PHYLOGENETIC ANALYSES AND TAXONOMY OF ANTHELIDAE (LEPIDOPTERA)

by

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DECLARATION

I hereby declare that this dissertation does not contain any material that has been submitted for the award of any degree or diploma at any tertiary institution or other institute of higher learning, except for cited material of other persons. The research presented herein is my own original work and all sources used are referenced.

Excluding indices, references, appendices and figure legends (423 figures with on average 39 words [n=40]), the dissertation has 91,400 words and remains well below the allowed maximum number of 100,000 words.

Andreas Zwick

December 2005

"MULTI FAMAM, CONSCIENTIAM PAUCI VERENTUR."

Gaius Plinius Caecilius Secundus (AD 103)
in a letter addressed to Messius Maximus (Book III, Epistle 20)
on a Roman Senate decision to use secret ballots.

To me, his words seem equally apposite for the current state of systematics.

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Growing up in a family of entomologists, I have been exposed to the study of insects from my early years on. My parents, Heide and Peter Zwick, managed to strike the right balance between fostering my interest in insects and not pressuring me. Being familiar with the poor and dwindling job market for entomologists, they always advised wisely against a career as an entomologist. However, once I had decided against their advice they gave me all the support one can think of for my studies, and for this I am very grateful to both of them. Not only did they support me financially during the long period of no or low income, but also with professional discussions, advice, proof-reading and simply by having a genuine interest in my study and an ear for my concerns.

I am equally grateful to my wife, Sandra, who always fully supported me and my unusual interest. We spent many nights collecting together in the bush, and some of our field trips to remote areas of the Philippines and Kenya were far from being a "walk in the park" – I doubt that without Sandra I would have undertaken all of these adventures. Not only did she sponsor my study and field trips substantially by generously sharing her truly hard-earned money with me, but ever since we met she quietly put up with the many restrictions in our private life caused by my studies. At last, her eternal "school-boy" – as her friends like to refer to me – has completed his subject, and I am glad and happy that finally we move on together as a growing family.

I was fortunate to spend one year as an exchange student from the University of Tübingen, Germany in the Department of Entomology at the University of Queensland, Australia in 1997. During that highly interesting and stimulating time, one of my main projects was supervised by David Yeates, who towards the end casually suggested that I proceed with a PhD project under his supervision. I was fortunate to be able to return to Australia, and relocate to the worlds best collection of Australian insects (CSIRO Entomology, Australian National Insect Collection [ANIC]). I have had a strong interest in the moth family Lasiocampidae and other bombycoid moths for many years, and a PhD in Australia seemed to provide an ideal opportunity to examine the alleged sistergroup of the Lasiocampidae – the Anthelidae, which are endemic to the Australian and New Guinean region. I applied for funding and was awarded an International Postgraduate Research Scholarship (IPRS) by the Department of Education, Science and Technology (DEST) as well as a PhD Scholarship by the School of Botany and Zoology

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ABSTRACT

The Anthelidae form a small family of bombycoid moths endemic to the Australian and New Guinean region. A critical review of all literature on Anthelidae and of the major publications on phylogeny of the bombycoid complex reveals limited and often inaccurate current knowledge. This study aims at elucidating the relationships within Anthelidae and of the family with other bombycoid moths based on comparative morphological and molecular genetic studies.

Morphology of genital structures and their muscles, antennae, wing venations and larval mouth parts are described and analysed in a Hennigian Argumentation, as well as with Maximum Parsimony. Sections of seven gene sequences (CO I & II, EF1a, CPS [CAD], 12S, 18S and 28S) are evaluated for their usefulness in phylogenetic analyses. CPS sequences were found to be least saturated and most parsimony informative and are, together with EF1a sequences, used in phylogenetic analyses. These analyses include Maximum Likelihood and Bayesian Inference of the molecular data, as well as individual and combined Maximum Parsimony Analyses of molecular and morphological data.

Methodological aspects of Hennigian Argumentation and Maximum Parsimony are critically discussed. Results of the different analyses are compared and found to be very similar, except for the placement of *Chenuala heliaspis* and an undescribed antheline species. The following hypotheses on anthelid and bombycoid phylogeny are proposed and require future testing by attempted falsification using additional character sets. The subfamilies Anthelinae and Munychryiinae are monophyletic, as is the family Anthelidae. The widely accepted hypothesis of Anthelidae as sistergroup to the Lasiocampidae, which together form the superfamily Lasiocampoidea, is falsified. Instead, a sistergroup relationship between Anthelidae and Lemoniidae / Brahmaeidae + Eupterotidae is proposed. Consequently, the monotypic Lasiocampoidea and Mimallonoidea are synonymized with the Bombycoidea, making the term "bombycoid complex" redundant.

Within the Anthelidae, the Munychryiinae comprise the genera *Munychryia* and *Gephyroneura*, as well as a monotypic, undescribed genus and species. The Anthelinae comprise twelve monophyla. The currently recognized genera *Chelepteryx*, *Chenuala*, *Pterolocera*, and *Omphaliodes* are confirmed. Genus *Anthela* is restricted to only five

species, *Nataxa* is enlarged to include twelve species and the other species are assigned to monophyletic genera for most of which names restored from synonymy are available (*Colussa*, *Pseudodreata* (*Corticomis* n. syn.), *Darala* and *Newmania*). Two additional monophyla require new generic names. A comprehensive synonymic list of all described taxa reflecting the proposed classification is included in the Appendix B.

NOTE:

None of the taxonomic changes proposed in this dissertation are intended as nomenclatural acts in the sense of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999)!

For easier reading taxonomic names of animal genera and species are generally used without author and year throughout this text. A list of all taxonomic names (species and genus level) in combination with their respective author and year of publication is given in the Appendices A & Q.

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CHAPTER ONE:

INTRODUCTION

I.1) What are Anthelidae?

The Anthelidae form a small family of moths restricted to Australia and New Guinea. At present the family comprises 74 species in 8 genera described from Australia and a few species from New Guinea (Edwards & Fairey 1996). Many as yet undescribed species are expected to exist as these moths are inconspicuous and widely distributed throughout the whole of Australia. Numerous distinct species have already been identified as undescribed in museum collections such as the Australian National Insect Collection (ANIC) in Canberra.

The large genus *Anthela* (56 described Australian species) is likely to be polyphyletic and the current unsatisfactory knowledge of its taxonomy is symptomatic of the current classification of the Anthelidae. This classification is based on superficial differences or similarities only and merely separates "odd" taxa from the principal genus *Anthela*. The original descriptions and the subsequent taxonomic revision of the family by Turner (1921b) have not utilised genital structures. These typically provide valuable characters for discrimination in other families. At present, a reliable identification of all taxa to species level using published keys is not possible. Similarly, the systematic position of the Anthelidae in the poorly defined bombycoid complex is unclear, stemming partly from the controversial concepts of the superfamilies constituting this complex (e.g., Brock 1971 versus Minet 1994) and partly from the lack of any phylogenetic study of the family.

Many adult Anthelidae resemble certain plesiomorphic Eupterotidae and Saturniidae with their "hairy" appearance, stout body, comparatively large wings, pectinate antennae and simple wing-pattern. Their caterpillars are typically external, nocturnal feeders, with a characteristic vertical stripe across the frons of the headcapsule, and densely covered with secondary hairs. At least in some (but more likely in most) anthelid species these hairs can cause considerable skin irritation if touched.

Numerous papers dealing at least partially with Anthelidae have been published, and the information contained in these is reviewed in this chapter.

I.2) Literature on Anthelidae

I.2.1) Taxonomy and systematics – getting a grip on variation

The first anthelid species was described in 1832 by the French entomologist Jean Baptiste Antoine Dechauffour de Boisduval. His description in Latin and French consists of four sentences only, but matches the female of *Anthela nicothoe* quite well – a species widespread and common in SE Australia today. Soon afterwards, Gray (1835) published a detailed description of a second anthelid species, *Chelepteryx collesi*, for which he erected *Chelepteryx* as a subgenus of *Endromis* [Bombycoidea: Endromidae]. Only two further species were described by other authors (Feisthamel (1839) and White (1841)) prior to Walker's catalogue of the Lepidoptera present in the collection of the British Museum in London. In his publications Walker (1855a, 1855b, 1860, 1862a, 1862b [1863], 1865, 1866, 1869) described new genera and species on a large scale, naming 8 anthelid genera and 46 anthelid species in total. While this undoubtedly had a major impact on anthelid taxonomy, the majority of his names are synonyms of species named by himself. The bulk of these species he described in his genera *Darala* and *Colussa*. *Darala* became the principal genus for new anthelid species described by subsequent authors until Turner (1902) synonymized *Darala* with *Anthela*. Ever since, *Anthela* has been the principal genus for the description of new anthelid species, and by now comprises 80% of all species recognized to date. Following the publication of Walker's catalogue, numerous anthelid species and genera have been described by various authors, namely Herrich-Schäffer (1850-[1869]), Newman (1856), Wallengren (1858), Butler (1874, 1882), Felder and Rogenhofer (1874-75), Rosenstock (1885), Tepper (1890), Meyrick (1891), T.P. Lucas (1891, 1892, 1895, 1898), Lower (1892, 1893a, 1902, 1905, 1908), Swinhoe (1892, 1902a, b, 1903, 1905), Turner (1902, 1904, 1914, 1915, 1920a, 1921b, 1922, 1924, 1926a, c, 1931, 1932, 1936, 1939a, 1944), Bethune-Baker (1904, 1908), Grünberg (1914), Joicey, Noakes and Talbot (1915), Joicey and Talbot (1917), Fawcett (1917), Hulstaert (1924a, b), van Eecke (1924), Strand (1925, 1929), Niepelt (1934), and Common and McFarland (1970). Among these, Turner's descriptions stand out in quality and number.

With the exception of Lower, Lucas and Turner, who lived and collected in Australia

themselves, all authors described species foreign to them after examining only one or a few specimens housed in an overseas collection. With such limited material at hand they did not recognize the existence of sexual dimorphism and the unusually strong variation of the habitus of adult Anthelidae. This resulted in the publication of many synonyms, a problem recognized and discussed early on by Turner (1921b). Many original descriptions are insufficient and the vast majority lacks illustrations. This renders the recognition of previously described species very difficult, as noted by Aurivillius (1920). Consequently, anthelid taxonomy was in a very confused state by the end of the 19th century. As early as 1864, Scott synonymized *Festra affabricata* with *Chelepteryx collesi*. More taxa were synonymized over time by Lower (1897, 1903), Turner (1912) and Collenette (1923). Extensive synonymic lists and revisions were published by Swinhoe (1903, 1922), Turner (1906, 1921b) and Strand (1925, 1929), as well as five catalogues by Kirby (1892), Swinhoe (1892), Lower (1893b), Hulstaert (1928) and Bryk (1934). Among these, Turner's revision of the Australian Anthelidae (1921b) is outstanding as it includes detailed descriptions of and keys to all species known at that time. For a Master's degree at the Macquarie University (Sydney), Fairey (1983[?]) revised the genus *Pterolocera*. He has made it inaccessible to the public by placing a ban on it as his subsequent, ongoing studies are based on his thesis. None of his results have been published so far. A comprehensive annotated synonymic list of Australian Anthelidae (Edwards & Fairey 1996) was published recently, and no further taxonomic acts within Anthelidae have since been published. Hassan *et al.* (2004) erroneously assumed the well known Palearctic saturniid species *Antheraea pernyi* belonged to the Anthelidae. This clearly is no more than a lapse and was not intended as a taxonomic act. In their checklist Edwards and Fairey (1996) regard more than half of the 153 names proposed for Australian taxa as subjective synonyms. This checklist is used as the taxonomic basis for Australian Anthelidae in this study. Very recently an Internet webpage on Australian moths has been made available by the Australian National Insect Collection (ANIC). It illustrates a large number of pinned anthelid specimens with verified species identifications and collecting data (Willan *et al.* 2004), complementing the checklist of Edwards and Fairey (1996).

While the Australian Anthelidae are excellently covered by the checklist of Edwards and Fairey (1996), no comprehensive list of non-Australian Anthelidae exists. The catalogues of Swinhoe (1922), Hulstaert (1928) and Bryk (1934) included non-

Australian taxa, but were very incomplete even at their time of publication. A complete annotated synonymic list of taxa, reproducing Edwards & Fairey 1996 for Australian taxa and adding non-Australian taxa from catalogues and additional literature, is given in Appendix A.

Despite the poor quality of Walker's descriptions of anthelid genera, the sheer number of species he described in *Darala* and *Colussa* provided guidance for subsequent authors. They, too, described new anthelid species in these two genera, which were regarded as members of the family Lymantriidae [Noctuoidea]. Turner recognized the unique nature of the species placed in these two genera, as well as of anthelid species in other genera. He separated them from all other Lymantriidae by erecting the new lymantriid subfamily Anthelinae (type genus *Anthela*), which he defined clearly by two characters of the wing venation (Turner 1904). Later Turner (1918, 1920a) formulated hypotheses on the evolution of the wing venation, which led him to the conclusion that the seemingly shared peculiarity in wing venation of Lymantriinae and Anthelinae, an areole, was not of the same origin. Consequently, Turner (1920a: 418, 1920b) separated the Anthelinae from the Lymantriidae by elevating the former to family level. While a subfamily Anthelinae within Lymantriidae was generally accepted, its elevation to family level was explicitly rejected by Swinhoe (1922), Strand (1925) and Bryk (1934), but accepted by Tillyard (1926), Hulstaert (1928) and later authors. Soon after the elevation to family level, Turner (1921b) re-examined the similarities between Lymantriidae and Anthelidae, and concluded that only a single character of wing venation linked the two families together, at best indicating only a remote relationship. He saw the family Anthelidae as a specialized group with some archaic characters (Turner 1947) and placed it within Noctuoidea as the sistergroup to all other families (Turner 1940, 1947). Later, Common (1963) pointed out the absence of tympanal organs and on this basis transferred the Anthelidae from Noctuoidea to Bombycoidea (Common 1966, 1970). Since then they have remained in the bombycoid complex, but within it have been transferred from Bombycoidea to Lasiocampoidea by Minet (1991).

With the exception of numerous, usually unexplained statements by Turner and a publication by Common and McFarland (1970), relationships within Anthelidae remain largely unknown. Turner (1904) proposed a subdivision of the genus *Anthela* based on a single character in the hind wing venation, but also noted some variation of this

character within one particular species. With his revised definition of the Anthelidae Turner (1920a) included the two "closely related" genera *Munychryia* and *Gephyroneura*, which he assumed to be "archaic". Later Turner (1921b: 164) concluded that they were "very distinct from the rest and could be regarded as a subfamily". Turner (1921b: 164) further considered the genera *Nataxa* and *Aprosita* [= *Omphaliodes*] to be "simple developments of *Anthela*", as well as the genera *Pterolocera* and *Chelepteryx* to be "nearly related collaterally". Later Turner (1922: 349) assumed the monotypic genus *Chenuala* to be closely allied to *Anthela*. He made further explicit statements on the presumed relationships between anthelid species, i.e., *Anthela ostra* being "nearest to" *A. denticulata* (Turner 1921b: 174), *A. acuta* and *A. varia* being "closely allied" (Turner 1921b: 176), *A. cnecias* being "nearly allied" to *A. ocellata* (Turner 1921b: 178), as well as *A. ariprepes*, *A. magnifica*, *A. asciscens* and *A. stygiana* forming "a natural group" (Turner 1921b: 179). Common and McFarland (1970) described and illustrated the pre-imaginal instars of *Munychryia senicula*, which they found to differ from those of other Anthelidae to such an extent that these authors followed Turner's suggestion (Turner 1921b: 164) and formally erected a new subfamily for the genera *Munychryia* and *Gephyroneura*, the Munychryiinae. They differentiated the new subfamily from the remaining Anthelinae by Turner's character of wing venation as well as a whole suite of differences in larval characters. However, only the caterpillars of *Munychryia* spp. but not those of the very similar *Gephyroneura cosmia* are known as yet. Hence, the larval characters given for the Munychryiinae by Common and McFarland (1970) are only generalisations of *Munychryia* characters, which remain to be confirmed for *G. cosmia*.

While some of these statements and assumptions on relationships might reflect evolution within the Anthelidae, no phylogenetic analysis at any taxonomic level has been carried out for Anthelidae. Genera other than *Anthela* have been erected for "odd" species and are not defined by autapomorphies, leaving the monophyly of all genera and in particular of *Anthela* highly questionable.

I.2.2) Morphology – a wealth of details, but for which taxa?

Typically, the original descriptions of anthelid species and genera (see above I.2.1) consist of a more or less detailed account of the colouration and wing pattern of the imagines and at best a few notes on the rest of their morphology. These morphological notes usually concern the specimen's size, absence of proboscis, shape of labial palpi, pectination of antennae, number of tibial spurs, shape of wings, and wing venation. The relatively modern and extremely detailed original description of *Munychryia periclyta* and the Munychryiinae by Common and McFarland (1970) is a rare exception. Secondary literature, namely by Scott (1864, 1893), Turner (1920a, 1921b), Strand (1925, 1929) and Hulstaert (1928), provide marginally more detailed descriptions of morphology, in particular of wing venation, seemingly based on new observations.

Rather recently, publications summarizing the available information on Lepidoptera in general and giving accounts of most lepidopteran families have appeared. Amongst these, the publications of Tillyard (1926), Common (1963, 1970, 1974), Munroe (1982), Nielsen and Common (1991), Scoble (1995), Holloway *et al.* (2001), and Gaedike and Häuser (2003) include illustrations of selected species and morphological information on Anthelidae, but only Common (1990) and Lemaire and Minet ([1998]) actually add new morphological details. In addition to the morphological structures usually described, Common (1990) gave details on genital structures, eggs, caterpillars and pupae, thereby providing an overall detailed general account of anthelid morphology. Lemaire and Minet ([1998]) based their account of Anthelidae largely on Turner (1920a, 1921b), Common and McFarland (1970), and Common (1990), but significantly corrected and added morphological details based on their own observations, e.g., of head morphology, abdominal sclerites, male genital structures and caterpillar setal arrangements. Furthermore, they explicitly proposed four autapomorphies for the family Anthelidae, three of which were new.

Thanks to Common and McFarland (1970), Common (1990), and Lemaire and Minet ([1998]) a good general morphological knowledge of Anthelidae is available. However, most morphological details have been published in general accounts of the family, from which it is not apparent which species have been examined, and hence what these general descriptions are based on. Lemaire and Minet ([1998]) sometimes point out peculiarities of certain genera, but as 80% of all species have been indiscriminately placed in the genus *Anthela*, this is of limited use.

I.2.3) Faunistic – ubiquitous in Australia

All descriptions of new species and most taxonomic works (see above I.2.1) include faunistic records, which usually consist of single records only, the type localities, as most descriptions of anthelid species are based on unique specimens. The specificity and hence the value of these records ranges from as vague as "New Holland" [Australia] (Walker 1855a: 889) to as exact as "Western Australia, Mt. Singleton, 2300 ft." (Common & McFarland 1970: 19). Similarly, most other publications dealing with Anthelidae contain some sort of geographic reference, in fact the value of many short notes in popular magazines amounts to no more than a local faunistic record: Aurivillius 1920; Bashford 1993, 1997; Borch 1927; Brown *et al.* 1993; Chisholm 1923, 1925, 1929; Common 1981; Common & Upton 1977; Coupar & Coupar 1989; D'Abrera 1975; Day *et al.* 1953; Fanning 1913; Fleay 1935; W.W. Froggatt 1914, 1923; Green & Osbourne 1994; Haines 1963; Hardy *et al.* 1979, 1980; Hill 1955; Hulstaert 1924a; Illidge 1925; Kershaw 1943; Kitching *et al.* 2000; Kühnert 1994; Landsberg 1988; Lane 1995; Lee 1975; Lithgow 1988; Lower 1892, 1893b, 1896, 1916, 1918; Martyn *et al.* 1972, 1974, 1975, 1977; McCoy 1890; McFarland 1970, 1979; McQuillan & Forrest 1985; Montague 1914; Moore 1963a; Moss & Popple 2000; Nikitin 1965; Oke 1923; Orr & Kitching 1999; Palmer 1885; Ramirez 1978; Riek 1962 [1963]; Roberts 1987; Scott 1864, 1893; Scott & Scott 1988; Southcott 1978; Spencer 1978; Stewart 1944; Strong 1971; Swarbreck 1946; Szent-Ivany & Carver 1967; Szent-Ivany & Catley 1960; Terauds *et al.* 1985, 1986; Turner 1921a, 1925, 1926a, b, 1939b; Wickham 1913; and Willan *et al.* 2004. Only Swinhoe (1892) and Common (1990) gave species distributions based on additional material they examined in collections.

The vast majority of faunistic records is for Australia. Anthelidae occur very widely in Australia, including the interior as well as mountains in Tasmania, and have been recorded from many different habitats, e.g., native grasslands, coastal heath, alpine swamps, dry sclerophyll forests, rainforests, and semi-arid to arid areas. Most of the few non-Australian records refer to the island of New Guinea, where Anthelidae have been recorded from both Papua [formerly known as Irian Jaya] and Papua New Guinea. Consequently, most general publications on Anthelidae state them to be endemic to Australia and New Guinea, with the great majority of species occurring in Australia (Tillyard 1926; Common 1970, 1990; Nielsen & Common 1991; Edwards & Fairey 1996; Lemaire & Minet [1998]; Holloway *et al.* 2001; Austin *et al.* 2004).

There are, however, a few records outside mainland Australia and New Guinea, which warrant special attention. In his original description of *Anthela brunneilinea* Hulstaert (1924) states for the type "1 ♂, Kei Is. (?)." and further notes: "Although this locality is not quite certain, and even somewhat strange, nevertheless I should not be surprised if it should be confirmed by further specimens, as this is not the unique animal of the peculiar Australo-Neoguinean fauna found on the Kei group." (Hulstaert 1924a: 137). The Kai islands belong to Indonesia and are located less than 100km south of the western end of Papua, on the western side of Lydekker's line. Lydekker's hypothetical, biogeographic line (Lydekker 1896) marks the western edge of the Sahul continental shelf, which lies less than 100m below sea level at present. During past glacial epochs when sea levels were at least 40m lower than at present, this continental shelf interconnected Australia, New Guinea and the Aru archipelago (Voris 2000). In contrast, the Kai islands are not part of the Sahul continental shelf. Despite their relative proximity to New Guinea and the Aru archipelago, they are separated from both of these by the Aru Basin, which at its most shallow point is currently 1,000m or more deep. As anthelid females are rather poor fliers, this permanent gap of about 100km width between the Kai islands and New Guinea and the Aru archipelago is likely to present a major dispersal barrier for Anthelidae. Hence, the uncertain record from the Kai islands appears unlikely to be correct.

In fact, I have a single male specimen of an *Anthela* sp., possibly *Anthela brunneilinea*, labelled as "Naigoeli, Trangan Ins 16.ii.08" [6°38'S 134°5'E, INDONESIA, Moluccas, Aru archipelago, Trangan island, Naiguli – about 100km SE of the Kai island and about 100km S of Papua] and bearing a subsequent, printed label "Kei-Ins. 1908 H. Merton" [*leg.*] on loan from the Senckenberg Museum in Frankfurt, Germany. Dr. Hugo Merton and Jean Roux had been collecting on the islands of Kai as well as Aru during a joint expedition from January 1907 until June 1908 (Merton & Roux 1910). Hulstaert, in contrast, was a Belgian catholic missionary who had spent many years in Africa, but had never been to the Australasian region (Vinck 2001). While many of the specimens he described were collected by fellow missionaries, including specimens from the Kai islands, the source of the type specimen of *A. brunneilinea* was not stated. Access to specimens from the Kai and Aru islands was and is limited, and it does not seem unlikely that Huelstaert examined specimens collected by Merton and Roux during their Kai and Aru expedition.

Under these circumstances, I assume the type locality of *A. brunneilinea* to be erroneous, with the type possibly originating from the Aru archipelago.

The original description of another species, *Anthela prima*, states for the type "Makiau, Celebes. In Mr. Saunders' collection." (Walker 1866: 1917). This locality record is most probably incorrect and the error is likely to have originated as follows: A. R. Wallace visited the island of Makian (0°32'N 127°4'E, about 20km W of Halmahera, Moluccas), which he sometimes erroneously referred to as "Makiau" (e.g., Wallace 1863: 221). In the preface of the first edition of his book "The Malay Archipelago", Wallace (1869) wrote that he had collected a total of 13,100 specimens of Lepidoptera and had given his private collection to Mr. William Wilson Saunders, who had arranged for the description of many specimens by entomologists. It is therefore most likely that the specimen described by Walker as *A. prima* had been collected by Wallace, in which case it might have been collected on Makian (Moluccas) or possibly any other location visited by Wallace during his long journey, including New Guinea. Wallace wrote further: "When I reached England in the spring of 1862, I found myself surrounded by a room full of packing cases containing the collections that I had, from time to time, sent home for my private use. These comprised nearly three thousand birdskins of about one thousand species, at least twenty thousand beetles and butterflies of about seven thousand species, and some quadrupeds and land shells besides. A large proportion of these I had not seen for years, and in my then weakened state of health, the unpacking, sorting, and arranging of such a mass of specimens occupied a long time." (Wallace 1869: preface). Under these circumstances it appears reasonable to assume that the type of *A. prima* was mislabelled by Wallace during the process of unpacking and sorting specimens, and rather than from Makian (Moluccas) the specimen might have originated from New Guinea. More recently, entomological staff from the Natural History Museum, London, and private collectors from Germany have collected rather intensively on Halmahera, but no Anthelidae were caught (J. D. Holloway, NHM London, pers. comm.), supporting the assumption that the original record from Makian is incorrect. Mention of Anthelidae as occurring on Celebes in secondary literature (e.g., Day *et al.* 1953) most probably only refers to this single erroneous record, the type locality of *A. prima*.

In his catalogue of Lepidoptera in the collection of the Oxford University Museum, Swinhoe lists *Colussa* [*Chelepteryx*] *chalepteryx* without quoting the type locality, but as occurring on "Lord Howe Island, Australia" (Swinhoe 1892: 211), which is a tiny island about 550km E of the New South Wales coast. In his original description however, which merely consists of an illustration and the caption "*Darala Chalepteryx* F. ♂, Cap. b. sp. (Trimen)", Felder (*in* Felder & Rogenhofer 1874-75: 3) does not mention Lord Howe Island or Australia. In fact, his abbreviation of the type locality "Cap. b. sp." generally stands for "Caput bonae spei" [Republic of South Africa, Cape of Good Hope], which is most probably as erroneous as is Lord Howe Island – no anthelid specimens have ever been recorded from South Africa or Lord Howe Island so far.

In summary, the occurrence of Anthelidae seems to be restricted to Australia (including Tasmania), New Guinea and the Aru archipelago (Fig. 1).

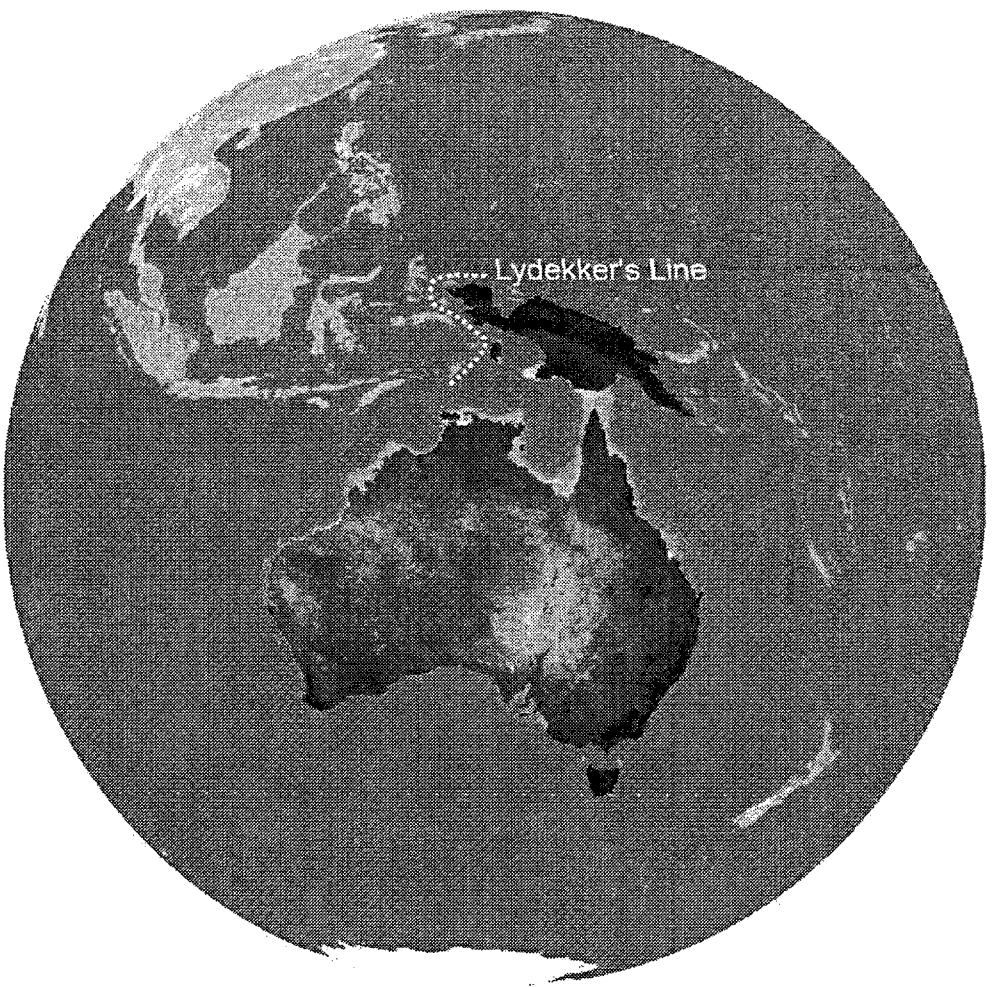

Fig. 1: Anthelidae are only known to occur in Australia (incl. Tasmania), New Guinea and the Aru archipelago – all of which have been interconnected by the Sahul continental shelf (western edge marked by Lydekker's Line) during past glacial epochs.

I.2.4) Life history – scratching the surface over and over again

Since the publication of the original species descriptions, which usually lacked illustrations and information on any stage of the life cycle other than the imagines, numerous photos, notes, observations and descriptions of the life history of Anthelidae have been published. However, despite the large quantity of publications our knowledge of anthelid life histories remains rather poor as the publications focus on a handful of taxa and repeat similar observations.

The anthelid species best known to the public is *Chelepteryx collesi*. This is due to the enormous size of the moth, the irritating hairs of caterpillars and cocoons (see below, I.2.5), and because it is frequently encountered even in large cities. Its caterpillar instars, pupa and cocoon have been illustrated and described in a number of publications, as well as the oviposition on bark, nocturnal feeding and the wandering of caterpillars prior to pupation: Scott 1864; Palmer 1885; Edwards 1890; McCoy 1890; Anderson 1892; Fanning 1913; Wickham 1914; G.H. Froggatt 1917; W.W. Froggatt 1923; McKeown 1942; Anonymous 1961; Common 1963, 1970, 1990; Hadlington 1972; Ramirez 1978; McMaugh 1985; and Coupar & Coupar 1992. Of all these references the unpublished Master's thesis of Ramirez (1978) on the life history of *C. collesi* stands out as the by far most detailed study.

For several species a small number of publications illustrates and describes almost all stages of the life cycle, and notes various observations on behaviour, e.g., nocturnal feeding, wandering of caterpillars, pupation in holes of wood-boring insects, emergence of moths being triggered by rain and moths feigning death upon disturbance: *Chelepteryx chalepteryx* (Scott 1864; Chisholm 1925; Gallard 1931; Common 1963, 1970; Moore 1963b; Coupar & Coupar 1991, 1992), *Anthela nicothoe* (Froggatt 1917; Fleay 1935, 1961; Common 1963, 1970; Moore 1963b; Coupar & Coupar 1992), *A. varia* (Moore 1963b; Teakle 1969; Edwards & Wanjura 1989; Monteith 1995), *A. ocellata* (Tepper 1890; Common 1963, 1970; Moore 1963b; McQuillan & Forrest 1985; Coupar & Coupar 1992), *A. excellens* (Moore 1963b), *Nataxa flavescens* (Common 1963, 1970; Webb 1990; Coupar & Coupar 1992), and *Pterolocera amplicornis* (Anderson 1892; Day *et al.* 1953 [very detailed]; Wakefield 1960; Common 1963, 1970; McFarland 1970; Coupar & Coupar 1992).

Only very short notes on observations exist for some other species. These include the diurnal feeding of *A. basigera* reported by McQuillan and Forrest (1985), and the nocturnal feeding of a species belonging to the species complex around *A. ekeikei* in New Guinea mentioned by Szent-Ivany and Catley (1960). Similar brief observations of various kinds have been noted by McFarland (1979) and Common (1990) for numerous species.

Rare exceptions from the typical short observations on common species are two publications by naturalists, each of them detailing their rearing of a poorly known anthelid species from their garden. McGauran (1951) described her observations on and rearing of *Pterolocera isogama*, providing particularly valuable information on host plants and pupation. Similarly, Mills (1954) reported on her rearing of *Anthela xantharcha*, during which she observed larval feeding behaviour involving the spinning of silken trails between resting and feeding sites.

As with all observations and records, species identity is absolutely crucial, and given the lack of illustrations and the taxonomic confusion prior to Edwards and Fairey (1996), misidentifications have to be expected and information, particularly from non-taxonomists, has to be treated with adequate caution. The very short note on the life history of *Anthela ocellata* by Brewster *et al.* (1920) may serve as an example – it apparently includes observations on at least three different species under one name, which unfortunately is not obvious from the text itself, but apparent if one is familiar with the life history of *A. ocellata.*

I.2.5) Economic and medical records – a nuisance to mankind

Apart from the original descriptions, Anthelidae have caught human attention most of the time only when perceived as harmful in one way or another.

In respect to Anthelidae, attacks on *Pinus radiata* plantations were the main concern in Australia and various records and reports have been published, most of them listing *Anthela nicothoe* as a pest: Campbell 1972; Common 1970, 1990; Hadlington 1963; Hardy *et al.* 1979; Moore 1963a, b. Other species reported are *A. connexa* by Elliott and de Little (1985), *Chenuala heliaspis* and *A. excellens* by Common (1970) and Moore (1963a), as well as *A. varia*, *Chelepteryx chalepteryx* and *A. ocellata* by Moore (1963a, b). For *Pinus patula* in Papua New Guinea, *Anthela ekeikei* has been recorded as a minor pest by Roberts (1987). Most of the recorded attacks on *Pinus* spp. were regarded as minor and/or occasional, but Hadlington (1963) reported *A. nicothoe* to "have consistently attacked pine in the highland areas", and Moore (1963b) even regarded Anthelidae in general as the second worst lepidopteran threat to pine plantations after Psychidae. His judgement appears to be based on the relatively large number of different anthelid species attacking pines (he lists 6 species) rather than on the actual damage caused by them. The "threat" posed by Anthelidae caused him to publish a major account of these species, including detailed life histories, descriptions of all instars, and keys to caterpillars and cocoons, as well as host and parasitoid records (Moore 1963b).

Native pastures were of major interest, too, and several records of "infestations" by anthelid caterpillars have been published. Most frequently, these infestations were caused by various *Pterolocera* spp., which are usually incorrectly referred to as *P. amplicornis*: Day *et al.* 1953; Edwards & Fairey 1996; Evans 1943; Hardy *et al.* 1980; Martyn *et al.* 1972, 1974, 1975, 1977; Swarbreck 1946 [mixing several species, probably including a *Pterolocera* spp.]; and Terauds *et al.* 1985, 1986. Occasionally, other species have been recorded as pasture pests as well, namely *Anthela ocellata* by French (1911) and Leach (1952), and *A. denticulata*, *A. euryphrica* and *A. ostra* by Common (1990), and Edwards and Fairey (1996). As with the attacks on pines, damage to native pastures was generally seen as insignificant to minor, even in cases of locally restricted mass occurrences of caterpillars – 500 caterpillars per square metre were counted in a Tasmanian pasture (Hardy *et al.* 1980)! French (1911) was the only author

to regard *A. ocellata* as a serious pest. He reported them to occur in thousands, moving in the same direction and eating up all sorts of plants in their path. As they not only ate grasses but further "defiled" pastures by their sheer number, he saw them as a "most destructive pest". In fact, as so dangerous that French (1911) recommended control of caterpillars during the wandering phase by running over thousands of them with brush harrows or rollers, or by digging pits and drains across their path.

Records of Anthelidae as pests of other plants are much rarer and usually limited to single references only. Ironside repeatedly listed and illustrated *A. varia* as a minor pest of macadamia foliage in QLD (Ironside 1973; subsequent publications in 1980, 1981 and 1995 merely repeated the information published in 1973). Hadlington (1963) reported *A. nicothoe* as a defoliator of the introduced Tree Lucerne (*Chamaecytisus prolifer*, Leguminosae). McMaugh (1985) recorded minor damage caused by *Chelepteryx collesi* to eucalypts in gardens and recommended several control measures. The same anthelid species was used by Hadlington (1969) as a test object for the effectiveness of insecticide implants in eucalypts. *A. denticulata* was reported as a pest of saltbush (*Atriplex* spp., Chenopodiaceae) in inland NSW (Froggatt 1910). However, this record is dubious as he did not see any live caterpillars feeding on saltbush. Instead, he only assumed the caterpillars, which were hanging dead in saltbushes and did not belong to the usual pest of saltbush, *Apina callisto* (Noctuidae), to be the same species as the cocoons of *A. denticulata*, which he had found in the soil beneath saltbushes. This anthelid species has otherwise only been recorded as feeding on various grasses, and as Froggatt (1910: 465) himself states that saltbushes are "still to be found in conjunction with the natural grasses over an immense area", it seems reasonable to assume that the grass-feeding caterpillars of *A. denticulata* might have merely pupated in the ground under saltbushes by chance or to shelter from the sun. Alternatively, a loss of the native host plant (e.g., by drought or from overpopulation defoliating the local host plants) could cause caterpillars to attempt to feed on non-host plants.

While numerous records of Anthelidae as pests exist, it seems as if only a few cause consistently serious damage. In fact, the more detailed reports indicate that many of the records as pests might be due to opportunistic feeding behaviour of Anthelidae combined with environmental changes or pressures. Terauds *et al.* (1985), for example, list a case in which caterpillars of a *Pterolocera* sp. "invaded" a lawn from an adjacent pasture, which was densely populated by this species. In a second case under very

similar circumstances the "invaders" fed on various garden plants (Terauds *et al.* 1986). This "opportunistic" feeding behaviour of Anthelidae is reflected in the great variety of host records, too, where anthelid species fed in captivity on various plants for some time, but in the end failed to survive on them (see below, I.2.6). Another example is a pest record of *A. ostra* from the Northern Territory by Edwards and Fairey (1996). A floodplain, probably with native grasses including *Oryza* spp., had been converted into a rice field. During the first year an "outbreak" of *A. ostra* in the paddy, with caterpillars feeding on the crop, was observed. Caterpillars were reared and sent to the ANIC for identification, and together with the old holotype these specimens remain the only ones ever found (E. D. Edwards, ANIC, pers. comm.). A likely explanation for this "phenomenon" is that this species had occurred in numbers on the floodplain unnoticed for a long time, and moths eclosed from pupae in the ground after their habitat had been destroyed for farming. With their native host plants gone, caterpillars "attacked" other plants, the crop, but failed to maintain the population. Records of *A. denticulata* and *A. euryphrica* as occasional pests of crops (Edwards & Fairey 1996) have similar backgrounds, with the species disappearing entirely from the agricultural area after an initial "outbreak". This also fits with the observation made by Hadlington for *A. nicothoe* that "severe infestations have been observed only in windbreaks and small woodlots, usually where the natural tree vegetation has been removed and the country utilised for grazing" (Hadlington 1963: 2).

In summary, Anthelidae are not dreaded economic pests, but some might have the potential to cause significant damage to crops, as they accept various plant species if their host plant is not available.

Apart from economic damage a characteristic of the caterpillars of some anthelid species drew even more public attention to the Anthelidae – urticating hairs. Almost all known anthelid caterpillars are densely covered with secondary setae, and in some species these include short, barbed, spine-like hairs, which are later incorporated into the cocoon in such a way that they radiate from it like the spines of a sea urchin. Two species with caterpillars and cocoons armed in this way are encountered by humans rather frequently, namely *Anthela nicothoe* and *Chelepteryx collesi,* the first two anthelid species to be described and named (see above, I.2.1). The following publications all mention their hairs, and almost all of them point out the urticating effect

these hairs have: Anonymous 1944 [about *A. nicothoe* as *A. acuta*], 1961; Anderson 1892; Balit *et al.* 2003, 2004; Bishop & Morton 1967, 1968; Common 1963, 1990; Coupar & Coupar 1992; D'Abrera 1975; Edwards 1890; Edwards & Fairey 1996; Fanning 1913; Fleay 1935, 1961, 1966; Hadlington 1972; Hardy *et al.* 1979; Kawamoto & Kumada 1984; Lee 1961, 1975; McKeown 1942; McMaugh 1985; Moore 1963b; Mulvaney *et al.* 1998; Musgrave 1924, 1941; Scott 1864; Scott & Scott 1988; Southcott 1973, 1978, 1983, 1987; Sutherland & Nolch 1999 [merely an exaggeration of Bishop & Morton 1967, 1968 without citing them], Swarbreck 1946 [as *A. acuta*; clearly a mix of species and probably including *C. collesi*], Tillyard 1926; Wakefield 1961; and Wickham 1916. However, it is obvious that several authors only repeat observations made and published by others. A single record of "considerable pain" caused by caterpillar hairs of *C. chalepteryx* exists, too (Gallard 1931). Touching *A. acuta* cocoons from the Northern Territory [probably a species of the *A. acuta* / *A. astata* complex] caused itching and erythema, with small papules remaining until the following day (Southcott 1987). Another record of *A. acuta* caterpillars having irritating hairs by Lee (1961, 1975) is only based on the erroneous record by an unknown author (Anonymous 1944).

The sensation of pain is subjective, and as such it comes as no surprise that contacts with caterpillars of *C. collesi* have been described as causing minor pain lasting less than one hour (Balit *et al.* 2004), as well as being very painful and causing a finger to swell to twice its size (Musgrave 1924). In addition, individual body reactions can be very different, and while allergic reactions to *C. collesi* caterpillar hairs are generally uncommon, some cases have been documented. Wakefield (1961) reports the case of a person allergic to iodine, who suffered from blisters caused by a few spines for three weeks. Mulvaney *et al.* (1998) detail two exceptional medical cases of severe allergic reaction to *C. collesi*, one even being systemic and requiring resuscitative measures (Mulvaney *et al.* 1998). All incidents with *C. collesi* have been caused by touching either caterpillars or cocoons, with the result that spines were embedded in the skin of hands or feet. In general, the irritation caused by *C. collesi* spines is assumed to be mechanical only (Anonymous 1961; Balit *et al.* 2003, 2004; Common 1990; Edwards & Fairey 1996; Lee 1961, 1975; McMaugh 1985; Scott 1864; Southcott 1983). However, at times *C. collesi* hairs have been assumed to possibly have a toxic effect (Mulvaney *et al.* 1998) or even to be "highly poisonous" (Edwards 1890; McKeown 1942). To some

extent this is also indicated by the observation that several-year-old cocoons retain their irritating characteristic, as reported by Anderson (1892).

The situation is different for *A. nicothoe*, where contact with hairs has usually caused more severe reactions ranging from painful rashes and pustules (Anonymous 1944) to "severe urticaria" (Common 1990) or even "maddening irritation" (Fleay 1935). Based on the severity of these reactions some authors assume them to be caused by an unknown poison (Balit *et al.* 2003; Bishop & Morton 1968), but Southcott (1973, 1983) assumes these irritations to be of mechanical nature only. No study to confirm the identity or even existence of any poison linked to anthelid caterpillar hairs has been undertaken to date. Unlike *C. collesi*, many particularly severe cases of injury by caterpillar hairs of *A. nicothoe* are believed to have been caused by airborne hairs and hair fragments (Bishop & Morton 1967, 1968; Lee 1961, 1975). Apart from causing dermatitis as reported by Lee (1961, 1975), Bishop & Morton recorded 132 cases of airborne hairs getting stuck in the eye-lid (1961), or even in the cornea (1975), with the hairs causing scratches on the cornea, photobia, lacrimation and foreign-body reactions. Most incidents occurred during the harvesting and handling of hay on fields during December and January. In all cases no caterpillars were touched or even seen, which gave rise to the hypothesis of airborne hairs, but the actual source was not located. A likely source had been mentioned by Hadlington many years earlier, unaware of the problem of airborne hairs: "When [*A. nicothoe*] caterpillars have attacked Tree Lucerne, they crawl into sheds and any sheltered, dark spot to pupate. Hundreds of these cocoons may be found attached to agricultural machinery near infested trees." (Hadlington 1963: 2).

A single, even more severe case of caterpillar hairs entering the eye was detailed by Southcott (1973, 1978) from the Northern Territory, where hairs of possibly an anthelid species got stuck in the eye of a person. Over time these hairs moved through the tissue of the anterior chamber, iris and the lens of the eye, perhaps causing the subsequent astigmatism reported. Southcott (1978) observed that after breaking off, anthelid caterpillar hairs had a very sharp base which, rather than the tip of the hair, penetrates the skin. The entire hair gets pushed deeper and deeper into the skin by the protruding barbed shaft, only allowing forward travel of the hair.

Edwards and Fairey (1996) mentioned one case of blindness being caused by anthelid caterpillar hairs. Their note refers to a case where a caterpillar had been rubbed into the

eye of a person with the intent to cause damage, but the reference and details were not revealed (E. D. Edwards, ANIC, pers. comm.).

The overall number of medical incidents is remarkably high – 13 confirmed and 13 probable cases of injuries caused by *C. collesi* caterpillar hairs were reported to the Poisons Information Centres of NSW over a two year period (Balit *et al.* 2004), and 132 cases of *A. nicothoe* caterpillar hairs found lodged in eyes were reported in Victoria alone during a 16-17 year period (Bishop & Morton 1968), with many more unreported cases certain to have occurred. This rather high number of incidents is likely to be due to the behaviour of the fully grown caterpillar, which in several anthelid species leaves its host plant and "wanders" around (Common 1990; French 1911, Monteith 1995; Ramirez 1978; Scott 1893) prior to pupating in a camouflaged cocoon under bark, rocks and other shelters – including barns, sheds and farm machinery (Hadlington 1963), as well as in mailboxes in residential areas. Of the few anthelid species which spin cocoons with irritating spines radiating from them, *C. collesi* and *A. nicothoe* (and possibly *A. connexa*) are the only ones to occur commonly in densely populated areas.

The general public perception of Anthelidae has been summed up by an unknown author:

"They are worth knowing, if only to avoid them."

(Anonymous 1944: 198)

I.2.6) Host records – to eat and to be eaten

Of the 167 valid original species descriptions only two include a host record (Turner 1936 and Common & McFarland 1970). In contrast, many secondary publications on Anthelidae mention host plants of certain anthelid species, but the link between an original species description and a subsequent host record is critical. The problem of correct species identification is even more pressing for host records than it is for most other records, as not only the anthelid species, but also the host plant has to be identified correctly. Further, the identification of the anthelid species is particularly difficult as it is the caterpillar feeding on the plant, while all original species descriptions are based on adults and secondary descriptions or illustrations of caterpillars are rare. Unless the adult has been reared from the caterpillar, a reliable species identification based on publications is currently impossible for most taxa. For the vast majority of host records no voucher specimens of either the anthelid specimen or the host plant have been preserved. Hence, most records cannot be verified and their value depends largely on the reliability of their author. The excellent publication by McFarland (1979) is a rare exception – all taxa were identified by specialists and voucher specimens of at least the Anthelidae were preserved.

An additional problem, typical for host records, is a lack of definition of what constitutes a host record. Does a single caterpillar observed to chew on a leaf, possibly only temporarily due to the lack of other plants, justify the assumption of this species feeding on this plant species in general? Do records of caterpillars reared from eggs obtained from a gravid female and initially feeding on a plant selected by the breeder (on which they might or might not complete their life cycle successfully) constitute host records? Or do only observations of caterpillars successfully completing their life cycle in the wild on a certain plant qualify as host records? More often than not the reader is left guessing as to the basis of host records. It is rather common practice to state a host plant for a species without giving any further information, and very often these "records" are merely repetitions of previously published records without citing the source.

A list of all available host records is given in Appendix C (sorted by anthelid species as well as by host plant). It has been compiled from my own observations and experiences breeding Anthelidae, from notes and records in the ANIC, as well as from publications and information on the Internet. As the majority of host records cannot be verified, no attempt to distinguish between host records of different quality was made,

but the source for each record is given and sometimes commented on. Consequently, the list of anthelid host records in Appendix C has to be used with extreme caution!

Despite all these problems linked to host records, certain tendencies are apparent. Some plant groups are clearly more widely accepted than others. For Anthelidae these are *Acacia* (Mimosaceae), *Eucalyptus* (Myrtaceae), grasses (Poaceae) and *Casuarina* (Casuarinaceae). In particular the host records of McFarland (1979) for different *Pterolocera* spp. and those for *Chelepteryx collesi* show that at least some anthelid species have a preferred or principal host plant, but readily switch to feeding on other plants if necessary. Apart from being a highly interesting trait in itself, the occurrence of this opportunistic feeding behaviour demonstrates clearly that single host records, in particular of species bred in captivity, do not do justice to the complex host plant usage by Anthelidae and easily result in a distorted picture.

While many host records exist for Anthelidae feeding on plants, only a few for Anthelidae being eaten have been published. These include odd notes, such as the record by Stewart (1947) of caterpillar remains of *Anthela denticulata* being found in the stomach of a fan-tailed cuckoo. Other records are of generalist predators, such as crows (Passeriformes: Corvidae, *Corvus* sp.), crickets (Orthoptera: Gryllidae, *Teleogryllus commodus*) and ants (Hymenoptera: Formicidae, *Iridomyrmex* sp. and *Pheidole* spp.) feeding on *Chelepteryx collesi* caterpillars (Ramirez 1978). Bats are major predators of Lepidoptera in general. One bat species, *Rhinolophus megaphyllus* (Chiroptera: Rhinolophidae), has been shown by Pavey and Burwell (1998) to have a preference for feeding on Anthelidae, presumably aided by the absence of tympanal organs in Anthelidae. A very large number of records of "caterpillars" as the food of birds are contained in Barker and Vestjens (1989, 1990), but rarely are these larvae identified even to family. Mites have been recorded several times on anthelid caterpillars by McFarland (1979), and Coupar and Coupar (1992), but of these at least the two identified mite species, *Charletonia feideri* (McFarland 1979) and *Leptus charon* (Southcott 1993) (both Acarina: Erythraeidae), have both been recorded from other hosts as well. Similarly, published records of Hymenoptera and Diptera from anthelid eggs, caterpillars and pupae either do not identify the parasitoid species (e.g., Turner 1936; Moore 1963b; Coupar & Coupar 1992) or refer to generalist parasitoids (e.g., Froggatt 1910; Riek 1962; Moore 1963b; Ramirez 1978). The only parasitoid

species described from an anthelid host (*Chelepteryx collesi*) is *Lioscinella australiensis* (Diptera: Chloropidae) by Spencer (1978). This species had also been recorded from a gall and hence was considered to be a scavenger rather than a parasitoid specific to *C. collesi*. Only two nuclear-polyhedrosis viruses have been recorded from Anthelidae. Day *et al.* (1953) described a virus as "*Borrelina anthelus*" from a *Pterolocera* sp., and Teakle (1969) gave details on a virus isolated from *Anthela varia*, without giving the new virus a name. Both nuclear-polyhedrosis viruses are probably rather host specific, as indicated by the negative cross-contamination experiments of Teakle (1969).

A complete list of all anthelid parasitoid records is given in Appendix D.

I.3) LITERATURE ON BOMBYCOID PHYLOGENY

The origin of the name "Bombycoidea" dates back as far as the introduction of our current nomenclatural system, when Linnaeus (1758) erected the subgenus *Bombyx* within the genus *Phalaena*. Latreille ([1802]: 404) introduced the family level name "Bombycinae" (Fletcher & Nye 1982: viii), which was used with various endings (e.g., "Bombyces", "Bombycites", "Bombycina") for similar groupings of taxa by subsequent authors. These names were applied in a very broad sense for taxa of superficially similar appearance, such as a medium to large size, a stout and densely scaled body, and reduced mouth parts. Under these group names moths of many distantly related families were included, e.g., Hepialidae, Cossidae, Zygaenidae, Notodontidae, Saturniidae, Lasiocampidae and Bombycidae. Dyar's studies of caterpillars (1894, 1895, 1896) initiated a gradual narrowing of these groups (Franclemont 1973: 15) to finally comprise those families which are currently placed in the "bombycoid complex" *sensu* Lemaire & Minet [1998]: Anthelidae TURNER, 1904; Bombycidae LATREILLE, [1802]; Brahmaeidae SWINHOE, 1892; Carthaeidae COMMON, 1966; Endromidae BOISDUVAL, 1828; Eupterotidae SWINHOE, 1892; Lasiocampidae HARRIS, 1841; Lemoniidae HAMPSON 1918[1]; Mimallonidae BURMEISTER, 1878; Mirinidae KOZLOV 1985; Saturniidae BOISDUVAL, 1834 [1837]; and Sphingidae LATREILLE, [1802].

Since the erection of *Bombyx* by Linnaeus (1758), a huge number of publications on taxa in the bombycoid complex has appeared. Some of these include statements on the presumed relationships between the families, often based on superficial similarities of imagines only. Most of these similarities concern wing venation, as well as the presence or absence of the wing coupling structures frenulum and retinaculum, the morphology of the labial palpi, and the haustellum. Hampson (1901) erected the family Sabaliadae [= Lemoniidae] for a small group of Palearctic and African bombycoid taxa. He assumed this family to be closely allied to Brahmaeidae, a bombycoid family likewise of Palearctic and African occurrence. Forbes (1955) distinguished the Sabaliadae from the

1 The nomenclatural situation of the family group name Lemoniidae is complicated and uncertain. While it is beyond the scope of this thesis to resolve the complications and mistakes, two principal situations are possible: If the name Lemoniidae is a junior homonym of the butterfly family group name Lemoniidae KIRBY, 1871, of which the validity is uncertain, the family group name Sabaliadae HAMPSON 1901 would be available as a replacement under the current definition of the family by Lemaire and Minet ([1998]). Alternatively, Lemoniidae is a valid family group name of uncertain authorship, possibly of Staudinger and Rebel (1901). In any case the authorship seems to be incorrectly accredited to HAMPSON, 1918 by Fletcher and Nye (1982: viii) and dates back earlier than 1918.

Eupterotidae by the approximation of the veins Sc+R to vein Rs beyond the cell in the hind wing of Sabaliadae. Forbes noted further that the Eupterotidae hardly differed from Bombycidae, but he distinguished them by the more apical forking of the fore wing veins Rs1+Rs2 versus Rs3+Rs4 in Eupterotidae. In this context it is noteworthy that his concept of the Eupterotidae included the subfamilies Apatelodinae and Prismostictinae, both of which have, in the past as well as are currently again, been placed in the family Bombycidae. In his revision of the Brahmaeidae and Eupterotidae of China, Mell ([1930]: 485) assumed the Eupterotidae to be closest to the Brahmaeidae and Notodontidae (Noctuoidea), but this idea was based on ancestral characters.

Forbes (1916) discovered the occurrence of tympanal organs in a number of moth families, and later noted the absence of these structures in Bombycoidea and Saturnioidea (Forbes 1923). In a short but excellent article Jordan (1923) presented a system to reliably distinguish various moth families by the occurrence of tympanal organs in combination with other characters. His system went unnoticed by subsequent authors for many years, but essentially forms the basis of our current "modern" classification. Classifications of early authors relied heavily on differences in wing venation, in particular on the relative position of vein M2 to veins M1 and M3 in the fore wing. Jordan (1923) drew attention to the median position of the vein M2 [his "R2"] in the fore wing, arguing that this position was ancient and hence insignificant for the understanding of evolutionary relationships. Similarly, he pointed out that the homoplastic loss of the veins CuP and 3A had very limited phylogenetic value. He further distinguished between primary and secondary absence of the wing coupling structures, the frenulum and retinaculum. In contradiction to his comment on the phylogenetic value of ancient characters he used the complete and hence, in his understanding, primary absence of the retinaculum and frenulum to define the superfamily Saturnioidea as a "natural group". Further, he assumed the Eupterotidae to be very closely related to the Lemoniidae, which in turn he regarded as very similar to the Brahmaeidae. Jordan (1923), like Forbes (1955) many years later, noticed the difficulty in distinguishing between Eupterotidae and Bombycidae. However, he separated these two families on the basis of differences in the wing structure near the frenulum base, as well as in the shape of the "merum" [meron] of the midcoxa.

Turner (1947) reviewed historic classifications of Lepidoptera and proposed his own classification, in which he divided the bombycoid complex into the monotypic

Lasiocampoidea, the monotypic Sphingoidea and the Bombycoidea. He relied heavily on differences in wing venation and emphasized the importance of the position of vein M2 in the fore wing, apparently unaware of Jordan's (1923) note on the insignificance of the median position of M2. Soon after, Michener (1952) published his extensive study of the Saturniidae of the western hemisphere, which remains the most detailed and most comprehensive morphological study of Saturniidae to date. This study includes a diagram of the relationships within the superfamily Saturnioidea, in which he literally placed the families Cercophanidae and Oxytenidae on the lowest branches of his dendrogram. Michener (1952) defined the Saturnioidea by two characters, the loss of the frenulum and the loss of at least one branch of vein Rs in the fore wing. Like Jordan (1924), Michener (1952) assumed the Cercophanidae, Oxytenidae and Saturniidae to form a monophyletic group (= Saturnioidea), but he deemed his two defining characters as too weak and inconsistent to warrant a separate superfamily for these families. Hence, he followed Turner (1947) and included the three families Cercophanidae, Oxytenidae and Saturniidae in the Bombycoidea.

Common (1963) was the first author to note the lack of tympanal organs in the Anthelidae. He subsequently transferred the Anthelidae from the Noctuoidea, which are defined by the presence of a pair of metathoracic tympana, to the Bombycoidea (Common 1966). In the same publication Common (1966) erected the monotypic Australian family Carthaeidae in the Bombycoidea. Because of the presence of a number of plesiomorphic structures in Carthaeidae, which are reduced in many other Bombycoidea, he assumed the Carthaeidae to be the most "primitive" member of the Bombycoidea. He drew attention to [plesiomorphic] similarities with "primitive" Saturniidae, as well as to minor similarities with Eupterotidae and Anthelidae.

Brock (1971) systematically studied morphological details of a large group of Lepidoptera, the Ditrysia. In an attempt to reconstruct ditrysian phylogeny, Brock examined and developed hypotheses on the evolution of the radial system of veins in the fore wing, as well as of thoracic sclerites and the articulation between thorax and abdomen. Based on his hypotheses, Brock proposed a phylogeny for all ditrysian superfamilies, with one major clade consisting of Bombycoidea and Cossoidea as sistergroups. According to his new classification, the Bombycoidea comprised the Bombycoidea, Lasiocampoidea, Saturnioidea, Sphingoidea and Psychoidea *partim* [Mimallonoidea] of previous authors, resulting in exactly the assemblage of families

later referred to as the "bombycoid complex" by Minet (1994). Within the Bombycoidea he regarded the Lasiocampidae as the most "primitive" family, while he proposed that the Anthelidae formed a link between the more "primitive" Eupterotidae and the more "advanced" Bombycidae. He further assumed the Saturniidae to be derived from Carthaeidae and Brahmaeidae. While he provided hypotheses of step-wise transformations for several structures within the Bombycoidea, he did not provide any characters defining this superfamily.

Brock's work was strongly criticized by Scott (1986), in particular for not mapping character changes onto the branches of his dendrogram. Scott further suggested that the Macrolepidoptera formed a monophyletic group, refuting Brock's proposed clade of Bombycoidea+Cossoidea. He compiled a character matrix largely based on morphological details published by others, and summarized his hypotheses in a dendrogram, with character changes mapped onto its branches. Most notably, he excluded Mimallonidae from the bombycoid complex and placed this family outside the Macrolepidoptera in the Pyraloidea – on the basis of several symplesiomorphies.

In a series of publications on the moths of America north of Mexico, the bombycoid complex was again split into several superfamilies by Franclemont (1973), namely the Mimallonoidea, Bombycoidea and Sphingoidea. In his treatment of the Bombycoidea, Franclemont (1973) characterized the Bombycoidea [*s. str.*] by "the loss of or loss of function of various structures, the reduction in the wing veins and the expansion of the humeral angle of the hind wing", without specifying these losses and reductions any further. Similarly, Holloway (1987) vaguely defined the Bombycoidea on the absence of the M-stem in fore wing venation and the loss of haustellum and frenulum. As these structures are not lost in some members of several bombycoid families and hence these losses appear to be homoplastic, he concluded that the monophyly of the Bombycoidea was not supported by these losses. However, he presented some characters which group larger parts of the Bombycoidea together. The dilemma of defining the Bombycoidea entirely by non-universal and homoplastic reductions and losses was also pointed out by Common (1990) and Scoble (1995).

In his classification of Lepidoptera, Minet (1986) included the Sphingidae in Bombycoidea and voiced doubts about the monophyly of this superfamily, as he proposed only a single supporting apomorphy, namely the occurence of secondary hairs in caterpillars, which is a characteristic widespread in Macrolepidoptera. Nevertheless,

Minet (1986) was the first to explicitly propose two synapomorphies for parts of the superfamily: the hypertrophy of the lateral setose plates of the anal prolegs in final instar caterpillars and the location of the D1 setae on an unpaired scolus on abdominal segment A8. Five years later he expanded his classification to a phylogeny of the Ditrysia, in which he split the Bombycoidea *sensu* Brock 1971 into three superfamilies, namely the Mimallonoidea, Lasiocampoidea and Bombycoidea *s. str.*, to assure monophyly of the latter (Minet 1991). This was achieved by excluding Lasiocampidae and Anthelidae from Bombycoidea and by placing the two families together in Lasiocampoidea. For the entire bombycoid complex he proposed six autapomorphies, while for Lasiocampoidea, Mimallonoidea and Bombycoidea he proposed four, one and two autapomorphies, respectively. In a subsequent study dedicated to the phylogeny of the Bombycoidea, Minet (1994) corrected and improved his argumentation, but most of all presented a proposal for a largely resolved phylogeny of the bombycoid complex based on individual character analyses (a priori determination of character polarity), summarized in a dendrogram. The classification based on this proposed phylogeny was maintained in Lemaire & Minet [1998], but the argumentation (proposed synapomorphies) was corrected and improved again. In their classification of the bombycoid complex Minet (1994), and Lemaire and Minet ([1998]) explicitly proposed urgently needed autapomorphies for each family.

The phylogeny of the bombycoid complex proposed by Minet (1994) rapidly attracted criticism from other authors. In their publication on the pre-imaginal instars of the "odd" African taxon *Spiramiopsis comma*, Oberprieler and Duke (1994) critically re-examined pre-imaginal synapomorphies proposed by Minet and pointed out several short-comings. They doubted the necessity of the split between Bombycoidea and Lasiocampoidea, and suggested synonymising Lemoniidae and Brahmaeidae [as was earlier done by Forbes (1955)]. In a study of the Australian eupterotid species *Ebbepterote expansa*, Oberprieler *et al.* (2003) re-examined several of Minet's proposed synapomorphies, in particular the autapomorphies of the family Eupterotidae. They pointed out numerous problems and concluded that the monophyly of the Eupterotidae was only potentially supported by a single character of thorax morphology not examined by them. Further criticism of Minet's concepts came from Niculescu (1988, 1989a, b), who proposed his own classification almost entirely based on thorax morphology. His classification included the Mimallonidae in the Bombycoidea, but re-instated the

monotypic superfamily Sphingoidea.

Kuznetzov and Stekolnikov studied the muscles of male genital structures across a wide range of Lepidoptera. One of their publications proposed a phylogeny of the bombycoid complex, based on male genital muscles only (Kuznetzov & Stekolnikov 1985) [Their publication is in Russian; according to their English summary, their phylogeny is based on male genital muscles and some additional larval and pupal characters. I translated the Russian text, but did not find mention of any larval or pupal characters other than the occurrence of hairs on scoli in some caterpillars.]. They provided a fully resolved dendrogram of the families Lasiocampidae, Sphingidae, Saturniidae, Brahmaeidae, Endromidae and Bombycidae, which they arranged in the monotypic Lasiocampoidea, the monotypic Sphingoidea and the Bombycoidea. In a more recent publication Kuznetzov and Stekolnikov (2001) modified their concept of these superfamilies to include the families Lasiocampidae, Anthelidae, Lemoniidae, Eupterotidae and Apatelodidae in the superfamily Lasiocampoidea, as well as the families Carthaeidae, Saturniidae, Brahmaeidae, Endromidae and Bombycidae in the superfamily Bombycoidea. However, they apparently lacked representatives of many families (including Anthelidae) and simply accepted the placement of these families by Minet (1994). Subsequently, Stekolnikov and Zolotukhin (2002) published a detailed description of the muscles of male genital structures of two species of Lemoniidae, confirming the placement of Lemoniidae in Lasiocampoidea by two presumed synapomorphies, namely the reduction of muscle *m2* and a gnatho-uncal articulation of the gnathos.

A tentative phylogeny of the bombycoid complex, very different from any previous one proposed, was presented by Heppner (1998). He derived a fully resolved phylogeny of 124 terminal taxa (families) from a character matrix with only 24 multi-state characters and a "review of the available literature" (Heppner 1998: 4). As his character states are remarkably constant among the bombycoid taxa and as previously published bombycoid phylogenies differ strongly from Heppner's dendrogram, the basis for Heppner's bombycoid phylogeny is not discernible. A bombycoid phylogeny of equally low value was published by Dolinskaya and Pljushch (2000), who examined the egg chorion of some bombycoid species. They illustrated a dendrogram of several bombycoid families based on their studies, but they did not list any characters or give any justifications for their hypotheses.

In a masterly study of the adhesive devices of caterpillars, Hasenfuss (1999) noted a unique modification of the structure of the proleg cuticle, which he casually proposed as a possible autapomorphy of the bombycoid complex. While his study did not include all bombycoid families, it nevertheless included all of the major ones as well as a very large number of non-bombycoid taxa from many different families. Such wide sampling paired with the uniqueness of this character is rare and renders it the most convincing autapomorphy of the bombycoid complex published so far.

With the advent of automated DNA sequencing, molecular phylogenies for bombycoid taxa appeared in quick succession. The first publication used a short stretch of a single nuclear gene (Arylphorin) to hypothesize the relationships between nine species of Saturniidae and two species of Bombycidae (Shimada *et al.* 1995). Phenetic trees were calculated by a neighbor-joining algorithm and showed support for closely related taxa only within the Saturniidae. Likewise, but even less informatively, Hwang *et al.* (1999) claimed support of more than 99% confidence for the monophyly of Saturniidae and Bombycidae, but their samples consisted of only two species of the saturniid genus *Antheraea* and the bombycid species *Bombyx mandarina* and *B. mori.*

A phylogeny of Macrolepidoptera was derived from ND1 and 28S ribosomal DNA sequences in a search of butterfly origins (Weller & Pashley 1995), but the resulting trees were inconclusive for the few bombycoid taxa involved (insignificant statistical support).

A small number of molecular phylogenies within bombycoid families were published by the labs of Jerome C. Regier and Charles Mitter at the University of Maryland. They used the "known lepidopteran relationships [of certain bombycoid families]" (Regier *et al.* 1998: 1173) in "concordance studies" to benchmark the suitability of the genes used in their phylogenetic analyses. These studies included phylogenies of Attacini [Saturniidae] based on EF1a and DDC sequences (Friedlander *et al.* 1998), of mainly North American Lasiocampidae derived from EF1a sequences only (Regier *et al.* 2000), as well as of Sphingidae (Regier *et al.* 2001) and of Saturniinae [Saturniidae] (Regier *et al.* 2002) based on EF1a and DDC sequences.

So far only Regier *et al.* (1998) targeted the phylogeny of the bombycoid complex up to family level, using a 909bp fragment of the *period* gene. The result, however, was largely inconclusive for relationships between families, as none of the clades proposed

had convincing statistical support. Interestingly, Apatelodinae and Bombycinae – both bombycid subfamilies according to Lemaire & Minet [1998] – were not grouped together, but the actual placement of each of them was inconclusive, too.

Relatively little progress has been made since the popular usage of the term "Bombyces". While the superfamily has been stripped of obviously unrelated taxa, its definition by homoplastic characters of loss is not convincing and its presumed monophyly is accordingly uncertain. Many of the earlier authors stated difficulties in separating several of the bombycoid families from each other, namely the Bombycidae, Eupterotidae, Brahmaeidae and Lemoniidae. Until now, the monophyly of most bombycoid families has been uncertain despite the autapomorphies proposed for them by Minet (1994), and Lemaire and Minet ([1998]). But even worse, the monophyly of these families has only been rarely questioned. With the exception of Minet's bombycoid phylogeny (Minet 1994) the vast majority of other "phylogenies" and classifications is based only on the uncritical use of similarities. While Minet's concept of the bombycoid complex represents by far the most significant contribution to our current understanding of bombycoid phylogeny, it suffers from numerous problems. In particular, these are the frequent *ad hoc* postulation of reversals, the common use of characters of low information content (losses and reductions), and the incorrect scoring of character state occurrence, probably due to a lack of samples in certain groups. His hypotheses and their problems are discussed in greater detail in Appendix P. The few molecular phylogenies published for bombycoid taxa so far contribute little to the higher classification of the bombycoid complex. The genes used were not informative at the family level and the claimed "support" for the monophyly of various bombycoid families is flawed because of very limited, unrepresentative sampling. Taxa presumed to be critical for the understanding of the phylogeny were not included in these studies, and statistical support was generally only found for relationships between relatively similar taxa, leaving the "critical" questions largely unanswered.

Upon closer examination, it seems as if despite – if not due to – 200 years of popular study of the bombycoid complex our knowledge of evolutionary relationships in this group is more of a guess.

I.4) AIMS OF THIS THESIS

The review of literature clearly demonstrates our overall lack of knowledge of the Anthelidae. While rather large quantities of information on various aspects of Anthelidae have been published, these are largely repetitive and often of limited value due to low quality (e.g., many faunistic, medical and host records) and/or uncertainty about the source (e.g., most morphological data). To a large extent this is caused by our current inability to reliably identify species based on publicly available taxonomic information alone. The publication of results based on incorrect species identification only obscures the available correct information. The current "taxonomic mess" deters people from attempting to resolve this problem by taxonomically revising the family, as is indicated by the virtual absence of taxonomic publications on Anthelidae for the last 60 years. Further, the interpretation and application of currently available information is severely limited by the lack of a phylogenetic system that, if used correctly, can provide a justifiable basis for the interpretation and generalisation of observations made on a few taxa only.

The key to opening this taxonomic deadlock is a phylogenetic system to serve as a framework for future taxonomic revisions, which in turn are the indices to and links between any other type of study of Anthelidae. This thesis aims at establishing such a phylogenetic system, which will provide a justifiable and stable classification based on natural groupings of taxa. The following three particular goals are to be achieved through a number of specific objectives:

A) To gain insights into the evolution of Anthelidae

- Re-examine phylogenetic hypotheses previously published.
- Test the monophyly of the family Anthelidae and its subfamilies.
- Develop phylogenetic hypotheses based on morphological and molecular data for
  a) the evolutionary relationships among anthelid taxa, and
  b) the origin of the family Anthelidae.
- Critically test these phylogenetic hypotheses by examining the plausibility of character state changes implied by the phylogenies, by mapping additional characters (e.g., host records) onto the phylogenies, and by statistical analyses.

B) To establish a stable classification on which subsequent taxonomic revisions can be based

- Revise the current classification to reflect natural groupings consistent with the phylogenetic hypotheses, adjusting existing genera and subfamilies accordingly.
- Introduce new genera, tribes and subfamilies in accordance with the phylogenetic hypotheses if required.

C) To make previously published and newly gained knowledge of Anthelidae accessible to the public

- Summarize all currently available information on Anthelidae in a critical review with comprehensive lists of records (e.g., of host plants and parasitoids).
- Summarize phylogenetic hypotheses in phylograms.
- Make high quality DNA sequences used as phylogenetic characters available on GenBank.

CHAPTER TWO:

MATERIALS & METHODS

II.1) MATERIALS

II.1.1) Museum collections and field collecting

Museum collections around the world house relatively large quantities of dried, pinned anthelid imagines as well as huge quantities of other taxa of the bombycoid complex. Their significance lies not only in the preservation of the unique type specimens, but also in their extensive spatial and temporal coverage, in historic records from habitats which have been changed or destroyed, and in knowledge potentially preserved in the arrangement of the specimens. Numerous collections were visited in person and/or loans were made in an attempt to obtain as broad a basis as possible for this study:

- Australian National Insect Collection C.S.I.R.O. (ANIC) – Australia, Canberra: visited
- Queensland Museum (QM) – Australia, Brisbane: visited
- University of Queensland Insect Collection (UQIC) – Australia, Brisbane: visited
- Insect collection of the Queensland Department of Primary Industries (QDPI) – Australia, Brisbane: visited
- Western Australia Museum (WAM) – Australia, Perth: visited
- Insect collection of the Western Australia Department of Agriculture (WADA) – Australia, Perth: visited
- Natural History Museum (formerly British Museum (Natural History)) (BMNH) – United Kingdom, London: visited
- Zoölogisch Museum, Universiteit van Amsterdam (ZMA) – The Netherlands, Amsterdam: visited

- Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie) (RMNH) – The Netherlands, Leiden: visited
- Museum für Naturkunde an der Humbolt-Universität zu Berlin (ZMB) – Germany, Berlin: visited
- Forschungsinstitut und Naturmuseum Senckenberg (SMF) – Germany, Frankfurt: visited
- Staatliches Museum für Naturkunde (SMNS) – Germany, Stuttgart: visited
- National Museum (NMK) – Kenya, Nairobi: visited
- National Museum of Natural History, Smithsonian Institution, (USNM) – USA, Washington: loan of all anthelid specimens
- National Agricultural Insect Collection Kila Kila (NAIC) – Papua New Guinea, Boroko: digital images of all anthelid specimens in NAIC
- private Bombycoidea collection of Dr. Rolf Oberprieler, CSIRO (CROC) – Australia, Canberra: visited
- private insect collection of the author (CAZS) – Germany, Schlitz

Of these, the ANIC is by far the most significant collection for the study of Anthelidae as it holds numerous type specimens by Turner and Lower. Further, it has the largest and most complete collection of Anthelidae, covering all of Australia and parts of Papua New Guinea (Brandt collection). Overseas collections, in particular the BMNH, preserve a rather small number of anthelid specimens with a rather poor representation of anthelid diversity, but hold a large proportion of anthelid type specimens.

While museum collections provide a good basis for the morphological examination of sclerotized imaginal structures (e.g., wing venation and genital structures), they are generally not suitable for molecular studies, as they mainly consist of old specimens in which the DNA has entirely degraded. This often is due to the practise of relaxing the specimens with water for setting their wings. Likewise, pre-imaginal instars are rarely preserved in museum collections, and first instar caterpillars are particularly scarce.

Again, the limited collection of preserved caterpillars and very few pupae in the ANIC is clearly the most significant one of its kind.

To obtain specimens for molecular studies as well as for morphological studies of soft imaginal parts (e.g., muscles and glands) and pre-imaginal instars, live specimens were collected in the field. Field collecting was carried out frequently in various habitats within 150km of Canberra from September until May. Numerous short and several longer field collecting trips were undertaken in Australia as well as overseas, specifically targeting species identified as critical for this study by imaginal morphology. Within Australia this included several short collecting trips to inland NSW and the Snowy Mountains, a five week collecting trip covering localities along coastal QLD from its southern border to as far north as Daintree NP north of Cairns as well as inland localities as far west as Charleville in autumn, a three week collecting trip to the Pilbara in WA during autumn, and a two week collecting trip to southern WA in spring. To obtain specimens of the bombycoid complex critical for molecular studies I further collected in south-eastern Kenya for two weeks, as well as on the Philippine island of Palawan. A comprehensive list of collecting localities and dates is given in Appendix E.

The field collecting of Australian specimens was covered by several permits:

area covered	licence type	licence number	licence holder	issuing body
ACT (National Parks & State Forests)	letter of agreement	[none]	Andreas Zwick	Environment ACT
NSW (National Parks & State Forests)	Scientific Research Licence	3319	Andreas Zwick	NSW National Parks and Wildlife Service
VIC (National Parks & State Forests)	Research Permit	10002076	Andreas Zwick	Department of Natural Resources and Environment
QLD (State Forests of the Atherton/Mareeba QPWS Wet Tropics District area)	permit to collect	1714	Dr. David Yeates	Queensland Parks and Wildlife Service
QLD (National Parks)	permit to collect	F1/000246/02/SAA	Dr. David Yeates	Queensland Parks and Wildlife Service
WA (National Parks & Nature Reserves)	licence to take fauna for scientific purposes	SF004145	Tom Weir	Dep. of Conservation and Land Management
WA (National Parks & Nature Reserves)	licence to take fauna for scientific purposes	SF004301	Dr. Christine Lambkin	Dep. of Conservation and Land Management

To collect specimens in the field, a white sheet was set up like a screen and a UV-emitting light source was placed in front of it. This was either a clear Mercury Vapour bulb (250W) powered by a Honda generator (EX650) [Fig. 2] or a 20W UV-fluorescent tube ("blacklight") powered by a sealed lead-acid battery (12V, 17Ah) through a voltage inverter. Usually, several such lights were set up in different habitats and run from dusk till dawn. The lights were attended throughout most of the night and specimens were collected manually.

In addition to material obtained during field collecting, specimens for molecular studies were purchased from amateur breeders in Europe. Further, five specimens of three North American bombycoid taxa were kindly provided by Bruce Walsh at the University of Arizona (USA, AZ, Tucson) and James Costa at the Western Carolina University (USA, NC, Cullowhee), and caterpillars and cocoons of two Australian anthelid species by Gerhard Weber (Australia, SA, Adelaide).

Fig. 2: Field collecting in the Pilbara (WA) – typical setup for moth collecting with light.

I.1.2) Taxa sampled for morphological study and DNA sequencing

The ANIC holds specimens of all described and most undescribed Australian anthelid species (about 150 spp.), as well as a number of New Guinean anthelid species (about 15-20 spp.). Of these, genitalia preparations of male specimens were made for all visually distinct taxa, often of more than one specimen to assess variation. Male genital structures are usually highly informative within the family and were used to identify closely related taxa, of which representatives were chosen for further morphological and molecular studies, depending on their availability. Unfortunately, no fresh specimens from New Guinea (including the endemic genus *Pseudodreata*) for DNA sequencing could be obtained, but members of all other identified species groups were collected.

For the phylogenetic analyses of the placement of Anthelidae within the bombycoid complex, taxa were targeted which are either "critical" (typical members of current families and subfamilies as well as "odd", monotypic or "primitive" taxa) according to the literature, or which are assumed to be so, based on previous own observations, as well as on the advice of Dr. Rolf Oberprieler (ANIC) and Dr. Wolfgang Nässig (SMF). Again, the final choice was restricted by the availability of specimens, but overall the bombycoid complex was well covered for morphological as well as molecular studies, with only two families (Mimallonidae and Mirinidae) and a few subfamilies not being available for molecular studies. For comprehensive lists of genitalia preparations, whole body preparations, SEM preparations and DNA samples see Appendices F-I.

II.2) Morphological methods

II.2.1) Dissections

II.2.1.A) Fresh and fixed specimens

Freshly killed specimens were pinned into a petri dish with a foam bottom and insect ringer solution (9.1g NaCl, 0.52g KCl, 1.2g $CaCl_2$, 0.8g $MgCl_2$, 1l H_20). Female genital structures and muscles of male genital structures were dissected by cutting open the abdomen with a pair of micro-scissors and carefully cleaning the abdomen of internal organs including the intestinal tract, tracheae and fat bodies with a pair of fine forceps. Muscles were stained by briefly dipping the entire preparation into aqueous, acidic Aniline Blue solution (1mg Aniline blue, 2ml glacial acetic acid, 98ml water) and rinsing it with water.

Specimens fixed in the field with Kahle's fluid (30 parts distilled water, 15 parts 95% ethanol, 6 parts 35% formalin, 2 parts glacial acetic acid) and stored in 80% ethanol were likewise dissected in 80% ethanol, rather than in insect ringer.

II.2.1.B) Maceration of specimens

To examine the sclerotized structures of dried specimens, their tissues had to be removed by maceration. Body parts (e.g., the entire abdomen for genitalia preparations) or entire specimens were individually placed in a vial with 10% aqueous potassium hydroxide (KOH) solution and brought to boil briefly in a water bath (electric water kettle), where they remained for another 10min after boiling. Scales were removed with a trimmed brush from the softened samples, and large pieces of tissue and internal organs were removed with a pair of forceps. If necessary, samples were boiled up a second time to remove smaller remnants of tissue.

For preparations of genital structures the abdominal membrane was cut with a pair of micro-scissors along the left pleura and detached from the genital structures by tearing the membrane with two pairs of fine forceps. For male genital structures the membrane was torn around the annulus, while for female genital structures it was torn along tergum VIII and ventrally along the lateral and proximal edges of sternite VII to preserve the ostium bursae with lamellae ante- and postvaginalis. All genital structures and the abdominal membrane were stored in vials with a mixture of 70% absolute ethanol and 30% glycerine (to protect them from drying out and to keep them flexible). Identical

labels with a unique index number and the collecting data were placed in the vial as well as on the specimen pin for every genitalia preparation. All other preparations were stored and labelled likewise.

Only the sclerotized parts of male genital structures remained after maceration and were generally preserved unmodified. They were not "flattened out" and slide-mounted as is commonplace for Lepidoptera, because their three dimensional structure is essential for the understanding of function as well as for forming hypotheses of homology.

Of the female genital structures not only the sclerotized structures and bursa copulatrix were preserved, but also spermatheca, accessory glands and the ducts of the ovarioles if possible. Membranous structures were stained by briefly dipping the entire preparation into a Chlorazol Black solution.

A comprehensive list of all preparations is given in Appendices F & G.

II.2.2) Observation and documentation

II.2.2.A) Photos

Photos of whole specimens (all instars) and larger structures were taken with a digital SLR camera (Canon EOS 300D), a dedicated macro lens (Tamron SP AF 90mm f/2.8), a set of extension tubes (Kenko C/AF) and a corded E-TTL flash (Sigma EF-500 DG Super). The same setup with a zoom lens (Canon EF-S 18-55mm f/3.5-5.6) was used for all other photos.

II.2.2.B) Light microscopy (drawings and images)

All specimens, fresh and macerated dissections and preparations were examined with a dissecting stereomicroscope (WILD M3C, Leica) and fibre-optic ring-light (Intralux 5000-1, Volpi) in the ANIC. Structures were either documented by drawing with help of a camera lucida (WILD M5 drawing tube) attached to the WILD M3C or by digital images taken with a video camera (Olympus DP70) mounted on a dissecting stereomicroscope (Leica MZ 8). Of most structures multiple digital images at different focal levels were taken and combined to a single image of greater depth of field with the software Auto-Montage™ version 4.02.0014 (Syncroscopy).

II.2.2.C) Scanning electron microscopy

Small structural details including the mouth parts of first instar caterpillars and the

sensilla of imaginal antennae were examined with a scanning electron microscope (SEM). SEM samples had to be either air-dried (all strongly sclerotized imaginal structures, e.g., imaginal antennae) or dehydrated through a series of ethanol baths of increasing concentrations and critical-point dried (all softer, ethanol-fixed samples, e.g., caterpillars). Dry samples were mounted on metal studs with a double-sided carbon sticky tape. They were gold sputtered (~30nm thickness: 4min, 0.15 Torr vacuum, 200V, 42.5mA) with a Balzers Union sputter coater at the Microscopy Centre of CSIRO Entomology. For samples which did not adhere well to the sticky tape due to scales or hairs, electric contact was improved by the addition of a droplet of conductivity silver to reduce electrostatic charging in the SEM. Samples were examined with a Cambridge S360 scanning electron microscope at the ANU Electron Microscopy Unit (EMU).

Anthelid caterpillars of *Munychryia senicula* and *Anthela ocellata*, as well as of *Cotana serranotata* (Eupterotidae) and an *Epicoma* species (Notodontidae), were examined by Cryo-SEM. The live specimens were shock-frozen when placed in a chamber cooled by liquid nitrogen. The frozen samples were gold sputtered if necessary and inserted into the cold stage of the Cambridge S360. Samples were examined with the SEM in this frozen state.

A total of 647 digital images of 66 preparations was taken directly through the SEM. A comprehensive list of all preparations is given in Appendix H.

II.2.2.D) X-ray microanalysis (EDXA)

Some vesicles on the surface of the caterpillar integument were qualitatively analysed by X-ray microanalysis. Frozen samles, which were not sputtered with gold, were examined in the cold stage of the Cambridge S360 SEM. The structures to be examined were hit with an electron beam at 10kV, which caused hit atoms to emit x-rays of intrinsic wavelengths. These x-rays were detected by an Energy Dispersive X-Ray Analyzer (Tracor Northern EDXA detector) and the resulting spectrum was recorded and documented as an image file. Peaks in this spectrum indicate which different elements are present in the examined structure.

II.2.2.E) Wing venation

Wings of dried specimens were broken off and their scales removed with a small brush. They were examined and their shape and venation illustrated by drawing as described for light microscopy in general (see above, II.2.2.B). Due to the large size of

the wings and their veins, bleaching and staining as described for Microlepidoptera by, e.g., Zimmerman (1978: 73-87) was not necessary.

For some specimens, in which only the arrangement of a few veins had to be checked, wings and scales were not removed, but instead wings were locally moistened with absolute ethanol to reveal the veins beneath the scales.

II.2.2.F) Pupal tracheation

Relatively recently hardened pupae (about one week after cocoon spinning) were removed from their cocoons and the semi-transparent cuticle over their developing wings was painted with clear nail polish. This resulted in a very smooth surface and thereby reduced diffuse reflections of light, which are caused by the microscopically rough cuticle. Pupae were examined periodically with a stereo-lens until the onset of scale pigmentation, which commenced close to eclosion of the moths. Visibility of tracheae was improved by illuminating the pupae laterally with a fibre-optic light source, causing reflections of light in the air-filled tracheae. The arrangements of tracheae in the developing wings were documented by taking pictures through the ocular of the stereo-lens with a digital camera (Nikon Coolpix 995) in one case, and illustrated by drawing with help of a camera lucida otherwise (see above, II.2.2.B).

II.3) Molecular methods

All molecular work was carried out in the molecular laboratory of the School of Botany and Zoology at the ANU.

II.3.1) Fixation and extraction of sample DNA

Live specimens, preferably male imagines for reliable identification, were fixed in 95% or absolute ethanol and immediately stored in a -20°C freezer. During longer field collecting trips as well as with specimens received by mail from overseas, freezing was not possible until several weeks after fixation in absolute ethanol.

For DNA extraction, thoracic muscles of imagines were used to avoid contamination with foreign DNA from gut contents or external particles. If caterpillar samples only were available, entire first instar caterpillars were used prior to the commencement of feeding, or only longitudinal abdominal and/or proleg muscles of older caterpillars were used. To reduce the usage of hazardous chemicals, DNA extraction was facilitated by salt extraction (see Appendix J.1 for the protocol).

II.3.2) Genes sampled

Due to time constrains and a very limited budget, only genes which had already been used successfully in other phylogenetic analyses and for which primer sequences were available were considered for sequencing. A search for novel genes and primers was beyond the scope and possibilities of this study. Gene choice was further restricted by sub-optimal fixation of DNA samples (fixed in ethanol with no possibility to freeze samples collected during longer field trips in hot climates), ruling out the sequencing of genes like DDC and PEPCK, which would have required the preservation of mRNA (fixation of samples in liquid nitrogen) for costly RT-PCRs.

Initially, gene fragments frequently used for lepidopteran phylogenies and with numerous primer sequences available were chosen: 1246bp of elongation factor 1 alpha (EF1a) and 2321bp of cytochrome oxidase I and II (CO I & II). Based on a preliminary examination of these sequences, which revealed variable codon positions to be saturated in both genes, fragments of more conserved genes were sequenced. These were fragments of the ribosomal genes 12S, 18S and 28S, and fragments of the protein coding genes *wingless* and carbamoylphosphate synthetase (CPS), which is a domain of the

fusion protein CAD (carbamoyl-phosphate synthetase, aspartate transcarbamylase, dihydroorotase).

II.3.3) Gene amplification

Gene fragments were amplified by standard polymerase chain reaction (PCR; see Appendix J.2 for the protocol), using a Cooled Thermal Cycler PC-960C from Corbett Research and a touch-down program with stepwise reduction of annealing temperature (down to 40°C) to increase chances of fragment amplification (see Appendix K.1 for the program). As the maximum sequence length was limited to about 630bp by the capillaries used in the sequencer, much longer gene fragments (EF1a and CO I & II) were subdivided into several shorter, overlapping fragments for PCR and sequencing, resulting in the following successful primer pair combinations (see Appendix L for primer sequences):

gene	fragment #	fwd primer	rev primer	fragment length [bp]
EF1a	A	M3	rcM51.1	540
EF1a	B	M44.1	rcM52.6	657
EF1a	C	M44.1	rcM4	1071
EF1a	D	M46.1	rcM4	766
EF1a	E	M51.9	rcM4	516
CO I & II	A	TY-J-1460	C1-N-1840a	379
CO I & II	B	C1-J-1751e	C1-N2329	577
CO I & II	C	C1-J-1751e	C1-N-2578f	826
CO I & II	D	C1-J-2495a	TL2-N-3014	518
CO I & II	E	C1-J-2792a	C2-N-3389a	596
CO I & II	F	C2-J-3138	TK-N-3782	643
wingless	A	LepWg1	ModLepWg2	378
CPS	A	806F	1124R	953
CPS	B	843F_BOM	1057R_BOM	641
CPS	C	806F	1057R_BOM	752
28S	A	S3660	A335	~780
12S	A	J14199	N14594	~439
18S	A	18S-2880	18S-B	510

PCR product quality and quantity was checked by electrophoresis in a 1% agarose gel (an example is shown in Fig. 3; see Appendix J.3 for the protocol). Weak PCR products as well as PCR products with more than one strong band were excised from a 1%

agarose gel and cleaned with an UltraClean 15™ DNA Purification Kit (see Appendix J.4 for the protocol). PCR products with a single strong band were cleaned directly by ammoniumacetate/ethanol precipitation (see Appendix J.5 for the protocol).

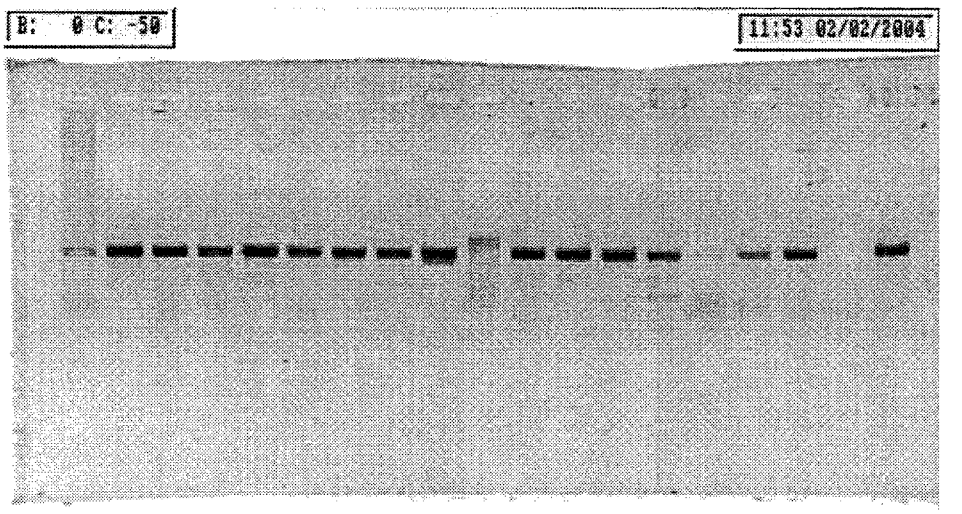

Fig. 3: Control of PCR product quality and quantity – an amplified EF1a fragment run out by electrophoresis in an agarose gel; weak PCR products (e.g., fifth lane from the right) were excised and purified; HyperLadder IV in central, negative and positive controls in most right-hand lanes.

II.3.4) Sequencing

Cleaned PCR products were prepared for sequencing in a sequencing reaction using the dye terminator mixture BigDye 3.1. Excess labelled nucleotides of the BigDye 3.1 mixture were removed in subsequent precipitation and wash steps (see Appendix J.6 for the protocol, and Appendix K.2 for the sequencing reaction program cycle times). Sequencing reaction products were sequenced by an automated cycle sequencer ABI 3100 Genetic Analyzer (Applied Biosystems/Hitachi). For all fragments the forward as well as the reverse strand were sequenced.

II.3.5) Sequence processing

Sequences were obtained from the sequencer in ABI format, which includes the chromatogram and the sequence interpreted from it by the ABI base-caller software. All sequences were processed with the software package Phred/Phrap/Consed (Ewing *et al.* 1998a, b; Gordon *et al.* 1998): Chromatograms were re-analysed with Phred (base-caller, version 0.020425.c) and alternative sequences with quality values for every base-call were generated. Contigs (combinations of forward and reverse strands of all gene fragments, resulting in a single consensus sequence) were assembled directly with Phrap

(assembler, version 0.990329), using the quality values generated by Phred as guidance and thereby eliminating the need to cut off stretches of low quality sequence (ends) prior to assembly. All contigs were manually checked against their chromatograms in Consed (graphical contig editor, version 13.39(β)), using ABI as well as Phred base calls and utilizing Consed's guidance functions to double-check for low quality areas and base-call mismatches between individual chromatograms. Primer sequences were excluded from contigs. All contigs were exported to FASTA format for sequence alignment.

Following initial sequence alignment of all contigs (see below, II.4.1.B) base-calls for all parsimony informative characters were re-checked in Consed and all contigs were entirely checked manually a second time to assure sequence quality. The double-checked contigs were all exported to FASTA format for final sequence alignment. For protein coding genes to be used in the phylogenetic analyses (EF1a and CPS), sequence quality was further checked by translating the final DNA sequences to amino acid sequences with the software MEGA version 3.0 (Kumar *et al.* 2004).

II.4) PHYLOGENETIC METHODS

II.4.1) Forming hypotheses of homology

II.4.1.A) Morphological characters

Based on the criteria of homology proposed by Remane (1952), hypotheses on the homology of structures in specimens of different species were formed. These sufficient criteria are:

a) the location of a structure relative to other structures (criterion of location),

b) the agreement in details of a structure (criterion of specific quality), and

c) the transformation of structures (criterion of continuity), which essentially represents an application of a) and b).

Hypotheses of homologous structures were coded as characters and hypotheses of homologous details of these structures as character states in a character matrix in Nexus format (Maddison *et al.* 1997). For the Hennigian Argumentation multi-state characters were split into a number of binary characters for ease of use and transparency. Transformation series were coded as additive binary characters.

The hypotheses of homology are formed in individual character analyses (sections III.1.4, III.2.4, III.3.2, III.4.2, III.5.2, III.6.2) and are the basis of the Hennigian Argumentation (section III.7). They are also used in the cladistic analyses (chapters IV & VI), in which the hypotheses of homologous details (character states) are regarded as primary homologies *sensu* de Pinna (1991).

II.4.1.B) Molecular characters

The alignment of sequences is the forming of hypotheses of homology for characters based on the criterion of location (see above, section II.4.1.A) alone, while the hypotheses of homology for character states is only based on the criterion of specific quality.

For each gene sequences of different specimens were aligned using the multiple alignment program ClustalX version 1.83 (Thompson *et al.* 1997) with default parameters. All alignments were visually checked in the program SeaView (Galtier *et al.* 1996) and manually corrected if necessary. Alignment of protein coding genes was straightforward, but alignments of ribosomal genes required a lot of manual aligning due to hyper-variable regions with multiple insertions and deletions ("indels").

Sequence alignments were directly used as character matrices by saving them in Nexus format.

II.4.2) Hennigian Argumentation

The development of phylogenetic hypotheses by Hennigian Argumentation of morphological characters is based on methods formalized by Hennig (1950, 1966; for a recent discussion of these methods and their theoretical basis see Wägele 2001). This method consists of individual character analyses (sections III.1.4, III.2.4, III.3.2, III.4.2, III.5.2, III.6.2) and a subsequent argumentation (section III.7), in which the results of the character analyses are evaluated and interpreted on the basis of parsimony.

The analysis of each character includes three steps:

- Firstly, a character and its character states are postulated by the formation of hypotheses of homology of morphological structures (see section II.4.1).
- Secondly, hypotheses of which character state is plesiomorphic and which states are apomorphic are formed. This determination of the polarity of the character is carried out *a priori* by outgroup comparison.

  For an outgroup comparison a group of monophyletic taxa is defined as the ingroup. As many as possible of the other known taxa (the outgroup) are screened for the occurrence of character states present in the ingroup. If a character state is shared by the ingroup and the outgroup it is hypothesized to be the plesiomorphic state of the character. On the contrary, any character states that are unique to the ingroup are hypothesized to be apomorphies within or of the ingroup. As the hypotheses of homology of structures as well as the hypotheses of monophyly of the ingroup taxa are axiomatic assumptions of the method of outgroup comparison, these hypotheses have to be well supported. If more than one character state of a character appears to be shared by the ingroup and the outgroup (= to be plesiomorphic), several causes of the error are possible and a re-examination of the actual specimens and subsequent hypotheses is necessary:

  - A hypothesis of homology of the structural details (character state) is incorrect, i.e., the structural details assumed to be present in a taxon are not homologous with the structural details observed in other taxa (the structural details are only superficial similarities).

- The hypothesis of homology of the character ("frame homology") is incorrect, i.e., some of its character states belong to a different (possibly not defined) character.
- The hypothesis of monophyly of the ingroup taxa is incorrect, i.e., taxa of the ingroup are regarded as members of the outgroup.
- A mistake has been made in the scoring of the characters.

- Thirdly, the quality of the hypothesis of homology of the postulated apomorphic character state is judged *a priori* on the basis of the quality and quantity of the indications of homology (additive use of the criteria of Remane). For every postulated apomorphic character state of each character (one for binary characters) an informal assessment of the quality of its hypothesis of homology is stated in the summary of the character analysis (sections III.1.4, III.2.4, III.3.2, III.4.2, III.5.2, III.6.2). The hypothesis is judged to be "very poorly", "poorly", "moderately", "well" or "very well" supported. The better the support for the hypothesis is, the stronger is the confidence in the hypothesis.

Only apomorphies (hypotheses of homology for structural details, which are hypothesized to be apomorphic) are considered in the subsequent argumentation. The occurrence of apomorphies in several taxa is interpreted as being caused by a single evolution of the apomorphy in a shared ancestor of these taxa, which, in the absence of other indications, is always the most parsimonious explanation for the distribution of the apomorphy amongst the taxa. Hence, taxa that share an apomorphy (= possess a synapomorphy) are hypothesized to form a monophylum, i.e., to be "a group of organisms sharing an ancestor only common to them" (Wägele 2001: 70). In contrast, the sharing of a plesiomorphic character state (= symplesiomorphy) by some taxa does not allow the postulation of monophyly for these taxa, because this group of taxa shares a common ancestor, but lacks those taxa with the apomorphic character state(s) as well as taxa in the outgroup with the plesiomorphic character state.

Different apomorphies can support the same or different monophyla. In the latter case they form an encaptic system of monophyla, i.e., a system, in which every monophylum is part of a larger monophylum (except for the largest one). Such an encaptic system of monophyla is a phylogenetic hypothesis of the evolutionary relationships between monophyla and can be visualized in a dendrogram. If the monophyla were given facts, the assembly of the encaptic system would be trivial. However, monophyla are

conceptual constructs based on hypotheses of homology and apomorphy, which in turn are based on observations (= interpretations of visual sensory signals). Hence, hypotheses of monophyly can be wrong. This is sometimes, but not necessarily, apparent as an incompatibility between monophyla, i.e., in a pair of monophyla both include only some of the taxa included in the other monophylum. This indicates an error in at least one of the hypotheses of synapomorphy supporting the monophyla. If a re-examination of the specimens and a repeated character analysis does not lead to a different hypothesis of apomorphy, the conflict might be decided in favour of the better supported hypothesis of monophyly (the hypothesis that one has greater confidence in). If incompatible monophyla differ in the number and/or quality of their supporting hypotheses of synapomorphy, it is possible to argue for the better supported monophylum and to refute the hypothesis of the other. If no distinction can be made on this basis, the conflict can be presented as an unresolved polytomy in a consensus dendrogram.

Refuting any monophylum requires an explanation other than monophyly for the observed distribution of its supporting synapomorphies. Such *ad hoc* explanations can be, e.g., the apparent secondary absence of structures due to strong reduction or loss, the modification of a structure beyond recognition, or the incorrect homologization of structural details in different taxa (superficial similarity of structural details due to analogy or convergence).

II.4.3) Cladistic analysis (Maximum Parsimony)

Unlike a Hennigian Argumentation (see section II.4.2), a cladistic analysis does not include character analyses, which determine *a priori* the quality and polarity of character states. Instead, directly observable similarities of structures in different taxa are defined as discrete character states, the primary homologies *sensu* de Pinna (1991). These primary homologies are tested in the cladistic analysis for congruence with other primary homologies, resulting in their confirmation (secondary homology) or rejection (homoplasy). As in a Hennigian Argumentation, the principle applied in the analysis is parsimony. Based on the assumption that the presence or absence of a specific character state in a number of taxa is likely to be caused by a single evolutionary event in a shared ancestor, that topology of a dendrogram is searched which requires the smallest number of evolutionary events (character state changes) to explain the given distribution of

character states (= most parsimonious topology). This requires the axiomatic assumptions that terminal taxa are monophyla represented by ground patterns as characters and that all character states, if they conflict with other states, have the same probability of being homologies or alternatively be weighted accordingly (Wägele 2001: 191).

I used morphological as well as molecular characters in separate as well as combined cladistic analyses. The morphological characters are based on the characters used in the Hennigian Argumentation (sections III.1.4, III.2.4, III.3.2, III.4.2, III.5.2, III.6.2), but unlike in the Hennigian Argumentation they are restricted to directly observable similarities. Some characters of the Hennigian Argumentation are merged into multistate characters, while other characters of the Hennigian Argumentation are split up. Occasionally, additional character states are introduced to reduce the number of inapplicables in the character matrix. The molecular characters are defined by the alignment of the sequences (see section II.4.1.B).

For both morphological and molecular characters Maximum Parsimony Analyses were carried out in PAUP* version 4.0B10 (Swofford 2002). Characters were generally analysed unweighted (with an implied equal weight) and unordered, but molecular characters were additionally analysed with arbitrary differential weights by codon position to reduce the impact of saturated third codon positions on the analyses. The sets of weights by codon position are 1-1-1, 2-3-1, 5-5-1, 10-10-1 and 1-1-0. In all analyses a heuristic search with branch swapping by tree-bisection-reconnection (TBR), random sequence additions and 1000 replicates was used. Resulting trees were rooted by outgroup addition.

II.4.4) Maximum Likelihood Analyses

For molecular characters, Maximum Likelihood Analyses were run in PAUP*. The best fitting models and their parameters for these analyses were chosen on the basis of hierarchical Likelihood Ratio Tests (hLRT) and Akaike Information Criterion (AIC) as implemented in the program ModelTest version 3.7 (Posada & Crandall 1998). The resulting parameters of the command "Lset" used in the Maximum Likelihood Analyses in PAUP are as follows:

taxa	*genes*	*model*	*parameters of the command "Lset" used in PAUP*
Anthelidae	EF1a	TIM+I+G	Base=(0.2773 0.2730 0.2301) Nst=6 Rmat=(1.0000 6.8966 1.5700 1.5700 10.6992) Rates=gamma Shape=1.3165 Pinvar=0.6594
Anthelidae	CPS	GTR+I+G	Base=(0.3949 0.1445 0.1735) Nst=6 Rmat=(2.7777 10.3144 2.5421 2.8590 21.3775) Rates=gamma Shape=1.4565 Pinvar=0.5051
Anthelidae	EF1a & CPS	GTR+I+G	Base=(0.3123 0.2257 0.2184) Nst=6 Rmat=(1.6646 9.8161 3.8357 1.8521 17.1106) Rates=gamma Shape=1.5018 Pinvar=0.6070
bombycoid complex	EF1a	GTR+I+G	Base=(0.2713 0.2602 0.2278) Nst=6 Rmat=(4.7168 30.5033 13.4963 3.1343 39.3659) Rates=gamma Shape=1.3620 Pinvar=0.6425
bombycoid complex	CPS	GTR+I+G	Base=(0.4312 0.1263 0.1361) Nst=6 Rmat=(3.6235 11.6608 0.6592 3.4994 32.4701) Rates=gamma Shape=0.5558 Pinvar=0.4363
bombycoid complex	EF1a & CPS	GTR+I+G	Base=(0.3149 0.2090 0.2151) Nst=6 Rmat=(5.4679 25.0920 10.3795 4.3979 47.5998) Rates=gamma Shape=1.0365 Pinvar=0.5899

II.4.5) Bayesian analyses

Bayesian analyses of molecular characters were carried out with the software MrBayes version 3.1.1 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003). Datasets were partitioned by codon positions for protein coding genes as well as by different genes in combined analyses. Default values were used for the prior probability distribution of the parameters of the likelihood model, with the exception of the rate multipliers of the partitions, which were specified to be variable ("prset ratepr=variable"). The likelihood model was set to be a GTR model with rates for a proportion of the sites being constant, while the rates for the remaining sites were drawn from a gamma distribution ("lset nst=6 rates=invgamma"). For all partitions the gamma shape parameter, proportion of invariable sites, character state frequencies and substitution rates of the GTR model were unlinked ("unlink shape=(all) pinvar=(all) statefreq=(all) revmat=(all)"). The Markov Chain Monte Carlo analysis was run for 2,000,000 to 5,000,000 cycles, and samples were take every 1,000 cycles ("mcmc ngen=5000000 samplefreq=1000"). Each analysis consisted of two simultaneous runs (separate analyses), and conservatively only those sampled trees were included in the majority rule consensus tree which were generated after the sampled trees converged

onto each other as indicated by the average standard deviation of split frequencies falling below 0.01. An average standard deviation of split frequencies of 0.01 or less was always reached much later in the analysis than convergence of log likelihood values of the cold chain, which was typically used to determine the number of sampled trees to be discarded as "burn in" in previous versions of MrBayes.

II.4.6) Statistical support values

Based on pairwise distances and transition/transversion ratios calculated in PAUP*, saturation plots of the codon positions of the different genes were created with the spreadsheet module of OpenOffice version 1.1.4. Likewise, statistics on parsimony informative character numbers and base frequency bias were generated in PAUP*.

Bootstrap percentages of 1,000 and 100 pseudoreplicates were calculated by the program PAUP* for Maximum Parsimony and Maximum Likelihood Analyses, respectively.

Partitioned Bremer Support (PBS; Baker *et al.* 1998) values for partitions by codon position and gene were calculated by the program TreeRot version 2b (Sorenson 1999) for strict consensus trees resulting from the Maximum Parsimony Analyses of molecular data.

Posterior probabilities were calculated by the program MrBayes as part of the majority rule consensus trees resulting from the Bayesian analyses of molecular data.

CHAPTER THREE:

HENNIGIAN ARGUMENTATION

BASED ON

MORPHOLOGICAL CHARACTERS

The Hennigian Argumentation based on morphological characters is presented as a second, independent line of evidence to be viewed in comparison to the cladistic analyses of morphological characters (chapter IV) and the phylogenetic analyses of molecular characters (chapter V).

Published morphological data accumulated over a long time and conclusions based on them are a treasure that, however, needs to be exploited with caution because interpretations of observed structural agreements changed with the changing theoretical basis of biology. The early interpretations not only vary between different authors because of different opinions, but also due to the lack of a general understanding that morphological resemblances may have different causes, i.e., be analogous or homologous. The morphological criteria to form hypotheses of homology were presented in detail by Remane (1952) and remain valid today (see section II.4.1.A).

Hennig (1950 in German; 1966 more lucidly and also in English) recognized that many different systematic approaches may be valid, depending on the particular purpose and use of the respective system of animal classification. However, only the approach attempting to trace the actual evolutionary history of organisms and depicting the resulting cladistic relations between organisms in its system is useful for the advancement of science *per se*.

The principles of the approach were derived directly from Mayr's biospecies concept (1942) and the speciation process. Hennig also recognized fundamental heuristic limitations in reconstructing past historical events from homologous structures and proposed formal ways of dealing with them, introducing the concepts and terms *apo-* and *plesio-* for this purpose.

The resulting phylogenetic (or cladistic) system is the formal expression of numerous

phylogenetic hypotheses that the systematist himself is supposed to continuously test by confrontation with new evidence, refuting or corroborating the existing hypotheses. However, in accordance with the principle of falsification (Popper 1934) as part of the philosophy of science the proposed system can never be proven to be correct and to be a true picture of evolutionary history. Details of the methodologies referred to above cannot be repeated here; the reader is referred to the original literature and modern summaries of systematic theories (e.g., Schuh 2000; Wägele 2001; Wiesenmüller *et al.* [2003]). Comprehensive syntheses of published and new information on Lepidoptera following the above principles was presented by Kristensen ([1998], 2003a).

In this chapter I present morphological characters and their phylogenetic interpretation based on Hennigian Argumentation. These morphological characters are arranged in sections on different stages of the life cycle and different parts of the body. Each section consists of an introduction and discussion of the structures in question, based on publications and own observations. The discussions and resulting hypotheses on ground plans are a key to the understanding of the character analyses, which complete each section. In these character analyses (sections III.1.4, III.2.4, III.3.2, III.4.2, III.5.2, III.6.2) the distribution of character states are not specified for individual species. Instead, this information is presented separately for the Anthelidae and the bombycoid complex in two matrices in Appendix N. At the end of this chapter the hypotheses of homologies and character polarity are discussed and summarized in a cladogram (section III.7).

The structures considered in the character analyses are often so complex and inconsistently named that for each character existing knowledge, new findings, interpretations and my conclusions need to be presented together, for the convenience of readers. To avoid any ambiguity, I use sideheads in bold italics for the character analyses as follows:

Introduction. To facilitate the understanding of details described in the present chapter it is often necessary to first provide a framework into which observed details are placed. Where necessary, sections on individual characters or character sets therefore begin with a short introduction presenting broader information, often from referenced literature.

Descriptions. Actual descriptions of structures are based on my own observations of Anthelidae, other Bombycoidea and occasionally additional specified taxa. Sometimes, information from literature had to be included also and is identified as such by reference to the source each time.

Discussion. Comprehensive syntheses of published and new information on Lepidoptera following the above principles of Remane was presented by Kristensen ([1998], 2003a).

I follow the same approach in the interpretation of my own new findings and in cases where described facts concerning the bombycoid complex and the (presumably) included Anthelidae had not yet been subjected to critical evaluation. My considerations are presented in the ***Discussion*** following the descriptions, with the identification of apomorphic hypothetical ground plan characters being the main goal.

Summary. For each character a summarizing statement about the hypothesized polarity and the strength of the presumed apomorphic hypothesis of homology is presented.

I re-examined characters used in publications, and a critical review of these publications and characters is presented in Appendix P. Overall, I regard only very few of these characters as suitable for phylogenetic hypotheses of the Anthelidae or the bombycoid complex. Consequently, the majority of characters presented in this chapter are based on own, new observations. In the few cases where I do use previously published characters I cite the respective publications.

III.1) THE SCLERITES OF MALE GENITAL STRUCTURES

The sclerites of male genital structures of Lepidoptera, as well as of insects in general, show typically little intraspecific variation, while at the same time interspecific variation is relatively high. These general characteristics of male genital structures make them extremely valuable diagnostic tools in lepidopteran taxonomy. While not all diagnostic modifications of male genital structures are suitable for phylogenetic analyses, male genital structures are frequently used as characters in phylogenies of lower (= younger) taxonomic ranks. The rather high interspecific variation results in most information being linked to more recent evolution of taxa. This is the case as these more recent modifications of sclerites often obscure or even wipe out older modifications, e.g., by a reduction or loss of a structure. The same problem exists for molecular data, where multiple substitutions in DNA sequences replace older information with newer one (saturation). To access the information pertaining to higher (= older) taxonomic ranks one has to look beyond obvious similarities of structures, such as their shape and size. It requires the understanding and abstraction of visible structures, based on the assembly of remnants of information in related taxa. These abstractions are hypotheses of homology, as are all other characters used in phylogenetic analyses.

Within the bombycoid complex, evolution of morphological structures frequently appears to consist of their reduction only. This tendency is particularly strong in taxa that have a shortened adult lifespan, which is the case for most families in the bombycoid complex, including the Anthelidae. These reductions result in less complex structures or even the total loss of structures, which hinders the development of sound hypotheses of homology and thereby reduces the phylogenetic value of these modifications – obviously, no indications of homology can be observed for absent structures. While reductions and losses of male genital structures are common in Anthelidae, too, their genital structures nevertheless exhibit more modifications towards equal or even higher morphological complexity than any other sclerotized body part of adult Anthelidae. This, combined with low intraspecific and high interspecific variation, predestines such non-reductive modifications of their male genital structures as characters in phylogenetic analyses.

Consequently, I avoid the use of reductions as characters, because they are likely to be homoplastic due to a general tendency towards reduction. I particularly avoid reductions that result in low structural complexity or even absence of a structure, as this makes the recognition of potential homoplasy more difficult to impossible. While this excludes quite a number of modifications from being used as phylogenetic characters, I believe this exclusion to be important.

Only the publications of Common and McFarland (1970), Common (1990), and Lemaire and Minet ([1998]) contain information on male genital structures of Anthelidae. This very limited information is of a descriptive nature and, with the exception of Common & McFarland 1970, not linked to species. Hence, this information is not suitable for phylogenetic analyses.

In contrast, a huge number of taxonomic publications on the bombycoid complex exists, many of which include descriptions and illustrations of male genital structures of species. However, as these descriptions were made for diagnostic purposes and are not based on comparative morphology, their phylogenetic value is typically low. While they detail visible structures more or less accurately, the homology of these structures was rarely of concern. Taxonomic literature on the bombycoid complex contains too many mistakes to detail and correct them. Many of these mistakes are linked to the male genital structures termed uncus, socii, gnathos and transtilla. The worst case scenario of examining, illustrating and even describing male genital structures upside down can be found in publications of well known lepidopterists, e.g., Pinhey (1972:44, Figs 6f, g; *Pselaphelia* spp.), and de Freina and Witt (1983; *Stoermeriana* n. gen.). While being the exceptional extreme, these examples highlight the main problems of publications on male genital structures of the bombycoid complex – they are based on poor, superficial observations and lack critical examination by the respective authors.

With approximately 5,150 described species in the bombycoid complex (numbers summarized from Lemaire & Minet [1998]) it is not possible to examine all of these taxa in this context. However, generally plesiomorphic male genital structures of taxa of all families are very similar. In the following sections, I present hypothetical ground plans of the sclerites of plesiomorphic male genital structures in the bombycoid complex and in Anthelidae in particular, as well as my hypotheses on modifications of these

structures in Anthelidae. Based on these descriptions and hypotheses I subsequently discuss the characters of male genital structures that I chose for my Hennigian Argumentation.

III.1.1) The principal male genital sclerites of the bombycoid complex

The sclerites of lepidopteran male genital structures are highly modified in many taxa. Authors frequently created new names for (parts of) such modified structures in the group of Lepidoptera they studied. Consequently, a large number of names exists for homologous structures in different taxa. The "Taxonomist's Glossary of Genitalia in Insects" by Tuxen (1970) summarizes many of the older names. The opposite, the application of available terms to non-homologous structures, is equally common. However, well established names exist for the generally present sclerites of male genital structures, and these terms can be applied in the bombycoid complex as well.

Tegumen and vinculum

The tegumen and vinculum are the sclerotized dorsal and ventral parts of the abdominal segment IX. According to Kristensen (2003b: 100), the dorsal and ventral sclerites of segment IX are part of a synscleritous ring in the hypothetical lepidopteran ground plan. Consequently, he assumes the separation of these sclerites in the Heteroneura – which include the Bombycoidea – to be secondary, possibly a "reversal". Kristensen's view is based on the most parsimonious explanation for the occurrence of a synscleritous ring in the hypothetical ground plan of Trichoptera and all non-neolepidopteran moth families except Heterobathmiidae. However, at least within Heteroneura the tegumen and vinculum are separated and a tendency towards a fusion of these two sclerites is apparent. This fusion strengthens the frame that supports the movable structures, and such a tendency is likely to exist for all Lepidoptera and Trichoptera. In the absence of other indications, simple parsimony is the only option to interpret the observed distribution of a synscleritous ring among the non-neolepidopteran taxa. However, in my opinion the apparent tendency to strengthen the ring weakens simple parsimony as a sufficient justification for Kristensen's hypothesis on the hypothetical ground plan of Lepidoptera.

Irrespective of the origin of a separation of tegumen and vinculum in Heteroneura, a tendency to fuse these two sclerites is very strong in the bombycoid complex (Fig. 4).

Very few extant taxa show a separation of tegumen and vinculum, which in some cases are clearly secondary reductions of the synscleritous ring, e.g., in the highly modified genital structures of *Bombyx mori* (one pair of partial reductions of the sclerotization within the tegumen and one reduction within the vinculum). It is difficult to structurally distinguish between primary and secondary separation of tegumen and vinculum, but incomplete fusions or the characteristic separation with an overlap between tegumen and vinculum (see below, sections III.2.2: 181ff. and III.2.4: 194ff.) are present in taxa with largely plesiomorphic genital structures. Such a characteristic separation can be found in non-bombycoid families, e.g., Gelechiidae (Kuznetzov & Stekolnikov 2001: 177, Fig. 52Б), Choreutidae (Kuznetzov & Stekolnikov 2001: 230, Fig. 70A), Zygaenidae (Kuznetzov & Stekolnikov 2001: 233, Fig. 71B) and Noctuidae (Fig. 122). I believe these characteristic separations to be homologous, and consequently the fusion of tegumen and vinculum to have evolved many times independently. The characteristic separation with an overlap of tegumen and vinculum is present in some taxa of the bombycoid complex, e.g., in the eupterotid species *Ganisa plana* (Fig. 138). I therefore assume the overlapping, separated tegumen and vinculum to be the plesiomorphic condition in the bombycoid complex, and the widespread, fused condition to have evolved independently in the bombycoid complex.

In the bombycoid complex, as in many other Ditrysia, the ventral part of the vinculum extends anteriad, forming a protrusion referred to as the saccus. The proportions of the saccus vary greatly, and its length is typically correlated to the length of the anteriad protruding part of the phallus (Fig. 4), to which it is connected by muscles *m6*.

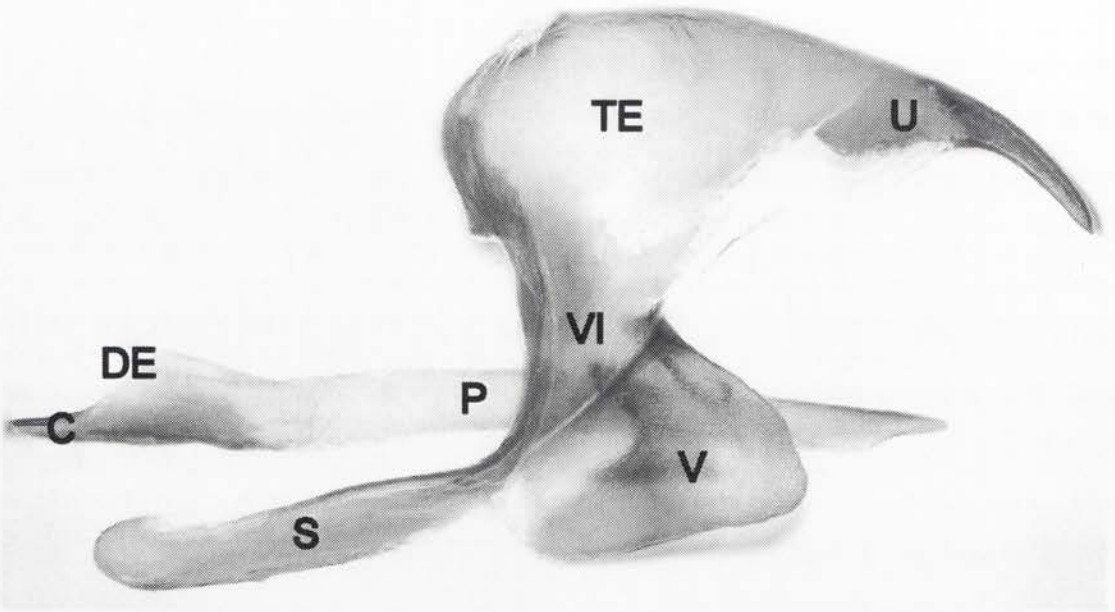

Fig. 4: *Omphaliodes obscura* (Anthelidae), ♂, lateral view – sclerotized genital structures; tegumen and vinculum are strongly fused with each other; note the example of the correlation between a long phallus and a long saccus.

Uncus

The uncus is the tergite of the abdominal segment X. Its anterior fusion with or separation from the tegumen is too variable and too simple to be homologized at higher phylogenetic levels. A (partly) fused condition is most common within the bombycoid complex. The anterior part of the uncus extends further laterad than the rest of the uncus. This anterior, lateral extension often appears as a short arm in lateral view (Figs 35, 37). The posterior edge of the uncus is frequently modified and typically bilobed (Fig. 5) or a simple hook (Figs 6, 7). Kristensen (2003b: 105) assigns a bilobed condition to the hypothetical lepidopteran ground plan, but notes that in some Ditrysia the bilobed condition is likely to represent "reversals" from the simple condition.

A bilobed posterior edge of the uncus occurs in at least some taxa of almost all families of the bombycoid complex. In the monotypic Carthaeidae the uncus apex is blunt and only faintly bilobed. In the Endromidae and Mirinidae, closely related to each other (Minet 1994), the uncus is strongly modified to generally protrude dorsad and to form a pair of little (Endromidae) to strongly (Mirinidae) developed antero-dorsal protrusions. This unusually shaped uncus is single-pointed, possibly as a result of a fusion as indicated by the weekly sclerotized and depressed median part of the uncus in Endromidae. The generally bilobed uncus of the bombycoid complex contrasts with the simple, pointed uncus typical for most other Macrolepidoptera, but the shape of the posterior uncus edge is too variable to be homologized and phylogenetically informative

at family or superfamily level.

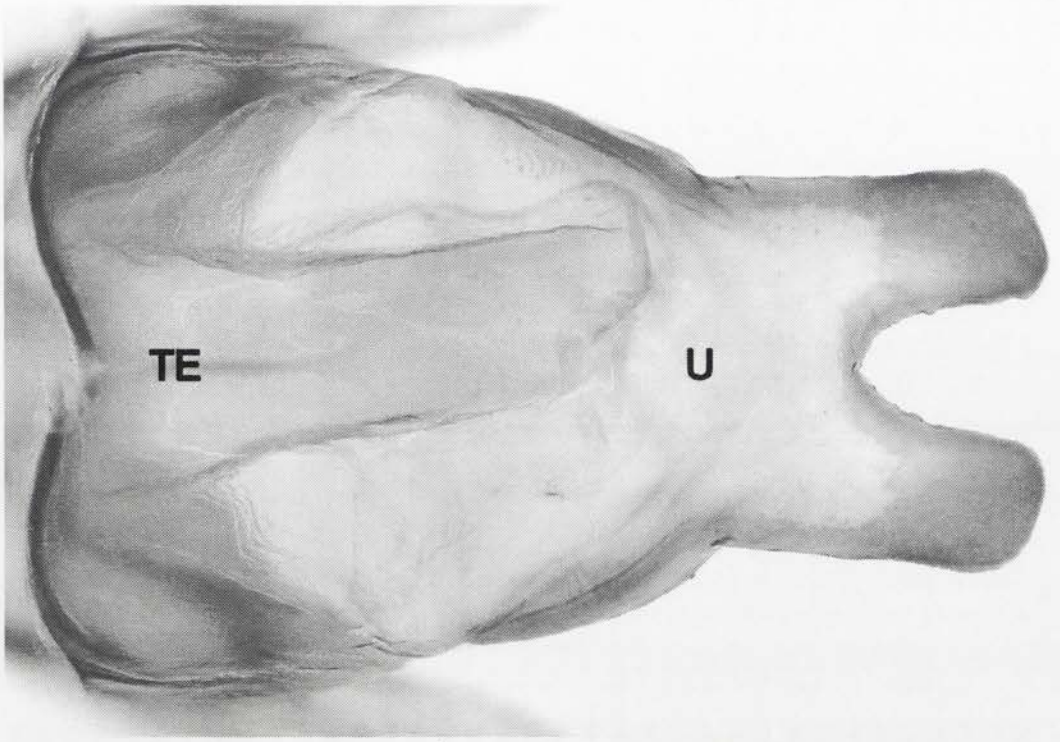

Fig. 5: *Anthela excellens* (Anthelidae), ♂, dorsal view – fused tegumen and uncus; the uncus apex is strongly bilobed [the large subscaphium is visible through the tegumen].

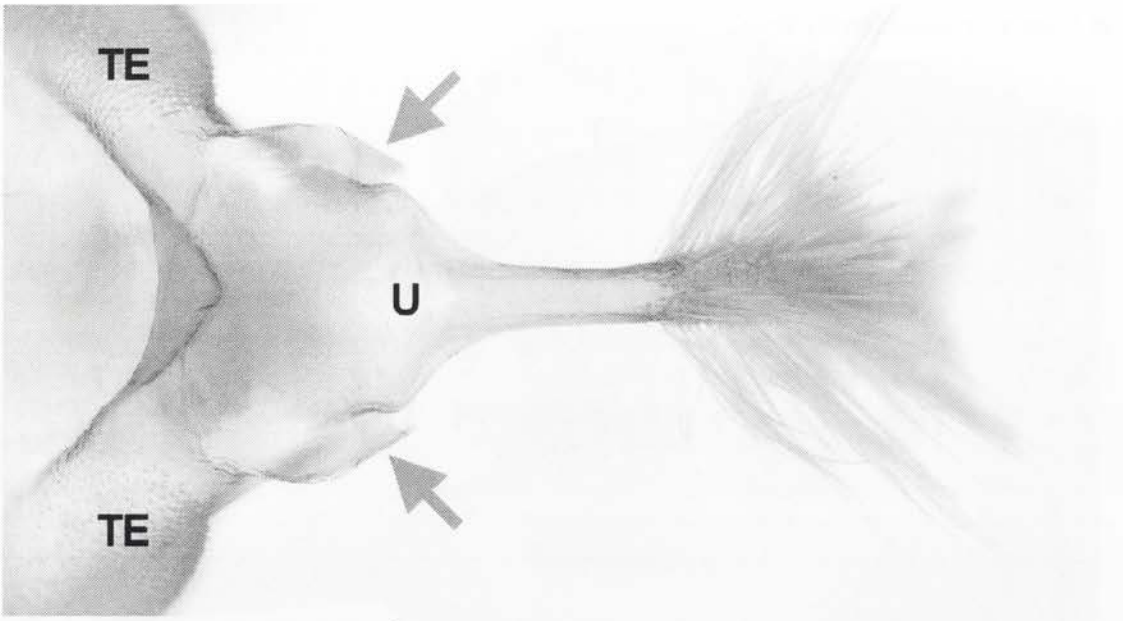

Fig. 6: *Agrotis infusa* (Noctuidae), ♂, dorsal view – fused tegumen and uncus; the uncus apex is single-pointed; note the "articulation" of the gnathos arms with the lateral side of the uncus (green arrows).

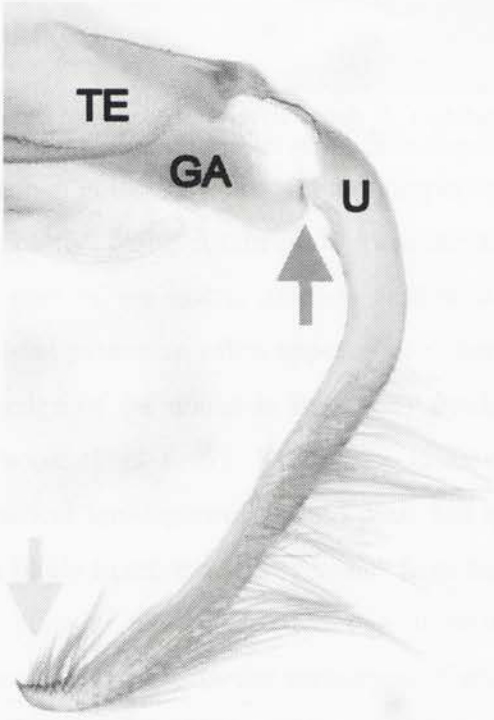

Fig. 7: *Agrotis infusa* (Noctuidae), ♂, lateral view – fused tegumen and uncus; the uncus apex is a single-pointed, apically pointed hook (yellow arrow); note the "articulation" of the gnathos arms with the lateral side of the uncus (green arrow).

Socii

The socii are a pair of posterior, setose processes located latero-ventrally of the uncus. The structures referred to as socii in various Lepidoptera are unlikely to be homologous in all cases. Within the bombycoid complex, a pair of setose patches latero-ventrally of

the uncus is often referred to as socii. These patches typically form moderate, membranous protrusions, which are sclerotized and/or enlarged in some taxa. They might represent remnants of socii, but even within the bombycoid complex their homology is hardly supported by anything other than the roughly identical location of some patches of hairs.

Subscaphium

The subscaphium is an unpaired, median sclerotization of the diaphragma, stretching from ventrally of the anal cone ventrad towards the gnathos. It is rather weakly sclerotized in the bombycoid complex and frequently absent.

Gnathos

The gnathos is an unpaired sclerite and assumed to be formed (in part) by the sternite of the abdominal segment X (Kristensen 2003b: 107) or by a process of it (Mehta 1934). It consists of a median plate ventrally of the anal cone and its lateral arms, which articulate either with the antero-lateral part of the uncus (Figs 50, 51) or with the posterior edge of the tegumen (Fig. 23). No muscles attach to this sclerite. The gnathos is frequently reduced or lost, and the reduction most commonly starts at the middle of the median plate, splitting it into halves. This led many authors, e.g., Klots (1970: 119), Common (1990: 26) and Scoble (1995: 96), to the popular perception of the gnathos as a paired structure, which fused mesally in some taxa.

In the bombycoid complex the gnathos is generally well developed, but reduced or lost in many taxa. Occasionally, the remnants of the mesally reduced plate of the gnathos fuse again with each other (e.g., some *Cicinnus* spp. (Mimallonidae), as indicated by their modified attachment of muscle *m4*), which might have been misinterpreted as indications of the gnathos being a paired structure by some authors as described above. The reduction of a well developed gnathos can even occur within a genus and in general is too homoplastic to be phylogenetically significant. In most cases a reduction of the gnathos starts mesally, and only rarely does it start from the dorsal end of the lateral arms. In the bombycoid complex, the arms of the gnathos articulate with the antero-lateral extension of the uncus. However, in some taxa the dorsal end of the gnathos arms is located further anteriorly, between the tegumen and uncus, which can appear as an articulation between gnathos and tegumen.

Valva

The valvae are the gonopods of the IX abdominal segment (Kristensen 2003b: 100), an

articulated pair of large, clasping structures. They are frequently highly modified in Ditrysia, and numerous terms have been coined for various regions of the valva.

In the bombycoid complex the valva is a large, lobe-shaped structure with a process in the ventro-distal area of its mesal side. This process is referred to as the "clasper" by most authors (Kristensen 2003b: 101). Muscle *m7* connects the base of the mesal clasper wall (or the area just proximally of it) with the basal area of the lateral valva wall. A contraction of muscle *m7* pulls the area basally of the clasper antero-laterad, which tilts the clasper and bends the distal part of the valva antero-mesad ("inwards"). Unlike muscle *m7*, the clasper is frequently reduced to absent. The attachment of muscle *m7* can be a valuable indication of the homology of highly modified or shifted processes on the mesal side of the valva.

At least in Macrolepidoptera the dorso-basal edge of the valva and the dorsal edge of the mesal side of the valva are strongly sclerotized. In many taxa they stand out from the remaining mesal side of the valva as a strong, smooth and hairless band. Together they extend mesad and form the attachment area of muscles *m2* and *m4*, the presumed abductor and adductor of the valva. Hence, I refer to this band as the "valva apodeme" (Figs 11, 22, 53, 74, 80). The mesal side of the valva goes over into the diaphragma, and hence the hairless valva apodeme extends mesad as a sclerotization of the diaphragma. The rather narrow basal part of the valva apodeme broadens into a hairless sclerotization in the diaphragma. This sclerotization can stretch far mesad, reaching and fusing with its counterpart from the other valva. In this fused condition it is often referred to as a "transtilla", while Kuznetzov and Stekolnikov (1985, 2001) refer to the typically shorter valva apodeme in the bombycoid complex as a "hemi-transtilla".

The term "transtilla" was introduced by Pierce (1914: xxi) for a structure he observed in Geometridae: "From the bases of the valvae arises a cross-bar which I term *The Transtilla* (*Ennomos autumnaria, pl. iv*). The cross-bar may be incomplete, the opposing arms not uniting, and whilst it is often simple, it is capable of great development, occasionally producing free arms, and becoming in the Tortricidae a highly complex part." To correctly homologize this structure across families it is necessary to understand its nature and origin. Pierce (1914) noted, in my opinion correctly, that the transtilla originates ("arises") from the valvae. He stated further that it was "a cross-bar", which arose from the left and the right valva. This is a minor contradiction, in as far as an origin from two sources clearly refers to two (possibly secondarily fused) structures, and

not a single, unpaired structure like "a cross-bar". Contrary to my opinion, most authors, e.g., Klots (1970), Common (1990) and Kristensen (2003b), regard the transtilla as a sclerotization of the diaphragma, and the occurrence of separate arms as a secondary, median reduction. This interpretation cannot be excluded, and in fact, an unpaired sclerite not connected to the valvae and without traces of a mesal fusion occurs in some taxa, e.g., the pyralid species *Indomyrlaea auchmodes*, possibly representing such an unpaired sclerotization of the diaphragma (Fig. 8).

However, at least within the representatives of the Macrolepidoptera I examined, a "cross-bar" between the valvae appears to have evolved several times independently from a paired structure, the "valva apodeme". The valva apodeme appears to function primarily as a lever for muscle *m4*, the adductor of the valva. Further, muscle *m2* attaches to it mesally of *m4* (Fig. 111). This muscle is generally assumed to function as the abductor of the valva (e.g., Kristensen 2003b; Kuznetzov & Stekolnikov 2001). A generalized diagram by Kuznetzov and Stekolnikov (2001: 32, Figs 8 Ж, 3, И) illustrates muscles *m2* and *m4* as attaching opposite to each other, being direct antagonists. However, in most Macrolepidoptera I examined these muscles do not exert force in opposite directions, but at an angle of roughly 90 degrees to each other. Moving the valva manually does not result in a significant change of the length of muscle *m2*. Likewise, moving the attachment point of muscle *m2* on the valva apodeme manually in the direction of its opposite attachment point on the tegumen does not open the valves – in fact, any forceful movement of the attachment point only results in a bending of the valva apodeme. In contrast, moving the opposite attachment point on the tegumen towards the valva apodeme tilts or bends the tegumen anteriad. This bend occurs at the weakest point of the annulus, which is either the point of articulation between tegumen and vinculum, or a secondary narrowing/reduction in the annulus. This anterior movement of the tegumen lifts the uncus and gnathos. I believe that in these taxa muscles *m2* are not abductors of the valvae, but instead raise the uncus and gnathos dorsally. Possibly, the frequent loss of *m2* is linked to a strengthening of the annulus, which does not allow for such an anterior movement of the tegumen.

In some taxa that retained muscle *m2* and have a very firm annulus, the function of *m2* might be a different one. In *Carthaea saturnioides* (Carthaeidae) and *Endromis versicolora* (Endromidae) muscles *m2* and *m4* appear to have an antagonistic function, with *m2* being an abductor of the valva as generally assumed. This antagonistic function

is possible because of a modification of the typical arrangement of muscles. In *C. saturnioides* muscle *m4* is located ventrally of a curved valva apodeme, rather than at the same level as and/or dorsally of it, which results in a roughly opposite position of muscles *m2* to *m4* (Fig. 9). In contrast, muscle *m2* attaches to the tegumen much further mesally than usual in *E. versicolora*, likewise resulting in a roughly opposite attachment of *m2* to *m4* (Fig. 114). Another modification of the function of muscle *m2* appears to be present in *Agrius convolvuli* (Sphingidae), in which muscles *m2* and *m4* exert force in almost the same direction, causing an adduction of the valva by both muscles (Fig. 116). It seems that at least within Macrolepidoptera the function of muscle *m2* is not uniform.

The variation of function of muscle *m2* and its frequent loss raise the question as to which mechanisms exist to open the valvae in these taxa. One mechanism is said to be the contraction of muscle *m3*, which opens the valvae either directly or indirectly, depending on its attachment to the valva or the vinculum (Kuznetzov & Stekolnikov 2001: 34, Figs 9 А-Г). Another mechanism could be an outward movement of the diaphragma, as it attaches to the mesal edge of the valvae, which are articulated with the vinculum along their lateral edge. With the diaphragma being suspended along its edges, the posterior movement of the diaphragma is furthest at its central point. Consequently, any sclerotized part of the valva stretching mesad within the diaphragma will assist in the opening of the valvae during a posterior movement of the diaphragma. The valva apodeme is such a structure, and the further it extends mesad as a sclerotization of the diaphragma and the larger this sclerotization is (Fig. 52), the stronger is the effect. As the diaphragma terminates the segment posteriorly, no muscle attaching to a simple valva apodeme [without a cephalo-ventral lever] can move it or the diaphragma posteriad. However, an increase in haemolymph pressure in the abdomen would push the diaphragma outwards (posteriad), and with it the valva apodeme and the mesal edge of the valva. While not contradicting the origin of the transtilla as an unpaired sclerotization of the diaphragma, this mechanism could be a reason for a mesal extension of the existing valva apodemes, which probably led to the secondary fusion and formation of a continuous "cross-bar" in Macrolepidoptera more than once.

Pierce (1914) coined the term "transtilla" for a continuous "cross-bar" in Geometridae, which I assume to have evolved independently several times in Macrolepidoptera. I further believe that the principal attachment area of muscles *m2* and *m4* is homologous within Macrolepidoptera, and therefore I prefer to refer to this

structure as the "valva apodeme", rather than as the "transtilla".

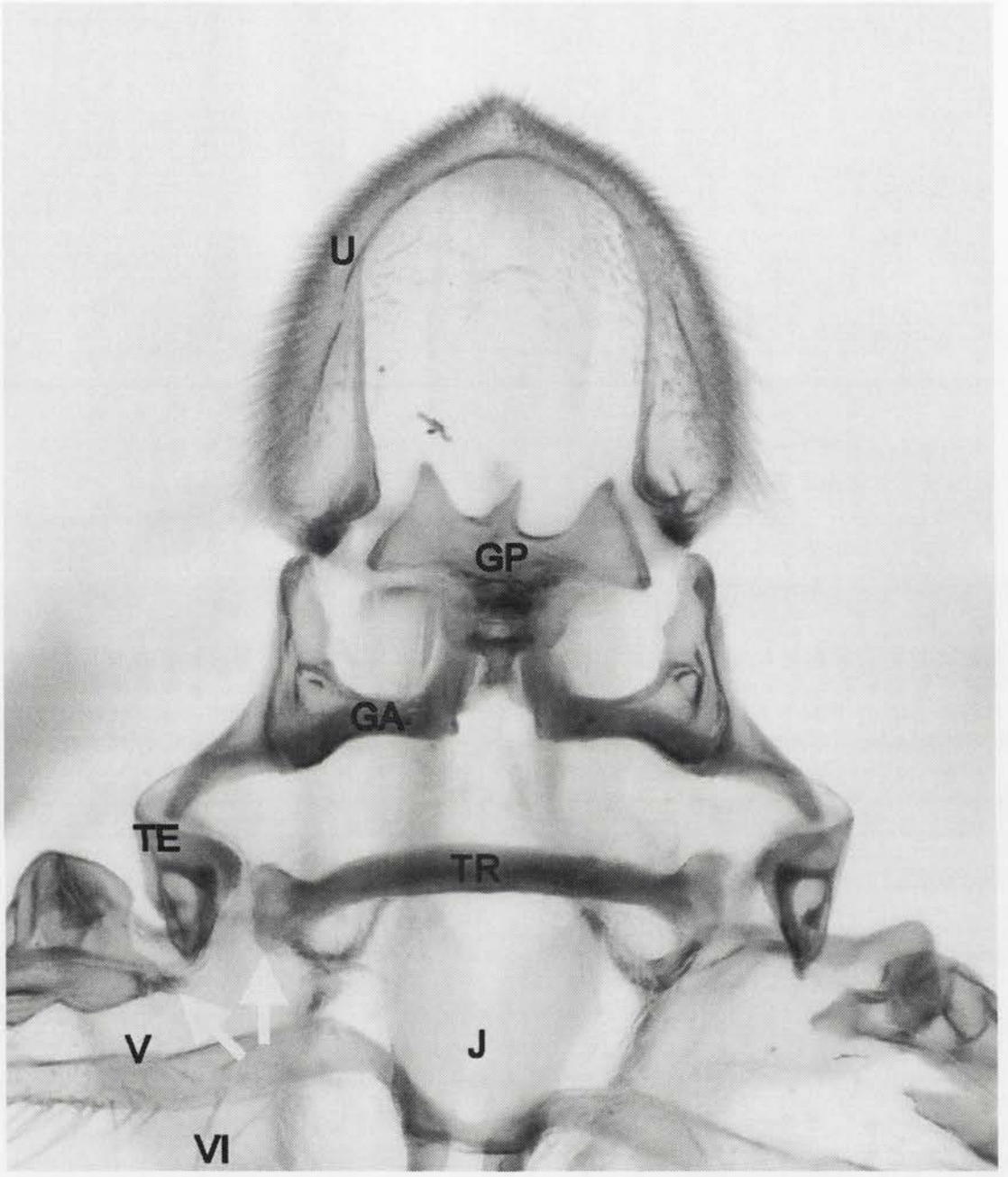

Fig. 8: *Indomyrlaea auchmodes* (Pyralidae), ♂, posterior view [phallus removed] – uncus, gnathos, tegumen, transtilla and dorsal part of valva; the transtilla appears to be formed by an unpaired sclerotization in the diaphragma, which is located between the ventral ends of the tegumen; note the distance between the dorsal corner of the valva and the transtilla (yellow arrows).

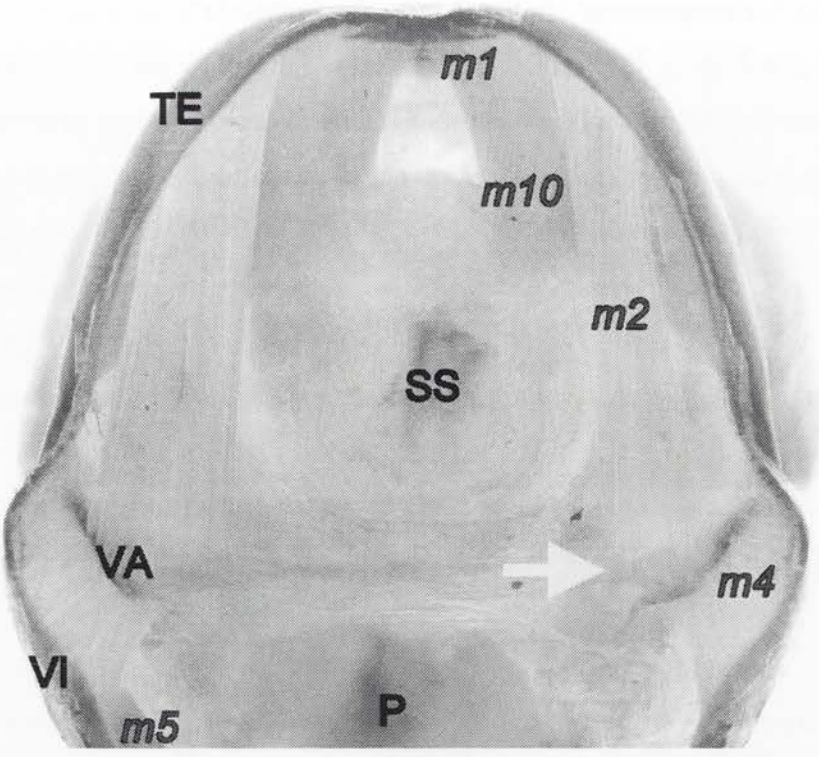

Fig. 9: *Carthaea saturnioides* (Carthaeidae), ♂, anterior view – unlike most other taxa of the bombycoid complex (e.g., Figs 112, 114), muscles *m2* and *m4* have a directly antagonistic function due to the ventrad curving of the valva apodeme and the position of *m4* ventrally of the valva apodeme; note the partial attachment of the unusually massive muscle *m2* to a fold between the valva apodemes (yellow arrow).

Juxta

The juxta is said to be an unpaired sclerotization of the diaphragma located ventrally of and supporting the phallus (Kristensen 2003b: 102). In the bombycoid complex this sclerite is V-shaped, and muscles *m3* attach to the dorso-lateral ends of the juxta. The mesal juxta edge borders a membranous fold (anellus) around an invagination of the diaphragma (manica) surrounding the phallus. Frequently, the juxta extends onto the anellus, and in some taxa this mesal edge of the juxta and the anellus form a distinct posterior protrusion of the juxta.

The anterior end of the membranous manica (invagination of the diaphragma) attaches to the penetrating phallus, with the attachment area referred to as the "zone". The membranous nature of the manica allows for the protraction of the phallus by muscles *m5*. In some taxa of the bombycoid complex the ventral part of the manica is sclerotized and firmly connects juxta and phallus. This sclerotization effectively changes the posterior protraction of the phallus into a postero-ventral movement. In all Lasiocampidae, the phallus and the juxta are directly fused with each other and the manica is virtually absent, which I interpret as an autapomorphy of the family

Lasiocampidae. In most Lasiocampidae, this fusion and probably the reduction of valvae led to a very strong reduction of the juxta and muscles *m3*.

Phallus / aedoeagus

The phallus of Lepidoptera is most commonly referred to as "aedeagus" or "aedoeagus". Kristensen (2003b: 103) argued convincingly for a preferential use of the term "phallus" over "aedeagus", as the phallic tube of most Lepidoptera does not appear to be homologous with the aedeagus of Agathiphagidae, Trichoptera and other insects. I therefore follow his suggestion and refer to the structure as "phallus", despite the overwhelmingly common use of the term "aedeagus" in literature.

The phallus of the bombycoid complex shows no special modifications compared to most other Lepidoptera. It has a coecum at its anterior end and an eversible, membranous vesica with cornuti at its posterior end.

III.1.2) The principal male genital sclerites of and their modifications in the Anthelidae

Within the bombycoid complex generally plesiomorphic genital structures of different families are very similar, and the Anthelidae are no exception. No male genital synapomorphies of families in the bombycoid complex have been published so far, but a fusion of some structures is shared by several families, including the Anthelidae. In this section the principal male genital structures of Anthelidae and their modifications are discussed. The fusion of certain structures shared by some families and the modifications of these fused structures in Anthelidae are discussed separately in the next section ("III.1.3) The fusion of gnathos, valvae, juxta and anellus").

Tegumen and vinculum

The tegumen and vinculum are firmly fused with each other in all Anthelidae. They form a strong, synscleritous annulus, which rarely allows the distinction between these two sclerites. Only in the Munychryiinae does the anterior edge of the annulus have a small gap, which I interpret as a remnant of the articulation between tegumen and vinculum (Fig. 10). In addition to this anterior gap, this area of the annulus shows patches of incomplete sclerotization in Munychryiinae. These patches are not necessarily identical in size and location between the left and right side of one specimen or between specimens. They might represent an incomplete fusion of tegumen and vinculum, or a secondary reduction of the sclerotization of an almost entirely fused

annulus. Because these patches are inconsistent between specimens and the interpretation of their origin is uncertain, I do not use this tendency towards incomplete sclerotization of the annulus as a character in my phylogenetic analyses.

As in most other members of the bombycoid taxa, the annulus is hood-shaped dorsally and gradually narrows ventrally in Anthelidae. The ventral part of the vinculum forms a well developed, tubular saccus of very variable length and shape.

Uncus

The anterior edge of the uncus is firmly fused with the posterior edge of the tegumen in all Anthelidae. Along the antero-lateral extensions of the uncus, the sclerotization of the fusion is weaker and does not reach the ventral end of the antero-lateral extension. Like the tegumen, the anterior part of the uncus does not carry any setae, while the posterior part of the uncus is setose on all sides.

The posterior part of the uncus is variously modified in many taxa, and while its general shape is constant within species, interspecific variation of its proportions can be conspicuous. This setose posterior part is mesally divided, resulting in an apically bilobed uncus.

A weakly bilobed uncus, which is typical of many taxa in the bombycoid complex, is present in Munychryiinae. In these taxa the uncus is laterally bowed ventrad over its entire posterior extent, like all tergites generally are. Consequently, the short posterior lobes are laterally drooping – their lateral edge is located further ventrally than the mesal edge (see character #H.1).

In all other Anthelidae the mesal split between the two lobes is much longer, resulting in two very prominent lobes. These lobes are never drooping laterally, but instead show mesally a ventral tilt in many taxa – the mesal edge of the posterior lobes is located further ventrally than the lateral edge (character #H.1). The degree of this tilt is very variable and the orientation of lobes ranges from almost horizontal to vertical (character #H.6). While being the most parsimonious interpretation, it is not certain by any means that this range represents a continuous ventral tilt only and that no subsequent tilt in the opposite direction occurred.

The mesally tilted lobes of the deeply split uncus apex appear to have fused again in a number of anthelid taxa, resulting in a single-pointed uncus apex. It is difficult to distinguish such a secondary fusion of lobes from a reduction of the lobes, and even

more so to distinguish between convergent fusions or reductions. However, several indications exist that – with the exception of a single, undescribed species in Munychryiinae – the single-pointed uncus apex found in Anthelidae is always the result of a secondary fusion of a deeply split uncus apex. Such indications of a fusion of lobes are a median crest on the ventral side of the single-pointed uncus apex, the lack of hairs on this ventral suture and a dorsal gap in the apex revealing the tilt of the lobes during fusion. Further, such fusions appear to have evolved several times independently, at the very least two times (characters #H.2, #H.3, #H.4, #H.5, #H.7).

In one case the fusion started anteriorly on the dorsal side between the two lobes, which are tilted mesally by about 90° (vertical orientation of the lobes). This is evident in the endemic New Guinea genera *Pseudodreata* and *Corticomis*, in which the lobes are partly fused antero-dorsally, but entirely separate ventrally (character #H.7). In another group of taxa, the lobes are tilted mesally by about 90° and fused entirely. This might be a completion of the partial fusion present in these New Guinean taxa, or it might be an independent fusion event (character #H.4).

In other anthelid taxa the fusion of the uncus lobes appears to have started ventrally, as the ventral crest reaches the uncus apex, but an apical gap or depression remains on the dorsal side of the uncus (characters #H.2, #H.3). This gap indicates that the lobes were mesally tilted at less than 90° degrees during their fusion. Such fused uncus lobes differ from each other in their overall shape and the length of their ventral crest, which separates them into distinct groups. Unfortunately, it is not possible to tell whether these differences are the result of modifications subsequent to the fusion of the uncus lobes, or whether these differences indicate independent fusion events.

Each of the different types of fused uncus lobes has some characteristics that distinguishes it from all other uncus lobes. However, as the indications are insufficient to conclude whether more than two fusion events occurred or not, I conservatively treat each distinct type of fusion as a separate character, as if these fusions evolved independently from each other. By doing this I avoid incorrectly homologizing independent fusion events if more than two fusion events occurred. However, if only two fusion events occurred I miss out on making a poorly supported hypothesis which would correctly group taxa together that I distinguish by assuming independent fusion events. While a hypothesis of anthelid phylogeny can never give proof of the homology of these potentially independent fusion events, the occurrence of presumed independent

fusion events in hypothesized sistergroups would indicate a higher likeliness of their homology.

Socii

A paired, small patch of a few setae is located on the membrane just ventrally of the lateral part of the uncus in all Anthelidae. This patch is always membranous and hardly protruding to flat. Judging from the presence of setae and its location, this patch of setae is likely to represent a remnant of the paired, setose protrusion referred to as a socius [*pl.* socii] in other taxa of the bombycoid complex.

Subscaphium

A subscaphium is present in most Anthelidae, stretching from the anal cone ventrad. Its degree of sclerotization is variable and not necessarily constant between specimens of the same species. It is rather strongly sclerotized and stiff in some taxa, and it frequently extends to and fuses with the gnathos plate or its remnants.

Gnathos

In Anthelidae the arms of the gnathos approach the ends of the antero-lateral uncus extensions, giving the gnathos the appearance of being "articulated" with the uncus (Figs 28, 35, 37, 43). This is the principal condition found in the bombycoid complex, which fits the hypothesis of the uncus and gnathos being the tergite and sternite of the Xth abdominal segment, respectively. In Munychryiinae the gnathos is strongly reduced or lost, except for small remnants of the dorsal part of the gnathos arms. These remnants are anteriorly fused to the tegumen, giving the impression of an "articulation" between tegumen and gnathos (Fig. 23).

The gnathos is strongly reduced or lost in most Anthelidae. In particular the median gnathos plate is frequently lost and only distinctly present in the genera *Chelepteryx* and *Pseudodreata/Corticomis* (Fig. 71).

The lateral gnathos arms or their remnants are frequently retained. In a group of anthelid taxa that lost the median gnathos plate these gnathos arms have a secondary, sclerotized, spinose mesal and dorso-lateral extension (character #H.9). This extension can fuse with the extension of the opposite gnathos arm and hence is easily mistaken for remnants of the gnathos plate.

In Anthelidae the gnathos is ventro-laterally fused with the dorsal part of the mesal side of the valva, and together they form a "bridge" between the valvae. This is not a continuous transtilla *sensu* Pierce (1914) [see above, section III.1.1: 63ff.], and this

construction is highly modified in Anthelidae and discussed more in detail separately (see below, section III.1.3).

Valva

The valva of the Anthelidae is large, lobe-shaped and has a strongly sclerotized clasper on its mesal side. Further, the valva apodeme protrudes mesad from the dorso-basal part of the valva. In these respects the principal structure of the valva in Anthelidae does not differ from that of other families in the bombycoid complex.

The mesal clasper of the valva is well developed in only one group of anthelid taxa. Within this group a transformation series can be constructed for the clasper (characters #H.25, #H.26). It ranges from a broad, plate-like structure, via a narrower arm with a dorsal process, to a simple, spine-like arm. In all other Anthelidae the clasper is strongly reduced or entirely absent.

In some Anthelidae the apex of the valva is flexed outwards along a transverse line (see character #H.27). This line of bending stretches from the dorsal edge of the valva ventro-distad to the ventral edge of the valva. How far distally this line reaches the ventral valva edge varies between species. The variation ranges from as little distal as the distal third of the ventral valva edge to as far distal as the valva apex itself. Consequently, a large proportion to just a small part of the valva is flexed outwards. Further, the degree to which the valva apex is flexed outwards varies greatly between taxa, and to a lesser degree between specimens of the same species. In some taxa the flexing of the valva apex is very conspicuous, in others it is hardly noticeable. Potentially, this is influenced by the time for which genital structures are boiled in potassium hydroxide during the process of preparation.

In some anthelid taxa a protrusion on the mesal valva side extends roughly along the dorsal part of the line at which the valva is flexed outwards (character #H.27). This transverse, mesal ridge is more strongly sclerotized and less setose than the surrounding area of the valva. Ventro-proximally this ridge almost borders a lateral, membranous depression in the mesal valva side. If the valvae are closed, this depression closes around and provides space for the phallus and juxta. However, the transverse ridge is more than just the edge of a depression, it protrudes distinctly from the mesal side of the valva.

Part of the mesal valva side stretches along the smooth, hairless valva apodeme. Together with the gnathos, juxta and anellus this part of the mesal valva side forms a

complex, fused structure. In some anthelid taxa a lobe originates from these fused structures. It is located at the base of the valva, just distally of the valva apodeme, and hence I refer to it as the "valva apodeme lobe". The shape and relative position of this lobe vary greatly between taxa, and I use its characteristics in my phylogenetic analyses (characters #H.17, #H.18, #H.19, #H.20, #H.21, #H.22, #H.23, #H.24). The complex, fused structure and its modifications are discussed in greater detail below (see section III.1.3).

Juxta

The juxta of Anthelidae is a V-shaped, sclerotized band as in all other families of the bombycoid complex. Its lateral edge is in the plane of the diaphragma, while its mesal edge extends onto the anellus and protrudes with the anellus posteriad (Fig. 62). In anthelid taxa in which the phallus is supported by other structures, the lateral arms of the V-shaped juxta are reduced. As this alternative support of the phallus is provided by different structures in different taxa (see characters #H.16, #H.29), the reduction of the juxta is likely to have evolved several times independently. The remnants of such a reduced juxta are too simple to be convincingly homologized, and hence I did not include the strong reduction of the juxta as a character in my phylogenetic analyses.

In many Anthelidae in which the juxta appears to be the sole support for the phallus, the juxta extends far dorsally and protrudes overall very far posteriad – it forms a very large, tall sheath around the phallus. While the lateral edge of this structure with its dorsal attachment of muscles *m3* is clearly part of the juxta, the far posteriad protruding part of the sclerotization probably only appears to be formed by the mesal juxta edge and a greatly extended anellus alone. Instead a partially everted vesica might form the dorsal part of the juxta, and this hypothesis is discussed in more detail below (see section III.1.3).

Phallus / aedeagus

The phallus of Anthelidae is a straight to slightly curved, well sclerotized tube. It has typically a prominent, straight coecum at its anterior end. The sclerotized posterior end is blunt and opens into a small, simple, sack-shaped vesica. In Munychryiinae this vesica carries a large, single cornutus formed by a sclerotization of the distal end of the phallic tube (character #H.32). In contrast, the vesica appears to be almost absent and does not carry a distinct cornutus in other Anthelidae. Instead, in posterior view, two right-hand twisted sclerotizations stretch onto the vesica, seemingly extending the

sclerotized part of the phallus and greatly shortening its eversible part, the vesica (character #H.33). The right member of these flat sclerotizations is distinctly larger than the left and forms apically a tubular or flat process (character #H.34). Structures at the apex of the left sclerotization might represent remnants of such a process or might be novel developments. In most anthelid taxa these spines are strongly reduced to absent, and in many taxa even the two secondary sclerotizations of the vesica are either strongly reduced and/or broadened, leaving no more than a small gap in the posterior edge of the phallus sclerotization. The anterior part of a sack-shaped vesica is entirely sclerotized in some taxa, giving the phallus apex an enlarged, funnel-shaped appearance overall (character #H.36).

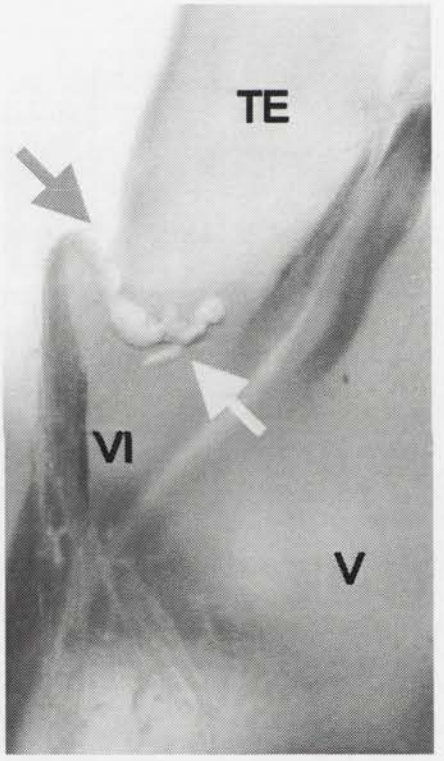

Fig. 10: *Munychryia periclyta* (Anthelidae), ♂, lateral view – tegumen and vinculum are fused with each other, but an anterior gap is still present (green arrow); note the irregular, incomplete sclerotization (yellow arrow).

III.1.3) The fusion of gnathos, valvae, juxta and anellus

The gnathos and the valvae are widely separated in most Macrolepidoptera (Fig. 11; see character #H.10). This is also the case in some families of the bombycoid complex, most distinctly so in the families Mimallonidae, Lasiocampidae, Bombycidae and Sphingidae. In these taxa the gnathos plate is located dorsally and posteriorly to the valvae. In taxa in which the gnathos extends further ventrad, gnathos and valvae are still

separated from each other by a large membrane which folds beneath the gnathos.

In contrast, the gnathos extends further ventrad than typical and is fused to the valvae in some families of the bombycoid complex (character #H.10). In these taxa the ventral wall of the gnathos is seamlessly fused with a part of the valva, and no large membrane separates the ventral wall of the gnathos from the valva. The actual fusion occurs between the gnathos and the setose, mesal side of the valvae, which extends mesad with and beyond the smooth valva apodeme in the plane of and going over into the diaphragma. This fusion connects the two valvae with each other like a "bridge", restricting their ability to move (Fig. 12). In the majority of these taxa a "weak area" within this fused construction allows for movement of the valvae – in some taxa the sclerotization near the base of the valva apodeme is lost (e.g., *Munychryia senicula* (Anthelidae), *Eacles imperialis* (Saturniidae)), and in other taxa a minute gap separates the structures along the ventral part of the gnathos (e.g., *Ganisa plana* (Eupterotidae), *Sabalia picarina* (Lemoniidae)). In the majority of taxa an extensive median reduction occurred, resulting in a loss of the sclerotization (e.g., *Lemonia dumi* (Lemoniidae)) or even part of the structure of the fused gnathos and valvae. Most frequently it is the gnathos that is lost in these taxa. Obviously, such reductions obscure the fusion of gnathos and valvae, in some cases beyond recognition.

Evidence of, or indications of, the fusion of gnathos and valvae are rather well preserved in Anthelidae. Even in anthelid taxa with a mesally reduced sclerotization, the composition of the remaining membranous "bridge" is often still apparent from the shape of the membranes (Fig. 14). The fusion of sclerites is not restricted to gnathos and valvae, but additionally includes the juxta and the anellus. As with the fused gnathos and valvae, these additional fusions are obscured by reductions in many taxa.

In Anthelidae, the dorsal part of the mesal side of the valva extends as a very shallow fold in the plane of the diaphragma far mesad along and beyond the valva apodeme. This fold is setose, (partly) sclerotized and of variable width. In Munychryiinae the basal part of this fold is membranous and devoid of setae, but forms a heavily sclerotized, setose protrusion distally (= mesally). I refer to this protrusion as the "mesal protrusion" (Figs 12, 15). In Munychryiinae, this mesal protrusion is located dorso-laterally of the anellus. While widely separated from each other, the mesal protrusions of the two valvae are mesally interconnected by a strong, hairless sclerotization, which extends

posteriad and latero-ventrally onto the anellus. In posterior view this sclerotized part of the anellus has the shape of an upside-down U, which borders the dorsal end of the juxta laterally with its ventral ends (Fig. 15). In *M. senicula* and *M. periclyta* this smooth sclerotization has reached and fused with the juxta (Figs 17, 18). The anellus appears to protrude unusually far posteriad in Munychryiinae, and this extreme posterior protrusion seems to be caused by a partial eversion of the manica. A part of the membranous manica forms the dorsal part of the anellus, which is still membranous in *M. senicula* and *M. periclyta* (Figs 17, 18), but strongly sclerotized in an undescribed munychryiine species (Fig. 16). The very distinct "hump" present in the middle of the posteriad protruding part of the juxta in *G. cosmia* might mark the position of the dorsal edge of the anellus prior to the eversion of the manica (Fig. 19, 20). The gnathos is lost in Munychryiinae, except for tiny remnants of the dorsal part of the gnathos arms (Fig. 23). It is possible that parts of the gnathos plate are included in the dorso- median sclerotization of the anellus.

In all other Anthelidae, the setose mesal protrusion and the anellus are not only connected by a hairless sclerotization, but are merged with each other. In the genus *Chelepteryx* the valva apodeme has been lost and the mesad extending fold formed by the dorsal part of the mesal side of the valva is very shallow. The mesal protrusion is strongly reduced to a tiny patch, which is located in a dorso-lateral position on a shallow fold around the posterior manica opening, the anellus (Fig. 96). This fused structure of the mesal protrusion and anellus carries tiny setae and has the same shape as the anellus in Munychryiinae – an upside-down U, which ends laterally of the (reduced) juxta. The ventral wall of the very well developed gnathos ends dorsally adjacent to the anellus. In this genus the phallus is fused to the juxta by a sclerotization of the entire manica. The remnants of the mesal protrusions are only visible if the phallus with the sclerotized manica is pushed outwards.

In a group of closely related taxa including *Anthela ferruginosa* the mesal protrusion is well developed and merged with the anellus dorso-laterally of the phallus (Fig. 62). This protrusion does not end laterally of the juxta, but instead goes directly over into the mesal wall of the juxta (Figs 64, 65, 66). As in Munychryiinae, the sclerotization of the mesal side of the valva is reduced around the valva apodeme.

In all Anthelidae other than the aforementioned taxa the mesal fold, which extends from the dorsal part of the mesal side of the valva and gives rise to the mesal protrusion,

is modified to form a second protrusion. In these taxa the valva apodeme is long and curves ventrad, "pushing up" a fold, which protrudes strongest basally. This fold is modified and enlarged in many taxa, forming a large protrusion posterior to the valva apodeme, which is why I refer to the protrusion as the "valva apodeme lobe" (Fig. 13). In many species the sclerotization of the dorsal edge of the valva (including the valva apodeme) extends onto the dorsal side of this fold, and in some taxa extends onto the ventral side, too.

The homology between protrusions is easy to hypothesise in all those taxa that have a mesal protrusion as well as a valva apodeme lobe, as the former is located dorso-laterally of and is fused with the anellus, while the latter is located at the base of the valva and synscleritous with the valva apodeme. However, the various modifications of these two protrusions, their similar cover of setae, and the more extensive sclerotization in Munychryiinae make a homologization of the protrusions between taxa with one and taxa with two protrusions more difficult. For these taxa my homologization of the single protrusion as the mesal protrusion is based on:

- The more mesal position of the protrusion,
- the fusion between the protrusion and the anellus,
- the fusion with the gnathos (if retained), and
- the lack of an attachment of muscles *m4*, which are attached to the valva apodeme.

In the group of taxa with two protrusions, both protrusions have been modified variously. In *Anthela basigera* and related taxa the mesal protrusion is entirely fused with the anellus. Together they form an elongate, setose, well sclerotized, lateral sheath around the phallus (Figs 67, 68, 69). The ventral ends of this sheath attach to the juxta dorso-laterally by a flat, hairless sclerotization. In these taxa a transformation series of the valva apodeme lobe is preserved. It is reduced from an upturned ventro-distal corner of the sclerotization in *A. basigera* and *A. repleta* over a flat, triangular protrusion to a minute protrusion and finally absence (Figs 73, 74, 75).

In the New Guinean genera *Pseudodreata* and *Corticomis* the gnathos is retained and entirely fused with the mesal protrusions – both mesal protrusions and gnathos are structures with double walls, but share a continuous dorsal wall in this fused state. Together they form a dorsal and ventral sheath around the aedeagus, which is fused onto the anellus and extends with it far posteriad (Figs 70, 71). The phallus is effectively

suspended from this structure and no longer supported by the juxta, which is reduced and only membranously connected to this complex of structures.

In all other taxa the mesal protrusion is extremely reduced or lost (Fig. 21). Sometimes it is still apparent as a shallow, weakly sclerotized protrusion with a few setae, which is connected to the dorso-lateral end of the juxta (e.g., an undescribed antheline sp. (Fig. 22), *C. heliaspis* and *Anthela nicothoe*). In many of these taxa the juxta forms a large, far posteriad protruding, hairless sheath, which is very similar to the one in Munychryiinae, but entirely sclerotized.

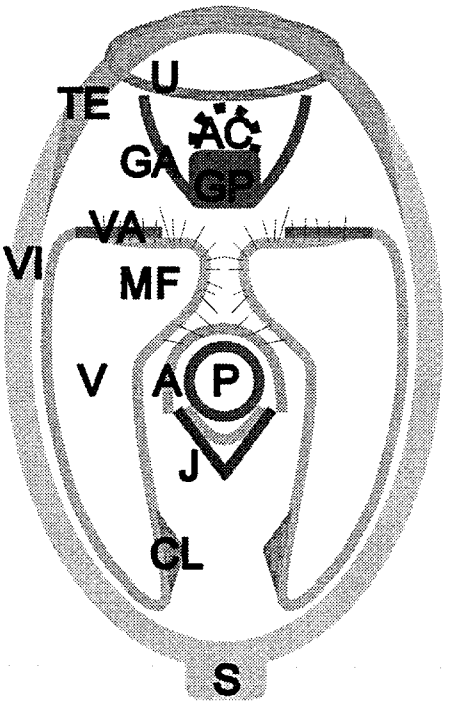

Fig. 11: Bombycoid complex, ♂, posterior view – general scheme of the principal genital sclerites; gnathos and valvae are widely separated.

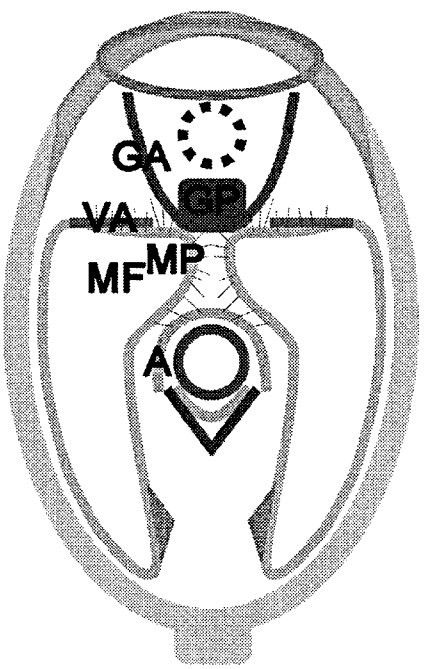

Fig. 12: Anthelidae, ♂, posterior view – general scheme of the principal genital sclerites; gnathos and valvae are fused; the fold formed by dorsal part of the mesal side of the valva forms the mesal process.

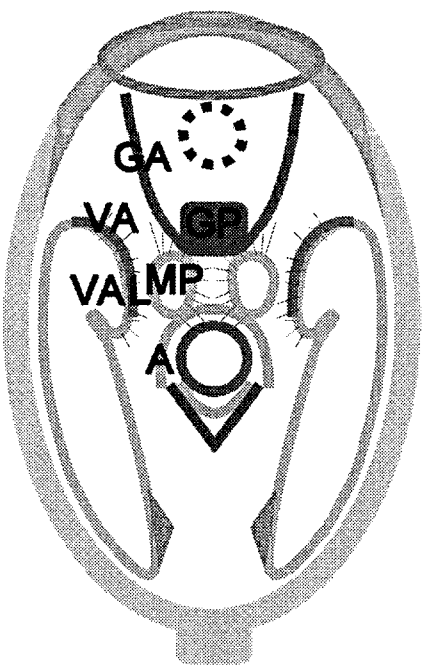

Fig. 13: Anthelidae, ♂, posterior view – general scheme of the principal genital sclerites; gnathos and valvae are fused; the fold formed by the dorsal part of the mesal side of the valva forms the mesal process; the mesal process and the anellus are fused; the long, ventrad curved valva apodeme "pushes up" a fold, which forms the valva apodeme lobe.

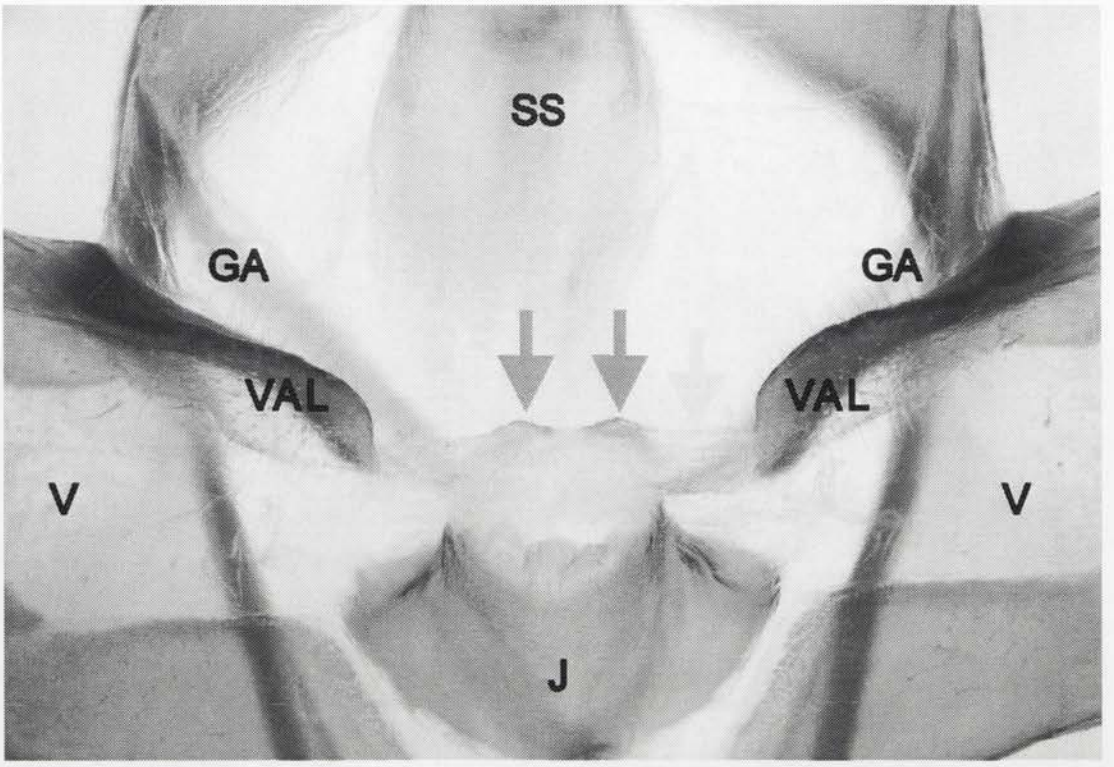

Fig. 14: *Anthela excellens* (Anthelidae), ♂, posterior view [phallus removed] – the mesal sides of the valva and gnathos are fused; the sclerotization of the fused structures is secondarily reduced, but the membranous connections (yellow arrows) between the valva apodeme lobes and the (reduced) gnathos plate (green arrows) are still apparent.

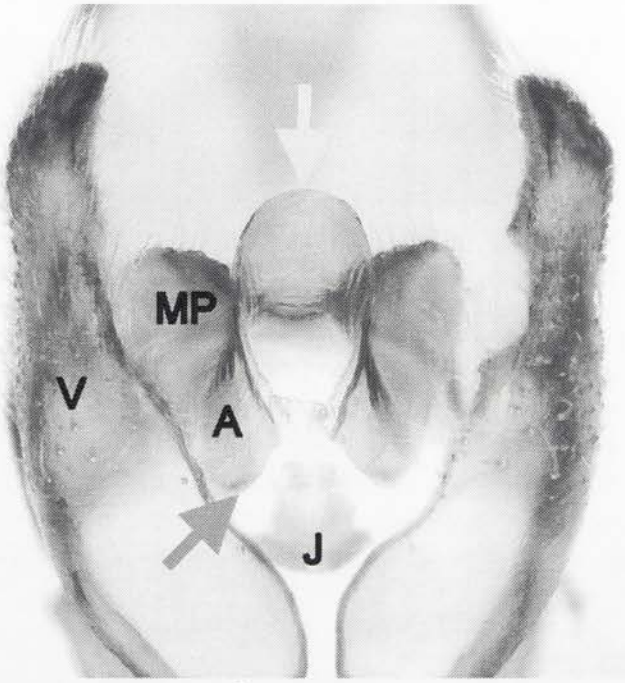

Fig. 15: Munychryiinae n. sp. (Anthelidae), ♂, (ventro-) posterior view [phallus removed] – valva, setose mesal protrusion, anellus and juxta; the two mesal processes are interconnected and fused with the anellus, which is sclerotized and extends laterad; the lateral sclerotization of the anellus ends dorsally of the reduced juxta (green arrow); note the extreme height of the sclerotized, everted manica (yellow arrow).

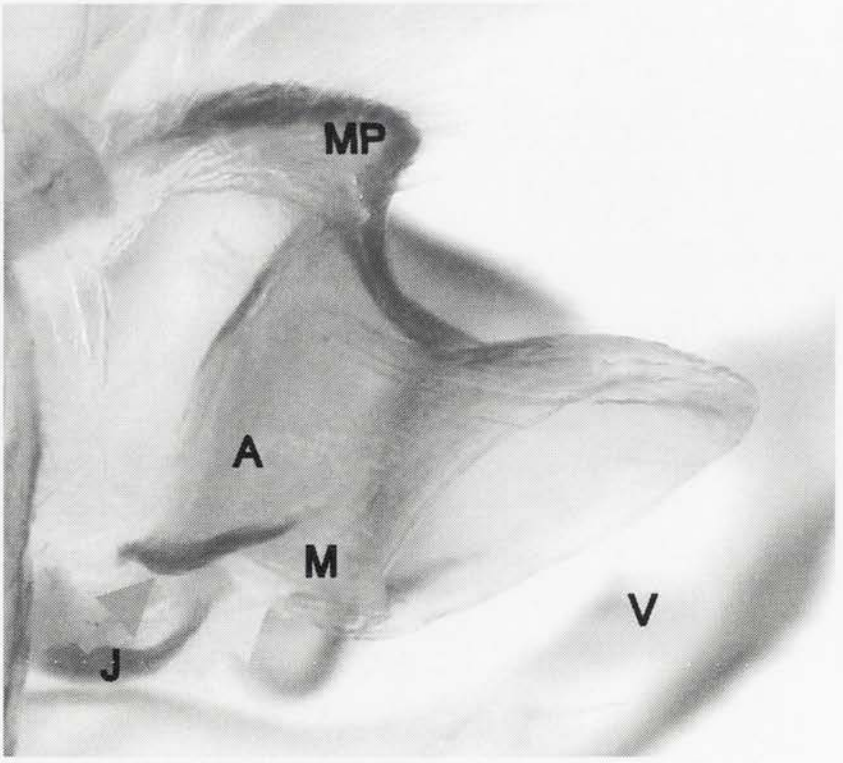

Fig. 16: Munychryiinae n. sp. (Anthelidae), ♂, lateral view [phallus removed] – the setose mesal protrusion and the anellus are fused with each other; the lateral sclerotization of the anellus ends dorsally of the reduced juxta (green arrow); the manica appears to be everted and sclerotized, forming a tall dorsal protrusion (yellow arrow marks the ventral side of the manica).

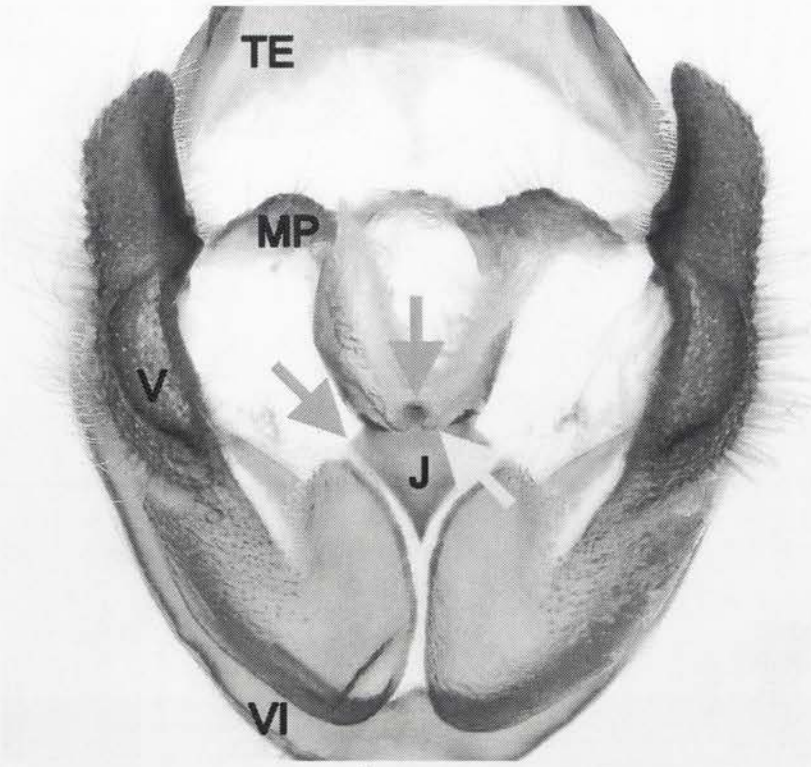

Fig. 17: *Munychryia periclyta* (Anthelidae), ♂, posterior view [phallus removed] – the setose mesal protrusion and the anellus are fused with each other; the lateral sclerotization of the anellus is fused with the juxta; the manica appears to be everted and partly sclerotized, forming a very tall ventro-lateral sheath around the phallus; muscles *m3* (not visible) attach to the dorso-lateral corner of the juxta (green arrow), clearly indicating the composite nature of the sheath; the lateral part of the everted manica protrudes ventrally (yellow arrow) over the median sclerotization (red arrow); this median sclerotization posteriorly to the juxta might have been formed prior to the eversion of the manica.

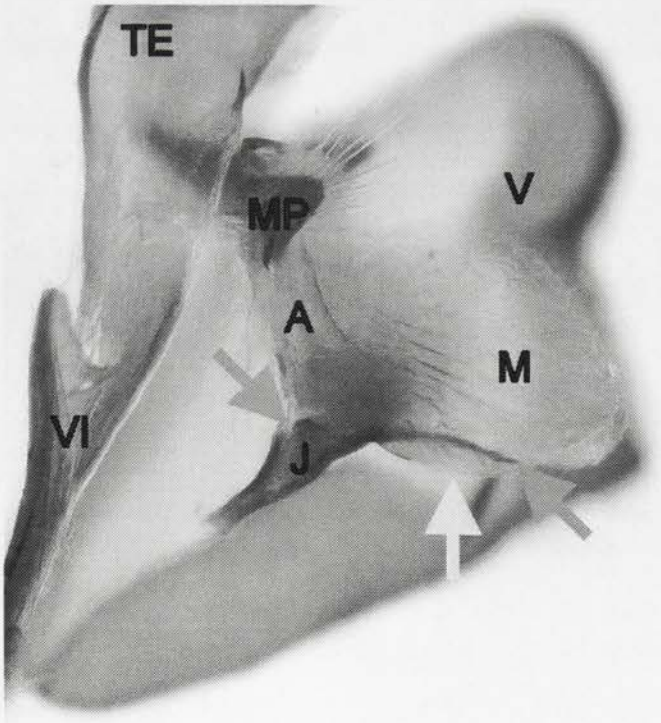

Fig. 18: *Munychryia periclyta* (Anthelidae), ♂, lateral view [phallus removed] – as Fig. 17.

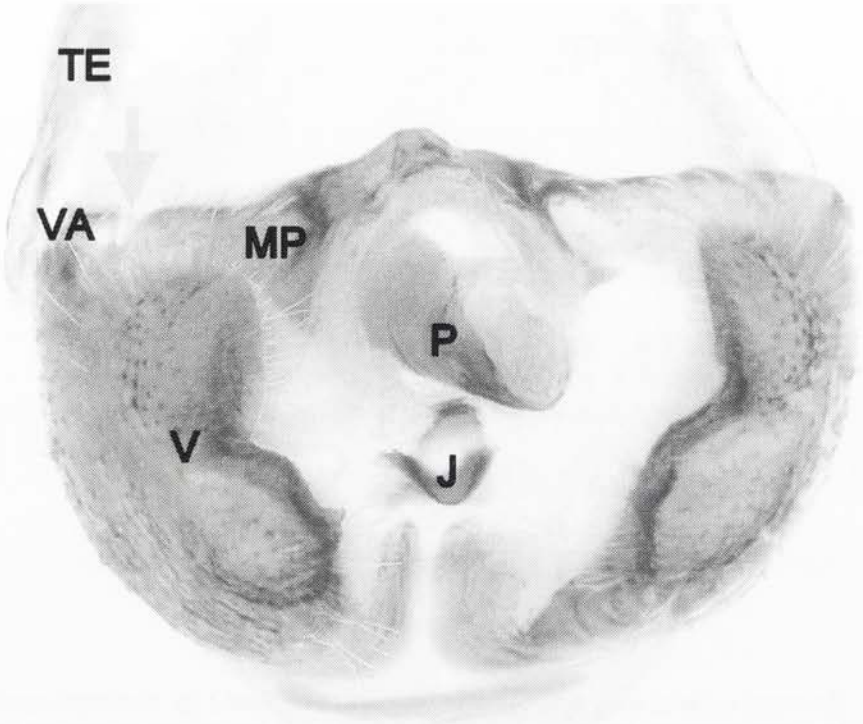

Fig. 19: *Gephyroneura cosmia* (Anthelidae), ♂, posterior view – the mesal protrusions are interconnected by a sclerotization, which might include parts of the gnathos plate.

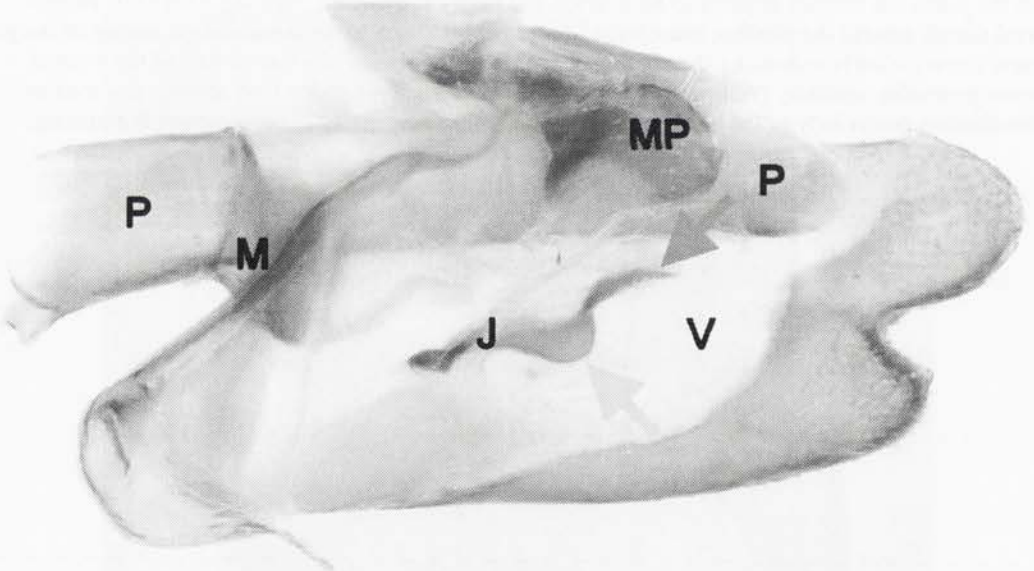

Fig. 20: *Gephyroneura cosmia* (Anthelidae), ♂, lateral view – juxta with a distinct ventral hump (yellow arrow), which might represent the original dorsal edge of the anellus prior to the eversion of the manica; the sclerotization dorsally of the juxta (red arrow) might have been stretching anteriad (towards the phallus) previously.

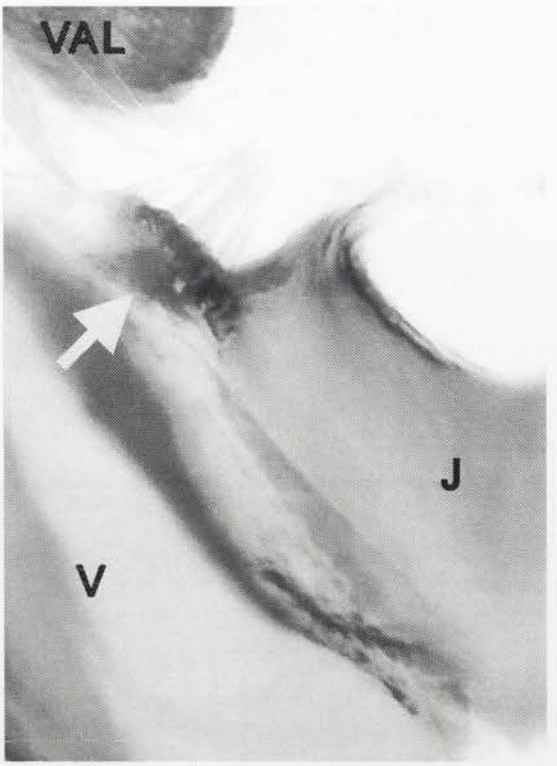

Fig. 21: *Anthela hyperythra* (Anthelidae), ♂, posterior view [phallus removed] – juxta with a remnant of the mesal protrusion (yellow arrow) fused to its dorso-lateral corner.

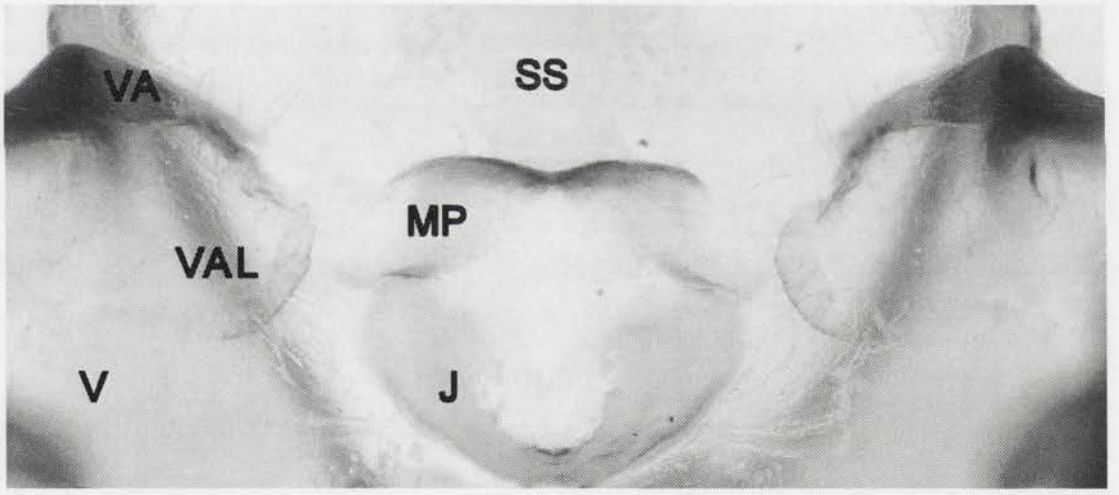

Fig. 22: Anthelinae n. sp. (Anthelidae), ♂, posterior view [phallus removed] – juxta with very distinct remnants of the mesal protrusion fused to its dorsal end.

III.1.4) Character analyses of male genital sclerite characters

Character #H.1: Bilobed uncus deeply divided, resulting in two mesally ventrad tilted lobes.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; poorly supported.

Introduction. Being derived from the tergite of the abdominal segment X (e.g., Kristensen 2003b), the uncus is laterally bowed ventrad over its entire length. The posterior part, which carries numerous setae on all sides and is ventrally sclerotized, is commonly referred to as the "apex" of the uncus (e.g., Scoble 1995), even though this term is not applicable to a tergite, as a tergite has an anterior and posterior end, but no distinct attachment at only one end. This "apex" of the uncus is frequently modified, and its general shape ranges from bilobed to single-pointed (e.g., Scoble 1995). These different shapes can be attained by various modifications, e.g., splits, fusions and reductions.

Descriptions. My examinations revealed two essential shapes and their modifications of the uncus among Anthelidae.

In the subfamily Munychryiinae the uncus apex is weakly bilobed (Fig. 23) and laterally bowed ventrad (Fig. 26). This bilobed shape is caused by a short, median indentation, which is shorter than roughly 10% of the length of the setose, ventral sclerotization. Only in an undescribed munychryiine species this bilobed condition appears to have been reduced to a blunt, simple shape (Fig. 25).

In all other Anthelidae the uncus apex is deeply split, with the split (almost) reaching the anterior end of the setose, ventral sclerotization (Fig. 24). The resulting prominent lobes are not laterally bowed ventrally, but instead show a tilt in the opposite direction – they are mesally tilted ventrad (Fig. 27). The tilt is strongest at the apex of the lobe and the absolute degree of this tilt can differ between specimens of a species. It is very variable between species and its angle ranges from near zero to 90 degrees. This range of tilts might represent a gradient in one direction, but the variation within species and differences in obviously closely related taxa argue for these differences to be caused by simple variability of the tilt and possibly subsequent changes in tilt. Hence, I do not use minor gradual differences in tilt as distinct character states. Several subsequent fusions of these two lobes occurred and are discussed as separate characters below (characters

#H.2-5, #H.7).

Discussion. Lateral curving of the uncus apex is the principal condition found in the non-anthelid taxa. Anthelidae have a weakly bilobed to deeply split uncus apex, and bilobed uncus "apices" occur also in some members of almost all families of the bombycoid complex. The length of the split varies from short to long in many families, but homologous splitting cannot convincingly be inferred alone from either the length of the split, or from the variable degree of tilt the lobes exhibit. However, the consistent combination of a particular length of split with one particular direction of tilt which I observed in the Anthelidae provides support to my hypothesis of homology for character state (1).

The deeply split and mesally ventrad tilted uncus apex is unique to some anthelid species, which is why I hypothesize this structure to be apomorphic.

Summary. This structure is characteristic, but varies in the degree of split and tilt between species. Further, the split is partly obscured by secondary fusions in some species (see characters #H.2-5, #H.7). Therefore, I regard my hypothesis of homology for the apomorphic character state (1) as poorly supported.

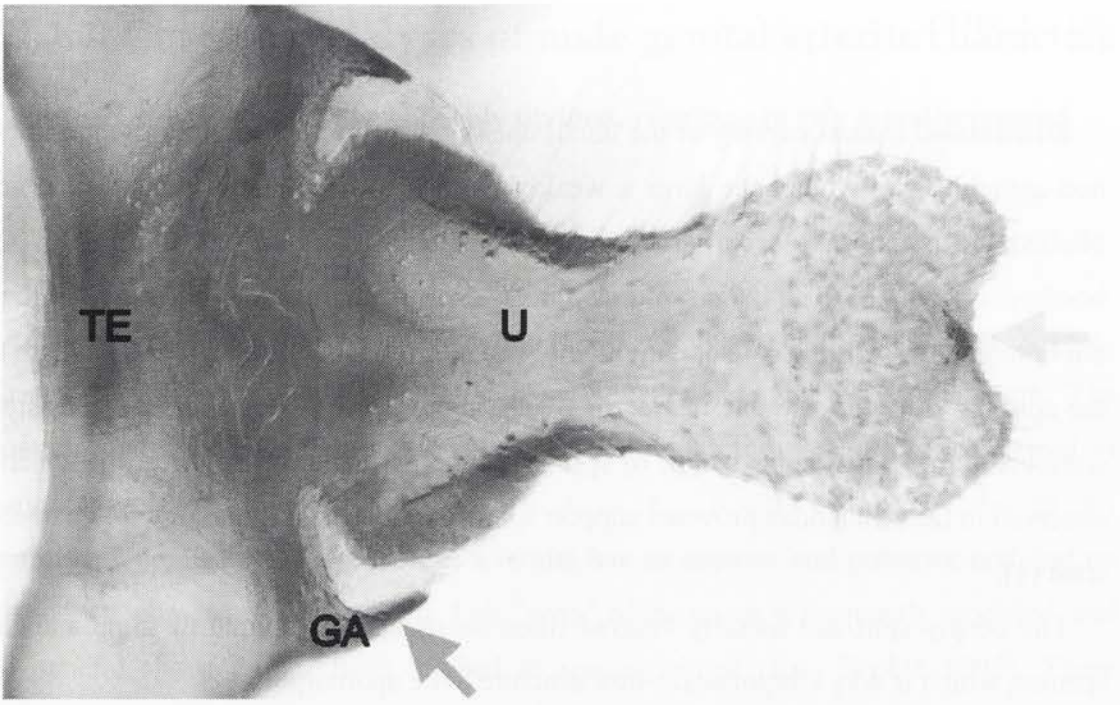

Fig. 23: *Munychryia periclyta* (Anthelidae), ♂, dorsal view – tegumen and weakly bilobed uncus apex (yellow arrow); note the fusion between tegumen and gnathos arm (green arrow).

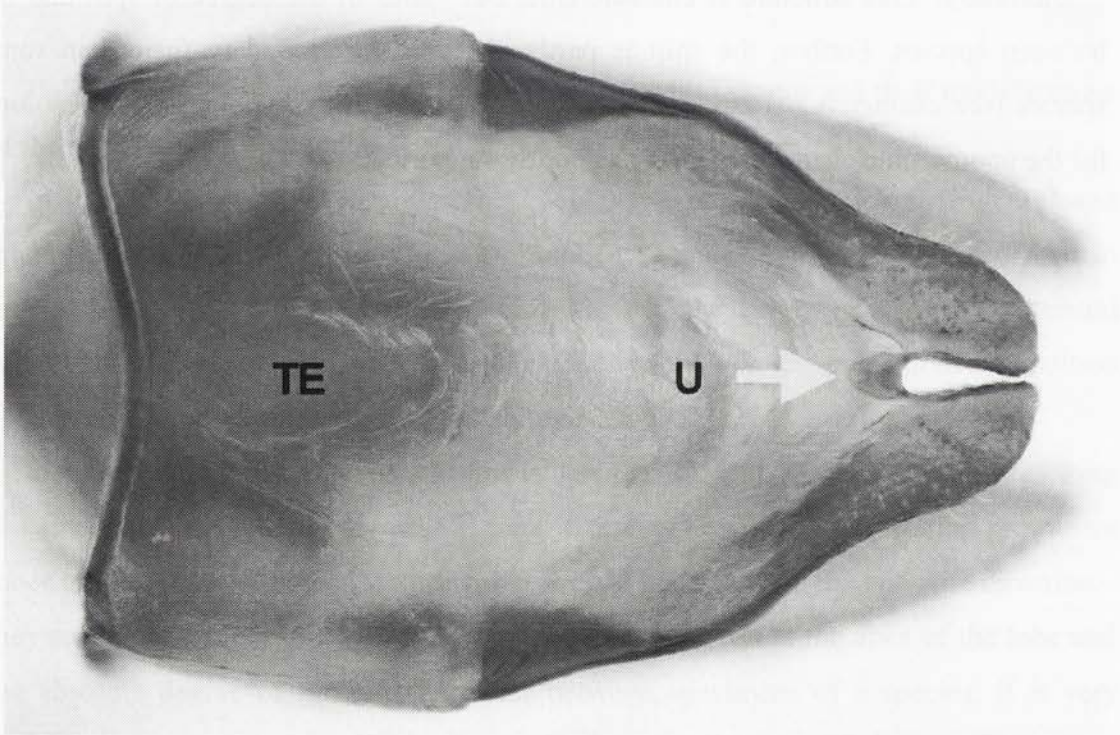

Fig. 24: *Anthela virescens* (Anthelidae), ♂, dorsal view – tegumen and deeply split uncus apex; note the tongue-shaped anterior end of the ventral sclerotization shining through (yellow arrow).

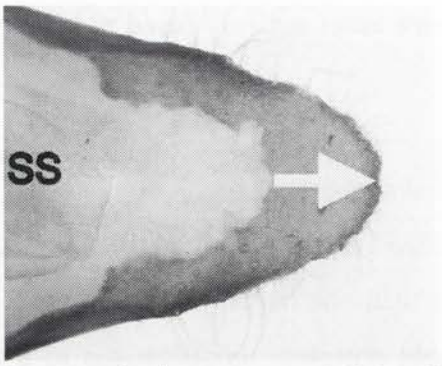

Fig. 25: Munychryiinae n. sp. (Anthelidae), ♂, ventral view – uncus apex with reduced lobes, as indicated by a tiny indentation (yellow arrow).

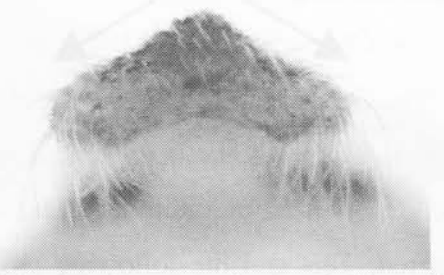

Fig. 26: *Munychryia periclyta* (Anthelidae), ♂, posterior view – weakly bilobed uncus apex laterally curving ventrad (yellow arrows symbolize direction).

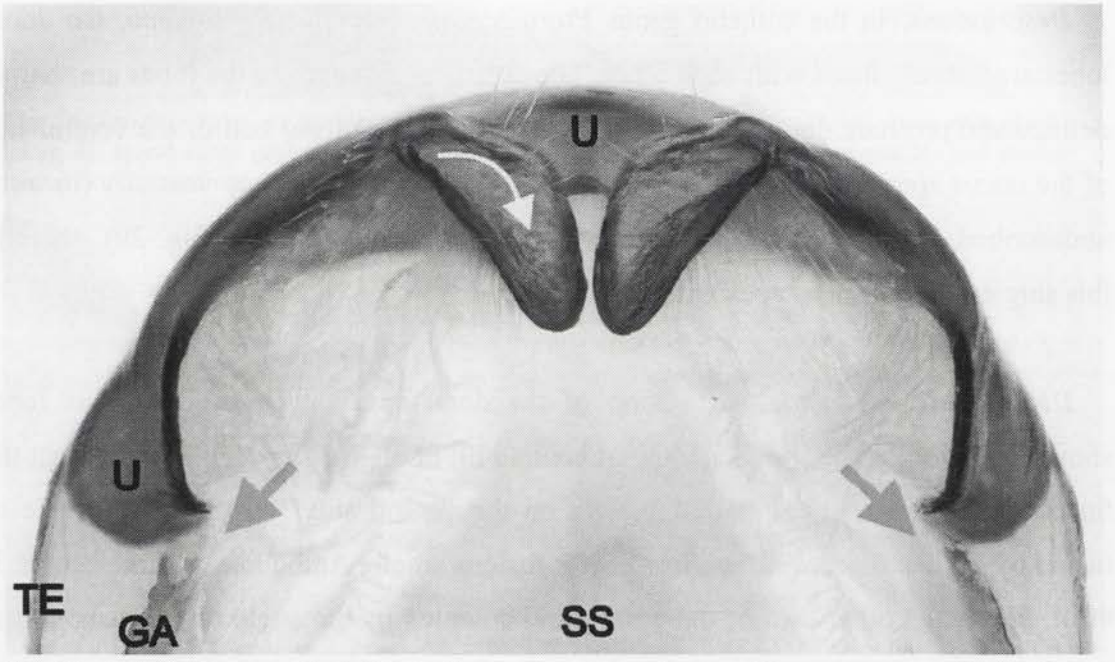

Fig. 27: *Anthela virescens* (Anthelidae), ♂, posterior view – deeply split uncus apex mesally tilted ventrad (yellow arrow symbolizes direction); note the "articulation" between antero-ventral extension of the uncus and the dorsal end of the gnathos arm (green arrows).

Character #H.2: Deeply divided uncus apex with lobes entirely fused at 60-70° angle, starting ventrally.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; well supported.

Introduction. The lobes of the deeply divided, mesally ventrad tilted uncus are secondarily fused in a number of taxa, and more than one fusion event appears to have occurred. This and the following characters might represent modifications of a single fusion event, but this is uncertain and hence they are conservatively treated as separate characters (see above, section III.1.2: 71).

Descriptions. In the anthelid genus *Pterolocera*, except for *P. isogama*, the uncus lobes are entirely fused with each other. The dorso-apical edges of the lobes are sharply defined and protrude dorsally and posteriad (Fig. 28). The distal half of the ventral side of the uncus apex forms a distinct crest, which protrudes a long way ventrally (in some undescribed *Pterolocera* species extremely) and is devoid of setae (Fig. 29). Overall, this single-pointed uncus apex enlarges apically.

Discussion. The partial separation of the dorso-apical edge of the uncus lobes showing the lobes to be fused at a mesal ventrad tilt of 60-70° (Fig. 30) suggests that the fusion of the uncus lobes started basally on the ventral side. This particular type of fusion of the uncus lobes differs from other fusions among Anthelidae (characters #H.3, #H.4, #H.7) and other taxa of the bombycoid complex by the angle of the fused lobes, the dorso-posteriad protruding, sharply defined apical edges and the strong ventral protrusion of the distal part of the ventral crest.

This particular type of fusion of the uncus lobes is unique to some anthelid species, which is why I interpret characters state (1) as apomorphic.

Summary. My hypothesis of homology for this type of fusion is well supported by several structural details.

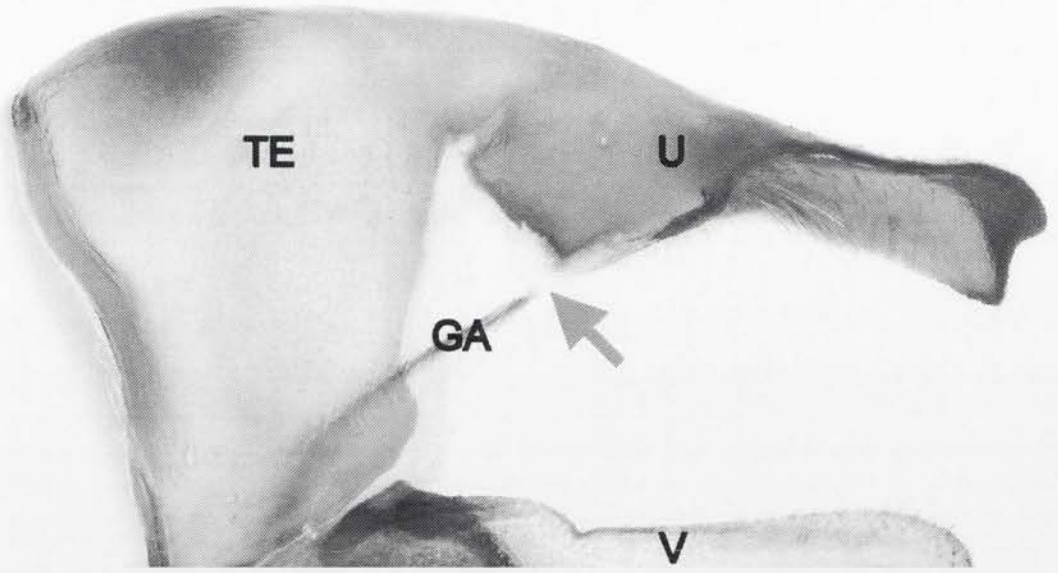

Fig. 28: *Pterolocera* sp. ex Tasmania (Anthelidae), ♂, lateral view – tegumen and uncus with fused lobes; the apical uncus edge protrudes dorso-posteriad; note the "articulation" of gnathos and antero-lateral extension of the uncus (green arrow).

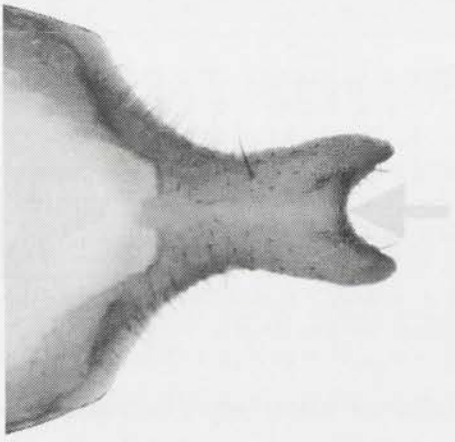

Fig. 29: *Pterolocera* sp. ex Tasmania (Anthelidae), ♂, ventral view – uncus apex; the median suture stretches along the entire apex (yellow arrows); posterior protrusion of dorso-apical edges very distinct.

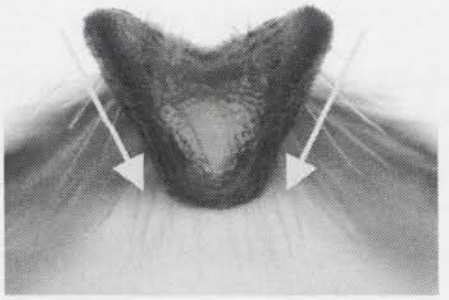

Fig. 30: *Pterolocera* sp. ex Tasmania (Anthelidae), ♂, posterior view – uncus apex; the dorso-apical edges show a mesal ventrad tilt of roughly 60-70° (indicated by yellow arrows).

Character #H.3: Deeply divided uncus apex with lobes entirely fused at less than 30° angle, starting ventrally

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; moderately supported.

Introduction. The fused lobes are similar to the ones described in the previous character (#H.2, state (1)) and I cannot rule out that they are merely a reduction of the previous character. However, a number of details differ and argue for these structures to represent independent fusion events.

Description. As in the previous character the lobes of the uncus apex are fused, apparently starting ventrally. The fused lobes are tilted at less than 30° (Fig. 34), the dorso-apical edges do not protrude and the apex shows at most a small indentation (Fig. 33). The median crest of the ventral side is very shallow to absent and only apparent in the apical half of the fused lobes (Fig. 32). Overall, the single-pointed uncus apex narrows apically (Fig. 31), rather than enlarges. The sclerotization of the ventral side does not extend anteriad, but shows an indentation instead (Fig. 33).

The above characteristic structure is present in a large group of species that includes the well-known *Anthela repleta*, *A. acuta*, *A. astata* and *A. varia*. In other members of this species group, namely *Anthela basigera* and sibling species, the fused uncus lobes are further modified. While these species have a very shallow, ventral, median crest and posteriorly a minute indentation, the entire fused uncus apex is laterally compressed and protrudes dorsally (Fig. 39).

Discussion. As in the previous character I assume this single-pointed uncus apex to be a secondary fusion of deeply divided, mesally ventrad tilted uncus lobes, as indicated by the ventral crest and the remnants of the dorso-apical edges in some species.

This type of fusion is unique to some anthelid species and hence I interpret character state (1) as apomorphic.

Summary. The characteristics of character state (1) are not strikingly distinct. Consequently, I regard my hypothesis of homology to be only moderately supported.

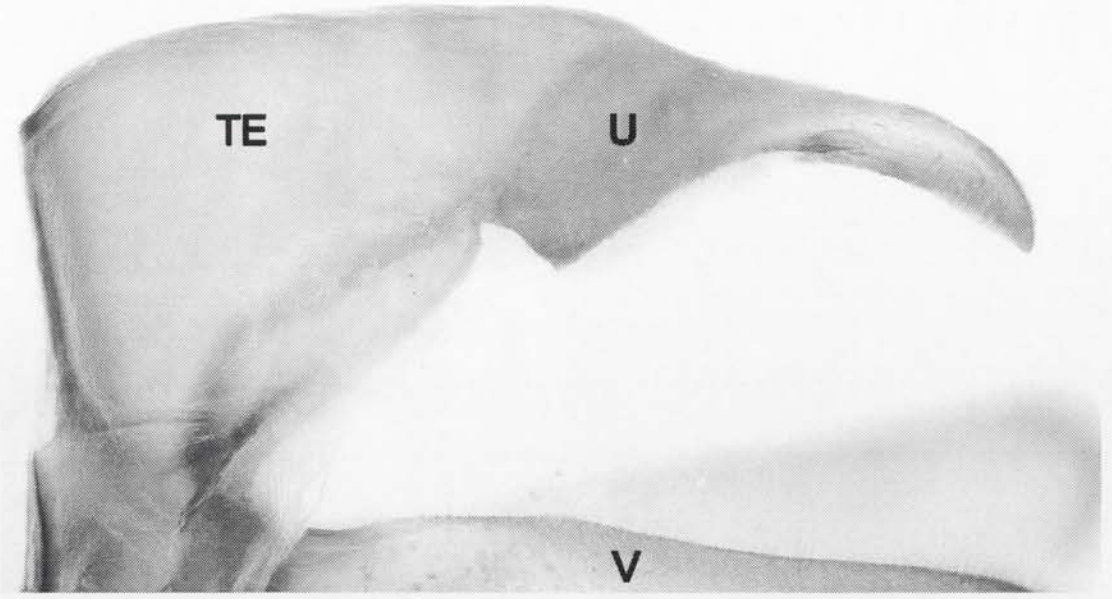

Fig. 31: *Anthela astata* (Anthelidae), ♂, lateral view – tegumen and uncus with fused lobes; the uncus apex is shallow and without a protruding dorso-apical edge.

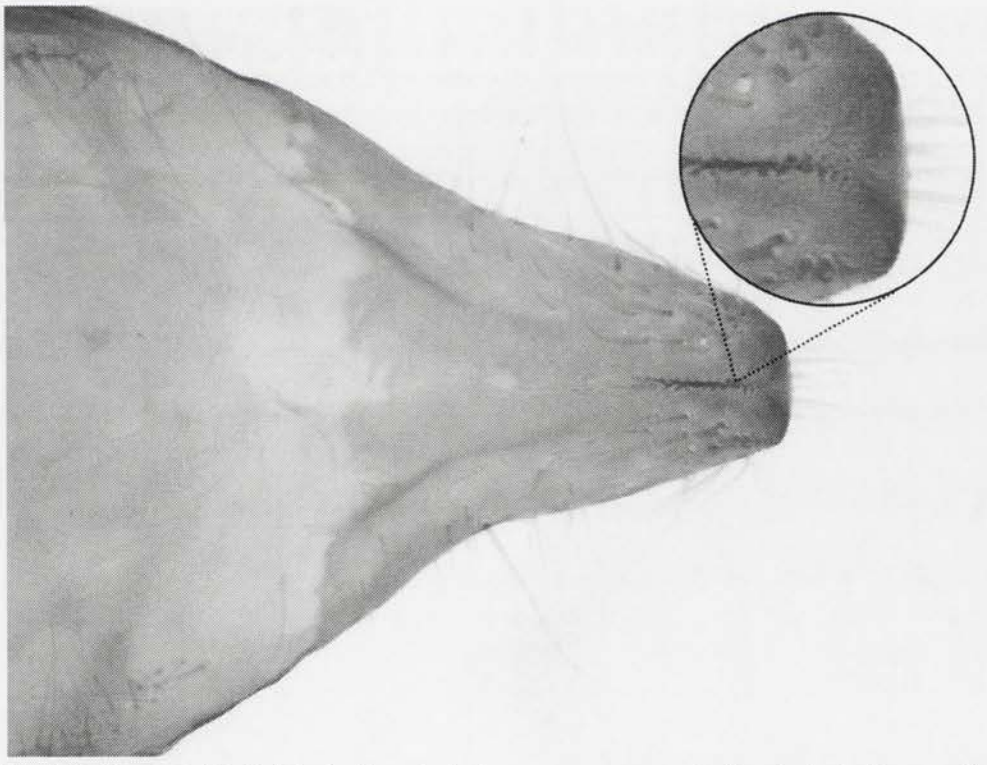

Fig. 32: *Anthela astata* (Anthelidae), ♂, ventral view – uncus apex; note the short, shallow, median suture.

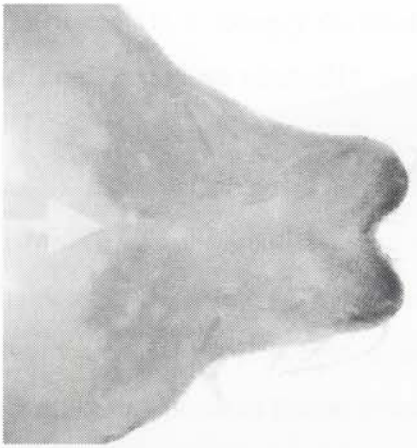

Fig. 33: *Anthela postica* (Anthelidae), ♂, ventral view – uncus apex; the median suture is hardly visible; note the anterior gap in the sclerotization (yellow arrow).

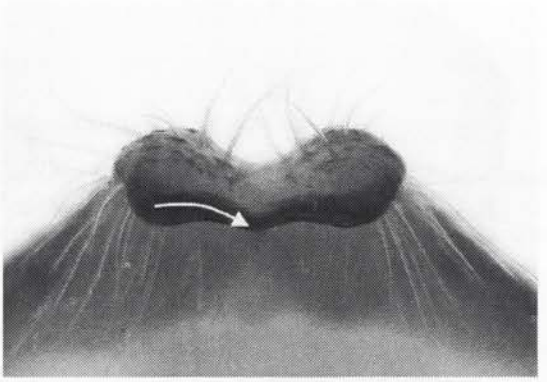

Fig. 34: *Anthela* sp. near *astata* ex PNG (Anthelidae), ♂, posterior view – uncus apex; the dorso-apical edges show a mesal ventrad tilt of less than 30° (symbolized by the yellow arrow).

Character #H.4: Deeply divided uncus with fused lobes forming a ventral blade.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; poorly supported.

Description. The fused uncus lobes are apically mesally tilted ventrad by 90° and stand vertically. This fused structure is dorsally broad and flat, with its lateral walls being strongly concave (Fig. 36) and form a median, ventral blade (Fig. 35). This blade extends over the length of the entire uncus apex, but is tallest posteriorly.

Discussion. I regard the present condition to be the first step in a transformation series, which is characterized by the formation of a ventral blade over the entire length of the uncus apex. Accordingly, I score this character as 1 in taxa exhibiting the further modification detailed in character #H.5, state (1). In their overall shape the fused lobes of the uncus recall a condition present in other anthelid species, namely separate, apically touching uncus lobes with a mesal ventrad tilt of roughly 90° (character #H.6, state (1)).

This fusion type of the uncus lobes is unique to some Anthelidae, which is why I interpret character state (1) as apomorphic.

Summary.

Because of the assumed subsequent modification my hypothesis of homology is only based on the shared formation of a ventral blade over the entire length of the uncus apex. Therefore, I regard my hypothesis of homology to be poorly supported.

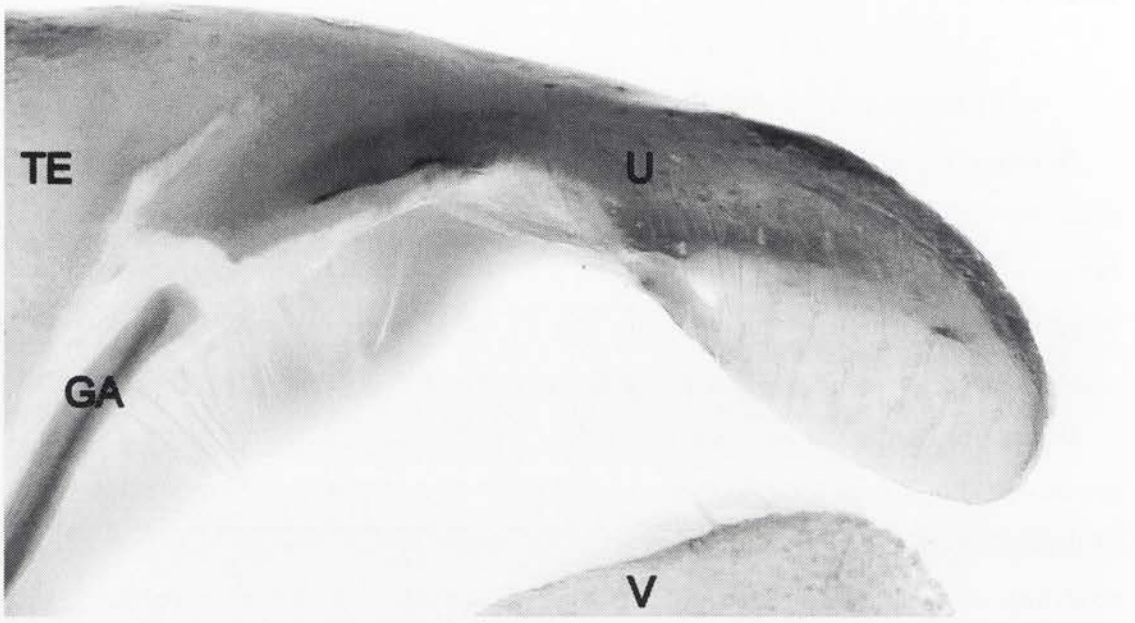

Fig. 35: *Anthela neurospasta* (Anthelidae), ♂, lateral view – uncus with fused lobes forming a ventral blade over entire length of uncus apex; note the "articulation" of gnathos and antero-lateral extension of the uncus.

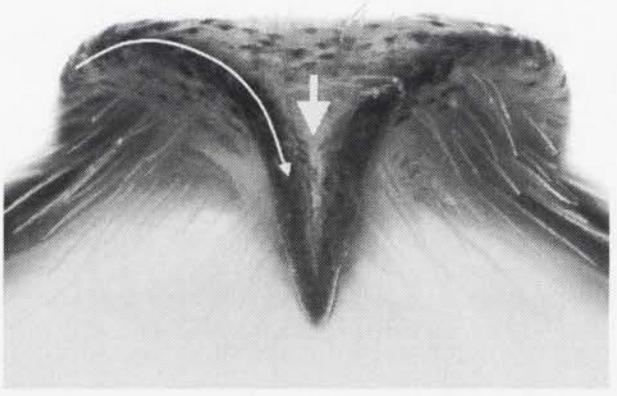

Fig. 36: *Anthela neurospasta* (Anthelidae), ♂, posterior view – uncus with fused lobes forming a ventral blade; note the concave lateral sides caused by the strong ventral tilt (long yellow arrow), the median indication of a fusion of separate lobes (short yellow arrow) and the flat dorsal side.

Character #H.5: Uncus with ventral blade laterally compressed.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; moderately supported.

Description. Some anthelid species have fused uncus lobes that form a ventral blade as in character #H.4 state (1), but these differ from it by being dorsally narrow (Fig. 37). This condition is superficially similar to the one found in the species group surrounding *Anthela basigera* (Fig. 39; see character #H.3), but can be distinguished from it by the blade-shaped part extending ventrad (rather than dorsad) and over the entire length of the uncus apex (rather than just distally). Further, the posterior edge of this ventral blade is rounded (not indented).

Discussion. I assume this structure to be a modification of character #H.4 state (1), in which the uncus apex is dorsally broad and flat, and has strongly concave lateral walls (Fig. 36). In the species with character #H.5 state (1) the lateral walls of the uncus blade are parallel and the posterior edge is rounded (no indentation) (Fig. 38).

Being part of a postulated transformation series, for which the polarity has been identified in the previous character, interpret character state (1) as apomorphic.

Summary. I regard my hypothesis of homology for the apomorphic character state (1) to be moderately supported.

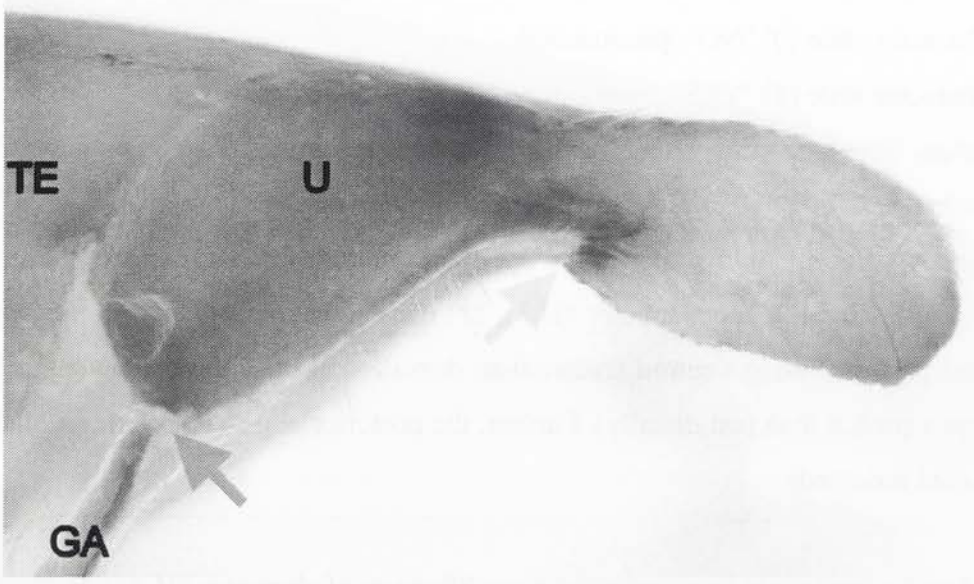

Fig. 37: *Anthela phoenicias* (Anthelidae), ♂, lateral view – uncus with fused lobes forming a ventral blade over entire length of uncus apex (yellow arrow); note the "articulation" of gnathos and antero-lateral extension of the uncus (green arrow).

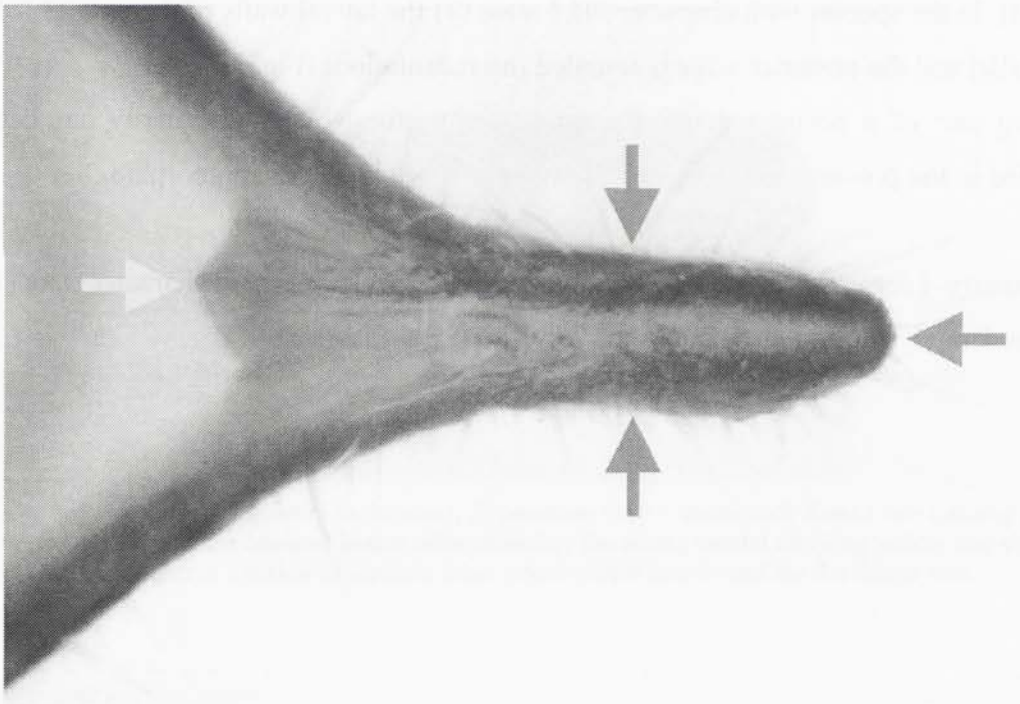

Fig. 38: *Anthela phoenicias* (Anthelidae), ♂, ventral view – uncus with fused lobes forming a ventral blade over entire length of uncus apex (yellow arrow); blade is laterally compressed (red arrows); note the rounded posterior edge (green arrow).

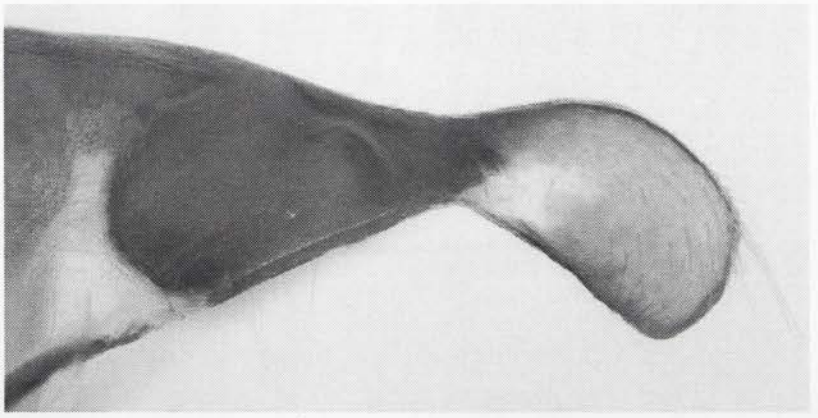

Fig. 39: *Anthela basigera* (Anthelidae), ♂, lateral view – uncus with fused lobes, which have a very shallow, short, ventral crest (yellow arrow), are laterally compressed ("blade-shaped") and protrude dorsally.

Character #H.6: Deeply divided uncus with vertical lobes distally touching.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; well supported.

Description. In some species the deeply divided uncus lobes are mesally distinctly more strongly tilted ventrad than in other taxa, they are distally in a vertical position (Fig. 42). In these species the lobes are distinctly separated from each other basally (elongate, oval gap; Fig. 41), but they are touching each other distally. Overall, these lobes are finger-shaped and curve ventrad (Fig. 40).

Discussion. The vertical position of the uncus lobes is the most extreme ventrad tilt, and the restriction of the contact between the uncus lobes to their apices is unique. I therefore interpret character state (1) as apomorphic.

I further regard this character state to be subsequently modified (character #H.7 state (1)) and score it accordingly as an additive binary character.

Summary. I believe my hypothesis of homology for this modification of the uncus lobes to be well supported.

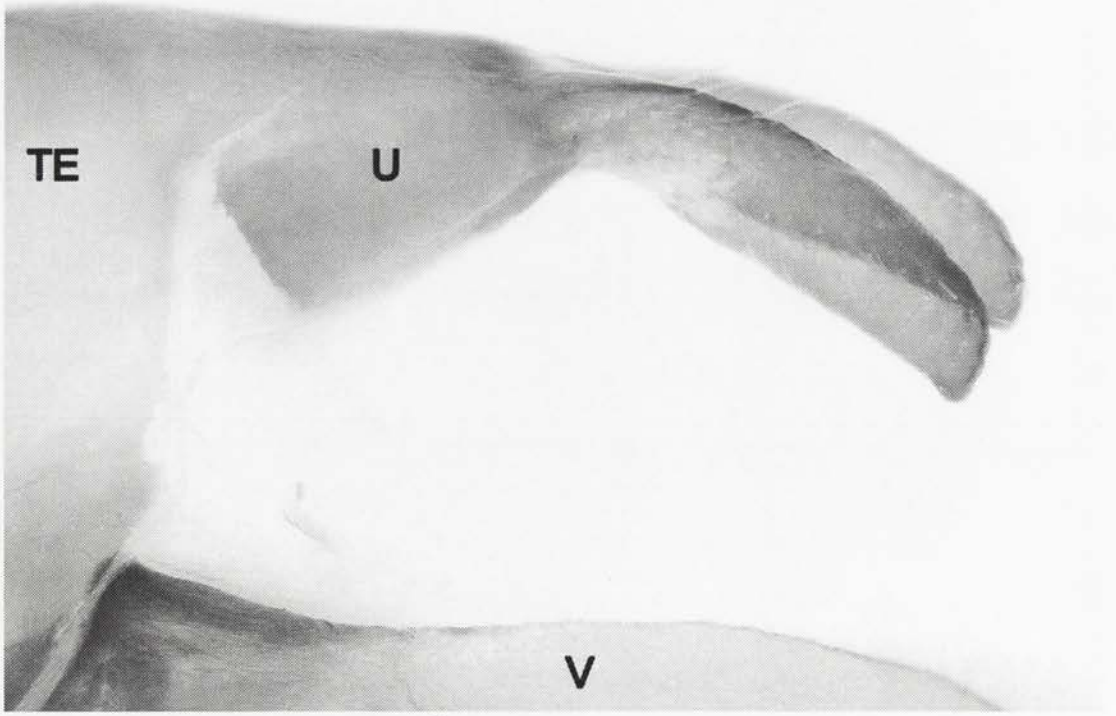

Fig. 40: *Anthela asterias* (Anthelidae), ♂, lateral view – uncus with finger-shaped, mesally strongly ventrad tilted lobes, which touch each other distally.

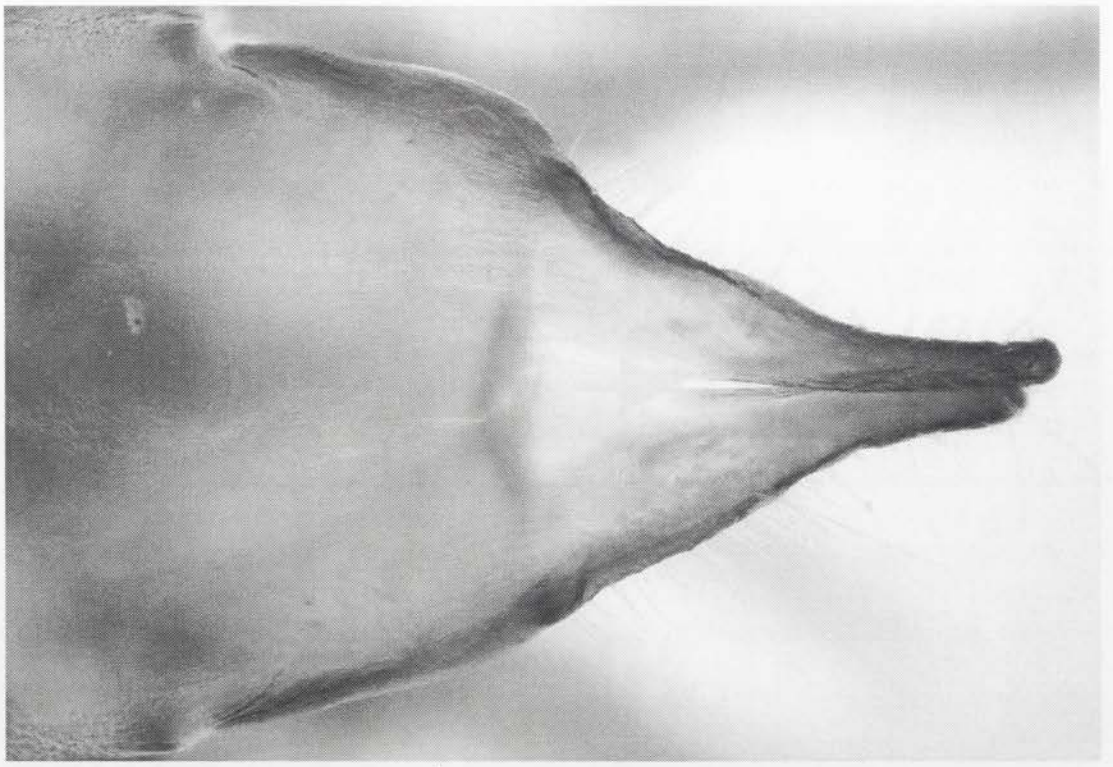

Fig. 41: *Anthela asterias* (Anthelidae), ♂, dorsal view – uncus with finger-shaped, mesally strongly ventrad tilted lobes, which touch each other distally; note the gap at the base of the two lobes (yellow arrow).

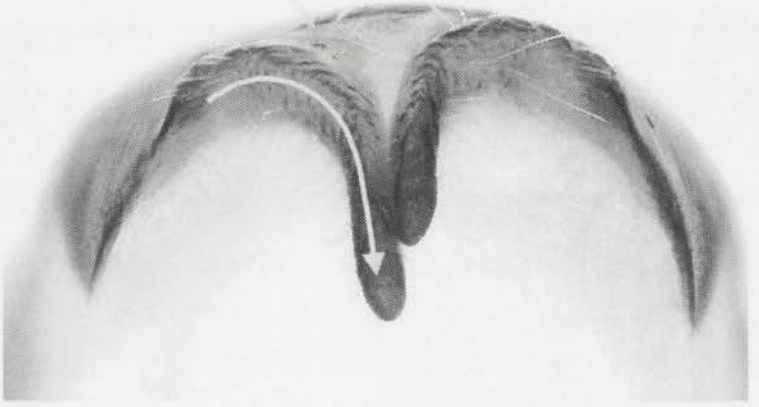

Fig. 42: *Anthela asterias* (Anthelidae), ♂, dorsal view – uncus with finger-shaped, mesally strongly ventrad tilted lobes (yellow arrow visualizes tilt; the lobes are distally oriented "vertically"), which touch each other distally.

Character #H.7: Deeply divided uncus with lobes only dorsally partly fused.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; very well supported.

Description. In a group of species endemic to New Guinea the deeply divided uncus lobes are long, flat and curve ventrad (Fig. 43). Their apex has a strongly sclerotized, pointed tip (Figs 43, 46). From the base to the apex, these lobes are tightly parallel to each other and are mesally tilted ventrad by 90° (vertical orientation) (Fig. 46). These lobes show a partial, proximal fusion of the dorsal sides, which ends well before the apices of the lobes (Fig. 44). The ventral sides of the lobes are still entirely separated (Fig. 45) and the two parts can be pulled apart physically.

Discussion. This apparent beginning of a fusion on the dorsal side contrasts with all other fusions, which are complete and appear to have originated on the ventral side as indicated by the apices of the fused uncus lobes. As the dorsal fusion is complete proximally, but the two lobes are separated distally, I assume this fusion to progress from the bases towards the apices of the uncus lobes.

In some species, e.g., the type species of the genus *Corticomis* (*C. eupterotioides*), it seems very apparent that the fused condition of the uncus lobes is a subsequent modification of the strongly ventrad tilted and apically touching uncus lobes described as character #H.6 state (1). Hence, I scored this character accordingly as an additive binary character, with character state (1) being apomorphic.

Summary. The fusion shows numerous indications of homology as described above. Hence, I regard my hypothesis of homology of the apomorphic character state (1) to be very well supported.

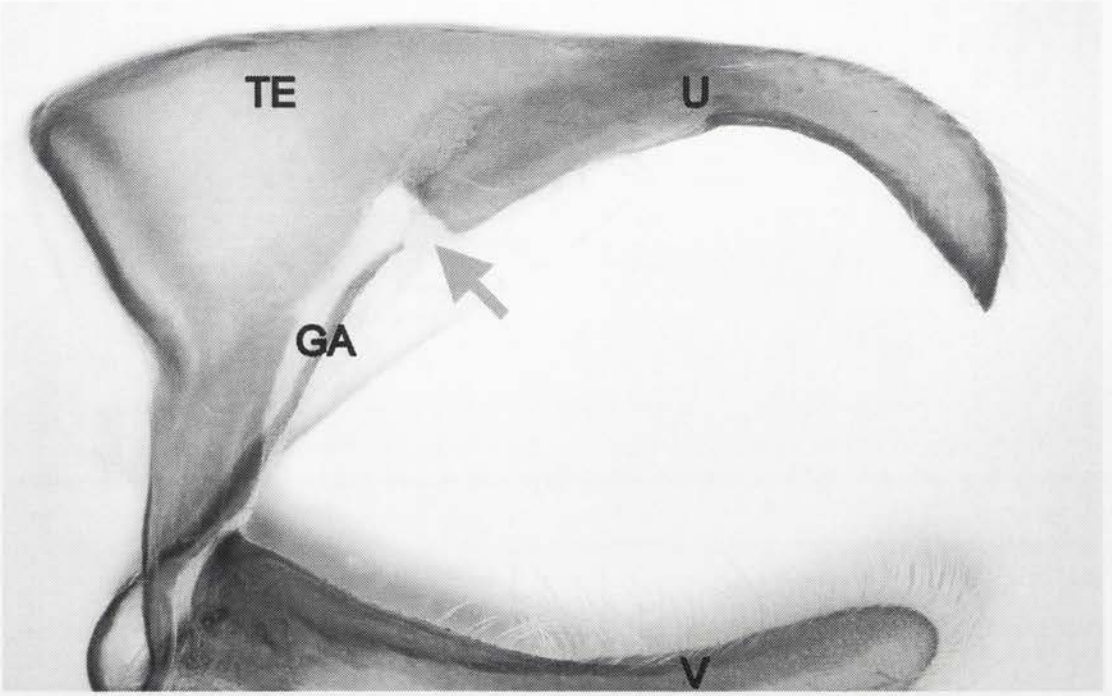

Fig. 43: *Pseudodreata* sp. (Anthelidae), ♂, lateral view – tegumen and uncus with dorsally partly fused, but ventrally separate lobes; lobe apex with strongly sclerotized, pointed tip; note the "articulation" between the gnathos and the antero-lateral extension of the uncus (green arrow).

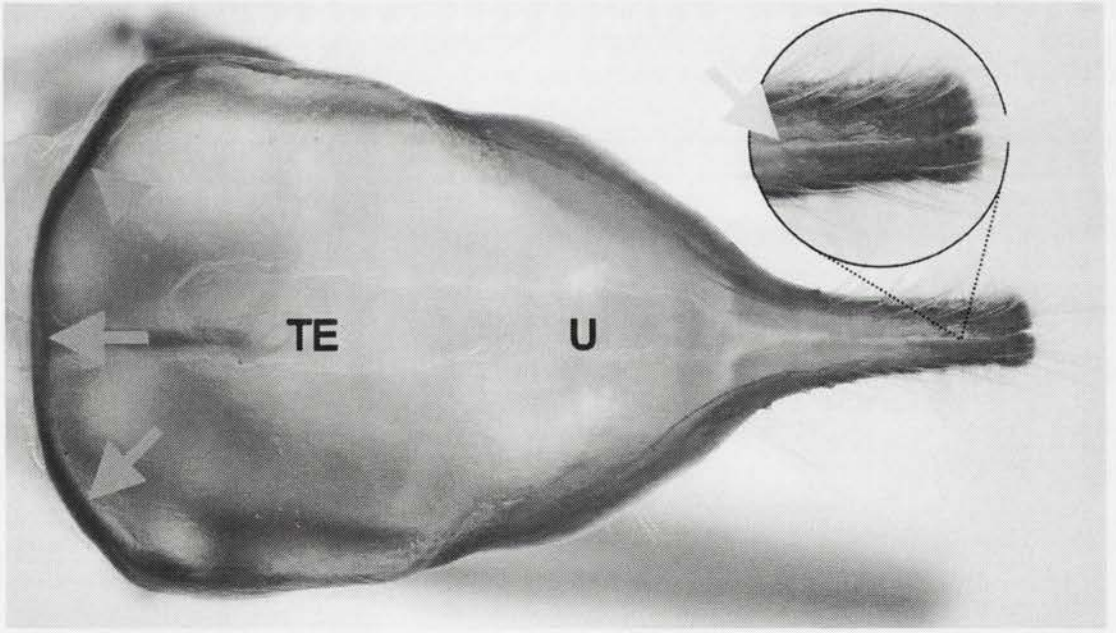

Fig. 44: *Pseudodreata* sp. (Anthelidae), ♂, dorsal view – tegumen and uncus with dorsally partly fused, but ventrally separate lobes; the dorsal side of the lobes' apex remained distally separated (yellow arrows); note the convex anterior edge of the tegumen (green arrows).

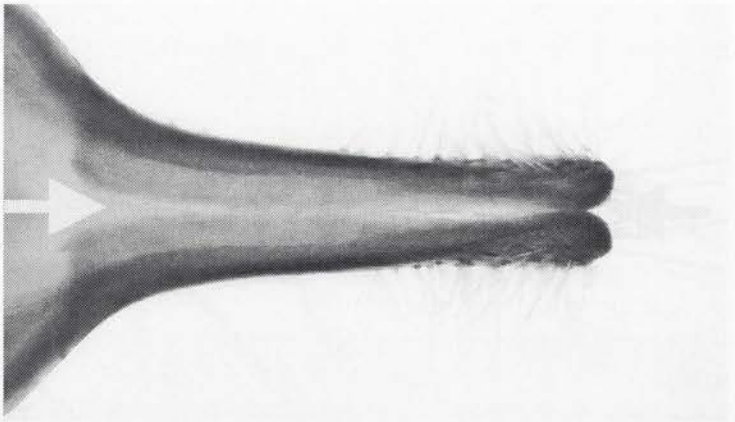

Fig. 45: *Pseudodreata* sp. (Anthelidae), ♂, ventral view – uncus with dorsally partly fused, but ventrally separate lobes; the ventral side is not fused as indicated by median membranous area (yellow arrows).

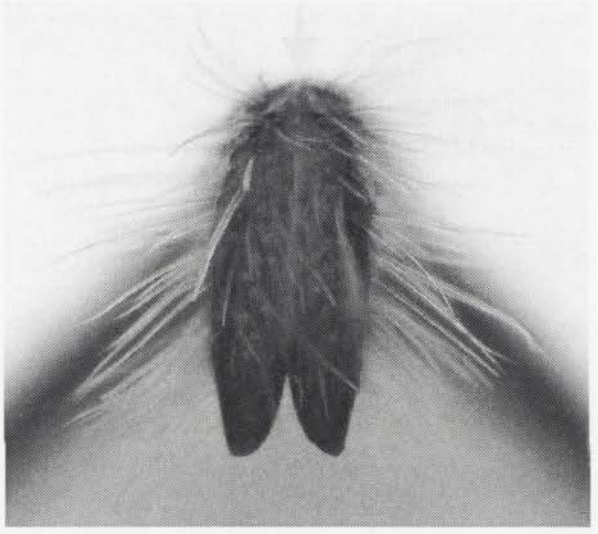

Fig. 46: *Pseudodreata* sp. (Anthelidae), ♂, posterior view – uncus with dorsally partly fused, but ventrally separated lobes; the lobe apices have a strongly sclerotized, pointed tip; note the median suture (yellow arrow) and gap.

Character #H.8: Gnathos arms dorsally reduced.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; poorly supported.

Introduction. The gnathos is one of the most frequently reduced structures in Macrolepidoptera. At least within the bombycoid complex these reductions and losses of the gnathos are obviously very homoplastic and hence I do not use them as characters in my phylogenetic analyses. If remnants of the gnathos are left, they typically show that the reductions started from the gnathos plate and extended laterad – the dorsal ends, which "articulate" with the antero-ventral extension of the uncus, are the last to disappear (Fig. 47).

Description. An unusual reduction starting from the dorsal end of the gnathos arms is present in some anthelid species (Fig. 48). The amount of the reduction varies between species, but a distinct ventral part of the gnathos arm is retained in all species, typically mesally fused to the modified mesal protrusions (character #H.15 state (1)).

Discussion. The fully developed gnathos or at least dorsal remnants of it are present in many anthelid species. The apomorphic condition is obviously the dorsal reduction of the gnathos arms, character state (1).

Summary. While being very unusual, this dorsal reduction of the gnathos arms is no more than a simple reduction, which could not be differentiated from similar reductions. Therefore, I regard my hypothesis of homology to be poorly supported.

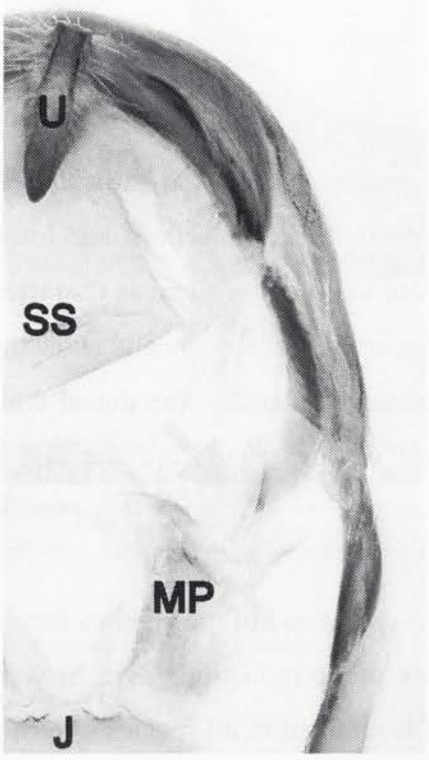

Fig. 47: *Anthela basigera* (Anthelidae), ♂, posterior view – the gnathos arm is dorsally well developed (yellow arrows).

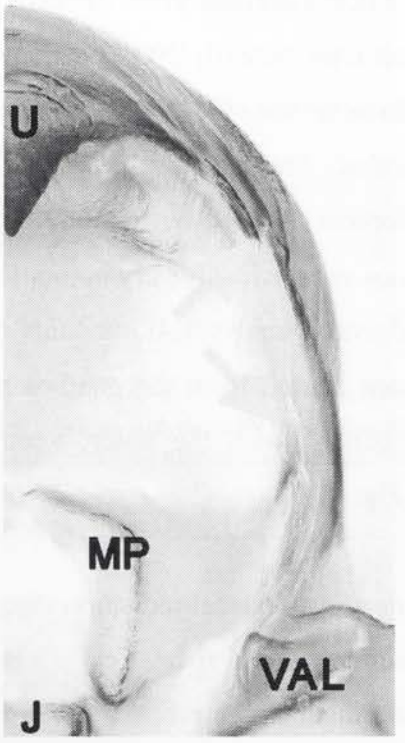

Fig. 48: *Anthela varia* (Anthelidae), ♂, posterior view – the gnathos arm is dorsally reduced (yellow arrows mark lost section; the sclerotized remnant of the gnathos arm starts dorsally at the ventral arrow and is seamlessly fused with the sclerotization of the mesal protrusion).

Character #H.9: Gnathos arms dorso-posteriorly with secondary, spinose sclerotization.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; very well supported.

Introduction. The sclerotization of the gnathos, in particular its median plate, is very variable within Macrolepidoptera. It ranges from smooth to very rough, but is essentially never setose. In Anthelidae the sclerotization of the gnathos arms as well as of the median plate is always smooth (Fig. 14).

Description. In a few anthelid species the median plate has been lost and the mesal ends of the retained lateral arms have a characteristic shape. They consist of a strongly sclerotized, posteriad protruding band and a weak sclerotization in the plane of the diaphragma, which extends further mesad than the posteriad protruding band. In addition, a secondary sclerotization of mainly the dorsal, posteriad protruding part exists. This sclerotization consists of numerous minute spines (Fig. 49). The degree of development of this secondary sclerotization differs between species. It ranges from a few minute spines on the strongly sclerotized band (*Anthela neurospasta* and *A. achromata*) to a very distinct posterior and mesal extension, which can even fuse with its counterpart from the opposite side, forming a continuous band. The remnants of the original gnathos are still clearly discernible with transmitted light.

Discussion. The entire gnathos has a smooth sclerotization in all Anthelidae and most Macrolepidoptera. The spinose secondary sclerotization of such gnathos arm remnants seems to be unique to some anthelid species, and hence I interpret character state (1) as apomorphic.

Summary. Despite the variation in extent and degree of sclerotization, this modification has numerous characteristic details as described above. This is why I regard my hypothesis of homology to be very well supported.

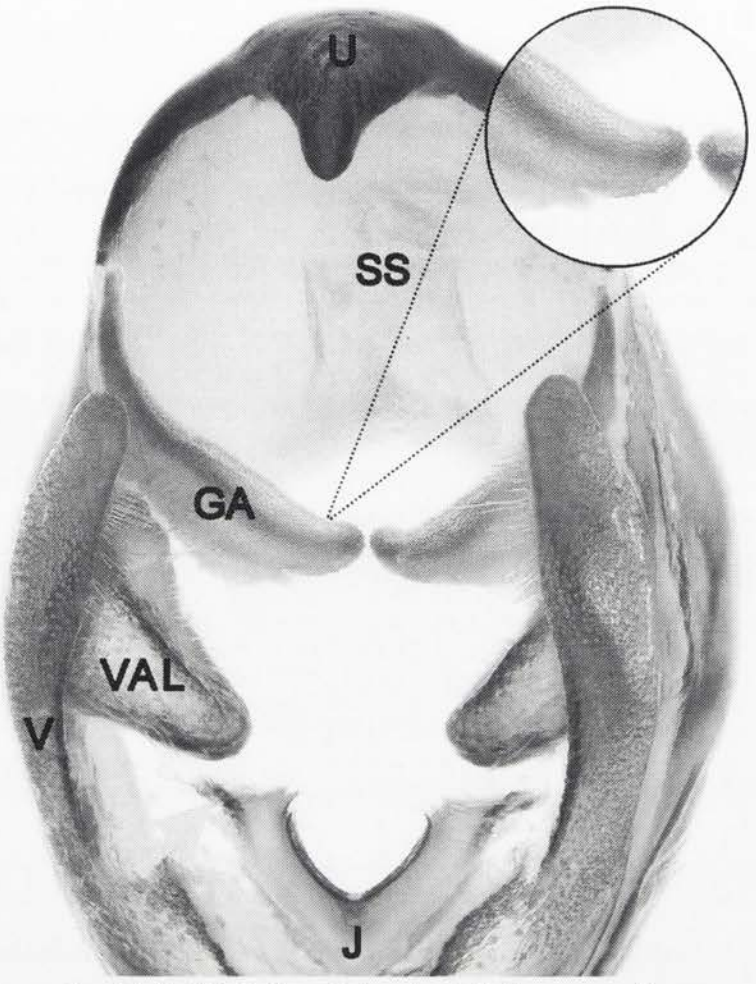

Fig. 49: *Anthela hyperythra* (Anthelidae), ♂, posterior view [phallus removed] – uncus with fused lobes, gnathos arms with secondary, spinose sclerotization, valvae with large valva apodeme lobe, and juxta with remnants of mesal protrusion (yellow arrow; see Fig. 21); note the remnants of the smooth sclerotization ventrally of the secondarily sclerotized gnathos arm ends, as well as the dorsal curving of the apex of these ends; note the concave, plate-like dorsal side of the valva apodeme lobe.

Character #H.10: Gnathos and mesal side of valva fused.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; moderately supported.

Introduction. With the exception of some families in the bombycoid complex, gnathos and valvae are separated from each other by the membranous diaphragma in Macrolepidoptera (Fig. 53). Typically, the gnathos ends far dorsally and somewhat posteriorly to the valva base. This condition is very distinct in a number of bombycoid families, namely Mimallonidae, Lasiocampidae (Figs 50, 51), Bombycidae and Sphingidae (Fig. 52).

Description. In a number of families of the bombycoid complex a seemingly unique fusion between the gnathos and a fold extending from the mesal side of the valva is present (see above, section III.1.3). This fold extends from the base of the valva mesad, along and beyond the valva apodeme. It is usually referred to as the transtilla or hemi-transtilla in literature, but see the discussion of these terms above (pp. 63ff). The fusion between this fold and the gnathos occurs near the transition from the double-walled gnathos plate to the gnathos arms. In the majority of species secondary reductions of the gnathos and/or the mesal fold obscure this fusion, often beyond recognition.

Discussion. The fusion of the gnathos and the mesal fold is obvious in some Anthelidae (Figs 70, 71) and many Saturniidae (Fig. 54), for which a fusion of gnathos and "transtilla" has already been mentioned occasionally in the literature (Michener 1952: 353-354; Rougerie 2003: 229), but more often was misunderstood and caused confusion in the application of the terms gnathos and transtilla (e.g., Pinhey 1972: 18). In many Saturniidae the connection between the gnathos arms and the gnathos plate is secondarily severed, while the gnathos plate and the mesal fold are strongly fused in many taxa (Figs 55, 56). This "relocated" gnathos plate can be mesally reduced, resulting in the appearance of a protrusion at the end of the "transtilla". In some species the situation is even more confusing as the membranous gnathos plate is fused to the mesal fold, while the severed mesal ends of the gnathos arms form secondary, coarse, posteriad protruding outgrowths (e.g., *Therinia buckleyi* (Saturniidae: Oxyteninae)). Despite all these confusing modifications, the most distinct fusions between gnathos and mesal fold can be found in Saturniidae with generally (for the family) plesiomorphic

genital structures (e.g., *Aglia tau* (Agliinae) and *Eacles imperialis* (Ceratocampinae) (Figs 54-56)).

In *Lemonia dumi* (Lemoniidae) Stekolnikov and Zolotukhin (2002: 682) noted the attachment of muscles *m4* to a "dense fold between the valves, close to the median plate of the gnathos". This describes a secondary reduction of the sclerotization of the mesal fold and gnathos. This is further indicated by the valva apodeme reaching the gnathos (Fig. 57). This condition can be more easily observed in the more heavily sclerotized structures of *Sabalia picarina* (Lemoniidae) (Fig. 58), as well as less heavily sclerotized in *Brahmophthalma hearseyi* (Brahmaeidae) (Fig. 59).

In most Eupterotidae the gnathos is entirely lost, but a well developed gnathos is present and fused with the mesal fold in, e.g., the genera *Ganisa* (Fig. 60) and *Apona.* This fusion is secondarily severed by a crack between the two structures, but the secondary nature of this condition is indicated by patches of sclerotization dorsally attached to the valva apodeme.

In (almost) monotypic families of the bombycoid complex the situation is difficult to judge. In Endromidae and Mirinidae the gnathos plate has the shape of a large wall with a reduced sclerotization, except for its dorsal edge in *Endromis versicolora* (Endromidae). While the membranous remnants of the gnathos appear to stretch far ventrad, it is not discernible where the sclerotization of the ventral gnathos wall ended originally. In *E. versicolora* the valva apodeme is very long and strongly curved antero-ventrad. As the valva apodeme borders the mesal fold dorsally, it appears unlikely that a fusion between gnathos and mesal fold existed, but I cannot rule out that this is a secondary modification. The valva apodeme and the sclerotization of the mesal side of the valva are strongly reduced in *Mirina christophi* (Mirinidae) and no conclusions can be drawn for this species. The situation is similar in the Australian *Carthaea saturnioides* (Carthaeidae, monotypic) (Fig. 61). In this species the gnathos is well developed, but the coarse, spinose sclerotization recalls the condition present in *Brahmophthalma hearseyi* (Fig. 59) and superficially the secondary sclerotization found in some Anthelidae (see above, character #H.9). A similar but finer scobination is also present at the distal end of the mesal fold of the valva, which could be an indication of a fusion between the gnathos and mesal fold, with a subsequent loss of sclerotization (Fig. 61). Alternatively, this scobination could have evolved independently. The gnathos is located far ventrally, and a membrane connects its ventral edge with the dorsal corner of

the valvae. This ventral membrane might have been the wall of the gnathos plate, if the visible plate should be a secondary sclerotization. However, the valva apodeme and with it the well sclerotized mesal fold are curved ventrad and therefore distinctly at a distance to the membrane ventrally of the gnathos, which argues against a fusion between gnathos and mesal fold.

While the gnathos and mesal fold are not as clearly separated from each other as in the families mentioned above, I also assume them to be separated in the three families Endromidae, Mirinidae and Carthaeidae based on the indications of a separation.

As the gnathos and mesal fold are distinctly separated in Macrolepidoptera and several bombycoid families, I interpret character state (1) as apomorphic.

Summary. This unique fusion is typically distinct in some representatives of each family, but the condition is obscured in three small bombycoid families (Endromidae, Mirninidae and Carthaeidae), for which I have possibly incorrectly scored this character as plesiomorphic. Subsequent reductions often obscure the visibility of the fusion within each family. I regard my hypothesis of homology to be well supported overall.

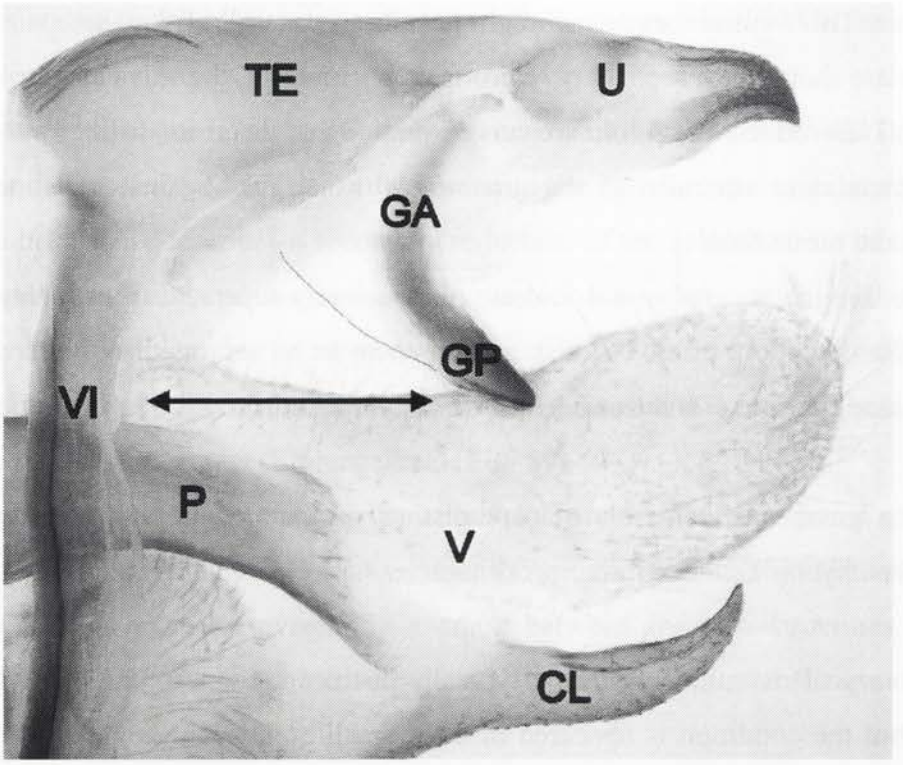

Fig. 50: *Poecilocampa populi* (Lasiocampidae), ♂, lateral view – uncus and gnathos; note the huge distance between the gnathos and the valva (black double-arrow) [dotted line traces membranous connection].

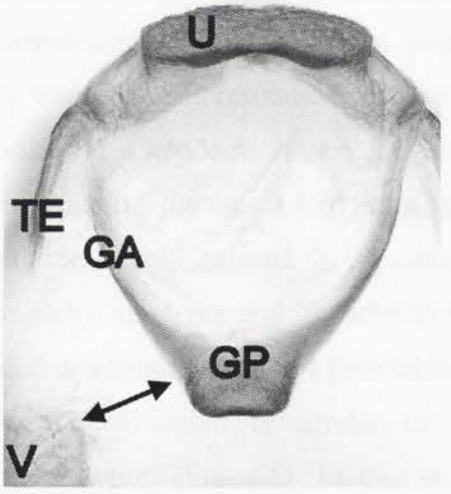

Fig. 51: *Poecilocampa populi* (Lasiocampidae), ♂, posterior view – uncus and gnathos; note the distance between the gnathos and the valva (black double-arrow).

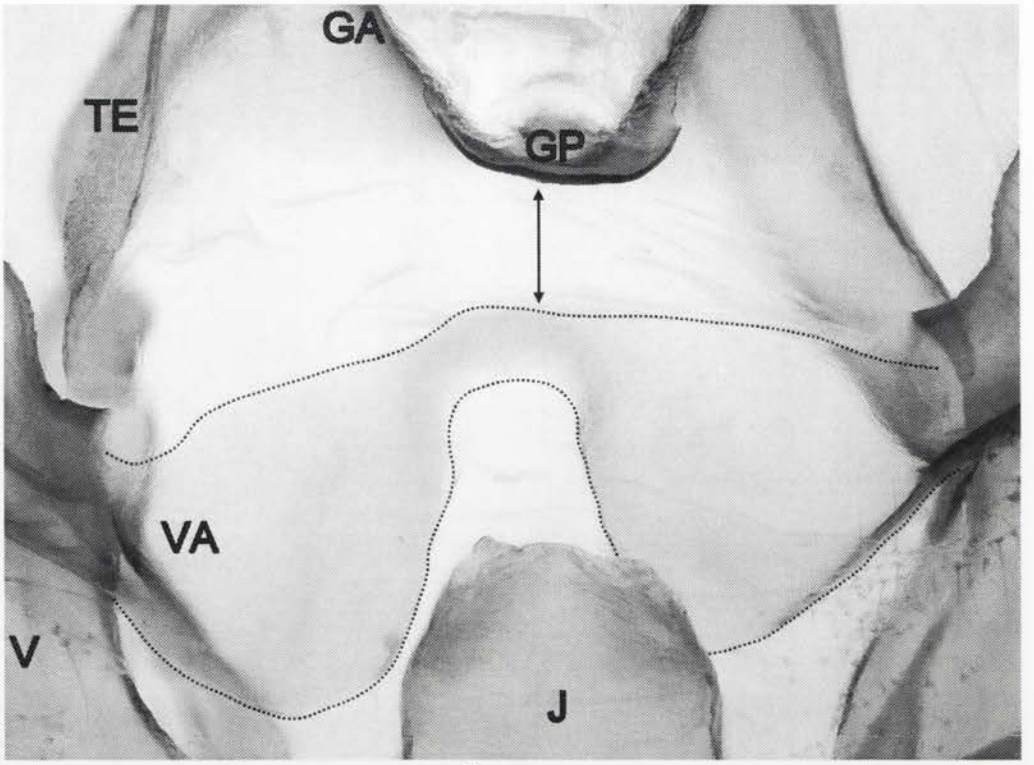

Fig. 52: *Coenotes eremophilae* (Sphingidae), ♂, posterior view – a hairless, smooth sclerotization of the mesal side of the valva (valva apodeme) extends mesad as a huge, weak sclerotization (dotted line marks extent) of the diaphragma and fuses with the valva apodeme of the opposite side; note the distance (black double-arrow) between the gnathos plate and the valva apodeme.

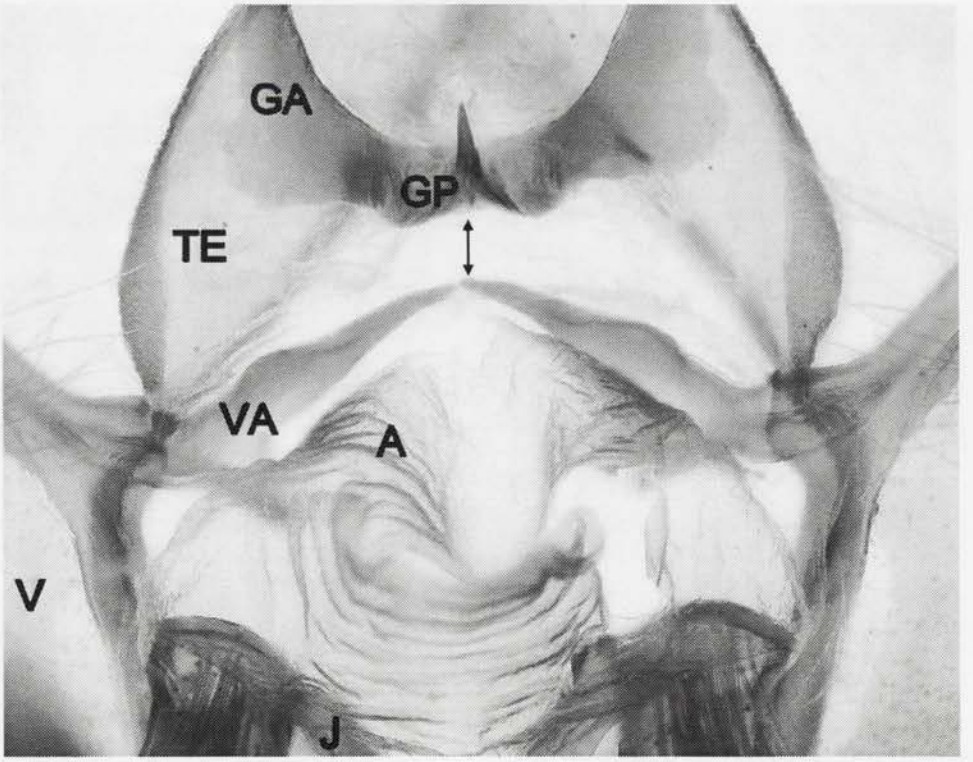

Fig. 53: *Paralaea jarrah* (Geometridae), ♂, posterior view – a hairless, smooth sclerotization of the mesal side of the valva (valva apodeme) extends mesad and almost fuses with the valva apodeme of the opposite side; note the distance (black double-arrow) between the gnathos plate and the valva apodeme.

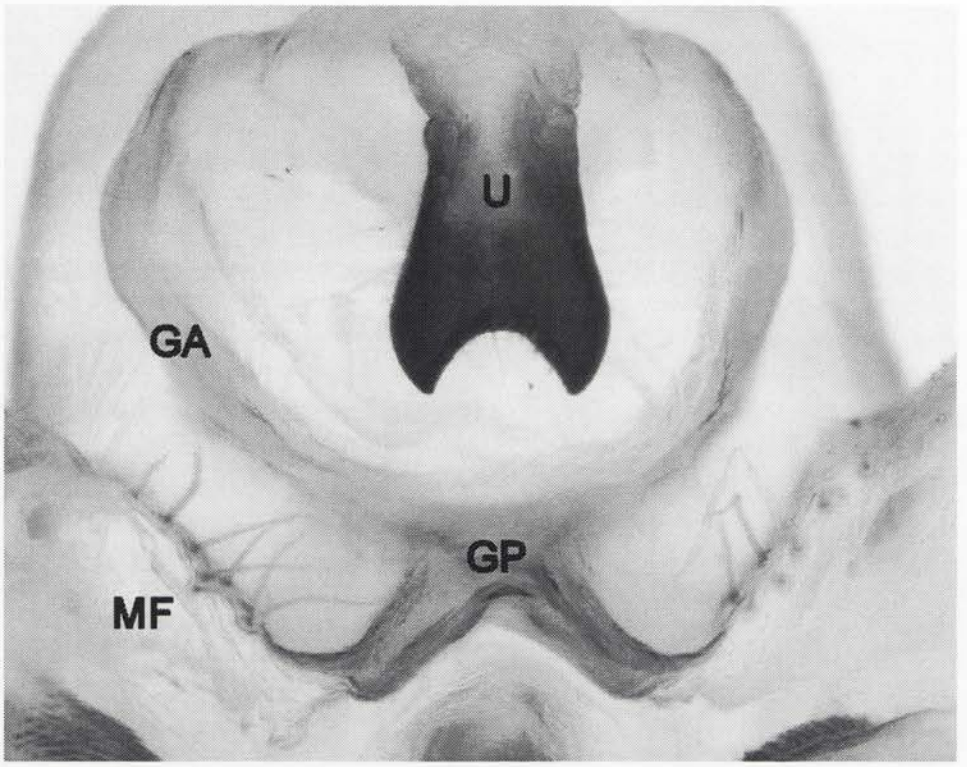

Fig. 54: *Aglia tau* (Saturniidae), ♂, posterior view – the gnathos plate and the setose, mesal fold of valva are firmly fused with each other.

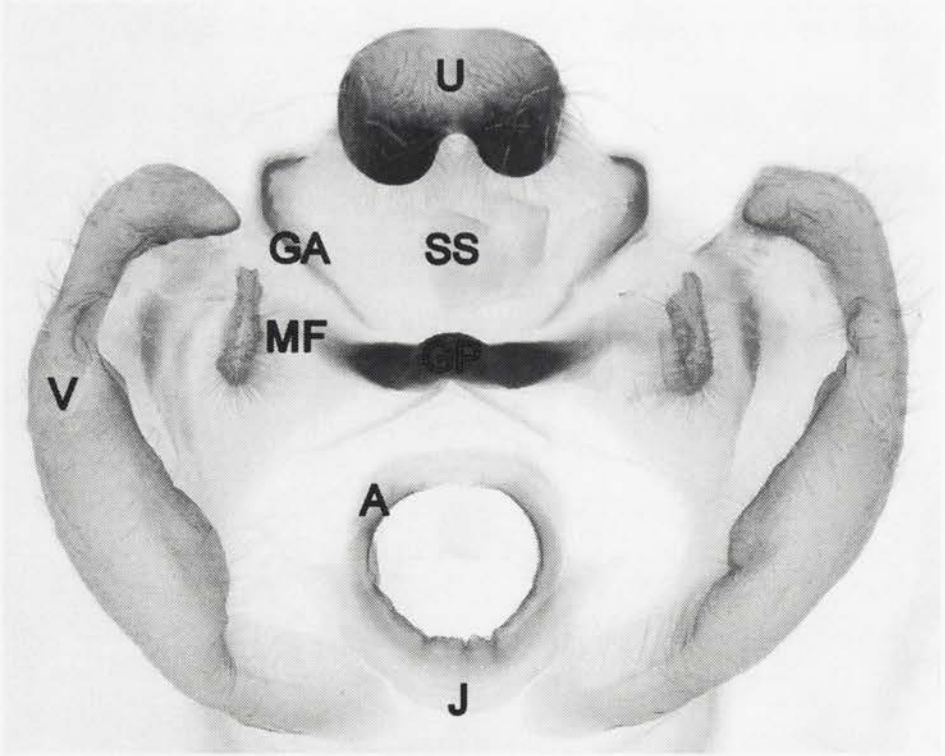

Fig. 55: *Eacles imperialis* (Saturniidae), ♂, posterior view [phallus removed] – the gnathos plate and the setose, mesal fold of valva are firmly fused with each other.

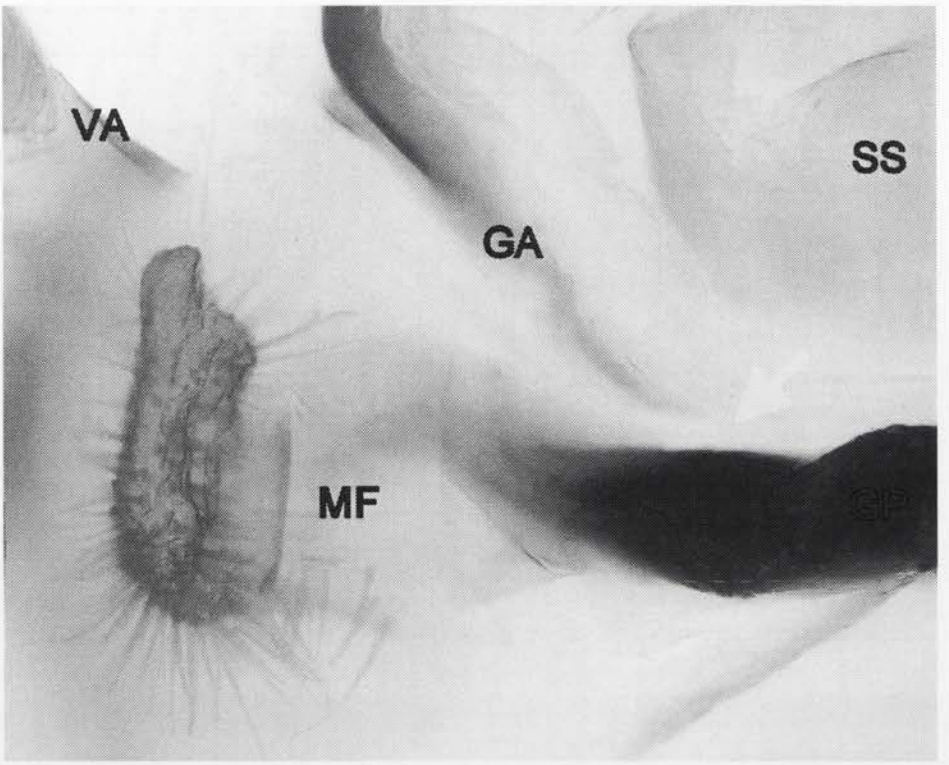

Fig. 56: *Eacles imperialis* (Saturniidae), ♂, posterior view – the gnathos plate and the setose, mesal fold of the valva (forming a strongly laterally compressed process) are firmly fused with each other; note the secondary reduction of the sclerotization between the gnathos arm and the gnathos plate (yellow arrow).

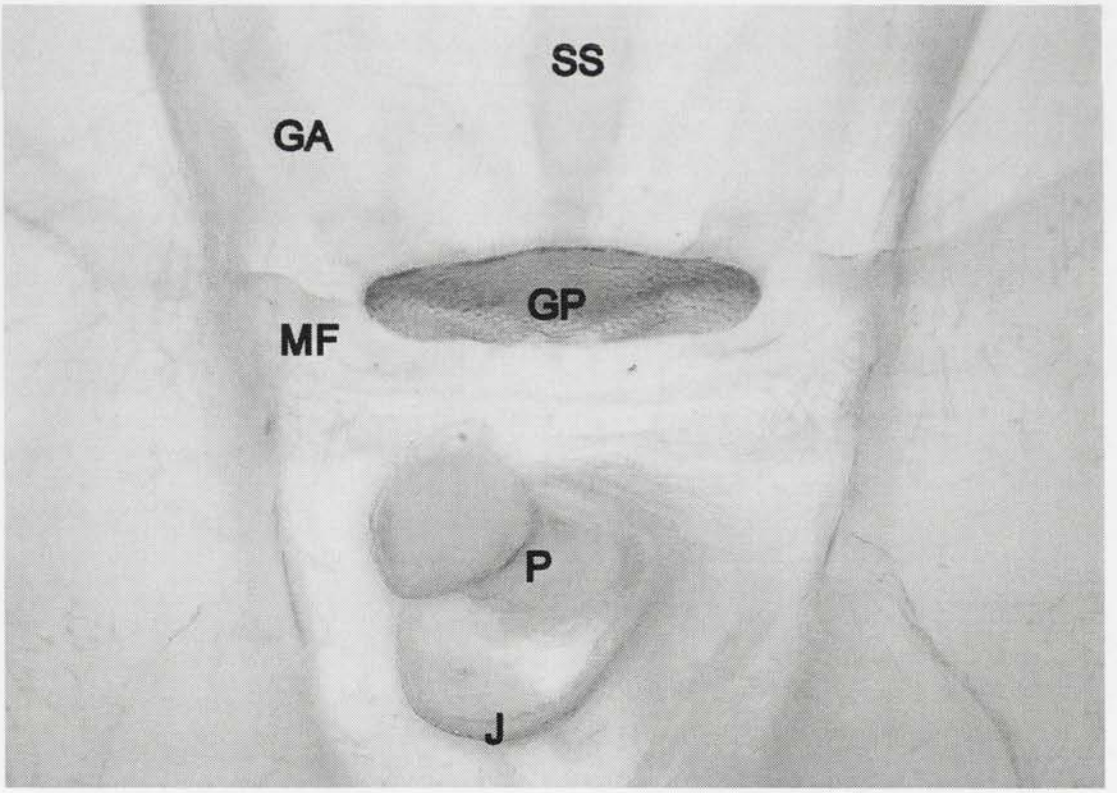

Fig. 57: *Lemonia dumi* (Lemoniidae), ♂, posterior view – the gnathos plate and the mesal fold of the valva (sclerotization reduced) are fused with each other.

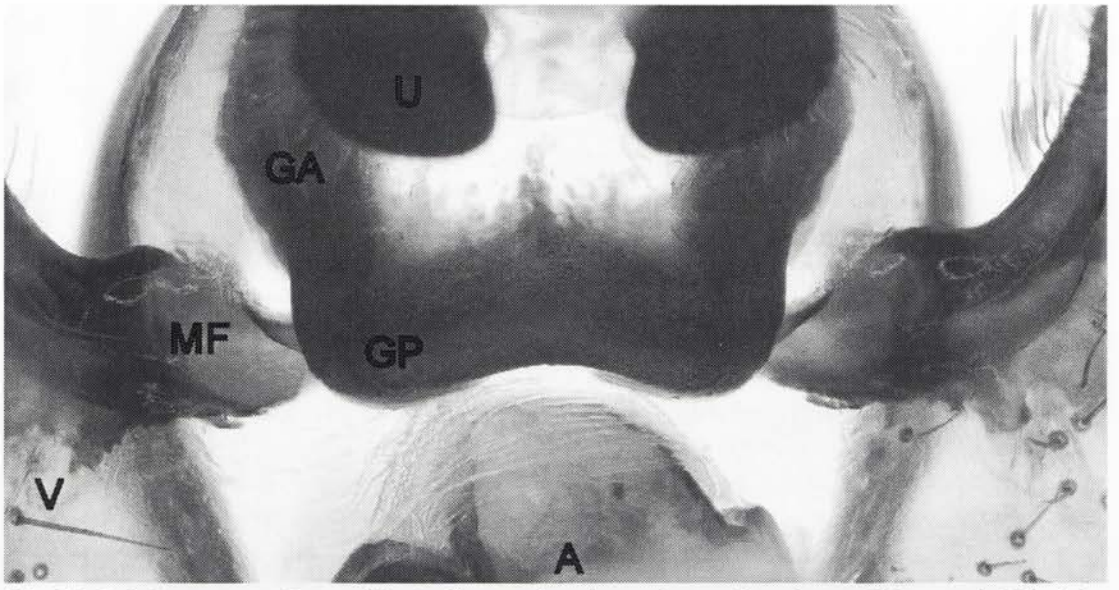

Fig. 58: *Sabalia picarina* (Lemoniidae), ♂, posterior view – the gnathos plate and the mesal fold of the valva are fused with each other.

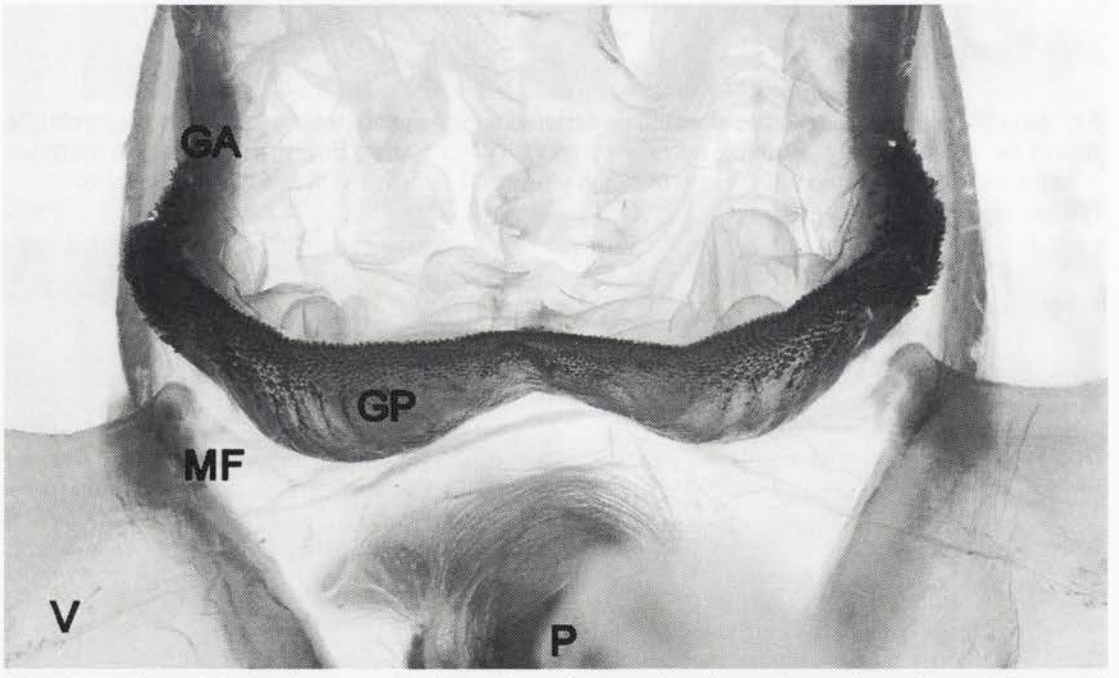

Fig. 59: *Brahmophthalma hearseyi* (Brahmaeidae), ♂, posterior view – the gnathos plate and the mesal fold of the valva (sclerotization reduced) are fused with each other.

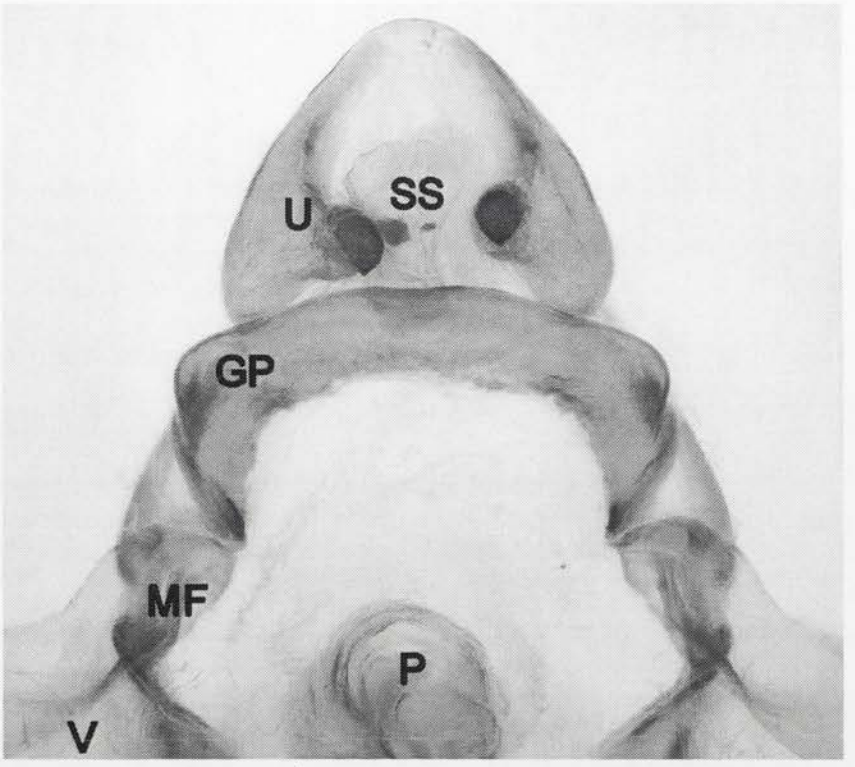

Fig. 60: *Ganisa plana* (Eupterotidae), ♂, posterior view – the gnathos plate and the mesal fold of the valva are fused with each other (separated by a minute cleft).

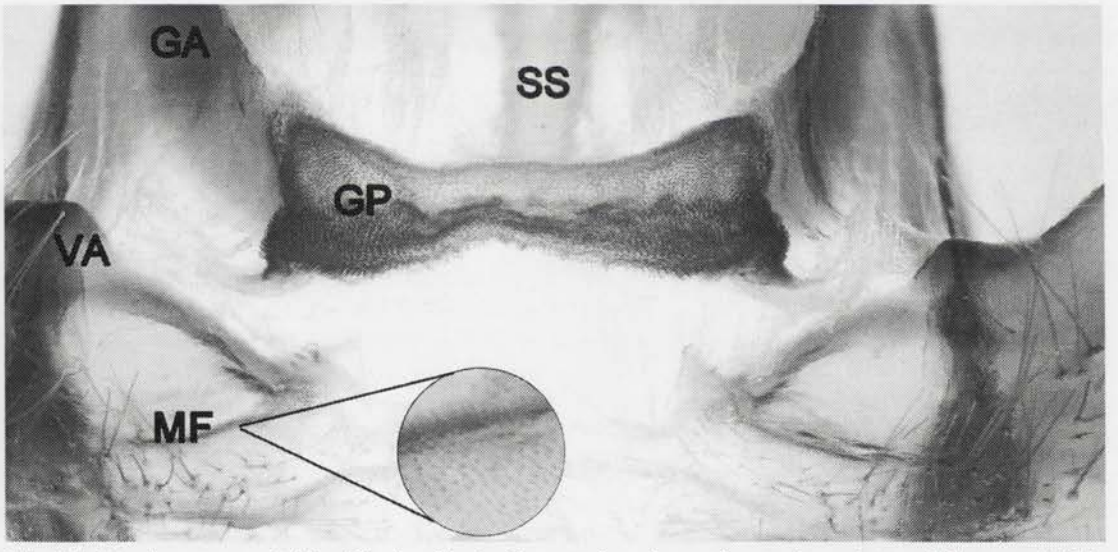

Fig. 61: *Carthaea saturnioides* (Carthaeidae), ♂, posterior view – the gnathos plate and the mesal fold of the valva are distinctly separated from each other; note the scobination of the gnathos and the finer scobination at the distal end of the mesal fold of the valva, which might indicate a secondarily reduced fusion between the gnathos and the mesal fold.

Character #H.11: Mesal protrusion and anellus merged.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; poorly supported.

Description. In Anthelidae the mesal fold that originates from the dorsal part of the mesal valva wall forms a setose, mesal protrusion (Figs 15, 17; see above, section III.1.3). In most Anthelidae, this setose protrusion is merged with the protruding anellus, which surrounds the phallus dorsally and laterally and which ends dorso-laterally of the juxta. Together they form a single, protruding structure (Figs 64, 66, 69).

Discussion. As the mesal protrusion originates from a fold of the mesal side of the valva, the mesal protrusion is a structure independent of the anellus. In Munychryiinae the physical separation of these structures as two individual protrusions is retained, but the structures are interconnected by a sclerotization. The fusion of these two protrusions into a single protrusion is unique to all other Anthelidae, which is why I interpret character state (1) as apomorphic.

Summary. This unique fusion is variously modified and frequently lost, which is why I regard my hypothesis of homology to be poorly supported.

Character #H.12: Mesal protrusion and anellus merged with juxta.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; moderately supported.

Description. The setose protrusion, formed by the merged mesal protrusion and anellus, ends laterally of the dorso-lateral ends of the juxta. In some anthelid species the lateral wall of this setose, merged protrusion goes directly over into the lateral wall of the protruding part of the juxta – the merged mesal protrusion and anellus are directly fused with the protruding part of the juxta (Figs 62, 63, 64, 65, 66) and no longer separated from each other by a simple sclerotization.

Discussion. The setose, mesal protrusion is formed by the mesal fold of the dorsal part of the mesal valva wall. In taxa of the bombycoid complex the mesal fold is never fused to the juxta except for a few anthelid species in which the mesal protrusion (a part of the mesal fold) is fused to the juxta. Therefore, I interpret character state (1) as apomorphic.

Summary. The direct merger between the mesal protrusion and the anellus with the protruding part of the juxta is unique but simple. Hence, I regard my hypothesis of homology to be moderately supported.

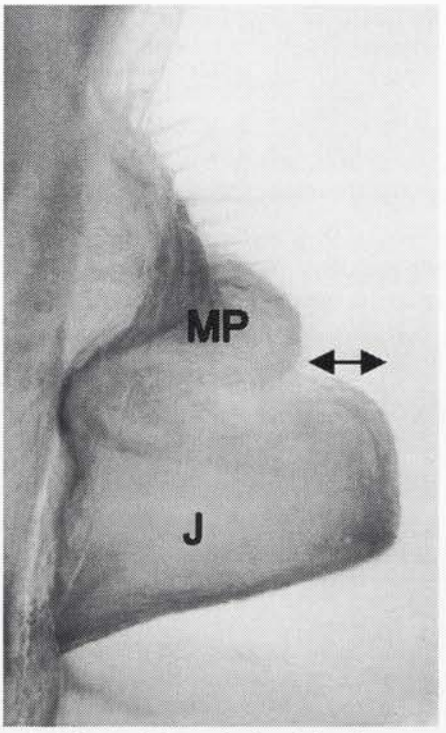

Fig. 62: *Anthela ferruginosa* (Anthelidae), ♂, lateral view [phallus removed] – the mesal protrusion/anellus and the posteriad protruding part of the juxta are directly fused with each other; note the relatively short length of the protruding juxta part (black double-arrow visualizes difference compared to mesal protrusion/anellus); note the conical shape of the mesal protrusion.

Character #H.13: Juxta forms a very long, apically narrowing and pointed trough.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; well supported.

Description. In some species that have a fused mesal protrusion/anellus and juxta (character #H.12 state (1)), the juxta protrudes a long way posteriad. This "long" juxta has the shape of a trough, narrows apically and ends in a pointed tip (Figs 63, 65).

Discussion. In other species with a protruding juxta, including those with a directly fused mesal protrusion and juxta, the juxta is much shorter and does not form a pointed trough (Fig. 62). Hence, I interpret character state (1) as apomorphic.

Summary. The juxta is of characteristic shape and unusual length, which is why I believe my hypothesis of homology to be well supported.

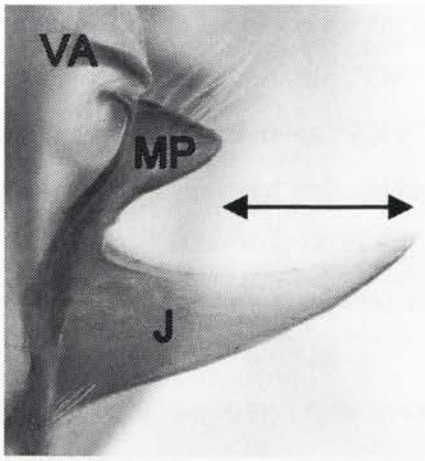

Fig. 63: *Anthela phaeodesma* (Anthelidae), ♂, lateral view [phallus removed] – the mesal protrusion/anellus and the posteriad protruding part of the juxta are directly fused with each other; the protruding juxta part is trough-shaped, apically pointed and very long (black double-arrow visualizes difference in length compared to mesal protrusion); note the conical shape of the mesal protrusion.

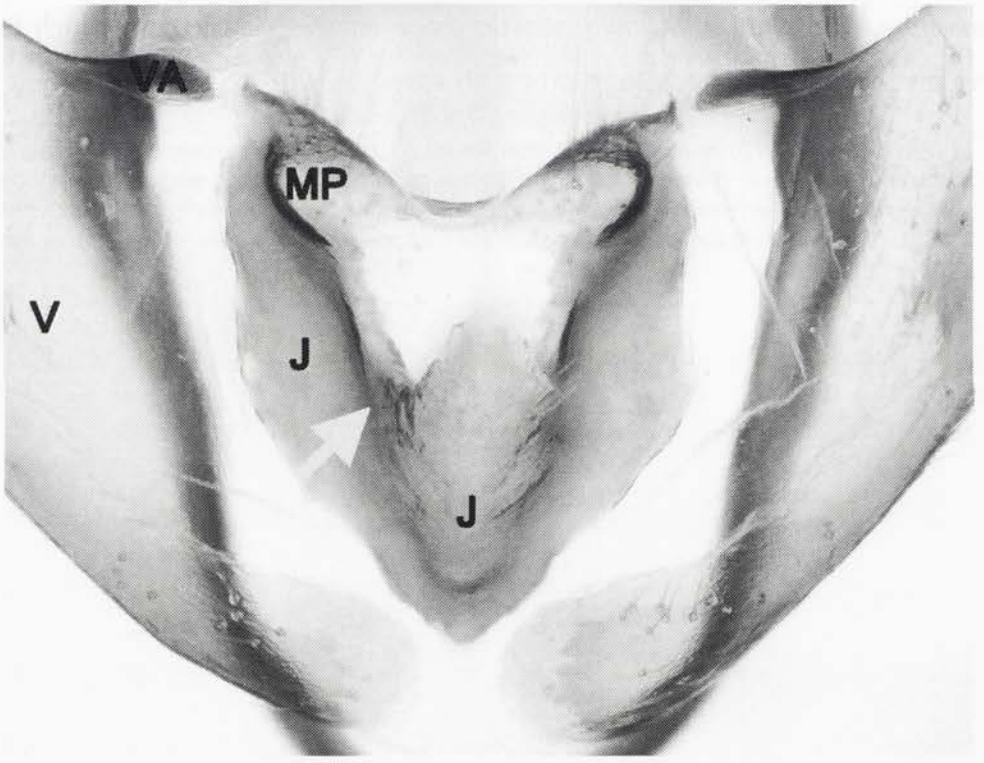

Fig. 64: *Anthela phaeodesma* (Anthelidae), ♂, posterior view [phallus removed] – the mesal protrusion/anellus and the posteriad protruding part of the juxta are directly fused with each other (yellow arrow marks continuous wall); the protruding juxta part is trough-shaped, apically pointed and very long; note the conical shape of the mesal protrusion.

Character #H.14: Mesal protrusions merged with the juxta form a pair of laterally bowed ridges.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; well supported.

Description. The rather conical mesal protrusion/anellus (Figs 62, 63, 64), which is directly fused to the posteriad protruding part of the juxta (character #H.12 state (1)), has been modified in a number of anthelid species. In these species the mesal protrusion/anellus forms an elongate ridge in dorso-ventral orientation, which near its middle is bowed laterally in a characteristic way (Figs 65, 66).

Discussion. The conical mesal protrusion occurs in species in which the mesal protrusion is separate from the protruding part of the juxta, as well as in species in which these structures are directly fused. A ridge-shaped and laterally bowed mesal protrusion occurs only in species in which the mesal protrusion and the protruding part of the juxta are fused. Therefore I interpret character state (1) as apomorphic.

Summary. The ridge-shaped and laterally bowed mesal protrusion has a unique and very characteristic shape, which has numerous details hard to describe with words. I therefore regard my hypothesis of homology to be well supported.

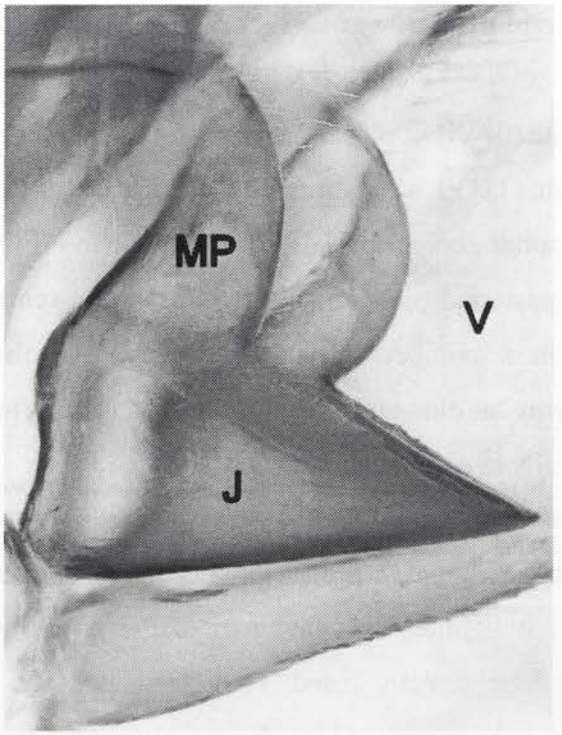

Fig. 65: *Anthela virescens* (Anthelidae), ♂, (postero-) lateral view [phallus removed] – the mesal protrusion/anellus and the posteriad protruding part of the juxta are directly fused with each other; note the elongate ridge-shape of the mesal protrusion; note the large difference in height between the mesal protrusion and the apex of the protruding part of the juxta.

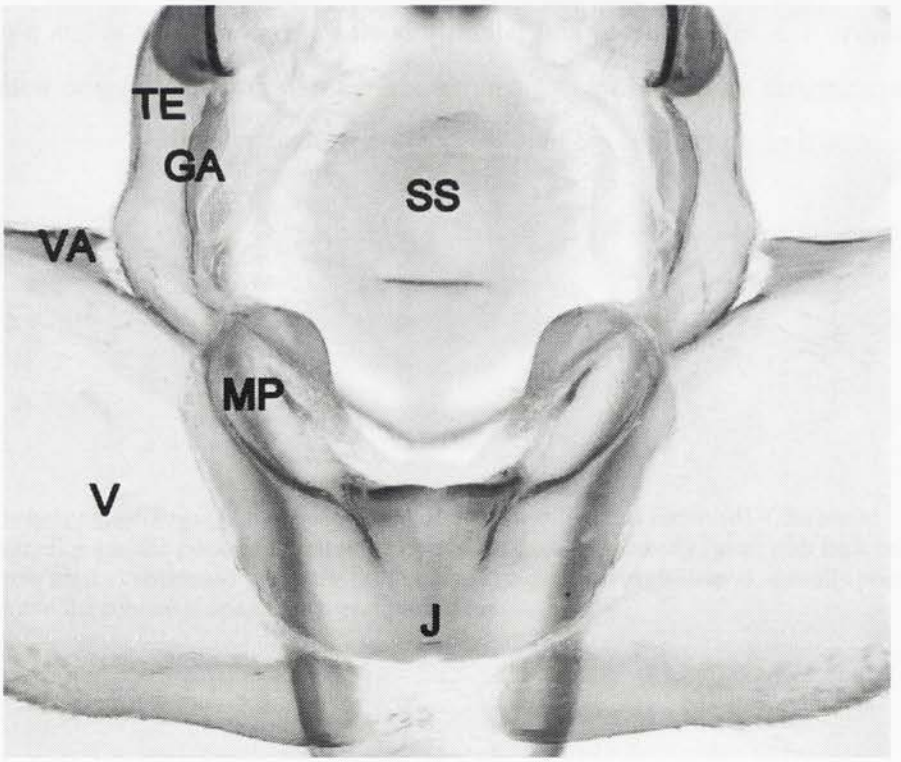

Fig. 66: *Anthela virescens* (Anthelidae), ♂, posterior view [phallus removed] – the mesal protrusion/anellus and the posteriad protruding part of the juxta are directly fused with each other; the elongate, ridge-shaped mesal protrusion is bowed laterally near its middle; note the total absence of a valva apodeme lobe and the lack of sclerotization of the mesal valva wall, resulting in an "isolated", very short valva apodeme.

Character #H.15: Mesal protrusion/anellus forms a well sclerotized, elongate, setose ridge laterally of the phallus.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; very well supported.

Description. In some anthelid species the phallus is bordered laterally by a pair of elongate, sclerotized and setose ridges, which are – with the exception of *Anthela denticulata* and its closest relatives – posteriad curved (Figs 67, 68). These setose ridges end laterally of the juxta (Fig. 67), to which they are connected by a simple, flat sclerotization (Fig. 69).

Discussion. These setose ridges are the mesal protrusions, which are entirely united with the anellus. Correlated with the ventral extension of the mesal protrusions/anellus is a dorsal shortening of the juxta (Fig. 69). This is because the lateral support for the phallus, which is normally provided by the lateral ends of the protruding juxta in other species, is provided by the elongate mesal protrusions/anellus in these taxa.

As described for character #H.14, the mesal protrusion is originally conical and located dorso-laterally of the phallus. Consequently I interpret character state (1) as apomorphic.

Summary. This modification of the mesal protrusion/anellus has numerous characteristic details as described above. Based on those details I regard my hypothesis of homology to be very well supported.

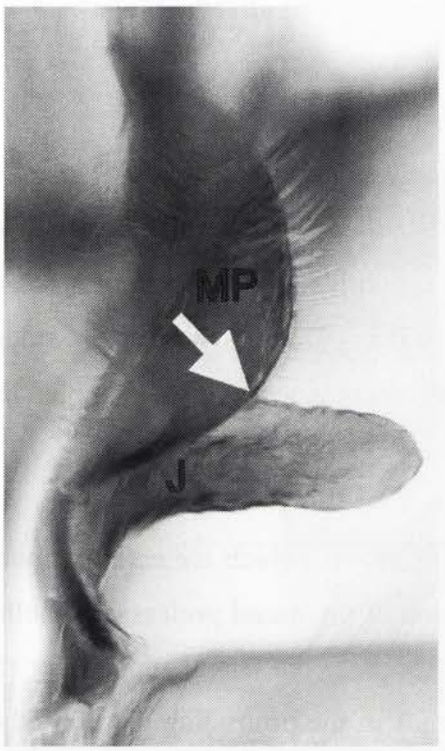

Fig. 67: *Anthela acuta* (Anthelidae), ♂, lateral view [phallus removed] – setose, elongate mesal protrusion/anellus and protruding juxta; note the distinct lateral overlap of the two structures (yellow arrow).

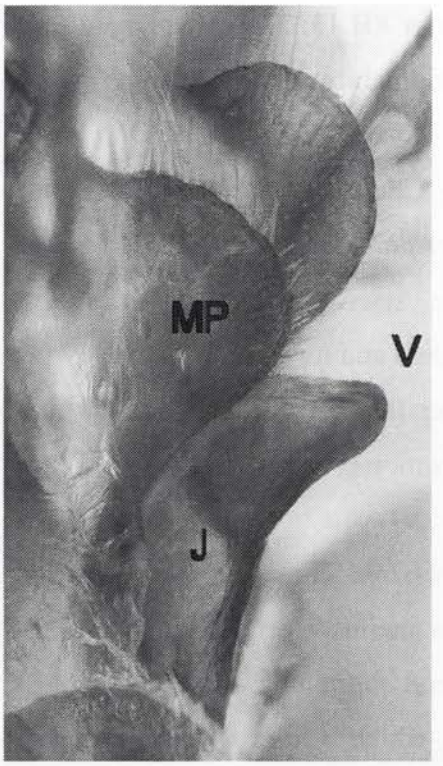

Fig. 68: *Anthela astata* (Anthelidae), ♂, lateral view [phallus removed] – setose, elongate mesal protrusion/anellus and protruding juxta; note the minor lateral overlap of the two structures.

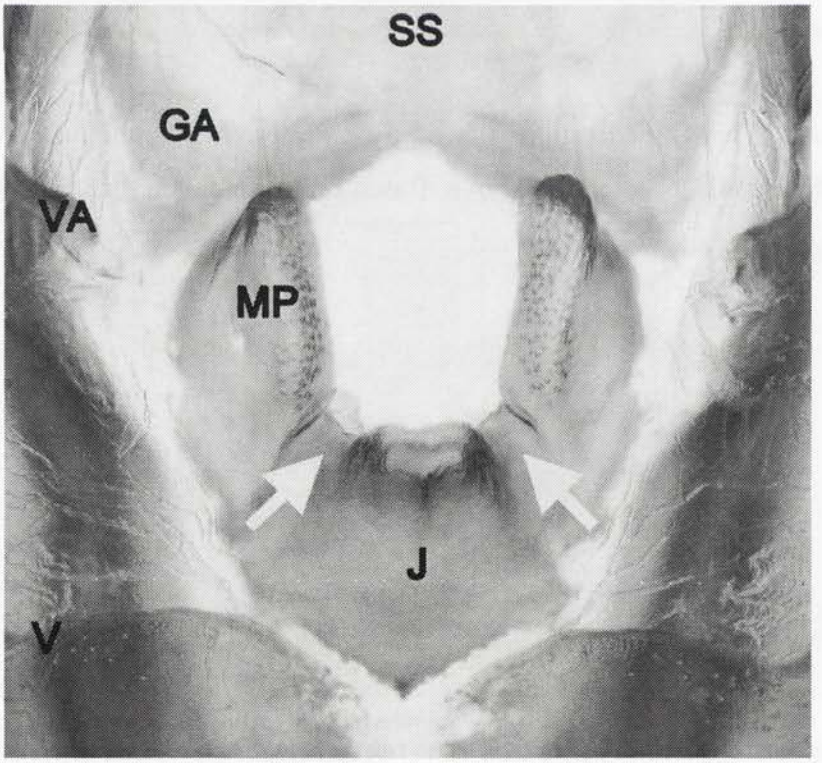

Fig. 69: *Anthela astata* (Anthelidae), ♂, posterior view [phallus removed] – setose, elongate mesal protrusion/anellus and protruding juxta; note the minor lateral overlap and the distinct gap bridged by a flat sclerotization (yellow arrows) between the two structures; note the remnants of the gnathos arms being fused ventrally to the mesal protrusions as well as mesally to the subscaphium.

Character #H.16: Mesal protrusions, anellus and gnathos form dorsal suspension of the phallus.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; very well supported.

Description. In the endemic New Guinean genera *Pseudodreata* and *Corticomis* (both Anthelidae) the setose mesal protrusions and the hairless gnathos plate are entirely fused (Fig. 71). They are ventrally fused onto the anellus which protrudes posteriad a long way (Fig. 70). In this fused structure the mesal protrusions extend further posteriad than in any other anthelid species, and their setae are minute. The long, thin phallus appears to be suspended dorsally (from the gnathos plate) in this sheath, while the "superfluous" juxta is reduced to a flat, U-shaped sclerotization in the diaphragma (Fig. 70).

Discussion. This unique and rather complex fusion of structures is a modification of the conical mesal protrusions, the latero-basally fused gnathos plate and the anellus. Therefore I interpret character state (1) as apomorphic.

Summary. This modification involves several structures and has numerous characteristic details as described above. Based on these details I believe my hypothesis of homology to be very well supported.

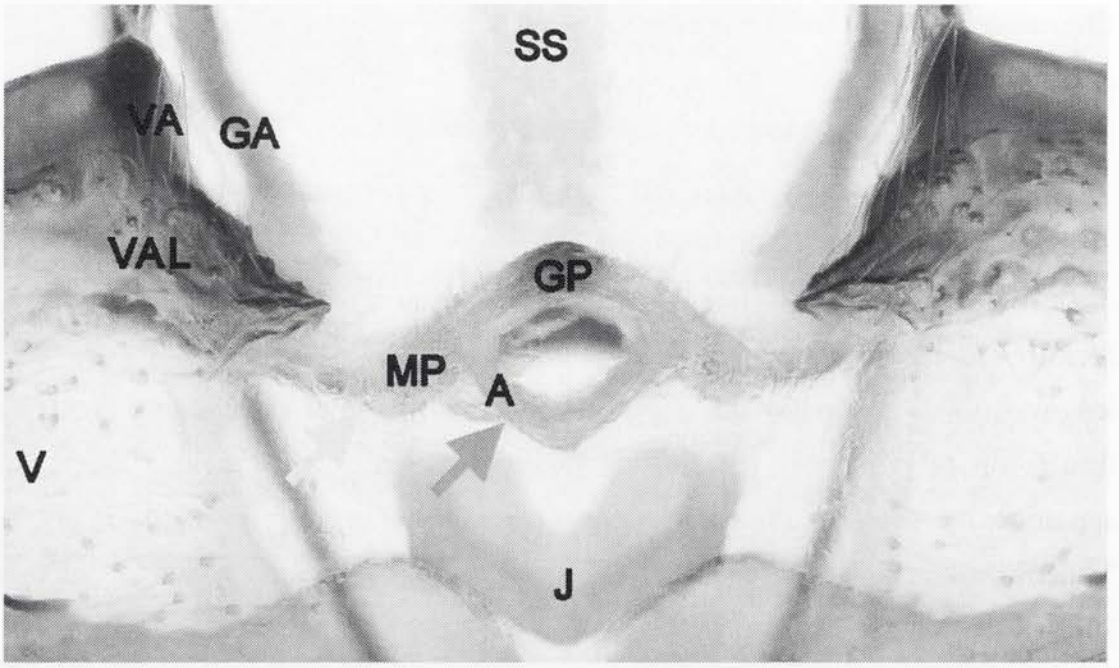

Fig. 70: *Pseudodreata* sp. (Anthelidae), ♂, posterior view [phallus removed] – the mesal protrusion with minute setae (yellow arrow) and the dorsal side of the hairless gnathos plate form the dorsal wall of a sheath, which is fused onto the anellus (green arrow); note the gap between this sheath and the simple, flat juxta.

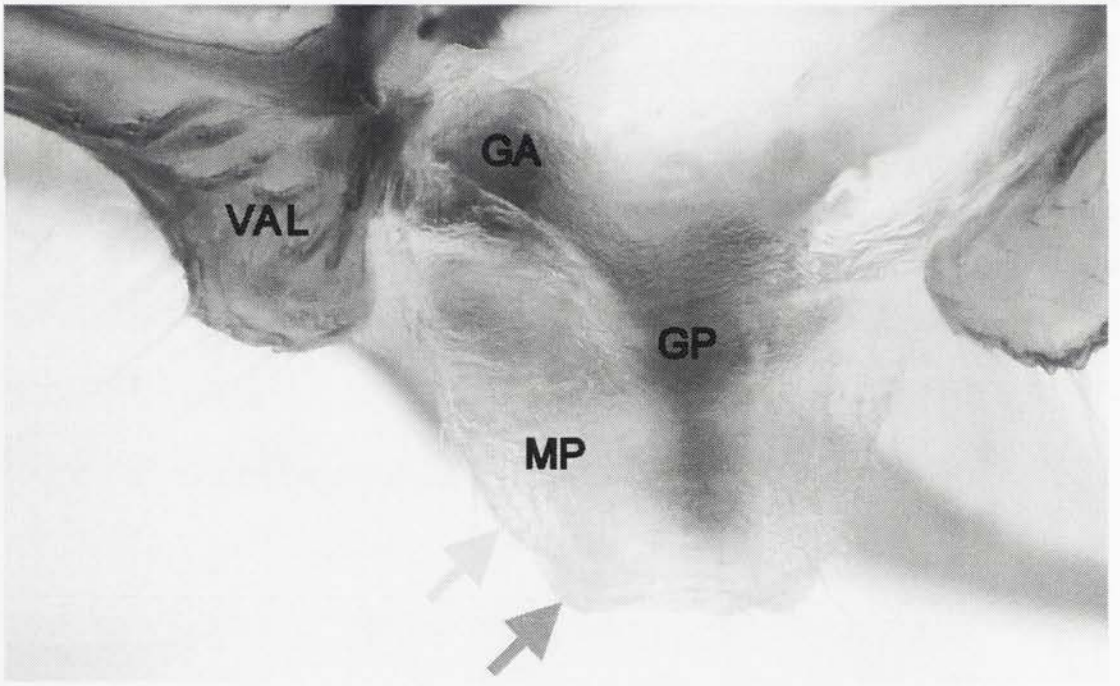

Fig. 71: *Pseudodreata* sp. (Anthelidae), ♂, dorsal view [phallus removed] – the mesal protrusion with minute setae (yellow arrow) and the dorsal side of the hairless gnathos plate form the dorsal wall of a sheath, which is fused onto the anellus (green arrow); this fused complex of structures suspends the phallus dorsally.

Character #H.17: Valva apodeme long and curved ventrad, giving rise to a second protrusion ("valva apodeme lobe").

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; well supported.

Description. In most anthelid species a second setose protrusion – in addition to the setose mesal protrusion – is formed by the dorsal part of the mesal side of the valva (see above, section III.1.3), ventro-posteriorly to the valva apodeme.

Discussion. This protrusion seems to have been caused by an extension of the valva apodeme, which curves ventrad and "pushes up" a membranous fold near its distal end (Fig. 72). This protruding fold appears to be secondarily (partly) sclerotized in many species. Due to the location of the fold ventro-posteriorly to the valva apodeme and its subsequent modification into a prominent, sclerotized lobe in many species, I refer to this protrusion as the "valva apodeme lobe".

The valva apodeme lobe is variously modified and has characteristic shapes and locations in many species. I use these characteristic modifications as characters but generally have too few indications to hypothesize on all the transformations of these shapes. As with the fusion of the uncus lobes (see above, section III.1.2: 71) I therefore treat these modifications conservatively as if they originated independently.

The valva apodeme lobe seems to be a modification of the mesal wall of the valva, caused by an extension and the ventral curving of the valva apodeme. This is unique to some anthelid taxa, which is why I interpret character state (1) as apomorphic.

A similarly ventrad curved long valva apodeme is present in *Carthaea saturnioides* (Carthaeidae). I assume the modification in *C. saturnioides* to be a parallelism as the curving of the valva apodeme enables a direct antagonistic function of muscle *m2* to muscle *m4* (see above, section III.1.1: 65); the former is absent and the latter is in a different position in Anthelidae.

Summary. While unique, the valva apodeme lobe has been modified frequently, which makes homologization of the various shapes rather difficult, other than by Remane's criterion of the specific location (1952), as well as by the length and curving of the valva apodeme. For some shapes transformation series can be hypothesized, for others not. Based on these indications, I regard my hypothesis of homology to be well

supported.

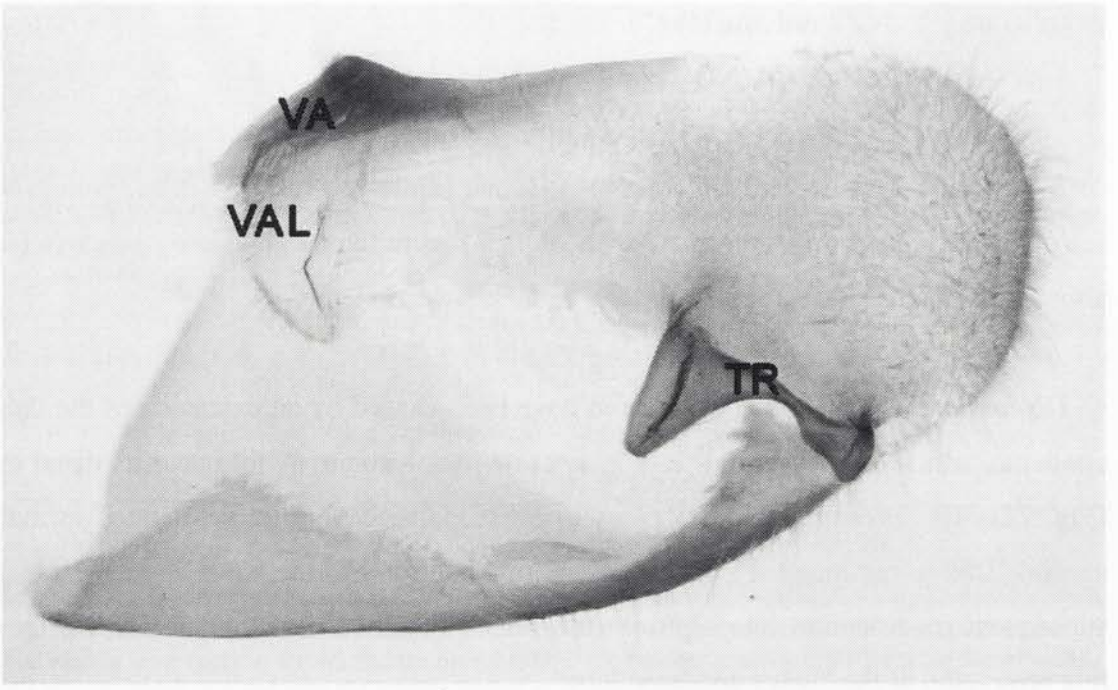

Fig. 72: Anthelinae n. sp. (Anthelidae), ♂, mesal view – mesal side of valva with protruding fold, caused by the extension and ventral curving of the valva apodeme; note the weak sclerotization; note the ventro-distal, sclerotized, transverse ridge, which forms a large and a small protrusion.

Character #H.18: Valva apodeme lobe forms a posterior, "upturned" process.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; moderately supported.

Description. In some anthelid species the valva apodeme lobe (Fig. 72) curves posteriad, forming an "upturned" process (Figs 73, 74).

Discussion. This posterior process is modified in most species and a transformation series of modifications can be constructed (characters #H.19, #H.20). As with other structures arranged in a transformation series, I code them as additive binary characters.

The posterior process is a unique modification of the simple, membranous valva apodeme lobe. Therefore I interpret character state (1) as apomorphic.

Summary. The posterior process on the membranous valva apodeme lobe is characteristic. However, subsequent reduction obscures some of its characteristics in many species, which is why I regard my hypothesis of homology to be moderately supported.

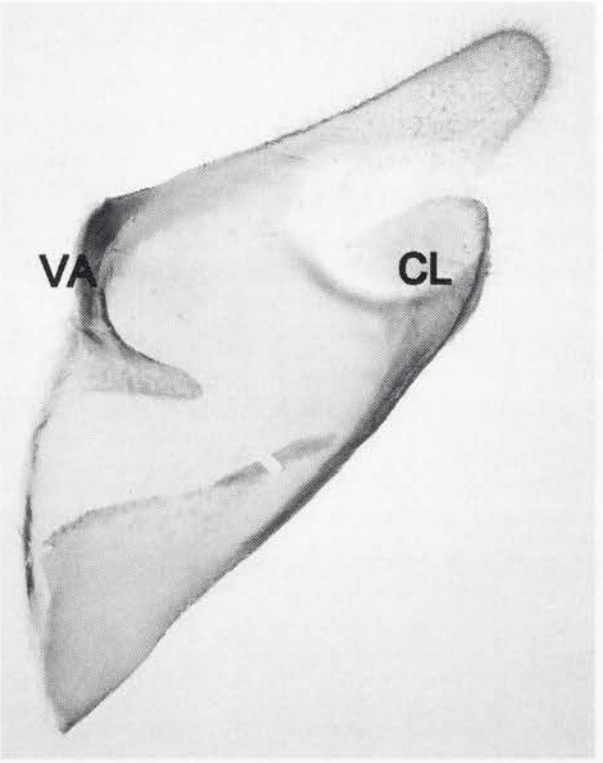

Fig. 73: *Anthela basigera* (Anthelidae), ♂, mesal view – mesal side of valva with the valva apodeme lobe forming a posterior process (yellow arrow); note the broad, almost rectangular, plate-shaped clasper (protruding postero-mesad from the plane of the valva).

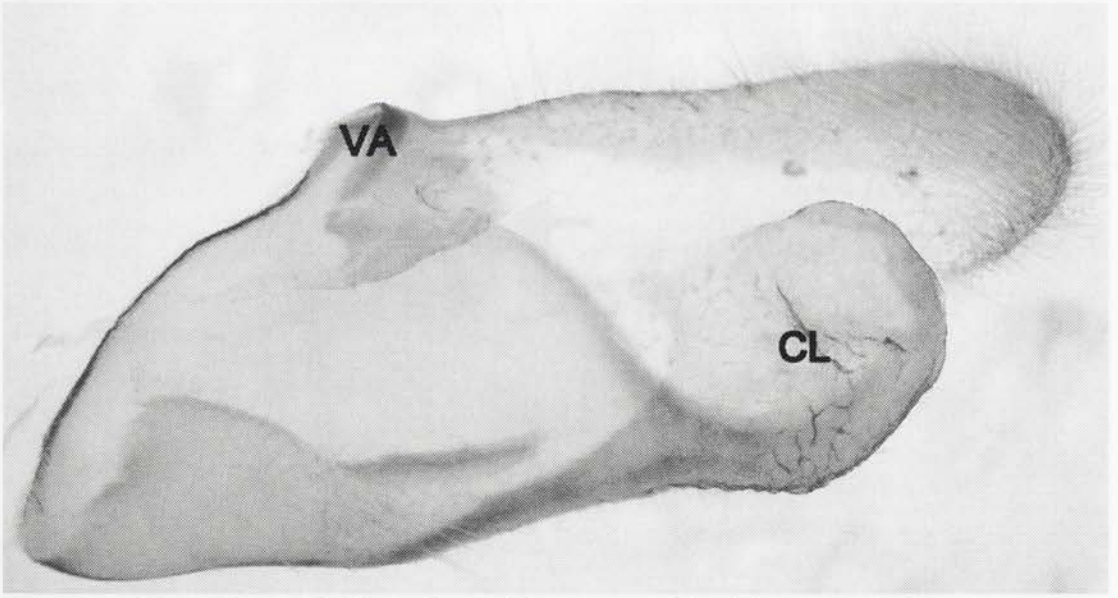

Fig. 74: *Anthela repleta* (Anthelidae), ♂, mesal view – mesal side of the valva with the valva apodeme lobe forming a posterior process (yellow arrow); note the broad, almost rectangular, plate-shaped clasper.

Character #H.19: Valva apodeme and valva apodeme lobe with posterior process shortened to a triangular process, which is orientated parallel to the valva apodeme.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; moderately supported.

Description. In a number of anthelid species a triangular, rather flat process is located parallel to a short valva apodeme (Fig. 75).

Discussion. In these anthelid species the valva apodeme and the valva apodeme lobe with a posterior process (character #H.18 state (1)) have been shortened basally. This basal reduction causes a dorsal shift of the process on the valva and results in the structure described above. Further simple reductions in size, including the total loss of the process and the valva apodeme, are common but do not affect the position of the process relative to the valva (Fig. 76). These reductions are too non-specific to allow sound hypotheses of homology, which is why I did not use these subsequent reductions as separate characters.

I assume character state (1) to be a subsequent modification of character #H.18 state (1), hence character state (1) to be apomorphic.

Summary. The triangular, rather flat process, which is located parallel to the shortened valva apodeme, is a characteristic structure despite being the result of a reduction. Its presence is obscured by subsequent reductions, which is why I regard my hypothesis of homology to be moderately supported.

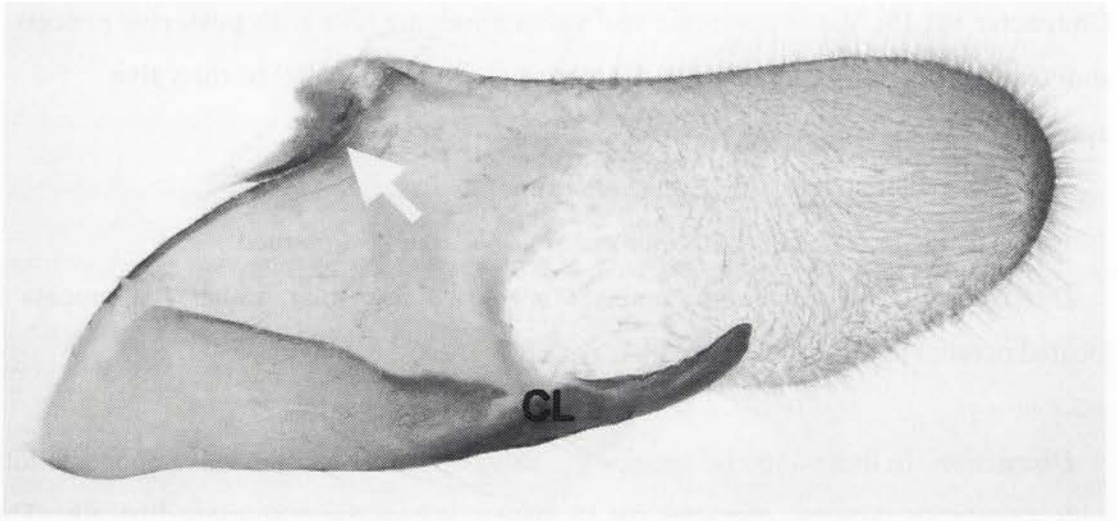

Fig. 75: *Anthela haemoptera* (Anthelidae), ♂, mesal view – mesal side of valva with the valva apodeme reduced to a flat process, which protrudes mesad and is parallel to the valva apodeme (in this view only visible as a line of darker sclerotization marked by the yellow arrow); note the simple, narrow clasper.

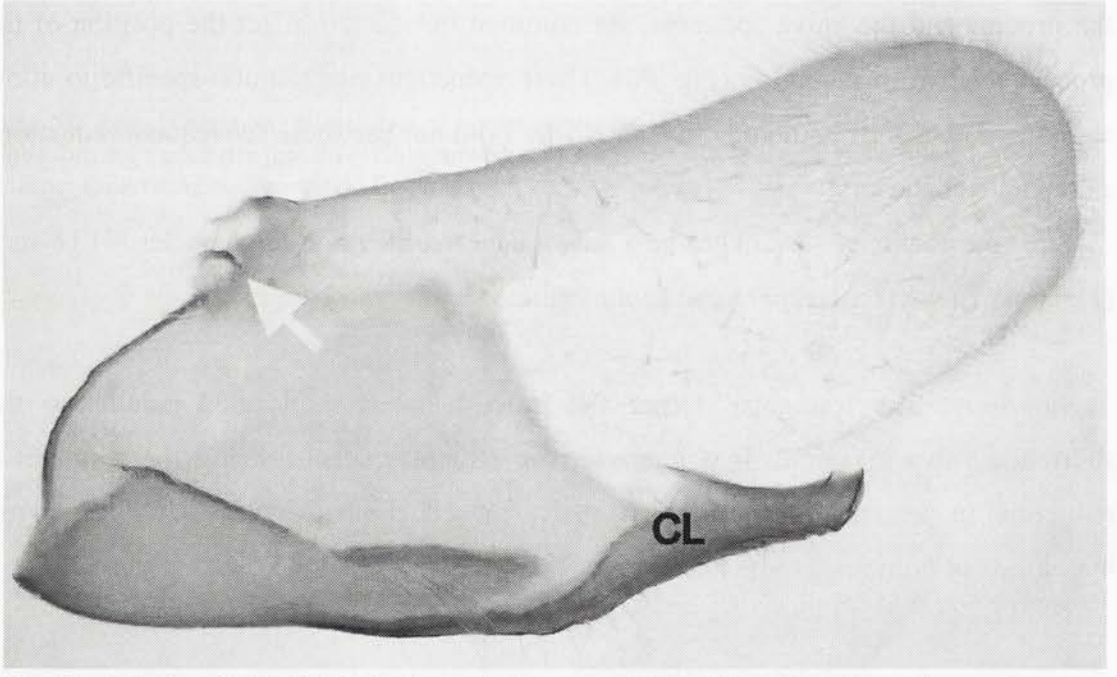

Fig. 76: *Anthela varia* (Anthelidae), ♂, mesal view – mesal side of the valva with a valva apodeme lobe that is reduced to a small process (yellow arrow); note the simple, narrow clasper with a shallow, triangular, dorsal protrusion near its apex.

Character #H.20: Triangular process, which is parallel to the valva apodeme, is heavily sclerotized, thereby forming a flat, serrate and pointed tooth.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; well supported.

Description. Currently included in the large species complex around *Anthela acuta* and *A. astata* is a small group of species, in which the process parallel to the valva apodeme forms a large, heavily sclerotized, flat, serrate and pointed tooth (Figs 77, 78).

Discussion. I assume character state (1) to be a subsequent modification of character #H.19 state (1), hence character state (1) to be apomorphic.

Summary. The sclerotized tooth is very distinct, and specific in location and orientation. Therefore I regard my hypothesis of homology to be well supported.

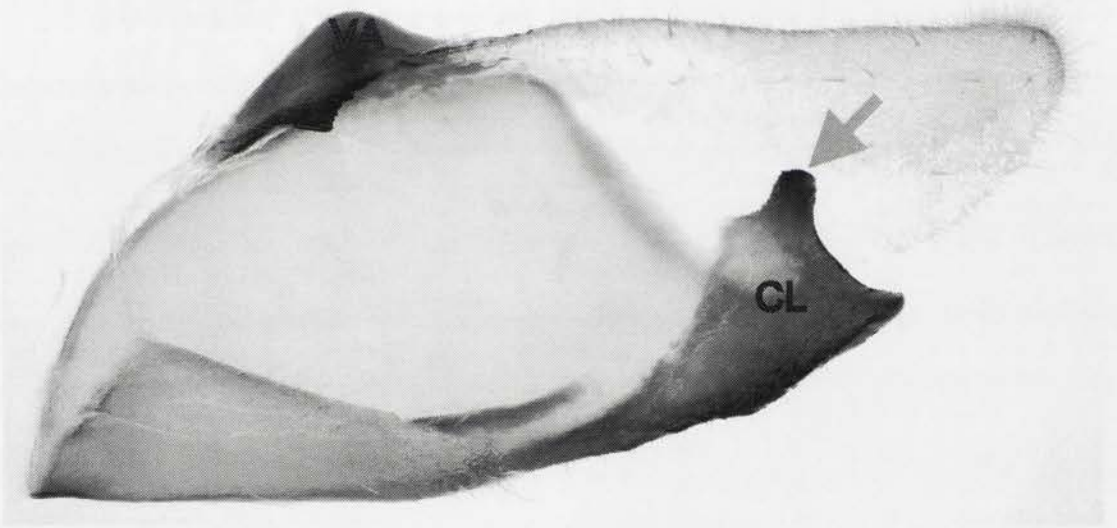

Fig. 77: *Anthela "acuta"* (Anthelidae), ♂, mesal view – valva apodeme with heavily sclerotized, flat, serrate tooth (yellow arrow); note the process (green arrow) formed by the reduction of the plate-shaped clasper.

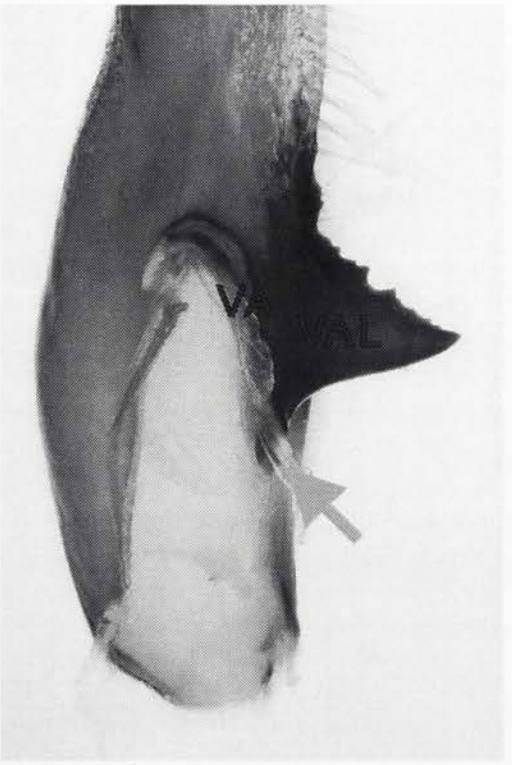

Fig. 78: *Anthela "acuta"* (Anthelidae), ♂, dorso-anterior view – valva apodeme (red arrow marks end) with heavily sclerotized, flat, serrate tooth (modified posterior process of valva apodeme lobe).

Character #H.21: Valva apodeme lobe lost.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; poorly supported.

Description. In a small number of anthelid species the membranous to weakly sclerotized mesal side of the valva does not form a fold or protrusion (Figs 79, 80), despite the distinct extension and very strong ventrad curving of the valva apodeme. In one species only, *Anthela ostra*, a very shallow protrusion is present. In these species the valva apodeme seems to be more "adpressed" (more strongly curved ventrad) to the mesal side of the valva than in other species, and the distal end of the valva apodeme is slightly bent or extended anteriad (Fig. 80).

Discussion. The ventrad curving of a long valva apodeme typically causes a fold in the membrane of the mesal side of the valva. As a long, strongly ventrad curved valva apodeme is present in these taxa, I interpret the lack of a membranous fold as a subsequent reduction, hence character state (1) as apomorphic.

Summary. The simple absence of any structure by itself has no indications of homology, and the additional modifications of the valva apodeme are minor. Therefore I regard my hypothesis of homology to be poorly supported.

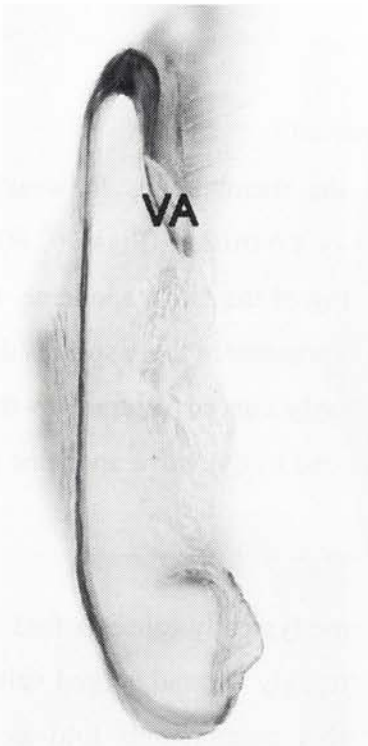

Fig. 79: *Anthela* sp. near *A. ocellata* group (Anthelidae), ♂, anterior view – valva with valva apodeme; note the absence of a valva apodeme lobe, despite the length and strong ventrad curving of the valva apodeme.

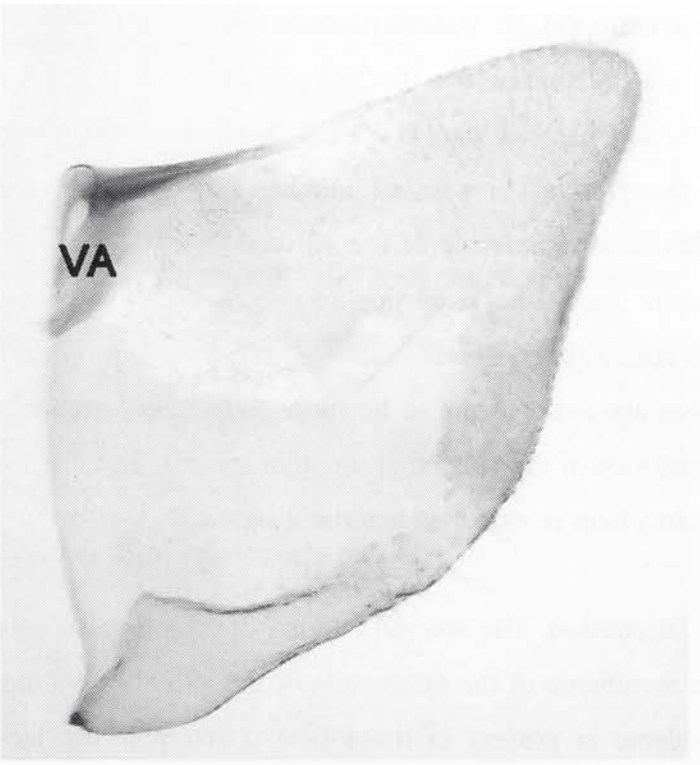

Fig. 80: *Anthela* sp. near *A. ocellata* group (Anthelidae), ♂, mesal view – valva with extended and ventrad curved valva apodeme; note the absence of a valva apodeme lobe and the minor anterior extension/bending at the distal end of the valva apodeme.

Character #H.22: Dorsally sclerotized valva apodeme lobe protrudes mesad at roughly 45° angle.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; moderately supported.

Description. In many anthelid species the fold caused by the ventrad curved valva apodeme extends on the mesal side of the valva from near the distal end of the valva apodeme far posteriad. In these species the dorsal side of the fold is typically strongly sclerotized and synscleritous with the dorsal edge of the valva. The baso-ventral end of this fold – and with it to a lesser degree the distal part of the valva apodeme – protrudes dorso-mesad in many species. This results in a characteristic shape of the valva apodeme lobe: its ventral side is at about a right angle to the plane of the valva, while its dorsal side is oblique to the plane of the valva (at roughly a 45° angle) and ends distinctly ventrally of the dorsal edge of the valva (the dorsal side appears angled near its dorsal end) (Figs 81, 82, 83, 84). In posterior view, the distal part of the valva apodeme is hidden beneath the valva apodeme lobe.

Discussion. The degree of sclerotization of the ventral side of the valva apodeme lobe ranges from membranous to fully sclerotized, which is a good diagnostic character but not suitable for phylogenetic analyses. In some taxa with a fully sclerotized ventral wall the valva apodeme lobe appears to be "pushed inwards" into the valva. While this is likely to be an apomorphy, the degree to which the valva apodeme lobe is "pushed inwards" is very variable between species, and hence I do not use this tendency as a phylogenetic character.

I hypothesize the dorsally sclerotized and dorso-mesad moved valva apodeme lobe to be a modification of the simple, membranous fold described as character #H.17 state (1). Therefore I interpret character state (1) as apomorphic.

A subsequent modification of this shape of the valva apodeme lobe is described as character #H.23.

Summary. The mesad protruding valva apodeme lobe is characterized by the two different angles of its dorsal and ventral walls, the "off-set" of the protrusion from the dorsal edge and the location of the distal part of the valva apodeme "beneath" the valva apodeme lobe. Differences in size, extent of sclerotization and minor variations in the

angle of dorsal and ventral walls of the valva apodeme lobe can obscure these characteristics in some species. Therefore I believe my hypothesis of homology to be moderately supported.

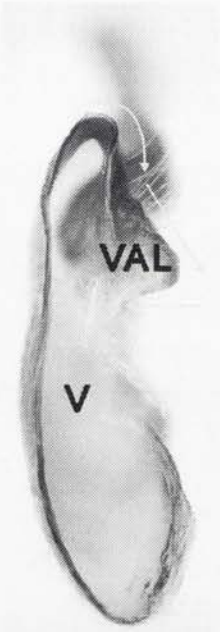

Fig. 81: *Anthela clementi* (Anthelidae), ♂, anterior view – valva with valva apodeme lobe protruding mesad at roughly 45° angle; yellow arrows symbolize angles of edges.

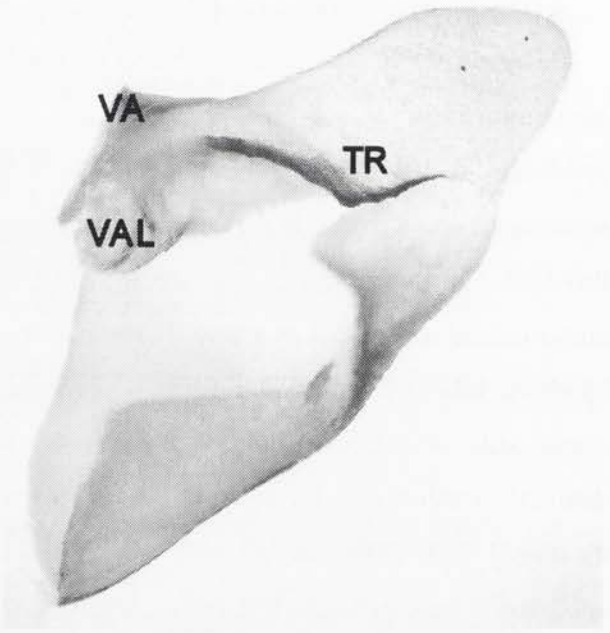

Fig. 82: *Anthela clementi* (Anthelidae), ♂, mesal view – valva with valva apodeme lobe protruding mesad at roughly 45° angle.

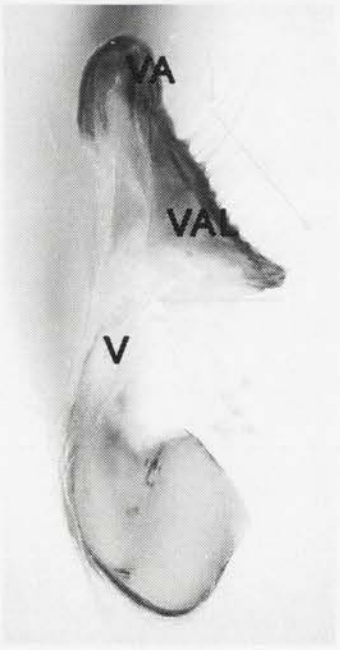

Fig. 83: *Pseudodreata* sp. (Anthelidae), ♂, anterior view – valva with valva apodeme lobe protruding mesad at roughly 45° angle; yellow arrows symbolize angles of edges; note the very short ventral sclerotization of the valva apodeme lobe.

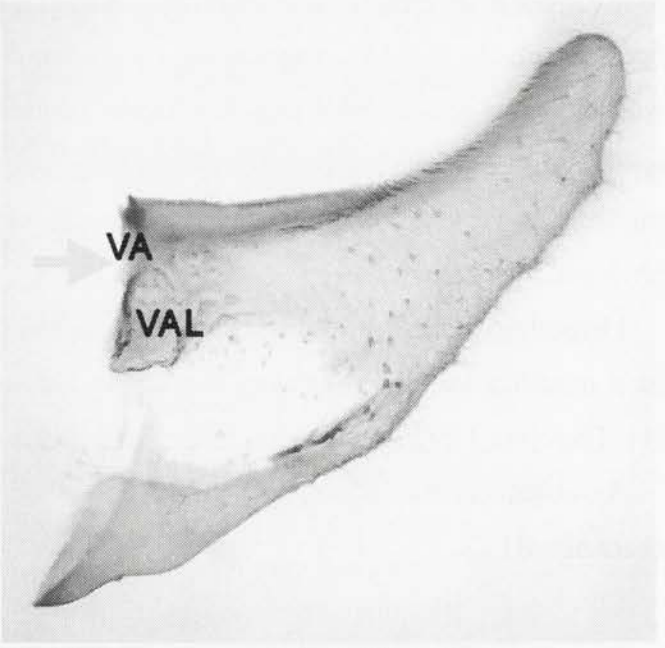

Fig. 84: *Pseudodreata* sp. (Anthelidae), ♂, mesal view – valva with valva apodeme lobe protruding mesad at roughly 45° angle (yellow arrow marks start of protrusion, distinctly ventrally of dorsal valva edge).

Character #H.23: Very long valva apodeme extends anteriad, and with it the valva apodeme lobe.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; moderately supported.

Description. In some anthelid species the long valva apodeme does not extend ventrad in the plane of the diaphragma, but rather (ventro-) anteriad. The valva apodeme is very long in these species, ending at or anteriorly to the anterior edge of the tegumen (Fig. 85). At its distal end the valva apodeme lobe forms a distinct postero-mesal protrusion (Fig. 86).

Discussion. The origin of this structure from character #H.22 state (1) is still apparent in some species, e.g., *Anthela nicothoe* and *A. ariprepes*. In many species the valva apodeme lobe is restricted to the apex of the valva apodeme (Fig. 87), but intermediate forms with more elongate valva apodeme lobes occur in a few species.

I assume this structure to be a modification of character #H.22 state (1), which is why I interpret character state (1) as apomorphic.

Summary. The anterior extent, the length of the valva apodeme and the location of the valva apodeme lobe at the distal end of the valva apodeme are the most constant characteristics. Differences in the actual shape and size of the valva apodeme and the angle between the valva apodeme and the plane of the valva can be confusing. Therefore I believe my hypothesis of homology to be moderately supported.

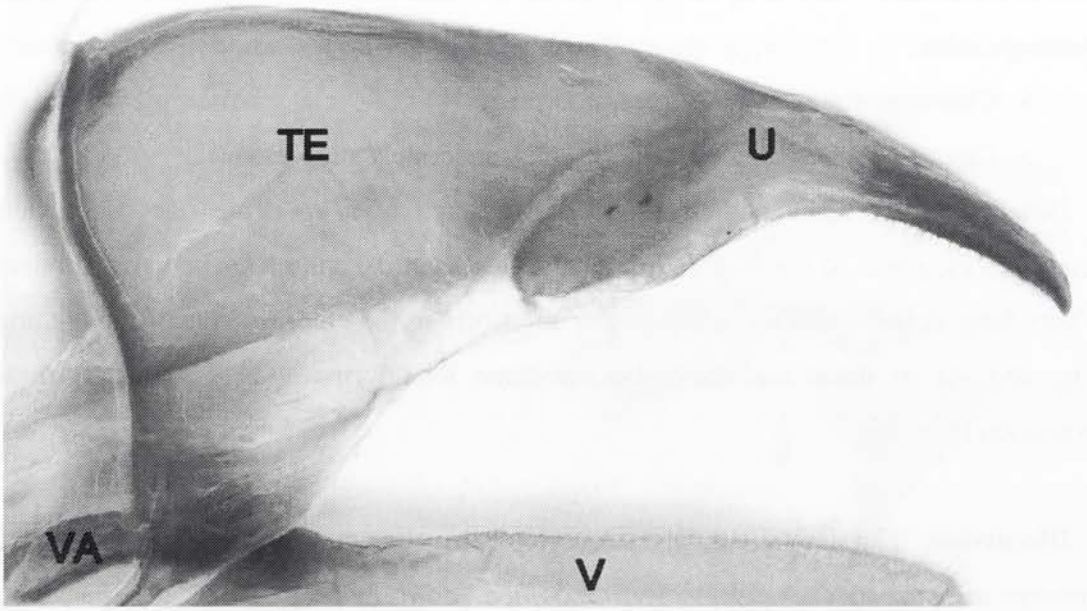

Fig. 85: *Anthela excellens* (Anthelidae), ♂, lateral view – tegumen, uncus and dorsal edge of valva; note the long anterior protrusion of the very long valva apodeme.

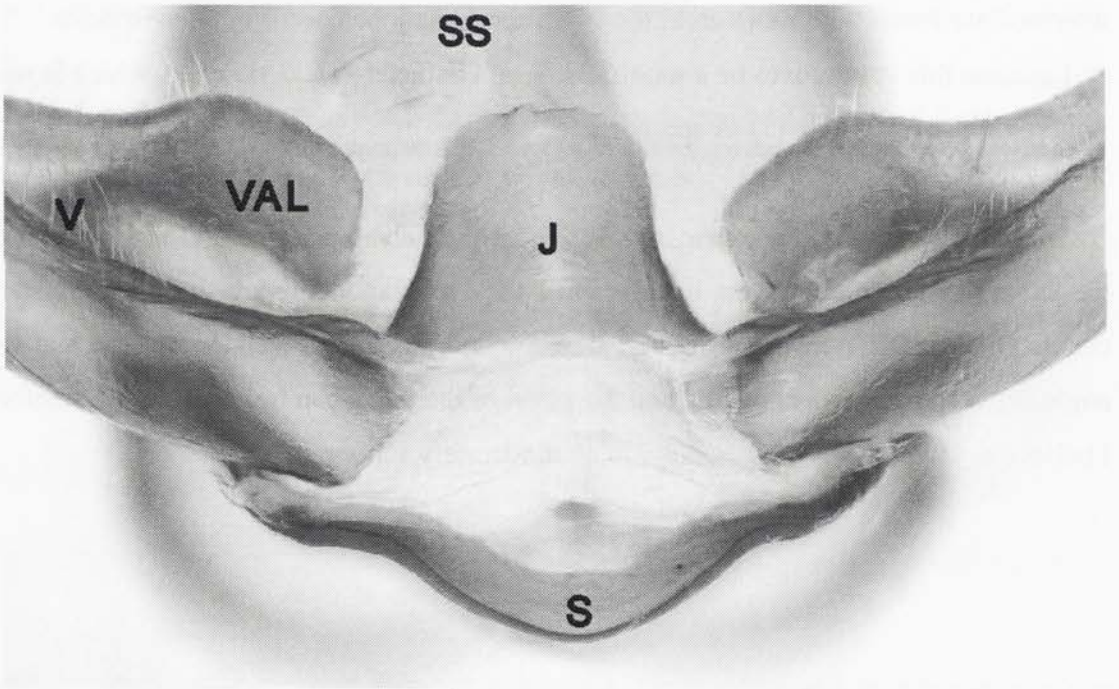

Fig. 86: *Anthela excellens* (Anthelidae), ♂, lateral view [phallus removed] – juxta and valvae with valva apodeme at distal end of the very long, anteriad extending valva apodeme (valvae are widely opened, which moves the valva apodemes and valva apodeme lobes posteriad).

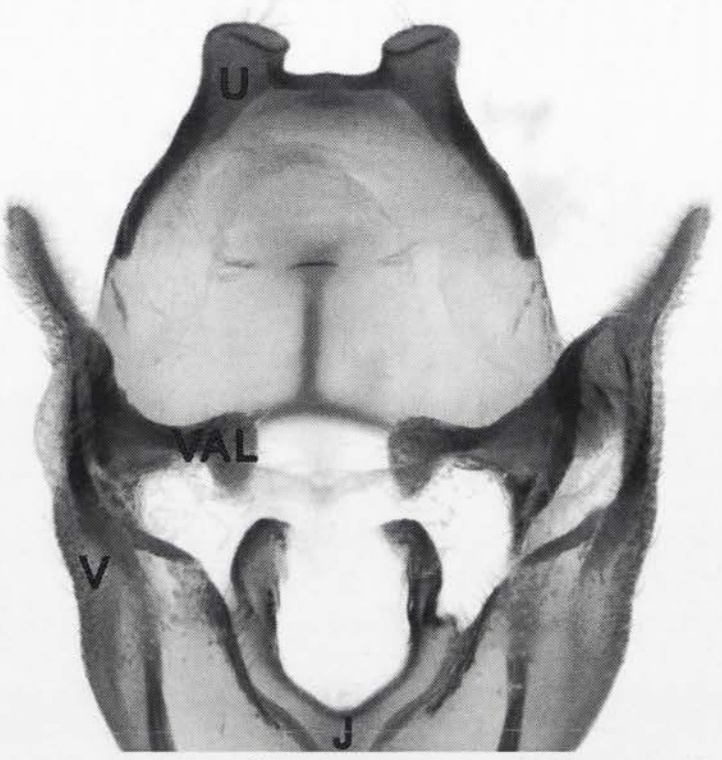

Fig. 87: *Nataxa flavescens* (Anthelidae), ♂, ventro-posterior view [phallus removed] – valva apodeme lobe at distal end of the very long, anteriad extending valva apodeme; note the laterally flexed valva apex.

Character #H.24: Conical valva apodeme lobe shifted distad on valva.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; well supported

Description. In the genus *Omphaliodes*, which consists of a small complex of cryptic species, the valva apodeme lobe has the shape of a conical process and is located on the dorsal edge of the valva, distinctly distally from the base of the valva (Fig. 88).

Discussion. This is a unique modification of the valva apodeme lobe, which is why I interpret character state (1) as apomorphic.

Summary. The shape of the valva apodeme lobe is simple, but in combination with its unique location provides good indications of homology. Therefore I regard my hypothesis of homology to be well supported.

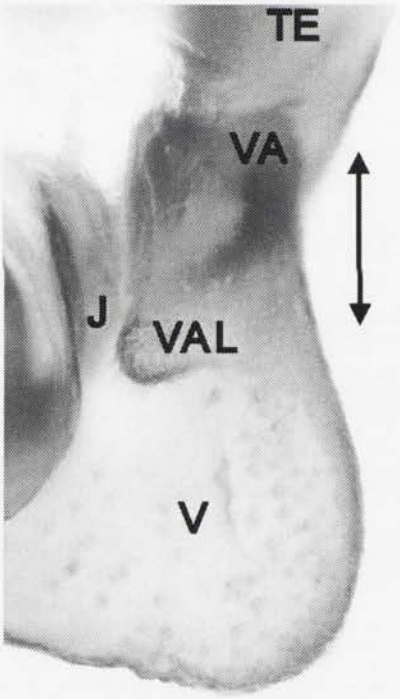

Fig. 88: *Omphaliodes obscura* complex (Anthelidae), ♂, dorso-posterior view – valva with conical, distad shifted valva apodeme lobe (black double-arrow indicates distance between the valva apodeme lobe and the base of the valva).

Character #H.25: Clasper reduced to a broad, roughly triangular plate with a massive, dorsal spine.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; well supported.

Introduction. The clasper is one of the basic elements of the valva (e.g., Kristensen 2003b: 101), which is variously modified or reduced in most Lepidoptera. In the majority of Anthelidae the clasper is entirely absent, but in a group of anthelid species it is retained and very well developed. In some Anthelidae the clasper is a broad, almost rectangular plate, which forms ventrally the ventral edge of the valva, but inserts dorsally on the mesal side of the valva (Figs 73, 74). For some of these Anthelidae a transformation series of reductions can be constructed for the clasper, leading from the broad, plate-shaped clasper to a simple, pointed one. As with other structures arranged in transformation series, I code them as additive binary characters. As the first, distinct step of the transformation series I postulate the following structure.

Description. In a small group of species the clasper has a broad, roughly triangular shape with a "hump" in its ventral edge. It carries a massive, spine-shaped, dorsad-pointing process near the base of its dorsal edge (Figs 77, 89).

Discussion. As mentioned above, a transformation series from a broad, plate-shaped clasper to a simple, pointed clasper with distinct intermediate states can be arranged. These transformations could be simple reductions of edges, if the transformation series started from a broad, plate-shaped clasper. The shape described above appears to be the result of a reduction of the dorso-posterior edge of the broad, almost rectangular plate. The posterior edge of such a broad, plate-shaped clasper is still apparent in anthelid species with otherwise strongly reduced claspers, e.g., in *Munychryia* spp. While undoubtedly the shape of the clasper has been variously modified in most macrolepidopteran families, a broad, plate-shaped clasper is a common denominator. Such a broad, plate-shaped clasper, which in overall shape, location and attachment is very similar to the one of Anthelidae, is present in several families of the bombycoid complex. Therefore I interpret character state (1) as apomorphic.

Summary. The roughly triangular shape with an additional ventral corner and a

massive dorsal spine is very distinct and constant. I regard my hypothesis of homology to be well supported.

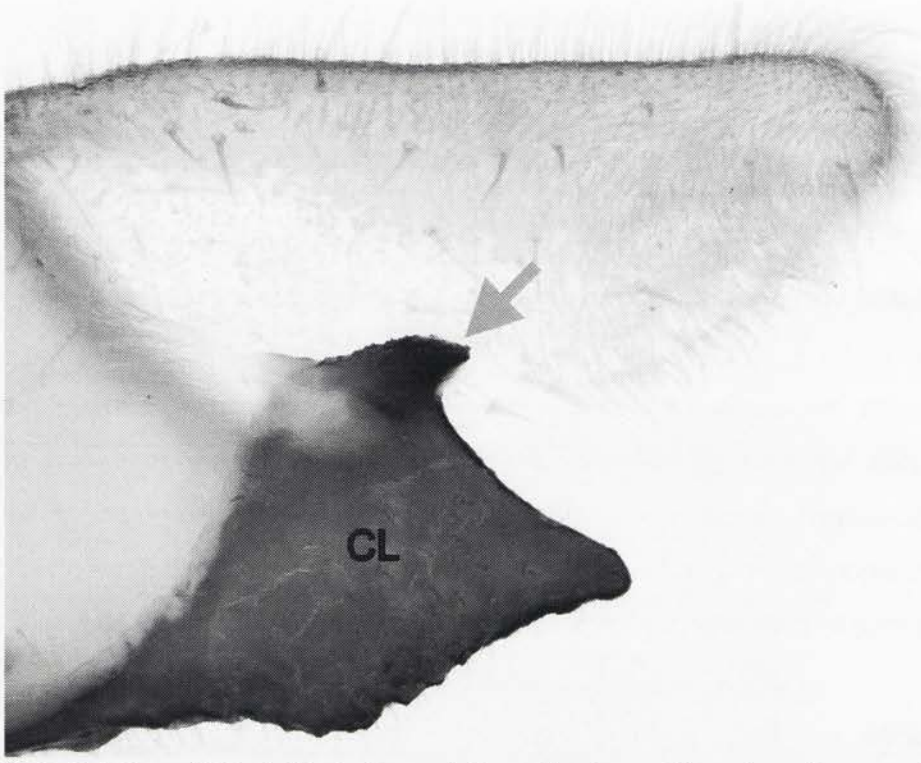

Fig. 89: *Anthela "acuta"* (Anthelidae), ♂, mesal view – distal part of the valva with a strongly sclerotized, roughly triangular, broad clasper, which has a ventral "hump" and carries a dorso-mesally protruding, spine-shaped process (green arrow) near the proximal end of its dorsal edge.

Character #H.26: Broad, triangular clasper reduced and elongated to a slender arm with a dorsal protrusion.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; poorly supported.

Description. In some species the clasper has the shape of a slender and blunt to pointed arm with a slender dorsal spine. The ventral "hump" of the roughly triangular clasper is located further proximally of the dorsal spine than in the previous character #H.25 state (1).

Discussion. In these species the broad, triangular clasper (character #H.25 state (1)) has been reduced in height and elongated to form a slender arm with a dorsal protrusion (Fig. 90). This shape has subsequently been variously modified, typically by a gradual reduction or loss of the dorsal spine and a reduction and curving of the slender arm. These modifications and changes in shape of the dorsal spine (towards a triangular shape) are valuable diagnostic characters, but currently useless for phylogenetic analyses as this group of species forms a large species complex and differences in shapes between species cannot be clearly separated from intra-specific variation.

Being part of a transformation series I interpret character state (1) as apomorphic.

Summary. The structure resulting from a reduction is merely characterized by its slender shape and the smaller dorsal process. Various modifications and reductions obscure the structure further, which is why I regard my hypothesis of homology to be poorly supported.

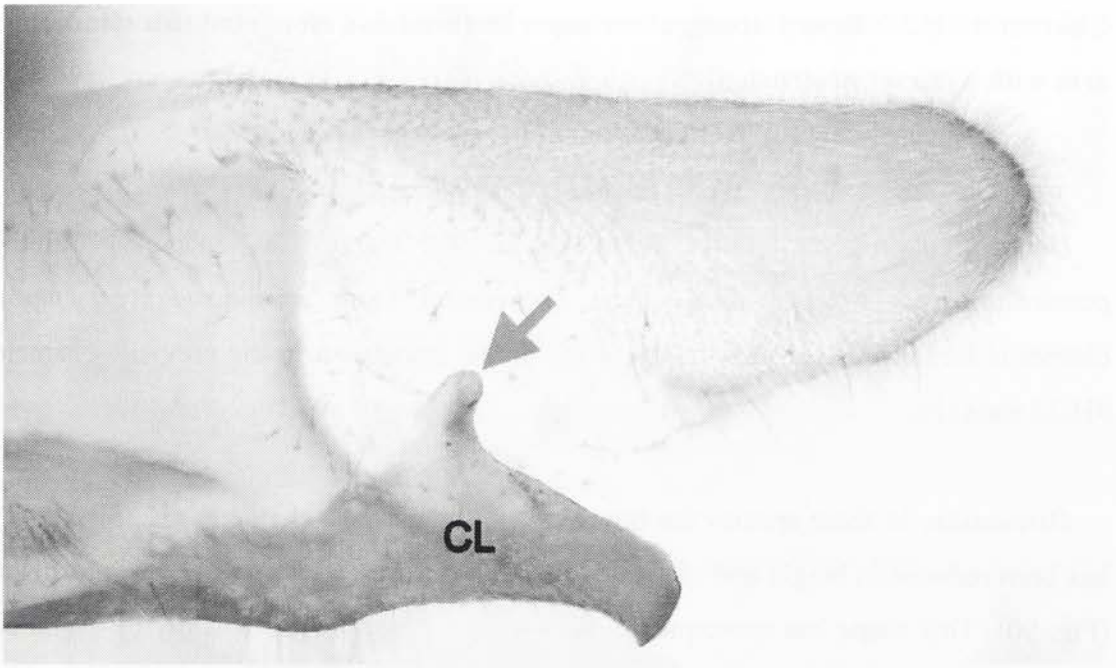

Fig. 90: *Anthela astata* (Anthelidae), ♂, mesal view – distal part of the valva with an elongate, slender clasper, which carries a dorso-mesally protruding, spine-shaped process (green arrow) near the base of its dorsal edge; note the further proximal location of the ventral "hump" relative to the dorsal spine.

Character #H.27: Valva apex flexed outwards and strengthened by a transverse ridge on the mesal side of the valva.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; poorly supported.

Introduction. In some anthelid species the lateral wall of the valva is convex – the valva curves slightly inwards. Such a valva is very stiff and strongly resists any sideways bending of its apex. This seems logical for a clasping structure, which exerts force in mesal direction. In contrast, the valva apex of many Anthelidae is slightly bent to strongly flexed outwards (Fig. 92). The line of bending runs from the dorsal edge of the valva transversely towards a more distal point on the ventral valva edge (Fig. 91). The point at which this straight line of bending reaches the ventral valva edge is very variable. It ranges from the distal third of the valva to the valva apex itself. Hence the size of the apical part of the valva, which is bent outwards, differs greatly. Likewise, the degree of bending ranges from not bent at all to strongly flexed outwards. Major differences exist between obviously closely related species. While this outward flexing of the valva apex is clearly a synapomorphy of these species, it is not possible to score this character accurately due to the great variation. Hence I did not use the apical outward flexing of the valva alone as a character in the phylogenetic analyses. Instead, I score the following modification of the valva, which is linked to the flexed valva apex.

Description. In some anthelid species in which the valva apex is distinctly flexed outwards, the line of bending is strengthened on the mesal side of the valva. In these species the mesal side of the valva forms a mesally protruding, transverse ridge along the line of bending, which is strongly sclerotized (Figs 91, 92, 93). Further, this ridge forms the distal wall of the central, membranous depression which surrounds the phallus if the valvae are closed (Fig. 91). The transverse ridge is typically straight, but in some species it (partly) follows the curving of the edge of the central depression. Likewise, the length and the extent of the mesal protrusion of this ridge are variable.

Discussion. The length, height, sclerotization and actual shape of the ridge are too variable to be good indications of the homology of this often prominent structure in all species. In contrast, its constant location and general orientation appear to be good indications of homology. However, this ridge appears to be a strengthening of the

outwards-flexed valva apex, which occurs in many more species than just in those with a transverse ridge. Possibly, a flexed valva apex favours the formation of such a transverse ridge, which is likely to assist in the grasping of the female abdomen.

In an undescribed antheline species the valva is strongly flexed outwards and the edge is strengthened by a transverse ridge. However, this ridge is located further ventrally than is typical and forms two large protrusions (Figs 72, 94). The homology of this structure with the transverse ridge of other anthelid taxa is uncertain. The distant attachment of muscle *m7* in this species indicates that this structure is not an unusually shaped clasper.

This ridge is unique to some anthelid species, which is why I interpret character state (1) as apomorphic.

Summary. While the structure is too prominent to be ignored, the strong variation of its characteristics and the potential preposition for such a ridge seem to make convergent evolution of this structure likely. Therefore I regard my hypothesis of homology to be poorly supported.

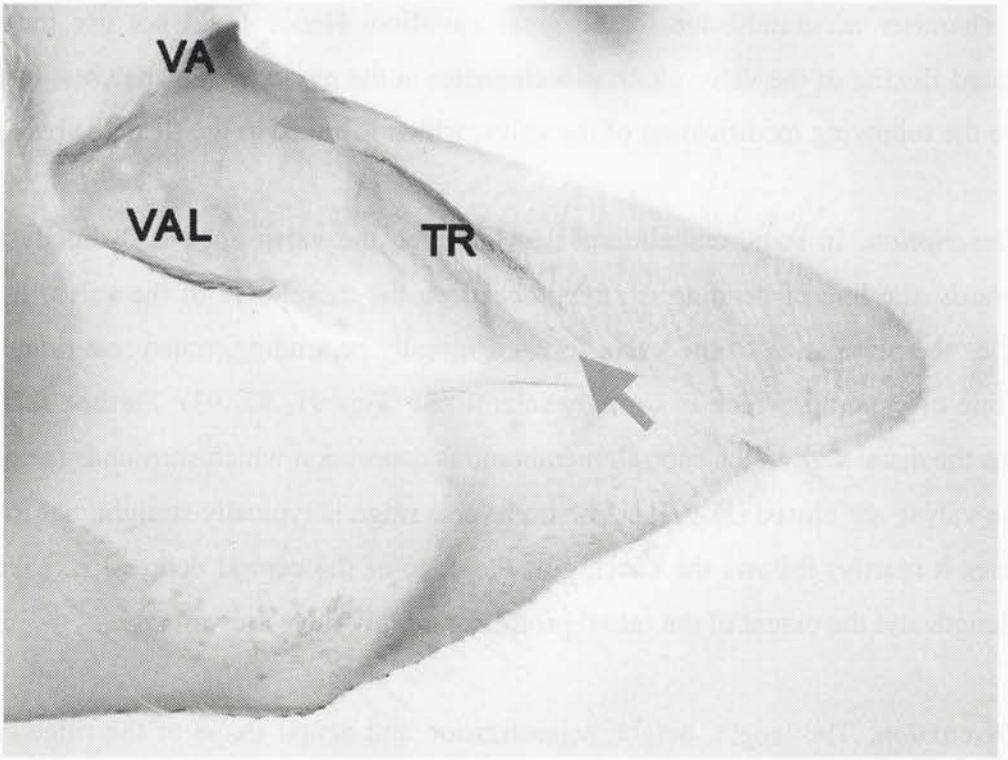

Fig. 91: *Anthela guenei* (Anthelidae), ♂, mesal view – valva with long valva apodeme, valva apodeme lobe and transverse ridge (green arrows show orientation of the ridge).

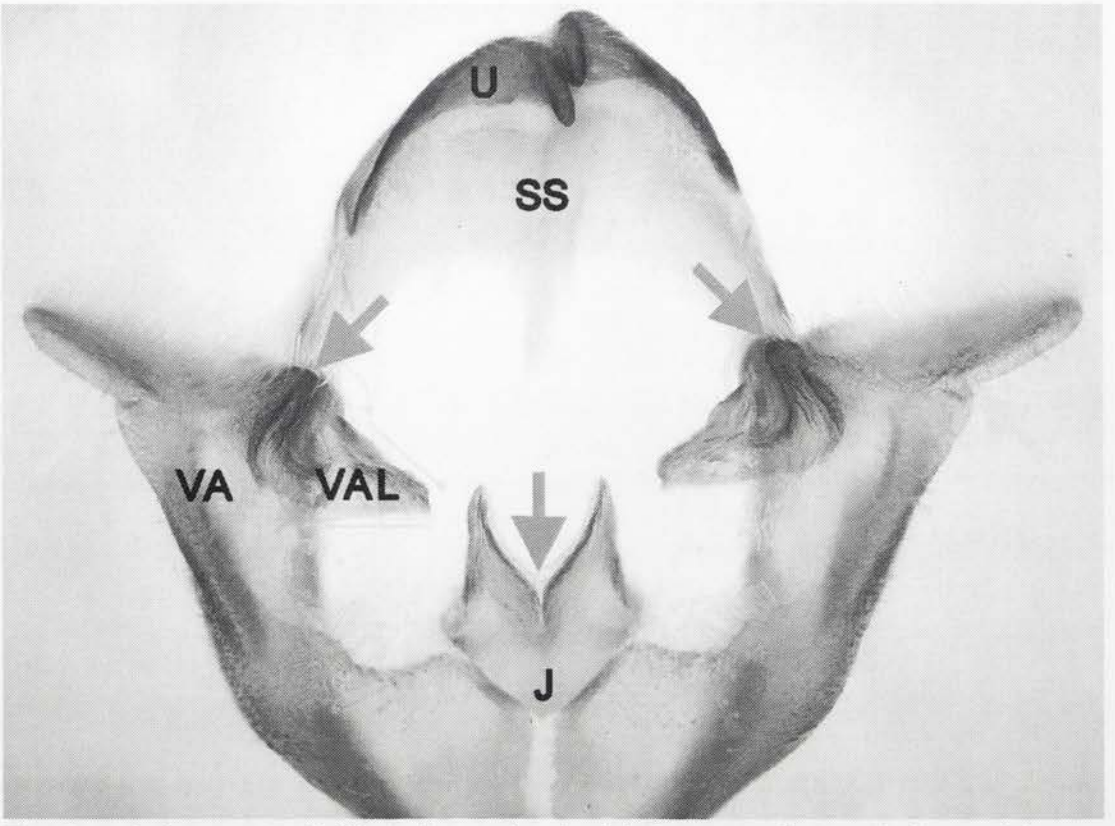

Fig. 92: *Anthela guenei* (Anthelidae), ♂, posterior view [phallus removed] – "vertical" uncus lobes, juxta with a median gap (red arrow), valvae with mesad protruding valva apodeme lobe, very strongly flexed valva apex (yellow arrows) and transverse ridge (green arrows).

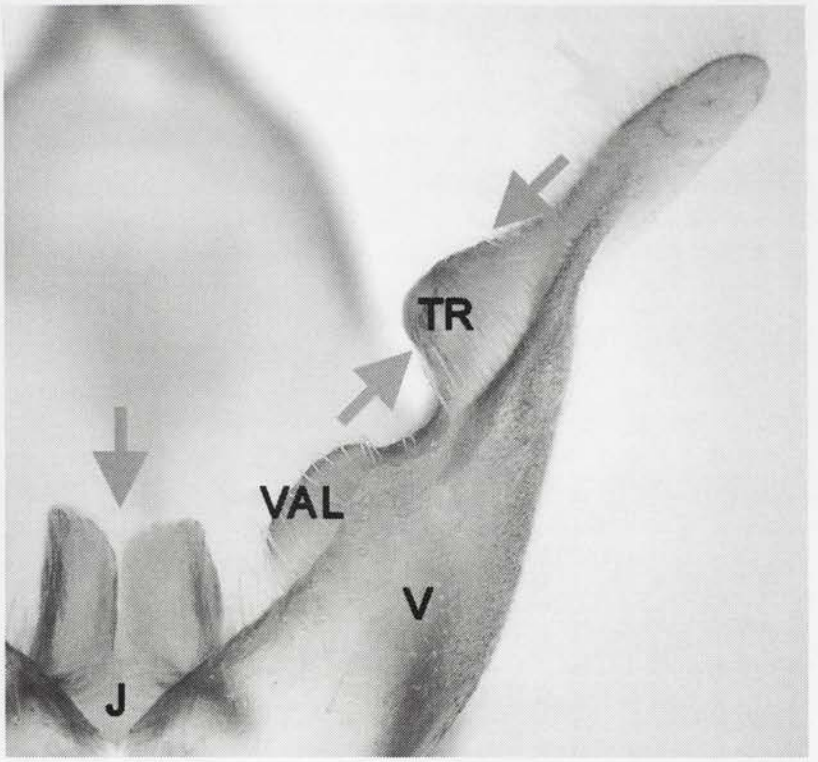

Fig. 93: *Anthela guenei* (Anthelidae), ♂, ventral view [phallus removed] – juxta with a median gap (red arrow), valvae with mesad protruding valva apodeme lobe, flexed valva apex (yellow arrow marks ventral end of line of bending) and transverse ridge (green arrows show orientation of the ridge).

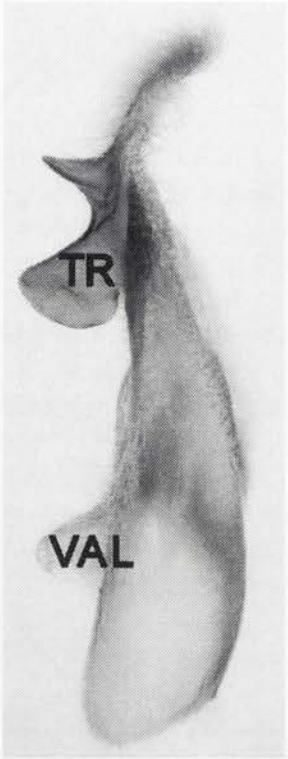

Fig. 94: Anthelinae n. sp. (Anthelidae), ♂, ventral view – valva with apex flexed outwards and with a unique, ventro-distal, transverse ridge, which forms a large and a small protrusion.

Character #H.28: Extremely wide manica sclerotized adjacent to zone.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; well supported.

Introduction. The phallus penetrates the diaphragma at the anterior end of a membranous invagination termed the "manica", which attaches to an area of the phallus termed the "zone" (e.g., Kristensen 2003b: 102).

Description. In some Munychryiinae the manica is extremely wide and the area of the manica adjacent to the zone is sclerotized (Fig. 95). In at least the two examined species of *Munychryia* the attachment of muscles *m6* extends from the phallus onto this sclerotization of the manica.

Discussion. The partial sclerotization of the manica near the zone is a unique modification, which is why I interpret character state (1) as apomorphic.

Summary. The combination of an extremely wide manica sclerotized in a certain area only is very characteristic. Therefore I regard my hypothesis of homology to be well supported.

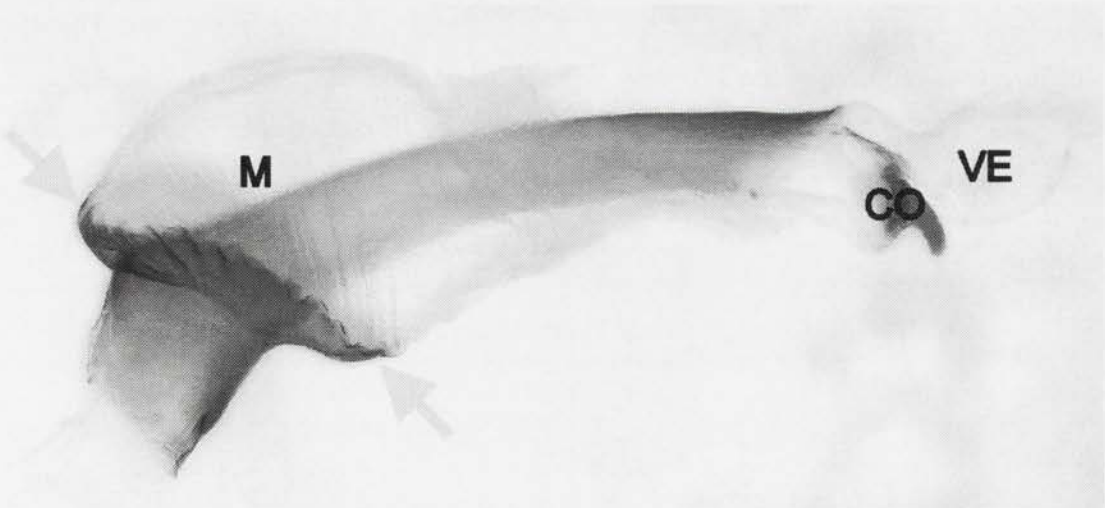

Fig. 95: *Munychryia periclyta* (Anthelidae), ♂, lateral view – phallus with a very wide manica, which is partly sclerotized adjacent to the zone (yellow arrows mark sclerotization).

Character #H.29: Juxta and phallus fused by sclerotization of entire manica.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; well supported.

Description. The typically membranous manica is entirely sclerotized on all sides in the genus *Chelepteryx* (Fig. 96). It connects the dorso-median area of the juxta firmly with the phallus. The juxta, which has no more guiding function, is strongly reduced to a ventral patch of sclerotization.

Discussion. This connection between juxta and phallus by the sclerotization of the entire manica is a unique modification, which is why I interpret character state (1) as apomorphic. Sclerotizations of the manica occur occasionally in other families, too, but usually differ in some details from the one present in *Chelepteryx*. It is noteworthy that within Anthelidae a partial sclerotization of the manica at the zone as well as near the anellus occurs in some Munychryiinae (Fig. 95) and the species group including *Anthela ferruginosa* (Fig. 110). However, the much larger part between these two sclerotizations remains membranous.

Summary. The relatively simple entire sclerotization of the manica and its attachment to the dorso-median area of a reduced juxta only are characteristic. Therefore I regard my hypothesis of homology to be well supported.

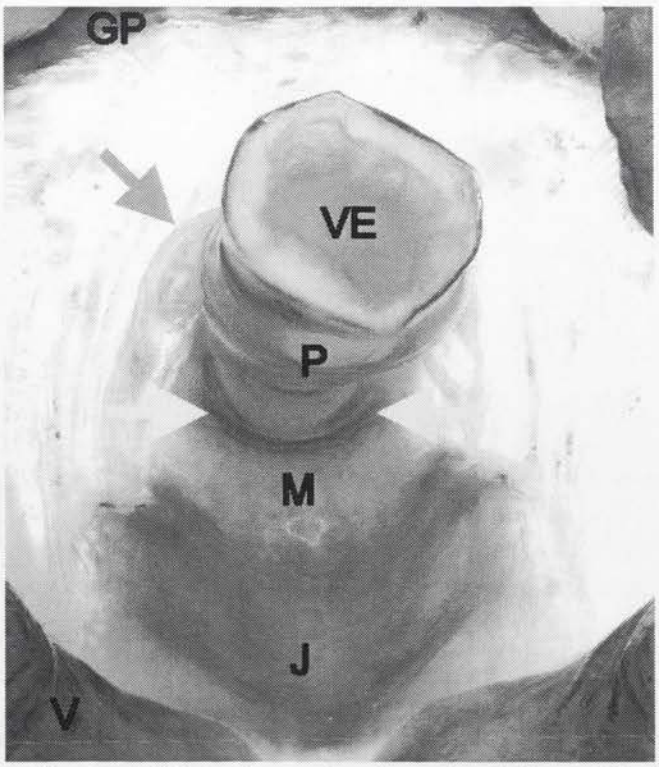

Fig. 96: *Chelepteryx collesi* (Anthelidae), ♂, posterior view – the phallus and the juxta are firmly connected to each other by the entirely sclerotized manica (yellow arrows mark the zone on the phallus); the mesal protrusion (red arrow) is merged with the anellus, forming a tiny protrusion with some minute setae.

Character #H.30: Apex of phallus coecum curved dorsad.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; moderately supported.

Introduction. As in many other Lepidoptera, the phallus of Anthelidae has a ventro-anteriad protruding, unpaired, tubular extension – a coecum. This coecum is typically rather short and straight (Fig. 97), and its rounded apex serves as an attachment area for muscles *m5*.

Description. In some anthelid species the ventro-anteriad protruding coecum is rather long and its distal part curves to bends dorsad (Fig. 98). The extent to which the coecum curves dorsad differs between species. At least in the examined specimen of *Anthela oressarcha*, which has a distinctly curved coecum apex, a few muscle fibres not observed in any other species connect the apex of the coecum with the apex of the saccus. No such fibres were found in the single examined specimen of *Anthela ocellata*, in which the coecum apex is less distinctly curved.

Discussion. The curving of the coecum apex seems to be a unique modification of the straight coecum present in many Lepidoptera, including the majority of Anthelidae, which is why I interpret character state (1) as apomorphic.

The unique muscle fibres observed in *A. oressarcha* represent a very distinct modification, but have not been observed in A. *ocellata*, while the muscles of other species with a curved coecum apex were not examined. Therefore these muscle fibres are not considered for this character.

Summary. I regard my hypothesis of homology to be moderately supported.

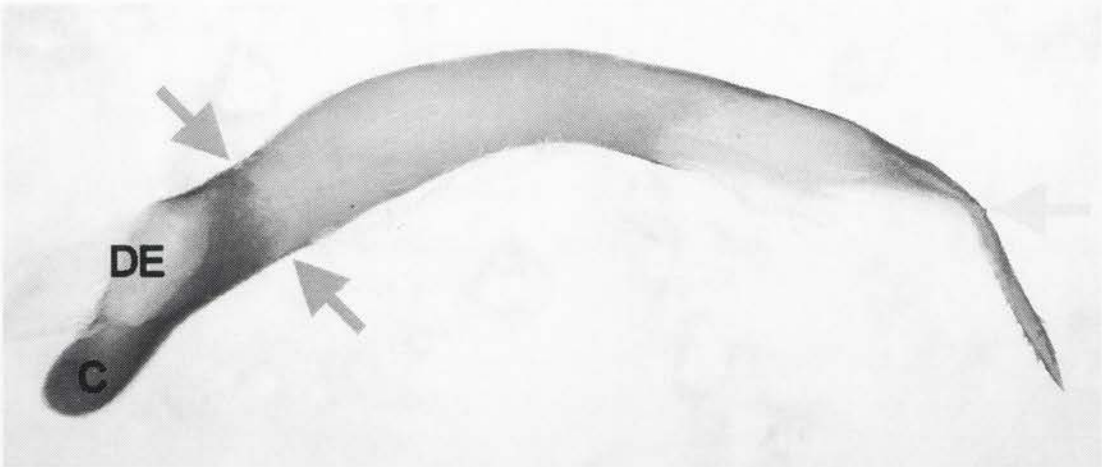

Fig. 97: *Anthela astata* (Anthelidae), ♂, lateral view – phallus with distinct, straight coecum; note the serrate, long, curved to bent (yellow arrow) process at the phallus apex; note the roughly continuous diameter of the phallus near the zone (red arrows).

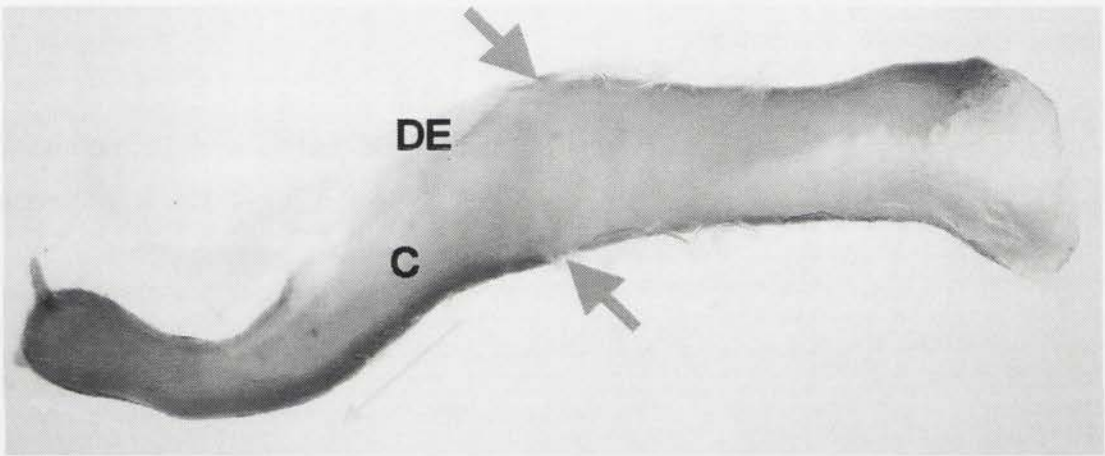

Fig. 98: *Anthela oressarcha* (Anthelidae), ♂, lateral view – phallus with very long, apically dorsad curved coecum (yellow arrows show curving of coecum); note the apophysis at the apex of the coecum; note the lateral gap in the sclerotization of the phallus apex; note the roughly continuous diameter of the phallus near the zone (red arrows).

Character #H.31: Phallus base bulbous.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; moderately supported.

Introduction. The phallus shape and size vary greatly between species, but its base has typically about the same diameter as the area distally of the zone (Figs 97, 98).

Description. In the species of the genus *Munychryia* the base of the phallus is distinctly wider than the part just distally of the zone (Fig. 95).

Discussion. The difference in diameter between the phallus proximally and distally of the zone seems to be unique to the genus *Munychryia*, which is why I interpret character state (1) as apomorphic.

Summary. The difference in diameter is a simple modification at a specific location and in a very specific environment (the partly sclerotized manica). Therefore I regard my hypothesis of homology to be moderately supported.

Character #H.32: Vesica ventrally with single cornutus, which originates from a sclerotization of the most distal part of the ductus ejaculatorius.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; well supported.

Introduction. The vesica of many bombycoid species carries numerous sclerotizations termed "cornuti". In Anthelidae only some Munychryiinae have a cornutus.

Description. In these Munychryiinae the vesica is simple and apically sack-shaped. A single cornutus is located on the ventral side proximally of the apical sack (Figs 99, 100). It originates from a sclerotization of the most distal part of the ductus ejaculatorius in a fully everted vesica, proximally of the opening of the phallic tube.

Discussion. Originating as a sclerotization of the distal part of the ductus ejaculatorius, this cornutus reminds of the "aedoeagus" present in other insects and postulated for Agathiphagidae by Kristensen (2003b). However, as no "aedoeagus" is known from Lepidoptera other than Agathiphagidae, this structure in Munychryiinae can hardly be interpreted other than a convergent sclerotization.

The cornuti of the vesica are typically too variable in number, location and shape to be homologized between more distantly related species, and certainly no homologies can be established between families. Within Anthelidae, however, the single cornutus is a unique sclerotization of the most distal part of the phallic tube and therefore not homologous with the simple sclerotizations found in various locations on the outside of the vesica in other species of the bombycoid complex. Consequently I interpret character state (1) as apomorphic. However, I cannot rule out that this single cornutus was present and subsequently lost in all other anthelid species, in which case the cornutus would be plesiomorphic for the species of Munychryiinae.

The cornutus can be straight or hook-shaped and differs greatly in size between closely related species – these differences are of taxonomic importance.

Summary. While the single cornutus is not similar between species, its unique origin and its location on the ventral side proximally of the apically sack-shaped vesica are valuable indications of homology, which is why I regard my hypothesis of homology to be well supported.

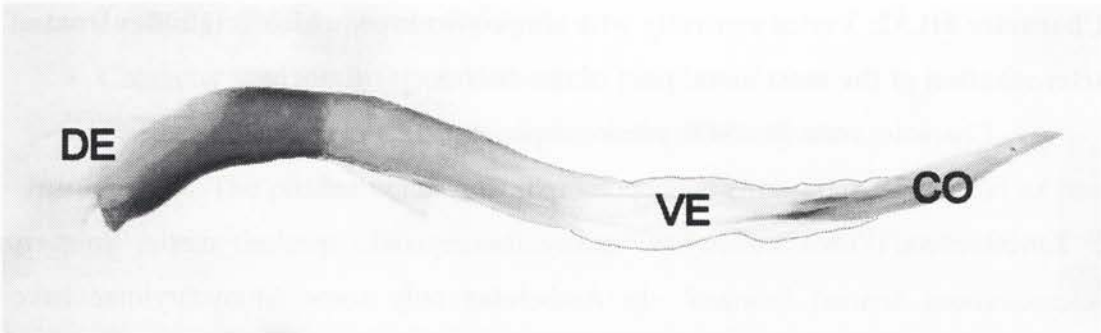

Fig. 99: Munychryiinae n. sp. (Anthelidae), ♂, lateral view [vesica shape traced by dotted line] – phallus with simple vesica (apical sack-shaped extension in different plane and not visible) and a single, long and straight cornutus.

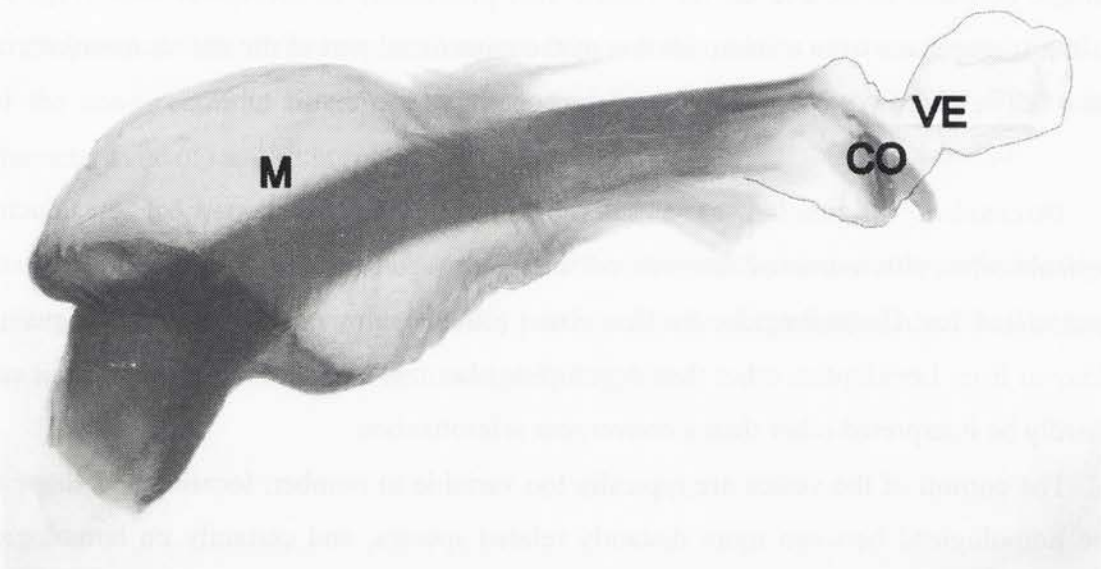

Fig. 100: *Munychryia periclyta* (Anthelidae), ♂, lateral view, stained [vesica shape traced by dotted line] – phallus with simple, apically sack-shaped vesica and a single, hook-shaped cornutus.

Character #H.33: Vesica largely sclerotized.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; poorly supported.

Description. The vesica of the Munychryiinae and the genus *Chelepteryx* are simple, membranous sacks, which can be everted. In all other Anthelidae the sclerotization of the phallus extends onto large parts of the vesica, which at large prevents a retraction of the latter – in these species the vesica appears to be absent. The sclerotization, which extends onto the vesica, starts as two clock-wise twisted bands (posterior view), of which the right-dorsal one is more prominent.

Discussion. The secondary nature of the two sclerotized bands is indicated by the partly patchy appearance of the sclerotization (Fig. 102). Numerous modifications of these bands exist, extensions (Fig. 103) as well as reductions. Two small, thin setae are present on the sclerotized part in some species (Fig. 104). They are easily overlooked or damaged, and they can be absent as part of intraspecific variation. Therefore I did not use these two setae as part of this or as a separate character. However, I interpret their presence on the sclerotized part as a further indication of the secondary sclerotization of the vesica, as setae are typically not found on the sclerotized part of the phallus, but occasionally on the vesica, e.g., in *Kunugia fae* (Lasiocampidae).

The distal end of the sclerotized part of the phallus is variously modified in Lepidoptera. Typically, the phallus apex distally of the sclerotization is an eversible sack, the vesica. Such an eversible vesica is present in some Anthelidae, while the sclerotization of the vesica from two sides appears to be unique to some anthelid species. Therefore I interpret character state (1) as apomorphic.

Summary. The sclerotization of the vesica from two sides has been variously modified and frequently reduced, which greatly obscures any characteristics. However, a hardly retractable/eversible vesica remains in all species independent of subsequent modifications, as does at least a minor gap in the sclerotization. Based on such limited indications I regard my hypothesis of homology to be poorly supported.

Character #H.34: Right sclerotized band on vesica forms long, curved to bent process.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; well supported.

Description. The right-dorsal sclerotization on the vesica forms a long process, which can be slightly curved to apically bent ventrad. The left process does not form an elongate spine in these species, it is stout and can be membranous to distinctly sclerotized (Fig. 101). The phallic tube ends ventrally of the bases of these two processes.

Discussion. The right process can be either tubular and spine-shaped (Fig. 101) or it can be flat and serrate (Fig. 105). In species of the *Anthela repleta* complex, either a simple tubular process (Fig. 101), a serrate tubular process (Fig. 102) or a flat, serrate process (Fig. 103) occur, which is why I do not distinguish between these shapes. In the case of the flat, serrate process, the vesica extends on the ventral side up to near the apex of the process (Fig. 104). This part of the vesica is sclerotized and forms part of the tubular, spine-shaped process in other species.

This process does not orriginate from the distal end of the ductus ejaculatorius, but from a lateral sclerotization of the vesica. Therefore, I interpret this spine as being non-homologous with the single cornutus present in some Munychryiinae (character #H.32).

The process is unique to a group of anthelid species, which is why I interpret character state (1) as apomorphic.

A similar, spine-like process occurs in the genus *Nataxa*, which I assume to be a convergence due to difference in details (see character #H.35).

Summary. The long, serrate process and its location are characteristic, and the existing variations are all linked together by intermediate forms. Therefore I regard my hypothesis of homology to be well supported.

Fig. 101: *Anthela repleta* complex (Anthelidae), ♂, left lateral view – phallus; right process tubular and spine-shaped (green arrow); left sclerotized band much shorter.

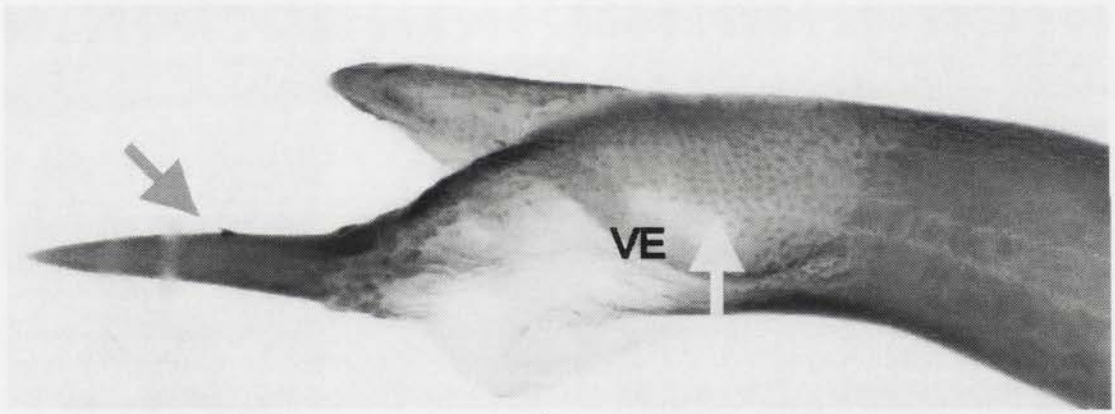

Fig. 102: *Anthela repleta* complex (Anthelidae), ♂, right lateral view – phallus apex; right sclerotized band on vesica partly sclerotized (yellow arrow) and with tubular, spine-shaped process with single "tooth" (green arrow); left sclerotized band distinct.

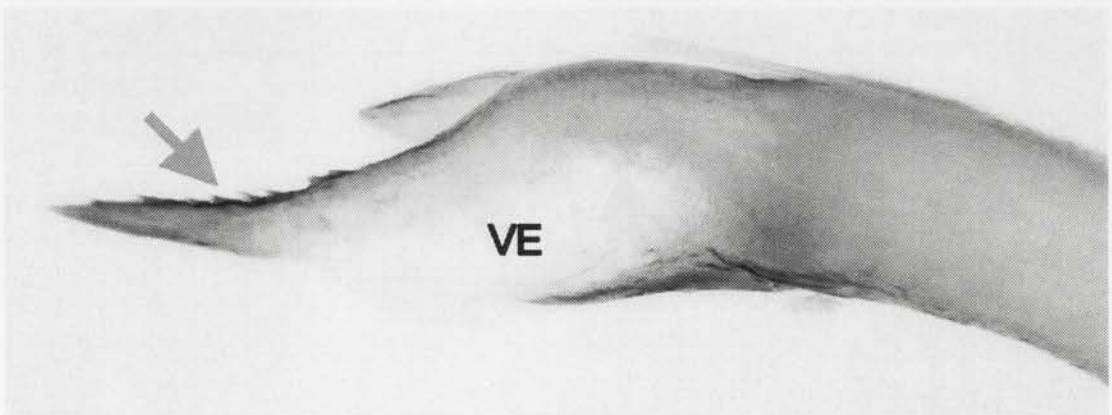

Fig. 103: *Anthela repleta* complex (Anthelidae), ♂, right lateral view – phallus apex; right sclerotized band on vesica partly sclerotized (yellow arrow) and with partly tubular, serrate process (green arrow); left sclerotized band distinct.

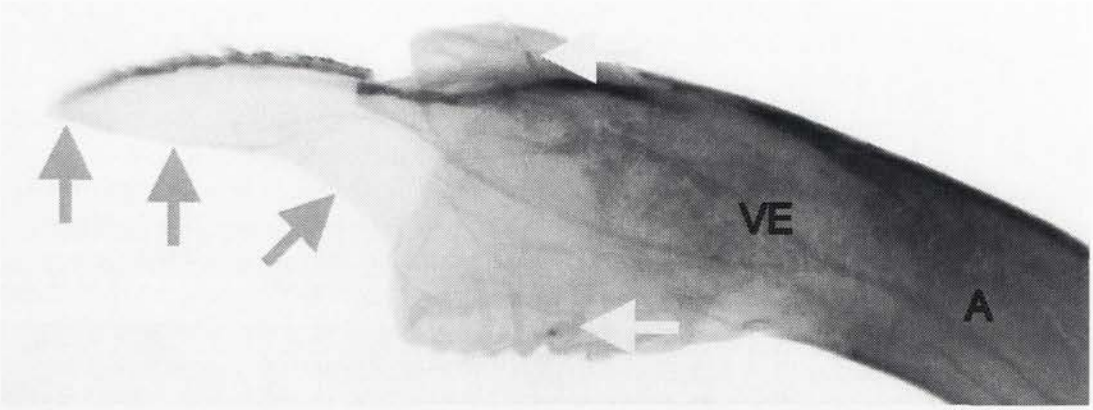

Fig. 104: *Anthela astata* complex (Anthelidae), ♂, right lateral view [stained] – phallus apex; right sclerotized band on vesica partly sclerotized and going over into a flat, serrate sclerotization [broken] on top of membranous protrusion of vesica (red arrows); left sclerotized band reduced to membranous lobe; note the two minute setae, which are located in other species on the sclerotized part of the vesica (yellow arrows).

Fig. 105: *Anthela limonea* (Anthelidae), ♂, left lateral view – phallus; right sclerotized band forms a flat, serrate and strongly curved to bent (yellow arrow) process; left sclerotized band lost.

Character #H.35: Both sclerotized bands on the vesica form a tubular spine.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; well supported.

Description. In the genus *Nataxa* both sclerotized bands on the vesica form long, slender, tubular spines of almost equal size (Fig. 106). These two spines follow the strong clock-wise twist of the sclerotized bands (posterior view). The phallic tube ends between the bases of these two spines.

Discussion. While being similar to the curved, single right process found in some anthelid species (see character #H.34), I believe the two twisted spines to be unique developments of the genus *Nataxa*. Consequently I interpret character state (1) as apomorphic.

Summary. The twisted pair of long spines is characteristic and therefore I regard my hypothesis of homology to be well supported.

Fig. 106: *Nataxa flavescens* (Anthelidae), ♂, left lateral view – phallus with the apical, sclerotized bands on the vesica forming two clock-wise twisted spines.

Character #H.36: Proximal sclerotization of vesica forms a funnel-shaped phallus apex.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; poorly supported.

Description. In the New Guinean genera *Pseudodreata* and *Corticomis* the apex of the phallus does not carry any processes, but is apically distinctly enlarged to form a very wide, funnel-shaped apex (Fig. 107). This shape is caused by an entire, but ventrally weaker, sclerotization of the proximal part of a short, sack-shaped vesica.

Discussion. A superficially similar phallus shape is present in some Australian species, in which the sclerotization extends even further distally on the vesica, giving the phallus apex more of a knob-shaped appearance (Fig. 108). This sclerotization has a distinct dorsal gap and the apical widening of the phallus is less abrupt than in the genera *Pseudodreata* and *Corticomis*. Therefore, I interpret the knob-shaped phallus apex as a convergent development.

The funnel-shaped apex is unique to anthelid genera *Pseudodreata* and *Corticomis*, differing from the equal width in other species with or without processes. Therefore I interpret character state (1) as apomorphic.

Summary. The funnel-shaped apex has a distinct shape, but this shape is caused by a simple sclerotization of the vesica, which is a rather simple and a poor indication for homology. Hence, I regard my hypothesis of homology to be poorly supported.

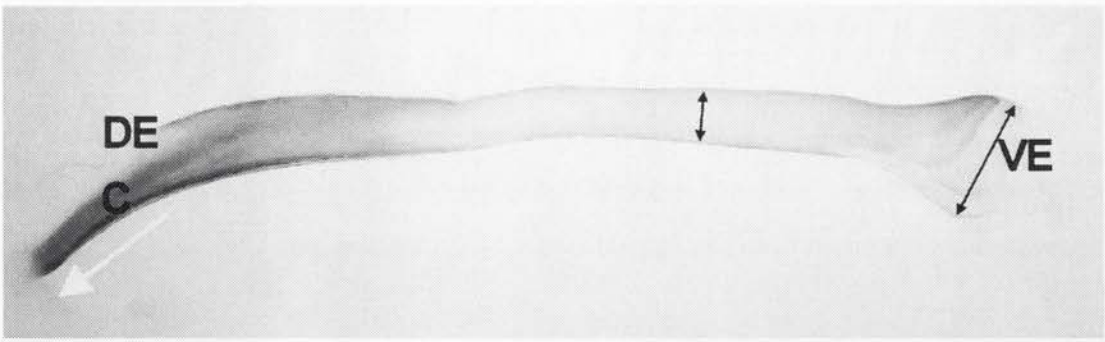

Fig. 107: *Pseudodreata* sp. (Anthelidae), ♂, left lateral view – phallus with funnel-shaped apex caused by the secondary sclerotization (large yellow arrow) of the vesica (black double-arrows indicate difference in diameter); note the straight coecum (small yellow arrow).

Fig. 108: *Anthela hyperythra* (Anthelidae), ♂, left lateral view – phallus with a knob-shaped apex, which is likely to be a convergent development of a widened phallus apex (black double-arrows indicate difference in diameter).

Character #H.37: Abdominal segment A1 with a lateral, spine-shaped projection.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; poorly supported.

Introduction. This character is not a character of male genital sclerites, but of the first abdominal segment in males. As I do not have other abdominal characters, I include this character in this section.

Description. Lemaire and Minet ([1998]: 324) proposed this character as an autapomorphy of the family Anthelidae: "A1 of male with postspiracular conical projections of tergal origin.". This refers to an outgrowth formed by a sclerotization of the abdominal integument, which extends from the marginotergite ventrad and is located between the A1 spiracle and the postspiracular tergosternal bar (Fig. 109). The convex outgrowth narrows gradually to a cone, which apically narrows abruptly to form a pointed, spine-like process. While the largest part of this outgrowth is just a convex part of the abdominal integument, its apical part is a discrete process, which occasionally curves away from the abdomen. The outgrowth is scaled, except for the apical process.

Discussion. Within Anthelidae this process varies very greatly in length, overall size and degree of sclerotization between specimens. Occasionally, such variation is even present within a single specimen. The spine is frequently reduced or lost, and this reduction can even occur within a species with otherwise well developed spine. No such outgrowth seems to be present in female specimens, and no obvious function is apparent.

The process was said to be unique to Anthelidae (Fig. 110) by Lemaire and Minet ([1998]), but I found a very well developed process in a single *Eupterote* species (Eupterotidae), too (Fig. 109). I did not observe this structure in other Lepidoptera, but given its frequent reduction in Anthelidae many more taxa have to be examined than I did. In many families of the bombycoid complex and in Noctuidae, Drepanidae and Epicopeidae a ventro-lateral brush of androconial scales occurs, which is not homologous with the "outgrowth" of Anthelidae and Eupterotidae. This androconial brush and its rather elaborate system of secretory invaginations is located in the ventral part of the pleura and connected to the sternite by a sclerotized lever, while the "outgrowth" is of "tergal origin" as pointed out by Lemaire and Minet ([1998]).

Therefore I interpret character state (1) as apomorphic.

Summary. The lateral protrusion of A1 is too simple and variable in size and sclerotization to offer many indications of its homology between different taxa. Mainly the abrupt narrowing to a spine-shaped protrusion and the specific location are such indications. Further, the frequent reduction to loss obscures the presence of this structure. Hence, I regard my hypothesis of homology to be poorly supported.

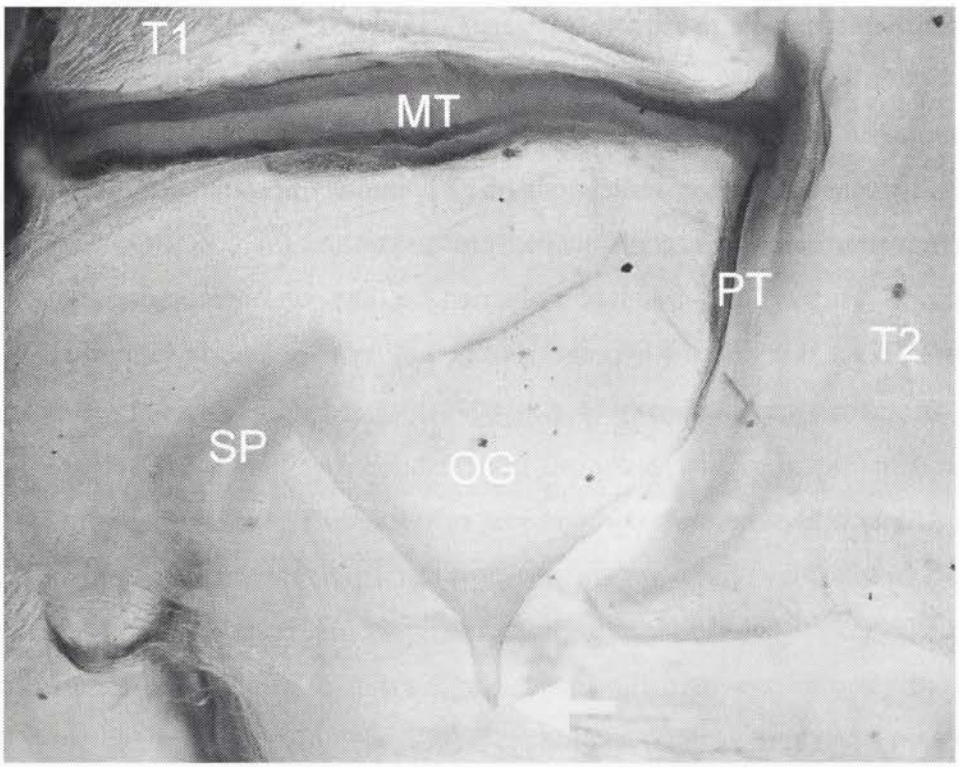

Fig. 109: *Eupterote* sp. (Eupterotidae), ♂, abdominal segment A1, left lateral view – the integument forms a sclerotized outgrowth (OG) with an apical spine (yellow arrow) [T1 = tergite I; T2 = tergite II; MT = marginotergite; PT = postspiracular tergosternal bar; SP = spiracle].

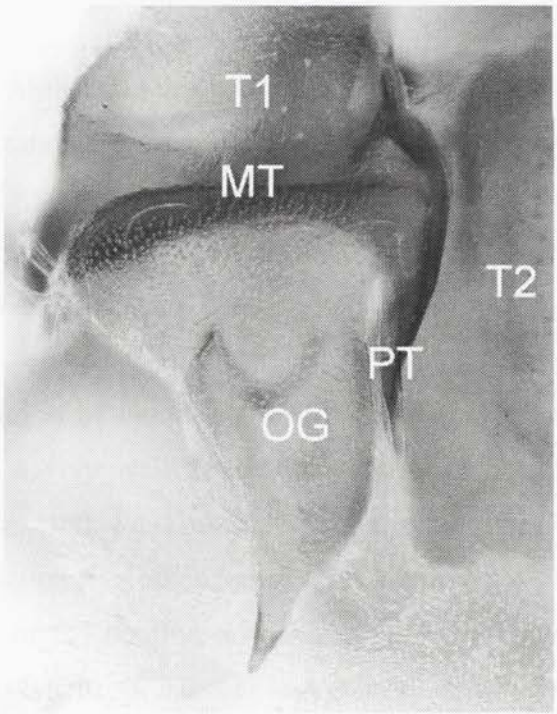

Fig. 110: *Pterolocera leucocera* (Anthelidae), ♂, abdominal segment A1, left lateral view – the integument forms a sclerotized outgrowth (OG) with an apical spine (yellow arrow) [T1 = tergite I; T2 = tergite II; MT = marginotergite; PT = postspiracular tergosternal bar].

III.2) THE MUSCLES OF MALE GENITAL STRUCTURES

Our knowledge of the male genital muscles in the bombycoid complex is limited to a relatively small number of publications, namely Birket-Smith 1974, Eaton 1988, Forbes 1939, Kuznetzov & Stekolnikov 1985, 2001, Libby 1961, Snodgrass 1935 and Stekolnikov & Zolotukhin 1994, 2002. Nevertheless, different authors created their own numbering systems and names for genital muscles, as well as made different assumptions about their origin. I am not in a position to judge the origin of these muscles, nor their homology across the entire order Lepidoptera. Hence I will not use terms relating to their origin, such as *musculus gonopodalis externus dorsomedialis* (Kuznetzov & Stekolnikov 2001). Instead, I use for practical reasons the simple numbering system outlined in a hypothetical scheme for Lepidoptera by Kuznetzov and Stekolnikov (2001: 24-25). By following their numbering system I imply homology with muscles of Macrolepidoptera labelled correspondingly by them, but not necessarily with muscles of other Lepidoptera.

The most comprehensive study of the male genital muscles of the bombycoid complex was published by Kuznetzov and Stekolnikov (1985, 2001). Their publications are based on the study of Palearctic taxa only, hence our knowledge of genital muscles within the cosmopolitan and predominantly tropical bombycoid complex is rudimentary.

I examined the genital muscles of male representatives of all bombycoid families, with the exception of Mirinidae, which, amongst others, have been studied by Kuznetzov and Stekolnikov (2001). Detailed examinations were made of the muscles attached to structures within the genital capsule formed by tegumen and vinculum, but not of muscles connecting the entire genital capsule to other abdominal segments. Minor muscles within the anal tube (muscle *m20*) and within the phallus (muscle *m21*) were not examined. Descriptions of my observations and of six illustrations from Kuznetzov & Stekolnikov 1985, 2001 and Stekolnikov & Zolotukhin 2002 are summarized for a total of 59 representatives of all bombycoid families and some Noctuoidea by means of a table in Appendix M. The illustrations of muscles are labelled with abbreviations, which are explained in Appendix R. While all genital muscles are paired, one muscle out of a pair might have been removed in some illustrations to reveal underlying structures. Any descriptions referring to muscles in the singular are applicable to both muscles of a pair.

III.2.1) The principal male genital muscles of the bombycoid complex

Based on my muscle preparations and the literature (Birket-Smith 1974; Kuznetzov & Stekolnikov 1985, 2001; Stekolnikov & Zolotukhin 2002), the principal male genital muscle pairs of the bombycoid complex are (Fig. 111):

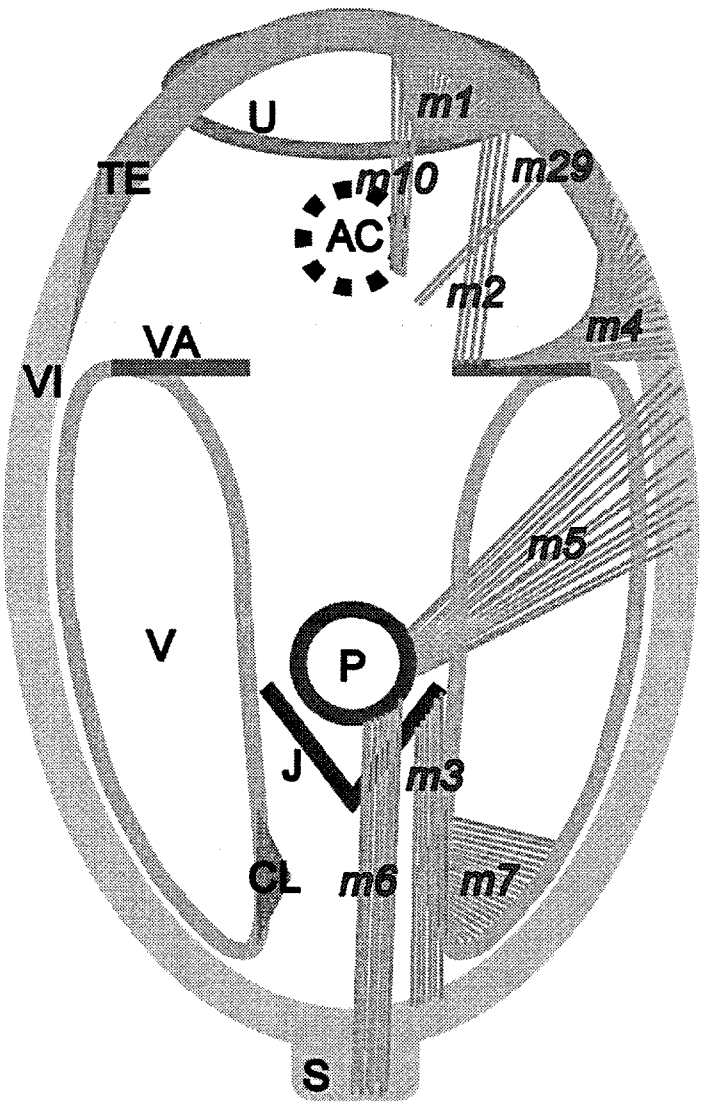

Fig. 111: Bombycoid complex, ♂, anterior view – general scheme of the principal genital muscles (muscles *m20*, *m21*, gnathos and subscaphium omitted; outer edge = anterior edge of structure; note that this two-dimensional illustration of three-dimensional structures does not necessarily represent relative muscle lengths correctly).

m1:

A massive muscle which connects the tegumen with the uncus and functions as an adductor of the uncus. Its attachment to the tegumen is very broad, occupying the dorso-lateral and dorsal parts of the tegumen over almost its entire width, except for the anterior edge of the tegumen. The other attachment point is focused onto the anterior edge of the ventral uncus side. No modifications of this muscle were observed, irrespective of modifications of the uncus shape (simple or bilobed). The muscle is entirely absent in taxa in which the uncus is strongly reduced to absent.

This muscle is typically referred to as the "uncus depressor" (e.g., Kuznetzov & Stekolnikov 2001; Kristensen 2003b), even though muscles can only contract, but never "press" or "push". Strictly speaking, the term "uncus adductor" is more appropriate. The function of this muscle as a "depressor" is not immediately obvious. The muscle attaches to the tegumen dorsally of its opposite attachment point on the ventral wall of the uncus, but nevertheless moves the apex of the uncus ventro-anteriad. This is the case as the tube-like uncus is dorsally "hinged" to the tegumen and muscle *m1* attaches to the ventro-anterior edge of the uncus. By pulling this ventro-anterior edge dorso-anteriad, *m1* tilts the uncus apex ventro-anteriad – the uncus is indirectly pulled towards the diaphragma. Hence, it is the uncus that depresses part of the female genital structures during copula, but the muscle is not "depressing" the uncus.

m2:

A rather thin, evenly wide and long muscle which connects the tegumen with the valva and is generally believed to function as an abductor of the valva (e.g., Kristensen 2003b; Kuznetzov & Stekolnikov 2001). Its function, however, might be a different one in some Macrolepidoptera (see above, section III.1.1: 65). Its attachment point on the tegumen is in a dorso-lateral position on the anterior tegumen edge, laterally of and adjacent to *m10*. The opposite attachment point is the distal end of the dorso-basal apodeme of the valva, at about the same level as and mesally of *m4* (Figs 112, 114). In the examined Sphingidae, but in no other examined family of the bombycoid complex, the dorso-basal valva apodeme forms a ventral lever, which protrudes cephalo-ventrad. In these taxa muscle *m2* attaches to the apex of the cephalo-ventral lever of the dorso-basal valva apodeme, and is located anteriorly and latero-ventrally of *m4* (Figs 113, 116). A very similar attachment of *m2* to the apex of a ventral lever is present in the examined Oenosandridae and Noctuidae (both Noctuoidea) (Fig. 115, 144). In the few

representatives I examined, the structure of the valva apodeme and the attachment of muscle *m4* differ between Sphingidae and Noctuoidea, which is why I assume the lever with apical attachment of muscle *m2* to be non-homologous between these two groups. A lever, which is most similar to the lever present in Noctuoidea, occurs in the geometrid genus *Paralaea* (muscles not examined). However, more material has to be examined to gain more certainty about the homoplasy or homology of these structures. If my assumption of non-homology of the lever system between Sphingidae and Noctuoidea (and possibly Geometridae) is wrong, it might be a symplesiomorphy within the bombycoid complex, rather than a synapomorphy of (some) Sphingidae. In most taxa of the bombycoid complex muscle *m2* has been lost.

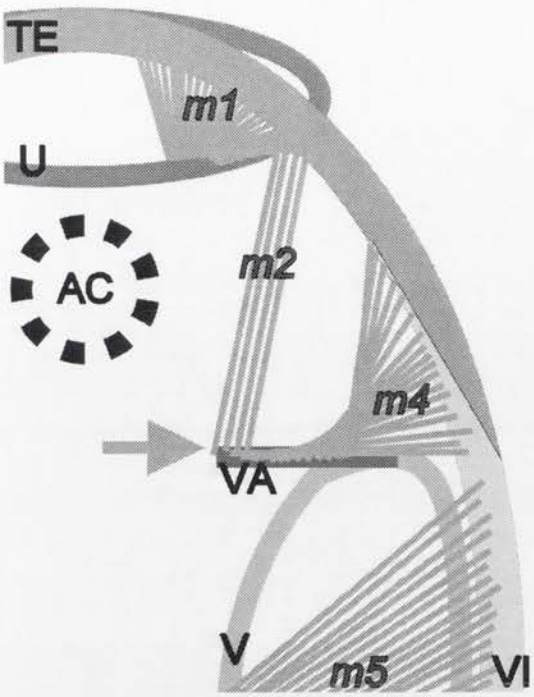

Fig. 112: Bombycoid complex, ♂, anterior view – scheme of *m2* attachment to the mesal end of the dorso-basal valva apodeme (green arrow).

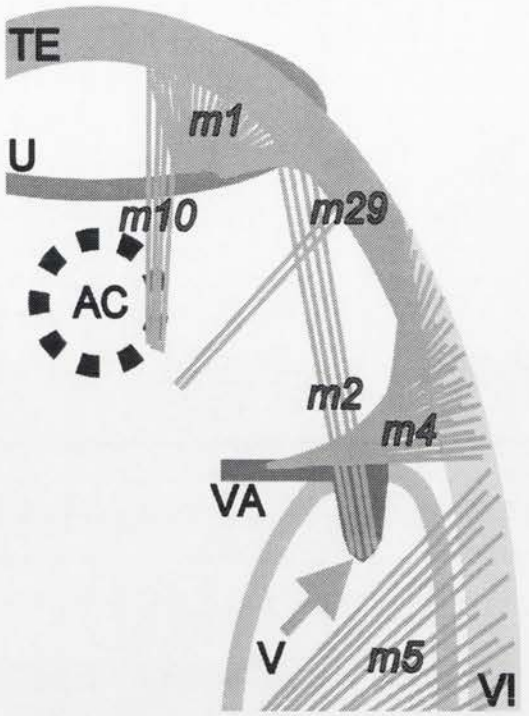

Fig. 113: Sphingidae, ♂, anterior view – scheme of *m2* attachment to the apex of the cephalo-ventral lever (green arrow) of the dorso-basal valva apodeme.

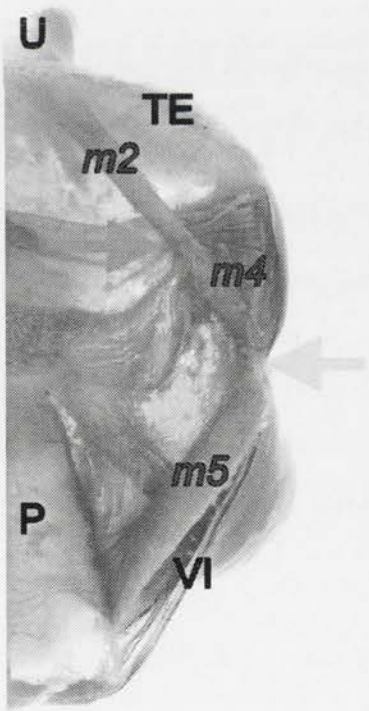

Fig. 114: *Endromis versicolora* (Endromidae), ♂, anterior view – *m2* attachment to the mesal end of the dorso-basal valva apodeme, mesally of *m4* (green arrow); note the unique median attachment of *m2* to the tegumen; note *m4* and *m5* proximity (yellow arrow).

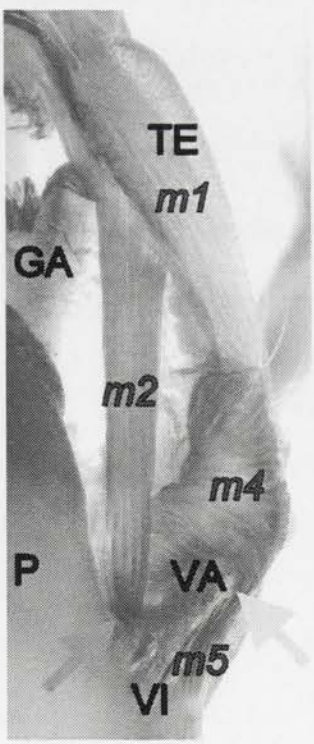

Fig. 115: *Agrotis infusa* (Noctuidae), ♂, anterior view – *m2* attachment to the apex of the cephalo-ventral lever of the dorso-basal valva apodeme (green arrow), ventrally of *m4*; note *m4* and *m5* proximity (yellow arrow).

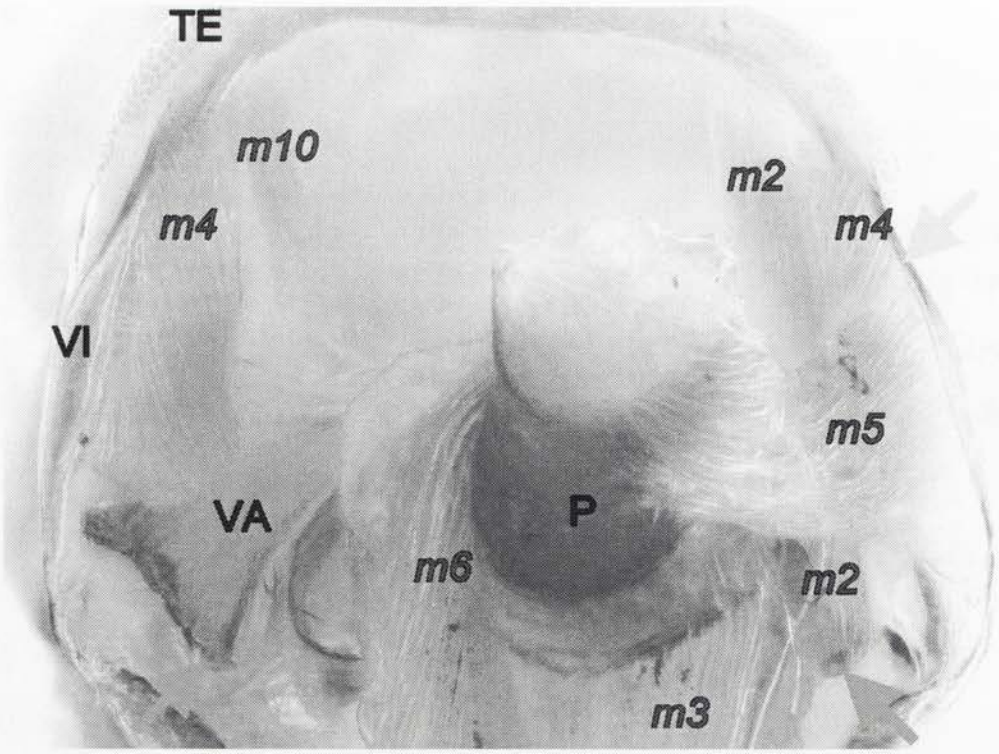

Fig. 116: *Agrius convolvuli* (Sphingidae), ♂, anterior view - *m2* attachment (green arrows) to the apex of the cephalo-ventral lever of the dorso-basal valva apodeme, ventrally of *m4*; *m2* and *m5* are removed in left half, revealing lever (left green arrow); note *m4* and *m5* proximity (right yellow arrow).

m3:

A strong and rather short muscle which connects the juxta with the vinculum or with the valva and which seems to function as an indirect adductor of the valva. Its attachment to the juxta is on the dorsal or dorso-lateral juxta edge, irrespective of modifications of the juxta shape. Consequently, the position of the muscle attachment relative to other genital structures changes with modifications of the juxta. The other attachment point varies between the dorsal edge of the saccus base, which is the ventral part of the vinculum (Fig. 117), and the basal area of the ventral valva wall (Fig. 118). Intermediate attachments to both of these closely approximated, sclerotized structures occur. The muscle is entirely absent in taxa in which the juxta is extremely reduced to almost absent, e.g., in most Lasiocampidae.

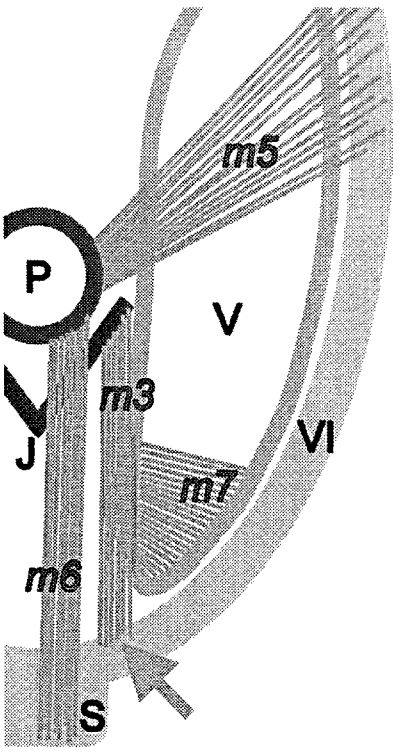

Fig. 117: Bombycoid complex, ♂, anterior view – scheme of *m3* attachment to the dorsal edge of the saccus base (green arrow).

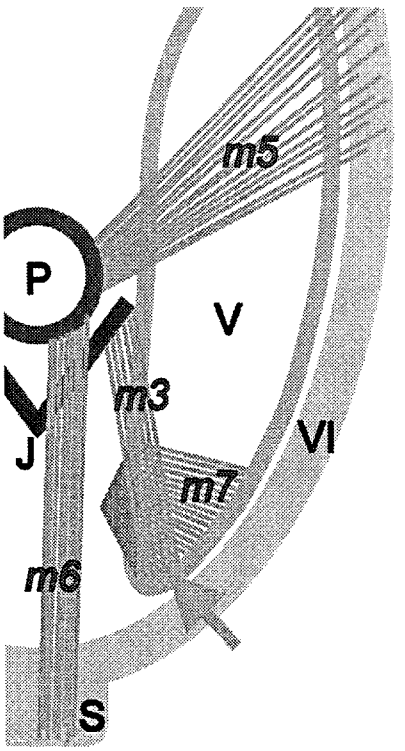

Fig. 118: Bombycoid complex, ♂, anterior view – scheme of *m3* attachment to the basal area of the ventral valva wall (green arrow).

m4 (Fig. 111):

A strong, rather broad and very short muscle which connects the vinculum with the valva and functions as an adductor of the valva. Its attachment to the anterior vinculum edge stretches from the dorsal vinculum end ventrad. Relative to the valva, this attachment to the vinculum is typically located at about the same level as – or slightly dorsally of – the dorsal valva edge. Further, this attachment of muscle *m4* to the vinculum is dorsally adjacent to muscle *m5*. The opposite attachment of muscle *m4* is along the lateral side of the dorso-basal apodeme of the valva, of variable length, and typically starting from near the apodeme base. The attachment of muscle *m4* to the vinculum is always spread out, while its attachment to the valva apodeme is focused onto a relatively smaller area in many taxa, resulting in a fan-shaped appearance of the muscle. The muscle is rarely lost, e.g., in some Lasiocampidae.

m5:

A strong, long muscle which connects the phallus with the vinculum and functions as a protractor of the phallus. Its attachment to the phallus is located at the lateral side of the anterior phallus end, which is typically the anterior end of a coecum. The opposite attachment point is the anterior edge and/or the mesal side of the dorso-lateral part of

the vinculum, just ventrally of *m4* (Fig. 119). A gradual shift from the mesal side of the vinculum onto the basal part of the inner lateral side of the valva can be concluded from transformation series, in which case the muscle functions not only as a phallus protractor but simultaneously as an adductor of the valva, too (Fig. 120). Any dorsal or ventral shift of the attachment to the vinculum, as well as the shape of the phallus and its coecum, influence the angle at which the phallus is pushed outwards. This muscle is present in all taxa.

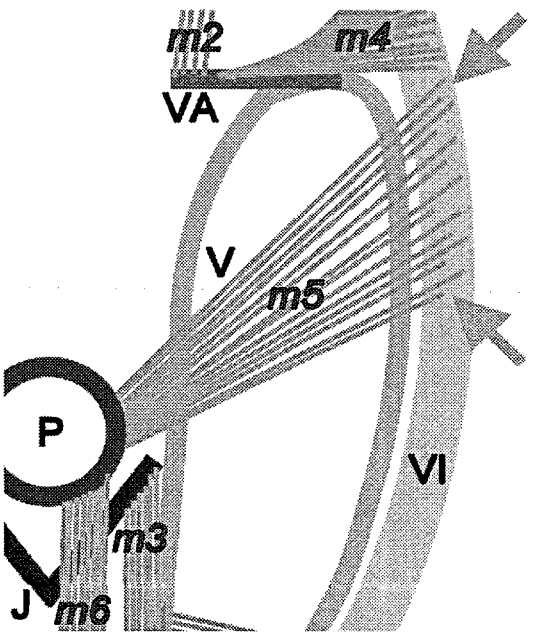

Fig. 119: Bombycoid complex, ♂, anterior view – scheme of *m5* attachment to the dorso-lateral part of the vinculum (green arrows).

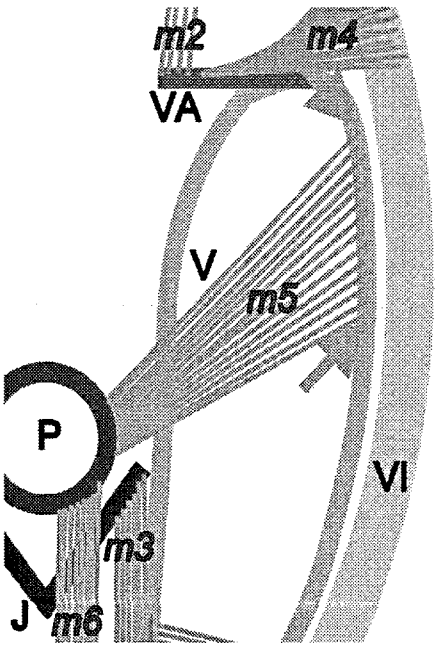

Fig. 120: Bombycoid complex, ♂, anterior view – scheme of *m5* attachment to the dorso-lateral part of the valva (green arrows).

m6 (Fig. 111):

A well developed muscle of variable length which connects the phallus with the vinculum and functions as a retractor of the phallus. Its attachment point on the phallus is located as far posteriorly as possible, at the zone, and can be on any side of the phallus – dorsal, lateral or ventral. Its other attachment is to the apex of the saccus, and/or to the lateral side of the saccus in some taxa. This muscle is present in all taxa.

m7 (Fig. 111):

A broad, flat muscle within the valva which tilts the clasper (if present) inwards and bends the distal part of the valva inwards, too. One attachment of the muscle is along the inner side of the basal valva edge. It is typically located in the ventral half of the lateral valva wall and frequently extends to the basal edge of the ventral or even ventro-mesal part of the wall. The opposite attachment is to the inner side of the mesal wall of

the valva, rather broadly spread out at or just proximally of the heavily sclerotized process termed "clasper". This position is retained in taxa which have lost the clasper. Even in taxa with very short valvae this muscle is present, but it is lost in some lasiocampid taxa with extremely modified valvae.

m10 (Fig. 111):

A feeble to moderately developed muscle of variable length which connects the tegumen with the anal cone and functions as an anal cone / subscaphium adductor in taxa of the bombycoid complex, rather than as an anal cone retractor as in other Lepidoptera. Its attachment to the tegumen is located near the tegumen middle, mesally of muscle *m2* if present, and adjacent to, but not on, the anterior tegumen edge. The opposite attachment is to the ventro-lateral part of the anal cone wall, at a variable distance from the anal cone apex. Depending on the degree of sclerotization of the ventral anal cone wall this might be to the lateral edge of a subscaphium. This muscle is easily destroyed during the preparation of samples, in particular by the removal of the anal tube in dried specimens, and hence its apparent absence in some taxa is likely to be an artefact in a number of my preparations.

m29 (Fig. 111):

A very feeble muscle which connects the lateral part of the ring formed by the fused tegumen and vinculum (the "annulus" of Kuznetzov and Stekolnikov (1985, 2001)) with the diaphragma. Its attachment to the annulus is at the fusion zone of tegumen and vinculum, between *m2* and *m4*. Its other attachment is to the diaphragma near the ventral end of the anal cone, in some taxa to the ventro-lateral end of the subscaphium. This muscle has been lost in most taxa, but occasional destruction of this thin muscle during preparation of the samples seems likely. The exact attachment to either tegumen or vinculum in the annulus is difficult to identify, and my hypotheses of homology of this muscle between the taxa examined as well as of homology with *m29 sensu* Kuznetzov and Stekolnikov (2001: 24-25) are only poorly supported. This is particularly the case in taxa in which this muscle attaches ventrally of muscle *m4* (potentially being part of *m4*), e.g., *Hoplojana* sp. near *rhodoptera* (Eupterotidae) (Fig. 121). Hence I do not use this muscle as a character for my phylogenetic hypotheses. However, I include it as "*m29*" in my descriptions of male genital muscles, as it potentially represents unique modifications and requires further study.

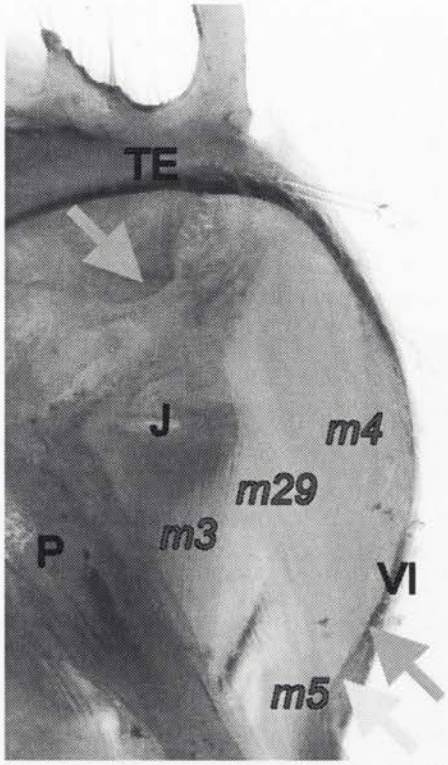

Fig. 121: *Hoplojana* sp. near *rhodoptera* (Eupterotidae), ♂, anterior view – muscle *m29* attaches to the diaphragma near the ventral end of the anal cone (green arrow) and ventrally of muscle *m4* to the annulus (rather than dorsally of *m4*, which is why this muscle might not be homologous with *m29* in other taxa).

III.2.2) Principles derived for the bombycoid complex

My study and the published illustrations of male genital muscles within the bombycoid complex allow some general conclusions to be drawn:

A) Genital muscles are highly conservative and show much less evolutionary modifications than the sclerotized, external genital structures to which they are attached. This is true for their points of attachment as well as for their size. Consequently, they can be valuable indicators of homologies between highly modified, sclerotized, external genital structures.

B) No intraspecific variation in muscle attachment or muscle size seems to occur.

C) Seemingly "new" muscles are merely the result of a division of the muscle fibres of one muscle at one attachment point of the muscle – the muscle splits up into two branches at one end (e.g., *m3* and *m6* in *Hopliocnema brachycera* (Sphingidae); *m5* in *Aurivillius fuscus* (Saturniidae)).

D) Within the bombycoid complex, if not within Macrolepidoptera, major modifications are typically limited to:

- A shift of the attachment point of muscle *m3* from the ventral part of the vinculum (Fig. 117) to the ventral edge of the valva (Fig. 118) (with intermediate forms), while the dorso-lateral edge of the juxta remains the opposite point of attachment.
- A shift of the point of attachment of muscle *m5* from the dorsal end of the vinculum (Fig. 119) to the latero-basal edge of the valva (Fig. 120) (with intermediate forms), while the lateral side of the anterior phallus end remains the opposite point of attachment.
- Loss of muscles *m2* and *m29*.
- Splits of muscles at one point of attachment.

These modifications occur rather frequently and can even be found within a genus (e.g., a shift of *m3* in *Lemonia*), which is why they are of very limited phylogenetic value. Between macrolepidopteran superfamilies and between at least some bombycoid families, these modifications are certainly homoplastic.

E) In most taxa the sclerites of the tegumen and vinculum are fused entirely to form a sclerotized ring, the "annulus" of Kuznetzov and Stekolnikov (1985). This fusion does not occur between the opposite tips of the lateral ends of the tegumen and vinculum, but along a lateral overlap of the sclerite ends, at which the tegumen is located posteriorly to the vinculum (Fig. 122). In a number of taxa of various families

the extent of the fused sclerites within the annulus can be deduced from minor marks and slight differences in the degree of sclerotization between tegumen and vinculum (Fig. 123). In all of these taxa, this mark corresponds with the position and extent of muscle *m4*, which always attaches to the dorsal end of the vinculum. Even in taxa with a broad annulus, muscle *m4* extends only on a narrow strip along the anterior edge of the annulus – along the vinculum, anteriad to the tegumen.

Muscle *m4* is a very short, broad and often seemingly fan-shaped muscle that connects the dorsal end of the vinculum with the dorso-basal apodeme of the valva. Depending on the dorsal extent of the valva, *m4* appears to be shifted correspondingly on the annulus. Hence in some cases *m4* appears to be shifted dorsad from the vinculum onto the tegumen, e.g., in *Opodiphthera eucalypti* (Saturniidae), in which the valva extends as far dorsad as to the uncus. However, careful examination of the sclerites indicates that *m4* is not shifted onto the tegumen, but that instead the vinculum extends further dorsad as a very narrow strip, and muscle *m4* with it. The most extreme dorsal extent of the vinculum is present in some Lasiocampidae, as discussed below (see section III.2.3.A).

These observations argue for an attachment of genital muscles to sclerites ontogenetically prior to secondary fusions of sclerites. Hence a transfer of a muscle attachment from one sclerite to another seems likely to occur by a gradual shift between sclerites that are closely approximated at the time of muscle development, rather than as a "jump" between widely separated or only secondarily fused sclerites. Such a transformation series can be observed in muscles *m3* and *m5*, which are relatively more variable in their attachment points than other muscles. They frequently show intermediate positions, attaching continuously across two very closely approximated sclerites as well as to the membrane between them (e.g., *m3* in *Actias artemis* (Saturniidae) and in *Lemonia balcanica* (Lemoniidae); *m5* in *Anthela excellens* (Anthelidae; Fig. 146) and in *Hopliocnema brachycera* (Sphingidae)).

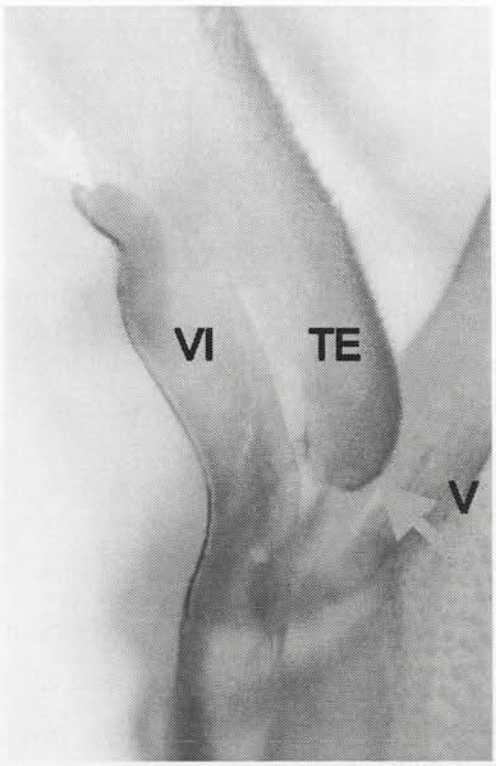

Fig. 122: *Agrotis infusa* (Noctuidae), ♂, lateral view (posterior to the right) – overlap of tegumen (green arrow marks end) and vinculum (yellow arrow marks end); note the difference in surface structure (tegumen "coarse" and with hairs).

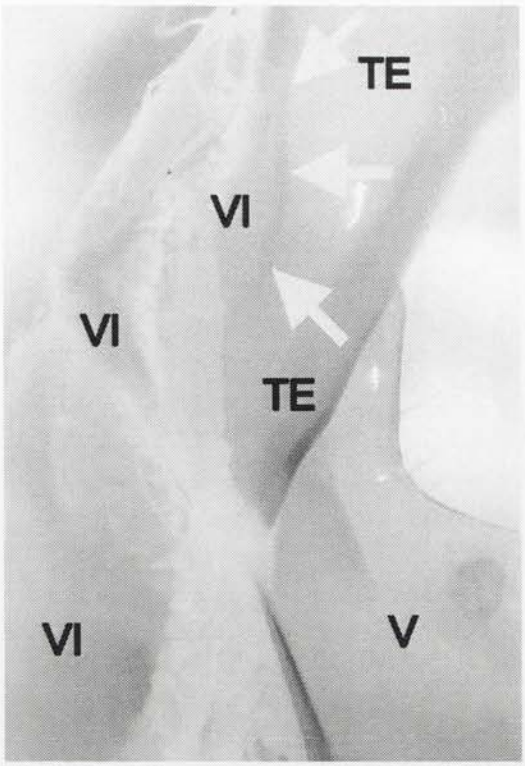

Fig. 123: *Endromis versicolora* (Endromidae), ♂, lateral view (posterior to the right) – overlap of fused tegumen and vinculum; note the dark line (yellow arrows) indicating the extent of the vinculum in the pharate specimen.

III.2.3) Errors in literature

Some publications contain mistakes that have been used in, or are significant for, phylogenetic hypotheses and need to be corrected.

III.2.3.A) The dorso-lateral attachment of muscle *m4* in Bombycoidea

A chain of mistakes led to a very significant erroneous conclusion, a presumed synapomorphy of Bombycoidea *sensu* Kuznetzov and Stekolnikov (1985) and later *sensu* Lemaire and Minet ([1998]). Kuznetzov and Stekolnikov (1985: 48) state in their English summary: "Bombycoidea (Saturniidae, Brahmaeidae, Endromidae, Bombycidae and oth.) is monophyletic. There is a secondary, common with Sphingoidea, type of muscules insertion in this superfamily, in which tergal flexors of valvae (m_4) insert to the **dorsoventral** area of annulus.". Probably referring to the English summary, Lemaire and Minet ([1998]: 324) list this statement as an unexplained synapomorphy of Bombycoidea: "male genitalia with a modified position of "muscles 4" (Kuznetzov & Stekolnikov 1985)".

An attachment point to the "**dorsoventral** area of annulus" is illogical and merely a mistake in the English summary of Kuznetzov & Stekolnikov (1985: 48). I have translated their original Russian text, which states in the conclusion (1985: 44): "Подтверждается монофилетичность надсем. Bombycoidea. У исследованных представителей этого таксона из сем. Saturniidae, Brahmaeidae, Endromidae и Bombycidae развит общий со Sphingoidea вторичный тип прикрепления флексоров вальв (m_4) в **дорсолатеральной** области аннулуса,..." ["The monophyly of the superfamily Bombycoidea is confirmed. In the examined representatives of this taxon of the families Saturniidae, Brahmaeidae, Endromidae and Bombycidae, shared with Sphingoidea, a secondary attachment of the valva flexor (m_4) to the **dorso-lateral** region of the annulus has developed,..."].

The drawings of Kuznetzov and Stekolnikov (1985) illustrate such an attachment of *m4* to the dorso-lateral area of the annulus, and my own observations confirm this for other taxa of the Bombycoidea *sensu* Lemaire and Minet ([1998]), as well as for Anthelidae. Muscle *m4* attaches, as in other Macrolepidoptera, to the dorsal end of the vinculum, at about the same level as the dorsal edge of the valva. Relative to the entire annulus, this is a dorso-lateral position in these taxa (Figs 124-126).

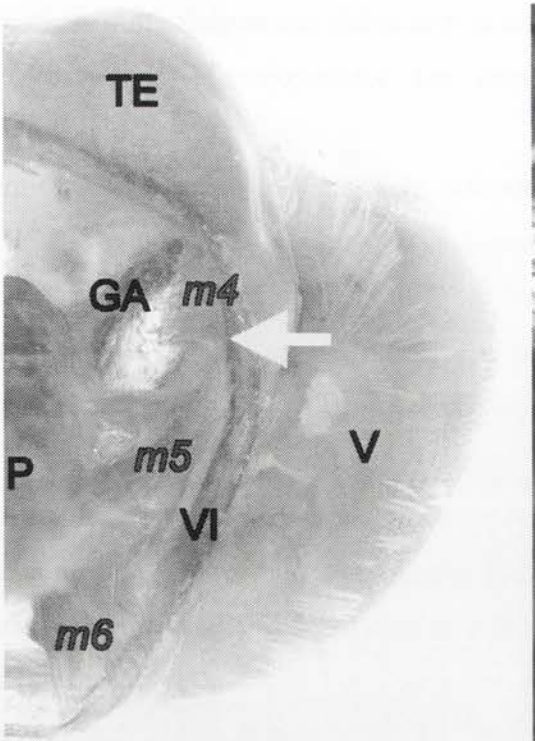

Fig. 124: *Aglia tau* (Saturniidae), ♂, anterior view – *m4* is in a dorso-lateral position on the annulus; note the proximity of *m4* and *m5* (yellow arrow).

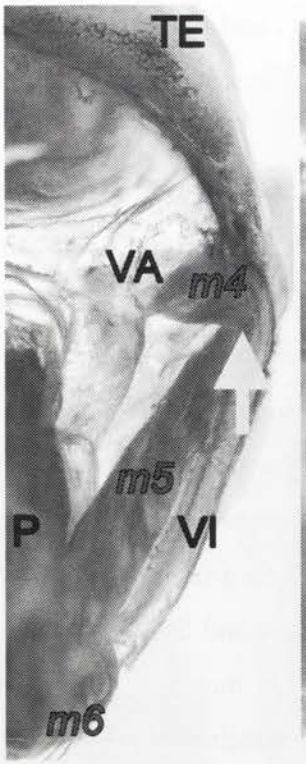

Fig. 125: *Anthela euryphrica* (Anthelidae), ♂, anterior view – *m4* is in a dorso-lateral position on the annulus; note the proximity of *m4* and *m5* (yellow arrow).

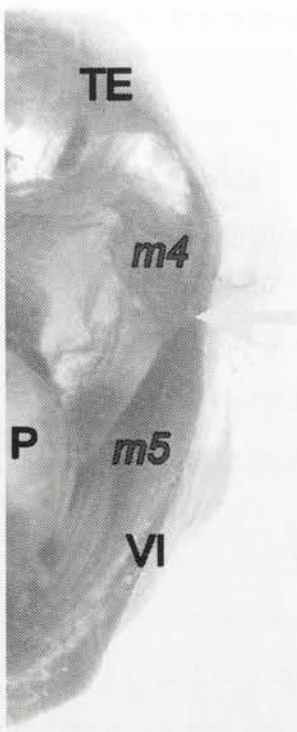

Fig. 126: *Poecilocampa populi* (Lasiocampidae), ♂, anterior view – *m4* is in a dorso-lateral position on the annulus; note the proximity of *m4* and *m5* (yellow arrow).

However, Kuznetzov and Stekolnikov assumed this dorso-lateral position to correspond to an attachment of *m4* to the tegumen, rather than to the vinculum: "... верхнебазальному углу вальв обычно подходят 2 пары мышц (m_2 и m_4), причем они начинаются на **тегумене**." ["... the upper-basal angle of the valva is usually approached by 2 pairs of muscles (m_2 and m_4), which originate on the **tegumen**."] (Kuznetzov & Stekolnikov 1985: 31). Such an attachment to the tegumen contrasts with an attachment to the vinculum, a condition Kuznetzov and Stekolnikov assumed to be present in Lasiocampoidea: "В надсем. Lasiocampoidea сохраняется первичное состояние мышц m_4 с прикреплением их к **винкулуму** и ряд других архаичных особенностей в строении гениталий у имаго, а также в признаках гусениц и куколок, что позволяет признать этот таксон более генерализованным и древним, чем Sphingoidea и Bombycoidea." ["In the superfamily Lasiocampoidea remains the primary state of muscles m_4 with their attachment to the **vinculum** and a number of other archaic special features in the structure of genitalia of the imago, and also in the

characters of caterpillars and pupae, which makes it possible to recognize this taxon as more generalized and ancient than Sphingoidea and Bombycoidea."] (Kuznetzov & Stekolnikov 1985: 43).

The occurrence of the presumed plesiomorphic attachment of muscle *m4* to the vinculum in the "archaic sistergroup Lasiocampoidea" (Kuznetzov & Stekolnikov 2001: 371) is probably the reason why Kuznetzov and Stekolnikov assumed the attachment of *m4* to the tegumen to be a synapomorphy of Bombycoidea (and Sphingoidea). Otherwise, such a dorso-lateral attachment, as present in Bombycoidea and Lasiocampoidea, is very widespread in at least Macrolepidoptera.

Unfortunately, the assumed ventro-lateral attachment of muscle *m4* to the annulus in Lasiocampidae is based on a misinterpretation of muscles. For the genera *Gastropacha* and *Odonestis*, Kuznetzov and Stekolnikov (1985) incorrectly identified part of the split intra-valvar muscle *m7* as muscle *m4*. This misinterpretation in these taxa is due to a modified valva and an attachment of a part of *m7* to the vinculum, rather than to the latero-basal edge of the valva. Consequently, they identified muscle *m4* as muscle *m2*, an interpretation seemingly supported by its attachment to the dorsal part of the annulus. In *Gastropacha* spp., a secondary, local reduction of the annulus further feigns an "obvious" separation into tegumen and vinculum, which led them to a misidentification of the dorsal part of the vinculum as the tegumen.

My own examinations of specimens belonging to the genera *Gastropacha*, *Odonestis*, *Trabala* and *Crinocraspeda* show that in these taxa the tegumen is extremely reduced and replaced by a dorsally enlarged vinculum. The vinculum ends are mesally fused with each other, as well as with the tegumen remnants. In some taxa a very distinct median gap is retained in the dorsal part of the annulus, indicating this condition (Figs 127, 128). No such median gap is present in a fully developed, "normal" lasiocampid tegumen (Fig. 129, 130). As in other Macrolepidoptera, muscle *m4* attaches to the dorsal end of the vinculum in *Gastropacha*, *Odonestis*, *Trabala* and *Crinocraspeda*. However, in these taxa the extreme dorsal growth of the vinculum results in a dorso-lateral to dorsal attachment of *m4* on the annulus (Fig. 127). While a strong to total reduction of the tegumen is common to many Lasiocampinae, the extreme dorsal expansion and mesal fusion of the vinculum coupled with a reduction of the tegumen and a strong enlargement of muscle *m4* is a very characteristic synapomorphy of those four and many other closely related genera, currently placed in separate tribes or subfamilies by some

authors (e.g., Zolotuhin & Witt 2000).

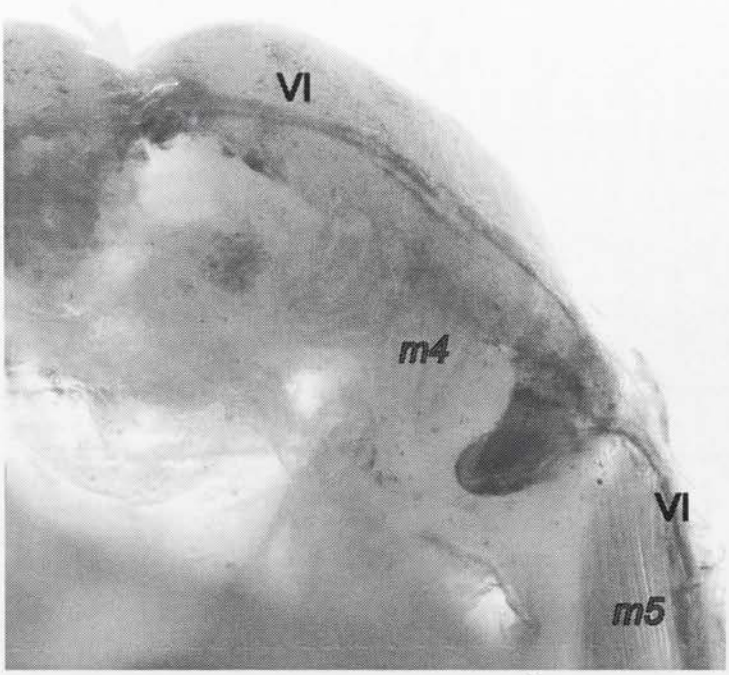

Fig. 127: *Gastropacha* n. sp. (Lasiocampidae), ♂, anterior view – *m4* is in a dorsal position on the annulus, filling the entire dome-shaped dorsal part of the enlarged vinculum; note the remaining gap between the two halves (yellow arrow), filled by the tegumen remnant (no median gap occurs within the tegumen).

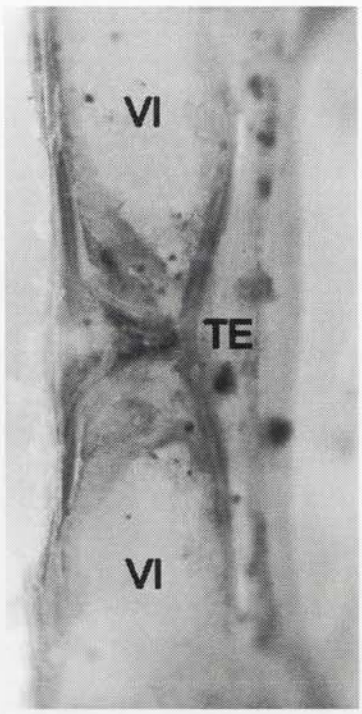

Fig. 128: *Crinocraspeda torrida* (Lasiocampidae), ♂, dorsal view (posterior to the right) – fusion between the two dorsally expanded vinculum ends, which are also fused to the posterior remnants of the tegumen.

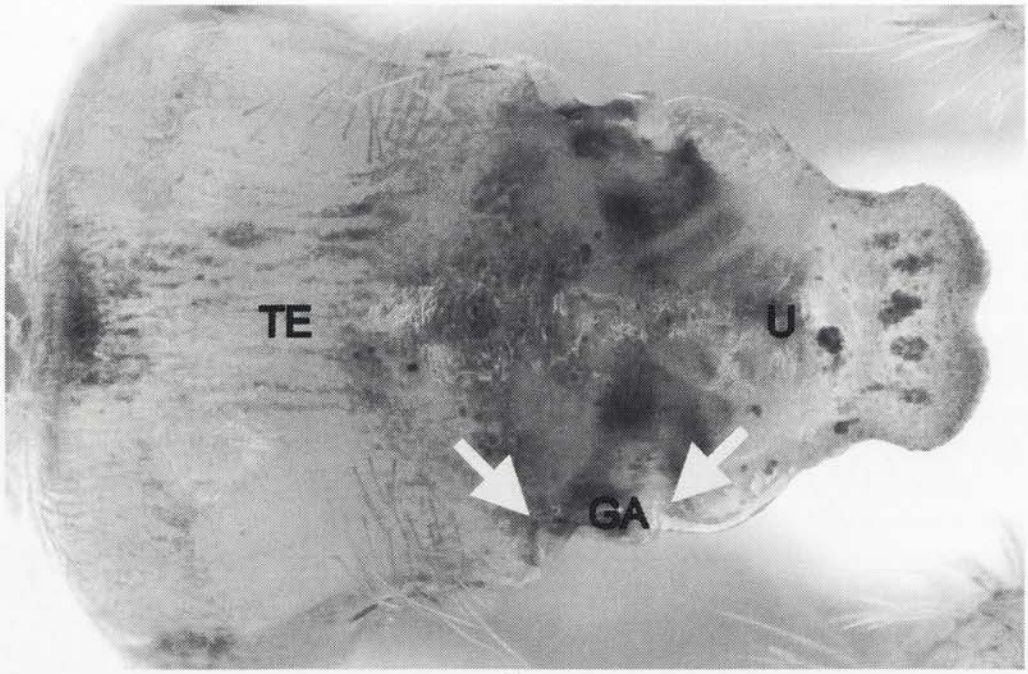

Fig. 129: *Poecilocampa populi* (Lasiocampidae), ♂, dorsal view (posterior to the right) – tegumen, uncus and gnathos attachment (yellow arrows mark the position of the gnathos arm attachment); note the absence of a gap in the tegumen.

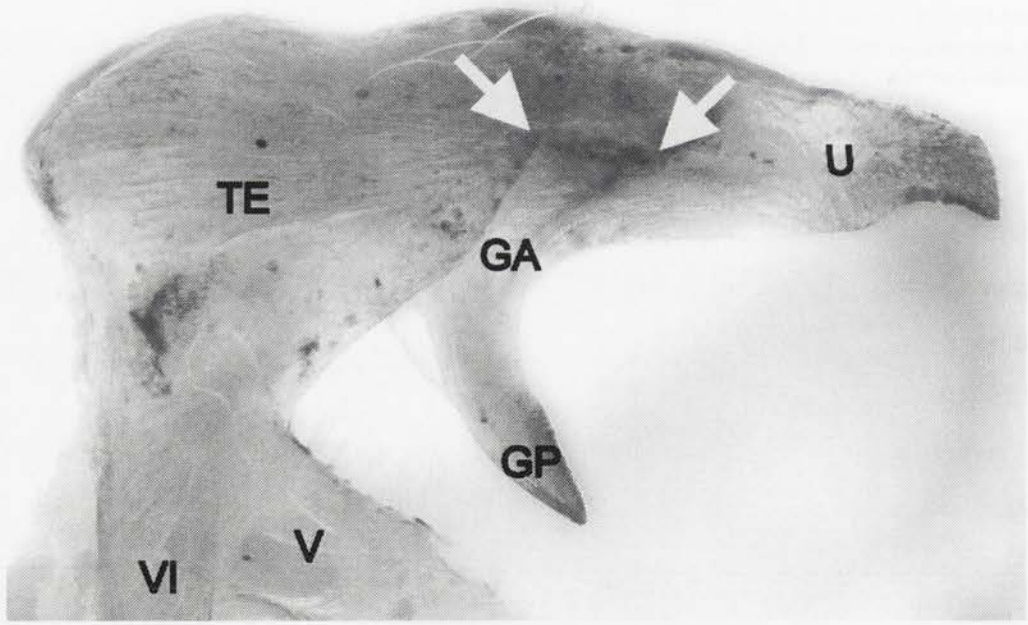

Fig. 130: *Poecilocampa populi* (Lasiocampidae), ♂, lateral view (posterior to the right) – tegumen, uncus and gnathos attachment (yellow arrows mark the position of the gnathos arm attachment); note the large distance between gnathos plate and valva.

In contrast to this greatly modified condition of the vinculum and muscle *m4*, muscle *m4* is located in the typical dorso-lateral position on the annulus in *Poecilocampa populi*. *P. populi* is a species with, for Lasiocampidae, largely plesiomorphic male genital structures (Fig. 126). This species was examined by Stekolnikov and Zolotukhin

(1994), and their drawing was reprinted in Kuznetzov and Stekolnikov (2001), illustrating *m4* in a distinctly more dorsal position than it is in the three specimens I examined.

Kuznetzov and Stekolnikov (2001; except for fig. 128Г) subsequently corrected their initial misidentification (1985) of muscles *m4* and *m7*. They retained the idea of a plesiomorphic type of *m4* attachment to the vinculum in some Lasiocampidae, as exemplified in *P. populi* (2001: 370). However, the previously assumed synapomorphic attachment of *m4* to the tegumen (the dorso-lateral position in the annulus) in Bombycoidea was quietly dropped, as reflected in their statement on the synapomorphies of Bombycoidea: "Надсем. Bombycoidea характеризуется единственным объединительным признаком гусениц, у которых хотя бы некоторые первичные щетинки замещены бородавками или колючками." ["Superfamily Bombycoidea is characterized by the only unifying character in caterpillars, in which at least some primary setae are substituted by scoli or thorns."] (2001: 372).

In summary, muscle *m4* attaches to the dorsal end of the vinculum, which is in a dorso-lateral position relative to the annulus in all families of the bombycoid complex. No difference exists between Lasiocampidae, Anthelidae or other members of the bombycoid complex, and this type of attachment is widespread in Macrolepidoptera. Hence no synapomorphic muscle attachment of muscle *m4* exists for Bombycoidea *sensu* Kuznetzov and Stekolnikov (1985) or *sensu* Lemaire & Minet ([1998]).

III.2.3.B) The presence of muscle *m2* in Saturniidae

Another error in literature concerns the alleged presence of muscle *m2* in Saturniidae. Birket-Smith studied male genital muscles of African moths in great detail, describing and illustrating them for a few bombycoid taxa (Birket-Smith 1974: 13-18). His drawings of *Pselaphelia gemmifera* (Saturniidae) show two muscles, labelled "4" and "3", respectively, as attaching to the dorso-basal valva edge, as well as a structure labelled "plica centripetalis" (1974: 16, fig. 12). Birket-Smith states in his description of *P. gemmifera* (1974: 17): "A well developed muscle, m. 3, runs from middorsally on tegumen to the dorso-proximal, heavily sclerotized corner of the valva; to the same part runs a very strong, fanshaped muscle, m. 4, originating from the entire lateral edge of vinculum, *vi.* The strongly sclerotized dorso-proximal corner of the valva apparently represents the proc. momenti, even if nothing like a process is visible; on the other hand, from this corner originates a small mesad directed hook, *pc*, probably the modified plica centripetalis."

His illustrations and his explicit description in particular match exactly those muscles that Kuznetzov and Stekolnikov (2001) refer to as muscles *m2* and *m4* in other Macrolepidoptera, leaving no doubt about their homology. Kuznetzov and Stekolnikov recognized the significance of the occurrence of muscle *m2* in *P. gemmifera*, as this muscle has not been found in any other saturniid species examined to date. They concluded: "Значительной архаичностью вальварной мускулатуры отличается африканский род *Pselaphelia* Auriv., так как только в гениталиях исследованного представителя (*P. gemmifera* Btl.) этого рода найдены мышцы m_2, хотя нарядус этим редуцирован ункус и его депрессоры (m_1)." ["The significant archaicness of valvar musculature is characterized by the African genus *Pselaphelia* Auriv., since only in the genitalia of the investigated representative of this genus (*P. gemmifera* Btl.) muscles m_2 are found, although otherwise the uncus and its depressors (m_1) are reduced."] (2001: 373).

I examined a specimen of *P. gemmifera* and of *P. flavivitta* (Saturniinae: Urotini *sensu* Oberprieler (1997)). None of my specimens had a muscle *m2* or traces of it (Fig. 131). My own observations on both *Pselaphelia* species differ from Birket-Smith's drawings in several aspects. In his drawings the tegumen is broader, the dorsal part of the vinculum narrower (in fig. 12B only), and the valva is located further ventrally. In exactly the position of his muscle "m. 3" (the presumed muscle *m2*) the lateral "arms" of

a well developed gnathos are located in my specimens, while the central "plate" of this gnathos is fused to the valvae at the position of his "plica centripetalis" (Fig. 132). He does not mention the occurrence of a gnathos, and as in a dried specimen the "gnathos arms" are of the same colour as the dried muscles, they might have been misinterpreted by him as such. In none of the two *Pselaphelia* species is muscle *m2* present. Only a huge, fan-shaped muscle *m4* connects the greatly expanded dorso-lateral part of the vinculum with the dorso-basal edge of the valva and the fused gnathos, as this muscle does in other saturniid species (e.g., *Aglia tau*). Hence no muscle *m2* has been found in any of the relatively few saturniid species examined so far, and the genital muscles of *Pselaphelia* do not represent an archaic type of valva musculature as interpreted by Kuznetzov and Stekolnikov (2001: 373). To the contrary, the male genital structures of *Pselaphelia* (and probably other Urotini *sensu* Oberprieler (1997)) are highly modified. Their sternite VIII and modified muscles form an unpaired, ventral "clasper", and the modified tergite VIII ("pseuduncus" of Birket-Smith, 1974) probably functions as its abutment.

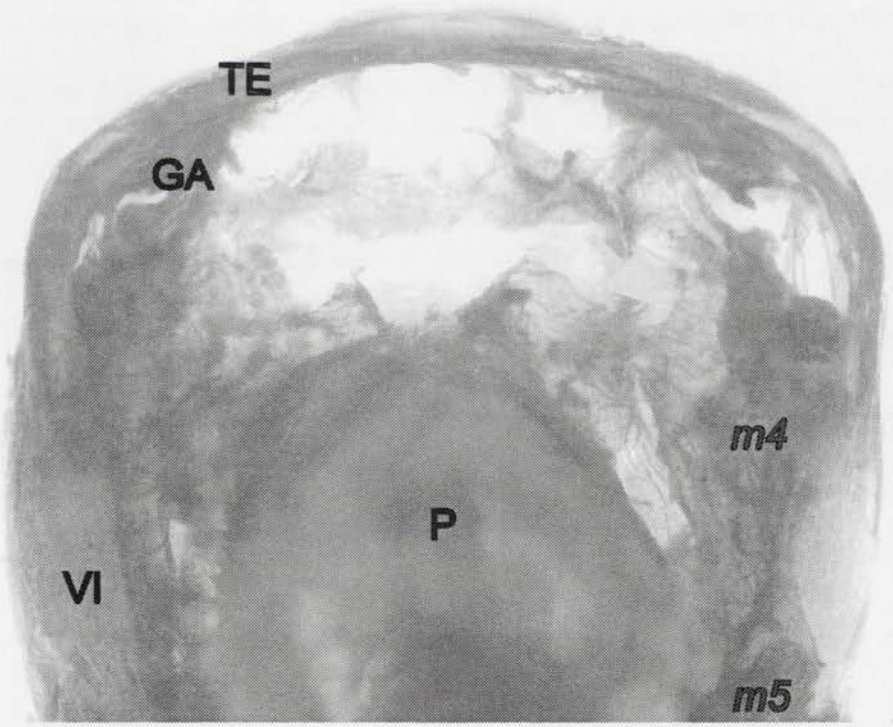

Fig. 131: *Pselaphelia flavivitta* (Saturniidae), ♂, anterior view – *m4* is well developed (yellow arrow marks attachment to the fused valva and gnathos), *m2* is absent; note the mesally protruding gnathos arm (GA) in dorso-lateral position.

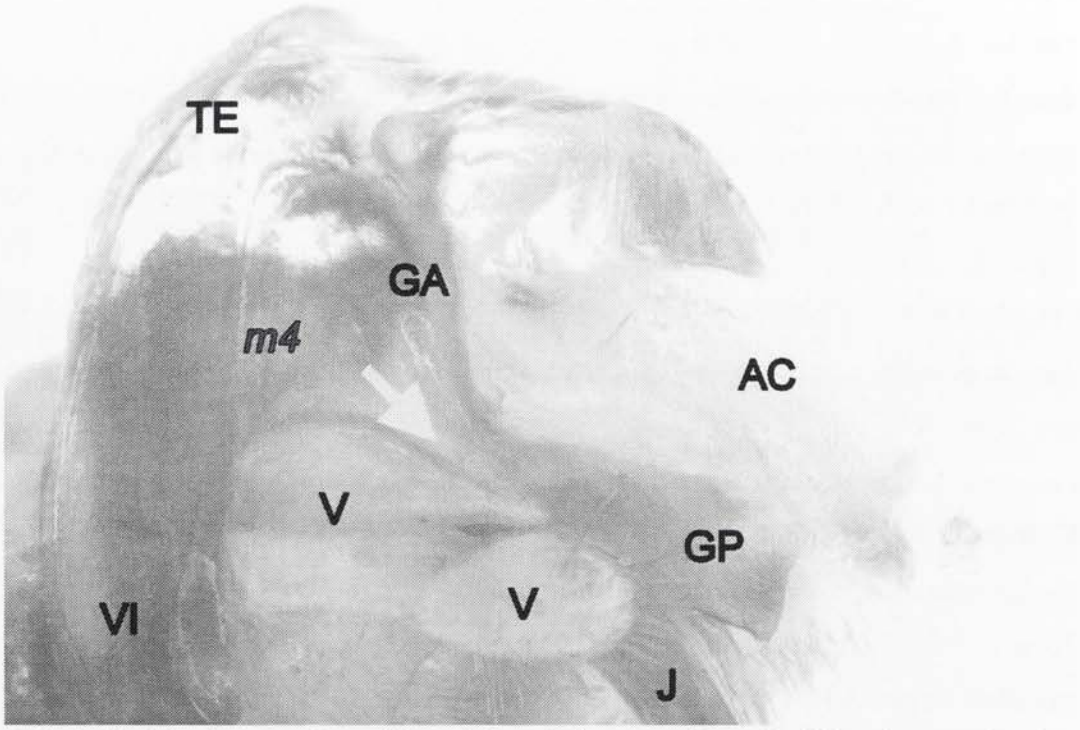

Fig. 132: *Pselaphelia flavivitta* (Saturniidae), ♂, lateral view (posterior to the right) – large gnathos is fused to valva (yellow arrow marks area of fusion).

III.2.3.C) The attachment of muscle *m3* in Endromidae

The male genital muscles of Endromidae were illustrated and described by Kuznetzov and Stekolnikov (1985, 2001). According to them, muscle *m3* attaches to the basal edge of the ventral valva wall in *Endromis versicolora* (Endromidae) as well as in *Mirina christophi* (Mirinidae). However, in the pharate male specimen of *Endromis versicolora* I examined, muscle *m3* only appears to attach to the valva, but instead attaches to the very closely approximated vinculum and the ventral edge of the connecting membrane (Fig. 133).

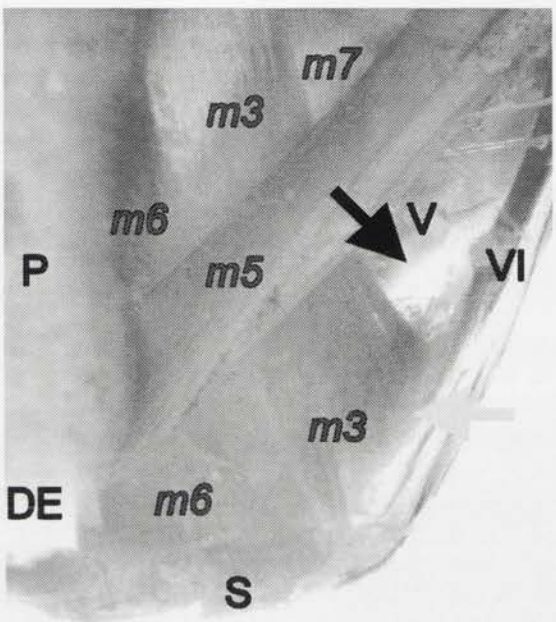

Fig. 133: *Endromis versicolora* (Endromidae), ♂, anterior view – *m3* attaches to the vinculum (yellow arrow), not to the valva; note the gap between the vinculum and the valva (black arrow).

III.2.4) Character analyses of male genital muscle characters

Of the few differences I observed in male genital muscles, I assume the following to be informative characters for my hypotheses on the phylogeny of Anthelidae and the bombycoid complex:

Character #H.38: Muscle *m5* attaches to the vinculum posteriorly to muscle *m4* ("overlapping").

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; moderately supported.

Introduction. In Macrolepidoptera muscles *m4* and *m5* both attach to the vinculum, with muscle *m5* being ventrally adjacent to *m4*, generally irrespective of the dorsal extent of the vinculum (Figs 114, 115, 126, 134, 135, 144). This attachment of *m5* is largely to the anterior edge, and in many taxa to a lesser degree to the mesal side of the vinculum, too. Muscle *m5* attaches directly ventrally of *m4* (Fig. 134, 135) and at the very most overlapping with *m4* by a few muscle fibres only. This condition is present in members of the bombycoid complex families Mimallonidae, Lasiocampidae, Endromidae and Bombycidae, as well as probably Mirinidae. In contrast, this position of *m5* has been modified as described below in some bombycoid complex families, namely Carthaeidae, Sphingidae, Saturniidae, Anthelidae and Eupterotidae, as well as probably Brahmaeidae and Lemoniidae.

Description. In the aforementioned families muscle *m5* attaches distinctly posteriorly to *m4*, at the same level as or even dorsally of *m4*, rather than to the anterior vinculum edge and directly ventrally of *m4*. Depending on the position and extent of *m4*, this arrangement appears as a minor to very large overlap of *m4* and *m5* in lateral view, with *m5* passing laterally of *m4* (Figs 136, 137). Irrespective of the extent of the overlap, *m5* attaches to the posterior area of the mesal side of the vinculum, rather than to the anterior edge of the vinculum.

Discussion. With *m4* attaching to the mesal side of the vinculum, an attachment of *m5* to the mesal side posterior to *m4* requires a broadening of the vinculum. In these bombycoid families the fused vinculum and tegumen form a particularly broad part of the annulus. The origin of such a broad annulus seems to be preserved in some taxa

with, for their respective family, largely plesiomorphic genital structures. In these taxa additional space for the attachment of *m5* is provided by a posteriad protruding lobe. This lobe is part of the dorsal end of the vinculum, not of the posteriorly located end of the tegumen. The basic structure of the dorsal vinculum end of this type is most distinct in the eupterotid species *Ganisa plana*, in which it appears to have two protrusions (Fig. 138). The dorsal, more anterior protrusion is the typical dorsal end of the vinculum, which is located anteriorly to the tegumen in Macrolepidoptera (Fig. 122). It is the principal attachment area of muscle *m4*. The other protrusion is located further ventrally, at the same level as or just ventral ly of the dorsal edge of the valva. It extends posteriad beyond the remainder of the vinculum and even beyond the membrane which connects the vinculum with the valva. Hence, together with the connecting membrane, it forms a double-walled lobe which extends for a short distance parallel to and laterally of the valva. The mesal side of the posterior protrusion is the principal attachment area of muscle *m5*. The dorsal and posterior protrusions are interconnected by a membranous, triangular area, which stretches transversely between their apices and fills the gap between them.

While tegumen and vinculum are articulated with each other in *G. plana*, and hence their extent and shape are obvious, both these sclerites are firmly fused with each other in most bombycoid taxa. Such a fusion is part of a very common and highly homoplastic tendency to strengthen the frame (annulus), to which other genital structures attach. Any fusion obscures the extent and shape of tegumen and vinculum, and in most members of all bombycoid families an additional heavy sclerotization of the annulus renders a reliable distinction between tegumen and vinculum impossible.

Despite such a fusion, the shape of the vinculum is still discernible in some species, e.g., *Arsenura ciocolatina* (Saturniidae). In this species, which overall has plesiomorphic genital structures for Saturniidae, the shape of the vinculum is indicated by a slightly depressed suture (Fig. 139). As in *G. plana* the vinculum has a dorsal and a posterior protrusion, the latter stretching slightly beyond the remainder of the vinculum, parallel to the valva. The fused ventral tegumen end fills the space between the two protrusions of the vinculum, seemingly "displacing" the membranous area postero-dorsad. I do not have a muscle preparation of *A. ciocolatina*, but in the related *A. xanthopus* muscle *m5* attaches to the posterior edge of the vinculum, distinctly overlapping with muscle *m4* as in the eupterotid species *G. plana*. In most other

saturniid taxa examined, the recognition of this character is obscured by a strong sclerotization of the annulus and modifications of the attachment of either *m4* or *m5*, but the posterior attachment of *m5* to the vinculum has generally been retained.

In Anthelidae the tegumen and vinculum are entirely fused with each other, too, but unlike in *A. ciocolatina* their lateral borders are no longer recognizable. However, the characteristic posterior protrusion of the vinculum beyond the membrane that articulates vinculum and valva is distinct in some taxa (Fig. 140). As in the eupterotid species *G. plana*, muscle *m5* attaches to the mesal side of this lobe, posteriorly to *m4*. The overlap of *m4* and *m5* is very distinct in these Anthelidae. However, in the majority of anthelid taxa, in all of which muscle *m5* is displaced far ventrad (see character #H.39), the posterior lobe of the vinculum is strongly reduced (Fig. 141). These taxa do not have an overlap of muscles *m4* and *m5*, because of the ventral shift of *m5*. Despite this ventral shift, muscle *m5* attaches still to the posterior edge of the vinculum or even further posteriorly to the basal edge of the valva, but never to the anterior edge of the vinculum. Consequently I score this character as present for all anthelid taxa with a ventrally shifted muscle *m5*, too, which is equivalent to combining the states of character #H.38 and #H.39 into a single, ordered multi-state character.

In the single examined specimen of *Anthela euryphrica*, which belongs to a group of taxa with a very distinct overlap of muscles *m4* and *m5*, a small but distinct gap separates the two muscles. This gap is much smaller than that in Anthelidae with a ventrally displaced muscle *m5*. As *A. euryphrica* is extremely similar in male genital structures to *A. repleta*, in which the overlap of muscles is very strong, I assume the minor gap in *A. euryprhica* to be either an anomaly of the examined specimen or to be a subsequent modification.

In some bombycoid taxa the complete fusion of tegumen and vinculum encloses the posterior lobe of the vinculum, e.g., in *Agrius convolvuli* (Sphingidae; Fig. 142). Independent of the exact arrangement of the fused tegumen and vinculum, this fusion eliminates many indications of the condition distinct in *G. plana*. Typically, only the posterior attachment of muscle *m5* and its overlap with *m4* remain, as well as a small to minute posterior extension of the vinculum sclerotization in some taxa, e.g., in *Carthaea saturnioides* (Carthaeidae; Fig. 143).

The attachment of *m5* to the anterior area of the vinculum, ventrally of *m4* [character state (0)], is common to many Lepidoptera examined by me or illustrated by Kuznetzov and Stekolnikov (2001), including some families of the bombycoid complex. Only in a number of other such families is a dorso-posterior shift of muscle *m5* present [character state (1)]. Hence I interpret character state (1) as apomorphic for these taxa.

As indications of character state (1) are typically obscured by the fusion of tegumen and vinculum, as well as by modifications of muscles *m4* and *m5*, many more taxa of all families of the bombycoid complex need to be examined than was feasible for this study. While I particularly examined representatives of the bombycoid complex that have, for their respective family, largely plesiomorphic genital structures, different character states might occur in non-examined members of these families. The problem of having examined only a comparatively small number of representatives of each family is accentuated by the only poorly supported monophyly of some families. In this respect the inclusion of Apatelodinae in Bombycidae is particularly critical, as the examined Bombycinae (*Ocinara* n. sp. and *Bombyx mori*) are inconclusive for this character due to a split of *m5*.

Summary. The modification of this muscle attachment is very characteristic in those taxa in which it is not obscured by the fusion of tegumen and vinculum. It consists of a dorso-posterior shift of the muscle *m5* attachment point, which is apparent as a distinct overlap with *m4*. Further, it involves the formation of a double-walled posterior lobe of the vinculum at a specific location to accommodate this attachment of *m5*. However, in the majority of taxa most of these indications are lost due to the secondary fusion of vinculum and tegumen. In these taxa, indications are frequently limited to an attachment of *m5* to the posterior edge of the vinculum and a (partial) overlap with *m4*. Further, subsequent modifications of the structures involved make the recognition of the original presence of the character state even more difficult. The ventral shift of muscle *m5* in most Anthelidae is an example of this problem. Consequently my hypothesis of homology of character state (1), the attachment of muscle *m5* to the vinculum posteriorly to muscle *m4*, is only moderately supported in the majority of taxa.

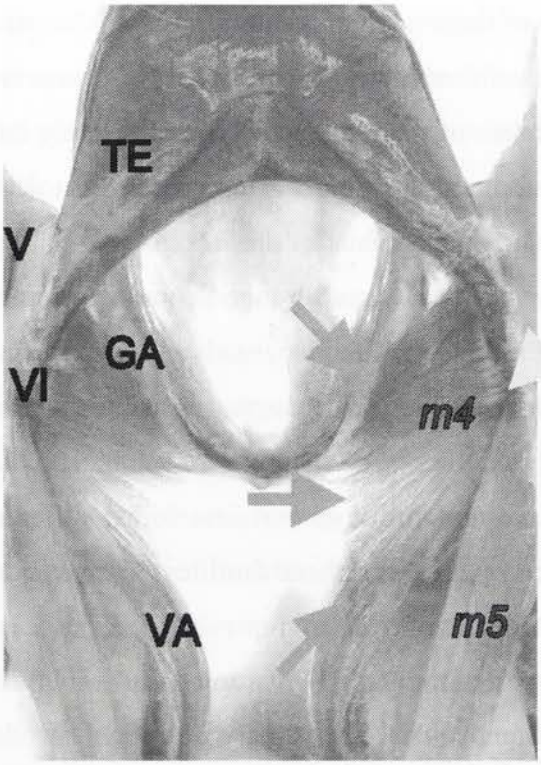

Fig. 134: *Cicinnus* sp. (Bombycidae: Apatelodinae), ♂, anterior view – *m5* attaches directly ventrally of *m4* to the anterior vinculum edge; note the unique shape of *m4*, which is mesally spread out (rather than focused) and largely attaches to the movable gnathos plate as well as to the valva (green arrows); note *m4* and *m5* proximity (yellow arrow).

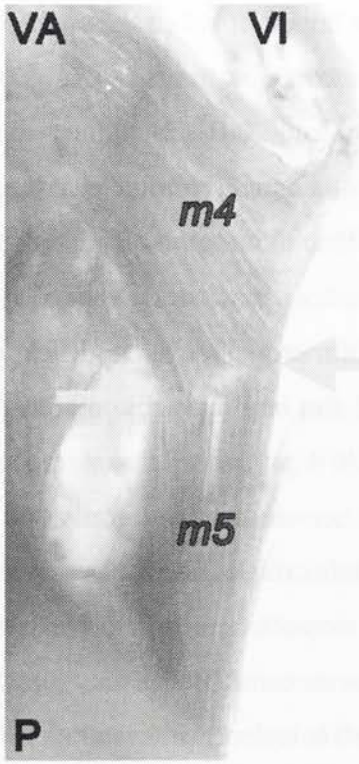

Fig. 135: *Poecilocampa populi* (Lasiocampidae), ♂, anterior view – *m5* attaches directly ventrally of *m4* to the mesal side and anterior edge of the vinculum (yellow arrows); note *m4* and *m5* proximity.

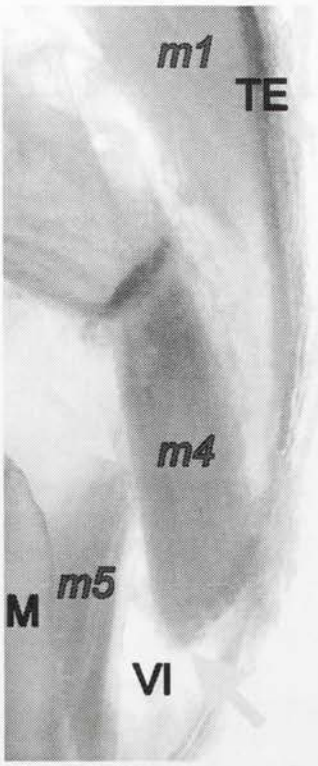

Fig. 136: *Munychryia senicula* (Anthelidae), ♂, anterior view – *m5* attaches to the vinculum dorsally of and posteriorly to *m4* ("overlapping" with *m4*; yellow arrows mark muscle ends); note *m4* and *m5* proximity.

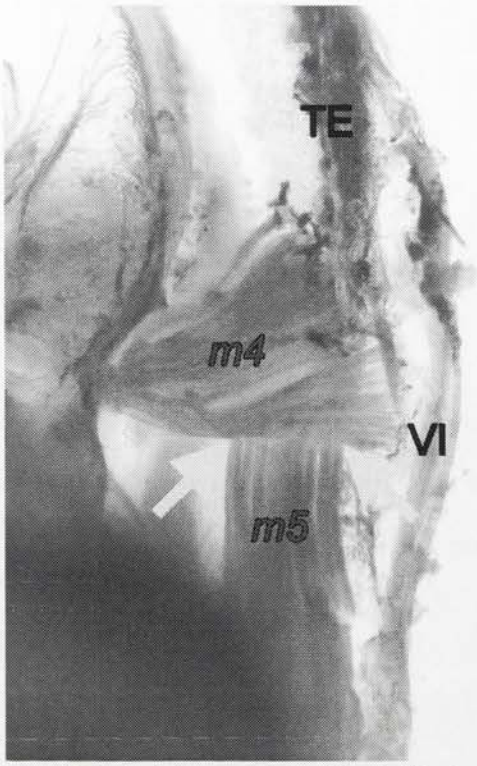

Fig. 137: *Anthela euryphrica* (Anthelidae), ♂, anterior view – *m5* attaches to the vinculum dorsally of and posteriorly to *m4* ("overlapping" with *m4*; yellow arrows); note *m4* and *m5* proximity.

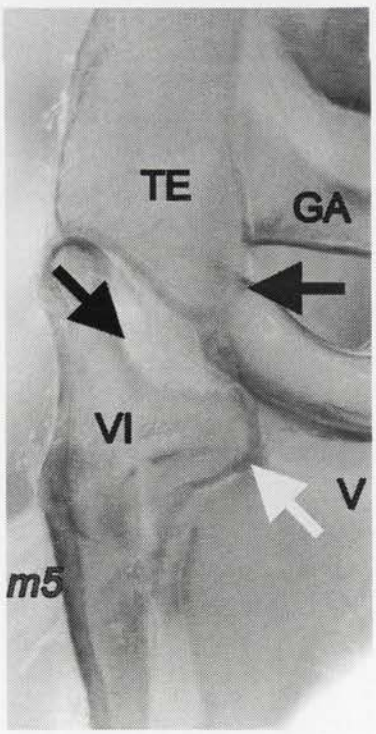

Fig. 138: *Ganisa plana* (Eupterotidae), ♂, lateral view (posterior to the right) – dorsal posteriad protruding lobe of the vinculum (yellow arrow) with *m5*; membranous area (black arrow) between vinculum and tegumen (blue arrow).

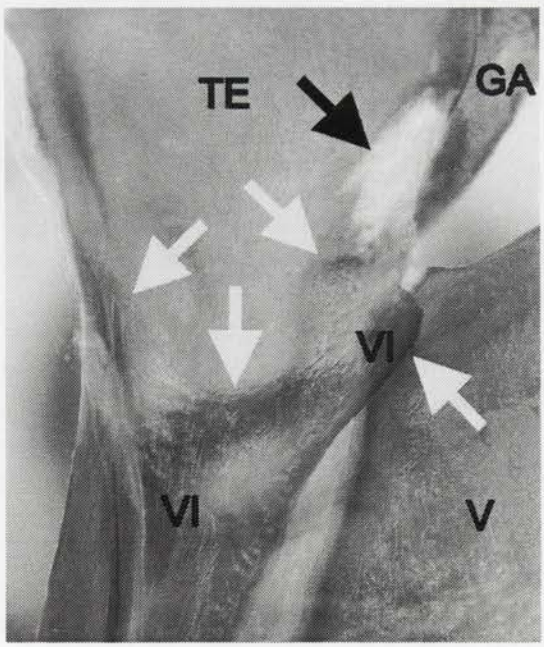

Fig. 139: *Arsenura ciocolatina* (Saturniidae), ♂, lateral view (posterior to the right) – dorsal posteriad protruding lobe and vinculum extent (yellow arrows); membranous area (black arrow) between vinculum and tegumen.

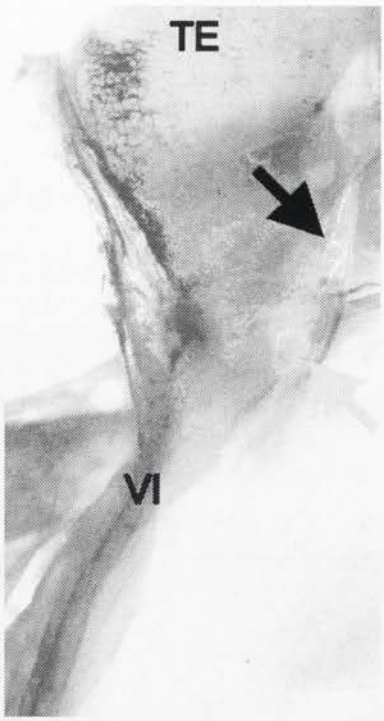

Fig. 140: *Anthela euryphrica* (Anthelidae), ♂, lateral view (posterior to the right) – dorsal posteriad protruding lobe of the vinculum (yellow arrow) with *m5* (not shown); membranous area (black arrow) between vinculum and tegumen.

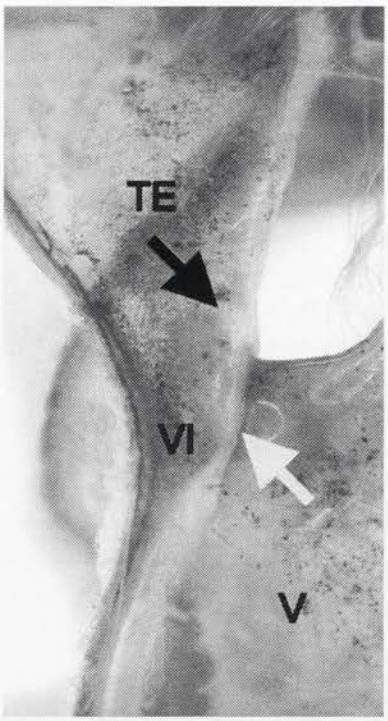

Fig. 141: *Chelepteryx chalepteryx* (Anthelidae), ♂, lateral view (posterior to the right) – reduced dorsal posteriad protruding lobe of the vinculum (yellow arrow), without muscle attachment (*m5* shifted ventrad; not shown); membranous area (black arrow) between vinculum and tegumen.

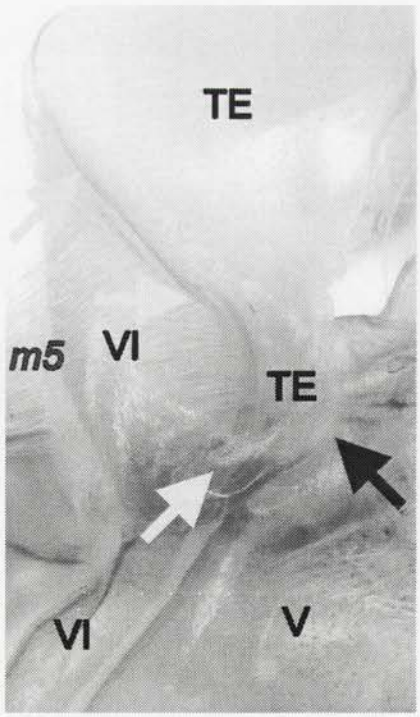

Fig. 142: *Agrius convolvuli* (Sphingidae), ♂, lateral view (posterior to the right) – *m5* attaches to the posterior enlargement of the vinculum (yellow arrows), anterior to the fused tegumen (blue arrow).

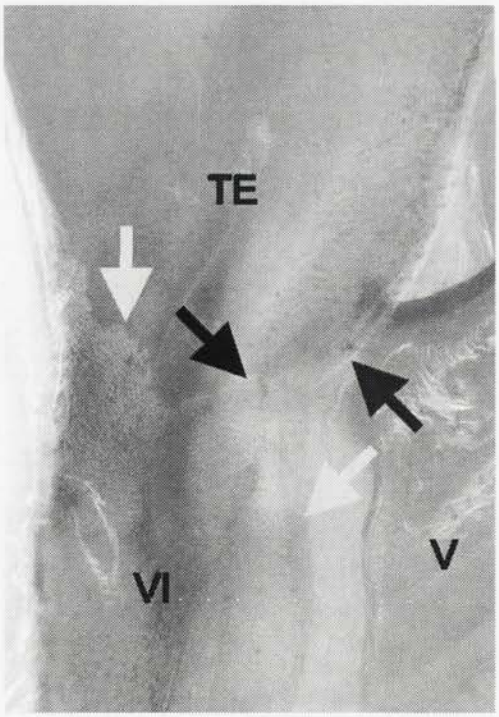

Fig. 143: *Carthaea saturnioides* (Carthaeidae), ♂, lateral view (posterior to the right) – dorsal extent of the vinculum and remnants of posterior protrusion (yellow arrows); membranous area (black arrow) between vinculum and tegumen (blue arrow).

Character #H.39: Muscle *m5* attaches to the vinculum far ventrally of muscle *m4*.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; moderately supported.

Introduction. As discussed in character #H.38, muscle *m5* attaches to a posterior lobe of the vinculum in Anthelidae, passing *m4* laterally and appearing as an overlap of *m4* and *m5* in lateral view (Figs 125, 136, 137). As in other Macrolepidoptera, in which *m5* attaches ventrally of *m4* (Figs 114, 115, 116, 124, 126, 134, 135, 144), this is an attachment of *m5* adjacent to *m4*. This arrangement is very constant, and only rarely is a distinct gap present between *m5* and *m4*. This can be the case if the valva is of great height and requires an extreme dorsal extension of the vinculum due to the short connecting muscle *m4* (e.g., *Opodiphthera eucalypti* (Saturniidae); *Dactyloceras widenmanni* (Brahmaeidae)). In these cases muscle *m4* has been moved dorsad with the dorsal extension of the vinculum, while *m5* seems to have remained in its typical position.

Description. In many Anthelidae the attachment of *m5* is not adjacent to *m4*. Instead, a very large gap exists between the attachment points of muscles *m5* and *m4* on the vinculum (Fig. 145), even though the valva is of typical height only, about half the height of the annulus. In these taxa the attachment point of muscle *m5* has moved ventrad, while *m4* remains attached to the dorsal end of the vinculum.

Discussion. The ventral shift of muscle *m5* in many Anthelidae changes the direction of the force which *m5* exerts on the phallus during contraction. The muscle attachment to the vinculum is at about the same level as the phallus, rather than far dorsally of it as in other taxa. Hence a contraction of *m5* does not pull the phallus base dorsad in these taxa. As a result, the phallus apex is extruded in a straight line, rather than in a ventral arc.

Unlike the very constant proximity of *m5* to *m4*, the relative position of *m5* to other structures, e.g., the valva, is rather variable and influenced by several factors. Such factors are the extent of the vinculum, the width of the *m5* attachment, and the size and position of those other structures *m5* is compared to.

With few exceptions, caused by dorsal shifts of *m4* (*O. eucalypti*, *D. widenmanni*, some Lasiocampidae), *m5* attaches adjacent to *m4* [character state (0)] in all

Macrolepidoptera examined, as well as in most Macrolepidoptera illustrated by Kuznetzov and Stekolnikov (2001). A modification of this attachment, which retains an attachment of *m5* adjacent to *m4*, is the principal arrangement in Anthelidae, as outlined in character #H.38. In contrast, the ventral shift of *m5*, which results in a very large gap between the attachment points of *m4* and *m5* [character state (1)], is only present in a number of Anthelidae. Hence I interpret character state (1) as apomorphic for these anthelid taxa.

Summary. While character state (1) is distinct due to the large size of the gap, it only consists of a simple, though seemingly unique, ventral shift of muscle *m5* along the vinculum. Hence my hypothesis of homology of this modification in all examined taxa is based on the enormous size and position of the gap only. Homoplastic occurrences of similar ventral shifts could not be easily distinguished as such. Therefore I consider this hypothesis to be moderately supported.

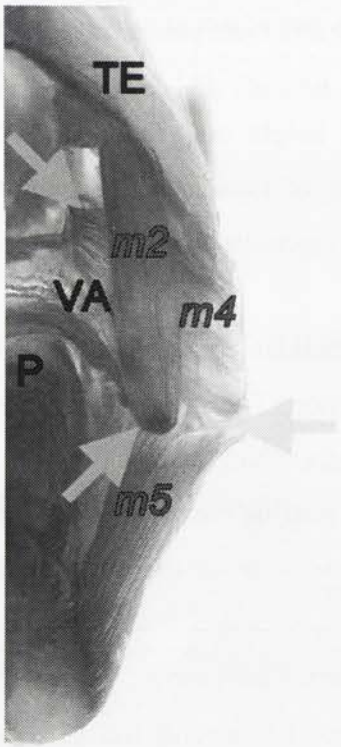

Fig. 144: *Oenosandra boisduvalii* (Oenosandridae), ♂, anterior view – proximity of the attachment of muscles *m4* and *m5* to the vinculum (yellow arrow); note *m2* attachment to the apex of the cephalo-ventral lever of the dorso-basal valva apodeme, ventrally of *m4* (green arrows).

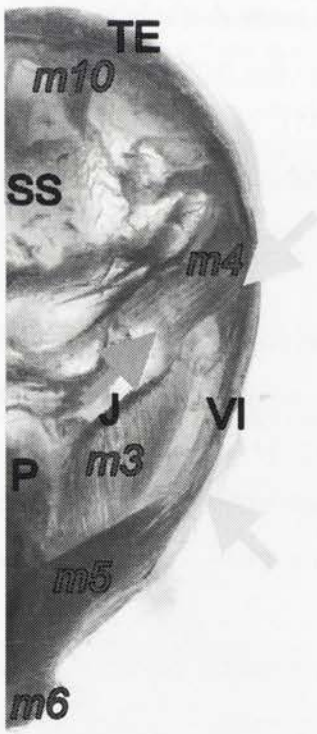

Fig. 145: *Anthela virescens* (Anthelidae), ♂, anterior view – note the large gap between the attachments of muscles *m4* and *m5* to the vinculum (yellow arrows), caused by a ventral shift of *m5*; note the attachment of *m4* to the lobe, which is dorsally fused to the juxta (green arrow).

Character #H.40: In taxa with a ventrad shifted muscle *m5*, this muscles attaches to the basal edge of the lateral valva wall only.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; poorly supported.

Introduction. Irrespective of dorso-ventral differences in attachment, muscle *m5* attaches to the vinculum only, the vinculum and the valva, or the valva only in different Macrolepidoptera. While the intermediate stage of attachment to both structures exists, the confinement to either structure represents a distinct state. In the intermediate state as found in Anthelidae, the majority of muscle fibres attaches to the vinculum. Hence the attachment to the valva only is more distinct from the intermediate state than is the attachment to the vinculum only. Therefore I only use the former as a character.

Description. In some of the anthelid taxa in which muscle *m5* has been shifted far ventrad [character #H.39 state (1)], an intermediate state with the majority of muscle fibres of muscle *m5* attached to the vinculum (Fig. 146), as well as a state with attachment to the valva only (Fig. 147), occur.

Discussion. While the attachment to the inside of the valva has been assigned to a hypothetical ground-plan of Lepidoptera (Kristensen [1998]: 110; Kuznetzov & Stekolnikov 2001: 24), all three positions of attachment occur in Macrolepidoptera, which makes a determination of their homology and polarity for the bombycoid complex impossible without prior knowledge of macrolepidopteran phylogeny. Obviously, if the families are monophyletic, at least two, but possibly all, states are homoplastic between families. However, this character applies only to a number of anthelid taxa in which muscle *m5* has been shifted far ventrad (character #H.39). Within this group only two character states occur, namely the intermediate attachment of *m5* and the attachment of *m5* to the valva only. Hence, the occurrence of either of these two character states within the other anthelid taxa indicates the polarity of this character for this group of anthelid taxa. The attachment of *m5* only to the vinculum and the intermediate state [united in character state (0)] are present in these other anthelid taxa, but not the attachment to the valva only. Hence I interpret character state (1) as apomorph for this group of anthelid taxa.

Summary. As the distinction between the character states consists of a shift in muscle attachment only, which is even less distinct due to the intermediate stage, my hypotheses of homology of these character states in all examined taxa is based on weak indications only. Hence I consider this hypothesis to be poorly supported.

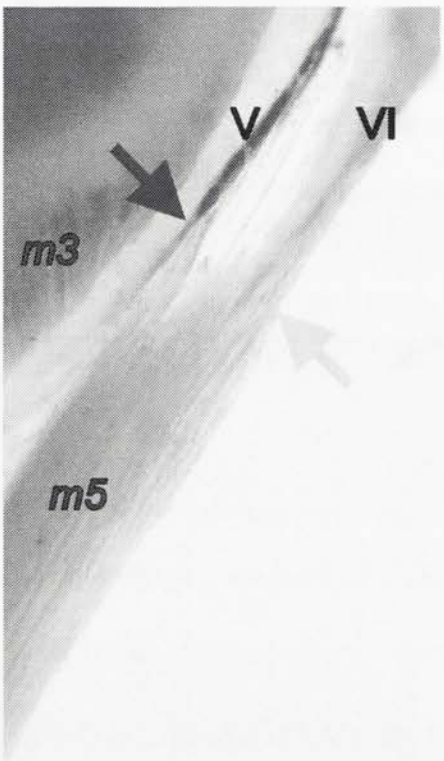

Fig. 146: *Anthela virescens* (Anthelidae), ♂, anterior view – intermediate attachment of the ventrad shifted muscle *m5*, partly to the basal edge of the valva (yellow arrow) and largely to the vinculum and the connecting membrane (red arrow).

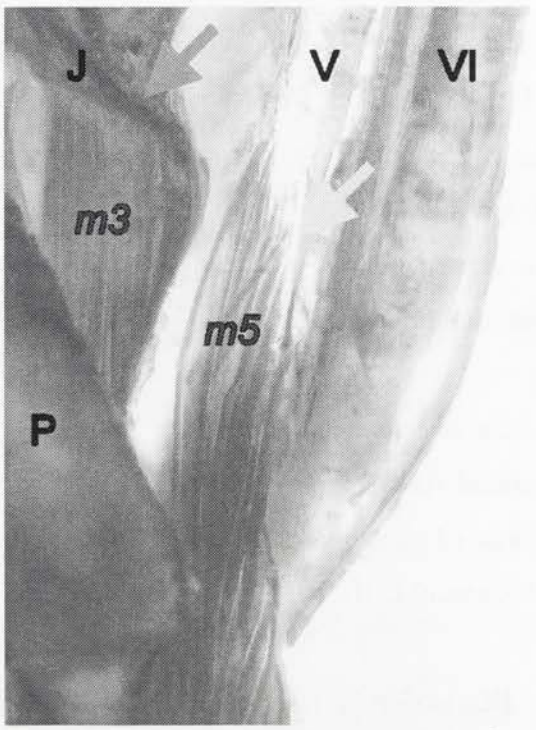

Fig. 147: *Anthela oressarcha* (Anthelidae), ♂, anterior view – attachment of the ventrad shifted muscle *m5* to the basal edge of the valva only (yellow arrow); note the invaginated dorso-lateral corner of the juxta, with *m3* attaching to the ventral side of the invagination only (green arrow).

Character #H.41: Muscle *m7* is seemingly displaced distad by muscle *m5*.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; moderately supported.

Description. Muscle *m7* attaches to the inside of the valva, along the basal edge of the latero-ventral part of the valva. In a few anthelid taxa, in which muscle *m5* is shifted ventrad [character #H.39, state (1)] and attaches to the basal edge of the valva [character #H.40, state (1); (Fig. 148)], this position of *m7* has been modified. In these taxa muscle *m5* occupies the typical position of *m7* on the inside of the ventro-lateral valva wall base, while *m7* attaches distinctly further distally of the basal valva edge (Fig. 149).

Discussion. Muscle *m7* attaches to the inside of the lateral valva wall at its basal edge in almost all Macrolepidoptera. This attachment has seemingly been displaced by a modified attachment of muscle *m5* in a few anthelid taxa only. Hence I interpret character state (1) as apomorph for these anthelid taxa.

Summary. While character state (1) is distinct due to the combined modification of two muscle attachments, it only consists of two shifts of muscles, with one of them likely to cause the other. My hypothesis of homology of this modification in all examined taxa is based on this seemingly unique indication only. Homoplastic occurrences of similar shifts could not easily be distinguished as such. Hence I consider this hypothesis to be moderately supported.

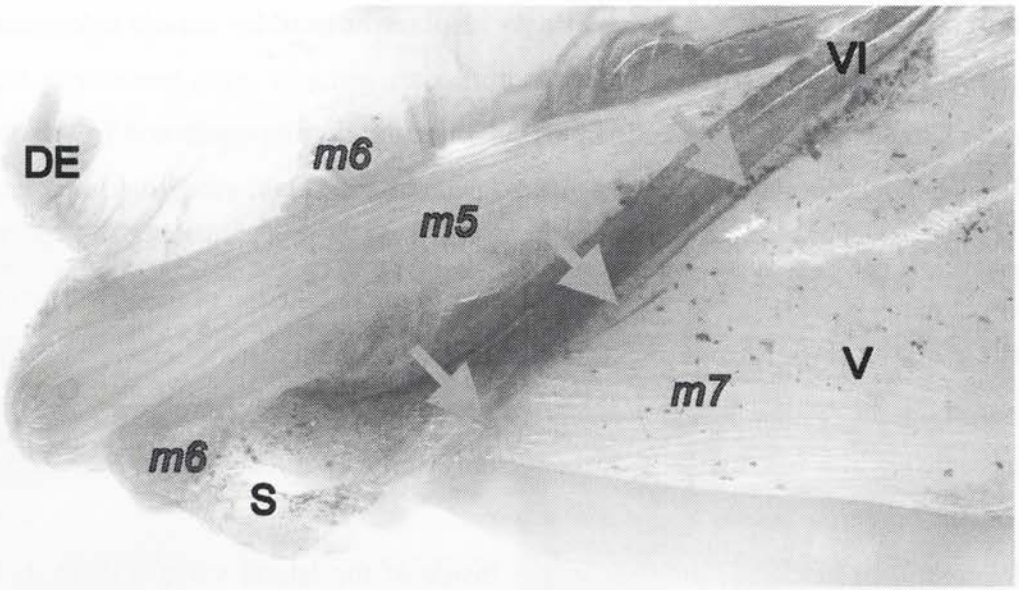

Fig. 148: *Anthela repleta* (Anthelidae), ♂, lateral view (posterior to the right) – muscle *m7* attaches along the basal edge of the valva (green arrows); *m5* attaches dorsally of *m7* (outside of picture).

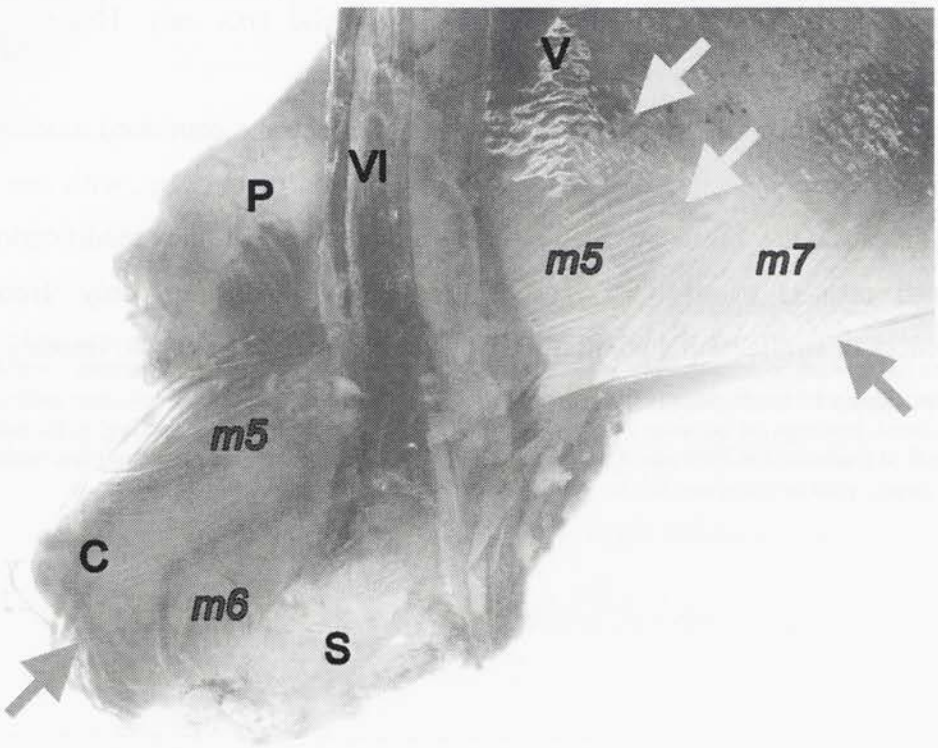

Fig. 149: *Anthela oressarcha* (Anthelidae), ♂, lateral view (posterior to the right) – ventrad shifted muscle *m5* reaches deeply into the valva (yellow arrows), seemingly displacing muscle *m7* distad (green arrows); note the unique muscle fibres connecting the coecum apex with the saccus apex (red arrow).

Character #H.42: Dorso-lateral corners of the juxta invaginated, with ventral attachment of muscle *m3*.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; very well supported.

Introduction. In Macrolepidoptera the juxta is an unpaired, U-shaped, flat sclerotization of the diaphragma, with muscle (*m3*) attached to the dorso-lateral edge of each lateral "arm". Hence the attachment of *m3* is located in the plane of the diaphragma, facing anteriad. These muscles connect to the ventral edge of the valvae or to the dorsal edge of the ventral vinculum wall, in both cases stretching ventrad, roughly parallel to the plane of the diaphragma. Consequently, the muscles are bent ventrad at their attachment to the juxta (Fig. 150). The shape of the juxta is modified in many Macrolepidoptera, and a posterior protrusion of the juxta is very common. In some taxa such a posterior protrusion changes the plane of the muscle attachment, reducing or eliminating the bend in the muscle and thereby improving the transmission of force during contraction of *m3*.

In most Anthelidae the juxta has been modified to protrude far posteriad (outwards) from the diaphragma, supporting the phallus ventrally and laterally. Nevertheless, the entire anterior edge of this modified juxta is located in the plane of the diaphragma, as it is the case in the flat juxta, or the anterior edge forms the dorsal part of the posterior protrusion. However, this condition is modified in many Anthelidae as described below.

Description. In many anthelid species the dorso-lateral corners of the juxta curve anteriad, resulting in an invagination of the diaphragma and the dorso-lateral corners of the juxta (Fig. 152). These dorso-lateral corners are broadly rounded and interconnected by a fold in the diaphragma caused by the invagination (Fig. 153). In these taxa the attachment of muscle *m3* is focused onto the apex and ventral wall of the invagination, which is at a steep angle to the diaphragma (Fig. 147). As a result, the muscle attachment faces ventrad and each muscle fibre runs in a straight line from the vinculum to the ventral valva wall (Fig. 151), rather than facing anteriad and being bent ventrad at the juxta.

Discussion. Superficially similar, but in their morphological detail different, modifications of the juxta can be observed in a number of non-anthelid taxa. The

examined specimen of *Aurivillius fuscus* (Saturniidae) has a posteriad protruding juxta with an invaginated dorsal juxta corner. However, in this species the dorso-mesal corner is invaginated, rather than the dorso-lateral corner as in some Anthelidae. In the examined *Hoplojana* sp. near *rhodoptera* (Eupterotidae) the dorso-lateral part of the juxta forms an invagination, too, but in this taxon it is elongate, pointed and extends at a different angle than in Anthelidae. I assume the invaginations of the juxta in these two taxa to be non-homologous with the one present in some anthelid taxa. Hence I score this character as character state (0) for these two non-anthelid taxa.

In the anthelid genus *Omphaliodes* the entire area around the phallus protrudes posteriad, raising the juxta out of the typical plane of the diaphragma. This makes a determination of this character difficult, but the curving of the juxta in lateral view argues for an invagination, even though no depression in the diaphragma is visible due to its posterior protrusion. While I presume the invagination to be present [character state (1)], I conservatively score this character as unknown for the genus *Omphaliodes*.

The entire anterior edge of the juxta is located in the plane of the diaphragma in some Anthelidae and many Lepidoptera other than Anthelidae. In contrast, the characteristically curved juxta with modified muscle attachment seems to be unique to a number of anthelid taxa. Hence I interpret character state (1) as apomorph for these anthelid taxa.

Summary. My hypothesis of homology of this modification in all examined taxa is based on numerous details as described above. Hence, I consider this hypothesis to be very well supported.

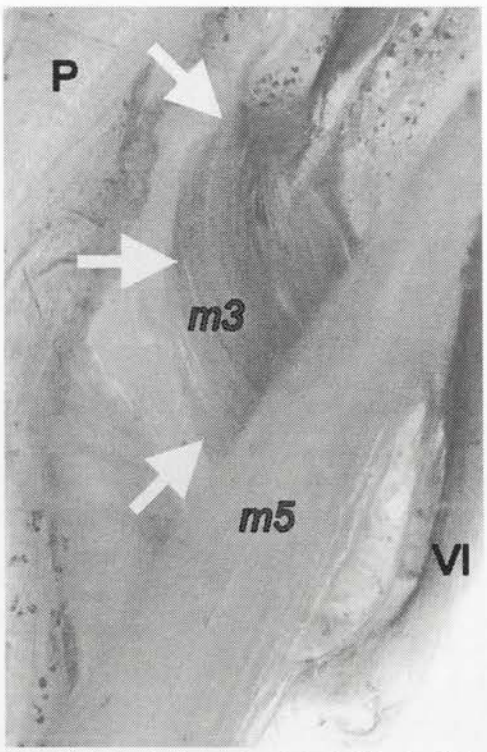

Fig. 150: *Anthela repleta* (Anthelidae), ♂, latero-anterior view (posterior to the right) – *m3* curves ventrad (yellow arrows), compensating the anteriad facing *m3* attachment area of the juxta [hidden beneath *m3*].

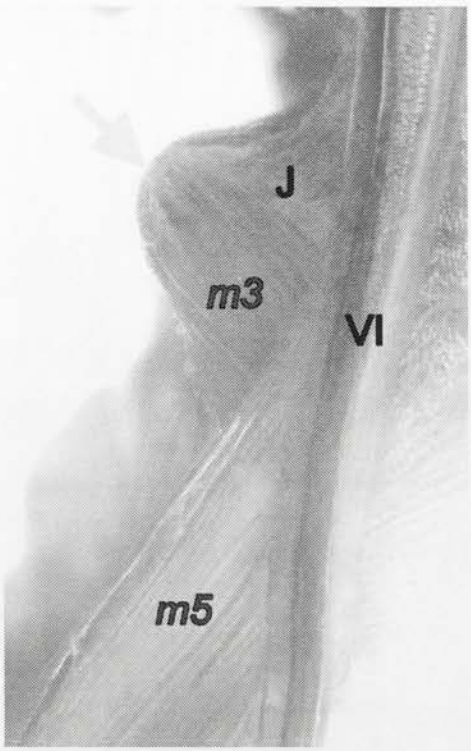

Fig. 151: *Anthela excellens* (Anthelidae), ♂, lateral view (posterior to the right) – *m3* stretches in a straight line from the ventral side and apex of the invaginated, dorso-lateral juxta corner (yellow arrow) to the ventral valva wall [hidden by *m5* and vinculum].

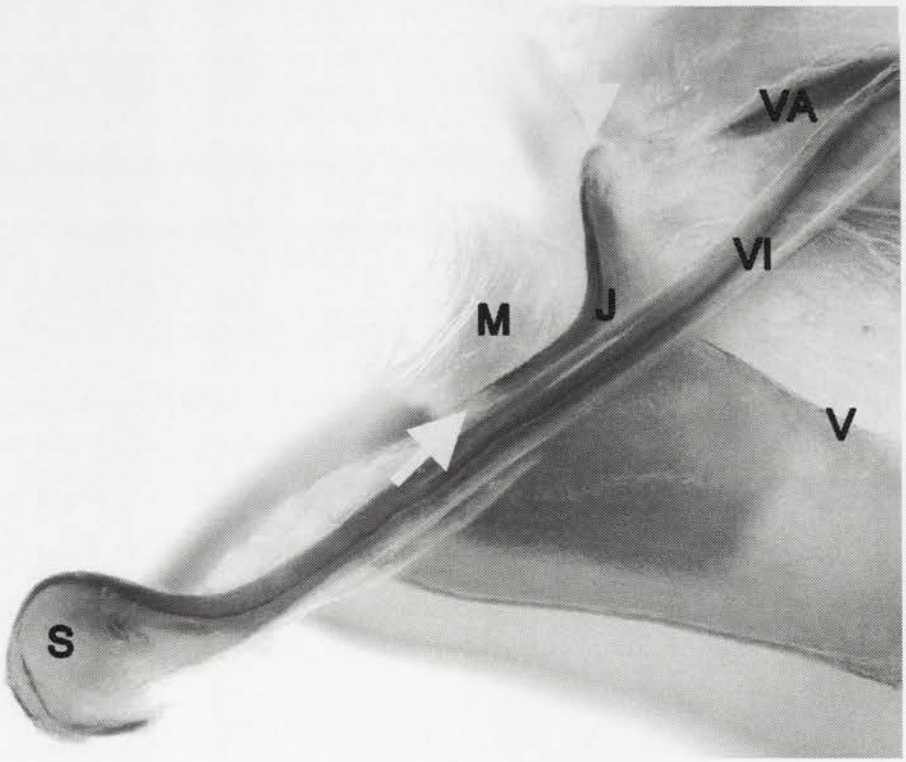

Fig. 152: *Anthela excellens* (Anthelidae), ♂, lateral view (posterior to the right) – dorso-lateral juxta corner invaginated (yellow arrows mark ventral and dorsal end of the juxta; note the angle between the two arrows).

Character #H.43: Coecum and phallus twisted righthand, with muscles *m5* crossing each other.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; very well supported.

Introduction. Muscle *m5* is the protractor of the phallus and attaches to the lateral side of the phallus end, typically the end of the coecum. In Anthelidae, as in most other Macrolepidoptera, the ductus ejaculatorius enters the phallus antero-dorsally, slightly anteriorly to the attachment point (zone) of the membranous manica. In anterior view the paired muscle *m5* and the phallus form a vertically symmetric structure, with muscle *m5* running in a straight line from the phallus base to the lateral part of the vinculum and/or to the valva (Fig. 153).

Description. In some anthelid taxa the coecum and phallus are twisted more than 100° clockwise in anterior view. This is indicated by the muscles *m5* crossing each other, as well as by the ductus ejaculatorius seemingly entering the phallus from the dorso-lateral right side (Figs 154, 155). In these taxa the two muscles *m5* seem to partly reach around the coecum and to attach to the dorso- and ventro-lateral sides of its end, respectively. During contraction of the muscles *m5*, the phallus is not only pushed outwards but also rotated to the rightanti-clockwise in anterior view. No corresponding twist is apparent in the ductus bursae of the females.

Discussion. No such twist or rotation of the phallus is apparent in any of the examined or illustrated Macrolepidoptera, other than a few anthelid taxa. Therefore I interpret character state (1) as apomorph for these anthelid taxa.

Summary. The twisted condition of the muscles *m5* can easily be differentiated from the non-twisted state. Superficially similar, homoplastic rotations could probably be identified as such by the amount of rotation and the difference in twist between the coecum end and the entrance of the ductus ejaculatorius into the phallus. No similar rotations or intermediate states have been observed, though. Given the number and quality of these details, which my hypothesis of homology of this modification in all examined taxa is based on, I consider this hypothesis to be very well supported.

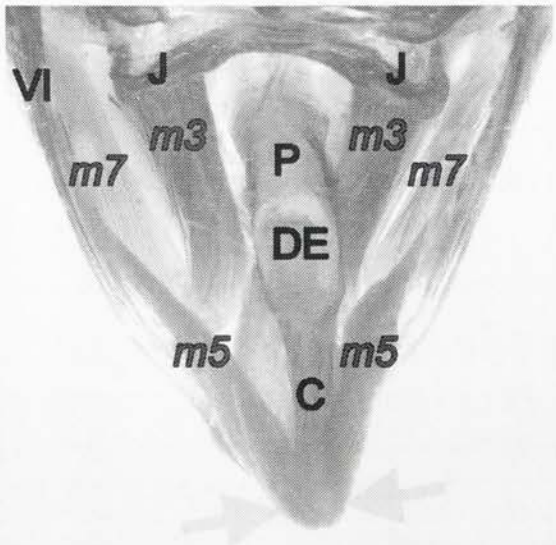

Fig. 153: *Anthela unisigna* (Anthelidae), ♂, anterior view – typical, straight coecum and phallus with vertically symmetric muscles *m5*, attaching laterally to the phallus (yellow arrows); note the minor anti-clockwise twist; note the invaginated, dorso-lateral juxta corners being interconnected by a fold in the diaphragma.

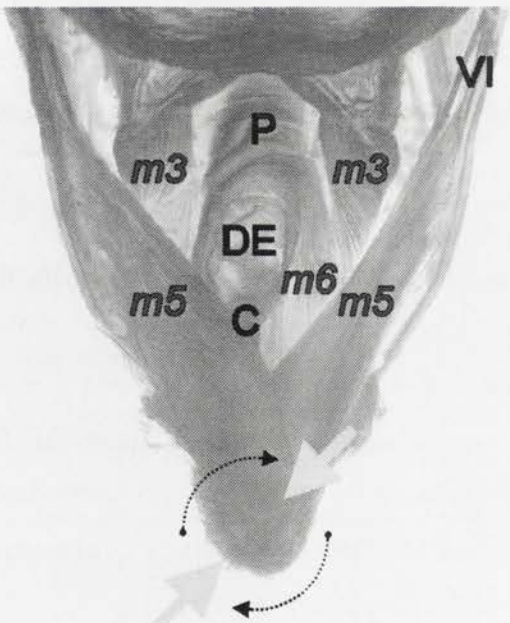

Fig. 154: *Anthela excellens* (Anthelidae), ♂, anterior view – coecum and phallus twisted clockwise by more than 100°, as indicated by the crossing over of the dorso- and ventro-laterally attached muscles *m5* (yellow arrows); note the difference in degree of twist between the *m5* attachment and the ductus ejaculatorius entrance.

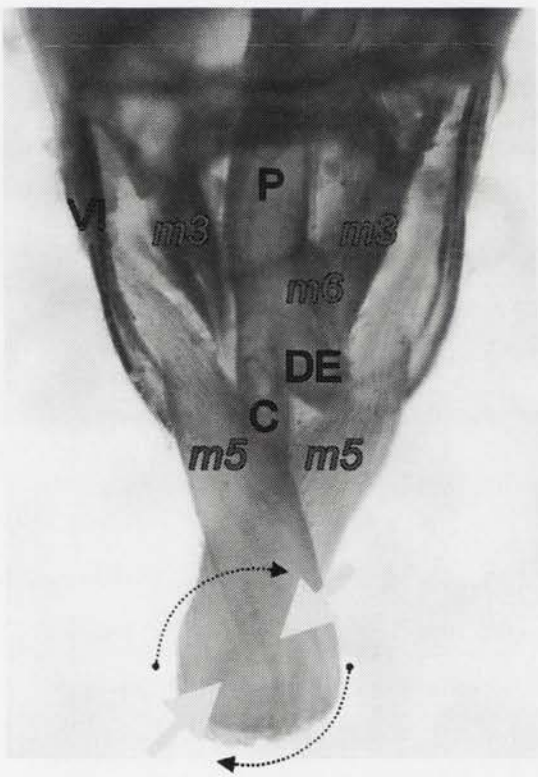

Fig. 155: *Nataxa flavescens* (Anthelidae), ♂, anterior view – coecum and phallus twisted clockwise by more than 100°, as indicated by the crossing over of the dorso- and ventro-laterally attached muscles *m5* (yellow arrows); note the difference in degree of twist between the *m5* attachment and the ductus ejaculatorius entrance.

III.3) THE FEMALE GENITAL STRUCTURES

The exoskeleton of female genital structures is less complex than that of male genital structures. It consists of the abdominal segments VIII-X and its general structure is rather uniform in Macrolepidoptera. In contrast, details of the copulatory opening (ostium bursae) and the surrounding structures are very variable and of taxonomic significance at lower taxonomic levels. These differences often concern the position of the ostium bursae, the sclerotization of the surrounding membranes (lamella antevaginalis and lamella postvaginalis), the shape, length and sclerotization of the ductus bursae, sclerotizations (signa) of the corpus bursae and the relative position of the ductus seminalis. At least within the bombycoid complex, these differences are typically too simple to be of high phylogenetic significance. Likewise, other sclerotized structures, e.g., the anal papillae, apophyses anterior and posterior, are either not very variable or their modifications are simple, e.g., changes in the degree of sclerotization. Further, the ductus bursae and corpus bursae are often reduced and signa are rare, which is probably linked to the full development of eggs during the pupal phase in non-feeding taxa with a very short adult lifespan. In these taxa the ductus bursae is strongly shortened, hence differences in the relative position of the joining ductus seminalis translate to rather small absolute distances.

Within the bombycoid complex the more delicate, internal genital structures, such as the spermatheca and the accessory glands, are hardly ever examined and typically removed during the process of making genitalia preparations for taxonomic studies. These structures are rather variable in the bombycoid complex and possibly more informative for phylogenetic studies than the structures typically examined for taxonomic diagnoses. However, as publications on these structures are very limited and they should ideally be examined in fresh or fixed specimens, a detailed comparative morphological study of these structures is beyond the scope of this thesis.

The female genital structures of Anthelidae are as reduced or simple as mentioned above for other taxa with non-feeding adults. Their principal genital structures do not differ much from the general descriptions given for Ditrysia in many text books, e.g., Scoble 1995. In the following sections I give a brief outline of the principal female genital structures of Anthelidae, followed by a discussion of the female genital characters that I use in my phylogenetic analyses.

III.3.1) The principal female genital structures of the Anthelidae

The copulatory opening (ostium bursae) is located just anteriorly to the sternite of abdominal segment VIII in Anthelidae and is surrounded by a sclerotization of the membrane (Fig. 156). Based on its relative location, the anterior part of this in Anthelidae continuous sclerotization is referred to as lamella antevaginalis and the posterior part as lamella postvaginalis. The lamella antevaginalis is not synscleritous with the weakly sclerotized sternite of the abdominal segment VII, but the lamella postvaginalis is part of the ventral sclerotization of abdominal segment VIII. This sclerotization typically extends into the posterior end of the ductus bursae, the antrum. Both lamellae are generally strongly sclerotized and in Anthelinae the lamella antevaginalis is at right angle to the lamella postvaginalis and the abdominal sternites (character #H.44). This unusually orientated lamella antevaginalis forms a sclerotized, arc-like plate, with the ostium bursae being located medially in the dorsal part of the lamella antevaginalis – hence the ostium bursae and posterior part of the antrum are in line with the body axis. The sclerotization of the lamella antevaginalis has been reduced in some species. The ductus bursae and bursa copulatrix are very simple and short, together typically not reaching the anterior end of the VII. abdominal segment. The condition appears to be modified in the genus *Munychryia*, and potentially in all Munychryiinae, but the female of *Gephyroneura cosmia* is unknown and the only available female specimen of the currently undescribed munychryiine species was not dissected. In *Munychryia* a protruding sclerotization, which might be a part of the lamella postvaginalis, forms a tube, which protrudes at an angle posteriad from the ventral side of the body (Fig. 157). This extension has an apical opening in the plane of the ventral side of the body. However, the actual ostium bursae, which is indicated by a sclerotized collar, and the antrum are roughly in line with the body axis as in other Anthelidae. The antrum is well sclerotized, while the remaining membranous part of the ductus bursae is rather long (coiled in *M. senicula*). The corpus bursae of *Munychryia* is distinctly larger than in other Anthelidae and has a weakly sclerotized signum.

The ductus seminalis joins the ductus bursae about midway between the ostium bursae and the bursa copulatrix in most Anthelidae (Fig. 156), but at the anterior end of the sclerotized antrum in *Munychryia*. As the ductus seminalis is a simple, membranous

structure, it is not possible to determine whether this more posterior position of the ductus seminalis in *Munychryia* is caused by an extension of the ductus bursae or by a shift of the ductus seminalis. Alternatively, the more central position of the ductus seminalis in other Anthelidae could have been caused by opposite mechanisms. The relative position of the ductus seminalis is a good example of a valuable diagnostic character with distinct differences, which nevertheless has no to very little phylogenetic significance. In Anthelidae the ductus seminalis is not widened to form a bulla seminalis and it opens into the ventral side of the anterior end of the genital chamber.

Roughly opposite of the ductus seminalis the genital chamber forms a protrusion ('papilla') and opens dorsally into the very thin and long ductus spermathecae. This membranous tube ends in the spermatheca, which is bilobed and consists of a balloon-shaped lagena and a tubular utriculus with annular folds and an apical, branched spermathecal gland.

As in most other Lepidoptera, the two ovaries each consist of four ovarioles, which open into a short lateral oviduct. The two lateral oviducts join to form the common oviduct, which opens into the anterior end of the genital chamber.

The paired accessory glands of Anthelidae are long to extremely long (e.g., *Anthela clementi*), simple tubes, which widen into very long, tubular reservoirs (Fig. 163). These reservoirs extend far beyond abdominal segment VII, have a wrinkled, membranous surface and can have several asymmetric expansions and constrictions. The two reservoirs join to form a common duct, which opens into the dorsal wall of the posterior part of the genital chamber. This common duct is an extension of the two joined reservoirs and posteriorly narrows gradually, but has been modified to form a set-off, very narrow duct in some anthelid taxa (character #H.45).

The anal tube ends separately from the genital chamber between the weakly sclerotized, setose, lateral anal papillae. From a sclerotization at the dorso-lateral edge of the anal papillae the paired, well developed, slender posterior apophyses originate. The anterior apophyses are of similar proportions and are attached to the tergite and sternite of the abdominal segment VIII by a well sclerotized fork.

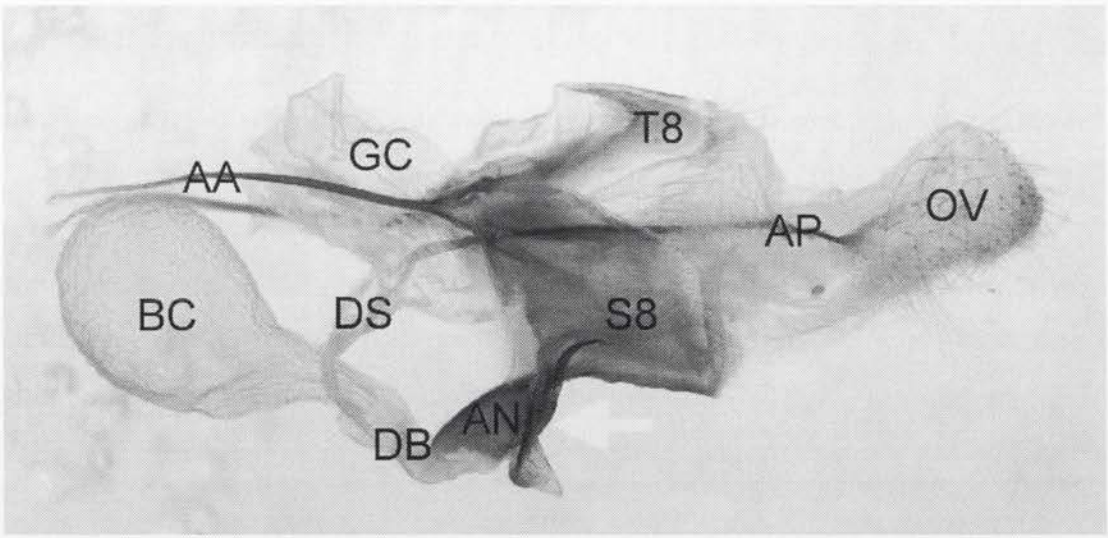

Fig. 156: *Anthela nicothoe* (Anthelidae), ♀, lateral view (posterior to the right; horizontally flipped) [ovaries, spermatheca and accessory glands removed] – female genital structures; yellow arrow marks ostium bursae in lamella antevaginalis.

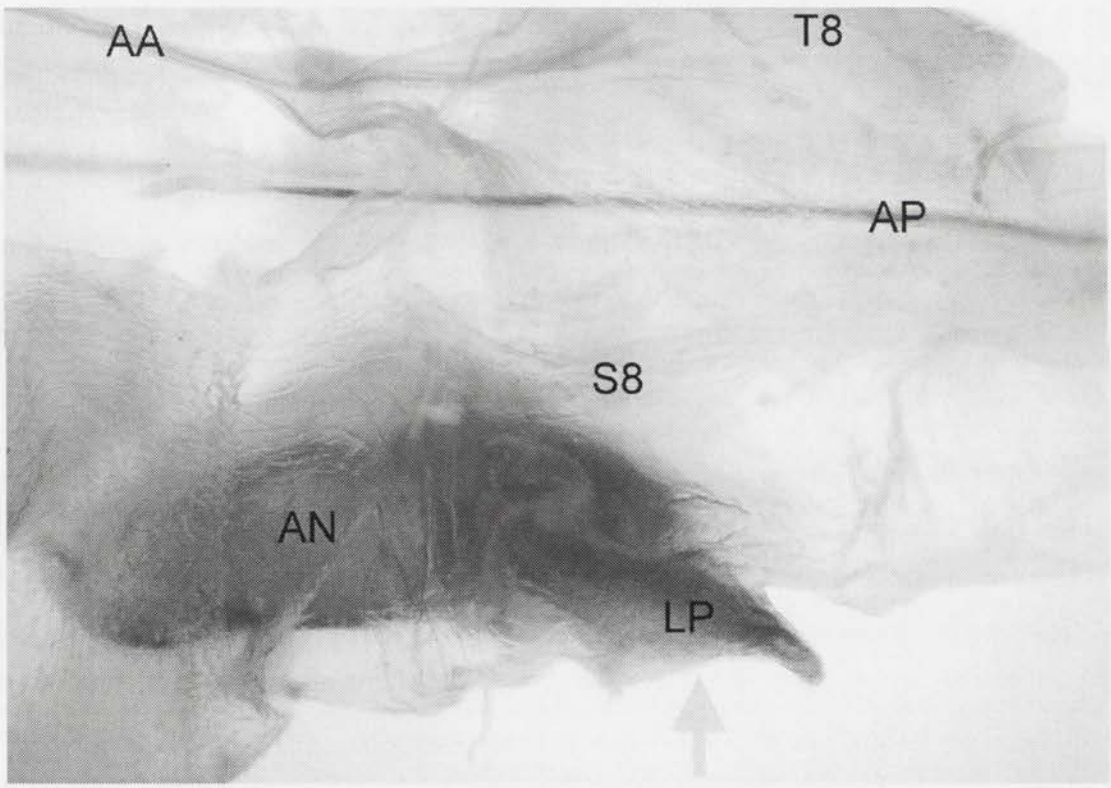

Fig. 157: *Munychryia senicula* (Anthelidae), ♀, lateral view (posterior to the right) – a sclerotized tube (probably formed by the lamella postvaginalis) is located posteriorly to the antrum, which relocates the copulatory opening (yellow arrow) into the plane of the (reduced) sternites.

III.3.2) Character analyses of female genital characters

Character #H.44: Lamella antevaginalis at right angle to lamella postvaginalis.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; poorly supported.

Introduction. The location and orientation of the ostium bursae and the adjoining antrum vary greatly between taxa, as does the sclerotization of the surrounding membrane (Figs 158, 159, 160). In Anthelidae, however, these characteristics are rather constant as described below.

Description. As in many other Lepidoptera, the posterior part of the sclerotization surrounding the ostium bursae (the lamella postvaginalis) is in the plane of the sternites in Anthelidae. In contrast, the lateral and anterior parts of this sclerotization (lamella antevaginalis) protrude from this plane at an angle of roughly 90°. The ostium bursae and antrum are located in the basal area of this ventrad angled lamella antevaginalis, and consequently are in line with the body axis (Fig. 161). This protruding lamella antevaginalis is typically strongly sclerotized, forming an arc ventrally of the ostium bursae (Fig. 162). However, this sclerotization is frequently reduced or lost, but the orientation of the membrane, ostium bursae and antrum remain.

Discussion. It is uncertain if the arrangement in the genus *Munychryia* is a subsequent modification of the condition found in all other Anthelidae, or if it is a different structure. In this genus a sclerotized, postero-ventrad protruding tube is formed by the surrounding membrane, which appears to be the lamella postvaginalis (Fig. 157). This tube ends internally at the sclerotized antrum, which extends in the orientation of the body axis as in all other Anthelidae. The posterior edge of this antrum, the ostium bursae, is surrounded by a sclerotized collar, which has a thick outer layer of transparent cuticle and is confluent with the surrounding membrane. The sclerotized part of this collar might be homologous with the lamella antevaginalis of other Anthelidae. As I am uncertain about this arrangement in *Munychryia* and do not have information on any other Munychryiinae, I score this character as unknown ("?") for Munychryiinae.

Due to the great variety of modifications in the area of the ostium bursae it is difficult to impossible to determine a plesiomorphic state for any group. In the bombycoid complex the ostium bursae is typically located in the posterior part of the intersegmental

fold between abdominal segments VII and VIII. The distinctly ventrad angled, sclerotized lamella antevaginalis including the ostium bursae and the antrum appears to be unique to Anthelidae. Therefore I assume character state (1) to be apomorphic.

Summary. The ventrad angled lamella antevaginalis with the ostium bursae and antrum is a distinct, but simple modification. It is obscured in some Anthelidae by a loss of the sclerotization, and the condition present in Munychryiinae is difficult to interpret. The ostium bursae and its surrounding membrane are very variable in families other than Anthelidae, and subsequent modifications might easily obscure the condition in these taxa, too. Hence I consider this hypothesis to be poorly supported.

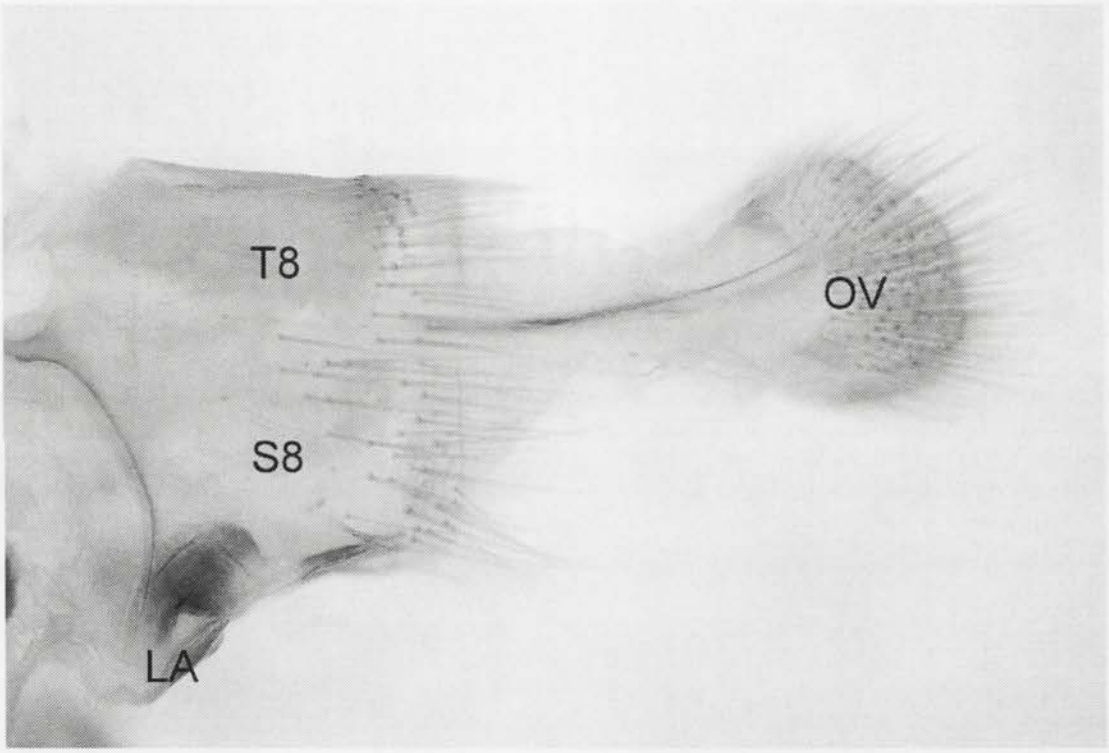

Fig. 158: *Oenosandra boisduvalii* (Oenosandridae), ♀, lateral view (posterior to the right) – the ostium bursae (yellow arrow) is covered by the transverse lamella antevaginalis.

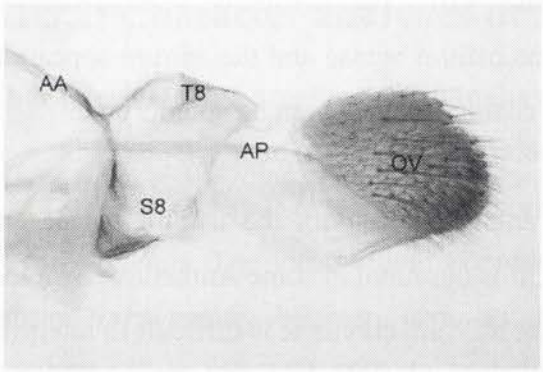

Fig. 159: *Agrius convolvuli* (Sphingidae), ♀, lateral view (posterior to the right) – the ostium bursae (yellow arrow) is located at the base of the postero-ventrally protruding lamella antevaginalis.

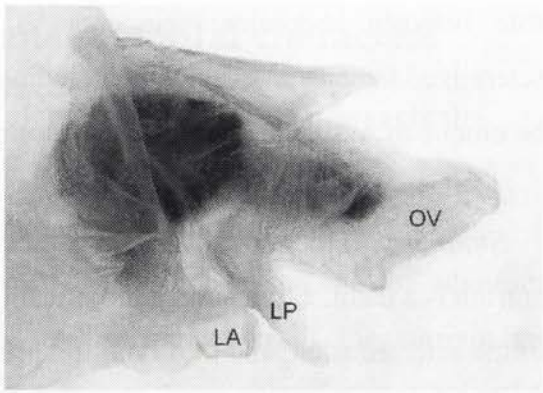

Fig. 160: *Rhodinia fugax* (Saturniidae), ♀, lateral view (posterior to the right) – the ostium bursae (yellow arrow) is located at the base of the lamella antevaginalis and is covered by a postero-ventrally protruding lamella postvaginalis.

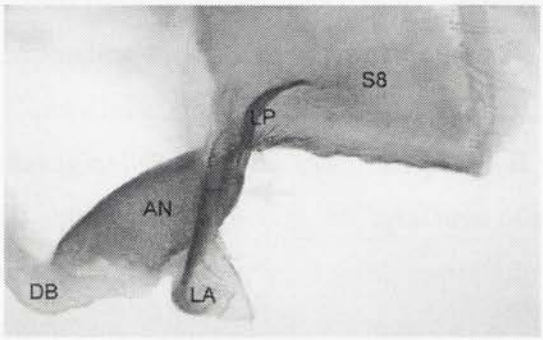

Fig. 161: *Anthela nicothoe* (Anthelidae), ♀, lateral view (posterior to the right; horizontally flipped) – the ostium bursae (yellow arrow) and antrum are located in the basal area of the lamella antevaginalis, which is at right angle to the lamella postvaginalis.

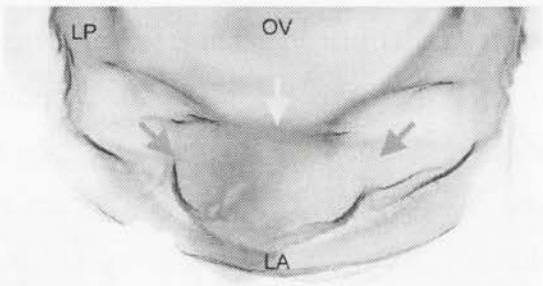

Fig. 162: *Anthela nicothoe* (Anthelidae), ♀, posterior view – the wide ostium bursae (yellow arrow) and antrum (green arrows mark lateral edges) are located in the basal area of the ventrad angled lamella antevaginalis.

Character #H.45: Common duct of accessory glands set off from and at right angle to accessory gland reservoirs.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; poorly supported.

Introduction. The reservoirs of the two accessory glands join posteriorly and form a common duct, which opens into the dorsal wall of the posterior part of the genital chamber (Fig. 163). This common duct is the posterior extension of the joined reservoirs and hence is in the plane of this V-shaped joined reservoir (Figs 166, 167). From the joined reservoirs towards the genital chamber the common duct typically narrows gradually, but it is slightly more set off from the joined reservoirs in some taxa.

Description. In some Anthelidae the common duct is much narrower than the joined reservoirs and not a posterior extension. Instead, the thin duct attaches to one side of the joined reservoirs, being at an angle of 90° to the plane of this V-shaped joined reservoirs (Fig. 165). This attachment is not to the posterior end of the joined reservoirs, but slightly further anteriorly, which results in the joined reservoirs forming a short coecum (Fig. 164).

Discussion. In some species (e.g., *Chenuala heliaspis*, *Anthela neurospasta*, *A. nicothoe*, *A. excellens*) the joint reservoirs do not form a distinct coecum, but the common duct is nevertheless at right angle to the plane of the accessory gland reservoirs. This appears as a bent in the common duct, which can be adjacent or at a short distance to the joint reservoirs. Either a simple bent in the common duct or a coecum can be present in closely related species. I have no basis to hypothesize, whether the bent in the common duct is formed by a reduction of the coecum, or whether it is the pre-cursor to the formation of a coecum. Therefore, I use only the common denominator as a character, namely the right angle in the set-off common duct.

The gradually narrowing, posterior extension of the joined reservoirs is present in all examined species of the bombycoid complex, Noctuoidea and some Anthelidae. In contrast, the thin and angled common duct is unique to some anthelid species. Therefore I interpret character state (1) as apomorphic.

Summary. While this modification appears to be more than just a simple angling of a duct in many species, a coecum is not always present and the location of the right angle seems to be somewhat variable. Therefore, the very strong, abrupt narrowing and the right angle in the common duct are the only characteristics, which is why I consider this hypothesis of homology to be poorly supported.

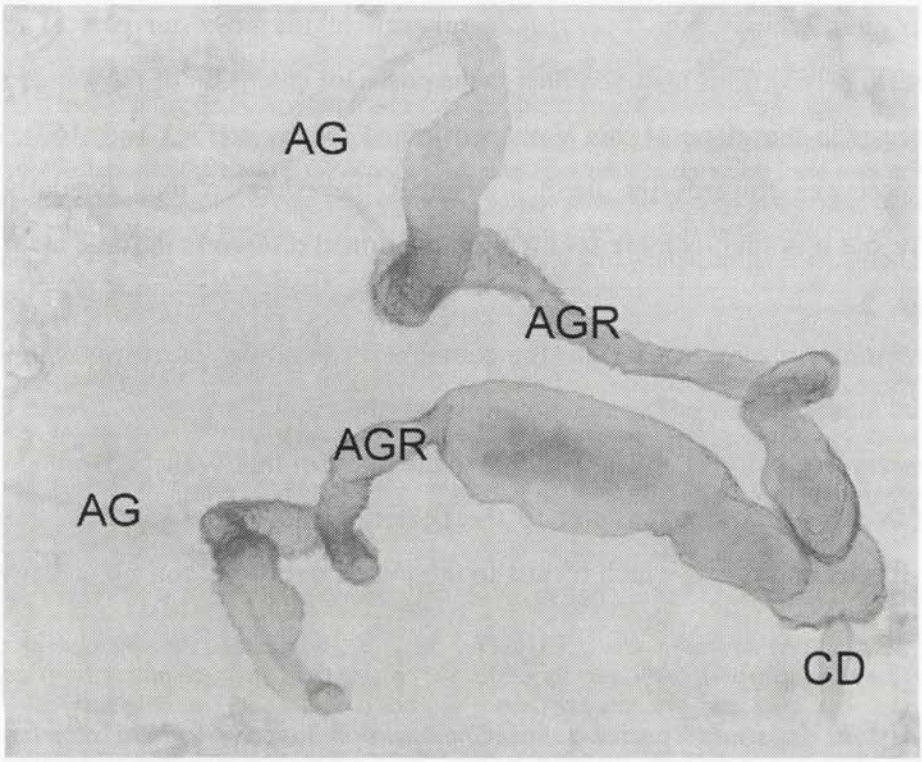

Fig. 163: *Anthela clementi* (Anthelidae), ♀, ventral view (posterior to the right) – the two accessory glands are long, thin tubes, which open into the wider accessory gland tubes and unite to form a common duct.

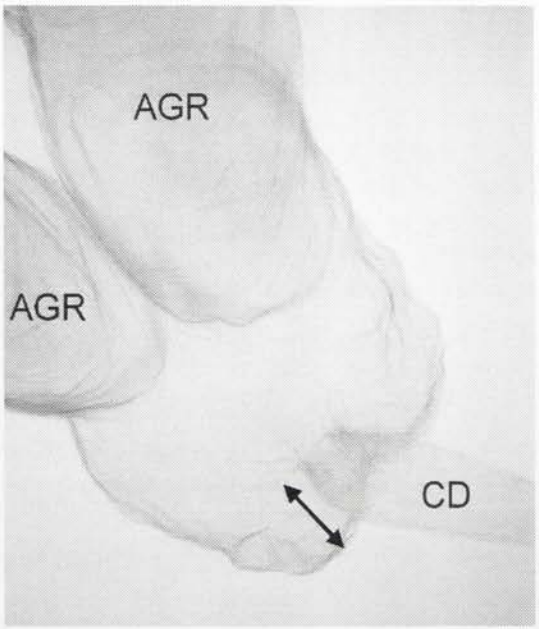

Fig. 164: *Anthela clementi* (Anthelidae), ♀, ventral view (posterior to the right) – the common duct connects to the ventral side of the merged accessory gland reservoirs, anteriorly to their merged posterior end (black double-arrow).

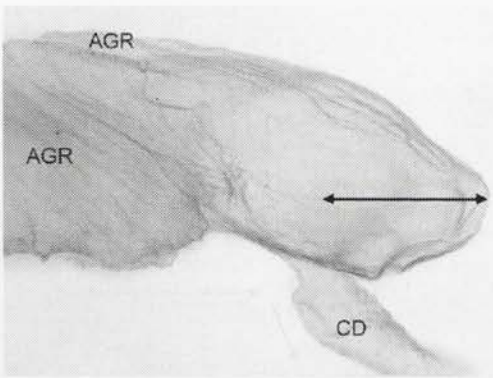

Fig. 165: *Anthela clementi* (Anthelidae), ♀, lateral view (posterior to the right) – the common duct connects to the ventral side of the merged accessory gland reservoirs, anteriorly to their merged posterior end (black double-arrow) and at an angle of roughly 90° to the merged reservoirs (yellow arrows indicate orientation).

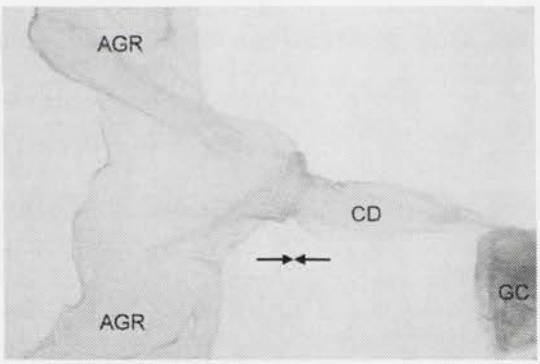

Fig. 166: *Chelepteryx chalepteryx* (Anthelidae), ♀, ventral view (posterior to the right) – the common duct connects to the posterior end of the merged accessory gland reservoirs.

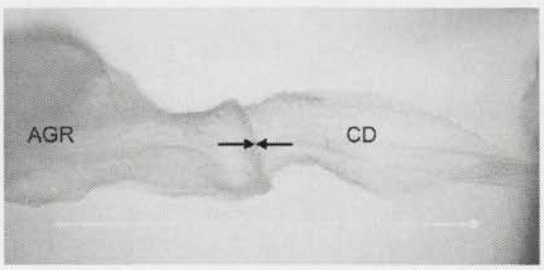

Fig. 167: *Chelepteryx chalepteryx* (Anthelidae), ♀, lateral view (posterior to the right) – the common duct connects to the posterior end of the merged accessory gland reservoirs, extending in the same plane (yellow arrows indicate orientation).

III.4) THE WINGS OF IMAGINES

The wings are THE most commonly used structures in publications on lepidopteran taxonomy and phylogeny. This is not surprising as wing pattern, colouration and to a lesser degree wing shape are often highly variable between species and differences are instantly observable without the need for preparations or tools. However, these differences are so variable and modifications so frequent that wing pattern, colour and shape have hardly any value in the reconstruction of higher phylogenies.

In contrast, wing venation has always played a major role in the classifications and later in phylogenetic hypotheses of Lepidoptera. Today's "modern" classification of Lepidoptera, in particular of Macrolepidoptera, relies heavily on differences in wing venation. This is problematic in as far as most differences in wing venation have high diagnostic value, but are of rather limited phylogenetic value. These limitations are caused by the characteristics of wing venations themselves as well as by our perception of them – they are structures of simple appearance, which form a rather complex system. Differences in wing venation essentially never pertain to qualities of veins, as at least external structural details of veins are very constant. Instead, these differences concern exclusively the relative position of veins to each other or the absence of veins. Obviously, differences in relative positions can be caused (or obscured) by changes in more than one vein. This problem of recognizing different origins as such is reflected by the simplistic use of descriptive terms that do not differentiate between the causes of an observed appearance. For example (Fig. 168), if the connate vein branches radial sector Rs1/Rs2 and Rs3/Rs4 change to Rs1/Rs2 being stalked with Rs3/Rs4, this appearance could have been caused by

a) the closing of the discoidal cell by the branch of the media M1 proximally of the unaltered split between Rs1/Rs2 and Rs3/Rs4 (a proximal shift of M1) [Fig. 168 B)], or
b) the split between Rs1/Rs2 and Rs3/Rs4 being located more distally of the unaltered termination of the discoidal cell by M1 (e.g., an incomplete primary split in Rs) [Fig. 168 C)].

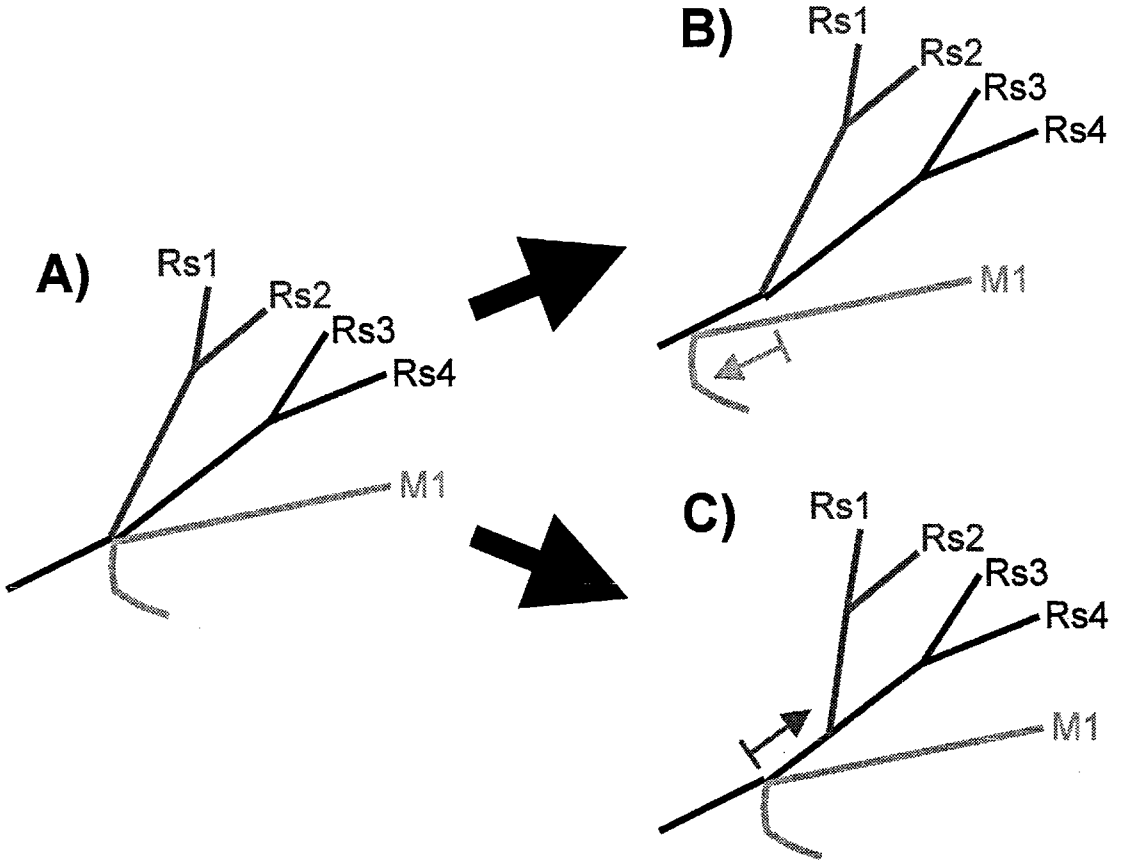

Fig. 168: Scheme illustrating the difficulty of recognizing different origins of similar venation patterns. The differences are easy to pick in these simple schemes, but not in actual wings of different shape, size or with slightly different arrangement of veins.
A) Rs1+Rs2 and Rs3+Rs4 are connate.
B) Rs1+Rs2 and Rs3+Rs4 are stalked due to a proximal shift of M1 (closing of the cell)
C) Rs1+Rs2 and Rs3+Rs4 are stalked due to a distal shift of the primary split in Rs

Further, the modifications of veins are typically simple and affect either the distance of a split between branches from the base of the wing, or the laterad bending of branches. Therefore certain appearances are very likely to evolve multiple times, such as the relative position of vein M2 being either closer to M1 or to M3. It is virtually impossible to structurally determine single or multiple evolutionary events. Additionally, the overall shape and size of the wing combined with functional constraints are likely to favour the evolution of certain wing venations, e.g., the fusion of the radial sector branches in Macrolepidoptera.

As the veins of a wing have hardly any external structural characteristics, the identification (= homologization) of vein branches between different taxa is typically only based on their relative position and the branching pattern of the vein. In taxa that "lack" vein branches, the reliable identification of the remaining branches by external characteristics is usually no longer possible. This is commonly the case with the "loss" of radial sector branches in, e.g., the bombycoid complex. The study of the wing

tracheae, which extend inside the veins, can help to homologize the remaining vein branches and to distinguish between true losses and fusions of vein branches. Observations on the developing wing in the pupa are particularly useful in this respect, but are rarely carried out.

It must be concluded that the typical differences in wing venations are less than ideal characters for phylogenetic analyses and have to be used much more cautiously than is generally done in literature. This caution certainly applies also to my own descriptions and characters of wing venation, which I discuss in the following sections.

III.4.1) The principal wing venation of the Anthelidae

Many different numbering systems and names have been applied to wing venations by various authors. I follow the notation suggested by Wootton (1979). With the exception of the radial sector of the fore wing, the wing venation of Anthelidae (Figs 177, 180, 185, 186, 187, 188, 197, 198) represents at large the principal arrangement of veins in the bombycoid complex.

In the fore wing of Anthelidae the costa (C) forms the anterior edge of the wing. The simple subcosta (Sc) runs almost parallel to C and fuses with it well proximally of the wing apex. The simple radius (R) diverges from its common stem with the radial sector (Rs) and reaches C distally of Sc. The radial sector splits into two main branches Rs1/Rs2 and Rs3/Rs4, each of which splits into two terminal branches. The fork in Rs1/Rs2 is located slightly distally (Figs 177, 185, 197, 198), at level (Fig. 187) or slightly proximally (Fig. 180) of the fork in Rs3/Rs4. The former condition is typical of the bombycoid complex (character #H.46), and usually much more distinct than in Anthelidae. A short sclerotization of the wing membrane between or touching of Rs2 and Rs3 just distally of their respective branching points results in an elongate, loop-shaped arrangement of veins, which is generally referred to as the "areole" (character #H.47). If perceived as a loop, Rs1-Rs4 branch off separately from the distal end of this areole. Despite this structural difference to other Lepidoptera having been pointed out by Turner (1920a), this areole is frequently regarded as homologous with a similar arrangement of veins found in Geometridae and Noctuoidea (e.g., Lemaire & Minet [1998], but see character #H.47). A transverse sclerotization ("cross-vein") is located just distally of the areole, stretching from the connection between Rs2 and Rs3 across

Rs1 towards R (Figs 181, 182, 183). This transverse sclerotization is unique to Anthelidae and discussed in greater detail in character #H.48. The media M is split into three terminal branches, of which M1 can be either free from or connate (occasionally short-stalked) with Rs3/Rs4. Branch M2 is closest to M3, with both branches arising from the lower distal corner of the discoidal cell. The two branches of the cubitus anterior (CuA1 and CuA2) split off separately from the distal half of the discoidal cell, well proximally of the cell's lower distal corner. The cubitus posterior (CuP) is occasionally distinct (Figs 180, 185), but typically reduced to a fold. The fused anal veins 1A+2A form basally a loop, while 3A is absent.

In the hind wing C forms a distinct humeral angle, but no humeral veins are present. Sc diverges from the radial stem basally, but after a short distance curves towards and almost touches the fork in the radial stem, prior to diverging again. There is a tendency towards a loss of this approximation between Sc and the radial stem. R fuses with Sc after a short distance, but its separate, basal part is occasionally reduced to absent. Rs and M1 can be free, connate or stalked with each other. M2 is closest to the M3, both branches arising from the lower distal corner of the discoidal cell. The two branches CuA1 and CuA2 split off separately from the distal half of the discoidal cell. CuP is absent, and the anal veins 1A+2A and 3A are simple.

III.4.2) Character analyses of wing-related characters

Character #H.46: The fork in Rs1/Rs2 is located distally of the fork in Rs3/Rs4 (fore wing).

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; moderately supported.

Introduction. According to Kristensen (2003b: 87) the radial sector (Rs) of the fore wing is "twice dichotomously forked (Rs1/Rs2 and Rs3/Rs4)" in the hypothetical ground plan of the Lepidoptera. In Heteroneura this basic dichotomy into Rs1/Rs2 and Rs3/4 is rarely obvious in the fully developed wing. It is obscured by partial fusions within Rs, which appear as either Rs branches diverging separately from the discoidal cell, or as the stalking of multiple Rs branches. In Macrolepidoptera, the branches Rs1/Rs2 and Rs3/Rs4 are still (or again) separated from each other, but more distally fused, which results in a loop-shaped appearance referred to as the areole (Fig. 178). Subsequent fusions, resulting in the "loss" of the areole, are very common. The at least basal separation of the branches is retained in families of most macrolepidopteran superfamilies, e.g., some Axiidae (Minet [1998]: 258, Fig. 15.1A), Drepanidae (Minet & Scoble [1998]: 303, Fig. 17.1B, C), Geometridae (Minet & Scoble [1998]: 314, Fig. 17.6A), families of the Noctuoidea (Miller 1991: 74-75, Figs 244-246; Kitching & Rawlins [1998]: 358, Fig. 19.3B, D-H) and families of the bombycoid complex. In most of these families the areole is very small and the separation of the two branches restricted to the base of the branches (Fig. 178). In contrast, this split into two radial branches is very obvious in some families of the Noctuoidea (Oenosandridae, Doidae, Notodontidae) and of the bombycoid complex (Mimallonidae (Fig. 176), Lasiocampidae (Fig. 169), Sphingidae (Fig. 170), Carthaeidae (Fig. 195), Anthelidae (Figs 177, 185, 186, 187, 188)). I examined the pupal tracheation (the "primary tracheation" of Pruscha (1985: 92)) of the developing wing of *Oenosandra boisduvalii* (Oenosandridae) (Fig. 171), *Anthela ferruginosa*, *A. guenei* and of *A. astata* (Anthelidae) (Figs 172, 173), which all show a split into the Rs1/Rs2 and Rs3/Rs4 branches. Based on the distribution of the partially split condition and my observations in the developing wing, I believe the forking into Rs1/Rs2 and Rs3/Rs4 to be the principal arrangement of veins in Macrolepidoptera – irrespective of it representing a synapomorphy or a symplesiomorphy of this group. Consequently I regard the common stalking of terminal Rs branches to merely represent secondary fusions between the terminal branches Rs2

and Rs3 or between the Rs1/Rs2 and Rs3/Rs4 branches, which must have evolved multiple times. Such a tendency towards a fusion of radial sector branches is not restricted to Macrolepidoptera, but typical of Heteroneura. Effectively, these fusions cause a compression of Rs, which together with the approximation of C, Sc, R and Rs causes a higher density of veins in the costal area than in any other part of the wing. This higher density of veins strengthens the costal area, which is likely to be important for flight.

With the exception of the Bombycoid complex, the fork in branch Rs1/Rs2 is located proximally of the fork in Rs3/Rs4. This is not obvious, as branches of the radial sector are typically fused, which results in a perception of the radial sector as a sequence of branches, rather than as a double dichotomy. Visualizing the sequential branching of the radial sector as a double dichotomy, the fork in branch Rs1/Rs2 is clearly located proximally of the fork in Rs3/Rs4 (Fig. 179). This condition can be observed in some species like *O. boisduvalii* (Oenosandridae), in particular in its developing wing (Fig. 171). There are, of course, also occasional exceptions, like the *Balacra* sp. (Arctiidae: Syntominae) illustrated by Kitching and Rawlins ([1998]: 358, Fig. 19.3I), in which the fork in Rs1/Rs2 is located distally of the fork in Rs3/Rs4.

Description. In all families of the bombycoid complex, the relative positions of the most distal dichotomies of the radial sector are reversed – the fork in Rs1/Rs2 is located distally of the fork in Rs3/Rs4.

Discussion. This condition is very obvious in the families Mimallonidae (Fig. 176), Lasiocampidae (Fig. 169), Bombycidae (Fig. 191), Carthaeidae (Fig. 195), Endromidae, Mirinidae (Fig. 196), Sphingidae (Fig. 170) and a few Eupterotidae (Fig. 192). It is obscured by a "loss" of Rs branches in Saturniidae, most Eupterotidae, most Lemoniidae (Fig. 194) and many Brahmaeidae, which appears to be caused by the extreme of a tendency to shift the fork in Rs1/Rs2 towards the apex of the wing (e.g., Fig. 170) – the fork is located at the very end of Rs1/Rs2 in some species and is frequently "lost" in many other species of Sphingidae as well as Eupterotidae. I assume this to be the case in Saturniidae, Lemoniidae and Brahmaeidae, too, but an examination of the pupal tracheation should be carried out. Pruscha (1985) published his observations on the

trachea of the developing wing of some Saturniidae (Fig. 174). In Saturniidae Rs4 and M1 are entirely "fused", which appears as a "loss" of one Rs branch (Fig. 175). A further branch is "lost" in many species, caused by the extreme distal movement of the Rs1/Rs2 fork.

Within the bombycoid complex, the Anthelidae are an exception in this regard. They possess a unique modification in the radial sector, a transverse, partly sclerotized fold (character #H.48). This fold is very close to or coincides with the two forks in Rs1/Rs2 and Rs3/Rs4, possibly affecting their locations. In the Anthelidae the two forks are at about the same distance from the base of the wing (e.g., Fig. 185). In many species the fork in Rs1/Rs2 is located slightly to distinctly more distally (e.g., Figs 197, 198), as in other families of the bombycoid complex. But in some taxa, e.g., the Munychryiinae with a particularly greatly developed modification of Rs, the fork in Rs1/Rs2 is located slightly proximally of Rs3/Rs4 (Fig. 188). In the pupal tracheation of the developing wing of *A. astata* (early stage), the fork in Rs1/Rs2 is located slightly proximally of the fork in Rs3/Rs4, too (Figs 172, 173). However, in the emerged moth of this species the fork in Rs1/Rs2 is positioned distinctly distally of the fork in Rs3/Rs4. While not being as distinct as in other families of the bombycoid complex, I nevertheless believe the principal location of the fork in Rs1/Rs2 to be distally of the fork in Rs3/Rs4 in Anthelidae.

The bombycid subfamilies Apatelodinae, Bombycinae and possibly Phiditiinae are further exceptions in this regard. Some Apatelodinae and some Bombycinae (with an extremely produced fore wing apex) have an entirely fused radial sector, in which Rs4 branches off most distally (Figs 189, 190). Hence, the fork in the fused Rs1/Rs2 is located proximally of the fork in Rs3/Rs4. In the bombycine Epiini and the Phiditiinae one branch of the radial sector (seemingly of the Rs1/Rs2 branch) is lost, which does not allow to distinguish between the relative locations of the forks. However, in the other bombycid subfamily Prismostictinae the configuration typical for the bombycoid complex is present (Fig. 191), which is why I assume the uniquely fused arrangements (not entirely fused in the apatelodine genus *Olceclostera* (Fig. 189)) found in the other bombycine subfamilies to be subsequent modifications. This is based on the assumption of monophyly of the Bombycidae *sensu* Minet (1994), which is at best very poorly supported.

The arrangement of veins in Lepidoptera other than the bombycoid complex and my observation of pupal tracheation in developing wings of *A. astata* indicate the more proximal position of the fork in Rs1/Rs2 to be the plesiomorphic condition. Therefore I interpret character state (1) as apomorphic.

Summary. The changes in relative position of forks in the radial sector are very unusual and for the majority of taxa very distinct to extreme. Apart from the relative position, no indications of homology exist. As explained below (III.5.1.C, pp 283ff.), the relative arrangement of veins can be caused by changes in various veins, and independent changes of the same vein could hardly be identified as such. However, in the bombycoid complex this arrangement appears to be caused by a change in the Rs1/Rs2 branch only. I therefore consider my hypothesis of homology to be moderately supported.

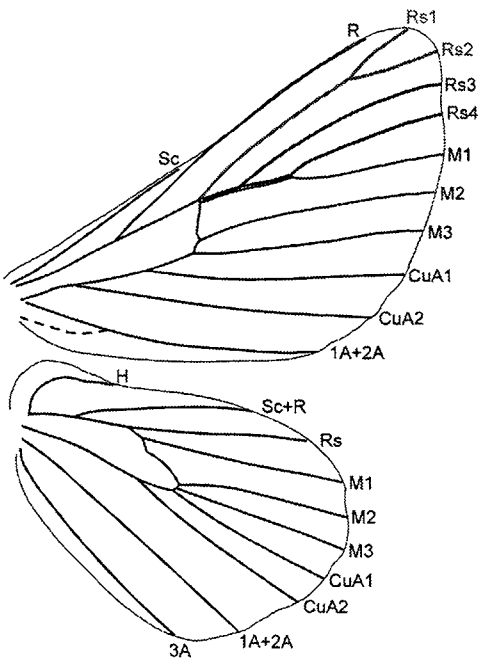

Fig. 169: *Artace cribraria* (Lasiocampidae), ♂, wing venation scheme [redrawn after Franclemont (1973: 32, Fig. 5c)]– the FW Rs branches Rs1/Rs2 (red) and Rs3/Rs4 (blue) are widely separated; note the far distal fork in Rs1/Rs2.

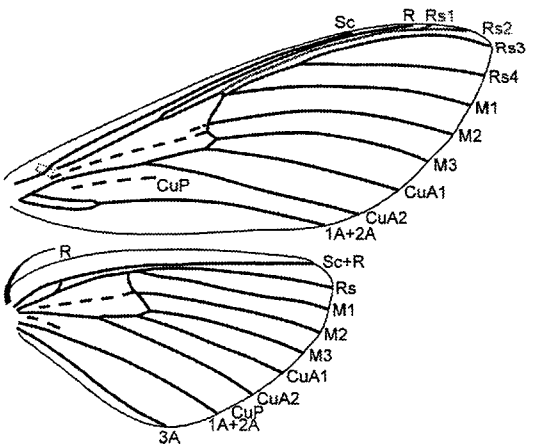

Fig. 170: *Leucophlebia afra* (Sphingidae), ♂, wing venation scheme [redrawn after Lemaire & Minet ([1998]: 339, Fig. 18.5I)]– the FW Rs branches Rs1/Rs2 (red) and Rs3/Rs4 (blue) are approximated, but entirely separated; note the far distal fork in Rs1/Rs2.

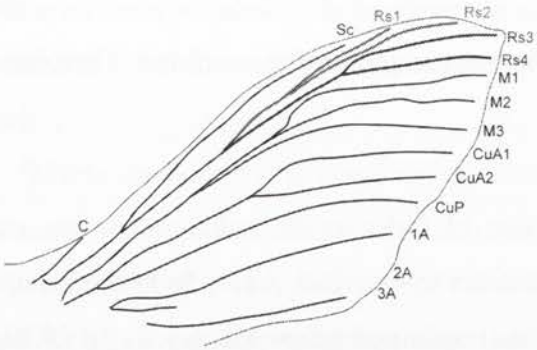

Fig. 171: *Oenosandra boisduvalii* (Oenosandridae), ♂, pupal fore wing tracheation scheme – the FW Rs branches Rs1/Rs2 (red) and Rs3/Rs4 (blue) entirely separated; note the more proximal position of the fork in Rs1/Rs2 compared to the one in Rs3/Rs4.

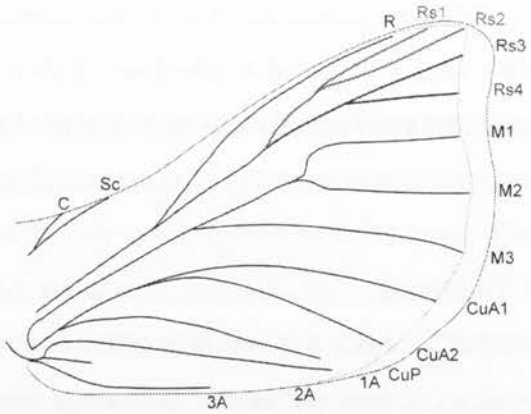

Fig. 172: *Anthela astata* (Anthelidae), ♂, pupal fore wing tracheation scheme – the FW Rs branches Rs1/Rs2 (red) and Rs3/Rs4 (blue) are entirely separated.

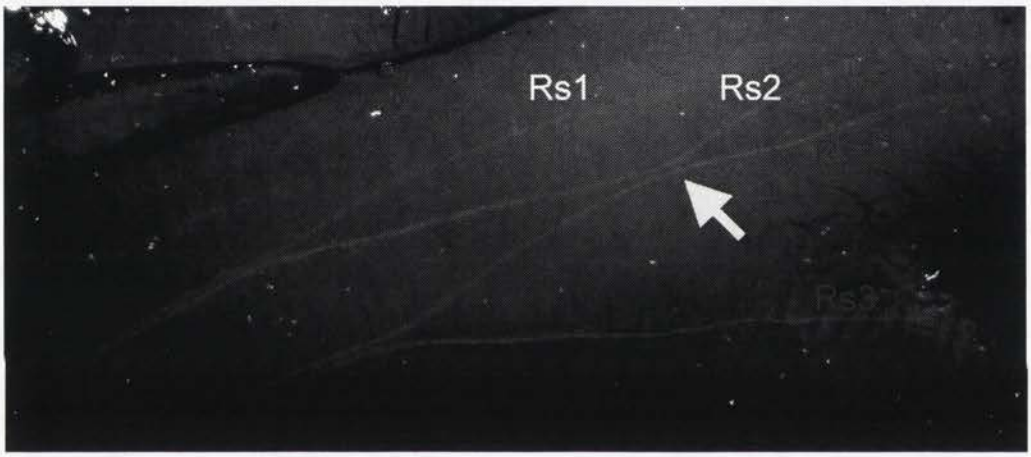

Fig. 173: *Anthela astata* (Anthelidae), ♂, pupal wing tracheation – the FW Rs branches Rs1/Rs2 and Rs3/Rs4 are entirely separated, but Rs2 and Rs3 are locally approximated (yellow arrow).

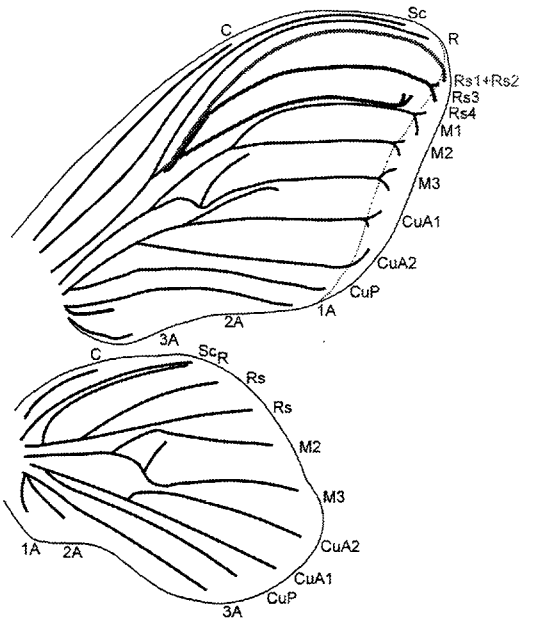

Fig. 174: *Samia cynthia* (Saturniidae), ♂, pupal wing tracheation scheme [redrawn after Pruscha (1985: 93, Fig. 1)] – the pupal FW Rs branches Rs1/Rs2 (red) and Rs3/Rs4 (blue) are entirely fused, and M1 and Rs4 are very closely approximated.

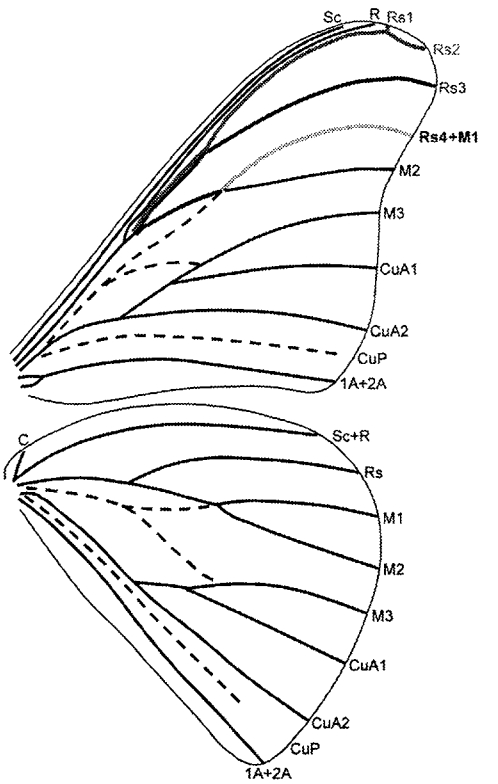

Fig. 175: *Samia cynthia* (Saturniidae), ♂, wing venation scheme [redrawn after Pruscha (1985: 94, Fig. 2)] – the imaginal FW Rs branches Rs1/Rs2 (red) and Rs3/Rs4 (blue) are entirely fused, the fork in Rs1/Rs2 is at its most distal position, and M1 and Rs4 are merged.

Character #H.47: "Areole" formed by a sclerotization between or the local touching of Rs2 and Rs3 (fore wing).

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; moderately supported.

Introduction. The radial sector branches Rs2 and Rs3 of the fore wing originate from two separate branches as described above (character #H.46; Fig. 176). In many Macrolepidoptera these two terminal branches (or even the two branches Rs1/Rs2 and Rs3/Rs4) are partly to entirely fused with each other, in which case Rs2 and Rs3 form a single vein over a certain distance (Figs 178, 179). This often appears as a "transfer" of one of these branches onto the other one.

Description. The situation is different in Anthelidae, in which Rs2 and Rs3 are connected to each other for a very short distance by a sclerotization of the wing membrane, just distally of their respective origins (Fig. 177). This appears as a separate origin of all Rs branches from a secondary cell, as opposed to the "stalked" origin of branches from an often tiny secondary cell – Turner's justification for separating the Anthelidae from the Lymantriidae (Turner 1920a: 418). This connection of Rs2 and Rs3 is neither a "cross-vein" containing a trachea, nor a fusion of Rs2 and Rs3. Instead, this connection is formed by a simple, sclerotized thickening. In quite a number of anthelid species, Rs2 and Rs3 are so closely approximated that they touch each other for a short distance, but without forming an anastomosis/fusion of the veins.

Discussion. Species have a tendency towards either a sclerotized thickening or a local contact between the veins, but occasionally both these conditions can be found in different specimens of the same species. This connection between Rs2 and Rs3 marks the posterior end of a sclerotized, transverse fold (see character #H.48), and the sclerotized thickening is likely to be part of it, while the local touching of these veins seems to be no more than an additional approximation of Rs2 and Rs3.

As Rs2 and Rs3 originate from separate branches and are not connected with each other in several bombycoid families, as well as during the development of anthelid wings, I interpret character state (1) as apomorphic.

Summary. The connection between Rs2 and Rs3 is unique to Anthelidae and not to be confused with the (partial) fusion of these branches (no longer distinguishable as two separate veins) or a "true cross-vein" with a trachea (if existing) in other taxa. While the sclerotized connection might be derived or be part of the fold described in character #H.48, this connection involves additionally the approximation and distal divergence of the two veins. Further, this connection occurs in a very specific arrangements of veins only. The actual connection itself is structurally very simple and does not offer any details indicating homology. Therefore I consider my hypothesis of homology to be moderately supported.

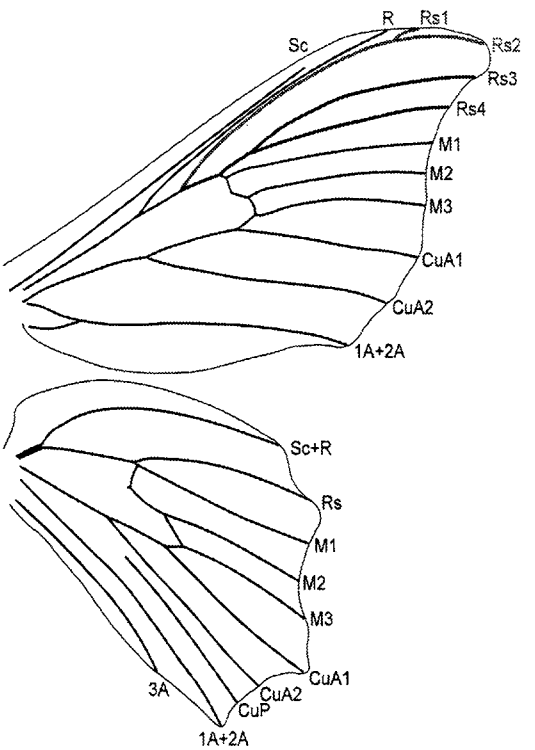

Fig. 176: *Mimallo amilia* (Mimallonidae), ♂, wing venation scheme [redrawn after da Costa Lima (1959: 248: Fig. 202)] – the FW Rs branches Rs1/Rs2 (red) and Rs3/Rs4 (blue) are widely separated and do not form an areole; note the distal fork in Rs1/Rs2.

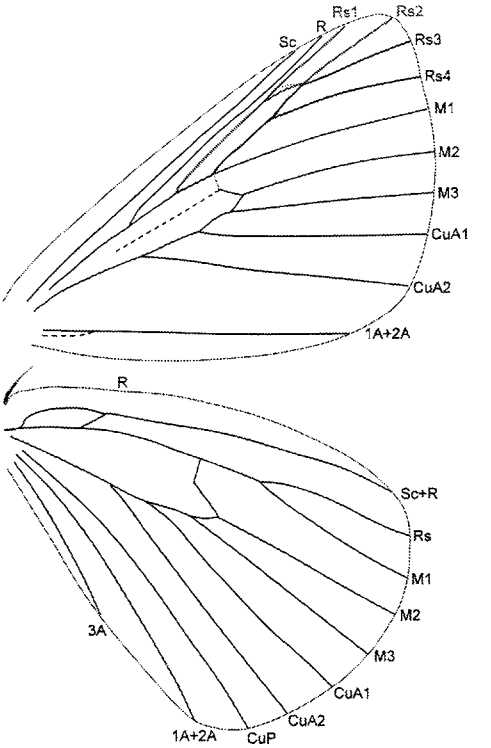

Fig. 177: *Anthela pudica* (Anthelidae), ♂, wing venation scheme – the FW Rs branches Rs1/Rs2 (red) and Rs3/Rs4 (blue) form the long edges of an areole, which is closed by a local contact between Rs2 and Rs3 near their origin.

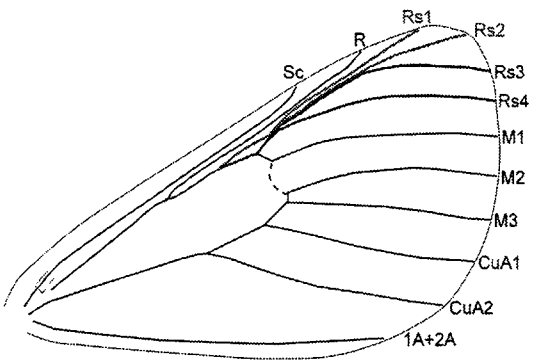

Fig. 178: *Laelia obsoleta* (Lymantriidae), ♂, fore wing venation scheme – the FW Rs branches Rs1/Rs2 (red) and Rs3/Rs4 (blue) are fused except for their basal part, which results in a very small areole.

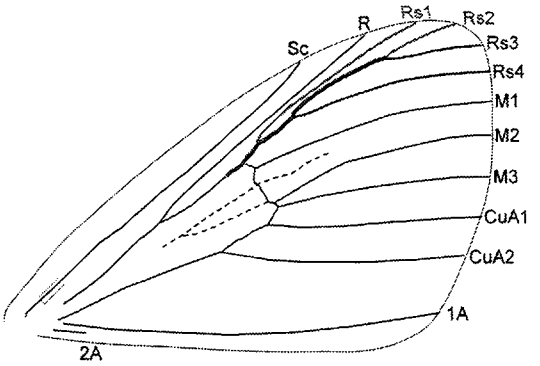

Fig. 179: *Leptocneria reducta* (Lymantriidae), ♂, fore wing venation scheme – the FW Rs branches Rs1/Rs2 (red) and Rs3/Rs4 (blue) are entirely fused; note the fork in Rs1/Rs2 being located more proximally than in Rs3/Rs4.

Character #H.48: Transverse, sclerotized fold connects Rs2 with Rs1 (fore wing).

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; very well supported.

Introduction. The fore wing of Anthelidae is not an entirely flat structure. The proximal 2/3 of the costal area are more strongly curved ventrad than in other families, while the distal 1/3 is slightly curved dorsad. The ventrad curved proximal area includes the costa, subcosta, and stem of the radius and radial sector. Near the base of the wing this area is at an angle of more than 45° to the rest of the wing (in cross-section). Obviously, any bend in a flat structure stiffens the whole structure – as employed technically by angled beams in construcions. Similarly, a stiffening of the wing edge is likely to be caused by the higher density of veins in the costal area, which is found in many other families of the bombycoid complex (e.g., Figs 189, 190), but not or less distinctively so in most Anthelidae (e.g., Figs 185, 186; the genus *Chelepteryx* with its giant wings is an exception (Fig. 180)). The increase in vein density appears to be positively correlated to wing length (size).

Description. The bend in the wing along the coastal area ends proximally of the wing apex in a transverse "step" or fold, distally of which the apex of the wing is not only in the plane of the wing, but even curves slightly dorsad. This transverse fold is located just distally of the forks in Rs1/Rs2 and Rs3/Rs4, stretching from Rs2 beyond Rs1 and converging onto R (Fig. 181). The beginning of this fold is formed by the basal section of Rs2, which is located dorsally of Rs1. In most anthelid species the ventral edge of this transverse fold is strengthened by a sclerotization, which connects Rs2 with Rs1 and extends slightly towards (Figs 182, 183) or even reaches R (character #H.49). Between Rs2 and Rs1, the dorsal edge of this transverse fold typically stretches at an angle to Rs2, but it occasionally overlies Rs2.

Discussion. The connection between Rs2 and Rs3 is formed by a sclerotized thickening (character #H.47), too, but as it is at an angle to the rest of the sclerotization its derivation from the sclerotized thickening of the fold is uncertain.

This partly sclerotized, transverse fold is unique to Anthelidae and has not been recorded from any other Lepidoptera, which is why I interpret character state (1) as apomorphic.

The development of truly new structures as opposed to the reuse of existing structures is very rare. The partly sclerotized transverse fold is such a new development, and its uniqueness and value were already recognized by Turner (1904).

Summary. The sclerotization of the fold is simple, but the fold itself consists of the basal section of Rs2 and a triangular part of the wing membrane. Further, the location and course of the fold are very constant and specific. Overall I consider my hypothesis of homology to be very well supported.

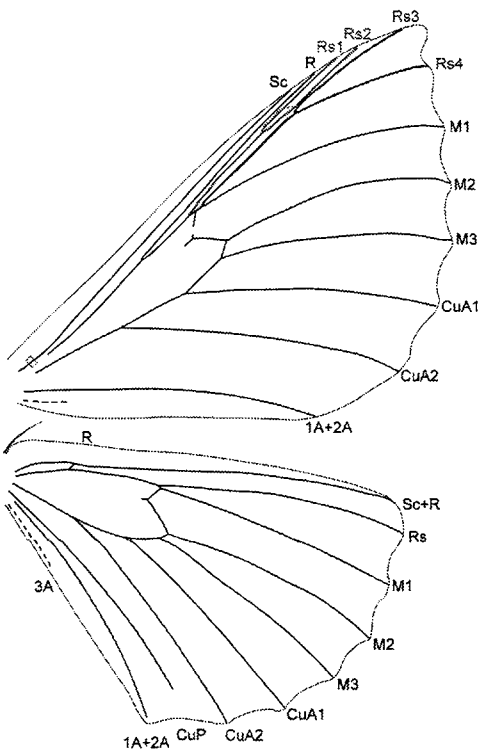

Fig. 180: *Chelepteryx chalepteryx* (Anthelidae), ♂, wing venation scheme – just distally of the closure of the areole in the FW a partly sclerotized cross-fold extends from Rs3/Rs2 towards R.

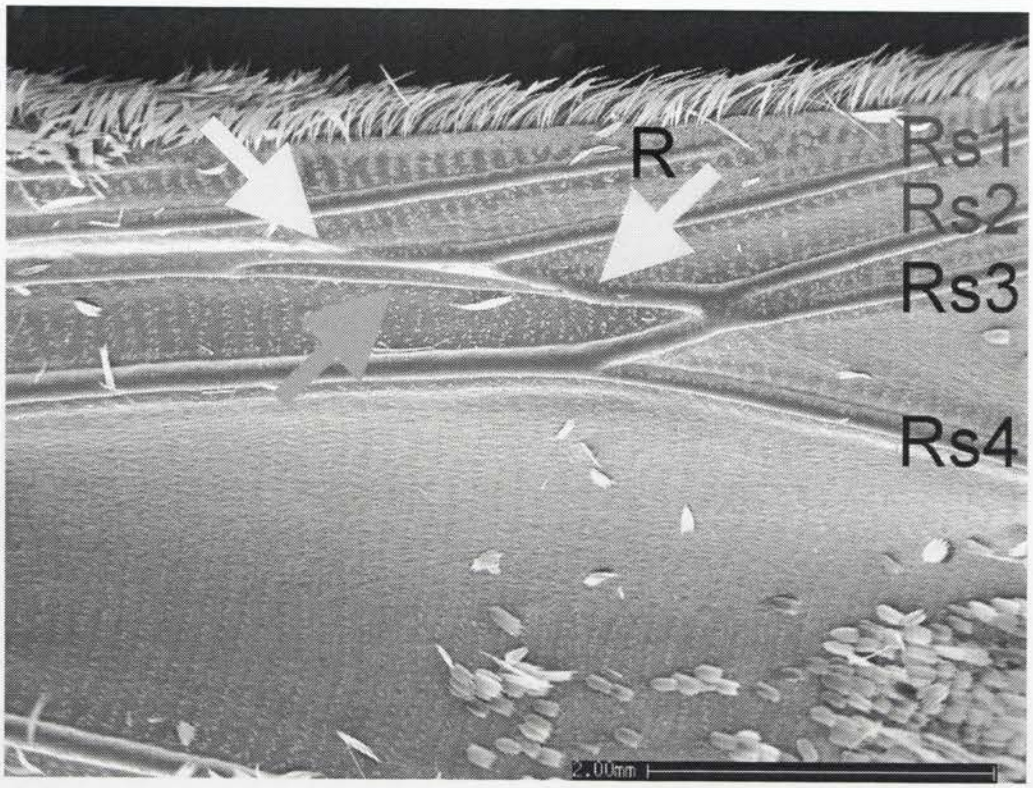

Fig. 181: *Chelepteryx chalepteryx* (Anthelidae), ♂, fore wing underside – a partly sclerotized cross-fold (green arrow) terminates the ventrad-angled costal area just distally of the origin of Rs2 and the contact between Rs2 and Rs3; the fold converges onto R, while the sclerotization (between yellow arrows) hardly extends beyond Rs1.

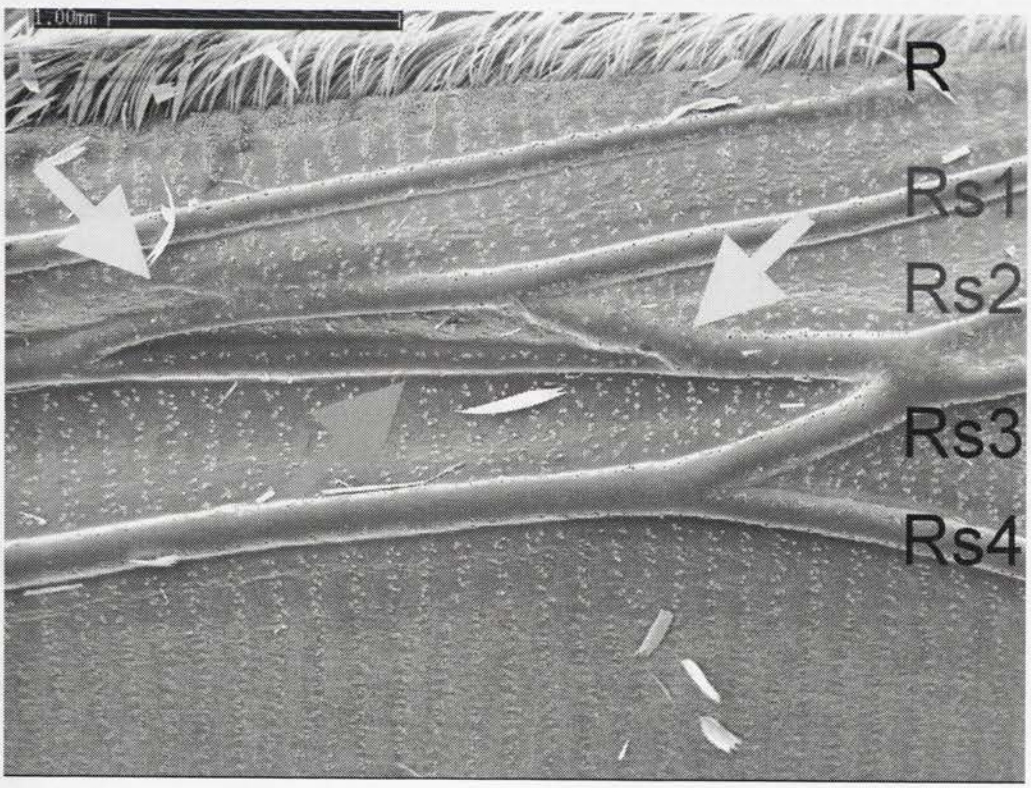

Fig. 182: *Chelepteryx chalepteryx* (Anthelidae), ♂, fore wing underside – a partly sclerotized cross-fold terminates the ventrad-angled costal area just distally of the origin of Rs2 and the contact between Rs2 and Rs3; the sclerotized part of the fold (between yellow arrows) is located dorsally and just slightly distally of the basal part of Rs2 (green arrow).

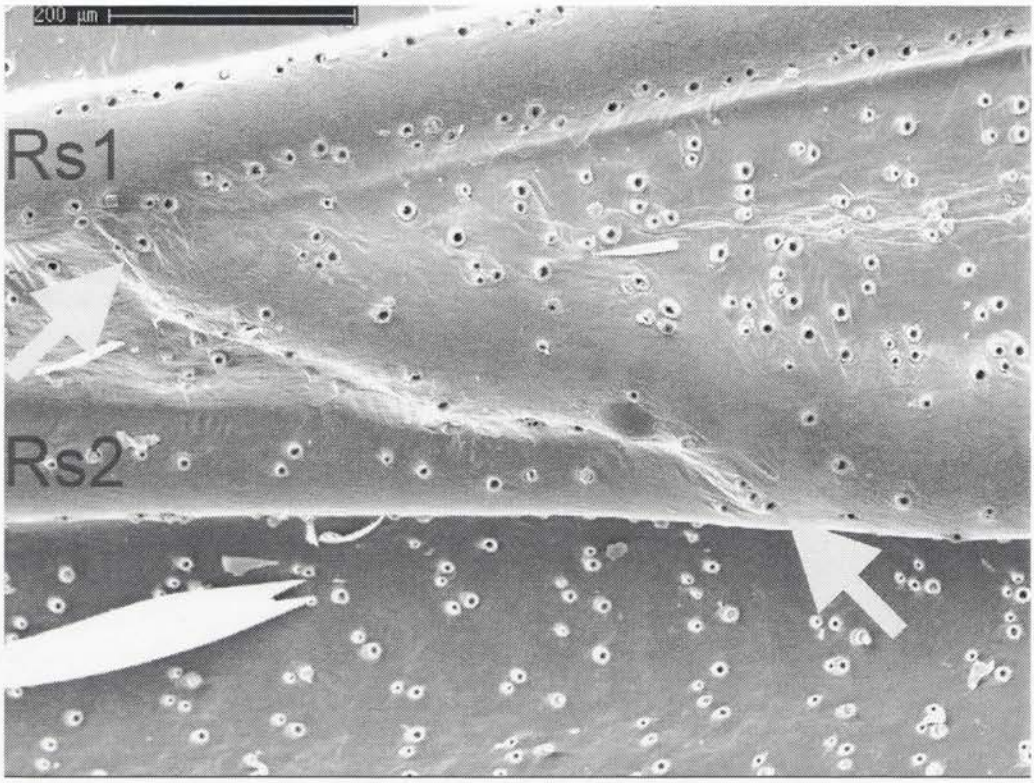

Fig. 183: *Chelepteryx chalepteryx* (Anthelidae), ♂, fore wing underside – sclerotized part (between yellow arrows) of the cross-fold in Rs, located dorsally and just slightly distally of the basal part of Rs2.

Character #H.49: Sclerotization of transverse fold extends onto R (fore wing).

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; poorly supported.

Description. The sclerotization of the transverse fold in the fore wing is of variable strength and variable extent. In most anthelid species it does not extend far beyond Rs1, ending before reaching R (Fig. 185). However, in some anthelid species it does extend further and reaches R (Fig. 184).

Discussion. This character has traditionally been used to characterize the anthelid subfamily Munychryiinae.

No sclerotization is present in species without a fold, and the sclerotization is not reaching R in most anthelid species. A gradual extension of the sclerotization is the most parsimonious explanation for the occurrence of the longest sclerotization, but while a reduction from a total sclerotization (which would have evolved initially) cannot be ruled out, I assume character state (1) to be apomorphic.

Summary. The extension of a sclerotization along an existing fold is a very simple modification, which does not allow the distinction between convergent evolution of such sclerotizations. Also I recorded such an extension of the sclerotization as part of infra-specific variation in *Omphaliodes obscura* (Fig. 186). Consequently I consider my hypothesis of homology to be poorly supported.

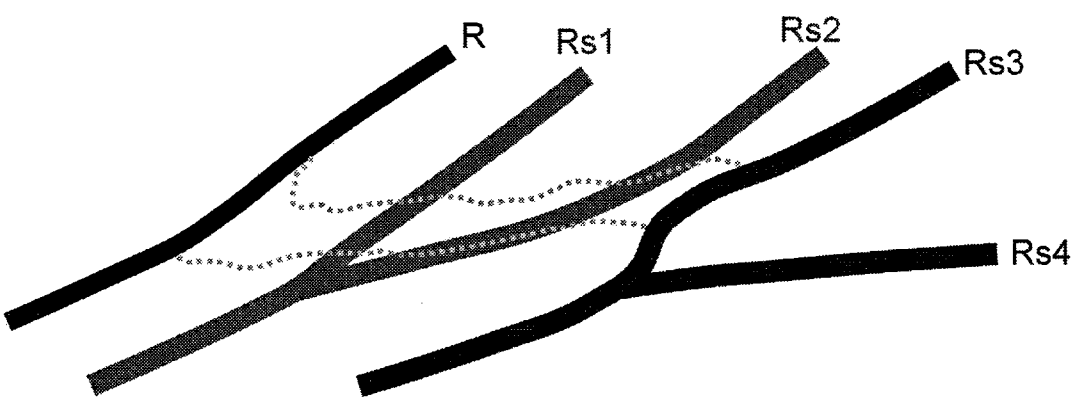

Fig. 184: *Munychryia* n. sp. nr *senicula* (Anthelidae), ♂, wing venation scheme – the sclerotization of the fold in the FW Rs (between the two green dotted lines) extends beyond Rs1 onto R.

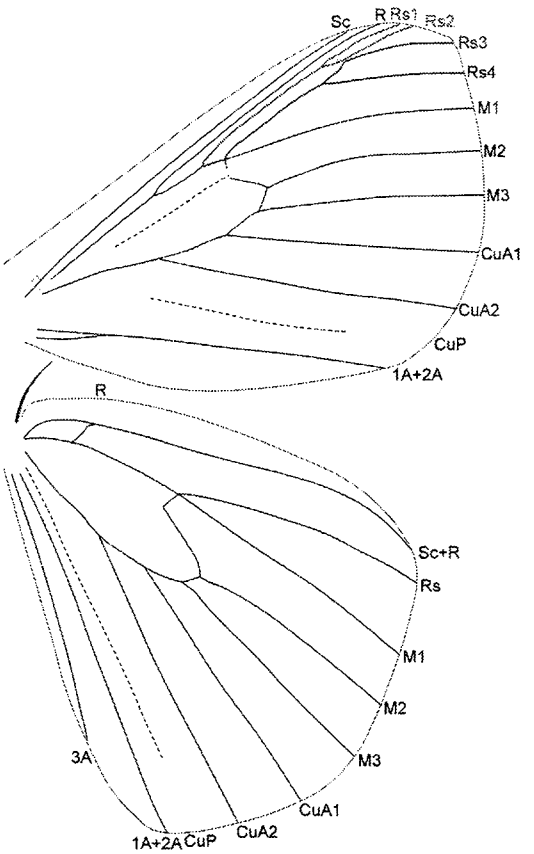

Fig. 185: *Pseudodreata* sp. (Anthelidae), ♂, wing venation scheme – the sclerotization of the cross-fold in the FW Rs hardly extends beyond Rs1.

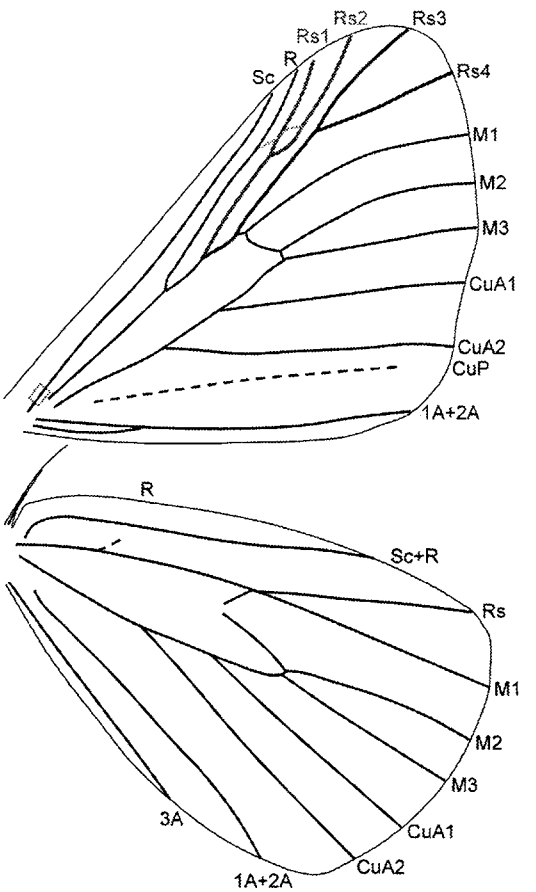

Fig. 186: *Omphaliodes obscura* complex (Anthelidae), ♂, wing venation scheme – the sclerotization of the cross-fold in the FW Rs extends beyond Rs1 as far as R in the illustrated specimen, but not in other specimens; note the open areole.

Character #H.50: Areole with Rs1/Rs2 "stalked" with Rs3/Rs4 (fore wing).

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; moderately supported.

Description. In almost all Anthelidae the branches Rs1/Rs2 and Rs3/Rs4 arise separately from the discoidal cell in the fore wing, extending parallel to each other from their origin (Fig. 187). Only in *Gephyroneura cosmia* and an undescribed munychryiine species are Rs1/Rs2 and Rs3/Rs4 "stalked" and gradually diverge from each other (Fig. 188).

Discussion. The "stalking" seems to be caused by a subsequent fusion of a short basal section of Rs1/Rs2 onto Rs3/Rs4, which ends well before the fork in both branches.

Both branches Rs1/Rs2 and Rs3/Rs4 arise separately from the discoidal cell and extend parallel to each other in most Anthelidae and other families of the bombycoid complex (e.g., Carthaeidae (Fig. 195), Sphingidae, some Brahmaeidae). Further, this condition is indicated in the developing wing of *Anthela astata*. Therefore I interpret character state (1) as apomorphic.

Summary. The only partial fusion of the two branches is unique in the context of the very specific arrangement of veins (as described in characters #H.47, #H.48), but is otherwise a rather simple modification. Much more extensive ("entire") and thereby less distinct fusions of these branches are common in other Lepidoptera (e.g., many Noctuoidea). Therefore I consider my hypothesis of homology to be moderately supported.

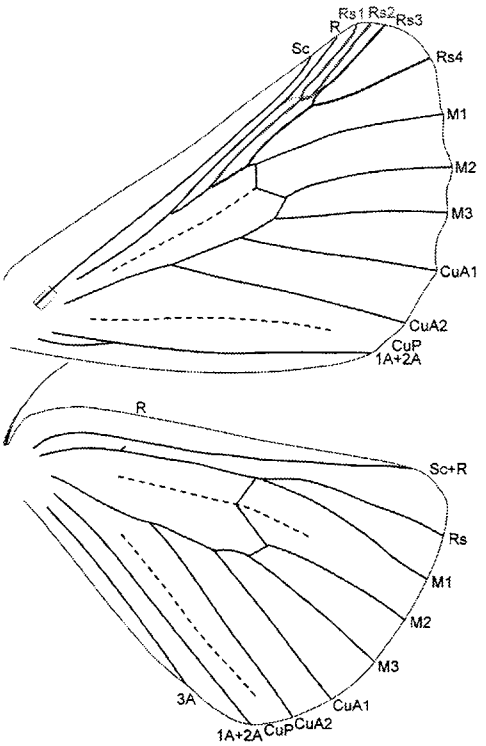

Fig. 187: *Anthela ferruginosa* (Anthelidae), ♂, wing venation scheme – FW Rs branches Rs1/Rs2 (red) and Rs3/Rs4 (blue) arise separately from the discoidal cell and form the long edges of the areole.

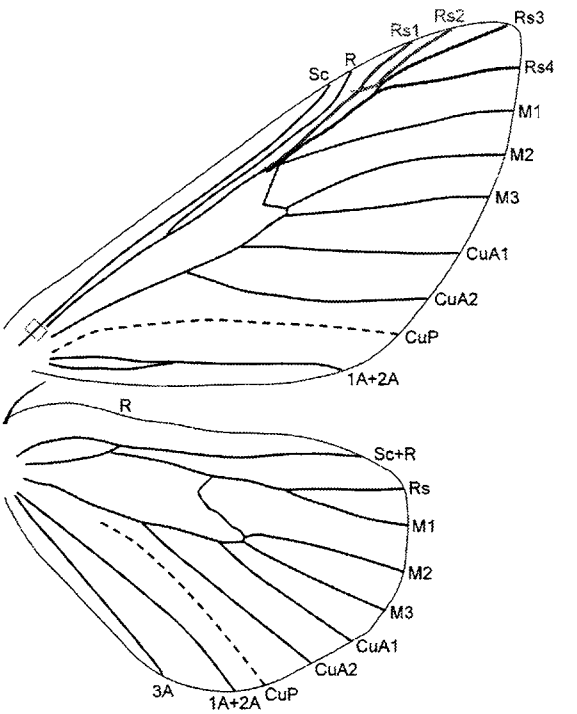

Fig. 188: Munychryiinae n. sp. (Anthelidae), ♂, wing venation scheme – FW Rs branches Rs1/Rs2 (red) and Rs3/Rs4 (blue) are stalked from the upper distal corner of the discoidal cell and form the long edges of the shortened areole.

Character #H.51: Rs fused, with Rs1 branching off most distally (fore wing).

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; very poorly supported.

Description. The radial sector of the fore wing with a distal fork in the Rs1/Rs2 branch (character #H.46) is largely fused in a number of families in the bombycoid complex. In these taxa the branches Rs1/Rs2 and Rs3/Rs4 are entirely fused with each other, which results in an appearance of "stalked" Rs branches, with Rs1 seemingly branching off most distally (Fig. 192).

Discussion. Minet (1994) proposed a similar character for this arrangement, namely "fore wing venation with Rs1 + Rs2 closely parallel to branch Rs3 + Rs4 (in Carthaeidae and Sphingidae), or even fused to it (in the remaining Bombycoidea)" (Minet 1994: 70). This definition includes the "stalking" present in many Bombycidae (see character #H.46), which differs from all other "stalkings" in the bombycoid complex by Rs1 seemingly branching off most proximally, rather than distally (Fig. 190). This, as well as the partly separate condition of the two branches in some Apatelodinae (Fig. 189), indicates a fusion of the two branches in an arrangement, in which the fork in Rs1/Rs2 is located proximally of the fork in Rs3/Rs4. Consequently, the fusion of the two branches in these Bombycidae does not seem to be homologous with the fusion found in many other families of the bombycoid complex. In the subfamily Prismostictinae the Rs branches are entirely fused, too, but with the fork in Rs1/Rs2 being more distal than the one in Rs3/Rs4 (Fig. 191), which is similar to but not identical with the condition present in other families of the bombycoid complex. The interpretation of these differences is difficult as the monophyly of Bombycidae *sensu* Minet (1994) is not convincingly supported.

In the family Brahmaeidae the branches are fused entirely in the genera *Dactyloceras* and *Acanthobrahmaea*. However, the branches are only stalked in the genera *Brahmaea* and *Brahmophthalma*. This condition is not identical with the entirely separated branches and could have originated from a partial fusion of the separate branches or from a partial split-back of the fused branches. An examination of the pupal tracheation might clarify the origin of the stalked condition, but at present I cannot decide between the two possible origins on a structural basis. Therefore, I cannot assign a character state to the hypothetical ground plan of the family Brahmaeidae.

Further, Minet's character definition implies the fused condition to be a subsequent modification of the Rs branches being "closely parallel", with "closely parallel" being the common denominator. How close the branch Rs1/Rs2 has to be to Rs3/Rs4 to qualify for being "closely parallel" was not specified (Minet (1994: 70) considered the arrangement in Anthelidae to be more "widely separated"). In any case, the proximity of these veins alone is a very poor indication of homology. Assuming that the fused conditions have separately originated from closely approximated branches only weakens this hypothesis of homology further.

The primary split in the radial sector results in the separation of the two branches Rs1/Rs2 and Rs3/Rs4, as present in a number of families of the bombycoid complex but not in any anthelid species. The fusion of these branches is a subsequent modification, which is why I interpret character state (1) as apomorphic.

Summary. The fusion of these branches is entire and rather unspecific. It is further obscured by the "loss" of one (or more) of the radial branches in a number of taxa (e.g., most Eupterotidae and Saturniidae, many Lemoniidae (Figs 193, 194)). The convergent occurrence of a fusion in Bombycidae (and potentially some Brahmaeidae) and the frequent occurrence of such fusions outside the bombycoid complex argue for a general tendency to fuse these branches. Therefore I regard my hypothesis of homology as very poorly supported.

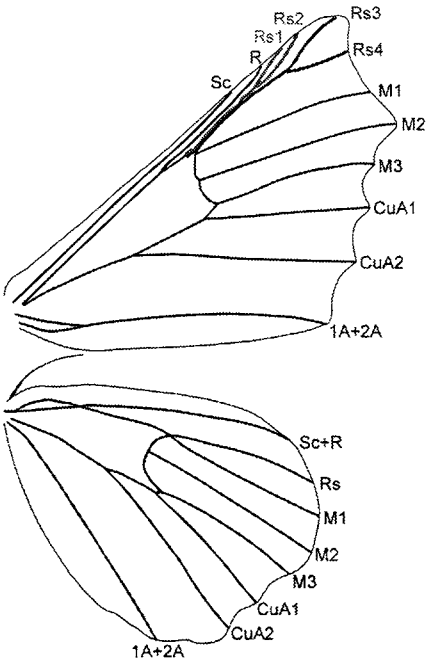

Fig. 189: *Olceclostera* sp. (Bombycidae: Apatelodinae), ♂, wing venation scheme [redrawn after da Costa Lima (1959: 282: Fig. 233)] – FW Rs branches Rs1/Rs2 (red) and Rs3/Rs4 (blue) partly fused, with most distal fork in Rs3/Rs4.

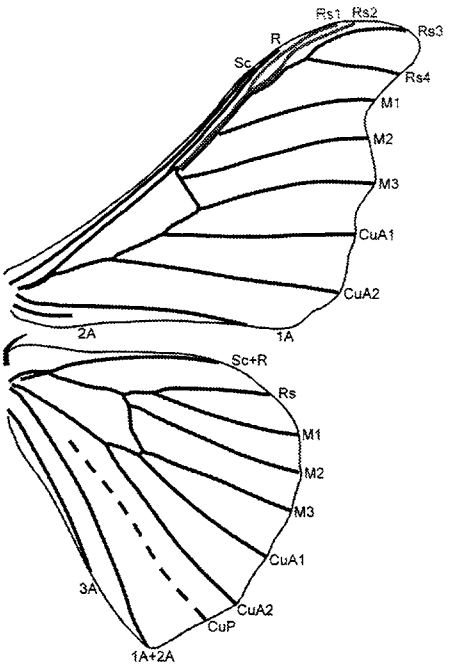

Fig. 190: *Bombyx huttoni* (Bombycidae: Bombycinae), ♂, wing venation scheme [redrawn after Lemaire & Minet ([1998]: 332: Fig. 18.3C)] – FW Rs branches Rs1/Rs2 (red) and Rs3/Rs4 (blue) entirely fused, with most distal fork in Rs3/Rs4.

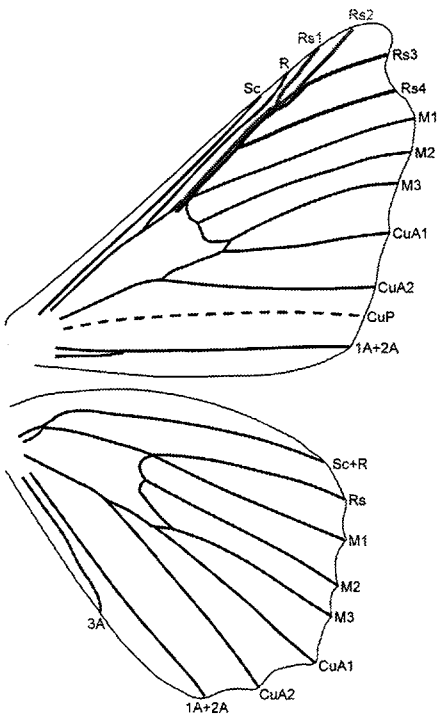

Fig. 191: *Prismosticta* sp. (Bombycidae: Prismostictinae), ♂, wing venation scheme – FW Rs branches Rs1/Rs2 (red) and Rs3/Rs4 (blue) entirely fused, with most distal fork in Rs1/Rs2.

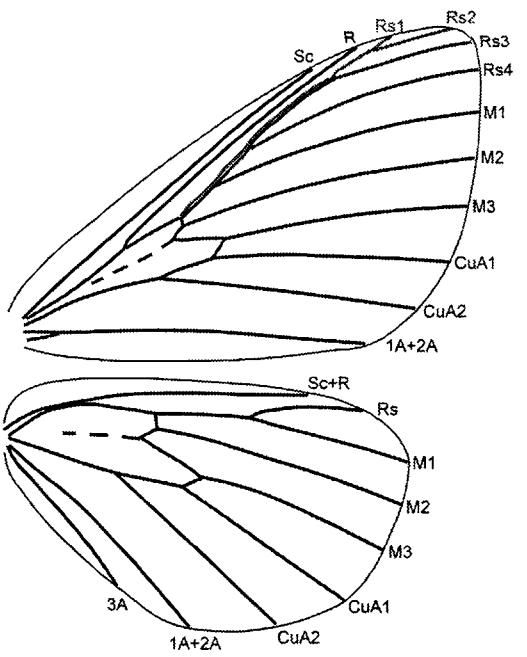

Fig. 192: *Phiala costipuncta* (Eupterotidae), ♀, wing venation scheme [redrawn after Aurivillius (1901: 15, Fig. 10)] – FW Rs branches Rs1/Rs2 (red) and Rs3/Rs4 (blue) entirely fused, with most distal fork in Rs1/Rs2.

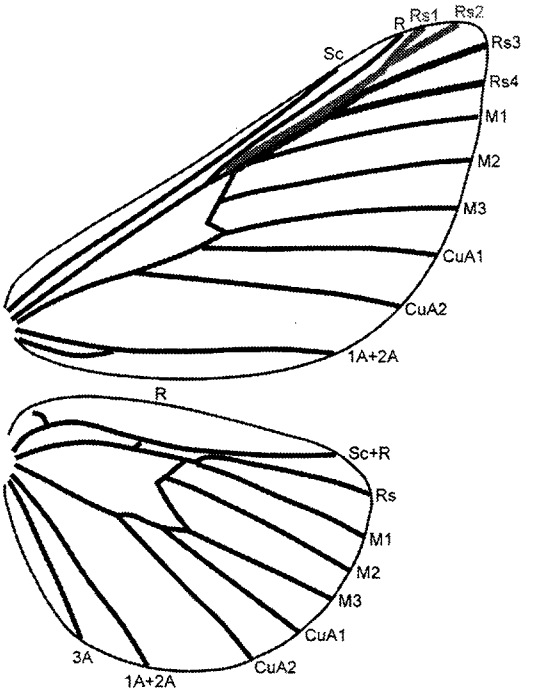

Fig. 193: *Lemonia dumi* (Lemoniidae), ♂, wing venation scheme [redrawn after Hampson (1901: 189)] – FW Rs branches Rs1/Rs2 (red) and Rs3/Rs4 (blue) entirely fused, with most distal fork in Rs1/Rs2.

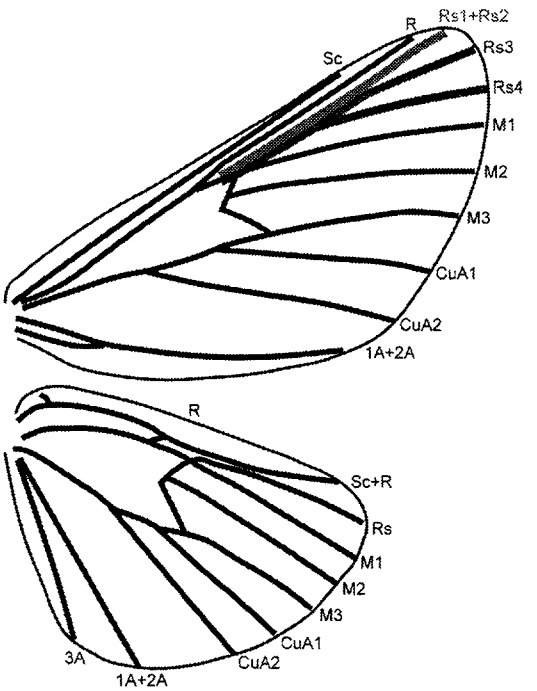

Fig. 194: *Lemonia sardanapalus* (Lemoniidae), ♂, wing venation scheme [redrawn after Hampson (1901: 188)] – FW Rs branches Rs1/Rs2 (red) and Rs3/Rs4 (blue) entirely fused, with no fork in Rs1/Rs2 (the fork is probably displaced as far distad as the edge of the wing).

Character #H.52: Anal loop of 1A+2A about half as long as length of 1A+2A (fore wing).

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; poorly supported.

Description. The anal veins 1A and 2A of the adult fore wing appear either to be separate or form a short, basal fork. In the small families Endromidae and Mirinidae this fork is unusually long, extending to about half the length of the anal veins.

Discussion. The long anal loop seems to be unique to Endromidae and Mirinidae, which is why I interpret character state (1) as apomorphic.

Summary. The length of the anal loop is significantly different from the typical lengths of anal loops in other Lepidoptera and a seemingly unique modification. Nevertheless, any differences in length are very simple modifications only. Therefore I regard my hypothesis of homology as poorly supported.

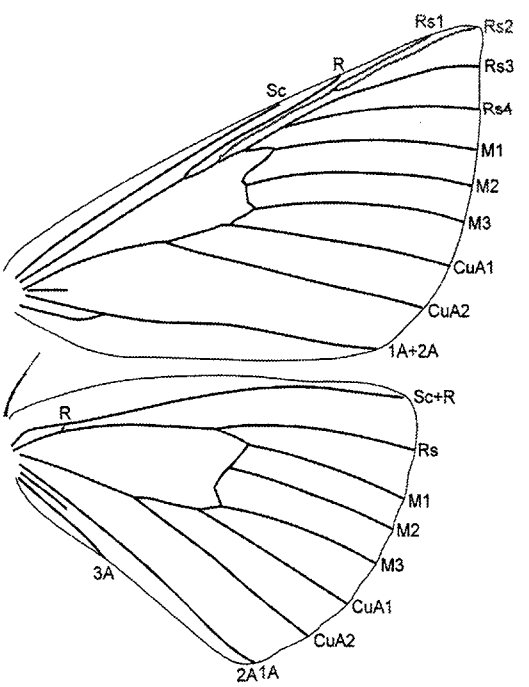

Fig. 195: *Carthaea saturnioides* (Carthaeidae), ♂, wing venation scheme [redrawn after Common (1966: 30, Fig. 1)] – the loop in the anal vein 1A+2A of the FW does not extend to about the middle of this vein; note the separate Rs1/Rs2 and Rs3/Rs4 branches in the FW.

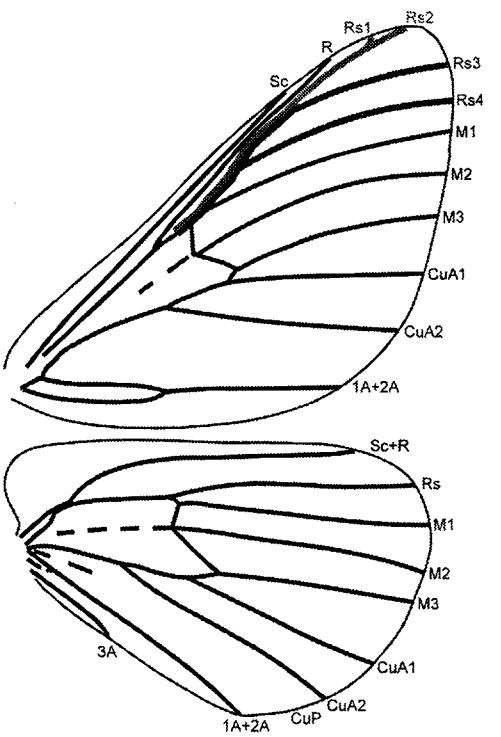

Fig. 196: *Mirina christophi* (Mirinidae), ♂, wing venation scheme [redrawn after Lemaire & Minet ([1998]: 339: Fig. 18.5F)] – the loop in the anal vein 1A+2A in the FW extends to about the middle of this vein.

Character #H.53: Termen with a subapical protrusion (fore wing).

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; very poorly supported.

Introduction. The shape of the wing is extremely variable, and obviously similar shapes have evolved many times. This is also true for the termen (distal edge) of the fore wing, which can have any shape from concave to convex. In Anthelidae the termen is always convex, and the subapical part is either smooth or weakly crenulate, but not forming a protrusion. The only exceptions are *Chenuala heliaspis* and an undescribed antheline species from northern Queensland, which possibly belongs to the genus *Chenuala*.

Description. In these two species the termen forms a subapical protrusion, which has its angular point at the vein M1 in *C. heliaspis*, but at vein M2 in the undescribed antheline species.

Discussion. Relative to the length of the termen the position is about the same in the two anthelid species, but relative to the veins this location differs slightly between them, which might be due to differences in the overall proportions of the wing.

Within the Anthelidae the subapical protrusion of the termen is unique to the aforementioned two species. However, subapical protrusions are occasionally present in other Lepidoptera, e.g., Bombycidae (Figs 189, 190, 191). In most cases it is not possible to decide about the homology or non-homology of these protrusions, which is why it is not possible to determine the polarity of this character based on an outgroup comparison. Hence, I only assume character state (1) to be apomorphic, based on the absence of a subapical protrusion in all other Anthelidae and in largely plesiomorphic taxa of the bombycoid complex.

Summary. The subapical protrusion of the termen has no indications of homology other than its extent and location. Given the slight difference in location and the lack of other indications of homology, I regard my hypothesis of homology as very poorly supported.

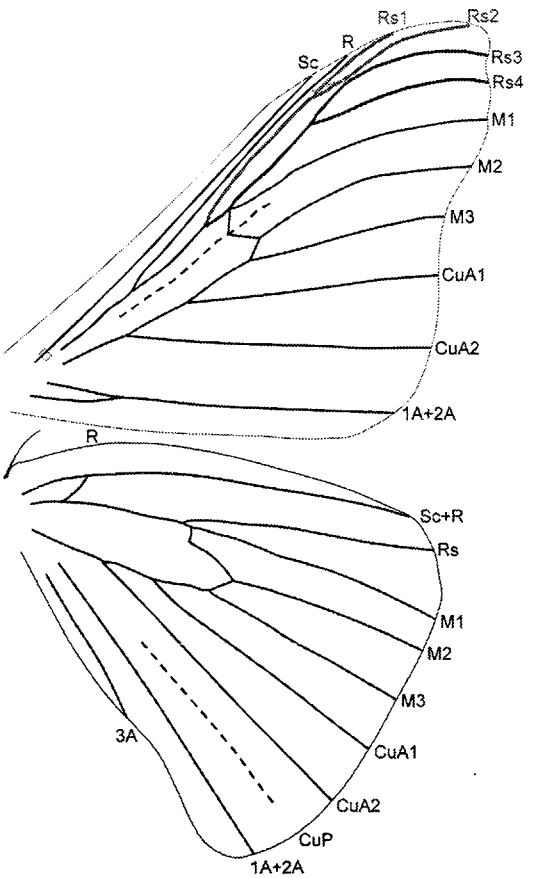

Fig. 197: *Chenuala heliaspis* (Anthelidae), ♂, wing venation scheme – fore wing termen with a subapical protrusion at M1; note the distinctly more distal position of the fork in the FW Rs branch Rs1/Rs2 compared to the one in Rs3/Rs4.

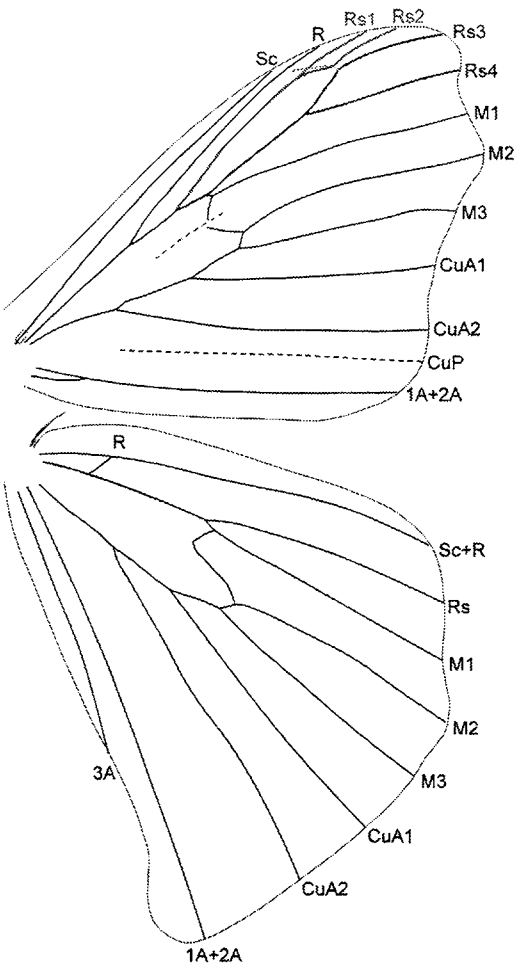

Fig. 198: Antheline n. sp. (Anthelidae), ♂, wing venation scheme – fore wing termen with a subapical protrusion at M2; note the distinctly more distal position of the fork in the FW Rs branch Rs1/Rs2 compared to the one in Rs3/Rs4.

Character #H.54: Female apterous.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; very poorly supported.

Description. In the anthelid genus *Pterolocera* the females have entirely reduced wings (Fig. 200), while the males have very well developed wings (Fig. 199).

Discussion. Undoubtedly, this loss of wings has a strong influence on the ecology of these species, in particular on their ability to disperse and to choose host plants as adults.

The female of the anthelid species *Omphaliodes obscura* is still unknown. As male specimens of this species are frequently collected at lights, it seems likely that the female is apterous.

The loss of wings in one gender is obviously a modification, which is why I interpret character state (1) as apomorphic.

Summary. As extreme as the loss of wings might appear, it is nevertheless only a loss, which does not provide any indications of its homology other than its restriction to females only. However, such a loss of wings is typically restricted to females, and apterous females occur occasionally in many lepidopteran families (Sattler 1991), including the bombycoid families Lasiocampidae (e.g., *Chondrostega*) and Eupterotidae (R. Oberprieler, ANIC, pers. comm.). Therefore I consider my hypothesis of homology as at best very poorly supported.

Fig. 199: *Pterolocera* sp. (Anthelidae), ♂ – males are fully winged; note the large antennae.

Fig. 200: *Pterolocera* sp. (Anthelidae), ♀ – females are wingless (apterous).

III.5) THE ADULT HEAD

The adult head of Lepidoptera is generally rich in rather complex structures, which are involved in orientation and feeding. In Anthelidae, as well as many other families, the emergence of females with fully developed eggs, and the rapid mating and oviposition result in a shortened adult lifespan without the need to feed, which is linked to a strong reduction or loss of many of the complex structures on the head. While a shortened lifespan does not require extensive feeding, the location of a mate has to be achieved more efficiently. In the bombycoid complex it is the male that searches actively for females. Not surprisingly, the sensory structures required for this task, the antennae, are very well developed in males. The correlation between a shortened adult lifespan, loss of feeding behaviour, reduction of mouthparts and strong development of antennae can be observed in many lepidopteran families. Consequently, many modifications of similar appearance have evolved convergently, e.g., the loss of the proboscis, maxillary palpi and pilifer bristles, or the development of lateral outgrowths (rami) of the antenna.

In the Anthelidae only the genus *Munychryia* retains a well developed proboscis and structures associated with it, namely a one-segmented maxillary palpus and well developed pilifer bristles. However, no feeding behaviour has yet been observed for *Munychryia*. In all other Anthelidae, including other Munychryiinae, these structures are very strongly reduced or lost. Anthelidae never have a median protrusion on the frons, ocelli, chaetosemata or a chaetosema-like sense organ on the labial palpus. Their labial palpi are three-segmented, upturned and fully scaled. Their compound eyes are large and without interommatidial setae, except for *Chelepteryx chalepteryx* (but not *C. collesi*), in which only the dorsal two-thirds of the eye have some interommatidial setae in both sexes. The antennae are very well developed and dorsally scaled to the apex. The antennal flagellum consists of about 50-55 segments, which each have a single pair of latero-ventrally protruding rami (the antenna appears "bipectinate") as well as a median, ventral protrusion with a ventro-distal sensory structure (the antenna appears "tripectinate"; character #H.55). The bipectinate, unipectinate, serrate or filiform antennae of female Anthelidae are merely stages of reduction of the tripectinate condition present in males. The antenna is tripectinate to the apex, with the size of the rami increasing gradually towards the apex of the antenna. The relative length of the

antenna as well as of the rami varies greatly between species. While certain taxa are characterized by particularly long rami, e.g., the genus *Pterolocera*, morphometric differences in size are very poor indications of homology, and in the case of Anthelidae a continuous range of antenna and ramus lengths seems to exist. Further, the length of rami is difficult to measure in dried specimens as the dried rami tend to curve or curl inwards. Therefore I did not use morphometric data of the antennae as characters for my phylogenetic hypotheses.

The different antennal structures in the bombycoid complex are discussed in the next section, followed by the character analyses of adult head-related characters.

III.5.1) The male antennal flagellum structure of the bombycoid complex

As in other Lepidoptera the antenna of the bombycoid complex seems to be mainly an organ for olfaction, but certainly has various other functions as well. Its flagellum consists of a series of segments (flagellomeres), which carry numerous sensilla of various types. These sensilla are mainly located on the ventral to latero-ventral side of the segments, while the dorsal to dorso-lateral side is typically scaled. As in many other Lepidoptera the sensory ventral surface of each segment is enlarged by a pair of latero-ventral extensions, the rami. These rami are tubular, hollow outgrowths near the anterior end of the segment (Fig. 201). They are not articulated to the antennal segment and carry a large number of long, sensory setae on their mesal side, which, based on appearance, have generally been classified as sensillum trichodeum, sensillum basiconicum and sensillum chaeticum in Lepidoptera (e.g., Hallberg *et al.* 2003). Less prominent and rarer sensilla on the ventro-median part of each flagellomere are sensillum coeloconicum, sensillum styloconicum and sensillum squamiformium (a sensory scale). Sensilla auricillica (Fig. 202) have occasionally been recorded for Lepidoptera, too (e.g., Faucheux 1985; Shields & Hildebrandt 1999a, b).

The flagellum of males is typically much more developed than that of females (the Mimallonidae are an exception, with equally well developed antennae in both sexes), which appear to be reduced forms of the male flagellum. Hence, in this and the following sections I discuss the structurally more diverse male flagellum only.

A sensillum styloconicum is located ventro-medially at the distal end of each flagellomere, pointing ventro-distad (Fig. 203). This arrangement can be found in Zygaenoidea (Bodine 1896: Pl. IV, Fig. 43), Pyraloidea (e.g., Bodine 1896: Pl. III, Fig. 21 & Pl. IV, Fig. 45; Nuss 1999: 121, Fig. 29), Macrolepidoptera and possibly also in other Lepidoptera. A sensillum styloconicum consists of a poreless peg, which is situated in the tip of a conical, sclerotized protrusion (Fig. 204). According to Hallberg *et al.* (2003: 273), just a single sensillum styloconicum is located at the distal edge of each flagellomere in most taxa. Lee and Strausfeld (1990) described a modification of such a sensillum styloconicum for *Manduca sexta* (Sphingidae), in which 3-6 sensilla styloconica are united within one sclerotized protrusion and fused with each other. They

referred to this "unique" modification as the "styliform sensillum complex" (Fig. 205). However, already one century earlier such sclerotized cones with multiple pegs were described and illustrated by Bodine (1896: 10; Pl. III, Fig. 21 & Pl. IV, Fig. 45). He illustrated a styliform sensillum complex for Megalopygidae (Zygaenoidea) and Geometridae (Geometroidea). In addition I observed a styliform sensillum complex in *Oenosandra boisduvalii* (Noctuoidea: Oenosandridae; Fig. 206) and most families of the bombycoid complex as well: *Andraca* n. sp. (Bombycidae), *Carthaea saturnioides* (Carthaeidae), *Smerinthus jamaicensis* (Sphingidae), *Periga* sp. (Saturniidae), *Pterolocera* sp. (Anthelidae), *Ganisa plana* (Eupterotidae), *Brahmophthalma hearseyi* (Brahmaeidae) and *Lemonia taraxaci* (Lemoniidae). In these taxa the number of pegs varies between flagellomeres of one specimen, as does their degree of fusion. Most taxa have 3-6 fused pegs within one sclerotized protrusion, but in the *Andraca* n. sp. I observed no more than two pegs.

The styliform sensillum complex located at the ventro-distal edge of flagellomeres is likely to be significant for hypotheses regarding the higher phylogeny of Lepidoptera. However, as it has been recorded only very rarely and incompletely so far, no conclusions can be drawn at this point and much more comprehensive examinations with a SEM are required. The sparse data merely show that this structure is not a synapomorphy of Noctuoidea and the bombycoid complex, as might appear from my own observations and modern literature alone.

In most families of the bombycoid complex the median ventral part of a flagellomere has been modified. This ventral area forms a ventro-median process, which carries the styliform sensillum complex at its apex (Figs 207, 208, 209; character #H.55). This process is further characterised by the occurrence and distribution of sensilla coeloconica on it. In species without such a process, sensilla coeloconica are "usually located on the mid-ventral part" of a flagellomere (Hallberg *et al.*, 2003: 272) and are low in numbers – the largest number I observed were up to seven, mainly near the distal flagellomere edge in *Hypsidia niphosema* (Drepanoidea: Drepanidae; Fig. 210). In contrast, the distal and lateral sides of the ventro-median process present in many families of the bombycoid complex are covered in sensilla coeloconica (Figs 211, 212, 213). Depending on the size of the process, they can number more than 30 (e.g., *Ganisa plana* (Eupterotidae) and *Periga* sp. (Saturniidae)). Unlike the distal and lateral sides,

the proximal side of the process does not carry any sensilla coeloconica, but sensory setae only (Fig. 214).

The ventro-median process is often very prominent, in which case the antenna appears to be tripectinate – the flagellomeres have a large ventro-median process and a pair of lateral rami (Fig. 215). The size of the process is very variable and differs not only between species, but between flagellomeres, too. Very often the size of a process increases the further distally a flagellomere is located. In species with a "simple" antenna apex (e.g., many Bombycidae) the apical rami are lost and the ventral process might be the only protrusion (Fig. 216).

However, in the majority of species this ventro-median process is not prominent or even reduced to a rather shallow protrusion with an apical styliform sensillum complex (Fig. 217). Various stages of reductions occur, in particular in female antennae. In Anthelidae the rami and ventro-median processes of some females are simply strongly shortened, resulting in a weakly tripectinate antenna. In other species the female antenna is bipectinate as the ventro-median process is entirely lost. Others have a "serrate" antenna, with the lateral rami lost and only the ventro-median process remaining. If this process is lost, too, the antenna appears to be filiform. I did not use these reductions as characters in my phylogenetic analyses, because a tendency towards a reduction of the pectination in females is almost universal in Lepidoptera (few exceptions exist, e.g., in the family Mimallonidae).

Shallow ventro-median protrusions to short processes have occasionally evolved in non-bombycoid taxa, too (Fig. 248). Superficially they resemble the processes of the bombycoid complex (in particular subsequently reduced processes), but they differ in details, which argues against a homology of these structures. In *O. boisduvalii* (Noctuoidea: Oenosandridae) a very short and laterally dilated process is present on apical flagellomeres, but it lacks any sensilla coeloconica (Fig. 206). A ventro-median protrusion of a totally different type is present in the genus *Trictena* (Hepialoidea: Hepialidae; Fig. 218).

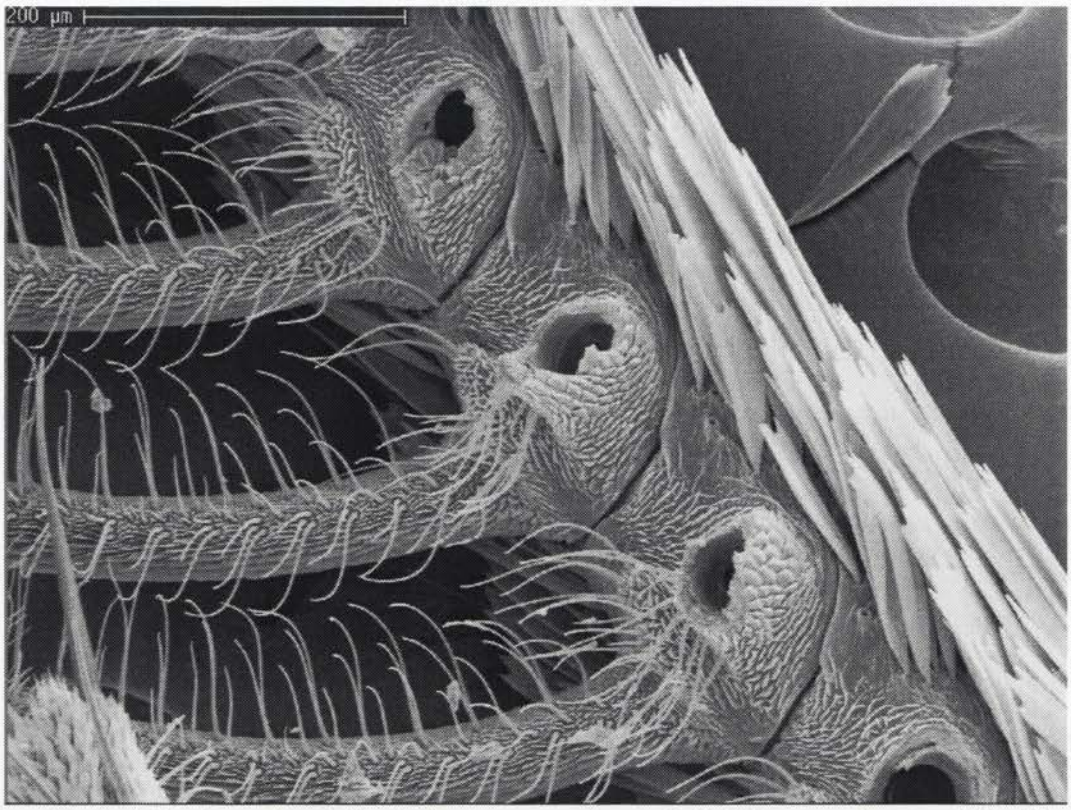

Fig. 201: *Anthela adriana* (Anthelidae), flagellomeres at basal third of ♂ antenna [rami on right side removed], latero-ventral view (top left = distal) – the flagellomeres are dorsally scaled and ventrally carry many s. trichodea; the flagellomeres form ventro-laterally a single pair of hollow rami near their proximal edge and a ventro-median process, which is reduced to a shallow protrusion in this species.

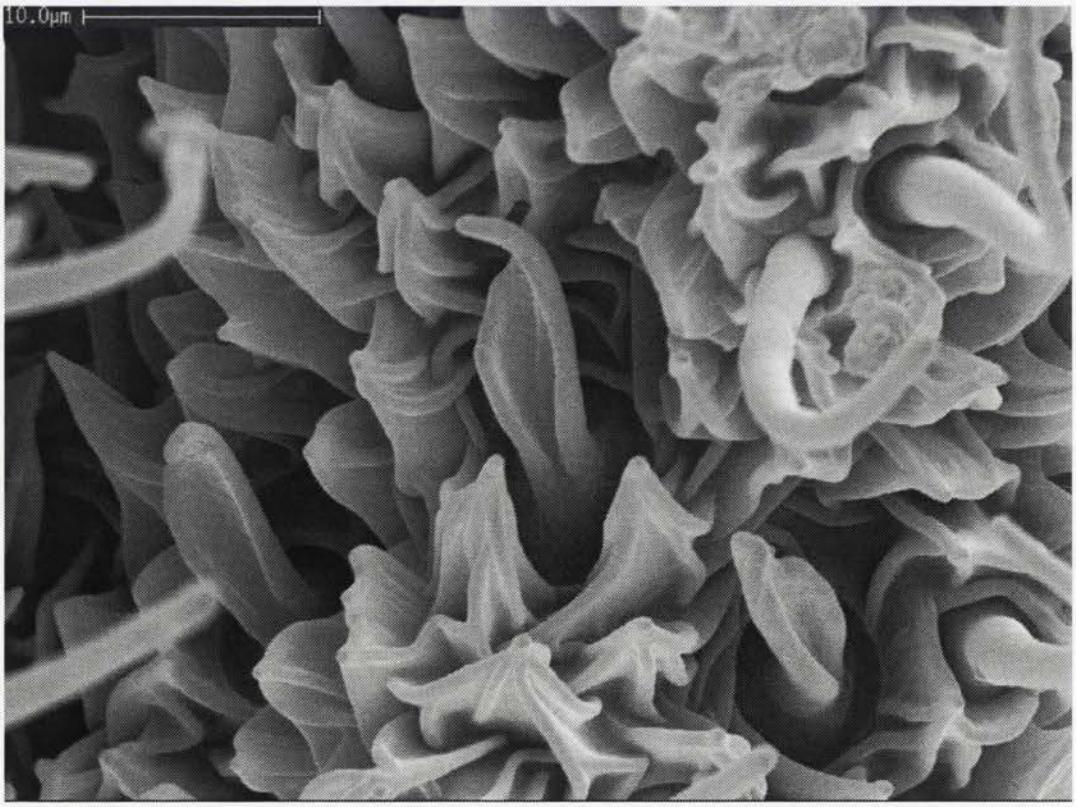

Fig. 202: *Carthaea saturnioides* (Carthaeidae), ventro-median process of a flagellomere at apex of ♂ antenna, latero-distal view (top = ventral) – sensilla auricillica on ventro-median process.

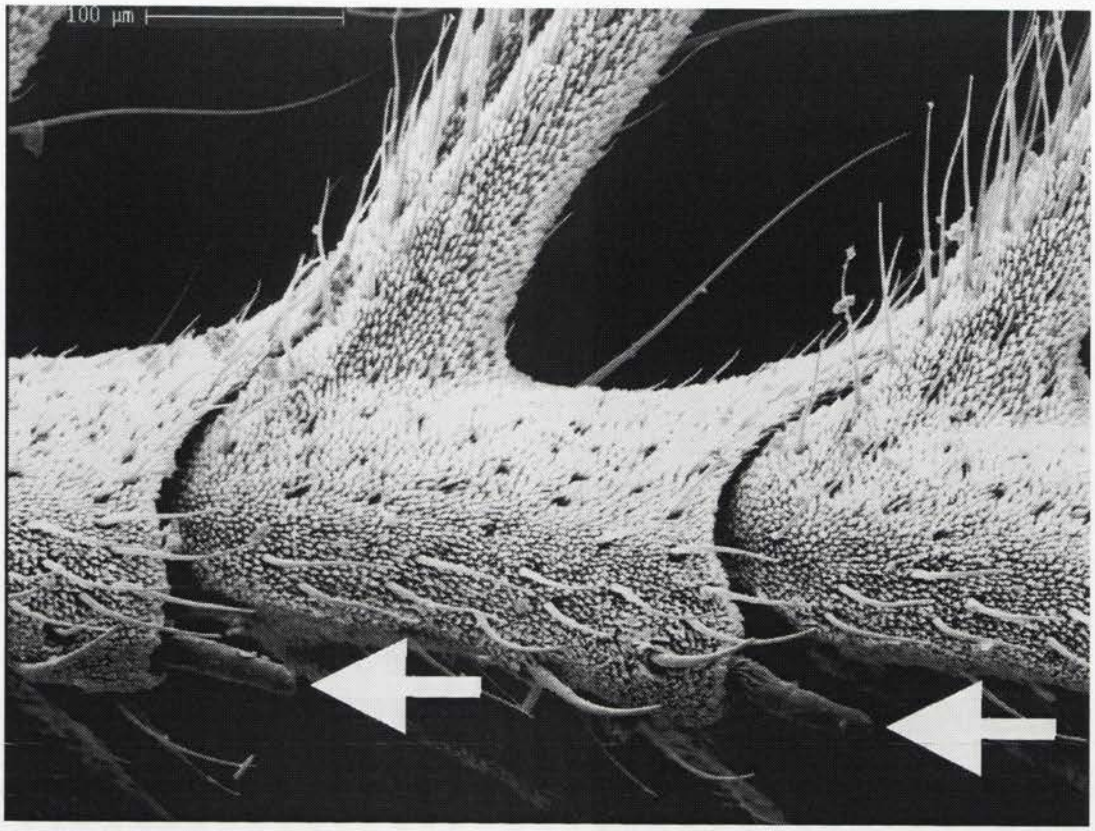

Fig. 203: *Bathyphlebia eminens* (Saturniidae), flagellomeres at distal third of ♂ antenna, ventral view (right = distal) – the antennal flagellomeres carry a median styliform sensillum complex at their distal edge.

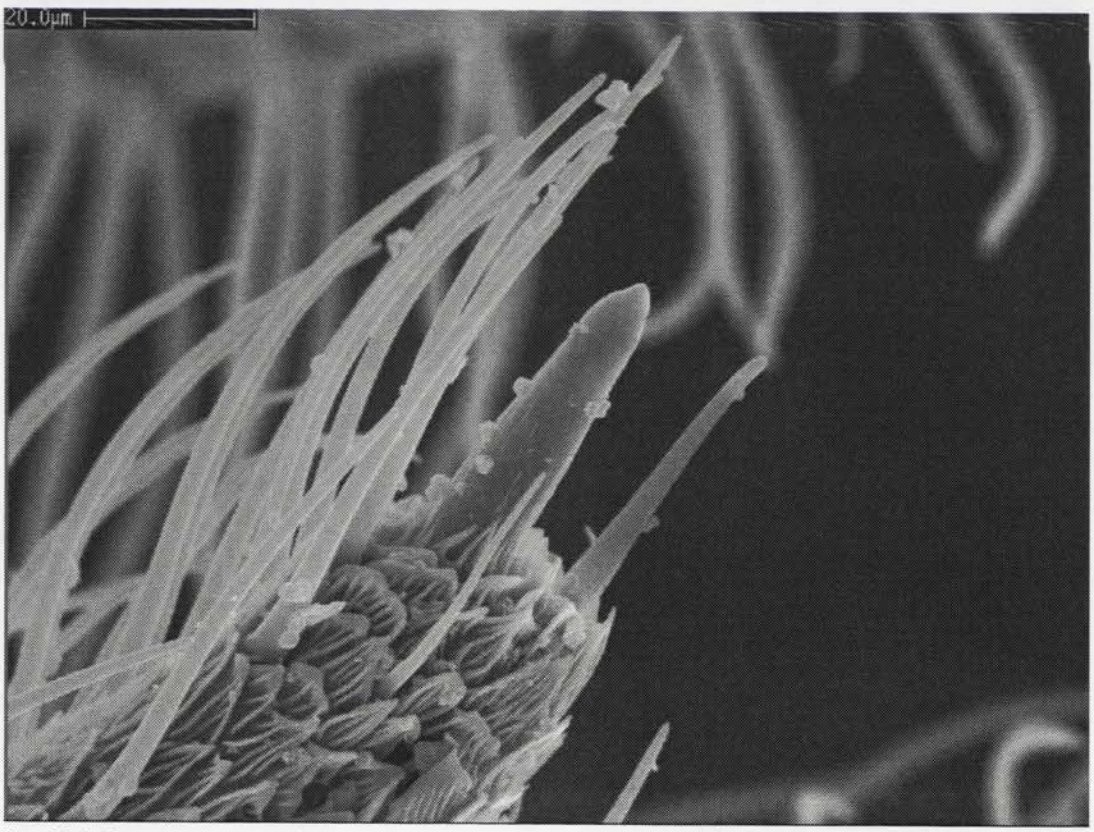

Fig. 204: *Entometa* sp. (Lasiocampidae), ramus apex at middle of ♂ antenna, distal view (left = ventral) – the apex of an antennal ramus carries a sensillum styliformium with a single peg.

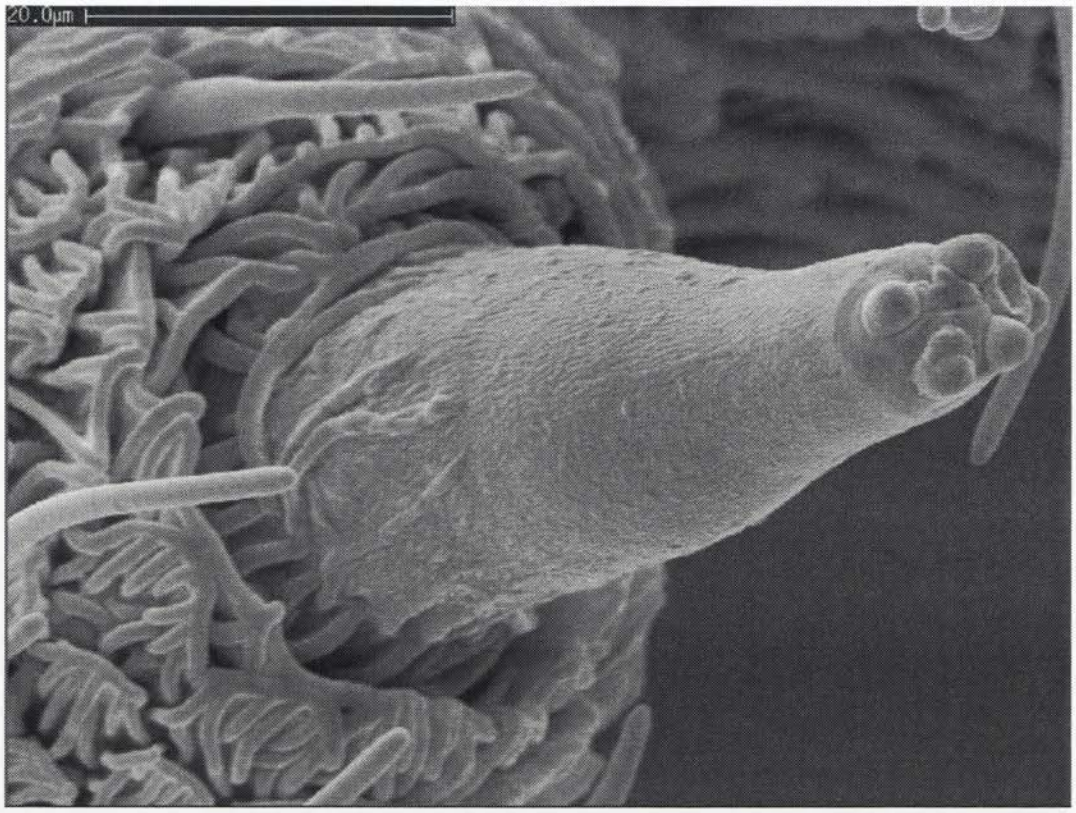

Fig. 205: *Periga* sp. (Saturniidae), apex of ventro-median process of a flagellomere at distal fifth of ♂ antenna, latero-ventral view (bottom = distal) – a styliform sensillum complex with five pegs is located at the apex of the ventro-median process of a flagellomere.

Fig. 206: *Oenosandra boisduvalii* (Oenosandridae), apex of ventro-median process of a flagellomere at apex of ♂ antenna, ventro-distal view (top = ventral) – a styliform sensillum complex with five pegs (yellow arrow) is located at the apex of the ventro-median process of a flagellomere.

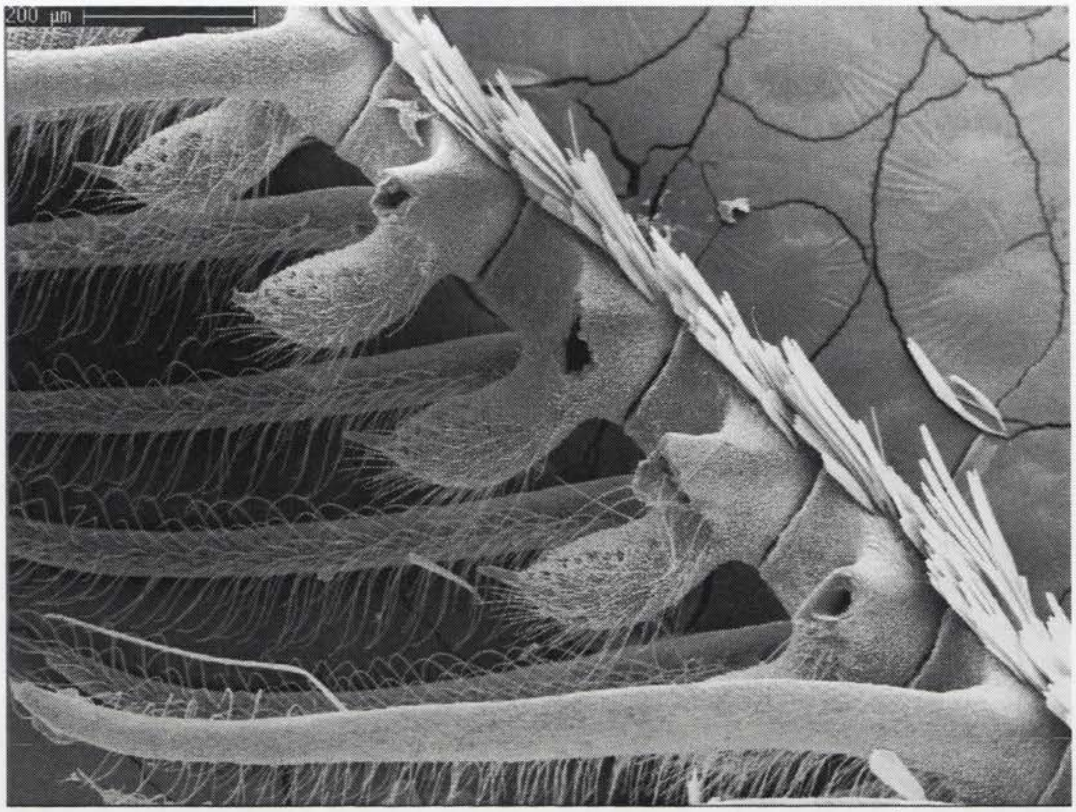

Fig. 207: *Brahmophthalma hearseyi* (Brahmaeidae), flagellomeres at distal third of ♂ antenna [some rami on right side removed], ventro-lateral view (top left = distal) – a ventro-median process with a styliform sensillum complex at its apex is located between the rami of each flagellomere.

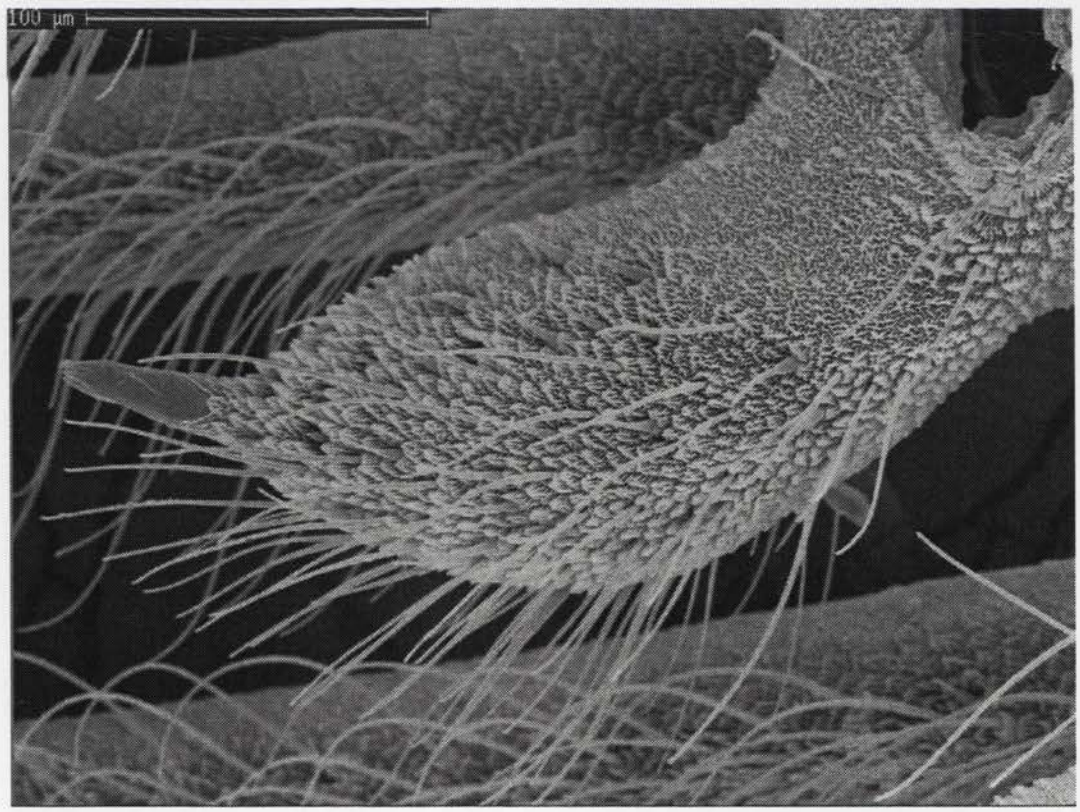

Fig. 208: *Brahmophthalma hearseyi* (Brahmaeidae), ventro-median process of a flagellomere at distal third of ♂ antenna [right ramus removed], ventro-lateral view (top left = distal) – the ventro-median process carries a styliform sensillum complex at its apex.

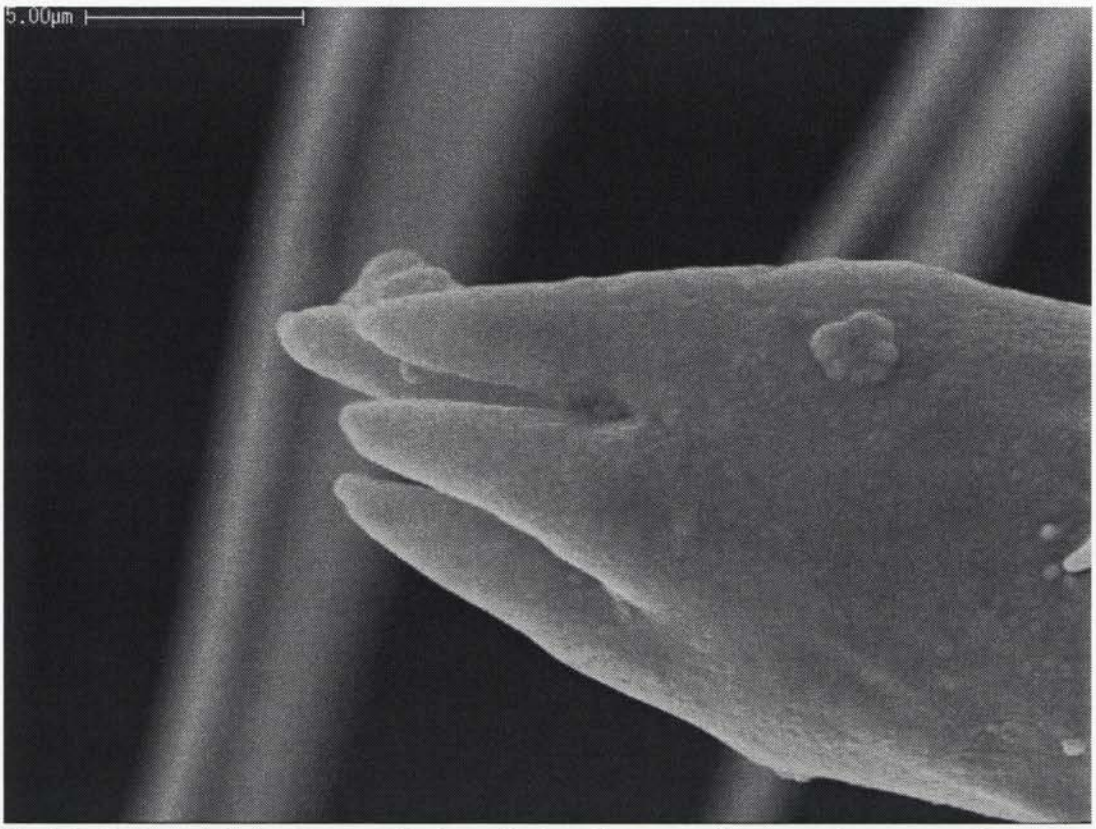

Fig. 209: *Brahmophthalma hearseyi* (Brahmaeidae), styliform sensillum complex at apex of a ventro-median process of a flagellomere at distal third of ♂ antenna, ventro-lateral view (top left = distal) – the styliform sensillum complex has four fused pegs.

Fig. 210: *Hypsidia niphosema* (Drepanidae), apex of ♂ antenna, ventral view – a small group of sensilla coeloconica is located at the distal edge of the ventral side of a flagellomere.

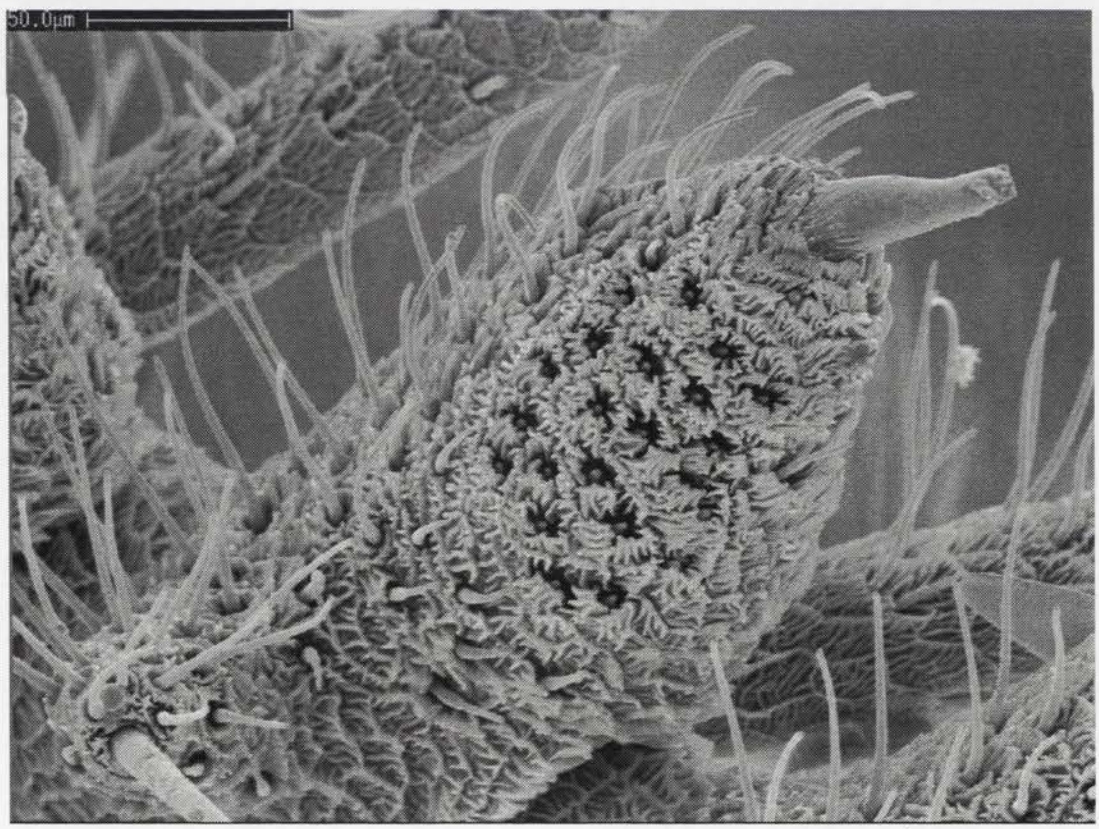

Fig. 211: *Periga* sp. (Saturniidae), ventral process of a flagellomere at distal fith of ♂ antenna, lateral view (bottom right = distal; top right = ventral) – the ventro-median process has a lateral field with numerous s. coeloconica (dark openings) and an apical styliform sensillum complex.

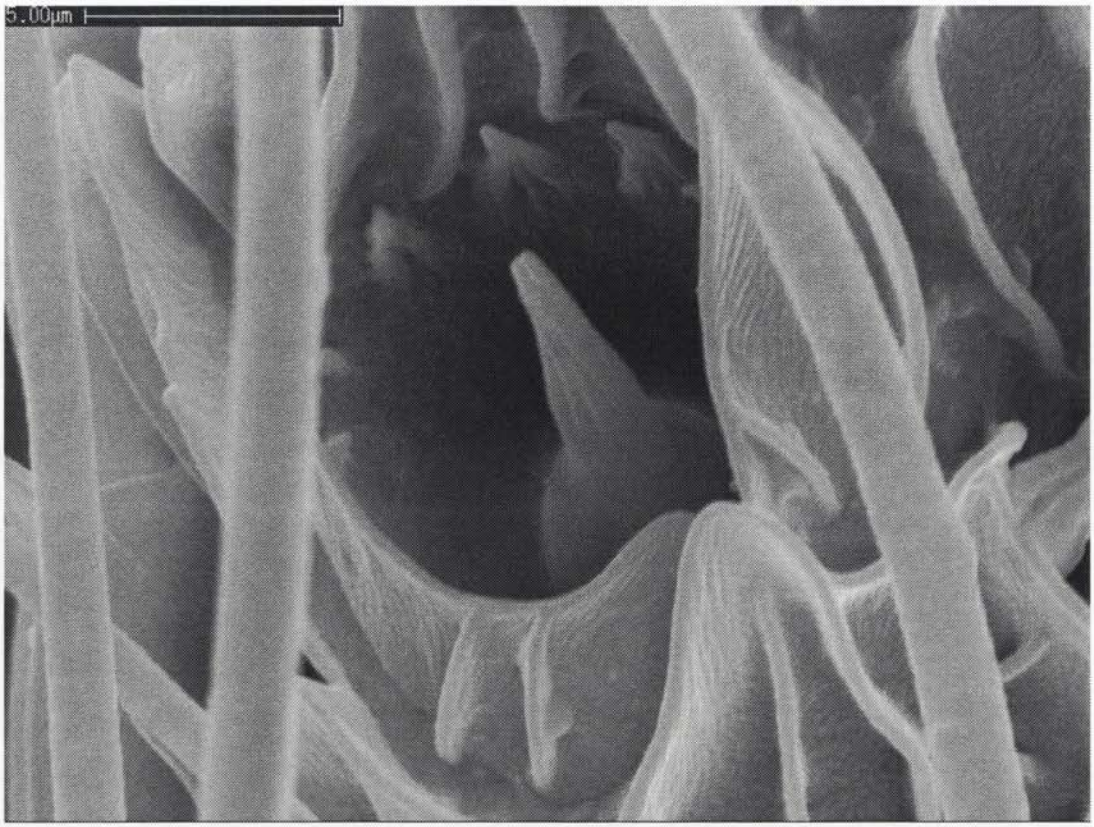

Fig. 212: *Anthela astata* (Anthelidae), ventro-median process of a flagellomere at distal fourth of ♂ antenna, latero-distal view (bottom left = distal; top = ventral) – the sensillum coeloconicum on a ventro-median process has a single peg surrounded by cuticular protrusions.

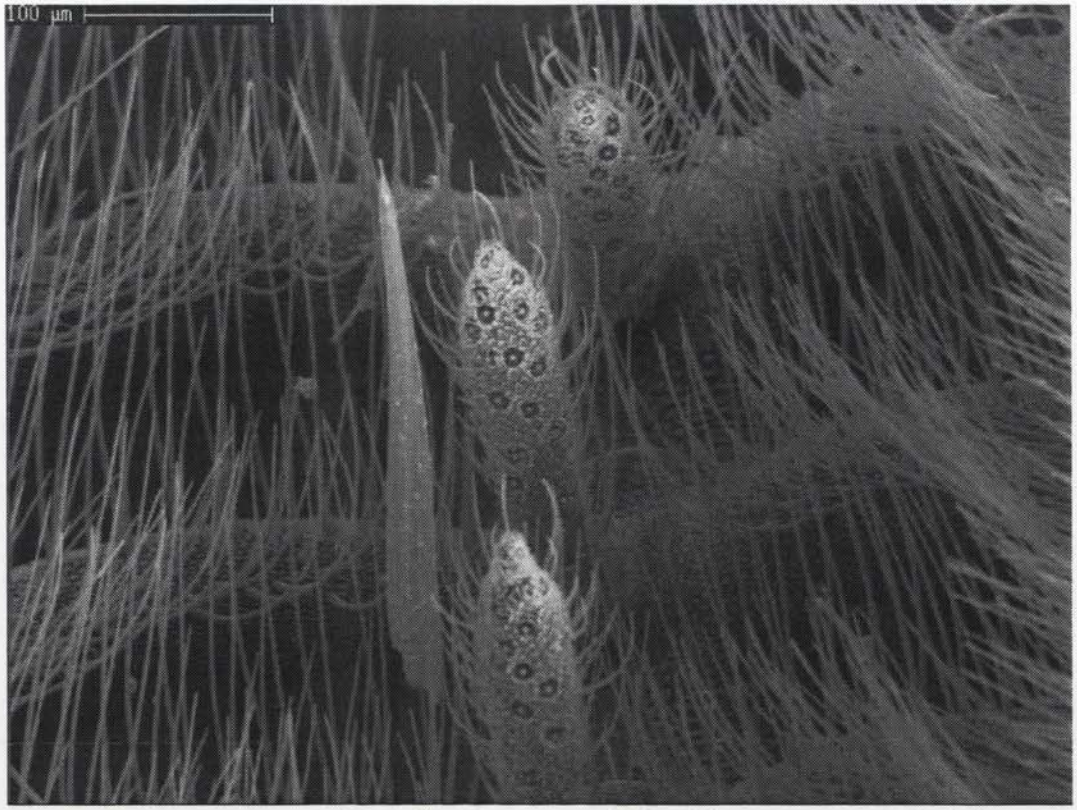

Fig. 213: *Pterolocera* sp. (Anthelidae), flagellomeres at middle of ♂ antenna, ventro-distal view (bottom = distal) – the ventro-median processes of each flagellomere has a distal and lateral fields with numerous sensilla coeloconica (dark openings) and an apical styliform sensillum complex.

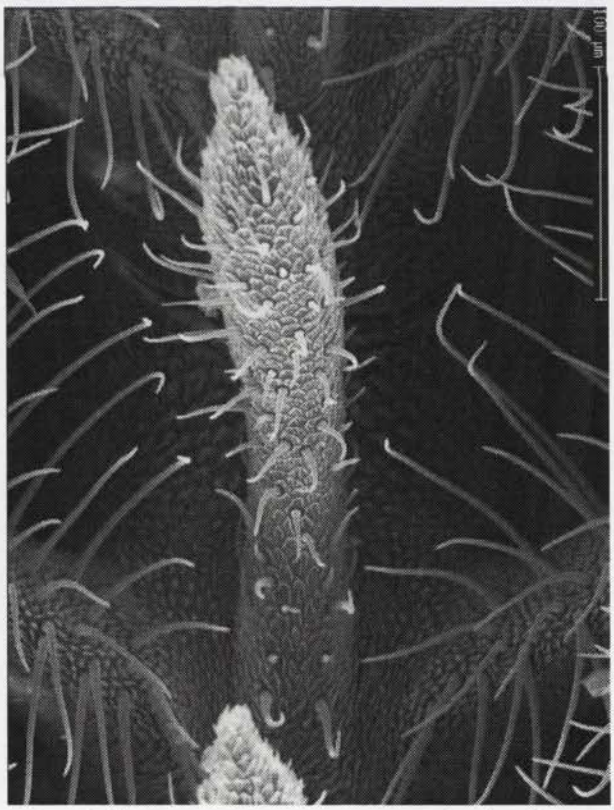

Fig. 214: *Pterolocera* sp. (Anthelidae), ventro-median process of a flagellomere at middle of ♂ antenna, ventro-proximal view (top = distal) – the proximal side of the ventro-median process carries sensory setae, but no sensilla coeloconica.

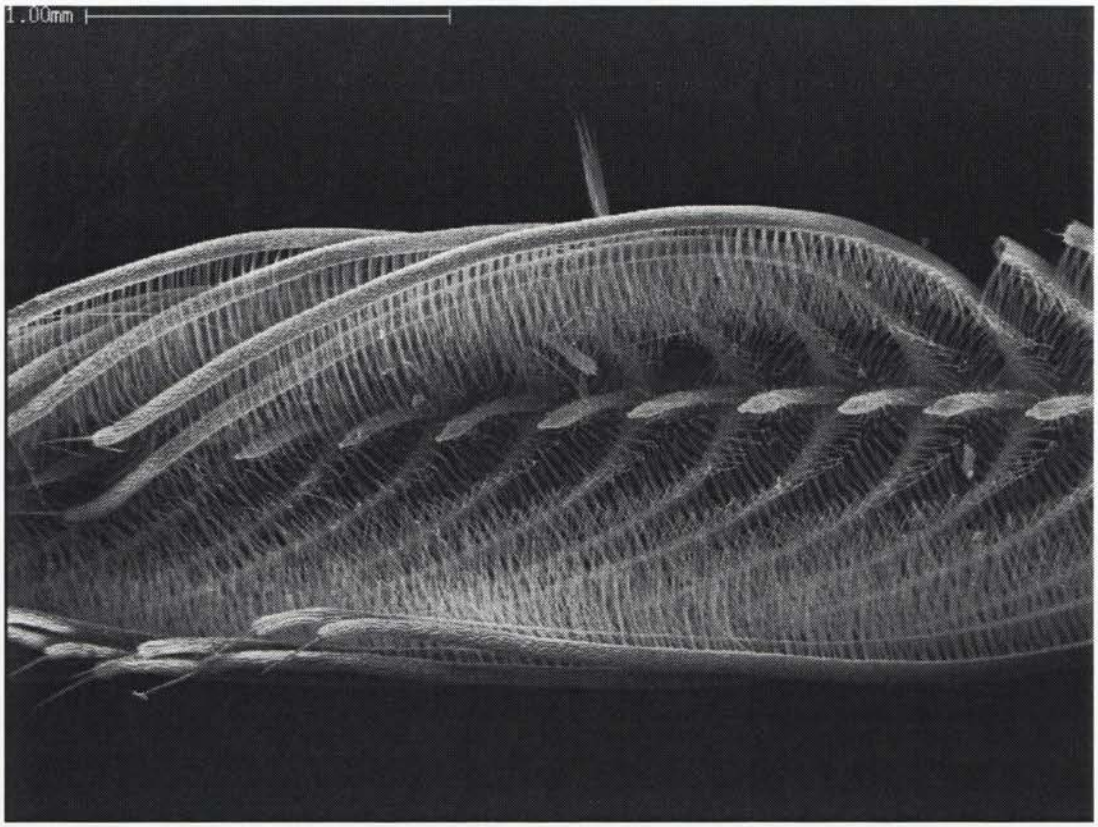

Fig. 215: *Pterolocera* sp. (Anthelidae), ♂ antenna, ventral view (left = distal) – the flagellomeres of a "tripectinate" antenna have a pair of lateral rami and a very prominent ventro-median process.

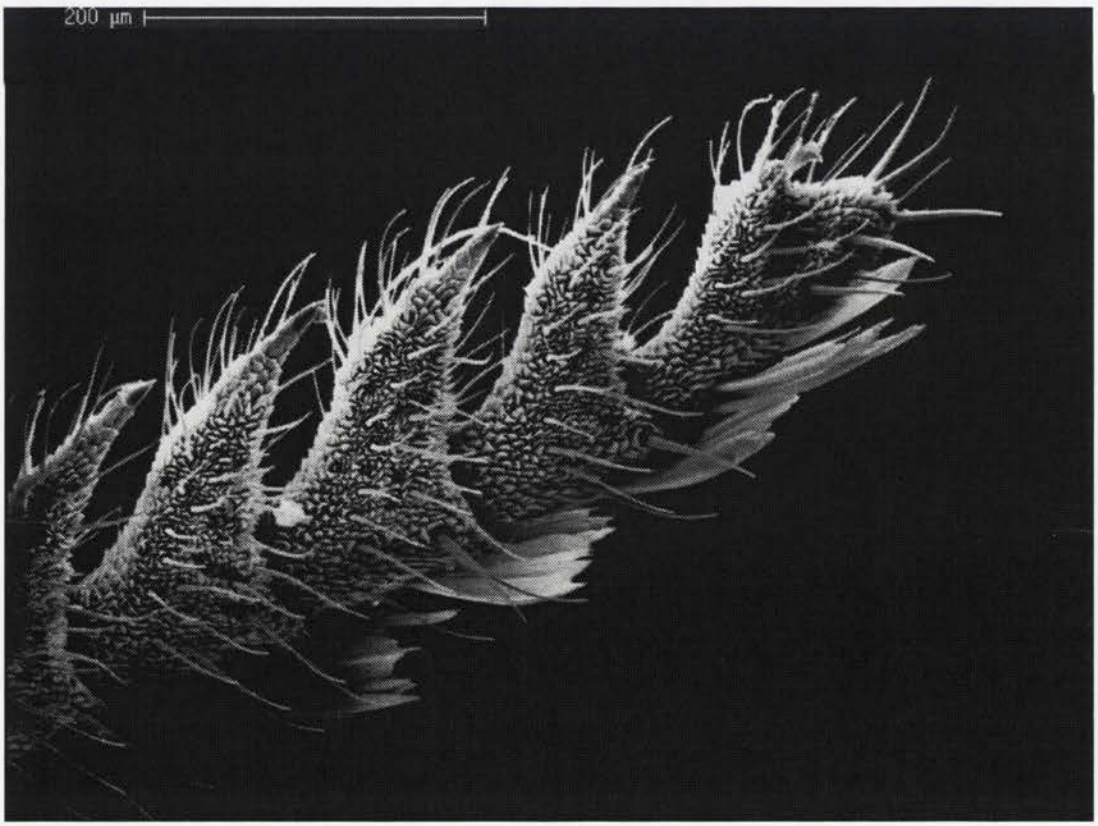

Fig. 216: *Andraca* n. sp. (Bombycidae), apex of ♂ antenna, ventro-lateral view (top = ventral) – the lateral rami decrease and the ventro-median processes increase in size towards the antennal apex.

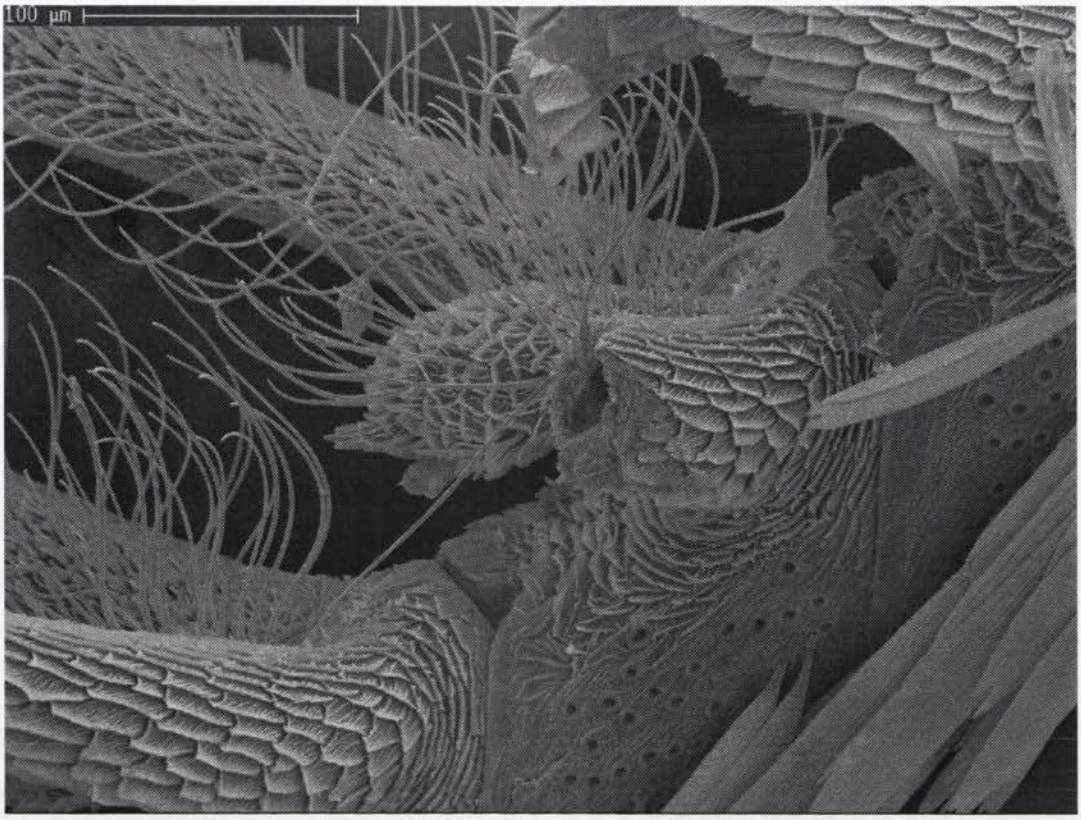

Fig. 217: *Anthela astata* (Anthelidae), flagellomere at distal fourth of ♂ antenna [one ramus removed], lateral view (bottom left = distal; top left = ventral) – the ventro-median process is reduced.

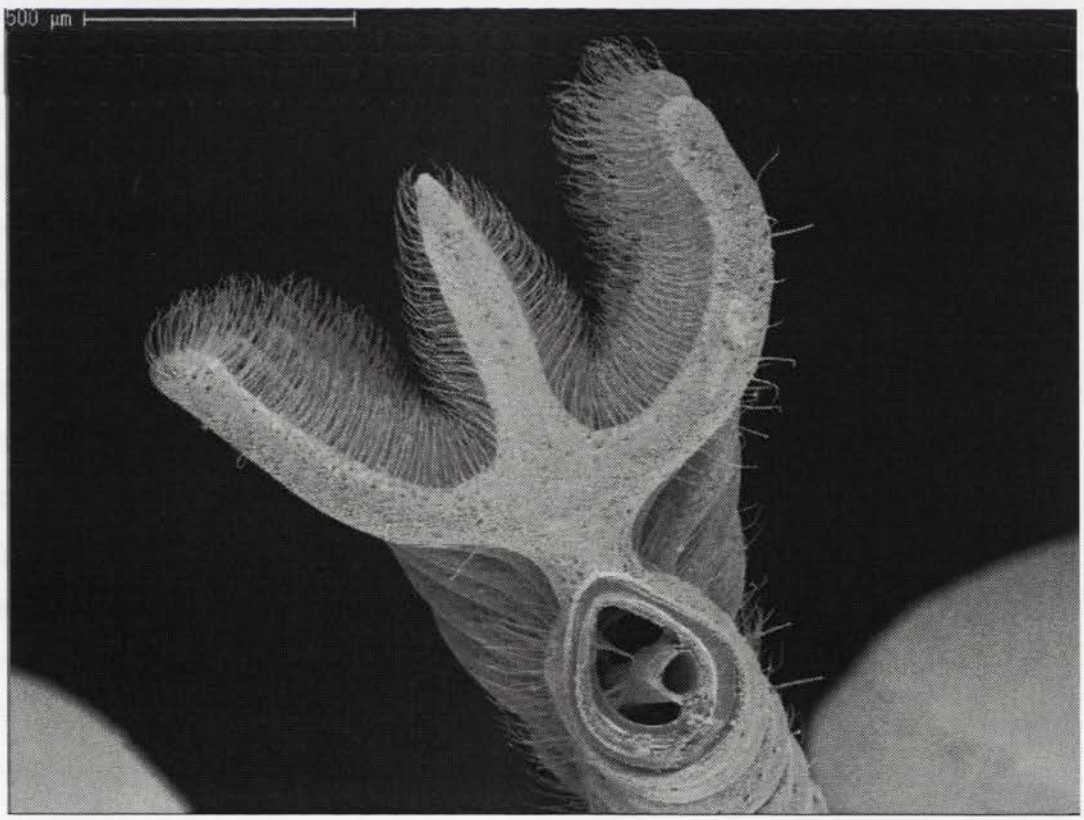

Fig. 218: *Trictena argyrosticha* (Hepialidae), flagellomere at basal fifth of broken ♂ antenna, distal view (top left = ventral) – a ventro-median protrusion forms three processes, which are unlikely to be homologous with the rami and the ventro-median process of the bombycoid complex.

III.5.1.A) The principal flagellum structure of the Sphingidae

As described for *Manduca sexta* (Sphingidae) by Sanes and Hildebrand (1976), Lee and Strausfeld (1990), and Shields and Hildebrand (1999a, b), the sphingid antenna differs in its orientation from that of most other Lepidoptera. In this family the scaled, dorsal side faces posteriad, while the sensory ventral side faces anteriad – against the flow of air during flight. The latter two studies distinguish a "leading edge" (= ventral side of other taxa) versus dorsal and ventral sides, but for easier comparison I use terms like dorsal and ventral in the following sections as if the antenna of Sphingidae was in the orientation typical for most Lepidoptera, with the sensory side facing ventrad.

The flagellum of the Sphingidae is a modification of the "tripectinate" antenna, which is most apparent in the subfamily Smerinthinae. The typical sphingid flagellum has been described as "prismatic" (e.g., Rothschild & Jordan 1903) or "lamellate ventrally" (Lemaire & Minet [1998]). These terms relate to the most prominent part of a sphingid flagellomere, a very large ventro-median process. In Sphingidae this process tends to extend over the entire length of the flagellomere and is very tall (Fig. 219). As typical for the ventro-median process of the bombycoid complex, it carries numerous sensilla coeloconica on its lateral sides and disto-apically a styliform sensillum complex. Unlike the process in other families of the bombycoid complex, however, the distal side of the process does not carry sensilla coeloconica (or any other sensilla) in the species I examined (*Smerinthus* spp.), possibly due to the extremely close proximity of these processes caused by their huge size (Fig. 220). This blade-shaped ventro-median process is laterally covered with sensory setae (small sensilla trichodea, sensilla chaetica and sensilla basiconica), but its proximal and distal lateral edges are fringed by a row of particularly long setae (sensilla trichodea) (Fig. 219). The very long sensilla trichodea of the lateral edges curve towards the sensilla trichodea of the opposite edge (Fig. 221). These fringes of setae extend over the lateral side of the ventro-median process onto the lateral side of the actual flagellomere "body", where they unite dorsally in an arc just ventrally of a protruding edge (Fig. 219). This protruding edge marks the end of the scaled, dorsal side of the flagellomere and might be a remnant of a reduced ramus.

Apart from proportional differences and reductions, this principal structure of the flagellum is rather constant. Only a few species with "odd" modifications exist in the subfamily Smerinthinae, most of which were already examined by Rothschild and Jordan (1903) and later mentioned by Kitching and Cadiou (2000). In the Central

American *Monarda oryx* the proximal and distal setose, lateral edges of the ventro-median process are extended and form two pairs of protrusions, which resemble rami. Unlike rami in other taxa, their sensory setae are not restricted to the ventral side, but run along the ventral and dorsal edge of this protrusion. Such a modification has been illustrated for *Amorpha juglandis*, too (Rothschild & Jordan 1903: Pl. LXI, Figs 3-5, as *Cressonia juglandis*). These antennae resemble the quadripectinate antennae of Saturniidae, particularly so because of the very long setae of proximal and distal rami of each flagellomere, which curve towards each other, and because of the arrangement of these setae around the outer edge of the "fake rami". Unlike in Saturniidae, the "fake rami" of *M. oryx* originate from the ventro-median process and not from the lateral side of the actual flagellomere "body". Based on structural differences, I do not regard the "quadripectinate" condition in those two sphingid species to be homologous with the quadripectinate condition present in most Saturniidae.

A different modification is present in the North American species *Smerinthus jamaicensis*, but in none of the other *Smerinthus* species. In this species the dorso-lateral protrusion of the flagellomere is very well developed and forms an unscaled ramus (Figs 222, 223). The arrangement of sensory setae on the mesal side of the ramus (Fig. 224) resembles the arrangement of setae present in other taxa of the bombycoid complex (Fig. 225). Two other species with rami were illustrated by Rothschild and Jordan (1903: Pl. LX, Figs 27-29), namely *Ceridia mira* and *Sphingonaepiopsis obscurus*.

The South African *Xenosphingia jansei* is another sphingid species with rami. Its flagellum does not differ from the typical tripectinate flagellum of other taxa in the bombycoid complex, except for the rami to be entirely scaled dorsally. Its flagellomeres have a single pair of well developed rami and a relatively slender, long, ventro-median process. As typical for Lepidoptera, the scaled side of the antenna faces dorsad, rather than posteriad as in other Sphingidae. The scales on the dorsal side of the rami indicate that these rami include parts of the scaled dorsal side of the flagellomere. Only the imago of *X. jansei* is known from a few specimens, and its current placement in the family Sphingidae seems to be based on general appearance and wing venation only. This species differs further from all known Sphingidae by a modification of the labial palpus. Kitching and Cadiou (2000: 2) listed the monotypic genus *Xenosphingia* as an example for the occurrence of short labial palpi in Smerinthini, but the opposite is the case. As already pointed out and illustrated in the original description and definition of

the genus by Jordan (1920: 168-169), *X. jansei* has prominent labial palpi with a very long third segment. Further, this third segment protrudes laterad due to a laterad curving of the second segment. In both length and lateral protrusion this third segment of the labial palpus differs from that of all other known Sphingidae. Within the bombycoid complex a long third segment occurs only in the monotypic Carthaeidae in Australia, but the second segment is not curved laterad in this taxon. While "typical" Sphingidae are very distinct, the autapomorphies proposed for the family Sphingidae by Lemaire and Minet ([1998]) are not as "unique" as desirable, and the placement of *X. jansei* in the Sphingidae should be re-examined, as already pointed out by Oberprieler and Duke (1994).

If one accepts the monophyly of the Sphingidae and Saturniidae, the rami in *S. jamaicensis*, *C. mira*, *S. obscurus* and *X. jansei* could be "remnants", which are lost in all other Sphingidae. In this case all other Sphingidae, including congeneric species, would form a monophylum supported by a modification of the sensory area of the antenna (see character H.56), and this modification would have to have evolved independently in Saturniidae, too. However, I have no reasons to doubt the monophyly of the genus *Smerinthus*, which includes a single species with and other species without rami. Further, such a monophylum of all other Sphingidae would not be compatible with the current subfamily and tribal classification of Sphingidae (e.g., Kitching & Cadiou 2000). Therefore, I reject the interpretation that the rami of the aforementioned sphingid species are "remnants" and homologous with the rami found in other Macrolepidoptera. Instead, I regard these rami as convergent developments, which possibly represent "reversals". The striking similarity between these "rami" and the rami of other Macrolepidoptera questions to some extend the homology of rami within Lepidoptera. Obviously, antennal outgrowths other than the rami in Macrolepidoptera did evolve (e.g., in Hepialidae, Fig. 218), and while the usage of the term rami implies homology, no detailed studies in support of this assumption have been published.

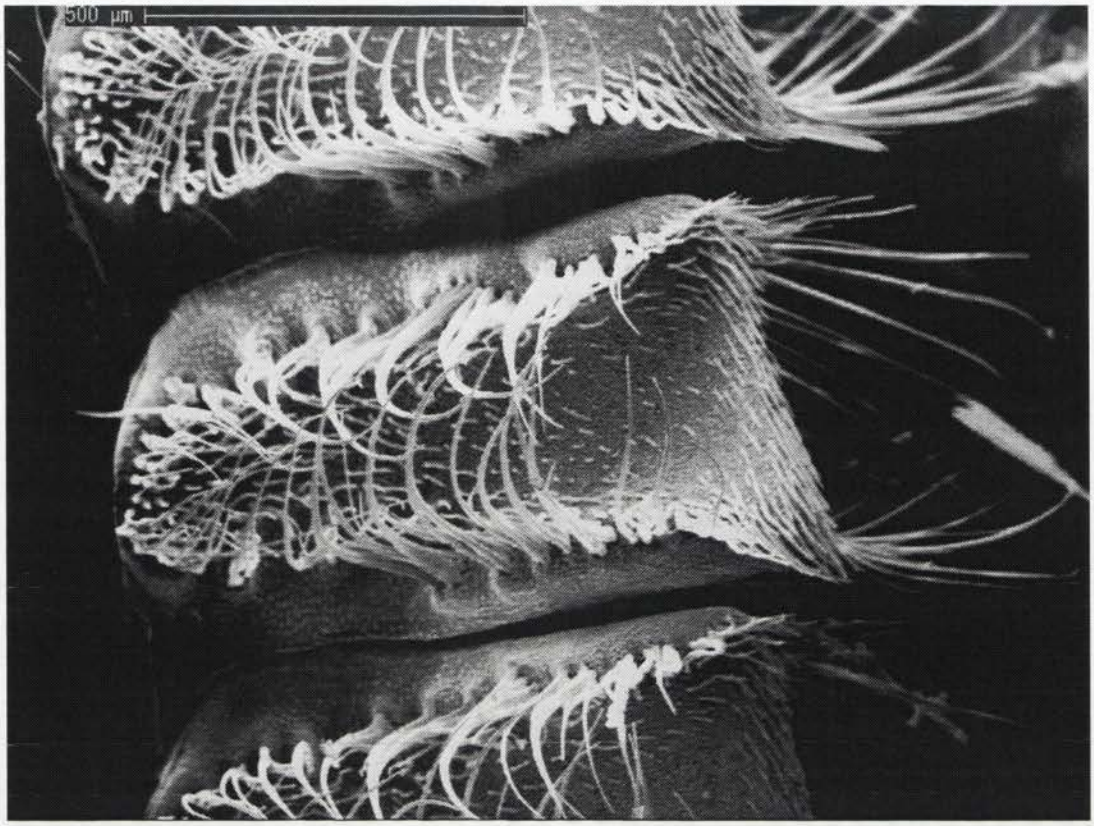

Fig. 219: *Smerinthus cerisyi* (Sphingidae), flagellomeres at middle of ♂ antenna, lateral view (bottom = distal; right = ventral) – the flagellomere has a very large ventro-median process, which extends over the entire length of the flagellomere; its proximal and distal rows of s. trichodea unite in an arc ventrally of a laterally protruding edge.

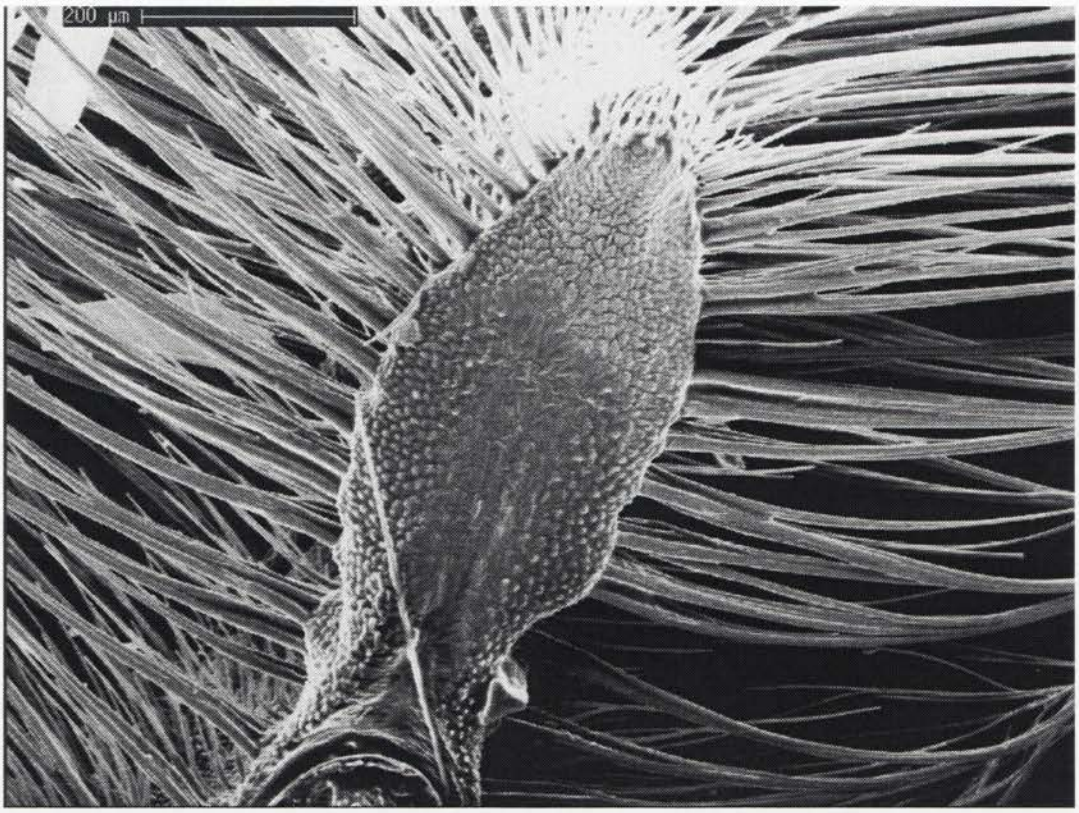

Fig. 220: *Smerinthus cerisyi* (Sphingidae), ventro-median process of a flagellomere at middle of ♂ antenna, distal view (top = ventral) – the very large ventro-median process carries no sensilla on its distal side.

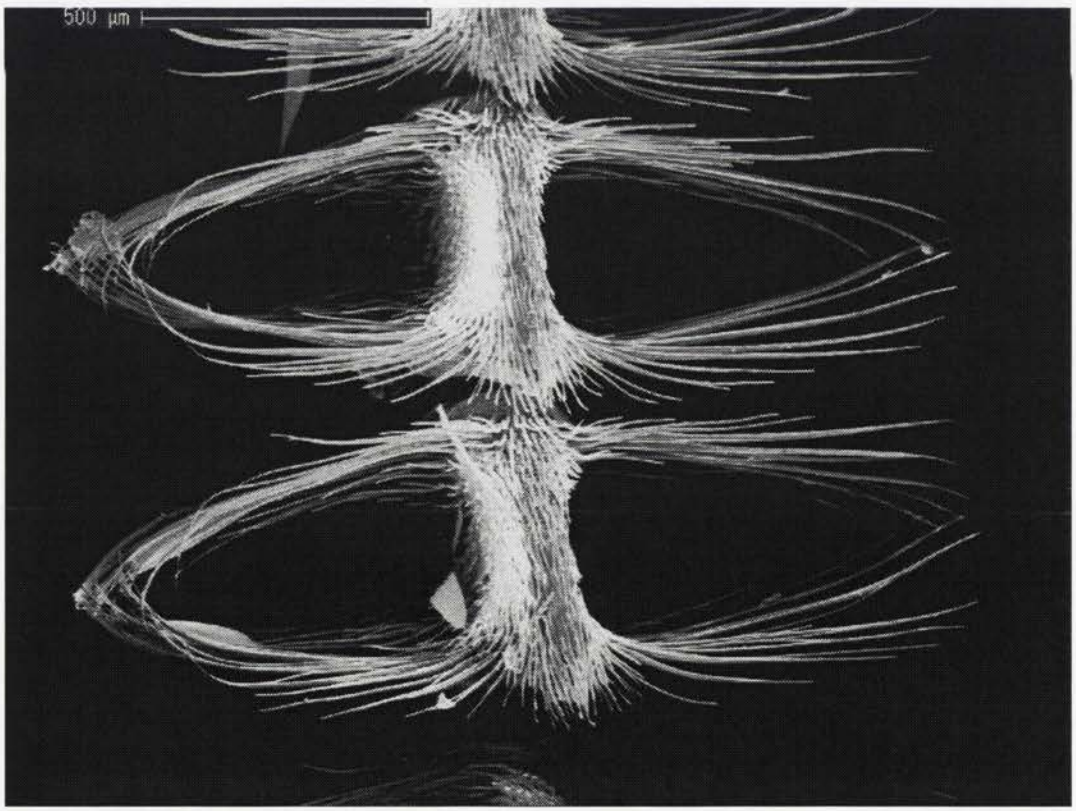

Fig. 221: *Smerinthus cerisyi* (Sphingidae), flagellomeres at middle of ♂ antenna, ventral view, (bottom = distal) – each flagellomere has laterally a proximal and a distal row of very long sensilla chaetica, which curve towards each other.

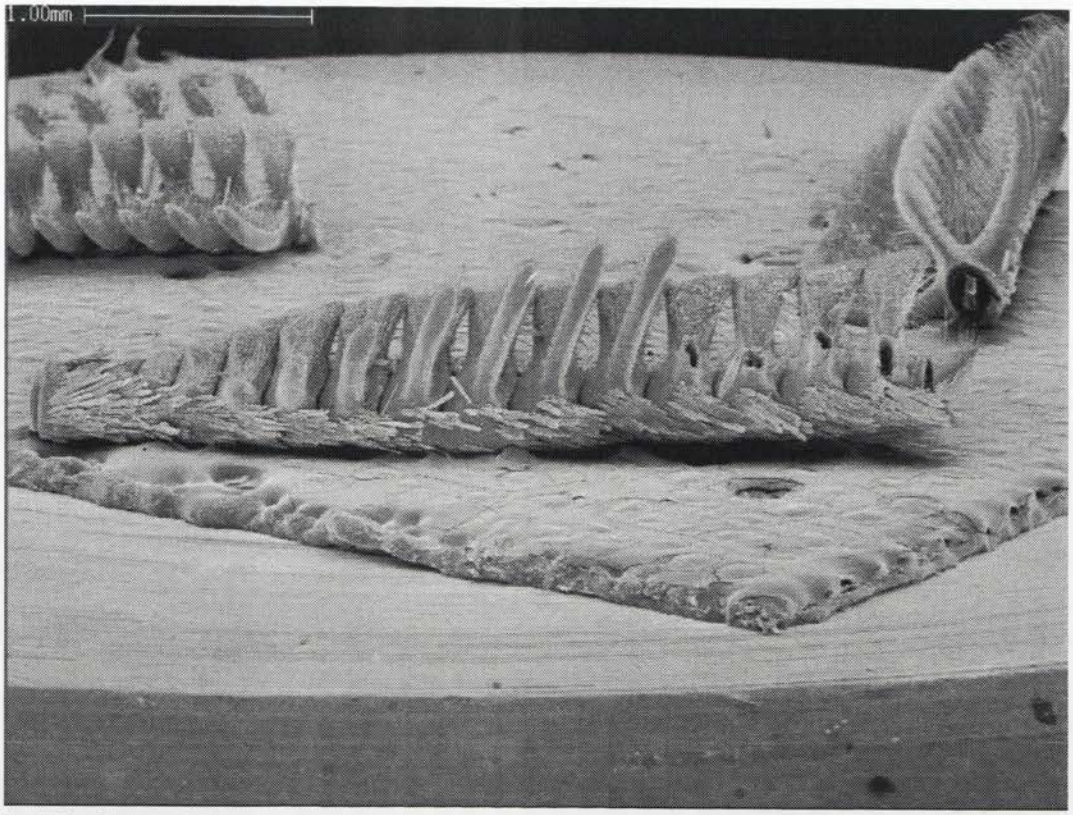

Fig. 222: *Smerinthus jamaicensis* (Sphingidae), basal fourth of ♂ antenna [some rami are partly broken off on one side], lateral view (right = distal; top = ventral) – each flagellomere has a single pair of lateral rami and a very large ventro-median process (both decreasing in size towards the antennal base).

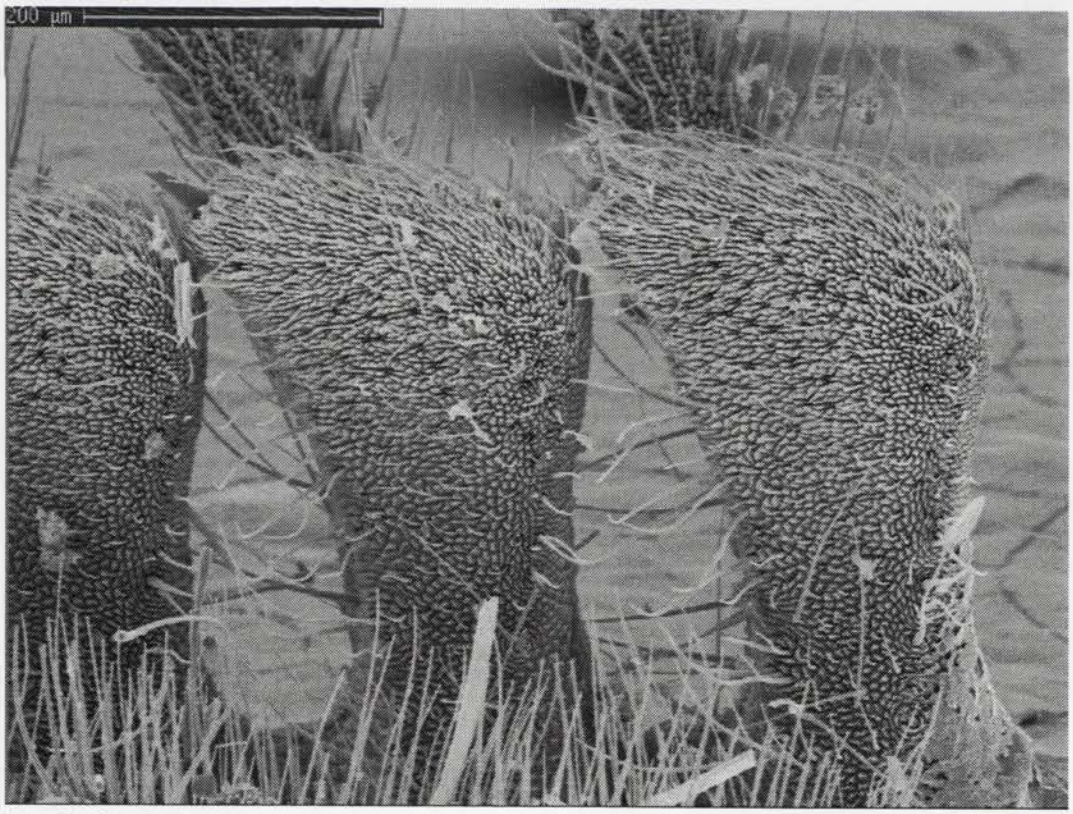

Fig. 223: *Smerinthus jamaicensis* (Sphingidae), ventro-median processes of flagellomeres at distal fourth of ♂ antenna, lateral view (left = distal; top = ventral) – each flagellomere forms a very large ventro-median process, which carries sensilla coeloconica laterally.

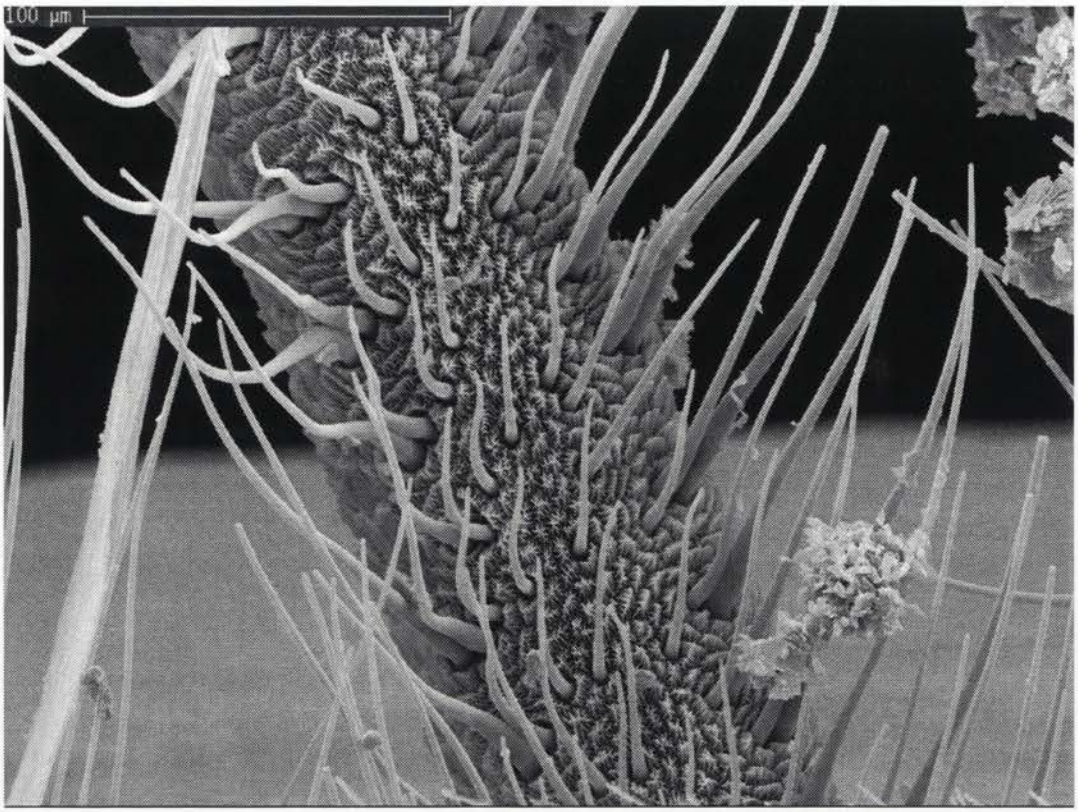

Fig. 224: *Smerinthus jamaicensis* (Sphingidae), ramus at middle of ♂ antenna, mesal view (left = distal; top = ventral) – the sensilla trichodea (and s. basiconica) on the mesal side of the ramus are arranged in groups similar to the arrangement in other taxa of the bombycoid complex.

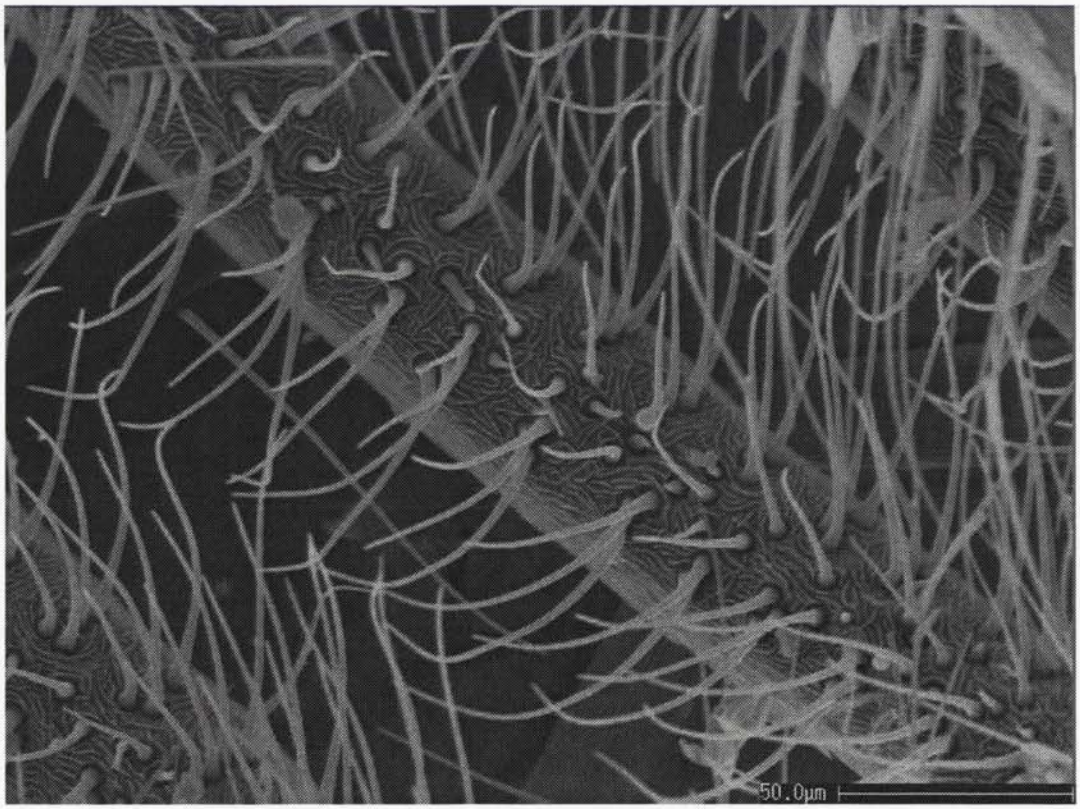

Fig. 225: *Munychryia senicula* (Anthelidae), rami at middle of ♂ antenna, mesal view (top right = distal; top left = ventral) – the sensilla trichodea and s. basiconica on the mesal side of each ramus are arranged in a rather complex pattern of groups.

III.5.1.B) The principal flagellum structure of the Saturniidae

Like Sphingidae, Saturniidae have an antenna with a modified orientation, in which the sensory ventral side faces (ventro-) anteriad in the active moth (Figs 226, 227). As above, I use terms like dorsal and ventral in the following sections as if the antenna of Saturniidae was in the orientation typical for most Lepidoptera, with the sensory side facing ventrad.

The "typical" antenna of Saturniidae is a highly derived structure, which is broad, flat, quadripectinate and without dorsal scales (Fig. 228). Its flagellomeres have a rather shallow, ventro-median process over the entire flagellomere length (larger at the apical segments), and the rami originate on the latero-dorsal to dorsal side (Fig. 230). These dorsal rami are directed dorso-laterad at the base but then curve slightly ventrad, which results in an orientation of opposite rami in one plane – the antenna appears to be "flat". Further, these two rami pairs originate directly at the proximal and distal edges of a flagellomere, respectively (Fig. 229), rather than like a single rami pair at a distance from the proximal edge (Figs 248, 249). As in other Lepidoptera these rami carry very long sensilla trichodea, but not only on their ventral side (Fig. 233), but as a continuous row along their ventral and dorsal sides (Fig. 231). The dorsal part of this row of sensilla of the proximal and distal rami of a flagellomere extends onto the dorsal side of the flagellomere "body", where the two rows unite in an arc in the middle. These two rami pairs of a flagellomere are dorsally slightly tilted against each other, which, together with the curving of their sensilla trichodea, results in a very characteristic pattern in lateral view: on the dorsal side the sensilla of the proximal and the distal rami of one flagellomere are closest together, while on the ventral side the sensilla of the distal and of the proximal rami of two neighbouring flagellomeres are closest together (Fig. 232). This arrangement of sensilla trichodea in "weirs", which alternately open ventrally and dorsally (anteriad and posteriad *in situ*), is likely to be a highly efficient filter for female pheromone molecules.

This unique, structurally very complex quadripectinate antenna allows for a very well supported hypothesis of homology and would have been proposed as an autapomorphy of the family Saturniidae [*sensu* Draudt (1929-1930), re-established by Minet (1994): including Oxyteninae and Cercophaninae], if it was not for a number of exceptional

taxa. These taxa have bipectinate antennae and belong to the Oxyteninae, Cercophaninae and various Hemileucinae (e.g., *Lonomia*, *Periga*, *Hemileuca* and *Dirphia*), as well as to some African Saturniinae (Urotini and *Decachorda* of the Micragonini). For most, if not all, of these taxa it can be convincingly demonstrated that their bipectinate antennae originated from a quadripectinate antenna by a reduction of the distal rami. Michener (1952) described the complete transformation series retained in the different subgenera of the genus *Dirphia* (Hemileucinae). He drew attention to the correlation between quadripectinate antennae with an orientation of sensilla trichodea as described above and a gradual change to ventrally orientated rami and sensilla trichodea in species with reduced distal rami (Michener 1952: 358-359), seemingly "reverting" to the condition present in most other families of the bombycoid complex.

No such distinct transformation series is apparent in the Cercophaninae, *Hemileuca* (Hemileucinae), Urotini and *Decachorda*. However, their rami originate far dorsally and at the proximal edge of the flagellomeres, as otherwise only found in the quadripectinate condition. In *Parusta thelxinoe* (Urotini) additionally a dorsal row of sensilla trichodea is retained, further indicating the bipectinate condition of this species to be a reduction of the quadripectinate condition. These dorsal setae are typically lost in taxa with secondarily bipectinate antennae, and no dorsal setae occur in primarily bipectinate antennae. The female of *Eosia insignis* (Saturniidae: Micragonini) is exceptional for African Saturniidae in as far as it has bipectinate antennae, but remnants of the reduced distal rami are still visible (Fig.).

The antennae of *Periga* (Hemileucinae; formerly treated as a subgenus of *Lonomia*, e.g., Lemaire 1973) have received much attention (e.g., Michener 1952; Lemaire 1973; Minet 1994; Balcázar-Lara & Wolfe 1994). Its antennal shaft is dorsally fully scaled, apically with large ventro-median processes, bipectinate and with the rami originating from the latero-ventral side (Fig. 234). This strong resemblance of an antenna typical of the bombycoid complex led to speculations as to whether the antenna might be primarily or secondarily bipectinate. As the latero-ventral rami originate directly at the proximal edge of flagellomeres (Fig. 236; not the case at the apex of the antenna) and as the seemingly closely related genus *Lonomia* has dorso-laterally originating rami and dorsally no scales on the antennal shaft, I interpret the bipectinate condition present in *Periga* to be a subsequent modification of the quadripectinate antenna, as did Michener (1952), Lemaire (1973) and Minet (1994).

A dorsally scaled, bipectinate antenna with ventrally originating and ventrally protruding rami is also present in all Oxyteninae. Minet (1994: 84) believed the Oxyteninae "... to represent the most 'primitive' lineage of the Saturniidae, since their male antennae have the bases of the rami directed ventrad (Fig. 5), a plesiomorphy not found in the other subfamilies ...". While the orientation of the rami is identical with the condition found in the bombycoid complex, indications exist that argue for the bipectinate condition to nevertheless be derived from the quadripectinate condition as in all other bipectinate Saturniidae. As in the quadripectinate antenna and its subsequent modifications, the single pair of rami originates directly from the proximal edge of the flagellomeres in Oxyteninae, instead of further distally. This is the case in both oxytenine species I examined, namely an *Oxytenis* species and *Therinia buckleyi* (Fig. 237). Further, the rami of *T. buckleyi* carry long sensilla trichodea not only on the ventral side, but additionally also dorsally – a single row of strongly distad curved sensilla trichodea (Figs. 238, 239). No rows of sensilla trichodea are present on the dorsal side of a ramus in the typical antenna of the bombycoid complex, while a dorsal row of many such curved sensilla trichodea is part of the flagellomere structure of the typical quadripectinate antenna. Such dorsal sensilla trichodea are absent in the *Oxytenis* species, but I assume the absence of these sensilla in the *Oxytenis* species to be a continuation of the reduction apparent in *T. buckleyi*, as the close relationship between *Oxytenis* and *Therinia* is convincingly supported by several synapomorphies of caterpillars (Aiello & Balcázar-Lara 1997) and adults. The monophyly of the entire subfamily Oxyteninae is likewise well supported by their highly apomorphic caterpillars with "sticky glands" (Aiello & Balcázar-Lara 1997), the extreme stalking of R with Rs in the fore wing, and to a lesser degree the lack of a claw on the tibial spurs (Minet 1994). The significance of the dorsal sensilla trichodea are explained in more detail below (III.5.1.C: 283ff.). On the basis of the proximal origin of the rami and the presence of dorsal sensilla trichodea on these rami in *T. buckleyi*, I conclude that the bipectinate antenna of the Oxyteninae is also derived from the quadripectinate antenna. Hence, the bipectinate antenna of the Oxyteninae does not support a sistergroup relationship between the Oxyteninae and all other subfamilies of the Saturniinae, as implied by Minet (1994: 84). Further, I propose the quadripectinate antenna not to be an autapomorphy of the Saturniidae "*sensu stricto*", but instead of the Saturniidae *sensu* Draudt (1929-1930), inclusive of Cercophaninae and Oxyteninae.

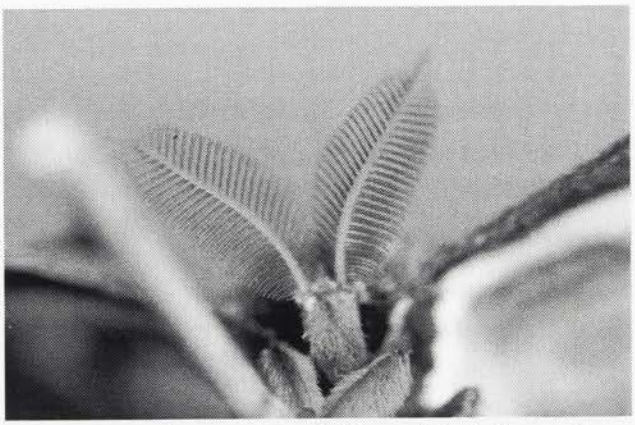

Fig. 226: *Epiphora mythimnia* (Saturniidae), ♂, anterior view [courtesy of R. Oberprieler, ANIC]– the active moth extends the antennae transversely forward, and the sensory side ("ventral" in other moths) is turned upwards, facing meso-anteriad as well as slightly ventrad.

Fig. 227: *Aurivillius fuscus*, ♂, dorsal view [courtesy of R. Oberprieler, ANIC] – the active moth extends the antennae transversely forward, and the sensory side ("ventral" in other moths) is turned upwards, facing meso-anteriad as well as slightly ventrad.

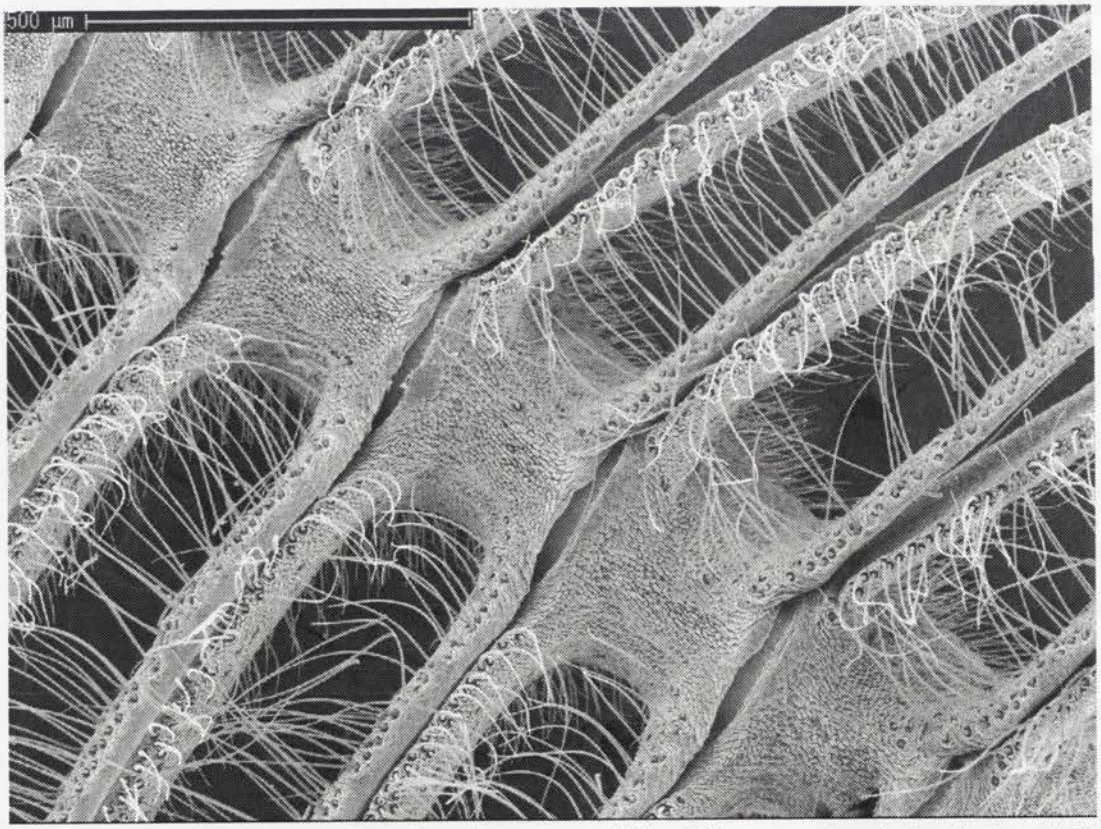

Fig. 228: *Coloradia* sp. (Saturniidae), flagellomeres at middle of ♂ antenna, dorsal view (bottom right = distal) – the flagellomeres carry dorsally no scales and have a proximal and a distal pair of dorso-lateral rami.

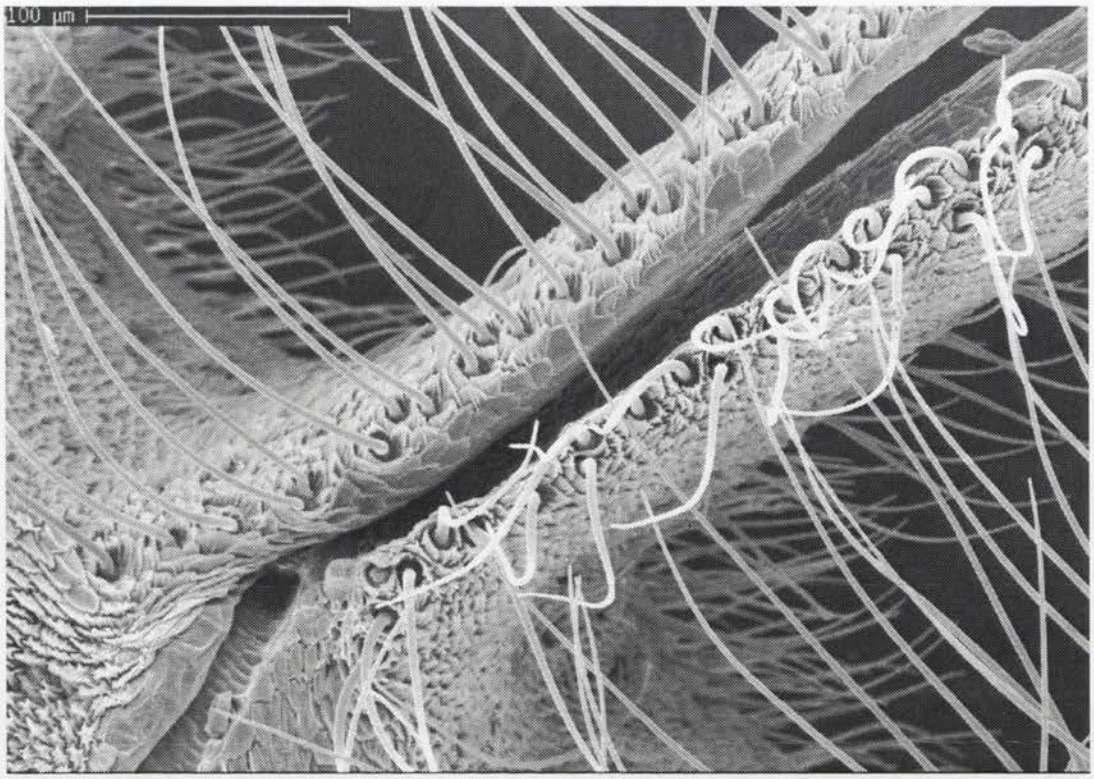

Fig. 229: *Coloradia* sp. (Saturniidae), flagellomeres at middle of ♂ antenna, dorsal view (bottom right = distal) – distal and proximal rami of two adjoining flagellomeres; note the proximity of the rami to the flagellomere edges.

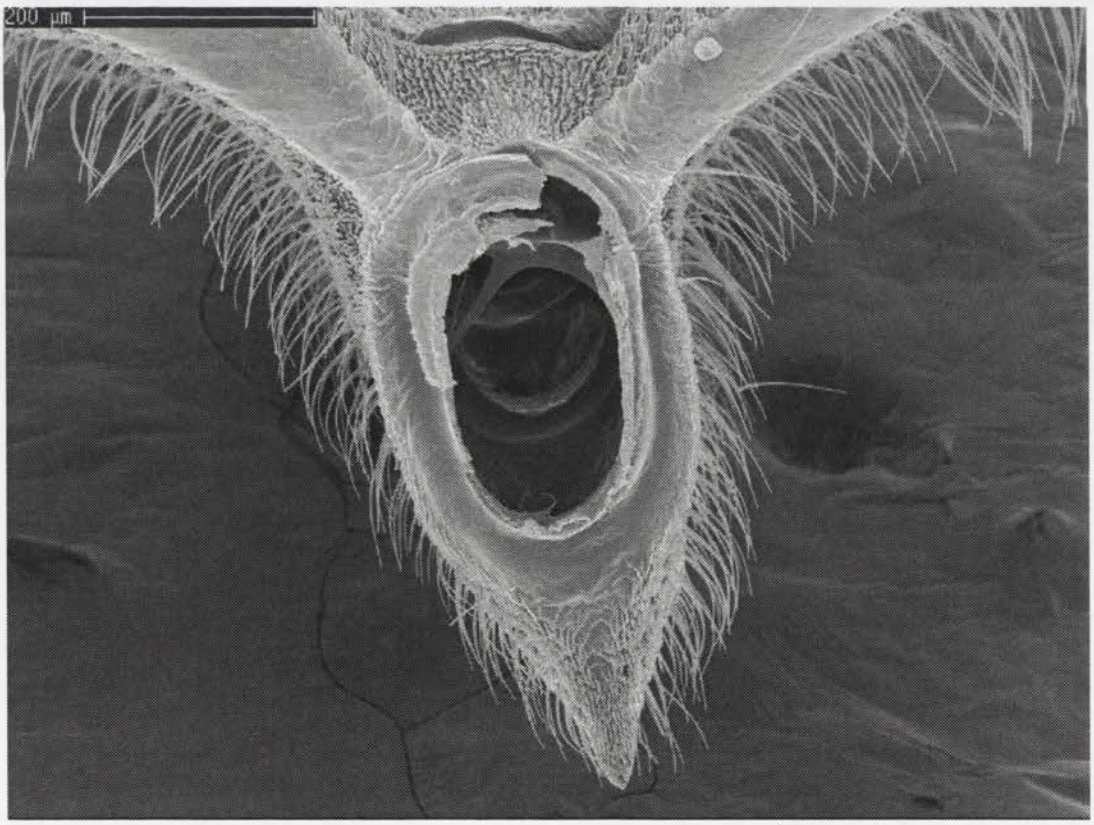

Fig. 230: *Coloradia* sp. (Saturniidae), flagellomere at middle of broken ♂ antenna, distal view (bottom = ventral) – the flagellomere has a rather shallow ventro-median process (crest) and dorso-lateral rami.

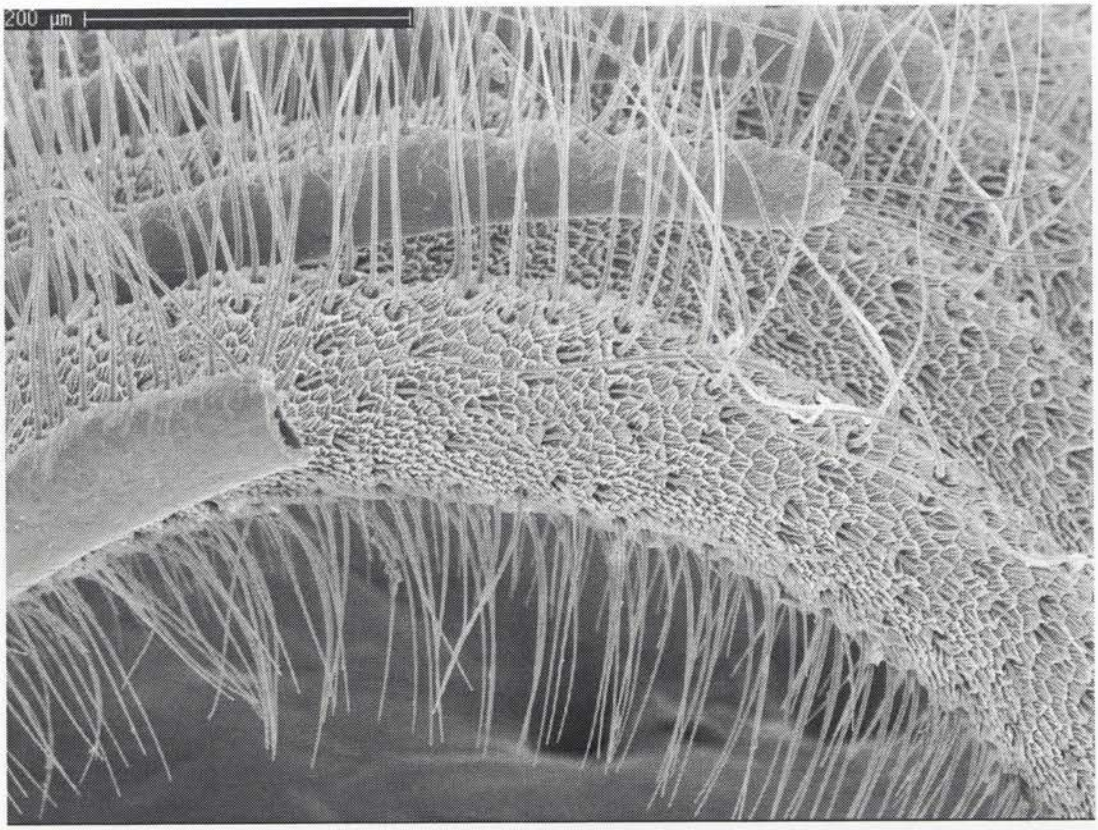

Fig. 231: *Coloradia* sp. (Saturniidae), rami at middle of ♂ antenna, distal view (bottom = ventral) – the rami have ventral and dorsal rows of very long sensilla trichodea (broken ramus / short rami = distal rami).

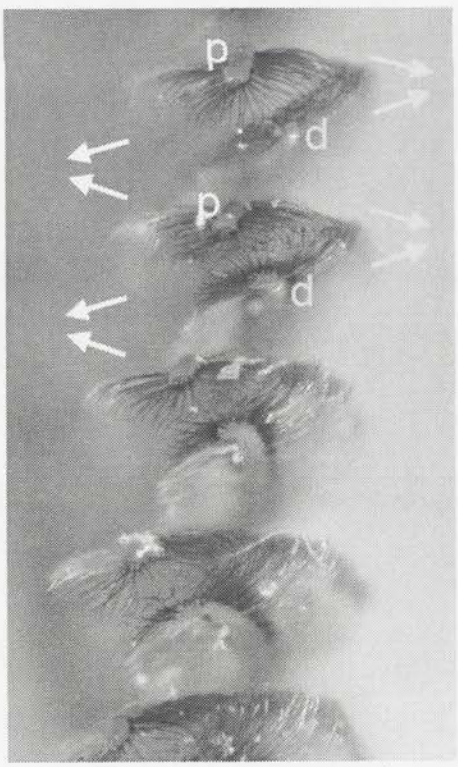

Fig. 232: *Rhodinia fugax* (Saturniidae), rami apices at middle of ♂ antenna, lateral view – the sensilla trichodea of the proximal (p) and distal (d) rami of flagellomeres form "weirs", which open alternately anteriad (left) and posteriad (right); arrows symbolize orientation of s. trichodea;.

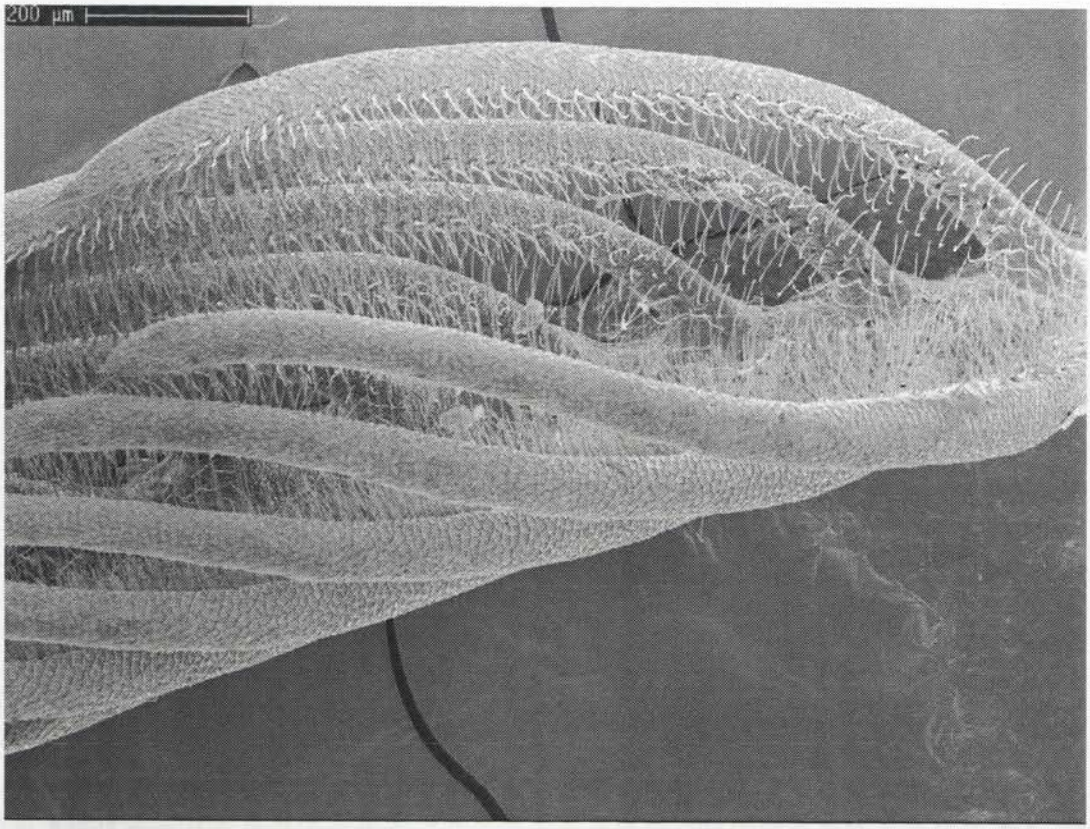

Fig. 233: *Endromis versicolora* (Endromidae), flagellomeres at base of ♂ antenna, latero-ventral view (bottom-left = distal) – only the ventral side of the rami carries a multiple row of very long sensilla trichodea.

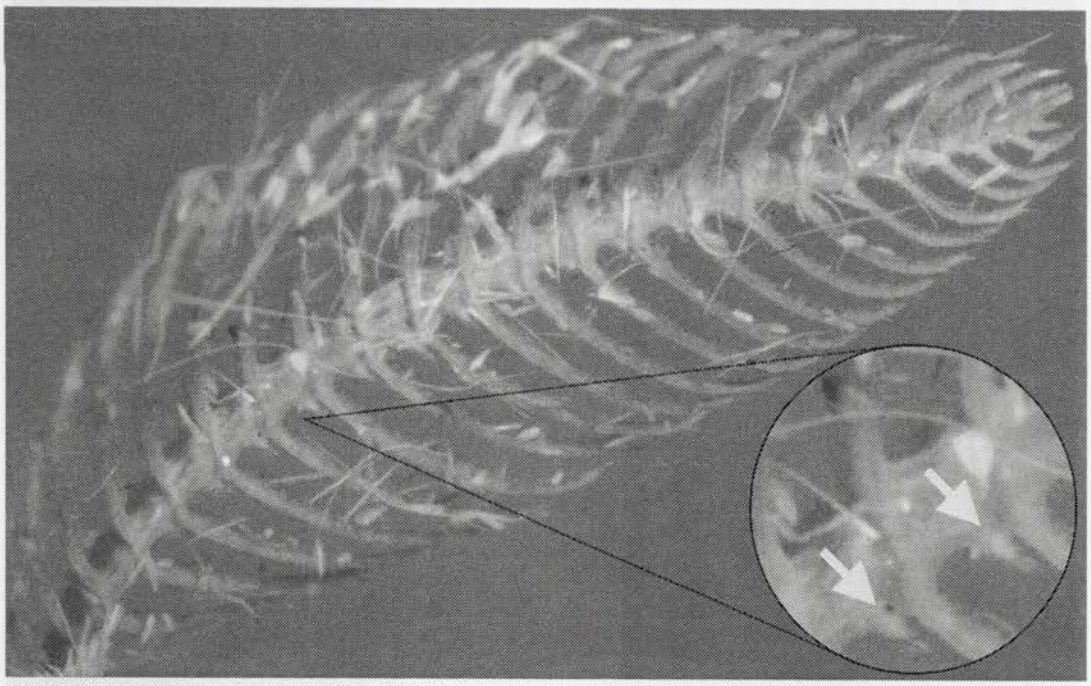

Fig. 234: *Eosia insignis* (Saturniidae), ♀ antenna, dorsal view [courtesy of R. Oberprieler, ANIC] – while the antenna with well developed proximal rami superficially appears to be bipectinate, tiny remnants of the distal rami (yellow arrows) and the location of the proximal rami directly at the proximal edge of each flagellomere indicate this bipectinate condition to be derived from the typical quadripectinate antenna of the Saturniidae.

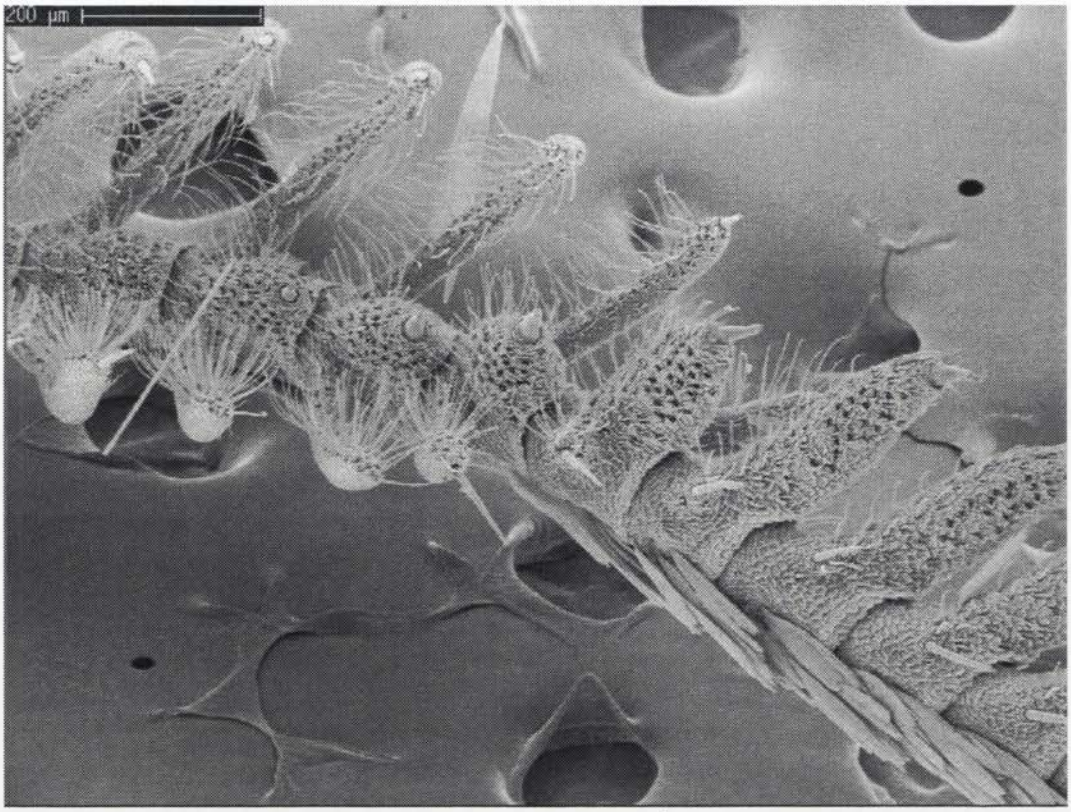

Fig. 235: *Periga* sp. (Saturniidae), flagellomeres near apex of ♂ antenna, latero-distal view (top = ventral) – each flagellomere is dorsally scaled, has laterally only a single pair of rami and forms a very large ventro-median process (increasing in size towards the antennal apex).

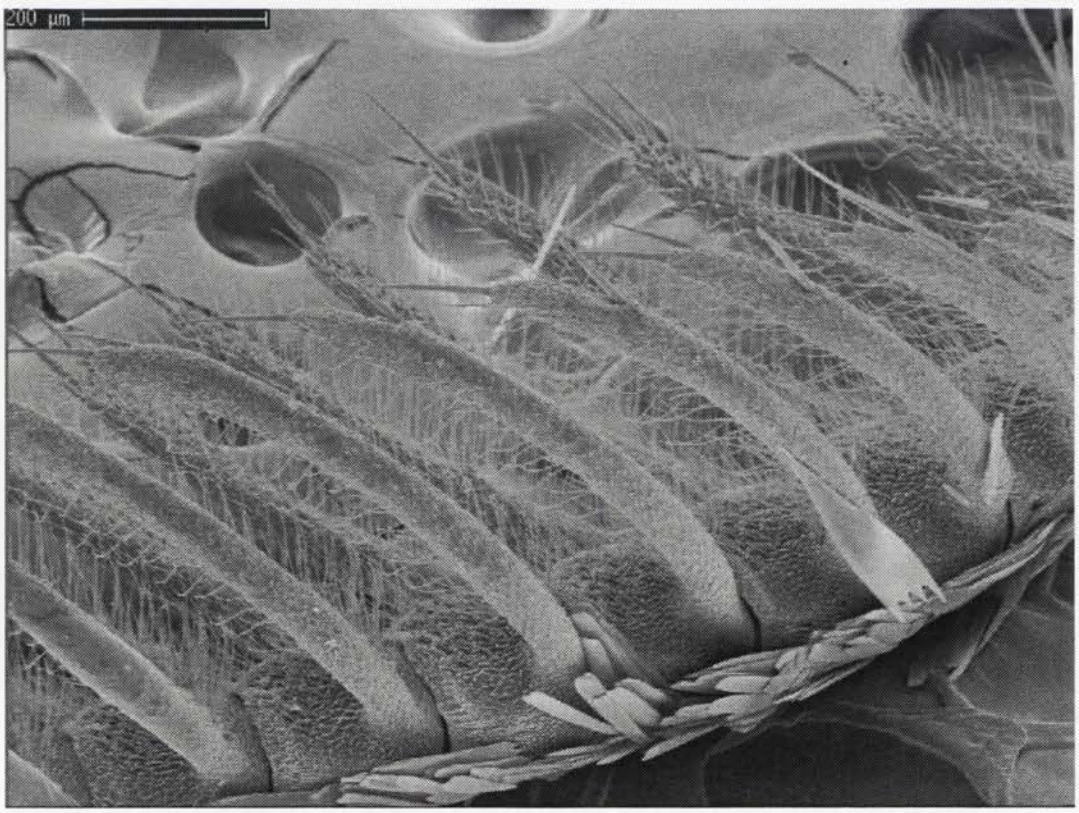

Fig. 236: *Periga* sp. (Saturniidae), flagellomeres at apical fifth of ♂ antenna, latero-distal view (top = ventral) – only a single pair of rami arises directly at the proximal edge of each flagellomere (further distally on flagellomeres at the apex of the antenna).

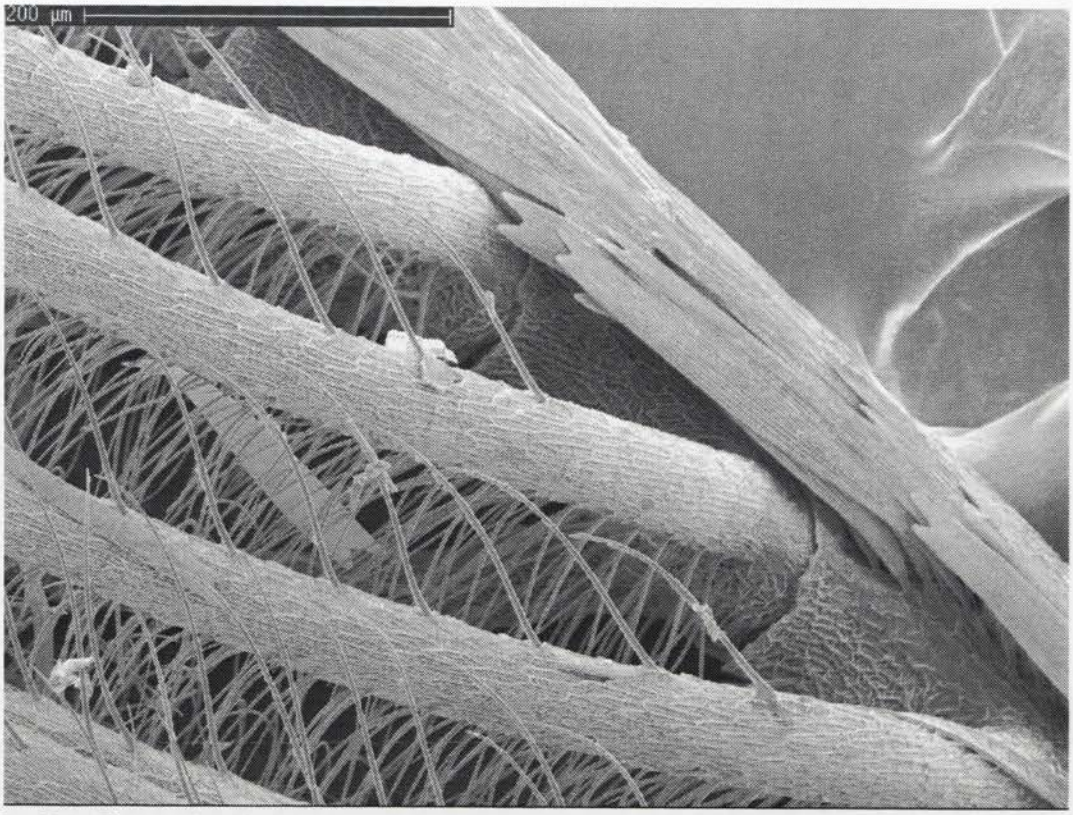

Fig. 237: *Therinia buckleyi* (Saturniidae), flagellomeres with rami at basal fourth of ♂ antenna, lateral view (top left = distal; bottom left = ventral) – from each flagellomere only a single pair of rami arises directly at its proximal edge; note the scaled dorsal side of the flagellomeres.

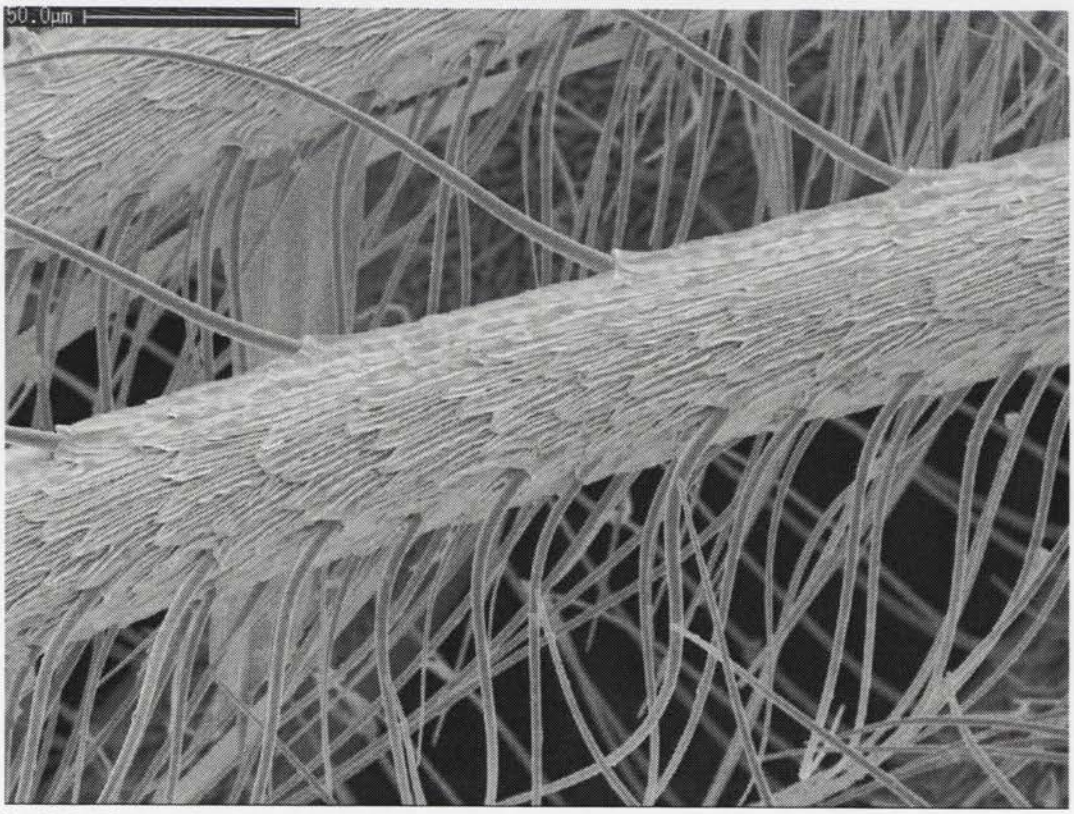

Fig. 238: *Therinia buckleyi* (Saturniidae), middle of rami at basal fourth of ♂ antenna, proximal view (bottom = ventral) – in addition to the ventral band of numerous sensilla trichodea, the ramus carries a single dorsal row of s. trichodea.

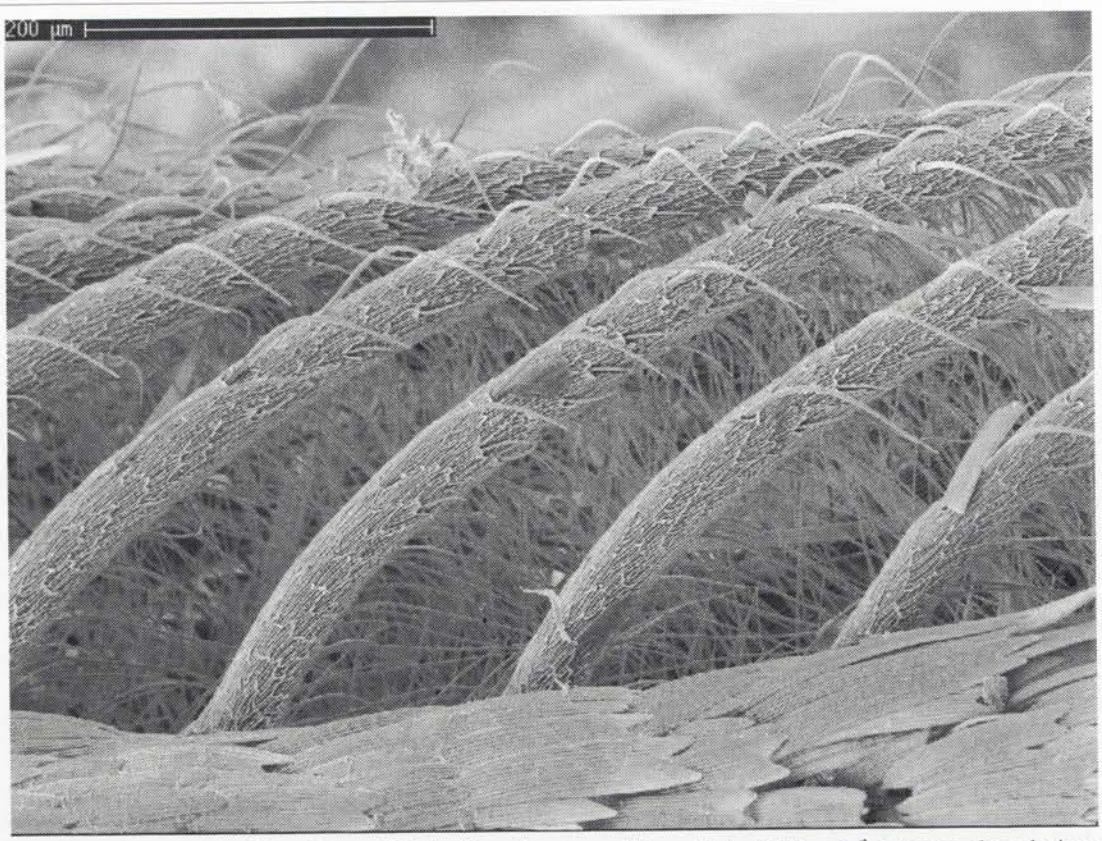

Fig. 239: *Therinia buckleyi* (Saturniidae), flagellomeres with rami at middle of ♂ antenna, dorsal view (right = distal) – the sensilla trichodea of the single dorsal row of the ramus are strongly curved distad.

III.5.1.C) The sensilla trichodea on the flagellomeres of the bombycoid complex

The antennal sensilla are not scattered over the antenna at random, but restricted to certain areas and arranged in specific patterns. The most prominent and by far most abundant type of sensilla are the long to very long, olfactory sensilla trichodea, which are apparent to the naked eye as tiny hairs. With the exception of the occasional sensillum trichodeum on the dorsal side of the flagellum, the vast majority (e.g., >70,000 in *Manduca sexta* (Sphingidae); Lee & Strausfeld 1990) is located on the lateral and ventral surface of the flagellum. The size of the long sensilla trichodea varies continuously from 70-600µm in *M. sexta* (Lee & Strausfeld 1990), but it is the very long sensilla trichodea that stand out and form those arrangements described above.

In Macrolepidoptera without rami, these very long sensilla trichodea are arranged in a row that is several sensilla trichodea wide and stretches roughly in the middle of a flagellomere from one dorsal end of a lateral side around the ventral side and on to the dorsal end of the other lateral side (Fig. 240). In taxa with bipectinate antennae the latero-ventral side of the flagellomere is expanded into rami. The band of sensilla trichodea stretches accordingly from the distal end of these rami along their ventral side and across the flagellomere "body" (Fig. 241). Within this band the sensilla trichodea appear to be arranged in a certain pattern, which seems to involve groups of two or three sensilla (Fig. 225). The restriction of the very long sensilla trichodea to a band on the ventral side of rami seems to be universal within Macrolepidoptera – the band extends hardly ever onto the dorsal side of these rami.

The seemingly only exception of such kind occurs in Sphingidae and Saturniidae. In both of these families the very long sensilla trichodea are arranged in two bands, which run along the proximal and distal margins of the lateral and ventral sides of a flagellomere and unite dorsally in an arc (Figs 242, 243, 244; see above, section III.5.1.A; character #H.56). Further, the sensilla trichodea of the opposite bands are curved towards each other, forming a very characteristic weir (Figs 221, 232, 242). This duplication and modified location of the sensory area is the shared structural basis of the otherwise very different antennae of Sphingidae and Saturniidae – the generally aerodynamically shaped, rapid-flying Sphingidae have slender, reduced antennae without rami, which contrasts with the greatly enlarged, quadripectinate antennae of the generally large-winged, relatively slowly flying Saturniidae.

Both rami pairs of a saturniid flagellomere differ from the typical single rami pair of the bombycoid complex flagellomere in structural details. While the single pair of rami has a row of diverging sensilla trichodea on the ventral side only, the unidirectional sensilla trichodea of the two rami pairs of Saturniidae extend over the ventral and dorsal side of the ramus (Fig. 231). From this arrangement it can be hypothesized that the sensory dorsal epithelium of the saturniid rami differs from the non-sensory dorsal epithelium of the typical bombycoid complex rami, while at the same time it seems to be identical with the sensory epithelium on the ventral side of the saturniid rami. A possible, simple explanation for this situation is that the epithelium of the dorsal side of saturniid rami is a continuation of the epithelium of the ventral side of the rami. Or in other words, the saturniid rami are outgrowths within the sensory epithelium only, while the typical rami of the bombycoid complex (and possibly all Macrolepidoptera) are "outgrowths" at the border between sensory and non-sensory epithelia. Occasionally, these "outgrowths" seem to contain even part of the dorsal epithelium, which produces the scales on the dorsal side of the flagellomere. In this case these rami are fully scaled to their apices (e.g., *Xenosphingia jansei* (Sphingidae) and many Limacodidae (Zygaenoidea)).

In Sphingidae the two bands of sensilla trichodea form an arc just ventrally of a shallow, laterally protruding edge (Fig. 219). The rather flat area dorsally of this edge is densely covered with scales, hence this edge probably marks the border between the dorsal scale-producing and the latero-ventral sensory epithelium. In Saturniidae the four rami originate dorso-laterally to dorsally on the flagellomere (rather than ventrally), the arc of sensilla trichodea is located on the dorsal side of the flagellomere, and the flagellomere typically lacks any scales (Fig. 244). It seems that this arrangement is caused by a dorsal shift and extension of the ventral, sensory epithelium, which displaces the dorsal, scale-producing epithelium to an extent that the dorsal ends of the ventro-lateral epithelium are (almost) touching each other dorsally (Fig. 245). This dorsal shift increases towards the apex of the flagellum, and it is only the basal flagellomeres that might still carry a few scales. In taxa with bipectinate antennae and secondarily ventrad shifted rami, the dorsal side of the flagellum is scaled, possibly as the dorsal epithelium is no longer displaced (e.g., *Periga* and Oxyteninae) (Figs 236, 237).

The dorsal shift of the rami "opens up" the antenna, fully exposing the alternating

anterior and posterior "weirs" formed by the sensilla trichodea. These "weirs" open anteriad in Saturniidae and Sphingidae, as the orientation of the antenna is modified in both taxa as described above. A similar effect is achieved by the ventral orientation of the primarily single rami pairs and the ventral, diverging sensilla trichodea in the antenna typical of the bombycoid complex. Their diverging sensilla trichodea form "weirs" between the rami of one side of adjacent flagellomeres, and because the rami face ventrad, these "weirs" of the anterior rami open anteriad and the ones of the posterior rami posteriad.

If the distal pair of rami of a quadripectinate antenna is reduced, the sensilla trichodea on the ventral side of the proximal rami diverge as in the primarily bipectinate antennae, by which they form "weirs" between each other. In contrast, the sensilla trichodea on the dorsal side of the remaining rami do not form "weirs" any longer. They are absent in most of the secondarily bipectinate species, but a single dorsal row of sparsely distributed sensilla trichodea is retained in a few species, e.g., *Therinia buckleyi* (Saturniidae: Oxyteninae; Figs. 237, 238; see above, section III.5.1.B) and *Parusta thelxinoe* (Saturniidae: Saturniinae, Urotini). This single row of very long, curved sensilla trichodea confirms the presence of the dorsal, sensory epithelium, which indicates the origin of these bipectinate antennae from the quadripectinate condition. It also indicates the secondary loss of these sensilla trichodea in most of the other Saturniidae with secondarily bipectinate antennae.

Keil and Steiner studied the development of the antenna of *Antheraea polyphemus* (Saturniidae) in great detail (Keil & Steiner 1990a, b, 1991; Steiner & Keil 1993, 1995a, b). They showed that the segmentation of the antenna into flagellomeres develops by incisions of a leaf-shaped precursor of the antenna and that the quadripectinate condition of each flagellomere develops by an additional, subsequent incision (Steiner & Keil 1993). These primary and secondary incisions are caused by different mechanisms (Steiner & Keil 1993, 1995a, b), as one might expect from the presence of segments in all antennae but the restriction of quadripectinate antennae to Saturniidae. Further, they concluded from disturbance experiments that the formation of rami by incisions and the development and orientation of sensilla trichodea are two independent processes (Steiner & Keil 1995b). This conclusion corroborates my hypothesis that the vastly differently shaped antennae of Sphingidae and Saturniidae are based on the same unique

arrangement of sensilla trichodea in a proximal and distal band.

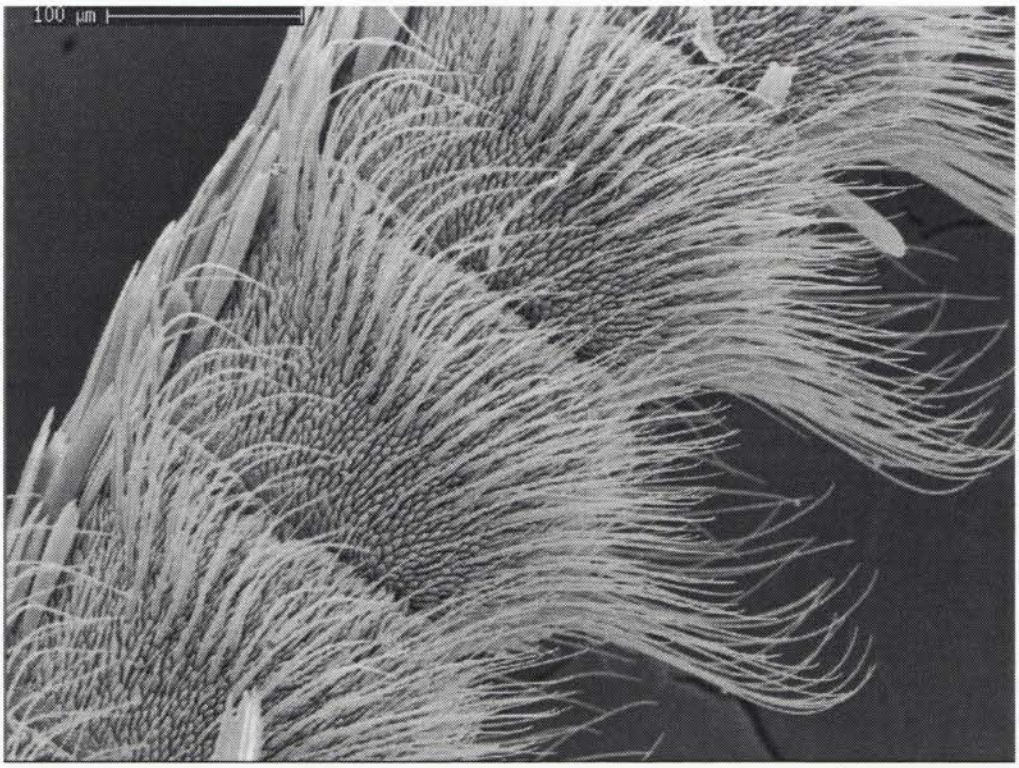

Fig. 240: *Hypsidia niphosema* (Drepanidae), flagellomeres at proximal fourth of ♂ antenna, lateral view (top right = distal; bottom right = ventral) – the sensilla trichodea are arranged in a single, median band across the lateral and ventral side of each flagellomere.

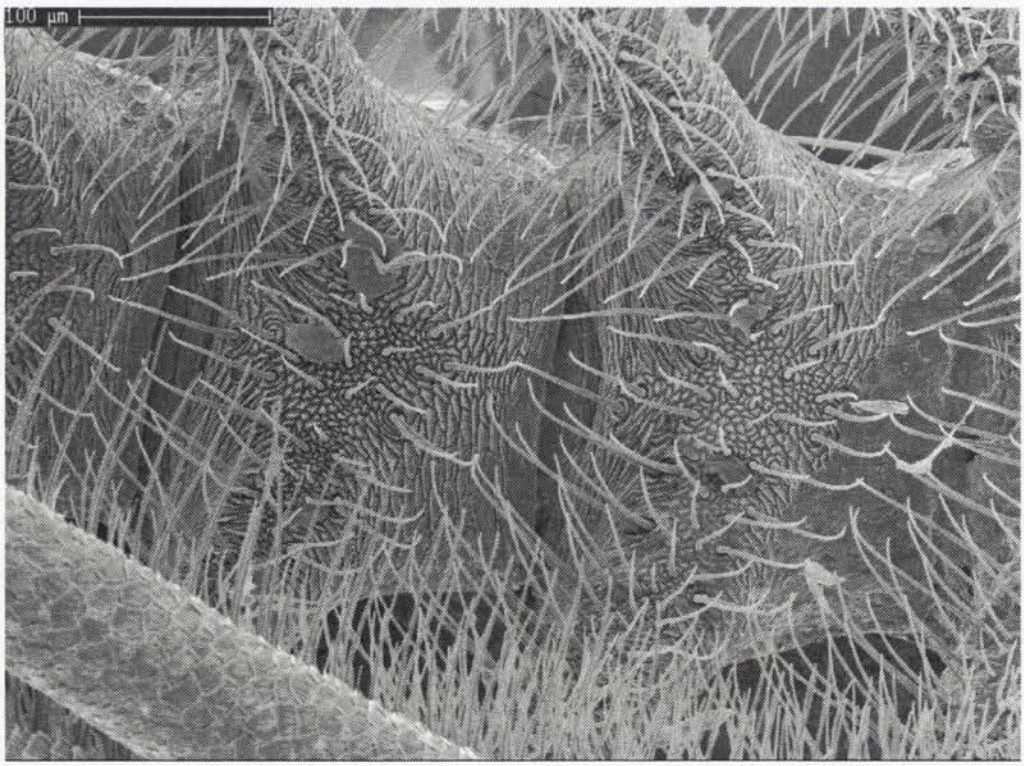

Fig. 241: *Endromis versicolora* (Endromidae), flagellomeres at proximal fifth of ♂ antenna, ventral view (left = distal) – the sensilla trichodea of each flagellomere are arranged in a single, median band, which runs along the ventral side of the rami and across the middle of the ventral side of the flagellomere.

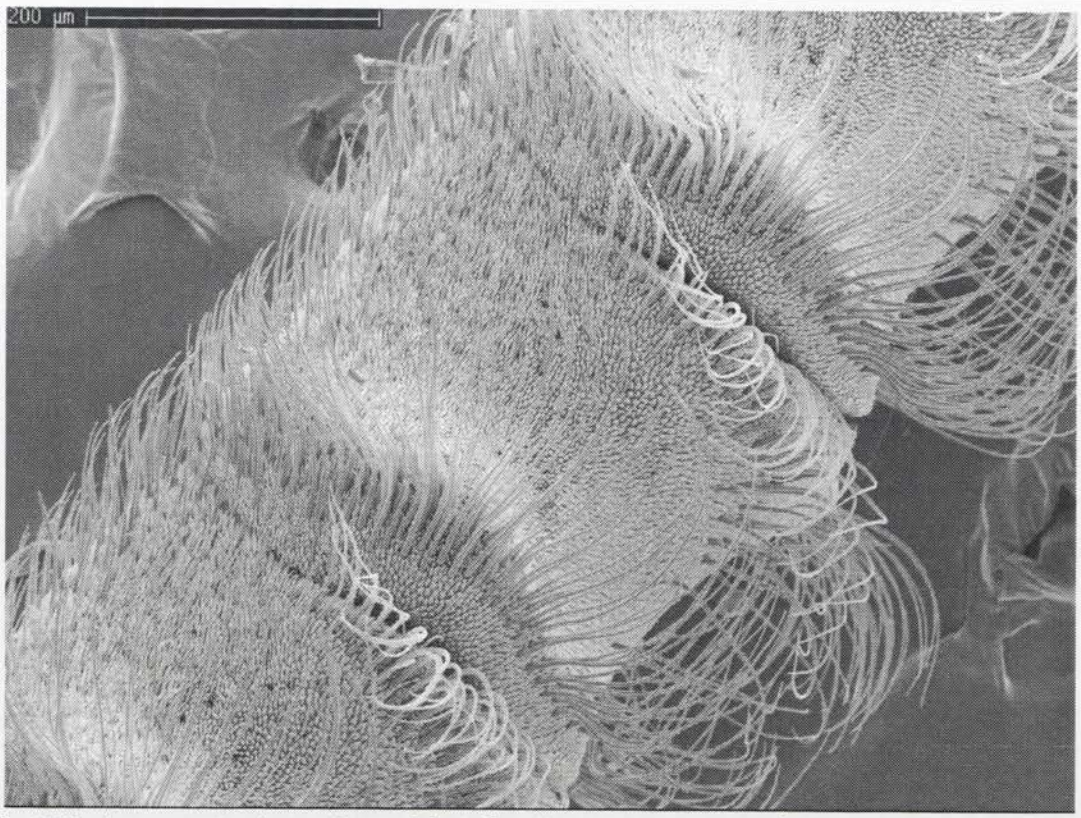

Fig. 242: *Arsenura ciocolatina* (Saturniidae), flagellomeres at middle of ♂ antenna, lateral view, (top right = distal; bottom right = dorsal) – the sensilla trichodea are arranged in a proximal and a distal band on the lateral and ventral side of each flagellomere.

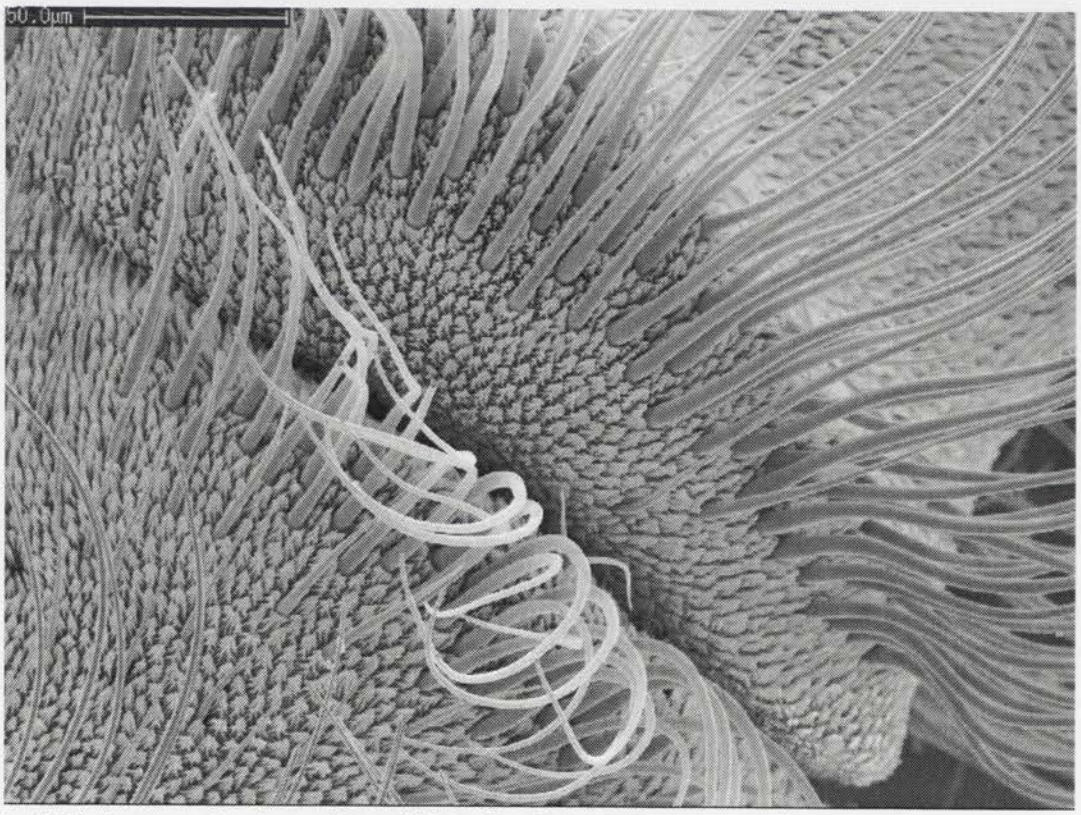

Fig. 243: *Arsenura ciocolatina* (Saturniidae), flagellomeres at middle of ♂ antenna, lateral view (top right = distal; bottom right = dorsal) – the sensilla trichodea form fringes at the distal and proximal edge of adjoining flagellomeres.

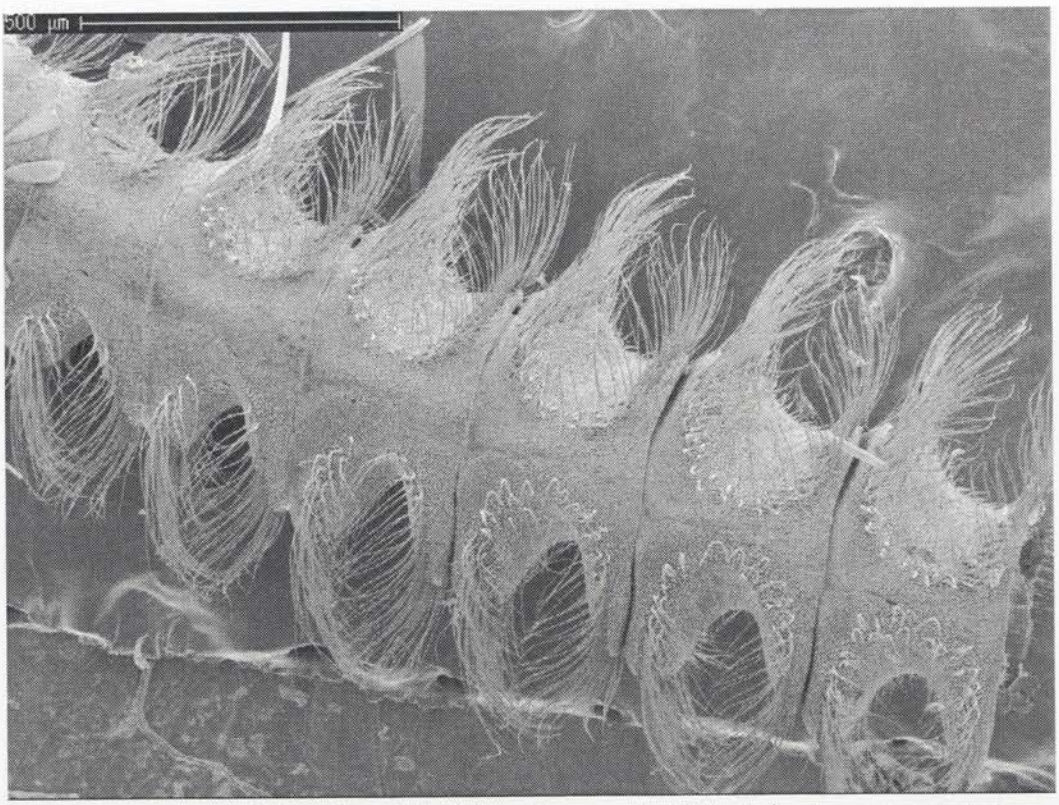

Fig. 244: *Arsenura ciocolatina* (Saturniidae), flagellomeres at middle of ♂ antenna, dorsal view (bottom right = distal) – the two lateral fringes of sensilla trichodea unite in an arc on the non-scaled dorsal side of each flagellomere.

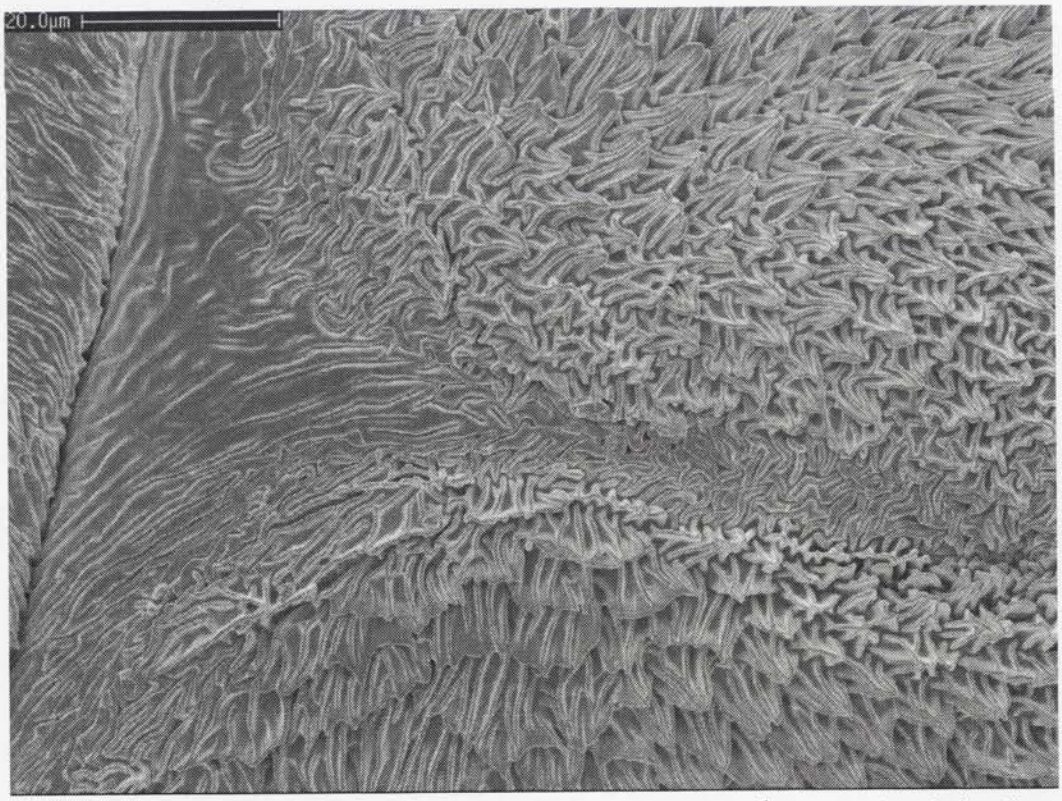

Fig. 245: *Arsenura ciocolatina* (Saturniidae), flagellomere at middle of ♂ antenna, dorsal view (bottom right = distal) – the ventro-lateral sides (top and bottom in picture) of the flagellomere appear to be shifted dorsad, entirely displacing the scaled dorsal side located between them, except for a small triangle remnant at the proximal edge of the flagellomere.

III.5.2) Character analyses of adult head-related characters

Character #H.55: Flagellomere with large, ventro-median process, which carries numerous sensilla coeloconica and an apical styliform sensillum complex.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; very well supported.

Introduction. As discussed in detail above (see section III.5.1), the flagellomeres of Macrolepidoptera, Pyralidae and at least some Zygaenoidea carry a single styliform sensillum complex (the sensory pegs of several sensilla styliformia are fused to form one peg with multiple tips) in a median position near the distal edge of their ventral sides (Figs 247, 257). In most taxa this styliform sensillum complex is located on the flagellomere "body" (Fig. 246), a shallow, ventral crest or a minor protrusion (Figs 248, 249). Occasionally a few sensilla coeloconica (Fig. 256) are located near the anterior edge, too.

Description. In many families of the bombycoid complex the ventral side forms a very large ventro-median process, which carries the styliform sensillum complex at its apex (Fig. 254). The lateral and distal sides of this process, but not the proximal side, are covered with numerous sensilla coeloconica (Fig. 255). Sensilla coeloconica are rather scarce on the flagellomeres of other Macrolepidoptera, but typically number 20-40 on this ventro-median process. The process occurs on all flagellomeres, but it is frequently reduced or lost on the majority of flagellomeres, in which case the remaining processes often increase in size on the last apical segments only. It seems that the process occupies most of the ventral side of a flagellomere in Bombycidae, Sphingidae and Saturniidae, while it is very slender and pointed in the Anthelidae (Fig. 253) and Eupterotidae (Fig. 254) I examined. However, in anthelid and eupterotid taxa with a secondarily reduced process the remnants can be rather broad, too (Fig. 201). Further, the process of Carthaeidae (Fig. 251), Brahmaeidae (Fig. 207) and Lemoniidae (Fig. 252) is intermediate in width, and therefore I do not distinguish between the overall shapes of these processes.

Discussion. The ventro-median process is absent in the other families of the bombycoid complex, namely in the Mimallonidae, Lasiocampidae, Endromidae and Mirinidae. In the Lasiocampidae (including the in many aspects plesiomorphic

Poecilocampa populi and *Chionopsyche montana*) and the few Mimallonidae I examined, even the styliform sensillum complex is lost and the rami are ventrally very closely approximated, occupying the location of the ventro-median process (Fig. 250). Possibly the median area of the ventral side is displaced by a mesal extension of the ventro-lateral region.

The very large ventro-median process of the flagellomere is unique to a number of taxa in the bombycoid complex, which is why I interpret character state (1) as apomorphic for these taxa.

Summary. While the process is of variable shape and frequently reduced, it occurs at a specific location and is characterised by the specific arrangement of its sensilla. This arrangement always includes one specific sensory structure, the ventro-apical styliform sensillum complex, as well as a large number of otherwise scarce sensilla coeloconica. Therefore I consider my hypothesis of homology to be very well supported.

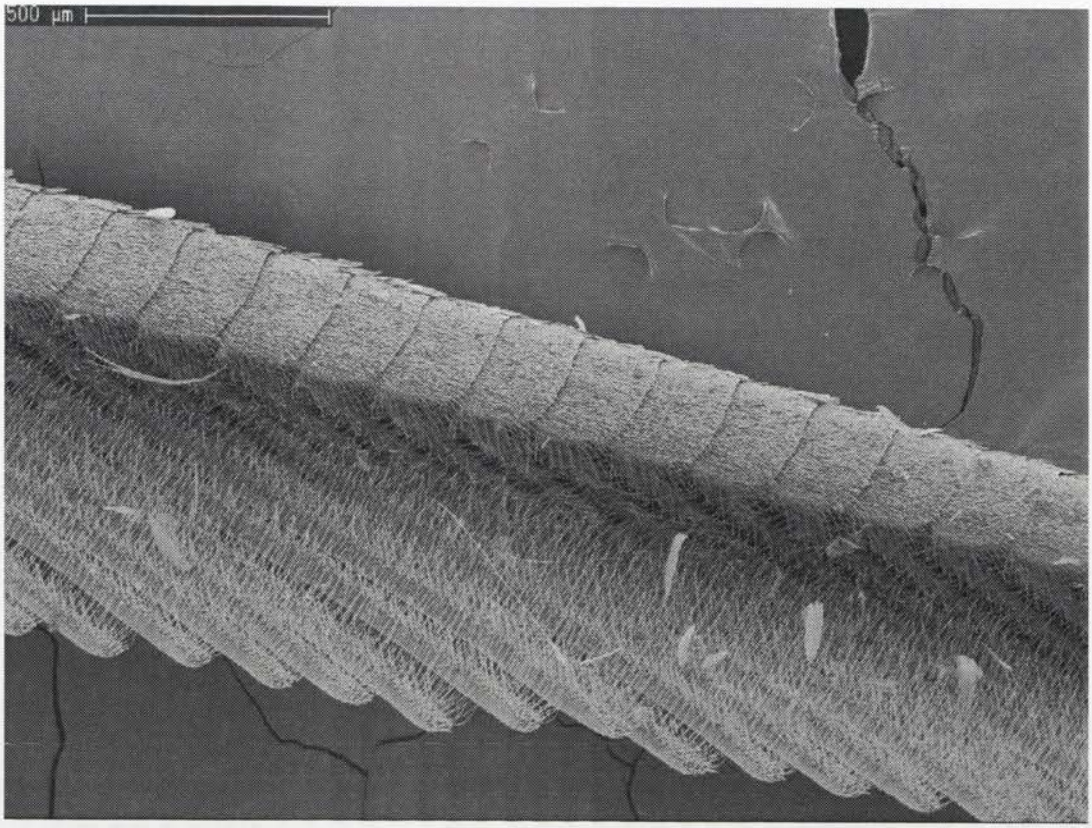

Fig. 246: *Oenochroma vinaria* (Geometridae), middle section of ♂ antenna, ventral view (right = distal) – the flagellomeres do not form a ventro-median process and have only a single ramus each.

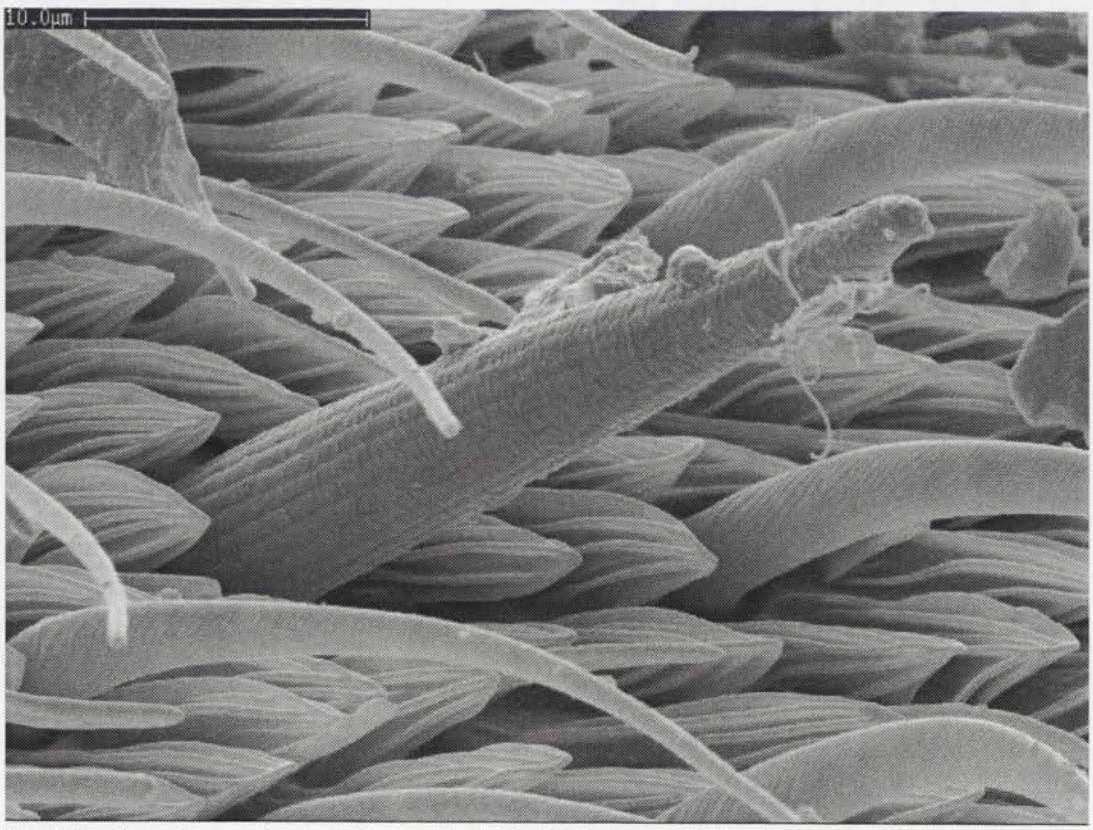

Fig. 247: *Oenochroma vinaria* (Geometridae), flagellomere at middle of ♂ antenna, latero-ventral view (right = distal) – a styliform sensillum complex is located directly on the flagellomere body, rather than on a ventro-median process.

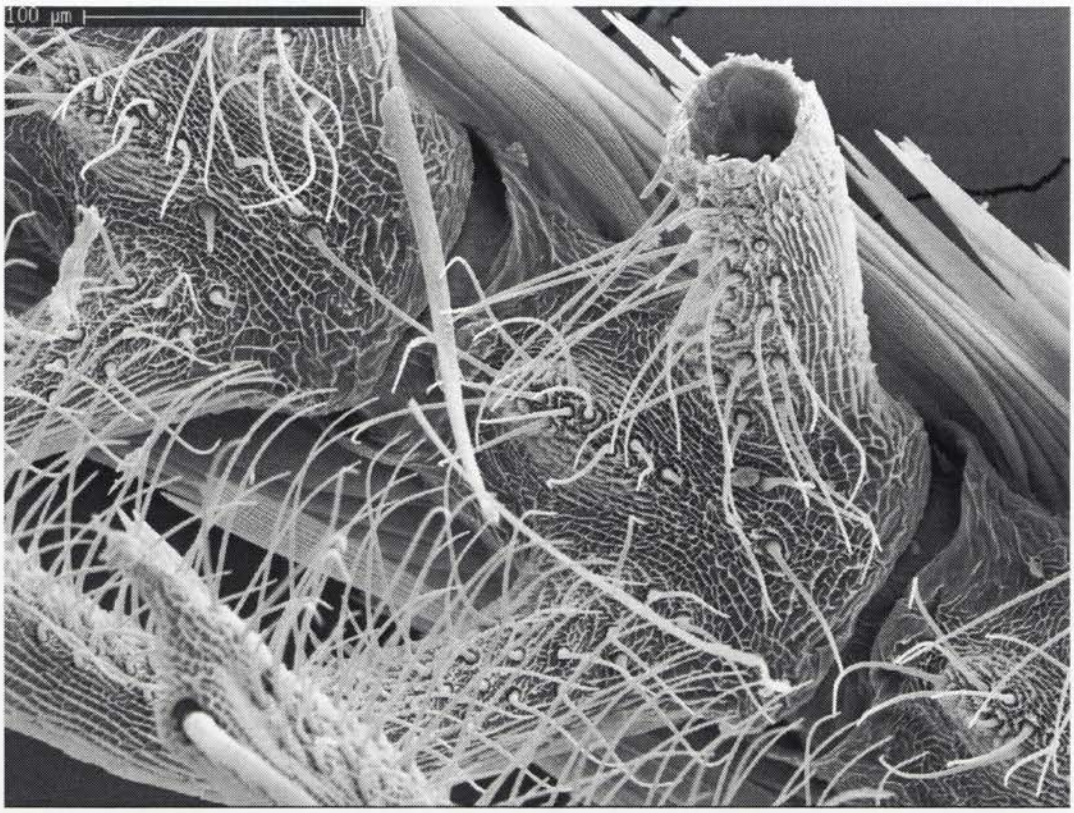

Fig. 248: *Lymantria nephrographa* (Lymantriidae), flagellomeres at distal fifth of ♂ antenna [one ramus partly broken off], ventral view (top left = distal) – each flagellomere has a small, shallow ventro-median protrusion, but no large ventro-median process.

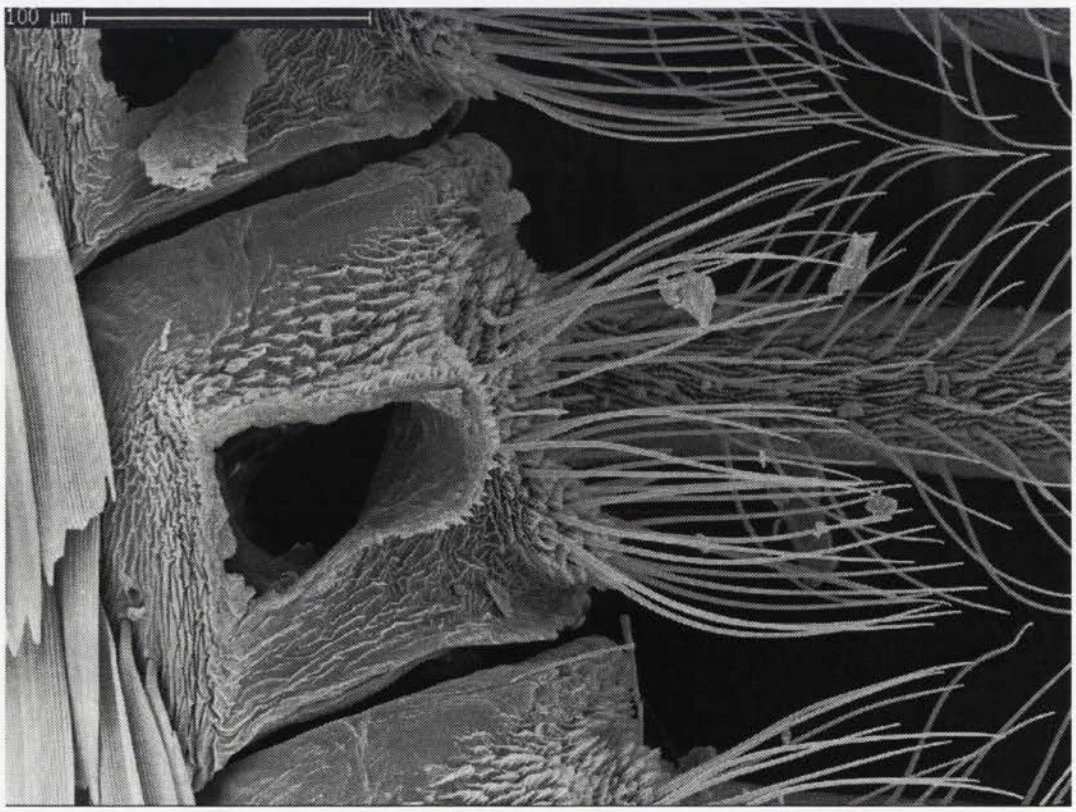

Fig. 249: *Lymantria nephrographa* (Lymantriidae), flagellomeres at proximal fifth of ♂ antenna [rami of one side removed], lateral view (bottom = distal; right = ventral) – each flagellomere has no more than a small, shallow ventro-median protrusion, but no large ventro-median process.

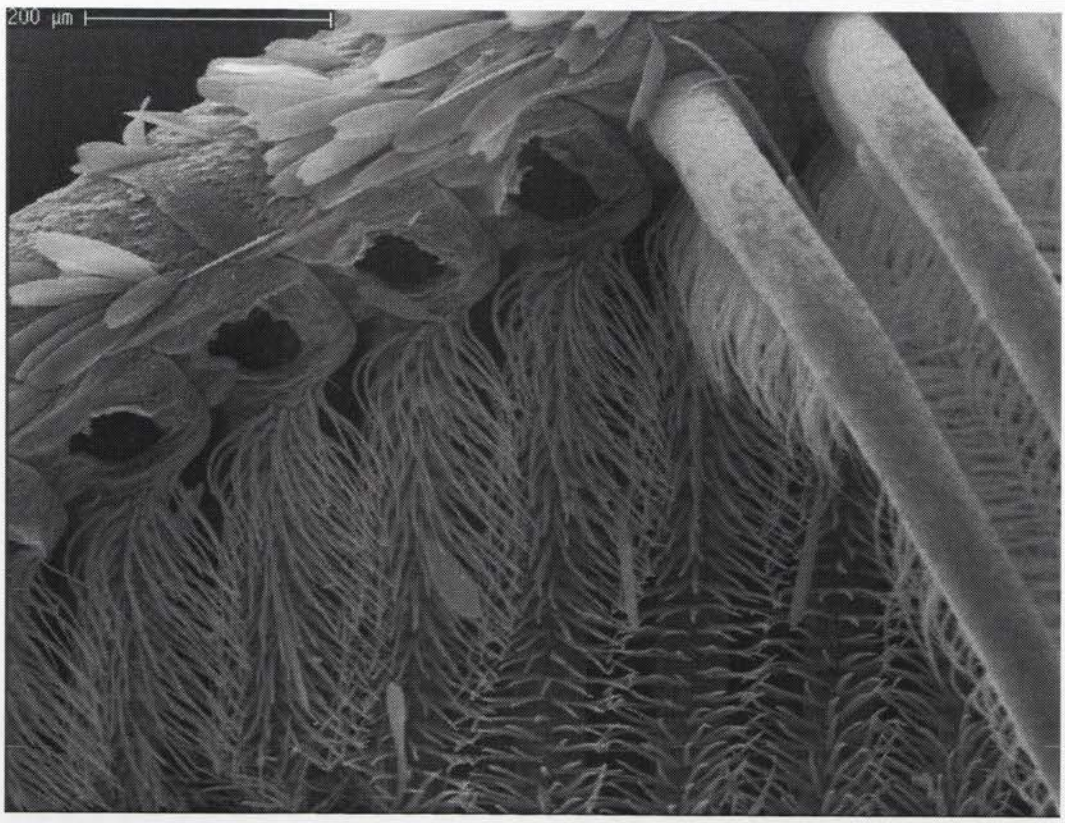

Fig. 250: *Entometa* sp. (Lasiocampidae), flagellomeres at middle of ♂ antenna [some of the rami of one side are removed], ventro-lateral view (bottom left = distal; top left = ventral) – the paired rami of each flagellomere are greatly approximated at their bases, displacing the styliform sensillum complex.

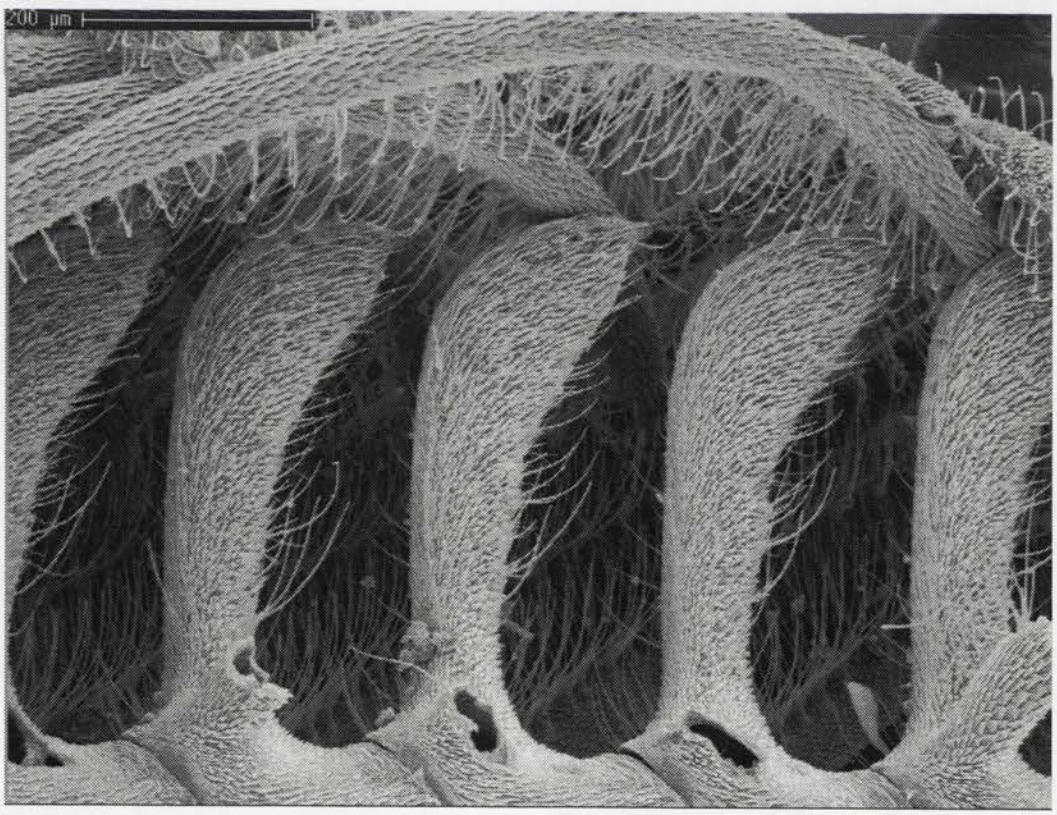

Fig. 251: *Carthaea saturnioides* (Carthaeidae), ventro-median processes of flagellomeres at distal fourth of ♂ antenna, lateral view [rami in foreground removed] (right = distal; top = ventral) – each flagellomere forms a very large, club-shaped ventro-median process.

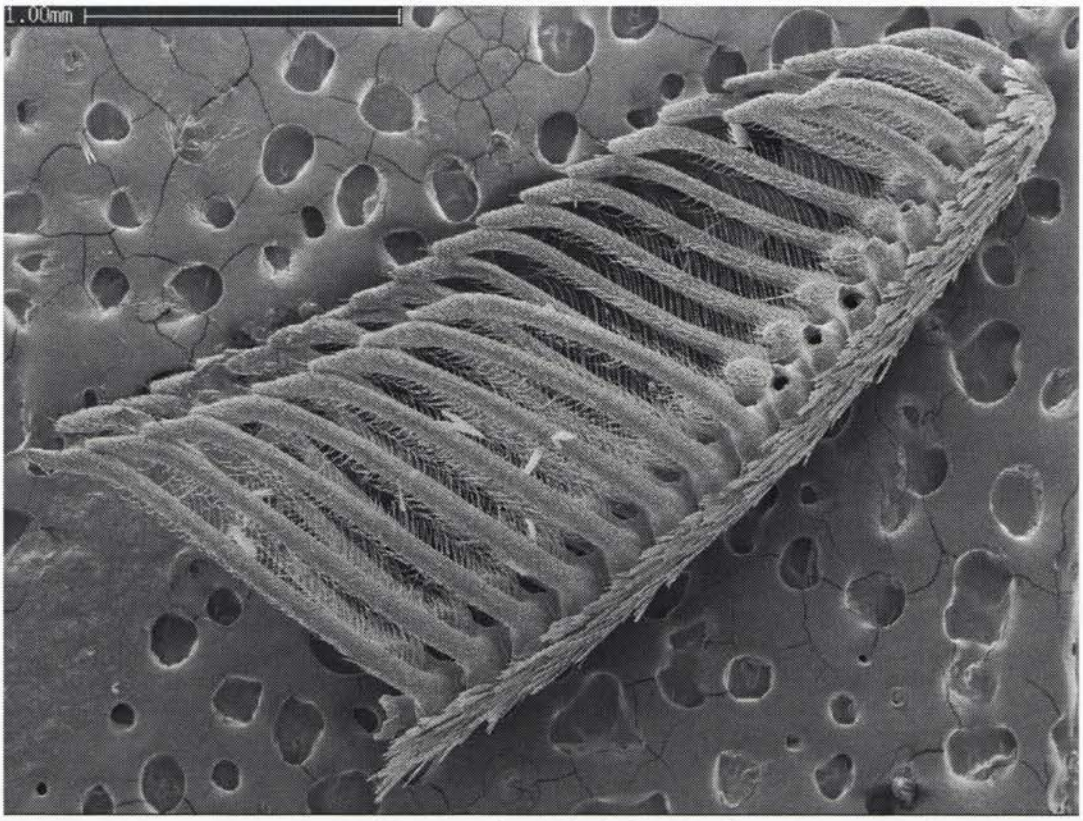

Fig. 252: *Lemonia taraxaci* (Lemoniidae), proximal third of broken ♂ antenna, lateral view [some rami on one side removed] (bottom left = distal; top left = ventral) – each flagellomere forms a short and wide ventro-median process.

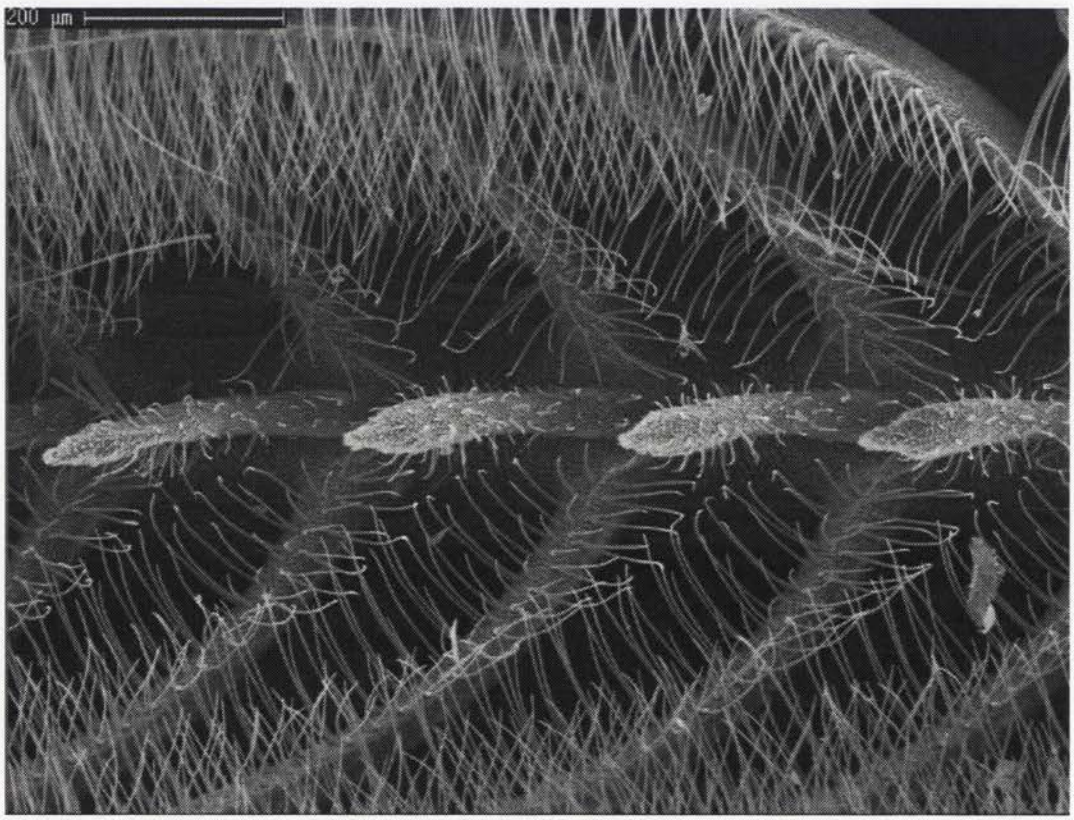

Fig. 253: *Pterolocera* sp. (Anthelidae), flagellomeres at distal third of ♂ antenna, ventral view (left = distal) – each flagellomere forms a huge, pencil-shaped ventro-median process.

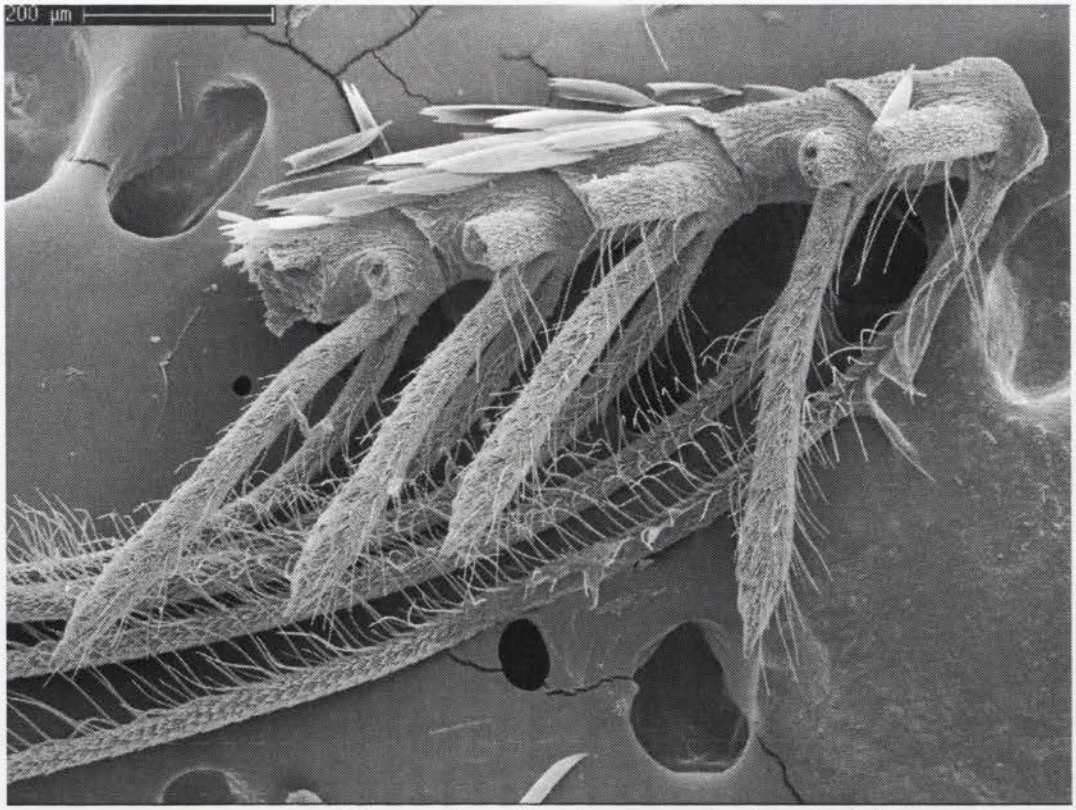

Fig. 254: *Ganisa plana* (Eupterotidae), section of flagellomeres at distal fourth of ♂ antenna [rami on one side partly broken off], lateral view (left = distal) – each flagellomere forms a huge, pencil-shaped, ventro-median process.

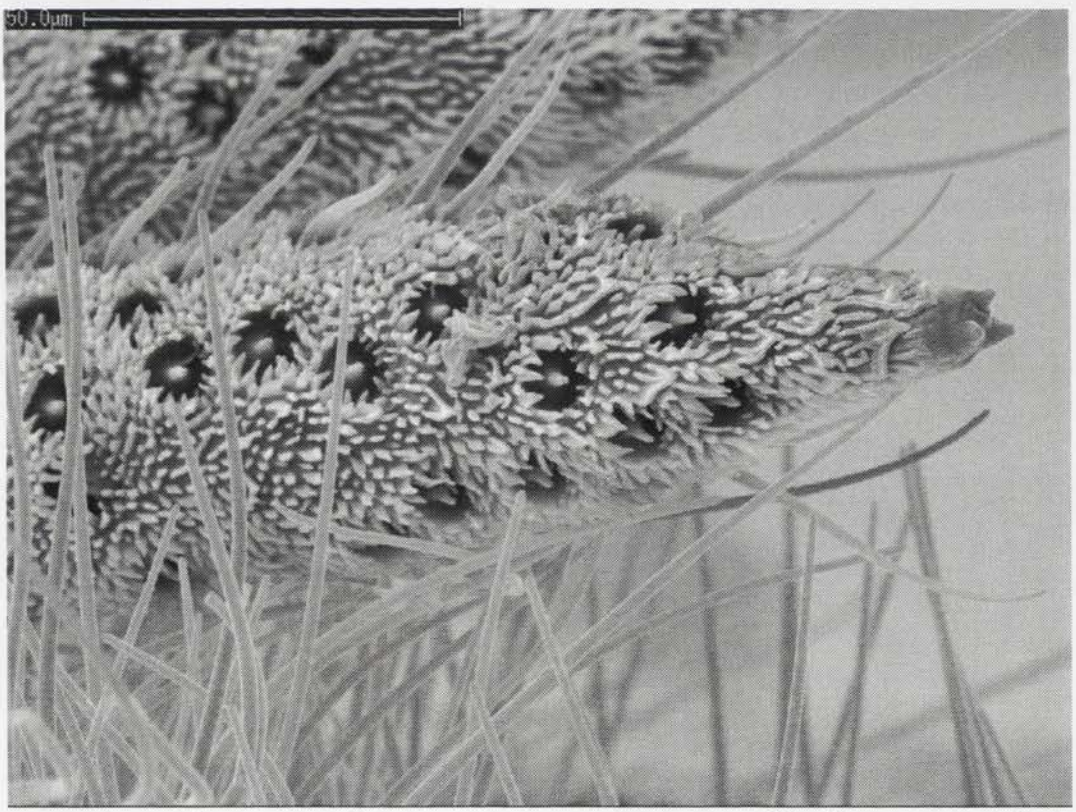

Fig. 255: *Ganisa plana* (Eupterotidae), apex of ventro-median process of flagellomere at distal fourth of ♂ antenna, lateral view (bottom = distal; ventral = right) – the apex of the ventro-median process carries laterally and distally many sensilla coeloconica, and apically a styliform sensillum complex.

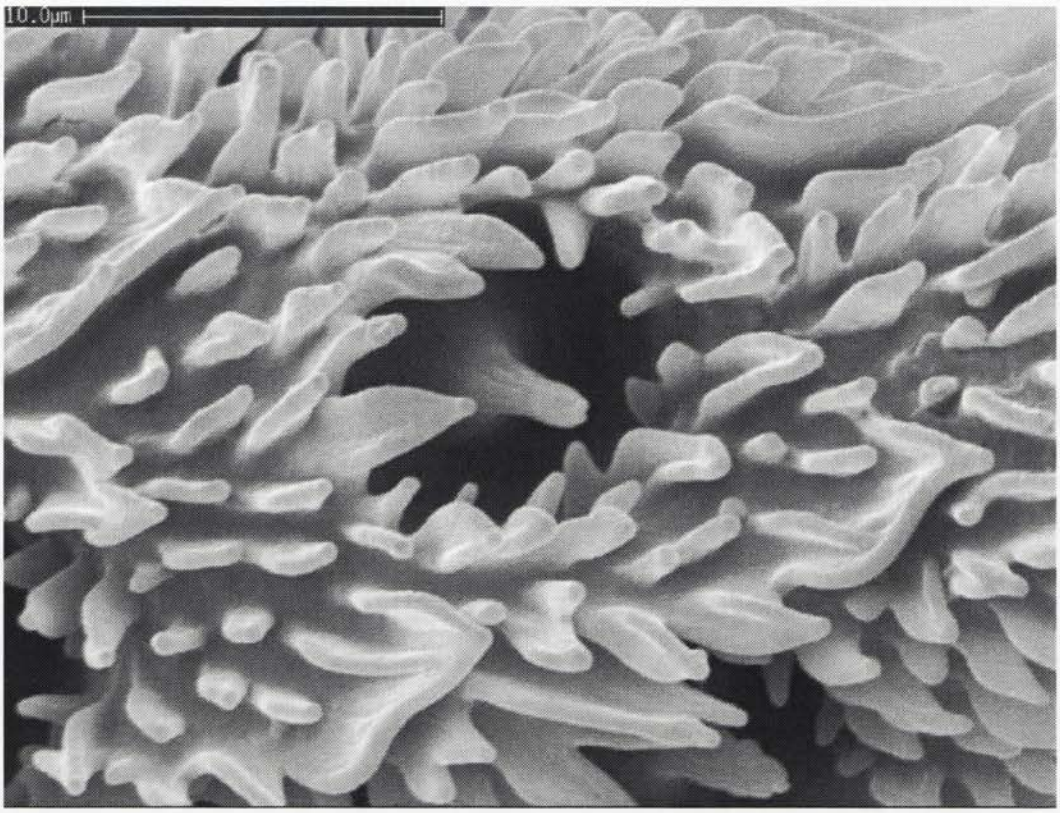

Fig. 256: *Ganisa plana* (Eupterotidae), ventro-median process of flagellomere at distal fourth of ♂ antenna, lateral view (bottom = distal; ventral = right) – sensillum coeloconicum on a lateral side of a ventro-median process.

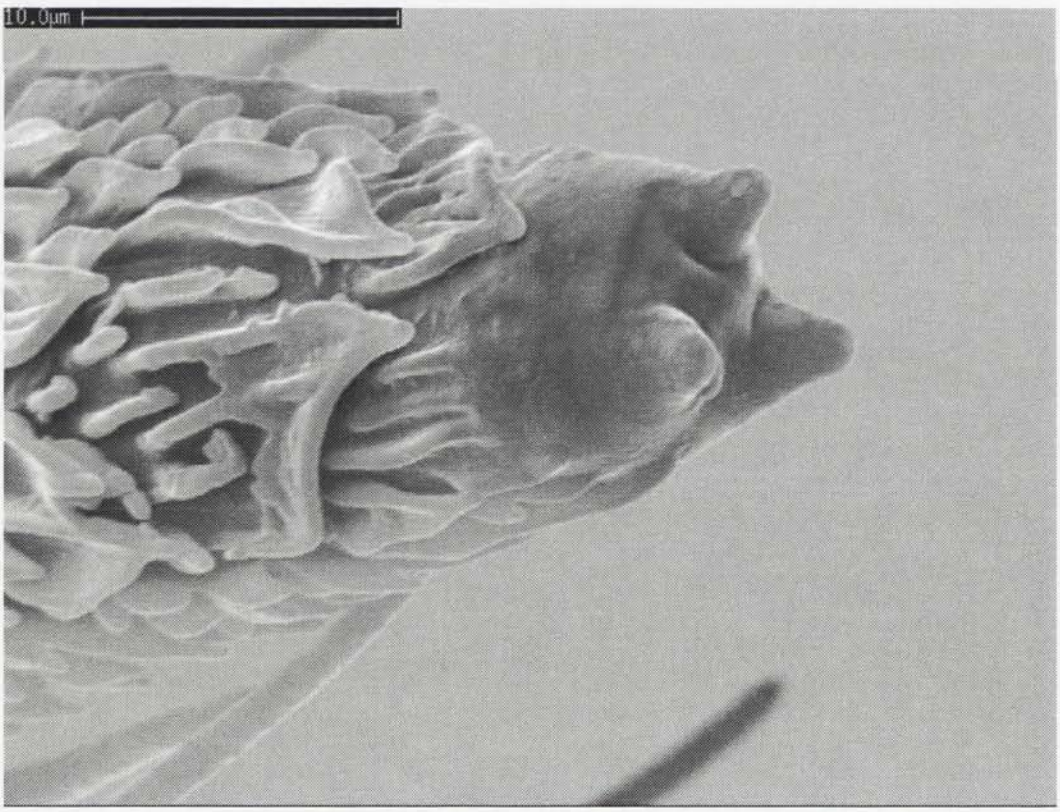

Fig. 257: *Ganisa plana* (Eupterotidae), apex of ventro-median process of flagellomere at distal fourth of ♂ antenna, lateral view (bottom = distal; ventral = right) – the styliform sensillum complex at the apex of a ventro-median process has three pegs in a single cuticular sheath.

Character #H.56: Antennal flagellomere with a proximal and a distal sensory band of very long sensilla trichodea.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; well supported.

Introduction. As discussed in detail in section above (see section III.5.1), the ventral side of the antennal flagellomeres is the sensory area, which carries the vast majority of the antennal olfactory sensilla. This sensory area extends as a single band across the lateral and ventral side of the flagellomere. In taxa with bipectinate antennae the band extends accordingly along the ventral side of the single pair of rami and across the median part of the flagellomere (Fig. 258). Amongst other sensilla this sensory band carries very long sensilla trichodea, which are arranged in a rather complex pattern of small groups. In taxa with bipectinate antennae this sensory band is restricted to the ventral side of the rami, hence no such sensilla trichodea occur on the dorsal side of rami.

Description. In Sphingidae (see above, section II.2.1.A) and Saturniidae (see above, section II.2.1.B) the principal arrangement of sensory setae is different. In these families two bands of very long sensory setae exist, one at the proximal and the other at the distal edge of each flagellomere (Fig. 260). Each sensory band of very long sensilla trichodea extends across the lateral and ventral side of a flagellomere, and the sensilla trichodea of one band curve towards the opposite band. This results in a "weir" of sensilla trichodea on each flagellomere (Fig. 221). While widely separated from each other on the ventral and lateral sides, these two bands unite in an arc (latero-) dorsally (Fig. 259).

Discussion. The principal condition is most easily recognized in the sphingid subfamily Smerinthinae (Fig. 219) and the saturniid subfamily Arsenurinae (Fig. 260), which might represent the plesiomorphic condition for their respective families.

In all Saturniidae other than the Arsenurinae the proximal and distal sensory bands form processes, which originate in a dorso-lateral position (Fig. 261). The band of sensory setae runs around these "rami", and hence long sensilla trichodea occur on the ventral and dorsal side of each "ramus" (Fig. 231). Neither of these rami pairs is homologous with the rami of bipectinate antennae of other Macrolepidoptera, but not all of these rami of bipectinate antennae are necessarily homologous structures either. The

typical, broad, quadripectinate antenna of Saturniidae appears superficially as very different from the slender, "prismatic" antennae of Sphingidae, but their principal structure is nevertheless identical.

The unique arrangement combined with the unique orientation of the very long sensilla trichodea is very characteristic. It consists not only of a distal and proximal band of setae, but these bands unite dorsally in an arc. However, these characteristics are obscured by subsequent modifications in a number of taxa, which can be identified as subsequent modifications as discussed in III.5.1 (pp 253ff.). The similarity of some of these independent modifications further indicates the existence of strong functional constraints that cause convergent modifications in the subsequent arrangement and orientation of these sensilla. Such functional constraints might exist for the arrangement and orientation of the sensilla trichodea, but they do not account for the initial duplication of the sensory area.

It is noteworthy that, while the duplication of the sensory area seems to be unique to the two families Sphingidae and Saturniidae, the secondary loss of the structures linked to the duplication occurred several times independently within the two families. These secondary reductions are often difficult to distinguish from the primarily bipectinate condition and appear as "reversals", but nevertheless must differ from them during their development.

The arrangement of the very long sensilla trichodea in a proximal and distal band on each flagellomere is unique to Sphingidae and Saturniidae, which is why I interpret character state (1) as apomorphic for these taxa.

Summary. While strong functional constraints might influence the characteristic arrangement and orientation of the very long sensilla trichodea, the duplication of the sensory area appears to be unique. Therefore I consider my hypothesis of homology to be well supported.

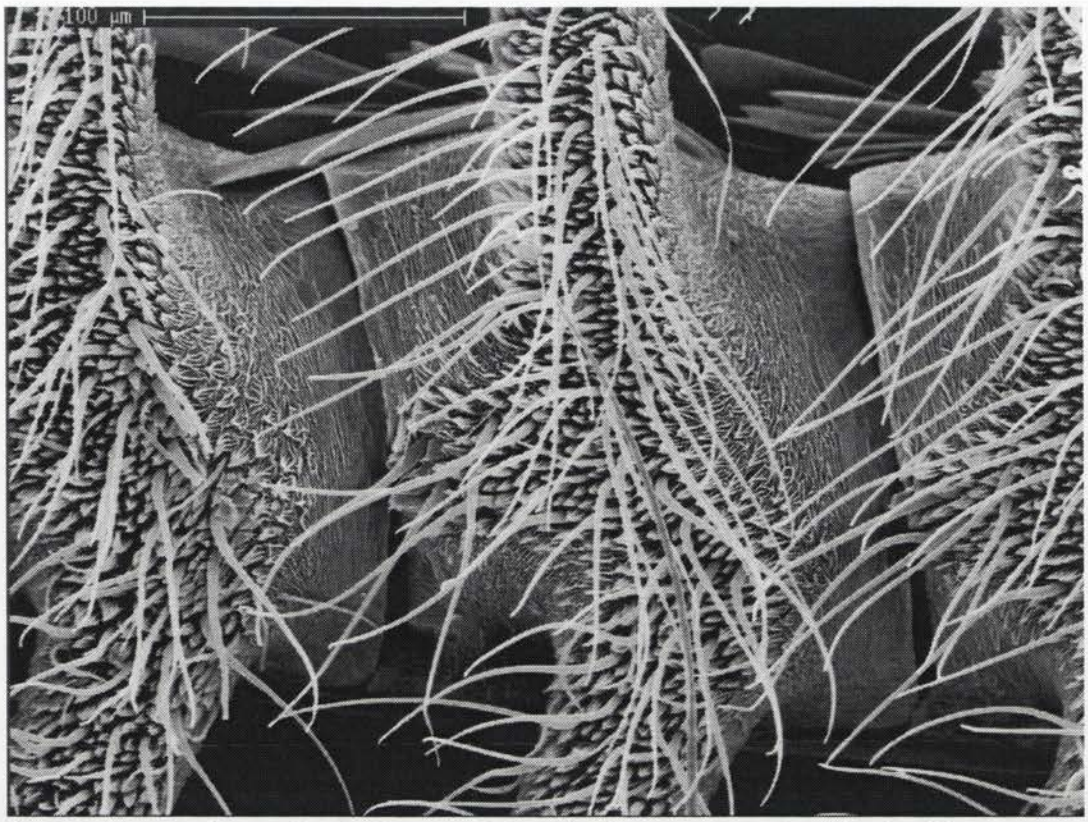

Fig. 258: *Oenosandra boisduvalii* (Oenosandridae), flagellomeres at proximal fourth of ♂ antenna, ventral view (left = distal) – each flagellomere has only a single, median sensory band on its ventral side.

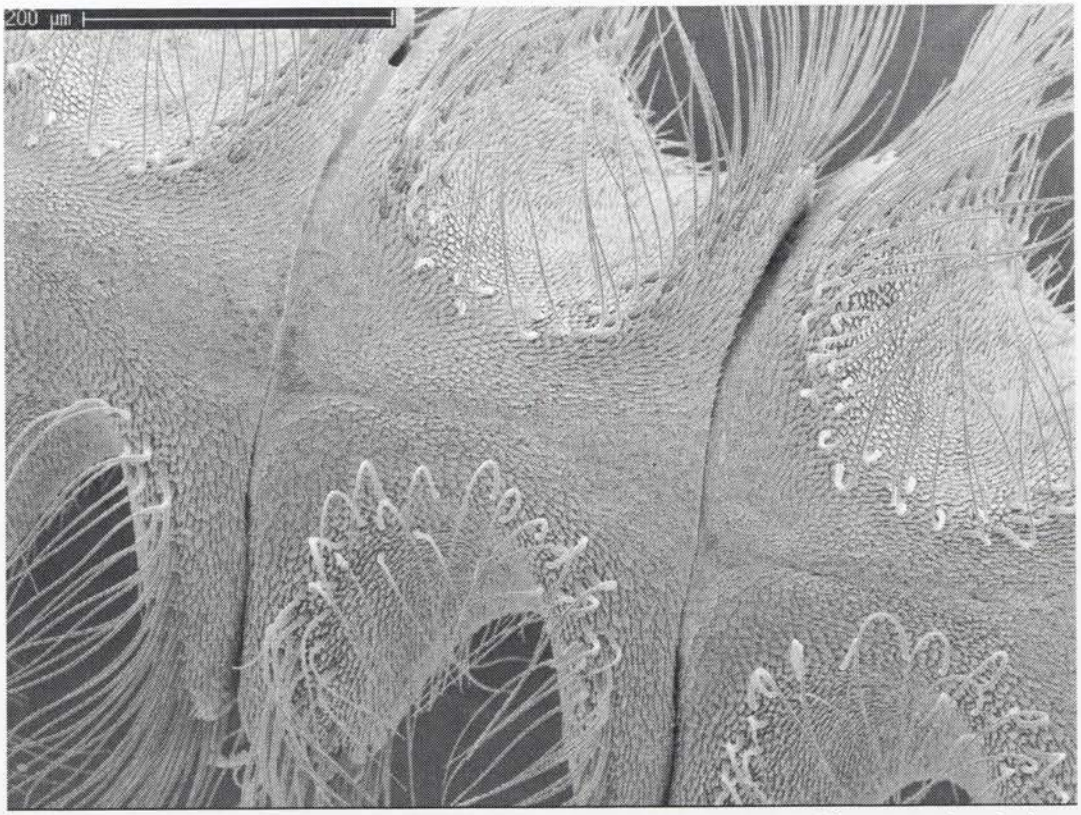

Fig. 259: *Arsenura ciocolatina* (Saturniidae), flagellomeres at basal fourth of ♂ antenna, dorsal view (right = distal) – each flagellomere has a proximal and a distal sensory band, which unite dorsally in an arc.

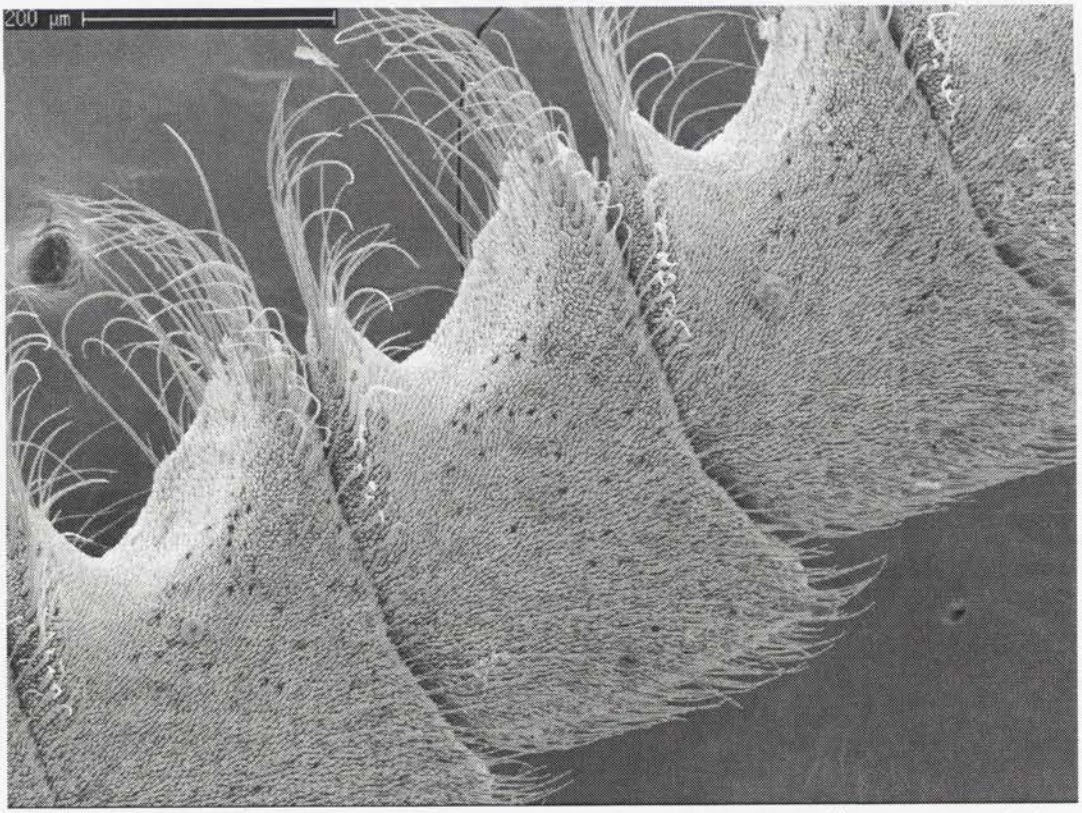

Fig. 260: *Arsenura ciocolatina* (Saturniidae), flagellomeres at distal fourth of ♂ antenna, lateral view (right = distal) – each flagellomere has a proximal and a distal sensory band, between which numerous sensilla coeloconica (dark spots) are located on the lateral side of the flagellomere "body".

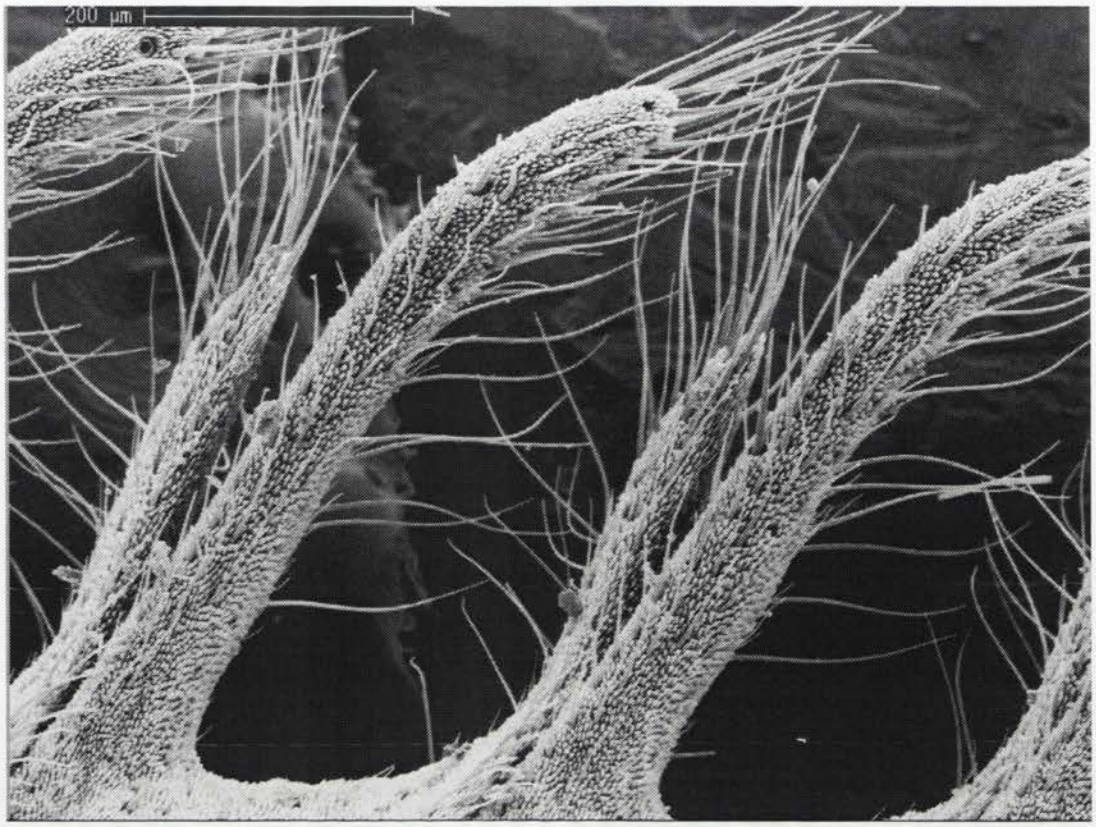

Fig. 261: *Bathyphlebia eminens* (Saturniidae), rami of flagellomeres at middle of ♂ antenna, ventral view (right = distal) – each antennal flagellomere has a proximal and a distal sensory band, each of which extends onto (and around) a lateral protrusion (= quadripectinate antenna).

III.6) THE PRE-IMAGINAL STAGES

In Lepidoptera with a shortened adult lifespan the caterpillars with their various instars (first instar larva [L1] to penultimate instar larva [Lp] and mature larva [Lm]) constitute the main physically active phase of the lifecycle. Yet our limited knowledge of adult moths is vastly larger than that of caterpillars, not to mention eggs or pupae. This is primarily caused by the limited availability of pre-imaginal instars, as only the adult moths are collected easily and in large quantities, usually by light-trapping. Most scientific collections house hundreds of thousands of pinned adult specimens, but often no more than a handfull of pre-imaginal instars.

The primary activity of caterpillars is obviously feeding, which in some taxa of the bombycoid complex with rapid larval development (e.g., many Sphingidae) takes place continuously during day and night. Consequently, mouthparts and associated sensory structures are particularly well developed and differentiated. Compared to many other animals, caterpillars are relatively slow-moving, which makes them easy prey for predators and parasitoids. Large numbers of offspring, avoidance of exposure, camouflage and occasionally defence structures appear to be the main mechanisms of protection. The latter two greatly influence the appearance of the externally feeding caterpillars of the bombycoid complex, and the larger the caterpillars are, the stronger these influences are. This leads to a strong adaptation and modification of the later, larger caterpillar instars in particular, which often possess highly derived structures, e.g., eye-spots and characteristic tufts of hairs. These derived structures have significance for phylogenetic hypotheses about younger taxa (e.g., at the level of species groups and genera) and are highly valuable characters for taxonomic diagnoses. At the same time these adaptations frequently result in the independent evolution of similar appearances (e.g., the gain and loss of secondary setae, the formation of verrucae and scoli, the development of camouflaging patterns and body shapes), and the strong modifications can obscure characteristics of older taxa (e.g., at the tribal and family level). Both of these tendencies decrease the value of the appearance of older caterpillar instars for higher phylogenetic hypotheses, but nevertheless it is typically caterpillars of the late instars that are preserved in collections due to their high diagnostic value at species level and because it is the larger caterpillars that get noticed in the environment most frequently.

The younger caterpillar instars, in particular the first instar, are more suitable for phylogenetic hypotheses of older taxa, as shared modifications are not yet obscured by the subsequent adaptations of the later instars. Younger instars are, however, scarce in collections as they generally have to be reared from eggs. With short-lived, non-feeding taxa of the bombycoid complex this is relatively easy as females collected at light have already mated in most cases and readily lay eggs in captivity. While the host plant might be unknown and hence the rearing of the caterpillars might fail, first instar caterpillars can always be hatched from such eggs. However, for most species of the bombycoid complex females are much more rarely collected at lights than males, and for quite a number of species the females are still unknown (e.g., *Gephyroneura cosmia* and *Omphaliodes obscura* in the Anthelidae). By collecting live females I obtained a substantial number of first instar caterpillars of different anthelid species over time, but, expectedly, this was not possible for all the species included in my phylogenetic hypotheses. Gathering first instar caterpillars of critical taxa in the cosmopolitan bombycoid complex was even more difficult, and as with Anthelidae I failed to obtain sufficient material for a comprehensive study of larval characters in the bombycoid study.

First instar caterpillars of the bombycoid complex typically range from about 2-10mm in size and their accurate examination requires high magnification. While setal arrangements (chaetotaxy) can still be observed by light microscopy, the laborious use of a SEM is advisable for the detailed examination of most structures. Hardly any such studies have been published for taxa of the bombycoid complex so far. In fact, even information on chaetotaxy in the bombycoid complex is surprisingly scarce. Chaetotaxy is often perceived as particularly valuable for systematic studies (e.g., Scoble 1995), but in my opinion its value is largely diagnostic, not phylogenetic. Differences in chaetotaxy typically consist only of shifts in the relative position of setae or the loss of individual setae, both of which are simple modifications with little if any indications of homology. Further, only the relative position of these setae indicates their homology, differences in structural characteristics do not identify individual setae. In these respects the shortcomings of the use of chaetotaxy are the same as those of wing venations.

Chaetotaxy is concerned with the naming of so-called "primary setae" and "punctures" based on topology. It refers to those setae and punctures that are present in first instar caterpillars only and highly conserved in their location in different taxa.

Other setae, which occur in later instars only and are not as conserved in their location, are referred to as "secondary setae". Such secondary setae, as are not present in the first instars of other taxa, occur in Anthelidae from the first instar on already (Figs 262, 263). In first instar caterpillars most but not all of these secondary setae are located together with primary setae on wart-like protrusions (verrucae), but in later instars they are scattered over the entire integument (including the headcapsule) and their number increases dramatically. This hinders the recognition and homologization of primary setae. Only the verrucae with multiple setae indicate the location of the primary setae within the very dense cover of secondary setae.

Given the relatively low phylogenetic value, the difficulties caused by the presence of "secondary setae" even in first instar caterpillars of Anthelidae, and the lack of first instar caterpillars for many taxa, I do not use characters of chaetotaxy for my phylogenetic analyses, with one exception. In the following section I define those differences of structures as characters, which I believe to be phylogenetically informative.

None of the following characters relates to the other pre-imaginal stages of Lepidoptera, the egg and the pupa. The eggs of the few species I examined with a SEM (Fig. 264) did not reveal any differences with good indications of their homology, only a few minor differences in the details of the surface pattern. The chorion of the anthelid egg has a pattern of irregular, multi-cornered (5-7 corners) cells formed by ridges (Fig. 265), and the corners of these cells have a pore-like depression (aeropyle) within a ring-shaped protrusion (Fig. 266). The basic, simple pattern of multi-cornered cells is caused by the follicle cells below (Fehrenbach 2003) and is very common for Lepidoptera and even other insect orders. The sculpturing of the micropylar area, which can be diagnostic at the species level, did not show any significant differences suitable for phylogenetic hypotheses.

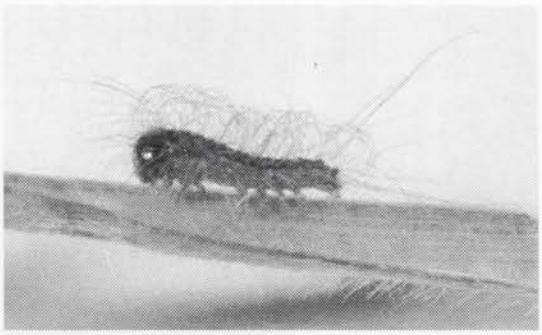

Fig. 262: *Anthela ferruginosa* (Anthelidae), caterpillar (L1) – first instar caterpillar with many "secondary" setae.

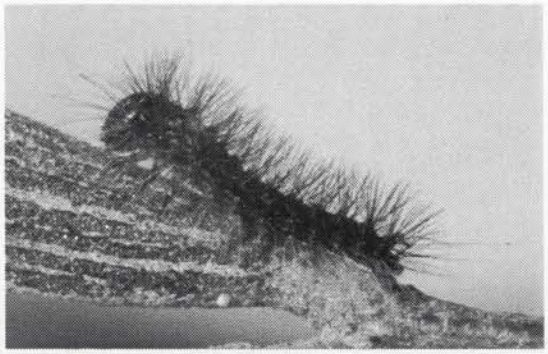

Fig. 263: *Anthela tetraphrica* (Anthelidae), caterpillar (L1) – first instar caterpillar with many "secondary" setae.

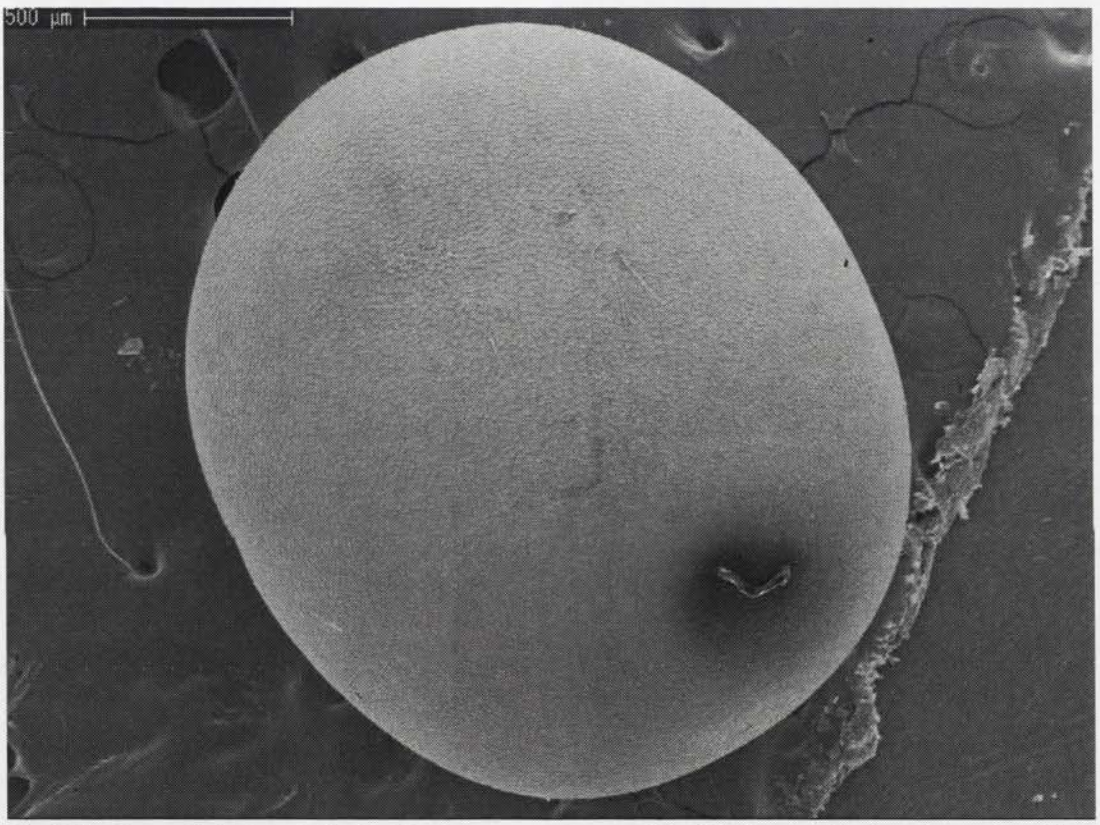

Fig. 264: *Chenuala heliaspis* (Anthelidae), egg – oval egg of the "flat" type with the micropyle at the centre of the broader end (bottom right).

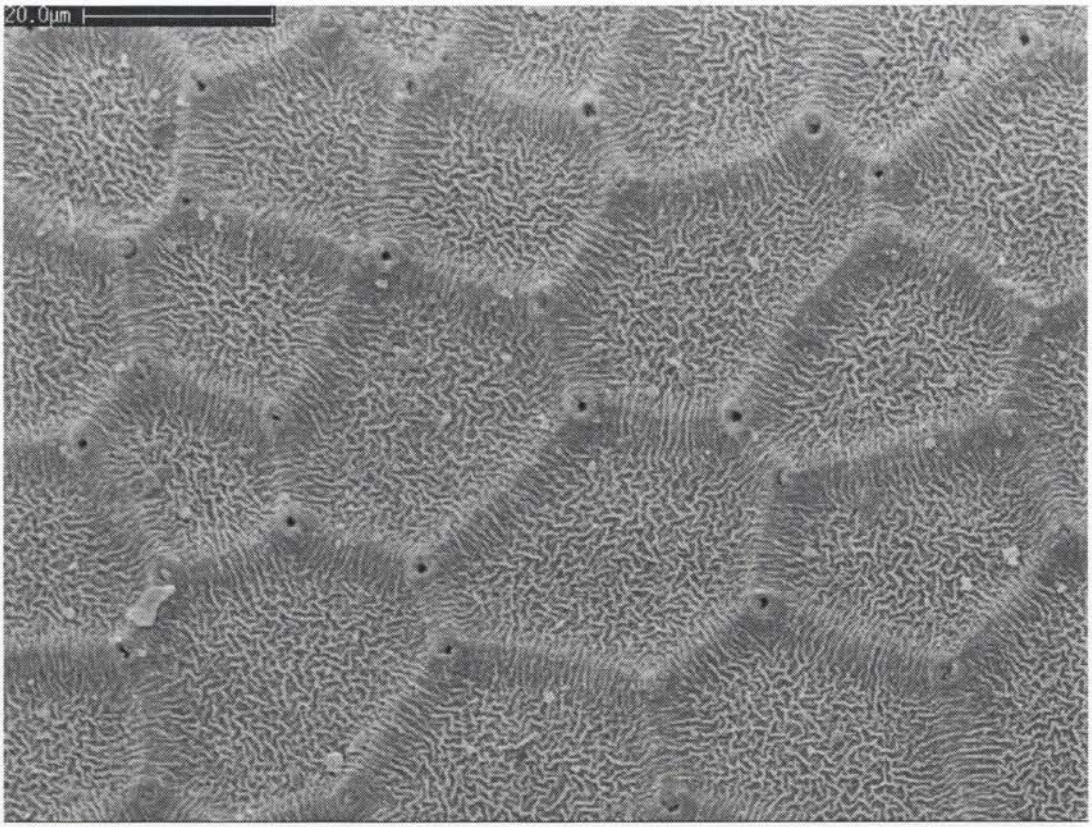

Fig. 265: *Chenuala heliaspis* (Anthelidae), egg – chorion pattern consisting of multi-cornered cells formed by ridges; note the pore-like depression in each corner.

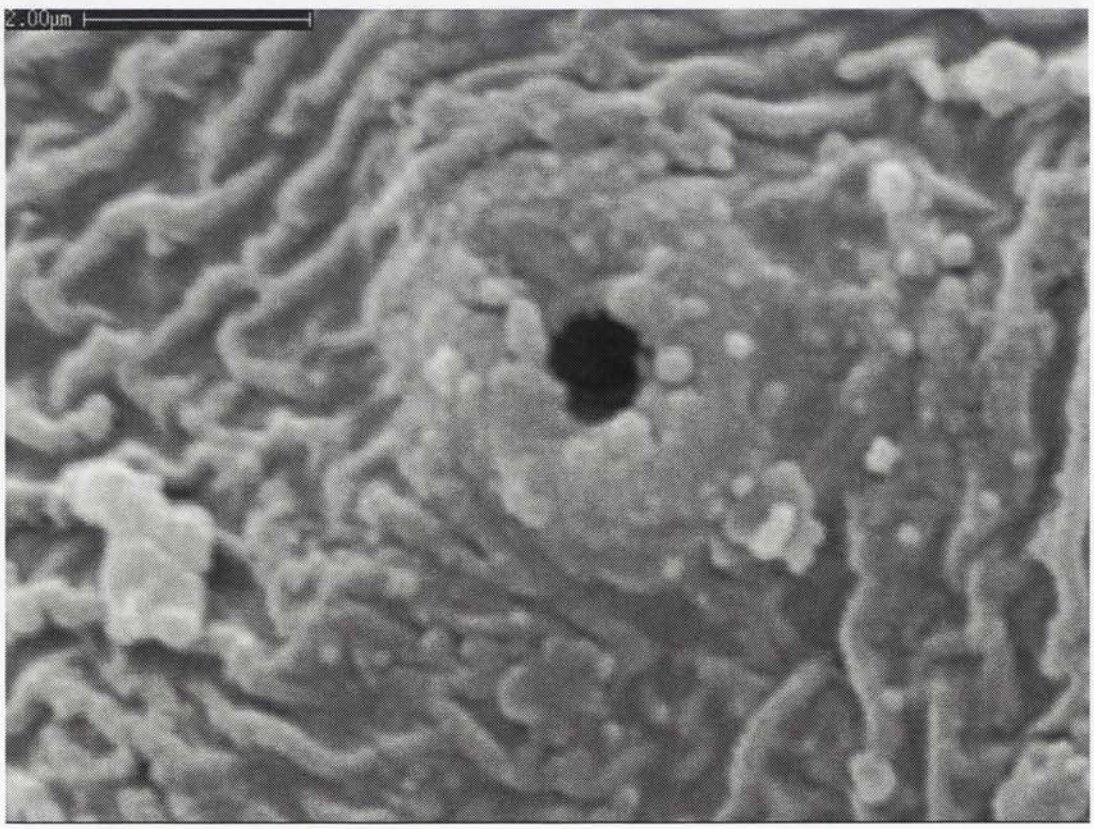

Fig. 266: *Chenuala heliaspis* (Anthelidae), egg – pore-like depression in the centre of a ring-shaped protrusion on the ridges of the chorion pattern.

III.6.1) The vesicles on the integument of anthelid caterpillars

The cuticular integument of caterpillars is the interface to the environment and naturally carries numerous structures of different types, e.g., sensilla, cuticular protrusions and secretory structures. Secretory structures are typically restricted to relatively few locations within an individual, e.g., the two glands on the sixth and seventh abdominal segments in Lymantriidae (Fig. 267) or the scoli of some Saturniidae (e.g., Deml & Dettner 2002). Further, their number and location does not change with different instars. The caterpillars of Anthelidae are exceptional in that they have hundreds of secretory structures scattered over large areas of the integument, which differ between instars in number and seemingly in location.

From the second instar on anthelid caterpillars are literally covered by vesicles, which appears under the light microscope as minute, strongly reflective drops of a clear liquid (Fig. 269). The number of these vesicles increases significantly with subsequent moults (Figs 269, 270, 271), and the vesicles are fully developed prior to the casting of the old skin during a moult (Fig. 272). The total number of vesicles varies not only between different instars, but between species, too. Except for the ventral side, legs, mouthparts and verrucae, these vesicles are distributed over the entire integument, including the headcapsule (Fig. 273) and intersegmental folds. Their density appears to be lower in strongly setose areas, or such that become strongly setose in later instars (compare Fig. 269 with Fig. 334). No groupings of vesicles are apparent, their distribution within the aforementioned limits is seemingly at random. With increasing numbers and uniform appearance it is difficult to keep track of the locations of individual vesicles. The actual vesicles are exchanged with every moult (they remain on the cast skin), but the source of the vesicles is likely to remain in the same position. Nevertheless, my simple attempts to track these sources by photography failed – vesicles present in a certain location on one specimen were absent in the same location of the next instar of the same specimen, while "new" vesicles were present in other locations. I cannot rule out that the sources of vesicles changed their position in different instars, but it seems more likely that they are replaced by vesicles from different sources. Observations on more specimens should be made to verify this unexpected turn-over or relocation of vesicles.

The vesicles of cast skins do not evaporate, even after years. They do, however, collapse after a couple of months, leaving an empty "shell" behind. Similarly, the vesicles are still preserved in 40 year old ethanol-fixed specimens. Probing the vesicles of a living caterpillar or a cast skin with a pin gives further indications that the vesicles are not small drops of a liquid, but consist of a firmer substance. It is surprisingly difficult to dislodge any of these vesicles. Using a pointed insect pin to push away any vesicles fails in most cases, even though the proportions of the pin to the vesicle are comparable to that of a large tree trunk to a soccer ball. If hit by the tip of the pin centrally from above or from the side the vesicles moves sideways and the pin passes it. If hit laterally with the side of the pin in an attempt to scrape the vesicles off, the cuticle around the vesicles bends and the pin passes above the vesicles. I attempted to puncture the vesicles with a drawn-out glass capillary for micro-injections using a micro-manipulator, but even with this extremely thin tip and the precise movements of a micro-manipulator it was not possible to puncture or dislodge the vesicles. They appear to be extremely firmly "glued" to the cuticle.

I attempted to dissolve the vesicles by washing caterpillars in hexane (non-polar, organic solvent) as well as in acetone (polar, aprotic [no exchange of protons], organic solvent), but neither of these solvents did so. Even after being stored in a hexane-chloroform mixture (4:1; wax solvent) for a month, the vesicles were still present and spherical. In contrast, the application of acetone quickly "discharged" the vesicles, but failed to dissolve the remaining collapsed "shells" (Figs 292, 293). However, vesicles are easily scraped off with a pin moistened with either of the two solvents.

Dr. Victoria Haritos (CSIRO Entomology) attempted to analyse a sample of more than 50 vesicles collected into hexane from an *Anthela ocellata* caterpillar. After processing and blowing down the solvent, an aqueous fraction became apparent, which was taken off and remains to be analysed. Gas chromatography of the non-polar fraction showed minute amounts of Palmitate (a 16-carbon saturated fatty acid), Stearate (a 18-carbon saturated fatty acid), Oleate (a 18-carbon unsaturated fatty acid) and other fatty acids of similar length, as well as small amounts of several longer hydrocarbons (25 to 30 carbons) not typically found in insects (Fig. 294). At least the shorter fatty acids are likely to be contaminations picked up with the pin from the caterpillar integument.

I further examined these vesicles qualitatively by x-ray microanalysis with an Energy Dispersive X-Ray Analyzer (EDXA) in a Cryo-SEM. The resulting weak spectrum (Fig.

295) indicates no heavier elements than phosphorus. This means that no inorganic substances are present within the vesicle, but it does not characterize the content of the vesicles any further as the elements of organic substances are too light to allow qualitative or quantitative analyses by EDXA.

Examination of the vesicles by Cryo-SEM showed that only minor differences in size exist and that most of them are almost perfectly spherical (Fig. 274). Many of these vesicles have a small protrusion at their most distal point, which might be formed by a substance released from the vesicles at that location (Figs 275, 277, 278). The vesicles "sit" directly on the integument, which is covered by closely approximated protrusions. Occasionally these protrusions end in a finger-shaped to hair-like tip (Figs 279, 280), but such protrusions with and without a hair-like process occur in caterpillars of taxa without such vesicles, too (Figs 281, 282). The attachment of the vesicles is difficult to observe and only visible at a certain viewing angle (proximo-lateral). Compared to the diameter of the vesicle (about 20µm), the diameter of the very short, connecting "stalk" is narrow (about 3µm) (Figs 285). It appears to have the shape of a socket on which the vesicle rests (Figs 286, 287, 288). During the x-ray microanalysis several vesicles were dislodged by the electron beam. The remaining "attachments" are damaged and do not provide much information. They usually consist of a central "stub" surrounded by a ring of a substance, which appears to have "melted" onto the surrounding protrusions of the cuticle (Fig. 289). Judging from the size of the central stub it is a remnant of the short, connecting "stalk", while the surrounding substance seems to be a remnant of the outer wall of the vesicles, which broke off from the central "stalk". In one case the damage was less severe and the outer wall and the "stalk" were not disconnected from each other. The central area, beneath which the "stalk" is presumably located, has an opening of approximately 2µm in diameter. From this opening a peg protrudes slightly (Fig. 290). I also examined vesicles that I had treated with acetone and in some cases manually damaged prior to the examination in the SEM. A picture of a remnant of such a damaged vesicle shows the presence of an outer wall and the central opening very clearly (Fig. 291), but only a minute part of the peg's apex is visible at high magnification due to the viewing angle. In a collapsed vesicle the outer wall is draped over the attachment area, but the shape of the central opening as well as the peg are recognizable (Fig. 292). All vesicles that had been treated with acetone are entirely collapsed and appear as an empty sack with folds (Figs 292, 293).

From all these above observations I conclude the following about the nature of these vesicles: Most parts of the integument of anthelid caterpillars are covered with minute, round vesicles from the second instar on. Like secondary setae, the number of these vesicles increases with older instars and the vesicles are randomly arranged. Each vesicle has an outer, probably membranous wall and is attached to the integument by this wall as well as by an external substance at the base of the vesicle. This external substance attaches the vesicle unusually firmly, while the connecting thin outer wall keeps the vesicle in place if the external substance has been dissolved by a polar or non-polar solvent. The contents of the vesicle is solid at room temperature and probably a polar, organic substance. This substance easily dissolves in acetone, but not in non-polar solvents like hexane. At room temperature the substance sublimates very slowly, probably through a minute opening in the distal end of the vesicle. The proximal end of the vesicle opens through a very short stalk into the integument, from which a peg protrudes slightly into the lumen of the vesicle.

These vesicles are present in caterpillars of all anthelid species, except for the genus *Munychryia* and possibly all other Munychryiinae, of which the caterpillars are yet unknown. Examination of the caterpillar of *M. senicula* by (Cryo-) SEM (L1 and L4) revealed no traces of vesicles or remnants of structures from which they might originate in other taxa. The integument surface of *M. senicula* differs from that of all other examined caterpillars, in as much as it does not have any protrusions, but instead consists of plaques (Fig. 283). No long setae are present, but instead numerous small, club-shaped pegs occur, which protrude from a large socket and are most probably reduced setae (Fig. 284).

The occurrence of vesicles in all Anthelinae irrespective of the host plant (e.g., Poaceae, Proteaceae, Mimosaceae and Myrtaceae) argues for a *de novo* synthesis of the vesicle contents. The function of the vesicles is unknown, but their obligatory occurrence argues for their importance. The vesicles might be a for caterpillars unusual way of disposing harmful chemicals, but the external "storage" of substances in vesicles and the occurrence independent of host plant usage make this explanation unlikely. Chemical communication is another possible function, but while anthelid caterpillars

can occasionally be (at least in captivity) gregarious (e.g., *Anthela nicothoe*), no "semi-social" behaviour, as occasionally found in other families of the bombycoid complex (e.g., *Malacosoma* spp. (Lasiocampidae), *Arsenura armida* (Saturniidae), *Andraca theae* (Bombycidae)), occurs. The most likely function is a defensive one, which might be by chemical "camouflage" or deterrence. The higher density of vesicles in more exposed locations as opposed to between hairs fits to this explanation, but simple spatial constraints might play a role in the density of vesicles, too. A constant, slow release of chemicals would suit a deterring function, particularly if the contact with the substance was direct, e.g., with the sensilla of the ovipositor of a parasitoid attempting to deposit eggs on the exposed parts of the caterpillar integument. Likewise, a direct contact of the substance with the mouthparts of ants might have a deterring or "appeasing" effect on these, in Australia, very abundant predators. In contrast, the slow sublimation of such minute amounts seems unlikely to be sufficient for airborne deterrence or camouflage in an open environment.

Fig. 267: *Euproctis baliolalis* (Lymantriidae), caterpillar (L2 or L3) – two unpaired, median glands (yellow arrows) are located on the dorsal side of the sixth and seventh abdominal segments.

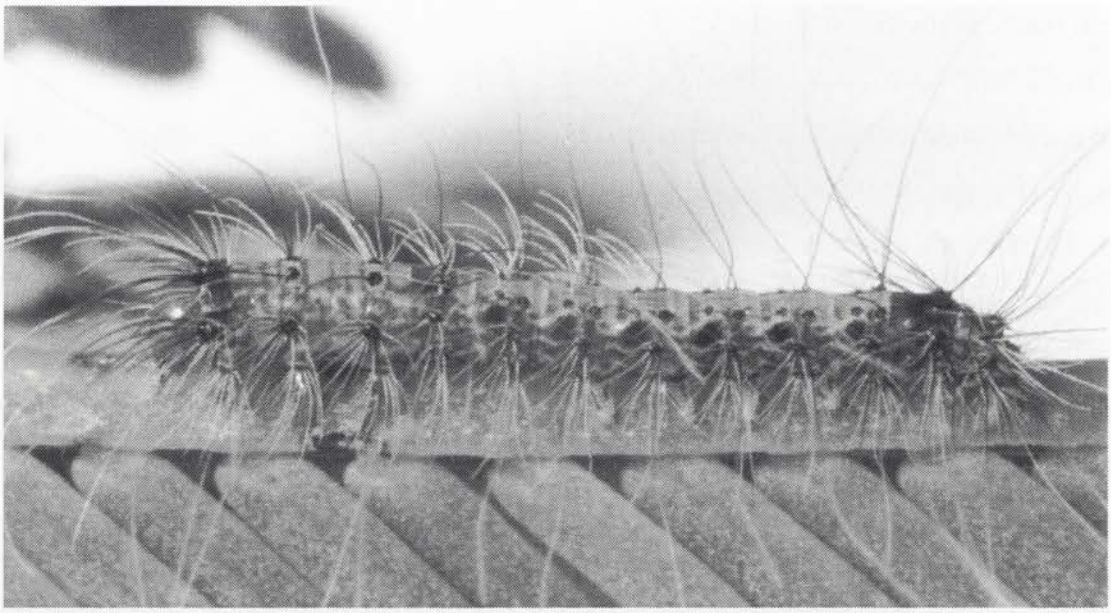

Fig. 268: *Anthela guenei* (Anthelidae), caterpillar (L1) – the integument carries numerous setae on verrucae, but no shiny vesicles.

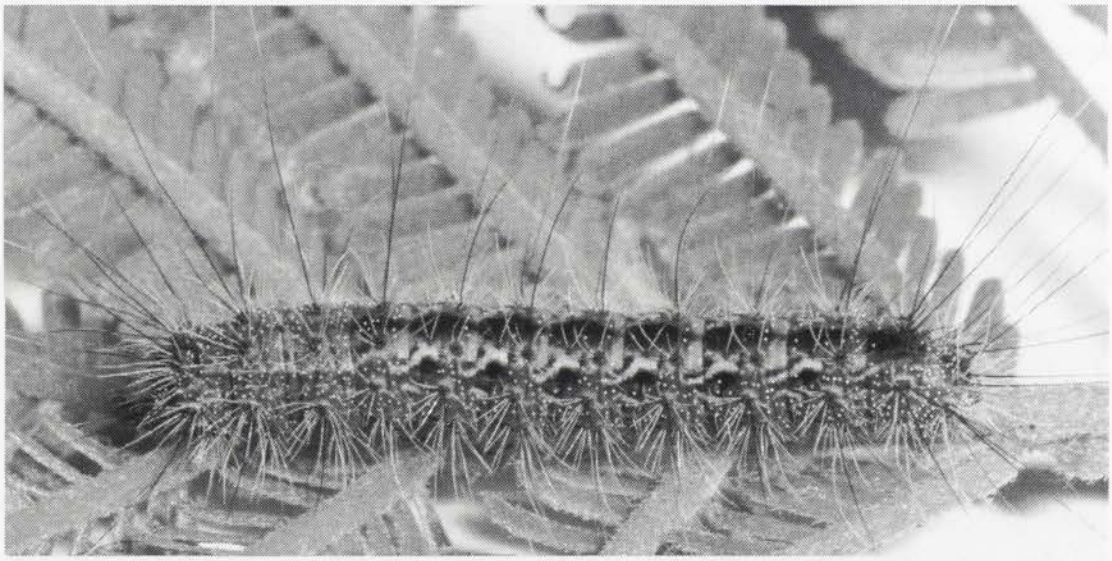

Fig. 269: *Anthela guenei* (Anthelidae), caterpillar (L2) – the integument carries numerous setae on verrucae, as well as a large number of tiny, shiny vesicles.

Fig. 270: *Anthela guenei* (Anthelidae), caterpillar (L3) – the integument carries numerous setae on verrucae, as well as hundreds of tiny, shiny vesicles.

Fig. 271: *Anthela guenei* (Anthelidae), caterpillar (L4) – the integument carries numerous setae on verrucae, as well as hundreds of tiny, shiny vesicles; note the vesicles on the headcapsule.

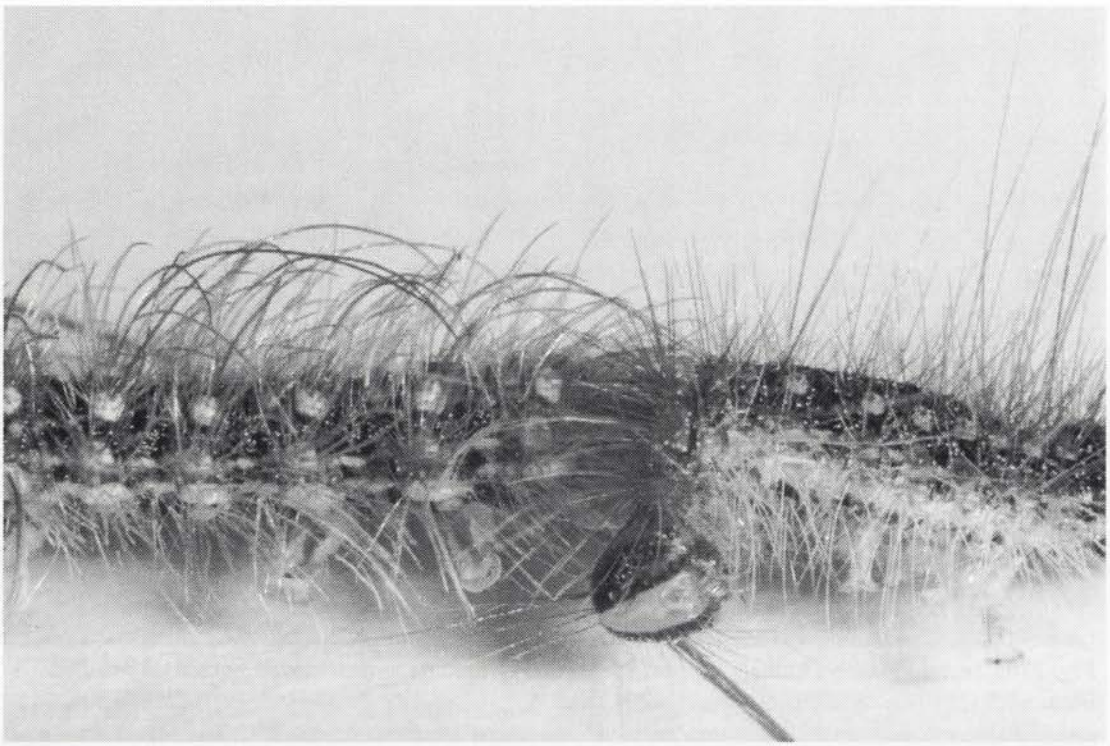

Fig. 272: *Anthela excellens* (Anthelidae), caterpillar (L3) – freshly moulted L3 caterpillar (left) leaving shed L2 skin (right); the minute vesicles (tiny, shiny spots) are fully developed prior to moulting.

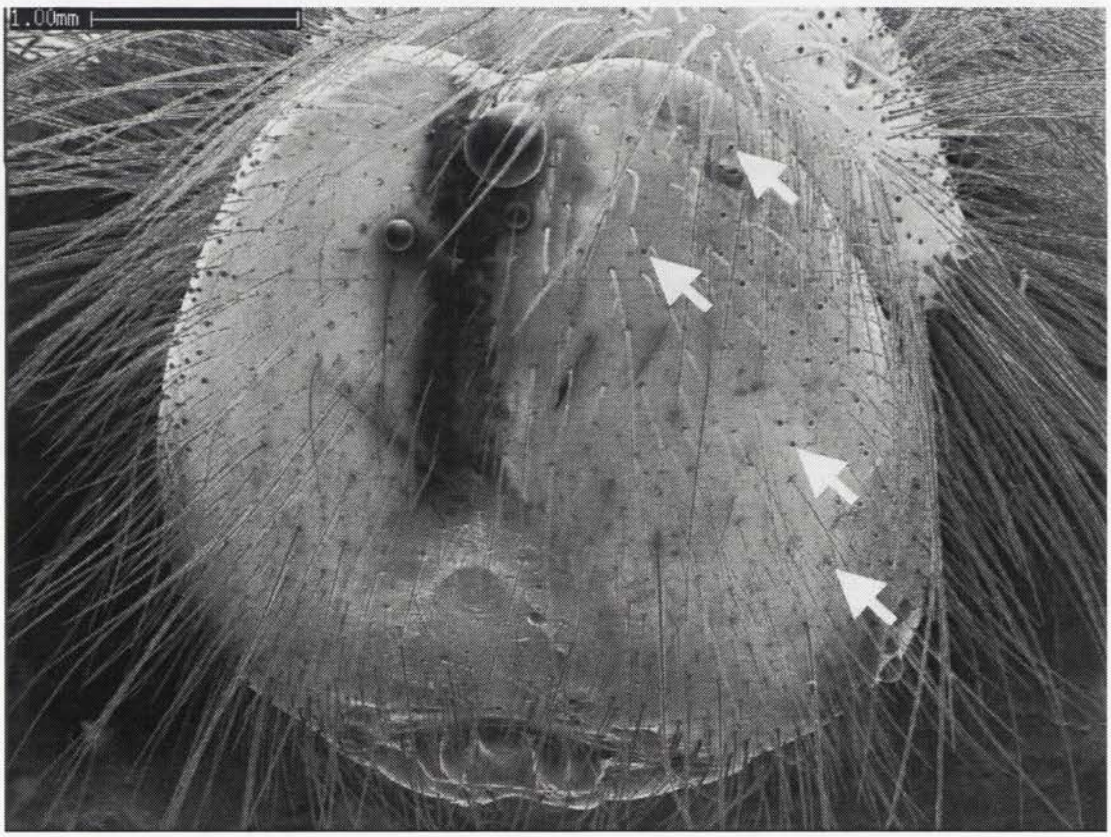

Fig. 273: *Anthela ocellata* (Anthelidae), caterpillar (L4), anterior view – headcapsule covered with secondary setae and minute vesicles (yellow arrows mark a few); the large median droplets are artefacts from freezing and the dark median area is caused by electrostatic charging of the sample.

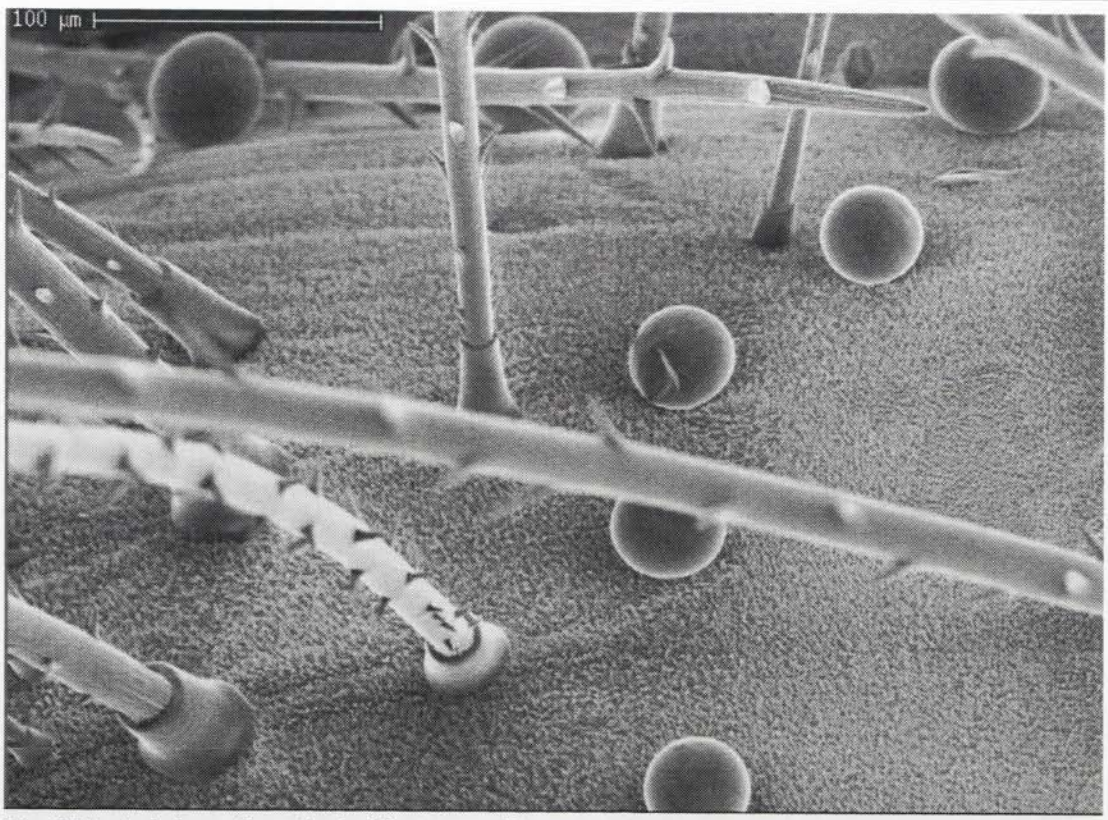

Fig. 274: *Anthela ocellata* (Anthelidae), caterpillar (L4), thorax – the vesicles are of roughly equal size and almost perfectly symmetrically round.

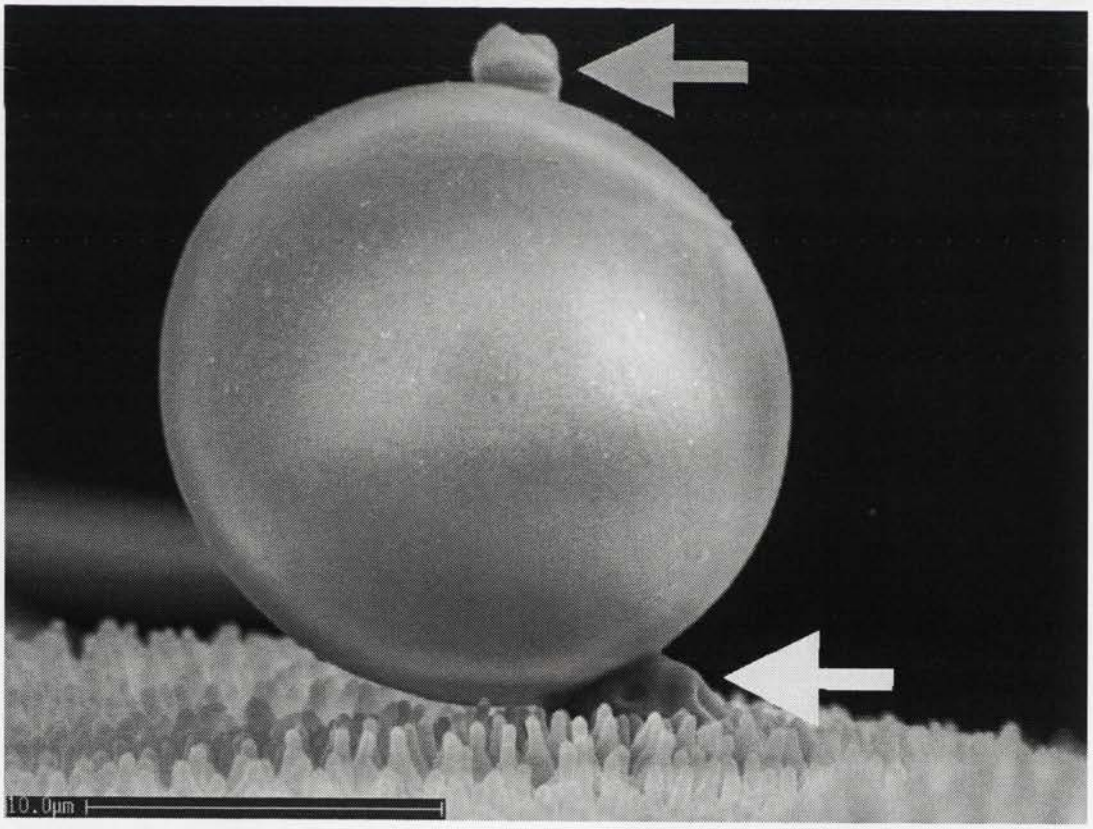

Fig. 275: *Anthela ocellata* (Anthelidae), caterpillar (L2) – the vesicle is attached to a short "stalk" (yellow arrow) and has a small protrusion at its distal end, probably formed by a substance released from the inside (green arrow).

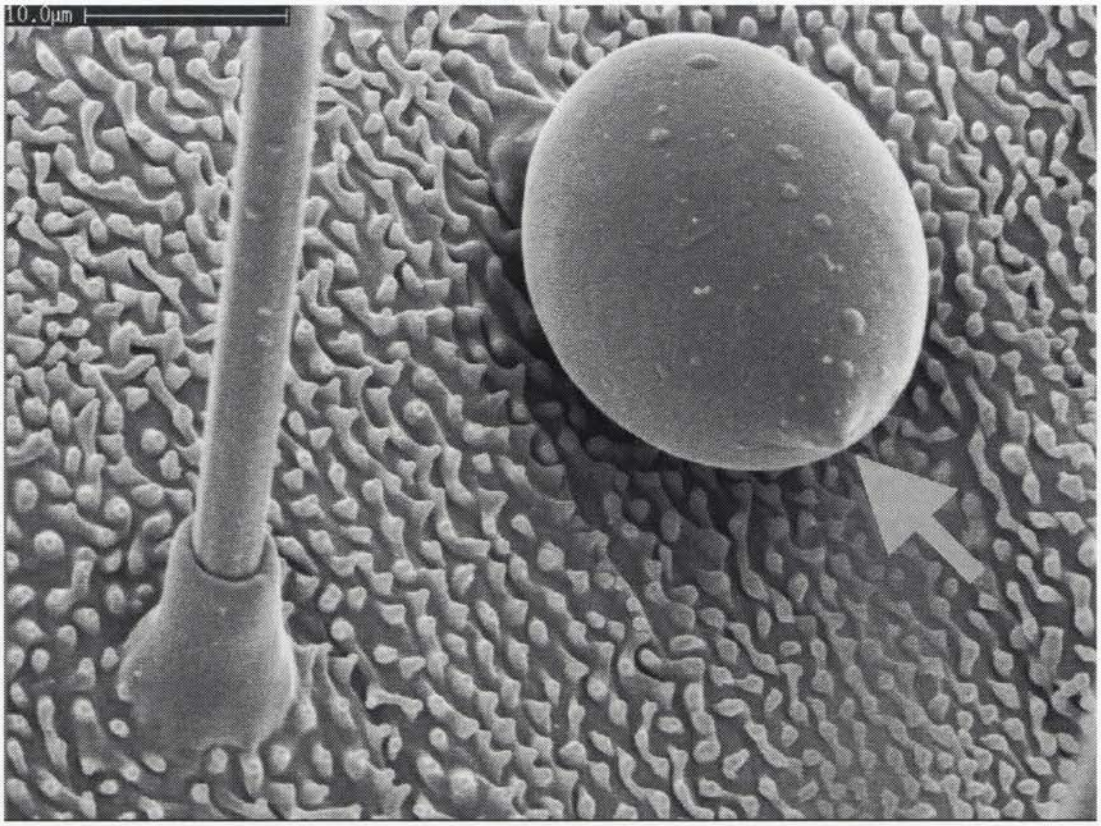

Fig. 276: *Anthela ocellata* (Anthelidae), caterpillar (L2) – the vesicle has a small protrusion at its distal end, probably formed by a substance released from the inside (green arrow).

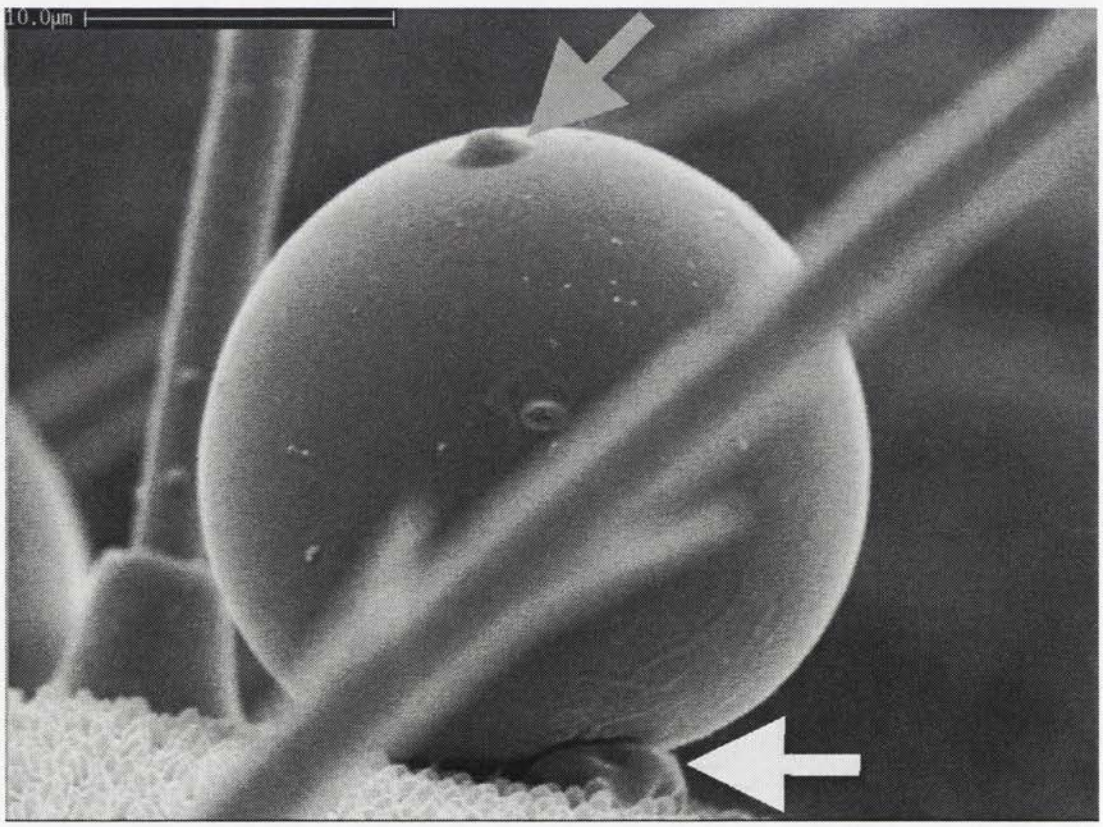

Fig. 277: *Anthela ocellata* (Anthelidae), caterpillar (L2) – the vesicle is attached to a short "stalk" (yellow arrow) and has a small protrusion at its distal end, probably formed by a substance released from the inside (green arrow).

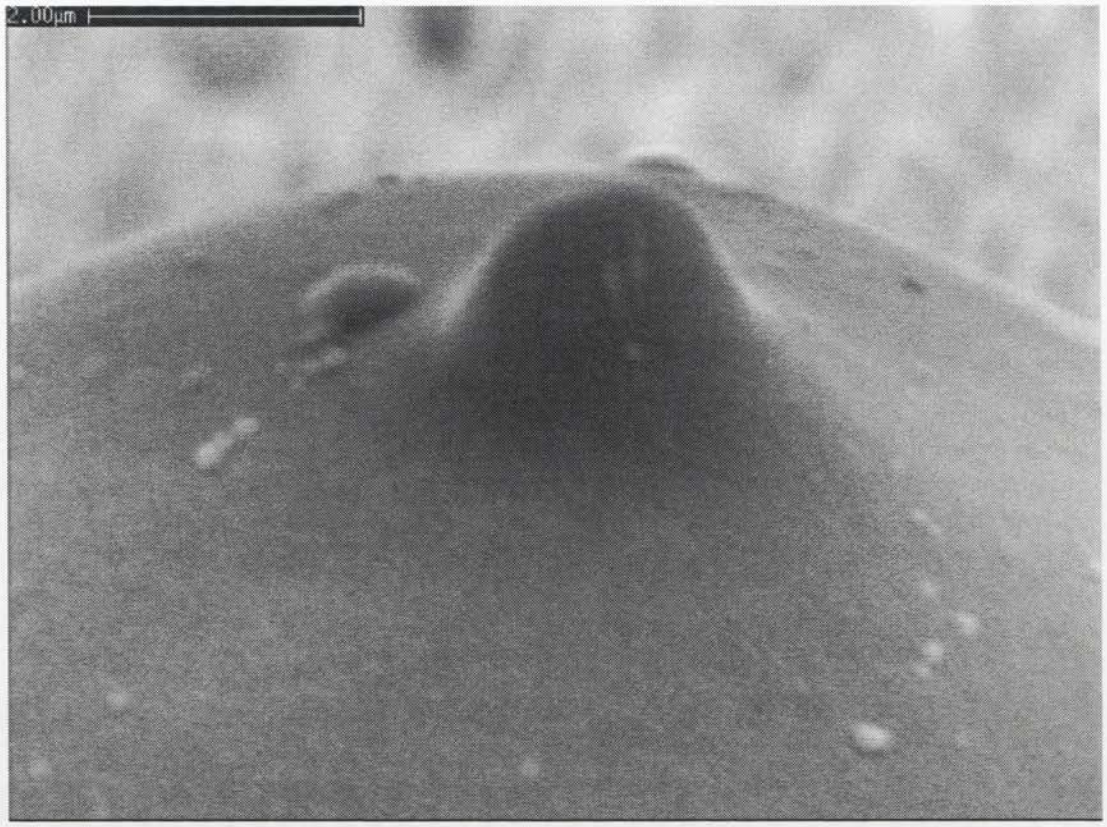

Fig. 278: *Anthela ocellata* (Anthelidae), caterpillar (L2) – small protrusion at the distal end of a vesicle, probably formed by a substance released from the vesicle.

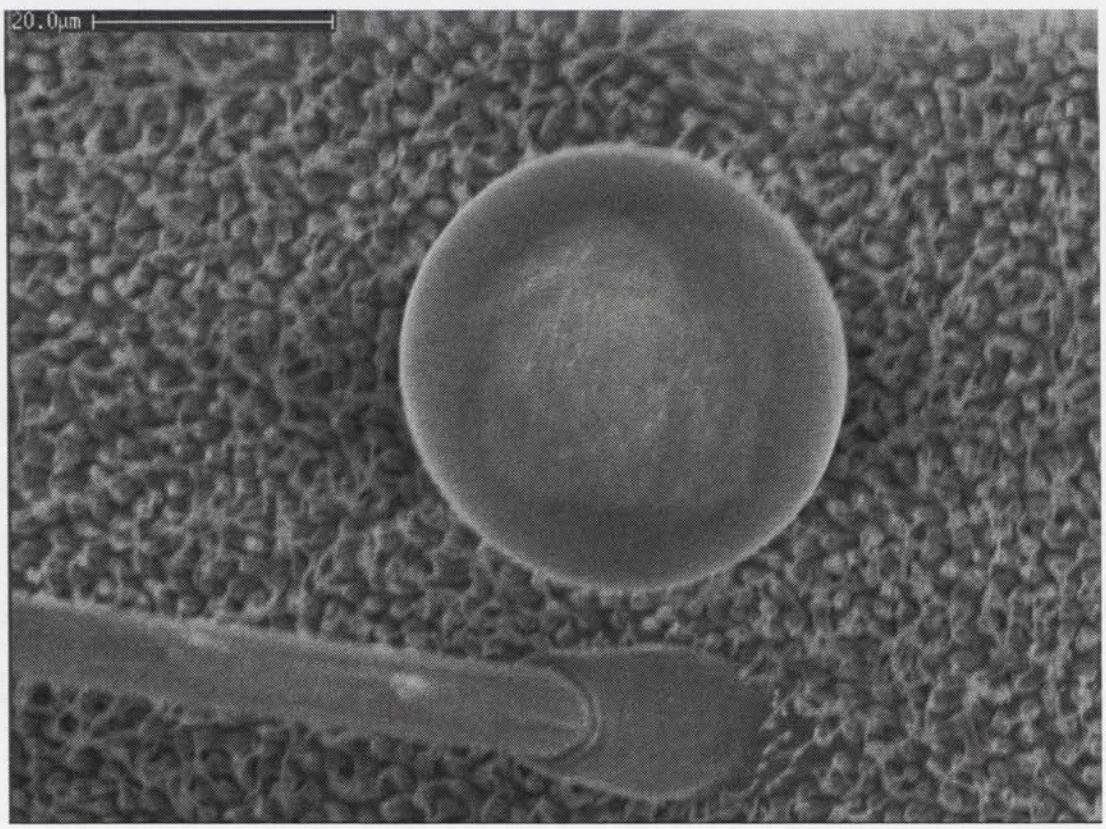

Fig. 279: *Anthela ocellata* (Anthelidae), caterpillar (L4) – the vesicle "sits" on top of tiny, closely approximated protrusions of the integument, which can end in a hair-like tip.

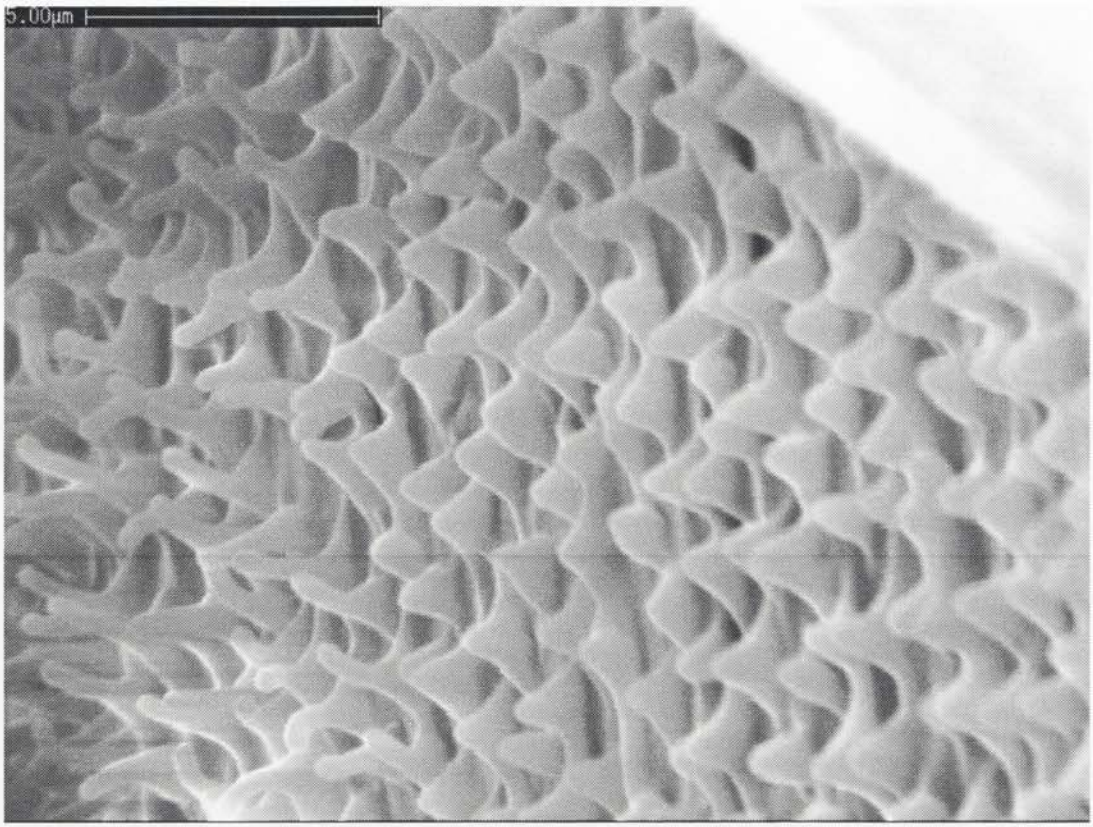

Fig. 280: *Anthela ocellata* (Anthelidae), caterpillar (L2) – the integument has tiny, closely approximated protrusions, which range in shape from blunt cones to cones with an apical, hair-like tip.

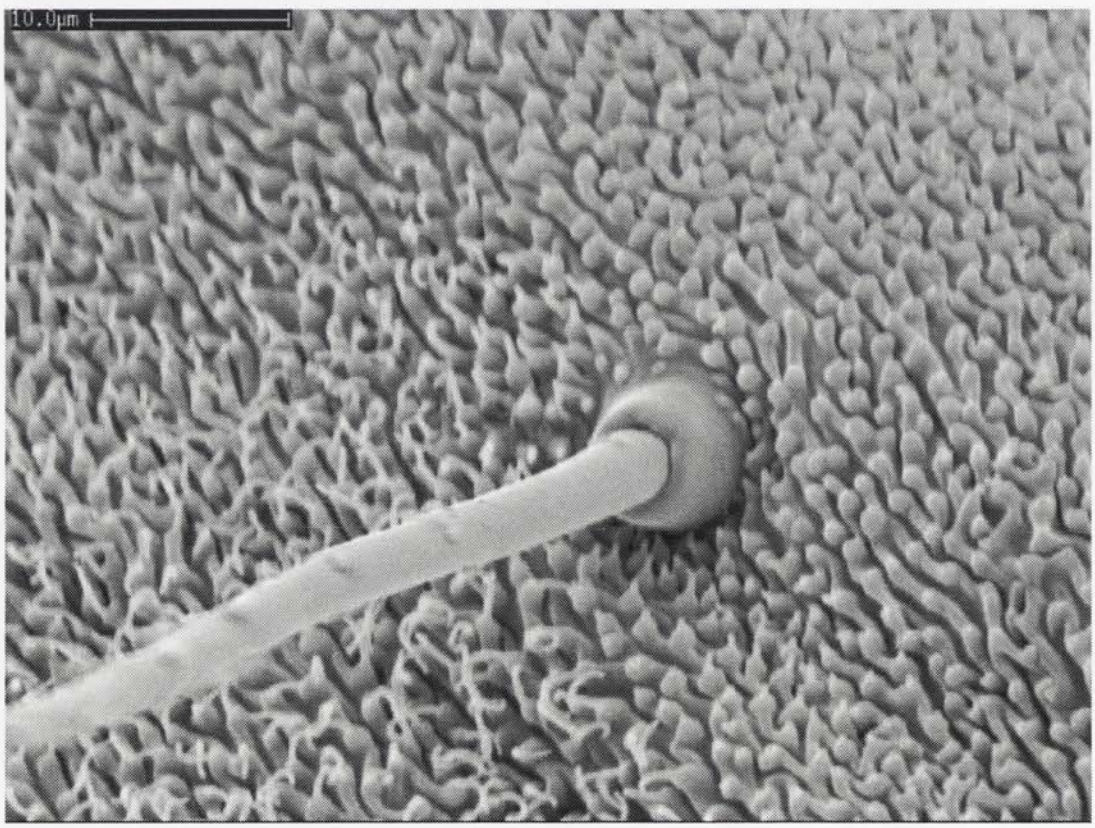

Fig. 281: *Cotana serranotata* (Eupterotidae), caterpillar (L4) – the integument has tiny, closely approximated protrusions, which range in shape from blunt cones to cones with an apical, hair-like tip.

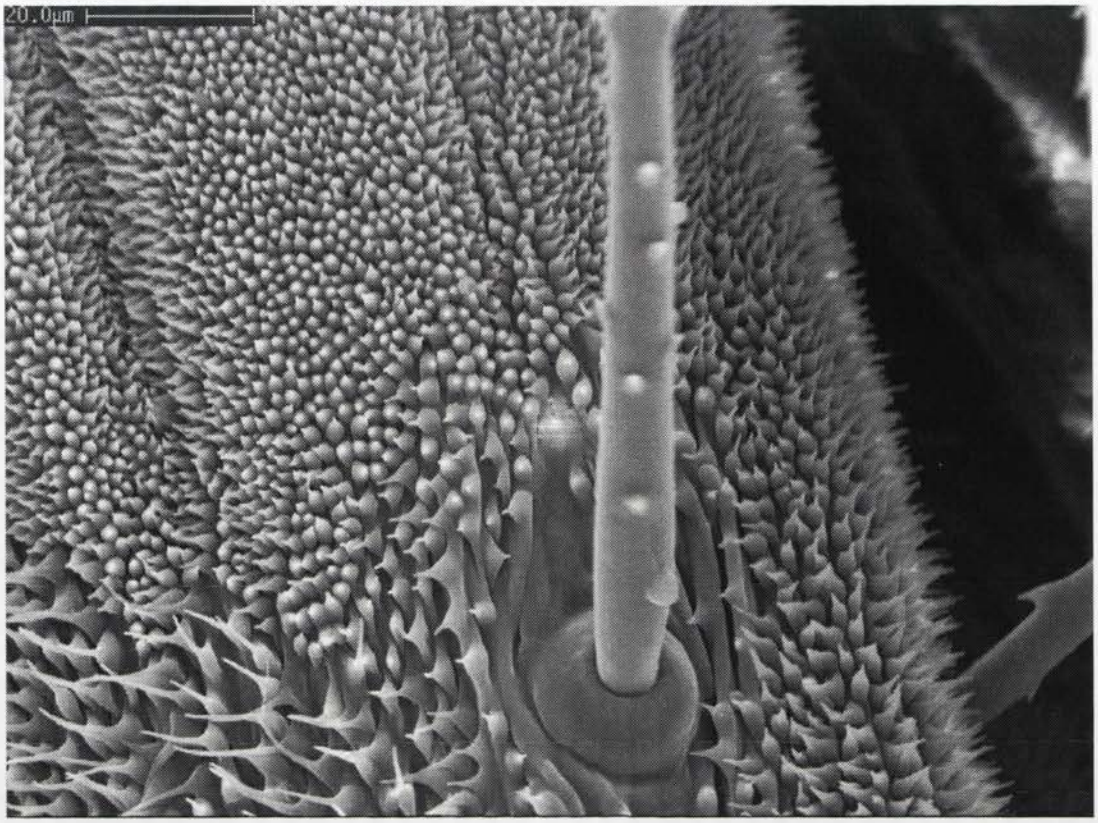

Fig. 282: *Epicoma* sp. (Notodontidae), caterpillar (L4) – the integument has tiny, closely approximated protrusions, which range in shape from blunt cones to cones with an apical, hair- or spine-like tip.

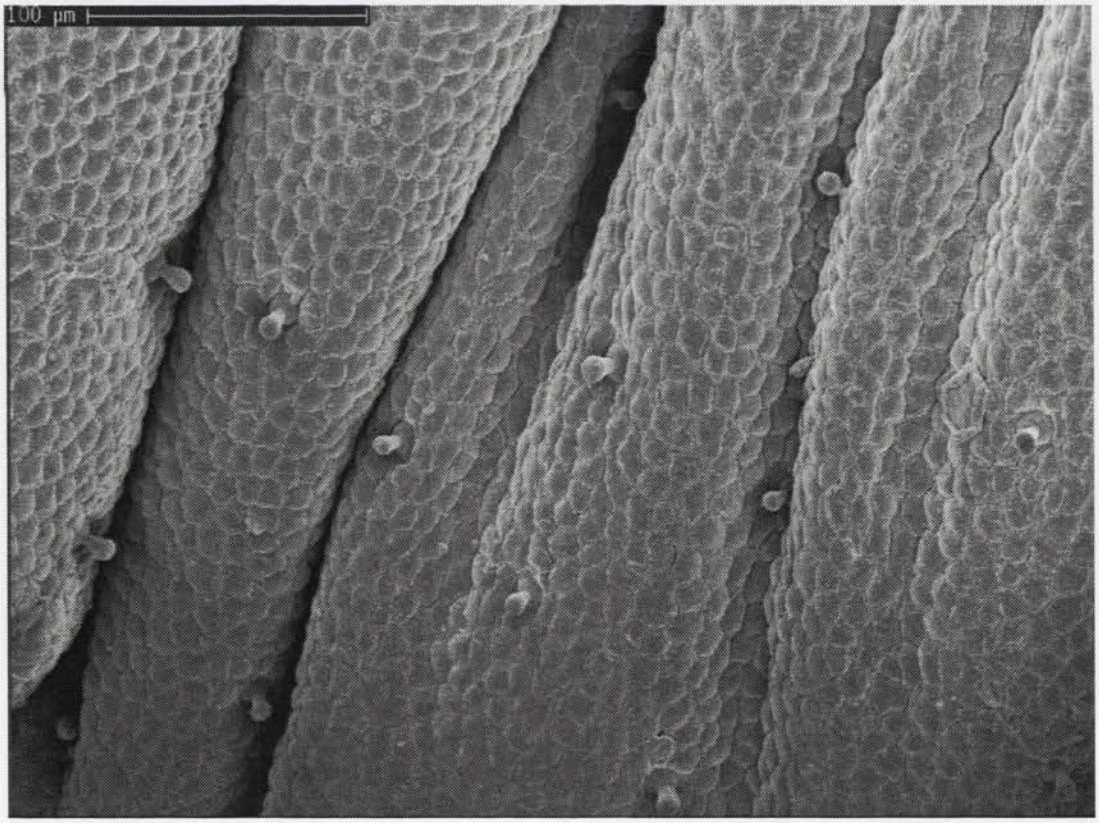

Fig. 283: *Munychryia senicula* (Anthelidae), caterpillar (L4) – the integument surface has no protrusions, but consists of plaques; note the numerous, short, club-shaped setae.

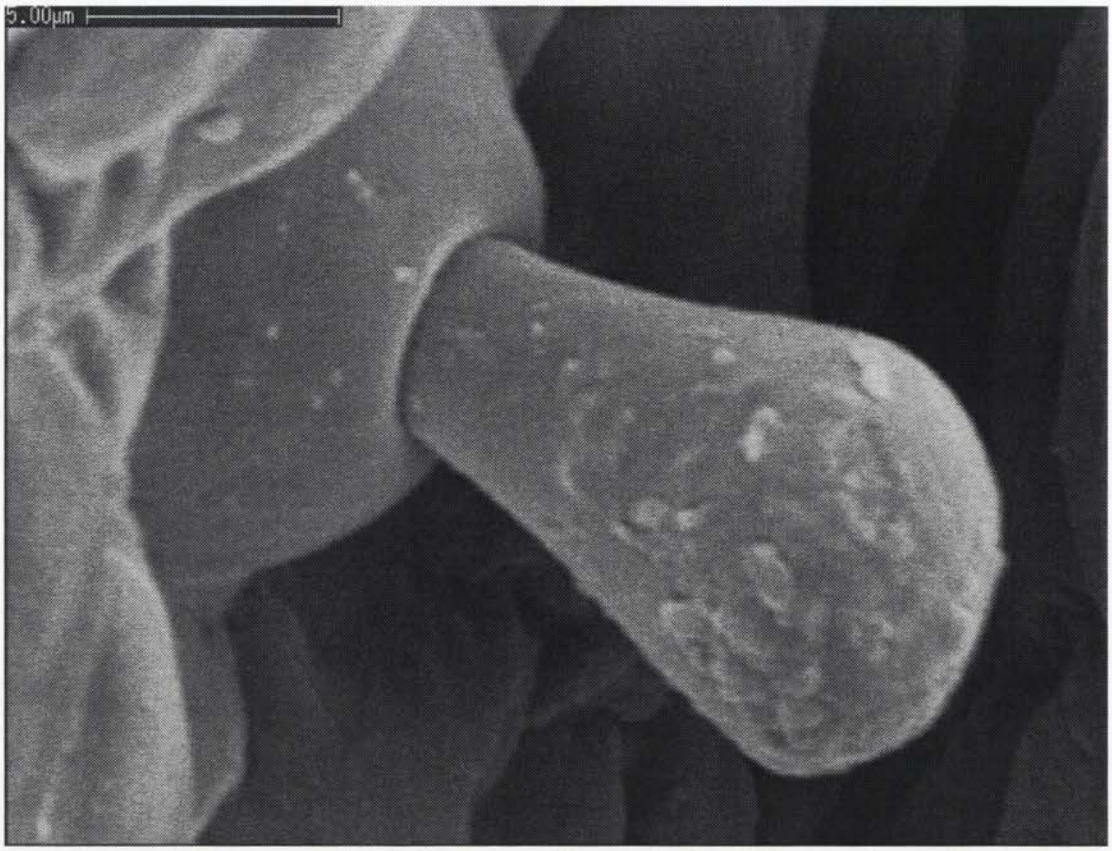

Fig. 284: *Munychryia senicula* (Anthelidae), caterpillar (L4) – short, club-shaped seta with a socket on the integument of an abdominal segment.

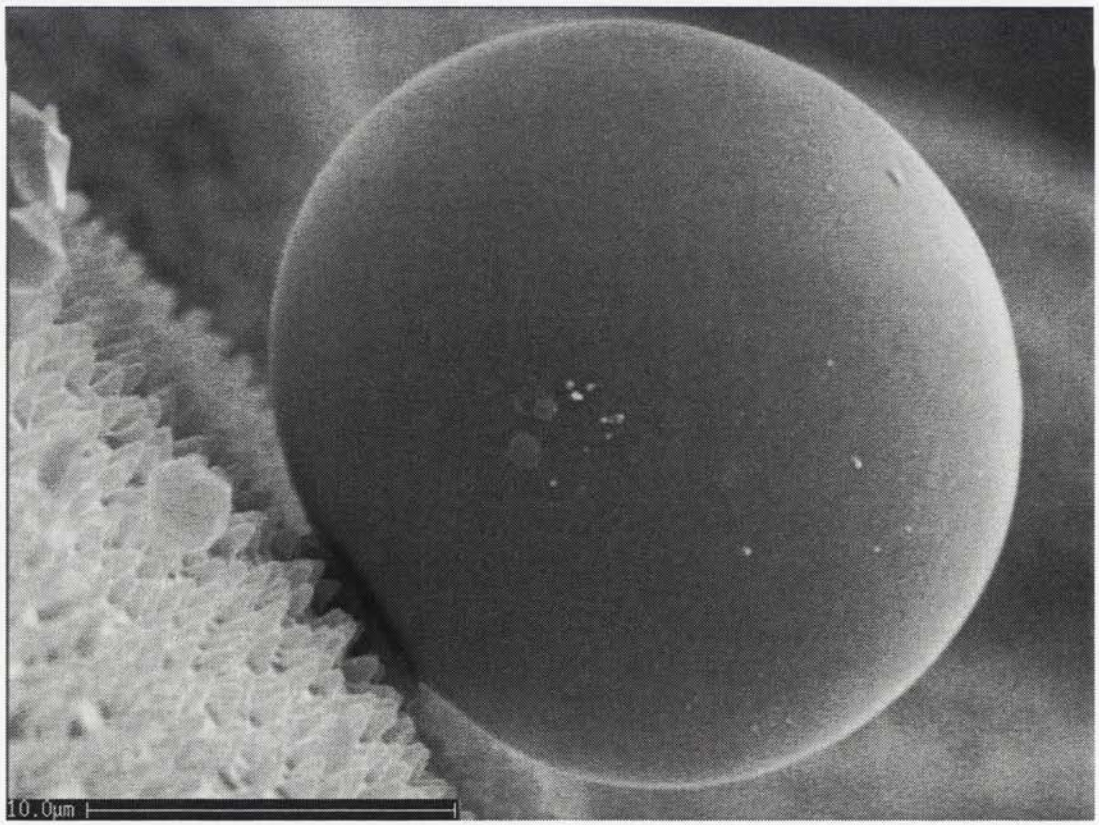

Fig. 285: *Anthela ocellata* (Anthelidae), caterpillar (L2) – the vesicle attaches through a very short and, relative to the vesicle diameter, narrow "stalk" to the integument.

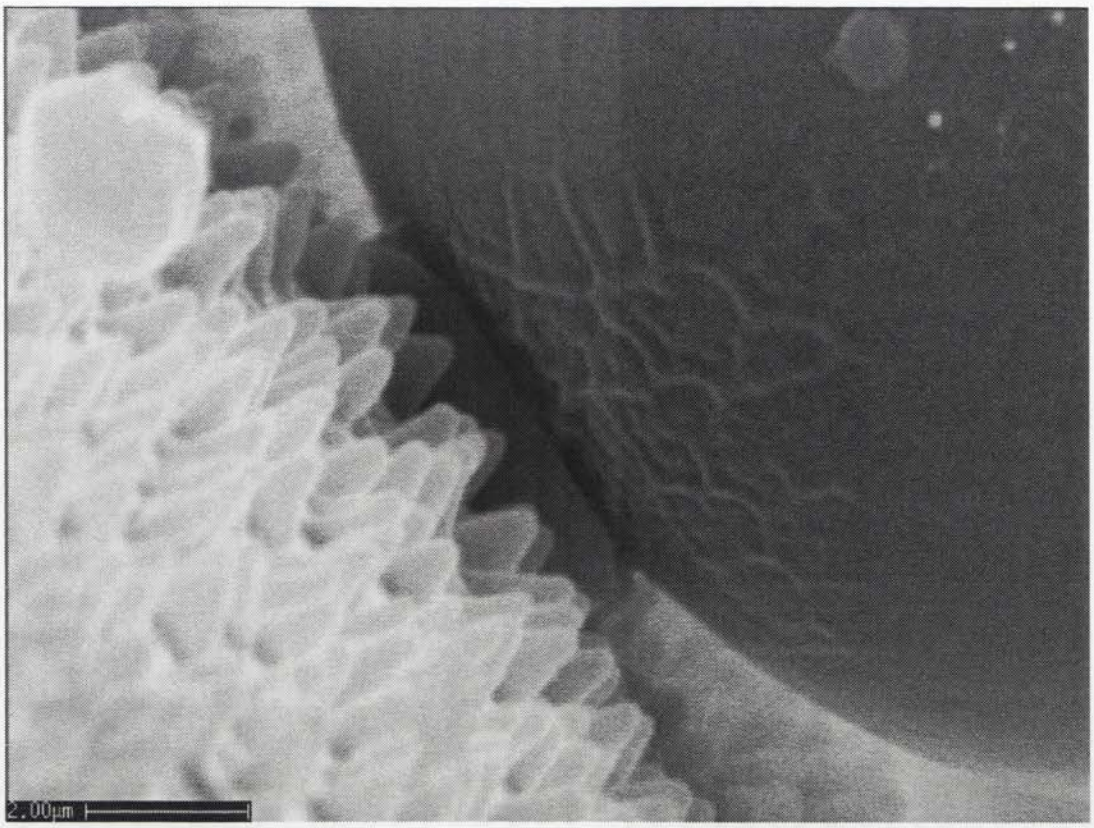

Fig. 286: *Anthela ocellata* (Anthelidae), caterpillar (L2) – the vesicle attaches through a very short "stalk" to the integument, which appears as if the vesicle rests on a socket.

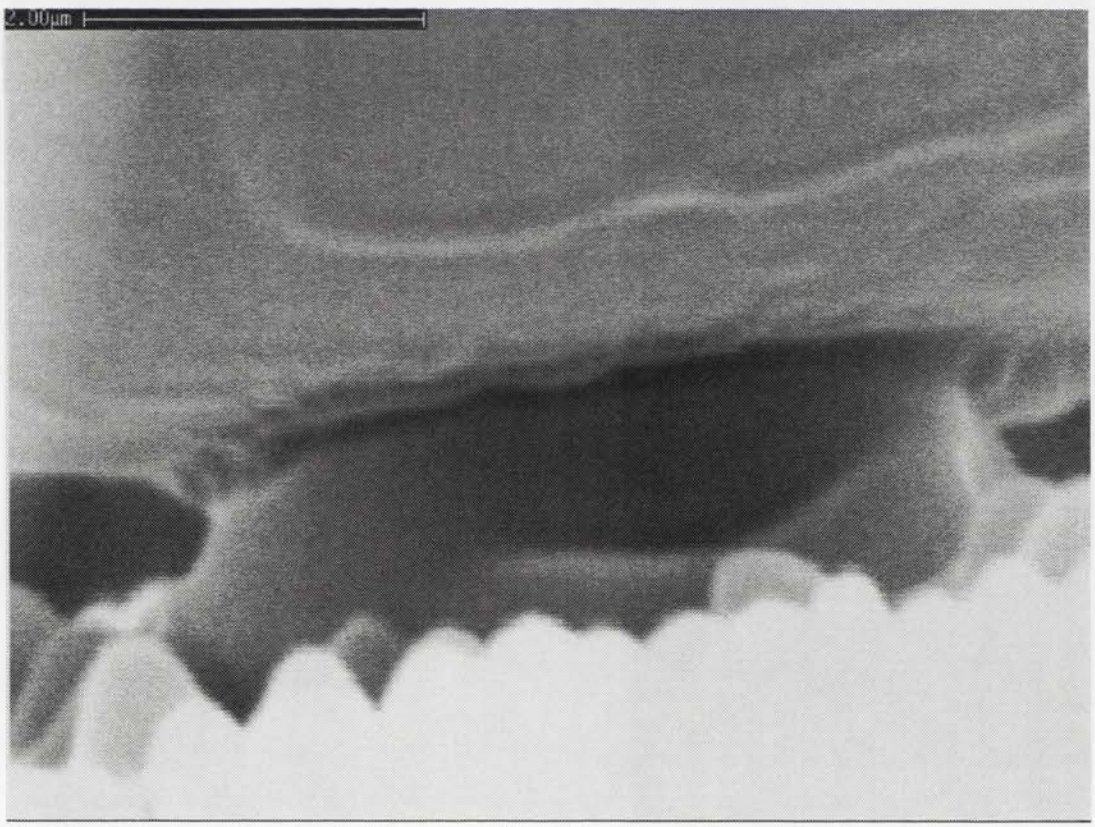

Fig. 287: *Anthela ocellata* (Anthelidae), caterpillar (L2) – the vesicle attaches through a very short "stalk" to the integument, which appears as if the vesicle rests on a socket.

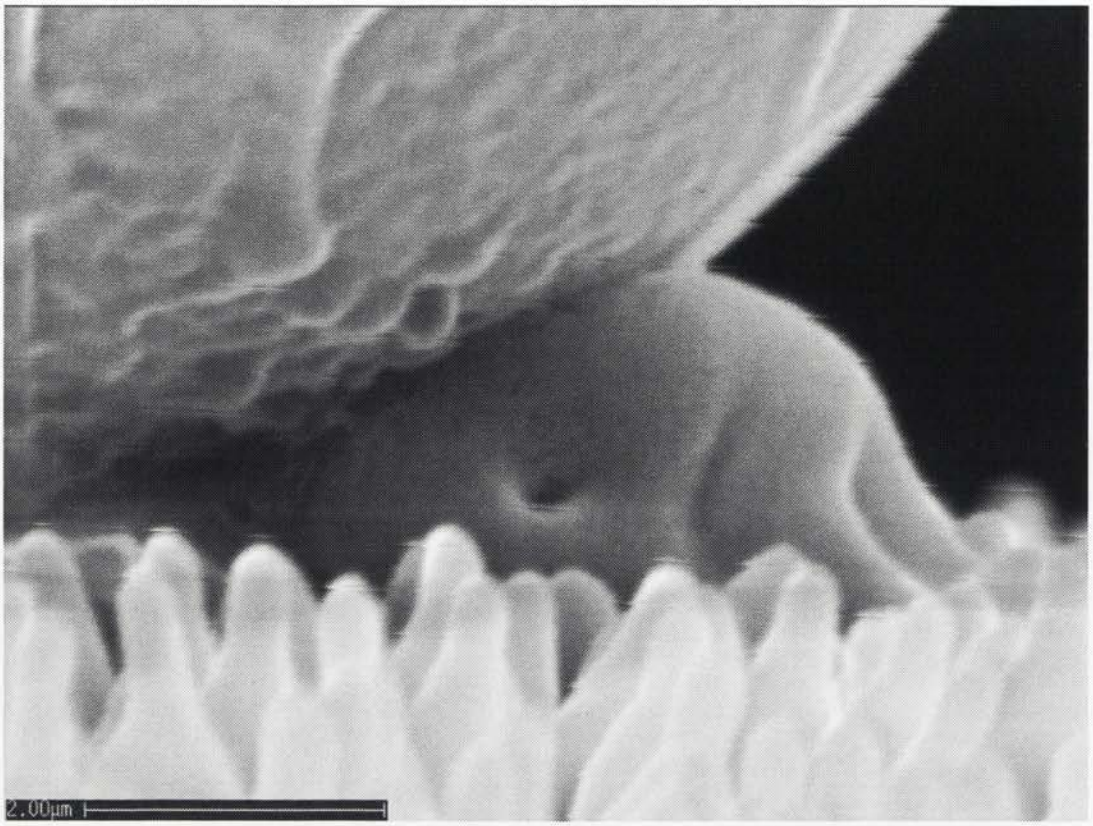

Fig. 288: *Anthela ocellata* (Anthelidae), caterpillar (L2) – the vesicle attaches through a very short "stalk" to the integument, which is probably covered externally by a substance, "glueing" the vesicle to the integument.

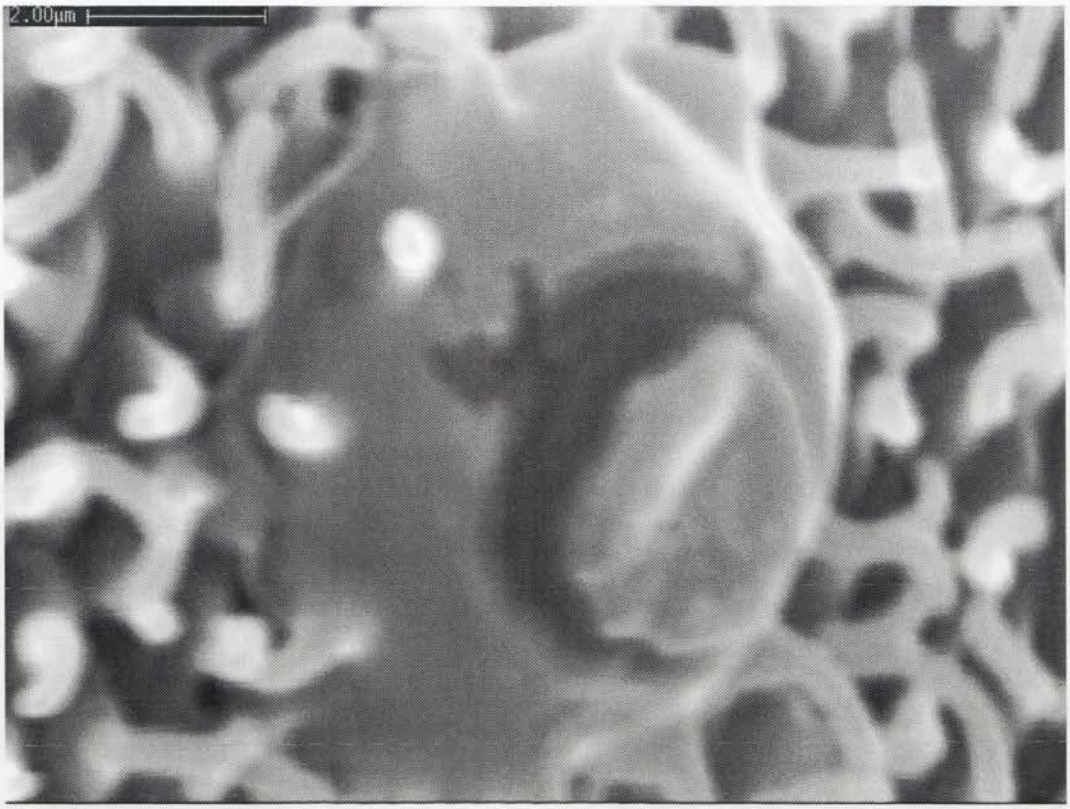

Fig. 289: *Anthela ocellata* (Anthelidae), caterpillar (L2) – the damaged remnants of the vesicle attachment after the vesicle was dislodged by the electron beam of the SEM; the central "stub" is the actual attachment, while the surrounding, possibly melted ring is the proximal part of the vesicle wall.

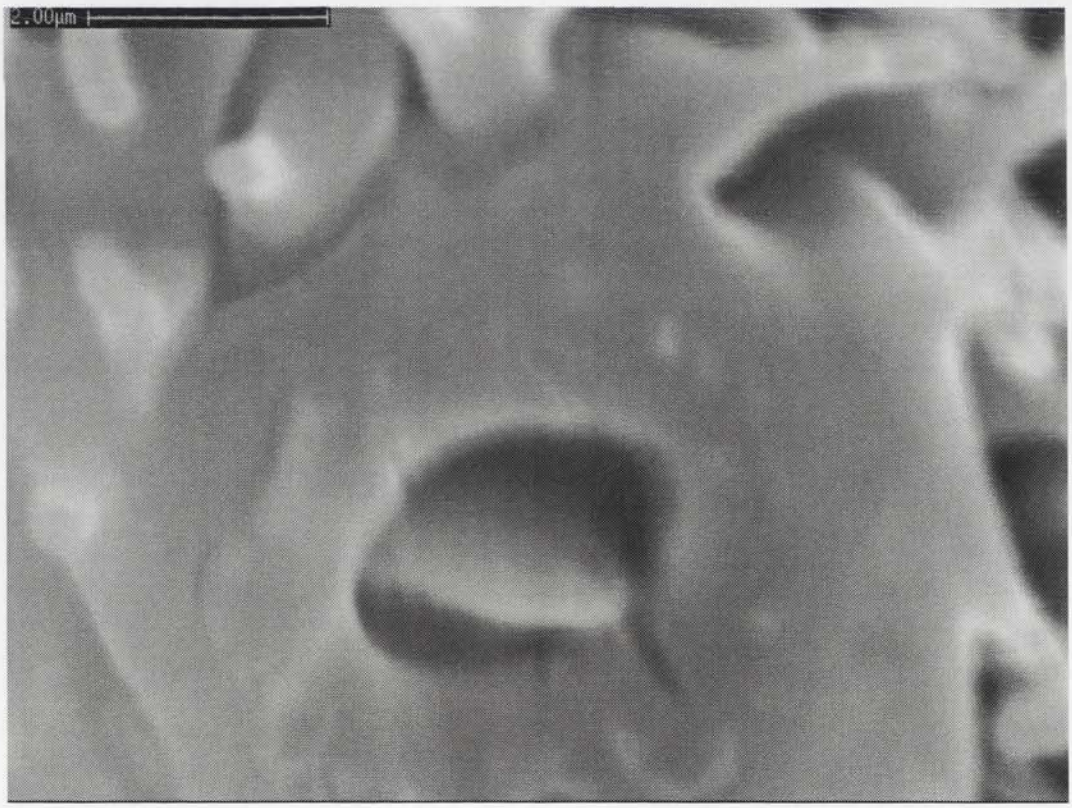

Fig. 290: *Anthela ocellata* (Anthelidae), caterpillar (L2) – the damaged remnants of the proximal part of the vesicle after the vesicle was dislodged by the electron beam of the SEM; a peg protrudes slightly through an opening in the "stalk" into the lumen of the vesicle.

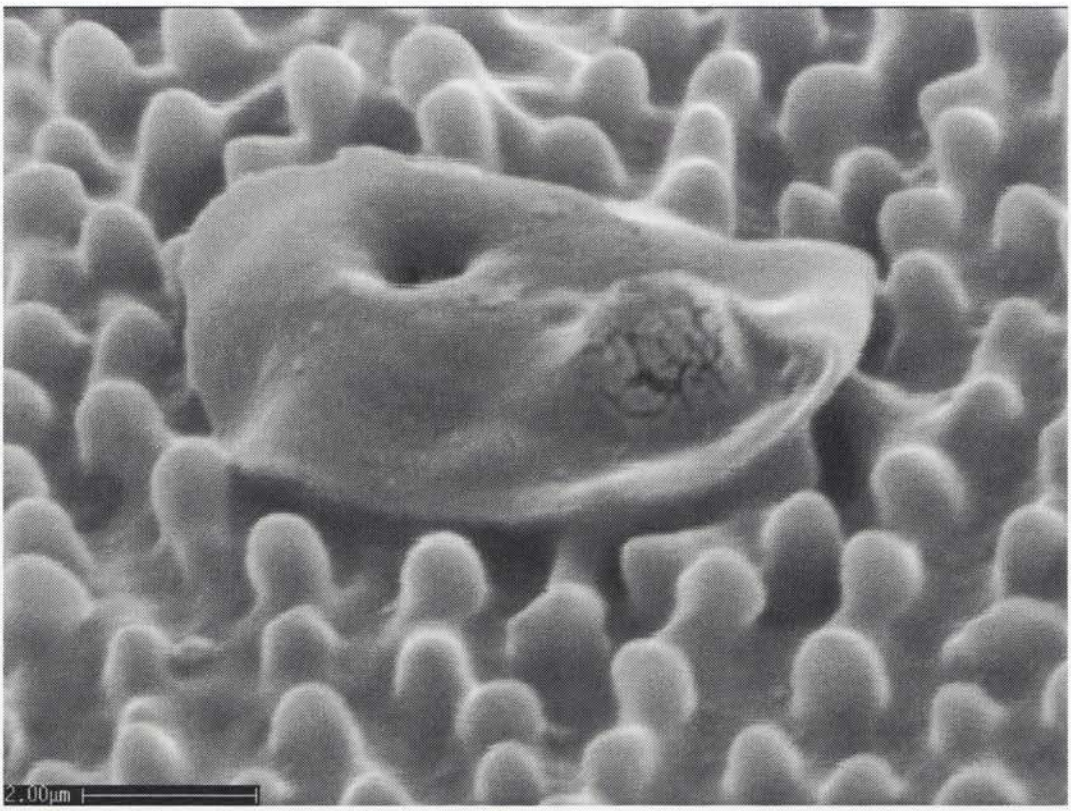

Fig. 291: *Anthela ocellata* (Anthelidae), caterpillar (L3) – the damaged remnants of the proximal part of the vesicle after the vesicle was dislodged manually with a pin and acetone; remnants of the proximal wall of the vesicle and the opening into the "stalk" are clearly visible.

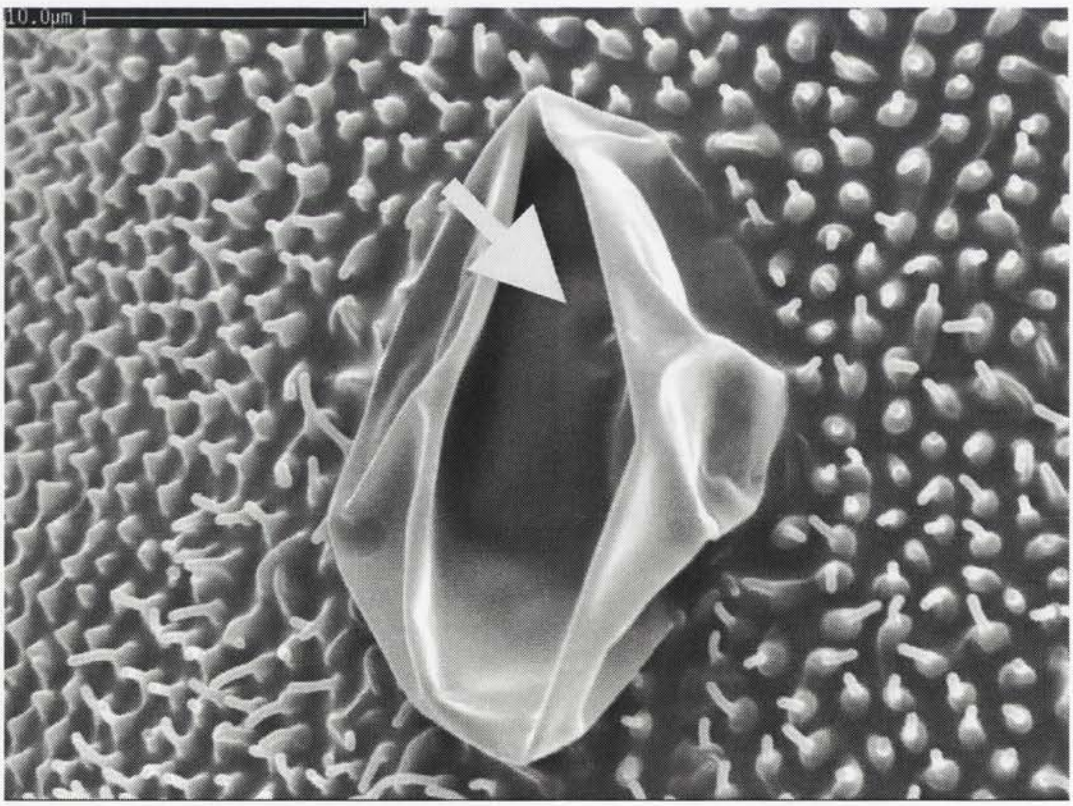

Fig. 292: *Anthela ocellata* (Anthelidae), caterpillar (L3) – collapsed vesicle after treatment with acetone; note the shape of the opening (yellow arrow) and the central peg (lighter-coloured line within opening), over which the vesicle wall is draped.

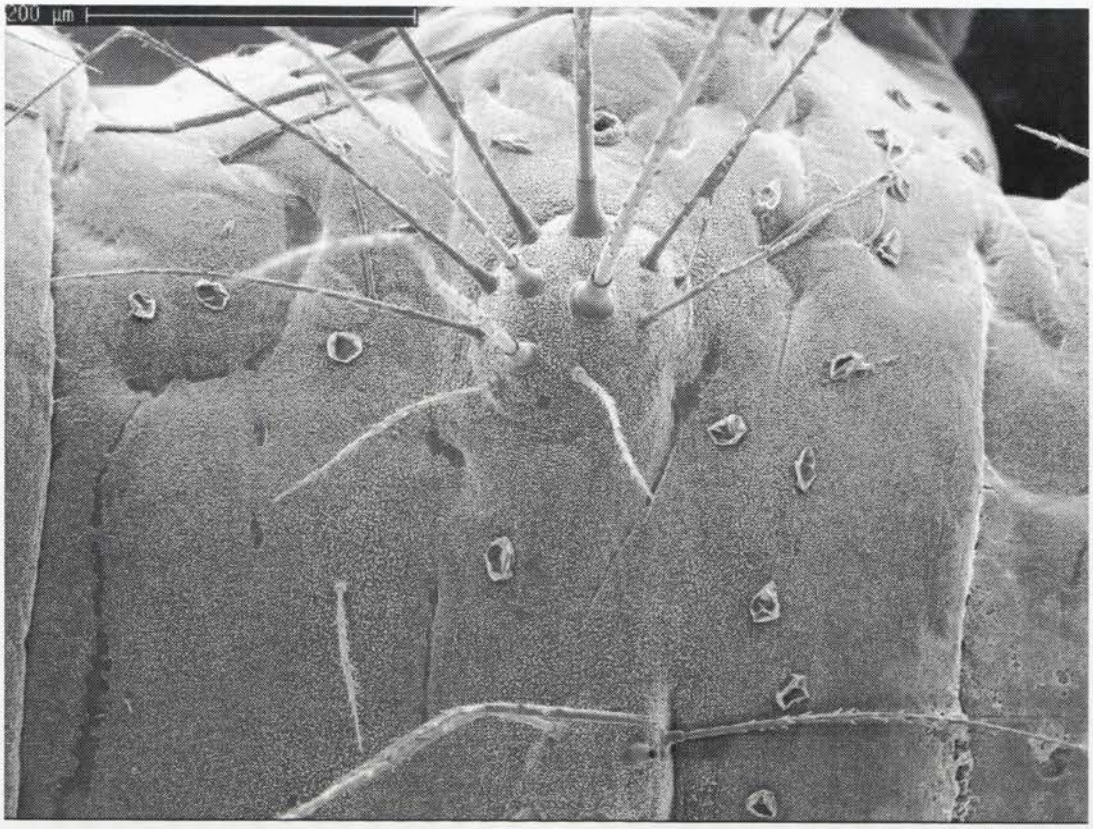

Fig. 293: *Anthela ocellata* (Anthelidae), caterpillar (L3) – during a treatment with acetone all vesicles discharge and collapse quickly.

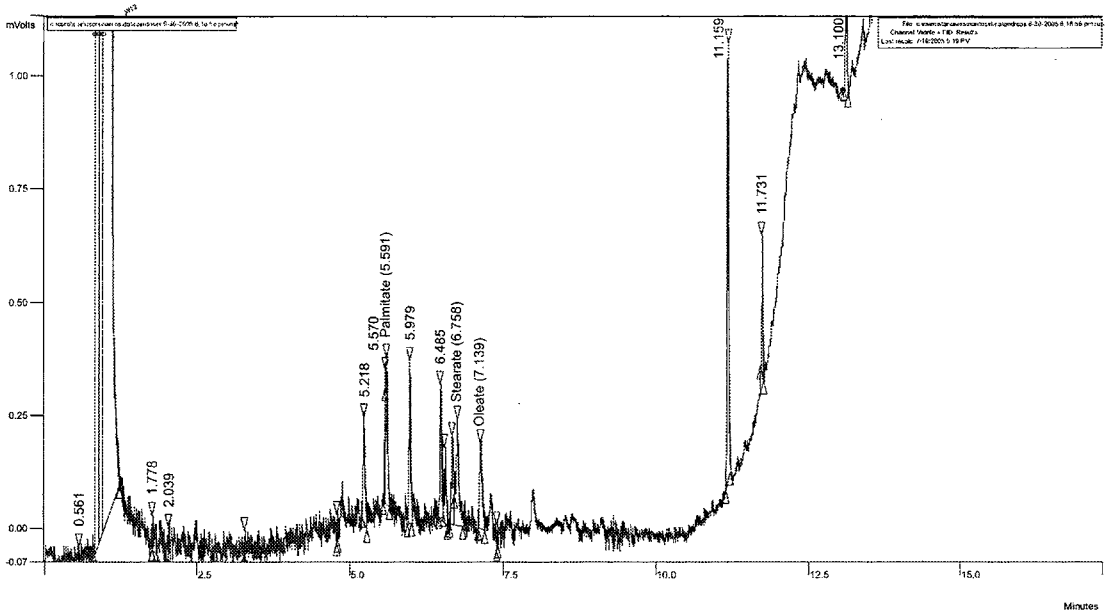

Fig. 294: Gas chromatography spectrum of the non-polar fraction obtained from dissolved vesicles of an *Anthela ocellata* (Anthelidae) caterpillar (Lm) – minute quantities of Palmitate, Stearate and Oleate as well as other fatty acids of similar length are present; note the for insects unusual, much higher peaks in the burn-off phase, probably caused by longer hydrocarbons (25-30 carbons).

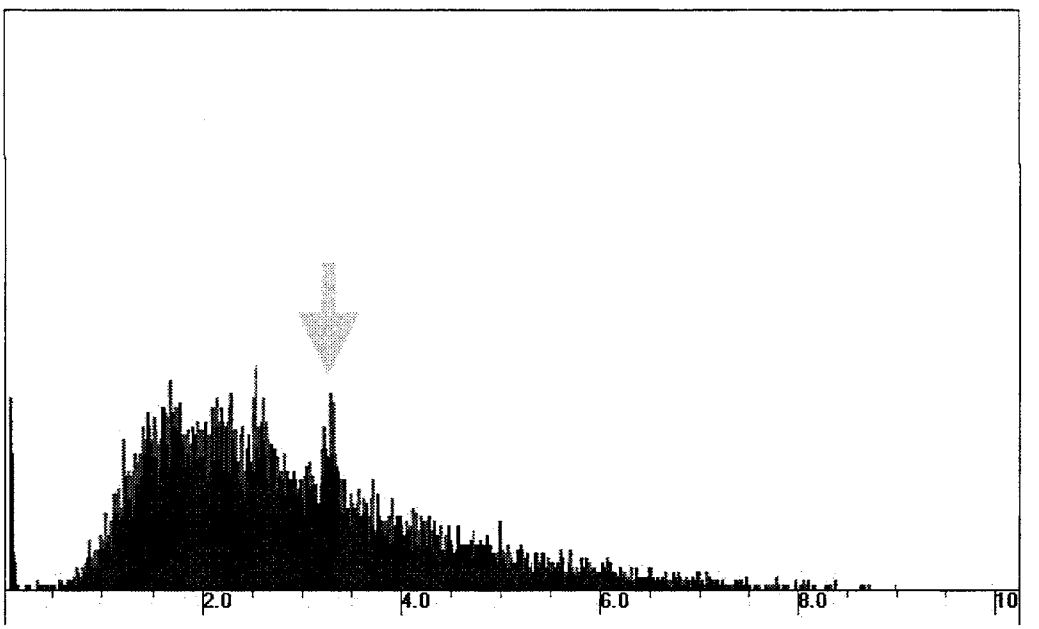

Fig. 295: *Anthela ocellata* (Anthelidae), caterpillar (L3) – EDXA spectrum (10kV) of a vesicle centre (red) overlaid with background noise (blue) as measured from the abdominal integument surface; note the minor but significant peak (yellow arrow) at about 3.3, indicating the presence of phosphorus as the heaviest element in the vesicle (no significant peaks further to the right).

III.6.2) Character analyses of pre-imaginal characters

Character #H.57: Headcapsule with triangular, pale frontal area.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; poorly supported.

Introduction. The headcapsule of macrolepidopteran caterpillars is typically uniformly coloured (Fig. 296), but has some pigment patterns in some taxa (e.g., *Danaus plexippus* (Nymphalidae) and many Lasiocampidae (Fig. 297)). The epicranial and lateral adfrontal sutures are often pale.

Description. In all Anthelidae an area laterally of the lateral adfrontal sutures, often including the frons, is pale. The pale area is relatively narrow in *Munychryia senicula* (Fig. 298) and not very distinct to absent in the genus *Pterolocera* (Fig. 301), but it is very obvious (Fig. 299) and often enlarged in other Anthelidae (Fig. 300). The pale area is typically of roughly triangular shape, narrowing dorsally, and often appears as a vertical stripe (Fig. 300).

Discussion. In *Nataxa flavescens* (Fig. 302), as well as very similarly in the Australian *Panacela lewinae* (Eupterotidae) (Fig. 303), the pale frontal area is very broad, almost circular in shape. A pale frontal area occurs in some African Eupterotidae (e.g., *Janomima mariana*, *Phyllalia patens* and *Rhabdosia patagiata*), too, but these areas are different in shape and not necessarily homologous.

The triangular, pale frontal area, which extends laterally of the lateral adfrontal sutures, is unique to Anthelidae, which is why I interpret character state (1) as apomorphic.

Summary. The shape of the pale frontal area is to some extent variable within the Anthelidae. The common denominator is merely the location of the pale area laterally of the lateral adfrontal sutures and the overall triangular shape. Therefore I consider my hypothesis of homology for the apomorphic character state (1) to be poorly supported.

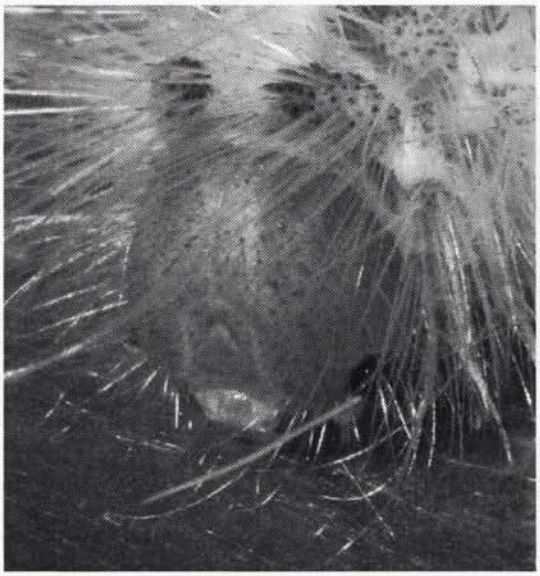

Fig. 296: *Cotana serranotata* (Eupterotidae), caterpillar (Lm) – headcapsule uniformly coloured to speckled.

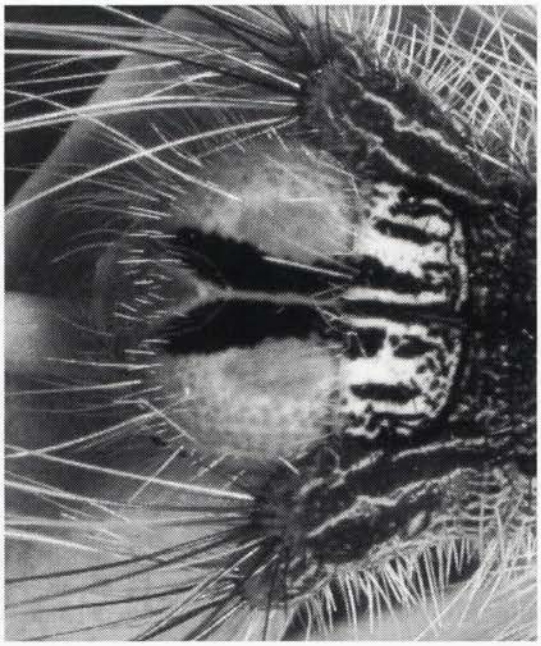

Fig. 297: *Pinara divisa* (Lasiocampidae), caterpillar (Lm) – headcapsule with colourful pigment patterns; note the pale epicranial and the lateral adfrontal sutures (pale, Y-shaped line).

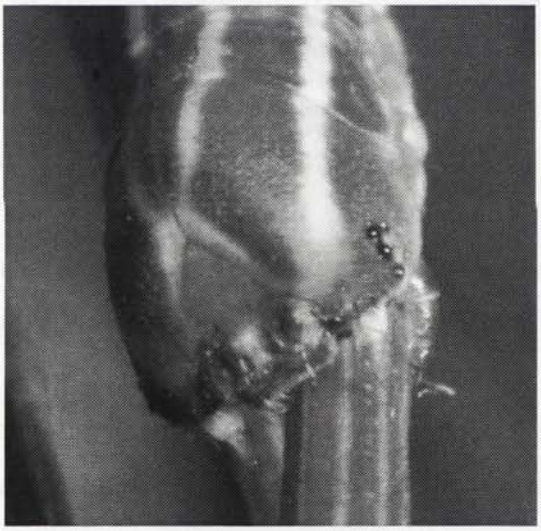

Fig. 298: *Munychryia senicula* (Anthelidae), caterpillar (L5) – headcapsule with pale area laterally of the lateral adfrontal suture.

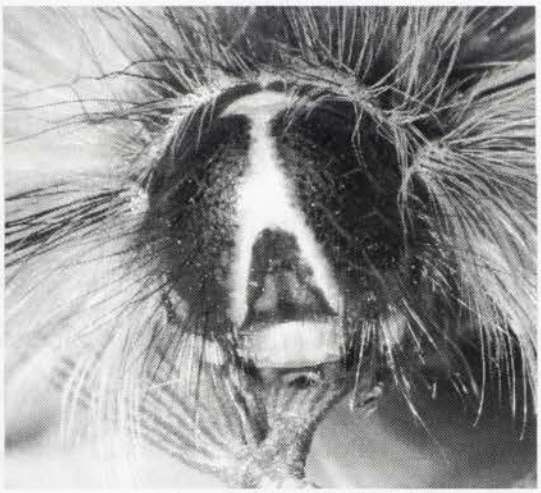

Fig. 299: *Anthela reltoni* (Anthelidae), caterpillar (L7) – headcapsule with pale area distinctly laterally of the lateral adfrontal suture, extending dorsad.

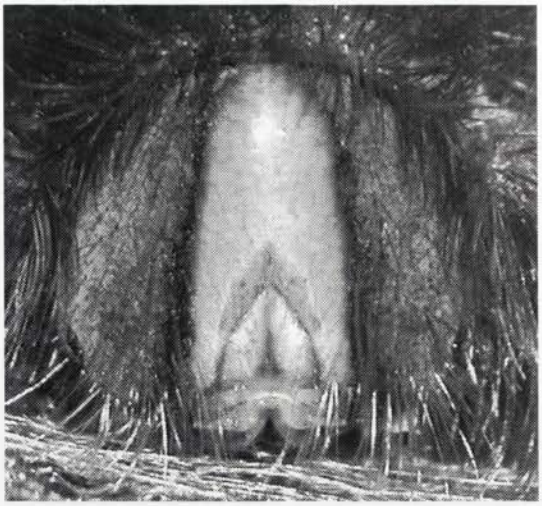

Fig. 300: *Anthela astata* (Anthelidae), caterpillar (Lm) – headcapsule with very large, pale area laterally of the lateral adfrontal suture and including the frons.

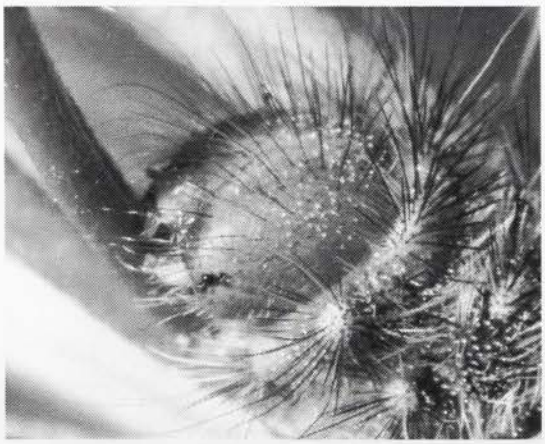

Fig. 301: *Pterolocera* sp. (Anthelidae), caterpillar (L5) – headcapsule with a very faint pale area laterally of the lateral adfrontal suture.

Fig. 302: *Nataxa flavescens* (Anthelidae), caterpillar (Lm) – headcapsule with broad, almost circular, pale area laterally of the lateral adfrontal suture, including large parts of the frons.

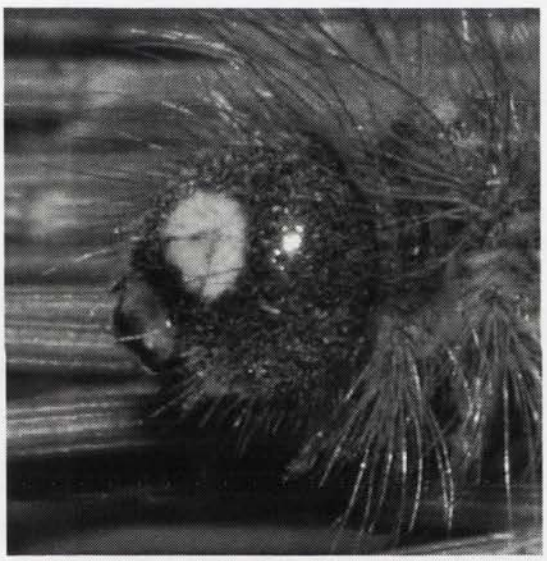

Fig. 303: *Panacela lewinae* (Eupterotidae), caterpillar (Lm) – headcapsule with broad, almost circular, pale area laterally of the lateral adfrontal suture, including large parts of the frons.

Character #H.58: Maxillar lobarium with a distinct apical "segment", exclusive of STI-III.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; well supported.

Introduction. The main externally visible structures of the caterpillar headcapsule are stemmata, antennae and mouth parts (Fig. 304). Of the mouthparts the maxilla is the structure with the largest number of sensilla. These are largely concentrated at the apex of two structures – the apical segment of the maxillary palpus and the lobarium (Kristensen 1984; "mesal lobe" *sensu* Grimes & Neunzig 1986b) (Fig. 305). Both structures were described externally in detail by Grimes and Neunzig (1986a, b) in a morphological survey of ditrysian caterpillars. Their publications are the most comprehensive accounts published on the maxillae of ditrysian caterpillars and I adopt their notation of sensilla. Some of their notations are based on the relative positions of the sensilla, which are correct for the mesal and lateral position, but the terms anterior and posterior were applied incorrectly in a reversed sense throughout the text. However, as none of their notations is based on the latter two terms, I use their notations without alterations.

The lobarium is located on the divided dististipes, which is fused with a basal segment of the maxillary palpus (Kristensen 1984). According to Eassa (1963) and Matsuda (1965) the lobarium is homologous with the galea, while Grimes and Neunzig (1986b) argue for it being a composite structure consisting of the fused galea and lacinia. Galea and lacinia are separate in *Sabatinca barbarica* (Micropterygidae) (Tillyard 1923), and this separation is a unique symplesiomorphy of Micropterygidae (Kristensen 2003b: 42). Accordingly, no separate lacinia was described or illustrated for Agathiphagidae by Kristensen (1984) and Heterobathmiidae by Kristensen and Nielsen (1983), and likewise no separate lacinia has been observed in Ditrysia. However, the lobarium of Ditrysia appears to consist of two fused structures, which Grimes and Neunzig (1986b) interpreted as the galea and remnants of the fused lacinia. The distinctiveness of this separation is variable between different taxa, and it is an extreme separation in some Anthelidae, which constitutes this character.

The ditrysian lobarium carries apically a rather constant arrangement of three sensilla trichodea (STI-III), two sensilla styloconica (SSI-II) and three sensilla basiconica (SBI-III) (Fig. 306). The three sensilla trichodea are typically arranged in a row along the

dorso-anterior edge of the lobarium (Fig. 307). This anterior edge ("lacinial ridge" *sensu* Grimes and Neunzig 1986b) is typically slightly set off from the rest of the lobarium (Fig. 308), and together with two of the sensilla trichodea (STII-III) is suggested to be a remnant of the lacinia (Grimes and Neunzig 1986b). While the lacinial ridge is distinct, it is posteriorly strongly fused to the remainder of the lobarium, with the sensilla trichodea arising from about the same level as the other sensilla. These other sensilla, including STI, arise from a rather shallow protrusion (the posterior part of the lobarium) (Fig. 309), which can have a sclerotized outside, except for its anterior (= fused) side.

Description. With the exception of *Munychryia senicula* (Fig. 306) (and possibly other Munychryiinae), this situation is modified in Anthelidae. Their lobarium carries apically a free-standing "segment" with all sensilla of the lobarium at its apex, except for all three sensilla trichodea, which remain as a row on the lacinial ridge (Figs 310, 311). This "segment" is formed by the posterior part of the lobarium and it has a completely sclerotized outer wall, which separates it from the lacinial ridge as well as the distal section of the dististipes (Fig. 312 versus Fig. 313).

Discussion. I interpret this condition as a subsequent separation of the majority of sensilla from the three sensilla trichodea by an extension of the sclerotized posterior wall of the lobarium and a separation of this posterior side of the lobarium from the distal part of the dististipes. The secondary nature of this condition is indicated by the exclusion of STI from this "segment" and the posterior segregation from the dististipes.

The separation of the posterior part of the lobarium from the lacinial ridge and segregation from the dististipes is not unique to Anthelidae. It has been illustrated for some Noctuidae, e.g., *Agrotis ipsilon* (Reese *et al.* 1974) and *Euxoa messoria* (Devitt & Smith 1982), but the typical ditrysian condition is present in other Noctuidae, e.g., *Heliothis* spp. (Baker *et al.* 1986). Grimes and Neunzig (1986b: 523, Figs 32 & 33) illustrate an American specimen of *Danaus plexippus* (Nymphalidae), in which a "segment" inclusive of STI is formed. This differs from my own observation of the Australian *D. plexippus*, in which a separate segment without STI is formed (Fig. 315). Such a formation of a "segment" inclusive of STI is present in the African eupterotid species *Poloma angulata* (Fig. 314). Based on the differences in location of STI I assume these rather rare formations to have evolved convergently.

As described above, a true separation of galea and lacinia seems to be restricted to the Micropterygidae, which according to Kristensen and Skalski ([1998]) are the sistergroup of all other Lepidoptera. The lobarium consists of the fused lacinial ridge and the posterior part of the lobarium in most Ditrysia, as apparent from the survey of Grimes and Neunzig (1986b). Therefore I interpret character state (1) to be apomorphic.

Summary. The homology of the subsequent formation of a "segment" in some Anthelidae is indicated by the extended sclerotization of the "segment", the exclusion of STI from it and the more proximal location of the sensilla trichodea relative to the remaining sensilla on the "segment" apex. While the actual length of this "segment" varies between species, this arrangement is very constant and distinct within Anthelidae. Therefore I consider my hypothesis of homology for the apomorphic character state (1) to be well supported.

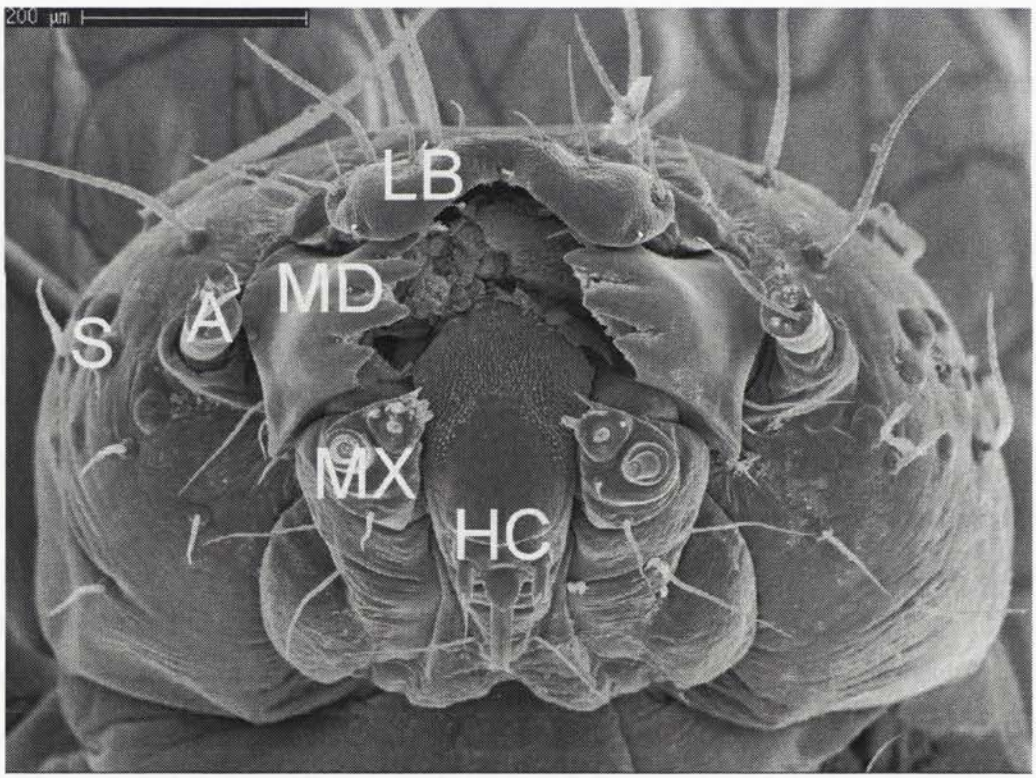

Fig. 304: *Carthaea saturnioides* (Carthaeidae), caterpillar (L1), ventral view (top=anterior) – headcapsule overview, showing the location of stemmata (S), antenna (A), labrum (LB), mandible (MD), maxilla (MX) and the hypopharyngeal complex (HC), consisting of hypopharynx, labium and spinneret.

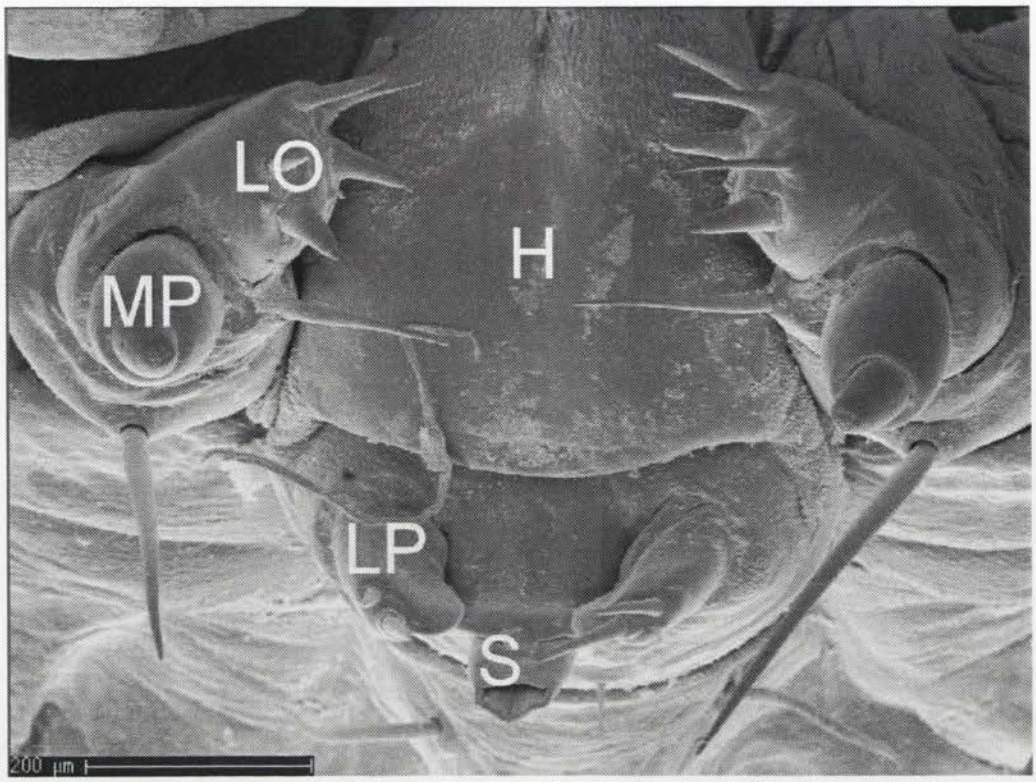

Fig. 305: *Spiramiopsis comma* (Brahmaeidae), caterpillar (Lm), ventral view (top=anterior) – mouthpart overview; the maxilla carries apically two structures, namely the maxillary palpus (MP) and the lobarium (LO); the hypopharynx (H) is located between the maxillae, and the labial palpi (LP) border the spinneret (S) antero-laterally; note the antero-mesal orientation of the lobarium.

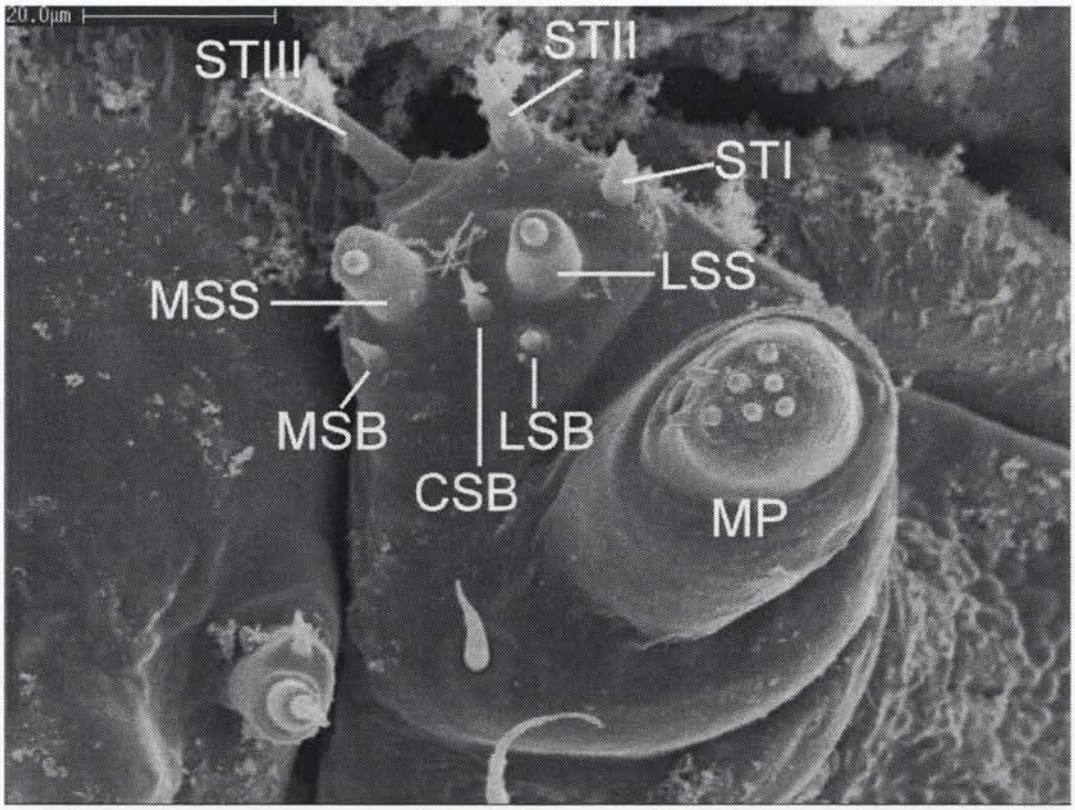

Fig. 306: *Munychryia* n. sp. near *senicula* (Anthelidae), caterpillar (L1), ventral view (top=anterior) – left maxilla apex with maxillary palpus (MP) and lobarium; the lobarium carries three sensilla trichodea (STI-III), a lateral (LSS) and a mesal styliform sensillum (MSS), as well as a lateral (LSB), central (CSB) and mesal sensillum basiconicum (MSB).

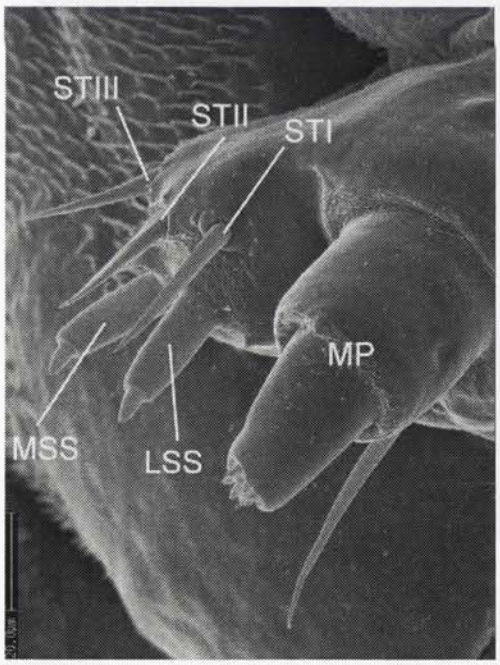

Fig. 307: *Carthaea saturnioides* (Carthaeidae), caterpillar (L1), ventro-lateral view (top=anterior) – left maxilla apex with maxillary palpus (MP) and lobarium; the three sensilla trichodea (STI-III) of the lobarium are arranged in a row along the lacinial ridge, slightly protruding distally [see Fig. 306 for abbreviations].

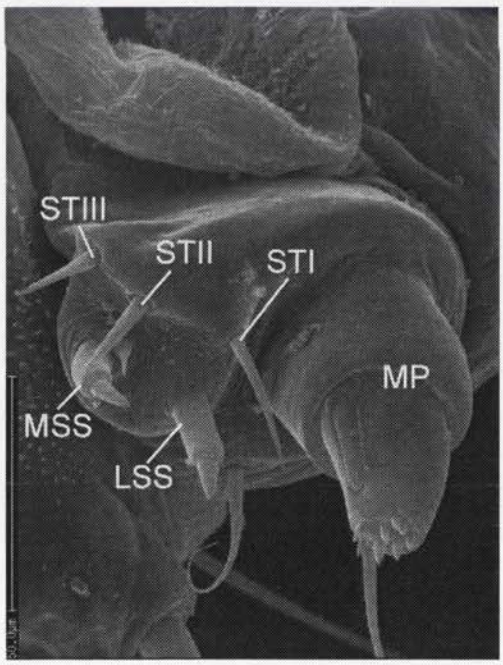

Fig. 308: *Opsirhina albigutta* (Lasiocampidae), caterpillar (L1), ventral view (top=anterior) – left maxilla apex with maxillary palpus (MP) and lobarium; the three sensilla trichodea (STI-III) of the lobarium are arranged in a row along the lacinial ridge, slightly protruding distally [see Fig. 306 for abbreviations].

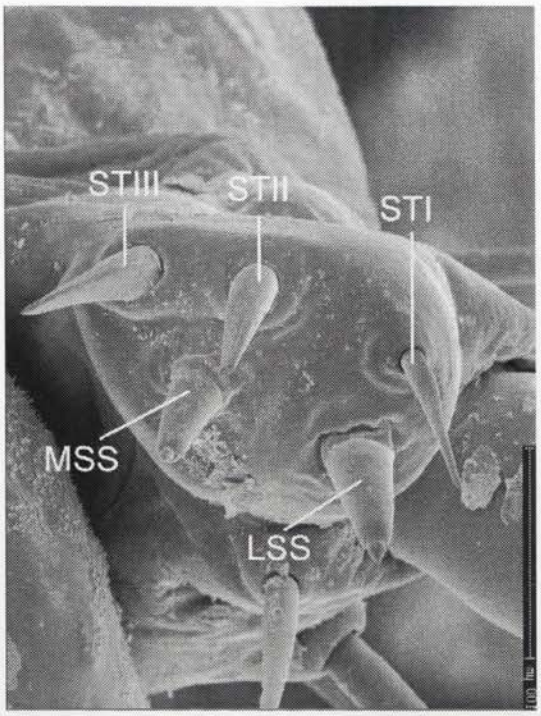

Fig. 309: *Spiramiopsis comma* (Brahmaeidae), caterpillar (Lm), ventral view (top=anterior) – left maxilla apex with lobarium; the three sensilla trichodea (STI-III) of the lobarium are arranged in a row along the lacinial ridge, with STI belonging to the protrusion carrying the sensilla styloconica [see Fig. 306 for abbreviations].

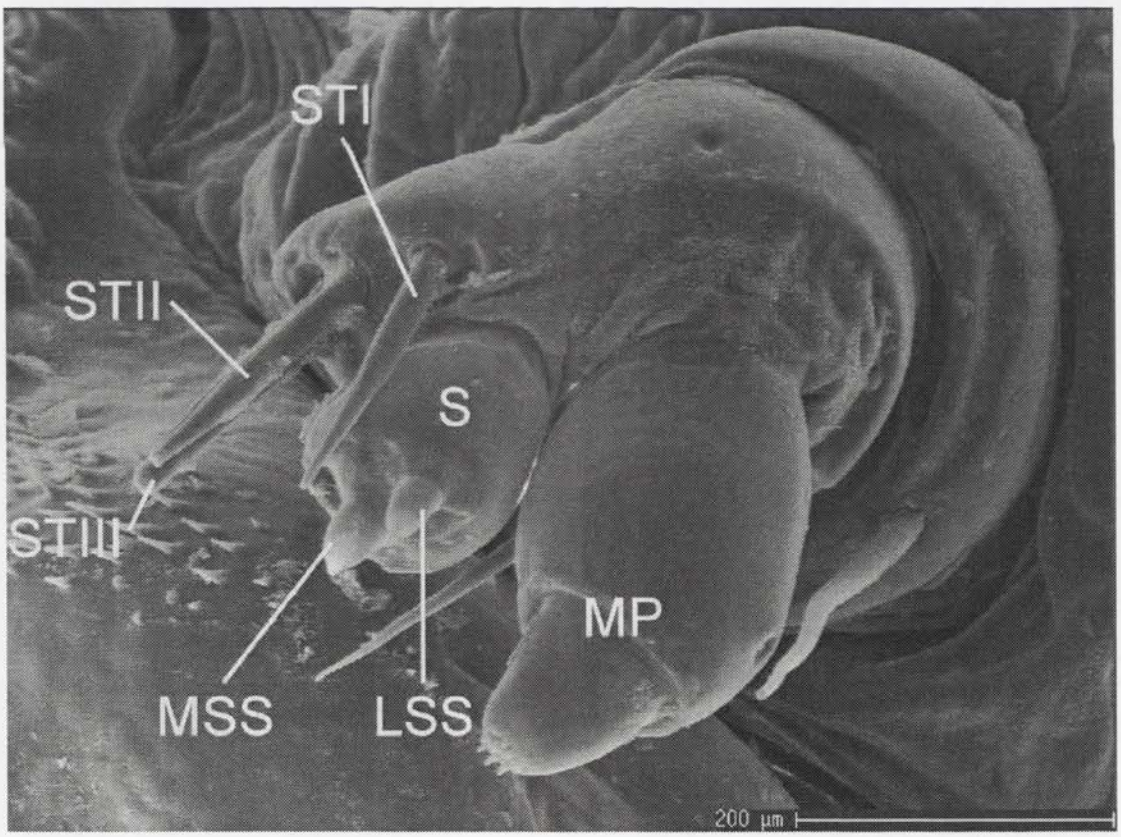

Fig. 310: *Anthela nicothoe* (Anthelidae), caterpillar (Lm), ventral view (top=anterior) – left maxilla apex with lobarium and maxillary palpus (MP); the three sensilla trichodea (STI-III) of the lobarium are arranged in a row along the lacinial ridge, while all other sensilla of the lobarium are located on a discrete "segment" (S) [see Fig. 306 for abbreviations].

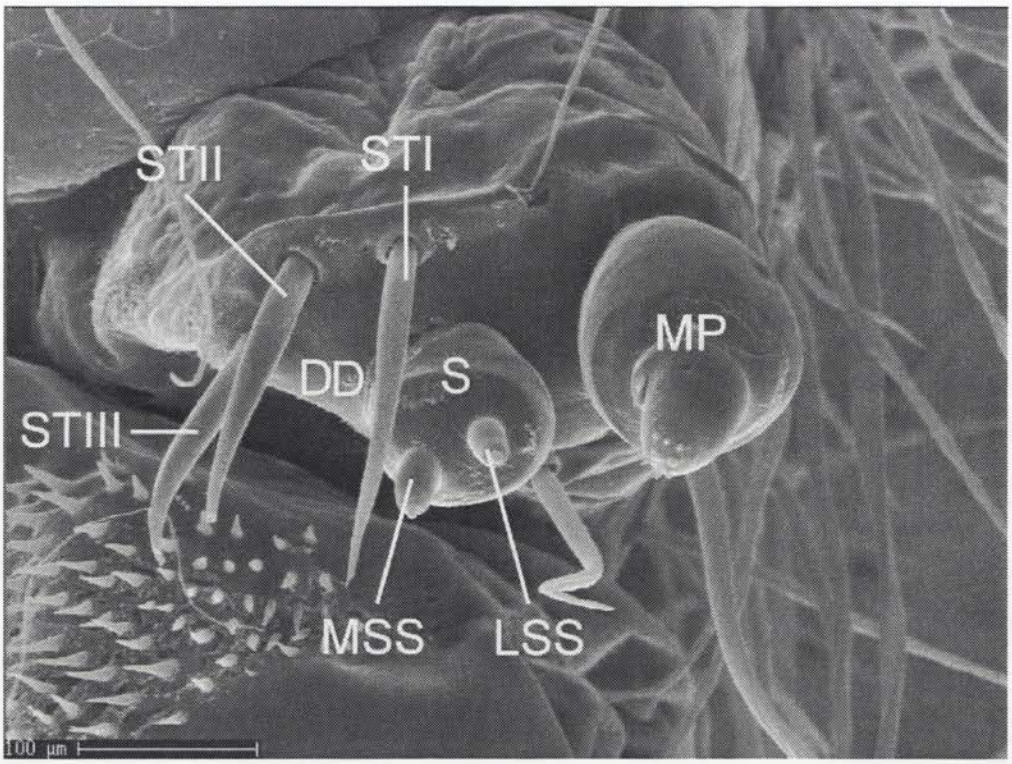

Fig. 311: *Pterolocera* sp. (Anthelidae), caterpillar (Lm), ventral view (top=anterior) – left maxilla apex with lobarium and maxillary palpus (MP); the three sensilla trichodea (STI-III) of the lobarium are arranged in a row along the lacinial ridge, while all other sensilla of the lobarium are located on a discrete "segment" (S) [see Fig. 306 for abbreviations].

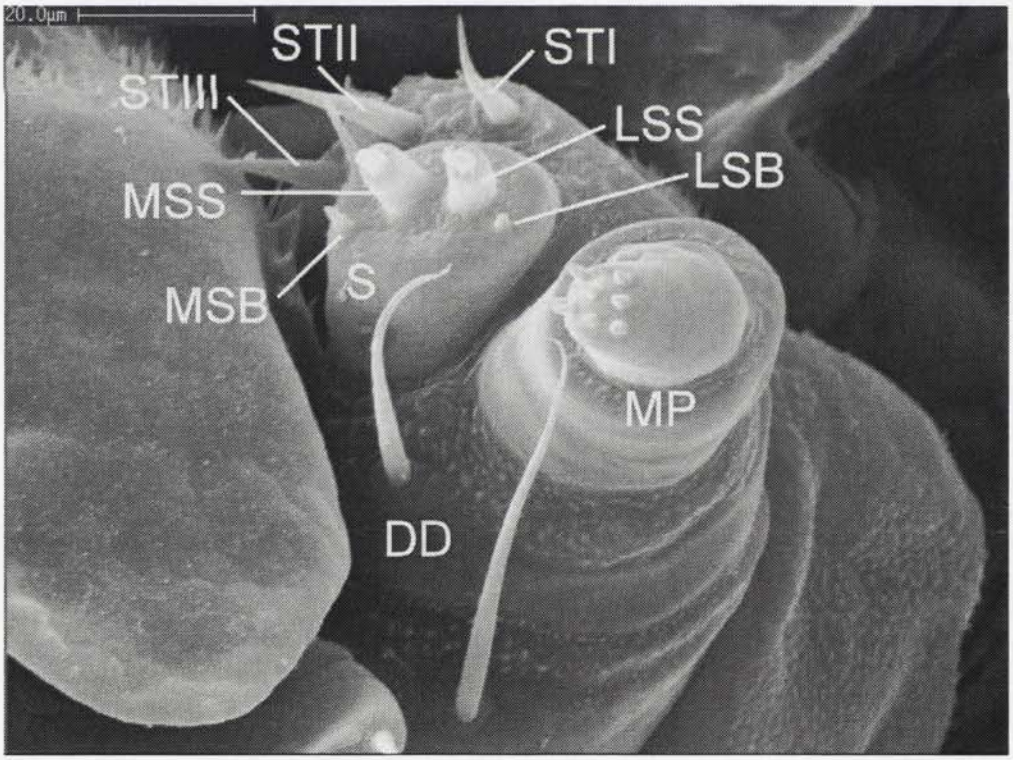

Fig. 312: *Anthela* n. sp. near *addita* (Anthelidae), caterpillar (L1), ventral view (top=anterior) – left maxilla apex with lobarium and maxillary palpus (MP); the three sensilla trichodea (STI-III) of the lobarium are arranged in a row along the lacinial ridge, while all other sensilla of the lobarium are located on a discrete "segment" (S), which is posteriorly separated from the distal part of the dististipes (DD) [see Fig. 306 for abbreviations].

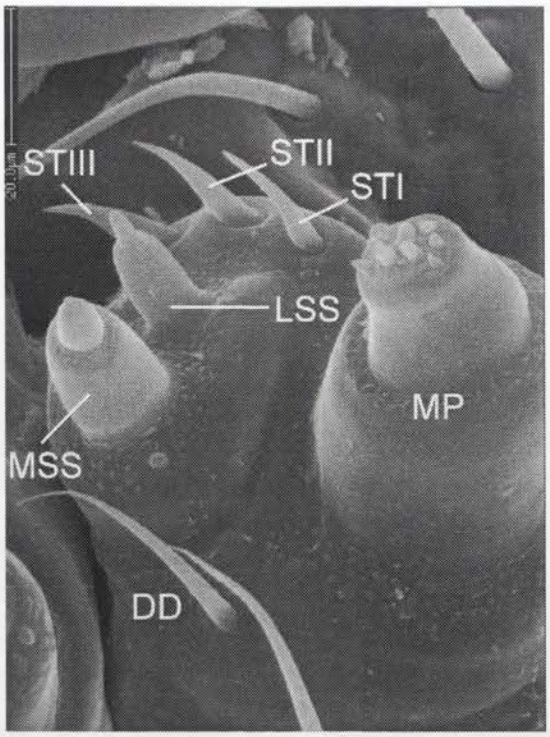

Fig. 313: *Chionopsyche montana* (Lasiocampidae), caterpillar (L1), ventral view (top=anterior) – left maxilla apex with lobarium and maxillary palpus (MP); the three sensilla trichodea (STI-III) of the lobarium are arranged in a row along the lacinial ridge, while all other sensilla of the lobarium are located on a shallow protrusion, which is anteriorly incompletely sclerotized and fused with the lacinial ridge, while posteriorly formed by the distal part of the dististipes (DD) [see Fig. 306 for abbreviations].

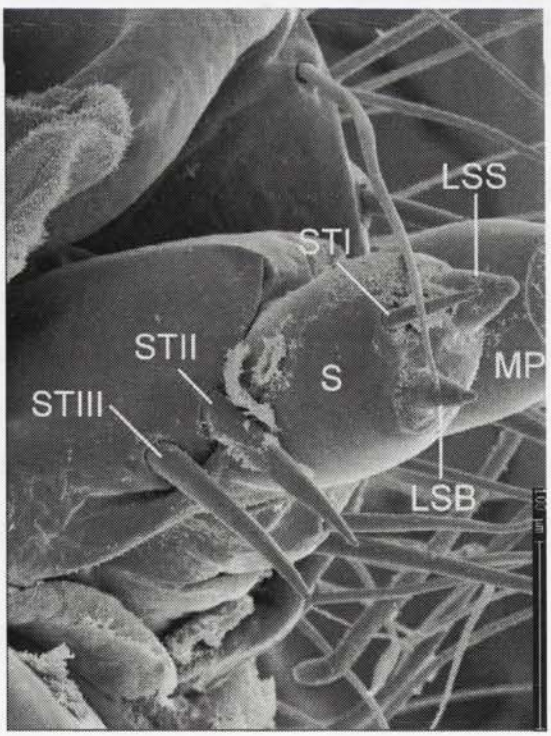

Fig. 314: *Poloma angulata* (Eupterotidae), caterpillar (Lm), ventral view (top=anterior) – left maxilla apex with lobarium and maxillary palpus (MP); only two sensilla trichodea (STII & III) of the lobarium are located along the lacinial ridge, while all other sensilla of the lobarium, including STI, are located on a discrete "segment" (S) [see Fig. 306 for abbreviations].

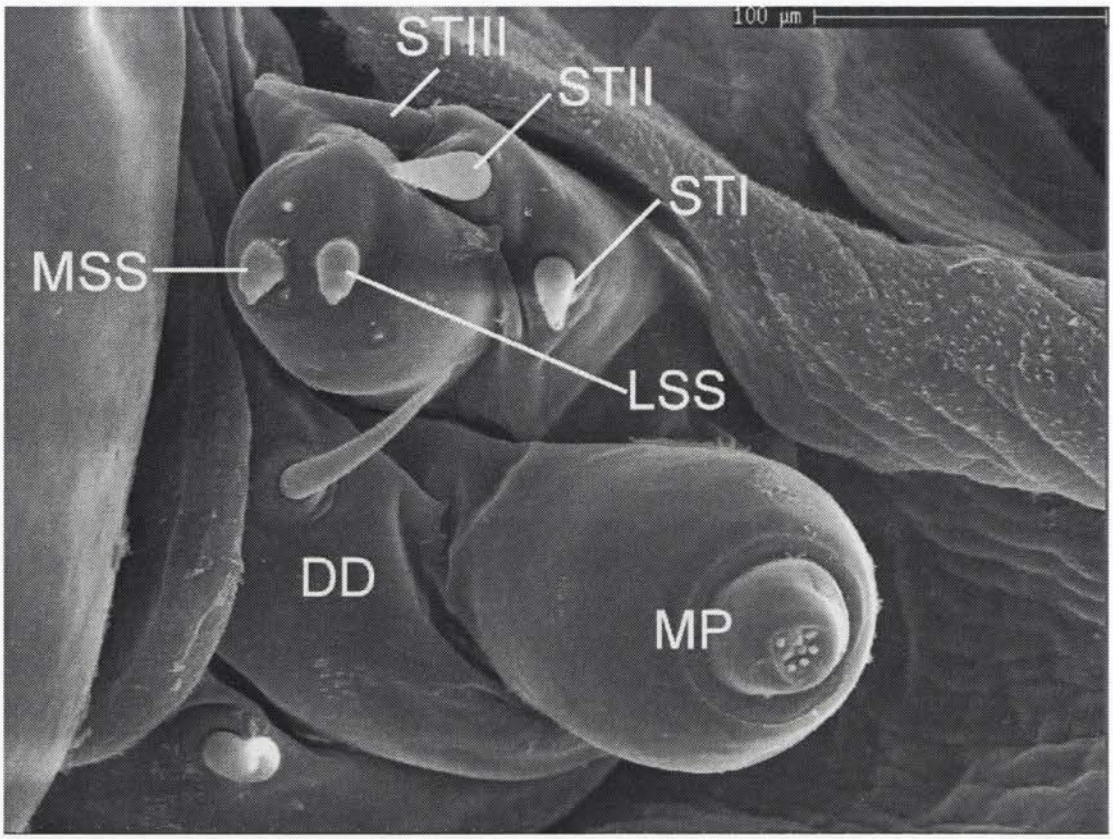

Fig. 315: *Danaus plexippus* (Nymphalidae), caterpillar (Lm), ventral view (top=anterior) – left maxilla apex with lobarium and maxillary palpus (MP); the three sensilla trichodea (STI-III) of the lobarium are arranged in a row along the lacinial ridge, while all other sensilla of the lobarium are located on a discrete "segment" (S), which is posteriorly separated from the distal part of the dististipes (DD) [see Fig. 306 for abbreviations]; note that this condition differs greatly from the illustration of *D. plexippus* in Grimes & Neunzig (1986b: 523, Figs 32 & 33).

Character #H.59: Maxillary palpus anteriorly with a paired "mammiform sensillum" SC4.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; poorly supported.

Introduction. The apical segment of the ditrysian maxillary palpus carries apically eight sensilla basiconica, as well as a sensillum digitiformium on the anterior and a variable number of up to five sensilla campaniformia on the anterior and lateral part of the sclerotized wall (Fig. 316) (Grimes & Neunzig 1986a). Externally these sensilla campaniformia appear as a shallow depression of variable shape in the cuticle, or as a shallow protrusion in a depression. The exact locations of these sensilla vary between species, and as the homologies implied by the notations of Grimes and Neunzig (1986a) are based on the location only, they are often dubious. According to these authors, one of these sensilla campaniformia (SC4) occurs as a single, small depression at the proximal end of the digitiform sensillum in a few species of different families (Pyralidae, Hesperiidae, Nymphalidae, Bombycidae).

Description. Grimes and Neunzig (1986a) noted two "most extraordinary" sensilla proximally of the latero-proximal end of the digitiform sensillum in *Actias luna* (Saturniidae) and less distinct in *Paonias myops* (Sphingidae), which taken together they regarded as SC4, too. They described these sensilla as consisting of "a swollen base supporting a sunken dome with one or two pores in the center", and they referred to them as a pair of "bulbous, mammiform sensilla" (Fig. 317) (Grimes & Neunzig 1986a: 496)).

I documented such paired SC4 sensilla in several families of the bombycoid complex, namely Lasiocampidae, Carthaeidae (Fig. 318), Saturniidae, Anthelidae (Fig. 319), Eupterotidae and *Spiramiopsis comma* (currently placed in Brahmaeidae, but *incerta sedis* – see Oberprieler & Duke 1994), but not in the non-bombycoid species *Danaus plexippus* (Nymphalidae). As with other sensilla campaniformia, the shape of these paired sensilla varies between shallow depressions and shallow protrusions in these taxa, but their location is constant – proximally of the latero-proximal end of the digitiform sensillum.

Discussion. A paired sensillum campaniformium SC4 seems to be unique to at least some members of the bombycoid complex, which is why I interpret character state (1)

as apomorphic for these taxa. However, many more taxa should be carefully examined than Grimes and Neunzig (1986a) and I did so far.

Summary. The appearance of these sensilla varies within a family from a shallow depressions over a depression with a protrusion to a shallow protrusion, and the shallow depressions in particular are easily overlooked. Merely the paired occurrence and specific location are indications of the homology of these structures. Therefore I consider my hypothesis of homology for the apomorphic character state (1) to be poorly supported.

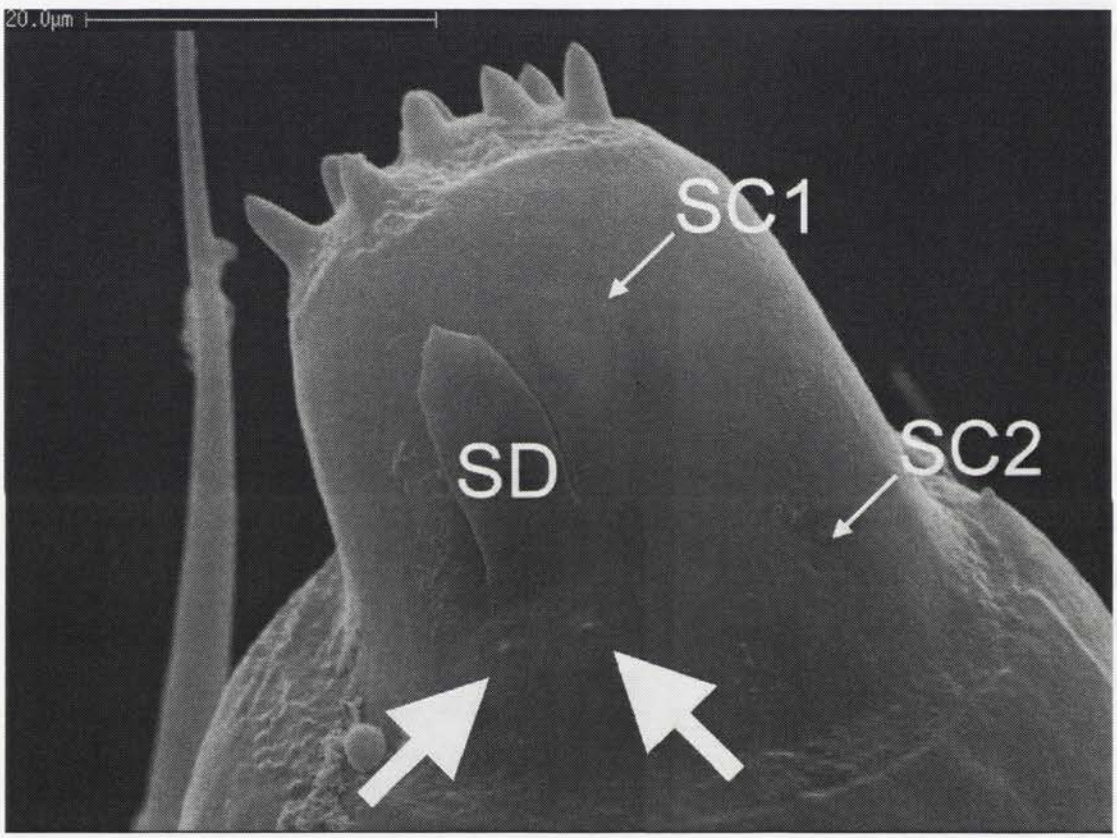

Fig. 316: *Opodiphthera helena* (Saturniidae), caterpillar (L1), anterior view (top=ventral) – apical segment of the maxillary palpus with a sensillum digitiformium (SD), two sensilla campaniformia (SC1 & SC2) and a pair of "mammiform sensilla" [SC4] (large yellow arrows).

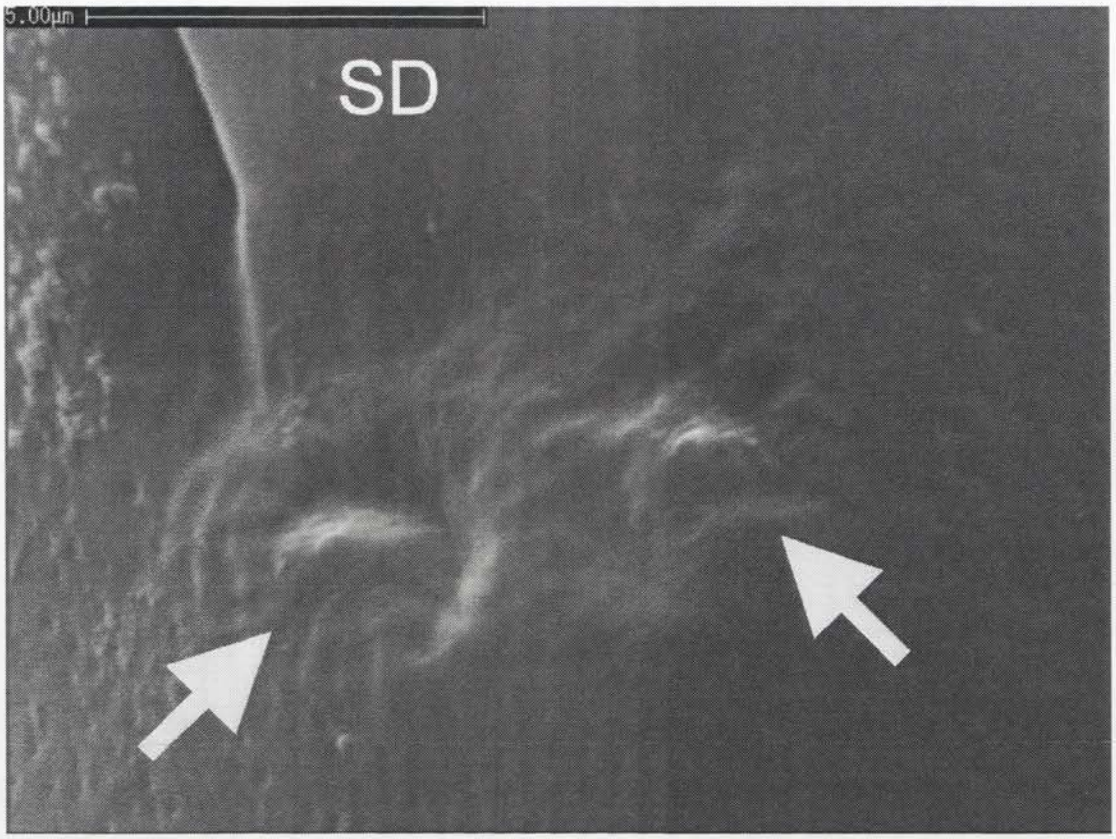

Fig. 317: *Opodiphthera helena* (Saturniidae), caterpillar (L1), anterior view (top=ventral) – the paired "mammiform sensilla" [SC4] (yellow arrows) of the apical segment of the maxillary palpus are located proximally of the sensillum digitiformium.

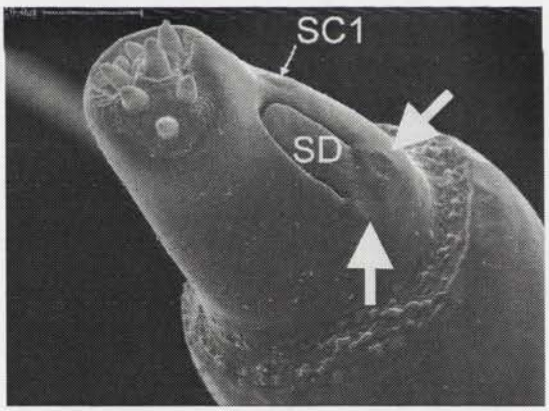

Fig. 318: *Carthaea saturnioides* (Carthaeidae), caterpillar (L1), meso-anterior view (left top=ventral) – apical segment of the maxillary palpus with a sensillum digitiformium (SD), a sensillum campaniformium (SC1) and a pair of sensilla campaniformia [SC4] in the position of the "mammiform sensilla" in other taxa (large yellow arrows).

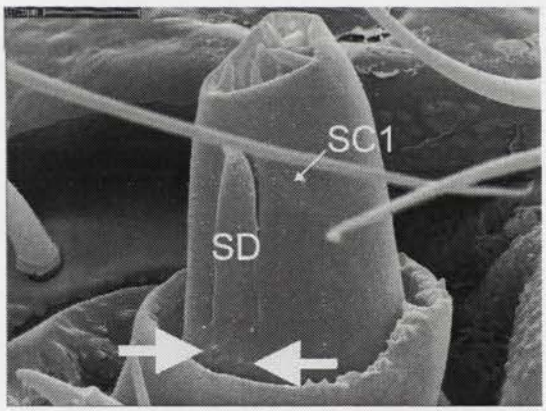

Fig. 319: *Nataxa flavescens* (Anthelidae), caterpillar (L1), anterior view (top=ventral) – apical segment of the maxillary palpus with a sensillum digitiformium (SD), a sensillum campaniformium (SC1) and a pair of "mammiform sensilla" [SC4] (large yellow arrows).

Character #H.60: Caterpillar labial palpus with a mesal lappet.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; well supported.

Introduction. In Glossata the fused prelabium and hypopharynx carry a spinneret, which is bordered latero-anteriorly by the two-segmented labial palpi. Taken together these structures are referred to as the hypopharyngeal complex (Grimmes & Neunzig 1986a, b; Fig. 320). In Macrolepidoptera, the basal segment of the palpi is typically short, broad and merged with the prelabium/hypopharynx, while the distal segment is simple, cylindrical and slender. The apical segment carries two apical setae, one of which has a pronounced tubular base and is particularly long (Fig. 325). This structure is remarkably constant within Macrolepidoptera.

Description. In some taxa, namely the bombycoid complex and the Notodontidae, the labial palpus is modified. The mesal side of the apical, cylindrical segment forms a lappet over its entire length. This lappet protrudes with a pointed tip slightly to distinctly beyond the apex of the labial palpus segment, but not beyond the two setae (Fig. 324). In many taxa this lappet is band-shaped (Fig. 321), but strongly enlarged to form a broad, apically rounded lobe in some taxa (Fig. 324). However, it is frequently strongly reduced to absent (Fig. 325). This mesal lappet is typically present in the first instar, but occasionally develops only in later instars (Figs 322, 323).

Discussion. Miller (1991: 134) had noticed these lappets in some Notodontidae ("Character 125. Mesal Flange of the Labial Palpus."), but not in any other taxa, which is why he used the structure as a synapomorphy in his cladistic analyses of notodontid phylogeny. He noted that although he felt confident to have scored the character correctly, its distribution within Notodontidae conflicted with other characters. Knowing that this modification occurs in the bombycoid complex, too, and that it is frequently reduced, this "conflict" is not surprising – the modification is a frequently reduced symplesiomorphy within the Notodontidae.

The function of these lappets is unknown, but it is noticeable that they protrude roughly as far distally as the prelabium/hypopharynx and that they close the gap between the labial palpi and the prelabium/hypopharynx (Fig. 324). Together they form a "wall", beyond which only the two setae of each labial palpus and the median spinneret protrude

distally. A further indication of the significance of the closing of the gap between labial palpi and prelabium/hypopharynx could be a different modification in the Saturniidae. None of the examined Saturniidae species have labial palpi with mesal lappets. Instead, the first instar caterpillars of most examined species (including the "critical" Oxyteninae and Agliinae; the modification seems to be an autapomorphy of the family Saturniidae) have a very broad spinneret, which extends laterally as far as or beyond the labial palpi (Fig. 326). The width of the spinneret is reduced in later instars, which indicates a function of the "wall" during the first instars only – a period during which caterpillars of the bombycoid complex are particularly actively producing silk, e.g., for "abseiling". Hence, it seems likely that this structure is linked to the production or processing of silken threads, possibly closing off some area if the spinneret is pushed against the substrate.

The mesal lappets of the labial palpi are only known from some Notodontidae and my own records in the bombycoid complex, which is why I interpret character state (1) as apomorphic for these taxa. However, my observations outside the bombycoid complex are not representative, and the absence of records of this structure in literature does not allow the ruling out of the occurrence of this structure, as indicated by the total lack of records for the relatively well studied bombycoid complex, in which the mesal lappets are common and widespread. Consultation with specialists of Geometridae (Dr. P. McQuillan, University of Tasmania) and Pyralidae (Dr. A. Solis, USDA) did not add any observations about the presence of this structure in these families. Nevertheless, as with the previous character, many more taxa have to be carefully examined specifically for the occurrence of this structure to gain more conclusive information on the distribution of the structure within Lepidoptera.

Summary. The modification of the labial palpus is characterized by the consistent location of the lappet on the mesal side of the apical segment, its extension over the entire length of the segment and the presence of a pointed tip distally of the segment's apex. Therefore I consider my hypothesis of homology for the apomorphic character state (1) to be well supported.

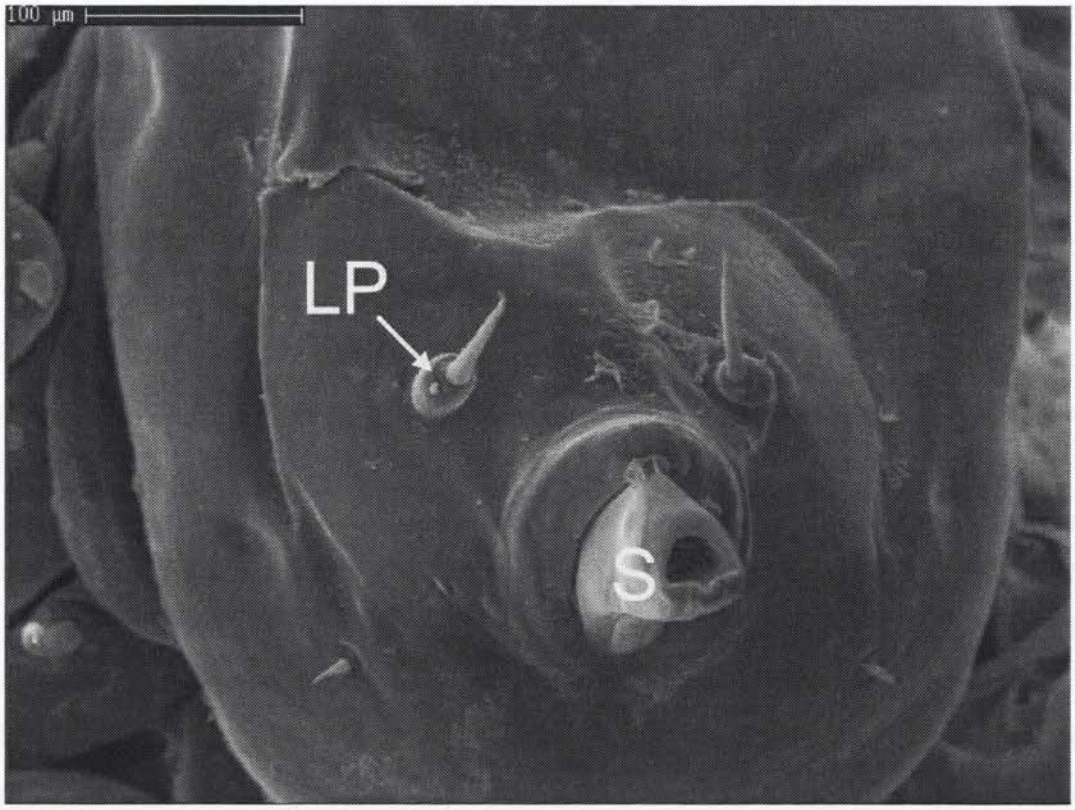

Fig. 320: *Danaus plexippus* (Nymphalidae), caterpillar (Lm), ventral view (top = anterior) – hypopharyngeal complex with labial palpus (LP) and spinneret (S); note the simple structure of the labial palpus.

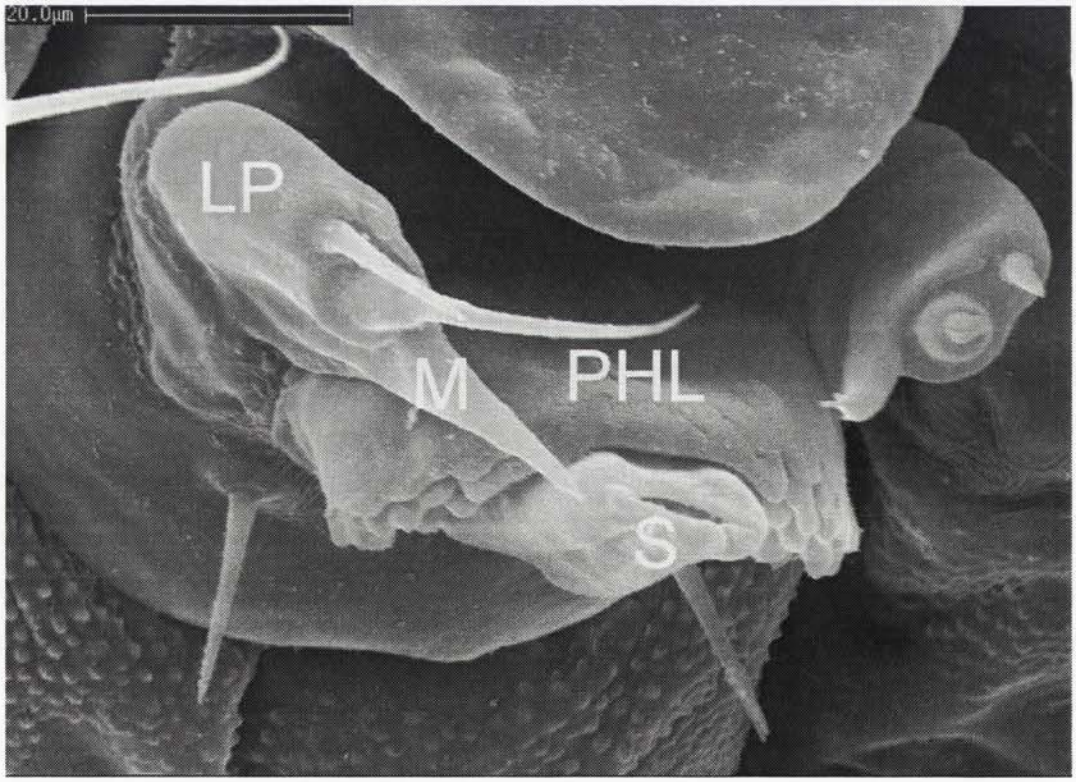

Fig. 321: *Anthela* n. sp. near *addita* (Anthelidae), caterpillar (L1), ventral view (top = anterior) – hypopharyngeal complex with labial palpus (LP), long mesal lappet (M) and spinneret (S); note the enlarged prementо-hypopharyngeal lobe (PHL); note how tightly even the narrow mesal lappet closes the gap between the LP and the PHL.

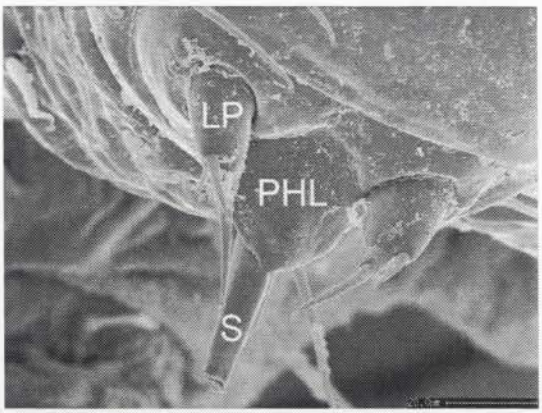

Fig. 322: *Spiramiopsis comma* (Brahmaeidae), caterpillar (L1), antero-ventral view (top right = anterior; bottom = ventral) – hypopharyngeal complex with simple labial palpus (LP), spinneret (S) and premento-hypopharyngeal lobe; note the absence of a mesal lappet on the labial palpus in L1.

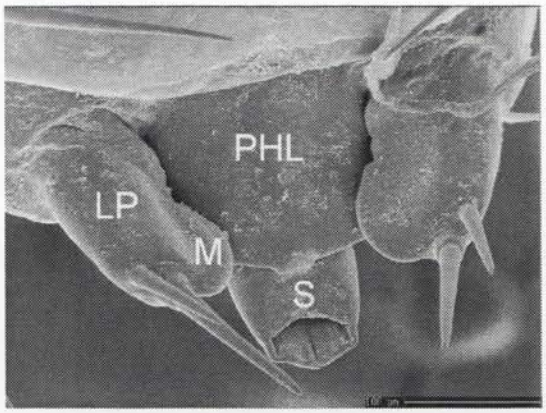

Fig. 323: *Spiramiopsis comma* (Brahmaeidae), caterpillar (Lm), anterior view (bottom = ventral) – hypopharyngeal complex with labial palpus (LP), rounded mesal lappet (M), spinneret (S) and premento-hypopharyngeal lobe; note the well developed mesal lappet on the labial palpus in Lm.

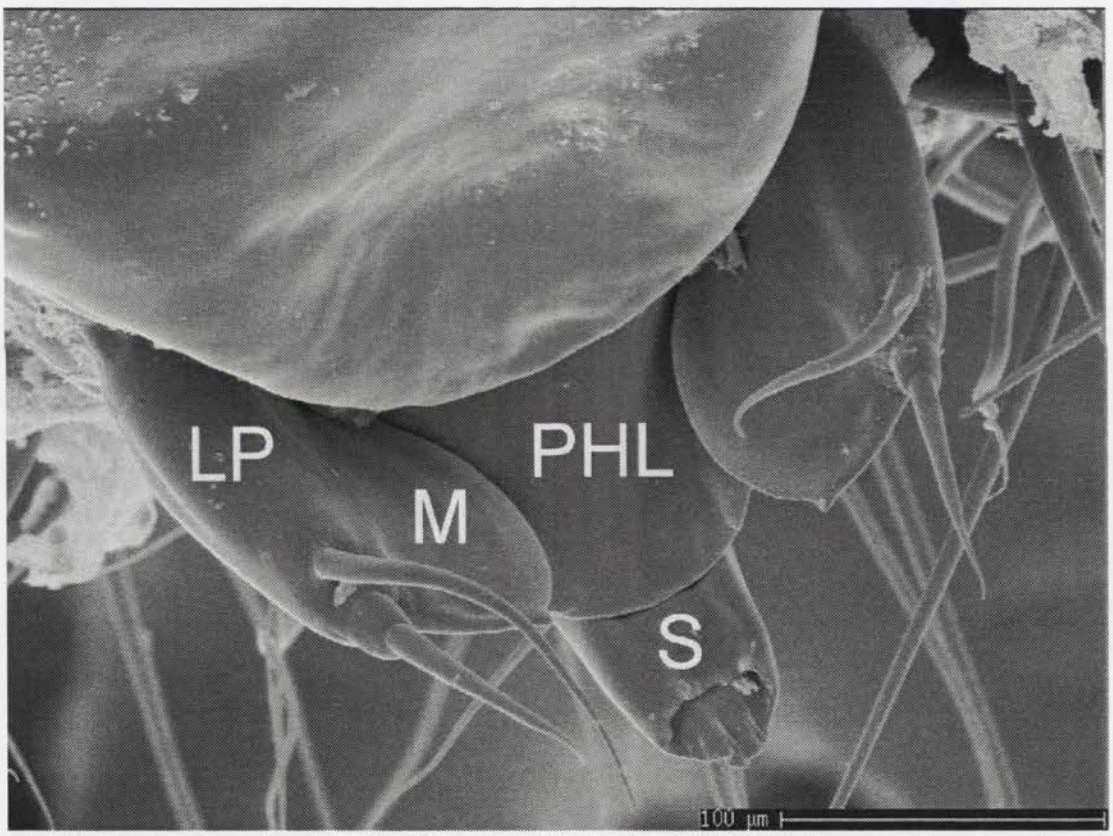

Fig. 324: *Poloma angulata* (Eupterotidae), caterpillar (Lm), anterior view (bottom right = ventral) – hypopharyngeal complex with labial palpus (LP), huge, rounded mesal lappet (M), spinneret (S) and premento-hypopharyngeal lobe; note how the mesal lappet closes the gap between the LP and the PHL.

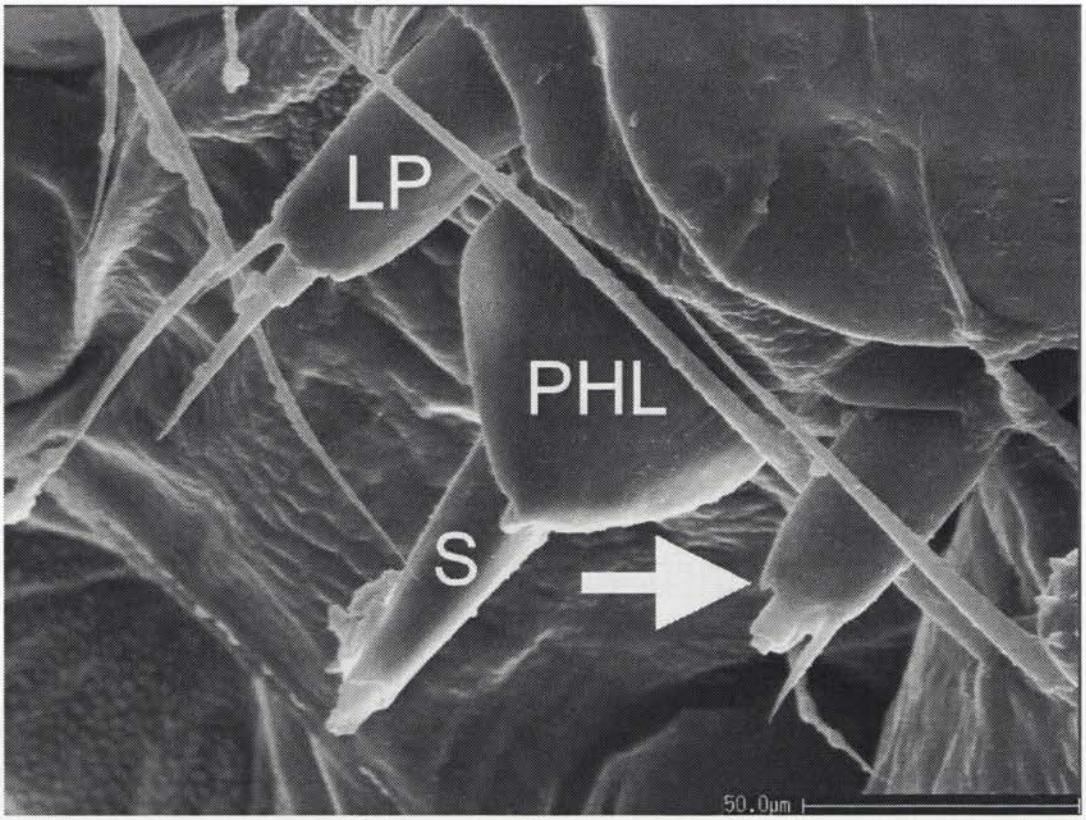

Fig. 325: *Anthela canescens* (Anthelidae), caterpillar (L1), anterior view (bottom right = ventral) – hypopharyngeal complex with labial palpus (LP), premento-hypopharyngeal lobe (PHL) and spinneret (S); note the remnant of the mesal lappet (yellow arrow).

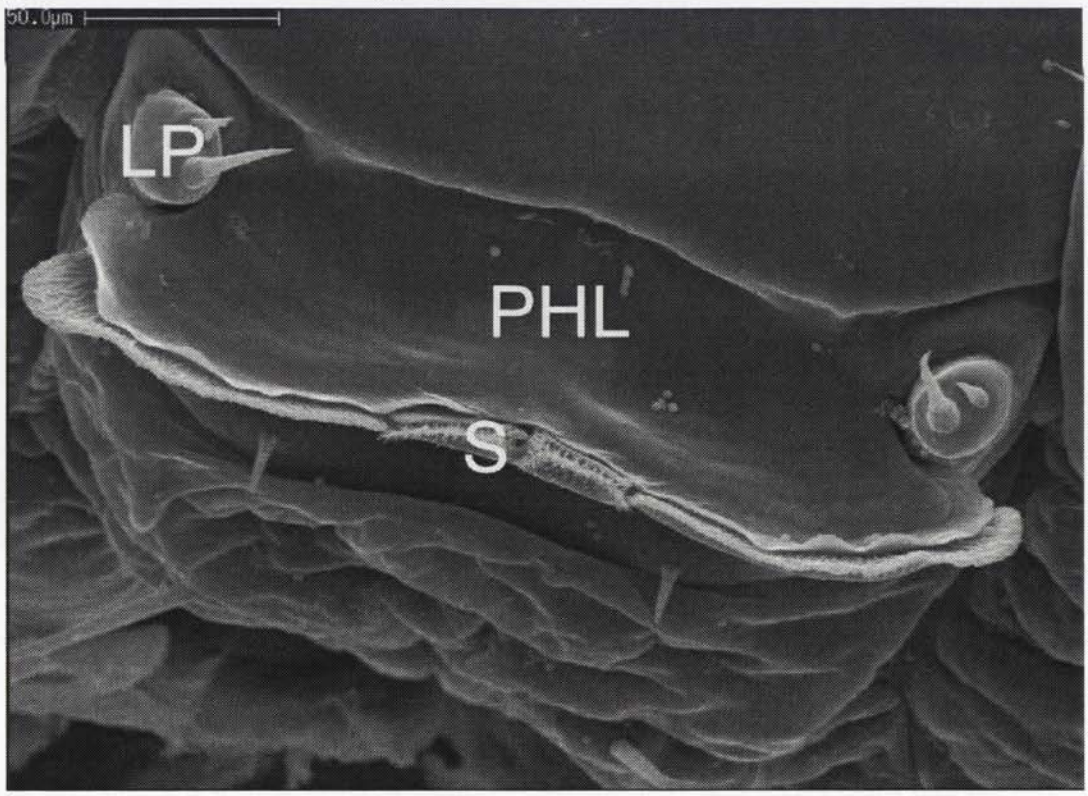

Fig. 326: *Opodiphthera helena* (Saturniidae), caterpillar (L1), ventral view (top right = anterior) – hypopharyngeal complex with labial palpus (LP), extremely broad premento-hypopharyngeal lobe and spinneret (S); note the absence of a mesal lappet and how the PHL extends laterally beyond the LP.

Character #H.61: Caterpillar integument covered with minute vesicles.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; very well supported.

Description. As discussed and illustrated in detail above (section III.6.1), the integument of most anthelid caterpillars is covered by hundreds of minute, shiny vesicles (Figs 269, 270, 271). These vesicles occur obligatorily from the second instar on, and their number increases with subsequent moults. The vesicles are seemingly randomly distributed on most areas of the body, including the headcapsule, but not on the legs, mouthparts, verrucae and the ventral side. Despite a connection between vesicle and integument by a very thin and short "stalk" only, the vesicles are extremely firmly attached to the integument, probably by some external substance on the "stalk". The vesicle has an opening into the "stalk", from which a peg protrudes slightly into the lumen of the vesicle. The distal end of the vesicle seems to have a smaller opening, through which the contents of the vesicle is released (Fig. 276). This contents is probably a polar, organic substance, which is solid at room temperature and sublimates very slowly. The function of the vesicles is unknown, but likely to be defensive.

Discussion. The vesicles are unique to the subfamily Anthelinae, in which they occur obligatorily in all species I examined. They are absent in the genus *Munychryia* and potentially in all other Munychryiinae, too (other caterpillars are unknown). As I found no traces of vesicles or structures that might produce or fill these vesicles, I assume the vesicles to be primarily absent in *Munychryia*. In Anthelinae the density of vesicles is particularly high in areas with few or no setae. If the function of the vesicles was a defensive one, this would corroborate my assumption of primary absence of vesicles in the secondarily "hairless" caterpillars of *Munychryia*. I did not observe such or similar vesicles in any non-anthelid caterpillars, and to my knowledge no such or similar vesicles have been recorded for any caterpillars in literature. Therefore, I interpret character state (1) as apomorphic.

Summary. The various details described above provide ample indications of the homology of these vesicles in different taxa, and their obligatory occurrence renders the scoring of this character very reliable. Therefore, I consider my hypothesis of homology for the apomorphic character state (1) to be very well supported.

Character #H.62: Abdominal segments A2-A7 with D2 verrucae larger than D1 verrucae.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; very poorly supported.

Introduction. The caterpillars of many taxa have shallow protrusions with multiple setae (verrucae) located in the position of the primary setae of other taxa. The different verrucae of one abdominal segment are different in location and size, and the dorsal verrucae are particularly prominent. In most taxa the dorsal D1 verrucae of the abdominal segments are distinctly larger than the D2 verrucae of the same segments (Fig. 328), and occasionally the D1 verrucae are even enlarged to the exclusion of the D2 verrucae (Fig. 329). In this case the identification of the remaining dorsal verrucae as either D1 or D2 is based on their location on the segment (more anteriorly or posteriorly) or the presence of the second pair of dorsal verrucae in earlier instars.

Description. In Anthelidae these proportions are reversed, their D2 verrucae of the abdominal segments A2-A7 are distinctly larger than the D1 verrucae in all instars (Fig. 327).

Discussion. The caterpillars of the *Munychryia* species do not have any setae or scoli at all. Within the Anthelinae, only in the highly apomorphic caterpillar of *Nataxa*, in which both pairs of dorsal verrucae are strongly reduced in mature caterpillars but present in earlier instars, is D1 slightly larger than D2. An enlarged D2 is rarely present in other families, e.g., in the Lymantriidae *Leptocneria reducta*, *Calliteara pura* and *Euproctis baliolalis.*

The abdominal D1 verrucae are larger than the D2 verrucae in most taxa. This is the case in all families of the bombycoid complex with verrucae or scoli, except for the Anthelidae. As the mere difference in relative size is only a very poor indication of homology, I only assume character state (1) to be apomorphic based on its absence in other families of the bombycoid complex and only sporadic occurrence in other taxa.

Summary. The difference in relative size is the only indication of homology and convergent, similar appearances as present in, e.g., Lymantriidae, cannot be distinguished as such on this basis. Therefore I consider my hypothesis of homology for

the apomorphic character state (1) to be very poorly supported.

Fig. 327: *Anthela acuta* (Anthelidae), caterpillar (L4) – abdominal segments A2-A7 with D2 verrucae (yellow arrows) larger than D1 verrucae (blue arrows).

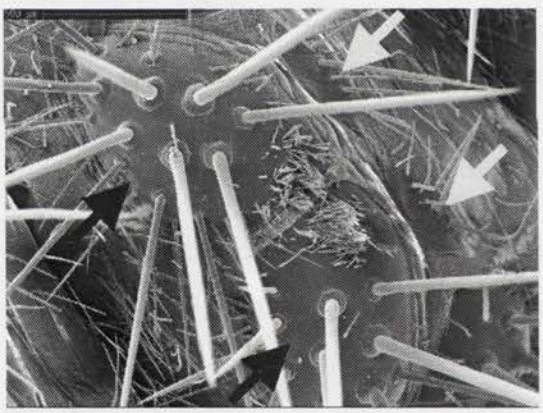

Fig. 328: *Epicoma* sp. (Notodontidae), caterpillar (L4), dorsal view (bottom left = anterior) – abdominal segment with D1 verrucae (blue arrows) much larger than D2 verrucae (yellow arrows).

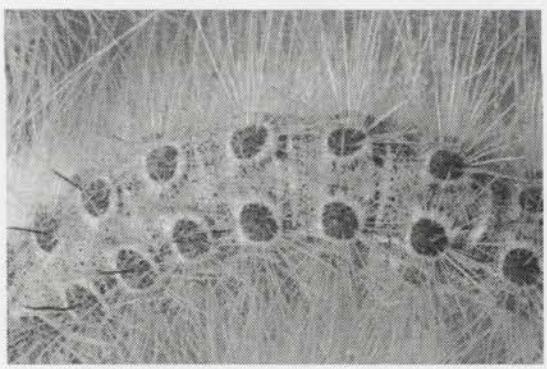

Fig. 329: *Cotana serranotata* (Eupterotidae), caterpillar (L6), dorsal view (bottom left = anterior) – abdominal segment with D1 verrucae greatly enlarged and D2 verrucae absent.

Character #H.63: Short secondary setae with serration restricted to apex.

- Character state (0) '**No**'; plesiomorph.
- Character state (1) 'Yes'; apomorph; poorly supported.

Introduction. All known caterpillars of Anthelinae are densely covered with secondary hairs of variable length in older instars. These secondary hairs are barbed in most species, and the degree varies from hardly visible to very prominent. The serration extends over the entire length of the hair and increases gradually from the base towards the apex of the hair (Fig. 330). Apically these hairs form a very prominent, pointed tip (Fig. 331).

Description. In a number of antheline species modified, short secondary hairs are located on the dorsal side of the abdominal segments, but never on the verrucae. These hairs are distinctly, densely barbed, but only at the apex of the hair (distal $1/16^{th}$ of the hair length), while the rest of the hair is remarkably smooth (Fig. 332). The size of the barbs is roughly equal for the apical 10-20 spines, but decreases rapidly towards the base of the hair (Fig. 333). The hair has a pointed tip, which is not larger than the most distal spines.

Discussion. This type of hairs seems to be unique to some antheline species, which is why I interpret character state (1) as apomorphic.

In some species these only apically barbed hairs are further modified and in a particular arrangement, which I interpret as a subsequent modification (character #H.64 (1) of the apomorphic character state (additive binary coding).

Summary.

The restriction of the barbs to the apex of the hair is characteristic but simple, and the shape and size of the apical serration are somewhat variable. Therefore, I regard my hypothesis of homology for the apomorphic character state (1) as poorly supported.

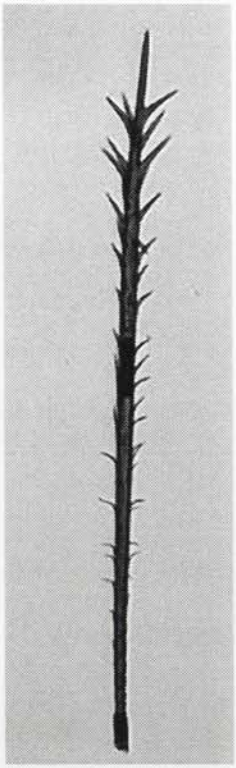

Fig. 330: *Pterolocera* sp. B (Anthelidae), caterpillar (Lm) – short, serrate secondary hair of the dorsal side of the abdomen; note the extent of the serration over most of the hair's length.

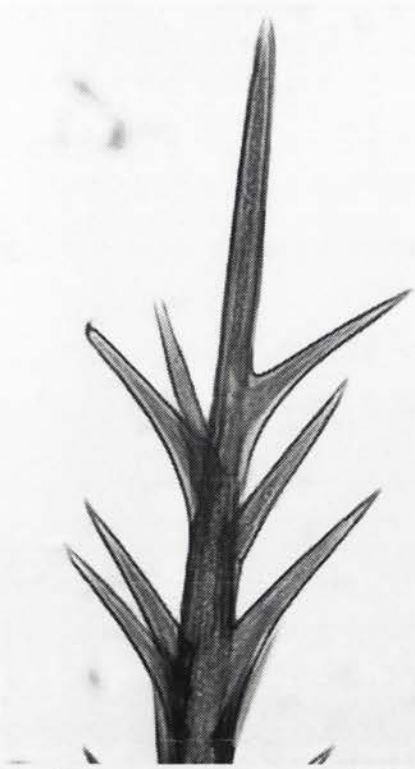

Fig. 331: *Pterolocera* sp. B (Anthelidae), caterpillar (Lm) – apex of a short, serrate secondary hair of the dorsal side of the abdomen; note the very long apical tip.

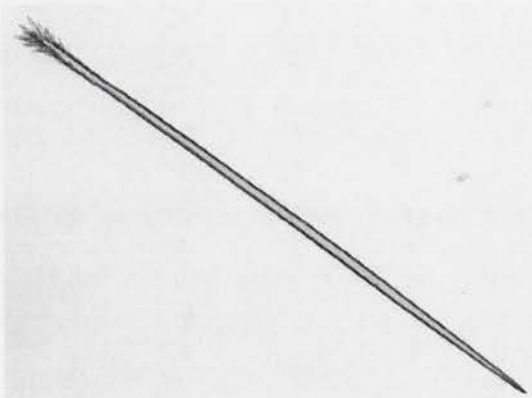

Fig. 332: *Anthela reltoni* (Anthelidae), caterpillar (L5) – short, serrate secondary hair of the dorsal side of the abdomen; note the restriction of the serration to the apex of the hair.

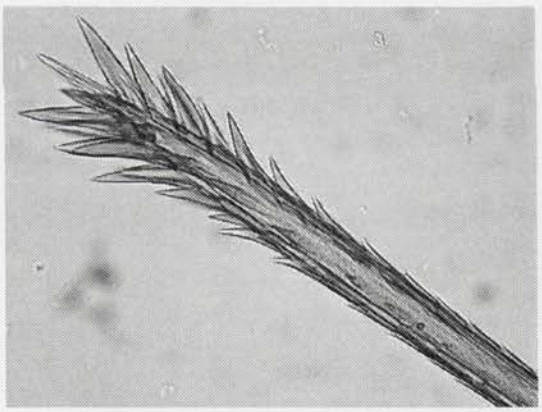

Fig. 333: *Anthela reltoni* (Anthelidae), caterpillar (L5) – apex of short, serrate secondary hair of the dorsal side of the abdomen; note the almost equal size and density of the distal 10-20 spines, as well as the short apical tip.

Character #H.64: Lm caterpillars with dense "cushions" of aposematically coloured, apically multiple-forked hairs on abdominal segments A2-A7.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; very well supported.

Description. Many caterpillars carry brushes, tufts or cushions of specialized hairs on the dorsal side of some segments, and these can be used as highly diagnostic characters. In some anthelid taxa the abdominal segments A2-A7 have a dorsal area of specialized, short hairs (Figs 334, 338). These "cushions" consist of densely packed, apically multiple-forked, short and stiff hairs, which are greyish-blue to blue (Figs 335, 337). The hairs are of the type described as character #H.63 state (1), but are unique in having apically 3 (occasionally 2 or 4) barbs, which are much larger than any other barbs of the hair and protrude a long way beyond the apex of the hair shaft (Figs 339, 340). The cushions of these hairs extend sagitally from anteriorly to the D1 verrucae up to the D2 verrucae, and transversely over most of the dorsal side, therefore surrounding the D1 verrucae, but not the D2 verrucae (Fig. 336). They are surrounded by an area of minute, red hairs, which are apically multiply forked (Figs 336, 337, 341).

Discussion. I never observed the function of these "cushions" directly, but the characteristics of these hairs and arrangement in dense cushions suggests a defensive function.

I reared two species with such hair cushions, namely *Anthela rubicunda* (Fig. 338) and *A. guenei* (Fig. 334). In both species these hair cushions were only present in the final instar caterpillars. As typical for the hairs of Anthelidae in general, these hairs were incorporated in the outer layer of the cocoon (see character #H.67). In two instances I found a few of such apically multi-forked hairs embedded in the abdominal skin of a male moth (ANIC/AZ 13: *A. callileuca*; ANIC/AZ 263: *A. callispila*). In *A. callileuca* the extreme apical spines are a bit smaller and with a larger apical tip than illustrated for *A. rubicunda* in Fig. 340, but they match exactly the hairs arranged in the typical cushion in an unidentified caterpillar from QLD, Biggenden, Bluff Range (ANIC caterpillar collection, vial #3061). In both cases the hairs found in the abdominal skins are likely to have penetrated the abdomen of the soft moth during eclosion from a cocoon "armed" with such hairs, and hence I score both species as possessing these cushions of hairs, even though their caterpillars are unknown.

Occasionally, cushions of densely packed hairs also occur in non-anthelid taxa, e.g., the final instar caterpillars of *Cotana serranotata* (Fig. 342), *Panacela lewinae* (both Eupterotidae) and *Epicoma* spp. (Notodontidae) (Figs 343, 344). However, their cushions differ from the ones in Anthelidae in structural details, e.g., their hairs are apically simple (Eupterotidae) or the cushions are restricted to an area between the D1 verrucae of one segment and the hairs are barbed differently (*Epicoma* spp.).

Abdominal hair cushions with the characteristics described above are unique to some anthelid species. Therefore, I interpret character state (1) as apomorphic.

Summary. These cushions of specialized hairs are characterized by several details, particularly their specific location and extent, the density, the multiple-forked tips of the spines and the aposematic colour. Given the number of indications of homology, I consider my hypothesis of homology for the apomorphic character state (1) to be very well supported.

Fig. 334: *Anthela guenei* (Anthelidae), caterpillar (Lm) – abdominal segments A2-A7 carry a dorsal, dense cushion of aposematically coloured, apically multiple-forked spines.

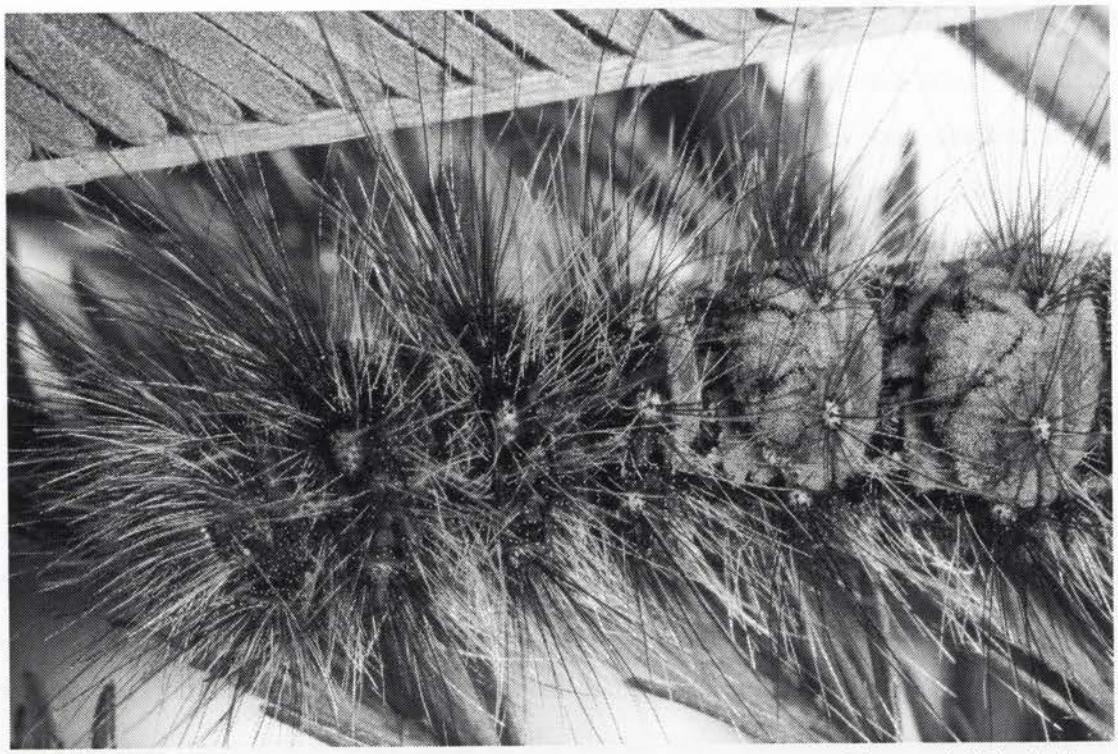

Fig. 335: *Anthela guenei* (Anthelidae), caterpillar (Lm) – thoracic segments without and abdominal segments A2-A3 with a dorsal, dense cushion of aposematically coloured, apically multiple-forked spines.

Fig. 336: *Anthela guenei* (Anthelidae), caterpillar (Lm) – abdominal segment with a dorsal, dense cushion of aposematically coloured, apically multiple-forked spines; cushion envelops D1 but not D2 verrucae.

Fig. 337: *Anthela guenei* (Anthelidae), caterpillar (Lm) – abdominal segment with a dorsal, dense cushion of aposematically coloured, apically multiple-forked spines.

Fig. 338: *Anthela rubicunda* (Anthelidae), caterpillar (Lm) – abdominal segments A2-A7 carry a dorsal, dense cushion of aposematically coloured, apically multiple-forked spines.

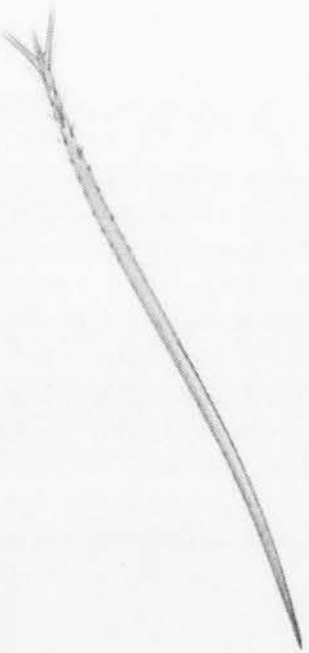

Fig. 339: *Anthela rubicunda* (Anthelidae), caterpillar (Lm) – specialized hair of hair cushion.

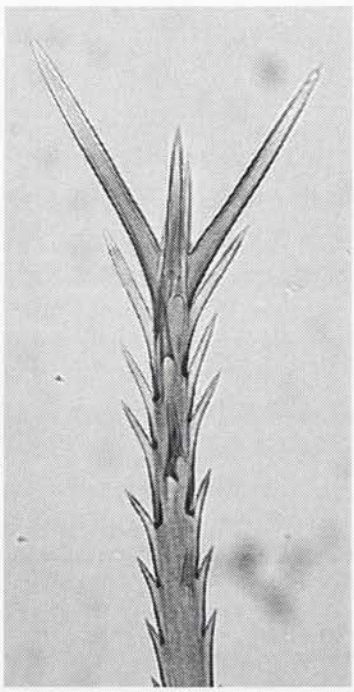

Fig. 340: *Anthela rubicunda* (Anthelidae), caterpillar (Lm) – apex of specialized hair with very long apical barbs (hair cushion).

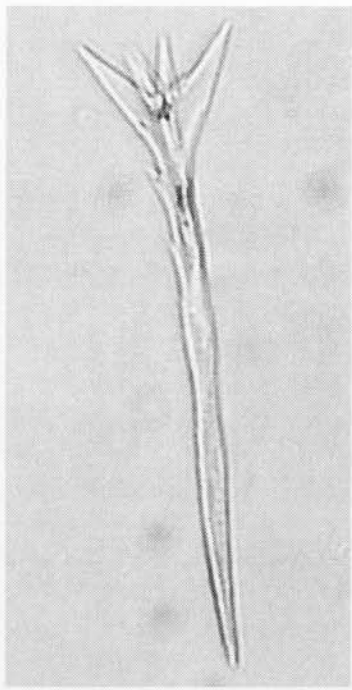

Fig. 341: *Anthela rubicunda* (Anthelidae), caterpillar (Lm) – minute hair of field of red hairs surrounding the hair cushions.

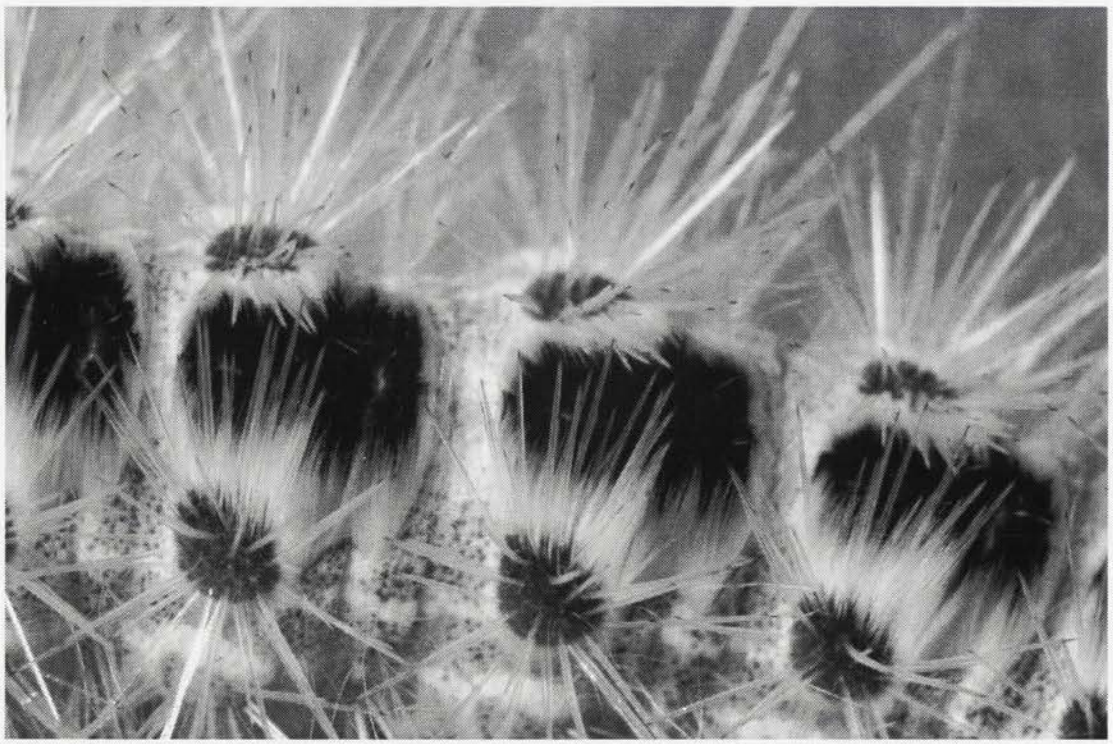

Fig. 342: *Cotana serranotata* (Eupterotidae), caterpillar (Lm), dorsal view (left = anterior) – abdominal segment with a dense cushion of short setae between the prominent D1 verrucae of one segment.

Fig. 343: *Epicoma* sp. (Notodontidae), caterpillar (L4), dorsal view (left = anterior) – two abdominal segments with a dense cushion of short setae between the prominent D1 verrucae of each segment.

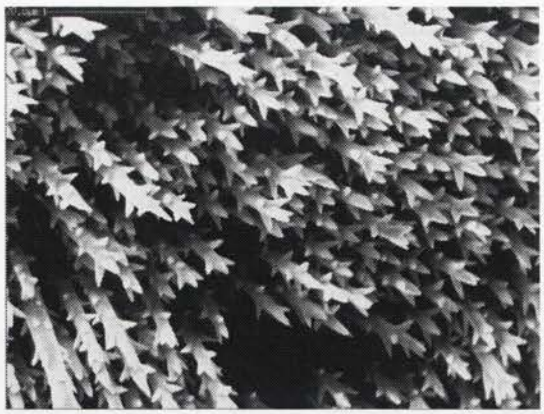

Fig. 344: *Epicoma* sp. (Notodontidae), caterpillar (L4), dorsal view (left = anterior) – short, stiff, serrate hairs of cushion on the abdominal segments.

Character #H.65: Abdominal segment A1 with a pair of hair brushes on the D2 verrucae.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; moderately supported.

Description. In many anthelid species the first abdominal segment carries a pair of hair pencils. These hair pencils consist of particularly long, thin and soft hairs, which arise closely approximated and largely parallel to each other from the D2 verrucae. In some taxa they form very prominent, white, red or black hair pencils, which protrude above the surrounding other setae (Figs 347, 348, 349). These brushes are absent in the first instar, but occur in the second and subsequent instars (Figs 345, 346). They are particularly well developed in the final instar in some taxa (e.g., *Anthela astata*), while they are only present in second and third instar but entirely lost in the final instar in other taxa (e.g., *A. nicothoe*). In other anthelid taxa they clearly do not occur in any instar.

Discussion. These hair brushes are unique to some Anthelidae, which is why I interpret character state (1) as apomorphic.

Summary. The main indications of the homology of these hair brushes in different taxa are their origin on the D2 verrucae of the abdominal segment A1 and their closely parallel arrangement. Other characteristics like length and colour are very variable and more useful for diagnostic purposes. The subsequent loss of these brushes in later instars makes an accurate scoring of this character difficult as it requires the rearing of caterpillars. Further, it seems likely that the absence of these hairs even in early instars of some taxa is a continuation of this tendency to reduce these hair brushes. Therefore I consider my hypothesis of homology for the apomorphic character state (1) to be moderately supported.

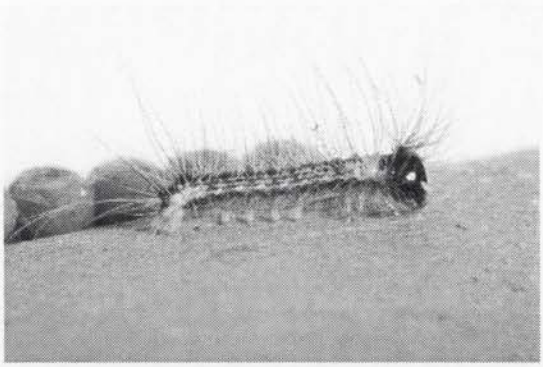

Fig. 345: *Anthela astata* (Anthelidae), caterpillar (L1) – abdominal segment A1 does not carry any hair brushes on the D2 verrucae.

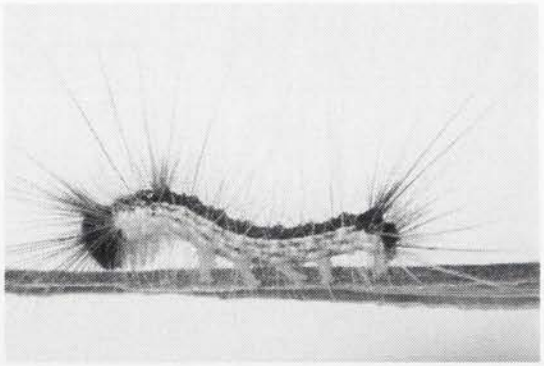

Fig. 346: *Anthela astata* (Anthelidae), caterpillar (L2) – abdominal segment A1 carries dorsally a pair of red hair brushes on the D2 verrucae.

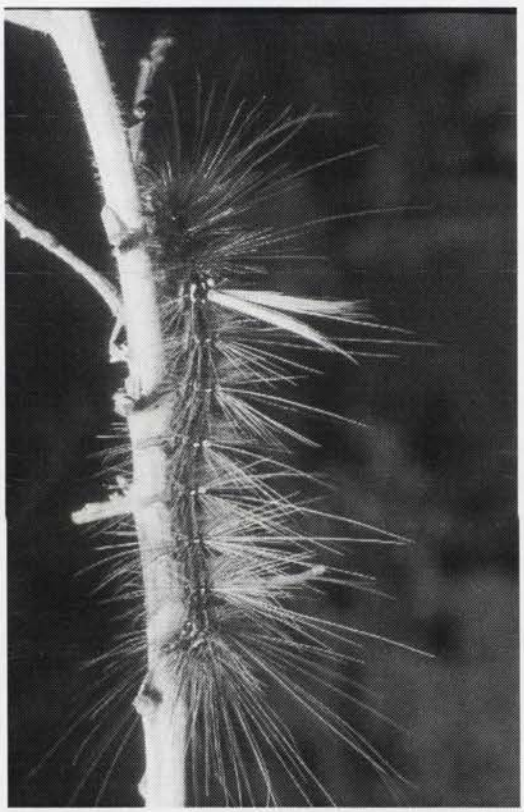

Fig. 347: *Anthela astata* (Anthelidae), caterpillar (L4) – abdominal segment A1 carries dorsally a pair of long, white hair brushes on the D2 verrucae.

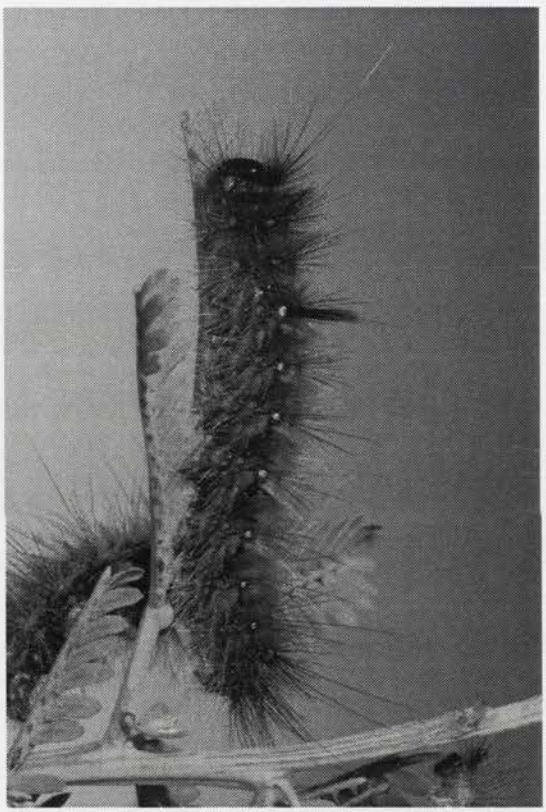

Fig. 348: *Anthela repleta* (Anthelidae), caterpillar (L4) – abdominal segment A1 carries dorsally a pair of short, black hair brushes on the yellow D2 verrucae.

Fig. 349: *Anthela reltoni* (Anthelidae), caterpillar (L4) – abdominal segment A1 carries dorsally a pair of small, white hair brushes on the D2 verrucae.

Character #H.66: Bending cuticle of proleg with two layers of transverse microfibrils.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; moderately supported.

Introduction. In an outstanding publication on the adhesive devices of caterpillars, Hasenfuss (1999) noted a peculiarity of the caterpillar proleg cuticle, which he proposed as a synapomorphy of Bombycoidea *sensu lato*. This rather recently discovered and not widely known characteristic might be the most convincing synapomorphy of the bombycoid complex proposed so far. I cannot add any own information and this character analyses is solely based on the descriptions and illustrations by Hasenfuss (1999: 146, 156, 158, Figs 3C & 13).

Hasenfuss (1999: 145) distinguishes three types of cuticle based on the arrangement of fibrillary chitin micelles. One of these types, which he termed "pad cuticle", has the fibrillary micelles arranged obliquely at an angle of 45° to the cuticle surface, rather than parallel to it.

Description. In the older caterpillar instars the mesal side of the "subcorona", which is an area of the proleg proximally of the crochets (chitinous hooks), consists of different cuticle types. In Macrolepidoptera a single layer of "pad cuticle" is located beneath the epicuticle, followed by a layer of "normal cuticle" and a layer of "undulated-type cuticle". All members of the bombycoid complex examined by Hasenfuss (1999) differ from this scheme in as much as they have a second layer of "pad cuticle" between the "normal cuticle" and the "undulated-type cuticle".

Discussion. The occurrence of a second layer of "pad cuticle" is restricted to a certain area, the mesal area of the "subcorona". Further, this pad-cuticle seems to extend no further than the "regular" layer of "pad cuticle" does – it appears as a duplication of the "pad cuticle", separated from the "regular" layer by a layer of "normal cuticle". The "pad cuticle" itself is a structure repeatedly found in different locations and hence its structural details provide no indications of the homology of this structure in a specific location, as it is the case with other repeatedly occurring structures, e.g., setae.

I did not examine any caterpillars for this characteristic myself, and Hasenfuss (1999) did not examine all families of the bombycoid complex. Nevertheless, with the

exception of Mimallonidae he examined members of all those families for which the placement in the bombycoid complex has been controversial – other families are linked to one of these by other characteristics. These are the Lasiocampidae, Endromidae, Sphingidae, Bombycidae (Bombycinae), Saturniidae, Lemoniidae and Brahmaeidae. The number of different species and instars he examined was unusually large and very representative of this group, but, probably even more important, also of non-bombycoid Macrolepidoptera. This is a better basis for the assessment of the occurrence of this characteristic than presently available for most other synapomorphies proposed for the bombycoid complex. According to Hasenfuss (1999: 158) this characteristic only occurs in members of the bombycoid complex, hence I interpret character state (1) as apomorphic for these taxa.

Summary. The only indications of homology are the specific location and extent, which is why I consider my hypothesis of homology for the apomorphic character state (1) to be moderately supported.

Character #H.67: Cocoon "double-walled".

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; moderately supported.

Introduction. Many Lepidoptera form a silken shelter for pupation, and the cocoons of most members of the bombycoid complex are particularly elaborate. Except for some taxa pupating in the ground (e.g., Sphingidae), the caterpillars spin sack-like cocoons with walls of variable thickness, occasionally incorporating the caterpillars hairs.

Description. In Anthelidae the wall of the cocoon consists of two distinct layers (Fig. 350). The hairs and spines of the caterpillar are incorporated in the outer wall, in some taxa apparently at random, but in others radiating from the cocoon (e.g., *Chelepteryx collesi*, *Anthela nicothoe*). The inner layer is a smooth lining, which covers the ends of the hairs incorporated in the outer layer and probably serves as a protection for the pupa and emerging moth. The basic structure of a double-walled cocoon is retained in taxa with more specialized cocoons. It is present in the subterranean cocoons of *Pterolocera* as well as in the hanging, smooth cocoons of a species group including, amongst others, *A. stygiana*, *A. xantharcha* and *A. unisigna*. In these species the hairs are not protruding through the outer layer, but are laying flat between the two closely approximated layers. This "thin" composite wall is covered by an additional substance externally. The opposite is the case in a species group including *A. acuta*, *A. astata* and *A. varia*. Their cocoons are particularly thick, consisting of a thin inner lining and multiple, loose outer layers of silk and hairs. Irrespective of these modifications, all of these cocoons are "double-walled".

Discussion. In the field I partly observed the spinning of a cocoon by *C. collesi*, which has spines radiating from the cocoon (see above, section I.2.5). Initially the outer wall is spun without hairs penetrating it. This indicates that the construction of the cocoon proceeds by spinning the outer layer, followed by the "rubbing off" and penetrating of the spines and a final spinning of the inner lining, with the latter two actions possibly occurring at the same time. Such a sequence is a possible explanation for the presence of two distinct silken layers.

I do not have a cocoon of the genus *Munychryia* available, as none are preserved in the ANIC and my own livestock of *M. senicula* died prior to pupation. No double-

walled cocoon is mentioned for this species in literature, but Common and McFarland (1970: 14) illustrated and described it as "Elongate-elliptical, of tough pale brown or pale tan silk, internal surface smooth, pupa not visible through walls.". The smooth internal surface and the visible outer surface argue for a double-walled cocoon as in other Anthelidae, which might not be obvious if the two walls were closely approximated as in some other species.

The wall of the silken cocoons of the bombycoid complex generally consists of a (or probably several) silken thread stuck onto objects like leaves and branches, as well as onto itself. Independently of how often a thread is stuck onto itself (how thick the wall is), the wall is a single structure. The double-walled cocoon, in which the wall consists of a smooth inner lining and at least one outer layer, seems to be unique to the Anthelidae. A smooth inner lining is also present in other taxa that incorporate hairs in their cocoon (e.g., *Calliteara pura* (Lymantriidae)), but in these taxa the inner lining is merged with the rest of the cocoon. Therefore I interpret character state (1) as apomorphic.

Summary. Without having observed the actual construction of the cocoon, the two layers and the incorporation of hairs either in the outer layer or between the two layers are the only indications of homology. Therefore I consider my hypothesis of homology for the apomorphic character state (1) to be moderately supported.

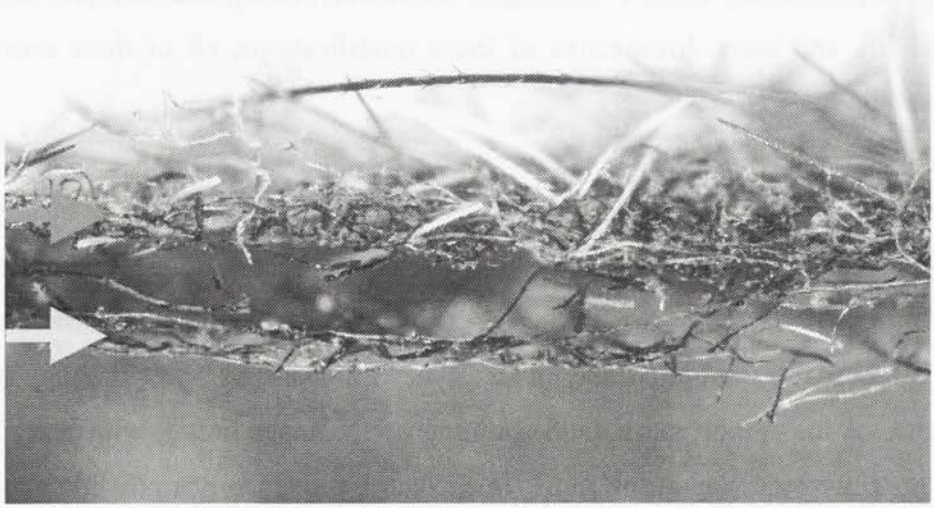

Fig. 350: *Anthela guenei* (Anthelidae), cocoon – cross-section through the double-walled cocoon; the outer wall (green arrow) is "armed" with protruding spines from the caterpillar, while the inner wall (yellow arrow) is a smooth lining, protecting the pupa and emerging moth against the embedded spines.

Character #H.68: Subterranean cocoon with silken exit tube.

- Character state (0) **'NO'**; plesiomorph.
- Character state (1) **'YES'**; apomorph; well supported.

Introduction. Silken cocoons are generally constructed in relatively exposed conditions – attached to a twig, under bark, between leaves at a tree or between debris on the ground. If pupation takes place in the ground, it is typically within a horizontal chamber formed in the soil, occasionally including a few silken threads, but without a silken cocoon.

Description. In some species of the anthelid genus *Pterolocera*, pupation takes place within a double-walled, silken cocoon with hairs embedded in the outer layer of the wall. Unlike other Anthelidae, this cocoon is constructed vertically within the soil and has a silken exit tube to the surface.

Discussion. The length of the cocoon exit tube depends on the depth at which the cocoon is constructed, and this is most probably linked to the climate and the density of the soil. A cocoon of this type has been described in detail for *Pterolocera isogama* by McGauran (1951).

Such a cocoon is typical of grass-feeding *Pterolocera* species and the pupation in the ground is likely to be an adaptation to either hot and dry conditions in the open habitat, or to burning of the habitat. Not all *Pterolocera* species feed on grasses, and a Western Australian species I raised on *Banksia* species pupated without restless searching for a pupation site in a silken cocoon within some tissue paper. However, this pupation occurred in captivity and in the absence of soil, hence a subterranean cocoon might have been constructed under natural conditions.

No other anthelid species, including those known to feed on grasses (*A. ferruginosa* group, *A. denticulata* group, *A. ocellata* group), pupate in this particular way. The subterranean cocoon with a silken exit tube is unique to the anthelid genus *Pterolocera*, which is why I interpret character state (1) as apomorphic.

Summary. The cocoon differs from other anthelid cocoons by its silken exit tube and the location in the soil. Further, the vertical orientation of the cocoon within the soil is very unusual for subterranean pupation, which is in a horizontal orientation in all other taxa. Therefore I consider my hypothesis of homology for the apomorphic character

state (1) to be well supported.

Fig. 351: *Pterolocera* sp. (Anthelidae), cocoon – subterranean cocoon with a short silken exit tube.

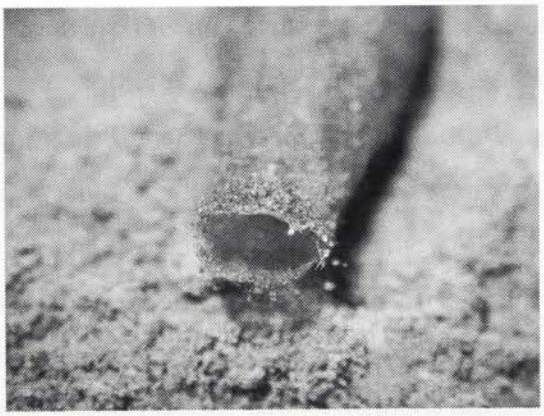

Fig. 352: *Pterolocera* sp. (Anthelidae), cocoon – opening of the short, silken exit tube of the subterranean cocoon.

III.7) PHYLOGENETIC HYPOTHESES

In the previous section I presented and discussed hypotheses of homology as well as hypotheses of character polarity of these proposed homologies. Taken together they form hypotheses of apomorphy, which are the basis for the postulation of monophyletic taxon groups, as argued for by Hennig (1950). Each monophylum identified by apomorphies is part of a larger monophylum identified by other apomorphies. This encaptic system of hypothesized monophyla establishes the hypothesized evolutionary relationships of these taxa and can be illustrated in a dendrogram ("Hennigian Argumentation scheme"). The better founded and the larger in number the hypotheses of apomorphy of one monophylum are, the better supported is the hypothesis of monophyly.

Based on my hypotheses of apomorphy I construct an encaptic system of hypothesized monophyla for the Anthelidae (Fig. 354) and the bombycoid complex (Fig. 355). The actual construction is simple for apomorphies that support compatible monophyla, and therefore I do not spell out the process for all apomorphies supporting compatible monophyla. An example of such compatible monophyla is the group of species consisting of *Anthela addita*, *A. virescens*, *A. phaeodesma* and *A. ferruginosa*. Apomorphy H.14(1) is shared by *A. addita* and *A. virescens*, which is why I postulate these species to form a monophylum. Apomorphy H.13(1) occurs in this monophylum and in *A. phaeodesma*, supporting a monophylum consisting of *A. addita*, *A. virescens* and *A. phaeodesma*. Apomorphy H.12(1) is present in the latter monophylum and *A. ferruginosa*, which supports the hypothesis of all four species forming a monophyletic group.

However, some hypotheses of apomorphy support hypotheses of monophyly that are not compatible with each other. For example, apomorphy H.41(1) supports a monophylum consisting of *Anthela ocellata*, *A. oressarcha* and *Nataxa flavescens*, while apomorphy H.43(1) supports a monophylum consisting of *N. flavescens*, *A. nicothoe* and *A. excellens*. *N. flavescens* alone cannot be a member of both monophyla, which is why these two monophyla are incompatible. If the character states have been scored correctly, one of the two hypotheses of apomorphy must be incorrect. The mistake can be within the hypothesis of homology or within the hypothesis of polarity of either apomorphy. A re-examination of both hypotheses is necessary, and if no mistake

can be found, only the hypothesis of monophyly is retained that is better supported by the number and quality of the hypotheses of apomorphy, while the less supported hypothesis of monophyly is refuted. If no decision between apomorphies supporting incompatible monophyla can be made on this basis, the conflict is presented as a polytomy in a consensus dendrogram. Any incompatibilities require an *ad hoc* explanation for one of the hypotheses of apomorphy, e.g., the postulation of a convergence, a "reversal" or a loss. In the chosen example the monophylum consisting of *N. flavescens*, *A. ocellata* and *A. oressarcha* is clearly refuted by the higher quality of apomorphy H.43(1) and additionally by apomorphy H.23(1). Being the most parsimonious explanation, I postulate *ad hoc* a convergent development of character #H.41 state (1), the distal displacement of muscle *m7* by muscle *m5* in the valva of *N. flavescens*.

III.7.1) The Anthelidae

My argumentation on anthelid phylogeny meets the two conditions required for Hennigian Argumentation (see section III.4.2), namely the use of monophyletic terminal taxa and the use of ground plan character states for these terminal taxa. I use species as terminal taxa, or occasionally combine species in species complexes if this reduces the number of unknown character states. The character states scored for these taxa are representative for all specimens examined and not variations of individual specimens. All apomorphies that appear to be autapomorphies of terminal taxa in my dendrogram are synapomorphies of species that are very similar to the terminal taxa (identical character states) and omitted for the sake of clarity. I now discuss individually all those monophyla within the Anthelidae that are incompatible with other monophyla and require *ad hoc* explanations.

The placement of *Nataxa flavescens* not only requires the *ad hoc* postulation of a convergence as discussed above (section III.7), but also an *ad hoc* postulation for a "reversal" of apomorphy H.62(1), the larger size of the larval D2 verrucae compared to the D1 verrucae. In this species the D2 verrucae are reduced and even entirely lost in the final instar caterpillar, hence the D1 verrucae are larger than the D2 verrucae. This appears as being the plesiomorphic character state. A large number of apomorphies, some of which are very well founded, supports the proposed placement of *N. flavescens* and clearly refutes an alternative placement suggested by character #H.62.

Anthela nicothoe lacks apomorphy H.23(1), while being a member of a well supported [H.43(1)] monophylum that otherwise shares apomorphy H.23(1). Apomorphy H.23(1) is the very long valva apodeme extending anteriad, together with the valva apodeme lobe. This structure is present in *A. nicothoe* but extends ventrad rather than anteriad. Therefore, I postulate a secondary reduction of this apomorphy for this species.

Character #H.40 concerns the attachment of muscle *m5* to the vinculum and/or the valva in male genital structures, which is an unusually variable attachment within other families (see section III.2.2; Kuznetzov & Stekolnikov 2001). Changes between the different attachments in either direction are so common in other families and are such simple modifications that I cannot argue for any preference of one direction of change over the other. Apomorphy H.40(1) provides weak support for a large monophylum that includes *A. excellens* and *A. adriana*, based on numerous other apomorphies. These two species have the presumed plesiomorphic character #H.40 state (0), which I interpret as a "reversal" in these two species. Further, apomorphy H.40(1) is present in the genus *Pseudodreata* and in an undescribed antheline species, but not in *Chenuala heliaspis* and *Pterolocera* sp. B. This distribution of apomorphies can be interpreted in different ways. Three equally parsimonious explanations are possible, each requiring the postulation of two independent *ad hoc* explanations of convergences and reversals (Fig. 353). I have no grounds for choosing between these alternative topologies supported by apomorphy H.40(1), which is why I present them as two polytomies in the dendrogram (Fig. 354).

Apomorphy H.65(1), the presence of hair brushes on abdominal segment A1 in the larva, is one of three apomorphies that support a very large monophylum. A strong tendency to reduce these brushes is apparent in *A. nicothoe*, in which poorly developed brushes are present only in the early caterpillar instars (see discussion of character #H.65 in section III.6.2). These brushes are entirely absent in all other species of a monophylum including *A. nicothoe*. Similarly, these brushes are absent in *A. guenei* and possibly other species related to it, for which the caterpillars are still unknown. In all cases several other apomorphies support the placement of these species lacking apomorphy H.65(1) within the monophylum supported by apomorphy H.65(1), which is why I postulate independent strong reductions or losses for these two taxa.

The interpretation of apomorphy H.27(1) is difficult. It is widespread within

Anthelidae and weakly supports a large monophylum that includes several taxa which are placed within it by other apomorphies but lack apomorphy H.27(1). Apomorphy H.27(1) is a sclerotized, transverse ridge on the mesal side of the valva and its loss seems likely for *A. ocellata*, in which the valva is generally only weakly sclerotized. Likewise, the very strong reduction of the entire valva in *Omphaliodes obscura* is a plausible explanation for the loss of this ridge and other features of the valva in this species. However, another two or three losses have to be postulated without any apparent reasons for the losses, namely for the monophylum supported by apomorphy H.23(1), the monophylum supported by apomorphy H.4(1) and all species of the genus *Pterolocera*, except for the generally less derived species *P. isogama*. If the absence of 27(1) in the former two monophyla was a secondary loss, this loss would very poorly support the monophyly of these two groups as shown in Fig. 354. As I assume the absence of H.27(1) in *O. obscura* to be caused by the overall reduction of the valva, I do not include this species in this tentative group. Further, the homologization of a structure present in an undescribed antheline species with apomorphy H.27(1) is poorly supported, as stated in the discussion of character #H.27. If this homologization is incorrect, apomorphy H.27(1) would, in addition to apomorphy H.42(1), support the current topology that is incompatible with a monophylum very weakly supported by apomorphy H.53(1).

In addition to this potential incompatibility with apomorphy H.27(1), apomorphy H.53(1) supports a monophylum consisting of an undescribed antheline species and *Chenuala heliaspis*, which is incompatible with the large monophylum supported by apomorphy H.42(1). The hypothesis of apomorphy H.42(1) is much better supported than the hypothesis of apomorphy H.53(1), which is why I assume similar subapical protrusions of the fore wing termen [H.53(1)] to have evolved independently in the undescribed antheline species and *C. heliaspis*. This is further indicated by a difference in location of the protrusion, as discussed for character #H.53 (section III.4.2).

Apomorphy H.44(1) is one of many characters supporting the monophyly of Anthelinae. Character #H.44 refers to the orientation of the lamella antevaginalis to the lamella postvaginalis in female genital structures. In *A. clementi* and *A. asterias* the sclerotization termed lamella antevaginalis is lost, which is why I scored character #H.44 as absent for these two taxa. However, while the lamella antevaginalis is absent, the remaining membrane has about the same orientation as the lamella antevaginalis in

species with apomorphy H.44(1), which is why I postulate the absence of apomorphy H.44(1) to be a loss in these two species. This loss might be an apomorphy of the monophylum supported by apomorphy H.63(1) [the states of H.63 are unknown for *A. rubicunda*, *A. guenei* and *A. callileuca*], but being a loss the remnants of the structures hardly support this hypothesis, and more species of this monophylum have to be examined in any case.

Apomorphy H.47(1), the areole formed in the fore wing, is very constant and supports the monophyly of the family Anthelidae. However, it is absent in *Omphaliodes obscura*, in which the areole forming veins Rs2 and Rs3 show intraspecific variation. Therefore, I interpret the condition present in *O. obscura* as a secondary loss.

Apomorphy H.22(1) supports a large monophylum including the genera *Pseudodreata* and *Corticomis*, which is incompatible with the monophyla supported by the apomorphies H.27(1) and H.42(1). Character #H.22 refers to the valva apodeme lobe and its mesad protrusion, which is rather variable between species as mentioned in the discussion of the character (section III.1.4). Therefore, I interpret the presence of apomorphy H.22(1) in *Pseudodreata* and *Corticomis* as a convergent development of a similar condition, which I homologized incorrectly with apomorphy H.22(1). The resulting topology also fits to the inapplicability of apomorphy H.11(1), which is caused by a secondary loss of the sclerotization of the gnathos and the mesal protrusion (as indicated by membranous remnants). A tendency towards a reduction of these sclerotizations is also apparent in *C. heliaspis*, but the sclerotization is partially present in some specimens of this species.

Another incompatibility concerns apomorphy H.6(1). This apomorphy supports a monophylum consisting of *A. rubicunda*, *A. guenei* and *A. asterias & callispila*, as well as *Pseudodreata & Corticomis*. I scored apomorphy H.6(1) as present for these two genera as part of additive binary coding, based on my hypothesis of apomorphy H.7(1) being a subsequent modification of H.6(1) (see the discussion of character #H.7 in section III.1.4). This hypothesis is refuted by numerous well supported other apomorphies that support the topology presented in Fig. 354. Therefore, I postulate the apparent apomorphy H.6(1) to be a convergence in *Pseudodreata* and *Corticomis*.

Apomorphy H.45(1) is one of three characters supporting a very large monophylum that includes a very well supported monophylum containing *A. varia* (state unknown for *A. astata*). In this species the plesiomorphy H.45(0) appears to be present, which I

interpret as a "reversal".

The same monophylum containing *A. varia* appears to have plesiomorphy H.39(0), while being part of a very well supported monophylum possessing apomorphy H.39(1). This appears to be a reversal of apomorphy H.39(1), an interpretation supported by the almost intermediate condition present in *A. euryphrica* (see the discussion of character #H.39 in section III.2.4).

Within the Munychryiinae different incompatible monophyla are supported by two apomorphies. Apomorphy H.32(1) supports the monophyly of an undescribed munychryiine species and *Munychryia senicula*, exclusive of *Gephyroneura cosmia*, in which the plesiomorphy H.32(0) appears to be present. This apparent plesiomorphy in *G. cosmia* is the lack of a cornutus, which could have been caused by a secondary loss. The second incompatible monophylum is supported by apomorphy H.50(1), which is the partial fusion of the primary Rs branches in the fore wing of the undescribed munychryiine species and *G. cosmia*. Such a monophylum would be incompatible with the chosen monophylum, which is supported by two other, better founded hypotheses of apomorphy. Two *ad hoc* explanations are possible for the present distribution of apomorphy H.50(1): Either plesiomorphy H.50(0) is a reversal in *M. senicula*, or apomorphy H.50(1) evolved convergently in *G. cosmia*. The condition present in *M. senicula* does not differ from the typical plesiomorphic condition. In contrast, the partial fusion of the veins [H.50(1)] differs moderately in length between the undescribed munychryiine species and *G. cosmia,* and the venation of the radial sector of *G. cosmia* differs further by the stalking with M1. Therefore, I favour the latter *ad hoc* explanation of a convergent development of H.50(1) in *G. cosmia*.

The phylogenetic hypotheses summarized for Anthelidae in Fig. 354 are not equally well supported. Most of the hypotheses concerning older splits are much better supported by a larger number of apomorphies than are hypotheses of younger splits. The large, unresolved polytomy supported by apomorphy H.22(1) is the extreme. However, within this polytomy several monophyla are based on single, well supported hypotheses of apomorphy.

III.7.2) The bombycoid complex

The Hennigian Argumentation of the bombycoid complex based on morphological characters is carried out as described above for the Anthelidae (section III.7.1). As in any other Hennigian Argumentation, the two conditions of using monophyletic terminal taxa and using ground plan character states for these terminal taxa must be met (see section III.4.2). In the case of the bombycoid complex the terminal taxa are not exemplar species but families for which the monophyly is hypothesized. It is beyond the scope of this study to examine the monophyly of these often cosmopolitan families. Instead, I rely on published hypotheses, namely the ones of Lemaire and Minet ([1998]; based on Minet 1994). Unlike the hypotheses of other authors, their hypotheses are based on explicitly stated and, hence, verifiable apomorphies. However, I believe several of their hypotheses of apomorphy to be poorly supported or incorrect, which is problematic for my assumption of monophyly of the terminal taxa. Of all their proposed hypotheses the monophyly of the family Bombycidae is least convincingly supported. To ensure monophyletic terminal taxa I originally scored all characters separately for the four bombycid subfamilies, but the information on these subfamilies available to me is too limited for this approach to be feasible, because of a lack of specimens and publications on morphology. In the absence of alternatives I tentatively accept the hypothesis of monophyly of the Bombycidae *sensu* Lemaire and Minet [1998] (based on Minet 1994) and construct a hypothetical ground plan for the family based on the limited information I have. The subfamilies differ only in two of the examined characters (#H.46 and #H.55), and these differences are discussed below in the context of *ad hoc* explanations.

The hypothetical ground plans used for scoring the characters are derived by outgroup comparison. The character states that are only present within a subset of taxa of the family but not the outgroup are apomorphies of these taxa, but not states of the hypothetical ground plan. In contrast, I interpret the character state that is present within as well as outside the family as the state to be assigned to the hypothetical ground plan of the family. If the state present within the family is absent in the outgroup, this is an autapomorphy of the familiy and hence its state in the ground plan (in the case of several unique states within the family its ground plan state remains to be worked out by phylogenetic hypotheses based on other apomorphies within the family). This interpretation requires that the hypothesis of homology of the apomorphic character

state is well supported. This is the case for complex structures, but not for character states involving strong reduction or absence. Hence, if a structure is present outside the family as well as in a subset of taxa within the family, but absent in a different subset within the family, I nevertheless assign the presence of the structure to the hypothetical ground plan of the family, assuming a (possibly repeated) loss in some taxa of the family. All characters used in this argumentation have been scored according to this principle. As for the Anthelidae, I now discuss individually all those monophyla within the bombycoid complex that are incompatible with other monophyla and require *ad hoc* explanations.

Apomorphy H.51(1), the fusion of the fore wing radial sector with Rs1 branching off most distally, supports a monophylum that is incompatible with several monophyla supported by other apomorphies. One of these is the better supported apomorphy H.37 (1), the lateral spine-shaped projection of the abdominal segment A1 of imagines, which supports a monophylum consisting of Anthelidae and Eupterotidae. As apomorphy H.51 (1) is present in some but not all Brahmaeidae and the state in the ground plan of the family can not be postulated with confidence (see character #H.51 in section III.4.2) this apomorphy is inconclusive for hypothesizing relationships between Lemoniidae, Brahmaeidae, Eupterotidae and Anthelidae. If all of these families are monophyletic as assumed, this apomorphy would have evolved independently in Lemoniidae, Eupterotidae and some Brahmaeidae. Alternatively, apomorphy H.51(1) supports a monophylum consisting of Eupterotidae, Lemoniidae and possibly Brahmaeidae (or even including Saturniidae and Anthelidae, in which case the plesiomorphic state H.51 (0) in Anthelidae would have to be explained as a reversal), in which case apomorphy H.37(1) would have been lost secondarily in Lemoniidae and Brahmaeidae. This possibility cannot be ruled out, especially as the abdominal spine [H.37(1)] is variably well developed and frequently reduced in Anthelidae, and so far the spine is only known from a single *Eupterote* species in Eupterotidae. A convergent evolution of the spine in Anthelidae and the *Eupterote* species is a further possibility, but more eupterotid species should be examined. In addition to these convergent fusions two further independent fusion events have to be postulated for the Saturniidae and for the Endromidae plus Mirinidae in the preferred topology. A reversal of apomorphy H.51(1) in Anthelidae, some Brahmaeidae and possibly Sphingidae, Carthaeidae and Bombycidae is yet another

possible *ad hoc* explanation. However, as the branches of the radial sector are rather widely separated from each other in the Anthelidae and a tendency to fuse rather than to split the radial sector seems to exist (see character #H.46 in section III.4.2), I prefer the less parsimonious but more plausible explanation (multiple independent fusion events) over the more parsimonious explanations of multiple evolution of the splitting of fused branches. The incompatibility of apomorphy H.51(1) with not only one but several other apomorphies supports the notion in section III.4 that differences in wing venation are not necessarily reliable characters as convergent developments are very difficult to recognize as such.

Fusions of radial sector branches differ also between subfamilies of the Bombycidae. A unique fusion, at least for the bombycoid complex with Rs1 branching off most basally, is present in the subfamilies Bombycinae, Apatelodinae and probably Phiditiinae (reduced), possibly being a synapomorphy of these three subfamilies. However, in the only other bombycid subfamily, Prismostictinae, the branches of the radial sector are fused differently from this unique fusion as well as from apomorphy H.51(1). In this subfamily the fork in the Rs1/Rs2 branch is located more distally than the fork in the Rs3/Rs4 branch [apomorphy H.46(1)], the opposite of the condition present in the other bombycid subfamilies, which appears as plesiomorphy H.46(0). Accepting the poorly supported hypothesis of monophyly of the Bombycidae, I assume the seemingly plesiomorphic condition to be part of the unique fusion present in these three bombycid subfamilies, and assign the apomorphy H.46(1) of the Prismostictinae to the hypothetical ground plan of the family Bombycidae.

A second difference between the bombycid subfamilies is present in character #H.55, which has the plesiomorphic state in the Apatelodinae, but the apomorphic state in Prismostictinae, Bombycinae and Phiditiinae. In the Apatelodinae the antennal flagellomeres of the imagines do not have a ventro-median process [plesiomorphy H.55 (0)], while such a process is present in at least some members of all other subfamilies. In these other subfamilies the occurrence of the process is limited to the most distal segments of the antenna only. Assuming the Bombycidae to be monophyletic, I assign apomorphy H.55(1) to the ground plan of the Bombycidae and interpret the absence in the Apatelodinae as a loss of the structure. Such losses occur frequently in other families of the bombycoid complex, too, which is problematic for the interpretation of the absence in the almost monotypic families Endromidae and Mirinidae. Due to species

numbers the situation is less uncertain in the large family Lasiocampidae and in the Mimallonidae, in which the rami of the flagellomeres are ventrally adjacent to each other and do not leave any space for even a reduced ventro-median process (which is potentially a synapomorphy of the two families).

Apomorphy H.56(1), the presence of two sensory bands on each antennal flagellomere of imagines, supports a monophylum that is incompatible with the equally well supported apomorphy H.10(1), the fusion between the gnathos and the mesal side of the valva in male genital structures. While I cannot rule out convergent fusions between the gnathos and the valva, this or similar fusions do not seem to occur outside the bombycoid complex. In contrast, the two sensory bands on the flagellomeres have been lost or merged several times in Sphingidae (e.g., *Xenosphingia jansei*, *Smerinthus jamaicensis*) as well as Saturniidae (e.g., Oxyteninae, *Periga*), resulting in antennal structures very strongly resembling the single sensory band and rami found in other Lepidoptera, including the other families of the bombycoid complex (see sections III.5.1.A - C). Therefore, I postulate *ad hoc* the condition H.56(0) in Anthelidae, Eupterotidae, Brahmaeidae and Lemoniidae to be a "reversal".

Apomorphy H.60(1), the mesal lappet of the larval labial palpus, supports a monophylum consisting of most families of the bombycoid complex and some Notodontidae (Noctuoidea). This monophylum is incompatible with several other monophyla, most noticeably the monophyly of the bombycoid complex, which is supported by apomorphy H.46(1) and tentatively H.66(1). The mesal lappet is absent in the three lasiocampid species I examined, but as the Lasiocampidae are a large family with about 2053 described species (Holloway *et al.* 2001), obviously many more species have to be examined by SEM to assign the absence of this structure with some certainty to the hypothetical ground plan of the family Lasiocampidae. In the family Saturniidae the spinneret is modified from a slender tube to a very broad, plate-shaped structure (see the discussion of character #H.60 in section III.6.2), which might have made the mesal lappets redundant in Saturniidae. The mesal lappet of the labial palpus is repeatedly reduced in some taxa of the Anthelidae and the Notodontidae. As *ad hoc* explanation of the absence of apomorphy H.60(1) in the Lasiocampidae, the monotypic Carthaeidae and the Saturniidae I also postulate a loss.

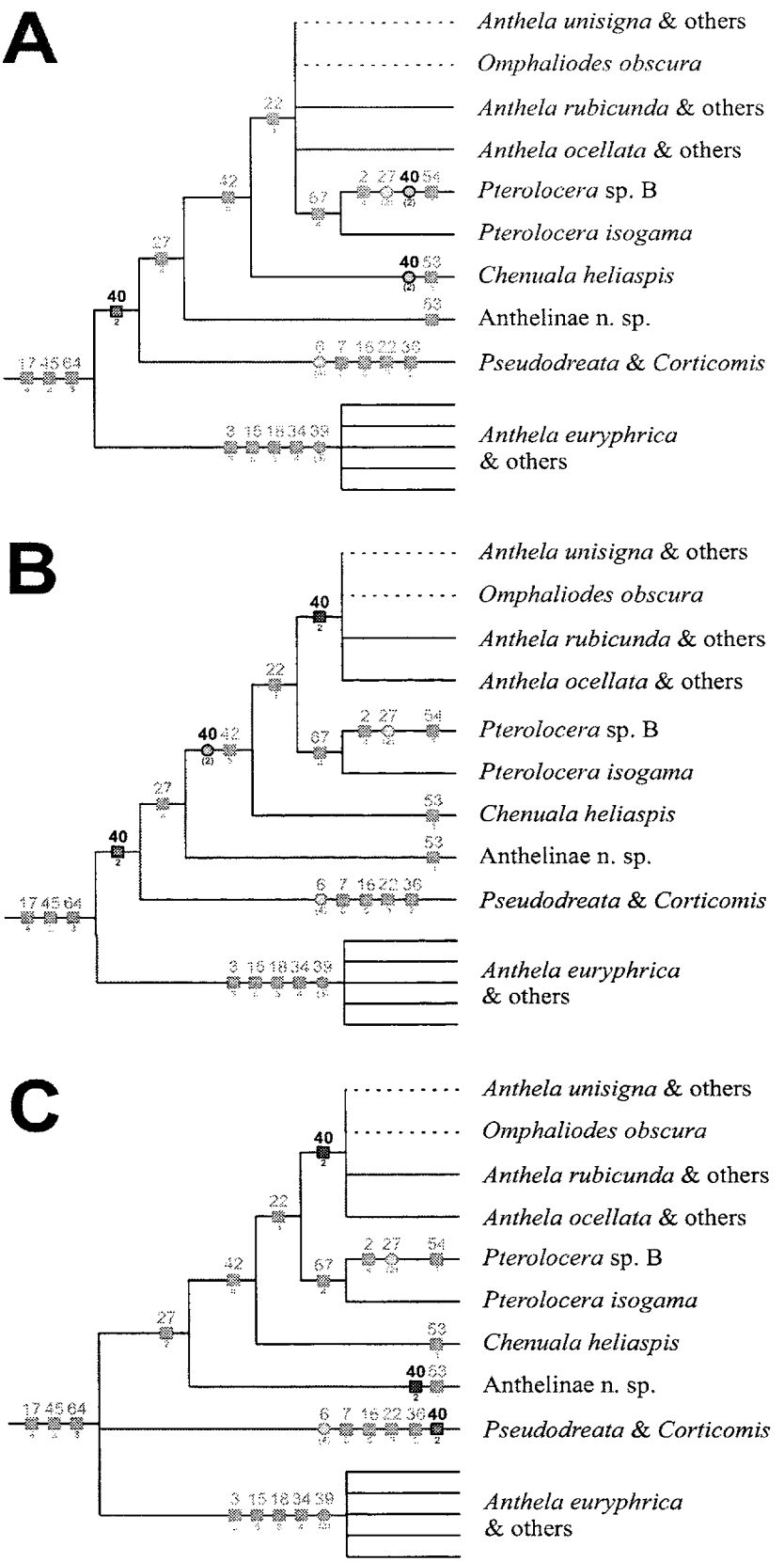

Fig. 353: Morphology-based Hennigian Argumentation scheme of Anthelidae – the incompatible apomorphy H.40(1) supports three different, equally parsimonious topologies (A, B, C; see Fig. 354 for legend).

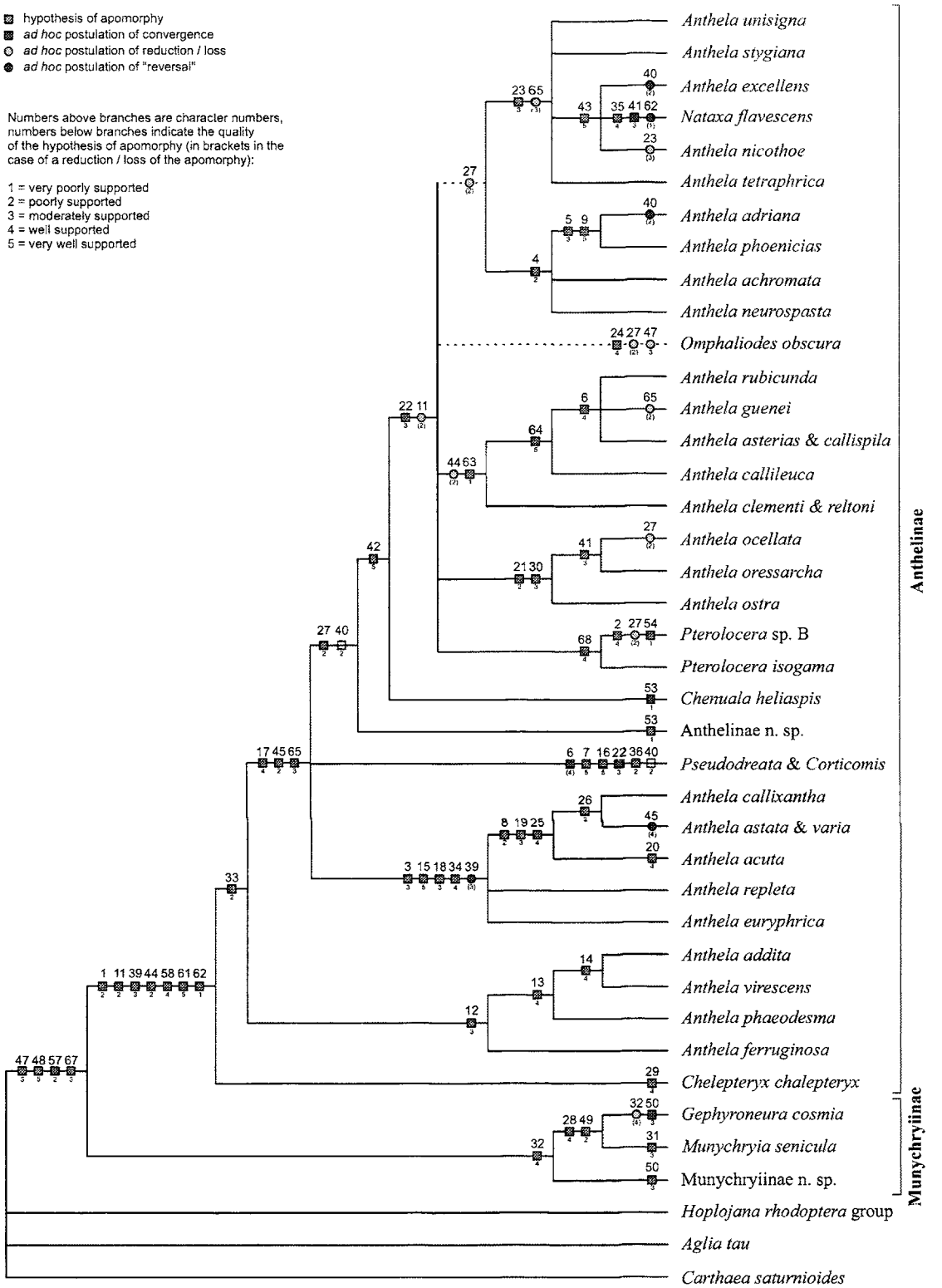

Fig. 354: Morphology-based Hennigian Argumentation scheme of the Anthelidae – the encaptic system of hypothesized monophyla establishes the hypothesized evolutionary relationships of taxa; the hypothesized apomorphies supporting these monophyla are symbolized on the branches, as well as the postulated *ad hoc* explanations for apormorphies supporting incompatible monophyla; the different topologies supported by apomorphy H.40(1) are presented as a consensus (apomorphies/convergences not coloured and losses omitted; see Fig. 353 for details); note that the genus *Anthela* is a polyphylum.

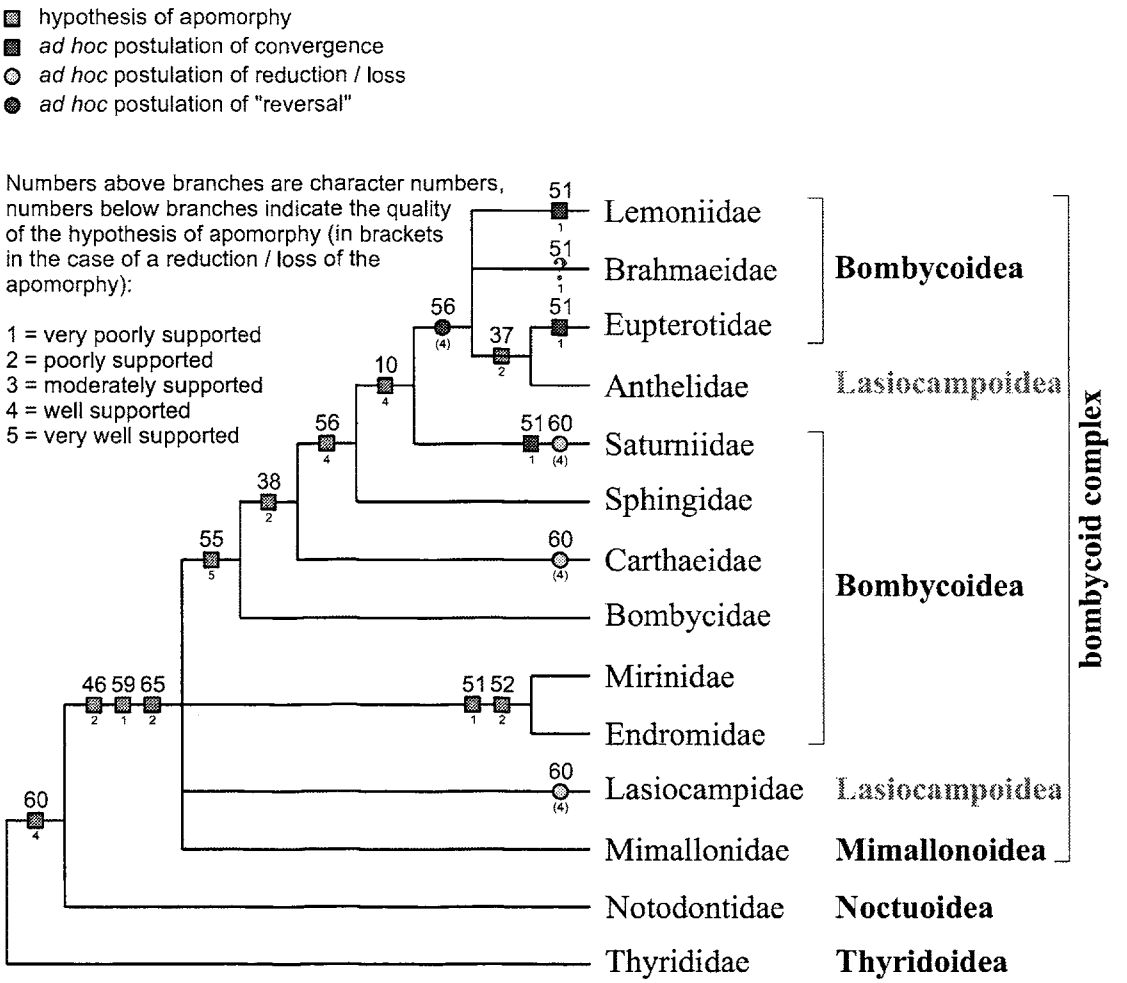

Fig. 355: Morphology-based Hennigian Argumentation scheme of the bombycoid complex – the encaptic system of hypothesized monophyla establishes the hypothesized evolutionary relationships of taxa; the hypothesized apomorphies supporting these monophyla are symbolized on the branches, as well as the postulated *ad hoc* explanations for apomorphies supporting incompatible monophyla; note that the current concept of Lasiocampoidea defines a polyphylum.

CHAPTER FOUR:

CLADISTIC ANALYSIS OF MORPHOLOGICAL CHARACTERS

The cladistic analysis of characters differs from the Hennigian Argumentation in several aspects (see sections II.4.2, II.4.3 and VII.1.1). They are different methods, which are applied to different types of "data". For a cladistic analysis these data consist of preliminary hypotheses of homology (the "primary homology" of de Pinna 1991) based on "directly observable facts" only, in an attempt to reduce the number of subjective hypotheses / interpretations. Hence, it is commonplace to use similarity of observable structures [the criterion of specific quality of Remane (1952)] as the basis for forming preliminary hypotheses of homology, without carrying out a character analysis as done for Hennigian Argumentation.

I use the same species, specimens and morphological structures in my cladistic analysis as in my Hennigian Argumentation (chapter III). However, characters used for the Hennigian Argumentation have to be recoded for the cladistic analysis to reflect "directly observable facts" only, ignoring any of the interpretations made in character discussions of the Hennigian Argumentation. This can lead to quite different coding of characters, e.g., in the case of the fused uncus lobes, where no distinction is made between structures hypothesized for the Hennigian Argumentation to have resulted from different fusion events (see section III.1.2). To further avoid interpretations, all character states are unordered.

In most cases the recoded characters and their states have been described in detail in the Hennigian Argumentation. No published characters were used other than cited in the Hennig Argumentation (chapter III; see Appendix P for a critical review of all published characters). In the following list of 67 cladistic characters (symbolized by a "C" preceding the character number) the corresponding numbers of the Hennigian characters (symbolized by an "H" preceding the character number) are stated in square brackets. The actual character matrices are presented in Appendix O and included as NEXUS files in an electronic appendix on the enclosed CDROM (rear cover page).

IV.1 List of cladistic characters

Characters of the male genital structures:

Character #C.1: Shape of the posterior uncus edge.

(0): Weakly bilobed (<10% of setose area length).

(1): Deeply bilobed (>80% of setose area length) [#H.1(1)].

(2): Single-pointed, blunt.

Character #C.2: Tilt of the uncus lobe.

(0): 30-40° laterad.

(1): 5-30° mesad [in part #H.3(1)].

(2): ~50° mesad.

(3): 60-70° mesad [in part #H.2(1)].

(4): ~90° mesad [in part #H.7(1)].

Character #C.3: Contact between the apices of the basally separated uncus lobes.

(0): Distinctly separated.

(1): Touching each other [#H.6(1)].

Character #C.4: Fusion of uncus lobes.

(0): Separate.

(1): Only (baso-) dorsally fused [#H.7(1)].

(2): Entirely fused [in part #H.2(1), #H.3(1) and #H.4(1)].

Character #C.5: Size of the ventral edge of the fused uncus lobes [#C.4(3)].

(0): A shallow to distinct crest over part of the uncus lobes.

(1): A distinct to prominent crest over part of the uncus lobes.

(2): A large, ventral blade over the entire length of the uncus lobes.

Character #C.6: Shape of the ventral blade formed by the fused uncus lobes [#C.5 (1)].

(0): Dorsally broad and laterally concave.

(1): Dorsally narrow and lateral sides straight (blade appears laterally "compressed") [#H.5].

Character #C.7: Development of the gnathos arms.

(0): Dorsally well developed.

(1): Dorsally reduced [#H.8(1)].

(2): Entirely absent.

Character #C.8: Presence of a spinose sclerotization that envelopes the smooth mesal ends of the gnathos arms posteriorly.

(0): Absent.

(1): Present [#H.9(1)].

Character #C.9: Merger of the gnathos and the valva.

(0): Widely separated from each other.

(1): Merged [#H.10(1)].

Character #C.10: Presence of the mesal protrusion.

(0): Absent.

(1): Present.

Character #C.11: Shape of the mesal protrusion.

(0): Simple, conical.

(1): Laterally bowed ridge [#H.14(1)].

(2): Well sclerotized, elongate, setose ridge laterally of the phallus [#H.15(1)].

Character #C.12: Merger of the mesal protrusion and the anellus.

(0): Separated from each other.

(1): Merged [#H.11(1)].

Character #C.13: Merger of the mesal protrusion/anellus and the juxta.

(0): Separated from each other.

(1): Merged [#H.12(1)].

Character #C.14: Posterior protrusion of the U-shaped juxta.

(0): Not protruding.

(1): The lateral arms protrude further than the ventral part.

(2): The entire juxta protrudes equally far posteriad.

(3): The ventral part of the juxta protrudes particularly far, giving the entire juxta the appearance of a very long, apically narrowing and pointed trough [#H.13 (1)].

Character #C.15: Support of the phallus.

(0): Supported by the juxta/mesal protrusion.

(1): Suspended in a membranous tube (anellus) from the fused gnathos and the mesal protrusions [#H.16(1)].

Character #C.16: Curving of the valva apodeme (VA)

(0): Extends mesad in a straight line.

(1): Curves ventrad [in part #H.17(1)].

Character #C.17: Length of valva apodeme (VA)

- (0): Minute to absent.
- (1): Short to moderately developed (< 1.5x the width of the valva)
- (2): Long (> 1.5x the width of the valva) [in part #H.17(1)].

Character #C.18: Presence of the valva apodeme lobe (VAL).

(0): Absent [including #H.21(1)].

(1): Present [#H.17(1)].

Character #C.19: Shape of the valva apodeme lobe (VAL).

(0): A mesal protrusion at an angle of roughly 45° [#H.22(1)].

(1): A posterior, "upturned" process [#H.18(1)].

Character #C.20: Modification of the posterior, "upturned" process (VAL) [#C19 (1)].

(0): Not modified.

(1): Triangular process, which is orientated parallel to the VA [#H.19(1)].

Character #C.21: Sclerotization of the triangular process [#C20(1)].

(0): Not sclerotized (membranous).

(1): Heavily sclerotized, thereby forming a flat, serrate and pointed tooth [#H.20 (1)].

Character #C.22: Orientation of the valva apodeme (VA) and valva apodeme lobe (VAL), if present.

(0): Dorso-ventrad (in the plane of the diaphragma).

(1): Antero-posteriad [#H.23(1)].

Character #C.23: Proximity of the valva apodeme lobe (VAL) to the further anteriorly located valva apodeme (VA).

(0): Directly adjacent.

(1): At a distance [#H.24(1)].

Character #C.24: Shape of the clasper.

(0): Broad, simple plate.

(1): Broad, roughly triangular plate with a massive, dorsal spine [#H.25(1)].

(2): Slender arm with a dorsal protrusion [#H.26(1)].

(3): Strongly reduced or absent.

Character #C.25: Structure of the mesal side of the valva.

(0): Flat.

(1): Forms a transverse ridge [#H.27(1)].

Character #C.26: Diameter of the manica.

(0): The manica surrounds the phallus tightly to loosely.

(1): The manica is extremely wide around the phallus and stretched to its full width by the circumferential sclerotization of its posterior end [#H.28(1)].

Character #C.27: Interconnection of the juxta and the phallus.

(0): By the membranous manica.

(1): By a sclerotization of the entire manica [#H.29(1)].

Character #C.28: Shape of the phallus coecum.

(0): Straight.

(1): Dorsad curved [#H.30(1)].

Character #C.29: Shape of the phallus base.

(0): Tubular.

(1): Bulbous [#H.31(1)].

Character #C.30: Armature of the vesica.

(0): Without cornuti.

(1): With a single cornutus, which originates from a sclerotization of the most distal part of the ductus ejaculatorius [#H.32(1)].

Character #C.31: Degree of the vesica sclerotization.

(0): Not sclerotized (membranous).

(1): Largely sclerotized [#H.33(1)].

Character #C.32: Shape of the distal end of the right sclerotized band on the vesica.

(0): Simple.

(1): Long, curved to bent process [#H.34(1)].

(2): Twisted, tubular spine [#H.35(1)].

Character #C.33: Shape of the distal end of the left sclerotized band on the vesica.

(0): Simple to forming a small protrusion.

(1): Twisted, tubular spine [#H.35(1)].

Character #C.34: Width of the sclerotization of the vesica.

(0): Equal over its entire length (forming a tubular phallus apex).

(1): Posteriorly widening (forming a funnel-shaped phallus apex) [#H.36(1)].

Characters of the abdomen:

Character #C.35: Presence of a protrusion on the male abdominal segment A1

(0): No protrusion.

(1): A lateral, spine-shaped protrusion of tergal origin [#H.37(1)].

Characters of the male genital muscles:

Character #C.36: Location of the muscle *m5* attachment to the vinculum.

(0): At the anterior edge of the vinculum, directly ventrally of *m4*.

(1): At the mesal side of the vinculum, posteriorly to *m4* ("overlapping") [#H.38 (1)].

Character #C.37: Dorso-ventral position of the muscle *m5* attachment to the vinculum.

(0): Adjacent to the muscle *m4* (about middle of vinculum).

(1): Far ventrally of the muscle *m4* (latero-ventral part of vinculum) [#H.39(1)].

Character #C.38: Attachment of the ventrally shifted muscle *m5* [#C.37(1)] to the vinculum and/or the valva.

(0): At most partly to the basal edge of the lateral valva wall, but mainly to the vinculum.

(1): Exclusively to the basal edge of the lateral valva wall [#H.40(1)].

Character #C.39: Attachment of muscle *m7* to the mesal side of the lateral wall of the valva.

(0): At the basal area of the lateral wall of the valva.

(1): Seemingly displaced distad by the muscle *m5* [#H.41(1)].

Character #C.40: Orientation of the attachment point of muscle *m3* on the juxta.

(0): The dorso-lateral corners of the juxta are in the plane of the diaphragma, requiring a bending of the muscles *m3*.

(1): The dorso-lateral corners of the juxta are invaginated, tilting the attachment points of the muscles *m3* by roughly 90° to the plane of the juxta and thereby facilitating a direct course of the muscles *m3* [#H.42(1)].

Character #C.41: Arrangement of the muscles *m5* to each other.

(0): The coecum and phallus are straight, with the muscles *m5* stretching parallel to each other from the coecum to the vinculum.

(1): Coecum and phallus are twisted righthand, with muscles *m5* crossing each other [#H.43(1)].

Characters of the female genital structures:

Character #C.42: Sclerotization of lamella antevaginalis.

(0): Distinctly sclerotized.

(1): Membranous.

Character #C.43: Angle of lamella antevaginalis to the body axis.

(0): 0 - 60°.

(1): ~90° [#H.44(1)].

Character #C.44: Orientation of the common duct of the accessory glands.

(0): The common duct of the accessory glands merges with the accessory gland reservoirs in the plane of the latter.

(1): The common duct of the accessory glands is at right angle to accessory gland reservoirs [#H.45(1)].

Characters of the fore wing:

Character #C.45: Relative location of the fork in the Rs1/Rs2 branch.

(0): Proximally of the fork in Rs3/Rs4.

(1): Distally of the fork in Rs3/Rs4 [#H.46(1)].

Character #C.46: Formation of an "areole" by Rs2 and Rs3.

(0): The veins Rs2 and Rs3 are not distally approximated to each other and hence do not form an "areole".

(1): A sclerotization or the distal, local touching of Rs2 and Rs3 forms an "areole" [#H.47(1)].

Character #C.47: Area between Rs2 and Rs1.

(0): Flat.

(1): With a transverse, sclerotized fold connecting Rs2 with Rs1 just distally of the fork in Rs1/Rs2 [#H.48(1)].

Character #C.48: Extent of the sclerotization of the fold in the radial sector [#C.47 (1)].

(0): From Rs2/Rs3 as far as or slightly beyond Rs1.

(1): From Rs2/Rs3 across Rs1 to R [#H.49(1)].

Character #C.49: Fusion of the primary radial sector branches Rs1/Rs2 and Rs3/Rs4 in the basal part of the "areole".

(0): The primary Rs branches diverge separately from the discoidal cell.

(1): The primary Rs branches are "stalked" with each other [#H.50(1)].

Character #C.50: Fusion of the radial sector with the fork in Rs1/Rs2 being located more distally than the one in Rs3/Rs4.

(0): The primary Rs branches are separated from each other.

(1): The primary Rs branches are entirely fused [#H.51(1)].

Character #C.51: Length of the anal loop formed by 1A+2A.

(0): Less than 1/3rd of the length of 1A+2A.

(1): About half the length of 1A+2A [#H.52(1)].

Character #C.52: Shape of the termen.

(0): Convex.

(1): With a subapical protrusion [#H.53(1)].

Character #C.53: Development of wings in females.

(0): Fully developed.

(1): Apterous [#H.54(1)].

Characters of the adult antenna:

Character #C.54: Antennal flagellomere shape.

(0): Without a ventro-median protrusion.

(1): With a large, ventro-median process that carries numerous sensilla coeloconica and apically the styliform sensillum complex [#H.55(1)].

Character #C.55: Number of sensory bands of very long sensilla trichodea on each antennal flagellomere.

(0): One median sensory band.

(1): One anterior and one posterior sensory band [#H.56(1)].

Characters of the caterpillar:

Character #C.56: Colouration of the frontal area of the headcapsule.

(0): Does not differ from the remainder of the headcapsule (uniformly coloured or patterned).

(1): With a pale triangle [#H.57(1)].

Character #C.57: Structure of the maxillar lobarium.

(0): Without a distinct apical "segment", carrying all sensilla.

(1): With a distinct apical "segment" that carries only some sensilla (exclusive of STI-III) [#H.58(1)].

Character #C.58: Presence of a paired "mammiform sensillum" SC4 on the anterior side of the maxillary palpus.

(0): Absent.

(1): Present [#H.59(1)].

Character #C.59: Presence of mesal lappets on the labial palpus.

(0): Absent.

(1): Present [#H.60(1)].

Character #C.60: Presence of numerous minute vesicles on the integument.

(0): Absent.

(1): Present. [#H.61(1)].

Character #C.61: Relative size of D2 verrucae of the abdominal segments A2-A7.

(0): D2 smaller than D1.

(1): D2 larger than D1 [#H.62(1)].

Character #C.62: Structure of short secondary hairs.

(0): Distinctly serrate from the base to the apex of the hair.

(1): Distinct serration restricted to the apex of the hair [#H.63(1)].

Character #C.63: Arrangement of specialized hairs [#C.62(1)].

(0): Scattered over the dorsal side of the abdomen.

(1): Only the final instar caterpillars have aposematically coloured, apically multiple-forked hairs arranged in dense "cushions" on the abdominal segments A2-A7 [#H.64(1)].

Character #C.64: Type of setae on the D2 verrucae of the abdominal segment A1.

(0): Uniform hairs/spines that do not differ from the hairs of other abdominal segments.

(1): A brush of hairs, which differ in colour and/or length from the hairs of all other abdominal segments [#H.65(1)].

Character #C.65: Structure of the bending cuticle of the prolegs.

(0): With only a single layer of transverse microfibrils.

(1): With two layers of transverse microfibrils [#H.66(1)].

Characters of the cocoon:

Character #C.66: Structure.

(0): Single-walled.

(1): Double-walled, with the hairs incorporated only in the outer wall [#H.67(1)].

Character #C.67: Location and shape.

(0): Spun above the soil and without an exit tube.

(1): Spun vertically within the soil and with a silken exit tube [#H.68(1)].

IV.2) Analyses of cladistic characters

The cladistic morphological characters of section IV.1 were scored for the same taxa as in the Hennigian Argumentation (chapter III), resulting in two character matrices for the Anthelidae and the bombycoid complex, respectively (electronic appendix; printed in Appendix O). Taxa that do not differ computationally in their character states (i.e., that differ only by missing data) were merged. The matrix of the Anthelidae has 56 characters for 32 taxa (including three outgroup taxa), while the matrix of the bombycoid complex has 11 characters and 11 taxa (including two outgroup taxa). These matrices of cladistic morphological characters were analysed with the Maximum Parsimony criterion as implemented in PAUP.

IV.2.1) Phylogeny of the Anthelidae

The matrix of 56 characters and 32 taxa contains 13 autapomorphies, which were excluded in PAUP prior to analysis, effectively resulting in a 43x32 matrix. Repeated heuristic search (1,000 replicates, random sequence addition) always resulted in 1080 most parsimonious trees, of which the strict consensus is presented in Fig. 356. The trees are 92 steps long and have a Consistency Index (CI) of 0.62 and a Retention Index (RI) of 0.79. Bootstrap percentages were estimated from 100 pseudo-replicates of 10 sequence-addition replicates, which were limited to 1,000,000 rearrangements each.

The consensus tree (Fig. 356) is largely resolved, but most nodes have bootstrap support < 50% and a Bremer Support value of only 1. Only very few groups are well supported in the bootstrap analysis (having a bootstrap percentage of ≥80%; see section V.2):

- *Anthela oressarcha*, *A. ostra* and *A. ocellata*,
- *A. guenei*, *A. rubicunda*, *A. asterias* and *A. callispila*,
- *A. astata*, *A. varia*, *A. callixantha* and *A. acuta* group,
- the latter group, *A. euryphrica* and *A. repleta*, and
- the family Anthelidae.

Given the misproportion of only 43 parsimony informative characters for 32 taxa, the resolution is better than one might expect, but the support of the topology is accordingly poor.

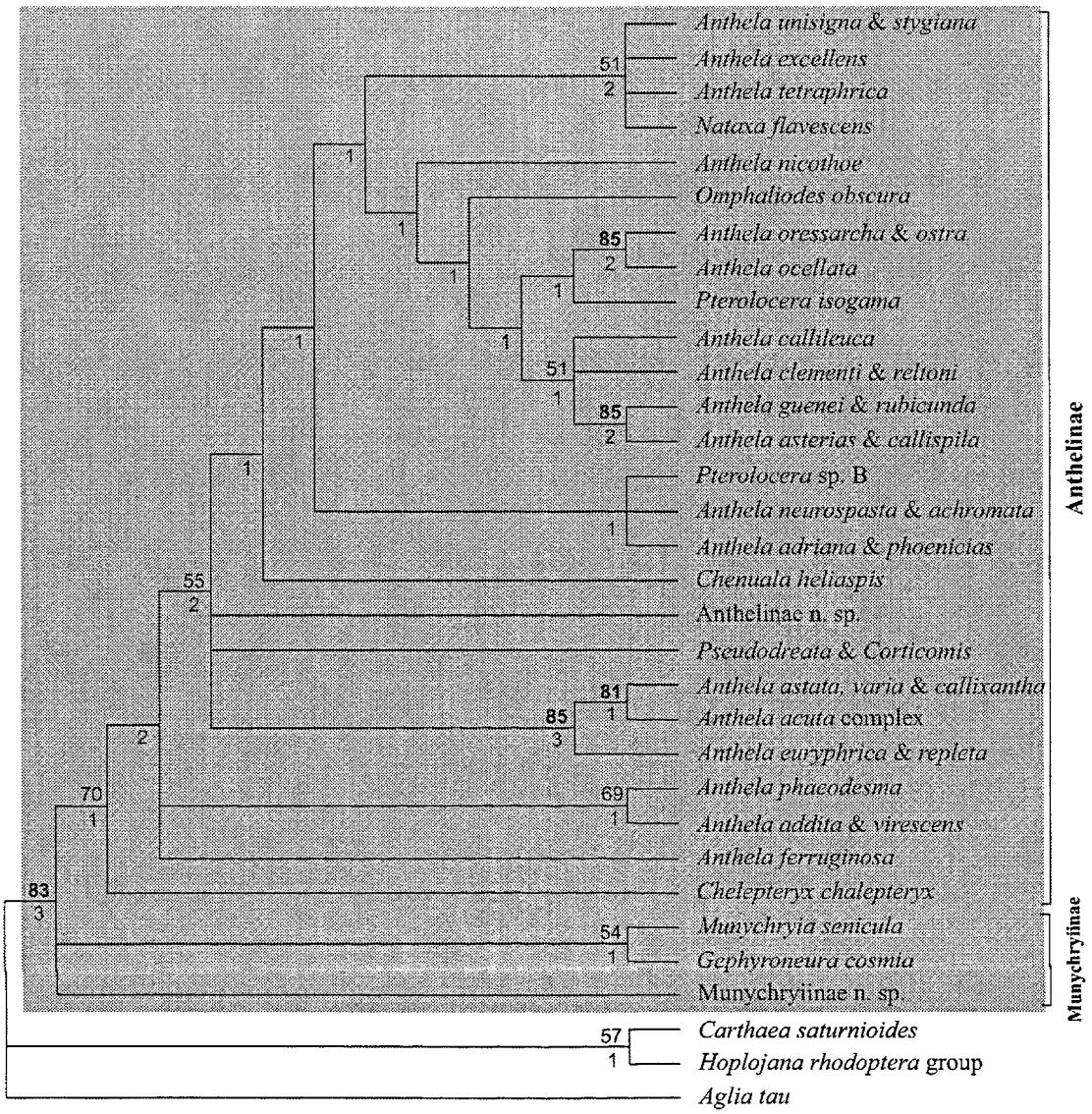

Fig. 356: Maximum Parsimony Analysis of cladistic morphological characters (43 parsimony informative characters, unordered, equally weighted) of Anthelidae (29 taxa on bluish background; three non-anthelid species as outgroup) – strict consensus tree of the 1080 most parsimonious trees (each 92 steps long; CI=0.62 ; RI=0.79). Numbers above branches are bootstrap percentages ≥50% (≥80% **bold**; 100 bootstrap replicates, with rearrangements limited to 1,000,000), numbers below branches are Bremer Support values.

IV.2.2) Phylogeny of the bombycoid complex

The matrix of 11 characters and 11 taxa contains 1 autapomorphy, which was excluded in PAUP prior to analysis, effectively resulting in a 10x11 matrix. Repeated heuristic search (1,000 replicates, random sequence addition) always resulted in 54 most parsimonious trees, of which the strict consensus is presented in Fig. 357. The trees are 17 steps long and have a Consistency Index (CI) of 0.63 and a Retention Index (RI) of 0.7. Bootstrap percentages were estimated from 100 pseudo-replicates of 10 sequence-

addition replicates, which were limited to 1,000,000 rearrangements each.

While ten non-contradicting, binary characters are the minimum number theoretically required to fully resolve relationships between eleven taxa, the ten characters I scored fail to resolve relationships due to missing data and most probably character conflicts. The strict consensus tree has only three nodes, of which only one is dichotomous. Amongst these three nodes, only the bombycoid complex sensu Minet (1994) is well supported by a bootstrap value of 84%, but the Bremer Support indicates that the hypothesis of monophyly of this group is supported by only two unambiguous autapomorphies.

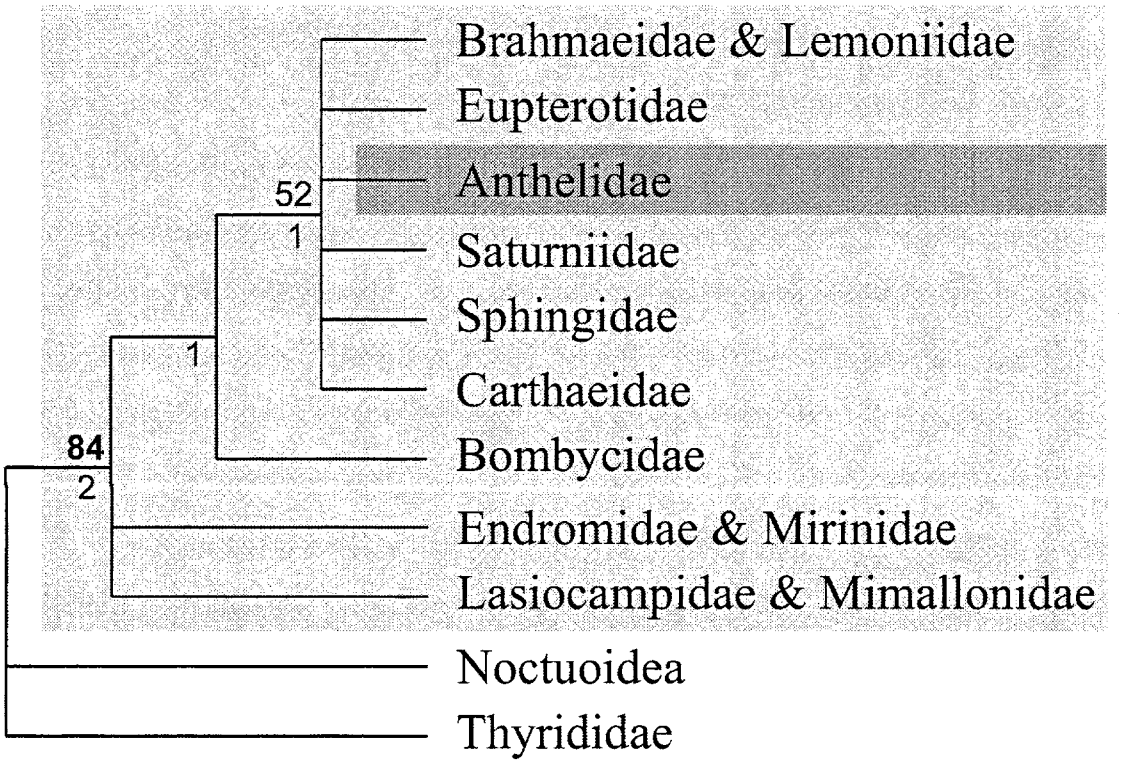

Fig. 357: Maximum Parsimony Analysis of cladistic morphological characters (10 parsimony informative characters, unordered, equally weighted) of the bombycoid complex (9 taxa on yellowish and bluish backgrounds; two non-anthelid species as outgroup) – strict consensus tree of the 54 most parsimonious trees (each 17 steps long; CI=0.63 ; RI=0.7). Numbers above branches are bootstrap percentages ≥50% (≥80% **bold**; 100 bootstrap replicates), numbers below branches are Bremer Support values.

CHAPTER FIVE:

ANALYSES OF MOLECULAR CHARACTERS

Initially I attempted to amplify and sequence (fractions of) the genes *wingless*, CO I & II, EF1a, CPS, 12S, 18S and 28S for ten anthelid species (*Anthela clementi*, *A. nicothoe*, *A. ocellata*, *A. varia*, *A. virescens*, *Chelepteryx chalepteryx*, *Chenuala heliaspis*, *Munychryia senicula*, *Omphaliodes obscura*, *Pterolocera* sp. B). From the sequences of this set of "test species" I judged by statistics (see below) and preliminary Maximum Parsimony Analyses whether the gene was suitable for my purposes, in which case I sequenced it for additional species. This was only the case with EF1a, CPS, 12S and 28S, and all aligned sequences of all successfully sequenced genes are included as NEXUS files in an electronic appendix on the enclosed CDROM (rear cover page).

V.1) General and quantitative characteristics of the molecular data

In this section I provide general information on the sequencing of individual genes/gene fragments, e.g., an overview of sequencing success, difficulties encountered with sequencing and species numbers. Further, I describe the major quantitative characteristics of these genes, e.g., the number of total sites and parsimony informative characters, and base frequencies and bias. At the end of this section (p. 399) I provide a table with details of all quantitative characteristics.

wingless

The sequencing of *wingless* failed for all ten species despite successful amplifications. I did not make further attempts to amplify and sequence *wingless*, because no further primers were available to me and the sequencing of the other genes had in principle been successful.

Cytochrome Oxidase I & II

The sequences of CO I (1534bp) and CO II (683bp) are complete, except for a gap of approximately 350bp in the CO I sequence of four species. I sequenced the two genes including the entire sequence of the tRNA for Leucine between the two genes and the partial tRNA sequences at the sequence ends. For the nine anthelid and one lasiocampid species sequenced, only 272bp (12%) of the 2217bp of the two genes are parsimony informative characters. The vast majority of these parsimony informative characters (84%) are third codon positions. Unlike first and second codon positions, the third codon positions have a very significant bias of base frequencies (χ^2 test with $P = 0.06$), which is problematic for phylogenetic analyses. The aligned ten sequences are included in the electronic appendix [file CO.nex on the CDROM].

Elongation Factor 1 alpha

The 1246bp fragment of EF1a was easy to sequence. With the exception of three species that lack about 400bp at the 3' end, the sequences for the 50 species are generally complete. Thirty-one of these species are Anthelidae, while the remaining 19 species belong to other families of the bombycoid complex, the Noctuoidea and the Thyrididae. In the alignment [file EF1aCPS.nex on the CDROM] I included sequences downloaded from Genbank of an additional 35 non-anthelid species of the bombycoid complex. Within the Anthelidae (plus three outgroup species) 285bp of the 1246bp are parsimony informative characters, which is 23% of all sites and almost double the proportion of parsimony informative characters present in CO I & II for Anthelidae. However, as in CO I & II the vast majority of the parsimony informative characters are third codon positions (94%), which have an extreme bias of base frequency (χ^2 test with $P < 0.01$). In contrast, no significant bias of base frequencies exists for first and second codon positions, but their contribution to the 285 parsimony informative characters is very small (18bp = 6%). Within the bombycoid complex (plus four outgroup species) the situation is very similar, but the proportion of parsimony informative characters is even higher (32%).

Carbamoylphosphate Synthetase

The sequencing of CPS was difficult, with the amplification and particularly the sequencing of the fragment with the published primers 806F and 1124R (Moulton & Wiegmann 2004) failing for most species. From the few sequences I obtained I designed a pair of custom primers (843R_Bom & 1057R_Bom), but taken as a pair these custom primers performed even worse. However, fragment amplification with a combination of one of the published and one of the custom primers was rather successful, but often resulted in the amplification of multiple fragments with large differences in length. Hence, the targeted fragments as identified by length had to be excised and extracted from the gel, after which direct sequencing was not difficult. The resulting sequences have up to 691bp, but the length of sequences varies greatly, depending on which primer combinations they are based on. I successfully sequenced 18 anthelid species, 25 non-anthelid species of the bombycoid complex and one species of the Thyrididae [file EF1aCPS.nex on the CDROM]. Within the Anthelidae (plus three outgroup species) of the up to 691bp a total of 195bp (28%) are parsimony informative characters, of which 80% are third codon positions. Unlike CO I & II and EF1a none of the codon positions of CPS have a significant base frequency bias (χ^2 test with P = 1.0). Within the bombycoid complex (plus one outgroup species) the total proportion of parsimony informative sites is even higher (43%), but the proportion of third codon positions is lower (73%).

Ribosomal genes 12S, 18S and 28S

The amplification and sequencing of the fragments of the ribosomal genes 12S (~439bp), 18S (510bp) and 28S (~780bp) was particularly easy, resulting in high quality sequences. The 18S fragment sequences [file 18S.nex on the CDROM] of the ten anthelid species initially sequenced are almost identical. Only four sites are variable, and of these three sites (0.6% of all sites) are parsimony informative characters.

I sequenced 12S for a total of 20 species of the bombycoid complex and the Noctuoidea [file 12S.nex on the CDROM]. As typical for rRNA molecules in general, the secondary structure consists of highly preserved stems and hyper-variable loops, which are unalignable (see below, section V.2). Excluding these unalignable loop regions and the ends of the sequences, the remaining 296bp have 85 variable sites, of which 46 sites (16% of all sites) are parsimony informative characters.

For 28S I sequenced a total of 22 species of the bombycoid complex and the Noctuoidea [file 28S.nex on the CDROM]. The numerous loop regions have even more extreme length differences than the loop regions of the 12S sequences and are unalignable. After the exclusion of these clearly unalignable regions 633 aligned sites with 140 variable sites remain, of which 108 sites (17% of all sites) are parsimony informative characters. Most of these parsimony informative sites are located near the edges of the unalignable regions, which is why the alignment of these sites is ambiguous. Hence, these alignments of 28S sequences do not present credible data for phylogenetic analyses.

The quantitative details of all genes, including the base frequencies, are summarized in the following table. The differences in the proportion of parsimony informative bases of the codon positions are visualized for Anthelidae and the bombycoid complex in Fig. 358 and Fig. 359, respectively.

taxa (number)	gene	codon position	number of total sites (length)	number of variable, parsimony uninformative sites	number of variable parsimony informative sites	proportion of sites being parsimony informative [%]	proportion of all parsimony informative sites [%]	base frequency of A [%]	base frequency of C [%]	base frequency of G [%]	base frequency of T [%]	χ^2 test of base frequency bias
Anthelidae (9) + outgroup (1)	CO I+II	1st	740	70	**37**	5.0	**13.6**	33	14	22	31	χ^2=11.7; df=27; **P=0.99540649**
		2nd	739	20	**7**	0.9	**2.6**	22	22	15	42	χ^2=2; df=27; **P=1**
		3rd	738	197	**228**	30.9	**83.8**	43	7	1	49	χ^2=39.1; df=27; **P=0.06147691**
		all	2217	287	**272**	12.3	-	33	14	12	40	χ^2=15.6; df=27; **P=0.96007564**
Anthelidae (31) + outgroup (3)	EF1a	1st	415	8	**14**	3.4	**4.9**	29	18	38	15	χ^2=4.6; df=99; **P=1**
		2nd	415	4	**4**	1.0	**1.4**	32	25	16	27	χ^2=1.1; df=99; **P=1**
		3rd	416	51	**267**	64.2	**93.7**	15	42	23	21	χ^2=198.8; df=99; **P=0.00000001**
		all	1246	63	**285**	22.9	-	25	28	26	21	χ^2=66.7; df=99; **P=0.994725**
bombycoid complex (58) + outgroup (4)		1st	415	10	**27**	6.5	**6.8**	29	18	38	15	χ^2=12.8; df=183; **P=1**
		2nd	415	8	**8**	1.9	**2.0**	32	25	16	27	χ^2=3.5; df=183; **P=1**
		3rd	416	19	**362**	87.0	**91.2**	18	37	19	26	χ^2=506.7; df=183; **P=0**
		all	1246	37	**397**	31.9	-	26	27	24	23	χ^2=182.6; df=183; **P=0.49418999**

taxa (number)	gene	codon position	number of total sites (length)	number of variable, parsimony uninformative sites	number of variable parsimony informative sites	proportion of sites being parsimony informative [%]	proportion of all parsimony informative sites [%]	base frequency of A [%]	base frequency of C [%]	base frequency of G [%]	base frequency of T [%]	χ^2 test of base frequency bias
Anthelidae (18) + outgroup (3)	CPS	1st	231	22	**26**	11.3	**13.3**	36	11	34	19	χ^2=7.01; df= 60; **P=1**
		2nd	230	14	**13**	5.7	**6.7**	35	18	16	31	χ^2=5.1; df=60; **P=1**
		3rd	230	44	**156**	67.8	**80.0**	40	13	13	34	χ^2=31.7; df=60; **P=0.99900488**
		all	691	80	**195**	28.2	-	37	14	21	28	χ^2=13.6; df=60; **P=1**
bombycoid complex (30) + outgroup (1)		1st	231	22	**55**	23.8	**18.6**	36	10	33	20	χ^2=14.2; df=90; **P=1**
		2nd	230	21	**24**	10.4	**8.1**	36	18	16	30	χ^2=7.9; df=90; **P=1**
		3rd	230	2	**217**	94.3	**73.3**	38	13	14	35	χ^2=66; df=90; **P=0.97311814**
		all	691	45	**296**	42.8	-	37	14	21	28	χ^2=30.1; df=90; **P=1**
bombycoid complex (28) + outgroup (5)	**12S**	-	296	42	**59**	19.9	-	43	12	6	39	χ^2=18.8; df=96; **P=1**
Anthelidae (9) + outgroup (1)	**18S**	-	510	1	**3**	0.6	-	26	22	26	25	χ^2=1.9; df=18; **P=0.99999935**
bombycoid complex (18) + outgroup (4)	**28S**	-	633	32	**108**	17.1	-	21	28	32	19	χ^2=10.1; df=63; **P=1**

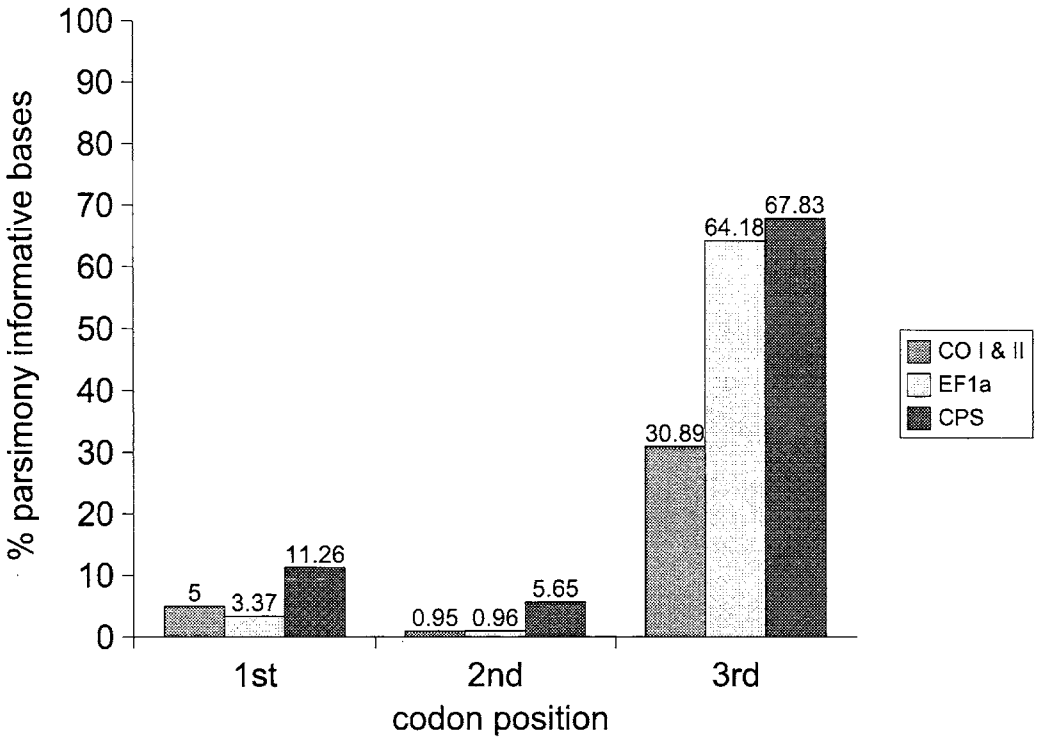

Fig. 358: Proportion of parsimony informative bases of the codon positions for the genes CO I & II, EF1a and CPS in the Anthelidae – note the much higher proportion of parsimony informative bases in 1st and 2nd codon positions of CPS relative to CO I & II and EF1a.

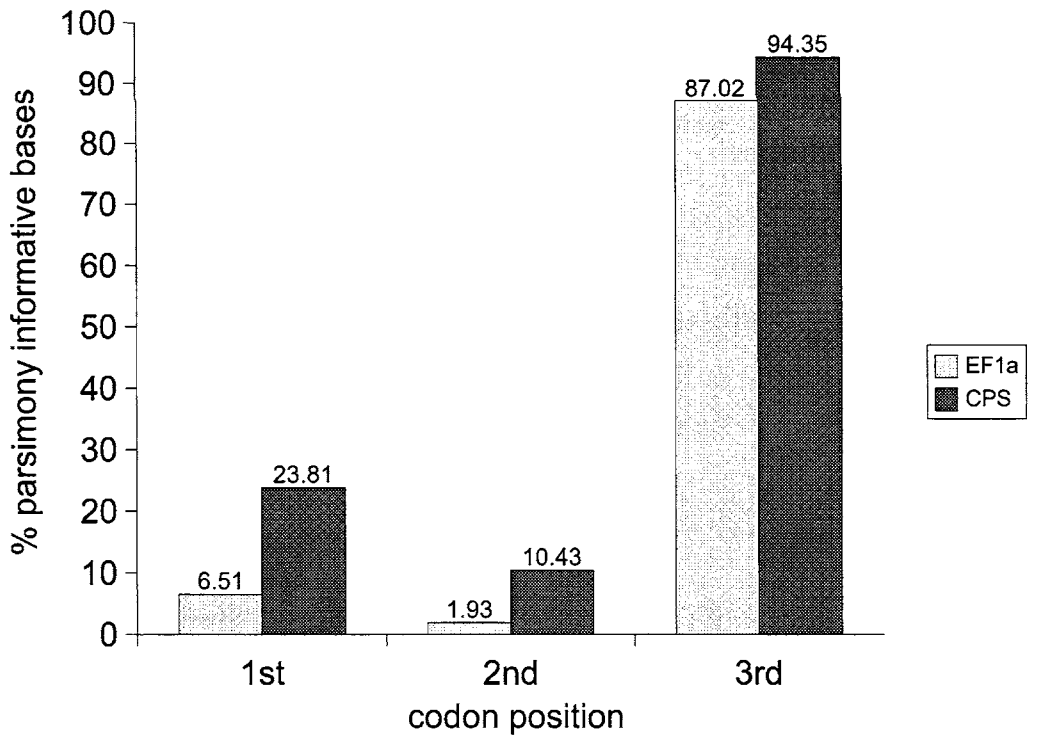

Fig. 359: Proportion of parsimony informative bases of the codon positions for the genes EF1a and CPS in the bombycoid complex – note the much higher proportion of parsimony informative bases in 1st and 2nd codon positions of CPS relative to and EF1a.

V.2) QUALITATIVE CHARACTERISTICS OF THE MOLECULAR DATA

The information content of data, including molecular characters, depends not only on the quantity of parsimony informative characters (see above, V.1), but also on their quality. Like morphological data, sequence data are not given facts. Instead, molecular characters are hypotheses of homology based on the alignment of sequences that are obtained through a series of complex, but highly reproducible technical processes. Each of these technical processes has a certain potential to introduce errors into the data. For the processes involved in sequencing, the noise in sequence chromatograms and the (automated or manual) interpretation of the chromatograms appear to be the most frequent source of error. Such errors cannot be excluded entirely, but I attempted to minimize the number of errors by sequencing the complementary forward and reverse strands of all genes, by using the alternative base-caller software Phred which assigns quality values (Ewing & Green 1998), and by manually checking all sequences in multiple ways as described above (section II.3.5). Ideally, these measures eliminate effectively all errors. However, it should be noted that mainly due to technical and financial limitations not all of these measures were always possible to realize. Occasionally, parts of sequences have been sequenced effectively as single strands only, because of stretches of low quality base-calls in one of the complementary strands. This is most frequently the case at the ends of sequences, where in addition sequence chromatograms are generally shallower and of lower quality for technical reasons. If base-calls in a final single-strand sequence or in all strands of the consensus sequence were ambiguous, I used the appropriate standard IUPAC Ambiguity Code [K, Y, W, S, R, M, B, D, H, V, N] instead of the originally called base.

While the technical quality of any character state can only be judged by an assessment of the quality of individual sequences at that specific site, overall sequence quality gives an indication of the number of errors to be expected. The overall quality of my sequences is high, as indicated by Phred quality scores for individual base-calls (Ewing & Green 1998), but I do not show these scores due to their large number (>140,000). Presenting and using the quality scores for the parsimony informative characters only would be useful, but the effort to manually identify them among all individual quality scores outweighs their usefulness in my opinion.

An indirect judgement of overall sequence quality is the comparison of independently obtained sequences of the same gene and taxon. While I did not sequence several specimens of the same species, my gene and taxon sampling overlaps in two cases with sequences deposited by other researchers on Genbank. These are the EF1a sequences of *Opodiphthera eucalypti* (Genbank accession number AF373938) and *Brahmaea certhia* (Genbank accession number AF234560), which are 100% identical with my own sequences. However, the exact match of only two sequences of one gene is no guarantee of similarly high quality of all of my sequences.

The alignment of sequences is the equivalent to the formation of hypotheses of homology for morphological characters. Hence, the information content of the aligned sequences stands or falls with the correctness of the alignment. The homologization of individual bases in different taxa is solely based on the position of the bases within the sequence, which is an application of Remane's criterion of location (see above, section II.4.1.A). Therefore, the absence of insertions and deletions is crucial for an unambiguous alignment of the sequences. In the coding sequence of protein coding genes, in which the triplet reading frame has to be maintained for the correct translation of the entire coding sequence, insertions and deletions ("indels") are very rare. If present at all, such indels occur in multiples of three, which makes a distinction from a typical sequencing mistake (the addition or absence of a single base) easy. In contrast, non-coding ribosomal genes are transcribed to rRNA, which forms secondary structures with highly conserved, double-strand stems and highly variable, single-strand loops. Between different taxa these loops often differ in size, which makes it impossible to align unambiguously those parts of the sequence that code for the loops in the rRNA. Substitutions in double-stranded stems pose a different problem, one of non-independence of characters. As stems are formed by the folding of the rRNA molecule onto itself, any established substitution of one base within one strand of the stem has induced the substitution of the complementary base in the opposite strand, which is a second base within the same (gene of the) rRNA molecule. Hence, substitutions within ribosomal genes are ideally subject to differential weighting schemes based on the secondary structure of the rRNA.

The alignments of my own sequences are no exception to the above principles. For the protein coding genes CO I & II, EF1a and CPS the alignment is straight forward and unambiguous. No indels are present and the successful translation of the sequences to amino acids without start or stop codons in the coding sequence (only done for EF1a and CPS, but not CO I & II) corroborates the correctness of the alignment. Likewise, no indels are present in the sequenced fragment of the ribosomal gene 18S. With hardly any variation between sequences, the alignment of the 18S sequences is straight forward. In contrast, the sequences of the ribosomal genes 12S and 28S show strong to extreme differences in length. These differences are confined to highly variable regions, which are located between very constant regions, and most probably correspond to loop and stem regions of the secondary structure of the rRNA molecules. While the alignment of the conserved stems is not difficult, the presumed loop regions cannot be aligned due to the differences in length. I excluded these hyper-variable regions in both genes for the phylogenetic analyses. Due to the differences in length, the alignment of the variable sections that border the hyper-variable loops is also somewhat ambiguous.

Apart from the technical quality of sequences and the quality of the alignment, the information content of the molecular data depends on the quality of the characters in a phylogenetic sense. This "phylogenetic quality" depends on the amount of noise (homoplasy), which is contained in the characters. The noise is caused by multiple substitutions of bases at one site, which wipes out any older phylogenetic information present at that site (saturation). Such multiple substitutions cannot be observed directly, but inferred from the transition/transversion ratio (Ti/Tv). Transitions are substitutions of bases, which replace one class of bases with the same class of bases, i.e., a purine base with a purine base or a pyrimidine base with a pyrimidine base. Transversions are the opposite type of substitution, in which one class of bases is replaced by the other class of bases, e.g., a purine base is replaced by a pyrimidine base. The rates at which transitions and transversions occur are not equal – transitions occur more frequently than transversions. Observed over time, the ratio of transitions to transversions (Ti/Tv ratio) decreases to a level at which it does not change any further, because of multiple substitutions. Hence, observing a convergence of the Ti/Tv ratio over time indicates saturation. As different taxa diverged from each other at different times, plotting sequence Ti/Tv ratios of different taxon pairs against the pairwise distances of these

taxon pairs gives a rough indication for the degree of saturation of the sequence. It should be noted that neither Ti/Tv ratios nor distances are corrected for multiple or silent substitutions, which is why the saturation plots do not provide an absolute measure of saturation, but just an indication for it.

I prepared saturation plots for my sequences of CO I & II (Fig. 360), EF1a (Figs 361, 362), CPS (Figs 363, 364), 12S (Fig. 365) and 28S (Fig. 366), but not for the almost invariable 18S sequences. For the protein coding genes CO I & II, EF1a and CPS the saturation plots present the three codon positions separately, because the different codon positions generally evolve differently due to the degeneration of the genetic code. For EF1a and CPS sequences I created separate plots for the taxa used in the analyses of the Anthelidae and of the bombycoid complex.

The saturation plot of the CO I & II sequences (Fig. 360) shows that the Ti/Tv ratios of first and second codon positions of Anthelidae do not converge onto a plateau with an increase in pairwise distance. This means that within Anthelidae first and second codon positions are not yet saturated, hence the number of multiple substitutions since the divergence of taxa within the Anthelidae seem to be rather low. With anthelid taxa compared to the outgroup the same codon positions start to approach saturation. In contrast, the Ti/Tv ratios of third codon positions essentially do not change with an increase of divergence between any taxon pairs. This indicates a very strong saturation of third codon positions even for species within the Anthelidae.

For Anthelidae the EF1a sequences are not saturated in first and second codon positions, but they are substantially saturated in third codon positions (Fig. 361). The same is true for the bombycoid complex, except for an increase in saturation of third codon positions, which are very strongly saturated (Fig. 362).

The CPS sequences of Anthelidae are not yet saturated in first and second codon positions, but if compared to the outgroup start to approach saturation (Fig. 363). Similarly, third codon positions are not yet saturated within Anthelidae, except for a small number of nodes that approach saturation. Within the bombycoid complex, first and second codon positions of CPS start to approach saturation, and third codon positions are strongly saturated (Fig. 364).

The ribosomal 12S sequences of the bombycoid complex show a range of Ti/Tv ratios across a relatively short range of pairwise distances, but for many taxon pairs the sequences appear to be saturated (Fig. 365).

For the ribosomal 28S sequences the Ti/Tv ratios are similarly scattered, but compared to 12S the 28S sequences of fewer taxon pairs seem to be saturated (Fig. 366).

In summary, for the protein coding genes only first and second codon positions are generally not saturated, both within Anthelidae and within the bombycoid complex. In contrast, the third codon positions of the protein coding genes other than CPS are largely to strongly saturated within the Anthelidae, and they are certainly saturated for all protein coding genes within the bombycoid complex. The ribosomal genes 12S and 28S both appear to be saturated within the bombycoid complex.

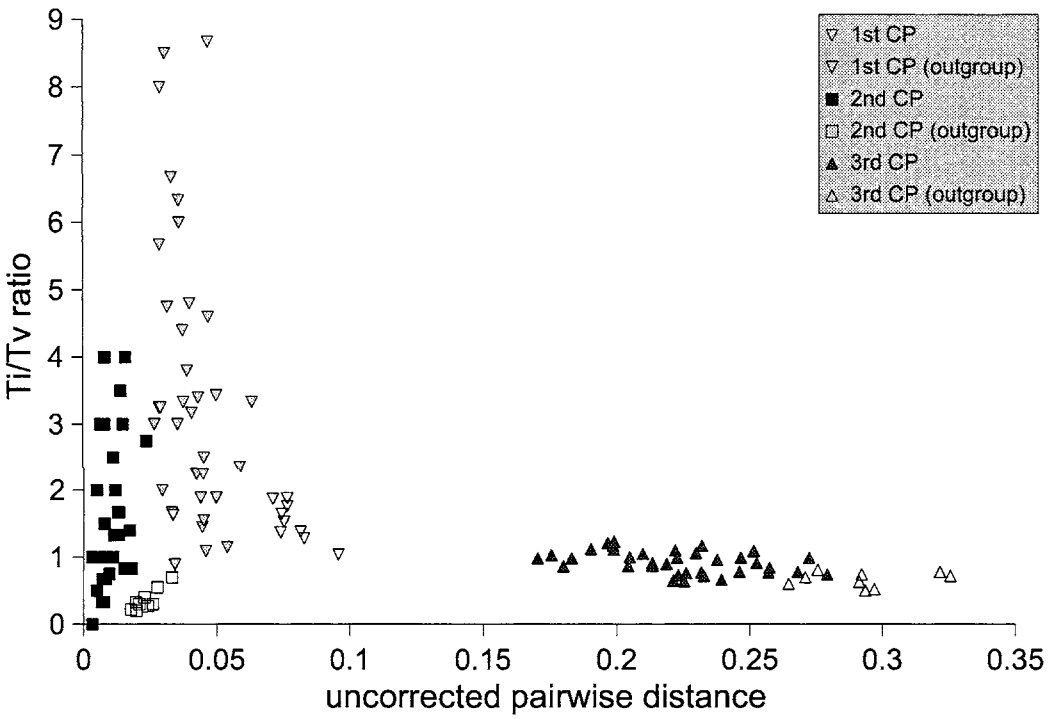

Fig. 360: Saturation plot for the three codon positions of CO I & II sequences of the Anthelidae plus outgroup (Lasiocampidae) – while first and second codon positions approach saturation only at the level of the outgroup, the third codon positions are very strongly saturated even within the Anthelidae.

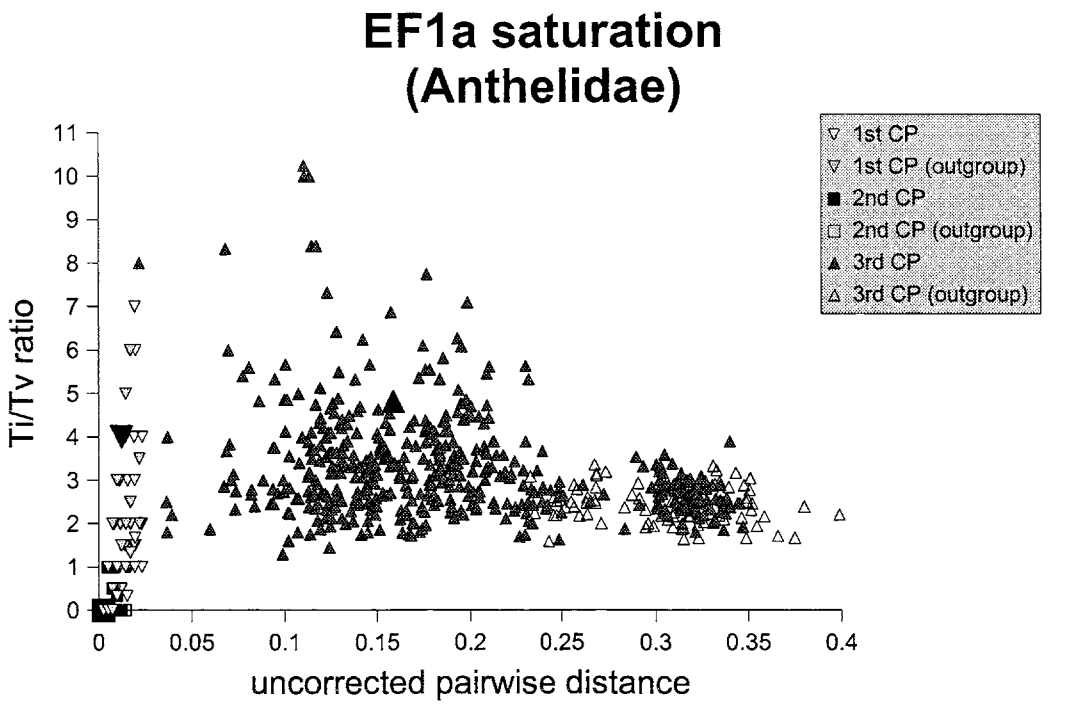

Fig. 361: Saturation plot for the three codon positions of EF1a sequences of the Anthelidae plus outgroup (Carthaeidae, Saturniidae & Eupterotidae) – while first and second codon positions are not saturated, the third codon positions are substantially saturated within the Anthelidae; symbols of *Chenuala heliaspis* / Anthelinae n. sp. black and enlarged.

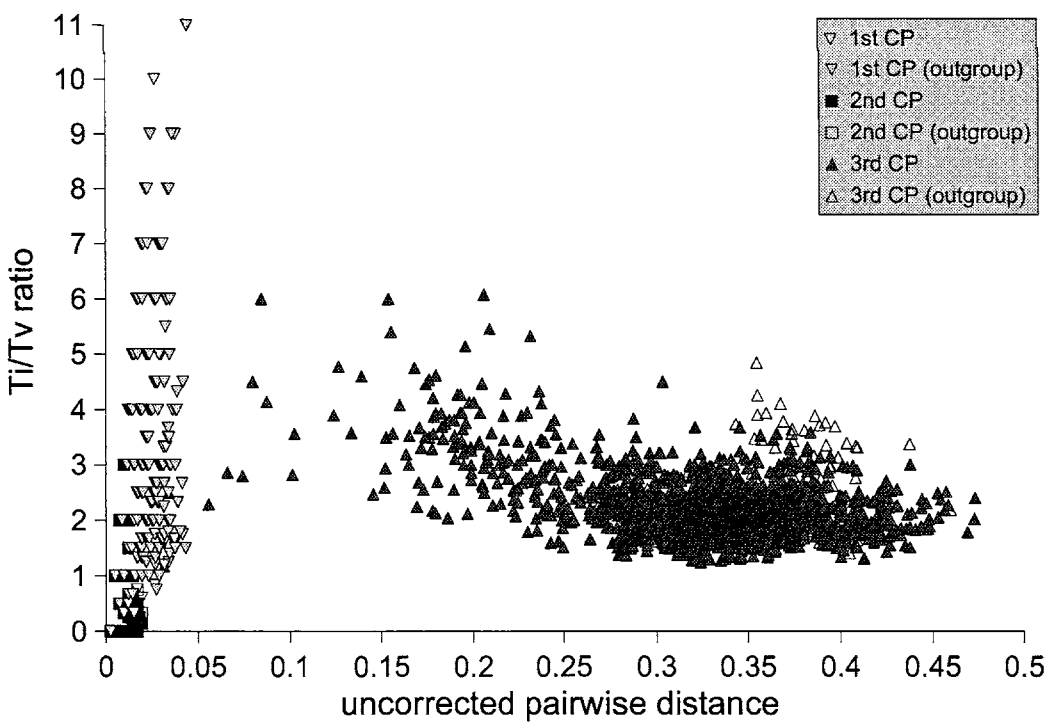

Fig. 362: Saturation plot for the three codon positions of EF1a sequences of the bombycoid complex plus outgroup (Thyrididae, Oenosandridae, Notodontidae & Lymantriidae) – while first and second codon positions are not saturated, the third codon positions are very strongly saturated within the bombycoid complex.

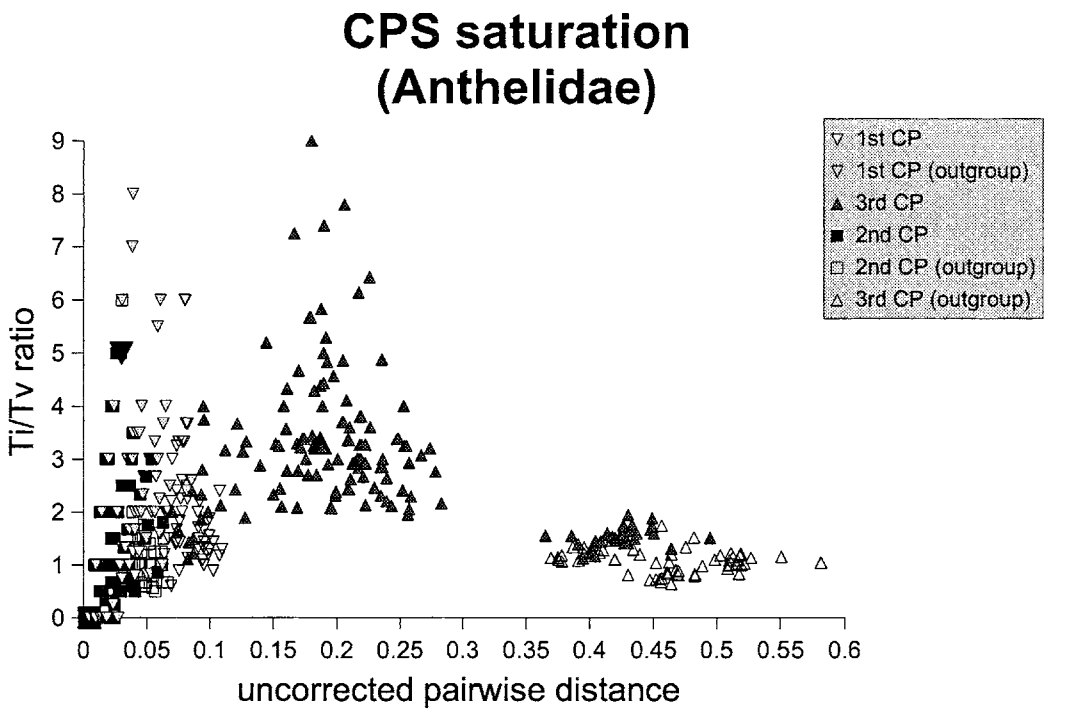

Fig. 363: Saturation plot for the three codon positions of CPS sequences of the Anthelidae plus outgroup (Carthaeidae, Saturniidae & Eupterotidae) – while first and second codon positions start to approach saturation only at the level of the outgroup, the third codon positions approach saturation for some nodes within the Anthelidae; symbols of *Chenuala heliaspis* / Anthelinae n. sp. black and enlarged.

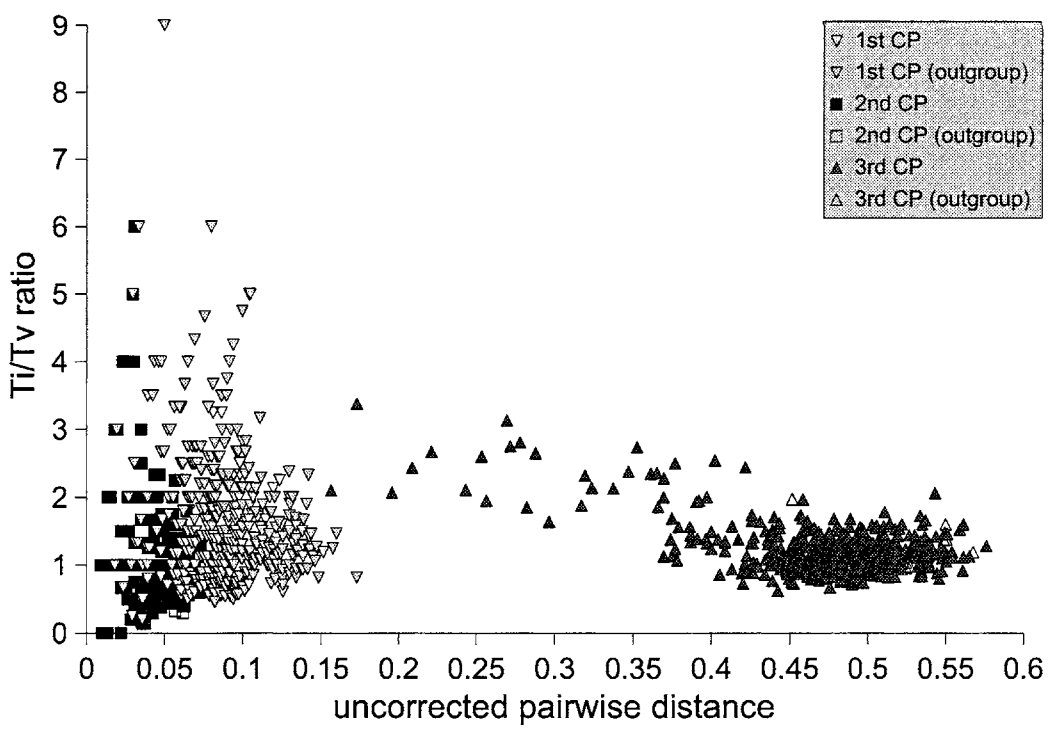

Fig. 364: Saturation plot for the three codon positions of CPS sequences of the bombycoid complex plus outgroup (Thyrididae) – while the first and second codon position start to approach saturation, the third codon positions are largely saturated within the bombycoid complex.

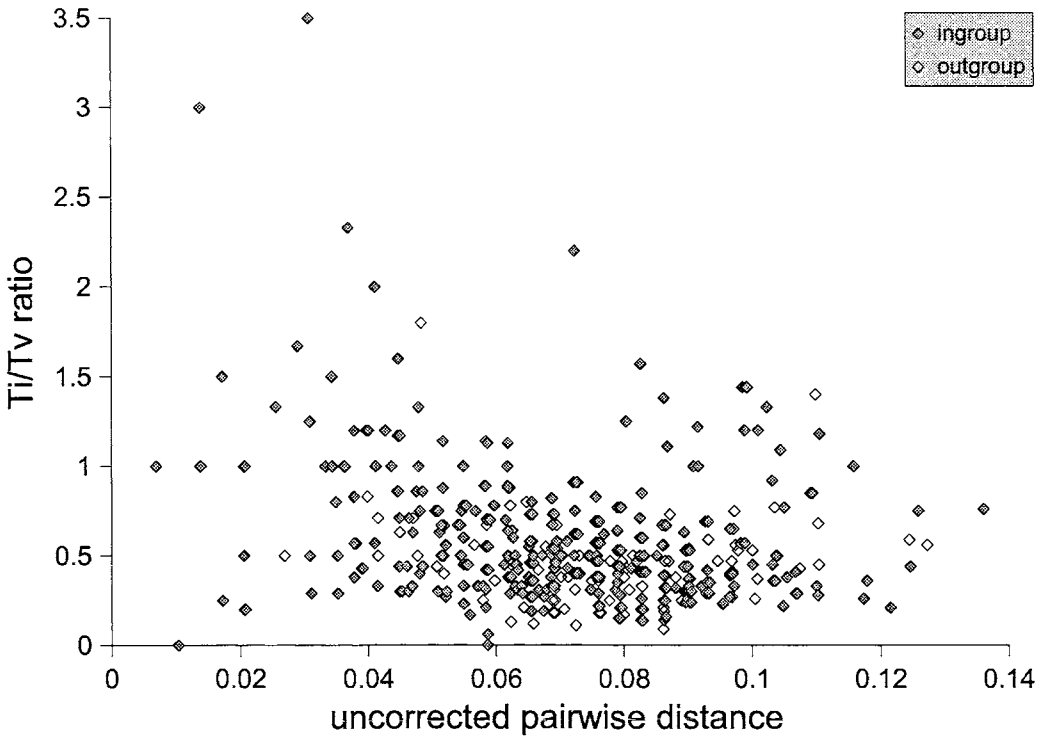

Fig. 365: Saturation plot for 12S sequences of the bombycoid complex plus outgroup (Pyralidae, Geometridae, Noctuidae & Lymantriidae) – the sequence is largely saturated within the bombycoid complex.

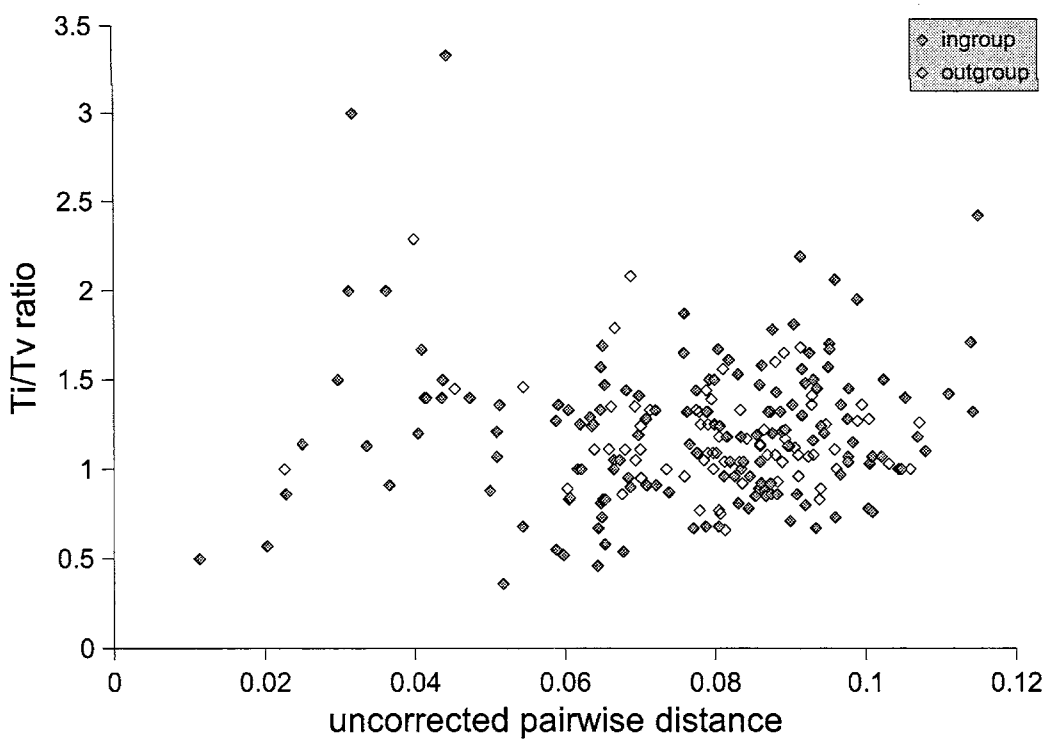

Fig. 366: Saturation plot for 28S sequences of the bombycoid complex plus outgroup (Thyrididae, Oenosandridae & Lymantriidae) – the sequence is substantially saturated within the bombycoid complex.

V.3) SELECTION OF MOLECULAR DATA

Based on the quantitative and qualitative characteristics of the different genes I decided to exclude some of the molecular data from the phylogenetic analyses.

COI & II sequences are very strongly saturated at the third codon positions and show a strong base-frequency bias, even within the Anthelidae. Excluding the third codon position leaves very few parsimony informative characters, which to obtain in quantity long stretches have to be sequenced. This is very inefficient and costly. As to be expected from these problems, a preliminary Maximum Parsimony Analysis of the ten test taxa did not resolve relationships within Anthelidae (results not shown). Hence, I did not sequence CO I & II for additional species, nor did I double-check the obtained sequences, exclude primers from them, or use the sequences for my analyses.

The 18S fragment provides only three parsimony informative characters, which is why I did not sequence this gene for additional species, nor use the three parsimony informative characters in my analyses. The sequence fragments of the other two ribosomal genes, 12S and 28S, are both unalignable in those regions that hold the majority of parsimony informative characters. For both genes preliminary parsimony analyses (unalignable regions excluded) neither resolved any relationships within the Anthelidae, nor within the bombycoid complex (results not shown). In the case of 12S, the addition of 13 lepidopteran sequences from Genbank did not improve the situation. Hence, I did not sequence additional species and do not use these data for my phylogenetic analyses.

Like COI & II, the EF1a and CPS sequences are at least partly saturated in third codon positions, but to a lesser degree. Their first and second codon positions are not saturated, and for CPS these codon positions provide a relatively large number of parsimony informative characters. Further, sequence alignment is unambiguous and the sequence data are complete for the majority of species. Therefore, of all the genes I sequenced I use only sequences of the two genes EF1a and CPS in my subsequent phylogenetic analyses.

V.4) PHYLOGENETIC HYPOTHESES

Ideally phylogenetic analyses should include all available taxa, because the length of the branches decreases with an increase of sampling density. This reduces the problem of "long branch attraction", which is the incorrect grouping of taxa due to analogies/convergences outnumbering homologies. Long branch attraction is particularly problematic for the rooting of trees by cladistic outgroup addition, as outgroups are typically rather distant to the ingroup and therefore might incorrectly root the ingroup at a long branch of the ingroup (Hendy & Penny 1989).

However, because of the extreme increase in computation time with an increasing number of taxa in Maximum Likelihood and Bayesian Inference analyses I analysed the molecular data separately for the phylogeny of the Anthelidae and the one of the bombycoid complex, including only a few anthelid representatives in the latter. In both cases I used outgroup taxa that other phylogenetic hypotheses indicate to be closely related. In the case of the analyses of the Anthelidae this is based on my hypothesis of phylogeny of the bombycoid complex (section III.7.2) and consists of the Carthaeidae, Saturniidae and Eupterotidae, the latter two presumably being more closely related to the Anthelidae. For the analyses of the bombycoid complex my choice of the outgroup is based on the phylogeny presented in Kristensen and Skalski ([1998]: 10) and my own, tentative hypothesis of the Noctuoidea possibly being the sistergroup of the bombycoid complex (section III.7.2). I always used the Thyrididae as an outgroup, and in the case of EF1a sequences I used additionally the Oenosandridae, Notodontidae and, in one case, Lymantriidae (the latter three all Noctuoidea).

I analysed the molecular data with the phenomenological method of Maximum Parsimony (MP), as well as with the process-dependent methods of Maximum Likelihood (ML) and Bayesian Inference (BI). While phenomenological and process-dependent methods are fundamentally different, I present and discuss the results of the different analyses together, first for the Anthelidae (section V.4.1) and then for the bombycoid complex (section V.4.2) by genes, rather than in the order of the different methods.

The phylograms and support values (bootstrap percentage, Partitioned Bremer Support [PBS] and posterior probability) are based on equal character weights. However, to test for the influence of saturation in predominantly third codon positions,

bootstrap percentages of MP analyses were calculated for by codon position equally as well as differentially weighted characters. This differential weighting influenced the bootstrap percentages as shown in the phylograms, but did not result in significantly different or even conflicting topologies (only branches with bootstrap support of less than 60% differed). Instead, downweighting third codon positions resulted in a decrease of resolution due to the low numbers of parsimony informative characters in first and second codon positions. Because the downweighting or even exclusion of saturated third codon positions did not result in different topologies and because the degree of saturation differes between taxon pairs, I did not exclude third codon positions in my ML and BI analyses.

General statistics of the phylograms, e.g., tree length, consistency index (CI), consistency index excluding uninformative characters (CIU), retention index (RI) *etc.*, are given in the figure caption of each phylogram (Figs 367-375, 377-385).

While support values are part of any modern phylogenetic analysis, no consensus exists as to which values should be regarded as "good" or "high" support. Similarly, controversy exists about the equality of different support values, with posterior probabilities often being seen as generally too high (e.g., Suzuki *et al.* 2002, Alfaro *et al.* 2003, Cummings *et al.* 2003, Douady *et al.* 2003). I conservatively but arbitrarily interpret bootstrap percentages of ≥80% and posterior probabilities of ≥90% as high support for the assumption of the topology correctly reflecting the given data analysed with the given method.

In the following sections I discuss the consensus trees resulting from the different analyses. These discussions are largely based on the support values specified in the respective phylograms. However, these support values reflect only the fit of the topology to the given data analysed with the given method, but cannot assess the quality of the data. Because the probability of any phylogenetic hypothesis being correct depends on the quality of underlying data in the first place, a high support value alone does not necessarily justify high confidence in the phylogenetic hypothesis. Therefore, I include in the discussion a rough judgement of the data quality as indicated by the saturation plots (section V.2) in those cases, in which high support values seem to be based on dubious data.

V.4.1) Phylogeny of the Anthelidae

V.4.1.1) Analyses of EF1a

All available EF1a sequences of Anthelidae (31) were included in the MP (Fig. 367) and BI analyses (Fig. 369), but only a subset of anthelid sequences (22 species) was used in the ML analysis (Fig. 368) to limit calculation time. Four nodes of the MP analysis of the EF1a sequences have a very high bootstrap percentage but a low negative PBS value for first and/or second codon position, indicating conflicting information between the different codon positions of EF1a. This is likely to be caused by the high proportion of probably largely saturated third codon positions (see sections V.1 and V.2), which drive the analyses. The paucity of parsimony informative characters in first and second codon positions (see section V.1) is reflected in the decrease of the bootstrap percentages with the down-weighting of third codon positions.

Most of the well supported nodes of the MP analysis are species pairs, but numerous additional well supported nodes are present in the phylogram of the BI analysis. The species pairs well supported by MP, BI and partly ML analyses are *A. unisigna* / *A. stygiana*, *A. oressarcha* / *A. ocellata*, *Pterolocera* sp. A / B, *A. rubicunda* / *A. asterias*, *A. adriana* / *A. phoenicias*, Anthelinae n. sp. / *Chenuala heliaspis* and *M. periclyta* / *M. senicula*. Of these species pairs the pair Anthelinae n. sp. / *C. heliaspis* stands out by a high bootstrap percentage and posterior probability in all analyses, which contrasts with the distinctly lower and conflicting PBS support. The grouping of these two taxa is only supported by third codon positions (PBS 4.5), but contradicted by first codon positions (PBS -0.5). The saturation plot (Fig. 361, species pair highligted in black) shows that the third codon positions of this species pair are probably saturated, while first codon positions are probably not. Hence, the grouping of these two species is not convincing, despite the high bootstrap support.

Other species groups that are well supported in all analyses are (*A. rubicunda* / *A. asterias*) / *A. clementi*, *A. virescens* / *A. addita* / *A. ferruginosa* and (*M. periclyta* / *M. senicula*) / *G. cosmia* [= Munychryiinae]. Further, a monophylum containing all sequenced antheline species except for *Chelepteryx chalepteryx* is moderately supported in the MP and well supported in the BI analysis. In the MP analysis one large clade including the species from *A. unisigna* to *A. euryphrica* is weakly supported by a bootstrap percentage of 81 but a PBS of 1.1 in the third codon position only. This large

clade is incompatible with a very well supported clade comprising the species from *A. stygiana* to *A. euryphrica* in the BI analysis, which differs from the former by the additional inclusion and position of *A. adriana* / *A. phoenicias*. Further, the BI analysis supports also a monophylum consisting of *A. acuta* complex / *A. astata* / *A. varia* / *A. callixantha*, as well as a monophylum additionally including *A. repleta* and *A. euryphrica*. The monophyly of the subfamily Anthelinae is well supported in ML and BI analyses, but only moderately so in the MP analysis.

Within the outgroup a monophylum consisting of *Aglia tau* (Saturniidae) and *H. rhodoptera* group (Eupterotidae) is moderately to well supported in all analyses. However, the PBS indicates that the monophylum is only supported by a few shared substitutions in the strongly saturated third codon position, but contradicted by the seemingly less saturated first and second codon position. Therefore, this monophylum is not credible, despite the high support values.

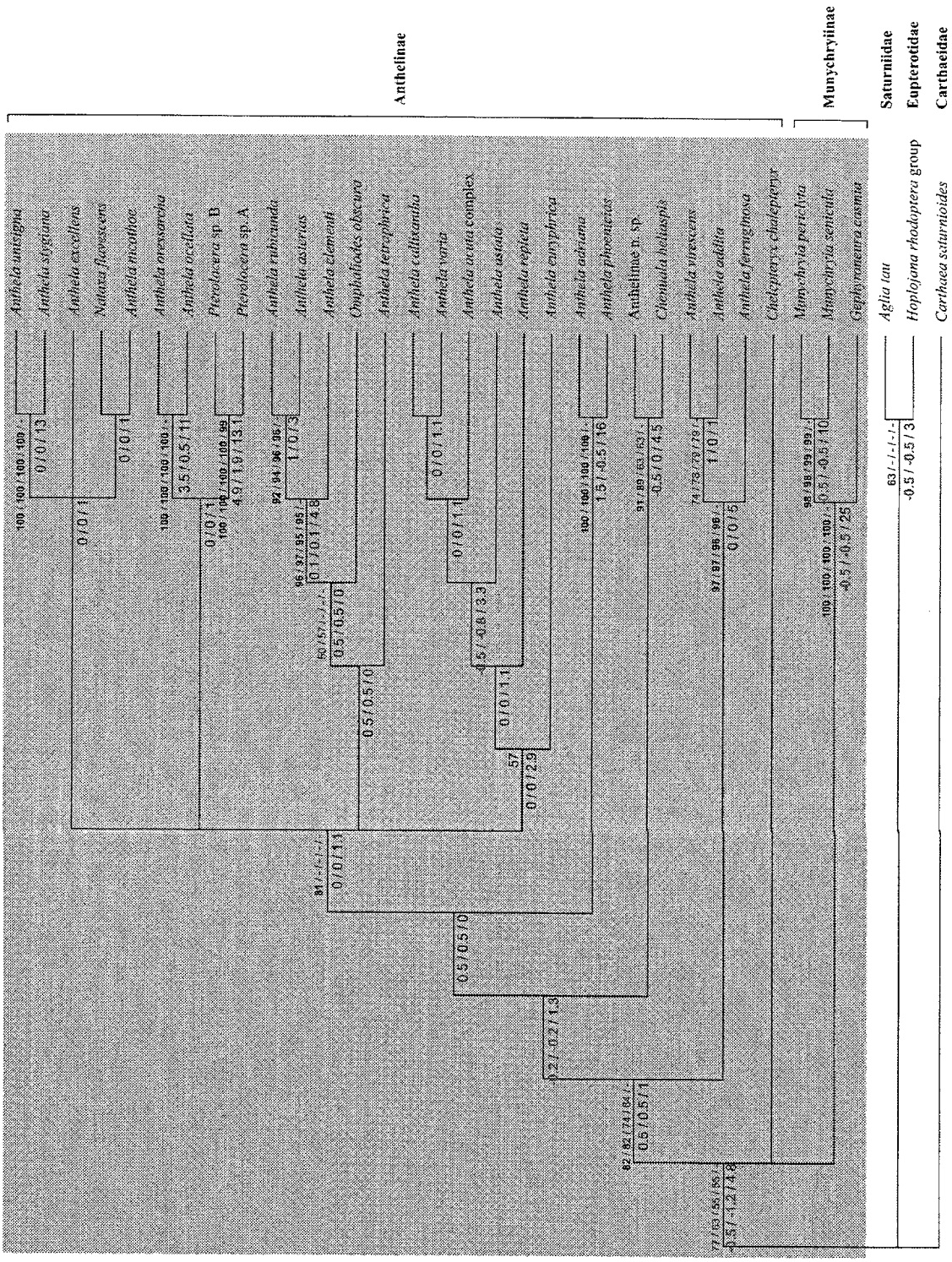

Fig. 367: Maximum Parsimony Analysis of EF1a sequences (1246bp, equally weighted) of Anthelidae (31 species on bluish background; three non-anthelid species as outgroup) – strict consensus tree of the 6 most parsimonious trees (each 1172 steps long; CI=0.44; CIU=0.4; RI=0.52). Numbers above branches are bootstrap percentages ≥50% (≥80% **bold**; 1000 bootstrap replicates) under differential weighting by codon positions (1-1-1 / 2-3-1 / 5-5-1 / 10-10-1 / 1-1-0); numbers below branches are Partitioned Bremer Support values (contradicting, negative values **bold red**), partitioned by codon positions.

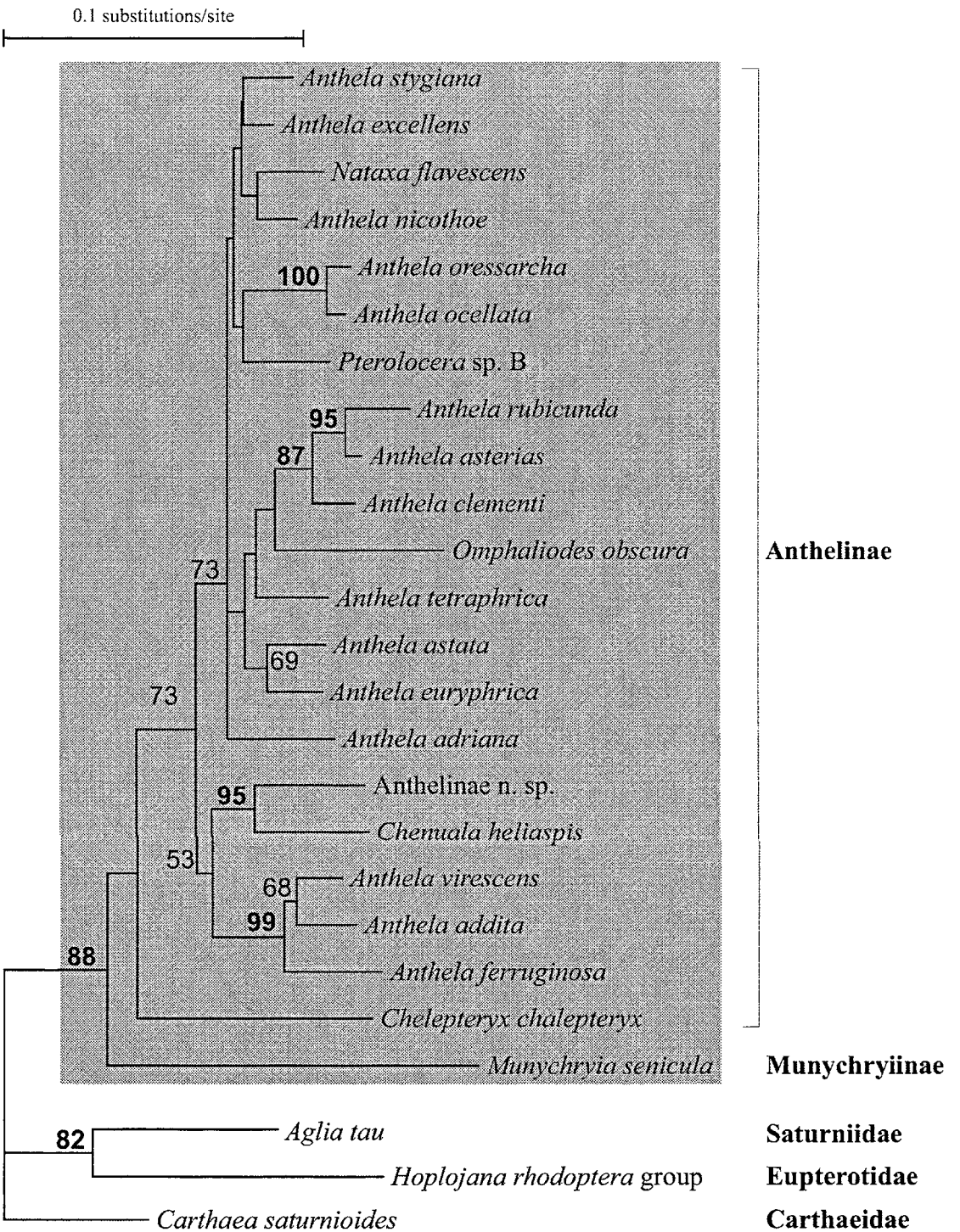

Fig. 368: Maximum Likelihood Analysis (TIM+I+Γ) of EF1a sequences (1246bp, equally weighted) of Anthelidae (22 species on bluish background; three non-anthelid species as outgroup) – phylogram (log-likelihood score = -6364.50311); numbers above branches are bootstrap percentages ≥50% (≥80% **bold**; 100 bootstrap replicates).

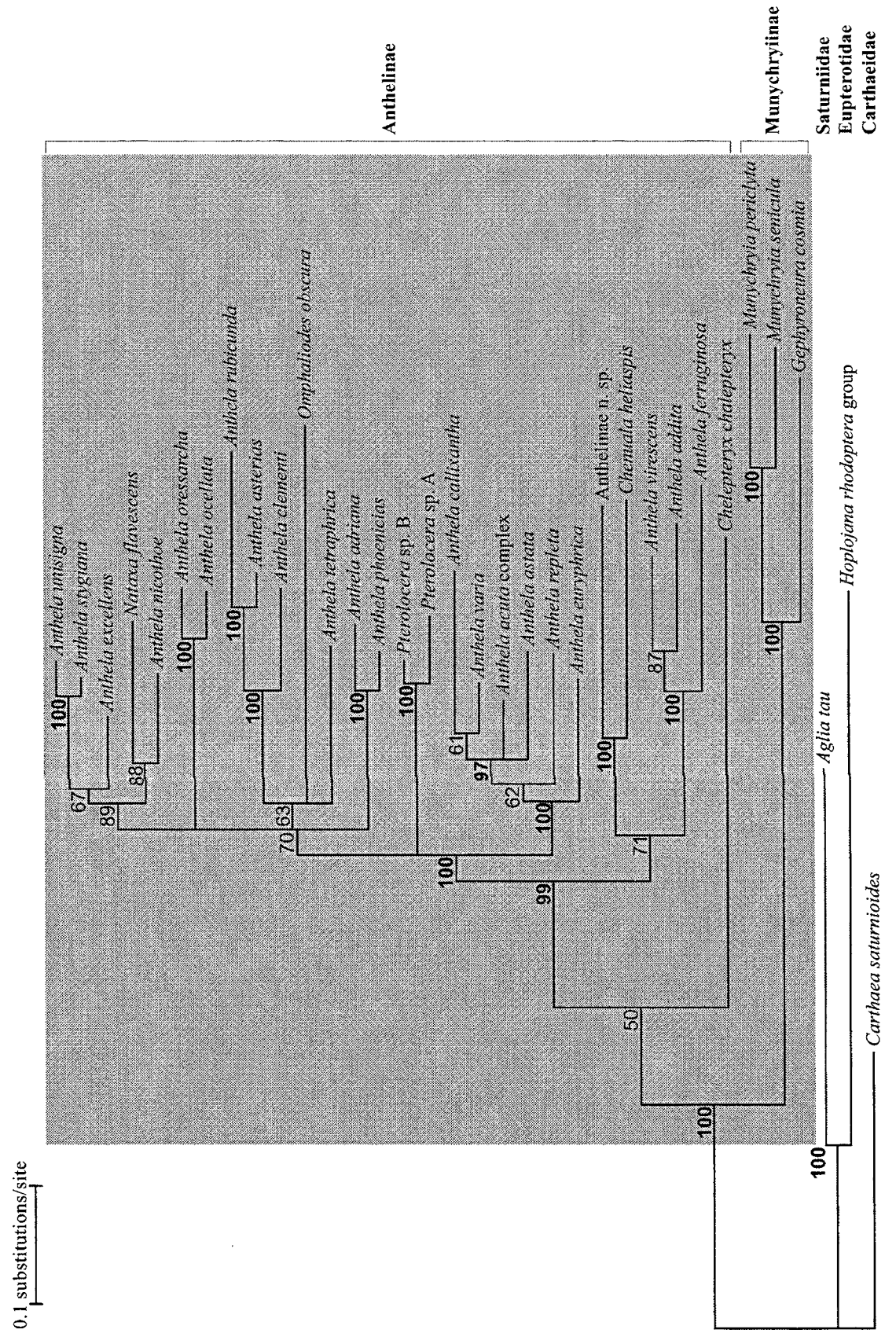

Fig. 369: Bayesian Inference analysis (GTR+I+Γ) of EF1a sequences (1246bp, equally weighted) of Anthelidae (31 species on bluish background; three non-anthelid species as outgroup) – majority rule consensus tree of 439 sampled trees; numbers above branches are posterior probabilities ≥50% (≥90% **bold**).

V.4.1.2) Analyses of CPS

Sequencing was generally less successful for CPS than it was for EF1a, and hence CPS sequences of only a subset of the taxa sequenced for EF1a is available for analyses.

Within the Anthelidae, nodes of the MP analysis of CPS [Fig. 370] with high bootstrap percentages do not have negative PBS values. This indicates that within the family saturation of even third codon positions is still too limited to strongly support conflicting topologies. This interpretation fits the decrease in bootstrap percentages with down-weighting of third codon positions.

Analyses of the CPS sequences alone result in only a few well supported hypotheses of monophyly, all of which are supported by the three different methods of analyses. Three of these monophyla are the very well supported species pairs of *Anthela varia* / *A. astata* (merged into one terminal taxon in the morphological analyses of sections III.7.1, IV.2.1 and VI.1), *A. adriana* / *A. phoenicias* and *Gephyroneura cosmia* / *Munychryia senicula*. The latter two have higher Bremer Support values for all codon positions than any of the other monophyla, including in the less variable and less saturated first and second codon positions. This accumulation of substitutions in all codon positions fits their long branch, which separates each of these two species pairs from all other species in the ML (Fig. 371) and BI analyses (Fig. 372). As the species pair of *G. cosmia* and *M. senicula* represents the Munychryiinae, the monophyly of this anthelid subfamily is very well supported. A larger well supported monophylum consists of *A. stygiana*, *A. excellens*, *Nataxa flavescens* and *A. nicothoe*, but hypotheses on the relationships between these taxa are not well supported. Similarly, the monophylum of *A. varia*, *A. astata*, *A. acuta* complex, *A. repleta* and *A. euryphrica* is well supported, but hypotheses about the relationships within it are only poorly supported. As with the Munychryiinae, the monophyly of the Anthelinae is well supported in MP (mainly first and third codon positions) and BI analyses, less so in the ML analysis. The split between the two subfamilies of the Anthelidae is distinct and seems to be rather old, as indicated by the long branches leading to each of the two subfamilies in ML as well as BI analyses. Nevertheless, the monophyly of the family Anthelidae is well supported in the BI and ML analyses, while the bootstrap support in MP analyses is very limited and restricted to the second and third codon position, as indicated by the PBS.

A monophylum within the outgroup consisting of *Carthaea saturnioides* (Carthaeidae) and *Hoplojana rhodoptera* group (Eupterotidae) is only supported in the

MP and BI analyses, but not in the ML analysis. The PBS shows that this support is based on the first and second codon position, but contradicted by the third codon position (negative PBS). While the third codon position is almost certainly saturated between these two families, first and second codon positions only start to approach saturation, which does not necessarily argue for this monophylum, but certainly not against it.

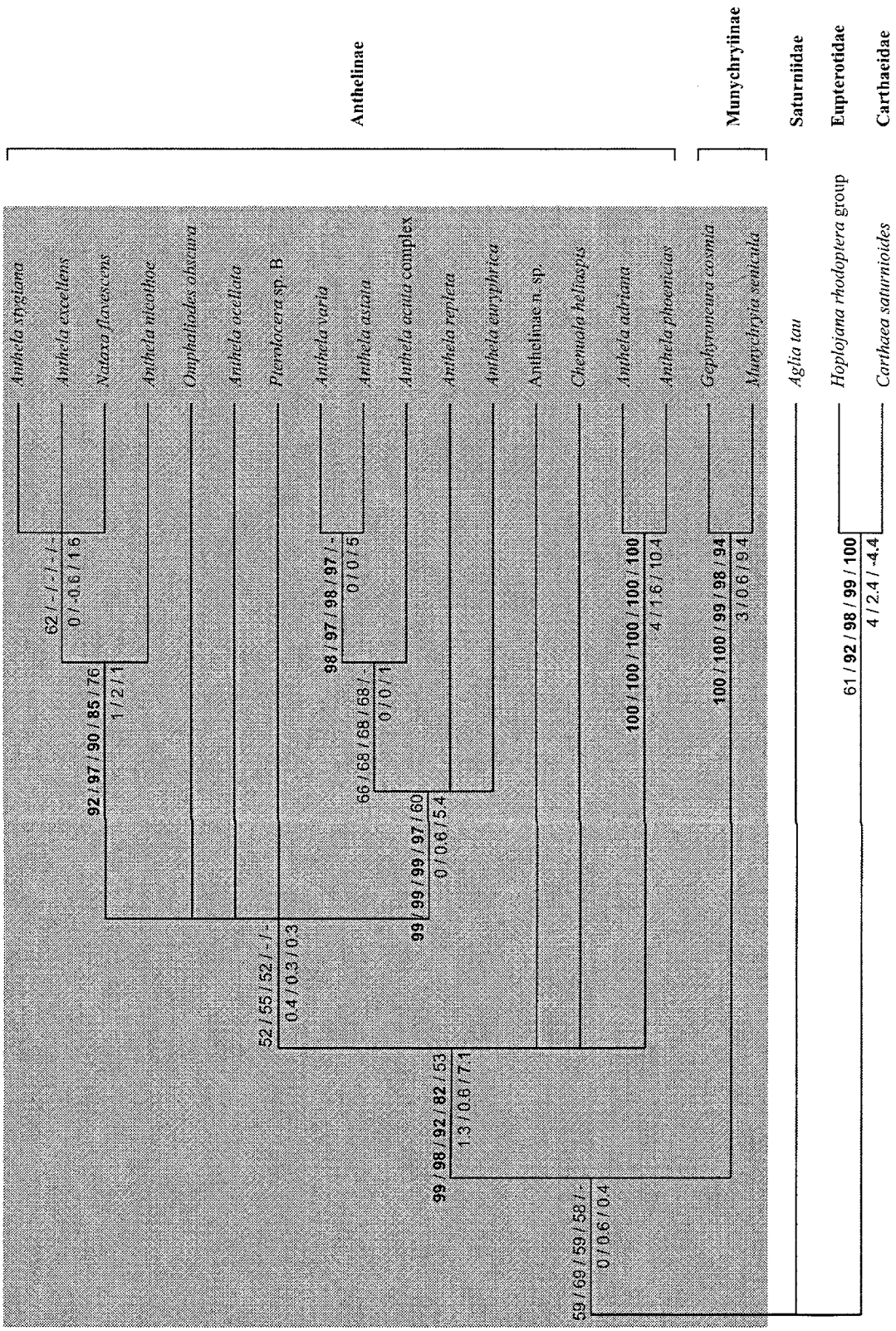

Fig. 370: Maximum Parsimony Analysis of CPS sequences (691bp, equally weighted) of Anthelidae (18 species on bluish background; three non-anthelid species as outgroup) – strict consensus tree of the 42 most parsimonious trees (each 686 steps long; CI=0.59; CIU=0.52; RI=0.56). Numbers above branches are bootstrap percentages ≥50% (≥80% **bold**; 1000 bootstrap replicates) under differential weighting by codon positions (1-1-1 / 2-3-1 / 5-5-1 / 10-10-1 / 1-1-0); numbers below branches are Partitioned Bremer Support values (contradicting, negative values **bold red**), partitioned by codon positions.

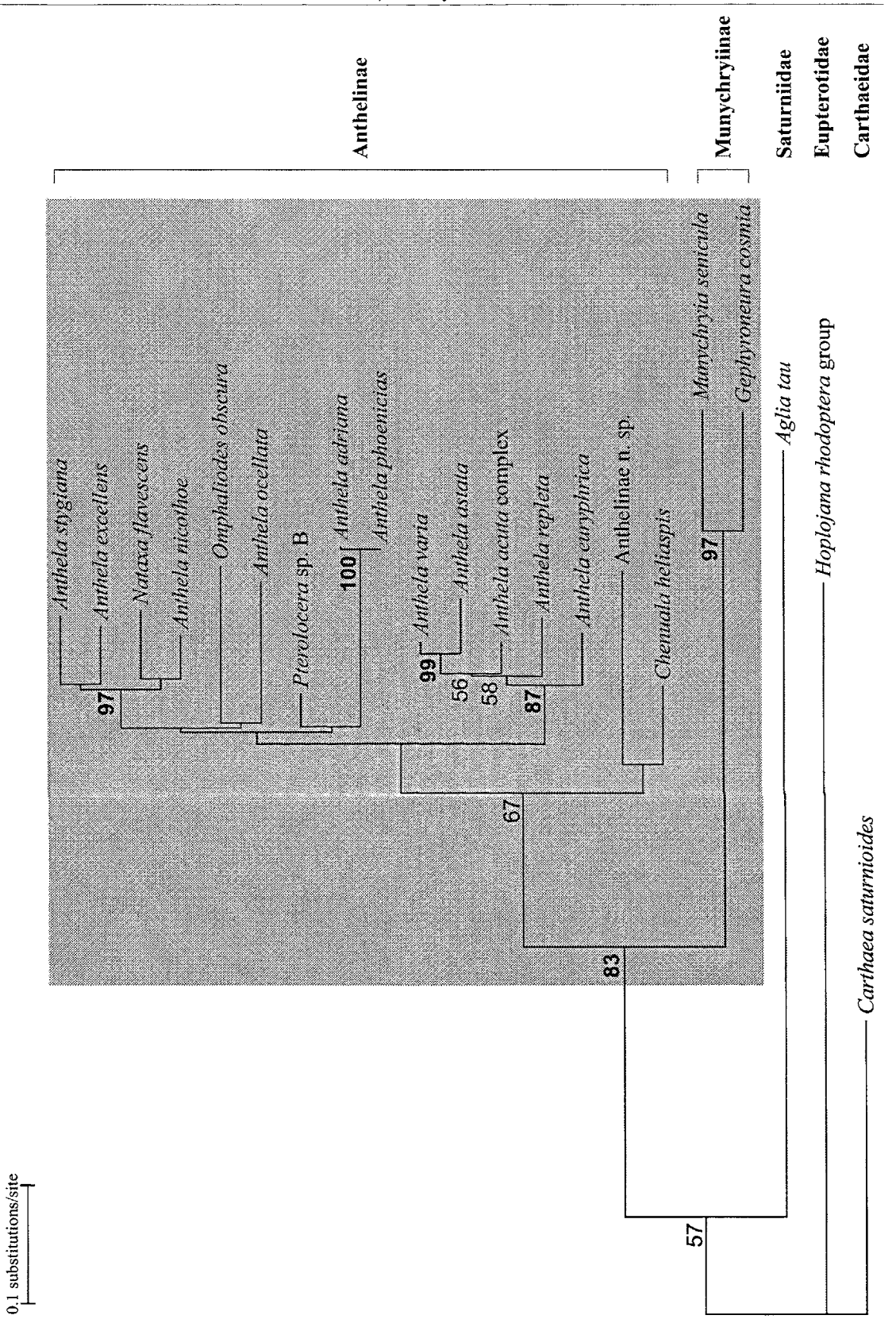

Fig. 371: Maximum Likelihood Analysis (GTR+I+Γ) of CPS sequences (691bp, equally weighted) of Anthelidae (18 species on bluish background; three non-anthelid species as outgroup) – phylogram (log-likelihood score = -3953.53714); numbers above branches are bootstrap percentages ≥50% (≥80% **bold**; 100 bootstrap replicates).

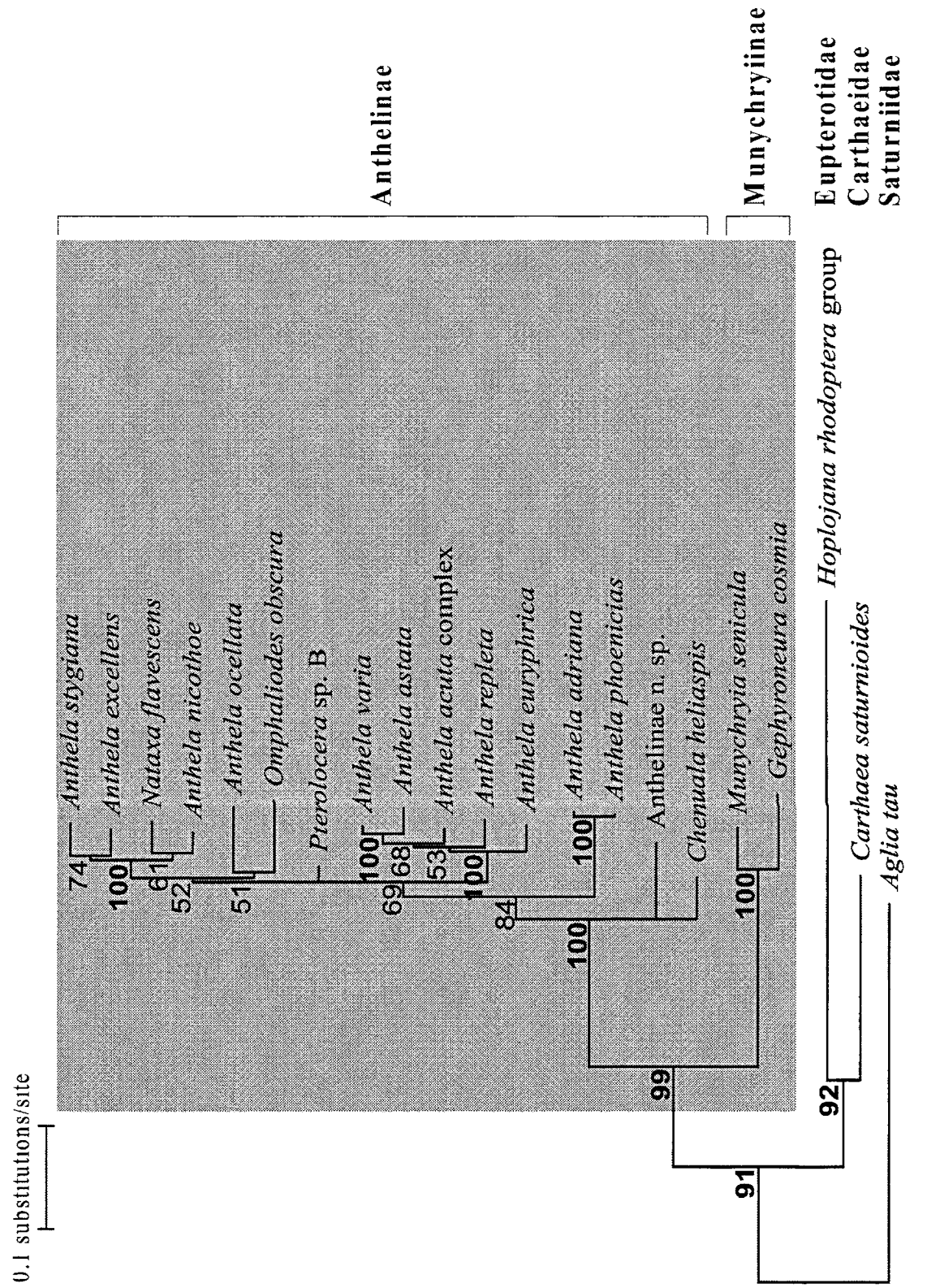

Fig. 372: Bayesian Inference analysis (GTR+I+Γ) of CPS sequences (691bp, equally weighted) of Anthelidae (18 species on bluish background; three non-anthelid species as outgroup) – majority rule consensus tree of 1001 sampled trees; numbers above branches are posterior probabilities ≥50% (≥90% **bold**).

V.4.1.3) Combined analyses of EF1a and CPS

The combined analyses of EF1a and CPS sequences are limited to those taxa for which sequences of both genes are available. These are the same taxa as in the analyses of the CPS sequences alone, and the resulting phylograms are better resolved than those of the CPS analyses and have generally higher support values. However, with few exceptions monophyla that are well supported are identical in all analyses. In addition to the monophyla discussed for CPS, a monophylum consisting of *N. flavescens* and *A. nicothoe* is moderately to well supported in all analyses of the combined EF1a and CPS sequences. A species pair consisting of *A. stygiana* and *A. excellens* is well supported in the ML (Fig. 374) and BI analyses (Fig. 375), but only poorly supported by the third codon position in the MP analysis (Fig. 373). As in the analyses of EF1a only (section V.4.1.1), a monophylum consisting of Anthelinae n. sp. and *C. heliaspis* is controversially supported. Its support by bootstrap percentage and posterior probability is well to very well in all analyses. However, the PBS shows that while the EF1a data support this clade it is significantly contradicted by the first and second codon position of CPS. In the CPS saturation plot (Fig. 363) the third codon positions of CPS fall into the area of beginning saturation. Again, this grouping is well supported by high bootstrap and posterior probability values, but is probably based on saturated third codon positions only.

Further, the ML and BI analyses, and to a lesser degree also the MP analysis, support strongly a monophylum that consists of *A. varia*, *A. astata* and *A. acuta* complex. The PBS shows some conflict between the codon positions of EF1a, but the support for this monophylum by the third codon positions of EF1a and CPS dominates. The ML and BI analyses both strongly support a larger monophylum that includes all Anthelinae of these analyses, except for the Anthelinae n. sp. and *C. heliaspis*. This grouping is also moderately supported by the bootstrap percentage of the MP analysis, but the PBS shows that this grouping is only supported by third codon positions of CPS, while first and second codon positions of CPS contradict this grouping. This contradiction questions the correctness of this hypothesis of homology, in particular as the only support for it is based on the at this level probably saturated third codon positions of CPS.

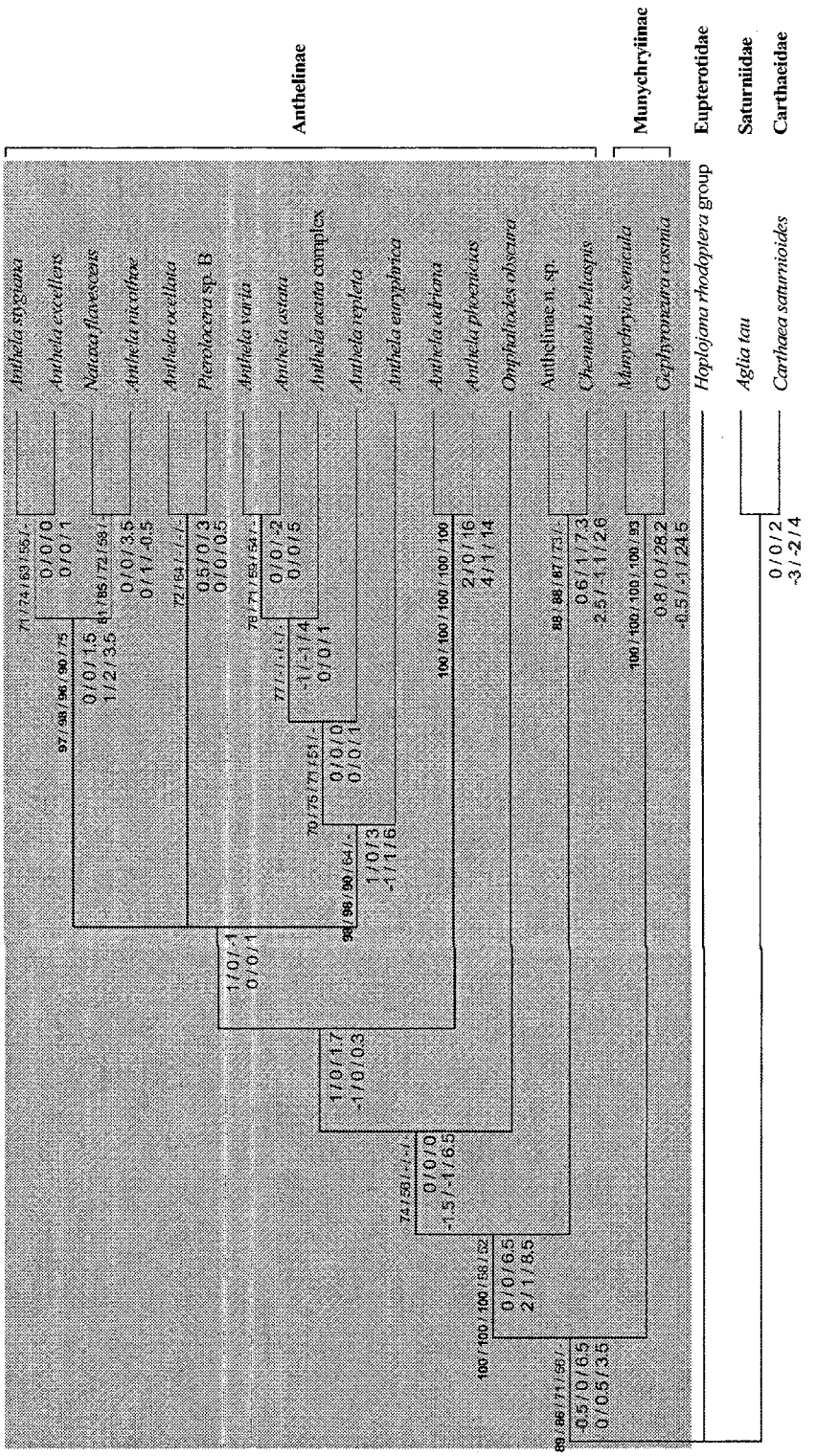

Fig. 373: Maximum Parsimony Analysis of the combined CPS and EF1a sequences (1937bp in total, equally weighted) of Anthelidae (18 species on bluish background; three non-anthelid species as outgroup) – strict consensus tree of the 2 most parsimonious trees (each 1504 steps long; CI=0.55; CIU=0.49; RI=0.5). Numbers above branches are bootstrap percentages ≥50% (≥80% **bold**; 1000 bootstrap replicates) under differential weighting by codon positions (1-1-1 / 2-3-1 / 5-5-1 / 10-10-1 / 1-1-0); numbers below branches are Partitioned Bremer Support values (contradicting, negative values **bold red**), partitioned by codon positions and genes (EF1a above CPS).

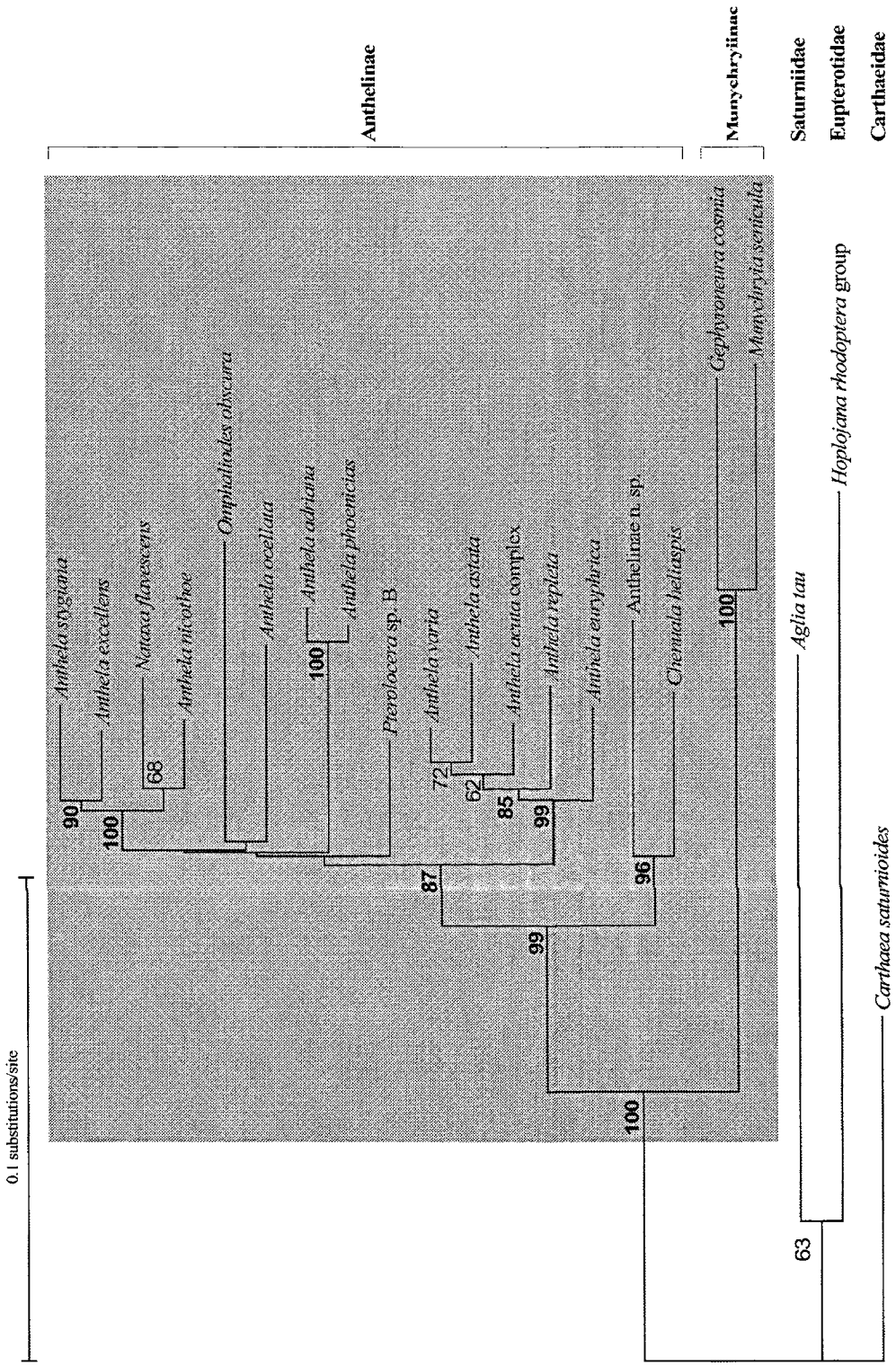

Fig. 374: Maximum Likelihood Analysis (GTR+I+Γ) of the combined CPS and EF1a sequences (1937bp in total, equally weighted) of Anthelidae (18 species on bluish background; three non-anthelid species as outgroup) – phylogram (log-likelihood score = -9624.48016); numbers above branches are bootstrap percentages ≥50% (≥80% **bold**; 100 bootstrap replicates).

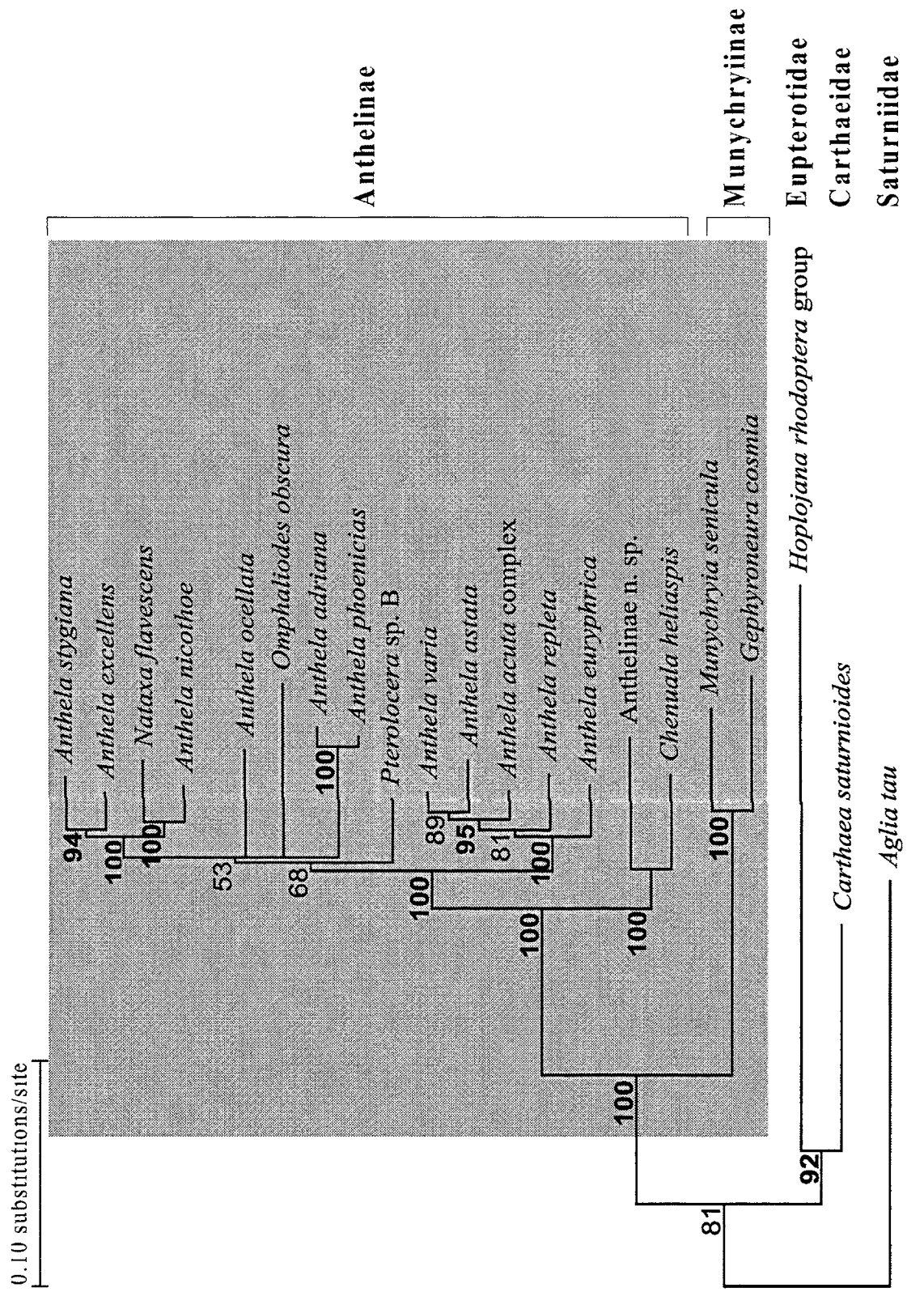

Fig. 375: Bayesian Inference analysis (GTR+I+Γ) of the combined CPS and EF1a sequences (1937bp in total, equally weighted) of Anthelidae (18 species on bluish background; three non-anthelid species as outgroup) – majority rule consensus tree of 1401 sampled trees; numbers above branches are posterior probabilities ≥50% (≥90% **bold**).

V.4.1.4) Conclusion

In summary, only some groups within the Anthelidae are well supported by molecular characters, but these groups are generally supported by all genes and all methods of analyses. These well supported hypotheses, as discussed in sections V.4.1.1 - V.4.1.3, are visually summarized in Fig. 376. The only dubious phylogenetic hypotheses with high support values are the sistergroup relationship between the undescribed species of Anthelinae and *C. heliaspis*, as well as the sistergroup relationship of these two species to the majority of other Anthelinae (exclusive of the monophyla of *A. ferruginosa* / *A. addita* / *A. virescens* and the genus *Chelepteryx*).

Various other hypotheses of monophyly are poorly to moderately supported, often by more than one gene and method of analysis. However, I regard them as too insufficiently supported to warrant their individual discussion. Nevertheless, some of them will be mentioned in the discussion of the results of all analyses below (see section VII.1.3.1).

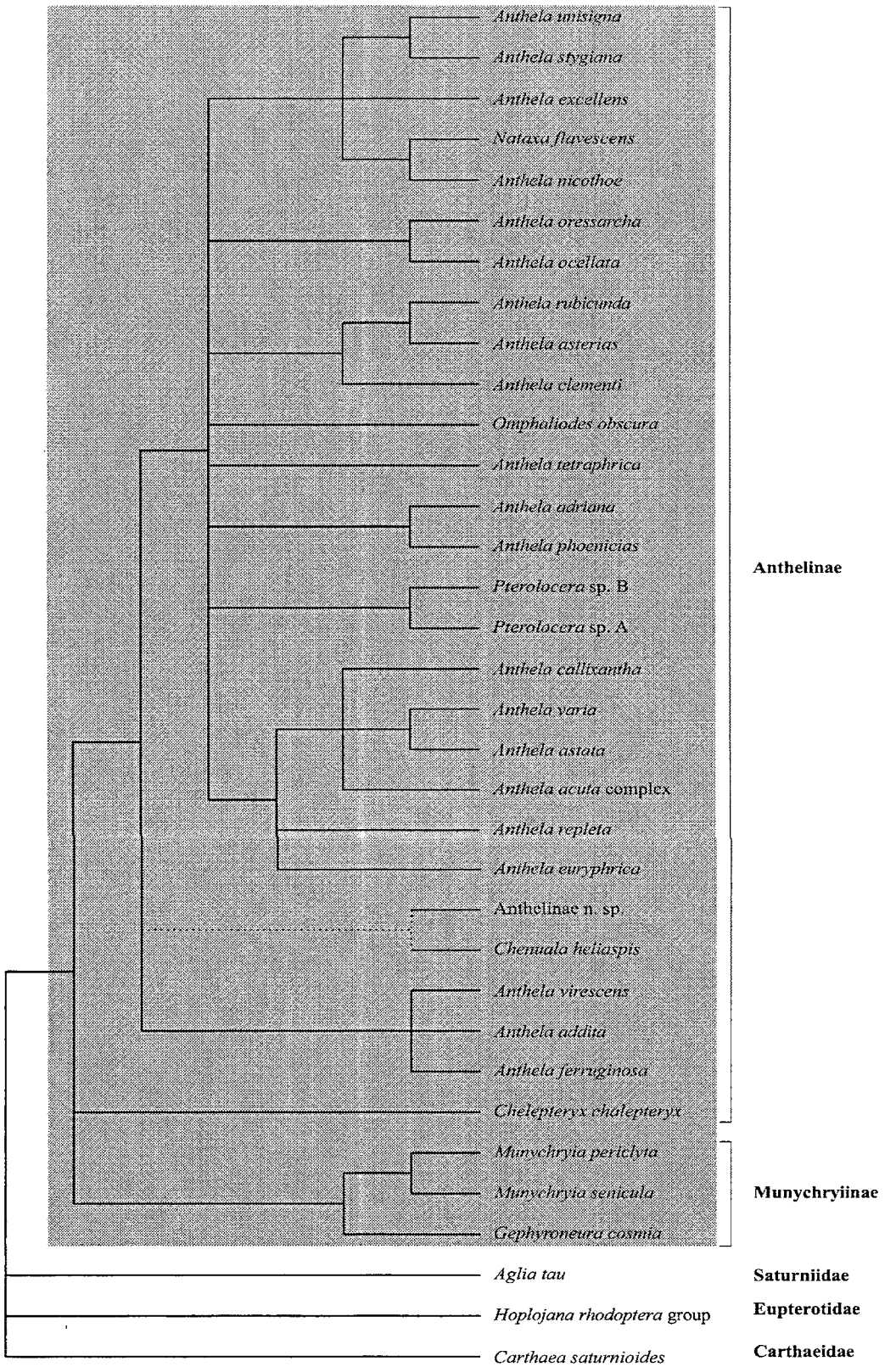

Fig. 376: Dendrogram visually summarizing the well supported hypotheses of monophyly within the Anthelidae based on MP, ML and BI analyses of EF1a, CPS and EF1a & CPS. Note the uncertain placement of the undescribed antheline species and *Chenuala heliaspis* (dotted line) due to saturation in third codon positions.

V.4.2) Phylogeny of the bombycoid complex

V.4.2.1) Analyses of EF1a

The analyses of the EF1a sequences are generally not informative at the family level within the bombycoid complex. Negative PBS values in first and second codon positions are abundant and reflect the dominance of the most probably entirely saturated third codon positions amongst the parsimony informative characters (see section V.2). At the same time the lack of parsimony informative characters in first and second codon positions results in a decrease of bootstrap percentages with the down-weighting of third codon positions.

The analyses of EF1a sequences rarely supports the monophyly of families of the bombycoid complex, and well supported monophyla are typically restricted to within families. The only supported relationship between families is the monophylum consisting of Lemoniidae and Brahmaeidae. This relationship is well supported in the BI analysis (Fig. 379), but only poorly supported in the ML analysis (Fig. 378). In the MP analysis (Fig. 377) *Dactyloceras widenmanni* group is placed outside this monophylum, and the grouping of the remaining species is contradicted by negative support values of PBS in first and second codon positions, possibly due to the exclusion of *D. widenmanni* group. The relationships between *Sabalia picarina* (Lemoniidae), *D. widenmanni* group (Brahmaeidae) and *Lemonia dumi* (Lemoniidae) are not well supported, but weak support for a monophylum comprising all three species is provided by ML and BI analyses. As the family Lemoniidae consists only of the genera *Lemonia* and *Sabalia*, this indicates that the apparent paraphyly of Brahmaeidae in respect to Lemoniidae is not simply caused by the incorrect inclusion of the genus *Sabalia* in the Lemoniidae, as might be concluded from the analyses lacking *L. dumi* (sections V.4.2.2 and V.4.2.3, respectively).

The negative PBS in first and second codon positions for the monophylum consisting of Lymantriidae (Noctuoidea) and Bombycidae (bombycoid complex) in the MP analysis indicates that this placement is caused by the total saturation of third codon positions at the phylogenetic level of superfamilies. Hence, this is most probably also the case for the unsupported inclusion of Oenosandridae and Notodontidae (both Noctuoidea) in the bombycoid complex in ML and BI analyses.

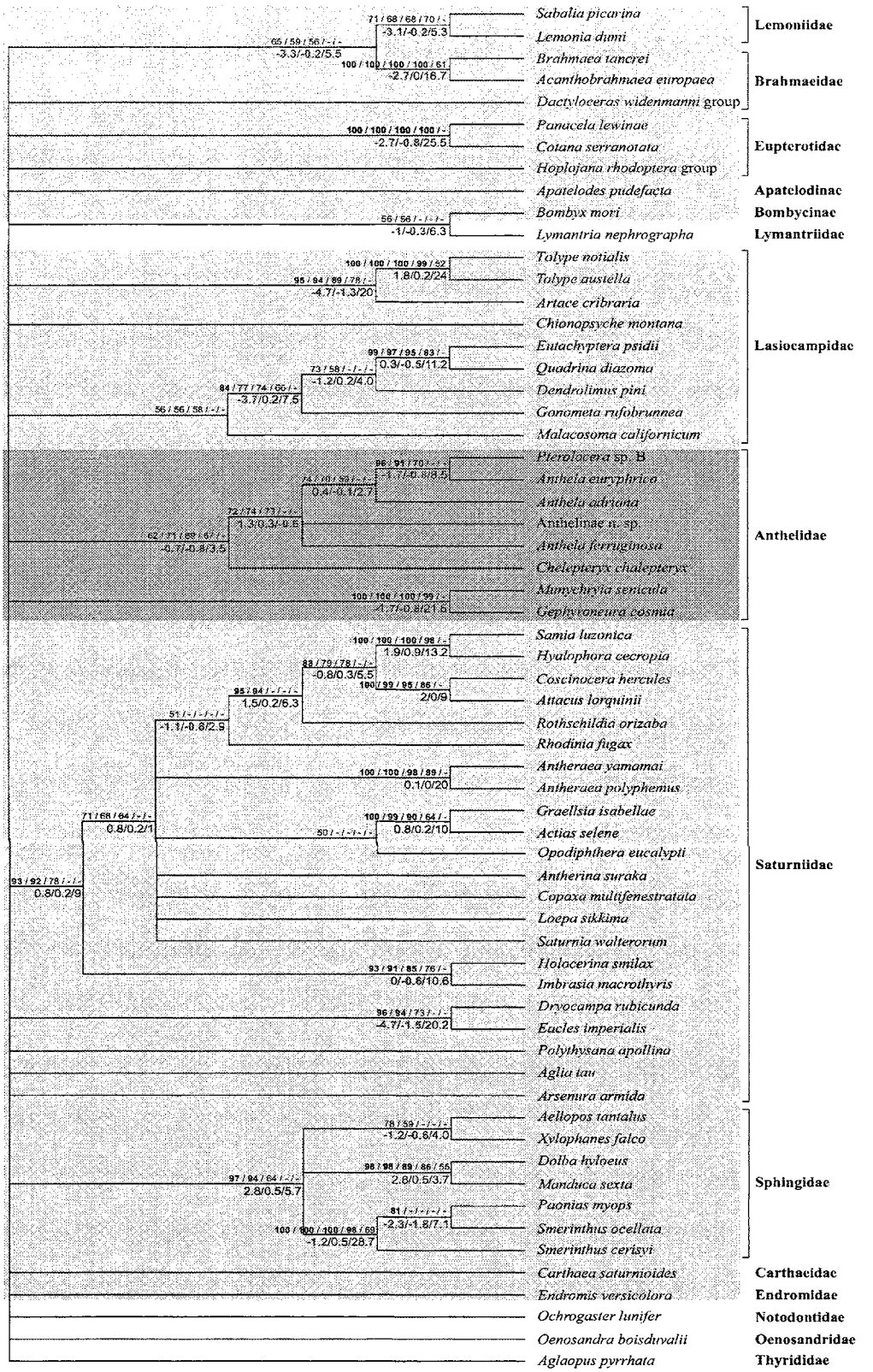

Fig. 377: Maximum Parsimony Analysis of EF1a sequences (1246bp, equally weighted) of the bombycoid complex (58 species on yellowish and bluish backgrounds; four non-bombycoid species as outgroup) – strict consensus tree of the 29 most parsimonious trees (each 3622 steps long; CI=0.21; CIU=0.2; RI=0.47). Branches with bootstrap percentages < 50% collapsed; numbers above branches are bootstrap percentages ≥50% (≥80% **bold**; 1000 bootstrap replicates) under differential weighting by codon positions (1-1-1 / 2-3-1 / 5-5-1 / 10-10-1 / 1-1-0); numbers below branches are Partitioned Bremer Support values (contradicting, negative values **bold red**), partitioned by codon positions.

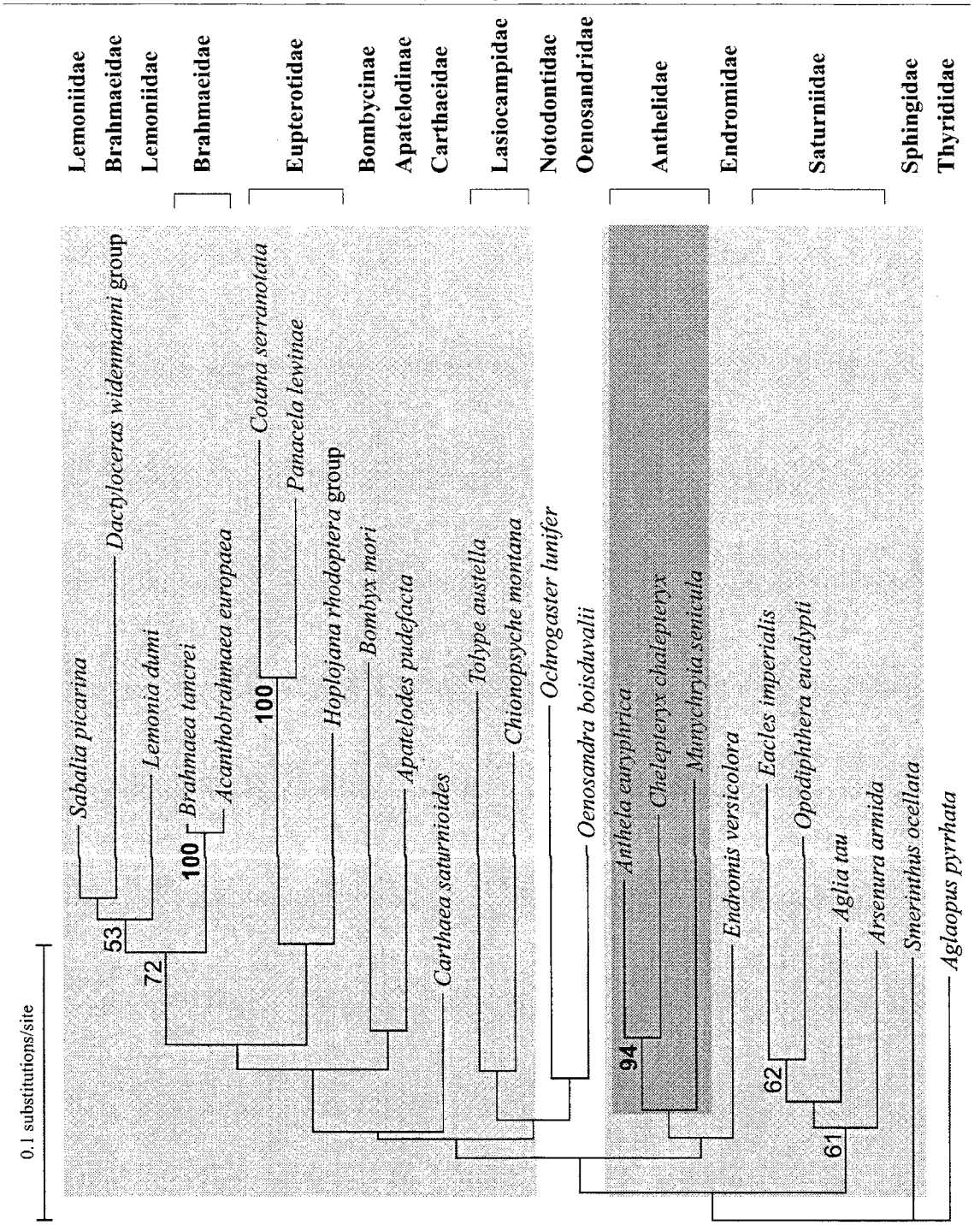

Fig. 378: Maximum Likelihood Analysis (GTR+I+Γ) of EF1a sequences (1246bp, equally weighted) of the bombycoid complex (22 species on yellowish and bluish backgrounds; three non-bombycoid species as outgroup) – phylogram (log-likelihood score = -8958.37187); numbers above branches are bootstrap percentages ≥50% (≥80% **bold**; 100 bootstrap replicates).

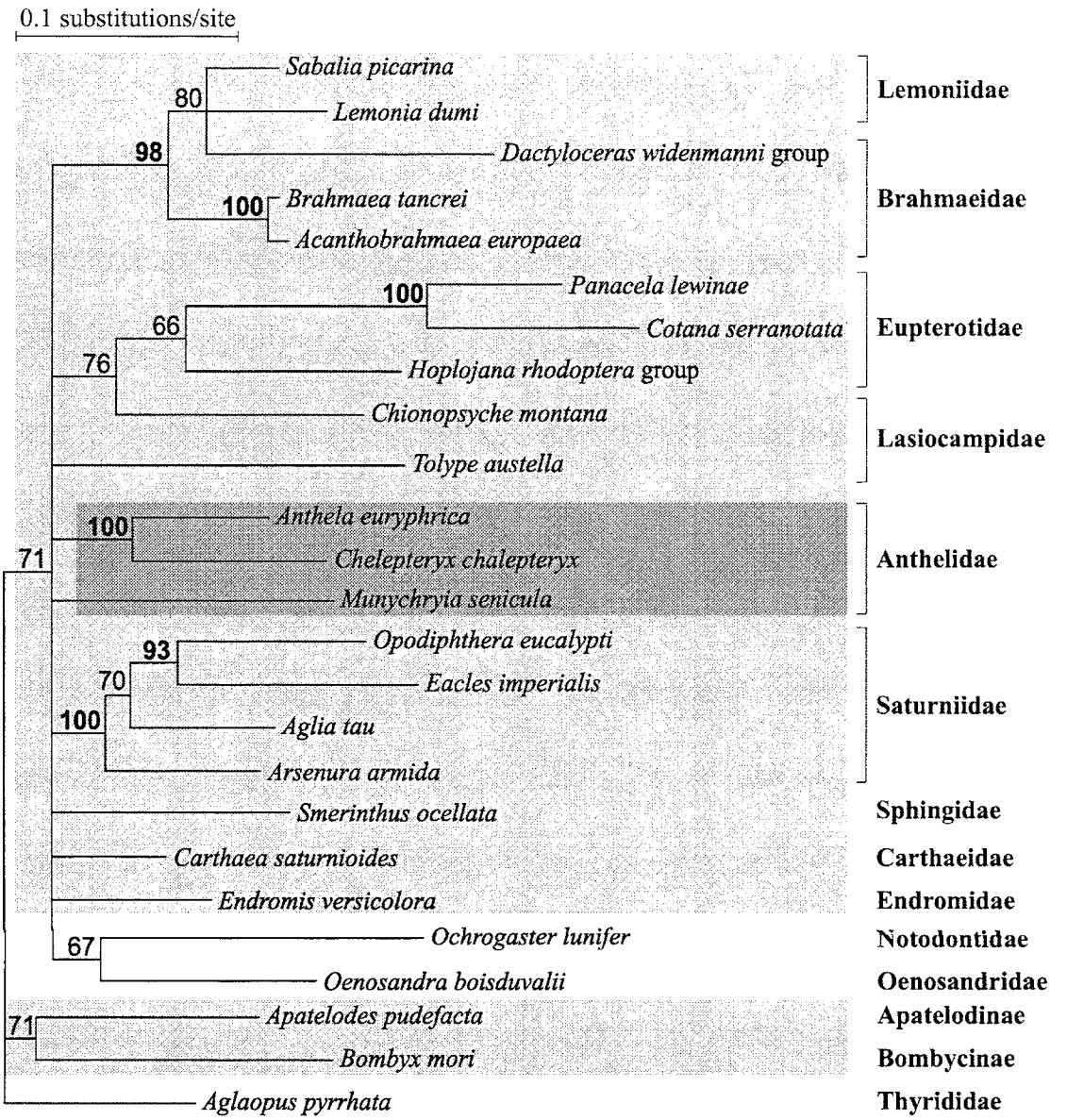

Fig. 379: Bayesian Inference analysis (GTR+I+Γ) of EF1a sequences (1246bp, equally weighted) of the bombycoid complex (22 species on yellowish and bluish backgrounds; three non-bombycoid species as outgroup) – majority rule consensus tree of 1001 sampled trees; numbers above branches are posterior probabilities ≥50% (≥90% **bold**).

V.4.2.2) Analyses of CPS

Like EF1a, the fragment of CPS is generally not informative within the bombycoid complex at the family level. The frequent occurrence of negative PBS values and the tendency for bootstrap percentages to initially increase with a down-weighting of third codon positions fit to beginning saturation of first and second but strong saturation of third codon positions, as indicated by the saturation plot (Fig. 364).

In many cases the monophyly of families is supported, as well as some relationships within each family, but little or no support exists for relationships between families. The family Bombycidae is an exception in as far as its two subfamilies Bombycinae and Apatelodinae do not form a monophylum. Instead, a placement of the Apatelodinae as the sistergroup of the Eupterotidae (MP analysis (Fig. 380)) or of the Lemoniidae, Brahmaeidae and Eupterotidae (ML (Fig. 381) and BI analyses (Fig. 382)) is suggested. In the case of the MP analysis this placement is contradicted by the negative PBS of first and second codon positions, and no bootstrap support exists for the ML analysis. However, a posterior probability of 90 indicates good support in the BI analysis. Further, BI analysis supports a sistergroup relationship between Carthaeidae and the monophylum of Lemoniidae, Brahmaeidae and Apatelodinae. This topology matches the unsupported topology of the ML analysis, but is incompatible with the poorly supported topology in the MP analysis. Similarly, BI analysis lends support to a monophylum consisting of Lemoniidae, Brahmaeidae, Eupterotidae, Apatelodinae, Carthaeidae, Anthelidae, Lasiocampidae and Endromidae, which is compatible with the essentially unsupported topologies of the MP and ML analyses. In the MP analysis one monophylum receives noticeable PBS support in first and second codon positions, but no bootstrap support due to the contradiction in the most probably totally saturated third codon position. This monophylum, which is poorly to moderately supported in the BI analysis, consists of all representatives of the bombycoid complex, except for *Ocinara* n. sp. (Bombycinae).

Only in one case is a relationship between families very well supported by all three analyses, namely the monophylum consisting of Lemoniidae and Brahmaeidae (see section V.4.2.1). Interestingly, a sistergroup relationship between *Sabalia picarina* and *Dactyloceras widenmanni* group within this monophylum is equally well supported in all analyses. Given the current classification of the families, this strongly supports the paraphyly of the Brahmaeidae in respect to the Lemoniidae, or at least the incorrect

placement of either the genus *Dactyloceras* or *Sabalia*.

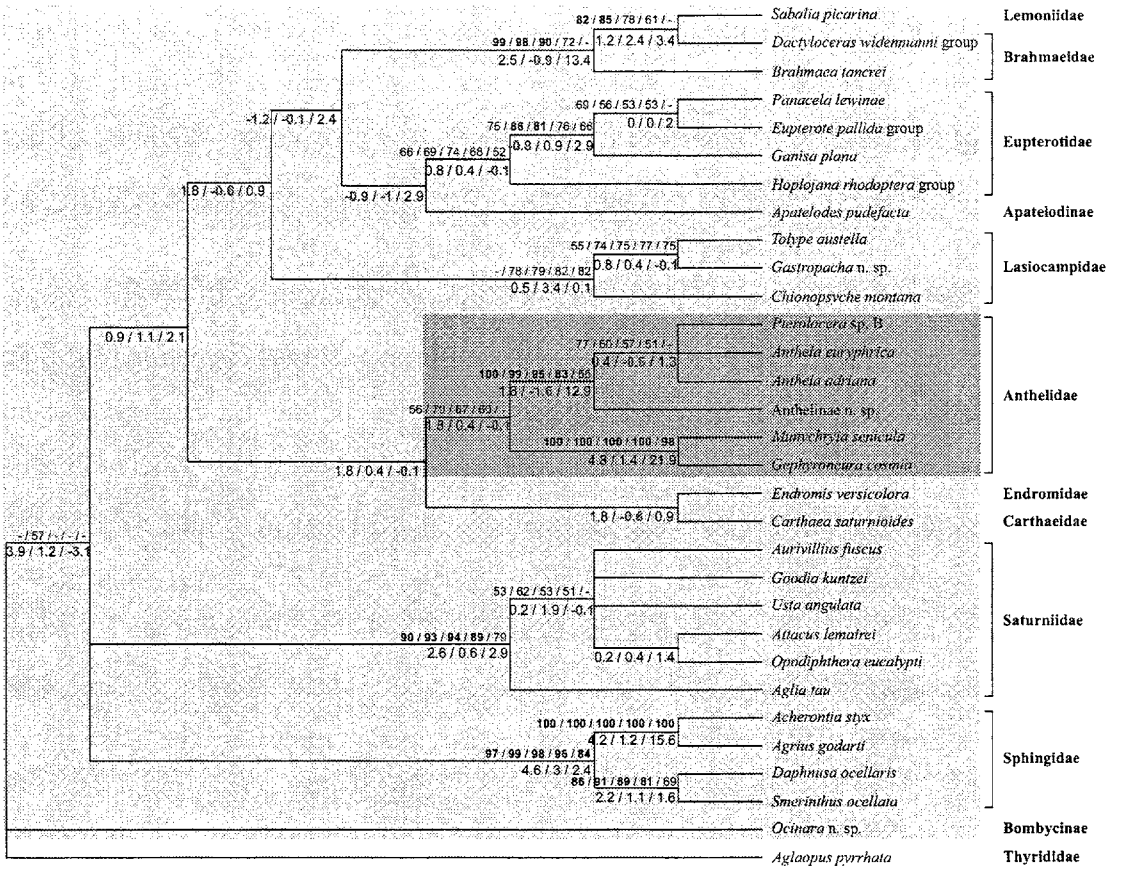

Fig. 380: Maximum Parsimony Analysis of CPS sequences (691bp, equally weighted) of the bombycoid complex (30 species on yellowish and bluish backgrounds; one non-bombycoid species as outgroup) – strict consensus tree of the 8 most parsimonious trees (each 1965 steps long; CI=0.31; CIU=0.29; RI=0.43). Numbers above branches are bootstrap percentages ≥50% (≥80% **bold**; 1000 bootstrap replicates) under differential weighting by codon positions (1-1-1 / 2-3-1 / 5-5-1 / 10-10-1 / 1-1-0); numbers below branches are Partitioned Bremer Support values (contradicting, negative values **bold red**), partitioned by codon positions.

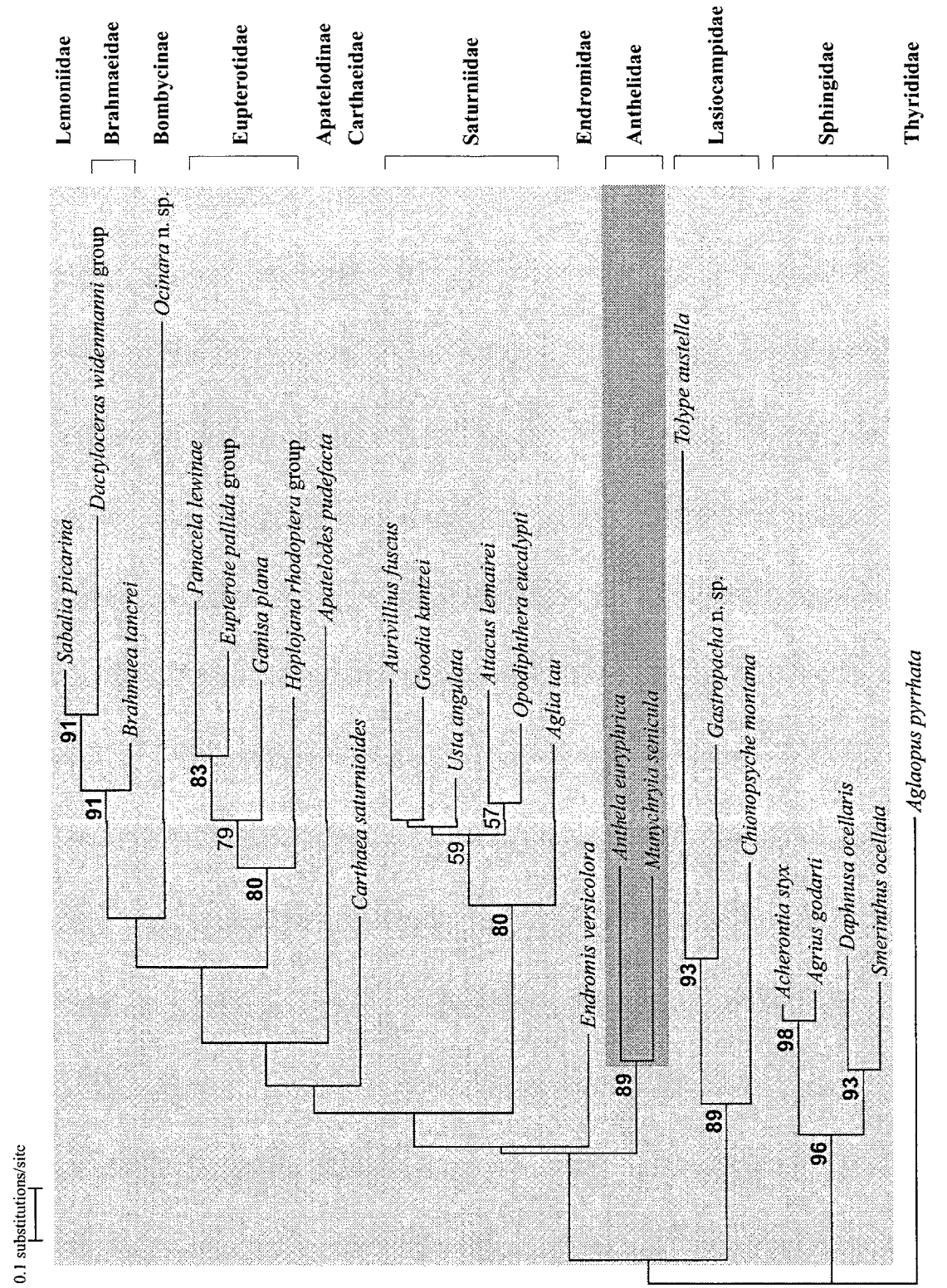

Fig. 381: Maximum Likelihood Analysis (GTR+I+Γ) of CPS sequences (691bp, equally weighted) of the bombycoid complex (26 species on yellowish and bluish backgrounds; one non-bombycoid species as outgroup) – phylogram (log-likelihood score = -7816.93865); numbers above branches are bootstrap percentages ≥50% (≥80% **bold**; 100 bootstrap replicates).

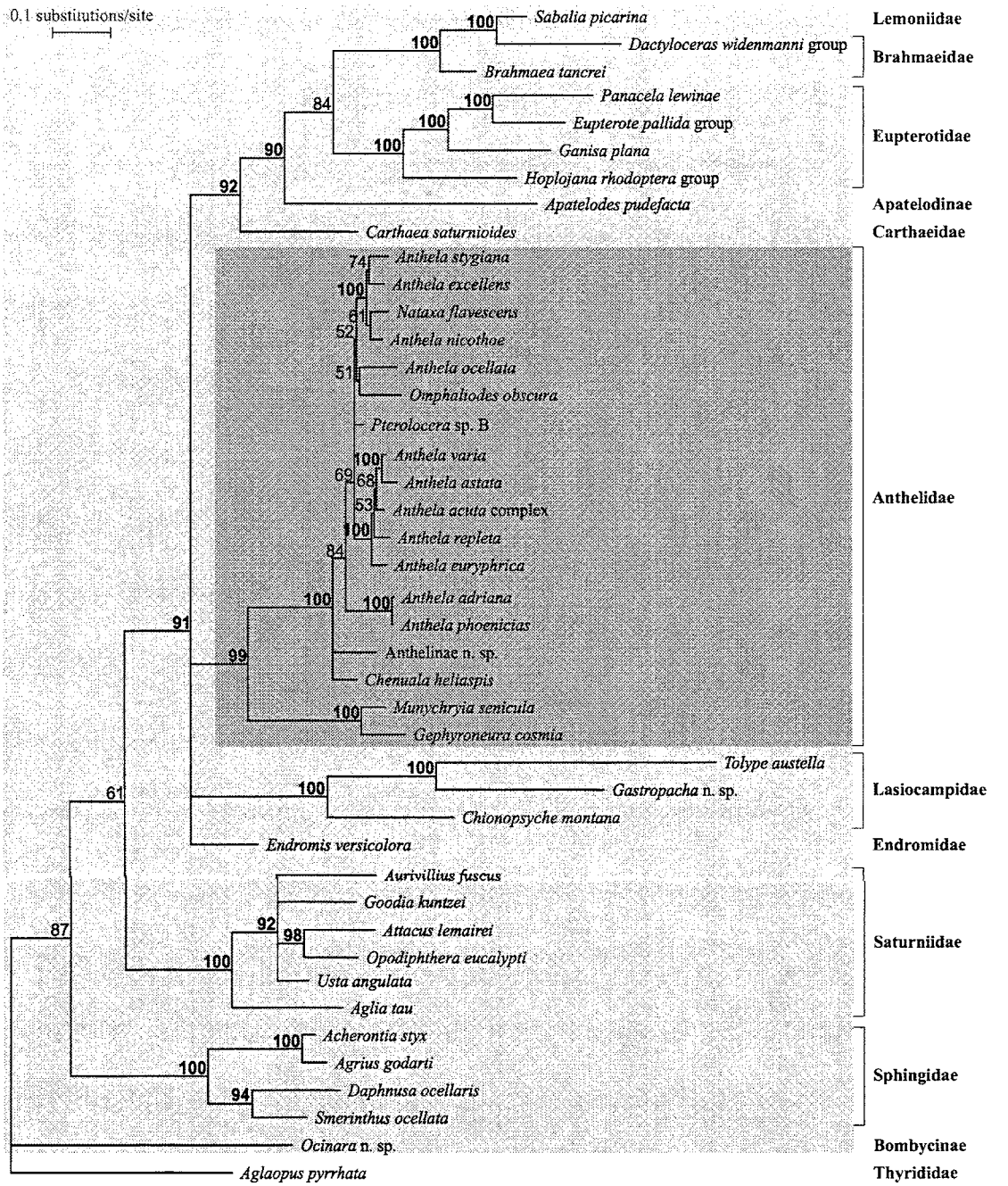

Fig. 382: Bayesian Inference analysis (GTR+I+Γ) of CPS sequences (691bp, equally weighted) of the bombycoid complex (42 species on yellowish and bluish backgrounds; one non-bombycoid species as outgroup) – majority rule consensus tree of 1001 sampled trees; numbers above branches are posterior probabilities ≥50% (≥90% **bold**).

V.4.2.3) Combined analyses of EF1a and CPS

The results of the MP analysis of the combined EF1a and CPS sequences is characterized by conflicting PBS values. Typically, it is the PBS of first and second codon positions of CPS, which is negative. As the saturated third codon positions of both genes dominate the parsimony informative characters, they largely drive the topology of the phylogram. If third codon positions are downweighted, the small number of parsimony informative characters in first and second codon positions is insufficient to resolve relationships.

Probably as a result of the conflict apparent from the PBS and the lack of non-saturated parsimony informative characters (see section V.2), the MP analysis (Fig. 383) indicates no well supported relationships between families other than the monophylum consisting of Lemoniidae and Brahmaeidae as discussed in section V.4.2.1. The situation is the same for the ML analysis (Fig. 384), except for a moderately to well supported monophylum comprising all representatives of the bombycoid complex except the Sphingidae. This monophylum is also supported by the BI analysis (Fig. 385). Further, the BI analysis supports the same topology as the BI analysis of the CPS sequences alone (see V.4.2.1) for the monophylum consisting of Lemoniidae, Brahmaeidae, Eupterotidae, Apatelodinae and Carthaeidae, but with in two cases distinctly higher posterior probabilities.

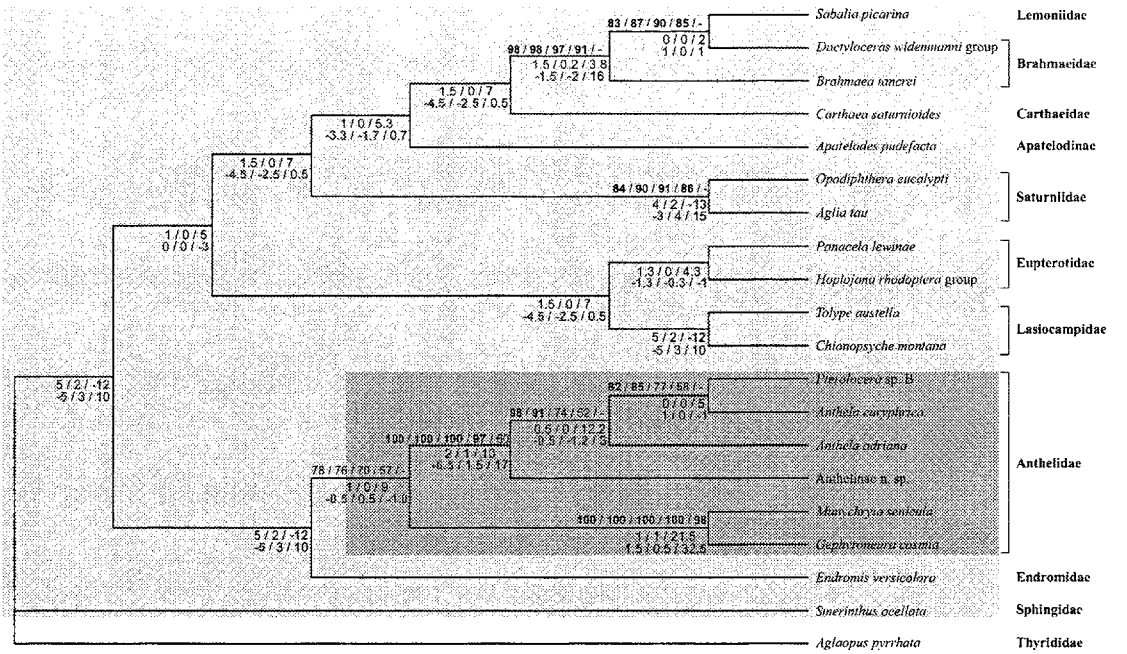

Fig. 383: Maximum Parsimony Analysis of the combined CPS and EF1a sequences (1937bp in total, equally weighted) of the bombycoid complex (19 species on yellowish and bluish backgrounds; one non-bombycoid species as outgroup) – single most parsimonious tree (2732 steps long; CI=0.41; CIU=0.38; CIU=0.37). Numbers above branches are bootstrap percentages ≥50% (≥80% **bold**; 1000 bootstrap replicates) under differential weighting by codon positions (1-1-1 / 2-3-1 / 5-5-1 / 10-10-1 / 1-1-0); numbers below branches are Partitioned Bremer Support values (contradicting, negative values **bold red**), partitioned by codon positions and genes (EF1a above CPS).

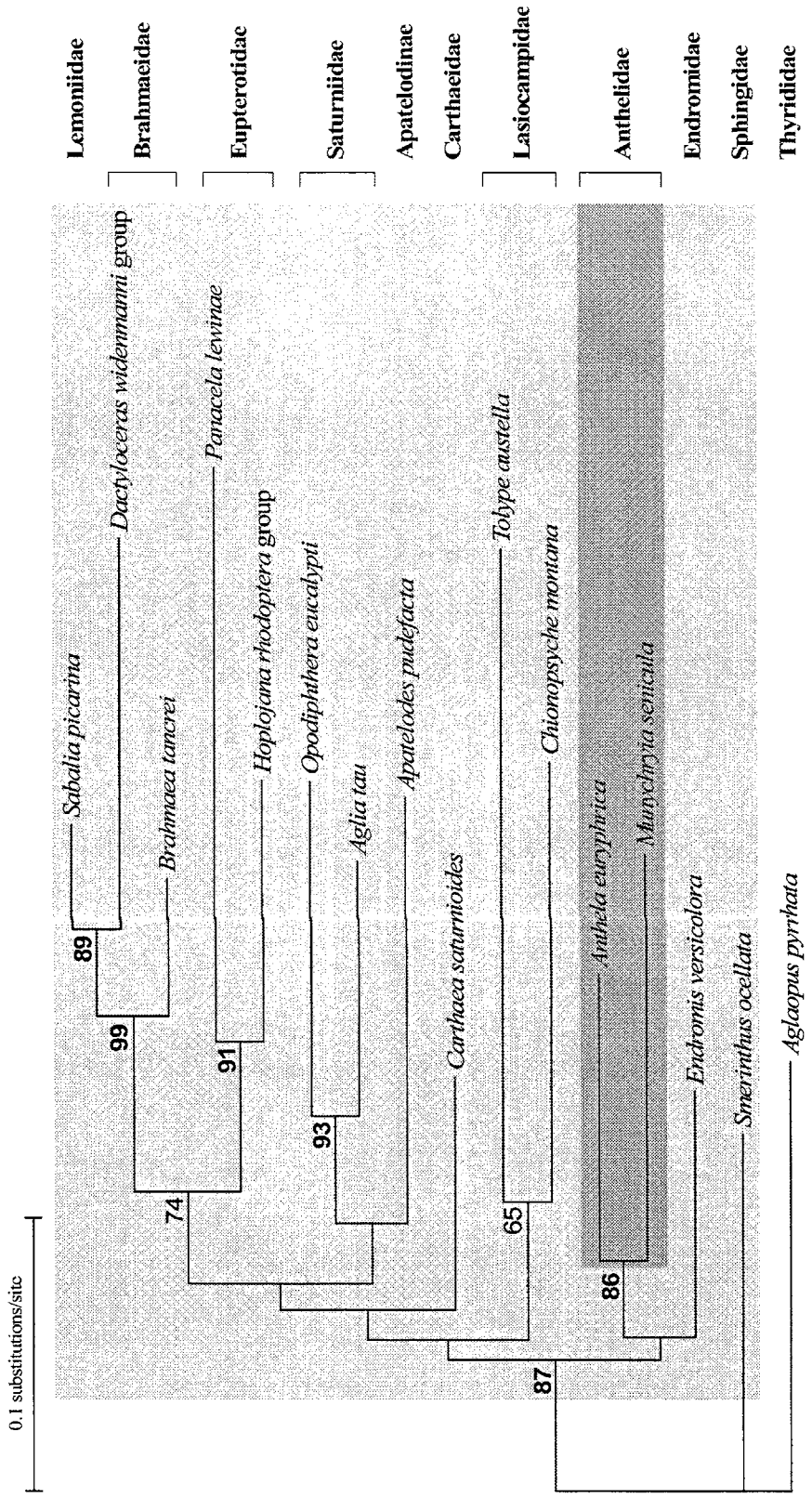

Fig. 384: Maximum Likelihood Analysis (GTR+I+Γ) of the combined CPS and EF1a sequences (1937bp in total, equally weighted) of the bombycoid complex (15 species on yellowish and bluish backgrounds; one non-bombycoid species as outgroup) – phylogram (log-likelihood score = -12027.75490); numbers above branches are bootstrap percentages ≥50% (≥80% **bold**; 100 bootstrap replicates).

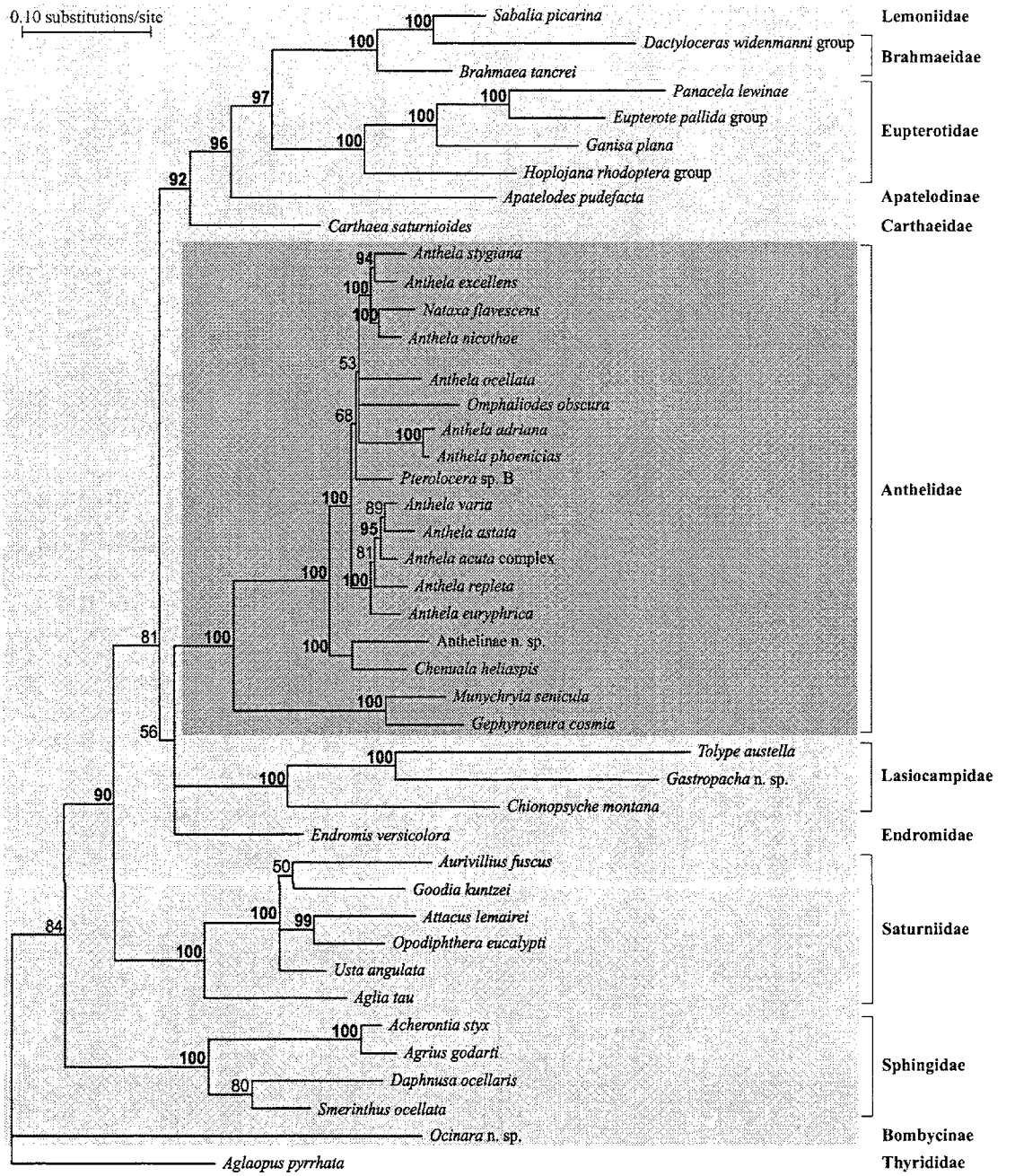

Fig. 385: Bayesian Inference analysis (GTR+I+Γ) of the combined CPS and EF1a sequences (1937bp in total, equally weighted) of the bombycoid complex (42 species on yellowish and bluish backgrounds; one non-bombycoid species as outgroup) – majority rule consensus tree of 1401 sampled trees; numbers above branches are posterior probabilities ≥50% (≥90% **bold**).

V.4.2.4) Conclusion

The dominance of the third codon positions, wich are entirely saturated at family level, is likely to drive all analyses. Hence, the resulting topologies contradict the very limited information potentially preserved in first and second codon positions. Consequently, proposed relationships between families are generally likely to be incorrect and are not supported by bootstrap percentages or posterior probabilities (Fig. 386A). However, the relationships between Lemoniidae and Brahmaeidae, and to a lesser extent also the Eupterotidae, Apatelodinae and Carthaeidae, show less conflict between PBS values and are supported by most analyses (Fig. 386B). No support exists for an exact placement of the Anthelidae within the bombycoid complex.

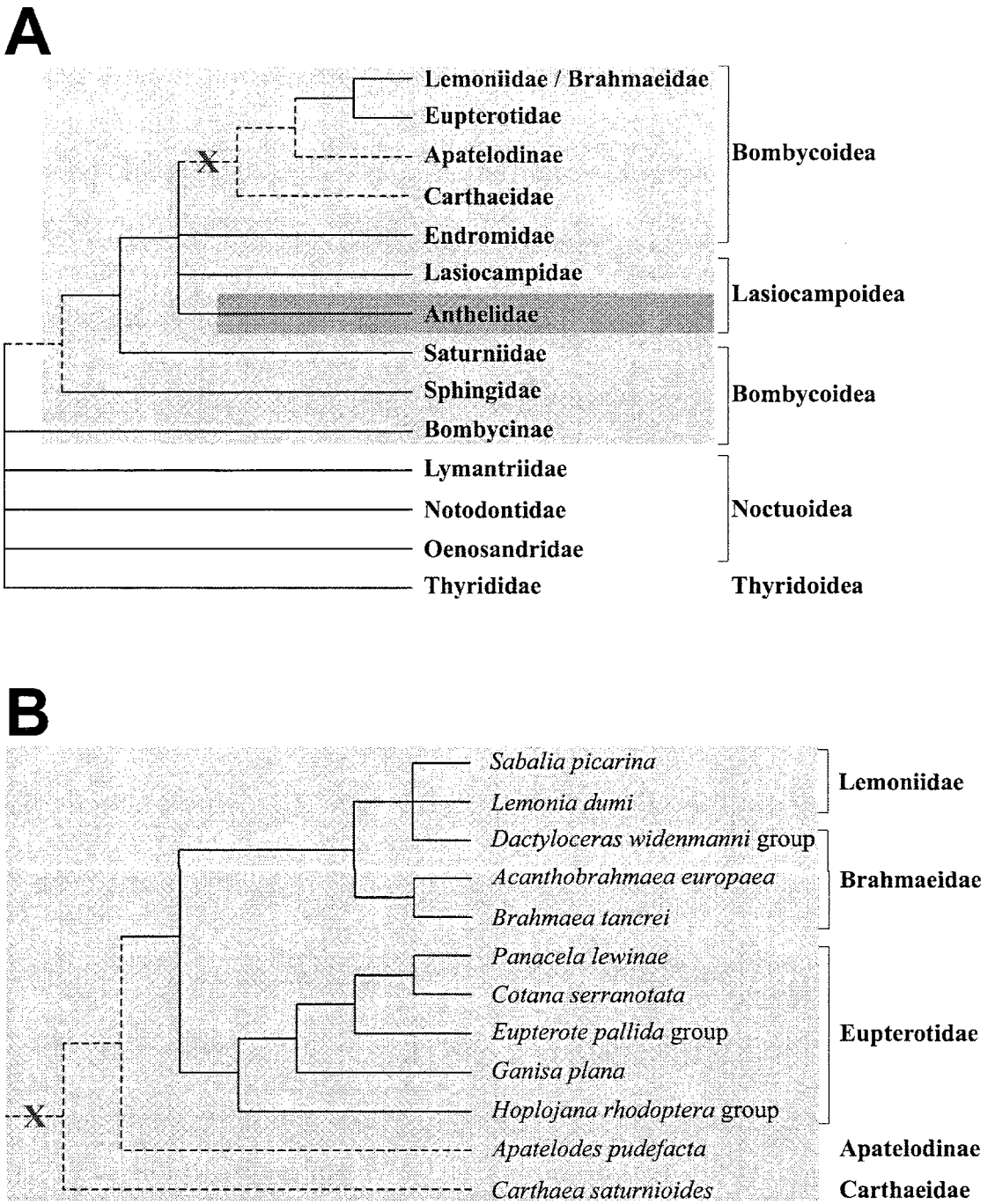

Fig. 386: Dendrograms visually summarizing only the well supported hypotheses of monophyly within the bombycoid complex (yellowish and bluish backgrounds) based on MP, ML and BI analyses of EF1a, CPS and EF1a & CPS. Note the less well supported and possibly incorrect placement of the Apatelodinae and Carthaeidae (dotted line).
A) Summary of the relationships between families. Note the polyphyly of the Bombycidae (Apatelodinae + Bombycinae). Note the paraphyly of the Bombycoidea in respect to the Lasiocampoidea.
B) Details of the relationships within the families Lemoniidae, Brahmaeidae and Eupterotidae [location in **A)** marked by X]. Note the paraphyly of Brahmaeidae in respect to Lemoniidae, or alternatively the misplacement of the genus *Dactyloceras* in the Brahmaeidae.

CHAPTER SIX:

CLADISTIC ANALYSES OF COMBINED MORPHOLOGICAL AND MOLECULAR CHARACTERS

While various models have been proposed for the evolution of molecular characters and are used for the process-dependent Maximum Likelihood and Bayesian Inference analyses, no models exist for the evolution of complex morphological structures. In contrast, morphological as well as molecular data can both be analysed with phenomenological methods, e.g., Maximum Parsimony (MP), and it is commonplace to analyse such data individually as well as combined in a "total evidence" approach. However, the principle axiomatic assumption of MP analyses, that conflicting character states have an equal probability of being homologies (see section II.4.3), seems even less likely to be met for a combination of such different kinds of characters than it is for the characters of only one kind. I cannot judge these probabilities objectively, and hence cannot compensate any differences by differential weighting. By not applying weights in the absence of objective measures, I inadvertently imply equal weights, which is likely to cause problems in the case of conflicting characters. Given the small number of morphological parsimony informative characters relative to the number of molecular parsimony informative characters, the latter are likely to dominate in conflicts.

A NEXUS file containing the merged cladistic morphological and molecular characters is included in the electronic appendix.

VI.1) Phylogeny of the Anthelidae

For the Anthelidae, the two data sets are not entirely overlapping as no molecular characters are available for 6 taxa, and only incomplete molecular data are available for 12 taxa (CPS missing). Consequently, I analysed the combined data twice, excluding and including the taxa with incomplete data.

Heuristic search (1,000 replicates, random sequence addition) for the taxa with complete data resulted in 5 most parsimonious trees, of which the strict consensus is presented in Fig. 387. The trees are 1587 steps long and have a Consistency Index (CI) of 0.56 (excluding uninformative characters of 0.5) and a Retention Index (RI) of 0.52. Bootstrap percentages were estimated from 100 pseudo-replicates of 10 sequence-addition replicates.

The strict consensus tree (Fig. 387) is largely resolved, but only some of the nodes are well supported in the bootstrap analysis (having a bootstrap percentage of ≥80%; see section V.2). With the exception of the species pair *Anthela adriana* / *A. phoenicias*, for which the species do not differ in their morphological characters, Partition Bremer Support (PBS) indicates character conflict between morphological characters and at least one codon position of the molecular characters for every node, irrespective of bootstrap support values. The species groups, which are well supported by bootstrap percentages and PBS, are:

- *Anthela stygiana*, *A. excellens*, *A. nicothoe* and *Nataxa flavescens*,
- *A. adriana* and *A. phoenicias*,
- *A. astata*, *A. varia* and *A. acuta* complex,
- the latter group, *A. repleta* and *A. euryphrica*,
- Anthelinae n. sp. and *Chenuala heliaspis*,
- *Munychryia senicula* and *Gephyroneura cosmia*,
- the subfamily Anthelinae, and
- the family Anthelidae.

As in the analysis of molecular characters, the group Anthelinae n. sp. and *C. heliaspis* is mainly supported by probably saturated third codon positions and distinctly contradicted by first and second codon positions of CPS. However, in this analysis the PBS indicates support by morphological characters, too.

Heuristic search (1,000 replicates, random sequence addition) including taxa with incomplete data resulted in 1032 most parsimonious trees, of which the strict consensus is presented in Fig. 388. The trees are 1972 steps long and have a Consistency Index (CI) of 0.5 (excluding uninformative characters of 0.45) and a Retention Index (RI) of 0.55. Bootstrap percentages were estimated from 100 pseudo-replicates of 10 sequence-addition replicates.

The strict consensus tree (Fig. 388) is poorly resolved, with most of the polytomies being caused by taxa with missing data. The topology of the tree is compatible with the one of the analysis including taxa with complete data only. While some of the nodes are less well supported by bootstrap values, some additional well supported nodes include some of the additional taxa:

- *Anthela unisigna* and *A. stygiana*,
- *A. oressarcha* and *A. ocellata*,
- *A. rubicunda* and *A. asterias*,
- *A. callixantha*, *A. astata*, *A. varia* and *A. acuta* complex,
- the latter group, *A. repleta* and *A. euryphrica*,
- *A. adriana* and *A. phoenicias*,
- Anthelinae n. sp. and *Chenuala heliaspis*,
- *A. phaeodesma*, *A. virescens*, *A. addita* and *A. ferruginosa*,
- *Munychryia periclyta* and *M. senicula*,
- the subfamily Anthelinae except *Chelepteryx chalepteryx*, and
- the family Anthelidae.

The large number of missing data appears to cause problems with the calculation of Partitioned Bremer Support. While taxa with missing molecular data correctly have PBS values of 0 for these genes, this is also the case for some taxa with complete data (e.g., *A. adriana* and *A. phoenicias*). Further, some taxa with missing CPS data have a negative PBS value for this gene (e.g., *A. unisigna* and *A. stygiana*). Obviously, the PBS values of this consensus tree are not reliable and should be ignored. Repetition of analyses did not solve the problem, nor could mistakes be traced in the log files (e.g., the consensus tree used for PBS calculation not being the shortes tree). Similar incorrect results were obtained for matrices with abundant missing data by other people, too (Christine Lambkin, ANIC, pers. comm.).

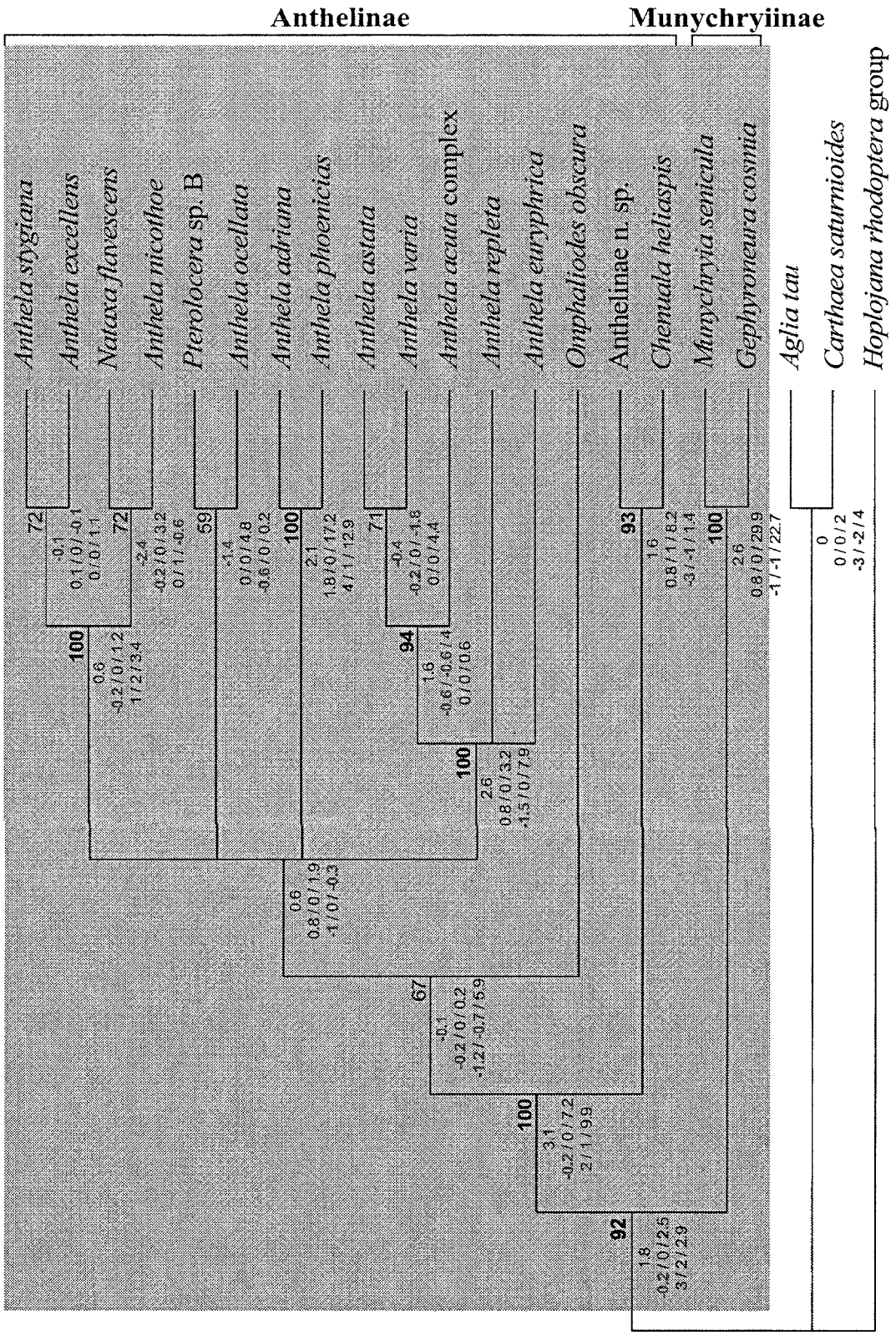

Fig. 387: Maximum Parsimony Analysis of the combined morphological and molecular characters (CPS and EF1a, all characters equally weighted) of Anthelidae (18 species on bluish background; three non-anthelid species as outgroup) with complete data – strict consensus tree of the 5 most parsimonious trees (each 1587 steps long; CI=0.56; CIU=0.5; RI=0.52). Numbers above branches are bootstrap percentages ≥50% (≥80% **bold**; 100 bootstrap replicates); numbers below branches are Partitioned Bremer Support values (contradicting, negative values **bold red**), partitioned into morphology, genes and codon positions (morphology above EF1a above CPS).

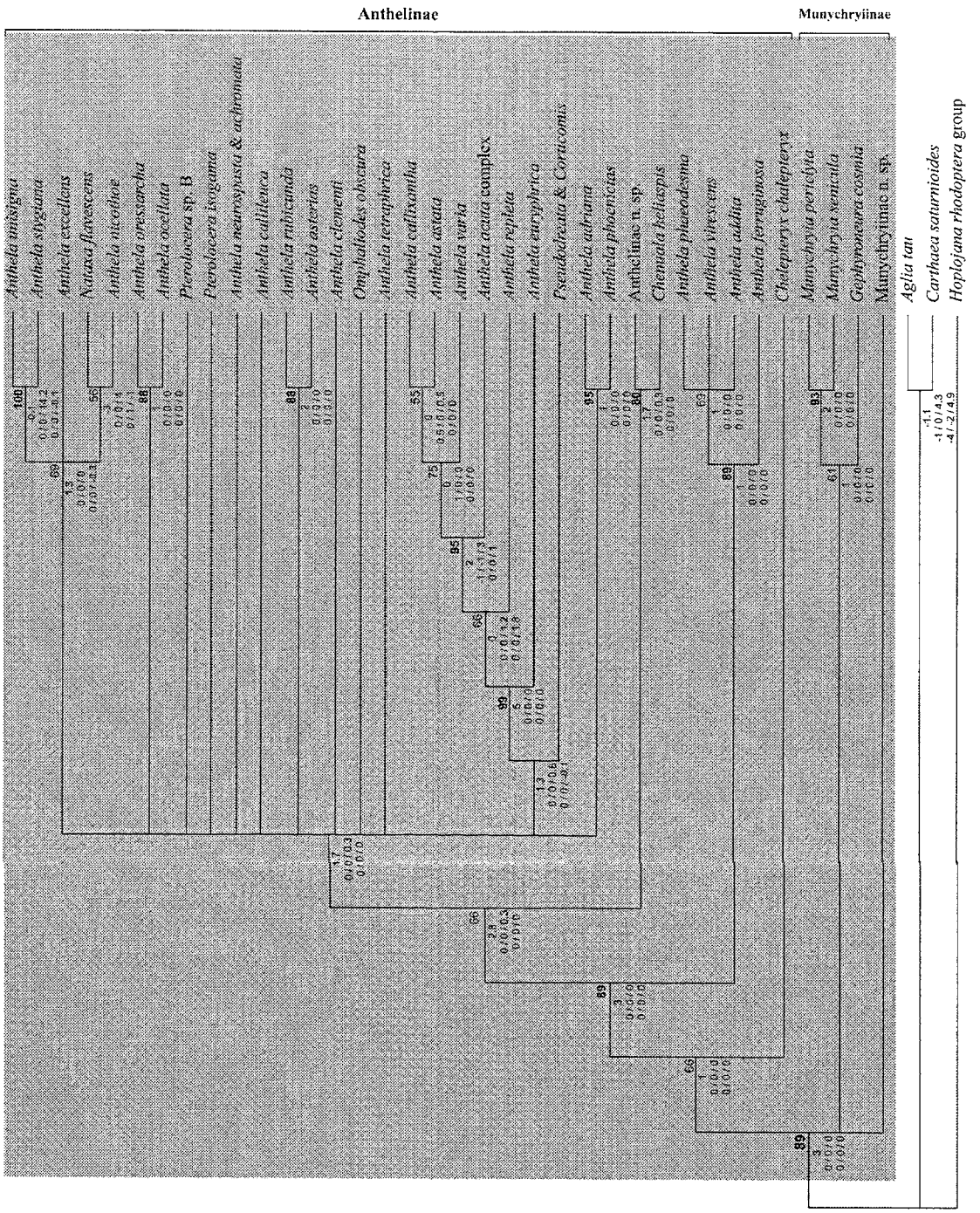

Fig. 388: Maximum Parsimony Analysis of the combined morphological and molecular characters (CPS and EF1a, all characters equally weighted) of Anthelidae (36 taxa on bluish background; three non-anthelid species as outgroup), including taxa with incomplete data (marked with ▒ = CPS missing; marked with ▒ EF1a and CPS missing) – strict consensus tree of the 1032 most parsimonious trees (each 1972 steps long; CI=0.5; CIU=0.45; RI=0.55). Numbers above branches are bootstrap percentages ≥50% (≥80% **bold**; 100 bootstrap replicates); numbers below branches are Partitioned Bremer Support values (contradicting, negative values **bold red**), partitioned into morphology, genes and codon positions (morphology above EF1a above CPS).

VI.2) PHYLOGENY OF THE BOMBYCOID COMPLEX

For the bombycoid complex, I scored the morphological matrix according to hypothetical ground plans of the families (see section III.7.2). Therefore, the morphological data included in the combined matrix do not differ for the sequenced exemplars of each family. In the MP analysis I only included taxa with complete data, because each bombycoid family distinguished for the morphological data is represented by at least one exemplar with complete data and the addition of taxa with mainly missing characters is detrimental for the analysis.

Heuristic search (1,000 replicates, random sequence addition) for the taxa with complete data resulted in a single most parsimonious tree (Fig. 389). The tree is 2815 steps long and has a Consistency Index (CI) of 0.42 (excluding uninformative characters of 0.38) and a Retention Index (RI) of 0.39. Bootstrap percentages were estimated from 100 pseudo-replicates of 10 sequence-addition replicates.

The single most parsimonious tree (Fig. 389) is almost fully resolved, but only few of the nodes are well supported in the bootstrap analysis (having a bootstrap percentage of ≥80%). Except for the placement of *Sabalia picarina* (Lemoniidae) as sistergroup of *Dactyloceras widenmanni* group (Brahmaeidae) in the Brahmaeidae, none of the well supported nodes represents relationships between families. The exclusion of the largely saturated third codon positions of EF1a or of EF1a and CPS did not result in well supported, alternative topologies. Consequently I did not estimate PBS values for this tree.

Clearly, this analysis failed to provide well supported hypotheses on relationships between families of the bombycoid complex, except for the paraphyly of the Brahmaeidae in respect to the Lemoniidae.

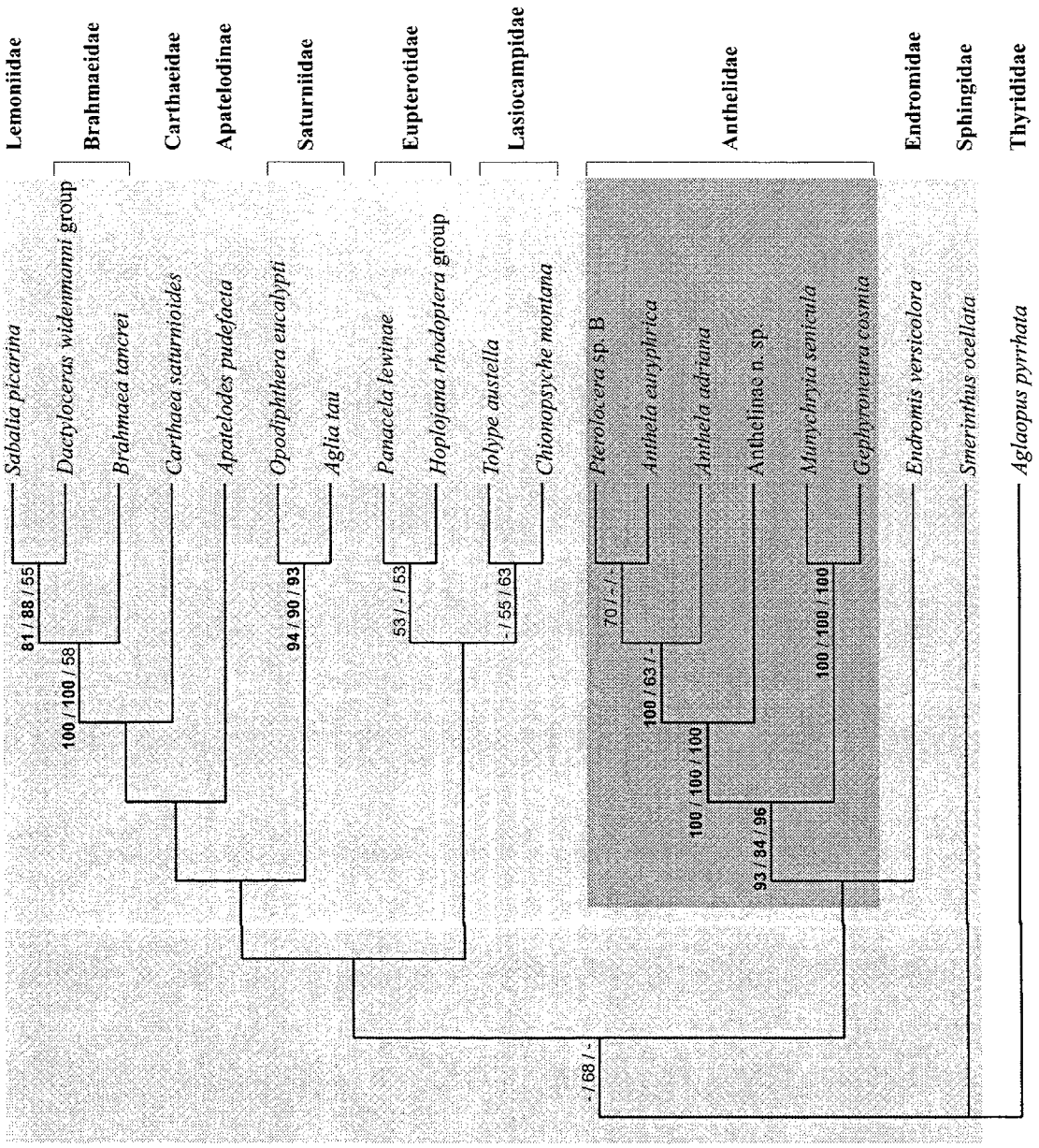

Fig. 389: Maximum Parsimony Analysis of the combined morphological and molecular characters (CPS and EF1a, all characters equally weighted) of the bombycoid complex (19 species on yellowish and bluish backgrounds; one non-bombycoid species as outgroup) – single most parsimonious tree (2815 steps long; CI=0.42; CIU=0.38; RI=0.39). Numbers above branches are bootstrap percentages ≥50% (≥80% **bold**; 100 bootstrap replicates) under differential weighting by gene and codon position (all data equal / 3rd codon positions of EF1a excluded / 3rd codon positions of EF1a and CPS excluded).

CHAPTER SEVEN:

DISCUSSION

VII.1) COMPARISON OF PHYLOGENETIC ANALYSES

VII.1.1) Principle problems of the methods of analysis

Hypotheses of evolutionary relationships between taxa can be derived with different methods, and various schools of thought on different methods exist. Each of these methods has its specific advantages and shortcomings, and irrespective of the school of thought, proponents of a particular method often strongly argue against alternative approaches, typically ignoring the shortcomings of their own method of choice. Particularly strong dissent exists on the value of Hennigian Argumentation and Maximum Parsimony Analyses. The shared use of terms like "cladistic", "homology" and "apomorphy" with slightly different meanings by proponents of both methods does not further the understanding of the alternative approach. Doubtlessly, Maximum Parsimony is worldwide the currently more popular approach of these two methods. I ascribe this popularity to the combination of ease and speed of automated use (in particular of large quantities of data), seeming redundancy of prior knowledge of organisms and structures, "justification" of the hypotheses by statistical support values, and that direct responsibility for explicitly stated hypotheses need not be taken. However, popularity by itself is not necessarily evidence of a method's quality or reliability, because the majority of users is neither interested in nor in a position to judge the different methods. Instead, they are users interested in some result for various purposes, and the situation resembles that of end-users and the popularity of computer operating systems. I certainly do not claim to have understood each of the methods in all its variations and intricacies, but I recognize several basic principles and assumptions of each method (see sections II.4.2 and II.4.3). Very many publications discuss principles, assumptions, advantages and shortcomings of Hennigian Argumentation as well as Maximum Parsimony, and this section is not intended as a literature review. Instead, I discuss these methods to clearly state my point of view on both approaches to the reader.

For Hennigian Argumentation the formulation of well supported hypotheses of homology is the most critical part. They do not only present the basis for character definitions and character states as in Maximum Parsimony Analyses. Additionally, hypotheses of homology are used for *a priori* determination of character polarity by outgroup comparison and *a priori* weighting of character state changes on the basis of the quality of the respective hypothesis of homology (see section II.4.2). The hypotheses of polarity and of weight are more than just additional information, they are crucial parts of the theoretical basis of Hennigian Argumentation – only shared apomorphies allow to conclude on evolutionary relationships, and conflicting hypotheses of apomorphy must have the same probability of being correct or otherwise be weighted accordingly (see Wägele 2001 for a recent discussion). At the same time they are additional hypotheses, and because hypotheses can be wrong, they are additional sources of error in any argumentation / analysis.

The *a priori* assignment of a specific weight is most frequently criticized, because no truly objective measure is known to quantify the quality of a hypothesis – utilizing the criteria of homology by Remane (1952) is merely a tool for assessment (see section II.4.2). The absolute values of weights are not critical, because relative differences between character state changes are decisive in Hennigian Argumentation, but errors in absolute values result in errors of relative values. Obviously, the lack of an objective measure is a serious shortcoming in Hennigian Argumentation. However, rejecting *a priori* weighting and not applying any weights means to assign equal weights to all character state changes. While this assumption of all hypotheses being equally well supported is very convenient, it has no objective basis and is most probably wrong for morphological as well as molecular characters (e.g., differences in codon positions and functionality of protein regions). Obviously, the assumption of equal weight is an additional hypothesis, too, and not necessarily better supported than the hypothesis of a weight based on an assessment of the criteria of homology.

Errors in hypotheses of polarity derived by outgroup comparison are strongly linked to errors in hypotheses of homology (see section II.4.2). Therefore, it is important to use only well supported hypotheses of homology in Hennigian Argumentation. However, this requirement is not a theoretical, but a practical shortcoming of Hennigian Argumentation, because different structures allowing for well supported hypotheses of

homology (e.g., compound eyes and tympanal organs) are limited in number. In adult Macrolepidoptera, for example, a tendency to reduce rather than to develop new structures exists. Not only are such reductions and losses homoplastic, but most of all they result in a loss of structural detail, which does not permit the postulation of well supported hypotheses of homology – the absence of a structure is the most extreme case, lacking any indication of homology. As a consequence, many of the hypotheses of monophyly are only supported by single or a few hypotheses of apomorphy, which is problematic if they are incorrect.

The actual argumentation of an Hennigian Argumentation is based on the principle of Maximum Parsimony. It is traditionally carried out manually, which often attracts the criticism of being inaccurate and limited (not covering the "entire tree-space"). Depending on the number of contradicting hypotheses of apomorphy and the number of taxa, this criticism can be justified. However, the additional information of weights helps to resolve many of the conflicts, keeping the number of plausible most parsimonious trees at a manageable number. Also, conflicting hypotheses of apomorphy could and should be re-assessed on the basis of a re-examination of structures and re-analysis of characters, rather than being accepted as facts. In principle, computer software used for Maximum Parsimony Analysis could be used as an alternative to a manual analysis if character polarity and weights can be implemented. However, the treatment of inapplicable characters by currently available software is problematic (treated equally to missing data), and I cannot judge if problems arise with the algorithms implemented in "black-box" software, which is not intended for Hennigian Argumentation. In the case of my two data matrices, manual analysis was not a problem as the data sets are relatively small and lack serious conflicts between hypotheses of apomorphy. Further, most of the *ad hoc* explanations required for conflicting hypotheses were typically simple reductions and plausible.

Maximum Parsimony Analysis ("cladistics") applies the same principle of parsimony as Hennigian Argumentation, but the theoretical basis of this method differs. In this case the principle of parsimony, that the smallest number of evolutionary events required to explain a given distribution of character states is the most preferred explanation, is applied to all character state changes. Consequently, no *a priori* hypotheses on the polarity of characters have to be made. Further, subjective hypotheses of *a priori*

weighting are seemingly avoided by typically assuming an equal weight for all character state changes. However, this assumption in itself is a subjective hypothesis, which is unlikely to be correct in most cases (see above). By assuming equal weights the analysis of data is restricted to the entirely quantitative criterion of parsimony, which is objective and consistently applied to all data. In an attempt to avoid the introduction of subjectivity and to obtain hypotheses with equal probability of being correct, the scoring of character states is typically limited to "observable facts" (yet still interpretations of visual signals and not facts), which are regarded as "primary homologies". If a conflict between primary homologies exists, this conflict can only be resolved quantitatively, or has to be expressed as a consensus. As quantitative decisions can only be made with sufficient quantities of primary homologies, a large number of characters is required.

If the distribution of a primary homology is incongruent with the estimated most parsimonious topology, its hypothesis of homology is rejected. Otherwise, it is regarded as tested and not falsified by incongruence, after which it is referred to as a "secondary homology" (*a posteriori* determination of homology, which depends on the correctness of the hypothesized topology). This test of congruence is limited to the homology of an individual character state present in different taxa, but cannot test the presumed homology of the character states of a character. Hence, if conflicting topologies are supported by different characters, non-homology of one state among some of the taxa is always assumed. However, this might not be the cause of the conflict. Instead, it might be caused by an incorrect homologization of different character states as belonging to the same character, i.e., the modifications (character states) of a structure (character) are in fact modifications of more than one structure. This is a principle error, which can only be avoided by re-examination and re-assessment of actual structures in case of conflicts.

For morphological characters, the need for large quantities of "observable facts" and the notion that the analysis "will sort out the true homologies" by congruence anyway, often result in the scoring of numerous similarities that provide few indications of homology, e.g., the relative length of a structure or the colour of a wing. The larger the number of incorrect hypotheses of homology that are included in an analysis (which is likely to increase with poorly supported hypotheses), the more hypotheses of homology are needed to resolve the resulting conflicts. However, in the case of morphological characters, the number of well supported hypotheses is limited by the number of

complex structures, which often causes the postulation of further poorly supported hypotheses in an attempt to increase quantity (problem of signal-noise ratio). Scoring numerous superficial similarities that are not homologous can easily lead to the rejection of a few well supported (and possibly correct) hypotheses of homology, in particular if the similarities are linked. An example for such a link are adaptations in various Macrolepidoptera – species with a shortened adult lifespan have typically non-feeding imagines and rather sessile females, which attract males over long distances by pheromones, while caterpillars are actively involved in dispersal. As a consequence of these adaptations, imagines (and to some extent pupae) have a reduced proboscis, reduced labial palpi, reduced maxillary palpi, enlarged and bipectinate antennae, females with reduced wing-coupling mechanisms, rapidly flying males with strengthened costal areas of the fore wing, first instar caterpillars with very long setae (aerial drift) and final instar caterpillars with a wandering behaviour prior to pupation. All of these characteristics match, e.g., Anthelinae (bombycoid complex) and Lymantriidae (Noctuoidea), in which the former were included in the past, despite only Noctuoidea having a metathoracic tympanal organ.

The *a posteriori* determination of character polarity by cladistic outgroup addition can cause problems in the determination of character polarity. Apomorphic conditions in the outgroup can be mistaken for the plesiomorphic condition in the ingroup, causing the plesiomorphic condition of the ingroup to be mistaken as an apomorphy. For example, if a primary homology, which happens to be a plesiomorphy of the ingroup, is secondarily lost in the exemplar chosen as an outgroup (an apomorphic condition), the plesiomorphy of the ingroup can incorrectly be interpreted as an apomorphy of the ingroup. The fewer taxa are used as an outgroup, the more likely is this type of mistake.

In summary, both Hennigian Argumentation as well as Maximum Parsimony Analysis have several serious shortcomings. In my opinion, Maximum Parsimony is not very suitable for the analysis of morphological data, but more suitable for molecular data if large quantities of parsimony informative characters are available. For well studied morphological characters and moderate numbers of taxa – as is the case in my study – I believe Hennigian Argumentation to provide better results, despite its unpopularity.

VII.1.2) Particular problems of the applied analyses

The Hennigian Argumentation of chapter III suffers from a shortage of well supported hypotheses of homology. Their number is insufficient to resolve all relationships, in particular in the presence of conflicting hypotheses. Consequently, many of the hypothesized monophyla are only supported by single hypotheses of apomorphy, which is not satisfying. The reduced adult lifespan of Anthelidae and most bombycoid taxa is linked to reductions of structures (e.g., mouth parts), and the immature stages are so far too poorly known (unavailable) to contribute many characters. Future more detailed studies of immatures and internal organs are likely to yield further well supported hypotheses.

As with the Hennigian Argumentation in chapter III, the number of morphological characters used in the Maximum Parsimony Analyses is insufficient. As this approach is a quantitative analysis, the lack of data is even more problematic than in Hennigian Argumentation. Conflicts, which are frequently caused by secondary losses of structures, could not be resolved on a quantitative basis due the shortage of parsimony informative data. Instead, alternative topologies are summarized in the strict consensus, which reduces its resolution. Further, probably incorrect groupings (e.g., the position of *Anthela nicothoe* if compared against Hennigian Argumentation and the analyses of molecular characters) are likely to be the result of the shortage of parsimony informative data, with a few homoplasies outnumbering other hypotheses of homology (in the case of *A. nicothoe* this could be the single, well supported hypothesis of homology used in the Hennigian Argumentation). The shortage of parsimony informative data and the homoplasy are also the probable cause of the low statistical support values. However, the few well supported nodes agree with the results of Hennigian Argumentation, as well as with molecular data. As the failure of the Maximum Parsimony Analyses of morphological characters to provide well supported phylogenetic hypotheses is probably largely caused by a lack of parsimony informative characters, no conclusions on the principle suitability of this method can be drawn from these analyses.

For the Maximum Parsimony Analyses of molecular data the situation is essentially similar. While the total number of parsimony informative characters is relatively high, their vast majority consists of third codon positions, which are most probably largely saturated for not all but many of the groups in question. This is a general problem of

data quality (signal-noise ratio), which affects not only Maximum Parsimony Analyses. If presumably wrong (saturated) data are excluded from the analyses (see the step-wise down-weighting of third codon positions in sections V.4), the remaining number of non-saturated data is too small to reliably resolve relationships by Maximum Parsimony. If these doubtful data are not excluded, they might result in incorrect topologies, either outnumbering alternative topologies (which is indicated by negative PBS values for other codon positions) or being uncontradicted due to a lack of non-saturated parsimony informative characters (PBS values of 0 for other codon positions). In the latter case I would expect contradictions from other saturated bases in third codon positions, probably causing low PBS values for third codon positions of incorrect taxon groups or ideally even reducing the effect of saturation to random noise.

I did not discuss process-dependent methods like Maximum Likelihood and Bayesian Inference in section VII.1.1. However, it should be noted that naturally the quality of any process-dependent method stands or falls with the fit of its model to the data. In the case of my molecular data, as well as with most published analyses, the best fitting model of all available models is the most complex (parameter richest) one, namely GTR+I+Γ. This indicates that none of the available models fits the complex evolutionary processes perfectly. An analysis of the molecular data partitioned by codon positions and with different models and/or parameters for each partition (as currently only possible in Bayesian Inference software) might have resulted in better fits between models and data than my combined analyses of all codon positions did.

VII.1.3) Consensus of well supported hypotheses

VII.1.3.1) Anthelidae

For the Anthelidae neither Hennigian Argumentation nor cladistic analyses of morphological, molecular or combined data resulted in well supported, fully resolved dendrograms. However, all analyses provide at least some well supported hypotheses of monophyla. For the various analyses of molecular data these monophyla have already been summarized in section V.4.1.4 (Fig. 376). Comparing the well supported monophyla of the cladistic analyses of morphological data (Fig. 356) and combined data (Figs 387, 388) with this summary, all of these monophyla are also supported by the analyses of molecular results. In general, the analyses of molecular data resulted in more and better supported hypotheses than any of the other two approaches, and no well supported contradictions exist between them. The cladistic analysis of morphological data has been particularly weak due to a lack of parsimony informative data, which is why the combined analysis of morphological and molecular data is dominated by the latter.

The Hennigian Argumentation is a second, independent line of evidence, which should be compared against the cladistic analyses. It shares the use of the same morphological structures with the cladistic analysis of morphological data, but the characters were scored differently and the methods of analyses differ, too. The independent postulation of the same hypotheses increases the probability of them being correct, but in accordance with the principle of falsification (Popper 1934) there can never be proof of their correctness. At the same time, any conflict between these hypotheses must result in the falsification of one of them.

The few well supported hypotheses resulting from the cladistic analysis of morphological data (Fig. 356) do not contradict the results of the Hennigian Argumentation (Fig. 354), but agree with them. This is also the case with most of the hypotheses summarized for the molecular analyses (Fig. 376), and a noticeable agreement exists also in the failure of either method to resolve relationships for a large number of groups within the Anthelinae. This might reflect a rapid radiation of their common ancestors, as indicated by the lack of synapomorphies for these taxon groups in the Hennigian Argumentation and the relatively short branches leading to these groups in the phylograms of Maximum Likelihood and Bayesian Inference analyses (Figs 374,

375). While numerous potential causes, e.g., changes in climate or access to new resources (plants), can be imagined, any conclusion on the cause for such a hypothesized rapid radiation without further information would be speculation.

However, differences between the hypotheses of Hennigian Argumentation and cladistic analyses of molecular data exist, too. In the summary of the cladistic analysis (based on EF1a only) the relationships between *Anthela callixantha*, *A. astata* & *varia* and *A. acuta* complex are not resolved, while *A. callixantha* is hypothesized to form a monophylum with *A. astata* & *varia* in the Hennigian Argumentation. The situation is similar for the polytomy of *A. virescens*, *A. addita* and *A. ferruginosa* in the cladistic summary, which is resolved in Hennigian Argumentation with *A. virescens* and *A. addita* forming a monophylum. This topology is also supported by all individual analyses of EF1a, but the support values were slightly lower than the self-imposed margins for the inclusion in the summary (80% bootstrap support or 90% posterior probability). Further, the summary of analyses of molecular data includes the monophyly of *A. unisigna* and *A. stygiana*, which form an unresolved polytomy in the Hennigian Argumentation.

The inclusion of *Anthela excellens* in an unresolved monophylum including *A. nicothoe* and *Nataxa flavescens* is rather well supported in Hennigian Argumentation, but is not supported by analyses of molecular data. However, as the species is placed in a polytomy as a potential sistergroup of *A. nicothoe* and *N. flavescens*, the inclusion of *A. excellens* in a polytomy with *A. nicothoe* and *N. flavescens* is not contradicted either. Neither of the hypotheses can be falsified as a possible consensus would be the placement shown in Fig. 390. Similarly, *A. tetraphrica* is part of an unresolved monophylum including *A. unisigna*, *A. stygiana*, *A. nicothoe*, *A. excellens* and *N. flavescens* in Hennigian Argumentation, while it is not included in this monophylum in the summary of analyses of molecular data. Instead, it is placed in a more inclusive, unresolved monophylum. Again, neither of the hypotheses can be falsified as a possible consensus would be the placement shown in Fig. 390.

The support of the sistergroup relationship between *Chenuala heliaspis* and the undescribed antheline species in analyses of molecular characters is dubious as discussed in section V.4.1.1. According to Hennigian Argumentation, the undescribed antheline species is not the sistergroup of *C. heliaspis*, but of *C. heliaspis* and a large number of antheline species, to which *C. heliaspis* forms the sistergroup. This

separation of Anthelinae n. sp. and *C. heliaspis* in the Hennigian Argumentation is based on a single, very well supported hypothesis of apomorphy. As the analyses of molecular data provide only dubious support, I favour the hypothesis of the Hennigian Argumentation. However, at the same time the analyses of molecular data support a different placement of both taxa than does Hennigian Argumentation, in which essentially this position is swapped with a large monophylum including *A. callixantha*, *A. astata* & *varia*, *A. acuta* group, *A. repleta* and *A. euryphrica*. This placement is only moderately well supported in Hennigian Argumentation and also affected by the unresolved placement of *Pseudodreata* & *Corticomis*, taxa for which no molecular data are available. Given the uncertainties in the Hennigian Argumentation (see section III.7.1) and the dubious support for the relationship between the critical taxa Anthelinae n. sp. and *C. heliaspis* in the analyses of molecular data, I cannot convincingly refute either hypothesis. As an alternative, I form an unresolved consensus in Fig. 390. This dendrogram summarizes all well supported groups of all methods of analysis and represents my phylogenetic working hypothesis.

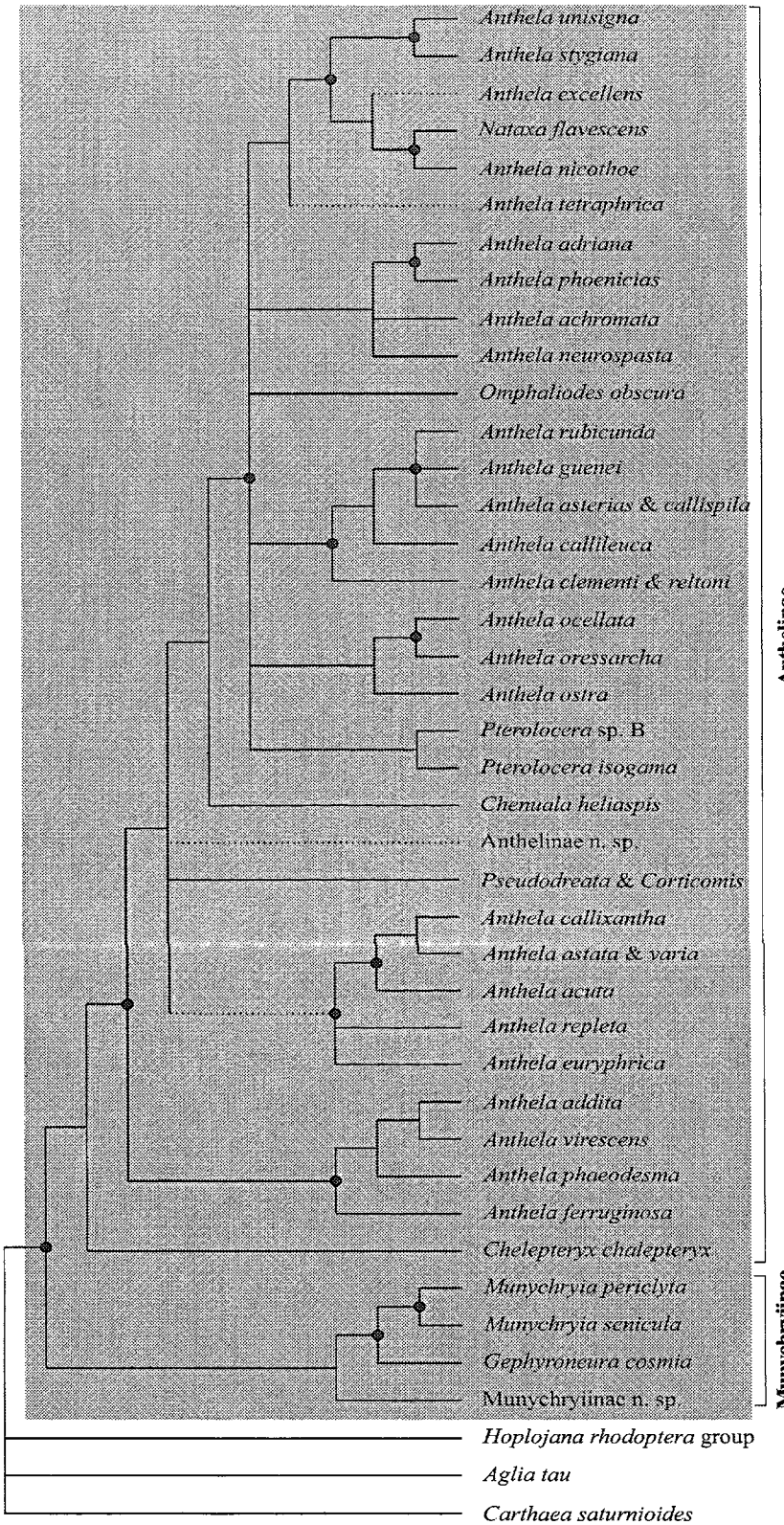

Fig. 390: Dendrogram visually summarizing all well supported hypotheses of monophyly within the Anthelidae (on bluish background) based on Hennigian Argumentation and cladistic analyses of morphological and molecular data. Consensus positions required by conflicting hypotheses of different methods of analysis are represented by dotted lines (note that this position is not postulated to be the correct position, but merely a compromise due to the inability to refute one of the hypotheses). Red dots mark nodes that are well supported by molecular characters.

VII.1.3.2) Bombycoid complex

The analysis of molecular data resulted in very few hypotheses of relationships between bombycoid families (Fig. 386). The only relationships well supported in most analyses are the inclusion of the Lemoniidae in the Brahmaeidae and the sistergroup relationship of this taxon with the Eupterotidae. A close relationship of Apatelodinae and Carthaeidae to this group is frequently but less strongly support, too. Otherwise, only relationships within families were supported by the majority of analyses. However, Bayesian Inference of data including CPS provided support for a monophylum including the Lemoniidae/Brahmaeidae, Eupterotidae, Apatelodinae, Carthaeidae, Endromidae, Lasiocampidae and Anthelidae, as well as including the Saturniidae in one instance. Given the saturation of the dominant third codon positions of CPS and EF1a at this phylogenetic level and the limited support (posterior probabilities of about 90; Figs 382, 385) provided by Bayesian Inference only, the monophyly of this group is rather questionable. The combined Maximum Parsimony Analysis of morphological and molecular characters (Fig. 389) did not provide additional support and the only well supported relationships between families are the inclusion of Lemoniidae in Brahmaeidae. As for Anthelidae, the combined analysis for the bombycoid complex is dominated by molecular characters. Unlike the previous two methods of analysis, the cladistic analysis of morphological characters provides support for the monophyly of the bombycoid complex. However, this is the only well supported hypothesis of the entire analysis.

Hennigian Argumentation results in moderately resolved hypotheses of relationships between families, but almost all are at best supported by a single hypothesis of apomorphy. The moderately to well supported monophyly of the bombycoid complex is the exception. Given the large number of missing data and the limited examination of family members, in particular of Macrolepidoptera other than of the bombycoid complex, the dendrogram derived by Hennigian Argumentation is no more than tentative, with some parts of the topology based on single well or very well supported hypotheses of apomorphy. A group including Lemoniidae & Brahmaeidae, Eupterotidae and Anthelidae is hardly resolved due to conflicting, homoplastic characters. The relationship between Lemoniidae & Brahmaeidae and Eupterotidae that is very well supported by the analyses of molecular data, matches one of several possible *ad hoc* explanations in the Hennigian Argumentation. A different *ad hoc* explanation was

favoured (see section III.7.2), but given the strong support of molecular characters, the favoured *ad hoc* explanation of the Hennigian Argumentation is refuted. The better supported topology is presented in the summary of all supported topologies (Fig. 391), which represents my phylogenetic working hypothesis [in the absence of well supported alternatives, this summary is largely identical with the result of the Hennigian Argumentation].

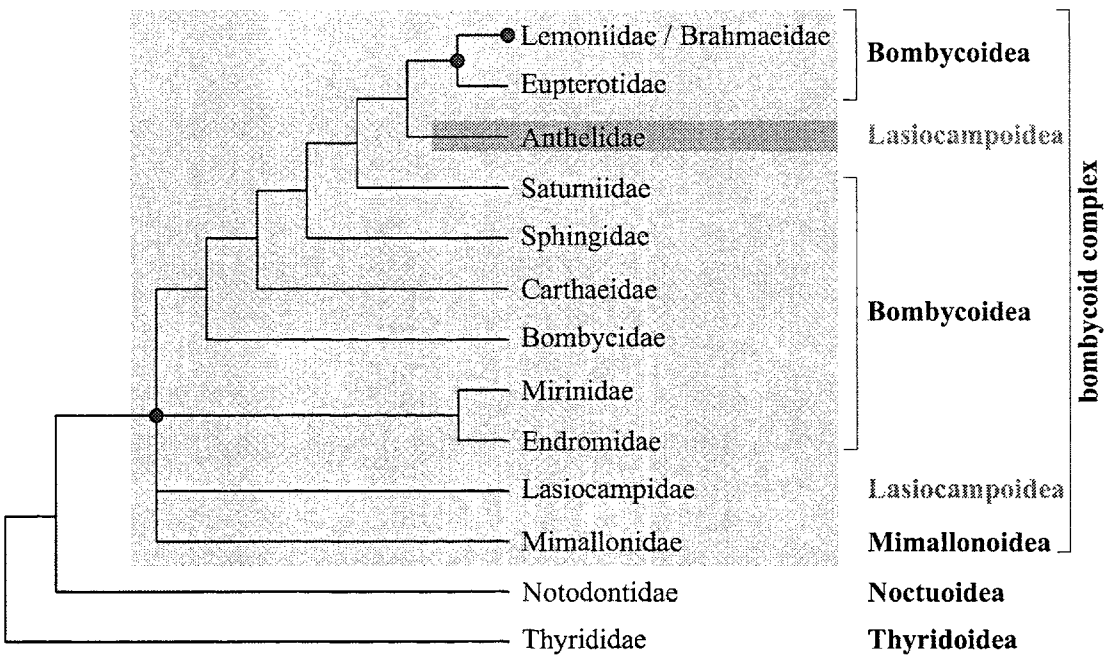

Fig. 391: Dendrogram visually summarizing all well supported hypotheses of monophyly within the bombycoid complex (on yellowish and bluish background) based on Hennigian Argumentation and cladistic analyses of morphological and molecular data. Red dots mark nodes that are well supported by molecular characters (however, no molecular data are available for Mimallonidae and Mirinidae). Note the hypothesized polyphyly of the Lasiocampoidea (orange).

VII.2) TESTING OF PHYLOGENETIC HYPOTHESES

If one accepts the theory of evolution as the explanation for the occurrence of different taxa, the presence of factual evolutionary relationships between taxa is a logic consequence. These relationships are *de facto* non-observable and the reconstruction of the single "true phylogeny" is the aim of any phylogenetic study. Dendrograms, such as in Figs 390 and 391, are intended to reflect the phylogeny of taxa. However, these dendrograms are merely graphical summaries of numerous phylogenetic hypotheses and do not necessarily match the unknown, true phylogeny. As all hypotheses in general, phylogenetic hypotheses can never be proven to be correct (Popper 1934). Consequently, no synapomorphy, no support value of any kind, no congruence between characters or even between independently derived, complex hypotheses can prove a phylogenetic hypothesis to be correct. Instead, a phylogenetic hypothesis has to be constantly questioned and tested, in an attempt to falsify it. While confidence in a hypothesis might grow with repeated failure to falsify it, a final proof of its correctness is not possible. Nevertheless, a very well tested hypothesis might eventually be accepted as factual for practical reasons, e.g., the hypothesis of gravity.

My own phylogenetic hypotheses, which are summarized in Figs 390 and 391, are no exceptions and require repeated attempts of falsification. Such falsification cannot be conducted with any data utilized for the formation of the hypotheses. Hence, the calculation of additional statistical support values based on the present data is not an attempt to falsify the hypotheses. Instead, new data are required that have to be assessed against the existing hypotheses. Only incongruence of the existing hypotheses with the new hypotheses can falsify the former, and only if the latter are better supported or equally well supported and more numerous.

In practical terms, such a falsification is rather difficult as usually all data available at the time have already been used for the generation of the phylogenetic hypotheses. New data could be additional gene sequences, as well as characters based on morphological structures not utilized in this study, e.g., potentially egg and pupal morphology or thoracal sclerites. The study of the organisms by other researchers is likely to provide such new data and hence I regard my data and dendrograms as working hypotheses, which are up for discussion and falsification by others.

Checking the plausibility of the proposed phylogeny is a form of falsification

attempts. It involves the assessment of additional hypotheses ("knowledge") against the existing phylogeny, typically in an informal way without explicitly stating the additional hypotheses. For example, a phylogeny appears to be implausible if it hypothesizes the repeated loss and re-gaining of complex structures such as wings or mouth parts. While this might not be a formal refutation of the proposed hypotheses, a check of the plausibility of the phylogenetic hypotheses can provide valuable indications and prompt a more rigorous examination.

Apart from mapping hypotheses of discrete character changes onto a proposed phylogeny, the mapping of other biological information can be useful to assess plausibility of phylogenetic hypotheses. Such information could be, e.g., data on distribution, behaviour or host usage. However, such "data" represent and require numerous hypotheses, too, and have to be used with caution. For example, several anthelid species have been recorded as feeding on grasses (see Appendix C). Grasses are generally poor in nutrients and "armed" with silicate crystals, which might be the reason for grass-feeding being very uncommon amongst the large caterpillars of bombycoid species. Hence, I hypothesize that grass-feeding did not evolve many times independently within the Anthelidae. As a check of plausibility, I mapped the host records of Appendix C onto my working hypothesis of anthelid phylogeny (Fig. 390). The result (Fig. 392) supports the hypothesis that the shared ancestors of all Anthelinae other than *Chelepteryx* (the vast majority of extant Anthelidae) fed on grasses, with shifts to other hosts evolving several times independently. These shifts in hosts appear to be mainly to *Acacia* species and to coincide with rapid speciation, which is indicated by the very short corresponding branches in phylograms (e.g., Figs 374 and 375) and results in the large polytomy within Anthelinae in Fig. 390.

Further, the proposed phylogeny of Anthelidae is not fully resolved, no host records exist for numerous taxa and the reliability of the host records used is not consistent and often poor. Therefore, my data are inconclusive to whether grass-feeding evolved only once or multiple times, and consequently, these current biological data are not suitable to falsify the proposed anthelid phylogeny.

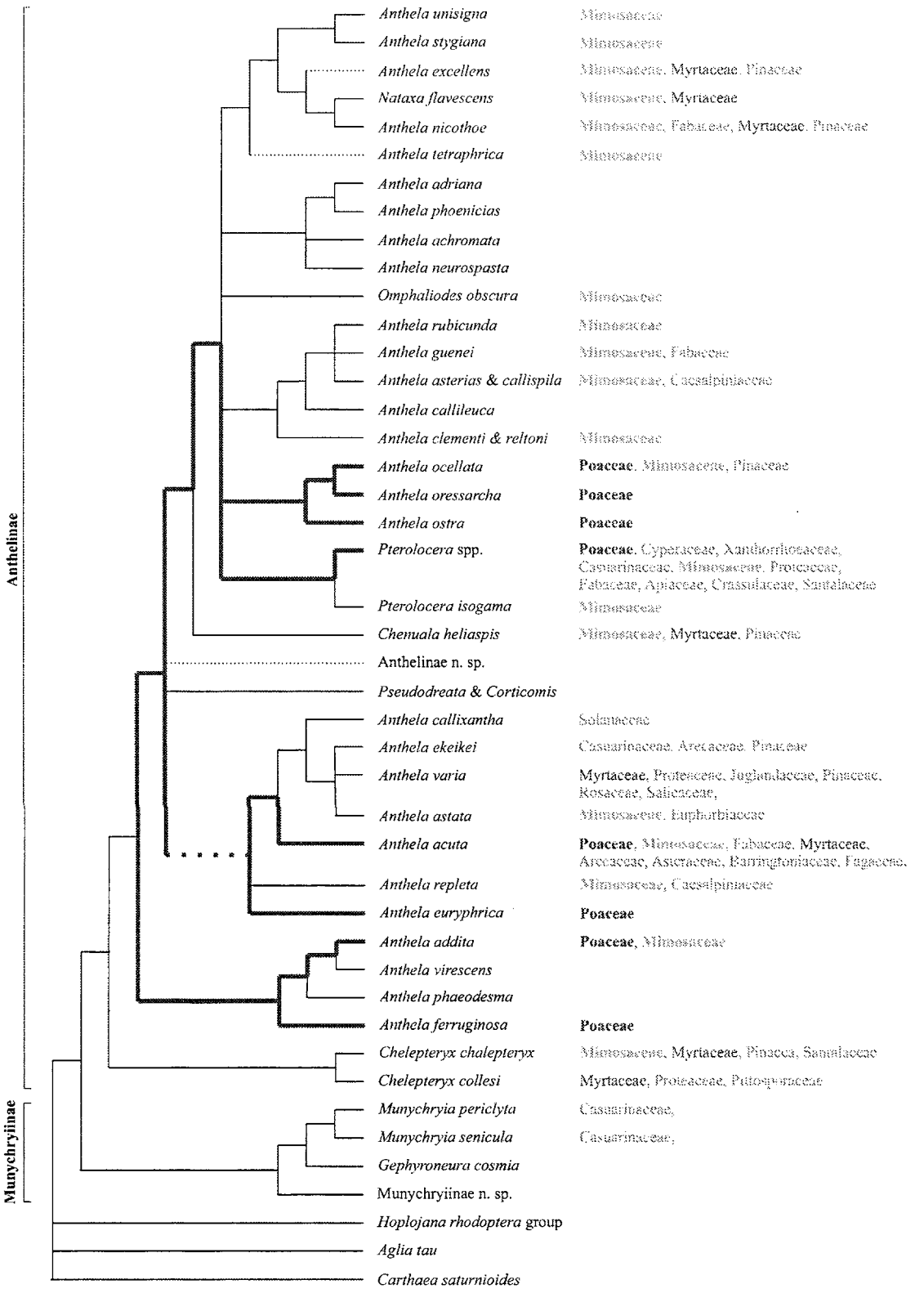

Fig. 392: Proposed anthelid phylogeny (Fig. 390) in combination with plant families of host records (Appendix C). Records of grasses (Poaceae) are marked blue, while *Acacia* species (Mimosaceae) are yellow and Myrtaceae (incl. *Eucalyptus* spp.) are red. Grass-feeding appears to have evolved rather early during anthelid evolution and possibly (but not necessarily) only a single time, while feeding on *Acacia* species (and other hosts) seems to have evolved multiple times. Note that many records other than of Poaceae and Mimosaceae represent single observations and that the records are not equally reliable.

VII.3) Revised taxonomic classifications

The number of available taxonomic ranks (species, genus, tribe, family, etc.) is obviously much smaller than the number of nodes of most phylogenetic hypotheses, let alone speciation events. While in theory each node could be named if required (neither necessary nor practical), not every node of my phylogenetic hypothesis can be assigned a formal rank due to the shortage in ranks. An arbitrary choice between nodes has to be made, and no binding rules exist for this process. It is desirable for comparison, but impossible in practice, to assign formal ranks at equivalent phylogenetic levels. Hence, the use of ranks in our current classification of living organisms is inconsistent and not comparable, e.g., a bird family is not necessarily equivalent to a moth family or a plant family. This is a major shortcoming of the classification system, limiting its usefulness.

I see the function of the classification in providing a nomenclatural index system to information on organisms. For practical reasons this index should be as stable as possible, which requires any classification to be exclusively based on well supported hypotheses. If the classification reflects phylogeny, it conveys additionally some limited information on relationships – all members of a rank (e.g., of a genus or family) are more closely related to each other than to any other organism, and this relationship is stable. Therefore, I believe that formal ranks should only be assigned to well supported monophyla. As a consequence, these ranks do not necessarily comprise only in habitus similar organisms, but can include highly modified, very distinct taxa. To isolate such distinct taxa by assigning an equivalent rank to them and the monophylum means creating paraphyletic taxa and is to be avoided. Isolating the distinct taxa and splitting the larger monophylum according to a phylogenetic hypothesis is an alternative. However, this often results in assigning ranks to poorly supported (=unstable) monophyla or in creating numerous very small or even monotypic taxa, which is not desirable either. In such a case I opt to assign a rank to a more inclusive but better supported monophylum, even if this means "lumping" distinct taxa together with in habitus less similar taxa (e.g., in the case of the anthelid genus *Nataxa*). If future research provides better hypotheses on the relationships within the more inclusive monophylum, then well supported and compatible splits might be possible.

Despite some differences between the phylogenetic hypotheses derived by Hennigian Argumentation, cladistic analyses and model-dependent analyses (see IV.1), numerous monophyla are proposed by most analyses (or are at least compatible with all analyses) and only a few contradictions exist. The phylograms are not fully resolved, but as the polytomies consist of monophyletic groups, these monophyla can be used as the basis of taxonomic classification despite lacking a hypothesis of the relationships between them.

In the following sections I propose revised taxonomic classifications based on hypothesized monophyla at the generic, subfamily, family and superfamily level. A checklist of all described anthelid genera and species in accordance with the proposed new classification is presented in Appendix B.

VII.3.1) Generic classification of Anthelidae

As currently perceived (see Appendix A), the genus *Anthela* includes 80% of all described species and is paraphyletic in respect to the genera *Nataxa*, *Omphaliodes*, *Pterolocera* and probably *Chenuala*, hence most other genera of the Anthelinae. Synonymizing these genera with *Anthela* would equate *Anthela+Chelepteryx* with Anthelinae, and little is to be gained from this. Instead, I propose to subdivide the large subfamily Anthelinae into monophyletic groups, restricting *Anthela* to its type species and closest relatives and resurrecting synonymized genera or defining new ones (see Appendix B). I propose the following genera for the family Anthelidae, to which all anthelid species in the ANIC can be assigned, including all undescribed species (only two of these undescribed species are listed in Appendix B):

- ***Munychryia* Walker, 1865**

  Type species: *Munychryia senicula* Walker, 1865 (Figs 393, 394).

  Autapomorphies: **(1)** Phallus base bulbous [H.31(1)].

  Notes: A small genus with only two described species, of which *M. senicula* is part of a small complex of sibling species (specimens from northern QLD as well as TAS/VIC/probably SA differ from the typical specimens from southern QLD/NSW in male genital structures, particularly the hook-shaped cornutus, and represent at least two undescribed species).

  The sistergroup relationship of the two described species relative to the superficially very similar *Gephyroneura cosmia* is very well supported by molecular characters. Relative to *G. cosmia* and an undescribed munychryiine species from WA the

monophyly is also supported by the proposed autapomorphy of the genus. The caterpillars of *Munychryia* show numerous apomorphies (e.g., the enlarged prothoracic legs; the membranous lobe of the thoracic tibiae (Fig. 395); the posteriad extended anal prolegs (Fig. 396); the minute, club-shaped secondary setae (Fig. 284); a prominent, unpaired median lobe (glandular sack?) located posteriorly to the hypopharyngeal complex (Fig. 397); the colour pattern of longitudinal stripes on the body (Fig.)), some of which have previously been proposed as autapomorphies of the Munychryiinae by Common and McFarland (1970). However, as long as the caterpillars of the other Munychryiinae (*G. cosmia* and the undescribed species from WA) are unknown, it is not possible to decide whether these peculiarities of the caterpillars are autapomorphies of the genus *Munychryia* or of (parts of) the subfamily Munychryiinae.

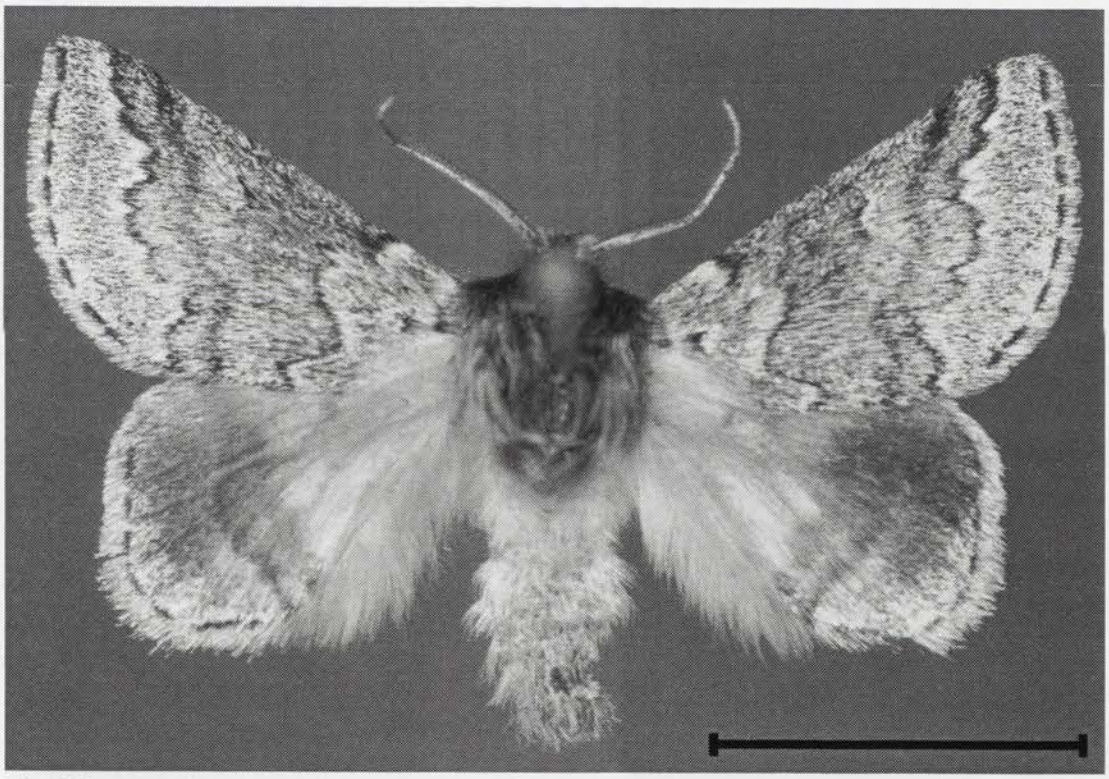

Fig. 393: *Munychryia senicula* WALKER, 1865, ♂ (NSW, Church Point) – type species of *Munychryia* WALKER, 1865 [scale bar = 1cm].

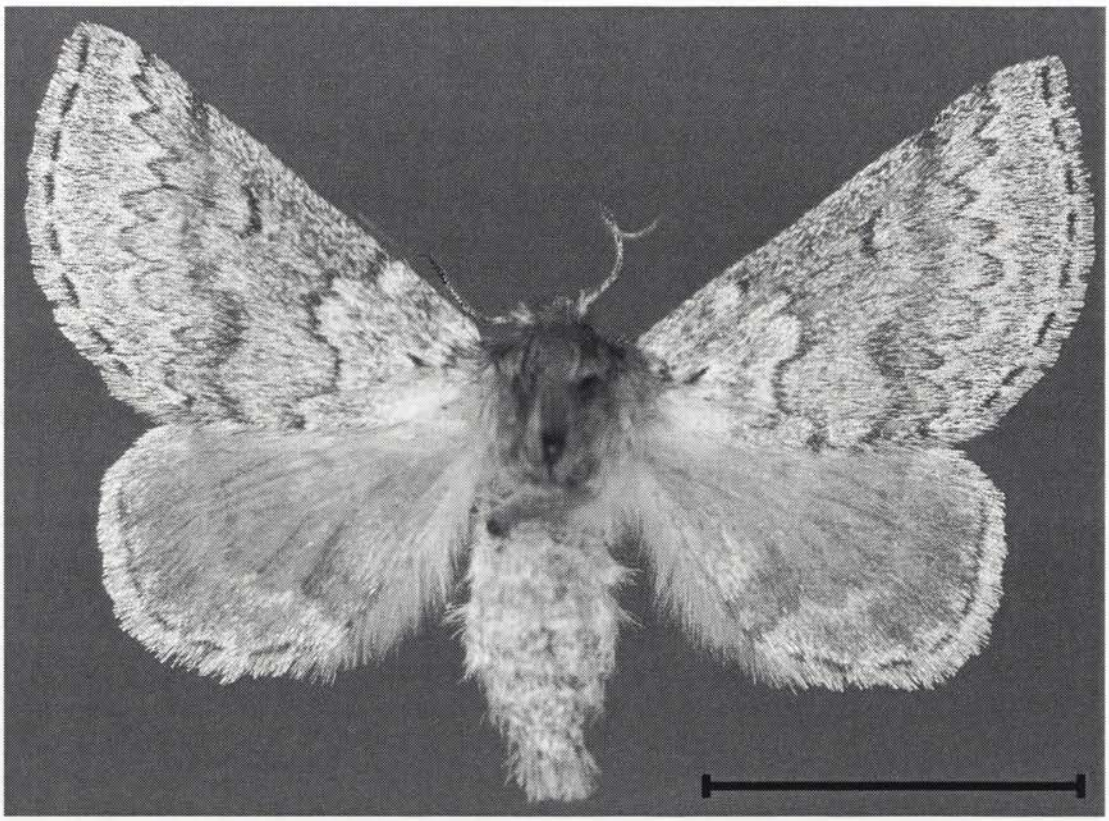

Fig. 394: *Munychryia senicula* WALKER, 1865, ♀ (NSW, Church Point) – type species of *Munychryia* WALKER, 1865 [scale bar = 1cm].

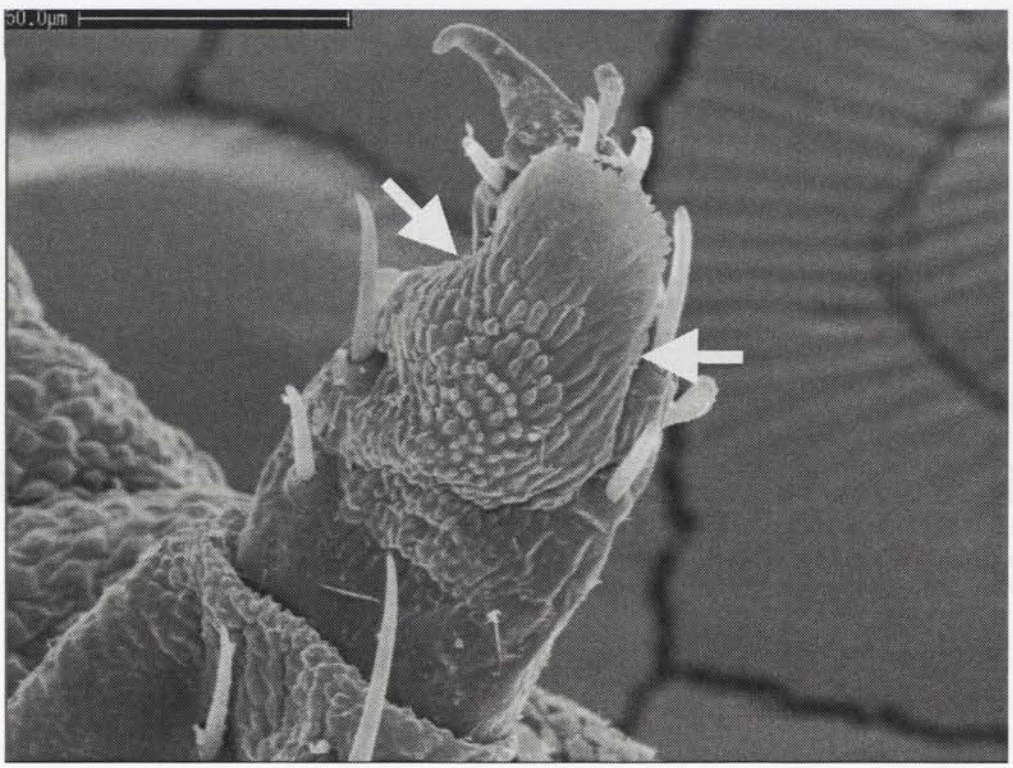

Fig. 395: *Munychryia senicula* (Anthelidae), caterpillar (L1), ventro-mesal view (top left=anterior) – left metathoracic leg with a membranous lobe on the mesal side of the tibia (between yellow arrows).

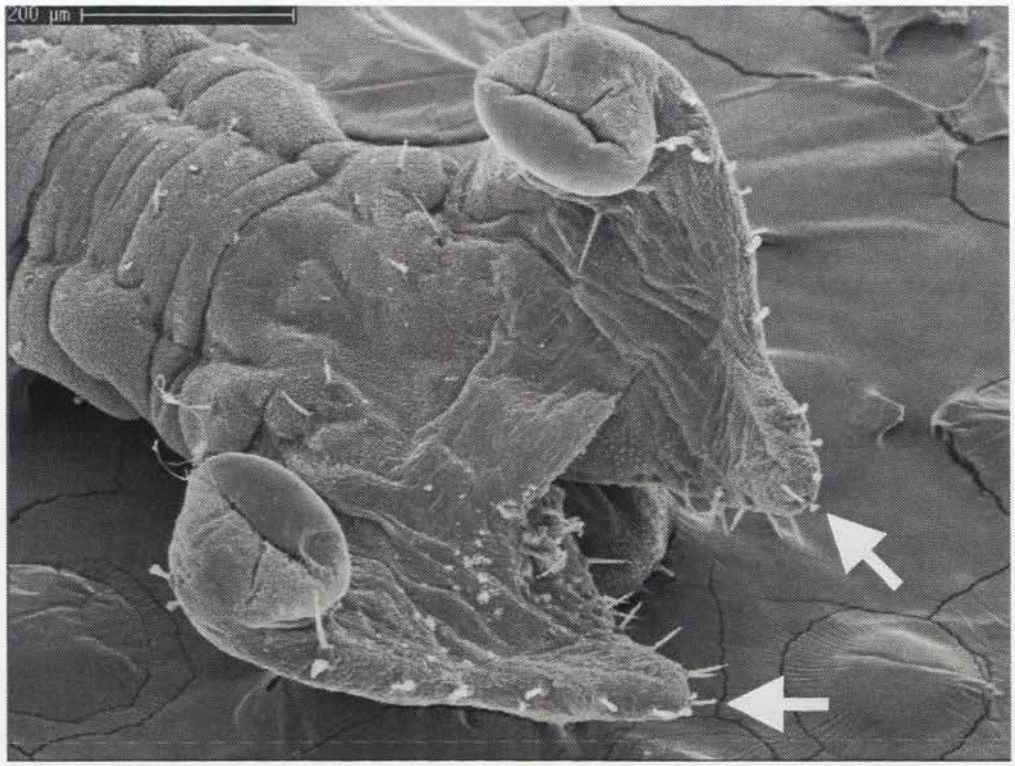

Fig. 396: *Munychryia senicula* (Anthelidae), caterpillar (L1), ventral view (top left=anterior) – anal prolegs posteriad extended (yellow arrows).

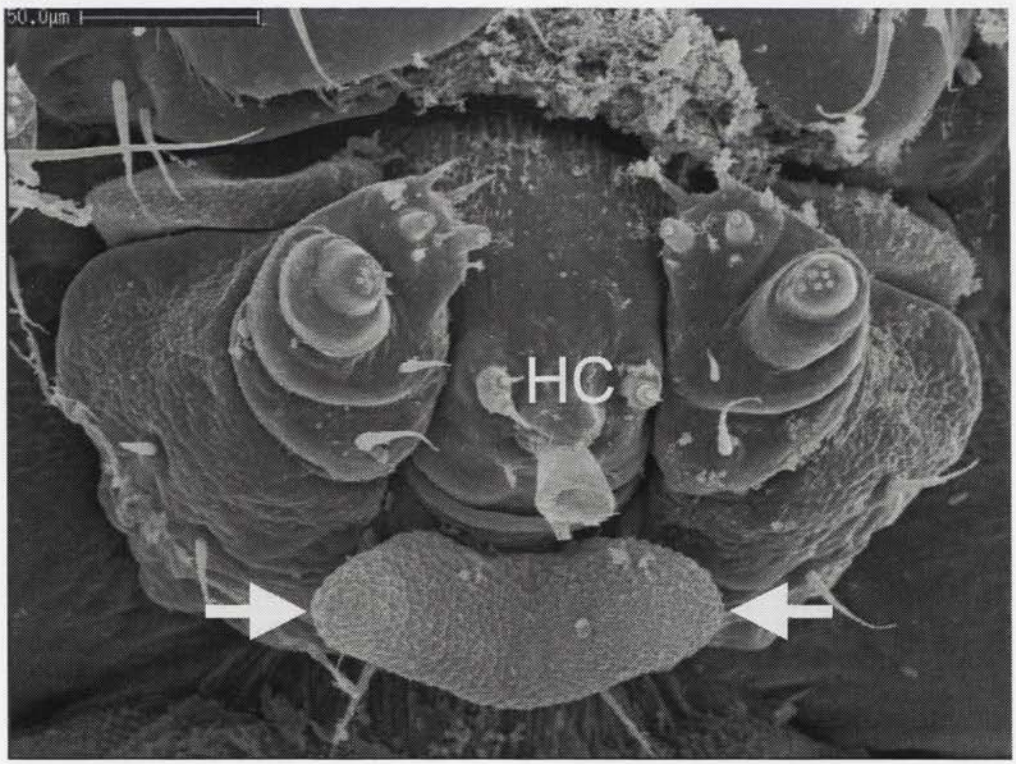

Fig. 397: *Munychryia senicula* (Anthelidae), caterpillar (L1), ventral view (top=anterior) – head capsule posteriorly of the hypopharyngeal complex (HC) with an unpaired, median membranous lobe (between yellow arrows; possibly glandular).

- ***Gephyroneura* TURNER, 1920**

  Type species: *Gephyroneura cosmia* TURNER, 1921 (Fig. 398).

  Autapomorphies: **(1)** Loss of the single cornutus [H.32(0)]. **(2)** Partial basal fusion of Rs1/Rs2 and Rs3/Rs4 branches in the fore wing [H.50(1)].

  Notes: A monotypic genus, which is only known from a few male specimens from the Atherton Tableland (north-eastern QLD) and Rockhampton (eastern QLD); the female and pre-imaginal instars are unknown. The sistergroup relationship of the genus to *Munychryia* is well supported by molecular characters (in the absence of other Munychryiinae!), but only poorly defined morphologically by the above autapomorphies. None of these apomorphies are unique and both depend on the interpretation of the phylogeny within the Munychryiinae (see section III.7.1). Common and McFarland (1970: 21) noted that *Gephyroneura* differs from the superficially very similar genus *Munychryia* additionally in the reduction of mouth parts and the absence of subapical spurs of the hind tibiae. Both of these characteristics are very common reductions in Lepidoptera (incl. Anthelidae) and not suitable to define a genus.

  Being the presumed sistergroup of *Munychryia* and being only poorly defined, *Gephyroneura* as well as the following genus ("Genus novum 1") could be included in *Munychryia*. However, this would equate *Munychryia* with Munychryiinae, and as *Gephyroneura* is already a described and recognized genus, I retain it as a genus distinct from *Munychryia*, despite any monotypic genus being *per se* uninformative.

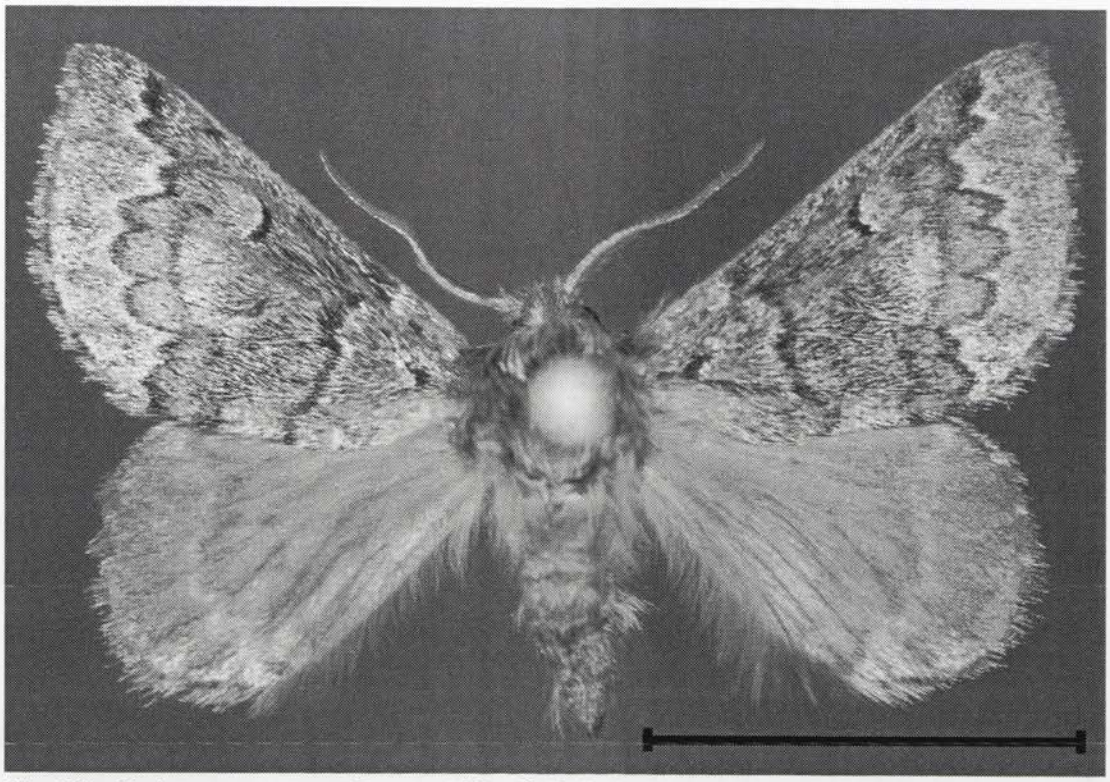

Fig. 398: *Gephyroneura cosmia* TURNER, 1921, ♂ (QLD, 7mi NNE Ravenshoe) – type species of *Gephyroneura* TURNER, 1920 [scale bar = 1cm].

- **"Genus novum 1"**

  Proposed type species: undescribed ["Munychryiinae n. sp." (Figs 399, 400)].

  Autapomorphies: **(1)** Partial basal fusion of Rs1/Rs2 and Rs3/Rs4 branches in the fore wing [H.50(1)]. **(2)** Uncus with a blunt posterior edge [C.1(2)].

  Notes: Like the preceding genus *Gephyroneura*, this undescribed genus is monotypic and morphologically poorly defined by an autapomorphy, which depends on the phylogeny of the Munychryiinae (the first apomorphy is also present in *Gephyroneura*, but *ad hoc* assumed to be a convergence; see section III.7.1). The blunt posterior edge of the rather broad and flat uncus seems to be a unique reduction of the weakly bilobed edge. According to the proposed phylogenetic hypothesis and because *Gephyroneura* is retained as a distinct genus, a new genus has to be described for the undescribed munychryiine species, despite its poor definition (see *Gephyroneura*).

  The species is only known from two male and one female specimens from southern WA in the ANIC.

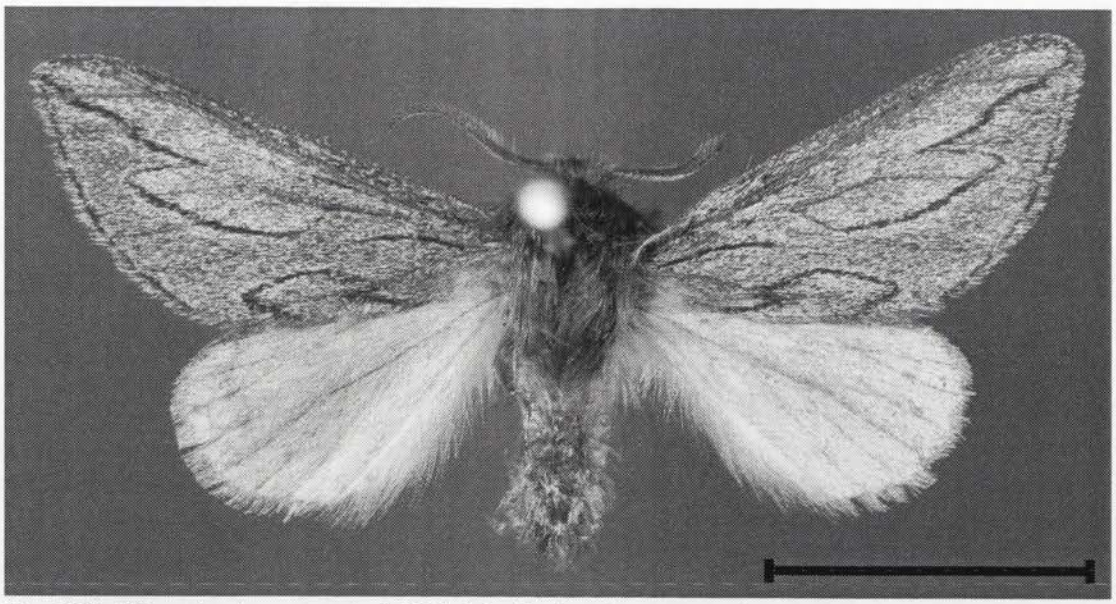

Fig. 399: "Munychryiinae n. sp.", ♂ (WA, Mt. Singleton) – proposed type species of "Genus novum 1" [scale bar = 1cm].

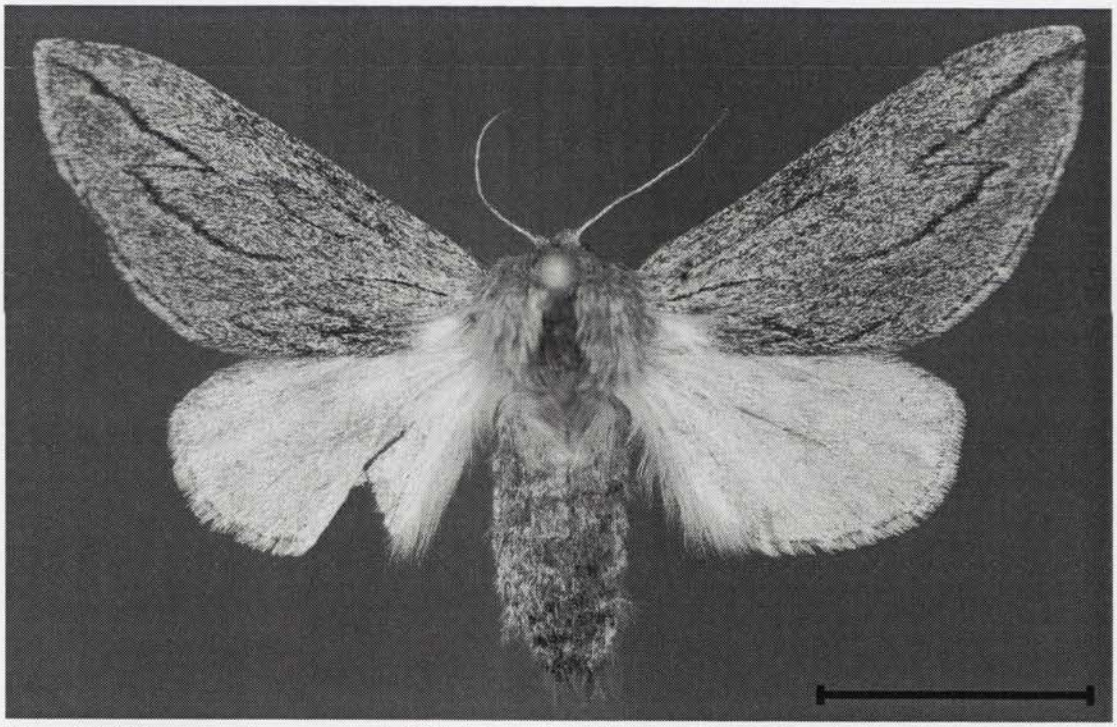

Fig. 400: "Munychryiinae n. sp.", ♀ (WA, Cane Grass Swamp 57km S Menzies) – proposed type species of "Genus novum 1" [scale bar = 1cm].

- ***Chelepteryx* GRAY, [1835]**

  Type species: *Chelepteryx collesi* GRAY [1835] (Figs 401, 402).

  Autapomorphies: **(1)** Fusion of juxta and phallus by sclerotization of entire manica [H.29(1)].

  Notes: A small genus with two very large species. The genus ranges in its distribution along the East coast and Tablelands from northern QLD to VIC. The huge, spiny caterpillars are frequently encountered in urban areas when wandering around prior to pupation.

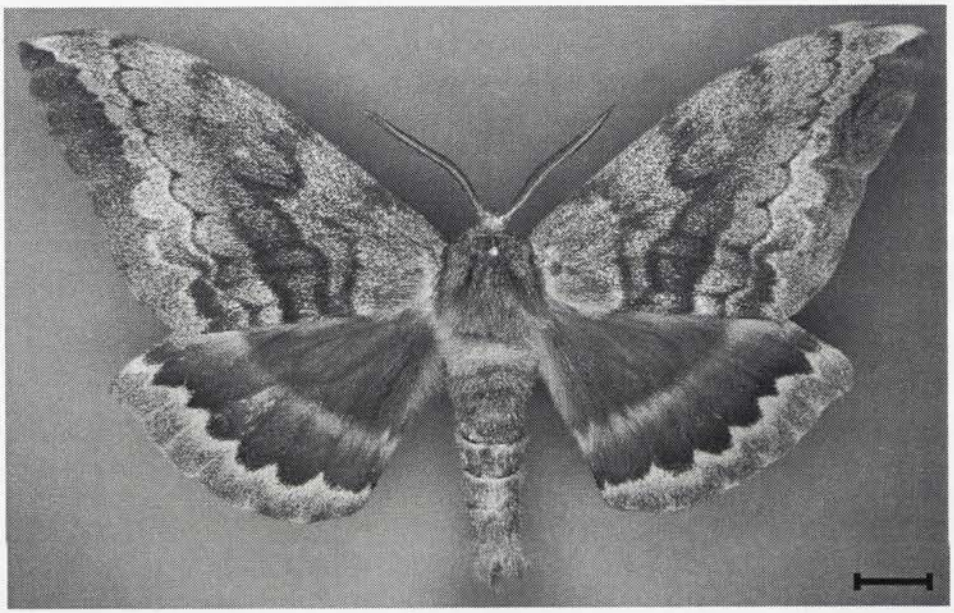

Fig. 401: *Chelepteryx collesi* GRAY [1835], ♂ (VIC, Hazelwood) – type species of *Chelepteryx* GRAY [1835] [scale bar = 1cm].

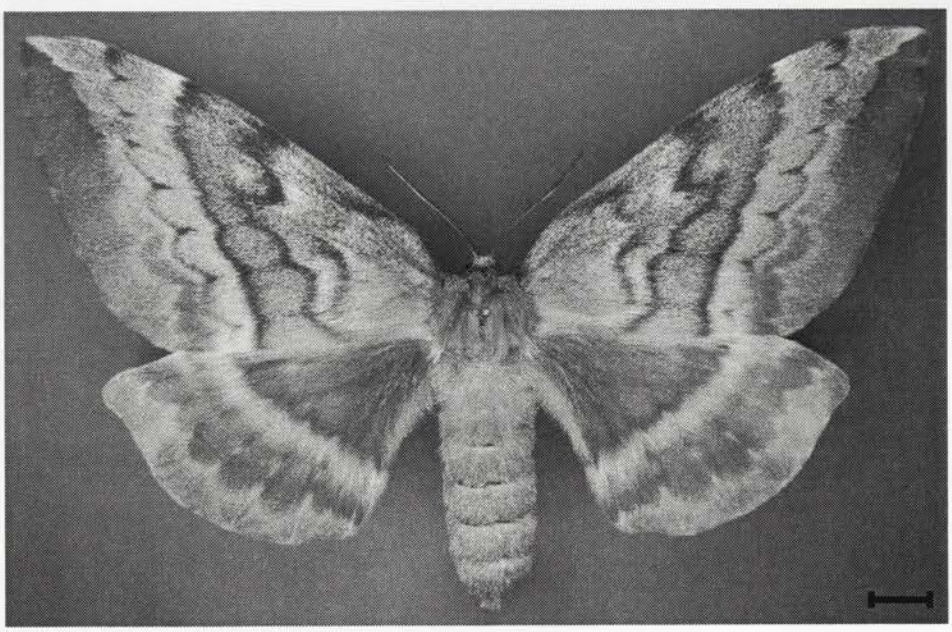

Fig. 402: *Chelepteryx collesi* GRAY [1835], ♀ (VIC, Morwell) – type species of *Chelepteryx* GRAY [1835] [scale bar = 1cm].

- ***Anthela* WALKER, 1855**

  Type species: *Anthela ferruginosa* WALKER, 1855 (Figs 403, 404).

  Autapomorphies: **(1)** Mesal protrusion and anellus merged with the juxta.

  Notes: By defining the principal anthelid genus *Anthela* by the above autapomorphy, the genus is restricted to *A. ferruginosa*, *A. virescens*, *A. phaeodesma* and the *A. addita* group (strongly supported by molecular characters). All other species so far included in *Anthela* should be placed in other genera as described below [see Appendix B for details]. In the *A. addita* group, the habitus of specimens can vary strongly, but only two sympatric species are easily recognizable by male genital structures. Similarly, *A. ferruginosa* is very variable in habitus, but only one undescribed species from WA (in the ANIC) differs consistently in habitus (greyish and with strongly marked wing pattern) and marginally in male genital structures. A further undescribed *Anthela* species occurs on the Atherton Tableland. The distribution of *Anthela* [*s. str.*] ranges mainly along the East coast and Tablelands from N QLD through NSW, VIC, TAS and SA to WA, but *A. ferruginosa* has occasionally been collected at locations further inland, too (e.g., QLD, Carnarvon Ranges, Mt. Moffat). *A. phaeodesma*, which inhabits Cape York Peninsula and north-eastern QLD, occurs also in coastal areas of PNG (a single specimen in the Brandt collection at the ANIC).

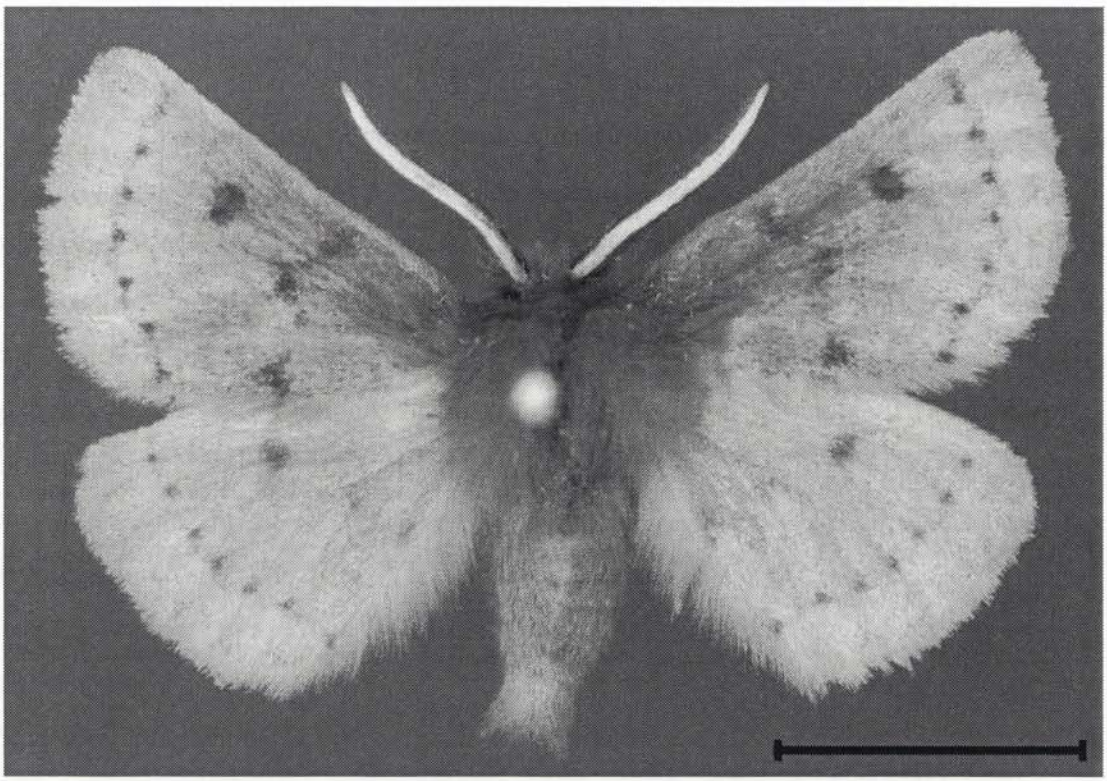

Fig. 403: *Anthela ferruginosa* WALKER, 1855, ♂ (NSW, Burrill Lake near Woodburn SF) – type species of *Anthela* WALKER, 1855 [scale bar = 1cm].

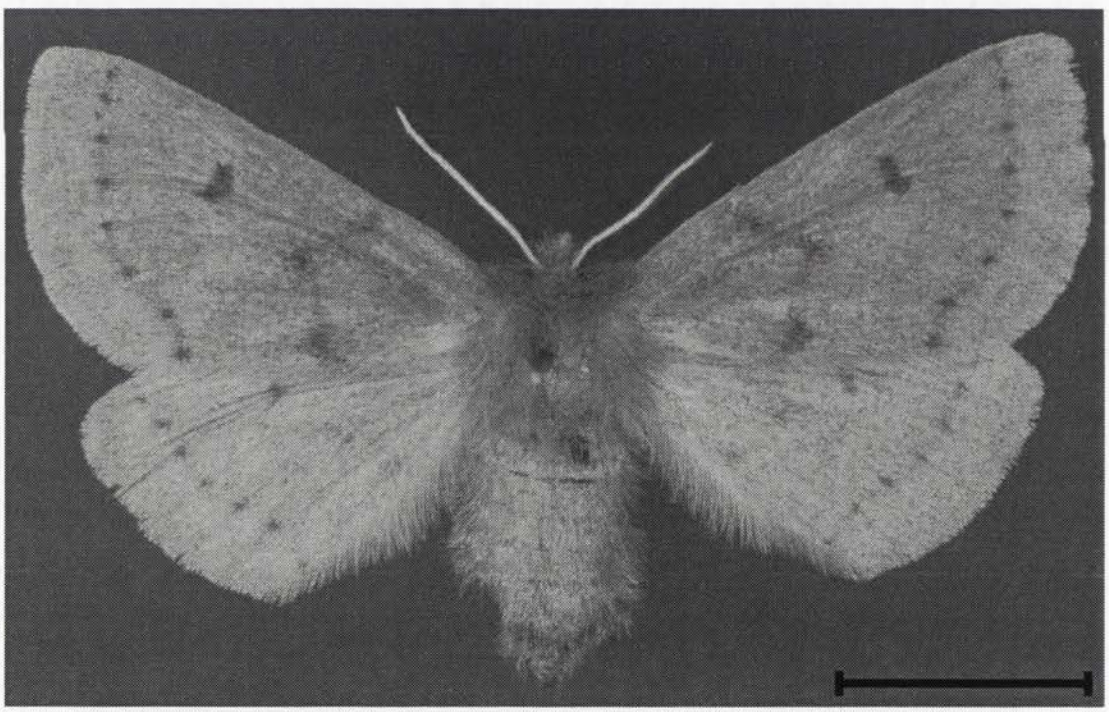

Fig. 404: *Anthela ferruginosa* WALKER, 1855, ♀ (NSW, Kanangra Walls, Boyd Ck) – type species of *Anthela* WALKER, 1855 [scale bar = 1cm].

- ***Colussa* WALKER, 1860, stat. rev.**

  Type species: *Colussa odenestaria* WALKER, 1860, a junior subjective synonym of *Darala varia* WALKER, 1855 (Figs 405, 406).

  Autapomorphies: **(1)** Uncus lobes with a mesad tilt of less than 30° entirely fused. **(2)** Mesal protrusion/anellus forms a well sclerotized, elongate, setose ridge lateral of the phallus. **(3)** Valva apodeme lobe forms a posterior, "upturned" process (reduced in many species). **(4)** Right sclerotized band on vesica forms a long, curved to bent process.

  Notes: This is the largest anthelid genus, comprising 20 currently recognized species from Australia and 9 described species from New Guinea and Aru. Many of these recognized species represent a complex of cryptic, sometimes synonymized but often undescribed species. The sympatric occurrence of two to three species of the *C. acuta / astata* complex is common along the East coast and Tablelands of Australia. Further, a small number of distinct, undescribed species mainly from WA is housed in the ANIC, most noticeably a species of unusual habitus from the Pinkerton Range (NT). In contrast, some currently recognized species are likely to represent synonyms. For example., *C. basigera* and *C. denticulata* are largely distinguished by distribution only, while being differentiated from *C. euryphrica* by their darker colour and distribution. However, mapping the distributions of specimens in the ANIC revealed an overlap in distribution, and no constant differences in male genital structures exist. Further, of 492bp of EF1a sequence of *C. basigera* (SA, Adelaide) and *C. euryphrica* (NSW, Orange) only a single base differs (0.2%; see *Omphaliodes* below for comparison). This argues for synonymizing these three species, with *C. denticulata* (Newman, 1856) being the most senior synonym. The total number of species comprised in this genus is difficult to judge, but based on preliminary dissections of male genital structures I expect the total number of species to range from 50 to 90.

  Molecular characters support the monophyly of this genus very strongly. Likewise, the male genital structures possess several unique and within the genus universal modifications (see apomorphies) that provide excellent support for the monophyly of the genus. Male genital structures differ surprisingly little, except for the various simple modifications of the clasper and the common reduction of the valva apodeme lobe. In contrast, species can differ tremendously in size and habitus. Further, the

wing pattern and colouration of many species are extremely variable, and the offspring of a single female can comprise the full range of variations of a species [own observation from rearing Anthelidae]. Sexual dimorphism is extreme, which contributed to the description of numerous synonyms. A careful revision of this genus is urgently needed, with the use of molecular characters, ideally combined with the study of caterpillars and male genital structures, seeming to be the most promising approach.

The genus is extremely widespread in Australia and New Guinea, but diversity appears to be particularly high along the East coast and Tablelands of Australia. Many of the New Guinean species can hardly be separated from the Australian species, but others (e.g., *Colussa charon*) are very distinct.

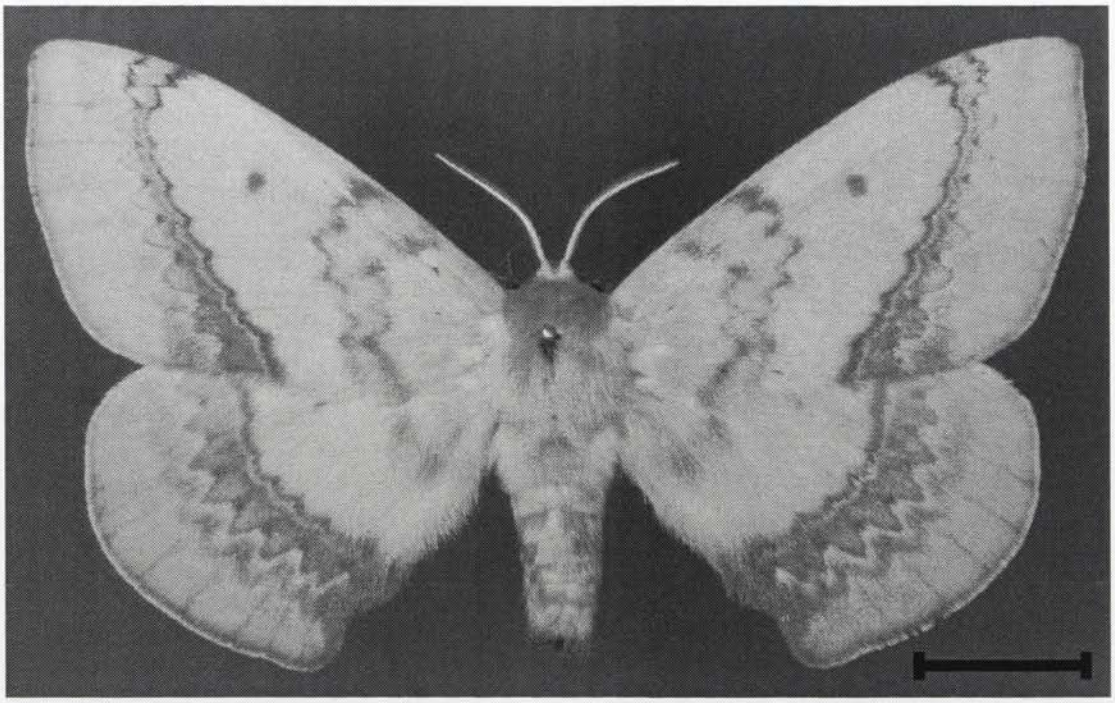

Fig. 405: *Colussa odenestaria* WALKER, 1860 [= *Colussa varia* (WALKER, 1855)], ♂ (NSW, Warrumbungles) – type species of *Colussa* WALKER, 1860 [scale bar = 1cm].

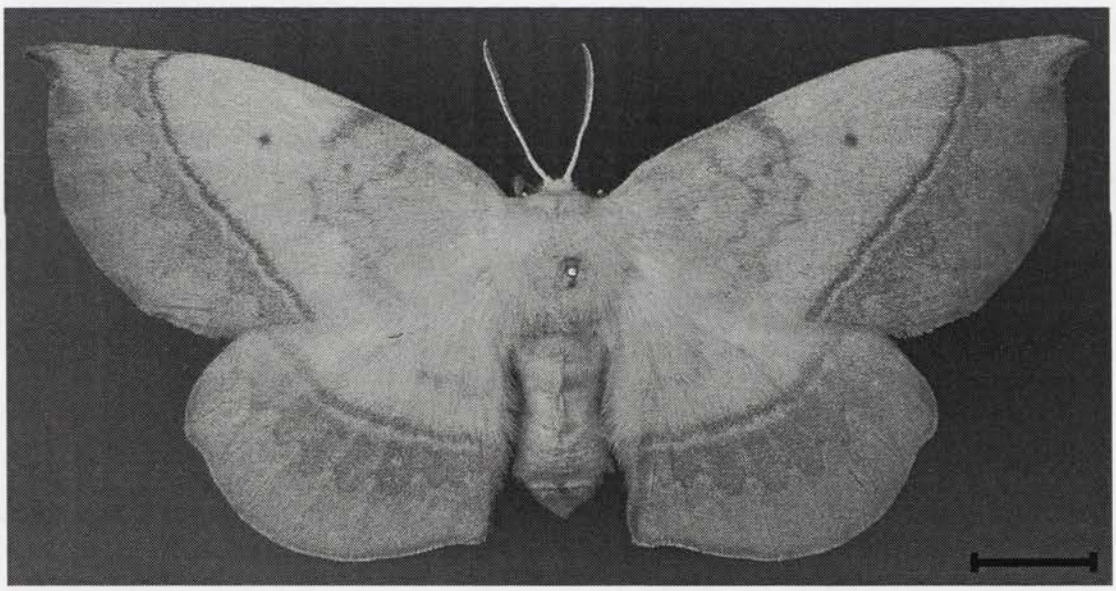

Fig. 406: *Colussa odenestaria* WALKER, 1860 [= *Colussa varia* (WALKER, 1855)], ♀ (QLD, Brisbane) – type species of *Colussa* WALKER, 1860 [scale bar = 1cm].

- ***Pseudodreata*** **BETHUNE-BAKER, 1904, stat. rev.**

  Type species: *Pseudodreata strigata* BETHUNE-BAKER, 1904 (Figs 407, 408).

  Autapomorphies: **(1)** Apically touching uncus lobes only dorsally and only partly fused. **(2)** Mesal protrusion, anellus and gnathos form a unique and complex dorsal suspension of the phallus. **(3)** Partial sclerotization of vesica forms funnel-shaped phallus apex.

  Notes: The genus comprises only four described species, two of which were described in the genus *Corticomis* VAN EECKE, 1924 **syn. nov.** and overlooked by subsequent authors. However, many undescribed species are represented by single specimens in collections around the world. The Brandt collection in the ANIC contains numerous very similar species, which are part of an extensive species complex around *Pseudodreata strigata / aroa*, rivalling the species complex around *Colussa astata / acuta / ekeikei* in complexity and possibly species number.

  Morphologically, male genital structures are very constant, possessing a unique and complex modification of the phallus support, but are very simple in all other aspects. Unlike genital structures, the habitus is extremely variable within this genus, ranging from fragile, small-bodied, large-winged moths to large and stout-bodied. Within the genus a probably monophyletic group of species (including the type species of *Pseudodreata*) can be defined by a pattern of the hind wing colouration unique for Anthelidae and a more extensive dorsal fusion of the uncus lobes. However, while the remaining taxa (including the type species of *Corticomis*) are characterized by a crenulate postmedian band in the fore wing and shorter as well as less extensively fused uncus lobes, these characteristics are unlikely to represent apomorphies and hence a separation of *Pseudodreata* and *Corticomis* would possibly render the latter paraphyletic, which is why I propose to synonymize *Corticomis* with *Pseudodreata*.

  Pseudodreata (as well as *Corticomis*) is endemic to New Guinea, where it occurs over the entire longitudinal range as well as over a large altitudinal range, from sea level to at least as high as 3500m. Despite the genus being widespread and rather regularly collected, females are relatively scarce in collections and the pre-imaginal instars are entirely unknown.

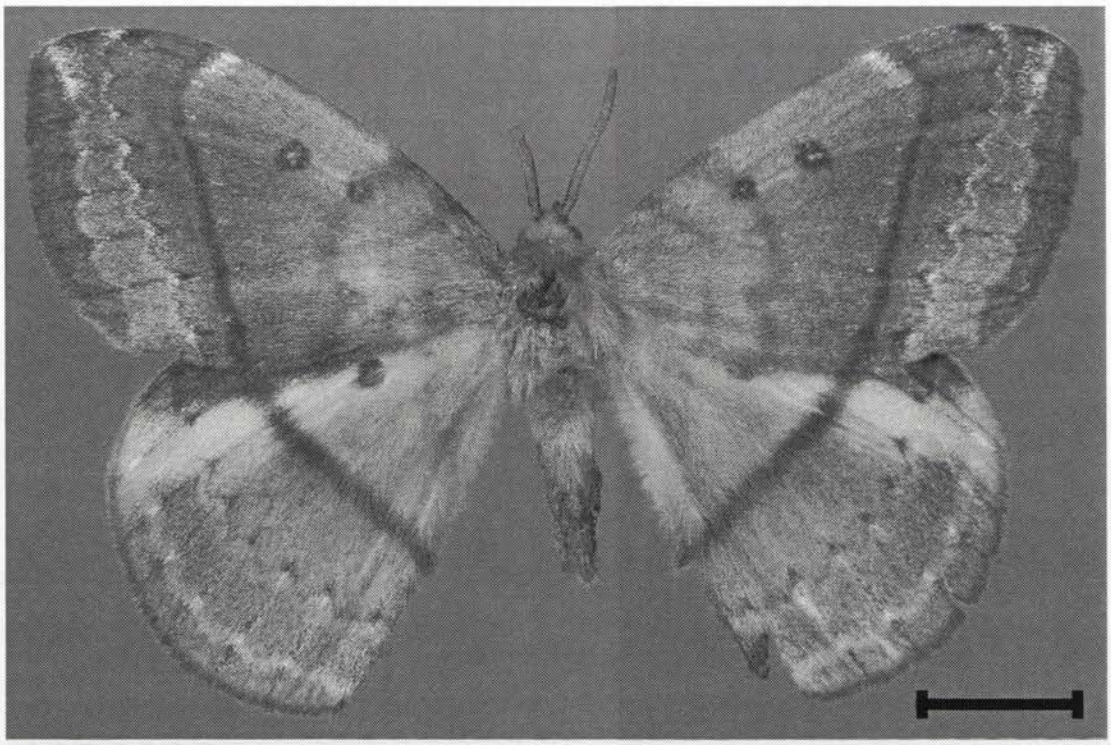

Fig. 407: *Pseudodreata strigata* BETHUNE-BAKER, 1904, Holotype (NHM, London), ♂ (PNG, Dinawa) – type species of *Pseudodreata* BETHUNE-BAKER, 1904 [scale bar = 1cm].

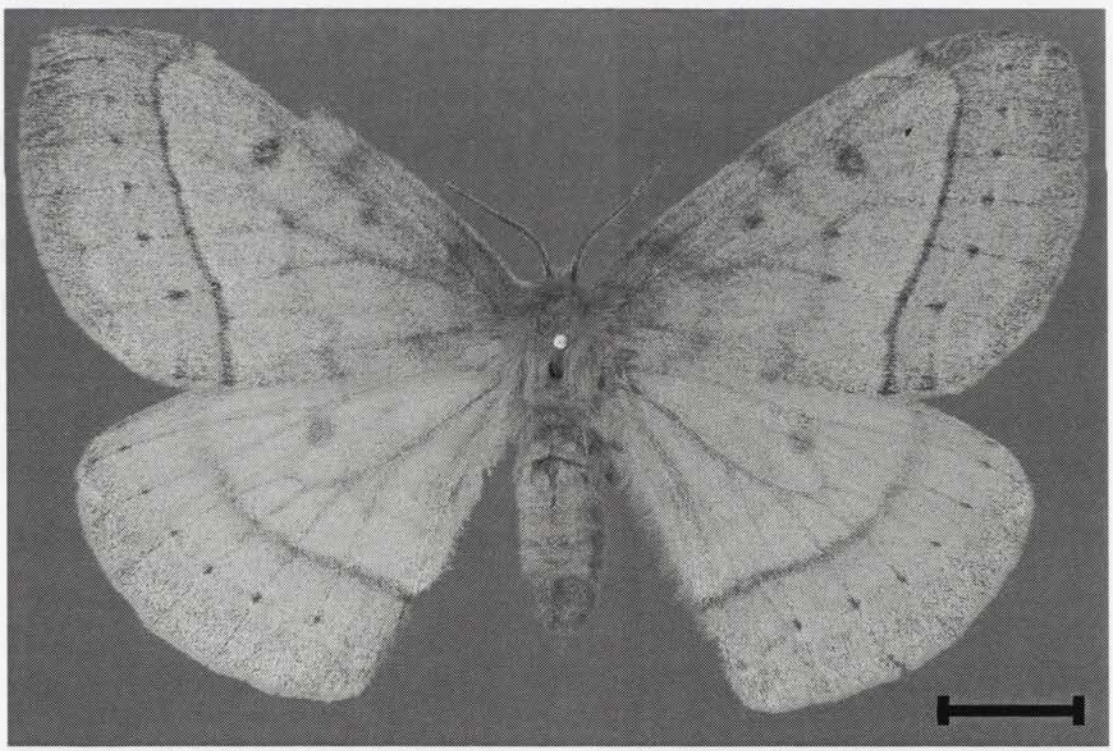

Fig. 408: *Pseudodreata strigata inconstans* (JOICEY, NOAKES & TALBOT, 1915), Paralectotype (NHM, London), ♀ (Indonesia, New Guinea, Arfak Mtns, Angi Lakes) – probably similar to the nominate subspecies, which is the type species of *Pseudodreata* BETHUNE-BAKER, 1904 [scale bar = 1cm].

- **"Genus novum 2"**

  Proposed type species: undescribed ["Anthelinae n. sp." (Figs 409, 410)].

  Autapomorphies: **(1)** Fore wing with a subapical protrusion. **(2)** Mesal side of valva with a uniquely shaped transverse ridge (forming two flattened protrusions, orientated at right angle to each other) **(3)** Shape of dorso-laterally protruding uncus lobes **(4)** Shape of the valva apodeme lobe (flat and ventrally up-curved).

  Notes: This monotypic genus includes a very unusual species, which has several unique modifications, but at the same time retains several plesiomorphic characteristics lost or modified in most other antheline species. Apomorphy (1) is shared with *Chenuala heliaspis*, but *ad hoc* assumed to be a convergence due to a conflict with another character (see section III.7.1). Molecular analyses either do not resolve the relationship of this species with *C. heliaspis* and others, or group it together with *C. heliaspis*. The latter appears to be caused by saturation in third codon positions (see section V.4.1.4). While monotypic genera are meaningless, I suggest placing this species in a genus of its own to allow the separation of the remaining Anthelinae into monophyletic groups. Being monotypic, the apomorphies of the species and genus are identical.

  The species seems to occur only in rainforest areas of northern QLD (Cooktown to Ingham, including the Atherton and Windsor Tableland). Numerous specimens are held in the ANIC, UQIC and QM, almost all of them being an in colouration variable series of males. Only three female specimens are known (in the ANIC and UQIC), which in appearance are somewhat similar to some females of the genus *Colussa*. The pre-imaginal instars are unknown.

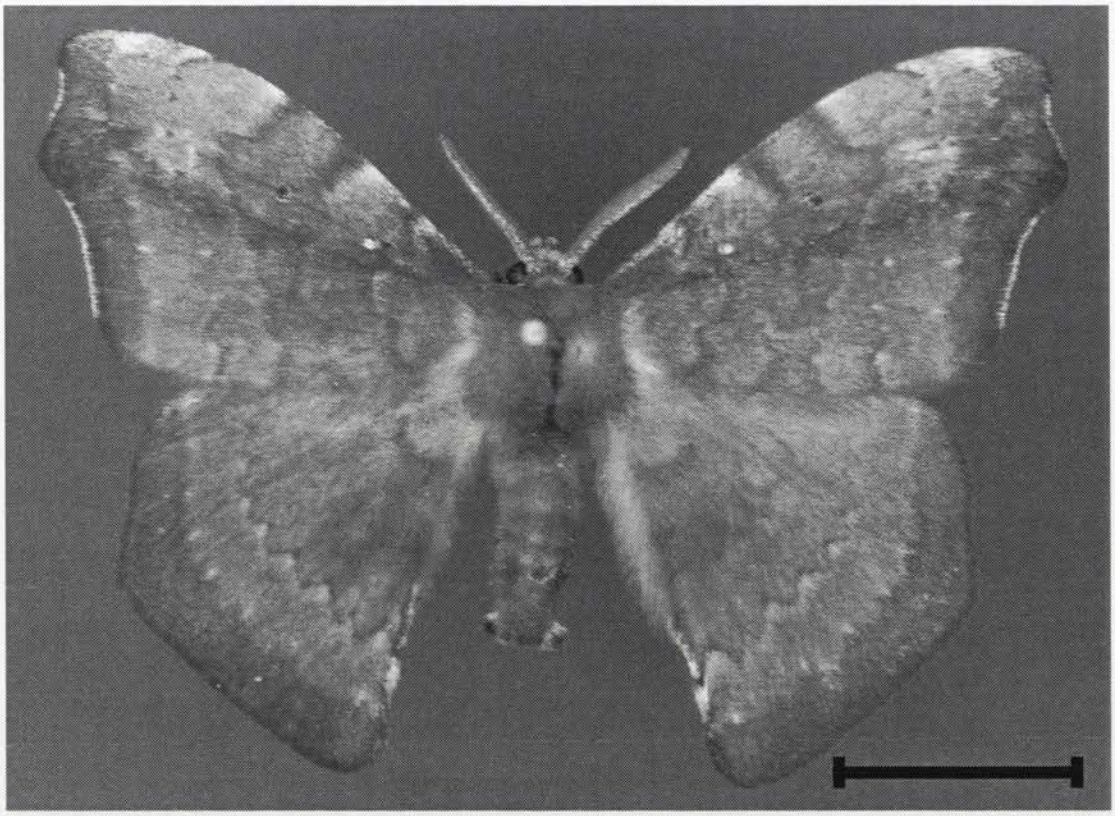

Fig. 409: "Anthelinae n. sp.", ♂ (QLD, 21km S Atherton) – proposed type species of "Genus novum 2" [scale bar = 1cm].

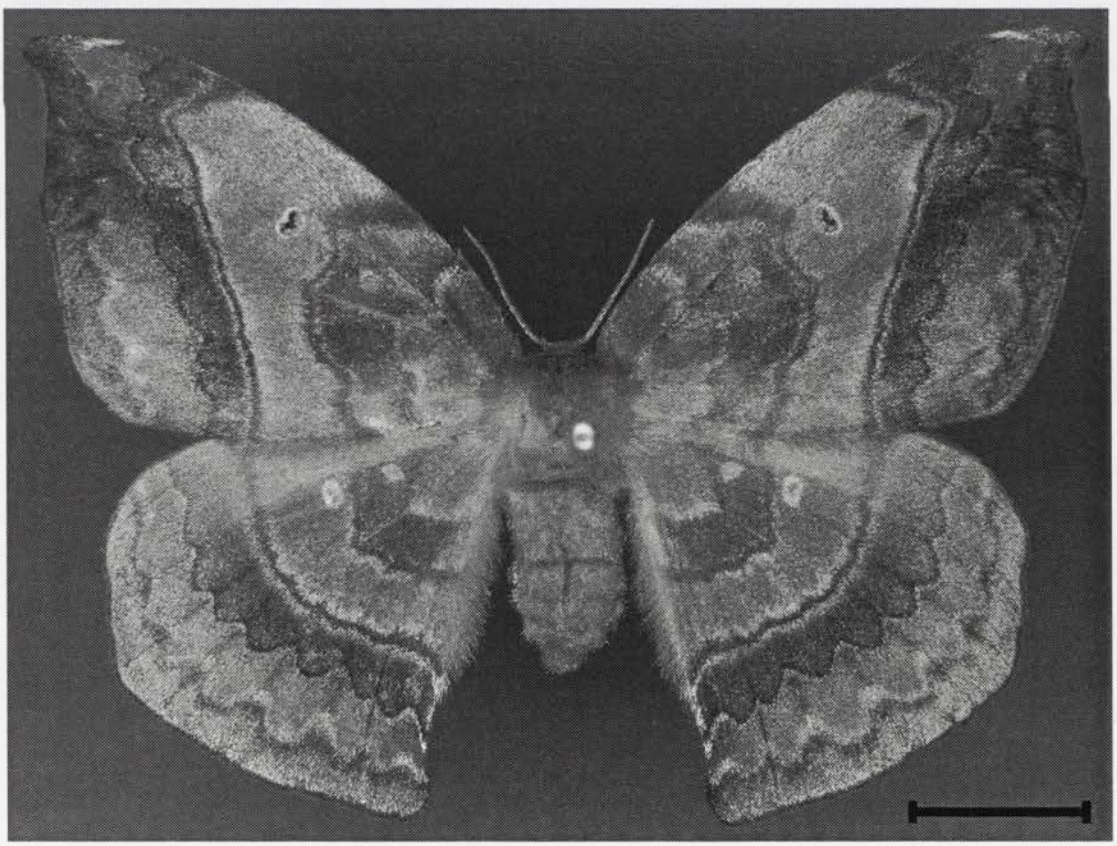

Fig. 410: "Anthelinae n. sp.", ♀ (QLD, SW Mossman, 25km on Mt. Lewis Rd) – proposed type species of "Genus novum 2" [scale bar = 1cm].

- ***Chenuala* SWINHOE, 1892**

  Type species: *Chenuala rufa* SWINHOE, 1892 (Figs 411, 412), a subjective junior synonym of *Ocneria heliaspis* MEYRICK, 1891.

  Autapomorphies: **(1)** Fore wing with a subapical protrusion. **(2)** Shape of the valva apodeme lobe (huge, dorso-ventrally expanded, distally wider than basally).

  Notes: As in the preceding genus apomorphy (1) is not unique, but shared with "Genus novum 2" (see above). The valva apodeme lobe has a very unusual shape (different from "Genus novum 2"), which is why the species is not included in the larger monophylum defined by the at roughly 45° protruding valva apodeme lobe.

  The species occurs along the East coast and Tablelands from southern QLD to VIC. Older caterpillars are occasionally found on *Eucalyptus* trees or wandering around prior to pupation.

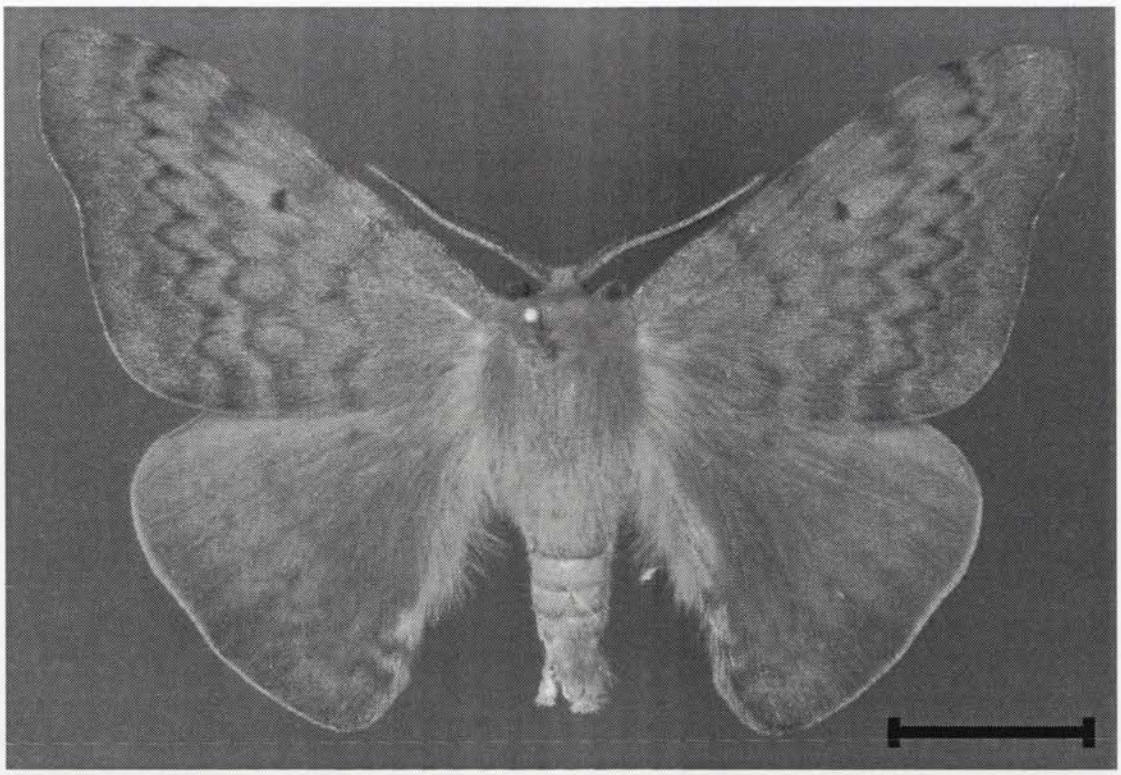

Fig. 411: *Chenuala rufa* SWINHOE, 1892 [= *Chenuala heliaspis* (Meyrick, 1891)], ♂ (VIC, Moe) – type species of *Colussa* WALKER, 1860 [scale bar = 1cm].

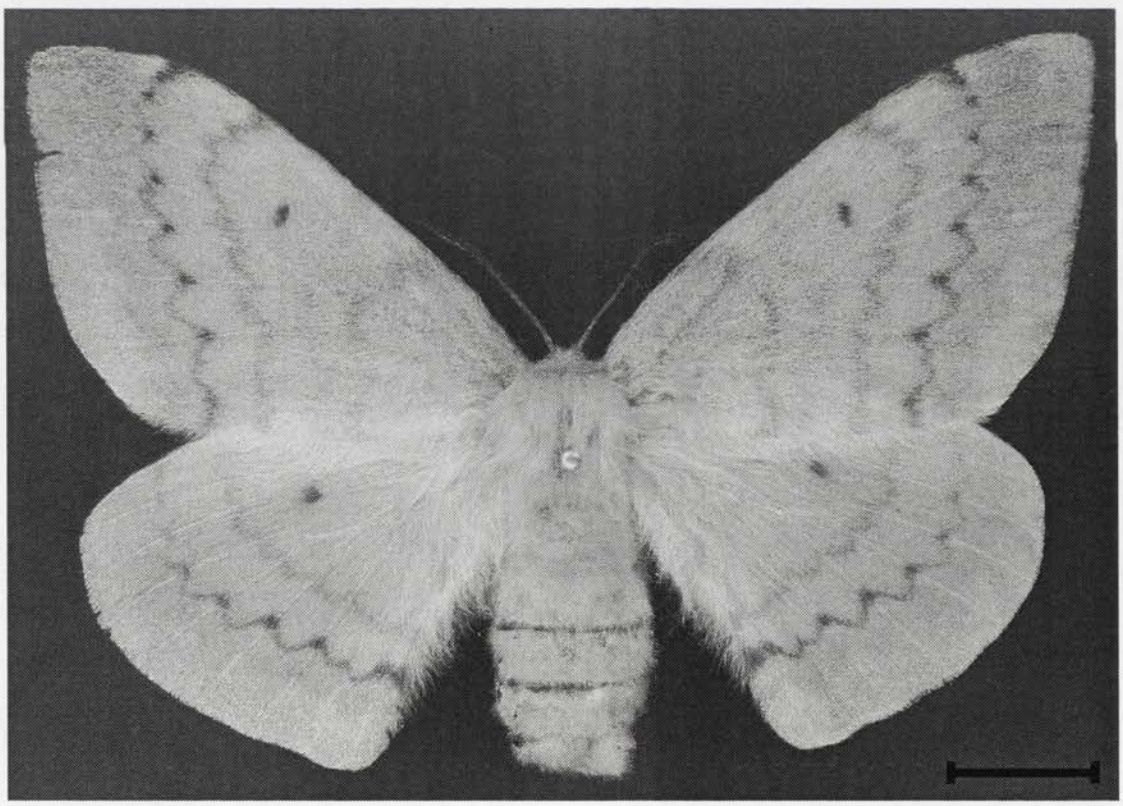

Fig. 412: *Chenuala rufa* SWINHOE, 1892 [= *Chenuala heliaspis* (Meyrick, 1891)], ♀ (NSW, 2.7km NE Queanbeyan) – type species of *Colussa* WALKER, 1860 [scale bar = 1cm].

- ***Pterolocera* WALKER, 1855**

Type species: *Pterolocera amplicornis* WALKER, 1855 (Figs 413, 414).

Autapomorphies: **(1)** Cocoon with exit tube in a vertical shaft in the soil.

Notes: The genus comprises eight currently recognized species, but many undescribed sibling species exist. Due to wingless females and the increasing patchiness of native grasslands in SE Australia gene-flow between populations is likely to be very limited for some species, which makes the occurrence of allopatric speciation likely. However, the habitat was probably less fragmented in the past and minor differences in habitus might be caused by genetic drift within currently small populations, which is part of the ongoing speciation process and makes the delineation of species very difficult.

The majority of species within this genus forms a monophyletic group, which is very well supported by molecular characters and apomorphies of male genital structures (the shape of the fused uncus lobes in particular), the apterous females and the particular arrangement of short spines in caterpillars (dense "cushions", which differ in extent, orientation and hair structure from character H.(1)). These apomorphies are in stark contrast to the conditions in *Pterolocera isogama* and an undescribed sibling species, which have very different male genital structures (of a type shared by members of several genera, e.g., *Darala ostra* and *Newmania clementi*, and probably representing the plesiomorphic condition for these genera). Further, their caterpillars seem to lack hair cushions and the females are fully winged. Probably, these species had originally been placed into the genus *Pterolocera* because of the habitus of the males, which have very prominent antennae with long rami and almost semi-transparent wings with strongly protruding veins (not all species). However, the latter condition is also typical of many anthelid females of other genera (e.g., *Pseudodreata aroa, N. clementi* and "Gen. nov. 3" *pudica*). The length of male antennal rami is linked to the search for pheromone releasing females, and similarly prominent antennae have evolved numerous times in some taxa of different lepidopteran families in Australia (e.g., Cossidae and Notodontidae) as well as in some other Anthelidae (e.g., "Gen. nov. 3" *pudica*; not obvious in dried collection specimens). The unique cocoon is, in my opinion, the only convincing apomorphy of this genus (no specimens of *P. isogama* were available for molecular studies), but the occurrence of such a cocoon in *P. isogama* is so far only known from a publication

by McGauran (1951). While she gave detailed descriptions of the cocoon and made a drawing of the adults, of which the male specimen resembles a typical *Pterolocera* spp., the specimens sent to the ANIC for identification were not the ones bred. This introduces some uncertainty to the identity of the species she bred, but her hand drawings clearly indicate that she did breed a *Pterolocera* species with fully winged females and the cocoon typical of the genus.

The genus occurs predominantly in the southern half of Australia, ranging from southern WA through SA, VIC, TAS and NSW to about the border of NSW and QLD; I am not aware of records from the dry interior. Caterpillars can be abundant and are more frequently encountered than the adults, which have a rather short flight period, often triggered by a drop in temperature and/or the onset of rains in autumn.

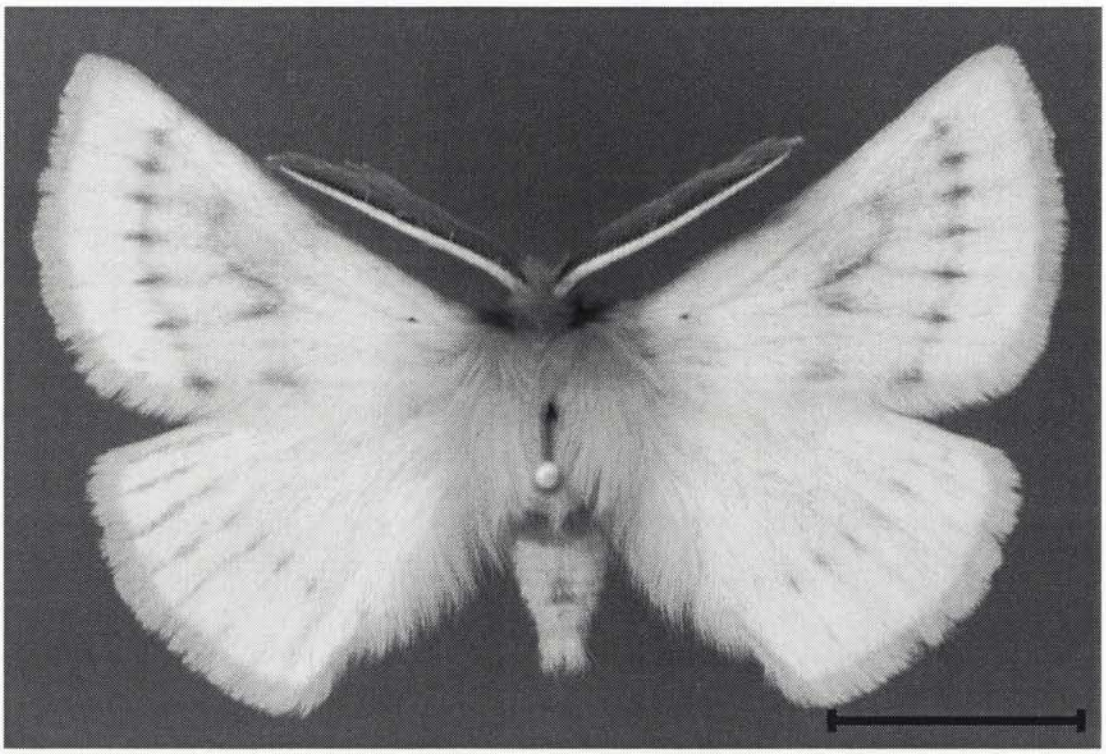

Fig. 413: *Pterolocera* sp. near *amplicornis* WALKER, 1855, ♂ (NSW, 3km EbyS Cooma) – *P. amplicornis* is the type species of *Pterolocera* WALKER, 1855 [scale bar = 1cm].

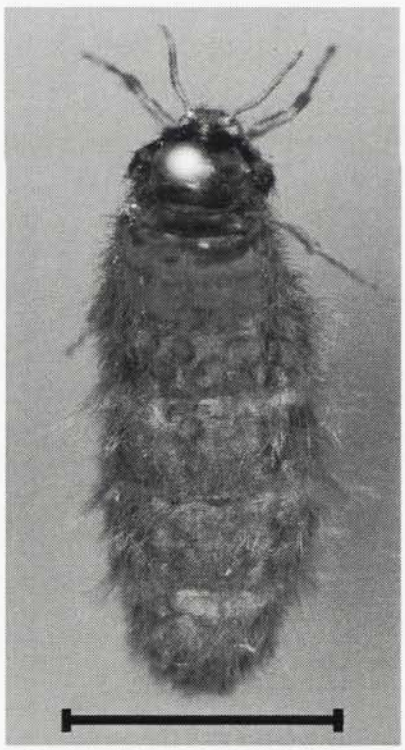

Fig. 414: *Pterolocera* sp. near *amplicornis* WALKER, 1855, ♀ (NSW, 3km EbyS Cooma) – *P. amplicornis* is the type species of *Pterolocera* WALKER, 1855 [scale bar = 1cm].

- ***Darala* WALKER, 1855, stat. rev.**

  Type species: *Darala ocellata* WALKER, 1855 (Figs 415, 416).

  Autapomorphies: **(1)** Apex of phallus curved dorsad. **(2)** Extreme reduction or loss of valva apodeme lobe, which occurs in combination with a seemingly unique slight ventro-anteriad angling of the valva apodeme apex.

  Notes: The genus includes only six currently recognized species, of which *D. ocellata* is likely to form a small complex of sibling species. Unlike other members of this genus, this species group seems to be rather variable in colouration and wing pattern, as well as colouration of the caterpillars. Further, the male genital structures are relatively simple, which adds to the difficulties of a sound taxonomic revision of this potential species complex. The use of molecular characters as an additional tool is an obvious choice for this group. In addition to these cryptic species, a small, brownish species from the Alice Springs area (NT; housed in the ANIC) should be included in *Darala*.

  The monophyly of this genus is well supported by the above autapomorphies and strongly supported by the analyses of molecular characters. However, some of the critical taxa were not available for sequencing, e.g., *D. ostra* and the undescribed species from the Alice Springs area. Only the caterpillars of *D. ocellata*, *D. cnecias* and *D. oressarcha* are known. All of them have not only a pair of white hair brushes on A1 only, but on every other abdominal segment, too, which is a synapomorphy of this group and potentially of all members of the genus.

  The genus is widespread in Australia. The species group around *D. ocellata* occurs from QLD through NSW, VIC, TAS, SA to WA, but not in the dry interior. The obviously closely related species *D. cnecias* and *D. oressarcha* occur on the higher mountains and parts of the Tablelands of south-eastern NSW and in Tasmania. In contrast, *D. ostra* (flood plains SE of Darwin) and the undescribed species from the Alice Springs area are only known from a few specimens and locations in the NT.

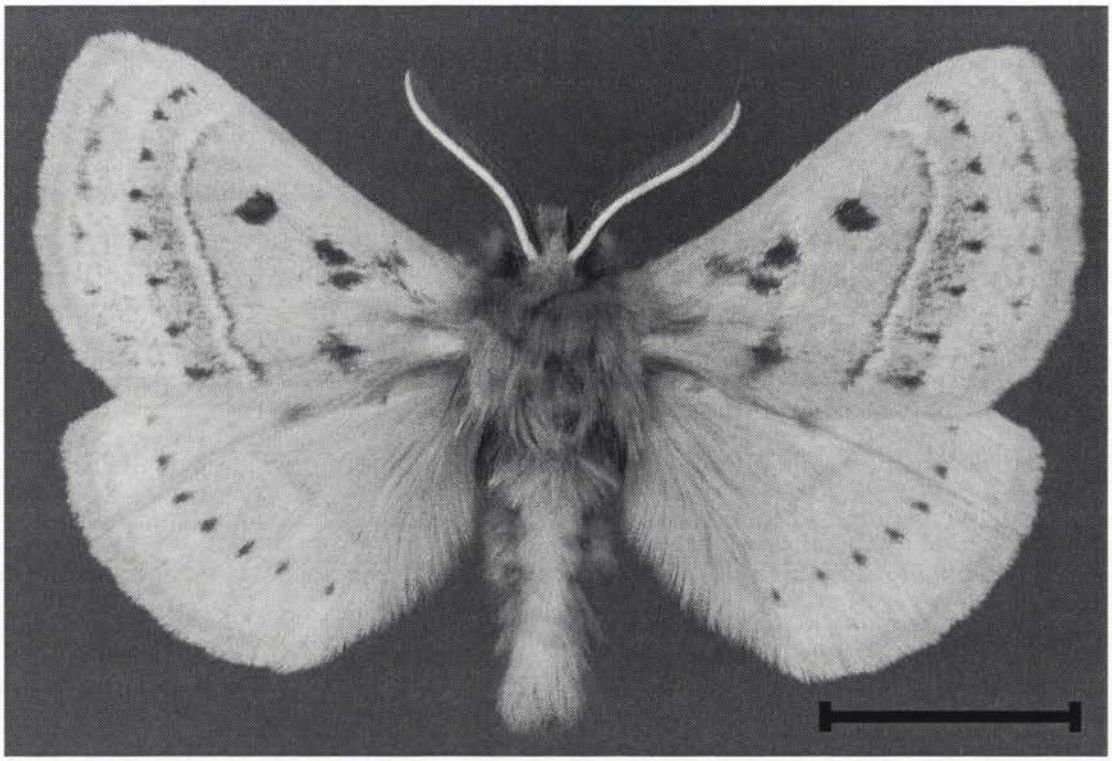

Fig. 415: *Darala ocellata* WALKER, 1855, ♂ (NSW, Wollongong) – type species of *Darala* WALKER, 1855 [scale bar = 1cm].

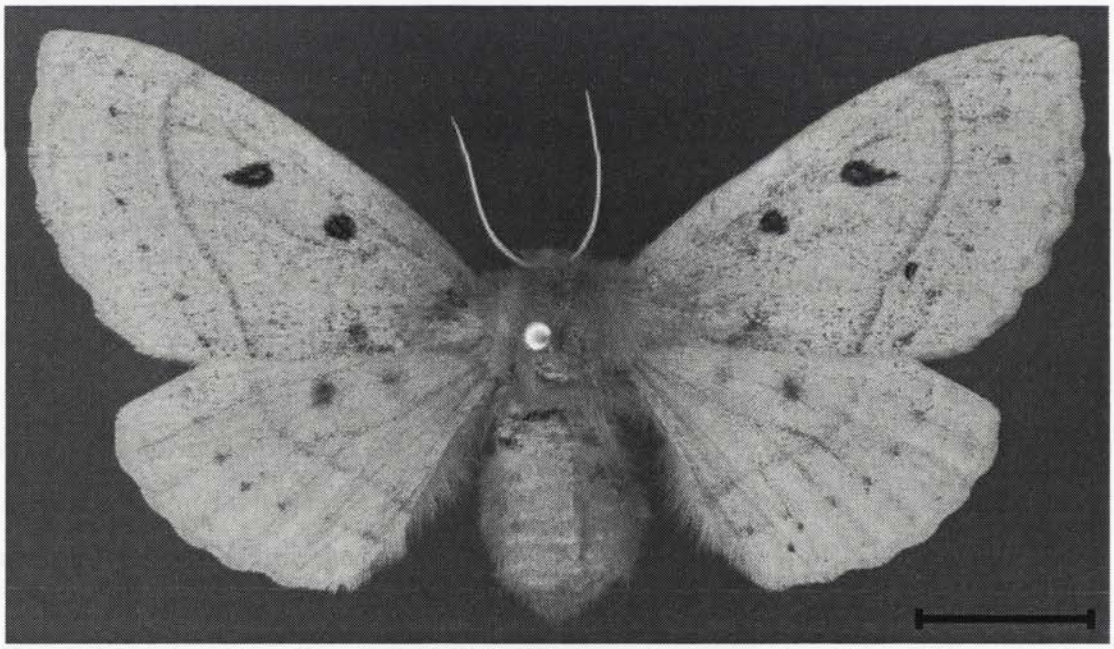

Fig. 416: *Darala ocellata* WALKER, 1855, ♀ (NSW, Caparra) – type species of *Darala* WALKER, 1855 [scale bar = 1cm].

- ***Newmania* SWINHOE, 1892, stat. rev.**

  Type species: *Teara guenei* NEWMAN, 1856 (Figs 417, 418).

  Autapomorphies: **(1)** Specialized setae with barbs restricted to the apex [caterpillar].

  Notes: The genus comprises nine recognized species and an undescribed species similar to *N. heliopa*. Most of these species are superficially quite different, e.g., *N. rubescens* is plain red, *N. callileuca* plain white with two black rings and *N. guenei* dark brown with two large white spots. The monophyly of the genus is only moderately supported by the above autapomorphy, but well supported by molecular characters (EF1a; not all members of the genus were available). Within the genus two encaptic monophyla that include the seemingly different taxa are well supported by other synapomorphies as well as molecular characters. In contrast, the inclusion of *N. exoleta* and *N. heliopa* in *Newmania* should be considered tentative as the caterpillars of these two species are unknown. However, their male genital structures match the other taxa in details of the shape of the valva apodeme lobe, and I know of no structural details that would argue against their inclusion in *Newmania*.

  With the exception of *N. guenei*, the genus occurs in very dry areas of all Australian states other than TAS. In contrast, *N. guenei* is restricted to the East coast and coastal slopes of the Tablelands of NSW and southern QLD; a single female specimen from south-eastern SA is present in the South Australian Museum.

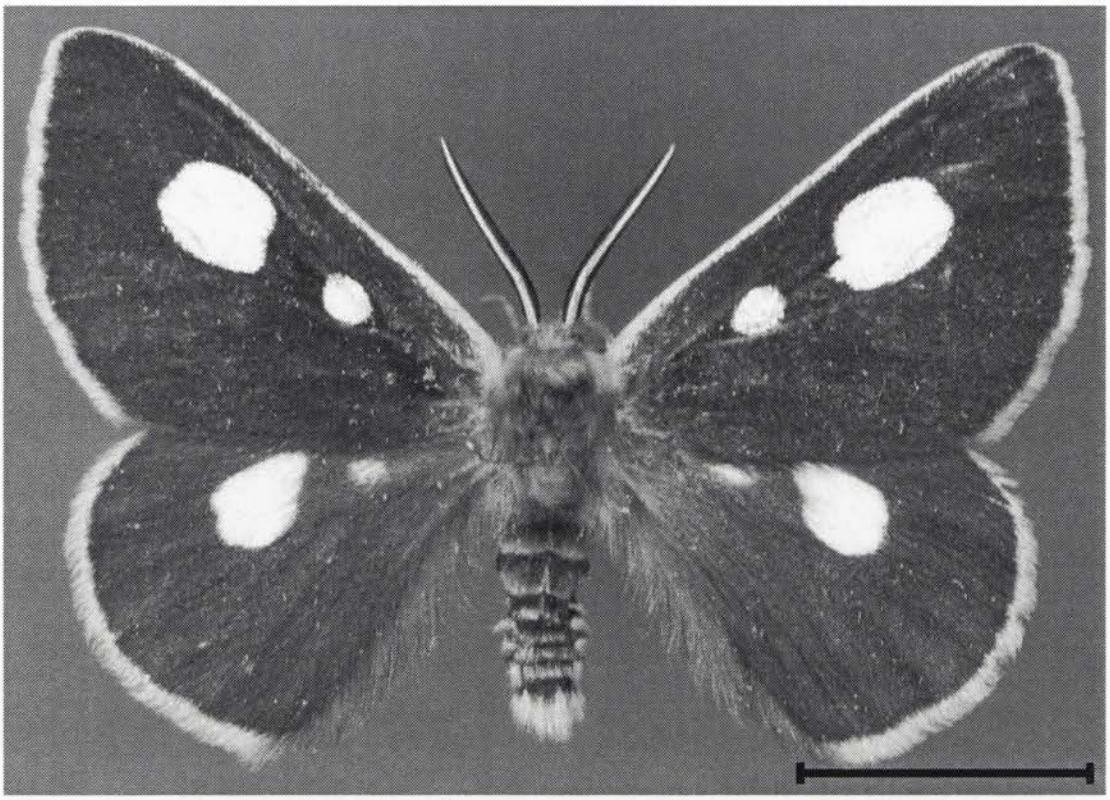

Fig. 417: *Teara guenei* NEWMAN, 1856, ♂ (NSW, CSIRO Exp. Farm Wilton) – type species of *Newmania* SWINHOE, 1892 [scale bar = 1cm].

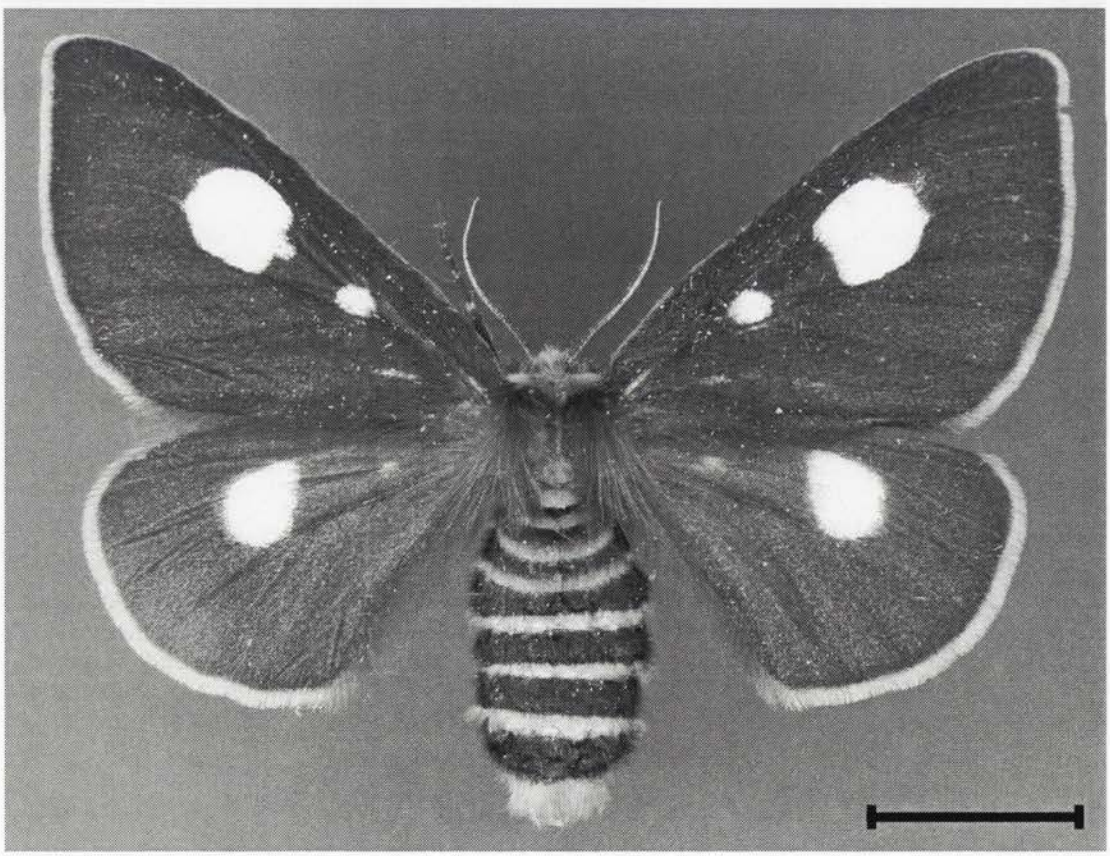

Fig. 418: *Teara guenei* NEWMAN, 1856, ♀ (NSW, CSIRO Exp. Farm Wilton) – type species of *Newmania* SWINHOE, 1892 [scale bar = 1cm].

- ***Omphaliodes* FELDER, 1874**

Type species: *Omphaliodes nana* FELDER, 1874, which is a subjective junior synonym of *Trichiura obscura* WALKER, 1855 (Fig. 419).

Autapomorphies: **(1)** Conical valva apodeme lobe shifted distally on valva. **(2)** Uncus lobes widely separated and reduced to two slender, pointed prongs. **(3)** Fore wing with Rs2 and Rs3 not touching ("opening" of the areole).

Notes: This currently monotypic genus actually consists of a small complex of sibling species with at least two undescribed species in WA, which can be distinguished by differences in the shape of the valva apodeme lobe and possibly wing pattern in one case (variations in pattern and colouration exist within the species). EF1a sequences of 658bp length differed in 32bp (4.9%) between two of these species (one from western NSW, the other from southern WA).

The relationships of this genus within the Anthelinae are uncertain. Its species have strongly reduced valvae and modified uncus lobes, obscuring many of the characters used for other taxa. Further, despite males coming frequently to light, the females are still unknown and possibly apterous. A single caterpillar has been reported by Jenkins (2005), but I have not seen any caterpillars so far.

The genus is widespread in dry and semi-arid areas of NT, QLD, NSW, VIC, SA and WA.

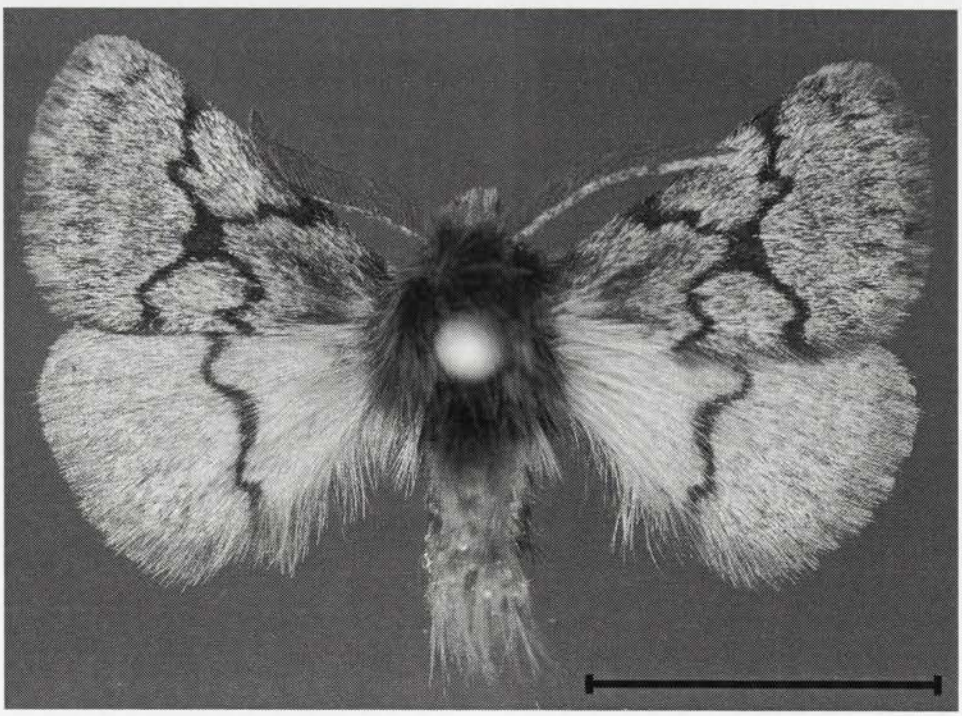

Fig. 419: *Omphaliodes nana* FELDER, 1874 [= *Omphaliodes obscura* (WALKER, 1855)], ♂ (SA, 50mi E Nullabor) – type species of *Omphaliodes* FELDER, 1874 [scale bar = 1cm].

- **"Genus novum 3"**

  Proposed type species: *Anthela neurospasta* TURNER, 1902 (Figs 420, 421).

  Autapomorphies: **(1)** Fused uncus lobes form a ventral blade.

  Notes: The genus includes only six recognized species, but male genital preparations and details of antennal structures indicate that "Gen. nov. 3" *phoenicias* consists of a widespread complex of numerous cryptic species, as does – to a lesser extent – "Gen. nov. 3" *pudica*.

  The monophyly of the genus is moderately supported by the above autapomorphy, while a subordinate monophylum exclusive of "Gen. nov. 3" *neurospasta* and "Gen. nov. 3" *achromata* is very well supported by other apomorphies. Sequences of only two representatives were available, both being part of the well supported monophylum and always very strongly supported as sistergroup taxa.

  The genus is widespread in dry and semi-arid areas of NT, QLD, NSW, VIC, SA and WA. Further, specimens of "Gen. nov. 3" *neurospasta* and an undescribed species in the complex of "Gen. nov. 3" *phoenicias* have been collected in coastal heath of Papua New Guinea (in CPMB). A single specimen of "Gen. nov. 3" *achromata* from south-western Papua New Guinea is present in the Brandt collection of the ANIC, too.

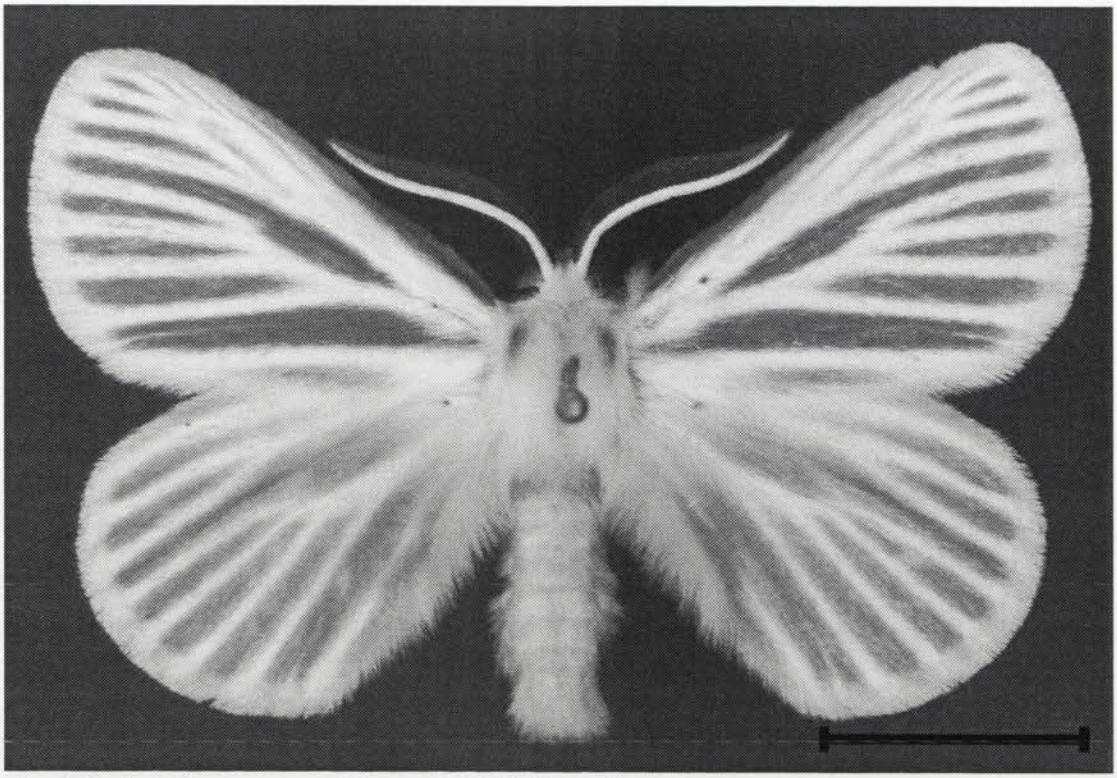

Fig. 420: *Anthela neurospasta* TURNER, 1902, ♂ (QLD, 8km W Dimbulah) – proposed type species of "Genus novum 3" [scale bar = 1cm].

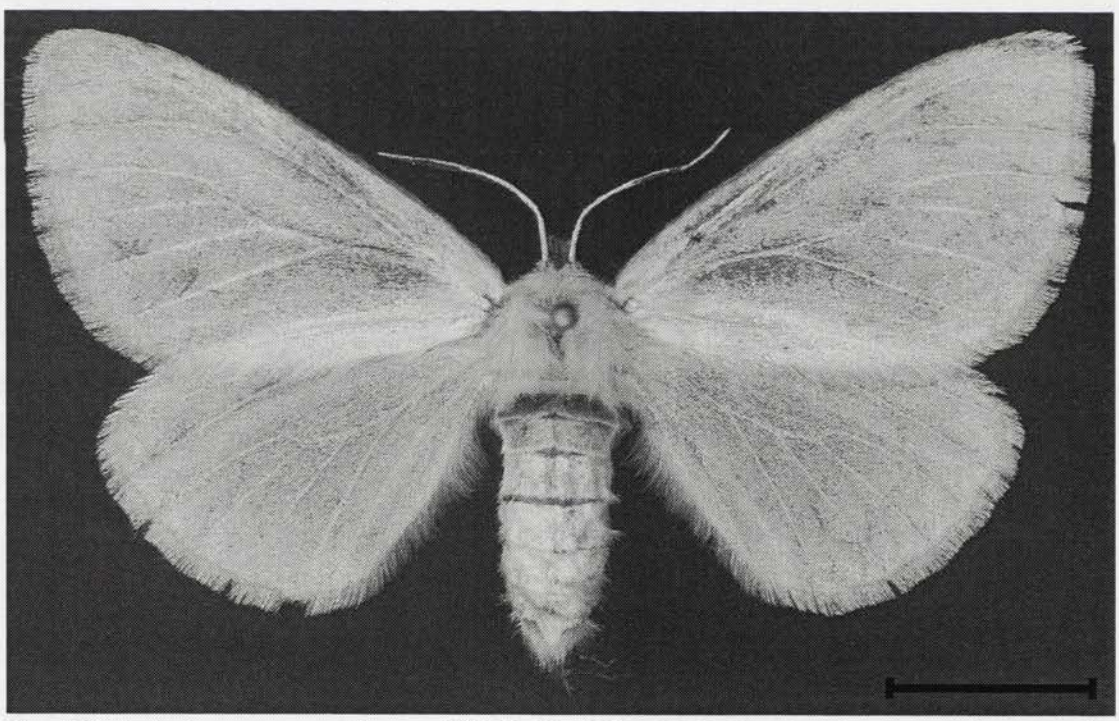

Fig. 421: *Anthela neurospasta* TURNER, 1902, ♀ (NT, 22km WSW Borroloola) – proposed type species of "Genus novum 3" [scale bar = 1cm].

- ***Nataxa* WALKER, 1855**

Type species: *Nataxa flavifascia* WALKER, 1855, a subjective junior synonym of *Perna flavescens* WALKER, 1855 (Figs 422, 423).

Autapomorphies: **(1)** Very long valva apodeme extends anteriad, and with it the valva apodeme lobe.

Notes: At present the genus *Nataxa* is very distinct and comprises only two recognized species. I propose to widen the genus to include numerous other species, which are superficially very different from these two species and which renders the genus externally indistinct. Obviously, this is not satisfactory. The reason for nevertheless doing so is that within a supported monophylum (the genus *Nataxa* [*sensu lato*]) some subordinate monophyla are more or less well supported (e.g., *Nataxa* [*sensu stricto*]), but their separation from *Nataxa s.lat.* would either cause paraphyly of the remaining group, or require splitting of the group into numerous smaller monophyla, some of which would be difficult to support (see section VII.3). Instead, I chose the compromise of including all these taxa in a larger genus, for which the name *Nataxa* is available. This ensures the monophyly of the genus and allows subsequent splitting if additional apomorphies for all subordinate monophyla become available. The monophyly of such a larger group is not only supported by the above autapomorphy, but also very well supported by molecular characters.

The proposed extension of *Nataxa* results in the inclusion of the following species groups, some of which are difficult to define as monophyla. A group consisting of the species from *N. asciscens* to *N. unisigna* in Appendix B, as well as several undescribed species, particularly from WA. Most species are easily recognizable as members of this group by habitus, and the two members of this group included in analyses of molecular characters formed a well supported monophylum. However, I have found it difficult to define the group other than by external similarities. Within this group a monophylum is supported by an apomorphic type of cocoon (hanging and, due to some substance, smooth-walled), but separating this monophylum would probably render the remaining group paraphyletic. Species of this group occur in dry inland areas of QLD, NSW, VIC, SA, WA and NT.

N. tetraphrica and three undescribed species from WA form a second species group that is difficult to define other than by similar wing pattern and maybe the rather shallow valva apodeme lobe. They, too, inhabit dry areas of WA, SA, VIC, NSW and

possibly QLD.

The remaining species, namely *N. excellens* and an undescribed sibling species, *N. nicothoe*, *N. connexa*, *N. allocota, N. flavescens* and *N. amblopis*, form a morphologically very well supported monophylum (coecum and phallus twisted clockwise in anterior view, with muscles *m5* crossing each other). This grouping is partly contradicted by molecular characters, which sometimes moderately to well support a grouping of *N. excellens* with the first species group (represented by *N. stygiana*) and a sistergroup relationship between *N. nicothoe* and *N. flavescens*. These species groups are externally as indistinct as the proposed concept of *Nataxa s.lat.*. Unlike the other species groups inhabiting dry areas, this group occurs along the East coast and the Tablelands of QLD, NSW and VIC, and in the case of *N. nicothoe* extends into TAS (possibly an undescribed sibling species).

Within this latter species group *N. flavescens* and *N. amblopis* (=*Nataxa s.str.*) form a very well supported monophylum. Synapomorphies of these species are the formation of two tubular spines on the vesica, the displacement of muscle m7, the unique loss of vein CuA1 in the hind wing, the reduction of D2 in older caterpillar instars and the presence of a pair of anteriad orientated hair brushes on lateral protrusions of T1 in the caterpillar. However, maintaining a generic rank for this species group would require the description of all species groups as genera, including the placement of *N. excellens* in a monotypic genus.

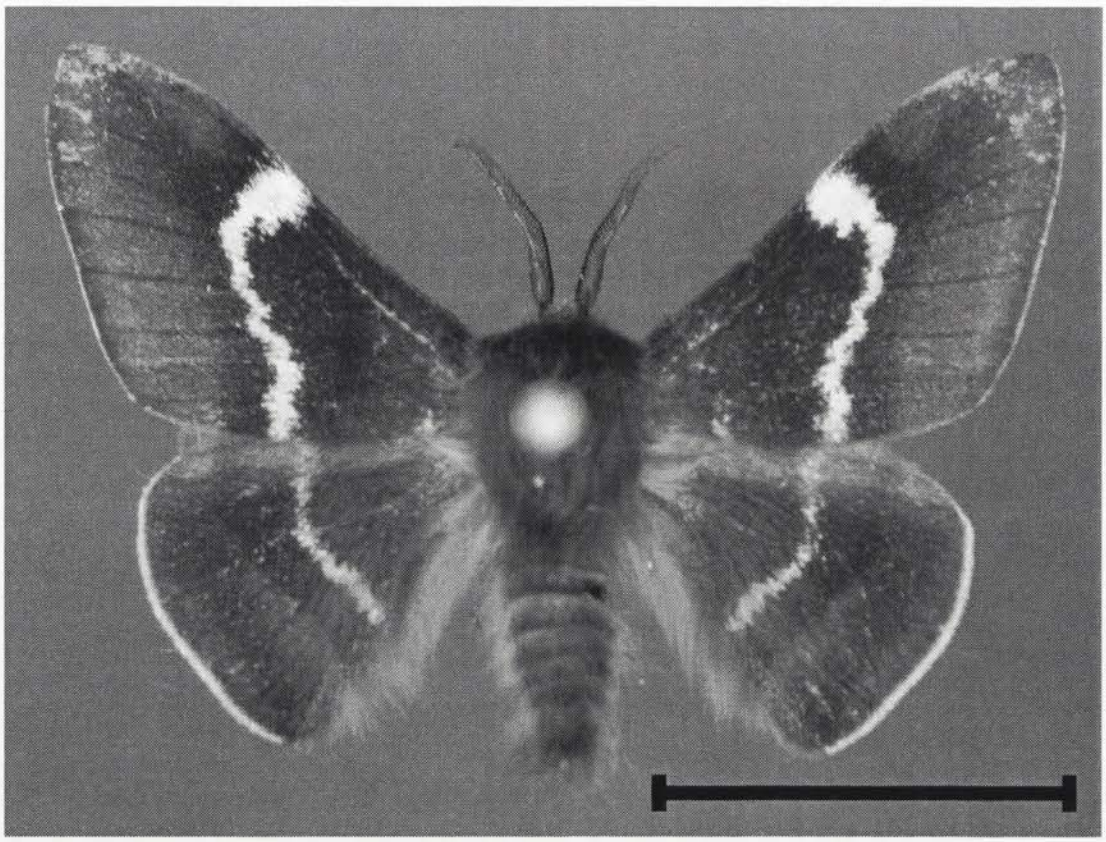

Fig. 422: *Nataxa flavifascia* WALKER, 1855 [= *Nataxa flavescens* (WALKER, 1855)], ♂ (ACT, Macquarie) – proposed type species of *Nataxa* WALKER, 1855 [scale bar = 1cm].

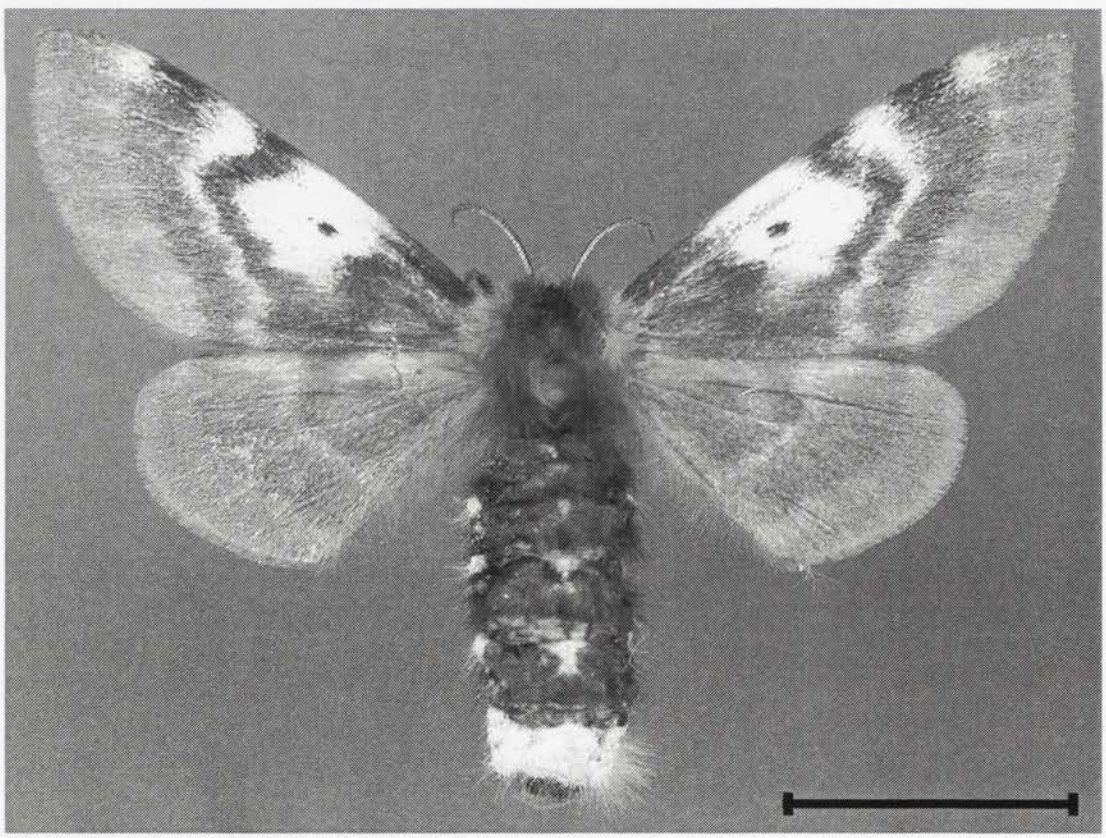

Fig. 423: *Nataxa flavifascia* WALKER, 1855 [= *Nataxa flavescens* (WALKER, 1855)], ♀ (ACT, Cotter Dam) – proposed type species of *Nataxa* WALKER, 1855 [scale bar = 1cm].

VII.3.2) Subfamily classification of Anthelidae

The current separation of the Anthelidae into two subfamilies, Anthelinae and Munychryiinae, stems from the separation of the genera *Munychryia* and *Gephyroneura* from the remaining Anthelidae by Common and McFarland (1970). Like Turner (1920a, 1921b) they noted several peculiarities of these two genera, only some of which are apomorphies. The highly adapted caterpillar of *Munychryia* was used in particular to justify the erection of a new subfamily, Munychryiinae COMMON & MCFARLAND, 1970, even though the caterpillar of the very similar monotypic genus *Gephyroneura* was only assumed to be the same. As a consequence, the monophyly of Munychryiinae is supported by a few apomorphies, while none have been proposed for the Anthelinae.

My Hennigian Argumentation as well as cladistic analysis of morphological characters support the monophyly of both subfamilies. Due to the addition of a previously unknown taxon ("Genus novum 1") to the Munychryiinae, the monophyly of this subfamily is less convincingly supported than it was for the superficially very similar genera *Munychryia* and *Gephyroneura* alone. The proposed autapomorphies of this subfamily are now limited to the presence of a unique cornutus (see character H.32 (1); *ad hoc* assumed assumed to be lost in *Gephyroneura*), because the previously used extension of the sclerotization of the cross-fold in the radius sector (character H.49(1)) is absent in "Genus novum 1" as well as in Anthelinae. The caterpillars, when finally known, are likely to provide additional, excellent apomorphies of the Munychryiinae (see section VII.3.1: *Munychryia*). No specimens of "Genus novum 1" were available for sequencing, which is why the strong support provided by molecular characters is restricted to the monophyly of *Munychryia* + *Gephyroneura*.

Unlike the Munychryiinae, the monophyly of the Anthelinae is supported by a large number of autapomorphies (H.1(1), H.11(1), H.39(1), H.44(1), H.58(1), H.61(1) and H.62(1)), of which the presence of minute vesicles on the integument is exceptionally convincing. Molecular characters strongly support the monophyly of the majority of Anthelinae, but fail to resolve the relationships between this monophylum, *Chelepteryx* and Munychryiinae. Hence, molecular characters do not provide support for the monophyly of the Anthelinae, but they do not contradict it either. This lack of support is likely to be due to the failure to sequence CPS for *Chelepteryx* and *Anthela*. The obtained EF1a sequences of *Chelepteryx* are very likely to be totally saturated in third codon positions at the level of divergence between Anthelinae and Munychryiinae,

which is why the relationships could not be resolved with EF1a sequences alone.

VII.3.3) Family classification of Anthelidae

Since the erection of the subfamily Anthelinae in the Lymantriidae by Turner (1904) and its subsequent elevation to family rank by Turner (1920a), the monophyly of this group of taxa has never been questioned in literature. This is probably due to Turner's definition of the group (1904) by the presence of unique modification in the fore wing radial sector, a "cross-bar" connecting Rs2 with Rs1. Minet (in Lemaire & Minet [1998]) subsequently proposed three additional autapomorphies for the family Anthelidae, but none of them are convincing (see section VII.1).

The monophyly of Anthelidae is supported in all of my molecular and morphological analyses, as well as by Hennigian Argumentation. Apart from the "cross-fold" in the radial sector, which was originally proposed by Turner (1904) and remains the most convincing autapomorphy of the family, I propose three new autapomorphies of the family Anthelidae:

- H.47(1): The formation of an areole by a sclerotization between, or the local touching of, Rs2 and Rs3 in the fore wing [not homologous with the condition present in some other Macrolepidoptera, e.g., some Noctuoidea].
- H.57(1): The triangular, pale frontal area of the caterpillar head capsule.
- H.67(1): The construction of a double-walled cocoon.

VII.3.4) Superfamily classification of the bombycoid complex

While it is not the aim of this thesis to propose a phylogenetic hypothesis for the entire bombycoid complex, hypotheses have to be formed to investigate the placement of the family Anthelidae within the Macrolepidoptera. The inclusion of the Anthelidae within the bombycoid complex had initially been proposed by Common (1966). Despite attempts by Minet (1991, 1994, in Lemaire & Minet [1998]) to define this complex by autapomorphies, the monophyly of the bombycoid complex remained poorly supported (see section VII.1). Hasenfuss (1999) was the first to propose a convincing autapomorphy for the complex, namely the presence of two layers of transverse microfibrils in the bending cuticle of the caterpillar proleg (H.66(1)). However, this condition remains to be checked in several families, including the critical Mimallonidae. Based on my studies I propose one additional autapomorphy of the bombycoid complex, namely the location of the fork in Rs1/Rs2 distally of the fork in Rs3/Rs4 in the fore wing (H.46(1)). Due to a modification in the radial sector of the fore wing, which approximates both forks, the inclusion of the Anthelidae within the bombycoid complex based on this apomorphy alone is not convincing. However, numerous other synapomorphies place the Anthelidae in monophyla with families that are clearly included in the bombycoid complex, thereby supporting the inclusion of the Anthelidae in the bombycoid complex.

Minet (1994) proposed a subdivision of the bombycoid complex into the monotypic Mimallonoidea, the Lasiocampoidea and the Bombycoidea. His concept of the Lasiocampoidea comprises the Anthelidae and the Lasiocampidae. As discussed in section VII.1, this sistergroup relationship between Anthelidae and Lasiocampidae is not convincingly supported. Instead, my studies support a placement of the Anthelidae within the Bombycoidea *sensu* Minet 1994, probably as the sistergroup of the Eupterotidae+Brahmaeidae/Lemoniidae (see section IV.1). By transferring the Anthelidae from the Lasiocampoidea to the Bombycoidea, the Lasiocampoidea become a monotypic superfamily within the bombycoid complex. Because monotypic taxa do not convey any phylogenetic information (even though they are often introduced to demonstrate the "remoteness" of a family from other families, e.g., Kuznetzov & Stekolnikov 1985, 2001) and in particular as the relationships between the three

superfamilies are not resolved, I propose to eliminate the monotypic superfamilies Mimallonoidea and Lasiocampoidea. Instead, I propose re-establishing the concept of Brock (1971) and to refer to the bombycoid complex sensu Minet 1994 as a single superfamily, the Bombycoidea.

Further, my studies raise doubts about the monophyly of some bombycoid families, namely the Bombycidae, Brahmaeidae and Lemoniidae (see section IV.1). However, my morphological studies did not focus on these groups and more detailed studies are needed before making any taxonomic changes! So far analyses of molecular characters indicate that the Apatelodinae are not a subfamily of the Bombycinae, as suggested by Minet (1994). Instead, they appear to be more closely related to the monophylum comprising Eupterotidae, Brahmaeidae and Lemoniidae, and their rank as a family might be restored. Further, analyses of molecular characters indicate the paraphyly of Brahmaeidae relative to Lemoniidae. While I did not study the phylogeny of these two families in detail, the unique wing pattern of Brahmaeidae alone argues against a transfer of *Dactyloceras* from the Brahmaeidae to the Lemoniidae. The alternative, to synonymize the Lemoniidae with the Brahmaeidae, seems to be advisable (also proposed by Oberprieler and Duke (1994) on different grounds). With the current attribution of family group name authorships, Brahmaeidae SWINHOE, 1892 would be the senior synonym over Lemoniidae HAMPSON 1918. However, the current attribution of authorship to Lemoniidae is incorrect as noted in the footnote of section I.3 and has to be resolved prior to determining the priority of the family group names Brahmaeidae or Lemoniidae.

VII.4) Conclusion

The critical review of literature on Anthelidae (section I.2) shows that our knowledge is rather limited and largely consists of poor species descriptions, limited morphological information and faunistic, medical, pest and host records. Most of this information suffers from unreliable species identifications or insufficient specificity to which taxa the studies are based on. Further, the critical review of literature on bombycoid phylogeny (section I.3 and Appendix P) demonstrates that our current phylogenetic concepts are base on very poorly or unsupported hypotheses of homology.

My own comparative morphological examinations (sections III.1-III.6) provide substantial, detailed new information for specified anthelid taxa (character matrix in Appendix N), in particular in the areas of antennal morphology, wing venation, male genital structures and their muscles, female reproductive organs and caterpillar mouth parts. Further, these sections (III.1-III.6) include new information on principal structures and their modifications in the bombycoid complex.

The molecular data (electronic appendix on the enclosed CDROM) are the only sequence data of Anthelidae available to date. Similarly, the sequence data of Eupterotidae and Carthaeidae are the first for these families. These data include a fragment of the CPS domain of the CAD gene, for which no lepidopteran sequences are available on GenBank so far. The CPS domain has been proven to be highly informative for the reconstruction of higher phylogenies of Diptera by Moulton and Wiegman (2004). My study demonstrates the superiority of this gene over frequently used genes (EF1a, COI & II, 28S, 18S and 12S) for lepidopteran phylogenies at the generic to family level in the bombycoid complex (sections V.1-V.3).

The development of phylogenetic hypotheses through Hennigian Argumentation, Maximum Parsimony, Maximum Likelihood and Bayesian Inference analyses (chapters III-VI) demonstrates the principle differences between these methods (see section II.4). Each of these methods has specific problems and limitations, which one has to be aware of for meaningful interpretation of the results (section VII.1.1). Likewise, the different data sets suffer from specific problems, in particular saturation in the case of molecular data and the abundance of reduction/loss of structures amongst morphological data (section VII.1.2). Nevertheless, the different methods of analysis of identical as well as different data sets (molecular and morphological characters) produce very similar

results, with the exception of the placement of and relationship between *Chenuala heliaspis* and an undescribed antheline species (section VII.1.3). All of the analyses failed to resolve relationships within Anthelinae completely, and the resulting large polytomy probably reflects rapid speciation. The summaries of all well supported nodes represent the first working hypothesis of anthelid phylogeny (section VII.1.3.1) and an alternative hypothesis of bombycoid phylogeny (section VII.1.3.2) to the proposal of Minet (1994).

Irrespective of polytomies and conflicting hypotheses, several monophyla are well supported and can be used for a revision of the current taxonomic classification of Anthelidae (section VII.3). The large genus *Anthela*, as perceived at present, is paraphyletic in respect to the currently recognized genera *Chenuala*, *Pterolocera*, *Omphaliodes*, *Nataxa* and *Corticomis*. Rather than to synonymize these genera with *Anthela*, I propose to split these genera into eleven monophyletic taxa (section VII.3.1), which brings the total number of proposed anthelid genera to fifteen. For most of these proposed genera names are already available (mainly subjective junior synonyms of *Anthela*), except for three unnamed genera (see Appendix B). Unfortunately, the proposed anthelid phylogeny is too poorly resolved to sensibly propose a tribal classification. In contrast, the monophyly of the two existing subfamilies Anthelinae and Munychryiinae is well supported (section VII.3.2), as is the monophyly of the family Anthelidae (VII.3.3). Further, the monophyly of the poorly defined bombycoid complex and the inclusion of the Anthelidae within it are supported by morphological characters (section VII.3.4). However, the proposed sistergroup relationship between Lasiocampidae and Anthelidae and the inclusion of the latter in the Lasiocampoidea (Minet 1994, Lemaire & Minet [1999]) is falsified. Alternatively, the Anthelidae are proposed as the sistergroup of the Lemoniidae/Brahmaeidae+Eupterotidae, and consequently I argue for the abolishment of the term "bombycoid complex" and for the synonymy of Lasiocampoidea and Mimallonoidea with Bombycoidea (section VII.3.4).

All proposed phylogenies require testing by attempting to falsify them through addition of new, independent data (section VII.2). For such future data I propose to focus on the generation of additional molecular data (in particular the extension of CPS sequences and other genes), the inclusion of taxa currently unavailable for sequencing (specifically the endemic New Guinean genus *Pseudodreata*, as well as the Australian *Pterolocera isogama* and the undescribed munychryiine species from WA), a more

detailed study of the at present largely unknown pre-imaginal instars and comparative morphological studies of internal organs of imagines. Further, the study of the antheline caterpillar vesicles, in particular their fine structure and contents, seems a very interesting area with potential future technical application (extreme strength of the adhesion). If attempts to falsify the phylogenetic hypotheses presented in this dissertation will fail, the proposed phylogeny-dependent classification (Appendix B) could serve as a framework for urgently needed alpha-taxonomic revisions of the numerous species complexes.

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APPENDIX A:

SYNONYMIC SPECIES LIST

[Currently accepted genera on red background.]

[Non-Australian taxa on cyan background.]

genus	species	synonym	author	year	orig. comb.	notes
MUNYCHRYIA			Walker	1865		type species: *M. senicula* Walker, 1865
		MUNYCHRYTA	Turner	1920		misspelled
		MUNICHRYIA	Turner	1921		misspelled
Munychryia	*senicula*		Walker	1865	*Munychryia*	
		nyssiata	Felder & Rogenhofer	1875	*Hypochroma*	
Munychryia	*periclyta*		Common & McFarland	1970	*Munychryia*	
GEPHYRONEURA			Turner	1920		type species: *G. cosmia* Turner, 1921
Gephyroneura	*cosmia*		Turner	1921	*Gephyroneura*	
CHENAULA			Swinhoe	1892		type species: *C. rufa* Swinhoe, 1892
		CHENAULA	Common	1970		misspelled
Chenuala	*heliaspis*		Meyrick	1891	*Ocneria*	
		rufa	Swinhoe	1892	*Chenuala*	
		expolitus	Scott	1893	*Chelepteryx*	unavailable published synonym
		epicrypha	Swinhoe	1905	*Anthela*	
NATAXA			Walker	1855		type species: *N. flavifascia* Walker, 1855
		DICREAGRA	Felder	1874		type species: *ochrocephala* Felder, 1874
		APROSCEPTA	Turner	1944		type species: *amblopis* Turner, 1944
Nataxa	*flavescens*		Walker	[Nov.] 1855	*Perna*	
		flavifascia	Walker	[Nov.] 1855	*Nataxa*	
		rubida	Walker	1865	*Nataxa*	
		ochrocephala	Felder	1874	*Dicreagra*	
Nataxa	*amblopis*		Turner	1944	*Aproscepta*	
CHELEPTERYX			Gray	[1835]		type species: *C. collesi* Gray, [1835]
		CHALEPTERYX	Walker	1855		misspelled
		MEGETHNA	Walker	1855		type species: *collesi* Gray, [1835]

genus	species	synonym	author	year	orig. comb.	notes
		FESTRA	Wallengren	1858		type species: *affabricata* Wallengren
		CHALEPTERIX	Koch	1872		misspelled
Chelepteryx	*collesi*		Gray	[1835]	*Chelepteryx*	
		laplacei	Feisthamel	1839	*Saturnia*	
		affabricata	Wallengren	1858	*Festra*	
		collesii	Koch	1872		misspelled
Chelepteryx	*chalepteryx*		Felder	1874	*Darala*	
		kochii	Koch	1872	*Chalepterix [sic!]*	nomen nudum
		cupreotincta	T.P. Lucas	1892	*Darala*	
		chelepteryx	Lower	1893		misspelled
		felderi	Turner	1904	*Chelepteryx*	replacement name
ANTHELA			Walker	[Aug.] 1855		type species: *ferruginea* Walker, 1855
		DARALA	Walker	[Aug.] 1855		type species: *ocellata* Walker, 1855
		OMMATOPTERA	Herrich-Schäffer	[Dec.] 1855		type species: *tetrophthalma* Herrich-Schäffer, 1856
		BAEODROMUS	Herrich-Schäffer	[1858]		unavailable published synonym
		LARANDA	Herrich-Schäffer	[1858]		unavailable published synonym
		COLUSSA	Walker	1860		type species: *odenestaria* Walker, 1860
		ARNISSA	Walker	1869		type species: *simplex* Walker, 1869
		NEWMANIA	Swinhoe	1892		type species: *guenei* Newman, 1856
		EULOPHOCAMPE	Scott	1893		unavailable published synonym

genus	species	synonym	author	year	orig. comb.	notes
		PSEUDODREATA	Bethune-Baker	1904		type species: *strigata* Bethune-Baker, 1904. Replacement name for *Cycethra* B.-B., 1904 and subjective junior synonym of *Colussa* Walker, 1860, a subjective junior synonym of *Anthela* Walker, 1855.
		CYCETHRA	Bethune-Baker	1904		type species: *aroa* Bethune-Baker, 1904, Joicey, Noakes and Talbot (1915: 379): junior synonym of *Colussa* Walker, 1860. Fletcher & Nye (1982: 136): junior homonym of *Cycethra* Bell, 1881 (Echinoderma); established *Pseudodreata* as replacement name (*C. aroa* is congeneric with *P. strigata*).
		COLLUSA	Bethune-Baker	1904		misspelled
		NEUMANIA	Swinhoe	1922		misspelled
		OMMATOPHORA	Swinhoe	1922		misspelled
		OMMALOPHORA	Dalla Torre	1927		misspelled
Anthela	*nicothoe*		Boisduval	1832	*Bombyx*	
		australasiae	Herrich-Schäffer	[June 1855]	*Laelia*	
		adusta	Walker	[Aug.] 1855	*Darala*	
		eucalypti	Herrich-Schäffer	[1858]	*Darala*	unavailable published synonym
		censors	Walker	1865	*Darala*	
		consors	Walker	1866	*Darala*	emended
Anthela	*allocota*		Turner	1921	*Anthela*	
Anthela	*connexa*		Walker	[Aug.] 1855	*Darala*	
		fervens	Walker	[Aug.] 1855	*Darala*	

genus	species	synonym	author	year	orig. comb.	notes
		zonata	Felder	1874	*Darala*	
Anthela	*repleta*		Walker	1855	*Darala*	
		diophthalma	Herrich-Schäffer	[1856]	*Ommatoptera*	
		repletana	Strand	?1928/29	*Anthela*	
Anthela	*protocentra*		Meyrick	1891	*Darala*	
Anthela	*rubeola*		Felder	1874	*Darala*	
		haemoptera	Lower	1893	*Darala*	
Anthela	*varia*		Walker	[Aug.] 1855	*Darala*	
		hamata	Walker	[Aug.] 1855	*Darala*	
		humata	Turner	1921		misspelled
		odenestaria	Walker	1860	*Colussa*	
		pinguis	Walker	1865	*Darala*	
		amoena	Scott	1893	*Eulophocampe*	unavailable published synonym
Anthela	*canescens*		Walker	1855	*Darala*	
		latifera	Walker	1862	*Colussa*	
		uvaria	Walker	1866	*Colussa*	
		tintinarra	Tepper	1890	*Opsirhina*	
		scortea	T.P. Lucas	1891	*Darala*	
		succinea	T.P. Lucas	1891	*Darala*	
		succinia	Swinhoe	1905		misspelled
		moretonensis	Strand	1925	*Anthela*	
Anthela	*inornata*		Walker	1855	*Darala*	
		complens	Swinhoe	1892	*Darala*	
		carneotincta	Swinhoe	1903	*Anthela*	
		crenulata	Swinhoe	1903	*Anthela*	
Anthela	*xanthocera*		Turner	1922	*Anthela*	
Anthela	*deficiens*		Walker	1865	*Dreata*	
Anthela	*excellens*		Walker	[Aug.] 1855	*Darala*	
		integra	Walker	[Aug.] 1855	*Darala*	
		caniceps	Walker	1862	*Dreata*	
Anthela	*astata*		Turner	1926	*Anthela*	
		cinerascens	Grünberg	1914	*Darala*	*nec* (Walker, 1855) (*Darala*)
Anthela	*cinerascens*		Walker	1855	*Darala*	
		rufifascia	Walker	1865	*Darala*	
		cervinella	Strand	?1928/29	*Anthela*	
Anthela	*subfalcata*		Walker	[Aug.] 1855	*Darala*	
		ferruginea	Walker	[Aug.] 1855	*Darala*	
		myrti	Herrich-Schäffer	[1858]	*Darala*	unavailable published synonym
		phaeozona	Turner	1926	*Anthela*	
Anthela	*acuta*		Walker	[Aug.] 1855	*Darala*	
		excisa	Walker	[Aug.] 1855	*Darala*	
		conspersa	Walker	[Aug.] 1855	*Darala*	

genus	species	synonym	author	year	orig. comb.	notes
		simplex	Walker	[Aug.] 1855	*Darala*	
		plana	Walker	[Aug.] 1855	*Darala*	
		quadriplaga	Walker	1862	*Darala*	
		potentaria	Walker	1863	*Ennomos*	
		delineata	Walker	1865	*Darala*	
Anthela	*virescens*		Turner	1939	*Anthela*	
Anthela	*addita*		Walker	1865	*Darala*	
		simplex	Walker	1869	*Arnissa*	*nec* (Walker, 1855) (*Darala*)
		vinosa	Rosenstock	1885	*Colussa*	
		venosa	Kirby	1892		misspelled
		pyrrhica	Turner	1921	*Anthela*	
Anthela	*pyrrhobaphes*		Turner	1926	*Anthela*	
Anthela	*ferruginosa*		Walker	[Aug.] 1855	*Anthela*	
		parva	Walker	[Aug.] 1855	*Darala*	
		minuta	Swinhoe	1892	*Darala*	
		walkeri	Strand	1925	*Anthela*	
		guttifascia	Strand	1925	*Anthela*	
Anthela	*phaeodesma*		Turner	1921	*Anthela*	
		intermedia	Hulstaert	1924	*Anthela*	
		phaedesma	Bryk	1934		misspelled
Anthela	*heliopa*		Lower	1902	*Darala*	
		prionodes	Turner	1932	*Anthela*	
Anthela	*limonea*		Butler	1874	*Darala*	
Anthela	*postica*		Walker	1855	*Darala*	
		callicesta	Turner	1924	*Anthela*	
Anthela	*callixantha*		Lower	1902	*Darala*	
		flavala	Swinhoe	1903	*Anthela*	
Anthela	*decolor*		Turner	1939	*Anthela*	
Anthela	*barnardi*		Turner	1922	*Anthela*	
Anthela	*asciscens*		T.P. Lucas	1891	*Darala*	
		tritonea	Swinhoe	1903	*Anthela*	
Anthela	*stygiana*		Butler	1882	*Darala*	
		magnifica	T.P. Lucas	1891	*Darala*	
Anthela	*ariprepes*		Turner	1921	*Anthela*	
Anthela	*xantharcha*		Meyrick	1891	*Darala*	
Anthela	*unisigna*		Swinhoe	1903	*Anthela*	
Anthela	*tetraphrica*		Turner	1921	*Anthela*	
		tetraphica	Hulstaert	1928		misspelled
Anthela	*ocellata*		Walker	1855	*Darala*	
		tetrophthalma	Herrich-Schäffer	1856	*Ommatoptera*	
		symphona	Turner	1904	*Anthela*	
		nigristigma	Fawcett	1917	*Anthela*	
		dama	Strand	?1928/29	*Anthela*	
Anthela	*ochroptera*		Lower	1892	*Darala*	
		psammochroa	Lower	1908	*Colussa*	
Anthela	*habroptila*		Turner	1921	*Anthela*	
Anthela	*cnecias*		Turner	1921	*Anthela*	
		tasmaniensis	Strand	?1928/29	*Anthela*	
Anthela	*oressarcha*		Turner	1921	*Anthela*	
Anthela	*denticulata*		Newman	1856	*Teara*	

genus	species	synonym	author	year	orig. comb.	notes
Anthela	*basigera*		Walker	1865	*Darala*	
		undulata	Felder	1874	*Darala*	
Anthela	*euryphrica*		Turner	1936	*Anthela*	
Anthela	*ostra*		Swinhoe	1903	*Anthela*	
		chrysocrossa	Turner	1915	*Anthela*	
Anthela	*hyperythra*		Turner	1921	*Anthela*	
Anthela	*achromata*		Turner	1904	*Anthela*	
Anthela	*guenei*		Newman	1856	*Teara*	
		gueneei	Tillyard	1926		misspelled
Anthela	*exoleta*		Swinhoe	1892	*Aroa*	
		figlina	Swinhoe	1902	*Darala*	
		glauerti	Turner	1939	*Anthela*	
Anthela	*reltoni*		T.P. Lucas	1895	*Darala*	
		pyromacula	Lower	1905	*Anthela*	
Anthela	*callileuca*		Turner	1922	*Anthela*	
Anthela	*callispila*		Lower	1905	*Anthela*	
Anthela	*asterias*		Meyrick	1891	*Darala*	
		uniformis	Swinhoe	1892	*Darala*	
		niphomacula	Lower	1905	*Anthela*	
Anthela	*phoenicias*		Turner	1902	*Anthela*	
		aspilota	Turner	1902	*Anthela*	
Anthela	*adriana*		Swinhoe	1902	*Darala*	
Anthela	*rubicunda*		Swinhoe	1902	*Darala*	
Anthela	*pudica*		Swinhoe	1902	*Darala*	
Anthela	*neurospasta*		Turner	1902	*Anthela*	
		ochroneura	Turner	1915	*Anthela*	
		linopepla	Turner	1921	*Anthela*	
Anthela	*clementi*		Swinhoe	1902	*Darala*	
		clementsi	Lower	1916		misspelled
Anthela	*strigata*		Bethune-Baker	1904	*Pseudodreata*	
	inconstans		Joicey, Noakes & Talbot	1915	*Colussa*	described as "subsp. nov." of *strigata* B.-B., 1904
Anthela	*aroa*		Bethune-Baker	1904	*Cycethra*	
	angiana		Joicey, Noakes & Talbot	1915	*Colussa*	described as "subsp. nov." of *aroa* B.-B., 1904
Anthela	*charon*		Bethune-Baker	1908	*Anthela*	
Anthela		*kebea*	Strand	?1928/29	*Anthela*	described as "n. ab." of *charon* B.-B., 1908

genus	species	synonym	author	year	orig. comb.	notes
Anthela	*ekeikei*		Bethune-Baker	1904	*Anthela*	B.-B. (1904) accidentially described *A. ekeikei* twice in the same paper. He subsequently corrected his mistake (B.-B., 1906: 13): *Collusa*[sic!] *ekeikei* B.-B., 1904 is an objective synonym of *Anthela ekeikei* B.-B., 1904. The illustration but not the label data ("Ekeikei, B.C. New Guinea, 1500 ft., March-April, 1903, A. E. Pratt. Coll.") in the original description match the specimen in the NHM London.
Anthela		*ekeikei*	Bethune-Baker	1904	*Collusa* [sic!]	[see *Anthela ekeikei* B.-B., 1904]
Anthela		*pupillifera*	Strand	?1928/29	*Anthela*	described as "form. nov." of *ekeikei* B.-B., 1904
Anthela		*mediana*	Strand	?1928/29	*Anthela*	described as "form. nov." of *ekeikei* B.-B., 1904
Anthela		*obsoletipicta*	Strand	?1928/29	*Anthela*	described as "form. nov." of *ekeikei* B.-B., 1904
Anthela	*intermedia*		Hulstaert	1924	*Anthela*	
Anthela	*brunneilinea*		Hulstaert	1924	*Anthela*	
Anthela	*julia*		Hulstaert	1924	*Anthela*	
Anthela	*prima*		Walker	1866	*Darala*	
Anthela	*odontogramm ata*		Joicey & Talbot	1917	*Colussa*	
Anthela	*laeta*		Grünberg	1914	*Darala*	
Anthela	*roberi*		Niepelt	1934	*Anthela*	
OMPHALIODES			Felder	1874		type species: *O. nana* Felder, 1874
		APROSITA	Turner	1914		type species: *ulothrix* Turner, 1914
Omphaliodes	*obscura*		Walker	1855	*Trichiura*	
		nana	Felder	1874	*Omphaliodes*	

genus	species	synonym	author	year	orig. comb.	notes
		ulothrix	Turner	1914	*Aprosita*	
		nuna	Swinhoe	1922		misspelled
PTEROLOCERA			Walker	1855		type species: *P. amplicornis* Walker, 1855
Pterolocera	*isogama*		Turner	1931	*Pterolocera*	
Pterolocera	*elizabetha*		White	1841	*Odonestis*	
		elisabetha	Strand	?1928/29		misspelled
Pterolocera	*rubescens*		Walker	1865	*Darala*	
Pterolocera	*leucocera*		Turner	1921	*Anthela*	
Pterolocera	*amplicornis*		Walker	1855	*Pterolocera*	
Pterolocera	*ferruginea*		Strand	1925	*Pterolocera*	
Pterolocera	*ferrugineofusca*		Strand	1925	*Pterolocera*	
		similis	Swinhoe	1922	*Pterolocera*	unavailable published synonym
		similis	Hulstaert	1928	*Pterolocera*	infrasubspecific
		similis	Bryk	1934	*Pterolocera*	unavailable published synonym
Pterolocera	*insignis*		Herrich-Schäffer	[1856]	*Ptilophora*	
CORTICOMIS			van Eecke	1924		type species: *C. eupterotioides* van Eecke, 1924
Corticomis	*eupterotioides*		van Eecke	1924	*Corticomis*	
Corticomis	*marmorea*		van Eecke	1924	*Corticomis*	
UNPLACED						
unplaced	*directa*		Walker	1862	*Colussa*	
unplaced	*linearis*		T.P. Lucas	1891	*Darala*	
unplaced	*rubriscripta*		T.P. Lucas	1891	*Darala*	
		rubroscripta	Swinhoe	1922		misspelled
		robroscripta	Bryk	1934		misspelled
unplaced	*macrota*		Lower	1892	*Darala*	nomen nudum
unplaced	*maculosa*		T.P. Lucas	1898	*Darala*	
unplaced	*trisecta*		T.P. Lucas	1898	*Darala*	

APPENDIX B:

REVISED SYNONYMIC SPECIES LIST

[Revised/proposed genera on green background.]

[Non-Australian taxa on cyan background.]

genus	species	synonym	author	year	orig. comb.	notes
MUNYCHRYIA			Walker	1865		type species: *M. senicula* Walker, 1865
		MUNYCHRYTA	Turner	1920		misspelled
		MUNICHRYIA	Turner	1921		misspelled
Munychryia	*senicula*		Walker	1865	*Munychryia*	
		nyssiata	R. Felder & Rogenhofer	1875	*Hypochroma*	
Munychryia	*periclyta*		Common & McFarland	1970	*Munychryia*	
GEPHYRONEURA			Turner	1920		type species: *G. cosmia* Turner, 1921
Gephyroneura	*cosmia*		Turner	1921	*Gephyroneura*	
"GENUS NOVUM 1"						proposed type species "Munychryiinae n. sp."
"Genus novum 1"	n. sp.					Referred to as "Munychryiinae n. sp." in the text.
CHELEPTERYX			Gray	[1835]		type species: *C. collesi* Gray, [1835]
		CHALEPTERYX	Walker	1855		misspelled
		MEGETHNA	Walker	1855		type species: *C. collesi* Gray, [1835]
		FESTRA	Wallengren	1858		type species: *F. affabricata* Wallengren, 1858
		CHALEPTERIX	Koch	1872		misspelled
Chelepteryx	*collesi*		Gray	[1835]	*Chelepteryx*	
		laplacei	Feisthamel	1839	*Saturnia*	
		affabricata	Wallengren	1858	*Festra*	
		collesii	Koch	1872		misspelled
Chelepteryx	*chalepteryx*		R. Felder	1874	*Darala*	
		kochii	Koch	1872	*Chalepterix [sic]*	nomen nudum
		cupreotincta	T.P. Lucas	1892	*Darala*	
		chelepteryx	Lower	1893		misspelled

genus	species	synonym	author	year	orig. comb.	notes
		felderi	Turner	1904	*Chelepteryx*	replacement name
ANTHELA			Walker	[Aug.] 1855		type species: *A. ferruginosa* Walker, 1855
		ARNISSA	Walker	1869		type species: *A. simplex* Walker, 1869
		BAEODROMUS	Herrich-Schäffer	[1858]		unavailable published synonym
		LARANDA	Herrich-Schäffer	[1858]		unavailable published synonym
		EULOPHOCAMPE	Scott	1893		unavailable published synonym
Anthela	*virescens*		Turner	1939	*Anthela*	
Anthela	*addita*		Walker	1865	*Darala*	
		simplex	Walker	1869	*Arnissa*	nec (Walker, 1855) (*Darala*)
		vinosa	Rosenstock	1885	*Colussa*	
		venosa	Kirby	1892		
		pyrrhica	Turner	1921	*Anthela*	
Anthela	*pyrrhobaphes*		Turner	1926	*Anthela*	
Anthela	*ferruginosa*		Walker	[Aug.] 1855	*Anthela*	
		parva	Walker	[Aug.] 1855	*Darala*	
		minuta	Swinhoe	1892	*Darala*	
		walkeri	Strand	1925	*Anthela*	
		guttifascia	Strand	1925	*Anthela*	
Anthela	*phaeodesma*		Turner	1921	*Anthela*	
		intermedia	Hulstaert	1924	*Anthela*	
		phaedesma	Bryk	1934		misspelled
COLUSSA			Walker	1860		**stat. rev.**; type species: *C. odenestaria* Walker, 1860
		COLLUSA	Bethune-Baker	1904		misspelled
Colussa	*denticulata*		Newman	1856	*Teara*	
Colussa	*basigera*		Walker	1865	*Darala*	
		undulata	R. Felder	1874	*Darala*	
Colussa	*euryphrica*		Turner	1936	*Anthela*	
Colussa	*repleta*		Walker	1855	*Darala*	
		diophthalma	Herrich-Schäffer	[1856]	*Ommatoptera*	
		repletana	Strand	?1928/29	*Anthela*	
Colussa	*protocentra*		Meyrick	1891	*Darala*	
Colussa	*rubeola*		R. Felder	1874	*Darala*	
		haemoptera	Lower	1893	*Darala*	
Colussa	*varia*		Walker	[Aug.] 1855	*Darala*	

genus	species	synonym	author	year	orig. comb.	notes
		hamata	Walker	[Aug.] 1855	*Darala*	
		humata	Turner	1921		misspelled
		odenestaria	Walker	1860	*Colussa*	
		pinguis	Walker	1865	*Darala*	
		amoena	Scott	1893	*Eulophocampe*	unavailable published synonym
Colussa	*canescens*		Walker	1855	*Darala*	
		latifera	Walker	1862	*Colussa*	
		uvaria	Walker	1866	*Colussa*	
		tintinarra	Tepper	1890	*Opsirhina*	
		scortea	T.P. Lucas	1891	*Darala*	
		succinea	T.P. Lucas	1891	*Darala*	
		succinia	Swinhoe	1905		misspelled
		moretonensis	Strand	1925	*Anthela*	
Colussa	*inornata*		Walker	1855	*Darala*	
		complens	Swinhoe	1892	*Darala*	
		carneotincta	Swinhoe	1903	*Anthela*	
		crenulata	Swinhoe	1903	*Anthela*	
Colussa	*xanthocera*		Turner	1922	*Anthela*	
Colussa	*deficiens*		Walker	1865	*Dreata*	
Colussa	*astata*		Turner	1926	*Anthela*	
		cinerascens	Grünberg	1914	*Darala*	nec (Walker, 1855) (*Darala*)
Colussa	*cinerascens*		Walker	1855	*Darala*	
		rufifascia	Walker	1865	*Darala*	
		cervinella	Strand	?1928/29	*Anthela*	
Colussa	*subfalcata*		Walker	[Aug.] 1855	*Darala*	
		ferruginea	Walker	[Aug.] 1855	*Darala*	
		myrti	Herrich-Schäffer	[1858]	*Darala*	unavailable published synonym
		phaeozona	Turner	1926	*Anthela*	
Colussa	*acuta*		Walker	[Aug.] 1855	*Darala*	
		excisa	Walker	[Aug.] 1855	*Darala*	
		conspersa	Walker	[Aug.] 1855	*Darala*	
		simplex	Walker	[Aug.] 1855	*Darala*	
		plana	Walker	[Aug.] 1855	*Darala*	
		quadriplaga	Walker	1862	*Darala*	
		potentaria	Walker	1863	*Ennomos*	
		delineata	Walker	1865	*Darala*	
Colussa	*limonea*		Butler	1874	*Darala*	
Colussa	*postica*		Walker	1855	*Darala*	
		callicesta	Turner	1924	*Anthela*	
Colussa	*decolor*		Turner	1939	*Anthela*	

genus	species	synonym	author	year	orig. comb.	notes
Colussa	*callixantha*		Lower	1902	*Darala*	
		flavala	Swinhoe	1903	*Anthela*	
Colussa	*barnardi*		Turner	1922	*Anthela*	
Colussa	*charon*		Bethune-Baker	1908	*Anthela*	
		kebea	Strand	?1928/29	*Anthela*	described as "n. ab." of *charon* B.-B., 1908
Colussa	*ekeikei*		Bethune-Baker	1904	*Anthela*	B.-B. (1904) accidentially described *A. ekeikei* twice in the same paper. He subsequently corrected his mistake (B.-B., 1906; 13): *Collusa* [sic!] *ekeikei* B.-B., 1904 is an objective synonym of *Anthela ekeikei* B.-B., 1904. The illustration but not the label data ("Ekeikei, B.C. New Guinea, 1500 ft., March-April, 1903, A. E. Pratt. Coll.") in the original description match the specimen in the NHM London.
		ekeikei	Bethune-Baker	1904	*Collusa[sic]*	[see *Anthela ekeikei* B.-B., 1904]
		pupillifera	Strand	?1928/29	*Anthela*	described as "form. nov." of *ekeikei* B.-B., 1904
		mediana	Strand	?1928/29	*Anthela*	described as "form. nov." of *ekeikei* B.-B., 1904
		obsoletipicta	Strand	?1928/29	*Anthela*	described as "form. nov." of *ekeikei* B.-B., 1904
Colussa	*intermedia*		Hulstaert	1924	*Anthela*	
Colussa	*brunneilinea*		Hulstaert	1924	*Anthela*	
Colussa	*julia*		Hulstaert	1924	*Anthela*	
Colussa	*prima*		Walker	1866	*Darala*	
Colussa	*odontogramm ata*		Joicey & Talbot	1917	*Colussa*	
Colussa	*laeta*		Grünberg	1914	*Darala*	

genus	species	synonym	author	year	orig. comb.	notes
Colussa	*roberi*		Niepelt	1934	Anthela	
PSEUDODREATA			Bethune-Baker	1904		**stat. rev.**; type species: *P. strigata* Bethune-Baker, 1904. Replacement name for *Cycethra* B.-B., 1904 and subjective junior synonym of *Colussa* Walker, 1860, a subjective junior synonym of *Anthela* Walker, 1855.
		CYCETHRA	Bethune-Baker	1904		type species: *C. aroa* Bethune-Baker, 1904. Joicey, Noakes and Talbot (1915: 379): junior synonym of *Colussa* Walker, 1860. Fletcher & Nye (1982: 136): junior homonym of *Cycethra* Bell, 1881 (Echinoderma); established *Pseudodreata* as replacement name (*C. aroa* is congeneric with *P. strigata*).
		CORTICOMIS	van Eecke	1924		**n. syn.**; type species: *C. eupterotioides* van Eecke, 1924
Pseudodreata	*strigata*		Bethune-Baker	1904	*Pseudodreata*	
		inconstans	Joicey, Noakes & Talbot	1915	*Colussa*	described as "subsp. nov." of *strigata* B.-B., 1904
Pseudodreata	*aroa*		Bethune-Baker	1904	*Cycethra*	
		angiana	Joicey, Noakes & Talbot	1915	*Colussa*	described as "subsp. nov." of *aroa* B.-B., 1904
Pseudodreata	*eupterotioides*		van Eecke	1924	*Corticomis*	
Pseudodreata	*marmorea*		van Eecke	1924	*Corticomis*	

genus	species	synonym	author	year	orig. comb.	notes
"GENUS NOVUM 2"						proposed type species "Anthelinae n. sp."
"Genus novum 2"	n. sp.					Referred to as "Anthelinae n. sp." in the text.
CHENUALA			Swinhoe	1892		type species: *C. rufa* Swinhoe, 1892
		CHENAULA	Common	1970		misspelled
Chenuala	*heliaspis*		Meyrick	1891	*Ocneria*	
		rufa	Swinhoe	1892	*Chenuala*	
		expolitus	Scott	1893	*Chelepteryx*	unavailable published synonym
		epicrypha	Swinhoe	1905	*Anthela*	
PTEROLOCERA			Walker	1855		type species: *P. amplicornis* Walker, 1855
Pterolocera	*isogama*		Turner	1931	*Pterolocera*	
Pterolocera	*elizabetha*		White	1841	*Odonestis*	
		elisabetha	Strand	?1928/29		misspelled
Pterolocera	*rubescens*		Walker	1865	*Darala*	
Pterolocera	*leucocera*		Turner	1921	*Anthela*	
Pterolocera	*amplicornis*		Walker	1855	*Pterolocera*	
Pterolocera	*ferruginea*		Strand	1925	*Pterolocera*	
Pterolocera	*ferrugineofusca*		Strand	1925	*Pterolocera*	
		similis	Swinhoe	1922	*Pterolocera*	unavailable published synonym
		similis	Hulstaert	1928	*Pterolocera*	infrasubspecific
		similis	Bryk	1934	*Pterolocera*	unavailable published synonym
Pterolocera	*insignis*		Herrich-Schäffer	[1856]	*Ptilophora*	
DARALA			Walker	[Aug.] 1855		**stat. rev.**; type species: *D. ocellata* Walker, 1855
		OMMATOPTERA	Herrich-Schäffer	[Dec.] 1855		type species: *O. tetrophthalma* Herrich-Schäffer, 1856
		OMMATOPHORA	Swinhoe	1923		misspelled
		OMMALOPHORA	Dalla Torre	1927		misspelled
Darala	*ocellata*		Walker	1855	*Darala*	
		tetrophthalma	Herrich-Schäffer	1856	*Ommatoptera*	
		symphona	Turner	1904	*Anthela*	
		nigristigma	Fawcett	1917	*Anthela*	

genus	species	synonym	author	year	orig. comb.	notes
		dama	Strand	?1928/29	*Anthela*	
Darala	*ochroptera*		Lower	1892	*Darala*	
		psammochroa	Lower	1908	*Colussa*	
Darala	*habroptila*		Turner	1921	*Anthela*	
Darala	*cnecias*		Turner	1921	*Anthela*	
		tasmaniensis	Strand	?1928/29	*Anthela*	
Darala	*oressarcha*		Turner	1921	*Anthela*	
Darala	*ostra*		Swinhoe	1903	*Anthela*	
		chrysocrossa	Turner	1915	*Anthela*	
NEWMANIA			Swinhoe	1892		**stat. rev.**; type species: *T. guenei* Newman, 1856
		NEUMANIA	Swinhoe	1922		misspelled
Newmania	*guenei*		Newman	1856	*Teara*	
		gueneei	Tillyard	1926		misspelled
Newmania	*callispila*		Lower	1905	*Anthela*	
Newmania	*asterias*		Meyrick	1891	*Darala*	
		uniformis	Swinhoe	1892	*Darala*	
		niphomacula	Lower	1905	*Anthela*	
Newmania	*callileuca*		Turner	1922	*Anthela*	
Newmania	*rubicunda*		Swinhoe	1902	*Darala*	
Newmania	*reltoni*		T.P. Lucas	1895	*Darala*	
		pyromacula	Lower	1905	*Anthela*	
Newmania	*clementi*		Swinhoe	1902	*Darala*	
		clementsi	Lower	1916		misspelled
Newmania	*exoleta*		Swinhoe	1892	*Aroa*	Only tentatively placed into *Newmania* – caterpillars are unknown, but male genital structures match this genus, except for deeply divided uncus lobes, which are not distally touching (possibly part of a transformation series leading from the condition in *N. clementi / reltoni / callileuca* to the one of *N. guenei / callispila / asterias / rubicunda.*
		figlina	Swinhoe	1902	*Darala*	
		glauerti	Turner	1939	*Anthela*	

genus	species	synonym	author	year	orig. comb.	notes
Newmania	*heliopa*		Lower	1902	*Darala*	As in *N. exoleta* (see above).
		prionodes	Turner	1932	*Anthela*	
OMPHALIODES			R. Felder	1874		type species: *O. nana* Felder, 1874
		APROSITA	Turner	1914		type species: *A. ulothrix* Turner, 1914
Omphaliodes	*obscura*		Walker	1855	*Trichiura*	
		nana	R. Felder	1874	*Omphaliodes*	
		ulothrix	Turner	1914	*Aprosita*	
		nuna	Swinhoe	1922		misspelled
"GENUS NOVUM 3"						proposed type species: *A. neurospasta* Turner, 1902
"Genus novum 3"	*neurospasta*		Turner	1902	*Anthela*	
		ochroneura	Turner	1915	*Anthela*	
		linopepla	Turner	1921	*Anthela*	
"Genus novum 3"	*achromata*		Turner	1904	*Anthela*	
"Genus novum 3"	*phoenicias*		Turner	1902	*Anthela*	
		aspilota	Turner	1902	*Anthela*	
"Genus novum 3"	*adriana*		Swinhoe	1902	*Darala*	
"Genus novum 3"	*pudica*		Swinhoe	1902	*Darala*	
"Genus novum 3"	*hyperythra*		Turner	1921	*Anthela*	
NATAXA			Walker	1855		type species: *N. flavifascia* Walker, 1855
		DICREAGRA	R. Felder	1874		type species: *D. ochrocephala* Felder, 1874
		APROSCEPTA	Turner	1944		type species: *A. amblopis* Turner, 1944
Nataxa	*flavescens*		Walker	[Nov.] 1855	*Perna*	
		flavifascia	Walker	[Nov.] 1855	*Nataxa*	
		rubida	Walker	1865	*Nataxa*	
		ochrocephala	R. Felder	1874	*Dicreagra*	
Nataxa	*amblopis*		Turner	1944	*Aproscepta*	
Nataxa	*nicothoe*		Boisduval	1832	*Bombyx*	
		australasiae	Herrich-Schäffer	[June 1855]	*Laelia*	
		adusta	Walker	[Aug.] 1855	*Darala*	
		eucalypti	Herrich-Schäffer	[1858]	*Darala*	unavailable published synonym
		censors	Walker	1865	*Darala*	
		consors	Walker	1866	*Darala*	emended
Nataxa	*allocota*		Turner	1921	*Anthela*	

genus	species	synonym	author	year	orig. comb.	notes
Nataxa	*connexa*		Walker	[Aug.] 1855	*Darala*	
		fervens	Walker	[Aug.] 1855	*Darala*	
		zonata	R. Felder	1874	*Darala*	
Nataxa	*excellens*		Walker	[Aug.] 1855	*Darala*	
		integra	Walker	[Aug.] 1855	*Darala*	
		caniceps	Walker	1862	*Dreata*	
Nataxa	*asciscens*		T.P. Lucas	1891	*Darala*	
		tritonea	Swinhoe	1903	*Anthela*	
Nataxa	*stygiana*		Butler	1882	*Darala*	
		magnifica	T.P. Lucas	1891	*Darala*	
Nataxa	*ariprepes*		Turner	1921	*Anthela*	
Nataxa	*xantharcha*		Meyrick	1891	*Darala*	
Nataxa	*unisigna*		Swinhoe	1903	*Anthela*	
Nataxa	*tetraphrica*		Turner	1921	*Anthela*	
		tetraphica	Hulstaert	1928		misspelled
UNPLACED						
unplaced	*directa*		Walker	1862	*Colussa*	
unplaced	*linearis*		T.P. Lucas	1891	*Darala*	
unplaced	*rubriscripta*		T.P. Lucas	1891	*Darala*	
		rubroscripta	Swinhoe	1922		misspelled
		robroscripta	Bryk	1934		misspelled
unplaced	*macrota*		Lower	1892	*Darala*	nomen nudum
unplaced	*maculosa*		T.P. Lucas	1898	*Darala*	
unplaced	*trisecta*		T.P. Lucas	1898	*Darala*	

APPENDIX C:

HOST RECORDS

C.1) ANTHELID HOST RECORDS SORTED BY ANTHELID SPECIES

HOSTS – an online-database of the hostplants of the world's Lepidoptera by the Natural History Museum, London:

http://www.nhm.ac.uk/research-curation/projects/hostplants/

anthelid species	host plant family	host plant species	source
Anthela acuta	Asteraceae	*Hypochoeris radicata*	own observation [field observation of two specimens; completed life cycle on host plant in captivity; host plant species not native to Australia]
Anthela acuta	Asteraceae	*Olearia argophylla*	Coupar & Coupar 1992; Herbison-Evans & Crossley
Anthela acuta	Fabaceae	*Vicia faba*	ANIC card [at Taree in Sept., "NSW Ins. Pest Survey, 1953, p. 18"]
Anthela acuta	Mimosaceae	*Acacia* spp.	Coupar & Coupar 1992; Herbison-Evans & Crossley
Anthela acuta	Mimosaceae	*Acacia baileyana*	own observation [bred in captivity]
Anthela acuta	Mimosaceae	*Acacia melanoxylon*	own observation [bred in captivity]
Anthela acuta	Myrtaceae	*Eucalyptus robusta*	Beutenmüller 1891
Anthela acuta	Myrtaceae	*Eucalyptus* spp. (and less frequently many other plants)	Illidge 1913
Anthela acuta	Poaceae	*Saccharum officinarum*	HOSTS
Anthela acuta	Poaceae	grasses (any soft sp.)	Haines 1963
Anthela acuta	Poaceae	grasses	VJ Robinson card; Herbison-Evans & Crossley
Anthela acuta (NT)	Barringtoniacea e	*Planchonia careya*	Southcott 1987
Anthela acuta (QLD, Brisbane)	Arecaceae	palm tree	Chew
Anthela acuta (TAS)	Fagaceae	*Fagus sylvatica*	Herbison-Evans & Crossley
Anthela acuta (TAS)	Fagaceae	*Quercus robur*	Herbison-Evans & Crossley
Anthela acuta (?)	Proteaceae	*Hakea sericea*	Moore 1964
Anthela addita	Mimosaceae	*Acacia dealbata*	Bashford 1997
Anthela addita	Poaceae	grasses (soft, introduced species)	own observation [bred in captivity]
Anthela asciscens	Mimosaceae	*Acacia harpophylla*	Common 1990
Anthela asciscens	Mimosaceae	*Acacia* sp.	HOSTS
Anthela astata	Euphorbiaceae	*Glochidion ferdinandi*	Nathan 1960 [probably wrong ID: *A. acuta / astata* grp or *A. excellens]*

anthelid species	host plant family	host plant species	source
Anthela astata	Mimosaceae	*Acacia baileyana*	own observation [bred in captivity]
Anthela astata	Mimosaceae	*Acacia melanoxylon*	own observation [bred in captivity]
Anthela asterias	Mimosaceae	*Acacia* spp. ("Broadleaf Wattles")	Herbison-Evans & Crossley
Anthela basigera	Poaceae	various grasses	Herbison-Evans & Crossley
Anthela basigera	Poaceae	grasses	McQuillan & Forrest 1985
Anthela callispila	Caesalpiniaceae	*Cassia nemophila*	McFarland 1979 [as *Anthela* sp. near *guenei*]
Anthela callispila	Caesalpiniaceae	*Cassia* sp.	McFarland 1979 [as *Anthela* sp. near *guenei*]
Anthela callixantha	Solanaceae	*Solanum cunninghamii*	ANIC specimen label [caterpillars found on *S. cunninghamii*]
Anthela callixantha	Solanaceae	*Solanum ellipticum*	ANIC specimen label [caterpillars found on *S. ellipticum*, bred on S. *elaeagnifolium*]
Anthela canescens	Myrtaceae	*Corymbia torelliana*	Herbison-Evans & Crossley
Anthela canescens	Myrtaceae	*Eucalyptus* spp.	own observation [bred in captivity]
Anthela clementi	Mimosaceae	*Acacia melanoxylon*	own observation [bred in captivity, but most caterpillars and finally single pupa died]
Anthela cnecias	Poaceae	native grasses	own observation [bred in captivity, but died in final instar]
Anthela connexa	Mimosaceae	*Acacia longifolia.*	Herbison-Evans & Crossley
Anthela connexa	Mimosaceae	*Acacia melanoxylon*	Herbison-Evans & Crossley
Anthela connexa	Mimosaceae	*Acacia* spp.	Elliott & de Little 1985
Anthela connexa	Pinaceae	*Pinus radiata*	Elliott & de Little 1985; Bashford 1990
Anthela denticulata	Chenopodiaceae	*Atriplex* spp.	Froggatt 1910 [dubious record, see "Introduction – economic and medical records"]
Anthela denticulata	Poaceae	naturalized and native grasses (esp. "soft" annual spp.)	naturalized and native grasses (esp. "soft" annual spp.) [McFarland 1979]
Anthela denticulata	Poaceae	various grasses	Herbison-Evans & Crossley
Anthela denticulata	Poaceae	grasses	Common 1990
Anthela denticulata	Poaceae	grass	Anderson 1892; HOSTS
Anthela denticulata	[Poaceae]	crops	Edwards & Fairey 1996
Anthela ekeikei	Arecaceae	*Cocos nucifera*	Szent-Ivany & Catley 1960 [as *Darala rubeola*, which certainly is a wrong ID: probably *A. ekeikei* species group]
Anthela ekeikei	Casuarinaceae	*Casuarina equisetifolia*	Szent-Ivany & Carver 1967
Anthela ekeikei	Pinaceae	*Pinus patula*	Roberts 1987; HOSTS
Anthela euryphrica	Poaceae	*Bromus arenaria*	Turner 1936
Anthela euryphrica	Poaceae	*Hordeum leporinum*	ANIC card [label data on specimen from NSW, Murrurundi, reared by Middleton, 26.5.34, CSIRO: "Fairy Grass" & "Barley Grass"]
Anthela euryphrica	Poaceae	*Sporobolus caroli*	ANIC card [label data on specimen from NSW, Murrurundi, reared by Middleton, 26.5.34, CSIRO: "Fairy Grass" & "Barley Grass"]
Anthela euryphrica	Poaceae	grasses	Common 1990
Anthela euryphrica	Poaceae	grass	HOSTS
Anthela euryphrica	Poaceae	Poaceae	ANIC rearing book 1980
Anthela euryphrica	Poaceae	*Triticum aestivum*	Herbison-Evans & Crossley

anthelid species	host plant family	host plant species	source
Anthela euryphrica	Poaceae	*Triticum* sp. ("wheat")	Common 1990
Anthela euryphrica	[Poaceae]	crops	Edwards & Fairey 1996
Anthela excellens	Mimosaceae	*Acacia baileyana*	own observation [bred in captivity]
Anthela excellens	Mimosaceae	*Acacia longifolia*	ANIC card [larvae feeding on phyllodes at NSW, Heathcote, 11.4.75 (M.v.d.B., det. IFBC, 1978)]; Berg 1982
Anthela excellens	Mimosaceae	*Acacia mearnsii*	Berg 1982
Anthela excellens	Mimosaceae	*Acacia melanoxylon*	VJ Robinson card
Anthela excellens	Mimosaceae	*Acacia* sp.	VJ Robinson card; HOSTS; Herbison-Evans & Crossley
Anthela excellens	Mimosaceae	*Acacia* spp.	Common 1990
Anthela excellens	Myrtaceae	*Eucalyptus camaldulensis*	VJ Robinson card
Anthela excellens	Myrtaceae	*Eucalyptus* sp.	VJ Robinson card
Anthela excellens	Pinaceae	*Pinus radiata*	Moore 1963a, b; HOSTS
Anthela exoleta	Mimosaceae	*Acacia ligulata*	McFarland 1979 [as *Anthela glauerti*, bred]
Anthela ferruginosa	Poaceae	*Pennisetum clandestinum*	VJ Robinson card
Anthela ferruginosa	Poaceae	*Stenotaphrum secundatum*	VJ Robinson card
Anthela ferruginosa	Poaceae	grasses (soft, introduced species)	own observation [bred in captivity]
Anthela ferruginosa	Poaceae	grasses	Common 1990
Anthela ferruginosa	Poaceae	grass	HOSTS; Herbison-Evans & Crossley
Anthela guenei	Fabaceae	*Jacksonia* sp.	Common 1990; HOSTS
Anthela guenei	Mimosaceae	*Acacia dealbata*	Common 1990; Herbison-Evans & Crossley
Anthela guenei	Mimosaceae	*Acacia decurrens*	VJ Robinson card; Common 1990; Herbison-Evans & Crossley
Anthela guenei	Mimosaceae	*Acacia melanoxylon*	own observation [bred in captivity]
Anthela guenei	Mimosaceae	*Acacia* spp.	Common 1990
Anthela guenei	Mimosaceae	*Acacia* sp.	VJ Robinson card; HOSTS
Anthela nicothoe	Fabaceae	*Chamaecytisus prolifer*	Hadlington 1963
Anthela nicothoe	Mimosaceae	*Acacia baileyana*	own observation [bred in captivity]
Anthela nicothoe	Mimosaceae	*Acacia dealbata*	Berg 1982; ANIC card ["Brindabella race", Mt. Coree, June 1957, emg. Aug. 1958 (R. Straatman), No. 24/1957)]; Common 1963, 1990; Hadlington 1963; HOSTS
Anthela nicothoe	Mimosaceae	*Acacia melanoxylon*	VJ Robinson card; own observation [bred in captivity]
Anthela nicothoe	Mimosaceae	*Acacia* spp. ("various broad leaved wattles")	Herbison-Evans & Crossley

anthelid species	host plant family	host plant species	source
Anthela nicothoe	Mimosaceae	*Acacia* spp.	Hadlington 1963; Moore 1963a, b; Elliott & de Little 1985; Coupar & Coupar 1992
Anthela nicothoe	Mimosaceae	*Acacia* sp.	VJ Robinson card; HOSTS
Anthela nicothoe	Myrtaceae	*Eucalyptus obliqua*	ANIC card [*Anthela* sp. near *A. nicothoe* defoliating trees at TAS, New Norfolk, 18.1.78, H. Elliott (emg 20.2.78; det. IFBC, 1978)]
Anthela nicothoe	Pinaceae	*Pinus radiata*	Hadlington 1963; Moore 1963a, b; Common 1970, 1990; Campbell 1972; HOSTS
Anthela nicothoe	Pinaceae	*Pinus* spp.	Coupar & Coupar 1992
Anthela ocellata	Mimosaceae	*Acacia dealbata*	Bashford 1997
Anthela ocellata	Pinaceae	*Pinus radiata*	Moore 1963a, b; HOSTS
Anthela ocellata	Poaceae	*Axonopus affinis*	Moore 1963b
Anthela ocellata	Poaceae	*Cynodon dactylon*	Moore 1963b
Anthela ocellata	Poaceae	*Ehrharta erecta*	Coupar & Coupar 1992; Herbison-Evans & Crossley
Anthela ocellata	Poaceae	*Lolium perenne*	McQuillan & Forrest 1985
Anthela ocellata	Poaceae	*Triticum* sp. ("wheat")	ANIC card ["published record"]
Anthela ocellata	Poaceae	*Themeda triandra*	own observation [field observation; completed life cycle on introduced grasses in captivity]
Anthela ocellata	Poaceae	mixed lawn grasses	McFarland 1979; own observation [bred in captivity]
Anthela ocellata	Poaceae	pastures	Leach 1952
Anthela ocellata	Poaceae	various native grasses	Moore 1963b
Anthela ocellata	Poaceae	various naturalized annual grasses	McFarland 1979
Anthela ocellata	Poaceae	various grasses	French 1911; Brewster et al.1920; VJ Robinson card; ANIC card [Canberra, No. 26/1956]; Common 1963, 1990; McQuillan & Forrest 1985
Anthela ocellata	Poaceae	grass	HOSTS
Anthela oressarcha	Poaceae	*Cynodon dactylon*	VJ Robinson card [L1 from female ex "The Long Plain" near Kiandra accepted "Turfgrass", "Bermudagrass", "Parramatta Grass"]
Anthela oressarcha	Poaceae	*Poa* sp.	VJ Robinson card [leaves and young spikes of "snowgrass" *Poa* sp.]
Anthela oressarcha	Poaceae	*Sporobolus indicus*	VJ Robinson card [L1 from female ex "The Long Plain" near Kiandra accepted "Turfgrass", "Bermudagrass", "Parramatta Grass"]
Anthela oressarcha	Poaceae	native grasses	own observation [bred in captivity, but died in L3]
Anthela oressarcha	Poaceae	various grasses	Herbison-Evans & Crossley

anthelid species	host plant family	host plant species	source
Anthela oressarcha	Poaceae	grass	Common 1990 [bred in captivity]; HOSTS
Anthela ostra	[Poaceae]	crops	Edwards & Fairey 1996
Anthela ostra	Poaceae	grass	HOSTS
Anthela postica	Mimosaceae	*Acacia decurrens*	VJ Robinson card [as *A. callicesta*]; Common 1990 [bred in captivity]; Herbison-Evans & Crossley
Anthela postica	Mimosaceae	*Acacia* sp	VJ Robinson card [as *A. callicesta*]; HOSTS
Anthela reltoni	Mimosaceae	*Acacia aneura*	own observation [bred in captivity]
Anthela reltoni	Mimosaceae	*Acacia melanoxylon*	own observation [bred in captivity, but died in final instar]
Anthela repleta	Mimosaceae	*Acacia binervata*	Berg 1982; ANIC card [NSW, Robertson, 26.4.76, M.v.d.B. (det. IFBC, 1976)]; Common 1990; Herbison-Evans & Crossley
Anthela repleta	Mimosaceae	*Acacia floribunda*	VJ Robinson card; Common 1990; Herbison-Evans & Crossley
Anthela repleta	Mimosaceae	*Acacia longifolia*	Berg 1982
Anthela repleta	Mimosaceae	*Acacia mearnsii*	ANIC card [NSW, Waterfall, 20.7.76, M.v.d.B. (det. IFBC, 1978)]; Berg 1982; Common 1990; Herbison-Evans & Crossley
Anthela repleta	Mimosaceae	*Acacia melanoxylon*	Berg 1982; Common 1990; Herbison-Evans & Crossley; own observation [bred in captivity]
Anthela repleta	Mimosaceae	*Acacia* sp. (prob. *penninervis*)	ANIC card [NSW, 13 mls SE Braidwood (No. 20/1957)]
Anthela repleta	Mimosaceae	*Acacia* spp.	Common 1990
Anthela repleta	Mimosaceae	*Acacia* sp.	VJ Robinson card; HOSTS
Anthela n. sp. near *repleta*	Caesalpiniaceae	*Cassia nemophila*	McFarland 1979
Anthela n. sp. near *repleta*	Mimosaceae	*Acacia pycnantha*	McFarland 1979
Anthela rubeola	Mimosaceae	*Acacia pycnantha*	Herbison-Evans & Crossley
Anthela rubicunda	Mimosaceae	*Acacia melanoxylon*	own observation [bred in captivity, but died in final instar]
Anthela rubicunda	Myrtaceae	*Eucalyptus* sp.	Lower 1903 [quoted G. Barnard]
Anthela stygiana	Mimosaceae	*Acacia excelsa*	VJ Robinson card [as *A. magnifica*]
Anthela stygiana	Mimosaceae	*Acacia harpophylla*	Common 1990 [as *A. magnifica*]
Anthela stygiana	Mimosaceae	*Acacia melanoxylon*	own observation [bred in captivity]
Anthela stygiana	Mimosaceae	*Acacia* sp.	HOSTS [as *A. magnifica*]
Anthela tetraphrica	Mimosaceae	*Acacia aneura*	own observation [bred in captivity]
Anthela unisigna	Mimosaceae	*Acacia melanoxylon*	own observation [bred in captivity]
Anthela varia	Juglandaceae	*Carya "diviformis"*	ANIC card [at QLD, Nambour, Mar. 1968, larvae on foliage (det. IFBC, 1970), D816]

anthelid species	host plant family	host plant species	source
Anthela varia	Juglandaceae	*Carya* sp.	Common 1990; HOSTS
Anthela varia	Mimosaceae	*Acacia decurrens*	VJ Robinson card
Anthela varia	Mimosaceae	*Acacia* sp.	VJ Robinson card
Anthela varia	Myrtaceae	*Eucalyptus blakelyi*	ANIC card [ACT, Canberra, NJR Mitchell (det. EDE), No. 44/1971]; Landsberg 1988
Anthela varia	Myrtaceae	*Eucalyptus fastigata*	VJ Robinson card
Anthela varia	Myrtaceae	*Eucalyptus leucoxylon*	Edwards & Wanjura 1989
Anthela varia	Myrtaceae	*Eucalyptus* spp.	Scott 1893 [as *A. hamata*]; Strand 1925 [as *A. hamata*]; Teakle 1969; Common 1990; Herbison-Evans & Crossley; own observation [bred in captivity]
Anthela varia	Myrtaceae	*Eucalyptus* sp.	VJ Robinson card; Monteith 1995; Chew; HOSTS
Anthela varia	Pinaceae	*Pinus radiata*	Moore 1963a, b
Anthela varia	Proteaceae	*Grevillea* sp.	Herbison-Evans & Crossley
Anthela varia	Proteaceae	*Macadamia tetraphylla*	Teakle 1969; HOSTS
Anthela varia	Proteaceae	*Macadamia integrifolia*	Herbison-Evans & Crossley
Anthela varia	Proteaceae	*Macadamia* sp.	Ironside 1973, 1980, 1981, 1995
Anthela varia	Proteaceae	*Stenocarpus* sp.	Herbison-Evans & Crossley
Anthela varia	Rosaceae	*Prunus armeniaca*	Teakle 1969
Anthela varia	Salicaceae	*Salix* sp.	Common 1990; HOSTS
Anthela varia	Sapindaceae	(?) *Atalaya hemiglauca*	ANIC card [near Longreach some frass apparently killed outright (Q. Dep. Agric. Ent.): "Whitewood"]
Anthela xantharcha	Mimosaceae	*Acacia acuminata*	Mills 1954
Anthela xantharcha	Mimosaceae	*Acacia melanoxylon*	own observation [bred in captivity]
Anthela xantharcha	Mimosaceae	*Acacia pycnantha*	McFarland 1979 [bred, probably *A. xantharcha*]
Anthela xantharcha	Mimosaceae	*Acacia* sp.	Common 1990; HOSTS
Anthela sp. (NSW, ACT)	Myrtaceae	*Eucalyptus viminalis*	Chisholm 1923; Riek 1962
Anthela sp. (NSW)	Chenopodiaceae	*Atriplex vesicaria*	ANIC card [NSW, Deniliquin, 30.9.1958, B. Fox (det. IFBC 1960 and 1976; examples in ANIC)]
Anthela sp. (QLD, Brisbane)	Mimosaceae	*Acacia* sp.	Chew
Anthela sp. (QLD, Brisbane)	Myrtaceae	*Eucalyptus* sp.	Chew
Anthela sp. (QLD, Mareeba)	Caesalpiniaceae	*Erythrophleum chlorostachys*	McFarland 1979
Anthela sp. (TAS)	Fagaceae	*Quercus* sp.	Bashford 1990
Anthela sp. (TAS)	Myrtaceae	*Eucalyptus amygdalina*	Bashford 1990
Anthela sp. (TAS)	Myrtaceae	*Eucalyptus obliqua*	Bashford 1990
Anthela sp. (TAS)	Pinaceae	*Pinus radiata*	Bashford 1990
Anthela sp. (TAS)	Pinaceae	*Pinus* sp.	Hardy *et al.* 1979
Anthela sp. (WA)	Mimosaceae	*Acacia decurrens*	VJ Robinson card [60mls. E. Geraldton]

anthelid species	host plant family	host plant species	source
Anthela sp.	Mimosaceae	*Acacia dealbata*	Bashford 1997
Chelepteryx chalepteryx	Fabaceae	*Trifolium* sp.	Gallard 1931 [initially]
Chelepteryx chalepteryx	Mimosaceae	*Acacia decurrens*	ANIC card [reared ex ovo (supplied by D.R. Holmes), No. 10/1958]
Chelepteryx chalepteryx	Mimosaceae	*Acacia mearnsii*	Coupar & Coupar 1991 [in captivity]
Chelepteryx chalepteryx	Mimosaceae	*Acacia* spp. (bipinnate)	Common 1990 [in captivity]; Coupar & Coupar 1992; Herbison-Evans & Crossley
Chelepteryx chalepteryx	Mimosaceae	*Acacia* sp.	Common 1963; VJ Robinson card; HOSTS
Chelepteryx chalepteryx	Myrtaceae	*Eucalyptus* sp.	Gallard 1931
Chelepteryx chalepteryx	Pinaceae	*Pinus radiata*	Moore 1963a, b; HOSTS
Chelepteryx chalepteryx	Pinaceae	*Pinus* spp.	Coupar & Coupar 1992; Herbison-Evans & Crossley
Chelepteryx chalepteryx	Poaceae	grasses	Gallard 1931 [occasionally]
Chelepteryx chalepteryx	Santalaceae	*Choretrum candollei*	Common 1990; Coupar & Coupar 1992; Herbison-Evans & Crossley
Chelepteryx chalepteryx	Santalaceae	*Choretrum* sp.	HOSTS
Chelepteryx chalepteryx	Santalaceae	*Exocarpos cupressiformis*	Common 1990; Coupar & Coupar 1992; Herbison-Evans & Crossley; own observation [bred in captivity, caterpillars died in L2/L3]
Chelepteryx chalepteryx	Santalaceae	*Exocarpos* sp.	ANIC card [VIC, Red Hill (D.R. Holmes pers. comm.)]; HOSTS
Chelepteryx collesi	Myrtaceae	*Angophora costata*	Ramirez 1978
Chelepteryx collesi	Myrtaceae	*Angophora* spp.	Herbison-Evans & Crossley
Chelepteryx collesi	Myrtaceae	*Eucalyptus andreana*	VJ Robinson card
Chelepteryx collesi	Myrtaceae	*Eucalyptus botryoides*	Ramirez 1978
Chelepteryx collesi	Myrtaceae	*Eucalyptus capitellata*	Ramirez 1978
Chelepteryx collesi	Myrtaceae	*Eucalyptus corymbosa*	Strand 1925
Chelepteryx collesi	Myrtaceae	*Eucalyptus globoidea*	Lee 1975; Ramirez 1978
Chelepteryx collesi	Myrtaceae	*Eucalyptus haemastoma*	Froggatt 1923; Hadlington 1969; McMaugh 1985
Chelepteryx collesi	Myrtaceae	*Eucalyptus haemastoma / racemosa / sclerophylla* ("Scribbly Gum")	Anonymous 1941
Chelepteryx collesi	Myrtaceae	*Eucalyptus macrorhyncha*	ANIC card [ACT, Canberra (No. 47/1956)]; Southcott 1978
Chelepteryx collesi	Myrtaceae	*Eucalyptus mannifera maculosa*	Southcott 1978; own observation [field observation, numerous caterpillars completing lifecycle]

anthelid species	host plant family	host plant species	source
Chelepteryx collesi	Myrtaceae	*Eucalyptus piperita*	Ramirez 1978
Chelepteryx collesi	Myrtaceae	*Eucalyptus rossii*	ANIC card [ACT, Canberra (No. 47/1956)]
Chelepteryx collesi	Myrtaceae	*Eucalyptus sideroxylon*	Ramirez 1978
Chelepteryx collesi	Myrtaceae	*Eucalyptus stellulata*	Glenn Cocking (ANIC, pers. comm.) [field observation]
Chelepteryx collesi	Myrtaceae	*Eucalyptus viminalis*	Chisholm 1923
Chelepteryx collesi	Myrtaceae	*Eucalyptus* sp. ("Box Gum")	Fanning 1913
Chelepteryx collesi	Myrtaceae	*Eucalyptus* sp.	HOSTS
Chelepteryx collesi	Myrtaceae	*Eucalyptus* spp. ("White-stemmed Gum"	Anonymous 1941
Chelepteryx collesi	Myrtaceae	*Eucalyptus* spp.	Scott 1864; Palmer 1885; McCoy 1890; Common 1963, 1970, 1990; Herbison-Evans & Crossley
Chelepteryx collesi	Myrtaceae	*Lophostemon confertus*	McMaugh 1985; Herbison-Evans & Crossley
Chelepteryx collesi	Myrtaceae	*Melaleuca quinquenervia*	Herbison-Evans & Crossley
Chelepteryx collesi	Myrtaceae	*Tristania conferta*	Ramirez 1978
Chelepteryx collesi	Pittosporaceae	*Pittosporum* sp.	Lee 1975
Chelepteryx collesi	Proteaceae	*Xylomelum pyriforme*	Chisholm 1925
Chenuala heliaspis	Mimosaceae	*Acacia decurrens*	VJ Robinson card
Chenuala heliaspis	Mimosaceae	*Acacia mearnsii*	Common 1990 [caterpillars found near Wilton by Jessop]; Coupar & Coupar 1992
Chenuala heliaspis	Mimosaceae	*Acacia* sp.	VJ Robinson card; HOSTS; Herbison-Evans & Crossley
Chenuala heliaspis	Myrtaceae	*Eucalyptus obliqua*	Coupar & Coupar 1992
Chenuala heliaspis	Myrtaceae	*Eucalyptus pauciflora*	ANIC card [ACT, Mt. Gingera, Feb. 1957, IFBC (No. 8/1957)]; Common 1990; Coupar & Coupar 1992; own observation [bred in captivity]
Chenuala heliaspis	Myrtaceae	*Eucalyptus* spp.	Scott 1893; Common 1970, 1990; Herbison-Evans & Crossley
Chenuala heliaspis	Myrtaceae	*Eucalyptus* sp	Moore 1963a, b; HOSTS
Chenuala heliaspis	Pinaceae	*Pinus engelmannii*	Moore 1963a, b; HOSTS
Chenuala heliaspis	Pinaceae	*Pinus patula*	Moore 1963a, b; HOSTS
Chenuala heliaspis	Pinaceae	*Pinus radiata*	Moore 1963a, b; ANIC card [nr Blayney (det. IFBC 1960)]; Common 1970, 1990; HOSTS
Chenuala heliaspis	Pinaceae	*Pinus* spp.	Coupar & Coupar 1992
Chenuala heliaspis	Pinaceae	*Pinus* sp.	HOSTS; Herbison-Evans & Crossley

anthelid species	host plant family	host plant species	source
Munychryia periclyta	Casuarinaceae	*Casuarina* sp.	Common & McFarland 1970; McFarland 1979; Common 1990; VJ Robinson card; HOSTS
Munychryia senicula	Casuarinaceae	*Casuarina muelleriana*	Common & McFarland 1970
Munychryia senicula	Casuarinaceae	*Casuarina striata*	Common & McFarland 1970
Munychryia senicula	Casuarinaceae	*Casuarina* spp.	McFarland 1979; Common 1990; VJ Robinson card; HOSTS; own observation [bred in captivity]
Nataxa flavescens	Mimosaceae	*Acacia dealbata*	Berg 1982; ANIC card [ACT, Mt. Coree, April 1958, R. Straatman (No. 4/1958)]; ANIC card [NSW, Yass, 27.9.76, M.v.d.B. (det. IFBC, 1978)]; Coupar & Coupar 1992
Nataxa flavescens	Mimosaceae	*Acacia decurrens*	Berg 1982; ANIC card [ACT, Mt. Coree, April 1958, R. Straatman (No. 4/1958)]; ANIC card [ACT, Canberra, 14. MAR 1959 (reared and det. IFBC, 28/1959)]; ANIC card [NSW, Goulburn, 27.9.76, pupa in hole in dead branch, M.v.d.B. (det IFBC, 1978)]; own observation [bred in captivity]
Nataxa flavescens	Mimosaceae	*Acacia mearnsii*	Berg 1982; Coupar & Coupar 1992
Nataxa flavescens	Mimosaceae	*Acacia melanoxylon*	Berg 1982; Coupar & Coupar 1992
Nataxa flavescens	Mimosaceae	Acacia sp.	VJ Robinson card; Common 1963, 1990; HOSTS; Herbison-Evans & Crossley
Nataxa flavescens	Myrtaceae	*Eucalyptus* sp.	VJ Robinson card
Nataxa flavescens	Santalaceae	*Exocarpos* sp.	VJ Robinson card
Omphaliodes obscura	Mimosaceae	*Acacia leiophylla*	Jenkins
Pterolocera elizabetha	Mimosaceae	*Acacia saligna*	ANIC card [at WA, Bullbrook, 17.8.75, M v.d.B., det. IFBC, 1976]; Berg 1980
Pterolocera elizabetha	Poaceae	*Phalaris aquatica*	ANIC card [WA, 4mls E Pinjarra, Aug. 1968, M.A.Mahon ("Larvae fed exposed on leaves and when supply was exhausted fed readily on "Phalaris Grass", p...ic and rye grasses (88/1965)")]

anthelid species	host plant family	host plant species	source
Pterolocera elizabetha	Xanthorrhoeaceae	*Xanthorrhoea preissii*	ANIC card [WA, 4mls E Pinjarra, Aug. 1968, M.A.Mahon ("Larvae fed exposed on leaves and when supply was exhausted fed readily on "Phalaris Grass", p...ic and rye grasses (88/1965)")]
Pterolocera isogama	Mimosaceae	*Acacia acuminata*	McGauran 1951; Day *et al.* 1953, most prob. based on McGauran 1951
Pterolocera isogama	Mimosaceae	*Acacia* spp.	McGauran 1951; HOSTS
Pterolocera sp. (ACT, Canberra)	Poaceae	native grasses	ANIC card [ACT, Canberra, Oct. 1958, emg. Feb. 1959, No. 23/1958]; own observation [bred in captivity]
Pterolocera sp. (ACT)	Poaceae	native grass pastures	Day *et al.* 1953 [as *Pterolocera amplicornis*]
Pterolocera sp. (NSW, Cobar area)	Poaceae	*Triodia irritans*	VJ Robinson card
Pterolocera sp. (TAS)	Cyperaceae	*Gymnoschoenus sphaerocephalus*	Brown *et al.* 1993
Pterolocera sp. (TAS)	Mimosaceae	*Acacia dealbata*	Bashford 1990
Pterolocera sp. (TAS)	Poaceae	pastures	Hardy *et al.* 1980 [as *Pterolocera amplicornis*]
Pterolocera sp. (TAS)	Poaceae	pastures	Martyn et al. 1972, 1975, 1977 [as *Pterolocera amplicornis*]; Terauds *et al.* 1985 [as *Pterolocera amplicornis*]
Pterolocera sp. (TAS)		various garden plants	Terauds *et al.* 1986 [as *Pterolocera amplicornis*]
Pterolocera sp. (WA)	Cyperaceae	sedge	own observation [field observation, three specimens, all parasitized by Tachinidae]
Pterolocera sp. (WA)	Mimosaceae	*Acacia cyclops*	Berg 1980
Pterolocera sp. (WA)	Proteaceae	*Banksia* spp.	own observation [field observation; found on *Banksia* sp., completed life cycle on various *Banksia* spp. in captivity]
Pterolocera sp. 0 (SA)	Cyperaceae	*Lepidosperma viscidum*	Andy Young (SA, Kangaroo Isl., pers. comm.) [field observation]
Pterolocera sp. 0 (SA)	Cyperaceae	*Gahnia hystrix*	Andy Young (SA, Kangaroo Isl., pers. comm.) [field observation]
Pterolocera sp. 0 (SA)	Fabaceae	*Daviesia genistifolia*	Andy Young (SA, Kangaroo Isl., pers. comm.) [field observation]
Pterolocera sp. 1 (SA)	Casuarinaceae	*Casuarina striata*	McFarland 1979
Pterolocera sp. 1 (SA)	Fabaceae	*Daviesia brevifolia*	McFarland 1979
Pterolocera sp. 1 (SA)	Fabaceae	*Platylobium obtusangulum*	McFarland 1979
Pterolocera sp. 1 (SA)	Mimosaceae	*Acacia pycnantha*	McFarland 1979 [readily switched to from other plants in captivity]
Pterolocera sp. 1 (SA)	Poaceae	tough, wiry perennial bunch-grasses	McFarland 1979
Pterolocera sp. 1 (SA)	Proteaceae	*Hakea* (?)*muelleriana*	McFarland 1979

anthelid species	host plant family	host plant species	source
Pterolocera sp. 1 (SA)	Proteaceae	*Hakea rostrata*	McFarland 1979
Pterolocera sp. 1 (SA)	Santalaceae	*Choretrum spicatum*	McFarland 1979
Pterolocera sp. 1 (SA)		woody shrubs	McFarland 1979
Pterolocera sp. 2 (WA)	Proteaceae	*Banksia marginata*	McFarland 1979 [accepted in captivity]
Pterolocera sp. 2 (WA)	Proteaceae	*Banksia sphaerocarpa*	McFarland 1979
Pterolocera sp. 3 (WA)	Cyperaceae	*Lepidosperma* sp.	McFarland 1979 [particularly]
Pterolocera sp. 3 (WA)	Cyperaceae	sedges	McFarland 1979
Pterolocera sp. 3 (WA)	Poaceae	grasses	McFarland 1979
Pterolocera sp. 4 (TAS)	Poaceae	*Boronia* sp.	Martyn 1974 [as *Pterolocera amplicornis*]
Pterolocera sp. 4 (TAS)	Poaceae	*Holcus lanatus*	Martyn 1974 [as *Pterolocera amplicornis*]
Pterolocera sp. 4 (TAS)	Poaceae	*Lolium perenne*	Martyn 1974 [as *Pterolocera amplicornis*]
Pterolocera sp. 5 (SA)	Apiaceae	*Daucus glochidiatus*	[McFarland 1979 [occasionally, as *Pterolocera* sp. near *amplicornis*]
Pterolocera sp. 5 (SA)	Apiaceae	*Hydrocotyle* sp.	[McFarland 1979 [occasionally, as *Pterolocera* sp. near *amplicornis*]
Pterolocera sp. 5 (SA)	Crassulaceae	*Crassula* sp.	[McFarland 1979 [occasionally, as *Pterolocera* sp. near *amplicornis*]
Pterolocera sp. 5 (SA)	Cyperaceae	*Gahnia lanigera*	[McFarland 1979 [occasionally, as *Pterolocera* sp. near *amplicornis*]
Pterolocera sp. 5 (SA)	Poaceae	*Poa bulbosa*	[McFarland 1979 [occasionally, as *Pterolocera* sp. near *amplicornis*]
Pterolocera sp. 5 (SA)	Poaceae	naturalized (annual) and (perennial) native grasses	McFarland 1979 [particularly, as *Pterolocera* sp. near *amplicornis*]
Pterolocera sp. (VIC)	Poaceae	*Danthonia spicata*	Herbison-Evans & Crossley [as *Pterolocera amplicornis*]
Pterolocera sp. ("mountain form")	Poaceae	*Poa* sp. ("Snowgrass")	VJ Robinson card
Pterolocera sp.	Fabaceae	*Trifolium* sp.	Common 1990; HOSTS
Pterolocera sp.	Poaceae	various grasses	Evans 1943 [as *Pterolocera amplicornis*]; VJ Robinson card [as *Pterolocera amplicornis*]
Pterolocera sp.	Poaceae	grasses	Common 1990
Pterolocera sp.	Poaceae	grass	Anderson 1892 [as *Pterolocera amplicornis*]; Common 1963, 1970 [as *Pterolocera amplicornis*]; HOSTS [as *Pterolocera amplicornis*]
Pterolocera sp.		low-growing shrubs	Common 1990
Pterolocera spp.	Poaceae	native pastures	Edwards & Fairey 1996

C.2) ANTHELID HOST RECORDS SORTED BY HOST PLANT

HOSTS – an online-database of the hostplants of the world's Lepidoptera by the Natural History Museum, London:
http://www.nhm.ac.uk/research-curation/projects/hostplants/

host plant family	host plant species	anthelid species	source
Apiaceae	*Daucus glochidiatus*	*Pterolocera* sp. 5 (SA)	[McFarland 1979 [occasionally, as *Pterolocera* sp. near *amplicornis*]
Apiaceae	*Hydrocotyle* sp.	*Pterolocera* sp. 5 (SA)	[McFarland 1979 [occasionally, as *Pterolocera* sp. near *amplicornis*]
Arecaceae	*Cocos nucifera*	*Anthela ekeikei*	Szent-Ivany & Catley 1960 [as *Darala rubeola*, which certainly is a wrong ID: probably *A. ekeikei* species group]
Arecaceae	palm tree	*Anthela acuta* (QLD, Brisbane)	Chew
Asteraceae	*Hypochoeris radicata*	*Anthela acuta*	own observation [field observation of two specimens; completed life cycle on host plant in captivity; host plant species not native to Australia]
Asteraceae	*Olearia argophylla*	*Anthela acuta*	Coupar & Coupar 1992; Herbison-Evans & Crossley
Barringtoniaceae	*Planchonia careya*	*Anthela acuta* (NT)	Southcott 1987
Caesalpiniaceae	*Cassia nemophila*	*Anthela* n. sp. near *repleta*	McFarland 1979
Caesalpiniaceae	*Cassia nemophila*	*Anthela callispila*	McFarland 1979 [as *Anthela* sp. near *guenei*]
Caesalpiniaceae	*Cassia* sp.	*Anthela callispila*	McFarland 1979 [as *Anthela* sp. near *guenei*]
Caesalpiniaceae	*Erythrophleum chlorostachys*	*Anthela* sp. (QLD, Mareeba)	McFarland 1979
Casuarinaceae	*Casuarina equisetifolia*	*Anthela ekeikei*	Szent-Ivany & Carver 1967
Casuarinaceae	*Casuarina muelleriana*	*Munychryia senicula*	Common & McFarland 1970
Casuarinaceae	*Casuarina striata*	*Pterolocera* sp. 1 (SA)	McFarland 1979
Casuarinaceae	*Casuarina striata*	*Munychryia senicula*	Common & McFarland 1970
Casuarinaceae	*Casuarina* spp.	*Munychryia senicula*	McFarland 1979; Common 1990; VJ Robinson card; HOSTS; own observation [bred in captivity]
Casuarinaceae	*Casuarina* sp.	*Munychryia periclyta*	Common & McFarland 1970; McFarland 1979; Common 1990; VJ Robinson card; HOSTS
Chenopodiaceae	*Atriplex vesicaria*	*Anthela* sp. (NSW)	ANIC card [NSW, Deniliquin, 30.9.1958, B. Fox (det. IFBC 1960 and 1976; examples in ANIC)]

host plant family	host plant species	anthelid species	source
Chenopodiaceae	*Atriplex* spp.	*Anthela denticulata*	Froggatt 1910 [dubious record, see "Introduction – economic and medical records"]
Crassulaceae	*Crassula* sp.	*Pterolocera* sp. 5 (SA)	[McFarland 1979 [occasionally, as *Pterolocera* sp. near *amplicornis*]
Cyperaceae	*Gahnia hystrix*	*Pterolocera* sp. 0 (SA)	Andy Young (SA, Kangaroo Isl., pers. comm.) [field observation]
Cyperaceae	*Gahnia lanigera*	*Pterolocera* sp. 5 (SA)	[McFarland 1979 [occasionally, as *Pterolocera* sp. near *amplicornis*]
Cyperaceae	*Gymnoschoenus sphaerocephalus*	*Pterolocera* sp. (TAS)	Brown *et al.* 1993
Cyperaceae	*Lepidosperma viscidum*	*Pterolocera* sp. 0 (SA)	Andy Young (SA, Kangaroo Isl., pers. comm.) [field observation]
Cyperaceae	*Lepidosperma* sp.	*Pterolocera* sp. 3 (WA)	McFarland 1979 [particularly]
Cyperaceae	sedge	*Pterolocera sp. (WA)*	own observation [field observation, three specimens, all parasitized by Tachinidae]
Euphorbiaceae	*Glochidion ferdinandi*	*Anthela astata*	Nathan 1960 [probably wrong ID: *A. acuta / astata* grp or *A. excellens]*
Fabaceae	*Chamaecytisus prolifer*	*Anthela nicothoe*	Hadlington 1963
Fabaceae	*Daviesia brevifolia*	*Pterolocera* sp. 1 (SA)	McFarland 1979
Fabaceae	*Daviesia genistifolia*	*Pterolocera sp. 0 (SA)*	Andy Young (SA, Kangaroo Isl., pers. comm.) [field observation]
Fabaceae	*Jacksonia* sp.	*Anthela guenei*	Common 1990; HOSTS
Fabaceae	*Platylobium obtusangulum*	*Pterolocera* sp. 1 (SA)	McFarland 1979
Fabaceae	*Trifolium* sp.	*Chelepteryx chalepteryx*	Gallard 1931 [initially]
Fabaceae	*Trifolium* sp.	*Pterolocera* sp.	Common 1990; HOSTS
Fabaceae	*Vicia faba*	*Anthela acuta*	ANIC card [at Taree in Sept., "NSW Ins. Pest Survey, 1953, p. 18"]
Fagaceae	*Fagus sylvatica*	*Anthela acuta* (TAS)	Herbison-Evans & Crossley
Fagaceae	*Quercus robur*	*Anthela acuta* (TAS)	Herbison-Evans & Crossley
Fagaceae	*Quercus* sp.	*Anthela* sp. (TAS)	Bashford 1990
Juglandaceae	*Carya "diviformis"*	*Anthela varia*	ANIC card [at QLD, Nambour, Mar. 1968, larvae on foliage (det. IFBC, 1970), D816]
Juglandaceae	*Carya* sp.	*Anthela varia*	Common 1990; HOSTS
Mimosaceae	*Acacia* sp.	*Anthela* sp. (QLD, Brisbane)	Chew
Mimosaceae	*Acacia acuminata*	*Anthela xantharcha*	Mills 1954
Mimosaceae	*Acacia acuminata*	*Pterolocera isogama*	McGauran 1951; Day *et al.* 1953, most prob. based on McGauran 1951
Mimosaceae	*Acacia aneura*	*Anthela reltoni*	own observation [bred in captivity]
Mimosaceae	*Acacia aneura*	*Anthela tetraphrica*	own observation [bred in captivity]

host plant family	host plant species	anthelid species	source
Mimosaceae	*Acacia baileyana*	*Anthela acuta*	own observation [bred in captivity]
Mimosaceae	*Acacia baileyana*	*Anthela astata*	own observation [bred in captivity]
Mimosaceae	*Acacia baileyana*	*Anthela excellens*	own observation [bred in captivity]
Mimosaceae	*Acacia baileyana*	*Anthela nicothoe*	own observation [bred in captivity]
Mimosaceae	*Acacia binervata*	*Anthela repleta*	Berg 1982ANIC card [NSW, Robertson, 26.4.76, M.v.d.B. (det. IFBC, 1976)]Common 1990Herbison-Evans & Crossley
Mimosaceae	*Acacia cyclops*	*Pterolocera* sp. (WA)	Berg 1980
Mimosaceae	*Acacia dealbata*	*Anthela addita*	Bashford 1997
Mimosaceae	*Acacia dealbata*	*Anthela guenei*	Common 1990; Herbison-Evans & Crossley
Mimosaceae	*Acacia dealbata*	*Anthela nicothoe*	Berg 1982; ANIC card ["Brindabella race", Mt. Coree, June 1957, emg. Aug. 1958 (R. Straatman), No. 24/1957)]; Common 1963, 1990; Hadlington 1963; HOSTS
Mimosaceae	*Acacia dealbata*	*Anthela ocellata*	Bashford 1997
Mimosaceae	*Acacia dealbata*	*Anthela* sp.	Bashford 1997
Mimosaceae	*Acacia dealbata*	*Nataxa flavescens*	Berg 1982; ANIC card [ACT, Mt. Coree, April 1958, R. Straatman (No. 4/1958)]; ANIC card [NSW, Yass, 27.9.76, M.v.d.B. (det. IFBC, 1978)]; Coupar & Coupar 1992
Mimosaceae	*Acacia dealbata*	*Pterolocera* sp. (TAS)	Bashford 1990
Mimosaceae	*Acacia decurrens*	*Anthela guenei*	VJ Robinson card; Common 1990; Herbison-Evans & Crossley
Mimosaceae	*Acacia decurrens*	*Anthela postica*	VJ Robinson card [as *A. callicesta*]; Common 1990 [bred in captivity]; Herbison-Evans & Crossley
Mimosaceae	*Acacia decurrens*	*Anthela* sp. (WA)	VJ Robinson card [60mls. E. Geraldton]
Mimosaceae	*Acacia decurrens*	*Anthela varia*	VJ Robinson card
Mimosaceae	*Acacia decurrens*	*Chelepteryx chalepteryx*	ANIC card [reared ex ovo (supplied by D.R. Holmes), No. 10/1958]
Mimosaceae	*Acacia decurrens*	*Chenuala heliaspis*	VJ Robinson card
Mimosaceae	*Acacia decurrens*	*Nataxa flavescens*	Berg 1982; ANIC card [ACT, Mt. Coree, April 1958, R. Straatman (No. 4/1958)]; ANIC card [ACT, Canberra, 14. MAR 1959 (reared and det. IFBC, 28/1959)]; ANIC card [NSW, Goulburn, 27.9.76, pupa in hole in dead branch, M.v.d.B. (det IFBC, 1978)]; own observation [bred in captivity]
Mimosaceae	*Acacia excelsa*	*Anthela stygiana*	VJ Robinson card [as *A. magnifica*]

host plant family	host plant species	anthelid species	source
Mimosaceae	*Acacia floribunda*	*Anthela repleta*	VJ Robinson card; Common 1990; Herbison-Evans & Crossley
Mimosaceae	*Acacia harpophylla*	*Anthela asciscens*	Common 1990
Mimosaceae	*Acacia harpophylla*	*Anthela stygiana*	Common 1990 [as *A. magnifica*]
Mimosaceae	*Acacia leiophylla*	*Omphaliodes obscura*	Jenkins
Mimosaceae	*Acacia ligulata*	*Anthela exoleta*	McFarland 1979 [as *Anthela glauerti*, bred]
Mimosaceae	*Acacia longifolia*	*Anthela excellens*	ANIC card [larvae feeding on phyllodes at NSW, Heathcote, 11.4.75 (M.v.d.B., det. IFBC, 1978)]; Berg 1982
Mimosaceae	*Acacia longifolia*	*Anthela repleta*	Berg 1982
Mimosaceae	*Acacia longifolia.*	*Anthela connexa*	Herbison-Evans & Crossley
Mimosaceae	*Acacia mearnsii*	*Anthela excellens*	Berg 1982
Mimosaceae	*Acacia mearnsii*	*Anthela repleta*	ANIC card [NSW, Waterfall, 20.7.76, M.v.d.B. (det. IFBC, 1978)]; Berg 1982; Common 1990; Herbison-Evans & Crossley
Mimosaceae	*Acacia mearnsii*	*Chelepteryx chalepteryx*	Coupar & Coupar 1991 [in captivity]
Mimosaceae	*Acacia mearnsii*	*Nataxa flavescens*	Berg 1982; Coupar & Coupar 1992
Mimosaceae	*Acacia mearnsii*	*Chenuala heliaspis*	Common 1990 [caterpillars found near Wilton by Jessop]Coupar & Coupar 1992
Mimosaceae	*Acacia melanoxylon*	*Anthela acuta*	own observation [bred in captivity]
Mimosaceae	*Acacia melanoxylon*	*Anthela astata*	own observation [bred in captivity]
Mimosaceae	*Acacia melanoxylon*	*Anthela clementi*	own observation [bred in captivity, but most caterpillars and finally single pupa died]
Mimosaceae	*Acacia melanoxylon*	*Anthela connexa*	Herbison-Evans & Crossley
Mimosaceae	*Acacia melanoxylon*	*Anthela excellens*	VJ Robinson card
Mimosaceae	*Acacia melanoxylon*	*Anthela guenei*	own observation [bred in captivity]
Mimosaceae	*Acacia melanoxylon*	*Anthela nicothoe*	VJ Robinson card; own observation [bred in captivity]
Mimosaceae	*Acacia melanoxylon*	*Anthela reltoni*	own observation [bred in captivity, but died in final instar]
Mimosaceae	*Acacia melanoxylon*	*Anthela repleta*	Berg 1982; Common 1990; Herbison-Evans & Crossley; own observation [bred in captivity]
Mimosaceae	*Acacia melanoxylon*	*Anthela rubicunda*	own observation [bred in captivity, but died in final instar]
Mimosaceae	*Acacia melanoxylon*	*Anthela stygiana*	own observation [bred in captivity]
Mimosaceae	*Acacia melanoxylon*	*Anthela unisigna*	own observation [bred in captivity]

host plant family	host plant species	anthelid species	source
Mimosaceae	*Acacia melanoxylon*	*Anthela xantharcha*	own observation [bred in captivity]
Mimosaceae	*Acacia melanoxylon*	*Nataxa flavescens*	Berg 1982; Coupar & Coupar 1992
Mimosaceae	*Acacia* sp. (prob. *penninervis*)	*Anthela repleta*	ANIC card [NSW, 13 mls SE Braidwood (No. 20/1957)]
Mimosaceae	*Acacia pycnantha*	*Anthela* n. sp. near *repleta*	McFarland 1979
Mimosaceae	*Acacia pycnantha*	*Anthela rubeola*	Herbison-Evans & Crossley
Mimosaceae	*Acacia pycnantha*	*Anthela xantharcha*	McFarland 1979 [bred, probably *A. xantharcha*]
Mimosaceae	*Acacia pycnantha*	*Pterolocera* sp. 1 (SA)	McFarland 1979 [readily switched to from other plants in captivity]
Mimosaceae	*Acacia saligna*	*Pterolocera elizabetha*	ANIC card [at WA, Bullbrook, 17.8.75, M v.d.B., det. IFBC, 1976]; Berg 1980
Mimosaceae	*Acacia* spp. (bipinnate)	*Chelepteryx chalepteryx*	Common 1990 [in captivity]; Coupar & Coupar 1992; Herbison-Evans & Crossley
Mimosaceae	*Acacia* spp. ("Broadleaf Wattles")	*Anthela asterias*	Herbison-Evans & Crossley
Mimosaceae	*Acacia* spp. ("various broad leaved wattles")	*Anthela nicothoe*	Herbison-Evans & Crossley
Mimosaceae	*Acacia* spp.	*Anthela acuta*	Coupar & Coupar 1992; Herbison-Evans & Crossley
Mimosaceae	*Acacia* spp.	*Anthela connexa*	Elliott & de Little 1985
Mimosaceae	*Acacia* spp.	*Anthela excellens*	Common 1990
Mimosaceae	*Acacia* spp.	*Anthela guenei*	Common 1990
Mimosaceae	*Acacia* spp.	*Anthela nicothoe*	Hadlington 1963; Moore 1963a, b; Elliott & de Little 1985; Coupar & Coupar 1992
Mimosaceae	*Acacia* spp.	*Anthela repleta*	Common 1990
Mimosaceae	*Acacia* spp.	*Pterolocera isogama*	McGauran 1951; HOSTS
Mimosaceae	*Acacia* sp	*Anthela postica*	VJ Robinson card [as *A. callicesta*]; HOSTS
Mimosaceae	*Acacia* sp.	*Anthela asciscens*	HOSTS
Mimosaceae	*Acacia* sp.	*Anthela excellens*	VJ Robinson card; HOSTS; Herbison-Evans & Crossley
Mimosaceae	*Acacia* sp.	*Anthela guenei*	VJ Robinson card; HOSTS
Mimosaceae	*Acacia* sp.	*Anthela nicothoe*	VJ Robinson card; HOSTS
Mimosaceae	*Acacia* sp.	*Anthela repleta*	VJ Robinson card; HOSTS
Mimosaceae	*Acacia* sp.	*Anthela stygiana*	HOSTS [as *A. magnifica*]
Mimosaceae	*Acacia* sp.	*Anthela varia*	VJ Robinson card
Mimosaceae	*Acacia* sp.	*Anthela xantharcha*	Common 1990; HOSTS

host plant family	host plant species	anthelid species	source
Mimosaceae	*Acacia* sp.	*Chelepteryx chalepteryx*	Common 1963; VJ Robinson card; HOSTS
Mimosaceae	*Acacia* sp.	*Chenuala heliaspis*	VJ Robinson card; HOSTS; Herbison-Evans & Crossley
Mimosaceae	Acacia sp.	*Nataxa flavescens*	VJ Robinson cardCommon 1963, 1990HOSTSHerbison-Evans & Crossley
Myrtaceae	*Angophora costata*	*Chelepteryx collesi*	Ramirez 1978
Myrtaceae	*Angophora* spp.	*Chelepteryx collesi*	Herbison-Evans & Crossley
Myrtaceae	*Corymbia torelliana*	*Anthela canescens*	Herbison-Evans & Crossley
Myrtaceae	*Eucalyptus amygdalina*	*Anthela* sp. (TAS)	Bashford 1990
Myrtaceae	*Eucalyptus andreana*	*Chelepteryx collesi*	VJ Robinson card
Myrtaceae	*Eucalyptus blakelyi*	*Anthela varia*	ANIC card [ACT, Canberra, NJR Mitchell (det. EDE), No. 44/1971]; Landsberg 1988
Myrtaceae	*Eucalyptus botryoides*	*Chelepteryx collesi*	Ramirez 1978
Myrtaceae	*Eucalyptus camaldulensis*	*Anthela excellens*	VJ Robinson card
Myrtaceae	*Eucalyptus capitellata*	*Chelepteryx collesi*	Ramirez 1978
Myrtaceae	*Eucalyptus corymbosa*	*Chelepteryx collesi*	Strand 1925
Myrtaceae	*Eucalyptus fastigata*	*Anthela varia*	VJ Robinson card
Myrtaceae	*Eucalyptus globoidea*	*Chelepteryx collesi*	Lee 1975; Ramirez 1978
Myrtaceae	*Eucalyptus haemastoma*	*Chelepteryx collesi*	Froggatt 1923; Hadlington 1969; McMaugh 1985
Myrtaceae	*Eucalyptus haemastoma / racemosa / sclerophylla* ("Scribbly Gum")	*Chelepteryx collesi*	Anonymous 1941
Myrtaceae	*Eucalyptus leucoxylon*	*Anthela varia*	Edwards & Wanjura 1989
Myrtaceae	*Eucalyptus macrorhyncha*	*Chelepteryx collesi*	ANIC card [ACT, Canberra (No. 47/1956)]; Southcott 1978
Myrtaceae	*Eucalyptus mannifera maculosa*	*Chelepteryx collesi*	Southcott 1978; own observation [field observation, numerous caterpillars completing lifecycle]
Myrtaceae	*Eucalyptus obliqua*	*Anthela nicothoe*	ANIC card [*Anthela* sp. near *A. nicothoe* defoliating trees at TAS, New Norfolk, 18.1.78, H. Elliott (emg 20.2.78; det. IFBC, 1978)]
Myrtaceae	*Eucalyptus obliqua*	*Anthela* sp. (TAS)	Bashford 1990
Myrtaceae	*Eucalyptus obliqua*	*Chenuala heliaspis*	Coupar & Coupar 1992

host plant family	host plant species	anthelid species	source
Myrtaceae	*Eucalyptus pauciflora*	*Chenuala heliaspis*	ANIC card [ACT, Mt. Gingera, Feb. 1957, IFBC (No. 8/1957)]; Common 1990; Coupar & Coupar 1992; own observation [bred in captivity]
Myrtaceae	*Eucalyptus piperita*	*Chelepteryx collesi*	Ramirez 1978
Myrtaceae	*Eucalyptus robusta*	*Anthela acuta*	Beutenmüller 1891
Myrtaceae	*Eucalyptus rossii*	*Chelepteryx collesi*	ANIC card [ACT, Canberra (No. 47/1956)]
Myrtaceae	*Eucalyptus sideroxylon*	*Chelepteryx collesi*	Ramirez 1978
Myrtaceae	*Eucalyptus stellulata*	*Chelepteryx collesi*	Glenn Cocking (ANIC, pers. comm.) [field observation]
Myrtaceae	*Eucalyptus viminalis*	*Anthela* sp. (NSW, ACT)	Chisholm 1923; Riek 1962
Myrtaceae	*Eucalyptus viminalis*	*Chelepteryx collesi*	Chisholm 1923
Myrtaceae	*Eucalyptus* spp. ("White-stemmed Gum"	*Chelepteryx collesi*	Anonymous 1941
Myrtaceae	*Eucalyptus* spp. (and less frequently many other plants)	*Anthela acuta*	Illidge 1913
Myrtaceae	*Eucalyptus* spp.	*Anthela canescens*	own observation [bred in captivity]
Myrtaceae	*Eucalyptus* spp.	*Anthela varia*	Scott 1893 [as *A. hamata*]; Strand 1925 [as *A. hamata*]; Teakle 1969; Common 1990; Herbison-Evans & Crossley; own observation [bred in captivity]
Myrtaceae	*Eucalyptus* spp.	*Chelepteryx collesi*	Scott 1864; Palmer 1885; McCoy 1890; Common 1963, 1970, 1990; Herbison-Evans & Crossley
Myrtaceae	*Eucalyptus* spp.	*Chenuala heliaspis*	Scott 1893Common 1970, 1990Herbison-Evans & Crossley
Myrtaceae	*Eucalyptus* sp. ("Box Gum")	*Chelepteryx collesi*	Fanning 1913
Myrtaceae	*Eucalyptus* sp	*Chenuala heliaspis*	Moore 1963a, b; HOSTS
Myrtaceae	*Eucalyptus* sp.	*Anthela excellens*	VJ Robinson card
Myrtaceae	*Eucalyptus* sp.	*Anthela rubicunda*	Lower 1903 [quoted G. Barnard]
Myrtaceae	*Eucalyptus* sp.	*Anthela* sp. (QLD, Brisbane)	Chew
Myrtaceae	*Eucalyptus* sp.	*Anthela varia*	VJ Robinson card; Monteith 1995; Chew; HOSTS
Myrtaceae	*Eucalyptus* sp.	*Chelepteryx chalepteryx*	Gallard 1931
Myrtaceae	*Eucalyptus* sp.	*Chelepteryx collesi*	HOSTS

host plant family	host plant species	anthelid species	source
Myrtaceae	*Eucalyptus* sp.	*Nataxa flavescens*	VJ Robinson card
Myrtaceae	*Lophostemon confertus*	*Chelepteryx collesi*	McMaugh 1985; Herbison-Evans & Crossley
Myrtaceae	*Melaleuca quinquenervia*	*Chelepteryx collesi*	Herbison-Evans & Crossley
Myrtaceae	*Tristania conferta*	*Chelepteryx collesi*	Ramirez 1978
Pinaceae	*Pinus engelmannii*	*Chenuala heliaspis*	Moore 1963a, b; HOSTS
Pinaceae	*Pinus patula*	*Anthela ekeikei*	Roberts 1987; HOSTS
Pinaceae	*Pinus patula*	*Chenuala heliaspis*	Moore 1963a, b; HOSTS
Pinaceae	*Pinus radiata*	*Anthela excellens*	Moore 1963a, b; HOSTS
Pinaceae	*Pinus radiata*	*Anthela nicothoe*	Hadlington 1963; Moore 1963a, b; Common 1970, 1990; Campbell 1972; HOSTS
Pinaceae	*Pinus radiata*	*Anthela ocellata*	Moore 1963a, b; HOSTS
Pinaceae	*Pinus radiata*	*Anthela* sp. (TAS)	Bashford 1990
Pinaceae	*Pinus radiata*	*Chelepteryx chalepteryx*	Moore 1963a, b; HOSTS
Pinaceae	*Pinus radiata*	*Chenuala heliaspis*	Moore 1963a, b; ANIC card [nr Blayney (det. IFBC 1960)]; Common 1970, 1990; HOSTS
Pinaceae	*Pinus radiata*	*Anthela connexa*	Elliott & de Little 1985; Bashford 1990
Pinaceae	*Pinus radiata*	*Anthela varia*	Moore 1963a, b
Pinaceae	*Pinus* spp.	*Anthela nicothoe*	Coupar & Coupar 1992
Pinaceae	*Pinus* spp.	*Chelepteryx chalepteryx*	Coupar & Coupar 1992; Herbison-Evans & Crossley
Pinaceae	*Pinus* spp.	*Chenuala heliaspis*	Coupar & Coupar 1992
Pinaceae	*Pinus* sp.	*Anthela* sp. (TAS)	Hardy *et al.* 1979
Pinaceae	*Pinus* sp.	*Chenuala heliaspis*	HOSTS; Herbison-Evans & Crossley
Pittosporaceae	*Pittosporum* sp.	*Chelepteryx collesi*	Lee 1975
Poaceae	*Axonopus affinis*	*Anthela ocellata*	Moore 1963b
Poaceae	*Boronia* sp.	*Pterolocera* sp. 4 (TAS)	Martyn 1974 [as *Pterolocera amplicornis*]
Poaceae	*Bromus arenaria*	*Anthela euryphrica*	Turner 1936
Poaceae	*Cynodon dactylon*	*Anthela ocellata*	Moore 1963b

host plant family	host plant species	anthelid species	source
Poaceae	*Cynodon dactylon*	*Anthela oressarcha*	VJ Robinson card [L1 from female ex "The Long Plain" near Kiandra accepted "Turfgrass", "Bermudagrass", "Parramatta Grass"]
Poaceae	*Danthonia spicata*	*Pterolocera* sp. (VIC)	Herbison-Evans & Crossley [as *Pterolocera amplicornis*]
Poaceae	*Ehrharta erecta*	*Anthela ocellata*	Coupar & Coupar 1992; Herbison-Evans & Crossley
Poaceae	*Holcus lanatus*	*Pterolocera* sp. 4 (TAS)	Martyn 1974 [as *Pterolocera amplicornis*]
Poaceae	*Hordeum leporinum*	*Anthela euryphrica*	ANIC card [label data on specimen from NSW, Murrurundi, reared by Middleton, 26.5.34, CSIRO: "Fairy Grass" & "Barley Grass"]
Poaceae	*Lolium perenne*	*Anthela ocellata*	McQuillan & Forrest 1985
Poaceae	*Lolium perenne*	*Pterolocera* sp. 4 (TAS)	Martyn 1974 [as *Pterolocera amplicornis*]
Poaceae	*Pennisetum clandestinum*	*Anthela ferruginosa*	VJ Robinson card
Poaceae	*Phalaris aquatica*	*Pterolocera elizabetha*	ANIC card [WA, 4mls E Pinjarra, Aug. 1968, M.A.Mahon ("Larvae fed exposed on leaves and when supply was exhausted fed readily on "Phalaris Grass", p...ic and rye grasses (88/1965)")]
Poaceae	*Poa bulbosa*	*Pterolocera* sp. 5 (SA)	[McFarland 1979 [occasionally, as *Pterolocera* sp. near *amplicornis*]
Poaceae	*Poa* sp.	*Anthela oressarcha*	VJ Robinson card [leaves and young spikes of "snowgrass" *Poa* sp.]
Poaceae	*Poa* sp. ("Snowgrass")	*Pterolocera* sp. ("mountain form")	VJ Robinson card
Poaceae	*Saccharum officinarum*	*Anthela acuta*	HOSTS
Poaceae	*Sporobolus indicus*	*Anthela oressarcha*	VJ Robinson card [L1 from female ex "The Long Plain" near Kiandra accepted "Turfgrass", "Bermudagrass", "Parramatta Grass"]
Poaceae	*Sporobolus caroli*	*Anthela euryphrica*	ANIC card [label data on specimen from NSW, Murrurundi, reared by Middleton, 26.5.34, CSIRO: "Fairy Grass" & "Barley Grass"]
Poaceae	*Stenotaphrum secundatum*	*Anthela ferruginosa*	VJ Robinson card
Poaceae	*Themeda triandra*	*Anthela ocellata*	own observation [field observation; completed life cycle on introduced grasses in captivity]
Poaceae	*Triodia irritans*	*Pterolocera* sp. (NSW, Cobar area)	VJ Robinson card
Poaceae	*Triticum aestivum*	*Anthela euryphrica*	Herbison-Evans & Crossley
Poaceae	*Triticum* sp. ("wheat")	*Anthela euryphrica*	Common 1990
Poaceae	*Triticum* sp. ("wheat")	*Anthela ocellata*	ANIC card ["published record"]
Poaceae	tough, wiry perennial bunch-grasses	*Pterolocera* sp. 1 (SA)	McFarland 1979

host plant family	host plant species	anthelid species	source
Poaceae	grasses (soft, introduced species)	*Anthela addita*	own observation [bred in captivity]
Poaceae	grasses (soft, introduced species)	*Anthela ferruginosa*	own observation [bred in captivity]
Poaceae	mixed lawn grasses	*Anthela ocellata*	McFarland 1979; own observation [bred in captivity]
Poaceae	native grass pastures	*Pterolocera* sp. (ACT)	Day *et al.* 1953 [as *Pterolocera amplicornis*]
Poaceae	native grasses	*Anthela cnecias*	own observation [bred in captivity, but died in final instar]
Poaceae	native grasses	*Anthela oressarcha*	own observation [bred in captivity, but died in L3]
Poaceae	native grasses	*Pterolocera* sp. (ACT, Canberra)	ANIC card [ACT, Canberra, Oct. 1958, emg. Feb. 1959, No. 23/1958]; own observation [bred in captivity]
Poaceae	native pastures	*Pterolocera* spp.	Edwards & Fairey 1996
Poaceae	naturalized (annual) and (perennial) native grasses	*Pterolocera* sp. 5 (SA)	McFarland 1979 [particularly, as *Pterolocera* sp. near *amplicornis*]
Poaceae	naturalized and native grasses (esp. "soft" annual spp.)	*Anthela denticulata*	naturalized and native grasses (esp. "soft" annual spp.) [McFarland 1979]
Poaceae	pastures	*Anthela ocellata*	Leach 1952
Poaceae	pastures	*Pterolocera* sp. (TAS)	Martyn et al. 1972, 1975, 1977 [as *Pterolocera amplicornis*]; Terauds *et al.* 1985 [as *Pterolocera amplicornis*]
Poaceae	pastures	*Pterolocera* sp. (TAS)	Hardy *et al.* 1980 [as *Pterolocera amplicornis*]
Poaceae	various naturalized annual grasses	*Anthela ocellata*	McFarland 1979
Poaceae	various native grasses	*Anthela ocellata*	Moore 1963b
Poaceae	various grasses	*Anthela basigera*	Herbison-Evans & Crossley
Poaceae	various grasses	*Anthela denticulata*	Herbison-Evans & Crossley
Poaceae	various grasses	*Anthela ocellata*	French 1911; Brewster et al.1920; VJ Robinson card; ANIC card [Canberra, No. 26/1956]; Common 1963, 1990; McQuillan & Forrest 1985
Poaceae	various grasses	*Anthela oressarcha*	Herbison-Evans & Crossley
Poaceae	various grasses	*Pterolocera* sp.	Evans 1943 [as *Pterolocera amplicornis*]VJ Robinson card [as *Pterolocera amplicornis*]
Poaceae	grasses (any soft sp.)	*Anthela acuta*	Haines 1963
Poaceae	grasses	*Anthela acuta*	VJ Robinson card; Herbison-Evans & Crossley
Poaceae	grasses	*Anthela basigera*	McQuillan & Forrest 1985
Poaceae	grasses	*Anthela denticulata*	Common 1990

host plant family	host plant species	anthelid species	source
Poaceae	grasses	*Anthela euryphrica*	Common 1990
Poaceae	grasses	*Anthela ferruginosa*	Common 1990
Poaceae	grasses	*Chelepteryx chalepteryx*	Gallard 1931 [occasionally]
Poaceae	grasses	*Pterolocera* sp.	Common 1990
Poaceae	grasses	*Pterolocera* sp. 3 (WA)	McFarland 1979
Poaceae	grass	*Anthela denticulata*	Anderson 1892; HOSTS
Poaceae	grass	*Anthela euryphrica*	HOSTS
Poaceae	grass	*Anthela ferruginosa*	HOSTS; Herbison-Evans & Crossley
Poaceae	grass	*Anthela ocellata*	HOSTS
Poaceae	grass	*Anthela oressarcha*	Common 1990 [bred in captivity]; HOSTS
Poaceae	grass	*Anthela ostra*	HOSTS
Poaceae	grass	*Pterolocera* sp.	Anderson 1892 [as *Pterolocera amplicornis*]; Common 1963, 1970 [as *Pterolocera amplicornis*]; HOSTS [as *Pterolocera amplicornis*]
[Poaceae]	crops	*Anthela denticulata*	Edwards & Fairey 1996
[Poaceae]	crops	*Anthela euryphrica*	Edwards & Fairey 1996
[Poaceae]	crops	*Anthela ostra*	Edwards & Fairey 1996
Proteaceae	*Banksia marginata*	*Pterolocera* sp. 2 (WA)	McFarland 1979 [accepted in captivity]
Proteaceae	*Banksia sphaerocarpa*	*Pterolocera* sp. 2 (WA)	McFarland 1979
Proteaceae	*Banksia* spp.	*Pterolocera sp. (WA)*	own observation [field observation; found on *Banksia* sp., completed life cycle on various *Banksia* spp. in captivity]
Proteaceae	*Grevillea* sp.	*Anthela varia*	Herbison-Evans & Crossley
Proteaceae	*Hakea* (?)*muelleriana*	*Pterolocera* sp. 1 (SA)	McFarland 1979
Proteaceae	*Hakea rostrata*	*Pterolocera* sp. 1 (SA)	McFarland 1979
Proteaceae	*Hakea sericea*	*Anthela acuta* (?)	Moore 1964
Proteaceae	*Macadamia integrifolia*	*Anthela varia*	Herbison-Evans & Crossley
Proteaceae	*Macadamia tetraphylla*	*Anthela varia*	Teakle 1969; HOSTS
Proteaceae	*Macadamia* sp.	*Anthela varia*	Ironside 1973, 1980, 1981, 1995
Proteaceae	*Stenocarpus* sp.	*Anthela varia*	Herbison-Evans & Crossley
Proteaceae	*Xylomelum pyriforme*	*Chelepteryx collesi*	Chisholm 1925
Rosaceae	*Prunus armeniaca*	*Anthela varia*	Teakle 1969
Salicaceae	*Salix* sp.	*Anthela varia*	Common 1990; HOSTS
Santalaceae	*Choretrum candollei*	*Chelepteryx chalepteryx*	Common 1990; Coupar & Coupar 1992; Herbison-Evans & Crossley

host plant family	host plant species	anthelid species	source
Santalaceae	*Choretrum spicatum*	*Pterolocera* sp. 1 (SA)	McFarland 1979
Santalaceae	*Choretrum* sp.	*Chelepteryx chalepteryx*	HOSTS
Santalaceae	*Exocarpos cupressiformis*	*Chelepteryx chalepteryx*	Common 1990; Coupar & Coupar 1992; Herbison-Evans & Crossley; own observation [bred in captivity, caterpillars died in L2/L3]
Santalaceae	*Exocarpos* sp.	*Chelepteryx chalepteryx*	ANIC card [VIC, Red Hill (D.R. Holmes pers. comm.)]; HOSTS
Santalaceae	*Exocarpos* sp.	*Nataxa flavescens*	VJ Robinson card
Sapindaceae	(?) *Atalaya hemiglauca*	*Anthela varia*	ANIC card [near Longreach some frass apparently killed outright (Q. Dep. Agric. Ent.): "Whitewood"]
Solanaceae	*Solanum cunninghamii*	*Anthela callixantha*	ANIC specimen label [caterpillars found on *S. cunninghamii*]
Solanaceae	*Solanum ellipticum*	*Anthela callixantha*	ANIC specimen label [caterpillars found on *S. ellipticum*, bred on S. *elaeagnifolium*]
Xanthorrhoeaceae	*Xanthorrhoea preissii*	*Pterolocera elizabetha*	ANIC card [WA, 4mls E Pinjarra, Aug. 1968, M.A.Mahon ("Larvae fed exposed on leaves and when supply was exhausted fed readily on "Phalaris Grass", p...ic and rye grasses (88/1965)")]
	low-growing shrubs	*Pterolocera* sp.	Common 1990
	woody shrubs	*Pterolocera* sp. 1 (SA)	McFarland 1979
	various garden plants	*Pterolocera* sp. (TAS)	Terauds *et al.* 1986 [as *Pterolocera amplicornis*]

APPENDIX D:

PARASITOIDS OF ANTHELIDAE

parasitoid family	parasitoid species	anthelid host species	source
Hymenoptera: Ichneumonidae	*Rhyssa semipunctata*	*Anthela denticulata* [pupa]	Froggatt 1910
Hymenoptera: Ichneumonidae	*Echtromorpha intricatoria* [as *Pimpla intricatoria*]	*Anthela denticulata* [pupa]	Froggatt 1910
Hymenoptera: Ichneumonidae	*Theronia tuberculicollis*	*Anthela nicothoe* [pupa]	Moore 1963b
Hymenoptera: Ichneumonidae	*Lissopimpla* sp.	*Anthela nicothoe* [pupa]	Moore 1963b
Hymenoptera: Ichneumonidae	*Echthromorpha intricatoria*	*Anthela varia* [pupa]	Moore 1963b
Hymenoptera: Ichneumonidae	*Gotra gilberti*	*Anthela varia* [pupa]	Moore 1963b
Hymenoptera: Ichneumonidae	*Cyanoxorides* sp.	*Anthela varia* [pupa]	Moore 1963b
Hymenoptera: Ichneumonidae	*Netelia producta*	*Chelepteryx collesi* [pupa]	Ramirez 1978
Hymenoptera: Ichneumonidae	*Enicospilus* sp.	*Anthela* sp. [pupa]	Riek 1962
Hymenoptera: Braconidae	*Apanteles* sp.	*Anthela* sp. [pupa]	Riek 1962
Hymenoptera: Braconidae	-	*Anthela acuta*	Coupar & Coupar 1992
Hymenoptera: Chalcidoidea	*Pteromalidae* sp.	*Chelepteryx collesi* [egg]	Ramirez 1978
Diptera: Tachinidae	-	*Anthela excellens* [caterpillar]	Moore 1963b
Diptera: Sarcophagidae	*Taylorimyia iota*	*Anthela nicothoe* [pupa]	Moore 1963b
Diptera: Chloropidae	*Lioscinella australiensis*	*Chelepteryx collesi*	Spencer 1978
Diptera	-	*Anthela euryphrica*	Turner 1936
Acarina: Erythraeidae	*Charletonia feideri*	*Pterolocera* sp. [younger caterpillar]	McFarland 1979
Acarina: Erythraeidae	*Leptus charon*	*Anthela* sp. [caterpillar]	Southcott 1993
Acarina	-	*Anthela* sp. [caterpillar]	Coupar & Coupar 1992
nuclear-polyhedrosis virus	"*Borrelina anthelus*"	*Pterolocera amplicornis* [*sic*!] [caterpillar]	Day *et al.* 1953
nuclear-polyhedrosis virus	[unnamed new virus]	*Anthela varia* [caterpillar]	Teakle 1969

APPENDIX E:

COLLECTING LOCALITIES & DATES

#	collecting locality, date and light source
120	35°19'11.1"S 148°51'32.0"E, AUSTRALIA, ACT, Brindabella Rd nr Condor Ck, 1. MAR 2002, MV-lamp
121	35°20'40.5"S 148°49'23.8"E, AUSTRALIA, ACT, Namadgi NP, 2.7km NE Piccadilly Circus, 7. MAR 2002, MV-lamp
122	35°20'33.8"S 148°49'32.7"E, AUSTRALIA, ACT, Namadgi NP, 3km NE Piccadilly Circus, 10. MAR 2002, MV-lamp
125	35°28.405'S 148°46.148'E, AUSTRALIA, ACT, Namadgi NP, Mt. Aggie, 1400m, 17. MAR 2002, MV-lamp
126	35°31.597'S 148°46.743'E, AUSTRALIA, ACT, Namadgi NP, Mt. Ginini, 1650m, 18. MAR 2002, MV-lamp
127	28°11.590'S 153°11.402'E, AUSTRALIA, QLD, Lamington NP, Binna Burra, bellbird clearing, 25.-27. MAR 2002, MV-lamp
128	28°11.590'S 153°11.402'E, AUSTRALIA, QLD, Lamington NP, Binna Burra, bellbird clearing, 25.-27. MAR 2002, MV-lamp
129	28°03.218'S 152°22.768'E, AUSTRALIA, QLD, Main Range NP, Cunningham's Gap, rest-area, 28. MAR 2002, MV-lamp
130	26°43.372'S 153°04.566'E, AUSTRALIA, QLD, Mooloolah River NP, heathland, 29. MAR 2002, MV-lamp
131	28°02.953'S 152°23.680'E, AUSTRALIA, QLD, Main Range NP, Cunningham's Gap, rainforest track, 30. MAR 2002, MV-lamp
132	28°04.838'S 152°25.147'E, AUSTRALIA, QLD, Main Range NP, Spicer's Gap, Moss's Well, 31. MAR 2002, MV-lamp
133	28°03.218'S 152°22.768'E, AUSTRALIA, QLD, Main Range NP, Cunningham's Gap, rest-area, 1. APR 2002, MV-lamp
134	25°48.815'S 148°15.658'E, AUSTRALIA, QLD, rd Injune to Mt. Moffat (Carnarvon NP) [dry sclerophyll bushes], 3. APR 2002, MV-lamp
135	24°59.397'S 147°58.409'E, AUSTRALIA, QLD, Carnarvon NP, Mt. Moffat sect., Marlong Plain [native grass, Casuarina & Eucalyptus], 4. APR 2002, MV-lamp
136	24°59.397'S 147°58.409'E, AUSTRALIA, QLD, Carnarvon NP, Mt. Moffat sect., well 4km N rangerst. [native grass & Eucalyptus], 5. APR 2002, MV-lamp
137	25°39.509'S 148°08.491'E, AUSTRALIA, QLD, rd Injune to Mt. Moffat (Carnarvon NP) [dry sclerophyll bushes], 6. APR 2002, MV-lamp
138	25°03.281'S 148°13.592'E, AUSTRALIA, QLD, Carnarvon NP, C. Gorge, 3rd cr. crossing, 7. APR 2002, MV-lamp
139	25°03.138'S 148°12.811'E, AUSTRALIA, QLD, Carnarvon NP, C. Gorge, 7th-8th cr. crossing, 8. APR 2002, MV-lamp
140	25°03.1'S 148°12.8'E, AUSTRALIA, QLD, Carnarvon NP, C. Gorge, Moss Garden, 8. APR 2002, UV-flt lighttrap
141	23°27.648'S 148°08.831'E, AUSTRALIA, QLD, ~10km N Emerald, powerline, 9. APR 2002, MV-lamp
142	21°08.7'S 148°29.4'E, AUSTRALIA, QLD, Eungella NP, Diggings Rd., 10. APR 2002, MV-lamp
143	21°09.150'S 148°30.145'E, AUSTRALIA, QLD, Eungella NP, walking track, 11. APR 2002, MV-lamp
144	19°00.510'S 146°12.955'E, AUSTRALIA, QLD, Paluma Range NP, reforest. site nr Windy Corner, 12. APR 2002, MV-lamp
145	17°35.923'S 145°45.540'E, AUSTRALIA, QLD, Palmerston Hwy, Henrietta Ck campgr., 350m, 13. APR 2002, MV-lamp
146	17°28.645'S, 145°22.182'E, AUSTRALIA, QLD, old Ravenshoe–Herberton rd, ~5km S Herberton, 900m, 14. APR 2002, MV-lamp
147	18°06.540'S 144°49.533'E, AUSTRALIA, QLD, Forty Miles Scrub NP, walking track, 780m, 15. APR 2002, MV-lamp
148	17°00.594'S 145°34.948'E, AUSTRALIA, QLD, Davies Ck NP, rd at falls, 630m, 16. APR 2002, MV-lamp

#	collecting locality, date and light source
149	16°14.311'S 145°25.959'E, AUSTRALIA, QLD, Daintree NP, Jindalba, 17. APR 2002, MV-lamp
151	16°03.763'S 145°27.726'E, AUSTRALIA, QLD, Daintree NP, Cape Tribulation, 3km N rangerstation, 18. APR 2002, MV-lamp
152	17°19.903'S 145°25.127'E, AUSTRALIA, QLD, Herberton, Baldy SF, ~1100m, 20. APR 2002, MV-lamp
153	17°44.461'S 145°32.017'E, AUSTRALIA, QLD, Ravenshoe SF, clearing at rd to Tully Falls, ~800m, 21. APR 2002, MV-lamp
154	16°35.060'S 145°16.215'E, AUSTRALIA, QLD, Mt. Lewis, ~900m, 22. APR 2002, MV-lamp
155	17°19.903'S 145°25.127'E, AUSTRALIA, QLD, Herberton, Baldy SF, ~1100m, 23. APR 2002, MV-lamp
156	19°00.510'S 146°12.955'E, AUSTRALIA, QLD, Paluma Range NP, reforest. site nr windy corner, 24. APR 2002, MV-lamp
157	26°30.486'S 147°07.444'E, AUSTRALIA, QLD, Tregole NP near Morven [ooline, belah open forest], ~500m, 26. APR 2002, MV-lamp
158	26°20.153'S 146°17.722'E, AUSTRALIA, QLD, ~10km N Charleville, dry riverbed [tall Eucalyptus, Acacia, grass], 27. APR 2002, MV-lamp,
159	29°14.892'S 145°51.416'E, AUSTRALIA, NSW, ~10km N Enngonia, ridge of well in bush/farmland, 28. APR 2002, MV-lamp
160	30°30.105'S 146°17.164'E, AUSTRALIA, NSW, 21km NW Byrock, Nightvale Station [*A. aneura* & *E. populnea*], 29. APR 2002, MV-lamp
161	30°40.396'S 146°24.872'E, AUSTRALIA, NSW, 1.65km SE Byrock, 3. AUG 2002, MV-lamp
162	30°36.157'S 146°21.132'E, AUSTRALIA, NSW, 8.21km NW Byrock, 4. AUG 2002, MV-lamp
163	30°40.396'S 146°24.872'E, AUSTRALIA, NSW, 1.65km SE Byrock, 13. SEP 2002, MV-lamp
164	30°36.157'S 146°21.132'E, AUSTRALIA, NSW, 8.21km NW Byrock, 14. SEP 2002, MV-lamp
165	35°19'11.1"S 148°51'32.0"E, AUSTRALIA, ACT, Brindabella Rd nr Condor Ck, 25. SEP 2002, MV-lamp
166	38°34.085'S 143°44.955'E, AUSTRALIA, VIC, Otway SF, Noonday Tk, 12. OCT 2002, MV-lamp
167	35°26.278'S 148°49.589'E, AUSTRALIA, ACT, Namadgi NP, Bendora Rd nr Bendora Dam, 750m, 29. OCT 2002, MV-lamp
168	35°21.343'S 148°50.159'E, AUSTRALIA, ACT, Namadgi NP, Blundells Ck Rd, 900m, 1. NOV 2002, MV-lamp
169	35°31.597'S 148°46.743'E, AUSTRALIA, ACT, Namadgi NP, Mt. Ginini, 1650m, 6. NOV 2002, MV-lamp
170	34°11.585'S 146°15.827'E, AUSTRALIA, NSW, Binya SF, 8. NOV 2002, MV-lamp
171	34°05.317'S 146°12.495'E, AUSTRALIA, NSW, Cocoparra NP, Woolshed Ck valley, 9. NOV 2002, MV-lamp
172	34°07.248'S 146°14.072'E, AUSTRALIA, NSW, Cocoparra NP, Mt. Bingar, 10. NOV 2002, MV-lamp
173	35°26.278'S 148°49.589'E, AUSTRALIA, ACT, Namadgi NP, Bendora Rd nr Bendora Dam, 750m, 19. NOV 2002, MV-lamp
174	36°22.249'S 148°28.349'E, AUSTRALIA, NSW, Kosciuszko NP, Smiggin Holes vic. (SE Guthega), 20. NOV 2002, MV-lamp
175	36°31.537'S 148°11.616'E, AUSTRALIA, NSW, Kosciuszko NP, Leatherbarrel Ck, 21. NOV 2002, MV-lamp
176	35°25.506'S 148°49.955'E, AUSTRALIA, ACT, Namadgi NP, Bendora Rd, 750m, 26. NOV 2002, MV-lamp
177	36°02.779'S 149°32.168'E, AUSTRALIA, NSW, Badja Swamp NR NE Numeralla, 1040m, 2. DEC 2002, MV-lamp
178	35°38.300'S 150°00.378'E, AUSTRALIA, NSW, Monga NP, rd to "Corn Trail" base, ~350m, 4. DEC 2002, MV-lamp
179	35°31.597'S 148°46.743'E, AUSTRALIA, ACT, Namadgi NP, Mt. Ginini, 1650m, 14. DEC 2002, MV-lamp
180	35°31.391'S 148°46.945'E, AUSTRALIA, ACT, Namadgi NP, Ginini Flat (swamp), 1600m, 30. DEC 2002, MV-lamp
181	35°47.300'S 148°47.865'E, AUSTRALIA, NSW, SW Old Yaouk, 4. JAN 2003, MV-lamp
182	35°47.300'S 148°47.865'E, AUSTRALIA, NSW, SW Old Yaouk, 7. JAN 2003, MV-lamp
183	35°11.796'S 149°07.830'E, AUSTRALIA, ACT, Gungahlin grassland nr Palmerston, 20. FEB 2003, MV-lamp

#	collecting locality, date and light source
184	35°09.231'S 149°09.408'E, AUSTRALIA, ACT, Mulligan's Flat NR NE Gungahlin, 28. FEB 2003, MV-lamp
185	34°08.758'S 151°01.840'E, AUSTRALIA, NSW, Royal NP, Bola Ck, 4. MAR 2003, MV-lamp
186	35°11.796'S 149°07.830'E, AUSTRALIA, ACT, Gungahlin grassland nr Palmerston, 10. MAR 2003, MV-lamp
200-203	2°27.938'S 37°54.988'E, KENYA, Kibwezi, Umani Springs Camp, ~1050m asl, 22.-27. MAR 2003, MV-lamp & UV-flt
204	2°52.339'S 38°3.768'E, KENYA, Tsavo West NP, slope ~7km NE Chyulu Gate, ~900m asl, 28. MAR 2003, UV-flt
205	2°54.002'S 37°38.900'E, KENYA, rd Tsavo West NP to Oloitokitok, river bed, ~1200m asl, 29. MAR 2003, MV-lamp
206	KENYA, Amboseli NP, campground, 30. MAR 2003, UV-flt
207	2°56.120'S 37°30.339'E, KENYA, Oloitokitok, Loi Forest (sec. regrowth), ~1800m asl, 31. MAR 2003, MV-lamp
208	2°56.725'S 37°30.350'E, KENYA, Oloitokitok, Loi Forest (remnants of prim. forest), ~1800m asl, 1. APR 2003, MV-lamp & UV-flt
209	3°26.599'S 37°36.348'E, KENYA, Taveta, Kitobo Forest, ~900m asl, 2. APR 2003, MV-lamp & UV-flt
210	3°19.866'S 38°26.919'E, KENYA, Tayta Hills, Mbololo Forest, ~1550m asl, 4. APR 2003, MV-lamp & UV-flt
211	21°37'04.1"S 117°06'35.2"E, AUSTRALIA, WA, Millstream-Chichester NP, Deep Reach campgrd, 5. MAY 2003, MV-lamp
212	21°40'38.7"S 116°58'30.4"E, AUSTRALIA, WA, 15km SW Millstream ranger stn, 6. MAY 2003, MV-lamp
213	21°35'42.9"S 117°04'01.1"E, AUSTRALIA, WA, Millstream-Chichester NP, pumping station at junction Snappy Gum Rd / Pipeline Rd, 7. MAY 2003, MV-lamp
214	21°34'37.6"S 117°05'11.8"E, AUSTRALIA, WA, Millstream-Chichester NP, Fortescue River, Crossing Pool campgrd, 8. MAY 2003, MV-lamp
215	21°34'46.4"S 117°05'29.9"E, AUSTRALIA, WA, Millstream-Chichester NP, Pipeline Rd, 6km NbyW ranger stn, 9. MAY 2003, MV-lamp
216	21°20'00.0"S 117°15'18.2"E, AUSTRALIA, WA, Millstream-Chichester NP, Black Hill Pool, 10. MAY 2003, MV-lamp
217	21°19'57.7"S 117°14'23.9"E, AUSTRALIA, WA, Millstream-Chichester NP, Python Pool, 10. MAY 2003, MV-lamp
218	21°19'57.7"S 117°14'23.9"E, AUSTRALIA, WA, Millstream-Chichester NP, Python Pool, 11. MAY 2003, MV-lamp
219	22°33'56.0"S 118°27'10.4"E, AUSTRALIA, WA, Karijini NP, junction Juna Downs Rd / Karijini Drive (Mulga), 13. MAY 2003, MV-lamp
220	22°35'48.5"S 118°27'05.1"E, AUSTRALIA, WA, Karijini NP, Djuna Downs Rd, ~2km S Ranger Stn (Mulga), 14. MAY 2003, MV-lamp
221	22°25'01.3"S 118°24'05.7"E, AUSTRALIA, WA, Karijini NP, Kalamina Falls, 15. MAY 2003, MV-lamp
222	22°33'40.5"S 118°43'01.7"E, AUSTRALIA, WA, E of Karijini NP, Fig Tree Crossing, 16. MAY 2003, MV-lamp
223	22°27'01.2"S 118°26'55.0"E, AUSTRALIA, WA, Karijini NP, Doug Frances Drive (Johnson Gorge?), 17. MAY 2003, MV-lamp
224	22°50'31.3"S 118°31'11.2"E, AUSTRALIA, WA, Karijini NP, gorge 5km N Juna Downs Stn (Callitris), 18. MAY 2003, MV-lamp
225	22°16'47.0"S 118°44'41.9"E, AUSTRALIA, WA, Fortescue River Basin ~12km N Auski RH, 19. MAY 2003, MV-lamp
	8°42'23.7"N 117°33'59.1"E, PHILIPPINES, Palawan, Bataraza, Malihud, Tagurida, ~500m asl, 25. JUN 2003
226	31°39'44.5"S 128°52'55.4"E AUSTRALIA, WA, Eucla, 29. OCT 2003, MV-lamp
229	33°27'07.2"S 123°26'16.2"E AUSTRALIA, WA, Cape Arid NP, track to Mt. Ragged, ~200m asl, 30. OCT 2003, MV-lamp
230	33°26'39.7"S 123°28'00.5"E AUSTRALIA, WA, Cape Arid NP, foot of Mt. Ragged, ~200m asl, 30. OCT 2003, MV-lamp
231	32°11'01.5"S 121°38'29.5"E AUSTRALIA, WA, W of Norseman (rd to Hyden), ~350m asl, 31. OCT 2003, MV-lamp

#	collecting locality, date and light source
234	33°55'52.3"S 119°59'34.0"E AUSTRALIA, WA, Fitzgerald River NP, Hammersley Drv., 10m asl, 1. NOV 2003, MV-lamp
235	34°23'32.2"S 118°03'46.2"E AUSTRALIA, WA, Stirling Range NP, W end of Toolbrunup Rd, ~300m, 2. NOV 2003, MV-lamp
236	34°26'03.1"S 118°04'23.8"E AUSTRALIA, WA, Stirling Range NP, Chester Pass Rd, ~250m, 2. NOV 2003, MV-lamp
237	34°26'01.3"S 116°38'04.1"E AUSTRALIA, WA, Talling SF, Lake Muir Rd, 200m asl, 3. NOV 2003, MV-lamp
238	34°27'49.3"S 116°41'13.9"E AUSTRALIA, WA, Lake Muir NR, Nabagup Rd, 200m asl, 3. NOV 2003, MV-lamp
241	34°51'38.3"S 116°13'11.8"E AUSTRALIA, WA, D'Entrecasteaux NP, 0.5km E Moore's Hut, 25m asl, 4. NOV 2003, MV-lamp
242	34°25'59.8"S 115°42'34.8"E AUSTRALIA, WA, D'Entrecasteaux NP, Lake Jasper, Woodarburrup/Lake Jasper Rd, ~50m asl, 5. NOV 2003, MV-lamp
243	34°25'47.9"S 115°44'33.1"E AUSTRALIA, WA, D'Entrecasteaux NP, Lake Jasper, Scott Rd, ~50m asl, 5. NOV 2003, MV-lamp
245	32°49'11.8"S 116°06'12.6"E AUSTRALIA, WA, Lane Pool Reserve, Icy Ck, ~300m, 6. NOV 2003, MV-lamp
246	35°00'20.1"S 150°09'05.5"E AUSTRALIA, NSW, Morton NP, ~11km on Talwong Rd, 550m asl, 28. NOV 2003, MV-lamp
248	35°31'27.6"S 150°02'09.3"E AUSTRALIA, NSW, Budawang NP, ~9km on Western Distributor Rd, 400m asl, 1. DEC 2003, MV-lamp
249	35°30'58.5"S 150°03'34.2"E AUSTRALIA, NSW, Budawang NP, Western Distributor Rd, Carters Ck, 200m asl, 1. DEC 2003, MV-lamp
250	35°26'54.6"S 150°05'33.4"E AUSTRALIA, NSW, Budawang NP, ~25km on Western Distributor Rd, ~400m asl, 4. DEC 2003, MV-lamp
251	35°11'36.4"S 149°08'05.2"E AUSTRALIA, ACT, Gungahlin grassland E Palmerston, 10. DEC 2003, MV-lamp
252	35°31'27.6"S 150°02'09.3"E AUSTRALIA, NSW, Budawang NP, ~9km on Western Distributor Rd, 400m asl, 14. DEC 2003, MV-lamp
253	35°30'58.5"S 150°03'34.2"E AUSTRALIA, NSW, Budawang NP, Western Distributor Rd, Carters Ck, 200m asl, 14. DEC 2003, MV-lamp
254	35°55'57.1"S 149°35'10.8"E AUSTRALIA, NSW, Tallaganda SF, Little Snowball Ck, native grassland, ~850m asl, 19. DEC 2003, MV-lamp
255	36°02'46.7"S 149°32'10.1"E AUSTRALIA, NSW, Badja Swamp NR NE Numeralla, 1040m, 19. DEC 2003, MV-lamp
256	34°38'06.4"S 150°43'22.4"E AUSTRALIA, NSW, Budderoo NP, Minamurra Falls, 200m asl, 30. DEC 2003, MV-lamp
257	35°30'58.5"S 150°03'34.2"E AUSTRALIA, NSW, Budawang NP, Western Distributor Rd, Carters Ck, 200m asl, 25. JAN 2004, MV-lamp
258	35°33'31.8"S 150°02'26.4"E AUSTRALIA, NSW, Budawang NP, ~5km on Western Distributor Rd, 200m asl, 25. JAN 2004, MV-lamp
259	35°25'49.2"S 149°32'21.7"E AUSTRALIA, NSW, Tallaganda NP, ~3km N on North Black Range Trail, ~1150m asl, 3. FEB 2004, MV-lamp
260	35°53'38.2"S 149°30'17.7"E AUSTRALIA, NSW, Tallaganda NP, Slap-Up Rd, ~1350m asl, 28. FEB 2004, MV-lamp
261	35°52'33.2"S 149°33'07.7"E AUSTRALIA, NSW, Tallaganda SF, Jinden Ridge Rd, ~950m asl, 28. FEB 2004, MV-lamp
262	35°56'04.9"S 149°34'51.2"E AUSTRALIA, NSW, Tallaganda SF, Little Snowball Ck, ~850m asl, 28. FEB 2004, UV-flt
263	35°58'20.5"S 149°31'06.8"E AUSTRALIA, NSW, Tallaganda NP, Slap-Up Rd, ~1400m asl, 28. FEB 2004, UV-flt
264	30°33'44.3"S 148°45'00.1"E AUSTRALIA, NSW, Pilliga West SF, Ginee Belah FR, ~200m asl, 13. MAR 2004, MV-lamp
265	30°35'38.5"S 148°48'00.9"E AUSTRALIA, NSW, Pilliga West SF, Western Way/B-H Line, ~200m asl, 13. MAR 2004, MV-lamp
266	30°31'57.4"S 149°39'10.9"E AUSTRALIA, NSW, Pilliga East SF, 5km on Bohena Ck Rd, ~200m asl, 14. MAR 2004, MV-lamp

#	collecting locality, date and light source
267	30°16'47.3"S 150°10'02.5"E AUSTRALIA, NSW, Mt. Kaputar NP, Dawson Spring, 1350m asl, 15. MAR 2004, MV-lamp
268	30°16'29.3"S 150°09'54.5"E AUSTRALIA, NSW, Mt. Kaputar NP, nr Mt. Kaputar summit, ~1450m, 15. MAR 2004, MV-lamp
269	30°17'23.5"S 150°08'30.5"E AUSTRALIA, NSW, Mt. Kaputar NP, nr Bark Hut, 1150m asl, 15. MAR 2004, MV-lamp
270	30°16'44.1"S 150°04'10.9"E AUSTRALIA, NSW, Mt. Kaputar NP, Mt. Ningadhun base, 800m asl, 15. MAR 2004, MV-lamp
271	33°09'18.6"S 149°15'15.0"E AUSTRALIA, NSW, Orange, Ophir, Miller's Crossing, ~650m asl, 20. MAR 2004, MV-lamp
272	36°39'24.3"S 150°00'10.5"E, AUSTRALIA, NSW, Mimosa Rocks NP, Gillard's Beach, ~10m asl, 27. MAR 2004, MV-lamp
273	AUSTRALIA, NSW, Mimosa Rocks NP, ~3km before Gillard's Beach, ~100m asl, 27. MAR 2004, MV-lamp
274	32°37'49.3"S 145°34'42.6"E AUSTRALIA, NSW, Yathong NR, nr airstrip, 150m asl, 9. APR 2004, MV-lamp
275	32°35'14.1"S 145°29'56.5"E AUSTRALIA, NSW, Yathong NR, ~4km W on Western Rd, 150m asl, 10. APR 2004, MV-lamp
276	31°30'31.9"S 145°47'05.6"E AUSTRALIA, NSW, ~3km W of Cobar, 200m asl, 11. APR 2004, MV-lamp
278	30°41'31.6"S 146°17'23.0"E AUSTRALIA, NSW, pwrlne 11.5km ENE Byrock, 150m asl, 12. APR 2004, MV-lamp
279	34°15'46.6"S 147°27'03.4"E AUSTRALIA, NSW, Temora, Barmedman SF, 200m asl, 23. APR 2004, MV-lamp
280	34°21'21.3"S 147°25'39.3"E AUSTRALIA, NSW, Temora, Big Bush SF, 200m asl, 23. APR 2004, UV-flt
281	35°30'58.5"S 150°03'34.2"E AUSTRALIA, NSW, Budawang NP, Western Distributor Rd, Carters Ck, 200m asl, 30. APR 2004, MV-lamp
282	35°33'31.8"S 150°02'26.4"E AUSTRALIA, NSW, Budawang NP, ~5km on Western Distributor Rd, 200m asl, 30. APR 2004, UV-flt
283	27°17'51.8"S 152°45'14.0"E AUSTRALIA, QLD, D'Aguilar NP, Mt. Glorious Rd nr Kobble Ck (South Branch), ~700m asl, 19. AUG 2004, MV-lamp
284	25°59'38.9"S 153°04'29.8"E AUSTRALIA, QLD, Great Sandy NP, vic. Rainbow Beach, 500m SE on Freshwater Rd, ~50m asl, 21. AUG 2004, MV-lamp
285	26°01'37.2"S 153°01'31.8"E AUSTRALIA, QLD, Great Sandy NP, vic. Rainbow Beach, ~1.5km S on Cooloolah Rd, <50m asl, 22. AUG 2004, MV-lamp
286	28°49'41.1"S 151°57'39.4"E AUSTRALIA, QLD, Girraween NP, 2km NE park headquarter, ~850m asl, 25. AUG 2004, MV-lamp
287	35°30'58.5"S 150°03'34.2"E AUSTRALIA, NSW, Budawang NP, Western Distributor Rd, Carters Ck, 200m asl, 22. SEP 2004, MV-lamp
288	35°33'15.2"S 150°02'04.5"E AUSTRALIA, NSW, Budawang NP, ~5km on Western Distributor Rd, 250m asl, 22. SEP 2004, MV-lamp & UV-flt
289	35°30'58.5"S 150°03'34.2"E AUSTRALIA, NSW, Budawang NP, Western Distributor Rd, Carters Ck, 200m asl, 25. OCT 2004, MV-lamp
290	35°33'15.2"S 150°02'04.5"E AUSTRALIA, NSW, Budawang NP, ~5km on Western Distributor Rd, 250m asl, 25. OCT 2004, MV-lamp
291	32°57'32.0"S 146°09'05.3"E, AUSTRALIA, NSW, Round Hill NR, The Round Hill, ~250m asl, 6. NOV 2004, MV-lamp
292	30°54'20.8"S 145°54'03.0"E, AUSTRALIA, NSW, pwrlne ~70km N Cobar, ~150m asl, 7. NOV 2004, MV-lamp
293	35°31'48.8"S 150°01'42.7"E, AUSTRALIA, NSW, Budawang NP, ~10km on Western Distributor Rd, ~350m asl, 18. NOV 2004, MV-lamp
294	35°30'58.5"S 150°03'34.2"E AUSTRALIA, NSW, Budawang NP, Western Distributor Rd, Carters Ck, 200m asl, 18. NOV 2004, MV-lamp
295	35°30'58.5"S 150°03'34.2"E AUSTRALIA, NSW, Budawang NP, Western Distributor Rd, Carters Ck, 200m asl, 20. NOV 2004, MV-lamp
297	35°31'48.8"S 150°01'42.7"E, AUSTRALIA, NSW, Budawang NP, ~10km on Western Distributor Rd, ~350m asl, 5. DEC 2004, MV-lamp

#	collecting locality, date and light source
298	35°30'58.5"S 150°03'34.2"E AUSTRALIA, NSW, Budawang NP, Western Distributor Rd, Carters Ck, 200m asl, 5. DEC 2004, MV-lamp
299	35°30'42.2"S 150°03'30.9"E AUSTRALIA, NSW, Budawang NP, Western Distributor Rd, ~500m N Carters Ck, 300m asl, 5. DEC 2004, MV-lamp & UV-flt
300	35°32'35.7"S 149°55'53.2"E, AUSTRALIA, NSW, Monga, River Rd, ~650m asl, 5. DEC 2004, UV-flt
301	35°55'57.1"S 149°35'10.8"E AUSTRALIA, NSW, Tallaganda SF, Little Snowball Ck, native grassland, ~850m asl, 10. DEC 2004, MV-lamp & UV-flt
302	36°02'46.7"S 149°32'10.1"E AUSTRALIA, NSW, Badja Swamp NR NE Numeralla, 1040m, 10. DEC 2004, MV-lamp & UV-flt

APPENDIX F:

GENITALIA PREPARATIONS

family	species	gender	collecting data	preparation #
Anthelidae	*Anthela achromata*	male	11°50'S 142°30'E, AUSTRALIA, QLD, Dulhunty R., 13km SW Heathlands, 21. MAR 1992	ANIC/AZ 16
Anthelidae	*Anthela acuta*	male	AUSTRALIA, QLD, Brisbane, 10. SEP [19]39	ANIC/AZ 239
Anthelidae	*Anthela acuta* (1)	male	28°24'S 153°17'E, AUSTRALIA, NSW, 1km E Mt. Warning, 500m, 22. NOV 1976	ANIC/AZ 69
Anthelidae	*Anthela acuta* (2)	male	AUSTRALIA, QLD, Eungella NP, 800m, 1. MAR 1964	ANIC/AZ 74
Anthelidae	*Anthela acuta* (3)	male	17°14'S 145°11'E, AUSTRALIA, QLD, Stannary Hills 11km SbyW Mutchilba, 700m, 26. MAY 1977	ANIC/AZ 75
Anthelidae	*Anthela acuta* (sp.)	male	AUSTRALIA, QLD, 18mls S Gympie, 28. FEB 1964	ANIC/AZ 238
Anthelidae	*Anthela acuta* (sp.)	male	AUSTRALIA, QLD, Carnarvon Range, 29. MAR 1957	ANIC/AZ 235
Anthelidae	*Anthela acuta* (sp.)	male	AUSTRALIA, NSW, Mt. Keira, 15. NOV 1960	ANIC/AZ 236
Anthelidae	*Anthela acuta* (sp.)	male	AUSTRALIA, NSW, Yabbra SF, N Yabbra Rd & Castle Spur Rd, 30. SEP 1999	ANIC/AZ 237
Anthelidae	*Anthela acuta* (sp.)	male	AUSTRALIA, QLD, Brisbane, 26. JUN [19]40	ANIC/AZ 243
Anthelidae	*Anthela acuta* (sp.)	male	AUSTRALIA, QLD, Brisbane, 12. DEC [19]37	ANIC/AZ 242
Anthelidae	*Anthela acuta* (sp.)	male	AUSTRALIA, QLD, Brisbane, 4. SEP [19]35	ANIC/AZ 244
Anthelidae	*Anthela acuta/astata* (sp.)	male	13°43'S 1143°19'E, AUSTRALIA, QLD, McIlwraith Ra., Weather Stn, 420m, 3. JUL 1989	ANIC/AZ 1
Anthelidae	*Anthela addita* (A)	male	35°46'S 149°35'E, AUSTRALIA, NSW, Little Snowball Ck, 960m, 17. DEC 1990	ANIC/AZ 45
Anthelidae	*Anthela addita* (A)	male	41°33'S 148'18E, AUSTRALIA, TAS, 6km S Falmouth, 21. MAR 1986	ANIC/AZ 217
Anthelidae	*Anthela addita* (A)	male	AUSTRALIA, NSW, Boyd River, Kanangra Walls, 25. JAN 1968	ANIC/AZ 216
Anthelidae	*Anthela addita* (A)	male	35°32'S 148°45'E, AUSTRALIA, ACT, Mt. Ginini, 1660m, 28. JAN 1984	ANIC/AZ 215
Anthelidae	*Anthela addita* (A)	male	36°13'S 148°34'E, AUSTRALIA, NSW, 12km SSW Eucumbene Dam, 1360m, 12. JAN 1964	ANIC/AZ 214
Anthelidae	*Anthela addita* (A)	male	42°10'S 146°08'E, AUSTRALIA, TAS, 9km WSW Derwent Bridge, 21. JAN 1983	ANIC/AZ 219
Anthelidae	*Anthela addita* (A)	male	42°10'S 146°08'E, AUSTRALIA, TAS, 9km WSW Derwent Bridge, 21. JAN 1983	ANIC/AZ 41
Anthelidae	*Anthela addita* (A)	male	AUSTRALIA, VIC, Moe, 10. DEC 1957	ANIC/AZ 42
Anthelidae	*Anthela addita* (A)	male	AUSTRALIA, TAS, lookout 20km N Launceston, 15. JAN 2003	ANIC/AZ 220
Anthelidae	*Anthela addita* (B)	male	AUSTRALIA, TAS, Mt. Wellington, 850ft, 30. APR 1963	ANIC/AZ 44
Anthelidae	*Anthela addita* (B)	male	AUSTRALIA, VIC, Kallista, 19. APR 1966	ANIC/AZ 46
Anthelidae	*Anthela addita* (B)	male	42°10'S 146°08'E, AUSTRALIA, TAS, 9km WSW Derwent Bridge, 21. JAN 1983	ANIC/AZ 218

family	species	gender	collecting data	preparation #
Anthelidae	*Anthela addita* (B)	male	AUSTRALIA, TAS, Tarraleah, 22. APR 1963	ANIC/AZ 43
Anthelidae	*Anthela addita* (B)	male	AUSTRALIA, TAS, Mt. Wellington, 850ft, 30. APR 1963	ANIC/AZ 213
Anthelidae	*Anthela addita* (B)	male	AUSTRALIA, TAS, Tarraleah, 22. APR 1963	ANIC/AZ 211
Anthelidae	*Anthela addita* (B)	male	AUSTRALIA, NSW, Jenolean SF, 24. APR 1968	ANIC/AZ 212
Anthelidae	*Anthela adriana*	male	32°15'S 125°32'E, AUSTRALIA, WA, 5km ENE of Caiguna, 11. APR 1983	ANIC/AZ 284
Anthelidae	*Anthela adriana*	male	[22°18'S 130°50'E, AUSTRALIA, NT,] 18mi East of Vaughan Springs HS, 2. JUL 1968	ANIC/AZ 286
Anthelidae	*Anthela adriana*	male	AUSTRALIA, WA, 8mi E of Carnarvon, 20. APR 1968	ANIC/AZ 280
Anthelidae	*Anthela adriana*	male	21°34'S 117°03'E, AUSTRALIA, WA, 3km NWbyW of Millstream HS, 11. APR 1971	ANIC/AZ 283
Anthelidae	*Anthela adriana*	male	AUSTRALIA, WA, 107mi S of Carnarvon, 21. APR 1968	ANIC/AZ 281
Anthelidae	*Anthela adriana*	male	AUSTRALIA, WA, Caiguna, 14. AUG 1963	ANIC/AZ 282
Anthelidae	*Anthela adriana*	male	23°36'S 133°34'E AUSTRALIA, NT, 33km WNW of Alice Springs, 30. SEP 1978	ANIC/AZ 285
Anthelidae	*Anthela ariprepes*	male	AUSTRALIA, NSW, Round Hill Fauna Reserve, 16. MAR 1969 (emerged)	ANIC/AZ 129
Anthelidae	*Anthela asciscens*	male	AUSTRALIA, QLD, Duaringa, 2. MAY [19]23 (bred)	ANIC/AZ 131
Anthelidae	*Anthela astata*	male	AUSTRALIA, QLD, 1km E Kuranda, 11. MAR 1964	ANIC/AZ 72
Anthelidae	*Anthela astata*	male	17°16'S 145°54'E, AUSTRALIA, QLD, Mt. Bellenden-Ker, base cableway, 80m, 31. OCT 1981	ANIC/AZ 71
Anthelidae	*Anthela astata*	male	AUSTRALIA, QLD, 1km E Kuranda, 11. MAR 1964	ANIC/AZ 70
Anthelidae	*Anthela astata*	male	AUSTRALIA, QLD, Iron Range NP, 7. APR 1964	ANIC/AZ 73
Anthelidae	*Anthela astata* (A)	male	AUSTRALIA, VIC, Blairgowrie, 10. OCT 1978	ANIC/AZ 47
Anthelidae	*Anthela astata* (A)	male	AUSTRALIA, ACT, Namadgi NP, Mt. Ginini, 1750m, 8. OCT 2002 (bred)	CAZS/AZ 217
Anthelidae	*Anthela astata* (A)	male	AUSTRALIA, ACT, Mt. Gingera, 6000ft., 10. OCT 1956 (bred)	ANIC/AZ 222
Anthelidae	*Anthela astata* (B)	male	AUSTRALIA, NSW, Gosford, 30. NOV 1967 (bred)	ANIC/AZ 228
Anthelidae	*Anthela astata* (B)	male	AUSTRALIA, VIC, Moe, 15. FEB 1931	ANIC/AZ 223
Anthelidae	*Anthela astata* (B)	male	AUSTRALIA, NSW, Jervis Bay, 17. MAR 1956	ANIC/AZ 227
Anthelidae	*Anthela astata* (B)	male	AUSTRALIA, NSW, Jervis Bay, 7. NOV 1956	ANIC/AZ 225
Anthelidae	*Anthela astata* (B)	male	35°51'S 150°11'E, AUSTRALIA, NSW, Broulee, 29. DEC 1995	ANIC/AZ 233
Anthelidae	*Anthela astata* (B)	male	AUSTRALIA, NSW, Jervis Bay, 7. NOV 1956	ANIC/AZ 226
Anthelidae	*Anthela astata* (B)	male	35°32'S 148°45'E, AUSTRALIA, ACT, Mt. Ginini, 1660m, 28. JAN 1984	ANIC/AZ 221
Anthelidae	*Anthela astata* (B)	male	AUSTRALIA, VIC, Moe, 2. MAR 1931	ANIC/AZ 224
Anthelidae	*Anthela astata* (C)	male	AUSTRALIA, VIC, Grampians, Barneys Ck, 14. NOV 1966	ANIC/AZ 229

family	species	gender	collecting data	preparation #
Anthelidae	*Anthela astata* (C)	male	AUSTRALIA, TAS, National Park, 14. DEC 1982	ANIC/AZ 230
Anthelidae	*Anthela astata* (PNG1)	male	PAPUA NEW GUINEA, Amazon Bay area, Doveta, 2400ft, W. W. Brandt leg., 24. JUL – 11. SEP 1962	ANIC/AZ 31
Anthelidae	*Anthela astata* (PNG1a)	male	PAPUA NEW GUINEA, Telefomin (Feramin), 4700ft, W. W. Brandt leg., 2. MAY – 18. JUN 1959	ANIC/AZ 33
Anthelidae	*Anthela astata* (PNG1b)	male	PAPUA NEW GUINEA, Telefomin (Feramin), 4700ft, 2. MAY – 18. JUN 1959	ANIC/AZ 101
Anthelidae	*Anthela astata (PNG2)*	male	PAPUA NEW GUINEA, Amazon Bay area, Dogon, 2300ft, 13. SEP – 11. DEC 1962	ANIC/AZ 99
Anthelidae	*Anthela astata* (PNG3)	male	PAPUA NEW GUINEA, Kiunga, Fly River, W. W. Brandt leg., 2. JUL – 31. OCT 1957	ANIC/AZ 32
Anthelidae	*Anthela astata/acuta*	male	AUSTRALIA, TAS, Hobart, Cambridge, JUN 1970 (bred)	ANIC/AZ 231
Anthelidae	*Anthela astata/acuta*	male	AUSTRALIA, QLD, Mt. Tamborine, NOV [19]06	ANIC/AZ 241
Anthelidae	*Anthela astata/acuta*	male	AUSTRALIA, VIC, Mt. Beauty, DEC 1960	ANIC/AZ 234
Anthelidae	*Anthela astata/acuta*	male	AUSTRALIA, TAS, Collinsvale, 11. OCT 1977	ANIC/AZ 232
Anthelidae	*Anthela astata/acuta*	male	AUSTRALIA, QLD, Mt. Tamborine, 3. NOV [19] 42	ANIC/AZ 240
Anthelidae	*Anthela asterias*	male	23°38'S 133°35'E, AUSTRALIA, NT, Todd River 9km NbyE Alice Springs, 1. OCT 1978	ANIC/AZ 121
Anthelidae	*Anthela barnardi*	male	AUSTRALIA, WA, Gladstone, 14. AUG 1963	ANIC/AZ 262
Anthelidae	*Anthela basigera*	male	AUSTRALIA, SA, Adelaide, 1. APR [19]42	ANIC/AZ 257
Anthelidae	*Anthela basigera*	male	34°21'S 139°31'E, AUSTRALIA, SA, Blanchtown, Brookfield Cons. Pk., 30. APR 1992	ANIC/AZ 114
Anthelidae	*Anthela basigera*	male	34°21'S 139°31'E, AUSTRALIA, SA, Blanchtown, Brookfield Cons. Pk., 30. APR 1992	ANIC/AZ 256
Anthelidae	*Anthela callileuca*	male	25°34'S 149°46'E, AUSTRALIA, QLD, 10km NbyW Taroom, 230m, 28. MAR 1994	ANIC/AZ 13
Anthelidae	*Anthela callispila*	male	30°20°'S 13922'E, AUSTRALIA, SA, 3.5km ESE Arkoroola Village, 24. OCT 1993	ANIC/AZ 263
Anthelidae	*Anthela callixantha*	male	18°27'S 123°03'E, AUSTRALIA, WA, 101km SEbyE Broome, 20. AUG 1976	ANIC/AZ 124
Anthelidae	*Anthela callixantha*	male	24°11'S 134°01'E, AUSTRALIA, NT, 56km SbyE Alice Springs, 3. OCT 1978	ANIC/AZ 17
Anthelidae	*Anthela charon*	male	PAPUA NEW GUINEA, Telefomin (Eliptamin), 4500-5500ft, W. W. Brandt leg., 19. JUN – 14. SEP 1959	ANIC/AZ 29
Anthelidae	*Anthela clementi*	female	21°14'S 119°16'E, AUSTRALIA, WA, Junction Shaw R. & Honeyeater Ck, 29. APR 1995	ANIC/AZ 291
Anthelidae	*Anthela clementi*	male	22°16'47.0"S 118°44'41.9"E, AUSTRALIA, WA, Fortescue River Basin ~12km N Auski RH, 19. MAY 2003	ANIC/AZ 251
Anthelidae	*Anthela clementi*	male	21°36'S 117°07'E, AUSTRALIA, WA, 4km ESE Millstream, 18. APR 1971	ANIC/AZ 118
Anthelidae	*Anthela clementi*	male	22°35'48.5"S 118°27'05.1"E, AUSTRALIA, WA, Karijini NP, Djuna Downs Rd, ~2km S Ranger Stn [Mulga], 14. MAY 2003	ANIC/AZ 247

family	species	gender	collecting data	preparation #
Anthelidae	*Anthela connexa*	male	AUSTRALIA, TAS, Cuvier R., 2500ft, 22. DEC [19]52	ANIC/AZ 50
Anthelidae	*Anthela connexa*	male	AUSTRALIA, VIC, Moe, 15. JAN 1937	ANIC/AZ 68
Anthelidae	*Anthela connexa*	male	AUSTRALIA, VIC, Moe, 6. JAN [19]39	ANIC/AZ 51
Anthelidae	*Anthela denticulata*	male	AUSTRALIA, NSW, Beni SF NE Dubbo, 20. APR 1966	ANIC/AZ 255
Anthelidae	*Anthela denticulata*	male	AUSTRALIA, NSW, Trangie, 3. APR 1979	ANIC/AZ 253
Anthelidae	*Anthela denticulata*	male	32°37'S 148°56'E, AUSTRALIA, NSW, Wellington Caves, 22.-26. APR 1990	ANIC/AZ 254
Anthelidae	*Anthela denticulata*	male	AUSTRALIA, VIC, Braybrook, 25. MAR 1945	ANIC/AZ 115
Anthelidae	*Anthela denticulata*	male	AUSTRALIA, NSW, Trangie, Mitchell Lab., 5. APR 1953	ANIC/AZ 252
Anthelidae	*Anthela euryphrica*	male	32°37'S 148°56'E, AUSTRALIA, NSW, Wellington Caves, 22.-26. APR 1990	ANIC/AZ 178
Anthelidae	*Anthela excellens*	male	35°30'S 150°24'E, AUSTRALIA, NSW, Bawley Point, 9. MAR 1998	ANIC/AZ 2
Anthelidae	*Anthela excellens*	male	AUSTRALIA, NSW, Narara, 25. FEB 1948	ANIC/AZ 92
Anthelidae	*Anthela excellens* (A)	male	AUSTRALIA, QLD, Mt. Edith 18mi NE Atherton, 3400ft, 17. MAR 1964	ANIC/AZ 93
Anthelidae	*Anthela excellens* (A)	male	AUSTRALIA, QLD, Mt. Lewis 8mi NW Mt. Molly, 3200ft, 18. APR 1964	ANIC/AZ 94
Anthelidae	*Anthela excellens* (B)	male	AUSTRALIA, QLD, 4km E Toowoomba, 340m, 27. FEB 1984	ANIC/AZ 95
Anthelidae	*Anthela exoleta*	male	AUSTRALIA, WA, 8mi E Carnarvon, 20. APR 1968	ANIC/AZ 116
Anthelidae	*Anthela ferruginosa*	female	AUSTRALIA, NSW, Barrington Tops [Len Willan leg.], 2004	CAZS/AZ 234
Anthelidae	*Anthela ferruginosa*	male	AUSTRALIA, ACT, Black Mtn, 28. MAR 1966	ANIC/AZ 35
Anthelidae	*Anthela ferruginosa*	male	AUSTRALIA, ACT, Black Mtn, 21. MAR 1966	ANIC/AZ 201
Anthelidae	*Anthela ferruginosa*	male	AUSTRALIA, QLD, Toowoomba, 6. OCT 1970	ANIC/AZ 39
Anthelidae	*Anthela ferruginosa*	male	AUSTRALIA, TAS, Richmond, 17. MAR 1985	ANIC/AZ 38
Anthelidae	*Anthela ferruginosa*	male	AUSTRALIA, ACT, Black Mtn, 12. MAR 1968	ANIC/AZ 202
Anthelidae	*Anthela ferruginosa*	male	AUSTRALIA, ACT, Black Mtn, 19. MAR 1969	ANIC/AZ 203
Anthelidae	*Anthela ferruginosa*	male	24°15'S 151°30'E, AUSTRALIA, QLD, 1km SSW Bororen, 12. OCT 1988	ANIC/AZ 206
Anthelidae	*Anthela ferruginosa*	male	AUSTRALIA, ACT, Black Mtn, 12. APR 1965	ANIC/AZ 198
Anthelidae	*Anthela ferruginosa*	male	AUSTRALIA, ACT, Black Mtn, 21. MAR 1966	ANIC/AZ 199
Anthelidae	*Anthela ferruginosa*	male	AUSTRALIA, NSW, Grafton, 20. NOV 1958	ANIC/AZ 36
Anthelidae	*Anthela ferruginosa*	male	AUSTRALIA, VIC, Maryvale, JAN 1970	ANIC/AZ 37
Anthelidae	*Anthela ferruginosa*	male	24°59.397'S 147°58.409'E, AUSTRALIA, Carnarvon NP, Mt. Moffat sect., Marlong Plain, 4. APR 2002	ANIC/AZ 209

family	species	gender	collecting data	preparation #
Anthelidae	*Anthela ferruginosa*	male	AUSTRALIA, ACT, Black Mtn, 21. MAR 1966	ANIC/AZ 200
Anthelidae	*Anthela ferruginosa*	male	AUSTRALIA, NSW, Pilliga SF, Telephone line Rd & Wanga Rds, 21. APR 1993	ANIC/AZ 207
Anthelidae	*Anthela ferruginosa*	male	AUSTRALIA, NSW, Rocky Hill, 17. OCT 1977	ANIC/AZ 210
Anthelidae	*Anthela ferruginosa* ssp. A	male	31°18'S 119°38'E, AUSTRALIA, WA, 2km WbyS of Yellowdine, 4. MAY 1983	ANIC/AZ 40
Anthelidae	*Anthela ferruginosa* ssp. A	male	AUSTRALIA, WA, Kojonup, 11. APR 1963	ANIC/AZ 204
Anthelidae	*Anthela ferruginosa* ssp. A	male	32°15'S 125°32'E, AUSTRALIA, WA, 5km ENE Caiguna, 8. MAY 1983	ANIC/AZ 205
Anthelidae	*Anthela ferruginosa* ssp. B (or A?)	male	35°57'S 141°51'E, AUSTRALIA, VIC, Lake Hindmarsh 15km WSW Rainbow, 26. APR 2001	ANIC/AZ 208
Anthelidae	*Anthela guenei*	male	AUSTRALIA, QLD, Millmerran, 2. NOV [19]29	ANIC/AZ 11
Anthelidae	*Anthela habroptila* [*ocellata* (3)]	male	34°22'S 139°27'E, AUSTRALIA, SA, Blanchtown, Brookfield Cons. Pk., 30. APR 1992	ANIC/AZ 112
Anthelidae	*Anthela haemoptera*	male	AUSTRALIA, SA, Blackwood, "Kurlge", 850ft, 20. MAY 1969	ANIC/AZ 49
Anthelidae	*Anthela heliopa*	male	AUSTRALIA, NT, Brook Creek Burnside, 8. FEB 1932	ANIC/AZ 126
Anthelidae	*Anthela hyperythra*	male	AUSTRALIA, NT, P. Darwin, NOV [19]08	ANIC/AZ 123
Anthelidae	*Anthela limonea*	male	AUSTRALIA, QLD, Cape York Pen., Silver Plains Homestead, 26. APR 1963	ANIC/AZ 77
Anthelidae	*Anthela limonea* ssp.	male	AUSTRALIA, NT, Mataranka Hsd, Waterhouse River, 23. DEC 1986	ANIC/AZ 78
Anthelidae	*Anthela limonea/astata* (A)	male	16°31'S 125°16'E, AUSTRALIA, WA, Synnot Ck, 17.-20. JUN 1988	ANIC/AZ 79
Anthelidae	*Anthela limonea/astata* (B)	male	15°44'S 129°07'E, AUSTRALIA, NT, Keep R. NP, 6km NEbyN Jarrnarm, 31. MAY 2001	ANIC/AZ 81
Anthelidae	*Anthela stygiana*	male	AUSTRALIA, QLD, 25mi N Emerald, 20. APR 1955	ANIC/AZ 130
Anthelidae	*Anthela* n. sp. (nsp-A) [*ocellata* (5)]	male	23°48'S 132°21'E, AUSTRALIA, NT, 3mi NE Gosses Bluff, 13. MAY 1969	ANIC/AZ 12
Anthelidae	*Anthela* n. sp. (nsp-B)	male	AUSTRALIA, WA, 107mi SSE Carnarvon, 21. APR 1968	ANIC/AZ 19
Anthelidae	*Anthela* n. sp. (nsp-C)	male	14°17'S 126°16'E, AUSTRALIA, WA, Kalumburu Mission [sandstone], 24. MAY 1993	ANIC/AZ 80
Anthelidae	*Anthela* n. sp. (nsp-D)	male	21°12'S 119°15'E (GPS), AUSTRALIA, WA, 50km W Marble Bar, 26.-27. APR 1995	ANIC/AZ 117
Anthelidae	*Anthela* n. sp. near *charon*	male	PAPUA NEW GUINEA, Telefomin (Eliptamin), 4500-5500ft, W. W. Brandt leg., 19. JUN – 14. SEP 1959	ANIC/AZ 28
Anthelidae	*Anthela* n. sp. (nsp-E) [*A. stygiana* group]	male	22°50'31.3"S 118°31'11.2"E, AUSTRALIA, WA, Karijini NP, gorge 5km N Juna Downs Stn [Callitris], 18. MAY 2003	ANIC/AZ 250

family	species	gender	collecting data	preparation #
Anthelidae	*Anthela neurospasta*	male	12°19'S 133°19'E, AUSTRALIA, NT, Nabarlek, 23. NOV 1983	ANIC/AZ 15
Anthelidae	*Anthela nicothoe*	female	AUSTRALIA, ACT, 3mi N Mt. Coree, 3000ft., 6. FEB 1957	ANIC/AZ 144
Anthelidae	*Anthela nicothoe*	male	AUSTRALIA, QLD, Stanthorpe [ex pupa?], 15. MAR [19]48	ANIC/AZ 66
Anthelidae	*Anthela nicothoe*	male	AUSTRALIA, VIC, Moe (ex ovo), 1. FEB 1932	ANIC/AZ 62
Anthelidae	*Anthela nicothoe*	male	AUSTRALIA, VIC, Moe, 9. MAR 1918	ANIC/AZ 65
Anthelidae	*Anthela nicothoe*	male	AUSTRALIA, VIC, Moe (ex ovo), 1. FEB 1932	ANIC/AZ 63
Anthelidae	*Anthela nicothoe*	male	36°20'S 148°29'E, AUSTRALIA, NSW, Kosciusko NP, Danera Gap, 22. JAN 1987	ANIC/AZ 64
Anthelidae	*Anthela ocellata*	female	AUSTRALIA, VIC, Morwell, 1. APR 1922	ANIC/AZ 295
Anthelidae	*Anthela ocellata* (1)	male	AUSTRALIA, VIC, Maryvale, 16. MAR 1969	ANIC/AZ 10
Anthelidae	*Anthela ocellata* (2)	male	AUSTRALIA, QLD, Ingham, 21. APR 1961	ANIC/AZ 111
Anthelidae	*Anthela oressarcha* [*ocellata* (4)]	male	36°23'S 148°25'E, AUSTRALIA, NSW, Kosciusko NP, Saddle 2km NW Smiggin Holes, 1680m, 23. JAN 1987	ANIC/AZ 113
Anthelidae	*Anthela ostra*	male	AUSTRALIA, NT, Tortilla Flats (ex rice), 27. JAN 1987	ANIC/AZ 146
Anthelidae	*Anthela phaeodesma*	male	AUSTRALIA, QLD, 10km W Kuranda, 20. MAR 1984	ANIC/AZ 125
Anthelidae	*Anthela phaeodesma*	male	PAPUA NEW GUINEA, Western District, Rouku, Morehead River, 19. MAR – 28. MAY 1962	ANIC/AZ 96
Anthelidae	*Anthela phoenicias*	male	AUSTRALIA, QLD, Stannary Hills,	ANIC/AZ 273
Anthelidae	*Anthela phoenicias*	male	AUSTRALIA, QLD, Mareeba, 31. JAN 1963	ANIC/AZ 119
Anthelidae	*Anthela phoenicias*	male	25°35'S 151°57'E, AUSTRALIA, QLD, 5.5km SWbyS of Mt. Biggenden, 11. OCT 1984	ANIC/AZ 278
Anthelidae	*Anthela phoenicias*	male	26°55'S 146°05'E, AUSTRALIA, QLD, 5km ENE of Yanna, 9. MAY 1973	ANIC/AZ 277
Anthelidae	*Anthela phoenicias*	male	15°18'S 145°00'E, AUSTRALIA, QLD, Isabella Ck 32km NWbyW of Cooktown, 22. MAY 1977	ANIC/AZ 270
Anthelidae	*Anthela phoenicias*	male	AUSTRALIA, QLD, Mareeba, 31. DEC 1962	ANIC/AZ 271
Anthelidae	*Anthela phoenicias*	male	AUSTRALIA, QLD, Cape York Pen., Silver Plains, Chester R., 4. DEC 1961	ANIC/AZ 272
Anthelidae	*Anthela phoenicias*	male	12°37'S 141°55'E, AUSTRALIA, QLD, Dinah Ck, 17. FEB 1994	ANIC/AZ 274
Anthelidae	*Anthela phoenicias*	male	AUSTRALIA, VIC, Moe, 7. DEC 1912	ANIC/AZ 276
Anthelidae	*Anthela phoenicias*	male	AUSTRALIA, QLD, 7mi SW of Mt. Garnet, 20. APR 1969	ANIC/AZ 275
Anthelidae	*Anthela postica*	male	AUSTRALIA, NSW, Wilton, CSIRO Exp. Fm., 19. MAR 1968 (emerged)	ANIC/AZ 52
Anthelidae	*Anthela postica*	male	AUSTRALIA, VIC, Moe, 30. MAR 1915	ANIC/AZ 53
Anthelidae	*Anthela protocentra*	male	AUSTRALIA, NSW, Blackheath, 6. DEC 1917	ANIC/AZ 59
Anthelidae	*Anthela pudica*	male	22°56'S 114°45'E, AUSTRALIA, WA, 23km WSW Barradale, 28. APR 1971	ANIC/AZ 120

family	species	gender	collecting data	preparation #
Anthelidae	*Anthela pudica* (X)	male	AUSTRALIA, NT, Victoria Hwy, 52km E Kununurra, 22. JAN 1998	CAZS/AZ 212
Anthelidae	*Anthela pudica* (X)	male	AUSTRALIA, WA, Kimberleys, 6km before El Questro Station, 23. JAN 1998	CAZS/AZ 213
Anthelidae	*Anthela reltoni*	male	26°43'S 146°08'E, AUSTRALIA, QLD, 35km SSW Charleville, 13. MAR 1990	ANIC/AZ 122
Anthelidae	*Anthela repleta*	male	AUSTRALIA, QLD, Main Range NP, Cunningham's Gap, 800m, 15. APR 1955	ANIC/AZ 27
Anthelidae	*Anthela repleta*	male	AUSTRALIA, VIC, Moe, 1. SEP 1950	ANIC/AZ 58
Anthelidae	*Anthela repleta*	male	36°30'S 148°19'E, AUSTRALIA, NSW, Kosciusko NP, Thredbo, 1400m, 22. JAN 1989	ANIC/AZ 57
Anthelidae	*Anthela repleta ssp.*	male	AUSTRALIA, TAS, Pot Hill 1km W Chimney, 370m, 19. OCT 1980	ANIC/AZ 55
Anthelidae	*Anthela rubicunda*	male	21°35'S 117°04'E, AUSTRALIA, WA, 1km N Millstream HS, 9. APR 1971	ANIC/AZ 14
Anthelidae	*Anthela rubicunda*	male	22°35'48.5"S 118°27'05.1"E, AUSTRALIA, WA, Karijini NP, Djuna Downs Rd, ~2km S Ranger Stn [Mulga], 14. MAY 2003	ANIC/AZ 245
Anthelidae	*Anthela rubicunda*	male	25°46'S 133°17'E, AUSTRALIA, NT, 8km N Kulgera, 21. SEP 1978	ANIC/AZ 266
Anthelidae	*Anthela rubicunda*	male	24°15'S 133°26'E, AUSTRALIA, NT, James Ranges, 22. SEP 1978	ANIC/AZ 267
Anthelidae	*Anthela rubicunda*	male	21°35'S 117°04'E, AUSTRALIA, WA, 1km N Millstream, 8. APR 1971	ANIC/AZ 269
Anthelidae	*Anthela rubicunda*	male	AUSTRALIA, SA, 1mi ESE Ooldea, 3. OCT 1968	ANIC/AZ 264
Anthelidae	*Anthela rubicunda*	male	21°35'S 117°04'E, AUSTRALIA, WA, 1km NE Millstream HS., 4. APR 1971	ANIC/AZ 268
Anthelidae	*Anthela rubicunda*	male	32°51'S 141°37'E, AUSTRALIA, NSW, 100km SbyE Broken Hill, 2. OCT 1988	ANIC/AZ 265
Anthelidae	*Anthela* sp. near *adriana*	male	22°35'48.5"S 118°27'05.1"E, AUSTRALIA, WA, Karijini NP, Djuna Downs Rd, ~2km S Ranger Stn [Mulga], 14. MAY 2003	ANIC/AZ 246
Anthelidae	*Anthela* sp. near *asciscens*	male	AUSTRALIA, WA, 28mi W Madura, 30. APR 1968	ANIC/AZ 132
Anthelidae	*Anthela* sp. near *basigera*	male	AUSTRALIA, WA, 11km N Geralton, Drummond Cove, 30. APR 1973	ANIC/AZ 259
Anthelidae	*Anthela* sp. near *basigera* or *A. basigera* ssp.	male	AUSTRALIA, WA, 11km N Geralton, Drummond Cove, 2. MAY 1973	ANIC/AZ 177
Anthelidae	*Anthela* sp. near *clementi*	male	21°19'57.7"S 117°14'23.9"E, AUSTRALIA, WA, Millstream-Chichester NP, Python Pool, 11. MAY 2003	ANIC/AZ 248
Anthelidae	*Anthela* sp. near *denticulata*	male	32°15'S 125°32'E, AUSTRALIA, WA, 5km ENE Caiguna, 11. APR 1983	ANIC/AZ 258
Anthelidae	*Anthela* sp. near *denticulata* or *A. denticulata* ssp.	male	32°15'S 125°32'E, AUSTRALIA, WA, 5km ENE Caiguna, 11. APR 1983	ANIC/AZ 176
Anthelidae	*Anthela* sp. near *nicothoe*	male	AUSTRALIA, TAS, 10mi E Marrawah, 15. FEB 1963	ANIC/AZ 67

family	species	gender	collecting data	preparation #
Anthelidae	*Anthela* sp. near *phoenicias*	male	21°56'S 115°39'E, AUSTRALIA, WA, 17km NbyE of Cane River HS, 27. APR 1971	ANIC/AZ 279
Anthelidae	*Anthela* sp. near *repleta*	male	AUSTRALIA, NSW, Barren Grounds, Fauna Res., 2. FEB 1971	ANIC/AZ 54
Anthelidae	*Anthela stygiana*	male	AUSTRALIA, WA, Madura, 20. MAR 1968	ANIC/AZ 193
Anthelidae	*Anthela stygiana*	male	AUSTRALIA, SA, 6mi W Iron Knob, 16. MAR 1968	ANIC/AZ 192
Anthelidae	*Anthela tetraphrica*	male	31°04'S 121°03'E, AUSTRALIA, WA, 16km SW of Coolgardie, 12. MAR 1996	ANIC/AZ 3
Anthelidae	*Anthela tetraphrica* (A)	male	29°54'S 121°07'E, AUSTRALIA, WA, 25km S Menzies, 5. MAY 1984	ANIC/AZ 133
Anthelidae	*Anthela tetraphrica* (B)	male	29°54'S 121°07'E, AUSTRALIA, WA, 25km S Menzies, 5. MAY 1984	ANIC/AZ 134
Anthelidae	*Anthela unisigna*	male	21°34'46.4"S 117°05'29.9"E, AUSTRALIA, WA, Millstream-Chichester NP, Pipeline Rd, 6km NbyW ranger stn, 09. MAY 2003	ANIC/AZ 249
Anthelidae	*Anthela varia*	female	AUSTRALIA, ACT, Black Mtn, 9. JAN 1964	ANIC/AZ 145
Anthelidae	*Anthela varia* (A)	male	23°46'S 133°47'E, AUSTRALIA, NT, 12km SWbyW Alice Springs, Roe Cr., 9. OCT 1978	ANIC/AZ 22
Anthelidae	*Anthela varia* (A)	male	21°37'S 117°06'E, AUSTRALIA, WA, 5km SE Millstream HS, 12. APR 1971	ANIC/AZ 23
Anthelidae	*Anthela varia* (A)	male	15°28'S 145°13'E, AUSTRALIA, QLD, 4km WbyS Cooktown, 21. MAY 1977	ANIC/AZ 85
Anthelidae	*Anthela varia* (A)	male	AUSTRALIA, QLD, Atherton Tableland, Millstream Falls, 3. DEC 1967	ANIC/AZ 21
Anthelidae	*Anthela varia* (B1)	male	AUSTRALIA, ACT, Black Mtn, 18. NOV 1959	ANIC/AZ 82
Anthelidae	*Anthela varia* (B2)	male	AUSTRALIA, NSW, Wilton, CSIRO, Exp. Fm., 30. DEC 1973	ANIC/AZ 84
Anthelidae	*Anthela varia* (B2)	male	AUSTRALIA, VIC, Moe, 20. FEB 1939	ANIC/AZ 83
Anthelidae	*Anthela varia* (B3)	male	31°49'S 141°12'E, AUSTRALIA, NSW, 9km NNW Silverton, Umberumberka Reservoir, 1. MAY 1976	ANIC/AZ 86
Anthelidae	*Anthela varia* (B4)	male	23°46'S 133°46'E, AUSTRALIA, NT, Roe Ck 12km SWbyW of Alice Springs, 27. SEP 1978	ANIC/AZ 87
Anthelidae	*Anthela varia* (C)	male	31°22'S 131°47'E, AUSTRALIA, SA, 14km NNW Yalata Mission, 9. APR 1983	ANIC/AZ 91
Anthelidae	*Anthela varia* (C)	male	AUSTRALIA, WA, Perth, 4. MAR [19]02	ANIC/AZ 90
Anthelidae	*Anthela varia* (C)	male	AUSTRALIA, WA, 28mi W Madura, 30. APR 1968	ANIC/AZ 89
Anthelidae	*Anthela varia* (PNG2)	male	PAPUA NEW GUINEA, Western Highlands, Kandep, 8000-8500ft, 23. DEC 1961 – 14. FEB 1962	ANIC/AZ 97
Anthelidae	*Anthela varia* (PNG3)	male	PAPUA NEW GUINEA, Western District, Rouku, Morehead River, 19. MAR – 28. MAY 1962	ANIC/AZ 98
Anthelidae	*Anthela varia* (PNG4)	male	PAPUA NEW GUINEA, Port Moresby (Mt. Lawe, 1300ft), 5. MAR – 12. MAY 1963	ANIC/AZ 100
Anthelidae	*Anthela varia* (sp.)	male	15°58'S 129°33'E (GPS), AUSTRALIA, NT, Pinkerton Range, 3. APR 1995	ANIC/AZ 127
Anthelidae	*Anthela varia/astata* (sp.)	male	AUSTRALIA, TAS, Collinsvale, 11. OCT 1977	ANIC/AZ 56

family	species	gender	collecting data	preparation #
Anthelidae	*Anthela varia/astata/acuta* (Z1)	male	AUSTRALIA, QLD, 9mi W Paluma, 830m, 15. APR 1969	ANIC/AZ 76
Anthelidae	*Anthela varia/astata/acuta* (Z2)	male	13°44'S 143°20'E, AUSTRALIA, QLD, McIlwraith Ra., Golden Nugget Ck Camp Site, 2. JUL 1989	ANIC/AZ 88
Anthelidae	*Anthela virescens*	male	AUSTRALIA, QLD, Springbrook, 11. FEB 43	ANIC/AZ 25
Anthelidae	*Anthela virescens*	male	28°11'S 153°11'E, AUSTRALIA, QLD, Lamington NP, Binna Burra, 700m, 1. MAY 1989	ANIC/AZ 26
Anthelidae	*Anthela virescens*	male	AUSTRALIA, NSW, Tooloom Scrub, 26. MAR [19]41	ANIC/AZ 24
Anthelidae	*Anthela xantharcha*	male	AUSTRALIA, NSW, Yanco, MAR 1970	ANIC/AZ 18
Anthelidae	*Anthela xanthocera*	male	AUSTRALIA, QLD, Millmerran, 12. JAN 1938	ANIC/AZ 48
Anthelidae	*Chelepteryx chalepteryx*	female	AUSTRALIA, VIC, Moe, 7. APR 1927	ANIC/AZ 287
Anthelidae	*Chelepteryx chalepteryx*	male	35°40'S 150°13'E, AUSTRALIA, NSW, 6.5km NE of Batemans Bay, 21. JUN 1980	ANIC/AZ 4
Anthelidae	*Chelepteryx collesi*	male	AUSTRALIA, ACT, Black Mtn, 26. APR 1968	ANIC/AZ 128
Anthelidae	*Chenuala heliaspis*	female	35°13'S 148°36'E, AUSTRALIA, NSW, 13km SWbyS Wee Jasper, 860m asl, 18. APR 1987	ANIC/AZ 289
Anthelidae	*Chenuala heliaspis*	female	AUSTRALIA, ACT, Mt. Ginini, 9. JAN 1957	ANIC/AZ 288
Anthelidae	*Chenuala heliaspis*	male	AUSTRALIA, NSW, 2.7km NE Queanbeyan, 670m, 4. APR 1976	ANIC/AZ 8
Anthelidae	*Chenuala heliaspis*	male	AUSTRALIA, VIC, Moe, 2. JAN 1936	ANIC/AZ 186
Anthelidae	*Chenuala heliaspis*	male	AUSTRALIA, NSW, Armidale, 8. APR 1956	ANIC/AZ 185
Anthelidae	Anthelinae n. sp.	male	17°16'S 145°51'E, AUSTRALIA, QLD, Mt. Bellenden Ker, Centre Peak, 1560m, 15. FEB 1988	ANIC/AZ 20
Anthelidae	*Corticomis eupterotioides* [HOLOTYPE]	male	INDONESIA, Irian Jaya, Doorman top, 3500m; W.C. van Heurn & Kapit. van Arkeldon leg. (N. Guinea Exp. 1920), OCT 1920	RMNH/AZ 3
Anthelidae	*Corticomis* sp. (1)	male	PAPUA NEW GUINEA, Mt. Giluwe, 11,000; Coode 432/2; with P. Wardk & P. Katik; moss forest/grass, JUN [19]69	RMNH/AZ 1
Anthelidae	*Corticomis* sp. (2)	male	INDONESIA, Irian Jaya, Sterren Mtns, Bivak 42, 3400m (Nieuw Guinea Ned. Exp. 1959), 26. JUL 1959	RMNH/AZ 2
Anthelidae	*Gephyroneura cosmia*	male	AUSTRALIA, QLD, 7mi NNE Ravenshoe, 22. APR 1969	ANIC/AZ 141
Anthelidae	*Gephyroneura cosmia*	male	23°18'S 150°32'E, AUSTRALIA, QLD, 8km NNE Rockhampton, 4. SEP 1980	ANIC/AZ 142
Anthelidae	*Munychryia periclyta*	male	34°09'S 115°31'E, AUSTRALIA, WA, 38km EbyN Karridale, 23. APR 1983	ANIC/AZ 137
Anthelidae	*Munychryia periclyta*	male	34°32'S 116°00'E, AUSTRALIA, WA, 10km SbyW Pemberton, 22. APR 1983	ANIC/AZ 138
Anthelidae	*Munychryia periclyta* [Paratypus]	male	AUSTRALIA, WA, Mt. Singleton, 2300ft, 20. JUN 1963	ANIC/AZ 135
Anthelidae	*Munychryia senicula*	female	AUSTRALIA, NSW, St. George's Basin, 16. MAR 1960	ANIC/AZ 290

family	species	gender	collecting data	preparation #
Anthelidae	*Munychryia senicula* (A)	male	17°39'S 145°27'E, AUSTRALIA, QLD, The Millstream Falls 5km SW of Ravenshoe, 820m, 25. NOV 1998	ANIC/AZ 34
Anthelidae	*Munychryia senicula* (B)	male	AUSTRALIA, VIC, Little Desert, 26. OCT 1946	ANIC/AZ 139
Anthelidae	*Munychryia senicula* (B)	male	AUSTRALIA, TAS, Northdown Heath, 24. APR 1987	ANIC/AZ 140
Anthelidae	N. gen. n. sp. near *Munychryia/ Gephyroneura*	male	AUSTRALIA, WA, Mt. Singleton, 2300ft, 29. AUG 1963	ANIC/AZ 136
Anthelidae	*Nataxa amblopis*	male	AUSTRALIA, QLD, Millmerran, 7. SEP [19]27	ANIC/AZ 107
Anthelidae	*Nataxa flavescens*	female	AUSTRALIA, VIC, Blairgowrie, 3. FEB 1962	ANIC/AZ 292
Anthelidae	*Nataxa flavescens*	male	27°33'S 151°59'E, AUSTRALIA, QLD, Toowoomba, Prince Henry Heights, 620m, 8. JAN 1986 (emgd)	ANIC/AZ 191
Anthelidae	*Nataxa flavescens*	male	AUSTRALIA, ACT, Black Mtn, 5. FEB 1969	ANIC/AZ 9
Anthelidae	*Omphaliodes obscura* (1)	male	24°20'S 31°35'E, AUSTRALIA, NT, Amadeus Basin, nr Reedy Rockhole, 31. JUL 1962	ANIC/AZ 108
Anthelidae	*Omphaliodes obscura* (1)	male	30°59'S 118°55'E, AUSTRALIA, WA, Karolin Rock 18km W Bullfinch, 11. MAY 1984	ANIC/AZ 5
Anthelidae	*Omphaliodes obscura* (2)	male	31°58'S 124°28'E, AUSTRALIA, WA, 49mi NE Balladonia HS, 10. OCT 1968	ANIC/AZ 109
Anthelidae	*Omphaliodes obscura* (3)	male	AUSTRALIA, WA, Mt. Singleton, 2300ft, 29. SEP 1948	ANIC/AZ 110
Anthelidae	*Pseudodreata* sp.	female	PAPUA NEW GUINEA, Western Highlands, Mt. Hagen Range, Murmur Pass, 8700 ft., 27. OCT – 20. DEC 1961	ANIC/AZ 294
Anthelidae	*Pseudodreata* sp.	male	[INDONESIA, Irian Jaya] "5" [K. Cerny leg., ex coll. B. Ploessel],	CAZS/AZ 190
Anthelidae	*Pseudodreata* sp.	male	PNG, Kodama Range, Mt. Kaindi, 4500ft., 27. FEB 1952	ANIC/AZ 260
Anthelidae	*Pseudodreata* sp. (1)	male	PAPUA NEW GUINEA, Amazon Bay area, Komania, 3400ft, W. W. Brandt leg., 11. – 26. NOV 1962	ANIC/AZ 30
Anthelidae	*Pseudodreata* sp. (2)	male	PAPUA NEW GUINEA, Finistere Range, N Freyberg Pass, 8500ft, 1. – 22. OCT 1958	ANIC/AZ 102
Anthelidae	*Pseudodreata* sp. (3)	male	PAPUA NEW GUINEA, Western Highlands, Jimi River, 4700ft, 16. JUL – 21. SEP 1961	ANIC/AZ 103
Anthelidae	*Pseudodreata* sp. (4)	male	PAPUA NEW GUINEA, Telefomin (Feramin), 4700ft, 2. MAY – 18. JUN 1959	ANIC/AZ 104
Anthelidae	*Pseudodreata* sp. (5)	male	PAPUA NEW GUINEA, Eastern Highlands, Mt. Wilhelm, Pengal River, 9200ft, 16. MAY – 9. JUN 1963	ANIC/AZ 105
Anthelidae	*Pseudodreata* sp. (6)	male	PAPUA NEW GUINEA, Western Highlands, Kandep, 8000-8500ft, 23. DEC 1961 – 14. FEB 1962	ANIC/AZ 106
Anthelidae	*Pseudodreata* sp. (6)	male	PAPUA NEW GUINEA, Kodama Range, Mt. Kaindi, 4500ft., 1951	ANIC/AZ 190
Anthelidae	*Pseudodreata* sp. (7)	male	PAPUA NEW GUINEA, Morobe D., Mt. Kaindi, 9. JUL 1976	CPMB/AZ 1
Anthelidae	*Pterolocera amplicornis*	male	35°19'S 149°08'E, AUSTRALIA, ACT, Barton, York Park, 13. MAR 1985	ANIC/AZ 7

family	species	gender	collecting data	preparation #
Anthelidae	*Pterolocera elizabetha* (?)	male	31°41'S 115°48'E, AUSTRALIA, WA, Neerabup, Flynn Drive, 19. MAR 1996	ANIC/AZ 6
Anthelidae	*Pterolocera isogama*	male	AUSTRALIA, WA, East Yuna ["Bunya Bunya"], JUN 1949	ANIC/AZ 172
Anthelidae	*Pterolocera leucocera*	male	AUSTRALIA, NSW, Wilton, CSIRO, Exp. Fm., 8. MAR 1971	ANIC/AZ 167
Anthelidae	*Pterolocera* n. sp. near *isogama*	male	31°01'S 120°51'E, AUSTRALIA, WA, 2km WbyS Bullabulling, 6. MAY 1984	ANIC/AZ 147
Anthelidae	*Pterolocera* sp (1)	male	43°25'S 146°09'E, AUSTRALIA, TAS, Melaleuca, 28. NOV 1991	ANIC/AZ 168
Anthelidae	*Pterolocera* sp (2)	male	35°05'S 177°54'E, AUSTRALIA, WA, 7km SbyE Albany, 18. APR 1983	ANIC/AZ 169
Anthelidae	*Pterolocera* sp (3)	male	AUSTRALIA, TAS, Tamar River, Exeter, 13. JUN 1963	ANIC/AZ 170
Anthelidae	*Pterolocera* sp (4)	male	AUSTRALIA, WA, 11km N Geralton, Drummond Cove, 8. JUN 1973	ANIC/AZ 171
Anthelidae	*Pterolocera* sp (5)	male	AUSTRALIA, VIC, East Malvern, MAR 1957	ANIC/AZ 173
Anthelidae	*Pterolocera* sp (6)	male	AUSTRALIA, VIC (SE), Mann's Beach, 2. MAR 1957	ANIC/AZ 174
Bombycidae	*Andraca* n. sp.	male	8°43'54"N 117°34'04"E, PHILIPPINES, Palawan, Bataraza, Malihud, prim. forest 6km N, hilltop, 730m, 02. JUN 2000	CAZS/AZ 231
Bombycidae	*Gastridiota adoxima*	male	27°33'S 151°59'E, AUSTRALIA, QLD, Toowoomba, Prince Henry Heights, 620m, 3. MAY 1989 (emgd)	ANIC/AZ 150
Bombycidae	*Mustilia gerontica*	female	THAILAND, vic. Pak Chong, Khao Yai NP, 4.-22. SEP 1998	CAZS/AZ 238
Bombycidae	*Mustilia gerontica*	male	TAIWAN, Nantou Prov., Puli Pref., 25.-28. FEB 1998	CAZS/AZ 232
Bombycidae	*Prismosticta tiretta*	male	INDONESIA, Sumatra Barat, Mt. Singgalang, 2100m, near Padang Panjang, 10.-11. FEB 1996	CAZS/AZ 233
Bombycidae	*Quentalia ephonia*	male	EL SALVADOR, San Salvador, 3. SEP 1951	CAZS/AZ 227
Bombycidae: Apatelodinae	*Olceclostera seraphica*	male	USA, Texas, Val Verde Co. male x Jeff Davis County female; bred, emgd. July 1994	CAZS/AZ 226
Brahmaeidae	*Brahmophtha lma hearseyi*	male	INDONESIA, Sumatra, NW of Pematang Siantar, Tinggi Raja, 350m, 15. FEB 1996	CAZS/AZ 215
Carthaeidae	*Carthaea saturnioides*	male	33°27'07.2"S 123°26'16.2"E AUSTRALIA, WA, Cape Arid NP, track to Mt. Ragged, ~200m asl, 30. OCT 2003	CAZS/AZ 224
Endromidae	*Endromis versicolora*	female	CZECHIA (?) [bred], 9. MAR 1991 (emg.)	CAZS/AZ 237
Endromidae	*Endromis versicolora*	male	CZECHIA, Bohemia, Chomliton [bred], 14. APR 1992	CAZS/AZ 216
Eupterotidae	*Eupterote styx* (?)	male	New Guinea, Araboebivak (Nieuw Guinea Exp. K.N.A.G. 1939), 1. NOV 1939	RMNH/AZ 4
Eupterotidae	Eupterotidae sp., not *Phiala* sp.?	male	ZIMBABWE [?], Kasangeji, 14.xi.1999	CAZS/AZ 189
Eupterotidae	*Melanergon* sp.	male	PAPUA NEW GUINEA, East Sepik P., Bagi (Gavien), 50m, 3. JUL 1975	CPMB/AZ 2
Eupterotidae	*Panacela nyctropa*	male	AUSTRALIA, NSW, Coffs Harbour, 16. MAY 1966	ANIC/AZ 61
Eupterotidae	*Panacela syntropha*	male	AUSTRALIA, QLD, 1mi E Kuranda, 22. MAR 1964	ANIC/AZ 60

family	species	gender	collecting data	preparation #
Eupterotidae	*Phiala arrecta* (?)	male	ZIMBABWE, Halfarag, house, 29.i.1998	CAZS/AZ 187
Eupterotidae	*Phiala* sp.	male	REP. SOUTH AFRICA, Mkuzi-Reserve, 16.i.2000	CAZS/AZ 93
Eupterotidae	*Phiala* sp.	male	ZIMBABWE, Nr. Chimanimani NP, Hayfield B, 20°01'S 32°58'E, 920m, 9.-25.i.1998	CAZS/AZ 188
Eupterotidae	*Preptos* sp.	male	MEXICO, Vera Cruz, road Coscomatepec to Tetelclngo, km 14, 1850m, 02. AUG 1992	CROC/AZ 1
Geometridae	*Paralaea jarrah* [Paratype]	male	34°58'S 116°56'E, AUSTRALIA, WA, 2km WSW Bow River Bridge, 20. APR 1983	ANIC/AZ 189
Geometridae	*Paralaea porphyrinaria*	male	AUSTRALIA, ACT, Black Mtn, 8. MAY 1950	ANIC/AZ 188
Lasiocampidae	*Artace cribraria*	male	USA, Texas, Huntsville, 18.v.1992	CAZS/AZ 186
Lasiocampidae	*Artace* sp.	male	BOLIVIA, Yungas la Paz, Unduavi/Coroico, 2500m, 19/23. NOV 1984	ANIC/AZ 166
Lasiocampidae	*Chionopsyche montana*	male	KENYA, Umani Springs, 1050m, 02°28'S 37°55'E, 26.-28.iv.1997	CAZS/AZ 49
Lasiocampidae	*Chondrostega* sp.	male	TURKEY, Adana, 1400m, 09.ix.1992	CAZS/AZ 50
Lasiocampidae	*Crinocrasped a torrida*	male	[THAILAND] "13.9. TB" [ex coll. Swen Loeffler, 2003],	CAZS/AZ 218
Lasiocampidae	*Eremaea coralliphora*	male	31°17'S 142°18'E, AUSTRALIA, NSW, Mootwingee NP, Homestd Gorge, 6. OCT 1988	ANIC/AZ 151
Lasiocampidae	*Eremaea* n. sp.	male	29°54'S 121°07'E, AUSTRALIA, WA, 25km S Menzies, 5. MAY 1984	ANIC/AZ 153
Lasiocampidae	*Eriogaster lanestris*	male	[bred, ex pupa], v.1991	CAZS/AZ 183
Lasiocampidae	*Euglyphis* sp.	male	BOLIVIA, Yungas la Paz, Ciacuata/Cajuata, 2400m, 3/5. DEC 1984	ANIC/AZ 165
Lasiocampidae	*Genduara fola*	male	21°35'S 117°04'E, AUSTRALIA, WA, 1km N Millstream, 1. NOV 1970	ANIC/AZ 179
Lasiocampidae	*Macromphali a* sp.	male	CHILE, E. Puerto Mountt, Correntoso, Hornohuinco, 3/5. MAR 1984	ANIC/AZ 164
Lasiocampidae	*Macromphali a* sp.	male	[CHILE,] San Sebastian, 14. FEB [19]61	ANIC/AZ 162
Lasiocampidae	*Macromphali a* sp.	male	[CHILE] Terma d. Rio Blanco (Cautin), 1200m, 14. FEB [19]64	ANIC/AZ 163
Lasiocampidae	*Macrothylaci a rubi*	female	GERMANY, Hohenfels, autumn 1984	CAZS/AZ 236
Lasiocampidae	*Malacosoma neustria*	male	[GREAT BRITAIN,] Portchester, Hants, 2. AUG 1911 (bred)	ANIC/AZ 195
Lasiocampidae	*Opsirhina albigutta*	male	35°32'S 148°34'E, AUSTRALIA, ACT, Mt. Ginini, 1660m, 28. JAN 1984	ANIC/AZ 182
Lasiocampidae	*Opsirhina alphaea*	male	12°52'S 132°50'E, AUSTRALIA, NT, 15km E Mt. Cahill, Koongarra, 8. MAR 1973	ANIC/AZ 184
Lasiocampidae	*Opsirhina lechriodes*	male	AUSTRALIA, ACT, Black Mtn, 17. APR 1963	ANIC/AZ 183
Lasiocampidae	*Pararguda rufescens*	female	35°33'15.2"S 150°02'04.5"E, AUSTRALIA, NSW, Budawang NP, ~5km on Western Distributor Rd, 250m asl, 22. SEP 2004	CAZS/AZ 235
Lasiocampidae	*Pernattia brevipennis*	male	AUSTRALIA, QLD, Carnarvon Gorge, 31. MAR 1957	ANIC/AZ 180
Lasiocampidae	*Pernattia chlorophrag ma*	male	31°47'S 136°21'E, AUSTRALIA, SA, Nooltana Ck 13km NWbyN Hawker, 16. SEP 1978	ANIC/AZ 181

family	species	gender	collecting data	preparation #
Lasiocampidae	*Pernattia pusilla*	male	AUSTRALIA, ACT, Black Mtn, 24. MAR 1960	ANIC/AZ 143
Lasiocampidae	*Pinara cana*	male	AUSTRALIA, ACT, Macquarie, 15. DEC 1989 (bred)	ANIC/AZ 196
Lasiocampidae	*Poecilocampa populi*	male	CZECHIA, Bohemia, Chomutov, 20.x.1990	CAZS/AZ 182
Lasiocampidae	*Trichiura crataegi*	male	GERMANY, Bonn, Kottenforst, 5.ix.1986	CAZS/AZ 194
Lemoniidae	*Sabalia picarina*	male	2°54.002'S 37°38.900'E, KENYA, rd Tsavo West NP to Oloitokitok, river bed, ~1200m asl, 29. MAR 2003	CAZS/AZ 220
Limacodidae	*Pseudanapaea transvestita*	male	AUSTRALIA, ACT, Black Mtn, 10. MAR 1957	ANIC/AZ 175
Lymantriidae	*Aroa cometaris*	male	INDONESIA, Solomon Islands, Gudalcanal Isl., Betikama River, 6. AUG – 2. OCT 1960	ANIC/AZ 261
Lymantriidae	*Euproctis baliolalis*	male	AUSTRALIA, NSW, Wollongong, APR 1953	ANIC/AZ 149
Megalopygidae	*Megalopyge opercularis*	male	USA, Texas, Huntsville, 11.v.1992	CAZS/AZ 185
Mimallonidae	*Mimallo amilia*	male	BRAZIL, South,	CAZS/AZ 229
Mimallonidae	*Trogoptera althora*	female	EL SALVADOR, San Salvador, 14. AUG 1951	CAZS/AZ 228
Mirinidae	*Mirina christophi*	male	RUSSIA, S. Primorye, 20km SE Ussuriisk, Gornotayozhnoe, 14.-22.JUN 1995	CAZS/AZ 230
Oenosandridae	*Discophlebia catocalina*	male	AUSTRALIA, ACT, Black Mtn, 4. JAN 1958	ANIC/AZ 159
Oenosandridae	*Oenosandra boisduvalii*	female	AUSTRALIA, VIC, Moe, 27. MAR 1941	ANIC/AZ 293
Oenosandridae	*Oenosandra boisduvalii*	male	AUSTRALIA, ACT, Black Mtn, 4. MAR 1955	ANIC/AZ 158
Pyralidae: Phycitinae	*Indomyrlaea auchmodes*	male	10°12'S 145°49'E, AUSTRALIA, QLD, Sue (Warraber) Island, 12. JAN 1978	ANIC/AZ 187
Saturniidae	*Eacles imperialis imperialis*	male	USA, Florida, Orlando, 26. SEP 1937	ANIC/AZ 154
Saturniidae	*Opodiphthera eucalypti*	male	AUSTRALIA, QLD, Mareeba, 31. DEC 1962	ANIC/AZ 197
Saturniidae	*Rhodinia fugax*	female	OCT [19]59	CAZS/AZ 239
Saturniidae	*Syntherata janetta*	male	AUSTRALIA, QLD, Julatten, 20. NOV 1979	ANIC/AZ 148
Saturniidae: Arsenurinae	*Arsenura ciocolatina*	male	PERU (NO), (Amazonasabhaenge), Depot. Amazonas, Strecke Bagua-Chica-Nazareth, 700-1100m, Oct-Dez. 1998	CAZS/AZ 223
Saturniidae: Cercophaninae	*Cercophana venusta*	male	CHILE, Colima, Santiago, Pena, 3. MAY [19]79	CAZS/AZ 222
Saturniidae: Oxyteninae	*Therinia buckleyi*	male	BOLIVIEN, Dept. Sta Cruz, Prov. Chapare, Alto Palmar, 1000-1200m, Haendlermaterial c/o Lampe, APR 1992	CAZS/AZ 221
Saturniidae: Saturniinae	*Loepa diversiocellata*	male	16°10'N 107°54'E, VIETNAM, Bach-ma NP, 1200m, 26. JUL – 6. AUG 1996	CAZS/AZ 225
Sphingidae	*Agrius convolvuli*	female	11°58'S 142°55'E, AUSTRALIA, QLD, Harmer Ck, riverine forest, 22. MAY 1993	ANIC/AZ 296
Sphingidae	*Coenotes eremophilae*	male	AUSTRALIA, QLD, Emerald, 2. JAN [19]20	ANIC/AZ 155

family	species	gender	collecting data	preparation #
Sphingidae	*Hopliocnema brachycera*	male	24°11'S 134°01'E, AUSTRALIA, NT, 56km SbyE of Alice Springs, 3. OCT 1978	ANIC/AZ 157
Sphingidae	*Marumba tigrina*	male	PHILIPPINES, Palawan, Malihud, 18.ix.-1.x.1998	CAZS/AZ 123
Sphingidae	*Smerinthus jamaicensis*	male	CANADA, Ontario, Dunnville, 4. JUN 1958	ANIC/AZ 194
Sphingidae	*Synoecha marmorata*	male	AUSTRALIA, QLD, Injune, 3. FEB [19]37	ANIC/AZ 156
Sphingidae	*Xenosphingia jansei*	male	18°03'S 22°11'E, SOUTH WEST AFRICA, Omega mil. base, Caprivi, 1000m, 05. FEB 1985	CROC/AZ 2
Thyrididae	*Aglaopus pyrrhata*	male	AUSTRALIA, ACT, Black Mtn, 20. JAN 1969	ANIC/AZ 160

APPENDIX G:

WHOLE SPECIMEN PREPARATIONS

family	species	gender	coll. locality	preparation #
Anthelidae	*Anthela acuta* grp.	male	AUSTRALIA, QLD, Brisbane, Mt. Coo-tha, Slaughter Falls	CAZS/AZ whole 5
Anthelidae	*Anthela adriana*	male	21°34'46.4"S 117°05'29.9"E, AUSTRALIA, WA, Millstream-Chichester NP, Pipeline Rd, 6km NbyW ranger stn	CAZS/AZ whole 4
Anthelidae	*Anthela virescens*	male	AUSTRALIA, QLD, Tooloom Scrub	CAZS/AZ whole 11
Anthelidae	*Chelepteryx chalepteryx*	male	AUSTRALIA, NSW, 13mi N Dungog	CAZS/AZ whole 10
Anthelidae	*Munychryia senicula*	male	AUSTRALIA, NSW, St. George's Basin	CAZS/AZ whole 9
Anthelidae	*Pterolocera* sp.	female	AUSTRALIA, ACT, Canberra, Gungahlin Grassland nr Palmerston; ex larva	CAZS/AZ whole 18
Bombycidae	*Apatelodes* sp.	male	PERU, Sierra de Dios	CAZS/AZ whole 3
Bombycidae	*Bombyx mori*	male	[bred]	CAZS/AZ whole 2
Bombycidae	*Ocinara ficicola*	male	2°27.938'S 37°54.988'E, KENYA, Kibwezi, Umani Springs Camp, ~1050m asl	CAZS/AZ whole 15
Bombycidae	*Ocinara* n. sp.	male	PHILIPPINES, Palawan, Malihud Mtns, house of Ceding	CAZS/AZ whole 14
Eupterotidae	*Eupterote* sp.	male	PHILIPPINES, Samar, Mt. Capotoan, 600m	CAZS/AZ whole 7
Eupterotidae	*Ganisa plana*	male	PHILIPPINES, Palawan, Salakot Falls, road, 300m asl	CAZS/AZ whole 17
Lasiocampidae	*Chionopsyche montana*	male	3°26.599'S 37°36.348'E, KENYA, Taveta, Kitobo Forest, ~900m asl	CAZS/AZ whole 8
Lasiocampidae	*Poecilocampa populi*	male	GERMANY, Berg-Land, Dhuenn-Tal, Boxberg	CAZS/AZ whole 1
Lemoniidae	*Lemonia dumi*	male	[no data]	CAZS/AZ whole 13
Saturniidae	*Aglia tau*	male	[bred]	CAZS/AZ whole 6
Sphingidae	*Daphnusa ocellaris*	male	PHILIPPINES, Palawan, Salakot Falls, road, 300m asl	CAZS/AZ whole 16
Sphingidae	*Laothoe populi*	male	GERMANY, Hesse, Schlitz [bred]	CAZS/AZ whole 12

APPENDIX H:

SEM PREPARATIONS

family	species	in-star	object	notes	collecting locality	prepara-tion #
Anthelidae	*Anthela rubicunda*	L1	entire specimen	cpd	AUSTRALIA, WA, Millstream-Chichester NP, Pipeline Rd, 6km NbyW ranger stn	SEM/AZ 27
Anthelidae	*Anthela phoenicias* group [ANIC/AZ 119]	I [male]	left antenna	air dried	AUSTRALIA, QLD, Mareeba	SEM/AZ 32
Anthelidae	*Anthela astata* [ANIC/AZ 71]	I [male]	left antenna	air dried	AUSTRALIA, QLD, Mt. Bellenden-Ker, base cableway	SEM/AZ 31
Anthelidae	*Anthela canescens*	L1	entire specimen, dorsal	cpd	AUSTRALIA, WA, Millstream NP	SEM/AZ 6
Anthelidae	*Anthela canescens*	L1	head, A10	cpd	AUSTRALIA, WA, Millstream NP	SEM/AZ 7
Anthelidae	*Anthela canescens*	L1	entire specimen, lateral	cpd	AUSTRALIA, WA, Millstream NP	SEM/AZ 5
Anthelidae	*Anthela ferruginosa* [ANIC/AZ 35]	I [male]	left antenna	air dried	AUSTRALIA, ACT, Black Mt.	SEM/AZ 33
Anthelidae	*Anthela* n. sp. near *addita*	L1	entire specimen	cpd	AUSTRALIA, QLD, Mt. Lewis	SEM/AZ 21
Anthelidae	*Anthela* n. sp. near *addita*	L2	entire specimen	cpd	AUSTRALIA, QLD, Mt. Lewis	SEM/AZ 22
Anthelidae	*Anthela neurospasta*	L1	3 entire specimens	air dried	AUSTRALIA, QLD, Cape York	SEM/AZ 30
Anthelidae	*Anthela nicothoe*	Lm	antenna, maxillae, labium, spinneret	cpd	AUSTRALIA, ACT, Namadgi NP, Mt. Ginini	SEM/AZ 1
Anthelidae	*Anthela nicothoe* [ANIC/AZ 63]	I [male]	left antenna	air dried	AUSTRALIA, VIC, Moe (ex ovo)	SEM/AZ 34
Anthelidae	*Chelepteryx chalepteryx*	I [male]	fore wing cross-fold	air dried	AUSTRALIA, NSW, Budawang NP, Carter's Ck	SEM/AZ 52
Anthelidae	*Chelepteryx collesi* [ANIC/AZ 128]	I [male]	left antenna	air dried	AUSTRALIA, ACT, Black Mt.	SEM/AZ 37
Anthelidae	*Chenuala heliaspis*	L1, E	entire specimen, eggs	cpd	AUSTRALIA, ACT, Mt. Aggie	SEM/AZ 26
Anthelidae	*Munychryia* n. sp. near *senicula*	L1	entire specimen	cpd	AUSTRALIA, QLD, old Ravenshoe–Herberton rd, ~5km S Herberton	SEM/AZ 23

family	species	in-star	object	notes	collecting locality	prepara-tion #
Anthelidae	*Munychryia senicula*	I [male]	right antenna, left antenna for cross section	air dried	AUSTRALIA, NSW, St. George Basin	SEM/AZ 9
Anthelidae	*Nataxa flavescens*	L1 & E	entire specimen	cpd	AUSTRALIA, NSW, Little Snowball Ck	SEM/AZ 47
Anthelidae	*Omphaliodes obscura* [ANIC/AZ 108]	I [male]	left antenna	air dried	AUSTRALIA, NT, Amadeus Basin, nr Reedy Rockhole	SEM/AZ 35
Anthelidae	*Pseudodreata* sp. [ANIC/AZ 102]	I [male]	left antenna	air dried	PAPUA NEW GUINEA, Finistere Range, N Freyberg Pass	SEM/AZ 36
Anthelidae	*Pterolocera* sp. near *amplicornis*	I [male]	right antenna, left antenna for cross section	air dried	AUSTRALIA, ACT, Canberra, York Park	SEM/AZ 8
Anthelidae	*Pterolocera* sp. near *amplicornis*	Lm	headcapsule	mazerrated, cpd	AUSTRALIA, ACT, Canberra, Gungahlin grassland	SEM/AZ 3
Anthelidae	*Pterolocera* sp. near *amplicornis*	Lm	labrum, maxillae, labium, spinneret	cpd	AUSTRALIA, ACT, Canberra, Gungahlin grassland	SEM/AZ 2
Bombycidae	*Andraca* n. sp. [CAZS/AZ 231]	I [male]	antenna	air dried	PHILIPPINES, Palawan, Malihud, primary forest 6km N	SEM/AZ 55
Bombycidae	*Mustilia gerontica*	I [male]	antenna	air dried	TAIWAN, Nantou Prov., Puli Pref.	SEM/AZ 56
Brahmaeidae	*Brahmophthalma hearseyi*	I [male]	left antenna	air dried	INDONESIA, Sumatra, NW of Pematang Siantar, Tinggi Raja	SEM/AZ 43
Brahmaeidae	*Spiramiopsis comma*	L1	entire specimen	cpd	SWAZILAND, Mbabane	SEM/AZ 48
Brahmaeidae	*Spiramiopsis comma*	Lm	headcapsule, left frontal "horn"	cpd	SWAZILAND, Mbabane	SEM/AZ 49
Carthaeidae	*Carthaea saturnioides*	I [male]	left antenna	air dried	AUSTRALIA, WA, Cape Arid NP, Mt. Ragged	SEM/AZ 46
Carthaeidae	*Carthaea saturnioides*	L1	entire specimen	cpd	AUSTRALIA, WA, Ravensthorpe	SEM/AZ 24
Carthaeidae	*Carthaea saturnioides*	Lm	headcapsule	cpd	AUSTRALIA, WA, Ravensthorpe	SEM/AZ 25
Drepanidae	*Hypsidia niphosema*	I [male]	antenna	air dried	AUSTRALIA, WA, Kojonup	SEM/AZ 54
Eupterotidae	*Ganisa plana*	I [male]	left antenna	air dried	MALAYSIA, Borneo, Sabah, Mt. Kinabalu NP	SEM/AZ 39
Eupterotidae	*Panacela lewinae*	Lm	headcapsule, labial palpus	cpd	AUSTRALIA, NSW, Mt. Keira	SEM/AZ 19
Eupterotidae	*Panacela lewinae*	Lm	legs	cpd	AUSTRALIA, NSW, Mt. Keira	SEM/AZ 20

family	species	in-star	object	notes	collecting locality	prepara-tion #
Eupterotidae	*Poloma angulata*	Lm	headcapsule	cpd	[AFRICA]	SEM/AZ 50
Hepialidae	*Oncopera alboguttata*	Lm (?)	legs	cpd	AUSTRALIA, NSW, Guyra	SEM/AZ 18
Hepialidae	*Oncopera alboguttata*	Lm (?)	headcapsule	cpd	AUSTRALIA, NSW, Guyra	SEM/AZ 17
Hepialidae	*Trictena argyrosticha*	I [male]	left antenna	air dried	AUSTRALIA, QLD, Carnarvon NP, Carnarvon Gorge	SEM/AZ 38
Lasiocampidae	*Chionopsyche montana*	I [male]	labial palpus	mazerrated, cpd	KENYA, Taveta, Kitobo Forest	SEM/AZ 15
Lasiocampidae	*Chionopsyche montana*	L1	caterpillar, egg	cpd	KENYA, Taveta, Kitobo Forest	SEM/AZ 14
Lasiocampidae	*Entometa* sp.	I [male]	right antenna, left antenna for cross section	air dried	AUSTRALIA, WA, Karijini NP	SEM/AZ 10
Lasiocampidae	*Opsirhina albigutta*	L1	prolegs, legs, mouth parts	cpd	AUSTRALIA, ACT, Namadgi NP, Mt. Ginini	SEM/AZ 13
Lasiocampidae	*Trabala vishnou*	L1	entire specimen	cpd	INDIA	SEM/AZ 29
Lemoniidae	*Lemonia taraxaci*	I [male]	left antenna	air dried	SWITZERLAND, St. Gotthard Pass	SEM/AZ 44
Lemoniidae	*Sabalia picarina*	I [male]	right antenna	air dried	KENYA, rd Tsavo West NP to Oloitokitok, river bed	SEM/AZ 45
Lymantriidae	*Lymantria nephrographa*	I [male]	left antenna	air dried	AUSTRALIA, NSW, Tooloom	SEM/AZ 41
Noctuidae	*Apina callisto*	Lm	headcapsule	mazerrated, cpd	AUSTRALIA, ACT, Canberra, Gungahlin grassland	SEM/AZ 4
Nymphalidae	*Danaus plexippus*	Lm	headcapsule	cpd	AUSTRALIA, QLD, Beenliegh, Bahr's Scrub	SEM/AZ 16
Oenosandridae	*Oenosandra boisduvalii*	I [male]	antenna	air dried	AUSTRALIA, NSW, Budawang NP, Carter's Ck	SEM/AZ 58
Saturniidae	*Bathyphlebia eminens*	I [male]	antenna	air dried		SEM/AZ 53
Saturniidae	*Periga* sp.	I [male]	left antenna	air dried	PERU, Dep. Piura, Abra Porculla	SEM/AZ 40
Saturniidae	*Ludia* sp.	L1	2 entire specimens	cpd	KENYA, rd Tsavo West NP to Oloitokitok, river bed	SEM/AZ 28
Saturniidae	*Opodiphthera helena*	L1	headcapsule, mouth parts	cpd	AUSTRALIA, ACT, Namadgi NP, Blundells Ck Rd	SEM/AZ 12
Saturniidae	*Opodiphthera helena*	L1	prolegs, legs	cpd	AUSTRALIA, ACT, Namadgi NP, Blundells Ck Rd	SEM/AZ 11
Sphingidae	*Smerinthus cerisyi*	I [male]	antenna	air dried	USA, Utah, Box Elder Co., Clear Ck	SEM/AZ 57
Sphingidae	*Smerinthus jamaicensis*	I [male]	left antenna	air dried	CANADA, Ontario, Dunnville	SEM/AZ 42

APPENDIX I:

DNA EXTRACTIONS

family	species	in-star	collecting data	preser-vation	prepara-tion #
Anthelidae	*Anthela acuta*	I	35°26'54.6"S 150°05'33.4"E AUSTRALIA, NSW, Budawang NP, ~25km on Western Distributor Rd, ~400m asl, 4. DEC 2003	EtOH abs.	DNA/AZ 19
Anthelidae	*Anthela adriana*	I	22°33'56.0"S 118°27'10.4"E, AUSTRALIA, WA, Karijini NP, junction Juna Downs Rd / Karijini Drive (Mulga), 13. MAY 2003	EtOH abs.	DNA/AZ 151
Anthelidae	*Anthela astata*	I	16°03.763'S 145°27.726'E, AUSTRALIA, QLD, Daintree NP, Cape Tribulation, 3km N rangerstation, 18. APR 2002	EtOH abs.	DNA/AZ 51
Anthelidae	*Anthela asterias*	I	30°30.105'S 146°17.164'E, AUSTRALIA, NSW, 21km NW Byrock, Nightvale Station [*A. aneura & E. populnea*], 29. APR 2002	EtOH abs.	DNA/AZ 45
Anthelidae	*Anthela basigera*	L3/4	AUSTRALIA, SA, Ferguson Conservation Park nr Adelaide	EtOH abs.	DNA/AZ 155
Anthelidae	*Anthela clementi*	I	[AUSTRALIA, WA, Karijini NP] 17.2km W of ranger t/o 20. APR 2003	EtOH abs.	DNA/AZ 127
Anthelidae	*Anthela clementi*	I	21°19'4"S 117°14'34"E, AUSTRALIA, WA, Millstream-Chichester NP, nr Python Pool, 3.-7. MAY 2003 [malaise trap MIL3]	95% EtOH	DNA/AZ 128
Anthelidae	*Anthela cnecias*	I	36°02'46.7"S 149°32'10.1"E AUSTRALIA, NSW, Badja Swamp NR NE Numeralla, 1040m, 19. DEC 2003	95% EtOH	DNA/AZ 4
Anthelidae	*Anthela euryphrica*	I	33°09'18.6"S 149°15'15.0"E AUSTRALIA, NSW, Orange, Ophir, Miller's Crossing, ~650m asl, 20. MAR 2004	EtOH abs.	DNA/AZ 156
Anthelidae	*Anthela excellens*	I	34°08.758'S 151°01.840'E, AUSTRALIA, NSW, Royal NP, Bola Ck, 4. MAR 2003	EtOH abs.	DNA/AZ 16
Anthelidae	*Anthela ferruginosa*	I	AUSTRALIA, NSW, Budderoo NP, off Budderoo Plateau Rd on abused track	95% EtOH	DNA/AZ 154
Anthelidae	*Anthela nicothoe*	I	35°31.597'S 148°46.743'E, AUSTRALIA, ACT, Namadgi NP, Mt. Ginini, 1650m, 18. MAR 2002	95% EtOH	DNA/AZ 29
Anthelidae	*Anthela ocellata*	I	AUSTRALIA, ACT, Canberra, Acton, ANU (BoZo bldg)	95% EtOH	DNA/AZ 27
Anthelidae	*Anthela phoenicias*	I	24°59.397'S 147°58.409'E, AUSTRALIA, QLD, Carnarvon NP, Mt. Moffat sect., Marlong Plain [native grass, *Casuarina & Eucalyptus*], 4. APR 2002	EtOH abs.	DNA/AZ 68

family	species	in-star	collecting data	preser-vation	prepara-tion #
Anthelidae	*Anthela addita*	I	35°55'57.1"S 149°35'10.8"E AUSTRALIA, NSW, Tallaganda SF, Little Snowball Ck, native grassland, ~850m asl, 19. DEC 2003	95% EtOH	DNA/AZ 1
Anthelidae	*Anthela repleta*	I	25°03.138'S 148°12.811'E, AUSTRALIA, QLD, Carnarvon NP, C. Gorge, 7th-8th cr. crossing, 8. APR 2002	EtOH abs.	DNA/AZ 57
Anthelidae	*Anthela rubicunda*	I	[AUSTRALIA, WA, Karijini NP] 17km W of ranger t/o 20. APR 2003	95% EtOH (partly dried out)	DNA/AZ 120
Anthelidae	*Anthela stygiana*	I	26°30.486'S 147°07.444'E, AUSTRALIA, QLD, Tregole NP near Morven [ooline, belah open forest], ~500m, 26. APR 2002	EtOH abs.	DNA/AZ 35
Anthelidae	*Anthela stygiana*	I	26°30.486'S 147°07.444'E, AUSTRALIA, QLD, Tregole NP near Morven [ooline, belah open forest], ~500m, 26. APR 2002	EtOH abs.	DNA/AZ 49
Anthelidae	*Anthela tetraphrica*	I	22°16'47.0"S 118°44'41.9"E, AUSTRALIA, WA, Fortescue River Basin ~12km N Auski RH, 19. MAY 2003	EtOH abs.	DNA/AZ 150
Anthelidae	*Anthela unisigna*	I	21°37'04.1"S 117°06'35.2"E, AUSTRALIA, WA, Millstream-Chichester NP, Deep Reach campgrd, 5. MAY 2003	EtOH abs.	DNA/AZ 152
Anthelidae	*Anthela varia*	I	AUSTRALIA, ACT, Gungahlin grassland E Palmerston	EtOH abs.	DNA/AZ 149
Anthelidae	*Anthela virescens*	I	28°03.218'S 152°22.768'E, AUSTRALIA, QLD, Main Range NP, Cunningham's Gap, rest area, 1. APR 2002	EtOH abs.	DNA/AZ 70
Anthelidae	*Anthela xantharcha*	I	21°37'04.1"S 117°06'35.2"E, AUSTRALIA, WA, Millstream-Chichester NP, Deep Reach campgrd, 5. MAY 2003	EtOH abs.	DNA/AZ 153
Anthelidae	*Chelepteryx chalepteryx*	I	28°04.838'S 152°25.147'E, AUSTRALIA, QLD, Main Range NP, Spicer's Gap, Moss's Well, 31. MAR 2002	EtOH abs.	DNA/AZ 80
Anthelidae	*Chelepteryx collesi*	I	ACT, Hawker	EtOH abs.	DNA/AZ 162
Anthelidae	*Chenuala heliaspis*	I	35°28.405'S 148°46.148'E, AUSTRALIA, ACT, Namadgi NP, Mt. Aggie, 1400m, 17. MAR 2002	EtOH abs.	DNA/AZ 28
Anthelidae	Anthelinae n. sp.	I	17°44.461'S 145°32.017'E, AUSTRALIA, QLD, Ravenshoe SF, clearing at rd to Tully Falls, ~800m, 21. APR 2002	EtOH abs.	DNA/AZ 38
Anthelidae	*Gephyroneura cosmia*	I	17°19.903'S 145°25.127'E, AUSTRALIA, QLD, Herberton, Baldy SF, ~1100m, 20. APR 2002 [20:45 o'clock]	EtOH abs.	DNA/AZ 40

family	species	in-star	collecting data	preser-vation	prepara-tion #
Anthelidae	*Munychryia periclyta*	I	33°27'07.2"S 123°26'16.2"E AUSTRALIA, WA, Cape Arid NP, track to Mt. Ragged, ~200m asl, 30. OCT 2003	EtOH abs.	DNA/AZ 158
Anthelidae	*Munychryia senicula* (A)	I	17°28.645'S, 145°22.182'E, AUSTRALIA, QLD, old Ravenshoe–Herberton rd, ~5km S Herberton, 900m, 14. APR 2002	EtOH abs.	DNA/AZ 52
Anthelidae	*Nataxa flavescens*	L1	35°26.278'S 148°49.589'E, AUSTRALIA, ACT, Namadgi NP, Bendora Rd nr Bendora Dam, 750m, 19. NOV 2002	EtOH abs.	DNA/AZ 24
Anthelidae	*Omphaliodes obscura* (A)	I	32°15.048'S 120°20.910'E, AUSTRALIA, WA, E of Hyden, 1.-17. NOV 2003, malaise trap	95% EtOH	DNA/AZ 10
Anthelidae	*Omphaliodes obscura* (B)	I	30°36.157'S 146°21.132'E, AUSTRALIA, NSW, 8.21km NW Byrock, 14. SEP 2002	EtOH abs.	DNA/AZ 25
Anthelidae	*Pseudodreata* sp.	I	[PAPUA NEW GUINEA] "PNG3 sp."	dried, papered	DNA/AZ 193
Anthelidae	*Pterolocera* sp. (A)	I	33°09'21"S 149°15'11"E, AUSTRALIA, NSW, Girralang NR 20.6km NE Orange, nr Lewis Ponds Ck, 15.-18. MAR 2002	95% EtOH	DNA/AZ 11
Anthelidae	*Pterolocera* sp. (B)	I	35°11.796'S 149°07.830'E, AUSTRALIA, ACT, Gungahlin grassland nr Palmerston, 10. MAR 2003	EtOH abs.	DNA/AZ 15
Apatelodinae	*Apatelodes pudefacta*	I	USA, AZ, Pima Co, Santa Rita Mtns, 5600 ft Santa Rita Mts, Madera Canyon, Upper Parking Lot, 31. JUL 2003, B. Walsh leg.	95% EtOH	DNA/AZ 159
Bombycidae	*Ocinara ficicola*	I	2°27.938'S 37°54.988'E, KENYA, Kibwezi, Umani Springs Camp, ~1050m asl, 22.-27. MAR 2003	EtOH abs.	DNA/AZ 147
Bombycidae	*Ocinara* sp.	I	8°42'23.7"N 117°33'59.1"E, PHILIPPINES, Palawan, Bataraza, Malihud, Tagurida, ~500m asl, 25. JUN 2003	95% EtOH	DNA/AZ 176
Brahmaeidae	*Brahmaea tancrei*	L2/3	[bred; origin unknown]	95% EtOH	DNA/AZ 191
Brahmaeidae	*Dactyloceras* sp.	I	2°56.725'S 37°30.350'E, KENYA, Oloitokitok, Loi Forest (remnants of prim. forest), ~1800m asl, 1. APR 2003	EtOH abs.	DNA/AZ 132
Carthaeidae	*Carthaea saturnioides*	I	33°27'07.2"S 123°26'16.2"E AUSTRALIA, WA, Cape Arid NP, track to Mt. Ragged, ~200m asl, 30. OCT 2003	95% EtOH	DNA/AZ 185
Carthaeidae	*Carthaea saturnioides*	I	33°27'07.2"S 123°26'16.2"E AUSTRALIA, WA, Cape Arid NP, track to Mt. Ragged, ~200m asl, 30. OCT 2003	EtOH abs.	DNA/AZ 184
Carthaeidae	*Carthaea saturnioides*	I	33°27'07.2"S 123°26'16.2"E AUSTRALIA, WA, Cape Arid NP, track to Mt. Ragged, ~200m asl, 30. OCT 2003	95% EtOH	DNA/AZ 183

family	species	in-star	collecting data	preser-vation	prepara-tion #
Endromidae	*Endromis versicolora*	P	CZECHIA	96% EtOH	DNA/AZ 181
Endromidae	*Endromis versicolora*	P	CZECHIA	95% EtOH	DNA/AZ 187
Eupterotidae	*Cotana serranotata*	I	17°00.594'S 145°34.948'E, AUSTRALIA, QLD, Davies Ck NP, rd at falls, 630m, 16. APR 2002	EtOH abs.	DNA/AZ 58
Eupterotidae	*Eupterote* sp. near *pallida*	I	8°42'23.7"N 117°33'59.1"E, PHILIPPINES, Palawan, Bataraza, Malihud, Tagurida, ~500m asl, 25. JUN 2003	95% EtOH	DNA/AZ 167
Eupterotidae	*Ganisa plana*	I	8°42'23.7"N 117°33'59.1"E, PHILIPPINES, Palawan, Bataraza, Malihud, Tagurida, ~500m asl, 25. JUN 2003	95% EtOH	DNA/AZ 168
Eupterotidae	*Hoplojana* sp. near *rhodoptera*	I	2°27.938'S 37°54.988'E, KENYA, Kibwezi, Umani Springs Camp, ~1050m asl, 22.-27. MAR 2003	EtOH abs.	DNA/AZ 144
Eupterotidae	*Panacela lewinae*	I	26°43.372'S 153°04.566'E, AUSTRALIA, QLD, Mooloolah River NP, heathland, 29. MAR 2002	EtOH abs.	DNA/AZ 69
Lasiocampidae	*Alompra roepkei pella*	I	8°42'23.7"N 117°33'59.1"E, PHILIPPINES, Palawan, Bataraza, Malihud, Tagurida, ~500m asl, 25. JUN 2003	EtOH abs.	DNA/AZ 180
Lasiocampidae	*Euthrix laeta austrina*	I	8°42'23.7"N 117°33'59.1"E, PHILIPPINES, Palawan, Bataraza, Malihud, Tagurida, ~500m asl, 25. JUN 2003	95% EtOH	DNA/AZ 171
Lasiocampidae	*Gastropacha* n. sp.	I	8°42'23.7"N 117°33'59.1"E, PHILIPPINES, Palawan, Bataraza, Malihud, Tagurida, ~500m asl, 25. JUN 2003	95% EtOH	DNA/AZ 170
Lasiocampidae	*Kunugia austroplacida*	I	8°42'23.7"N 117°33'59.1"E, PHILIPPINES, Palawan, Bataraza, Malihud, Tagurida, ~500m asl, 25. JUN 2003	EtOH abs.	DNA/AZ 179
Lasiocampidae	*Odonestis erectilinea*	I	8°42'23.7"N 117°33'59.1"E, PHILIPPINES, Palawan, Bataraza, Malihud, Tagurida, ~500m asl, 25. JUN 2003	95% EtOH	DNA/AZ 175
Lasiocampidae	*Paralebeda crinodes uniformis*	I	8°42'23.7"N 117°33'59.1"E, PHILIPPINES, Palawan, Bataraza, Malihud, Tagurida, ~500m asl, 25. JUN 2003	95% EtOH	DNA/AZ 174
Lasiocampidae	*Poecilocampa populi*	P	GERMANY	96% EtOH	DNA/AZ 182
Lasiocampidae	*Tolype austella*	I	USA, AZ, Santa Cruz Co, Pena Blanca Cyn, Atascosa highlands, 4000ft., 22. AUG 2003, B. Walsh leg.	95% EtOH	DNA/AZ 160
Lasiocampidae: Chionopsychinae	*Chionopsyche montana*	I	2°27.938'S 37°54.988'E, KENYA, Kibwezi, Umani Springs Camp, ~1050m asl, 22.-27. MAR 2003	EtOH abs.	DNA/AZ 100
Lemoniidae	*Lemonia dumi*	L1	CZECHIA	95% EtOH	DNA/AZ 190

family	species	in-star	collecting data	preser-vation	prepara-tion #
Lemoniidae	*Sabalia picarina*	I	2°54.002'S 37°38.900'E, KENYA, rd Tsavo West NP to Oloitokitok, river bed, ~1200m asl, 29. MAR 2003	EtOH abs.	DNA/AZ 131
Lymantriidae	*Leptocneria reducta*	I	25°48.815'S 148°15.658'E, AUSTRALIA, QLD, rd Injune to Mt. Moffat (Carnarvon NP) [dry sclerophyll bushes], 3. APR 2002	EtOH abs.	DNA/AZ 66
Lymantriidae	*Lymantria nephrographa*	I	28°11.590'S 153°11.402'E, AUSTRALIA, QLD, Lamington NP, Binna Burra, bellbird clearing, 25.-27. MAR 2002	EtOH abs.	DNA/AZ 90
Oenosandridae	*Oenosandra boisduvalii*	I	33°09'18.6"S 149°15'15.0"E AUSTRALIA, NSW, Orange, Ophir, Miller's Crossing, ~650m asl, 20. MAR 2004	EtOH abs.	DNA/AZ 157
Saturniidae	*Aglia tau*	I	AUSTRIA	95% EtOH	DNA/AZ 186
Saturniidae	*Arsenura armida*	L1	VENEZUELA	95% EtOH	DNA/AZ 189
Saturniidae	*Attacus lemairei*	I	8°42'23.7"N 117°33'59.1"E, PHILIPPINES, Palawan, Bataraza, Malihud, Tagurida, ~500m asl, 25. JUN 2003	EtOH abs.	DNA/AZ 178
Saturniidae	*Cricula trifenestrata treadawayi*	I	8°42'23.7"N 117°33'59.1"E, PHILIPPINES, Palawan, Bataraza, Malihud, Tagurida, ~500m asl, 25. JUN 2003	95% EtOH	DNA/AZ 165
Saturniidae	*Eacles imperialis opaca*	L1	ARGENTINIA, Missiones	96% EtOH	DNA/AZ 161
Saturniidae	*Goodia kuntzei*	I	2°27.938'S 37°54.988'E, KENYA, Kibwezi, Umani Springs Camp, ~1050m asl, 22.-27. MAR 2003	EtOH abs.	DNA/AZ 146
Saturniidae	*Gynanisa* sp.	I	2°54.002'S 37°38.900'E, KENYA, rd Tsavo West NP to Oloitokitok, river bed, ~1200m asl, 29. MAR 2003	EtOH abs.	DNA/AZ 135
Saturniidae	*Opodiphthera eucalypti*	I	35°55'57.1"S 149°35'10.8"E AUSTRALIA, NSW, Tallaganda SF, Little Snowball Ck, native grassland, ~850m asl, 19. DEC 2003	95% EtOH	DNA/AZ 8
Saturniidae	*Aurivillius fuscus*	I	2°27.938'S 37°54.988'E, KENYA, Kibwezi, Umani Springs Camp, ~1050m asl, 22.-27. MAR 2003	EtOH abs.	DNA/AZ 141
Saturniidae	*Usta angulata*	I	2°27.938'S 37°54.988'E, KENYA, Kibwezi, Umani Springs Camp, ~1050m asl, 22.-27. MAR 2003	EtOH abs.	DNA/AZ 136
Sphingidae	*Acherontia styx*	I	8°42'23.7"N 117°33'59.1"E, PHILIPPINES, Palawan, Bataraza, Malihud, Tagurida, ~500m asl, 25. JUN 2003	95% EtOH	DNA/AZ 163
Sphingidae	*Agrius godarti*	I	23°27.648'S 148°08.831'E, AUSTRALIA, QLD, ~10km N Emerald, powerline, 9. APR 2002	EtOH abs.	DNA/AZ 54
Sphingidae	*Daphnusa ocellaris*	I	8°42'23.7"N 117°33'59.1"E, PHILIPPINES, Palawan, Bataraza, Malihud, Tagurida, ~500m asl, 25. JUN 2003	EtOH abs.	DNA/AZ 177
Sphingidae	*Smerinthus ocellata*	P	GERMANY	95% EtOH	DNA/AZ 188

family	species	in-star	collecting data	preser-vation	prepara-tion #
Sphingidae	*Smerinthus ocellata*	L1	GERMANY	95% EtOH	DNA/AZ 192
Thyrididae	*Aglaopus pyrrhata*	I	35°47.300'S 148°47.865'E, AUSTRALIA, NSW, SW Old Yaouk, 4. JAN 2003	95% EtOH	DNA/AZ 103

APPENDIX J:

PROTOCOLS

- MQ-water: distilled, millipore-filtered and sterilized water
- Tris: tris (hydroxymethyl) aminomethane
- EDTA: ethylenediaminetetraacetic acid
- TAE: Tris-Acetate-EDTA
- TNES: 50 mM Tris buffer, 0.5% SDS, 20 mM EDTA, and 400 mM NaCl

J.1) DNA EXTRACTION FROM ETHANOL FIXED SAMPLES

[After Summucks & Hales 1996]

- remove scales from sample's thorax with forceps
- sterilize forceps with absolute ethanol and flaming
- open thorax with forceps and pull out bundles of muscle fibres
- dip muscles onto filter paper to remove excess ethanol
- place 2 bundles of muscle fibres in a sterile 2ml Eppendorf vial
- add 25µl TNES buffer
- grind with pestle
- flush pestle with additional 275µl TNES [bringing the total volume of TNES to 300µl]
- add 5µl Proteinase K
- mix by vortexing
- incubate 3h at 55°C, flicking or vortexing the vial once every hour [add more Proteinase K and incubate longer if tissue should not have dissolved entirely]
- add 85µl 5M NaCl and vortex
- spin 5min at 14,000rpm in centrifuge
- transfer supernatant to another sterile vial and discard old vial with pellet

- add 400µl chilled, absolute ethanol
- mix gently by inverting the vial for a minute
- spin 10min at 14,000rpm in centrifuge
- discard supernatant [pour off]
- wash pellet with 500µl chilled, 70% ethanol
- mix gently by inverting the vial 3 times
- spin 5min at 14,000rpm in centrifuge
- discard supernatant [take off with pipette and narrow tip]
- air dry pellet over night [covered with tissue on bench] or 30min at 37°C, until all traces of ethanol have disappeared
- resuspend pellet in 30µl MQ-water by brief vortexing
- store DNA extract in freezer at -20°C until processed further

J.2) PCR REACTION

The following steps are all to be carried out on ice! Reagents should be recently thawed or chilled. Vortex and spin down all reagents prior to use.

- label 0.5ml Eppendorf tubes and place in rack on ice
- set up master mix in the following order for the total number of reactions [number of samples + positive control + negative control, multiplied by 1.1 to compensate for loss of liquid in pipette tips: n = (samples + 2) * 1.1], for each reaction consisting of:

reagent	quantity [µl]
MQ-water	14.0
$MgCl_2$ [25mM]	3.0
Taq-ti buffer [10x]	2.5
dNTPs [2mM]	2.0
fwd primer [10µM]	0.5
rev primer [10µM]	0.5
Taq-ti [0.75U/µl]	1.0
total	**23.5**

- vortex master mix
- aliquot 23.5µl master mix into cooled vials
- briefly vortex DNA extracts to dislodge DNA from vial wall and add 2µl [pipetting up and down in vial 3 times to minimize loss in tip]; 2µl MQ-water for negative control
- pre-heat PCR machine to 94°C
- vortex vials and take care to remove any air bubbles in the tip of the vials [touch vortexer or flick vials with finger]
- load PCR machine with vials directly from ice and start PCR program [see Appendix K.1]
- after completion store vials at 4°C until processed further

J.3) Electrophoresis in a 1% agarose gel

- make 1% agarose gel:
  - mix 2g agarose powder and 200ml TAE in 250ml conical flask
  - heat in microwave until boiling and agarose powder fully dissolved [about 1min at full power and 3 min at defrost power setting; watch to avoid spilling]

ATTENTION:

Agarose gel retains heat for a long time!

  - cool to about 50°C [rotate flask under running cold water]
  - add 7µl ethidiumbromide [10mg/ml] and mix

ATTENTION:

Ethidiumbromide is highly carcinogenic – wear double gloves and dispose of gloves and pipette tip in appropriate contaminated waste bins as soon as ethidiumbromide has been added to gel! Wear single gloves whenever handling agarose gels with ethidiumbromide and dispose of gloves as

well as agarose gel in the contaminated waste bin. Avoid exposure of ethidiumbromide stock to light!

- pour gel into tray with plastic combs, destroy air bubbles with pipette tip
- let gel solidify for > 30min and remove combs (add TAE if difficult)
- store in sealed plastic bag in 4°C fridge until used

- run PCR product electrophoresis:
  - place 1% agarose gel in electrophoresis basin and fill up with TAE until liquid level 1cm above agarose gel
  - samples: mix 3µl loading dye with 2µl PCR product [drops on Parafilm]
  - reference ladder: mix 3µl loading dye with 2µl quantitative DNA ladder [100ng/µl HyperLadder IV: BioLine, London, UK]
  - slowly load samples and reference ladder with a narrow tip and pipette into separate wells of submerged agarose gel
  - run electrophoresis for 25min at 130V
- check and document PCR product quality and quantity with a UV-transilluminator/Video Printer [UVP UV-transilluminator and Sony Video Graphic Printer UP-895CE]

ATTENTION:

UV-radiation is carcinogenic – keep door of UV-transilluminator closed and generally avoid exposure of yourself to UV-radiation!

J.4) Excising PCR products from an agarose gel

[According to manufacturer's instructions of UltraClean 15™ DNA Purification Kit.]

- make a thick 1% agarose gel (as in Appendix J.3, but use 5g agarose powder, 500ml TAE, large tray and large combs)
- run PCR product electrophoresis:

- place thick 1% agarose gel in electrophoresis basin and fill up with TAE until liquid level 1cm above agarose gel
- mix 15µl loading dye with 20µl PCR product [in well plate]
- slowly load samples with a narrow tip and pipette into separate wells of submerged agarose gel, leaving one empty well between samples
- run agarose gel for 65 min at 100V
- slice agarose gel into separate blocks containing one sample each [to avoid prolonged exposure of samples to UV-light in the following step]
- place single gel block onto UV transilluminator, narrowly excise target band with a sterile scalpel blade and store excised band in 2µl Eppendorf vial

ATTENTION:

UV-radiation is carcinogenic – wear face shield and gloves; reduce exposure time of yourself and samples to UV-radiation as much as possible!

- Use UltraClean 15™ DNA Purification Kit [MoBio Laboratories Inc., Solana Beach, CA, USA] to clean excised bands:
  - weigh excised gel pieces and add 3µl UltraSalt [Sodium Iodine solution] per mg of gel [e.g., 540µl UltraSalt to a 0.18g piece of gel]
  - mix well and incubate for 5min at 55°C in water bath [until gel has melted entirely]
  - resuspend UltraBind [uniform size silica matrix] by vortexing for 1min at highest speed
  - add 8µl UltraBind [5µl + 1µl for every µg of expected DNA yield]
  - vortex briefly and mix gently by inverting vial for 5min

- spin 5sec in centrifuge and discard supernatant [take off with pipette]
- add 1ml UltraWash [NaCl, Tris, EDTA and ethanol solution] and vortex 10sec
- spin 5sec in centrifuge and discard supernatant [pour off]
- add 1ml UltraWash and vortex 10sec
- spin 5sec in centrifuge and discard supernatant [pour off]
- spin 5sec in centrifuge and discard supernatant [take off with pipette and narrow tip]
- dry off at 37°C for 5-10min
- resuspend in 15µl MQ-water by pipetting up and down [do NOT vortex!]
- mix gently by inverting vial for 5min
- spin 1min at 14,000rpm in centrifuge
- transfer supernatant [cleaned PCR product] to another sterile vial and discard old vial with pellet
- check DNA quality and quantity by electrophoresis in a 1% agarose gel (see Appendix J.3) and add MQ-water to cleaned PCR products to roughly equalize concentrations if necessary
- store at 4°C until processed further

J.5) Cleaning of PCR products

- add a mixture of 5µl 5M ammoniumacetate and 50µl chilled, absolute ethanol to the PCR product
- vortex and precipitate 10min at room temperature
- spin 20min at 14,000rpm in a centrifuge
- discard supernatant [pour off]
- wash with 150µl chilled 70% ethanol
- spin 10min at 14,000rpm in a centrifuge
- discard supernatant [take off with a pipette and a narrow tip]

- dry 30min at 37°C
- resuspend in 15µl MQ-water by vortexing
- spin down
- check DNA quality and quantity by electrophoresis in a 1% agarose gel (see Appendix J.3) and add MQ-water to cleaned PCR products to roughly equalize concentrations if necessary
- store at 4°C until processed further

J.6) SEQUENCING REACTION

Avoid exposure of BigDye to light by keeping vials in a closed box or wrapped in aluminium foil! The following steps are all to be carried out on ice! Reagents should be recently thawed or chilled. Vortex and spin down all reagents prior to use.

- label 0.5ml Eppendorf tubes [one forward and one reverse for each sample] and place in rack on ice
- set up master mix in the following order for the total number of sequencing reactions [number of samples multiplied by 2 for forward and reverse reaction and multiplied by 1.1 to compensate for loss of liquid in pipette tips: n = samples * 2.2], for each reaction consisting of:

reagent	**quantity [µl]**
MQ-water	14.0
sequencing buffer [5x]	3.0
BigDye 3.1	1.0
total	**18.0**

- vortex master mix
- split master mix into half and add 1µl forward to one half and 1µl reverse sequencing primer [3µM each] to the other half of the master mix
- aliquot 19µl master mix into the corresponding cooled vials

- briefly vortex and spin down cleaned PCR products to dislodge DNA from vial wall and add 1µl [pipetting up and down in vial 3 times to minimize loss in tip]
- pre-heat PCR machine to 94°C
- vortex vials and take care to remove any air bubbles in the tip of the vials [touch vortexer or flick vials with finger]
- load PCR machine with vials directly from ice and start sequencing program [see Appendix K.2]
- after completion wrap vials in aluminium foil and store at 4° C if not processed further immediately
- add 80µl 75% isopropanol to each vial
- precipitate >30min in the dark
- spin 30min at 14,000rpm in centrifuge
- discard supernatant [pour off]
- wash with 150µl 70% isopropanol
- spin 10min at 14,000rpm in centrifuge
- discard supernatant [pour off]
- wash with 150µl 70% isopropanol
- spin 10min at 14,000rpm in centrifuge
- discard supernatant [take off with pipette and narrow tip]
- dry 30min at 37°C in darkness
- resuspend sequencing reaction products in 20µl absolute HiDi formamid by slowly shaking on vortexer [wrapped in aluminium foil]
- spin down and load into 96 well plate
- denaturate sequencing reaction products at 94°C for 90sec
- store wrapped in aluminium foil at 4°C until sequenced

APPENDIX K:

THERMOCYCLER PROGRAMS

K.1) PCR PROGRAM (TOUCH-DOWN PROGRAM)

temperature [°C]	period [sec]	repetition of cycle
94	240	1
94	30	2
65	20	
72	90	
94	30	2
60	20	
72	90	
94	30	2
55	20	
72	90	
94	30	2
50	20	
72	90	
94	30	2
45	20	
72	90	
94	30	35
40	20	
72	90	
72	260	1
4	300 & hold	

K.2) SEQUENCING REACTION PROGRAM

temperature [°C]	period [sec]	repetition of cycle
96	20	35
50	15	
60	180	
4	300 & hold	

APPENDIX L:

PRIMER SEQUENCES

L.1) MITOCHONDRIAL GENES

gene	primer name	direc-tion	sequence [5'-3']	source
12S	J14199	fwd	TAC TAT GTT ACG ACT TAT	Kambhampati & Smith 1995
12S	N14594	rev	AAA CTA GGA TTA GAT ACC C	Kambhampati & Smith 1995
18S	18S-2880	fwd	CTG GTT GAT CCT GCC AGT AG	von Dohlen & Moran 1995
18S	18S-B	rev	CCG CGG CTG CTG GCA CCA GA	von Dohlen & Moran 1995
CO I + II	TY-J-1460	fwd	TAC AAT TTA TCG CCT AAA CTT CAG CC	Simon *et al.* 1994
CO I + II	C1-J-1751e	fwd	GGA GCT CCA GAT ATA GCT TTC CC	Simon *et al.* 1994
CO I + II	C1-J-2495a	fwd	CTT CTA TAC TTT GAA GAT TAG G	e.g., Caterino & Sperling 1999
CO I + II	C1-J-2792a	fwd	ATA CCT CGA CGT TAT TCA GA	e.g., Caterino & Sperling 1999
CO I + II	C2-J-3138	fwd	AGA GCC TCT CCT TTA ATA GAA CA	Simon *et al.* 1994
CO I + II	C1-N-1840a	rev	AGG AGG ATA AAC AGT TCA yCC	e.g., Caterino & Sperling 1999
CO I + II	C1-N2329	rev	ACT GTA AAT ATA TGA TGA GCT CA	Simon *et al.* 1994

gene	primer name	direc-tion	sequence [5'-3']	source
CO I + II	C1-N-2578f	rev	TGA AAA TGA GCA ACA ACA TAA TA	Sperling Lab, University of Alberta, Edmonton, Canada
CO I + II	TL2-N-3014	rev	TCC AAT GCA CTA ATC TGC CAT ATT A	Simon *et al.* 1994
CO I + II	C2-N-3389a	rev	TCA TAA GTT CAr TAT CAT TG	Simon *et al.* 1994
CO I + II	TK-N-3782	rev	GAG ACC ATT ACT TGC TTT CAG TCA TCT	Harrison Laboratory, Cornell University, Ithaca, NY, USA

L.2) Nuclear genes

gene	primer name	direc-tion	sequence [5'-3']	source
28S D2/D3	S3660	fwd	GAG AGT TmA AsA GTA CGT GAA AC	Sequeira *et al.* 2000
28S D2/D3	A335	rev	TCG GAr GGA ACC AGC TAC TA	Sequeira *et al.* 2000
CPS	806F	fwd	GTn GTn AAr ATG CCn mGn TGG GA	Moulton & Wiegmann 2004
CPS	843F	fwd	TTy CAA AAA GCw TTr CGd ATG GTy TGA	custom
CPS	1057R	rev	CTC Awr TCA TAA TCw GTr CTh AC	custom
CPS	1124R	rev	CAT nCG nGA rAA yTT rAA rCG ATT yTC	Moulton & Wiegmann 2004
EF1a	M3	fwd	CAC ATy AAC ATT GTC GTs ATy GG	Cho *et al.* 1995
EF1a	M44.1	fwd	GCT GAG CGy GAr CGT GGT ATC AC	Cho *et al.* 1995

gene	primer name	direc-tion	sequence [5'-3']	source
EF1a	M46.1	fwd	GAG GAA ATy AAr AAG GAA G	Cho *et al.* 1995
EF1a	M51.9	fwd	CAr GAC GTA TAC AAA ATC GG	Cho *et al.* 1995
EF1a	rcM51.1	rev	CAT rTT GTC kCC GTG CCA kCC	Cho *et al.* 1995
EF1a	rcM52.6	rev	GCy TCG TGG TGC ATy TCs AC	Cho *et al.* 1995
EF1a	rcM4	rev	ACA GCv ACk GTy TGy CTC ATr TC	Cho *et al.* 1995
wingless	LepWg1	fwd	GAr TGy AAr TGy CAy GGy ATG TCT GG	Brower & DeSalle 1998
wingless	ModLepWg2	rev	ACT ICG CrC ACC ArT GGA ATG TrC A	Brower & DeSalle 1998

APPENDIX M:
MALE GENITAL MUSCLE DESCRIPTIONS

species	family	*m1*: a	*m1*: b	*m2*: a	*m2*: b	*m3*: a	*m3*: b	*m4*: a	*m4*: b	*m5*: a	*m5*: b	*m6*: a	*m6*: b	*m7*: a	*m7*: b	*m10*: a	*m10*: b	*m29*: a	*m29*: b
Oenosandra boisduvalii	Oenosandri-dae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	dorso-lateral on anterior tegumen edge [far from *m4*]	apex (only) of valva apodeme [[long lever ventral of m4 attachment; not at apparent "transtilla" (flat sclerotization in diaphragma)]	dorsal edge of juxta [anteriorly and "inside"]	ventro-lateral corner of valva [basal edge and outside/lateral]	dorsal end of vinculum [over long stretch, bridging secondary gap in vinculum; dorsal of dorsal valva edge]	along mesal edge of transtilla plate [which is part of the diaphragma]	lateral side of coecum-penis end	partly dorsal part of vinculum, partly basal edge of lateral valva wall [adjacent to *m4*; dorsal half of valva edge]	along entire ventral phallus side [from zone to short coecum end]	reduced saccus apex	inner side of basal valva edge [lateral, ventral]	inner side at base of clasper [remnants]	near centre of anterior tegumen edge [just mesal of *m2*]	lateral wall of anal cone [lateral of subscaphium]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Discophlebia sp.	Oenosandri-dae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	dorso-lateral on anterior tegumen edge [far from *m4*]	apex (only) of valva apodeme [long lever ventral of m4 attachment; not at apparent "transtilla" (flat sclerotization in diaphragma)]	dorsal edge of juxta [anteriorly and "inside"]	reduced saccus apex [beneath *m6*]	dorsal end of vinculum [over long stretch; dorsal of dorsal valva edge]	along mesal edge of transtilla plate [which is part of the diaphragma]	lateral side of coecum-penis end	largely dorsal part of vinculum, partly basal edge of lateral valva wall [adjacent to *m4*; dorsal half of valva edge]	along most of ventral phallus side [from zone to near end of short coecum]	reduced saccus apex	inner side of basal valva edge [lateral, ventral]	inner side at base of clasper [remnants]	near centre of anterior tegumen edge [just mesal of *m2*]	lateral wall of anal cone [lateral of subscaphium]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Agrotis infusa	Noctuidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	dorso-lateral on anterior tegumen edge [far from *m4*]	apex (only) of valva apodeme [long lever ventral of m4 attachment]	dorsal edge of juxta [anteriorly]	basal edge of ventral valva wall	dorsal end of vinculum [over long stretch; dorsal of dorsal valva edge]	on membrane dorsal of and on entire lateral side of valva apodeme	latero-ventral side of coecum-penis end [proximal of apex, beneath ductus ejaculatorius]	lateral part of vinculum [adjacent to *m4*; along entire hight of narrow valva]	lateral phallus side [at zone]	saccus apex	inner side of basal valva edge [lateral, ventral]	inner side at base of clasper	near centre of anterior tegumen edge	lateral edge of subscaphium, near posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]

species	family	*m1*: a	*m1*: b	*m2*: a	*m2*: b	*m3*: a	*m3*: b	*m4*: a	*m4*: b	*m5*: a	*m5*: b	*m6*: a	*m6*: b	*m7*: a	*m7*: b	*m10*: a	*m10*: b	*m29*: a	*m29*: b
Ocinara n. sp. (Palawan)	Bombycidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	absent	absent	dorsal end of vinculum [dorsal of dorsal valva edge]	diaphragma dorso-mesal of reduced valva	lateral side of phallus end (lateral of ductus ejaculatorius)	Split: A) dorsal end of vinculum [lateral of *m4*] B) inside dorsal part of reduced valva	ventral phallus/coecum-penis side	saccus apex	absent	absent	[destroyed]	[destroyed]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Apatelodes sp. [DRIED SPECIMEN]	Bombycidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorsal edge of juxta	posterio-dorsal edge of saccus centre [= ventral vinculum edge]	dorsal end of vinculum [dorsal of dorsal valva edge]	apical half of valva apodeme	lateral side of coecum-penis end	anterior edge of dorsal end of vinculum [just ventral of *m4*]	latero-ventral phallus side [at zone]	saccus apex	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Agrius convolvuli	Sphingidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	dorso-lateral on anterior tegumen edge [just dorsal of *m4*]	apex (only) of valva apodeme [long lever ventral of m4 attachment; not at apparent "transtilla" (flat sclerotization in diaphragma)]	dorso-lateral edge of juxta [anteriorly]	posterio-dorsal edge of saccus centre [= ventral vinculum edge]	dorsal end of vinculum [dorsal of dorsal valva edge]	along basal third of valva apodeme [not on apparent "transtilla"]	lateral side of coecum-penis end	dorsal part of vinculum [adjacent to *m4*; dorsal half of valva]	dorsal phallus side [at zone]	split and crossed: A) saccus apex; B) lateral edge of saccus base	inner side of basal valva edge [lateral, ventral, mesal]	inner side at base of clasper	near centre of anterior tegumen edge [just mesal of *m2*]	lateral wall of anal cone end [dorso-lateral of posterior subscaphium end]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Hopliocnema brachycera	Sphingidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	dorso-lateral on anterior tegumen edge	apex (only) of valva apodeme [long lever ventral of m4 attachment]	anterio-dorsal juxta apodeme	split and diverging: A) posterio-dorsal edge of saccus centre [= ventral vinculum edge] B) mesal edge of lateral vinculum part [at hight of valva]	dorsal end of vinculum [over very long stretch; dorsal of dorsal valva edge]	along entire lateral side of valva apodeme	lateral side of coecum-penis end	partly dorsal part of vinculum, partly basal edge of lateral valva wall [adjacent to *m4*; dorsal half of valva edge]	dorsal phallus side [at zone]	split and diverging: A) saccus apex; B) lateral edge of saccus base	inner side of basal valva edge [lateral, ventral, mesal]	inner side at base of clasper	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	ventral end of tegumen (?) [dorsal, but adjacent to what appears to be the fusion between vinculum and tegumen; ventral of *m2*, dorsal of *m4*]	ventro-lateral end of subscaphium
Laothoe populi [LITERATURE: K. & S., 1985]	Sphingidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	dorso-lateral on anterior tegumen edge [far from *m4*]	apex (only) of valva apodeme [long lever ventral of m4 attachment]	dorso-lateral edge of juxta [anteriorly]	basal edge of ventral valva wall	dorsal end of vinculum [at hight of dorsal valva edge]	basal third of valva apodeme [apparent "transtilla"]	lateral side of coecum-penis end	dorsal part of vinculum [adjacent to *m4*; dorsal half of valva]	dorsal phallus side	saccus [lateral	inner side of basal valva edge [lateral]	inner side at base of clasper	near centre of anterior tegumen edge [just mesal of *m2*]	lateral wall of anal cone end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]

species	family	*m1*: a	*m1*: b	*m2*: a	*m2*: b	*m3*: a	*m3*: b	*m4*: a	*m4*: b	*m5*: a	*m5*: b	*m6*: a	*m6*: b	*m7*: a	*m7*: b	*m10*: a	*m10*: b	*m29*: a	*m29*: b
Aurivillius sp.	Saturniidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	ventral side of dorsal invagination of juxta [= dorsal edge of juxta, anteriorly]	posterio-dorsal edge of saccus centre [= ventral vinculum edge]	dorsal end of vinculum [at hight of dorsal valva edge; vinculum and tegumen entirely fused]	apex of valva apodeme and lateral corner of gnathos (both fused with each other)	lateral apodeme of phallus base, split: A) dorsal side of apodeme B) ventral side of apodeme	split: A) dorsal part of vinculum [adjacent to *m4*; dorsal half of valva] B) saccus	ventral phallus side [at zone]	saccus apex	inner side of ventral valva wall	inner side of valva [where clasper occurs in other taxa]	[destroyed]	lateral wall of anal cone base	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Pselaphelia flavivitta	Saturniidae	absent	absent	absent	absent	dorso-lateral edge of juxta [anteriorly]	posterio-dorsal edge of saccus centre [= ventral vinculum edge]	dorsal end of vinculum [at hight and dorsal of dorsal valva edge; huge]	valva apodeme and gnathos arm (both fused with each other)	lateral side of coecum-penis end	dorsal part of vinculum [adjacent to *m4*; middle of reduced valva]	ventral phallus side	saccus apex	lateral part of vinculum [ventral and adjacent to *m4*]	basal part of inner side of ventral valva lobe	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Pselaphelia gemmifera [DRIED SPECIMEN]	Saturniidae	absent	absent	absent	absent	dorso-lateral edge of juxta [anteriorly]	posterio-dorsal edge of saccus centre [= ventral vinculum edge]	dorsal end of vinculum [at hight and dorsal of dorsal valva edge; huge]	valva apodeme and gnathos arm (both fused with each other)	lateral side of coecum-penis end	dorsal part of vinculum [adjacent to *m4*; middle of reduced valva]	ventral phallus side	saccus apex	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Actias artemis [LITERATURE: K. & S., 1985]	Saturniidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorso-lateral edge of juxta [anteriorly]	split: A) ventro-lateral vinculum edge B) ventral valva wall	dorsal end of vinculum [at hight of dorsal valva edge]	base of valva apodeme	lateral side of coecum-penis end	dorsal part of vinculum [adjacent to *m4*; dorsal half of valva]	dorsal phallus side	saccus apex	inner side of basal valva edge [lateral]	inner side at base of clasper	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Opodiphthera helena	Saturniidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	almost entire lateral edge of juxta [anteriorly]	ventro-lateral vinculum edge	dorsal end of vinculum [at hight of dorsal valva edge; over long stretch]	along entire lateral side of valva apodeme	lateral phallus base	lateral part of vinculum [far from *m4*; ventral half of valva; both caused by giant valva stretching over entire hight of whole genitalia structures]	phallus base [ventral; phallus extremely short]	entire reduced saccus [laterally and apically]	inner side of basal valva edge [lateral]	inner side of valva [about position of base of clasper in other taxa]	near centre of anterior tegumen edge	ventro-lateral wall of anal cone, distinctly anterior of posterior end [position of lateral edge of subscaphium in other taxa]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Syssphinx quadrilineata	Saturniidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	ventro-lateral edge of juxta [anteriorly]	saccus apex [reduced; beneath *m6*]	dorso-lateral edge of vinculum [at hight and dorsal of dorsal valva edge]	basal 1/3 of valva apodeme [which is strongly fused to very distinct gnathos plate]	lateral side of coecum-penis end [on lateral apodeme]	dorsal part of vinculum [adjacent to *m4*; dorsal half of valva]	lateral phallus side [at zone]	saccus apex	inner side of basal valva edge [lateral]	inner side at base of clasper	near centre of anterior tegumen edge	lateral edge of subscaphium, distinctly anterior of posterior end	ventral end of tegumen (?) [dorsal, but adjacent to what appears to be the fusion between vinculum and tegumen]	ventro-lateral end of subscaphium [ventral of *m10*]

species	family	*m1*: a	*m1*: b	*m2*: a	*m2*: b	*m3*: a	*m3*: b	*m4*: a	*m4*: b	*m5*: a	*m5*: b	*m6*: a	*m6*: b	*m7*: a	*m7*: b	*m10*: a	*m10*: b	*m29*: a	*m29*: b
Aglia tau	Saturniidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	attachment of juxta to phallus [= antero-dorsal edge of juxta in other taxa]	latero-dorsal edge of reduced saccus [=ventro-lateral vinculum edge]	dorsal end of vinculum [at level and dorsal of dorsal valva edge; over longer stretch]	sclerotized part of gnathos (or diaphragma), which connects gnathos and valva apodeme	lateral side of coecum-penis end	dorsal part of vinculum [adjacent to *m4*; dorsal half of valva]	ventro-lateral phallus side [anterior of fused juxta = at zone]	saccus [ventro-laterally; reduced]	inner side of basal valva edge [latero-ventral]	inner side at base of clasper	near centre of anterior tegumen edge	ventro-lateral wall of anal cone [lateral of where subscaphium is located in other taxa], near posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Arsenura xanthopus [DRIED SPECIMEN]	Saturniidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorsal end of juxta	posterio-dorsal edge of saccus centre [= ventral vinculum edge]	dorsal end of vinculum [at level of dorsal valva edge]	along almost entire fused valva apodeme and gnathos	Split: A) lateral side of coecum-penis end B) dorsal side of phallus, just posterior of ductus ejaculatorius	dorsal part of vinculum [adjacent to *m4*; dorsal half of valva]	ventral phallus side	saccus apex	inner side of basal valva edge [lateral, ventral, mesal]	inner side at base of clasper	near centre of anterior tegumen edge	ventro-lateral wall of anal cone	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Carthaea saturnioides	Carthaeidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	dorso-lateral on anterior tegumen edge [far from *m4*]	distal half of valva apodeme [sclerotization of membranous fold only; NOT ventral of m4]	dorsal edge of juxta [anteriorly and inside]	posterio-dorsal edge of saccus centre [= ventral vinculum edge]	dorsal end of vinculum [ventral of dorsal valva edge; over longer stretch;]	along entire lateral side of valva apodeme	lateral side of coecum-penis end	partly lateral part of vinculum, partly basal edge of lateral valva wall [adjacent to *m4*; ventral half of valva edge]	dorsal phallus side [at zone]	saccus apex	inner side of basal valva edge [ventral]	inner side of valva [about position of base of clasper in other taxa]	near centre of anterior tegumen edge [just mesal of *m2*]	lateral edge of subscaphium, distinctly anterior of posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Pseudodreata spp. [2 DRIED SPECIMENS of 2 species]	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorsal edge of juxta [anteriorly]	basal part of meso-ventral valva wall	dorsal end of vinculum [dorsal of dorsal valva edge]	distal half of valva apodeme	lateral side of coecum-penis end	inside valva on ventro-lateral wall [stretching deep into valva; far from *m4*; ventral half of valva edge]	latero-ventral phallus side [at zone]	saccus apex	absent	absent	near centre of anterior tegumen edge	lateral edge of subscaphium, distinctly anterior of posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Omphaliodes n. sp.	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorsal edge of juxta [anteriorly]	entire ventral valva wall	dorsal end of vinculum [dorsal of dorsal valva edge, adjacent to *m1*; very long]	distal end of valva apodeme	lateral side of coecum-penis end	inside valva on lateral wall, filling almost entire valva[far from *m4*; middle of valva edge]	dorsal phallus side [at zone]	saccus apex	absent	absent	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Anthela oressarcha	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	ventral side of dorsal invagination of juxta [= dorsal edge of juxta, anteriorly]	basal part of ventral valva wall	dorsal end of vinculum [dorsal of dorsal valva edge]	partly along most of valva apodeme on lateral side and mainly on adjacent membrane dorsal of valva apodeme	lateral side of coecum-penis end	basal edge of lateral valva wall [far from *m4*; ventral half of valva edge]	split and diverging: A) ventral phallus side [at zone] B) upturned apex of coecum	entire saccus	inner side of valva wall [lateral, ventral, mesal; not along basal edge, but displaced distad by *m5*]	inner side of valva [about position of base of clasper in other taxa]	near centre of anterior tegumen edge	lateral edge of subscaphium, distinctly anterior of posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]

species	family	*m1*: a	*m1*: b	*m2*: a	*m2*: b	*m3*: a	*m3*: b	*m4*: a	*m4*: b	*m5*: a	*m5*: b	*m6*: a	*m6*: b	*m7*: a	*m7*: b	*m10*: a	*m10*: b	*m29*: a	*m29*: b
Anthela ocellata	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	ventral side of dorsal invagination of juxta [= dorsal edge of juxta, anteriorly]	basal part of ventral valva wall	dorsal end of vinculum [dorsal of dorsal valva edge]	partly along most of valva apodeme on lateral side and mainly on adjacent membrane dorsal of valva apodeme	lateral side of coecum-penis end	basal edge of lateral valva wall [far from *m4*; ventral half of valva edge]	ventral phallus side [at zone]	saccus apex	inner side of valva wall [lateral, ventral; not along basal edge, but displaced distad by *m5*]	inner side of valva [about position of base of clasper in other taxa]	near centre of anterior tegumen edge	lateral edge of subscaphium, distinctly anterior of posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Anthela clementi	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	ventral and slightly dorsal side of dorsal invagination of juxta [= dorsal edge of juxta, anteriorly]	basal part of ventral valva wall	dorsal end of vinculum [dorsal of dorsal valva edge]	on diaphragma slightly dorsal of distal half of valva apodeme	lateral side of coecum-penis end	basal edge of lateral valva wall [far from *m4*; ventral half of valva edge]	ventral phallus side and manica [at zone]	saccus apex	inner side of basal valva edge [lateral, ventral, mesal]	inner side of valva [about position of base of clasper in other taxa]	near centre of anterior tegumen edge	lateral edge of subscaphium, distinctly anterior of posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Anthela unisigna	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	ventral side of dorsal invagination of juxta [= dorsal edge of juxta, anteriorly]	basal part of ventral valva wall	dorsal end of vinculum [dorsal of dorsal valva edge]	along entire lateral side of valva apodeme	lateral side of coecum-penis end	basal edge of lateral valva wall [far from *m4*; ventral half of valva edge]	ventral phallus side [at zone]	saccus apex	inner side of basal valva edge [lateral, ventral, mesal]	inner side of valva [about position of base of clasper in other taxa]	near centre of anterior tegumen edge	lateral edge of subscaphium, distinctly anterior of posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Nataxa flavescens [1 FIXED & 1 DRIED SPECIMEN]	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	ventral side of dorsal invagination of juxta [= dorsal edge of juxta, anteriorly]	basal part of meso-ventral valva wall	dorsal end of vinculum [at hight of dorsal valva edge]	along basal half of valva apodeme	lateral side of coecum-penis end	basal edge of lateral valva wall [far from *m4*; ventral half of valva edge]	latero-ventral phallus side [at zone; phallus rotated clock-wise by 90° in anterior view]	saccus apex	inner side of ventral valva wall	inner side of valva [about position of base of clasper in other taxa]	near centre of anterior tegumen edge	lateral edge of subscaphium, distinctly anterior of posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Anthela nicothoe [2 SPECIMENS]	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	ventral side of dorsal invagination of juxta [= dorsal edge of juxta, anteriorly]	basal part of ventral valva wall	dorsal end of vinculum [dorsal of dorsal valva edge]	along almost entire lateral side of valva apodeme [from near base to apex]	lateral side of coecum-penis end	basal edge of lateral valva wall [far from *m4*; ventral half of valva edge]	latero-ventral manica side [just posterior of zone; phallus rotated clock-wise by 90° in anterior view]	saccus apex	inner side of basal valva edge [lateral, ventral]	inner side of valva [about position of base of clasper in other taxa]	near centre of anterior tegumen edge	lateral edge of subscaphium, distinctly anterior of posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Anthela excellens	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	ventral side of dorsal invagination of juxta [= dorsal edge of juxta, anteriorly]	basal part of ventral valva wall	dorsal end of vinculum [dorsal of dorsal valva edge]	along distal half of valva apodeme	lateral side of coecum-penis end	partly lateral part of vinculum, partly basal edge of lateral valva wall [far from *m4*; ventral half of valva edge]	latero-ventral phallus side [at zone; phallus rotated clock-wise by 90° in anterior view]	saccus apex	inner side of basal valva edge [lateral, ventral]	inner side of valva [about position of base of clasper in other taxa]	near centre of anterior tegumen edge	lateral edge of subscaphium, distinctly anterior of posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]

species	family	*m1*: a	*m1*: b	*m2*: a	*m2*: b	*m3*: a	*m3*: b	*m4*: a	*m4*: b	*m5*: a	*m5*: b	*m6*: a	*m6*: b	*m7*: a	*m7*: b	*m10*: a	*m10*: b	*m29*: a	*m29*: b
Anthela adriana	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	ventral side of dorsal invagination of juxta [= dorsal edge of juxta, anteriorly]	basal part of ventral valva wall	dorsal end of vinculum [dorsal of dorsal valva edge]	along basal 2/3 of valva apodeme	lateral side of coecum-penis end	partly lateral part of vinculum, partly basal edge of lateral valva wall [far from *m4*; ventral half of valva edge]	ventral phallus side [at zone]	saccus apex	inner side of basal valva edge [lateral, ventral]	inner side of valva [about position of base of clasper in other taxa]	near centre of anterior tegumen edge	lateral edge of subscaphium, distinctly anterior of posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Pterolocera sp.	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	ventral side of dorsal invagination of juxta [= dorsal edge of juxta, anteriorly]	basal part of ventral valva wall	dorsal end of vinculum [dorsal of dorsal valva edge]	along distal quarter of valva apodeme	lateral side of coecum-penis end	partly lateral part of vinculum, partly basal edge of lateral valva wall [far from *m4*; middle of valva edge]	ventral phallus side [at zone]	saccus apex	inner side of basal valva edge [lateral, ventral, meso-ventral]	inner side at base of clasper	near centre of anterior tegumen edge	lateral edge of subscaphium, distinctly anterior of posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Chemuala heliaspis	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorsal edge of juxta [anteriorly]	basal part of ventral valva wall	dorsal end of vinculum [at hight of dorsal valva edge]	along valva apodeme	lateral side of coecum-penis end	partly lateral part of vinculum, partly basal edge of lateral valva wall [far from *m4*; ventral half of valva edge]	ventral phallus side [at zone]	saccus apex	inner side of basal valva edge [lateral, ventral]	inner side of valva [about position of base of clasper in other taxa]	near centre of anterior tegumen edge	lateral edge of subscaphium, distinctly anterior of posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Chemuala n.sp.	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorsal edge of juxta [anteriorly]	basal part of ventral valva wall	dorsal end of vinculum [dorsal of dorsal valva edge]	distal half of valva apodeme	lateral side of coecum-penis end	basal edge of lateral valva wall [far from *m4*; ventral half of valva edge]	ventral phallus side [at zone]	saccus apex	inner side of basal valva edge [lateral, ventral]	inner side of valva [about position of base of clasper in other taxa; far from the two mesal protrusions, indicating non-homology with clasper]	near centre of anterior tegumen edge	lateral edge of subscaphium, distinctly anterior of posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Anthela ferruginosa [1 FIXED & 1 DRIED SPECIMEN]	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorsal edge of juxta [anteriorly]	basal part of ventral valva wall	dorsal end of vinculum [dorsal of dorsal valva edge]	diaphragma up to and including dorso-lateral edge of setose protrusion [position of valva apodeme in other taxa; indication for fusion of transtilla and juxta!]	lateral side of coecum-penis end	partly lateral part of vinculum, partly basal edge of lateral valva wall [far from *m4*; ventral half of valva edge]	ventral phallus side [at zone]	saccus apex	inner side of basal valva edge [lateral, ventral]	inner side of valva [about position of base of clasper in other taxa]	near centre of anterior tegumen edge	lateral edge of subscaphium, distinctly anterior of posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]

species	family	*m1*: a	*m1*: b	*m2*: a	*m2*: b	*m3*: a	*m3*: b	*m4*: a	*m4*: b	*m5*: a	*m5*: b	*m6*: a	*m6*: b	*m7*: a	*m7*: b	*m10*: a	*m10*: b	*m29*: a	*m29*: b
Anthela virescens	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorsal edge of juxta [anteriorly]	basal part of ventral valva wall	dorsal end of vinculum [at hight of dorsal valva edge]	inside dorsal part of setose protrusion [position of valva apodeme in other taxa; indication for fusion of transtilla and juxta!]	lateral side of coecum-penis end	largely lateral part of vinculum, partly basal edge of lateral valva wall [far from *m4*; ventral half of valva edge]	ventral phallus side [at zone]	saccus apex	inner side of basal valva edge [lateral only]	inner side of valva [about position of base of clasper in other taxa]	near centre of anterior tegumen edge	lateral edge of subscaphium, distinctly anterior of posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Anthela euryphrica	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorsal edge of juxta [anteriorly and partly inside]	basal part of ventral valva wall	dorsal end of vinculum [at hight of dorsal valva edge]	diaphragma beneath distal half of upturned valva apodeme	lateral side of coecum-penis end	largely dorsal part of vinculum, partly basal edge of lateral valva wall [adjacent to *m4*; dorsal half of valva edge]	ventral phallus side [at zone]	saccus apex	inner side of basal valva edge [lateral only]	inner side at base of clasper	near centre of anterior tegumen edge	lateral edge of subscaphium, near posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Anthela repleta	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorsal edge of juxta [anteriorly and partly inside]	basal part of ventral valva wall	dorsal end of vinculum [at hight of dorsal valva edge]	along distal half of valva apodeme [lateral side]	lateral side of coecum-penis end	middle to dorsal part of vinculum [adjacent to *m4*, but with a distinct small gap; dorsal half of valva edge, from just dorsal of middle up to near dorsal end]	ventral phallus side [at zone]	saccus apex	inner side of basal valva edge [lateral, ventral]	inner side at base of clasper	near centre of anterior tegumen edge	lateral edge of subscaphium, near posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Anthela acuta grp. [3 SPECIMENS of 2 species]	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorsal edge of juxta [anteriorly and partly inside]	basal part of ventral valva wall	dorsal end of vinculum [dorsal of dorsal valva edge]	along valva apodeme, on diaphragma and on lateral edge of fused transtilla lobe [indicates homology of fused lobe and transtilla]	lateral side of coecum-penis end	largely dorsal part of vinculum, partly basal edge of lateral valva wall [adjacent to *m4*; dorsal half of valva edge]	ventral phallus side and manica [at zone]	saccus apex	inner side of basal valva edge [lateral, ventral]	inner side at base of clasper	near centre of anterior tegumen edge	lateral edge of subscaphium, near posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]

species	family	*m1*: a	*m1*: b	*m2*: a	*m2*: b	*m3*: a	*m3*: b	*m4*: a	*m4*: b	*m5*: a	*m5*: b	*m6*: a	*m6*: b	*m7*: a	*m7*: b	*m10*: a	*m10*: b	*m29*: a	*m29*: b
Anthela varia	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorsal edge of juxta [anteriorly and partly inside]	basal part of ventral valva wall	dorsal end of vinculum [dorsal of dorsal valva edge]	lateral edge of sclerotized triangles attached dorsally to the fused transtilla lobe and juxta [dorso-mesal of reduced valva apodeme]	lateral side of coecum-penis end	dorsal part of vinculum [adjacent to *m4*; dorsal half of valva edge]	ventral phallus side and manica [at zone]	saccus apex	inner side of basal valva edge [lateral, ventral]	inner side at base of clasper	near centre of anterior tegumen edge	lateral edge of subscaphium, near posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Chelepteryx chalepteryx	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorsal edge of juxta [anteriorly]	basal part of ventral valva wall	dorsal end of vinculum [at hight of and slightly ventral of dorsal valva edge]	diaphragma at position of valva apodeme in other taxa [secondarily reduced]	lateral side of coecum-penis end	largely lateral part of vinculum, partly on articulating membrane and just touching basal edge of lateral valva wall [far from *m4*; ventral half of valva edge, just ventral of middle]	ventral phallus side [at zone]	saccus apex	inner side of basal valva edge [lateral only]	inner side of valva [about position of base of clasper in other taxa]	near centre of anterior tegumen edge	lateral edge of subscaphium, distinctly anterior of posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Chelepteryx collesi	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorsal edge of juxta [anteriorly]	basal part of ventral valva wall	dorsal end of vinculum [at hight of dorsal valva edge]	diaphragma at position of valva apodeme in other taxa, very close to ventro-latera edge of gnathos sclerite [indication for fusion of gnathos and transtilla! Secondarily reduced]	lateral side of coecum-penis end	largely lateral part of vinculum, very few fibres on articulating membrane [far from *m4*; ventral half of valva edge, just ventral of middle]	ventral phallus side [at zone]	saccus apex	inner side of basal valva edge [lateral only]	inner side of valva [about position of base of clasper in other taxa]	near centre of anterior tegumen edge	lateral edge of subscaphium, at its posterior end [anterior of anal cone apex]	probably point of fusion between tegumen and vinculum [not distinct]	diaphragma far lateral of ventral end of subscaphium, close to gnathos arm]

species	family	*m1*: a	*m1*: b	*m2*: a	*m2*: b	*m3*: a	*m3*: b	*m4*: a	*m4*: b	*m5*: a	*m5*: b	*m6*: a	*m6*: b	*m7*: a	*m7*: b	*m10*: a	*m10*: b	*m29*: a	*m29*: b
Munychryia senicula	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorsal edge of juxta [anteriorly; smooth, ventral sclerite of unusually "high juxta", indicating non-homology of secondarily reduced juxta and dorso-lateral lappets => probably derived from manica]	basal part of ventral valva wall	dorsal end of vinculum [at hight of dorsal valva edge]	along lateral side of valva apodeme remnant	lateral side of coecum-penis end	partly lateral part of vinculum, partly basal edge of lateral valva wall [adjacent to *m4*; dorsal half of valva edge]	ventral phallus side and sclerotized part of manica [sclerotized, bulbous part]	saccus apex	inner side of basal valva edge [lateral, ventral, mesal]	inner side at base of clasper	near centre of anterior tegumen edge	lateral edge of subscaphium, distinctly anterior of posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Munychryia periclyta [2 SPECIMENS]	Anthelidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorsal edge of juxta [anteriorly; smooth, ventral sclerite of unusually "high juxta", indicating non-homology of secondarily reduced juxta and dorso-lateral lappets => probably derived from manica]	basal part of ventral valva wall	dorsal end of vinculum [at hight and a bit ventral of dorsal valva edge; muscle across reduced patch, indicating reduction to be secondary]	along lateral side of valva apodeme remnant	lateral side of coecum-penis end	partly lateral part of vinculum, partly basal edge of lateral valva wall [adjacent to *m4*; dorsal half of valva edge]	ventral phallus side and sclerotized part of manica [sclerotized, bulbous part]	saccus apex	inner side of basal valva edge [lateral, ventral, mesal]	inner side at base of clasper	near centre of anterior tegumen edge	lateral edge of subscaphium, distinctly anterior of posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]

species	family	*m1*: a	*m1*: b	*m2*: a	*m2*: b	*m3*: a	*m3*: b	*m4*: a	*m4*: b	*m5*: a	*m5*: b	*m6*: a	*m6*: b	*m7*: a	*m7*: b	*m10*: a	*m10*: b	*m29*: a	*m29*: b
Cicinnus sp.	Mimallonidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	lateral edge of reduced juxta	latero-dorsal edge of saccus [= ventral vinculum edge]	dorsal end of vinculum [at hight and slightly ventral of dorsal valva edge]	fan-shaped spread over ventral edge of gnathos arm, diaphragma and base of valva apodeme [gnathos protrudes as a pair of separate arms from diaphragma in *Mimallo* sp., and these armes are possibly secondarily fused in *Cicinnus* sp.; the shift of *m4* onto the gnathos is likely to be due to a secondary clasping function of the modified gnathos and NOT an indication for fusion of gnathos and transtilla, which are widely separated.]	lateral side of coecum-penis end [entire lateral apodeme]	dorsal part of vinculum [adjacent to *m4*; dorsal half of valva]	latero-ventral phallus side [at zone]	lateral saccus part [saccus forms a frame, which points posteriorly!]	membranous centre of saccus frame?	base of sheath formed around process (clasper?) by mesal valva side?	near centre of anterior tegumen edge	lateral edge of subscaphium, at its posterior end [anterior of anal cone apex]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Chionopsyche montana	Lasiocampidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	juxta [juxta reduced; muscle extremely thin]	valva [reduced to setose patch, shifted dorsal beneath uncus]	dorsal end of vinculum [over long stretch; ventral of valva remnants]	valva [reduced to setose patch, shifted dorsal beneath uncus]	dorsal side of lateral phallus apodeme [at phallus end]	valva [reduced to setose patch, shifted dorsad beneath uncus]	ventral side of lateral phallus apodeme [at phallus end]	saccus remnant [reduced, pointing posteriorly]	POSSIBLE INTERPRETATION: asymmetric and split – one side dorsal valva remnants to sack, other side ventral valva remnant basal edge to base of spine and apex of valva remnant to base of spine	(see *m7*a)	near centre of anterior tegumen edge	posterior end of anal cone	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]

species	family	*m1*: a	*m1*: b	*m2*: a	*m2*: b	*m3*: a	*m3*: b	*m4*: a	*m4*: b	*m5*: a	*m5*: b	*m6*: a	*m6*: b	*m7*: a	*m7*: b	*m10*: a	*m10*: b	*m29*: a	*m29*: b
Poecilocampa populi [1 FIXED & 2 DRIED SPECIMENS]	Lasiocampidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorsal edge of juxta [anteriorly]	posterio-dorsal edge of saccus centre [= ventral vinculum edge]	dorsoal end of vinculum [over longer stretch; at hight of dorsal valva edge and ventral of it]	basal edge of dorso-mesal wall of dorsal valva end and diaphragma dorsal of it [= valva apodeme in other taxa]	lateral side of coecum-penis end	dorsal part of vinculum [adjacent to *m4*; dorsal half of valva edge]	ventral phallus side [at zone]	saccus apex [reduced]	inner side of basal valva edge [lateral & mesal only, not ventral]	inner side at base of clasper	near centre of anterior tegumen edge	ventro-lateral wall of anal cone, distinctly anterior of posterior end [position of lateral edge of subscaphium in other taxa]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Chondrostega sp. [DRIED SPECIMEN]	Lasiocampidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	dorsal end of vinculum [ventral of dorsal valva edge?]	diaphragma ventro-mesal of valva apodeme	lateral side of phallus end	lateral part of vinculum [adjacent to *m4*; middle of valva edge]	ventro-lateral phallus side [at zone]	saccus apex [reduced]	absent	absent	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Macromphalia sp. [2 SPECIMENS of 2 species]	Lasiocampidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	absent	absent	lateral side of coecum-penis [strongly reduced]	dorsal part of vinculum [m4 absent, but would be adjacent if present; dorsal half of valva]	ventro-lateral side of phallus [at zone]	saccus apex [reduced]	inner side of basal valva edge [lateral & mesal only, not ventral]	inner side at ventral valva arm [about middle]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Trabala vishnou [DRIED SPECIMEN]	Lasiocampidae	absent	absent	absent	absent	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	dorsal end of vinculum [dorsal of dorsal valva edge; far from centre on dorso-lateral parts and over entire width of the "fake tegumen"; huge]	along basal edge of dorsal valva wall [= valva apodeme]	lateral side of phallus end	dorsal part of vinculum [m4 absent, but would be adjacent if present; dorsal half of valva; stretching across bent in annulus, supporting interpretation that vinculum reaches across bent, and ends shortly after]	ventral phallus side [at zone]	largely saccus apex [reduced], partly basal edge of the ventro-lateral valva wall	Split: A) basal edge of ventro-lateral valva wall; B) distal end of ventro-lateral valva wall	Split: A) base of mesal side of ventral valva part [=> split of valva into two is split into valva and clasper!]; B) dorsal vinculum end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	dorsal end of vinculum [seems to be located on a very narrow strip belonging to vinculum, but could be ventral end of tegumen, too]	latero-ventral end of subscaphium (?) remnant on fold
Crinocraspida torrida [DRIED SPECIMEN]	Lasiocampidae	absent	absent	absent	absent	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	dorsal end of vinculum [dorsal of dorsal valva edge; distinctly distant of centre on dorso-lateral parts and over entire width of the "fake tegumen"; huge]	along basal edge of dorsal valva wall [= valva apodeme]	lateral side of phallus end	dorsal part of vinculum [m4 absent, but would be adjacent if present; dorsal half of valva]	ventral phallus side [at zone]	largely lateral side of saccus [reduced], partly basal edge of the ventro-lateral valva wall	basal edge of ventro-lateral valva wall	base of mesal side of ventral valva part [=> split of valva into two is split into valva and clasper!]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	dorsal end of vinculum [rather clearly on a very narrow strip belonging to vinculum]	centre of diaphragma on fold beneath anal tube

species	family	*m1*: a	*m1*: b	*m2*: a	*m2*: b	*m3*: a	*m3*: b	*m4*: a	*m4*: b	*m5*: a	*m5*: b	*m6*: a	*m6*: b	*m7*: a	*m7*: b	*m10*: a	*m10*: b	*m29*: a	*m29*: b
Gastropacha n. sp. (ex Philippines, S. Palawan)	Lasiocampidae	absent	absent	absent	absent	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	dorsal end of vinculum [dorsal of dorsal valva edge; from centre to lateral parts and over entire width of the "fake tegumen"; huge]	along basal edge of dorsal valva wall [= valva apodeme]	ventro-lateral side of phallus end	dorsal part of vinculum [m4 absent, but would be adjacent if present; dorsal half of valva]	ventral phallus side [at zone]	saccus apex [reduced]	posterior edge of lateral vinculum part	posterior edge of lateral valva wall just dorsal of beginning of serrate, ventral process [broadening compared to attachment at base of valva; lateral wall curves inwards, resulting in posterior edge being at almost right angle to proximal edge]	near centre of anterior tegumen edge	lateral wall of anal cone end [dorso-lateral of posterior subscaphium end]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Odonestis erectilinea	Lasiocampidae	absent	absent	absent	absent	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	dorsal end of vinculum [dorsal of dorsal valva edge; from centre to lateral parts and over entire width of the "fake tegumen"; huge]	along basal edge of dorsal valva wall [= valva apodeme]	dorso-lateral side of phallus end [caudal of ductus ejaculatorius!]	dorsal part of vinculum [m4 absent, but would be adjacent if present; dorsal of valva]	ventro-lateral phallus side [at zone]	ventral side of saccus [about middle; saccus apex occupied by other muscle connecting to sternite]	partly basal edge of ventro-lateral valva wall, partly posterior edge of lateral vinculum part	inner side at base of clasper	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]

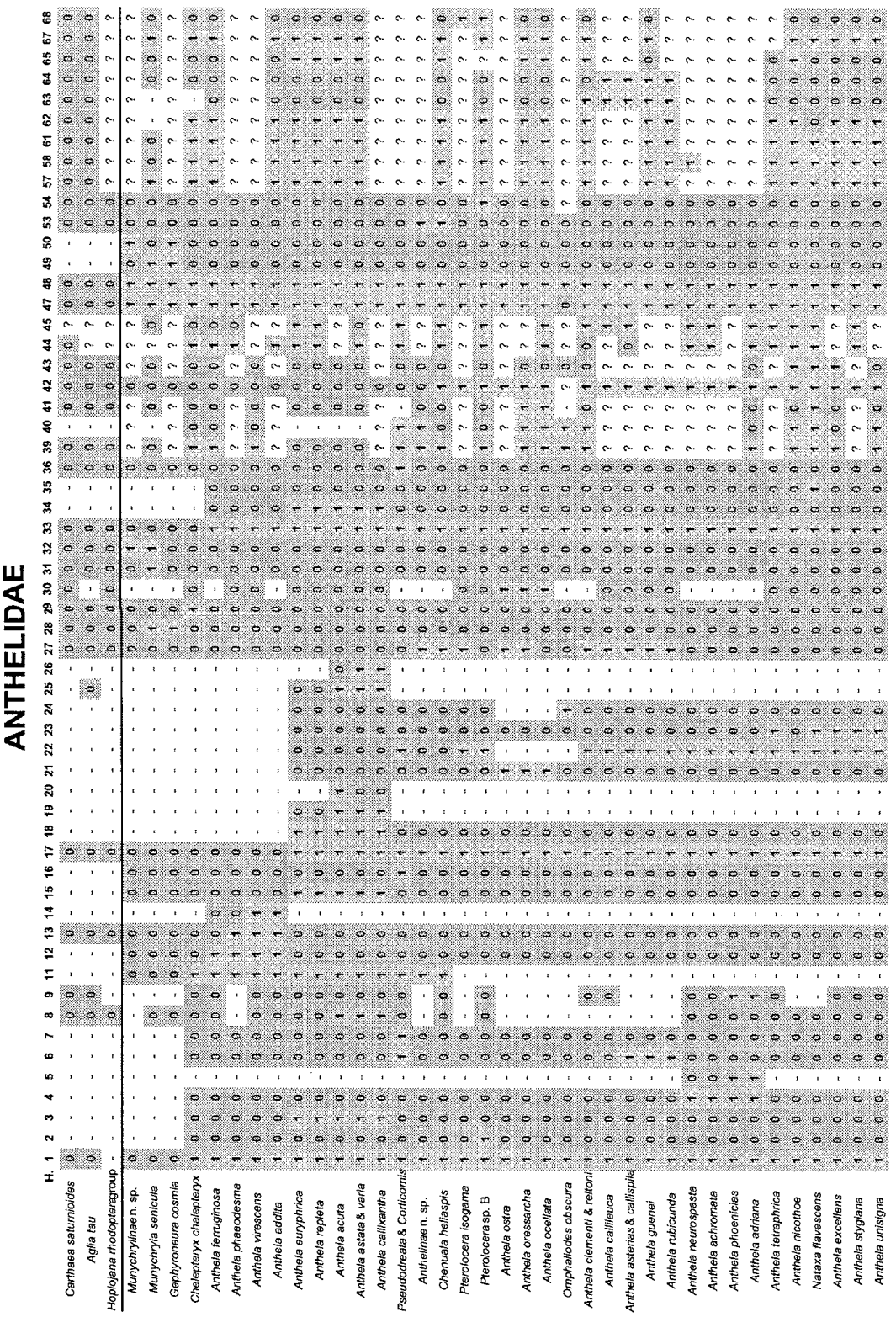
species	family	*m1*: a	*m1*: b	*m2*: a	*m2*: b	*m3*: a	*m3*: b	*m4*: a	*m4*: b	*m5*: a	*m5*: b	*m6*: a	*m6*: b	*m7*: a	*m7*: b	*m10*: a	*m10*: b	*m29*: a	*m29*: b
Prorifrons prosper	Lasiocampidae	absent	absent	absent	absent	absent	absent	absent	absent	dorsal side of phallus end	dorsal part of vinculum [m4 absent, but would be adjacent if present; dorsal of valva]	split and diverging: A) ventral side of phallus [at zone] B) dorsal edge of lateral phallus apodeme at base of phallus	split and diverging: A) very distal end of sclerotized centre between cubile [= end of ventral side of saccus, with muscle stretching over saccus]; B) cubile proximo-lateral of sclerotized cubile apex [= lateral side of the end of the ventral side of saccus; can move cubile proximad (clasping)]	absent	absent	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Ganisa plana	Eupterotidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorso-lateral edge of juxta [anteriorly]	basal part of ventral valva wall	dorsal end of vinculum [at hight of dorsal valva edge]	largely on entire lateral side of broad valva apodeme and to a lesser degree on diaphragma and on gnathos [=>indicating secondary reduction of sclerotization of gnathos and transtilla]	lateral side of coecum-penis end	dorsal part of vinculum [adjacent to *m4*; dorsal half of valva edge]	ventral phallus side [at zone]	saccus apex	inner side of basal valva edge [lateral only]	inner side at base of clasper	near centre of anterior tegumen edge	lateral edge of subscaphium, near posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]

species	family	*m1*: a	*m1*: b	*m2*: a	*m2*: b	*m3*: a	*m3*: b	*m4*: a	*m4*: b	*m5*: a	*m5*: b	*m6*: a	*m6*: b	*m7*: a	*m7*: b	*m10*: a	*m10*: b	*m29*: a	*m29*: b
Iloplojana sp. near *rhodoptera*	Eupterotidae	absent	absent	absent	absent	dorso-lateral edge of juxta [anteriorly]	basal part of ventral valva wall	dorsal end of vinculum [at hight and ventral of dorsal valva edge]	along entire valva apodeme	lateral side of coecum-penis end	dorsal part of vinculum [adjacent to *m4*; ventral half of valva edge]	ventral phallus side [anterior of zone]	saccus apex	inner side of basal valva edge [lateral, ventral]	inner side at base of clasper	absent	absent	[lateral vinculum [ventral of *m4*!]	lateral wall of anal cone base
Lemonia dumi [LITERATURE: S. & Z., 2002]	Lemoniidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorso-lateral edge of juxta [anteriorly]	posterio-dorsal edge of saccus centre [= ventral vinculum edge]	dorsal end of vinculum [dorsal of dorsal valva edge]	fold in diaphragma between valves and adjacent to gnathos plate	lateral side of coecum-penis end	basal edge of lateral valva wall [adjacent to *m4*; dorsal half of valva edge]	ventral phallus side [at zone]	saccus apex	inner side of basal valva edge [lateral, ventral]	inner side at base of clasper	near centre of anterior tegumen edge	lateral wall of anal cone base	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Lemonia balcanica [LITERATURE: S. & Z., 2002]	Lemoniidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	absent	absent	dorso-lateral edge of juxta [anteriorly]	partly posterio-dorsal edge of saccus centre [= ventral vinculum edge], partly basal edge of ventral valva wall	dorsal end of vinculum [dorsal of dorsal valva edge]	fold in diaphragma between valves and adjacent to gnathos plate	lateral side of coecum-penis end	?	ventral phallus side [at zone]	saccus apex	inner side of basal valva edge [lateral, ventral]	inner side at base of clasper	near centre of anterior tegumen edge	lateral wall of anal cone base	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Brahmaea tancrei [LITERATURE: K. & S., 2001]	Brahmacidae	broadly spread across dorsal part of tegumen	focused on anterior edge of ventral side of uncus	dorso-lateral on anterior tegumen edge [far from *m4*]	dorsal of valva apodeme (?), NOT ventral of m4	dorsal edge of juxta [anteriorly]	posterio-dorsal edge of saccus centre [= ventral vinculum edge]	dorsal end of vinculum [dorsal of dorsal valva edge]	valva apodeme	lateral side of coecum-penis end	dorsal part of vinculum [adjacent to *m4*; dorsal half of valva edge]	dorsal phallus side	saccus apex	inner side of basal valva edge [lateral]	inner side at base of clasper	near centre of anterior tegumen edge	lateral edge of subscaphium, near posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Dactyloceras sp.	Brahmaeidae	broadly spread across dorsal part of tegumen	anterior edge of ventral side of uncus	absent [see *m4*]	absent [see *m4*]	dorsal edge of juxta [anteriorly]	basal part of meso- ventral valva wall	dorsal end of vinculum and ventral end of tegumen [*m4* adjacent to *m1*; very massive muscle; possibly including *m4*]	along entire valva apodeme [reduced], diaphragma mesal and dorsal of it, and gnathos arm [supports hypothesis of gnathos/transtilla fusion]	lateral side of phallus end	lateral part of vinculum [far from *m4*; middle to ventral half of valva; both caused by giant valva stretching over entire hight of whole genitalia structures]	dorsal phallus side	saccus apex	inner side of basal valva edge [lateral, ventral]	inner side at base of clasper	dorso-lateral tegumen edge	lateral edge of subscaphium, distinctly anterior of posterior end	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Endromis versicolora	Endromidae	broadly spread across dorsal part of tegumen	anterior edge of ventral side of uncus	centre of anterior tegumen edge [far from *m4*]	apex of valva apodeme, NOT ventral of m4	dorsal edge of juxta [anteriorly]	posterio-dorsal edge of saccus centre [= ventral vinculum edge]	dorsal end of vinculum [at hight of dorsal valva edge]	along entire valva apodeme [including apex]	lateral side of coecum-penis end [reduced]	dorsal part of vinculum [adjacent to *m4*; dorsal half of valva edge]	ventral phallus side	saccus apex	inner side of entire ventral valva wall	along entire median fold [which runs from juxta to base of clasper]	dorso-lateral tegumen [near edge; very thin]	ventro-lateral wall of anal cone [distinctly anterior of posterior end]	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]

species	family	*m1*: a	*m1*: b	*m2*: a	*m2*: b	*m3*: a	*m3*: b	*m4*: a	*m4*: b	*m5*: a	*m5*: b	*m6*: a	*m6*: b	*m7*: a	*m7*: b	*m10*: a	*m10*: b	*m29*: a	*m29*: b
Mirina christophi [LITERATURE: K. & S., 1985]	Mirinidae	broadly spread across dorsal part of tegumen	anterior edge of ventral side of uncus	absent	absent	dorsal edge of juxta [anteriorly]	basal part of latero- ventral valva wall	dorsal end of vinculum [dorsal of dorsal valva edge]	along reduced valva apodeme and mesal of it	lateral side of coecum-penis end	dorsal part of vinculum [adjacent to *m4*, but with distinct gap; dorsal half of valva edge]	dorsal phallus side	saccus apex	inner side of ventral valva wall	inner side of valva [about position of base of clasper in other taxa]	near centre of anterior tegumen edge	lateral wall of anal cone	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]
Oberthueria caeca	Bombycidae	broadly spread across dorsal part of tegumen	anterior edge of ventral side of uncus	dorso-lateral on anterior tegumen edge [far from *m4*]	mesal of valva apodeme, NOT ventral of m4	ventro-lateral edge of juxta [anteriorly; dorsal end is fused to phallus]	basal part of mesal valva wall	dorsal end of vinculum [a bit ventral of dorsal valva edge]	apex of short valva apodeme	lateral side of coecum-penis end	dorsal part of vinculum [adjacent to *m4*; dorsal half of valva edge]	ventral coecum-penis side and dorsal end of fused juxta	saccus apex	inner side of basal valva edge [lateral, possibly mesal – different between left and right asymmetric valva]	inner side at base of clasper	near centre of anterior tegumen edge	arms of mesally divided/reduced gnathos	[destroyed, overlooked or absent]	[destroyed, overlooked or absent]

APPENDIX N:

CHARACTER MATRIX OF HENNIGIAN ARGUMENTATION



BOMBYCOID COMPLEX

H.	10	37	38	46	51	52	55	56	59	60	66
Thyrididae	0	0	0	0	0	0	0	0	0	0	0
Notodontidae	0	0	0	0	0	0	0	0	0	1	0
Mimallonidae	0	0	0	1	0	0	0	0	?	?	?
Lasiocampidae	0	0	0	1	0	0	0	0	1	0	1
Endromidae	0	0	0	1	1	1	0	0	?	1	1
Mirinidae	0	0	0	1	1	1	0	0	?	?	?
Bombycidae	0	0	0	1	0	0	1	0	?	1	1
Prismostictinae	0	0	?	1	0	0	1	0	?	?	?
Apatelodinae	0	0	?	0	0	0	0	0	?	?	?
Bombycinae	0	0	0	0	0	0	1	0	?	1	1
Phiditiinae	?	?	?	-	-	0	1	0	?	?	?
Carthaeidae	0	0	1	1	0	0	1	0	1	0	?
Sphingidae	0	0	1	1	0	0	1	1	1	1	1
Saturniidae	1	0	1	1	1	0	1	1	1	0	1
Anthelidae	1	1	1	1	0	0	1	0	1	1	?
Eupterotidae	1	1	1	1	1	0	1	0	1	1	?
Brahmaeidae	1	0	1	1	?	0	1	0	?	1	1
Lemoniidae	1	0	1	1	1	0	1	0	?	1	1

APPENDIX O:

CHARACTER MATRIX OF CLADISTIC ANALYSES

ANTHELIDAE

	C.1	2	3	4	5	6	7	8	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	37	38	39	40	41	42	43	44	46	47	48	49	52	53	56	57	60	61	62	63	64	66	67
Aglia tau	0	?	0	0	-	-	0	0	0	-	-	-	0	0	1	1	0	-	-	-	0	-	-	0	0	-	-	0	0	0	-	-	-	0	-	0	0	0	?	?	?	0	0	-	-	0	0	0	0	0	0	-	-	-	0	0
Carthaea saturnioides	2	-	-	-	-	-	0	0	0	-	-	-	2	0	1	2	0	-	-	-	0	-	3	0	0	0	0	0	-	0	-	-	-	0	-	0	0	0	0	0	?	0	0	-	-	0	0	0	0	0	-	-	-	-	0	0
Hoplojana rhodopteragroup	-	-	-	-	-	-	0	-	0	-	-	-	2	0	-	0	0	-	-	-	-	-	0	0	0	0	0	0	-	0	-	-	-	0	-	0	0	0	?	?	?	0	0	-	-	0	0	?	?	?	?	?	?	?	?	?
Anthela acuta	1	1	-	2	0	-	1	0	1	2	1	0	2	0	1	{12}	1	1	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	-	0	0	0	?	?	?	1	1	0	0	0	0	1	1	1	1	0	-	1	1	0
Anthela addita & virescens	1	1	0	0	-	-	0	0	1	1	1	1	3	0	0	1	0	-	-	-	0	-	3	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	?	1	1	0	0	0	0	1	1	1	1	0	-	0	1	0
Anthela adriana & phoenicias	1	-	-	2	2	1	0	1	0	-	-	-	2	0	1	1	1	0	-	-	0	0	3	0	0	0	-	0	0	1	0	0	0	1	0	0	1	0	0	1	1	1	1	0	0	0	0	?	?	?	?	?	?	?	?	?
Anthela astata varia & callixantha	1	1	-	2	0	-	1	0	1	2	1	0	2	0	1	1	1	1	1	0	0	0	2	0	0	0	0	0	0	1	1	0	0	0	-	0	0	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	-	1	1	0
Anthela asterias & callispila	1	4	1	0	-	-	2	-	0	-	-	-	2	0	1	1	1	0	-	-	0	0	3	1	0	0	0	0	0	1	0	0	0	?	?	?	1	?	1	1	1	1	1	0	0	0	0	?	?	?	?	1	1	?	?	?
Anthela callileuca	1	2	0	0	-	-	2	-	0	-	-	-	2	0	1	1	1	0	-	-	0	0	3	1	0	0	0	0	0	1	0	0	0	?	?	?	1	?	?	?	1	1	1	0	0	0	0	?	?	?	?	1	1	?	?	?
Anthela clementi & reltoni	1	2	0	0	-	-	2	-	0	-	-	-	2	0	1	1	1	0	-	-	0	0	3	1	0	0	-	0	0	1	0	0	0	1	1	0	1	0	1	1	1	1	1	0	0	0	0	1	1	1	1	1	0	1	1	0
Anthela euryphrica & repleta	1	1	-	2	0	-	0	0	1	2	1	0	2	0	1	2	1	1	0	-	0	0	0	0	0	0	0	0	1	1	0	0	0	-	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	1	0	-	1	1	0
Anthela excellens	1	1	0	0	-	-	0	0	0	-	-	-	2	0	1	1	1	0	-	-	1	0	3	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	?	?	?	1	1	0	0	0	0	1	1	1	1	0	-	0	1	0
Anthela ferruginosa	1	2	0	0	-	-	0	0	1	0	1	1	2	0	0	1	0	-	-	-	0	-	3	0	0	0	-	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	-	0	1	0
Anthela guenei & rubicunda	1	4	1	0	-	-	2	-	0	-	-	-	2	0	1	1	1	0	-	-	0	0	3	1	0	0	0	0	0	1	0	0	0	?	?	?	1	?	?	?	?	1	1	0	0	0	0	1	1	1	1	1	1	0	1	0
Anthela neurospasta & achromata	1	{34}	-	2	2	0	0	0	-	-	-	-	2	0	1	1	1	0	-	-	0	0	3	0	0	0	-	0	0	1	0	0	0	?	?	?	1	?	0	1	1	1	1	0	0	0	0	?	1	?	?	?	?	?	?	?
Anthela nicothoe	1	2	0	0	-	-	0	-	0	-	-	-	2	0	1	1	1	0	-	-	0	0	3	0	0	0	0	0	0	1	0	0	0	1	1	0	1	1	0	1	1	1	1	0	0	0	0	1	1	1	1	0	-	1	1	0
Anthela ocellata	1	2	0	0	-	-	2	-	0	-	-	-	2	0	1	2	0	-	-	-	0	-	3	0	0	0	1	0	0	1	0	0	0	1	1	1	1	0	0	1	1	1	1	0	0	0	0	1	1	1	1	0	-	1	1	0
Anthela oressarcha & ostra	1	{12}	0	0	-	-	2	-	0	-	-	-	2	0	1	2	0	-	-	-	0	-	3	1	0	0	1	0	0	1	0	0	0	1	1	1	1	0	?	?	?	1	1	0	0	0	0	1	1	1	1	0	?	1	1	0
Anthela phaeodesma	1	1	0	0	-	-	0	-	1	0	1	1	3	0	0	1	0	-	-	-	0	-	3	0	0	0	0	0	0	1	0	0	0	?	?	?	0	?	0	1	0	1	1	0	0	0	0	?	?	?	?	?	?	?	?	?
Anthela tetraphrica	1	1	0	0	-	-	0	0	0	-	-	-	2	0	1	1	1	0	-	-	1	0	3	0	0	0	0	0	0	1	0	0	0	?	?	?	1	?	0	1	1	1	1	0	0	0	0	1	1	1	1	0	-	0	?	?
Anthela unisigna & stygiana	1	1	0	0	-	-	0	0	0	-	-	-	2	0	1	1	1	0	-	-	1	0	3	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	1	1	1	0	0	0	0	1	1	1	1	0	-	0	1	0
Anthelinae n. sp.	1	1	0	0	-	-	2	-	1	0	1	0	2	0	1	2	1	?	-	-	0	0	3	1	0	0	-	0	0	1	0	0	0	1	1	0	0	0	?	?	?	1	1	0	0	1	0	?	?	?	?	?	?	?	?	?
Chelepteryx chalepteryx	1	2	0	0	-	-	0	0	1	0	1	0	0	0	-	0	0	-	-	-	-	-	-	3	0	0	1	0	0	0	0	-	-	-	1	0	0	0	0	0	1	0	1	1	0	0	0	0	1	1	1	1	-	-	0	1	0
Chenuala heliaspis	1	1	0	0	-	-	0	0	1	0	1	0	2	0	1	1	1	?	-	-	0	0	3	1	0	0	-	0	0	1	0	0	0	1	0	0	1	0	0	1	1	1	1	0	0	1	0	1	1	1	1	0	-	1	1	0
Gephyroneura cosmia	0	0	0	0	-	-	0	-	1	0	0	0	0	0	0	1	0	-	-	-	0	-	3	0	1	0	-	0	0	0	-	-	-	?	?	?	0	?	?	?	?	1	1	1	1	0	0	?	?	?	?	?	?	?	?	?
Munychryia senicula	0	0	0	0	-	-	0	-	1	0	0	0	0	0	0	1	0	-	-	-	0	-	3	0	1	0	-	1	1	0	-	-	-	0	-	0	0	0	0	?	0	1	1	1	0	0	0	1	0	0	-	-	-	-	1	0
Munychryiinae n. sp.	2	-	-	-	-	-	2	-	1	0	0	0	0	0	0	1	0	-	-	-	0	-	3	0	0	0	-	0	1	0	-	-	-	?	?	?	0	?	?	?	?	1	1	0	1	0	0	?	?	?	?	?	?	?	?	?
Nataxa flavescens	1	1	0	0	-	-	0	-	0	-	-	-	1	0	1	1	1	0	-	-	1	0	3	0	0	0	0	0	0	0	1	2	1	0	1	1	1	1	1	0	1	1	1	1	0	0	0	0	1	1	1	1	0	0	-	0	1	0
Omphaliodes obscura	1	?	0	0	-	-	2	-	0	-	-	-	2	0	1	1	1	?	-	-	0	1	3	0	0	0	-	0	0	1	0	0	0	1	1	-	?	0	?	?	?	?	0	1	0	0	0	?	?	?	?	?	?	?	?	?
Pseudodreata & Corticomis	1	4	-	1	-	-	0	0	1	0	1	0	0	1	1	2	1	0	-	-	0	0	3	0	0	0	-	0	0	1	0	0	0	1	1	1	-	0	0	0	1	1	1	1	0	0	0	0	?	?	?	?	?	?	?	?	?
Pterolocera isogama	1	2	0	0	-	-	2	-	0	-	-	-	2	0	1	2	1	0	-	-	0	0	3	1	0	0	0	0	0	1	0	0	0	?	?	?	1	?	?	?	?	1	1	0	0	0	0	?	?	?	?	?	?	?	?	1
Pterolocera sp. B	1	3	-	2	1	-	0	0	0	-	-	-	2	0	1	2	1	0	-	-	0	0	3	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	1	1	1	0	0	0	1	1	1	1	1	0	-	?	1	1

BOMBYCOID COMPLEX

C.	9	35	36	45	50	51	54	55	58	59	65
Thyrididae	0	0	0	0	0	0	0	0	0	0	0
Noctuoidea	0	0	0	0	0	0	0	0	0	1	0
Lasiocampidae & Mimallonidae	0	0	0	1	0	0	0	0	1	0	1
Endromidae & Mirinidae	0	0	0	1	1	1	0	0	?	1	1
Bombycidae	0	0	0	1	0	0	1	0	?	1	1
Carthaeidae	0	0	1	1	0	0	1	0	1	0	?
Sphingidae	0	0	1	1	0	0	1	1	1	1	1
Saturniidae	1	0	1	1	1	0	1	1	1	0	1
Anthelidae	1	1	1	1	0	0	1	0	1	1	?
Eupterotidae	1	1	1	1	1	0	1	0	1	1	?
Brahmaeidae & Lemoniidae	1	0	1	1	?	0	1	0	?	1	1

APPENDIX P:

PUBLISHED BOMBYCOID APOMORPHIES

P.1) CRITICAL REVIEW OF PUBLISHED PHYLOGENETIC HYPOTHESES OF THE BOMBYCOID COMPLEX

Numerous publications relate to the systematics of the bombycoid complex (see I.3), but only very few propose hypotheses of phylogenetic relationships between its families based on apomorphies. These particular publications are Brock 1971, Kuznetzov & Stekolnikov 1985, 2001, Stekolnikov & Zolotukhin 2002, Niculescu 1988, Scott 1986, Minet 1986, 1991, 1994, and Lemaire & Minet [1998] (based on Minet 1994). Of these only Brock (1971), Minet (1986, 1991, 1994), and Lemaire and Minet ([1998]) examined Anthelidae. However, as the Anthelidae were placed in the Bombycoidea by Common (1966), the characters proposed for the bombycoid complex by the other authors cannot be simply ignored and are also briefly discussed in this appendix.

Brock (1971) formed hypotheses on the evolutionary relationships between ditrysian superfamilies based on hypotheses of transformation series of wing venation, thoracic sclerites and the abdominal articulation within each superfamily. He was the first author to propose an assemblage of families for the Bombycoidea that is equivalent to our current concept of the bombycoid complex, but he did not present any apomorphies to support this grouping. While he did not explicitly state apomorphies supporting monophyla, his transformation series of changes in the fore wing radial sector included the Anthelidae. He regarded the areole of the Anthelidae as an intermediate form between the radial sector of the "primitive" Eupterotidae and that of the "more advanced" Bombycidae. Thereby, Brock postulated the areole of the Anthelidae to be different from the areole present in other Lepidoptera (e.g., Noctuoidea). I agree with Brock on this conclusion and include this autapomorphy of the Anthelidae as character H.47. However, I disagree with him on the transformation series, which is not based on detailed morphological studies (Brock explicitly rejected the imaginal tracheation to be based on the pupal tracheation (p. 39)), but on his perception of the superficial branching pattern of the radial sector and his ideas on how this pattern might have

evolved by distad movements of certain branches.

Kuznetzov and Stekolnikov (1985, 2001) extensively studied the musculature of lepidopteran male genital structures. They hypothesized relationships between families of the bombycoid complex, constructing a dendrogram (1985: 31) on the basis of some families being "more plesiomorphic" than others and "consequently" being the sistergroup to these other families, which is neither a Hennigian nor a cladistic method. On this basis, they separated the Lasiocampidae from the Bombycoidea and Sphingoidea, placing them in a superfamily of their own – Lasiocampoidea. Nevertheless, they indirectly proposed one synapomorphy ("secondary modification") for the Sphingoidea and Bombycoidea, namely the attachment of muscle *m4* to the dorso-lateral part of the annulus (the tegumen). However, this synapomorphy is illusory, as argued in detail in section III.2.3.A.

In a subsequent publication, Kuznetzov and Stekolnikov (2001: 370) presented a dendrogram of all families of the bombycoid complex, this time including Lasiocampidae, Lemoniidae, Anthelidae, Eupterotidae and Apatelodinae in the Lasiocampoidea, despite not having examined any Anthelidae, Eupterotidae or Apatelodinae. They defined this expanded superfamily by two characteristics, namely the dense hair coverage of caterpillars and the "functional morphology of genitalia". While the latter was not specified further, the dense hair coverage of caterpillars is widespread in Noctuoidea (e.g., Thaumetopoeinae, Lymantriidae, Arctiidae) and occasionally occurs in other families of the bombycoid complex (e.g., the Saturniidae *Loepa, Vegetia, Ludia, Decachorda* and *Micragone*). Similarly, the Bombycoidea were defined by a single character, namely the substitution of primary setae in caterpillars with verrucae/scoli. Such verrucae are very widespread, occurring in Noctuoidea as well as all members of the Lasiocampoidea *sensu* Kuznetzov and Stekolnikov (2001). In summary, none of their proposed characters are suitable for phylogenetic hypotheses within the bombycoid complex.

Stekolnikov and Zolotukhin (2002) examined the genital structures and musculature of the genus *Lemonia* (Lemoniidae), confirming that Lemoniidae should be included in the Lasiocampoidea *sensu* Kuznetzov and Stekolnikov (2001). This hypothesis is based on two proposed synapomorphies of Lemoniidae and Lasiocampidae, namely the loss of

muscle *m2* and the articulation of the gnathos with the lateral angles of the uncus. As the authors themselves stated, the former apomorphy is very widespread and common within Macrolepidoptera (at least some taxa in all superfamilies), hence of very little significance. In contrast, the articulation between gnathos and uncus was said to be of importance due to "virtually total absence in other families and superfamilies of Lepidoptera" (p. 685), except for Papilionoidea. However, this type of articulation is likely to be the ground plan condition in Lepidoptera due to the origin of the uncus from the 10th tergite and of the gnathos from the 10th sternite (Kristensen 2003b: 107; see section III.1.1). This articulation is typically at the proximal end of the uncus (sometimes represented by lateral extensions), near its articulation with the tegumen. As with the fusion between uncus and tegumen in many species, a secondary sclerotization between the dorsal end of the gnathos arm and the posterior edge of the tegumen can connect the two structures, giving the false impression of an articulation between the gnathos and the tegumen+uncus or even the tegumen only. The, in my opinion, plesiomorphic type of gnathos articulation (with the proximal edge of the uncus) is by no means "virtually absent" in Lepidoptera. Even if the sclerotization is also approximated to the tegumen, its direct connection to the uncus is apparent in numerous species of various families, e.g., *Agrotis infusa* (Noctuidae), *Aurivillius fuscus*, *Pselaphelia flavivitta*, *Opodiphthera helena*, *Syssphinx quadrilineata* (all Saturniidae), *Carthaea saturnioides* (Carthaeidae), *Anthela euryphrica*, *A. excellens*, *Pterolocera* spp. (all Anthelidae), *Poecilocampa populi* (Lasiocampidae) and *Cicinnus* sp. (Mimallonidae).

Niculescu (1988, 1989a: 105) claimed to have defined the Bombycoidea by 18 characters of the exo-skeleton in Niculescu 1988, but none of his characters actually did so. Instead, he presented a list of characters claimed to be apomorphies or plesiomorphies, respectively of Lasiocampidae, Lemoniidae, Attacidae [= Saturniidae], Mimallonidae or Endromidae. Seemingly based on the number of presumed apomorphies relative to plesiomorphies he regarded a family as the "most advanced of Bombycoidea" (Lasiocampidae), belonging to the "advanced families" (Lemoniidae) and so on. Further, each of these presumed plesiomorphies and apomorphies was at best presented as a simple line-drawing and a short sentence regarding the occurrence or shape of the structure within a single family of the bombycoid complex. No information

on the occurrence of the character in other families of the bombycoid complex or outside of it was provided. Under these circumstances I deem it futile to discuss his characters in detail.

Scott (1986), who himself stated not to have "great personal experience with moth anatomy" (p. 30), hypothesized on the relationships between superfamilies of Macrolepidoptera. He did not specify which families he included in the Bombycoidea, but he excluded Sphingidae and Mimallonidae from it. His cladogram showed three characters that he regarded as autapomorphies of the Bombycoidea. These are the concealed fore leg femur in the pupa, the non-roofed position of the wings over the abdomen and the absence of chaetosemata. The former two characters are not universal within the bombycoid complex, and whether they represent the ground plan condition of each of its families remains to be shown. Further, none of these characters are unique to the Bombycoidea, in fact, Scott's "matrix" (1986: 36, table 1) showed that they occur at least in some taxa of every macrolepidopteran superfamily, except for the universal presence of chaetosemata in Hesperioidea and Papilionoidea. Obviously, none of these three characters is suitable to define the superfamily Bombycoidea.

Minet's studies of the bombycoid complex are the by far most specific and comprehensive published to date. He refined and expanded his hypotheses on the relationships within the bombycoid complex in several publications (1986, 1991, 1994, and in Lemaire & Minet [1998]). While his hypotheses are currently widely accepted (e.g., Regier *et al.* 1998, Holloway *et al.* 2001, Gaedike & Häuser 2003; but see Oberprieler & Duke 1994, Oberprieler *et al.* 2003), he explicitly stated that the "cladogram proposed hereafter (Fig. 71) should only be considered a reasonable working hypothesis" (1994: 65). I acknowledge Minet's notion and now discuss with particular scrutiny his characters supporting the monophyly of the bombycoid complex, of the Bombycoidea, of the Lasiocampoidea and of the Anthelidae. A detailed discussion of his proposed apomorphies supporting other monophyla within the bombycoid complex is out of the scope of this thesis, but an annotated list of all his characters is presented below (Appendix P.2).

Minet (1986) initially specified a single synapomorphy for the bombycoid complex (exclusive of Mimallonidae), namely the presence of many secondary setae in

caterpillars. Caterpillars with many secondary setae are also typical of many other Lepidoptera (e.g., Thaumetopoeinae, Arctiidae, Lymantriidae, Riodinidae and Megalopygidae), and Minet himself never mentioned this character again in his later publications. Instead, he subsequently proposed six other synapomorphies to support the monophyly of the bombycoid complex inclusive of the Mimallonidae:

1. The presence of secondary setae on the larval prolegs (Minet 1991, 1994). This characteristic also occurs in some taxa of the Noctuoidea and of Minet's "A-G group", which includes the remaining macrolepidopteran superfamilies Axioidea, Calliduloidea, Hedyloidea, Hesperioidea, Papilionoidea, Drepanoidea and Geometroidea. Further, the presence of secondary setae *per se* is not a good indication of homology.
2. The maxillary palpi of the pupa are either concealed or only indicated by minute triangular sclerites (Minet 1991, 1994). Apart from uniting two different conditions in one character state, these conditions are also present in some taxa of the Noctuoidea and of Minet's "A-G group". At least the reduction of maxillary palpi is linked to the loss of the proboscis, which occurred many times independently in families within and outside the bombycoid complex.
3. The absence of functional ocelli in the adult moth (Minet 1991, 1994) This is a simple loss of function, which not only occurred repeatedly within various families (e.g., Cossidae), but which is even the ground plan condition of several non-bombycoid families, e.g., the Drepanidae, Uraniidae, Geometridae, Notodontidae and Hepialidae.
4. The mesothorax of the adult moth lacks the upper sector of the precoxal sutures (Brock 1971; Minet 1991). Minet (1994) himself rejected this apomorphy, because the upper sector is distinctly present in some Bombycidae and faintly in Mirinidae. Further, the upper sector is also absent in other families, e.g., the Zygaenidae, Metarbelidae and Megalopygidae (Brock 1971).
5. The long line of junction between the mesepimeron and the meron (Minet 1991, 1994). The distinction of this character state is only relative to the hypothesized ground plan of the "A-G" group (Minet 1991) and the Noctuoidea, for both of which Minet assumed a shorter junction. Minet's assumption for the Noctuoidea seems to be merely based on the condition present in *Oenosandra boisduvalii* (Oenosandridae) and the hypothesis of Miller (1991) of the Oenosandridae being the sistergroup of all

other Noctuoidea. However, Minet's equation of the length in one representative of the Oenosandridae with the condition in the hypothetical ground plan of all Noctuoidea is highly presumptuous and not empirically supported.

6. The relative closeness of the dorsal extremities of the prescutal clefts on the mesothorax (Minet 1991, 1994; Lemaire & Minet [1998]). This condition is less distinct in some taxa of the bombycoid complex, e.g., the Mirinidae (Lemaire & Minet [1998]). However, it is also present in the Hedylidae (Minet 1994) and *Oenosandra boisduvalii* (Oenosandridae). The "closeness" of these clefts is relative to the condition present in the "hypothetical ground plan of the Macrolepidoptera" (Lemaire & Minet [1998]), which unfortunately was not specified further.

The first three of these proposed synapomorphies are very widespread and common in Macrolepidoptera, as even Minet noted himself when defining the characters, and hence are not convincing synapomorphies of the bombycoid complex. The fourth proposed synapomorphy was subsequently rejected by Minet (1994) himself, and in his latest publication (Lemaire & Minet [1998]) he presented only the sixth synapomorphy as convincing support for the monophyly of the bombycoid complex.

In support of the monophyly of the superfamily Bombycoidea (exclusive of Anthelidae, Lasiocampidae and Mimallonidae) Minet (1991, 1994) proposed four synapomorphies, all of which were repeated in Lemaire & Minet [1998]:

1. The fore coxae of the final instar caterpillar are anteriorly firmly fused with each other (Minet 1991, 1994; Lemaire & Minet [1998]). This condition is not present in the Apatelodinae (Bombycidae), which Minet (1994) explained *ad hoc* as a reversal. Further, the fore coxae of some Eupterotidae (Oberprieler & Duke 1994) and of the monotypic family Carthaeidae are not fused, the latter of which was not examined by Minet (1991). As stated by Minet (1991), the fore coxae are generally not distinctly fused in Anthelidae (not included in Bombycoidea). However, they are so closely approximated in all Anthelidae that they touch each other and are typically partly fused at their base. In *Anthela basigera* they are even distinctly fused, as in the Bombycoidea. Due to their shape, even fused fore coxae always diverge from each other distally, leaving a distal gap between them. This gap renders the distinction between an anterior basal and an entire fusion difficult. The correct scoring of the

fused condition is further hindered by variation in length and degree of sclerotization of the fore coxae in different taxa.

2. In the male genitalia, the "flexors" of the valvae (muscles *m4*) originate on the tegumen, not on the vinculum (Minet 1991, 1994; Lemaire & Minet [1998]). As stated by Minet (1991, 1994), this character had previously been proposed by Kuznetzov and Stekolnikov (1985). It is discussed in detail in section III.2.3.A, where I argue that muscle *m4* attaches to the dorsal end of the vinculum (not the tegumen) in Bombycoidea, Lasiocampoidea and most other Lepidoptera, and that this proposed synapomorphy is based on a chain of errors in interpretation.
3. In the caterpillar, the D1 setae of abdominal segment A8 arise from a middorsal protuberance (Minet 1994; Lemaire & Minet [1998]). Minet (1994) assumed this character to be present in the hypothetical ground plan of his three main lineages within the Bombycoidea and explained the absence of this apomorphy in Eupterotidae, Apatelodinae, *Lemonia* and some Saturniidae *ad hoc* as a secondary loss. Based on a setal map of the first instar caterpillar of *Munychryia senicula* in Common & McFarland (1970: Fig. 15), Minet (1994) assumed the D1 setae to be separated from each other in the hypothetical ground plan of the Anthelidae. However, as already pointed out by Oberprieler and Duke (1994), the caterpillars of *Munychryia* are highly adapted, camouflaging as a *Casuarina* leaf, which includes the extreme reduction of secondary setae and the total loss of verrucae (protuberances). In contrast, the D1 setae are located on distinctly merged verrucae on A8 in, e.g., *Chelepteryx* (Figs 424, 425), *Anthela basigera* and relatives, and *A. excellens*, but are located on more distantly merged verrucae in some Anthelinae (e.g., *A. ferruginosa*). The occurrence of both conditions within the Anthelidae as well as outside this family makes a determination of the hypothetical ground plan of the family by outgroup comparison impossible. Judging from the phylogeny of Anthelidae proposed in section VII.1.3.1 and the general loss of verrucae in *Munychryia*, the condition of the merged verrucae (a middorsal protuberance) might be assigned to the hypothetical ground plan of Anthelidae. Taxa with (e.g., *Entometa* (Fig. 426), *Gastropacha* (Minet 1994)) and without a middorsal protuberance on A8 (e.g., *Chionopsyche montana* (Fig. 427), *Chondrostega*, *Genduara*) occur in Lasiocampidae, providing further evidence of the homoplasy of this character. In general, these middorsal protuberances vary significantly in structural details within

the Bombycoidea (e.g., a naked horn in Sphingidae versus a spiny verruca in Saturniidae), raising doubts about the homology of the character as defined by Minet (1994).

4. Fore wing with branch Rs1/Rs2 closely parallel or even fused with Rs3/Rs4 (Minet 1994; Lemaire & Minet [1998]). The closely parallel condition is present in the families Carthaeidae, Sphingidae and Anthelidae, and differs in the latter from the former two only by the larger distance between the two branches. However, very closely approximated Rs branches occur in *Chelepteryx* (Fig. 180). The extreme proximity of the branches in Sphingidae (Fig. 170) is likely to be linked to the very narrow wing shape. As discussed in character H.51 (section III.4.2), Minet's definition of the character assumes that all fusions in other families have originated from the closely parallel condition, which is not necessarily the case.

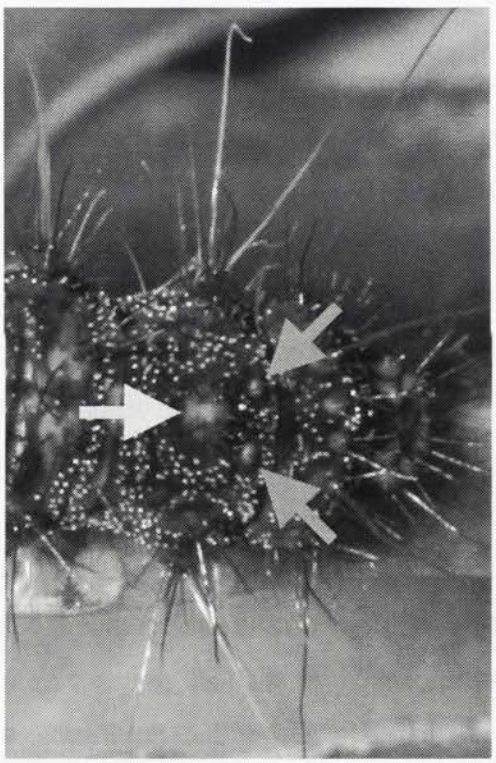


Fig. 424: *Chelepteryx collesi* (Anthelidae), caterpillar (L3) – abdominal segment A8 with merged D1 (yellow arrow) and separate D2 verrucae (green arrows).

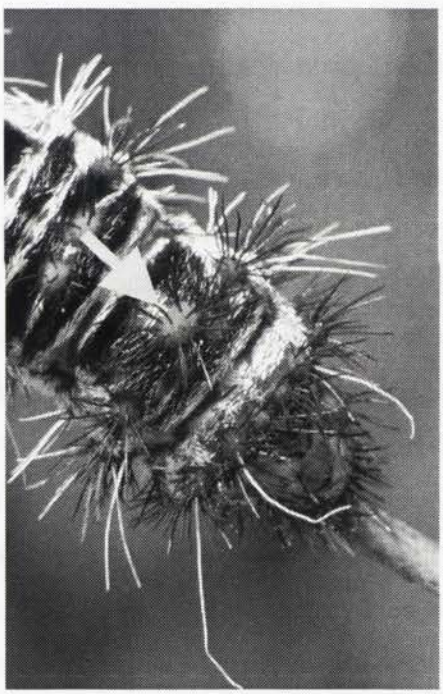


Fig. 425: *Chelepteryx collesi* (Anthelidae), caterpillar (Lm) – abdominal segment A8 with merged D1 (yellow arrow) and separate D2 verrucae.

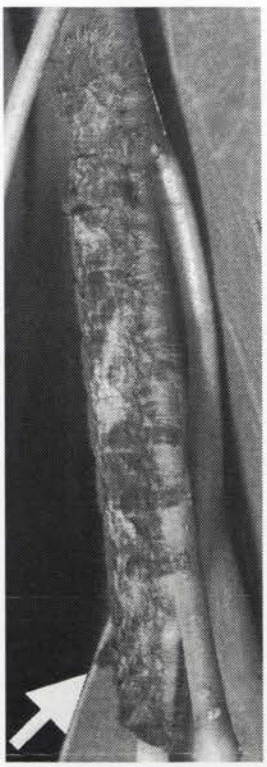


Fig. 426: *Entometa fervens* (Lasiocampidae), caterpillar (L3/4) – abdominal segment A8 with a middorsal protuberance (yellow arrow), but no verrucae.

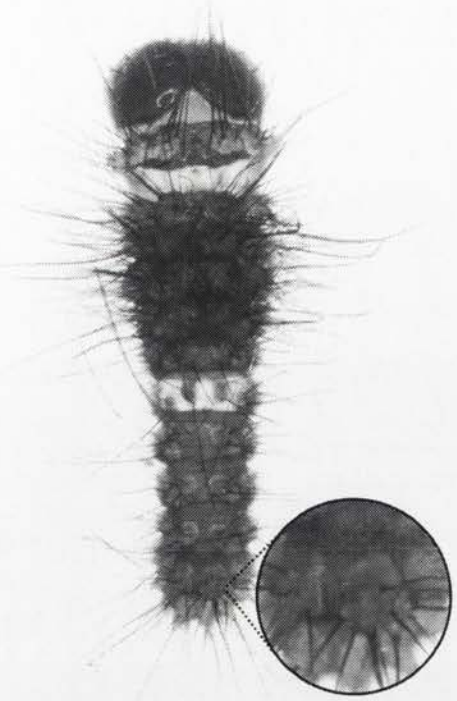


Fig. 427: *Chionopsyche montana* (Lasiocampidae), caterpillar (L1) – abdominal segment A8 with two separate, distinct D1 verrucae (magnified).

For the Lasiocampoidea (Lasiocampidae and Anthelidae), Minet (1991, 1994) postulated 5 synapomorphies, none of which are unique as subsequently stated in Lemaire & Minet [1998] without further details. These proposed synapomorphies are:

1. Epiphysis of the female reduced or lost, while well developed or less reduced in the male (Minet 1991, 1994). Such a "sexual dimorphism" is also present in other families, e.g., Endromidae, Mirinidae, some Eupterotidae and some Saturniidae. The relative difference in length of a structure is never a good indication of homology. Additionally, the reduction of the epiphysis in females is likely to be linked to its function, the cleaning of the antennae, which are distinctly less well developed in the females of the bombycoid complex.
2. Female hind wing without frenular bristle (Minet 1994). The frenular bristle is absent in anthelid females, but not males, while it is absent in both sexes of the Lasiocampidae. Further, the frenular bristle is absent in females of Endromidae, Mirinidae, Saturniidae, Lemoniidae, some Eupterotidae and some Brahmaeidae. The loss of part of the wing-coupling mechanism consisting of retinaculum and frenulum in females is likely to be linked to the almost sessile behaviour of these non-feeding

females, which do not fly prior to mating and tend to lay almost all eggs during the following night.

3. Fore wing vein M2 arising closer to M3 than to M1 (Minet 1991, 1994; Lemaire & Minet [1998]). This relative position of M2 is also present in various other lepidopteran families, e.g., some Pyraloidea, Drepanidae, Noctuoidea, Eupterotidae, Endromidae, Sphingidae and Bombycidae. It can be caused by various factors, e.g., the extent of fusion between M1 and Rs4, an actual change in the position of M2 and the extent of splitting between M2 and M3. Without differentiating between these possible causes of the proximity between M2 and M3, which is difficult, this character state is certainly not representing homologous arrangements of veins.
4. Mandible of the mature caterpillar provided with some secondary setae (Minet 1991, 1994). This character is also present in other families, e.g., Eupterotidae, Apatelodinae and some Saturniidae (*Hemileuca nevadensis*). In the examined anthelid species, numbers range from 14 to 55 and in Lasiocampidae from 7 to 45 setae on each mandible. Such variable numbers and the varying positions of the setae do not provide indications of homology. As with secondary setae on the integument, the mere presence of such setae is not a good indication of homology.
5. Ventral prolegs with the subventral [SV] area divided into two sclerites by a median, vertical membrane (Minet 1991, 1994) (Fig. 429). The SV-sclerite is typically entire (Fig. 428). Minet's description of the SV area fits not only Lasiocampidae and Anthelidae, but also some Eupterotidae, Apatelodinae and Bombycinae. However, in Lasiocampidae two dark sclerites are separated from each other by a pale, membranous area (Fig. 431), while in the other families two pale sclerotizations are separated by a dark membranous area (Fig. 430). In the latter the sclerites themselves are not white but translucent, with the underlying tissue shining through. Unlike all other Anthelidae, the sclerite is dark and not divided in the caterpillar of *Munychryia senicula* (Fig. 432), which is uniquely modified in many aspects. Among the Eupterotidae are species with an entire SV sclerite (e.g., *Janomima mariana*, *Phyllalia patens*, *Poloma angulata, Ebbepterote expansa, Cotana serranotata, Panacela lewinae* [the observation of a split sclerite by Oberprieler *et al.* 2003: 109 is based on a misidentified caterpillar in the ANIC, which belongs to the anthelid genus *Newmania*]) as well as with a divided SV sclerite (e.g., *Rhabdosia patagiata* and *Trichophiala devylderi*; see Oberprieler & Duke 1994: 237-238). Further, the degree

of sclerotization ranges within a family from faintly sclerotized (e.g., *Argema mimosae*, *Urota sinope* (both Saturniidae)) to heavily sclerotized (e.g., *Opodipthera eucalypti*, *Micragone cana* (both Saturniidae)). This indicates that secondary sclerotizations of the median membranous area are possible, as is the loss of one of the sclerites. The function of the SV sclerite is unknown. Dissections of prolegs of *A. astata* (Anthelidae) did not reveal any muscle attachments. Instead, the muscle moving the crochets attaches dorsal of the sclerite. The stiffening of the proleg between the muscle attachment points might contribute to the unhooking of the crochets. It prevents a compression of this part of the proleg upon contraction of the muscle, which instead tilts (unhooks) the crochets.

While the divided SV sclerite can be prominent, the differences in structure and the occurrence of both entire and divided SV sclerites within several families cast doubt on the hypotheses of homology regarding this structure.

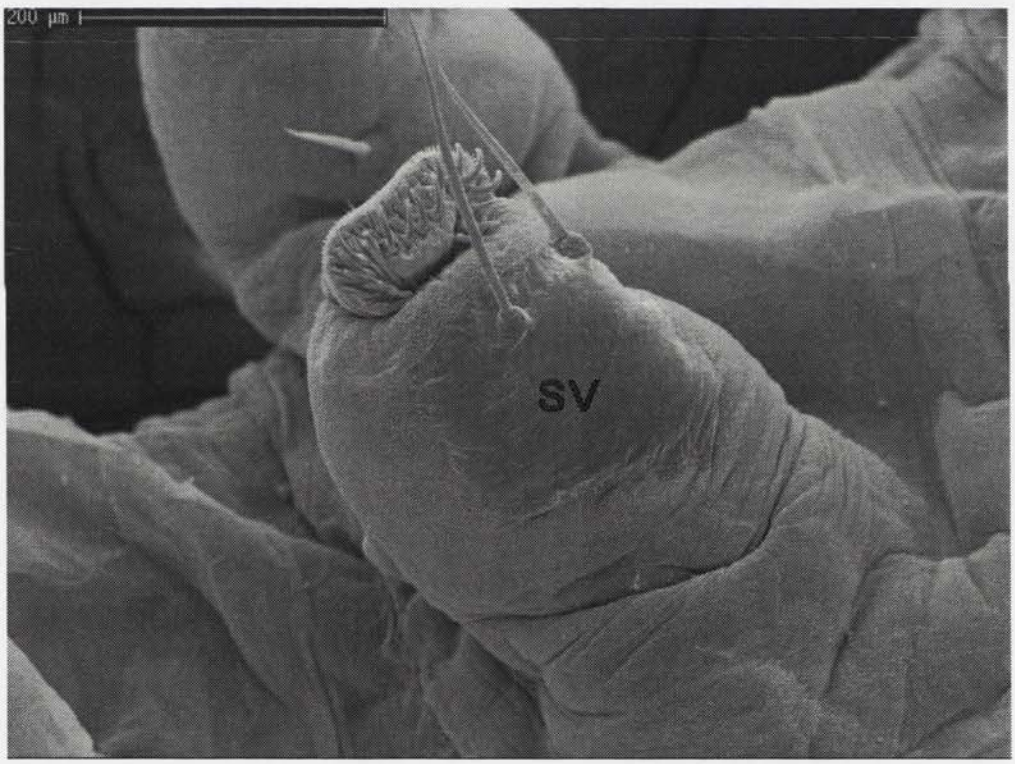


Fig. 428: *Carthaea saturnioides* (Carthaeidae), caterpillar (L1) – abdominal proleg with undivided SV-sclerite (SV).

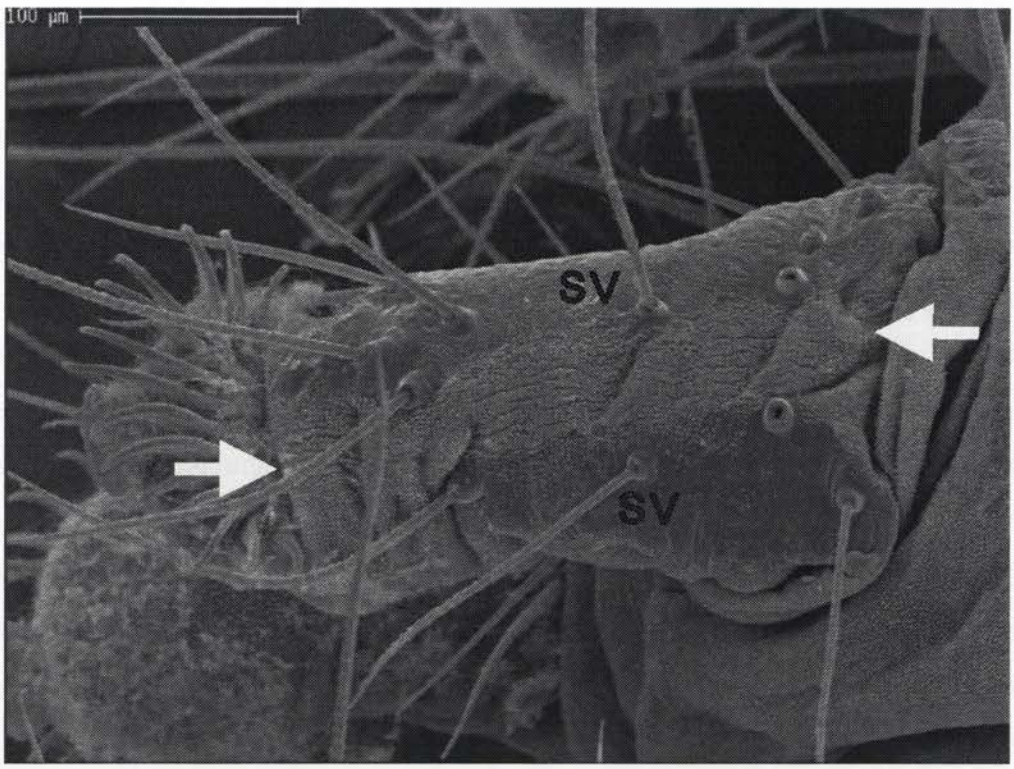


Fig. 429: *Anthela rubicunda* (Anthelidae), caterpillar (L1) – SV-sclerite (SV) of abdominal proleg divided by a median, membranous strip (yellow arrows).

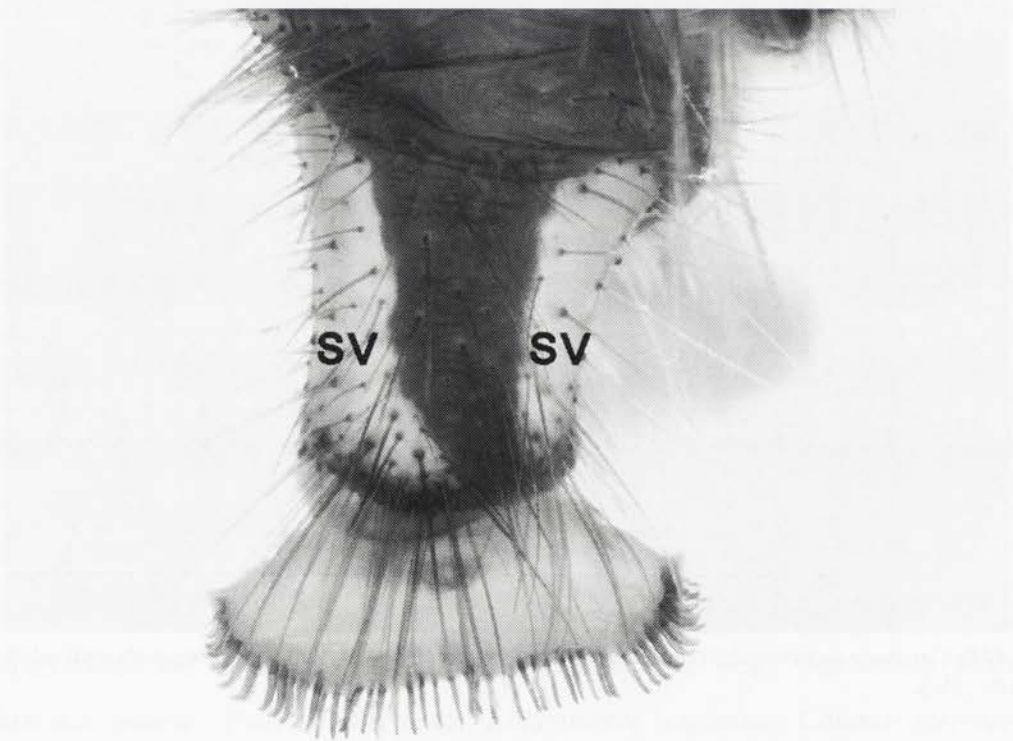


Fig. 430: *Anthela astata* (Anthelidae), caterpillar (Lm) [impinging light] – white (transparent) SV-sclerite (SV) of abdominal proleg divided by a median, membranous, dark strip.

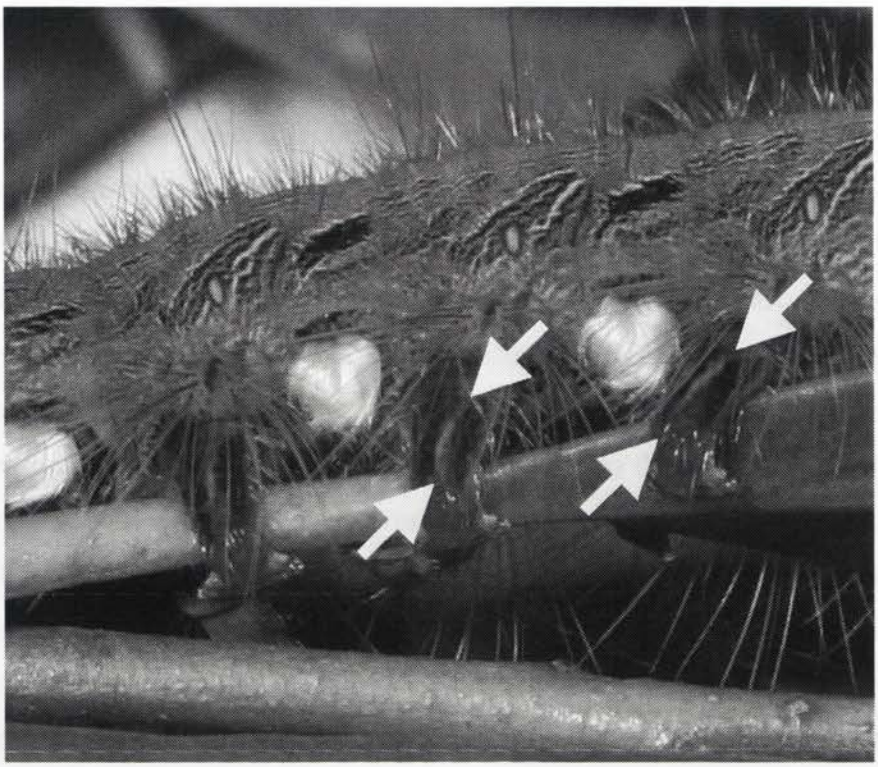


Fig. 431: *Porela* sp. (Lasiocampidae), caterpillar (L5) – dark SV-sclerite of abdominal prolegs divided by a median, membranous, pale strip (between two arrows).

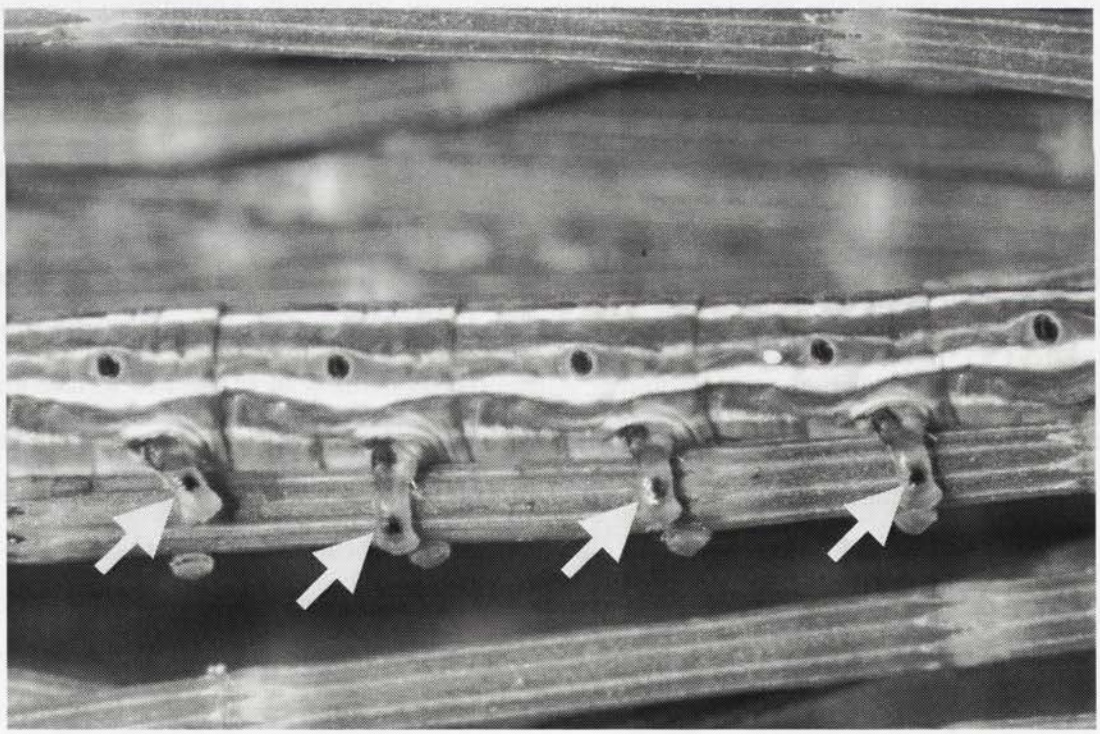


Fig. 432: *Munychryia senicula* (Anthelidae), caterpillar (L6) – prolegs with an undivided, dark SV-sclerite (yellow arrows); note the colour pattern of longitudinal stripes.

Minet (in Lemaire & Minet [1998]) proposed 4 autapomorphies in support of the monophyly of the Anthelidae:

1. Fore wing with an oblique fold or cross-bar between R and Rs1, near the apex of the areole (Lemaire & Minet [1998]). The uniqueness of this structure had already been noted by Turner (1904), who – unlike Minet – stated correctly that the cross-bar extends from Rs2 over Rs1 as far as R in some species. This apomorphy has been included in my analyses as character H.48 / C.47.
2. Fore wing without spinarea (Lemaire & Minet [1998]). The spinarea are cuticular spines arranged in a patch on the ventral side of the anal area of the fore wing (Minet 1991), which together with a similar patch on the metascutum supposedly functions as a wing-locking mechanism if the wings are at rest (e.g., Kristensen 2003b: 85). This structure is well developed in many Lepidoptera, but it is absent in all families of the bombycoid complex, except for the Lasiocampidae. As Minet (1994; in Lemaire & Minet [1998]) assumed the Lasiocampidae to be the sistergroup of the Anthelidae, he interpreted the absence of this structure in Anthelidae as an autapomorphy of the family. This autapomorphy of the family Anthelidae stands or falls with the hypothesis of the sistergroup relationship between Lasiocampidae and Anthelidae based on other characters. Even if this hypothesis is correct, this autapomorphy has no practical value as it is a loss common to many lepidopteran families.
3. Hind wing with base of M2 distinctly closer to M3 than to M1 (Lemaire & Minet [1998]). This arrangement of veins in the hind wing was originally part of the third synapomorphy of the Lasiocampoidea, namely the proximity of M2 to M3 in fore and hind wing (Minet 1991). Subsequently, Minet (1994) restricted this character to the fore wing, because M2 is slightly closer to M1 in the hind wing of *Chionopsyche*, which he regarded as possibly "the most primitive lasiocampid genus" (Minet 1994: 69). Apparently, Minet (1994, in Lemaire & Minet [1998]) assumed the proximity of M2 to M1 to be the condition present in the hypothetical ground plan of the Lasiocampidae and Lasiocampoidea, which is not justified by the presence of this condition in *Chionopsyche*. Seemingly on this basis Minet (in Lemaire & Minet [1998]) proposed the proximity of M2 to M3 in the hind wing as an autapomorphy of the family Anthelidae, despite this condition being present in all Lasiocampidae other than *Chionopsyche*, as well as in many macrolepidopteran families (e.g., some

Callidulidae, Drepanidae, Geometridae and Noctuidae).

4. Abdominal segment A1 of male with postspiracular conical projections of tergal origin (Lemaire & Minet [1998]). This seemingly unique modification is not restricted to Anthelidae but present in some Eupterotidae. It is used and discussed as character H.37.

In summary, none of the apomorphies of Minet (1986, 1991, 1994, in Lemaire & Minet [1998]) discussed above support the monophyly of his proposed groupings convincingly, except for the cross-bar in the fore wing of the Anthelidae. The vast majority of his apomorphies occurs not only in the taxa he named, but additionally also in numerous other families (often some of them mentioned by himself). Many of his apomorphies are compared against hypothetical ground plans of taxa hypothesized to be sistergroups, which stands or falls with these phylogenetic hypotheses. Minet's ground plans often seem to be derived by equation with the "most primitive" member of that group, a taxon with particularly many plesiomorphic structures. This method ignores that such seemingly "primitive taxa" can possess apomorphic structures, too, and the method is neither based on *a priori* Hennigian outgroup comparison nor on cladistic *a posteriori* ground plan reconstruction. Based on the postulated phylogenetic hypotheses and hypothetical ground plans, Minet often used the occurrence of a structure in different parts of his tree (homoplasies) as support for more than one monophylum, often without drawing attention to it. Further, many of Minet's characters are reductions, losses or simple structures, which do not provide strong support for any hypothesis of homology. These principle shortcomings of Minet's proposed apomorphies are not restricted to the ones discussed above, but apply to most of his characters. An annotated list of these characters is given below (Appendix P.2).

P.2) Annotated list of bombycoid apomorphies proposed by Minet

(Compiled from Minet 1991, 1994 and Lemaire & Minet [1998])

bombycoid complex	
proposed autapomorphy	**comment**
Larval prolegs with secondary setae.	Mere presence of secondary setae provides hardly any indication of homology. Also present in some Noctuoidea and Minet's "A-G" group.
Imago without functional ocelli.	Reduction or loss. Also present in Drepanidae, Uraniidae, Geometridae, Notodontidae, Hepialidae and some Cossidae.
Mesepimeron and meron with a long line of junction.	Relative to incorrectly determined ground plan (*Oenosandra boisduvalii* = Noctuoidea) only.
Maxillary palpi of the pupa entirely concealed or only indicated by minute triangular sclerites.	Two different conditions united. Reduction of maxillary palpi linked to very homoplastic reduction of proboscis. Also present in some Noctuoidea and Minet's "A-G" group.
Adult mesonotum with the dorsal extremities of the prescutal clefts varying from moderately distant from each other to distinctly joined together.	Relative to hypothetical ground plan of Macrolepidoptera only, which does not exclude presence in Noctuoidea or Minet's "A-G" group. Also present in Hedylidae and *Oenosandra boisduvalii* (Oenosandridae).

Mimallonoidea (Mimallonidae)	
proposed autapomorphy	**comment**
On the dorsal surface of the abdomen of the pupa, presence of conspicuous grooves that have dentate edges and lie along the anterior margins of abdominal segments A2-A7.	Seemingly a unique apomorphy of Mimallonidae.
Antenna of the male imago unevenly bipectinate, provided proximally with well developed rami, distally with shorter rami, which may even disappear entirely.	Simple reduction, which occurred repeatedly within several families, e.g., Bombycidae, Saturniidae, Notodontidae, Limacodidae and Cossidae.
Proboscis short to absent.	Simple reduction or loss, which occurred repeatedly within numerous families, e.g., Anthelidae, Sphingidae, Lymantriidae and Arctiidae.
Second segment of the labial palpus short, its length never exceeding that of segment 1.	Unusual reduction, which is probably an apomorphy of Mimallonidae.
Hind tibiae without medial spurs.	Simple loss, which occurred in at least some taxa of most macrolepidopteran families (e.g., Lasiocampidae, Anthelidae, Endromidae and Mirinidae).
In the hind wing, vein Sc+R strongly arched beyond wing base.	Simple curving of a single vein. Also present in many other families (e.g., Lasiocampidae, Lemoniidae, Eupterotidae, Sematuridae and Callidulidae).

Lasiocampoidea (Lasiocampidae+Anthelidae)	
proposed autapomorphy	**comment**
Imago with a sexually dimorphic fore leg, the female epiphysis varying from distinctly reduced to entirely absent.	Simple reduction or loss, which is likely to be linked to the reduction of antennae in females. Also present in Endromidae, Mirinidae, some Eupterotidae and some Saturniidae.
Fore wing vein M2 arising closer to M3 than to M1.	Superficial description of relative position of a vein, which can be caused by multiple modifications. Also present within many other families (e.g., some Pyraloidea, Drepanidae, Noctuoidea, Eupterotidae, Endromidae, Sphingidae and Bombycidae).
Female hind wing without frenular bristles.	Simple loss, which is likely to be linked to the almost sessile behaviour of the females. Also present in many other families (e.g., Endromidae, Mirinidae, Saturniidae, Lemoniidae, some Eupterotidae and some Brahmaeidae).
Mandible of the mature larva provided with secondary setae.	The mere presence of secondary setae provides hardly any indication for homology. Also present in Eupterotidae, Apatelodinae and some Saturniidae (*Hemileuca nevadensis*).
Each ventral proleg showing, in lateral view, a "vertical" membranous area which may lie either medially, thus dividing the SV plate into two parts, or posteriorly, thus giving an elongate shape to the SV plate.	Structural differences between families and differences in degree of sclerotization within families. Also present in some Eupterotidae, Apatelodinae and Bombycinae.

Bombycoidea	
proposed autapomorphy	**comment**
In the last stage larva, fore coxae distinctly fused anteriorly.	Difficult to identify due to differences in size, degree of sclerotization and extent of fusion of coxae. Also present in some Anthelidae (*Anthela basigera*). Absent in Apatelodinae, some Eupterotidae and Carthaeidae.
Segment A8 of the larva with the D1 setae arising from a middorsal scolus, sometimes replaced by a conical protuberance (the scolus often being better developed in younger larvae).	Unspecific merger of verrucae, which also occurs in some Lasiocampidae (e.g., *Entometa*) and several Anthelidae (e.g., *Chelepteryx*, *Anthela basigera* and *A. excellens*). Absent in Eupterotidae, Apatelodinae, *Lemonia* and some Saturniidae (e.g., *Salassa*).
Fore wing venation with Rs1/Rs2 closely parallel to or fused with branch Rs3/Rs4.	Simple relative position of veins and unjustified assumption that all fusions originated from the closely parallel condition. Also present in Anthelidae, except for wider distance between branches (closely approximated in *Chelepteryx*).
Male genitalia with the "flexors" of the valvae arising from the tegumen, not from the vinculum.	No modification present (series of mistakes by Kuznetzov & Stekolnikov 1985), muscle attaches to dorsal end of vinculum as in other Macrolepidoptera.

Eupterotidae+Bombycidae+Endromidae+Mirinidae+Saturniidae	
proposed autapomorphy	**comment**
Pupa with the proboscis cases shortened to a varying extend.	Equivalent to simple reduction or loss of the proboscis, which occurred repeatedly within numerous families, e.g., Mimallonidae, Anthelidae, Lasiocampidae, Sphingidae, Lymantriidae and Arctiidae.
In the adult, maxillary palpi vestigial, without a distinct segmentation.	Simple reduction or loss linked to reduction of proboscis. Also present in numerous other Lepidoptera (e.g., Lasiocampidae and Anthelidae).
Fore wing with all Rs branches stalked together.	Poorly defined; merger of Rs branches in Bombycidae is not homologous, but possibly homologous condition also present in Lemoniidae and Brahmaeidae. Merger of Rs branches, as defined by Minet (1994), occur additionally in numerous families, e.g., Geometridae and various families of the Noctuoidea.
Metepimeron provided, in lateral view, with a vertical (or slightly oblique) strip of weakly sclerotized cuticle, which reaches the ventral edge of the epimeron.	Weak area near middle of metepimeron, which can be membranous, partly/weakly sclerotized or strongly sclerotized (Lasiocampidae). Occasionally a strongly sclerotized median area with a fold (?) indicating the secondary nature of the sclerotization (e.g., Carthaeidae, for which Minet (1994) implies the absence of the membranous area). Also present in *Munychryia senicula* (Anthelidae; partly weakly sclerotized, but distinct; distinctly sclerotized in *Chelepteryx chalepteryx*, *Anthela adriana*, *A. acuta* group, *Pterolocera*). Very large membranous area in *Oenosandra boisduvalii* (Oenosandridae). Difficult to interpret, more extensive screening required. Possibly the presence of a membranous area is the plesiomorphic condition, with a tendency towards a secondary sclerotization of the area.
Fore femora concealed in the pupa.	According to Minet (1994) "widespread in the bombycoid complex", but absent in Sphingidae, which Minet incorrectly equated with being the ground plan condition for the proposed clade Carthaeidae+Lemoniidae+Brahmaeidae+Sphingidae.

Endromidae+Mirinidae+Saturniidae	
proposed autapomorphy	**comment**
Posterior arm of the mesepimeron wholly divided by a transverse area of weakly sclerotized cuticle.	The definition of this apomorphy is difficult. In most taxa a gap in the sclerotization of the mesepimeron extends dorsad, almost reaching the pleural membrane. This weakened area is part of a fold or overlap (posterior side overlapping anterior part), and in taxa with an overlap the weak sclerotization and line of overlap reach the pleural membrane. The difference between almost and distinctly reaching the pleural membrane is small, but the variation in shape and position of this weakly sclerotized overlap is strong. This character certainly requires some more detailed comparative morphology. An overlap that distinctly reaches the pleural membrane is also present in *Ganisa plana* (Eupterotidae), *Munychryia senicula*, *Pterolocera* sp. (both Anthelidae), *Carthaea saturnioides* (Carthaeidae), *Apatelodes* (Bombycidae: Apatelodinae) and, according to Minet (1994), Phiditiinae (Bombycidae).
In the fore wing venation, Rs1 and Rs2 either entirely fused or stalked for a very long distance (the free section of Rs1 being much shorter than the distance between its origin and that of the free section of Rs3).	Simple distal shift of fork in Rs1/Rs2, which is a general tendency and also present in Eupterotidae, Lemoniidae and Sphingidae.
In both sexes, hind wing entirely devoid of frenulum.	Simple loss, which also occurred in various other families, e.g., Lasiocampidae, Lemoniidae and some Brahmaeidae.

Endromidae+Mirinidae	
proposed autapomorphy	**comment**
Imago with the labial palpi never 3-segmented.	Relatively unusual loss, which differs between the two families (Endromidae short and non-segmented, Mirinidae 2-segmented), possibly an autapomorphy of the group. A reduction of the number of segments to one or two is also present in some Saturniidae (Urotini), which most probably is a convergence.
Fore leg epiphysis with a pronounced sexual dimorphism, that of the female varying from reduced to wholly absent.	Simple reduction or loss that is likely to be linked to the reduction of antennae in females. Also present in Lasiocampidae, Anthelidae,some Eupterotidae and some Saturniidae.
Tibial spurs numbering 0-2-2.	Simple loss, which occurs in at least some taxa of most macrolepidopteran families (e.g., Mimallonidae, Lasiocampidae and Anthelidae).
Fore wing with a long "anal loop", the length of which equals or exceeds half the length of the fused section of the anal veins.	Simple, but unique change in relative position of the anal veins – an autapomorphy of the group.

Carthaeidae+Lemoniidae+Brahmaeidae+Sphingidae	
proposed autapomorphy	**comment**
In both wings, vein CuP absent or replaced by a fold.	Simple reduction or loss, which occurs in almost all families of the bombycoid complex and most other Macrolepidoptera. Postulation as apomorphy based on proposed sistergroup relationship with a clade including Bombycidae, in which CuP is retained.
In hind wing venation, Sc+R closely parallel to a section of Rs lying before or beyond the end of the discal cell.	Relative position of veins only. Probably not homologous in Carthaeidae (diverges from cell much further basally than in other families). Also present in Axiidae, Callidulidae and Drepanidae.
Adult abdomen with the lateral bars of dorsum I distinctly produced laterad, in the rear.	Present in many other families, possibly extreme in Anthelidae and some Eupterotidae (lateral spine).
Female abdomen with the posterior third of venter 7 either membranous or very weakly sclerotized.	Simple reduction, which is often present in the group consisting of Eupterotidae, Bombycidae, Endromidae, Mirinidae and Saturniidae.
Adult mesothorax with the "lower" sector of the precoxal suture distinctly prolonged up to the anapleural cleft.	According to Minet (1994) also present in most other taxa of the bombycoid complex, except for *Mirina* (Mirinidae). The postulation as an apomorphy for this group can only be based on the unjustified equation of the condition present in *Mirina* with the one of the ground plan of the group Eupterotidae, Bombycidae, Endromidae, Mirinidae and Saturniidae.
Adult mesothorax without parepisternal membrane.	The parepisternal membrane varies in size and extent. It can be distinctly present or absent within a family, e.g, present in *Ganisa plana* and absent in *Eupterote* sp. (both Eupterotidae). It is distinctly present in Lasiocampidae, Oenosandridae and Geometridae, but apart from the monophylum proposed by Minet also absent in the Anthelidae, Saturniidae and Bombycidae (incl. Apatelodinae) I examined.

Lemoniidae+Brahmaeidae+Sphingidae	
proposed autapomorphy	**comment**
Metanotum of the pupa conspicuously sculptured.	Without a specific pattern a very simple character, which also occurs within several other families (e.g., Eupterotidae, Saturniidae and Endromidae); see discussion in Oberprieler & Duke 1994: 233-235.
In the adult, maxillary palpi at most 2-segmented.	Simple reduction or loss linked to reduction of proboscis. Also present in numerous other Lepidoptera (e.g., some Lasiocampidae, Lemoniidae, Eupterotidae, Endromidae, Mirinidae and Saturniidae).
Posterior "arm" of the mesepimeron distinctly shortened, its weakly sclerotized area lying near the rear end of the meron-epimeron junction line.	This character, which is present in most families of the bombycoid complex, is [incorrectly] assumed to be apomorphic for the proposed monophylum due to the hypothesized sistergroup relationship with Carthaeidae. In Carthaeidae the membranous area is said to be located further posteriorly than in the proposed monophylum, at about the position shown in Fig. 36 of Minet 1994. This is not the case, the membranous area is located even anteriorly of the posterior end of the meron-epimeron junction. The structure probably observed by Minet in the specified position is the suture between the mesepimeron and metanepisternum. This "apomorphy" requires more detailed examination.
In the hind wing, vein Sc+R approximated to the postdiscal section of Rs (i.e. that section of Rs which leaves the discal cell).	Relative position of veins only, which is also present in Axiidae and Drepanidae.

On each side of the adult mesoscutum, "notal incision" dorsally extended into a fairly narrow, tapering cleft.	Simple reduction of sclerotization, also present in other families, e.g., Lasiocampidae, Anthelidae and Eupterotidae (proposed autapomorphy of the family).
All Rs branches stalked together in the fore wing.	Poorly defined; also present in Lemoniidae and Brahmaeidae. Merger of Rs branches, as defined by Minet (1994), occur additionally in numerous families, e.g., Geometridae and various families of the Noctuoidea.
Female hind wing without frenular bristles.	Simple loss, which is likely to be linked to the almost sessile behaviour of the females. Also present in many other families (e.g., Lasiocampidae, Anthelidae, Mirinidae, Saturniidae and some Eupterotidae).
In the male abdomen, sternum 8 distinctly smaller than sternum 7.	Simple reduction, which according to Minet (1994) occurs in "several bombycoid taxa".
In the male abdomen, intersegmental membrane 8-9 dorsally provided with scales.	Structurally unspecific/simple and according to Minet (1994) also present in a few other bombycoid taxa. Possibly an autapomorphy of the group.

APPENDIX Q:

USED TAXONOMIC NAMES WITH AUTHOR AND YEAR

Acanthobrahmaea SAUTER, 1967

Acherontia styx (WESTWOOD, 1847)

Actias artemis (BREMER & GREY, 1853)

Actias luna (LINNAEUS, 1758)

Aglaopus pyrrhata (WALKER, 1866)

Aglia tau LINNAEUS, 1758

Agrius convolvuli (LINNAEUS, 1758)

Agrius godarti (W.S. MACLEAY, [1826])

Agrotis infusa (BOISDUVAL, 1832)

Agrotis ipsilon (HUFNAGEL, 1766)

Alompra roepkei pella TAMS, 1953

Amorpha juglandis (SMITH, 1797)

Andraca theae (MATSUMURA, 1909)

Andraca WALKER, 1865

Antheraea HÜBNER, 1819

Antheraea pernyi (GUÉRIN-MÉNÉVILLE, 1855)

Antheraea polyphemus (CRAMER, 1776)

Apanteles FÖRSTER, 1862

Apatelodes PACKARD, 1864

Apatelodes pudefacta DYAR, 1904

Apina callisto (ANGAS, 1847)

Apona WALKER, 1856

Argema mimosae (BOISDUVAL, 1847)

Aroa cometaris (BUTLER, 1887)

Arsenura armida (CRAMER, 1779)

Arsenura ciocolatina DRAUDT, 1930

Arsenura xanthopus (WALKER, 1855)

Artace WALKER, 1855

Artace cribraria (LJUNGH, 1825)

Attacus lemairei PEIGLER, 1985

Aurivillius fuscus (ROTHSCHILD, 1895)

Balacra WALKER, 1856

Bathyphlebia eminens (DOGNIN, 1891)

Bombyx LINNAEUS, 1758

Bombyx huttoni WESTWOOD, 1847

Bombyx mandarina (MOORE, 1872)

Bombyx mori (LINNAEUS, 1758)

"*Borrelina anthelus*" DAY, COMMON, FARRANT & POTTER, 1953

Brahmaea WALKER, 1855

Brahmaea certhia (FABRICIUS, 1793)

Brahmaea tancrei AUSTAUT, 1896

Brahmophthalma MELL, [1930]

Brahmophthalma hearseyi (WHITE, 1862)

Calliteara pura (T.P. LUCAS, 1892)

Carthaea saturnioides WALKER, 1858

Cercophana venusta (WALKER 1856)

Ceridia mira ROTHSCHILD & JORDAN, 1903

Charletonia feideri SOUTHCOTT, 1966

Chionopsyche montana AURIVILLIUS, 1909

Chondrostega LEDERER, 1858

Cicinnus BLANCHARD, 1852

Coenotes eremophilae (T.P. LUCAS, 1891)

Coloradia BLAKE, 1863

Corvus LINNAEUS, 1758

Cotana serranotata (T.P. LUCAS, 1894)

Cricula trifenestrata treadawayi NÄSSIG, 1989

Crinocraspeda HAMPSON, 1892

Crinocraspeda torrida (MOORE, 1879)

Cyanoxorides CAMERON, 1903

Dactyloceras MELL, [1930]

Dactyloceras widenmanni (KARSCH, 1895)

Danaus plexippus (LINNAEUS, 1758)

Daphnusa ocellaris WALKER, 1856

Decachorda AURIVILLIUS, 1898

Dirphia HÜBNER, 1819

Discophlebia catocalina R. FELDER, 1874

Eacles imperialis (DRURY, 1773)

Eacles imperialis opaca (BURMEISTER, 1878)

Ebbepterote expansa (T.P. LUCAS, 1891)

Echthromorpha intricatoria (FABRICIUS, 1804)

Endromis OCHSENHEIMER, 1810

Endromis versicolora (LINNAEUS, 1758)

Enicospilus STEPHENS, 1835

Ennomos autumnaria (WERNEBURG, 1859)

Entometa WALKER, 1855

Entometa fervens (WALKER, 1855)

Eosia insignis LE CERF, 1911

Epicoma HÜBNER, 1819

Epiphora mythimnia (WESTWOOD, 1849)

Eremaea TURNER, 1915

Eremaea coralliphora (LOWER, 1900)

Eriogaster lanestris (LINNAEUS, 1758)

Euglyphis HÜBNER, 1820

Euproctis HÜBNER, 1819

Euproctis baliolalis (SWINHOE, 1892)

Eupterote HÜBNER, 1820

Eupterote pallida (WALKER, 1855)

Euthrix laeta austrina (DE LAJONQUIÈRE)

Euxoa messoria (HARRIS, 1841)

Ganisa WALKER, 1855

Ganisa plana WALKER, 1855

Gastridiota adoxima (TURNER, 1902)

Gastropacha OCHSENHEIMER, 1810

Genduara WALKER, 1856

Genduara fola (SWINHOE, 1902)

Goodia kuntzei (DEWITZ, 1881)

Gotra gilberti (TURNER, 1919)

Gynanisa WALKER, 1855

Hemileuca WALKER, 1855

Hemileuca nevadensis STRETCH, 1872

Hopliocnema brachycera (LOWER, 1897)

Hoplojana rhodoptera (GERSTÄCKER, 1871)

Hypsidia niphosema (LOWER, 1908)

Indomyrlaea auchmodes (TURNER, 1905)

Iridomyrmex MAYR, 1862

Janomima mariana (WHITE, 1843)

Kunugia austroplacida HOLLOWAY, 1987

Kunugia fae ZOLOTUHIN, TREADAWAY & WITT, 1997

Laelia obsoleta (FABRICIUS, 1775)

Laothoe populi (LINNAEUS, 1758)

Lemonia HÜBNER, 1820

Lemonia balcanica (HERRICH-SCHÄFFER, 1847)

Lemonia dumi (LINNAEUS, 1761)

Lemonia sardanapalus STAUDINGER, 1887

Lemonia taraxaci ([DENIS & SCHIFFERMÜLLER], 1775)

Leptocneria reducta (WALKER, 1855)

Leptus charon SOUTHCOTT, 1991

Leucophlebia afra KARSCH, 1891

Lioscinella australiensis SPENCER, 1978

Lissopimpla KRIECHBAUMER, 1889

Loepa MOORE, 1860

Loepa diversiocellata BRYK, 1944

Lonomia WALKER, 1855

Ludia WALLENGREN, 1865

Lymantria nephrographa TURNER, 1915

Macromphalia FELDER, 1874

Macrothylacia rubi (LINNAEUS, 1758)

Malacosoma HÜBNER, 1820

Malacosoma neustria (LINNAEUS, 1758)

Manduca sexta (LINNAEUS 1763)

Marumba tigrina GEHLEN, 1936

Megalopyge opercularis (SMITH, 1797)

Melanergon BETHUNE-BAKER, 1904

Micragone WALKER, 1855

Micragone cana (AURIVILLIUS, 1893)

Mimallo amilia (CRAMER 1780)

Mirina christophi (STAUDINGER, 1887)

Monarda oryx DRUCE, 1896

Mustilia gerontica WEST,1932

Netelia producta (BRULLÉ, 1846)

Ocinara WALKER, 1856

Ocinara ficicola (WESTWOOD & ORMEROD, 1889)

Odonestis GERMAR, 1812

Odonestis erectilinea (SWINHOE, 1904)

Oenochroma vinaria GUENÉE, 1857

Oenosandra boisduvalii NEWMAN, 1856

Olceclostera BUTLER, 1878

Olceclostera seraphica (DYAR, 1906)

Oncopera alboguttata TINDALE, 1933

Opodiphthera eucalypti SCOTT, 1864

Opodiphthera helena (WHITE, 1843)

Opsirhina albigutta WALKER, 1855

Opsirhina alphaea (FABRICIUS, 1775)

Opsirhina lechriodes (TURNER, 1911)

Oxytenis HÜBNER, 1819

Panacela lewinae (LEWIN, 1805)

Panacela nyctropa (TURNER, 1922)

Panacela syntropha TURNER, 1922

Paonias myops (SMITH, 1797)

Paralaea GUEST, 1887

Paralaea jarrah MCQUILLAN, YOUNG & RICHARDSON, 2001

Paralaea porphyrinaria (GUENÉE, 1857)

Paralebeda crinodes uniformis HOLLOWAY, 1976

Pararguda rufescens (WALKER, 1855)

Parusta thelxinoe FAWCETT, 1915

Periga WALKER, 1855

Pernattia brevipennis (WALKER, 1865)

Pernattia chlorophragma (TURNER, 1924)

Pernattia pusilla (DONOVAN, 1805)

Phalaena LINNAEUS, 1758

Pheidole WESTWOOD, 1839

Phiala WALLENGREN 1860

Phiala arrecta DISTANT, 1899

Phiala costipuncta (HERRICH-SCHÄFFER, [1855])

Phyllalia patens (DE BOISDUVAL, 1847)

Pinara cana WALKER, 1855

Pinara divisa (WALKER, 1855)

Poecilocampa populi (LINNAEUS, 1758)

Poloma angulata WALKER, 1855

Porela WALKER, 1855

Preptos SCHAUS, 1892

Prismosticta BUTLER, 1880

Prismosticta tiretta SWINHOE, 1903

Pselaphelia AURIVILLIUS, 1904

Pselaphelia flavivitta (WALKER, 1862)

Pselaphelia gemmifera (BUTLER, 1878)

Pseudanapaea transvestita HERING, 1931

Quentalia ephonia (STOLL, 1791)

Rhabdosia patagiata (AURIVILLIUS, 1911)

Rhinolophus megaphyllus GRAY, 1834

Rhodinia fugax (BUTLER, 1877)

Rhyssa semipunctata KIRBY, 1883

Sabalia WALKER, 1865

Sabalia picarina WALKER, 1865

Sabatinca barbarica PHILPOTT, 1918

Samia cynthia (DRURY, 1773)

Smerinthus LATREILLE, 1802

Smerinthus cerisyi KIRBY, 1837

Smerinthus jamaicensis (DRURY, 1773)

Smerinthus ocellata (LINNAEUS, 1758)

Sphingonaepiopsis obscurus (MABILLE, 1880)

Spiramiopsis comma HAMPSON, 1901

Stoermeriana DE FREINA & WITT, 1983

Synoecha marmorata (T.P. LUCAS, 1891)

Syntherata janetta (WHITE, 1843)

Syssphinx quadrilineata (GROTE & ROBINSON, 1867)

Taylorimyia iota (JOHNSTON & TIEGS, 1921)

Teleogryllus commodus (WALKER, 1869)

Therinia buckleyi JORDAN, 1924

Therinia HÜBNER, 1823

Theronia tuberculicollis (CAMERON, 1912)

Tolype austella FRANCLEMONT, 1973

Trabala WALKER, 1856

Trabala vishnou (LEFEBVRE, 1827)

Trichiura crataegi (LINNAEUS, 1758)

Trichophiala devylderi AURIVILLIUS, 1879

Trictena MEYRICK, 1890

Trictena argyrosticha TURNER, 1929

Trogoptera althora SCHAUS, 1928

Urota sinope (WESTWOOD, 1849)

Usta angulata ROTHSCHILD, 1895

Vegetia JORDAN, 1922

Xenosphingia JORDAN, 1920

Xenosphingia jansei JORDAN, 1920

APPENDIX R:

FIGURE ABBREVIATIONS

Male genital structure sclerites		
A	=	anellus
AC	=	anal cone
C	=	coecum
CL	=	clasper
CO	=	cornutus
DE	=	ductus ejaculatorius
G	=	gnathos
GA	=	gnathos arm (lateral)
GP	=	gnathos plate (median)
J	=	juxta
M	=	manica
MF	=	mesal fold
MP	=	mesal protrusion
P	=	phallus
S	=	saccus
SS	=	subscaphium
T	=	transtilla
TE	=	tegumen
TR	=	transverse ridge
U	=	uncus
V	=	valva
VA	=	valva apodeme
VAL	=	valva apodeme lobe
VE	=	vesica
VI	=	vinculum

Male genital structure muscles		
m1	=	muscle *m1*
m2	=	muscle *m2*
m3	=	muscle *m3*
m4	=	muscle *m4*
m5	=	muscle *m5*
m6	=	muscle *m6*
m7	=	muscle *m7*
m10	=	muscle *m10*
m29	=	muscle *m29*

Female genital structures		
AA	=	apophysis anterior
AG	=	accessory gland
AGR	=	accessory gland reservoir
AP	=	apophysis posterior
AN	=	antrum
BC	=	bursa copulatrix
CD	=	common duct of accessory gland
DB	=	ductus bursae
DS	=	ductus seminalis
GC	=	genital chamber
LA	=	lamella antevaginalis
LP	=	lamella postvaginalis
OV	=	ovipositor
S8	=	abdominal sternite VIII
T8	=	abdominal tergite VIII