Pseudogyris gen. nov. (Lepidoptera: Lycaenidae), a new genus for two rare thecline butterflies from New Guinea, including the description of a new species

Michael F. Braby[1,2] and Chris J. Müller[3]

1. Division of Ecology and Evolution, Research School of Biology, RN Robertson Building, 46 Sullivans Creek Road, The Australian National University, Acton, ACT 2601, Australia; 2. Australian National Insect Collection, GPO Box 1700, Canberra, ACT 2601, Australia; 3. Australian Museum, 6 College Street, Sydney, NSW 2010, Australia.

Date of issue online: 18 March 2022
Zoobank Registered: urn:lsid:zoobank.org:pub:8D349BA6-11E1-4D23-9BFF-A62DDB24F88E
Electronic copies (ISSN 2575-9256) in PDF format at: https://journals.flvc.org/troplep; https://zenodo.org; archived by the Institutional Repository at the University of Florida (IR@UF), http://ufdc.ufl.edu/ufir; **DOI**: 10.5281/zenodo.6360550

Abstract: The lycaenid tribe Ogyrini Waterhouse & Lyell, 1914 is endemic to the Australian Region, where it is restricted to mainland New Guinea and Australia. It currently includes 15 species, all assigned to the genus *Ogyris* Angas, 1847, and most of these are endemic to Australia. One species, *Ogyris meeki* (Rothschild, 1900) from mainland New Guinea, has been rarely collected, being previously known only from nine specimens (7 ♂, 2 ♀). However, comparative study of the morphology, including adult wing structure and genitalia, and wing color pattern elements based on examination of existing and additional material (9 ♂, 3 ♀), indicate that *O. meeki* comprises a complex of two species, and differs fundamentally from *Ogyris* by 14 unique characters, many of which are considered to be synapomorphies. We therefore propose a new genus, *Pseudogyris* **gen. nov.**, and a new species to classify this unusual pair of species, which are among the largest and perhaps most spectacular theclines. Unlike *Ogyris*, *Pseudogyris meeki* (Rothschild, 1900) **comb. nov.** and *Pseudogyris brandti* **sp. nov.** are restricted to mainland New Guinea (West Papua and Papua of Indonesia, and Papua New Guinea) and the neighboring island of New Ireland (PNG), where they occur in tropical lowland rainforest and lower montane forest. The two species of *Pseudogyris* are allopatric, being separated by the Central Cordillera, with *P. meeki* **comb. nov.** restricted to the southern lowlands and *P. brandti* **sp. nov.** to the northern lowlands and New Ireland.

Resumen: La tribu Ogyrini Waterhouse & Lyell, 1914 de la Lycaenidae es endémica de la región Australiana, donde está restringida a la parte continental de Nueva Guinea y Australia. Actualmente incluye 15 especies del género *Ogyris* Angas, 1847, y la mayoría de éstas son endémicas de Australia. La especie, *Ogyris meeki* (Rothschild, 1900) de la parte continental de Nueva Guinea, ha sido recolectada pocas veces, y sólo se conocían nueve especímenes (7 ♂, 2 ♀). Sin embargo, el estudio comparativo de la morfología, incluyendo la estructura del ala y las genitalias de los adultos y los elementos del patrón de color del ala, basados en el examen de material existente y adicional (9 ♂, 3 ♀), indica que *O. meeki* comprende un complejo de dos especies y difiere fundamentalmente de *Ogyris* por 14 caracteres únicos, muchos de los cuales se consideran sinapomórficos. Por lo tanto, proponemos el nuevo género *Pseudogyris* **gen. nov.** y una nueva especie para dar cabida a este inusual conjunto de especies, las cuales se encuentran entre las más grandes y quizás más espectaculares theclines. A diferencia de *Ogyris*, *Pseudogyris meeki* (Rothschild, 1900) **comb. nov.** y *Pseudogyris brandti* **sp. nov.** están restringidas a la parte continental de Nueva Guinea (Papua Occidental y Papua de Indonesia, y Papua Nueva Guinea) y la vecina isla de Nueva Irlanda (PNG), donde se encuentran en la selva tropical de tierras bajas y en la selva montana baja. Las dos especies de *Pseudogyris* son alopátricas y están separadas por la Cordillera Central, con *P. meeki* **comb. nov.** restringida a las tierras bajas del sur y *P. brandti* **sp. nov.** a las tierras bajas del norte y Nueva Irlanda.

Key words: Australian zoogeographic region, biosystematics, taxonomy, Theclinae, tropical forest, vicariance biogeography

INTRODUCTION

The lycaenid genus *Ogyris* Angas, 1847 belongs to the monotypic tribe Ogyrini Waterhouse & Lyell, 1914 and is endemic to the Australian Region (Eliot, 1973). It currently includes 15 species, of which 13 are restricted to the Australian mainland and the adjacent islands of Melville and Kangaroo Islands (Field, 1999; Braby, 2000; Williams & Hay, 2001; Schmidt & Hughes, 2006; Schmidt, 2007; Braby & Douglas, 2008; Grund, 2010; Braby *et al.*, 2011). Only two species occur on mainland New Guinea (Parsons, 1998), one of which, *O. zosine* (Hewitson, 1853), also occurs widely in western, central, northern and eastern Australia (Braby *et al.*, 2014; Braby *et al.*, 2018), whereas the other, *O. meeki* (Rothschild, 1900) (Fig. 1), is restricted to mainland New Guinea (Papua and Papua New Guinea) (Parsons, 1998). The adults are robust and of medium

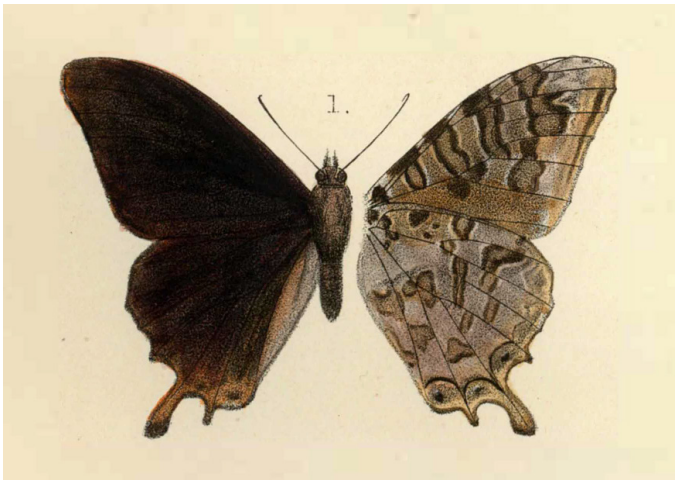


Figure 1. Syntype male of *Ogyris meeki* illustrated by Rothschild (1900).

to large size, and their flight is rapid and powerful. Many of them are brilliantly colored. The male lacks androconia (sex-scales), and a few species are strongly sexually dimorphic. All species in Australia occur in eucalypt open-forest, or eucalypt and acacia woodland or shrubland, with several species adapted to low rainfall areas of the semi-arid and arid zones (Braby, 2000). Only *O. meeki* occurs in rainforest, where it has been collected from lowland areas up to 800 m (Parsons, 1998).

Waterhouse & Lyell (1914) and Eliot (1973) provided a diagnosis of Ogyrini, noting that the forewing has 11 veins, with the radial branches R_4 and R_5 fused into a single vein R_{4+5} which reaches the costa just before the apex; vein Sc reaches the costa before the end of the discal cell; veins R_1 and R_2 are separated and not anastomosed; vein M_2 arises closer to vein M_1 than M_3; veins M_1 and $R_3 + R_{4+5}$ are connate at the apex of the discal cell in some species; the hind wing is generally without a tail and has the termen highly dentate and sometimes strongly produced at the end of vein CuA_2; the tornal lobe (between veins CuA_2 and 1A+2A) is present but weakly developed; the eye is smooth; the labial palpus is clothed with long appressed scales, with the third (apical) segment very short; and the male fore tarsus is fused into a single segment, terminating in a short down-turned point. Bethune-Baker (1905) provided illustrations of the male genitalia for 10 species of *Ogyris* and summarized their comparative differences; however, he did not examine the genitalia of *O. meeki*. The male genitalia of *Ogyris* possess juxta and brachia, and Parsons (1998) noted that the genitalia are simple and similar to those of *Arhopala* Boisduval, 1832, but the valva is shorter with the distal margin bearing a concave, U-shaped indentation. The female genitalia of *Ogyris* are also simple in which the ostium bursae is broad and weakly sclerotized, the ductus bursae is membranous, non-sclerotized and moderately long and expands into the corpus bursae, which is rounded and membranous without signa (Field, 1999). Braby (2000) observed that the antenna is about half or less than half the length of the forewing costa (nudum segments about 45 - Eliot, 1973); the flagellum of the antenna generally expands gradually into a slender club, but in the *O. olane* species-group it expands abruptly into a conspicuous club.

Bethune-Baker (1905), Parsons (1998) and Braby (2000) all independently noted that *O. meeki* is distinctive on account of fundamental differences in wing shape and pattern, including the presence of a long, clubbed tail on vein CuA_1, rather than a tornal projection on CuA_2. Indeed, Rothschild (1900, p. 274) stated "This is the largest and most aberrant species of the genus…" Braby (2000) remarked that *O. meeki* appears to be misplaced in this genus. Moreover, Parsons (1998, p. 395) perceptively stated that "…the ♂ und is somewhat variable, although this variability may eventually be found to correlate somewhat with geographical position when longer series of the species become available." However, comparative morphological studies of the adults, including the genitalia and other structures, have so far been lacking due to the paucity of material. D'Abrera (1971) and Parsons (1998) noted that the species was known only from a total of nine specimens (7 ♂, 2 ♀) in museum collections. Since that publication a further 11 specimens (8 ♂, 3 ♀) have come to our attention, preserved in three private collections (AYC, CJMC, MFBC; see Materials and Methods below). There is also an additional specimen (1 ♂) in KSP (Schröder, 2021). The purpose of this study is to examine the morphology of *O. meeki* and critically reassess its generic placement and taxonomic status based on these new acquisitions. Based on this comparative study we demonstrate that *O. meeki* comprises a complex of two species, one of which is new, and that both belong in a new genus distinct from *Ogyris*.

MATERIALS AND METHODS

There has been taxonomic confusion regarding the nomenclature of the genus-group name *Ogyris* because it was introduced twice by different authors, first by Angas (1847) with *O. amaryllis* Hewitson, 1862 as type species by subsequent monotypy, and then by Westwood (1851) in Doubleday and Westwood (1846-1852) with *O. abrota* Westwood, 1851 as type species by monotypy (Edwards, 1996; Edwards *et al.*, 2001). *Ogyris* Angas, 1847 was introduced for two undescribed species and thus the name was established without a nominal type species. Tepper (1893) was the first to correctly identify one of the figures illustrated by Angas (1847) as *Ogyris amaryllis*. This action was accepted by Edwards (1996) as the first reviser to include a valid species in *Ogyris* Angas; hence, *O. amaryllis* is the type species of *Ogyris* Angas by subsequent monotypy. Thus, prior to 1996, all published literature refers to *Ogyris* Westwood, 1851, which is a junior subjective synonym of *Ogyris* Angas, 1847.

Ogyris includes a number of informal species-groups according to similarities in adult phenotype, antennal structure and life history (Bethune-Baker, 1905; Braby, 2000). These groups are the *O. aenone* species-group of at least three species (*O. aenone* (Waterhouse, 1902), *O. ianthis* (Waterhouse, 1900) and *O. iphis* (Waterhouse & Lyell, 1914)), the *O. olane* species-group of three species (*O. oroetes* (Hewitson, 1862), *O. olane* (Hewitson, 1862) and *O. barnardi* (Miskin, 1890)), the *O. genoveva* species-group of two species (*O. genoveva* (Hewitson, [1853]) and *O. zosine* (Hewitson, [1853])), and the *O. idmo* species-group of four species (*O. otanes* (C. & R. Felder, 1865), *O. halmaturia* (Tepper, 1890), *O. idmo* (Hewitson, 1862) and *O. subterrestris* Field, 1999), which is closely related to the *O.*

genoveva species-group. *Ogyris amaryllis* (Hewitson, 1862) and *O. abrota* (Westwood, [1851]), as well as *O. meeki*, appear to be more isolated from these species-groups but their exact phylogenetic relationships are unclear.

Although Bethune-Baker (1905) illustrated the male genitalia of 10 species of *Ogyris* and provided diagnoses for each, his drawings are insufficient for modern comparative purposes. Since that publication the male genitalia have been illustrated for *O. genoveva* (Eliot, 1973), *O. subterrestris* (Field, 1999) and *O. halmaturia* (Braby & Douglas, 2008), whereas the female genitalia have been described and illustrated only for *O. subterrestris* (Field, 1999). We therefore dissected and examined the genitalia of both sexes of one species representing each of the various species-groups noted above, notably *O. abrota*, *O. aenone*, *O. amaryllis*, *O. olane*, *O. zosine* and *O. idmo*, for comparison with *O. meeki*. Dissection of the genitalia was performed using standard techniques: the entire abdomen was removed and placed in 10% KOH and boiled for 20 minutes, and then transferred to 30% ethanol for cleaning, dissection and examination. Completed dissections were fixed in 95% ethanol and then 100% isopropanol. The genitalia were placed in an alcohol-based gel in an excavated glass block and photographed using a Leica M205A microscope and were stacked using Helicon Focus 5.3 according to the technique of Su (2016). Terminology for genitalia follows Klots (1970) and Eliot (1973).

Adult size was estimated by measuring the length of the forewing, that is, the straight-line distance between the apex and base (i.e., the point of attachment of the wing with the thorax), using digital photographs or a digital caliper to an accuracy of 0.1 mm. Geo-coordinates (latitude and longitude) for each location were determined using Google Earth, converted to decimal degrees with a precision of approximately 10–100 km, and then plotted in ArcGIS version 10.7.1 using a projected coordinate system (WGS84_MGA_zone 55).

For species concept we follow Mayr's biological species concept based on phenotypic or morphological criteria, especially the reproductive structures, as a surrogate of reproductive isolation.

The following acronyms refer to repositories where specimens have been examined or deposited: **ANIC**: Australian National Insect Collection, Canberra, Australia; **AYC**: Akira Yagishita private collection, Japan; **NHMUK**: Natural History Museum, London, England (formerly British Museum of Natural History); **CJMC**: Chris J. Müller private collection, Sydney, Australia; **KONE**: National Insect Collection, Port Moresby, Papua New Guinea; **KSP**: Koleksi Serangga Papua, Jayapura, Indonesia (see Gassó Miracle, 2017); **MCZ**: Pierce Lab, Museum of Comparative Zoology, Harvard University, USA; **MFBC**: Michael F. Braby private collection, Canberra, Australia (now largely incorporated into ANIC); **MfN**: Museum für Naturkunde, Berlin, Germany (formerly Zoologisches Museum der Humboldt-Universität); **NMW**: Naturhistorisches Museum Wien, Vienna, Austria (The Natural History Museum Vienna).

TAXONOMY

***Pseudogyris* gen. nov.**

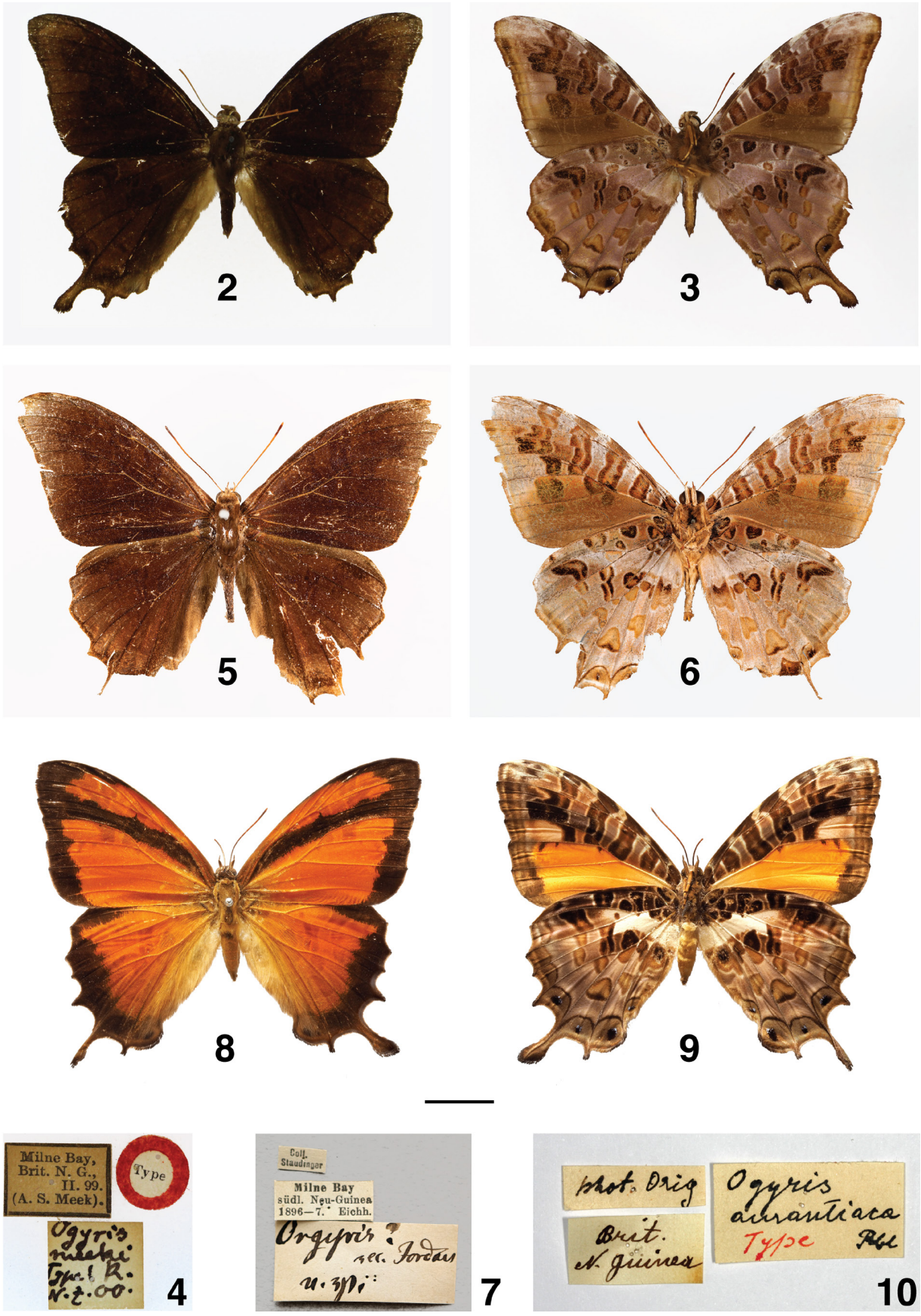
(Figs. 1-45)

http://zoobank.org/urn:lsid:zoobank.org:act:4C727BD8-3594-4669-8436-AE109F743B43

Type species. *Ogyris meeki* Rothschild, 1900 (designated here)

Diagnosis: Adults of *Pseudogyris* differ structurally from *Ogyris* in several fundamental ways. Although the wing venation (Figs. 23, 24) is similar to *Ogyris* (see Waterhouse & Lyell, 1914, Fig. X, p. 115), the forewing of male *Pseudogyris* differs in shape, being more strongly arched with the apex produced and termen distinctly concave. The hindwing of *Pseudogyris* has a prominent tail, which is long (ca. 6 mm) and spatulate at the end of vein CuA_1, whereas in *Ogyris* tails are absent. Although in three species of *Ogyris* (*O. genoveva*, *O. zosine* and *O. aenone*) there is a pronounced tornal projection at the end of vein CuA_2 and in two of these species (*O. genoveva* and *O. zosine*) there is an additional conspicuous projection at the end of vein M_3, in *Pseudogyris* there is no broad tornal projection but, rather, a small, narrow projection at the end of vein CuA_2, as well as a series of three smaller projections at the ends of veins M_1 to M_3. In contrast, in most species of *Ogyris* there is a series of five small projections from veins M_1 to CuA_2, giving the termen of the hindwing a dentate pattern. Also, the wings are larger than *Ogyris*: in male *Pseudogyris*, the forewing length (from base to apex) ranges from 30.3–36.5 mm (mean = 32.7 mm, $n = 15$), whereas in the four largest species of *Ogyris* (*O. genoveva*, *O. zosine*, *O. idmo* and *O. halmaturia*) the male forewing never exceeds 30 mm in length. The body (thorax and abdomen) of *Pseudogyris* is not as large or as robust relative to the size of the wings compared with *Ogyris*.

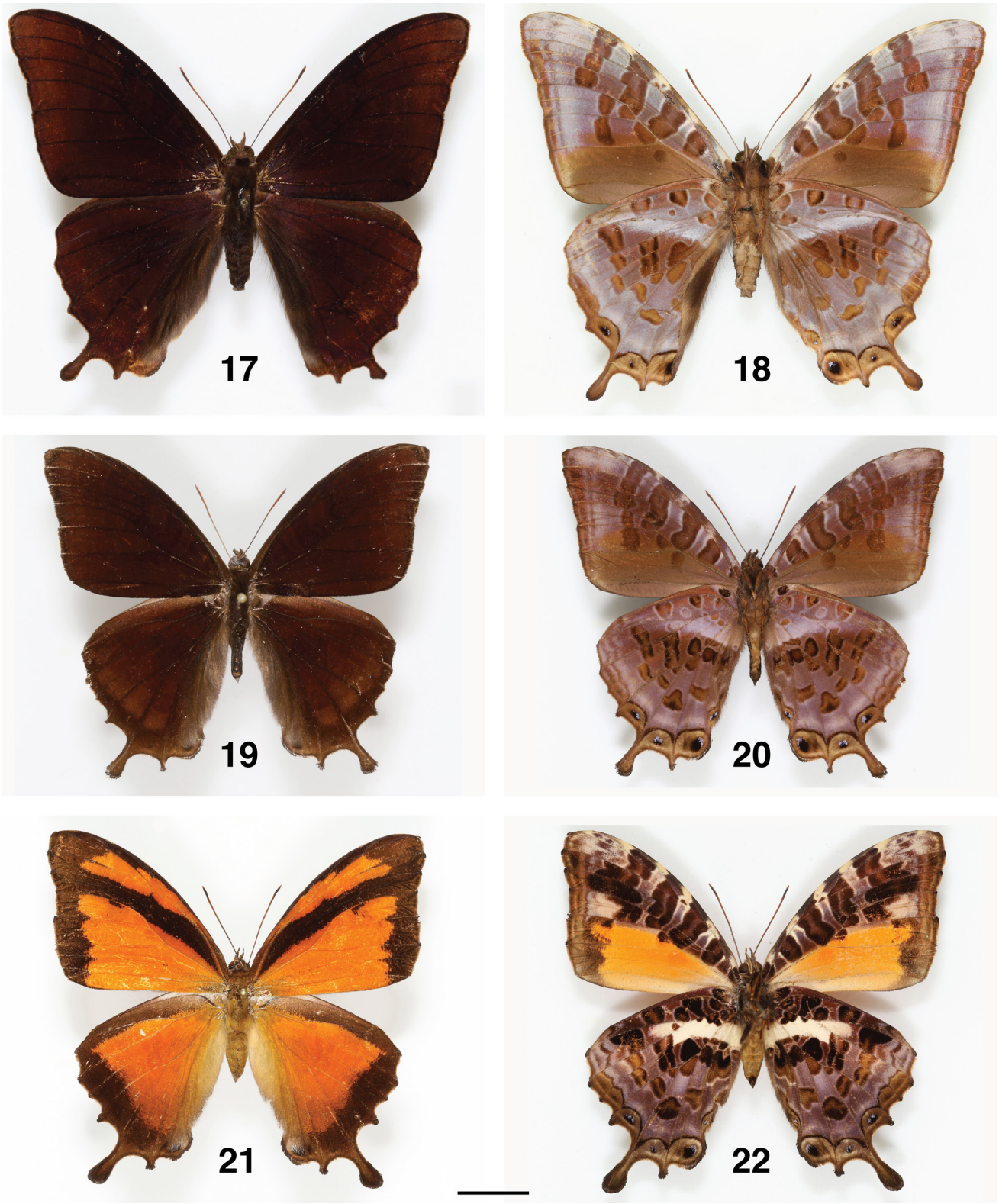
In addition, *Pseudogyris* differs from *Ogyris* by the following six wing color pattern characters. (1) The upperside of the wings in the male (Figs. 2, 5, 11, 13, 17, 19) have a different color pattern. In *Pseudogyris*, the color is uniformly dark brown with a deep purple suffusion, whereas in *Ogyris* the color is brighter purple, purplish-bronze, or metallic pale blue. (2) The upperside of the wings in the female (Figs. 8, 15, 21) have a different color pattern. In *Pseudogyris*, the ground color is bright orange, with the forewing possessing a broad black transverse band that extends from the base through the discal cell to the broad black termen with which it connects between veins M_2 and M_3, whereas the basal and central areas in females of most species of *Ogyris* are bright iridescent blue or purple. The inner edge of the black terminal band on the forewing in *Pseudogyris* is dentate, extending proximally along veins CuA_1 and CuA_2, whereas in *Ogyris* it is straight or evenly curved. In *Ogyris*, pronounced sexual dimorphism in which the female lacks iridescence scales occurs only in two species (*O. abrota* and *O. ianthis*), but these species do not have the broad black transverse band on the forewing that effectively divides the orange or yellow area into two separate patches, a pattern element which is unique to *Pseudogyris.* (3) The underside of the forewing in both sexes (Figs. 3, 6, 9, 12, 14, 16, 18, 20, 22) has a different color pattern. In *Pseudogyris*, there is



Figures 2-10. Type material of *Pseudogyris meeki* comb. nov.: (2-4) lectotype male of *Ogyris meeki*, showing upperside, underside and labels (NHMUK), © The Trustees of the Natural History Museum London; (5-7) paralectotype male of *Ogyris meeki*, showing upperside, underside and labels (MfN), © Museum für Naturkunde Berlin; (8-10) holotype female of *Ogyris aurantiaca*, showing upperside, underside and labels (NMW), © H. Bruckner photo collection. Scale bar = 10 mm.

Figures 11-16. Adults of *Pseudogyris meeki* comb. nov., showing: (11, 12) male upper- and underside, Yahukimo, Papua (AYC); (13, 14) male upper- and underside, Yahukimo, Papua (CJMC); (15, 16) female upper- and underside, Timika, Papua (AYC). Scale bar = 10 mm.

a basal spot followed by a series of three conspicuous broad brown bars in the discal cell, followed by a broad but variable postmedian band. The cell bars occur from the subbasal area to the discocellulars, and each bar extends from the costa to the cubital vein. The bars form a complex pattern, with each bar comprising a paler brown band or line broadly edged with darker chocolate brown and then narrowly edged with white or grey. In contrast, in *Ogyris* the basal spot is absent or reduced



Figures 17-22. Adults of *Pseudogyris brandti* sp. nov., showing: (17, 18) holotype male upper- and underside, Torricelli Mountains, Mokai, Papua New Guinea (ANIC); (19, 20) paratype male upper- and underside, Sorong, Doberai Peninsula, West Papua (AYC); (21, 22) paratype female upper- and underside, Avona, Kaimana, West Papua (AYC). Scale bar = 10 mm.

to a minute dot, and the cell bars are narrower, dark brown or black and usually edged with iridescent blue, with the two outer bars sometimes enclosing a narrow dark blue line. Moreover, the bars in *Ogyris* are shorter in length, extending between the radial and cubital veins and do not reach the costa. (4) The underside of the hind wing in both sexes (Figs. 3, 6, 9, 12, 14, 16, 18, 20, 22) has a different color pattern. In *Pseudogyris*, there is a series of variable but conspicuous discrete brown spots and markings which are edged with dark brown or black and then narrowly with grey, somewhat similar to the pattern

of *Arhopala antharita* Grose-Smith, 1894, whereas in *Ogyris* the pattern is far more complex, with the markings typically comprising a mosaic of irregularly shaped brown bands, edged narrowly with black, from the subbasal area to the postmedian area. In the *O. aenone* species-group, the markings are more discrete but faintly developed and less well defined. (5) The underside of the hindwing of *Pseudogyris* has a broad transverse submedian band, a pattern element which is absent in *Ogyris*. In *Pseudogyris*, the band is grey (male) or cream (female) and it extends from vein Rs through the discal cell to the dorsum. (6) The underside of the hindwing of *Pseudogyris* has a series of terminal lunules or crescent-shaped marks, with three of those between veins M_3 and 1A+2A, each enclosing a conspicuous black spot each of which has a patch of iridescent bluish-white scales; the largest of these spots comprises the tornal lobe. There is also a similar but smaller spot along the dorsum between veins 1A+2A and 3A. In *Ogyris*, these terminal and tornal marks and spots are absent.

The male genitalia of *Pseudogyris* (Figs. 30, 31, 39–44) are similar to those of *Ogyris*, but the valvae are more deeply divided or excavated apically into two long processes. In *Ogyris* (Figs. 33–38), the processes, when present, are more asymmetrical, with the lower process generally much shorter and the apex rounded posteriorly. The valvae in *Ogyris* are variable in shape: the apical indentation and bifurcated processes are well developed in *O. abrota* (Fig. 33), the *O. aenone* (Fig. 34) and *O. genoveva* (Fig 37) species-groups, less pronounced in *O. amaryllis* (Fig. 35), and poorly developed or absent in the *O. idmo* species-group (Fig. 38). In the *O. olane* species-group (Fig. 36), the valvae are long and narrow with the lower process residual or absent.

The female genitalia of *Pseudogyris* (Fig. 32) are similar to those of *Ogyris* with respect to the form of the sterigma of the ostium bursae, which comprises a simple sclerotized column. However, in *Pseudogyris*, the corpus bursae is exceptionally enlarged and elongated with the posterior half sclerotized, whereas in *Ogyris* the corpus bursae comprises a membranous rounded or oval-shaped sack that is not sclerotized. The corpus bursae is comparatively short in the *O. idmo* species-group; in *O. abrota*, there is a pair of weakly sclerotized signa located posteriorly. The shape of the ductus bursae is variable: in *Pseudogyris*, *Ogyris abrota*, *O. aenone* species-group and *O. olane* species-group it is relatively long and narrow and usually weakly sclerotized, in *O. amaryllis* it is short and narrow and weakly sclerotized, but in the *O. genoveva* and *O. idmo* species-groups it is relatively short and broad. In *Pseudogyris*, the ductus seminalis is located approximately midway between the ostium bursae and corpus bursae, whereas in *Ogyris* it is usually located near the anterior end of the ductus bursae close to the corpus bursae.

The morphology of the wing venation (Figs. 23, 24), antenna (Fig. 25), labial palpus (Fig. 26) and legs (Figs. 27-29) is similar to *Ogyris*. The number of segments of the flagellum in *Pseudogyris* ranges from 52-55, whereas in *Ogyris* it varies from 38 (*O. idmo* species-group - Field, 1999), 46 (*O. abrota*, *O. amaryllis*, *O. olane* species-group) to 56 (*O. genoveva* species-group).

Variation: The underside pattern of *Pseudogyris* varies among males, particularly the ground color, the form and extent of the brown markings and spots, and the shape of the brown postmedian band on the forewing. Available data suggest the underside pattern varies geographically and partitions into two distinct groups: (1) areas to the south of the Central Cordillera or Central Highlands of mainland New Guinea; and (2) areas to the north of the Central Cordillera. Investigation of these pattern differences indicates that there are in fact two species in the complex, with the latter group warranting specific status and a new name (see below).

Etymology: The genus-group name *Pseudogyris* is derived from the Greek word pseudos or pseudes, which means false, and refers to the fact that *Pseudogyris* is similar and closely related to, but otherwise taxonomically distinct from, *Ogyris*.

Distribution: *Pseudogyris* was previously known only from mainland New Guinea (Papua Province of Indonesia, and Papua New Guinea). However, over the past 20 years material has been collected from West Papua (AYC and MFBC) and New Ireland of Papua New Guinea (CJMC). Thus, spatial data of the known 21 specimens (16 ♂, 5 ♀) indicates that the geographical distribution of *Pseudogyris* (Fig. 45) extends from West Papua (including Sorong, Kaimana and Wasior), through Papua (including Timika, Lower Oetakwa River, Yahukimo and Jayapura) to Papua New Guinea (mainland PNG and New Ireland). In Papua New Guinea, it has been collected on the mainland from the Prince Alexander Range (CJMC), Torricelli Mountains (ANIC), Amahop near Maprik, Rawlinson Mountains Huon Peninsula, Mamai plantation near Port Glasgow (Parsons, 1998), and Milne Bay (Rothschild, 1900). It may also occur in New Britain, which lies between the New Guinea mainland and New Ireland. Most specimens appear to have been collected from lowland areas (<500 m) dominated by tropical forest; however, the altitudinal range is uncertain because the labels of most specimens do not report altitude. The highest recorded altitudes on the mainland include two males collected from the West Sepik Province: at approximately 650 m in the Prince Alexander Range (CJMC), and at 760 m (2,500 ft) from Mokai in the Torricelli Mountains by WW Brandt (ANIC). In central New Ireland, a male was collected in lower montane forest at approximately 1,100 m in the Schleinitz Mountains (CJMC). Thus, available spatial data suggests *Pseudogyris* is absent from the higher elevated mid-montane forest (1,600-2,100 m). As far as is known it does not occur together with *Ogyris zosine faciepicta* Strand, 1911, which is known from two males from the East Sepik and Northern Provinces (Parsons, 1998). *Ogyris zosine faciepicta* is the only taxon of *Ogyris* known to occur on mainland New Guinea.

Biology: Little is known of the biology of *Pseudogyris.* Adults have been collected in each month from September to April, as well as in June. Two males captured by one of us (CJM) were flying rapidly in the lower canopy approximately 6-8 m above the ground during the afternoon.

***Pseudogyris meeki* (Rothschild, 1900) comb. nov.**
(Figs. 1, 2-10, 11-16, 39-41, 45)

Ogyris meeki Rothschild, 1900: p. 274, pl. V fig 1. [genus *Ogyris* Westwood, 1851]

Ogyris meeki Rothschild. - Bethune-Baker (1905), pp. 271, 278; Rebel (1912), pp. 219-220; Meek (1913), p. 238; Seitz (1926), p. 940, fig. 161g; D'Abrera (1971), p. 321; D'Abrera (1990), p. 321; Common and Waterhouse (1972), p. 336; Common and Waterhouse (1981), p. 471; Parsons (1998), pp. 395-396, pl. 60 Figs. 1633-1635. [genus *Ogyris* Westwood, 1851]

Ogyris meeki (Rothschild, 1900). - Braby (2000), p. 693; Tennent (2006), pp. 39, 161. [genus *Ogyris* Angas, 1947]

Ogyris aurantiaca Rebel, 1912: pp. 219-221, Figs. 2, 3. [genus *Ogyris* Westwood, 1851]

Ogyris aurantiaca Rebel. - Seitz (1926), p. 941; D'Abrera (1971), p. 321; D'Abrera (1990), p. 321; Parsons (1998), p. 395. [genus *Ogyris* Westwood, 1851]

Material examined:

Lectotype: ♂ **PAPUA NEW GUINEA:** "Milne Bay, Brit. N. G., II. 99, (A. S. Meek).", "Ogyris meeki Type! R., N. z. 00.", "Type", "NHMUK 010923731" (NHMUK).

Paralectotype: ♂ **PAPUA NEW GUINEA:** "Milne Bay, südl. Nue Guinea, 1896-7, Eichh.", "Coll. Staudinger", "*Orgyris* [sic], sec. Jordan n. sp.", "http://coll.mfn-berlin.de/u/ca880d" (MfN).

Other material: 6♂, 3♀. **INDONESIA:** 1 ♂, 1 ♀ "Lower Oetakwa R., Dutch South N.G., 17.-28. Nov. 1910., (A.S. Meek)", "Specimen photographed by B. D'Abrera, 1970" (NHMUK); 1 ♀ "Timika, Irian Jaya, INDONESIA, NOV. 2001", "Genitalia No. MFB-125, P. meeki ♀" (AYC); 1 ♂ "Timika, Irian Jaya, INDONESIA, MAR. 2003" (AYC); 1 ♂ "Timika, Irian Jaya, INDONESIA, NOV. 2018" (AYC); 1 ♂ "Yahukimo, central Irian Jaya, INDONESIA, JAN. 2013", "Genitalia No. MFB-136, P. meeki ♂" (AYC); 1 ♂ "INDONESIA, Yahukimo Regency, JAN, 2013", "CJM-21-3225" [DNA leg voucher in MCZ] (CJMC). **PAPUA NEW GUINEA:** 1 ♀ "Brit. N. guinea", "Phot. Orig.", "Ogyris aurantiaca Rbl, Type" (NMW) [holotype of *Ogyris aurantiaca*]; 1 ♂ "Mamai Estate, near Amazon Bay, CeP" (KONE) as illustrated in Parsons (1998).

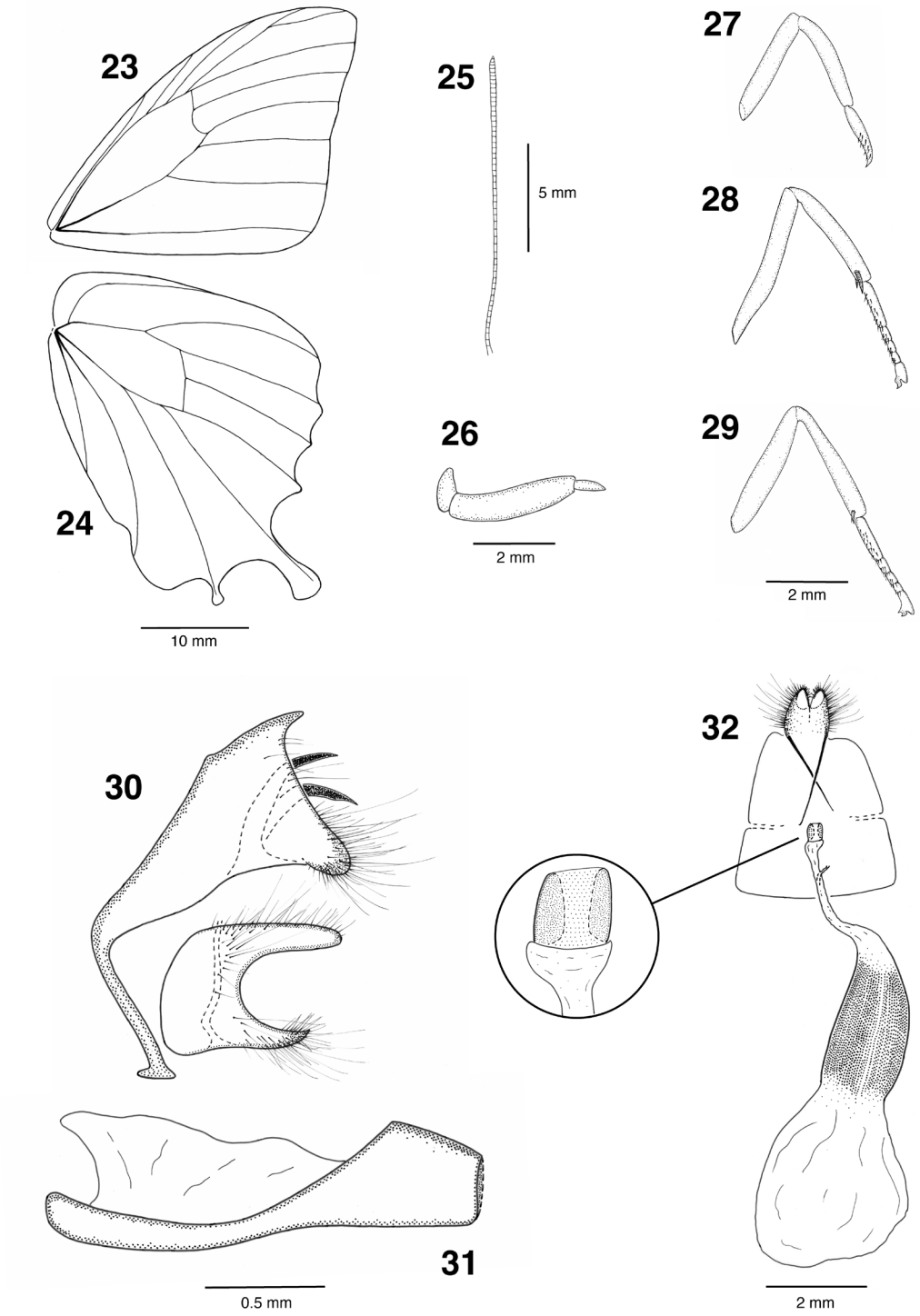
Diagnosis: *Pseudogyris meeki* males (Figs. 11-14), compared with *P. brandti* sp. nov. males, have the underside ground color darker purple or purplish-brown, the underside markings larger and more distinct (i.e., darker brown with pronounced white edges), a broader transverse submedian band on the hindwing, and the postmedian band on the forewing extended distally towards the termen between veins M_1 and M_3. The lower section of the forewing postmedian band between veins M_1 and CuA_1 is narrower and about half the width of the section between veins CuA_1 and CuA_2. Also, the double postmedian mark between veins M_3 and Rs on the underside of the hindwing has the outer edge distinctly curved (concave) in *P. meeki* males, whereas it is relatively straight in *P. brandti* sp. nov. males. In addition, adult males appear to be smaller in size (forewing length: 30.3-32.5 mm; mean = 31.4 mm, n = 8). The male genitalia of *P. meeki* (Figs. 39-41) differ fundamentally from those of *P. brandti* sp. nov. (Figs. 42-44) in the following respects: the apical processes of the valvae (in lateral view) are more widely divergent from one another, with the lower (ventral) process rounded apically and the upper (dorsal) process of uneven width; the uncus (in posterior view) is obtuse rather than rounded; the uncus lobes (in lateral view) are shorter and narrower and (in posterior view) relatively straight; the brachia are broader throughout their length and enlarged near the base; and the anterior margin of the tegumen (in dorsal view) is sinuate without the middorsal projection. Females of the two species are difficult to distinguish, but in *P. meeki* the cream transverse submedian band on the underside of the hindwing is slightly broader with a relatively straight posterior margin.

Remarks: Rothschild (1900) originally illustrated (Fig. 1) and described *Ogyris meeki* Rothschild, 1900 based on two syntype males from Milne Bay, Papua New Guinea, one of which was collected by A. S. Meek, but he did not designate a holotype. Of the two syntypes, one is housed in NHMUK (Figs. 2-4) and the other in the MfN Staudinger collection (Figs. 5-7). Parsons (1998) referred to the syntype in NHMUK as the 'holotype'. We interpret Parsons' (1998) incorrect reference to a holotype as a lectotype designation according to Article 74 of the ICZN (1999). It therefore follows that the second specimen in MfN automatically becomes a paralectotype.

Association of the sexes of *P. meeki* was first hypothesized by Meek (1913) and then later by D'Abrera (1971) and Parsons (1998), but to date has not been confirmed by captive breeding of the immature stages or by field observations on adult courtship or mating. However, we consider that the male and female illustrated here from Papua to belong to the same species given their similarities in size, underside pattern and the shape of the hindwing. At the time of description of *P. meeki* the female was unknown (Bethune-Baker, 1905; Seitz, 1926). Meek (1913, p. 97) collected a female some years later, noting that "I did not get a female specimen until the year 1910." Meek's female (as well as a second male) was collected from the Lower Oetakwa River, Papua, and is housed in NHMUK; it was subsequently illustrated by both D'Abrera (1971; 1990) and Parsons (1998).

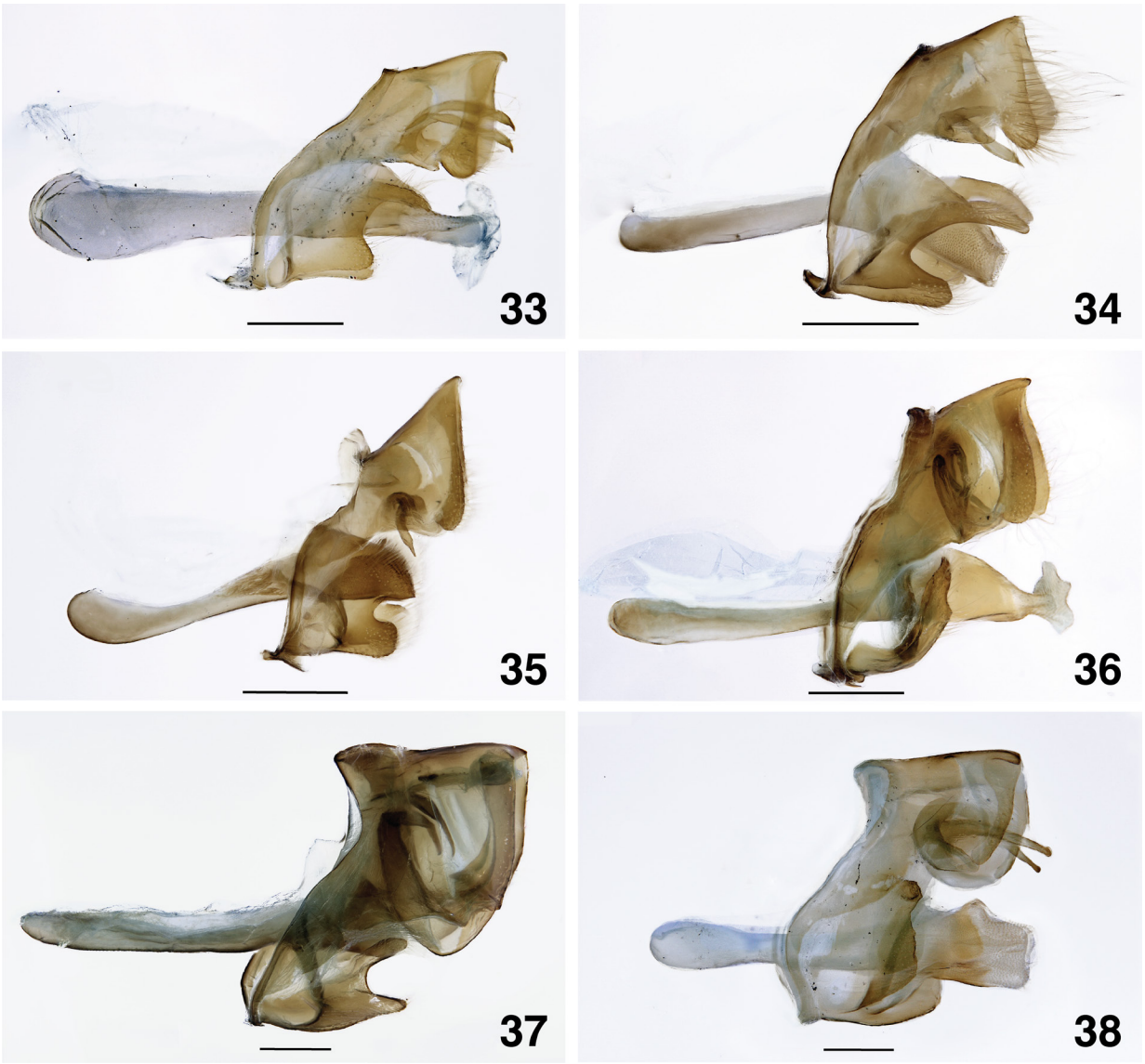
Hans Rebel (1861-1940) described and illustrated the species *Ogyris aurantiaca* Rebel, 1912 based on a single female from an unspecified location in southern Papua New Guinea (given as 'British New Guinea') (Rebel, 1912). Parsons (1998) considered the holotype female of *Ogyris aurantiaca* (Rebel, 1912) to be the opposite sex of the lectotype male of *Pseudogyris meeki* (Rothschild, 1900); he therefore synonymized *O. aurantiaca* as an objective junior synonym of *P. meeki*. Parsons (1998) stated that the whereabouts of the holotype female of *O. aurantiaca* is not known, but we have traced it in NMW (Figs. 8-10). Since *P. meeki* is restricted to areas south of the Central Cordillera and the far east of Papua New Guinea (see below), and British New Guinea refers to this same area of Papua New Guinea, it can be safely assumed that Rebel's type specimen came from within the distribution of *P. meeki*. Moreover, the *O. aurantiaca* holotype female agrees with two females of *P. meeki* from Papua south of the Central Cordillera, bearing a prominent, broad cream transverse submedian band on the underside of the hindwing. Therefore, we agree with Parsons in that *O. aurantiaca* is indeed synonymous with *P. meeki*.

The exact locality from which the *O. aurantiaca* holotype female was obtained, and the person responsible for the collection, may never been known. Rebel was an Austrian entomologist who specialized in Lepidoptera (Hermkens, 2013). He was keeper of the Lepidoptera collection of the Naturhistorisches Museum in Vienna, a post he held from 1897



Figures 23-32. Adult morphology of *Pseudogyris brandti* sp. nov., showing: (23, 24) wing venation of fore- and hindwings; (25) antenna; (26) labial palpus; (27-29) male fore-, mid- and hindlegs, (30, 31) male genitalia, lateral view with phallus removed, and phallus, lateral view; (32) *P. meeki* comb. nov. female genitalia, ventral view.

to 1932. He directed the Department of Zoology in 1923 and was the museum's Director General in 1925. Rebel secured vast acquisitions for the museum, and this included four accessions from New Guinea, between 1906 and 1912, though information for two of the purchases is unknown. The annual reports of the museum from 1906 to 1912 indicate that Karl Rechinger (botanist) and Rudolf Pöch (doctor, anthropologist and ethnologist) donated specimens they collected from New Guinea, in 1906 and 1911, respectively (Sabine Gaal-Haszler, pers. comm. 2021). It appears that Rechinger collected in German New Guinea, whereas Pöch spent nearly two years (1905-1906) in New Guinea, including three months in British New Guinea where he visited areas just north of Milne Bay (Goodenough and Collingwood Bays). In addition to anthropological objects, Pöch gathered geological data as well as biological specimens, such as mammals, birds, shells and reptiles (Hermkens, 2013). Thus, it is possible that the *O. aurantiaca* type was collected by Pöch in 1905/1906, possibly somewhere near Milne Bay, and



Figures 33-38. Male genitalia of *Ogyris*, lateral view: (33) *O. abrota*; (34) *O. aenone*; (35) *O. amaryllis*; (36) *O. olane*; (37) *O. zosine*; (38) *O. idmo.* Scale bars = 0.5 mm.

deposited by Pöch in NMW when he donated his collection in 1911; the species was subsequently described by Rebel in 1912.

Distribution: *Pseudogyris meeki* occurs on mainland New Guinea where it is known from lowland areas south of the Central Cordillera (Fig. 45). It has been recorded from Milne Bay, PNG (type locality) (Rothschild, 1900), Mamai plantation near Port Glasgow, PNG (Parsons, 1998), Lower Oetakwa River (NHMUK), Timika and Yahukimo (AYC, CJMC), Papua, Indonesia. Two females from Timika (AYC) and the Lower Oetakwa River, Papua (illustrated in D'Abrera, 1971; 1990; Parsons, 1998) are considered to belong here. Adults have been collected in the months of November and from January to March.

Pseudogyris brandti sp. nov.

(Figs. 17-22, 23-31, 42-44, 45)

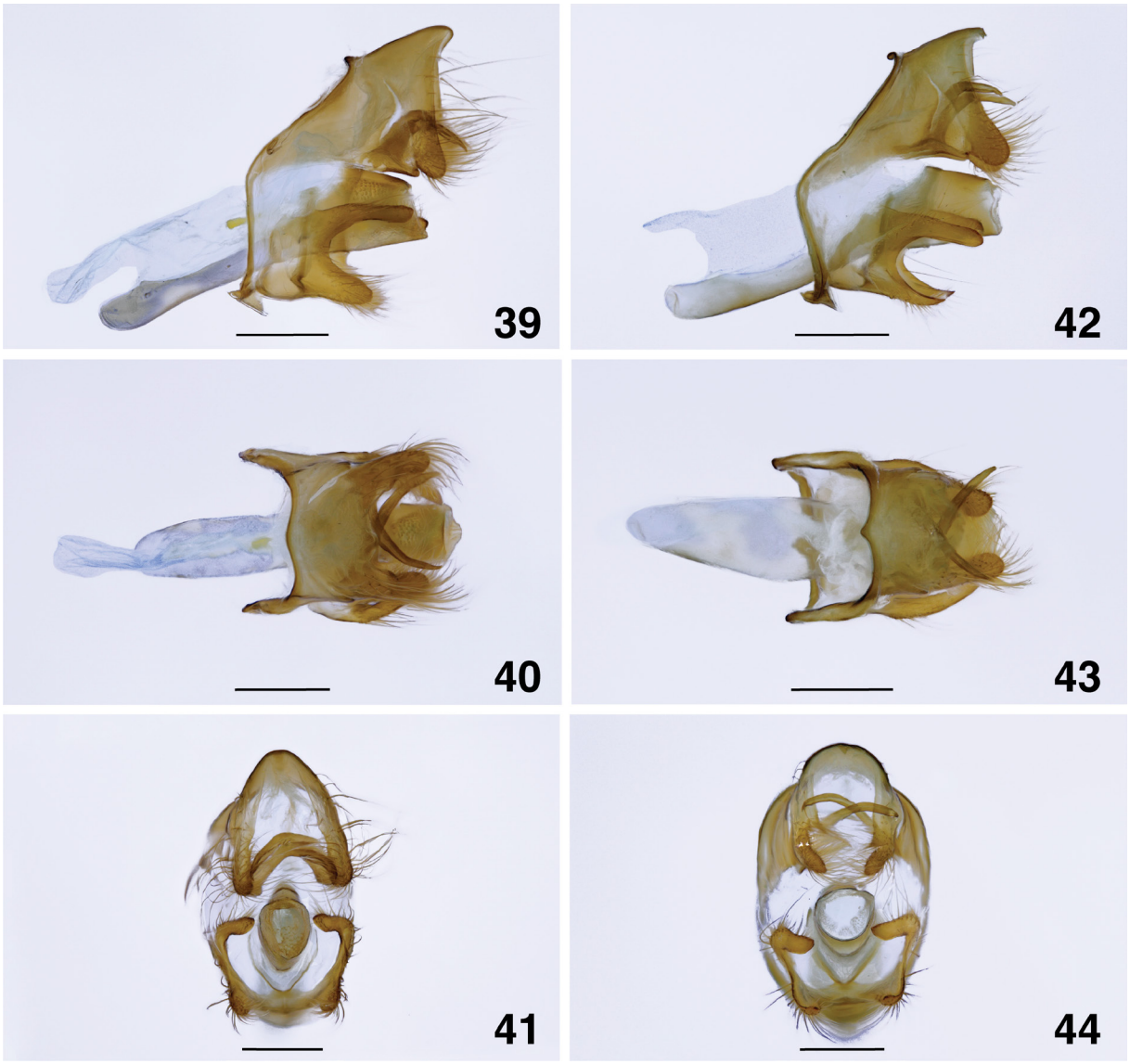
http://zoobank.org/urn:lsid:zoobank.org:act:436E93CB-8F3E-4207-91C4-585C20CC6DFE

Ogyris meeki Rothschild. - D'Abrera (1971), p. 321; D'Abrera (1990), p. 321; Parsons (1998), p. 395, pl. 60, Figs. 1628-1632. [genus *Ogyris* Westwood, 1851]

Material examined:

Holotype: ♂ **PAPUA NEW GUINEA:** "NEW GUINEA, Torricelli Mountains, Mokai, 2500 ft., 8 Dec. 1958-23 Jan. 1959, W. W. Brandt" (ANIC).

Paratypes: 5♂, 2♀. **INDONESIA:** 1 ♂ "Sorong, W-Irian, Nov. 1999", "Genitalia No. MFB-120, P. brandti ♂", "MFB-13-P039" [DNA leg voucher in MCZ], "M.F. Braby Collection, Donated ANIC 2020" (MFBC); 1 ♂ "Sorong, Doberai Pen., Irian Jaya, INDONESIA, Apr. 2005" (AYC); 1 ♀ "Avona, Kaimana. Etna, INDONESIA, Sep. 2006 (AYC); 1 ♀ "Wasior, Wondiwoi Mts., Wandammen Pen, Irian Jaya, INDONESIA, Dec. 2013" (AYC). **PAPUA NEW GUINEA:** 1 ♂ "Rawlinson Mts, inland Huon Gulf, (Keysser)", "Specimen



Figures 39-44. Male genitalia of *Pseudogyris*: (39-41) *P. meeki* comb. nov., showing lateral, dorsal and posterior views, Yahukimo, Papua (AYC); (42-44) *P. brandti* sp. nov., showing lateral, dorsal and posterior views, Sorong, West Papua (MFBC). Scale bars = 0.5 mm.

photographed by B. D'Abrera, 1970", "NHMUK 014047073" (NHMUK); 1 ♂ "PAPUA NEW GUINEA, Schleinitz Mts, New Ireland Province, ca. 1100m, 3.33 S, 151.94 E, Oct, 2005, C.J. Müller", "CJM-21-3223" [DNA leg voucher (RE-05-D041) in MCZ] (CJMC); 1 ♂ "PAPUA NEW GUINEA, Prince Alexander Range, West Sepik Province, ca. 650m, 3.52 S, 142.97 E, Jun. 2012, C.J. Müller", "CJM-21-3224" [DNA leg voucher in MCZ] (CJMC).

Other material: 2 ♂. **INDONESIA:** 1 ♂ "Jayapura, Papua" (KSP) as illustrated in Schröder (2021). **PAPUA NEW GUINEA:** 1 ♂ "Amahop, near Maprik, ESP" (KONE) as illustrated in Parsons (1998).

Diagnosis: *Pseudogyris brandti* males (Figs. 17-20), compared with *P. meeki* males, have the underside ground color paler lilac or lilac-grey with the underside markings smaller and less contrasted, a narrower transverse submedian band on the hindwing, and the postmedian band on the forewing of approximately even width but frequently displaced proximally between veins M_3 and CuA_2. This displaced, lower section of the forewing postmedian band is of even width, whereas in *P. meeki* the section between veins CuA_1 and CuA_2 is about twice the width of the adjacent section between veins M_3 and CuA_1. Also, the double postmedian mark between veins M_1 and Rs on the underside of the hindwing has the outer edge relatively straight in *P. brandti* males, whereas it is distinctly curved (concave) in *P. meeki* males. In addition, adult males appear to be larger (forewing length: 32.7-36.5 mm; mean = 34.3 mm, n = 7). The male genitalia of *P. brandti* (Figs. 42-44) differ fundamentally from those of *P. meeki* (Figs. 39-41) in the following respects: the apical processes of the valvae (in lateral view) are parallel with one another, with the lower process terminating in a spine and the upper process of uniform width; the uncus (in posterior view) is evenly curved rather than obtuse; the uncus lobes (in lateral view) are longer and broader and (in posterior view) inwardly curved towards their apices; the brachia are narrower and more slender throughout their length; and the anterior margin of the tegumen (in dorsal view) has a middorsal projection. Females of the two species are difficult to distinguish, but in *P. brandti* the cream transverse

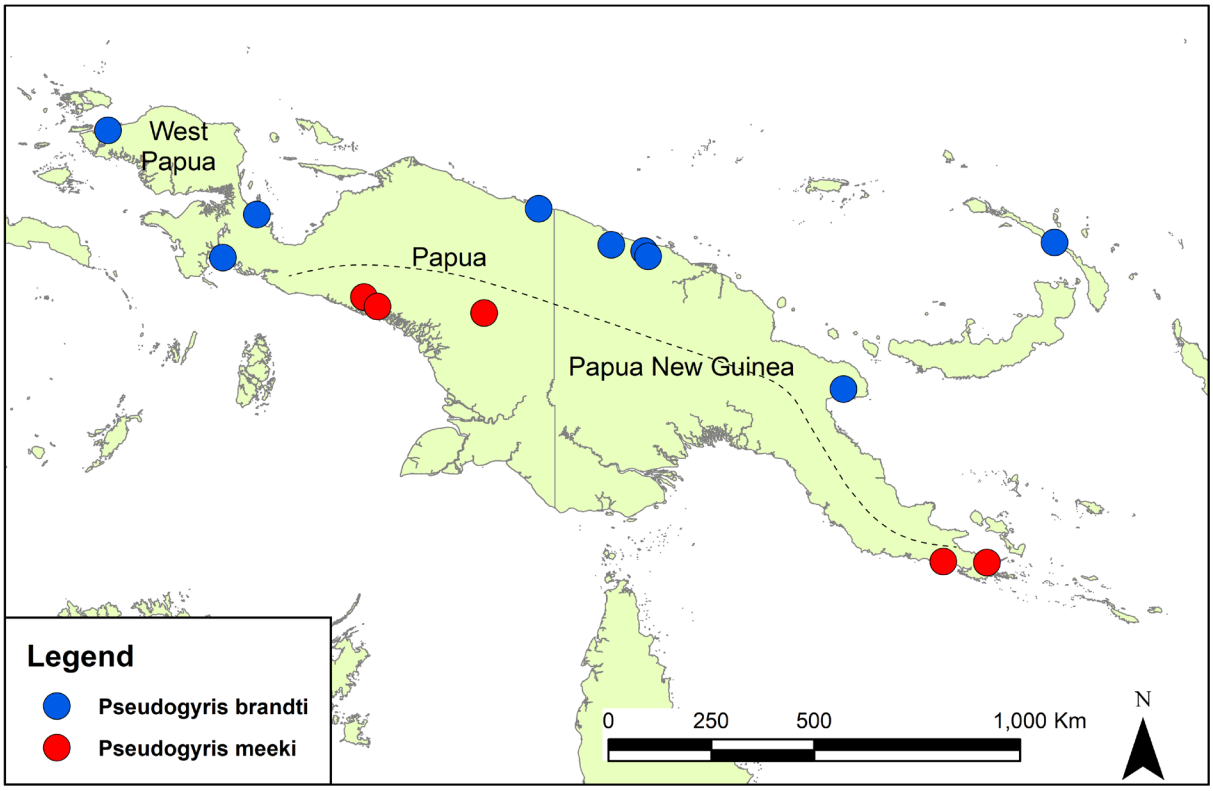


Figure 45. Distribution map of *Pseudogyris* and the geographical distribution of its two species *P. meeki* comb. nov. and *P. brandti* sp. nov. based on vouchered specimens in museum and private collections. Dashed line indicates approximate location of the Central Cordillera, a biogeographic barrier that divides the lowland areas of northern and southern mainland New Guinea.

submedian band on the underside of the hindwing is slightly narrower and constricted with the posterior margin concave.

Description:

Male: *Head*: eyes black; frons brown; labial palp clothed with brown piliform scales, a paler brown narrow mid-ventral line, third (apical) segment short and slender, second (middle) segment four times longer than third segment; antenna 14-15 mm long, flagellum with 52-55 segments (shaft 39-42, club 13-14), shaft gradually expands into club, shaft orange, club black tipped with orange. *Thorax*: dorsal surface black, ventral surface brown; legs brown; foreleg with tarsus fused into a single segment, terminating in a point; mid- and hindlegs each with a pair of tibial spurs. *Forewing*: length 36.5 mm (holotype); upperside uniformly dark brown with a deep purple suffusion (iridescent under white light), a narrow black terminal line, termen slightly concave; underside ground color lilac or lilac-grey, with posterior third of wing (below cubitus and CuA_2) brown, discal cell with a basal spot, followed by a series of three conspicuous broad purplish-brown subbasal, submedian and median bars extending from costa to cubital vein, each bar comprises a paler band broadly edged with darker purplish-brown and then narrowly with white or grey, a purplish-brown submedian spot between veins CuA_2 and 1A+2A below submedian bar, a purplish-brown median spot between veins CuA_1 and CuA_2 distal to submedian bar, median bar extends along discocellular veins into space between veins M_3 and CuA_1, a broad postmedian band from costa to vein CuA_2 often displaced proximally at vein M_3, pattern of postmedian band similar to discoceullar cell bars, a narrow purple subterminal line from veins M_1 to CuA_2, followed by a darker and broader terminal line from veins M_1 to just below CuA_2. *Hindwing*: upperside uniformly dark brown with a deep purple suffusion (iridescent under white light), a black terminal band that widens towards tornus, costa and dorsum paler brown, termen concave between veins with slight projections at end of veins Rs, M_1, M_2 and M_3, the largest of these projections on M_3, end of vein CuA_1 with a prominent spatulate tail, end of vein CuA_2 with a conspicuous projection, tornal lobe between veins CuA_2 and 1A+2A; underside ground color lilac or lilac-grey, a series of three subbasal spots, two or three submedian spots just below costa between veins $Sc+R_1$ and Rs, a broad grey transverse submedian band from vein Rs through discal cell to dorsum, a complex series of brown median and postmedian spots and markings frequently edged with dark brown or black, an irregular faint whitish subterminal line from veins Rs to 1A+2A, followed by a series of dark brown terminal lunules or crescent-shaped marks, those marks between veins M_3 and CuA_1, CuA_1 and CuA_2, CuA_2 and 1A+2A, and 1A+2A and 3A each enclose a brown area centered with a conspicuous black spot bearing a patch of iridescent bluish-white scales, the largest of these spots comprises the tornal lobe. *Abdomen*: dorsal surface black, ventral surface brown. *Genitalia*: vinculum (in lateral view) relatively straight but bent at an internal angle of ca. 135º approximately two-fifths along its length; saccus short; tegumen relatively large, broad and sclerotized; uncus evenly rounded (in posterior view) with a pair of lateral lobes, uncus lobes broad and long, extending beyond ventral surface of tegumen, and sclerotized with numerous setae; brachium (=gnathos) long and narrow, strongly curved, heavily sclerotized and terminating in a spine; valva deeply divided with a U-shaped indentation and bifurcated into two long apical sclerotized processes furnished with numerous setae, with upper (dorsal) process longer and of uniform width and inwardly curved, lower (ventral) process terminating in a spine; phallus (in lateral view) very broad posteriorly, coecum narrower beyond alula, cornutus absent.

Female: *Head*: similar to male; antenna 12-13 mm long, flagellum with 53 segments (shaft 39, club 14). *Thorax*: dorsal surface orange-brown, ventral surface brown; legs brown. *Forewing*: length 30.2-31.0 mm ($n = 2$); upperside orange, costa narrowly black, apex and termen broadly black with inner edge extending proximally along veins CuA_1 and CuA_2, a broad black curved transverse band extending from base through discal cell to termen between veins M_2 and M_3, termen slightly concave; underside ground color purplish-grey, with posterior third of wing (below cubitus and CuA_1) orange except for termen which is broadly brown, markings and pattern similar to male except spots and bands darker, postmedian band shorter (stops at vein CuA_1) with section between veins M_1 and M_3 broadly edged distally with dark purplish-brown, a broad whitish rectangular spot between veins M_3 and CuA_1 distal to postmedian band. *Hindwing*: upperside orange, costa and termen broadly black, dorsum paler orange, margin of wing similar shape to male but projections at the end of veins Rs, M_1, M_2 and M_3 more pronounced so that termen appears dentate; underside ground color purplish-grey, markings and pattern similar to male except spots and marks darker, broad transverse submedian band cream. *Abdomen*: dorsal surface orange-brown, ventral surface pale brown.

Remarks: This species has previously been confused with *P. meeki*. For example, a male specimen from the Rawlinson Mountains illustrated by D'Abrera (1971; 1990) and Parsons (1998) (plate 60, fig. 1632) and a further two males from Mokai and Amahop illustrated as *Ogyris meeki* by Parsons (1998) (plate 60, Figs. 1628-1631) are in fact *P. brandti*.

Etymology: The species-group name *brandti* is in honor of William Waldemar Brandt (1904-1982), who collected a fine specimen of this species, in 1958-59. Brandt spent many years (1949-1963) conducting field work throughout Papua New Guinea and he made a substantial contribution to knowledge of the entomology of the country, especially Lepidoptera (Upton, 1997).

Distribution: *Pseudogyris brandti* occurs on mainland New Guinea and New Ireland where it is restricted to lowland and lower montane areas (up to 1,100 m) north of the Central Cordillera (Fig. 45). It has been recorded from Sorong, West Papua (MFBC, AYC), Jayapura, Papua (KSP) (Schröder, 2021), and in Papua New Guinea from the Prince Alexander Range (CJMC), Mokai Torricelli Mountains (type locality) (ANIC) (also illustrated in Parsons, 1998), Amahop near Maprik (KONE) (illustrated in Parsons, 1998), the Rawlinson Mountains Huon Peninsula (NHMUK) (illustrated in D'Abrera, 1971; 1990; Parsons, 1998), and the Schleinitz Mountains in central New Ireland (CJMC). Two females from Avona, Kaimana and Wasior, Wondiwoi Mountains, Wandammen Peninsula, West Papua (AYC) are considered to belong here.

Adults have been collected in the months of June, from September to December and in April. The relatively long flight season suggests the species is multivoltine.

DISCUSSION

Two genera are now included in the tribe Ogyrini, which is endemic to the Australian region (Eliot, 1973). Morphology of the wing venation, labial palpus and male and female genitalia clearly place *Pseudogyris* in the Ogyrini. Although a phylogenetic hypothesis of all members of the tribe is required to determine their evolutionary relationships and confirm monophyly of *Ogyris*, the large number of unique phenotypic characters observed in the two sister species *meeki* and *brandti* (total of at least 14 characters - 5 morphological based on wing/body features, 6 wing color pattern elements, and 3 morphological based on genitalia) strongly suggests they fall outside the *Ogyris* lineage. The relationships of the Ogyrini are somewhat uncertain, but the tribe appears to be closely related to the *Lucia* section of the polyphyletic Luciini Waterhouse & Lyell, 1914 (Espeland *et al.*, 2018 and unpublished data). The *Lucia* section of the Luciini includes four genera: *Lucia* Swainson, 1833, *Paralucia* C. & R. Felder, 1860, *Pseudodipsas* Waterhouse & R.E. Turner, 1905 and *Acrodipsas* Sands, 1980 (Eliot, 1973; Sands, 1980). The likely phylogenetic hypothesis of genera of these two tribes is: ((*Lucia* + *Paralucia*) + (*Pseudodipsas* + *Acrodipsas*)) + (*Ogyris* + *Pseudogyris*).

Compared with *Ogyris*, character states unique to *Pseudogyris* include the large body size (forewing length); the elongated and almost falcate forewing of the male; the prominent spatulate tail on vein CuA_1 of the hindwing; the broad black transverse band on the forewing upperside of the female; the broad and long discal cell bars with filled (brown) color pattern on the forewing underside; the broad cream or grey transverse submedian band on the hindwing underside; the series of conspicuous discrete brown spots and markings on the hind wing underside; and the series of four terminal crescent-shaped marks enclosing a black spot overlaid with iridescent bluish-white scales between veins M_3 and 3A on the hindwing underside, with one of these marks and spots being particularly pronounced on the tornal lobe between veins CuA_2 and 1A+2A. These eight character-states are absent in the *Lucia* section of the Luciini and thus they may be considered synapomorphies for *Pseudogyris*. The polarity of the other characters that differentiate *Pseudogyris* from *Ogyris*, such as morphology of the genitalia, await further study. The single, conspicuous spatulate tail on the hindwing of *Pseudogyris* is most unusual and reminiscent of the tail of papilionids, such as *Graphium weiskei* (Ribbe, 1900), except it is located on vein CuA_1 instead of CuA_2. In the Theclinae and Polyommatinae, the tail, when present, is filamentous and always located on vein CuA_2 adjacent to the tornal lobe (Eliot, 1973; Ackery *et al.*, 1999), whereas in *Pseudogyris* the tail is of a different shape and on a different vein. In some thecline genera there is a second filamentous tail on vein 1A+2A or, very occasionally, on CuA_1, such as in the Neotropical Eumaeini (e.g., *Arcas* Swainson, 1832, *Evenus* Hübner, 1819, *Paiwarria* Kaye, 1904 and *Pseudolycaena* Wallengren, 1858). Pronounced sexual dimorphism in *Pseudogyris* is remarkable and, to some extent, parallels that observed in *Ogyris ianthis* but is even more striking.

Pseudogyris is considered to be polytypic, containing two allopatric species, *P. meeki* and *P. brandti*, hypothesized to have diverged vicariantly by the uplift of the Central Cordillera of mainland New Guinea during the Pliocene-Pleistocene (Toussaint *et al.*, 2014). As such, the genus adds to the growing number of cases of butterflies endemic to mainland New Guinea that have putative vicariant, sister taxa on either side of the Central Cordillera. Examples of species pairs which have allopatric, lowland distributions on the northern and southern sides of the Cordillera, respectively, include: *Ornithoptera paradisea* + *O. meridionalis*; *Chaetocneme critomedia* + *C. caristus*; *Parantica kirbyi* + *P. schenkii*; *Parthenos sylvia* + *P. tigrina*; *Mydosama durga* + *M. bazochii*; *Praetaxila satraps* + *P. albiplaga*; *Hypochrysops thesaurus* + *H. cleonides*; and *Hypochrysops heros* + *H. herdonius*.

Ogyris has radiated on the Australian continent (14 species are now recognized) where they mainly specialize on parasitic plants in the family Loranthaceae growing in dry, non-rainforest habitats (Braby, 2000). The larvae of one species (*O. otanes*) feeds on related Santalaceae (Burns & Angel, 1952; Williams *et al.*, 1992; Hart & Powell, 1997; Williams & Hay, 2001), but three species are myrmecophagous and specialize on ants (Pierce, 1995; Hunt *et al.*, 1998; Moore, 1999; Field, 1999; Douglas & Allen, 2002; Braby & Douglas, 2008; Schmidt *et al.*, 2014; Williams *et al.*, 2020). In addition, three species-groups of *Ogyris* have specific, obligate associations with

ants: the *O. aenone* species-group with Dolichoderinae, and the *O. genoveva* and *O. idmo* species-groups with Formicinae (*Camponotus*) (Eastwood & Fraser, 1999). The remaining five species (*O. amaryllis*, *O. abrota* and the *O. olane* species-group) have non-specific, facultative associations with ants. In contrast, *Pseudogyris* is largely allopatric, containing two putative vicariant species restricted to tropical lowland rainforest and lower montane forest in mainland New Guinea and New Ireland, but the extent to which it associates with ants is not known. Limited diversification of the lineage implies *Pseudogyris* may not be associated with Loranthaceae, unlike the pierid genus *Delias* Hübner, 1819 which appears to have radiated explosively on aerial hemi-parasites in the Santalales (especially Loranthaceae and Viscaceae) in montane New Guinea (Braby, 2006; Braby & Pierce, 2007; Müller *et al.*, 2013). This lack of diversification, together with its relatively small spatial distribution and habitat association, suggests *Pseudogyris* may be a relict. An investigation into the historical biogeography and divergence times of these lineages in the context of the drying of Australia during the Tertiary would make a fascinating study. Espeland *et al.* (2018) estimated the stem group of the Ogyrini to have evolved in the Eocene, which is well before the major period of aridification of the Australian continent and concomitant contraction of the Gondwanan rainforests (White, 1994, 1998).

Further work on the life history, biology, and host plant specialization of *Pseudogyris* may provide additional evidence supporting the distinctiveness of this lineage. On recounting his adventures in New Guinea and the discovery of *P. meeki* at Milne Bay, Meek (1913, p. 98) reminisced that "I had taken… one male specimen of the large blue butterfly (*Orgyris* [sic] *meeki*) which pupates under the ground at the trunk of the food-plant (the tree on which the mistletoe lives)." However, given that the life history of *P. meeki* is unknown it is likely that Meek was referring more generally to the biology of the genus *Ogyris* rather than to the species *P. meeki* in particular. Before working in New Guinea, Meek had spent time as a cattleman with G. Barnard on the pastoral property at Coomooboolaroo Station (near Duaringa), QLD, in the 1890s (Tennent, 2021). George Barnard was the first naturalist to discover the life history of *Ogyris*, and his observations and descriptions of the immature stages of *O. genoveva* (and *O. zosine*, see Waterhouse, 1941), together with a beautifully colored plate illustrating the life histories of these two butterflies, was published by Miskin (1883). Thus, Meek would have been aware that the larvae of *Ogyris* feed on Loranthaceae and that those of *O. genoveva* and *O. zosine* often pupate beneath the surface of the ground at the base of the trunk of the host tree.

ACKNOWLEDGMENTS

We thank You Ning Su (ANIC) for technical advice and preparing several images for the photographic plates; William Hastie (CSIRO) for providing the digital image of Rothschild's painting of *Ogyris meeki*; Blanca Huertas, Nicola Lowndes and John Tennent (NHMUK) for providing digital images of the lectotype male of *O. meeki* and other material in the Natural History Museum London under their care; Théo Léger and Eran Wolff (MfN) for organizing and providing digital images of the paralectotype male of *O. meeki*; and Sabine Gaal-Haszler (NMW) for historical information and providing digital images of the holotype female of *O. aurantiaca*. Material examined and photographed in NHMUK was made available under Creative Commons License 4.0 (https://creativecommons.org/licenses/by/4.0). Akira Yagishita kindly assisted with the loan of valuable material from his extensive private collection in Japan, Motoki Saito assisted in various other ways, and Andrei Sourakov (McGuire Center for Lepidoptera and Biodiversity) checked the Florida Museum of Natural History collection, Gainesville, USA, for material. David J. Lohman, Frank Hsu, Rod Eastwood and John Tennent are thanked for critically reading and improving a draft of the manuscript. Leonora Rodríguez Sevilla and Kenji Nishida assisted with translation of the Abstract into Spanish.

LITERATURE CITED

Ackery, P. R., de Jong, R., Vane-Wright, R. I. 1999. *The Butterflies: Hedyloidea, Hesperioidea and Papilionoidea*, pp. 263-300. *In*: Kristensen, N.P., (Ed.) *Lepidoptera, Moths and Butterflies. Volume 1. Evolution, Systematics and Biogeography*. Berlin, de Gruyter.

Angas, G. F. 1847. *South Australia Illustrated*. London, Thomas McLean. pp. i-xii, pls I-LX.

Bethune-Baker, G. T. 1905. A monograph of the genus *Ogyris*. *Transactions of the Entomological Society of London* 1905: 269-292, pl XV.

Braby, M. F. 2000. *Butterflies of Australia. Their Identification, Biology and Distribution*. Collingwood, Melbourne, CSIRO Publishing. xx + 976 pp.

Braby, M. F. 2006. Evolution of larval food plant associations in *Delias* Hübner butterflies (Lepidoptera: Pieridae). *Entomological Science* 9: 383-398.

Braby, M. F., Douglas, F. 2008. The nomenclature, taxonomy and conservation status of *Ogyris waterhouseri* (Bethune-Baker, 1905) stat. nov. (Lepidoptera: Lycaenidae), a threatened butterfly from southern Australia. *Australian Journal of Entomology* 47: 315-329.

Braby, M. F., Douglas, F., Peterson, M. 2014. New and interesting records of *Ogyris zosine* (Hewitson, [1853]) (Lepidoptera: Lycaenidae) from inland Western Australia. *The Australian Entomologist* 41: 107-114.

Braby, M. F., Douglas, F., Willan, R. C. 2011. The nomenclature of *Ogyris halmaturia* (Tepper, 1890) (Lepidoptera: Lycaenidae). *The Australian Entomologist* 38: 29-36.

Braby, M. F., Franklin, D. C., Bisa, D. E., Williams, M. R., Williams, A. A. E., Bishop, C. L., Coppen, R. A. M. 2018. *Atlas of Butterflies and Diurnal Moths in the Monsoon Tropics of Northern Australia*. Canberra, ANU Press. xxxii + 430 pp.

Braby, M. F., Pierce, N. E. 2007. Systematics, biogeography and diversification of the Indo-Australian genus *Delias* Hübner (Lepidoptera: Pieridae): phylogenetic evidence supports an 'out-of-Australia' origin. *Systematic Entomology* 32: 2-25.

Burns, A. N., Angel, F. 1952. The Small Brown Azure (*Ogyris atanes* [sic] Feld) (description and notes on the life history). *The Victorian Naturalist* 68: 183-186.

Common, I. F. B., Waterhouse, D. F. 1972. *Butterflies of Australia*. Sydney, Angus and Robertson. xii + 498 pp.

Common, I. F. B., Waterhouse, D. F. 1981. *Butterflies of Australia. Revised Edition*. Sydney, Angus and Robertson. xiv + 682 pp.

D'Abrera, B. 1971. *Butterflies of the Australian Region*. Melbourne, Lansdowne Press. 415 pp.

D'Abrera, B. 1990. *Butterflies of the Australian Region. Third Edition*. Melbourne, Hill House. 416 pp.

Doubleday, E., Westwood, J. O. 1846-1852. *The genera of diurnal Lepidoptera: comprising their generic characters, a notice of their habits and*

transformations, and a catalogue of the species of each genus. Illustrated with eight-six plates by William C. Hewitson. London, Longman, Brown, Green and Longmans.

Douglas, F., Allen, G. G. 2002. The known distribution at Hattah-Kulkyne National Park and current conservation status in Victoria of *Ogyris subterrestris subterrestris* Field, 1999, Lepidoptera: Lycaenidae (Arid Bronze Azure or Mildura Ogyris Butterfly). Unpublished report to the Department of Natural Resources and Environment. 16 pp.

Eastwood, R. G., Fraser, A. M. 1999. Associations between lycaenid butterflies and ants in Australia. *Australian Journal of Ecology* 24: 503-537.

Edwards, E. D. 1996. Lycaenidae, pp. 249-254, 360-363. *In*: Nielsen, E.S., Edwards, E.D., Rangsi, T.V., (Eds.) *Checklist of the Lepidoptera of Australia. Monographs on Australian Lepidoptera. Volume 4*. Collingwood, Melbourne, CSIRO Publishing.

Edwards, E. D., Newland, J., Regan, L. 2001. *Lepidoptera: Hesperioidea, Papilionoidea. Zoological Catalogue of Australia. Vol. 31.6*. Collingwood, Melbourne, CSIRO Publishing. x + 615 pp.

Eliot, J. N. 1973. The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. *Bulletin of the British Museum (Natural History) Entomology* 28: 371-505.

Espeland, M., Breinholt, J. W., Willmott, K. R., Warren, A. D., Vila, R., Toussaint, E. F. A., Maunsell, S. C., Aduse-Poku, K., Talavera, G., Eastwood, R. G., Jarzyna, M. A., Guralnick, R., Lohman, D. J., Pierce, N. E., Kawahara, A. Y. 2018. A comprehensive and dated phylogenomic analysis of butterflies. *Current Biology* 28: 770-778.

Field, R. P. 1999. A new species of *Ogyris* Angas (Lepidoptera: Lycaenidae) from southern arid Australia. *Memoirs of Museum Victoria* 57: 251-259.

Gassó Miracle, E. 2017. Koleksi Serangga Papua: collection management and digitization. *Suara Serangga Papua (SUGAPA digital)* 10: 36-41.

Grund, R. 2010. The taxonomy of *Ogyris halmaturia* (Tepper, 1890) stat. nov. (Lepidoptera: Lycaenidae). *Australian Journal of Entomology* 49: 114-120.

Hart, R., Powell, M. 1997. Status of the northern population of the butterfly, the Western Dark Azure (*Ogyris otanes*) in Western Australia. *Western Australian Naturalist* 21: 185-190.

Hermkens, A. 2013. *Engendering Objects. Dynamics of Barkcloth and Gender among the Maisin of Papua New Guinea*. Leiden, Sidestone Press. 384 pp.

Hunt, L., Moore, M., Moore, D. 1998. Rediscovery of *Ogyris idmo halmaturia* (Tepper 1890). *Victorian Entomologist* 28: 113-116.

ICZN. 1999. *International Code of Zoological Nomenclature. Fourth Edition*. London, The International Trust for Zoological Nomenclature. xxix + 126 pp.

Klots, A. B. 1970. *Lepidoptera*, pp. 115-130. *In*: Tuxen, S.L., (Ed.) *Taxonomist's Glossary of Genitalia in Insects. Second Edition*. Copenhagen, Munksgaard.

Meek, A. S. 1913. *A Naturalist in Cannibal Land*. London, T. Fisher Unwin. 238 pp.

Miskin, W. H. 1883. On *Ogyris genoveva*, Hewitson, and its life-history. *Transactions of the Entomological Society of London* 1883: 343-345.

Moore, M. 1999. Some field notes on the as yet unnamed *Ogyris* species (formerly included in the species *Ogyris idmo halmaturia*) from Waikerie. *Victorian Entomologist* 29: 12-17.

Müller, C. J., Matos-Maraví, P. F., Beheregaray, L. B. 2013. Delving into *Delias* Hübner (Lepidoptera: Pieridae): fine-scale biogeography, phylogenetics and systematics of the world's largest butterfly genus. *Journal of Biogeography* 40: 881-893.

Parsons, M. J. 1998. *The Butterflies of Papua New Guinea. Their Systematics and Biology*. London, Academic Press. xvi + 736 pp.

Pierce, N. E. 1995. Predatory and parasitic Lepidoptera: carnivores living on plants. *Journal of the Lepidopterists' Society* 49: 412-453.

Rebel, H. 1912. VIII Herr Prof. Rebel legt die Diagnosen zweier neuer Tagfalterarten aus dem Naturhistorischen Hofmuseum vor. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 62: 218-221.

Rothschild, L. W. 1900. Some new or recently described Lepidoptera. *Novitates Zoologicae* 7: 274-276.

Sands, D. P. A. 1980. A new genus, *Acrodipsas*, for a group of Lycaenidae (Lepidoptera) previously referred to *Pseudodipsas* C. & R. Felder, with descriptions of two new species from northern Queensland. *Journal of the Australian Entomological Society* 18: 251-265.

Schmidt, D. J. 2007. *Congeneric Phylogeography of Australian* Ogyris *butterflies (Lepidoptera: Lycaenidae)*. Brisbane, Griffith University, Australian Rivers Institute, Faculty of Environmental Sciences, School of Environmental Science. PhD Thesis.

Schmidt, D. J., Grund, R., Williams, M. R., Hughes, J. M. 2014. Australian parasitic *Ogyris* butterflies: east-west divergence of highly-specialized relicts. *Biological Journal of the Linnean Society* 111: 473-484.

Schmidt, D. J., Hughes, J. M. 2006. Genetic affinities among subspecies of a widespread Australian lycaenid butterfly, *Ogyris amaryllis* (Hewitson). *Australian Journal of Zoology* 54: 429-446.

Schröder, S. 2021. *The Blues (Lepidoptera: Lycaenidae, Lycaeninae) of Papua Indonesia.* Ogyris meeki *Rothschild, 1900*. https://www.papua-insects.nl/insect%20orders/Lepidoptera/Lycaenidae/Lycaeninae/Ogyris/Ogyris%20meeki.htm. Accessed 13 July 2021.

Seitz, A. 1926. *Genus:* Ogyris*. Family: Lycaenidae. Vol. 9. The Indo-Australian Rhopalocera*, pp. 940-942. *In*: Seitz, A., (Ed.) *The Macrolepidoptera of the World*. Stuttgart, Alfred Kernen.

Su, Y. N. 2016. A simple and quick method of displaying liquid-preserved morphological structures for microphotography. *Zootaxa* 4208: 592-593.

Tennent, W. J. 2006. A checklist of the butterflies of Melanesia, Micronesia, Polynesia and some adjacent areas. *Zootaxa* 1178: 1-209.

Tennent, W. J. 2021. *The Man Who Shot Butterflies. Albert Stewart Meek (1871-1943) - Naturalist and Explorer*. Oxfordshire, England, Storm Entomological Publications. 603 pp.

Tepper, J. G. O. 1893. Notes and remarks on South Australian Rhopalocera. *Transactions, Proceedings and Reports of the Royal Society of South Australia* 17: 281-286.

Toussaint, E. F. A., Hall, R., Monaghan, M. T., Sagata, K., Ibalim, S., Shaverdo, H. V., Vogler, A. P., Pons, J., Balke, M. 2014. The towering orogeny of New Guinea as a trigger for arthropod megadiversity. *Nature Communications* 5: 1-10.

Upton, M. S. 1997. *A Rich and Diverse Fauna: The History of the Australian National Collection 1926-1991.* Collingwood, Melbourne, CSIRO Publishing. xx + 386 pp.

Waterhouse, G. A. 1941. Notes on Australian Lycaenidae. Part VIII. On *Ogyris zosine* Hew. and *O. genoveva* Hew. *Proceedings of the Linnean Society of New South Wales* 66: 234-238.

Waterhouse, G. A., Lyell, G. 1914. *The Butterflies of Australia. A Monograph of the Australian Rhopalocera*. Sydney, Angus and Robertson. vi + 239 pp.

White, M. E. 1994. *After the Greening: The Browning of Australia*. East Roseville, NSW, Kangaroo Press. 288 pp.

White, M. E. 1998. *The Greening of Gondwana. Third Edition*. East Roseville, NSW, Kangaroo Press. 256 pp.

Williams, A. A. E., Williams, M. R., Heterick, B. E. 2020. Notes on the distribution, habitat, behaviour and flight times of the Large Bronze Azure, *Ogyris idmo* (Hewitson, 1862) (Lepidoptera: Lycaenidae), a rare myrmecophilous butterfly from south-western Western Australia. *The Australian Entomologist* 47: 221-247.

Williams, M. R., Atkins, A. F., Hay, R. W., Bollam, H. H. 1992. The life history of *Ogyris otanes* C. & R. Felder in the Stirling Range, Western Australia (Lepidoptera: Lycaenidae). *The Australian Entomologist* 19: 55-60.

Williams, M. R., Hay, R. W. 2001. Two new subspecies of *Ogyris otanes* C.&R. Felder (Lepidoptera: Lycaenidae) from Western Australia. *The Australian Entomologist* 28: 55-63.