SYSTEMATICS OF THE AUSTRALIAN NASUTITERMITINAE
WITH REFERENCE TO EVOLUTION WITHIN
THE TERMITIDAE (ISOPTERA)

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A thesis submitted for the degree of
Doctor of Philosophy
of the
Australian National University

Canberra July 1997
DECLARATION

I declare that the research described in this thesis is my own original work

Leigh Robin Miller

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ACKNOWLEDGEMENTS

Because of the circumstances of my employment, I have had to carry out much of this work in greater isolation than was optimal for good research. Fortunately, members of the CSIRO Division of Entomology Termite Group, including G.F.Hill who founded it, have maintained a comprehensive collection of termite literature.

While I intend no disrespect towards any who have published work on termites, the persons acknowledged below have helped me to maintain, I hope, a path somewhere between:

"soldiers with beak"

[Dudley's (1890) description of the genus *Nasutitermes*

and:

"2nd usually shortest of all, sometimes of the same length as, or a little shorter or a little longer than 3rd,....3rd as long as, or a little shorter or distinctly longer than 4th;"

[Part of Gerald Freer Hill's (1942) two hundred and thirty-one word description of the soldier of *Eutermes pastinator*]

My most sincere thanks are due to my late colleague, friend, and supervisor, Dr Tony Watson, without whose long-term support and encouragement, I would not have embarked upon a second, and very late, course of education. I thank all who continued that support after Tony's death.

Dr Penny Gullan, Dr Peter Cranston, and Dr Michael Lenz have provided helpful criticism, guidance, advice and support. I am also indebted to Dr David Grimaldi and Dr Kumar Krishna for their generous help in providing access to the AMNH collection, and particularly to Kumar for helpful discussion.

I thank the staff of CSIRO Division of Entomology and Division of Plant Industry Electron Microscopy Laboratory for technical help and access to equipment.

Lastly, I am grateful for the patience, support, and sometimes over-enthusiastic assessment of my scientific ability provided by my wife, Eveline Goy.

All of the above helped me to keep in mind that:

"exhausted patience induces strong wish for a conclusion; and it is then that the difficulty arises of keeping the influence of wish from upsetting the even balance of judgement."

ABSTRACT

This thesis describes a systematic study of the Australian species of a widely-distributed group of termites, the Nasutitermitinae, which is characterised by having soldiers which possess the ability to squirt the defensive secretions of a well-developed frontal gland a considerable distance.

The Nasutitermitinae in general, and the type genus, *Nasutitermes*, have never been well-defined and it has long been recognised that the generic placement of some species has been confused. I examined a series of criteria by which earlier authors had placed species and found that phylogenies based on differing character sets were not compatible. This study set out to determine whether analysis of a previously unused set of characters, combined with "traditional" character sets, would reveal an acceptable phylogeny for the group. In addition to characters based on external and internal morphology, I examined termite behaviour, expressed as tunnelling, nesting, feeding and other behaviour, in order to determine whether the expression of such was phylogenetically determined. While it is clear that there is convergence of behaviour across families, patterns of behaviour can correlate with phylogeny based on morphological characters.

After examining a large number of characters, in order to better understand evolution and polarity of those characters under consideration, I used a reduced set of characters common to most families and subfamilies of the order to determine the position of the Nasutitermitinae relative to other subfamilies and to determine suitable outgroups. The analysis showed that the mandibulate group long regarded as sister group of the true nasute group, and always placed within the subfamily Nasutitermitinae, namely the *Syntermes* group of genera, is a sister group of the Termitidae minus the Macrotermintinae, and deserves subfamily status.
I then analysed the Australian species in detail, using a set of 67 characters. The results generally supported the currently recognised genera, with the exception that some species presently placed in *Nasutitermes* were placed in *Tumulitermes*, and conversely, some species were removed from *Tumulitermes*. Also, a number of species currently placed in *Nasutitermes* were removed and form a sister group of the *Subulitermes*-group. The inclusion of the type species of *Nasutitermes*, *N. cornigera* (Motschulsky), in the analysis indicates that the Australian "*Nasutitermes*" are a sister group of, and not congeneric with, *Nasutitermes s. str*.

Finally, I argue that the results of the analysis should be more or less accepted, with the provision that the positions of some species, for which the data are incomplete owing to the fact that not all castes are known, are best left unchanged for the present. I present a revised taxonomy of the Australian Nasutitermitinae. The genus *Nasutitermes* is defined and stabilised by the re-description of the type species *N. cornigera*, current Australian genera are re-diagnosed in the light of the results of this study, and diagnoses are given for the suggested new genera. However, for reasons discussed in the text, new taxa are not formally named in this work, although formal publication will follow when relevant type material can be examined.
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CHAPTER 1

SYSTEMATICS OF AUSTRALIAN NASUTITERMITINAE

1.1 INTRODUCTION

The Nasutitermitinae Hare (1937) is a tropical and subtropical group which is generally regarded as the most highly specialised subfamily of the Termitidae (Krishna 1970). The following diagnosis is based on that given by Sands (1965), who referred mainly to species of the Ethiopian region.

Subfamily NASUTITERMITINAE Hare

Nasutitermitinae Hare, 1937 : 462. Type genus, Nasutitermes Dudley, 1890.

Winged Adult  Labrum broader than long, without transverse sclerotised band, tip partly hyaline; mandibles with apical tooth slightly shorter to distinctly longer than first marginal, left third marginal with anterior edge at most only slightly longer than posterior (up to $1\frac{1}{2}$ times); fontanelle commonly slit-like, often bifurcate, sometimes nearly obsolete. Tibial spurs $2 : 2 : 2$ (Syntermes with $3 : 2 : 2$). Styli absent.

Soldier  Frontal gland well-developed. Head capsule often modified to form proboscis terminating in opening of frontal gland; mandibles often reduced to vestiges, with or without "points". Tibial spurs $2 : 2 : 2$. Styli absent.

Digestive Tract  Gizzard with reduced armature. Malpighian tubules always attached at midgut-P1 junction, usually in two pairs, sometimes all together.

The subfamily is reasonably well-defined, and although Sands (1972) suggested that they were derived from the same stock as the Termitinae, he retained them as a valid subfamily. The Nasutitermitinae is traditionally divided into two sections. The first consists of a Neotropical group of genera in which the soldier mandibles have a biting function and the area of the head capsule surrounding the fontanelle, into which the well-developed frontal gland opens, is variously modified. The second is a group of genera, supposedly derived from the former group, in which the soldier mandibles are greatly reduced, the fontanelle opening is reduced to a very small aperture and the area surrounding it is always elongated into a sharply-pointed nasus or rostrum, through
which the secretions of the frontal gland can be squirted a considerable distance. All of the Australian genera belong to the latter section which is represented in mainland Australia by 42 described species in six genera. Various species were described as *Eutermes* Hagen = *Nasutitermes* Dudley by Brauer (1865), Froggatt (1898), Silvestri (1909), Mjöberg (1920) and Hill (1915, 1921, 1922, 1923, 1925, 1927, 1932 & 1942). Several Australian species were assigned to the subgenera *Occasitermes* Holmgren and *Tumulitermes* Holmgren by Holmgren (1912). Snyder (1949) gave these subgenera full generic rank, and included several species in *Subulitermes* Holmgren. The genera *Macrosubulitermes* Emerson, *Australitermes* Emerson and *Occultitermes* Emerson were erected by Emerson (1960) to contain the species included in *Subulitermes* by Snyder. Gay (1974, 1977) described new species of *Occasitermes* and *Occultitermes* and Watson and Gay (1980) transferred one species of *Nasutitermes* to another subfamily. One species was transferred from the Termitinae to the genus *Australitermes* by Miller (1984). Roisin & Pasteels (1996) recently revised the genera from Papua New Guinea, which include three species which also occur on mainland Australia. The Australian genera and species currently recognised are:

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<thead>
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<th>Australitermes Emerson</th>
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<tr>
<td><em>N. carnarvonensis</em> (Hill)</td>
<td><em>T. apioccephalus</em> (Silvestri)</td>
<td><em>A. dilucidus</em> (Hill)</td>
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<td><em>N. centraliensis</em> (Mjöberg)</td>
<td><em>T. comatus</em> (Hill)</td>
<td><em>A. insignitus</em> (Hill)</td>
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<td><em>N. coalescens</em> (Mjöberg)</td>
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<td><em>N. dixoni</em> (Hill)</td>
<td><em>T. dalbiensis</em> (Hill)</td>
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<td><em>N. eucalypti</em> (Mjöberg)</td>
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<td><em>N. fumigatus</em> (Brauer)</td>
<td><em>T. marcidus</em> (Hill)</td>
<td><em>O. occasus</em> (Silvestri)</td>
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<td><em>N. graveolus</em> (Hill)</td>
<td><em>T. mareebensis</em> (Hill)</td>
<td><em>O. watsoni</em> Gay</td>
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<td><em>N. kimberleyensis</em> (Mjöberg)</td>
<td><em>T. nichollsi</em> (Hill)</td>
<td><em>Occultitermes</em> Emerson</td>
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<td><em>N. longipennis</em> (Hill)</td>
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<td><em>O. occultus</em> (Hill)</td>
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<td><em>T. petilus</em> (Hill)</td>
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<td><em>N. projectus</em> (Hill)</td>
<td><em>T. pulleini</em> (Mjöberg)</td>
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<td><em>N. smithi</em> (Hill)</td>
<td><em>T. recalvis</em> (Hill)</td>
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<td><em>T. subaquilis</em> (Hill)</td>
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<td><em>N. triodiae</em> (Froggatt)</td>
<td><em>T. tumuli</em> (Froggatt)</td>
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<td><em>N. walkeri</em> (Hill)</td>
<td><em>T. westraliensis</em> (Hill)</td>
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Although this assignment of species is currently accepted (Watson & Gay 1991), some authors have doubted the validity of some genera and Hill (1942) summarised his misgivings in the following statement.

"Holmgren (1912, p. 59) divided the genus Eutermes into a number of subgenera, which have since been adopted by various writers as either subgenera or genera. This classification is considered by many authors to be unsatisfactory and has not been adopted in this work, inter alia, for the following reasons: -

The species are more easily identified specifically than subgenerically; in some dimorphic species the large soldier could not be placed in the same subgenus as the small soldier, so it follows that if the winged adult is unknown the subgenus could not be determined; several species with almost identical winged adults would be separated into different subgenera if the characters of the soldier only were considered. It may be mentioned that the type of one subgenus is now considered to be a species of another genus (Mirotermes), and one subgenus (Grallatoterms), which is based on the soldier form only, is characterised (twice) in different terms."

This single paragraph suggests that the characters upon which the Australian genera were established are inadequate to reflect the true relationships between species, and provides ample justification for a comprehensive study of this diverse, albeit small, group.

Most of the anomalies occur within the genera Nasutitermes and Tumulitermes. Soldiers of Nasutitermes generally have a rounded head capsule with a relatively short, more or less conical rostrum and well-developed points on the mandibles; whereas soldiers of Tumulitermes usually have a constricted head capsule, are often dimorphic, have a relatively slender rostrum (Gay 1970) and usually have vestigial or absent mandibular points. In addition, the left imago mandible of Nasutitermes has a straight or evenly curved cutting edge between the fused first plus second marginal tooth and the third marginal tooth; in Tumulitermes the cutting edge is sinuate, with a notch anterior to the third marginal tooth. However, some species have a constricted soldier head capsule and mandibles of the "Nasutitermes" type, whereas others possess a rounded head capsule and short stout rostrum combined with mandibles of the "Tumulitermes" type. Also, as discussed by Hill (1942), dimorphic species may have soldiers with both rounded and constricted head capsules.
Prior to the present study the winged adult was unknown in 15 of the 42 named species and classification has in the past relied heavily on characters of external morphology of the soldier and, to a lesser extent, patterns of dentition of mandibles of the winged adult and worker, which are basically similar in the two castes and will be referred to throughout this work as imago/worker mandibles.

It has been shown that the structure of the digestive tract provides many useful taxonomic characters (Noirot & Kovoor 1958; Kovoor 1969; Noirot & Noirot-Timothee 1969; Sands 1972; Miller 1986, 1991). Miller (1984) used characters of the digestive tract to resolve the relationships between Australian species of the nasute genera *Australitermes* and *Macrosubulitermes* and the present study combines such characters with "traditional" characters of external morphology of the soldier and winged adult.

The primary aim of this work is to resolve the anomalies evident in the accepted classification of the Australian Nasutitermitinae by a detailed examination of external morphology of all species to determine whether the present divisions are real, or Hill's statement is justified, and an examination of previously unused characters of gut structure to determine whether or not divisions based on such characters could be correlated with divisions based on external morphology. In order to effect this aim, it is necessary to achieve an understanding of termite morphology, behaviour and evolution in a broader context than at genus or subfamily level, so that interpretation of observed character states will have the consistency necessary for an unambiguous classification to be presented.

The family Termitidae Westwood 1840, to which more than 80% of extant termite species currently belong, is in reality a "default" conglomeration of taxa which comprises the remainder of the order Isoptera after the other six families have been excised. Although it is beyond the scope of this study to re-define the subfamilies, it is nevertheless necessary to recognise the structure and position of the Nasutitermitinae in order to define the type genus, *Nasutitermes*, so that it can be used as a baseline against which the Australian taxa may be compared.

A recurring theme throughout the course of this study is the fact that much of the morphological change associated with termite evolution has been in the form of reductions or losses (Emerson 1962, Hennig 1981). A few examples are loss of ocelli, loss of antennal segments, loss of tarsal segments, loss of tibial spines and spurs, reduction of wing venation, loss of Malpighian tubules, reduction of gizzard armature, and reduction of styli and cerci. In consequence, a great deal of weight must be given to characters which can unequivocally be regarded as gains, such as the development of the
"mixed segment" at the junction of the mid- and hindgut, elongation of the first proctodeal segment, elongation of colonic region, and enlargement of mandibular teeth.

1.2 HISTORICAL

1.2.1 Holmgren 1912
Holmgren's monumental Termitenstudien of 1909-1913 (Holmgren 1912, pp. 45-72 refer to what is currently recognised as Nasutitermitinae) formed a solid framework for all termite taxonomy upon or with which all more recent revisions and phylogenetic trees have been based or compared (e.g. Hare 1937; Snyder 1949; Ahmad 1950; Krishna 1970). Holmgren's "Syntermes-Reihe" (Fig. 1.1) included the currently-recognised Nasutitermitinae, as well as Anoplotermes Fr. Müller and Speculitermes Wasmann, which are now included in the Apicotermitinae Grassé & Noirot (Sands 1972).

Holmgren included in *Eutermes = Nasutitermes* the Australian species *E. fumigatus, E. hastilis, E. magnus, E. pyriformis (=E. triodiae), and E. triodiae*. *Tumulitermes* Holmgren and *Occasitermes* Holmgren were described as subgenera of *Eutermes* Hagen and included the species *T. tumuli, T. apiocephalus*, and *O. occasus*.

Note that Holmgren's tree (Fig. 1.1) implied that *Eutermes = Nasutitermes* was derived, through *Armitermes* Wasmann, from *Syntermes* Holmgren. This notion formed the basis of a paradigm, strengthened by Hare (1937), Emerson (1941, 1949), Ahmad (1950), Sands (1957) and Krishna (1970), which remained unquestioned until challenged by Miller (1986, 1992). Emerson (1941) also introduced the concept that the Nasutitermitinae was diphyletic in the sense that the fully-nasute soldier evolved twice from different mandibulate stems. This hypothesis also was widely accepted until questioned by Prestwich & Collins (1981) and Miller (1986).

1.2.2 Hare 1937
Hare (1937) formally raised Holmgren's Syntermes-Reihe to subfamily rank, namely the Nasutitermitinae, and her placement of fully-nasute genera substantially agreed with that of Holmgren in that the mandibulate genus *Armitermes* appeared as the sister group of the fully nasute genera (Fig. 1.2).

1.2.3 Hill 1942
Hill described many species from Australia, as summarised in his monograph (Hill 1942). As noted in the introduction, Hill did not recognise Holmgren's subgenera and explicitly stated his reasons. He placed all Australian nasutes in *Eutermes (>
Figure 1.1. Holmgren's "Syntermes-Reihe". Redrawn from Holmgren (1912, p. 53).

Figure 1.2. Hare's Nasutitermitinae. Redrawn from Hare (1937, p. 477).
Nasutitermes) and although Hill never illustrated relationships by trees, he often implied relatedness in his descriptions.

1.2.4 Snyder 1949
The subgenera of Holmgren were raised to genera by Snyder (1949), and it was his inclusion of many Australian species in Holmgren's genera, particularly Tumulitermes, that has expanded and perpetuated the confusion alluded to by Hill (1942). Snyder's justification for such synonymies was apparently based on Emerson's advice or notes (Snyder 1949 p. 4). Snyder included in Subulitermes the four species Eutermes dilucidus Hill, E. perlevis Hill E. greavesi Hill, and E. occultus Hill.

1.2.5 Emerson 1960
Emerson (1960) described the genera Australitermes, Macrosubulitermes and Occultitermes to include A. dilucidus (Hill), M. greavesi (Hill) and M. perlevis (Hill), and O. occultus (Hill). Gay (1974) later added Occasitermes to the "Subulitermes branch" of Emerson.

1.2.6 Sen-Sarma 1968
Sen-Sarma (1968) followed Snyder's (1949) placement of Tumulitermes and Nasutitermes on the "Procornitermes branch" while including the genera Occasitermes, Occultitermes, Macrosubulitermes and Australitermes on the "Paracornitermes branch".

1.2.7 Krishna 1970
Krishna (1970) summarised what are still the most commonly accepted relationships within the families of Isoptera, with the exception that some authors (myself included) follow Grassé's recognition of the Termopsidae, and Sand's (1972) re-definition of the Termitidae. Figure 1.3 illustrates a synthesis of various authors' views of the possible relationships of the Nasutitermitinae.

1.2.8 Miller 1984, 1986
Miller (1984) clarified the relationships of the Australian species of the genera of the Subulitermes branch, on the basis of gut structure. Prestwich & Collins' (1981) evidence of frontal gland secretions, and the observation that differences in gut structure did not correlate with the accepted diphyletic theory of the subfamily led me to propose a monophyletic phylogeny (Miller 1986) (Fig. 1.4).

1.2.9 Summary
When the literature discussed above is examined in detail it becomes evident that there has been little justification for the present placement of Australian species of Nasutitermitinae
Figure 1.3. Currently accepted relationships between relevant genera of Nasutitermitinae, based on Krishna (1970). * Endemic Australian genera.
Figure 1.4. Miller's (1986) suggested phylogeny of the Nasutitermitinae, showing differences in soldier mandibles and rostrum development in some mandibulate and fully nasute genera. Numbers on branches are the original character numbers of apomorphies. Australian genera lie within "Nasutitermes" and "Subulitermes" groups.
within the genera *Nasutitermes* and *Tumulitermes*. Most species were assigned to either genus by Snyder (1949), apparently on the basis of Emerson's determination, without stating formally the case for doing so. Since Holmgren's generic diagnoses were brief and generalised, and referred to only seven Australian species in three genera/subgenera, it is necessary to re-examine the type species before assessing the extent of the anomalies referred to by Hill (1942).

### 1.3 CURRENT GENERIC DIAGNOSES

#### 1.3.1 *Nasutitermes* Dudley 1890

The extensive synonymy of *Nasutitermes* has been given by Snyder (1949). Watson *et al.* (1997) clarified the confusion surrounding the authorship of the genus, and the identity of the type species *Termes cornigera* Motschulsky. Dudley's (1890) description, "soldiers with beak", is hardly illuminating since it covers all of the fully nasute genera and a substantial portion of the mandibulate genera. Sands' (1965) generic diagnosis referred only to African species, and Sen-Sarma & Verma's (1983) to Oriental species. I have not seen the type of *N. cornigera*, listed by Snyder (1949) as being in the Hagen collection, Museum of Comparative Zoology. Consequently, the following description of *N. cornigera*, based on a winged adult and associated soldier and worker from the type locality Panama, determined and compared with the Type by A. E. Emerson, is presented as a basis against which Australian genera and species can be compared.

*N. cornigera* (Motschulsky) (Fig. 1.5)

**Winged Adult**


**Measurements**

<table>
<thead>
<tr>
<th>Description</th>
<th>mm.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length with wings</td>
<td>14.08</td>
</tr>
<tr>
<td>Length without wings</td>
<td>13.50</td>
</tr>
<tr>
<td>Head length to apex of labrum</td>
<td>1.72</td>
</tr>
</tbody>
</table>
Head length to clypeofrontal suture 1.07
Head width 1.46
Eye, maximum diameter 0.34
Ocellus, maximum length 0.12
Pronotum length 0.70
Pronotum width 1.16
Forewing length 10.30
Forewing width 3.08

Soldier
Colour dark chestnut brown. Head capsule more or less circular, not constricted. Rostrum relatively short and very stout at base. Antennae of 13 segments, 3rd segment long and slender in basal half. Mandibles with long points. Head capsule and dorsal sclerites with few scattered long hairs. Hairs more dense ventrally.

Measurements
Head length to apex of rostrum 1.60
Head length to genal corners 1.10
Maximum head depth 0.78
Minimum head depth 0.72
Maximum head width 1.14
Head width at genal corners 0.64
Pronotum width 0.60
Left hind tibia length 1.34
Left fore tibia length 0.98
Left fore tibia width 0.12

Digestive Tract
Mixed segment moderately long. Malpighian tubules attached in two separate pairs, not markedly swollen at proximal ends. P1 relatively long, looped before insertion into P3. Enteric valve with relatively long section posterior to proximal armature, the position of which is indicated by a slight dilation. Colonic region relatively short, without anterior loop.

1.3.2 Tumulitermes Holmgren 1912
Eutermes (Tumulitermes) Holmgren 1912, 59-61, 64.
Tumulitermes, Snyder 1949, 301.
(In press)
Figure 1.5 *Nasutitermes cornigera* (Motschulsky). Winged adult head capsule, A dorsal, B lateral. Soldier head capsule, C dorsal, D lateral. E Mixed segment and attachment of Malpighian tubules.
Type species *Eutermes tumuli* Froggatt. Lectotype ANIC No 9059 major soldier.

Froggatt (1898) described only the major soldier of *T. tumuli*. Hill's (1942) comprehensive descriptions of the winged adult, major and minor soldiers, and worker of *Tumulitermes tumuli* (Froggatt) form an adequate basis for the genus. In addition, *T. tumuli* differs substantially from *N. cornigera* in the following aspects.

**Winged adult.** Postclypeus inflated, length much more than half width. Wing membrane almost hyaline between micrasters, so that body is clearly visible through wings when folded at rest. Left mandible with distinct notch anterior to 3rd marginal tooth; right mandible with short concave molar plate, first molar ridge greatly enlarged.

**Soldier.** Always dimorphic. Head capsule slightly constricted behind antennae. Rostrum relatively long and narrow.

1.3.3 *Australitermes Emerson 1960*

*Australitermes*, Emerson 1955, 515 (no description).

*Australitermes* Emerson 1960, 24-25.


Type species *Eutermes dilucidus* Hill. Holotype ANIC No 9069 dealate female.

Emerson's (1960) and Miller's (1984) descriptions adequately distinguish this genus. Key characters are as follows.

**Winged adult.** Eyes and ocelli extremely large and prominent, eye diameter > 0.3 head width, left mandible index > 1.5. Enteric valve heavily sclerotised with extensive spiny armature.

1.3.4 *Macrosubulitermes Emerson 1960*

*Macrosubulitermes*, Emerson 1955, 503, 515 (no description).

*Macrosubulitermes* Emerson 1960, 18-19.

*Macrosubulitermes*, Miller 1984, 119-120.


Type species *Eutermes greavesi* Hill. Holotype ANIC No 9070 alate female.


1.3.5 *Occasitermes Holmgren 1912*

*Eutermes (Occasitermes)* Holmgren 1912, 59-60, 64.
Occasitermes, Snyder 1949, 304.
Occasitermes, Gay 1974, 275-283.
Occasitermes, Watson et al. (In press).^1\footnote{1907-72}

Type species Eutermes occassus Silvestri. Lectotype ZMH soldier.

Gay (1974) translated Silvestri's (1909) description of *O. occassus*. In addition, the following serves to distinguish *O. occassus* from all other described genera.

*Winged adult.* Second marginal tooth, right mandible, with very short anterior, and long posterior margin; margins forming distinctly obtuse angle. Right molar plate relatively very long and slightly convex.

Emerson (1960) and Gay (1977) suggested a close relationship between *Occasitermes* and *Occultitermes*. However, the mandibular dentition of *Occasitermes* is very different from that of *Occultitermes occultus*.

1.3.6 *Occultitermes Emerson 1960*

*Occultitermes*, Emerson 1955, 515 (no description).
*Occultitermes* Emerson 1960, 17-19.
*Occultitermes*, Watson et al. (In press).^1\footnote{1907-72}

Type species Eutermes occultus Hill. Lectotype NMV T-10885 alate female.

Emerson's (1960) and Gay's (1977) descriptions adequately distinguish *O. occultus* from all other genera. The high left mandible index, > 0.6, combined with the very long first proctodeal segment, and very small size of all castes, are key diagnostic characters.

1.4 ANOMALIES

1.4.1 General

Figure 1.6 illustrates the currently accepted (Krishna 1970, Watson & Gay 1991) relationships of the Australian genera of the Nasutitermitinae. Miller (1984) indicated that, as Emerson (1960) had suggested, *Australitermes* and *Macrosubulitermes* are related on the basis of their reduced or absent mixed segment, the form of the soldier, and their soil-feeding habit. However, on the basis of gut structure, there is no justification for placing *Occasitermes* and *Occultitermes* on the "Subulitermes branch" (Miller 1984).

Most of the apparently anomalous placement of species lies within the genera *Nasutitermes* and *Tumulitermes*, and most of Hill's (1942, see section 1.1) comments apparently referred to species in these genera. As Hill noted, placement of species is
most difficult when the winged adult is unknown, but as discussed below, the discovery of adults which were unknown to Hill has added further confusion.

The following discussion refers in detail to some examples which illustrate these anomalies.

1.4.2 *Nasutitermes eucalypti* (Mjöberg)

Mjöberg's material consisted of mixed series, and he wrongly described *N. eucalypti* as dimorphic. Soldiers of *N. eucalypti* are monomorphic and have a more or less round head capsule with relatively short rostrum, which, although not so stout as that of *N. cornigera*, is not slender like that of *T. tumuli*. The general shape of the head capsule and rostrum of the soldier is more similar to that of *N. cornigera* and Australian species such as *N. longipennis* than to *T. tumuli* and the species was regarded as belonging to *Nasutitermes* by Snyder (1949). However, examination of the winged adult shows that it is morphologically very similar to that of *T. tumuli*. On the basis of colour, pilosity, wing membrane, mandibular dentition, and form of the postclypeus, the adult of *N. eucalypti* would intuitively be placed with that of *T. tumuli*. The gut structure resembles that of *T. tumuli* in that the Malpighian tubules are attached together rather than in two pairs, and the colon is relatively long.
Further evidence of the uncertainty of the placement of *N. eucalypti* in *Nasutitermes* is provided by its associated inquilines. Watson (1973 p. 309) described *Austrospirachtha mimetes* Watson, an extremely specialised staphylinid beetle associated with *"Nasutitermes* sp. near *N. eucalypti* (Mjöberg) (ANIC series 14258).” I have examined this series and determined it to be an undescribed species of *Tumulitermes*. However, a second, undescribed species of *Austrospirachtha* was recently collected with what is undoubtedly *N. eucalypti* (Appendix 1).

Termitophilous staphylinids are highly host-specific and it is claimed (Seevers 1957; Kistner 1969) that their phylogeny closely reflects that of their hosts. Kistner (1968), discussing the *Spirachtha* Schiödte group of genera, to which *Austrospirachtha* Watson belongs, suggested that their hosts were genera possessing soldiers with constricted head capsules and it is unlikely that the group would be associated with any species of the genus *Nasutitermes*. Sands & Lamb (1975) later verified Kistner's hypothesis. Although the soldier head capsule of *N. eucalypti* is not constricted, many *Tumulitermes*, which have similar alates to *N. eucalypti*, have soldiers with constricted heads.

### 1.4.3 *Tumulitermes pastinator* (Hill)

The soldiers of *T. pastinator* have markedly constricted head capsules, even more so than *T. tumuli*. Apparently on this basis the species was assigned to *Tumulitermes* by Snyder (1949). The soldiers differ from those of *T. tumuli* in that they are always monomorphic and have well-developed points on the mandibles. The winged adult is almost indistinguishable from that of *N. longipennis* in colour, pilosity, size and placement of eyes and ocelli, postclypeus, wing length and membrane, and mandibular dentition. Although the soldier would be intuitively placed with other constricted-headed species, the adult morphologically resembles many placed in *Nasutitermes*, rather than *T. tumuli*. The gut structure is like that of *N. cornigera* in that the Malpighian tubules are attached in two pairs and the colon is short. Overall, *T. pastinator* appears more closely related to the *N. triodiae* group than to *Tumulitermes s. str.*, with the constricted head capsule of the soldier being the single character linking it to that genus.

### 1.4.4 *Tumulitermes recalvus* (Hill)

*T. recalvus* has dimorphic soldiers. The large form resembles the soldier of *N. longipennis* whereas in the small form the head capsule is markedly constricted. The winged adult is unknown, but the worker postclypeus is of the *Tumulitermes* form. The left mandible of the worker lacks the notch anterior to the 3rd marginal tooth found in *T. tumuli* but the right molar region is concave with an enlarged first molar ridge. Thus, postclypeus and right molar region of worker, dimorphism, and constricted-headed small soldier place *T. recalvus* close to *T. tumuli*, whereas morphology of the large soldier and
worker left mandibular dentition resemble *Nasutitermes*. The gut is like that of *T. tumuli*, with Malpighian tubules attached together and a long colonic region.

1.5 AIMS AND HYPOTHESIS

As stated in the introduction, this study aims to resolve anomalies of the kind alluded to above. Characters presently regarded as diagnostic will be examined critically in an attempt to determine whether they are homologous and consequently to assess their true value as taxonomic indicators. In addition to "traditional" characters, a series of previously unused external and internal characters will be examined, as well as behavioural characteristics.

It is suggested that the current generic placement of species of Australian Nasutitermitinae do not reflect their true relationships. The main objective of this thesis is to analyse an expanded character set of traditional and new characters to propose an unambiguous phylogeny of the subfamily. In addition, the position of the subfamily relative to other Termitidae, and the overall phylogeny of the Isoptera will be reviewed.
CHAPTER 2

MATERIALS AND METHODS

2.1 SPECIMENS EXAMINED

Most material examined is in the Australian National Insect Collection (ANIC), Canberra. Type material lodged in other institutions was borrowed and examined during the preparation of the Zoological Catalogue of Australia: Isoptera Section (Watson, Miller & Abbey 1997). Type material examined, including type material borrowed from other institutions, is listed below. Many of the species discussed in Chapter 7 are not represented in the ANIC: verified specimens of those species were examined at the American Museum of Natural History (AMNH), New York.

I did not see the type soldier of *Termes cornigera* Motschulsky, lodged in the Hagen collection, Museum of Comparative Zoology, Harvard. The description in section 1.3.1 is based on a winged adult and associated soldier and worker of *N. cornigera* from the type locality, "Panama", compared with the type by A.E. Emerson.

All material is ethanol preserved and was examined, measured and, where necessary, dissected under ethanol.

2.1.1 Type material examined

In addition to more than 2,500 series of Nasutitermitinae in the Australian National Insect Collection, representatives of genera and species not represented in the ANIC, as well as type material lodged in other institutions was borrowed and examined.

Abbreviations below refer to the following institutions.

AMNH American Museum of Natural History, New York.
ANIC Australian National Insect Collection, Canberra.
NHRM Naturhistoriska Riksmuseet, Stockholm.
NHMW Naturhistorisches Museum, Vienna.
NMV National Museum of Victoria, Melbourne.
ZMH Zoologisches Museum der Universität Hamburg, Hamburg.
Nasutitermes corniger


Nasutitermes carinarvonensis

ANIC. Holotype 9055 male adult. Type colony series 10 3971, adult, soldiers, workers (paratypes).

Nasutitermes centraliensis


Nasutitermes coalescens

NHRM. Lectotype soldier. Type colony series, soldiers, workers (paralectotypes).

Nasutitermes dixoni

ANIC. Lectotype 9053 male adult. Type colony series 10 732, adults, soldiers, workers (paralectotypes).

Nasutitermes eucalypti

NHRM. Lectotype soldier. Type colony series, soldiers, workers.

Nasutitermes exitiosus

NMV. Lectotype T-10878 Male adult. Type colony series, adults, soldiers, workers (paralectotypes).

Nasutitermes fumigatus

NHRM. Lectotype female adult.

Nasutitermes graveolus

NMV. Lectotype T-10879 soldier. Type colony series, adults, nymphs, soldiers, workers (paralectotypes). ANIC. Type colony series 10 127, adults, nymphs, soldiers, workers (paralectotypes).

Nasutitermes kimberleyensis

NHRM. Lectotype soldier. Type colony series, soldiers, workers (paralectotypes).

Nasutitermes longipennis

AMNH. Lectotype soldier. ANIC. Type colony series 10 87, adult, soldiers (paralectotypes).

Nasutitermes magnus

AMNH. Lectotype soldier. ANIC. Adult, soldier, workers (paralectotypes).

Nasutitermes pluvialis

NHRM. Lectotype soldier. Type colony series, soldiers, workers (paralectotypes).
Nasutitermes projectus
   ANIC. Holotype soldier 9067. Type colony series 10 1544, soldier, worker (paratypes).

Nasutitermes smithi
   ANIC. Holotype soldier 9056. Type colony series 10 2241, adults, soldiers, workers (paratypes).

Nasutitermes torresi
   ANIC. Holotype soldier 9057. Type colony series 10 17707, Adults, soldiers, workers (paratypes).

Nasutitermes triodiae
   ANIC. Lectotype soldier 9054. Type colony soldiers, workers (paralectotypes).

Nasutitermes walkeri
   ANIC. Holotype soldier 9058. Female adult, worker (paratypes).

Tumulitermes apioccephalus
   ZMH. Lectotype soldier

Tumulitermes comatus
   ANIC. Holotype soldier 9060. Type colony series 10 75, soldier (paratype).

Tumulitermes curtus
   ANIC. Holotype soldier 9061.

Tumulitermes dalbiensis
   ANIC. Holotype soldier 9062. Type colony series 10 1926, soldiers, workers (paratypes).

Tumulitermes hastilis
   AMNH. Lectotype male adult. Soldier, worker (paralectotypes).

Tumulitermes kershawi
   NMV. Holotype soldier T-10880. Worker (paratype).

Tumulitermes marcidus
   ANIC. Holotype soldier 9064. Type colony series 10 199, queen soldiers workers (paratypes).

Tumulitermes mareebensis
   NMV. Lectotype major soldier T-10881. Type colony, soldiers, workers (paralectotypes).

Tumulitermes nichollsi
   ANIC. Holotype soldier 9065. Type colony series 10 17696, soldiers, workers (paratypes).

Tumulitermes pastinator
   NMV. Lectotype soldier T-10882. Male adult (paralectotype).
Tumulitermes peracutus

NMV. Lectotype major soldier T-10883. Type colony, minor soldiers queen (paralectotypes).

Tumulitermes petilus

ANIC. Holotype major soldier 9066. Type colony series 10 1545, major soldier, minor soldiers, workers (paratypes).

Tumulitermes pulleini

NHMR. Lectotype major soldier. Type colony series minor soldier, worker (paralectotypes).

Tumulitermes recalvus

ANIC. Holotype major soldier 9068. Type colony series 10 2204, major soldiers, minor soldiers, workers (paratypes).

Tumulitermes subaquilis

ANIC. Holotype soldier 9169. Type colony series 10 1556, nymph, soldier, workers (paratypes).

Tumulitermes tumuli

ANIC. Lectotype major soldier 9059. Type colony, nymphs, major soldier, workers (paralectotypes).

Tumulitermes westraliensis

NMV. Lectotype soldier T-10884.

Australitermes dilucidus

ANIC. Holotype female adult 9069. Type colony series 10 4139, adults, nymph, soldiers, workers (paratypes).

Australitermes insignitus

ANIC. Holotype male adult 9118. Type colony series 10 4149, adults (paratypes).

Australitermes perlevis

ANIC. Holotype soldier 9071. Type colony series 10 72, soldiers (paratypes).

Macrosubulitermes greavesi

ANIC. Holotype female adult 9070. Type colony series 10 2659, adults (paratypes).

Occasitermes occasus

ZMH. Lectotype soldier. Adults, workers (paralectotypes).

Occasitermes watsoni

ANIC. Holotype soldier 9072. Type colony series 10 14725, adults, nymphs, soldiers, workers (paratypes).

Occulitermes aridus

Holotype ANIC soldier 9073. Type colony series 10 4333, adults, soldiers, workers (paratypes).
**Occultitermes occultus**

NMV. Lectotype female adult T-10885. Adult (paralectotype).

### 2.2 TERMS USED

Termite literature contains some terms not generally applicable to the majority of insect orders and it is useful to define some of these.

#### 2.2.1 Lower termites

Lower termites refers to all families other than the Termitidae. I regard it as an unfortunate term since it seems to imply that less highly derived taxa are less than perfect. However, I have used it, sparingly, since it remains a convenient alternative to listing the six families Mastotermitidae, Kalotermitidae, Termopsidae, Hodotermitidae, and Serritermitidae by name.

#### 2.2.2 Left mandible index

The left mandible index is the linear distance from the apex of the fused first plus second marginal tooth to the apex of the apical tooth, divided by its linear distance to the apex of the third marginal tooth. The index is widely used to indicate elongation of the apical tooth, which often occurs in derived species.

#### 2.2.3 Series

Series refers to a colony sample. It may consist of any number of specimens of one or more castes from a single colony. Series rarely contain all forms since, even if the sample is large and from a nest rather than a foraging group, all instars/larval stages may not be present concurrently.

#### 2.2.4 Gut segments

The segmentation of the termite gut is discussed in Chapter 4. P1-P4 refer to the proctodeal segments between the midgut and rectum. Most Termitidae possess a "mixed segment", consisting of an overlap of midgut tissue and the first proctodeal segment. The mixed segment has high phylogenetic significance.
2.3 MEASUREMENTS

Measurements of the winged adult and soldier caste generally follow the guidelines of Roonwall (1969). Most were carried out using an eyepiece micrometer fitted to a Wild M5 stereomicroscope. Measurements of mandibular dentition were made using an eyepiece micrometer attached to a Nikon Alphaphot.

Measurements of gut segments are difficult to make due to the fact that the guts of preserved specimens can seldom be uncoiled and straightened into a single plane. Dissected guts were drawn, usually in sections, using a camera lucida attached to the stereomicroscope and the drawings were measured to calculate relative lengths of gut segments.

2.4 DISSECTION

Dissection was carried out under ethanol using jewellers' forceps generally, or "home-made" needles consisting of insect micro-pins mounted on glass or aluminium handles for dissection of the enteric valve. Conventional dissecting needles proved far too large for the enteric valves of smaller species.

Coiling of the gut in situ can sometimes be observed through the cuticle of the abdomen, but usually the cuticle, fat body and malpighian tubules must be removed before all segments can be clearly seen. Guts were drawn in situ to record the relative position of insertion of the enteric valve and the coiling and position of the first proctodeal segment.

Enteric valves were mounted in Berlese fluid or Euparal, either whole or slit down one side and opened out flat. Imago-worker mandibles were mounted in Berlese fluid or Euparal.

2.5 RECORDS

In addition to measurements and observations on colour, pilosity, etc. of adults, workers and soldiers, drawings were made of head capsules, gut segments in situ and uncoiled, and in some cases mandibles. Mounts of mandibles and enteric valves were photographed.
There is a great deal of variation in size, and consequently overall gut length among species. Therefore, schematic drawings of guts reproduced at a common scale were made to facilitate comparison.

2.6 PHYLOGENETIC ANALYSIS

Phylogenetic analyses were carried out using the computer program PAUP 3.0 (Swofford 1990). Throughout Chapters 6 & 7, both the terms "cladograms" and "trees" are used to describe results generated by PAUP. I regard the terms as interchangeable, but generally use "trees" to refer to one or more possible arrangements of taxa, including consensus trees, and "cladogram" to refer to a final chosen or preferred result.

The program MacClade (Maddison & Maddison 1987) was used to manipulate trees in order to quickly evaluate the effect of rearranging the position of particular taxa. MacClade is also useful in that it graphically illustrates the state of a particular character for all branches and taxa.
CHAPTER 3

EXTERNAL MORPHOLOGY

3.1 INTRODUCTION

With the exception of *Occasitermes watsoni* Gay (1974) and *Occultitermes aridus* Gay (1977), there have been no nasute species described from Australia since Hill's (1942) monograph. Early descriptions used characters based on colour, pilosity and antennal segmentation of adults and soldiers, shape of head capsule and rostrum of soldiers, and eyes, ocelli, fontanelle and wings of adults. Following Ahmad's (1950) work on mandibular dentition, mandibular characters were used to help define genera (Emerson 1960) and species (Gay 1974, 1977).

3.2 SOLDIERS

3.2.1 Mandibles

Within the fully nasute genera of the Nasutitermitinae the soldiers show varying degrees of reduction of the mandibles. In what has always been regarded as the most primitive state, as occurs in *Longipeditermes* Holmgren or *Angularitermes* Emerson, the bulk of the mandible is reduced to the level of the molar region but the remains of the blade portion persists as a long conical process, the apex of which corresponds to the apical tooth, and which may bear vestiges of the marginal teeth. The most highly derived mandibles bear no traces of the blade portion. Although Sands (1957) persisted with a diphyletic arrangement of genera, based on imago/worker mandibles, he recognised that the true relationships between them were probably complex and that various stages of "degeneration" were not necessarily homologous.

It is useful to note that, although the soldier mandible is derived from the worker mandible, dissimilar worker mandibles ultimately give rise to remarkably similar soldier mandibles (cf Hare 1937). Emerson regarded this phenomenon as evidence that the fully nasute soldier had evolved twice but Miller (1986) disagreed, arguing that the constriction of the fontanelle was the single mutation which made biting mandibles obsolete. I regard the persistence of points or marginal teeth on the mandibles as an indication of a high degree of conservatism within the mechanisms controlling soldier mandibular patterns.
Although widely used by other authors, I have avoided the term "functionless" when referring to the reduced form of mandible. Such mandibles have several functions: they form a seal for the buccal cavity; the presence of a definite, though reduced, molar region indicates that they probably still perform some function in processing food presented by the workers; and, most importantly, since the adductor muscles serve to compress the frontal gland and expel its secretions, they provide an anchor point against which the contraction of those muscles can work. The macrostructure of the frontal gland and its associated musculature is discussed in Appendix 2.

The Australian genera show varying degrees of reduction of the soldier mandibular blade portion. Some species have relatively long points and a vestigial marginal tooth is sometimes present. In its most advanced form, the anterior edge of the mandible does not bear any trace of a tooth, and is broadly angular or very slightly curved. This character is variable within species and therefore relatively unreliable. Some specimens within a single colony may have mandibular points while others lack points, or bear a point on one mandible only. In spite of this variability, the character is useful as an indicator of trends within genera. Although the degree of loss of the point is erratic, it is extremely unlikely that it could reappear once totally lost in a genus.

In the Australian genera, I regard the loss of all traces of the mandible blade as an apomorphic state. The retention of a point on one or both mandibles, and the presence of a marginal tooth on the mandibular point are plesiomorphic states. The molar tooth (Sands 1957) is rarely present in Australian species. When it does occur, it is regarded as plesiomorphic. The thin patch of cuticle present in some genera discussed by Sands (1957) does not occur in any Australian species.

### 3.2.2 Head capsule

The form of the soldier head capsule has been used extensively as an indicator of relatedness of species or genera (Fig. 3.1). For example, see discussion of the "constricted-headed genera" in Ahmad (1950) and Sands (1957). Constriction of the head capsule must always be regarded as a derived character and Gay (1970) suggested that it is characteristic of the Australian genus *Tumulitermes*.

I suggest that constriction of the head capsule may be a result of overall reduction in soldier size, relative to the workers, from which they are derived, without a corresponding reduction of the soldier's single weapon of defence, the frontal gland. Species with constricted-headed soldiers are often grass or leaf harvesters, which forage on the soil surface or in trees. Such species are more vulnerable to predators and it would be an advantage to have a greater proportion of soldiers to workers in the
Figure 3.1. Examples of unconstricted A, B, and constricted C, D, nasute soldier head capsules. A, B; dorsal and lateral view of soldier head of *Nasutitermes exitiosus* (Hill). C, D; dorsal and lateral view of soldier head of *Tumulitermes marcidus* (Hill). From Hill (1942).
colony for protection. Traniello & Busher (1984), referring to Neotropical nasutes, stated that such species invest in large numbers of soldiers for defence and also showed that the soldiers of Nasutitermes costalis (Holmgren) initiate location of food and communicate its whereabouts to workers. The cost of maintaining a higher proportion of soldiers is lessened if those soldiers are reduced in size. However, there is an allometric problem associated with reduction of soldier size. If for convenience the frontal gland is regarded as spherical, a 20% reduction in diameter results in a 36% reduction in surface area, i.e. secretory surface, and almost 49% reduction in volume. This represents a disproportionate reduction in the colony's capacity to both secrete and store the frontal gland secretions, virtually its sole weapon of defence. It would therefore be an advantage not to reduce the size of the frontal gland in the same proportion as the reduction in size of the rest of the soldier. Since the bulk of the gland is contained in the posterior portion of the head capsule, the result would be a constricted head capsule, with a bulbous rear portion posterior to the antennae. Note that in dimorphic species, the large soldier often has an unconstricted head while the head of the small soldier is constricted.

If constriction of the head capsule is indeed directly linked to a reduction of soldier size, then it would be expected that such soldiers should be smaller, relative to the worker caste from which they are derived, than soldiers with unconstricted heads. Figure 3.2 summarises indices of soldier head-width relative to large worker head-width. Although there is some overlap, it is clear that soldiers with constricted heads are generally smaller, relative to workers, than soldiers without constricted heads. It should be noted that although some data were based on large (n = 10 - 25) samples of each caste from full nest series, such samples were not available for many species and the possibility remains that such series did not contain large workers. In such case, the results would be biased towards the null hypothesis, i.e there is no difference in size, relative to large workers, between soldiers with constricted heads and those with non-constricted heads. The data which generated Fig. 3.2 are discussed more fully in Appendix 3.

I suggest that T. pastinator appears to provide convincing support for the above hypothesis. As will be shown in Chapters 7 & 8, T. pastinator's nearest relatives are unequivocally the N. triodiae group, the workers of which are similar in size. The soldier/worker head-width indices of the other species of the group range between 0.65 and 0.80, whereas that of the constricted-headed T. pastinator is < 0.45 (Fig. 3.2).

As discussed above, constriction of the head capsule is undoubtedly an apomorphic state.
Figure 3.2. Summary of soldier/worker head-width indices for 37 Australian nasute species for which a reasonable range of measurements was available. Although there is some overlap, soldiers with constricted heads are generally smaller than soldiers with unconstricted heads.

- Soldiers with unconstricted heads.
- Soldiers with constricted heads.
- Soldiers of dimorphic species with constricted heads.
3.2.3 Polymorphism

Caste differentiation and polymorphism in the soldier caste in the Nasutitermitinae have been discussed by Noirot (1955, 1969), Pasteels (1965), and McMahan & Watson (1975). Mechanisms of soldier development within the subfamily are variable (Noirot 1969); different-sized soldiers can arise from different (male and female) workers, in which the male or female may be the larger, or from larvae. In the Australian species *Nasutitermes exitiosus* large female soldiers are derived from large workers and small male soldiers from small workers (McMahan & Watson 1975). The two types show very different behavioural patterns and probably have different functions within the colony but although the small soldier's role is obviously aggressive defense, the precise nature of the role of the large soldier is unknown (McMahan 1974).

I observed a marked behavioural difference between the large and small soldiers of *T. recalvus*. In all other species I have collected, the frontal gland secretions are expelled in a series of contractions before or immediately after the soldier is touched, and the gland is usually almost completely emptied when specimens are placed in ethanol. Large soldiers of *T. recalvus* are relatively slow-moving, and could not be induced to contract the frontal gland to expel its contents, either by "teasing", gripping with forceps, or placing in ethanol. The fontanelle pore in the large soldier is relatively large in diameter (Fig. 3.3), and consequently the distance the secretions could be squirted must be reduced compared with a similar-sized soldier with a more constricted fontanelle. This evidence implies a different, but unknown, function of the large soldier within the colony's defence system from that of the small soldier.

Polymorphism is variable within the Australian genera. Some species appear to be rarely dimorphic (Hill 1942; Gay 1974) whereas some are always dimorphic and at least one undescribed species is trimorphic. Throughout this work polymorphism generally refers to "obvious" polymorphism, in which all or nearly all series examined contained more than one form of soldier. If polymorphism is rare it may remain undiscovered in cryptic species known only from a few series of foraging parties. Different behavioural characteristics, for example non-aggression in the large soldier of *N. exitiosus*, may result in one form appearing to be much less common than in reality. Note that an intermediate soldier form in the polymorphic rhinotermitid *Schedorhinotermes seclusus* (Hill) remained undiscovered for more than 50 years because of its close association with the reproductive centre of the colony, with no nests having been examined in detail (Miller 1987).
Figure 3.3. Apex of rostrum and fontanelle pore of major soldier (A) and minor soldier (B) of *Tumulitermes recalvus* (Hill). A & B X390
There is also a possibility that an extremely rare morph may be an aberration; development does not always follow a precise pattern and intercastes are often found in Isoptera (see Watson 1974). Disease or parasitisation may also affect morphology.

In the Nasutitermitidae, and indeed all of the Termitidae, distinct soldier polymorphism must always be regarded as apomorph. Distinct partitioning of forms and functions of different castes is an advanced feature of social insect evolution and more numerous specific morphs indicate a high degree of specialisation (Oster & Wilson 1978; Noirot 1985).

3.2.4 Pigmentation
It is difficult to assess the significance of colour of the soldier and worker. Generally, species which move on the surface either at night or in daylight are much darker than cryptic species. However there are some relatively pale-coloured species which are harvesters and, conversely, cryptic wood-feeding species which are nearly black.

For the purposes of this study, soldier pigmentation has been divided into three broad classes.
- Brown. Soldier head capsule ranges from almost black to light brown.
- Yellow. Basic colour yellow or yellow-brown (sometimes tinged with brown) to very pale yellow.
- Red. Basic colour reddish or orange, but sometimes tinged with very dark brown.

3.2.5 Legs
Species which harvest grass or forage epigeally often have relatively long legs and antennae. This character, expressed as head width/length of hind tibia, is always apomorphic and undoubtedly polyphyletic, occurring in species which are otherwise substantially different morphologically.

3.3 WINGED ADULT

3.3.1 Pigmentation
As with soldiers, slight differences in colour are difficult to quantify. However, pigmentation of nasute adults can be divided into the following broad categories.
- Brown. Entire body more or less uniformly light brown to dark brown, with ventral sclerites, legs and antennae, and sometimes pronotum, uniformly paler than head and dorsal sclerites.
• Yellow-brown. As above, but predominantly yellow rather than predominantly brown.
• Dark brown. Entire body uniformly dark brown. Ventral sclerites, legs, antennae, and pronotum the same colour as, or only very slightly paler than, head and dorsal sclerites.

3.3.2 Pilosity
Pilosity is extremely variable within genera, as is the case for other subfamilies of Termitidae. However, a combination of dull rather than shiny cuticle, and slightly more pilose body and wings, can give a general impression of hairiness rather than smoothness which is readily obvious when comparing specimens.

3.3.3 Wings
Wing venation is more or less uniform throughout the subfamily. Two forms of wings can be distinguished in the Australian species. In the first, the wing membrane is relatively hairy, has many closely-spaced micrasters, and has a smoky appearance. In the second type, hairs, if present, are generally fewer, micrasters more widely-spaced, and the membrane is more or less hyaline, so that the body can be clearly seen through the four wings when folded dorsally. Wings of the second type are usually slightly shorter, relative to total body length, than those of the first type.

3.3.4 Postclypeus
As is the case with mandibular dentition, elongation and inflation of the postclypeus is equivalent in the adult and worker castes, and consequently a valuable character in species in which the adult is unknown. An elongated postclypeus is apomorphic.

3.3.5 Eyes and ocelli
Watson & Perry (1981) related eye diameter and prominence within the termitine genus *Drepanotermes* Silvestri to time of flight, with night-flying species having larger eyes than day-flying species. Little information on time of flight is available for the Nasutitermitinae, other than that both small-eyed and large-eyed species have been collected at lights (personal data and ANIC records), which seems to indicate that eye diameter bears no relationship to time of flight and consequently may have phylogenetic significance.

Eye and ocelli size can be broadly divided into three categories.
• Eyes and ocelli very large and prominent, eyes > 0.3 head width. *(Australitermes)*.
• Eyes large, posterior margins behind posterior limit of fontanelle. Ocelli large, less than their length from, or in contact with, margins of eyes.
• Eyes relatively small, posterior margins not extending past fontanelle. Ocelli relatively small and widely separated from eyes.

3.4 IMAGO/WORKER MANDIBLES

3.4.1 INTRODUCTION
Ahmad (1950) presented a detailed discussion of the phylogeny of termite genera based on the dentition of the imago/worker mandibles. The overall relationships of his proposed phylogenies for various families are generally accepted and are based on the concept that characters of imago/worker mandibular dentition are conservative and that similarities in mandibular structure are indicative of relatedness. Within the Nasutitermitinae, this concept led to the hypothesis that subfamily is diphyletic: two lines with different mandibular structures independently evolved through a mandibulate soldier stage to a series of genera with fully nasute soldiers. The hypothesis was formulated by Emerson (1941) and generally persisted (Emerson 1949, 1960; Ahmad 1950; Sen-Sarma 1968; Krishna 1970) until questioned by Prestwich & Collins (1981) and Miller (1986). However, Sands (1965) had commented that some species did not fit this division exactly, and that although earlier authors stated there was no relationship between mandibular structure and diet, suggested that the loss of transverse grinding ridges on the molar plate was an adaptation to feeding on humus. It must also be noted here that Emerson (1960) "hedged his bets" by stating that species with similar mandibles "are not necessarily closely related because of this character alone" although he reiterated the conservative hypothesis in the same paragraph with the statement "there is no indication that a functional adaptation of the imago-worker mandible is involved" (in the evolution of mandibular dentition) (Emerson 1960, p. 7).

As noted above, Sands (1965) was the first to suggest that alteration of mandibles in the Nasutitermitinae was related to change in diet, implying that elongation of the apical teeth, reduction of marginals, and modification of the molar plate need not be monophyletic. Miller (1986) noted that almost identical mandibular structures arose elsewhere in the Termitidae, in genera or groups of genera adapted to humus feeding. Some mandibular structures, for example the "Subulitermes-type", are clearly linked to diet since they appear in unrelated groups with similar feeding habits, and within the Nasutitermitinae are likely to be polyphyletic. However, there is evidence that change of diet is not necessarily accompanied by marked changes in mandibular structure and that a high degree of conservatism does exist and persists throughout some, but not all, of the genera or groups of genera of the Nasutitermitinae.
Although the most marked modifications to mandibular patterns are usually associated with soil and humus feeding, it is worth discussing at this point an additional example of what I believe is convergence within the subfamily, since it involves reduction rather than elongation of the apical teeth. *Hospitalitermes* Holmgren is an Oriental nasute genus which has become a specialised lichen feeder that forages in the open (Miura & Matsumoto 1995). The mandibles are modified in that the apical teeth are greatly reduced, and the molar plate is very long. The Neotropical genus *Constrictotermes* Holmgren is also a specialised lichen feeder (Mathews 1977) and has similar mandibles to those of *Hospitalitermes*. However, apart from having a similarly large crop, presumably for transporting forage back to the nest, the gut structures of the two genera are very different, particularly in the position of the Malpighian tubules and the form of the mixed segment. This suggests that although lichen feeding requires a particular mandibular pattern, the processing of that food source can be accommodated by different gut structures.

As an example of the converse situation it is useful to refer to the Hodotermitidae as an example of conservatism in the face of dietary change and as a basis for comparison with parallels in the Nasutitermitinae. The proto-termite diet was almost certainly relatively damp decaying wood and the primitive family Termopsidae still largely retains this diet. The Hodotermitidae are undoubtedly close to the Termopsidae but they are specialised grass harvesters and the structure of their imago-worker mandibles is very different from that of the Termopsidae and it must be assumed that it is an adaptation for grass-feeding. *Anacanthotermes* Jacobson is a desert-dwelling hodotermitid genus which, although it does feed on wood, still retains the harvester habit, storing its forage in underground chambers (Harris 1970), and has no modification to its mandibles. This strongly suggests that the adaptation of *Anacanthotermes* to wood-feeding is secondary to the grass-feeding habit which gave rise to the hodotermitid mandibular pattern. The genus *Nasutitermes* contains both wood-feeding and grass-feeding species and although, as will be discussed later, there are slight differences in mandibular patterns, the overall structure is conservative.

Within the Australian nasute genera, there are several recognisably different mandibular patterns. The true humus-feeding genera *Australitermes* and *Macrosubulitermes* have "typical" humus-feeding mandibles with elongate apical teeth, reduced marginals and modified molar plate. As discussed in section 6.2.1, *Nasutitermes* has mandibles of a primitive type, more primitive even than those of the Neotropical genus *Syntermes* Holmgren which has been regarded as closest to the ancestral stock which gave rise to the Nasutitermitinae (Krishna 1970). All species of *Syntermes* are specialised grass and leaf harvesters (Constantinò 1995). Many *Nasutitermes* feed entirely on relatively undecayed
wood whereas others harvest grass but show very little alteration in mandibular structure from the basic pattern. In genera other than *Nasutitermes*, the mandibles are variously modified but so little is known of the biology of most species that it is difficult to relate such changes to diet.

Throughout this work, while recognising that departures from the basic pattern of *Nasutitermes*-like mandibles are probably a result of dietary change, I have regarded the imago/worker mandibular structure as a conservative character and recognise that dietary changes can occur without corresponding mandibular changes. Dissimilarities in mandibular structures, therefore, must be given a great deal of weight when comparing otherwise similar taxa. In contrast, similarities in mandibular dentition have been regarded with caution and the likelihood of possible convergence has been examined thoroughly.

3.4.2 Relative size of apical tooth
Throughout the Isoptera a relatively small apical tooth, approximately equal in size to the first marginal tooth, must generally be regarded as plesiomorphic. In the Termopsidae and Rhinotermitidae there are three marginal teeth on the left mandible, as occurs in cockroaches, and the apical tooth is small. Dentition is modified in Mastotermitidae and Kalotermitidae but the apical teeth remain small. Within the Termitidae, the apical tooth remains relatively small throughout the Macrotermitinae but all other subfamilies contain genera in which the apical tooth is enlarged, with a relatively wide angle between its posterior edge and the anterior edge of the first plus second marginal teeth, which are fused.

Within the Australian genera, I regard the pattern found in *N. exitiosus*, in which the apical tooth of the left mandible is about the same size as the fused first plus second marginal tooth, as the plesiomorphic state. Elongation or reduction of the apical tooth are derived states. Elongation of apical teeth in *Occasitermes, Occultitermes, Australitermes* and *Macrosubulitermes* has been discussed by Emerson (1960), Gay (1974, 1977) and Miller (1984). Marked reduction of the apical teeth occurs in only one described Australian species, namely *N. projectus*.

3.4.3 Cutting edge of left mandible
On the left mandible, there is a blade-like cutting edge between the posterior edge of the first plus second marginal tooth and the anterior edge of the third marginal tooth. In *Nasutitermes* it is straight or slightly concave as in *Syntermes*, and this state is plesiomorphic. In its more derived form, a distinct indentation appears immediately anterior to the third marginal tooth (Fig. 3.4). This rounded notch is not homologous
with the well-defined posterior edge of the second marginal tooth evident in some Macrotermiteinae (see section 6.2.3).

3.4.4 Vestigial subsidiary tooth
In some species, there is evidence of a vestigial subsidiary tooth at the base of the anterior edge of the first marginal tooth of the right mandible. This tooth is well-developed in the Termopsidae and Rhinotermitidae and also occurs in the Macrotermiteinae. It is always regarded as a plesiomorphic character (Ahmad 1950).

3.4.5 Second marginal tooth, right mandible
This tooth is never well-developed; in its primitive state it has short anterior and long posterior edges, with the angle between them ca 90°. This angle, and the angle between the posterior edge of the first and the anterior edge of the second marginal, become more obtuse as the tooth undergoes reduction. In the highly derived Australitermes it is vestigial or absent.

3.4.6 Molar region
The basal part of each mandible consists of a region variously adapted for grinding. In its plesiomorphic form, as found in the families of lower termites, it is a broad plate, the surface of which consists of a series of more or less equal-sized transverse ridges. On the right mandible the plate is almost flat or slightly convex; on the left it is slightly concave, with fewer ridges. Sands (1965) discussed the modification of the molar region with reference to Ethiopian genera and suggested changes were related to changes in diet. In the Australian species, I regard the reduction in number and prominence of the molar ridges, the increase in size and/or modification in shape of the anterior first and second ridges, the shortening of the molar area relative to the mandible blade, and a deeply concave molar plate as apomorphic states.

3.4.7 Summary
There are two disadvantages in reliance on patterns of imago/worker mandibular structure. The first is that mandibles are subject to wear and the apparent dentition may be greatly altered as the mandibles are ground down. It is not always possible in a small series to select a recently-moulted individual with unworn mandibles for study. The second disadvantage is that mandibular dentition may vary between castes, i.e. the winged adult and the worker, or between various worker forms or nymphal instars. For these reasons, characters are based on a rather more general view of trends in mandibular patterns, rather than individual measurements and indices. However, when large series of individuals are available for study, for example from mound-building species, indices based on measurements of mandibular teeth can be useful.
Figure 3.4. Worker mandibles of A *Nasutitermes exitiosus* and B *Tumulitermes hastilis*, showing notch (arrowed) anterior to left 3rd marginal, and highly modified right molar region typical of *Tumulitermes*. 
CHAPTER 4

GUT STRUCTURE

4.1 INTRODUCTION

Although the digestive tract of termites has undergone considerable modification within families and lower groups (Noirot 1969), only comparatively recently have characteristics of such modifications been used to illustrate taxonomic relationships. Grassé & Noirot (1954) proposed the subfamily Apicotermitinae largely on the basis of the digestive tract. Noirot & Kovoor (1958) and Kovoor (1969) made comparative studies of some genera of the Termitinae and Nasutitermitinae. Sands (1972) and Miller (1986) used a complex of characters of the digestive tract to revise the phylogenies of the Apicotermitinae, the Termitinae and the Nasutitermitinae, and as diagnostic characters in determining relationships at genus and species level in the Apicotermitinae (Sands 1972) and Termitinae (Miller 1991).

The basic structure of the gut of the Australian genera of Nasutitermitinae (Fig. 4.1) is close to that of the Termitinae. The oesophagus passes through the thorax and opens into an asymmetric crop which lies more or less centrally in the anterior part of the abdomen. The crop terminates in a funnel-shaped muscular gizzard whose narrow end is inserted into the midgut.

The beginning of the midgut is often asymmetric, with a single anterior bulge which represents a vestigial caecum. The midgut usually forms an oblique junction of varying length with the hindgut, the so-called mixed segment, although in some genera the junction is straight. In the Australian genera, the Malpighian tubules are always attached to the midgut at its junction with the hindgut.

The first segment of the hindgut is tubular and is very variable in length between genera. It terminates in a muscular enteric valve, variously armed with sclerotised spiny plates (usually termed cushions), which is inserted into a voluminous sac-like paunch. The paunch tapers into a variously dilated colonic region, terminating in the rectum.
The gut can usually be seen through the armor of the abdomen and details its subunits can sometimes be seen by dissection. Although the structure of the gut in termite is variable by species, it is composed of the following segments: the oesophagus, crop, gizzard, midgut, mixed segment, first proctodaeal segment, enteric valve, second proctodaeal segment, colon, and rectum.

4.1 THE GUT

The oesophagus is a short tube that connects the mouth to the crop. The crop is a large, thin-walled sac where the termite grinds down the food. The gizzard is a muscular, thick-walled segment that helps to further break down the food. The midgut is the longest segment of the gut and is divided into the mixed segment and the first and second proctodaeal segments. The mixed segment is a narrow tube that leads to the enteric valve, which is a muscular valve that controls the flow of food into the second proctodaeal segment. The second proctodaeal segment is a short, thick-walled segment that leads to the colon. The colon is a large, thin-walled segment that stores undigested food. The rectum is the final segment of the gut and is where the termite evacuates waste products.

Figure 4.1. Schematic diagram of gut of Nasutitermitinae.
4.2 COILING OF THE GUT IN SITU

The gut can usually be seen through the cuticle of the abdomen and, with experience, subfamilies and sometimes genera of the Termitidae can be determined without dissection. Johnson (1979) showed that workers could be identified to species in some cases. For the Australian Nasutitermitinae, the coiling of the gut is rather uniform but the relative length of various segments and consequently the way in which they lie in the abdomen often gives an indication of genus or genus-group. Although quantitative comparisons are difficult, it is useful to compare the overall appearance of the gut structure in situ for various species and genera (Fig. 4.2). Noirot (1995a), noted that coiling of the gut in situ is not only determined by the relative lengths of various segments, but also by torsion of the P3/colonic region, and has phylogenetic significance at family level.

4.3 THE GIZZARD

The armature of the gizzard is reduced in the higher termites (LeBrun and Lequet 1985) and there appears to be little variation in the Australian nasute genera.

4.4 THE MIDGUT

The midgut always appears to be relatively uniform in length in situ because of variation in the way in which the gut is coiled, with the midgut forming part of an anticlockwise loop enclosing the posterior paunch/colon junction and the salivary gland reservoirs. Most of the variation in gut proportions is in the relative lengths of the various segments of the hindgut. Because of variation in size between individuals and between species, comparisons can only be made if measurements are related to a constant. Throughout this study, comments on the length of various gut segments, including the mixed segment, are relative to the length of the tubular portion of the midgut.

In the lower termites, the midgut is always relatively short (Noirot 1969). Lengthening of the midgut and its extension into a mixed segment are derived states, although, as discussed in the following section, the mixed segment may be secondarily reduced.
Figure 4.2. Coiling of gut in situ in representative genera of Nasutitermitinae. A *Nasutitermes cornigera*. B *Tumulitermes hastilis*. C *Occasitermes occasus*. 
4.5 MIXED SEGMENT

Variation in relative length of the mixed segment in the Nasutitermitinae always involves reduction. In the lower termites and in the Macrotermiteinae, there is no mixed segment and the Malpighian tubules are evenly spaced at the junction of the mid- and hindgut. In the Nasutitermitinae the tubules are attached in two pairs, variously spaced but always in the same half of the midgut, on the opposite side to the mesenteric extension of the mixed segment. The extension is bilobed in some primitive mandibulate genera in which the first proctodeal segment is dilate, but its usual form in most of the subfamily is parallel-sided and about the same length as the tubular portion of the midgut. In this respect, it resembles the form found in many Termitinae.

A well-developed mixed segment is the plesiomorphic state in the subfamily. Evidence that change in length involves reduction rather than elongation is given by the position of attachment of the Malpighian tubules. If the extension is absent, as in Macrosubulitermes, the Malpighian tubules all remain on the same side, indicating that the absence of the extension is a secondary loss in the subfamily. A reduced or absent mixed segment, therefore, is an apomorphic state. The mixed segment and a possible mechanism determining the place of attachment of the Malpighian tubules is discussed more fully in Appendix 4.

4.6 FIRST PROCTODEAL SEGMENT (P1)

The first segment of the hindgut, the first proctodeal segment or P1, is uniformly tubular in all the Australian species. The length is variable, it is relatively short in the "Subulitermes" group of genera, and very long in Occasitermes.

A medium-length P1, as found in many Termitinae, entering the P3 in the position shown in Fig. 4.2 B, would appear to be plesiomorphic. Reduction of the P1, as occurs for example in Australitermes, or elongation, so that the junction with the P3 moves to the right and/or the end of the P1 is looped, are apomorphic character states.

In some species in which the end of the P1 forms a loop before its insertion into the paunch, there is a peculiar feature associated with the loop. The inside of the loop is held closed by several bands of longitudinal muscle on both sides which have become detached from the outer wall of the intestine (Fig. 4.3). This character is only easily observed in fresh specimens and extremely careful dissection is necessary. However, such dissection of freshly-killed material has shown that it is not an artefact of dissection.
Figure 4.3A-B. A Posterior loop of P1 of *Nasutitermes longipennis* (Hill) showing detached bands of longitudinal muscle (mb); a anterior, and p posterior spinous areas of enteric valve. B detail of muscle bands (mb).
itself. I assume that the function of the muscle bands is an aid to peristaltic movement of gut contents around the rather tight loop.

4.7 ENTERIC VALVE

In many groups of the Termitidae, the armature of the enteric valve provides extremely useful characters at generic and specific level (Sands 1972; Miller 1991). In most of the Australian Nasutitermitinae, the valve is relatively weakly armed and not very well sclerotized but several patterns of armature do exist. In *Nasutitermes* and some *Tumulitermes* the armature is in two distinct sections; the most anterior has a somewhat asymmetric pattern of large and small cushions with numerous spines, and the posterior part is armed with shorter, alternatively large and small cushions (Fig. 4.4). In some species, the armature is greatly reduced, the anterior part sometimes disappearing almost completely (Figs 4.5, 4.6). In other species, the anterior part may be reduced while the posterior armature is strengthened with increased sclerotisation or long spines (Fig. 4.6).

The extended armature of the *Nasutitermes* type is plesiomorphic, as similar structures are found in some Termitinae. Reduction of armature, or increase in size of spines or degree of sclerotisation are apomorphic character states.

4.8 THIRD PROCTODEAL SEGMENT (P3 OR PAUNCH)

The size of the P3 varies greatly with gut contents so that it is difficult to make comparisons. However in some species the P3 is very weakly subdivided, with a small anterior and a large posterior section. The subdivision of the P3 is an apomorphic character.

4.9 COLONIC REGION

The junction of the P3 and the colon lies anteriorly in the abdomen and is encircled by a loop formed by the midgut/mixed segment and P1. The colon is variable in length and, when short, is straight and more or less dorsal. When elongate, the extra length is accommodated by looping slightly at its anterior end (Fig. 4.2 B-C). In *N. projectus* and some related undescribed species, the colonic region is always slightly dilated. As with other segments of the hindgut (Noirot 1969), a short colonic region is plesiomorphic. Elongation or dilation of the colon are apomorphic character states.
Figure 4.4A-B. Armature of enteric valve of A worker of *Nasutitermes longipennis* (Hill), and B soldier of *Tumulitermes tumuli* (Froggatt). a anterior and p posterior spinous areas.
Figure 4.5. Enteric valve of worker of *Tumulitermes petilus* (Hill). Armature of anterior (a) spinous area is greatly reduced, posterior (p) part less so.

Figure 4.6. Enteric valve of worker of *Tumulitermes marcidus* (Hill). Anterior part (a) is virtually unarmed, posterior part (p) is well-armed with long stout spines.
4.10 MALPIGHIAN TUBULES

4.10.1 General
Noirot (1995a) summarised the information reported to date on the Malpighian tubules, and discussed the taxonomic significance of their number at family and subfamily level. In the Termitidae, there are always four Malpighian tubules. Bignell et al. (1983) discussed the histology of the tubules of two genera of soil-feeding Termitinae, and Noirot et al. (1967) briefly described their course within the gut of the termite genus Cephalotermes. Sands (1972) described the "malphigian knot" formed by the tubules in the Apicotermitinae and discussed its usefulness as a taxonomic character. In the Nasutitermitinae the tubules always have their origin at the junction of the midgut and hindgut and terminate next to the rectum. Morphological aspects of the tubules which were examined as having possible relevance to this study are their point of attachment at the midgut-hindgut junction, their degree of dilation at their proximal ends, and the position of each tubule relative to the others and to other parts of the gut.

4.10.2 Attachment to the midgut
In cockroaches, in all the "lower" families of termites, and in the Macrotermiteinae and some Termitinae, the junction of the mid- and hindgut is a simple transverse join and the Malpighian tubules are evenly spaced around the gut. Noirot (1995a), on the basis that embryonic and first-instar cockroaches and termites have four evenly spaced tubules regardless of the final number, suggests that four is the basal number common to cockroaches and termites. The number and spacing has relevance to discussion of the mixed segment, treated in detail in Appendix 4.

In the Australian Nasutitermitinae, the tubules are attached either in two distinctly separated pairs, or all four tubules arise very close together. In some species in which the tubules are attached together, the point of attachment is at the apex of a short extension of the midgut which forms a "peninsula" into the hindgut portion of the mixed segment (Fig. 4.7). Since outgroup comparison shows even spacing to be primitive in Isoptera, the attachment of all tubules together, and the extension of the midgut at the point of attachment, are derived states. In Nasutitermes cornigera and most of the Australian species currently recognised as Nasutitermes, the Malpighian tubules are attached in two pairs, whereas in Tumulitermes tumuli and many other species currently placed in Tumulitermes, they are attached together.

Roisin & Pasteels (1996) suggested that attachment could vary within a species (N. gracilirostris Desneux from Papua New Guinea) but qualified that suggestion by stating
Figure 4.7. Mixed segment and attachment of Malpighian tubules in two undescribed species of *Tumulitermes*. Tubules are swollen at their proximal ends and are attached together at the apex of a narrow extension of the mesenteron.
that "N. gracilirostris" possibly represented "several closely related species". I have not noted "variation" of the extent referred to by Roisin & Pasteels in any Australian species.

4.10.3 Proximal dilation
Marked dilation of the proximal portion of the Malpighian tubules (Noirot & Noirot-Timothee 1969) appears to be unique to the Nasutitermitinae. In the Macrotermnitinae and some Termitinae the tubules are slightly thicker at their proximal end, but never to the degree found in, for example, Nasutitermes and Tumulitermes. In some species, for example N. projectus, dilation is not well-developed and this must be regarded as retention of a primitive state. Degree of dilation within species and even within colonies was found to be variable and too difficult to quantify to be useful as a reliable taxonomic character.

4.10.4 Position of tubules
Malpighian tubules in termites are long; many times the length of the abdominal cavity. In some families, for example Mastotermitidae or Rhinotermitidae, they are relatively robust and thick-walled. In the Nasutitermitinae, apart from the short proximal portion, they are narrow and fragile.

There is very little information on the position of the tubules within the gut, other than their point of attachment and the fact that they are closely associated with the mesenteric part of the mixed segment where it exists (Noirot et al. 1967, Noirot 1995a). Consequently, I traced the precise position of the tubules in a variety of species in order to determine: 1) whether their position was fixed as opposed to "floating" within the haemocoel, and 2) if fixed, whether there is variation in position which could be used as a taxonomic character.

Tracing of Malpighian tubules requires extremely delicate, fine dissection and is often difficult or impossible to carry out with preserved specimens. Removal of fat or other obscuring tissue in such specimens, or "untangling" of the tubules themselves, causes them to break. Consequently, freshly-killed termites were partially dissected (to the extent that the abdominal cuticle and some fat body were removed), and left for 24 hours in absolute ethanol to harden tissue before attempting to trace tubules. A comparative study of the course of the Malpighian tubules was carried out on the following species for which fresh material was readily available; Nasutitermes smithi, N. triodiae, N. longipennis, N. graveolus, N. eucalypti, Tumulitermes tumuli, T. pastinatoor, and T. hastilis. In addition, Microcerotermes nervosus, Amitermes vitiosus, Macrognathotermes sunteri and Lophoterms septentrionalis, all Termitinae, were examined for outgroup comparison.
4.10.5 Pathways of tubules

4.10.5.1 Tubules 1 & 2
Tubules were numbered 1-4. No. 1 has its proximal end most antero-dorsal in situ, that is, to the left when facing the attachment point(s) with the gut uncoiled and midgut uppermost (Fig. 4.1). Tubule 1 follows the curve of the midgut-P1 loop, tightly encircling the P3-colon junction. When adjacent to its starting point, it closely adheres to the mesenteric part of the mixed segment (the mesenteric extension), doubles back close to the attachment point and then passes beneath the midgut and proceeds towards the rectum to the left of the colon, forming an anterior loop before terminating at the rectum (Fig. 4.8). Tubule 2 follows the same path, except that its final loop is shorter and close to the rectum.

4.10.5.2 Tubule 3
Tubule 3 follows the same path as 1 and 2 until it is opposite its attachment point. It then passes under the midgut and joins the mesenteric extension from the opposite side to 1 and 2. After forming a loop which adheres to the mesenteric extension, it proceeds towards the rectum to the right of the colon, forming another loop anterior to the rectum (Fig. 4.8).

4.10.5.3 Tubule 4
Tubule 4 follows the curve of the midgut-P1 only as far as the end of the mixed segment. It does not encircle the P3-colon junction, but instead forms a long posterior loop before attaching to the distal end of the mesenteric extension. It does not form a long loop on the mesenteric extension, but proceeds to a point approximately opposite its origin, then passes to the right of the colon towards the rectum (Fig. 4.8). From near the rectum, tubule 4 forms a narrow anterior loop, the apex of which lies very close to the apex of its first posterior loop, before terminating close to the rectum.

4.10.5.4 Summary
The patterns described above were more or less the same in all species examined, with the exception that the "mesenteric loops" were of course shorter in species with very short mixed segments. I had no opportunity to examine fresh specimens of the comparatively rare *Macrosubulitermes*, which lacks a mixed segment.

There were slight variations in the lengths of the posterior loops, but these are difficult to quantify. Overall, the pathway taken by each tubule relative to each of the others is constant for all of the Nasutitermitinae examined and consequently, if this uniform pattern
Figure 4.8. Schematic representation of pathways of proximal portions of Malpighian tubules of *Nasutitermes exitiosus*. 

a = tubules 1 & 2  
b = tubule 3  
c = tubule 4.
persists across the subfamily, it has little taxonomic value in the context of this study. It will be useful to continue to examine further species whenever fresh material is available, particularly those Termitidae which lack a mixed segment, and a wider range of genera within each subfamily.

The general pattern of the Malpighian tubules in all the Nasutitermitinae examined can be briefly described as follows.
1 & 2 encircle the posterior P3-anterior colon junction, form a loop along the mesenteric extension beginning and ending at its proximal end, then pass under the midgut and proceed towards the rectum to the left of the colon, forming a loop in the posterior part of the abdomen.
3 encircles the posterior P3-anterior colon junction, passes under the midgut, forms a loop along the mesenteric extension beginning and ending at its proximal end, then proceeds towards the rectum to the right of the colon, forming a loop in the posterior part of the abdomen.
4 forms a long loop posterior to the mixed segment, then joins the mesenteric extension at its distal end; when close to its point of origin, it passes towards the rectum to the right of the colon, forming a long loop from near the rectum to near the apex of its first loop.

**4.10.6 Other Termitidae**

Of the Termitinae examined, the basic patterns in *M. nervosus* and *A. vitiosus* are similar to that of the Nasutitermitinae, except that the initial loop of tubule 4 is shorter, as are the most distal loops. Given that the Macrotermitinae lack a mixed segment and have a primitive arrangement of evenly-spaced Malpighian tubules, and the structure of the mixed segment and attachment of the Malpighian tubules of the Apicotermitinae are unique to that subfamily (Sands 1972), this observed similarity suggests a common origin of Nasutitermitinae and Termitinae.

In *M. sunteri*, which is a highly specialised soil-feeding genus (Miller 1991), the basic pattern remains the same, but tubules 1, 2 and 3 form loops which closely adhere to the mesenteric extension before looping the P3-colon junction, and each then forms a second loop, corresponding to the first mesenteric loop of *N. exitiosus* or *M. nervosus*, over the mesenteric extension before proceeding to the rectum. Tubule 4 also adheres to the mesenteric extension before forming its posterior loop and returning to pass once from distal to proximal over the mixed segment (Fig. 4.9). The path of tubule 4 in *L. septentrionalis* is even more convoluted, forming a series of short and long loops closely associated with the mesenteric extension (Fig. 4.10).
Figure 4.9. Coiling of Malpighian tubules in *Macrognathotermes sunteri* (Hill). Secondary mixed segment loops separated to avoid obscuring primary loops.
Figure 4.10. Coiling of Malpighian tubule 4 in *Lophotermes septentrionalis* (Hill).
It is worth discussing at this point Noirot et al.'s (1967) illustration of part of the gut of *Cephalotermes rectangularis* (Termitinae). This genus is regarded as close to the *Amitermes* group (Snyder 1949; Ahmad 1950), but the pathways of the Malpighian tubules are illustrated as being different from that described above in the following ways. Tubule 3 does not pass under the gut before looping on the mesenteric extension, 1 & 2 do not pass under the gut after looping, and 4 joins the mesenteric extension at its proximal, rather than distal end. I had no access to fresh specimens of *Cephalotermes* and consequently could not verify the pathways, but if Noirot et al.'s interpretation is correct, there may be variation within subfamilies which could be taxonomically useful.

### 4.10.7 Conclusion

In summary, the Malpighian tubules of all Australian Nasutitermitinae examined follow the same well-defined pathways from their origin at the mesenteron-proctodaeum junction to their termination close to the rectum. For part of their length they are closely associated with the mesenteric part of the mixed segment where one exists. There is too little variation in the species examined for reliable taxonomic characters to be derived from the pathways. The basic patterns observed occur outside the Nasutitermitinae, and examination of some highly specialised soil-feeding Termitinae indicate that there is sufficient variation in some groups that the pathways taken by their Malpighian tubules may provide useful taxonomic information.
CHAPTER 5

BEHAVIOUR

5.1 INTRODUCTION

Although behaviour, as expressed for example in the form of nest construction or feeding habit, has occasionally been discussed in terms of its relevance to phylogeny (Emerson 1938; Noirot 1970; Constantino 1995), there is often so little information available for the majority of taxa under review that it is disregarded in phylogenetic analyses. This section sets out to examine behaviour in order to try to determine at what level(s) it can usefully be incorporated into phylogenetic analyses.

I have discussed elsewhere diet and foraging behaviour within the Nasutitermitinae and at higher levels (Miller 1992 (Appendix 5)). Variation in behaviour between individual species within a particular taxonomic group may be considerable. Emerson (1938) noted that although there were close similarities among groups of related species, which supported his hypothesis that nesting behaviour reflected phylogeny, there were also striking differences for which he offered no explanation. I here investigate the possibility that the development of a particular behaviour is governed by parameters which delineate a track or pathway which reflects evolution of behaviour generally within Isoptera, and that end behaviour is the observed result of a fixed life habit pattern. If this is true, then close similarities in observed behaviour between species need not reflect phylogenetic relatedness.

Abe (1984, 1987, 1991) introduced the concept that 'life types' of termites could be divided into six forms of nesting-feeding behaviour within three broad categories (Fig. 5.1), although he did not link behaviour with phylogeny.

- One-piece: termites which consume only the wood in which they nest.
- Intermediate: termites which construct galleries and consume wood in addition to the nest wood.
- Separate: termites in which nesting and feeding sites are separate.

I propose to use Abe's concept as a starting point and expand it to the extent that a model can be designed (Fig. 5.2) which covers known isopteran life habits and the rules or constraints governing their development. The model illustrates the major termite
behavioural traits described below (section 5.2) and implies that derived forms of behaviour have prerequisite patterns which reflect general patterns of evolution of behaviour in Isoptera.

![Diagram of termite life types]

**Figure 5.1.** Abe’s termite"life type" categories. Based on Abe (1984).

It is important that the model be developed fully before assigning a particular species or other taxon a position within it, although of course during the development process the known behaviour of all members of the order must be considered. For example, much discussion of termite phylogeny begins with Mastotermidae, since morphological characters suggest that the family is closest to the hypothetical "proto-termite", and it is tempting to place *Mastotermes* near the base of any developmental model. However, it will be seen that in terms of behaviour, *Mastotermes* is far removed from the assumed ancestral pattern.
Derived behaviour such as parasitism or food storage always implies, and is dependent on, a series of steps or stages of development.

It is far beyond the scope of this work to investigate the much-discussed relationships between termites and the remainder of the Dictyoptera, but I believe it reasonable to assume the ancestral form to be more or less cockroach-like, as originally indicated by Cleveland (1934), and discussed by Hennig (1981), Nalepa (1984) and Thorne & Carpenter (1992). Therefore, in the absence of fossil or other evidence to the contrary, the model relies on a basic assumption that the ancestor of the Isoptera lived at or close to the forest floor and had an omnivorous or predominantly xylophagous diet. This is the only assumption made in constructing the model that is not supported either by personal...
observation or the literature\(^1\). Before discussing the range of behaviour exhibited by modern Isoptera, it is necessary to mention that this assumption actually consists of two possibilities that have been fundamental to arguments on behaviour (particularly nesting behaviour) to date (Sewell 1978). Emerson (1938), combining dry wood and moist decayed wood, regarded excavation within wood, with no contact with soil, as the most primitive form of nesting behaviour. Weidner (1966) proposed that the ancestral termite dwelt in soil and loss of soil connections evolved independently in different groups. Both views are untestable since they are based on the behaviour of an unknown, supposed ancestor. In the absence of evidence, it remains that the ancestral habit could be regarded as either, or both, and either can be accommodated by the proposed model (Fig. 5.2).

### 5.2 BEHAVIOURAL PATTERNS

#### 5.2.1 Dampwood feeding

In the form illustrated by Figure 5.2, the model assumes that the basic expression of isopteran behaviour is living within, and consuming, the food source in the form of decayed, \textit{i.e.} partially digested, wood. This corresponds with Abe’s (1984) "one piece type", and is shared by some xylophagous cockroaches. Note that there is also the implied assumption at this point that the "proto-termite" or its immediate descendant is already partially or totally reliant on cellulose or its by-products.

#### 5.2.2 Drywood feeding

An alternative "one piece" option in terms of diet is the development of the ability to colonise and consume dry, relatively undecayed wood. Such a change could be initiated in response to drier conditions generally, or simply by expansion into an unexploited niche, thereby avoiding competition. Such a niche is generally in the form of dead wood in standing trees rather than wood, in contact with the soil, which is rapidly subject to decay, and therefore drywood feeding is unlikely to be ancestral to feeding on moist decayed wood. Colonisation in this sense refers to the founding of a new nest by newly paired adults which have flown from an established colony or colonies. As with dampwood feeding, colonies are confined to, and consume, their food source.

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\(^1\)Hennig (1981) qualified his and other authors’ assumptions concerning cockroach-termite relationships with the following statement: "In themselves these \textit{ad hoc} hypotheses have no value. However, they can be useful, as here, when they are used simply to get around the difficulties that stand in the way of a suggestion which, for other reasons, appears to be entirely plausible."
5.2.3 Soil tunnelling

The great disadvantage of consuming the nest site, as is the case in the preceding two behavioural patterns, is ultimate starvation, and the only way to avoid it is to seek additional sources of food. This has been accomplished in termite colonies in two ways. The first is by relatively quickly and synchronously completing adult development and seeking to establish new colonies as described above. A disadvantage of this is that the social structure of the parent colony is lost, and it runs the risk of becoming extinct if there are no suitable new nest sites available, or if all alates are killed by predators or fail to find a partner. A second method is by extending living/feeding tunnels, commonly referred to as galleries, into the soil and thence to additional food either within the soil or on its surface. I suggest that the ability to establish and maintain a network of galleries, *i.e.* a territory with the nest or reproductive centre as its focal point, has been enormously important in determining the success of the Isoptera. Soil tunnelling is vital to almost all of the known life habits and in those cases where it does not occur, as will be discussed later, it has probably been secondarily lost.

As noted above, there is an alternative that affects the order of discussion of patterns, although not the importance nor placement within the model of soil tunnelling. The alternative is Weidner’s (1966) view that the ancestral termite was an animal that tunnelled within soil rather than ranging at the soil-litter interface. This option does not affect the model at all when it comes to placement of taxa within it. For example, as a general rule, modern termopsids and kalotermitids do not tunnel in soil. However, under some circumstances, such as in an island environment where there is little or no competition from other families (Lenz 1994), tunnelling does occur. This suggests either an expression of a previous behavioural trait which has been lost, or a latent ability to proceed through the developmental pathways described here which is normally suppressed. Both possibilities are implied by the reciprocal arrows at the base of the model. The true pattern could only be resolved by the unlikely discovery of fossils which illustrate behaviour.

5.2.4 Nest moveable/not reliant on wood

The next two characteristics are considered together because they are very often, although not exclusively, linked. Following the establishment of connections between food sources is the ability to move not only foraging workers, but also the reproductive centre of the colony, to a new site. This can be, but is not necessarily, linked to the presence in the colony of reproductives which are supplementary to the founding pair. An important aspect, in terms of sociality, of this behaviour is that the new nest site is chosen by workers and soldiers, the sterile castes, rather than by the reproductives (Emerson 1938). At this point in behavioural development there occurs the opportunity to establish a nest
site which is no longer necessarily also a food source. This can be achieved by maintaining the original position of the nest but replacing the consumed wood with an alternative, surrounding, protective substance (mound construction). Alternatively, a nest can simply be excavated within the soil, or constructed of woody material (carton).

5.2.5 Wood/other food source outside nest
If the termite colony no longer relies on a single, relatively massive volume of wood as both food source and nest site, it has the opportunity to begin to vary its diet. Many groups have retained wood as a food source, but there are a variety of other diets ranging from living or dead grass or leaves, to litter or even lichen (Noirot 1992; Bignell 1994).

5.2.6 Nest as food store
Harvesting/foraging activity has associated problems. Since the harvesters can no longer work within the shelter of their food source, some mechanism must be evolved for protection during feeding. This can be resolved by not feeding at the source, but instead carrying the food to the nest to be stored within specially-constructed chambers. An alternative form of food storage is associated with construction of a nest largely from partly digested food, so-called "carton" nests, which still have value as food.

5.2.7 Fungus cultivation
Once the nest is established as a food store, there arises the opportunity to modify the food in some way before final consumption. Maceration and/or partial digestion of the collected material (the manufacture of "carton") is the first phase, and this has led in one taxon, the Macrotermiteinae, to the deliberate cultivation of symbiotic fungi to assist in the digestion of the food (Sands 1969).

5.2.8 Humus feeding
This, and the following, behavioural characteristics are slightly less easily defined than those discussed so far. In several groups, and probably often but not exclusively as a consequence of litter feeding, there has developed an ability to utilise humus and soil as a food source. This ability is clearly highly derived and is usually accompanied by marked morphological change, particularly in the worker caste, which is in contrast with all other behavioural steps discussed. However, there is some overlap with other patterns. Wood- or grass-feeders sometimes ingest mineral soil, possibly as a consequence of soil tunnelling, and some humus-feeders occasionally ingest decayed wood or litter (Honigberg 1970).
5.2.9 Inquilinism/parasitism

The soil-feeding habit can lead in turn to inquilinism/parasitism, of which many degrees exist, the most basic being consumption of parts of the nests of other termites. "Parasite" in this sense refers to a colony, rather than an individual, level. For example, I regard the termitine genus *Incolitermes* Gay as a parasite since its habit of consuming the fabric of the nursery of its host (Gay 1966) must surely affect host colony vigour. Parasitism could also develop from a harvesting/storing habit, in the form of "stealing" other termites' food stores.

A theoretical next step from parasitism is carnivory, whereby not only the nest or food stores of the host are consumed, but the hosts themselves are eaten. This behaviour would not involve radical change, since termites very often eat their dead, and Thorne (1990) has shown that they will consume other insects. Carnivory as a life habit is not known to exist within Isoptera, although Sands (in Emerson & Krishna 1975) suggested it as a possible function of the unusual worker mandibles of *Serritermes serrifer* (Bates), a unique species which may be an obligatory inquiline of *Cornitermes* (Costa-Leonardo & Camargo 1990).

The model, or portions of it, can provide graphic representation of relatively simple or more complex aspects of termite behaviour (Fig. 5.3). It should be noted that although most patterns figured later in this chapter are represented, for simplicity, as portions of the total model, the actual representation of the life habit of a mature termite colony is circular, as indicated in Figure 5.3. In this respect, the ontogeny of behaviour of a colony, from founding adult pair to mature colony in which all castes and instars are represented, reflects the evolutionary development of termite behaviour generally.

5.3 SPECIFIC TAXA AS EXAMPLES

It remains to consider some specific taxa in terms of the model illustrated and discuss whether there are indications for its usefulness in phylogenetic discussions.

5.3.1 *Mastotermes*

As discussed above, on the basis of its many primitive morphological character states, *Mastotermes* is very often placed at the base of phylogenetic trees (Krishna 1970). However, its colonies construct extensive and often elaborate (Hill 1942) gallery systems, are highly mobile in terms of moving their reproductive centre (Miller & Paton, unpublished data) although they are still reliant on a woody supporting/protective frame, and feed on a large variety of woody materials, often within a single colony's territory.
Figure 5.3. Primitive, *Archotermopsis wroughtoni* Desneux, and derived, *Nasutitermes magnus* (Froggatt), patterns of behaviour in termites.
The very large colony size and rigid caste structure (Watson & Sewell 1985) of *Mastotermes* are additional derived features (see also section 5.4). Thus a form resembling modern *Mastotermes* in its behaviour could not possibly be ancestral in behavioural terms to either the Termopsidae or Kalotermitidae. Thorne and Carpenter (1992) noted that the Mastotermitidae is defined by ancestral rather than derived character states and Noirot (1995) suggested that sternal gland structure indicated a sister-group relationship between Kalotermitidae and Termopsidae rather than between Mastotermitidae and Kalotermitidae.

Clearly, the traditional placement of *Mastotermes* is unsatisfactory, and behavioural information seems to strengthen this view. The particular case of *Mastotermes*, with its multitude of primitive morphological character states combined with complex nesting and soil tunnelling behaviour, would appear to support Weidner’s (1966) opinion that soil tunnelling was primitive, and has been largely lost in the Kalotermitidae and Termopsidae.

5.3.2 Termopsidae/Hodotermitidae
The Hodotermitidae as recognised by Grassé (1949) is often regarded as a subfamily of the Termopsidae (Snyder 1949; Krishna 1970). However, while the Termopsidae generally feed within relatively moist decayed wood, all hodotermitid genera are specialised harvester/foragers which store forage in nests that are not reliant on wood. I suggest that hodotermitid behaviour strongly supports Grassé’s conclusions.

5.3.3 Prorhinotermes
It is worth discussing *Prorhinotermes* as an apparently anomalous example. Despite their general classification as “lower” termites on a morphological basis, Rhinotermitidae exhibit many highly advanced behavioural traits and the Rhinotermitinae is regarded as the most specialised subfamily. *Prorhinotermes* is usually regarded as the most primitive genus of the subfamily (Ahmad 1952; Gay & Barrett 1983), an assumption that would appear to be supported by its habit of nesting in logs (see Abe 1984). However, an examination of wing venation (Miller unpublished data) reveals highly derived morphological character states anomalous with its supposed primitiveness.

A predominantly seashore- or island-dwelling termite has its dispersal capabilities reduced simply by the possibility that alates have a high chance of ending their flight in water. At least one other derived feature, the regular production of large numbers of apterous neotenic reproductives, enhances the ability of *Prorhinotermes* to perfect what could be regarded as a highly specialised form of behaviour, namely dispersal by way of floating logs. The production of apterous neotenics ensures that high reproductive capability is
retained within the colony rather than dispersed as is the case with alate production. *Prorhinotermes* often exhibits primitive (Abe’s one-piece) behaviour, but is perfectly capable, once established at a new location, of complex soil tunnelling (Gay & Barrett 1983; Miller, unpublished data from Cocos Island). The "one-piece" habit in *Prorhinotermes*, which is in contrast with the remainder of the Rhinotermitidae, is anomalous in that it would appear to be a reversal of the pathways illustrated by the model, given its position as a member of the most highly derived subfamily (Krishna 1970). I suggest that such a reversal would only occur if there were some enormous advantage to be gained. In the case of *Prorhinotermes*, i.e. the advantage of being able to disperse over water and consequently colonise new territory free from competition, as has been recently illustrated in the case of Krakatau (Abe 1984).

5.3.4 Nasutitermitinae

Given the apparent usefulness, as discussed above, of analysing behaviour in tandem with morphology as a tool to help determine polarity of observed states, can the process be applied within the vastly diverse Termitidae? The examples given above refer to taxa which are generally acknowledged as relatively primitive. Within the Termitidae generally, and certainly within the Nasutitermitinae, there are examples of morphologically very similar taxa exhibiting very different behaviour.

As noted at the beginning of this section, many collections lack data on biology or behaviour. However, the Nasutitermitinae can be divided broadly into soil and humus feeders, grass and litter feeders, and wood feeders. There are further sub-divisions, such as wood feeders which construct arboreal versus epigeal nests. For the purposes of this discussion, it is necessary to consider only a small group which is relatively uniform in terms of morphology.

The species presently included in the genus *Nasutitermes* contains a subset of species (*N. triodiae*, *N. smithi*, *N. magnus*, *N. torresi*, *N. graveolus*, *N. exitiosus*², *N. centraliensis* and *N. walkeri*) which are all relatively large, usually with dark-headed soldiers, large brown hairy adults with long hairy wings, and closely similar mandibular dentition and gut morphology (as noted elsewhere, *T. pastinator* has a similar adult). However, some feed on sound wood whereas others harvest and store grass and litter including, rarely, decayed wood (Fig. 5.4). In the absence of the latter information and using the criteria of, for example, Sands (1957, 1965), all would be placed on a single clade.

² As noted by Hill (1942) *N. carnarvonensis* adults are almost indistinguishable from *N. exitiosus* and were consequently excluded from the graph illustrated in Fig. 5.5.
Figure 5.4. Comparison of life habit patterns of *Nasutitermes magnus*, left, and *Nasutitermes exitiosus*, right.
If diet is considered and, more importantly, an attempt is made to link diet with morphology, a different conclusion can be drawn. As stated above, the external morphology of all the species under consideration appears similar, and when indices calculated from measurements of adult heads are plotted the group appears homogeneous and distinct from *Tumulitermes* and other groups (Fig. 5.5). However, when dietary information is considered the two trophic groups of the Australian *"Nasutitermes"* each form a distinct cluster (Fig. 5.5), with species which feed on relatively sound wood separated from grass/litter/decayed-wood feeders. It is noteworthy that the indices plotted are not based on mandibular nor digestive tract characters, which may be directly related to diet. Note also (Fig. 5.5) that the soil-feeding genera (*"Subulitermes"*) are distinct from other groups.

### 5.3.5 Schedorhinotermes

It is useful to discuss a final example to illustrate a different situation from that described above. *Schedorhinotermes actuosus* (Hill) and *S. seclusus* (Hill), originally regarded as subspecies of *S. intermedius* (Brauer), are of similar size, are morphologically more or less similar, and both feed on wood. Until recently, very little was known of their nesting behaviour (Miller 1987, 1994), although incipient colonies are often found beneath logs on the soil surface. It is now known that *S. seclusus* builds moveable nests which are not necessarily dependent on wood to contain them, whereas although the nests of *S. actuosus* are also moveable, they are always constructed within wood. Therefore, although their ultimate feeding habit is the same, their track or pathway to that habit in terms of the proposed model is slightly different (Fig. 5.6). A third, also morphologically similar species, *S. derosus* (Hill), originally regarded as another subspecies of *S. intermedius*, is a harvester (Watson 1969). Thus, behavioural differences supplement morphological differences in helping to distinguish closely related species.

### 5.4 CASTE STRUCTURE

Throughout the above discussion, behaviour usually refers to overall colony behaviour. However, there remains to briefly discuss one variable aspect of termite sociality in terms of its link with behaviour, namely, caste structure. Caste differentiation (developmental pathways) follows a multitude of patterns within the Isoptera (see various authors in Watson, Okot-Kotber & Noiroit, Eds. *Caste Differentiation in Social Insects* 1985), and can be quite different in relatively closely related genera or species (Noiroit 1985). I have briefly referred above to the common occurrence of aperous reproductives in *Prorhinotermes* and its relevance to dispersal behaviour. Roisin (1992) noted that
Figure 5.5. Head shape of winged adults of some Australian Nasutitermitinae, plus *N. cornigera*. Australian “*Nasutitermes*” form two species groups, only readily apparent when dietary information is added.
Figure 5.6. Comparison of life habit patterns of *Schedorhinotermes seclusus*, left, *Schedorhinotermes actuusus*, centre, and *Schedorhinotermes derosus*, right.
reduction of worker instars is associated with feeding behaviour. Abe (1990) argued that a significant aspect of caste development, i.e. the evolution of a true worker caste, is directly linked to life habit and "one piece" termites do not have sterile workers.

If Abe's proposal is correct, and, as illustrated above, there is convergence of life habit behaviour across families, then a true worker caste must be polyphyletic. This hypothesis is supported by the findings of Noirot & Pasteels (1988). There is some dispute (Watson & Sewell 1985, Noirot 1985a) as to the precise status of the "worker" of Mastotermes, which retains reproductive capability throughout its life. I suggest that this stems from a desire to place it in either of two categories ("true worker" or "pseudergate"), rather than recognise it as a unique response, at family level, to a critical point in behavioural and colony size development as proposed by Higashi et al. (1991). The response in Mastotermes is to develop a caste, not found in other termites, which is worker-like in most aspects and not nympha1 in origin, but whose end point is neotenic production (Watson & Abbey 1985). I have further suggested elsewhere (Miller 1986a) that this aspect of Mastotermes' caste development is linked to behaviour in terms of its pest status.

5.5 CONCLUSION

Emerson's (1938) discussion of nesting behaviour implied that it was directly related to phylogeny at family level, but that within the Termitidae there was convergence of highly specialised behaviour. Within the Nasutitermitinae there is evidence of the convergence referred to by Emerson, but I suggest that my model disagrees with Emerson's views in that there is convergent behaviour across families (Fig. 5.7).

However, although the examples discussed above are by no means an exhaustive test, they appear to indicate that aspects of behaviour can correlate with and supplement information derived from morphological characters. Further, the suggested model is useful in that it also distinguishes differing pathways to similar observed results, provided that sufficient information is available. It can, of course, be expanded at any level (Fig. 5.8) to include more detailed expressions of behaviour such as physical characteristics of nests, whether forage is stored as finely chaffed material versus straw, whether foraging is in the open or under cover of a constructed shelter, etc. Some such details, where known, have been incorporated into the data matrices used in phylogenetic analyses.
Figure 5.7. Convergence of life habit patterns in three families of Isoptera.

- Hodotermitidae: *Hodotermes mossambicus*
- Rhinotermitidae: *Schedorhinotermes derosus*
- Termitidae: *Tumulitermes spp*
Figure 5.8. Expanded portion of behaviour model illustrating differences between closely related species. *Tumulitermes westraliensis* stores grass as straw, whereas *Tumulitermes tumuli* stores a variety of forage as finely ground material compacted into balls.
CHAPTER 6

HIGHER TAXONOMY

6.1 INTRODUCTION

Before concentrating on specific characters of the Australian nasute species in detail, it is necessary to examine the broad relationships within the subfamily and the affinities of the subfamily itself to establish polarity of character states and to provide a basis for comparison. Such examination/comparison enables the identification of the sister group and consequently selection of a suitable outgroup.

Although there is general consensus that the Termitidae is the sister group of the Rhinotermitidae, interpretations of the relationships between the subfamilies vary. Emerson (1945) and Ahmad (1950) considered that the Macrotermitinae and Nasutitermitinae had a common ancestor, although Ahmad stated that the subfamilies could not be arranged in any linear order. Krishna (1970) placed the Amitermitinae and Termitinae together and stated that the Amitermitinae was the most primitive subfamily on the basis of the mandibular dentition of Protohamitermes Holmgren, and was derived from the Rhinotermitidae. Sands (1972), on the basis of gut structure, stated that the Nasutitermitinae were derived from the same stock as the Termitinae and grouped those subfamilies.

As discussed in sections 1.2 & 3.4, relationships between genera and between groups of genera within the Nasutitermitinae have been largely based on mandibular patterns in the adult and worker castes (imago/worker mandibles). All phylogenies proposed for the subfamily have also been based on the concept that genera with mandibulate soldiers are more primitive than genera with fully nasute soldiers, that Syntermes Holmgren is the most primitive genus of the subfamily, and that all other genera are derived from a Syntermes-like ancestor. This concept was discussed in detail by Emerson (1945). A close examination of mandibular patterns, however, reveals that Syntermes has derived characters which clearly indicate that the ancestor of the fully nasute genera must have had more primitive mandibular dentition than Syntermes (Miller 1992 (Appendix 5)).

Sands (1965) discussed the concept that alteration of diet from wood or leaves and litter to humus and soil is usually accompanied by elongation of the apical teeth and reduction of the marginal teeth and molar plate. This pattern has arisen many times within the
Termitidae (Miller 1986). In all the lower families the right molar plate is a relatively long, flat or slightly convex area, with a series of transverse grinding ridges. In many genus-groups within the Termitidae, the length of the molar region is reduced, the ridges are reduced in number and may become greatly differentiated in size and prominence or disappear altogether. Such reduction is usually accompanied by an alteration of the plate from flat, convex, or slightly concave to deeply concave.

This section broadly discusses some primitive mandibular patterns found in the Nasutitermitinae and their possible affinities outside the subfamily, and a complex of other characters, in an attempt to determine polarity and relationships within the Termitidae and also speculates on the possible origins of the family.

6.2 AFFINITIES OF NASUTITERMITINAЕ

Emerson (1945) suggested that the origins of the Nasutitermitinae were close to the Macrotermiteinae and listed characters of Syntermes which were possibly homologous with those of some Macrotermiteinae. The characters included thoracic spines on the soldier, a hyaline tip to the labrum and 3:2:2 tibial spur formula. I would add the very large size of some species and foraging behaviour to this list of characters, and believe that the type of imago/worker mandible found in for example N. exitiosus and related species is similar to some Macrotermiteinae. The following complex of characters are examined to determine whether they link the Nasutitermitinae, through the Macrotermiteinae, to the Rhinotermitidae. Since, as discussed below, some characters are hodotermitid-like, the possibility that the Hodotermitidae (rather than the Rhinotermitidae as is generally accepted) is the sister group of the Termitidae is also examined.

6.2.1 Mandibular patterns
An examination of the dentition of the Australian species reveals that many degrees of modification of the right molar plate are present. The relatively long, more or less convex type found in Nasutitermes graveolus (Hill), N. exitiosus (Hill) and allied species (Fig. 6.1) must be regarded as more primitive than the modified form found in, for example, Tumulitermes (Fig. 6.2). In addition, N. graveolus and related species possess a vestigial subsidiary tooth at the base of the anterior edge of the first marginal tooth, right mandible (Fig. 6.3). This tooth is present in the lower families Termopsidae, Hodotermitidae and Rhinotermitidae, in the termitid subfamily Macrotermiteinae, and the primitive termitine genus Protohamitermes. The presence of the subsidiary tooth is always regarded as the primitive character state (Ahmad 1950, Krishna 1970).
Figure 6.1. Right molar region of *Nasutitermes exitiosus* (X300)

Figure 6.2. Right molar region of *Tumulitermes hastilis*. The number of ridges is reduced, the area is concave, and the 1st ridge is greatly enlarged. (X400).
Figure 6.3. Mandibles of worker of *Nasutitermes exitiosus* (Hill), showing vestigial subsidiary tooth at base of anterior edge of right first marginal tooth (arrowed).
Figure 6.4. Right mandible of *Syntennes dirus* X60. The subsidiary tooth is lacking, and the molar region is reduced.

Figure 6.5. Right molar region of *S. dirus* X200. Molar plate is concave, with a reduced number of ridges, and the 1st ridge is greatly enlarged.
The Neotropical genus *Syntermes*, which has long been regarded as the most basal genus of the Nasutitermitinae, nevertheless has imago/worker mandibles in which the right molar plate is of the derived type. The length of the plate relative to the rest of the mandibular blade is greatly reduced and the plate is concave. In addition, the subsidiary tooth is lacking (Fig. 6.4, 6.5). Other mandibulate genera, for example *Cornitermes* Wasmann which is regarded as the next most basal, have similar mandibles. Since such mandibles are more advanced than those of *N. exitiosus*, it follows that the origin of the monophyletic line which led to the fully nasute genera as proposed by Prestwich & Collins (1981) and discussed by Miller (1986) must have been pre-*Syntermes*. Note that although examples of Australian species are referred to above, some fully nasute genera have an even more primitive molar plate than *N. exitiosus*. The Papuan species *Grallatortermes grallator* (Desneux) for example, has an even longer molar plate with ca 14 ridges, and the second marginal tooth, left mandible, is represented by an angular convexity (Fig. 6.6). In Sands' (1972) illustration of the left mandible of *G. africanus* Harris, the convexity is even more pronounced.

The presence of the subsidiary tooth, a second marginal tooth on the left mandible in *Protohamitermes* and related genera of the Termitinae, and the presence of the subsidiary tooth in the Macrotermiteidae, have led to the hypothesis that the Termitidae is derived from the Rhinotermitidae or a rhinotermitid-like ancestor (Ahmad 1950). The Rhinotermitidae in turn are believed to be derived from an ancestral form which had plesiomorphic character states shared by the Rhinotermitidae and Termopsidae/Hodotermitidae. If the hypothesis that the type of mandible found in some fully nasute species is more primitive than that of any mandibulate genus of the Nasutitermitinae is accepted, the question arises as to whether that type of mandible can be linked to any other subfamily or family, and whether its primitive features are rhinotermitid-like.

**6.2.2 Protohamitermes (Termitinae)**

The imago-worker mandibles of *Protohamitermes* are regarded as the most primitive of the Termitidae (Ahmad 1950) on the basis of the retention of a second marginal tooth on the left mandible, and a subsidiary tooth at the base of the first right marginal tooth. It is significant that the second right marginal has a convex anterior margin and concave posterior margin, an apparently derived state. Sands (1972) argued that a second right marginal tooth with a convex anterior and concave posterior margin is primitive, on the basis that a similar tooth occurs in some cockroaches. However, his suggestion that the imago-worker mandibles adapted to a particular diet revert to a primitive state when the function of the soldier mandibles changes seems unnecessarily complicated. I would think it more likely that the convex/concave second marginal is a positive adaptation to
Figure 6.6. Mandibles of *Grallatotermes grallator* (Desneux). The right molar region is primitive in that it is relatively long, with many ridges.
diet. Even if this type of mandible does contain dentition which has regressed and reappeared, the reappearance itself must be regarded as a derived condition. Note that the majority of genera with mandibles of this form, including those of the Apicotermitinae, which are largely soldierless, are soil feeders, and it is widely accepted that soil feeding is an advanced habit which requires specialised mandibles (Sands 1965; Miller 1986).

I suggest that the issue can be resolved by examination of the corresponding region of the left mandible. Although the ground plan of left mandibular dentition for all the Isoptera is: apical tooth, three marginal teeth, molar region; there has developed in some groups a form of "false" fourth marginal tooth. In the Termopsidae and some Rhinotermitidae, this has been effected by an indentation of the edge of the molar region (Fig. 6.7). In Protohamitermes, some other Termitinae, and all of the Apicotermitinae, it has been effected by reduction of the molar region proper, and the movement and fusion into the gap between the third marginal and reduced molar region of the blade-like process referred to as "wedge-shaped" by Ahmad (1950) and termed the "submolar tooth" by Mathews (1977) (Figs 6.8 - 6.10).

Such a radical change to the left mandible would be expected to be accompanied by a change in dentition of the corresponding region of the right mandible and I propose that the convex-concave right second marginal is the expression of that change. In all species in which the submolar tooth is fused with, and more or less in line with, the 3rd marginal tooth, the right 3rd marginal is convex-concave. Since this form of false marginal tooth is found throughout the soil-feeding Apicotermitinae, in Protohamitermes which feeds on decaying wood, and in Procapritermes Holmgren and related genera, some of which feed on sound wood, it appears to be a relatively conservative character, persisting across subfamilies and, whatever its origins, is not now directly related to diet. This raises the possibility that it arose only once, and consequently the Termitidae is diphyletic. I have discussed the implications this hypothesis has on the currently accepted phylogeny of the Termitinae elsewhere (Miller 1994a (Appendix 5)).

6.2.3 Hodotermitidae
The Hodotermitidae are harvesters which store their forage in underground chambers. The hodotermitid mandibles vary from the termopsid pattern in that the second marginal tooth, left mandible, is reduced, with its posterior edge forming a blade (Fig. 6.11). In some Macrotermidae, the mandibles are very similar, the second marginal is blade-like and the form illustrated in Figure 6.11, Macrotermes subhyalinus (Rambur), is actually less derived than that of Hodotermes mossambicus (Hagen) in that the posterior margin is well-defined. In this respect it appears intermediate between the termopsid and the
Figure 6.7. Left mandible of adult of *Porotermes adansonii* (Froggatt), Termopsidae X94. There are three marginal teeth (1-3) and a false fourth marginal (f4), formed by an indentation of the molar region.

Figure 6.8. Ventral view of left mandible of *P. adansonii* X180, showing the submolar tooth (sm). The form and position of the submolar tooth is representative of that found in all the "lower" families, and in the majority of the Termitidae.
Figure 6.9. Dorsal (A X 100) and ventral (B X130) views of left adult mandible of a species of *Cubitermes* Wasmann. The false fourth marginal tooth is the submolar tooth, more or less in the same plane as, and fused with the posterior margin of, the 3rd marginal.

Figure 6.10. Detail of Fig. 6.9 (X440). The submolar tooth (f4 (sm)) is fused with the posterior margin of the third marginal tooth (3). In all species of Termitidae in which the submolar tooth occupies this position, the right second marginal tooth is convex/concave.
Figure 6.11. Worker mandibles of *Hodotermes mossambicus* (Hagen) (A, B) and *Macrotelmes subhyalinus* (Rambur) (C, D). Second and third marginal teeth are labelled 2 & 3.
hodotermitid forms. Both have a subsidiary tooth (worn in the specimen of M. subhyalinus illustrated) and a flat molar plate on the right mandible.

As discussed above, the mandibles of Nasutitermitinae show a similar overall pattern but they are more derived in that both the anterior and posterior edges of the second marginal tooth, left mandible, are not well-defined although the tooth remains as the blade-like edge between the first and third marginal teeth. Although in many genera the length of the molar plate is reduced, some species retain a long molar plate similar to that of some termopsid and hodotermitid genera.

6.2.4 Size
Emerson (1945) regarded the large size of adults and soldiers of Syntermes as a primitive feature, and reduction in size, usually accompanied by reduction in the number of antennal segments, appears as a derived character state throughout the Isoptera. Many Macrotermitinae, Hodotermitidae and Termopsidae are very large, whereas all living Rhinotermitidae are comparatively small.

6.2.5 Wing scales
The possession of large forewing scales, which overlap those of the hindwing, is a character state found in most of the lower termites. Most Rhinotermitidae possess such scales but those of all of the Termitidae are small. The less derived members of the Termopsidae, for example Zootermopsis Emerson, have large overlapping forewing scales but in the genera Porotermes Hagen and Stolotermes Hagen the suture is oblique, so that the lateral margin of the scale is longer than the inner margin and the overall area of the scale is reduced. The Hodotermitidae have small forewing scales, similar in relative size to those of the Termitidae, which do not overlap those of the hindwing.

The relative sizes and shapes of the sclerotized plates which represent the proximal sections of the costal, radius/media/cubitus and anal regions of the wing and form its articulation are relatively uniform at family level (Miller unpublished data). The wing scales of the mandibulate Nasutitermitinae, and of some fully nasute genera, are remarkably similar to those of the Macrotermitinae, particularly in the size and shape of the anal region (Fig. 6.12).

6.2.6 Foraging behaviour
The "proto-termite" diet was almost certainly damp decayed wood (5.2.1, 5.2.2) and the Termopsidae retain this diet. The Hodotermitidae, the Macrotermitinae and many Nasutitermitinae including Syntermes are foragers and harvesters which store their forage within their nests. Some Rhinotermitidae, for example Parrhinotermes or some
Figure 6.12. Wing scales of A *Macrotermes* & B *Syntermes*. Note similarity with C *Microhodotermes* (Hodotermitidae) rather than Kalotermitidae & Rhinotermitidae (D-E), from which line Termitidae is supposedly derived. 
AR = anal region.
Prorhinotermes, live in relatively damp wood and almost all eat wood in varying stages of decay. Only one member of a relatively advanced genus, Schedorhinotermes derosus (Hill) is known to be a harvester (Watson 1969). In the case of S. derosus the foraging habit is probably a secondary adaptation to its arid environment. It should also be noted here that although some fully nasute species, for example N. graveolus, eat relatively sound wood their mandibles are indistinguishable from those of closely related species which are harvesters. At least one mandibulate species, Cornitermes bequaerti Emerson, also eats wood (Mathews 1977) but its mandibles are similar to those of other Cornitermes and Syntermes.

6.2.7 Ocelli
Ahmad (1950) suggested that the presence of ocelli in the Rhinotermitidae (and subsequently the Termitidae) indicated that they could not have been derived from the Hodotermitidae (=Hodotermitidae+Termopsidae) which have lost their ocelli. The Termopsidae do not possess ocelli but all three genera of the Hodotermitidae, Hodotermes, Microhodotermes and Anacanthotermes have what appear to be vestigial ocelli in both the adults and soldiers. Although Emerson & Krishna (1975) suggested that these were not ocelli but muscle insertion points, sectioning reveals thinning of the cuticle (Fig. 6.13) with no evidence of muscle attachment. Ocelli would have been present in a common ancestor of the Hodotermitidae and Termitidae.

6.2.8 Pronotum
The pronotum of the Termitidae is usually saddle-shaped, whereas that of almost all of the lower termites, including most Rhinotermitidae, is more or less flat. The Hodotermitidae is exceptional among the lower termites in that all castes have a saddle-shaped pronotum, indistinguishable from that of many Termitidae.

6.2.9 Gut structure
Noirot & Noirot-Timothee (1969) compared the gut structures of most of the families of Isoptera, and Kovoor (1969) described in detail the gut of 21 genera of the Nasutitermitinae. Two characters appear to be significant in determining relationships at generic and subfamily level; they are the presence or absence of a mixed segment, and the position of the attachment of the Malpighian tubules.

Noirot & Noirot-Timothee (1969) discussed the origin of the mixed segment and suggested that it had evolved only once and that its absence in the subfamilies of the Termitidae, apart from the Macrotermitinae, were instances of regressive evolution. Sands (1972) showed that the mixed segment of the Apicotermitinae was not homologous with that of the Termitinae and Nasutitermitinae. I believe that any
Figure 6.13 A-B. A Scanning electron micrograph of section through head capsule of worker of *Hodotermes mossambicus* (Hagen) at level of Emerson & Krishna's (1975) "muscle insertion point" (arrow). The cuticle is extremely thin, and there is no evidence of muscle attachment, although mandibular adductor muscles (1) and the broken optic nerve (2) can be clearly seen (X110). B Detail of domed thinning of cuticle (X360).
interpretation of the evolution of the mixed segment is closely linked to the position of attachment of the Malpighian tubules (Appendix 4).

In the lower families, there is no mixed segment and the Malpighian tubules, which number eight or more, are evenly spaced around the junction of the midgut and hindgut. In the Termitidae there are invariably four Malpighian tubules and in the Macrotermitinae they are evenly spaced at the midgut/hindgut junction. In Termitidae which possess a mixed segment, the Malpighian tubules are attached very close together, or in two separate pairs. There are two further divisions, discussed by Sands (1972): in the Apicotermitinae the Malpighian tubules are attached to the midgut, some distance from its junction with the hindgut; in the Termitinae and Nasutitermitinae they are attached at the junction of the midgut and hindgut. Since in all the lower termites the attachment of the Malpighian tubules is at the junction of the midgut and hindgut, attachment directly to the midgut must be regarded as a derived condition. In this respect the gut of the Apicotermitinae is more advanced than any other subfamily of the Termitidae.

In the Nasutitermitinae which lack a mixed segment, all of which are humus and soil feeders, the Malpighian tubules are not evenly spaced, always being in one half of the circumference of the gut at their level of attachment, as occurs in all species which possess a mixed segment. I suggest a possible reason for such positioning is that they have secondarily lost the mixed segment, the formation of which altered the even spacing of the ancestral form. Because of the even spacing of the Malpighian tubules of the Macrotermitinae there is no doubt that they never possessed a mixed segment and, conversely, all living Nasutitermitinae are derived from a form which did have a mixed segment. The question now arises as to whether there exists a gut structure which may be a link between the forms which have or had a mixed segment, and the gut type found in the Macrotermitinae.

Sands (1972) described the gut structure of what he regarded as primitive genera of the Termitinae, namely *Labritermes* Holmgren and *Foraminitermes*. He considered that these genera have gut characters similar to some Macrotermitinae, although the first proctodeal segment (the P1) is dilated. The P1 is also dilated in *Protohamitermes*, which on the basis of the imago/worker mandibles is regarded as the most primitive genus of the Termitinae (Ahmad 1976). The P1 is also dilated in *Syntermes* and other mandibulate genera of the Nasutitermitinae, but is uniformly tubular in all of the fully nasute genera. Dilation of the P1 must be regarded as a derived state at family level since it is always tubular in the lower families, although there is evidence of its regression in the Termitinae (Miller 1991).
There remains one further anomalous termitine genus for which information on gut structure is available, namely *Pseudomicrotermes* Holmgren. Sands (1972) described and illustrated its gut and discussed similarities with *Labritermes* and *Foraminitermes*. The gut has no mixed segment but the Malpighian tubules are attached as bilaterally opposed pairs, and the P1 is uniformly tubular. Sands suggested that it is an extremely primitive offshoot of the Termitinae.

Considering only the gut features described above, it appears that:
1) the Apicotermitinae are a well-differentiated group which could not have given rise to any other subfamily.
2) the basal Termitinae have some affinities with the Macrotermiteinae which are not found in any Nasutitermitinae, and
3) the fact that the fully nasute genera all possess a mixed segment or evidence of one, but show no evidence of a dilate P1, further separates them from the mandibulate genera of the Nasutitermitinae.

### 6.3 PHYLOGENETIC HYPOTHESES

Some species of Nasutitermitinae with fully nasute soldiers have imago/worker mandibles which resemble in several ways the mandibles of some Macrotermiteinae. It may be argued that such similarities are a result of convergence and that the subsidiary tooth and the reduction of the second marginal tooth are adaptations to harvesting. However, this cannot be true since the subsidiary tooth is present in the Termopsidae and Rhinotermitidae, and the second marginal tooth is reduced in the Mastotermitidae and Kalotermitidae, all of which are basically wood feeders. The most simple explanation of the occurrence of such mandibles in the fully nasute line is that the Nasutitermitinae are derived from a macrotermid- or even hodotermitid-like ancestor. Most of the other characters discussed above appear to strengthen the argument that the Macrotermiteinae and Nasutitermitinae, and by association the Termitinae and Apicotermitinae, are closer to the Hodotermitidae than to the Rhinotermitidae.

Relationships between gut structures are less clear, there is a great diversity of forms within subfamilies of the Termitidae, with the exception that the Apicotermitinae form a clearly-defined group (Sands 1972), and the issue is complicated by the fact that some genera regarded as close to the base of the Termitinae exhibit a combination of primitive and highly derived characters. For example *Protohamitermes*, which is generally regarded as having the most primitive imago/worker mandibles of the Termitidae (Ahmad 1950; Sands 1972), possesses the following derived features: loss of the soldier caste;
the presence of a well-developed mixed segment; a dilated P1; Malpighian tubules attached to evaginations of the midgut; 2.2.2 tibial spur formula; a reduced molar plate with only seven ridges; and 14-segmented antennae in the adult (cf Ahmad 1976).

*Labritermes* and *Foraminitermes* possess the primitive form of midgut and evenly-spaced Malpighian tubules found in the Macrotermitinae but the P1 is dilute and the mandibles are more advanced than those of *Protohamitermes*. In *Pseudomicrotermes* the gut is very like that of the *Macrotermitinae*, with a tubular P1, but the Malpighian tubules are attached in two pairs rather than evenly spaced. Is this evidence of the beginning of a mixed segment, or an indication that a mixed segment has been lost? I suggest the latter (see Appendix 4). The molar plate of *Pseudomicrotermes* is of the derived type.

Sands (1972) noted close relationships between soldiers and adults of *Labritermes*, *Foraminitermes* and *Pseudomicrotermes*. It is worth noting that these genera have an open fontanelle, at the apex of a projection in the soldier of *Foraminitermes* and in the adults of *Foraminitermes* and *Pseudomicrotermes*, and the soldiers have a hyaline tip to the labrum. A fontanelle opening at the apex of some form of frontal process is the basis of the Nasutitermitinae, and Emerson (1945) has noted that primitive Nasutitermitinae have a hyaline tip to the labrum, as do some Macrotermitinae.

The close similarities between the gut structures of *Labritermes*, *Foraminitermes*, *Pseudomicrotermes* and the Macrotermitinae would appear to indicate that they have a common derivation.

Although Sands (1972) noted similarities in gut structure between basal Termitine genera and the Macrotermitinae, he stated that the Macrotermitinae were distinct from the other three subfamilies and that the gut of the Nasutitermitinae was derived from the same stock as the Termitinae. *Syntermes* and some other mandibulate genera have a dilate P1, similar to that of some Termitinae. The dilation is greatest in basal genera such as *Syntermes* and is markedly reduced in relatively highly derived genera such as *Rhynchotermes* (Kovoor 1969). The basal mandibulate genera possess a mixed segment unlike that of any other group, having two unequal extensions of the mesenteron overlapping the P1. This is reduced to a single extension in *Armitermes* and *Rhynchotermes*. Since it is unlikely that a double extension would develop from a single extension and then revert to its primitive form, the bilobed mixed segment evident in mandibulate genera further separates them from the fully nasute line. Such a gut type could well have been derived from a type similar to that of, for example, *Foraminitermes* but since the derived molar plate of *Foraminitermes* and related genera is more advanced than that of the least derived of the fully nasute genera, no existing genus of the
Termitinae could be ancestral to the Nasutitermitinae and there is no reason to believe that the fully nasute line ever had a dilate Pl.

The hypothetical ancestor of the Termitinae, Nasutitermitinae and Apicotermitinae would have possessed a primitive molar plate, well developed second marginal tooth and subsidiary tooth, four evenly spaced Malpighian tubules, a short tubular Pl and no mixed segment. All of these characters are also present in the Macrotermitinae, with the exception that the second marginal tooth is modified, so that it could not be ancestral to the other subfamilies.

In summary, the characters discussed above indicate that:

1) The fully nasute branch of the Nasutitermitinae is not derived from any extant mandibulate genus; reduction of the molar plate and loss of the subsidiary tooth in the fully nasute line is not homologous with that of the mandibulate line.
2) There is no unequivocal evidence clarifying the origins of the Nasutitermitinae but it appears more likely that they are derived from an ancestral generalized termitid form rather than directly from the Termitinae or the Macrotermitinae.
3) The Apicotermitinae, on the basis of their gut structure, form a distinct homogeneous group.
4) The Macrotermitinae, the most primitive termitid subfamily in terms of gut structure, appear to have affinities with the Hodotermitidae and it is likely that the Termitidae arose early, temporally as well as in an evolutionary sense, from a common ancestor of the Termopsidae, Hodotermitidae and Rhinotermitidae rather than directly from the Rhinotermitidae.

Many of the arguments presented above widen the gap between the mandibulate and fully nasute genera of the Nasutitermitinae. Although throughout this discussion I have adhered to the concept that the two branches had a common origin, an extensive comparative study of more genera, particularly of less-specialised fully nasute genera, may suggest that they arose separately.

6.4 PHYLOGENETIC ANALYSIS

The hypotheses suggested above, that the fully-nasute genera are not derived directly from the mandibulate Nasutitermitinae, that the assignment of genera not included in the Macrotermitinae or Apicotermitinae to a monophyletic Termitinae (Sands 1972) is not valid, and that the Hodotermitidae rather than the Rhinotermitidae is the sister group of the Termitidae, were subjected to cladistic analysis using PAUP 3.0. (Swofford 1990).
The data matrix (Table 6.1) contained nineteen taxa, as discussed below.

**Table 6.1.** Data set for major groups of Isoptera as discussed in text.

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<th>Taxon</th>
<th>Matrix</th>
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| In addition to the existing families Mastotermitidae, Kalotermitidae, Termopsidae, Hodotermitidae and Rhinotermitidae, the Macrotermitinae and Apicotermatinae were regarded as discrete units. Genera relevant to the discussion above were selected from the Nasutitermitinae and Termitinae. Such genera are representative of groups of genera, except in the case of *Protohamitermes* and *Foraminitermes*. The highly-derived monotypic Neotropical family Serritermitidae, which has affinities with Rhinotermitidae (Emerson & Krishna 1975), was omitted. The outgroup Blattodea, often suggested as the ancestor (Krishna 1970) or sister group (Hennig 1981) of Isoptera, is represented by the wood-feeding cockroach *Panesthia*.

Taxa used in the analysis were therefore:

- *Panesthia* representing Blattodea
- *Mastotermes* representing Mastotermitidae
- *Kalotermes* representing Kalotermitidae
- *Archotermopsis* representing Termopsidae
- *Hodotermes* representing Hodotermitidae
- *Coptotermes* representing Rhinotermitidae
- *Macrotermes* representing Macrotermitinae
- *Apicotermes* representing Apicotermatinae
- *Syntermes* representing mandibulate nasute genera
6.4.2 Characters selected

It proved difficult to select characters which could unambiguously be regarded as "gains" rather than losses at family and subfamily level and the resulting character set is small. As stated elsewhere in this work (see also Emerson 1962, Hennig 1981), much evolutionary change in Isoptera is in the form of losses or reductions so that there is always a possibility that such losses are the result of convergence. Characters that are not losses but which have been definitely shown to be convergent, such as a soil-feeding habit and the associated mandibular modifications, were also omitted. It should also be noted that some character states may not be universal within the representative taxa due to the losses or reductions referred to above. For example, the highly derived, bilobed mixed segment found in *Syntermes* and other primitive mandibulate genera is secondarily lost in e.g. *Rhynchotermes*. Similarly, the mixed segment is scored as present in fully-nasute genera, as represented by *Nasutitermes* and *Tumulitermes*, even though it is lost in many of the *Subulitermes* group of genera (see discussion in Appendix 4).

It may be argued that I have selected only characters which indicate particular relationships, thereby biasing the results of the analysis. I would counter that argument by suggesting that, if both are included, characters which unambiguously change at family or subfamily level should be given more weight than characters in which change may or may not be the result of convergence, but that weighting and bias are surely the same thing. I examined and considered many characters during the course of this study (See section 7.2.1) and chose to use a small set of unordered, equal-weight characters rather than selectively weighting some characters from a large set. Differential character weighting is not always considered a good option (e.g. Brower et al. 1996) in cladistic analyses.
The characters selected are as follows. Further discussion of character states and polarity is found in the sections in parentheses.

1. Molar tooth free = 0; molar tooth fused as 'false 4th marginal' = 1. The molar tooth is free in all the lower families and in Ponesthesia. In its derived state it is fused with the posterior edge of the third marginal tooth. (See 6.2.2.).

2. Right 2nd marginal tooth with straight posterior margin = 0; convex/concave = 1. In all of the lower families and much of the Termitidae the posterior margin is predominantly straight. (See 6.2.2.).

3. Right molar region slightly convex with many ridges = 0; concave = 1. A long, grinding molar plate is characteristic of wood-feeding termites. A concave plate is derived. (See 3.4.6.).

4. Malpighian tubules 12 or more = 0; 8-10 = 1; always 8 = 2; always 4 = 3. Malpighian tubules are multituidinous in cockroaches, reduced to ca 12 in Mastotermes, and further reduced in other families. Although embryological studies indicate that four may be the groundplan for cockroaches and termites (Noirot 1995), a reduced number is apomorphic in living adult termites.

5. Malpighian tubules evenly spaced = 0; not = 1. Spacing of the Malpighian tubules appears to be associated with development of the mixed segment. Uneven spacing is derived. (See 4.10.4.).

6. Mixed segment absent = 0; 2-lobed = 1; 1-lobed external = 2; 1-lobed internal = 3. Where present, the mixed segment is of three forms. In the Syntermes group it is often bilobed; in the Apicotermitinae it is internal to the curve of the anterior hindgut; in all other genera it is external to the curve (Sands 1972).

7. Malpighian tubules attached midgut/P1 junction = 0; attached to midgut = 1. In cockroaches and most termites, the Malpighian tubules are attached to the junction of the mid- and hindgut and that state is primitive (Noirot 1995).

8. P1 tubular = 0; dilate = 1. A short, tubular first proctodeal segment is primitive (Noirot 1995).
9. Soldier labrum not hyaline = 0; hyaline = 1. A hyaline tip to the soldier labrum is found in some Rhinotermitidae, some Macrotermitinae, and "primitive" (Emerson 1945) Nasutitermitinae and Termitinae.

10. Ocelli present = 0; absent = 1. Although ocelli are not present in the oldest known termite fossils (termopsids from the Lower Cretaceous (Ruis & Delclos 1986)), their presence in mantids, roaches and all families of Isoptera except Termopsidae and Hodotermitidae indicates that absence is derived.

11. Soldier mandibles biting = 0; snapping = 1; vestigial = 2. Soldier mandibles are derived from worker mandibles and in their primitive state retain worker-like dentition and a biting function.

12. Frontal gland absent = 0; present = 1. The frontal gland is unique to termites and its occurrence is derived.

13. Sternal gland on 3 sternites = 0; on one = 1. Mastotermes possesses sternal glands on sternites 3, 4 & 5. In other families the single sternal gland is on sternite 4 or 5.

14. Sternal gland on sternite 4 = 0; sternite 5 =1; more than one sternite = 2.

15. Left second marginal tooth well-developed = 0; reduced = 1. A well-developed second marginal tooth, present in cockroaches, is absent in Mastotermitidae, Kalotermitidae and Hodotermitidae, and persists as a plesiomorphic state in Termopsidae, Rhinotermitidae, and some Termitidae.

16. Postclypeus indistinct = 0; well-developed = 1. An elongate and inflated postclypeus is derived (by outgroup comparison).

17. Ano-jugal lobe present in hindwing = 0; absent = 1. In cockroaches and in Mastotermes, posterior anal veins of the hindwing are well-developed. Kukalova-Peck & Peck (1993 p. 346) regard the lobe as "convincingly blattoid" and as such its presence is plesiomorphic.

18. Flagellate protists present in hindgut = 0; absent = 1. The apparent non-reliance of the Termitidae on the families of cellulose-feeding protists found in lower termites and the wood-feeding roach Cryptocercus is derived.
Although not regarded as closely related (Ahmad 1950), the *Angulitermes* group and the *Pericapritermes* group are identical with respect to the above 18 characters. Similarly, the *Termes* and *Neocapritermes* groups also appear identical. Consequently, the following character, exclusive to the *Termes-Capritermes* group of genera, and considered diagnostically important by Ahmad (1950) and Krishna (1968, 1970), was added.

Soldier mandibles relatively symmetrical = 0; strongly asymmetrical = 1.

### 6.4.3 Analysis

The number of taxa was too large to allow the use of PAUP's exhaustive search option, which required extensive (days) computer time for each search on the available computer, a Macintosh LC 575. However, the data set (Table 6.1) was small enough (19 taxa, 19 characters) so that the PAUP Branch-and-bound algorithm, which identifies all optimal trees (Swofford 1990), could be applied. PAUP also provides several heuristic (approximate) options, combinations of which may be used to increase the likelihood that shortest trees will be found. During the course of the analysis, several combinations of heuristic options were tried, all of which found the same trees as the branch-and-bound algorithm. All characters were of equal weight and multistate characters were unordered.

### 6.4.4 Results and discussion

PAUP produced 112 most parsimonious cladograms of length = 36, Consistency Index = 0.694. All cladograms were identical as far as node seven (Figs 6.14, 6.15). The ten terminal taxa consisting of part of the Termitidae were largely unresolved. However, *Nasutitermes* + *Tumulitermes* always formed one branch of the polycladogram. In terms of the above discussion and hypotheses, the suggestion that the Termitidae may be close to the Hodotermitidae was not supported. Instead, Rhinotermitidae was always placed in its "traditional" position as sister group of the Termitidae. Macrotermiteinae appears as sister group of the remainder of the Termitidae, also supporting the "traditional" view (e.g. Krishna 1970) and perhaps supporting the suggestion that the subfamily be elevated to family status (Noitot & Noirot-Timothee 1969).

The sister group relationship between Kalotermitidae and Mastotermitidae suggested by Krishna (1970) and Thorne & Carpenter (1992) is not supported. This result agrees with that of Khambhampati *et al.* (1996) and the tentative suggestion of Noirot (1995).

With the exception of the Macrotermiteinae, the trees produced cast doubts on the validity of the current subfamilies of the Termitidae. The position of *Foraminitermes* would
appear to justify Sands' (1972 p. 40) assessment of it as "primitive". However, the arrangement of the remainder of the Termitidae bears no resemblance to Sands' (1972 p. 38) tree. Although the lack of resolution within the Termitidae indicates that a detailed analysis of a wider range of genera is necessary, the most significant difference in terms of this study is that the mandibulate group, represented by *Syntermes*, always appears as a sister group of all remaining genera, suggesting that the currently recognised subfamily Nasutitermitinae is not monophyletic. This result appears to confirm Miller's (1992 (Appendix 5), and above) suggestion that the mandibulate and fully-nasute genera are not closely related. The evidence of high intestinal pH in *Cornitermes* compared with nasute genera, although incomplete (Bignell & Eggleton 1995), further supports the separation of the two groups. The extreme diversity of the undoubtedly homogeneous mandibulate group, from the relatively unspecialised *Syntermes* to e.g. *Rhynchopterms*, parallels that found across, for example, the Rhinotermitidae, and raises the question of whether the group deserves subfamily status.

It is clear that a comprehensive analysis of the genera of the Termitidae needs to be undertaken, with Macrotermiteinae as the outgroup, using characters which are significant at subfamily/genus level. I suggest that such an analysis will most likely produce a different cladogram. Since the above analysis is mostly based on characters which are significant at family level, characters which are significant at genus level should provide resolution within and between subfamilies (note comments regarding character 19, above). It is not unusual in Isoptera for taxa to exhibit a combination of primitive and derived characters. The supposedly primitive genus *Protohamitermes* has already been discussed above. I had no opportunity to examine *Pseudomicrotermes*, regarded by Sands (1972 p. 40) as "an extremely primitive offshoot near the base of the Termitinae", in detail, and consequently did not include it in the analysis. However, I did examine poorly-preserved Wasmann cotypes in the AMNH, and although some aspects of the gut as described by Sands are primitive, the genus exhibits derived features such as the very long colonic region, its very small size, the distinctive black/white colour of the adult and a reduced and indistinct wing venation.

Apart from *Foraminitermes*, the genera currently placed in Termitinae are divided, with several genera on the same clade as the Apicotermitinae, and several genera forming a polyclotomty with the fully-nasute genera and the *Apicotermes* group. In 77% of the 112 trees, *Amitermes* (and related genera) are a sister group of the remainder (Fig. 6.15). As stated above, an analysis of the Termitidae alone using characters significant at subfamily/genus level may provide further resolution, but, since the Apicotermitinae is a valid subfamily (I agree with Sands' (1972) definitions), the current Termitinae will almost certainly need to be divided. A cladogram constructed from the data matrix shown
**Figure 6.14.** Strict consensus of 112 minimum-length cladograms, length 36, Consistency Index 0.694, showing characters which unambiguously change on each branch (apomorphies) with character states in parentheses. Trees are identical below node 7.

**Figure 6.15.** Majority rule consensus of 112 minimum-length cladograms found by PAUP
in Table 6.1, using MacClade (Maddison & Maddison 1987) but arranged according to Sands (1972) had a length of 43, seven steps (more significantly, more than 19%) longer than the trees found by PAUP.

It is useful to add a final note regarding the position of *Foraminitermes*. Its apparent affinity with the Macrotermitinae and position as sister group of the remainder of the Termitidae is determined by the form of its Malpighian tubules and lack of mixed segment. However, the states of both characters in *Foraminitermes* are plesiomorphic and the genus does share apomorphic mandibular characters with the Apicotermitinae and genera on node 8. Placement of *Foraminitermes* with that group requires one additional step.

In summary, on the basis of the most parsimonious trees generated by PAUP the following points are of note.

- Kalotermitidae, often regarded as a sister group of Mastotermitidae (Krishna 1970; Thorne & Carpenter 1992), is closer to Termopsidae/Hodotermitidae, as suggested by Noirot (1995).
- The Termitidae is the sister group of the Rhinotermitidae. Similarities between Hodotermitidae, Macrotermitinae, and genera such as *Syntermes* are convergent, possibly as a consequence of a harvesting/foraging habit. If so, then morphological characters correlate with behaviour, and, in contrast with Emerson's (1938) view, there is convergence of behaviour across families, as suggested in section 5.4.
- The currently recognised Nasutitermitinae is not monophyletic. *Syntermes* and related mandibulate genera should be removed and a new subfamily erected to contain them.
- The fully-nasute genera (Nasutitermitinae *s. str.*) remain distinct from all other genera.
- The status of the current Apicotermitinae+Termitinae remains largely unresolved, but, provided the false fourth marginal tooth evolved only once, the complex is at least diphyletic.
CHAPTER 7

PHYLOGENETIC ANALYSIS OF AUSTRALIAN NASUTITERMITINAE

7.1 INTRODUCTION

Current relationships within the Australian Nasutitermitinae are based on a small number of characters of either imago-worker mandibles (Emerson 1960, Gay 1970), soldier head capsule morphology (Holmgren 1912, Gay 1970), or gut structure (Kovoor 1969, Miller 1986). As discussed at length in preceding sections, phylogenetic hypotheses based on such character sets are often incompatible. This section examines an analysis of an extensive combination of the characters previously used, plus a series of characters not hitherto considered, in order to determine whether anomalies between current hypotheses can be resolved.

7.2 PHYLOGENETIC ANALYSIS

The 42 named species of Australian Nasutitermitinae, plus the type species of the genus Nasutitermes, N. cornigera, were subjected to cladistic analysis using PAUP 3.0 (Swofford 1990). The complete data set (Table 7.1) consisted of 19 imago-worker characters, 19 soldier characters, 25 gut characters, and 4 life habit characters. All characters were of equal weight and unordered. Table 7.2 lists the species for which adults are known, and the character matrix used in the analyses of that reduced set.

Two species, Amitermes modicus (Hill), a generalised termitine, and Syntermes wheeleri Emerson, representing the mandibulate group of "Nasutitermitinae", were selected as outgroup taxa. Syntermes was chosen for the reason that it has long been regarded as sister group of the fully-nasute genera, although this is not supported by the results of the analysis carried out above (Section 6.4.4). Amitermes was chosen on the basis that its relatively unspecialised morphology may be assumed to be close to the basic termitine from which it has been suggested the Nasutitermitinae is derived (Sands 1972).

7.2.1 Discussion of characters selected

It would be tedious and uninformative to list all characters examined during the course of this study. Many were found to be either too variable, for example antennal segment size or wing venation which can differ on either side of an individual, or too constant, such as
Table 7.1. Full data set for all species, including those for which adults are unknown. As noted in the text, uninformative characters are included in the matrix, but were excluded from the analyses using PAUP's "exclude characters" option. Habit characters are also included.

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Table 7.2. Reduced data set, containing only species for which adults are known. Uninformative characters have been excluded, habit characters are included.

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form, number and position of setae on structures such as the gula, to be included. Since
some relevant worker characters are closely similar to those of adults, they were regarded
as imago-worker characters and included with adult characters. Gut structure was
examined in the worker and gut characters always refer to the worker gut. There is a
possibility that adult or soldier guts may differ significantly from that of the worker, but it
is a rare occurrence in termites (Miller 1991).

Many characters have already been discussed in preceding chapters. The following brief
notes complement that discussion.

7.2.1.1 Adults
Some aspects of adult morphology are easily defined. For example *Tumulitermes s. str.*
are very dark, with very pale intersegmental membranes, have a glossy rather than dull
appearance, more or less hyaline wings and a long postclypeus. Adults of the *N. triodiae*
group are large, markedly hairy, have long wings and a short postclypeus. However,
some characteristics are difficult to quantify, particularly in "intermediate" forms such as
*N. fumigatus*. Consequently, it was useful to calculate a series of indices to represent
otherwise indefinable states such as head shape. Most useful was a combination of
relative eye diameter with relative postclypeus length.

7.2.1.2 Soldiers
Scoring characters of soldier morphology is complicated by the fact that some species are
dimorphic and the forms may greatly differ. For such species, e.g. *T. recalvus*, soldiers
were scored as having constricted heads and the large form was disregarded other than to
score the occurrence of "real" dimorphism. The reason for doing this is that personal
collecting experience (see also Hill 1942 p. 248) indicates that the large form is often
extremely rare and the possibility always remains that it may occur, but is as yet
unknown, in any constricted-headed species.

7.2.2 Character states and polarity
Based on the above discussion, the following characters were included in the analysis.
Polarity is indicated unless more than one state occurs in the outgroups or elsewhere in
the Termitidae or the character is equivocal in lower families.

Some characters have long been expressed as indices (e.g. imago/worker left mandible
index (Ahmad 1952)). In such cases the range of indices was often split by an arbitrary
division, usually the median unless there was marked clustering of plotted data. Such
arbitrary divisions are not totally satisfactory; but I considered that disregarding such
characters, and thus significantly reducing the data set, as a less attractive alternative than
their inclusion, particularly in the light of the discussion presented in sections 1.1 and 6.4.2 and their long history of use as "traditional" characters.

**Adult/worker characters**

1. **Eye size.** Eye diameter less than 0.33 times head width at genal corners = 0. Eye diameter > 0.33 times head width = 1. Within the Termitidae, increased eye diameter is derived.

2. **Postclypeus length.** Postclypeus short, less than 0.25 times head width at genal corners = 0. Postclypeus long, > 0.25 times head width = 1. In most families, the postclypeus is indistinct. In Rhinotermitidae, Serritermitidae and Termitidae a long and/or inflated postclypeus is derived.

3. **Head shape.** Eye diameter index minus postclypeus index > 0.1 = 0. < 0.1 = 1. Combining eye diameter and postclypeus length gives an overall index of head shape, representing the relative area of head capsule visible dorsally. A reduced head capsule is derived.

4. **Ocelli.** Ocelli separated from eyes by at least their diameter = 0. Ocelli close to compound eyes = 1. Ocelli, when present, are close to or in contact with eyes in primitive families. Widely separated or greatly enlarged ocelli are derived.

5. **Wing membrane.** Wing membrane dark = 0. Wing membrane relatively clear = 1. In the Termitidae generally, the wing membrane is dark. In some Nasutitermitinae, the body can be clearly seen through the wings when folded. This character is not related to presence or density of hairs or micrasters.

6. **Pronotum colour.** Pronotum more or less the same colour as head capsule = 0. Pronotum noticeably paler than head capsule = 1. Sclerites more or less uniform in colour is primitive in all families. In some relatively dark species, the pronotum is very pale to almost yellow.

7. **Sternites.** Sternites more or less the same colour as tergites = 0. Sternites noticeably paler than tergites = 1.

8. **Antennae.** Antennae more or less the same colour as head = 0. Antennae paler than head capsule = 1.

9. **Body appearance.** Overall appearance dull or hairy = 0. Overall appearance glossy = 1.

10. **Apical tooth.** Mandibular apical tooth more or less equal to first marginal tooth = 0. Longer than first marginal = 1. Shorter than first marginal = 2. Reduction and elongation of apical teeth are derived states.

11. **Left mandible index.** Apical-first marginal/first marginal-third marginal > 1.0 = 0. Apical-first marginal/first marginal-third marginal < 1.0 = 1. In some species the apical teeth are greatly enlarged. Elongation of apical teeth is always derived.
12. **Right molar region.** First molar ridge much less than 0.25 times length of molar region = 0. > 0.25 times length of molar region = 1. An enlarged first molar ridge is derived.

13. **Right molar region.** Right molar region straight or slightly convex = 0. Right molar region concave = 1. Reduction of molar ridges and concavity of the region is always derived.

14. **Left mandible notch.** Left mandible without notch anterior to third marginal tooth = 0. Left mandible with undulating blade or faint indentation = 1. Left mandible with distinct notch = 2. A notched mandibular blade is derived.

15. **Right second marginal tooth.** Apical angle of right second marginal tooth ca 90° or less = 0. Apical angle of tooth markedly obtuse = 1. Tooth vestigial = 2. An obtuse second marginal tooth occurs in only a few species and is derived.


17. **Rostrum shape.** Rostrum stout, width at base/length > 0.185 = 0. Rostrum slender, width at base/length < 0.185 = 1.

18. **Adult size.** Head width of adult < 1.40mm = 0. Head width 1.40mm or more = 1. Head width > 2.20mm = 2.

19. **Adult antennae.** Adult with 15 antennal segments = 0. 15 - 17 = 1. Less than 15 = 2. More than 17 = 3.

**Soldier characters**

20. **Soldier tarsi.** Tarsus more or less similar in colour to femur = 0. Tarsus markedly paler than femur, "white feet" appearance = 1.

21. **Soldier tibiae.** Tibiae not swollen = 0. Tibiae markedly swollen = 1. Swollen tibiae are derived.

22. **Soldier colour.** Basic head capsule colour more or less brown = 0. Basic colour red = 1. Basic colour yellow = 2.

23. **Dimorphism.** Soldier dimorphism unknown = 0. Dimorphism recorded = 1.

24. **Dimorphism frequency.** Dimorphism rarely recorded = 0. Always dimorphic = 1.

25. **Dimorphism type.** Soldiers morphologically similar but of different sizes = 0. Soldiers morphologically different, "real" dimorphism = 1. "Real" dimorphism is undoubtedly derived.

26. **Constriction.** Soldier head capsule not constricted = 0. Soldier head capsule constricted = 1. Constriction of the head capsule is derived.

27. **Mandibular points.** Soldier mandibles with well-developed points = 0. Points reduced = 1. Points always absent = 2. Complete loss of the vestigeal blade area of the mandible, the "point", is derived.
28. Tibia length. Soldier hind tibiae length relative to head width 0.4-0.6 = 0. Length relative to head width < 0.4 = 1. Length relative to head width > 0.6 = 2.

29. Gula shape. Gula length/width index < 0.5 = 0. Gula length/width index > 0.5 = 1.

30. Gula+foramen. This index is an indicator of soldier head shape which is otherwise difficult to define. It is derived from the ratio between gula length and gula+occipital foramen length. Gula+foramen index 0.42 or greater = 0. Gula+foramen index 0.41 or less = 1.

31. Tibia colour. Tibia and femur more or less the same colour as ventralsclerites = 0. Tibia paler than femur and ventral sclerites = 1. Tibia and femur paler than ventral sclerites = 2. Tibia dark, the same colour as femur, both darker than ventral sclerites = 3.

32. Bristles. Soldier without stout bristles = 0. Soldier with many stout bristles = 1. The presence of many stout bristles is derived.

33. Rostrum length. Rostrum short, < 0.43 times head length = 0. Rostrum > 0.43 times head length = 1. Both states (soldiers dimorphic) = 2. Elongation of the rostrum is derived. This, and the following three characters, are indicative of overall head capsule shape.

34. Rostrum length. Rostrum short, < 0.8 times head width = 0. Rostrum long, > 0.8 times head width = 1. Both states (soldiers dimorphic) = 2.

35. Head shape. Head broad, length/width < 1.05 = 0. Head long, length/width > 1.05 = 1. Both states (soldiers dimorphic) = 2.

36. Head shape. Rostrum-head shape index < 0.45 (short rostrum-broad head) = 0. Index > 0.45 (long rostrum-long head) = 1. Both states (soldiers dimorphic) = 2.

37. Soldier size. Soldier large, head width/worker head width > 0.75 = 0. Soldier medium sized, head width/worker head width 0.55-0.75 = 1. Soldier small, head width/worker head width < 0.55 = 2. Soldier non-nasute = 3.

38. Worker size. Worker head width medium-sized, 1.00-1.45mm = 0. Head width < 1.00mm = 1. Head width > 1.45mm. = 2. Head width > 1.90mm. = 3.

**Gut characters**


40. Malpighian tubules. Malpighian tubules attached in two pairs = 0. Malpighian tubules attached together = 1. Attachment of malpighian tubules close together is derived.

41. Pl. Pl simple and relatively short = 0. Pl always with a distinct posterior loop = 1.
42. P1 muscle bands. Posterior loop of P1 without free muscle bands (see section 4.6) = 0. P1 with free muscle bands = 1. The detachment of muscle from the intestinal wall is derived.

43. Colon. Colonic region relatively short and straight = 0. Colonic region relatively long = 1. A long colonic region is derived.

44. Enteric valve. Enteric valve variously armed for a considerable length = 0. Only distal end of enteric valve armed = 1.

45. Enteric valve. Distal armature with varied spines = 0. Distal area weakly armed with more or less equal-sized spines = 1.

46. Enteric valve. Anterior armature well developed and strongly sclerotised = 0. Anterior armature present but reduced = 1.

47. Enteric valve. Anterior armature with fewer, slender spines = 0. Anterior armature very spiny = 1.


50. Enteric valve. Posterior armature well developed = 0. Posterior armature reduced = 1.

51. Enteric valve. Posterior armature with slender or peg-like spines = 0. Posterior armature with stout triangular spines = 1.

52. P1. P1 relatively short = 0. P1 longer, looped = 1. P1 reduced, insertion into P3 more lateral = 2.

53. P1. P1 loop relatively indistinct = 0. P1 loop easily visible = 1. P1 loop tightly closed = 2. P1 loop very long and open = 3.

**Overall gut pattern**

The following series of characters (54-62) refers to the gut as it lies in situ within the abdomen. In addition to differences in length of various segments, there are recognisable differences in the way in which the gut is coiled. Noirot (1995a) stressed the importance of such coiling, and showed that different patterns of coiling between guts which are otherwise more or less equal is due to torsion of the P3/colonic region. The inclusion of overall gut pattern as a character is problematic in that it is difficult to quantify, and, since it relies on the position of segments already scored, it may appear that some gut characters are unfairly weighted (although Noirot showed that coiling patterns can be independent of relative segment lengths and the "relative position of the different parts" (Noirot 1995a p. 197) was phylogenetically significant). Consequently, the final analysis of the reduced data set was run with and without characters 54-62.

54. Overall gut structure. Gut pattern not as in *N. triodiae* = 0. Gut as in *N. triodiae* = 1.
55. Overall gut structure. Gut pattern not as in *N. projectus* = 0. Gut as in *N. projectus* = 1.

56. Overall gut structure. Gut pattern not as in *Occasitermes* = 0. Gut as in *Occasitermes* = 1.

57. Overall gut structure. Gut with well developed mixed segment and longer P1 = 0. Gut with reduced mixed segment, short P1 and very long colonic region = 1.


59. Overall gut structure. Gut pattern not as in *N. eucalypti* = 0. Gut as in *N. eucalypti* = 1.

60. Overall gut structure. Gut pattern not as in *T. kershawi* = 0. Gut as in *T. kershawi* = 1.


62. Overall gut structure. Gut with long, looped P1 and relatively short colonic region = 1. Gut not as above = 0.

63. Mixed segment. Proximal part of mesenteric section of mixed segment parallel-sided = 0. Proximal part with slightly concave sides = 1. Proximal part with short neck, about half diameter of gut = 2. Proximal part with short neck obviously less than half gut diameter = 3. Proximal part with long, extremely narrow neck = 4.

**Habit characters**

The following four characters were added to the above data set in order to determine the effect, if any, of the inclusion of behavioural characters on cladograms otherwise based on morphological characters.

64. Diet. Wood feeder = 0. Other diet = 1.

65. Diet. Decayed wood = 0. Forage, grass, litter etc. = 1. Soil = 2.

66. Diet. Forage stored as finely ground material = 0. Forage stored as straw = 1.


Three characters included above (44, 45 & 55) were listed as uninformative under PAUP's Show Character Status option. All were autapomorphies but are included in the above list since they occur in undescribed taxa not included in the data set. However, they were excluded from the analysis, although discussion of characters in the text or on figures refers to the numbers above.

**7.2.3 Analysis**

The data set was too large to allow the use of PAUP's Exhaustive and Branch-and-bound options. Instead, several combinations of heuristic settings were used to search for
shortest trees. PAUP's Branch Swapping algorithm using TBR (Tree-Bisection-Reconnection) and Simple, Closest and Random addition sequences were most successful in finding minimum-length cladograms. Other combinations produced fewer cladograms.

The various heuristic searches of the complete (all taxa, characters 54-62 included) data set produced a large number (225) of minimum-length cladograms. The various combinations of settings described above produced the same cladograms of length 198, consistency index 0.48. However, the consensus tree (Figs 7.1) shows that much of the lack of resolution is within what is currently recognised as *Tumulitermes*. Since the winged adult is known for only eight of the sixteen species, and I was unable to dissect a worker of one species, such lack of resolution could be due to missing data. Consequently the data set was reduced to include only species for which all castes are known (with the single exception of *Australitermes insignitus*, which is known only from alates). The reduced data set rendered a further five characters (25, 50, 59, 60, 61) uninformative and they were excluded from the final analysis.

### 7.3 RESULTS AND DISCUSSION

As described above, heuristic searches of the full data set found 225 minimum-length cladograms of length 198 and consistency index 0.48. One thousand random addition sequence replicates failed to find additional cladograms. The consensus tree (Fig. 7.1) shows that all cladograms are well-resolved more or less at the level of currently recognised genera, with some lack of resolution within *Nasutitermes* and *Tumulitermes*. Consequently, it is most useful to discuss genera and species groups in terms of their placement on the consensus tree. Note that node labels are for convenience of discussion and have no other significance.

All cladograms show the following:

- A clade (6) consisting of *Nasutitermes cornigera* as the sister group of ten Australian species currently placed in *Nasutitermes*, plus *Tumulitermes pastinator*.
- A clade (9) which supports the genera *Occasitermes*, *Occultitermes*, *Australitermes* and *Macrosubulitermes*.
- A clade (10) consisting of *Nasutitermes pluvialis*, *N. fumigatus* and *N. dixoni*, with *T. comatus* as sister group.
- A clade (4) consisting of sixteen species including the type species of *Tumulitermes*, *Tumulitermes tumuli*, with *N. kimberleyensis*, *N. coalescens* and *N. eucalypti* forming a sister group.
Figure 7.1. Strict consensus of 255 minimum-length cladograms, length 198, consistency index 0.48, derived from the full (all taxa) data set. With the exclusion of outgroup species, generic names indicate type species. Nodes discussed in text are indicated by bold numerals. Characters which unambiguously change (apomorphies) are indicated for some relevant branches.
Analysis of the reduced data set found 1914 minimum-length trees of length 168 and consistency index 0.536. Most of the existing genera and species groups discussed above were again supported, but formed a polychotomy, due to PAUP's collapsing zero-length branches, at node 2 (Fig. 7.2).

When characters 54-62 were excluded as discussed above (p. 109), PAUP found 488 minimum-length trees of length 189 and consistency index 0.524 (Fig. 7.3). Once again, the genera and species groups discussed above were supported in the consensus tree, which only differed from those generated by the full and reduced (only species for which alates are known) data sets in that node 3 forms a trichotomy, and Occasitermes appears as a sister group of "Subulitermes" plus Occultitermes. The close similarity of the trees generated with and without the "gut pattern" characters discussed above indicates a lack of significant bias resulting from the inclusion of those characters.

7.3.1 Habit characters in relation to morphology
In order to test the hypothesis that habit characters can correlate with trees based on morphological characters, various states of the four habit characters were plotted on the consensus tree produced from the reduced data set, and are discussed below.

Character 64. Several species of Australian nasutes, and N. cornigera, are capable of attacking sound, relatively undecayed wood, and construct their nests largely or entirely from woody "carton" material. Figure 7.4a verifies that this group of Australian Nasutitermes are morphologically distinct from a largely grass- and litter-feeding sister group.

Character 65. When the remaining species are considered in terms of their varied diet, this also correlates well with the morphology-based tree (Fig. 7.4b). Two points are of note. 1) Since Tumulitermes differs greatly from grass-feeding Nasutitermes in mandibular structure, which might be expected to be related directly to diet, as well as in other morphological aspects, the grass-feeding habit in the two groups is clearly not homologous. 2) A soil-feeding habit has developed many times within the Termitidae (Noirot 1992). If it arose as a result of ingesting soil during tunnelling, it could be expected to appear almost at random. However, if the pattern shown by the Australian nasutes is representative of the order, a soil-feeding habit is most likely derived from litter-feeding. If such were the case, Weidner's (1966) argument that the proto-termite tunnelled within soil is weakened, since very few "lower" termites are litter-feeders, and soil-feeding does not exist outside the Termitidae.
Figure 7.2. Strict consensus of 1914 minimum-length cladograms, length 168, consistency index 0.536, derived from the reduced data set (species for which all castes are known). Annotations as in Fig. 7.1.
Figure 7.3. Strict consensus of 488 minimum-length cladograms, length 189, consistency index 0.524, derived from the reduced data set with characters 54-62 excluded.
Character 66. Further to point 1 above, although *Tumulitermes* and some *Nasutitermes* share a grass- and litter-feeding habit, the method of processing food differs. Although a trend is clear, this character does not precisely correlate with the morphology-based tree (Fig. 7.4c).

Character 67. Bearing in mind that *Tumulitermes* is a relatively much larger group than appears on the tree, almost all species which build epigeal or arboreal nests are *Nasutitermes*. Note also that *carnarvonensis* is scored as subterranean because the only recorded nest was in a cave, and the nest of *centraliensis* has not been recorded, but may be constructed within tree trunks. The construction of epigeal nests by a few species of *Tumulitermes* would appear to be convergent.

In summary, Figure 7.4a-d illustrates that the four habit characters discussed correlate reasonably closely with a phylogeny based on morphological characters, as suggested in section 5.4.

Unless otherwise stated, the following discussion refers to the analyses of the full (all taxa included) data set.

### 7.3.2 *Nasutitermes*

The total support for *Nasutitermes cornigera* as the sister group of the Australian "*Nasutitermes*" would appear to suggest that the group is close to, but not congeneric with, *N. cornigera*. Node 6 (Fig. 7.1) is supported by two apomorphies (four in Fig. 7.2) and the apparent sister-group status of *N. cornigera* may be an artefact resulting from the absence of included species from the Neotropical or other regions. In other words, the placement of the Australian species on a single clade may simply reflect endemic speciation within *Nasutitermes*. On the other hand, node 7 is supported by nine apomorphies, at least as many, or more, than those supporting currently recognised genera or groups of genera. The placement of *T. pastinator* on this clade supports the hypothesis, discussed above in Section 3.2.2, that constriction of the soldier head capsule is not necessarily phylogenetically determined.

### 7.3.3 *Tumulitermes*

With the exception of *T. pastinator*, as discussed above, and *T. comatus*, the genus *Tumulitermes* is fully supported. In the analysis of the full data set, *N. projectus* is included in *Tumulitermes*, while *T. comatus* is removed. Both are discussed in greater detail below.
Figure 7.4a-d. Habit characters 64-67 superimposed on consensus tree derived from analysis of reduced data set (characters 54-62 excluded).
**Nasutitermes eucalypti**, together with, in the full analysis, *N. coalescens* and *N. kimberleyensis*, forms a sister group of *Tumulitermes s. str*. However, node 4 is supported by four apomorphies which suggests that *N. eucalypti*, *N. coalescens* and *N. kimberleyensis* should be included in *Tumulitermes*.

**7.3.4 Occasitermes-Macrosubulitermes**

The third major clade (node 8 Fig.7.1) fully supports the current genera *Occasitermes, Occultitermes, Australitermes* and *Macrosubulitermes* as recognised by Miller (1986), and supports Kovoor's (1969) and Miller's (1986) separation of *Occasitermes* and *Occultitermes* from *Australitermes* and *Macrosubulitermes*.

*N. dixoni, N. fumigatus* and *N. pluvialis*, plus *T. comatus*, form a sister group of the *Occasitermes-Macrosubulitermes* clade. The first three species, given the generic status of more terminal branches (nodes 12, 16, Fig. 7.1) on the clade, should be included in a new genus. The status of *T. comatus* remains uncertain until the alate caste is recognised.

**7.3.5 Tumulitermes comatus**

Although excluded from the reduced data set, *Tumulitermes comatus* is worth further discussion. The soldier morphology is similar to some undescribed species, for which the adult is known, that undoubtedly belong in *Tumulitermes*. However, the Malpighian tubules are attached in two pairs and in all cladograms of the full data set (node 8, Fig. 7.1) *T. comatus* is placed on the *Occasitermes-Macrosubulitermes* clade. Only the discovery of the winged adult can resolve the phylogenetic position of the species, but its present position would appear to predict that the adult would not be *Tumulitermes*-like.

**7.3.6 Nasutitermes projectus**

In spite of the soldier having a constricted head capsule, *N. projectus* was placed in *Nasutitermes* by Snyder (1949), who apparently never saw a specimen. The soldier is morphologically similar to some species of *Tumulitermes* and is placed on the *Tumulitermes* clade in all cladograms generated by the full data set (Fig. 7.1). However, the species has a series of autapomorphic gut and worker mandibular characters which it shares with a group of undescribed taxa, while retaining extremely primitive soldier mandibles. Once again, only the discovery of the winged adult will resolve its position.
CHAPTER 8

GENERAL DISCUSSION AND CONCLUSIONS

8.1 INTRODUCTION

An examination of representative genera from all families of Isoptera except the monotypic Serritermitidae, with reference to a series of "traditional" and new characters, raised the possibility that the currently accepted relationships between families and between subfamilies, particularly within the Termitidae, were not valid. A cladistic analysis based on those characters generally supported the accepted phylogeny at family level, but did not support the current subfamilies of the Termitidae.

A cladistic analysis of all described Australian species of Nasutitermitinae generally supported current genera, but suggested that some species have been wrongly assigned.

Although diagnoses are given below for the proposed species groups of the Australian Nasutitermitinae, I do not formally nominate them here as new genera for the following reasons:

1. In recent years there have been many new genera described from neighbouring regions, particularly by Chinese taxonomists, in which case the descriptions are usually in Chinese. I have had no opportunity to examine representatives of these genera, or even translations of the descriptions, and the possibility remains that some Australian species or species groups may belong to extant genera.

2. Similarly, Roisin & Pasteels (1996) recently revised the Nasutitermitinae of Papua New Guinea and described new genera and species. I have not yet examined paratypes of their new taxa, so consequently could not subject them to the character analysis used in this study. However, from their descriptions and illustrations, it appears that if the criteria used in this study were applied to the PNG species, those currently included in Nasutitermes by Roisin & Pasteels would be divided into sub-groups.

3. Following from points 1 & 2, I suggest that before additional genera be described, the type species of all extant genera should be examined to determine the states of the characters used in this study.

4. Finally, with specific reference to the Australian species under discussion, I suggest that the erection of further genera be postponed until more winged adults are known, particularly those of the apparently "intermediate" species such as T. comatus, N. projectus, and the N. eucalypti group.
8.2 PROPOSED PHYLOGENY: HIGHER TAXA

8.2.1 Isoptera

On the basis of the analysis carried out using PAUP, and a synthesis of earlier authors' hypotheses, it seems reasonable to accept the phylogeny illustrated by the consensus trees of Figs 6.14, 6.15.

The recognition of Mastotermitidae as a sister group of all other Isoptera conflicts with Krishna's (1970) and Thorne & Carpenter's (1992) view, but, as discussed in Chapter 5, the unique morphological and behavioural characteristics of Mastotermes appear to justify its position.

Similarly, although the Hodotermitidae clearly have affinities with the Termopsidae, a series of highly derived morphological and, significantly, behavioural characteristics separate the three hodotermitid genera from all termopsids. Emerson's justification for linking the families was that they shared the "wide area occupied by the radial sector (Rs) in the outer fourth of the forewing" (Emerson 1967 p. 277). However, Kukalová-Peck (1991) has shown the "inferior branches" (of the radial sector) of Emerson (1967 p. 279) to be the remains of the anterior median vein (MA). Since the retention of MA veins in primitive groups is a plesiomorphic state it therefore has little diagnostic value.

Although Serritermitidae was not included in the analysis, the evidence of Emerson & Krishna (1975), Costa-Leonardo & Camargo (1990) and Costa-Leonardo & Kitayama (1991) clearly indicate its affinities with Rhinotermitidae. Rhinotermes, as suggested by Krishna (1970) and others, is the sister group of the Termitidae.

8.2.2 Termitidae

It is within the Termitidae that the relationships indicated by Figure 6.15 disagree with current phylogenetic hypotheses. Macrotermes forms a morphologically and behaviourally distinct sister group of all other Termitidae, as suggested by other authors, but the most recently recognised subfamilies as defined by Sands (1972) are not supported. The mandibulate Nasutitermitinae, represented by Syntermes in Figure 6.14, form a sister group of all remaining genera (excluding Foraminitermes as discussed in section 6.4.4). Such placement not only removes the mandibulate genera from the Nasutitermitinae, represented by Nasutitermes and Tumulitermes, but casts doubt on the validity/composition of the remaining subfamilies Apicotermitinae and Termitinae.
It is clear that the Termitidae needs re-examination, using an expanded set of characters which are significant at subfamily/genus level. As noted in Chapter 1 (section 1.1), it is beyond the scope of this work to re-define the subfamilies of the Termitidae. However, as tentatively indicated in the final point in section 6.4.4, and elsewhere (Miller 1992 (Appendix 5)), I suggest that the Apicotermitinae + Termitinae is diphyletic, and that the following hypothesis should be tested by more rigorous cladistic analysis.

The current Apicotermitinae + Termitinae consists of at least five genus-groups:
1. Apicotermitinae
2. Genera with biting soldier mandibles and false worker fourth marginal tooth
3. Genera with snapping soldier mandibles and false worker fourth marginal tooth
4. Genera with snapping soldier mandibles, lacking false worker fourth marginal tooth (<Termitinae Sjöstedt)
5. Genera with biting soldier mandibles, lacking false worker fourth marginal tooth (<Amitermitinae Kemner).

Since Sands' (1972) arguments for the validity of the Apicotermitinae as a subfamily are convincing, it would appear that if the hypothesis was supported, two new subfamilies would need to be erected. Amitermitinae would remain a junior synonym of Termitinae (Sands 1972; 4 & 5 above). The fully nasute genera would comprise the Nasutitermitinae, and a new subfamily would need to be erected to contain Syntermes and related genera. A second new subfamily, of which Apicotermitinae is the sister group, would be comprised of groups 2 & 3, above (Fig. 8.1) and include Foraminitermes for the reasons discussed in section 6.4.4.

I cannot formally propose here the changes discussed above, since I have not examined all of the genera referred to by Sands (1972) when he re-defined the subfamilies of the Termitidae. Also, since the tentative phylogeny is partly based on previously unexamined characters, the states of those characters in at least the type species of all genera need to be examined before genera can be assigned to subfamilies.

8.3 PROPOSED PHYLOGENY: NASUTITERMITINAE

As discussed above, the Nasutitermitinae should contain only those genera that possess soldiers with a fully developed conical rostrum with a constricted fontanelle, and vestigial mandibles. All of the Australian genera and species lie within this large group.
Figure 8.1 Proposed phylogeny of Termitidae, with Rhinotermitidae as outgroup. Tree is one step longer (due to inclusion of Foraminitermes with "false marginal" genera) than most parsimonious trees found by PAUP. As noted in text, genera shown represent genus groups.

On the basis of the cladistic analysis carried out as described in Chapter 7, and the following discussion, Figure 8.2 illustrates the proposed phylogeny of the described Australian species for which all castes are known.

8.3.1 General
As noted in section 7.3, the Australian species consist of the following three distinct groups.

1. The *N. exitiosus-N. triodiae* group, with close affinities with *Nasutitermes cornigera*

2. A group of genera regarded by Emerson (1960) as part of the "Subulitermes group" and including several species currently placed in *Nasutitermes*

3. *Tumulitermes s. str.* and related species, including some currently placed in *Nasutitermes*.

The composition of these three broad groups is discussed below.

8.3.2 *N. exitiosus - N. triodiae*
Since *N. cornigera* forms a sister group of the Australian species on this clade, it would seem reasonable to exclude them from *Nasutitermes*. As Tho (1992) pointed out,
Figure 8.2. Proposed phylogeny of Australian Nasutitermitinae, plus Nasutitermes cornigera. Bold type indicates type species of described genera. See text for discussion of species (not included) for which adults are unknown. The tree is unrooted.
Nasutitermes is a cosmopolitan, heterogeneous assemblage representing an "historical taxonomic artifact", consisting of species which could not be assigned to subsequently erected genera and, there has never been a satisfactory generic diagnosis. However, the establishment of *N. cornigera* as the type species (Watson et al. 1997) and the description above (section 1.3.1) provide a basis for comparison, and differences between *N. cornigera* and the *N. exitiosus-N. triodiae* group are consistent with generic differences within Australian Termitinae (Miller 1991) or other Australian Nasutitermitinae (Miller 1986).

The position of *T. pastinator* within the group appears incongruous, in the light of the constricted head capsule of the soldier. However, given the ability of some nasute species to express head capsule shape as both round and constricted, I see no reason why one species in an otherwise round-headed group should not produce soldiers with constricted heads.

### 8.3.3 Occasitermes-Macrosubulitermes

I prefer to interpret the cladogram as supporting Kovoor's (1969) and Miller's (1984) separation (Fig. 7.1, node 9) of *Occasitermes* and *Occultitermes* from the true soil-feeding *Subulitermes*-like genera. However, the sister group relationship of the *Occasitermes + Occultitermes* clade with the *Australitermes + Macrosubulitermes* clade illustrates the closeness which led Emerson (1960) to include them in the *Subulitermes* group.

The three closely similar species *N. dixoni*, *N. fumigatus* and *N. pluvialis* should be included in a new genus. In addition to morphological similarities, they have similar, cryptic life habits and diet and, although the range of *N. fumigatus* is slightly more extensive, all are found within the narrow eastern coastal strip of Australia.

The inclusion of *T. comatus* on this clade in the analysis of the full data set requires discussion. The data available for *T. comatus* are restricted due to the fact that the winged adult is unknown. Some aspects of its morphology, notably the attachment of the Malpighian tubules in two pairs, distinguish it from the *Tumulitermes* group which it otherwise resembles. Until the winged adult is found, it seems prudent to continue to regard it as a species of *Tumulitermes*, while noting that it may be close to the base of that group.

### 8.3.4 Tumulitermes

With the exceptions (*T. pastinator, T. comatus*) noted above, the genus *Tumulitermes* remains a discrete monophyletic unit. One species, namely *N. projectus*, has already
been discussed with reference to Snyder's (1949) placement in *Nasutitermes*, and is discussed in more detail below.

Three additional species currently placed in *Nasutitermes* form a sister group of *Tumulitermes* s. *str*. Those species, *N. eucalypti*, *N. coalescens* and *N. Kimberleyensis*, are distinguished from *Tumulitermes* s. *str.* by subtle differences in gut structure and the fact that the soldier head capsule is not constricted. I do not consider the group to be sufficiently different from *Tumulitermes* to warrant inclusion in a separate genus, particularly since the winged adult is unknown in two of the three species.

8.3.5 *N. projectus*

Although *N. projectus* is included in *Tumulitermes* in the cladistic analysis, it will be discussed in detail here since it illustrates the limitations of this study and some of the problems which will be encountered when a comprehensive revision of the subfamily, or of the genus *Nasutitermes*, is undertaken. In short, this example illustrates the points made in the introduction to this chapter.

While carrying out termite work (not directly related to this study) in Uluru National Park, I collected, among other Nasutitermitinae, three undescribed species in very close proximity on a single dune. The three species are morphologically very distinct from one another (Fig. 8.3 B-D) One is a large *Tumulitermes* type resembling *T. westraliensis*, the soldier having a very dark, constricted head capsule and very long legs. The soldier mandibles have very long points, uncharacteristic of *Tumulitermes*. The second is relatively large round-headed form somewhat resembling *N. longipennis*. The mandibular points are reduced. The third is an extremely small species having a soldier with a slightly elongate, but not constricted, head and no trace of points on its mandibles.

Dissection of all three species revealed that, in spite of their external morphology being dissimilar, they have virtually identical gut structures which are unlike any described genus, notably an extremely short mixed segment, dilate colonic region, weakly divided P3 and Malpighian tubules distinctly curved at their proximal ends. In addition, the imago/worker left apical tooth is always obviously much shorter than the 1st marginal tooth and the notch anterior to the 3rd marginal is deep and narrow (Fig. 8.4).

Examination of undetermined specimens in the ANIC revealed a further nine species with similar gut and mandibular structures. Only one described species, *N. projectus*, has similar features. Although the gut and imago/worker mandibles are so distinctive that I would unhesitatingly place all thirteen species in a single new genus, soldier morphology, in particular head capsule shape (Fig. 8.3), size, relative leg length and mandibular points
Figure 8.3. Comparison of head capsule shape and size in eight species including *Nasutitermes projectus* (A), all of which have closely similar gut structures and worker mandibles. Species B-H are undescribed.
Figure 8.4 A-C. Gut and worker mandibles of an undescribed species of the *N. projectus* group. The mixed segment is very short and the Malpighian tubules are distinctly curved close to their attachment (A). The P3 is weakly subdivided, and the colon is distinctly dilate (B). The apical teeth (C) are shorter than the first marginals, and the notch (arrowed) anterior to the third marginal is very deep.
are highly variable. The winged adult is not known for any of the thirteen species, and in their absence and on the basis of external morphology, some species would be placed in *Nasutitermes* and some in *Tumulitermes*.

The significance of this discussion is that, given the extreme variability in external morphology within what is undoubtedly a homogeneous group on the basis of characters used throughout this study, the criteria used by other authors to define genera are insufficient basis for comparison with the species groups/genera revealed by this study.

Finally, the analysis has included *N. projectus* in *Tumulitermes* on the basis that its unique gut is autapomorphic and therefore uninformative. The inclusion of the undescribed species would undoubtedly separate the groups. I suggest that the retention of very primitive soldier mandibles (long points with vestigial marginal teeth) in some species of the *N. projectus* group indicate an early separation from *Tumulitermes*, the soldier mandibles of which never possess long points.

### 8.4 TAXONOMY

As discussed at length in the preceding section, I consider it premature to formally erect new genera until the data are more complete. However, this study would be incomplete without definition of the groups discussed above. Although diagnoses, or relevant references, have been given for the existing genera in section 1.3, that section is partially reproduced here, with relevant additions, to maintain continuity of this section.

#### 8.4.1 *Nasutitermes* Dudley 1890

Type species *Termes cornigera* Motschulsky 1855 (see Fig. 1.5).

Species included: No Australian species is congeneric with *N. cornigera* (see section 8.3.2).

#### 8.4.2 Genus A

Type species *Eutermes exitiosus* Hill 1925. Lectotype NMV No. T-10878 Adult male.

Winged Adult (Fig. 8.5 B-C, 8.6 A)
Moderately large species. Entire body with many long and short hairs. Moderately dense long hairs on wings. Colour brown to dark brown, pronotum always noticeably paler than head, as pale as legs and ventral sclerites, antennae pale (except in E. torresi). Eyes very large and prominent, posterior margins always well behind posterior limit of fontanelle in dorsal view. Ocelli large, always close to or in contact with compound eyes. Postclypeus short, relatively longer than N. cornigera, length ca one-third width. Antennae of 15 or 16 segments. Left mandible without distinct notch anterior to 3rd marginal tooth. Right molar region straight or slightly convex, first molar ridge not enlarged or only slightly enlarged.

Soldier (Fig. 8.6 B)
Head capsule colour brown to very dark brown, almost black. Head capsule usually round, constricted in E. pastinator. Rostrum always relatively longer and more slender than N. cornigera. Body usually with stout bristles. Mandibles always with points, but never so strongly developed as in N. cornigera.

Digestive Tract (Figs 8.6 C-D)
Mixed segment well developed, often with markedly narrowed mesenteric section at proximal end. Malpighian tubules attached in two pairs, markedly dilate at proximal ends. P1 long, always with tight loop at distal end; loop closed by muscle bands. Region prior to enteric valve proper with asymmetric spiny armature; terminal part of enteric valve with long unarmed region with lobed end. Colonic region always short, never looped.

8.4.3 Genus B
Type species Eutermes dixoni Hill 1932. Lectotype ANIC No 9053 Adult male. Species included: E. dixoni Hill, E. fumigatus Brauer, E. pluvialis Mjöberg. There are no undescribed species recognised.

Winged Adult (Fig 8.5 D-E, 8.7 A)
Small pale brown to dark brown species. Head width 1.00-1.20mm. Postclypeus length always less than half width, relatively longer than that of N. cornigera, relatively shorter than that of genus "A". Eyes small but often highly convex. Ocelli small, always separated from compound eyes by at least their long diameter. Head and body with many long hairs. Wings with very dense, thick-armed micrasters. Left mandible without notch anterior to 3rd marginal tooth. Right molar region very slightly convex, 1st molar ridge not greatly enlarged.
Figure 8.5. Comparison of adult head/postclypeus of A Nasutitermes cornigera: with genus "A", B N. longipennis, C N. centraliensis; genus "B", D N. dixoni, E N. pluvialis; and F Tumulitermes tumuli.
Figure 8.6. Genus "A". A-C Nasutitermes exitiosus (Hill); A head of winged adult, B head of soldier, C mixed segment and attachment of Malpighian tubules. D Mixed segment and attachment of Malpighian tubules of N. magnus (Froggatt).
Figure 8.7. Genus "B". *Nasutitermes dixoni* (Hill), A head of winged adult, B-C head of soldier.
Soldier (Figs 8.7 B-C)
Relatively small species with yellow head capsules (suffused with brown in E. dixoni).
Not markedly hairy. Head capsule never constricted. Mandibles usually with well
developed points. Rostrum relatively longer and more slender than N. cornigera.

Digestive Tract (Fig. 8.8.B).
Malpighian tubules attached in two pairs, slightly swollen at proximal ends. P1 very
long, with open loop at distal end (loop obscured in situ in E. dixoni). Colonic region
very long, with long anterior loop. Anterior armature of enteric valve reduced.

8.4.4 Occasitermes Holmgren 1912
Eutermes (Occasitermes) Holmgren 1912, 59-60, 64.
Occasitermes, Snyder 1949, 304.
Occasitermes, Gay 1974, 275-283.
Occasitermes, Watson et al. (In press)
Type species Eutermes occasus Silvestri. Lectotype ZMH soldier.
Species included: Occasitermes occasus (Silvestri); Occasitermes watsoni Gay. There are
no undescribed species recognised.

Gay (1974) translated Silvestri's (1909) description of O. occasus. In addition, the
following serves to distinguish O. occasus from all other described genera.
Winged adult.
Second marginal tooth, right mandible, with very short anterior, and long posterior
margin; margins forming distinctly obtuse angle. Right molar plate relatively very long
and slightly convex.
Emerson (1960) and Gay (1977) suggested a close relationship between Occasitermes
and Occultitermes. However, the mandibular dentition is very different from
Occultitermes occultus in which the right second marginal tooth is never obtuse.

8.4.5 Occultitermes Emerson 1960
Occultitermes, Emerson 1955, 515 (no description).
Occultitermes Emerson 1960, 17-19.
Occultitermes, Watson et al. (In press)
Type species Euterme occultus Hill. Lectotype NMV T-10885 Adult female.
Species included: Occultitermes occultus (Hill); Occultitermes aridus Gay. There are no
undescribed species recognised.
Figure 8.8. Comparison between gut of genus "A" A (Eutermes longipennis Hill) and genus "B" B (Eutermes dixoni Hill). Significant differences are in the terminal loop of the P3 and length of the colon C. Note that a significant terminal P3 loop occurs in E. dixoni but is obscured in this view.
Emerson's (1960) and Gay's (1977) descriptions adequately distinguish *O. occultus* from all other genera. The high left mandible index, > 0.6, combined with a very long first proctodeal segment, and very small size of all castes, are key diagnostic characters.

8.4.6 Australitermes Emerson 1960

* Australitermes*, Emerson 1955, 515 (no description).
* Australitermes* Emerson 1960, 24-25.
* Australitermes*, Watson et al. 1984, 49.

Type species *Eutermes dilucidus* Hill. Holotype ANIC No 9069 dealate Adult female.
Species included: *Australitermes dilucidus* (Hill); *Australitermes insignitus* (Hill); *Australitermes perlevis* (Hill). There are no undescribed species recognised.

Emerson's (1960) and Miller's (1984) descriptions adequately distinguish this genus. Key characters are as follows.

*Winged adult.*
Eyes and ocelli extremely large and prominent, eye diameter > 0.3 head width, left mandible index > 1.5.

*Digestive Tract*
Mixed segment extremely short, an oblique join with hindgut. Enteric valve heavily sclerotised with extensive spiny or peg-like armature.

8.4.7 Macrosubulitermes Emerson 1960

* Macrosubulitermes*, Emerson 1955, 503, 515 (no description).
* Macrosubulitermes* Emerson 1960, 18-19.
* Macrosubulitermes*, Miller 1984, 119-120.

Monotypic, type species *Eutermes greavesi* Hill. Holotype ANIC No 9070 Adult female.
There are no undescribed species recognised.


*Digestive Tract*
Mixed segment entirely absent.
8.4.8 Tumulitermes Holmgren 1912

*Eutermes (Tumulitermes)* Holmgren 1912, 59-61, 64.

*Tumulitermes*, Snyder 1949, 301.  
Type species *Eutermes tumuli* Froggatt. Lectotype ANIC No 9059 major soldier.

Species included: *Tumulitermes apioccephalus* (Silvestri); *Tumulitermes coalescens* (Mjöberg); *Tumulitermes comatus* (Hill); *Tumulitermes curtus* (Hill); *Tumulitermes dalbiensis* (Hill); *Tumulitermes eucalypti* (Mjöberg); *Tumulitermes hastilis* (Froggatt); *Tumulitermes kershawi* (Hill); *Tumulitermes kimberleyensis* (Mjöberg); *Tumulitermes marcidus* (Hill); *Tumulitermes mareebensis* (Hill); *Tumulitermes nichollsi* (Hill); *Tumulitermes peracutus* (Hill); *Tumulitermes petilus* (Hill); *Tumulitermes pulleini* (Mjöberg); *Tumulitermes recalvus* (Hill); *Tumulitermes subaquilis* (Hill); *Tumulitermes tumuli* (Froggatt); *Tumulitermes westraliensis* (Hill). In addition, there are approximately 700 undetermined series, representing at least 25 undescribed species, in the ANIC.

Froggatt (1898) described only the major soldier of *T. tumuli*. Hill's (1942) comprehensive descriptions of the winged adult, major and minor soldiers, and worker of *Tumulitermes tumuli* (Froggatt) form an adequate basis for the genus. In addition, *Tumulitermes* differs substantially from *N. comigera* in the following aspects.

**Winged Adult.** (Figs 8.5 F, 8.9 A-B)

Postclypeus inflated, length much more than half width. Wing membrane almost hyaline between micrasters, so that body is clearly visible through wings when folded at rest. Left mandible with distinct notch anterior to 3rd marginal tooth; right mandible with short concave molar plate, first molar ridge greatly enlarged.

**Soldier** (Figs 8.9 C-D)

Head capsule usually constricted behind antennae. Often dimorphic, major and minor soldiers may be similar in form, or distinctly different. Rostrum often relatively long and narrow.

**Digestive Tract** (Figs 4.2 B, 4.7)

Malpighian tubules attached together (2 pairs in *T. comatus*), often at the apex of a "peninsula" of mesenteric tissue. Enteric valve usually short and muscular. Armature associated with enteric valve region short.
Figure 8.9. *Tumulitermes tumuli* (Froggatt). A-B head of winged adult. The small eyes and small, widely separated ocelli and the long inflated postclypeus distinguish *Tumulitermes*. C major and D minor soldiers. The head capsule is constricted and the mandibles lack points.
8.4.9 **Genus C**

Type species *Eutermes projectus* Hill. Holotype ANIC No 9067 soldier. In addition, there are 42 undetermined series, representing 12 undescribed species, in the ANIC.

*Winged Adult*

Not known. Worker mandibles differ from all other Australian genera in that the apical tooth is always much shorter than the first marginal tooth (1st + 2nd on left mandible), and the notch anterior to the third marginal, left mandible, is very deep and acute (Fig. 8.3).

*Soldier* (Fig. 8.3)

Highly variable in size and head capsule shape. Maximum head width 0.58mm - 1.28mm (*projectus*). Abdominal tergites deeply pigmented. Mandibular points present or absent, if present, often with vestigial marginal teeth.

*Digestive Tract* (Figs 8.4 A-B)

Mixed segment very short, always much less than half, usually less than one quarter length of remainder of mesenteron. Malpighian tubules attached together, not markedly dilate at proximal ends, proximal ends distinctly curved. Colonic region distinctly dilate. P3 weakly subdivided. Armature associated with enteric valve region relatively short.

8.5 **SUGGESTED FURTHER RESEARCH**

Very little work is needed in order to formally publish the revision of Australian Nasutitermitinae outlined above, but comparisons need to be made between the new genera of Roisin & Pasteels, as well as the PNG "*Nasutitermes*", using the characters discussed above. I recognise many series of undescribed species in the ANIC (referred to in the above diagnoses), mostly lacking adults, but all fall within one or other of the genera suggested above.

The Termitidae and the genus *Nasutitermes* as currently recognised are alike in that they are a default collection of taxa which do not fit into other groups and are consequently very large, diverse, and cosmopolitan. Both are in urgent need of comprehensive revision. As pointed out in the introduction to this Chapter, I suggest that in both cases it is important to clarify the relationships among existing taxa before describing new ones.
Although there have been recent advances in new techniques for establishing relatedness between taxa, and the phylogenetic significance of characters based on chemical composition of secretions (e.g. Prestwich & Collins 1981; Pasteels et al. 1988), DNA analysis (e.g. Kambhampati et al. 1996), or analysis of cuticular hydrocarbons (e.g. Watson et al. 1989), have been much discussed, rarely have they been combined with earlier techniques.

I suggest the greatest value of new techniques lies in the opportunity to test relationships based on other criteria, and to increase the overall data set to be analysed; i.e. they should not be used in isolation. Since a single worker rarely has the expertise or facilities needed for all techniques, co-operative research is needed.
References


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APPENDIX 1

AUSTROSPIRACHTHA

The closely parallel phylogenies of termites, in particular the Nasutitermitinae, and their staphylinid inquilines have been extensively discussed (summarised by Seevers, 1957; and Kistner, 1969).

Inquilines have been recorded in few Australian nasute species, with the exception of species which build epigeal or arboreal nests (e.g. Watson & Kistner 1985), in which cases it is easy to examine relatively large samples.

During the course of this study, I noted a species of what is undoubtedly Austrospirachtha Watson (Watson 1973) associated with a small series of Nasutitermes eucalypti (Mjöberg) from Gunn Point near Darwin.

The specimen is distinct from A. mimetes Watson (Figs A1 A-B) in the following major aspects (Figs A1 C-F).

The swollen II/III intersegmental membrane is relatively much larger overall, is widest about the middle rather than towards sternite III, and relatively much deeper.

The two pairs of lateral "appendages" are much longer, with relatively less swollen ends. The terminal "appendages" arising between sternites VI and VII are club-shaped rather than more or less cylindrical, as is the case in A. mimetes.

The terminal part of the abdomen is shorter and less upright.

The host of A. mimetes (ANIC series 10-14258) is an undescribed species of Tumulitermes, somewhat similar, as Watson suggested, to N. eucalypti.

Figure A1 A-B. Left lateral (A) and dorsal (B) views of Austrospiractha mimetes Watson, reproduced from Watson (1973).
Figure A1 C-F. Camera lucida drawings of *Austrospirachtha* sp.; left lateral (C) and dorsal (D) views of abdomen, compared with holotype of *A. mimetes* Watson (E, F).
APPENDIX 2

MACROSTRUCTURE OF FRONTAL GLAND

Noirot (1969) discussed the frontal gland, which is unique to the Isoptera, and summarised its presence and form at family level. More recent studies have dealt mainly with the chemical composition of its secretions (e.g. Moore 1964; Prestwich 1983; Pasteels et al. 1988). In the Rhinotermitidae and Termitidae the frontal gland is sometimes greatly differentiated, particularly in the soldier caste in which case it produces defensive secretions.

The fontanelle, through which the frontal gland opens, is often at the apex of an extension of the head capsule. The most derived form of such an extension is expressed in the rostrum of the fully-nasute soldiers of the Nasutitermitinae, through which the secretions are forcibly expelled, and the rostrum of genera of Nasutitermitinae with biting mandibles such as *Rhynchotermes* or *Cyranotermes*. The rostrum of both groups is generally considered homologous but Miller (1986) pointed out that the relatively open fontanelle of *Rhynchotermes* and related genera differed greatly from the constricted pore found in fully-nasute genera.

When considering affinities of the fully-nasute genera during the course of this study, I examined the overall structure of the gland and associated musculature in greater detail to determine the extent of differences in form and operation of the gland.

*Rhynchotermes* Holmgren

*Rhynchotermes* and related genera have the most highly developed rostra of the mandibulate group of Nasutitermitinae and if the hypothesis that the fully-nasute genera are derived from this line was correct (Sands 1957; Emerson 1961; Sen-Sarma 1968; Krishna 1970), then possibly there would be evidence in the form of similarities in frontal gland structure.

Dissection of soldier head capsules revealed that the frontal gland of *Rhynchotermes* is a relatively simple sac (Fig. A2.1 A-B), albeit with a long neck, similar to that found in, for example, some Termitinae such as *Amitermes* or *Termes*. The content of the gland is expelled by contraction of the mandibular adductor muscles (Holmgren 1909), which are attached to the interior of, and occupy a large portion of, the head capsule.
Nasutitermes Dudley

Both the structure of the frontal gland and the form of the mandibular adductor muscles are very different in fully-nasute soldiers compared with those of mandibulate soldiers. As discussed in section 3.2.3 and as illustrated by Holmgren (1909), soldiers usually empty the frontal gland when killed so that it is collapsed when sectioned. Soldiers of N. exitiosus were gradually cooled to the point of inertia to prevent them expelling the frontal gland contents before killing and sectioning.

The gland of N. exitiosus is in four distinct sections. The rostral tube is narrowly constricted at its distal end and opens in the posterior half of the head capsule into a chamber formed by the junction of paired sacs which project into the anterior part of the head capsule (Fig. A2.2 A-C).

The adductor muscles are extremely highly derived. The muscle bands are attached to a concave plate of cuticle into which the antero-ventral portions of the paired sacs fit. The cuticle is in the form of a long-stemmed but very flat wine glass, or an "inside-out umbrella" with its handle attached to the vestigial mandible.

In the absence of transitional forms, it is always possible that the fully-nasute soldier with its complex of highly derived characters arose as a 'hopeful monster' from a mandibulate soldier which already possessed a rostrum. However, the evidence that all the mandibulate genera, including those which lack rostra such as Syntermes (section 6.2.1), possess more derived imago/worker mandibles than some Nasutitermes would appear to indicate that this is unlikely.

As already proposed (Miller 1986), I suggest that the constriction of the fontanelle, thence the ability to squirt rather than dribble secretions, occurred pre-Syntermes but after the ancestor of the fully-nasute line had developed a rostrum analogous to that of the mandibulate group.
Figure A3.1 A-B. Frontal gland and associated musculature of Rhynchotermes A dorsal and B lateral view. The gland (G) is a relatively simple sac.

Figure A2.2 A-C. Frontal gland and associated musculature of Nasutitermes exitiosus A lateral, B dorsal and C ventral view. The gland is 4-chambered, the rostral tube (1) opens into a broad reservoir (2) which is connected to two lateral sacs (3, 4).
APPENDIX 3

SOLDIER/WORKER HEAD-WIDTH INDEX

As stated by Roonwall (1969, p. 13), "only the chitinised external body-parts" are suitable for reliable measurements. The most easily-measured of these are the head capsule, pro-, meso-, and metanotum, and the leg segments.

Only the head capsule is a reliable indicator of overall size. Leg length is often related to behaviour rather than size, eg. species which forage on the surface often have very long legs. Roonwall (1969, p. 42) dismissed the meso- and metanotum as indicators of size, and Miller (1991) showed that the pronotum is variable to the extent that it can be sexually dimorphic.

Calculation of means.
For large samples, maximum head diameter of at least ten large workers and ten soldiers was measured. In some cases in which there was obviously a high degree of variability in head width, more were selected to try to ensure that extremes were included.

Soldier head-width/worker head-width was calculated for all soldier/worker combinations, giving 100 indices for which a mean was calculated. Those means are summarised in Figure 3.2.

In some cases in which only a very small sample was available, head widths listed in Hill (1942) were included in the calculation. Although this could give a false index since it includes comparisons between soldiers and workers from different colonies, such species were included in the graph to show that the overall trend is consistent. An additional problem with small samples is the possibility that they do not contain large workers, in which case the apparent index would be higher than the true index. As above, the inclusion of such species did not affect the overall trend.

Small-sample species were:

- *N. coalescens*
- *N. kimberleyensis*
- *T. subaquilis*  
- *T. curtus*
- *T. nichollsi*
- *T. kershawi*
- *T. kershawi*
- *N. carnarvonensis*
The following shows the method of calculation, based on a small sample of three workers and four soldiers, without and with two worker and one soldier measurement from Hill (1942).

*N. coalescens* soldier/worker head-width index

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Mean excl. Hill (1942) 0.721
Mean incl. Hill (1942) 0.701

The following are calculations for *N. longipennis*. Note that figures from Hill (1942) give almost the same mean, probably indicating that Hill's sample was large, although such is not always the case. It should also be noted that Hill's or other authors' measurements possibly include small workers.

*N. longipennis*

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Mean 0.689

From Hill (1942)
| 143 | 0.84 | 0.587 |
| 143 | 1.17 | 0.818 |
| 150 | 0.84 | 0.56  |
| 150 | 1.17 | 0.78  |

Mean 0.686
APPENDIX 4

DEVELOPMENT OF MIXED SEGMENT

As discussed at length by Sands (1972) the mixed segment is found only in the subfamilies Apicotermitinae, Termitinae and Nasutitermitinae. Sands suggested that the mixed segment of the Apicotermitinae was not homologous with that of the other two subfamilies. He further suggested that the mixed segment of the Termitinae resulted from a need to extend the P3 rather than the mesenteron. Bignell et al. (1983) disagree, stating that the segment is formed by a "posterior extension of the mesenteron rather than an anterior extension of the proctodaeum". I suggest that the form of the mixed segment within the Nasutitermitinae, combined with the attachment of the Malpighian tubules, supports the view of Bignell et al. (1983).

Some Nasutitermitinae, including the Australian species Macrosubulitermes greavesi, have no mixed segment, and in some other species it is very short (Miller 1984). Since all the lower families, and the Macrotermiteinae, have no mixed segment, it would appear that the lack of a mixed segment in the Nasutitermitinae would be plesiomorphic. However, in the Nasutitermitinae in which the mixed segment does not occur, all of which are humus and soil feeders, the Malpighian tubules are not evenly spaced, always being in one half of the circumference of the gut at their level of attachment, as occurs in all species which possess a mixed segment. I suggest a possible reason for such positioning is that they have secondarily lost the mixed segment, the formation of which altered the even spacing of the ancestral form. The even spacing of the Malpighian tubules of the Macrotermiteinae indicates that they never possessed a mixed segment and, conversely, all living Nasutitermitinae are derived from a form which did have a mixed segment.

In all of the Nasutitermitinae, the Malpighian tubules are attached at the junction of the mid- and hindgut. If they are to maintain their position relative to the midgut proper, they must migrate around the circumference of the gut as the mesenteron extends (Fig. A4 A-D). The attachment points of the two outer tubules move towards the inner tubules, forming two pairs (Fig. A4 C). In the most highly derived form of the mixed segment, all four tubules are crowded together at the anterior limit of the proctodaeum (Fig. A4 D).
Figure A4 A-D. Schematic representation of transverse section of gut at level of Malpighian tubule attachment showing theoretical development of mixed segment from A to D and consequent movement of attachment points of Malpighian tubules. L = lumen of P1. Stippled area = mesenteric tissue. MT = attachment of tubule.
APPENDIX 5

The following two conference papers are appended for the reason that they contain more detailed discussion of some issues included in the text (mainly Chapters 6 & 7). Both are based on data gathered during the course of this study. Both were illustrated by slides, of which copies are not included; consequently, figure references have been omitted.

ORIGINS OF MANDIBULAR AND OTHER STRUCTURES IN THE NASUTITERMITINAE, AND A DISCUSSION OF THE ORIGINS OF THE TERMITIDAE

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Paper prepared for 19th International Congress of Entomology, Beijing, 1992

Abstract
The pattern of imago/worker mandibular dentition in some fully nasute genera of the Nasutitermitinae is clearly more primitive than that of Syntermes or any other mandibulate genus. The polarity of a series of characters, including mandibular dentition, is discussed in order to clarify relationships within the Nasutitermitinae, between the subfamilies of the Termitidae, and between the Termitidae and other families. The precise origins of the Nasutitermitinae and the Termitinae are unclear but the primitive mandibulate Nasutitermitinae have characters possibly homologous with those of some Macrotermitinae, which in turn are similar to the Hodotermitinae. It appears likely that the Termitidae is derived independently from the Termopsid/Hodotermitid line, rather than directly from the Rhinotermitidae.

Introduction
Although there is general consensus that the family Termitidae is derived from the Rhinotermitidae, interpretations of the relationships between the termitid subfamilies vary. Emerson (1945) and Ahmad (1950) considered that the Macrotermitinae and Nasutitermitinae had a common ancestor, although Ahmad stated that the subfamilies could not be arranged in any linear order. Krishna (1970) stated that the "Amitermitinae" (<Termitinae) was the most primitive subfamily on the basis of the mandibular dentition of Protohamitermes. Sands (1972), on the basis of gut structure, stated that the Nasutitermitinae were derived from the same stock as the Termitinae.

As discussed by many authors (Ahmad 1950, Sands 1957, Emerson 1961, Sen-Sarma 1968, Krishna 1970, and Miller 1986), relationships between genera, and groups of genera, within the Nasutitermitinae have been based largely on patterns of mandibular teeth in the adult and worker castes (imago/worker mandibles). All phylogenies proposed for the subfamily also have been based on the concept that genera with mandibulate soldiers are more primitive than genera with fully nasute soldiers, that Syntermes is the most primitive genus of the subfamily, and that all other genera are derived from a Syntermes-like ancestor. Emerson (1945) discussed this concept in detail.

An examination of mandibular structures within the Australian species of Nasutitermitinae has revealed some confusing anomalies in the presently accepted pattern of relationships. This paper discusses these structures and a series of other characters in an attempt to determine relationships within the Nasutitermitinae, between the subfamilies of Termitidae (Nasutitermitinae, Macrotermitinae, Apicotermitinae and Termitinae [Sands 1972]), and also the possible origin of the family.
Mandibular patterns of Nasutitermitinae

Sands (1965) stated that alteration of diet from wood or leaves and litter to humus and soil is usually accompanied by elongation of the apical teeth and reduction of the marginal teeth and molar plate. This pattern has arisen many times within the Termitidae (Miller 1986). In families other than the Termitidae the right molar plate is a relatively long, flat or slightly convex area, with a series of transverse grinding ridges. In many branches of the Termitidae, the length of the molar region is reduced, the ridges are reduced in number and may become greatly differentiated in size and prominence or disappear altogether. Such reduction is usually accompanied by an alteration of the plate from flat, convex, or slightly concave to deeply concave.

An examination of the imago/worker dentition of the Australian Nasutitermitinae revealed that many degrees of modification of the right molar plate are present. The relatively long, more or less convex type found in Nasutitermes graveolus (Hill) and N. exitiosus (Hill) must be regarded as more primitive than the form found in, for example, Tumulitermes tumuli (Froggatt) in which the plate is reduced. In addition, N. graveolus and related species possess a vestigial subsidiary tooth at the base of the anterior edge of the first marginal tooth, right mandible. This tooth is present in the families Termopsidae, Hodotermitidae and Rhinotermitidae, in the termitid subfamily Macrotermitinae, and the primitive termite genus Protohamitermes, and is always regarded as a primitive character (Ahmad 1950, Krishna 1970).

The Neotropical genus Syntermes, which has long been regarded as the most primitive genus of the Nasutitermitinae, nevertheless has imago/worker mandibles in which the right molar plate is of the derived type. The length of the plate relative to the rest of the mandibular blade is greatly reduced and the plate is concave. In addition, the subsidiary tooth is lacking. Other mandibulate genera, for example Cornitermes, a genus which is also regarded as primitive, have similar mandibles. Since such mandibles are more specialised than those of N. graveolus, it follows that the origin of the monophyletic line which led to the fully nasute genera as proposed by Prestwich & Collins (1981) and discussed by Miller (1986) must have been pre-Syntermes. Note that although examples of Australian species are referred to above, some fully nasute genera have an even more primitive molar plate than N. graveolus. The Papuan species Grallatotermes grallator (Desneux) for example, has an even longer molar plate with ca 14 ridges, and the second marginal tooth, left mandible, is represented by an angular convexity. In Sands’ (1972) illustration of the left mandible of G. africanus Harris, the convexity is even more pronounced.

The presence of the subsidiary tooth, and a second marginal tooth on the left mandible in Protohamitermes and related genera of the Termitinae, and the presence of the subsidiary tooth in the Macrotermitinae, have led to the hypothesis that the Termitidae is derived from the Rhinotermitidae or a rhinotermid-like ancestor (Ahmad 1950). The Rhinotermitidae in turn are believed to be derived from an ancestral form which had primitive characters of the Rhinotermitidae and the Termopsidae/Hodotermitidae. If the hypothesis that the type of mandible found in some fully nasute species is more primitive than that of any mandibulate genus of the Nasutitermitinae is accepted, the question arises as to whether that type of mandible can be linked to any other subfamily or family, and whether its primitive features are rhinotermid-like.

Origins of Nasutitermitinae

Emerson (1945) suggested that the origins of the Nasutitermitinae were close to the Macrotermitinae and listed features of Syntermes which were possibly homologous with those of some Macrotermitinae. These included thoracic spines on the soldier, a hyaline tip to the labrum and 3:2:2 tibial spur formula. I would add the very large size of some species and foraging behaviour to this list, and believe that the type of imago/worker mandible found in N. graveolus and related species is similar to some Macrotermitinae. I also believe that there is a complex of character states including those listed above which link the Nasutitermitinae, and the Macrotermitinae, to a generalized termid ancestor which may have been hodotermitid-like, and consequently indicate that the origins of the Termitidae lie much closer to the hodotermitid/terrnopsid group than to the Rhinotermitidae. The characters are discussed below.
Imago/worker mandibles

*Hodotermitidae* and *Microhodotermitidae* are harvesters which store their forage in underground chambers and although *Anacanthotermes* is a more generalized feeder it also has this habit and possesses similar imago/worker mandibles. The hodotermitid mandibles differ from the termopsid pattern in that the second marginal tooth, left mandible, is reduced, with its posterior edge forming a blade. In some *Nasutitermitinae*, the mandibles are similar to those of the Hodotermitidae, the left second marginal is blade-like and the form illustrated, *Macrotermes subhyalinus* (Rambur), is actually more primitive than that of *Hodotermites mossambicus* (Hagen) in that the posterior margin is well-defined. In this respect it appears intermediate between the termopsid and the hodotermitid forms.

As discussed above, the mandibles of many *Nasutitermitinae* show a similar overall pattern to those of the *Macrotermes* and Hodotermitidae but they are more specialised in that neither the anterior and posterior edges of the second marginal tooth, left mandible, are well-defined although the tooth persists as the blade-like edge between the first and third marginal teeth. Although in many genera the length of the molar plate is reduced, some species retain a long molar plate as primitive as that of some termopsid and hodotermitid genera.

Size

Emerson (1945) regarded the large size of adults and soldiers of *Synterms* as a primitive feature, and reduction in size, usually accompanied by reduction in the number of antennal segments, appears as a derived character state throughout the Isoptera. Many *Nasutitermitinae*, Hodotermitidae and Termopsidae are very large, whereas all living *Rhinotermitidae* are comparatively small.

Wing scales

The possession of large forewing scales, which overlap those of the hindwing, is always regarded as a primitive state. Most *Rhinotermitidae* possess such scales but those of all *Termes* are small. The more primitive members of the Termopsidae, for example *Zootermopsis*, have large overlapping forewing scales but in the genera *Porotermes* and *Stiolotermes* the suture is oblique, so that the lateral margin of the scale is longer than the inner margin and the overall area of the scale is reduced. The Hodotermitidae have small forewing scales, similar in relative size and shape to those of the *Termitidae*.

The relative sizes and shapes of the sclerotized plates which represent the proximal sections of the costal, radius/media/cubitus and anal regions of the wing and form its articulation are relatively uniform at family level Miller, unpublished data). The wing scales of all the mandibulate *Nasutitermitinae*, and of some fully nasute genera, are remarkably similar to those of the *Macrotermes*, particularly in the size and shape of the anal region.

Foraging behaviour

The "proto-termite" diet was almost certainly damp decayed wood and the *Termopsidae* retain this diet. The Hodotermitidae, the *Macrotermes* and many *Nasutitermitinae* including *Synterms* are foragers and harvesters which store their forage within their nests. Some *Rhinotermitidae*, for example *Paraheterotermes* or some *Proterotermes*, live in relatively damp wood and almost all species eat wood in varying stages of decay. One member of a relatively advanced genus, *Schedorkhinotermes derosus* (Hill), is known to be a harvester (Watson 1969). In the case of *S. derosus* the foraging habit is probably a secondary adaptation to its arid environment, as in the genus *Psammotermes* which eats wood but is able to exist on almost any kind of vegetable debris in more or less complete desert regions (Harris 1970) although its mandibles remain unmodified. It should also be noted here that although some fully nasute species, for example *N. graveolus*, eat relatively sound wood their mandibles are indistinguishable from those of closely related species which are harvesters. At least one mandibulate species, *Coriternes beguaerti* Emerson, also eats wood (Mathews 1977) but its mandibles are similar to those of other *Coriternes* and *Synterms*. I suggest that
this indicates that wood feeding is secondary in the Nasutitermitinae.

Ocelli

Ahmad (1950) stated that the presence of ocelli in the Rhinotermitidae (and subsequently the Termitidae) indicated that they could not have been derived from the "Hodotermitidae" (=Hodotermitidae + Termopsidae) which have lost their ocelli. The Termopsidae certainly do not possess ocelli but all three genera of the Hodotermitidae, Hodotermes, Microhodotermes and Anacanthotermes have what appear to be vestigial ocelli in both the adults and soldiers. Although Emerson & Krishna (1975) suggested that these were not ocelli but muscle insertion points, sectioning reveals thinning of the cuticle with no evidence of muscle attachment. Only a more detailed histological examination of these structures will reveal their true origins. Ocelli would have been present in any common ancestor of the Hodotermitidae and Termitidae.

Pronotum

The pronotum of the Termitidae is usually saddle-shaped, whereas that of almost all other termites, including most Rhinotermitidae, is more or less flat. The Hodotermitidae is exceptional in that all castes have a saddle-shaped pronotum, similar to that of many Termitidae.

Gut structure

Noirot & Noirot-Timothée (1969) compared the gut structures of most of the families of Isoptera, and Kovoor (1969) described in detail the gut of 21 genera of the Nasutitermitinae. Two characters appear to be significant in determining relationships at generic and subfamily level; the presence or absence of a mixed segment, and the position of attachment of the malpighian tubules.

Noirot & Noirot-Timothée (1969) discussed the origin of the mixed segment and suggested that it had evolved only once and that its absence in the subfamilies of the Termitidae, apart from the Macrotermiinae, were instances of regressive evolution. I believe that any interpretation of the evolution of the mixed segment is closely linked to the position of attachment of the malpighian tubules.

In the generalized insect gut and termites other than the Termitidae, there is no mixed segment and the malpighian tubules, which number eight or more, are evenly spaced around the junction of the midgut and hindgut. In the Termitidae there are invariably four malpighian tubules and in the Macrotermiinae they are evenly spaced at the midgut/hindgut junction. In Termitidae which possess a mixed segment, the malpighian tubules are attached very close together, or in two separate pairs. There are two further divisions, discussed by Sands (1972): in the Apicotermitinae the malpighian tubules are attached to the midgut, some distance from its junction with the hindgut; in the Termitinae and Nasutitermitinae they are attached at the junction of the midgut and hindgut. Since the attachment of the Malpighian tubules is at the junction of the midgut and hindgut in most insects, attachment directly to the midgut must be regarded as a derived condition. In this respect the gut of the Apicotermitinae is more specialised than any other subfamily of the Termitidae.

In the Nasutitermitinae which lack a mixed segment (all of which are humus and soil feeders) the malpighian tubules are not evenly spaced, always being in one half of the circumference of the gut at their level of attachment, as occurs in all species which possess a mixed segment. I suggest a possible reason for such positioning is that they have secondarily lost the mixed segment, the formation of which altered the even spacing of the ancestral form. Because the Macrotermiinae have evenly spaced malpighian tubules there is no doubt that the subfamily never possessed a mixed segment and, conversely, all living Nasutitermitinae are derived from a form which did have a mixed segment. The question now arises as to whether there exists a gut structure which may be a link between the forms which have or had a mixed segment, and the gut type found in the Macrotermiinae.

Sands (1972) described the gut structure of what he regarded as primitive genera of the Termitinae, namely Labritermes and Foraminitermes. He considered that these genera have gut characters similar to some Macrotermiinae, although the first proctodeal
segment (the P1) is dilated. The P1 is also dilated in *Protohamitermes*, which on the basis of the imago/worker mandibles is regarded as the most primitive genus of Termitinae (Ahmad 1976). The P1 is also dilated in *Syntermes* and other mandibulate genera of the Nasutitermitinae, but is uniformly tubular in all of the fully nasute genera. Dilation of the P1 must be regarded as a derived state at family level since it is always tubular in families other than the Termitidae, although there is evidence of its regression in the Termitinidae (Miller 1991).

There remains one further primitive termite genus for which information on gut structure is available, namely *Pseudomicrotermes*. Sands (1972) described and illustrated its gut and discussed similarities with *Labritermes* and *Foraminitermes*. The gut has no mixed segment but the malpighian tubules are attached as bilaterally opposed pairs, and the P1 is uniformly tubular. Sands suggested that it is an extremely primitive offshoot of the Termitidae.

Considering only the gut features described above, it appears that:
1) the Apicotermitinae are a well-differentiated group which could not have given rise to any other subfamily,
2) the primitive Termitinae share some features with the Macrotermiteinae which are not found in any Nasutitermitinae, and
3) the fact that the fully nasute genera all possess a mixed segment or evidence of one, but show no evidence of a dilated P1, further separates them from the mandibulate genera of the Nasutitermitinae.

**Discussion**

Some species of Nasutitermitinae with fully nasute soldiers have imago/worker mandibles which resemble in several ways the mandibles of some Macrotermiteinae. It may be argued that such similarities are a result of convergence and that the subsidiary tooth and the reduction of the second marginal tooth are adaptations to harvesting. This cannot be true since the subsidiary tooth is present in the Termopsidae and Rhinotermitidae, and the second marginal tooth is reduced in the Mastotermitidae and Kalotermitidae, all of which are basically wood feeders. I believe the most simple explanation of the occurrence of such mandibles in the fully nasute line is that the Nasutitermitinae are derived from a macrotermitid- or even hodotermitid-like ancestor. Most of the other characters discussed above appear to strengthen the argument that the Macrotermiteinae and Nasutitermitinae, and by association the Termitinae and Apicotermitinae, are closer to the Hodotermitidae than to the Rhinotermitidae.

Relationships between gut structures are difficult to resolve. The gut structure of the Macrotermiteinae is uniformly primitive, the Apicotermitinae form a clearly-defined derived group (Sands 1972), and there is a great diversity of forms within the subfamilies Termitinae and Nasutitermitinae. The issue is complicated by the fact that some genera regarded as close to the base of the Termitinae exhibit a combination of primitive and highly derived conditions. For example *Protohamitermes*, which is generally regarded as having the most primitive imago/worker mandibles of the Termitidae, possesses the following derived features: loss of the soldier caste; the presence of a well-developed mixed segment; a dilated P1; malpighian tubules attached to evaginations of the midgut; 2.2.2 tibial spur formula; a reduced molar plate with only seven ridges; and 14-segmented antennae in the adult.

*Labritermes* and *Foraminitermes* possess the primitive form of midgut and evenly-spaced malpighian tubules found in the Macrotermiteinae but the P1 is dilated and the mandibles are more advanced than those of *Protohamitermes*. In *Pseudomicrotermes* the gut is very like that of the Macrotermiteinae, with a tubular P1, but the malpighian tubules are attached in two pairs rather than evenly spaced. Is this evidence of the beginning of a mixed segment, or an indication that a mixed segment has been lost? The molar plate of *Pseudomicrotermes* is of the derived type.

Sands (1972) noted close similarities between soldiers and between adults of *Labritermes*, *Foraminitermes* and *Pseudomicrotermes*. It is worth noting that these genera have an open fontanelle, at the apex of a projection in the soldier of *Foraminitermes* and in the adults of *Foraminitermes* and *Pseudomicrotermes*, and the soldiers have a hyaline tip to the labrum. A fontanelle opening at the apex of some form
of frontal process is the basis of the Nasutitermitinae, and Emerson (1945) has noted that primitive Nasutitermitinae have a hyaline tip to the labrum, as do some Macrotermiteinae.

The close similarities between the gut structures of Labritermes, Foraminitermes, Pseudomicrotermes and the Macrotermiteinae would appear to indicate that they have a common derivation, and the apparent closeness of Nasutitermitinae, Macrotermiteinae and Hodotermitidae indicate divergence of the Termitidae from a common ancestor of the Hodotermitidae. The structure of the imago/worker mandibles of Protohamitermes, and to a lesser extent, Labritermes, Foraminitermes and Pseudomicrotermes in which the second marginal tooth is angular rather than blade-like is close to the termopsid form. This is also similar to the rhinotermitid form but I believe that when other characters discussed above are considered, the Termitidae do not appear to be derived from the Rhinotermitidae. The combination of characters present in the Termitidae indicates an origin or divergence from a termopsid/hodotermitid branch from which the Rhinotermitidae independently split.

Although Sands (1972) noted similarities in gut structure between primitive termitine genera and the Macrotermiteinae, he stated that the Macrotermiteinae were distinct from the other three subfamilies and that the gut of the Nasutitermitinae was derived from the same stock as the Termitinae. Syntermes and some other mandibulate nasute genera have a dilated P1, similar to that of some primitive Termitinae. The dilation is greatest in primitive genera such as Syntermes and is markedly reduced in relatively advanced genera such as Rhynchopterme (Kovoor 1969). The primitive mandibulate genera possess a mixed segment unlike that of any other group, having two unequal extensions of the mesenteron overlapping the P1. This is reduced to a single extension in Armintermes and Rhynchopterme. Since it is unlikely that a double extension would develop from a single extension and then revert to its primitive form, the bilobed mixed segment of the primitive mandibulate genera further separates them from the fully nasute line. Such a gut type could well have been derived from a type similar to that of, for example, Foraminitermes but since the derived molar plate of Foraminitermes and related genera is more advanced than that of the most primitive of the fully nasute genera, no existing genus of the Termitinae could be ancestral to the Nasutitermitinae and there is no reason to believe that the fully nasute line ever had a dilated P1.

The hypothetical ancestor of the Termitinae, Nasutitermitinae and Apicotermitinae would have possessed a primitive molar plate, well developed second marginal tooth and subsidiary tooth, four evenly spaced malpighian tubules, a short tubular P1 and no mixed segment. All of these features are also present in the Macrotermiteinae, with the exception that the second marginal tooth is modified, so that it could not be ancestral to the other subfamilies.

In summary, the characters discussed above indicate that:

1) The fully nasute branch of the Nasutitermitinae is not derived from any extant mandibulate genus; reduction of the molar plate and loss of the subsidiary tooth in the fully nasute line is not homologous with that of the mandibulate line.
2) There is no unequivocal evidence clarifying the origins of the Nasutitermitinae but it appears more likely that they are derived from an ancestral generalized termitid form rather than directly from the Termitinae or the Macrotermiteinae.
3) The Apicotermitinae, on the basis of their gut structure, form a distinct homogeneous group.
4) The Macrotermiteinae, the most primitive termitid subfamily in terms of gut structure, appear to have affinities with the Hodotermitidae and it is likely that the Termitidae arose early, temporally as well as in an evolutionary sense, from the termopsid/hodotermitid line rather than directly from the Rhinotermitidae.

Many of the arguments presented above widen the perceived gap between the mandibulate and fully nasute genera of the Nasutitermitinae. Although throughout this discussion I have adhered to the concept that the two branches had a common origin, an extensive comparative study of more genera, in particular primitive fully nasute genera, may suggest that they arose separately.
References


POLYPHyleTIC ORIGINS OF THE SNAPPING MANDIBLE AND ASYMMETRY, AND THE BIOGEOGRAPHY OF SOME TERMITINAE (ISOPTERA: TERMITIDAE)

L.R. Miller


Abstract
The Termitinae contains a number of genera related to Termes Linnaeus and Capritermes Wasmann, in which the mandibles of the soldiers are highly specialised and are not used for biting but as springs to strike enemies. Current interpretations of the relationships between those genera suggest that they are derived from an Ethiopian group of genera, related to Cubitermes Wasmann, with slender biting mandibles. The group is further divided into genera with symmetrical mandibles, and those with asymmetrical mandibles, the latter being derived monophyletically from the former. An examination of a number of characters, including imago-worker mandibular dentition, gut structure and soldier morphology, and considering geographical distribution, suggests that asymmetry is not monophyletic, and that the snapping mandible itself is diphylectic. The hypothesis also suggests that a stock with snapping mandibles, which gave rise to a group of relatively primitive genera related to Termes, was widely distributed in Gondwana before it fragmented into the present southern landmasses. A second large group of genera, related to Procapritermes Holmgren, is likely to be derived from a separate primitive stock which also gave rise to the Cubitermes group, and possibly the subfamily Apicotermitinae.

Introduction
The Termes-Capritermes group of genera is a highly derived branch of the Termitinae. It is broadly characterised by having soldiers with highly modified, so-called “snapping” mandibles which are not used for biting but, by being compressed and suddenly released (Deligne 1965), are used as springs to strike and tear enemies. The group is distributed widely throughout the Tropics and extends into warm temperate regions in the Australian, Ethiopian, and Neotropical regions. The greatest diversity of genera and species occurs in the Oriental region and in tropical parts of the Australian and Neotropical regions. Emerson (1955) suggested that the group originated in the Ethiopian region and was derived from a group with biting mandibles, which includes Cubitermes Wasmann and related genera. Ahmad (1950) and Krishna (1968) divided the group on the basis of the degree of symmetry of the soldier mandibles and Krishna indicated a monophyletic origin of a group of genera which often have markedly asymmetrical mandibles. Both authors based their conclusions on imago/worker and soldier mandibular structure but Sands (1972) and Miller (1991) suggested that gut structure more accurately reflects phylogenetic relationships within the Termitinae. Miller (1991) also suggested that marked asymmetry is not monophyletic. This paper discusses characters based on the structure of the imago-worker and soldier mandibles, and of the digestive tract, which appear to support the hypothesis of a polyphyletic origin for both the snapping mandible and marked asymmetry. The rôle of present distribution in this hypothesis is discussed.

Phylogeny
Most of the species from the Ethiopian, Neotropical and Oriental regions, which are regarded as having symmetrical snapping mandibles, are presently placed in the genus Termes Linnaeus. However, they are recognised as a heterogeneous assemblage
(Krishna 1970, Matthews 1977). Miller (1991) showed that none of the 54 Australian species were congeneric with the type species *T. fatalis* Linnaeus. Krishna (1968) revised the genera with asymmetrical mandibles and suggested that the group was monophyletic, derived from an ancestor with symmetrical mandibles, but that two Neotropical genera (*Neocapritermes* Holmgren and *Planicapritermes* Emerson), which possess a combination of primitive and derived characters, separated early from the remaining genera. This interpretation is unsatisfactory in that it requires that the retention of extra segments in the antennae, and the apparently primitive mandibular dentition of the adult, be regarded as derived states. Ahmad (1950) had considered the mandibular dentition not only to be more primitive than any of the symmetrical *Termes*-related genera, but also the Ethiopian *Cubitermes*-related genera with biting mandibles from which the group with snapping mandibles was supposedly derived.

I believe that asymmetry, possibly because of the bizarre appearance of its most extreme development, has been given far too much weight in most phylogenetic reconstructions. In fact, asymmetry is extremely difficult to define or quantify within the group. Miller (1991) has pointed out that snapping mandibles must be asymmetrical to some degree to be able to function, and that interpretations of degree of asymmetry alone led to *Paracapritermes kraepelinii* (Silvestri) being confused with four other species in two other genera.

I suggest that since all of the group should be regarded as having asymmetrical soldier mandibles, any interpretation of their phylogenetic relationships should be based on a combination of characters such as those of imago/worker mandibular dentition and gut structure, which have been shown to be useful in other sections of the Isoptera.

**Imago-worker mandibular dentition.**

As indicated by Ahmad (1950) the most primitive imago-worker mandibular dentition found in the *Termes-Capritermes* group is that of *Neocapritermes* and *Planicapritermes*. Apical teeth which are more or less the same size as the first marginal teeth are plesiomorphic throughout the Isoptera, as is a right second marginal tooth with a short anterior margin and long straight posterior margin. It should be noted that Sands (1972) argued that a second right marginal tooth with a convex anterior and concave posterior margin is primitive, on the basis that a similar tooth occurs in some cockroaches. However, his suggestion that the imago-worker mandibles adapted to a particular diet revert to a primitive state when the function of the soldier mandibles changes seems unnecessarily complicated. I would think it more likely that the convex/concave second marginal is a positive adaptation to diet. Even if this type of mandible does contain dentition which has regressed and reappeared, the reappearance itself must be regarded as a derived condition. Note that the majority of genera with mandibles of this form, including those of the Apicotermitinae, which are largely soldierless, are soil feeders, and it is widely accepted that soil feeding is an advanced habit which requires specialised mandibles (Sands 1965, Miller 1986).

*Protohamitermes* Holmgren is regarded as the most primitive of the termitine genera in which the right second marginal tooth is prominent and acute, with a convex anterior and concave posterior edge. The genera related to *Procapritermes* Holmgren possess such a tooth, and the structure of their mandibles is similar to those of the *Cubitermes* group of genera with biting mandibles, and to those of the subfamily Apicotermitinae.

Genera with mandibles derived from the *Neocapritermes* form, including the Neotropical *Termes s. str.* are distributed throughout all regions, whereas the *Procapritermes* group is largely Oriental, with one exception which will be discussed later. Within the *Termes-Capritermes* group, as in other sections of the Termitidae, there has occurred modification of the mandibles consisting of elongation of the apical teeth and reduction of the marginal teeth. The mandibles of the Australian genera *Paracapritermes* Hill, *Protohamitermes* Holmgren and *Xylochomitermes* Miller are only slightly more derived than those of *Neocapritermes*. In all other genera the apical teeth are elongated to varying degrees.

Further discussion of the variation found in either group is not relevant at this stage, but it is useful to repeat that such variation does occur within sections of the Termitinae and convergent mandibular dentition is found in other subfamilies of the Termitidae (Miller 1986).
I suggest that the mandibular dentition found in *Termes* and related genera is derived from a type similar to that of *Neocapritermes*, but that of *Procapritermes* and related genera is more closely allied to that of the *Cubitermes* group. On the basis of imago-worker mandibular structure alone, and assuming that the convex-concave second right marginal tooth appeared only once in the Termitidae, the Termitinae with snapping mandibles can be divided into two groups. The most primitive mandibles of the first group (to which *Procapritermes* and related genera belong) resemble those of *Protohamitermes*, and of the second (*Termes* and related genera), those of *Neocapritermes*.

**Gut structure.**

Characters based on the morphology of the various sections of the gut have long been shown to be useful tools in determining phylogenetic relationships (e.g., Noirot & Kovoor 1958, Sands 1972, Miller 1986). Miller (1991) examined in detail the gut structure of the Australian genera, but there has been no comparative study of representative genera of the whole *Termes-Capritermes* group. Since the precise origins of the subfamily are unclear, and many genera exhibit a combination of primitive and derived features, polarity of gut character states within the Termitinae is difficult to determine without an extensive examination of all genera. The most comprehensive discussion is that of Sands (1972), and it seems probable that in the genera under discussion a relatively short, dilate first proctodeal segment can be regarded as plesiomorphic. *Neocapritermes* has a dilate first proctodeal segment, as do the genera with biting soldier mandibles from which it has been suggested the genera with snapping mandibles were derived (Ahmad 1950, Krishna 1968). However, the *Cubitermes* group have imago-worker mandibles which resemble those of the *Procapritermes* group, with a prominent convex-concave right second marginal tooth. On the basis of gut structure alone, *Procapritermes* and related genera could not be regarded as having affinities with the *Cubitermes* group. *Pericapritermes* Silvestri does have a relatively dilated first proctodeal segment, but in *Dicuspiditermes* Krishna, and in *Homallotermes* John and *Procapritermes* which are regarded as more primitive than *Pericapritermes*, the segment is more or less tubular. *Termes* s. str. and related genera have a slightly dilate first proctodeal segment, with a short tubular section immediately preceding the enteric valve, and often have the paunch subdivided into two sections. More highly derived genera in the *Termes* group often have a long tubular first proctodeal segment. The dilate first proctodeal segment of *Neocapritermes* would at first appear to be close to that of the *Cubitermes* group but the extreme development of that portion of the midgut which overlaps the first proctodeal segment to form the mixed segment is a highly derived feature which suggests that the overall gut structure is derived.

In *Promirotermes* Silvestri and *Angulitermes* Sjöstedt the first proctodeal segment is markedly dilate and the colonic region is very long, so that the overall gut structure resembles most closely that of the *Cubitermes* group.

**Frontal projection.**

There remains one further character which has been regarded as significant by Ahmad (1950) and Krishna (1968); namely, the frontal projection, or frontal tubercle. In many genera of the *Termes* line, the area of the soldier head capsule posterior to the fontanelle is variously developed into a more or less conical, acutely pointed tubercle, sometimes with smaller lateral tubercles at its base. Krishna (1968) has stated that the frontal tubercle has been independently lost several times and Miller's (1991) study of the Australian genera of the *Termes* line reinforces that hypothesis.

Genera of the *Procapritermes* group sometimes have the area posterior to the fontanelle weakly developed into a ridge or hump, but it is never acutely pointed and the line possibly never had such a tubercle. Krishna argued that the presence of a frontal projection is primitive in the genera with snapping mandibles, on the basis that *Angulitermes*, *Promirotermes* and *Termes* all have a frontal projection. I suggest that the frontal projection in *Promirotermes* and *Angulitermes* is not homologous with that of *Termes*, but a more developed version of the rounded ridge found in, for example, *Cubitermes fungifaber* (Sjöstedt). *Promirotermes* and *Angulitermes* have an identical gut structure, similar to that of *Basidentitermes* Holmgren; the imago-worker mandibles of
the three genera are also closely similar, and I suggest that the development of a rounded tubercle is a derived state in Promirotermes and Angulitermes. Promirotermes and Angulitermes are therefore highly derived members of the Cubitermes group, rather than primitive members of the Termes group. It should be noted that some genera of the Cubitermes group, such as Noditermes Sjostedt or Proboscitermes Sjostedt, have a projection equally or even more developed than Promirotermes and Angulitermes, but have biting mandibles. Unguitermes Sjostedt is always placed in the Cubitermes group, but its soldier mandibles are both dorso-ventrally curved and possess hooked tips; both characteristic of snapping mandibles. I suggest that the soldier mandibles of Unguitermes could be considered morphologically intermediate between Cubitermes and Promirotermes, but the genus is not ancestral to the latter since the frontal projection of Unguitermes is particularly well-developed. Although I regard an acutely pointed tubercle within the Termes group as a relatively primitive, homologous character which has been lost several times, the development of an elevated, rounded or pointed projection posterior to the fontanelle is a derived character which has appeared in several branches of the Termitinae.

**Biogeography**

Throughout the range of the group, genera with both relatively symmetrical and markedly asymmetrical soldier mandibles occur together; for example, Termes s. str. with Neocapritermes in the Neotropics, Xylacomitermes with Paracapritermes in Australia, ‘Termes’ with Pericapritermes in the Ethiopian and Oriental regions, and ‘Termes’ with Capritermes in Madagascar.

The Cubitermes group, from which the genera with snapping mandibles are supposed to have evolved, are confined to the Ethiopian region. Angulitermes and Promirotermes, hitherto regarded as most closely related to Termes, are also Ethiopian, although Angulitermes extends through the Palearctic to the Oriental region. The Cubitermes group does not occur in Madagascar. The Procapritermes group is widely distributed throughout the Oriental region, with one genus, Pericapritermes, extending into the Ethiopian region and through South-east Asia to the Papuan region and the extreme North of Australia.

Bouillon (1970) regarded the vast geographical dispersion of ‘Termes’ as indicative of its primitiveness. Relatively primitive, seemingly related genera are found in all tropical regions including, significantly, Madagascar. In the Australian and Neotropical regions a large number of endemic genera have diversified from the basic ‘Termes’-like stock. One genus from the Neotropical region is worth further discussion. Spinitermes Wasmann is paradoxical in that the form of the soldier head capsule is closely similar to that of some genera of the Termes group, with an acutely-pointed frontal projection which sometimes has lateral tubercles at its base, but the mandibles are of the biting type. Mathews (1977) subdivided the genus, stating that the mandibles of some genera were better adapted for “clicking” (=snapping) and therefore closer to those of Termes. It is tempting to suggest that Spinitermes may be close to the ancestor of Termes and related genera, and this may well be true of its soldier morphology. However, the imago-worker mandibles and gut structure are highly derived, with adaptations similar to those of soil-feeding genera.

**Discussion**

When the points above are considered separately, it appears that:

- The imago-worker mandibles of the Termitinae with snapping mandibles are of two forms; one derived from a type resembling those of Neocapritermes, and a form derived from a type resembling those of the Cubitermes group
- The gut structure of Promirotermes and Angulitermes is like that of the Cubitermes group, whereas that of Termes and related genera is more derived. The gut structure of the Procapritermes group is more primitive than that of the Termes group in that the first proctodeal segment is sometimes dilated, but in other aspects, such as the complex spiny armature of the paunch, it is highly derived.
• An acutely conical frontal projection is primitive in the *Termes* group, and has been lost several times. When present in the *Procapritermes* group, and in *Promirotermes* and *Angulitermes*, the frontal projection is a poorly-developed rounded hump or ridge rather than a sharp cone.

If these points are to be related to the presently accepted theory of a single origin of the snapping mandible, followed by a single origin of asymmetry, then at some stage one of the two imago-worker mandible types must have arisen from the other, since asymmetry is present in both groups. All of the *Procapritermes* group are regarded as asymmetrical, so it follows that the *Neocapritermes* form of imago-worker mandible must have been the original form. However, since *Promirotermes* and *Angulitermes* have imago-worker mandibles of the *Procapritermes* form, combined with symmetrical snapping mandibles and some *Cubitermes*-like features, they have either undergone several reversals, or have convergently developed the snapping mandible. Also, if the hypothesis that asymmetry is monophyletic is correct, it must antedate the *Procapritermes* form of imago-worker mandible and both symmetrical and asymmetrical genera would have had to disperse independently from their supposed Ethiopian origin to their present distributions before the *Procapritermes* form developed. This would necessitate a multiple origin of the *Procapritermes* type.

I propose the following to explain the present geographical distribution of genera, and the distribution of the morphological characters discussed above.

A basic stock which gave rise to the two main groups of Termitinae with snapping soldier mandibles, the *Procapritermes* group and the *Neocapritermes* group, was established in Gondwana before the Indian plate separated. The *Neocapritermes* group has retained imago-worker mandibles of a generalised termitid form, resembling those of some Nasutitermitinae, Termitinae of the *Amirteen* branch, and, in the form of the right second marginal tooth and apical teeth, Macrotermitinae. On the basis of the imago-worker mandibular dentition the *Procapritermes* group appears to share a common ancestry with the *Cubitermes* group of genera, and the Apicotermitinae.

After the breakup of Gondwana and at time periods when each, or part of each, of the separate land masses experienced tropical conditions, four distinct faunas developed. Each of these faunas consists of a number of derived genera showing varying degrees of specialisation but with obvious connections, and one or more relatively primitive genera which show affinities with primitive genera in other regions.

1. An Australian fauna which, although it has produced 53 species in 12 endemic genera, has remained relatively conservative in terms of external soldier morphology. The genera *Paracapritermes* and *Protocapritermes* have developed moderately asymmetrical soldier mandibles. The Australian species have evolved a wide variety of gut structures to enable them to exploit a range of food sources and are particularly adapted to soil feeding (Miller 1991).

2. A Neotropical fauna which has produced many endemic genera, including *Termes* s. str., some of which have developed extremely asymmetrical soldier mandibles but have retained primitive imago-worker mandibular dentition. No Neotropical genus has reached the Nearctic region.

3. An Ethiopian-Malagasy fauna which remained small and relatively undiversified. The soil-feeding niche exploited by related Australian Termitinae was filled in Africa by a large group of genera with biting mandibles, the *Cubitermes* group. This group diversified after the separation of Madagascar since none occur there. Two genera belonging to the *Cubitermes* group, *Promirotermes* and *Angulitermes*, developed snapping mandibles convergent with those of the *Termes* group. One of these genera, *Angulitermes*, dispersed through the Palearctic region to the Oriental region. On Madagascar, marked asymmetry developed in two genera derived from a form with *Neocapritermes*-like imago-worker mandibles.

4. An Indian/Oriental fauna, which is diphylectic in origin. A group of about ten species, presently designated 'Termes', remains morphologically similar to relatively conservative species from the Australian, Ethiopian and Neotropical regions.
A second group, the Procapritermes group, has greatly diversified within the region, resulting in many genera and species distributed throughout India, South-east Asia and China. One genus, Pericapritermes, has extended its range into the Ethiopian region and through South-east Asia and the Papuan region to northern Cape York Peninsula. The early separation and rapid northward movement of India, and its subsequent long association with tropical Asia, possibly favoured diversification and dispersal of the group through the Oriental region. A contributing factor may also have been the lack of competition from other Termitinae, such as the Cubitermes group which remained confined to the Ethiopian region, or the Amitermes group, which became extremely diverse in the Australian region.

Finally, it should be noted here that Bouillon (1970), without giving details, suggested that Termes could be more primitive than Promirotermes, and that Pericapritermes was derived separately from the same stock as Promirotermes, which is more or less a summary of some of the above arguments. However, he suggested that the dispersion of the Procapritermes group was the reverse of that which I have outlined, that is, from Africa to India and the rest of tropical Asia. Since Pericapritermes is not the most primitive genus of the group, but is the only Ethiopian representative, this would necessitate the extinction of all related genera in the region.

References


