

**Fauna of  
New Zealand**  
Ko te Aitanga Pepeke  
o Aotearoa

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**Erotylidae**  
(Insecta: Coleoptera: Cucujoidea):  
phylogeny and review

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**Lincoln, Canterbury, New Zealand**  
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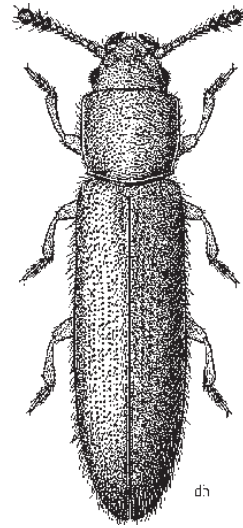
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## POPULAR SUMMARY

## HE WHAKARĀPOPOPOTOTANGA

Class **Insecta**Order **Coleoptera**Family **Erotylidae**

**Illustration / Whakaahua:** *Hapalips prolixus* (Sharp) (Illustrator / Kaiwhakaahua: D. W. Helmore).

**Erotylid beetles**

The family Erotylidae (here combined with Languriidae) is composed of approximately 3500 species worldwide, and is another one of those beetle groups that has had few researchers because most species are small, brown, and not considered attractive. But this is true only for the bulk of the species, because many plant-feeding (Languriinae) and fungus-feeding (Erotylini) forms are big, beautiful, and easy to collect and identify. It is only by unfortunate evolutionary reasons that these bigger forms don't occur in New Zealand: New Zealand split off from the ancient continent Gondwana before these bigger groups evolved.

Part of this contribution deals with the development of a classification for the world fauna. Biological classifications allow scientists and the public to communicate about the world of plants and animals by providing a natural reference system that conveys, among other things, where species belong in the tree of life and what taxa they are related to. This taxonomic reference system is typically based on phylogenetic trees that are graphic representations of how life evolved. How the New Zealand members of Erotylidae fit into this new classification is of primary importance for understanding the origins of our local fauna and how they relate to other erotylids.

The New Zealand fauna is rather small, and the 9 species are treated here, while the remaining species in the tribe Erotylini (*Thallis* and *Cryptodacne*) are treated elsewhere. The family can be easily separated from other groups, but a microscope will be necessary to discriminate these species from similar families such as Cryptophagidae. The included

**Ngā Pītara Erotylid**

Kei te āhua 3500 ngā momo o te whānau Erotylidae (kua uru mai ngā Languriidae ki tēnei tatauranga) puta noa i te ao. Heoi anō, he tokoiti noa te hunga rangahau i te whānau nei, i te mea he pakupaku, he parauri te tae, ā, ki ētahi, he anuanu anō ki te titiro atu. Engari ahakoa kei te tika pea tēnei kōrero mō te nuinga, kāore e tika ana mō te katoa. He maha hoki ngā momo kai tipu (ngāi Languriinae) me ngā momo kai harore (ngāi Erotylini) he rahi tonu te hanga, he ātaahua, he māmā anō ki te kohikohi, ki te tautohu. Ko te āhua o te kunenga mai te take kāore a Aotearoa e nohoia ana e ngā momo rahi ake. Arā nē, i wehe mai a Aotearoa i Te Uri Māroa i mua i te kunenga mai o ngā momo rahi ake.

E aro ana tētahi wāhanga o tēnei tuhinga ki te hanganga o tētahi pūnaha whakarōpū mō ngā erotylid huri i te ao. Mā ngā whakarōpūtanga koiora ka takoto he pūnaha tohutoro māori e whakaatu ana kei hea ake o te ao koiora tēnā me tēnā momo, ā, ko wai mā ngā uri tata, e taea ai e ngā tohunga pūtaiao me te hunga tūmatanui te whakawhiti kōrero mō ngā aitanga a Tāne. I te nuinga o te wā, ka noho ko ngā 'rākau whakapapa' hei tāhuhu mō te pūnaha whakapapa, e māmā ai te whakaahua pēhea te kunenga mai o ngā uri maha. He mea tino nui kia mōhiotia te tūranga o ngā momo Erotylidae o Aotearoa i roto i tēnei whakapapa hou, i te mea mā reira e mōhiotia ai tō rātau pūtakenga mai, me ō rātau hononga ki ētahi atu erotylid.

(continued overleaf)

(haere tonu)

identification keys will help. The species are not difficult to identify, and some, like *Loberus* and *Cathartocryptus*, have distinctive colour patterns that make for easy recognition.

What is extraordinary about the New Zealand species is that these have phylogenetic or family relationships with erotylid beetles throughout the rest of the world. Many species have close relationships with species in Australia, New Caledonia, South America, and possibly South Africa. The unusual genus *Loberonotha*, found only in New Zealand, may be related to taxa distributed in Boreal Europe, but its exact relationship is unclear and requires additional study.

The family Erotylidae is composed of a mixture of feeding types, and this is reflected in New Zealand's fauna. *Cathartocryptus*, *Cryptodacne*, and *Thallis* are strictly fungus feeding, *Loberonotha* is plant feeding, perhaps specialising on pollen, and the remaining species are scavengers feeding on plant and fungus tissues. Some species are restricted to certain habitats; for example, *Loberus depressus* is found commonly at the leaf axes of cabbage trees, and *Hapalips* can be found in the sheaths of nikau palms. These species can be collected in traps (flight intercept traps) and by sifting leaf-litter. Looking on host plants and fungi provide the best areas for collecting some species.

Like many beetles in New Zealand, most species of *Cryptodacne*, *Loberus*, and *Thallis* are flightless and must walk between food sources. When habitat is destroyed, it may take a long time for these beetles to re-establish themselves in regenerating bush.

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Contributor **Rich Leschen** was born in Newport, Arkansas, a small rural community in the southern United States, and raised in the large city of St Louis, Missouri. He spent his early life interested in paleontology, herpetology, and music. After graduating from Southwest Missouri State University (Springfield) with a major in biology and a minor in geology, he worked as a soil consultant, during which time fieldwork helped him develop interests in edible mushrooms and bird watching. Missing academic pursuits, he eventually began a Masters program at the University of Arkansas (Fayetteville), and started work that would form the basis for his ongoing studies on the systematics, evolution, and ecology of mycophagous Coleoptera. His Masters project was a list of the fungus-feeding Coleoptera of Arkansas, and much of his time was spent collecting bee-

(continued overleaf)

E 9 noa iho ngā momo erotylid e kitea ana i Aotearoa, ā, koirā ngā mea e āta tirohia ana i konei. Ko ērā atu momo o te iwi Erotylini (ngāi *Thallis* me ngāi *Cryptodacne*), kei te kōrerotia i wāhi kē. He māmā te wehewehe i tēnei o ngā whānau i ētahi atu rōpū, engari me whakamahi rawa he karu whakarahi hei wehewehe i ēnei momo mai i ētahi whānau āhua rite te hanga, pērā i ngā Cryptophagidae. Heoi, he āwhina kei ngā ara tautohu e mau mai ana ki te tuinga nei. Kāore e pērā rawa te uaua o te tautohu i ngā momo. He whai taurira kano ētahi e mārama ana te kitea atu, pērā i ngā *Loberus* me ngā *Cathartocryptus*, e māmā ai te tautohu i a rātou.

Ko te mea rerekē o ngā momo o Aotearoa, he whai hononga ā-whānau rātou ki ērā atu pītara erotylid i ngā tōpito katoa o te ao. Arā ngā momo maha he hononga tata a ō rātou ki ngā momo o Ahitereiria. o New Caledonia, o Amerika ki te Tonga, tae atu ki Āwherika ki te Tonga. Arā tētahi puninga korokē o Aotearoa, ko *Loberonotha* te ingoa, tērā pea he hononga ōna ki ngā rōpū e kitea ana i Ūropi ki te Raki; heoi anō, he rehurehu te āhua o te hononga – me haere tonu he rangahautanga e mārama ake ai.

He rerekē te āhua o te kai a tēnā, a tēnā o te whānau Erotylidae, ā, e whakaataria ana tēnei āhua i ngā momo o Aotearoa. He kai harore te *Cathartocryptus*, te *Cryptodacne*, me te *Thallis*. He kai tipu te *Loberonotha*, otirā, ko te hae anake pea tāna kai. Ko ērā atu momo, ka hamuhamu noa i ngā tipu me ngā harore kua mate. He ripoina whāiti ō ētahi, hei taurira, kitea nuitia ai a *Loberus depressus* i te tī, i te wāhi e hono ana ngā rau ki te kahiwi. Waihoki, ko ngā pūkoro o ngā rau o te nīkau te kāinga o te *Hapalips*. Ka taea te whakatū āhei kokoti rere hei hopu i ngā momo nei, ka taea rānei te tātari ngā rau popo. Hei kohikohi i ētahi atu momo, ka whaihua ake te āta tiroiro i ngā rākau, i ngā harore rānei e noho ana hei kāinga mō rātou.

Pērā i te maha tonu o ngā pītara i Aotearoa, he rerekore te nuinga o ngā *Cryptodacne*, ngā *Loberus*, me ngā *Thallis*, ā, me hīkoi haere rawa hei kimi kai mā rātou. Ki te takakinotia ō rātou ripoina, ka roa tonu pea ngā taupori pītara nei e whakapau kaha ana kia mano, kia rea i ngā ngahere hou.

---

I whānau mai te kaituhi, a **Rich Leschen**, i Newport, he paenoho tāngata i te taiwhenua, rohe o Arkansas, i te taha tonga o Amerika. Ka tipu ake ia i te tāone nui o St Louis, i Missouri. Ko te mātai mātātoka, te mātai ngārara, nukuwai, me te puoro ngā kaupapa i ngākau nuitia e ia i ōna tau tuatahi i te whare wānanga. Nōna ka whiwhi i tana tohu paetahi (ko te koirā te kaupapa mātāmua, ko te tātai arowhenua te kaupapa mātāmuri) i te Whare Wānanga

(haere tonu)

tles and becoming familiar with the North American fauna. After completing his Masters he went to University of Kansas to work on the systematics of Cryptophagidae, but spending more time working on other groups, including other members of Cucujoidea (e.g., Erotylidae) and Staphylinoidea (scaphidiine staphylinids). This work was facilitated by a curatorial assistant position at the Snow Entomological Museum that allowed Rich to be more broadly trained in the identification and systematics of world Coleoptera and to collect beetles throughout Latin America. Several grants allowed him to visit museums in North America, Europe, and Latin America. After a 2-year period of being unemployed and periodically teaching systematics at Michigan State University (Lansing) he joined Landcare Research, Auckland. He maintains a high level of academic interest in Coleoptera systematics and involvement with the local and international beetle community; his main objectives being to produce useful beetle classifications and to promote the study of natural history, especially systematics and taxonomy. Apart from his systematics career, he maintains an interest in improvisational acoustic music, and combines western folk and classical Indian influences into a unique guitar style.



o te Rohe Nui o Missouri ki te Uru-mā-tonga (i Springfield), ka haere hei mātanga oneone. I roto i āna mahi tiroiro oneone, ka tūmata tana aro nui ki ngā harore e taea ana te kai, me te mātakitaki manu. Ka mea ā, ka tupu ake te hiahia ki te whāwhā anō i ngā mahi whare wānanga. Ka tūmata a Leschen i tana tohu paerua i te Whare Wānanga o Arkansas (Fayetteville), me te uru ki ētahi mahi ka noho hei tūāpapa mō āna mahi e pā ana ki te whakarōpūtanga, te kunenga mai, me te taupuhi kaiao o ngā Coleoptera kai harore. He whakarārangi i ngā Coleoptera kai harore o Arkansas te aronga o tana Tohu Paerua. He nui te wā i pau i a ia ki te kohikohi pītara, me te whai kia taunga ia ki ērā o Amerika ki te Raki. Nō te otinga o tana Tohu Paerua, ka haere te tangata nei ki te Whare Wānanga o Kansas, ko tōna tikanga he whakarōpū i ngā Cryptophagidae tana kaupapa matua. Heoi anō, i pau te nuinga o ōna kaha ki te tiroiro i ētahi atu rōpū, tae atu ki ētahi atu o ngā Cucujoidea (hei tauira, ngā Erotylidae) me ngā Staphylinoidea (ngā scaphidiine staphylinid). He waimarie i riro i a ia tētahi tūranga kaitiaki tuarua i te Whare Mātai Pepeke o Snow. I taua tūranga ka whānui ake tana mōhio ki te tautohu, ki te whakarōpū i ngā Coleoptera o te ao nui tonu, ā, i āhei ia ki te kohikohi pītara puta noa i ngā whenua Rātini o Amerika. Ka whakawhiwhia anō hoki a Leschen ki ētahi pūtea i āhei ai ia ki te toro i ngā whare taonga maha o Amerika ki te Raki, o Ūropi, me ngā whenua Rātini o Amerika.

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---

Translation by **H. Jacob**  
Huatau Consultants, Levin





## ABSTRACT

Nine species of New Zealand Erotylidae (excluding Erotylinae) belonging to five genera are described. Two of these species from the Three Kings Islands are described as new: *Loberus wattii* Leschen and *Loberus borealis* Leschen. One species is transferred from Cryptophagidae to Erotylidae (*Loberus anthracinus* (Broun), new combination) and another is synonymised with *Loberonotha olivascens* (Broun) (= *Telmatophilus vestitus* Broun). *Cryptophilus integer* (Heer) is newly reported from New Zealand.

An amended world classification of the Erotylidae is proposed. A cladistic analysis of the families Erotylidae and Languriidae based on 120 adult morphological characters and 57 terminal taxa demonstrates that the family Languriidae is paraphyletic with respect to the placement of Erotylidae. The subfamily Xenoscelinae and its tribes are paraphyletic with respect to the placements of other subfamilies of Languriidae. The name Erotylidae has nomenclatural priority and the name Languriidae is treated as a synonym of the former. A new classification is proposed and recognises six subfamilies: Xenoscelinae (7 genera), Pharaxonothinae (5 genera), Loberinae (6 genera), Languriinae (72 genera), Cryptophilinae (13 genera), and Erotylinae (5 tribes). The monophyly of Loberinae is questionable because of the placement of *Loberus* and the uncertain generic status of some of its relatives. Cladoxenini is shown to be paraphyletic, and three tribes are recognised in Languriinae: Hapalipini (new tribe, type genus *Hapalips* Reitter), Languriini, and Thallisellini. Three tribes are recognised in Cryptophilinae: Cryptophilini, Empocryptini (new tribe, type genus *Empocryptus* Sharp), and Toramini. The monotypic tribes Loberonothini and Xenoscelinini are redundant and are synonymised with Xenoscelinae and Cryptophylini, respectively.

The following changes in generic status and family-group placements are made for the world fauna: *Rhopalocryptus* Arrow is transferred to Salpingidae (Prostominiinae), *Cryptophagops* Grouvelle is synonymised with *Henoticus* (the type species *Cryptophilus alluaudi* Grouvelle is transferred to *Henoticus* (Cryptophagidae)), the three species described by Bruce in *Cryptophagops* are transferred to *Cryptophilus* Reitter (*C. allotrius* Bruce, *C. leonensis* Bruce, and *C. mnionomoides* Bruce), *Leucohimatiops javanus* Heller is synonymised with *Ahasverus advena* Waltl (Silvanidae), *Tomarops* Grouvelle is synonymised with *Cryptophilus* Reitter (resulting in one new combination), and the genus *Loberolus* is shown to be paraphyletic. Two genera are newly described: *Protoloberus* (type species *Telmatophilus singularis* Blackburn) from Australia and *Neoloberolus* (type species *Loberolus cursor* Grouvelle) from Central and South America. The following Australian species of *Telmatophilus* described by Blackburn are transferred to *Loberus*: *L. breviformis*, *L. koebeli*, *L. sharpi*, *L. stygius*, and *L. sublautus*, new combinations. Annotated keys to the higher taxa and genera of all subfamilies except Erotylinae and Languriini are provided and biological information, including cycad feeding and mycophagy, is summarised.

Keywords: Coleoptera, Cucujoidea, Erotylidae, Languriidae, taxonomy, classification, key, phylogeny, generic status changes, family placement changes, new species, new synonymy, distribution, ecology, biology, species endemism, fauna.

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Paul Skelley confirmed characters for Erotylidae and John Lawrence made available Beta versions of his world adult key that provided additional cladistic and identification characters. For notes pertaining to type specimens I thank Eric Matthews and Malcolm Kerley. For relevant literature I thank the staff librarians of the University of Kansas, FMNH, HortResearch, and Landcare Research as well as copies of papers supplied by John Lawrence, Al Newton, Rolf Oberprieler, Paul Skelley, Adam Slipinski, Margaret Thayer, and Piotr Wegymowicz. Dany Azar (MHNP) tried to locate Crowson's fossil "beautiful clavicorn" at various museums: the specimen is still missing. I thank Bernd Franzen and Piotr Wegymowicz for use of their draft catalogues of the species of Languriidae. Des Helmore provided habitus drawings for each genus and Fig. 14 and 15 and, with a keen sense for the microscopic,

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## INTRODUCTION

Groups of microcoleoptera, especially those in the superfamily Cucujoidea, are taxonomically challenging because similar body forms exist among completely unrelated lineages and they require careful dissection to confirm taxonomic placement. Confusion about the family limits of Cryptophagidae, Erotylidae, Languriidae and other cucujoids has resulted in a complex history of paraphyletic groupings requiring detailed phylogenetic study. The objectives of this study were three-fold:

- (1) reconstruct the phylogeny of Languriidae and Erotylidae using adult characters,
- (2) provide a higher classification for these families, and
- (3) review the species of Languriidae *sensu lato* occurring in New Zealand.

Leschen & Wegrzynowicz (1998) reviewed many of the problems with the higher classification of Languriidae and their treatment serves as an appropriate introduction to this work. The phylogenetic study of Languriidae presented here grew from previous work on the systematics of Cryptophagidae because many languriid taxa were described as cryptophagids, and members of both families are usually misidentified together in insect collections. While Cryptophagidae appears to be a monophyletic group (Leschen 1996), a two-century long controversy remains

about the status of Languriidae: this family is either monophyletic or should be included in a broadly defined family Erotylidae (see references in Leschen & Wegrzynowicz 1998). A cladistic analysis based on genera and adult characters forms a major portion of this study to support the monophyly of Erotylidae plus Languriidae as well as determine the monophyly of the higher taxa within these two families. An arrangement based on the phylogenetic relationships shown in this study will, in turn, provide a better classification for placing the New Zealand species in a global taxonomic context. In light of the new phylogenetic information I broaden the taxonomic concept of Erotylidae to include all Languriidae.

In this paper the New Zealand species that were included in the Languriidae *sensu lato* are reviewed and a future publication to be co-authored with P. Skelley will treat the species of erotylids currently placed in *Cryptodacne* and *Thallis*.

## SYNOPSIS OF THE SYSTEMATIC PROBLEMS

Leschen & Wegrzynowicz (1998), in their review of Languriidae classification, included comments on salient characters of Languriidae and the discussion here is limited to major points relevant to questions to be addressed by the cladistic analysis. The major issues concern the monophyly of the higher taxa at the familial, subfamilial, and tribal levels (current arrangement of Languriidae is provided in Table 1).

The family Erotylidae, which originally included the large-bodied, colourful, and plant-feeding members of Languriidae (Crotch 1876; Gorham 1887a, b; Fowler 1908), was considered separate from languriids by Crotch (1873) and this classification was followed by others (Arrow 1925; Crowson 1952; Schenkling 1923, 1928; Sen Gupta & Crowson 1971; Lawrence & Newton 1982, 1995; Pakaluk *et al.* 1995). These two families were separated largely on the basis of different biologies (Lewis 1884), with Erotylidae being mycophagous and Languriidae being phytophagous. This two-family system spans two centuries (Lawrence *et al.* 1995), and when the classification of Languriidae was re-examined in light of taxa transferred to it from Cryptophagidae, the morphological grade between Languriidae and Erotylidae remained (Leschen & Wegrzynowicz 1998). Some authors (e.g., Rymer Roberts 1939, 1958; Lawrence 1991; Sen Gupta & Crowson 1971; Leschen & Wegrzynowicz 1998) have questioned the separation of Erotylidae and Languriidae, though the two-family system is followed presently. While there are unambiguous characters that support the monophyly of Erotylidae (Leschen & Wegrzynowicz 1998, Lawrence

Table 1. Current (summarised in Leschen & Wegrzynowicz 1998) and proposed classifications of Languriidae and Erotylidae.

Sen Gupta & Crowson System	Proposed New System
Languriidae	Erotylidae
Cryptophilinae	Cryptophilinae
Cryptophilini	Cryptophilini
Xenoscelinini	Empocryptini
Languriinae	Toramini
Cladoxenini	Languriinae
Languriini	Thallisellini
Thallisellini	Languriini
Setariolinae	Hapalipini
Toraminae	Xenoscelinae
Xenoscelinae	Pharaxonothinae
Loberonothini	Loberinae
Pharaxonothini	Erotylinae
Loberini	
Xenoscelini	
Erotylidae	

1991), Languriidae is not a monophyletic taxon, as shown below.

Several problems exist with the monophyly of the family-group taxa of Languriidae (Leschen & Wegrzynowicz 1998). A key problem is the monophyly of the heterogeneous subfamily Xenoscelinae: synapomorphies have not been identified for the subfamily, the monophyly of all of the three tribes is questionable, the pharaxonothine genus *Loberopsyllus* may be a member of Cryptophilinae (Leschen & Ashe 1999), and the widespread and diverse genus *Loberus* may be paraphyletic with respect to similar genera that were described as distinct (Leschen & Wegrzynowicz 1998). The two tribes of Languriinae (Languriini and Cladoxenini) which contain the highest diversity in Languriidae are thought to be paraphyletic (Crowson 1955, Sen Gupta & Crowson 1971).

While the emphasis of this study is adult morphology, larval characters have been used to clarify the relationships among some of the higher taxa (e.g., Rymer Roberts 1939, 1958; Sen Gupta & Crowson 1971) and information about larval work is contained in Leschen & Wegrzynowicz (1998) and is not repeated here. Meanwhile, a phylogenetic study using larval characters is in progress by Joseph McHugh.

## TAXONOMIC HISTORY OF NEW ZEALAND LANGURIIDAE (now Erotylidae)

The Languriidae fauna of New Zealand is relatively small and consists of only 8 endemic species (Watt 1982, Klimaszewski & Watt 1997). It is, however, an important group historically and taxonomically, and from two scientific perspectives led by two pairs of contemporaries. David Sharp and Thomas Broun (late 1800's and early 1900's) described the New Zealand species, and later Roy Crowson and Tapan Sen Gupta (mid 1960's and early 1970's) placed the fauna in a world classification of Cucujoidea.

The New Zealand languriid species were originally described as members of the families Cryptophagidae or Cucujidae. David Sharp (1876, 1886) described two species (now placed *Loberus*) in the holarctic genus *Telmatophilus* (Cryptophagidae), the only species of *Hapalips* in the mediterranean genus *Xenoscelis* (Cucujidae), and erected a genus *Cathartocryptus* for the species *C. obscurus* (Cucujidae), a species that was described previously by Broun in *Paramecosoma*. Thomas Broun (1881, 1893) was busy describing the entire beetle fauna and placed his languriid species into holarctic cryptophagid genera (*Cryptophagus anthracinus*, *Paramecosoma maculosa*, *Telmatophilus vestitus*, and *T. olivascens*).

The incorrect placement of New Zealand taxa may not have been a case of messy taxonomy for the industrious Major Broun or the distinguished and world-renowned

Sharp, but rather a conservative decision to accept the premodern concepts of cucujoid classification. Sharp influenced Broun's career in entomology (Zimmerman 1993) and the classifications accepted by these coleopterists reflected the uncertain status Cryptophagidae, Cucujidae, and Languriidae and their subordinate genera. Concepts of these taxa were questionable at the time and in some respects continue to be so.

While Broun and Sharp were working, *Telmatophilus* was a paraphyletic genus consisting of members of Cryptophagidae (the true Holarctic *Telmatophilus* is in Cryptophagidae) and many taxa now included in *Loberus*. Polyphyletic groups like *Telmatophilus* existed because the concept of homology in Victorian England and elsewhere was very different from that accepted today, especially in connection with classification. The distinction between homology and analogy was being discussed fervently, typically in light of Darwinian theory (Russell 1916), and there was no adequate empirical method to distinguish between these two classes of similarity. For example Sharp thought that *Xenoscelis prolixus* (now in *Hapalips*) resembled *Xenoscelis deplanatus* (Wollaston), a taxon once included in Cucujidae. These two species are dorsoventrally compressed (as is the genus *Cathartocryptus*, which was also once included in Cucujidae) and the morphological connection between similar and unrelated taxa made by Sharp resulted in an error in classification recognised later using other methods that differentiate homology and analogy. Also, the cultural goals of Victorian taxonomists were different from those of modern systematists, and Broun and Sharp were trying to describe as quickly and as adequately as possible the new taxa brought to them by local and foreign naturalists. Accusing these predecessors of their taxonomic errors is easy, but we have the luxury of modern approaches, training, and skills that did not exist over 100 years ago.

In the 1900's the use of light microscopy and dissection increased, and entomologists began examining characters in more detail and testing existing taxonomies. Roy Crowson, whose influence on modern Coleoptera classification was unprecedented, came to New Zealand in the 1950's to collect its rich relictual fauna (Leschen 2000) and together with, or in an advisory role to, his student Tapan Sen Gupta provided the first modern attempts to classify Languriidae into monophyletic taxa. (Actually, Sen Gupta was supposed to be working on a world review of Cryptophagidae for his Ph.D. thesis at the University of Glasgow, but spent most of his time transferring cryptophagid species to Languriidae and working on the classification of this group.) Sen Gupta (1968a) transferred Sharp's *Xenoscelis prolixus* to *Hapalips* (subgenus *Xenosceloides*), and with Crowson (1969), erected

*Loberonotha* for Broun's *Telmatophilus* species, and placed this genus in the tribe Loberonothini. The work of Crowson and Sen Gupta is considered in more detail elsewhere (Leschen & Wegrzynowicz 1998).

Crowson and Sen Gupta are credited for being the first modern systematists to study Languriidae, but Crowson was philosophically opposed to cladistics, a "postmodern" method developed in the mid to late 1900's and credited to Willi Hennig (see the English translation of Hennig 1966). Cladistics provides systematists with a rigorous method to distinguish between similarity (or analogy) and homology (synapomorphy), the latter of which is taken as evidence for the monophyly of a group. The resultant tree is a cladogram that is produced by grouping taxa by synapomorphies and minimising the number of character changes over the entire tree. Though he did recognise the need to differentiate between primitive and derived characters, one reason why Crowson was opposed to cladistics was that character weighting could not be applied explicitly and he preferred a detailed narrative approach to homology and classification (Crowson 1991a). Crowson also acknowledged that a character could be derived in one group and primitive in another group, a pattern that "sometimes leads to false conclusions" (Sen Gupta & Crowson 1971: 29). Though Sen Gupta & Crowson (1971) did not produce a phylogenetic tree that represented languriid relationships, they provided three box or chart diagrams. Each chart was a sort of periodic table of selected Cucujoidea that tabulated larval and adult characters. The cladistic analysis that follows is a third phase in the development of a classification for Languriidae.

An important and somewhat neglected addition to this short history is the contribution made by Charles Watt, one of my predecessors at NZAC. Watt was New Zealand's specialist on tenebrionoids (among other groups) and was very active in collection management and curation. He made many unpublished observations on NZAC specimens and indicated syntypes that he recognised were original specimens contained in Broun's type series. These labels are easily identified and have handwritten labels with locality (usually one word) and Broun's unique species numbers followed by a full stop (.) (T. K. Crosby, pers. comm.). Watt (1982) transferred two of David Sharp's species of *Telmatophilus* to *Loberus* (unaware of Bruce 1952b) and, based on his curation labels, he thought that *C. anthracinus* should be a new genus of Languriidae. However, *C. anthracinus* is actually a member of *Loberus* and is similar to other species, especially to one montane South American form that is also apterous.



## MATERIAL EXAMINED AND GENERAL METHODS

This study is the continuation of a project initiated during work on Cryptophagidae (Leschen 1996). In contrast to the previous study, I have not attempted to examine every species of languriid in detail because of time restrictions. Type species of most genera were examined externally (except for Languriinae) for a previous study (Leschen & Wegrzynowicz 1998), and a few others were examined more recently. Over the years, museum specimens on loan and those retained from identifications have provided the foundation for understanding the morphological variation necessary to determine the monophyly of the higher taxa and some genera. Approximately 400 species of cucujoidea have been dissected for this and other studies and an annotated list of dissected species is provided in Appendix 1. Collections and curators are cited in Leschen (1996) and important and additional material examined in this work were borrowed from the collections listed in the Acknowledgments.

In the descriptions of New Zealand species, diagnostic characters are not repeated in the body of the description and two-letter codes on labels and for New Zealand distributions follow Crosby *et al.* (1998). Total length of the beetle is measured from the anterior edge of the pronotum to the apex of the elytra. Lectotype designation was necessary for *Loberolus cursor* Grouvelle, *Xenoscelis prolixus* Sharp (= *Hapalips*), and New Zealand species described by Broun because holotypes were not designated in the type series. Paralectotypes were designated for New Zealand taxa, because original type material, especially Broun syntypes, are contained in the BMNH and NZAC. Type specimens are listed under each species, while material examined is listed in Appendix 3.

Adult morphology is the focus of this study, and to properly evaluate cladistic and taxonomic characters slide-mounted specimens are mandatory for examination with a compound microscope. Duplicate specimens (especially males) stored in glycerine such that the structures can be rotated easily are also important. Specimen preparation and dissection follows that of Leschen (1996) and was influenced in a large part by methods used by A. Newton (FMNH). There is no quick and easy way to prepare a specimen for light microscopy. Perfect and intact specimens of the species to be dissected are best. Observations of the specimens throughout the preparation process is necessary so that they are not damaged. The specimen should be removed from its paper point or card by placing the specimen into a test tube with a small amount of water and holding the tube over a flame until the specimen floats off (the "Slipinski method"). A piece of cotton inserted at the

top will prevent the specimen from boiling out in case of overheating. The wings are removed from the softened specimen and stored in glycerine. The body is placed in weak potash (10% KOH) for maceration of soft tissues, a technique that was advocated by 19<sup>th</sup> Century coleopterist George H. Horn, and deemed unsafe by David Sharp (Zimmerman 1993). Maceration requires 1 to 4 days, maybe longer depending on the size of the beetle. After maceration, specimens with darkly pigmented cuticle are placed in hydrogen peroxide for a period of up to 5 minutes for further clearing. Once clearing is completed washing in distilled water is necessary to stop the clearing or macerating process. While some entomologists prefer xylene-based mounting media, I prefer alcohol-based mounting media which makes transfer between alcohol preservative, stains, and mounting media easy and practical. After clearing and washing, specimens are transferred to 90% ethanol prior to staining in Chlorazol Black. Staining often requires washing or staining repeatedly until the membranes are clearly visible. To destain, the specimen can be diluted in alcohol until the desired level of penetration is made. The treatment of wings requires special attention to see the veins (Kukalová-Peck & Lawrence 1993) and I do not stain them because these are visible using Nomarski differential contrast under the compound microscope. The wings are removed from the glycerine, washed in water, and placed in graded series up to 90% alcohol. Wings and the rest of the beetle are washed briefly in alcohol and placed directly into the mounting media on a microscope slide where dissection is performed.

Specimens are dissected in Euparal (Chroma-Gessellschaft) mounting medium. A droplet of Euparal is placed on one end of the slide (making room for labels) and the specimen is placed in it. For dissecting tools, two wooden applicators with minutens attached apically are used to disarticulate the specimens. Just as entomologists are idiosyncratic about the way they dissect, likewise each beetle group requires certain procedures. Some groups dissect well and require less finesse, while others are difficult and require patience. Erotylidae are not difficult to manage because their bodies are relatively hard and the sclerites do not distort during dissection. I start with the head by removing the mouthparts and usually keep one mandible and maxilla attached and articulated. The left legs are disarticulated from the body at the coxa, and the genitalia and terminalia are removed. Then the parts are arranged sequentially on the slide and the dissection is laid aside for a period of 3–6 hours while the Euparal sets. The specimens are periodically checked so that the pieces are arranged appropriately until stable. Arrangement of the structures is made with forceps dipped into alcohol (to break the surface skin). Removal of bubbles from the Euparal is

done by applying the tips of a closed forceps dipped in alcohol to the edge of the bubble. After setting, four vinyl slide props are set into the media and the slide is placed on a slide warmer set at 40° C for 24 hours. Once hardened, Euparal is applied to the dissection, an 8 x 8 mm cover slip is applied on top of the dissection and the slide dried for a period of 2–4 weeks depending on the thickness of the mount. Slide ringer is not necessary. Disarticulated specimens can easily be removed from the slide mounts by soaking them in a bath of alcohol for approximately 15 minutes.

## MORPHOLOGY

Basic morphology of Erotylidae and Languriidae is covered in this section. The most comprehensive references for adult morphology of lower cucujoids are Evans (1961), for his treatment of the cryptophagid *Atomaria ruficornis* (Marsham), and McHugh *et al.* (1997), for their treatment of the erotylid *Megalodacne heros* (Say). For gross structure I adopt the terminology used by Lawrence & Britton (1991) and Lawrence *et al.* (1999a) and for microsculpture I follow Harris (1979, 1998). Key features used in the cladistic analysis are italicised and details about each character are discussed in Appendix 2 under numbers listed at the end of each entry. Structures discussed below are labelled in the following figures: dorsal body (Fig. 8), ventral body (Figs. 9, 14, 15), male genitalia (Fig. 19), female genitalia (Fig. 31, 32) and wing (Fig. 34).

### Surface and internal cuticular features

**Abdominal calli** (Fig. 15): lineate structures present on the internal surfaces of the abdominal ventrites (characters 83, 84).

**Cuticular gland ducts** (Fig. 10–12, 14, 15): *Unitubular* or *multitubular* ducts which extend internally into the cuticle from a distinct *pore* (or pores) visible at the surface at high magnification. These structures may be associated with various raised lines, deep grooves, or carinae where excretions are dispersed via capillarity or by evaporation from special *platforms* or *callosities* (Fig. 11, 68) via evaporation (characters 5, 18, 19, 46–48, 50, 61, 80, 81, 82).

**Microsculpture**: small cuticular surface features in the form of transverse lines (*imbricate*) or oval (*alveolate*) patterns.

**Pores**: small cuticular openings which are associated with well developed glandular ducts or may be scattered in clusters on sclerites (character 79).

**Punctures**: shallow pit-like impressions which extend into

the cuticle and are often marked by a seta and/or a pore; these also form the striae and the *scutellary striole* on the elytron (characters 113–114).

**Setae**: hair-like extensions of the cuticle which are *erect*, *suberect*, or *decumbent* (closely pressed to the surface of the cuticle).

### Head and its appendages

**Antenna**: typically clavate or capitate, consisting of 11 antennomeres and a 3–5 segmented club (characters 24–26).

**Frons**: anterodorsal portion of the head between the eyes where a *frontoclypeal suture* (Fig. 6) or *supraocular lines* (Fig. 53) may be present (characters 1, 29, 30).

**Gena**: ventrolateral portion of the head which may be anteriorly produced into *genal spines* (Fig. 40) (characters 16, 27).

**Gula**: ventral region of the head which usually has a *transverse groove* and rarely a well developed *pit* or *fovea* (Fig. 35, 39) (characters 20–23).

**Labium**: ventral mouthparts which include the mentum, ligula, prementum and labial palpi (characters 13–15).

**Mandible** (Fig. 56–59): dorsoventrally flattened appendage consisting mainly of apical teeth, a membranous prosthema, and a basal striate mola (2–4).

**Maxilla** (Fig. 60, 61): tripartite appendage located below the mandible consisting of an outer palp of three segments and a palpiger, a middle *galea*, and inner *lacinia* with one to three apical teeth (characters 6–8).

**Mentum** (Fig. 41, 42): posterior portion of the labium which consists of a transverse and median carinae, sometimes with lateral pits or pockets formed by well defined rims along the carinae (characters 9–12).

**Ocular setae** (Fig. 47): setae which are located between the eye facets (character 28; = interfacetal setae of Lawrence *et al.* 1999a).

**Tentorium**: internal structure which may have an anterior median spine which arises from a bridge-like corporotentorium (17).

**Vertex** (Fig. 53, 54): dorsal portion of the head which may have *stridulatory files* or a transverse *vertexal line* (= occipital carina, Lawrence *et al.* 1999a) and is sometimes bounded laterally by temples which extend posteriorly from the eyes (characters 31–34).

### Thorax

**Hypomeron**: deflexed portion of the pronotum which lies beneath the lateral carina; it may have a *notch* (Fig. 70) or

*spine* (Fig. 13) along its posterior margin, and may connect with the prosternal process posteriorly behind the procoxa (character 54).

**Procoxal cavity:** fossa which serves as the point of insertion for the procoxa which may have a narrow anterior extension, the *trochantinal notch* (Fig. 13, 76), which is the posterior extension of the notosternal suture (characters 51–53, 55).

**Pronotum:** dorsal portion of the prothorax consisting of a *disc* (portion of the pronotum above the carina) and may have well developed *posterior* and *anterior angles*, a *basal sulcus* and *pits*; the lateral margin or *lateral carina* may have teeth, a well developed marginal *bead* or raised rim, and other structures (characters 35–38, 40–45).

**Prosternum:** ventral portion of the prothorax which may have teeth along its anterior edge, forms the walls of the coxal cavities, and has a posterior *procoxal process* (Fig. 76) which may have lateral flanges which extend partly behind the procoxal cavities (characters 39, 49).

### Pterothorax

**Mesoventrite:** ventral portion of the mesothorax which often has anterior *procoxal rests*; rarely a pair of median carinae or lines (Fig. 87) or foveae, and meets the metaventrite posteriorly by the mesoventral process between the mesocoxae, articulating by means of internal *mono-* (Fig. 83) or *dicondylate articulations* or a simple flat edge (characters 56–60, 62, 64, 66).

**Mesepisternum and mesepimeron:** lateral or pleural elements of the mesothorax, a pit may be present in the mesepisternum (character 63).

**Metaventrite:** ventral portion of the metathorax which articulates anteriorly with the mesoventrite and posteriorly with the first ventrite of the abdomen (a notch may be present medially, Fig. 85) and usually has a median *discrimen* or longitudinal groove, *subcoxal lines* (or femoral lines), and *precoxal lines* on the external surface; there may be internal pores or hemidesmosomes. The metaventrite encloses the lateral portion of the mesocoxal cavities and connects with the lateral extensions of the mesoventrite. The metendosternite is an internally bifurcate structure which functions in muscle attachment (characters 64, 65, 67–72, 79, 85, 86).

**Metepisternum and metepimeron:** pleural region of the metathorax; the metepisternum may have a *ctenidium* (Fig. 89), a comb-like line of setae along its inner margin (character 73).

### Abdomen

**Aedeagus** (Fig. 19, 27): male intromittent organ of the cucujoid type (Crowson 1955) consisting of a ring-like tegmen, a median lobe, *articulated parameres*, internal sac (sometimes with a flagellum, internal sclerites and an apical apodeme), and posterior struts (characters 87–89).

**Ovipositor** (Fig. 31): female genitalia and egg-laying structure consisting of paired basal *gonocoxites* usually with an apical *gonostyle* or style (characters 92–96).

**Spiracles:** spiracles are present in the dorsal (tergal) membranes and may be absent from the apical abdominal terga (character 102).

**Sternites 8–10:** sternites 9 and 10 are fused in the male and form a ring around the apical portions of the aedeagus with an anterior extension or *spiculum gastrale* (characters 90, 91); sternite 8 is in the form of long ventral strut in the female and is referred to here as a *spiculum ventrale* (character 97).

**Spermatheca** (Fig. 32–33): female sperm storage structure consisting of a *basal bulb*, which may have an *apical pit*, an *accessory gland*, and a *spermathecal duct* (characters 98–101).

**Ventrite 1:** first visible ventral segment of the abdomen which articulates with the metaventrite medially by an *intercoxal process* and forms the posterior portion of the metacoxal cavities; its surface may have *subcoxal lines*; the intersegmental membrane between ventrites 1 and 2 may be absent and the two sclerites may be fixed or connate (characters 74–78).

### Body appendages

**Elytron:** hardened forewing consisting of a dorsal disc which may have well developed longitudinal *striae* consisting of punctures, a small *scutellary striole* (a short rudimentary stria that begins near the *scutellum*), a *humeral spine* near its base, and with a lateral *epipleuron* which is clearly visible in ventral view (characters 112–117).

**Hind wings** (Fig. 34): typically well developed with up to 9 veins and cross veins, including two cells, the *radial* and *wedge cells* (characters 118–120).

**Legs:** consisting of the basal coxa (with a small trochantin that is hidden), a short trochanter, elongate femur and tibia, and 5 segmented tarsus, with tarsomere 5 having a well developed empodium, *empodial setae*, tarsal claws, and sometimes a *tarsal shelf* which is a ventral extension of tarsomere that covers the empodium (Fig. 96–98) (characters 103–111).



## CLADISTIC ANALYSIS

### Terminals used in cladistic analysis

The analysis here is designed to test the monophyly of Languriidae and Erotylidae, and the higher taxa of Languriidae. These families combined probably form a monophyletic group supported by a combination of adult characters (Sen Gupta & Crowson 1971, Leschen & Wegrzynowicz 1998). Adult characters taken from an unpublished preliminary analysis of the cucujoidea families are indicative of this monophyletic group: presence of cuticular glandular ducts (especially in the head, Fig. 10), gular sutures mainly absent (Fig. 40, 45, 48), and mesocoxal cavities laterally closed (Fig. 9, 14, 82). None of these features are unique to Erotylidae and Languriidae. Perhaps correlated with these characters is the distinctive aedeagus which is usually retracted on its side in the abdomen, has a laterally compressed median lobe, and usually one or two elongate and narrow penile struts (Fig. 16, 19). These characters in combination may be unique to the erotylid complex and a more detailed survey is needed to assess the range of variation and distribution of uni- or biflagellate penile struts.

Choosing a member of Cucujoidea that is a likely sister taxon to Erotylidae and Languriidae is difficult because the relationships of the superfamily are so obscure. Several members of the cerylonid series (Alexiidae, Endomychidae; Arrow 1925, Crowson 1955, Sen Gupta & Crowson 1971) may be sister taxa to Erotylidae and Languriidae because these have a laterally closed mesocoxal cavity. This feature also occurs in members of the lower Cucujoidea and the metaventrite in these, as well as Erotylidae and Languriidae, overlaps the apical part of the mesepimeron, a feature mentioned by Sen Gupta & Crowson (1971: 36). Some members of the lower Cucujoidea (Cryptophagidae, Propalticidae; Sen Gupta & Crowson 1969, 1971, Leschen 1996, McHugh 1995 and in prep.) have also been suggested or used as sister taxa to root trees of Erotylidae and Languriidae, based in part by the presence of the characters listed above. Sen Gupta & Crowson (1971: 37) considered Biphyllidae as a likely sister taxon to Languriidae because Cryptophilinae and Biphyllidae both share a unisetose tarsungulus in the larva, even though the remaining members of Languriidae have a bisetose tarsungulus (see also Lawrence 1991). In the preliminary cladistic analysis of Cucujoidea mentioned above, Erotylidae and Languriidae are placed together as a relatively basal taxon to the remaining Cucujoidea, one step above the sister pair Sphindidae + Protocucujidae, which are at the root of Cucujoidea (no outgroups to Cucujoidea were included in the preliminary study). Based on these data I chose outgroups conservatively.

I chose four taxa to serve as outgroups to polarise

characters in the cladistic analysis from a broad range of Cucujoidea: Cryptophagidae (*Cryptophagus*), Phloeostichidae (*Myriabola*; Myriabolinae), Biphyllidae, and Lamingtoniidae (*Lamingtonium*). Cryptophagidae shares a number of features with Erotylidae and Languriidae, including mesocoxal cavities closed laterally (also occurs in cerylonid series, Passandridae, and Phalacridae), mesepisternum with pockets or foveae (variable in Erotylidae and Languriidae and present in Cavognathidae, Lamingtoniidae, and some Endomychidae), and presence of cuticular glandular ducts in the body (see discussion for character 48 in Appendix 2). One character suggesting further phylogenetic relationship among these outgroups is the lack of gular sutures in Erotylidae and most Languriidae, Biphyllidae, *Myriabola*, and Lamingtoniidae. Note that Biphyllidae and related Byturidae may actually be part of the Cleroidea (Lawrence & Leschen 2003) and are considered here as a distant outgroup. I did not include Endomychidae as an outgroup because this family may be paraphyletic (but see Tomaszewska 2000) and is probably not related to members of Languriidae and Erotylidae (as indicated in preliminary analyses) by having the following characters which define also a portion of the cerylonid series: frontoclypeal suture absent in many taxa (Fig. 51–53, though present mainly in Languriinae), absence of articulated parameres, tarsal formula 3–3–3 or 4–4–4, and medial fleck of the hind wing absent.

The cladistic study is challenging because it is meant to examine the relationships for a group exceeding 3500 described species. Also, there is an incredible amount of taxonomic work necessary to describe the diversity in Erotylidae and Languriidae and I have examined several undescribed languriine, toramine, and xenosceline genera from South Africa and tropical regions of Southeast Asia and Central and South America. Therefore, terminal taxa are species examined internally and externally and represent genera (or higher taxa of Erotylidae) in the data matrix (Table 2). I have examined specimens of all described genera of Languriidae except for most of the 51 genera contained in the tribe Langurini and the genus *Chinophagus* Ljubarsky, 1997, a flightless cryptophiline similar to *Atomarops*. The genus *Loberolus* contains two species, one from Costa Rica and the other from Madagascar, and the treatment of this taxon in the analysis is discussed below. The examination of types of some taxa necessitated changes in taxonomic status of some genera which are covered in the taxonomic sections following the cladistic analysis.

Males of *Anadastus*, *Atomarops*, *Bolerus*, *Cladoxena*, *Henoticonus*, *Macrophagus*, *Othniocryptus*, *Penolanguria*, and *Telmatoscius* were not available for study, and these are coded as unknown for characters 79 and 87–91 as listed

**Table 2.** Data matrix used in the phylogenetic analyses of Erotylidae. Character numbers refer to those in the text and in Appendix 2 and an asterisk (\*) refers to polymorphic character states.

	10	20	30	40	50	60	70	80	90	100	110	120
Biphylidae	0010000000	000?111000	?00000000?	10?0*10110	000000??00	1200101000	000000001*	0100111*00	??10000100	100?002101	10000000?0?	100*001000
Cryptophagus	00*1021000	000?0*1100	?00100000?	10?0000111	0000010001	00?0100?00	0011110010	1100000?01	1100001110	000?000101	?0000000?0?	201?000011
Lamingtonium	0010021000	010?001001	000100000?	00?0000110	1?0100??00	00?0000?00	0000021000	1100110?00	??10001110	000?000101	00000001?10	0001000000
Myriabola	0000021000	010?100000	?00000000?	010000000?	000100??210	1110101000	0000000010	1100010?00	??0?001010	100?002100	1000001?0?	2001001011
Ancestor	*0*0**000	0*0?***0*	000*000000?	**00**011*	*00*0*00**	**0*0*000	00***0*0*	*100***0*	*11*000**0*	*00?00*10*	*00000*?0*	*0**00*0**
Dacninae	10100**00	000?001010	?0000*0*1	0*10*10*00	1?010*0000	021000*000	0001110*0*	0001101100	??1**00110	120?1?0001	00000000?10	2001001000
Encausatinae	*000020110	0011001101	2001010111	00?0*10100	1?01010000	0210100?00	1002110101	0001101001	100?000110	100?000101	1000010110	2001001000
Erotylinae	000002*110	00110111*1	100*01011*	00?0210100	1?01010001	0210*0*000	1001120*?1	0001100?0	??0?000110	100?000101	1002010110	*001001000
Megalodacninae	000000000	010?001111	2000010111	0*10010100	1?01010001	0210000?00	1001121010	0001100?01	1010000110	100?000001	1000010110	2001001000
Tritominae	00*0021**0	00**001101	1000000011*	0*10*10100	1?0101000*	0210*0*000	1001110*11	000110*000	??10*00110	100?00*0**	0000010110	2001001000
Acryptophagus	0010030000	000?001011	2001000010	00?0011011	0110111001	10?*-100?00	1*10100111	0010101101	1110*00111	1301010011	000011010?	1100111000
Anadastus	1100131000	010?111011	2001110011	00?0000000	1?1000?000	10?1100?00	1010100011	00001111?1	111100????	?20?012010	1001010111	2101011000
Atomarops	0001000000	00*0*0101	000000000?	00?0000*10	000100??00	10?0001100	*001120100	00001010?1	011011????	?10?011101	010101000?	20110011??
Bolerus	0010030000	0010001011	000100000?	0110010100	0110011001	1111100?00	1010100101	00101010?1	101000????	?00?000?0?	000001010?	1000001000
Brachypterosa	0000000000	010?001011	2000000010	0110000100	1?0100??00	1200000?00	0001100001	0000101001	1010110110	100?000?0?	?00211000?	20110011??
Cathartocryptus	00*1020000	010?001000	?0000000*1	00?0110110	0100010010	120001??00	1002110001	0010101000	??10110110	110?001101	0000000?0?	20110*1011
Cladoxena	1100020000	010?111011	2001000010	0110000*00	1?1000?00	10?1000?0	0000100011	00001010?0	??1000????	?20?010001	000101010?	1101001000
Crotchia	0100030000	000?1*1001	200*000011	0110000*00	1?1000?00	10?0100?00	0000100111	001010*101	1010000111	120?010011	000001010?	2101001000
Crowsenguptus	0001020000	001110*101	0000000010	0100100100	1?1000?00	120011??00	0001100011	100010*001	0110110110	100?000001	100211010?	1011011*11
Cryptophilus	0010020000	00*001011	00000000*1	01000*0110	0000010000	1200*00?00	10011*0011	1000101001	1110110110	110?00*011	000*01000?	10110*1011
Dasydactylus	1110130000	000?111011	2001110111	00?0000200	1?10011000	10?0000?00	1000100011	0000100?01	1110000111	120?012001	000001010?	2101001000
Empocryptus	0001020000	0*1*001011	0000000010	0100001010	000*010000	10?0*00?00	0001110*11	1000101010	??10000110	100?000001	001001000?	2001011011
Fitoa	0010020000	0110011011	2000000010	0110300100	*11001*101	10?0000?00	1010100011	00001**000	??10000111	100?000001	100001010?	1001011001
Hapalips	00*0030000	0010001011	**000000**	0*1*000*10	*10*00*1*0	*10*100?00	0000100111	1*011100*	**10000111	100?0001*1	000001010?	210***100*
Henoticonus	0000020000	100?001010	?010000011	1111000010	1?00011100	11?0000?01	0010100011	1000110?01	010?00????	?00?000101	00000000?0?	20000001000
Languria	1100031000	010?111011	2001110111	00?0000*00	1?00010010	1100000?00	1000100011	0000110?01	1111000111	120?01210?	0002010111	2101001000
Lepidotaramus	0001020000	000?001011	0000000010	0100000110	0000010000	10?0000?00	1001121010	1000101000	??10000110	110?000111	0010010010	2001001011
Leucohimatium	0000010000	100?101010	?00000000?	10?0000001?	0000010110	1100000?00	0010100001	1010110?00	??0?000010	1300001100	10000000?0?	2001001001
Loberogosmus	0010020000	100?101010	?010000011	10?1010110	1?0000?00	1100000?00	0010100001	1010110?01	010?000?0	1?00000?0	?0010000?0?	20000001001
Neoloberolus	*100030000	0010011011	20010000011	00?0100100	1?10000?00	?0?1100?00	0110100011	0000100?00	??10000011	120?012100	000001010?	2001001000
Loberolus	0000020000	0110100011	2000000010	0110100110	1?10010001	1111100?00	1010100011	0100100?01	1010000110	100?000001	000001010?	10000001001
Loberonotha	0010020000	000?001011	20000000011	1111002010	010100?00	00?1100?01	0000100011	1100110?00	??10000110	110?010001	000001000?	211?000000

Loberopsyllus	10*0020000 000?101011 0000000**0 0070000110 1?0000?00 11000*0?00 0002110000 000110*000 0001101011 100?001101 100?001101 10020000?0? 201?0*11??
Loberoschema	00*1020000 00100*1011 0000000*10 00700*0111 *100010001 10?0101000 0101100001 000010*0*1 101010001? 110?000101 110211010? 2001001011
Loberus	00*0030000 0*100*1011 *0000001* 01100001*0 *1*001*001 *0?*100?00 *0?0101000** *0*010*001 1100000111 100?000*01 000*1010? 20*10*1*01
Lobosternum	0001020000 0010001011 000000011 0100000110 0000010000 10?0100?00 0001120101 0000101010 0000101010 1??0000000? 000101000? 20010011??
Macrophagus	0010020000 000?101011 2000000010 0110000010 1?0100?00 1100000?00 0000100001 1111110?0 0001100?00 0001010000 0001000?11 201?001000
Microfanguria	0000030000 000?111011 2001000010 0070000110 1?1001*001 10?1000?00 0010100111 0010101101 1110000010 120?010101 0000010111 1001001000
Nomotus	1100031000 000?111111 0001110111 0100000200 1?10010001 10?0000?00 1000100001 0001110?01 1110000110 1??000000? 0001010111 21010*1000
Othniocryptus	0000010000 0010001011 200000010? 0110000110 1?0100?00 10?0000?00 0000100001 1111110?0 0001000?00 0001000?0? 001?001000
Paphezia	0000020000 0110011011 2000000010 0070300100 1?10010000 10?0100?00 0000101000 0000100?01 1110110111 100?01?101 000111010? 20010011??
Paracladoxena	1*00030000 010?111011 2001000010 01100*0*00 1?10010000 10?1000?00 0010100001 0000101001 0110*00?11 120?010101 0001010111 1*010*1100
Penolanguria	1100030000 000?111000 0001001011 0070000*00 1?01010000 10?0100?10 0000100001 0000100?01 111000?00? 220?010101 0000010111 10*1001001
Pharaxoatha	0010020000 100?101110 0000000*0 111*0*0*10 1?0*011100 110*000?0* 1010100001 1000110?01 110?000110 100?010100 0000000?0? 2000001001
Platoberus	0100022010 010?011011 200100010? 00?0011110 1?10011101 10?0100?00 0010120111 00*010*011 110?100111 04101?0010 000011010? 0001*11001
Protoloberus	0000020011 000?111000 0101000100 0000010000 10?01000?01 0010100010 1110110?00 0001000100 0001000100 0001000?0? 2000001001
Pseudhappalips	0000020000 0010001011 2000000010 0110011111 0110111001 1100100?00 1010100110 1010111101 1110000110 100?010010 000011010? 1000011000
Setariola	00*0020000 100?001011 200020000? 1100000110 0001011101 1100000?00 1010100000 1000100?00 000100?00 110?0000101 100101000? 201?011001
Stengita	00010*0000 00100*1011 0000000110 00?0010111 1?00010000 10?0*01100 0101120001 100010*001 1010100?10 1*0?0*0101 110201000? 2001011011
Stenodina	0000030000 0010000011 2000000010 0110300110 0100010001 1112100?01 1010100011 1100111001 101000011? 00?000001 000001010? 2001001001
Telmatoscus	0010020000 0110011111 2000000010 0110200100 1?00010000 10?0100?01 1010100001 00101010?1 111000?00? 00?0000101 000101010? 001?011001
Thalassella	0000030000 000?011011 2001*0010? 00700*0101 *10000?00 10?1000?00 0000100111 001010110* *10?000?011 1510010111 000111010? 1001011000
Toramus	00**000000 00001*1011 2000000001* 10?00*01** 1?000*0000 10?0*01100 00*11000*1 *00010*00* 0110100110 110?001100 *102*10*0? 201?*1*11
Truquella	0000030000 0010001111 000000000? 00?00000010 1?00011000 1100100?00 0010100111 0001011001 100?1?0111 1010000110? 000001010? 20000101000
Xenocryptus	0010030000 000?101011 111000000011 1110000110 1?0100?00 1101000?00 0000100001 1110110?00 0001010100 000000?10 20000011000
Xenocscelis	0000020000 0010100010 000001011 1110001200 1?0100?00 121201?00 0010100000 1110110?00 000100000? 0000000?10 2001011000
Zavaljus	0010010001 000?101000 011100001011 01110000100 000000?00 1100000?00 0010100010 11110110?00 0001010100 10000001?10 10000011001

in Appendix 2. Males of the type specimens of *Loberolus*, *Neoloberolus*, and *Stenodina* were not fully dissected but were cleared partially in KOH to allow examination of the genitalia *in situ*. Male genitalic characters that were scored for *Setariola*, are based on the detailed morphological study by Falcoz (1921). Females of *Loberogosmus*, *Lobosternum*, and *Nomotus* were not available for study, and are coded as unknown for characters 93–101. I chose representative species from each of the five subfamilies of Erotylidae and these are represented as tribes in the analysis. Species examined internally and externally are listed in Appendix 1 and include slide-mounted specimens prepared by Tapan Sen Gupta (and possibly Roy Crowson) and maintained in the BMNH. The condition of these slide mounts was reasonable though due to inappropriate storage of the slides on edge, articulated parts in many slides accumulated on one side beneath the cover slip obscuring some important characters from view.

### Characters and polymorphic taxa

Identifying cladistic characters, or homologies, is usually considered a two-step process by morphologists. The first step involves the identification of a set of character states for a similar structure based on positional criteria (Remane 1956) and coding them in a data matrix as primary homologies (de Pinna 1991). The second step is subjecting these characters to a cladistic analysis and the resultant trees (cladograms) are used to determine the status of the characters as synapomorphies, or secondary homologies (de Pinna 1991). Characters useful for cladistic analysis were identified from dissected material on microslides and from pinned specimens. Dissected specimens were examined by a compound microscope with Nomarski differential interference contrast. A detailed survey of adult characters resulted in an inventory of 120 characters that are variable among terminal taxa: coding and other issues of homology and morphology are outlined in Appendix 2.

Coding polymorphic taxa relates directly to the assumptions about the monophyly of terminal taxa (Nixon & Davies 1991). Coding the variation in a taxon as independent terminals is best (e.g., Leschen (1997) following the method of Nixon & Davies (1991)), but this may be difficult in large data sets, or in diverse taxa such as Coleoptera. In a recent review, Kornet & Turner (1999) suggested that identifying and scoring plesiomorphic character states for polymorphic terminals was preferable. Because the objective was to test the monophyly of higher taxa, and since I wanted to examine microscopically as many species as possible, I coded most genera and all the higher groups of Erotylidae as single terminal taxa with their polymorphic character states. This was not the case for *Loberolus* because the two described species of the

genus are reported from two widely disparate localities and external characters suggested that this taxon is paraphyletic. The type species, *L. agilis* Grouvelle from Madagascar, was coded as *Loberolus* and *L. cursor* from Bolivia are coded separately as *Neoloberolus* new genus. Other Neotropical species similar to *L. cursor* were also examined and were treated as members of *Neoloberolus*.

The assumption of monophyly for polymorphic taxa has some consequences and my decision could be viewed as a shortcut to circumvent a more complex problem. For example, *Loberus* is a highly variable genus and it has been suggested that *Fitoa*, *Paphezia*, and *Telmatoscius* may be contained in the range of variation for the genus (Leschen & Wegrzynowicz 1998). These three genera are treated separately from *Loberus* in the data matrix because there are characters present in these that are absent in *Loberus*. *Toramus* is a large polymorphic taxon (with 21 polymorphic characters) and is retained as a single terminal taxon, mainly because all taxa I have examined microscopically have a transverse line on the vertex of the head (Fig. 53). *Loberus* and *Toramus* are probably polyphyletic taxa, but an analysis of these taxa requires more detailed study of the described species. In total, 22 of the characters in Appendix 2 are coded as polymorphic for some terminal taxa.

The toramine genera *Loberoschema* and *Stengita*, ranging from southern Chile (and the Juan Fernandez Islands) northward to Central America, are also very variable. Though these appear to be a monophyletic group based on the presence of two carinae on the mesoventrite (Fig. 87), the separation of *Loberoschema* and *Stengita* is difficult when variation is considered for undescribed species. In this study *Loberoschema* and *Stengita* are maintained as separate taxa.

### Analytical methods

Parsimony criteria are used for most of the phylogenetic analyses in this study. The data were coded and entered into MacClade version 3 (Maddison & Maddison 1992) and analysed using PAUP\* version 4.0b3a (Swofford 2001). The settings used in PAUP\* for heuristic tree searches included a 100 random addition sequence with stepwise addition (holding 25 trees at each step) set with steepest descent; character states were treated as unordered; TBR branch swapping on all trees; and zero-length branches were collapsed. Polarity of character states was determined after the trees were produced (Nixon & Carpenter 1993) using the outgroups Biphylidae, Cryptophagidae, Lamingtoniidae, and Phloeostichidae. The outgroups are treated as separate terminal taxa (STT) or were combined into a hypothetical ancestor (HAL) for Lundberg rooting

with the variable characters coded as uncertain (?) in parsimony analyses. Twenty-one of the total 120 characters were coded as inapplicable (?) for some terminals in the HAL analyses. Successive approximation character weighting (SAW) with a base weight of 100 set in PAUP\* was applied to characters after the parsimonious trees were produced (Farris 1969, Carpenter 1988, 1994) and polymorphic taxa were treated either as uncertainty (UNC) or as polymorphic with the minimum-possible single-character length (MIN) or the ranges (RAN) option to decrease the number of internal steps while character weighting (Rognes 1999).

Morphologists are inclined to use cladistic parsimony because characters treated as homologies (de Pinna 1991) are assumed to reflect evolutionary novelty after they have been identified as synapomorphies. Moreover, morphological characters are often more subjective (requiring individual description and definition), and *a priori* weights are not easily applied to them or arguing for any evolutionary model for character change is difficult (as is the case for sequence data used routinely in likelihood, Bayesian, and other methods). Phenetic analyses (distance criteria) may be useful for identifying groups based solely on similarity (without regard for synapomorphy) because most, if not all, classifications were, and still are, based on similarity and not synapomorphy. Therefore, empirical determination of whether languriid taxonomic groups recognised previously are phenetic is rational. Numerical methods were just being developed at the time Crowson and Sen Gupta were studying languriids and I decided to analyse the STT data matrix using distance criteria with the following options used in PAUP\*: negative branch lengths allowed (but set to zero for tree-score calculation), distance measure = mean character difference, starting tree obtained by neighbour-joining, branch-swapping algorithm tree-bisection-reconnection (TBR) with steepest descent option in effect, zero-length branches collapsed.

Large morphological data sets with many terminal taxa are problematic because the ratio of characters to taxa may be low, resulting in little to no branch support for groups that are otherwise supported in parsimony trees by one or a few characters. Moreover, bootstrap, jackknife, and Bremer support analyses may be exceedingly time consuming. Bremer support values reflect the best support for phylogenetic relationships, especially for morphological characters, because these measure the amount of “decay” a clade has as tree length is increased. Based on preliminary analyses to determine Bremer support using Autodecay 4.0.2' ppc (Eriksson 2000), I estimate it would require over 2 days to complete a full analysis with 100 random addition replications using the settings as above. Smaller random addition replications (10) required over 4 hours per step to

complete so other options were investigated. Widely used alternatives to Bremer support are bootstrap (Felsenstein 1985, Sanderson 1995) and jackknife analyses (Farris *et al.* 1994), which determine branch support by resampling (or not resampling) a certain percentage of characters or taxa per replication. Fast methods that build trees without branch swapping (Mort *et al.* 2000) may be useful for large data sets and these algorithms were employed with the STT data set using 1000 replicates and including groups compatible with 50% majority rule consensus trees; in the bootstrap analyses 120 characters were resampled and jackknifing was set with 50% of the characters deleted at each replicate. Note that fast methods seem to have variable performance in contrast to their counterparts with branch swapping, and fast bootstrap analyses appear to be more predictable in comparison to jackknifing (Mort *et al.* 2000). To summarise, determining confidence intervals was difficult with this data set and I chose to use fast bootstrap and parsimony jackknifing to test branch support.

Characters were optimised onto cladograms using ACCTRAN and DELTRAN optimisations (Maddison *et al.* 1984) and, in the discussion below, characters that reverse or transform to other states are indicated by superscripts C<sup>-</sup> and C<sup>+</sup>, respectively.

## RESULTS OF CLADISTIC ANALYSIS

The results of all the analyses are presented with reference to the family-group taxa that I will recognise formally in the following section. The groups are listed in Table 3 and the relationships are shown in the cladograms provided in Fig. 101–109.

Results using polymorphic MIN and RAN options were the same for all analyses and are referred to by the acronym MIN in following discussions and in Table 3. The STT analysis resulted in 526 trees (MIN, tree length (TL) = 904, consistency index (CI) = 0.37, retention index (RI) = 0.51; UNC, TL = 707, CI = 0.20, RI = 0.51). A strict consensus of these trees is poorly resolved but with the clades or sister pairs indicated by an asterisk in Fig 101: The trees are rooted at *Myriabola* and Biphylidae; Erotylinae and a four-taxon branch of Languriinae are fully resolved. STT–SAW analysis, using each of the polymorphic settings, resulted in one tree each by two iterations. MIN and UNC trees were identical except the relationships Pharaonothinae and Xenoscelinae (Fig. 101, 102). *Loberonotha* is placed among the outgroup and all of the groups listed in Table 3 are monophyletic except for Loberinae, Cryptophilinae, and Cryptophilini which are paraphyletic with respect to the placements of *Loberus* (as sister taxon to Languriinae) and *Brachypterosa* (as sister

**Table 3.** Higher taxa and clades supported in cladistic analyses ("yes"). BOOT = Bootstrap; DIS = distance; HAL = hypothetical ancestor; JACK = Jackknife; NW = wingless taxa *Brachyptera* and *Paphezia* eliminated; STT = separate terminal taxa as outgroups; MIN = SAW tree with multistate taxa coded as polymorphic; UNC = SAW tree with multistate taxa coded as uncertainty.

Higher Taxa	STT	STT MIN	STT UNC	HAL	HAL MIN	HAL UNC	BOOT	JACK	NW	NW UNC	DIS†
<b>Xenoscelinae</b> <sup>1</sup>	no	no	no	no	no	yes	no†	yes	no	no	no
<b>Pharaxonothinae</b> <sup>2</sup>	no	yes	yes	no	yes	yes	yes	yes	yes	yes	yes
<b>Group 1</b>											
Loberinae, Languriinae	no	yes	yes	no	yes	yes	yes	yes	yes	yes	yes
<b>Loberinae</b> <sup>3</sup>	no	no	no	no	no	no	no*	no*	no	no	yes
<b>Languriinae</b>											
Hapalipini, Languriini, Thalisellini	no	yes	yes	no	yes	yes	yes	yes	yes	yes	no
<b>Hapalipini</b> <sup>4</sup>	no	yes	yes	yes	yes	yes	no	no	yes	yes	no
<b>Languriini</b>											
(=Cladoxenini, Languriini)	no	yes	yes	no	yes	yes	yes	yes	no	yes	yes
<b>Thalisellini</b> <sup>5</sup>	no	yes	yes	no	yes	yes	no	no	yes	yes	no
<b>Group 2</b>											
Erotylinae, Cryptophilinae	no	yes	yes	no	yes	yes	yes	yes	no	yes	yes
<b>Cryptophiliinae</b>											
Empocryptini, Cryptophilini, Toramini	no	no*	no*	no	yes	yes	no	no	yes	yes	yes
<b>Empocryptini</b> <sup>6</sup>	no	yes	yes	yes	yes	no	yes	yes	yes	yes	no
<b>Cryptophilini</b> <sup>7</sup>	no	no*	no*	no	no	no	no	no*	no	yes	yes
<b>Toramini</b> <sup>8</sup>	no	yes	yes	no	yes	yes	yes	yes	no	yes	no
<b>Erotylinae</b>											
Dacnini, Encaustini, Erotylini, Megalodacnini, Tritomini	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes

<sup>1</sup>Loberonotha, Macrophagus, Othniocryptus, Protoloberus, Xenocryptus, Xenoscelis, Zavajlus

<sup>2</sup>Henoticonus, Leucohimatium, Loberogomus, Pharaxonotha, Setariola

<sup>3</sup>Fitia, Loberus, Loberolus, Paphezia, Stenodina, Telmatoscus

<sup>4</sup>Bolerus, Hapalips, Truquiella

<sup>5</sup>Acryptophagus, Platoberus, Pseudhapalips, Thalisella

<sup>6</sup>Empocryptus, Lepidotarum, Lobosternum

<sup>7</sup>Brachyptera, Cathartocryptus, Crowsonguptus, Cryptophilus, Loberopsyllus

<sup>8</sup>Atomarops, Loberoschema, Stengita, Toramus

\*Placements of *Brachyptera* or *Paphezia* make these groups paraphyletic.

† Support for family groups *sensu lato* is not shown (see results section).



taxon to Erotylidae).

The second set of analyses (HAL) using Lundberg rooting resulted in 184 trees (MIN, TL = 889, CI (excluding uninformative characters) = 0.42, RI = 0.53; UNC, TL = 640, CI (excluding uninformative characters) = 0.21, RI = 0.53. These trees are better resolved (see consensus tree in Fig. 103) and resulted in the following monophyletic groups: Erotylinae, Languriinae + Loberinae, Hapalipini, and Empocryptini. HAL-SAW analysis, using each of the polymorphic settings, resulted in one tree each by two iterations. These trees differ in the arrangements of Xenoscelinae, Pharaonothinae, and Cryptophilini (Fig. 104, 105).

Bootstrapped and jackknifed STT trees are identical with the exception of the relationships among the genera as *Xenocryptus* (*Loberonotha* (*Macrophagus*, *Othniocryptus*)) in the latter analysis. The bootstrap tree is presented as 50% majority consensus trees in Fig 106. These trees differ from the original parsimony trees as is shown by the alternate placements for genera not seen in the previous analyses. There is no support for the tribes Hapalipini and Thallisellini, which are paraphyletic, though these are included in Languriinae. Loberinae is shown as a monophyletic taxon, though it is paraphyletic as a result of the placement of *Paphezia* in Cryptophilinae as sister taxon to *Brachypterosa*. If the numbers of replications are increased for fast analyses, results should tend to converge on the results for normal bootstrap and, in some cases, for jackknifing using branch swapping (Mort *et al.* 2000). As a check, I examined support for lineages among the fast searches with replicates of 3000. In this case, the trees are similar to the initial jackknife tree with the resolution of the four xenosceline taxa as indicated above.

While the trees resulting from the fast analyses support many groups seen in the parsimony trees, branch support is generally poor and the consensus trees account for a majority but not all of the parsimony trees. Interestingly, *Brachypterosa* and *Paphezia* are placed as sister taxa: these two genera are completely flightless. Flightless taxa often have homoplasious features that could bias routine cladistic analyses. An STT-UNC analysis deleting *Brachypterosa* and *Paphezia* resulted in 1174 trees (a consensus tree is shown in Fig. 107; TL = 684, CI (excluding uninformative characters) = 0.20, RI = 0.52), and one tree was produced by SAW with 2 iterations, similar to the tree shown in Fig. 102.

Finally, the STT-distance tree (score = 532.12) is interesting because some of the family-groups recognised by Sen Gupta & Crowson (1971) are seen in the phenogram (Fig. 108). There is support for Xenoscelini *sensu lato* (excluding *Loberopsyllus* and including *Setariola* and *Loberonotha*), Loberini *sensu lato* (exclusive of Hapalipini),

Toraminae *sensu lato*, and Cryptophilinae *sensu lato*.

The presence of family-groups in one or more trees is basis enough for recognising natural and monophyletic taxa, despite the poor branch support seen in the fast analyses. The lack of strong support for some groups may be symptomatic of the problems associated with the enigmatic relationships of Cucujoidea (i.e., specific outgroups may need to be identified) and the presence of primitive characters in the basal taxa of Languriidae. There are specific concerns regarding the morphological data set and terminal taxa. In future analyses, some of the characters should be deleted (or down-weighted) as they may or may not be well defined, or may be poor indicators of phylogenetic relationship (e.g., tarsal length characters). Moreover, certain character systems require detailed study (wing, aedeagal and terminalia characters) and could provide additional support for some of the groups recognised below. Coding terminal taxa as genera or family-group taxa resulted in a relatively high number of multistate terminals that may have created some of problems in recognising monophyletic taxa. Inclusion of more terminals for diverse taxa (*Loberus*, *Stengita* and its relatives, and *Toramus*) and fewer ones for clearly monophyletic groups (Languriini) might be best. Additional characters from immatures and DNA data sets will be useful for testing the relationships for the groups recognised here.

### Monophyly of higher taxa

The monophyly of Erotylidae and Languriidae has been discussed periodically in the literature but the formal separation of the families has been accepted for over a century. Though the relationships among most lineages of Cucujoidea is uncertain and the monophyly of the group is questionable, there are several adult characters that strongly suggest that the Erotylidae and Languriidae should be combined into a monophyletic taxon, Erotylidae, despite the placement of *Lamingtonium* and *Cryptophagus* inside the group in the SST trees. In the reference tree SAW-SST-MIN (Fig. 102) with the ancestor replaced by the outgroups with the relationship Biphylidae (*Myriabola* (*Lamingtonium*, *Cryptophagus*)) (Fig. 109), Erotylidae in this broad sense is monophyletic based on the following synapomorphies: subocular glandular ducts present (19-1<sup>r</sup>, Fig. 10), supraocular line present (29-1<sup>r</sup>, Fig. 52, 53), pronotal carina smooth (41-1<sup>r</sup>, Fig. 9), trochantinal notch present (55-0<sup>r</sup>, Fig. 13, 76), and mesocoxal cavities laterally closed by the metaventrite (65-1, Fig. 9). Though all but character 65 reverse in some lineages the first two characters are not present, or are rare, in the outgroups and in other Cucujoidea. The smooth pronotal carina (41), which is present in *Lamingtonium* and widespread in Cucujoidea, is probably not a reliable synapomorphy, nor is the presence of a trochantinal notch (55), which is also

variable in Cucujoidea. The mesocoxal closure by the metaventre is present in other Cucujoidea, including the cerylonid series. Within the lower Cucujoidea it is also present in Cryptophagidae, Passandridae, and Phalacridae. These characters, in addition to the aedeagal characters mentioned earlier, indicate that this group is monophyletic within Cucujoidea. Other characters concordant with the aforementioned characters are too variable to be considered synapomorphies for Erotylidae-Languriidae: two stridulatory files on the vertex of the head (32–1<sup>r</sup> and 33–1<sup>r</sup>, Fig. 53), procoxal rests divided (57–0<sup>r</sup>, Fig. 79), mesepisternal pocket present (63–1<sup>r</sup>, ACCTAN, Fig. 82), length of spiculum ventrale to level of ventrite 2 or 3 (97–1<sup>r</sup>), and spermathecal duct coiled (101–0<sup>r</sup>).

In the following discussions regarding the internal relationships of Erotylidae, I refer to the group names provided in Tables 1 and 3 and the reference tree STT–MIN–SAW in Fig 102 unless specified otherwise. A nexus file containing the data matrix and trees referred to in this paper are located at <http://www.LandcareResearch.co.nz/>.

### Xenoscelinae

The subfamily Xenoscelinae is clearly a polyphyletic group in all of the analyses and requires reclassification into monophyletic or, in one case, phenetic groups. Interestingly, the groups more or less corresponding to Xenoscelini *sensu lato* (including *Setariola*) and Loberini *sensu lato* are supported in the distance tree as phenetic assemblages, confirming that the old classification for Xenoscelinae tribes was based entirely on morphological similarity; however, to maintain the present classification for these groups as evolutionary units may be unjustified. Significant phylogenetic relationships that must be reflected in the new classification are

- (1) the placement of the monotypic subfamily Setariolinae within members of Xenoscelinae,
- (2) four genera newly placed in Languriinae (*Hapalips*, *Neoloberolus*, *Truquiella*, and *Boleros*), and
- (3) *Loberopsyllus* confirmed as a member of Cryptophilinae.

Xenoscelinae *sensu lato* is divided into three subfamilial groups: Xenoscelinae (*Loberonotha*, *Macrophagus*, *Othniocryptus*, *Protoloberus*, *Xenocryptus*, *Xenoscelis*, *Zavaljus*), Pharaxonothinae (*Henoticomus*, *Leucohimatium*, *Loberogosmus*, *Pharaxonotha*, *Setariola*), and Loberinae (*Fitoa*, *Loberus*, *Loberolus*, *Paphezia*, *Stenodina*, *Telmatoscius*).

Xenoscelinae *sensu stricto* appears as a monophyletic group in the trees derived from STT–UNC, HAL–UNC, and distance analyses. Clearly Xenoscelinae is a mixture of primitive species that have a combination of symplesiomorphic characters (e.g., vertexal line present

(Fig. 33), tarsomeres 2 or 3 not strongly lobed below, elytra with confused punctuation in some species (Fig. 1), hind wing lacking an wedge cell, etc.) shared with some members of the outgroup (*Cryptophagus* and *Lamingtonium*) and other basal languriids. This group is one that may be recognised based more on similarity rather than on synapomorphy.

Xenoscelinae is supported by three unambiguous characters: the presence of a metepisternal ctenidium (73–1, Fig. 89, which is not present in *Loberonotha* and is usually poorly developed in taxa outside this group), accessory gland of spermatheca absent (100–0<sup>r</sup>, reverses in *Othniocryptus* and unknown in *Xenoscelis*) and tarsal shelf of tarsomere 5 present (109–1<sup>r</sup>, Fig. 100, reverses in *Othniocryptus* and *Protoloberus*). The strongest evidence for this grouping is character 73, and in these xenosceline taxa, the ctenidium is well developed with tightly packed setae often arising from distinct punctures. In other taxa (except *Hapalips*, Fig. 89) the ctenidium is composed of diffuse setae and do not arise from well developed punctures. The following characters are concordant with the presence of a ctenidium: elytra explanate (116–1<sup>r</sup>, ACCTAN, Fig. 91) and scutellary striole present (114–1<sup>r</sup>, ACCTAN; coded as inapplicable for some taxa). These characters are very variable and taken together may not be strong evidence for the monophyly for Xenoscelinae.

### Pharaxonothinae

The monophyly of Pharaxonothinae is supported in most analyses by the following synapomorphies: lateral pockets present on the mentum (11–1, Fig. 41), presence of multitubulate cuticular ducts on the pronotum (48–1<sup>r</sup>, Fig. 11), abdominal calli absent (83–0). Presence of character 11 is unique and unreversed and is strong evidence for the monophyly of this group. However, this character is poorly developed in some *Pharaxonotha* examined and should be examined in closer detail in other members of the genus. Multitubulate glandular ducts on the pronotum are rare in erotylids and this character is present in also *Fitoa*, *Hapalips*, and *Platoloberus*. Concordant with these characters are the presence of glandular ducts below the lateral carina of the pronotum (47–1<sup>r</sup>, ACCTAN; coded as inapplicable for some taxa) and mesepisternal fovea present (63–1<sup>r</sup>, DELTRAN).

### Group 1: Loberinae and Languriinae

The monophyly of Languriinae + Loberinae together is supported in most cladograms. In all of the trees except the distance tree and those derived from fast analyses, *Loberus* does not place with the remaining members of Loberinae, making this subfamily group paraphyletic (discussed be-



low). I discuss character support for Loberinae and various lineages on the assumption that Loberinae is monophyletic by fixing *Loberus* to the base of Loberinae in the reference tree shown in Fig. 109. Loberinae and Languriinae are monophyletic based on the following synapomorphies: teeth of pronotal carina widely spaced (42–1, coded as inapplicable for most terminals), transverse depression at base of pronotum present (43–1<sup>r</sup>, Fig. 6), prosternal cuticular glandular ducts present (50–1<sup>r</sup>), trochantal notch present (55–1<sup>r</sup>, Fig. 76), and tarsomere 4 hidden (108–1, inapplicable in basal taxa). Concordant with these characters are the width of apical labial palpomere greater or equal to its length (13–1<sup>r</sup>, ACCTTRAN, Fig. 42), mesepisternal fovea present (63–1<sup>r</sup>, DELTRAN), abdominal glandular ducts present (80–1<sup>r</sup>, DELTRAN, Fig. 15), male spiculum gastrale of sternite IX asymmetrical (90–1<sup>r</sup>, ACCTTRAN) and tarsal shelf bifid (110–1<sup>r</sup>, ACCTTRAN; note that most taxa are coded as inapplicable for this character, Fig. 97).

### Loberinae

*Loberus* is very similar in body form to other members of Loberinae (*Fitoa*, *Paphezia*, *Telmatosciscus*, and *Stenodina*) as mentioned by Leschen & Wegrzynowicz (1998) and this is clearly indicated by their grouping in the distance tree (Fig. 108) a position supported only in the fast analyses (though *Paphezia* is placed elsewhere). In the context of the distance tree, three characters support this group: width of apical labial palpomere greater or equal to its length (13–1, a feature shared with Hapalipini, Fig. 42), stridulatory files present on the vertex of the head (32–1<sup>r</sup>, reverses in *Paphezia*), and pronotum constricted at base (35–3<sup>t</sup>, coded as 35–0 in *Loberus* and transforms in other taxa). Other characters concordant with these are: medial carina of mentum absent (12–1<sup>r</sup>, ACCTTRAN; coded as 12–0 in *Loberus*, Fig. 44), supraocular line present to level above eye (30–0, DELTRAN, present beyond level of eye in some *Loberus*), prosternal cuticular glandular ducts present (50–1<sup>r</sup>, ACCTTRAN, reverses in *Paphezia* and *Telmatosciscus*), external closure of procoxal cavity by the prosternum and hypomeron (53–1, ACCTTRAN; inapplicable for most taxa including *Loberus* and present only in *Loberolus* and *Stenodina*, Fig. 9), mesoventral glandular ducts present (61–1<sup>r</sup>, ACCTTRAN; polymorphic in *Loberus* and also present in *Bolerus*), mesepisternal pocket present (63–1<sup>r</sup>, DELTRAN, reverses in *Paphezia*, Fig. 82), and absence of the wedge cell in the hind wing (120–1, DELTRAN, inapplicable in *Paphezia*). By fixing *Loberus* to the remaining loberines as in the reference tree (Fig. 109), which adds one step to the tree shown in Fig. 102, Loberinae is defined by six ambiguous characters as in the distance tree: 12–1, 13–1 (DELTRAN), 53–1, 61–1, 98–0<sup>r</sup>

(ACCTTRAN, spermatheca round, reverses in *Paphezia* and *Telmatosciscus*), 120–1.

Characters that support the placement of *Loberus* outside Loberinae and as sister taxon to Languriinae are the presence of three lacinial spines (6–3<sup>t</sup>, Fig. 62), position of glandular ducts below the pronotal carina (47–1<sup>r</sup>, ACCTTRAN), metepisternal ctenidium present (73–1<sup>r</sup>, ACCTTRAN, Fig. 89), and spiculum gastrale asymmetrical (90–1<sup>r</sup>, DELTRAN; coded as inapplicable for many taxa): two of these characters (47 and 73) are coded as polymorphic in *Loberus* and character 6 is unambiguous.

The placement of *Loberus* outside of Loberinae might be related to the high number of polymorphic characters coded for it in the data matrix. To examine the effect that the high number of polymorphic characters has on the placement of *Loberus*, I fixed polymorphisms to their plesiomorphic states (as recommended by Kornet & Turner 1999) based on the character states present in Xenoscelinae (3–0, 16–0, 21–2, 30–0, 39–1, 41–1, 43–1, 47–0, 51–1, 54–0, 61–0, 69–0, 70–1, 71–0, 73–0, 78–0, 98–1, 104–0, 105–0, 113–0, 116–0, 118–0). Reanalysis using the STT data set resulted in no new trees and the placement of *Loberus* remained contentious.

### Languriinae

This group is supported in most of the analyses, and included in it are the groups *Bolerus*, *Hapalips*, and *Truquiella* (Hapalipini), and *Acryptophagus* and *Pseudhapalips* (Thallisellini) which were previously placed in Xenoscelinae. Note that Hapalipini and Thallisellini are not supported in the distance and fast analyses (Fig. 106, 108). Languriinae is supported by three unambiguous characters (*Loberus* is treated as the sister taxon to Languriinae): presence of submesocoxal lines (68–1<sup>r</sup>, Fig. 14), apical pit of spermatheca present (99–1<sup>r</sup>, Fig. 32), and wedge cell present (120–0<sup>r</sup>, Fig. 34). Concordant with these characters are the antennal insertion exposed in dorsal view (24–1<sup>r</sup>, ACCTTRAN, Fig. 6), absence of stridulatory files on vertex of the head (32–0<sup>r</sup>, ACCTTRAN), metepisternal ctenidium present (73–1<sup>r</sup>, DELTRAN; coded as variable in *Loberus* and present in Thallisellini and basal Languriini, Fig. 89) and presence of a single empodial seta (111–1<sup>r</sup>, ACCTTRAN). If *Loberus* is fixed to the base of the Loberinae, Languriinae is supported unambiguously by characters 68–1<sup>r</sup>, 73–1<sup>r</sup> and 99–1<sup>r</sup> and by 6 ambiguous characters including some as in the reference tree: presence of 3 lacinial spines (6–3<sup>t</sup>, DELTRAN, Fig. 62), 24–1, 32–0, glandular ducts present below the pronotal carina (47–1<sup>r</sup>, ACCTTRAN; coded as inapplicable in many taxa), 111–1, and wedge cell present (120–0<sup>r</sup>, DELTRAN).

### Hapalipini

This triad of genera (*Bolerus*, *Hapalips*, and *Truqiella*) forms a monophyletic group that is supported by the following unambiguous characters: transverse gular line shallow or weakly developed as a line or groove (21–0<sup>r</sup>, Fig. 47), supraocular line absent (29–0<sup>r</sup>, Fig. 5), external closure of procoxal cavity slightly open (52–1, widespread in Erotylidae, Fig. 72), absence of glandular ducts near the margin of the ventrites (82–0<sup>r</sup>), and scutellary striole present (114–0<sup>r</sup>). Concordant with these characters is the position of the cuticular glandular ducts below the carina of pronotum (47–1, coded as inapplicable in *Hapalips*). An additional ambiguous character supports this group if *Loberus* is fixed to Loberinae: terminal labial palpomere wider than or equal to its length (13–1, DELTRAN, Fig. 42).

### Languriini and Thallisellini

These sister taxa are well supported in all of the analyses by the following unambiguous characters: submetacoxal lines parallel (78–1<sup>r</sup>, coded as inapplicable for many Languriini), and gonostyle at a subapical position on the gonocoxite (96–1<sup>r</sup>, inapplicable in *Platoberus*, Fig. 30). Concordant with these characters are the following synapomorphies: length of apical labial palpomere greater than its width (13–0<sup>r</sup>, ACCTAN, Fig. 42), genal spines absent or poorly developed (16–1<sup>r</sup>, ACCTAN; reverses in *Acryptophagus* and *Pseudhapalips*), antennal insertion visible in dorsal view (24–1<sup>r</sup>, DELTRAN), and presence of one empodial seta (111–1<sup>r</sup>, DELTRAN).

### Languriini

Languriini is supported in most of the analyses by two unambiguous characters: width of ligular membrane greater than that of prementum (15–1<sup>r</sup>, reverses only in *Neoloberolus*) and gonocoxite acute (92–2, coded as inapplicable for *Nomotus*, Fig. 95). The following characters are concordant with these: genal spines absent or poorly developed (16–1<sup>r</sup>, DELTRAN; reverses in larger species of *Crotchia*) and tarsal shelf bifid (110–1, coded as inapplicable for many groups though present in some of the Languriini and *Macrophagus* outside this group, Fig. 97). It is likely that character 15 is associated with the size of the beetle (most Languriini are larger than 3 mm) and both unambiguous characters may be correlated with phytophagy.

While some members of Languriini are well defined by the presence of a frontoclypeal suture (character 1), and a flattened antennal club (character 26, Fig. 61) consisting of 4 or more segments, in this study the group corresponds to the combined tribes Languriini and Cladoxenini, with the second tribe forming a grade of taxa and Languriini forming

a monophyletic group (inclusive of *Neoloberolus*). This confirms the hypothesis proposed by Crowson (1955) and Sen Gupta & Crowson (1971) that the tribes are paraphyletic.

### Thallisellini

The tribe Thallisellini is a well defined group and is broadened here from the original concept proposed by Sen Gupta (1968b) to include *Acryptophagus* and *Pseudhapalips*. This group is supported by the following unambiguous characters: anterior angles of pronotum well developed (36–1, variable in *Thallisella*, Fig. 9), tarsomere 2 lobed (105–1), and elytra strongly explanate (116–1). The following characters are concordant with these: pronotal carina relatively thick (37–1<sup>r</sup>, ACCTAN; reverses in *Thallisella*), pronotal callosities present (40–1, ACCTAN; absent in *Platoberus*, Fig. 11), position of cuticular glandular ducts below pronotal carina (47–1<sup>r</sup>, DELTRAN; coded as inapplicable for many languriines and *Thallisella*), spermatheca round (98–0<sup>r</sup>, ACCTAN). The ovipositor of this group is variable and departs from the typical ovipositor seen in Fig. 31 (with the exception of *Pseudhapalips*). Some ovipositors in this group are similar to those present in basal Xenoscelinae (see Fig. 29–30).

### Group 2: Cryptophilinae and Erotylinae

The sister relationship of Cryptophilinae + Erotylinae is relatively strongly supported based on two unambiguous synapomorphies: mesometaventral articulation dicondylic (64–1<sup>r</sup>, transforms to 64–2 in Encaustini, *Cathartocryptus* and *Loberopsyllus*, Fig. 14) and metaventral pores absent (69–0<sup>r</sup>, reverses in many taxa). Two ambiguous synapomorphies support this group: mesepisternal fovea absent (63–0<sup>r</sup>, ACCTAN; reverses in some species of *Toramus* and is weakly developed in *Cathartocryptus* and many Toramini) and marginal ducts of the abdominal ventrites absent (82–0<sup>r</sup>, ACCTAN, coded as inapplicable for many taxa). Cryptophilinae and Erotylinae have been considered by some authors as closely related on the basis of the genus *Cryptophilus* which has been placed in Erotylidae, Languriidae, and in some cases its own family (Leschen & Wegrzynowicz 1998). The wingless taxon *Brachypterosa* is grouped with Erotylinae, based on four unambiguous characters (39–0, 44–1, 52–2, 82–0). In Fig. 109 I have joined *Brachypterosa* with Cryptophilini as shown in the distance tree (Fig. 108), which adds one step to the reference tree (Fig. 102). The following discussions on character distribution are based on this phylogenetic arrangement.

The dicondylic meso-metaventral articulation is the strongest synapomorphy for the erotyline–cryptophiline group, though this character occurs in other cucujoids.

## Cryptophilinae

Cryptophilinae is supported as a monophyletic group based on two unambiguous characters: transverse gular line shallow or present as a weakly-developed line or groove (21–0<sup>r</sup>, transforms to character state 2 in *Brachypterosa* and *Toramus*, Fig. 48, 49) and the radial cell reduced or absent (119–1, coded as inapplicable for wingless taxa). Five characters are concordant with these: subapical serrations of mandible present (4–1<sup>r</sup>, ACCTTRAN, reverses in some *Toramus* and most Cryptophilini), presence of two stridulatory files on the vertex of the head (33–0<sup>r</sup>, inapplicable for most taxa, Fig. 53), *Toramus* type of procoxal rest bead (58–1<sup>r</sup>, ACCTTRAN; coded as inapplicable for most taxa and is present only in *Atomarops*, *Toramus*, and *Stengita*, Fig. 82), tarsomere 4 exposed in ventral view (108–0<sup>r</sup>, ACCTTRAN; reverses in *Loberoschema*, *Crowsonguptus* and some *Toramus*, Fig. 100), and absence of the wedge cell in the hind wing (120–1, DELTRAN, inapplicable in wingless taxa and *Loberopsyllus*). This lineage is a well defined monophyletic group, based firmly on the reduction or absence of the radial cell, though the remaining characters may be poor indicators of monophyly. Moreover, the placement of *Cathartocryptus* within Cryptophilinae may be questionable because of its aberrant body form and ovipositor (see below and Sasaji 1989): perhaps a more detailed study of its placement should be undertaken since it has been considered, maybe erroneously, as a relative of Propalticidae (see Crowson & Sen Gupta 1969).

## Empocryptini

This group, formerly referred to as the *Empocryptus* group by Leschen (1997), is supported in all of the parsimony analyses by two unambiguous synapomorphies: pronotal carina serrate (41–0) and width of mesoventral process equal to mesocoxa (66–2<sup>t</sup>, transforms to character state 1 in *Empocryptus*, Fig. 14). Six ambiguous synapomorphies also support this group: subapical serrations present on mandible (4–1, DELTRAN), width of apical labial palpomere greater than its length (13–1<sup>r</sup>, ACCTTRAN; reverses in *Lepidotoramus*, Fig. 42), stridulatory files present on the vertex of the head (32–1, ACCTTRAN) in the form of one broad file (33–0, DELTRAN, coded as inapplicable for many cryptophiline taxa, Fig. 53), submesocoxal lines present (68–1<sup>r</sup>, DELTRAN; reverses in some species of *Empocryptus*, Fig. 14), and abdominal pores present (79–1<sup>r</sup>, ACCTTRAN; reverses in *Lepidotoramus*, Fig. 15).

## Cryptophilini

The placement of the cryptophiline *Brachypterosa* at the base of Cryptophilinae in some of the trees is probably

due to characters that are linked with brachyptery. The placement of *Brachypterosa* in Cryptophilini, and the monophyly of this group, is consistent with the previous classification of the group (Leschen & Wegrzynowicz 1998). Cryptophilini is a monophyletic group based on two unambiguous synapomorphies: procoxal cavity completely closed externally (52–2<sup>t</sup>, transforms to character state 1 in *Loberopsyllus*, Fig. 9) and median stalk of metendosternite poorly developed (86–1). Concordant with this character is the confused punctuation of the elytron (113–1, DELTRAN, Fig. 8).

## Toramini

This group, formerly recognised as a subfamily, is supported by the following unambiguous characters, one of which is unique and unreversed (\*): procoxal rests contiguous (57–1, Fig. 82), dilated gonocoxite (92–1<sup>t</sup>, transforms to character state 0 in some *Stengita*, Fig. 93), and absence of spiracles from terga 6 and 7 (102–1\*, present on tergite 6 in some species of *Toramus*). Three characters are concordant with these: serrations of mandible present (4–1<sup>r</sup>, DELTRAN, reverses in some *Toramus*), absence of stridulatory files on vertex of the head (32–0, DELTRAN), and abdominal glandular ducts present (80–1<sup>r</sup>, DELTRAN, reverses in some *Toramus*, Fig. 15).

## Erotylinae

This group is well supported in all of the analyses and the group is determined to be monophyletic by the following unambiguous synapomorphies (many of which are unreversed): anterior angles of pronotum well developed (36–1, Fig. 9, 12), anterior edge of prosternal margin smooth (39–0, Fig. 9), basal pronotal pits absent (44–1), internal closure of procoxal cavity open (51–0, Fig. 76), external closure of procoxal cavity completely closed (52–2, also present in Cryptophilini, Fig. 9), external closure of procoxal cavity by a flange of the prosternum and the hypomeron (53–1, coded as inapplicable in many taxa outside erotylids, Fig. 9), width of mesoventral process greater than mesocoxa (66–1<sup>t</sup>, transforms to 66–2 in Erotylini and Megalodacnini, Fig. 9), abdominal ventrites 1 and 2 connate (74–1), spermatheca round (98–0<sup>r</sup>, reverses in Encaustini and Erotylini), and tarsal shelf of tarsomere 5 present (109–1, Fig. 98). Concordant with these characters are the securiform labial palp (14–1, ACCTTRAN, coded as inapplicable for Dacnini and Megalodacnini and polymorphic for Tritomini, Fig. 9), supraocular line present to level beyond eye (30–1<sup>r</sup>, ACCTTRAN and is coded as polymorphic in Erotylini and Tritomini, Fig. 53), and wedge cell present (120–0, uncertain ancestral reconstruction, Fig. 34).

## FORMAL CHANGES IN CUCUJOID CLASSIFICATION

Results from the cladistic analysis fully demonstrate that changes in the classification of Erotylidae and Languriidae are warranted. First, and foremost, is the confirmation of the paraphyly of Languriidae with respect to the placement of Erotylidae. Because of nomenclatural priority, Languriidae Crotch, 1873 is synonymised with Erotylidae Latreille, 1802. The former subfamilies of Erotylidae are ranked as tribes (Dacnini, Encaustini, Erotylini, Megalodacnini, and Tritomini) and are included in the subfamily Erotylinae.

Changes in the names and status of the higher taxa of Languriidae are extensive and the preferred arrangement of the genera is provided in Fig. 109. The subfamily Xenoscelinae is clearly polyphyletic and it is divided into four higher taxa. The basal group is classified here as the subfamily Xenoscelinae and consists of *Loberonotha*, *Macrophagus*, *Othniocryptus*, *Protoloberus*, *Xenocryptus*, *Xenoscelis*, and *Zavaljus*, which corresponds to the previously recognised tribe Xenoscelini Ganglbauer, 1899 and includes the monogeneric taxon Loberonothini. Taxa excluded from the subfamily Xenoscelinae are *Henoticonus*, *Leucohimatiops* (synonym of the silvanid genus *Ahasverus*), *Leucohimatium*, *Loberogosmus*, *Loberolus* (two species, one transferred to Languriini the other one transferred to Loberinae), *Loberopsyllus* (transferred to Cryptophilinae), *Pharaxonotha*, and *Rhopalocryptus* (transferred to Salpingidae). *Setariola*, together with *Henoticonus*, *Leucohimatium*, *Loberogosmus*, and *Pharaxonotha* are classified as the subfamily Pharaxonothinae Crowson, 1952, an available name that was previously included as a synonym of Xenoscelini. The monotypic subfamily Setariolinae Crowson, 1952 that includes the single species *Setariola sericea* (Mulsant and Rey), is redundant.

The group consisting of *Fitoa*, *Loberus*, *Loberolus*, *Paphezia*, *Stenodina*, and *Telmatoscius* corresponds to the tribe Loberini Bruce, 1951 and is here raised to subfamily rank. Loberinae excludes *Acryptophagus*, *Bolerus*, *Hapalips*, *Pseudhapalips*, and *Truquiella*, which are placed into a more broadly defined Languriinae. *Bolerus*, *Hapalips*, and *Truquiella* are placed into the new tribe Hapalipini and the sister taxa *Acryptophagus* and *Pseudhapalips* are placed together with *Platoberus* and *Thallisella* in Thallisellini Sen Gupta, 1968b. The tribe Cladoxenini is a paraphyletic group that forms a morphological grade into Languriini and the members of both of these groups are combined into the single tribe Languriini.

Cryptophilinae, Toraminae, and the *Empocryptus* group are classified together in the subfamily Cryptophilinae.

The subfamily rank of Cryptophilinae and Toraminae is lowered to tribe (Cryptophilini and Toramini), and the name Xenoscelini Sen Gupta & Crowson, 1971 for the single genus *Cathartocryptus* is redundant. The *Empocryptus* group is formally recognised as Empocryptini.

The formal changes proposed here are in no way final because detailed analysis of poorly resolved or unsupported groups (i.e., Cryptophilini, Loberinae, Xenoscelinae, and basal Languriinae) and descriptions of new taxa could easily provide new interpretations of erotylid classification. New character sets as well as detailed study of some of the characters provided here will also provide significantly new and different conclusions. Moreover, the problem of choosing appropriate outgroups for Erotylidae remains and will certainly require a detailed study of the Cucujoidea as a whole.

## TAXONOMY OF WORLD FAUNA

### EROTYLIDAE Latreille, 1802: 233

**Diagnosis.** Glandular ducts usually present in the head (below the eye and behind the maxillary articulation), prothorax (along the lateral carina and on the prosternum in front of the coxae), and the ventrites (mesoventrite, metaventrite, and abdomen). Head with frontoclypeal suture present or absent; antennal insertions concealed or visible in dorsal view; mandible without a deep cavity or mycangium; genal spines present or absent; gula usually with a transverse line that is weakly or strongly-developed; vertexal line present or absent; tentorium typically without median spine. Prothorax with well developed lateral carina that is smooth, serrate, or rarely undulate, prosternum usually short in front of procoxae, procoxal cavities internally closed or open (Erotylinae), externally open, slightly closed, or completely closed; closure by hypomeron or flange of prosternal process, procoxal rests usually present. Mesometaventral junction flat, monocondylic or dicondylic. Mesocoxal cavity closed laterally by the meeting of the meso- and metaventrite. Metepisternal ctenidium present or absent. Metafurcal laminae present or absent. Ventrites 1 and 2 connate or free; ventrite 1 equal to length of ventrite 2. Aedeagus usually on side at rest; usually with articulated parameres, median lobe usually laterally compressed, penile struts narrow and either biflagellate or fused (uniflagellate). Spiculum gastrale (sternite IX) broad, symmetrical or asymmetrical. Gonocoxite usually narrowed, but may be dilated, acute, or modified; gonostyle usually present and apical or subapical. Spermatheca rounded or elongate, with



or without accessory gland. Spiracles present or absent (Toramini) on terga 7 and sometimes 6. Tarsomeres lobed below or not, or tarsomeres 2 and 3 only, or 3 only lobed; tarsomere 4 usually reduced and may be hidden in ventral view by lobe on tarsomere 3, tarsal shelf present or absent, empodium usually with 2 setae. Elytron striate or with confused punctation, scutellary striole usually absent, epipleuron usually distinct to apex (except *Loberonotha*), hind wing with radial cell and wedge cell present, reduced, or absent.

**Remarks.** Each higher taxon is provided with a diagnosis of their key phylogenetic characters with their character number in Appendix 2.

## ANNOTATED KEYS TO THE WORLD GENERA OF EROTYLIDAE

Many erotylids may be misidentified as other members of Cucujoidea, especially Cryptophagidae. Characters that distinguish Erotylidae from Cryptophagidae are as follows: well developed stridulatory files on the head (weakly-developed in some atomariine cryptophagids); length of abdominal ventrite 1 equal to 2 (ventrite 1 much longer than 2 in Cryptophagidae), well developed elytral epipleura that extend to the apex (poorly developed in *Loberonotha* and Cryptophagidae), hind wing with a closed wedge cell, 555 tarsomeres in both sexes (many Cryptophagidae in the subfamily Cryptophaginae have 554 male tarsal formula).

All of the genera examined in this study are included in the following keys with the exception of Languriini and Erotylinae. Two keys are provided. The first is a phylogenetic key that will aid systematists in identifying taxa that may not fit well into the higher categories described in this study. Dissection of the specimens will be necessary for the first key. The second key, which does not necessarily require dissection of specimens, is developed for non-specialists and does not include variation present in undescribed forms covered in the phylogenetic study (e.g., *Loberus* species that do not have punctate striae on the elytra).

### Phylogenetic Key (dissection required)

1 Pockets present on the mentum (reduced or absent in some species of *Pharaxonotha*, Fig. 41); cuticular glandular ducts of prothorax multitubate (when present, Fig. 11); abdominal calli absent .....  
..... (Pharaxonothinae, p. 35)... 10

—Pockets absent on the mentum; cuticular glandular ducts of prothorax typically unitubulate when present (Fig. 12), abdominal calli usually present (Fig. 15) ..... 2

2(1) Metaventral articulation dicondylic (Fig. 14) or flat; procoxal cavities completely closed behind by flange of prosternal process (Erotylinae, Fig. 9), open (Empocryptini and Toramini Fig. 73) or slightly open (*Loberopsyllus*, Fig. 13) ..... 7

—Metaventral articulation monocondylic (Fig. 82), procoxal cavities open (Fig. 69), slightly open (Fig. 72), or rarely completely closed behind (*Xenoscelis*, Fig. 9) ..... 3

3(2) Pronotal pits typically absent (present in *Protooberus* and *Zavaljus*, Fig. 89); metepisternal ctenidium usually present and well developed (Fig. 89); tarsomere 3 not lobed (except *Loberonotha*); submesocoxal lines absent; abdominal glandular ducts absent .....  
..... (Xenoscelinae, p. 33)... 14

—Pronotal pits present (absent in *Penolanguria*, Fig. 6); metepisternal ctenidium, if present, poorly developed; tarsomere 3 lobed; submesocoxal lines present or absent (Fig. 14); abdominal glandular ducts present or absent (Fig. 15) ..... 4

4(3) Submesocoxal lines absent (Fig. 9); gonostyle apical (except for *Paphezia*, Fig. 31); wedge cell of hind wing absent; antennal insertions more or less hidden in dorsal view (Fig. 3, 4) ..... (Loberinae)... 20

—Submesocoxal lines present (absent in groups with acute gonocoxite); gonostyle, if present, subapical (Fig. 29) or apical (Fig. 31); wedge cell of hind wing present (absent in *Platoberus* and possibly winged *Penolanguria*, Fig. 34); antennal insertions visible in dorsal view in most taxa (except *Hapalips*, *Pseudhapalips*, *Truquiella*, and some *Crotchia*, Fig. 5, 6) ..... (Languriinae)... 5

5(4) Gular line usually very deep (Fig. 39); gonocoxite stylate or flattened and typically not of the normal cylindrical type with subapical gonostyle (absent in some taxa, Fig. 29, 95) ..... 6

—Gular line usually very shallow; gonocoxite of the normal cylindrical type with apical gonostyle (if present, Fig. 94) ..... (Hapalipini, p. 38)... 25

6(5) Tarsomere 2 strongly lobed below; anterior angles of prothorax usually well developed (Fig. 9) .....  
..... (Thallisellini, p. 39)... 27

—Tarsomere 2 not strongly lobed, anterior angles of prothorax usually poorly developed (Fig. 6) .....  
..... **Languriini** (p. 38) (not keyed further)

- 7(2) Procoxal cavities internally open; hind closure complete and by prosternum (Fig. 9); ventrites 1 and 2 connate ..... **Erotylinae** (not keyed further)
- Procoxal cavities internally closed; hind closure open or if complete, closure mainly by hypomeron (Fig. 72); ventrites 1 and 2 rarely connate (*Loberopsyllus*) .....  
..... (Cryptophilinae)... 8
- 8(7) Procoxal cavities externally slightly open or closed completely (Fig. 72) . ... (Cryptophilini, p. 41)... 30
- Procoxal cavities externally open (Fig. 73) ..... 9
- 9(8) Procoxal rests divided (Fig. 14); stridulatory files present (Fig. 53) ..... (Empocryptini, p. 41)... 34
- Procoxal rests contiguous or of the *Toramus* type (Fig. 82); stridulatory files absent ... (Toramini, p. 42)... 36
- 10(1) Antennal club 2-segmented ..... **Setariola**
- Antennal club 3-segmented ..... 11
- 11(10) Pronotal callosity present (Fig. 11); vestiture of modified setae (Fig. 11) ..... **Leucohimatium**
- Pronotal callosity absent; vestiture of simple setae 12
- 12(11) Dorsal punctation strong and impressed; dorsum subglabrous; procoxal cavities open .... **Henoticonus**
- Dorsal punctation usually weak and not strongly impressed; dorsum subglabrous to glabrous; procoxal cavities slightly open ..... 13
- 13(12) Metepisternal ctenidium absent; U-shaped fovea absent from gular region; supraocular line (if present) extending to level beyond eye (Fig. 53) .....  
..... **Pharaxonotha**
- Metepisternal ctenidium present (Fig. 89); U-shaped fovea present in gular region; supraocular line present only to level of eye ..... **Loberogosmus**
- 14(3) Mentum with well developed lateral pits (Fig. 36) ..... 15
- Mentum without well developed lateral pits ..... 16
- 15(14) Tarsomere 4 not reduced; northern Europe .....  
..... **Zavaljus**
- Tarsomere 4 reduced; Australia .....  
..... (p. 34) ... **Protoloberus** new genus
- 16(14) Elytron with a single well developed lateral carina ..... **Xenoscelis**
- Elytron without a well developed lateral carina .... 17
- 17(14) Elytra well developed with punctate striae (Fig. 6) ..... **Xenocryptus**
- Elytra without punctate striae (Fig. 8) ..... 18
- 18(17) Vertexal line present (Fig. 53); prothoracic carina poorly developed; shape of gonocoxite dilated (Fig. 93); New Zealand ..... **Loberonotha**
- Vertexal line absent; prothoracic carina well developed; lateral outline of gonocoxite sinuate (Fig. 28); not New Zealand ..... 19
- 19(18) Unicolorous light brown; tarsal shelf present and bifid (Fig. 97); Eurasia ..... **Macrophagus**
- Elytra bicoloured and mottled; tarsal shelf absent; Neotropical ..... **Othniocryptus**
- 20(4) Stridulatory files absent; mesepisternal pocket absent; metaventral discrimen absent; procoxal lines absent; New Caledonia ..... **Paphezia**
- Stridulatory files present (Fig. 53); mesepisternal pocket present (Fig. 82); metaventral discrimen present (Fig. 14); procoxal lines present (Fig. 14) ..... 21
- 21(20) Procoxal cavity slightly open behind (Fig. 13); tentorium with a median spine; Madagascar ..... 22
- Procoxal cavity completely open behind (Fig. 69); tentorium without a median spine; widely distributed ..... 23
- 22(21) Pronotum constricted at base with basal area of disc flat or convex; medial carina of mentum present (Fig. 42) ..... **Stenodina**
- Pronotum widest in apical half with basal area of disc depressed; medial carina of mentum absent (Fig. 44) ..... **Loberolus**
- 23(21) Pronotum widest at base; mesoventral fovea present; empodial setae apparently absent .....  
..... **Telmatoscius**
- Pronotum constricted at base or parallel-sided; mesoventral fovea absent; empodial setae present (Fig. 98) ..... 24
- 24(23) Pronotum at base distinctly constricted; median carina of mentum absent (Fig. 44); trochantinal notch absent; abdominal glandular ducts absent; Madagascar ..... **Fitoa**
- Pronotum at base not constricted or slightly so and parallel-sided; median carina of mentum present (Fig. 42); trochantinal notch present in most species (Fig. 13); abdominal glandular ducts present (Fig. 15); widespread ..... **Loberus**
- 25(5) Antennal insertion exposed (Fig. 6); 2 submetacoxal lines present on each side; stridulatory files present (Fig. 53) ..... **Bolerus**
- Antennal insertion hidden (Fig. 5); 1 submetacoxal line present on each side (Fig. 14); stridulatory files absent ..... 26
- 26(25) Mesepisternal pit and transverse prosternal impression absent; male without a well developed anterior projection on pronotum; widespread .....  
..... **Hapalips**

- Mesepisternal pit (Fig. 82) and transverse prosternal impression present; male with a well developed anterior projection on pronotum; Neotropical .... *Truquiella*
- 27(6) Scutellary striole absent; supraocular line absent; pronotum lacking broad pronotal groove at base . 28
- Scutellary striole present, supraocular line present (Fig. 53); pronotal groove at base present ..... 29
- 28(27) Mandible falcate (Fig. 58, 59); pronotal callosities absent; body convex ..... *Thallisella*
- Mandible not falcate (Fig. 56); pronotal callosities present; body dorsoventrally compressed *Platoberus*
- 29(27) Male with laminate process on frons; antennal insertion hidden in dorsal view; stridulatory files of head present; intercoxal process on metaventrite narrow (Fig. 85); humeral spine absent ..... *Pseudhpalips*
- Male with head unmodified; antennal insertion exposed in dorsal view; stridulatory files of head absent; intercoxal process on metaventrite broad (Fig. 86); humeral spine present ..... *Acryptophagus*
- 30(8) Stridulatory files of head absent; mesometaventral articulation flat; tarsomere 2 not lobed ..... 31
- Stridulatory files of head present (Fig. 53); mesometaventral articulation dicondylic (Fig. 14); tarsomere 2 lobed ..... 32
- 31(30) Body dorsoventrally flattened; frontoclypeal suture absent; hind wings present; free living ..... *Cathartocryptus*
- Body convex; frontoclypeal suture present (Fig. 6); hind wings reduced or absent; mainly associated with rodents ..... *Loberopsyllus*
- 32(30) Anterior margin of prosternum serrate; pronotal carina more or less serrate; tarsomere 2 not lobed ..... *Cryptophilus*
- Anterior margin of prosternum smooth; pronotal carina smooth; tarsomere 2 lobed ..... 33
- 33(32) Pronotum widest in apical half; Neotropical ..... *Crowsonguptus*
- Pronotum widest at middle; Fiji ..... *Brachypterosa*
- 34(9) Femoral crenulations absent; hind wings absent; Chile ..... *Lobosternum*
- Femoral crenulations present (Fig. 92); hind wings present; Neotropical ..... 35
- 35(34) Anterior pronotal angles well developed (Fig. 9); width of mesoventral process equal to or greater than coxa (Fig. 14); abdominal pores in male present (Fig. 14); gonocoxite relatively narrow; tarsal shelf absent ..... *Empocryptus*
- Anterior pronotal angles poorly developed; width of mesoventral process equal to coxa; abdominal pores in male absent; gonocoxite dilated (Fig. 93); tarsal shelf present (Fig. 98) ..... *Lepidotoramus*
- 36(9) Elytra with punctate striae (Fig. 6); labial palpomere wider than long; mesoventral lines present (Fig. 15) . ..... 37
- Elytra without punctate striae (Fig. 8); labial palpomere longer than wide; mesoventral lines absent ..... 38
- 37(36) Tarsomere 2 lobed; tarsomere 4 hidden in ventral view ..... *Loberoschema*
- Tarsomere 2 not lobed, tarsomere 4 visible in ventral view ..... *Stengita*
- 38(36) Vertexal line present (Fig. 53); gular line deep; basal pronotal pits present; submesocoxal lines absent ..... *Toramus*
- Vertexal line absent; gular line shallow; basal pronotal pits absent, submesocoxal lines present (Fig. 14) ..... *Atomarops*

### Identification Key

- 1 Procoxal cavities completely or nearly completely closed externally by well developed flanges of the prosternum (Fig. 9) ..... 2
- Procoxal cavities open externally, or, if closed, not by flanges of the prosternum (Fig. 13) ..... 6
- 2(1) Abdominal ventrites 1 and 2 connate ..... *Erotylinae* (not keyed further)
- Abdominal ventrites 1 and 2 free ..... 3
- 3(2) Antennal insertion visible in dorsal view (Fig. 6) ..... *Bolerus*
- Antennal insertion not visible in dorsal view (Fig. 5) 4
- 4(3) Pronotum completely parallel-sided; procoxal cavities completely closed behind ..... *Xenoscelis*
- Pronotum widest at apical third; procoxal cavities partially open behind ..... 5
- 5(4) Pronotal margin lacking undulations or spines; scutellary striole present ..... *Loberolus*
- Pronotal margin with undulations or spines; scutellary striole absent ..... *Stenodina*
- 6(1) Mandible falcate (Fig. 58, 59); gonocoxite acute (Fig. 95); frontoclypeal suture usually present (Fig. 6); antennal insertions well exposed and often dorsally on the frons (Fig. 6) ..... *Languriini* (not keyed further)
- Mandible not falcate (Fig. 56); gonocoxite never acute; clypeal suture usually absent; antennal insertions usually hidden in dorsal view (Fig. 5) ..... 7

- 7(6) Elytra without punctate striae (Fig. 6) ..... 8  
 —Elytra with punctate striae (Fig. 8) ..... 19
- 8(7) Prosternum relatively elongate in front of coxa (Fig. 72) ..... *Cathartocryptus*  
 —Prosternum relatively short in front of coxa (Fig. 73) 9
- 9(8) Frontoclypeal suture present (Fig. 6); most species associated with rodents; hind wings reduced or absent ..... *Loberopsyllus*  
 —Frontoclypeal suture absent; species free-living; hind wings usually present ..... 10
- 10(9) Elytral epipleuron complete to level of metaventrite ..... *Loberonotha*  
 —Elytral epipleuron complete to apex of elytron (Fig. 9) ..... 11
- 11(10) Vertexal line of head present (Fig. 53) ..... 12  
 —Vertexal line of head absent ..... 13
- 12(11) Antennal club 2-segmented; supraocular line absent ..... *Setariola*  
 —Antennal club 3-segmented; supraocular line present ..... *Toramus*
- 13(11) Prothorax parallel-sided and widest at middle (Fig. 8) ..... 15  
 —Prothorax not parallel-sided, widest anteriorly or posteriorly (Fig. 7) ..... 14
- 14(13) Prothorax widest at base with sides converging anteriorly ..... *Telmatoscius*  
 —Prothorax widest at apical third (Fig. 7) ..... *Crowsonguptus*
- 15(13) Ctenidium well developed (Fig. 89); metaventral notch well developed (Fig. 85) ..... 16  
 —Ctenidium absent; metaventral notch absent (Fig. 86) ..... 17
- 16(15) Body unicolorous; subocular bead present ..... *Macrophagus*  
 —Body bicolorous, often with reticulate elytral pattern of dark setae contrasting with light background; subocular bead absent ..... *Othniocryptus*
- 17(15) Body glabrous and black; supraocular line present and well developed (Fig. 53); gular line deep (Fig. 39) ..... *Brachypterosa*  
 —Body moderately shining and punctate, colour variable; supraocular line absent or present; gular line shallow ..... 18
- 18(17) Stridulatory file present on vertex of head (Fig. 53); submesocoxal lines absent; body usually parallel-sided (Fig. 8) ..... *Cryptophilus*  
 —Stridulatory file absent from vertex of head; submesocoxal lines present (Fig. 14); body broadly oval *Atomarops*
- 19(7) Antennal insertions clearly exposed in dorsal view (Fig. 6); anterior angles of prothorax usually well developed (Fig. 9) ..... 20  
 —Antennal insertions not exposed in dorsal view (Fig. 5); anterior angles of prothorax poorly developed (Fig. 5) ..... 22
- 20(19) Supraocular line present (Fig. 53); basal groove of pronotum broad ..... *Acryptophagus*  
 —Supraocular line absent; basal groove of pronotum narrow or absent ..... 21
- 21(20) Pronotal callosity present; mentum wider than long (Fig. 47); body more or less convex; subocular bead present ..... *Thallisella*  
 —Pronotal callosity absent; mentum narrow, longer than wide (Fig. 50); body dorsoventrally compressed; subocular bead absent ..... *Platoberus*
- 22(19) Gula with distinct setose fovea (Fig. 36) ..... 23  
 —Gula usually without distinct setose fovea (present in *Hapalips* (*Cavophorus*)) ..... 24
- 23(22) Supraocular line present (Fig. 53); procoxal cavity externally open behind (Fig. 69); tarsomere 4 reduced in size ..... (p. 34) ... *Protoloberus* new genus  
 —Supraocular line absent; procoxal cavity slightly open; tarsomere 4 not reduced in size ..... *Zavaljus*
- 24(22) Vertexal line of head present (Fig. 53) ..... 25  
 —Vertexal line of head absent ..... 29
- 25(24) Pronotal callosity present (Fig. 11); supraocular line absent; cuticle heavily punctured with modified scalelike setae (Fig. 40) ..... *Leucohimatium*  
 —Pronotal callosity absent; supraocular line present (Fig. 8); cuticle not heavily punctured and lacking modified scale-like setae ..... 26
- 26(25) Ctenidium present (Fig. 89); mesoventral fovea absent ..... 27  
 —Ctenidium absent; mesoventral fovea absent or present ..... 28
- 27(26) Antenna short and reaching to level of middle of the pronotum; anterior angles of pronotum not produced; Australia and South Africa ..... *Xenocryptus*  
 —Antenna long and reaching beyond level of middle of the pronotum; anterior angles of pronotum produced; Mediterranean ..... *Loberogosmus*
- 28(26) U-shaped fovea present on gula; supraocular line present and extending posteriorly beyond eye (Fig. 8); body highly punctate and subglabrous *Henoticonus*



- U-shaped fovea absent from gula; supraocular line when present not extending posteriorly beyond eye; body usually lightly punctate and glabrous *Pharaxonotha*
- 29(24) Pronotal bead thick, about as wide as antennal funicle; male with transverse lamina on head; pronotal base with broad groove ..... *Pseudhaplips*
- Pronotal bead narrow; male without transverse lamina on head; pronotal base lacking broad groove ..... 30
- 30(29) Pronotal callosities usually present; mesoventrite bicarinate (Fig. 87); spiracles on terga 6 and 7 absent ..... 31
- Pronotal callosities absent; mesoventrite not strongly bicarinate; spiracles on terga 6 and 7 present ..... 32
- 31(30) Tarsomere 2 not lobed; tarsomere 4 not visible in ventral view; elytra narrowly explanate (Fig. 90) ..... *Stengita*
- Tarsomere 2 lobed; tarsomere 4 exposed in ventral view; elytra widely explanate (Fig. 91) ..... *Loberoschema*
- 32(30) Tibial crenulations present (Fig. 92) ..... 33
- Tibial crenulations absent ..... 34
- 33(32) Elytra widely explanate (Fig. 91); anterior pronotal angles well developed ..... *Empocryptus*
- Elytra narrowly explanate (Fig. 90); anterior pronotal angles poorly developed ..... *Lepidotoramus*
- 34(32) Submesocoxal lines present (Fig. 14); gular line usually shallow ..... 35
- Submesocoxal lines absent; gular line usually deep (Fig. 39) ..... 37
- 35(34) Ctenidium absent; length of tarsomere 1 greater than 2; intercoxal process of ventrite 1 broad (Fig. 86); hind wings absent; small species (2 mm); southern Chile ..... *Lobosternum*
- Ctenidium present; length of tarsomere 1 not greater than 2; intercoxal process of ventrite 1 narrow (Fig. 85); hind wings present; large species (greater than 3.5 mm); widely distributed ..... 36
- 36(35) Male with median pronotal horn; gonostyle absent ..... *Truquiella*
- Male without median pronotal horn; gonostyle present ..... *Haplips*
- 37(34) Prothorax widest at middle and more or less parallel-sided (Fig. 3, 4) with weak notch at base sometimes present ..... *Loberus*
- Prothorax widest anteriorly and not parallel-sided. 38
- 38(37) Subocular bead present; tarsomere 2 not lobed below; Madagascar ..... *Fitoa*
- Subocular bead absent; tarsomere 2 lobed below; New Caledonia ..... *Paphezia*

## XENOSCELINAE Ganglbauer

Xenoscelini Ganglbauer, 1899: 649. Type genus: *Xenoscelis* Wollaston, 1864

Eicolycetini Vogt, 1967: 103. Type genus: *Eicolycetus* Sahlberg, 1919

Loberonothini Sen Gupta and Crowson, 1969: 127. Type genus: *Loberonotha* Sen Gupta & Crowson, 1969

**Diagnosis.** Subapical serrations of mandible absent (4); lacinia usually with 2 lacinial spines, 1 or 3 may be present (6); lateral pockets absent on mentum (11); medial carina of mentum present (12); width of apical labial palpomere variable (13) and not securiform (14); width of ligular membrane usually greater than prementum (15); transverse gular line absent or present as a shallow or weakly-developed line or deep groove (21); antennal insertion hidden in dorsal view (24); supraocular line usually present (29) and to a level beyond eye (30); transverse line present or absent on vertex of head (31); two stridulatory files present on vertex of head (32, one broad file is present in *Protoloberus*, 33); pronotum parallel-sided (35); anterior angles of pronotum poorly developed (36); anterior margin of prosternum serrate or not (39); pronotal pits usually absent (44, present in *Protoloberus* and *Zavaljus*); pronotal glandular ducts typically absent (46, though present in bead (47) and unitubulate (48) in *Protoloberus*); prosternal glands absent (50); internal closure of procoxal cavity closed (51, open in *Loberonotha*); external closure of procoxal cavity open, slightly open, or closed (52) usually by hypomeron (53, except for *Xenoscelis*, closure by prosternal process and hypomeron); edge of hypomeron notched, smooth, or spinose (54); mesoventral glandular ducts absent (61); mesepisternal fovea present or absent (63); mesometaventral articulation monocondylic (64); width of mesoventral process narrower than mesocoxa (66); submesocoxal lines absent (68); metaventral pores usually present (69); metepisternal ctenidium present (73, absent in *Loberonotha*); abdominal ventrites 1 and 2 free (74); abdominal glandular ducts absent (80, 82); abdominal calli present (83); metafurcal lamina present (85) with median stalk of metendosternite well developed (86); form of spermatheca rounded or elongate (98); apical pit of spermatheca absent (99); accessory gland of spermatheca present or absent (100); length of tarsomere 1 greater than or equal to tarsomere 2 (104); tarsomere 4 usually reduced (107, except *Zavaljus*) and exposed in ventral view (108); tarsal shelf of tarsomere 5 present or absent (109); empodium usually with two setae (111, absent or one present in *Othniocryptus* and *Zavaljus*, respectively); elytral punctation striate or confused (113); scutellary striole present or absent (114); elytra narrowly or strongly explanate (116); radial cell present (119); wedge cell of hind wing present or absent (120).

**Remarks.** This group may be paraphyletic with respect to other basal groups of erotylids and is composed mainly of monotypic genera, including *Protoloberus*, which is described below. There may be three additional species of Australian *Xenocryptus* and the generic placement of the African species *X. africanus* Wegrzynowicz (2000) requires confirmation. A group of *Xenocryptus*-like species from South Africa occurring on cycads are under study by P. Wegrzynowicz and A. Slipinski. These differ from *Xenocryptus* in many respects, including having elongate antennae, dilated tarsomeres, and strongly excavated tibial apices. There is considerable colour variation among specimens of the species *Othniocryptus variegatus* Sharp from Central and South America, and it is possible that there is more than one species in the genus.

**Taxonomic notes.** Two genera discussed here were included in Xenoscelini and are now transferred to other families. *Leucohimatiops* Heller, 1923 was described for a single species *L. javanus* Heller collected from a shipment of tea leaves. Based on the examination of the type specimens, *L. javanus* is synonymised with *Ahasverus advena* Walzl (Silvanidae, see description and illustration of this species in Thomas (1993)).

Based on the examination of the holotype of *Rhopalocryptus pulcher* Arrow, 1929 (BMNH), this species is transferred to Salpingidae (Prostominiinae) and is very similar to *Trogocryptoides* Champion because of the presence of the following characters: transverse line of gula absent, tenebrionoid aedeagus (based on partial dissection), 4-4-4 tarsomere formula, and heteromeroid metatrochanter.

**Biology.** Most xenosceline species are found on live vegetation and some of the taxa are associated with cycads and may be involved with pollination. *Xenocryptus* is associated with Australian *Macrozamia* (Crowson 1991b). Donaldson (1997) reported 2 species of Xenoscelinae as pollinators of *Encephalartos* in South Africa (one has been referred to as a large *Hapalips*-like species by Crowson 1991; R. Oberprieler, pers. comm.) which are members of the *Xenocryptus*-like taxa examined from South Africa mentioned in Remarks above. *Loberonotha* has been collected from a variety of angiosperms in New Zealand, and *Macrophagus* has been collected from bee nests (*Anthophora* and *Halictus*) and in thatched grass (Horion 1960).

Other xenosceline species are associated with rotting wood (some specimens of *Protoloberus*) or perhaps under bark (*Xenoscelis*). The European boreal species *Zavaljus brunneus* (Gyllenhal) has been commonly collected in rotting wood in Finland and not in association with wasps as has been suggested by Lundberg (1966). There is some indication that this species may be subsocial (J. Muona,

pers. comm.). The presence of setose cavities in the ventral portion of the head, which is homologous with the structure seen in *Protoloberus* (Fig. 35–38), suggests complex behaviour. Some pyrochroids with similar-looking cuticular cavities on the head use them for storing secretions used in mating (Eisner *et al.* 1996).

**Included genera.** *Loberonotha* (1 species; New Zealand), *Macrophagus* (1 species; Asia and Europe), *Othniocryptus* (1 species; Neotropical), *Protoloberus* (1 species; Australia), *Xenocryptus* (2 species; Africa and Australia), *Xenoscelis* (1 species; Mediterranean), *Zavaljus* (1 species; Northern Europe).

**Type material examined.** *Leucohimatiops javanus* Heller (SNFT): 3 [mounted on two cards], Java [yellow label]; 1922 [yellow label]; *Leucohimatiops javanus* H. Types/Staatl. Museum für Tierkunde Dresden/*Leucohimatiops javanus* Heller [hand].

### *Protoloberus* new genus

Fig. 2, 17, 35–38, 69–71, 80

Type species: *Telmatophilus singularis* Blackburn, 1895.

**Diagnosis.** Mandible with two apical teeth and on the same plane; mentum slightly transverse with setose fovea and two small lateral pits; genal spines poorly developed; subocular cuticular glandular ducts absent; gular line absent; gular fovea present; subocular groove present; supraocular line absent; vertexal line absent; vertexal files present and single; temples of head present and in the form of postocular carinae; pronotal carina present and mainly smooth and slightly undulate, with a well developed rim; pronotal width greater than its length, and narrower than the combined width of the elytra; pronotal pits present; pronotal cuticular glandular ducts present; procoxal cavity internally closed and externally open; edge of hypomeron notched; trochantinal notch absent; mesoventral fovea present; mesepisternal fovea present; metepisternal tentidium present; precoxal lines absent; gonocoxite narrow; gonostyle subapical; spermatheca elongate and lacking accessory gland; length of tarsomere 1 greater than tarsomere 2; tarsomere 3 not lobed; tarsal shelf absent; elytral punctation striate; elytral length 2–2.5× that of width; elytra narrowly explanate.

**Remarks.** This genus is described for a single species, *Protoloberus singularis* (Blackburn), new combination, that was originally placed in the genus *Telmatophilus* by Blackburn (1895), who noted that it differed from the other Australian species of the genus by ocular, pronotal, and elytral characters. In addition to the diagnostic characters

provided above, *Protoloberus* has a lineate group of sensory pegs located at the apex of apical labial palpomere, and the following male characters: presence of 2–3 lance-like setae at the dorsolateral margins of the tergum 9; aedeagus with biflagellate strut that is 5.25x the length of the median lobe, internal sac not spinose and is about 1/2 the length of the aedeagal struts; parameres about 4x as long as wide, with three major apical setae and numerous shorter setae. The gut of dissected specimens was empty.

**Type material examined.** *Telmatophilus singularis* Blackburn: Holotype, [mounted on a card] with 5999 and N.Qu. [hand, red ink] and T [black ink]/ TYPE [round and red bordered label] / Blackburn coll. 1910-236/ *Telmatophilus singularis*, Blackb. [hand] (BMNH). Paratypes (SAMC). 1, 5999, N.Qu. [hand, black ink, card mounted]/ *Telmatophilus singularis* cotype [handwritten]/ 15886 *Telmatophilus singularis* Bk Queensland [black ink] Co-type [red ink]/S.A. Museum specimen [red label]; 2 (mounted together) 5999, N.Qu. [hand, red ink, card mounted]/N. Queensland Blackb's Coll/ *Telmatophilus singularis* cotype [handwritten]/ *Telmatophilus singularis* Bk Queensland [black ink] Co-type [red ink]/ S.A. Museum specimen [red label].

**Other material examined:** see Appendix 3.

**Distribution.** Australia: Queensland, New South Wales.

## PHARAXONOTHINAE Crowson

Pharaxonothinae Crowson, 1952: 127. Type genus: *Pharaxonotha* Reitter, 1875a

Setariolinae Crowson, 1952: 127. Type genus: *Setariola* Jakobson, 1915

Setariini Casey, 1900: 77. Type genus: *Setaria* Mulsant and Rey, 1863

**Diagnosis.** Subapical serrations of mandible absent (4); lacinia usually with 1 (*Leucohimatium*) to 2 lacinial spines (6); lateral pockets present on mentum (11); medial carina of mentum present (12); width of apical labial palpomere variable (13) and not securiform (14); width of ligular membrane greater than or equal to prementum (15); transverse gular line absent or present (*Setariola*) as a deep groove (20, 21); antennal insertion hidden in dorsal view (24); supraocular line present or absent (29) and length variable (30); transverse line present on vertex of head (31); stridulatory files present or absent on vertex of the head (32), with one or two present (33); pronotum parallel-sided (35); anterior angles of pronotum poorly developed (36, well developed in *Loberogosmus*); anterior margin of prosternum serrate (39); pronotal pits usually present (44, absent in some *Pharaxonotha* and *Setariola*); glandular ducts usually present (46, absent in *Leucohimatium*) be-

low lateral carina of pronotum (47) and multitubulate (48); prosternal glandular ducts absent (present in *Setariola*) (50); internal closure of procoxal cavity closed (51); procoxal cavity slightly open behind (52) and partial closure by the hypomeron (53); edge of hypomeron usually smooth (54); mesoventral glandular ducts present or absent (61); mesepisternal fovea present (63); mesometaventral articulation monocondylic (64); width of mesoventral process narrower than mesocoxa (66); submesocoxal lines absent (68); metaventral pores present or absent (69); metepisternal ctenidium usually absent (73, present in *Leucohimatium* and *Loberogosmus*); abdominal ventrites 1 and 2 free (74); abdominal glandular ducts absent or present (80), at margin (81) or disk (82); abdominal calli absent (83); metafurcal lamina present (85) with median stalk of metendosternite well developed (86); form of spermatheca elongate (98); apical pit of spermatheca absent (99); accessory gland of spermatheca present or absent (100); length of tarsomere 1 greater than or equal to tarsomere 2 (104); tarsomere 4 usually reduced and exposed in ventral view (108); tarsal shelf of tarsomere 5 absent (109); empodium with two setae (111); elytral punctation usually striate (113, confused in *Setariola*) with scutellary striole absent (114, present in *Leucohimatium*); elytra narrowly explanate (116, widely explanate in *Setariola*); radial cell present (119) and wedge cell of hind wing absent (120, present in *Henoticomus*).

**Remarks.** The genus *Pharaxonotha*, with 11 species described, requires revision as there are many undescribed species from Africa, Asia, Neotropics, and Southeast Asia. Most species are fairly similar in body form and type of setation, however, closer study, especially of the mouthparts, gular region of the head, and glandular ducts may determine that the genus is not monophyletic. Crowson (1991b) mentioned that there were differences in the glandular duct morphology between Neotropical and Asian forms. This variation should be studied in more detail to better understand the monophyly of Pharaxonothinae as well as the genus *Pharaxonotha*. I have examined an undescribed genus from Papua New Guinea (MHNG) that is similar to *Pharaxonotha* but with relatively elongate labial palpomeres and a dorsoventrally compressed body.

In unpublished notes on beetles from Lebanese amber (120–135 mya), Roy Crowson described and illustrated in pencil a “*Pharaxonotha*-like” specimen that he called “The Beautiful Clavicorn” supposedly deposited in the BMNH (see also Crowson 1981, p. 668). This species is unlike any pharaxonothine, or other erotylid, I have examined, and can be distinguished from all erotylids by having a deep transverse sulcus on the frons.

**Biology.** Many pharaxonothines are associated with plants. *Setariola sericea* Mulsant & Rey is associated with *Cistus* (Cistaceae) (Falcoz 1929) and several species of Asian, Neotropical, and North American *Pharaxonotha* were collected from *Cycas* (Old World) and *Zamia* (New World) cycads (Tang 1987; Norstog *et al.* 1986; Pakaluk 1988; Norstog *et al.* 1992; Tang *et al.* 1999). Many of these *Pharaxonotha* are undescribed, and the Asian forms have been erroneously attributed to *Xenocryptus* (Tang *et al.* 1999) indicating the need for further taxonomic study. *Leucohimatium arundinaceum* (Forskål) has been collected from rotting vegetation (Falcoz 1929) and breeding in numbers in smut fungi (*Ustilago* sp.) infesting beach *Spinifex* along the western part of the southern Australian coastline (Lawrence 1991); it, as well as *Pharaxonotha kirschi*, are often associated with stored products and have worldwide distributions (exclusive of New Zealand) (Hinton 1945; Booth *et al.* 1990; Delobel & Tran 1993).

**Included genera.** *Henoticonus* (1 species; Japan), *Leucohimatium* (8 species; widespread), *Loberogosmus* (1 species; southern Europe), *Pharaxonotha* (11 species; Africa, Asia, Neotropics, and Southeast Asia), *Setariola* (1 species; southern Europe).

## LOBERINAE Bruce

Loberinae Bruce, 1951: 4, Type genus: *Loberus* LeConte, 1861

**Diagnosis.** Subapical serrations of mandible absent (4); lacinia usually with 2 or 3 lacinial spines (6); lateral pockets absent on the mentum (11); medial carina of mentum usually absent (12, present in some *Loberus* and in *Stenodina*); width of apical labial palpomere greater or equal to its length (13) and not securiform (14); width of ligular membrane equal to prementum (15, greater in *Loberolus*); transverse gular line present usually as a deep groove (20, 21, variable in *Loberus*); antennal insertion hidden in dorsal view (24); supraocular line present (29) usually to level above eye (30, variable in *Loberus*); transverse line absent on vertex of head (31); two stridulatory files present on vertex of the head (32, 33, absent in *Paphezia*); pronotum constricted or not at base (35); anterior angles of pronotum poorly developed (36); anterior margin of prosternum serrate or not (39); pronotal pits present (44); glandular ducts usually present (46) in lateral carina of pronotum (47, variable in *Loberus* and *Fitoa*) and unitubulate (48, multitubulate in *Fitoa*); prosternal glandular ducts present or absent (50); procoxal cavity internally closed (51, open in some *Loberus*); procoxal cavity completely or partially open externally (52), closure by prosternum and hypomeron (53, in *Loberolus* and *Stenodina*); edge of hypomeron usually smooth (54, variable in *Loberus*,

notched in *Loberolus* and spinate in *Stenodina*); mesoventral glandular ducts present (61, absent in *Paphezia* and some *Loberus*); mesometaventral articulation monocondylic (64); mesepisternal pockets absent (present in *Paphezia*) (63); width of mesoventral process narrower than mesocoxa (66); submesocoxal lines absent (68); metaventral pores present or absent (69); metepisternal ctenidium absent (73, present in some *Loberus* and *Telmatoscius*); abdominal ventrites 1 and 2 free (74); abdominal glandular ducts present (80, absent in *Fitoa*) at disk (81) and margin (82, in *Loberolus* and *Stenodina*); abdominal calli present (83); metafurcal lamina present (85, absent in *Paphezia*) with median stalk of metendosternite well developed (86, poorly developed in *Paphezia*); form of spermatheca rounded or elongate (98); apical pit of spermatheca absent (99); accessory gland of spermatheca present (100); length of tarsomere 1 equal to tarsomere 2 (104, variable in *Loberus*, and greater than tarsomere 2 in *Paphezia* and *Telmatoscius*); tarsomere 4 usually reduced and hidden in ventral view (108); tarsal shelf of tarsomere 5 absent (109); empodium (111) with 1 (*Fitoa* and *Loberolus*), 2 (most taxa), or no setae (*Telmatoscius*); elytral punctation usually striate (113, confused in some *Loberus* and *Telmatoscius*) with scutellary striole absent (114, present in *Loberolus*); elytra narrowly or widely explanate (116); radial cell present (119), and wedge cell of hind wing absent (120).

**Remarks.** This group requires additional study, especially focusing on the diverse and variable genus *Loberus*. Some of the presently recognised genera (*Fitoa* and *Stenodina*) are clearly similar to members of *Loberus*, but in this study these were retained as distinct taxa because they have at least one character that separated them from the other members of the subfamily and the type species of *Loberus*. I have examined at least six well defined species groups within *Loberus* that includes *Loberus*-like forms from tropical (Indonesia, New Caledonia, South America) and temperate (Chile) regions.

Since the description of *Paphezia* by Zablotny & Leschen (1996), I have examined several additional species from New Caledonia (NZAC) that appear to form a morphological grade linking *Paphezia* with *Loberus*, though *Paphezia* remains morphologically distinct, with elongate antennae and a constricted prothoracic base. (Note that *Paphezia* was erroneously listed from Asia by Leschen & Wegrzynowicz (1998) but is endemic to New Caledonia.) There are other *Loberus*-like taxa from New Caledonia, including forms that are strongly dorsoventrally compressed and others with confused punctures of the elytra. Males in at least one species have extravagant processes on the head, gula, and frons that vary according to body size. A single specimen of a *Loberus*-like species collected from



New Caledonia resembles the anthicid genus *Ischalia*.

A similar radiation of morphological forms is also present on Madagascar with four genera represented there from this subfamily. I have examined an indeterminate number of undescribed species of *Loberus* from throughout the world and there are at least five species of *Fitoo* from Madagascar.

I have examined one undescribed genus of Loberinae from lowland Amazon rainforest (Bolivia).

**Biology.** Members of this group are associated with leaf litter, rotting and live vegetation, and may also have specific associations with host plants. Some *Loberus* feed on fungi, plant pollen, and other material, and may be saprophagous. The larva and biology of *Loberus impressus* LeConte was described by Carlton *et al.* (2000) based on populations living on *Iris hexagona* in Louisiana, U.S.A.

**Taxonomic notes.** Based on examination of type specimens (SAMC) of the Australian species in the genus *Telmatophilus* described by Blackburn (1895, 1903), the following species are here transferred to the genus *Loberus* resulting in the following new combinations: *L. brevipennis* (Blackburn, 1895), *L. koebeli* (Blackburn, 1895), *L. sharpi* (Blackburn, 1895), *L. stygius* (Blackburn, 1895), and *L. sublaetus* (Blackburn, 1903). I did not indicate lectotype specimens in the type series, and this should be done when a full revision of the Australian species is undertaken.

**Included genera.** *Fitoo* (1 species; Madagascar), *Loberus* (75 species; widespread), *Loberolus* (1 species; Madagascar), *Paphezia* (1 species; New Caledonia), *Stenodina* (1 species; Madagascar), *Telmatoscius* (1 species; Central America).

## LANGURIINAE Crotch

Languriinae Crotch, 1873: 349. Type genus: *Languria* Latreille, 1802

**Diagnosis.** Subapical serrations of mandible absent (4); lacinia usually with 3 lacinial spines (6, two in some Thallisellini and *Cladoxena*); lateral pockets absent on the mentum (11); medial carina of mentum usually present (12, absent in *Platoberus* and some Languriini); width of apical labial palpomere greater than or equal to, its length (13) and not securiform (14); width of ligular membrane equal to (Thallisellini and Hapalipini) or greater than prementum (most Languriini; 15); transverse gular line present (absent in *Penolanguria*) usually as a deep groove (20, 21, variable in *Hapalips*); antennal insertion usually hidden in dorsal view (24, visible in *Pseudhapalips*, *Hapalips*, *Truquiella*, and some *Crotchia*); supraocular line absent or present (29) usually to level above or beyond eye (30, variable in *Hapalips*); transverse line absent on

vertex of head (31); two stridulatory files present (one in *Nomotus*) or absent on vertex of the head (32, 33); pronotum not constricted at base (35); anterior angles of pronotum well (most Thallisellini, *Bolerus*, and some *Paracladoxena*) or poorly developed (36); anterior margin of prosternum serrate or not (39); pronotal pits present (44, absent in some *Hapalips* and *Penolanguria*); glandular ducts usually present (46) below or in the lateral carina of pronotum (47) and unitubulate (48, multitubulate in *Hapalips* and *Platoberus*); prosternal glandular ducts present or absent (50); procoxal cavity internally closed (51); procoxal cavity sparsely (*Languria*, *Pseudhapalips*, and Hapalipini) or completely open behind (52), closure by the prosternum and hypomeron (in *Bolerus*) (53) or hypomeron; edge of hypomeron usually smooth (54); mesoventral glandular ducts present or absent (61); mesepisternal fovea present or absent (63); mesometaventral articulation monocondylic (64); width of mesoventral process narrower than mesocoxa (66, equal to coxa in *Platoberus*); submesocoxal lines present or absent (68); metaventral pores absent (*Bolerus* and *Paracladoxena*) or present (69); metepisternal ctenidium present or absent (73); abdominal ventrites 1 and 2 free (74, connate in *Nomotus*); abdominal glandular ducts usually present (80) at disk (81) and margin (82, not most Hapalipini and *Crotchia*); abdominal calli present (83, absent in *Platoberus* and *Thallisella*); metafurcal lamina present (85, absent in *Platoberus* and some *Paracladoxena*) with median stalk of metendosternite well developed (86); form of spermatheca rounded or elongate (98); apical pit of spermatheca present or absent (99); accessory gland of spermatheca usually present (100); length of tarsomere 1 usually equal to, or sometimes longer than, tarsomere 2 (104, longer than tarsomeres 2 and 3 in *Languria*); tarsomere 4 reduced and hidden in ventral view (108); tarsal shelf of tarsomere 5 present or absent (109); empodium with one, two (most taxa), or lacking setae (*Platoberus*) (111); elytral punctation striate (113, confused in some *Penolanguria*) with scutellary striae present or absent (114); elytra usually narrowly explanate (116, wide in Thallisellini and variable in *Hapalips*, *Nomotus*, and *Paracladoxena*); radial cell (119) and wedge cell of hind wing present (120, absent in *Penolanguria* and *Platoberus*).

**Remarks.** This predominantly phytophagous group is the second most diverse lineage in the family and requires major revision and review. Some members of this group may actually be members of other lineages. This includes the tribe Hapalipini which are doubtful members of this group because they have many characters in common with Pharaxonothinae and Xenoscelinae (e.g., procoxal cavities slightly open and scutellary striae present).

**Included tribes.** Hapalipini, Languriini, Thallisellini.



### HAPALIPINI, new tribe

Hapalipini, new tribe. Type genus: *Hapalips* Reitter, 1877

**Diagnosis.** Frontoclypeal suture absent (1); terminal labial palpomere wider or equal to its length (13); width of ligular membrane equal to prementum (15); genal spines present (16); transverse gular line a shallow or weakly developed line or groove (21, deep in some *Hapalips*); antennal insertion hidden in dorsal view (24, exposed in *Bolerus*); antennal club 3-segmented (25), rounded in cross section (26); supraocular line absent (29, present in some *Hapalips*); anterior angles of pronotum poorly developed (36, well developed in *Bolerus*); pronotal carina relatively narrow (37); pronotal callosities absent (40); cuticular glandular ducts, if present, located below pronotal carina (47, in the bead of some *Hapalips*); procoxal cavity slightly open behind (52); submetacoxal lines divergent (78); cuticular glandular ducts at ventrite margins usually absent (82, present in some *Hapalips*); gonocoxite narrow (92); apical position of gonostyle on gonocoxite (96, absent in *Truquiella*); tarsomere 2 not lobed below (105); tarsal shelf not present (109, 110); two empodial setae present (111, one in *Bolerus*); scutellary striole present (114, absent in some *Hapalips*); elytra narrowly explanate (116, strongly explanate in some *Hapalips*).

**Remarks.** This group is supported in most of the phylogenetic analyses, however, all of the unambiguous characters are coded as polymorphic in *Hapalips*, thus making the apparent resolution and placement of this group suspect.

**Taxonomic Notes.** *Hapalips* is a large genus requiring revision. It includes species ranging in body forms from those that are highly dorsoventrally compressed (like *H. prolixus* and other species in Australasia) to tubulate forms with short legs and lacking the scutellary striole from Australia and Mexico (these were not coded for in the phylogenetic analysis). The work by Bruce (1952a) is useful for this genus, but is incomplete and limited in scope. Sen Gupta (1968a) recognised three subgenera, including *Cavophorus* for a species with large ventral fovea on the head similar to that in Fig. 35–38. A detailed study of the subgenera is warranted. *Truquiella* is similar in body form to certain species of *Hapalips*, and may eventually be placed in this genus. It differs from all other erotylids examined by the presence of a deep transverse furrow on the prosternum in front of the procoxae. I examined only one species of *Bolerus* and the placement in this group is questionable, especially as it is very similar to some members of basal Languriini.

**Biology.** Members of *Hapalips* appear to be exclusively phytophagous and have been collected from cacti (*Opuntia*), tree ferns, palms, cycads (*Cycas*), and other

plants (Sen Gupta 1968a).

**Included genera.** *Bolerus* (16 species; Asia), *Hapalips* (57 species; widespread), *Truquiella* (1 species; Central and North America (Texas)).

### LANGURIINI Crotch

Languriini Crotch, 1873: 349: Type genus: *Languria* Latreille, 1802

Cladoxenini Arrow, 1925: 166 (key) and 253 (description).  
Type genus: *Cladoxena* Motschulsky, 1866

**Diagnosis.** Frontoclypeal suture present (1, absent in *Crotchia*, *Microlanguria*, and some *Neoloberolus*); terminal labial palpomere longer than wide in most taxa (13, except for *Neoloberolus*); width of ligular membrane greater than that of prementum in most taxa (15, except for *Neoloberolus*); genal spines absent (16, present in some *Crotchia*); transverse gular line deep (21, shallow or weak in *Nomotus*); antennal insertion exposed in dorsal view (24, hidden in some *Crotchia*); antennal club 3-, 4- or 5-segmented (25) and rounded or flattened in cross-section (26); supraocular line present (29); anterior angles of pronotum poorly developed (36, well developed in some *Paracladoxena*); pronotal carina relatively narrow (37); pronotal callosities absent (40); cuticular glandular ducts, if present, located in pronotal carina (47, below the carina in *Dasydactylus*); procoxal cavity open behind (52, slightly open in *Languria*); submetacoxal lines, when present, divergent or parallel (78); cuticular glandular ducts of ventrites usually present at margins (82, not present in *Crotchia*); gonocoxite acute (92); gonostyle subapical on gonocoxite when present (96); tarsomere 2 not lobed below (105); tarsal shelf, when present, bifid (109, 110); one or two empodial setae present (111); scutellary striole absent (114); elytra narrowly explanate (116, strongly explanate in some *Anadastus*, some *Nomotus*, and some *Paracladoxena*).

**Remarks.** I have not examined this group thoroughly, focussing rather on cladoxenines and representative languriines for the phylogenetic study. Accurately identifying the species and determining the limits of the genera are difficult problems. *Paracladoxena* may be paraphyletic because there are forms similar to *Paracladoxena flavicornis* (Arrow) with a high pronotal volume, but other species of the genus with a dorsoventrally compressed prothorax. Moreover, *P. flavicornis* has a well developed ventral carina on each side of the head, suggesting that it may be a member of *Penolanguria* which has a similar feature in some of its species.

This group has a diversity second to that of Erotylinae and seems to share the taxonomic characteristics of cerambycids and other charismatic megataxa where genera

are, in many cases, not monophyletic, poorly defined, or monotypic. Although the major works for Languriini are very well illustrated and the morphological work by Villiers (1943) is exceptional, much work is needed to clarify the limits of the genera and to classify them into monophyletic groups. I have had limited success with identifying Neotropical taxa with the keys and descriptions provided in Martins & Pereira (1966) and required identified specimens for reference. I examined two undescribed Neotropical genera that are similar to members of *Crotchia*.

**Taxonomic notes.** Alfred Newton (pers. comm.) noted that *Slipinskiella*, listed as a new name by Leschen & Wegrzynowicz (1998), was intended to name a section of *Promecolanguria* which was misidentified by previous authors and is actually a new genus and does not replace a pre-existing genus. The name *Slipinskiella* is therefore a nomen nudum and remains unavailable because no description of the genus (or reference to one) was included.

**Biology.** Members of this group are all phytophagous (Leschen & Wegrzynowicz 1998) with two species of *Anadastus* and 1 species of *Languria* being of economic importance (Baker & Ellsbury 1989, Ellsbury & Baker 1989, Booth *et al.* 1990). Some species of the Neotropical genus *Nomotus* has been observed to feed on the frons of cycads (Windsor *et al.* 1999). Females of *Languria mozardi* chew a hole in their host plant and excavate a cavity into which the elongate egg is laid, then covering the opening with shredded plant material (Ellsbury & Baker 1989).

**Included genera.** 56 genera, including those listed in the tribes Languriini and Cladoxenini in Wegrzynowicz & Leschen (1998) and the genus described below.

### *Neoloberolus* new genus

Fig. 6

Type species: *Loberolus cursor* Grouvelle, 1919: 114.

**Diagnosis.** Frontoclypeal suture present in most specimens; mandible falcate with two apical teeth; mandibular cuticular glandular ducts absent; lacinia with three spines; width of galea equal to that of lacinia; medial carina of mentum absent; width of labial palpomere greater or equal to its width, subulate; width of ligular membrane equal to sclerite; cephalic glandular ducts absent; subocular cuticular glandular ducts present; transverse gular line present and deeply impressed; antennal insertion exposed in dorsal view; antennal club 3-segmented and round in cross-section; subocular groove or carina absent; ocular setae present; supraocular line present beyond eye; stridulatory files absent; width of pronotum widest in apical half and greater than its length; anterior margin of prosternum smooth; pronotum at base depressed and lacking pits in most speci-

mens; pronotal cuticular glandular ducts absent; prosternum short in front of procoxa relatively short; prosternal glandular ducts absent; procoxal cavities externally open; edge of hypomeron notched; trochantal notch present; foveae in procoxal rest absent; mesoventral glandular ducts absent; paired longitudinal mesoventral lines present; mesepisternal pocket present; submesocoxal lines absent; metaventral pores present; precoxal lines present; metepisternal ctenidium absent; ventrites 1 and 2 free; intercoxal process of ventrite 1 relatively broad; submetacoxal lines absent; abdominal cuticular glandular ducts absent; calli of ventrites lineate; aedeagus at rest on side; spiculum gastrale asymmetrical; spiculum ventrale extended in abdomen to level of ventrite 1; spermatheca elongate, lacking apical pit and accessory gland, duct coiled; tarsomere 1 equal to length of tarsomere 2; tarsal shelf absent; empodium with 2 setae; elytral length 2–2.5x greater than their width; wing present and with wedge cell.

**Comments.** This genus is described for the Neotropical species *Loberolus cursor* which is clearly different from the loberine *Loberolus agilis* Grouvelle. *Neoloberolus* has many characters in common with Languriini (including the distinctive ovipositor) and differs externally from *Loberolus* by having a pronotum that is wider than the width of the head and a well developed basal sulcus. *Neoloberolus cursor* is a relatively small species of languriine that is similar to members of the genus *Crotchia*, but lacks male setiferous sex patches on the abdominal ventrites, has a well developed frontoclypeal suture (in most specimens), and a pronotum with the greatest width in the apical half. The description of the genus is based on the type specimens and two undescribed species.

Nothing is known about the biology of the genus and the gut of a dissected specimen contained unidentifiable material.

**Type material examined** (MHNP). *Loberolus agilis* Grouvelle: 4 (1 slide mounted), Madag. Mang. [olive label]/Type [pink label]/Museum Paris, 1917, Coll. Grouvelle.

*Loberolus cursor* Grouvelle: 6 (1 slide mounted, 1 designated as Lectotype, so as to assure correct and consistent application of the name in the future), Cochabamba (Bolivie) Germ. [olive label]/Type [pink]/Museum Paris, 1917, Coll. Grouvelle.

### THALLISELLINI Sen Gupta

Thallisellini Sen Gupta, 1968b: 470. Type genus: *Thallisella* Crotch, 1876

**Diagnosis.** Frontoclypeal suture absent (1); terminal labial palpomere longer than wide in most taxa (13, except for *Pseudhapalips*); width of ligular membrane equal to

prementum in most taxa (15); genal spines absent or present (16); transverse gular line deep (21); antennal insertion exposed in dorsal view (24, hidden in *Pseudhupalips*); antennal club 3-segmented (25, 4- or 5-segmented in some *Thallisella*) and rounded in cross section (26); supraocular line absent or present (29); anterior angles of pronotum well developed (36, poorly developed in some *Thallisella*); pronotal carina relatively thick (37, narrow in *Thallisella*); pronotal callosities present (40, absent in *Platoberus* and one undescribed *Acryptophagus*); position of cuticular glandular ducts below pronotal carina (47, absent in *Thallisella*); procoxal cavity open behind (52, slightly open in *Pseudhupalips*); submetacoxal lines parallel (78, divergent in *Platoberus*); cuticular glandular ducts of ventrites present at margins (82); gonocoxite variable (92); gonostyle subapical, when present (96); tarsomere 2 lobed below (105); tarsal shelf absent (109, 110); empodium with one seta (111, absent in *Platoberus*); scutellary striole present or absent (114); elytra strongly explanate (116).

**Remarks.** This appears to be a well defined monophyletic group. Sen Gupta (1968a) stated that the tibial spurs are absent in this group, however both of the genera he included in the tribe have them, though they are diminutive and rather poorly developed.

The genera of this tribe are easy to identify and each contains several new species. The modified head of the male of *Pseudhupalips* is distinctive (see Fig. 15 in Champion 1913) as is the strongly falcate galea of *Platoberus* (see Fig. 23 in Sen Gupta 1968b). There are at least 7 undescribed species of *Acryptophagus* ranging from Panama to Brazil, and one undescribed genus (Ecuador) that is similar to members of *Acryptophagus*.

**Biology.** Species of *Platoberus* appear to be commonly collected in rotting vegetation and leaf litter and *Thallisella* is primarily associated with live vegetation with some extraordinary species that have been collected from the canopy (USNM). Members of *Acryptophagus* have been taken by beating vegetation.

**Included genera** (all Neotropical). *Acryptophagus* (1 species), *Platoberus* (10 species), *Pseudhupalips* (1 species), *Thallisella* (13 species).

## CRYPTOPHILINAE Casey

Cryptophilinae Casey, 1900: 77. Type genus: *Cryptophilus* Reitter, 1874

**Diagnosis.** Subapical serrations of mandible usually present (4, absent in some *Brachypterosa*, *Cryptophilus*, *Loberopsyllus*, and *Toramus*); lacinia with one or no lacinial spines (6); lateral pockets absent on the mentum (11);

medial carina of mentum usually present (12, absent in *Brachypterosa*, *Cathartocryptus*, and some *Empocryptus*); width of apical labial palpomere greater or equal to its length (13) and usually not securiform (14) except in some *Crowsonguptus* and *Empocryptus*; width of ligular membrane equal to (most taxa) or greater than (some *Atomarops*, *Toramus*, and *Loberopsyllus*) prementum (15); transverse gular line present (absent in *Cathartocryptus*) usually as a shallow groove (20, 21, deep in *Brachypterosa* and *Toramus*); antennal insertion hidden in dorsal view (24); supraocular line present (29, absent in some *Cathartocryptus*, *Cryptophilus*, and *Loberopsyllus*) usually to level above eye (30, variable in *Toramus* and beyond eye in *Lobosternum*); transverse line absent on vertex of head (31, present in *Toramus*); one stridulatory file present (two in *Brachypterosa*) or absent on vertex of head in some Cryptophilini and Empocryptini (32, 33); pronotum not strongly constricted at base (35) except for *Chinophagus*; anterior angles of pronotum poorly or well developed (36); anterior margin of prosternum serrate (39, smooth in *Brachypterosa*, *Crowsonguptus*, and some *Toramus*); pronotal pits present (44, absent in *Brachypterosa*, and some *Empocryptus*); glandular ducts present or absent (46) in the lateral carina of the pronotum (47) and unitubulate (48); prosternal glandular ducts absent (present in *Loberoschema*) (50); procoxal cavity internally closed (51); procoxal cavity usually open behind (52, closed or slightly open in Cryptophilini and closure by hypomeron, 53); edge of hypomeron usually smooth (54); mesoventral glandular ducts usually absent (61, present in *Cathartocryptus*, *Cryptophilus*, and *Lepidotoramus*); well developed mesepisternal fovea absent (present in some *Toramus*) (63); mesometaventral articulation dicondylic (64, not present *Cathartocryptus* and *Loberopsyllus*); width of mesoventral process variable but usually less than coxa (66, greater or equal to coxa in Empocryptini and other taxa); submesocoxal lines absent (68, present in *Atomarops* and most Empocryptini); metaventral pores usually absent (69); metepisternal ctenidium absent (73, present in *Cathartocryptus*); abdominal ventrites 1 and 2 free (74, connate in *Loberopsyllus*); abdominal cuticular glandular ducts absent (Empocryptini, *Cathartocryptus*, *Loberopsyllus*, and some *Toramus*) or present (80) at disk (81) and margins (82); abdominal calli present (83); metafurcal lamina absent (85, present in Empocryptini) with median stalk of metendosternite poorly or well developed (86); form of spermatheca rounded or elongate (98); apical pit of spermatheca usually absent (99); accessory gland of spermatheca usually present (100, absent in *Toramus*); length of tarsomere 1 usually greater than tarsomere 2 and 3 (104, equal to tarsomere 2 in *Cathartocryptus*, *Empocryptus*, *Lepidotoramus*, greater

than 2 in *Atomarops* and *Lobosternum*, and variable in *Cryptophilus*); tarsomere 4 usually exposed in ventral view (108); tarsal shelf of tarsomere 5 absent (109, present in *Lepidotoramus*); empodium with two (most taxa) or one seta (*Cryptophilus* and *Crowsonguptus*) (111); elytral punctation striate or confused (113) with scutellary striole absent (114); elytra usually narrowly explanate (116); radial cell (119) and wedge cell of hind wing absent (120).

**Remarks.** This group appears to be a well defined monophyletic group, though the inclusion of *Cathartocryptus* requires verification.

**Included tribes.** Cryptophilini, Empocryptini, Toramini.

### EMPOCRYPTINI, new tribe

Type genus: *Empocryptus* Sharp, 1900

**Diagnosis.** Subapical serrations present on mandible (4); length of apical labial palpomere usually greater than or equal to its width (13, except for *Lepidotoramus*); stridulatory files present on vertex of head (32), pronotal carina serrate (41); external closure of procoxal cavity completely open (52); procoxal rests divided (57); width of mesoventral process equal to mesocoxa (66, greater in *Empocryptus*); submesocoxal lines present (68, absent in some *Empocryptus*); abdominal pores present in male (79, absent in *Lepidotoramus*); abdominal glandular ducts absent (80); median stalk of metendosternite well developed (86, poorly developed in *Lobosternum*); gonocoxite narrow (92, dilated in *Lepidotoramus*); spermatheca rounded or elongate (98); spiracles present on terga 6 and 7 (102); elytral punctation striate (113).

**Remarks.** A phylogenetic study of the genera was published by Leschen (1997). This is a strictly Neotropical group with many species of *Empocryptus* requiring description. Two specimens of *Lepidotoramus*, outside its published range of Brazil and Ecuador, have been examined from northern Argentina near Iguazu National Park (CMNC) and Paraguay (AAPC).

**Biology.** Members of this group are mainly litter inhabitants and are saprophagous. The species *Lepidotoramus grouvellei* Leschen may have been reared from a lepidopteran cocoon (Leschen 1997).

**Included genera.** *Empocryptus* (15 species, Neotropical), *Lepidotoramus* (1 species, South America), *Lobosternum* (1 species, Chile).

### CRYPTOPHILINI Casey

Cryptophilini Casey, 1900: 77. Type genus: *Cryptophilus* Reitter, 1874

Xenoscelinini Sen Gupta & Crowson, 1971: 25. Type genus: *Xenoscelinus* Grouvelle, 1910.

**Diagnosis.** Subapical serrations absent on mandible (present in *Crowsonguptus* and *Cathartocryptus*) (4); length of apical labial palpomere usually greater than its width (13, except for *Crowsonguptus* and some *Cryptophilus*); subocular bead absent from head (27); stridulatory files present on vertex of head (32, absent in *Cathartocryptus* and *Loberopsyllus*); pronotal carina smooth (41, serrate in *Cathartocryptus* and *Cryptophilus*); external closure of procoxal cavity completely closed (52, slightly open in *Loberopsyllus*); procoxal rests, when present, divided (57); width of mesoventral process less than mesocoxa (66, greater in *Cathartocryptus*, *Loberopsyllus*, and some *Cryptophilus*); submesocoxal lines absent (68); abdominal pores absent in male (79); abdominal glandular ducts present (absent in *Cathartocryptus* and *Loberopsyllus*) (80); median stalk of metendosternite poorly developed (86); gonocoxite narrow (92, dilated in *Cryptophilus* and somewhat dilated in *Cathartocryptus* which has a broad gonostyle); spermatheca rounded or elongate (98); spiracles present on terga 6 and 7 (102); elytral punctation confused (113).

**Remarks.** As previously mentioned, the phylogenetic composition of this group may be contingent on the placement on the rather unusual genus *Cathartocryptus*, which differs from the remaining members of cryptophilines previously classified in the separate tribe Xenoscelinini by Sen Gupta & Crowson (1971). *Cathartocryptus* is unique in the tribe and differs from the remaining members of the group by several characters: subocular glandular ducts absent (19), transverse gular line absent (20, Fig. 48), prosternum long in front of procoxae (49), metepisternal ctenidium present (73), gonostyle somewhat dilated with a large gonocoxite (see figures in Sen Gupta & Crowson 1971 and Sasaji 1989), and tarsal claws slightly notched at the base. All of these features may be associated with the presence of species in subcortical habitats. I disagree with Sen Gupta & Crowson (1971) that *Cathartocryptus* as a whole has striate elytra, though in *C. maculosa* there are weak striae on the disc (Fig. 7), not seen in other species.

The placement of *Chinophagus* in this group requires confirmation, but is placed here provisionally because the procoxal cavities are completely closed externally (Ljubarsky 1994).

There are many species of *Cryptophilus* throughout the world that require description, and classifying these into species groups would be useful. I have examined a



few undescribed species of *Crowsonguptus*, including a brachypterous species from montane Honduras, and of *Cathartocryptus*. The Fijian endemic genus *Brachypterosa* was erroneously listed from Asia by Leschen & Wegrzynowicz (1998).

Included in this group is an undescribed Neotropical genus with at least two species (Bolivia, Panama, and Trinidad) with a silvanid-like habitus and is possibly related to *Cathartocryptus*.

**Taxonomic notes.** The type species of *Cryptophagops* Grouvelle, 1919, *Cryptophilus alluaudi* Grouvelle, is clearly a member of *Henoticus* and is transferred to this genus based on the presence of typical cryptophagid characters (e.g., incomplete elytral epipleura and ventrite 1 equal in length to remaining ventrites) and “reductive” characters seen in many flightless African *Henoticus* which have caused confusion in the generic limits of the group (Leschen 1996). Grouvelle (1919) noted correctly that the completely open procoxal cavities of *C. alluaudi* placed it within Cryptophagidae, but the definition of the family at that time included many members of Languriidae. The three species initially described as members of *Cryptophilus* by Bruce (1953) and subsequently transferred to *Cryptophagops* (Bruce 1957) are transferred back to *Cryptophilus*: *C. allotrius* Bruce, *C. leonensis* Bruce, and *C. mnionomoides* Bruce. Although *Cryptophilus* is a moderately variable genus, these taxa do not fall outside the range of variation for the genus.

*Tomarops punctatus* Grouvelle, the type species of the genus *Tomarops* Grouvelle, 1903 (presently composed of three species including *T. bimaculatus* Bruce, *T. longitarsis* Bruce) is clearly congeneric with *Cryptophilus*. The species placed into this genus by Bruce, however, are both probably members of *Toramus* (only *T. longitarsis*), but the type specimens of these have not been examined.

**Biology.** Most members of this group are found in decaying leaf litter and under bark and are saprophagous or mycophagous. The species *Cryptophilus integer* (Heer) has been introduced throughout the world (see below).

#### Type Material Examined.

*Henoticus alluaudi* (Grouvelle), new combination: Holotype (MNHP); TYPE [pink label]/Museum Paris Coll. Grouvelle 1915 [powder blue label]/*Cryptophagops alluaudi* Grouv.

*Cryptophilus allotrius* Bruce: Holotype (BMNH); Type [red circular label]/Sierra Leone: Freetown, 1–2.iv.1915, Dr. M. Cameron/Typus [red label]/*Cryptophagops allotrius* Bruce [hand].

*Cryptophilus leonensis* Bruce: 3 Paratypes (BMNH); Cotype [yellow circular label]/Sierra Leone: Freetown, 1–2.iv.1915, Dr. M. Cameron/ Cotypus [red label]/

*Cryptophagops leonensis* Bruce [hand].

*Cryptophagops mnionomoides* Bruce: Holotype (BMNH); Type [red circular label]/Tonkin: Hoabinh., Aug. 1918, R.V. de Salvaza; Typus [red label]/ *Cryptophagops mnionomoides* Bruce [hand].

*Tomarops punctatus* Grouvelle (MNHP; lectotype not designated): 6 [card mounted], Coonour, 15–30 Juill, 1901, 1500–2000 m. alt./Nilghiris, N. Maindron/Type [labels pink, red or white]/Museum Paris, 1917, Coll. Grouvelle.

**Included genera.** *Brachypterosa* (1 species, Fiji), *Chinophagus* (1 species, Asia), *Crowsonguptus* (4 species, Neotropical), *Cryptophilus* (19 species, widespread), *Cathartocryptus* (8 species, Africa, Asia, Australia, New Zealand).

### TORAMINI Sen Gupta

Toramini Sen Gupta, 1967: 168. Type genus: *Toramus* Grouvelle, 1916

**Diagnosis.** Subapical serrations present on mandible (absent in some *Toramus*) (4); length of apical labial palpomere usually less than its width (13, except for *Toramus* and some *Atomarops*); subocular grooves absent on head (27, except for some *Toramus*); stridulatory files absent on vertex of head (32); pronotal carina smooth (41, serrate in *Atomarops*, some *Loberoschema* and possibly some *Toramus*); external closure of procoxal cavity completely open (52); procoxal rests contiguous (57); width of mesoventral process less than or equal to mesocoxa (66); submesocoxal lines absent (68, present in *Atomarops*); abdominal pores absent in male (79, present in some *Loberoschema*); abdominal glandular ducts present (absent in some *Toramus*) (80); median stalk of metendosternite well developed (86, poorly developed in *Atomarops*); gonocoxite dilated (92); spermatheca elongate (98); spiracles absent on terga 6 and 7 (102); elytral punctation confused or striate (113).

**Remarks.** The large and diverse genus *Toramus* appears to be monophyletic based on the presence of a transverse line on the vertex of the head, and deserves global study at the species level. Most species are very colourful and come in an assortment of body forms. Perhaps the most critical problem at the generic level in this group is the taxonomic limits of the genera *Loberoschema* and *Stengita*. These genera together are monophyletic, defined mainly by the presence of parallel carinae on the mesoventrite (Fig. 87) and presence of punctate stria on the elytra (Fig. 91). There are several undescribed species in the *Loberoschema-Stengita* group from Chile, Columbia, Panama, Ecuador, Juan Fernandez Islands, and Venezuela. An unusual undescribed genus related to these, which in-



cludes two very different species from montane Venezuela, have a well defined medial tooth on the tarsal claws. Unidentate claws are rare in Erotylidae and I have seen this feature only in some species of *Toramus*.

**Taxonomic Notes.** As mentioned in the preceding section on Cryptophilini, at least the type species of *Tomarops* is clearly congeneric with *Toramus* and requires transfer to this genus. Both of Bruce's (1954, 1963) species need to be examined thoroughly before any action is taken.

**Biology.** Toraminae occur in many habitats and are mostly saprophagous or mycophagous. I have collected larvae and adults of *Toramus* and *Loberoschema* from Xylariaceae (Costa Rica and Chile, respectively) and Neotropical *Toramus* from banana leaves and other aerial vegetation infected with phylloplane fungi. Larvae were taken in numbers in rotten *Pseudobombax* (Bombacaceae) flowers on the forest floor (Lawrence 1991; note that these were listed incorrectly as *Loberoschema* in this publication as well as in Lawrence *et al.* 1999b). Some larval *Toramus* and *Loberoschema* retain exuviae on the abdomen throughout the larval development.

**Included genera.** *Atomarops* (3 species, Asia), *Loberosyllus* (4 species, Central America), *Loberoschema* (7 species, South America and Juan Fernandez Islands), *Stengita* (1 species, South America), *Toramus* (43 species, widespread (not Australia or New Zealand)).

## EROTYLINAE Latreille

Erotylinae Latreille, 1802: 233. Type species: *Erotylus* Fabricius, 1775

**Diagnosis.** Subapical serrations of mandible absent (4); lacinia usually with two lacinial spines (6, absent in Megalodacnini which have a brushy lacinia); lateral pock-ets absent on mentum (11); medial carina of mentum usually present (12, absent in Megalodacnini); width of apical labial palpomere greater or equal to its length (13) and securiform (14) in Encaustini, Erotylini and some Tritomini; width of ligular membrane equal to prementum (15); transverse gular line present (absent in Dacninae) usually as a shallow or beadlike groove (20, 21); antennal insertion hidden in dorsal view (24, visible in dorsal view in Encaustini and some Erotylini); supraocular line typically present to level beyond eye (29, 30, absent in some Dacnini); transverse line absent on vertex of head (31); two stridulatory files present or absent on vertex of head (32, 33); pronotal shape variable and not constricted at base (35); anterior angles of pronotum well developed (36); anterior margin of prosternum smooth (39); pronotal pits absent (44); glandular ducts present (46, absent in some Dacnini) in lateral carina of pronotum (47) and unitubulate (48); prosternal

glandular ducts present or absent (50); procoxal cavity internally open (51) and externally closed (52), external closure by prosternum and hypomeron (53); edge of hypomeron smooth (54); mesoventral glandular ducts present (61, absent in Dacnini); mesepisternal fovea absent (63); mesometaventral articulation dicondylic (64, straight-line form in Encaustinae); width of mesoventral process usually greater or equal to mesocoxa (66); submesocoxal lines present or absent (68); metaventral pores present or absent (69); metepisternal ctenidium absent (73); abdominal ventrites 1 and 2 connate (74); abdominal cuticular glandular ducts present or absent (80) at disk (81) and margin (82); abdominal calli present or absent (83); metafurcal lamina present (85, absent in some Dacnini) with a well developed median stalk (86); form of spermatheca rounded or elongate (98); apical pit of spermatheca usually absent (99, present in some Tritomini); accessory gland of spermatheca present (100, absent in some Tritomini); length of tarsomere 1 usually equal to tarsomere 2 (104, equal to tarsomere 2 and 3 in Erotylini); tarsomere 4 reduced and hidden in ventral view in most taxa (108); tarsal shelf of tarsomere 5 present (109); empodium with two setae (none in Erotylini) (111); elytral punctation striate (113) without scutellary striole (114); elytra usually narrowly explanate (116); radial cell present (119); wedge cell absent (120).

**Remarks.** This is the largest subfamily in the Erotylidae and is currently under study by J. McHugh (larval characters), P. Skelley (adult characters), and P. Wegrzynowicz (adult characters). Perhaps the most interesting problems are the monophyly of the tribes and many genera and a number of unusual taxa are requiring description. The results of the present study should be considered minor because characters were not scored to determine the relationships of Erotylinae, but rather to determine the monophyly of the other subfamilies and the status of the family Languriidae. McHugh (1995), in a study based on larvae, reports the phylogenetic relationships, Dacnini ((Encaustini, Megalodacnini) (Tritomini + Erotylini)), with a paraphyletic Tritomini.

The genus *Hoplepiscapha* Lea (1922) was originally described as a member of Erotylidae, and was later transferred to Xenoscelinae (Pharaxonothini) by Sen Gupta & Crowson (1971), and then back to Erotylidae by Lawrence (1988). Dissections of this genus confirmed the placement of this species in Erotylinae.

**Biology.** All species are associated with fungi, especially macroscopic Basidiomycetes (Skelley *et al.* 1991).

**Included tribes.** Dacnini Gistel, 1856; Megalodacnini Sen Gupta, 1969; Encaustini Crotch, 1876/Chapuis, in Lacordaire 1876; Tritomini Curtis, 1834; Erotylini Latreille, 1802.

## KEY TO NEW ZEALAND EROTYLIDAE TAXA

- 1 Prothorax with distinct anterior angles projecting forward (Fig. 9); procoxal cavities completely closed externally by lateral extensions of the prosternal process and the hypomeron (Fig. 9) ..... (Erotylinae)... 2
- Prothorax anterior angles rounded or angulate but not projecting forward (Fig. 1, 3–5, 7, 8); procoxal cavities narrowly open (Fig. 76) or closed by extensions of the hypomeron only (Fig. 72) ..... 3
- 2(1) Body lacking dorsal vestiture of setae ..... *Thallis polita* Broun
- Body with vestiture of setae, setae often short or sparse ..... *Cryptodacne* spp.
- 3(1) Elytra with punctate striae (Fig. 3, 4, 5) ..... 4
- Elytra lacking punctate striae (Fig. 1, 7, 8) ..... 10
- 4(3) Antennal insertions completely concealed above (Fig. 5); length of body more than 3 mm; strongly elongate with length of elytra well over 3x that of prothorax .. ..... (p. 52)... *Hapalips prolixus* (Sharp)
- Antennal insertions partially visible from above (Fig. 3, 4); length of body less than 3 mm; length of elytra about 3x that of prothorax ..... 5
- 5(4) Body dorsoventrally compressed; sides of pronotum narrowed at base (Fig. 7); prosternal process wide, about as wide as exposed portion of procoxa ..... (p. 53)... *Cathartocryptus maculosus* (Broun)
- Body form convex; sides of pronotum evenly rounded (Fig. 3, 4); prosternal process narrower than procoxa (Fig. 74–78) ..... (*Loberus* spp.)... 6
- 6(5) Dorsal surface of body, especially pronotum, with well developed reticulated microsculpture visible at low magnification ..... 7
- Dorsal surface of body without well developed reticulated microsculpture ..... 8
- 7(6) Body unicolorous dark brown; Three Kings Islands ..... (p. 47)... *Loberus borealis* n. sp.
- Body typically bicoloured with infusate elytra which are sometimes unicolorous black or brown elytra; North and South Island... (p. 48)... *Loberus depressus* (Sharp)
- 8(6) Elytron bimaculate (Fig. 3); pronotum widest at middle with sides evenly arcuate ..... 9
- Body unicolorous black or chocolate-brown; pronotum widest just behind middle (Fig. 4) ..... (p. 46)... *Loberus anthracinus* (Broun)
- 9(8) Dorsal setae elongate, length of elytral setae about equal to width of eye; Three Kings Islands ..... (p. 50)... *Loberus watti* n. sp.
- Dorsal setae short, elytral setae less than width of eye (Fig. 3); North and South Island ..... (p. 49)... *Loberus nitens* (Sharp)
- 10(3) Width of pronotum less than combined width of elytra (Fig. 1); pronotal sides lacking well developed carina and having well developed setiferous tubercles ..... (p. 45)... *Loberonotha olivascens* (Broun)
- Width of pronotum equal to minimum width of elytra (Fig. 8); pronotal sides with well developed carina and lacking well developed setiferous tubercles ..... (p. 55)... *Cryptophilus integer* (Heer)

## DESCRIPTIONS

## Xenoscelinae

*Loberonotha* Sen Gupta & Crowson

Fig. 1, 16, 39, 53–55, 71, 93

*Loberonotha* Sen Gupta & Crowson, 1969: 127. Type species: *Telmatophilus olivascens* Broun, 1893: 1104 (original designation).

**Diagnosis.** With the characters of the subfamily Xenoscelinae. Mandible with three apical teeth on different horizontal planes, lateral margin lacking tooth; mentum relatively large and lacking pits; genal spines present; gular line present and deep, extending posteriorly to level of the posterior margin of the eye; subocular cuticular glandular ducts present; gular fovea absent; subocular bead absent; supraocular line present; vertexal line present; vertexal files present and double; temples of head present; genal spines present; width of pronotum narrower than combined width of elytra; pronotal carina absent, but side with four setiferous tubercles widely spaced and present; pronotal cavity equal to its length; pronotal pits absent; procoxal cavity internally and externally open; edge of hypomeron notched; pronotal cuticular glandular ducts absent; trochantal notch present; mesoventral fovea present; mesepisternal pocket absent; metepisternal ctenidium absent; gonocoxite dilated; precoxal lines present; gonostyle apical; spermatheca round with an accessory gland; length of tarsomere 1 equal to tarsomere 2; tarsomere 3 lobed; tarsal shelf absent; elytral length 3x that of width; elytral punctation confused; elytra narrowly explanate; epipleuron incomplete, with carina weakly developed in posterior 1/3; male abdominal segment 9 symmetrical.

**Distribution.** New Zealand (1 species).

***Loberonotha olivascens* (Broun)**

Fig. 1, 16, 39, 53–55, 71, 93, Map 9

*Telmatophilus olivascens* Broun, 1893: 1104.

*Telmatophilus vestitus* Broun, 1910: 25. **New synonymy.**  
*Loberonotha olivascens* (Broun, 1893: 1104). Combination  
by Sen Gupta & Crowson, 1969: 127.

**Description.** With the characters for the genus. Length 2.60–3.46 mm, mean = 3.07 (n = 12). Colour of body uniformly light to dark olive brown, often with head and pronotum darker, funicle and abdomen lighter. Punctuation dense, average width of puncture 1.3 µm. Body setae moderately long, decumbent with scattered erect setae. Dorsal surfaces strongly punctate, punctures of vertex separated by about 1 diameter. Eye prominent, finely faceted, 10–13 facets at greatest length; circumocular bead present; area of temple glabrous. Antenna relatively long, extending to beyond posterior margin of pronotum; antennomere relative lengths 9 : 7 : 10 : 7 : 8 : 6 : 7 : 6 : 9 : 9 : 12. Pronotum parallel-sided, about 0.90x as long as wide (pronotal length/maximum pronotal width = 0.85–0.94, mean = 0.90); depth = 0.28–0.44, mean = 0.34 mm; punctuation dense. Abdominal depth = 0.48–0.76 mm, mean = 0.57. Elytra about 1.60x as long as wide (elytral length/maximum elytral width = 1.37–1.66, mean = 1.60) and 3.21x as long as pronotum (elytral length/pronotal length = 2.86–3.42, mean = 3.21). Metaventrite without subcoxal lines; punctuation strong on disc, punctures on sides separated by 1–3 diameters. Abdominal punctation strong, separated by 1–3 diameters; vestiture decumbent with scattered suberect lateral setae, group of 3–4 medial setae present at edge of ventrite 5; internal calli on ventrites 1–4. Abdominal tergite 7 hidden in dorsal view. Elytron with sutural stria present at apical 1/3. Aedeagus with paramere 2.1x longer than wide, multisetose; biflagellate strut fused with apical swellings, 1.8x longer than median lobe; ventral striations present; median lobe with ventral lineate callus along margin; internal sac simple.

**Type material examined.** *Telmatophilus olivascens*: 1959 [hand] / Mount Arthur. / New Zealand Broun Coll. Brit. Mus. 1922-482 / *Telmatophilus olivascens* [hand] / *Telmatophilus olivascens* Broun, LECTOTYPE, Desig. Leschen 2001 [red label] (here designated, so as to assure correct and consistent application of the name in the future) (BMNH); 2, mounted on the same card, 1959 [hand] / New Zealand Broun Coll. Brit. Mus. 1922-482 / *Telmatophilus olivascens* Broun, PARALECTOTYPE, Desig. Leschen 2001 [yellow label] (BMNH); 4, 1959 [hand] / T. Broun Collection / A.E. Brookes Collection / PARALECTOTYPE, Desig. Leschen 2001 [yellow label] (NZAC); 3, same, but with Syntype [typed], *Telmatophilus olivascens* Broun, 1895 [hand]; 2, same but with Mount Arthur [hand].

*Telmatophilus vestitus*: 3055 [hand] / Mount Cook. [hand] / New Zealand Broun Coll. Brit. Mus. 1922-482 / *Telmatophilus vestitus* [hand] / LECTOTYPE, Desig. Leschen 2001 [red label] (here designated, so as to assure correct and consistent application of the name in the future) (BMNH); 1, same but PARALECTOTYPE [yellow label] (BMNH); 4, same but with T. Broun Collection / A.E. Brookes Collection / Syntype [typed], *Telmatophilus olivascens* Broun, 1895 [hand] (NZAC).

**Material examined.** Type specimens plus 470 non-type specimens — see Appendix 3 for collection details of specimens examined.

**Distribution** (Map 9). Central North Island and the South Island.

RI, TO / NN, WD, MB, KA, NC, MK, OL, CO, FD, SL, SI.

**Comments.** This species is easily distinguished from all other New Zealand Erotylidae by having the pronotum narrower than the elytra, absence of a well developed prothoracic carina, and confused punctuation of the elytra. Most specimens have been collected in the South Island (with the exception of three records from RI) and taken from vegetation and flowers. Guts of dissected specimens contained unidentifiable matter and mainly pollen in two specimens (see also Sen Gupta & Crowson 1969), suggesting that this species is phytophagous as an adult. Host associations include plant species in the genera *Brachyglottis*, *Cassinia*, *Celmisia*, *Coprosma*, *Hebe*, *Nothofagus*, *Olearia*, *Pseudopanax*, *Senecio*, and *Traversia*.

The type material of both species described by T. Broun in the genus *Telmatophilus* differ in their coloration (those from Mt. Cook are lighter) but are indistinguishable based on external morphology, and the synonymy is formalised here: the colour varies throughout the range of the species. Broun (1893) mentioned that numerous specimens were examined of *T. olivascens* collected from Mt. Arthur: three specimens from this series were present in the Broun Collection (BMNH) and nine were present in NZAC. One of the BMNH specimens was designated as the lectotype of *T. olivascens*. Broun (1910) listed eight specimens examined in the description of *T. vestitus*, and there were two present in the (BMNH), one of which was designated as the lectotype, and four specimens in the NZAC. The synonymy of these two species may have been an oversight by Sen Gupta & Crowson (1969) who listed both species in their study.

## Loberinae

### Genus *Loberus* LeConte

*Loberus* LeConte, 1861: 98. Type species: *Loberus impressus* LeConte, 1861: 98 (by monotypy)

*Glisonotha* Motschulsky, 1863: 430. Type species: *Glisonotha* [sic!] *setosa* Motschulsky, 1863 (designated by Leschen & Wegrzynowicz 1998)

*Glisonotha* Motschulsky. Mis-spelling by Motschulsky, 1863: 431 and Grouvelle, 1919: 66.

**Diagnosis.** With the characters of the subfamily Loberinae. Mandible usually with lateral tooth (present in all New Zealand forms); three lacinial spines present; medial carina absent or present on mentum; tentorium without medial spine; cephalic cuticular glandular ducts absent; subocular groove absent; stridulatory files present on vertex of head; pronotal margins parallel; cuticular glandular ducts of body usually unitubulate, when present; prosternal cuticular glandular ducts present; procoxal cavities externally open; trochantal notch present; mesoventral foveae absent; mesepisternal pocket absent; metaventral discrimen present; metaventral notch absent; intercoxal of ventrite 1 relatively broad; abdominal cuticular glandular ducts present in discal and marginal positions; spiculum gastrale asymmetrical; gonostyle apical; spermathecal duct coiled; empodium with two setae; scutellary striole absent.

**Distribution.** Worldwide, except for Europe (75 species, 5 in New Zealand).

### *Loberus anthracinus* (Broun), new combination

Fig. 4, 18, 24, 31, 42, 74, 84, Map 4

*Cryptophagus anthracinus* Broun, 1893: 1446.

**Diagnosis.** Body black to chocolate-brown, glabrous without obvious microsculpture, vestiture of short sparse setae; mandible with two apical teeth; median carina of mentum present; genal spines absent or reduced; transverse gular line weakly developed; supraocular line present above eye; anterior prosternal margin smooth; pronotal carina smooth; pronotum at base weakly depressed; cuticular glandular ducts in bead poorly developed; procoxal cavities internally open; edge of hypomeron smooth; mesoventral cuticular glandular ducts absent; metaventral pores absent; precoxal lines absent; metepisternal ctenidium present; submetacoxal lines absent; spermatheca elongate, accessory gland present; tarsomere 1 equal to tarsomere 2; tarsomere 2 not lobed; elytron striate, with 9 striae; elytron narrowly explanate; wing reduced to a small flap.

**Description.** With the characters for the genus and in the diagnosis. Length 1.40–2.07 mm, mean = 1.73 (n = 12). Punctuation sparse, average width of puncture 1 µm. Body relatively convex with dorsal setae very short, decumbent with average length of elytral setae 4 µm; ventral setae longer and decumbent, average length of abdominal setae 6

µm. Head moderately punctate, punctures of vertex separated by about 1–3 diameters, punctures absent on gula, punctures present behind eye. Eye prominent, finely faceted, 6–7 facets at greatest length, ocular setae absent. Antenna moderately short, extending to edge of pronotum; antennomere relative lengths 6 : 4 : 4 : 3 : 4 : 3 : 4 : 3 : 5 : 5 : 7. Pronotum widest in basal 1/3, about 0.76x as long as wide (pronotal length/maximum pronotal width = 0.71–0.87, mean = 0.76); depth = 0.23–0.32, mean = 0.26 mm; punctuation dense, punctures of disc separated by about 0.51 diameters; weak depressions or punctures present at base. Abdominal depth = 0.35–0.50 mm, mean = 0.48. Elytra about 1.27x as long as wide (elytral length/maximum elytral width = 1.13–1.48, mean = 1.27) and 2.60x as long as pronotum (elytral length/pronotal length = 2.11–2.70, mean = 2.80); 9 striae present with 1 punctate and confluent with sutural stria, 2–7 present to about apical 1/2 or 1/3, 8 short and present at basal 1/4, 9 confluent with epipleural fold, stria punctures separated by 15 diameters. Metaventrite lacking subcoxal lines; punctuation fine on disc, punctures on sides separated by 1–2 diameters. Abdomen with pairs of internal calli on ventrites 1–4 (weakly developed on 4); punctuation diffuse on disc, punctures on sides separated by 1 diameter. Abdominal tergite 7 exposed in dorsal view.

Aedeagus with separate biflagellate struts 2.9x length of median lobe, internal sac approximately 1/2 length of struts; sclerotised ejaculatory duct present, internal sac with median asymmetrical sclerites (though weakly sclerotised). Paramere 4x longer than wide, with 15 minor and 17 major setae (apex and shaft setae of equal length).

Gonocoxite 3.2x longer than wide, campaniform sensillae sparse, apex with 9 setae, gonostyle bearing 5 setae (central one elongate).

**Type material examined.** 2509 / Ashburton [hand] / New Zealand Broun Coll. Brit. Mus. 1922-482 / Languriidae - Loberini [hand] det. R. A. Crowson / *C. anthracinus* Broun, LECTOTYPE, Desig. Leschen 2001 [red label] (here designated, so as to assure correct and consistent application of the name in the future) (BMNH); Coll. W. W. Smith [no date] Ex Broun Coll. [hand] / Ashburton Canterbury South Isld [hand] / 2509 [hand] / *Cryptophagus anthracinus* Broun [hand] / T. Broun Collection / A. E. Brookes Collection / *C. anthracinus* Broun, PARALECTOTYPE, Desig. Leschen 2001 [yellow label] (NZAC).

**Material examined.** Type specimens plus 165 non-type specimens — see Appendix 3 for collection details of specimens examined.

**Distribution** (Map 4). Throughout New Zealand except for northern North Island.

WO, BP, TO, HB, WA / SD, NN, BR, WD, MB, MC, SC, DN, CO, SL, FD.



**Comments.** *Loberus anthracinus* can be distinguished from all other New Zealand erotylid species by its small size, glabrous black or dark brown body, and pronotal shape. Most specimens of this brachypterous species have been collected at relatively high altitudes in the South Island and from moss, carpet plants, and in leaf litter. Specimens have also been collected in dry conditions in Otago under rocks. The guts of dissected specimens were empty.

Broun (1893) based this species on five specimens collected from Ashburton by W. W. Smith. Only one specimen was located in the BMNH that matched this locality, although a second one located in the NZAC with handwritten labels could be from the original series.

Charles Watt labelled specimens of *L. anthracinus* in the NZAC as a new genus and there are several characters, besides the small convex body, that differ from the remaining New Zealand species (e.g., mentum with a median carina, tarsomere 2 not lobed below). I have seen at least one Chilean species that is very similar in body form to *L. anthracinus*, though with the more typical characters of *Loberus*, and it is best to place this species in *Loberus* until the genus is studied more closely.

### ***Loberus borealis*, new species**

Fig. 19, 27, 43, 51, 63, 75, Map 5

**Diagnosis.** Body brown to dark brown, moderately shining, with obvious microsculpture, vestiture consisting of very widely scattered short erect setae; mandible with two apical teeth; median carina of mentum absent; genal spine reduced to a tiny acute process; transverse gular line weakly developed; supraocular line weakly developed; anterior prosternal margin smooth; pronotal carina smooth; pronotum at base slightly depressed; cuticular glandular ducts in bead; procoxal cavities internally open; edge of hypomeron smooth; mesoventral cuticular glandular ducts present; metaventral pores present; precoxal lines present and impunctate; metepisternal ctenidium present and poorly developed; submetacoxal lines incomplete and poorly developed; spermatheca elongate, accessory gland present; tarsomere 1 subequal to tarsomere 2; tarsomere 2 lobed; elytron striate, with 9 striae; elytron slightly explanate; wing present.

**Description.** With the characters for the genus and in the diagnosis. Length 1.50–2.02  $\mu\text{m}$ , mean = 1.82 ( $n = 12$ ). Colour of body uniformly brown to dark brown, very rarely with light maculae on the elytron; funicle, tibia, tarsi, and sometimes the mouthparts pale. Punctuation dense, average width of puncture 1  $\mu\text{m}$ ; most of the body covered with imbricate microsculpture, strongly developed on vertex of the head and pronotum, absent from elytra. Body relatively flattened with dorsal setae very short and widely

scattered, erect with average length of elytral setae 3  $\mu\text{m}$ ; ventral setae longer and decumbent, average length of abdominal setae 7  $\mu\text{m}$ . Head moderately punctate, punctures of vertex separated by about 1 diameter, punctures absent on gula, punctures present behind the eye. Eye prominent, strongly faceted, 9–10 facets at greatest length, ocular setae present. Antenna moderately elongate, extending slightly beyond edge of pronotum; antennomere relative lengths 8 : 5 : 5 : 3 : 4 : 3 : 4 : 3 : 5 : 5 : 7. Pronotum widest at middle, about 0.68 $\times$  as long as wide (pronotal length/maximum pronotal width = 0.60–0.75, mean = 0.68); depth = 0.23–0.28, mean = 0.23 mm; punctuation dense, punctures of disc separated by about 1.53 diameters. Abdominal depth = 0.31–0.44 mm, mean = 0.34. Elytra about 1.45 $\times$  as long as wide (elytral length/maximum elytral width = 1.19–1.56, mean = 1.45) and 2.96 $\times$  as long as pronotum (elytral length/pronotal length = 2.39–3.20, mean = 2.96); 9 striae present with 1 often weakly punctate and confluent with sutural stria, 2–8 present to about apical 1/6, 8 starting slightly beyond humerus, 9 confluent with epipleural fold and bifurcating at apical 1/3; stria punctures separated by 15 diameters. Metaventrite without subcoxal lines; punctuation moderately fine on disc, punctures on sides separated by about 3 diameters. Abdomen with internal calli on ventrites 1–4. Abdominal punctuation of ventrites well developed on disc, punctures on sides separated by about 3 diameters.

Aedeagus with separated biflagellate struts 2.9 $\times$  length of median lobe, internal sac approximately 2/3 length of struts (or struts 1.6 $\times$  its length); sclerotised ejaculatory duct present, internal sac with median symmetrical sclerites. Paramere 9 $\times$  longer than wide, with 8 minor setae and 9 major setae.

Gonocoxite 7 $\times$  longer than width at middle, campaniform sensillae relatively dense, apex with 7 major setae, gonostyle bearing 5 setae (central one elongate).

**Comments.** This new species can be distinguished from most species of New Zealand erotylids by the presence of a unicolorous, subglabrous body which has an imbricate microsculpture on the pronotum. *Loberus borealis* closely resembles *L. depressus* which also has a well developed imbricate microsculpture, but differs from it by having a unicolorous body and the lateral margins of the pronotum which are evenly arcuate (compare Fig. 63 & 64). A few light brown specimens from West Island have two poorly developed maculae on the elytra like those seen in *L. nitens* (Fig. 3).

This species is restricted to the Three Kings Islands and has been collected from various plants and their flowers including grasses and tussocks, *Cordyline*, *Kunzea* (= *Leptospermum*) *ericoides*, *Muehlenbeckia*, *Myoporum laetum*, and *Mertya*. The gut of one female specimen was



packed with fungal spores and hyphae, and a male contained what could be plant matter, indicating that this species may be opportunistic and saprophagous.

**Material examined.** Holotype and 230 paratypes. **Holotype** (deposited in NZAC). Three Kings Is, North East I, 1 Dec 1983, J. C. Watt, beating *Meryta*, Duplicate specimens in alcohol, HOLOTYPE, desig. R. Leschen, 2001 [red label]. **Paratypes** (all NZAC except where noted). **TH.** Three Kings Is. **Great Island:** 5, 3 Jan 1963; 44, Nov 1970, beating at night; 10, Nov 1970, at night, G Kuschel, G. W. Ramsay, or J. C. Watt (5 each in MONZ and OMNZ); 85, Castaway Camp, Nov 1970, G. Kuschel or G. W. Ramsay; 1, same label except, suction collection, G Kuschel; 3, same label except, flowering *Leptospermum*, J. C. Watt; 5, Tasman Valley, Nov 1970, G. W. Ramsay or J. C. Watt; 1, same label except, beating at night, J. C. Watt; 5, same label except, *Cordyline* flowers, J. C. Watt; 5, Lighthouse Bush NZMS 260 L01 316827, 5.xii.1996, J. W. M. Marris, beaten from *Kunzea* (LUNZ); 2, same label except, 8.xii.1996, general beating (LUNZ); 1, Castaway Camp, NZMS 260 L01 319829, 9.xii.1996, J. W. M. Marris, ex litter from bird-burrowed *Kunzea* forest (LUNZ); 1, Tasman Valley, NZMS 260 L01 316823, 7–10.xii.1996, J. W. M. Marris, ex yellow pan trap in *Kunzea* forest (LUNZ); 4, 27 Nov 1983, C. F. Butcher, sweeping *Leptospermum ericoides* and *Muehlenbeckia*; 1, 27 Nov 1983, C. F. Butcher, ex *Myoporum laetum*; 2, 30 Nov 1983, C. F. Butcher, beating plants; 1, Castaway Saddle, 30 Nov 1983, J. C. Watt, beating at night; 2, Tasman Valley, 2 Dec 1983, J. C. Watt, under bark dead *Leptospermum*; 1, 30 Nov 1983, C. F. Butcher; 2, saddle, sweeping from Tussock, *Scirpus-Carex*, 2 Jan 1953, J. S. Edwards, AMNZ 2947029471 (AMNZ); 2, saddle, under prostrate *L. scoparium* scrub, 2 Jan 1953, J. S. Edwards, AMNZ 29472–29473, (AMNZ); 2, Tasman Valley, sweepings from grasses and tussock, 31 Dec 1952, J. S. Edwards, AMNZ 29474–29475 (AMNZ); 5, same data except, sweeping *L. ericoides*, AMNZ 29476 (3) and 29477 (2) (AMNZ); 1, eastern arm, sweeping ground layer, 1 January 1953, J. S. Edwards; AMNZ 29478 (AMNZ); 1, beating kanuka by depot, 10 May 1946, E. G. Turbott; AMNZ 29480 (AMNZ). **North East Island:** 6, same label as Holotype. **South West I:** 10, 26 Nov 1983, J. C. Watt, beating *Meryta* forest; 15, Nov 1970. **West I:** 2, 29 Nov 1983, C. F. Butcher; 6, 28–29 Nov 1983, J. C. Watt, beating.

**Distribution** (Map 5). Three Kings Islands only.

TH / – / –.

**Etymology.** From the Latin word, *borealis*, referring to its distribution in northern New Zealand.

### ***Loberus depressus* (Sharp)**

Fig. 20, 44, 64, 76, Map 6

*Telmatophilus depressus* Sharp, 1876: 28.

*Loberus depressus* (Sharp, 1876). Combination by Watt (1982: 301).

**Diagnosis.** Body usually light to dark brown with infusate elytra (elytra may be unicolorous), body with obvious microsculpture and subglabrous (except elytra glabrous), vestiture of very widely scattered short erect setae; mandible with two apical teeth; median carina of mentum absent; genal spines acute; transverse gular line weakly developed; supraocular line well developed above eye; anterior prosternal margin smooth; pronotal carina slightly undulate and slightly narrowed at base; pronotum at base slightly depressed; cuticular glandular ducts in bead; procoxal cavities internally open; edge of hypomerion smooth; mesoventral cuticular glandular ducts present; metaventral pores present; precoxal lines present and impunctate; metepisternal ctenidium present; submetacoxal lines present; spermatheca elongate, accessory gland present; tarsomere 1 subequal to tarsomere 2; tarsomere 2 lobed; elytron striate, with 9 striae; elytron slightly explanate; wing present.

**Description.** With the characters for the genus and in the diagnosis. Length 2.15–2.48 mm, mean = 2.28 (n = 12). Colour of body variable, yellow brown to dark chocolate-brown, with elytron infusate and brown near scutellum and along sides, legs and antennae lighter, metasternum and sometimes abdomen darker; or, body dark brown with pale-yellow epipleuron with paler legs and mouthparts; or completely unicolorous dark brown to black; funicle, tibia, tarsi, and sometimes the mouthparts pale. Punctuation dense, average width of puncture 1 µm; most of the body covered with imbricate microsculpture, absent from elytra and strongly developed on vertex of the head and pronotum. Body relatively flattened with dorsal setae very short and widely scattered, erect with average length of elytral setae 4 µm; ventral setae longer and decumbent, average length of abdominal setae 5 µm. Head moderately punctate, punctures of vertex separated by about 1–3 diameters, punctures absent on gula, punctures present behind the eye. Eye prominent, strongly faceted, 8–9 facets at greatest length, ocular setae present. Antenna moderately elongate, extending slightly beyond edge of pronotum; antennomere relative lengths 8 : 7 : 7 : 5 : 6 : 5 : 6 : 4 : 6 : 6 : 9. Pronotum widest at middle and narrowest at base, about 0.82x as long as wide (pronotal length/maximum pronotal width = 0.74–0.97, mean = 0.82); depth = 0.19–0.29, mean = 0.19 mm; punctuation dense, punctures of disc separated by about 1–3 diameters. Abdominal depth = 0.25–0.48 mm, mean = 0.32. Elytra about 1.49x as long as wide (elytral length/maximum elytral width = 1.33–1.61, mean = 1.49) and

3.25x as long as pronotum (elytral length/pronotal length = 3.15–3.45, mean = 3.25); 9 striae present with 1 punctate and confluent with sutural stria, 2–8 present to about apical 1/6 or 1/7, 8 starting slightly beyond humerus, 9 confluent with epipleural fold and in many specimens bifurcating at apical 1/6; strial punctures separated by 0.3 diameters. Metaventrite with subcoxal lines well developed; punctation fine on disc, punctures on sides separated by 2–3 diameters. Abdomen with internal calli on ventrites 1–4, ventrites lacking punctures.

Aedeagus with separate biflagellate struts 3.5x length of median lobe; median lobe with hook-like apex, internal sac approximately 2.5x length of struts; sclerotised ejaculatory duct present, internal sac with weak median symmetrical sclerites. Paramere 8x longer than wide, with 10 minor setae and 7 major setae.

Gonocoxite 7x longer than width at middle, campaniform sensillae relatively dense, apex with 7 major setae, gonostyle bearing 5 setae (central one elongate).

**Type material examined.** Holotype: *Telmatophilus depressus* Type D. S. N. Zeal. / Type H.T. [red circle] / Sharp Coll. 1905-313 (BMNH).

**Material examined.** Holotype plus 190 non-type specimens — see Appendix 3 for collection details of specimens examined.

**Distribution** (Map 6). Throughout New Zealand.

ND, AK, BP, HB, WA, WN / NN, MB, MC, SC, DN.

**Comments.** This species can be distinguished from all other New Zealand erotylids by the prothorax with a sinuate lateral margin and imbricate microsculpture on the pronotum (Fig. 64). The infusate elytron is also characteristic of the species, though this colour pattern is not present in all specimens. It most closely resembles *L. borealis* (see comments for that species).

This is a very widespread and variable species that has been collected from various plants (Kuschel 1990), but is clearly more commonly associated with *Cordyline australis* as suggested by Hudson (1934) in lower altitudes of the North and South Islands. The exact adult diet is unclear because the guts of dissected specimens were empty.

Two subfossil pronota and three elytra of this species were collected from surface ponding habitats alongside the Awatere Fault (KA) dated at 13 kaBP (M. Marra, pers. comm.).

### ***Loberus nitens* (Sharp)**

Fig. 3, 25, 45, 56, 57, 77, Map 7

*Telmatophilus nitens* Sharp, 1876: 70.

*Loberus nitens* (Sharp, 1876). Combination by Bruce (1952b: 171).

**Diagnosis.** Body usually light to dark brown with maculate elytra, body with weak microsculpture and somewhat shining, vestiture of very short suberect and decumbent setae; mandible with two apical teeth; median carina of mentum absent; genal spines absent; transverse gular line weakly developed; supraocular line present above eye; anterior prosternal margin smooth; pronotal carina slightly undulate and edge smooth; pronotum at base slightly depressed; cuticular glandular ducts in bead; procoxal cavities internally open; edge of hypomerion smooth; mesoventral cuticular glandular ducts present; metaventral pores absent; precoxal lines absent; metepisternal ctenidium present; submetacoxal lines present but very short; spermatheca oval, accessory gland present; tarsomere 1 subequal to tarsomere 2; tarsomere 2 lobed; elytron striate, with 9 striae; elytron slightly explanate; wing reduced to a broad flap.

**Description.** With the characters for the genus and in the diagnosis. Length 1.67–2.30 mm, mean = 2.01 (n = 12). Colour of body variable, brown, orange, or red-brown, elytron bimaculate (one macula in basal 1/4, the other in the apical 1/4) with yellow to orange or red maculae, mouthparts, funicle, and legs light to yellow-brown. Punctation dense, average width of puncture 1 µm (those of venter larger); most of the body covered with weak microsculpture of points and meshes, absent from elytra. Body relatively convex with dorsal setae relatively short, decumbent (with scattered erect setae on the elytra) with average length of elytral setae 4 µm; ventral setae longer and decumbent, average length of abdominal setae 6 µm. Head moderately punctate, punctures of vertex separated by about 1–1.5 diameters, punctures present on gula and behind the eye. Eye prominent, strongly faceted, 7–9 facets at greatest length, ocular setae present. Antenna moderately elongate, extending slightly beyond edge of pronotum; antennomere relative lengths 9 : 6 : 6 : 5 : 7 : 5 : 6 : 4 : 6 : 6 : 8. Pronotum widest at middle, about 0.78x as long as wide (pronotal length/maximum pronotal width = 0.72–0.93, mean = 0.78); depth = 0.23–0.38, mean = 0.32 mm; punctation dense, punctures of disc separated by about 0.51 diameter. Abdominal depth = 0.35–0.48 mm, mean = 0.42. Elytra about 1.41x as long as wide (elytral length/maximum elytral width = 1.12–1.78, mean = 1.49) and 2.62x as long as pronotum (elytral length/pronotal length = 1.90–2.75, mean = 2.62); 9 striae present with 1 punctate and confluent with sutural stria, 2–8 present almost to apex, 7 starting slightly beyond humerus, 9 confluent with epipleural fold bifurcating at apical 1/3–1/4; strial punctures separated by 0.5 diameters. Metaventrite without subcoxal lines; punctation strong on disc, punctures on sides separated by 0.5–1 diameter. Abdomen with internal calli on ventrites 1–4. Abdomen lacking punctation on ventrites.

Aedeagus with separate biflagellate struts 3.8x length of median lobe, shape of median lobe as in *L. borealis*, internal sac approximately 3/4 length of struts (or struts 1.6x its length); sclerotised ejaculatory duct present, internal sac with median asymmetrical sclerites (though weakly sclerotised). Paramere 9x longer than wide, with 9 or 12 minor setae and 14 major setae (apex with 1 or 2 minor setae on dorsal or left paramere).

Gonocoxite 7x longer than width at middle, campaniform sensillae relatively dense, apex with 9 major setae, gonostyle bearing 5 setae (central one elongate).

**Type material examined.** Holotype: *Telmatophilus nitens* Type D. S. N. Zeal. / Type H.T. [red circle] / Sharp Coll. 1905-313 (BMNH).

**Material examined.** Holotype and 785 non-type specimens — see Appendix 3 for collection details of specimens.

**Distribution** (Map 7). North Island and northern South Island.

ND, AK, CL, BP, WN / SD, NN.

**Comments.** This species is perhaps the most common erotyloid in New Zealand, found mainly in the North Island and the northern portion of the South Island. *Loberus nitens* can be distinguished from all other species by the quadrimaculate elytra and glabrous body with relatively short setae. *Loberus nitens* and *L. watti* are similar, having the same colour pattern and pronotal shape, but the elytral setae of *L. watti* are markedly longer.

*Loberus nitens* is common throughout its range and has been taken from *Carmichaelia*, *Coprosma*, *Melicytus*, *Pittosporum*, and *Senecio* by Watt (1962, 1982); Kuschel (1990) reported it from coastal cliff plants (*Gahnia*, *Phormium*, and grasses) in Northland and Auckland. Hudson (1934) stated that *L. nitens* was abundant in the flowers of speargrass (*Aciphylla squarrosa*) in Wellington. I have examined a large series of this species collected from the introduced weed boneseed (*Chrysanthemoides monilifera*) in the Nelson area (collected by C. J. Winks) and additional hosts are *Hymenanchera*, *Muehlenbeckia*, *Xeronema*, and *Metrosideros*. A few specimens have been taken from the nests of birds and sandy beaches, probably in association with roots of dune plants. The guts of dissected specimens included fungal spores and possibly hyphae (2 specimens), and pollen (1 specimen). Some specimens had guts that were packed with unidentified particulate matter suggesting that the species is opportunistic, saprophagous, and may feed on a variety of foods.

### ***Loberus watti*, new species**

Fig. 26, 46, 52, 65, 78, 88, Map 8

**Diagnosis.** Body light to dark brown with maculate elytra, body lacking microsculpture, and shining, vestiture of long suberect setae; mandible with two apical teeth; median carina of mentum absent; genal spines absent; transverse gular line weakly developed; supraocular line absent; anterior prosternal margin smooth and slightly undulate; pronotal carina smooth; pronotum at base slightly depressed; cuticular glandular ducts in bead; procoxal cavities internally open; edge of hypomerion smooth; mesoventral cuticular glandular ducts present (microtubulate); metaventral pores absent; precoxal lines absent; metepisternal ctenidium present; submetacoxal lines present; spermatheca elongate, accessory gland present; tarsomere 1 equal to tarsomere 2; tarsomere 2 lobed; elytron striate, with 9 striae; elytron slightly explanate; wing reduced to a broad flap.

**Description.** With the characters for the genus and in the diagnosis. Length 1.73–2.25 mm, mean = 2.19 (n = 12). Colour of body brown (light brown in some specimens) with elytron bimaculate with yellow to orange-brown maculae (one in basal 1/4, the other in the apical 1/4); mouthparts, funicle, epipleuron, and legs light to yellow-brown. Punctuation dense, average width of puncture 1 µm (those of venter slightly larger); body lacking weak microsculpture. Body relatively convex with dorsal setae relatively long, suberect with average length of elytral setae 8 µm; ventral setae shorter and decumbent, average length of abdominal setae µm. Head moderately punctate, punctures of vertex separated by about 1–1.5 diameters, punctures present on gula and behind eye. Eye prominent, strongly faceted, 8–9 facets at greatest length, ocular setae present. Antenna moderately elongate, extending slightly beyond edge of pronotum; antennomere relative lengths 8 : 5 : 6 : 4 : 5 : 4 : 5 : 4 : 7 : 7 : 8. Pronotum widest at middle, about 0.74x as long as wide (pronotal length/maximum pronotal width = 0.67–0.86, mean = 0.74); depth = 0.19–0.38, mean = 0.28 mm; punctuation dense, punctures of disc separated by about 0.5 diameter. Abdominal depth = 0.35–0.53 mm, mean = 0.44. Elytra about 1.49x as long as wide (elytral length/maximum elytral width = 1.08–1.64, mean = 1.49) and 2.40x as long as pronotum (elytral length/pronotal length = 1.70–2.66, mean = 2.40); 9 striae present with 1 punctate and confluent with sutural stria, 2–8 present almost to apex, 7 starting slightly beyond humerus, 9 confluent with epipleural fold bifurcating at apical 1/3; stria punctures separated by 0.3 diameter. Metaventrite with subcoxal lines; punctuation well developed on disc, punctures on sides separated by 1 diameter. Abdomen with internal calli on ventrites 1–4. Abdominal punctuation of

ventrites moderately well developed on disc, punctures on sides separated by about 1 diameter.

Aedeagus with separate biflagellate struts 3.8x length of median lobe, internal sac approximately 1/2 length of struts, shape of muscular tendon as in *L. anthracinus* and with a forked apex; sclerotised ejaculatory duct present, internal sac with median symmetrical sclerites (weakly sclerotised). Paramere 9x longer than wide, with 6 major (plus 2 shorter apical setae) and 11 minor setae; dorsal parameres and 7 major (plus 3 shorter apical setae) and 8 minor setae on ventral paramere (apex and shaft setae differ in length).

Gonocoxite 7x longer than width at middle, campaniform sensillae relatively dense, apex with 7 major setae, gonostyle bearing 5 setae (central one elongate).

**Material examined.** Holotype and 194 paratypes.

**Holotype** (NZAC). TH Three Kings Is, West I, 28 Nov 1983, C. F. Butcher, plants and rushes litter 83/120.

**Paratypes** (all NZAC except where noted). **Great Island:** 96, Tasman Valley, Nov 1970, litter, G. Kuschel (5 each in LUNZ, MONZ, and OMNZ); 8, Castaway Camp, Nov 1970, G. Kuschel; 33, same except, litter; 1, same except, nest, J. C. Watt; 7, same except, soil, G. Kuschel; 19, NZ, Nov 1970, on grass at night, J. C. Watt; 2, Nov 1970, *Hebe*, J. McBurney; 11, 28–30 Nov 1983, C. F. Butcher, pan traps shore and coastal forest; 1, Nov 1976, NZ. Ent. Div. Exp., J. C. Watt; 1, South East Bay, *Arthropodium* slope, 10 m, 23 Nov–1 Dec 1983, J.C. Watt, pit trap 83/133; 1, Tasman Valley, sweepings from grasses and tussock, 31 Dec 1952, J. S. Edwards; AMNZ 28081 (AMNZ); 2, saddle, sweeping from tussock, *Scirpus/Carex*, 2 Jan 1953, J. S. Edwards; AMNZ 2808283 (AMNZ); 4, NW Bay, 15.I.1951, E. G. Turbott, leaf litter under ngaio and karaka at site of *Placostylus bollonsi caperatus* colony, P/S 1 L8734, AMNZ 32833–36 (AMNZ). **Princess I:** 3, Hinemoa, Nov 1983, C. F. Butcher, nesting material 83/131. **South West I:** 2, TH Three Kings Is, 25 Nov 1983, C. F. Butcher, sweeping; 1, 25 Nov 1983, C. F. Butcher, on stem of *Mariscus*; 1, 26 Nov 1983, C. F. Butcher, sweeping *Myoporum laetum*, *Coprosma*, and *Arthropodium* near shore; 1, 26.ii.1997, collector unknown, ex litter from various sites mostly broadleaf forest shrubland (LUNZ).

**Distribution** (Map 8). Three Kings Islands only.

TH / - / -.

**Comments.** This species is similar in body form and colour to *L. nitens*, and differs mainly by the presence of long elytral setae.

*Loberus watti* is restricted to the Three Kings Islands and has been collected mainly from leaf litter and by beating various plants, including *Mariscus*, *Myoporum*, *Coprosma*,

*Arthropodium*, and sedges and rushes (*Scirpus* and *Carex*). Some specimens have been collected in bird nests of *Larus*. The guts of dissected specimens included mainly unidentifiable matter, fungal spores (including a single septate fungal spore) and hyphae, and possibly plant tissue. These observations suggest that the species is saprophagous and opportunistic.

**Etymology.** Named in honour of Charles Watt for his contributions to the knowledge of world and New Zealand Coleoptera, and as collector of many of the specimens on which this new species is based.

## Languriinae: Hapalipini

### *Hapalips* Reitter

Fig. 5, 21, 72, 81, 85, 89, 94

*Hapalips* Reitter, 1877: 122. Type species: *Hapalips mexicanus* Reitter, 1877: 124, 128 (designated by Sen Gupta, 1968: 6).

*Loberina* Grouvelle, 1902: 485. Type species: *Loberina taprobanae* Grouvelle, 1902: 485 (by monotypy). First synonymised by Grouvelle, 1919: 66.

*Isolanguria* Lea, 1929: 240. Type species: *Hapalips investigatus* Leschen & Wegrzynowicz, 1998: 233 (= *Isolanguria fusca* Lea, 1929: 241, nec *Hapalips fuscus* Reitter, 1877) (by monotypy).

Subgenus *Cavophorus* Sen Gupta, 1968: 8. Type species: *Hapalips fuscus* Reitter, 1877: 124, 127 (original designation).

Subgenus *Xenosceloides* Sen Gupta, 1968: 8. Type species: *Xenoscelis prolixus* Sharp, 1876: 26 (original designation).

**Diagnosis.** With the characters of the tribe Hapalipini. Antennal insertion hidden in dorsal view; cephalic glandular ducts absent; stridulatory files absent; anterior angles of pronotum poorly developed; anterior prosternal margin serrate; pronotum at base flat or convex; pronotal cuticular glandular ducts present and microtubulate; prosternal glandular ducts absent; procoxal cavities slightly closed behind by hypomerion; mesoventral cuticular glandular ducts absent (scattered and ungrouped microtubulate ducts present); mesepisternal pocket absent; metaventral glandular flecks present; precoxal lines punctate; intercoxal process of ventrite 1 narrow; gonostyle present; empodium with 2 setae; elytral length 3x greater than width.

**Distribution.** Widespread (57 species, 1 species in New Zealand).



***Hapalips prolixus* (Sharp)**

Fig. 5, 21, 72, 81, 89, Map 3

*Xenoscelis prolixus* Sharp, 1876: 26.

*Hapalips prolixus* (Sharp, 1876: 26). Combination by Champion, 1913: 96.

**Diagnosis.** Body strongly elongate, dorsoventrally compressed; mandible with two apical teeth; gular line relatively shallow; gular fovea absent; supraocular line absent; temples present and somewhat glabrous and lacking setae; stridulatory files absent; pronotal width subequal to pronotal length; pronotal carina explanate with well developed rim, dentate (especially at base), with tooth present at posterior corner; pronotal pits present; procoxal cavities internally open; edge of hypomeron notched; metaventral notch present; abdominal glandular ducts absent; spermatheca somewhat elongate with a deep apical pit extending about 2/3 the length of the bulb; scutellary striole present; humeral spine present; elytra narrowly explanate; wedge cell absent.

**Description.** With the characters listed for the genus and the diagnosis. Length 3.55–4.05 mm, mean = 4.05 ( $n = 12$ ). Colour of body dark to light brown, ventral portions, including epipleura and appendages often paler. Punctuation dense over entire body. Body setae long, decumbent, with a few widely scattered erect setae, average length of seta 6–8  $\mu\text{m}$ . Head strongly punctate, punctures of vertex about 1  $\mu\text{m}$  separated by about 0.5–1 diameters, alveolate punctures of 2  $\mu\text{m}$  present more posteriorly and along sides and lateral areas of gena and postmentum, becoming more transverse at occiput. Eye well developed, moderately coarsely faceted, 8–12 facets at greatest length; ocular setae present and well developed. Antenna relatively short, extending to middle of pronotum; antennomere relative lengths 8 : 5 : 6 : 4 : 4 : 4 : 4 : 4 : 6 : 6 : 11. Pronotum more or less parallel-sided, serrate, gradually narrowed in posterior 1/6, about 0.96x as long as wide (pronotal length/maximum pronotal width = 0.90–1.08, mean = 0.96), longer in males and also with well developed anterior bead; 8 lateral teeth present, one in anterior half at apical 1/4; the remaining in posterior half with posterior 2 more prominent; depth = 0.25–30, mean = 0.25 mm; punctuation dense, punctures ranging from 1 (disc) to 2 (margins)  $\mu\text{m}$  and separated of disc by about 0.5–0.7 diameters, median longitudinal “line” apunctate. Elytra about 2.57x as long as wide (elytral length/maximum elytral width = 2.35–2.80, mean = 2.57) and 3.39x as long as pronotum (elytral length/pronotal length = 3.33–3.44, mean = 3.39); 9 striae present, 1 (scutellary striole) sometimes poorly developed and when well developed present to level of basal 1/6, 2–9 well developed to apical 1/8, 9 split at apical 1/4 and confluent with epipleural fold, punctures of 1  $\mu\text{m}$  separated by 0.5 diameters. Prosternum punctate, weaker at disc and stronger at sides. Metaventrite

lacking subcoxal lines; punctuation moderately coarse on disc, stronger and larger at sides and separated by 0.3 diameter. Abdominal depth = 0.35–0.45 mm, mean = 0.40. Abdomen with short subcoxal lines; internal calli present on ventrites 1–3; punctuation of ventrites coarse on disc especially ventrites 1 and 2, punctures separated by 1–2 diameters on ventrite 1; imbricate microsculpture present; male with curved ligulate process at apex of ventrite 5.

Aedeagus with biflagellate strut 5.75x longer than median lobe, parameres elongate, about 5x long as wide, and bisetose apically, and two elongate setae lateral, subsetae absent. Internal sac spinose, length of internal sac about 1/2 length of struts, flagellum present and not projecting anteriorly from sac.

Gonocoxite and styli with well developed short apical setae, coxite with scattered short setae.

**Type material examined** (BMNH). *Xenoscelis prolixus* Type, D.S., N. Zeald. [hand]; Round, red bordered “TYPE” label. / Sharp Coll. 1905-313/Belongs to *Hapalips* Reitt. [hand, in pencil] / Tr. Ent. Soc. L. 1913. det. Champion / LECTOTYPE *Xenoscelis prolixus* Sharp, Desig. by R. Leschen 2001 (blue label) (here designated, so as to assure correct and consistent application of the name in the future). *Xenoscelis prolixus* Type, D.S., N. Zeald. [hand]/ Sharp Coll. 1905-313 / Auckland [hand, dark red oval label] / PARALECTOTYPE *Xenoscelis prolixus* Sharp, Desig. by R. Leschen 2001 [blue label]. *Xenoscelis prolixus* Type, D.S., N. Zeald. [hand] / Sharp Coll. 1905-313 / PARALECTOTYPE *Xenoscelis prolixus* Sharp, Desig. by R. Leschen 2001 [blue label].

**Material examined.** Lectotype and paralectotypes plus 460 non-type specimens — see Appendix 3 for collection details of specimens examined.

**Distribution** (Map 3). North Island, and northern and western South Island.

ND, AK, CL, WO, BP, TK, WN / SD, NN, BR.

**Comments.** This is one of the largest and most distinct species of the New Zealand erotylids, and can be distinguished from all of the other species by its flattened, elongate parallel-sided body, antennal insertions hidden in dorsal view, and male with a rather robust pronotum and a curved ligulate process on apex of ventrite 5. *Hapalips prolixus* is quite widespread and present in the North Island and mainly in northern parts of the South Island.

Sharp (1876) described this species based on “4 or 5 specimens” from Auckland and Tairua and it was noted to have been collected from *Cyathea dealbata*. Only three specimens were located in the type series (BMNH), and one of these was selected as a lectotype.

*Hapalips prolixus* has been collected on *Rhopalostylis sapida*, *Cordyline banksii*, *Cyathea dealbata*, *Cyathea*



*medullaris*, and *Dicksonia squarrosa* in Auckland by Kuschel (1990) and other localities by Hudson (1934). Watt (1961) considered this species as a possible obligate associate of nikau palm. Additional plant records for this species are *CollospERMUM*, *Leptospermum*, and *Phormium*. The guts of dissected specimens were packed with mainly unidentifiable material, but there were numerous fungal spores and hyphae, suggesting this species is a fungus feeder or saprophagous.

The aedeagus, wing, and larva of *Hapalips prolixus* were illustrated and described by Sen Gupta (1968a) who placed this species in its own subgenus, *Xenosceloides*, based on the absence of an wedge cell in the hind wing, flattened body form, and several other features. *Hapalips prolixus* is similar in form to other members of the genus found in Australasia.

## Cryptophilinae: Cryptophilini

### Genus *Cathartocryptus* Sharp

Fig. 7, 22, 47, 86, 99

*Cathartocryptus* Sharp, 1886: 392. Type species: *Cathartocryptus obscurus* Sharp, 1886: 393 (= *Paramecosoma maculosa* Broun, 1881: 670) (by monotypy).

*Xenoscelinus* Grouvelle, 1910: 143. Type species: *Xenoscelinus malaicus* Grouvelle, 1910: 144 (by monotypy). First synonymised by Leschen & Wegrzynowicz, 1998: 231.

**Diagnosis.** With the characters of the subfamily Cryptophilinae. Frontoclypeal suture absent; subapical serrations present on mandible; mentum without median carina; length of labial palpomere greater than its width and not subulate; width of ligular membrane equal to the sclerite; subocular cuticular glandular ducts absent; gular line absent; supraocular line present or absent; stridulatory files absent; prothoracic margin widest in its apical half (just slightly so in *C. maculosa*); anterior pronotal angles well developed; anterior prosternal margin serrate; pronotal carinae undulate with undulations widely separate; pronotum flat at base; pronotal cuticular glandular ducts present; length of prosternum in front of coxae relatively elongate (at least 2x the length of the procoxae); procoxal cavities externally closed; trochantal notch absent; procoxal rests absent; mesoventral cuticular glandular ducts present (a small carina is present in this area in a species from Brunei); mesometaventral junction straight-line type; width of mesoventral process greater than width of mesocoxa; metaventral pores absent; precoxal lines present and impunctate; metepisternal ctenidium present; ventrites 1 and 2 free; abdominal cuticular glandular ducts absent (present as small pores); elytra with punctate striae; spicu-

lum gastrale broad and symmetrical; gonocoxite dilated with large style of about equal size; length of spiculum ventrale to level of ventrite 4; spermatheca elongate and lacking apical pit, duct coiled; length of tarsomere 1 equal to tarsomere 2; tarsomeres 2 and 3 not lobed; empodium with 2 setae; tarsal claws notched at base; hind wing present.

**Remarks.** The history of this genus, with regard to the name and placement of *C. maculosus*, is a bit confusing. The first name for this species is *Paramecosoma maculosa* Broun, 1881, and the combination *Cathartocryptus maculosus* was listed by Kuschel (1990). Sharp (1886) independently named the same species *Cathartocryptus obscurus* and originally included it in the family Cucujidae. It was later transferred to Languriidae (Cladoxeninae) by Lefkovitch (1961). Meanwhile, Grouvelle (1910) described the genus *Xenoscelinus* for a Sumatran species he placed in Erotylidae. The generic name was used by Sen Gupta & Crowson (1971) who placed the species, *Xenoscelinus maculosus*, in Cryptophilinae (Xenoscelinini). Leschen & Wegrzynowicz (1998) noted that *Cathartocryptus* was congeneric with *Xenoscelinus*, though its taxonomic status was known previously but unaccounted for in the literature (Sen Gupta & Crowson 1971, Klimaszewski & Watt 1997).

**Distribution.** Africa, Asia, Australasia (8 species, 1 in New Zealand).

### *Cathartocryptus maculosus* (Broun)

Fig. 7, 22, 47, 86, 99, Map 1

*Paramecosoma maculosa* Broun, 1881: 670.

*Xenoscelinus maculosus* (Broun, 1881: 670). Combination by Bruce (1943: 60).

*Cathartocryptus obscurus* Sharp, 1886: 392.

*Cathartocryptus maculosus* (Broun, 1881: 670). Combination by Kuschel (1990: 31).

**Diagnosis.** Body light to dark brown with elytral maculae; head not strongly transverse; supraocular line present; terminal antennomere slightly narrower than penultimate; mandible apically bidentate; pronotum slightly transverse and only slightly widened apically; sides of elytron narrowly explanate, disc with weakly punctate striae.

**Description.** With the characters listed for the genus and the diagnosis. Length 1.61–2.00 mm, mean = 1.82 (n = 12). Colour of body dark to light brown, mouthparts, legs, and sometimes antenna light brown, head and pronotum typically darker, pronotum sometimes with a discal macula, elytron light brown usually with mediolateral and subapical maculae, sometimes a fourth posterior macula is present near the suture. Body surfaces subglabrous, entirely covered with imbricate microsculpture. Body setae very short

and decumbent, average length of dorsal setae about 2 µm; ventral setae longer, especially on abdomen. Head moderately punctate, punctures of vertex separated by about 1 diameter, fine punctures present on gula separated by 1–2 diameters. Eye prominent, finely faceted, 11 facets at greatest length, ocular setae present. Antenna relatively long, extending to posterior edge of pronotum; antennomere relative lengths 6 : 4 : 4 : 3 : 3 : 3 : 3 : 3 : 5 : 5 : 6. Pronotum slightly transverse and widest at apex, about 0.73x as long as wide (pronotal length/maximum pronotal width = 0.73–0.86, mean = 0.70); depth = 0.19–0.23, mean = 0.19 mm; slightly undulate at side; punctation dense like that on head. Elytra about 1.49x as long as wide (elytral length/maximum elytral width = 1.41–1.64, mean = 1.49) and 2.80x as long as pronotum (elytral length/pronotal length = 2.82–2.71, mean = 2.80); 4–5 weakly impressed striae present on dorsal surfaces, punctures separated by about 0.5–1 diameters. Abdominal depth = 0.23–0.38 mm, mean = 0.28. Metaventrite without subcoxal lines; punctation fine on disc, punctures on sides separated by 1 diameter. Abdomen with internal calli on ventrites 1–4; ventrite 1 with subcoxal lines; punctation of ventrites fine, absent in anterior portions of ventrites 2–5.

Aedeagus with internal sac longer than biflagellate struts, flagellum present, struts about 4x length of median lobe. Parameres 3x as long as wide, multisetose.

**Type material examined.** *Cathartocryptus obscurus*: Type D.S. Picton [card-mounted specimen and handwritten] / Type [round label with red border] / Picton New Zealand Helms. / Sharp coll. 1905-313. Note that the following material was examined at the time of description: 1, same as Holotype [lacking type label]; 1, same, but Picton Helms. [card-mounted specimen and handwritten] / Picton New Zealand Helms; 1, same, but Picton New Zealand Helms. 1884.

*Paramecosoma maculosa*: 1169 [green label] / Parua [hand] / New Zealand Broun Coll. Brit. Mus. 1922-482 / *Paramecosoma maculosa* Broun, LECTOTYPE, Desig. Leschen 2001 [red label] (here designated, so as to assure correct and consistent application of the name in the future) (BMNH); 2 (together on plastic card), 1169 [green label] / Parua [hand] / New Zealand Broun Coll. Brit. Mus. 1922-482 / *Paramecosoma maculosa* [hand] / *Paramecosoma maculosa* Broun, PARALECTOTYPE, Desig. Leschen 2001 [yellow label] (BMNH).

**Material examined.** Type specimens (above) plus 42 non-type specimens — see Appendix 3 for collection details of specimens examined.

**Distribution** (Map 1). North Island and northern South Island.

ND, AK, CL, WO, BP, TK, GB, WI, WN / NN, BR, MB.

**Comments.** *Cathartocryptus maculosus* is an uncommon species that is widespread through the North Island and in the northern part of the South Island. It can be readily distinguished from all other New Zealand species by the small and flattened body form, maculae on the elytra, and pronotum that is widest in the apical half.

This species has been collected on *Dysoxylum spectabile* and dead branches in Auckland by Kuschel (1990) and new records are for *Beilschmiedia tawa* and *Coprosma robusta*. Some specimens have been found under bark. Guts of dissected specimens were packed with small dark fungal spores confirming that this species is mycophagous. If any New Zealand erotyloid species deserves special conservation status it is this one, because *C. maculosus* may be an indicator of special subcortical habitats that are presently uncommon.

*Cathartocryptus maculosus* may not be congeneric with other members of the genus because it differs in many features, mainly those listed in the diagnosis. However, the broad form of the ovipositor of the genus is unique supporting the placement of *C. maculosus* in the genus, and the elongate form may be primitive. The wing, thoracic ventrites, and ovipositor of *Cathartocryptus maculosus* were illustrated in Sen Gupta & Crowson (1971).

Broun (1881) described the species *Paramecosoma maculosa* from specimens collected from Parua (ND) and three specimens matching this description were located in the BMNH, one of which was selected as a lectotype. Later, Sharp (1886) described *Cathartocryptus obscurus* and stated that three specimens were examined: four specimens were examined in the BMNH, with a single Holotype designated by Sharp (see above). The fourth specimen listed above probably was an additional specimen not noted in the original publication (note that the first three specimens were not dated).

## Introduced Species

### Genus *Cryptophilus* Reitter

Fig. 8

*Cryptophilus* Reitter, 1874: 381. Type species: *Cryptophagus integer* Heer, 1841: 426 (subsequent designation by Chûjô, 1969: 277).

*Tomarops* Grouvelle, 1903: 343. Type species *Tomarops punctatus* Grouvelle, 1903: 343 (by monotypy). **New synonymy** (see page 42).

**Diagnosis.** With the characters of the subfamily Cryptophilinae. Frontoclypeal suture absent; mandible with three apical teeth; mandible lacking subapical serrations; mentum with median carina; labial palp subulate; length of labial palpomere greater than its width; subocular cuticular glandular ducts present; gular line present and

shallowly impressed; supraocular line present or absent; stridulatory files present as single broad file; prothoracic margins parallel-sided; anterior prosternal margin serrate; pronotal carinae serrate or dentate; pronotum convex at base; pronotal cuticular glandular ducts present; length of prosternum in front of coxae relatively short; procoxal cavities externally closed; trochantinal notch absent; procoxal rests present; mesoventral cuticular glandular ducts present; mesometaventral junction dicondylic; metaventral pores present; precoxal lines present and punctate; metepisternal ctenidium absent; ventrites 1 and 2 free; abdominal cuticular glandular ducts present; elytral punctation confused; spiculum gastrale symmetrical; gonocoxite dilated; length of spiculum ventrale to level of ventrite 3 or 4, spermatheca round with a apical pit, duct coiled; tarsomere 2 not lobed; tarsomere 3 lobed, not obscuring 4 from view; empodium with 1 seta; tarsal claws not notched at base; hind wing present.

**Distribution and notes.** Widely distributed (19 species, 1 introduced to New Zealand).

### *Cryptophilus integer* (Heer)

Fig. 8, Map 2

*Cryptophagus integer* Heer, 1841: 426.

*Cryptophilus integer* (Heer, 1841: 426). Combination by Heyden *et al.* (1883: 79).

**Diagnosis.** Body uniformly light brown; mandible with two apical teeth; length of labial palpomere subequal to its width; anterior pronotal angles well developed but not strongly prominent; pronotum not explanate; width of mesoventral process narrower than width of mesocoxa; metatrochanter of male prolonged into a distal tooth; length of tarsomere 1 greater than tarsomere 2, and subequal to 2 and 3 on metatarsus; elytra moderately explanate.

**Description.** With the characters listed for the genus and the diagnosis. Length 1.59–2.00 mm, mean = 1.88 (n = 7). Colour of body light brown, head and pronotum sometimes darker. Body surfaces subglabrous. Body setae moderately elongate and decumbent, average length of dorsal setae about 5 µm. Head strongly punctate, punctures of vertex separated by about 0.5 diameters, well developed punctures present on gula separated by 0.5–1 diameters; one broad stridulatory file present. Eye prominent, coarsely faceted, 8–10 facets at greatest length, ocular setae present. Antenna relatively long, extending to posterior edge of pronotum; antennomere relative lengths 5 : 4 : 5 : 2 : 4 : 3 : 3 : 3 : 4 . 5 : 4 . 5 : 5. Pronotum transverse and widest at middle; about 0.63x as long as wide (pronotal length/maximum pronotal width = 0.61–0.71, mean = 0.63); depth = 0.40–0.50, mean = 0.48 mm; evenly arcuate at side with fine teeth; punctation dense like that on head. Elytra

biseriate, about 0.66x as long as wide (elytral length/maximum elytral width = 0.60–0.76, mean = 0.66) and 1.66x as long as pronotum (elytral length/pronotal length = 1.26–3.00, mean = 1.66), punctures slightly larger than those on head and pronotum, not strongly impressed and separated by about 0.5–1 diameters. Abdominal depth = 0.51–0.60 mm, mean = 0.54. Mesoventrite lacking well developed coxal rests. Metaventricle without subcoxal lines; punctation moderately coarse on disc, stronger at side with punctures separated by about 0.75 diameter. Abdomen with internal calli on ventrites 1–4; ventrite 1 with subcoxal lines; punctation of ventrites generally fine, absent or weakly developed in anterior portions of ventrites 2–5.

Aedeagus with internal sac slightly shorter (about 1/6) than biflagellate struts, flagellum present, struts about 5.6x the length of median lobe. Parameres 10x as long as wide, multisetose with long setae.

Gonocoxite with two or three lateral setae, style well developed with apical setae.

**Material examined.** 17 specimens — see Appendix 3 for collecting details of specimens.

**Distribution** (Map 2). Auckland City area only.

AK / –.

**Comments.** This is a species found in many countries, and is associated commonly with stored products and found in other modified habitats (Hinton 1945, Booth *et al.* 1990; Delobel & Tran 1993). This species occurs in leaf litter and is associated with grass clippings and wood chips in the Auckland City area (S. Thorpe, pers. comm.). The gut of a single dissected male contained a septate fungal spore, a few crushed simple fungal spores, and unidentifiable matter.

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**APPENDIX 1:** Species dissected for this study. Slide-mounted specimens of examined BMNH material are indicated by an asterisk (\*). Distribution and other acronyms are as follows: f = female, m = male, ? = sex or distribution unknown, t = type species of genus; AS = Asia; AU = Australia; BR = Brasil and tropical South America ; CA = Central America; CH = Chile and Juan Fernandez Islands; EU= Europe; IN = Indonesia; JA = Japan; MA = Madagascar; ME = Middle East; NC = New Caledonia; NZ = New Zealand; PR = Pacific region; SA = South Africa; TA = Tropical Africa; NA = Canada and United States.

### BIPHYLLIDAE

*Diplocoelus rudis* LeConte (m, f; NA)  
*Gonicoelus* sp. (m; CA)

### CRYPTOPHAGIDAE

*Cryptophagus* sp. nr. *difficilis* Casey (m, f; NA)

### PHLOEOSTICHIDAE (Myriabolinae)

*Myriabola grouvelliana* Reitter (f; AU)  
*Myriabola* sp. 1 (m; AU)

### LAMINGTONIIDAE

*Lamingtonium binnaburens* Crowson (m, t; AU)  
*L. thayerae* Lawrence & Leschen (f; AU)

### EROTYLIDAE

#### Xenoscelinae

*Loberonotha olivascens* (Broun) (m, f, t; NZ)  
*Macrophagus robustus* Motschulsky (f, t; EU)  
*Othniocryptus* sp. (f; BR)  
*Protoloberus singularis* (Blackburn) (m, f, t; AU)  
*Xenocryptus tenebroides* Arrow (m, f, t; AU)  
*Xenoscelis deplanatus* Wollaston\* (m, f, t; EU)  
*Zavaljus brunneus* (Gyllenhal) (m, f, t; EU)  
Genus 1 sp. 1 (f; SA)  
Genus 1 sp. 2 (m; SA)

#### Pharaxonothinae

*Henoticonus triphylloides* Reitter (f; JA)  
*Leucohimatium elongatum* Erichson\* (f; m, EU)  
*Leucohimatium* sp. (m; ME)  
*Loberogosmus fasciatus* Kolenati (m, t; EU)  
*Pharaxonotha kirschi* Reitter (m, t; NA)  
*Pharaxonotha* sp. (f; NA)  
*Pharaxonotha* sp. (m; CA)  
*Pharaxonotha* sp. (m; IN)  
*Setariola sericea* Mulsant & Rey (f, t; EU)

### Loberinae

*Fitoa* sp. 1 (m; MA)  
*Fitoa* sp. 2 (f; MA)  
*Loberus anthracinus* (Sharp) (m, f; NZ)  
*L. borealis* Leschen (m, f; NZ)  
*L. depressus* (Sharp) (m, f; NZ)  
*L. guatemalensis* Sharp\* (m, f; CA)  
*L. humeralis* Reitter\* (m, f; CA)  
*L. impressus* LeConte\* (m, f, t; NA)  
*L. nitens* (Sharp) (m, f; NZ)  
*L. suturalis* Sharp\* (m; CA)  
*L. watti* Leschen (m, f; NZ)  
*Loberus* sp. 1 (m; NC)  
*Loberus* sp. 2 (f; NC)  
*Loberus* sp. 3 (f; NA)  
*Loberus* sp. 4 (m; CA)  
*Loberus* sp. 5 (f; CH)  
*Loberus* sp. 6 (m; CH)  
Genus nr *Loberus* sp. 1 (m; IN)  
Genus nr *Loberus* sp. 2 (m; IN)  
Genus nr *Loberus* sp. 3 (m; NC)  
*Loberolus agilis* Grouvelle (m, f, t; MA)  
*Paphezia detritophila* Zablotsky & Leschen (m, f, t; NC)  
*Paphezia* sp. 1 (m; NC)  
*Stenodina quadriguttata* Fairemaire (m, f, t; MA)  
*Telmatoscius claviger* Sharp\* (f, t; CA)

### Languriinae: Hapalipini

*Bolerus* sp. (f; IN)  
*B. minutus* (Fleutieux)\* (f, t; IN)  
*Hapalips cribricollis* Gorham\* (f; CA)  
*H. eichelbaumi* Grouvelle\* (f; TA)  
*H. filum* Reitter\* (m; CA)  
*H. fuscus* Reitter\* (f; CA)  
*H. grouvelli* Gorham\* (m; CA)  
*H. nitidulus* Champion\* (m; CA)  
*H. prolixus* (Sharp)\* (m, f; NZ)  
*H. scotti* Grouvelle\* (f; IN)  
*Hapalips* sp. 1 (m; CA)  
*Hapalips (Cavophorus)* sp. 2 (m; CA)  
*Hapalips* sp. 3 (f; NA)  
*Truquiella gibbifera* Champion (m, f, t; CA)

### Languriinae: Thalliselini

*Acryptophagus* sp. 1 (f; BR)  
*Acryptophagus* sp. 2 (m; CA)  
*Acryptophagus* sp. 3 (m; CA)  
*Platoberus latus* Sharp\* (?; t; CA)  
*Platoberus* sp. 1 (f; CA)  
*Platoberus* sp. 2 (m; CA)  
*Pseudhapalips* sp. 1 (m; BR)



*Pseudhupalips* sp. 2 (f; BR)  
*Thallisella crotchi* Gorham\* (f; CA)  
*Thallisella* sp. (m; BR)  
 Genus 1 sp. 1 (m; BR)

#### **Languriinae: Languriini**

*Anadastus harmandi* Villiers (f; JA)  
*Cladoxena maculata* Motschulsky\* (f; AS)  
*Crotchia hondurana* Gorham\* (f; CA)  
*Crotchia* sp. (m; BR)  
*Dasydactylus* sp. 1 (f; CA)  
*Dasydactylus* sp. 2 (m; CA)  
*Languria mozardi* Latreille (m; NA)  
*L. trifasciata* Say (f; NA)  
*Microlanguria jansoni* (Crotch)\* (f; t; JA)  
*Neoloberolus cursor* (Grouvelle) (m, f, t; BR)  
*Neoloberolus* sp. (f; CA)  
*Nomotus* sp. (m; CA)  
*Paracladoxena abundans* Arrow\* (m, t; AS)  
*P. bipustulata* Fowler\* (f; t; AS)  
*Penolanguria* sp. (f; TA)  
 Genus 1 sp. 1 (m; BR)

#### **Cryptophilinae: Empocryptini**

*Empocryptus* sp. 1 (f; BR)  
*Empocryptus* sp. 2 (m; CA)  
*Empocryptus* sp. 3 (f; CA)  
*Empocryptus* sp. 4 (f; BR)  
*Empocryptus* sp. 5 (m; BR)  
*Empocryptus* sp. 6 (m; BR)  
*Empocryptus ovalis* Sharp\* (f, t; CA)  
*Lepidotoramus grouvellei* Leschen (m, f, t; BR)  
*Lobosternum clavicorna* Reitter (m; CH)

#### **Cryptophilinae: Toramini**

*Atomarops curvitalis* Sasaji (f; AS)  
*Atomarops lewisi* Reitter (f, t; JA)  
*Loberoschema bimaculata* Reitter (m, t; CH)  
*Loberoschema* sp. 1 (m; CH)  
*Loberoschema* sp. 2 (f; CH)  
*Stengita* sp. 1 (m; CH)  
*Stengita* sp. 2 (f; CH)  
*Stengita* sp. 3 (f; CH)  
*Toramus hirtellus* (Shwarz) (m, f; NA)  
*Toramus* sp. 1 (f; CA)  
*Toramus* sp. 2 (f; CA)  
*Toramus* sp. 3 (f; CA)  
*Toramus* sp. 4 (f; CA)  
*Toramus* sp. 5 (f; CA)  
 Genus 1 nr *Loberoschema* sp. 1 (f; BR)  
 Genus 1 nr *Loberoschema* sp. 2 (m; BR)  
 Genus 2 nr *Loberoschema* sp. 1 (f; BR)  
 Genus 2 nr *Loberoschema* sp. 2 (f; BR)

#### **Cryptophilinae: Cryptophilini**

*Brachypterosa peckorum* Zablotty & Leschen, (m, f, t; PA)  
*Cathartocryptus maculosus* (Broun) (m, f, t; NZ)  
*Cathartocryptus* sp. (f; IN)  
*Cryptophilus integer* (Heer)\* (f, t; AS)  
*Cryptophilus* sp. 1 (m, f; AU)  
*Cryptophilus* sp. 2 (m, f; NA)  
*Cryptophilus* sp. 3 (m; AS)  
*Crowsonguptus mexicanus* Sharp\* (m, f; CA)  
*Crowsonguptus* sp. 1 (f; CA)  
*Crowsonguptus* sp. 2 (f; CA)  
*Crowsonguptus* sp. 3 (m; CA)  
*Loberopsyllus explanatus* Leschen & Ashe (m, f; CA)  
*L. oculus* Leschen & Ashe (m, f; CA)  
*L. traubi* Martins & Barrera (m, f; CA)

#### **Erotylinae: Dacnini**

*Cryptodacne* sp. 1 (m; NZ)  
*Dacne quadrimaculata* (Say) (f; NA)  
*Hoplepiscapha longicornis* Lea (f, t; AU)  
 Genus 1 sp. 1 (m; AU)

#### **Erotylinae: Encaustini**

*Aulachochilus* sp. 1 (m; AS)  
*Aulachochilus* sp. 2 (f; AS)

#### **Erotylinae: Tritomini**

*Lybanodes bicolor* Skelley (m; BR)  
*L. castaneus* Gorham (m, t; CA)  
*L. lescheni* Skelley (m; BR)  
*L. rostratus* Skelley (f; CA)  
*L. sasquatch* Skelley (m; CA)  
*L. stigmatus* Skelley (m; BR)  
*L. similis* Skelley (m; BR)  
*Tritoma atriventris* LeConte (f; NA)  
 Genus 1 sp. 1 (f; BR)

#### **Erotylinae: Megalodacnini**

*Megalodacne fasciatus* Fabricius (f; NA)

#### **Erotylinae: Erotylini**

*Brachysphaenus* sp. (m, f; BR)  
*Coccimorphus* sp. (m; BR)  
*Erotylus* sp. (f; BR)  
*Homoeotelus* sp. (f; BR)

#### **Uncertain Placement**

Genus 1 sp. 1 (m; AU)

## APPENDIX 2. Character state definitions and argumentation.

1. Frontoclypeal suture. (0) absent (Fig. 51), (1) present (Fig. 6). This character is coded as polymorphic in *Myriabola*, *Encaustini*, and *Neoloberulus*.
2. Shape of mandible. (0) "normal" (Fig. 56), (1) falcate (Fig. 8). The outer angle of the mandible forms a more or less straight line towards the apex in most languriines, but is more angulate in remaining taxa where the leading edge is perpendicular to the inner edge. This character is coded as polymorphic in *Paracladoxena* where the falcate form occurs in *P. bipustulata* Fowler and is normal in *P. abundans* Arrow.
3. Number of apical teeth of mandible. (0) two (Fig. 56, 58), (1) three. This is a very variable character. Sometimes in the same specimen where the mandibles are asymmetrical, e.g., some species of *Hapalips* and *Setariola*, the number of apical teeth is recorded from the right mandible. Sometimes secondary teeth are weakly produced (one specimen of *Platoberus*) or they are extraordinarily well developed (male *Pseudhapalips*). This character is coded as polymorphic in *Cryptophagus*, Tritomini, *Cathartocryptus*, *Hapalips*, *Loberopsyllus*, *Loberoschema*, *Loberus*, *Setariola*, and *Toramus*.
4. Subapical serrations of mandible. (0) absent, (1) present. In *Crowsonguptus* the serrations are in the form of very well defined teeth, but normally they are not that prominent in the taxa that have them. This character is coded as polymorphic in *Toramus*.
5. Mandibular glandular ducts. (0) absent, (1) present. These unitubulate glandular ducts (see character 48) are present in the middle of the mandibles of some Languriinae.
6. Lacinial spines. (0) absent, (1) one, (2) two, (3) three (Fig. 61). Lawrence *et al.* (1999a) refers to these structures as lacinial hooks. Their absence is sometimes correlated with having a brushy lacinial apex (Megalodacnini and Toraminae). This character is coded as polymorphic in Dacnini and *Stenodina* (1/2).
7. Width of galea (g) to that of lacinia (l). (0)  $g = 1$ , (1)  $g > 1$  (Fig. 60), (2)  $g < 1$ . This character is coded as polymorphic in Dacnini (0/1) and Erotylini (0/2).
8. Relative length (l) to width (w) of apical maxillary palpomere. (0)  $l > w$  (Fig. 44), (1)  $w > \text{or} = l$  (Fig. 9). The shape of the apical maxillary palpomere is variable among erotylids and in those taxa with state 1 it is subulate or securiform. The apical palpomere appears to be very flattened in the type species of *Loberoschema* while in *Platoberus* it is aciculate. This character is coded as polymorphic in Dacnini and Tritomini.
9. Relative length (l) to width of mentum (w). (0)  $l < \text{or} = w$  (Fig. 44), (1)  $l > w$  (Fig. 50). The size and proportion of the mentum varies in erotylids and appears to be associated with the relative position of the mandibles. For example, in *Encaustini* the ventral mouthparts are retracted and enclosed by the mandibles (Skellely 1997) and in these the position of the mandible is correlated with a relatively small mentum. The mentum in *Platoberus* is about 2 times as long as wide, much longer than any other genus examined in this study. This character is coded as polymorphic in Tritomini.
10. Pits of mentum. (0) absent (Fig. 42), (1) present (Fig. 36). There are well defined pits located at the middle of the mentum in *Protoloberus* and *Zavaljus*.
11. Lateral pockets of mentum. (0) absent (Fig. 42), (1) present (Fig. 41). In contrast to the well developed pits coded in character 10, there are well developed pockets present on the lateral margins of *Henoticonus*, *Loberogosmus*, many *Pharaxonotha* (including the type species), and *Setariola*.
12. Medial carina of mentum. (0) present (Fig. 42), (1) absent (Fig. 44). The external surface of the mentum is composed typically of two carinae, one that is medial and which is perpendicular to one that is transverse. Care should be taken while scoring this character, because if the carina is not delimited by distinct steep sides, it may appear as a weak line or ridge along the mentum as it does in some *Loberus*. The presence of pits (characters 10 and 11) may also be correlated with shape differences and the occurrence of the medial carina (compare Fig. 36, 41, and 42). The medial carina is weakly developed in *Stenodina*, though coded as present, and present as a weak ridge in some *Cathartocryptus*, where it is coded as absent in this taxon. This character is coded as polymorphic in *Empocryptus* and *Loberus*.
13. Relative length (l) to width (w) of apical labial palpomere. (0)  $l > w$ , (1)  $w > \text{or} = l$  (Fig. 42). The relative proportions of the apical palpomere varies, and this and the following character refers to this variation. Typically the apical palpomere is wider than the penultimate one, but in some taxa these are equal in width. *Penolanguria* is the only genus examined in Languriinae with the apical palpomere narrower than penultimate one. The apical palpomere of *Platoberus* is aciculate. This character is coded as polymorphic in Tritomini, *Atomarops*, and *Cryptophilus*.

14. Form of labial palp. (0) subulate, (1) securiform, (?) inapplicable for taxa coded as 13–0. The relative shape of relatively wide apical palpomeres varies and I have scored two forms here. This character is coded as polymorphic in Tritomini and *Empoecryptus*.
15. Relative width of membrane (m) of the ligula to that of prementum (p). (0)  $m = p$ , (1)  $m > p$ . There is variation in the form of the ligula, especially in the arrangement of the microtrichia, which deserves further study. The weakly sclerotised ligular membrane rests on the well sclerotised internal portion of the prementum. The shape of the membrane varies: Anteriorly it may be in the form of a pair of weakly, or well developed, “free” lobes bearing microtrichia or setae. The apex may be deeply emarginate in those taxa coded as 15–1. This character is coded as polymorphic in *Atomarops*.
16. Genal spines. (0) present (Fig. 40), (1) absent or poorly developed (Fig. 43). The form of the genal spines may be directly associated with the relative position of the mouthparts in the head. In many Cucujoidea the genal spines are present and may be rather acute or rounded. The genal spines are lobate in *Aulachochilus* and some Erotylini, broad in *Xenocryptus*, rounded in *Thallisella*, acute and ventrally directed in *Loberolus* and *Stenodina*, and poorly developed in the larger species of *Crotchia*, *Henoticonus*, and many species of *Loberus* (Fig. 43–46). The genal spines of some *Penolanguria* are contiguous with ventral carinae that extend posteriorly below the eye. This character is coded as polymorphic in *Cryptophagus*, *Crotchia*, *Crowsonguptus*, *Loberus*, *Stengita* (present in the type species), and *Toramus*.
17. Medial spine of tentorium. (0) present, (1) absent. A well developed medial spine (or tendon) is present in *Xenoscelinus* and the genera *Loberolus* and *Stenodina* from Madagascar. Relatively poorly developed spines are present in *Xenocryptus* (coded as absent for this taxon).
18. Cephalic glandular ducts. (0) absent, (1) present. These are typically unitubulate ducts present on the anterior portion of the head at the margin of the frons. They are present but very poorly developed and scarcely visible in dissections of *Telmatoscius* and *Truquiella*.
19. Subocular glandular ducts. (0) absent, (1) present (Fig. 10). These are unitubulate glandular ducts that are present below the eye and end in external pores on the lateral margins of the postmentum or at the base or along the length of genal spines. There are groups of tiny pores attached to small ductules in *Henoticonus* and *Loberogosmus* (these do not form microtubules, see character 48) below the eyes, but associated with shallow grooves (see character 23) there are glandular ducts similar in form to those in *Setariola*. It was difficult to observe the presence of ducts in *Leucohimatium* because of the highly punctate cuticle. Typically the ducts originate deep in the thorax (Leschen 1997, see also McHugh *et al.* 1997) but in some taxa the ducts do not extend beyond the head, e.g., *Pharaxonotha*. In *Neoloberolus* and *Pharaxonotha* the ducts are multitubulate. Only in some Erotylini are there evaporative setae (trichomes) present at the openings of these ducts. This character is coded as polymorphic in Erotylini.
20. Transverse gular line. (0) absent (Fig. 48), (1) present (Fig. 47). In many Erotylidae there is a transverse gular ridge, carina, or groove, all referred to here as a transverse gular line. The gular line is absent in *Leucohimatium* and instead there are deep grooves at either side of the gula. The groove is very short in *Setariola*. In some taxa the gular line may not be clearly visible at the surface (i. e., some *Toramus*), but upon dissection, an internal carina is plainly visible. Sometimes the gular groove is lined with distinct setae, e.g., *Platoberus*.
21. Form of transverse gular line. (0) shallow or weakly developed line or groove, (1) ridge-like, (2) deep groove (Fig. 39), (?) inapplicable for taxa coded as 20–0. The form of the transverse gular line is variable, and in most Erotylinae it is ridge-like, while in other taxa it may be developed as a deep groove or gutter or a shallow or weak line. This character is coded as polymorphic for *Hapalips* and *Loberus* (0/2).
22. Gular fovea. (0) absent (Fig. 39), (1) present (Fig. 36). There are well developed foveae present in *Hapalips* (*Cavophorus*), *Protooberus*, and *Zavaljus* in the same location as the gular lines in other taxa. It could be argued that this character may be homologous with, and derived from, a gular groove, but it is coded separately in this study because it does not extend across the width of the head. In *Protooberus* and *Zavaljus* there are internal chambers that appear to empty laterally into the externally visible fovea. This character is coded as polymorphic in *Hapalips*.
23. Shallow U-shaped fovea. (0) absent, (1) present. Like the previous character, the u-shaped fovea could be derived from a shallow gular line (characters 19 and 21) but is coded as a separate character because these “foveae” are short and not transverse. These foveae are also associated with unitubulate glandular ducts that empty into them laterally and terminate a short distance into the head, and are similar to the ducts present in *Setariola*. These are present in *Henoticonus* and *Loberogosmus*.

24. Antennal insertion in dorsal view. (0) hidden (Fig. 5), (1) exposed (Fig. 6). Although a little difficult to score objectively, the antennal insertion is considered hidden when the antenna is inserted on the lateral side of the head, and the articulation is obscured in dorsal view, and not only when the base of the funicle is completely hidden from dorsal view as in *Hapalips* (Fig. 5). The insertion is slightly visible in *Fitoa* and it is scored as 24–0. This character is coded as polymorphic in Erotylini.
25. Number of segments of the antennal club. (0) three (Fig. 1), (1) four or five (Fig. 62), (2) two. The number of antennomeres included in the club is variable and in Languriinae the number is four or five, which is combined into character state 1. This character is coded as polymorphic in *Thallisella* (0/1).
26. Shape of antennal club in cross section. (0) rounded, (1) flattened (Fig. 62). The cross-sectional shape of the antennal club varies within Languriinae and Erotylinae, and in some languriine taxa where the club is flattened it is also asymmetrical. This character is coded as polymorphic in Dacnini.
27. Sub- or postocular carinae. (0) absent, (1) present. This character refers to well developed sub- and postocular carinae in a few taxa. In *Xenoseclis* and *Zavaljus* the carina is present behind and below the eye, and continues anteriorly to the gena or to the gular fovea, respectively. *Protooberus* has a postocular carina that does not extend much ventrally and in *Penolanguria* the carina is subocular. In many Erotylidae there may be weak antennal grooves near the anteroventral margin of the eye where the antenna can be retracted below the head, e. g., *Hapalips* and *Truquiella*. The antennal grooves are not marked by well developed carinae or sharp lines as seen in other beetles and this feature should be examined in more detail. Also in this region of the head there may be a weak subocular bead that is probably not associated with antennal retraction and present at the ventral margin of the eye in various taxa. A bead surrounding the antennal fossa is present in *Lobosternum*. These features are not confluent, or homologous, with the posterior extension of the transverse gular groove or line (character 20) which is also positioned below the eye (Fig. 55).
28. Ocular setae. (0) present (Fig. 40), (1) absent. The ocular setae are easily viewed on dissected specimens under high magnification and in many taxa these are restricted to the posterior facets of the eye (Fig. 46). These are in the form of nipple-like processes in at least one species of *Dasydactylus* and the setae in *Leucohimatium* typify the modified setae that cover the entire body. This character is coded as polymorphic in *Loberopsyllus* (present only in *L. oculatus* Leschen & Ashe) and *Loberoschema*.
29. Supraocular line. (0) absent, (1) present. In many Erotylidae there are lines present along the lateral margin of the frons and vertex of the head above and beyond the eye. In erotylines these may extend onto the anterior margin of the clypeus. In *Acryptophagus* the line is not easily distinguishable from the dorsal margin of the eye, nor is it well developed. This character is coded as polymorphic in Dacnini, *Cathartocryptus*, *Cryptophilus*, *Hapalips*, *Loberopsyllus*, and *Pharaxonotha*.
30. Supraocular line. (0) present to level above eye, (1) present to level beyond eye, (?) inapplicable for taxa coded as 29–0. The relative length of the supraocular line is variable, and can be subdivided into two character states. The line in *Stenodina* ends at the middle of eye. This character is coded as polymorphic in Erotylini, Tritomini, *Hapalips*, *Loberus*, and *Toramus*.
31. Vertexal line. (0) absent, (1) present (Fig. 53). Presence and absence of a transverse line or carina on the vertex of the head is a useful character in Cucujoidea, and is present mainly in basal Erotylidae and appears to be a synapomorphy for *Toramus*. A weakly impressed line on the vertex is present in *Stenodina* though it is coded as absent in this study.
32. Stridulatory files on vertex of the head. (0) absent, (1) present (Fig. 53). In many taxa, stridulatory files are usually present in both sexes though they may be present in one sex only, e.g., males of *Lepidotoramus*, an undescribed Ecuadorean genus near *Paracladoxena*, and females of *Loberolus*. The exact function of the files is unknown, but they have been implicated in sexual behaviour in Japanese *Dacne* (Ohya 1996a, b). This character is coded as polymorphic in *Hapalips*, Dacnini, Megalodacnini, and Tritomini.
33. Number of files. (0) one, (1) two (Fig. 53), (?) inapplicable for taxa coded as 32–0. Stridulatory files occur either as a broad single band or as two narrow rows.
34. Temples. (0) absent, (1) present. Temples are present behind the eyes in a few erotylids. They are weakly developed and coded as absent in *Loberolus*. The temples in *Protooberus* (Fig. 35) and *Zavaljus* also are associated with strong carinae (see character 27). This character is coded as polymorphic in *Hapalips* and *Pharaxonotha*.
35. Shape of prothorax. (0) parallel-sided (Fig. 1–5), (1) widest in apical half (Fig. 6), (2) widest at base, (3)



- constricted at base. The general shape of the prothorax is very variable in Erotylidae and can be coded in several ways. I decided to treat the variation under one character. Character state 0 refers to a prothorax that is parallel-sided, though it may be evenly arcuate or slightly sinuate but it is always widest at the middle. States 1 and 3 differ where the latter state refers to a pronotum which has a distinct constriction at the base that may be associated with a basal impression or sulcus on the pronotum, e.g., *Fitoa*, *Paphezia*, and *Stenodina*. The pronotum of *Cathartocryptus maculosus* is slightly widened anteriorly (Fig. 7), and is not as distinctly widened apically as other members of the genus. This character is coded as polymorphic in Dacnini, Encaustini, and Tritomini (0/2).
36. Anterior angles of pronotum. (0) poorly developed (Fig. 8), (1) well developed (Fig. 9). The anterior pronotal angles may be acute projections that extend beyond the mid-anterior margin of the pronotum. The angles are weakly developed in some species of *Thallisella* (coded as 36–1). This character is coded as polymorphic in *Cryptophilus*, *Loberoschema*, *Paracladoxena*, *Pharaxonotha*, *Thallisella*, and *Toramus*.
37. Pronotal carina. (0) narrow, (1) thick, (2) absent. A pronotal carina is usually present in Cucujoidea, but the carina and its bead can vary in thickness. In a few taxa, the carina may be as thick as the width of the antennal funicle. A sublateral line is present on the pronotum in many Biphylidae, but this character is not treated here.
38. Width (w) to length (l) of prothorax. (0)  $w = l$ , (1)  $w > l$ , (2)  $w < l$ . This character relates to the overall proportions of the prothorax, especially to the elongate form usual in many of the large-bodied languriines. Character state 1 is present in larger species of *Crotchia* while the prothorax of *Protoloberus* is slightly wider than long and is here only coded as 38–0. This character is coded as polymorphic in Dacnini (0/1), *Atomarops* (0/1), *Cladoxena* (1/2), *Crotchia* (0/1), *Hapalips* (0/1), *Languria* (0/2), *Paracladoxena* (0/1), *Penolanguria* (0/2), and *Pharaxonotha* (0/1).
39. Anterior edge of prosternum. (0) smooth, (1) serrate. The anterior margin of the prosternum may be serrate or smooth and this is sometimes correlated with the relative depth of the sockets of the anterior setae. In *Loberus* the margin is smooth except in the group with confused punctate elytra, a flattened species from Sumatra, an apterous species from Chile, and one Mexican species. The margin of *Xenocryptus* has well developed teeth that are associated with relatively elongate setae. Typically the anterior setae are arranged in a well defined row or rows though in *Zavaljus* the setae are scattered along the margin. This character is coded as polymorphic in *Loberus* and *Toramus*.
40. Pronotal callosities. (0) absent, (1) present. Pronotal callosities are thickened portions of the anterior angles of the pronotum that may have a small, posteriorly directed spine. The callosities are usually present in *Acryptophagus* and *Thallisella*, but can be reduced in some species. Callosities are present in most species of *Loberoschema*, but they are reduced in one apterous species from Juan Fernandez Islands (Chile). Three broad teeth or lobes are present on the carina of *Stenodina*, each appearing as separate callosities, much like those present in some Cryptophagidae (see Leschen 1996). This character is coded as polymorphic in *Toramus*.
41. Pronotal carina. (0) serrate or undulate (Fig. 7), (1) smooth (Fig. 6). Having a serrate pronotal carina corresponds to the presence of evenly or unevenly spaced undulations, spines, teeth, and setiferous tubercles. Examination under high magnification is necessary to determine the character state for some taxa, e.g., *Cryptophilus*, *Loberonotha*, and *Setariola*. In some species of *Atomarops* and *Cathartocryptus*, the margin is crenulate, or weakly so, and these are treated as being serrate. *Cladoxena maculata* Motschulsky has a small basal tooth and the remaining species of the genus have a smooth carina. *Stengita*, which has callosities, contains a few species that have a very weak undulate margin, and the genus is coded as 41–1. One specimen, possibly a member of *Toramus* (USNM), has distinct lateral teeth though the genus is treated as 41–0. This character is coded as polymorphic in *Fitoa*, *Hapalips*, *Loberoschema*, *Loberus*, and *Thallisella*.
42. Relative separation of the teeth on the pronotal carina. (0) approximate, (1) widely spaced, (?) inapplicable for taxa coded as 41–1. Though the number of teeth or undulations on the carina varies, here the relative separation of the teeth is accounted for. Teeth that are separated by less than 3x the width of an individual tooth or process are coded as state 0. Taxa that have a few or widely spaced teeth are coded state 1.
43. Transverse depression at base of pronotum. (0) absent (Fig. 5, 7), (1) present (Fig. 6). At the base of the pronotum there may be a distinct transverse impression or sulcus. This character is coded as polymorphic in *Loberus*.
44. Pronotal pits. (0) present (Fig. 6), (1) absent (Fig. 1). Pronotal pits are often clearly visible at the base of the pronotum though sometimes present as short longitudi-



dinal slits, e.g., *Anadastus*. In other taxa, dissections are necessary to locate the pronotal pits because these may be difficult to see under normal lighting. The pits are very weakly developed in *Lepidotoramus* and *Loberopsyllus* and these are coded as absent. This character is coded as polymorphic in *Empocryptus*, *Hapalips*, and *Pharaxonotha*. Although the pits are present in *Truquiella gibbifera* Champion, they are absent in a single specimen, possibly the same species, collected in Texas (not dissected).

45. Basal pronotal groove. (0) absent, (1) present. This character refers to a submarginal transverse groove present at the base of the pronotum of species of *Acryptophagus* and *Pseudhapalips*.
46. Pronotal glandular ducts. (0) absent, (1) present (Fig. 11, 12). These glandular ducts are present typically in the anterior portion or along the entire lateral edge of the pronotum inside the carina or just below it (see next character). It is difficult to determine the occurrence of these ducts in some taxa because of the relative thickness of the carina and the overall texture of the external cuticle, especially in species that are heavily punctured. The glandular ducts are poorly developed in *Anadastus*, *Crotchida*, and *Crowsonguptus*. There are numerous tiny pores in the carina of *Hapalips* and in the callosity of *Thallisella* but these taxa are coded as lacking ducts because the pores do not form well defined microtubules as shown in Fig. 11. This character is coded as polymorphic in Dacnini and *Toramus*.
47. Location of glandular ducts on pronotum. (0) in carina, (1) below carina, (?) inapplicable for taxa coded as 46–0. This character refers to the location of glandular ducts present in the callosity or carina (state 0) or just below the carina (state 1). This character is coded as polymorphic in *Fitoa*, *Loberus*, and *Microlanguria*.
48. Glandular duct type. (0) unitubular (Fig. 10, 12), (1) multitubular (microtubules, Fig. 12), (?) inapplicable for taxa coded as 46–0. Cuticular glandular ducts are fairly widespread and variable in Cucujoidea and are present in Discolomatidae (John, 1959; Slipinski, 1990), Cryptophagidae (Crowson, 1980, Leschen 1996), Boganiidae (Crowson, 1990), and Erotylidae (Arrow, 1925; Boyle 1956; Sen Gupta & Crowson, 1969; Crowson, 1990; McHugh *et al* 1998). In this study there are 11 characters relating to glandular ducts (in Cryptophagidae there were 12 characters scored, Leschen 1996). In other groups of cucujoids other forms of ducts or glandular pits are present. In Erotylidae there are several forms of ducts that are classified based on the arrangement of primary (large diameter ducts) and secondary ducts, which are smaller in diameter and sometimes attached to primary ducts. Unitubular (primary condition) ducts are simple, sometimes bifurcating ducts that are clearly visible in the cuticle. Multitubular (secondary) ducts are smaller, arranged into clusters of parallel groups and are often confined to certain areas in the cuticle on the pronotum or head. Secondary tubules may be present on a primary duct and are axiotubulate (arrangement along the primary tubule as in many Languriinae) or radiotubulate (arrangement at the end of primary tubule as is the case for *Acryptophagus*). Because of the complexity of glandular ducts I restrict this analysis to unitubular or multitubular systems on the lateral prothoracic margin, although under careful study, secondary tubule arrangement and position will probably provide phylogenetic information (especially for Languriinae). The multitubulate type is present in *Setariola* but with a common large pore.
- The function of the glandular ducts is presently unknown, and only among the larger erotylines have I seen evidence of fluid release in the laboratory under light microscopy. The chemicals released from Neotropical erotylids are distasteful. The presence of lines (supraocular lines), wells (foveae on the venter of the head), and evaporative structures (callosities) indicates active release and distribution of secretions, probably for defense, as these are present in both sexes.
49. Prosternum in front of procoxae. (0) short (Fig. 73), (1) long (Fig. 72). State (0) refers to an anterior portion of the prosternum in front of the procoxae that is 0.5–2x the length of the procoxa. State (1) refers to a condition that is 3.5–4x the length of the procoxae. This character is coded as polymorphic in *Hapalips* (members of the subgenus *Cavophorus* have a short prosternum).
50. Prosternal glandular ducts. (0) absent, (1) present. Prosternal glandular ducts are typically present as a single pair on the disk, but location may vary, and in some taxa two pairs of ducts are present, e.g., *Bolerus*. Male *Leucohimatium* has a microtuberculate ridge on the prosternum which does not appear to be glandular (Fig. 66, 67). The ducts may be poorly developed in *Pseudhapalips* (coded as absent and should be confirmed in other specimens) and this character is coded as polymorphic in Tritomini.
51. Internal closure of procoxal cavity. (0) open (Fig. 76), (1) closed (Fig. 69, 73). Character state 1 refers mainly to the internal closure of the procoxal cavity by a narrow slender bar (Lawrence *et al.* 1999a). In Biphyllidae the cavity is completely internally closed, while in an

- Argentinian specimen of *Acryptophagus* the cavity appears to be completely open. A Mexican species of *Hapalips* and several species of *Loberus* (e.g., *L. impressus* and *L. nitens*) have a poorly developed closure or internal bar, and this character is coded as unknown for *Neoloberulus* because the slide preparation was poor and the type specimens were not completely dissected. This character is coded as polymorphic in *Hapalips* and *Loberus*.
52. External closure of procoxal cavity. (0) open (Fig. 69, 73), (1) slightly open (Fig. 72), (2) completely closed (Fig. 9). State (2) refers to the condition where the postcoxal projection on the hypomeron meets the prosternum behind the procoxa without a space or opening. In Erotylinae hypomeral and lateral prosoternal processes are fused and interlocked. A slightly open coxal cavity is present when there is a gap between the postcoxal projection and the prosternal process. In the open condition there is a small postcoxal projection, or none at all. The prosternal process may be expanded laterad at its apex in taxa with 52-1 (i.e., *Bolerus*, *Loberulus*, and *Stenodina*) and 52-2 (e.g., many Erotylinae and *Xenoscelis*).
53. Form of external closure of procoxal cavity. (0) by the hypomeron, (1) by the prosternum and hypomeron (Fig. 9), (?) inapplicable for taxa coded as 52-0. This character refers to the type of closure in 52-1 and 52-2.
54. Edge of hypomeron. (0) smooth or unmodified (Fig. 78), (1) notched (Fig. 70), (2) spinate (Fig. 13). At the posterior edge of the hypomeron there may be a notch or a well developed spine. This structure is well developed (in *Acryptophagus*), weakly developed, or absent, and in *Loberus* it is usually absent (it is present in a group with confused elytral punctuation and a flattened form that is similar to *Cathartocryptus*). In one specimen of *Crotchia* the notch is very weakly developed and it is coded as absent for this genus. In *Hapalips* (*H. prolixus*) and *Pharaxonotha* (*P. kirschi*) the notch is present in some species but it is small, though more or less distinct, in *Loberonotha* and *Microlanguria*. This character is coded as polymorphic in *Acryptophagus*, *Hapalips*, *Loberus*, and *Pharaxonotha*.
55. Trochantinal notch. (0) absent (Fig. 73), (1) present (Fig. 76). The notch is variable among erotylids and is well developed in *Hapalips*, *Loberonotha*, most species of *Loberus*, and *Pseudhapalips*. The notosternal suture is absent in *Leucohimatium* (Fig. 66). This character is coded as polymorphic in Erotylini, Tritomini, *Cryptophilus*, *Empocryptus*, *Stengita*, and *Toramus*.
56. Procoxal rests. (0) present (Fig. 14, 79, 80), (1) absent or reduced. This character is present at the anterior margin of the mesoventrite, and is weakly developed in *Xenoscelis* and coded as 56-1 for the genus. This character is coded as polymorphic in *Loberopsyllus*.
57. Form of procoxal rests. (0) divided (Fig. 14, 79, 80), (1) contiguous (Fig. 82), (?) inapplicable for taxa coded as 56-1. The form of the procoxal rest is very variable and it typically consists of two rounded and shallow fossae with a median carina. A contiguous form refers to the absence or reduction of the median carina creating a broad transverse procoxal rest. This character is coded as polymorphic in Dacnini, Erotylini, and Tritomini.
58. Form of procoxal rest bead or carina. (0) normal, (1) *Toramus* type (Fig. 82), (?) inapplicable for taxa coded as 57-0. The *Toramus* type of carina is a well developed and characteristic median v-shaped ridge that is attached to an anterior bridge. Behind the bridge and surrounding the v-shaped ridge are fossae that may be analogous to those featured in character 57-0. The ridge is present in most *Toramus* (Fig. 82) and may be present as 'effaced' carinae in *Atomarops* and *Stengita* (Fig. 87).
59. Fovea of procoxal rest. (0) absent, (1) present. These are well developed foveae located in the procoxal rest (not outside of it) of *Cladoxena* and *Penolanguria*. There are poorly developed small fovea-like depressions in an Argentinian specimen of *Acryptophagus* and in this genus the foveae are coded as absent.
60. Mesoventral fovea. (0) absent, (1) present (Fig. 80). At lateral edge or corner of an individual procoxal rest fossa, there is a setose fovea in some basal erotylids. Shallow or weak impressions that bear setae located in this area are not considered as mesoventral foveae, e.g., *Atomarops*. The foveae are present in one species of *Pharaxonotha* and this genus is coded as polymorphic.
61. Mesoventral glandular ducts. (0) absent, (1) present (Fig. 14). These unitubulate glandular ducts are present on the mesoventrite, typically in the disc, but sometimes at the lateral margins proximal to the mesocoxae, e.g., some *Cryptophilus* and *Setariola*. The ducts are weakly developed and coded as present in *Anadastus*, *Lepidotoramus*, and *Pharaxonotha kirschi*. In some taxa there are two pairs of ducts per side and in *Telmatoscius* the anterior pair are well developed while the posterior pair are barely visible. In a specimen of *Cathartocryptus* from Brunei a small carina is present in association with the glandular ducts. In some specimens of *Hapalips* there are groups of microtubules on

- the disc while in *Loberogosmus* there are groups of tiny pores: in these taxa the unitubular glandular ducts are considered absent. This character is coded as polymorphic in *Atomarops* (present in *A. lewisi* Reitter) and *Loberus*.
62. Mesovenral carinae. (0) absent (Fig. 82), (1) present (Fig. 87). Longitudinal carinae that extend to the posterior edge of the mesoventrite are present in *Loberoschema*, *Stengita*, *Neoloberolus* (*N. cursor* (Grouvelle)), and one species of *Acryptophagus* from Panama. In the latter genus this character is coded as polymorphic. A pair of weak lines that do not form strong carinae are present in some species of *Empocryptus*, *Toramus*, and *Stenodina* but in these taxa carinae are coded as absent. In some Central American species of *Toramus* there are strong ridges, but not well defined carinae as those present on specimens of *Loberoschema* and *Stengita*.
  63. Mesepisternal fovea. (0) absent (Fig. 81), (1) present (Fig. 82). The mesepisternal fovea, pocket, or pit is considered present if there is a distinct invagination of the cuticle into the body. These are weakly developed shallow pockets and coded as absent in several taxa (*Atomarops*, *Cathartocryptus*, *Loberonotha*, *Loberoschema*, and *Stengita*). The foveae are relatively small though distinct in *Pseudhpalips* and *Truquiella* and are located more or less in the middle of the mesepisternum in *Protoloberus*. This character is coded as polymorphic in *Toramus*.
  64. Mesometaventral articulation. (0) monocondylic (Fig. 83), (1) dicondylic (Fig. 14), (2) flat. The mesometaventral articulation is an important internal feature present in various Cucujoidea, with three character states recognised here. A monocondylic form has a single ball-like process arising from the metaventrte that fits into a corresponding fossa located on the posterior margin of the mesoventrite. A dicondylic form is one that has two processes arising from the metaventrte, and a flat form (straight-line type) lacks well developed anterior processes.
  65. Mesocoxal closure by the metaventrte. (0) open, (1) closed (Fig. 9, 14). The metaventrte encloses the procoxal cavities laterally in erotylids. In some members of the outgroup the cavities are open and are in anterior contact with the metepisternum.
  66. Relative width of mesovenral process (p) to mesocoxa (c). (0)  $p < c$  (Fig. 88), (1)  $p > c$  (Fig. 9, 14), (2)  $p = c$ . The width of the mesovenral process between the mesocoxae is variable and here I compare its width to that of the mesocoxa. This character is coded as polymorphic in *Cryptophilus* (0/1).
  67. Metaventral discrimen. (0) present (Fig. 14), (1) absent. The discrimen is present in all Erotylidae examined, with the exception of *Paphezia*, and is variable in the outgroup. The discrimen is usually present in the posterior portion of the metaventrte, though it is present throughout its length in Erotylinae examined.
  68. Submesocoxal lines. (0) absent (Fig. 9, 82, 84), (1) present (Fig. 14). There are divergent lines present on the metaventrte that are often called femoral lines. This character is coded as polymorphic in Dacnini, Erotylini, Tritomini, and *Empocryptus*.
  69. Metaventral "pores." (0) absent, (1) present (Fig. 14). These metaventral "pores" are internal flecks that are present in the cuticle of the metaventrte. These structures may be the hemidesmosomes and pore canals associated with the attachment points for the flight muscles. If so, it is interesting to note that their presence (or absence) is not necessarily associated with hind wing reduction. Similar cuticular features are present on the lateral areas of the abdominal ventrites of some taxa, especially compact apterous taxa, but are not considered in this study. This character is coded as unknown in Erotylini because the internal structure of the metaventrte is difficult to observe in dissections. This character is coded as absent for *Telmatoscus* (this may be related to slide preparation) and as polymorphic for *Loberus* and *Toramus*.
  70. Premetacoxal lines. (0) absent (Fig. 84), (1) present (Fig. 14, 85). These are transverse lines that are present just in front of the metacoxal cavities on the metaventrte. The lines are weakly developed in *Loberoschema* and *Truquiella* (coded as present) and very weakly developed in *Xenoscelis* (coded as absent). This character is coded as polymorphic in Biphylidae, Dacnini, and *Loberus*.
  71. Precoxal line area. (0) impunctate, (1) punctate (Fig. 14, 85). Well developed punctures are present in the precoxal area of *Hapalips*, *Henoticonus*, *Leucohimatium*, *Loberogosmus*, *Pharaxonotha*, and *Protoloberus*. This character is coded as present in taxa that have imbricate microsculpture (*Cathartocryptus*, *Stenodina*, and *Xenoscelis*) or relatively weak punctures (*Macrophagus*). This character is coded as polymorphic in *Loberus* and *Toramus*.
  72. Metaventral notch. (0) absent (Fig. 84), (1) present (Fig. 85). This character refers to a notch that may be present at the base of the fossa of the metaventrte which articulates with the intercoxal process on abdominal ventrite 1. This feature is coded as present where there is a distinct and well defined invagination and not just a slight separation of the cuticle. A weak

notch (coded as absent) is present in *Anadastus*, *Languria*, *Microlanguria*, *Paracladoxena* (*P. bipustulata*), *Thallisella*, and an Australian dacinine. This character is coded as polymorphic for *Hapalips* (present in the subgenus *Cavophorus*).

73. Metepisternal ctenidium. (0) absent, (1) present (Fig. 89). The ctenidium, which is similar in position to the sclerolepidia in Curculionidae (Kuschel *et al.* 2000), is a series of closely aligned setae present at the border of the metepisternum. It is particularly well developed in some xenoscelines (e.g., *Xenoscelis*) where the setae may arise from punctures. In other taxa, the ctenidium is less well developed, may not arise from punctures and the setae may be separated from each other to form a row of more or less evenly scattered setae. For example, in a specimen of *Cathartocryptus* from Brunei and an undescribed genus near *Paracladoxena* from Ecuador, the ctenidium is in the form of a weak line of scattered setae, whereas in *Platoberus latus* the ctenidium is present only in the anterior half of the metepisternum. This character is coded as polymorphic in *Loberus*.

The function of the ctenidium is unknown. There are no obvious corresponding features on the middle legs as might be expected in a stridulatory structure. It is possible that the ctenidium is used in grooming.

74. Abdominal ventrites 1 and 2. (0) free, (1) connate. The condition where the intersegmental membranes are not visible between ventrites 1 and 2, and is referred to as connate (compare Fig. 9 and 15).
75. Length of abdominal ventrite 1 (V1) relative to the length of ventrite 2 (V2). (0)  $V1 > V2$ , (1)  $V1 = V2$  (Fig. 9, 15). The utility of this character is at the family level, especially since the character is variable among the outgroups.
76. Relative width of intercoxal process of abdominal ventrite 1. (0) broad (Fig. 86), (1) narrow (Fig. 85). Defining this character is somewhat difficult, as it relates to the relative width of the intercoxal process and the degree of metacoxal separation. I consider a process narrow if it is longer than wide (length is measured from an imaginary line connecting the posterior margins of the metacoxal cavities on ventrite 1 to the anterior tip of the process) and has an acute apex. A broad process is typically wider than long and has a more or less rounded apex. The intercoxal process of *Penolanguria* is coded as broad, although it falls between states 0 and 1.
77. Submetacoxal lines. (0) absent, (1) present (Fig. 15, 86). Sometimes referred to as femoral lines, these are present as single lines that arise from the inside corner of metacoxal cavity (for *Thallisella* the lines arise from the middle of the coxal cavity). These are paired in some Biphyllidae and *Bolerus*. The lines are poorly developed in *Paphezia*, though the subcoxal bead is relatively broad (they are coded as absent in this taxon). This character is coded as polymorphic in Tritomini, *Crotchia*, *Crowsonguptus*, *Fitoa*, *Loberopsyllus*, *Loberoschema*, *Loberus*, *Platoberus*, *Stengita*, and *Toramus*.
78. Submetacoxal lines. (0) divergent (Fig. 15), (1) parallel (Fig. 85), (?) inapplicable for taxa coded as 77–0. The lines are slightly divergent in *Hapalips*, and somewhat parallel in some species of *Loberus* (the later genus is coded as polymorphic).
79. Abdominal pores. (0) absent (Fig. 9), (1) present (Fig. 15). These individual micropores are found scattered in the male ventrites in some Toraminae (Leschen 1997). They are present in at least one species of erotyline (coded as present in this taxon), though difficult to observe in larger Erotylini because of their size. In some tritomines and Cryptophagidae, fields of pores may be located on the prosternum and hypomeron (Leschen 1996; Skelley *et al.* 1997). Paired setiferous sex patches (Faustini & Halstead 1982) that are subtended by modified cuticle similar to that described for character 69, are present in *Crotchia*, *Thallisella*, and at least one species of *Loberus* from Mexico: this character is not treated in detail in this study.
80. Abdominal glandular ducts. (0) absent, (1) present (Fig. 15). These unitubulate glandular ducts (see character 48) are present at the disc and posterior edges of the ventrites and are coded if the ducts are observed to penetrate clearly through the cuticle. For example *Cathartocryptus* and *Protoloberus* have small pores at homologous positions where ducts occur in other taxa, though the ducts are considered absent in these taxa because distinct tubules are absent. The form of the glandular ducts is usually unitubulate, but in *Henoticonus*, *Hapalips*, and a male specimen of *Thallisella* they are multitubulate. In addition to unitubulate glandular ducts, *Truquiella* also has scattered clusters of multitubulate ducts on the ventrites in both sexes. These unitubulate ducts may be restricted to certain ventrites although they are usually present on ventrites 1–4 (see next character). For example, they are present on the disc of ventrite 1 in one species of *Loberoschema*. For a discussion on how the variation is coded for the abdomen in Cryptophagidae see Leschen (1996). This character is coded as polymorphic in *Hapalips*, *Thallisella*, and *Toramus*.



81. Glandular ducts of the disc of ventrites. (0) absent, (1) present (Fig. 15), (?) inapplicable for taxa coded as 80–0. These ducts are clearly visible in the disc of the ventrites. They are restricted to ventrite 1 in *Paphezia*, *Platoberus*, *Telmatoscius*, and one species each of *Loberoschema* and *Stengita*. This character is coded as polymorphic in *Hapalips* and *Thallisella*.
82. Glandular ducts at the margin of ventrites. (0) absent, (1) present (Fig. 15), (?) inapplicable for taxa coded as 80–0. These ducts are present at the posterior edge of ventrites 1–4 and in Encaustini these are also present at the posterior edge of ventrite 5. In an Argentinian species of *Acryptophagus* there are six unitubulate ducts present in the disc. This character is coded as polymorphic in *Hapalips*.
83. Abdominal calli. (0) absent, (1) present (Fig. 15). Abdominal calli are internal thickenings of the cuticle located in the disk of many taxa. The function of the calli is unclear and they are probably not involved with musculature attachment but rather aid in the strengthening of the ventrites. Calli may be difficult to observe in larger taxa, and in Erotylini this character is coded as absent.
84. Distribution of abdominal calli. (0) lineate (Fig. 15), (1) scattered, (?) inapplicable for taxa coded as 83–0. The arrangement of calli is typically lineate, but in *Zavaljus*, *Anadastus*, and *Languria* the calli are scattered within the segment. This character is coded as polymorphic in Dacnini.
85. Metafurcal lamina. (0) present, (1) absent. The metafurcal laminae are well developed processes that arise from the metendosternite, and in Cryptophilinae, and a few other taxa, especially apterous forms, these are reduced to rounded processes or are absent. This character is coded as polymorphic in Dacnini, Tritomini, *Acryptophagus*, and *Paracladoxena*.
86. Median stalk of metendosternite. (0) well developed, (1) poorly developed. The median stalk is variable in its development, but if present, it is usually a broad (or slender) shaft branching into lateral arms. It is reduced or absent in many apterous species and may be correlated with the modifications of the preceding character.
87. Penile strut. (0) narrow (Fig. 16), (1) broad, (2) absent. There is usually a single narrow strut on the aedeagus in many species of Erotylidae, and it may be split-ended or biflagellate. This character is only informative among the outgroup.
88. Aedeagus at rest. (0) horizontal, (1) on side. Most of the ingroup have aedeagi that rest on their sides, but they rest horizontally in *Leucohimatium*, *Microlanguria*, and some toramines. It is possible that the aedeagus has rotated upon the death of the specimen due to muscle relaxation and additional dissections of certain taxa would confirm the coding of this character.
89. Articulated parameres. (0) absent, (1) present. The parameres are typically articulated in the terminal taxa with the only exceptions being some members of the outgroup and *Setariola*.
90. Form of spiculum gastrale (sternite IX). (0) symmetrical, (1) asymmetrical (Zablotny & Leschen 1996, Fig. 13). The shape of the spiculum gastrale is variable, and in the Erotylinae dissected it is only slightly twisted but not asymmetrical as in other taxa, especially Loberinae. The character states for *Loberoschema* (male was damaged) and *Stenodina* (partially cleared and dissected) could not be determined, so these taxa are coded as unknown (?). It is interesting that sternite IX is symmetrical in the type species of *Xenocryptus* and asymmetrical in the African species recently described by Wegrynowicz (2000): the codification for this character is based on the morphology of the type species.
91. Form of spiculum gastrale (sternite IX). (0) narrow, (1) broad. Most erotylids have a broad sternite IX, but it is narrow in *Platoberus*. This character could not be assessed for *Stenodina* and it is coded as unknown (?).
92. Form of gonocoxite. (0) narrow (Fig. 31, 94), (1) dilated (Fig. 93), (2) acute (Fig. 96), (3) sinuate (Fig. 28), (4) *Platoberus* type (Fig. 30), (5) *Thallisella* type (Fig. 29). Gonocoxae are diverse in erotylids and I recognise five character states. A narrow gonocoxite refers to the primitive condition of a typical shaft-like coxite that bears a terminal gonostyle and setae along its flanks. The dilated condition refers to a gonocoxite that is wider than long and often dorsoventrally flattened. The gonostyli of *Cathartocryptus* are extremely large and attached apically to the gonocoxae which are also somewhat dilated (see Sasaji 1989). An acute gonocoxite that is stylate with an elongate shaft is present in most Languriinae, and a sinuate form occurs in *Acryptophagus*, *Leucohimatium*, *Macrophagus*, and *Othniocryptus*. Two other forms are coded here that are quite different from the remaining forms and are referred to as the *Platoberus* and *Thallisella* types. They resemble character states 1 and 3 most closely but are well sclerotised and flattened.
93. Margin of gonocoxite. (0) unmodified, (1) calloused (Fig. 29 30). The gonocoxae and terminalia of some erotylids may be quite extraordinary (e.g., see Boyle



- (1956) for description of the dacinine ovipositor) and the lateral margins of the gonocoxae of *Platoberus* and *Thallisella* are calloused and striate. The inside margin of the gonocoxite of *Xenocryptus* is microreticulate and somewhat bevelled. With regard to terminalia, the tips of the abdominal sclerites of *Leucohimatium* are granulate, and the terminalia of *Loberopsyllus* inquilines are covered with pores.
94. Margin of gonocoxite. (0) unmodified, (1) granulate (Fig. 28), (?) inapplicable for taxa that are coded as 92–0, 1, and 2. This character is restricted to those taxa with rather broad gonocoxae that are well sclerotised (92–3, 4, and 5). A granulate appearance is present in *Acryptophagus* and *Macrophagus*.
95. Gonostyle. (0) present (Fig. 29), (1) absent (Fig. 30). The gonostyli are typically present in erotylids, but are reduced in *Penolanguria* and *Pseudhupalips* and absent in some Languriinae, probably correlated with ovipositing in plant tissue. The gonostyli appear to be completely absent in two dissected females of *Truquiella*, otherwise the gonocoxites are very similar to *Hupalips* but the apices are unpigmented and slightly irregular as if the gonostyli are deciduous.
96. Placement of gonostyle on gonocoxite. (0) apical (Fig. 31), (1) subapical (Fig. 29), (?) inapplicable for taxa coded as 95–0. The gonostyle is typically in a terminal location on the gonocoxite, but in all Languriinae and a few other taxa the gonostyle is subapical and inserted at the side of the coxite. *Bolerus lateralis* (Arrow) as figured by Villiers (1943) has the female ovipositor with a subapical gonostyle, and the specimens of the same genus I have examined have an apical gonostyle. This character is coded as polymorphic in *Stengita*.
97. Level of spiculum ventrale (sternite 7) in female abdomen. (0) present to V2 or V3, (1) to V4 or V5, (2) to V1. The scoring of this character can be determined by locating the level to which the anterior strut of the spiculum ventrale is present in the abdomen of dissected and cleared specimens. This character is coded as polymorphic in Tritomini.
98. Form of spermatheca. (0) round (Fig. 32), (1) elongate (Fig. 33). The shape of the spermatheca is variable and can be classified as either longer than wide (98–1) or round (98–0). The spermatheca in some specimens was collapsed (*Loberonotha*, *Platoberus*, *Stenodina*, and *Telmatosciscus*), but could still be easily coded. The spermatheca was missing in the dissection of *Bolerus* and this genus is coded as unknown for characters 98–101. This character is coded as polymorphic in *Loberus*.
99. Apical pit of spermatheca. (0) absent (Fig. 33), (1) present (Fig. 32). At the apex of the spermatheca there may be a well developed pit. A small dimple is present in *Penolanguria*, however this is not prominent and it is coded as absent. This character is coded as polymorphic in Tritomini and *Hupalips*.
100. Accessory gland of spermatheca. (0) absent, (1) present (Fig. 32). If not stained properly these tiny accessory glands may be difficult to observe because they are not very well sclerotised. Therefore the coding for *Loberoschema* and *Loberus* (present) and *Macrophagus*, *Pharaxonotha*, *Platoberus*, and *Pseudhupalips* (absent) should be verified in additional specimens. This character was coded as unknown (?) for *Xenoscelis* because the preparation was not suitable for scoring this character.
101. Spermathecal duct. (0) coiled, (1) straight. The spermathecal duct is typically a well sclerotised feature that is coiled within the abdomen. The ducts are not well sclerotised in the genus *Cryptophagus*, so this taxon is coded as unknown (?). This character is coded as polymorphic in *Toramus*.
102. Spiracles on terga 6 and/or 7. (0) present, (1) absent. This character was treated in Lawrence *et al.* (1999a), and the absence of the spiracles is a feature of Toraminae. Note that the spiracles are present on tergite 6 in two Costa Rican species of *Toramus*.
103. Femoral crenulations. (0) absent, (1) present (Fig. 92). Femoral crenulations are present on the profemur of *Lepidotoramus* and *Empocryptus*.
104. Relative length of tarsomere 1 (T1) to tarsomeres 2 (T2) or 2 and 3 (T2+3). (0) T1 = T2, (1) T1 > T2, (2) T1 > T2+3 (Fig. 100). Tarsal characters have created problems in the taxonomy of erotylids and other cucujoids, especially with respect to the presence/absence of tarsal pads which is closely linked with body size (see below and Leschen & Wegrzynowicz 1998; Leschen 1999). The relative lengths of the tarsomeres to one another are variable and are scored here and in the next four characters. The length of T1 is slightly greater than T2 in *Loberogosmus*, *Macrophagus*, *Othniocryptus*, *Paphezia*, *Protoloberus*, and *Telmatosciscus* (these are coded with character state 1) and is subequal to T2 in one species of *Cathartocryptus* (Fig. 99, the genus is coded with character state 0). This character is coded as polymorphic in *Cryptophilus* (1/2) and *Loberus* (0/1).
105. Tarsomere 2. (0) not lobed, (1) lobed. A tarsal pad is the name applied to the dense setal area below the

- tarsomere (see Fig. 99). In beetles there may also be a well developed ventral lobe that extends below the following tarsomere. This and the following characters refer to the presence of a lobe and not necessarily the presence of dense tarsal pads. This character is coded as polymorphic in *Loberus* and *Toramus*.
106. Tarsomere 3. (0) not lobed (Fig. 99), (1) lobed (Fig. 100). See previous character. Though tarsomere 3 is slightly lobed in Dacnini and *Protoloberus*, these taxa are coded for character state 0.
107. Tarsomere 4. (0) reduced (Fig. 99, 100), (1) not reduced. The relative size of tarsomere 4 is variable in the outgroup and it is not reduced in size in *Zavaljus* among the ingroup.
108. Tarsomere 4. (0) exposed, (1) hidden (Fig. 100), (?) inapplicable for taxa coded as 106–0. This character relates to the relative development of tarsomere 3 where tarsomere 4 may be concealed in ventral view by the lobe of tarsomere 3.
109. Tarsal shelf of tarsomere 5. (0) absent, (1) present (Fig. 96–98). A small ventral flattened process or apical extension of tarsomere 5 that I call a tarsal shelf may be present in various taxa, especially Erotylinae, Languriinae, and some Xenoscelinae. The tarsal shelf appears to be present on all legs, but in *Zavaljus* these are present only on the pro- and mesotarsomeres. This should be checked in detail because the shelf may be difficult to observe in smaller taxa, and on slide-mounted material this feature may be obscured from view. The apex of tarsomere 5 is notched above the empodium in *Platoberus*, so that it is visible in ventral view. Although not coded in this study, the tarsal claws of some *Cathartocryptus*, *Fitoa*, and *Telmatoscus* are notched at their bases, and some *Toramus* and an undescribed genus near *Loberoschema* have a well developed tooth on the claws.
110. Tarsal shelf. (0) unmodified (Fig. 98), (1) bifid (Fig. 97), (?) inapplicable for taxa coded as 109–0. The tarsal shelf may be in the form of a bifid process in some Languriinae and *Macrophagus*.
111. Number of empodial setae. (0) 0, (1) 1, (2) 2 (Fig. 96–98). The number of empodial setae varies and on small species these are only visible when specimens are mounted on slides, especially when the empodial setae are highly reduced as in *Paphezia*. It is possible that the number of empodial setae may be related to the ease of their loss in living or dead specimens, but all tarsi were examined to score this character. The empodial setae are long and whip-like in *Paracladoxena bipustulatus*. A ligulate process that is perhaps a modification of the empodial setae is present on the empodium of some Erotylinae, and may be a useful feature for identifying a monophyletic Neotropical group. This character is coded as polymorphic in Erotylinae.
112. Ratio of elytral length to width. (0) 2–2.5x width (Fig. 2), (1) 3x width (Fig. 5). The relative length of the elytra varies; in Languriinae they may be very elongate. In the erotyline *Coccimorphus* the elytral width is equal to its length. This character is coded as polymorphic in *Paracladoxena*.
113. Elytral punctation. (0) striate (Fig. 2, 3, 6), (1) confused (Fig. 1, 8). This is a key feature that is useful in defining some groups in Cucujoidea. The striae are weakly impressed and present in *Loberolus*. This character is coded as polymorphic in *Loberus* and *Penolanguria*.
114. Scutellary striole. (0) present, (1) absent (Fig. 6, 9), (?) inapplicable for taxa coded as 113–1. This character refers to the small incomplete stria (striole) that flanks the sides of the scutellum that typically extends only a short distance along side the elytral suture. This feature has been used in Erotylidae previously by Sen Gupta & Crowson (1971), though its utility in defining groups is questionable because taxa that have elytral punctation lack the striae altogether. The striole is very weakly developed and coded as absent in *Loberolus*. This character is coded as polymorphic in *Hapalips*.
115. Humeral spine. (0) absent, (1) present. This character refers to the short spine that extends posteriorly from the humeral angle in *Acryptophagus*, *Truquiella*, and some species of *Hapalips*, *Platoberus*, and *Toramus*. There is a basal transverse carina that extends along the entire base of the elytron in wingless *Cryptodacne* (Dacnini) and *Loberopsyllus*: this is not considered homologous to the humeral spine. This character is coded as polymorphic in *Hapalips*, *Platoberus*, and *Toramus*.
116. Elytra. (0) narrowly explanate (Fig. 90), (1) relatively widely explanate (Fig. 91). In most taxa there is a well developed epipleural fold separating the dorsal portion of the elytron from the ventral epipleuron. This fold forms a ridge that may be widened and explanate (character state 1) or narrow (character state 0). Character state 1 is present in taxa that may also have a depression at the side of the elytron above the epipleural fold, e.g., *Loberus* and its relatives. The elytra of *Paracladoxena abundans* flatten out to form an explanate apex. This character is coded as polymorphic in *Cathartocryptus*,

*Cryptophilus*, *Hapalips*, *Loberopsyllus*, *Loberus*, *Nomotus*, *Paracladoxena*, and *Toramus*.

117. Epipleuron. (0) incomplete, (1) complete to apex of elytron (Fig. 9). This character is variable in the outgroup, but with the exception of *Loberonotha*, all erotyliids have character state 1.
118. Hind wing. (0) present, (1) absent or reduced. This cladistic character is useful for some groups of beetles, but its utility as a character for determining relationships is questionable for Erotyliidae. Wing loss is variable in *Paracladoxena*, where the hindwings are absent in *P. bipustulatus* and reduced and lacking veins in *P. abundans*. In *Penolanguria* the radial cell is present, but the primary veins are reduced. This character is coded as polymorphic in *Crowsonguptus*, *Loberus* and *Toramus*.
119. Radial cell. (0) present (Fig. 34), (1) reduced or absent, (?) inapplicable for taxa coded as 118–1. The radial cell is variously developed with regard to its relative sclerotisation and its absence is diagnostic for Cryptophilinae and Toraminae. The radial cell is reduced, but present, in *Paracladoxena abundans*.
120. Wedge cell. (0) Present (Fig. 34), (1) absent, (?) inapplicable for taxa coded as 118–1. The wedge cell of *Henoticonus* is very small and present only on one side of the wing, and this character was difficult to observe in dissection of *Xenoscelis deplanatus*. This character is coded as polymorphic in *Hapalips* (Sen Gupta 1968a).

**Appendix 3.** Information for specimens examined for previously described species. All NZAC except where noted.

*Chathartocryptus maculosus* (Broun)

**North Island:** AK. 1, Papakura, Pukekohe [Kirks Bush], 20 m, on fungus on stump at bush margin, NZMS 260 Q12/R12 828567, 24 Jun 2000 (AMNZ); 2, Karekare, Feb 1916; 3, Hunua, 1 Jan 1916 (2 BMNH). **BP/WO.** 2, Okauia, Matamata, 23 Jan 1927, C. E. Clarke Collection (AMNZ); 1, Okauia, Dec 1924. **CL.** 1, Thames, Kauaeranga V., 18–20 Jan 1960; 1, Coromandel, 6 Feb 1977, under bark fallen tree (JNIC). **GB.** Te Koa, 300 m, NZMS 260 Z14 769885, 26 Oct 1992, beaten from scrub and low vegetation (LUNZ). **ND.** 4, Paihia Opuā SF, 22 Jan 1981, stream bank; 1, Waipoua SF, Yakas Track, 27 Jul–7 Aug 1998, FIT 1, RL235; 2, Maunu, 4 Feb 1927 (FWNZ); 1, Whangarei, ?Tauraroa, 12 Feb 1929. **TK.** 1, Tangarakau, 27 Oct 1941, C. E. Clarke Collection (AMNZ). **WI.** 2, Kakariki, Rangitawa Bush, Dec 1997, Malaise Trap. **WN.** 1, Ohau R, Kimberley Scenic Res, 8 Mar 1978, fogging branches with fungus; 3, Rimutuka FP, Tawa Grove, 11 Sep 1994, under bark, dead tawa tree (JNIC). **South Island:** BR. 17 (9 are general), Fletchers Ck, 6 km SW of Rotokohu, 25 Jan 1972, litter. **MB.** 1, Pelorus Bridge, 25 Jul 1967, *Coprosma robusta*; 1, Pelorus Bridge, 20 Sep 1967, bark of dead *Beilschmiedia tawa*. **NN.** 1, Whangamoa SdLe, 9 Aug 1966. **Unknown locality:** 1, A.E. Brookes Collection; 2, T. Broun Collection (1 AMNZ).

*Cryptophilus integer* (Heer)

(All AMNZ). **AK.** 1, Waterview, Auckland, AK, on dead foliage in grounds of Unitec, 4 Feb 2000; 1, same but Titirangi Beach, ex wrack and debris at back of beach, 6 Feb 2000; 1, same but Herne Bay, ex pile of grass clippings, 1 Apr 2000; 6, same but Auckland Domain, 11 Apr 2000 (1, NZAC); 1, same but 12 Apr 2000; 5, same but 13 Apr 2000; 2, same data but Newmarket, ex pile of tree mulch in park, 13 May 2000.

*Hapalips prolixus* (Sharp)

**North Island:** AK. 1, Auckland, Domain, 4 Jan 1927 (FWNZ); 2, Lynfield, Tropicana Dr, 25 May 1974; 1, same but 20 Oct 1974; 2, same but 29 Jun 1974, on plants; 1, same but 1 Sep 1974; 1, same but 20 Oct 1974; 1, same but 1 Feb 1975; 2, same but 10 May 1975, litter 75/108; 3, same but litter 75/152; 1, same but 10 Oct 1975, litter 75/154; 1, same but 4 Dec 1975; 2, same but 22 Jan 1976, ex *Cordylone banksii*; 13, same but 26 Jan 1976, on tree fern; 2, same but 26 Jan 1976, decayed wood; 9, same but 28 Feb 1976, ex *Rhopalostylis sapida*; 3, same but 10 Jul 1976, decayed wood; 1, same but 5 Sep 1976, decayed wood; 1, same but 18 Sep 1976, mixed litter; 1, same but 14 Jan 1979; 1, same but 2 Mar 1980, Malaise trap; 1 same but 9 Mar 1980; 2, same but 22 Mar 1980; 2, same but 27 Apr 1980; 1, same but 2 Jun 1980; 2, same but 4 May 1980; 1, same but 8 Mar 1981; 1, same but 15 Mar 1981; 2, same but 4 Apr 1980, on dead *Rhopalostylis sapida* fronds; 7, same but 27 Sep 1981, dead *Rhopalostylis sapida*; 3, Waitakere Ranges, 15 Feb 1973, (LUNZ); 3, Waitakere Ra, Scenic Drive, 18 Aug 1951; 3, Titirangi, 7 Jul 1964, dead frond *Cyathea medullaris*; 7, Huia, 29 Nov 1983, ex decayed frond *Rhopalostylis sapida*; 1, Waitakere Ra, 5 Nov 1946; 1, Hunua Ra, Parker Bush, 21 May 1960; 1, Waivera Nth, 7 Dec 1961; 1, Pukapuka, 18 Mar 1959; 1, Anawhata, 9 Jul 1954; 2, Swanson, 5 Apr 1954; 1, Waitakere Ra, Cascade park, 12 Jan 1975; 1, Waitakere Ra, Cascade park, 26 Feb 1968; 1, Huia, 22 Jan 1966; Auckland City, Grafton Gully, 3 May 1941, decayed tree fronds; 3, Hunua Falls, 2 Dec 1961, ex stems *Cyathea*; 4 (3 larvae), Mt Auckland, 18 Nov 1983, beating *Cyathea dealbata*; 1, Riverhead SF reserve, 18 Feb 1987, *Rhopalostylis sapida*; 3, Manurewa, Olive Davis Reserve, 7 Aug 1983, beating; 3, Waitakere Ra, Scenic Drive, 7 Sep 1980, *Cyathea medullaris*; 1, Mt Auckland, 10 Jan 1974, *Collospermum*; 2, Cornwallis, 20 Dec 1978; 1, Waitakere Ra, Cutty Grass Tk, 14 Dec 1973. **BP.** 87+ (and associated larvae) Mt Te Aroha, 25 Oct 1967, dead frond *Cyathea medullaris*; 20, Waenga, NZMS 260 Y14 652913, 27 Jan 1993, in dead nikau frond (LUNZ); 1, Papatea, NZMS 260 Y14 386806, 19–30 Oct 1992, malaise trap lowland/broadleaf forest (LUNZ); 2, Lottin Pt Rd, Waenga Bush, 16 Sep–20 Oct 1992, Malaise trap; 1, Lottin Pt Rd, Waenga Bush, 10 Mar–27 Apr 1993, Malaise trap; 3, Hicks Bay, 4 Feb–14 Mar 1993, Malaise trap; 1, Hicks Bay, 25 Oct–26 Nov 1992, Malaise trap; 9, Papatea, 5 Feb–8 Mar 1993; 2, Papatea, 24 Sep–19 Oct 1992, Malaise trap; 1, Papatea, 30 Oct–23 Nov 1992, Malaise trap; 8, Papatea, 4 Dec 1992–5 Feb 1993, Malaise trap; 3, Papatea, 5 Feb–8 Mar 1993, Malaise trap. **CL.** 1, Coromandel Forest Pk, Track to Mt Moehau, 400–500 m, 12 Nov 1978, beating (LUNZ); 1, Coromandel Forest Pk, Kauaeranga V, 10 Nov 1978, beaten ex bushes (LUNZ); 2, Coromandel Forest Pk, Track to Mt Moehau, 400–500m, 12 Nov 1978, Nikau

frond (LUNZ); 1, Maruia, 6 May 1957; 3, Little Barrier I, 4 Mar 1959, rotten log; 1, Gt Barrier, Mt Hobson, 18 Nov 1954; 2, Ongohi Stm, 18 Mar 1980, *Rhopalostylis sapida*; 2, Gt Barrier I, Mt Hobson, 27 Nov 1957, beating *Leptospermum* sp.; 1, Little Barrier I, Tirikakawa Stm, 5 Apr 1984, *Rhopalostylis sapida*; 1, Tapu Hill, 26 Jan 1960; 4, Little Barrier I, Te Titoki Flat, 25 Aug–4 Sep 1958; 2, Gt Barrier I, Kaiarara V, 27 Nov 1957, dead leaf *Cyathea medullaris*; 1, Gt Barrier I, Port Fitzroy, 8 Apr 1982, beating. **ND**. 2, Mt Tiger, 4 Jan 1927 (FWNZ); 11, Waipoua, 7 Feb 1966 *Cyathea medullaris*; 3, Te Pahi Coastal Park, Pandora S, 7 Feb 1975; 19, Omahuta SF, 9 Oct 1974, *Cyathea medullaris* rachides; 1, Waipoua SF, 3 Feb 1975, beaten at night; 3, Spirits Bay, 10 Jan 1957; 1, Spirits Bay, 17 Jan 1966; 19, Whangarei Heads, 7 Dec 1961; 3, Herekino, 22 Sep 1958; 1, Waiare, 17 Sep 1958; 1, Paparoa, 29 Sep 1958; 1, Peria, 23 Sep 1958; 1, Whangarei, Bream Head, 6 Jan 1957; 1, Waipoua SF, Waipoua Stm, 120 m, 10–11 Dec 1983, litter (BMNH); 1, Waipoua SF, Waipoua Stm, 16–21 Mar 1978, malaise trap; 2, Waipoua Forest, Yakas Tk, 6 Feb 1995, litter, bracket fungus & *Rhopalostylis sapida* fronds; 4, Mt Manaia, 300–400 m, 4 Nov 1981, litter and decayed wood 81/121; 10, nr Kaiwhetu, Tauranganui Estate, 19 Nov 1985, litter; 1, Tangihua Ra, nr Lodge, 13 Feb 2000; 6, Kaiwhetu, N of Hihi, A. Krause property, 15 Feb 2000, RL533; 1, Kaitia Walkway, 29 Mar 1999, beating at night, RL361; 1, Puketi SF, 21 Jan–31 Mar 1999, FIT, RL368; 1, Puketi SF, 31 Mar–3 May 1999, FIT, RL400. **TK**. 2, Egmont NP, Dawson Falls Rd, 550 m, 6–7 Dec 1983, litter (BMNH). **WN**. 7, Wiltons Bush, 12 Dec 1941; 1, Orongorongo, 15–17 Sep 1969, dead *Cyathea medullaris*. **WO**. 15, Hapuakoe Ra, Mangakawa 500 m, 3 Jan 1984, nikau leaf bases (BMNH); 1, same but standing tree (BMNH); 2, Onewhero, 8 Apr 1985, Malaise trap; 2, Onewhero, 24 Mar 1985, Malaise trap; 1, Onewhero, 10 Mar 1985, Malaise trap; 2, Onewhero, 23 Feb 1985, Malaise trap; 3, Onewhero, 9 Feb 1985, Malaise trap; 6, Onewhero, 27 Jan–10 Feb 1985, Malaise trap; 1, Herangi Ra, Mangatooa Sdle, 10 Dec 1982, to light at dusk; 1, Okauia, 20 Mar 1931. **South Island: BR**. 1, Rapahoe, 3 Nov 1940; 1, Punakaiki Scenic Res, Bullock Ck, 20 m, 2–28 Dec 1983, Malaise trap (LUNZ); 2, 1 km S of Pahautane, 24 Dec 1976, in rotting Nikau frond (LUNZ). **NN**. 1, Oparara, 13 Mar 1939; 3, N.E. Karamea, Kohaihai R, 10 Nov 1957; 1, Kaihoka Lakes, 12 Jan 1966; 1, Totaranui, Awaroa Rd, 7 Oct 1965, moss. **SD**. 7, Chetwode Is, 15–16 Jan 1964; 2, Stephens I, 14–28 Jan 1933; 18, Ship Cove, 27–30 Nov 1972, *Cyathea medullaris*, 1, Ship Cove, 27–30 Nov 1972, *Thormium tenax*; 1 (larva), Ship Cove 27–30 Nov 1972 ex *Cyathea medullaris*; 1, Ronga V, 7 Mar 1957; 1, Okivi Bay, Sep 1984, Malaise trap; 1, Queen Charlotte Sd, Bay of Many Coves, 24 Dec 1991–4 Jan 1992, malaise trap mixed kanuka/coastal bush (LUNZ). **Unknown localities**: 2, T. Broun Collection; 6, J.C. Watt Collection.

#### *Loberonotha olivascens* (Broun)

**North Island: RI**. 1, Ruahine Ra, Purity Ridge, 16 Jan 1960; 7, Ruahine Ra, Armstrong Sdle, 8 Feb 1980 *Senecio bidwillii*. **TO**. 1, Ruapehu, Tongariro NP, 25 Jan 1982, sweeping above bushline. **South Island: CO**. 4, Eyre Mts, Jane Peak, 6 Jan 1987, beating *Brachyglottis cassinioides* (BPBC). **FD**. 1, Hunter Mts, T. Broun Collection; 1, Hollyford V, 11 Dec 1966; 13, Kaherekaou Mts, Monowai 29 Jan 1963; 1, East Eglington, 3000 ft, 28 Jan 1961, on *Cassinia* flowers (PANZ). **KA**. 1, Seaward Kaikoura Ra, 13 Dec 1993 (OMNZ); 1, Puhupuhi, 15 Jan 1967. **MB**. 1, Richmond Ra, Mt Fell, 13 Mar 1969; 1, Black Birch Ra, 17 Feb 1970, *Cassinia*. **MK**. 1, Mt Cook NP, Sealy 1160 m, 1 Mar 1976, ex sticky trap (LUNZ); 1, Mt Cook, Broun Collection (AMNZ); 4, Mt Cook, T. Broun Collection. **NC**. 2, Arthurs Pass, Jan 1923, (AMNZ); 1, Arthurs Pass, 2 Jan 1943, (AMNZ); 1, Arthurs Pass, 17 Feb 1941; 2, Arthurs Pass, 8 Jan 1943; 1, Arthurs Pass, 3 Jan 1943 (MONZ); 1, Arthurs Pass, Dobson Nature Walk, 8 Feb 1982, sweeping; 2, Arthurs Pass, 8–11 Jan 1957; 2, Arthurs Pass, 26 Jan 1978, sifted litter. **NN**. 1, Mt Owen, 23–26 Feb 1960; 13, L. Sylvester, 9–10 Mar 1967, *Traversia* flowers; 3, Takaka Hill, Smt, 14 Mar 1971; 2, L. Sylvester, 1310 m, 8 Feb 1985, ex *Hebe* sp (LUNZ); 3, L. Sylvester, 1310 m, 8 Feb 1985, on *Celmisia* (LUNZ); 3, Mt Burnett, 600 m, 8 Feb 1981, beating (LUNZ); 1, Mt Burnett, 600 m, 8 Feb 1981, ragwort (LUNZ); 1, Mt Burnett, 450 m, 8 Feb 1981 (LUNZ); 1, Iron Hill 1350–1550 m, 9 Feb 1985, beaten from subalpine scrub (LUNZ); 3, Richmond Ra, Mt Johnson Sdle, 17 Mar 1969; 1, Takaka Hill, 17 Dec 1933; 3, Mt Arthur, Tableland, 27 Jan 1931; 2, Salisbury Hut, Mt Arthur Tableland, 16 Jan 1943 (AMNZ); 1, Balloon Hut, Mt Arthur, 1944 (AMNZ). **OL**. 8, Otago, Kinloch, 1933; 5, Bold Peak, 9 Mar 1943 (MONZ); 76, Dart Valley, 17 Feb 1980, beaten from shrubs; 17, Dart Hut, 15 Feb 1980, beaten at night; 6, Dart Hut, 13–15 Feb 1980, Malaise trap; 1, Mt Earnslaw, 9 Jan 1945; 1, Dart Hut, 19 Feb 1980, beaten from *Hebe salicifolia* at night; 10, Dart Valley, 17 Feb 1980, beaten at night; 9, W. Br. Matukituki Liverpool Stm, 5 Feb 1986, beating *Olearia moschata* (BPBC); 3, Otago, Bold Peak, 21 Feb 1933 (FWNZ). **SC**. 1, Moa Basin, T. Broun Collection; 1, Moa Hut, T. Broun Collection. **SI**. 1, Codfish I, North Hut Tk, 6 Dec 1991, litter; 1, Codfish I, Summit Tk, 30 Nov 1991,

sifted litter; 8, same but 8 Nov 1981–12 Jan 1982 mixed podocarp (LUNZ); 8, same but Malaise trap (LUNZ); 10, same but *Senecio-Olearia* scrub (LUNZ); 31, Big S Cape I, Feb 1969, *Senecio* flowers; 1, same but Nov 1968, general beating (LUNZ); 2, Pegasus, 21–25 Jan 1968; 3, Table Hill, 6 Feb 1947 (AMNZ). **SL**. 8, Takatimu Mts, 12 Feb 1963. **WD**. 60 (30 in alcohol), West Olivevine Ra, Simonin Pass, 23 Jan 1975, beating *Nothofagus Coprosma* & *Olearia*; 1, W. Olivevine Ra, Tempest Spur, 25 Jan 1975, litter; 1, Mt Aspiring NP, Arawata Biv, 840 m, 5 Feb 1989, LUNZ 89/2, scrub litter (LUNZ). **Unknown localities**. 13, Alfred, 4 Feb 1914; 12, T. Broun Collection; 3, Broun Collection (AMNZ).

#### *Loberus anthracinus* (Broun)

**North Island: BP**. 3, Te Aroha summit, 3 Nov 1977, lichen; 3, Te Aroha summit, 3 Nov 1977, moss. **GB**. 4, Huaiarau Ra, Putahinu Ridge, 2 Mar 1971, moss. **HB**. 1, Havelock North, 14 Nov 1977, nest of *Sturmus vulgaris*. **TO**. 1, Tongariro NP, Mauia Camp, 11 Nov 1976, litter; 1, Waituhi Sdle, 20 Nov 1966, moss; 1, Ruapehu, Whakapapa, 29 Nov 1965, moss. **WA**. 1, Mt Bruce, 4 Sep 1965, moss. **WO**. 2, Pirongia, Whararua S. face, 9 Jun 1977, moss; 7, Pirongia, Whararua, 9 Jun 1977, moss/lichen. **South Island: BR**. 5, Reefton, Rahu Sdle, 12 Nov 1964, moss. **CO**. 1, Rock and Pillar Ra, 28 Oct 1987 (LUNZ); 1, Cromwell, Beetle Res, 13 Mar 1979, litter; 3, S Sutton, 9 Sep 1968, litter; 1, McRaes Flat, Sailors Cutting, 7 Sep 1968, *Raoulia*; 5, Logan Burn, 7–21 Oct 1983; 1, nr Luggate, 6 Oct 1995 (OMNZ); 2, Rocklands, 5–19 Dec 1978, pitfall; 6, Sutton Ck, 14 Feb 1968, moss; 1, Rocklands, 30 Oct–15 Nov 1975, pit traps in tussock (BPBC); 1, Teviot R, Bridge Huts, 11 Oct 1968, litter; 7, E. Clutha V, Craig Flat, 17 Mar 1986, moss; 1, Raggedy Ra, Ophir, 10 May 1968; 1, Umbrella Mts, Crown Rock, 19 Dec 1995 (OMNZ); 1, Garvie Mts, 7–16 Nov 1984 (BPBC); 3, Nardoo Reserve, 25 Nov 1984, ex lichen on rock (BPBC); 14, South Rough Ridge, 7 Dec 1984 (BPBC); 1, North Rough Ridge, 8 Dec 1984 (BPBC); 1, Lammemoor Ra, 29 Dec 1984 (BPBC); 1, Lammemoor Ra, 6 Dec 1986 (BPBC). **DN**. 1, Mt Maungatua, 27 Mar 1973, litter; 4, Flagstaff, 8 May 1982, moss (BPBC); 1, Flagstaff, 8 Apr 1980, moss on rock (BPBC); 13, Swampy Smt, 17 Nov 1984, ex lichen on rock (BPBC); 1, Swampy Smt, 16 Dec–12 Jan 1985, pitfall trap (BPBC); 2, Swampy Smt, 17 Nov–16 Dec 1984, pitfall trap (BPBC). **FD**. 2, Homer Tunnel, 13 Jan 1967, moss (2); 2, Homer Tunnel, Milford side, 12 Dec 1966, moss; 8, Hunter Mts, S Borland R, Jan 1970, litter; 1, Eglington V, Cascade Lodge, 10 Jan 1967, moss. **MB**. 1, Richmond Ra, Fell Pk, 13 Mar 1969, litter; 3, Molesworth, Kennet R, 18 Aug 1966, moss; 1, Upcot Sdle, 28 Feb 1965, moss; 1, L. Sedgemere, 7 Sep 1966, moss; 3, Upper Wairau V, Wairau Bridge, 6 Sep 1966, lichen. **MC**. 2, Methven, Pudding Hill Ck, 14 Jul 1966, moss; 1, Banks Peninsula, Kennedy's Bush, 15 Aug 1966, moss; 1, Alford F, Staveley, 14 Jul 1966, moss; 1, Moa Basin. **MK**. 1, Hakataramea Pass, 17 Jan 1966, moss. **SD**. 1, Port Underwood Sdle, Sep 1969, moss. **NC/MB**. 1, Hope R Bridge, 12 Nov 1964, moss. **NN**. 1, Aorere V, Brown R, 27 Oct 1965, moss; 1, Wangapeka V 18 Nov 1934. **OL**. 4, Upper Hollyford V, 13 Jan 1967, moss; 1, Wanaka, 7 Dec 1966, *Raoulia*. **SL**. 1, Blue Mts, 5 Jan 1985 (BPBC). **WD**. 1, Haast R, W of Pivot Ck, 28 Oct 1966, moss; 8, Franz Josef, 2 Nov 1965; 2, 4 km S Haast, 26 Mar 1967, moss; 4, Haast, 11 Nov 1968, moss; 1, Haast Pass, 28 Feb 1966, moss; 1, Franz Josef 2, Apr 1965; 1, Pyke V Hd L. Alabaster, 11 Jan 1967, moss; 1, Mt Aspiring NP, Arawata R, 760 m, 2 Feb 1989, on moss by river (LUNZ). **Unknown localities**. 1, E. S. Gourlay Acc; 5, T. Broun Collection.

#### *Loberus depressus* (Sharp)

**North Island: AK**. 5, Lynfield, Tropicana Dr, 27 Nov 1976; 2, Tiritiri Matangi I, 23 Nov 1997, ex *Cordyline australis* flowers; 1, Auckland, coll. E. Fairburn, 4 Jan 1927 (FWNZ); Titirangi, coll. E. Fairburn, 21 Nov 1929 (FWNZ); 2, Woodhill; 1, Riverhead SF Res, 25 Apr 1982, in seed heads sedges; 7, Bayswater, Oct 1913; 1, Titirangi, 21 Nov 1914; 1, Titirangi, 5 Nov 1942; 1, Takapuna, 13 Mar 1915; 26, Huapai, Station Rd, 10 Nov 1985, *Cordyline australis* inflorescence; 2, Mangere, 10 Sep 1950, ex *Cordyline* sp.; 1, Bethells, Matuku Res, 18 Oct 1980; 1, Mt Albert, 16 Oct 1959 ex *Leptospermum* flowers; 4, Mt Albert, 6 Nov 1958, *Cordyline australis*; 1, Mt Albert, 24 Dec 1958, in house; 7, Muriwai, 14 Jun 1991, *Cordyline australis*; 1, Sandringham, 12 Feb 1981, at light; 5, Auckland, 1940. **BP**. 5, Rereauira Swamp, 16 Sep–20 Oct 1992, Malaise trap; 1, Waenga NZMS Y14 652913, 20 Oct 1992, on tree at night (LUNZ); 1, Cape Runaway, 4 Mar 1983; 6, Waenga Bush, Lotin Pt Rd, 24 Nov 1992, in *Cordyline* flws (BPBC). **HB**. 6, Waitere, 600 m, 1 Dec 1984–22 Jan 1985, Malaise trap. **ND**. 1, Whangarei, 21 Mar 1984, ex Nikau seeds (PANZ); 1, Kaitia Walkway, 20 Jan 1999, at night, RL264; 5, Te Pahi, Kauaeaparaou Stm, 30 Jul 1998, ex *Cordyline australis* sheath, RL214; 6, Spirits Bay, Waipuna Stm, Nov 1967, beating; 4, Spirits Bay, Tom Bowling Bay, Akura Stm, Nov



1967, ex pohutukawa; 1, Kerikeri, 5 Sep 1981; 10, Whangarei Heads, Peach Cove, 8 Jul 1957 *Cordylinae*; 2, Kohukohu, Hicks Bush, 15 Nov 1948, leaf mould; 5, Twin Bridges, 16 Jan 1951; 1, Tutukaka Hbr, 12 Dec 1980; 1, Kawakawa, 15 Jan 1951; 9, Ngaiotonga Sdle, 16 Jul 1983, beating understorey; 1, Pekaerau, 24 Nov 1918; 1, Omapere, Hunoke, 30 Oct 1985; 1, Kapowairoa (?) Nov 1994 (JNIC); 1, Trounsen Kauri Park, 25 Nov 1994 (JNIC); 1, Te Paki Stm, 18 Nov 1994 (JNIC). **RI**. 1, Mataroa, Main Trunk, 18 Nov 1917. **WA**. 1, Cape Palliser, Putangirua Stm, 29 Oct 1985, beating (JNIC). **WN**. 3, 2 km S Paekakariki, 13 Nov 1977; 1, Tinakori Hill, 30 May 1991, ex dead wood (JNIC); 1, Tinakori Hill, 30 Feb 1992, decaying *Cordylinae* branch (JNIC). **WO/BP**. 1, Okauia, 8 Apr 1924. **South Island**: **DN**. 9, Dunedin, Bradford, 19 Oct 1996 ex *Cordylinae* (OMNZ); 5, Dunedin, Bradford, 25 Oct 1996 ex *Cordylinae* (OMNZ). **MB**. 1, Hamner, Leslie Hills, 17 Nov 1958. **MC**. 2, Peel Forest, 26 Mar 1977, Deg. 1 Field trip Flax (LUNZ); 1, Christchurch, Riccarton Bush, 5 Dec 1941; 1, Christchurch, Riccarton Bush, 4 Dec 1941; 1, Christchurch, Riccarton Bush, 10 Dec 1941. **NN**. 9, Pupu Springs, 18 Feb 1999, beating, RL338; 1, 7.5 km S Mokihinui R, 9 Feb 1999, under bark at beach/ex cabbage tree, RL277; 1, Kongahu, Nov 1980, Malaise; 4, Kaihoka Lakes, West Haven, 28 Oct 1965, litter. **SC**. 2, Upper Pareora Gorge, Lindisfame Camp Area, 21 Mar 1970, Ento Dept Field Trip (LUNZ). **Unknown localities**: 1, flaxpod; 7, 391, T. Broun collection.

### *Loberus nitens* (Sharp)

**North Island**: **AK**. 1, Lynfield, Tropicana Dr, 16 Jan 1977, coastal; 2, same but 29 Jan 1977; 1, same but 27 Dec 1977, *Phormium tenax*; 1, same but 24 Mar 1979; 1, Auckland, coll. E. Fairburn, 4 Jan 1927 (FWNZ); 2, Auckland, Mt Eden, 4 Jan 1924 (MONZ); 1, Titirangi, 4 Dec 1927; 2, Takapuna, 8 Mar 1915; 1, Noises Is, Otatai, 1 Nov 1977, beating *Coprosma repens*; 182, Noises Is, Maria I, 29 Apr 1979, Litter 79/68; 1, Noises Is, Maria I, 29 Apr 1979, Litter 79/69; 64, Noises Is, Maria I, 25 Oct 1978, Litter 78/202; 29, Noises Is, Maria I, 10 Dec 1979, beating; 31, Noises Is, Orapapa I, 24 Oct 1978, Litter 78/196; 3, Whatipu, 26 Jan 1975, beating *Senecio*; 1, Mangere, Ihumatao, 10 Jan 1978, nest of *Turdus philomelos*; 1, Cornwall Park, 31 Mar 1979, nest of *Fringilla coelebs*; 1, Bucklands Beach, 10 Jan 1977, birds nest in *Ulex* sp.; 1, Bucklands Beach, Jan 1979, nest of *Passer domesticus*; 8, Karekare, 14 Apr 1984, under dune vegetation; 8, Waikowhai, Captain's Bush, 22 Sep 1986, Litter 86/20. **BP**. 25, Karewa I, 9 Nov 1972, Litter 72/261; 2, Motunau I, 14 Nov 1972, litter 72/262; 1, Whangaparaoa Bch, 25–26 Nov 1992 (BPBC). **CL**. 3, Ohena Is, Koruenga I, 27 Nov 1972, litter 72/246; 18, Ohena Is, Old Man Rock, 26 Nov 1972, litter 72/240; 2, Ohena Is, Ohena I, 25 Nov 1972, *Coprosma, Melicytus*; 1, Mercury Is, Korapuke I, 28 Nov 1972, litter; 8, Hot Water Beach, 24 Jan 1974, in sand; 11, Aldermen Is, Hongiora I, 11 Nov 1972, litter 72/194; 28, Aldermen Is, Hongiora I, 11 Nov 1972, Litter 72/195; 3, Aldermen Is, Ruamahuaiti I, 8–12 Nov 1972, *Hymenanthera* sp.; 5, Aldermen Is, Ruamahuaiti I, 8–12 Nov 1972, *Muehlenbeckia* sp.; 14, Aldermen Is, Ruamahuaiti I, 10 Nov 1972, *Carmichaelia* sp.; 13, Aldermen Is, Ruamahuaiti I, 8–12 Nov 1972, beating; 21, Aldermen Is, Ruamahuaiti I, 16 Nov 1972, litter 72/207; 1, Aldermen Is, Ruamahuaiti I, 12 Nov 1972, litter 72/200; 2, Little Barrier I, Dec 1931–Oct 1932 (MONZ); 1, Waitete Bay, 24 Oct 1981, sweeping *Muehlenbeckia*. **ND**. 4, Kawerua, 20–24 May 1974; 1, Kawerua, 4 Jun 1982, *Phormium* at night; 3, Poor Knights Is, Tawhiti Rahi, 11 Sep 1980, *Xeronema callistemon*; 7 (larvae), Poor Knights Is, Tawhiti Rahi, 11 Sep 1980, litter; 2, Spirits Bay, 20–28 Aug 1957, beaten ex karaka; 2, Spirits Bay, 17 Jan 1966; 5, Spirits Bay, Nov 1967, sand dunes; 13, Whangarei Heads, Smugglers Cove, 6 Dec 1958, beating rushes; 1, Whangarei Heads, Smugglers Bay, 27 Dec 1926; 2, Mokohinau Is, 392; 5, Mokohinau Is, Burgess I, Landing Bay NE, 1 Jan 1984, beating *Metrosideros excelsa*; 1, Mokohinau Is, Lizard I, 3–6 Jan 1984, beating *Hymenathera*; 2, Ninety Mile Beach, 22 Jan 1966; 2, Whangarei, Ocean Beach, 7 Dec 1958, *Muehlenbeckia*. **WN**. 2, Te Horo, 22 Oct 1946 (MONZ); 3, Wellington, Mahanga Bay, 14 Jan 1930 (FWNZ); 4, Waitarere Bch, 3 Oct 1980, sweeping at night; 1, Titahi Bay, 11 Apr 1971, *Muehlenbeckia complexa*, 6 (plus 2 larvae), Titahi Bay, Rocky Bay, 28 Dec 1980, litter 80/163; 18, Wanganui Bch, 28 Oct 1968, *Muehlenbeckia*; 4, Wellington, Red Rocks, 25 Nov 1941; 1, Wellington (MONZ); 6, Te Ikaamaru Bay, 26 Jan 1981, *Phormium* (MONZ); 4, Island Bay, 27 Apr 1991, under seaweed, wrack zone (JNIC); 1, Island Bay, 27 Oct 1992, on *Coprosma repens* flowers (JNIC); 1, Island Bay, 22 Nov 1995, under seaweed, sandy beach (JNIC); 5, Tinakori Hill, 26 Oct 1991, garden rubbish (JNIC); 1, Paekakariki Bch, 24 Dec 1977 (JNIC); 1, Somes I, 18 Jan 1996, in seagulls nest (JNIC). **South Island**: **NN**. 1, Farewell Spit, 1 Feb 1979, *Muehlenbeckia* flowers; 25, Farewell Spit Lighthouse, 9 Feb 1981 (LUNZ); 3, Takaka, Pohara Beach, 3 May 1967, in sand; 1, Takaka, Pohara Bch, 18 Jan 1973; 1, Karamea, Te Namu, 31 May 1963; 1, Upper Maitai, 25 May 1933. **SD**. 1, French Pass, 6 Oct 1972, beating *Phormium*; 1, French Pass, 16 Feb 1971, *Phormium colensoi*; 1,

Chetwode Is, Te Kakaho, 14 Feb 1988, beating/sweeping mixed scrub (LUNZ); 5, Chetwode Is, Te Kakaho, 15 Feb 1988, *Coprosma repens* at night (LUNZ); 1, Chetwode Is, Te Kakaho, 15 Feb 1988, on trees at night (LUNZ); 1, Chetwode Is, Te Kakaho, 15 Feb 1988, beating seaside vegetation at night (LUNZ); 13, The Brothers Is, 12–19 May 1954 (MONZ); 2, The Brothers Is, 17 Jan 1952; 2, Stephens I, 21 Feb 1971; 6, Stephens I, 14–28 Feb 1933; 2, Stephens I, 29 Apr 1975, beating *Muehlenbeckia*; 11, North Brother Island, 7 Feb 1993, on *Disphyma* and *Senecio* flowers at night; 3, same but 20–22 Nov 1993, ex pitfall trap in *Hebe/Coprosma/Disphyma* and *Salicornia* vegetation; 4, same but, 10 Feb 1993, beaten from *Coprosma* and *Hebe*; 2, same but, 9–10 Feb 1993, yellow pan trap in *Hebe* and *Coprosma* scrub; 9, same but, 10 Feb 1993, ex *Coprosma/Hebe/Pittosporum* litter; 2, Stephens I, 16 Jan 1933; 1, Stephens I, 9–12 Jan 1931; 38, Stephens I, 16 Feb 1971, litter; 2, Stephens I, Feb 1971, sweeping; 14, Stephens I, Feb 1971, sweeping tussock. **Unknown localities**: 32, J. C. Watt Collection, 1966; 3, E. S. Gourlay Collection.

### *Protoloberus singularis* (Blackburn)

**AUSTRALIA. QUEENSLAND**: 1, Kuranda 3/50 GB J.G. Brookes Bequest 976 (ANIC); 1, 17.37S 145.34E Massey Creek, BS3 4 Sept–3 Oct 1995, 1000 m F I Traps (ANIC); 1, 17.19S 145.29E Wongabel SF, botanic walk, 8 Nov 1992, beating trees and bushes (ANIC); 1, 17.10S 145.39E, 1 km N Cathedral Fig, Danbulla SF, 8 Nov 1992, beating bushes trees by stream (ANIC); 1, 26 km up Tinaroo Ck Rd at Mareeba, 23 xii 82–12 i 83 (ANIC); 30.22S 145.39E, Blackbutt Track, Dorrigo NP, 13–15 Nov 1990, beating rainforest vegetation (ANIC); 1, 40 km W Ingham, nr Wallaman Falls, 22 Jun–7 Aug 1982, SBP45, 600 m, flight intercept trap, rainforest (ANIC); 1, Curtain Fig, 17.17S 145.34E ca 800 m, rainforest by tower, vii 1997, (ANIC); 3, Binna Burra, Lamington Nat. Pk., 27 Oct 1983, under bark in rotten wood and fungi (ANIC); 1, Mt Lewis via Jullaten, 12 Oct 1980, Rainf.; 2, Mt William, 1240 m, 21 Dec 1992–10 Jan 1993, ANZ SES Expdn. FIT 5951 (NQMC); 2, Bulburin SF, 600 m, 9 km E Many Peaks, 17 Sep 1989, pyrethrum, rainforest (NQMC); 2, Davies Ck Road, 750 m, 20 km SE Mareeba, 17 Dec 1989, pyrethrum logs & trees (NQMC); 1, Bellenden Ker Range, NQ, Cableway Base Stn, 100 m, 17 Oct–9 Nov 1981, Earthwatch (NQMC); 1, Mt Glorious, nr. Brisbane, 635 m, 11.XII.1988 (AAPC); 1, Mt Tambourine (SAMC); 3, Cairns District (SAMC); 1, Tully Falls SF, 730 m, 18 km SSW Ravenshoe, 7.XII.87–7.1.88, Malaise trap (DPIM); 1, Tully Falls SF 730m, 18 km SSW Ravenshoe, 1.X–5.XI.87, Malaise trap (DPIM); 1, 25 km up Tinaroo Ck Rd, via Mareeba, 17.ii.1983, sweeping (DPIM). **NEW SOUTH WALES**: 41 (mounted on 5 pins and most have 6+ specimens on 1 card), Upper Williams R, Oct 1926 (SAMC); 1, 3 km N Lansdowne via Taree, 26 Aug 1985, ex wet scler. for. interface, beaten from foliage (ANIC); 1, Sheepstation Ck, 16 km NE of Wiangaree, 600 m, 13 Jun–24 Aug 1982, SBP36, flight intercept trap rainforest (ANIC); 6.5 km S Monga NSW, 28 Oct 1988 (ANIC); 9, Comboyne, (ANIC); 2, Mt Glennie, 16 km E Woodenbong, 25 Nov 1982–3 Feb 1983, Qld. Mus. Rainfor., 910 m, flight intercept trap (NQMC).



## ILLUSTRATIONS

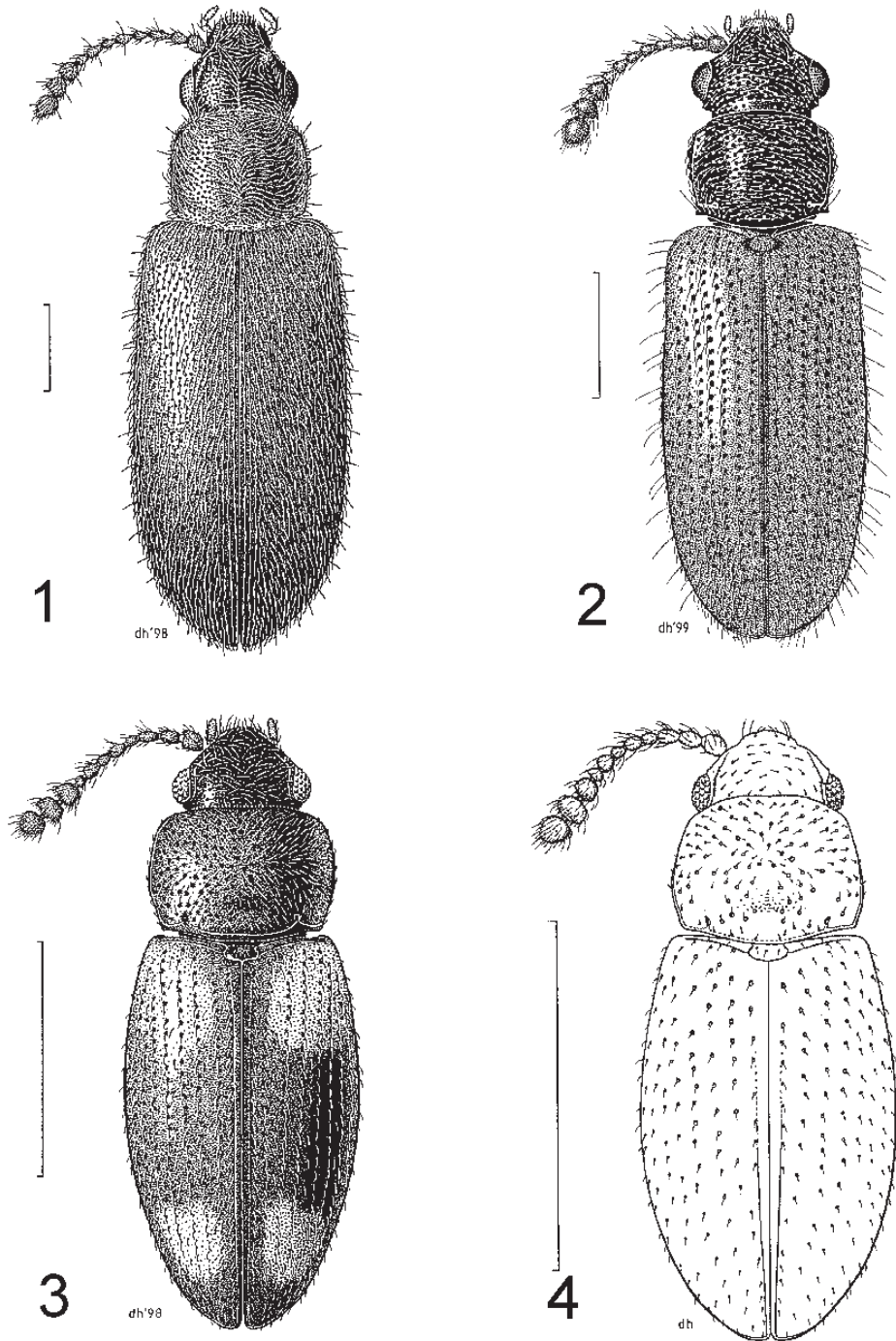
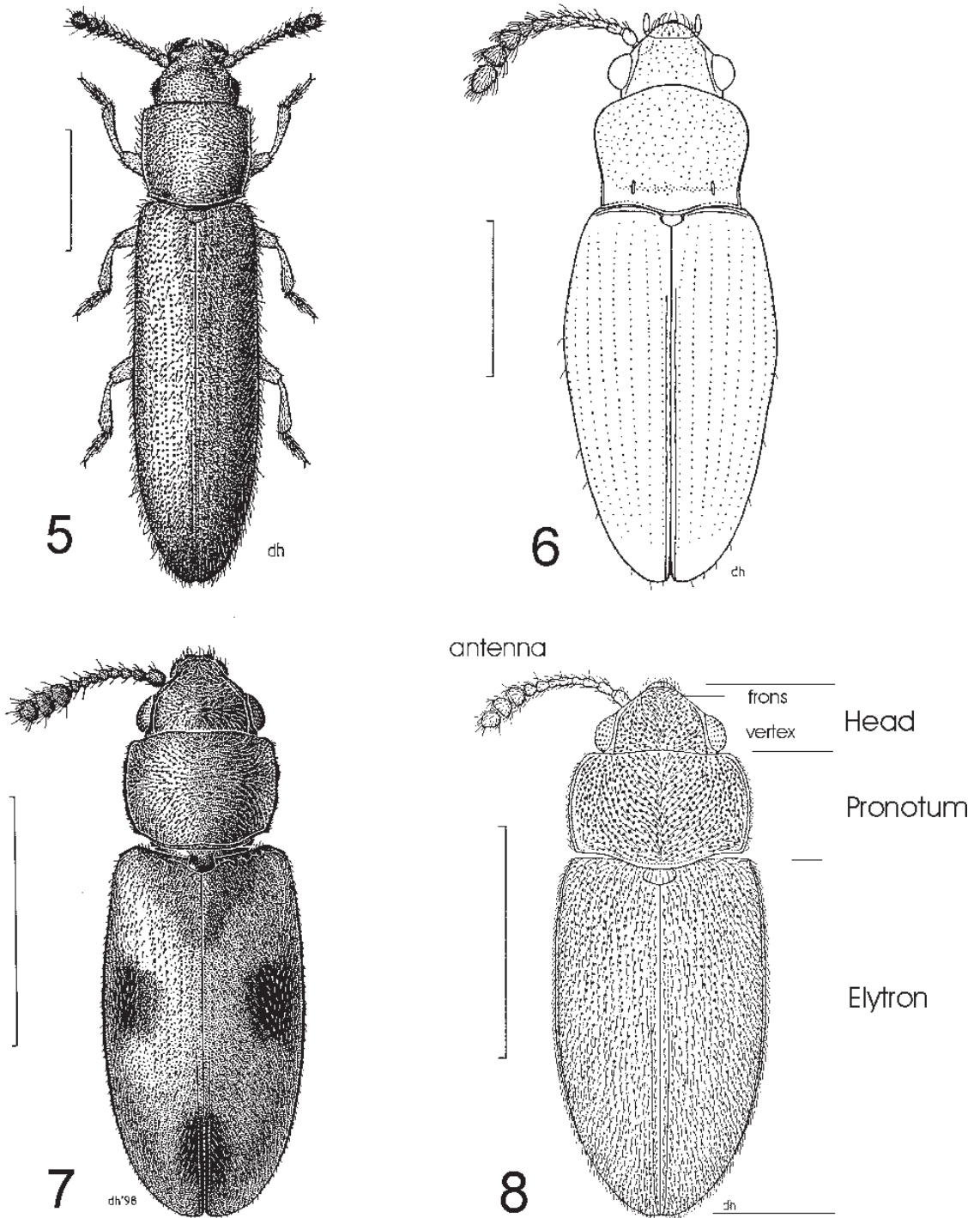
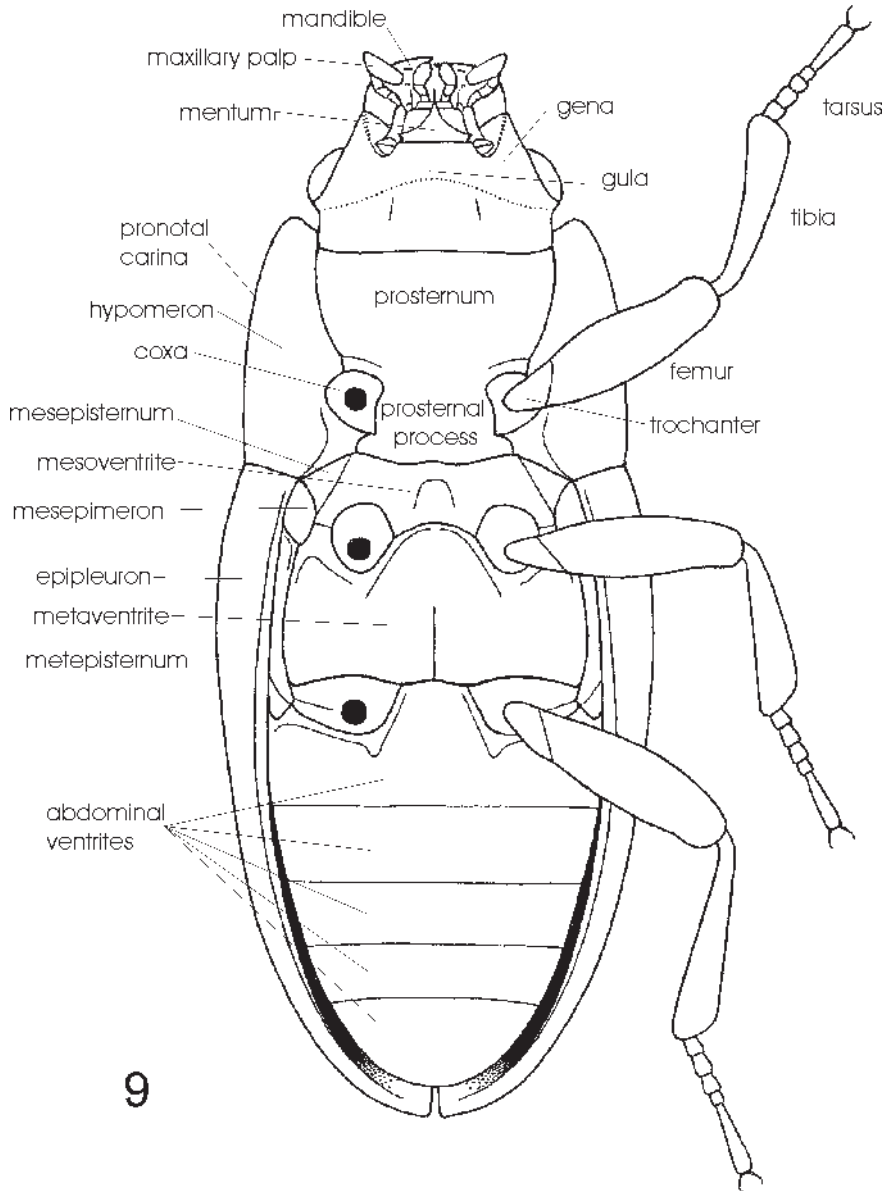


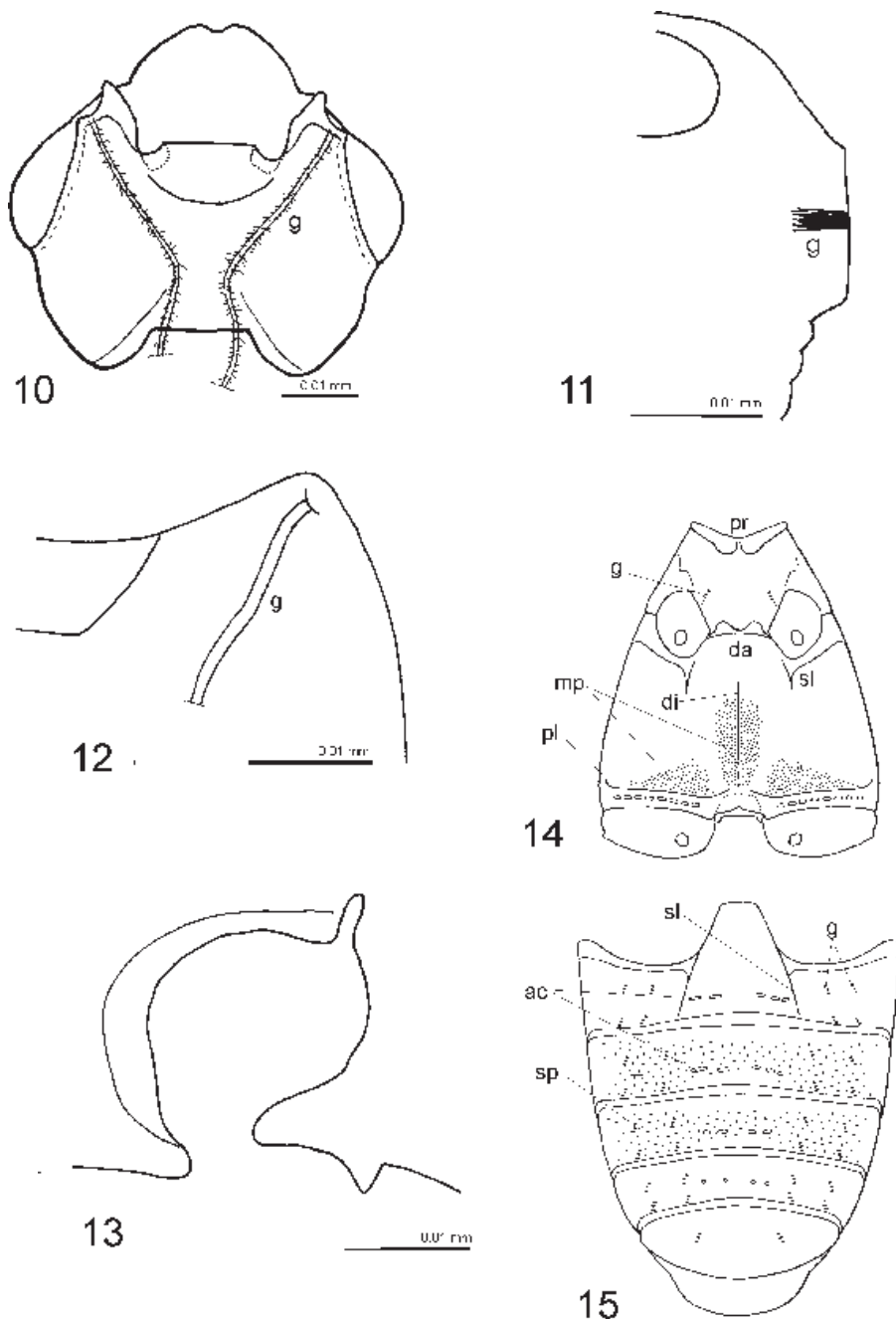
Fig. 1–4 Dorsal habitus, scale bar = 1 mm : (1) *Loberonotha olivascens* ; (2) *Protoloberus singularis* ; (3) *Loberus nitens* ; (4) *Loberus anthracinus*.



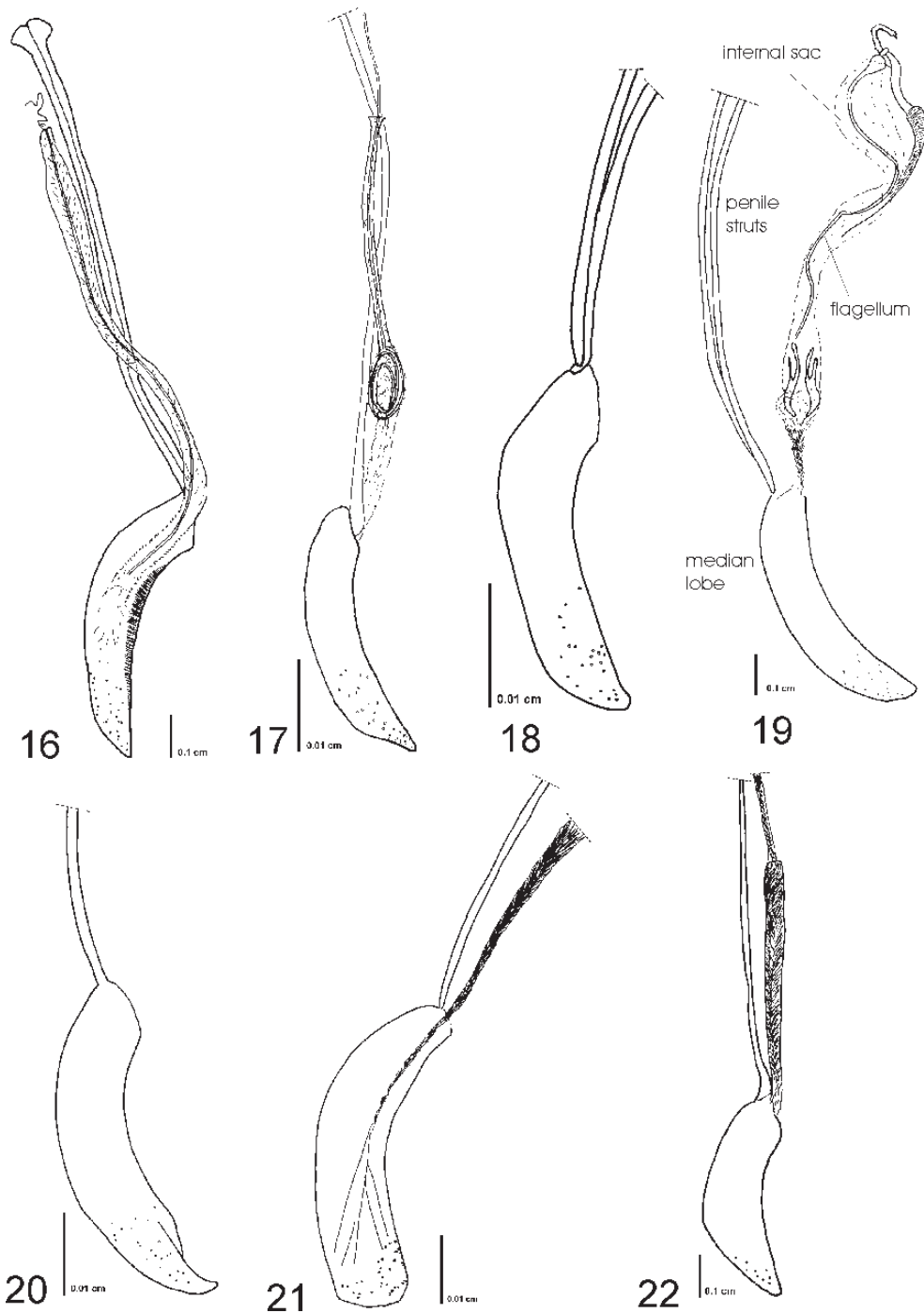
**Fig. 5–8** Dorsal habitus, scale bar = 1 mm : (5) *Hapalips prolixus* ; (6) *Neoloberus cursor*; (7) *Cathartocryptus maculosus*; (8) *Cryptophilus integer*.



**Fig. 9** *Cryptodacne synthetica* Sharp, ventral habitus, scale bar = 1 mm.

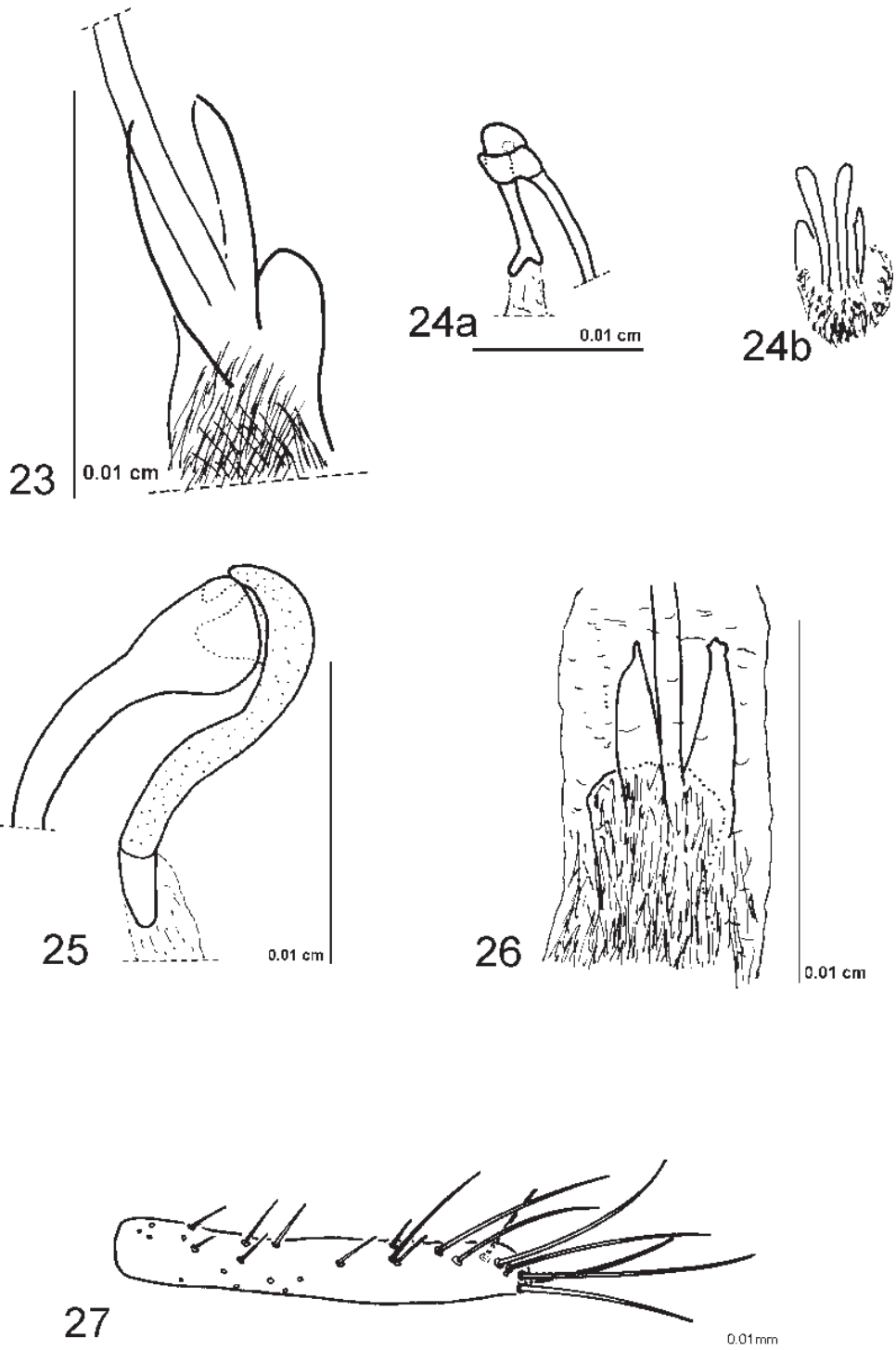


**Fig. 10–15** Ventral views and structures: (10) *Lepidotoramus grouvellei* head, with unitubulate glandular duct (g); (11) *Leucohimatium arundinaceus*, left anterior portion of the pronotum, with multitubulate glandular duct (g); (12) *Lybanodes bicolor* Skelley, left anterior portion of the pronotum, with unitubulate glandular duct (g); (13) *Stenodina quadriguttata*, left procoxal cavity; (14) diagrammatic figure of meso- and metaventrites showing external and internal features (da = dicondylic articulation; di = discrimin; g = glandular duct (dotted line); mp = metaventral pores; pl = precoxal line; pr = procoxal rest; sl = subcoxal line); (15) diagrammatic figure of the abdominal sterna showing external and internal features (ac = abdominal calli; g = glandular duct (dotted line); sl = subcoxal line; sp = sexual pores).

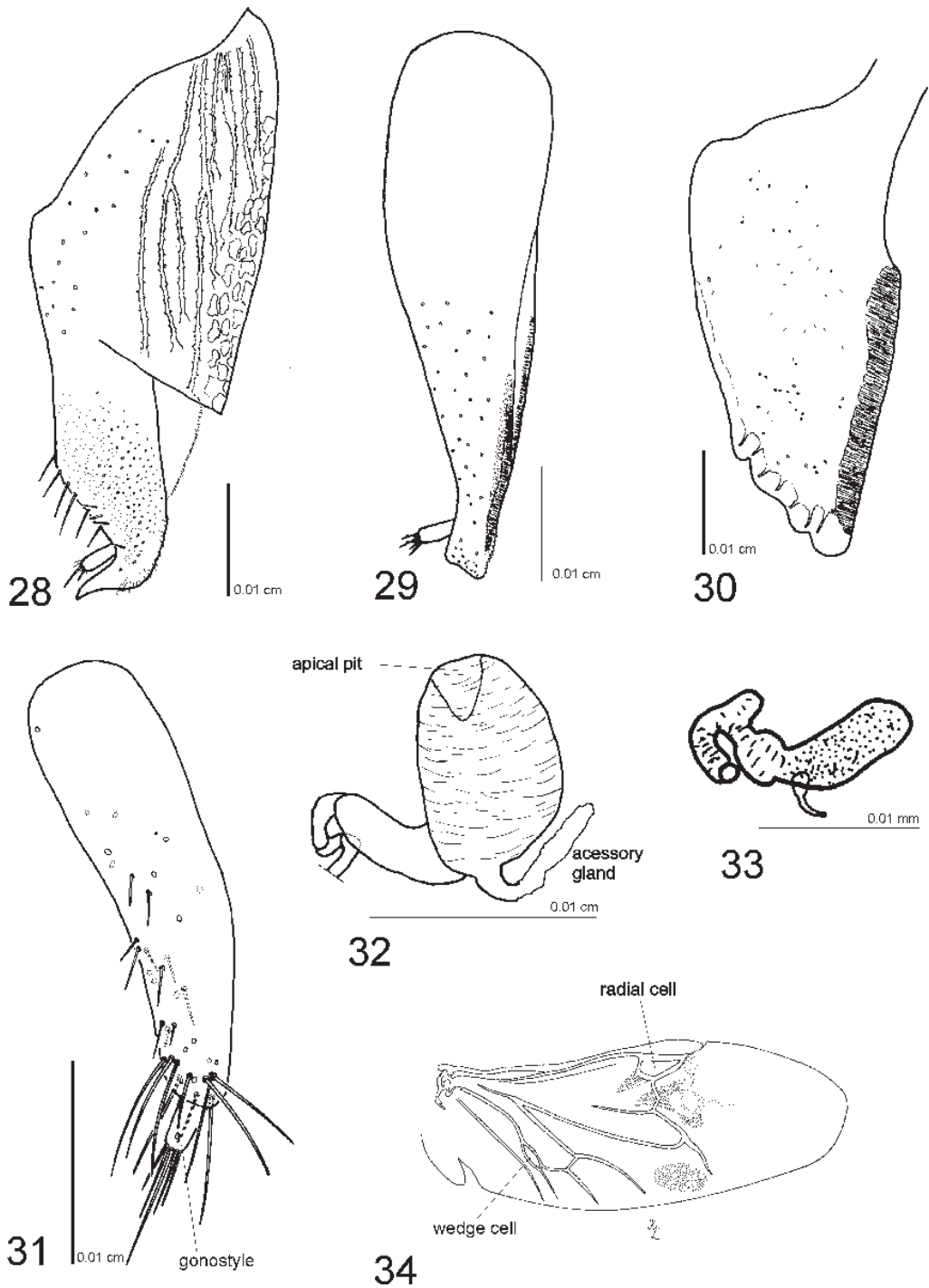


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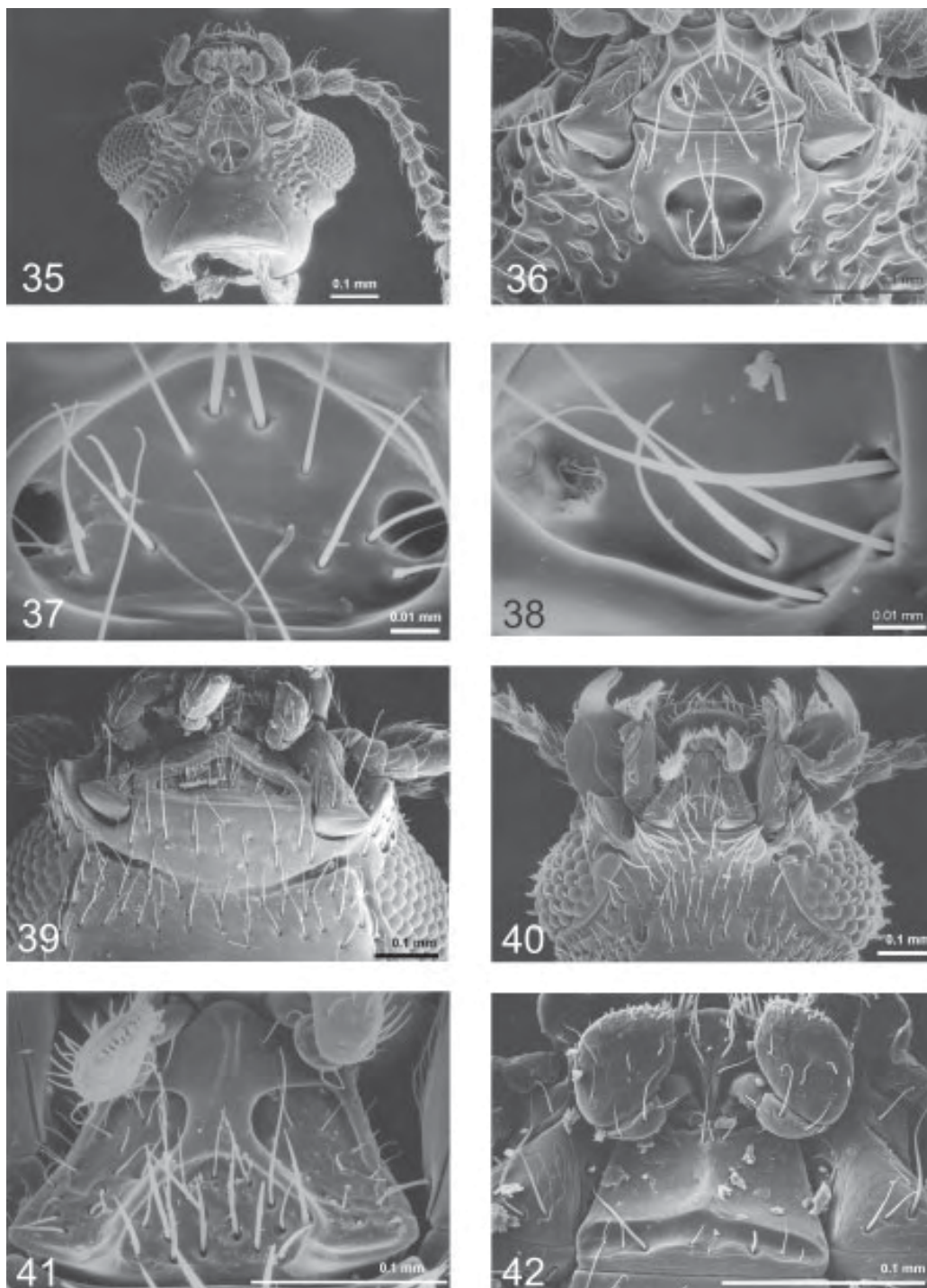




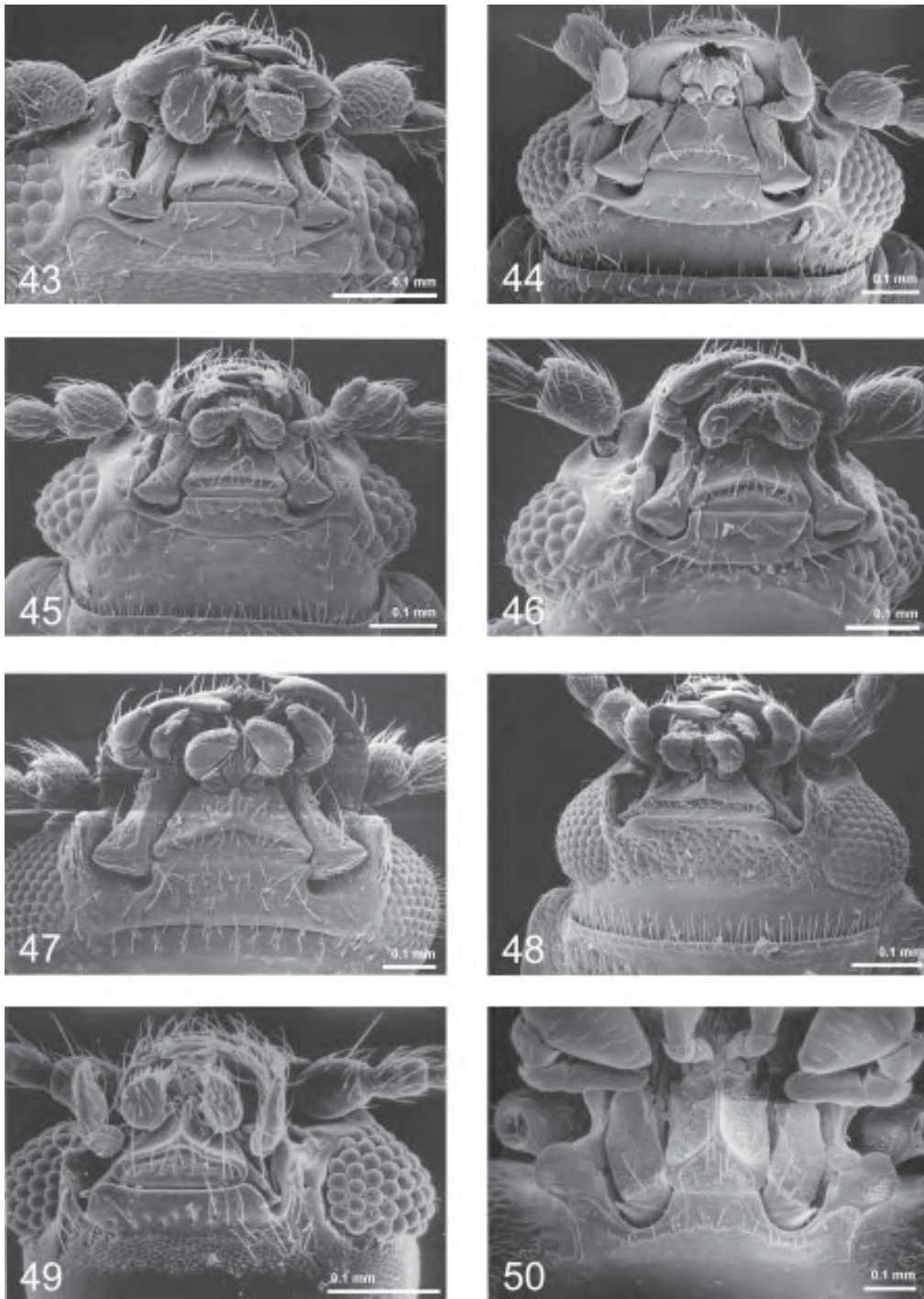
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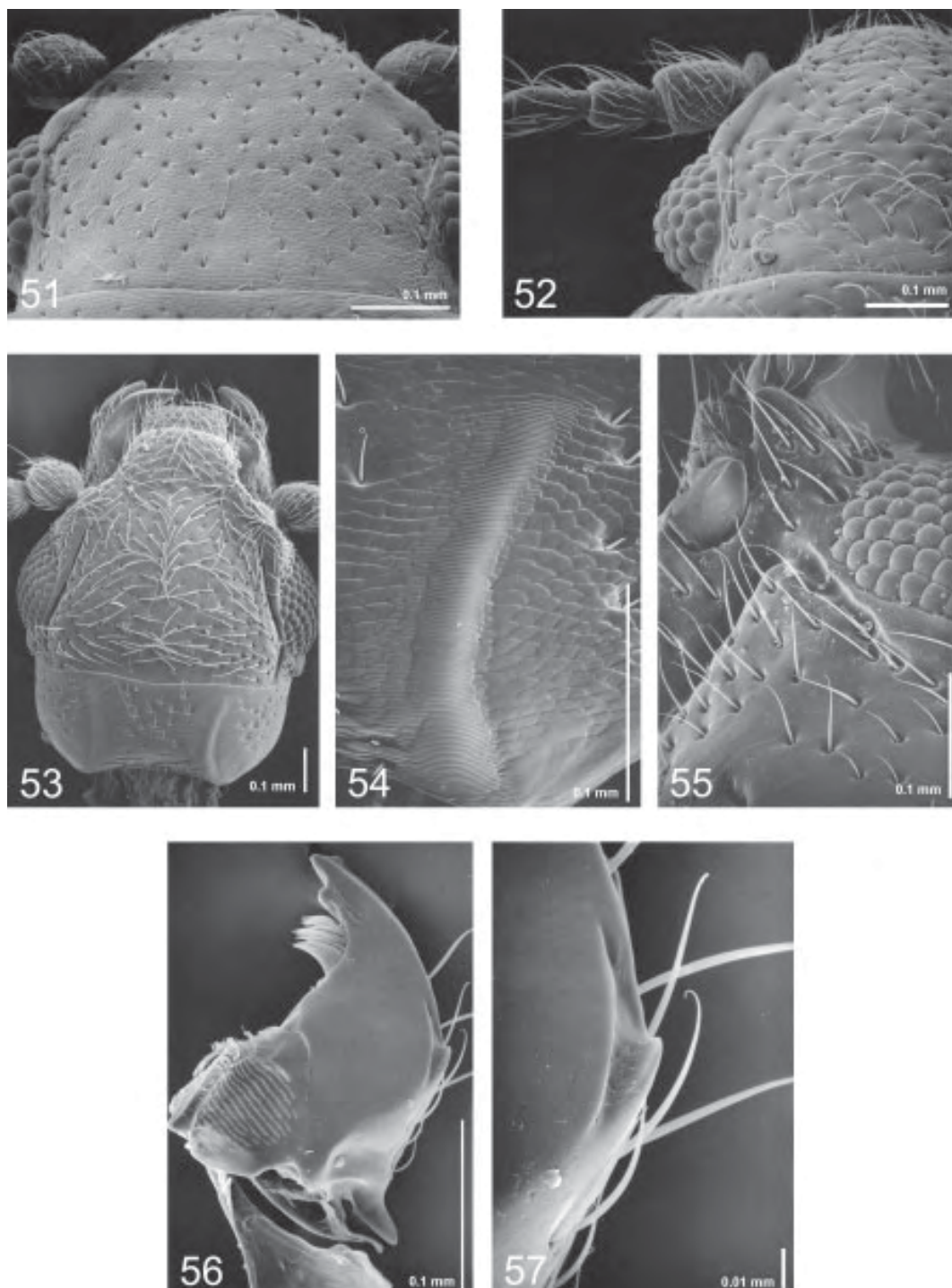


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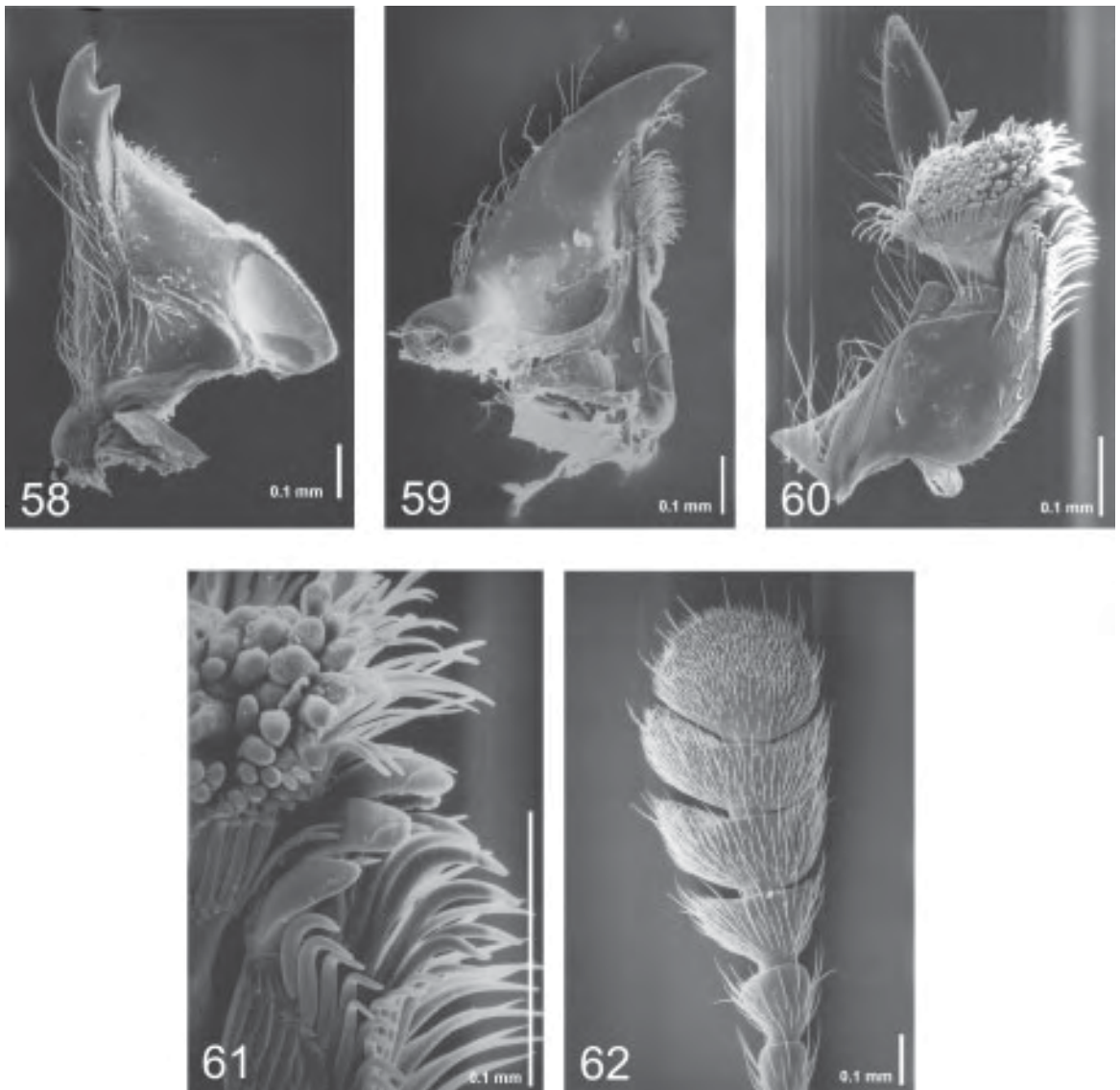
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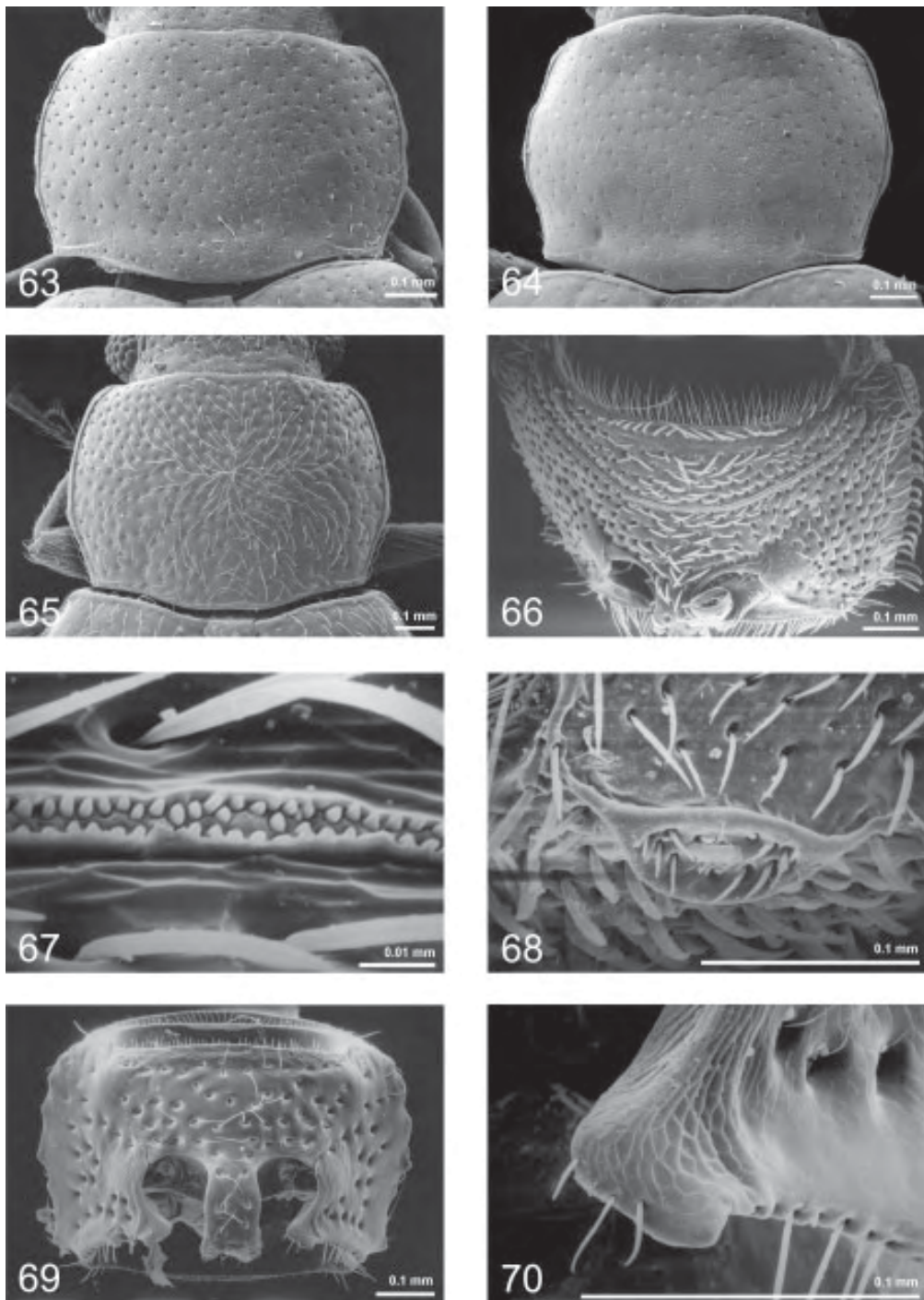


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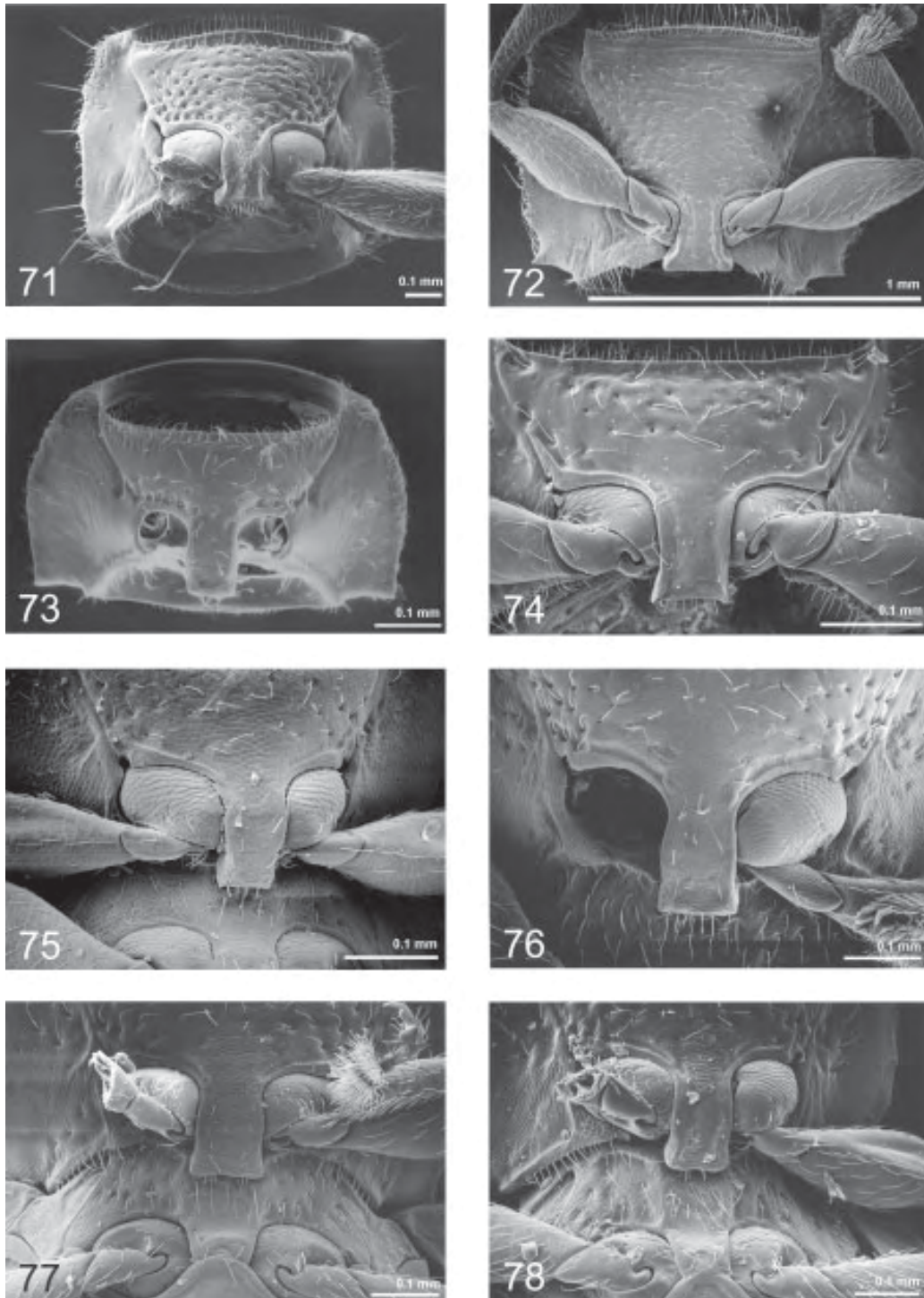




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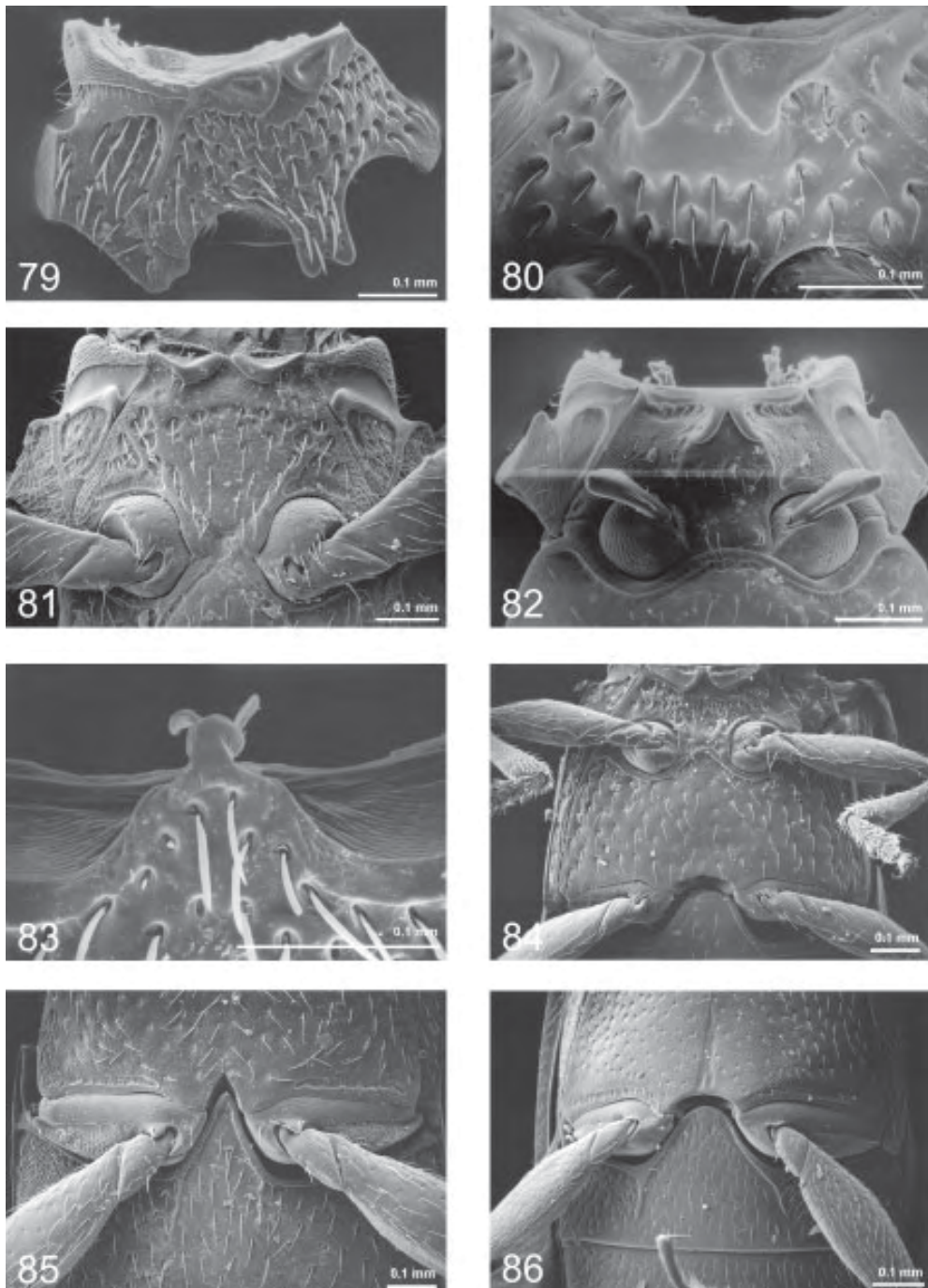


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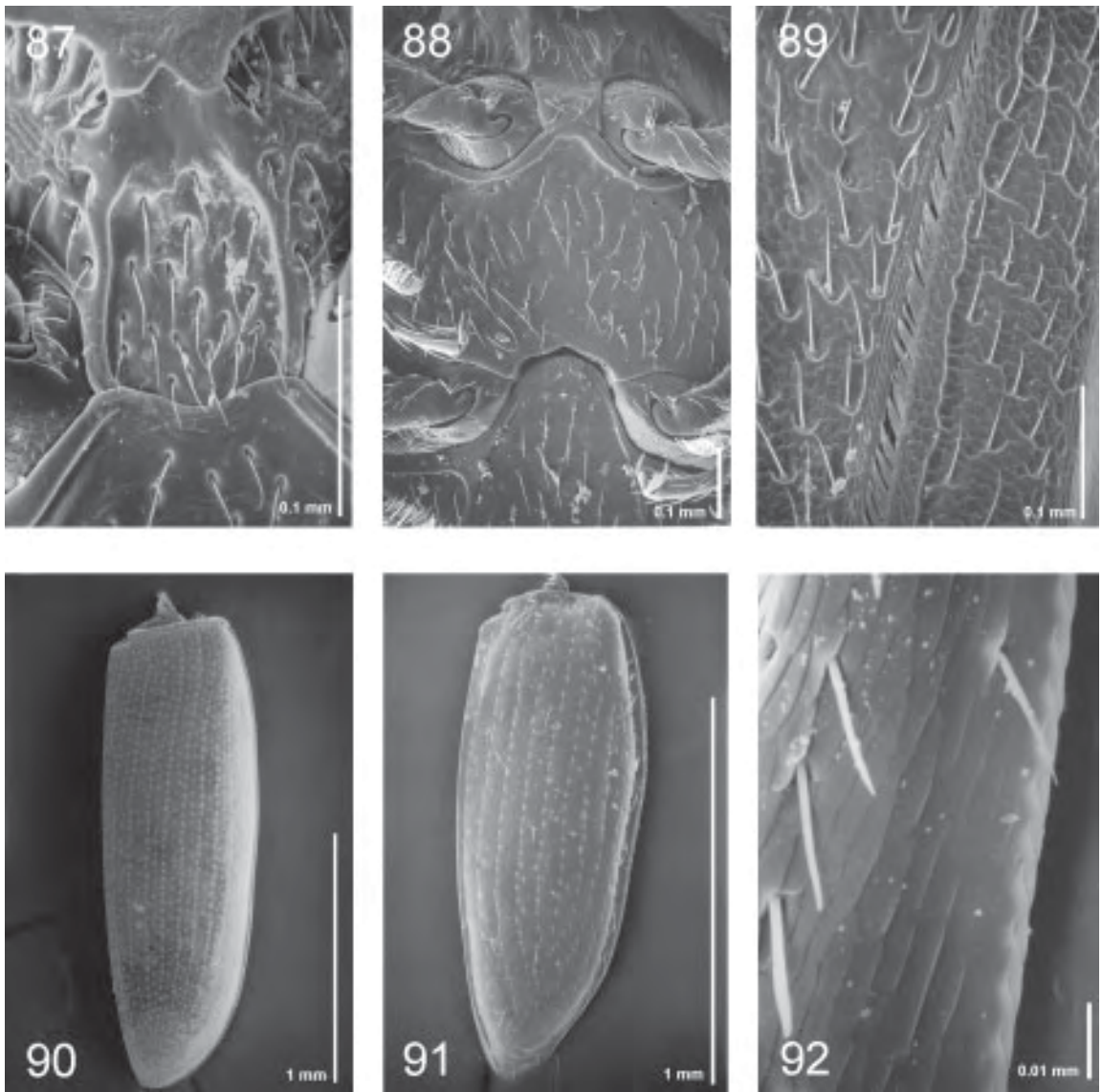


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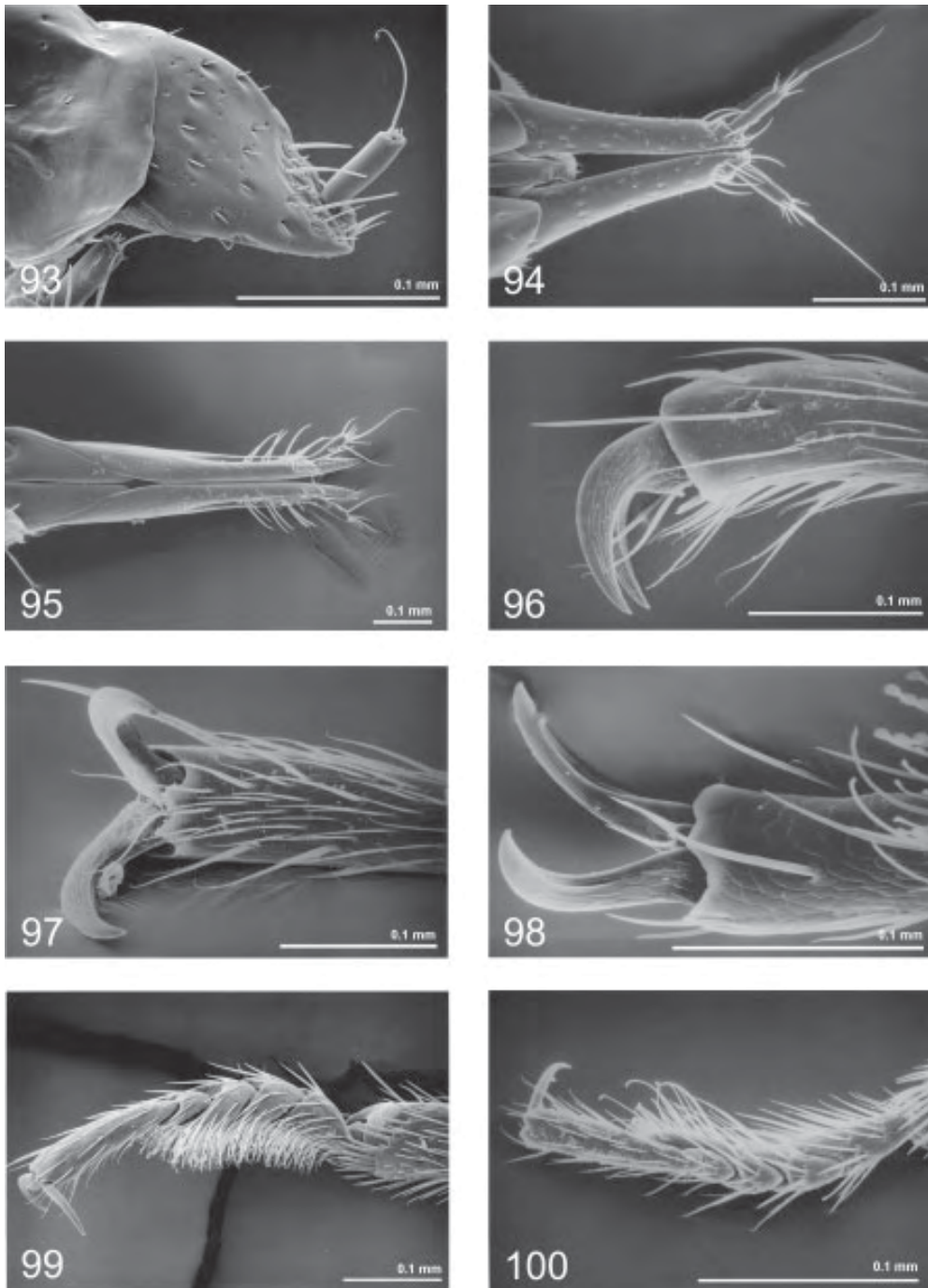


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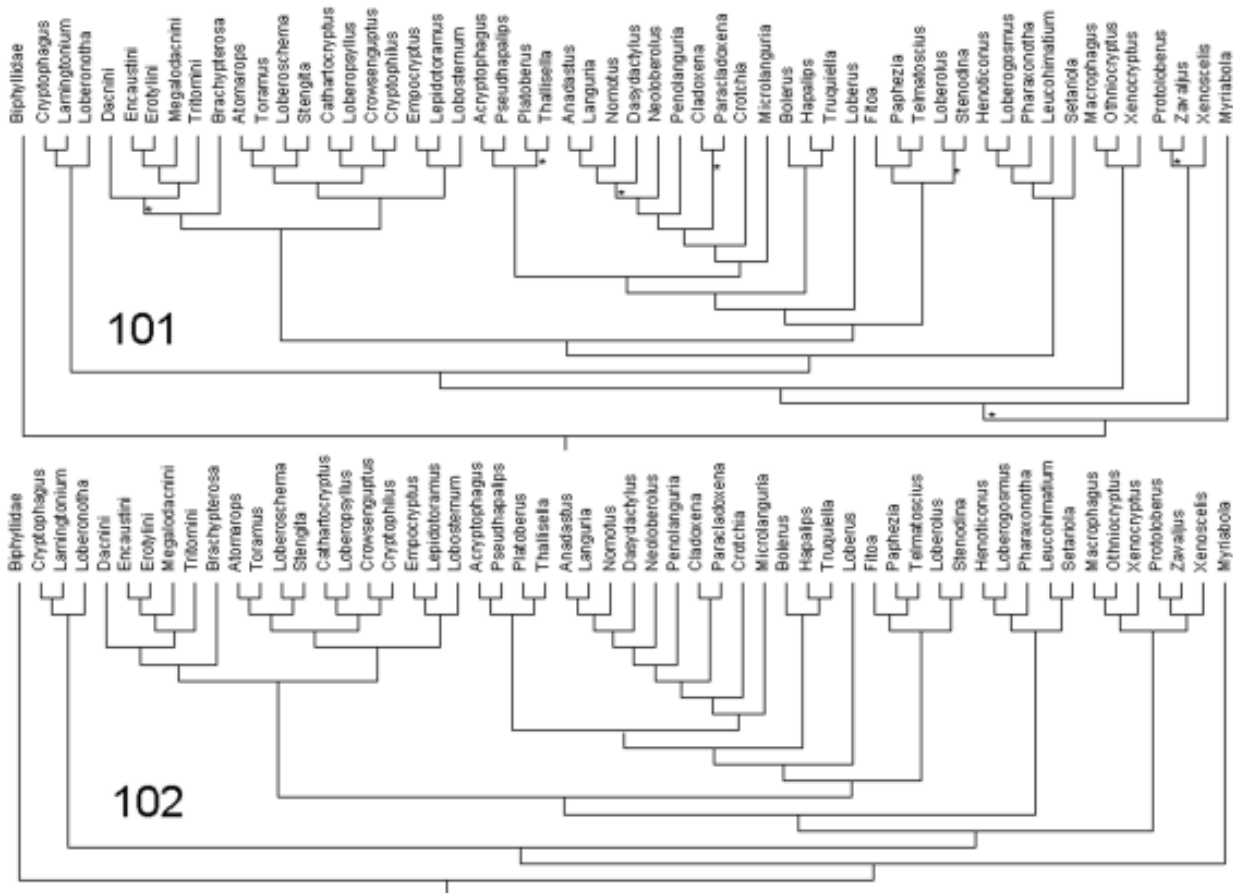


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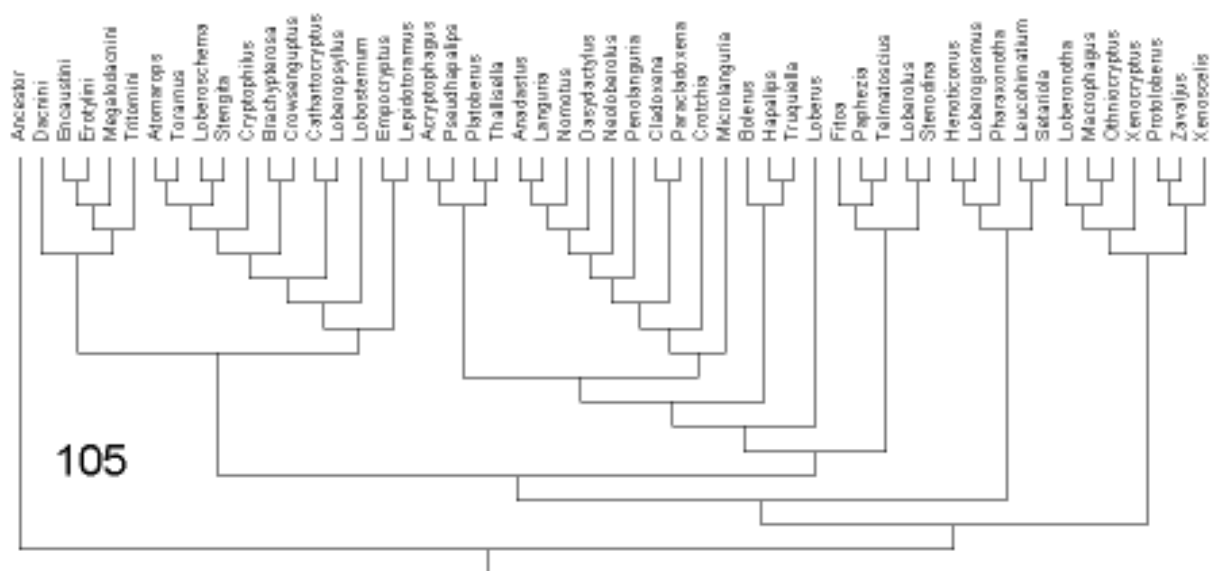
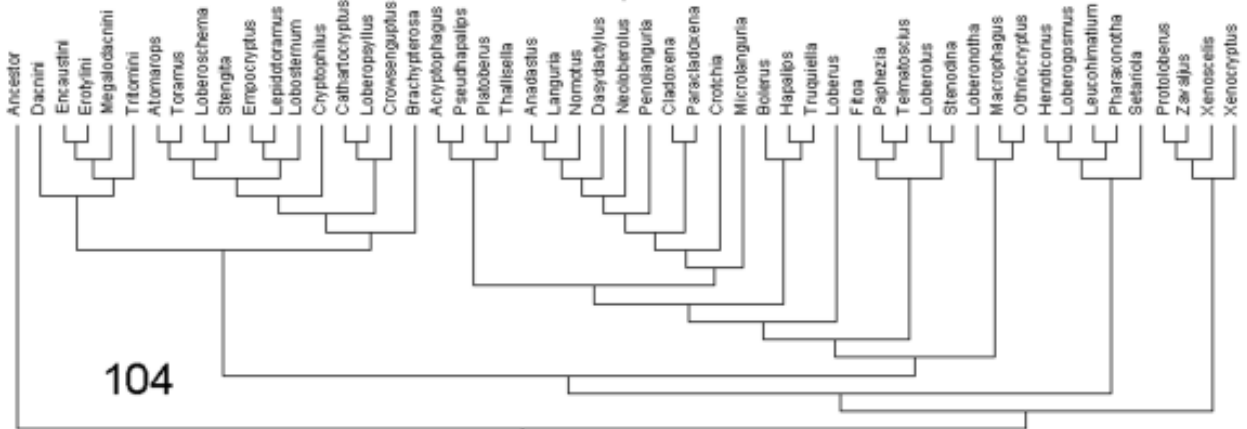
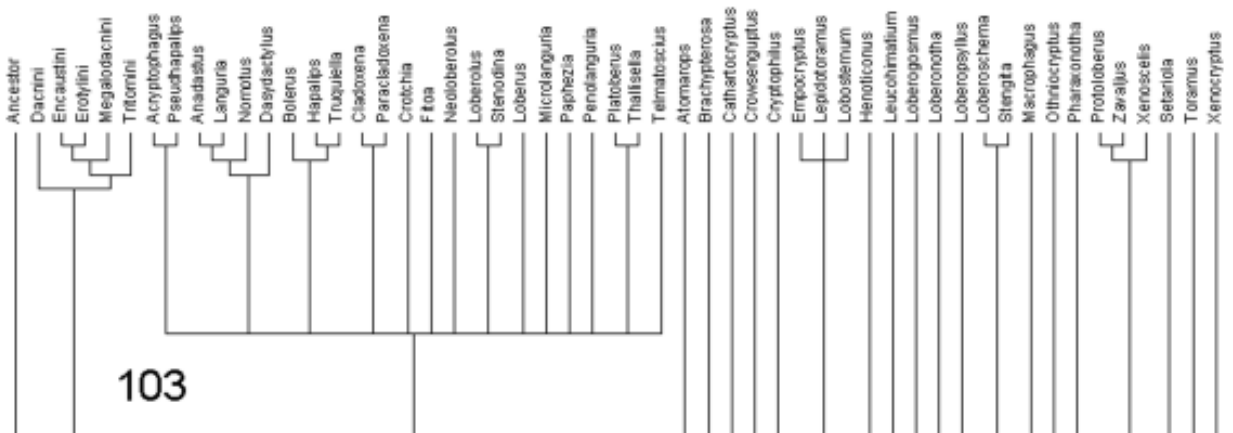




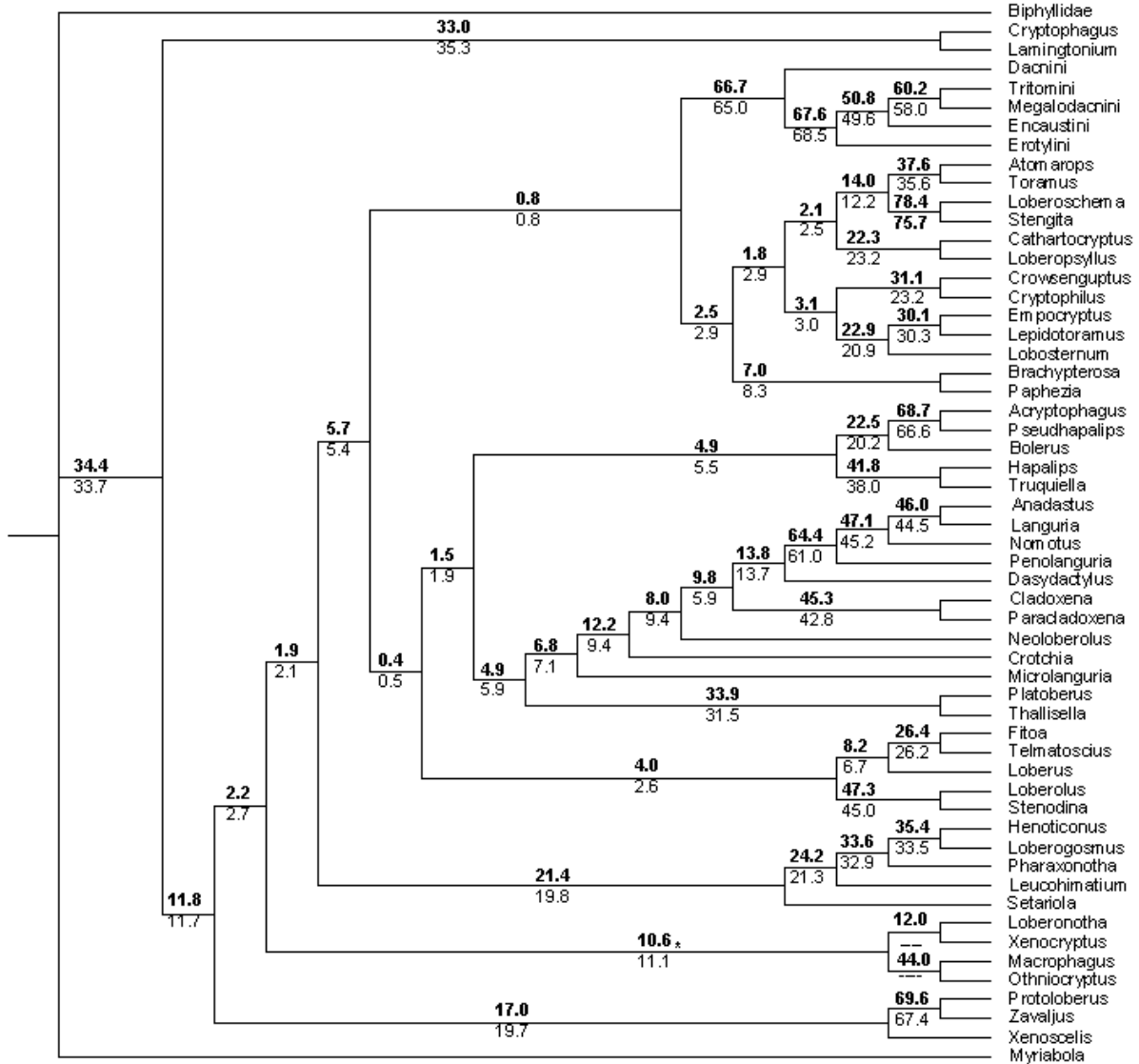
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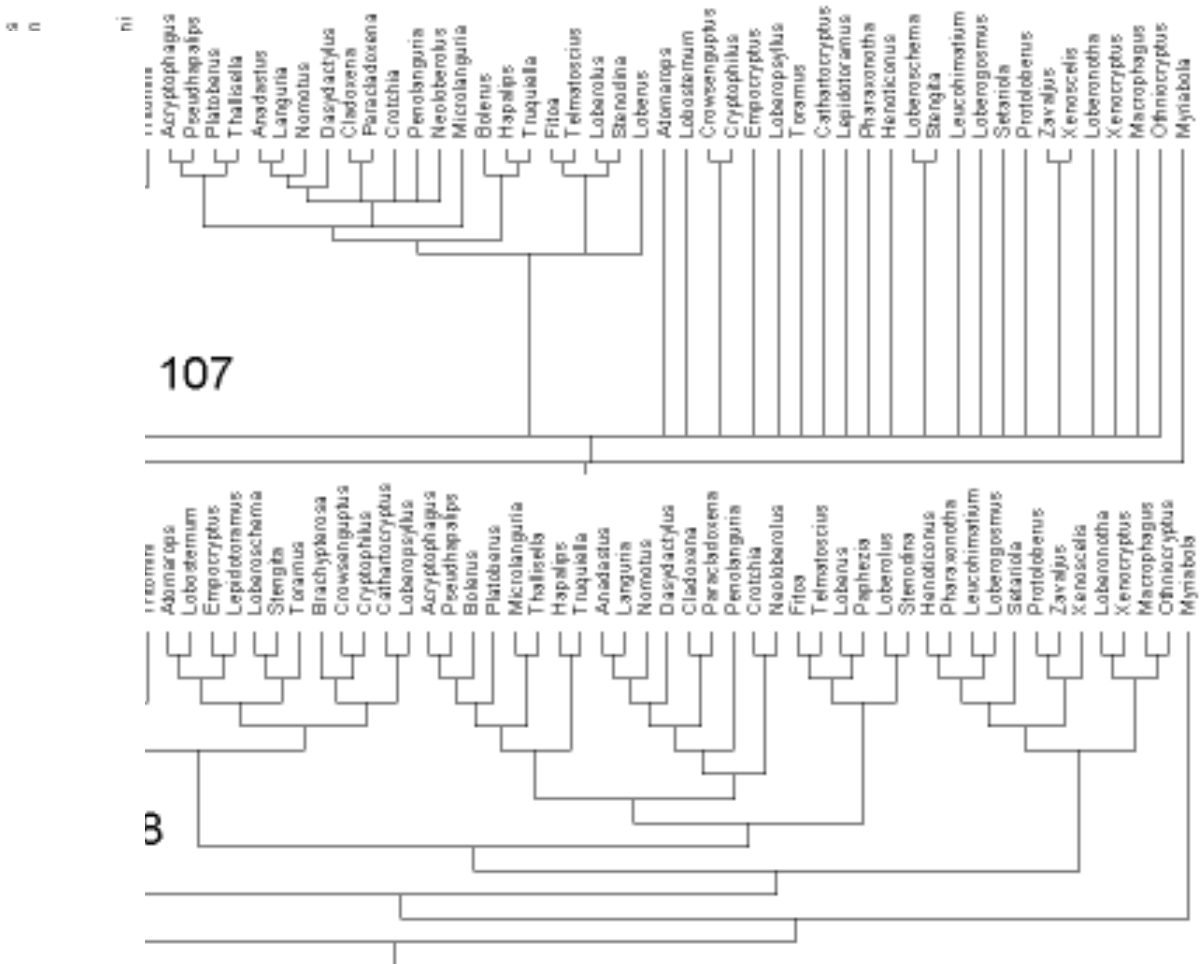


SAW of 184 trees rooted with an ancestor and using the polymorphic option (MIN) for reconstructing changes for polymorphic taxa (105) One tree derived from SAW of 184 trees rooted with an ancestor and using the uncertainty option (UNC) for reconstructing changes for polymorphic taxa.



**Fig. 106** 50% majority rule consensus tree derived by fast bootstrap and jackknife analyses of 1000 replications. Branch support derived by bootstrap is above the branch (in bold) and the support derived by jackknife is below the branch. The arrangement shown for four taxa belonging to Xenoscelinae is based only on the bootstrap analysis.





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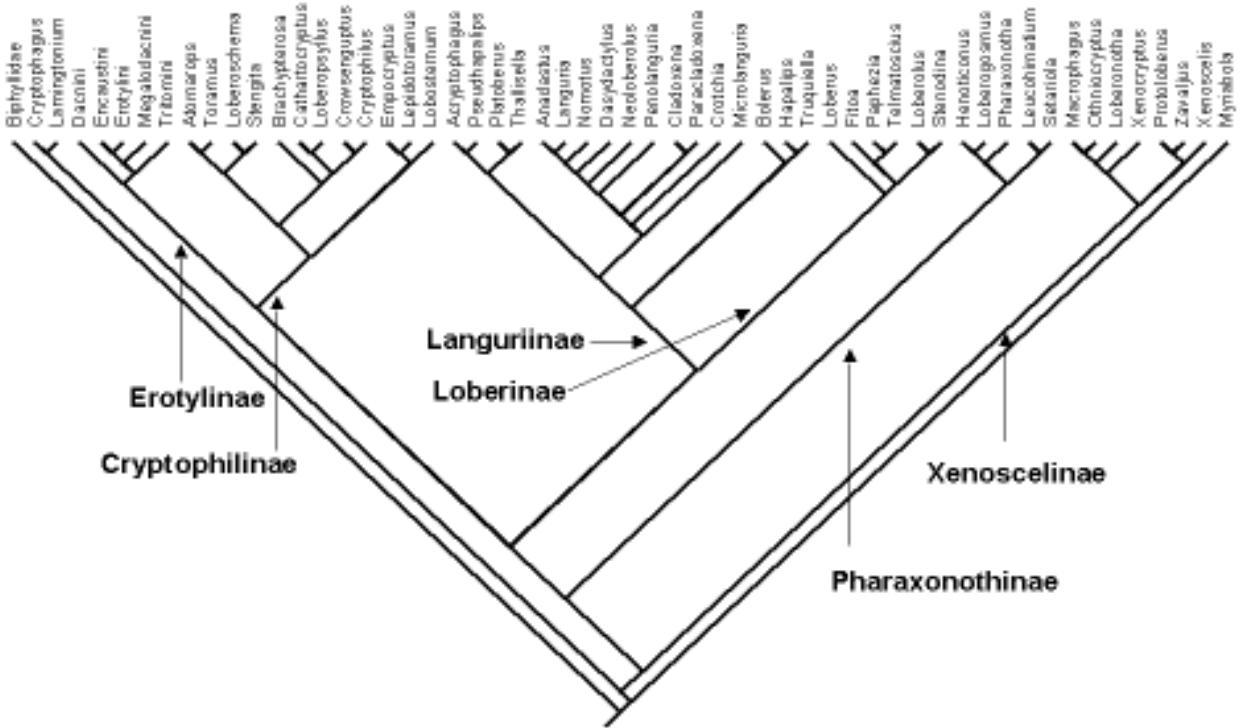
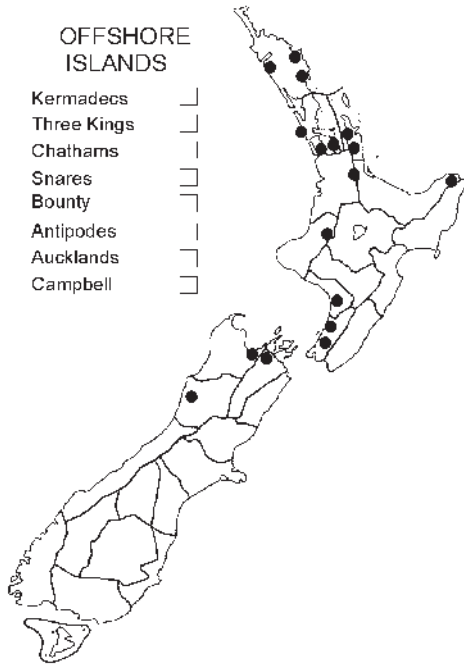
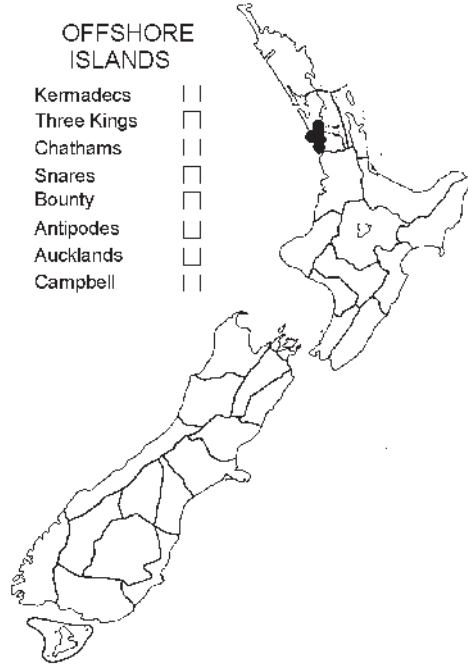


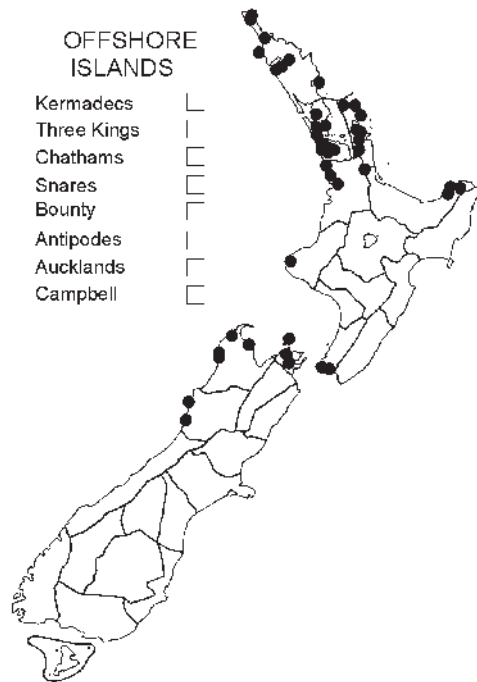
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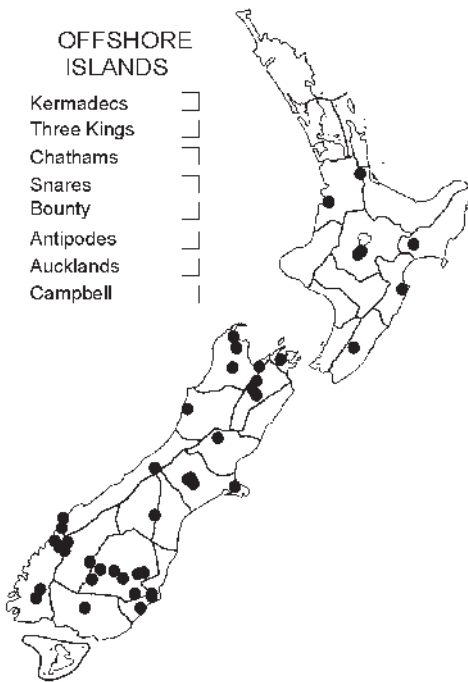
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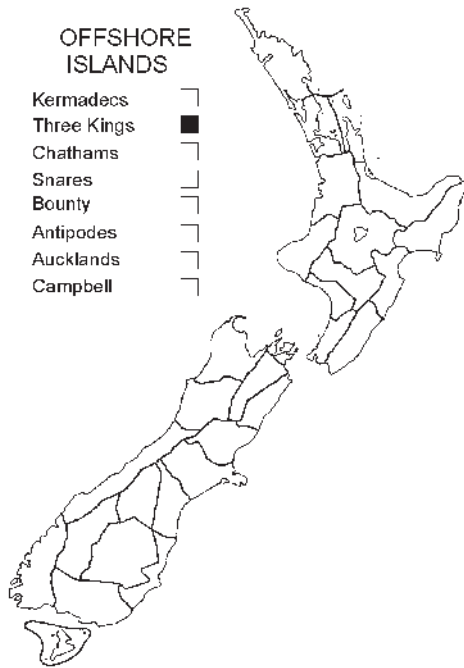
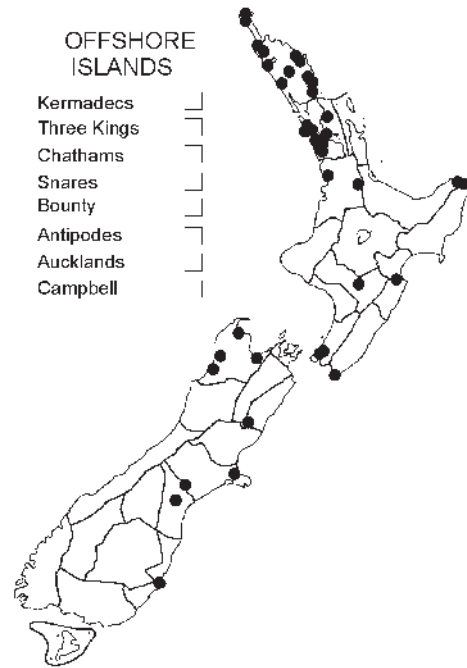
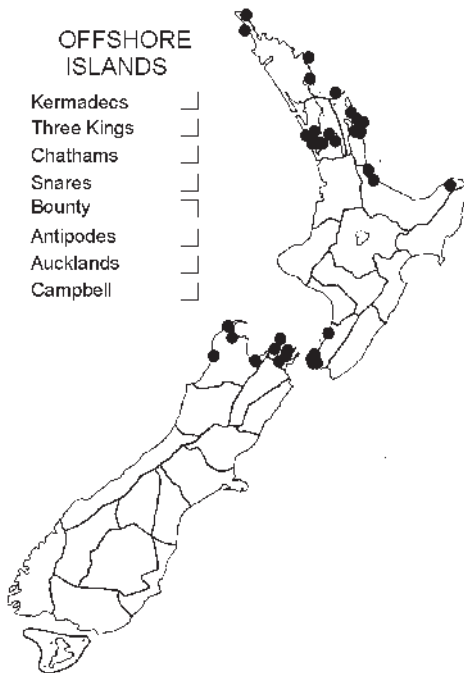
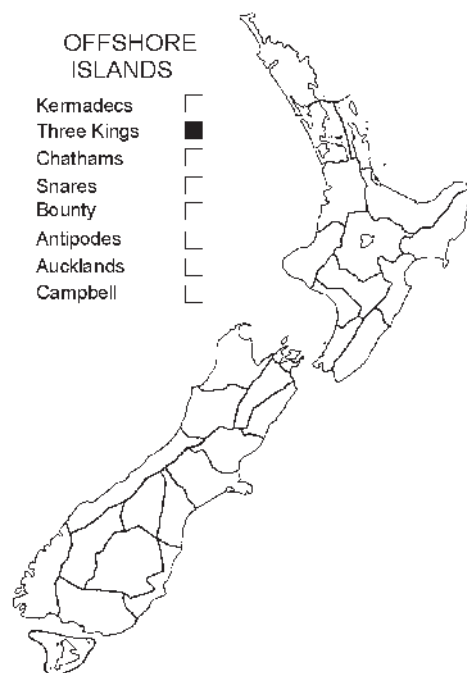
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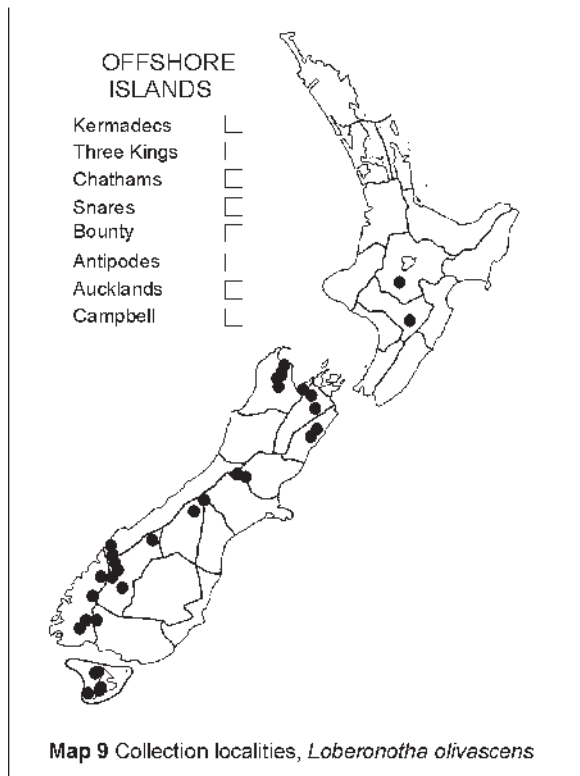


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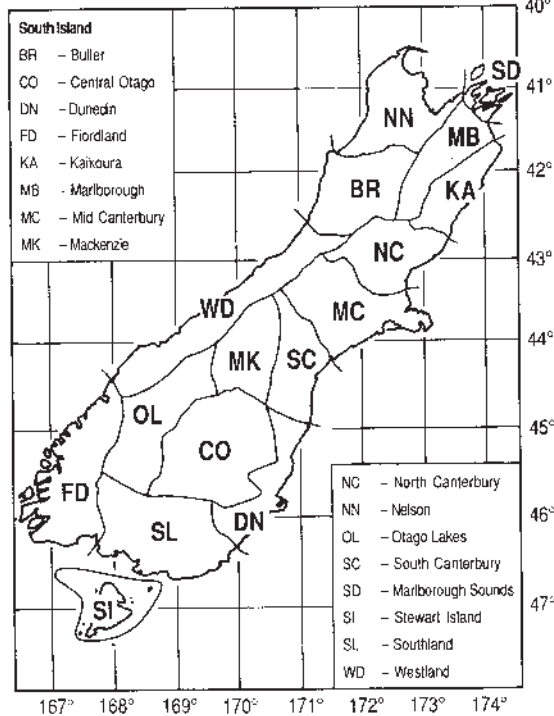
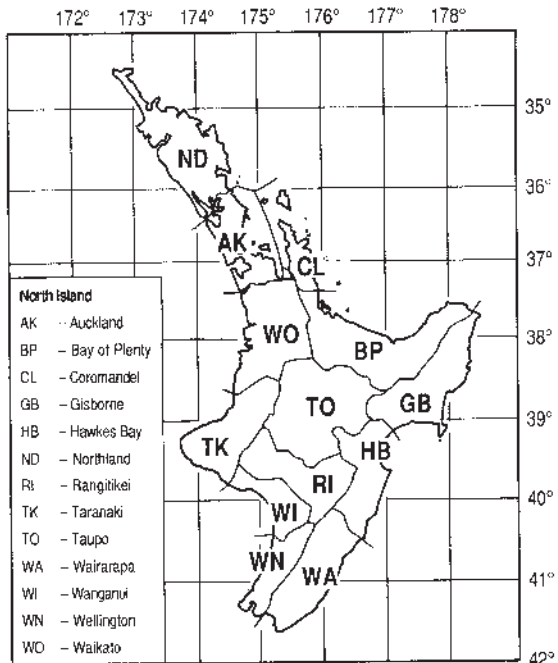
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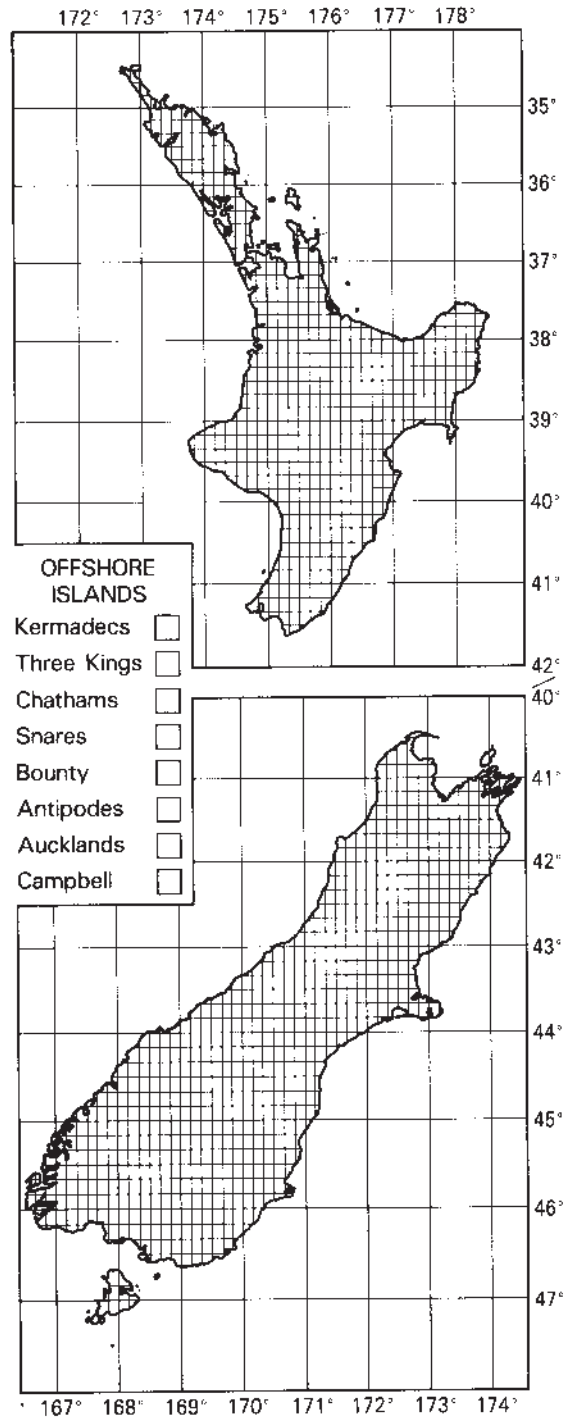
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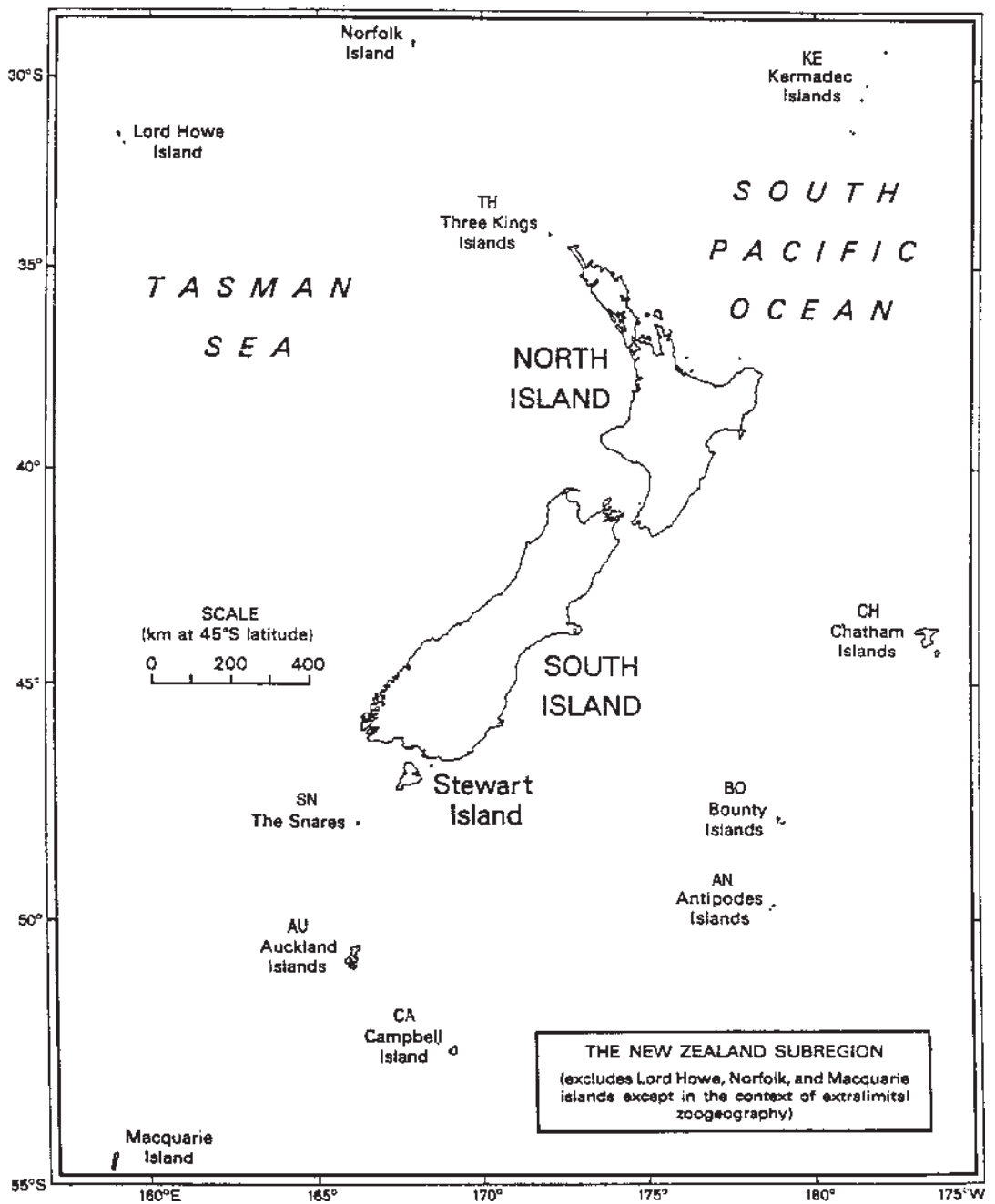
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Area codes and boundaries used to categorise specimen locality data (after Crosby *et al.* 1998)



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The New Zealand subregion with area codes (from Crosby *et al.* 1998).

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