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Phylogenetic relationships of the Australasian Coelometopini (Coleoptera: Tenebrionidae); a quantitative cladistic analysis with a review of biology

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Abstract

The phylogeny of a number of diverse, tropical Australian lineages has been studied recently to lay the groundwork for biogeographic analyses. As part of this effort, we present here a cladistic analysis of the Australasian Coelometopini (Coleoptera: Tenebrionidae: Coelometopinae). A total of 101 morphological characters were coded for 50 taxa. Results show that the Australasian Coelometopini comprises several well-supported clades and that the majority of flightless species from Australian high elevation rainforests form a single monophyletic group. Features of the female genital tube and ovipositor were especially useful in determining close relationship within the tribe. The Coelometopini has been redefined over recent years, and we synthesize and summarize the biology and ecology of the group taking into account the most current circumscription.

Key words: Coelometopinae, Coelometopini, north Queensland, wet tropics, phylogenetics, flightlessness, character evolution, genitalia

Introduction

The rainforests of northeastern Australia support a fascinating and diverse biota (Keto & Scott, 1986) and the evolutionary history of taxa in this area has intrigued biologists for several decades. The region consists of a narrow apron of forest at sea level, flanked by a series of mountains and dissected plateaus rising to as much as 1600 meters in altitude (Nix & Switzer, 1991). Historical climate and habitat changes in the Quarternary Period have combined to promote speciation and endemism in the region (Schneider & Moritz, 1998). Data from vertebrates suggest that high altitude refugia were available during rainforest contractions associated with ice age maxima and, as a result, several unrelated taxa show congruent patterns of distribution today (Joseph et al., 1995; Williams et al., 1996; Williams, 1997; Schneider & Moritz, 1998; Schneider et al., 1998, 1999). Although data on invertebrate taxa are scant, it is clear that insects, especially those with low vagility, are excellent tools for the study of mechanisms that resulted in high species diversity and endemism in these rainforests (Baehr, 1995; Russell, 1997; Monteith, 1997). This paper aims to contribute to the understanding of these evolutionary and biogeographic processes in Australia's tropical rainforests using the tribe Coelometopini (Coleoptera: Tenebrionidae: Coelometopinae).

The first entomologist who attempted to classify the large and morphologically diverse family Tenebrionidae was Lacordaire (Lacordaire, 1859). His classification was based entirely on the external morphological features of adults and with relatively few exceptions, the subfamilies, tribes and subtribes listed in his work remained unchanged for over 100 years (Watt, 1967). Classifications based entirely on larvae were available subsequently but the first revized classification of the family (including both larval and adult characters) came only 25 years ago (Watt, 1974). The comprehensive investigation of internal features of adults made by Tschinkel & Doyen (1980) has revealed several phylogenetically important characters which were incorporated in a phylogenetic analysis of the entire family (Doyen & Tschinkel, 1982). The currently accepted higher classification of the family Tenebrionidae is summarized in Doyen et al. (1990).

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According to these revised classifications, the "coelometopine lineage" (subfamily Coelometopinae) has been regarded as the best defined higher group within the family. Doyen & Tschinkel (1982: p. 164) state that the characters that differentiate the Coelometopinae from other lineages are "unequivocal, and with the exception of a few genera are fully expressed in all members". The characters alluded to are all internal features of adults: 1) highly specialized ovipositor with modifications involving the paraprocts and coxites, 2) derivation of the spermatheca from the distal part of the spermathecal gland and 3) large abdominal defence reservoirs supported by annular sclerotized bands, and gland secretions reaching the reservoirs through one or a few collecting tubules. Unfortunately, members of the subfamily Coelometopinae are often difficult to differentiate from members of other subfamilies on the basis of external morphology of adults and dissection is often required for adequate placement. The subfamily includes three tribes: Coelometopini, Strongyliini and Talanini (Doyen, 1989) and the present paper deals principally with one of them, the Coelometopini.

In catalogues and checklists published before the revized classification of the Tenebrionidae, members of the tribe Coelometopini were often included in several other tribes such as Tenebrionini, Cnodalonini, Diaperini, Misolampini, Helopini, Bolitophagini and Nodotelini (= Eutelini) (Doyen & Tschinkel, 1982; Doyen, 1989; Doyen et al, 1990). Based on characteristics of the internal female genital tube, ovipositor and defence reservoirs, the tribes Misolampini, Nodotelini (= Eutelini), Hegemonini and Cnodalonini are now considered junior synonyms of the tribe Coelometopini (Doyen, 1989; Doyen et al, 1990). In this modern sense, the tribe Coelometopini contains a morphologically diverse group of taxa distributed worldwide, with the largest number of species being found in tropical and subtropical forests (Doyen, 1989). Phylogenetic hypotheses within the Coelometopini are unavailable and the production of a meaningful generic classification remains a major task (Doyen, 1989), both within zoogeographical realms and in a world sense.

Approximately 100 described species in the tribe Coelometopini are known to occur in Australia. The bulk of these species, as for most of the Australian tenebrionid fauna, were described late last century and in the early 1900's (Doyen et al., 1990). More recently, Kaszab included a number of Australian Coelometopinae species in his treatments of the Indo-Pacific tenebrionid fauna (e.g. *Scotoderus* Perroud (Kaszab, 1973), *Derosphaerus* Thomson (Kaszab, 1987), *Promethis* Pascoe (Kaszab, 1988a, b) and Strongyliini (Kaszab, 1977)). Additionally, Matthews & Doyen (1989) described the new genus *Kaszaba* from four species previously included in *Menephilus* Carter & Bouchard (in press)

described two species in a new Australian tropical genus.

Because the tribe Coelometopini contains genera and species which were previously placed in several different tribes, and subfamilies, the retrieval of the biological information on its members is often complex. Here, we present a first review of various aspects of the biology and ecology of the species of Coelometopini. The information presented is somewhat biased because the most significant work to date on the tribe has been done on the fauna of America north of Colombia. Data on tropical fauna is especially poor and this review is intended to trigger interest and information gathering on all biological aspects related to this understudied, species-rich tribe.

Several species of Coelometopini, because of their nocturnal habits, restriction to more or less intact forest habitats and inability to fly are often scarce in collections (Doyen, 1995). However, recent sampling of northern Australia's rainforest invertebrates has revealed a large number of previously undescribed Coelometopini species (Monteith, 1995; Fig. 1). In this paper, we present the first phylogenetically based assessment of the members of the diverse tribe Coelometopini. This preliminary analysis, based entirely on morphological features of adults, includes undescribed species from the northern Queensland wet tropics as
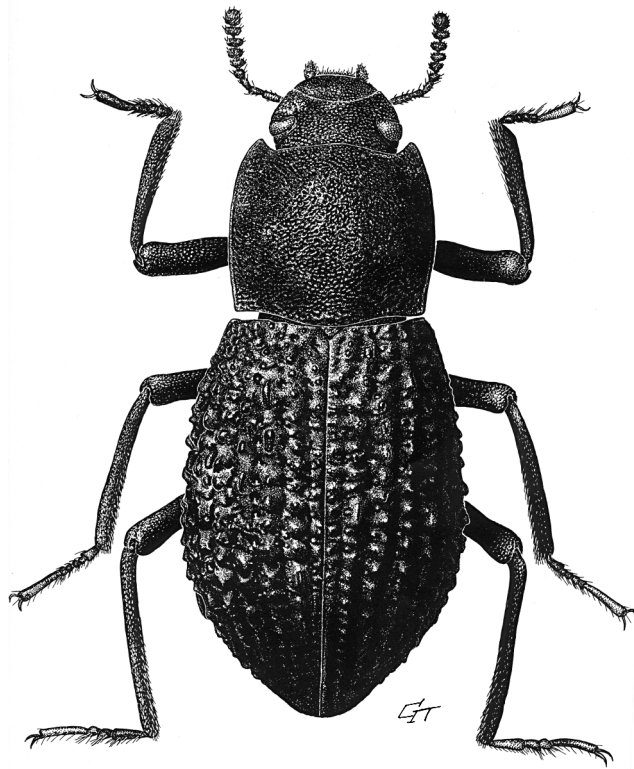

Fig. 1. Dorsal view of *Caxtonana* CM06, ♀. Body length = 12 mm.

well as representatives of Coelometopini genera present in Australia and surrounding countries.

The three main goals of the study are: 1) to summarize the information on the biology and ecology of the members of the tribe Coelometopini for the first time, 2) to quantitatively test the hypothesis, using cladistic methodology, that the largely undescribed northern Australia tropical fauna forms one or more natural, monophyletic group (s) and 3) identify a set of potentially closely related taxa (sibling taxa) of the northern Australia fauna which will be included in a future species level analysis.

Biology and Ecology

Habitat

Coelometopini primarily occupy forested habitats, with the largest number of species being found in tropical and subtropical regions of the world (Doyen, 1989). Adults are seldom seen during the day in tropical rainforests because of their nocturnal lifestyles (Doyen, 1995), but when found, they usually occur under loose bark and either in or under dead logs. In temperate regions, adults have been collected under the bark of several species of trees (Doyen, 1973; Miller, 1978b) during all seasons of the year. In a study of habitat preferences in several species of Tenebrionidae in an oak-conifer woodland in Arizona, Doyen and Tschinkel (1974) found that the species *Coelocnemis magna* LeConte shows a strong preference for a substrate of standing dead wood, which the adults use as daytime shelters and in which the larvae develop. They also found that adults of *Coelocnemis* Mannerheim, which are flightless and therefore less vagile than other tenebrionid species, are "specialists" in their substrate requirements in that they are almost exclusively found around decaying wood. This specialisation is thought to increase sexual contacts in low vagility species (Doyen & Tschinkel, 1974).

Label data can often be useful in determining both habitat preferences and elevation at which the beetles live. Of the 22 Coelometopini species reported from the Fiji Islands, Kaszab (1955; p. 441) demonstrates that eight of them prefer habitats above 150 meters (3 of them were collected only above 900 meters) while six species were only collected below 150 meters. The other species were found in various elevation zones. In this case, winged and flightless species were found at all altitudes although there was a tendency for flightless *Asopidiopsis* Kaszab species to be found only at high altitudes (Kaszab, 1955). The flightless Coelometopini species described by Kaszab (1986) were all collected above 1500 meters and two females of *Apterobrachys*

wilhelminae Kaszab were collected at an altitude of 3600 meters. In the northern tropical forests of Australia, the tribe Coelometopini seems to show pronounced restriction to high altitude rainforests (Monteith, 1995). It should be mentioned here that a large number of flightless taxa inhabit only small patches of intact forest habitats and are potentially subject to local extinction if habitat degradation occurs. Of the three tenebrionid species listed on the IUCN Red List of Threatened Animals, only one receives the status of "critically endangered", the Coelometopini species *Polposipus herculeanus* Solier (World Conservation Monitoring Centre, 2000).

Kaszab (1955) summarizes the trapping method found on label data of tenebrionids from Fiji. This list shows that most of the specimens of Coelometopini were collected by beating of shrubs and other surfaces or found on dead branches. Three winged species were collected "at light" (*Bradymerus amicorum* (Fairmaire), *Chariotheca kulzeri* Kaszab and *Thesilea versicolor* Haag-Rutenberg) while two other species (*Thesilea impressipennis* Haag-Rutenberg and *Asopidiopsis csikii* Kaszab) were collected on the "seashore". The large collection of adults from northern Australia's tropics (over 3000 specimens) were mostly collected at night with a headlamp (harvesting specimens browsing on the surface of trees or fallen branches) while others were collected during the day using a pyrethrum knockdown technique on dead trees (see Baehr, 1995 for details of technique).

As mentioned before, the majority of species in the tribe Coelometopini are found in subtropical and tropical forests. However, some species such as *Hypaulax orcus* Pascoe are known to occur in arid areas (Matthews, 1987) and several genera have evolved in higher latitudes where they have to survive during several months with temperatures below the freezing point. Bousquet (1991) reported 11 species of Coelometopini from Canada and Alaska in seven genera. The most interesting of these, in terms of survival under extreme cold temperatures, is *Upis ceramboides* Fabricius. This species, which overwinters as adult under the bark of various trees, can survive prolonged freezing to at least -50°C (Miller, 1975; Miller & Smith, 1975; Miller, 1978a, b; Lundheim & Zachariassen, 1993).

Life history

The most comprehensive published data of Coelometopini life history was gathered by Doyen (1973) for the North American genus *Coelocnemis* Mannerheim. Through his laboratory work, Doyen demonstrated that females can remain reproductive for several years and that only a minority of individuals are responsible for the pairings at any one time. Impregnation is by means of an

elongate, threadlike spermatophore and viable sperm may be stored in females for at least a few months. Up to about 50 eggs were laid by females in cracks in the substrate (especially rotten wood) under laboratory conditions, however, oviposition has yet to be observed in the field. Approximately 14 days elapse between oviposition and emergence of the first instar larva. After five or six moults, the larva reaches its mature size (usually requiring one to two years to reach maturity in laboratory conditions) and excavates an irregular cell for pupation in the substrate. Pupation occurs after that last instar larva has spent 12–15 days in the pupal cell. The pupal stage of the different *Coelocnemis* species varies between 19 to 27 days and occurs in the summer months. After emergence, the adults remain teneral for two to three weeks and are apparently not capable of reproducing before the next spring. The lifespan of adults is relatively long among insects and specimens of *C. californica* Mannerheim have been kept under laboratory conditions in excess of five years (Doyen, 1973). Larvae of *Polposipus herculeanus* Solier have also been reared from egg to adult (Marshall, 1982). A total of seven instars were recorded for this species.

In both studies mentioned above, adults reared from the eggs under laboratory conditions were found to be smaller than wild adults. Two main explanations have been suggested for this: 1) insufficient or improper stage of decomposition of the larval food (usually pieces or bark and wood from the same species of tree where the adults were collected from) and 2) the absence of eugregarine protozoans in specimens reared from "artificial diet". It has been reported that absence of eugregarines in the gut of *Tenebrio molitor* Linnaeus (Tenebrioninae: Tenebrionini) significantly reduces final pupal weight and pupation success of larvae reared on suboptimal diets (Harry, 1969 in Doyen, 1973). No published data are available on the life history of Australian Coelometopini although associations of a few larvae with adults are known in collections.

Adults of the tribe Coelometopini are often found only around dead and decaying wood and all members of the subfamily Coelometopinae feed and develop almost exclusively in dead and decaying wood as larvae. This life history trait is one way to determine whether a certain species or genus belongs to the Coelometopini or the morphologically similar (as adults) tribe Tenebrionini. Tenebrionini larvae and adults are frequently found in caves, nests of vertebrates, stored products, etc. and the larvae in this tribe lack the strongly sclerotized, recurved urogomphi characteristic of Coelometopine larvae (Marshall, 1982; Doyen, 1989). The presence of these characteristic urogomphi in the Coelometopinae is attributed to their lifestyle and is thought to be important for locomotion in burrows and may also serve a protective function (Marshall, 1982).

The members of a group of genera from Africa and Madagascar previously placed in the coelometopine tribe Strongyliini (subtribe Praeugenina of DeMoor, 1970) are known to be associated with nests of mammals (Penrith, 1982). *Praogena, Nesogena* and related genera were recently transferred from Strongyliini to the tenebrionine lineage (possibly near Heleini) by Doyen & Tschinkel (1982) making the subfamily Coelometopinae uniform in terms of larval habitat requirements. The small number of described Coelometopini larvae have been found in a wide variety of host trees (data summarized in Marshall, 1982).

Chemical secretions

All the members of the subfamily Coelometopinae possess abdominal defensive glands which secrete hydroquinones, often in combination with other substances. These secretions are stored in a pair of reservoirs which empty their contents between sternites seven and eight when the beetles are disturbed. Tschinkel (1975c) isolated the principal chemical components of nearly 150 species of tenebrionids in an attempt to assess their potential as diagnostic characters for some higher taxa. Species from seven North American Coelometopini genera were included in Tschinkel's study (all placed in the tribe Tenebrionini). Some of these taxa had uncommon compounds in their secretions such as 1-heptadecene in *Merinus* LeConte and *Cibdelis* Mannerheim as well as *p*-benzoquinone in amounts greater than five percent in *Alobates* Motschulsky and *Iphthiminus* Spilman.

Seven Asian Coelometopini species (placed in the subfamilies Tenebrioninae, Cnodaloninae and Misolampinae by the author at the time) were investigated in a study of abdominal defensive systems of tenebrionids by Kanehisa (1978). Results showed that species of *Promethis* Pascoe, *Derosphaerus* Thomson and *Hemicera* Castelnau et Brullé contained relatively large amounts of *p*-quinone.

The New Zealand endemic species *Chrysopeplus expolitus* Broun was found to have benzoquinones, pentadecene, heptadecene as well as methyl esters in its defence secretions (Gnanasunderam et al., 1984). The detection of the methyl esters of 6-methyl- and 6-ethylsalicylic acids in this species constituted the first observation of these compounds in the family Tenebrionidae (the latter being a new arthropod natural product).

The defence secretions of Australian tenebrionids were recently investigated by Brown et al. (1992). A total of 11 species of Coelometopini were included in the analysis. Results of this investigation showed that, apart from the benzoquinones found in all tenebrionids, members of the tribe Coelometopini also contain additional compounds such as limonene, a-pinene, a-phellandrene, 1-tridecene and others.

Although analyses of the defence secretions of a wide range of Coelometopini species have yet to yield diagnostic components for the entire tribe, the chemical composition of secretions has potential significance at a generic level. Doyen (1973) reported that the composition of the defensive secretions clearly separates *Coelocnemis* from other related genera, although variations between the different species within the genus were not consistent. His analyses also showed that *Iphthiminus zopheroides* Horn had strikingly different chemical compositions in its defence secretions from other *Iphthiminus* species and was transferred to the genus *Oenopion* Champion (Doyen, 1971).

The defensive secretions of tenebrionid beetles have been demonstrated to repel a number of vertebrate predators (Eisner & Meinwald, 1966; Raske, 1967). However, remains of tenebrionid beetles have been found in the excretions of a considerable number of mammals and birds (summarized in Tschinkel, 1975c). Doyen (1974) reports that Channel Islands foxes have more remains of tenebrionids without glands (subfamily Pimeliinae) in their scats than tenebrionids which possess glands.

Doyen (1973) suggested that the defensive secretions may also function as general attractant serving to assemble several specimens in suitable shelters. This suggestion was based on observations that overwintering in *Coelocnemis* entails marked aggregations of adults. Doyen records masses of up to 50 adults of the genus *Coelocnemis* in a single overwintering site. This effect would also tend to explain why adults of different tenebrionid genera (within the tribe Coelometopini as well as distantly related ones) are often found in mixed aggregations in suitable shelters. Aggregating masses have not been observed in overwintering Australian species and this behavior may be restricted to latitudes where low temperatures are a threatening process for overwintering adults.

A number of tenebrionids (e.g. Ulomini, Tenebrionini, Diaperini) also have a pair of prothoracic glands used for defence against predators (Kendall, 1974). These glands are absent in members of the subfamily Coelometopinae.

Defence behavior

The first extensive study of the defence behavior of tenebrionids was that of Tschinkel (1975a). In his work, the mode of delivery and the behavior of the beetles before and after the release of secretions was investigated in several taxa. The tribe Coelometopini was represented by nine species in seven genera (all were included in the tribe Tenebrionini at the time). The results showed that eight of the nine species "exude" their defence secretions. The other species (genus *Mylaris* Motschul-sky) was recorded as using a "spray" for the mode of delivery. Both exuding and spraying are considered derived behaviors as opposed to the "everting" mode of delivery of more primitive tenebrionids (Tschinkel, 1975a; Tschinkel & Doyen, 1980). When exuded, the defensive secretion spreads anteriorly over the elytra and ventrites (Doyen, 1973). The spread of the secretions onto the source of disturbance (i.e. potential predator) is sometimes aided by a transfer of the substance from the sternites to the predator by movement of the hind legs. This behavior was recorded in the Coelometopini in two genera (*Cibdelis* Mannerheim and *Alobates* Motschulsky) (Tschinkel, 1975a).

Two other types of behavior have been recorded in the tribe Coelometopini: death-feints and "headstanding". The former occurs when the legs and antennae of the beetles are folded flat against the ventrum when disturbed (Weiss, 1944; Tschinkel, 1975a). This position is usually maintained for a period of time before the specimens start moving again. In laboratory experiments, it was demonstrated that the sensitivity to external stimuli and period of recovery after disturbance varies between individuals and is also dependent on temperature (Weiss, 1944).

The North American genus *Coelocnemis* Mannerheim is peculiar in that it is the only member of the Coelometopini to exhibit the behavior of headstanding when disturbed (Doyen & Somerby, 1974; Tschinkel, 1975a). A number of *Coelocnemis* species, which occur in sympatry with species of the genus *Eleodes* Eschscholtz (Tenebrioninae: Eleodini), raise the posterior part of their body at an angle between 30 and 60 degrees from the horizontal when approached or touched. Headstanding in *Eleodes* is thought to be of help in directing the "sprayed" secretion towards the disturbance. Most of the tenebrionids which spray their secretion usually show some form of headstanding (Tschinkel, 1975a). The fact that some species of *Coelocnemis*, which "exude" their secretions, perform headstanding has been interpreted as a case of Müllerian mimicry (Doyen, 1973; Doyen & Somerby, 1974; Tschinkel, 1975a). Australian Coelometopini species exude their secretions and combine this behavior with death-feints (authors, personal observations).

Materials and methods

Over 4000 specimens of Coelometopini from Australia and surrounding countries (Papuan and Pacific subregions of the Oriental region (Gressitt, 1961)) were examined during the course of this study. A large number of these represent specimens from undescribed species found in Australia's northern wet tropics. The material included in the present analysis was obtained from the following collections: University of

Queensland Insect Collection, Brisbane, Queensland, Australia (UQ); Hungarian Natural History Museum, Budapest, Hungary (HNHM); Bernice P. Bishop Museum, Honolulu, Hawaii, USA (BPBM); Australian National Insect Collection, Canberra, Australian Capital Territory, Australia (ANIC); Australian Museum, Sydney, New South Wales, Australia (AMS); Department of Primary Industries, Mareeba, Queensland, Australia (QPIM); Queensland Museum, South Brisbane, Queensland, Australia (QM); Tony Hiller Insect Collection, Mount Glorious, Queensland, Australia (THIC); Museum of Victoria, Abbotsford, Victoria, Australia (MVMA). All codens in parentheses follow Evenhuis (1997) except for Tony Hiller's Insect Collection for which the acronym was determined by the authors. Label data as well as deposition of specimens for the 50 taxa included in the phylogenetic analysis is available from the senior author upon request. When large series of an exemplar were available for study, 5 males and 5 females were selected to represent the taxon. Both male and female specimens of all species were studied except for *Rhophobas burgersi* Gebien, *Microphenus sp., Cataphanus sp., Strongylium fuscovestitum* Carter and *Papuamisolampus toxopeusi* Kaszab where only one sex was available. Types were included when available.

Terminology describing the skeletal anatomy follows Lawrence & Britton (1994) and Lawrence et al. (1999). Terminology associated with the defensive glands, ovipositor and female genital tube follows Tschinkel & Doyen (1980). For observation of female genitalic features, the abdomen of the specimen was first removed from the body after soaking the specimen in hot water to soften tissues. The abdomen was then placed in boiling five to ten percent KOH for a few minutes. The tergites on one side of the abdomen (usually the left hand side) were cut or torn along the junction with the ventrites. The ovipositor as well as the defence glands were then separated independently from the abdomen (the length of the defence reservoirs was noted before removal). The complete clearing of the female ovipositor and genital tube sometimes required a few more minutes in KOH. All structures treated in KOH were rinsed several times with distilled water and with 80% ethanol. The female genital tube as well as the defence glands were stained with a saturated solution of Chlorazol Black in 40% ethanol. Dissections were done in 80% ethanol.

Tschinkel and Doyen (1980) recommended cutting off the membrane below the ovipositor (paraprocts) after clearing for the simultaneous study of the coxites, paraprocts and genital tube. We found that a number of phylogenetically important characters that describe the shape, size and relative position of structures between the base of the paraprocts and segment eight are lost using this technique. The change from Tschinkel and Doyen's dissecting technique (1980) is as follows: once cleared, the genital tube is cut off at the base of the still folded ovipositor, the apex of the ovipositor is then held with forceps while pulling the sternite and tergite of the eighth abdominal segment in the opposite direction. This enables the full extension of the ovipositor and associated structures critical for scoring characters relating to the paraprocts, proctiger and extra baculi.

The length of the hind wings was assessed by first putting the specimen in hot water for a few minutes and gently pulling the two elytra apart from the apex. This was easily done in species with macropterous hind wings but more difficult in flightless species with "fused" elytra. In the latter case, teneral specimens were used when available.

At least two specimens of each sex were dissected for each of the species. The dissected genitalia are stored in glycerine in vials on the same pin as the specimens. Preparations were illustrated in 80% ethanol using a camera lucida mounted on a Zeiss Stemi SV-6 stereomicroscope (Germany). Measurements were made using a graticule with the same microscope.

Measurements were taken as follows: character 9: distance between eyes as well as eye width taken from dorsal view; character 17: width of penultimate antennal segment is greatest width when the antenna is perpendicular to plane of lens; characters 22 and 26: length of tarsal segments taken in lateral view; character 24: length of tarsal segments taken in dorsal view; character 50: length of procoxa and area anterior to procoxa taken in ventral view; character 66: length of scutellary striole and distance between striae one to three taken in dorsal view, distance between striae one to three taken near the middle of elytra; character 75: distance between meso and metacoxae as well as length of mesocoxa taken along a longitudinal axis in ventral view; character 79: length of defence reservoirs taken in dorsal view while still attached to sternites, once tergites and genitalia were moved to the side; character 88: length of extra baculus and paraproct baculus taken after full extension of ovipositor in either ventral, lateral or dorsal view depending on the specimens; character 90: length of proctiger and tergite eight taken in lateral view; character 92: maximum length of spiculum ventrale taken from posterior edge of sternite eight to the apex of spiculum in ventral view, length of ovipositor taken from the apex of coxite four to the apex of coxite one baculus in lateral view; character 94: length of coxites taken in lateral view.

The specimen used for Fig. 2G was dehydrated through a graded series of ethanol (from 70% to 100%), mounted on a stub and sputter coated with gold. The image was digitally captured from a JEOL JSM-6400F (Japan) scanning electron microscope (SEM) at 5kv.

Characters

A total of 101 morphological characters of adults (both internal and external) were included in this analysis (Appendix 1). The phylogenetic importance of female genitalic characters for studies above the genus level in the family Tenebrionidae has been observed previously (Tschinkel & Doyen, 1980; Doyen & Tschinkel, 1982). Variation in the structures associated with the female ovipositor and genital tube were also found to be useful in this analysis. The male genitalia are often highly variable in species within a single genus (e.g. Kaszab, 1987, 1988b) and were found to be of little value in the present analysis. However, secondary sexual dimorphism in the legs of males was found to be useful for some clades.

Only 40 coelometopine larvae have been described throughout the world (Marshall, 1982). Certain features

associated with the ninth abdominal segment, mouthparts and antennae clearly have potential phylogenetic value. However, none of the described larvae occur in the region under study. Although a small number of Coelometopini larvae are present in Australian institutions or have been reared by the senior author, the data at hand are unfortunately too little for inclusion in this analysis.

A discussion of the principal characters as well as a brief overview of the data relating to important Coelometopinae features follow.

Head

Completely exposed clypeal membranes are present in all Strongyliini (Fig. 2C), parts of Coelometopini (e.g. *Cuemus* Bouchard, *Neotheca* Carter) as well as other unrelated tribes such as Amarygmini and Helopini (Watt, 1974; Doyen, 1989). All the species included in this analysis were coded as having either completely exposed or hidden clypeal membranes. However, a distinction was made between the clypeal membranes in the genus *Strongylium* (including basal clade in the tribe
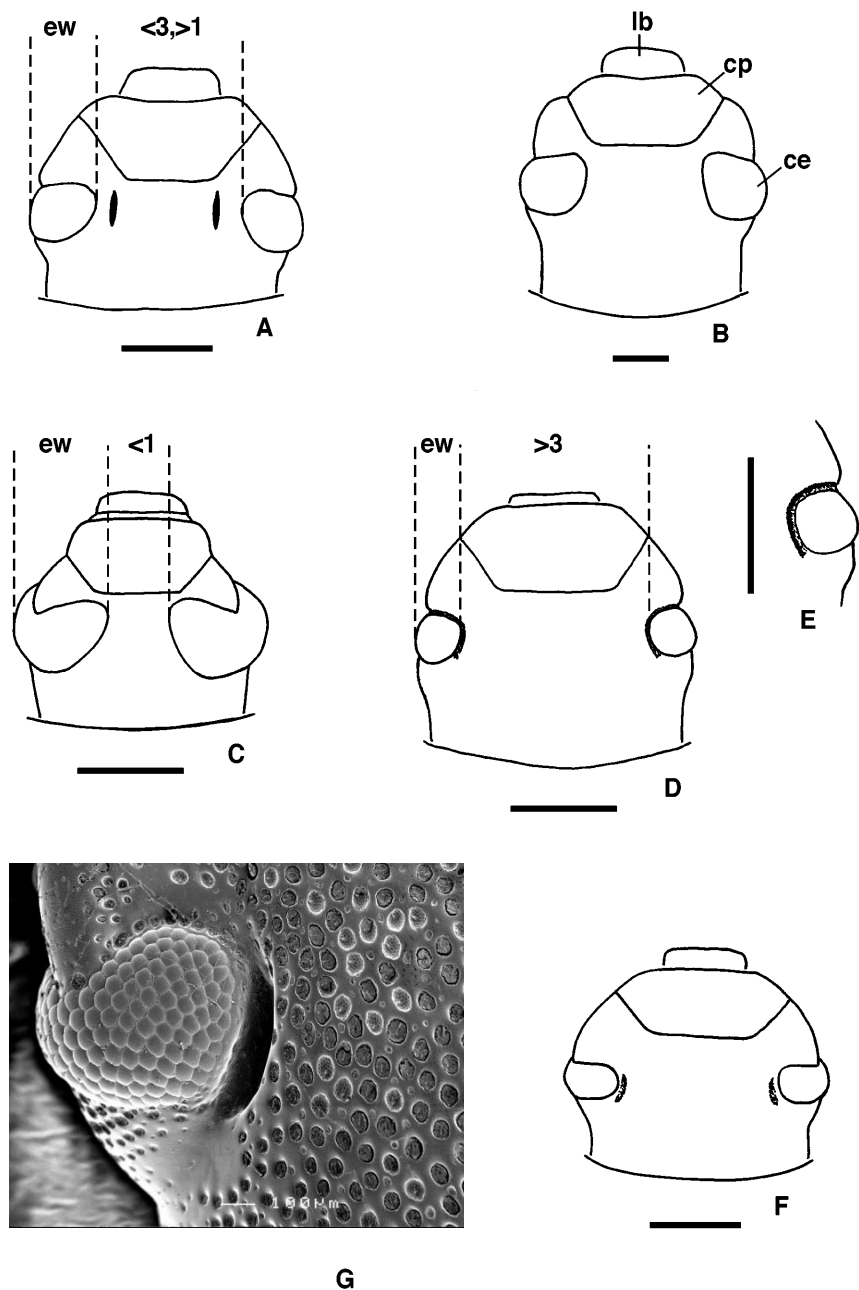
Fig. 2. Head features: A) *Zophophilus curticornis*, ♀ (distance between eyes greater than width of single eye lobe but less than three times width of eye lobe); B) *Promethis sulcigera*, ♀; C) *Strongylium* sp.1, ♀ (distance between eyes less than width of a single eye lobe); D) *Irianobates krikkeni*, ♂ (distance between eyes greater than three times width of single eye lobe); E) same as D), close up of the right compound eye showing groove between eye and frontal canthus; F) *Caxtonana costata*, ♂; G) same as F), SEM of the left eye. ce: compound eye, cp: clypeus, ew: eye width, lb: labrum. Scale A–F = 1 mm; G = 100 μm.

Coelometopini) and clade D (character 1; Fig. 14). The clypeal membrane of *Strongylium*, *Cuemus*, *Micromenandris* and *Asopidiopsis* originates posteriorly from the anterolateral corners of the clypeus. Species with this type of clypeal membrane usually have a broadly incized anterior edge of clypeus as reported by Bouchard (in press) and are the only taxa included here with setae present on the anterior corners of the clypeus (character 5). On the other hand, the clypeal membrane of *Neotheca*, *Thesilea* and *Agymnonyx* originates from under the clypeus and not as far laterally as in the taxa in the outgroup (see character 1). A smaller than usual labrum was recorded in *Neotheca*, *Thesilea* and *Agymnonyx* (character 3) and seems to be associated with a clypeal membrane originating from under the clypeus.

A small portion of the clypeal membrane is exposed in *Phenus latitarsus* Gebien which has a deep median notch in the anterior edge of the clypeus. This species was coded as having a hidden clypeal membrane (character 1) with the anterior edge of clypeus incized medially (character 4).

The presence of deep supraorbital grooves are characteristic of the type genus of the tribe Coelometopini (*Coelometopus* Solier). The majority of Australasian Coelometopini also possess this feature (character 8: Figs 2F, G) although it is not present in all taxa.

Doyen (1989) used the distance between the eyes in dorsal view as a distinguishing feature between the tribes Stongyliini and Coelometopini. He mentioned that the Coelometopini had eyes separated by much more than the width of a single eye lobe as opposed to usually separated by less than the width of a single eye lobe for Strongyliini. Although most males in the latter tribe usually have nearly contiguous eyes, it is not always the case for females. In the taxa included here, all Strongyliini had a short distance between the eyes (Fig. 2C) while the Coelometopini had at least the width of one eye lobe separating the eyes (character 9; Figs 2A, B, D, F). Compound eyes are usually smaller in size in flightless taxa.

The structure of the maxilla is fairly constant within the Tenebrionidae but variation is known to occur in the form of the lacinia (Doyen, 1993; Doyen & Tschinkel, 1982). The tribes Coelometopini and Strongyliini were coded as having a bifid and a single lacinial tooth respectively in Doyen and Tschinkel's phylogenetic analysis of the Tenebrionidae (1982). Data from the present study indicates that members of the Strongyliini always have a single tooth on the lacinia (Fig. 3A) whereas Coelometopini taxa either completely lack (character 14: Fig. 3B) or have a bifid tooth (Fig. 3C). Although variation in the lacinia did not show any consistent patterns in tribes of the subfamily Pimeliinae (Doyen, 1993), the absence or presence of a bifid tooth is a useful tool to group certain Coelometopini genera. Australasian Coelometopini genera with bifid lacinial tooth include *Derosphaerus* plus the clades B and C (Fig. 14).

A gular furrow was present only in the species *Hypaulax tenuistriata* (character 16; Fig. 4A). At the time of description of *Hypaulax*, Bates (1868: p. 260) mentions the following: "throat deeply and transversely channelled (as in *Coelometopus*)". The Palaearctic
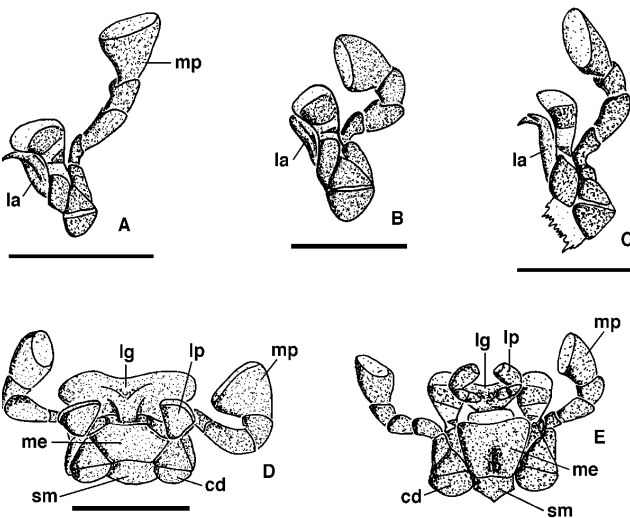
Fig. 3. Mouthparts: A–C left maxilla: A) *Strongylium* sp.1, ♀; B) *Caxtonana costata*, ♂; C) *Omolipus* CM18, ♂; D–E mouthparts: D) *Strongylium* sp.1, ♀; E) *Caxtonana costata*, ♂. cd: cardo of maxilla, la: lacinia, lg: ligula, lp: labial palp, me: mentum, mp: maxillary palp, sm: submentum. Scale = 1 mm.
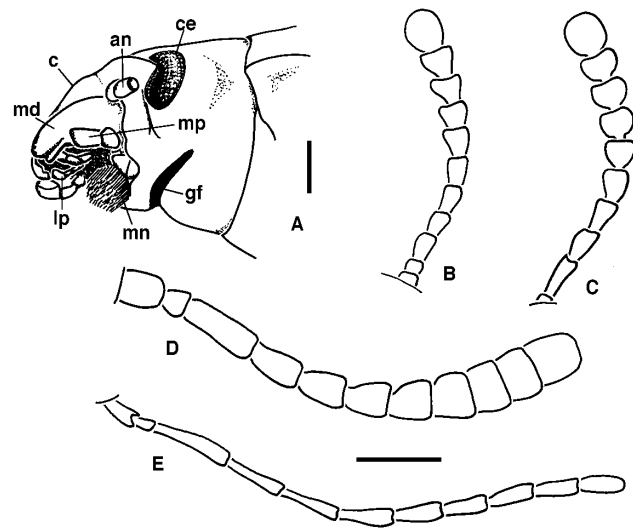
Fig. 4. Lateral view of head: A) *Hypaulax tenuistriata*, ♂. Antenna: B) *Pezophenus submetallicus*, ♂; C) *Caxtonana costata*, ♂; D) *Rhophobas buergersi*, ♂; E) *Strongylium* sp.1, ♂. an: antennal segments 1 and 2, ce: compound eye, c: clypeus, gf: gular furrow, lp: labial palp, md: mandible, mp: maxillary palp. Scale = 1 mm (scale bar for b–e below d).

genus *Coelometopus* Solier could have developed the same structure as in *Hypaulax* independently although this hypothesis still needs to be tested. The members of *Hypaulax* usually live in drier forests than members of other Coelometopini genera in Australia and the presence of a gular furrow might have evolved due to life in drier habitats.

All the members of the subfamily Coelometopinae are known to possess "compound" or "tenebrionoid" sensoria on their apical antennal segments (Medvedev, 1977; Doyen & Tschinkel, 1982). These sensoria are also found rather uniformly throughout most of the tribes of Tenebrioninae, Alleculinae as well as in Diaperini and related tribes (Doyen & Tschinkel, 1982). However, according to Doyen (1989), the number of antennal segments bearing compound sensoria seems to be fairly constant within the different tribes of Coelometopinae. Species in the tribe Coelometopini are thought to possess compound sensoria on the apical five or six segments (rarely seven or eight), whereas members of Strongyliini and Talanini are thought to bear compound sensoria on the apical seven or eight segments (Doyen, 1989). Australasian taxa from the tribe Coelometopini were found to have tenebrionoid sensoria on the apical four to seven segments with the most common number being six (character 20). The three species of Strongyliini had compound sensoria on the apical six segments.

Legs

The presence of an additional lateral seta on each side of the apical tarsal segments (near the apex) seems to be a phylogenetically informative character (character 21; Fig. 5A). These setae are only present in the outgroup and basal Coelometopini clades (clade A, *Derosphaerus* plus clade B; Fig. 14). Clades C, D and F have a pair of dorsal setae at the apex of the last tarsal segments.

The presence of a thick pad on the ventral surface of the apical tarsal segment (character 23, Fig. 5C) seems to be closely correlated with the presence of a cupiliform or slanted penultimate tarsal segment (clade C; character 25; Fig. 5C). The number of setae on the empodium (character 27; Fig. 5A–C) also seems to follow distinct patterns. For example, only the species *Rhophobas burgersi* and *Graptopezus crenaticollis* have lost these setae, whereas the group of taxa with blade-like ovipositors (clade D) as well as clade C have several setae on the empodium. All members of the clade E possess a pair of setae on the empodium which project ventrally.

A tooth on the apical portion of the hind tibia in the males of *Chariotheca besti* Blackburn and *Chariotheca amaroides* Pascoe was noted by Gebien (1920) when he placed the species in the new genus *Apterotheca*. Carter
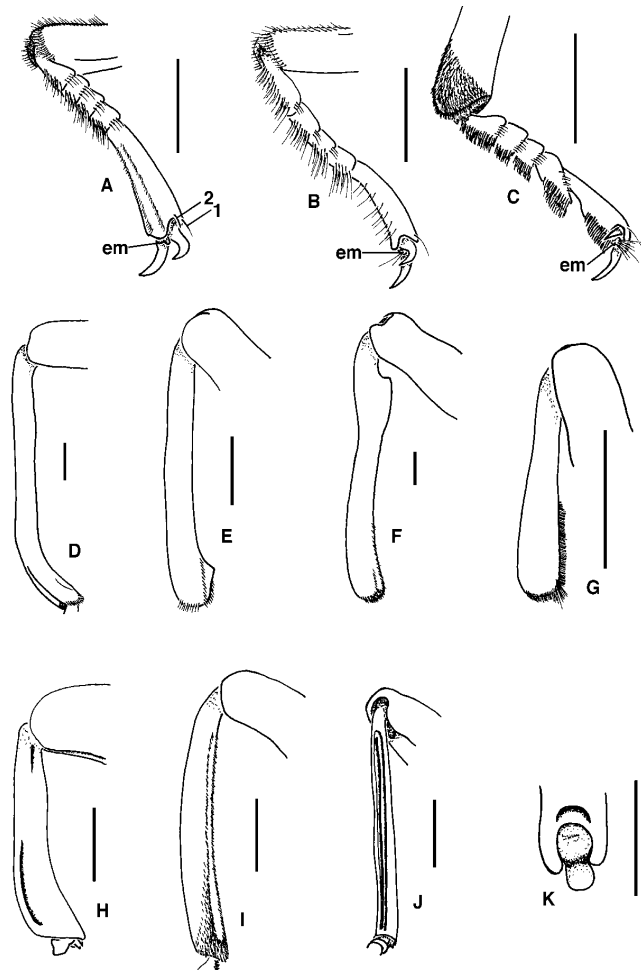
Fig. 5. Legs: A–C mesotarsi: A) *Graptopezus crenaticollis*, ♂; B) *Caxtonana costata*, ♂; C) *Hydissus* CM17, ♂; D) *Hypaulax tenuistriata*, ♂, protibia; E) *Apterotheca* CM16, ♂, metatibia; F) *Promethis sulcigera*, ♂, metatibia; G) *Scotoderus cancellatus*, ♂, metatibia; H) *Zophophilus curticornis*, ♀, protibia; I) *Caxtonana costata*, ♂, protibia; J) *Papuamisolampus toxopeusi*, ♀, protibia; K) same species, apex of metafemur. 1, 2: first and second pairs of setae near apex of fifth tarsal segment, em: empodium. Scale = 1 mm.
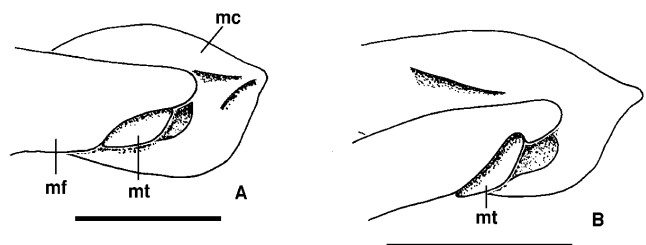
Fig. 6. Base of metafemur: A) *Hydissus* CM17, female; B) *Strongylium* sp.1, ♂. mc: metacoxa, mf: metafemur; mt: metatrochanter. Scale = 1 mm.

(1924) subsequently added a third species in the genus, *Apterotheca punctipennis*, which also has a tooth on the hind tibia in males. A large number of morphospecies collected in the northern Australia tropics (tentatively placed in *Apterotheca* and *Caxtonana*) also have this feature which is uncommon among the Australasian Coelometopini. In the present analysis, only males in the genera *Apterotheca*, *Campolene*, *Caxtonana*, *Zophophilus* and *Promethis* were found to have teeth on their hind tibiae. Although homology for the position of the apical tooth on the hind tibia of males in the clade F was established (character 29; Fig 5E), the same could not be done with *Zophophilus* and *Promethis* (Fig. 5F). Because males in these two genera (as well as in some species of *Derosphaerus*; see Kaszab, 1987) often have more than one tooth / depression on their tibiae, homology of these structures will need to be assessed more thoroughly with a large number of exemplars before revealing any phylogenetic potential. Males of *Promethis sulcigera* and *Zophophilus curticornis* were both coded as having no apical tibial tooth here (character 29). Additional useful sexually dimorphic features in the legs of male Coelometopini include the strongly curved apex of protibia (character 34; present only in males of clade B) and the presence of a thick patch of setae on the hind tibia of a number of males (character 34; Fig. 5G).

Clubbed femora were only found in the genus *Derosphaerus* in this analysis (character 38). However, this character is present in a number of other Coelometopini genera (e.g. *Ahexaroptrum* Kaszab, *Hexarhopalus* Fairmaire, *Asbolodes* Fairmaire, *Misolampidius* Solsky) and may become more useful when a larger number of taxa from the tribe are included (Becvar, 1997).

Pterothorax

One of the main reasons why members of tribe Coelometopini were originally placed in different tenebrionid tribes, and sometimes subfamilies, was because early groupings were made based on the presence or absence of functional hind wings. Most of the Coelometopini species previously placed in the tribe Tenebrionini (subfamily Tenebrioninae) (e.g. *Zophophilus*, *Promethis*, *Graptopezus*, *Derosphaerus*, etc.) are fully winged. On the other hand, groups of flightless genera from different zoogeographic regions were placed in different tribes (Gebien, 1938–1944). The Australasian Coelometopini included here represent a mixture of fully winged and brachypterous taxa (character 58) with the loss of flight occurring independently in several clades. Matthews (1986) mentioned that a characteristic venation pattern (merging of veins CuP and 1A for a short distance) occurs in some Australian Coelometopini (e.g. *Derosphaerus atroviridis* Macleay). However, some

other Coelometopini were found to have a more typical tenebrionine venation (e.g. *Tetragonomenes* Chevrolat and *Chariotheca* Pascoe). Because some variation in hind wing venation was observed between various specimens of a single species (e.g. *Apterophenus* sp., *Neotheca fusca*), the feature mentioned by Matthews (1986) was not coded here.

A short distance between the meso and metacoxae (character 75) is usually an indication that the specimen at hand is incapable of flight. The reduction in length of
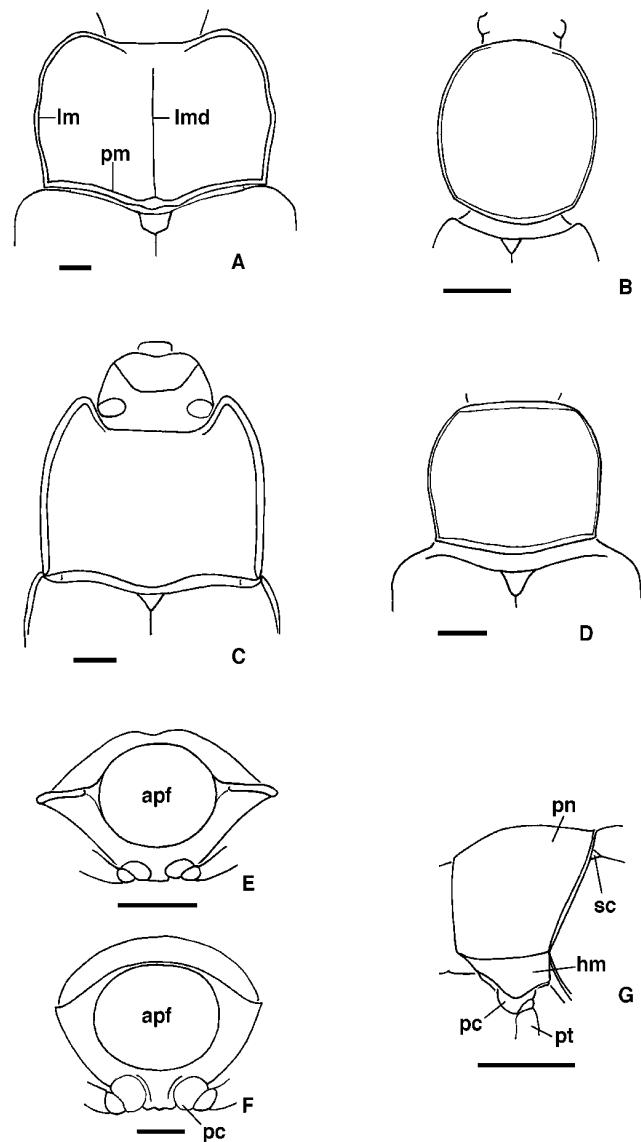
Fig. 7. Prothorax features: A–D dorsal view: A) *Promethis sulcigera*, ♂; B) *Oectosis cylindrica*, ♀; C) *Apterophenus* sp., ♀; D) *Strongylium* sp.1, ♂. E and F prothorax, anterior view: E) *Bradymerus raucipennis*, ♂; F) *Strongylium* sp.1, ♀; G) *Asopidiopsis* sp., ♀ prothorax, lateral view. apf: anterior prothoracic foramen, hm: hypomeron, lm: lateral margin, lmd: longitudinal median depression, pc: procoxa, pm: posterior margin, pn: pronotum, pt: protibia, sc: scutellum. Scale = 1 mm.
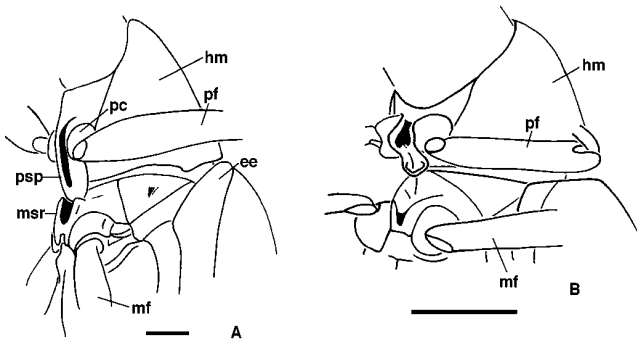
Fig. 8. Pro and mesothorax, lateral view: A) *Pezophenus submetallicus*, ♀; B) *Cuemus monteithi*, ♀. ee: elytral epipleuron, hm: hypomeron, msr: mesoventral receptacle, mf: mesofemur pc: procoxa, psp: prosternal process, pf: profemur. Scale = 1 mm.

the metathorax is due to a decrease in flight muscle mass which usually occurs after the reduction in length of the hind wings (Smith, 1964). Specimens of *Apterophenus* sp. were the only ones with short meso to metacoxa distance as well as fully developed hind wings.

The complete absence of a scutellum is only seen in the genus *Isopus* Montrouzier. The scutellum is very small in the closely related genera *Episopus* Bates and *Metisopus* Bates (character 67).

Abdomen – defence glands

Kendall (1974) presented a comprehensive account of the gross structure of the abdominal glands of several tenebrionids. The paired coelometopine glands rest ventrally at the posterior end of the abdomen and consist of reservoirs and associated secretory cells. The reservoirs are invaginations of the integument and open between sternites seven and eight. At the time of release of the secretions, the dilator muscles associated with each reservoir opens the reservoir's efferent duct. The discharge of secretion is usually associated with an increase in blood pressure. Two types of secretory cells are usually present in the tribe Coelometopini (Kendall, 1974). Their contents reach the reservoirs by means of collecting tubules, a feature considered derived in the family Tenebrionidae (Tschinkel, 1975b; Tschinkel & Doyen, 1980).

The Coelometopinae genera included in Tschinkel and Doyen's treatment of the defensive glands of tenebrionids (1980) were separated into three distinct defensive gland classes. The Strongyliini genera *Cuphotes* Champion and *Strongylium* Kirby were included in the *Catapiestus* type which also included the Coelometopini genus *Catapiestus* Perty. The glands in this group possess collecting tubules but are small in size and lack helical thickenings. The second class, which includes

the Coelometopini genera *Eucyrtus* Pascoe, *Apsida* Lacordaire, *Camaria* Serville and *Hemicera* Castelnau et Brullé belong to the cnodalonine type. The reservoirs of these genera are usually enlarged compared to those of the *Catapiestus* type. The third group includes most Coelometopini genera and is characterized by the presence of sclerotized annulations or helical thickenings on the reservoir walls as well as collecting tubules.

Doyen & Tschinkel (1982) mention that the large reservoirs strengthened by annulations and glands attached to the reservoirs by means of collecting tubules are characteristic features of the subfamily Coelometopinae. In their data matrix, the tribe Coelometopini is coded as having: few large ducts for tubule terminations (character 42: 5), defence reservoir wall accordion pleated (character 56: 2), large defence reservoirs (character 40: 3), reservoirs with common volume (character 41: 1) as well as long, straight and saccate reservoirs (character 69: 1). It should be noted that the tribe Strongyliini was coded for the same states as Coelometopini for characters 40 and 69 but these data disagree with the findings of the present study.

In the present analysis, three characters were included to describe the variation in Australasian coelometopine glands. The Coelometopini reservoirs usually have distinct darker color helical bands (Fig. 9D). Some species have heavily crinkled reservoir walls but the presence of sclerotized thickenings is sometimes difficult to see. All taxa included in this study have "coelometopine" reservoirs with distinct sclerotized thickenings and / or heavily crinkled reservoir walls (sensu Doyen & Tschinkel, 1982: character 56). The length (character 79) and shape (character 80) of the reservoirs as well as the number of collecting tubules leading to the reservoirs (character 81) were found to be informative. Short conical defence reservoirs were found only in the species *Strongylium fuscovestitum*, all other taxa had saccate reservoirs (i.e. with the basal part of the reservoirs slightly constricted). Tschinkel (1975a) recorded "everting" of glands for the mode of delivery of three species of *Strongylium*. Species with short conical defence reservoirs might be able to evert their contents when attacked whereas species with longer, saccate glands (such as *Strongylium* sp. 1 and 2) might instead "exude" their secretions like in most Coelometopini. A detailed description of tenebrionid defence glands and reservoirs can be found in Tschinkel & Doyen (1980).

Abdomen – ovipositor and associated structures

The major trends in the evolution of the tenebrionid ovipositor were discussed in Tschinkel and Doyen (1980). The subfamily Coelometopinae, as it is currently defined, is rather diverse in terms of ovipositor char-

acteristics. The "coelometopine type" of ovipositor of Tschinkel & Doyen (1980) is by far the most common in the subfamily and is found in members of the tribe Coelometopini and Strongyliini. It is characterized by a long coxite one (longer than coxites two to four combined), very long longitudinal baculus of coxite one and transverse orientation of the paraproct baculus. These features are all derived within the family Tenebrionidae according to Tschinkel & Doyen (1980). Doyen & Tschinkel (1982) mention that this highly specialized ovipositor is characteristic of the subfamily Coelometopinae and may function differently than other tenebrionids. Three other types of ovipositor were also recognized.

The "Talanine type" of Tschinkel & Doyen (1980) included only the genus *Talanus* Mäklin which has a blade-like ovipositor. The particular ovipositor of the genus *Talanus* was first described by Champion (1887) and is one of the main reasons why Doyen (1989) separated this genus from the rest of the Coelometopinae by recognizing the tribe Talanini. A blade-like ovipositor has also been found in a small number of Coelometopini genera (*Hegemona* Champion, *Saziches* Champion, *Promorphostenophanes* Kaszab and *Morphostenophanes* Pic). However, because of slight differences in the paraprocts and coxites of those genera, when compared to *Talanus*, Doyen (1987) mentioned that they are probably a separate derivation. Blade-like ovipositors are recorded for the first time in genera from Australasia in the present analysis (synapomorphy for clade D; Fig. 16).

The third ovipositor type recognized by Tschinkel & Doyen (1980) is the "Cnodalonine type". The genera *Eucyrtus*, *Hemicera*, *Apsida* and *Taphrosoma* Kirsch, with transverse paraproct baculi, coxite one shorter than the next three combined and coxite lobes three and four fused, were included in this group. The tribe Cnodalonini is now a synonym of Coelometopini (Doyen, 1989).

The fourth group includes three Coelometopini genera (*Catapiestus*, *Menephilus* Mulsant and *Zophophilus* Fairmaire) and is characterized by a short sclerotized ovipositor, sclerotized paraprocts with the baculi oblique and paraprocts partly enclosing coxite one. According to Tschinkel & Doyen (1980), this type of ovipositor is more primitive.

In their phylogenetic analysis of the Tenebrionidae, Doyen & Tschinkel (1982) coded the tribe Coelometopini as having the following states: paraproct much shorter than coxites (character 36: 3), paraproct transverse (character 37: 3), paraproct triangular (character 38: 3) and baculus of coxite 1 longitudinal (character 39: 3).

In the present analysis, a total of 12 characters relating to the female ovipositor and associated structures were included. Apart from the phylogenetically impor-

tant variation mentioned above concerning the orientation of the baculi and sclerotization of the paraproct, shape of ovipositor, orientation of the baculus and length of coxite lobe one, a number of relatively novel characters were also included. These refer to the shape, size and relative position of structures that are found between the base of the ovipositor and abdominal segment eight. In the past, the membrane below the paraprocts was cut off transversally, leaving for observation the ovipositor, paraprocts and genital tube (see Tschinkel & Doyen, 1980). More recently, structures between the abdominal segment eight and the ovipositor proved useful in assessing the relationship of Pimeliinae genera (Doyen, 1993) and are also used here.

The majority of Australasian Coelometopinae genera possess a pair of baculi or sclerotized plates in the membrane between the paraproct baculi and the proctiger
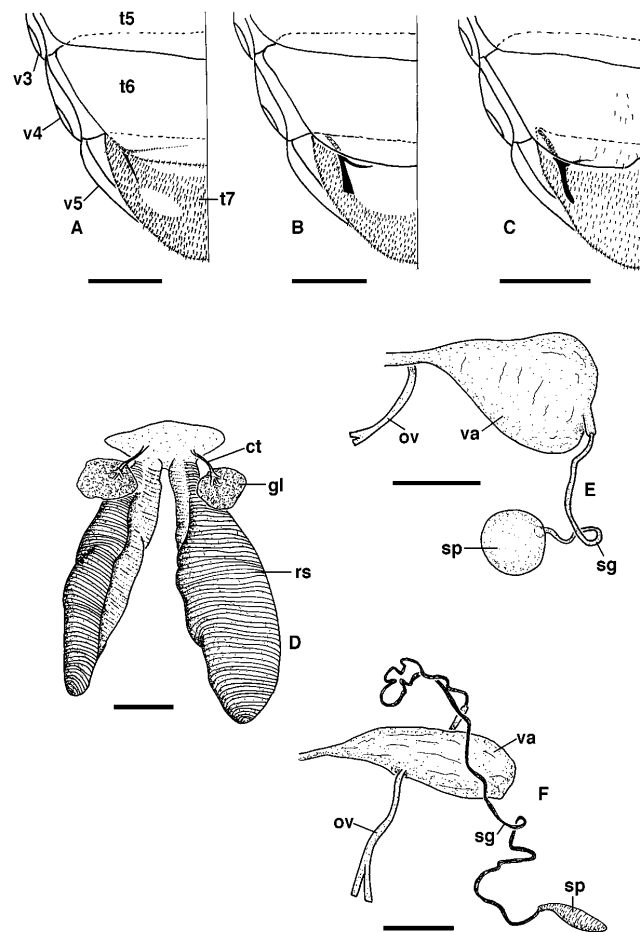
Fig. 9. Abdominal features: A–C tergites as seen dorsally: A) *Zophophilus curticornis*, ♀; B) *Chariotheca* sp.1, ♀; C) *Apterotheca* CM16, ♀. Internal structures: D) *Apterophenus* sp., ♀, defense glands and reservoirs; E) *Apterobrachis wilhelminae*, ♀ genital tube; F) *Hypaulax tenuistriata*, ♀ genital tube. ct: collecting tubule, gl: gland, ov: oviduct, rs: reservoir, sg: spermathecal gland, sp: spermatheca, t5-t7: tergites, v3 -v5: ventrites, va: vagina. Scale = 1 mm.

(character 87, 88; Figs 10D, 11B, C, D, 12D, 13A, C, D). These extra baculi, as briefly mentioned by Tschinkel & Doyen (1980: 325) are found in species which have very elongate ovipositors. The function of these extra baculi is not well understood but they are expected to serve as muscle attachments for the extension of the long ovipositors, which sometimes extend for the entire length of the abdomen when retracted. The presence of additional support between the paraproct baculi and the proctiger is restricted to genera where the para-procts are membranous instead of sclerotized. The genus *Derosphaerus* and members of clade B have scle-rotized paraprocts rather than membranous (Fig. 10A, 11A, 12A and 13B) and all lack additional support between the paraproct baculi and proctiger. Four other taxa lack additional support even though their para-procts are membranous. These are the three species with blade like ovipositor (clade D; Figs 12B, 16) and *Oecto-sis cylindrica* (Figs 13F, G).

In their brief discussion of the structures associated with the ovipositor, Tschinkel & Doyen (1980) mention that the proctiger usually has a pair of proctigeral baculi at its lateral margins and these interact with the extra ba-culi in species which have them. This was found to be true in most cases for the genera examined here. How-ever, the presence of extra baculi is not always associat-ed with proctigers with long sclerotized arms. In the taxa of clade C, short extra baculi are present but the
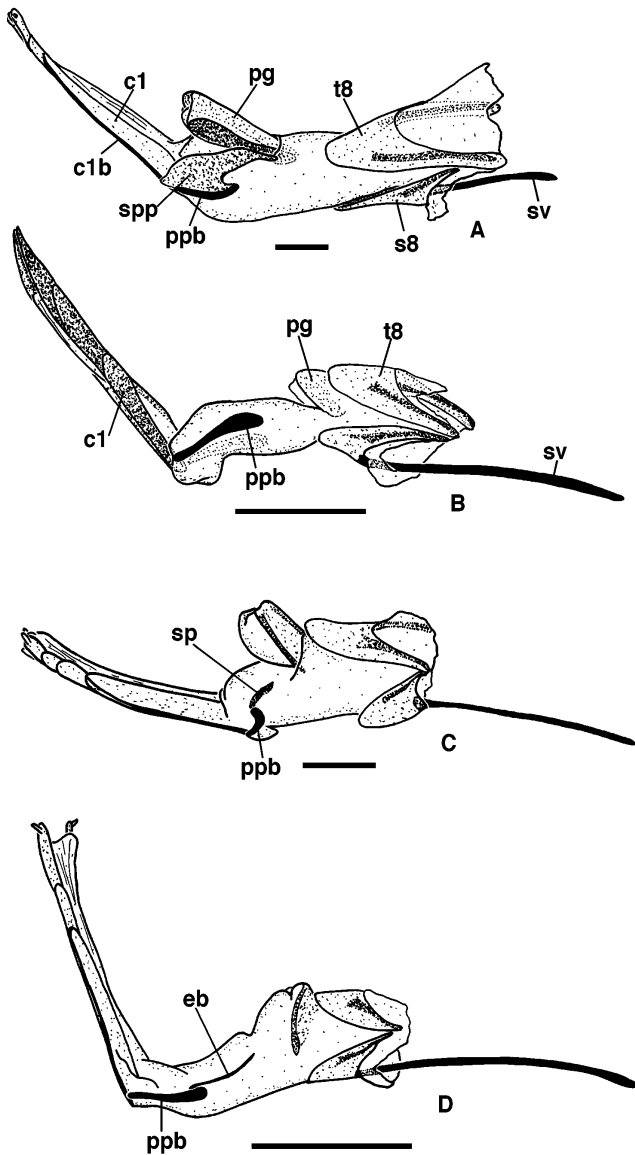
Fig. 10. Ovipositor and associated structures, lateral view: A) *Hy-paulax tenuistriata*; B) *Neotheca fusca*; C) *Strongylium* sp.1; D) *Mi-cromenandris* sp. c1: coxite 1, c1b: coxite 1 baculus, eb: extra bacu-lus,, pg: proctiger, ppb: paraproct baculus, sp: sclerotized plate, spp: sclerotized paraproct, s8: sternite 8, sv: spiculum ventrale, t8: tergite 8. Scale = 1 mm.
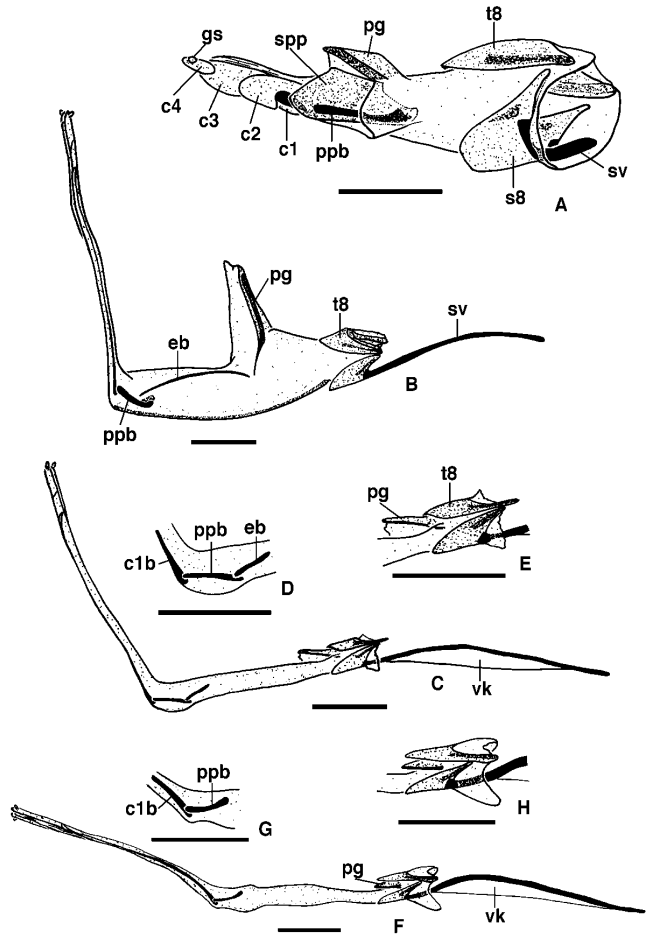
Fig. 11. Ovipositor and associated structures, lateral view: A) *Zophophilus curticornis*; B) *Apterotheca amaroides*; C–E) *Espites basalis*; F–H) *Oectosis cylindrica*. c1–4: coxite 1–4, c1b: coxite 1 bac-ulus, eb: extra baculus, gs: gonostylus, pg: proctiger, ppb: paraproct baculus, spp: sclerotized paraproct, s8: sternite 8, sv: spiculum ven-trale, t8: tergite 8, vk: ventral keel. Scale = 1 mm.
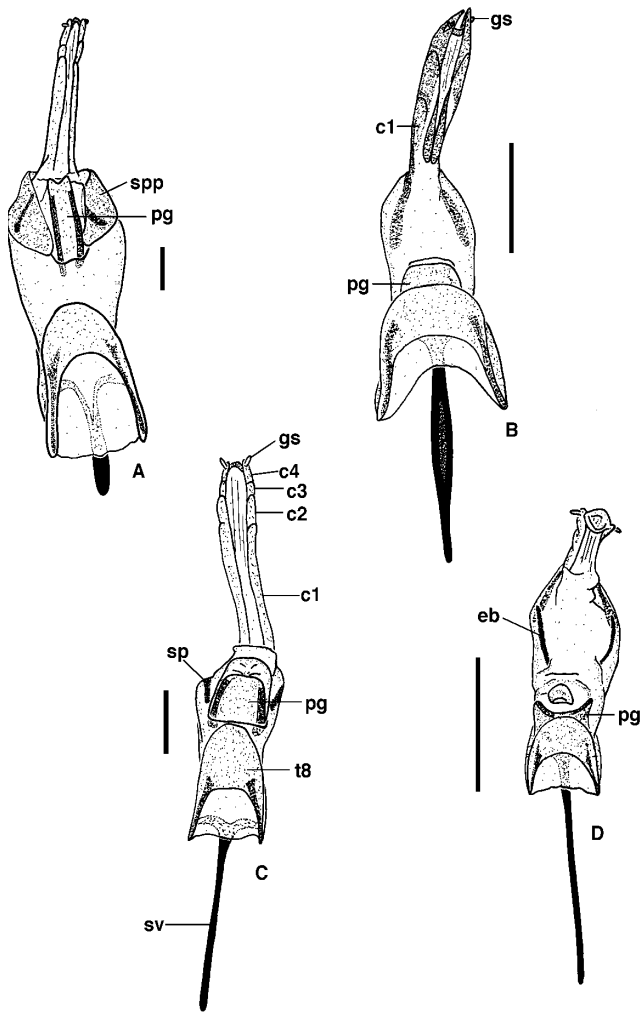
Fig. 12. Ovipositor and associated structures, dorsal view: A) *Hypaulax tenuistriata*; B) *Neotheca fusca*; C) *Strongylium* sp.1; D) *Micromenandris* sp. c1–4: coxite 1–4, eb: extra baculus, gs: gonostylus, pg: proctiger, sp: sclerotized plate, spp: sclerotized paraproct, sv: spiculum ventrale, t8: tergite 8. Scale = 1 mm.

Fig. 13. Ovipositor and associated structures, dorsal view: A) *Apterotheca amaroides* (ovipositor projecting toward lens); B) *Zophophilus curticornis*; C–E) *Espites basalis*; F–H) *Oectosis cylindrica*. c1–4: coxite 1–4, c1b: coxite 1 baculus, eb: extra baculus, pg: proctiger, spp: sclerotized paraproct, sv: spiculum ventrale, t8: tergite 8. Scale = 1 mm.

proctiger is positioned near tergite eight (Figs 11C, D, E, 13C). A similar position of the proctiger is also found in taxa with blade-like ovipositors (clade D). Members in clade E all have long extra baculi which interact with the elongated sclerotized arms of the proctiger when the ovipositor is extended (Figs 11B, 13A).

The relative length of the spiculum ventrale (character 92) as well as the presence of a clear keel on the spiculum in some genera (character 93; Figs 11C, F) were found to be useful taxonomically. Finally, the presence / absence of a pair of longitudinal baculi near the tip of the ovipositor in some species (character 96) was also found informative.

Abdomen – female genital tube

The first extensive survey of the structures associated with the female genital tube across the Tenebrionidae was done by Tschinkel & Doyen (1980). Their study revealed that these characters, as previously hypothesized by Watt (1974), have a great phylogenetic potential for resolution above the genus level. All of the members of the subfamily Coelometopinae are well defined based on the female genital tube and share a single, unique characteristic; the presence of a spermatheca derived distally from the spermathecal gland (Tschinkel & Doyen, 1980; char. 59 in Doyen & Tschinkel, 1982).

Most of the variation in the female genital tube of Coelometopinae has been reported in the position of origin of the spermathecal gland (whether at the anterior apex of the vagina or laterally) and the shape of the spermatheca (Tschinkel & Doyen, 1980). The Coelometopinae genera included in Doyen & Tschinkel (1980) were separated into six main types with only details separating them. In the present study, two characters (characters 82 and 83; Figs 9E, F) were included to cover the variation in the Australasian fauna. Only three genera were found to have a spermathecal gland derived laterally on the vagina (*Hypaulax*, *Promethis* and *Graptopezus*; Fig. 9F). The same taxa were also found to have a tapered spermatheca rather than spherical in all other Coelometopinae included in this study. It is predicted that females in the genus *Rhophobas* also have laterally derived spermathecal gland and tapered spermatheca although none were available for study.

Phylogenic analysis

The tribe Coelometopini is thought to be a monophyletic group (Doyen, 1989; Doyen et al., 1990) which contains over 250 genera worldwide. The present analysis does not endeavor to provide a thorough treatment of the world Coelometopini, but is a preliminary attempt to derive a meaningful generic classification of the entire fauna. The tribe Strongyliini was selected as the outgroup because it is closely related to the Coelometopini based on features of the female ovipositor, defence glands and genital tube (Tschinkel & Doyen, 1980; Doyen & Tschinkel, 1982; Doyen et al., 1990). The three outgroup taxa are Australian *Strongylium* species. Character polarity was determined using outgroup comparison (Maddison et al., 1984; Nixon & Carpenter, 1993).

A total of 47 species from the tribe Coelometopini (ingroup) were selected for this study. These represent 10 undescribed species from the rainforests of northern Australia (identified by CM-numbers in figures 14, 16 and 18), species in all genera of Coelometopini occurring in Australia (sensu Doyen et al., 1990) as well as representatives of other genera present in surrounding regions. Over 50 Coelometopini morphospecies from the northern Australia tropics have been identified to date from a number of genera. The bulk of these taxa are thought to form two monophyletic groups, near or within the genera *Apterotheca* Gebien and *Caxtonana* Buck (E.G. Matthews, pers. comm.). A database containing information for all specimens within each of these morphospecies is currently held at the Queensland Museum. The eight undescribed *Apterotheca* and *Caxtonana* taxa from the wet tropics included in this study were chosen to represent the variation of the entire material available.

Because groups of genera from particular regions of world appear to represent monophyletic clades within the Coelometopini (Doyen et al., 1990), we believe that the sister group (s) of the undescribed north Australian fauna will be present in the area under study (Australia plus Papuan and Pacific subregions of the Oriental region sensu Gressitt, 1961) and not in other zoogeographic realms, hence the selection of taxa. Current taxonomical knowledge shows that genera present in Australia are either endemic or are shared with New Guinea, New Caledonia and nearby islands which suggests a south Asian influence rather than gondwanan connections. The tribe Coelometopini contains approximately 40 genera in the region (Gebien, 1920; Kaszab, 1985; Doyen et al., 1990). Thirty six of these were included in the present study.

Character coding (see Appendix 2 for complete matrix) was conducted using MacClade version 3.08a (Maddison & Maddison, 1999). The number of character states varied between two and five. The total number of informative characters is 96 (five are phylogenetically uninformative using the present combination of taxa). All characters with more than two states were coded as unordered and all characters had equal weight. Inapplicable characters (i.e. characters that cannot possibly be coded for variation of a particular structure when that structure is absent) were coded as ? in the analysis. A good example of this is found in character 68 where the taxon *Isopus kanak* Fauvel was coded as ? for shape of scutellum because this taxon does not have a scutellum (character 67).

Cladistic analyses were performed as heuristic searches using PAUP*4.0b2a (Swofford, 1999). Fifty random step-wise addition searches with tree-bisection-reconnection (TBR) branch swapping were used. Branches having maximum length of zero were collapsed. The same data matrix was analysed using Hennig86 version 1.5 (Farris, 1988) with the same results and character evolution on the most parsimonious trees was analysed using Clados version 1.2 (Nixon, 1992; Figs 15–18) and MacClade. A strict consensus tree was generated using PAUP*4.0b2a (Fig. 14). Bremer support values (Bremer, 1994) were calculated using TreeRot version 2 (Sorenson, 1999) with 20 heuristic searches for each constrained node.

Results

Australasian clades

Analysis of the data matrix (Appendix 2) including 101 morphological characters coded for 50 Coelometopinae taxa yielded a total of 32 most parsimonious cladograms with a length of 383 steps (consistency index = 0.32, re-
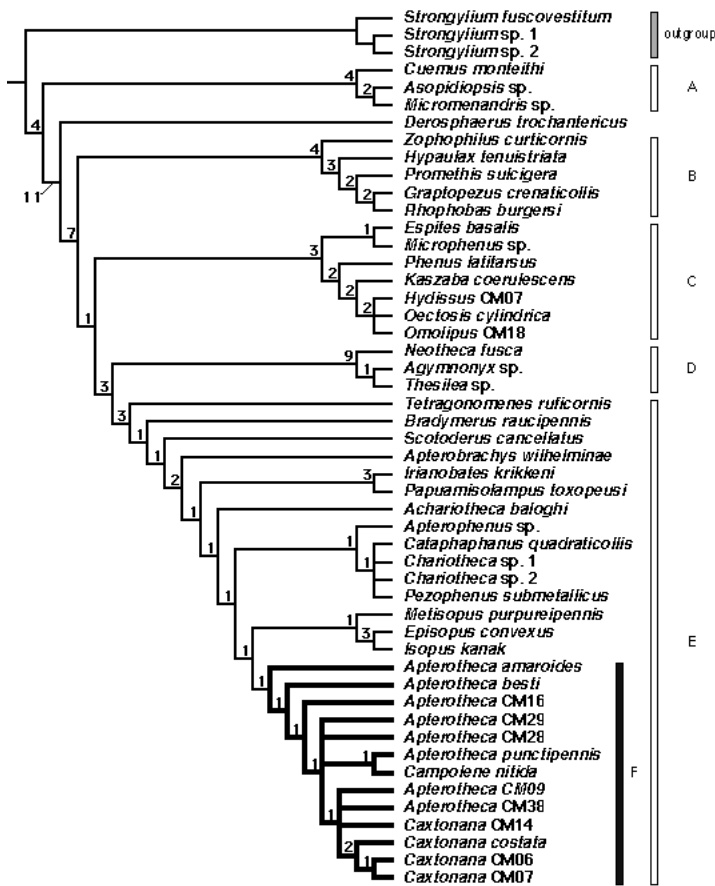
Fig. 14. Strict consensus cladogram of 32 most parsimonious cladograms (length = 383 steps). Three *Strongylium* species (outgroup) and 47 Coelometopini species (ingroup) were included in the analysis with 101 morphological characters. Numbers above the nodes represent Bremer support values for the tribe Coelometopini. Clades referred to in the text shown on the right hand side. Taxa included in the clade with thicker branches (F) will be the subject, along with other species, of a more detailed species-level analysis in the near future. Consistency index = 0.32, retention index = 0.72.

Fig. 15. Phylogenetic relationship of Australasian Coelometopini with character state distribution shown on each node. A) base of the cladogram shown in Fig. 14 (including outgroup, clade A plus *Derosphaerus trochantericus*); B) clade B from Fig. 14. Character numbers are represented above each hash, and character states below (see Appendix 1 for character descriptions). Non-homoplasious forward changes shown with black hashes and homoplasious changes shown in grey.

tention index = 0.72). The resulting strict consensus cladogram (Fig. 14) shows that the Australasian Coelometopini fauna can be separated in several clades. The Bremer support values shown in Fig. 14 indicate that the tribe Coelometopini is in fact monophyletic when compared to the Strongyliini (support of 4).

Synapomorphies for the Coelometopini taxa include: distance between the eyes greater than the width of one eye lobe (character 9), rectangular-shaped apical segment on the labial palp (character 13), length of the apical tarsal segment of hind legs equal or greater in length than first tarsal segment (character 22), incomplete elytral epipleuron (character 63; however states reversed in clade B) and long defence reservoirs (character 79). The distance between the eyes was also used by Doyen (1989) as a character separating Strongyliini and Coelometopini but other characters that he used, such as the number of antennal segments with tenebrionoid sensoria, did not appear useful in the present analysis.

The first clade to branch off at the base of the Coelometopini includes three flightless taxa (*Cuemus monteithi*, *Micromenandris* sp. and *Asopidiopsis* sp.; clade A; Figs 14, 15A). These three taxa share a number of characteristics with the outgroup such as reported by Bouchard (in press). A completely exposed clypeal membrane attached to the anterior corners of the clypeus (character 1), a broadly incized clypeus (character 4, state 1) and setae present on the anterior corners of the clypeus (character 5) are only found in the outgroup and clade A. The presence of long, cylindrical antennae is also characteristic of these taxa. An extra baculus equal in length to paraproct baculus (character 88; Figs 10D, 12D) is only found in *Cuemus*, *Micromenandris* and *Asopidiopsis* in the region. Taxa in clade A (support of 4; Fig. 14) lack a lacinial tooth, are usually small in size, are very convex and also have a strongly curved prosternal process in lateral view. The genus *Cuemus* has only been reported from the high altitude rainforests in the northern Australian tropics whereas *Asopidiopsis* Kaszab and *Micromenandris* Kaszab are endemic to Fiji. Kaszab (1955) included the latter two genera in the Misolampini along with *Menandris* Haag-Rutenberg and *Asopis* Haag-Rutenberg. The genus *Micromenandris* is unique among Australasian Coelometopini by having short rounded knobs for hind wings (character 58) and scutellary strioles which reach the apex of the elytra (character 66).

The genus *Derosphaerus*, along with the remainder of the Coelometopini form a distinct clade with a high Bremer support of 11 (Fig. 14). This clade is characterized by a hidden clypeal membrane (character 1; membrane exposed in clade D but differs from state 1 present in the outgroup and clade A), penultimate antennal segment wider than long (character 17; also found in *Micromenandris*) and flattened apical antennal segments

(character 19). The genus *Derosphaerus* has lateral expansions between procoxae also present in the outgroup and clade A (character 55). As mentioned before, the genus *Derosphaerus* is the only taxon with clubbed femora in this analysis (character 38) but this feature has also been recorded in the Coelometopini genera *Ahexaroptrum* Kaszab, *Hexarhopalus* Fairmaire, *Asbolodes* Fairmaire, *Misolampidius* Solsky. Along with clade B, the genus *Derosphaerus* is quite unique in that it has sclerotized paraprocts (character 89).

The next grouping includes clades B to E (Fig. 14). These are separated from the rest of the Australasian Coelometopini by having short antennae (character 18), triangular lateral angles of prothorax in anterior view (except for *Oectosis* and *Omolipus*; character 49; Fig. 7E) and prosternal process without lateral expansions between procoxae (character 55) (Fig. 15A).

Clade B includes the fully winged genera *Zophophilus*, *Promethis*, *Graptopezus* and *Rhophobas* as well as the Australian endemic flightless genus *Hypaulax* (support 4; Fig. 14, 15B). Apart from their large body size, the members included in clade B share the following unique combination of morphological features: curved apex on the protibia in males (character 34), oblique paraproct baculi (except for *Promethis*; character 91) and an row of setae on posterior edge of tergite six (except for *Graptopezus*; character 76). In *Promethis sulcigera* the paraproct baculi are transversal and the sclerotized part of the paraproct is only present dorsally, not ventrally as in *Hypaulax* and *Zophophilus*. Figure 15B also shows that the clade formed by *Promethis*, *Graptopezus*, *Rhophobas* and *Hypaulax* is supported by three non-homoplasious synapomorphies. These are: a tapered spermatheca (character 83; Fig. 9F), a spermathecal gland derived laterally from the vagina (character 82) and a row of short hairs where the metacoxae come in contact with the transversal ridge on sternite two (character 97). As mentioned before the genera *Graptopezus* and *Rhophobas* are the only taxa included in this analysis which lack setae on the parempodia (character 27: Fig. 5A). In Gebien's catalogue of Tenebrionidae (1938-1944), *Hypaulax* was included in the tribe Coelometopini whereas the other four genera, which are all winged, were included in the Tenebrionini.

Species in the genera *Espites*, *Microphenus*, *Hydissus*, *Oectosis*, *Omolipus*, *Kaszaba* and *Phenus* all grouped together in a monophyletic group in this analysis (clade C, support 3; Figs 14, 16). All these taxa have a curved spiculum ventrale with a clear keel (character 93; Figs 11C, F, 13C, F), cupiliform or slanted penultimate tarsal segments (also found in the genus *Asopidiopsis*; character 24; Figs 6C) and a thick pad of setae on the apical tarsal segments (character 22; Fig. 6C). A short extra baculus between the paraprocts and the abdominal segment eight may or may not be present but

the proctiger in those taxa always lies beneath tergite eight when the ovipositor is fully extended (Figs 11C, E, F, H, 13C, E, F, H). The species *Espites basalis* and *Microphenus* sp. only differ in detail and probably belong to the same genus. *Phenus latitarsus* was the only taxon with a deeply incized clypeus anteriorly (character 4) which exposed part of the clypeal membrane. The most basal members of clade C (*Espites*, *Microphenus*, *Phenus* and *Kaszaba*) are all fully winged, *Oectosis cylindrica* has hind wings shortened apically whereas the species of *Omolipus* and *Hydissus* only have strap-like wings (character 58). *Hydissus* CM07 and *Omolipus* CM18 are restricted to the northern Australian tropics. The taxa in clade C were included in the following tribes in the most recent catalogue of tenebrionids (Gebien, 1938-1944): Cnodalonini (*Phenus*, *Microphenus*, *Espites*), Tenebrionini (*Hydissus*, *Oectosis*) and Misolampini (*Omolipus*). Matthews & Doyen (1989) mentioned that the new genus *Kaszaba* was probably close to *Espites* based on diagnostic characters. These two genera are also closely related in the present analysis although they do not come up as sisters. The genus *Derosphaerus* also has a short lateral transparent longitudinal projection on the spiculum ventrale but this structure is not believed to be homologous to the ventral keel present in members of clade C.

The rest of the Coelometopini (clades D plus E; support of 3) are characterized by having no tooth on the lacinia (character 14) and long defence reservoirs (character 79). One of the clades with the highest Bremer support in Fig. 14 (support of 9) is composed of fully winged taxa from the genera *Neotheca*, *Thesilea* and *Agymnonyx*. These taxa share the following unique characters: a fully exposed clypeal membrane originating from under the clypeus (character 1), small labrum (character 3), an anterior edge of clypeus sharply incized laterally (character 4), reduced gonostyli found in depressions on the sclerotized coxite four (character 85), a strongly sclerotized blade-like ovipositor (character 87; Figs 10B, 12B), short baculus one (character 94; Fig. 10B; also found in the ovipositor of *Zophophilus*) and the baculi of coxite one immovable near the base (character 95; Fig. 16). Blade-like ovipositors were previously only known in a handful of genera in the tribe Coelometopini (*Talanus*, *Hegemona*, *Saziches*, *Promorphostenophanes* and *Morphostenophanes*). Doyen (1987) mentioned that this type of ovipositor may have evolved independently more than once in the tribe Coelometopini based on the striking differences in the female genital tube between the genus *Talanus* and the other genera with blade-like ovipositors in the New World (*Saziches*, *Hegemona*). The other two genera mentioned by Doyen (*Promorphostenophanes* and *Morphostenophanes*) are Asian in origin. Blade-like ovipositors have also been recorded in the unrelated
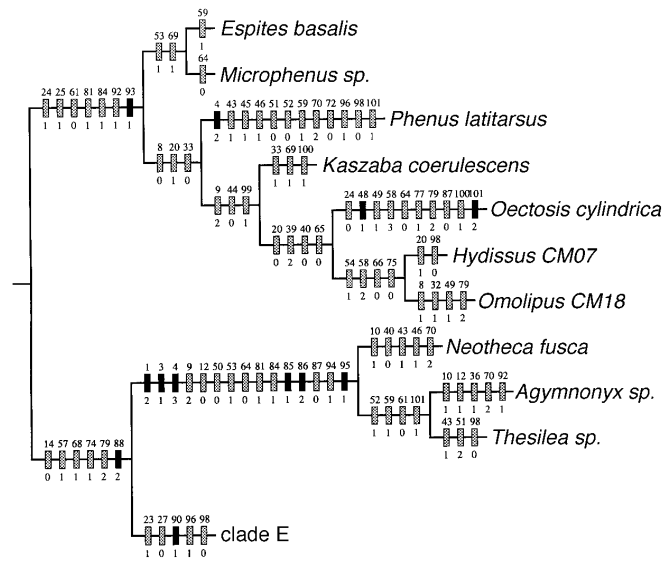
Fig. 16. Phylogenetic relationship of Australasian Coelometopini with character state distribution shown on each node. Clades C and D from Fig. 14. Character numbers are represented above each hash, and character states below. Non-homoplasious forward changes shown with black hashes and homoplasious changes shown in grey.

tenebrionid tribe Acropteronini (Doyen, 1989). The ventral orientation of the apex of the ovipositor in Acropteronini differs from the dorsally projecting blade-like ovipositors in Coelometopini. The reduction of gonostyli in females with blade-like ovipositors mentioned by Doyen (1987) was also found in *Neotheca*, *Thesilea* and *Agymnonyx* females. The three genera in clade D were included in the tribe Cnodalonini in Gebien's catalogue (1938–1944).

The rest of the taxa on the strict consensus cladogram (clade E, Fig. 14, 17 and 18; support of 3) share the following features: two sparse rows of setae on the ventral surface of the last tarsal segments (character 23; Fig. 5B), two setae on the empodium projecting ventrally (character 27), a pair of long extra baculi between the paraprocts and proctiger (character 88; Figs 11B, 13A), a long proctiger (character 90; Figs 11B, 13A) and a pair of longitudinal, narrow, sclerotized plates at the apex of the ovipositor (character 96; also found in *Phenus latitarsus*). The long extra baculi and long proctiger are unique to the members of this clade. The narrow, sclerotized plates at the apex of the ovipositor have never been reported in this group before and usually appear as darker areas next to the pleated membrane between the apex of the ovipositor and coxite one. Clade E contains a mixture of taxa that are both fully winged (*Tetragonomenes, Scotoderus, Bradymerus, Cataphanus, Chariotheca, Pezophenus* and *Apterophenus*) and flightless taxa (*Apterobrachys, Irianobates, Papuamisolampus, Achariotheca, Metisopus, Episopus, Isopus, Apterothe-*
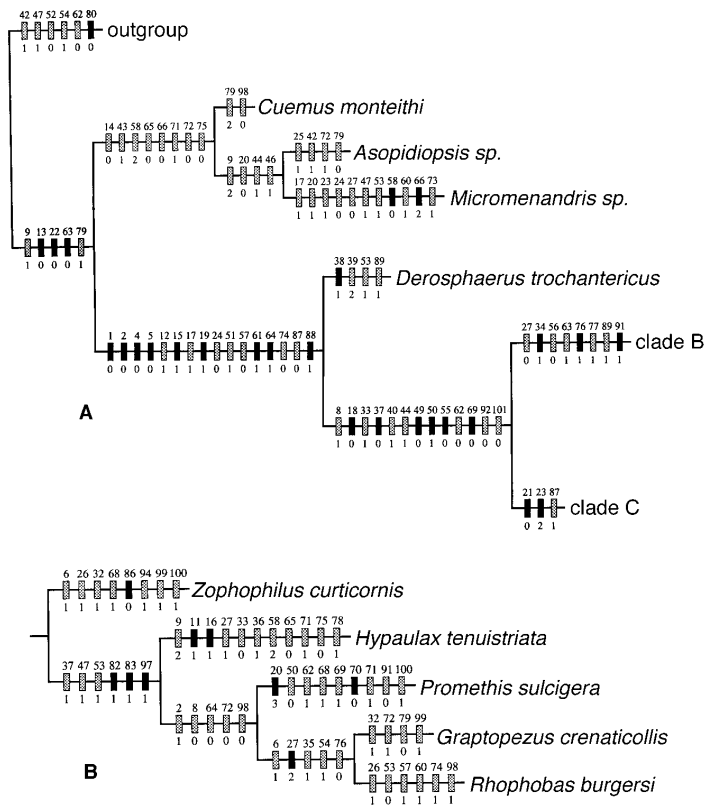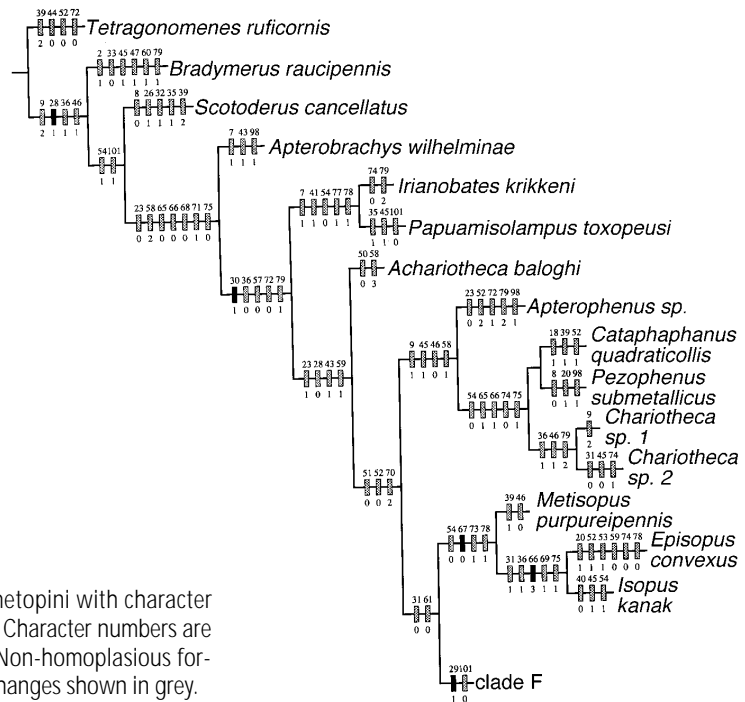
Fig. 17. Phylogenetic relationship of Australasian Coelometopini with character state distribution shown on each node. Clade E from Fig. 14. Character numbers are represented above each hash, and character states below. Non-homoplasious forward changes shown with black hashes and homoplasious changes shown in grey.

ca, *Caxtonana* and *Campolene*). Figure 14 shows that flightlessness has evolved in four separate occasions in this clade. It should be noted that even if the distance between the meso and metacoxae is short in *Apterophenus* sp. (character 75), usually an indication that the specimens are flightless, fully developed hind wings are present in this taxon.

Several restricted endemic taxa are found in clade E. For example, the genera *Papuamisolampus*, *Irianobates* and *Apterobrachys* are all restricted to high elevation forests in New Guinea (Kaszab, 1986), the clade composed of *Metisopus*, *Isopus* and *Episopus* (three genera with either absent or small scutellum; character 67) are restricted to New Caledonia and surrounding islands and the clade containing *Apterotheca* and *Caxtonana* species is more or less restricted to high elevation rainforests in northeastern Australia. All of the restricted genera are flightless. *Bradymerus*, *Scotoderus* and *Chariotheca*, species-rich fully-winged genera are widely distributed within the region under study. Internal support within clade E is generally rather low, however figure 17 and 18 indicate that some of the clades are supported by unique derived characters. For example, distinct rows of setae on the inner side of the protibia are found only in *Irianobates*, *Papuamisolampus* and all other taxa from that node on (character 30).

Clade F, which includes all species from the northern Australian tropics tentatively placed in the genera *Apterotheca* and *Caxtonana* (E.G. Matthews, pers. comm.) as well as *Campolene nitida*, contains all the

taxa which possess a single apical tooth on the hind tibia in males (Fig. 18; character 29). Two unique characters support clade F minus *Apterotheca amaroides*: the presence of thick setae on tergite seven which covers most of the segment without the trace of an oval patch lacking
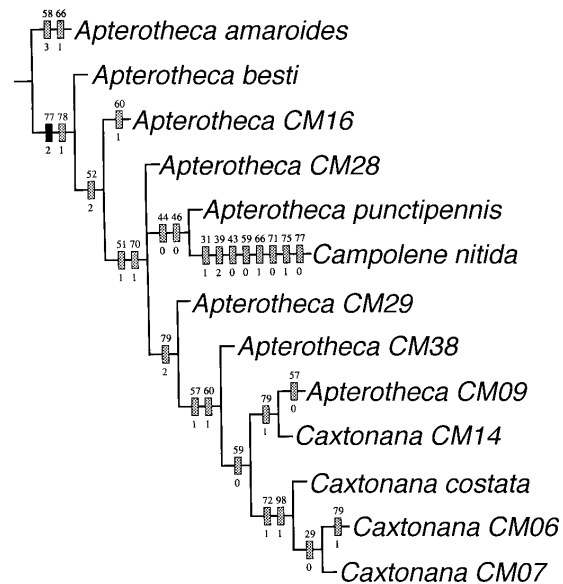
Fig. 18. Phylogenetic relationship of Australasian Coelometopinae with character state distribution shown on each node. Clade F from Fig. 14. Character numbers are represented above each hash, and character states below. Non-homoplasious forward changes shown with black hashes and homoplasious changes shown in grey.

thick setae (character 77) and the presence of thick setae medially on tergite six (chancre 78; Fig. 9C). The three basal species in clade F (*Apterotheca amaroides besti*, *A. amaroides* and *A.* CM16) have straight prosternal process (character 51) and mesoventral receptacle with high walls (character 70) similar to the ones in the *Metisopus – Episopus – Isopus* and *Apterophenus – Chariotheca – Cataphanus – Pezophenus* groups whereas the other species have a slightly curved pronotal process and a receptacle with low walls. Elytral interstriae with sharp ridges characteristic of *Caxtonana costata* are also present in *Apterotheca* CM38, *A.* CM09 as well as the three undescribed species tentatively placed in *Caxtonana* (character 60). From clade E, *Bradymerus* and *Scotoderus* were included in the tribe Bolitophagini based on early classifications, *Tetragonomenes* in the Diaperini, *Irianobates*, *Apterobrachys* and *Papuamisolampus* in the Misolampini and the remainder in Cnodalonini.

Character evolution

This first attempt at elucidating the phylogenetic relationship of the members of the tribe Coelometopini has revealed patterns in the evolution of different sets of characters. For example, the homology of an exposed clypeal membrane in species of Coelometopini has never been questioned previously but the results presented here clearly shows that there are two distinct types of membranes. The outgroup and basal members of Coelometopini have a clypeal membrane which is joined laterally at the anterior edge of the clypeus. Species with this type of clypeal membrane usually have a number of setae near the anterior corners of the clypeus, have the anterior edge of the clypeus broadly and smoothly incised and have rather large clypeus with the lateral edges extending beyond the frontoclypeal suture (Fig. 2C). On the other hand, species of *Neotheca*, *Agymnonyx* and *Thesilea* have a clypeal membrane which originates under the anterior edge of the clypeus, very small labrum and rather short clypeus with broadly and sharply incised anterior edge.

The evolution of characters relating to the Coelometopini ovipositor is rather complex although some patterns are evident. In all taxa studied here, only females in the genera *Zophophilus*, *Thesilea*, *Agymnonyx* and *Neotheca* have ovipositors with the first coxite shorter than the length of coxites two to four combined. Of those, *Zophophilus* is the only genus with a short, slightly sclerotized ovipositor. Tschinkel & Doyen (1980) mention that tenebrionids with all coxite lobes subequal is the primitive state. If this is the case then all members of Coelometopini have a derived ovipositor because all have different size coxites. However, Doyen & Tschinkel also mentioned that sclerotized paraprocts

with oblique paraproct baculi are primitive states in Tenebrionidae. This combination of features is found in some members of clade B (*Zophophilus*, *Promethis*, *Hypaulax* and *Graptopezus*). Additionally, members of clade B lack any support between the paraproct baculi and the proctiger.

The loss of sclerotization of the paraprocts, characteristic of most Coelometopinae, has probably led to the evolution of a unique feature in the subfamily, the presence of extra baculi between the paraprocts and the proctiger. These extra baculi potentially serve as muscle attachments during the complete extension of the long ovipositor. The extra baculi come in a variety of shape and length and have probably evolved independently in different clades. For example, Strongyliini have a short sclerotized plate, species in clade A have extra baculi the same length as the paraproct baculi whereas the members of clade E always have a pair of long extra baculi which interact with an elongated proctiger. The short extra baculi of clade C (*Espites*, *Hydissus*, *Omolipus*, *Phenus* and *Omolipus*) are unique in that they do not interact with the proctiger, which is always found next to tergite eight.

Species with blade-like ovipositors (*Thesilea*, *Neotheca* and *Agymnonyx*) do not have any extra baculi in the membrane between the paraprocts and proctiger but the length of the ovipositor in these taxa is usually shorter, in comparison to the body length, than other species with extra baculi. The fused or immoveable baculi of coxite one near the base of the ovipositor could have evolved as a means of providing extra support in these species. Extra baculi in the ancestors of *Thesilea*, *Neotheca* and *Agymnonyx*, if present, could have been lost with the evolution of a blade-like ovipositor.

Discussion

The subfamily Coelometopinae, as defined by Doyen & Tschinkel (1982), Doyen (1989) and Doyen et al. (1990) is a very well supported clade within the family Tenebrionidae. Its members share a number of apomorphic features (e.g. ovipositor and female genital tract) first brought to light by Tschinkel & Doyen (1980). The subfamily is currently divided into 3 tribes: Strongyliini, Coelometopini and Talanini (Doyen, 1989). The tribe Coelometopini is distributed world wide but is especially species-rich in tropical and subtropical regions. The small amount of data available on the biology and ecology of the members of this tribe indicates that the adults are often restricted to undisturbed forest patches and are usually found around dead standing trees, the source of nutrient for the immature stages. The Coelometopini larva usually goes through six or seven larval stages before pupation.

The long-lived adults are nocturnal in habit and usually uncommon in entomological collections. This is especially true for the flightless taxa which are often very restricted in distribution and rarely collected with typical trapping methods. Although characteristics of the defence behavior and chemical secretions of the Coelometopini could potentially reveal strong patterns within the tribe and clearly need more attention, the accumulation of basic morphological data is still in its infancy. The brief summary of the biological and ecological information presented in this work will hopefully trigger more interest in this diverse group and lead to the future publication of much needed data.

Here we present the first phylogenetic analysis of the Australasian Coelometopini. Results show that the tribe can be separated in several well supported higher clades. Features of the female genital tube and ovipositor and associated structures are usually stable within the different higher clades and a further understanding of the evolution of these will no doubt be useful in obtaining a meaningful generic classification of the entire tribe. Until recently (Doyen, 1989), the members of the Coelometopini had been placed in different tribes and subfamilies based on the presence or absence of fully functional hind wings (Gebien, 1938-1944). It is now clear that flightlessness has evolved on several occasions within the tribe.

Several undescribed Coelometopini taxa were recently collected in rainforests of northeastern Australia. The bulk of these new species were temporarily placed in the genera *Apterotheca* and *Caxtonana* by the Australian tenebrionid expert (E.G. Matthews, South Australian Museum). The restricted distribution of most of the undescribed wet tropics taxa to high elevation rainforests makes this fauna an ideal tool for the future monitoring and assessment of habitat health in this unique region. However, before starting the descriptive process, two questions had to be answered: do these taxa represent one or more monophyletic lineages? and what are their closest relatives? The results presented here show that the species of *Apterotheca*, *Campolene* and *Caxtonana* form a single monophyletic clade within the Australasian Coelometopini fauna. This clade includes all species with a tooth on the hind tibia in males, a character used by Gebien (1920) to separate *Apterotheca* from *Chariotheca*. Other characters that are unique to these taxa include the presence of continuous thick setae on tergite seven and the presence of thick setae medially on tergite six. Furthermore, features of the prosternal process and elytral interstriae also seem to suggest close affinity. Because some branches within clade F are still unresolved (Fig. 14), any internal subdivisions will have to include a larger number of species-level characters. The sister group of the monophyletic clade which includes all wet tropics taxa includes three flightless genera from New Caledonia and surrounding islands (*Metisopus*, *Isopus* and *Episopus*). These will be included in the species-level analysis as outgroups of the northeastern Australian tropics fauna in order to assess character polarity.

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Appendix captions

Appendix 1. List of the 101 internal and external morphological characters used for the phylogenetic analysis of Australasian Coelometopini.

1 – Clypeal membrane: 0: hidden (Figs 2A, B, D, F); 1: exposed, lateral edges attached to corners of clypeus (Fig. 2C); 2: exposed, lateral edges originating under the clypeus.
2 – Clypeus: 0: not extending laterally beyond frontoclypeal suture (Figs 2A, D, F); 1: extending laterally beyond frontoclypeal suture (Figs 2B, C).
3 – Size of labrum: 0: normal; 1: small.
4 – Anterior edge of clypeus: 0: straight or slightly convex; 1: broadly incized, lateral angles of clypeus smoothly incized; 2: incized in midline only; 3: broadly incized, lateral edges of clypeus sharply incized. (see text for details)
5 – Setae on anterior corners of clypeus: 0: absent; 1: present.
6 – Longitudinal frontal depression: 0: absent (Figs 2B, C, D, F); 1: present (Fig. 2A).
7 – Shallow groove between eye and frontal canthus: 0: absent (Figs 2A, B, C, F, G); 1: present (Figs 2D, E).
8 – Deep supraorbital groove: 0: absent (Figs 2A, B, C, D); 1: present (Figs 2F, G).
9 – Distance between the eyes: 0: less than width of single eye (Fig. 2C); 1: greater than width of single eye but less than three time as wide (Fig, 2A); 2: equal or three times as wide as single eye (Fig. 2D).
10 – Constriction of head behind the eyes (dorsal view): 0: gradual; 1: sharply constricted.
11 – Mentum: 0: with median keel or slightly convex; 1: flat.
12 – Anterior margin of submentum: 0: extending beyond anterior margin cardo (Fig. 3D); 1: not (Fig. 3E).
13 – Apical labial palp: 0: longitudinal or rectangular-shaped (Fig. 3E); 1: securiform or triangular-shaped (Fig. 3D).
14 – Apical tooth on lacinia: 0: absent (Fig. 3B); 1: present (Figs 3A, C).
15 – Lacinial tooth: 0: single (Fig. 3A); 1: bifid (Fig. 3C).
16 – Gular furrow: 0: absent; 1: present (Fig. 4A).
17 – Penultimate antennal segment: 0: longer than wide (Fig. 4E); 1: equal or wider than long (Figs 4B, C, D).
18 – Length of antennae: 0: not extending beyond posterior base of prosternum; 1: extending beyond posterior base of prosternum.
19 – Last antennal segments: 0: not flattened; 1: flattened.
20 – Number of antennal segments with stellate sensoria: 0: four; 1: five; 2: six; 3: seven.
21 – Lateral setae at apex of last tarsal segment: 0: absent (Figs 5B, C); 1: present (Fig. 5A).
22 – Length of apical tarsal segment of hind legs: 0: equal or greater than first tarsal segment; 1: less than first tarsal segment.
23 – Ventral surface of last tarsal segment: 0: with two distinct rows of setae, rows of several setae (Fig. 5A); 1: with two distinct rows of setae, rows of setae sparse (usually less than 10 pairs) (Fig. 5B); 2: with a thick pad (Fig. 5C).
24 – Penultimate tarsal segment of hind leg (dorsal view): 0: subequal to previous segment; 1: shortest of all tarsal segments.
25 – Penultimate tarsal segment: 0: not cupiliform nor slanted (Figs 5A, B); 1: cupiliform or slanted (Fig. 5C).
26 – Length of first tarsal segment of hind leg: 0: longer than tarsal segments 2 and 3 combined; 1: equal or shorter than tarsal segments 2 and 3 combined.
27 – Number of setae on empodium: 0: two (Fig. 5B); 1: greater than two (Fig. 5C); 2: zero (Fig. 5A).
28 – Apex of femora: 0: without semicircular depression; 1: with semicircular depression (Fig. 5K).
29 – Apical tibial tooth on hind leg of males: 0: absent (Figs 5F, G); 1: present (Fig. 5E).
30 – Distinct rows of setae on protibia: 0: absent; 1: present (Fig. 5I).
31 – Length of rows of setae on protibia: 0: greater than half of the length of protibia (Fig. 5I); 1: equal or less than half the length of protibia.
32 – Apex of protibia: 0: not wider than base; 1: wider than base (Fig. 5H).
33 – Pilosity at apex of tibia: 0: continuous (Fig. 5C); 1: with a distinct bare area above the row of apical tibial spines (Figs 5A, B).
34 – Protibia of males: 0: not strongly curved at apex; 1: strongly curved at apex (Fig. 5D).
35 – Outer longitudinal depression on tibia: 0: absent; 1: present (Fig. 5J).
36 – Metatibia of males with a patch of thick setae near apex: 0: absent (Figs 5E, F); 1: present (Fig. 5G).
37 – Base of metafemur: 0: without a notch near the trochanter (Fig. 6A); 1: with a notch near the trochanter (Fig. 6B).
38 – Clubbed femora: 0: absent; 1: present.
39 – Anterior edge of pronotum behind the head: 0: straight (Figs 7A, C, D); 1: concave (with median portion broadly curved towards posterior); 2: convex (with median portion slightly curved towards anterior) (Fig. 7B).
40 – Posterior edge of pronotum: 0: straight or convex (Fig. 7B); 1: bisinuate (Figs 7A, C).
41 – Anterior margin of pronotum: 0: incomplete or absent (Figs 7A, B); 1: complete (Fig. 7D).
42 – Lateral margin of pronotum: 0: complete (Figs 7A, B, C, D); 1: incomplete or absent (Fig. 7G).
43 – Hind margin of pronotum: 0: complete (Figs 7A, B, D); 1: incomplete or absent (Figs 7C).
44 – Anterior projections of pronotum: 0: absent (Fig. 7B); 1: present (Fig. 7C).
45 – Anterior corners of pronotum: 0: not reaching to middle of eyes; 1: produced anteriorly at least to middle of eye (Fig. 7C).
46 – Anterior corners of pronotum: 0: rounded (Figs 7B, D); 1: acute.
47 – Median longitudinal depression on pronotal disc: 0: absent (FigS 7 B, C, D); 1: present (Fig. 7A).
48 – Shape of pronotum: 0: wider than long (Fig. 7A, C, D); 1: longer than wide (Fig. 7B).
49 – Lateral angles of prothorax in anterior view: 0: triangular (Fig. 7E): 1: rounded (prothorax cylindrical) (Fig. 7F).
50 – Lateral portion of prosternum in front of procoxa: 0: shorter than 3/4 length of procoxa (Fig. 8B); 1: equal or longer than 3/4 length of procoxa (Fig. 8A).

 51 – Prosternal process in lateral view: 0: straight (Fig. 8A); 1: slightly curved; 2: strongly curved (Fig. 8B).
 52 – Prosternal process: 0: single longitudinal depression between procoxae (Fig. 8A); 1: flat; 2: with longitudinal margins near procoxae.
 53 – Apex of prosternal process: 0: acute or narrowly curved; 1: truncated, broadly rounded or incized medially.
 54 – Thick setae on prosternal process: 0: absent; 1: present.
 55 – Prosternal process between procoxae: 0: without lateral expansions (Fig. 8A); 1: with lateral expansions (Fig. 8B).
 56 – Posterior margin of hypomeron: 0: margined; 1: not margined.
 57 – Circular punctations on hypomeron: 0: absent; 1: present.
 58 – Hind wings: 0: short rounded knob; 1: macropterous (full wings present, with folded apex); 2: strap-like (long and narrow wings, usually extending to half the length of elytron or shorter); 3: reduced apically (hind wing only as long as elytron).
 59 – Metallic iridescence on elytra: 0: absent; 1: present.
 60 – Elytral interstriae: 0: flat or slightly convex; 1: with sharp ridges or tubercles (at least near posterior apex of elytron).
 61 – Bifurcation of stria 9 near posterior apex of elytron: 0: absent; 1: present.
 62 – Anterior edge of elytral epipleuron: 0: well defined; 1: feebly defined.
 63 – Elytra epipleuron: 0: incomplete; 1: complete.
 64 – Longitudinal groove on elytral epipleuron: 0: present; 1: absent.
 65 – "Squared" elytral humerus: 0: absent; 1: present.
 66 – Length of scutellary striole: 0: equal or shorter than distance between elytral striae one and three; 1: greater than distance between elytral striae one and three but shorter than half the length of elytra; 2: complete (reaching apex of elytra).
 67 – Scutellum: 0: absent or very reduced; 1: present, of normal size.
 68 – Shape of scutellum: 0: triangular; 1: pentagonal.
 69 – Anterodorsal corners of elytron: 0: with a notch to receive the prothorax; 1: without a notch to receive the prothorax.
 70 – Mesoventral receptacle: 0: flat or with median region as high as metaventrite; 1: median region depressed, with low walls (Fig. 8B); 2: median region depressed, with high walls (Fig. 8A).
 71 – Metaventral process: 0: margined anteriorly between mesocoxae; 1: not margined anteriorly.
 72 – Crenulations behind mesocoxae: 0: absent; 1: present.
 73 – Transversal depression on metaventrite anterior of metacoxae: 0: deep; 1: shallow or absent.
 74 – Circular punctations on mesepisternum: 0: absent; 1: present.
 75 – Distance between meso and metacoxae: 0: less than the length of one mesocoxa; 1: equal or wider than length of one mesocoxa.
 76 – Row of setae on posterior edge of tergite six: 0: absent (Figs 9B, C); 1: present (Fig. 9A).
 77 – Pilosity on tergite seven: 0: setae present on apical half or less (Fig. 9B); 1: setae covering 2/3 of segment, with two lateral oval patches lacking thick setae (Fig. 9A); 2: setae covering 2/3 of segment, lacking oval patch without setae (Fig. 9C).
 78 – Thick setae in middle of tergite six: 0: absent (Figs 9A, B); 1: present (Fig. 9C).
 79 – Length of defence reservoirs: 0: shorter than anterior base of ventrite four; 1: posterior apex between anterior base ventrites four and two; 2: longer than anterior base ventrite two.
 80 – Shape of defence reservoirs: 0: conical; 1: saccate (Fig. 9D).
 81 – Number of tubules leading to each reservoir: 0: one (Fig. 9D); 1: two or more.
 82 – Spermathecal gland derived: 0: anterior end of vagina (Fig. 9E); 1: laterally (Fig. 9F).
 83 – Shape of spermatheca: 0: spherical (Fig. 9E); 1: tapered (Fig. 9F).
 84 – Position of proctiger when ovipositor extended: 0: lateral arms close to paraprocts or extra baculi (Figs 10A, 11A, B); 1: under tergite 8 (Figs 10B, 11C, E, F, H, 13C, E, F, H).
 85 – Gonostyli reduced: 0: no (Fig. 10D, 12C); 1: yes (Fig. 12B).
 86 – Ovipositor shape: 0: short, slightly sclerotized (Figs. 11A, 13B); 1: long, flexible (Figs 10C, 11B, C, F); 2: blade-like (Figs 10B, 12B).
 87 – Extra baculus: 0: absent (Figs 10A, B, 11F, G, 12A, B, 13B, F, G); 1: present (Figs 10C, D, 11B, C, D, 12C, D, 13A, C, D).
 88 – Extra baculus: 0: about equal in length to paraproct baculus (Figs 10D, 12D); 1: shorter than paraproct baculus (Figs 11C, D, 13C, D); 2: longer than paraproct baculus (Figs 11B, 13A); 3: short sclerotized plate (Figs 10C, 12C).
 89 – Paraprocts: 0: membranous (Figs 10B, D, 11C, F, 13A, G); 1: sclerotized (Figs 10A, 11A, 12A, 13B).
 90 – Length of proctiger (lateral view): 0: equal or shorter than tergite eight (Figs 10A, B, C, D, 11A, C, E, F, H); 1: longer than tergite eight (Fig. 11B).
 91 – Orientation of paraproct baculus: 0: transversal; 1: oblique.
 92 – Length of spiculum ventrale (lateral view): 0: equal or shorter than ovipositor (Figs 10A, B); 1: longer than ovipositor (Figs 11C, F).
 93 – Clear keel on spiculum ventrale: 0: absent (Figs 13A, B); 1: present (Figs 11C, F, 13C, F).
 94 – Length of coxite one: 0: longer than coxites two to four combined (Figs 10A, D); 1: shorter than coxites two to four combined (Fig. 10B).
 95 – Baculi of coxite one near base: 0: separate; 1: immoveable.
 96 – Sclerotized area at apex of ovipositor: 0: absent; 1: present.
 97 – Row of hairs inside metacoxal cavity: 0: absent; 1: present.
 98 – Crenulations behind metacoxae on ventrite one: 0: absent; 1: present.
 99 – Crenulations on the anterior border of ventrites two and three: 0: absent; 1: present.
100 – Border on ventrite five: 0: absent; 1: present.
101 – Anterior corners of ventrite four: 0: depressed; 1: not depressed; 2: with a longitudinal margin.

ters CM are undescribed Coelometopini taxa collected in northern Queensland's wet tropics and are used in a database currently maintained at the Queensland Museum.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
Strongylium sp. 1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	2	1	1	1	0	0	1	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0
Strongylium sp. 2	1	1	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	2	1	1	1	0	0	1	0	0	?	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	2
Strongylium fuscovestitum	1	1	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	2	1	1	1	0	0	1	0	0	?	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	2
Achariotheca baloghi	2	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	2	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1
Agymnonyx sp.	0	1	3	0	0	0	0	1	1	2	1	0	1	1	0	0	0	1	0	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1
Apterobrachys wilhelminae	0	0	0	0	0	0	1	1	2	0	0	1	1	0	0	?	0	1	0	1	2	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0	0	1
Apterophenus sp.	0	0	0	0	0	0	1	1	2	0	0	1	0	0	0	?	0	1	0	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0	1	0
Apterotheca amaroides	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	?	0	1	0	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	1	0
Apterotheca besti	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	1	0
Apterotheca punctipennis	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	2	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	1	0
Apterotheca CM09	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	1	0
Apterotheca CM16	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	2	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	1	1	0	0	1	0	1	1
Apterotheca CM28	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0
Apterotheca CM29	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	1	0
Apterotheca CM38	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	2	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	1	0
Asopidiopsis sp.	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	2	1	0	0	0	0	1	0	0	?	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	2
Bradymerus raucipennis	0	1	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	2	0	0	0	0	0	1	0	0	?	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	1	1
Campolene nitida	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1
Cataphanus quadraticollis	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	?	0	1	0	1	2	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	2	0	0	0	1
Caxtonana costata	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	0	2	0	0	1	0	0	0	0	1	1	?	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Caxtonana CM06	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Caxtonana CM07	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Caxtonana CM14	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1
Chariotheca sp. 1	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	2	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1
Chariotheca sp. 2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	?	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	2
Ctenus monteithi	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	2	1	0	1	0	0	1	0	0	?	0	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0
Derosphaerus trochantericus	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	1	0	2	1	0	1	0	0	1	0	0	?	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2
Episopus convexus	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Espites basalis	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	1	0	0	?	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1
Graptopezus crenaticollis	0	1	0	0	0	0	1	0	0	2	0	0	0	0	1	1	0	0	1	0	2	1	0	1	0	0	1	0	0	?	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Hydissus CM 17	0	0	0	0	0	1	0	0	2	0	0	1	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	1	0	0	1	0	0	1
Hypaulax tenuistriata	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	1	0	2	1	0	1	0	0	1	0	0	?	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Irianobates krikkeni	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1
Isopus kanak	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	0	1	0	0	1	0	0	?	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Kaszaba coerulescens	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	1	0
Metisopus purpureipennis	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	2	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	2
Micromenandris sp.	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	0	1	0	0	1	0	0	?	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	2
Microphenus sp.	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1
Neotheca fusca	2	0	1	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1
Oectosis cylindrica	0	1	0	0	0	0	0	0	1	2	1	0	0	0	0	?	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	1	0	0	1	0	0	1
Omolipus CM18	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	2	0	0	0	0	1	1	0	0	0	0	0	1
Papuamisolampus toxopeusi	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	?	0	1	0	1	2	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1
Pezophenus submetallicus	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1
Phenus latitarsus	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	?	0	1	0	1	2	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	1
Promethis sulcigera	0	1	0	0	0	0	1	0	0	2	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	1	0	0	?	0	0	0	1	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1
Rhophobas burgersi	0	1	0	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	2	0	0	0	0	0	1	0	0	?	0	0	0	1	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1
Scotoderus cancellatus	0	0	0	0	0	0	0	1	2	0	0	1	1	0	0	?	0	1	0	1	2	0	0	0	0	0	1	0	0	1	1	1	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1
Tetragonomenes ruficornis	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	?	0	1	0	1	2	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1
Thesilea sp.	2	0	1	0	0	0	0	0	1	2	0	0	0	0	0	?	0	1	0	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	2
Zophophilus curticornis	0	0	0	0	0	1	0	1	1	0	0	1	1	0	0	?	0	1	0	1	2	1	0	0	0	0	1	0	0	?	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1

Character matrix (characters 52–111):

```
                                  5 5 5 5 5 5 5 5 6 6 6 6 6 6 6 6 7 7 7 7 7 7 7 7 7 7 8 8 8 8 8 8 8 8 8 8 9 9 9 9 9 9 9 9 9 9 1 1
                                  2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1
Strongylium sp. 1                 2 0 0 1 1 0 0 0 0 1 1 0 0 0 1 1 0 0 0 0 1 0 0 1 1 0 0 1 1 0 0 1 1 0 0 1 1 0 0 1 0 0 1 0 0 1 0 1
Strongylium sp. 2                 2 0 0 1 1 0 0 0 0 1 1 0 0 0 1 1 0 0 0 0 1 0 0 1 1 0 0 1 1 0 0 1 1 0 0 1 1 0 0 1 0 0 1 0 0 1 0 1
Strongylium fuscovestitum         0 0 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 1 0 0 1
Achariotheca baloghi              2 0 0 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0
Agymnonyx sp.                     1 1 0 1 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 0 0
Apterobrachys wilhelminae         2 0 1 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1
Apterophenus sp.                  2 0 1 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0
Apterotheca amaroides             0 0 1 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0
Apterotheca besti                 0 0 1 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0
Apterotheca punctipennis          2 0 1 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0
Apterotheca CM09                  2 0 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0
Apterotheca CM16                  2 0 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0
Apterotheca CM28                  2 0 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0
Apterotheca CM29                  2 0 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0
Apterotheca CM38                  2 0 1 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0
Asopidiopsis sp.                  2 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0
Bradymerus raucipennis            2 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 1
Campolene nitida                  2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 1
Cataphanus quadraticollis         1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 1
Caxtonana costata                 2 0 1 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0
Caxtonana CM06                    2 0 1 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0
Caxtonana CM07                    2 0 1 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0
Caxtonana CM14                    2 0 1 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0
Chariotheca sp. 1                 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 1
Chariotheca sp. 2                 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 1
Cuemus monteithi                  2 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 1
Derosphaerus trochantericus       2 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1
Episopus convexus                 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 1
Espites basalis                   2 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0
Graptopezus crenaticollis         2 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1
Hydissus CM 17                    2 1 1 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 1
Hypaulax tenuistriata             2 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1
Irianobates krikkeni              2 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0
Isopus kanak                      0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 1
Kaszaba coerulescens              2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1
Metisopus purpureipennis          0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0
Micromenandris sp.                ? 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 1
Microphenus sp.                   2 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 1
Neotheca fusca                    2 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1
Oectosis cylindrica               2 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 1
Omolipus CM18                     0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 1
Papuamisolampus toxopeusi         2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 1
Pezophenus submetallicus          0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 1
Phenus latitarsus                 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 1
Promethis sulcigera               2 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0
Rhophobus burgersi                2 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1
Scotoderus cancellatus            2 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0
Tetragonomenes ruficornis         0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 1
Thesilea sp.                      1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 1 0 0
Zophophilus curticornis           2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 1
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