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The Larva of *Sirrhas variegatus*, sp. nov., with Notes on the Perimylopidae, Ulodidae (stat. nov.), Zopheridae and Chalcodryidae (Coleoptera : Tenebrionoidea)

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Abstract

Sirrhas Champion and its type, *S. limbatus* Champion, are redescribed and *S. variegatus*, sp. nov., is described, along with its presumed larva. The two species are distinguished in a key and comments are made on their geographic distribution and habits. *Sirrhas* is compared with members of the Chalcodryidae, in which the genus is currently placed, and with the tenebrionoid taxa *Melytra* Pascoe, *Parahelops* Waterhouse, Perimylopidae and Zopheridae, each of which is discussed and delimited. A phylogenetic analysis is carried out on a matrix of 21 genera of Tenebrionoidea and 31 characters taken from both larvae and adults. As a result, the following taxonomic changes are proposed: (1) *Sirrhas* to be moved from Chalcodryidae to Perimylopidae, and the latter group expanded to include *Melytra* and *Parahelops*, and (2) the zopherid subfamily Ulodinae, including *Pteroderes* Germain and *Trachyderastes* Kaszab, but excluding *Melytra* and *Parahelops*, to be raised to family rank. The remaining Zopheridae form a monophyletic group with Colydiidae and Monommatidae, but relationships within that complex are not discussed further. A key to the genera of Ulodidae and Perimylopidae based on adults is given. The following new combinations are proposed in Ulodidae: *Ganyme tuberculata* (Carter) and *G. demarzi* (Kulzer).

Introduction

The Tasmanian genus *Sirrhas* Champion was placed by its author in Lacordaire's group Lagriides : Trachelostenides (Trachelostenidae according to Watt 1987). Carter (1915) placed his *Notolea* (= *Sirrhas*) in the tenebrionid subfamily Strongyliinae. Watt (1974*a*) combined *Sirrhas* with three New Zealand genera – *Onysius* Broun from Melandryidae, and *Chalcodrya* Redtenbacher and *Philpottia* Broun from Tenebrionidae – to form a new family Chalcodryidae. The last two genera were considered by Crowson (1967) to 'probably belong in or near Zopheridae'.

A new species, apparently congeneric with *S. limbatus* Champion, was collected from several sites in western and southern Tasmania, mainly in flight-intercept trap samples and in pyrethrin-fogging samples from moss-covered trunks and logs and tree fern crowns. Unusual tenebrionoid larvae were collected twice in the same samples with adults of the new species, and similar larvae were collected from areas where *S. limbatus* occurs (see below). These larvae possess attributes in common with Perimylopidae and some Zopheridae (e.g. *Syrphetodes* Pascoe), but lack most of the diagnostic features of *Chalcodrya* (globular head with Y-shaped epicranial suture, mandibular molae, simple mala, lack of urogomphi, terminal 10th segment, anal asperities, and annular spiracles). Although no direct association of these larvae with adult *Sirrhas* was made through rearing, the following make such an association probable, if not certain: (1) the multiple occurrence of larvae with adults; (2) the systematically important features of the larvae; (3) the large size, which eliminates the genus *Melytra* Pascoe (see below); and (4) the lack of other suitable taxa to which the larvae could belong among the relatively restricted Tasmanian fauna (especially at higher elevations).

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These larvae are described below, along with a redescription of the genus *Sirrhas*, descriptions of the two *Sirrhas* species, notes on putative larvae of *Melytra ovata* Pascoe, and a discussion of phylogenetic relationships of *Sirrhas*, *Melytra*, *Onysius* and other taxa presently included in Zopheridae, Perimylopidae and Chalcodryidae.

Terminology

The following abbreviations are used in descriptions: PL, median length of prothorax; PW, greatest prothoracic width; EL, median length of elytra (along suture); EW, greatest elytral width.

The following acronyms are used for institutions housing specimens cited: ANIC, Australian National Insect Collection; BMH, Bishop Museum, Honolulu; FMNH, Field Museum of Natural History, Chicago; MVM, Museum of Victoria; NHML, The Natural History Museum, London; SAM, South Australian Museum; TDPI, Tasmanian Department of Primary Industries and Fisheries.

Genus *Sirrhas* Champion

Sirrhas Champion, 1893: 367. Type species, by monotypy, *S. limbatus* Champion 1893: 368.
Notolea Carter, 1915: 530.—Watt 1974*a*: 36 (synonymy). Type species, by monotypy, *N. limbata* Carter 1915: 530.

Redescription

Body elongate with elytra subparallel or slightly wider posteriorly and distinctly wider than prothorax.

Head elongate, median length at least 1·3× as great as width behind eyes, slightly to moderately narrowed behind eyes; neck broad. Antennae with very weak club, last 3 antennomeres elongate but slightly wider than preceding segments and more densely clothed with fine sensory hairs; antennal insertions exposed, anterolaterally oriented, not or only slightly elevated, located well in front of eyes, which are prominent, and weakly emarginate anteriorly (reniform). Frontoclypeal impression very weak or absent. Clypeus truncate apically, with a broad strip of membrane between it and labrum. Labrum transverse; mesal arms of tormae bearing anterior and posterior projections; epipharynx with a number of coarse, anteromesally directed bristles on either side of midline near anterior edge; sensory pegs forming 2 small anterior patches behind which are 2 longitudinally oriented patches, one on either side of midline; median epipharyngeal rod short and very lightly sclerotised (*S. limbatus*) or longer and more heavily sclerotised (*S. variegatus*). Mandibles stout, bidentate; externally setose; asymmetrical molae heavily sclerotised, without transverse ridges or asperities; prostheca a large, pubescent membrane. Galea relatively large, apically expanded, rounded and densely setose; lacinia setose, with (*S. variegatus*) or without (*S. limbatus*) slender, curved spine at apex; apical segment of maxillary palp securiform; palp organ of 12 thin-walled, blunt-tipped, proclinate sensilla.

Prothorax slightly transverse, widest near the middle and narrower anteriorly and posteriorly, slightly explanate laterally, with complete anterior and posterior margins contiguous with slightly raised lateral pronotal carinae, which are somewhat sinuate in lateral view; anterior and posterior angles very broadly rounded to absent; disc only slightly convex; pronotal hypomera relatively steeply inclined. Procoxal cavities slightly transverse, internally open, externally closed by lateral expansions of the prosternal (intercoxal) process and mesal extensions of the hypomera, the former broadly overlapping the latter; procoxae conical and projecting; trochantin moderately well developed but completely concealed; cryptopleuron freely movable. Prosternal intercoxal process narrow (less than 0·2× as wide as a coxal cavity) and more or less flattened, not arched. Scutellum more or less semicircular.

Elytra at base distinctly broader than base of pronotum and slightly broader than greatest pronotal width; sides slightly to moderately diverging to posterior three-fifths; disc moderately flat at middle but steeply sloping laterally; humeri well-developed; punctation confused or forming irregular puncture rows, broken up in either case by slightly elevated

areas of varying shape. Epipleuron widest beneath humerus, gradually narrowing posteriorly and ending at or just before elytral apex, with a distinct, slightly elevated carina between it and disc.

Hind wings fully developed, apical membrane about two-fifths wing length; connection between medial and cubital systems (MP_4 and CuA) absent or incomplete; wedge cell long and narrow (about 7× as long as wide), acute at apex; medial fleck present but faint.

Mesosternum moderately flat, narrowly truncate to subacute anteriorly, posteriorly with intercoxal process somewhat elevated (as seen from below), very narrow (less than 0·15× as wide as mid coxal cavity), and extending beyond posterior third of coxal cavity; mid coxa globular, slightly projecting; trochantin well-developed and exposed; coxal cavity closed laterally by mesepimeron and a small portion of mesepisternum. Metasternum moderately convex; discrimen short to moderately long; visible portion of metepisternum moderately broad, less than 4× as long as greatest width; metepimeron visible, lying between hind coxa and epipleuron. Metendosternite with well-developed laminae.

Legs long and slender; trochanter strongly oblique; tarsi without lobed segments, basal and terminal tarsomeres longest, penultimate shortest, all segments densely clothed beneath with fine hairs; claws simple.

Abdomen with ventrites 1–3 connate; membrane visible at bases of 4 and 5. Aedeagus normally oriented, moderately lightly sclerotised; tegmen divided into distinct basale and apicale, the former at least 1·6× as long as the latter; apicale distinctly emarginate and with 2 tufts of setae at apex; penis slightly longer than tegmen. Ovipositor with paraprocts longer than coxites, bearing distinct baculi; coxites divided into 3 parts, basal one with short, straight, transverse baculus, apical one as long as first two taken together, styli well-developed, attached just before apex. Genital tract with bursa short and broad, barely separated from apex of vagina (*S. limbatus*) or relatively long and well-defined, narrower at apex (*S. variegatus*); spermathecal gland attached apically to bursa; spermatheca simple (*S. variegatus*) or divided into 3 lobes (*S. limbatus*).

Comments

The female genital tract of *S. variegatus* (Fig. 4) appears to be strikingly different from that of *S. limbatus* illustrated by Watt (1974*a*, figs 41, 42); the latter has a complex, three-lobed spermatheca, with two of the lobes annulated. Watt's figure does not show a short extension of the bursa between the spermathecal complex and the common oviduct. In my dissection a slender gland is attached at this point. This slight bulge appears to be homologous to the long, curved bursa in *S. variegatus*, which also has a slender gland attached at its apex. What Watt called a 'spermathecal gland' appears to be part of the complex spermatheca, which in *Sirrhas* (Fig. 4) is a simple structure. In *Onysius*, there is a two-part, annulated spermatheca located at the anterior end of the genital tract, and no glands can be seen. Annulated spermathecae are also found in *Syrphetodes* (two lobes, one on each side of the tract and well away from the enlarged terminal bursa) and in *Pteroderes* Germain (large, terminal and trilobed). In *Meryx* Latreille and in Perimylopidae the female tract is simple with a terminal sac-like bursa and basal gland; *Dipsaconia* Pascoe is similar, but there are two small spermathecae at the base of the bursa. Both *Melytra* and *Parahelops* have a terminal bursa which is subdivided. Although variable, these tracts bear little or no resemblance to those of *Chalcodrya* and *Philpottia* (Watt 1974*a*, figs 38–40, 44), which have a large, sclerotised bursa with a gland attached at the middle.

Sirrhas adults also have many features in common with members of the family Perimylopidae; this is especially striking when *S. variegatus* is compared with *Hydromedion magellanicum* (Fairmaire). Features of *Hydromedion* Waterhouse that distinguish it from *Sirrhas* include the distinct frontoclypeal impression, non-emarginate eyes, ovoid (rather than securiform) terminal maxillary palp segment, exposed prothoracic trochantins, and absence of hind wings. The small, flightless Tasmanian species *Melytra ovata*, while superficially very different from the species of *Sirrhas*, shares a number of features with them (see discussion of *Melytra* below).

Key to Species of *Sirrhas* Champion

1. Prothorax widest just behind middle, sides slightly converging anteriorly, more strongly so posteriorly; elytra subparallel; elevated areas on elytra punctate, dark, forming a reticulate pattern; mesepisterna separated by a distance much greater than the width of the mesosternal intercoxal process ..... *S. limbatus* Champion

   Prothorax subquadrate, widest just in front of and behind middle, sinuate in between; elytra distinctly widened posteriorly; elevated areas on elytra impunctate, yellow, forming an irregular pattern; mesepisterna separated by a distance less than width of mesosternal intercoxal process ..... *S. variegatus*, sp. nov.

Sirrhas limbatus Champion

Sirrhas limbatus Champion 1893: 368. Type locality: Goulds Country, north-east Tasmania. Holotype ♀ in NHML (examined).

Notolea limbata Carter 1915: 531. Type locality: Mt Horror, Tasmania. Holotype, ♂ in SAM, paratype ♀ in SAM, paratype ♀ in MVM (examined).

Redescription

Length 14·6–17·1 mm. Body elongate, parallel-sided, moderately convex; dark reddish-brown with a broad, yellow to light brown band along lateral edge of each elytron, legs and antennal apex slightly lighter. Surface shiny and subglabrous, clothed with very short setae. Head very slightly narrowed behind eyes, moderately densely punctured, punctures about as large as eye facets and separated by a puncture diameter or less; frontoclypeal impression weakly indicated. Pronotum about four-fifths as long as wide (PL/PW = 0·75–0·83, $\bar{x}$ = 0·78), widest at middle, sides slightly converging anterior to broadly rounded front angles, more strongly converging posterior to hind angles, which are almost obsolete; disc slightly, somewhat unevenly convex; punctation slightly coarser than on head but on mesal portion punctures tend to be contiguous and longitudinally aligned. Elytra about 2·4× as long as wide (2·27–2·43, $\bar{x}$ = 2·36) and 3·8× as long as pronotum (3·63–3·96, $\bar{x}$ = 3·79), moderately convex, more or less flattened on either side of suture, but gradually sloping posteriorly and steeply sloping laterally; mesal portions of elytra with a number of elevations forming an irregular, reticulate pattern; punctures slightly larger than those on pronotum, more or less uniformly distributed. Punctures on ventral surfaces of prothorax and pterothorax similar to that on pronotal disc, those on abdomen slightly finer and denser in female, much finer and denser in male. Fore tibia in male with weak tooth at about middle of inner edge. Aedeagus slightly curved; basale about 2·2× as long as apicale, apical notch relatively shallow.

Distribution

Tasmania: north-eastern and south-eastern portions and from one locality (Savage R.) in the north-western part of the island (Fig. 12). Watt (1974*a*) examined specimens (including the types) from Cascades, near Hobart (42·54 S, 147·17 E), Goulds Country (41·14 S, 148·03 E), Launceston (41·26 S, 147·06 E) and Mt Horror (41·04 S, 147·44 E). Additional specimens examined with the following data: 2, Big Sassy Ck (42·42 S, 147·52 E), 12.v.1989, pyrethrin knockdown *Atherosperma*, J. Diggle, H. Mitchell (ANIC); 2, Mt Mangana, Bruny I. (43·21 S, 147·13 E), 4.iv.1989, pyrethrin knockdown *Phyllocladus*, P. Greenslade, J. Diggle, ANIC Coleoptera Voucher 88-0188 (ANIC); 2, same locality and date, pyrethrin knockdown *Nothofagus*, P. Greenslade, J. Diggle (ANIC); 1, Savage River Pipeline Rd (41·30 S, 145·20 E), 20.iv.1989, pyrethrin knockdown *Nothofagus*, J. Diggle (ANIC).

Comments

Watt (1974*a*) recorded a specimen 12·5 mm long, outside the range of the small series available to me.

Sirrhas variegatus, sp. nov.

(Figs 1–4, 12)

Material Examined

Holotype. ♂, The Gap, Florentine Rd, 15 km WNW of Maydena (42·43 S, 146·29 E), Tasmania, 600 m, 1.iii.1980, pyrethrin fogging tree ferns, A. Newton, M. Thayer (ANIC).

Paratypes. **Tasmania:** 2, same data as holotype (ANIC, FMNH); 2, same locality and date, pyrethrin fogging *Nothofagus cunninghamii* bark, A. Newton, M. Thayer (ANIC, FMNH); 1, Florentine Valley, 22 km NW of Maydena (42·35 S, 146·29 E), 700′, 15.ii.1977, mosses on logs, FM(HD) #77–141, J. Kethley (FMNH); 1, Lake St Clair (42·06 S, 146·10 E), 750 m, 25–27.i.1980, pyrethrum spray tree ferns, J. Lawrence, T. Weir (ANIC); 1, Lower Gordon R. (42·48 S, 145·51–145·54 E), H. E. C. Survey, 5R-2480, Mar. 1977, moss, Howard, Hill etc. (ANIC); 1, Mt Murchison (41·50 S, 145·37 E), 18.iv.1989, pyrethrin knockdown, P. Greenslade, ANIC Coleoptera Voucher No. 88-0189 (ANIC); 1, 4 km S of Mt Oakleigh (41·51 S, 146·03 E), Malaise #3, 880 m, 7.xi.1990, malaise trap, W.E.B.S. (ANIC); 1, 2 km NE by N of Mt Ossa (41·52 S, 146·93 E), FIT #3, 1000 m, 30.ix.1990–8.i.1991, ANIC 1146, flight intercept trap, E. Nielsen, T. Edwards (ANIC); 1, same locality, 8.i–12.ii.1991, ANIC 1152, flight intercept trap, A. Calder, W. Dressler (ANIC); 1, Mt Read (41·51 S, 145·33 E), 800 m, 9.i.1989, P. B. McQuillan, E. S. Nielsen (TDPI); 1, 4 km SSE of Mt Rufus (42·10 S, 146·07 E), 800 m, 26–28.i.1980, J. Lawrence, T. Weir (ANIC); 2, Pelion Hut, 3 km S of Mt Oakleigh (41·50 S, 146·03 E), FIT #1, 860 m, 28–30.xi.1990, surfaces at night, ex fungi, T. Weir (ANIC); 1, same locality, 30.ix.1990–8.i.1991, ANIC 1144, flight intercept trap, E. Nielsen, T. Edwards (ANIC); 1, same locality, 7.iii–9.iv.1991, Malaise trap #5, E. Edwards, J. Berry (ANIC); 1, Pieman R., nr Lower Rapids (41·38 S, 145·07 E), 5.i.1954, T. G. Campbell (ANIC); 5, 2 km ENE of Tim Shea (42·43 S, 146·29 E), 600 m, 1.ii.1980, moss-covered trunks and logs, J. F. Lawrence, T. A. Weir (ANIC).

Description

Length 10·0–12·7 mm ($\bar{x}=11·3$, s.d. $=0·7$, $n=24$). Body moderately elongate (Fig. 1), elytra slightly wider posteriorly; reddish-brown to dark brown, elytra with an irregular pattern of yellow markings, which in some specimens coalesce so that yellow, rather than brown is the dominant elytral colour; antennae, legs and palps yellow, except for first 2 and last 3 antennal segments, apical segment of maxillary palp and large patch on each

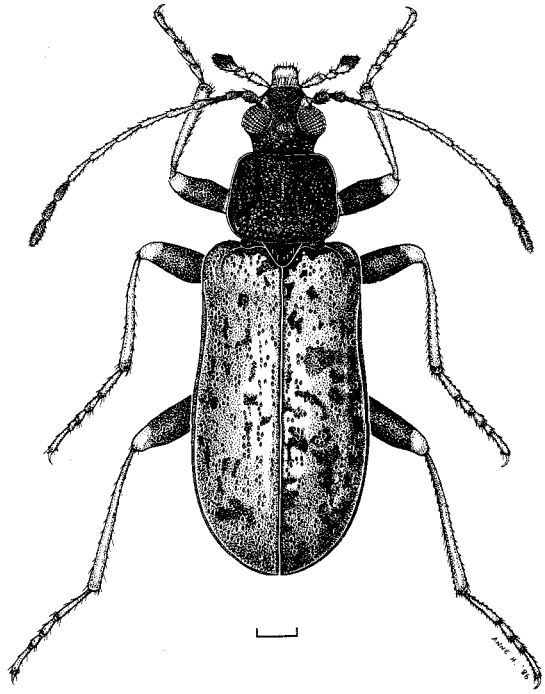
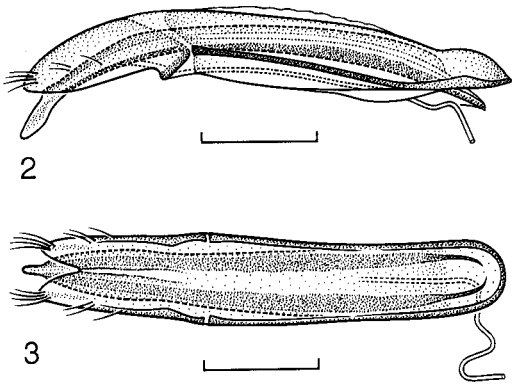


Fig. 1. *Sirrhas variegatus*, sp. nov., adult female, dorsal. Scale bar 1 mm.

femur, all of which are darker. Surface shiny, subglabrous, clothed with very short setae not visible under lower magnifications plus a few scattered longer setae. Head more abruptly narrowed immediately behind eyes than in *S. limbatus*, punctation similar to that in *S. limbatus*; frontoclypeal impression absent. Pronotum about seven-eights as long as wide (PL/PW = 0·78–0·92, $\bar{x}$ = 0·86), subquadrate with slightly sinuate sides, front and hind angles broadly rounded; disc slightly and irregularly convex; punctation similar to that in *S. limbatus*, but orientation of punctures less regular and those in centre tending to form concentric circles. Elytra about 1·9× as long as wide (EL/EW = 1·81–2·10, $\bar{x}$ = 1·93) and 3·5× as long as pronotum (3·33–3·74, $\bar{x}$ = 3·56), slightly convex, sides and posterior portions moderately sloping; surface with many elevated areas, which are impunctate and form a highly irregular pattern; punctation highly irregular, forming clusters and some incomplete longitudinal rows. Punctation of ventral surfaces similar to that in *S. limbatus*, with abdominal punctures, especially in male, finer and sparser than those of thorax. Fore tibia in male similar to that in female. Aedeagus (Figs 2, 3) more strongly curved than in *S. limbatus*; basale about 1·75× as long as apicale, apical notch moderately deep.



Figs 2, 3. *Sirrhas variegatus*, sp. nov., adult male: *2*, aedeagus, lateral; *3*, aedeagus, dorsal. Scale bar 0·5 mm.

Comments

This species differs from *S. limbatus* Champion in several respects, the most obvious being the less parallel-sided elytra, which have a distinctive sculpture and colour, and the differently shaped pronotum. In addition, mesosternum is strongly narrowed anteriorly and the male fore tibia is simple. The differences between the two species in the female genital tract were discussed above.

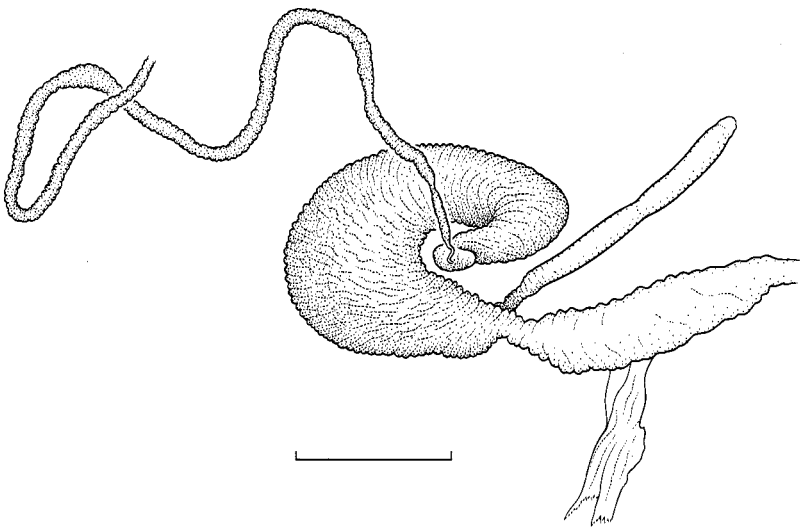


Fig. 4. *Sirrhas variegatus*, sp. nov., adult female, internal genital tract, lateral. Scale bar 0·5 mm.

Presumed Larva of *Sirrhas variegatus*

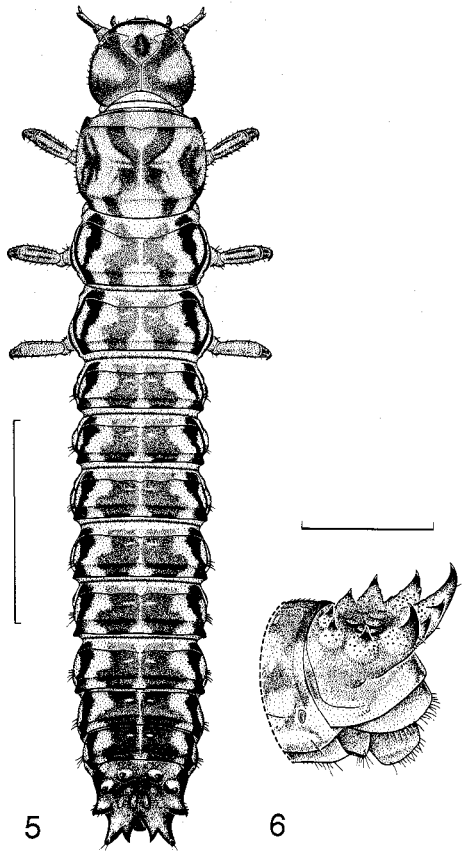
(Figs 5–11)

Material Examined

Tasmania: 1, West side Lake St Clair (42·06 S, 146·10 E), 750 m, 25–27.i.1980, under bark and in rotten logs, J. Lawrence, T. Weir (ANIC); 2, same locality, 25.i.1980, pyrethrin spray tree ferns, A. Newton, M. Thayer (ANIC); 1, Mt Murchison (41·50 S, 145·37 E), 18.iv.1989, pyrethrin knockdown, P. Greenslade (ANIC); 1, same locality, 17.iv.1989, rainforest hand-collecting, J. Diggle (ANIC).

Description of Mature Larva

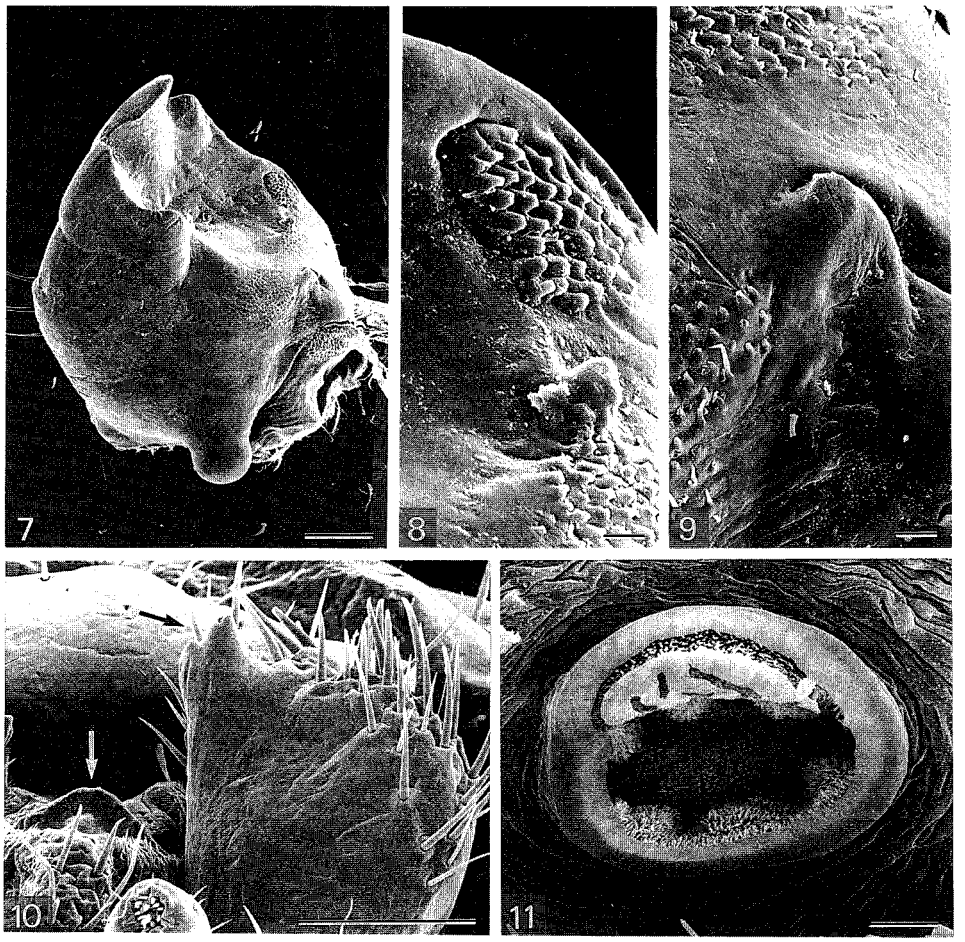
Length 18·2 mm. Body elongate, subcylindrical, moderately sclerotised dorsally, yellow with a pattern of light to dark brown markings forming four broad, wavy, longitudinal bands extending from protergum to tergum 9: a paramedian one on either side of midline and a lateral one extending to tergal edge on each side; each lateral band with a series of larger, subquadrate, yellow maculae (one per segment) and a yellow area around each spiracle; each paramedian band (on tergites 1–8 only) with a pair of small, transverse yellow maculae near midline; other dark markings laterally on anterior and a portion of posterior laterotergites. Dorsal surfaces having a dull appearance, finely granulate to weakly rugose anteriorly, becoming asperate or tuberculate posteriorly. Vestiture of very short, inclined hairs and a few scattered long hairs.



Figs 5, 6. *Sirrhas variegatus*, sp. nov., larva: *5*, dorsal; *6*, abdominal apex dorsolateral. Scale bar 5 mm.

Head slightly transverse, slightly flattened, widest at posterior fourth; sides broadly rounded; posterior edge not emarginate. Epicranial stem moderately long, about $\frac{1}{3}$ as long as head width; frontal arms lyriform and incomplete (ending well before antennal

insertions). Stemmata well developed, usually 5 in vertical rows of 3 and 2 (see *Variation* below). Antennae moderately long, about 0·4× as long as head width, sparsely setose; segment 2 about twice as long as 1 and 3× as long as 3; sensorium conical and about a $\frac{1}{4}$ as long as segment 3. Antennal insertions separated from mandibular bases by a clearly visible strip of cuticle which is more than half the width of antennal segment 1. Frontoclypeal impression distinct. Labrum transverse, about 0·63× as long as wide, slightly convex, clothed with several pairs of longer and shorter setae; tormae connected by a transverse bridge, without anterior projections, with 2 narrow posterior projections expanded at apex; epipharynx relatively simple, with 5 stout, anterolateral bristles, a field of fine, mesally directed hairs on either side, an irregular, transverse row of 6 sensilla near anterior edge and 3 pairs of sensilla, one behind the other, at midline near posterior edge.



Figs 7–11. *Sirrhas variegatus*, sp. nov., larva: *7*, right mandible, ventral (scale bar 100 μm); *8*, same portion of mesal surface at about middle (scale bar 100 μm); *9*, same, portion of mesal surface near base (scale bar 100 μm); *10*, portion of left maxilla and labium-hypopharynx, ventral, showing cleft malar apex with uncus (black arrow) at inner angle and blade-like hypopharyngeal sclerome (white arrow) (scale bar 100 μm); *11*, abdominal spiracle, showing incomplete sieve plate (scale bar 10 μm).

Mandibles (Figs 7–9) broad, obliquely bidentate, with 1 preapical ventral tooth and 1 (right) or 2 (left) preapical dorsal teeth, incisor edge more or less concave between preapical teeth; mola absent, a small tooth sometimes present in molar area (see *Variation* below).

Ventral mouthparts slightly protracted and not deeply embedded in hypostomal recess; ventral epicranial ridges absent; hypostomal rods absent or very weakly indicated, short and diverging. Cardo divided; maxillary articulating area narrow; stipes elongate; mala (Fig. 10) apically expanded, cleft and with well-developed, bidentate uncus. Labium distinctly separated from gula; submentum and mentum indistinctly separated; labial palps separated by the width of basal palp segment; ligula slightly longer than basal palp segment; hypopharyngeal sclerome (Fig. 10) consisting of a simple bar-like structure. Gula about as long as wide.

Prothorax about 1·75 × as long as mesothorax, which is subequal to metathorax; surface of protergum relatively smooth with finely, transversely rugulose patches near midline and granulose areas laterally; setae very short and inconspicuous, except for one long seta on lateral portion of tergum near anterior edge. Meso- and metatergites, near anterior edge, each with a fine, transverse carina, which is slightly curved posteriorly at each end; surfaces more or less as on protergum, but with lateral granules more distinct and extending mesally along posterior edge. Abdominal tergites 1–8 subequal in length, each with an anterior carina similar to those on thorax but with more well-developed lateral curvature; surfaces similar to those of thorax, but with granules better developed and more widely distributed. Tergum 9 (Figs 5, 6) more uniformly darkly pigmented than anterior terga, sometimes with lighter patches anteriorly; surface covered with prominent granules; urogomphi well developed, each with smaller mesal and larger lateral, acute process near base, the latter forming a semicircle with 2 pairs of acute pregomphi occupying anterior portion of tergum.

Thoracic venter lightly pigmented, except for spiracular sclerite, laterotergites, episterna and epimera, which are slightly darker; cervicosternum well developed but other sternal sclerites absent or only vaguely indicated. Thoracic spiracle annular, about 3 × as long as wide, posteriorly, obliquely oriented and located on subtriangular, mesothoracic anterior laterotergite; posterior laterotergite forming an irregular, transverse trapezoid; metathorax with small, subtriangular anterior laterotergite bearing a spircular scar and a posterior laterotergite similar to that on mesothorax. Legs long and slender, moderately lightly pigmented but with dark brown pretarsus, clothed with long and short, fine setae, without spines; coxae strongly projecting, separated by about 1·5 basal diameters on prothorax and 2 basal diameters on meso- and metathorax; femur slightly longer than tibiotarsus; pretarsus well developed, forming slender claw and bearing 2 long setae which are transversely aligned.

Abdominal sternites usually lightly sclerotised, but sometimes darker posteriorly, subtrapezoidal with a transverse, curved laterosternite attached to each posterolateral angle. Anterior laterotergites small, subtriangular and darkly pigmented, obsolete on segments 7 and 8; posterior laterotergites larger, transversely oval and more lightly pigmented. Spiracles (Fig. 11) of a cribriform type, with sieve plate covering only part of opening, 1 to 7 oval, only slightly longer than wide, anteriorly, obliquely oriented, and subequal, each located within an anterolateral notch in tergum; spiracle 8 larger, about 1·5 × as long as wide, posteriorly, obliquely oriented and located in a posterolateral notch in tergum. Sternum 9 strongly transverse, simple, lightly sclerotised. Segment 10 transverely oval, with distinct tergum and sternum, more or less fused laterally, and with distinct pygopods, but with membranous anal lobes in two lateral groups and thus resembling weakly-developed pygopods.

Variation

The late instar from Lake St Clair is the only specimen with only 4 stemmata on each side, but earlier instars from the same site have 5, as does the late instar from Mt Murchison, which differs from the other three in being more darkly pigmented (with narrower longitudinal bands of yellow). The first instar from Mt Murchison has the entire mesal portions of tergites 1, 2, 5, 6 and 7 completely yellow with dark pigment only at the sides. Antennal segment lengths differ somewhat in the earlier instars, with 1 being shorter and 3 longer. In early instars, the mesal edge of the mandibular base is armed with a

number of asperities absent in the mature larva; these are still evident as patches of fine tubercles in intermediate instars (Figs 7–9). The spiracles in early instars are more clearly cribriform, with large and complete sieve plates.

Habitat Data and Larval Associations

The description was based primarily on a mature larva (18·2 mm) collected at the same site as adult *S. variegatus* on the edge of Lake St Clair at 750 m elevation; it is labelled 'under bark and in rotten logs', referring to a hand-collected sample taken among rotten logs in rainforest. Two intermediate instars (9·0 and 9·5 mm long) were collected with several adults at the same site by spraying tree ferns with pyrethrin. One adult and an apparent first instar (2·5 mm) were collected by pyrethrin fogging in rainforest near Mt Murchison, while a late instar (18·6 mm) was hand-collected at the same time.

Several other very similar larvae were collected at the following sites where *S. variegatus* is not known to occur, but near localities recorded for *S. limbatus*: Mt Victoria (41·20 S, 147·50 E), 900 m; 20 km S of Scotsdale (41·20 S, 147·31 E), Simon's Rd; Thumbs Parallel Gullies (42·35 S, 145·28 E); 4 km SE of Weldborough, 450 m. Although a preliminary examination of these specimens revealed no consistent differences from the *S. variegatus* larvae described above, it is likely that they represent *S. limbatus*, the only species collected so far in north-eastern and south-eastern Tasmania.

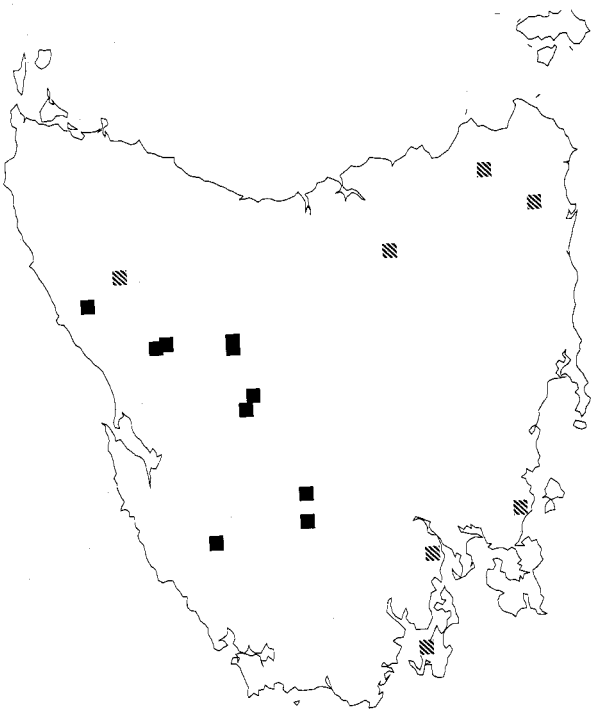


Fig. 12. Geographic distribution of *Sirrhas limbatus* Champion (hatched squares) and *S. variegatus*, sp. nov. (black squares).

Comments

Sirrhas larvae superficially resemble those of the New Zealand species of *Syrphetodes*, especially with respect to colour pattern and the complex armature of tergum 9 (see Hudson 1934, pl. II fig. 2a.); *Syrphetodes* larvae differ from those of *Sirrhas* in having well-developed mandibular molae and hypostomal rods, in lacking a frontoclypeal suture, and in having annular-biforous spiracles. Other very similar larval types are those of *Melytra* and the Perimylopidae, which are discussed below. *Chalcodrya* larvae are not only very different superficially from those of *Sirrhas*, being very lightly sclerotised, except for the globular head, and lacking urogomphi, but they have more fundamental differences, such as the presence of V-shaped frontal arms joined anteriorly by a transverse ecdysial line, distinct frontal ridges, well-developed mandibular molae, simple malar apex, molar-like hypopharyngeal sclerome, paired pygopods, and annular spiracles.

Genus *Melytra* Pascoe

Melytra Pascoe, 1869: 34. Type species, by monotypy, *M. ovata* Pascoe, 1869: 34.

Pascoe placed this genus in the subfamily Apocryphinae of Tenebrionidae, and Watt (1974*a*) retained it there, although noting its resemblance to members of the Perimylopidae, as well as 'Ulodinae and Parahelopinae'. The latter name (apparently based on the South American genus *Parahelops* Waterhouse) is a *nomen nudum*, since no included genus was mentioned and no distinguishing features were given that were not also found in Ulodinae. Doyden *et al.* (1990) transferred *Melytra to Zopheridae. M. ovata* is superficially very different from the two species of *Sirrhas* in that it is small and flightless, with small eyes, shortened metasternum, reduced metendosternal laminae, and no lateral pronotal carinae or elytral humeri. The genus has all of the basic features of the Ulodinae, as presently defined, but differs from them (and resembles *Sirrhas*) in having strongly projecting fore coxae without exposed trochantins. The female genital tract resembles that of *S. variegatus* in being somewhat constricted anterior to the common oviduct, delimiting a relatively large bursa; however, the bursa is divided into two parts. In two dissections, no gland could be found either basal to or at the apex of the bursa. In *Parahelops* the bursa is similarly divided, but the main or larger portion is also subdivided and there is a gland attached posterior to the constriction and thus at the apex of the vagina.

In some of the same collections from which *Sirrhas* larvae were collected, smaller larvae of the same type occurred which differed in having shinier and much less granulate upper surfaces, a relatively long first antennal segment (about three-fourths as long as the 2nd segment), and different armature on tergum 9 (longer urogomphi with better developed mesal and basal processes and no paramedian pregomphal tubercles). The lengths of these smaller larval specimens varied from 2·0–7·5 mm, which is consistent with the adult size (about 5–7 mm) of *M. ovata*, which was collected in four of the six samples. It is very likely that these are *Melytra* larvae, and although not formally described here, they were included in the analysis below. These larvae also resemble those of *Sirrhas* in having reduced mandibular molae, cribriform spiracles and no hypostomal rods.

Genus *Parahelops* Waterhouse

Parahelops Waterhouse, 1875: 333. Type species, by subsequent designation, *P. darwini* Waterhouse, 1875: 334 (Kulzer 1963: 603).

Watt (1967) mentioned the similarities between perimylopids and the genus *Parahelops*, which also occurs in southern Chile, Argentina and the Falkland Islands (Kulzer 1963), but he noted that the differences between the two taxa were more numerous and seemed more important than those between *Parahelops* and the Ulodini. The female genital tract is similar to that in both *Melytra* and the perimylopid genera *Hydromedion* and *Perimylops* in being constricted anterior to the median oviduct to form a distinct bursa anterior to the constriction; like the perimylopids, but unlike *Melytra*, there is a slender spermatheca near the base of the bursa. The *Parahelops* larva has a short, simple pair of urogomphi and lacks the complex armature of tergum 9 characteristic of Perimylopidae, *Sirrhas* and *Melytra*; however, it resembles all of these in lacking a mola and the last two in having cribriform spiracles.

Family **PERIMYLOPIDAE** St George

Perimylopidae St George 1939: 212.

This family was defined by St George on the basis of the larval features of two sub-antarctic genera *Perimylops* Müller and *Hydromedion* Waterhouse. Watt (1967, 1970) added *Darwinella* Enderlein and *Chanopterus* Boheman and gave a formal definition of the family based on both adults and larvae. These four genera occur only in the cooler parts of southern South America (Patagonia and Tierra del Fuego) and on the Falkland Islands and

South Georgia. Watt (1970) noted that *Hydromedion* had the most primitive features in the group, and that the abbreviated prosternal process, externally open fore coxal cavities and widely separated mid and hind coxae in *Perimylops* and *Chanopterus* were derived within the group. Perimylopid larvae differ from those of *Sirrhas* in having annular spiracles, no frontoclypeal suture and a different type of armature on tergum 9 (a single long process at the base of each urogomphus, no mesal urogomphal teeth and no pregomphi).

Genus *Onysius* Broun

Onysius Broun, 1886: 843.—Broun, 1915: 323; Watt, 1974*a*: 35. Type species, by monotypy, *Onysius anomalus* Broun, 1886: 843 (=*Malacodrya pictipes* Sharp, 1886).

Malacodrya Sharp, 1886: 412.—Broun, 1915: 323 (synonymy). Type species, by monotypy, *M. pictipes* Sharp, 1886: 413.

This genus was considered by Watt (1974*a*) to be most closely related to *Sirrhas* and he suggested that the two were different enough from *Chalcodrya* and *Philpottia* to be placed in a separate tribe or subfamily. *Sirrhas* and *Onysius* share the following attributes, which are absent in both *Chalcodrya* and *Philpottia*: (1) eyes reniform (emarginate); (2) antennae moderately long, extending posteriorly beyond the basal third of the elytra; (3) frontoclypeal suture not or only very weakly impressed; (4) lacinia without a stout apical tooth (although sometimes with small spine as in *S. variegatus*); (5) prothoracic trochantin concealed; (6) scutellum semicircular or subtriangular (not widened and truncate at apex as in *Chalcodrya* and *Philpottia*); (7) elytra distinctly broader than prothorax at base; (8) metendosternite with well-developed anterior process; (9) tegmen divided into basal and apical parts; (10) apicale cleft, forming 2 lobes, which are setose at apex; and (11) female tract without large, thick-walled bursa.

The above features are mainly plesiomorphic, and those derived features may be found in one or more of the tenebrionoid taxa discussed below. While they emphasise the distinctiveness of the *Chalcodrya–Philpottia* lineage, they lend little support to the hypothesis that *Sirrhas* and *Onysius* are sister groups. *Onysius* differs from *Sirrhas* as follows: (1) the eyes are much larger and extend onto the dorsal part of the head (the interocular distance, as seen from above, only half as great as the longest eye diameter); (2) the eyes are more deeply emarginate, with the antennal insertions lying partly within the emarginations; (3) the pronotum is subquadrate, with straight sides slightly diverging apically; (4) the pronotum and elytra are tuberculate; (5) the fore coxae are somewhat transverse and project only slightly below the prosternal process; (6) the scutellum is subtriangular; (7) the 4th ventrite is connate with the 3rd (as in Chalcodryidae); and (8) the metendosternite lacks laminae (as in Chalcodryidae).

Family **ZOPHERIDAE** Solier

Zopherites Solier 1841: 29.

The history of the family Zopheridae is complex. Typical zopherids, the so-called 'ironclad beetles', belonging to *Zopherus* Laporte and related genera, were recognised as a discrete subgroup of Tenebrionidae by most early workers, but it was Böving and Craighead (1931) who first elevated the Zopheridae to family rank, on the basis of the characteristics of their larvae. Crowson (1953) defined the group on the basis of adult features and noted the similarities between zopherids and members of the family Monommatidae. He also called attention to the presence of an 'inverted' type of aedeagus in the group (with the tegmen ventral to the penis). Kamiya (1963) confirmed that the Usechinae (*Usechus* Motschulsky and *Usechimorpha* Blaisdell) also belonged to this family, and Watt (1967, 1974*a*, 1974*b*) added a few 'typical' zopherids from Australia (*Cotulades* Pascoe, *Docalis* Pascoe and *Latometus* Erichson) plus a group of Southern Hemisphere taxa differing from tenebrionids in having the: (1) prosternal process relatively flat and expanded at the apex, forming paired lateral processes which partly or completely close the coxal cavities by joining or nearly joining mesal extensions of the hypomera; (2) aedeagus with setose parameres and without

inflected alae characteristic of Tenebrionidae; (3) larvae with divided cardines; (4) larvae without frontoclypeal suture; (5) larvae with lyriform frontal arms; and (6) larvae with hypostomal rods. These taxa also differ from typical zopherids in having: (A) exposed antennal insertions, (B) 'open' mid coxal cavities (closed partly by the mesepimera) and (C) an uninverted aedeagus (tegmen dorsal to penis). Watts' second group, including the Australian Ulodini and various genera from New Zealand and Chile, were placed by Doyen and Lawrence (1979) in a subfamily Ulodinae, to which *Meryx* Latreille (placed in the family Merycidae by Crowson 1953), *Trachyderas* Fairmaire & Germain, *Phaennis* Champion and *Notocerastes* Carter were added. This group is discussed further below under the heading Ulodidae.

Phylogenetics

The recognition of the *Sirrhas* larva casts serious doubt on its inclusion in the family Chalcodryidae; however, the true phylogenetic positions of this genus and other Notogean tenebrionoid taxa discussed above are far from obvious. Furthermore, a consideration of this problem must also involve an assessment of the limits of the family Zopheridae, which have been greatly expanded in recent years.

To throw some light on the problem, *S. variegatus* was compared with the following representatives of 20 tenebrionoid genera, for which both larval and adult characters were available:

Mycetophagidae. *Mycetophagus punctatus* Say.
Colydiidae: Colydiinae. *Namunaria pacifica* (Horn).
Colydiidae: Pycnomerinae. *Pycnomerus* sp.
Monommatidae. *Hyporhagus gilensis* Horn.
Zopheridae: Ulodinae. *Brouniphylax* sp., *Dipsaconia pyritosa* Pascoe, *Meryx rugosa* Latreille, *Syrphetodes* sp. and *Ulodes verrucosus* Erichson.
Zopheridae: Usechinae. *Usechus lacerta* Motschulsky.
Zopheridae: Zopherinae. *Nosoderma* sp. and *Phellopsis obcordata* (Kirby).
Zopheridae. *Cotulades* sp., *Melytra ovata* Pascoe and *Parahelops* sp.
Perimylopidae. *Hydromedion magellanicum* Fairmaire and *Perimylops antarcticus* Müller.
Chalcodryidae. *Chalcodrya variegata* Redtenbacher.
Tenebrionidae. *Tanylypa morio* Pascoe and *Tenebrio molitor* Linnaeus.

These taxa were coded for 17 larval and 14 adult characters, as follows.

Larva

(1) Posterior edge of head capsule: 1, straight or very slightly emarginate; 2, distinctly emarginate or cleft.

(2) Epicranial stem: 1, less than 0·20× as long as greatest head width; 2, more than 0·20× as long as greatest head width.

(3) Frontal arms: 1, lyriform; 2, V- or U-shaped.

(4) Frontoclypeal impression: 1, absent or very weakly indicated; 2, distinct.

(5) Ratio of antennal length to head width: 1, less than 0·25; 2, between 0·25 and 0·50; 3, greater than 0·50.

(6) Antenna separated from mandible by a distance: 1, less than 0·5× as great as basal antennal width; 2, more than 0·5× as great as basal antennal width.

(7) Mandibular mola: 1, well developed; 2, highly reduced or absent.

(8) Malar apex: 1, simple; 2, cleft and/or with subapical sclerome.

(9) Mala: 1, without distinct uncus at inner apical angle; 2, with distinct uncus at inner apical angle.

(10) Hypopharyngeal sclerome: 1, well developed and molar-like; 2, consisting of a flat plate or elevated carina; 3, absent.

(11) Hypostomal rods: 1, absent or very weakly indicated; 2, well developed.

(12) Anterior abdominal terga and/or posterior thoracic terga: 1, without transverse rows or patches of asperities; 2, with transverse rows or patches of asperities.

(13) Urogomphi: 1, simple or absent; 2, with one or more teeth or processes (sometimes located at base).

(14) Pregomphal tubercles: 1, absent, 2, 2 in number; 3, 4 or more in number.

(15) Paired pygopods: 1, absent; 2, present.

(16) Spiracles: 1, annular-biforous; 2, annular; 3, cribriform.

(17) Spiracles on segment 8: 1, about the same size as those on 1–7; 2, distinctly larger than those on 1–7.

Adult

(18) Antennal insertions: 1, exposed; 2, concealed.

(19) Frontoclypeal impression: 1, absent or weakly indicated; 2, distinct.

(20) Fore coxae: 1, not strongly projecting; 2, strongly projecting.

(21) Fore coxae: 1, with internal lateral extensions less than 0·7× as long as exposed portion of coxae; 2, with internal lateral extensions more than 0·7× as long as exposed portion of coxa.

(22) Propleuron: 1, freely movable; 2, fused to notum near junction of notosternal suture and coxal cavity.

(23) Fore coxal cavities: 1, without lateral notches; 2, with distinct lateral notches that partly expose trochantins.

(24) Fore coxal cavities: 1, externally open; 2, externally closed.

(25) Prosternal process: 1, narrow (less than 0·25× coxal width); 2, moderately to very broad (more than 0·25× coxal width).

(26) Prosternal process: 1, relatively flat, not strongly curved dorsally at apex; 2, convex and strongly dorsally at apex.

(27) Apex of prosternal process: 1, not or only slightly and/or gradually expanded laterally; 2, distinctly and abruptly expanded laterally.

(28) Mid coxal cavities: 1, open laterally (partly closed by mesepimera); 2, closed laterally by meeting of meso- and metasterna.

(29) Mid coxal cavities: 1, contiguous or narrowly separated (by less than 0·25× coxal width); 2, moderately to widely separated (by more than 0·25× coxal width).

(30) Hind coxae: 1, contiguous or narrowly separated; 2, moderately to very widely separated.

(31) Aedeagus: 1, 'normally' oriented, with tegmen dorsal to penis; 2, inverted, with tegmen ventral to penis.

The resulting matrix (Fig. 13) was subjected to a cladistic analysis using HENNIG86 and PAUP 3.0 with all characters ordered. A heuristic search produced 21 trees of length 92, with a CI of 0·38 and an RI of 0·66. A majority consensus tree of these data is given in Fig. 14. The major features of this cladogram are as follows:

(1) *Chalcodrya* consistently clusters with the two tenebrionid genera, *Tenebrio* and *Tanylypa*, and never with *Sirrhas*.

(2) *Sirrhas* always clusters with the two perimylopid genera *Hydromedion* and *Perimylops*.

(3) *Parahelops* and *Melytra* form a monophyletic group with *Sirrhas* and the Perimylopidae.

	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
Brouniphylax	1	2	1	2	1	1	1	2	2	2	2	1	2	3	1	1	2	1	2	1	1	2	1	2	2	1	2	1	2	2	1
Chalcodrya	1	2	2	2	1	1	1	1	1	1	1	2	1	1	2	2	1	1	2	2	1	1	2	2	1	1	2	1	2	1	1
Cotulades	2	2	2	1	1	1	1	2	2	2	2	2	1	1	1	1	1	2	1	1	2	1	1	1	2	1	2	2	2	2	2
Dipsaconia	1	1	1	2	1	1	1	2	1	2	2	1	2	2	1	1	1	1	1	1	1	1	1	2	2	1	2	1	2	1	1
Hydromedion	1	1	1	1	3	2	2	2	2	3	1	1	2	1	1	2	1	1	2	2	1	1	2	2	1	1	2	1	1	1	1
Hyporhagus	2	1	1	1	2	1	2	2	1	3	2	2	1	1	1	1	1	2	1	1	2	1	1	1	2	1	1	2	2	2	2
Melytra	1	2	1	2	2	1	2	2	2	2	1	1	2	1	1	3	2	1	1	2	1	1	1	2	2	1	2	1	1	2	1
Meryx	1	1	1	1	1	1	1	2	1	2	2	1	2	1	1	1	1	1	1	1	1	1	1	2	2	1	2	1	2	1	1
Mycetophagus	1	1	1	1	2	1	1	1	1	2	2	1	1	1	1	1	1	1	2	1	1	1	2	1	2	1	1	1	1	1	1
Namunaria	1	1	1	1	2	1	1	2	2	2	2	1	1	1	1	1	1	2	1	1	1	1	1	2	2	1	2	2	2	1	2
Nosoderma	2	2	2	1	1	1	1	2	2	2	1	2	1	1	1	1	1	2	1	1	2	1	1	2	2	1	2	2	2	2	2
Parahelops	1	1	1	2	1	1	2	2	1	2	1	1	1	1	1	3	1	1	1	2	1	1	1	2	2	1	2	1	2	2	1
Perimylops	1	2	1	1	3	2	2	2	2	3	1	1	2	1	1	2	1	1	2	2	1	1	2	1	1	1	1	1	2	2	1
Phellopsis	2	1	1	1	1	1	1	2	2	2	2	2	1	1	1	1	1	2	1	1	2	1	1	2	2	1	2	2	2	2	2
Pycnomerus	2	1	2	1	1	1	2	2	1	2	2	2	1	1	1	1	1	2	1	1	2	1	1	2	2	1	2	2	2	2	2
Sirrhas	1	2	1	2	2	2	2	2	2	2	1	1	2	3	1	3	2	1	1	2	1	1	1	2	1	1	2	1	1	1	1
Syrphetodes	1	2	1	1	2	1	1	2	2	2	2	2	2	3	1	1	2	1	1	1	1	2	2	2	2	1	2	1	2	1	1
Tanylypa	1	1	2	2	2	1	1	1	1	1	1	1	1	1	2	2	1	2	1	1	2	2	1	1	2	2	1	1	2	1	2
Tenebrio	1	2	2	2	2	1	1	1	1	1	1	1	1	1	2	2	1	2	2	1	2	2	1	2	2	2	1	1	2	1	1
Ulodes	1	1	1	1	1	1	1	2	2	2	1	1	2	2	1	1	1	1	1	1	1	1	1	2	2	1	2	1	2	1	1
Usechus	2	1	1	1	1	1	1	2	2	2	2	2	1	1	1	1	1	2	1	1	2	1	1	2	2	1	2	2	2	2	2

Fig. 13. Matrix of 21 taxa and 31 characters used in PAUP analyses.

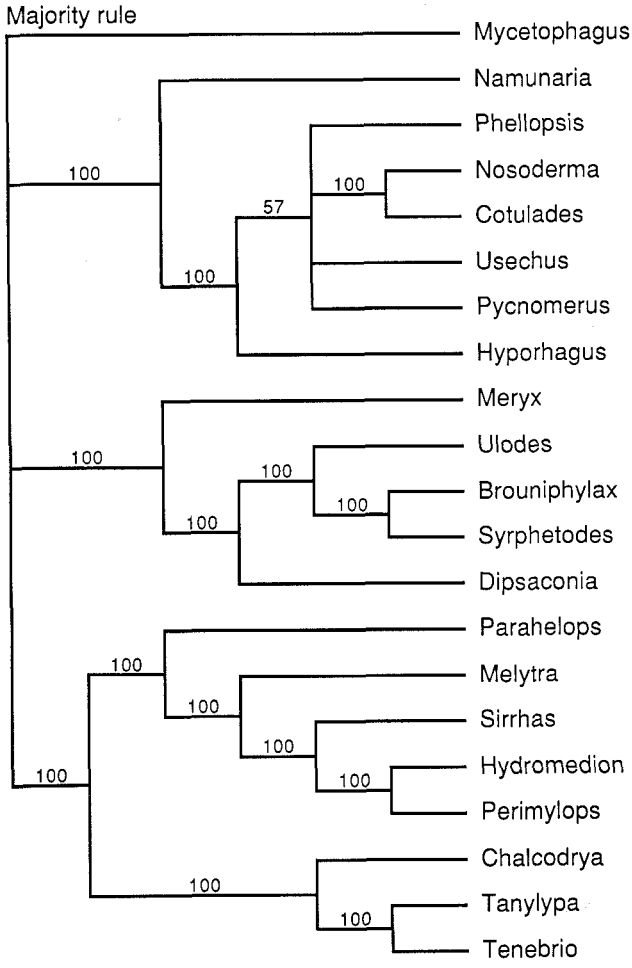


Fig. 14. Majority consensus of 21 shortest trees resulting from a PAUP 3.0 analysis of 21 genera of Tenebrionoidea and 17 larval and 14 adult characters (ordered).

(4) The ulodine Zopheridae form a monophyletic group, which is never part of the same lineage as the Zopherinae.

(5) The Colydiidae, Monommatidae, zopherine Zopheridae, plus *Usechus* and *Cotulades*, form a monophyletic group in all cladograms.

(6) *Pycnomerus* belongs to a monophyletic group including the Zopherinae and Monommatidae but excluding *Namunaria*, the other colydiid genus used in the analysis.

A search of the same data with all characters treated as unordered produced 193 trees 91 steps in length. The majority consensus in Fig. 15 shows much less resolution in the ulodine complex, although *Parahelops*, *Melytra*, *Sirrhas* and the perimylopids still form a monophyletic group. The isolation of *Chalcodrya* from *Sirrhas* is even more striking in this cladogram, and the zopherine lineage is also well supported.

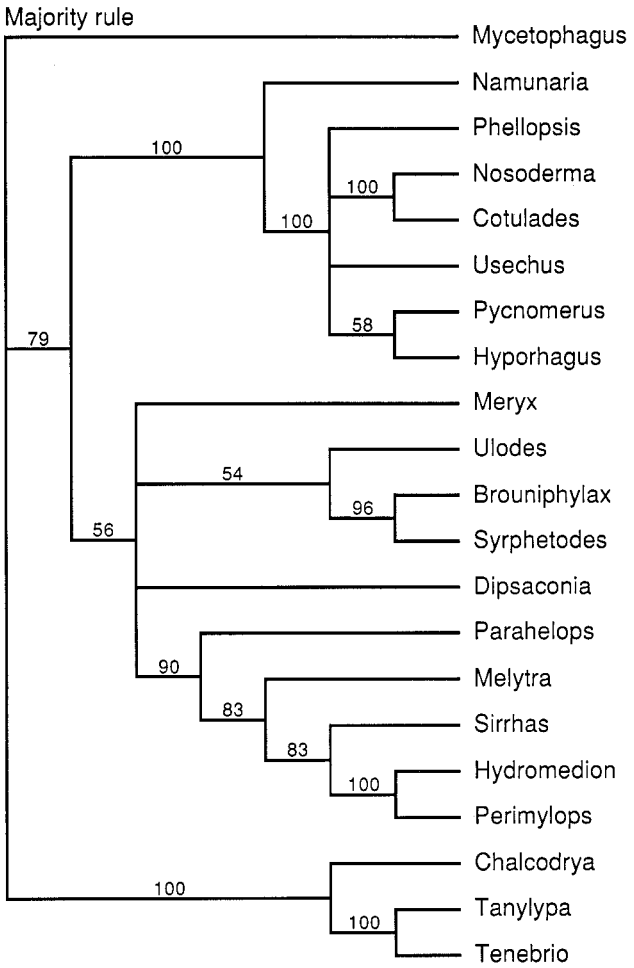


Fig. 15. Majority consensus of 193 shortest trees resulting from a PAUP 3.0 analysis of 21 genera of Tenebrionoidea and 17 larval and 14 adult characters (unordered).

This analysis must be considered somewhat preliminary for various reasons, including the small number of characters used relative to the number of taxa and the lack of some critical taxa (e.g. *Onysius*) for which only adult characters were available. Futhermore, large families, such as Tenebrionidae and Colydiidae were underrepresented, and the character states exhibited by the selected genera may not in all cases be basal for the group.

Classification

The above analyses clearly show that the placement of *Sirrhas* in the family Chalcodryidae is untenable, and a reasonable case can be made for the inclusion of this genus, along with *Melytra* and *Parahelops*, in an expanded Perimylopidae, which will now include Tasmanian species as well as those from the cool temperate and subantarctic portions of South America.

Members of this group share a number of features with the ulodine complex, but may be distinguished by the relatively thin cuticle and projecting fore coxae of the adults and the lack of a mola in the larva. Whether this complex should be retained as a family or combined with the ulodine complex is a more difficult question, since many characters uniting the Ulodinae are plesiomorphic ones. In spite of the lack of obvious synapomorphies occurring throughout the group (not subsequently reversed), the recognition of a family Ulodidae would seem to be a practical solution until the entire complex can be studied in more detail (see below).

The family placement of *Onysius* is not obvious on the basis of adult features alone. As mentioned above, the genus has no derived character states that unite it with *Sirrhas*, and few in common with *Chalcodrya* and *Philpottia*, one of the latter being the connation of ventrites 3 and 4. The type of spermatheca illustrated by Watt (1974*a*) for *Onysius anomalus* is similar to that of *Sirrhas limbatus* in that both have a complex, annulate spermatheca; however, as shown above, complex spermathecae are also found in some ulodines, including *Syrphetodes* and *Pteroderes*. The procoxae in *Onysius* are more or less transverse but project below the intercoxal process, as in chalcodryids, and in both taxa the trochantin is often visible in the slit-like extension of the coxal cavity. Although *Onysius* lacks several distinctive features of *Chalcodrya* and *Philpottia*, such as the reduced and fused apicale of the tegmen, the large, thick-walled bursa, the shortened antennae and the blunt tooth on the lacinia, it does share with them the prothoracic structure, lack of metendosternal laminae and connate 4th ventrite. Until the larva is discovered, the genus should remain in the family Chalcodryidae.

The analysis clearly indicates that the true Zopheridae, including *Usechus* and *Cotulades*, form a monophyletic group with the Monommatidae and the two colydiid genera used in the analysis. These taxa are being studied by M. A. Ivie, and relationships among them are not discussed further in this paper.

Family **Ulodidae** Pascoe, stat. nov.

Ulodinae Pascoe 1869: 31.

This family, as here delimited, contains all of the ulodine genera listed by Doyen and Lawrence (1979: 337–8) except *Parahelops*, plus two other genera, *Pteroderes* Germain and *Trachyderastes* Kaszab. The former contains a single species, *P. tuberosa* German (1894) from Chile, and is currently included in the tenebrionid tribe Nodotelini (=Eutelini) (Gebien 1940; Koch 1950). Specimens matching the description of *P. tuberosa*, including one identified by L. E. Peña were examined. *Trachyderastes* is based on a New Caledonian endemic, *T. dipsaconiae* Kaszab (1982), included by its author in Ulodini of Tenebrionidae. The type (BMH) is a distinctive looking ulodid with a very weak but distinctly 4-segmented antennal club and finely tuberculate elytra bearing rows of large, deep, complex punctures, the walls of which are lined with small tubercles. Similar complex and subseriate punctures are also found in the Chilean *Trachyderas* and the Australian *Meryx*.

The ulodids display a great deal of variation in general form, but they have a tuberculate upper surface (except in *Arthopus*) and a vestiture of stout hairs or scale-like setae (except in *Meryx* and *Trachyderastes*). Typical ulodids, such as species of *Ulodes* and *Dipsaconia*, have globular fore coxae, which are relatively widely separated and a distinct 3-segmented antennal club with apical sensory areas, as in true Zopheridae; however, they always lack the long internal extensions of the procoxae, the inverted aegeagus, and other diagnostic features mentioned above and in the key below. Other taxa, like *Syrphetodes* and *Trachyderastes* have very weak antennal clubs with generally distributed sensilla, as in Perimylopidae or Chalcodryidae. In *Meryx*, the antennal club is well-defined, but the fore coxae are slightly transverse and have a small slit-like extension of the cavity. The rather abrupt lateral expansion of the apex of the prosternal process leading to the external closure of the coxal cavities by both prosternum and hypomeron distinguishes this group from both Trachelostenidae and Tenebrionidae, as does the movable cryptopleuron, which is fused to the notum in the latter two taxa.

Known ulodid larvae often associate with basidiomycete fungi. *Meryx* larvae are usually found under bark amid hyphae of wood-rotting fungi and are less highly modified than are those of *Ulodes*, *Dipsaconia* and *Brouniphylax*, which feed internally in the fruiting bodies of *Pleurotus*, *Piptoporus* and *Ganoderma*, respectively, and are usually lightly sclerotised and subcylindrical, with upturned urogomphi. *Syphetodes* larvae have been reported to feed in dead branches (Hudson 1934), although their colour pattern and complex 9th tergum are suggestive of surface activity similar to that in *Sirrhas*.

The Australian ulodids have never been revised and the generic concepts are not well defined. The most obvious feature distinguishing *Ganyme* Pascoe from *Ulodes* and *Dipsaconia* is the angulate appearance of the pronotum, caused by a pair of broad basal excavations at the sides; however, the two species *Ulodes tuberculatus* Carter (1926) and *U. demarzi* Kulzer (1964) also have this feature. These are here transferred to *Ganyme*, the new combinations being *Ganyme tuberculata* (Carter) and *G. demarzi* (Kulzer). The genus *Phaennis* appears to be closely related to *Notocerastes*, and males in both groups have frontal projections; however, the prothoracic structure, general body form and vestiture easily distinguish the two taxa. The following key will distinguish adults of all genera of Ulodidae and the related Perimylopidae.

Key to the Genera of Ulodidae, Perimylopidae and Chalcodryidae

Based on adults

1. Antennal insertions concealed from above by frontal ridges; fore coxa with internal extension, which is longer than globular exposed portion of coxa; mid coxal cavities closed laterally by meeting of meso- and metasterna; aedeagus inverted (with tegmen lying below penis) ..... Zopheridae (not keyed further)

   Antennal insertions exposed from above; fore coxa with short internal extension, which is never longer than exposed portion of coxa; mid coxal cavities 'open' laterally (partly closed by mesepimera); aedeagus normally oriented (with tegmen above penis) 2

2. Procoxae transverse and slightly projecting below prosternal process, which is narrow (less than $0{\cdot}25\times$ coxal width); trochantin slightly exposed by slit-like lateral extension of coxal cavity; prothorax subquadrate, anterior and posterior angles more or less distinct, anterior ones not produced forward and acute, hind wings present and metasternum distinctly longer than first ventrite; ventrites 3 and 4 connate; upper surfaces subglabrous; New Zealand ..... (Chalcodryidae) 3

   Procoxae usually globular or strongly projecting ventrally; if transverse or if trochantins exposed, prosternal process broader and anterior prothoracic angles acute or hind wings absent and metasternum shorter than first ventrite; ventrites 3 and 4 not connate; if upper surfaces subglabrous, anterior angles acute or hind wings absent 5

3. Eyes large and distinctly emarginate; interocular distance (across frons) much less than longest eye diameter; antennae much longer than combined length of head and prothorax; basal elytral width much greater than basal width of prothorax; elytra tuberculate ..... *Onysius* Broun

   Eyes smaller and not emarginate; interocular distance much greater than longest eye diameter; antennae shorter than or only slightly longer than combined length of head and prothorax; basal elytral width only slightly greater than basal width of prothorax; elytra not tuberculate 4

4. Elytra with 3 or 4 distinctly raised longitudinal costae; dorsal surfaces more or less uniformly clothed with coarse greyish pubescence ..... *Philpottia* Broun

   Elytra without distinct longitudinal costae; dorsal surfaces with only a few small patches of coarse yellowish pubescence ..... *Chalcodrya* Redtenbacher

5. Procoxae distinctly projecting ventrally below prosternal process; anterior pronotal angles obsolete or very broadly rounded, neither produced nor acute; lateral pronotal carinae simple or absent; upper surfaces usually subglabrous or clothed with fine, decumbent hairs, never with coarse setae or scales ..... (Perimylopidae) 6

   Procoxae not or only slightly projecting ventrally below prosternal process; anterior pronotal angles usually produced and often acute or, if not, then lateral pronotal carinae serrate or crenulate; upper surfaces usually clothed with coarse setae or scales and often distinctly costate or tuberculate, rarely subglabrous ..... (Ulodidae) 12

6. Prosternal intercoxal process incomplete, not extending posteriorly behind coxae and not extending laterally to close cavities; mid coxae widely separated, the distance between them almost as great as coxal width 7
   Prosternal intercoxal process complete, extending posteriorly behind coxae and extending laterally to close cavities; mid coxae narrowly separated, the distance between them much less than coxal width 8
7. Lateral pronotal carinae absent; prosternal intercoxal process acute at apex; mid coxae separated by less than coxal width; hind coxae separated by less than half coxal width; South Georgia ..... *Perimylops* Müller
   Lateral pronotal carinae present; prosternal intercoxal process blunt at apex; mid coxae separated by slightly more than coxal width; hind coxae separated by just less than coxal width; Tierra del Fuego and Patagonia ..... *Chanopterus* Boheman
8. Hind winds present; metasternum distinctly longer than first ventrite; eyes weakly emarginate; Tasmania ..... *Sirrhas* Champion
   Hind wings absent; metasternum shorter than first ventrite; eyes not emarginate 9
9. Lateral pronotal carinae absent; elytral humeri absent; scutellum sharply triangular; Tasmania ..... *Melytra* Pascoe
   Lateral pronotal carinae present; elytral humeri present; scutellum semicircular; southern South America 10
10. Hind angles of pronotum distinct, sharp; elytra with distinct puncture rows; Magallanes Region, Chile and Falkland Islands ..... *Parahelops* Waterhouse
    Hind angles of pronotum rounded; elytra without distinct puncture rows 11
11. Lateral pronotal and elytral carinae explanate; form broadly oval; Falkland Islands ..... *Darwinella* Enderlein
    Lateral pronotal and elytral carinae not explanate; body narrow, elongate-oval; southern Chile and South Georgia ..... *Hydromedion* Waterhouse
12. Antennal club 4-segmented; sides of prothorax broadly rounded and coarsely crenulate; outer edges of fore and mid tibiae lined with sharp, spine-like tubercles; elytra finely, densely tuberculate with coarse punctures forming regular rows; New Caledonia ..... *Trachyderastes* Kaszab
    Antennal club 3-segmented; outer edges of fore and mid tibiae without or with finer, indistinct tubercles 13
13. Hind wings absent; metsternum shorter than or as long as first ventrite 14
    Hind wings present; metasternum distinctly longer than first ventrite 17
14. Antenna with all club segments distinctly longer than wide and without concentrations of sensilla at apices; anterior angles of pronotum strongly produced forward and acute; elytral epipleura broad, complete and separated from disc by distinct carina; New Zealand ..... *Syrphetodes* Broun
    Antenna with club segment not or only slightly longer than wide and with sensilla concentrated at apices; anterior angles of pronotum not or only slightly produced forward; elytral epipleura absent or contiguous with disc, which curves ventrally to embrace pterothroax and abdomen 15
15. Lateral edges of prothorax strongly raised, so that they are on a higher plane than the highest portion of the pronotal disc, which is smooth, without tubercles or protuberances; scutellum absent; New Zealand ..... *Exohadrus* Broun
    Lateral edges of prothorax not or only slightly elevated, not higher than pronotal disc; scutellum present 16
16. Sides of pronotum laterally explanate and posteriorly excavate, forming a pair of narrowly rounded, posteriorly curved, lateral processes; antennal segments 10 and 11 distinctly broader than 9, so that club appears 2-segmented; segment 10 strongly transverse; outer edges of fore tibiae armed with teeth; Chile ..... *Pteroderes* Germain
    Sides of pronotum explanate but without posterior excavations; antennal segments 10 and 11 not distinctly broader than 9; segment 10 not strongly transverse; outer edges of tibiae without teeth; New Zealand ..... *Brouniphylax* Strand
17. Tarsal formula 4-4-4; antennal club relatively weak, at least segments 9 and 11 distinctly longer than wide; lateral edges of prothorax crenulate; anterior angles of pronotum not or very weakly produced forward; Australia ..... *Meryx* Latreille
    Tarsal formula 5-5-4; antennal club usually stronger, without elongate segments and usually with at least one segment transverse; anterior angles of pronotum usually produced forward and subacute, or if not, then lateral edges of prothorax with several sharp teeth 18

18. Upper surfaces glabrous, shiny and metallic; New Zealand ..... *Arthopus* Sharp
Upper surfaces more or less densely clothed with coarse hairs or scale-like setae, sometimes mixed with finer, erect hairs, neither shiny nor metallic 19
19. Anterior angles of pronotum not produced forward; lateral edges of pronotum with several sharp teeth; males with short lateral processes on frons just above antennal insertions; Australia ..... *Phaennis* Champion
Anterior angles of pronotum distinctly produced forward; lateral edges of pronotum without sharp teeth (sometimes with finer crenulations) 20
20. Lateral edges of pronotum distinctly crenulate; males with prominent, dorsally projecting processes on frons just above antennal insertions; Australia ..... *Notocerastes* Carter
Lateral edges of pronotum without distinct crenulations 21
21. Elytra elongate, more than 1·8× as long as combined width; elytral punctures forming distinct rows with at least some interspaces forming longitudinal costae; Chile ..... *Trachyderas* Philippi
Elytra shorter and broader, less than 1·7× as long as combined width; elytral punctures not forming distinct rows; interspaces not costate; Australia 22
22. Base of prothorax much narrower than combined elytral bases; sides of prothorax broadly excavate at base; elytra tuberculate ..... *Ganyme* Pascoe
Base of prothorax not or only slightly narrower than combined elytral bases; sides of pronotum not broadly excavate at base; elytra not tuberculate (sometimes clothed with patches of erect scales which appear to be tubercles) 23
23. Lateral edges of pronotum strongly explanate and elevated; upper surfaces clothed with scale-like setae, which also occur on antennal segments 1–9 ..... *Ulodes* Erichson
Lateral edges of pronotum slightly explanate and not strongly elevated; upper surfaces clothed with scale-like setae or coarse, decumbent hairs mixed with fine, erect hairs, but antennae always clothed with fine hairs ..... *Dipsaconia* Pascoe

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