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Larva and pupa of *Cyphopisthes descarpentriesi* Paulian (Coleoptera: Scarabaeoidea: Ceratocanthidae) and their phylogenetic implications

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Abstract Pupae and mature larvae of the Australian ceratocanthid beetle, *Cyphopisthes descarpentriesi* Paulian 1977, are described and extensively illustrated. This is the sixth species of the family for which immature stages are known and the first from the Australian region. Unlike other ceratocanthid larvae described before, those of *Cyphopisthes* Gestro lack stridulatory teeth on the middle and hind legs and any trace of a frontoclypeal suture on the cranium. Reduced one-segmented labial palpi in *Cyphopisthes* are unique in Scarabaeoidea. Monophyly of the family is not corroborated by larval characters. Absence of spiracular closing apparatus in larvae is reported in the family for the first time. Like pupae of *Ceratocanthus* White and *Germarostes* Paulian, those of *Cyphopisthes* have thoracic projections, but their shape and location are different. Spiracles are found on abdominal segments 2–4 of pupa; that on segment 2 differs in colour and location from the others.

Key words beetle immatures, morphology, phylogeny, taxonomy.

INTRODUCTION

The Ceratocanthidae (formerly known as Acanthoceridae) are a medium-sized family of beetles belonging to the geotrupid line of the passalid lineage of the Scarabaeoidea (Browne & Scholtz 1999). They number about 320 recognised species, divided into 40 genera (Ballerio 2000; Howden & Gill 2000, and extensive references therein), but these figures are likely to be soon substantially increased because of the large number of undescribed taxa that have been detected in recent years.

Ceratocanthids are small (2–7 mm), usually very convex beetles, capable of rolling up their body, with all body parts perfectly fitting together to form a compact ball. Five New World genera show very strong adaptations to termitophily and recently (Howden & Gill 2000) the family has been divided into three subfamilies in order to find a proper placement to these five unusual genera. However, there is no agreement on the placement to give to these unusual Ceratocanthids (see for instance Nikolajev 1999), as well as on the degree of relationship with the Hybosoridae, commonly considered to be the sister group of the Ceratocanthidae.

The Ceratocanthidae exhibit a pantropical distribution, with few species living in the temperate regions of the Americas, South Africa and the Oriental transition zone. Most species are found in tropical rainforests, although a few species are known to occur also in temperate or seasonal tropical forests and savanna/forest mosaics.

The biology of the subfamily is poorly known. Since the early authors, it has been argued that the rolled up posture typical to the subfamily was an adaptation to life under bark and in dead wood (see also Iwata *et al*. 1992). Actually, most species are readily found in dead logs (usually the ones occupied by termites or passalid beetles) or are collected from Berlese samples of leaf litter. They are supposed to feed on soft food, probably fungi. Recently, evidence arose of the existence of canopy-dwelling species (Ballerio 1999b).

In spite of their wide pantropical distribution, relative abundance in suitable habitats and significant morphological diversity of adults, the immature stages (third-instar larva and/or pupa) of the family Ceratocanthidae are known only for five species from four genera (but with sufficient detail only for two species and one genus). Böving and Craighead (1931) included the family (under the name Acanthoceridae) in their larval key using characters of the genus *Germarostes* Paulian (under the generic name *Cloeotus* Germar). Ritcher (1966) dealt with larvae of Ceratocanthidae of the USA (under the name Acanthocerinae) by providing a detailed description of the third-instar larva of *Germarostes* (= *Cloeotus*) *aphodioides* (Illiger) and included two drawings of an unidentified '*Philharmostes*' larva (Ritcher 1966). Ritcher did not indicate the locality of collection and therefore it is not possible to state whether the author illustrated the larva of a true *Philharmostes* Kolbe, a genus restricted to the Afrotropical region, or the larva of *Astaenomoechus* Martínez and Pereira, a Neotropical genus whose species were previously included in *Philharmostes*. Because of this ambiguity, the

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genus will be hereinafter quoted in inverted commas. Iwata *et al.* (1992) provided a photograph of a third-instar larva of *Madrasostes kazumai* Ochi, Johki and Nakata and provided some observations on its habitat and food. Choate (1987) published some biological observations on larvae, pupae and adults of North American *Ceratocanthus aeneus* (Macleay) and gave a brief description of the pupa illustrated by two photographs. Costa *et al.* (1988) described a putative third-instar larva of the South American *Germarostes macleayi* (Perty), while Scholtz (1990) summarised and discussed the available data about Ceratocanthidae larvae in a phylogenetic context. Lawrence *et al.* (1999) treated the family as a single unit in a data matrix comprising 174 morphological features of larvae. Morón and Arce (in press) described larvae and pupae of *Ceratocanthus relucens* (Bates). However, ceratocanthid eggs, first- and second-instar larvae have not yet been described.

The genus *Cyphopisthes* Gestro presently numbers 10 species and ranges from north-eastern India to New Guinea, Queensland and possibly also New Caledonia (Ballerio 1999b). The single Australian species *C. descarpentriesi* Paulian, one of three known Australian ceratocanthid species (Cassis & Weir 1992), is being revised by one of us (A.B.) and will be divided into more species. The larvae dealt with herein belong to the true *C. descarpentriesi*. The purpose of this paper is to describe mature larvae and pupae of this species, placing particular emphasis on details of larval chaetotaxy, and to discuss some larval and pupal morphological characters of ceratocanthid beetles.

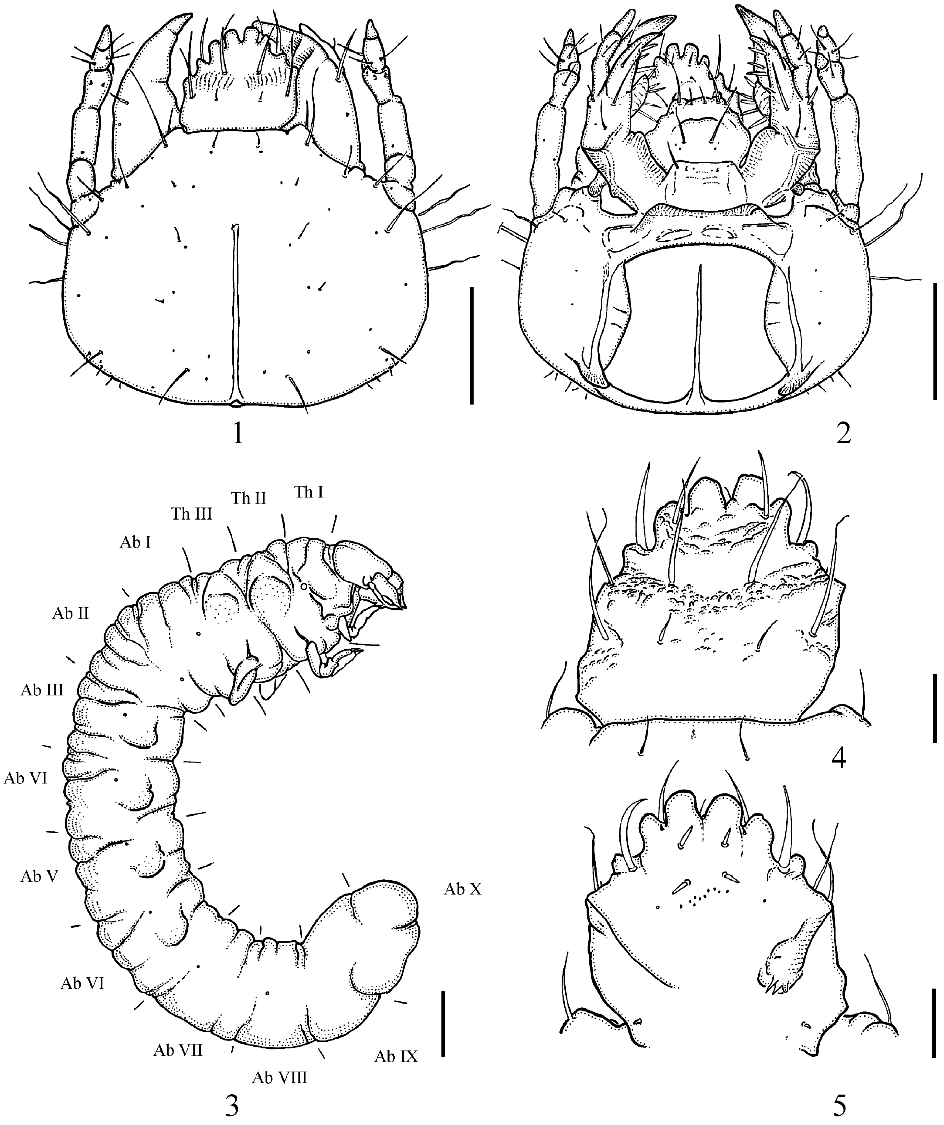
MATERIALS AND METHODS

For this work, about 30 putative third-instar larvae and several pupae of *C. descarpentriesi* were borrowed from the collection of the Australian National Insect Collection, CSIRO Entomology, Canberra. The larvae and pupae have the following collecting information: 'Queensland, Cape Pallarenda, Townsville, 1 July 1974, #51 J.A.L. Watson, in galleries of *Mastotermes* Froggatt nest in dead *Acacia*'. They were collected together with adults, paratypes for the original description of the species (Paulian 1977). One larva was disarticulated, cleaned in a hot-water solution of KOH and studied first on a temporary microscope slide mounted with glycerol and then on a permanent slide with Euparal under compound microscope with magnification up to 600 times. All measurements and counts were performed using this larva. Two remaining larvae and two pupae were studied in ethanol using a dissecting microscope with magnification up to 80 times. For comparison, older-instar larvae of two apparently different genera (presumably *Pterorthochaetes* Gestro and *Madrasostes* Paulian, because the larvae were collected together with adults belonging to these genera) of Ceratocanthidae from the Malay Peninsula were studied (A. Ballerio collection). Additionally, specimens of ceratocanthid larvae collected in western Ecuador (apparently belonging to the genus *Astaenomoechus*) were borrowed from the Humboldt-Univeristät Museum für Naturkunde, Berlin, Germany. The concept of the superfamily Scarabaeoidea follows Lawrence and Newton (1995). Morphological terms used in this work are those explained by Lawrence (1991). Terms of chaetotaxy ('seta' and 'pores') follow the concept used in descriptions of coleopteran larvae by Bousquet and Goulet (1984) for Carabidae, Ashe and Watrous (1984) for Staphylinidae–Aleocharinae, Kovarik and Passoa (1993) for Histeridae, and Alarie and Balke (1999) for Dytiscidae–Colymbetinae. In the present work we describe a number of sensory structures (setae and pores) on the body and show their location and relative size on illustrations. As we deal only with one species, we do not designate every sensory structure on the larval body.

DESCRIPTIONS

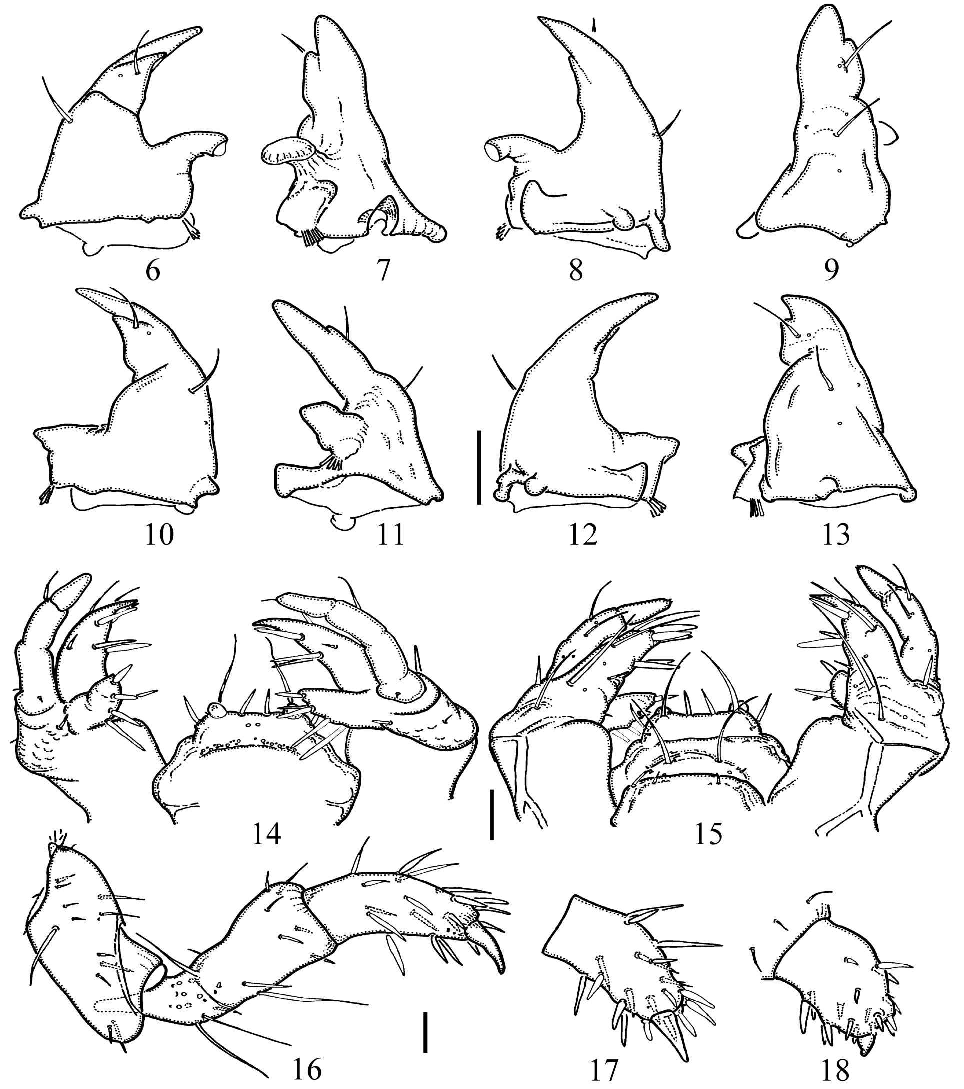
Larva

General appearance (Fig. 3)**.** Typical C-shaped melolonthid-looking larva, body rather small, uniformly cylindrical, markedly elongate and slender, without dorsal expansions. Pubescence yellowish. ***Head capsule*** (Figs 1,2)**.** Relatively large, protracted and hypognathous, nearly symmetrical, approximately 1.3 times wider than long. Sides slightly divergent posteriorly with maximum width in basal fourth (1.24 mm, *n* = 1). No stemmata. Frontoclypeal (= epistomal) suture and epistomal ridge absent, clypeo-labral suture present. Attachment of dorsal tentorial arms undetectable. Frontal stems of epicranial sutures markedly reduced and detectable as thin lines in their basal half; epicranial stem undetectable dorsally. Internal endocarina located on medial line of dorsal surface of cranium originating from occipital foramen and anteriorly reaching level of insertion of antennae. Chaetotaxy: cranium with 21 setae and 20 pores, ventrally with 2–3 irregular cuticular dots. ***Antenna*** (Figs 1,2,23,24)**.** 4-Segmented, with apex at about same level as those of maxillae, mandibles and labrum. Two basal antennomeres indistinctly separated by weak fold dorsally and laterally; on ventral surface antennomeres completely fused with no visible separation between them. Antennomeres I, III, and IV of about same length; antennomere II about 1.5 times longer. Antennomere III with conical sensorium ventrally and distally. Antennomere IV conical, with markedly developed hyaline sensory part apically. Chaetotaxy: antennomere I with no setae or pores; antennomere II with no setae and four pores, of them three located proximally and one distally on ventral surface; antennomere III with seta in middle on ventral surface, six conical sensilla and two apparently placoid sensilla in distal fourth; antennomere IV with five setae in proximal half, pore at middle of lateral surface and group of 5–6 conical sensilla at apex. ***Mandibles*** (Figs 6–13)**.** Asymmetrical, each with ventral process and molar part; that on left mandible notably elongate and medially protracting at proximal part. Median parts of mandibles without brushes of small hairs except one consisting of about four flat, apparently cuticular strips of



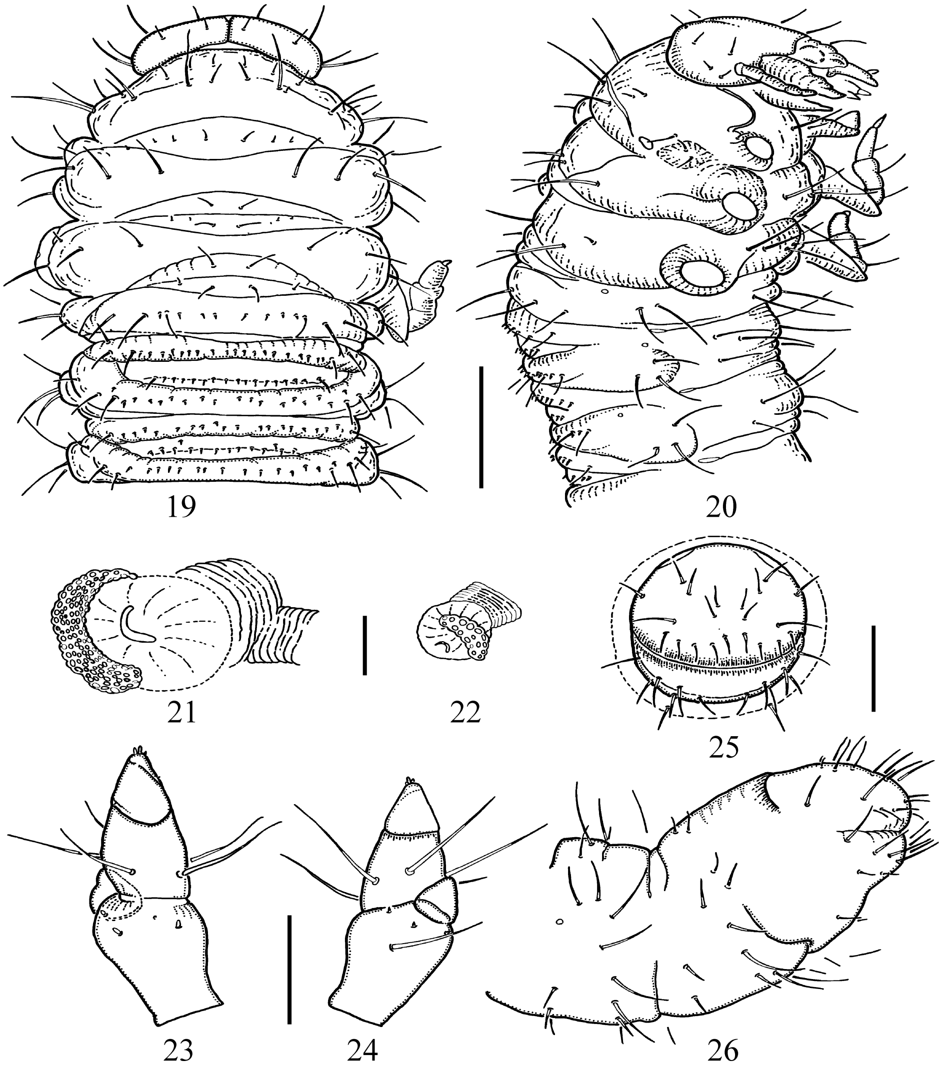
Figs 1–5. Larva of *Cyphopisthes descarpentriesi*. (**1–2**) Head: (**1**) dorsal; (**2**) ventral. (**3**) Habitus, lateral. (**4**) Labrum, dorsal. (**5**) Epipharynx, ventral. Scale bars: figs 1,2 = 0.4 mm; fig. 3 = 1.0 mm; figs 4,5 = 0.1 mm.

distal edge of mola on medial surface. Stridulatory area absent. Apices of mandibles with larger ventral and smaller and shorter dorsal tooth. Chaetotaxy: Each mandible with two setae and three pores. ***Ventral mouthparts*** (Figs 14,15)**.** Galea and lacinia not fused; lacinia (and possibly part of stipes; homologuey unclear) directed markedly dorsad relative to galea surface. Dorsal surface of stipes near base with about 10 tubercles (= stridulatory teeth, see Discussion). Maxillary palp of three segments and palpifer. Labial palp 1-segmented and as wide as long. Definite hypopharyngeal sclerites (= oncyli) absent; hypopharynx with some sclerotisation above maxillary attachments. Chaetotaxy: apical maxillary palpomere with no sensilla; middle palpomere with two setae and one pore, basal palpomere with two pores and short seta close to palpifer on lateral surface; palpifer with two setae, short dorsal and long ventral; lacinia with five stout setae; ligula (and, possibly, stipes, homologuey unclear) with four stout and large setae directed medially, four pores and seven more setae (two of them short); cardo with pore; labium with seven setae on each side (two long, two medium and three short), dorsal surface with pore on each side and transverse group of pores in centre, ventral surface with pore close to gula on each side; labial palp with no sensilla; gula with pore and seta on each side; on right side additionally with long seta, on left side with two pores. ***Labrum–Epipharynx*** (Figs 4,5)**.** Slightly asymmetrical, markedly enlarged and apically protracted. Distal part of lateral edges and apical edge with six projections (might be called ‘serration’), excluding the outer angles. Dorsal surface with some irregular ridges and microsculpture declining distally. Ventral surface with oblique carina on each side, no distinct beak-like process visible; left carina with three cuticular hair-like projections in proximal part. Torma unrecognisable; phobae absent. Chaetotaxy: dorsally with two pores and five setae on each side, ventrally with six setae on each side and central group of pores. ***Thorax*** (Figs 19,20)**.** Prothorax



Figs 6–18. Larva of *Cyphopisthes descarpentriesi.* (**6–9**) Left mandible: (**6**) dorsal; (**7**) mesal; (**8**) ventral; (**9**) lateral. (**10–13**) Right mandible: (**10**) dorsal; (**11**) mesal; (**12**) ventral; (**13**) lateral. (**14–15**) Ventral mouthparts: (**14**) dorsal; (**15**) ventral. (**16**) Left middle leg, anterior. (**17**) Left middle tarsungulus and femur, posterior. (**18**) Left hind tarsungulus and femur, anterior. Scale bars: figs 6–13 = 0.2 mm; figs 14–18 = 0.1 mm.

dorsally without secondary folds; both meso- and metathorax three folds each. Chaetotaxy: as on Figs 19,20. ***Legs*** (Figs 16,17,18)**.** Not markedly reduced in length but appear to be shorter than in similarly looking melolonthid larvae and those ceratocanthid genera studied. Stridulatory organs absent. Consist of coxa, trochanter, femur, tibia, and tarsungulus (= claw). Fore coxa shorter than middle coxa, hind coxa longest. Hind tarsungulus about half length of those on fore and middle leg. Junction between trochanter and femur marked by suture anteriorly and ventrally; no trace of junction visible dorsally and posteriorly and, consequently, trochanter and femur partly fused. Chaetotaxy: tarsungulus with no setae or pores; tibia with 20 setae and four pores, setae on hind tibia markedly shorter than those on middle and fore tibia, pore located on dorsal surface proximally near junction with femur, three pores located distally near junction with tarsungulus, one of them on dorsal surface and two on ventral; femur with nine setae and pore, six setae located distally around femur; two longer setae located on ventral surface in proximal third, and seta located on dorsal surface in proximal fifth; dorsally pointed long seta located on junction between femur and trochanter; trochanter with three setae in distal half, two of them markedly longer, four pores on anterodorsal surface and two pores on posterior surface; coxa with 17 setae, no pores. ***Abdomen*** (Figs 3,19, 20,25,26)**.** Segments I–VI with three dorsal folds (those on segments IV–VI indistinctly shaped); segment VII with two folds; segments VII–X without secondary subdivision. Anus transverse. Chaetotaxy: as in Figures 19,20,25,26; raster without palidia. ***Spiracles*** (Figs 21,22)**.** Functional cribriform spiracles present on posterior part of lateral side of prothorax and anterior part of lateral side of abdominal segments I–VIII. Spiracles on prothorax markedly larger than those on abdomen. Second abdominal spiracle located markedly ventrad relative to other spiracles. Spiracle closing apparatus not found. Mesothorax in posterior part of lateral side with trachea approaching wall of body from inside and attached to it by means of remnant of spiracle. This remnant forms



Figs 19–26. Larvae of Ceratocanthidae. (**19–20**) *Cyphopisthes descarpentriesi*, anterior part of body: (**19**) dorsal; (**20**) lateroventral. (**21–22**) Unidentified genus from the Malay Peninsula left spiracles: (**21**) prothorax; (**22**) abdominal segment III. (**23–26**) *Cyphopisthes descarpentriesi*: (**23–24**) right antennal segments III and IV: (**23**) dorsal; (**24**) ventral; (**25–26**) posterior part of body: (**25**) view from behind; (**26**) lateral. Scale bars: figs 19,20,25 = 1.0 mm; figs 21,22 = 0.05 mm; figs 23,24,26 = 0.1 mm.

narrow strip of sclerotisation without opening (= external ecdysial scar; Hinton 1967b: 949).

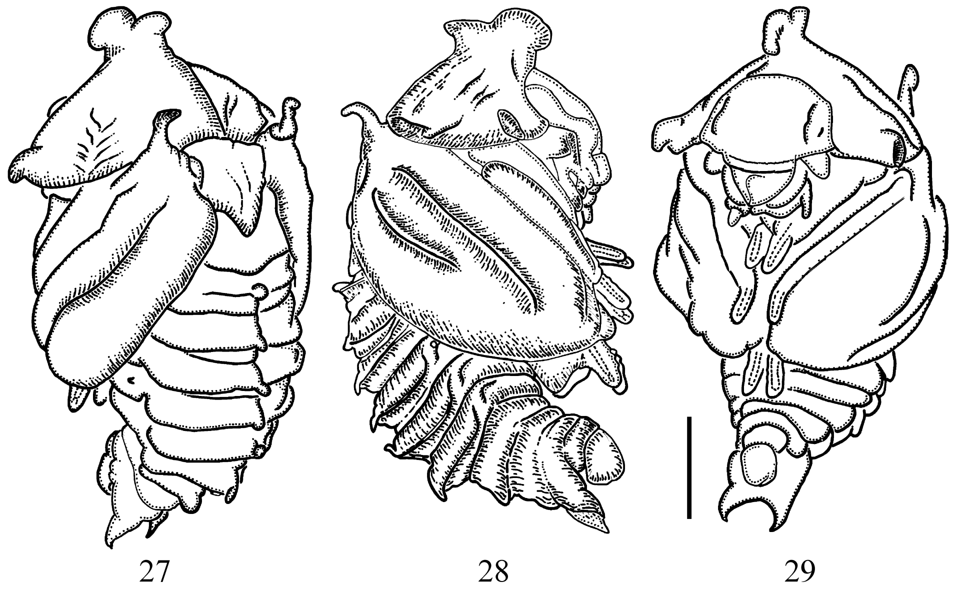
Pupa (Figs 27–29)

Exarate pupa. Head deflexed downward, with eyes, genal canthus, mouthparts and antennae distinctly visible. Prothorax with one markedly developed central and two smaller lateral projections. Base of each elytron with relatively long and narrow projection, each elytron with two distinct longitudinal carinae. Each abdominal tergum I–VII with transversally directed keel and short projection on it at body medial line. Gin-traps absent. Abdominal spiracles present on segments III and IV as dark and sclerotised spots; those on segment II moved ventrad, appear not to be sclerotised and with the same colour as rest of body. Spiracles on remaining segments not found. Last abdominal segment ending with two acutely pointed urogomphi, ventrally (males only) with developed genital capsule.

DISCUSSION

Preliminary diagnosis of the family Ceratocanthidae based on larval characters

Ritcher (1966) listed the following larval features to characterise the family Ceratocanthidae: (i) anterior margin of labrum strongly serrate; (ii) epipharynx with a dextral beak-like process; (iii) maxilla with separate galea and lacinia; (iv) maxillary stridulatory area with a row of conical teeth; (v) antenna 4-segmented; (vi) last antennal segment not reduced in diameter and with a dorsal sensory spot; (vii) thoracic spiracle with concavity of respiratory plate facing posteriorly; (viii) abdominal spiracles with concavities of respiratory plates facing anteriorly; (ix) dorsa of abdominal segments 2–5 plicate; (x) raster with a transverse palidia of spatulate setae; (xi) legs 4-segmented, with well-developed claws; (xii) stridulatory organ present on mesothoracic and metathoracic legs.



Figs 27–29. Pupa of *Cyphopisthes descarpentriesi*, habitus: (**27**) dorsolateral; (**28**) lateral; (**29**) ventrolateral. Scale bar = 1.0 mm.

Larvae of *Cyphopisthes* share with those of *Germarostes* and ‘*Philarmostes*’ (see: Ritcher 1966; Costa *et al.* 1988) a strongly serrate anterior margin of the labrum (character i). The ‘dextral beak-like process’ (character ii) is present in *Germarostes* (and in larvae from Malay Archipelago collected together with *Pterorthochaetes* adults) and absent in *Cyphopisthes* larvae. ‘*Philarmostes*’ larvae have the ‘dextral beak-like process’ absent, according to the drawing of Ritcher (1966), while unidentified larvae from the Malay Archipelago demonstrate both presence and absence of this structure. Character iii (separate galea and lacinia) is found in *Cyphopisthes* larvae, as well as in all known non-pleurostict Scarabaeoidea larvae. Character iv (a row of conical teeth on the ‘stridulatory’ area of the maxilla) should be modified, because in *Cyphopisthes* the larval shape and location of the tubercles do not correspond to those drawn by Ritcher (1966) and Costa *et al.* (1988). Antennal characters v and vi are shared by *Cyphopisthes* larvae, of which character vi (presence of markedly enlarged sensory spot on apical segment that is not reduced in size) noted for all ceratocanthid larvae known to us as well as for those of *Cryptogenius fryi* Arrow (Costa *et al.* 1988) and of some genera of the subfamily Orphninae (Paulian & Lumaret 1982; Morón 1991; but not in Barbero & Palestrini 1993). Characters vii–ix (orientation of concavities of sieve plates and presence of tergal folds) are shared by a majority of Scarabaeoidea larvae (except the Passalidae and Lucanidae). Character x (transverse orientation of palidia) might be used to separate *Germarostes* larvae from those of *Cyphopisthes* that have no palidia. Character xi (4-segmented legs with well-developed claws) is present in all known Ceratocanthidae larvae, as well as those of the majority of other scarabaeoid groups. Character xii (presence of stridulatory organ on mesothoracic and metathoracic legs) is absent in *Cyphopisthes* and other cartocanthid larvae we have studied and, consequently, is apparently unique only for *Germarostes*. In addition, all ceratocanthid larvae that we have studied are characterised by a markedly elongate and slender body.

Monophyly of Ceratocanthidae based on larvae

Cyphopisthes is the second ceratocanthid genus whose larva has been described in detail. We found no character of larval morphology that we could consider a synapomorphy for the Ceratocanthidae. Thus, the monophyly of the family is not corroborated.

Pupal characters

Some characters should be emphasised when *Cyphopisthes* pupae are compared to those of other ceratocanthid taxa (*Ceratocanthus* described by Choate 1987; *Germarostes* described by Costa *et al.* 1988). Presumably important similarities of all of them are the presence of one projection on the base of each elytron and the presence of transverse keels on the terga of at least the six basal abdominal segments. Pupae of *Cyphopisthes* have large central prothoracic projections, which are apparently shared only with *Pterorthochaetes* (Ballerio 1999a). The pupae differ from those of *Ceratocanthus* by the absence of two projections (‘knob-like structures’ *sensu* Choate 1987 on the head; they are similar (in contrast to *Germarostes*) in possessing one short central projection on the transversally directed dorsal abdominal keels. We regard these as ‘support projections’ (Ballerio 1999a), following the interpretation provided by Edmonds and Halffter (1978) for Scarabaeinae. However, Choate (1987) observed that these structures appeared to serve as sound-producing structures.

The number of functional spiracles has not been described for ceratocanthid pupae, except *Cyphopisthes* and that of an unidentified genus from Panama with functional spiracles on four basal abdominal segments (A.F. Newton, pers. comm., 2001).

Unique characters of *Cyphopisthes* larvae

Cyphopisthes larvae have a markedly reduced 1-segmented labial palp with the length about equal to the width. Larvae of *Germarostes* have a 2-segmented labial palp (Costa *et al.* 1988); the only ceratocanthid taxon where this character is described. As far as we are aware, the described larvae of other Scarabaeoidea also have 2-segmented labial palps (Browne & Scholtz 1999). In the material we have studied, larvae of two apparently different and unidentified genera of Ceratocanthidae from the Malay Peninsula have either a 2- or a 1-segmented labial palp. When 1-segmented, the segment is nearly twice as long as that present in *Cyphopisthes*.

The second unique *Cyphopisthes* larval character is the absence of the frontoclypeal suture. This structure in other ceratocanthid larvae studied is represented as a rigid, internally directed carina on the internal surface of the cranium, and is extended between the dorsal mandibular articulation. The frontoclypeal suture is partly (Trogidae, Ochodaeidae) or completely (some Bolboceratidae, Geotrupidae) reduced in a few other scarabaeoid lineages (Ritcher 1966; Baker 1968; Carlson & Ritcher 1974; Browne & Scholtz 1999).

Another character of *Cyphopisthes* larvae worthy of noting is the complete absence of setae on the tarsungulus (= 'claw'). Ritcher (1966) did not describe the number of setae on tarsungulus for '*Philarmostes*' or *Germarostes aphodioides*, while those of *G. macleayi* have at least two claw setae (Costa *et al.* 1988). Ceratocanthid larvae from Ecuador have a few setae on the claws, while those from the Malay Archipelago have no setae.

Larval spiracles of Ceratocanthidae

Contributions by Hinton (1947, 1967a, 1967b), Lotz (1962) and Galbreath (1976) have provided a reliable background for the comparative analysis of spiracles of larval coleopterans. The true non-functional and markedly reduced in size metathoracic spiracles in *Cyphopisthes* are reported here for the first time for Ceratocanthidae. This supports Edmonds and Halffter (1978), who mentioned that these structures are probably normally overlooked.

The study of Hinton (1967b) was handicapped by an unavailability of ceratocanthid larvae, particularly in respect to his search for the spiracle-closing apparatus. He stated that the presence of this structure is a primitive condition in larvae of pterygote insects which had been secondarily lost in many groups (i.e., larvae of Diptera). For the common ancestor of Scarabaeoidea, Hinton hypothesised the presence of a closing apparatus and, indeed, he found these structures in larvae of some basal families such as Trogidae, Lucanidae, Passalidae and Glaphyridae, while those of Scarabaeidae, Pleocomidae and Geotrupidae lack this structure (Hinton 1967b). We could not find the spiracle-closing apparatus, nor associated apodeme, in *Cyphopisthes* and other ceratocanthid larvae. Thus, the family might be one more group within the Scarabaeoidea sharing this derived character state.

Larval chaetotaxy of Ceratocanthidae

Larvae of *Cyphopisthes* and other Ceratocanthidae larvae that we studied possess quite numerous and nearly symmetrical setae and pores, which apparently might be compared to those of a so-called 'primary' set of sensilla in some other coleopteran groups (see Material and Methods). It might be plausible to assume that ceratocanthid larvae possess a set of sensilla more similar to that of the common ancestor of scarabaeoid beetles, than other larval Scarabaeoidea with normally highly modified and generally reduced chaetotaxy. We hope, that by using ceratocanthid chaetotaxy patterns, it will be possible to determine the closest relative of the Scarabaeoidea, which is one of the enigmatic questions in coleopteran phylogeny (Iablokoff-Khnzorian 1977; Lawrence & Newton 1982; Kukalová-Peck & Lawrence 1993; Hansen 1997; Browne & Scholtz 1999).

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