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Larvae of Ceratocanthidae and Hybosoridae (Coleoptera: Scarabaeoidea): study of morphology, phylogenetic analysis and evidence of paraphyly of Hybosoridae

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Abstract. Larvae of the scarabaeoid genera *Germarostes* Paulian, *Cyphopisthes* Gestro, *Paulianostes* Ballerio, *Ceratocanthus* White, *Pterorthochaetes* Gestro, *Madrasostes* Paulian, *Astaenomoechus* Martínez & Pereira (Ceratocanthidae) and *Hybosorus* Macleay, *Phaeochrous* Castelnau, and *Anaides* Westwood (Hybosoridae) are described, keyed and illustrated with fifty-seven drawings. A phylogenetic analysis of these two families based on larval morphology is presented. Fifty-four larval morphological and three biological characters from twenty-seven taxa revealed nineteen equally parsimonious cladograms. The monophyly of (Ceratocanthidae + Hybosoridae) is supported by four unambiguous unique synapomorphies: dorsal medial endocarina on cranium extended anteriorly into frontal sclerite; presence of large membranous spot on apical antennomere; labium dorsally with four pores in centre (secondarily reduced to two pores in some groups); and presence of stridulatory organ on fore- and middle legs (secondarily reduced in some groups). Our analysis suggests that the family Hybosoridae is paraphyletic with respect to Ceratocanthidae. The clade comprising the hybosorid genera *Hybosorus* and *Phaeochrous* is the sister group of the remaining Hybosoridae plus Ceratocanthidae. It is supported by two unambiguous synapomorphies: two apical antennomeres completely joined and the stridulatory organ represented by seven to nine large teeth anteriorly on the middle leg. The hybosorid genus *Anaides* is a sister group to the remaining Hybosoridae plus Ceratocanthidae (without *Hybosorus* and *Phaeochrous*) and the ceratocanthid genus *Germarostes* is a sister group to the remaining Hybosoridae plus Ceratocanthidae (without *Hybosorus*, *Phaeochrous* and *Anaides*). The ceratocanthid genera *Cyphopisthes*, *Astaenomoechus*, *Paulianostes*, *Pterorthochaetes*, and *Madrasostes* constitute a sister group to the hybosorid genus *Cryptogenius* and are supported by the presence of two reversions: two dorsal pores on labium and completely reduced stridulatory organs on fore- and middle legs.

Introduction

The primarily tropical family Ceratocanthidae (Fig. 1A–D) includes forty genera and about 320 species (Ballerio, 1999, 2000a, b; Howden & Gill, 2000; Scholtz & Grebennikov, in press, and references therein), with many undescribed taxa detected in recent years (Ballerio, unpublished data).

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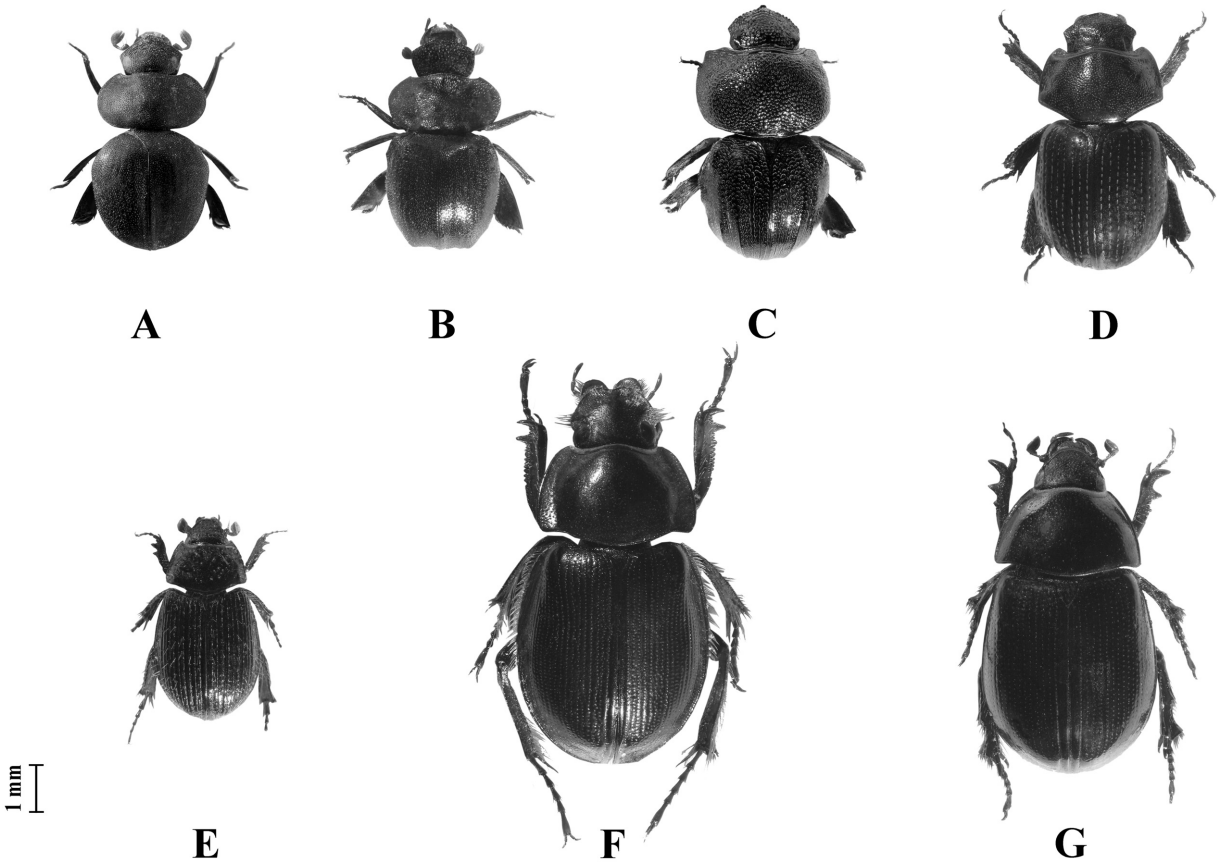

Fig. 1. Auto-montage images of some Ceratocanthidae and Hybosoridae adults. A, *Cyphopisthes* sp. (Sulawesi); B, *Paulianostes acromialis* (Malaysia); C, *Madrasostes sculpturatum* (Malaysia); D, *Germarostes* cfr. *macleayi* (Paraguay); E, *Chaetodus allsoppi* (Brazil); F, *Phaeochrous lobatus* (Philippines); G, *Hybosorus illigeri* (Kenya).

The first larval morphology was described by Ohaus (1909) for the stridulatory organs of the larva of *Cloeotus globosus* Say, 1835, from Brazil (likely to be a *Germarostes macleayi* (Perty, 1830)). More recently, larvae of six species in five genera of Ceratocanthidae have been described: *Germarostes aphodioides* (Illiger, 1800) and '*Philharmostes*' sp. (in Ritcher, 1966; the latter likely to be *Astaenomoechus* sp.); *Madrasostes kazumai* Ochi, Johki & Nakata, 1990 (in Iwata *et al*., 1992); *Germarostes macleayi* (Perty, 1830) (in Costa *et al*., 1988); *Ceratocanthus relucens* (Bates, 1887) (in Morón & Arce, 2003) and *Cyphopisthes descarpentriesi* Paulian, 1977 (in Grebennikov *et al*., 2002). A detailed summary of the present day knowledge of Ceratocanthidae larvae is provided in Grebennikov *et al*. (2002).

The nearly cosmopolitan family Hybosoridae (Fig. 1E–G), which is best represented in the tropics, includes thirty-two genera and approximately 210 described species (Allsopp, 1984; Ocampo, 2002a; Scholtz & Grebennikov, in press) and these numbers keep increasing (Ratcliffe & Ocampo, 2001; Ocampo & Vaz-de-Mello, 2002; Ocampo, 2002b, 2c, 2003). Late-instar larvae of five species, representing four genera, have been described. Gardner (1935) described the larvae of *Phaeochrous emarginatus* Laporte, 1840, which Ritcher (1966) re-described, together with a description of *Hybosorus orientalis* Westwood, 1845. Patil & Veeresh (1988) re-described the larva of *Hybosorus orientalis*. Costa *et al*. (1988) described the larvae of *Chaetodus* sp. and *Cryptogenius fryi* Arrow, 1909. Paulian (1939) first indicated that some hybosorid larvae stridulate by rubbing the front legs against the anterior margin of the epipharynx, a character justifying the monophyly of Hybosoridae (Jameson, 2002). Additionally, the description of the larva of *Brenskea coronata* Reitter, 1891 by Medvedev (1964), is, in fact, that of *Hybosorus illigeri* Reiche, 1853 (Nikolajev, 1987: 125).

The Hybosoridae are hypothesized to be related to Ochodaeidae and Ceratocanthidae (Scholtz *et al*., 1988; Browne & Scholtz, 1999) and Nikolajev (1995a, b) suggested that both Ceratocanthidae and Hybosoridae are closely related to the family Glaresidae. Browne & Scholtz (1995, 1999) suggested that the clade (Ceratocanthidae + Hybosoridae) + Ochodaeidae is the adelphotaxon to Geotrupinae, Taurocerastinae and Lethrinae (excluding Bolboceratidae). Howden & Gill (2000) agreed that Ceratocanthidae and Hybosoridae constitute a monophyletic group. Ocampo & Hawks (unpublished data), based on

molecular data, indicated that Ceratocanthidae and Hybosoridae constitute a monophyletic group which is sister to Glaphyridae and these three are a sister group of Ochodaeidae. The monophyly of Hybosoridae and Ceratocanthidae has been questioned by Nikolajev (1999) who proposed that Ceratocanthidae might be derived from Hybosoridae.

The aims of the present paper are to: (1) review critically published descriptions of Ceratocanthidae and Hybosoridae larvae and to describe unknown larvae; (2) provide an identification key to genera of Hybosoridae and Ceratocanthidae larvae; (3) conduct a phylogenetic analysis of Ceratocanthidae and Hybosoridae based on larval morphology and biology characters; and (4) seek the closest relatives of Ceratocanthidae and Hybosoridae by including a wide variety of members of possible sister groups in the analysis.

Materials and methods

Specimens' depository

Larval specimens for the present study were borrowed from and/or studied at the following collections: ANIC, Australian National Insect Collection, Canberra, Australia (T. Weir, S. A. Ślipiński); CMNC, Canadian Museum of Nature, Ottawa, Canada (H. F. Howden, R. Anderson); BMNH, The Natural History Museum, London, U.K. (S. Hine, M. Kerley); FMNH, Field Museum of Natural History, Chicago, U.S.A. (M. K. Thayer, A. F. Newton); MNHU, Museum für Naturkunde, Humboldt-Universität, Berlin, Germany (H. Wendt, M. Uhlig); NMNH, National Museum of Natural History, Washington DC, U.S.A. (D. G. Furth, N. Adams); ZISP, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (G. S. Medvedev); PZC, Peter Zwick Collection, Schlitz, Germany; MMC, Miguel A. Morón Collection, Xalapa, Mexico; ABC, Alberto Ballerio Collection, Brescia, Italy.

Specimen preparation and terminology

At least one larva of each available species was disarticulated, cleaned in a hot water solution of KOH, mounted on a microscope slide in Euparal medium, and studied under dissecting and compound microscopes with magnification up to 900×. Drawings were made with the aid of a camera lucida. The morphological terms used in this work are those of Lawrence (1991: 147–177). 'A' refers to adult; 'L3' to third-instar larva; 'P' to pupa.

Ingroup taxa

We performed a cladistic analysis of larvae of all studied species of Ceratocanthidae and Hybosoridae. We also included the Ceratocanthidae and Hybosoridae species described by Costa *et al*. (1988), which were unavailable to us for re-examination. Different authors have proposed Ochodaeidae (Browne & Scholtz, 1995, 1999), Glaresidae (Nikolajev, 1995a, b) and Glaphyridae (David Hawks, personal communication) as the closely related group to the clade of Ceratocanthidae + Hybosoridae. Larvae of Ochodaeidae are unavailable and relatively poorly known (*Pseudochodaeus estriatus* (Schaeffer, 1906) was described by Carlson & Ritcher (1974)); the description of the larva of *Codocera ferruginea* Eschscholtz, 1818 by Medvedev (1960) belongs in fact to a species of the genus *Trox* Fabricius, 1775 (Carlson & Ritcher, 1974), whereas larvae of Glaresidae are unknown. We included in the present analysis two representatives of Glaphyridae: *Amphicoma vulpes* Fabricius, 1792 (ZISP) and *Licnanthe vulpina* Hentz, 1826 (NMNH). The family Geotrupidae (s.str., *sensu* Scholtz & Browne, 1996) was proposed as a sister group to the clade comprising Hybosoridae, Ceratocanthidae and Ochodaeidae (Browne & Scholtz, 1999) and thus we included in the analysis *Geotrupes spiniger* Marsham, 1802 (MNHU), *Frickius variolosus* Germain, 1897 (CMNC), *Taurocerastes patagonicus* Philippi, 1866 (CMNC) and *Lethrus apterus* (Laxman, 1770) (ABC), representing three subfamilies of Geotrupidae (s.str.). It was argued recently (Scholtz & Browne, 1996) that the family Bolboceratidae, formerly included as a subfamily in Geotrupidae is in fact an independent lineage unrelated to Geotrupidae s.str., but this view was recently challenged by Verdú *et al*. (2004), who concluded, based on the study of larval morphology, that Bolboceratidae belongs to Geotrupidae. To address this question, we also included one species of Bolboceratidae in the analysis: *Odonteus darlingtoni* Wallis, 1928 (CMNC).

Outgroup taxa

The superfamilies Dascilloidea and Hydrophiloidea (*sensu* Lawrence & Newton, 1995; Hansen, 1997) have been proposed by different authors as sister groups to the superfamily Scarabaeoidea (for a detailed discussion and references on this subject see Grebennikov & Scholtz, 2003). It was shown recently that Dascillidae are unlikely to be closely related to Scarabaeoidea, because the larvae of the former family demonstrate characters suggesting dryopoid, particularly Eulichadidae, affinities (Grebennikov & Scholtz, 2003). We avoided using larvae of any Hydrophiloidea taxa as an outgroup due to numerous adaptive characters associated with the predatory way of life in water (family Hydrophilidae s.l.; see: Hansen, 1991; Beutel, 1994, 1999; Archangelsky, 1998a, b, 1999) or in other substrates (family Histeridae, see: Kovarik & Passoa, 1993; Caterino & Vogler, 2002). We chose the genus *Necrophilus* Latreille, 1829, a representative of the relatively early branching staphylinoid family Agyrtidae (Zwick, 1981; Newton, 1997) as an outgroup to polarize the character states. We studied larvae of two *Necrophilus* species: *N. hydrophiloides* Guérin-Méneville, 1835 (FMNH) and *N. subterraneus* Dahl, 1807 (PZC).

Phylogenetic analysis

Reconstruction of the phylogeny of the studied taxa was performed based on a matrix comprising fifty-four larval morphological and three biological characters (Table 1), compiled in WINCLADA version 1.00.08 (Nixon, 2002), and then spawned in HENNIG86 (Farris, 1988) using the exhaustive search option (i.e. *) to search for the shortest trees. We obtained nineteen equally parsimonious trees with length = 95 steps, consistency index = 0.76 and retention index = 0.89. The strict consensus of these trees (command 'n;' in HENNIG86) is shown in Fig. 2. Character state distributions were examined with WINCLADA (Nixon, 2002).

Characters

Morphological characters

(Characters treated as nonadditive, unless otherwise indicated.)

1. *Body shape*: (0) nearly straight, not or only slightly curved ventrally; (1) broadly C-shaped (Fig. 3).

Character state 1 is observed in all Scarabaeoidea, except Passalidae.

2. *Body shape*: (0) flattened dorsoventrally; (1) not flattened, nearly round in cross-section (Figs 3, 4A, B).

Character state 1 is an autapomorphy of Scarabaeoidea.

3. *Thoracic and abdominal segments dorsally and laterally*: (0) complete, not subdivided into folds; (1) subdivided into two or three folds (Fig. 4A, B).

Subdivided body segments are characteristic of all Scarabaeoidea except Passalidae and Lucanidae.

4. *Number of folds on thoracic and abdominal segments*: (0) two; (1) three.
5. *Defined body sclerites*: (0) present; (1) absent, body mainly membranous (Fig. 4A, B).

Character state 1 is an autapomorphy for Scarabaeoidea.

6. *Body, head and all appendages*: (0) with few setae; (1) moderate number of covering setae (Fig. 4A, B); (2) covered with numerous setae and larvae appear hairy (additive).

Character state 0 is a synapomorphy for Geotrupidae and Bolboceratidae; state 2 is an autapomorphy for Glaphyridae.

7. *Primary coleopteran chaetotaxy*: (0) ancestral type; (1) highly advanced type.

Larvae of many lineages of Coleoptera and Neuroptera have a characteristic set of similarly located primary sensilla (Ashe & Watrous, 1984; Bousquet & Goulet, 1984; Hoffman & Brushwein, 1992; Kovarik & Passoa, 1993; Alarie & Balke, 1999; Grebennikov & Beutel, 2002). Larvae of some groups of Coleoptera, including Scarabaeoidea, possess highly modified chaetotaxy hardly comparable with those of the coleopteran ground plan.

8. *Clypeus*: (0) uniformly sclerotized (Fig. 5A, C, G–I); (1) with basal sclerotization and apical membranous parts.

Table 1. Larval character state matrix for Ceratocanthidae and Hybosoridae (Coleoptera: Scarabaeoidea).

	1 2 3 4 5 12345678901234567890123456789012345678901234567890123456
Necrophilus subterraneus	000-0100000200000001100000000000000000001000000000000000
Necrophilus hidrophiloides	000-0100000200000001100000000000000000001000000000000000
Lethrus apterus	1110101001021021011120001111011000100000102010011211111100
Odonteus darlingtoni	1110101001021021001010001111011100200000-2121101311111100
Taurocerastes patagonicus	1110101011000021001110001111011100102001102111100211111100
Frickius variolosus	1110101011000021001110001111011100100001102111100211111100
Geotrupes spiniger	1110101021021021001120001111111100100001102111100211111100
Amphicoma vulpes	1111121111001111001231001111111001300100230000000011111000
Lichnanthe vulpina	1111121111001021101121001111011001300100230000000011111000
Paulianostes acromialis	1111111001112021001001101111011010111101111000000011111011
Astaenomoechus Ecuador	1111111001022021001001101111001010211101111000000011111011
Astaenomoechus Costa Rica	1111111001022021001001101111001010221101111000000011111011
Cyphopisthes descarpentriesi	1111111001022021001001101111011010211010-100000011111011
Pterorthochaetes insularis	1111111001012021001001101111011010111010-100000011111011
Madrasostes variolosum	1111111001012021001001101111011010101010-100000011111011
Madrasostes sculpturatum	1111111001012021001001101111011010101010-100000011111011
Ceratocanthus relucens	1111111001002021001001101111011020101111111000000011111011
Germarostes aphodioides	1111111001012021001001101111011020102111111000000011111011
Germarostes globosus	1111111001012021001001101111011020102111111000000011111011
Germarostes macleayi	1111111001012021001001101111011020102-11-11100000011111011
Chaetodus sp.	1111111001002021001001101111011020102111-11100000011110--
Cryptogenius fryi	1111111001002021001001101111011020102-10-12100000011111101-
Hybosorus illigeri	1111111001002021001011111111011020102120121000000011111000
Phaeochrous emarginatus	1111111001002021001011111111011020102120121000000011111000
Anaides simplicicollis	1111111001002021001001101111011020102111111000000011111000
Anaides Mexico	1111111001002021001001101111011020102111111000000011111000

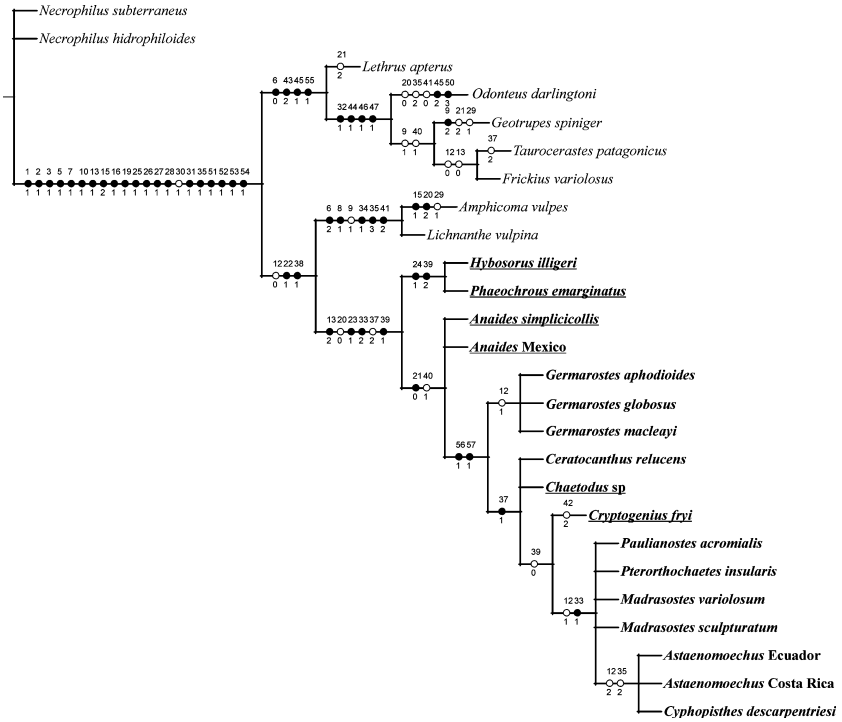

Fig. 2. Strict consensus of nineteen trees with length = 95, consistency index = 0.76 and retention index = 0.89. Taxa in bold represent Ceratocanthidae and Hybosoridae; underlined taxa represent Hybosoridae.

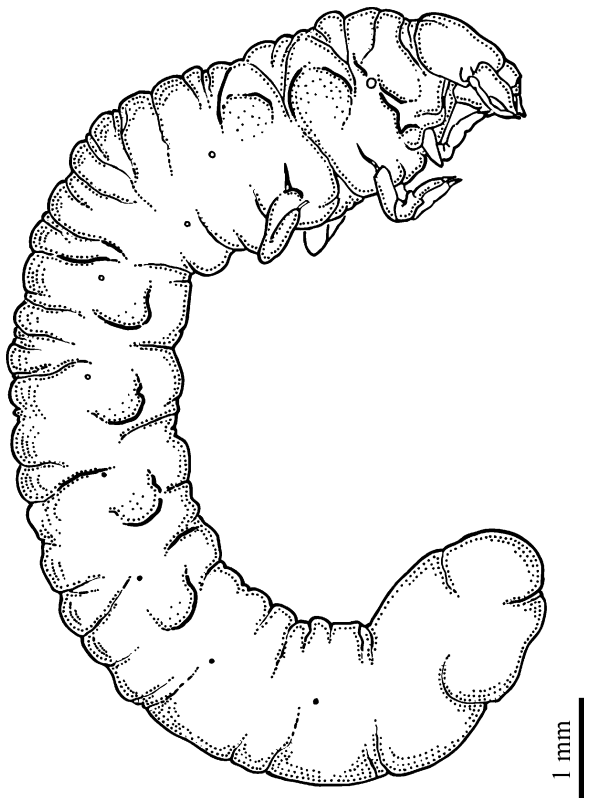

Fig. 3. Larva of *Cyphopisthes descarpentriesi*, habitus, lateral. From Grebennikov *et al*. (2002).

9. *Shape of clypeus*: (0) symmetrical (Fig. 5A, C, G–I); (1) asymmetrical, right side about one tenth longer than left; (2) asymmetrical, right side more than one fifth longer than left (additive).
10. *Cranium*: (0) prognathous; (1) hypognathous (Fig. 4B).

A hypognathous cranium is characteristic of all Scarabaeoidea except Passalidae.

11. *Two slightly divergent apodemes connecting frontoclypeal suture with anterior angles of clypeus*: (0) absent; (1) present (Fig. 5I).

Autapomorphy for *Paulianostes*, deactivated.

12. *Frontoclypeal suture between dorsal mandibular articulation*: (0) present, straight (Fig. 5A, C, G); (1) present, bent anteriorly (Fig. 5H, I); (2) absent (Fig. 5E).
13. *Median dorsal endocarina*: (0) absent; (1) present, poorly developed, not extending into frontal sclerite; (2) present, well developed, extending well into frontal sclerite (Fig. 5A, C, E, G–I).
14. *Length of epicranial suture*: (0) short, not extending beyond middle of cranium; (1) long, extending beyond middle of cranium.

Character state 1 is an autapomorphy for *Amphicoma*, deactivated.

15. *Number of stemmata*: (0) six; (1) one; (2) nil (Fig. 4B) (additive).

The majority of Scarabaeoidea larvae have no stemmata, whereas in a few groups there is one stemma on each side of the cranium (*Amphicoma*, all Trogidae, some pleurostict Scarabaeidae).

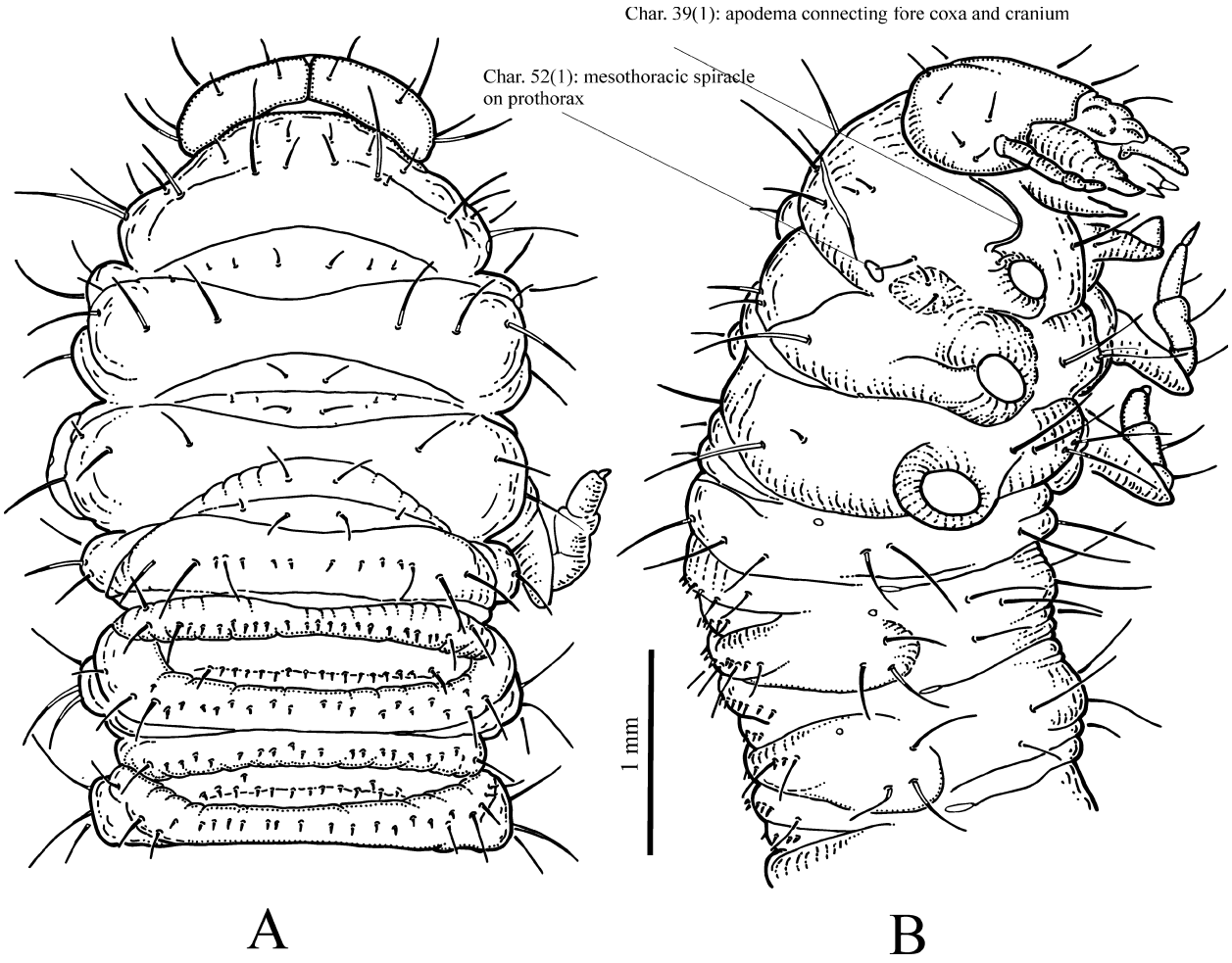

Fig. 4. Larva of *Cyphopisthes descarpentriesi*, anterior part of body, dorsal (A) and lateroventral (B). From Grebennikov *et al.* (2002).

16. *Antennal fossa*: (0) clearly separated from mandibular base; (1) not or weakly separated from mandibular base.

Character state 1 is a synapomorphy of all Scarabaeoidea.

17. *Characteristic sensoriumlike projection on second antennomere bearing a small and flat sensorium*: (0) absent; (1) present.

Character state 1 is an autapomorphy for *Lichnanthe*, deactivated.

18. *Length of antenna*: (0) long, extending to the level of clypeal apex; (1) short, not extending to the level of clypeal apex.

Character state 1 is an autapomorphy for *Lethrus*, deactivated. Within Scarabaeoidea, Passalidae are also unique with their short and two-segmented antennae.

19. *Markedly developed antennifer*: (0) absent; (1) present.

Character state 1 is a synapomorphy of all Scarabaeoidea.

20. *Antennomere 2 and 3*: (0) subequal in size; (1) antennomere 3 markedly smaller; (2) antennomere 3 absent (additive).
21. *Size and shape of antennal sensorium*: (0) medium-sized, conical; (1) markedly reduced in size, conical; (2) flat; (3) not recognizable/absent.
22. *Membranous subdivision of basal antennomere*: (0) absent, three true antennomeres; (1) present (Fig. 5G), antenna apparently consisting of four antennomeres.

The majority of authors consider Scarabaeoidea as having antennae two- (Passalidae), three- (Trogidae, Lucanidae, Pleocomidae, Geotrupidae, Bolboceratidae), and four-segmented (majority of other groups with few exceptions). During the course of our study, we preferred to consider four-segmented antennae of Scarabaeoidea as truly three-segmented with the basal antennomere secondarily subdivided by a membranous ring giving the antenna a four-segmented appearance. This question cannot be firmly solved before the study of antennal muscles and innervations is completed.

23. *Large membranous spot on apical antennomere*: (0) absent; (1) present, covering more than one third of surface.

Character state 1 is a synapomorphy of Ceratocanthidae + Hybosoridae. A similar-looking structure was observed in Scarabaeidae: Orphninae (Morón, 1991; Paulian & Lumaret, 1982; but not by Barbero & Palestrini, 1993).

24. *Antennomeres 2 and 3*: (0) separate (Fig. 6G–J, L, M); (1) fused (Fig. 6A, B, D, F).

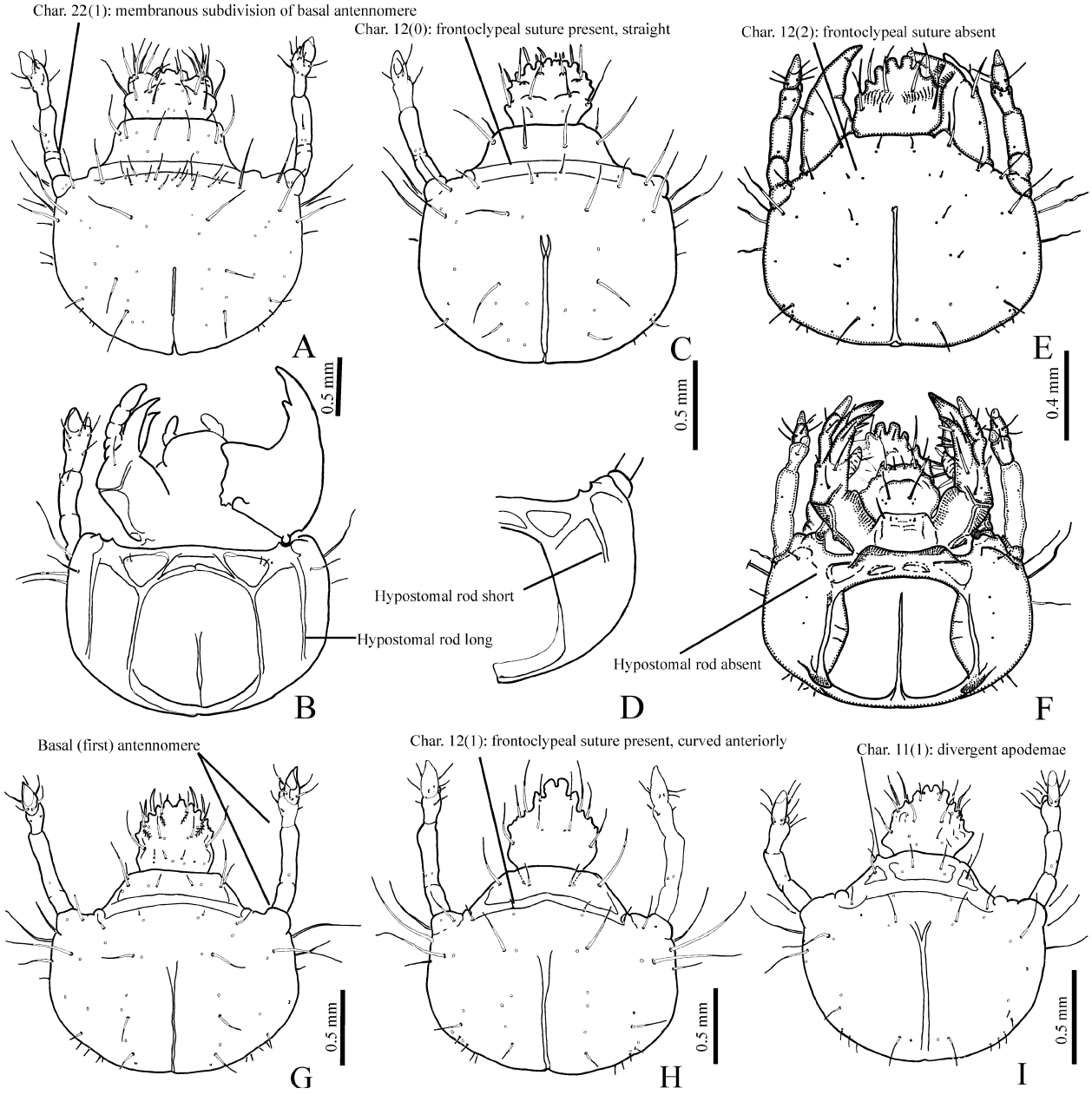

Fig. 5. Larvae of Hybosoridae and Ceratocanthidae, details. A, B, *Hybosorus illigeri*, cranium dorsal (A) and ventral (B); C, D, *Anaides simplicicollis*, cranium dorsal (C) and ventral (D); E, F, *Cyphopisthes descarpentriesi*, cranium dorsal (E) and ventral (F) (from Grebennikov *et al.*, 2002); G, *Pterorthochaetes insularis*, cranium, dorsal; H, *Madrasostes variolosum*, cranium, dorsal; I, *Paulianostes acromialis*, cranium, dorsal.

Character state 1 is a synapomorphy of *Hybosorus* + *Phaeochrous*.

25. *Direction of mandibular apex*: (0) medial; (1) anterior.

Character state 1 is a synapomorphy for all Scarabaeoidea.

26. *Shape of molar part of mandible viewed from above*: (0) round; (1) straight.

Character state 1 is an autapomorphy for Scarabaeoidea.

27. *Mandibles*: (0) symmetrical; (1) asymmetrical.

Character state 1 is a synapomorphy of Scarabaeoidea, except Passalidae.

28. *Ventral mandibular process*: (0) absent; (1) present (Fig. 7B, C, F).

Character state 1 is a synapomorphy of all Scarabaeoidea, except Passalidae.

29. *Lateral joint of stipes and cardo*: (0) not protruding laterally; (1) markedly protruding laterally.

30. *Dorsal stridulatory teeth on stipes*: (0) absent; (1) present (Fig. 8D, F, H, I).

Character state 1 is a synapomorphy for Scarabaeoidea; secondarily reduced in some Ceratocanthidae (*Astaenomoechus*).

31. *Maxillary palpifer*: (0) absent or not developed, palpi clearly with three palpomeres; (1) present, palpi appearing with four palpomeres (Fig. 8A–I).

Character state 1 is an autapomorphy of Scarabaeoidea.

32. *Anteroventral longitudinal suture on prementum between palps*: (0) absent; (1) present.
33. *Number of dorsal pores on prementum*: (0) nil; (1) two (Fig. 8D, F); (2) four (Fig. 8H, I).
34. *Characteristic medial curvature of basal labial palpomere with medially directed apical palpomere*: (0) absent; (1) present.

Character state 1 is an autapomorphy of Glaphyridae.

35. *Oncylus*: (0) absent; (1) present, well developed; (2) present, markedly reduced; (3) absent, substituted by numerous stout setae.
36. *Number and size of labial palpomeres*: (0) two, normal size (Fig. 8F–I); (1) one, 1.5–2× longer than wide (Figs 8D, 5K); (2) one, as long as wide (additive).
37. *Transverse line of dorsal sensilla on prementum*: (0) absent; (1) present, pores (Fig. 8F); (2) present, setae (Fig. 8I).
38. *Markedly developed sclerotized apodemes connecting the coxal base with the cranium*: (0) absent; (1) present (Fig. 4B).
39. *Stridulatory organ on fore- and middle legs*: (0) absent; (1) present, middle leg with field of microsculpture anteriorly and without large teeth (Fig. 9G); (2) present, middle leg with a few large teeth (Fig. 9E) (additive).

Ritcher (1966: 67) mistakenly indicated the presence of a larval stridulatory organ in Ceratocanthidae on meso- and metathoracic legs. When present, the stridulatory organ in Ceratocanthidae is always located on pro- and mesothoracic legs, as in all Hybosoridae larvae known to us. Besides Ceratocanthidae and Hybosoridae, the presence of stridulatory organs on fore- and middle legs has never been recorded in Scarabaeoidea and, consequently, this is a unique and unambiguous synapomorphy for these two families. The clade of 'advanced' Ceratocanthidae consisting of *Cyphopisthes*, *Astaenomoechus*, *Paulianostes*, *Pterorthochaetes* and *Madrasostes* lacks the stridulatory organs and it is considered as a secondary loss.

40. *Tarsi and claws on hind legs*: (0) similar to those on fore- and middle legs; (1) markedly reduced in size (Fig. 9H).
41. *Claw setae*: (0) absent; (1) two; (2) four.

Character state 2 is a synapomorphy for Glaphyridae (additive).

42. *Location and length of claw setae*: (0) located in basal part, not longer than 1.5× claw width; (1) located in apical part, not longer than 1.5× claw width; (2)

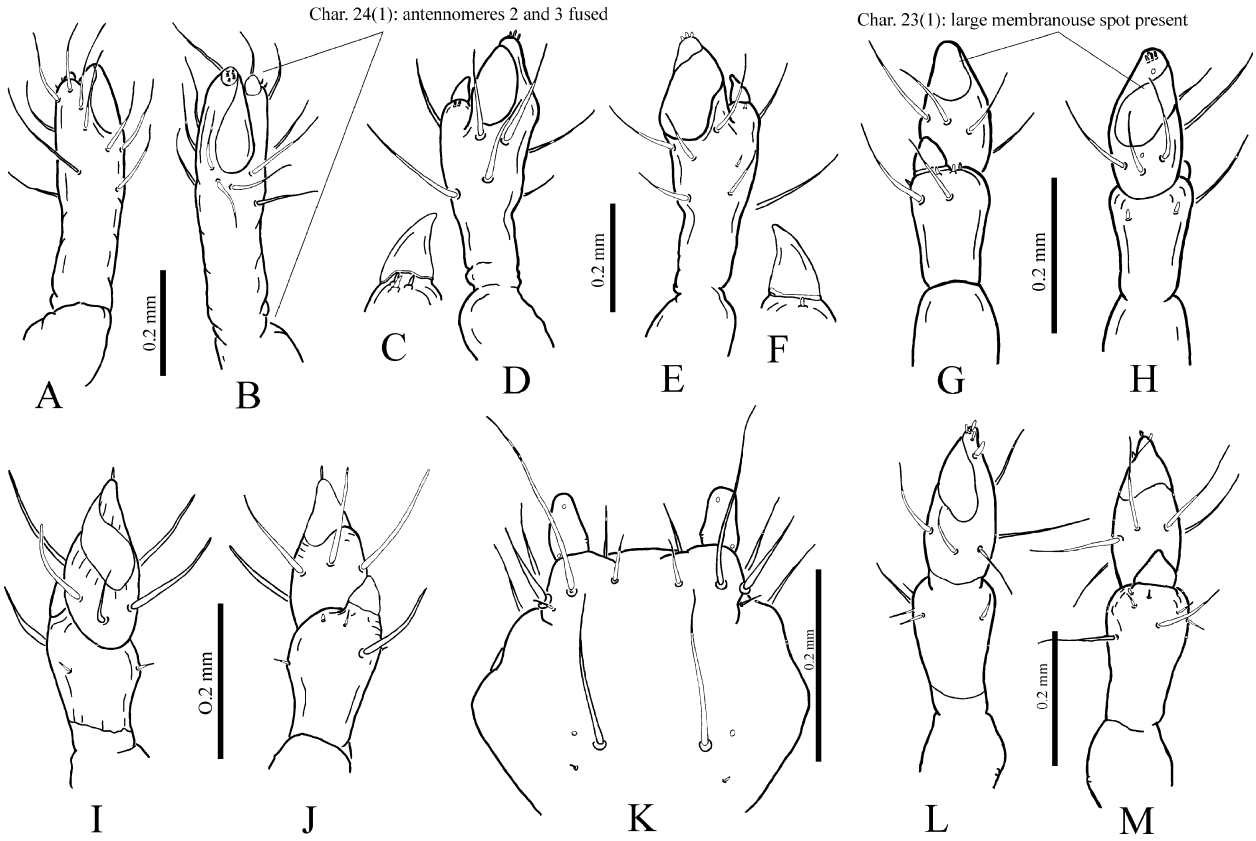

Fig. 6. Larvae of Hybosoridae and Ceratocanthidae, details. A–B, *Phaeochrous emarginatus*; C–F, *Hybosorus illigeri*; G, H, *Anaides simplicicollis*; I, J, *Pterorthochaetes insularis*; K, *Paulianostes acromialis*; L, M, *Madrasostes variolosum*. A, B, D, E, G–J, L, M, Two apical antennomeres; C, F, sensorium; K, labium, ventral.

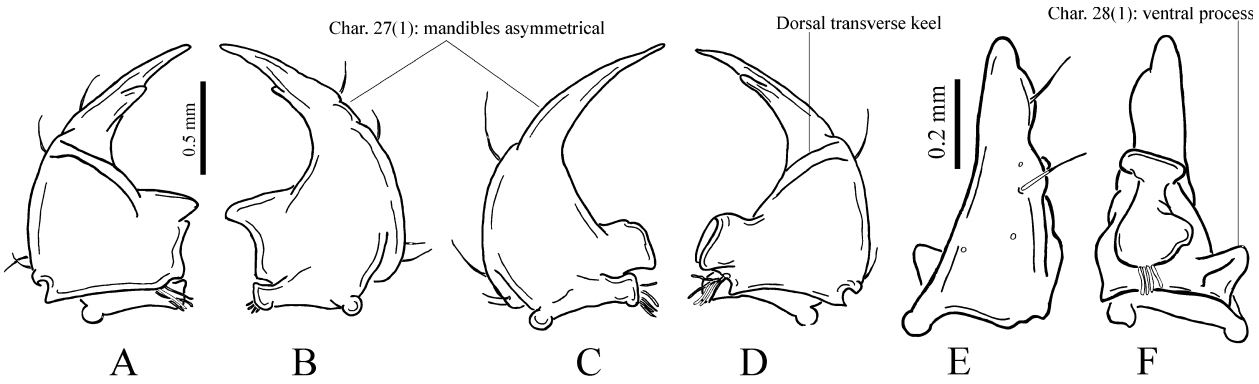

Fig. 7. Larvae of Hybosoridae and Ceratocanthidae, mandibles, dorsal (A, D), ventral (B, C), lateral (E) and medial (F). A–D, *Phaeochrous emarginatus*; E, F, *Astaenomoechus* sp. (Ecuador). A, B, E, F, left mandible; C, D, right mandible.

located in apical part, markedly longer than 1.5× claw width (Fig. 9F); (3) located in basal part, markedly longer than 1.5× claw width.

43. *Suture between trochanter and femur*: (0) present and complete; (1) anteriorly present, posteriorly absent (Fig. 9D, E, G); (2) absent, trochanter and femur completely fused (additive).
44. *Stridulatory organ on middle and hind legs*: (0) absent; (1) present.
45. *Claw size*: (0) normal; (1) all claws markedly reduced; (2) claws absent (additive).
46. *Size of trochanter and femur on fore- and middle legs*: (0) normal; (1) markedly enlarged.
47. *Ventral part of femur on fore- and middle legs*: (0) normal; (1) markedly protruding anteriorly, attachment of tibiotarsus appears shifted dorsally.
48. *Tibiotarsus and femur*: (0) not fused; (1) fused.

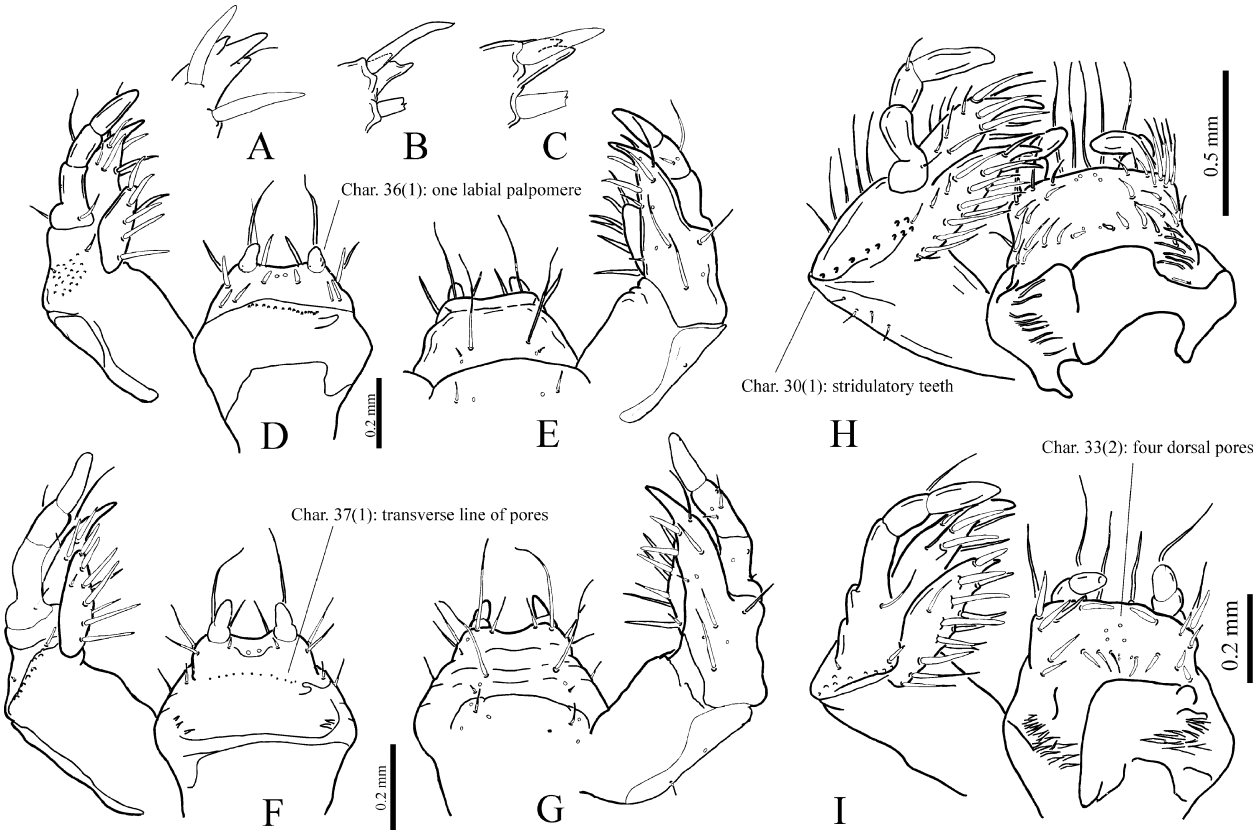

Fig. 8. Larvae of Hybosoridae and Ceratocanthidae, mouthparts, details. A, *Hybosorus illigeri*; B, *Germarostes globosus*; C, I, *Germarostes aphodioides*; D, E, *Pterorthochaetes insularis*; F, G, *Madrasostes variolosum*, H, *Phaeochrous emarginatus*. A–C, Apex of left lacinia, dorsal; D, F, H, I, left maxilla and labium, dorsal; E, G, left maxilla and labium, ventral.

Character state 1 is autapomorphic for *Lethrus*, deactivated.

49. *Size of legs*: (0) normal; (1) markedly reduced.
50. *Shape of abdominal apex*: (0) conically narrowed into pygidium; (1) broadly rounded (Fig. 3); (2) obliquely flattened; (3) narrowly rounded.
51. *Urogomphi on tergum IX*: (0) present; (1) absent (Fig. 3).

Character state 1 is an autapomorphy for Scarabaeoidea.

52. *Location of mesothoracic spiracles*: (0) anteriorly on mesothorax; (1) posteriorly on prothorax (Fig. 4B).

Character state 1 is an autapomorphy for Scarabaeoidea.

53. *Metathoracic spiracles*: (0) absent; (1) present on mesothorax, nonfunctional and reduced (Fig. 4B).

Character state 1 is an autapomorphy for Scarabaeoidea.

54. *Type of spiracles*: (0) annular-biforous; (1) cribriform (Fig. 9C).

Biological characters

55. *Larval food provisioned by adults*: (0) absent; (1) present.
56. *Larval habitat*: (0) soil; (1) wood.
57. *Larval association with termites*: (0) absent; (1) present.

Larval morphological characters excluded from the analysis due to incompatibility with the outgroup, but used in the description of larvae of Ceratocanthidae and Hybosoridae

58. *Hypostomal rods on ventral cranial surface*: very short or not detectable (Fig. 5F); short, not reaching posteriorly midlength of cranium (Fig. 5D); long, extending posteriorly beyond two thirds length of cranium (Fig. 5B).
59. *Transverse row of setae on front between mandibular articulation*: absent (Fig. 5C, G–I); present (Fig. 5A).
60. *Number of setae on apical antennomere*: five; six.
61. *Number of long setae on penultimate antennomere*: one (Fig. 6I, J); two (Fig. 6M).
62. *Number of setae on basal antennomere*: nil (Fig. 5C, E, G–I); two or three (Fig. 5A).
63. *Number of pores on basal antennomere*: three; four; five.
64. *Dorsal transverse keel on both mandibles*: present, distinct (Fig. 7A, D); present, poorly detectable; absent.
65. *Beaklike structure on epipharynx*: absent; present (Fig. 10G).
66. *Tormae*: united (Fig. 10B); not united (Fig. 10D, F, H).
67. *Longitudinal medial sclerite on epipharynx*: absent (Fig. 10D, F, H); present, small (Fig. 10I); present, large (Fig. 10G).
68. *Number of setae on lacinia*: nine and less (Fig. 8D); ten to fifteen (Fig. 8I); fifteen and more (Fig. 8H).
69. *Shape of apex of lacinia*: no points, rounded (Fig. 8D–F); one point; two points; three points (Fig. 10A).
70. *Length of apical maxillary palpomere compared with penultimate*: shorter (Fig. 8H, I); subequal (Fig. 10D, E); longer.
71. *Apex of lacinia*: extending beyond two thirds of galea (Fig. 10H); not extending beyond two thirds of galea (Fig. 10D).
72. *Palida*: absent; present, disperse flattened short setae; present, one row of flattened stout setae.

Diagnosis of third-instar Hybosoridae and Ceratocanthidae larvae

Typical C-shaped scarabaeiform larva (Fig. 3), body uniformly cylindrical, markedly elongate and slender, without dorsal expansions. Cranium protracted and

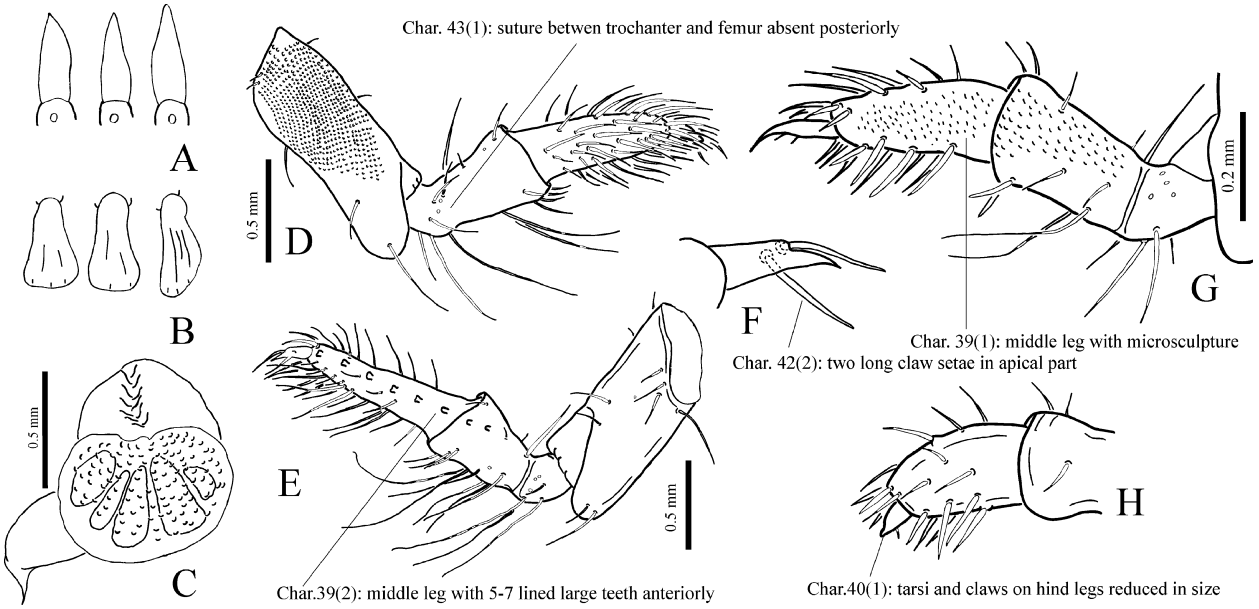

Fig. 9. Larvae of Hybosoridae and Ceratocanthidae. A, *Hybosorus illigeri*; B–F, *Phaeochrous emarginatus*; G, H, *Anaides simplicicollis*. A, B, Setae from palida; C, abdominal spiracle; D, right foreleg, posterior; E, G, right middle leg, anterior; F, claw, right foreleg, posterior; H, right hind leg, anterior.

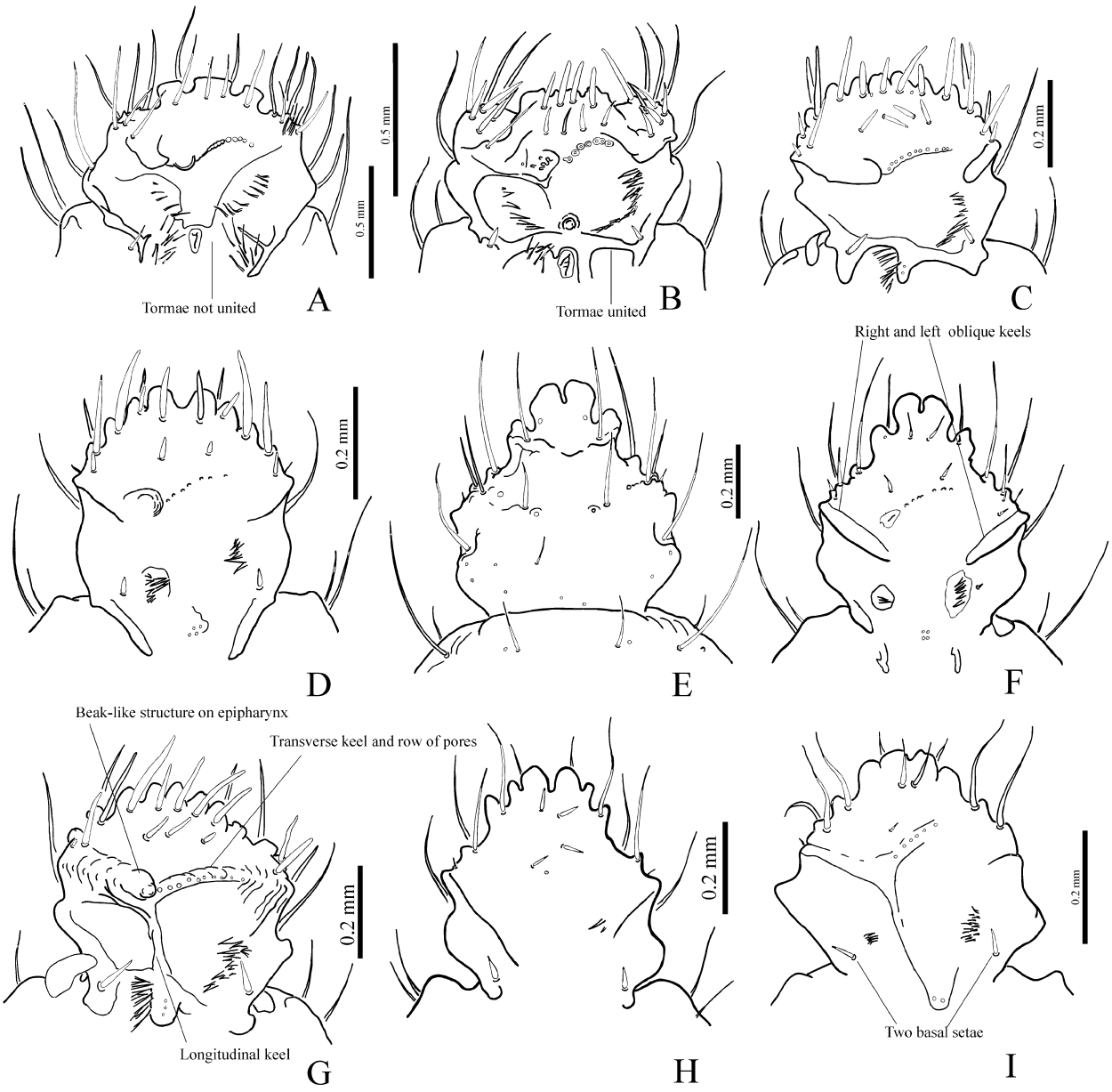

Fig. 10. Larvae of Hybosoridae and Ceratocanthidae, labrum, ventral (= epipharynx, A–D, F–I) and dorsal (E). A, *Phaeochrous emarginatus*; B, *Hybosorus illigeri*; C, *Anaides simplicicollis*; D, *Pterorthochaetes insularis*; E, F, *Madrasostes variolosum*; G, *Germarostes aphodioides*; H, *Astaenomoechus* sp. (Costa Rica); I, *Paulianostes acromialis*.

hypognathous (Fig. 4B), nearly symmetrical (Fig. 5A–C, E–I), about 1.3 times wider than long. Stemmata absent. Frontoclypeal (= epistomal) suture absent (Fig. 5E) or present, when present relatively straight (Figs 5, 8, 9) or markedly bent anteriorly (Figs 1, 2). Clypeolabral suture present (Figs 1, 2, 5, 7–9). Clypeus symmetrical and uniformly sclerotized (Fig. 5A, C, E, G–I). Internal longitudinal endocarina at medial line of dorsal surface of cranium originating from occipital foramen, extending anteriorly on frontal sclerite with its apex reaching level of antennal insertion (Fig. 5A, C, E, G–I). Frontal arms of epicranial suture poorly visible (Fig. 5A, C, E, G–I). Antenna with three true segments; basal one subdivided by membranous ring and thus antenna appearing four-segmented; sometimes two apical antennomeres fused with no visible separation (Fig. 6A, B, D, E). Two apical antennomeres subequal in size (Fig. 6G–J, L, M); basal subdivided antennomere markedly longer. Antennal apex at about same level as those of maxillae, mandibles and labrum (Fig. 5A–C, E–I). Penultimate (second) antennomere with conical sensorium (Fig. 6C, F) ventrally and distally (Fig. 6B, D, E, G–J, L, M). Apical antennomere conical, with markedly developed

hyaline sensory part apically covering not less than 30% of segment surface (Fig. 6A, B, D, E, G–J, L–M). Mandibles (Fig. 7A–F) asymmetrical, each with ventral process and molar part; that on left mandible notably elongate and medially protracted. Median parts of mandibles without brushes of small hairs dorsally and ventrally, except a group of about three to four flat apparently cuticular strips of distal edge of mola on medial surface (Fig. 7F). Stridulatory area on ventral surface of mandibles absent (Fig. 7B, C). Apices of mandibles with larger ventral and smaller and shorter dorsal tooth (Fig. 7A–F). Galea and lacinia separate (Fig. 8D, F, H, I). Stipes dorsally with eight to fifteen stridulatory teeth arranged in an oblique line (Fig. 8D, F, H, I), rarely (*Astaenomoechus*) without. Maxillary palp consists of three true segments and basal palpifer. Labial palp one- or two-segmented (Figs 6K, 8D–I). Hypopharyngeal sclerite (= oncylus) poorly defined or absent (Fig. 8D, F, H, I). Labrum slightly to markedly asymmetrical (Fig. 10A–I), slightly to markedly enlarged and apically protracted; with variable number of apical projections (might be called 'serration'), its dorsal surface with some irregular ridges and microsculpture (Fig. 6E). Ventral surface (= epipharynx) variable, with or without oblique carina on each side and beaklike process (Fig. 10A–D, F–I). Tormae joined (Fig. 10B, C, G) or not joined mesally (Fig. 10A, D, F, H, I). Base of each foreleg connected with ventral side of cranium by markedly sclerotized ridge (Fig. 4B). Meso-, metathoracic and six basal abdominal segments each subdivided into three folds (Figs 3, 9A, B). Defined thoracic and abdominal sclerites absent. Legs not reduced in length (Fig. 3). Stridulatory organs absent or present on fore- and middle legs (Fig. 9D, E, G). Legs consist of coxa, trochanter, femur, tibiotarsus and claw. Hind tarsungulus about half length of those on fore- and middle leg (Fig. 9H). Junction between trochanter and femur marked by suture anteriorly (Fig. 9E, G) and ventrally; no trace of junction visible dorsally and posteriorly (Fig. 9D) and, consequently, trochanter and femur partly fused. Anus transverse (Fig. 3). Raster with or without palida. Functional cribriform spiracles present on posterior part of lateral side of prothorax and anterior part of lateral side of abdominal segments I–VIII (Fig. 4B). Spiracles on prothorax markedly larger than those on abdomen. 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 (Fig. 4B). This remnant forms a narrow strip of sclerotization without opening (see also Edmonds & Halffter, 1978).

Key to genera of third-instar Ceratocanthidae and Hybosoridae larvae

1. Antennomeres 2 (bearing sensorium) and 3 fused (Fig. 6A, B, D, E); basal antennomere (subdivided by membranous ring) with two or more setae; hypostomal rods on ventral surface of cranium long, extending about two thirds of cranial length (Fig. 5B); lacinia with more than seventeen setae (Fig. 8G); middle tarsi and tibiae with longitudinal line of about seven to nine large stridulatory teeth on anterior surface (Fig. 9E). 2
1′ Antennomeres 2 (bearing sensorium) and 3 separate, not fused (Fig. 6G–J, L, M); basal antennomere (subdivided by membranous ring) without setae; hypostomal rods on ventral surface of cranium absent (Fig. 5F) or short (Fig. 5D), not extending beyond two thirds of cranial length; lacinia with less than fourteen setae (Fig. 8D, F, I); middle tarsi and tibiae without stridulatory teeth or with field of pointed microsculpture covering most of anterior surface, but without line of seven to nine large teeth (Fig. 9G)..... 3
2 Combined apical antennomere with markedly narrowed base and widened apex (Fig. 6D, E); lacinia with one large and two smaller apices (Fig. 8A); two joined apical antennomeres with ten long setae (Fig. 6D, E); tormae united (Fig. 10B); short and flattened setae of palida pointed towards apex (Fig. 9A) . .. .*Hybosorus*
2′ Combined apical antennomere with about same width at base and top (Fig. 6A, B); lacinia with one large central and one smaller apex; two joined apical antennomeres with fourteen long setae (Fig. 6A, B); tormae not united (Fig. 10A); short and flattened setae of palida widened towards apex (Fig. 9B)..... .... *Phaeochrous*
3 Labial palp two-segmented (Fig. 8D, H, G); labium normally with four dorsal pores (Fig. 8I; except *Madrasostes* with two dorsal pores, Fig. 8F) 4
3′ Labial palp one-segmented (Figs 6K, 8D); labium always with two dorsal pores (Fig. 8D)..... 9
4 Claw with two setae; labium with four dorsal pores (Fig. 8I); stridulatory teeth on fore coxa and middle tarsus and femur present as fields of fine tubercles (Fig. 9G)..... 5
4′ Claw without setae; labium with two dorsal pores (Fig. 8D, F); fore coxa and middle tarsus without stridulatory teeth .... *Madrasostes*
5 Apical antennomere with five long setae (except *Ceratocanthus* with six long setae); epipharynx with markedly developed beaklike structures (Fig. 10G) 6
5′ Apical antennomere with six long setae; epipharynx without beaklike structure (Fig. 10C)..... 7
6 Dorsal transverse keel on both mandibles absent .... *Ceratocanthus*
6′ Dorsal transverse keel present on both mandibles (like Fig. 7A, D)..... ....*Germarostes*
7 Claw setae markedly longer than basal width of claw (like Fig. 9F); fore- and middle legs without stridulatory apparatus ....*Cryptogenius*
7′ Claw setae shorter than basal width of claw (Fig. 9G); fore- (like Fig. 9D) and middle (Fig. 9G) legs with stridulatory apparatus 8
8 Two short claw setae, one in middle and another in apical quarter of claw (Fig. 9G)..... ....*Anaides*
8′ Two short claw setae both located in apical eighth of claw..... ....*Chaetodus*

9 Frontoclypeal suture present, markedly bent anteriorly (Fig. 5G, I, seen in translucent light)..... 10
9′ Frontoclypeal suture completely absent (Fig. 5E, seen in translucent light)..... 11
10 Frontoclypeal suture connected with anterior angles of clypeus by two slightly divergent apodemes (Fig. 5I); second antennomere (bearing sensorium) with two long setae; first antennomere with four pores; lacinia with seven setae along medial side; claws with two setae ....*Paulianostes*
10′ Frontoclypeal suture not connected with anterior angles of clypeus and no apodemes present; second antennomere (bearing sensorium) with one long seta (Fig. 6I, J); first antennomere with five pores; lacinia with six setae along medial side (Fig. 8D); claws without setae..... ....*Pterorthochaetes*
11 Claw with two setae; stridulatory teeth on maxilla present as poorly visible and almost not sclerotized rounded tubercles.... ....*Cyphopisthes*
11′ Claw without setae; stridulatory teeth on maxilla absent..... ....*Astaenomoechus*

Germarostes Paulian, 1982

Larval diagnosis

Clypeus without divergent apodemes connecting frontoclypeal suture with anterior clypeal angles; frontoclypeal suture between dorsal mandibular articulation present and markedly bent anteriorly; hypostomal rods on ventral cranial surface short, not reaching posteriorly midlength of cranium; transverse row of setae on front between mandibular articulation absent; antennal sensorium medium-sized, conical; antennomeres 2 and 3 separate; apical antennomere with five long setae, penultimate antennomere with one long seta, basal antennomere without setae and with five pores; dorsal transverse keel on both mandibles present, distinct; beaklike structure on epipharynx present; tormae united; longitudinal medial sclerite on epipharynx present, large; number of setae on lacinia ten to fifteen; apex of lacinia with one point; apical maxillary palpomere longer than penultimate; apex of lacinia extending beyond two thirds of galea; stridulatory teeth on stipes dorsally present; prementum dorsally with four pores; oncylus present, well developed; labium with two palpomeres; transverse line of dorsal sensilla on prementum present, consists of setae; sound-producing organ on fore- and middle legs present, middle leg with field of microsculpture anteriorly and without large teeth; claw with two setae located in apical part each not longer than 1.5× claw width; palida present, one row of flattened setae.

Diversity and geographical distribution

As currently defined (Howden & Gill, 2000: 323), the genus *Germarostes* consists of two subgenera *Germarostes* s.str. and *Haroldostes* Paulian, 1982 with forty-three and twenty-five species, respectively, distributed from Argentina and Chile to the U.S.A. and Canada. Some of the *Germarostes* species were previously referred under the generic name *Cloeotus* Germar, 1843. As presently defined, the genus *Cloeotus* consists of three species (*C. latebrosus* Germar, 1843, *C. petrovitzi* Paulian, 1982, and *C. semicostatus* Germar, 1843) from Brazil and Colombia (Howden & Gill, 2000: 232).

Material

Germarostes aphodioides (Illiger, 1800). Head width L3 = 1.73 mm ($n = 1$). 2 A, 5 L3. 26.vi.1949, College Park, Missouri, U.S.A. Under bark of standing red or black oak. H. S. Barber and G. B. Vogt leg. (NMNH). 4 L3, 1 P. 23.viii. 1963, Shenandoah, Iowa, U.S.A. Under bark of fallen tree. D. R. Riley leg., O. L. Cartwright det. (NMNH). 1 A, 2 P, 1 L3, 3 L2. 6.viii.1959, Louisville, Kentucky, under dead oak bark. T. J. Spilman leg. O. L. Cartwright det. (NMNH).

Germarostes globosus (Say, 1835). Head width L3 = 2.03 mm ($n = 1$). 1 A, 1 Ex. 3.ix.1949, Cedar Mt., near Rapidan, Virginia, U.S.A. Reared from pupa under bark. O. L. Cartwright leg., det. (NMNH). 2 A, 2 L3. Haw Creek, Florida, U.S.A. (NMNH).

Germarostes macleayi (Perty, 1830). See Costa *et al.* (1988). We could not examine larvae of this species. However, the description provided by Costa *et al.* (1988) is detailed enough for this species to be included in the analysis. It must be stressed that *Germarostes macleayi* is very similar to *Germarostes globosus* and that the former may be a synonym of the other (Woodruff, 1973).

Cyphopisthes Gestro, 1899

Larval diagnosis

Clypeus without divergent apodemes connecting frontoclypeal suture with anterior clypeal angles; frontoclypeal suture between dorsal mandibular articulation absent; hypostomal rods on ventral cranial surface very short or not detectable; transverse row of setae on front between mandibular articulation absent; antennal sensorium medium-sized, conical; antennomeres 2 and 3 separate; apical antennomere with five long setae, penultimate antennomere with one long seta, basal antennomere without setae and with three pores; dorsal transverse keel on both mandibles present, distinct; beaklike structure on epipharynx absent; tormae not united; number of setae on lacinia five to six; apex of lacinia without points, rounded; apical maxillary palpomere shorter than penultimate; apex of lacinia not extending beyond two thirds of galea; stridulatory teeth on stipes dorsally present; prementum dorsally with two pores; oncylus present, markedly reduced; labium with one palpomere as long as wide; transverse line of dorsal sensilla on prementum present, consists of pores; sound-producing

organ on fore- and middle legs absent; claw without setae; palida absent. See also Grebennikov *et al*. (2002).

Diversity and geographical distribution

This genus consists of about ten species distributed from eastern India (Assam) to Queensland and possibly New Caledonia (Ballerio, 2000a)

Material

Cyphopisthes descarpentriesi Paulian, 1977. Head width L3 = 1.24 mm ($n = 1$); see also Grebennikov *et al*. (2002). 30 L3. 1.vii.1974, Cape Pallarenda, Townsville, Queensland, larvae and pupae in galleries of *Mastotermes darwiniensis* Froggatt, 1897 nest in dead acacia tree. J. A. L. Watson leg. (ANIC). *Remark:* adults, pupae and larvae were collected together in the same galleries, see also Grebennikov *et al*. (2002).

Paulianostes Ballerio, 2000

Larval diagnosis

Clypeus with two divergent apodemes connecting frontoclypeal suture with anterior clypeal angles (Fig. 2); frontoclypeal suture between dorsal mandibular articulation present and markedly bent anteriorly; hypostomal rods on ventral cranial surface very short or not detectable; transverse row of setae on front between mandibular articulation absent; antennal sensorium medium-sized, conical; antennomeres 2 and 3 separate; apical antennomere with five long setae, penultimate antennomere with two setae, basal antennomere without setae and with four pores; dorsal transverse keel on both mandibles absent; beaklike structure on epipharynx absent; tormae not united; longitudinal medial sclerite on epipharynx present, small; number of setae on lacinia nine and less; apex of lacinia without points, rounded; apical maxillary palpomere shorter than penultimate; apex of lacinia not extending beyond two thirds of galea; stridulatory teeth on stipes dorsally present; prementum dorsally with two pores; oncylus present, well developed; labium with one palpomere 1.5–2× longer than wide; transverse line of dorsal sensilla on prementum present, consists of pores; sound-producing organ on fore- and middle legs absent; claw with two setae located in apical part, each not longer than 1.5× claw width; palida absent.

Diversity and geographical distribution

The genus *Paulianostes* was erected recently by Ballerio (2000a) and comprises three described species occurring in the Oriental region.

Material

Paulianostes acromialis (Pascoe, 1860). Head width L3 = 1.30 mm ($n = 1$). 1 L3. 24.xi.1987, Malaysia, Pahang, Bukit Fraser, Jeriau Falls. L. Bartolozzi leg. in a nest of *Hospitalitermes* sp. prope *medioflavus* (ABC). *Remark:* our species identification is based on the fact that one of the collected larvae was reared in a laboratory to adults representing *Paulianostes acromialis* (L. Bartolozzi, personal communication).

Ceratocanthus White, 1842

Larval diagnosis

Clypeus without divergent apodemes connecting frontoclypeal suture with anterior clypeal angles; frontoclypeal suture between dorsal mandibular articulation straight, present; hypostomal rods on ventral cranial surface short, not reaching posteriorly midlength of cranium; transverse row of setae on front between mandibular articulation absent; antennal sensorium medium-sized, conical; antennomeres 2 and 3 separate; apical antennomere with six long setae, penultimate antennomere with two long setae, basal antennomere without setae and with five pores; dorsal transverse keel on both mandibles absent; beaklike structure on epipharynx present; tormae united; longitudinal medial sclerite on epipharynx present, large; number of setae on lacinia ten to fifteen; apex of lacinia with one point; apical maxillary palpomere longer than penultimate; apex of lacinia extending beyond two thirds of galea; stridulatory teeth on stipes dorsally present; prementum dorsally with four pores; oncylus present, well developed; labium with two palpomeres; transverse line of dorsal sensilla on prementum present, consists of pores; sound-producing organ on fore- and middle legs present, middle leg with field of microsculpture anteriorly and without large teeth; claw with two setae located in apical part, each not longer than 1.5× claw width; palida present, one row of flattened setae.

Diversity and geographical distribution

The genus *Ceratocanthus* (= *Acanthocerus* Macleay, 1819; = *Sphaeromorphus* Germar, 1843; = *Gymnoropterus* Gestro, 1899) consists of fifty-four species distributed from Argentina to the U.S.A. (Ballerio, 2000c; Howden & Gill, 2000).

Material

Ceratocanthus relucens (Bates, 1887). Head width L3 = 2.20 mm ($n = 2$); see also Morón & Arce (2003). 2 L3, 26.vii.1999. Mexico, Veracruz, Xalapa, compost, R. Arce leg. (MMC).

Pterorthochaetes Gestro, 1899

Larval diagnosis

Clypeus without divergent apodemes connecting frontoclypeal suture with anterior clypeal angles; frontoclypeal suture between dorsal mandibular articulation present and markedly bent anteriorly; hypostomal rods on ventral cranial surface short, not reaching posteriorly midlength of cranium; transverse row of setae on front between mandibular articulation absent; antennal sensorium medium-sized, conical; antennomeres 2 and 3 separate; apical antennomere with six long setae, penultimate antennomere with one long seta, basal antennomere without setae and with five pores; dorsal transverse keel on both mandibles present, distinct; beaklike structure on epipharynx present; tormae not united; longitudinal medial sclerite on epipharynx absent; lacinia with nine and less setae; apex of lacinia without points, rounded; apical maxillary palpomere subequal to penultimate; apex of lacinia not extending beyond two thirds of galea; stridulatory teeth on stipes dorsally present; prementum dorsally with two pores; oncylus present, well developed; labium with one palpomere 1.5–2× longer than wide; transverse line of dorsal sensilla on prementum present, consists of pores; sound-producing organ on fore- and middle legs absent; claw without setae; palida absent.

Diversity and geographical distribution

This genus consists of twenty-one species distributed in the Oriental and Australasian regions.

Material

Pterorthochaetes ?insularis Gestro, 1899. Head width L3 = 1.65 mm ($n = 1$). 3 L3. 17.–19.iv.1999, Malaysia, Kelantan, 30 km northeast of Tanah Rata, A. Ballerio leg., det. (ABC). *Remark:* mature larvae, pupae and adults of *Pterorthochaetes insularis* were collected together under the bark of a dead log, the only other Ceratocanthidae collected there was an undescribed small species of *Pterorthochaetes*. However, due to the large size of the larvae collected, we think that they belong to *Pterorthochaetes insularis* and not to the smaller undescribed species.

Madrasostes Paulian, 1975

Larval diagnosis

Clypeus without divergent apodemes connecting frontoclypeal suture with anterior clypeal angles; frontoclypeal suture between dorsal mandibular articulation present and markedly bent anteriorly; hypostomal rods on ventral cranial surface short, not reaching posteriorly midlength of cranium; transverse row of setae on front between mandibular articulation absent; antennal sensorium medium-sized, conical; antennomeres 2 and 3 separate; apical antennomere with six long setae, penultimate antennomere with two long setae, basal antennomere without setae and with five pores; dorsal transverse keel on both mandibles present, distinct; beaklike structure on epipharynx absent; tormae not united; longitudinal medial sclerite on epipharynx absent; lacinia with nine and less setae; apex of lacinia without points, rounded; apical maxillary palpomere subequal to penultimate; apex of lacinia not extending beyond two thirds of galea; stridulatory teeth on stipes dorsally present; prementum dorsally with two pores; oncylus present, well developed; labium with two palpomeres; transverse line of dorsal sensilla on prementum present, consists of pores; sound-producing organ on fore- and middle legs absent; claw without setae; palida present, disperse flattened short setae.

Diversity and geographical distribution

This genus consists of about twenty-eight species distributed from India and southern Japan to New Guinea.

Material

Madrasostes ?variolosum (Harold, 1874). Head width L3 = 1.65 mm ($n = 1$). 3 L3. 16.iv.1999, Malaysia, Perak, near Kuala Woh, A. Ballerio leg., det. (ABC). *Remark:* adults and mature larvae of this species were collected together in a termite nest, inside a dead log. Other Ceratocanthidae adults collected in the same nest were *Pterorthochaetes insularis*, an undescribed small species of *Pterorthochaetes* and *Cyphopisthes* sp. Due to the large size of larvae and to the fact that they are different from the described larvae of *Cyphopisthes* and *Pterorthochaetes*, we suppose that they belong to *Madrasostes variolosum*.

Madrasostes sculpturatum Paulian, 1989. Head width L3 = 1.68 mm ($n = 1$). 2 L3. January 1999, Malaysia, Perak, Gunung Korbu, P. Cechovski leg., A. Ballerio det. (ABC, VGV). *Remark:* adults, teneral adults, pupae and mature larvae were collected together (P. Cechovski, personal communication) and, therefore, we suppose they belong to the same species.

Astaenomoechus Martínez & Pereira, 1959

Larval diagnosis

Clypeus without divergent apodemes connecting frontoclypeal suture with anterior clypeal angles; frontoclypeal suture between dorsal mandibular articulation absent; hypostomal rods on ventral cranial surface very short or not detectable; transverse row of setae on front between mandibular articulation absent; antennal sensorium medium-sized, conical; antennomeres 2 and 3 separate; apical antennomere with five long setae, penultimate

antennomere with two long setae, basal antennomere without setae and with five pores; dorsal transverse keel on both mandibles present, poorly detectable or absent; beaklike structure on epipharynx absent; tormae not united; longitudinal medial sclerite on epipharynx absent; lacinia with nine and less setae; apex of lacinia without points, rounded; apical maxillary palpomere subequal to penultimate; apex of lacinia not extending beyond two thirds of galea; stridulatory teeth on stipes dorsally absent; prementum dorsally with two pores; oncylus present, markedly reduced; labium with one palpomere 1.5–2× longer than wide or as long as wide; transverse line of dorsal sensilla on prementum present, consists of pores; sound-producing organ on fore- and middle legs absent; claw with two setae each located in apical part and each not longer than 1.5× claw width; palida absent.

Diversity and geographical distribution

The genus *Astaenomoechus* consists of about eleven species distributed from Mexico to Argentina (Howden & Gill, 2000).

Material

Astaenomoechus sp. 01. Head width L3 = 1.40 mm ($n = 1$); L2 = 1.00 mm ($n = 1$). 3 A, 2 P, about 15 L2–3. 06.vi. 1905, Pucay, W. Ecuador. (MNHU).

Astaenomoechus sp. 02. Head width L3 = 1.40 mm ($n = 1$). 2 A, 2 P, 5 L3. 29.i.1935, Costa Rica, F. Neverman leg., Van Emden coll. (BMNH).

Hybosorus Macleay, 1819

Larval diagnosis

Clypeus without divergent apodemes connecting frontoclypeal suture with anterior clypeal angles; frontoclypeal suture between dorsal mandibular articulation straight, present; hypostomal rods on ventral cranial surface long, extending posteriorly beyond two thirds length of cranium; transverse row of setae on front between mandibular articulation present; antennal sensorium markedly reduced in size, conical; antennomeres 2 and 3 fused; two fused apical antennomeres with ten long setae, basal antennomere with two to three setae and five pores; dorsal transverse keel on both mandibles present, distinct; beaklike structure on epipharynx present; tormae united; longitudinal medial sclerite on epipharynx absent; lacinia with more than fifteen setae; apex of lacinia with three points; apical maxillary palpomere longer than penultimate; apex of lacinia extending beyond two thirds of galea; stridulatory teeth on stipes dorsally present; prementum dorsally with four pores; oncylus present, well developed; labium with two palpomeres; transverse line of dorsal sensilla on prementum present, consists of setae; sound-producing organ on fore- and middle legs present, middle leg with a few large teeth anteriorly; claw with two setae located in apical part each markedly longer than 1.5× claw width; palida present, one row of flattened setae.

Diversity and geographical distribution

This genus consists of five species and is distributed in North, Central America, and the Caribbean region, Africa, Asia and Europe.

Material

Hybosorus illigeri Reiche, 1853. Head width L3 = 2.15 mm ($n = 1$); L2 = 1.25–1.30 mm ($n = 2$). 1 L3. 1.vii.1947, Mystic, Irwin Co., Georgia, U.S.A., ex soil, roots of fennel. F. R. Majure leg. (NMNH). 5 L3, 8 L2. 12.vii.1989, Tex. Ward Co., Monahans, U.S.A., in Bermuda grass turf. M. Guelker leg. (NMNH).

Phaeochrous Castelnau, 1840

Larval diagnosis

Clypeus without divergent apodemes connecting frontoclypeal suture with anterior clypeal angles; frontoclypeal suture between dorsal mandibular articulation straight, hypostomal rods on ventral cranial surface long, extending posteriorly beyond two thirds length of cranium; transverse row of setae on front between mandibular articulation present; antennal sensorium markedly reduced in size, conical; antennomeres 2 and 3 fused; two joined apical antennomeres with fourteen long setae, basal antennomere with two to three setae and five pores; dorsal transverse keel on both mandibles present, distinct; beaklike structure on epipharynx present; tormae not united; longitudinal medial sclerite on epipharynx absent; lacinia with more than fifteen setae; apex of lacinia with two points; apical maxillary palpomere longer than penultimate; apex of lacinia extending beyond two thirds of galea; stridulatory teeth on stipes dorsally present; prementum dorsally with four pores; oncylus present, well developed; labium with two palpomeres; transverse line of dorsal sensilla on prementum present, consists of setae; sound-producing organ on fore- and middle legs present, middle leg with a few large teeth anteriorly; claw with two setae located in apical part each markedly longer than 1.5× claw width; palida present, one row of flattened setae.

Diversity and geographical distribution

This genus consists of forty-three species distributed in Africa, Asia, and Oceania.

Material

Phaeochrous emarginatus Laporte, 1840. Head width L3 about = 2.30 mm ($n = 1$; single specimen slightly damaged). 3 L3. India: Dehra Dun, U.P.G.#3082, adult reared, ex soil in forest. (NMNH).

Anaides Westwood, 1846

Larval diagnosis

Clypeus without divergent apodemes connecting frontoclypeal suture with anterior clypeal angles; frontoclypeal suture between dorsal mandibular articulation straight, present; hypostomal rods on ventral cranial surface short, not reaching posteriorly midlength of cranium; transverse row of setae on front between mandibular articulation absent; antennal sensorium medium-sized, conical; antennomeres 2 and 3 separate; apical antennomere with six long setae, penultimate antennomere with two long setae, basal antennomere without setae and with two pores; dorsal transverse keel on both mandibles present, distinct; beaklike structure on epipharynx present; tormae united; longitudinal medial sclerite on epipharynx present, small; lacinia with ten to fifteen setae; apex of lacinia with one point; apical maxillary palpomere longer than penultimate; apex of lacinia extending beyond two thirds of galea; stridulatory teeth on stipes dorsally present; prementum dorsally with four pores; oncylus present, well developed; labium with two palpomeres; transverse line of dorsal sensilla on prementum present, consists of setae; sound-producing organ on fore- and middle legs present, middle leg with field of microsculpture anteriorly and without large teeth; claw with two setae located in apical part each not longer than 1.5× claw width; palida present, one row of flattened setae.

Diversity and geographical distribution

This genus consists of thirteen species distributed in the Central, South America and Caribbean region.

Material

Anaides simplicicollis Bates, 1887. Head width L3 = 2.30 mm ($n = 1$). 1 L3. 15.viii.1932, Rio Durazno 1700 m, W.-Abharg, Irazu, Costa Rica. (NMNH). *Remark:* the identification of this larva is based on the fact that it is nearly identical to the second studied larval specimen of *Anaides* (see below). Moreover, the vial with this larva bears an identification label without the specialist's name, which we consider trustworthy.

Anaides sp. Head width L3 or L2 = 1.53 mm ($n = 1$). 1 L3. 19.viii.1938, Laredo Tx., Mexico, A.H. Lewis leg., A. Böving det. (NMNH). *Remark: Anaides laticollis* Harold, 1863 is the only species of this genus recorded from Mexico.

Discussion

Monophyly of Ceratocanthidae + Hybosoridae

The phylogenetic analysis yielded nineteen equally parsimonious cladograms represented by the strict consensus tree (Fig. 2). The analysis strongly supports the monophyly of Ceratocanthidae and Hybosoridae with four unambiguous and unique synapomorphies: dorsal medial endocarina on cranium extending anteriorly into frontal sclerite (character 13/2); presence of large membranous spot on apical antennomere (character 23/1); labium dorsally with four pores (character 33/2; two of four pores are lost secondarily in derived members of this clade) and fore- and middle legs have a stridulatory organ (character 39/1; reduced secondarily in derived members of this clade). The last feature is unique within Scarabaeoidea and, to our knowledge, has not been recorded in Coleoptera larvae previously. Thus, it provides strong support for the Ceratocanthidae + Hybosoridae monophyly. Howden & Gill (2000: 284) additionally listed adult synapomorphies for Ceratocanthidae + Hybosoridae: ability to flex the pronotum downwards (this character is present only in some hybosorid species); exposed labrum and tips of the mandibles; the ocular canthus of the gena dividing the eye (a genal canthus intruding at least partly into the eyes in a few Ceratocanthidae; also there are a few exceptions in Hybosoridae); antennal club three-segmented; and anterior tarsus inserted on the underside of fore tibia posterior to the anterior tooth. All these characters provide support for Hybosoridae and Ceratocanthidae having unique common ancestry.

Paraphyly of Hybosoridae in respect to Ceratocanthidae

The major result of this study is the discovery that the family Hybosoridae is paraphyletic with respect to Ceratocanthidae. Previously, Nikolajev (1999) suggested this possibility, but without a formal cladistic analysis. The clade formed by the two hybosorid genera *Hybosorus* and *Phaeochrous* is the sister group of the remaining (Hybosoridae + Ceratocanthidae) (Fig. 2) and is supported as a monophylum by two unambiguous synapomorphies: two apical antennomeres completely joined (character 24/1) and the presence of seven to nine large sound-producing teeth on the middle leg anteriorly (character 39/2). The group of derived ceratocanthid genera *Paulianostes*, *Pterorthochaetes*, *Madrasostes*, *Astaenomoechus* and *Cyphopisthes* form a rather poorly resolved clade due to the presence of two derived and conflicting character states. They are character state 36/1–2 (one-segmented labial palp observed in *Paulianostes*, *Astaenomoechus* and *Cyphopisthes*) and character state 39/0 (absence of claw setae observed in *Pterorthochaetes*, *Madrasostes and Cyphopisthes*). These character states are only once (one-segmented labial palp) or never (claws without setae) observed within Scarabaeoidea and this conflict implies that at least one of them evolved twice in these four genera. Such ambiguity

resulted in an unresolved polytomy of the genera *Paulianostes*, *Pterorthochaetes* and *Madrasostes* (Fig. 2). The remaining genera *Cryptogenius*, *Anaides*, *Germarostes*, *Ceratocanthus* and *Chaetodus* occupy an intermediate position on the cladogram between *Hybosorus* + *Phaeochrous* and the clade of more derived Ceratocanthidae. Resolution of this part of the tree is low, and this topology suggests that the differences between 'primitive' 'Ceratocanthidae' and 'derived' 'Hybosoridae' might not be significant, at least based on larval morphology. The hypothesis of Ceratocanthidae being an advanced clade within Hybosoridae does not contradict the fossil data revised by Krell (2000). The former family is known from Miocene, whereas the latter was first recorded from Lower Cretaceous (Krell, 2000: fig. 1)

Taxonomic position of the genera Paulianostes *and* Cryptogenius

Our results indicate that the 'ceratocanthid' genera *Paulianostes* and *Cyphopisthes* are not closely related, and support recent separation of two species from the former genus into the newly erected genus *Paulianostes* (Ballerio, 2000a). Our analysis also indicates that the aberrant genus *Cryptogenius* from the Amazon Basin, whose phylogenetic affinities were discussed on a number of occasions (Krikken, 1975; Scholtz *et al*., 1987; Ide *et al*., 1990), does belong to the Ceratocanthidae–Hybosoridae clade.

Sister group of Ceratocanthidae + Hybosoridae

Two genera of the family Glaphyridae, *Amphicoma* and *Lichnanthe*, are linked on the cladogram (Fig. 2) with five unambiguous larval synapomorphies and appear as an adelphotaxon to Ceratocanthidae + Hybosoridae. This sister group relationship is supported by three derived characters, of which two appear as unambiguous synapomorphies on the cladogram (membranous subdivision of the basal antennomere: character 22/1 and markedly developed sclerotized apodemes connecting fore coxae with the cranium: character 38/1). Both of these characters, however, are known in Scarabaeoidea outside of the sampled taxa (for example, larvae of the family Scarabaeidae have them both) and therefore do not provide strong support to Glaphyridae as the sister group to Ceratocanthidae + Hybosoridae if more scarabaeoid taxa are included in the analysis. A third character (12/0), the presence of a frontoclypeal suture between dorsal mandibular articulation, appears as a synapomorphy, because larvae of the outgroup (Agyrtidae; the genus *Necrophilus*) lack this suture. Polarization of this character is uncertain; it is plausible to assume that the loss of this suture once in *Necrophilus* and a second time in Geotrupidae and Bolboceratidae happened independently twice and the presence of this suture is indeed a symplesiomorphy. Therefore, the present analysis provides no strong evidence that Glaphyridae are indeed a sister group to Ceratocanthidae + Hybosoridae.

Concluding remarks

A few points of the present study should be emphasized. Two scarabaeoid families, Hybosoridae and Ceratocanthidae, form a well-supported monophyletic group based on both larval and adult morphological characters, but the sister group of this clade remains uncertain. Larval morphology suggests that Hybosoridae could be paraphyletic with respect to Ceratocanthidae, supporting the hypothesis of Nikolajev (1999). It is highly desirable to study larvae of more taxa from the 'hybosorid–ceratocanthid' clade, particularly in many respects the intermediate 'hybosorid' genus *Liparochrus* Erichson, 1847 from Australia and Papua New Guinea, morphologically modified 'hybosorid' genera from the South American tribe Cryptogeniini, and even more strangely shaped South American genera of presumably myrmecophilous or termitophilous 'ceratocanthids', currently placed in two separate subfamilies within the Ceratocanthidae: Scarabatermitinae and Ivieolinae (Howden, 1971, 1973, 2001; Howden & Gill, 1988a, b, 1995, 2000).

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