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Rolling into a ball: phylogeny of the Ceratocanthinae (Coleoptera: Hybosoridae) inferred from adult morphology and origin of a unique body enrollment coaptation in terrestrial arthropods

Alberto Ballerio[1] & Vasily V. Grebennikov[2]

[1] Viale Venezia 45, I-25123 Brescia, Italy; Alberto Ballerio [alberto.ballerio.bs@aballerio.it] — [2] Canadian Food Inspection Agency, Ottawa Plant Laboratory, KW Neatby Bldg., 960 Carling Ave, Ottawa, Ontario K1A 0Y9, Canada; Vasily V. Grebennikov [vasily.grebennikov@inspection.gc.ca]

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Abstract

Results of a phylogenetic analysis of all but one of the 43 recognized extant genera of Ceratocanthinae scarab beetles (Coleoptera: Hybosoridae) are reported. The analysis is based on 97 parsimony informative adult morphological characters scored for 61 ingroup and 10 outgroup terminals. This pantropical subfamily of some 366 species is remarkable for the adults' ability to pack their body into a tight sub-sphere using interlocking exoskeletal structures (= enrollment coaptations). An overview on known biological and fossil data on the subfamily is provided, as well as a list, an overview, a key and illustrations of adults of all Ceratocanthinae genera. The phylogenetic analysis supports a monophyletic Ceratocanthinae (bootstrap 76%) and a basal dichotomy between pantropical Ceratocanthini (97%) and the South American clade (98%) of Scarabatermitini. Ivieolini renders Scarabatermitini paraphyletic. Another well supported internal clade is the *Philharmostes* group of seven Afrotropical genera (85%). All other inclusive clades detected in the analysis have low bootstrap support (51–65%), likely indicative of limitations of the adult morphological dataset. We also provide a detailed distribution map of Ceratocanthinae and hypothesize about the South American origin of the subfamily, and that of its two subclades: Ceratocanthini and Scarabatermitini + Ivieolini. Overall this paper summarizes all existing information on Ceratocanthinae beetles in an evolutionary context in order to facilitate and stimulate further research on this subfamily.

Key words

Ceratocanthini, Ivieolini, Scarabatermitini, conglobation, coaptation, key to genera, distribution, fossils, biogeography.

1. Introduction

Ceratocanthinae are a pantropical subfamily of Hybosoridae (Coleoptera: Scarabaeoidea) comprising some 366 described species. Most species are easily recognized by the remarkable ability of the adult to form a nearly perfect ball. This, along with some other shared similarities, led to an early recognition of Ceratocanthinae as a natural group, although for a long time it was treated as a family distinct, but allied with, Hybosoridae. Phylogenetic placement of Ceratocanthinae within Hybosoridae (but not monophyly of the former) was first demonstrated by Grebennikov et al. (2004) using 57 larval characters from 17 Hybosoridae (of which 11 were Ceratocanthini) and nine outgroup terminals. Ocampo (2006) used 117 adult morphological characters of 40 Hybosoridae terminals (of which two were Ceratocanthini) to corroborate monophyly of Ceratocanthinae, as well as that of four other extant subfamilies: Anaidinae, Hybosorinae, Liparochrinae and Pachyplectrinae. Ocampo & Hawks (2006)

Fig. 1. Ceratocanthinae, live beetles. **A**: *Ceratocanthus* sp., Belize; **B**: *Eusphaeropeltis* sp., China; **D**: *Ebbrittoniella gestroi*, Malaysia; **C**: *Philharmostes* sp., Madagascar; **E**: *Madrasostes agostii*, Malaysia.

used a 2061 bp alignment of 28S and 18S rDNA for 36 terminals, of them 20 belonging to Hybosoridae (seven of them being Ceratocanthini), to recover all extant Hybosoridae subfamilies as monophyletic, and Ceratocanthinae forming a weakly supported clade (78% bootstrap) with Liparochrinae. Smith et al. (2006) extended the same rDNA dataset to include 600 (28S) and 150 (18S) Scarabaeoidea terminals to corroborate the placement of Ceratocanthinae within Hybosoridae. The subfamily comprises three tribes (Howden & Gill 2000): Ceratocanthini, Ivieolini and Scarabatermitini, whose monophyly and interrelationships have never been cladistically tested. The former includes 38 genera and > 95% of the extant species, while the latter two are comprised of five genera and eight bizarre species restricted to South America.

As highlighted above, adult Ceratocanthinae are best known by their ability to conglobate (Fig. 1A–E). This ability to roll into a tight compact structure probably has anti-predatory and physiological (moisture retention, thermoregulation) advantages. Some members of the subfamily are capable of forming a subsphaerical structure, with elytra, pronotum, head, and all six tibiae forming a tightly connected external surface. These structures interlock with each other by means of grooves and corresponding ridges. The degree of mechanical coaptation is so high, that unrolling a dead Ceratocanthini specimen requires significant practice and some understanding of the body mechanics. Other Ceratocanthini species are less morphologically committed, although they can still have their head and pronotum markedly deflexed in a similar manner to three other Coleoptera line-

ages exhibiting parallel morphological adaptations. This ball-forming capacity among the non-Ceratocanthini beetles is restricted, however, to bending the pronotum and head in the ventral direction and pressing the ventral side of the latter against the meso- (Cybocephalidae) and metathorax (Clambidae, Leiodidae: *Agathidium* Panzer, 1797), thus leaving at least some apical abdominal segments partly exposed. Moreover, in Ceratocanthinae, the tibiae of all six legs participate in forming the external hard surface of the sphere, unlike in other beetles. The very different, and perhaps no less weirdly shaped, Ivieolini and Scarabatermitini are incapable of deflexing their body, let alone forming a tight ball. This could be a reversal, since some non-Ceratocanthinae members of Hybosoridae (e.g., *Liparochrus*) have at least some capacity of body deflexion.

The subfamily Ceratocanthinae has a mainly pantropical distribution (Fig. 2), with only a few genera and species recorded from the adjacent parts of the northern and southern temperate regions (Ocampo & Ballerio 2006 and unpublished data). The subfamily is particularly diverse in the New World with 16 genera and at least 170 species recorded from Chile to Canada. Only three species occur north of Mexico, mainly in eastern North America, with their distributions extending west to western Nebraska and north to Ontario. Many species occur in Central America (including the Caribbean, where the endemic genus *Nesopalla* is found) and in South America, south to northern Argentina. Chile and the Valdivian temperate forests that intrude into Argentina have the endemic genus *Martinezostes* and the likely congeneric *"Germarostes" posticus* (Germar, 1843). Ceratocanthinae are abundant in suitable habitats in the Afrotropical region (including Madagascar), with 17 genera and 86 species recorded from southern Burkina Faso and Ethiopia in the north to the Eastern Cape province of South Africa in the south. Unpublished insular records exist for Sao Tomé and Annobon Island. One species is known from the Comoros, while many species, all of them endemic, occur throughout Madagascar (excepting the dry South-West). In Asia and Australasia Ceratocanthinae are represented by 10 genera and 110 species. The subfamily record from Micronesia is probably due to a recent human introduction (Cartwright & Gordon 1971). Finally Paulian (1991) recorded an unidentified species from New Caledonia, which is, however, of doubtful veracity. Local faunas of Ceratocanthinae might be relatively diverse. The highest species richness was recorded for rainforests, e.g., the Belvédère de Saül forest in French Guiana (38 species, Ballerio 2014) and Ulu Gombak forest in Peninsular Malaysia (18 species, Ballerio & Maruyama 2010). Members of Ceratocanthinae occur also in temperate moist forests of North America and Chile, in seasonal tropical and subtropical forests all over their distribution range, in woodlands (Miombo woodlands in Africa and open eucalypt woodlands in Queensland, Australia), in savannah habitats (such as the Brazilian Cerrado) and in coastal deserts (*Germarostes posticus* in the Atacama desert, Alfaro et al. 2014).

Very little is known about Ceratocanthinae life history and immature stages. Larvae are markedly elongate and have been described for representatives of seven genera (Grebennikov et al. 2004). Larvae were collected together with adults in termite nests (*Pterorthochaetes*, *Cyphopisthes*, *Paulianostes* and *Madrasostes*) and under bark (*Pterorthochaetes*). Pupae of some species have support projections (Grebennikov et al. 2002), which suggest the existence of a pupal cell. Adults of many species of Ceratocanthinae are found in termite nests. Scarabatermitini (and probably Ivieolini) seem to be adapted to life with termites such as *Neocapritermes* Holmgren, 1912, *Cornitermes* Holmgren, 1906 and *Procornitermes* Emerson, 1949, which involves the development of several morphological traits like physogastry and depigmentation (Silvestri 1940; Howden 1973). Possible termitophily of Ceratocanthini is, however, not well understood or corroborated with data. The capability to roll the body into a sphere has possible defensive purposes and might have evolved to support a lifestyle in the hostile environment of a termite nest. Several records of Ceratocanthini species found in termite nests of *Coptotermes* Banks, 1919, *Dicuspiditermes* Krishna, 1965, *Hospitalitermes* Holmgren, 1912, *Mastotermes* Froggatt, 1897 and *Nasutitermes* Dudley, 1890 (Ballerio & Maruyama 2010; Iwata et al. 1992; Paulian 1977, 1978) do not provide indications of the exact kind of relationship between the beetles and termites. Iwata et al. (1992) suggested that the beetles might be termitariophilous, i.e. attracted to termite nests. This hypothesis is further corroborated by the observation of *Astaenomoechus* species seemingly being attracted to fragments of arboreal termite nests (Howden & Gill 2000). Ceratocanthini adults have also been found in rotten wood or under bark, sometimes in association with Passalidae beetles (Ohaus 1909; Kon et al. 2014). Adults of *Germarostes aphodioides* (Illiger, 1800) stridulate (Alexander et al. 1963), while larvae of some genera (e.g., *Germarostes*) possess stridulatory organs (Grebennikov et al. 2004). Specimens are often found by sifting forest leaf litter, many of them being flightless. Flightlessness is a relatively common trait within the tribe, affecting about 20% of species. *Germarostes posticus* is often found under stones in arid environments in Chile. Several volant species inhabit the forest canopy (Ballerio & Wagner 2005), mainly its lower part. The canopy habitat is normally linked to adults having bright metallic colours and large eyes (chiefly the genera *Ceratocanthus* and *Eusphaeropeltis*). Canopy dwellers are often found on leaves or by beating dead twigs of bushes (Bates 1887). Adults and larvae of *Ceratocanthus aeneus* (MacLeay, 1819) have been observed in tree holes (Choate 1987). The feeding habits of Ceratocanthinae are almost entirely unknown. Bates (1887) observed *Germarostes plicatus* (Erichson in Germar, 1843) adults and other species feeding on old "woody boleti" and another species of the same genus "on gall-like excrescences" on the midrib of a leaf. A single observation reports two specimens of *Cloeotus* grazing at night on the underside of a polypore fungus in

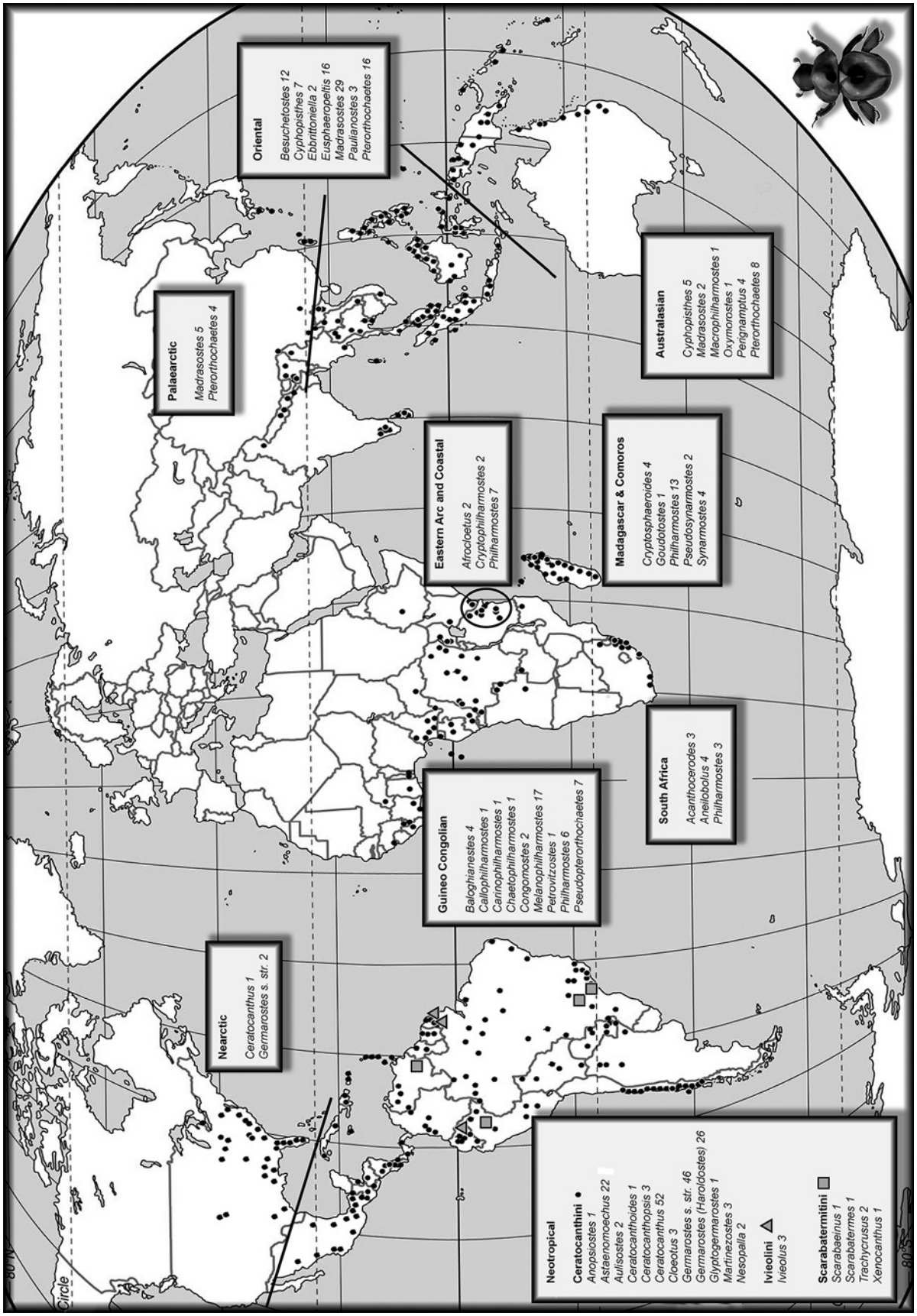


Fig. 2. Ceratocanthinae, global distribution (including unpublished records).

Colombia (Bruce Gill, personal communication). Adults of *Martinezostes* and *Germarostes posticus* are attracted by carrion, fungi and dung, although perhaps it is the moisture, which lures them. The Ceratocanthini mouthparts are quite diverse, suggesting diverse feeding habits. A common trait is the presence of a large membranous

galea covered by long dense setae (Fig. 11V–Y), usually ending with a spatulate/comb-like apex, which suggests that filtering plays an important role in the feeding process.

Although twenty-two fossil Hybosoridae species are known (http://edna.palass-hosting.org/ accessed on 01.05.2015; Yan et al. 2012a,b), establishing a minimal age of this family, or that of its subordinate clades such as Ceratocanthinae is not a straightforward matter. Only recently (Ocampo 2006) the first phylogenetic analysis of Hybosoridae provided a list of adult morphological synapomorphies to be used for fossil attribution. The assignment of fossils in question to Hybosoridae was not made by either cladistic analysis (as done for other insect groups, e.g. Cassis & Schuh 2010; Solodovnikov et al. 2013; Parker & Grimaldi 2014) nor by citing known clade synapomorphies detected on the fossil (as done for Hydrophiloidea beetles by Fikáček et al. 2012). Instead, they were associated with the family by listing "diagnostic" phenotypic features (Yan et al. 2012a; Kirejtshuk et al. 2011). In our opinion, these fossils should be critically re-examined before being used to provide minimal clade ages. Below we cite published fossil information without any attempt to verify the accuracy of the original taxonomic assessment.

The oldest fossil attributed to Ceratocanthinae is *Mesoceratocanthus tuberculifrons* Nikolajev et al., 2010. It is known from a poorly preserved two-dimensional impression of the Lower Cretaceous of Inner Mongolia. The fossil does not show the beetle's ability to deflect its body and was placed in Hybosoridae based on the alleged presence of a few diagnostic characters: (1) prominent mandibles and labrum; (2) elongate antennal club consisting of three antennomeres; (3) contiguous pro- and mesocoxae. It was attributed to Ceratocanthinae based on three features: (4) elongate antennal club; (5) lack of transverse carinae on meso- and metatibiae and (6) tarso-tibial junction proximal to the anterior tibial tooth. The fossil's further attribution to Ivieolini was based three characters: (7) elongate body; (8) deep V-shaped groove posteriorly on the pronotum and (9) labrum about a quarter as wide as head. The only other Ceratocanthinae fossils are those from Dominican amber dating between Upper Eocene to Lower Miocene and likely belonging to the extant genus *Germarostes* (if the latter is monophyletic, see Results below), including *"Ceratocanthus" emarginatus* Poinar, 2014. Such scarce and unevenly distributed geological records of the subfamily are inadequate to detect the minimal time of the clade's origin. No more conclusive would be an attempt to date Ceratocanthinae by using the time of origin of its sister group. The latter is only preliminary hypothesized (Ocampo & Hawks 2006) and remains uncertain. Among the non-Ceratocanthinae Hybosoridae the oldest fossils are the Upper Jurassic *Jurahybosorus* Nikolajev, 2005 and *Protohybosorus* Nikolajev, 2010, although their phylogenetic placement within Hybosoridae: Hybosorinae is open to debate. Cretaceous fossils include representatives of one extinct (Mimaphodiinae, Nikolajev 2007) and three extant Hybosoridae subfamilies (Anaidinae: *Protanaides sibericus* Nikolajev, 2010; Liparochrinae: *Libanochrus calvus* Kirejtshuk et al., 2011; Hybosorinae: *Fortishybosorus ericeusicus* Yan et al., 2012b and *Pulcherhybosorus tridentatus* Yan et al., 2012a).

For decades knowledge of Ceratocanthinae beetles was accumulated by means of species descriptions, taxonomic revisions of genera, biological records, larval descriptions or surveys of local faunas. Comprehensive revisions for major biogeographical regions were published for South America (Paulian 1982), New World (Howden & Gill 2000), continental Africa (Paulian 1977), Madagascar (Paulian 1979), and Asia and Oceania (Paulian 1978). Phylogenetic hypotheses, apart from the mere assumption of the group's monophyly, have never been addressed using cladistic methods. The main purpose of this paper is to bring together information on Ceratocanthinae beetles in a phylogenetic framework and to provide a single reference for those who want to know more about these peculiar beetles. More specifically, we have eight goals: 1. to provide an overview of the relationship, biology, distribution and fossil record of the subfamily; 2. to list, comment on, and illustrate by exemplars from all 43 currently recognized extant Ceratocanthinae genera; 3. to undertake a phylogenetic analysis based on adult morphological characters in order to test monophyly of the subfamily and its tribes, and search for previously unrecognised internal clades; 4. to highlight cases where current taxonomic consensus disagrees with our phylogenetic findings; 5. to illustrate and document diversity of adult morphological structures; 6. to trace the evolution of conglobation and enrollment coaptation in Ceratocanthinae; 7. to shed light on the geographical aspect of the present-day pantropical distribution of the subfamily; and 8. to provide an adult-based identification key to genera.

2. Extant genera of Ceratocanthinae

Below we list all 43 currently recognized extant Ceratocanthinae genera arranged in three tribes: Ceratocanthini (38 genera), Ivieolini (monogeneric) and Scarabatermitini (four genera). For each genus we provide taxonomic and biological information: type species, type species designation (only when not fixed by original designation or by monotypy), the number of named species, their distribution, a short diagnostic description of the adult, and a brief comment on biology. Unless otherwise mentioned, each genus is believed to be monophyletic. These hypotheses have not yet been explicitly tested, but are accepted following the historical taxonomic arrangement, which, in turn, was based on a number of shared attributes, such as adult similarity or coherent distribution (i.e. without inexplicable gaps).

Fig. 3. Ceratocanthinae, habitus. **A**,**B**,**D**,**E**: Scarabatermitini; **C**: Ivieolini, **F**–**L**: Ceratocanthini. **A**: *Scarabaeinus termitophilus*, Brazil, 5.6 mm; **B**: *Scarabatermes amazonensis*, Colombia, 4.1 mm; **C**: *Ivieolus brooksi*, French Guiana, 4.0 mm; **D**: *Trachycrusus lescheni*, Ecuador, 4.9 mm; **E**: *Xenocanthus* sp., Colombia, 3.2 mm; **F**: *Germarostes* (*Germarostes*) *oberthueri*, French Guiana, 3.9 mm; **G**: *Aulisostes* sp., Brazil, 5.0 mm; **H**: *Germarostes* (*Germarostes*) *pullus*, Ecuador, 3.8 mm; **I**: *Aneilobolus lawrencei*, South Africa, 3.0 mm; **J**: *Acanthocerodes* sp., South Africa, 4.2 mm; **K**: *Germarostes* (*Germarostes*) *posticus*, Chile, 4.1 mm; **L**: *Martinezostes fortecostatus*, Chile, 4.5 mm.

Tribe Ceratocanthini Martínez, 1968

Acanthocerodes Péringuey, 1901 (Fig. 3J) — Type species: *Acanthocerodes singularis* Péringuey, 1901. — Three medium-sized flightless species from South Africa. Head with genal canthus not extending through eyes, first antennomere of antennal club with outer surface almost completely glabrous, dorsum black and convex, with simple striae and/or punctures. In forest leaf litter.

Afrocloetus Petrovitz, 1968 (Fig. 6B) — Type species: *Afrocloetus gibbosus* Petrovitz, 1968. — Two large or medium-sized flightless species from Tanzania (Eastern Arc Mountains and coastal forests). Genal canthus indistinct, first antennomere of antennal club with outer surface almost completely glabrous, dorsum with tubercles and/or carinae. Adults resemble those of the genus *Congomostes* from the Guineo-Congolian forests. In forest leaf litter.

Aneilobolus Hesse, 1948 (Fig. 3I) — Type species: *Aneilobolus lawrencei* Hesse, 1948. — Four small or medium-sized flightless species from South Africa. Head with genal canthus indistinct, first antennomere of antennal club with outer surface almost completely

Fig. 4. Ceratocanthinae-Ceratocanthini, habitus. **A**: *Germarostes* (*Haroldostes*) *diffundus*, Argentina, 4.5 mm; **B**: *Ceratocanthoides undatus*, French Guiana, 5.0 mm; **C**: *Germarostes (Germarostes) degallieri*, French Guiana, 6.4 mm; **D**: *Germarostes (Germarostes) aphodioides*, U.S.A., 5.2 mm; **E**: *Germarostes (Germarostes) globosus*, U.S.A., 5.0 mm; **F**: *Germarostes (Haroldostes) senegalensis*, French Guiana, 5.0 mm; **G**: *Ceratocanthopsis fulgida*, French Guiana, 4.6 mm; **H**: *Ceratocanthus amazonicus*, French Guiana, 6.3 mm; **I**: *Ceratocanthus* sp., French Guiana, 4.5 mm; **J**: *Congomostes janssensi*, Zambia, 5.9 mm; **K**: *Eusphaeropeltis* sp., Malaysia, 4.6 mm; **L**: *Paulianostes panggoling*, Brunei, 6.3 mm.

glabrous, pronotum with posterior and anterior margins raised, dorsum black and convex, with striae and punctures. In forest leaf litter.

Anopsiostes Paulian, 1982 (Fig. 6J) — Type species: *Anopsiostes punctatus* Paulian, 1982. — One small volant species from Ecuador and Peru. Superficially resembles *Astaenomoechus*, but distinct by wing venation, shape of aedeagus, antennae (first antennomere of antennal club with outer surface almost completely glabrous) and mouthparts (mandibles are remarkably elongate). In forest leaf litter.

Astaenomoechus Martínez & Pereira, 1959 (Fig. 6K,L) — Type species: *Sphaeromorphus hospes* Wasmann, 1902. — Thirty one variably sized species from Central and South America. First antennomere of antennal club with outer surface setose, mandibles pointed and sharp, labrum distally depressed. Most species are volant and collected in forest understory by flight intercept traps. Might be biologically linked to arboreal termite nests.

Aulisostes Howden & Gill, 2000 (Fig. 3G) — Type species: *Aulisostes pseudoparadoxus* Howden & Gill, 2001 (designated by Howden & Gill 2001). — Two medium-sized flightless species from Colombia and Brazil. Dorsum black and convex, usually smooth with a few punctures and tubercles and elytral apex thickened. In forest leaf litter.

Baloghianestes Paulian, 1968 (Fig. 7C,D) — Type species: *Baloghianestes lissoubai* Paulian, 1968. — Four convex and setose small-sized flightless species from Cameroon, Congo and Gabon. Fore tibiae arcuate, genal canthus indistinct. Although recovered as a

Fig. 5. Ceratocanthinae-Ceratocanthini, habitus. **A**: *Cyphopisthes* sp., Malaysia, 3.8 mm; **B**: *Ebbrittoniella gestroi*, Malaysia, 5.5 mm; **C**: *Pterorthochaetes insularis*, Malaysia, 5.6 mm; **D**: *Madrasostes sculpturatum*, Malaysia, 5.6 mm; **E**: *Madrasostes clypeale*, Malaysia, 3.5 mm (photo by Munetoshi Maruyama); **F**: *Madrasostes mirificum*, Malaysia, 3.7 mm; **G**: *Macrophilharmostes major*, New Guinea, 5.0 mm; **H**: *Madrasostes* cf. *granulatum*, New Guinea, 4.0 mm; **I**: *Perignamptus* sp., New Guinea, 4.0 mm; **J**: *Oxymorostes riedeli*, New Guinea, 2.6 mm; **K**: *Besuchetostes* sp., Sri Lanka, 3.5 mm; **L**: *Besuchetostes jaccoudi*, Malaysia, 5.2 mm.

clade in the present analysis, the genus is likely non-monophyletic (probably paraphyletic with respect to some *Philharmostes*). In forest leaf litter.

Besuchetostes Paulian, 1972 (Fig. 5K,L) — Type species: *Besuchetostes taprobanae* Paulian, 1972. — Eleven species from southern India and Sri Lanka; Malaysian species probably belong to *Madrasostes*. Small and medium-sized flightless beetles. Genal canthus indistinct, pronotum with posterior median swelling, dorsum often with strong carinae and sculpturing. Likely monophyletic if excluding *B. jaccoudi* Paulian, 1977 (Fig. 8B–D) and *B. howdeni* Paulian, 1979. In forest leaf litter.

Callophilharmostes Paulian, 1968 (Fig. 7F) — Type species: *Philharmostes fleutiauxi* Paulian, 1943. — One medium-sized volant species from the Guineo-Congolian rainforests block. Fore tibiae arcuate, genal canthus complete, antennae with 7 antennomeres, recognizable by characteristic dorsal sculpturing and by a large trichome on head. In rainforests, collected by fogging or beating.

Carinophilharmostes Paulian, 1968 (Fig. 7E) — Type species: *Philharmostes vadoni* Paulian, 1937. — Monotypic genus endemic to the Guineo-Congolian rainforests block. Body medium-sized. Fore tibiae arcuate, genal canthus complete, dorsum with characteristic sculpturing of tubercles. Collected by canopy fogging or by leaf beating, as well as by sifting leaf litter or dead wood.

Ceratocanthoides Paulian, 1982 (Fig. 4B) — Type species: *Acanthocerus undatus* Petrovitz, 1973. — One medium-sized and volant species from the northern

Fig. 6. Ceratocanthinae-Ceratocanthini, habitus. **A**: *Nesopalla iviei*, Virgin Islands, 3.7 mm; **B**: *Afrocloetus* sp., Tanzania, 5.9 mm; **C**: *Cloeotus latebrosus*, South America, 6.1 mm; **D**: *Synarmostes* sp., Madagascar, 4.8 mm; **E**: *Pseudosynarmostes mitsinjo*, Madagascar, 4.0 mm; **F**: *Cryptosphaeroides hystrix*, Madagascar, 3.0 mm; **G**: *Goudotostes* sp., Madagascar, 5.8 mm; **H**: *Melanophilharmostes* sp., Uganda, 4.0 mm; **I**: *Pseudopterorthochaetes endroedyi*, Cameroon, 3.9 mm; **J**: *Anopsiostes punctatus*, Ecuador, 3.1 mm; **K**: *Astaenomoechus setosus*, French Guiana, 5.9 mm; **L**: *Astaenomoechus criberrimus*, French Guiana, 5.8 mm.

part of South America. Very similar to, and likely nested within, *Germarostes*, differing from it by the pronotal sculpturing made of transverse wrinkles. In forest leaf litter.

Ceratocanthopsis Paulian, 1982 (Fig. 4G) — Type species: *Acanthocerus fulgidus* Martínez, 1967. — Three small species from the northern part of South America. A poorly-defined genus, probably should be synonymized with *Ceratocanthus* (from which differs only by the number of antennomeres). In rainforests, *C. fulgida* is probably a canopy dweller.

Ceratocanthus White, 1842 (Fig. 4H,I) — Type species: *Acanthocerus aeneus* MacLeay, 1819 (designated by Martínez 1968). — Fifty-three variously-sized volant species from tropical and temperate regions of the Americas. Dorsum convex, in most cases with metallic color and large eyes. Meso- and metatarsi can be folded along the longitudinal axis of tibiae. Closely related to, and perhaps paraphyletic with respect to, *Ceratocanthopsis*. In forests, probably canopy dwellers.

Chaetophilharmostes Paulian, 1977 (Fig. 7L) — Type species: *Philharmostes chevalieri* Paulian, 1937. — One medium-sized volant species from the Guineo-Congolian region. Fore tibiae arcuate, genal canthus complete, dorsal setation present. In forests and in termite nests.

Cloeotus Germar, 1843 (Fig. 6C) — Type species: *Cloeotus latebrosus* Germar, 1843 (designated by Mar-

tínez 1968). — Three medium-sized or large flightless species from the northern part of South America. Genal canthus indistinct, head subpentagonal, meso- and metatibiae relatively thick, dorsum with strong sculpturing. Known by very few specimens mostly collected in the 19th century. Biology unknown.

Congomostes Paulian, 1968 (Fig. 4J) — Type species: *Congomostes baloghi* Paulian, 1968. — Two volant and one flightless species from the Congo basin (DRC, Cameroon, Zambia). Large beetles, dorsum black, genal canthus visible and incomplete, first antennomere of antennal club with outer surface almost completely glabrous; similar to the East African *Afrocloetus*. In forest leaf litter; volant species attracted by light.

Cryptophilharmostes Ballerio, 2000 (Fig. 7A,B) — Type species: *Cryptophilharmostes mahunkai* Ballerio, 2000. — Two small flightless species from Tanzania (Eastern Arc Mountains and coastal forests). Fore tibiae arcuate, genal canthus indistinct, head subrectangular, dorsum with complex sculpturing (tubercles and/or carinae). In forest leaf litter.

Cryptosphaeroides Ballerio, 2009 (Fig. 6F) — Type species: *Cryptosphaeroides hystrix* Ballerio, 2000. — Four small flightless species from Madagascar. Antennae with pedicel strongly bent inwards, body setose, parameres strongly asymmetrical. In forest leaf litter.

Cyphopisthes Gestro, 1898 (Fig. 5A) — Type species: *Synarmostes amphicyllis* Sharp, 1875. — Twelve small species found from India to Queensland, Australia; either volant or flightless. Labrum truncate, mesotibiae elongate, humeral callus indistinct, pronotum regularly convex. Species externally very similar to each other (except for *Cyphopisthes inexpectatus* Paulian, 1981). Monophyletic if excluding *C. inexpectatus*, which likely belongs to the *Perignamptus* generic group as defined in Ballerio (2009). In rainforests and woodlands, sometimes with termites.

Ebbrittoniella Martínez, 1962 (Fig. 5B) — Type species: *Acanthocerus ignitus* Westwood, 1883. — Two medium-sized volant species from south East Asia (Sundaic region). Dorsum metallic, labrum truncate, pronotum regularly convex, mesotibiae relatively short and wide. In rainforests, adults found by beating leaves or in window traps.

Eusphaeropeltis Gestro, 1898 (Fig. 4K) — Type species: *Synarmostes aurora* Lansberge, 1887. — Sixteen small to medium-sized volant species from south East Asia reaching northwards to Southern China. Dorsum brightly metallic, elytra in lateral view without strong development of apical portion. Species externally similar to each other, except for *E. sabah* Paulian, 1989 (which belongs to the *Perignamptus* generic group as defined in Ballerio 2009). Likely monophyletic, if excluding *E. sabah*. In rainforests, probably canopy dwellers, also in termite nests.

Germarostes Paulian, 1982 (Figs. 3F,H,K, 4A,C,D,E,F) — Type species: *Melolontha aphodioides* Illiger, 1800. — Seventy-one variously-sized and mainly volant species occurring from Canada to Argentina. Species with diverse morphology and forming two poorly-defined subgenera: *Germarostes* s.str. and *Haroldostes* Paulian, 1982. Likely non-monophyletic. Biology diverse, in forests, in savannah, in the canopy, in leaf litter, in rotten wood or under bark of trees, sometimes in association with Passalidae beetles.

Glyptogermarostes Ocampo & Ballerio, 2006 (Fig. 8A) — Type species: *Glyptopterus oberthueri* Paulian, 1982. — This monotypic genus (the name is a recent replacement name for *Glyptopterus* Paulian, 1982) is the only one not included in our analysis, being known from a single Brazilian specimen. Possibly an aberrant *Germarostes*, characterized by strong dorsal sculpturing. Biology unknown.

Goudotostes Paulian, 1979 (Fig. 6G) — Type species: *Acanthocerus scabrosus* Laporte, 1840. — One small to medium-sized flightless species from Madagascar. Antennae with pedicel strongly bent inwards, pronotum with posterior and anterior margins raised, dorsum with carinae and/or tubercles, parameres strongly asymmetrical. In forest leaf litter.

Macrophilharmostes Paulian, 1978 (Fig. 5G) — Type species: *Cyphopisthes major* Paulian, 1975. — One medium-sized flightless species from New Guinea. Probably congeneric with *Perignamptus*. In forest leaf litter.

Madrasostes Paulian, 1975 (Fig. 5D,E,F,H) — Type species: *Madrasostes nigrum* Paulian, 1975. — Thirty-four small to medium-sized mainly flightless species from Asia (India to Sulawesi, northwards to Japan; New Guinean species likely congeneric with *Perignamptus*). Externally diverse and likely non-monophyletic. Mandible with strongly developed mesal brush, mandibular base with large ventral pore, labial palpi with palpomere three swollen and strongly widened compared to other palpomeres. In forests, in leaf litter or in termite nests.

Martinezostes Paulian, 1982 (Fig. 3L) — Type species: *Acanthocerus asper* F. Philippi, 1859. — Three medium-sized flightless species from Chile and Argentina. Body black, convex, head with genal canthus developed, first antennomere of antennal club with outer surface almost completely glabrous. Likely monophyletic, if including *Germarostes posticus*. Most variable biologically with specimens found in such habitats as the Atacama coastal desert and cool forests of northern Patagonia. Under stones, in forest leaf litter, under carrion, mushrooms or dung.

Melanophilharmostes Paulian, 1968 (Fig. 6H) — Type species: *Philharmostes zicsii* Paulian, 1968. — Seventeen small and mainly volant species from the Afrotropical region (Burkina Faso to South Africa). Black to brown beetles, with homogeneous morphology. Genal canthus complete, fore tibiae straight. Closely related to *Pseudopterorthochaetes*, while reciprocal monophyly of both is questionable. In forest leaf litter, in savannah and in termite nests.

Fig. 7. Ceratocanthinae-Ceratocanthini, habitus. **A**: *Cryptophilharmostes merkli*, Tanzania, 4.2 mm; **B**: *Cryptophilharmostes mahunkai*, Tanzania, 4.3 mm; **C**: *Baloghianestes lissoubai*, Cameroon, 4.0 mm; **D**: *Baloghianestes oribatidiformis*, Cameroon, 4.0 mm; **E**: *Carinophilharmostes vadoni*, Uganda, 5.9 mm; **F**: *Callophilharmostes felutiauxi*, Uganda, 5.9 mm; **G**: *Philharmostes grebennikovi*, Tanzania, 2.1 mm; **H**: *Philharmostes* sp., South Africa, 2.3 mm; **I**: *Petrovitzostes guineensis*, Gabon, 4.5 mm; **J**: *Philharmostes basicollis*, Madagascar, 5.0 mm; **K**: *Philharmostes badius*, Uganda, 2.3 mm; **L**: *Chaetophilharmostes chevalieri*, Guinea, 5.8 mm.

Nesopalla Paulian & Howden, 1982 (Fig. 6A) — Type species: *Nesopalla iviei* Paulian & Howden, 1982. — Two small flightless species from Puerto Rico and the Virgin Islands. Very convex body, with genal canthus indistinct and labrum distally depressed. In forest leaf litter.

Oxymorostes Ballerio, 2009 (Fig. 5J) — Type species: *Oxymorostes riedeli* Ballerio, 2009. — One small flightless species from New Guinea. Characterized by the wide prothorax having two deep ventral excavations at each side. Closely related to *Perignamptus*, with which it shares similar mouthpart morphology. In forest leaf litter.

Paulianostes Ballerio, 2000 (Fig. 4L) — Type species: *Cyphopisthes georyssoides* Gestro, 1898. — Three medium-sized volant species from south East Asia (Sundaic region). Labrum truncate, pronotum strongly raised anteriorly, humeral callus always well marked, body sometimes covered by large scales. In rainforests, in leaf litter and in termite nests.

Perignamptus Harold, 1877 (Fig. 5I) — Type species: *Perignamptus sharpi* Harold, 1877. — Four small to medium-sized flightless species from New Guinea and adjacent islands. Closely related to *Madrasostes*, with which it shares similar mouthpart morphology. In forest leaf litter.

Petrovitzostes Paulian, 1977 (Fig. 7I) — Type species: *Pterorthochaetes guineensis* Petrovitz, 1968. — One medium-sized volant species from the Guineo-Congolian rainforest block. Fore tibiae arcuate, genal can-

thus complete, antennae with 7 antennomeres. Characterized by the pronotal sculpturing and the dorsum uniformly covered by short thick setae. In rainforests, collected by canopy fogging and by beating leaves.

Philharmostes Kolbe, 1895 (Fig. 7G,H,J,K) — Type species: *Philharmostes aeneoviridis* Kolbe, 1895 (designated by Fairmaire 1899). — Thirty-one small to medium-sized and mainly volant species from the Afrotropical region. Besides Madagascar, the other centers of species richness are the Guineo-Congolian rainforest block, South African forests, the Eastern Arc and coastal forests of Tanzania and Kenya. The subgenus *Holophilharmostes* Paulian, 1968 is poorly-defined. It is morphologically diverse and likely non-monophyletic. Fore tibiae arcuate, genal canthus complete, antennae with 9 antennomeres in most species. Closely related to, and perhaps paraphyletic with other genera, including *Baloghianestes*. In forest leaf litter, in termite nests and in lower canopy.

Pseudopterorthochaetes Paulian, 1977 (Fig. 6I) — Type species: *Pterorthochaetes elytratus* Paulian, 1946. — Seven small and mainly volant species from continental Africa (Guineo-Congolian rainforest block extending southwards to Mozambique). Black to brown, genal canthus complete, fore tibiae straight. A poorly-defined genus likely closely related to *Melanophilharmostes*. In forest leaf litter and in Miombo woodlands.

Pseudosynarmostes Ballerio, 2009 (Fig. 6E) — Type species: *Pseudosynarmostes mitsinjo* Ballerio, 2009. — Two small flightless and sexually dimorphic species from Madagascar with several unusual morphological characters on tibiae, mouthparts, antennae and aedeagus. In termite nests and in forest litter.

Pterorthochaetes Gestro, 1898 (Fig. 5C) — Type species: *Synarmostes gestroi* Harold, 1874. — Twenty-six small to medium-sized volant species from India and Southern China to Queensland, Australia. Morphologically homogenous species are characterized by having 9 antennomeres, spiculiform bursal sclerites. In forest leaf litter, under bark of trees, sometimes in association with Passalidae, or in termite nests.

Synarmostes Germar, 1843 (Fig. 6D) — Type species: *Acanthocerus tibialis* Klug, 1832. — Four small to medium-sized volant or flightless species from Madagascar and Comoros. Apical portion of elytra with several carinae. In forest leaf litter and in termite nests.

Tribe Ivieolini Howden & Gill, 2000

Ivieolus Howden & Gill, 1988 (Fig. 3C) — Type species: *Ivieolus pseudoscutellatus* Howden and Gill, 1988. — Three small to medium-sized volant species from the northern part of South America with depigmented elongate legs and oddly shaped pronotum having a "pseudoscutellum". All known species collected at light or in window traps, sometimes in large numbers. Biology unknown, probably termitophilous.

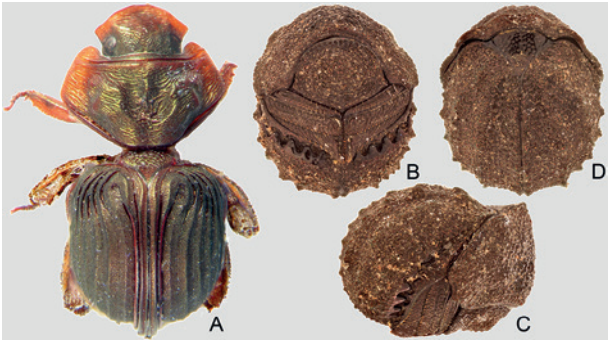


Fig. 8. Ceratocanthinae-Ceratocanthini, habitus. **A**: *Glyptogermarostes oberthueri*, holotype, Brazil, 5.3 mm, the only genus of Ceratocanthinae not represented in our analysis; **B**–**D**: *Besuchetostes jaccoudi*, Malaysia, 4 mm, dorsal (B), lateral (C) and ventral (D).

Tribe Scarabatermitini Nikolajev, 1999

Scarabaeinus Silvestri, 1940 (Fig. 3A) — Type species: *Scarabaeinus termitophilus* Silvestri, 1940. — One small and oddly shaped winged species from Brazil. Clypeus not serrated, pronotum weakly embossed, abdomen with lateral glands. Found with termites.

Scarabatermes Howden, 1973 (Fig. 3B) — Type species: *Scarabatermes amazonensis* Howden, 1973. — One small and oddly shaped winged species from Colombia. Clypeus not serrated, pronotum weakly embossed, abdomen without lateral glands. Found with termites.

Trachycrusus Howden & Gill, 1995 (Fig. 3D) — Type species: *Trachycrusus lescheni* Howden & Gill, 1995. — Two small, volant species from Peru and Ecuador. Morphologically less aberrant than the rest of the tribe, having meso- and metatibiae flattened and widened, in contrast with the rest of the subfamily. Clypeus weakly serrated. Specimens taken in flight interception traps. Biology unknown, probably termitophilous.

Xenocanthus Howden & Gill, 1988 (Fig. 3E) — Type species: *Xenocanthus singularis* Howden & Gill, 1988. — One small and oddly shaped volant species from Venezuela and Colombia. Clypeus distinctly serrated, pronotum strongly embossed with sides of pronotum tumid anteriorly and posteriorly. Collected from a flight interception trap. Biology unknown, probably termitophilous.

3. Material and methods

Due to the scarcity, inapplicability, or unavailability of data, no attempt was made to utilize, for phylogenetic

purposes, characters other than those based on the adult exoskeleton (all listed in Apppendix 1). Three potentially informative sources of adult morphological characters were excluded from the analysis due to the lack of adequate research: the detailed structure of enrollment coaptation interlocking devices, many morphometric characters (shapes), and the internal structure of male genitalia. Pinned adult specimens were assembled from a variety of sources (see Appendix 2), mainly from the collection of the first author. At least one specimen of each sex, if available, was softened in warm water, placed in glycerol and then disarticulated and studied under a dissecting microscope for character scoring. Hind wing venation nomenclature follows Kukalová-Peck & Lawrence (1993). The subfamily Ceratocanthinae (= ingroup) was represented by at least one species (= terminal) from each of its 43 recognized genera and all three tribes. The only unrepresented genus was *Glyptogermarostes*, the single known specimen of which was unavailable (Fig. 8A). We attempted to provide terminals in proportion to the size and diversity of each genus, so speciose genera like *Germarostes*, *Philharmostes* or *Madrasostes* were represented by 8, 5 and 4 terminals, respectively. In total, the matrix contained 61 Ceratocanthinae (= ingroup) terminals, 56 of which were Ceratocanthini. The outgroup consisted of five terminals representing five genera of three other Hybosoridae subfamilies (Anaidinae, Hybosorinae, Liparochrinae), as well as five additional terminals representing Belohinidae, Glaphyridae, Ochodaeidae, Scarabaeidae, and the genus *Orubesa* Reitter, 1895. Belohinidae, Glaphyridae and Ochodaeidae and the genus *Orubesa* were chosen since they have been hypothesised to be closely related to Hybosoridae (e.g. Smith et al. 2006; McKenna et al. 2015; A. Ballerio et al., ongoing work). The trees were consistently rooted on a representative of the distantly related Scarabaeidae.

The resulting matrix contained 71 terminals and 107 adult morphological characters (Table 1) and was assembled in Winclada (Nixon 2002). Ten parsimony-uninformative characters (13, 42, 47, 52, 55, 72, 76, 81, 96, 103) were deactivated, while the remaining 97 characters were activated and marked as unordered and unweighted, thus making no assumptions about character evolution. The matrix was spawned from Winclada to Hennig86 (Farris 1989). A search for the most parsimonious (= shortest) topologies was initiated using the command <mhennig*> (constructing several trees and then applying branch-swapping to each) followed by the command <bb*> (branch-swapping to trees constructed by mhennig* and retaining the shortest trees up to the limits of the computer memory space). The resulting shortest topologies were saved as a tree file by command <tsave> and then opened and further explored in Winclada by applying unambiguous character optimization to individual trees (Fig. 9) or by exporting the data to Nona (Goloboff 1999) for bootstrap analysis with 1000 replications (Fig. 10).

We were specifically interested in tracing the evolution of two morphological and behavioral traits: (a) the capacity to conglobate, and (b) the ability to form a tight sphere by employing enrollment coaptation. While the former is known in at least three other unrelated beetle clades (see Introduction), the latter is the most distinctive feature of most Ceratocanthini and its unique origin is the most likely assumption. Even though all three possibilities (no conglobation; conglobation without enrollment coaptation; conglobation with enrollment coaptation) might perhaps be treated as three ordered states of a single character, we opted to treat them conservatively as two independent binary characters (deflexion absent/present in character 2 and enrollment coaptation absent/present in character 3). To trace their origin, all most parsimonious individual trees were opened in Winclada and explored with respect for both states of each of these characters using the "Character Diagnoser" tool and the option "unambiguous optimisation".

Photographs were taken by the first author unless otherwise stated, with a Canon Eos D5 MII with a macro objective MP 65 mm, photos were then mounted with the Zerene Stacker software and cleaned and unmasked using photo processing software. Drawings were made by Mario Toledo (Parma, Italy), unless otherwise stated. SEMs were obtained with a Zeiss EVO 40 XVP Scanning Electron Microscope at MUSE (Trento, Italy) after gold coating.

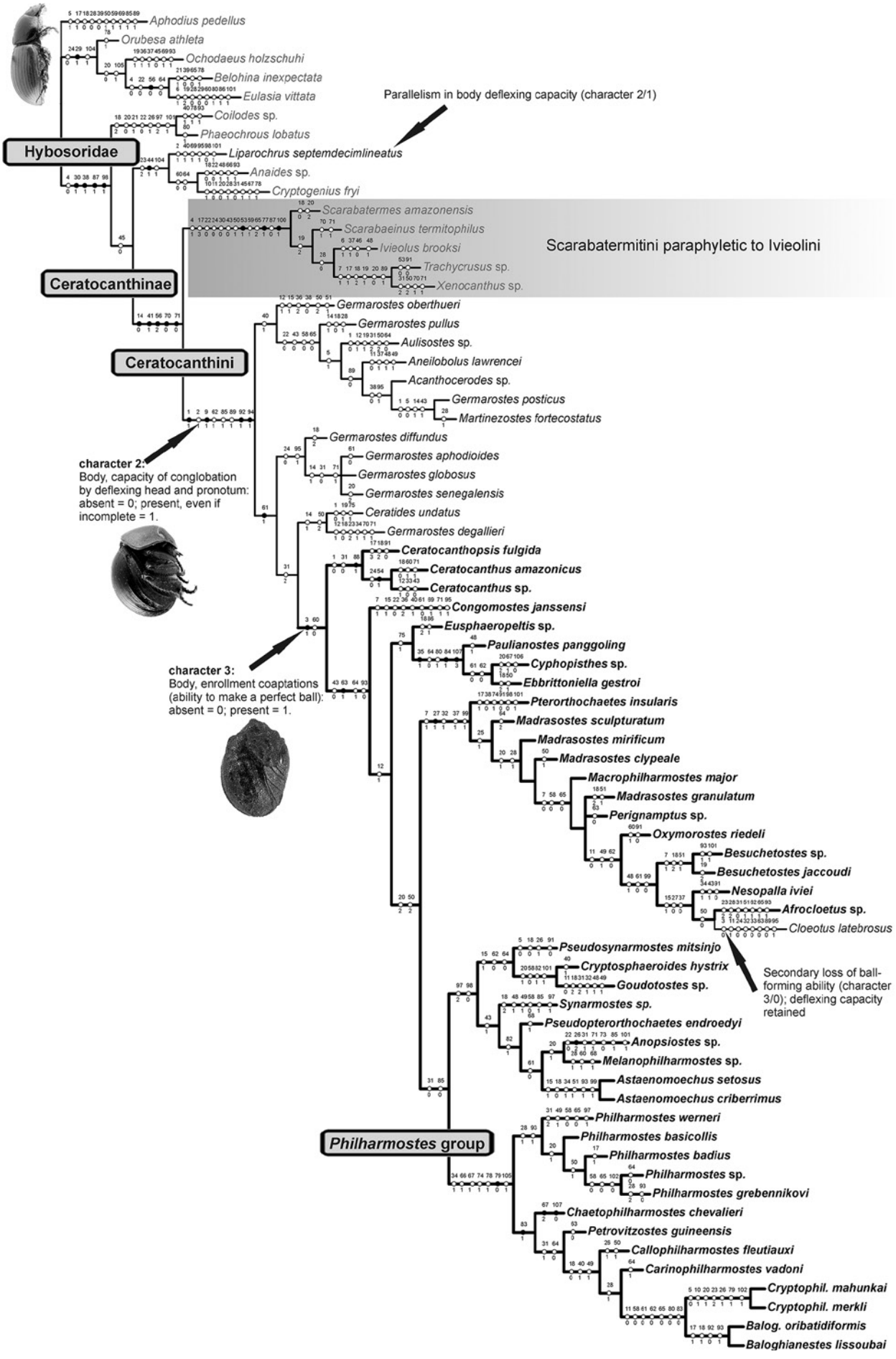
4. Results

The phylogenetic analysis resulted in an overflow of 1343 shortest trees, each with the length of 474 steps, consistency index of 0.24 and retention index of 0.69. A randomly selected tree (= first among output trees) with unambiguously optimized characters shown on internodes is depicted in Fig. 9, while the bootstrapping consensus topology is shown on Fig. 10.

The subfamily Ceratocanthinae consistently emerged as an internal clade (bootstrap support 76%) of a monophyletic Hybosoridae (Fig. 10). Three other inclusive clades containing five or more ingroup terminals were recovered (Fig. 10): Scarabatermitini + Ivieolini (98%), Ceratocanthini (97%) and *Philharmostes* group of seven genera (85%). All other inclusive clades had low bootstrap support (51–65%) and were judged as unreliable (Fig. 10).

Below we list unambiguous and ambiguous (* = fast, ** = slow optimization) synapomorphies for each of four strongly supported (bootstrap > 75%) Ceratocanthinae clades containing five or more terminals. Character number and synapomorphic state (as in Appendix 1) are given in brackets and separated by a slash, followed after a semicolon by character's consistency and retention indices separated by an n-dash.

Ceratocanthinae: labrum and clypeus in lateral view not on the same plane (8/1**; 50–80); fore margin of head


Aphodius pedellus
Orubesa athleta
Ochodaeus holzschuhi
Belohina inexpectata
Eulasia vittata
Coilodes sp.
Phaeochrous lobatus
Hybosoridae
Liparochrus septemdecimlineatus
Anaides sp.
Cryptogenius fryi
Parallelism in body deflexing capacity (character 2/1)
Scarabatermes amazonensis
Scarabaeinus termitophilus
Ivieolus brooksi
Trachycrusus sp.
Xenocanthus sp.
Scarabatermitini paraphyletic to Ivieolini
Ceratocanthinae
Ceratocanthini
Germarostes oberthueri
Germarostes pullus
Aulisostes sp.
Aneilobolus lawrencei
Acanthocerodes sp.
Germarostes posticus
Martinezostes fortecostatus
character 2:
Body, capacity of conglobation by deflexing head and pronotum: absent = 0; present, even if incomplete = 1.
Germarostes diffundus
Germarostes aphodioides
Germarostes globosus
Germarostes senegalensis
Ceratides undatus
Germarostes degallieri
Ceratocanthopsis fulgida
Ceratocanthus amazonicus
Ceratocanthus sp.
Congomostes janssensi
Eusphaeropeltis sp.
Paulianostes panggoling
Cyphopisthes sp.
Ebbrittoniella gestroi
character 3:
Body, enrollment coaptations (ability to make a perfect ball): absent = 0; present = 1.
Pterorthochaetes insularis
Madrasostes sculpturatum
Madrasostes mirificum
Madrasostes clypeale
Macrophilharmostes major
Madrasostes granulatum
Perignamptus sp.
Oxymorostes riedeli
Besuchetostes sp.
Besuchetostes jaccoudi
Nesopalla iviei
Afrocloetus sp.
Cloeotus latebrosus
Secondary loss of ball-forming ability (character 3/0); deflexing capacity retained
Pseudosynarmostes mitsinjo
Cryptosphaeroides hystrix
Goudotostes sp.
Synarmostes sp.
Pseudopterorthochaetes endroedyi
Anopsiostes sp.
Melanophilharmostes sp.
Astaenomoechus setosus
Astaenomoechus criberrimus
Philharmostes group
Philharmostes werneri
Philharmostes basicollis
Philharmostes badius
Philharmostes sp.
Philharmostes grebennikovi
Chaetophilharmostes chevalieri
Petrovitzostes guineensis
Callophilharmostes fleutiauxi
Carinophilharmostes vadoni
Cryptophil. mahunkai
Cryptophil. merkli
Balog. oribatidiformis
Baloghianestes lissoubai

capsule without a distinct angle delimiting genae (14/0; 20–76); prosternal apophyses reaching inner wall of pronotum (41/1; 100–100); lateroventral expansion of prothoracic hypomeron present (46/1**; 25–62); sides of the distal portion of exposed scutellum weakly concave forming acutely pointed apex (56/2; 100–100); posterior projection beyond posterior metatergite edge on metascutal furrow present (57/1**; 50–83); loop of wing vein RP MP 1+2 absent (70/0; 14–68); sinuation of wing vein AA even (71/0; 12–50).

Ceratocanthini: horseshoe-shaped punctures on dorsum present (1/1; 20–80); capacity of body conglobation by deflexing head and pronotum present (2/1; 50–92); vertical dimension of apical clypeal extremity present (9/1; 100–100); extension of sutural stria continuing from elytral apex along elytral lateral sides present (62/1; 16–82); longitudinal carina on ventral side of protibia present (85/1; 20–87); meso- and metatibiae in cross section parallel-sided (89/1; 20–75); inner apical spur in male mesotibiae curved (92/1; 50–93); posterior projection of posterior angle of metatrochanter beyond posterior edge of metafemora present (93/1*; 7–53); metatibiae triangular (94/1; 100–100).

Scarabatermitini + Ivieolini: body depigmented (4/1; 33–71); antenna with eight antennomeres (17/3; 22–36); proximal club antennomere without setae (22/0; 14–64); mandibles not conjunctive (24/0; 14–62); medial notch on anterior edge of labium absent (30/0; 50–88); labium with three palpomeres (33/0*; 16–0); longitudinal crest on prothoracic basisternum absent (43/0; 11–66); anterior pronotal angles broadly rounded (50/1; 16–71); embossed sculpturing on pronotum present (53/1; 50–66); thoracic metaventrite triangular (59/1; 50–80); metathoracic wings short, about 100% elytral length (65/2; 25–68); procoxae vertical (77/1; 100–100); distal emargination on posterior edge of meso- and metafemora absent (87/0; 50–88); abdominal physogastry present (100/1; 100–100).

***Philharmostes* group of genera:** distal longitudinal furrow on labrum present (34/1; 25–81); wing vein MP4 longer than half length of CuA (66/1; 25–70); distal part of wing vein MP4 bent towards CuA (67/1; 50–66); short proximal expansion of vein CuA3+4 present (74/1; 25–66); protibiae curved (78/1; 20–75); dentation on distal third of protibiae outer side absent (79/0; 50–90); basal apophyses on parameres present (102/1*; 25–40); vaginal palpi elongate, at least twice as long as wide (105/1; 50–92); sclerites on bursa copulatrix present (106/1**; 25–81); sclerites on bursa copulatrix spiculelike (107/1**; 100–100).

Body conglobation capacity (character 2/1) evolved without reversals at least twice: once in the common ancestor of Ceratocanthini and again in a member of Hybosoridae: Liparochrinae (Fig. 9). Body enrollment coaptations (= ability to make a perfect ball interlocked with exoskeletal devices, character 3/1) evolved in the common ancestor of a subclade of Ceratocanthini consisting of *Ceratocanthopsis* + *Ceratocanthus* and the sister group, with a single subsequent reversal in *Cloeotus* (Fig. 9).

5. Discussion

5.1. Phylogenetic interpretations

The consensus topology of Ceratocanthinae beetles depicted in Fig. 10 has a number of notable features. Monophyly of the subfamily, although not greatly doubted prior to the analysis, is only moderately corroborated (bootstrap 76%). This can perhaps be attributed to an hypothesis that the subfamily branches into two strongly supported subclades, each having a long list of autapomorphies, including those affecting the entire body architecture. One of these subclades (97%) corresponds to the tribe Ceratocanthini containing > 95% of all Ceratocanthinae species, whose most recent common ancestor likely recently developed a conglobate body. Its sister group (98%) is formed by representatives of the two remaining tribes, Scarabatermitini and Ivieolini, the former paraphyletic with respect to the latter. Unlike the most recent common ancestor of Ceratocanthini acquiring conglobation capacity, that of Scarabatermitini + Ivieolini acquired physogastry. Such dramatically different and profound morphological changes affected the entire adult body architecture of both sister clades and likely obscured at least some of the subfamily synapomorphies, which in turn might account for the relatively low subfamily bootstrap support. Because the analysis design focused on Ceratocanthinae (and not on the more inclusive clade of Hybosoridae), its putative sister group (as depicted in Fig. 10 and consisting of three Hybosoridae genera *Liparochrus*, *Anaides* and *Cryptogenius*) should not be considered phylogenetically tested.

Besides detecting the basal-most dichotomy of monophyletic Ceratocanthinae, our analysis revealed little phylogenetic results. Even though some non-congeneric

← **Fig. 9.** Randomly selected (first) among 1343 most parsimonious trees with unambiguously optimized evolutionary events indicated at respective branches. Solid circles indicate unique synapomorphies, while open circles indicate reversals or homoplasies. Numbers above and below circles are character numbers and states, respectively. Note double origin of capacity of body conglobation by deflexing head and pronotum in *Liparochrus* and again in all Ceratocanthini (character 2/1, terminals in black, including those in **bold**) and single origin of body enrollment coaptation in a subset of Ceratocanthini (character 3/1, branches and terminals in **bold**) with one subsequent loss in *Cloeotus*.

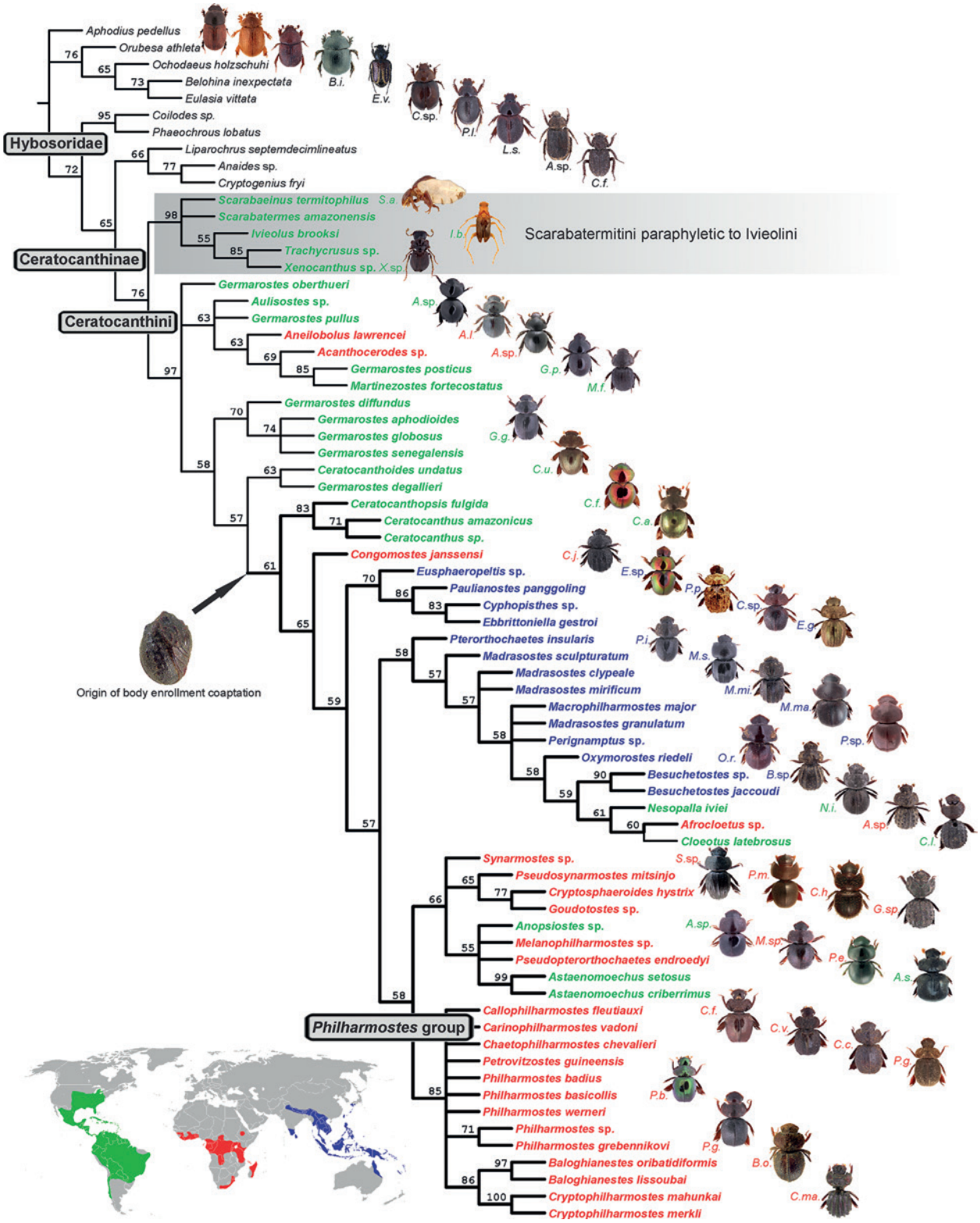


Fig. 10. Bootstrap consensus phylogenetic tree of Ceratocanthinae. Terminals are colored according to three areas of endemism (map inserted). Numbers at internodes are bootstrap values. Thick branches show presence of body enrollment coaptation. Note the suggestively Neotropical origin of monophyletic Ceratocanthinae and Ceratocanthini, as well as exclusively Afrotropical distribution of the monophyletic *Philharmostes* group.

terminals were occasionally linked in strongly supported clades (*Trachycrusus* + *Xenocanthus* 85%, *Germarostes posticus* + *Martinezostes* 85%, *Ceratocanthopsis* + *Ceratocanthus* 83%, *Paulianostes* + *Cyphopisthes* + *Ebbrittoniella* 86%, *Cryptosphaeroides* + *Goudotostes* 77%, *Balaghianestes* + *Cryptophilharmostes* 86%), they

never form sizable groups. The only exception was the *Philharmostes* group of seven genera (*Balaghianestes* + *Callophilharmostes* + *Carinophilharmostes* + *Chaetophilharmostes* + *Cryptophilharmostes* + *Petrovitzostes* + *Philharmostes* 85%). Recovery of this clade was not unexpected, since its existence had already been hypothesised (Ballerio 2000, 2001). Such low support for most of the Ceratocanthinae and particularly Ceratocanthini internal clades suggests that at least some of them are likely artefacts resulting from using a single and relatively small dataset for the analysis (i.e., adult morphology only).

No less interesting is that some speciose genera failed to form clades. Most notably, eight terminals of *Germarostes* formed six clades, while none of the four *Madrasostes* terminals linked to each other. Five terminals of *Philharmostes* branched off in four clades from the basal comb of the *Philharmostes* group suggesting a highly paraphyletic nature for this genus. These observed discrepancies between the current taxonomy and our findings suggest that much work remains before all taxonomically valid Ceratocanthinae genera become reciprocally monophyletic.

Summing up, the results of our first phylogenetic analysis of Ceratocanthinae based on adult morphological characters are not surprising. They corroborate previous phylogenetic findings that the subfamily is a clade subordinate to Hybosoridae. They further corroborate intuitive thoughts of early authors that the small South American tribes of odd Scarabatermitini and Ivieolini form a sister lineage to the rest of the subfamily united as the large tribe Ceratocanthini. The latter comprises over 95% of all Ceratocanthinae species. The backbone of the tribe is most unsatisfactorily resolved, offering no significant insight on its structure. Equally unsatisfactory are the current taxonomic arrangements of three speciose Ceratocanthini genera (*Germarostes*, *Madrasostes*, *Philharmostes*), which are highly polyphyletic with respect to those containing one or a few easy-to-distinguish species. This generic-level discrepancy between taxonomy and phylogeny is likely a result of the non-cladistic approach common in phylogenetically neglected clades, a practice in which small genera are routinely erected for charismatic species without any attempt to maintain reciprocal monophyly and equal taxonomic status between sister groups.

5.2. Geographical interpretations

Figure 10 illustrates the geographical aspect of Ceratocanthinae evolution and reveals their markedly pantropical distribution which is notably similar to that of some other clades such as the well-studied primates (Jaffe & Nijman 2008). Another notable biogeographical feature of the subfamily is that none of its 43 genera are known from more than one area of endemism (Neotropical, Afrotropical, Asian + Oceanic; Fig. 10). The lack of adequately identified fossils makes it uncertain whether Ceratocanthinae have been in existence before the Gondwana breakup, although this seems unlikely. The subfamily seems younger than the age of the oceanic barriers separating its present distribution, since the molecular clock estimations placed the origin of the more inclusive Hybosoridae clade in mid- or late Cretaceous at about 100 Mya (McKenna et al. 2015), which is some 20–50 My after the main Gondwana breakup events. If indeed so, then how did Ceratocanthinae cross the oceans and has long-range dispersal (de Queiroz 2014) been involved? At present we are unable to shed any light on when and how the representatives of the clade acquired their current trans-oceanic distribution.

The most significant positive geographical feature of the consensus tree (Fig. 10) is that the exclusively Neotropical clade of Scarabatermitini + Ivieolini forms the sister group to the rest of the subfamily. This implies that among all three areas of Ceratocanthinae endemism as depicted in Fig. 10, the Neotropics have at least a 50% chance of being the place of the subfamily origin. This hypothesis seems to be further strengthened by having the predominantly Neotropical clades branching off on the way leading to the common ancestor of the clade consisting of Afrotropical *Congomostes* and its predominantly non-Neotropical sister group. The likelihood of this "out of Neotropics" Ceratocanthinae and Ceratocanthini pattern is, however, slightly compromised by two Afrotropical genera, *Aneilobolus* and *Acanthocerodes*, edging themselves among the Neotropical terminals and, even more so, by the relatively low bootstrap support of the tree backbone. With all these limitations, it is still more likely to think that the Neotropical Region, and not two other areas of Ceratocanthinae endemism, was the place of origin of both the subfamily Ceratocanthinae and the tribe Ceratocanthini.

Another well-supported clade, the *Philharmostes* group consisting of seven genera, is exclusively Afrotropical. The majority of other Ceratocanthini clades in Fig. 10 are either small (such as the Asian and Australasian clade of *Paulianostes* + *Cyphopisthes* + *Ebbrittoniella* with 86% bootstrap) or have bootstrap support too low to be of biogeographical significance. With such limited data we cannot, therefore, assess the role of vicariance versus dispersal to explain the present distribution of Ceratocanthini subclades. The vicariance hypothesis seems to gain support from the fact that none of Ceratocanthinae genera are found in more than one area of endemism (Fig. 10). On the other hand species of all three Ceratocanthini genera occurring in southern India and in Sri Lanka (Fig. 2, *Pterorthochaetes*, *Madrasostes* and *Besuchetostes*) have their congeners in East Asia, and not in Africa and/or Madagascar, as would be implied by the classical Gondwanan scenario. The latter observation suggests a dispersal scenario. More likely, however, the processes causing both patterns played their roles, which cannot be adequately elucidated by our weakly resolved tree.

5.3. Ball-forming capacity

Our analysis weakly supports a hypothesis that the enrollment capacity accompanied by the development of

interlocking exoskeletal devices evolved in Ceratocanthinae only once (Fig. 9), followed by a single reversal in *Cloeotus*.

Examples of animals capable of compacting their body under protective cover by deflexing their body segments are not very numerous. Species- and specimen-wise, they appear to be more frequently found in water, rather than on land. Extinct and speciose trilobites were predominantly capable of some form of body deflection, or even of a complete enrollment facilitated by the use of complex interlocking (= coaptative) devices (for which the established term "enrollment" is used, Levi-Setti 1995, a terminology followed in the present paper since it describes the same phenomenon, see also Ortega-Hernández et al. 2013; Yuan et al. 2014). The recently discovered example of innovative body enrollment in mantis shrimp larvae (Malacostraca: Stomatopoda) also shows complex interlocking structures (Haug & Haug 2014), comparable only to those found in some trilobites and some Ceratocanthini beetles. In terrestrial habitats the ball-forming capacity by deflexing body segments (but not enrollment coaptation) has also evolved on a number of occasions. Pill bugs (Isopoda: Armadillidiidae) and the two likely unrelated Diplopoda orders Glomerida and Sphaerotheriida represent parallel cases among extant non-insect terrestrial arthropods. Surprisingly, no member of the exceptionally diverse clade Insecta can be justly compared in enrollment capacity to Ceratocanthinae, except perhaps females of *Perisphaerus* Serville, 1831 cockroaches. They lack coaptative devices, but are capable of forming a tight ball when disturbed (Schal et al. 1984). Even in three other beetle clades mentioned in the Introduction (Clambidae, Cybocephalidae and some Leiodidae) the capacity to conglobate is incomplete and coaptative devices are lacking. The body enrollment as displayed by oribatid mites is termed "ptychoidy" and consists of the retraction of the legs and gnathosoma into the idiosoma and complete body encapsulating by means of a deflected prodorsum. This phenomenon appears to have independently evolved in at least three Oribatidae clades (Schmelzle et al. 2015) and without development of coaptative devices. A preliminary survey of arthropod diversity suggests that trilobites, mantis shrimp larvae, and the majority of Ceratocanthini are the only arthropods having body enrollment coaptations facilitated by means of interlocking devices. Ceratocanthini appear to be unique in having the legs involved in the enrollment coaptation process.

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Appendix 1

List of 107 morphological characters used in the phylogenetic analysis of Ceratocanthinae.

1. Body, horseshoe-shaped punctures on dorsum: absent = 0; present = 1.
2. Body, capacity of conglobation by deflexing head and pronotum: absent = 0; present, even if incomplete (Fig. 11B) = 1.
3. Body, enrollment coaptations (ability to make a perfect ball): absent (Fig. 11B) = 0; present (Fig. 11A) = 1.
4. Body, exoskeleton: fully pigmented = 0; depigmented = 1.
5. Head capsule, pentagonal shape in dorsal view: absent = 0; present (Fig. 11F) = 1.
6. Head capsule, length/width ratio in dorsal view: less than one = 0; more than one = 1.
7. Head capsule, clypeus, anterior serration: absent (Fig. 11F) = 0; present (Fig. 11E) = 1.
8. Head capsule, labrum and clypeus, whether on same plane in lateral view: yes = 0; no (Fig. 11C) = 1.
9. Head capsule, vertical dimension of apical clypeal extremity: absent = 0; present (Fig. 11C) = 1.
10. Head capsule, vertical dimension of apical clypeal extremity, as compared to one fourth clypeal length: smaller (Fig. 11C) = 0; greater (Fig. 11D) = 1.
11. Head capsule, externally visible genal canthus: absent (Fig. 11H) = 0; present (Fig. 11G) = 1.
12. Head capsule, genal canthus, whether reaching postocular area: no (Fig. 11F) = 0; yes (Fig. 11G) = 1.
13. Head capsule, trichome at center of frons: absent = 0; present (Fig. 7F) = 1 [deactivated].
14. Head capsule, fore margin with a distinct angle delimiting genae: absent (Fig. 11G) = 0; present (Fig. 11J) = 1.
15. Head capsule, genal suture: absent (Fig. 11F) = 0; present (Fig. 11I) = 1.
16. Head capsule, genal suture generating a slight discontinuity in the fore margin: absent = 0; present (Fig. 11H) = 1.
17. Antennae, number of antennomeres: 10 = 0; 9 = 1; 8 = 2; 7 = 3.
18. Antennae, antennomere 3: wider than long = 0; as long as wide = 1; longer than wide = 2.
19. Antennae, each of antennomeres 4 to 7, proportion: wider than long = 0; as long as wide = 1; longer than wide = 2.
20. Antennae, club length as compared to that of funicle: shorter = 0; subequal = 1; longer = 2.

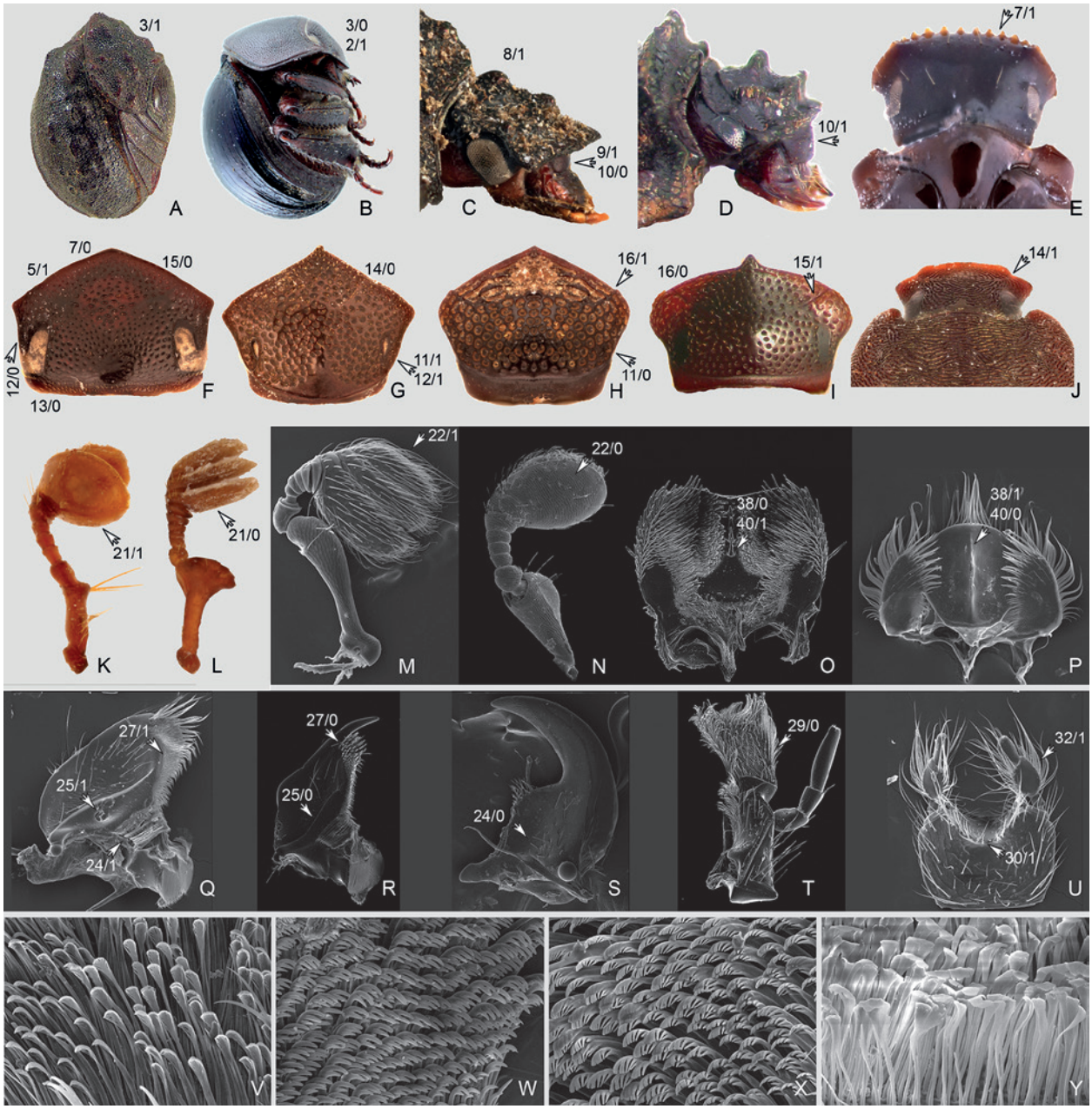

Fig. 11. Ceratocanthinae, heads and mouthparts. **A**: *Carinophilharmostes vadoni*, rolled up specimen in lateral view showing coaptations; **B**: *Acanthocerodes* sp., rolled up specimen lacking coaptations; **C**: *Afrocloetus* sp., head, lateral; **D**: *Cryptophilharmostes mahunkai*, head, lateral; **E**: *Xenocanthus* sp., head, dorsal; **F**: *Ceratocanthus amazonicus*, head, dorsal; **G**: *Astaenomoechus criberrimus*, head, dorsal; **H**: *Nesopalla iviei*, head, dorsal; **I**: *Pseudosynarmostes mitsinjo*, head, dorsal; **J**: *Ceratocanthoides undatus*, head, dorsal; **K**: *Phaeochrous lobatus*, antenna; **L**: *Ceratocanthus amazonicus*, antenna; **M**: *Cryptosphaeroides hystrix*, antenna; **N**: *Acanthocerodes* sp., antenna; **O**: *Acanthocerodes* sp., epipharynx; **P**: *Oxymorostes riedeli*, epipharynx; **Q**: *Oxymorostes riedeli*, mandible; **R**: *Synarmostes* sp., mandible; **S**: *Hybosorus illigeri*, mandible; **T**: *Synarmostes* sp., maxilla; **U**: *Oxymorostes riedeli*, labium; **V**: *Astaenomoechus* sp., galear brush; **W**: *Cyphopisthes* sp., galear brush; **X**: *Madrasostes* sp., galear brush; **Y**: *Germarostes* sp., galear brush.

21. Antennae, proximal club antennomere encapsulating rest of the club: absent (Fig. 11L) = 0; present (Fig. 11K) = 1.

22. Antennae, proximal club antennomere, setae on proximal face: absent (Fig. 11N) = 0; present (Fig. 11M) = 1.

23. Antennae, proximal club antennomere, setae on proximal face covering: whole surface = 0; only proximal area = 1; only distal area = 2.

24. Mandibles, conjunctive (sensu Nel & Scholtz 1990): absent (Fig. 11S) = 0; present (Fig. 11Q) = 1.

25. Mandibles, ventral pore on basal part: absent (Fig. 11R) = 0; present (Fig. 11Q) = 1.

26. Mandibles, apical part, number of teeth in addition to mandibular apex: 0 = 0; 1 = 1; 2 = 2.

27. Mandibles, mesal brush very developed with mandibular apex not exceeding it: absent (Fig. 11R) = 0; present (Fig. 11Q) = 1.

Table 1. Data matrix of 107 adult morphological characters used for the phylogenetic analysis of Ceratocanthinae (Coleoptera: Hybosoridae). Character numbers are given on top, written vertically. Ten parsimony uninformative characters (13, 42, 47, 52, 55, 72, 76, 81, 96, 103) deactivated form the analysis are indicated by U beneath the character numbers.

	00000000000000000000	**00000000000000000000**	**00000000000000000000**	**00000000000000000000**	**00000000000000000001**	**1111111**
	00000000011111111112	**22222222233333333334**	**44444444455555555556**	**66666666677777777778**	**88888888899999999990**	**0000000**
	12345678901234567890	**12345678901234567890**	**12345678901234567890**	**12345678901234567890**	**12345678901234567890**	**1234567**
	----------U-------	----------	-U----U----U--U-----	----------U---U----	U--------------U----	--U----
Aphodius pedellus	0001100--00-010-1001	0101000000101----00-	0010100001000001011 1	00023000111000000010	00001000111000000200	0000-0-
Belohina inexpectata	0000000-000-010-0000	10-0000210211----000	0000100000000000??01	00000----------0110	00000000011000000200	000????
Eulasia vittata	0000010000010010-0220	00-00100002010020010	0000100000000000000	00003100011000000011	00000100001000000200	100110-
Orubesa athleta	0001000000010010-0101	0100000210000002001 0	0000100000000010101	0002310001-000000110	00000000011000000200	000100-
Ochodaeus holzschuhi	0001000000-010-0110	0100010210210001101 0	0010000000000010101	0002310011-000000010	00000000001010000200	000110-
Coilodes sp.	0000000000010010-0200	10-10102011010000111	0010100000000010101	0002310001-000000110	00000010011010002100	100000-
Phaeochrous lobatus	0000000000010010-0200	10-10102011010000110	0010110000000010101	00023100011000000011	00000010001000002100	100000-
Anaides sp.	0000010100010010-0001	00-10002011010010110	0011000100000001 1100	00003100011000000010	00000010001010000100	000100-
Cryptogenius fryi	0000000101 0-010-0100	0121000101001003 0110	0011100000000001 1100	00003010011000000110	00000010001000000100	000???-
Liparochrus septemdecimlineatus	0100010000010010-0101	0121000201101000011 1	0011010000000001 0101	00023000111000000010	00000010001000100000	100100-
Ivieolus brooksi	0001010100100 00-3121	00-0000000?0?0001???	110000010-0110021111	00002--0000-00001010	0000000000100000020?	???????
Scarabaeinus termitophilus	0001000100100 00-3121	00-0000200100000???	1000010001001002111 1	00022--0011-00001010	0000000000100000010 1	???????
Scarabatermes amazonensis	0001000100100 00-3002	00-0000200100000???	1000010001001002111 1	00022--0000-00001010	0000000000100000010 1	???????
Trachycrusus sp.	0001001100100 00-1210	00-???0??0101000???	1000010001000002??11	00002--0000-00001010	0000000010000000020 1	???????
Xenocanthus sp.	0001001100100 00-1210	00-0000000201000???	1000010002001002111 1	00022--0011-00011010	0000000010100000010 1	???????
Acanthocerodes sp.	1100100110100 00-0101	00-1000201101000001 1	1000010000000002100 1	01020----------0010	0000101000111110010 0	000000-
Afrocloetus sp.	1110100110001 00101	0121000201011002011 0	1000010110100002100 0	01101----------0010	0000101010111110010 0	000000-
Aneilobolus lawrencei	1100100110001 00-0101	00-1000201101000111 1	1000010110000002100 1	01020----------0010	0000101000111110010 0	000000-
Anopsiostes sp.	1110100110110 00-0101	00-1020201101000011 0	1010010002000002110 0	01113000011-01100012	????101010?10100?0-0	100????
Astaenomoechus setosus	1110100110110 01001 0	0101000201001100011 0	1010010002100002110 0	01113000010-11100011	0100001010111110020 1 0	000000-
Astaenomoechus criberrimus	1110100110110 01001 0	0101000201001100011 0	1010010002100002110 0	01113000010-11100011	0100001010111110020 1 0	000000-
Aulisostes sp.	0100100110110 00-0111	00-1000201201000???	1000010002000002100 1	01000----------0010	0000101010110100010 0	000000-
Baloghianestes oribatidiformis	1110100110001 00-1102	0101000101101100011 1	1000010112000002100 0	00100----------0100	0000001010101100010 0	0000111
Baloghianestes lissoubai	1110100110001 00-1102	0101000101101100011 1	1000010112000002100 0	00100----------0100	0000001010101100010 0	0000111
Besuchetostes sp.	1110101110001 00-0201	0101001101211000111 0	1000010112100002100 0	00100----------0010	0000101010111110010 0	100000-
Besuchetostes jaccoudi	1110101110001 00-0221	0101101101211000111 0	1000010112100002100 0	00100----------0010	0000101010110100010 0	000000-
Callophilharmostes fleutiauxi	1110100110111 00-3022	0101010201101100011 1	1000010011000002110 0	11103110000-01000101	0010001010110100010 0	0000111
Carinophilharmostes vadoni	1110100110110 00-0002	0101000101101100011 1	1000010112000002110 0	11113110000-01000101	0010001010110100010 0	0000111
Ceratocanthoides undatus	0100000110100 10-0111	0101000201201000011 0	1010010002000002110 1	11023000000-00100010	0000101010111110010 0	000000-
Ceratocanthopsis fulgida	0110100110100 00-3202	0101000201001000011 0	1010010000000002110 0	11023000000-00000010	0000101110011000010 0	000000-
Ceratocanthus amazonicus	0110100110100 00-0002	0100000201001000011 0	1010010000000102110 1	11023000001-00000010	0000101110111110010 0	000000-
Ceratocanthus sp.	0110100110110 00-0101	0100000201000000011 0	1000010000000102110 0	11023000000-00000010	0000101110111110010 0	000000-
Chaetophilharmostes chevalieri	1110100110110 00-0102	0101000201001100011 0	1000010002000002110 0	11113120000-01000101	0010001010110100010 0	0100110
Cloeotus latebrosus	1100100110100 01101 0	0100000101200001011 0	1000010110000002100 0	00000----------0010	0000101000??01100100	000????
Congomostes janssensi	1110101110100 01101 0	00-1000201201002011 1	1000010000000002110 0	01113000101100000010	0000101010110110010 0	000????
Cryptophilharmostes mahunkai	1110000111 0-000-0001	0121010101101100011 1	1000010112000002100 0	00100----------0110	0000001010110100010 0	0100111
Cryptophilharmostes merkli	1110000111 0-000-0001	0121010101101100011 1	1000010112000002100 0	00100----------0110	0000001010110100010 0	0100111
Cryptosphaeroides hystrix	1110100110110 01101 0	0101000201001000011 1	1000010002000002100 0	10101----------0011	0100001010110100200 0	100000-

Table 1 continued.

	00000000000000000000	00000000000000000000	00000000000000000000	00000000000000000000	00000000000000000001	1111111
	00000000011111111112	22222222233333333334	44444444455555555556	66666666677777777778	88888888899999999990	0000000
	12345678901234567890	12345678901234567890	12345678901234567890	12345678901234567890	12345678901234567890	1234567
	----------U-------	--------------------	-U----U----U--U-----	----------U---U----	U--------------U----	--U----
Cyphopisthes sp.	111010011011000-0102	01010002012010100110	10000100000000021100	00103010010-00100011	00011010101101000100	001000-
Ebbrittoniella gestroi	111010011011000-0201	01010002012010100110	10000100010000021100	00103000010-00100011	00011010101101000100	0000013
Eusphaeropeltis sp.	111010011011000-0201	01000002012010000110	10000100000000021100	11113000010-00100010	00001110101101000100	0000012
Germarostes aphodioides	110000011010010-0101	01000002010010000110	10100100000000021101	01023000001-00000010	00001010101111100100	000000-
Germarostes degallieri	110010011011010-0001	01210002012011000110	10100100020000021101	11023000011-00000010	00001010101111000100	000000-
Germarostes diffundus	110000011010000-0201	01000002011010000110	10100100000000021101	11023000000-00000010	00001010101111100100	000000-
Germarostes globosus	110000011010010-0101	01000002010010000110	10100100000000021101	11023000001-00000010	00001010101111100100	000000-
Germarostes oberthueri	110000011011100110101	01010002011010020011	10100100021000021101	01023000000-00000010	00001010101101000100	000000-
Germarostes posticus	010000011010010-0101	00-10002011010000011	10100100000000021001	01020----------0010	00001010001111100100	000000-
Germarostes pullus	110000011010010-0001	00-10001011010000111	10000100000000021001	01020----------0010	00001010101111000100	000000-
Germarostes senegalensis	110000011010010-0102	01000002010010000110	10100100000000021101	11023000001-00000010	00001010101111100100	000000-
Goudotostes sp.	111010011100-00110201	01010002012110000110	10000101120000021000	10100----------0011	01000010101101002000	100000-
Macrophilharmostes major	111010011011000-0101	01011011012110001110	10000100020000021000	11110----------0010	00001010101101000110	000000-
Madrasostes clypeale	111010111011000-0101	01011011012110001110	10000100010000021100	11103000010-00000010	00001010101101000110	000000-
Madrasostes granulatum	111010011011000-0201	01011011012110001110	10000100021000021000	11100----------0010	00001010101101000110	000000-
Madrasostes mirificum	111010111011000-0101	01011011012110001110	10000100020000021100	11113000010-00000010	00001010101101000110	000000-
Madrasostes sculpturatum	111010111011000-0102	01011012012110001110	10000100020000021100	11123000010-00000010	00001010101101000110	000000-
Martinezostes fortecostatus	010000011010010-0101	00-10001011010000011	10100100000000021001	01020----------0010	00001010001111100100	000000-
Melanophilharmostes sp.	111010011011000-0101	01010001010010000110	10100100020000021101	01113--1010-10100011	01000010101101002000	000000-
Nesopalla iviei	111010011100-00110101	01010001012111000110	10100101120000021000	00100----------0010	00001010100-01000100	000000-
Oxymorostes riedeli	111010011100-000-0101	01011011012110001110	10000110120000021001	10100----------0010	00001010100-01000110	000000-
Paulianostes panggoling	111010011011000-0101	01000002012010100110	10000101000000021100	11103000010-00100011	00011010101101000100	0000013
Perignamptus sp.	111010011011000-0101	01011011012110001110	10000100020000021000	11000----------0010	00001010101101000110	000000-
Petrovitzostes guineensis	111010011011000-3122	01010002011011000110	10000101020000021100	11003-10000-01000101	00100010101101000100	0000111
Philharmostes sp.	111010011011000-0101	01010001010011000110	10000100010000021000	11100----------0100	00000010101111000100	0000111
Philharmostes badius	111010011011000-1101	01010001010011000110	10000100010000021100	11113110000-01000100	00000010101111000100	0100111
Philharmostes basicollis	111010011011000-0101	01010001010011000110	10000100020000021100	11113110000-01000100	00000010101111000100	0100111
Philharmostes grebennikovi	111010011011000-0101	01010002010011000110	10000100010000021000	11110----------0100	00000010101101000100	0000111
Philharmostes werneri	111010011011000-0102	01010001012011000110	10000100120000021000	11110----------0100	00000010101111001100	0100111
Pseudopterorthochaetes endroedyi	111010011011000-0102	01010002010010000110	10100100020000021100	11113--1010-10000011	11000010101101002000	000000-
Pseudosynarmostes mitsinjo	111000011011001000002	01010102010010000110	10000100020000021100	10102--0000-00100011	00000010100-01002000	000000-
Pterorthochaetes insularis	111010111011000-1102	01010012012110001010	10000100020000121100	11113000010-01000010	00001010100-01010010	1000012
Synarmostes sp.	111010011011000-0202	01010002010010000110	10100101120000021000	11110----------0011	00001010101101001000	000000-

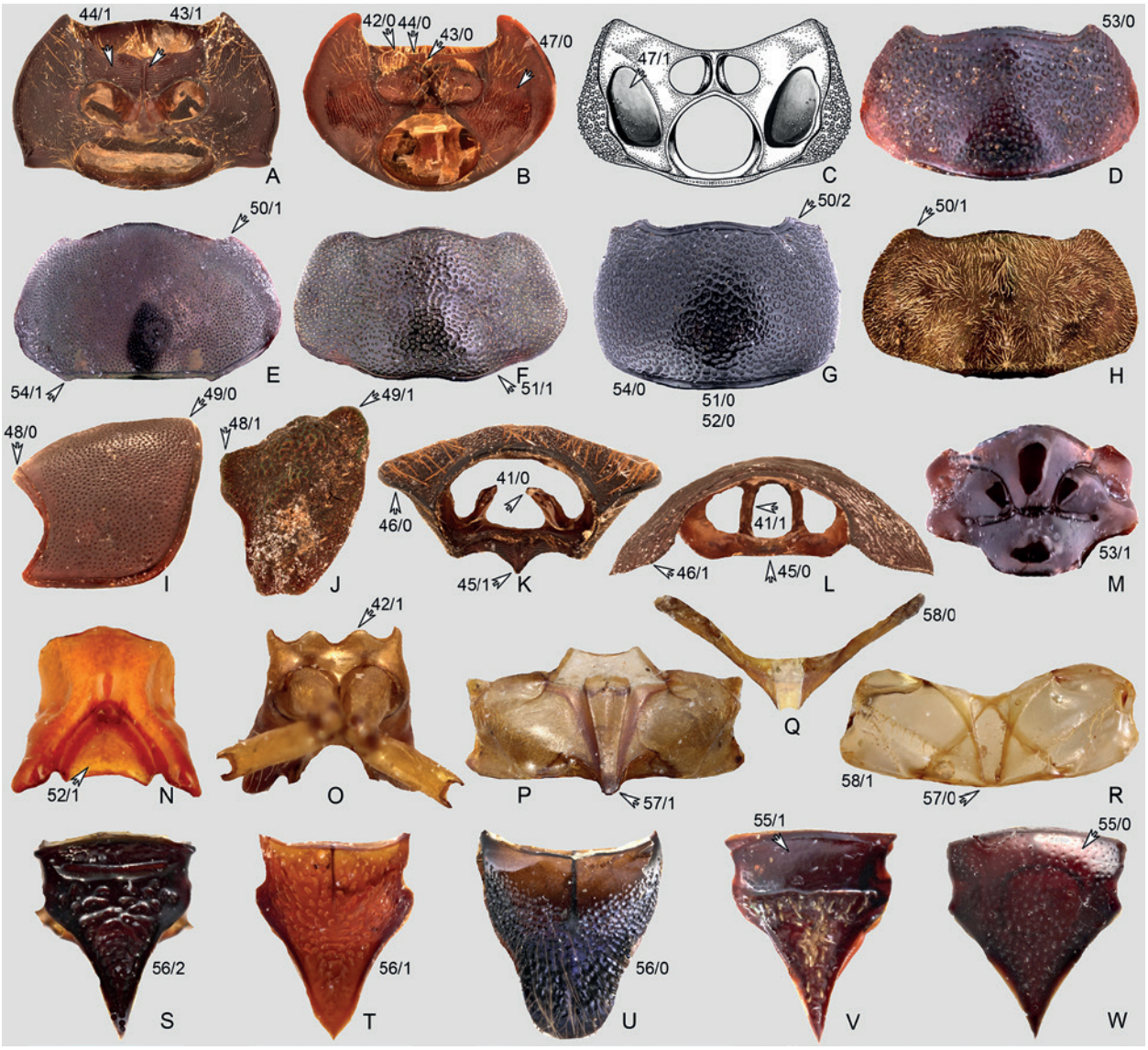

Fig. 12. Ceratocanthinae, thorax. **A**: *Anaides* sp., thorax, ventral; **B**: *Ebbrittoniella gestroi*, thorax, ventral; **C**: *Oxymorostes riedeli*, thorax, ventral (drawing by Aura Paucar Cabrera); **D**: *Philharmostes* sp., pronotum, dorsal; **E**: *Ceratocanthus* sp., pronotum, dorsal; **F**: *Astaenomoechus criberrimus*, pronotum, dorsal; **G**: *Madrasostes sculpturatum*, pronotum, dorsal; **H**: *Ebbrittoniella gestroi*, pronotum, dorsal; **I**: *Acanthocerodes* sp., pronotum, lateral; **J**: *Goudotostes* sp., pronotum, lateral; **K**: *Anaides* sp., prothorax, frontal; **L**: *Ebbrittoniella gestroi*, prothorax, frontal; **M**: *Xenocanthus* sp., pronotum, dorsal; **N**: *Ivieolus brooksi*, pronotum, dorsal; **O**: *Ivieolus brooksi*, basisternum; **P**: *Ceratocanthus amazonicus*, mesotergite; **Q**: *Martinezostes fortecostatus*, mesotergite; **R**: *Ochodaeus holzschuhi*, mesotergite; **S**: *Madrasostes sculpturatum*, scutellum; **T**: *Liparochrus septemdecimlineatus*, scutellum; **U**: *Eulasia vittata*, scutellum; **V**: *Pterorthochaetes insularis*, scutellum; **W**: *Ceratocanthus amazonicus*, scutellum.

28. Maxillae, length of distal palpomere compared to that of two preceding: shorter = 0; subequal = 1; longer = 2.
29. Maxillae, sclerotization of galea: absent (Fig. 11T) = 0; present = 1.
30. Labium, medial notch on anterior edge: absent = 0; present (Fig. 11U) = 1.
31. Labium, length of distal palpomere compared to that of two preceding: longer = 0; shorter = 1.
32. Labium, lateral expansion of third palpomere making it dissimilar to others: absent = 0; present (Fig. 11U) = 1.
33. Labium, palpomeres, number: 3 = 0; 4 = 1.
34. Labrum, distal longitudinal furrow, even if shallow: absent = 0; present = 1.
35. Labrum, anterior truncation: absent = 0; present = 1.
36. Labrum, surface: smooth = 0; wrinkled = 1; granulose = 2; punctate = 3.
37. Labrum, apical fringe: absent = 0; present = 1.
38. Epipharynx, longitudinal carina on median process: absent (Fig. 11O) = 0; present (Fig. 11P) = 1.
39. Epipharynx, sclerotization: absent = 0; present = 1.
40. Epipharynx, setae on median process: absent (Fig. 11P) = 0; present (Fig. 11O) = 1.
41. Prothorax, prosternal apophyses, whether reaching inner wall of pronotum [internal view, dissection re-

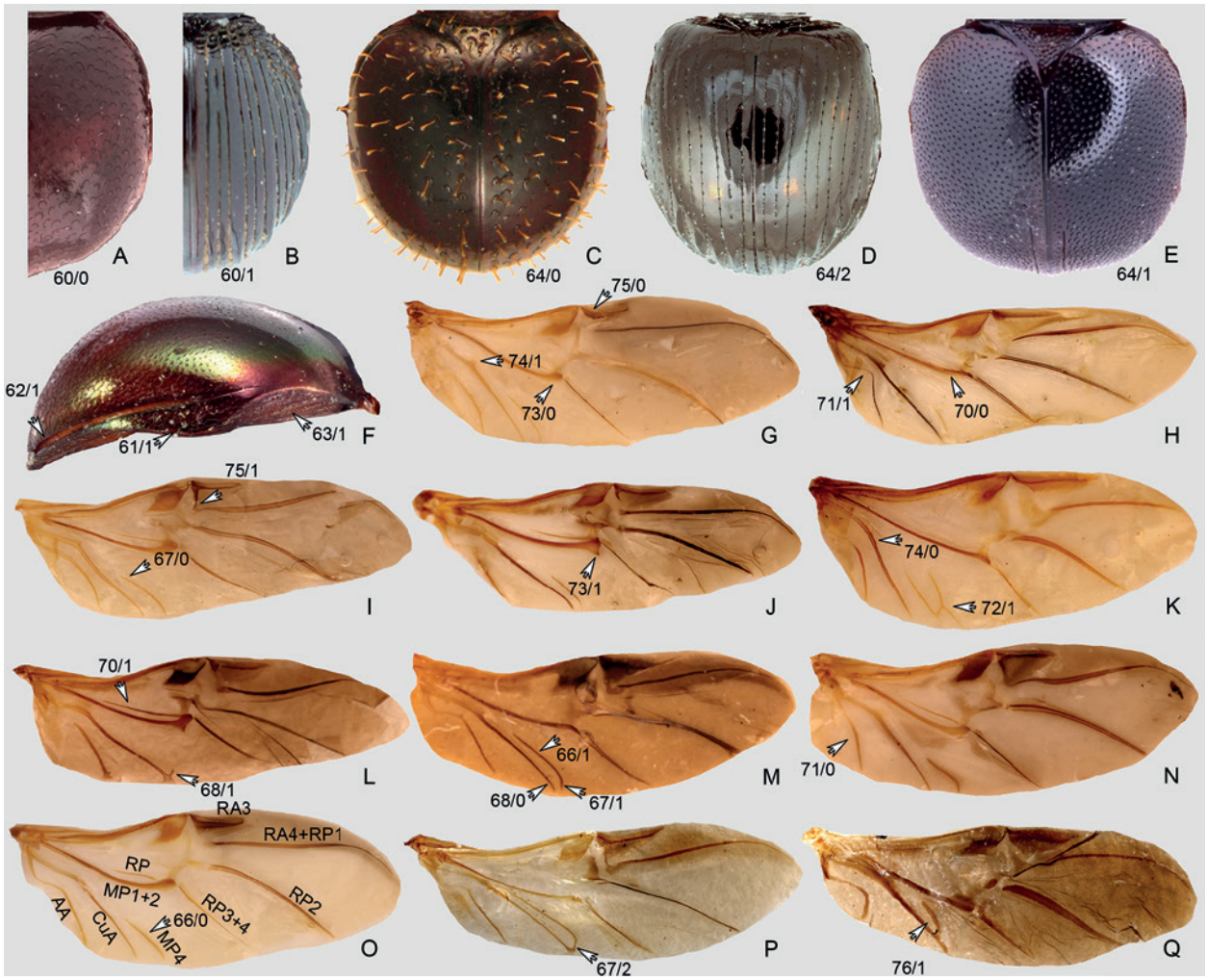

Fig. 13. Ceratocanthinae, elytra and hind wings. **A**: *Perignamptus* sp., right elytron, dorsal; **B**: *Aneilobolus lawrencei*, right elytron, dorsal; **C**: *Cryptosphaeroides hystrix*, elytra, dorsal; **D**: *Germarostes degallieri*, elytra, dorsal; **E**: *Anopsiostes punctatus*, elytra, dorsal; **F**: *Eusphaeropeltis* sp., right elytron, lateral. **G–Q:** right hind wing; **G**: *Pterorthochaetes insularis*; **H**: *Ceratocanthus amazonicus*; **I**: *Ebbrittoniella gestroi*; **J**: *Astaenomoechus criberrimus*; **K**: *Congomostes janssensi*; **L**: *Melanophilharmostes* sp.; **M**: *Petrovitzostes guineensis*; **N**: *Cyphopisthes* sp.; **O**: *Madrasostes sculpturatum*; **P**: *Chaetophilharmostes chevalieri*; **Q**: *Xenocanthus* sp.

quired]: not reaching (Fig. 12K) = 0; reaching (Fig. 12L) = 1.

42. Prothorax, basisternum, fore margin distinctly bilobed: absent (Fig. 12B) = 0; present (Fig. 12O) = 1 [deactivated].

43. Prothorax, basisternum, longitudinal crest: absent (Fig. 12B) = 0; present (Fig. 12A) = 1.

44. Prothorax, basisternum, deep transverse anteriorly opened depression: absent (Fig. 12B) = 0; present (Fig. 12A) = 1.

45. Prothorax, sternellum, ventral projection: absent (Fig. 12L) = 0; present (Fig. 12K) = 1.

46. Prothorax, lateroventral expansion of hypomeron: absent (Fig. 12K) = 0; present (Fig. 12L) = 1.

47. Prothorax, pit on hypomeron: absent (Fig. 12B) = 0; present (Fig. 12C) = 1 [deactivated].

48. Pronotum, swollen anterior margin: absent (Fig. 12I) = 0; present (Fig. 12J) = 1.

49. Pronotum, swollen posterior margin: absent (Fig. 12I) = 0; present (Fig. 12J) = 1.

50. Pronotum, anterior pronotal angles: acutely pointed (Fig. 12E) = 0; broadly rounded (Fig. 12H) = 1; truncate (Fig. 12G) = 2.

51. Pronotum, posterior median swelling: absent (Fig. 12G) = 0; present (Fig. 12F) = 1.

52. Pronotum, pseudoscutellum: absent (Fig. 12G) = 0; present (Fig. 12N) = 1 [deactivated].

53. Pronotum, embossed sculpturing: absent (Fig. 12D) = 0; present (Fig. 12M) = 1.

54. Pronotum, vestigial hind angles: absent (Fig. 12G) = 0; present (Fig. 12E) = 1.

55. Thoracic dorsum, transverse carina on rectangular part of scutellum: absent (Fig. 12W) = 0; present (Fig. 12V) = 1 [deactivated].

56. Thoracic dorsum, distal part of exposed scutellum, sides: markedly convex forming rounded obtuse apex (Fig. 12U) = 0; weakly convex forming lanceolate apex (Fig. 12T) = 1; weakly concave forming acutely pointed apex (Fig. 12S) = 2.

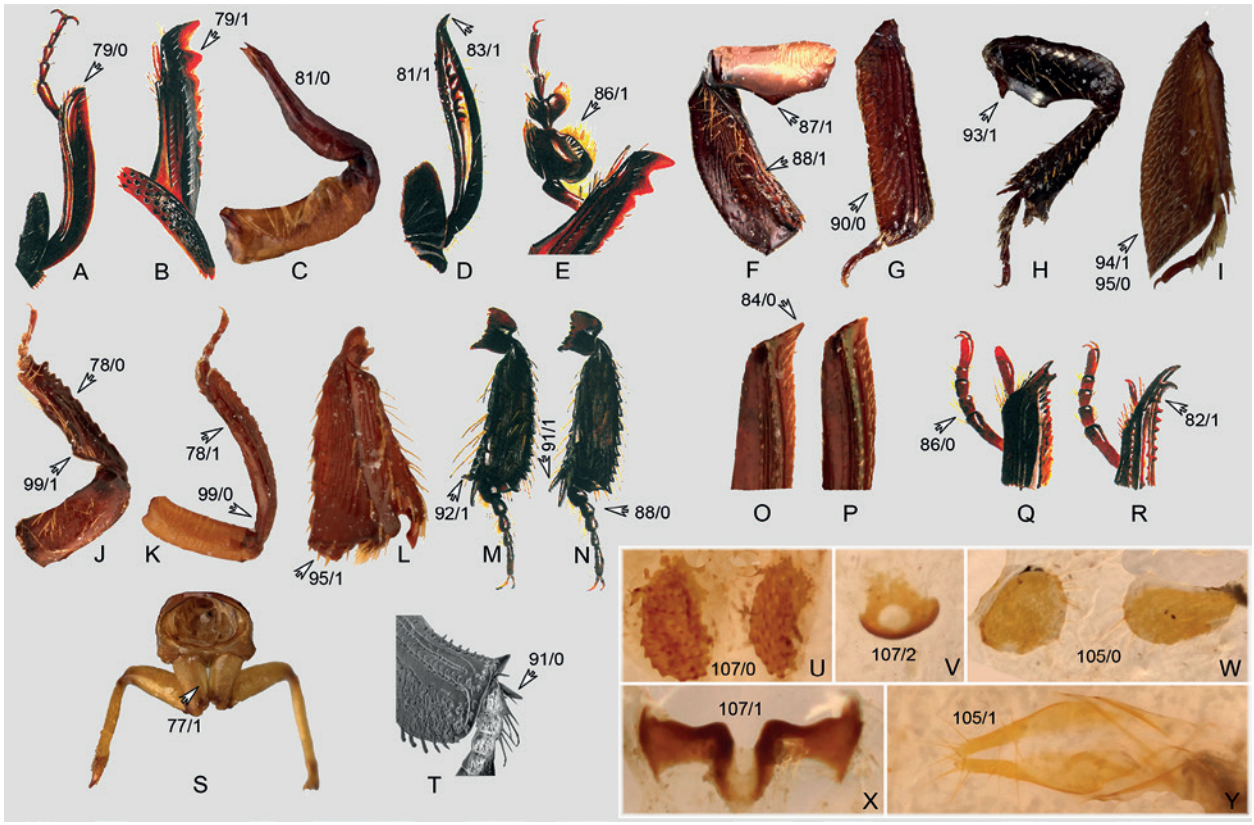

Fig. 14. Ceratocanthinae, legs and female genitalia. **A**: *Carinophilharmostes vadoni*, female protibia; **B**: *Eusphaeropeltis* sp., protibia; **C**: *Pseudosynarmostes mitsinjo*, female protibia, dorsal; **D**: *Callophilharmostes fleutiauxii*, female protibia, dorsal; **E**: *Eusphaeropeltis* sp., male protarsus, dorsal; **F**: *Ceratocanthus amazonicus*, mesotibia and mesotarsus, ventral; **G**: *Callophilharmostes fleutiauxi*, mesotibia; **H**: *Germarostes posticus*, metatibia; **I**: *Ebbrittoniella gestroi*, metatibia; **J**: *Madrasostes sculpturatum*, protibia, ventral; **K**: *Callophilharmostes fleutiauxi*, male protibia; **L**: *Germarostes diffundus*, metatibia; **M**: *Germarostes diffundus*, male mesotibia; **N**: *Germarostes diffundus*, female mesotibia; **O**: *Ebbrittoniella gestroi*, apex of female protibia; **P**: *Ebbrittoniella gestroi*, apex of male protibia; **Q**: *Goudotostes* sp., apex of male protibia; **R**: *Goudotostes* sp., apex of female protibia; **S**: *Ivieolus brooksi*, procoxae; **T**: *Oxymorostes riedeli*, apex of male mesotibia; **U**: *Carinophilharmostes vadoni*, bursal sclerites; **V**: *Ebbrittoniella gestroi*, bursal sclerite; **W**: *Ebbrittoniella gestroi*, vaginal palpi; **X**: *Pterorthochaetes insularis*, bursal sclerites; **Y**: *Philharmostes werneri*, vaginal palpi.

57. Thoracic tergite, mesotergite, metascutal furrow, posterior projection beyond posterior metatergite edge: absent (Fig. 12R) = 0; present (Fig. 12P) = 1.

58. Thoracic tergite, mesotergite, length compared to that of elytra: 1/4 the length of elytra (Fig. 12Q) = 0; 1/3 the length of elytra (Fig. 12R) = 1.

59. Thoracic venter, metaventrite: rectangular = 0; triangular = 1.

60. Elytra, longitudinal striation on dorsal side: absent (Fig. 13A) = 0; present (Fig. 13B) = 1.

61. Elytra, area between striated articular area and inferior sutural stria ("marginal area" sensu Paulian 1977): absent = 0; present (Fig. 13F) = 1.

62. Elytra, extension of sutural stria continuing from elytral apex along elytral lateral sides ("inferior sutural stria" sensu Paulian 1977): absent = 0; present (Fig. 13F) = 1.

63. Elytra, striated articular area (sensu Paulian 1977): absent = 0; present (Fig. 13F) = 1.

64. Elytra, sutural stria: absent (Fig. 13C) = 0; present (incomplete) (Fig. 13E) = 1; present (complete) (Fig. 13D) = 2.

65. Metathoracic wings: absent = 0; present, vestigial, < 30% elytral length = 1; present, short, about 100% elytral length = 2; present, long, about 200% elytral length = 3.

66. Wings, vein MP4, length relative to half length of CuA: shorter (Fig. 13O) = 0; longer (Fig. 13M) = 1.

67. Wings, distal part of vein MP4: straight and parallel to CuA (Fig. 13I) = 0; bent towards CuA (Fig. 13M) = 1; joining apically CuA (Fig. 13P) = 2.

68. Wings, vein CuA, distal fork: absent (Fig. 13M) = 0; present (Fig. 13L) = 1.

69. Wings, vein MP3: absent = 0; present = 1.

70. Wings, loop of vein RP MP 1+2: absent (Fig. 13H) = 0; present (Fig. 13L) = 1.

71. Wings, sinuation of vein AA: even (Fig. 13N) = 0; at right angle (Fig. 13H) = 1.

72. Wings, distal connection between veins MP4 and MP3: absent = 0; present (Fig. 13K) = 1 [deactivated].

73. Wings, distal expansion of vein MP1+2: absent (Fig. 13G) = 0; present (Fig. 13J) = 1.

74. Wings, short proximal expansion of vein CuA3+4: absent (Fig. 13K) = 0; present (Fig. 13G) = 1.

75. Wings, vein RA3, vertical secondary sclerification at base: absent (Fig. 13G) = 0; present (Fig. 13I) = 1.
76. Wings, vein CuA3+4 joining MP4: absent = 0; present (Fig. 13Q) = 1 [deactivated].
77. Legs, procoxae, orientation of longest axle: horizontal = 0; vertical (Fig. 14S) = 1.
78. Legs, protibiae: straight (Fig. 14J) = 0; curved (Fig. 14K) = 1.
79. Legs, protibiae, dentation on distal third of outer side: absent (Fig. 14A) = 0; present (Fig. 14B) = 1.
80. Legs, protibiae, sexual dimorphism in shape: absent = 0; present = 1.
81. Legs, female protibiae, S-shaped: present (Fig. 14C) = 0; absent (Fig. 14D) = 1 [deactivated].
82. Legs, female protibiae, apically elongate: absent = 0; present (Fig. 14R) = 1.
83. Legs, female protibiae, pointed: absent = 0; present (Fig. 14D) = 1.
84. Legs, female protibiae, with longer apical tooth: present (Fig. 14O) = 0; absent = 1.
85. Legs, protibiae, longitudinal carina on ventral side: absent = 0; present = 1.
86. Legs, protarsi, widening of male tarsomeres: absent (Fig. 14Q) = 0; present (Fig. 14E) = 1.
87. Legs, meso- and metafemora, distal emargination on posterior edge: absent = 0; present (Fig. 14F) = 1.
88. Legs, meso- and metatarsi, capability to be folded along the inner side of tibia: absent = 0; present (Fig. 14F) = 1.
89. Legs, meso- and metatibiae in cross section: rounded = 0; parallel sided = 1.
90. Legs, mesotibiae, transverse carinae on outer surface: absent (Fig. 14G) = 0; present = 1.
91. Legs, mesotibiae, number of apical spurs: one (Fig. 14T) = 0; two = 1.
92. Legs, mesotibiae, inner apical spur in males: straight = 0; curved (Fig. 14M) = 1.
93. Legs, posterior angle of metatrochanter, posterior projection beyond posterior edge of metafemora: absent = 0; present (Fig. 14H) = 1.
94. Legs, metatibiae: subrectangular = 0; triangular (Fig. 14I) = 1.
95. Legs, metatibiae, apical corbel (sensu Thompson 1992): absent (Fig. 14I) = 0; present (Fig. 14L) = 1.
96. Legs, metatibiae, inner apical spur: straight = 0; twisted = 1 [deactivated].
97. Legs, protarsi, length of female first tarsomere, to that of all others: distinctly shorter = 0; subequal = 1; distinctly longer = 2.
98. Legs, protarsi, tarsal insertion at: middle = 0; distal third = 1; apex = 2.
99. Legs, protibiae, proximal third swollen, ventral view: absent (Fig. 14K) = 0; present (Fig. 14J) = 1.
100. Abdomen, physogastry: absent (Fig. 3F) = 0; present (Fig. 3B) = 1.
101. Male genitalia, parameres: more or less symmetrical = 0; strongly asymmetrical = 1.
102. Male genitalia, parameres, basal apophyses: absent = 0; present = 1.
103. Male genitalia, parameres, dorsal apophyses: absent = 0; present = 1 [deactivated].
104. Female genitalia, styli: absent = 0; present = 1.
105. Female genitalia, vaginal palpi: rounded, about as long as wide (Fig. 14W) = 0; elongate, at least twice as long as wide (Fig. 14Y) = 1.
106. Female genitalia, bursa copulatrix, sclerites: absent = 0; present = 1.
107. Female genitalia, bursa copulatrix, shape of sclerites: plate-like (Fig. 14U) = 0; spicule-like (Fig. 14X) = 1; ring-like (Fig. 14V) = 2.

Appendix 2

Label data for Ceratocanthinae adults specimens used for scoring morphological characters. All specimens, unless followed by a museum abbreviation, are stored in the collection of the first author. Museum abbreviations (followed by the name of curator):
CNC – Canadian National Collection of Insect (P. Bouchard); **DEZA** – Dipartimento di Entomologia e Zoologia Agraria dell'Università, Portici, Italy (F. Pennacchio); **LSAM** – Louisiana State University, Louisiana State Arthropod Museum, Baton Rouge, U.S.A. (C. Carlton); **MNHN** – Muséum National d'Histoire Naturelle, Paris, France (O. Montreuil).

Non-Hybosoridae
Aphodius pedellus (de Geer, 1774): Italy, Brescia, 21.VI.1985, A. Ballerio;
Belohina inexpectata Paulian, 1958: Madagascar, near Beloha, XII.2007, A. Ballerio;
Orubesa athleta (Fairmaire, 1896): Turkmenistan, Merw, Badchys NP, 20.IV.1993, P. Cate & A. Dostal;
Eulasia vittata (Fabricius, 1775): Greece, Thrace, 15 km E of Alexandropolis, 3.VI.1992, A. Ballerio;
Ochodaeus holzschuhi Petrovitz, 1971: Turkey, Mugla, Fethiye, 2.V.1990, S. Dacatra & S. Graziosi.

Non-Ceratocanthinae Hybosoridae
Coilodes sp.: French Guiana, Piste de Kaw, PK 36, 17.VII.2012, O. Boilly;
Phaeochrous lobatus Kuijten, 1978: Philippines, Basilan Island, IV.1993, D. Mohagan;
Anaides sp.: French Guiana, Piste de Kaw, PK 36, 17.VII.2012, O. Boilly;

Cryptogenius fryi Arrow, 1909: Brazil, Nueva Teutonia, V.1977, F. Plaumann (CNC);
Liparochrus septemdecimlineatus Petrovitz, 1968: Australia, Northern Territory, Batchelor, 20.VII.1997, M. Leech.

Non-Ceratocanthini Ceratocanthinae
Ivieolus brooksi Howden & Gill, 2000: French Guiana, Saul, 7 km N, 1 km NW Les Eaux Claires, 4–8. VI.1997, J. Ashe & R. Brooks;
Scarabaeinus termitophilus Silvestri, 1940: Brazil, Rio dos Coros (Sao Paulo), 28.V.1937, F. Silvestri (DEZA);
Scarabatermes amazonensis Howden, 1973: Colombia, Leticia, Amazonas, 20–25.II.1972, S. & J. Peck (CNC);
Trachycrusus lescheni Howden & Gill, 1995: Ecuador, Orellana, Tiputini, 3–6.VIII.2008, LSAM team leg. (LSAM);
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Afrocloetus sp.: Tanzania, Kaguru Mountains, 28.XII. 2011, V. Grebennikov;
Aneilobolus lawrencei Hesse, 1948: South Africa, KwaZulu-Natal, Ngome Forest, 24–27.XI.2006, J. Janak;
Anopsiostes punctatus Paulian, 1982: Ecuador, Orellana, Tiputini, 4.VI.2011, A. Tishechkin;
Astaenomoechus setosus (Boucomont, 1936): French Guiana, Regina, 2012, J.L. Giuglaris;
Astaenomoechus criberrimus Paulian, 1982: French Guiana, Regina, 2012, J.L. Giuglaris;
Aulisostes sp.: Brazil, Rio de Janeiro, Nova Friburgo, Macaé de Cima, III.2000, C. Lopes-Andrade;
Baloghianestes oribatidiformis Ballerio, Gill & Grebennikov, 2011: Cameroon, Mt. Kupé, 19–21.V.2006, V. Grebennikov;
Baloghianestes lissoubai Paulian, 1968: Cameroon, Bakingili, 24–26.V.2006, V. Grebennikov;
Besuchetostes sp.: Sri Lanka, Sabarangamuwa, 31.XII. 2000, collector unknown;
Besuchetostes jaccoudi (Paulian, 1977): Malaysia, Pahang, Gunung Jasar, 7.VIII.2013, M. Maruyama;
Callophilharmostes fleutiauxi (Paulian, 1943): Uganda, Budongo Forest, 6–12.X.2004, T. Wagner;
Carinophilharmostes vadoni (Paulian, 1937): Uganda, Budongo Forest, 6–12.X.2004, T. Wagner;
Ceratocanthoides undatus (Petrovitz, 1973): French Guiana, Regina, 2012, J.L. Giuglaris;
Ceratocanthopsis fulgida (Martínez, 1967): French Guiana, Regina, no date, J.L. Giuglaris;
Ceratocanthus amazonicus Paulian, 1982: French Guiana, Regina, no date, J.L. Giuglaris;
Ceratocanthus sp.: French Guiana, Regina, no date, J.L. Giuglaris;
Chaetophilharmostes chevalieri (Paulian, 1937): Guinea, Nimba Mounts, 29.VI.1991, C. Girard (MNHN);
Cloeotus latebrosus Germar, 1843: no locality data, no date, collector unknown;
Congomostes janssensi (Basilevski, 1955): Zambia, 50 km E of Mwinilunga, 28.X.2008, M. Snizek;
Cryptophilharmostes mahunkai Ballerio, 2000: Tanzania, East Usambara, Amani NR, 15.XII.2011, V. Grebennikov (CNC);
Cryptophilharmostes merkli Ballerio, 2005: Tanzania, Kimboza Forest, 8.I.2012, V. Grebennikov;
Cryptosphaeroides hystrix (Paulian, 1991): Madagascar, Antsiranana, Réserve Spéciale d'Ambre, 26–31.I.2001, B. Fisher et al.;
Cyphopisthes sp.: Malaysia, Perak, Banjaran Bintang, Bukit Berapit, 20–23.II.1997, I. Jenis;
Ebbrittoniella gestroi (Paulian, 1942): Malaysia, Kelantan, between Kampong Raja and Gua Musang, 1–28. IV.2006, P. Cechovsky;
Eusphaeropeltis sp.: Malaysia, Perak, Banjaran Bintang, Bukit Berapit, 20–23.II.1997, I. Jenis;
Germarostes (*Germarostes*) *aphodioides* (Illiger, 1800): USA, Kansas, Oswego, Labette County, 8.IV.1968, G.F. Hevel;
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Germarostes (*Germarostes*) *globosus* (Say, 1835): USA, Virginia, Cape Henry Seashore SP, 10.VI.1974, D. & M. Davis;
Germarostes (*Germarostes*) *oberthueri* Paulian, 1982: French Guiana, Regina, 2012, J.L. Giuglaris;
Germarostes (*Germarostes*) *posticus* (Germar, 1843): Chile, Coquimbo, Los Villas, 28.X.1987, L. Peña;
Germarostes (*Germarostes*) *pullus* Paulian, 1982: Ecuador, Pichincha, San José de Guaramal, 3.VIII.2004, G. Osella;
Germarostes (*Haroldostes*) *diffundus* (Petrovitz, 1976): Argentina, Corrientes, Laguna Ibera, Colonia Pellegrini, 6–14.II.1999, G. Carpaneto et al.;
Germarostes (*Haroldostes*) *senegalensis* (Laporte, 1840): French Guiana, Regina, 2012, J.L. Giuglaris;
Goudotostes sp.: Madagascar, Antisranana, foret de l' Orangea, 22–28.II.2001, B. Fisher et al.;
Macrophilharmostes major (Paulian, 1975): Papua New Guinea, Morobe, Wau, 26.V.1992, G. Cuccodoro;
Madrasostes clypeale Paulian, 1993: Malaysia, Selangor, Ulu Gombak, no date, M. Maruyama;
Madrasostes granulatum (Paulian, 1975): Indonesia, Papua, Kekamatan, Abenaho, Pass valley, 18–25. II.2005, T. Lackner;
Madrasostes mirificum Ballerio & Maruyama, 2010: Malaysia, Perak, Banjaran Titit Wangsa, Gunung Korbu, 11–31.I.1999, P. Cechovsky;
Madrasostes sculpturatum Paulian, 1989: Malaysia, Selangor, Ulu Gombak, 7.IV–6.V.2007, M. Maruyama;
Martinezostes fortecostatus (Gutierrez, 1949): Chile, Concepcion, Periquillo, 2.V.1997, T. Cekalovic;
Melanophilharmostes sp.: Uganda, 20–50 km NNE Fort Portal, 26.XI.2001, M. Snizek;
Nesopalla iviei Paulian & Howden, 1982: Virgin Islands, St. John, Annaberg Ruins, 14.VI.1980, W.B. Muchmore;

Oxymorostes riedeli Ballerio, 2009: Indonesia, Papua, Sorong, Makbon, Malawor, 28.I.2001, A. Riedel;
Paulianostes panggoling Ballerio, 2000: Malaysia, Sabah, Sipitang, Mendolong, 4.XII.1987, S. Adebratt;
Perignamptus sp.: Indonesia, Papua, Kekamatan, Nipsan, Walmak, 10–17.II.2005, T. Lackner;
Petrovitzostes guineensis (Petrovitz, 1968): Uganda, Budongo Forest, 6–12.X.2004, T. Wagner;
Philharmostes sp.: South Africa, KwaZulu-Natal, Hluhluwe NP, 6.I.2004, A. Ballerio;
Philharmostes badius (Petrovitz, 1967): Uganda, Budongo Forest, 6–12.X.2004, T. Wagner;
Philharmostes basicollis Paulian, 1977: Madagascar, Fianarantsoa, 7 km W Ranomafana, 20–31.I.1990, W.E. Steiner;
Philharmostes grebennikovi Ballerio, 2004: Tanzania, West Usambara, Mikuso Forest, 14.I.2013, V. Grebennikov;
Philharmostes werneri Ballerio, 2001: Tanzania, Eastern Usambara, Amani NR, 10–11.X.2002, V. Grebennikov;
Pseudopterorthochaetes endroedyi (Paulian, 1974): Cameroon, Mt. Kupé, 19–21.V.2006, V. Grebennikov;
Pseudosynarmostes mitsinjo Ballerio, 2009: Madagascar, Andasibe, Mitsinjo Forest Reserve, 6.I.2011, A. Ballerio;
Pterorthochaetes insularis Gestro, 1899: Malaysia, Kelantan, 30 km NE Tanah Rata, IV.1999, A. Ballerio;
Synarmostes sp.: Madagascar, Antsiranana, Réserve Spéciale d'Ambre, 26–31.I.2001, B. Fisher et al.

Appendix 3

Identification key to genera of Ceratocanthinae.

1 New World genera **2**
1' African genera (including Madagascar) **12**
1" Asian and Oceanian genera **27**

New World genera

2 Body incapable of conglobation, always depigmented **3**
2' Body capable of conglobation by deflexing head and pronotum and by contracting legs, fully pigmented … **7**
3 Pronotum with distinct V-shaped basal depression ("pseudoscutellum", Fig. 12N) ..... ***Ivieolus***
3' Pronotum without V-shaped basal depression (e.g. Fig. 3D) **4**
4 Hind tibia flattened and widened ..... ***Trachycrusus***
4' Hind tibia elongate and narrow **5**
5 Pronotum distinctly embossed, lateral margins indented (Fig. 12M); fore margin of clypeus distinctly serrate (Fig. 11E) ..... ***Xenocanthus***
5' Pronotum feebly embossed (e.g. Fig. 3D), lateral margins not indented; fore margin of clypeus weakly serrate or smooth **6**
6 Abdomen without lateral glands ..... ***Scarabatermes***
6' Abdomen with protruding lateral gland on each side of first segment ..... ***Scarabaeinus***
7 Enrollment coaptations absent (Fig. 11B) **8**
7' Enrollment coaptations present (Fig. 11A) **9**
8 Head subpentagonal (Fig. 6C), dorsum always with tubercles and/or carinae ..... ***Cloeotus***
8' Head irregularly subpentagonal (fore margin with an angle delimiting genae) (e.g. Fig. 11J), dorsum variably sculptured ..... ***Martinezostes***, ***Germarostes*****,** ***Ceratocanthoides***, ***Glyptogermarostes***, ***Aulisostes***
9 Meso- and metatarsi capable to being folded along inner side of tibia (Fig. 14F) ..... ***Ceratocanthus*** and ***Ceratocanthopsis***
9' Meso- and metatarsi incapable to being folded along inner side of tibia (Fig. 14N) **10**
10 Genal canthus indistinct, genal suture forming slight discontinuity in fore margin, dorsal ocular area absent (Fig. 11H) ..... ***Nesopalla***
10' Genal canthus distinct, genal suture forming slight discontinuity in fore margin, at least small dorsal ocular area present (Fig. 11G) **11**
11 First article of antennal club with proximal face hairy; mandibles without tooth in addition to mandibular apex ..... ***Astaenomoechus***
11' First article of antennal club with proximal face glabrous; mandibles with distinct tooth in addition to mandibular apex ..... ***Anopsiostes***

Afrotropical genera

12 Enrollment coaptations absent (Fig. 11B) **13**
12' Enrollment coaptations present (Fig. 11A) **14**
13 Genal canthus indistinct; base of pronotum raised (Fig. 3I) ..... ***Aneilobolus***
13' Genal canthus distinct (although very short); base of pronotum not raised (Fig. 3J) ..... ***Acanthocerodes***
14 Protibiae broadly arcuate, outer margins smooth with weak tooth apically or at most finely serrate, without distinct teeth (e.g. Fig. 14A,D,K) **15**

14' Protibiae straight, outer margin apically with one or more distinct teeth (e.g. Fig. 14B,J) (or S-shaped with outer margin almost smooth) **21**
15 Head dorsally with trichome (Fig. 7F) ..... ***Callophilharmostes***
15' Head dorsally without trichome, rarely with short sparse setae **16**
16 Genal canthus indistinct, without dorsal ocular area (e.g. Fig. 7C) **17**
16' Genal canthus distinct, with dorsal ocular area (e.g. Fig. 7J) **18**
17 Head broadly subpentagonal (Fig. 7C,D); vertical dimension of apical clypeal extremity about one fourth of clypeal length ..... ***Baloghianestes***
17' Head subrectangular (Fig. 7B); vertical dimension of apical clypeal extremity about half of clypeal length (Fig. 11D) ..... ***Cryptophilharmostes***
18 Dorsal surface of elytra and pronotum with several distinct tubercles (Fig. 7E) ... ***Carinophilharmostes***
18' Dorsal surface of elytra and pronotum without carinae or tubercles (Fig. 7J) **19**
19 Dorsal surface setate (Fig. 7I,L) **20**
19' Dorsal surface glabrous (20×) (Fig. 7G,H,J) ..... ***Philharmostes***
20 Dorsal surface with relatively long claviform setae; pronotum without paradiscal depressions; antennae 10-segmented (Fig. 7L) ..... ***Chaetophilharmostes***
20' Dorsal surface with short and thick setae; pronotum on each side with deep paradiscal depression; antennae 7-segmented (Fig. 7I) ..... ***Petrovitzostes***
21 Genal canthus indistinct, dorsal ocular area absent (Fig. 6B) ..... ***Afrocloetus***
21' Genal canthus distinct, dorsal ocular area present (Fig. 11G) **22**
22 Genal canthus not reaching postocular area (Fig. 4J) ..... ***Congomostes***
22' Genal canthus reaching postocular area **23**
23 Apical portion of elytra with several carinae (Fig. 6D) ..... ***Synarmostes***
23' Apical portion of elytra with the same sculpturing of the remaining elytral surface, lacking any carinae (e.g. Fig. 6E) **24**
24 Dorsal ocular area always present and normally developed; antennal pedicellus straight or slightly curved **26**
24' Dorsal ocular area vestigial or absent; antennal pedicellus strongly curved backwards (Fig. 11M) **25**
25 Dorsal surface sculpturing formed by sparse horseshoe-shaped punctures, covered with setae; posterior margin of pronotum not raised (Fig. 6F) ..... ***Cryptosphaeroides***
25' Dorsal surface sculpturing formed by tubercles, carinae and strong punctures, not covered by setae; posterior margin of pronotum raised (Fig. 6G) ..... ***Goudotostes***
26 Head not subpentagonal, as in Fig. 11I ..... ***Pseudosynarmostes***
26' Head subpentagonal, as in Fig. 11G ... ***Melanophilharmostes*** and ***Pseudopterorthochaetes***

Asian and Oceanian genera

27 Labrum distally distinctly truncate by slight carina bearing a transverse row of long, fine, erect setae, frontal surface irregularly elliptical or semicircular **28**
27' Labrum distally not truncate **30**
28 Fore angles of pronotum broadly rounded (Fig. 12H); mesotibiae short and wide (W/L ratio about 0.3) ..... ***Ebbrittoniella***
28' Fore angles of pronotum triangular (Fig. 12D); mesotibiae slender and relatively narrow (W/L ratio about 0.2) **29**
29 Pronotum evenly convex, with fore margin not raised; humeral callus not marked by longitudinal cariniform process; interocular distance about 7× maximum width of dorsal ocular area; antennal club distinctly longer than funicle ..... ***Cyphopisthes*** (except *C. inexpectatus*)
29' Pronotum depressed, with fore margin distinctly raised; humeral callus marked by distinct longitudinal short carina; interocular distance about 16× maximum width of dorsal ocular area; antennal club subequal in length to funicle ..... ***Paulianostes***
30 Dorsum always metallic; genal canthus complete (reaching postocular area); elytra in lateral view evenly rounded (Fig. 13F) ..... ***Eusphaeropeltis*** (except *E. sabah*)
30' Dorsum of variable colour; genal canthus complete or incomplete or indistinct; elytra in lateral view irregularly swollen towards apex **31**
31 Antennae 9-segmented; dorsum always back or brown and always setate (Fig. 5C) ..... ***Pterorthochaetes***
31' Antennae 10-segmented; dorsal color variable; dorsum either glabrous or setate **32**
32 Mandibles with ventral pore on basal part (Fig. 11Q); volant or flightless species; South India, South East Asia and Australasia ..... ***Perignamptus***, ***Madrasostes***, ***Macrophilharmostes***, ***Oxymorostes***, ***Cyphopisthes inexpectatus***, ***Eushaperopeltis sabah***, ***Besuchetostes howdeni***, ***Besuchetostes jaccoudi***
32' Mandibles without ventral pore on basal part; flightless species; only South India and Sri Lanka .... ***Besuchetostes*** (except *B. howdeni* and *B. jaccoudi*)

Correction added in the proofs: At the page proof stage the authors discovered that the character 107, although correctly illustrated on Fig. 14, wrongly has four (not three, as needed) states scored in the matrix. It turned out that the plate-like shape of bursa copulatrix sclerites was inconsistently scored as either 0 or 1, while the spicule-like and ring-like shapes were consistently scored as either 2 or 3, respectively. This unfortunate error was noted too late to have it adequately addressed. Considered that only 16 among 71 terminals have this character scored (and 44 of the latter have this character inapplicable by lacking these sclerites), it is highly unlikely that this error will notably affect the topology. The only correction this error necessitates is that the list of synapomorphies for the Philharmostes group of genera on p. 37 should have its last character read as "sclerites on bursa copulatrix plate-like".