



Cleonini (Coleoptera: Curculionidae: Lixinae) are monophyletic and flightless: tribe overview, rampant adult homoplasy and illustrated global diversity

YURI G. ARZANOV¹ & VASILY V. GREBENNIKOV²

¹*apt. 36, bul'var Komarova 13/1, Rostov-on-Don, 344092, Russia. E-mail: arz99@mail.ru*

²*CFIA, 960 Carling Ave., Ottawa, ON, K1A 0C6, Canada. E-mail: vasily.grebennikov@inspection.gc.ca*

Dedication

This work is dedicated to the memory of Margarita E. Ter-Minassian (born on May 16, 1910 in Leipzig, Germany, died on April 9, 1995 in St. Petersburg, Russia; obituary: Korotyaev 2010; list of described taxa: Arzanov & Korotyaev 2011), former PhD supervisor of one of us (YuA), in recognition of her outstanding contribution to the knowledge of the Palae-arctic Cleonini weevils.

Abstract

We summarize knowledge of the weevil tribe Cleonini worldwide, including its monophyly, relationships, distribution, biology, immature stages, economic significance and paleontology. We score adult morphological characters for 79 of a total of 96 extant genus-group Cleonini taxa considered valid to date. The resulting matrix contains 121 parsimoniously informative characters scored for 145 ingroup (Cleonini) and 29 outgroup terminals. Maximum Parsimony (MP) and Bayesian Inference (BI) analyses consistently recover monophyletic Lixinae and Cleonini. Relationships within the latter remain unresolved with either 47 (BI) or 37 (MP) branches radiating from the tribe's most recent common ancestor. Most of the speciose genera of Cleonini emerge as monophyletic in both BI and MP analyses (generic names followed by the number of terminals, then by BI posterior probability / MP bootstrap): *Adosomus* (5, 94/77), *Asproparthenis* (6, 99/98), *Chromonotus* (6, 98/85), *Cleonis* (3, 64/76), *Coniocleonus* (10, 95/41), *Conorhynchus* (5, 95/51), *Cyphoclenus* (4, 65/76), *Maximus* (4, 84/68), *Mecaspis* (4, 95/91), *Scaphomorphus* (4, 90/84), *Temnorhinus* (8, 99/62) and *Xanthochelus* (6, 84/71). The genera *Pseudocleonus* (6, -/26) and *Stephanocleonus* (22, -/23) are not recovered in BI and weakly supported in MP. No genera are here added to, or removed from, Cleonini. We suggest that adult morphology of Cleonini was subject to widespread homoplasy obscuring the phylogenetic signal of morphological characters. Unlike the rest of Lixinae, all extant Cleonini are hypothesised to be flightless, even though often being macropterous. All 145 ingroup terminals are illustrated in three standard views; images of the type species of 15 of the 17 genus-group taxa that are not represented in our analysis are provided.

Key words: Lixini, Hennigian comb, beet pests

Introduction

Definition, composition and the neglected phylogeny of Cleonini. Cleonini is a traditionally recognized tribe of curculionid weevils presently consisting of 96 valid genus-group taxa (see Appendix 1) and approximately 545 valid species (Figs 1D-F, 2–6; Alonso-Zarazaga & Lyal 1999, Meregalli & Fremuth 2013). The tribe is included in the subfamily Lixinae (Meregalli 2014), together with two other tribes: Lixini (Figs 1A,B; about 40 genus-group taxa, Alonso-Zarazaga & Lyal 1999) and Rhinocyllini (Fig. 1C; two genus-group taxa; sometimes incorporated in Lixini, Gültekin & Fremuth, 2013). This taxonomic arrangement remained relatively stable since the dawn of Linnaean taxonomy (for historical details see Motschulsky 1860, Chevrolat 1873, Faust 1904, Aslam 1963, Ter-Minassian 1967, 1988). It has, however, always contained one significant logical flaw precluding its satisfactory application, namely that none of these three tribes have ever had their monophyly tested. Highlighting, embracing, and attempting to solve these fundamental phylogenetic uncertainties form the purposes of this paper.

This fundamental ambiguity plaguing the tribe Cleonini (and, in fact, all phylogenetically neglected taxa on all levels of the hierarchical taxonomy) deserves special consideration. Phylogenetic hypothesis is not merely a desirable attribute, but the indispensable and routine pre-requirement of any rational thought pertaining to a biological object, either an individual or their group, such as a species or a tribe. The paramount importance of phylogenetic thinking can be traced from Darwin (1859) through Dobzhansky (1937) to Felsenstein (1985a) and is inevitable. Still, the disciplined phylogenetic approach can be rarely observed not only among the general public, but even among professional biologists. Widespread lack of the consistent “tree thinking” (Omland *et al.* 2008) and the lamentable practice of tolerating non-monophyletic taxa (Zachos 2014), be they “fishes” or non-Avian “dinosaurs”, are hard-to-die examples of such widely practiced logical errors. Unsubstantiated statements are being made about a taxon of questionably monophyly without the necessary disclaimer that there might be no such entity in existence. The persistent logical fault of evading phylogeny when dealing with potentially non-monophyletic groups such as Cleonini, even if commonly practiced, should not be tolerated any longer, let alone indulged.

In this paper we want to avoid falling into this commonly encountered logical trap when handling a taxonomic group of questionable monophyly. From the very beginning we want to state that the “tribe Cleonini” is a taxonomic name historically and uncritically applied to Lixinae weevils of similar adult appearance (cylindrical body with robust rostrum) and biology (preference for arid habitats, no documented active adult flight, larvae in roots and lower stems). This tribe is further taxonomically divided into 96 genus-group taxa. Except for a few members of the native North American fauna (Anderson 1988), none of the latter has been demonstrated as monophyletic using formal cladistic analysis. The sister group of Cleonini is unknown, and indeed the monophyly of the tribe is in question. Even though monophyly of the subfamily Lixinae seems likely, it remains inadequately tested and has rarely been explicitly questioned. Among a number of broadly-sampled, DNA-based phylogenies of Coleoptera (e.g., McKenna *et al.* 2015) and Curculionioidea (e.g., McKenna *et al.* 2009, Gillett *et al.* 2014), none sampled Lixinae with sufficient density to address the monophyly of the group, let alone to hypothesize its sister clade. Analysis of a fragment of elongation factor 1-alpha gene for 34 ingroup Lixinae rooted on a single Molytinae (Arzanov & Stradomsky 2015) was limited in scope and inconclusive. The only exception is the analysis of 157 predominantly West Palaearctic weevils (of them, nine Lixinae representing all three tribes were included) based on 16S and 18S rDNA, wherein Lixinae was the only Curculionidae subfamily consistently recovered as a clade (Hundsdoerfer *et al.* 2009).



FIGURE 1. Lixini (A, B), Rhinocyllini (C) and Cleonini (D–F), live adult beetles. A: *Lachnaeus crinitus* (Russia, Rostov-on-Don); B: *Lixus (Phillixus) subtilis* (Russia, Rostov-on-Don); C: *Rhinocyllus conicus* (Russia, Adygea); D: *Adosomus (Adosomus) roridus* (Russia, Volgograd); E: *Ammocleonus aschabadensis* (Iran, Hormozgan); F: *Apleurus saginatus* (USA, Arizona).



FIGURE 2. Cleonini, live adult beetles. A: *Asproparthenis carinata* (Russia, Rostov-on-Don); B: *Asproparthenis carinicollis* (Russia, Rostov-on-Don); C: *Asproparthenis obsoletefasciata* (Kazakhstan, Karynzharyk); D: *Asproparthenis punctiventris* (Russia, Rostov-on-Don); E: *Bothynoderes affinis* (Russia, Volgograd reg.); F: *Bothynoderes declivis* (Russia, Volgograd); G: *Brachycleonus fronto* (Kazakhstan, Priaral Karakum); H: *Calodemus errans* (Namibia, Khomas); I: *Chromonotus* (*Chromonotus*) *pictus* (Kazakhstan, Koksem).

The review of North American Cleonini by Anderson (1988) was the first, and until the present, the only attempt to apply strict phylogenetic methodology to the members of the tribe Cleonini (and, more inclusively, to any Lixinae). This is the only phylogenetically-conscious, Cleonini-focussed work where the lack of the underlying phylogenetic hypothesis has been clearly articulated. Part of this uncertainty was explicitly addressed in that paper by analysing two native and supposedly monophyletic North American Cleonini radiations: the genus *Apleurus* and the North American members of the genus *Scaphomorphus* (as *Cleonidius*) using 31 and 22 adult morphological characters, respectively. In the same work the historical changes in taxonomic composition of Lixinae (as Cleoninae) were discussed, while the subfamily's monophyly was accepted by referring to the unique shape of the adult labial palpi (small, telescoped, three-segmented). Some other characters seemingly characteristic of Lixinae (such as paired symbiont bacteria pouches attached to the vagina, hind wing venation characters, ventral attachment of palpi to labium, testes structure, generalized stem- or root-mining larvae) were not scored for the analysis but were interpreted as plesiomorphic.

Meregalli & Silvestro (2008) were reportedly the first to attempt analysing the entire tribe Cleonini using a formalized approach. They constructed a matrix comprising 68 Cleonini genera scored for 30 adult morphological characters. They also reported that the clade of three genera (South African *Centrocleonus* and *Xenomacrus*, plus Indo-African *Xanthochelus*) is "...morphologically intermediate between the tribes Lixini and Cleonini..." (Meregalli & Silvestro 2008: 128) and forms the sister to the rest of Cleonini. The data (list of terminals, matrix, list of characters) and methods have not, however, been reported. Moreover, the analysis could not test monophyly of the ingroup (=the tribe Cleonini), since a single non-Cleonini terminal (Lixinae: *Lixus*) employed to root

topologies automatically forced monophyly of Cleonini. Because of these methodological shortcomings their results (partly repeated in Meregalli 2014) are not verifiable.

The sister-group and phylogenetic position of Lixinae have been addressed a few times, though as long as the subfamily is questionably monophyletic, any attempt to search for its sister-group is logically impossible. Zherikhin & Egorov (1990: 86, as Cleoninae) boldly considered the subfamily to be undoubtedly monophyletic and "...undoubtedly derived from within Molytinae...", with either of the the questionably monophyletic tribes Mecyslobini or Paipalesomini forming the sister group. Oberprieler *et al.* (2007) stated that "the boundary is also hazy between Molytinae and traditional Lixinae...". On the DNA-based tree of McKenna *et al.* (2009) the sister clade of Lixinae was formed by *Baris* and *Smicronyx*, while in that of Gillett *et al.* (2014) it was an unidentified molytine from China. Thus, the sister group of Lixinae, if the latter is indeed monophyletic, is currently inadequately tested and remains entirely unknown.



FIGURE 3. Cleonini, live adult beetles. A: *Chromonotus (Chromonotus) vittatus* (Russia, Astrakhan reg.); B: *Chromosomus fischeri* (Kazakhstan, Onere); C: *Cleonis pigra* (Russia, Rostov reg.); D: *Coniocleonus (Augustecleonus) turbatus* (Russia, Rostov reg.); E: *Coniocleonus (Plagiographus) nigrosuturatus* (Russia, Rostov reg.); F: *Conorhynchus lacerta* (Kazakhstan, Karynzharyk); G: *Conorhynchus nigrivittis* (Russia, Volgograd reg.); H: *Cyphocleonus cenchrus* (Kazakhstan, Karynzharyk); I: *Cyphocleonus dealbatus* (Russia, Rostov-on-Don).

Distribution and regional diversity of Cleonini. Recent Cleonini are known from most of the Northern Hemisphere (Fig. 7). Only in continental Africa and Madagascar can they be found south of the equator. Three most comprehensive species-level treatments of regional faunas cover most of the Holarctic Region and target the former USSR (Ter-Minassian 1988, 245 species in 43 genera), the Nearctic Region (Anderson 1988, 35 species in five genera; of them two genera each with one species not native), and the northern part of the West Palaearctic Region north of the Pyrenees, the Alps and the Balkans (Skuhrovec *et al.* 2014; 55 species in 18 genera). The rich Cleonini fauna of Mongolia was summarized by Ter-Minassian (1974, 1979, 1984). Japan, on the other hand, has only seven Cleonini species-group names listed by Kojima & Morimoto (2004). The 25 Cleonini species of Central

Europe are placed in 12 genera and were illustrated by Stejskal & Trnka (2014). The Catalog of the Palearctic Coleoptera lists 483 species and subspecies in 60 genera (Meregalli & Fremuth 2013). Outside of these areas regional diversity of Cleonini is poorly studied, with many Oriental and Afrotropical species (and some genera; see below) known only from the original descriptions. By far the greatest regional diversity of Cleonini is in the arid semi-desert areas of the Palearctic region, where up to 52 species might be found sympatrically (Fig. 7). The most recent online catalogue by Meregalli (2017) aims to summarize all geographic and/or taxonomic information on all available genus- and species-group names of Cleonini, often accompanied by images of the type specimens.



FIGURE 4. Cleonini, live adult beetles. A: *Cyphocleonus trisulcatus* (Russia, Volgograd reg.); B: *Entymetopus (Entymetopus) lineolatus* (Kazakhstan, Kendirli); C: *Eurycleonus talamellii* (Morocco, Tan-Tan prov.); D: *Glebius confluens* (Kazakhstan, Karatau); E: *Leucochromus imperialis* (Kazakhstan, Akkuduk); F: *Leucomigus candidatus* (Kazakhstan, Balkhash); G: *Maximus granulatus* (Kazakhstan, Ustyurt); H: *Maximus strabus* (Russia, Volgograd reg.); I: *Mecaspis alternans* (Ukraine, Kharkiv).

Biology of Cleonini. Scattered data on the biology of Cleonini were summarized by Anderson (1988), Volovik (2010), Meregalli (2014) and Stejskal & Trnka (2014). Members of the tribe show notable preference for xeric habitats and sandy soil. Endophagous larvae are either mono-, oligo- or polyphagous on herb and shrub eudicots, depending on the species and data availability. The phylogenetic pattern of Cleonini host-plant preferences, though suggestive, has never been addressed as thoroughly as it deserves (see, for example, Kobayashi *et al.* 2012 on Attelabidae or Winter *et al.* 2017 on Apionini).

Perhaps more than half of the species of Cleonini are to some degree brachypterous, since fully developed versus vestigial hind wings might be found within the same species (Anderson 1988). When present, the fully developed hind wings seem to be never used for locomotion, since Cleonini have never been documented to fly (unlike markedly more volant Lixini and Rhinocyllini).



FIGURE 5. Cleonini, live adult beetles. A: *Menecleonus virgatus* (Kazakhstan, Mametkazgan); B: *Pleurocleonus quadrivittatus* (Russia, Rostov-on-Don); C: *Pleurocleonus sollicitus* (Russia, Rostov reg.); D: *Pseudocleonus cinereus* (Russia, Rostov reg.); E: *Pseudocleonus marginicollis* (Kyrgyzstan, Osh reg.); F: *Rhabdorhynchus karelini* (Kazakhstan, Kendirli); G: *Scaphomorphus quadrilineatus* (USA, Arizona); H: *Scaphomorphus vibex* (Kazakhstan, Malye Barsuki); I: *Trichocleonus leucophyllus* (Kazakhstan, Khantau).

As in all Lixinae, external sexual dimorphism in Cleonini is weakly developed. The most prominent sexually dimorphic character is the surfaces of the first two abdominal ventrites, which are weakly concave in ♂s and weakly convex in ♀s (Fig. 11). Furthermore, ♀s tend to be larger in size and with body scales more abraded (although minute ♀s and much larger ♂s might be regularly encountered, with their size likely mainly determined by the larval nourishment, rather than by the sex). In the temperate Palaearctic with a single generation per year ♂s are more abundant in early spring, since ♀s tend to emerge slightly later (personal observations).

Unlike the rest of Lixinae, immature Cleonini (Fig. 6) tend to inhabit the lower parts of the host plant, mainly roots and rarely lower stems, and have never been reported from inflorescences frequented by other Lixinae. Cleonini larvae normally live inside the plant tissue of the root neck or collar of large plants (fig. 4E in Trnka *et al.* 2015), or form a characteristically swollen gall on a narrow root of the host plant (Fig. 6B,C) where larvae and pupae orient themselves head up and parallel to the root axis (Fig. 6D). The strategy of gall formation permits immature Cleonini to utilize roots otherwise much thinner than the body of the fully mature larvae (fig. 2 in Volovik 2010). An alternative approach to the narrow root problem is deployed by larvae of some North American *Scaphomorphus*, which construct peculiar “sand tubes” (O’Brien & Marshall 1987, Hooper & Holdaway 2007). Construction of such seemingly protective underground (Fig. B, Stejskal *et al.* 2014) or sometimes aerial (Gültekin 2012) chambers is not infrequent and might perhaps be linked to the improved moisture retention in arid environments. The extremely arid conditions of the Negev Desert were linked with a seemingly unique example of *Conorhynchus pistor* living most of its adult life underground in a mud structure affixed to the plant roots and benefiting the host plant (*Salsola inermis*) through a tri-party symbiotic interaction with a bacterium (*Klebsiella*

pneumonia) that supplies nitrogen to the system (Shelef *et al.* 2013). It should be noted, however, that such seemingly protective structures are not unique to Cleonini, since aerial pupation chambers termed “trehala” have also been reported in some Lixini (*Larinus*; Gültekin 2008, Gültekin & Shahreyary-Nejad 2015). With so much variety among a few species adequately known, it is plausible to think that behavioral aspects of the developmental biology of Cleonini will form a future fertile research ground.

Immature stages of Cleonini. The morphology of immature Cleonini is remarkably poorly known and has never been used as a source of phylogenetically-informative data. Only recently the first adequately illustrated larval descriptions became available (Zotov 2011), supplying a wealth of morphological data, including larval chaetotaxy (Stejskal *et al.* 2014, Trnka *et al.* 2015).



FIGURE 6. Cleonini, immature stages. A-F: *Rhabdorrhynchus* sp.: habitat in Kazakhstan (Kegen) with host plant *Lappula* sp. (Boraginaceae) flowering blue (A); roots of *Lappula* sp. with gall formed by immature beetle (B-D); immature stages (E-F). G-I: *Adosomus* (*Adosomus*) *roridus*: egg (G), larva (H) and pupa (I); from Trnka *et al.* (2015). J-L: *Coniocleonus* (*Plagiographus*) *nigrosuturatus*; larva (J, K) and pupa (L), from Stejskal *et al.* (2014).

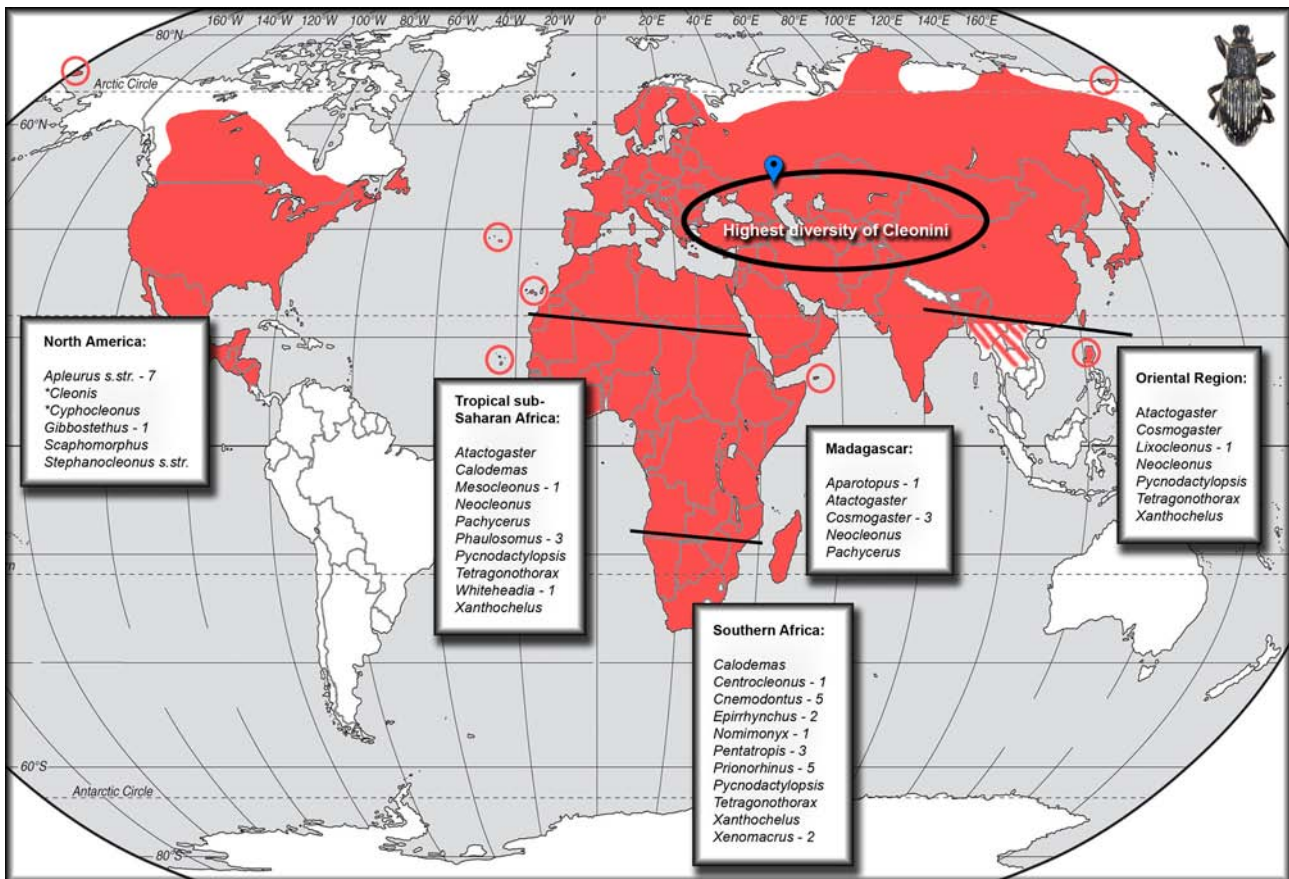


FIGURE 7. World distribution of Cleonini. The presence of the tribe in Indochina is poorly documented and shown as striped. Northern limits in North America are from Bouchard *et al.* (2013). Text boxes list genus-group taxa in five main “peripheral” regions; those endemic have the number of species indicated. Asterisk (*) denotes non-native taxa introduced by humans. Point on the map denotes the Baskunchak-Elton locality on the Kazakhstan-Russia border with the highest documented diversity of Cleonini containing at least the following 52 species: *Adosomus* (*Adosomus*) *roridus*, *Asproparthenis* *carinata*, *A. carinicollis*, *A. foveocollis*, *A. obsoletefasciata*, *A. punctiventris*, *A. vexata*, *Bothynoderes* *affinis*, *B. declivis*, *Chromonotus* (*Chevrolatius*) *bipunctatus*, *Ch.* (*Chevrolatius*) *hirsutulus*, *Ch.* (*Chevrolatius*) *pilosellus*, *Ch.* (*Chromonotus*) *pictus*, *Ch.* (*Chromonotus*) *vittatus*, *Cleonis* *pigra*, *Coniocleonus* (*Augustecleonus*) *hollbergi*, *C.* (*Plagiographus*) *crinipes*, *C.* (*Plagiographus*) *nigrosaturatus*, *Conorhynchus* *excavatus*, *C. lacerta*, *C. nigrivittis*, *C. pulverulentus*, *Cyphocleonus* *achates*, *C. adumbratus*, *C. cenchrus*, *C. dealbatus*, *C. trisulcatus*, *Epexochus* *lehmani*, *Eumecops* *kittaryi*, *Eurysternus* *limis*, *Leucomigus* *candidateus*, *Leucophyes* *pedestris*, *Maximus* *strabus*, *M. verrucosus*, *Mecaspis* *alternans*, *Pachycerus* *segnis*, *Pleurocleonus* *quadrivittatus*, *P. sollicitus*, *Pseudocleonus* *cinereus*, *P. grammicus*, *P. marginicollis*, *Rhabdorrhynchus* *echii*, *Scaphomorphus* *vibex*, *Stephanocleonus* (*Sanzia*) *microgrammus*, *S.* (*Sanzia*) *tetragrammus*, *Temnorhinus* (*Massimocleonus*) *elongatus*, *T.* (*Massimocleonus*) *nasutus*, *T.* (*Temnorhinus*) *hololeucus*, *T.* (*Temnorhinus*) *kirghisicus*, *T.* (*Temnorhinus*) *verecundus*, *Terminasiana* *granosa*, *Xanthochelus* *nomas*.

Economic significance of Cleonini as beetroot pests and biocontrol agents. Palaearctic Cleonini are infamous for being notorious pests of *Beta vulgaris* (beetroot or sugar beet, Amaranthaceae; Ter-Minassian 1988). Approximately half of the known genera have at least one of their species mentioned as damaging beet. Fourteen nominal species are listed as economically significant pests in the global database of the European and Mediterranean Plant Protection Organization (EPPO 2015). This list contains, however, significant taxonomic irregularities, thus underlying the practical importance of a stable and phylogenetically-based taxonomy. For example, the genus *Bothynoderes* is listed twice using both its valid name and a synonym. Also, the generic name *Cleonis* is erroneously treated as a masculine noun and further contains species epithets never assigned to it. In the Western Palaearctic, where the beet industry is most developed, significant efforts have been invested to mitigate the economic risks from Cleonini pests, including development of attractants enhancing field trap performance (Tóth *et al.* 2007, Lemic *et al.* 2016). *Cleonis pigra*, the only unintentionally adventive species of Cleonini in North America introduced before 1919 (Anderson 1988) has not yet been reported as a significant pest of beets in the

New World, though potential introduction of likely more aggressive species of such genera as *Asproparthenis* or *Bothynoderes* might have a markedly profound economic effect. Besides damaging beetles, various species of *Adosomus* are significant pests of *Artemisia* L. (Asteraceae) preventing formation of healthy plants and sand fixation in the arid parts of northern China (Wang *et al.* 2009), while adults of *Cosmogaster lateralis* are injurious to cotton in Ivory Coast, biting off the young plants (Marshall 1944).

Cleonini have a proven potential as biocontrol agents against invasive Palaeartic plants. *Cyphocleonus achates* has been released in North America against invasive spotted knapweed (*Centaurea stoebe* L., Asteraceae; Stinson *et al.* 1994, Story *et al.* 2006). Another Palaeartic beetle, *Pachycerus segnis*, was tested for release in Australia against invasive *Heliotropium europaeum* L. (Boraginaceae; as *P. cordiger*, Huber & Vayssieres 1990). With the ever increasing number and economic impact of invasive Palaeartic plants, the role of Cleonini as biological agents is likely only to rise. In a few cases native Cleonini have been considered as biocontrol agents against native weeds, such as *Scaphomorphus trivittatus* used against purple locoweed (*Astragalus mollissimus* Torrey, Fabaceae) in the western United States (Pomerinke *et al.* 1995).

Paleontology of Cleonini. Fossils of Cleonini, although relatively numerous, are of little help in establishing a realistic minimal age for the group, if the latter is indeed monophyletic. The only two taxonomically valid extinct genera, *Cleonolithus* Bassi and *Pliocleonus* Gersdorf, were named from fossils of the Lower Pliocene of Italy and the Upper Pliocene of Germany (Alonso-Zarazaga & Lyal 1999), respectively. Records as old as Lower Oligocene in age have been vaguely attributed to the genus *Cleonis* (listed in Alonso-Zarazaga & Lyal 1999), although at least some of them have been misidentified (Kingsolver 1962). All historical pre-Hennigian attributions were based on the phylogenetically misleading criterion of general similarity. Morphological synapomorphies for the tribe are still lacking, rendering any fossil attribution to Cleonini questionable. No fossil has been assigned to Cleonini by either cladistic analysis (as done for other insect groups, e.g. Parker & Grimaldi 2014, Yamamoto *et al.* 2016) or by citing known clade synapomorphies detected on the fossil (e.g. Fikáček *et al.* 2012). A sobering example of such non-cladistic palaeontological practices is *Troxites germari* Goldenberg originally reported as a scarab beetle, but later thought to be a weevil, then ‘probably a fruit’ and then a part of a crustacean (see Krell 2000). In our opinion all fossils of Cleonini should be critically re-examined from the phylogenetic standpoint, as routinely done in other groups (e.g. Cassis & Schuh 2010) before becoming useful for the clade calibration purpose. On the other hand, Cleonini fossils of the late Pleistocene attributable to extant genera (mainly *Coniocleonus* and *Stephanocleonus*) and sometime to extant species are abundant in and around the former Beringia, particularly in Russia, and are often and seemingly justifiably employed for the paleo-climatic reconstructions (Sher *et al.* 2005, Kuzmina *et al.* 2008).

Goals of this work. This project was designed as a way to summarize results of a life-long engagement with Cleonini weevils by the senior author delivered and analysed in a strict phylogenetic format. The main goal of this paper, therefore, is to utilize information contained in adult morphological diversity of Cleonini weevils in an attempt to propose the first phylogeny of the tribe. By doing so, we attempt to test the tribe’s monophyly and shed light on its sister-group. We also attempt to test the taxonomically implied monophyly of all genus-group taxa of Cleonini (if represented by two or more terminals), hypothesize their respective sister-groups, assess statistical support for each hypothesis and make an overall attempt to develop the first phylogenetic framework for the classification of Cleonini. The second goal of this paper is to stimulate further work on Cleonini by summarizing the current state of knowledge for this tribe. We provide illustrations of adult beetles representing all 145 ingroup terminals and all but two among 96 currently valid genus-group Cleonini taxa, along with a list of the latter. Our overall intent is to focus the attention of phylogenetically-minded biologists on Cleonini and propel, to the extent possible, this somewhat neglected group into the current age of integrative evolutionary biology.

Material and methods

Museum abbreviations (with the name of contact person/persons in brackets; an asterisk [*] indicates people who took images for Figs 30–32):

HNHM Hungarian Natural History Museum, Budapest, Hungary (Szél Győző, Tamás Németh*);
IARI Division of Entomology, Indian Agricultural Research Institute, New Delhi, India (Vilayanoor V. Ramamurthy*);

MCZ	Museum of Comparative Zoology, Harvard University, Oxford, USA (Philip D. Perkins);
MNHN	Muséum National d'Histoire Naturelle, Paris, France (Antoine Mantilleri*, Hélène Perrin);
MTD	Senckenberg Naturhistorische Sammlungen Dresden, Dresden, Germany (Olaf Jäger, Marc Srouer*, Klaus-Dieter Klass);
MZLU	Museum of Biology (Entomology), Lund University, Lund, Sweden (Christoffer Fägerström*);
ZIN	Zoological Institute, St. Petersburg, Russia (Boris A. Korotyaev, Andery M. Shapovalov*);
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (Bernd Jäger*, Johannes Frisch);
ZMUH	Universität von Hamburg, Zoologisches Institut und Zoologisches Museum, Hamburg, Germany (Martin Husemann*);
ZMUM	Zoological Museum, Moscow State University, Moscow, Russia (Alexey Gussakov);
YuAC	collection of Yuri G. Arzanov, Rostov-on-Don, Russia (Yuri G. Arzanov).

Design and workflow of this project follow those of Ballerio & Grebennikov (2016). Due to scarcity and/or unavailability of other data (fossils, immatures, DNA, biology), adult external and internal morphological characters of recent species were the only source of all information scored in a matrix for phylogenetic analysis. Dry pinned adult specimens were assembled from a variety of sources (see Appendix 3), predominantly from YuAC. At least one specimen of each sex, if available, was softened in warm water, placed in glycerol, disarticulated and studied under a dissecting microscope for character scoring.

Matrix construction. The ingroup for this analysis was defined to correspond to the tribe Cleonini in its current taxonomic delimitation (see above). We were unable to receive and adequately study specimens representing the 17 most obscure genus-group Cleonini taxa: *Aparotopus*, *Arabocleonus*, *Bodemeyeria*, *Centrocleonus*, *Ephimeronotus*, *Epirrhynchus*, *Gibbostethus*, *Hemeurysternus*, *Lixocleonus*, *Lixoglyptus*, *Mesocleonus*, *Nomimonyx*, *Pajnisoodes*, *Paraleurochromus*, *Phaulosomus*, *Pseudeumecops* and *Trichotocleonus*; for them (excepting *Epirrhynchus* and *Paraleucochromus*) we provide adult images of the type species. For the remaining 79 genus-group Cleonini taxa we studied and scored in the matrix at least one species, preferring whenever possible, the type species. The most speciose genus-group taxa such as the genus *Asproparthenis* or the subgenus *Stephanocleonus* are represented by 6 and 11 terminals respectively (for details see Appendix 3). Overall we scored and illustrated 145 ingroup Cleonini terminals.

To test the taxonomically implied monophyly of Cleonini, the closer outgroup consisted of 18 terminals representing 18 genus-group taxa of non-Cleonini Lixinae of both remaining tribes: Lixini (16) and Rhinocyllini (2). To test the taxonomically implied monophyly of Lixinae, the more distant non-Lixinae outgroup consisted of 10 terminals representing 10 genus-group taxa: Molytinae (7), Curculioninae (1), Entiminae (1) and Hyperinae (1). All topologies were consistently rooted on a branch leading to a representative of the most distantly related Anthribidae. The resulting matrix (Table 1) containing 174 terminals and 121 parsimoniously informative adult morphological characters was assembled in Winclada (Nixon 2002).

Analyses. Two analyses, each utilizing a different topology-building algorithm, were implemented: Bayesian Inference (BI) and Maximum Parsimony (MP). In both analyses all multistate characters were treated as unordered (including 12 linear quantitative variations, such as length or size or ratio: characters 1, 2, 3, 18, 19, 35, 36, 64, 72, 102, 106, 109). All characters were equally weighted.

For the Bayesian inference (BI) analysis, MrBayes 3.2.3 (Ronquist *et al.* 2012) was used. The settings included the Mkv common-mechanism Maximum Likelihood model for morphology (Lewis 2001), two MCMC runs of four chains run for 15 million generations, convergence judged to have occurred when the standard deviation of split frequencies was <0.01. The first 25% of trees were discarded as burn-in. The nexus file from Yamamoto *et al.* (2016, Supplement 2) was used, and the original rove-beetle matrix was substituted with that for Cleonini and then exported from Winclada in the nexus format (Electronic Supplement). Commands executed at the command line were as follows (in square brackets []): [Begin mrbayes; lset nst=1 rates=gamma coding=variable; mcmc ngen=15000000 samplefreq=1000 printfreq=1000 nruns=2 nchains=4 mcmcdiag=yes diagfreq=1000 savebrlens=yes relburnin=yes burninfrac=0.25; END;]. Posterior probabilities of 50% and above were used as a measure of clade support; clades with posterior probabilities <50% were collapsed.

The relatively large size of the matrix precluded use of exhaustive searches for the MP topology and, therefore, various heuristic approaches were tested to find the best performing analysis. Hennig86 (Farris 1989) was unable to do an adequate search, while searches using PAUP (Swofford 2003) and NONA (Goloboff 1999) consistently

resulted in suboptimal topologies some 3–20 steps longer than the overflow of 100 shortest trees obtained with TNT (Goloboff *et al.* 2008). The latter tree-building software was therefore chosen to detect the MP trees, while their consensus (Fig. 9) was obtained using 1000 bootstrap (Felsenstein 1985b) recalculations. The following command string was used in a TNT script file (in square brackets []; the matrix was named “unordered.tnt”; slash “/” separating lines): [procedure unordered.tnt;/log unordered.out;/mult;/bbreak=tbr;/nelsen */;/resample replications 1000;]. Considering the widespread homoplasy and low branch support, only the most consistently recovered taxa had their unambiguously optimized synapomorphies reported (Fig. 10) by opening the randomly selected (=first) among the most parsimonious trees in Winclada and plotting evolutionary events on branches.

Comments on selected characters. In preparation for the herein reported analysis, the senior author conducted preliminary studies illustrating diversity and assessing phylogenetic applicability of the following structures: internal sac of aedeagus (=endophallus; Arzanov 2003, 2008b, 2009b; Figs 41–43), rostrum (Arzanov 2007a; Figs 33–35) and elytral scales (Arzanov & Valov 2011; Fig. 40), as well as submentum (Fig. 36), maxillae (Fig. 37), tarsi (Fig. 38), claws (Fig. 39), ♀ abdominal sternite 8 (Fig. 45), hemisternites 9 (Fig. 45) and spermatheca (Fig. 46).

To maintain data consistency when scoring morphological structures in the matrix, certain assumptions have to be made, documented and consistently implemented. For example, monophyly of Lixinae (Anderson 1988), or at least their morphological distinctness from other weevils, was historically linked to the highly unusual structure of their prementum. Labial palpi of Lixinae are always indicated as unusually small (wider than long, which is achieved by significant length reduction and likely telescopic arrangements of palpomeres; fig. 90 in Anderson 2002). The exact number of palpomeres, however, was conflictingly given as either three (externally appearing as one due to telescoping arrangement; Anderson 2002), or one, two, or three (Zherikhin & Egorov 1990). An attempt to use this structure for cladistic purposes by delimiting discrete independent characters and their states was not trivial. Counting exact number of minute palpomeres was technically challenging and we were unable to do so consistently for all 174 terminals. Instead we scored this character by assessing palpomeres externally as either clearly three-segmented (non-Lixinae) or, alternatively, externally appearing as one-segmented (Lixinae, Character 35).

We originally attempted to consistently score the dorso-apical versus ventral attachment of labial palpi to the prementum, but were unable to do so due to the numerous intermediate situations defying discrete scoring. Furthermore, the size of the prementum is often referred to as “large” and diagnostic for the subfamily (Anderson 2002). It is indeed exceptionally large in at least one ingroup taxon, the monotypic genus *Mongolocleonus*, where it covers base of the mandibles when viewed ventrally. Most other times we were unable to distinctly separate the “large” prementum of Lixinae from the “small” one in the outgroups and, therefore, this character has not been scored for the matrix.

Lixinae, and particularly Cleonini, have a notably complex and diversified endophallus, equipped with numerous lobes (Figs 41–43). Following the pioneering work by Anderson (1988), we specifically attempted to utilize the morphological diversity of Cleonini genitalia. For ♂s we studied the shape of the inflated internal sac of the aedeagus (=endophallus, Fig. 41) following preparation methods and terminology of Arzanov (2003) and Van Dam (2014). Scoring the structures of the endophallus of Lixinae and non-Lixinae terminals was challenging due to uncertain homology. We decided to treat the presence of the complete and diversified endophallus similarly to such complex character as presence and structure of hind wings in a situation, when the hind wings might be absent. Thus the first endophallus character refers to the absence versus presence of complex and diversified endophallus as a whole and was scored for all terminals. All other characters dealing with various endophallus structures were scored only for those terminals that were deemed to have a complex and diversified endophallus. In other words, all outgroup terminals scored as having a simple endophallus were consistently scored as “-“ (=inapplicable character) for absence/presence (or shape) of individual endophallus lobes (and not as “0”). We recognize that such a formalized approach might not be the best reflection of the observed reality, however it is judged as the most suitable for converting complex evolutionary phenomena into the rigid shape of a machine-read matrix. For ♀s, three internal structures were studied: sternite 8 (Fig. 44), hemisternite 9 (Fig. 45) and spermatheca (Fig. 46); their terminology is explained on respective illustrations.

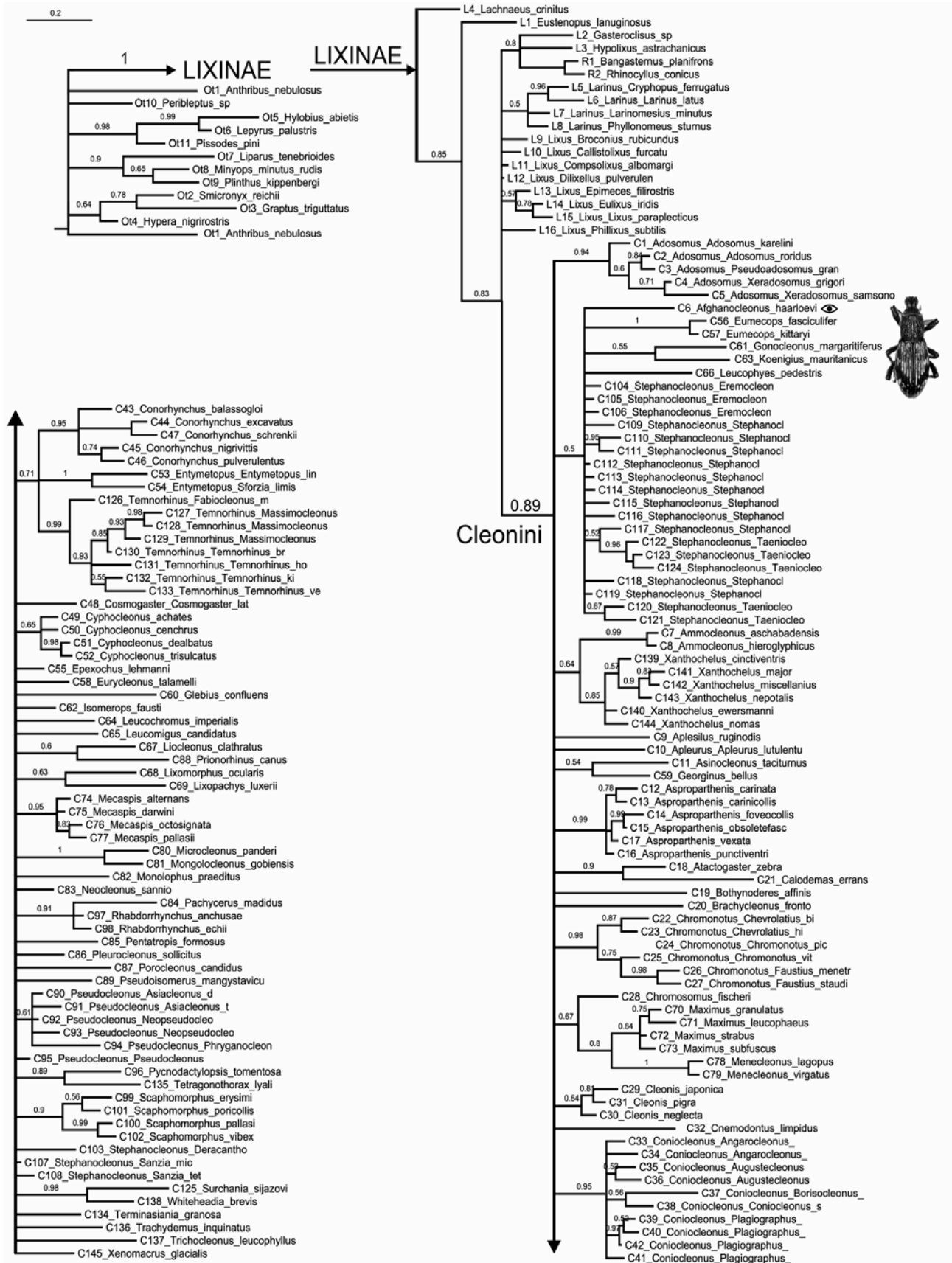


FIGURE 8. Bayesian inference majority rule consensus phylogram of Cleonini. Numbers on branches are posterior probabilities. Terminal names are truncated to the first 32 symbols; see Appendix 3 for the full names.

At least two potentially informative sources of adult morphological characters were excluded from the analysis due to the lack of adequate research and/or necessity to disarticulate specimens: the hind wing venation (also inapplicable for numerous brachypterous terminals) and the shape of the metendosternite. We also did not attempt to consistently check the presence and record the shape of paired symbiont sacs attached to vagina and thought to be characteristic of Lixinae, though not necessarily synapomorphic (Anderson 1988).

Results

The BI analysis ran for about 20 hours on a desktop PC and resulted in a topology depicted in Fig. 8. Both Lixinae and Cleonini are found to be monophyletic, with posterior probabilities 100 and 89%, respectively. Relationships within Cleonini are remarkably unresolved, with 47 branches forming the basal-most polytomy. The majority of genus-group taxa represented in the analysis by two or more terminals form variably supported clades, such as the genera *Adosomus* (94%), *Asproparthenis* (99%), *Chromonotus* (98%), *Cleonis* (64%), *Coniocleonus* (95%), *Conorhynchus* (95%), *Cyphoclenus* (65%), *Maximus* (84%), *Mecaspis* (95%), *Scaphomorphus* (90%), *Temnorhinus* (99%), *Xanthochelus* (84%). Only three clades of two (or more) genera with posterior probabilities exceeding 90% are found: *Atactogaster* + *Calodemus*; *Microcleonus* + *Mongolocleonus*; *Pachycerus* + *Rhabdorrhynchus*.

The MP analysis ran for about three minutes on the same desktop PC and resulted in an overflow of 100 shortest trees, each with the length of 2276 steps, consistency index 0.06 and retention index 0.59. The bootstrap consensus topology (Fig. 9) recovered a monophyletic Lixinae (bootstrap support 60%) and monophyletic Cleonini (bootstrap support 24%). As in the BI topology (Fig. 8), the main feature of the MP topology is the basal-most Cleonini polytomy formed by 37 branches. Similar to the BI topology, the majority of congeneric terminals form variously supported clades, including the genera *Pseudocleonus* (bootstrap support 26%) and *Stephanocleonus* (bootstrap support 23%) not recovered in BI. Unambiguously optimized synapomorphies of the subfamily Lixinae, the tribe Cleonini and 24 genus-group Cleonini taxa are depicted in Fig. 10.

Discussion

Both BI and MP topologies (Figs 8 and 9, respectively) are highly congruent, suggesting that both analyses, even though they are based on different methods, converged in detecting the most realistic trees that best represent the data.

Monophyletic Lixinae and Cleonini. The most remarkable feature of both BI and MP trees is that they corroborate the pre-existing vague taxonomically implied thoughts on Cleonini without, however, providing significant new insights. Both family-group taxa targeted in the analysis, the subfamily Lixinae and the tribe Cleonini, consistently emerge as monophyletic, which is in line with historical and current taxonomic treatments. Statistical support for monophyly of Lixinae is consistently stronger than that of Cleonini, which also agrees with the vaguely expressed ideas of the pre-Hennigian authors. Both Lixinae and Cleonini withstood the scrutiny of not only molecular phylogenetic analysis (Hundsdoerfer *et al.* 2009), but also that based on adult morphology and, unless explicitly challenged, should be considered monophyletic.

Synapomorphies of Cleonini. Four unambiguously optimized synapomorphies of Cleonini, namely: 26/0 (head, antenna, antennomere 5, ratio length to width: <1x), 39/1 (prothorax, anterior contour, postocular lobes, lateral view: present), 102/0 (female genitalia, sternite 8, ratio of length of apodeme to that of lamellae: <0.9x) and 112/0 (female genitalia, basal part of hemisternite 9, large depression on its surface: absent, sclerite relatively flat) have never been previously suggested as characteristic of the tribe and, indeed, none of them is uniquely optimized (Fig. 10) on the randomly selected most parsimonious topology. Being homoplasies, and the two latter being internal and sex-specific, they are not expected to be of much utility in identifying fossil members of Cleonini.

Unresolved internal phylogeny of Cleonini. The basal-most polytomy (=Hennigian comb) of Cleonini recovered in both analyses with 47 (BI) or 37 (MP) branches radiating from the most recent common ancestor of Cleonini is another most remarkable result. Such a topology suggests at least two non-mutually exclusive explanations. The first is that the basal-most splits within Cleonini occurred relatively rapidly and without accumulation of detectable morphological signatures. Another interpretation suggests that the amount of homoplasy in Cleonini is so widespread that it fully obscures any phylogenetic signal. Yet another interpretation would call for a need to include additional morphological characters and to rework the coding of existing characters to better describe variation in their states. More likely, all three factors have played their roles. The completely foggy early evolution of Cleonini undetected in our analyses agrees well with the historical taxonomic treatment of this sizable tribe of relatively large and noticeable beetles, which has never been subdivided into subtribes. So it should remain, at least for the time being.

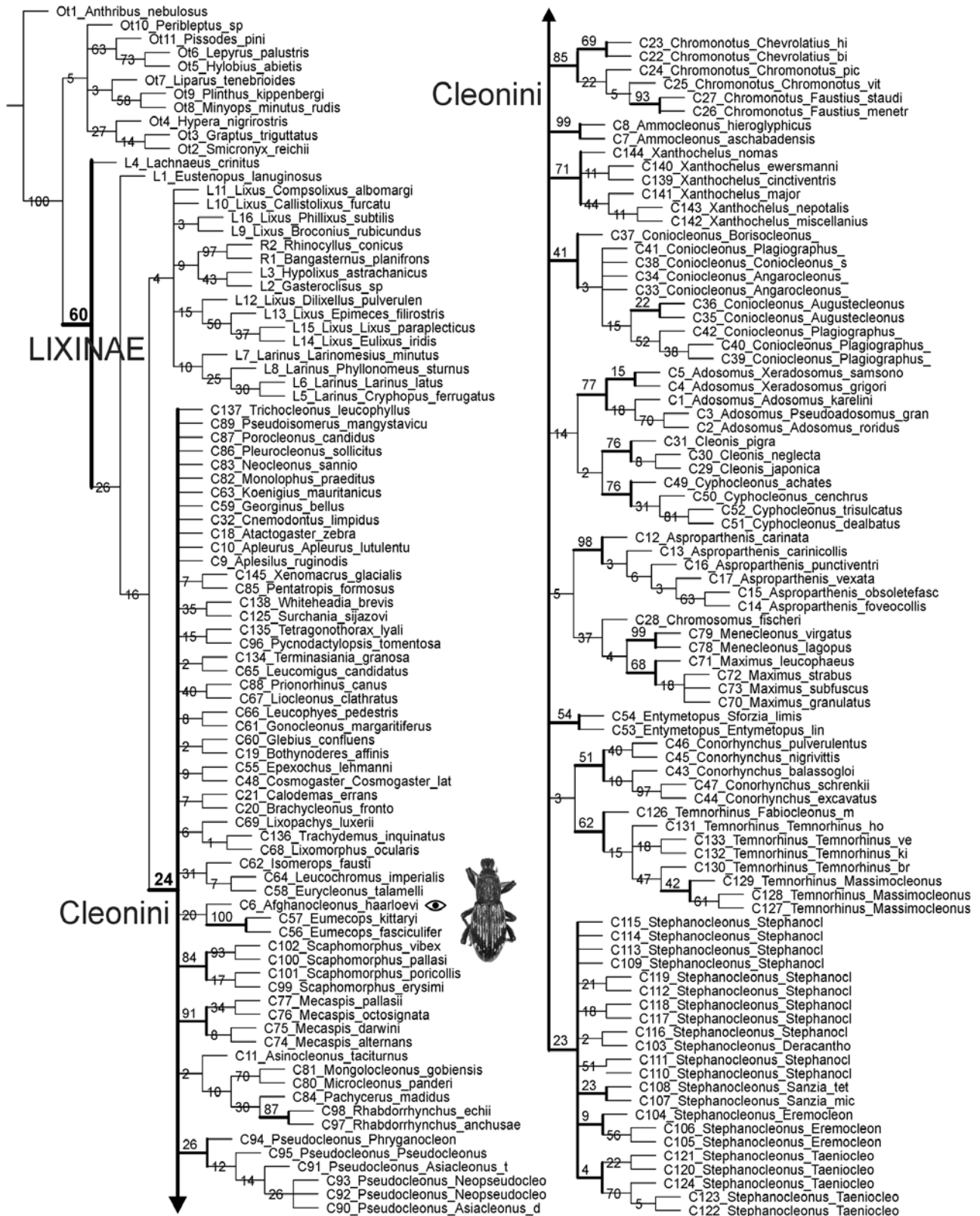


FIGURE 9. Maximum Parsimony majority rule bootstrap consensus phylogram of Cleonini. Numbers on branches are bootstrap values. Terminal names are truncated to the first 32 symbols; see Appendix 3 for the full names. Wide branches are those leading to monophyletic taxa, either Lixinae or Cleonini, or the genera or subgenera of Cleonini.

Are Cleonini truly flightless? The hypothesis that all extant Cleonini are flightless has been put forward by Anderson (1988: 446). It is based on the fact that to the best of our knowledge not a single observation refuting this statement is presently available. Flightlessness is a frequent phenomenon in weevils (Grebennikov 2017) and indeed in all Pterygota, Neoptera or Holometabola. In beetles it is normally accompanied by varying degrees of hind wing reduction and other presumably correlated modifications, such as rounding of elytral shoulders and shortening of the metaventrite. In Cleonini, the hind wings are variously developed, with at least some species having brachypterous and macropterous specimens either in sympatry, or allopatrically (Anderson 1988). One peculiarity of Cleonini is that even the fully macropterous specimens with seemingly full-sized wings (particularly in the genera *Asproparthenis*, *Bothynoderes*, *Coniocleonus* and *Cyphocleonus*) have never been observed in active flight. In this respect Cleonini differ markedly from the rest of Lixinae, most of which (perhaps all?) do fly. Thus, if Cleonini are indeed monophyletic, functional flightlessness might be the tribe's synapomorphy. The same phenomenon, on the other hand, might perhaps be the main driver of parallel evolution of unrelated Lixinae lineages independently dispensing with flight, developing a similar "flightless" phenotype to mislead taxonomists and linking them with the non-monophyletic Cleonini. The herein presented phylogeny refutes the latter hypothesis, although we will need a much better resolved and supported tree to shed adequate light on this intriguing evolutionary question.

Too many genus-group Cleonini taxa. At the genus-group level, our results again mainly corroborated the present taxonomic arrangement, with most of the genera and subgenera recovered as monophyletic. This, however, is not surprising, since, similar to the situation encountered in birds, every minimally morphologically distinct lineage of Cleonini has by now received a genus-group name of its own. Recovery of predominantly monophyletic genus-group taxa should, therefore, be mainly considered as an unavoidable by-product of excessive taxonomic splitting in Cleonini. The most speciose genus-group taxon, the subgenus *Stephanocleonus*, so far remains unaffected by the taxonomic splitters, and has emerged in our study as non-monophyletic. We suggest that no more genus-group taxa should be introduced in Cleonini, particularly for already-named species, unless newly named taxa are supported by a phylogenetic analysis.

The latter suggestion has significant applied implications. Practical utility of the Linnaean taxonomy in Cleonini weevils was compromised by excessive introduction of new genus-group taxa (14 new non-replacement names since 2000) and by seemingly random transfers of species-group names among genus-group taxa. This is exemplified by a nominal species currently known (Meregalli & Fremuth 2013) as *Temnorhinus (Fabiocleonus) mendicus*. This species was originally described as *Bothynoderes*, referred to as *Cleonus* when its biology and immatures were reported (Isart 1972), then made the type species for the monotypic subgenus *Fabiocleonus* (Arzanov 2006e), while Tóth et al. (2007), being unaware of the latter taxonomic action, referred to it as *Conorrhynchus (Cleonus)*. All these taxonomic actions were done based on variously documented phenetic, rather than on phylogenetic, grounds and are not phylogenetically justified (Zachos 2014).

Directions for further Cleonini research. Four main lines of promising research on Cleonini seem most likely to emerge from our herein reported results and experience with these beetles. Firstly, the phylogeny of the tribe will be hopefully eventually resolved by utilizing large amounts of information stored in the genome (i.e. McKenna et al. 2016). A coordinated accumulation of the DNA/RNA-suitable specimens of Cleonini leading to such an analysis is, therefore, desirable. Secondly, our weakly resolved topology of Cleonini suggests a need for inclusion of additional morphological characters and implies importance of reworking the coding of those employed. Thirdly, biology of Cleonini, and specifically that of their immature stages, is still a mainly untapped source of remarkable evolutionary discoveries, some of which are seemingly unique in their complexity (Shelef et al. 2013). Fourthly, the taxonomic identity of numerous Asian *Stephanocleonus* needs to be elucidated and this genus, by far the largest in the tribe, needs to be revised. We therefore hope that our attempt to document, illustrate and analyse Cleonini can at the very least stimulate others to explore the tribe further and along all aforementioned directions.

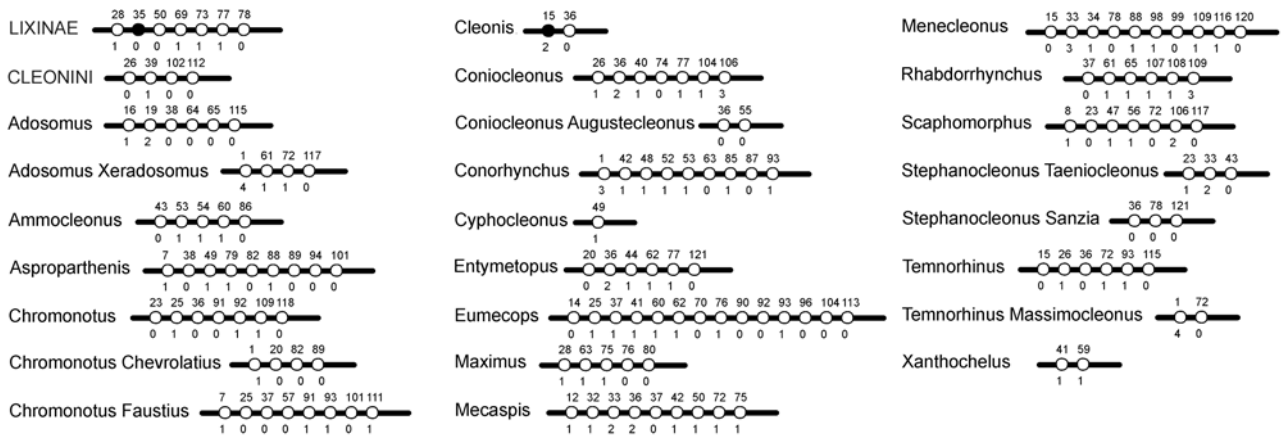


FIGURE 10. Unambiguously optimized synapomorphies of Lixinae, Cleonini and 24 genus-group Cleonini taxa from a randomly selected (=first) among the overflow of 100 most parsimonious trees. Solid circles indicate unique synapomorphies, open circles indicate reversals or homoplasies. Numbers above and below circles are character numbers and states, respectively. Note that the genera *Pseudocleonus*, *Stephanocleonus* and the subgenus *Eremocleonus* recovered as monophyletic on the MP consensus tree (Fig. 9) were not recovered as such on the selected most parsimonious tree.

Acknowledgements

The late Margarita E. Ter-Minassian (see Dedication) greatly influenced one of us (YuA) in choosing Cleonini as a study subject. Numerous and sometimes anonymous collectors mentioned in Appendix 3 made Cleonini specimens available for our study; among them Pavel P. Ivliev (Rostov-on-Don, Russia), Eduard A. Khachikov (Rostov-on-Ron, Russia), Evgeny V. Komarov (Volograd, Russia) and Alexander V. Napolov (Riga, Latvia) contributed most by repeatedly joining one of us (YuG) for fieldwork. Part of YuA fieldwork in Russia was facilitated by administrations of the Bogdo-Baskunchak Nature Reserve (Astrakhan Reg.) and Rostovskiy Nature Reserve (Rostov Reg.) represented by Konstantin A. Grebennikov and Alexander D. Lipkovich, respectively. Sergey V. Kolov (Almaty, Kazakhstan) found the Kegen locality where the immatures of *Rhabdorrhynchus* sp. in roots of *Lappula* sp. (Fig. 6A–D) could be reliably detected and guided one of us (VG) to the spot during the 2016 fieldwork.

Robert S. Anderson (Ottawa, Canada) through his PhD thesis on the North American Cleonini (Anderson 1988) inspired conception and completion of this project; he also provided North American specimens of *Apleurus* and *Scaphomorphus* used in the analysis, commented on the map (Fig. 7) and critically read an earlier version of this paper prior to its submission (as did Alexander Riedel, Karlsruhe, Germany; Jiří Skuhrovec, Prague, Czech Republic and Filip Trnka, Olomouc, Czech Republic).

Individual photographers and/or copyright holders provided images on Figs 1–6 and permitted their use: Andrey E. Abramov (Leningradskaya, Krasnodar reg., Russia), Mark H. Brown (North Liberty, IA, USA), Sergey V. Dementiev (Moscow, Russia), Pavel Yu. Gorbunov (Ekaterinburg, Russia), Boris M. Loboda (Kharkiv, Ukraine), Sergey O. Kakunin (Krasnodar, Russia), Evgeny V. Komarov (Volograd, Russia), Filip Trnka (Olomouc, Czech Republic), Hartmut Wisch (Pasadena, CA, USA), National Museum (Prague, Czech Republic) and Magnolia Press (Auckland, New Zealand). Images of 15 obscure Cleonini genus-group taxa not available for scoring (Figs 30–32) were generously made on our requests by various colleagues (see their names in the list of Museum abbreviations), while the respective Museums holding the copyright permitted image usage.

Sukhbir Kaur (Chandigarh, India) helped us to trace the weevil collection of H. R. Pajni, which has been transferred from the Panjab University to IARI. Jeffrey H. Skevington and Andrew D. Young (both Ottawa, Canada) advised on PAUP analysis. The Willi Hennig Society made TNT freely available. One of us (YuA) wants to affectionately mention his first mentor in entomology, the late Alexander I. Fomichev (1947–2008).

TABLE 1. Data matrix of 121 adult morphological characters used for the phylogenetic analysis of Cleonini (Coleoptera: Curculionidae: Lixinae); for full names of terminals see Appendix 3.

	20	40	60	80	100	120
Ot1_Anthrribus_nebulosus	0001010000?????0100	000000112111100221000	00000?0000110000?01000	000100100002000000100	0100???????????????	1200000000111107???????
Ot2_Smicronyx_reichii	0120000001100?000110	0011000?????????010	00000?00011000?10001	101100101002100000111	0100?????????????????	110000000000101107???????
Ot3_Graptus_triguttatus	10100110110?001010	0000001010?010210000	00010?0011010?10001	101100101002000000111	0000?????????????????	110100110000100?0?10?0?1
Ot4_Hypera_nigrirostris	01110000001100?000010	001100001111010200000	00000?00011000?10001	30210000100020000000111	0000?????????????????	11000010001111011010?0?1
Ot5_Hylobius_abietis	212000001110?0001010	001100120??030210010	10100?00011000?10000	202110110001000011111	000120?0?10010001000	10011011111111110110111
Ot6_Lepyrus_palustris	11200001011100001010	0011001120??030210000	10100?001100110000	202110110001000011111	001120?0?10010001000	100103111111111101101110
Ot7_Liparus_tenebrioides	21100000000100101010	0001011120??000220010	00000?00010000?10000	000000011001100000100	010110?0?101100100110	1200001011111011001110
Ot8_Minypops_minutus_rudis	10000000001100001010	001000020??010220000	00100?001000000?11111	10000011000000000101	0000?????????????????	1200001011111011010?0?1
Ot9_Plinthus_kippenbergi	211000000101100001010	101001021111010110000	20100?011100000?11011	10001011000200000101	0001000?001000000100	1000001011111011000?0?1
Ot10_Feribleptus_sp	23300000010010000020	00100002111010110000	00011000111?00?11000	011?1011000200000?111	0000?????????????????	120101010110110107?????
Ot11_Fissodes_pini	1230000001100?000010	00100102111130210100	10101100111001010000	101100111001000011111	010120?0?1100110000100	1200001011111011010?0?1
L1_Eustenopus_lanuginosus	0210000001100?000120	00100101101010010100	00000?000010010000001	31010111100001001001	01010100101011100111	1200001000010010011011
L2_Gasteroclisus_sp	133100010000?0?000120	1110000010?010000100	00011000101001000000	001101111100111001011	01010101111001011111	121101001110011010?0?1
L3_Hypolixus_astrachanicus	12310001010?10000121	001000010??110001100	00011000101001000000	0021001110011001201	0101111111111111?1111	1100011111111011000?0?1
L4_Lachnaeus_crintitus	01100000000?000120	0011001010?010001000	00000?00001000?00000	01010011100210001001	010100?0000111000011	0??010000110110000?0?1
L5_Larinus_Cryphopus_ferrugatus	10100001011010000120	001000001111120010100	00011000101000?00000	001101111002100001001	0001011011111?1?1?1	120111000110110000?0?1
L6_Larinus_Larinus_latus	302000010110?000120	10100002110020010100	00111100011000?10000	00110111100211001001	000101011?11?1?1?1?1	120111000011011011011
L7_Larinus_Larinomesius_minutus	00000000000?000120	001000001111020010100	00010?00101001000000	001101111002111001001	000101011?11?11?1?1?1	1201010000111011011011
L8_Larinus_Phylonomes_sturnus	2110000001100?000120	001000001111020010100	00011000011001010000	001101111002111001001	0001011000?111?1?1?111	120000100011011011011
L9_Lixus_Brocchius_rubicundus	1330000001100?000120	0010000100010001100	00011000101001000000	00210011111111001001	010101010?1?11?1?1111	120000100011011011011
L10_Lixus_Callistolix_furcatus	3330000001100?000120	00101011000020001100	00011000101001100000	003101111100211001001	000101000111111?1?11	12010100011011001001
L11_Lixus_Compsolixus_albomargi	1330000001100?000120	001000001100010001100	00011000101001100000	00210011100211101001	0101010001111111?1?11	12010100001101101101111
L12_Lixus_Dilixellus_pulverulen	3330000001100?000120	00100101100010001100	00011000101001000000	001101111002111001001	0101011011?1?1?111111	12010100011011011011111
L13_Lixus_Epimeces_filirostris	0330000001100?000120	001001010?0100001100	10000?00101001000000	001100111111211001001	0101011011?1?1?111111	12010100011011011011111
L14_Lixus_Eulixus_iridis	2330000001100?000120	001001010?01100001100	00010?00101001100000	00110111110211001001	010101011?1?1?111111	0??0110000110110011111
L15_Lixus_Lixus_paraplecticus	2330000001100?000120	001001010?0100001000	00000?00100100110000	001101111112100001001	0101011011?1?1?111111	0??01100001101101101110
L16_Lixus_Phillixus_subtilis	1330000001100?000120	0010010101100010001100	00010?00101001010000	00110011100210101001	0101010101?1?1?11?1?11	10011100001110110000?0?1
R1_Bangasterius_planifrons	01210111000010000120	00000001100020001100	00010?00101001000000	00110011100210001001	000101011111?11111111	100101000011011011011
R2_Rhincyllus_conicus	02210111000010000120	00000001100020001100	00010?00001001000000	00110011100221001001	01010101111?11111111	1011100001101101101110
C1_Adosomus_Adosomus_karelini	31101100011010010120	100100120??020010000	20000?100001000?10010	001000011000210101011	01010110111001101011	0??011000100010001001010
C2_Adosomus_Adosomus_roridis	32100000011010010120	10010012100020011100	2010101001101010010	00100111100210101011	01010110111001101011	0??011000100010001001010
C3_Adosomus_Pseudodosomus_gran	32100000011010010120	10010012100030010000	201011000011011010010	00100111100210101011	01010110111001101011	0??01100010000110101?1
C4_Adosomus_Xeradosomus_grigori	42201100011010010120	10010012100020020000	20100?10011011010010	1010011110011001101011	01010110111001101011	0??030001000100000?0?1
C5_Adosomus_Xeradosomus_samsono	41201100011010110120	10010012110030001000	20101111011000?10010	10300011100110101001	01011101111001101011	0??0300001000100001111
C6_Afghanocleonus_haarloevi	3120111001011111121	10010112111020020101	011010110000010?11000	103000111110110100001	01010110111011011011	11010311011011011011000?0?1
C7_Ammocleonus_aschabadensis	41200110011010100120	101001010?010010110	00000?0?11110110100001	00310011100111110001	0001000?1110011010111	0??0110001100010101110
C8_Ammocleonus_hieroglyphicus	31100111011010100120	101001010?010010110	00000?00111011010001	0031001110011110001	0001000?111001101011	0??0110001100010111110
C9_Aplesilus_ruginodis	41101100011010110120	100100120??130020110	10000?10111010?10000	000?0001100110100001	00010110111111101111	10000200010001101101101
C10_Apleurus_Apleurus_lutulentu	4320000001100?000110	000000010?0300010111	01100?10110100?10000	000?00001111111101001	00010110111001101011	0??0000001000101101110
C11_Asinocleonus_taciturnus	4220000001110?011120	1001101120??120021010	20100?0?11010100?10000	000?0001111011000001	01010101111101101011	0??0010001?00011010?0?1
C12_Asprorparthenis_carinata	32210110011010100111	001000001110110010010	211010000101001010001	303100011111011000111	00010110011000101011	0??02000110011010111
C13_Asprorparthenis_carinicolis	12210110011010100111	001000001110110011010	00101000101000?10000	103100111111011000111	00010111011011000101011	0??02000110011010111

TABLE 1. (Continued)

C103_Stephanocleonus_Deracantho	10001110110110001111	001100010??010010110	001011110010010700001	100000111110110000001	01010110101001101011	1107001?3100111000?00
C104_Stephanocleonus_Eremocleon	11101110111011001111	000100010??010010011	011010000010010701100	000000111110110000100	01010110101110011???	110700003100111010???
C105_Stephanocleonus_Eremocleon	21101110111011001111	000100010??010010111	00101010010010701100	000000111110110001001	01010110111001101011	11070003100111010???
C106_Stephanocleonus_Eremocleon	21101110111011001111	000100010??010010011	00101010010010701100	001000011110110001001	0101000??111001101011	110000103100111001101
C107_Stephanocleonus_Sanzia_mic	21101110011011000111	001100010??010000111	00101000000010700000	003000111110110000000	01010110111001101011	110001010100111010???
C108_Stephanocleonus_Sanzia_tet	21101110111011000111	001100020??010000010	00101010000011100000	00300011111011100000	0101000??111000101011	110002000100111010???
C109_Stephanocleonus_Stephanocl	11101110111011001111	000100010??010010110	00100700710010700000	003000011110110000200	000101000110111011011	110103102100111010???
C110_Stephanocleonus_Stephanocl	31201110111011001111	000100020??010010010	00100700010010701000	003000111110110000101	0111000??1101101111111	110103002100111010???
C111_Stephanocleonus_Stephanocl	21201110111011000111	000100020??010010010	001010000100107010010	003000111110111000011	0101000??1111011011111	110103102100111010???
C112_Stephanocleonus_Stephanocl	31101110111011000111	000100010??010010010	00101000010010700000	0030000111110110000200	0101000??1111011011111	110003002100111010???
C113_Stephanocleonus_Stephanocl	11101110111011000111	000100010??010010010	00101000110010700000	0030001111101110010010	0101000??111001111111	1101031021001110000???
C114_Stephanocleonus_Stephanocl	11101111111011000111	000100010??010010010	00101000010010700000	003000111110110000100	0101000??111001110111	1101011121001110000???
C115_Stephanocleonus_Stephanocl	31201110111011000111	000100010??010010010	01101000000010700000	001000011110110000100	1101000??111100111011	110101112100111010???
C116_Stephanocleonus_Stephanocl	10001110111011000111	000100010??010010010	01101000000010700100	00300011111011100001	0101000??11100111011?	110101102100111010???
C117_Stephanocleonus_Stephanocl	21101110111011001111	00010001100010010010	01110000010010700000	003000111110110000101	0111000??0111011011011	110001110100111010???
C118_Stephanocleonus_Stephanocl	21101110111011000111	00010001100010010010	01110700010010701000	003000111110110000110	1101000??1111011011111	110103012100111010???
C119_Stephanocleonus_Stephanocl	21101110111011000111	000100010??010010010	00101700010010700000	0030001111101110200	0101000??11110111111	110002000100111010???
C120_Stephanocleonus-Taeniocleo	11101110111011000111	001100010??020010010	00001000010010700000	003000111110110000100	0101000??011101111111	110102200100111011011
C121_Stephanocleonus-Taeniocleo	21101111111011001111	001100010??020010010	01001000010010701000	00300011111011100200	0101000??00100111???	110103002100111011011
C122_Stephanocleonus-Taeniocleo	31101110111011001111	000100010??020010010	01001000010010700001	103000111110110000200	0101000??011101111011	110000113100111011101
C123_Stephanocleonus-Taeniocleo	21201110011011000111	000100010??020010010	01001000010010701000	103000111110110000200	0101000??011101111011	110000113100111011101
C124_Stephanocleonus-Taeniocleo	20101110111011000111	001100010??020010010	01111010010010701000	103000111110110000200	0101000??001101110111	110000113100111011101
C125_Surchania_sijazovi	412001100110110001120	000001121110020010110	0100007001100000701001	20300001100000010101	0001000??111000011111	110012001100011010???
C126_Temnorhinus_Fabioocleonus_m	31210000010010000111	00100111110010001110	0000101001110000700000	303100111110111010101	010101101011101101011	110001000100111000???
C127_Temnorhinus_Massimocleonus	43310000010010000111	00101011110010001110	01101000111010000000	103100111110110000???	??F111101101101101011	1100010001001110101111
C128_Temnorhinus_Massimocleonus	33310000010010000111	001001010??010001110	01101000111110000000	103100111110111000000	01010101111711101011	1100010001001110101011
C129_Temnorhinus_Massimocleonus	41210001010010000111	00100101110010001110	00001000011111000000	30310011111011100101	0101011111011101111	1100010001001110101011
C130_Temnorhinus_Temnorhinus_br	22310000010010000111	00100101110010001110	00001000111101000000	00310011111110000101	010101011101110111011	110001000100110101011
C131_Temnorhinus_Temnorhinus_ho	22210000010010000111	00100101100110001110	000070000111000000	000100111100111000010	010101111111101101011	1100010001001110101011
C132_Temnorhinus_Temnorhinus_ki	22310010010010000111	00100101110110001110	00001000001101010000	3031001111111111010101	010101111111111101111	11000200010011100110011
C133_Temnorhinus_Temnorhinus_ve	333101111010010000111	00100101110110001110	00001010001101010000	00310011111111110000101	0101110011101110101011	110000000001100110111
C134_Terminasiana_granosa	11101110011110011120	10100102111010001010	00100710001010700000	00310011111010000001	01010110111000010111	110001001100011010???
C135_Tetragonothorax_lyali	31200110011011000111	011100111110001111	00101001111700710000	2037001111111111111101	010111000011011111111	0??F11000100011011010
C136_Trachydemus_inquinatus	32200110110100001120	00001010??F00000110	0010100011010000710010	000710111100210101000	00010100011111111011	????????????????????
C137_Tribocheleonus_l_eucophyllus	23301100111101101120	000100001111020010110	000007100110011110000	311010111100000101101	000101000110111111111	110001002100011001110
C138_Whiteheadia_brevis	41101100011011001110	1100011120??030020110	00000710010011010000	003700111100200010101	00010100111001011011	????????????????????
C139_Xanthochelus_cinctiventris	3220011001102?1101120	101101010??010010110	200110000010000700010	000700111100211010001	000101011011001101011	110711001100001011111
C140_Xanthochelus_ewersmanni	20000110011002?1001120	101101010??010010110	2010007000010000700010	003700111100211010001	0001010111001101011	110711001100001011111
C141_Xanthochelus_majior	322001100110070001120	1010000121110010010110	10011000101001700010	003700111100211010001	0001010111001101011	110711001100001011111
C142_Xanthochelus_miscellanianus	322001100110070001120	1010000??F0010010110	100110001010000700010	000700111100211010101	0101110111001101011	110711001100001011111
C143_Xanthochelus_repotalis	332001100110071001120	10100001070010010110	100110001010000700010	003700111100211010101	01010110111001101011	1107110011000110011001111
C144_Xanthochelus_nomas	42200110011002?1001120	10110101070010010110	101007001010000700010	003700111100211010101	0101110111001101011	111101001100001011111
C145_Xenomacrus_glacialis	311011101110110001110	110100010??0120010110	111110000010000700000	0037001111002111111001	010700100111001101011	0??F02000100111011011011

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APPENDIX 1. Extant genus-group taxa of Cleonini

Below we list in alphabetical order all 96 currently valid genus-group names of extant Cleonini. Taxonomic information was verified against the most up-to-date sources (Alonso-Zarazaga & Lyal 1999, 2002, Meregalli & Fremuth 2013) and when variable, the later source was deemed correct. No new taxonomic acts are herein proposed. Of the total of 96 genus-group names, 66 are those of genera containing no subgenera, 9 are those of nominotypical subgenera, and 21 are those of non-nominotypical subgenera. For each genus-group name we provide the following information: current valid name with its author and the year of publication, habitus image of one or more representatives, the type species in original combination, taxonomic status (genus, nominotypical subgenus or non-nominotypical subgenus), number of species included in the herein reported analysis, the approximate minimal number of valid species, generalized distribution summarized from published sources (mainly Alonso-Zarazaga & Lyal 1999 and Meregalli & Fremuth 2013), a comment (if applicable) and the most recent relevant publication. Lack of the latter indicates taxa where the original taxonomic description forms most of the available data and, therefore, the recent catalogues should be consulted (Alonso-Zarazaga & Lyal 1999, Meregalli & Fremuth 2013).

- 1: *Adosomus* Faust, 1904 (Figs 12A,B). Type species: *Curculio roridus* Pallas, 1781. Nominotypical subgenus. Species studied: 2; total species: 2. Temperate Palaearctic between Italy and Russian Far East. Arzanov (2005b).
- 2: *Afghanocleonus* Ter-Minassian, 1976 (Fig. 12F). Type species: *Aplesilus haarloevi* Voss, 1955. Genus with no subgenera. Species studied: 1; total species: 1. Afghanistan. Ter-Minassian (1988).
- 3: *Ammocleonus* Bedel, 1907 (Figs 12G,H). Type species: *Lixus hieroglyphicus* Olivier, 1807. Genus with no subgenera. Species studied: 2; total species: 5. Asia between Kazakhstan, Iran and Oman; Afrotropical and Oriental regions. Arzanov (2014).
- 4: *Angarocleonus* Arzanov, 2006b (Figs 15H, 16A). Type species: *Cleonus cineritius* Gyllenhal, 1834. Subgenus of *Coniocleonus*. Species studied: 2; total species: 7. Mongolia, China and Asian Russia; Nearctic region. Arzanov (2006b).
- 5: *Aparotopus* Faust, 1904 (Fig. 30A). Type species: *Pachycerus cribrosus* Fairmair, 1896. Genus with no subgenera. Species studied: 0; total species: 1. Madagascar. Only the type series is known.
- 6: *Aplesilus* Reitter, 1913 (Fig. 13A). Type species: *Aplesilus ruginodis* Reitter, 1913. Genus with no subgenera. Species studied: 1; total species: 1. Afghanistan and Iran.
- 7: *Apleurus* Chevrolat, 1873 (Fig. 13B). Type species: *Cleonus lutulentus* LeConte, 1859. Nominotypical subgenus. Species studied: 1; total species: 7. South-western USA and Mexico. Sister to *Bothynoderes* (as *Chromoderes*); trans-Beringian in late Eocene (Anderson 1988).
- 8: *Arabocleonus* Arzanov, 2009a (Fig. 30B). Type species: *Arabocleonus medvedevi* Arzanov, 2009. Subgenus of *Cosmogaster*. Species studied: 0; total species: 1. Saudi Arabia. Only the type series is known. Arzanov (2009a).
- 9: *Asiacleonus* Arzanov, 2005b (Fig. 13 C). Type species: *Cleonus dauricus* Gebler, 1830. Subgenus of *Pseudocleonus*. Species studied: 2; total species: 2. Asia between Uzbekistan and Russian Far East. Arzanov (2005b).
- 10: *Asinocleonus* Faust, 1904 (Figs 23A,B). Type species: *Pachycerus taciturnus* Faust, 1885. Genus with no subgenera. Species studied: 1; total species: 2. Kazakhstan, Kyrgyzstan, Tajikistan and Uzbekistan. Ter-Minassian (1988).
- 11: *Asproparthenis* Gozis, 1886 (Figs 13E-H, 14A). Type species: *Lixus punctiventris* Germar, 1824. Genus with no subgenera. Species studied: 6; total species: 22. Most of Palaearctic region. Arzanov (2006c).

- 12: *Atactogaster* Faust, 1904 (Fig. 14B). Type species: *Neocleonus orientalis* Chevrolat, 1873. Genus with no subgenera. Species studied: 1; total species: 10. Most of Oriental and Afrotropical regions (including Madagascar).
- 13: *Augustecleonus* Arzanov, 2006b (Figs 16B,C). Type species: *Curculio nebulosus* Linnaeus, 1758. Subgenus of *Coniocleonus*. Species studied: 2; total species: 3. Most of Europe and Asia eastwards including Kazakhstan. Arzanov (2006b).
- 14: *Bodemeyeria* Reitter, 1913 (Fig. 30C). Type species: *Bodemeyeria plicata* Reitter, 1913. Genus with no subgenera. Species studied: 0; total species: 1. Iran. Only the type series is known. Reitter (1913).
- 15: *Borisocleonus* Arzanov, 2006d (Fig. 16D). Type species: *Lixus mesopotamicus* Olivier, 1807. Subgenus of *Coniocleonus*. Species studied: 1; total species: 2. South-eastern Europe, Egypt, Asia eastwards including Afghanistan. Arzanov (2006d).
- 16: *Bothynoderes* Schoenherr, 1823 (Fig. 14C). Type species: *Curculio albidus* Fabricius, 1787. Genus with no subgenera. Species studied: 1; total species: 2. Most of temperate Palaearctic between Italy and Japan. Sister (as *Chromoderus*) to *Apleurus* (Anderson 1988). Ter-Minassian (1988), Volovik (2010).
- 17: *Brachytleonus* Faust, 1904 (Fig. 14D). Type species: *Cleonus fronto* Fischer von Waldheim, 1835. Genus with no subgenera. Species studied: 1; total species: 1. Iran, Kazakhstan, Turkmenistan and Uzbekistan. Ter-Minassian (1988).
- 18: *Calodemus* Faust, 1904 (Fig. 14E). Type species: *Cleonus errans* Fähræus, 1871. Genus with no subgenera. Species studied: 1; total species: 7. Most of southern and eastern Africa northwards including Ethiopia. Sister to *Pseudeumecops* (Meregalli 2004).
- 19: *Centrocleonus* Chevrolat, 1873 (Fig. 30D). Type species: *Cleonus fallax* Fähræus, 1842. Genus with no subgenera. Species studied: 0; total species: 1. Republic of South Africa. Only the type series is known.
- 20: *Chevrolatius* Arzanov, 2006e (Figs 14F,G). Type species: *Cleonis bipunctata* Zoubkoff, 1829. Subgenus of *Chromonotus*. Species studied: 2; total species: 4. Palaearctic between southern European Russia, Armenia, Asian Russia and central China. Arzanov (2006e).
- 21: *Chromonotus* Motschulsky, 1860 (Figs 14H, 15A). Type species: *Cleonis vittata* Zoubkoff, 1829. Nominotypical subgenus. Species studied: 2; total species: 4. Palaearctic between southern Russia, Armenia, Asian Russia and Xinjiang. Arzanov (2006a).
- 22: *Chromosomus* Motschulsky, 1860 (Fig. 15D). Type species: *Cleonus fischeri* Fähræus, 1842. Genus with no subgenera. Species studied: 1; total species: 3. Asia between Iran and Kazakhstan. Arzanov (2006c).
- 23: *Cleonis* Dejean, 1821 (Figs 11, 15E,F). Type species: *Curculio sulcirostris* Linnaeus, 1767. Genus with no subgenera. Species studied: 3; total species: 5. Palaearctic between Great Britain and Japan; Oriental region; *C. pigra* adventive in North America. Arzanov (2005b).
- 24: *Cnemodontus* Chevrolat, 1873 (Fig. 15G). Type species: *Cleonus limpidus* Gyllenhal, 1834. Genus with no subgenera. Species studied: 1; total species: 5. Republic of South Africa.
- 25: *Coniocleonus* Motschulsky, 1860 (Fig. 16E). Type species: *Cleonus carinirostris* Gyllenhal, 1834. Nominotypical subgenus. Species studied: 1; total species: 1. Temperate Palaearctic between Kazakhstan and North Korea. Arzanov (2006b).
- 26: *Conorhynchus* Motschulsky, 1860 (Figs 17B-F). Type species: *Cleonus bartelsii* Fähræus, 1842. Genus with no subgenera. Species studied: 5; total species: 17. Temperate Palaearctic between Italy and Mongolia. Homonym of five genus-group names, one in Neotropical catfishes in prevailing use. Arzanov (2005a).
- 27: *Cosmogaster* Faust, 1904 (Fig. 17G). Type species: *Cleonus lateralis* Gyllenhal, 1834. Nominotypical subgenus. Species studied: 1; total species: 3. Southern Palaearctic between Egypt and Xinjiang; most of Afrotropical region (including Madagascar).
- 28: *Cyphocleonus* Motschulsky, 1860 (Figs 17H, 18A-C). Type species: *Curculio cenchrus* Pallas, 1781. Genus with no subgenera. Species studied: 4; total species: 15. Most of Palaearctic (except Japan and Pacific coast); *C. achates* adventive in North America. Arzanov (2005b).
- 29: *Deracanthopsis* Voss, 1967 (Fig. 24F). Type species: *Stephanocleonus gemellus* Voss, 1967. Subgenus of *Stephanocleonus*. Species studied: 1; total species: 2. Mongolia. Ter-Minassian (1974, 1979).
- 30: *Entymetopus* Motschulsky, 1860 (Fig. 18D). Type species: *Entymetopus lineolatus* Motschulsky, 1860. Nominotypical subgenus. Species studied: 1; total species: 4. Morocco and between Syria and Kazakhstan. Ter-Minassian (1988).
- 31: *Epexochus* Reitter, 1913 (Fig. 18F). Type species: *Cleonus lehmanni* Ménériés, 1849. Genus with no subgenera. Species studied: 1; total species: 4. Asia between Turkmenistan and Mongolia. Arzanov (2005c), Meregalli & Talamelli (2009).
- 32: *Ephimeronotus* Faust, 1904 (Fig. 30E). Type species: *Cleonus miegii* Fairmaire, 1855. Genus with no subgenera. Species studied: 0; total species: 2. Mediterranean between Portugal, Morocco and Turkey. Sister to *Rhabdorrhynchus* (Arzanov 2007b).
- 33: *Epirrhynchus* Schoenherr, 1823 (not imaged). Type species: *Curculio argus* Sparrmann, 1785. Genus with no subgenera. Species studied: 0; total species: 2. Republic of South Africa. Only the type series is known. Faust (1904). The holotype could not be located in MTD, even though it is expected to be there (email from Olaf Jäger on Nov. 30, 2016).
- 34: *Eremocleonus* Ter-Minassian, 1974 (Figs 24G,H, 25A). Type species: *Cleonus bicostatus* Gebler, 1833. Subgenus of *Stephanocleonus*. Species studied: 3; total species: 9. Asia between Kyrgyzstan and Russian Far East. Ter-Minassian (1974, 1979).
- 35: *Eumecops* Hochhuth, 1851 (Figs 18G,H). Type species: *Eumecops kittaryi* Hochhuth, 1851. Genus with no subgenera. Species studied: 2; total species: 4. Palaearctic between southern European Russia and Russian Far East. Ter-Minassian (1988).
- 36: *Eurycleonus* Bedel, 1907 (Fig. 19A). Type species: *Leucochromus gigas* Marseul, 1868. Genus with no subgenera. Species studied: 1; total species: 5. Southern Palaearctic between Morocco and Pakistan. Meregalli (2000, 2005).
- 37: *Fabioacleonus* Arzanov, 2006c (Fig. 27E). Type species: *Bothynoderes mendicus* Gyllenhal, 1834. Subgenus of *Temnorhinus*. Species studied: 1; total species: 1. Southern Palaearctic between France and Tunisia. Arzanov (2006c).
- 38: *Faustius* Arzanov, 2006e (Figs 15B,C). Type species: *Cleonus albilineatus* Ménériés, 1849. Subgenus of *Chromonotus*. Species studied: 2; total species: 4. Asia between Pakistan and Kazakhstan. Arzanov (2006e).
- 39: *Georginus* Jakobson, 1913 (Fig. 19B). Type species: *Georginus bellus* Jakobson, 1913. Genus with no subgenera. Species studied: 1; total species: 2. Iran, Turkmenistan, Afghanistan. Ter-Minassian (1988).
- 40: *Gibbstethus* R. Anderson, 1988 (Fig. 30F). Type species: *Dinocleus hystrix* Fall, 1913. Subgenus of *Apleurus*. Species studied:

- 0; total species: 1. Sand dunes in southern California. Sister to *Apleurus* s. str. (Anderson 1988).
- 41: *Glebius* Arzanov 2006e (Fig. 19C). Type species: *Cleonus confluens* Fähræus, 1842. Genus with no subgenera. Species studied: 1; total species: 2. Palaearctic between southern European Russia, Iran and Xinjiang. Arzanov (2006e).
- 42: *Gonocleonus* Marseul, 1866 (Fig. 19D). Type species: *Cleonus helferi* Chevrolat, 1844. Genus with no subgenera. Species studied: 1; total species: 12. Mediterranean between Morocco, Tunisia and Sicily.
- 43: *Hemeurysternus* Voss, 1960 (Fig. 31A). Type species: *Eurysternus bakvaensis* Voss, 1960. Subgenus of *Entymetopus*. Species studied: 0; total species: 1. Asia between Kazakhstan and Afghanistan.
- 44: *Isomerops* Reitter, 1913 (Fig. 19E). Type species: *Isomerus fausti* Petri, 1908. Genus with no subgenera. Species studied: 1; total species: 5. Pakistan, Iran and Afghanistan. Ter-Minassian (1988).
- 45: *Koenigi* Heyden, 1900 (Fig. 19F). Type species: *Koenigi* *palaestinus* Heyden, 1900. Genus with no subgenera. Species studied: 1; total species: 2. Southern Mediterranean between Morocco and Israel.
- 46: *Leucochromus* Motschulsky, 1860 (Fig. 19G). Type species: *Cleonis imperialis* Zoubkoff, 1837. Genus with no subgenera. Species studied: 1; total species: 1. Asia between Kazakhstan and Iran. Ter-Minassian (1988).
- 47: *Leucomigus* Motschulsky, 1860 (Fig. 19H). Type species: *Curculio candidatus* Pallas, 1771. Genus with no subgenera. Species studied: 1; total species: 2. Southern Palaearctic between Morocco, France, Xinjiang and west Siberia. Ter-Minassian (1988).
- 48: *Leucophyes* Marshall, 1946 (Fig. 20A). Type species: *Curculio ophthalmicus* Rossi, 1790. Genus with no subgenera. Species studied: 1; total species: 6. Most of temperate Europe and Algeria. Arzanov (2008a).
- 49: *Lioocleonus* Motschulsky, 1860 (Fig. 20B). Type species: *Lixus clathratus* Olivier, 1807. Genus with no subgenera. Species studied: 1; total species: 2. Northern Africa between Morocco and Egypt; Armenia in Europe; Asia between Turkey, Israel and Mongolia; Oriental region. Record from southern European Russia (Meregalli & Fremuth 2013) is not corroborated. Ter-Minassian (1988).
- 50: *Lixocleonus* Marshall, 1923 (Fig. 31B). Type species: *Lixocleonus incanus* Marshall, 1923. Genus with no subgenera. Species studied: 0; total species: 1. India. Only the type series is known. Marshall (1923).
- 51: *Lixoglyptus* Reitter, 1916 (Fig. 31C). Type species: *Lixus spartii* Olivier, 1807. Genus with no subgenera. Species studied: 0; total species: 2. Mediterranean between Morocco and France.
- 52: *Lixomorphus* Faust, 1904 (Fig. 20C). Type species: *Curculio ocellaris* Fabricius, 1792. Genus with no subgenera. Species studied: 1; total species: 2. Mediterranean between France, Turkey and Algeria.
- 53: *Lixopachys* Reitter, 1916 (Fig. 20D). Type species: *Lixus cleoniformis* Petri, 1904. Genus with no subgenera. Species studied: 1; total species: 1. Mediterranean between Morocco and Syria.
- 54: *Massimocleonus* Arzanov, 2006c (Figs 27F-H). Type species: *Lixus arabs* Olivier, 1807. Subgenus of *Temnorhinus*. Species studied: 3; total species: 10. Palaearctic between Mongolia, Pakistan, and Armenia. Arzanov (2006c).
- 55: *Maximus* Alonso-Zarazaga et Lyal, 2009 (Figs 20E-H). Type species: *Cleonus verrucosus* Gebler, 1830. Genus with no subgenera. Species studied: 4; total species: 15. Palaearctic: north Africa between Morocco and Egypt; between Moldova, Xinjiang and Jordan. Ter-Minassian (1988).
- 56: *Mecaspis* Schoenherr, 1823 (Figs 21A,D). Type species: *Lixus palmatus* Olivier, 1807. Genus with no subgenera. Species studied: 4; total species: 18. Palaearctic around the Mediterranean Sea; temperate Europe and Asia eastwards including Kashmir and Kazakhstan; Oriental region. Ter-Minassian (1988).
- 57: *Meneocleonus* Faust, 1904 (Figs 21E,F). Type species: *Bothynoderes anxius* Gyllenhal, 1834. Genus with no subgenera. Species studied: 2; total species: 6. Palaearctic between Morocco, Jordan, southern European Russia and Xinjiang; Afrotropical and Oriental regions. Ter-Minassian (1988).
- 58: *Mesocleonus* Faust, 1904 (Fig. 31D). Type species: *Cleonus implicatus* Faust, 1885. Genus with no subgenera. Species studied: 0; total species: 1. Ghana. Only the type series is known.
- 59: *Microocleonus* Faust, 1904 (Fig. 21G). Type species: *Cleonus panderi* Fischer von Waldheim, 1835. Genus with no subgenera. Species studied: 1; total species: 3. Mongolia and neighbouring lands.
- 60: *Mongolocleonus* Ter-Minassian, 1974 (Fig. 21H). Type species: *Eumecops gobiensis* Voss, 1967. Genus with no subgenera. Species studied: 1; total species: 1. Mongolia and Inner Mongolia. Ter-Minassian (1974).
- 61: *Monolophus* Faust, 1904 (Fig. 22A). Type species: *Mecaspis praeditus* Faust, 1883. Genus with no subgenera. Species studied: 1; total species: 1. Asia between Iran and Mongolia.
- 62: *Neocleonus* Chevrolat, 1872 (Fig. 22B). Type species: *Curculio mucidus* Germar, 1813. Genus with no subgenera. Species studied: 1; total species: 3. Eastern Mediterranean between Israel and Egypt; Afrotropical region.
- 63: *Neopseudocleonus* Arzanov, 2005b (Figs 23C,D). Type species: *Curculio grammicus* Panzer, 1789. Subgenus of *Pseudocleonus*. Species studied: 2; total species: 7. Palaearctic between Morocco and Mongolia. Arzanov (2005b).
- 64: *Nomimonyx* Faust, 1904 (Fig. 31E). Type species: *Nomimonyx perturbans* Faust, 1904. Genus with no subgenera. Species studied: 0; total species: 1. Republic of South Africa. Only the type series is known.
- 65: *Pachycerus* Schoenherr, 1823 (Fig. 22C). Type species: *Lixus madidus* Olivier, 1807. Genus with no subgenera. Species studied: 1; total species: 12. Most of Palaearctic between Portugal and northern China; Afrotropical and Oriental regions. Meregalli (2002, 2009).
- 66: *Pajnisoodes* Alonso-Zarazaga et Lyal, 2002 (Fig. 31F). Type species: *Dirodes flavomaculatus* Pajni et Sood, 1982. Genus with no subgenera. Species studied: 0; total species: 2. India. Only the type series is known. Pajni & Sood (1982).
- 67: *Paraleucochromus* Obst, 1908 (not imaged). Type species: *Paraleucochromus pleurocleonides* Obst, 1908. Genus with no subgenera. Species studied: 0; total species: 1. Qinghai. Only the type series is known. The holotype could not be located in ZMHB, even though it is expected to be there (email from Bernd Jäger on Nov. 24, 2016).
- 68: *Pentatropis* Faust, 1904 (Fig. 22D). Type species: *Pachycerus formosus* Fähræus, 1842. Genus with no subgenera. Species studied: 1; total species: 3. Republic of South Africa.

- 69: *Phaulosomus* Faust, 1904 (Fig. 32A). Type species: not yet designated. Genus with no subgenera. Species studied: 0; total species: 3. Tropical Africa between Senegal and Tanzania.
- 70: *Phryganocleonus* Arnol'di, 1956 (Fig. 23E). Type species: *Pseudocleonus guldarensis* Arnol'di, 1956. Subgenus of *Pseudocleonus*. Species studied: 1; total species: 4. Afghanistan, Tajikistan and Uzbekistan. Meregalli & Talamelli (2017).
- 71: *Plagiographus* Chevrolat, 1869 (Figs 16F-H, 17A). Type species: *Stephanocleonus saintpierreorum* Chevrolat, 1969. Subgenus of *Coniocleonus*. Species studied: 4; total species: 14. Palaearctic between Portugal and Uzbekistan. Arzanov (2006b).
- 72: *Pleurocleonus* Motschulsky, 1860 (Fig. 22E). Type species: *Cleonis quadrivittata* Zoubkoff, 1829. Genus with no subgenera. Species studied: 1; total species: 3. Palaearctic between Moldova and Russian Far East. Ter-Minassian (1988).
- 73: *Porocleonus* Motschulsky, 1860 (Fig. 22F). Type species: *Porocleonus scrobicollis* Motschulsky, 1860. Genus with no subgenera. Species studied: 1; total species: 1. Southern Palaearctic between Morocco and Iran; Afrotropical region.
- 74: *Prionorhinus* Chevrolat, 1873 (Fig. 22 G). Type species: *Lixus canus* Wiedemann, 1823. Genus with no subgenera. Species studied: 1; total species: 5. Republic of South Africa. Faust (1904).
- 75: *Pseudeumecops* Meregalli, 2004 (Fig. 32B). Type species: *Cleonus lutulentus* Fairmaire, 1888. Genus with no subgenera. Species studied: 0; total species: 2. Kenya and the Horn of Africa. Sister to *Calodemas* (Meregalli 2004).
- 76: *Pseudisomerus* Ter-Minassian, 1988 (Fig. 22H). Type species: *Isomerus mangystavicus* Ter-Minassian, 1976. Genus with no subgenera. Species studied: 1; total species: 1. Kazakhstan. Ter-Minassian (1988).
- 77: *Pseudoadosomus* Arzanov, 2005b (Fig. 12C). Type species: *Cleonus granulatus* Mannerheim, 1825. Subgenus of *Adosomus*. Species studied: 1; total species: 4. Eastern Palaearctic between Japan, central China and eastern Siberia. Arzanov (2005b).
- 78: *Pseudocleonus* Chevrolat, 1872 (Fig. 23 F). Type species: *Curculio costatus* Fabricius, 1787. Nominotypical subgenus. Species studied: 1; total species: 8. Southern Palaearctic between Portugal, Morocco, Xinjiang and Kazakhstan. Arzanov (2005b).
- 79: *Pycnodactylopsis* Voss, 1963 (Fig. 23G). Type species: *Pycnodactylus schaeuffelei* Voss, 1963. Genus with no subgenera. Species studied: 1; total species: 2. Southern Palaearctic between Morocco and Iran; Afrotropical and Oriental regions.
- 80: *Rhabdorrhynchus* Motschulsky, 1860 (Figs 23H, 24A). Type species: *Pachycerus menetriesii* Gyllenhal, 1842. Genus with no subgenera. Species studied: 2; total species: 13. Southern Palaearctic between France, Algeria and Afghanistan. Sister to *Ephimeronotus* (Arzanov 2007b). Meregalli (2008).
- 81: *Sanzia* Alonso-Zarazaga et Lyal, 1999 (Figs 25B,C). Type species: *Curculio tetragrammus* Pallas, 1781. Subgenus of *Stephanocleonus*. Species studied: 2; total species: 4. Temperate Palaearctic between Romania and Mongolia. Ter-Minassian (1988).
- 82: *Scaphomorphus* Motschulsky, 1860 (Figs 24B-E). Type species: *Curculio vibex* Pallas, 1781. Genus with no subgenera. Species studied: 4; total species: 25. Temperate Holarctic between southern European Russia and Japan; 19 endemic species widespread in North America (Anderson 1988), south into Mexico and Honduras. Trans-Beringian late Eocene vicariance (Anderson 1988, as *Cleonidius*). Ter-Minassian (1988).
- 83: *Sforzia* Alonso-Zarazaga et Lyal, 1999 (Fig. 18E). Type species: *Cleonus limis* Ménétériés, 1849. Subgenus of *Entymetopus*. Species studied: 1; total species: 2. Palaearctic between Southern European Russia, Iran and Xinjiang.
- 84: *Stephanocleonus* Motschulsky, 1860 (Figs 25D-H, 26A-F). Type species: *Curculio flaviceps* Pallas, 1781. Nominotypical subgenus. Species studied: 11; total species: 103. Holarctic between Southern European Russia, Russian Far East and Northern China; 6 endemic species widespread in northern and montane North America (Anderson 1988). By far the largest genus-group taxon of Cleonini with the highest and inadequately documented diversity in, and around, Mongolia. Ter-Minassian (1974, 1979, 1984).
- 85: *Surchania* Lebedev, 1931 (Fig. 27D). Type species: *Surchania sijazovi* Lebedev, 1931. Genus with no subgenera. Species studied: 1; total species: 1. Kazakhstan, Tajikistan, Turkmenistan and Uzbekistan. Ter-Minassian (1988).
- 86: *Taenioleonus* Ter-Minassian, 1974 (Figs 26G,H, 27A-C). Type species: *Cleonus thoracicus* Fischer von Waldheim, 1835. Subgenus of *Stephanocleonus*. Species studied: 5; total species: 23. Asia between Kazakhstan, Russian Far East and northern China. Ter-Minassian (1974, 1979).
- 87: *Temnorhinus* Chevrolat, 1872 (Figs 28A-D). Type species: *Bothynoderes brevirostris* Gyllenhal, 1834. Nominotypical subgenus. Species studied: 4; total species: 17. Palaearctic between Spain, Morocco, Kazakhstan and Xinjiang; Afrotropical and Oriental regions. Arzanov (2006c).
- 88: *Terminasiania* Alonso-Zarazaga et Lyal, 1999 (Fig. 28E). Type species: *Cleonis granosa* Zoubkoff, 1833. Genus with no subgenera. Species studied: 1; total species: 1. Palaearctic between southern European Russia and Xinjiang. Ter-Minassian (1988).
- 89: *Tetragonothorax* Chevrolat, 1872 (Fig. 28F). Type species: *Curculio retusus* Fabricius, 1801. Genus with no subgenera. Species studied: 1; total species: 8. Most of Afrotropical and Oriental regions; Egypt and Palestine in Palaearctic.
- 90: *Trachydemus* Chevrolat, 1872 (Fig. 28G). Type species: *Pachycerus rugosus* Lucas, 1846. Genus with no subgenera. Species studied: 1; total species: 3. Mediterranean between Morocco and Iran.
- 91: *Trichocleonus* Motschulsky, 1860 (Fig. 28H). Type species: *Cleonus leucophyllus* Fischer von Waldheim, 1821. Genus with no subgenera. Species studied: 1; total species: 1. Asia between Iran, Kazakhstan and Xinjiang. Ter-Minassian (1988).
- 92: *Trichotocleonus* Voss, 1959 (Fig. 32C). Type species: *Trichotocleonus longipilis* Voss, 1959. Genus with no subgenera. Species studied: 0; total species: 1. Afghanistan. Only the type series is known.
- 93: *Whiteheadia* Alonso-Zarazaga et Lyal, 1999 (Fig. 29A). Type species: *Cleonus brevis* Fähræus, 1842. Genus with no subgenera. Species studied: 1; total species: 1. Afrotropical region between Chad, Ethiopia and Tanzania.
- 94: *Xanthochelus* Chevrolat, 1873 (Figs 29B-G). Type species: *Curculio nomas* Pallas, 1771. Genus with no subgenera. Species studied: 6; total species: 18. Most of Afrotropical and northern part of Oriental regions; between Spain and Japan in Palaearctic.
- 95: *Xenomacrus* Faust, 1904 (Fig. 29H). Type species: *Curculio glacialis* Herbst, 1797. Genus with no subgenera. Species studied: 1; total species: 2. Republic of South Africa.
- 96: *Xeradosomus* Arzanov, 2005b (Figs 12D,E). Type species: *Cleonus samsonowii* Gebler, 1844. Subgenus of *Adosomus*. Species studied: 2; total species: 3. Asia between Turkmenistan, Kazakhstan and northern China. Arzanov (2005b).

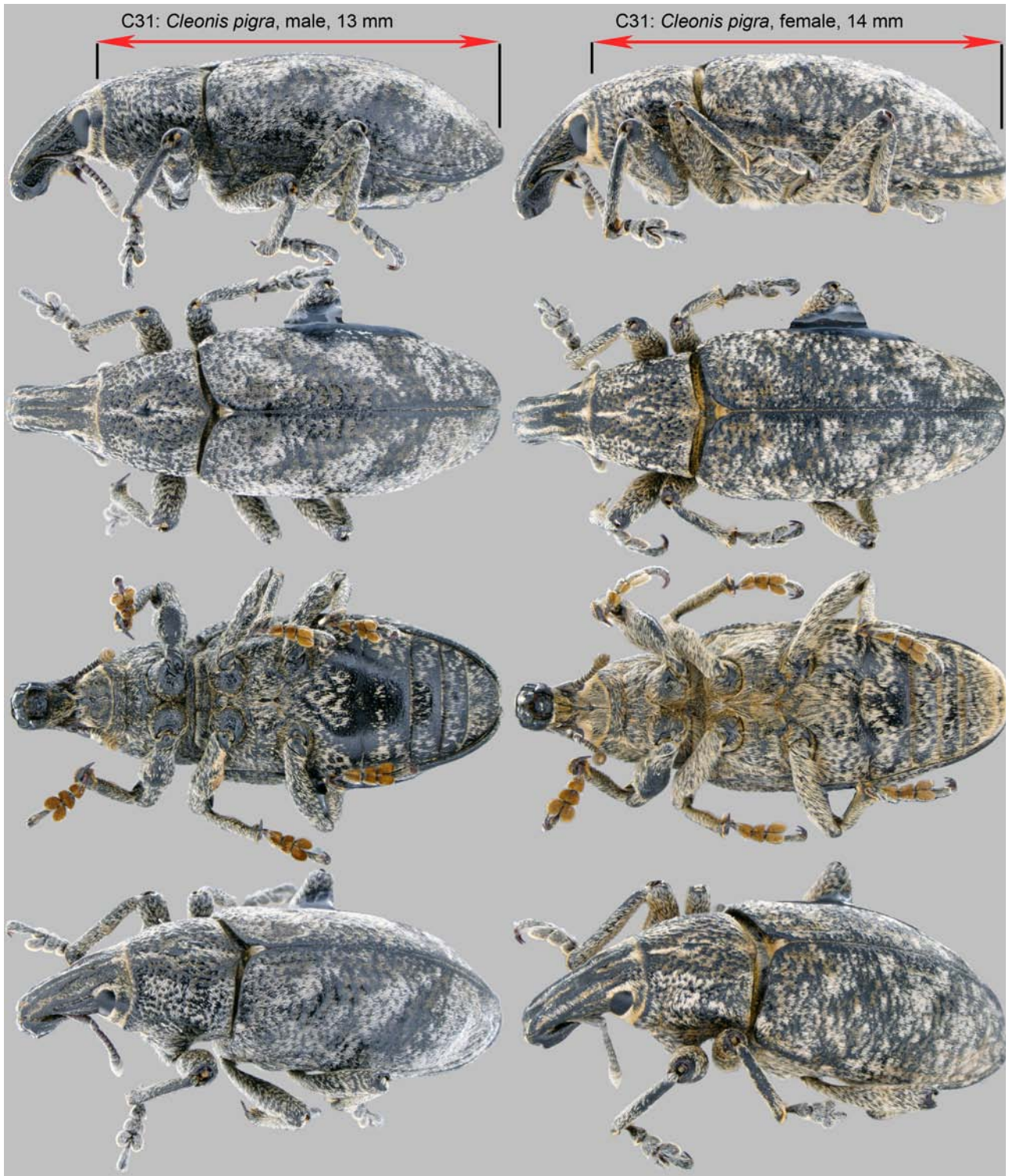


FIGURE 11. Cleonini terminal C31: *Cleonis pigra*, the type species of the tribe's type genus.

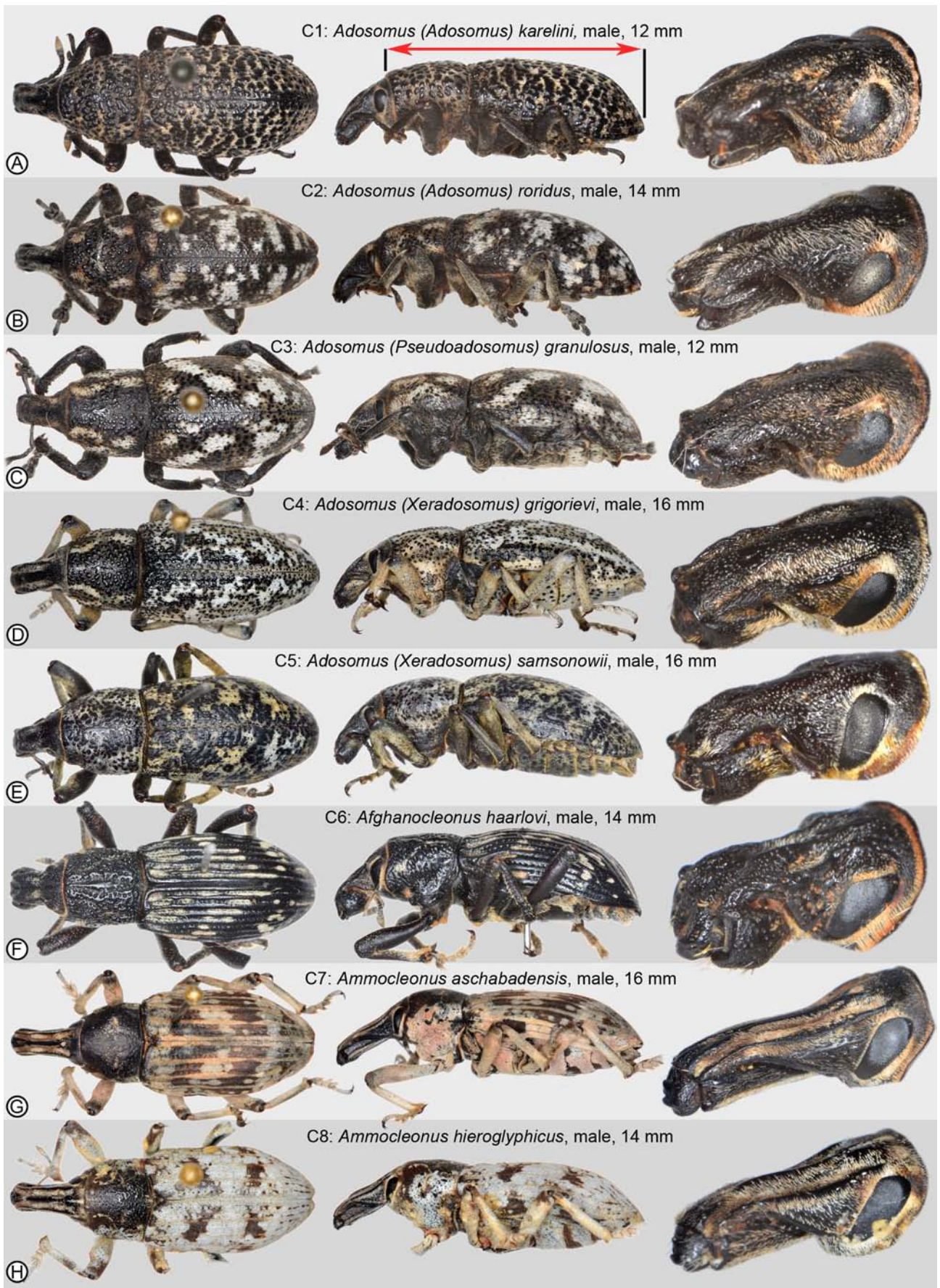


FIGURE 12. Cleonini terminals C1–C8.

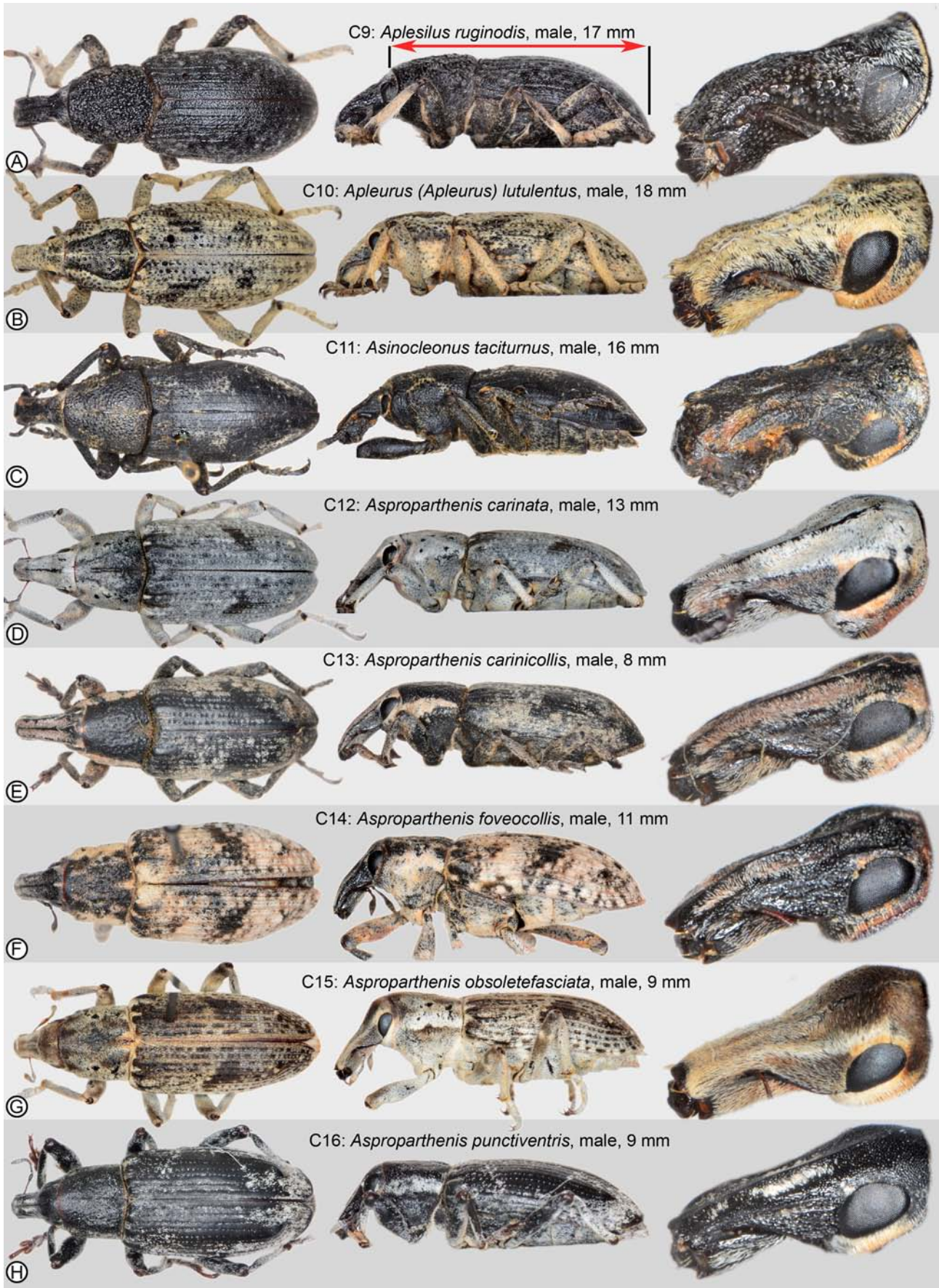


FIGURE 13. Cleonini terminals C9–C16.

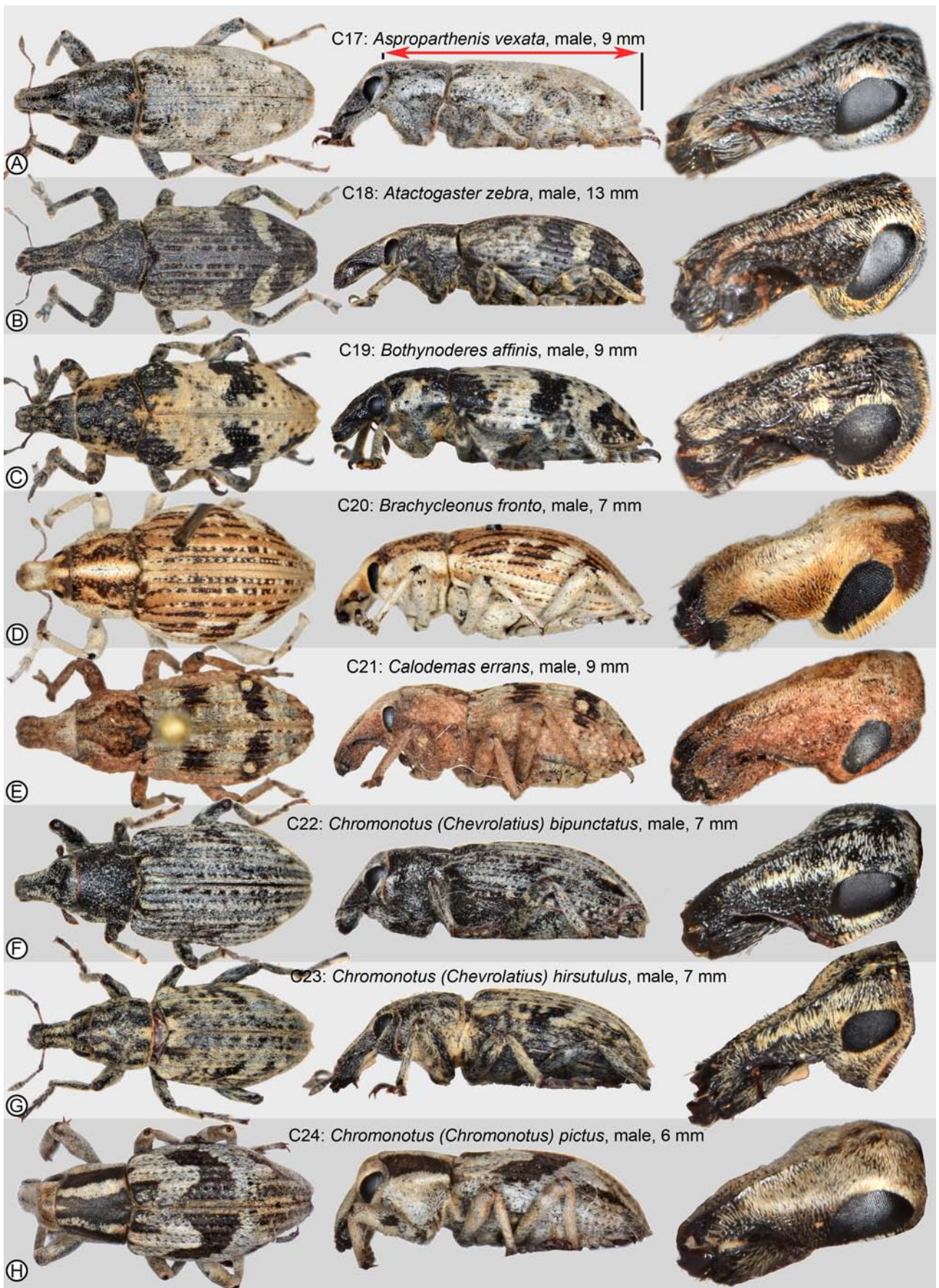


FIGURE 14. Cleonini terminals C17–C24.



FIGURE 15. Cleonini terminals C25–30 and 32–33.

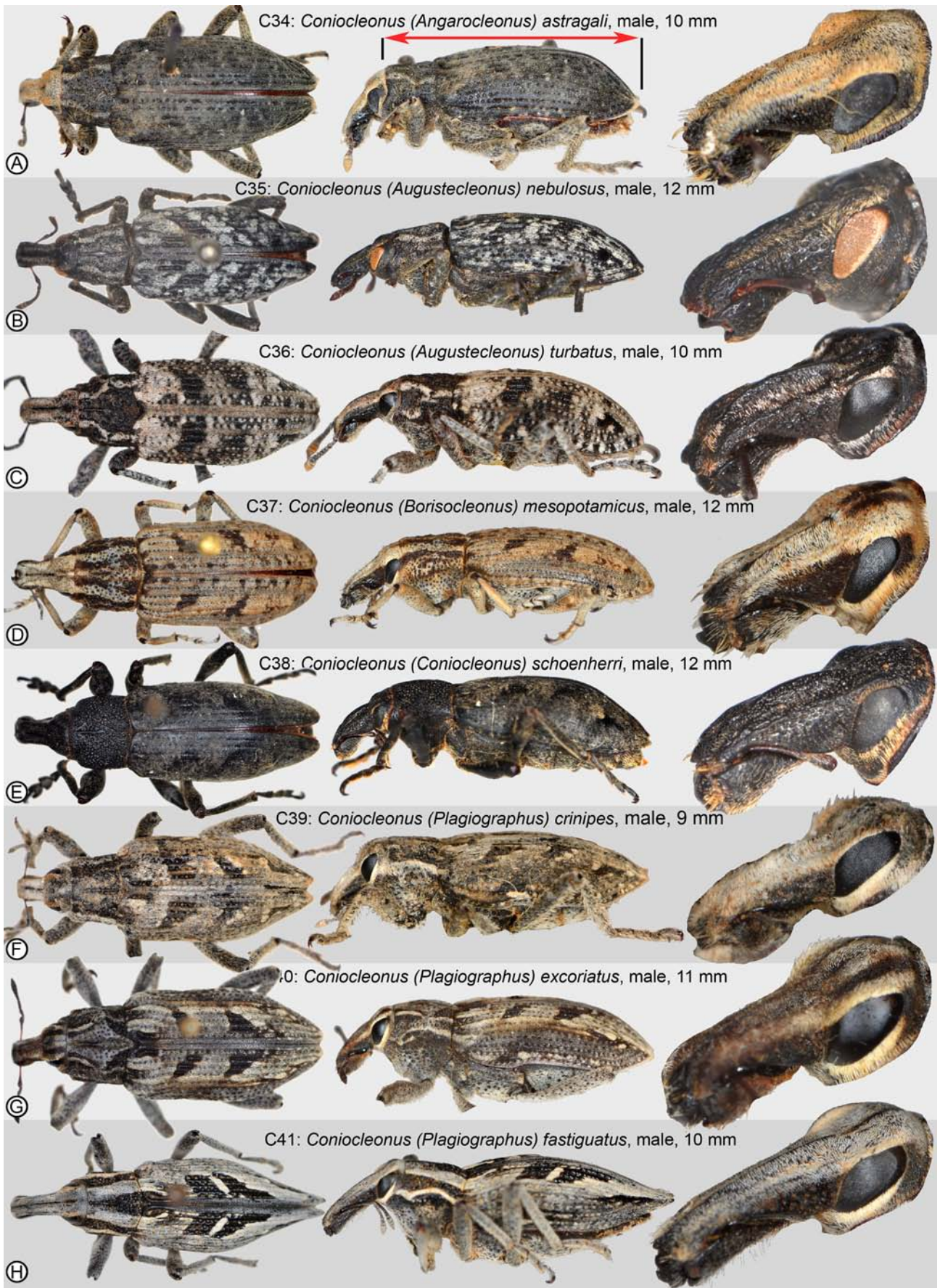


FIGURE 16. Cleonini terminals C34–C41.

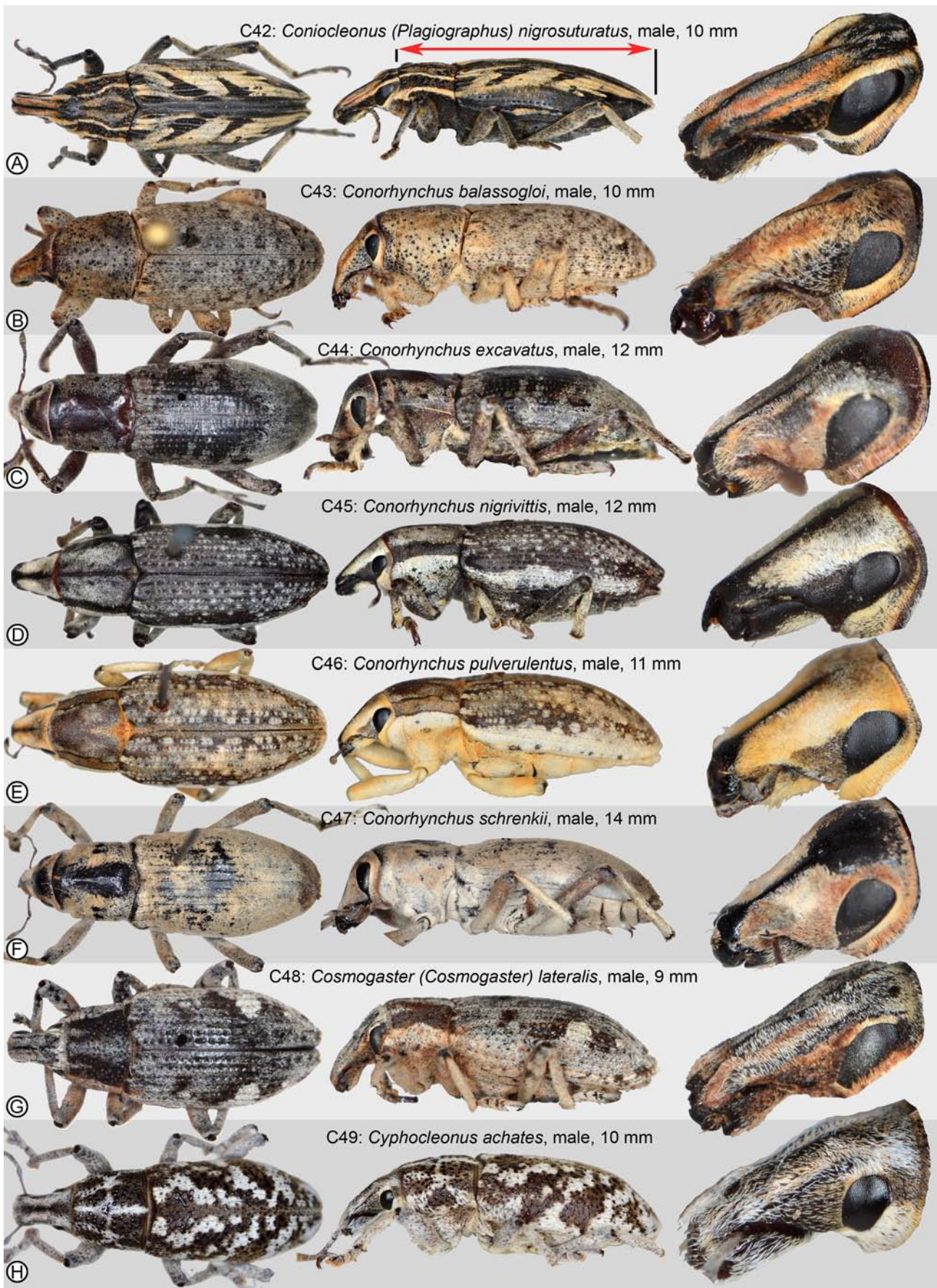


FIGURE 17. Cleonini terminals C42–C49.

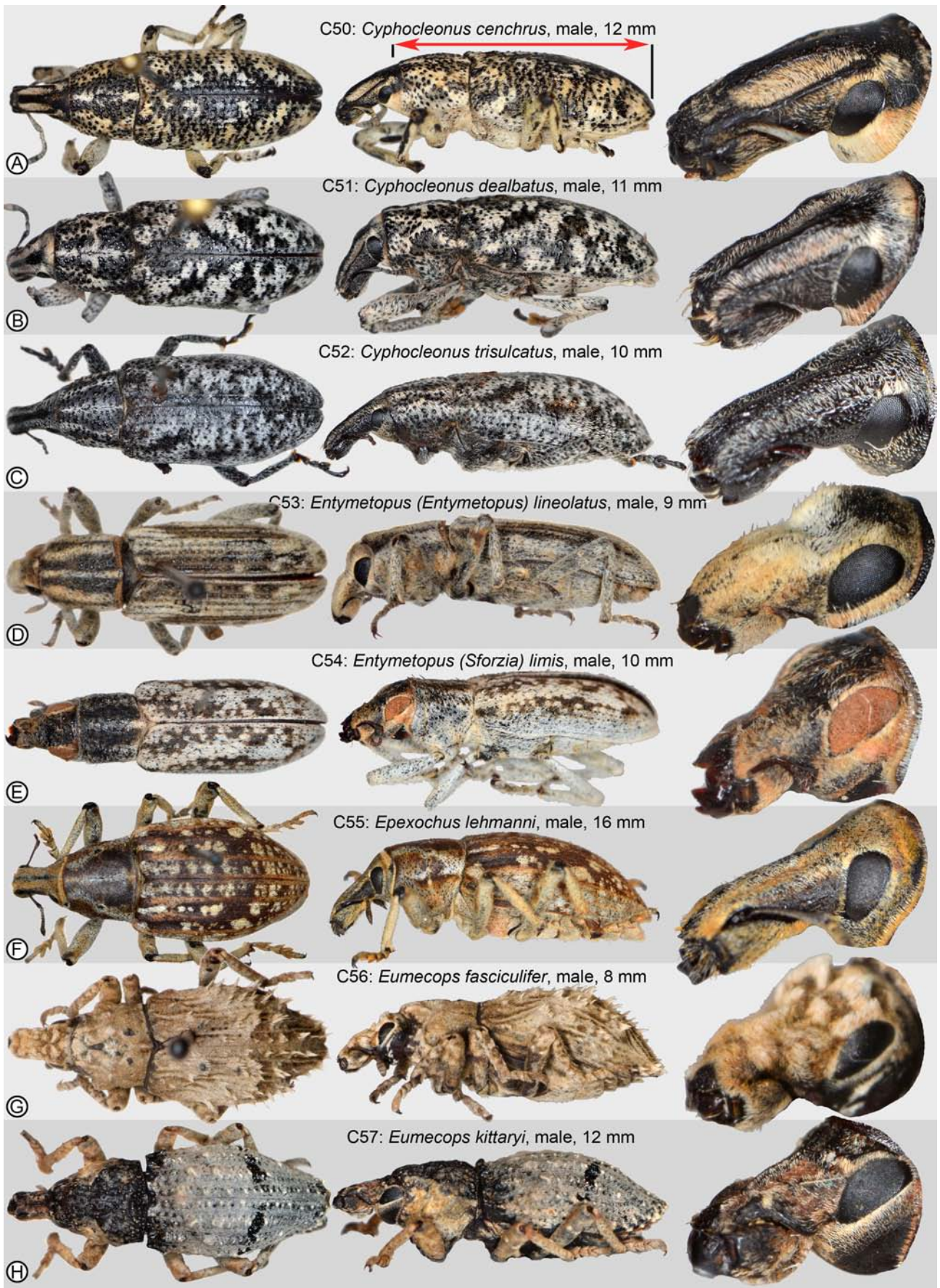


FIGURE 18. Cleonini terminals C50–C57.



FIGURE 19. Cleonini terminals C58–C65.



FIGURE 20. Cleonini terminals C66–C73.

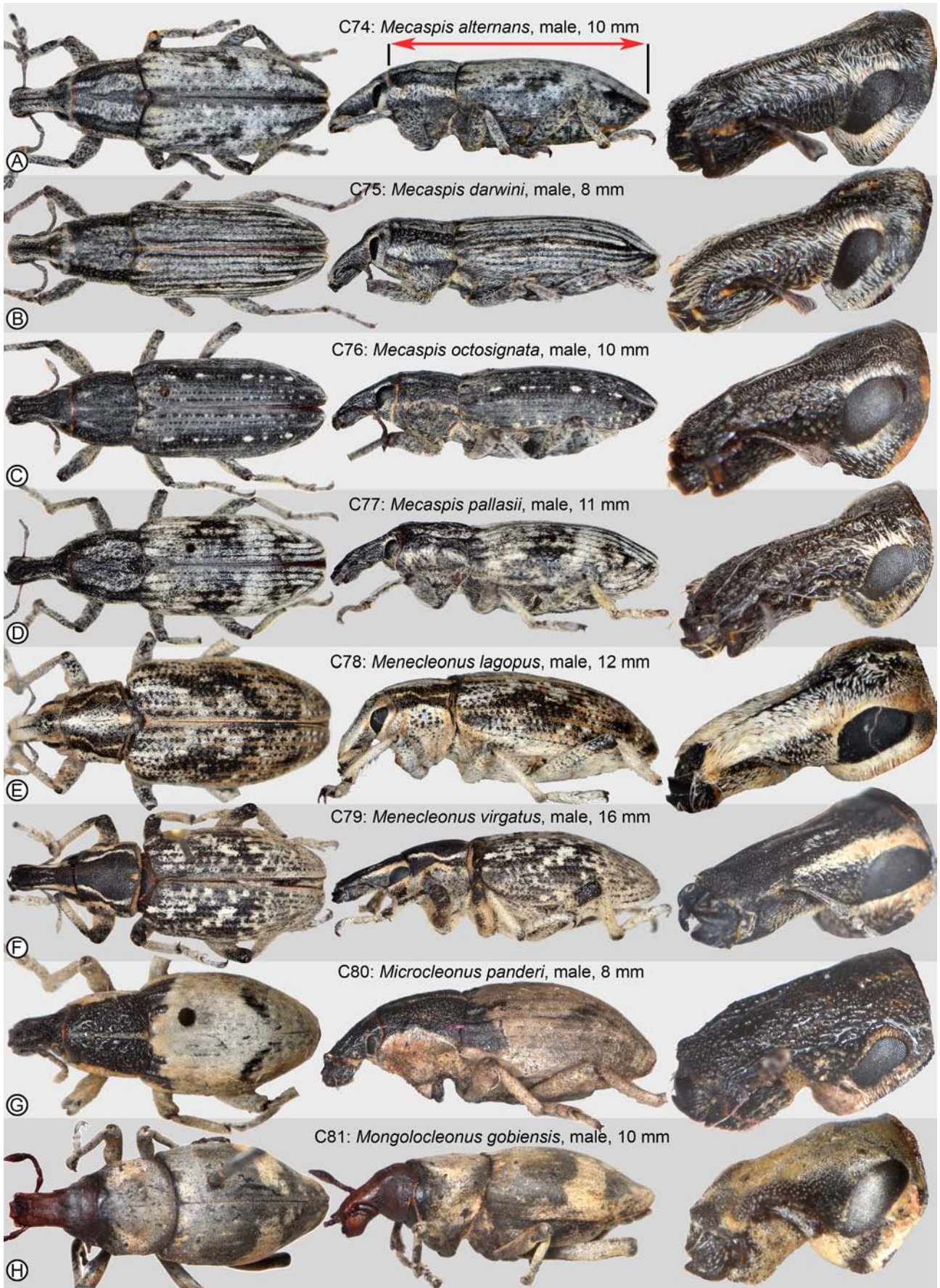


FIGURE 21. Cleonini terminals C74–C81.



FIGURE 22. Cleonini terminals C82–C89.



FIGURE 23. Cleonini terminals C90–C97.

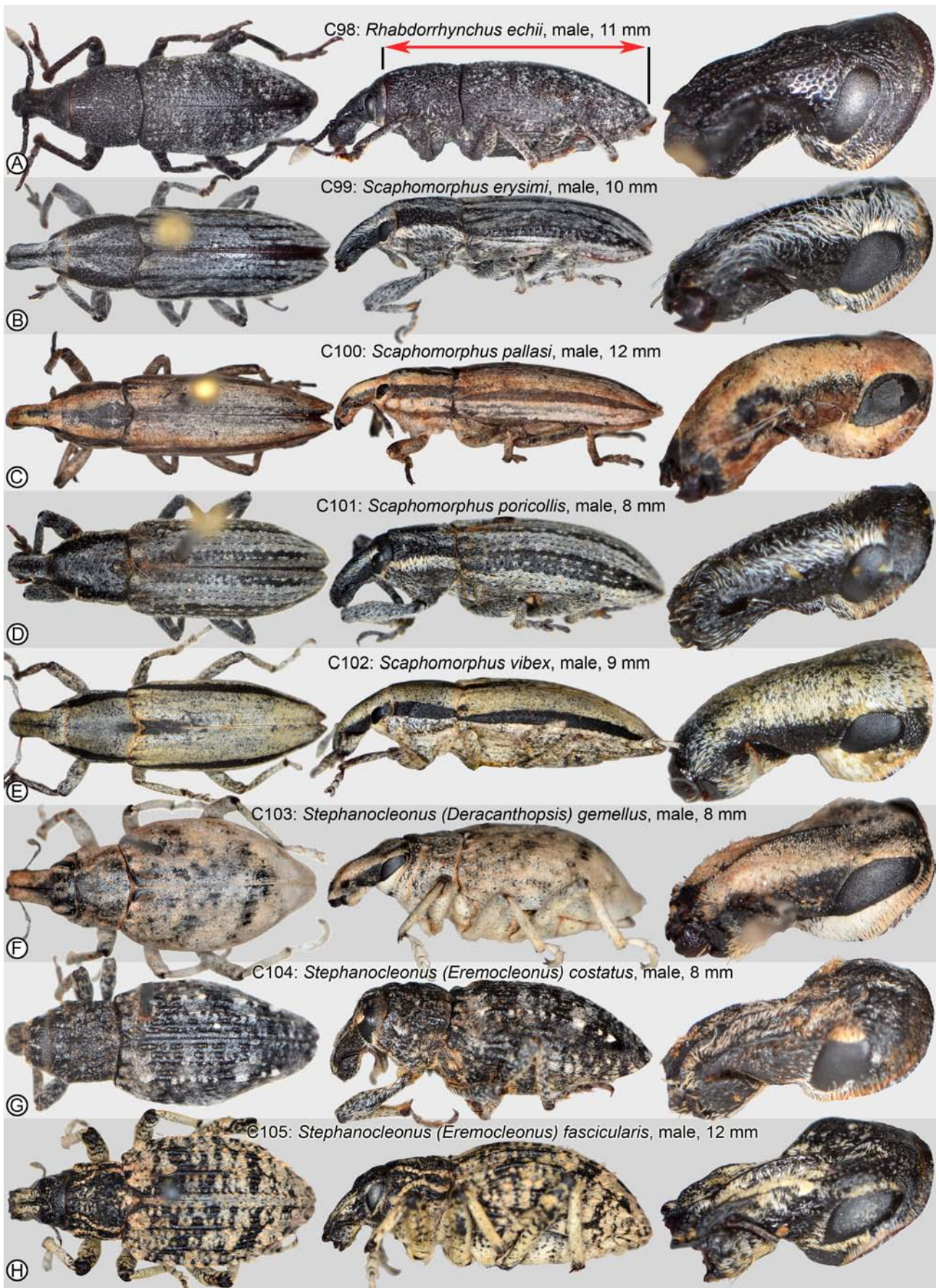


FIGURE 24. Cleonini terminals C98–C105.

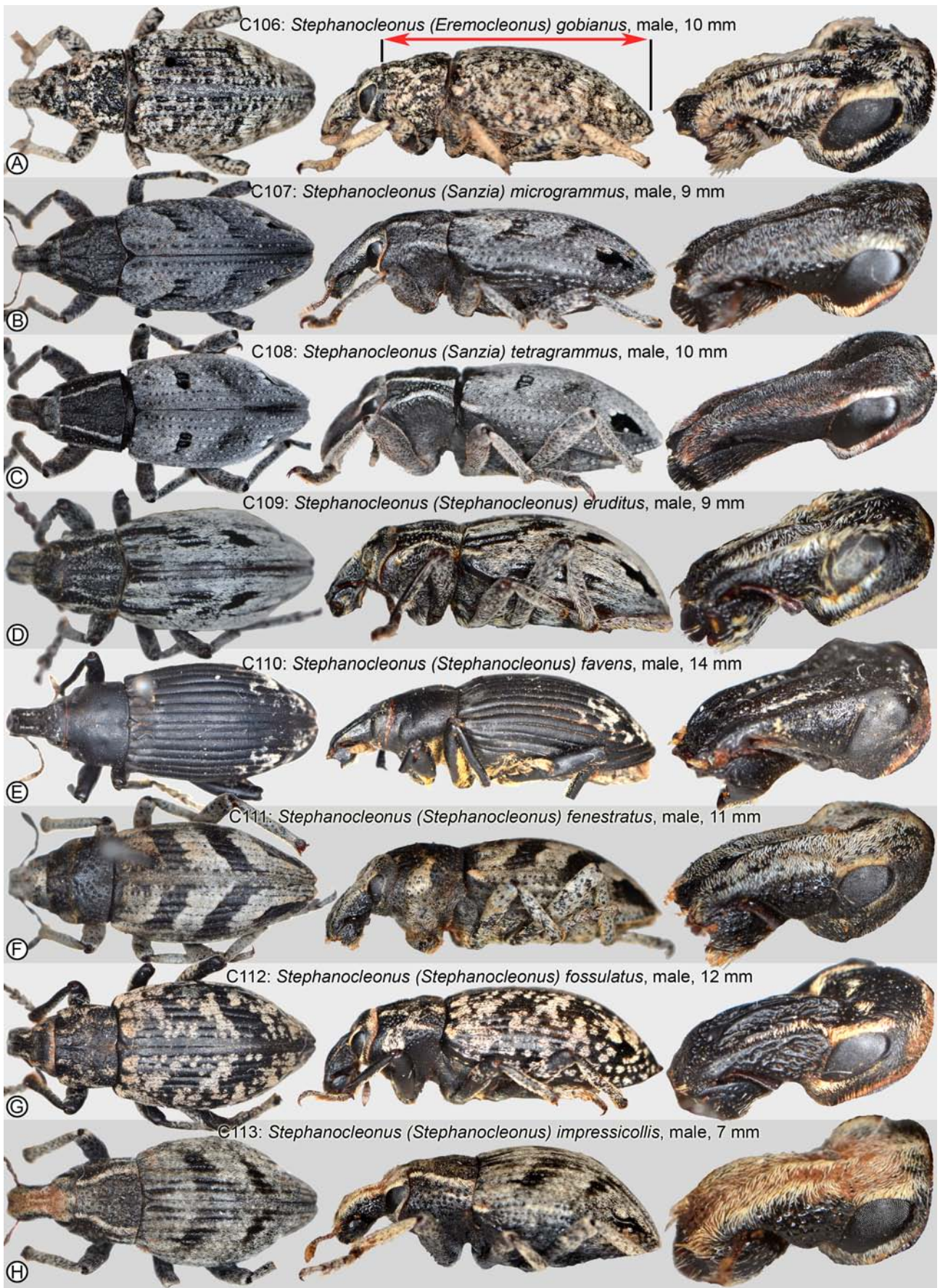


FIGURE 25. Cleonini terminals C106–C113.



FIGURE 26. Cleonini terminals C114–C121.



FIGURE 27. Cleonini terminals C122–C129.

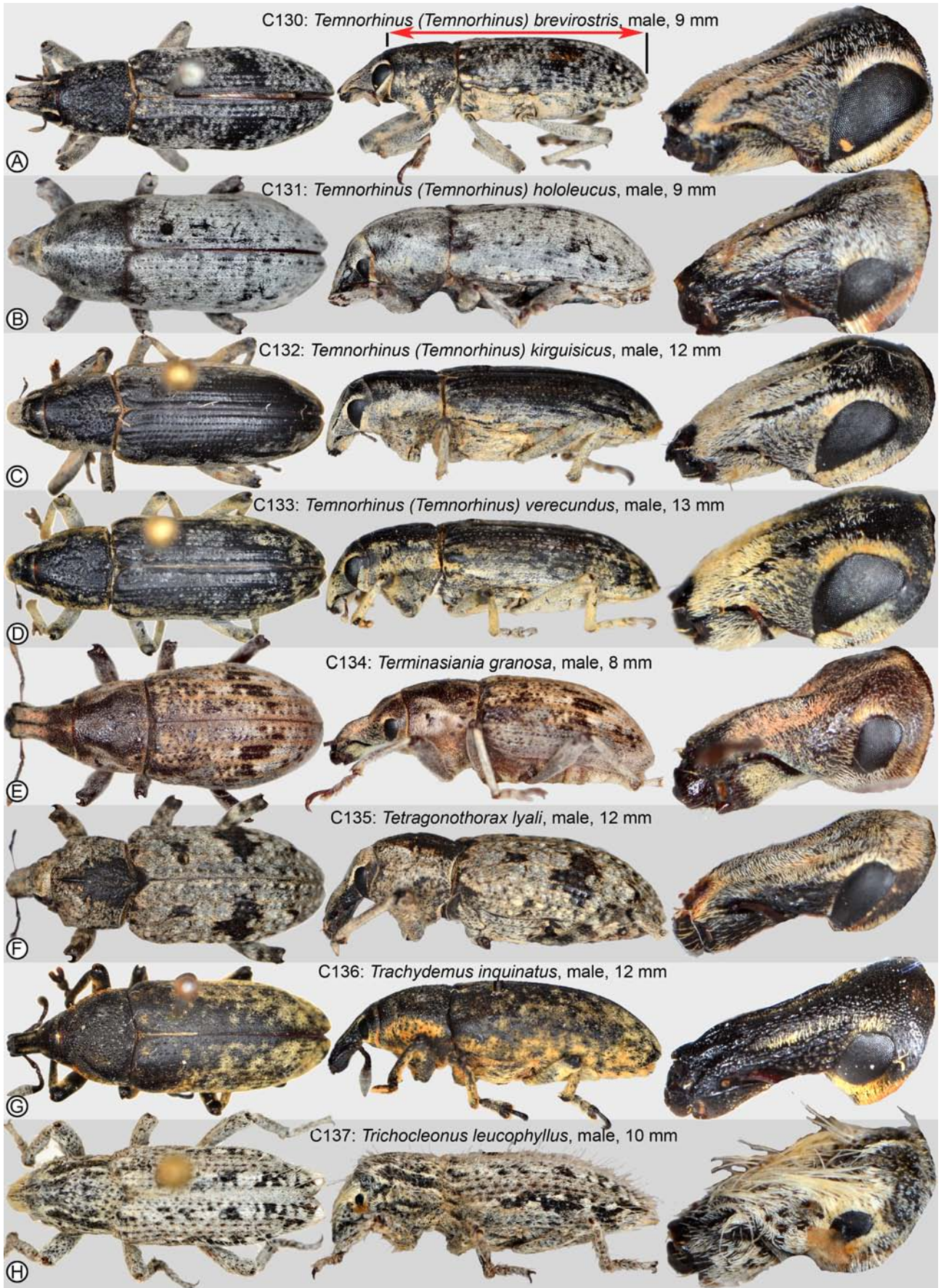


FIGURE 28. Cleonini terminals C130–C137.

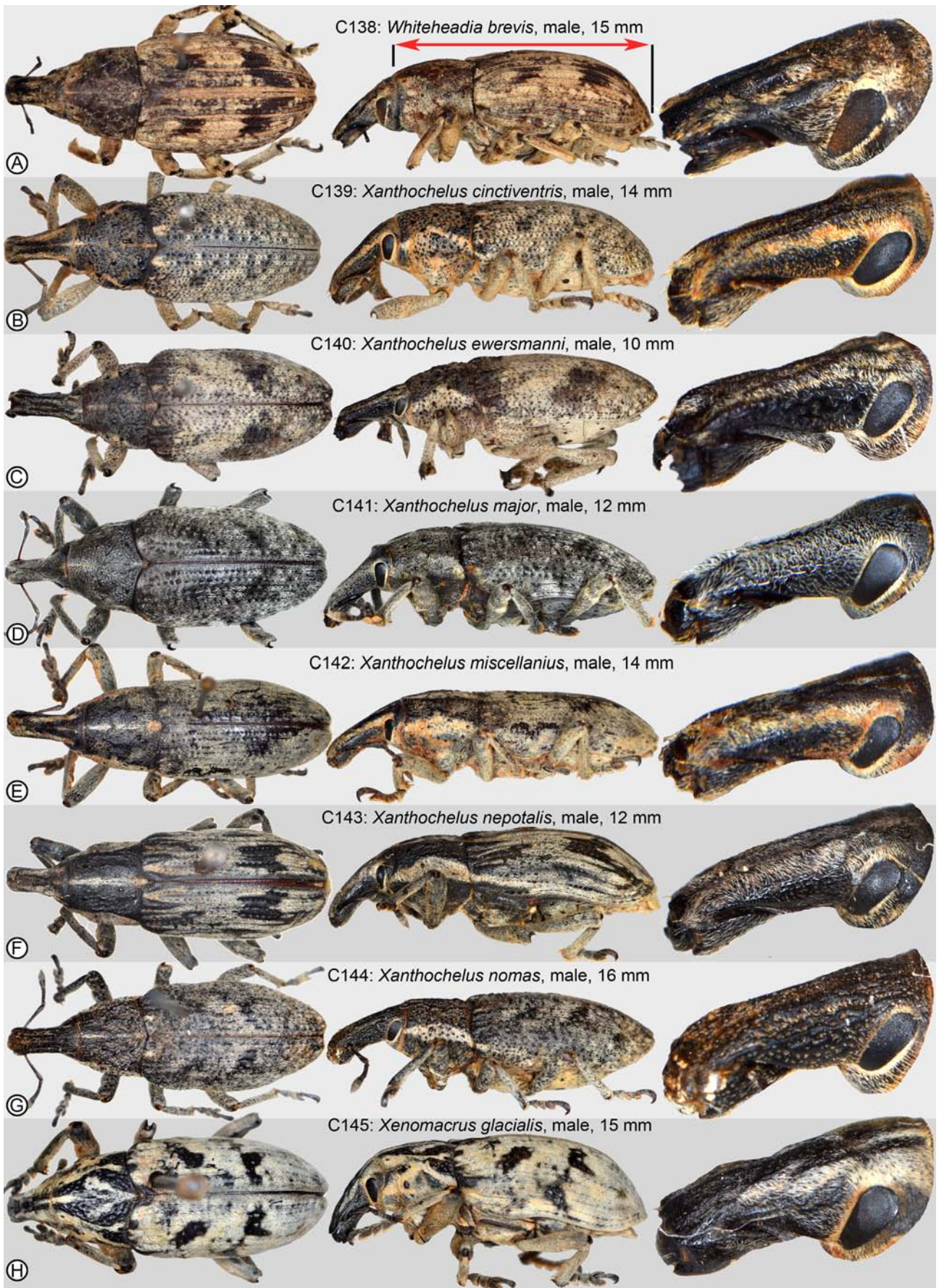


FIGURE 29. Cleonini terminals C138–C145.

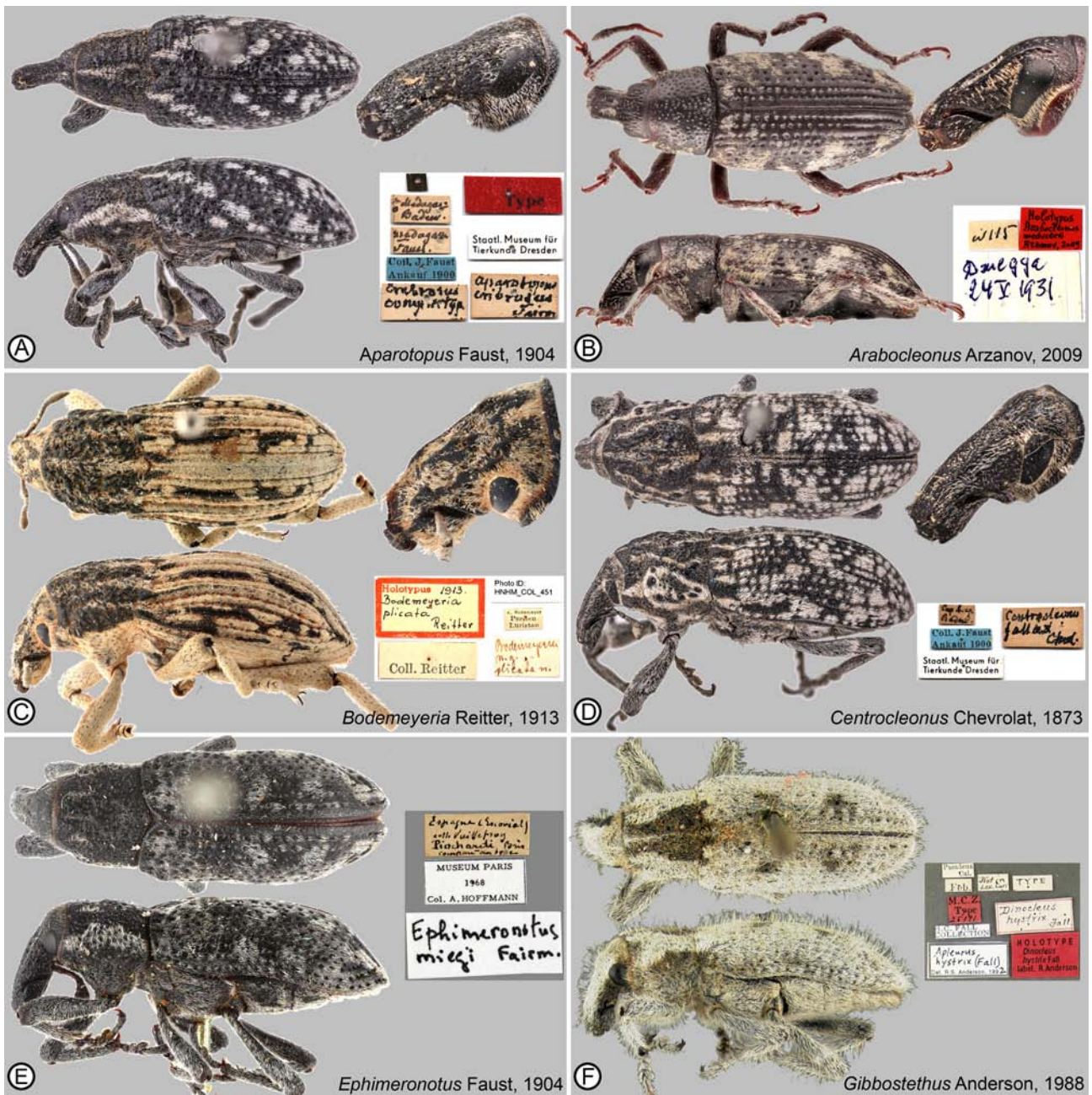


FIGURE 30. Cleonini genus-group taxa not represented in the analysis. A: *Aparotopus* Faust, 1904 (syntype of the type species *Pachycerus cribrusus* Fairmair, 1896; photo: Marc Srour, ©: MTD); B: *Arabocleonus* Arzanov, 2009 (holotype of the type species *Arabocleonus medvedevi* Arzanov, 2009; photo: Andery M. Shapovalov, ©: ZIN); C: *Bodemeyeria* Reitter, 1913 (holotype of the type species *Bodemeyeria plicata* Reitter, 1913; photo: Tamás Németh; ©: HNHM); D: *Centrocleonus* Chevrolat, 1873 (non-type specimen of the type species *Cleonus fallax* Fåhraeus, 1842; Marc Srour; ©: MTD); E: *Ephimeronotus* Faust, 1904 (non-type specimen of the type species *Cleonus miegii* Fairmaire, 1855 from Adolphe Hoffmann's collection; photo: Antoine Mantilleri; ©: MNHN; type specimens could not be located in MNHN, email from H el ene Perrin on Jan. 6, 2017); F: *Gibbostethus* Anderson, 1988 (holotype of the type species *Dinocleus hystrix* Fall, 1913; photo: MCZ, ©: President and Fellows of Harvard College).

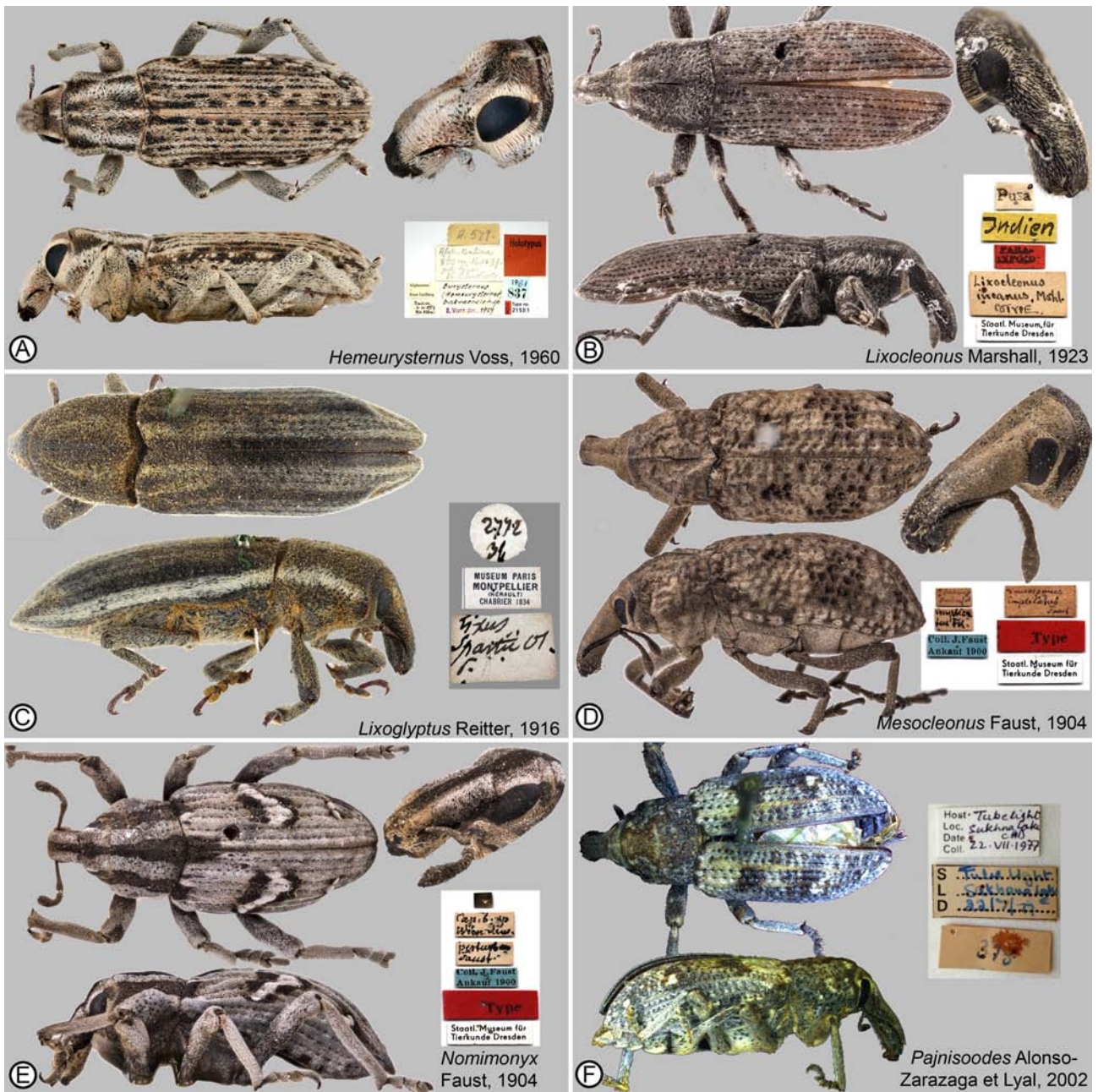


FIGURE 31. Cleonini genus-group taxa not represented in the analysis. A: *Hemeurysternus* Voss, 1960 (holotype of the type species *Eurysternus bakvaensis* Voss, 1960; photo: Christoffer Fägerström; ©: MZLU); B: *Lixocleonus* Marshall, 1923 (paratype of the type species *Lixocleonus incanus* Marshall, 1923; photo: Marc Srouf; ©: MTD); C: *Lixoglyptus* Reitter, 1916 (non-type specimen of the type species *Lixus spartii* Olivier, 1807; photo: Antoine Mantilleri; ©: MNHN; type specimens could not be located in MNHN, email from Hélène Perrin on Jan. 6, 2017); D: *Mesocleonus* Faust, 1904 (syntype of the type species *Cleonus implicatus* Faust, 1885; photo: Marc Srouf; ©: MTD); E: *Nomimonyx* Faust, 1904 (syntype of the type species *Nomimonyx perturbans* Faust, 1904; photo: Marc Srouf; ©: MTD); F: *Pajnisoodes* Alonso-Zarazaga et Lyal, 2002 (paratype of the type species *Dirodes flavomaculatus* Pajni et Sood, 1982; photo: Vilayanoor V. Ramamurthy; ©: IARI).

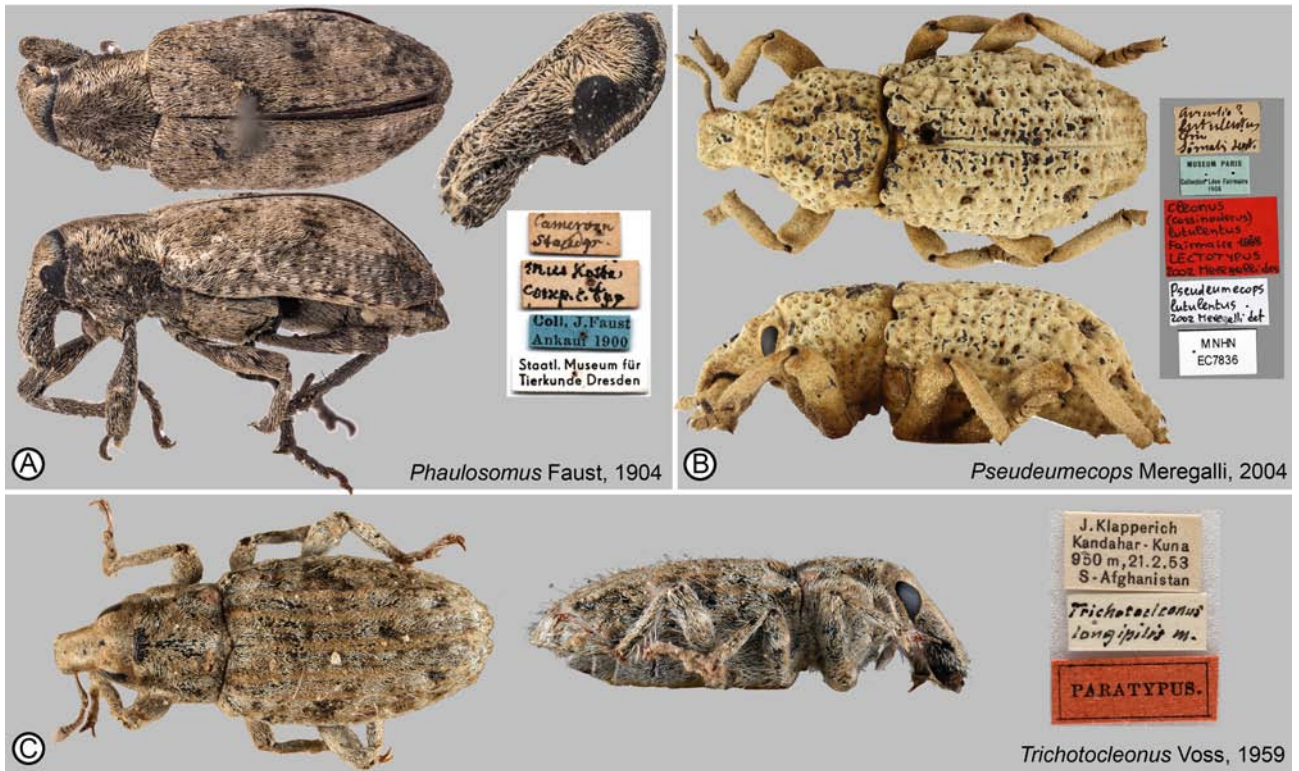


FIGURE 32. Cleonini genus-group taxa not represented in the analysis. A: *Phalosomus* Faust, 1904 (non-type specimen of the type species *Cleonus mus* Kolbe, 1883; photo: Marc Srour; ©: MTD); B: *Pseudeumecops* Meregalli, 2004 (lectotype of the type species *Cleonus lutulentus* Fairmaire, 1888; photo: Antoine Mantilleri; ©: MNHN); C: *Trichotocleonus* Voss, 1959 (paratype of the type species *Trichotocleonus longipilis* Voss, 1959; photo: Martin Husemann; ©: ZMUH).

APPENDIX 2. List of 121 morphological characters used in the phylogenetic analysis of Cleonini.

- 1: Body, length from anterior margin of pronotum to elytral apex, dorsal view: less than 6mm = 0; 6 to less than 9mm = 1; 9 to less than 12mm = 2; 12 to less than 15mm = 3; 15mm and more = 4.
- 2: Body, ratio body length to elytral width at midlength, dorsal view: less than 2.0 = 0 (Fig. 26C); 2.0 to less than 2.5 = 1 (Fig. 12A); 2.5 to less than 3.0 = 2 (Fig. 18D); 3.0 and more = 3 (Fig. 20D).
- 3: Body, ratio body length to maximum height, lateral view: less than 2.5 = 0 (Fig. 26C); 2.5 to less than 3.0 = 1 (Fig. 12E); 3.0 to less than 3.5 = 2 (Fig. 27G); 3.5 and more = 3 (Fig. 24C).
- 4: Head, rostrum, shape, fronto-dorsal view: parallel-sided = 0 (Fig. 34A); markedly narrowed apicad = 1 ((Fig. 34F).
- 5: Head, rostrum, dorsal contour, shape, lateral view: straight = 0 (Fig. 33D); convex = 1 (Fig. 33Q).
- 6: Head, rostrum, shape, cross-section at middle: round or oval = 0; square or trapezoid = 1.
- 7: Head, rostrum, markings separating epistome from the rest of dorsal surface, dorsal view: absent = 0 (Fig. 34O); present = 1 (Fig. 34B).
- 8: Head, rostrum, epistome, anterior edge, notch at middle, dorsal view: absent = 0 (Fig. 34B); present = 1 (Fig. 34H).
- 9: Head, rostrum, transverse depression separating rostrum from frons, lateral view: absent = 0 (Fig. 33A); present = 1 (Fig. 33J).
- 10: Head, rostrum, ratio of rostral length to pronotal length, dorsal view: $<0.5x$ = 0 (Fig. 12F); $>0.5x$ = 1 (Fig. 12H).
- 11: Head, rostrum, ratio of rostral length to rostral width at middle, fronto-dorsal views: $<1.5x$ = 0 (Fig. 34J); $>1.5x$ = 1 (Fig. 34K).
- 12: Head, rostrum, apical third, shape, fronto-dorsal view: parallel-sided = 0 (Fig. 34E); widening apicad by about fifth its width = 1 (Fig. 34K).
- 13: Head, rostrum, number of dorsal longitudinal keels: 0 = 0; 1 = 1 (Fig. 34Q); 2 = 2 (Fig. 34D); 3 = 3 (Fig. 34O)/.
- 14: Head, rostrum, central dorsal longitudinal keel, shape: parallel-sided = 0 (Fig. 34Q); widening apicad to at least twice its width = 1 (Fig. 34I).
- 15: Head, rostrum, number of dorsal longitudinal grooves: 0 = 0 (Fig. 34F); 1 = 1 (Fig. 34D); 2 = 2 (Fig. 34H); 3 = 3 (Fig. 34G).
- 16: Head, rostrum, ventral surface: smooth = 0 (Fig. 35H); wrinkled = 1 (Fig. 35A).

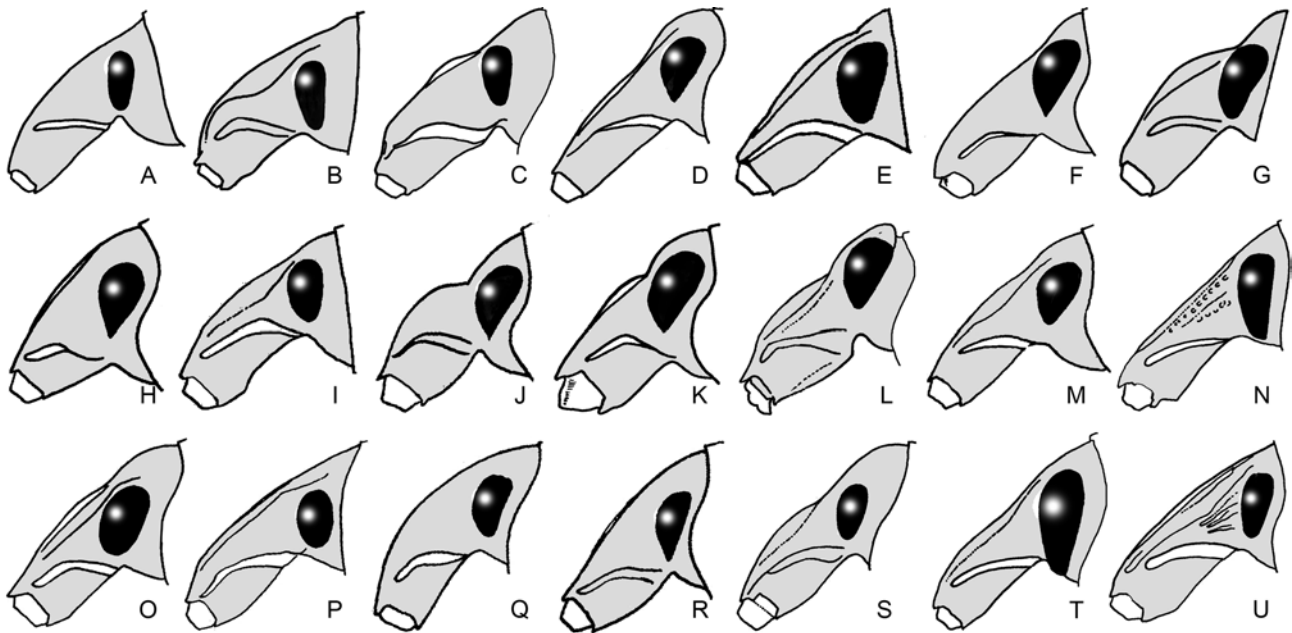


FIGURE 33. Cleonini, adults, head, left lateral view. A: *Adosomus* (*Adosomus*) *roridus*; B: *Adosomus* (*Xeradosomus*) *samsonovi*; C: *Aplesilus* *ruginodis*; D: *Asproparthenis* *carinata*; E: *Bothynoderes* *affinis*; F: *Chromonotus* (*Chromonotus*) *vittatus*; G: *Coniocleonus* (*Coniocleonus*) *schoenherrii*; H: *Conorhynchus* *pulverulentus*; I: *Cyphocleonus* *dealbatus*; J: *Entymetopus* (*Entymetopus*) *lineolatus*; K: *Glebius* *confluens*; L: *Koenigius* *palaestinus*; M: *Maximus* *strabus*; N: *Neocleonus* *sannio*; O: *Pleurocleonus* *sollicitus*; P: *Pseudocleonus* (*Pseudocleonus*) *cinereus*; Q: *Scaphomorphus* *vibex*; R: *Temnorhinus* (*Temnorhinus*) *hololeucus*; S: *Terminasiania* *granosa*; T: *Tetragonothorax* *senectus*; U: *Xenomacrus* *glacialis*.

- 17: Head, rostrum, lateral dish-shaped widening of scrobes accommodating antennal attachment (=pterygia), dorsal view: absent = 0 (Fig. 34E); present = 1 (Fig. 34K).
- 18: Head, rostrum, antennal attachment, location: in apical third = 0; in central third = 1.
- 19: Head, rostrum, scrobes, direction basad of antennal attachments and location: parallel-sided (not extending to ventral sides) = 0; weakly convergent (extending on ventral side), not joining = 1 (Fig. 33M); markedly convergent basad (extending on ventral side), joining = 2 (Fig. 33A).
- 20: Head, eyes, shape, lateral view: oval = 0 (Fig. 33O); narrowed ventrad (=inverted teardrop-shaped) = 1 (Fig. 33H).
- 21: Head, anterior margin of eyes, lateral view: evenly curved = 0 (Fig. 33E); straight = 1 (Fig. 33T).
- 22: Head, lower part of eyes, extension to ventral surface, lateral view: absent = 0 (Fig. 33A); present = 1 (Fig. 33T).
- 23: Head, antenna, ratio of scapus length to length of flagellum: <1x (scapus short) = 0; >1x (scapus long) = 1.
- 24: Head, antenna, ratio of pedicel length to length of antennomere 3: <1x (pedicel short) = 0; >1x (pedicel long) = 1.
- 25: Head, antenna, ratio of club length to that of flagellum: <0.65x (club normal) = 0; >0.65x (club large) = 1.
- 26: Head, antenna, antennomere 5, ratio length to width: <1x (short, transverse) = 0; >1x (long, elongated) = 1.
- 27: Head, stipes of maxilla, number of long setae on lateral side: 1 = 0 (Fig. 37C); 2 and more = 1 (Fig. 37M).
- 28: Head, palpiger of maxilla, number of long setae: 0 = 0; 1 = 1 (Fig. 37D); 2 and more = 2 (Fig. 37K).
- 29: Head, lamella of maxilla, internal teeth: absent = 0 (Fig. 37R); present = 1 (Fig. 37U).
- 30: Head, lamella of maxilla, internal teeth, length: short, <1.5x their basal width = 0 (Fig. 37B); long, >2x their basal width = 1 (Fig. 37C).
- 31: Head, lamella of maxilla, internal teeth, length compared to length of external ones: smaller = 0 (Fig. 37Q); subequal or greater = 1 (Fig. 37U).
- 32: Head, lamella of maxilla, external teeth, relative size: subequal = 0 (Fig. 37G); differ in size twice and more = 1 (Fig. 37I).
- 33: Head, prementum, number of setae on each side, ventral view: 0 = 0; 1 = 1 (Fig. 36C); 2 = 2 (Fig. 36D); 3 and more = 3 (Fig. 36J).
- 34: Head, prementum, transverse suture on ventral surface: absent = 0 (Fig. 36E); present = 1 (Fig. 36I).
- 35: Head, prementum, labial palps externally, ventral view: indistinct (=absent) = 0; 1-segmented, wider than long = 1; 3-segmented, longer than wide = 2.
- 36: Head, postmentum, ratio of minimal length to its minimal width: longer than width = 0 (Fig. 35E); subequal = 1 (Fig. 35P); shorter than width = 2 (Fig. 35R).
- 37: Head, postmentum, ratio of maximal apical width to minimal basal width (=constriction): <1.5x = 0 (Fig. 35E); >1.5x = 1 (Fig. 35Y).

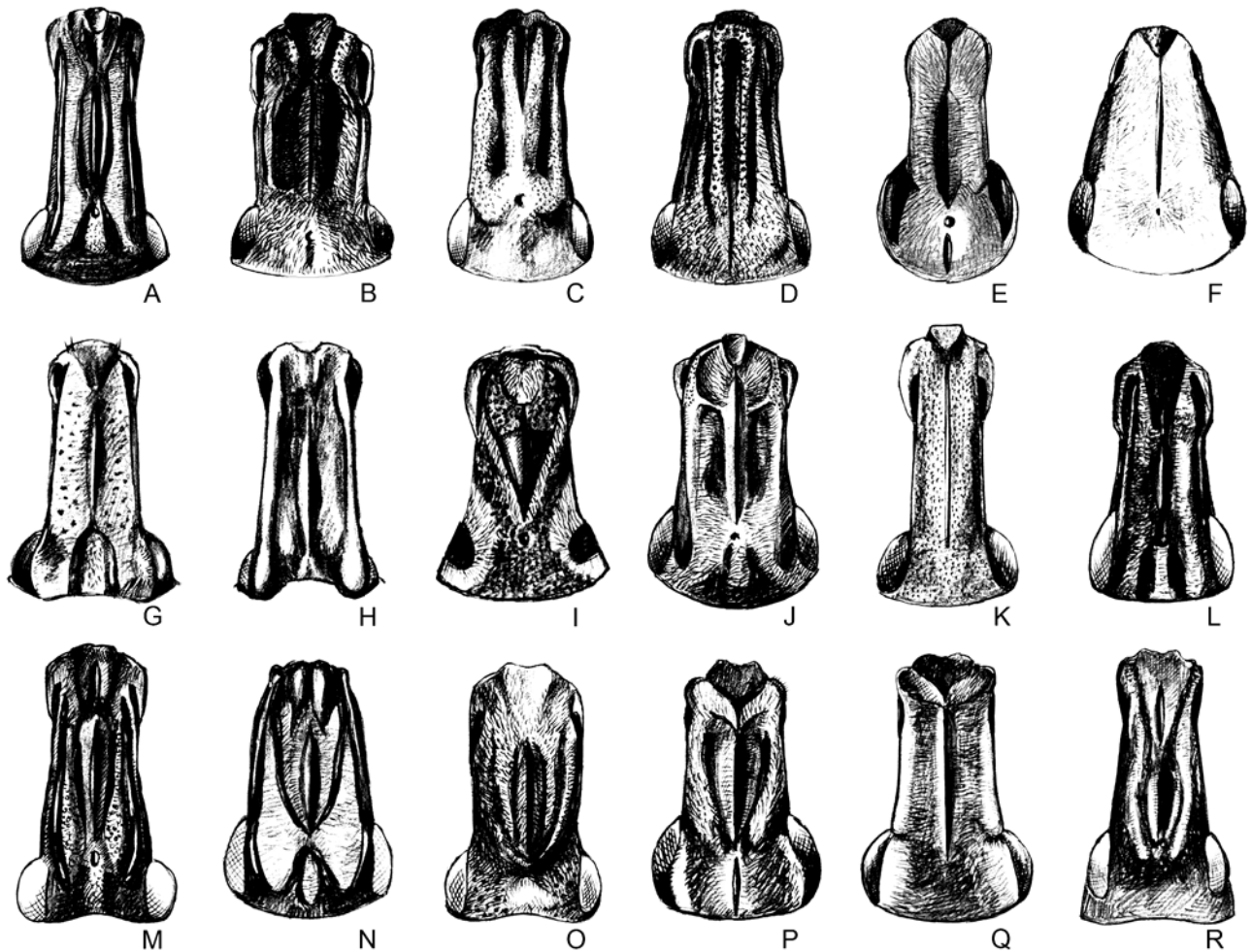


FIGURE 34. Cleonini, adults, head, fronto-dorsal view. A: *Ammocleonus aschabadensis*; B: *Atactogaster zebra*; C: *Calodemus errans*; D: *Cleonis pigra*; E: *Coniocleonus (Augustecleonus) turbatus*; F: *Conorhynchus pulverulentus*; G: *Gonocleonus margaritiferus*; H: *Koenigijs palaestinus*; I: *Leucomigus candidatus*; J: *Leucophyes pedestris*; K: *Lixomorphus algius*; L: *Monolophus praeditus*; M: *Neocleonus sannio*; N: *Pentatropis formosus*; O: *Prionorhinus canus*; P: *Stephanocleonus (Eremocleonus) gobianus*; Q: *Stephanocleonus (Stephanocleonus) colossus*; R: *Xenomacrus glacianus*.

- 38: Prothorax, posterior contour, angle between left and right halves, dorsal view: 180, posterior contour straight = 0 (Fig. 12A); <180, posterior contour forming obtuse angle protruding posterad = 1 (Fig. 19H).
- 39: Prothorax, anterior contour, postocular lobes, lateral view: absent = 0 (Fig. 18A); present = 1 (Fig. 12A).
- 40: Prothorax, anterior half, longitudinal protuberance forming lateral contour, dorsal view: absent = 0 (Fig. 12C); present = 1 (Fig. 18H).
- 41: Prothorax, sculpture, dorsal view: small dot-shaped rounded depressions = 0 (Fig. 22H); wrinkled = 1 (Fig. 16A); small protruding granules = 2 (Fig. 12E).
- 42: Prothorax, depression on each side of disk, dorsal view: absent = 0 (Fig. 12A); present = 1 (Fig. 22A).
- 43: Prothorax, medial longitudinal keel on disk, dorsal view: absent = 0 (Fig. 20C); present = 1 (Fig. 20B).
- 44: Prothorax, medial longitudinal groove on disk, dorsal view: absent = 0 (Fig. 12C); present = 1 (Fig. 21G).
- 45: Prothorax, medial longitudinal depression at base, dorsal view: absent = 0 (Fig. 12E); present = 1 (Fig. 16G).
- 46: Prothorax, thread-like keel in medial longitudinal depression at base, dorsal view: absent = 0 (Fig. 21A); present = 1 (Fig. 17A).
- 47: Prothorax, pre-coxal swellings, lateral view: absent = 0; present = 1.
- 48: Prothorax, intercoxal process, ventral view: absent = 0; present = 1.
- 49: Prothorax, ratio of thoracic length anterior of procoxae to length of procoxae, ventral view: <1x = 0; 1 or >1x = 1.
- 50: Mesothorax, scutellum externally, dorsal view: absent = 0 (Fig. 12C); present = 1 (Fig. 21A).
- 51: Metathorax, ratio of thoracic length along midline to length of mesocoxae, ventral view: <1x = 0; 1 or >1x = 1.
- 52: Metathorax, longitudinal intercoxal keel, ventral view: absent = 0; present = 1.

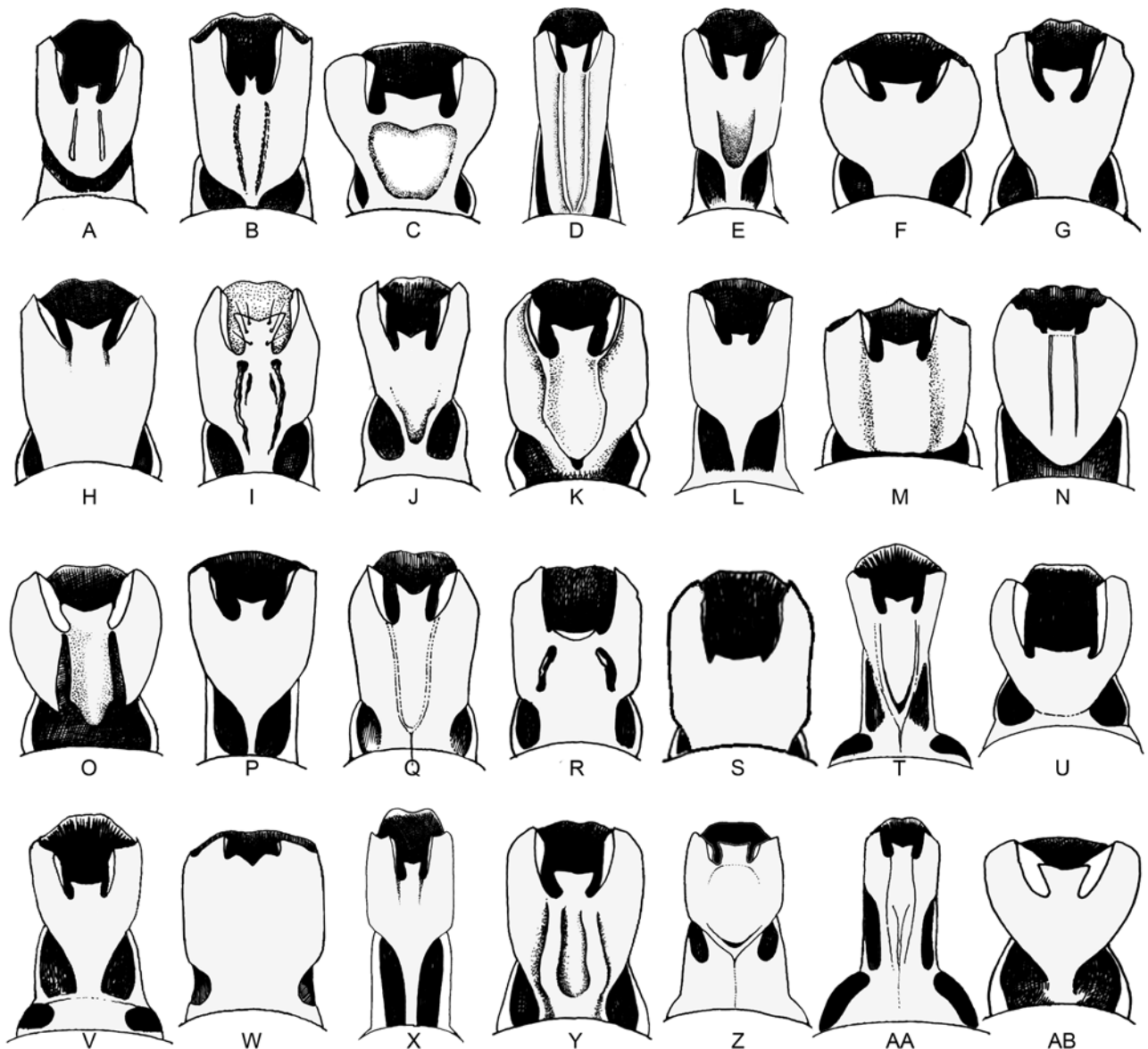


FIGURE 35. Cleonini, adults, head, mouthparts removed, ventral view. A: *Adosomus (Adosomus) roridus*; B: *Adosomus (Xeradosomus) samsonovi*; C: *Afghanocleonus haarloevi*; D: *Ammocleonus aschabadensis*; E: *Aplesilus ruginodis*; F: *Chromonotus (Chromonotus) vittatus*; G: *Eumecops kittaryi*; H: *Georginus bellus*; I: *Leucomigus candidatus*; J: *Leucophyes pedestris*; K: *Mecaspis alternans*; L: *Menecleonus lagopus*; M: *Microcleonus panderi*; N: *Mongolocleonus gobiensis*; O: *Neocleonus sannio*; P: *Pycnodactylopsis tomentosum*; Q: *Rhabdorrhynchus echii*; R: *Scaphomorphus pallasi*; S: *Stephanocleonus (Stephanocleonus) paradoxus*; T: *Tetragonothorax senectus*; U: *Trichocleonus leucophyllus*.

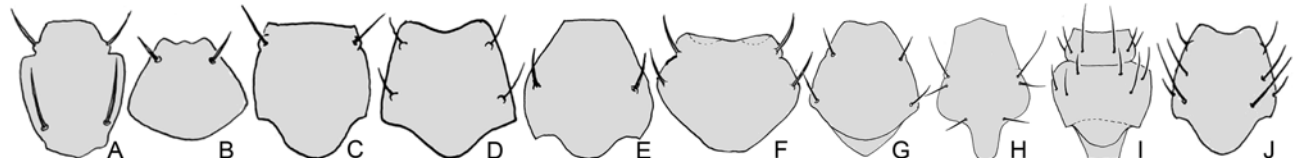


FIGURE 36. Cleonini, adults, head, submentum, ventral view. A: *Bothynoderes declivis*; B: *Chromonotus (Chromonotus) vittatus*; C: *Chromonotus (Faustius) menetriesi*; D: *Coniocleonus (Plagiographus) excoriatus*; E: *Georginus bellus*; F: *Glebius confluens*; G: *Leucophyes pedestris*; H: *Leurochromus imperialis*; I: *Menecleonus lagopus*; J: *Porocleonus candidus*.

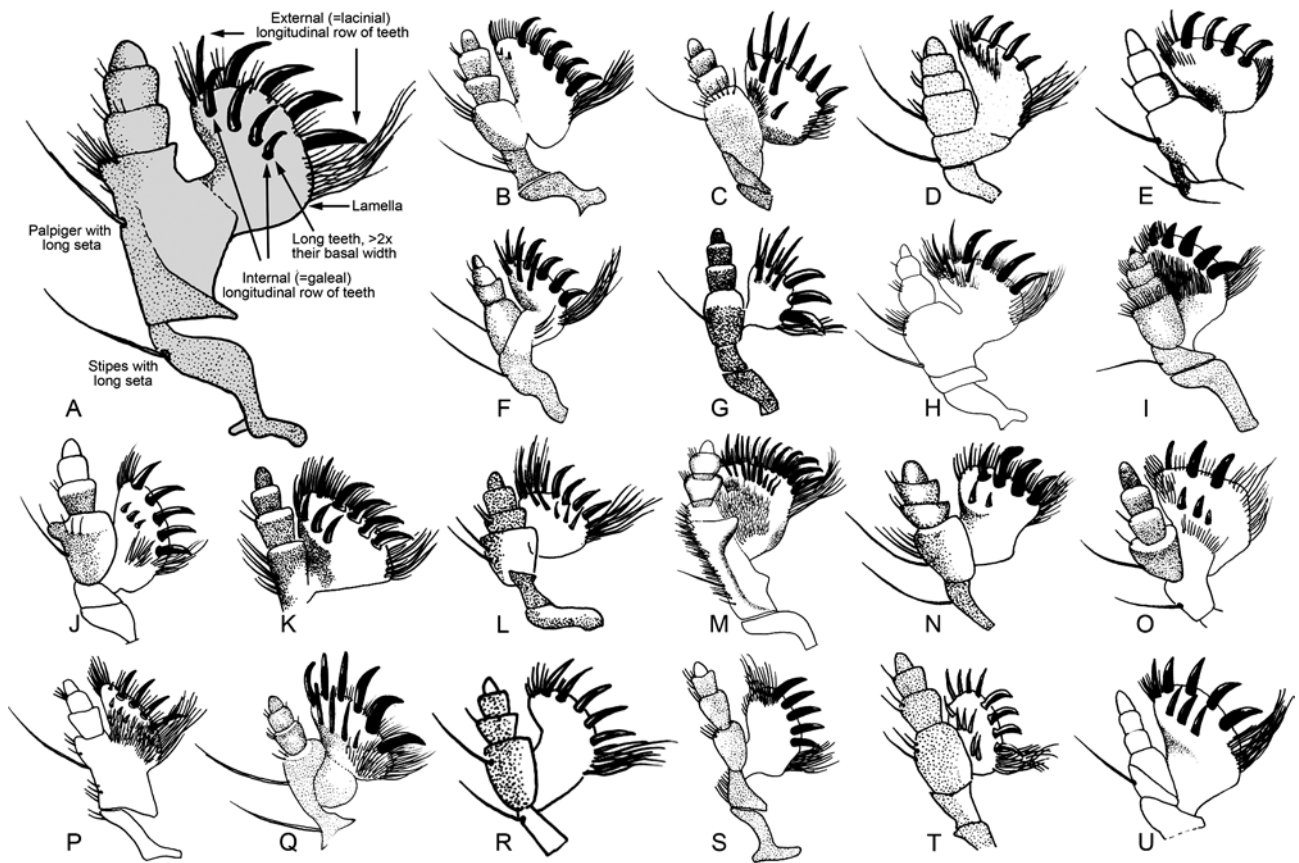


FIGURE 37. Cleonini, adults, head, left maxilla, dorsal view. A: scheme; B: *Adosomus (Adosomus) roridus*; C: *Asproparthenis punctiventris*; D: *Bothynoderes affinis*; E: *Brachycleonus fronto*; F: *Chromonotus (Chromonotus) vittatus*; G: *Chromonotus (Faustus) menetriesi*; H: *Chromosomus fischeri*; I: *Cleonis pigra*; J: *Coniocleonus (Borisocleonus) mesopotamicus*; K: *Georginus bellus*; L: *Isomerops fausti*; M: *Leucochromus imperialis*; N: *Leucomigus candidatus*; O: *Leucophyes pedestris*; P: *Liocleonus clathratus*; Q: *Maximus strabus*; R: *Neocleonus sannio*; S: *Pachycerus madidus*; T: *Terminasiania granosa*; U: *Trichocleonus leucophyllus*.

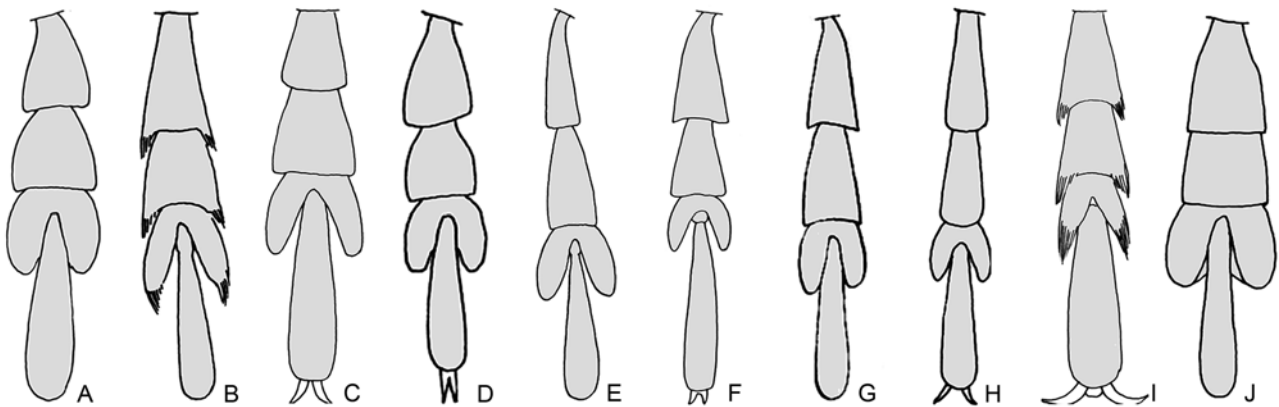


FIGURE 38. Cleonini, adults, tarsus, dorsal view. A: *Adosomus (Adosomus) roridus*; B: *Ammocleonus ganglbaueri*; C: *Aplesilus ruginodis*; D: *Bothynoderes affinis*; E: *Coniocleonus (Coniocleonus) schoenherri*; F: *Georginus bellus*; G: *Meneocleonus virgatus*; H: *Pleurocleonus sollicitus*; I: *Surchania sijazovi*; J: *Trachydemus rugosus*.

- 53: Elytra, lateral contour in basal (=anterior) half, dorsal view: straight and parallel to each other = 0 (Fig. 21B); rounded and diverging posterad = 1 (Fig. 14D).
- 54: Elytra, apices, joined or separated, dorsal view: forming join elytral apex for both elytra = 0 (Fig. 13A); separated in two elytral apices, one per elytron = 1 (Fig. 16H).

- 55: Elytra, apices, when separated, then individually rounded or pointed, dorsal view: rounded = 0 (Fig. 13E); pointed = 1 (Fig. 16H).
- 56: Elytra, shoulders, dorsal view: effaced = 0 (Fig. 14D); markedly developed = 1 (Fig. 11).
- 57: Elytra, interstriae, elevation, posterior view: all flat = 0 (Fig. 13E); even flat, odd protruding dorsad = 1 (Fig. 23E).
- 58: Elytra, width of interstriae at middle of elytra, dorsal view: subequal, maximal width difference <math><1.5x</math> = 0 (Fig. 23A); unequal, maximal width difference >math>>2x</math> = 1 (Fig. 17A).



FIGURE 39. Cleonini, adults, claws, dorsal view. A: *Adosomus (Adosomus) roridus*; B: *Afghanocleonus haarloevi*; C: *Ammocleonus hieroglyphus*; D: *Bothynoderes declivis*; E: *Gonocleonus margaritiferus*; F: *Isomerops fausti*; G: *Leucochromus imperialis*; H: *Maximus strabus*; I: *Pleurocleonus quadrivittatus*; J: *Terminasiania granosa*; K: *Trichocleonus leucophyllus*.

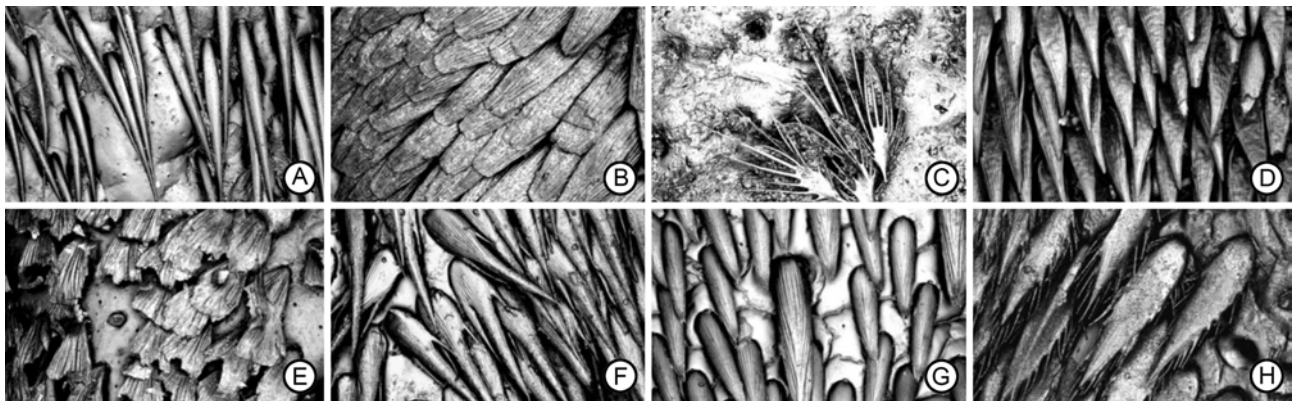


FIGURE 40. Scanning electron microscopy images of scales, dorsal surface of right elytron in basal third. A: *Entymetopus (Entymetopus) lineolatus*; B: *Eumecops kittaryi*; C: *Liocleonus clathratus*; D: *Lixomorphus algirus*; E: *Mongolocleonus gobiensis*; F: *Prionorhinus canus*; G: *Tetragonothorax lyali*; H: *Trichocleonus leucophyllus*.

- 59: Elytra, interstriae, protuberances, dorsal view: absent = 0 (Fig. 12A); present = 1 (Fig. 18G).
- 60: Elytra, density of recumbent scale, dorsal view: sparse, not fully concealing elytral surface = 0 (Fig. 13A); dense, fully concealing elytral surface = 1 (Fig. 23G).
- 61: Elytra, disk, shape pilosity-forming elements (setae or scales), dorsal view: seta-like, pointed = 0 (Fig. 40A); leaf- or lancet-shaped, pointed = 1 (Fig. 40D); parallel-sided, not pointed = 2 (Fig. 40G); scale-shaped, sides diverging apically and notched = 3 (Fig. 40H).
- 62: Elytra, protruding long setae on interstriae contrasting with recumbent pilosity, dorsal views: absent = 0 (Fig. 12H); present = 1 (Fig. 28H).
- 63: Elytra, colour patter, dorsal view: even, not forming patterns = 0 (Fig. 13A); irregular spots forming marble pattern = 1 (Fig. 12B); longitudinal stripes = 2 (Fig. 19C); oblique stripes = 3 (Fig. 19H).
- 64: Metathoracic wings, dissection required: absent = 0; present, vestigial, <math><1/3x</math> elytral length = 1.
- 65: Legs, front femora, femoral tooth, lateral view: absent = 0; present = 1.
- 66: Legs, tibiae, serration on internal surface, lateral view: absent = 0; present = 1.
- 67: Legs, front tibiae, mucro, lateral view: absent = 0; present = 1.
- 68: Legs, front tibiae, uncus, lateral view: absent = 0; present = 1.
- 69: Legs, front tibiae, short apical stout setae, lateral view: absent = 0; present = 1.
- 70: Legs, hind tarsi, length compared to half length of hind tibiae: shorter or subequal = 0; longer = 1.
- 71: Legs, tarsi, second tarsomere, length compared to that of third tarsomere, dorsal view: shorter or subequal = 0 (Fig. 38H); longer = 1 (Fig. 38J).
- 72: Legs, hind tarsi, dense setal fields on ventral surface, ventral view: absent = 0; present, in small patches not covering tarsal length = 1; present, covering most of tarsal length = 2.
- 73: Legs, claws, free = 0 (Fig. 39K); connate = 1 (Fig. 39C).
- 74: Legs, claws, shape in proximal half: evenly narrowed = 0 (Fig. 39A); parallel-sided = 1 (Fig. 39J).
- 75: Abdomen, ventrites, numerous black rounded punctures, ventral view: absent = 0; present = 1.
- 76: Abdomen, scale pattern on ventrites, dark pigmented spots, ventral view: absent = 0; present = 1.

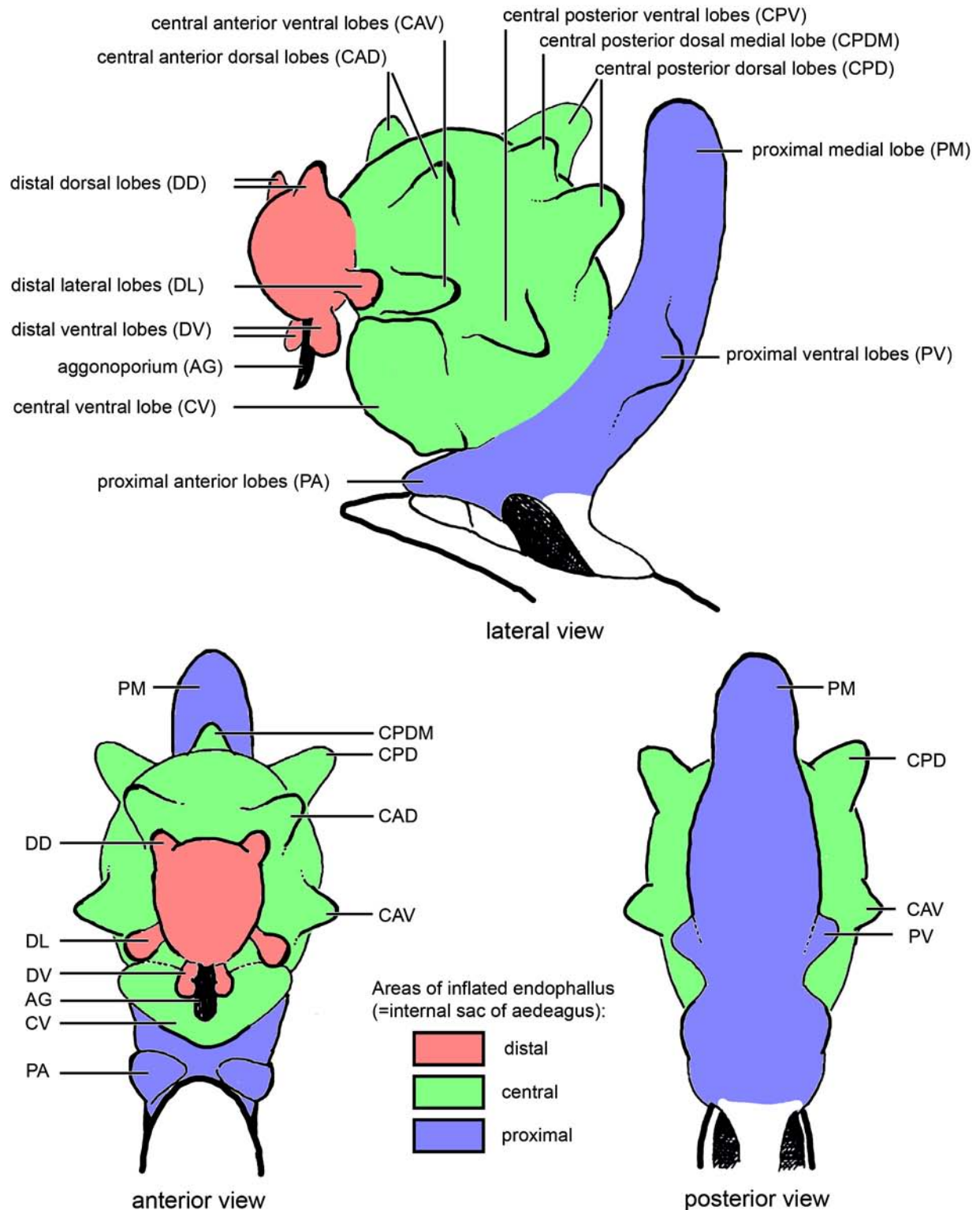


FIGURE 41. Cleonini, adult, ♂, generalized scheme of erected and inflated endophallus (=internal sack of aedeagus).

77: Abdomen, suture between metathorax and first visible ventrite, shape between hind coxae, ventral view: straight = 0; forming anteriorly directed angle = 1.

78: Male genitalia, aedeagus, cross-section at middle, shape: circular = 0; oval, compressed dorso-ventrally = 1; oval, compressed laterally = 2.

79: Male genitalia, aedeagus, dorsal surface, sclerotization compared to that of lateral surface: much weaker, appears

- membranous = 0; similar, appears well sclerotized = 1.
- 80: Male genitalia, aedeagus, ventral surface, sclerotization compared to that of lateral surface: much weaker, appears membranous = 0; similar, appears well sclerotized = 1.
- 81: Male genitalia, aedeagus, ventral surface, membranous window in apical part: absent = 0; present = 1.
- 82: Male genitalia, aedeagus, apex, dorsal or ventral view: evenly rounded = 0; pointed = 1.
- 83: Male genitalia, aedeagus, lateral projections of contour close to apex (=stabilizing structures), dorsal or ventral view: absent = 0; present = 1.
- 84: Male genitalia, endophallus, shape when fully everted and erected: simple, undifferentiated, rounded = 0 (Fig. 42F); complex, with lobes, not round = 1 (Fig. 42K).
- 85: Male genitalia, endophallus, central and distal areas, size: distal smaller than central = 0 (Fig. 43V); subequal = 1 (Fig. 43F); distal larger than central = 2 (Fig. 42J).

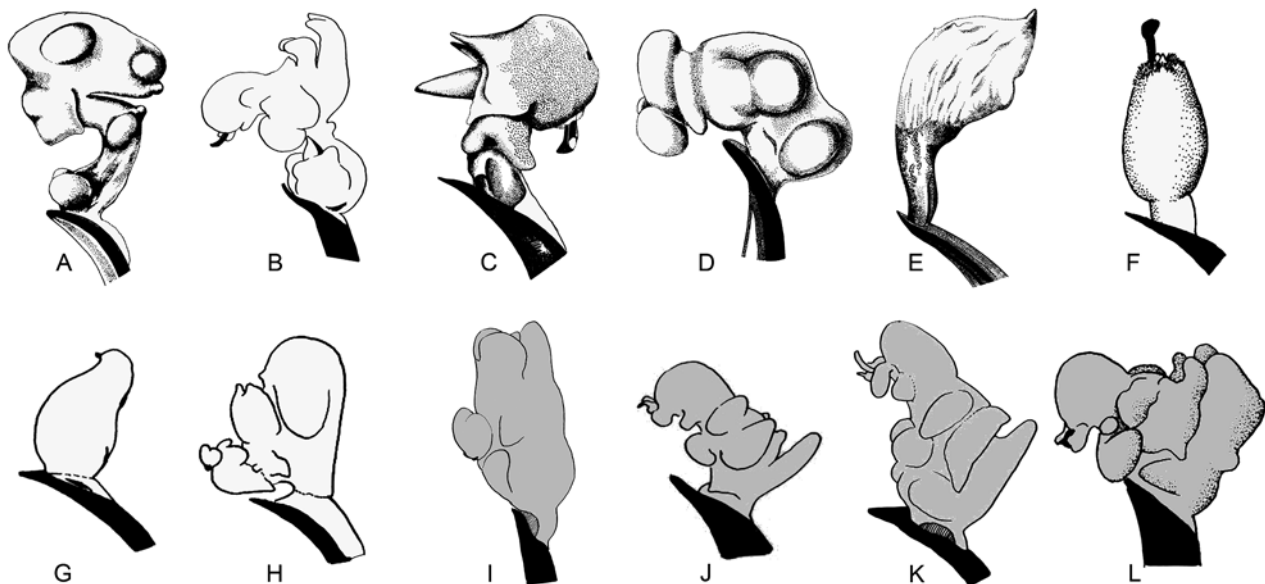


FIGURE 42. Non-Cleonini weevils, adults, ♂s, endophallus, lateral view. A: *Hylobius abietis*; B: *Hypolixus astrachanicus*; C: *Lepyrus palustris*; D: *Liparus tenebrioides*; E: *Minyops minutus rudis*; F: *Peribleptus* sp.; G: *Lachnaeus crinitus*; H: *Larinus obtusus*; I: *Larinus sturnus*; J: *Lixus albomarginatus*; K: *Lixus furcatus*; L: *Rhinocyllus conicus*.

- 86: Male genitalia, endophallus, PM lobe: absent = 0 (Fig. 43V); present = 1 (Fig. 43A).
- 87: Male genitalia, endophallus, PM lobe, length to width ratio: <2x = 0 (Fig. 43E); 2x and greater = 1 (Fig. 43F).
- 88: Male genitalia, endophallus, PM lobe, apex: entire, evenly rounded = 0 (Fig. 43H); subdivided in two = 1 (Fig. 43C).
- 89: Male genitalia, endophallus, PV lobes: absent = 0 (Fig. 43P); present = 1 (Fig. 43Q).
- 90: Male genitalia, endophallus, PA lobes: absent = 0 (Fig. 43V); present = 1 (Fig. 43W).
- 91: Male genitalia, endophallus, CPD lobes: absent = 0 (Fig. 43N); present = 1 (Fig. 43H).
- 92: Male genitalia, endophallus, CAD lobes: absent = 0 (Fig. 43L); present = 1 (Fig. 43C).
- 93: Male genitalia, endophallus, CPDM lobe: absent = 0 (Fig. 43B); present = 1 (Fig. 43N).
- 94: Male genitalia, endophallus, CV lobe: absent = 0 (Fig. 43V); present = 1 (Fig. 43U).
- 95: Male genitalia, endophallus, CPV lobes: absent = 0 (Fig. 43B); present = 1 (Fig. 43I).
- 96: Male genitalia, endophallus, CAV lobes: absent = 0 (Fig. 43N); present = 1 (Fig. 43H).
- 97: Male genitalia, endophallus, DL lobes: absent = 0 (Fig. 43F); present = 1 (Fig. 43O).
- 98: Male genitalia, endophallus, DD lobes: absent = 0 (Fig. 43E); present = 1 (Fig. 43Q).
- 99: Male genitalia, endophallus, DV lobes: absent = 0 (Fig. 43W); present = 1 (Fig. 43N).
- 100: Male genitalia, endophallus, aggonopodium, pointing: dorsad = 0; ventrad = 1.
- 101: ♀ genitalia, sternite 8, apodeme: absent = 0 (Fig. 44B); present = 1 (Fig. 44C).
- 102: Female genitalia, sternite 8, ratio of length of apodeme to that of lamellae: <0.9x = 0 (Fig. 44K); 0.9-1.1x = 1 (Fig. 44G); >1.1x = 2 (Fig. 44C).
- 103: Female genitalia, sternite 8, apodeme, composition: entire = 0 (Fig. 44E); longitudinally subdivided by groove as if consisting of two parts = 1 (Fig. 44G).
- 104: Female genitalia, sternite 8, apodeme, abrupt widening in distal quarter: absent = 0 (Fig. 44I); present = 1 (Fig. 44G).
- 105: Female genitalia, sternite 8, both lamellae, internal angle: pointed, between 70 and 120 degrees = 0 (Fig. 44H); rounded = 1 (Fig. 44B).

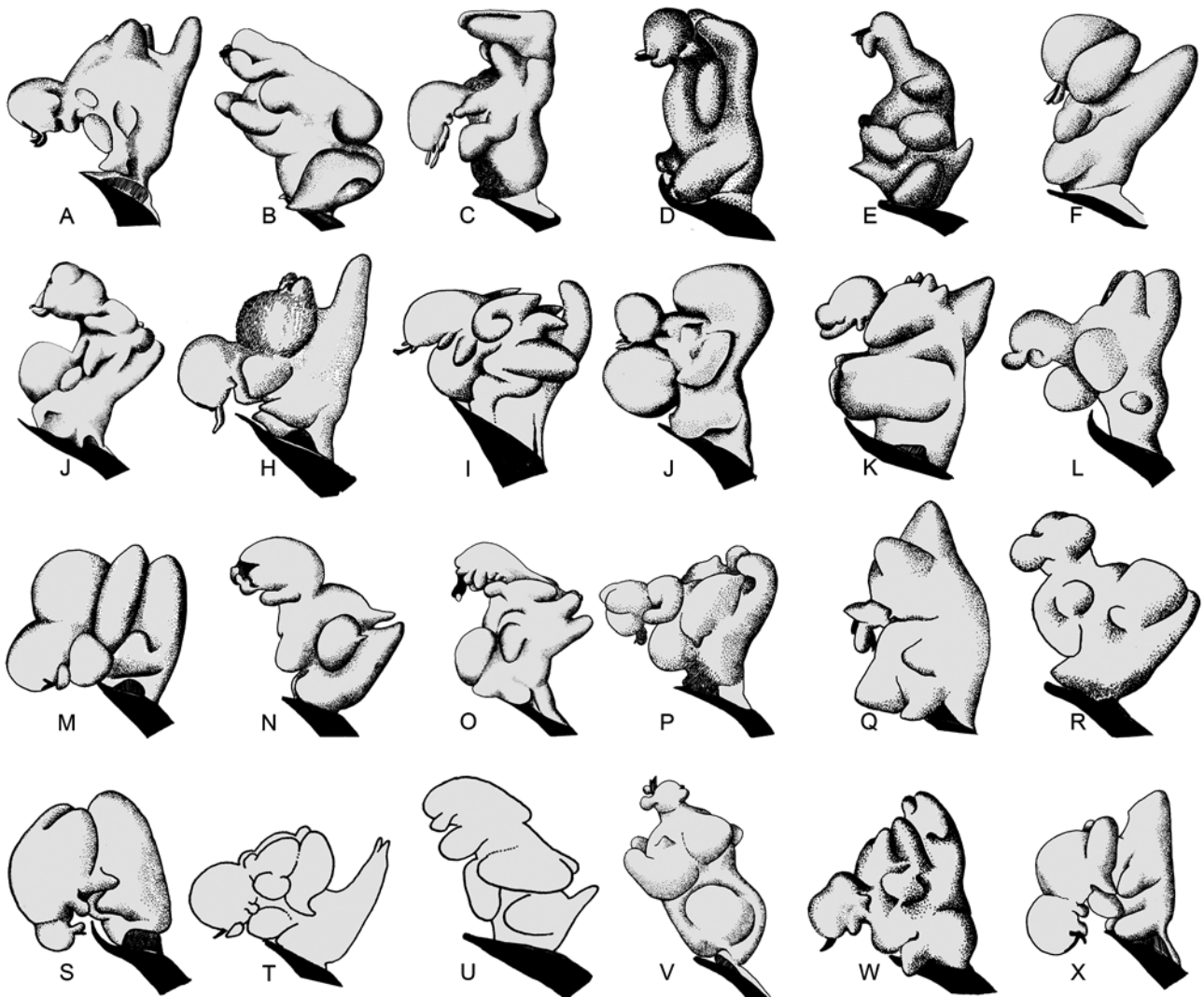


FIGURE 43. Cleonini weevils, adults, ♂s, endophallus, lateral view. A: *Adosomus (Adosomus) roridus*; B: *Ammocleonus aschabadensis*; C: *Asproparthenis punctiventris*; D: *Bothynoderes affinis*; E: *Brachycleonus fronto*; F: *Chromonotus (Chromonotus) vittatus*; G: *Chromosomus fischeri*; H: *Cleonis japonica*; I: *Coniocleonus (Plagiographus) nigrosuturatus*; J: *Conorhynchus pulverulentus*; K: *Epexochus lehmanni*; L: *Eumecops kittaryi*; M: *Leucomigus candidatus*; N: *Liocleonus clathratus*; O: *Maximus strabus*; P: *Menecleonus lagopus*; Q: *Monolophus praeditus*; R: *Porocleonus candidus*; S: *Pseudocleonus (Pseudocleonus) cinereus*; T: *Scaphomorphus vibex*; U: *Stephanocleonus (Deracanthopsis) gemellus*; V: *Surchania sijazovi*; W: *Temnorhinus (Temnorhinus) hololeucus*; X: *Xanthochelus eversmanni*.

106: Female genitalia, sternite 8, proximal part (=both lamellae), length to maximal width ratio: $<1.5x = 0$ (Fig. 44D); $1.5-2.0x = 1$ (Fig. 44C); $2.1-3.0x = 2$ (Fig. 44L); $>3.0x = 3$ (Fig. 44H).

107: Female genitalia, sternite 8, membrane between lamellae: indistinct (=not visible or absent) = 0 (Fig. 44B); distinct (=visible) = 1 (Fig. 44E).

108: Female genitalia, sternite 8, membrane between lamellae: not sclerotized = 0 (Fig. 44L); sclerotized = 1 (Fig. 44C).

109: Female genitalia, sternite 8, blades: separate by no less than individual diameter = 0 (Fig. 44J); separate by less than individual diameter and not contiguous = 1 (Fig. 44G); contiguous and not broadly joined mesally = 2 (Fig. 44I); broadly joined mesally = 3 (Fig. 44B).

110: Female genitalia, sternite 8, each blade, shape: circular, length to width ratio $<1.2x = 0$ (Fig. 44D); oval, length to width ratio $>1.2x = 1$ (Fig. 44H).

111: Female genitalia, basal part of hemisternite 9 (=coxite, gonocoxite), length to width ratio: $<1.5x = 0$ (Fig. 45J); $>1.5x = 1$ (Fig. 45F).

112: Female genitalia, basal part of hemisternite 9, large depression on its surface: absent, sclerite relatively flat = 0 (Fig. 45A); present, sclerite distinctly depressed on one side = 1 (Fig. 45E).

113: Female genitalia, basal part of hemisternite 9, shape: forming isosceles and acute triangle = 0 (Fig. 45A); bottle-shaped, with distinct basal and apical parts = 1 (Fig. 45H).

114: Female genitalia, apical part of hemisternite 9 (=stylus): absent = 0; present = 1 (Fig. 45J).

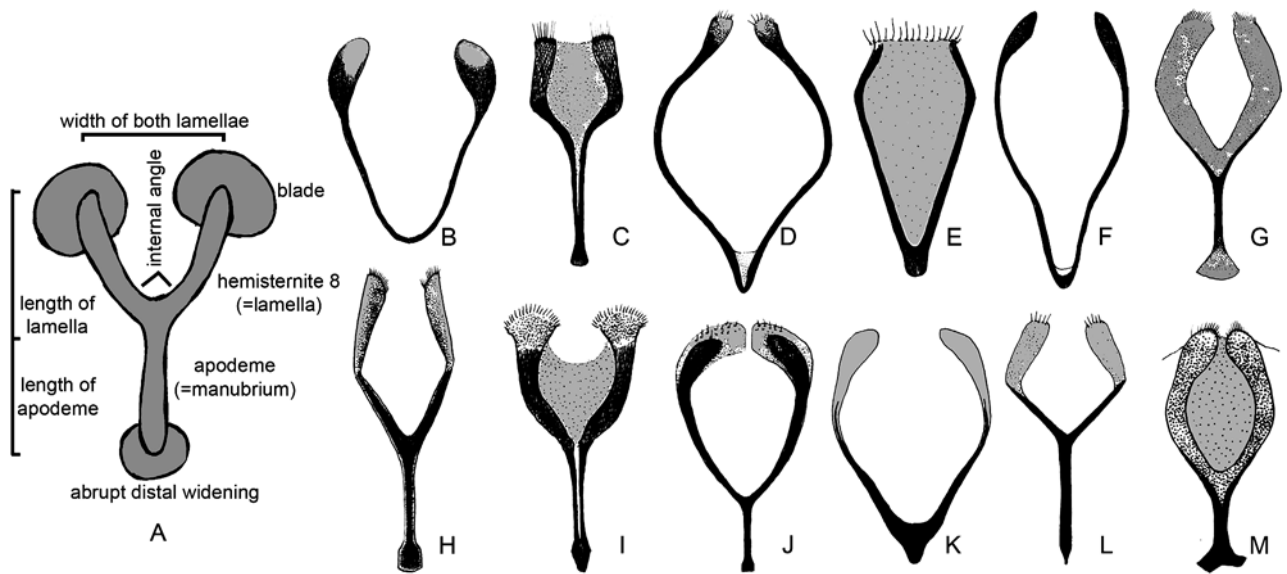


FIGURE 44. Cleonini weevils, adults, ♀s, sternite 8. A: scheme; B: *Adosomus (Adosomus) roridus*; C: *Afghanocleonus haarloevi*; D: *Asproparthenis punctiventris*; E: *Bothynoderes affinis*; F: *Cleonis pigra*; G: *Coniocleonus (Angarocleonus) cineritius*; H: *Coniocleonus (Coniocleonus) schoenherrri*; I: *Glebius confluens*; J: *Leucomigus candidatus*; K: *Maximus strabus*; L: *Pseudocleonus (Pseudocleonus) cinereus*; M: *Stephanocleonus (Stephanocleonus) paradoxus*.

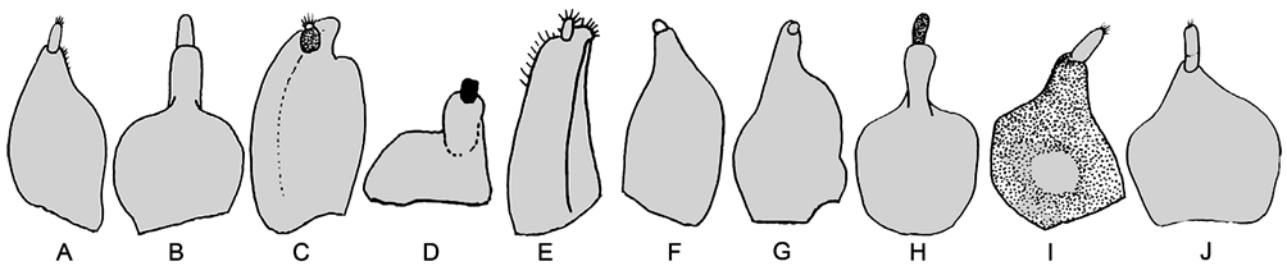


FIGURE 45. Cleonini weevils, adults, ♀s, hemisternite 9. A: *Asproparthenis punctiventris*; B: *Coniocleonus (Angarocleonus) alpinus*; C: *Conorhynchus pulverulentus*; D: *Glebius confluens*; E: *Leucophyes pedestris*; F: *Microcleonus panderi*; G: *Pleurocleonus quadrivittatus*; H: *Stephanocleonus (Taenioleonus) giganteus*; I: *Temnorhinus (Massimocleonus) elongatus*; J: *Xenomacrus glacialis*.

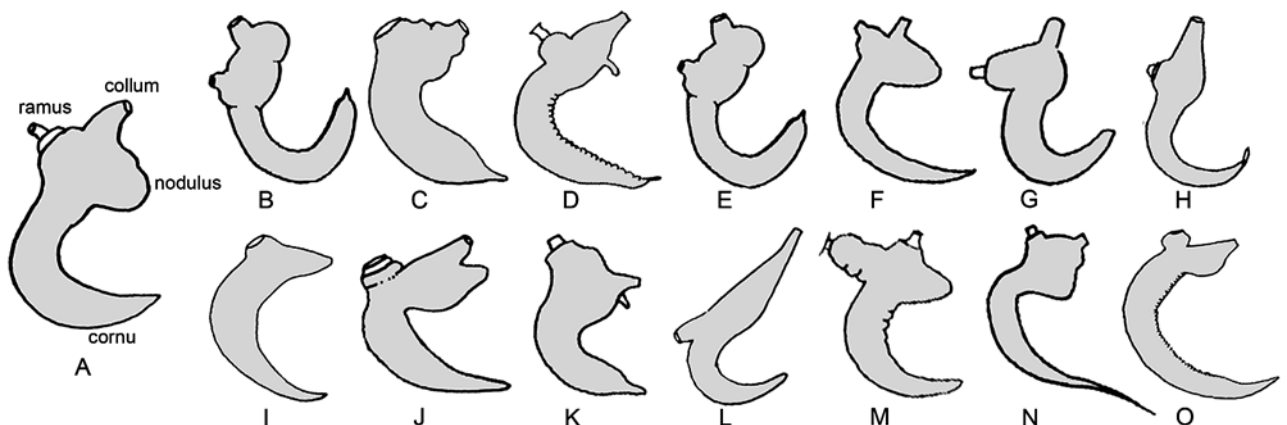


FIGURE 46. Cleonini weevils, adults, ♀s, spermatheca. A: scheme; B: *Adosomus (Adosomus) roridus*; C: *Ammocleonus aschabadensis*; D: *Asinocleonus taciturnus*; E: *Asproparthenis punctiventris*; F: *Coniocleonus (Angarocleonus) astragali*; G: *Coniocleonus (Plagiographus) crinipes*; H: *Conorhynchus pulverulentus*; I: *Leucochromus imperialis*; J: *Leucomigus candidatus*; K: *Neocleonus sannio*; L: *Pachycerus madidus*; M: *Porocleonus candidus*; N: *Pseudocleonus (Neopseudocleonus) grammicus*; O: *Surchania sijazovi*.

- 115: Female genitalia, apical part of hemisternite 9, length to width ratio: $<1.5x = 0$ (Fig. 45G); $>1.5x = 1$ (Fig. 45H).
 116: Female genitalia, attachment of apical part of hemisternite 9 to basal part: apical = 0 (Fig. 45A); subapical = 1 (Fig. 45C).
 117: Female genitalia, spermatheca, shape of cornu apex: rounded = 0 (Fig. 46G); pointed = 1 (Fig. 46N).
 118: Female genitalia, spermatheca, collum: indistinct (=not visible) = 0 (Fig. 46C); distinct (=visible) = 1 (Fig. 46G).
 119: Female genitalia, spermatheca, width of ramus and collum: ramus not wider than collum = 0 (Fig. 46E); ramus wider than collum = 1 (Fig. 46M).
 120: Female genitalia, spermatheca, distance between ramus and collum: lesser than diameter of ramus = 0 (Fig. 46B); not lesser than diameter of ramus = 1 (Fig. 46G).
 121: Female genitalia, spermatheca, nodulus: absent = 0 (Fig. 46B); present = 1 (Fig. 46M).

APPENDIX 3. Label data for Cleonini (and the outgroups) adult specimens used for scoring morphological characters. Lack of data such as dates or collector's initials indicates that these data were not found on the specimen label. Vague localities are cited verbatim in quotation marks. All specimens, unless followed by a museum abbreviation, are stored in the collection of one of us (YuAC).

Non-Lixinae. Ot1: *Anthribus nebulosus* Forster, 1770, ♂ & ♀: Russia, Rostov-on-Don, 24.vi.2012, Yu. Arzanov. Ot2: *Smicromyx reichii* (Gyllenhal, 1835), ♂ & ♀: Russia, Rostov reg., Krymsky, 9.v.2010, Yu. Arzanov. Ot3: *Graptus triguttatus* (Fabricius, 1775), ♂ & ♀: Russia, Rostov reg., Mitiakinskaya, 8.vi.2002, Yu. Arzanov. Ot4: *Hypera nigrirostris* (Fabricius, 1775), ♂ & ♀: Russia, Rostov reg., Kagalnik, 27.iv.2010, Yu. Arzanov. Ot5: *Hylobius abietis* (Linnaeus, 1758), ♂ & ♀: Russia, Karachay-Cherkessia, Arkasara Mt. R., 18.vii.1996, Yu. Arzanov. Ot6: *Lepyrus palustris* (Scopoli, 1763), ♂ & ♀: Russia, Rostov reg., Rogozhkino, 2.v.2013, Yu. Arzanov. Ot7: *Liparus tenebrioides* (Pallas, 1781), ♂ & ♀: Russia, Rostov reg., Nedvigovka, 27.iv.1999, Yu. Arzanov. Ot8: *Minyops minutus rudis* Menetries, 1849, ♂ & ♀: Russia, Rostov reg., Morskoy Chulek, 17.iv.2000, D. Kasatkin. Ot9: *Plinthus kippenbergi* Meregalli, 1985, ♂ & ♀: Russia, Adygea, Mt. Oshten, 14.viii.1992, Yu. Arzanov. Ot10: *Peribleptus* sp., ♂ & ♀: Thailand, Mae Hong Son prov., Pai, 27.iv.2013, I. Melnik. Ot11: *Pissodes pini* Linnaeus, 1758, ♂ & ♀: Russia, Karachay-Cherkessia, Mukhu gorge, 25.vi.1995, Yu. Arzanov.

Non-Cleonini Lixinae. L1: *Eustenopus lanuginosus* (Faust, 1885), ♂ & ♀: Turkey, Bashkhan, 2007, I. Shokhin. L2: *Gasteroclisus* sp., ♂ & ♀: Thailand, Mae Hong Son prov., Pai, 27.iv.2013, I. Melnik. L3: *Hypolixus astrachanicus* (Faust, 1883), ♂ & ♀: Russia, Astrakhan reg., Buruny, 21.v.2013, Yu. Arzanov. L4: *Lachnaeus crinitus* Schoenherr, 1826, ♂ & ♀: Russia, Stavropol reg., Podkumok, 13.vi.2010, D. Gapon. L5: *Larinus (Cryphopus) ferrugatus* Gyllenhal, 1835, ♂ & ♀: Russia, "Altay", Khamor riv., 11.vii.1983, I. Soloviev. L6: *Larinus (Larinus) latus* (Herbst, 1783), ♂ & ♀: Russia, Krasnodar reg., Sennoy, 28.v.1998, Yu. Arzanov. L7: *Larinus (Larinomesius) minutus* Gyllenhal, 1835, ♂ & ♀: Russia, Rostov reg., Kazanskaya, 14.vi.1987, Yu. Arzanov. L8: *Larinus (Phyllonomeus) sturnus* (Schaller, 1783), ♂ & ♀: Russia, Karachay-Cherkessia, Daut, 14.vi.1994, Yu. Arzanov. L9: *Lixus (Broconius) rubicundus* Zoubkoff, 1833, ♂: Russia, Astrakhan reg., Buruny, 21.v.2013, Yu. Arzanov; ♀: Russia, Rostov reg., Krasnopartizansk, 29.vi.2003, D. Gapon. L10: *Lixus (Callistolixus) furcatus* Olivier, 1807, ♂ & ♀: Armenia, Shorzha, 20.v.1999, M. Nabozhenko. L11: *Lixus (Compsolixus) albomarginatus* Boheman, 1842, ♂: Russia, Dagestan, Sarykum sands, 17.vii.1997, D. Kasatkin; ♀: Russia, Astrakhan reg., Bogdo Mt., 27.v.2003, Yu. Arzanov. L12: *Lixus (Dilixellus) pulverulentus* (Scopoli, 1783), ♂ & ♀: Ukraine, Crimea, Kerch, 4.iv.1997, S. Volovnik. L13: *Lixus (Epimeces) filirostris* (Fabricius, 1781), ♂ & ♀: Russia, Rostov-on-Don, 10.vii.2002, D. Gapon. L14: *Lixus (Eulixus) iridis* Olivier, 1807, ♂ & ♀: Russia, Stavropol reg., Kislovodsk, 21.vi.1981, Yu. Liman. L15: *Lixus (Lixus) paraplecticus* (Linnaeus, 1758), ♂ & ♀: Russia, Ulianovsk reg., Chernaya Rechka, 4.viii.2001, A. Zotov. L16: *Lixus (Phillixus) subtilis* Boheman, 1835, ♂: Russia, Rostov reg., Rogozhkino, 13.v.2010, Yu. Arzanov; ♀: Russia, Rostov reg., Krasnopartizansk, 29.vi.2003, D. Gapon. R1: *Bangasternus planifrons* (Brullé, 1832), ♂ & ♀: Kyrgyzstan, Kara-Balta, 27.viii.1998. R2: *Rhinocyllus conicus* (Frolich, 1792), ♂ & ♀: Armenia, Aratzag Mt., 22.vi.1997, V. Savitsky.

Cleonini. C1: *Adosomus (Adosomus) karelini* (Fähræus, 1842), ♂ & ♀: Kazakhstan, Karagandy, Karakhel, 30.iv.1996, M. Danilevsky. C2: *Adosomus (Adosomus) roridus* (Pallas, 1781), ♂ & ♀: Russia, Rostov reg., Nedvigovka, 9.vi.1974, Yu. Arzanov. C3: *Adosomus (Pseudoadosomus) granulatus* Mannerheim, 1825, ♂ & ♀: Russia, Jewish A.O., Radde, 19.vii.2004, I. Melnik. C4: *Adosomus (Xeradosomus) grigorievi* Suvorov, 1915, ♂ & ♀: Mongolia, Sukhe-Bator Aimak, Dariganga, 17.viii.2002, M. Danilevsky. C5: *Adosomus (Xeradosomus) samsonowii* (Gebler, 1844), ♂ & ♀: Kazakhstan, Karaganda reg., Kense, 8.vii.1962, G. Mevdedev (ZIN). C6: *Afganocleonus haarloevi* (Voss, 1955), ♂ & ♀: Afghanistan, Ghor, Caghcaran, 10.viii.1970, O. Kabakov. C7: *Ammocleonus aschabadensis* (Faust, 1884), ♂ & ♀: Iran, Isfahan, Kashan, 26.iv.2007, A. Anichenko. C8: *Ammocleonus hieroglyphicus* (Olivier, 1807), ♂ & ♀: Israel, Elifas, 3.vi.2003, V. Chekatunov. C9: *Aplesilus ruginodis* Reitter, 1913, ♂ & ♀: Iran, "Varamin", xii.1948, Zarazagi (ZIN). C10: *Apleurus (Apleurus) lutulentus* (LeConte, 1859), ♂ & ♀: "N. Mexico" (ZIN). C11: *Asinocleonus taciturnus* Faust, 1885, ♂: Uzbekistan, Chatkal N.P., 1.vi.1963, G. Mevdedev (ZIN); ♀: Uzbekistan, Fergana Mt. R., Kaldama pass, 2.vi.1961, E. Gureva (ZIN). C12: *Asproparthenis carinata* (Zoubkoff, 1829), ♂ & ♀: Kazakhstan, Aktau, 20.vi.2013, G. Abdurakhmanov. C13: *Asproparthenis carinicornis* (Gyllenhal, 1834), ♂ & ♀: Russia, Stavropol reg., Kievka, 1-6.vi.2002, A. Krukov. C14: *Asproparthenis foveocollis* (Gebler, 1834), ♂: Russia, Khakassia, W. Sayan Mt. R., Taskylkay Mt., 10.vi.2002, A. Brinev; ♀: Russia, Altai Kr., Pavlovsk, 25.vi.1944, V. Stark (ZIN). C15: *Asproparthenis obsoletefasciata* (Menetries, 1849), ♂: Turkmenistan, Lebap, Amudarya N.R., 6.vi.1988, V.

Gratschev; ♀: Tajikistan, Asht, 23.iv.1958, I. Lopatin (ZIN). C16: *Asproparthenis punctiventris* (Germar, 1824), ♂ & ♀: Kazakhstan, Aktau, 20.vi.2013, G. Abdurakhmanov. C17: *Asproparthenis vexata* (Gyllenhal, 1834), ♂ & ♀: Russia, Rostov reg., Krasnopartizansk, 26.v.2015, Yu. Arzanov. C18: *Atactogaster zebra* Chevrolat, 1873, ♂ & ♀: Cambodia, Kep, 8.vi.2014, I. Melnik. C19: *Bothynoderes affinis* Schrank, 1781), ♂ & ♀: Russia, Ulianovsk reg., Proskovino, 15-19.vii.2009, A. Zotov. C20: *Brachyleonius fronto* (Fischer von Waldheim, 1835), ♂ & ♀: Turkmenistan, Balkanabat, Chilmamedkum, 20-28.v.1993, Yu. Arzanov. C21: *Calodemus errans* Fåhræus, 1871, ♂ & ♀: Tanzania, Kigonsera (ZIN). C22: *Chromonotus (Chevrolatius) bipunctatus* (Zoubkoff, 1829), ♂ & ♀: Russia, Stavropol reg., Arbali, 22.v-4.vi.2002, A. Krukov. C23: *Chromonotus (Chevrolatius) hirsutulus* Faust, 1883, ♂ & ♀: Kazakhstan, Mangystau, Tazhen, 4.iv.2014, Ya. Kovalenko. C24: *Chromonotus (Chromonotus) pictus* (Pallas, 1771), ♂ & ♀: Russia, Astrakhan reg., Baskunchak, 12.v.2001, O. Brekhov. C25: *Chromonotus (Chromonotus) vittatus* (Zoubkoff, 1829), ♂ & ♀: Kazakhstan, Kyzylorda, Kumsagyz, 28.iv.2014, A. Shapovalov. C26: *Chromonotus (Faustius) menetriesi* (Faust, 1884), ♂: Turkmenistan, Repetek, 1.v.1970, G. Mevdedev (ZIN); ♀: Turkmenistan, Uzboy, Yaskha, 31.iii.1951, O. Kryzhanovskij (ZIN). C27: *Chromonotus (Faustius) staudingeri* (Faust, 1894), ♂ & ♀: Tajikistan, Aktau Mt. R., Garauty, 10.v.1974, Kh. Nasreddinov (ZIN). C28: *Chromosomus fischeri* (Fåhræus, 1842), ♂ & ♀: Turkmenistan, Balkanabat, Chilmamedkum, 20-28.v.1993, Yu. Arzanov. C29: *Cleonis japonica* (Faust, 1904), ♂: Russia, Primorsky, Yakovlevka, 25.vii.1926, Filipiev (ZIN); ♀: Russia, Amur reg., Klimoutsy, 7.vi.1959, Zinov'ev (ZIN). C30: *Cleonis neglecta* (Ter-Minasian et Egorov, 1981), ♂ & ♀: Russia, Primorsky, Yenoteevka, 1.v.1910, Shipgarev (ZIN). C31: *Cleonis pigra* (Scopoli, 1763), ♂ & ♀: Ukraine, Donetsk, 16.vii.2013, V. Martynov. C32: *Cnemodontus limpidus* Gyllenhal, 1834, ♂: Africa (ZIN). C33: *Coniocleonus (Angarocleonus) alpinus* (Gebler, 1833), ♂: Russia, Chita reg., Drov'yanskaya, 10.vii.1977; ♀: Russia, Amur reg., Zeya, 19.v.1914, V. Kazhanchikov (ZIN). C34: *Coniocleonus (Angarocleonus) astragali* Ter-Minasian et Korotyayev, 1977, ♂ & ♀: Russia, Vrangel island, 1989, O. Khruleva (ZIN). C35: *Coniocleonus (Augustecleonus) nebulosus* (Linnaeus, 1758), ♂ & ♀: Russia, Leningrad reg., 18.v.1870, Artobolovsky (ZIN). C36: *Coniocleonus (Augustecleonus) turbatus* (Fåhræus 1842), ♂ & ♀: Russia, Rostov reg., Polushkin, 25.iv.2009, P. Ivliev. C37: *Coniocleonus (Borisocleonus) mesopotamicus* Olivier, 1807, ♂ & ♀: Afganistan, Qargha, 9.i.1970, O. Kabakov (ZIN). C38: *Coniocleonus (Coniocleonus) schoenherri* (Gebler, 1830), ♂ & ♀: Russia, Amur reg., Ulunga, 17.vi.1910, Mishin (ZIN). C39: *Coniocleonus (Plagiographus) crinipes* (Fåhræus, 1842), ♂ & ♀: Russia, Dagestan, Sary-Kum dunes, 10.x.1986, E. Komarov. C40: *Coniocleonus (Plagiographus) excorinatus* (Gyllenhal, 1834), ♂ & ♀: Jordan, 29.iii.1897, Davidov (ZIN). C41: *Coniocleonus (Plagiographus) fastiguatus* (Erichson, 1841), ♂ & ♀: Algeria, Oran, 1889, Desbroschers (ZIN). C42: *Coniocleonus (Plagiographus) nigrosuturatus* (Goeze, 1777), ♂ & ♀: Iran, Gulan, Maryan, 19.v.2007, A. Anishenko. C43: *Conorhynchus balassogloi* (Faust, 1883), ♂: Kazakhstan, South Kazakhstan reg., Zhana Kuduk val., 13.vi.1958, Ler (ZIN); ♀: Kazakhstan, East Kazakhstan reg., Dzhan-Daria (ZIN). C44: *Conorhynchus excavatus* (Zoubkoff, 1833), ♂: Kazakhstan, Atyrau reg., lake Inder, 7.vii.1909, Uvarov (ZIN); ♀: Kazakhstan, Say Utes, 10.ix.1973, Zaitsev (ZIN). C45: *Conorhynchus nigrivittis* (Pallas, 1781), ♂: Russia, Stavropol reg., Arbali, 22.v.2002, Kryukov; ♀: Kazakhstan, Kostanay, 20.vi.2013, T. Bragina. C46: *Conorhynchus pulverulenta* Zoubkoff, 1829, ♂: Russia, Kalmykia, Rybachy, 20.vii.1974, A. Fomichev; ♀: Russia, Kalmykia, Utta, 23.v.1975, Yu. Arzanov. C47: *Conorhynchus schrenkii* (Gebler, 1844), ♂ & ♀: Kazakhstan, Barsa-Kelmes, 16.vii.1980, V. Vasilchenko. C48: *Cosmogaster (Cosmogaster) lateralis* (Gyllenhal, 1834), ♂ & ♀: Djibuti, Ambuli, 15.xii.1897, Kakhovsky (ZIN). C49: *Cyphocleonus achates* (Fåhræus 1842), ♂ & ♀: Russia, Rostov reg., Veshenskaya, 16.vii.2011, A. Zotov. C50: *Cyphocleonus cenchrus* Pallas, 1781, ♂: Russia, Kalmykia, Bol'shoy Tsaryn, 13.ix.1976, P. Ivliev; ♀: Kazakhstan, Kostanay reg., Rakhmet, 19.x.2014, T. Bragina. C51: *Cyphocleonus dealbatus* (Gmelin, 1790), ♂ & ♀: Kazakhstan, Kostanay reg., Rakhmet, 19.x.2014, T. Bragina. C52: *Cyphocleonus trisulcatus* (Herbst, 1795), ♂ & ♀: Russia, Ulianovsk reg., Vyazovka, 3.v.2001, A. Zotov. C53: *Entymetopus (Entymetopus) lineolatus* (Motschulsky, 1860), ♂: Turkmenistan, Meshed-Messer, 22.iv.1971, G. Medvedev (ZIN); ♀: Turkmenistan, Rustam-Kala, 7.v.1952, Romadina (ZIN). C54: *Entymetopus (Sforzia) limis* (Menetries, 1849), ♂: Turkmenistan, Uzboy, Yaskhan, 13.iv.1951, O. Kryzhanovskij (ZIN); ♀: Uzbekistan, Kyzil Kum, Bukantau, 13.v.1965, G. Medvedev (ZIN). C55: *Epexochus lehmanni* (Ménétriés, 1849), ♂: Kazakhstan, Karagandy reg., Zhana-Arka, 16.iv.1958, M. Loginova (ZIN); ♀: Kazakhstan, Taldykorgan reg., Ak-Tau, 10.v.1990, V. Prasolov (ZIN). C56: *Eumecops fasciculifer* Reitter, 1895, ♂ & ♀: Russia, Buryatia, Nikolsk, 27.viii.1998, A. Anishenko. C57: *Eumecops kittaryi* (Hochhuth, 1851), ♂: Kazakhstan, Atyrau reg., Beskala, 5.vii.1980, A. Ponomarev; ♀: Russia, Krasnodar reg., Taman, 5.v.1997, D. Kasatkin. C58: *Eurycleonus talamelli* Meregalli, 2005, ♂ & ♀: Morocco, Tan-Tan, 10.ii.2015, M. Nabozhenko. C59: *Georginus bellus* Jakobson, 1913, ♂ & ♀: Turkmenistan, West Kopetdag, Firuza, 17.iv.1987, V. Dubatolov (ZIN). C60: *Glebius confluens* (Fåhræus, 1842), ♂ & ♀: Uzbekistan, Qashqadaryo reg., Sechankul lake, 14.iv.2014, Ya. Kovalenko. C61: *Gonocleonus margaritifera* (Lucas, 1844), ♂ & ♀: Algeria, Laghonat, 1935, Clermont (ZIN). C62: *Isomerops fausti* Petri, 1908, ♂ & ♀: Iran, Iezda, 31.iii.1904, Matissen (ZIN). C63: *Koenigius mauritanicus* Hustache, 1932, ♂ & ♀: Morocco, Azemmour, Antoin. C64: *Leucochromus imperialis* (Zoubkoff, 1837), ♂ & ♀: Turkmenistan, Balkan reg., Chilmamedkum, 7.v.1985, E. Khachikov. C65: *Leucomigus candidatus* (Pallas, 1771), ♂ & ♀: Russia, Rostov reg., Rostovsky N.P., 10.viii.2002, Yu. Arzanov. C66: *Leucophyes pedestris* (Poda, 1761), ♂ & ♀: Russia, Rostov reg., Nedvigovka, 16.iv.1999, Yu. Arzanov. C67: *Liocleonus clathratus* (Olivier, 1807), ♂ & ♀: Georgia, Kakheti, Eldar, v. 1896, Mlakosevich (ZIN). C68: *Lixomorphus ocellaris* (Fabricius, 1792), ♂ & ♀: Italy, Sardinia, 4.v.1908, Krause (ZIN). C69: *Lixopachys luxerii* (Chevrolat, 1873), ♂: Iran (ZMUM). C70: *Maximus granulatus* (Fischer von Waldheim, 1821), ♂ & ♀: Kazakhstan, Atyrau reg., Kulsary, 11.v.1989, L. Ishkov. C71: *Maximus leucophaeus* (Menetries, 1849), ♂ & ♀: Kazakhstan, Atyrau reg., lake Inder, 4.x.1986, A. Ponomarev. C72: *Maximus strabus* (Gyllenhal, 1834), ♂ & ♀: Russia, Saratov reg., Dyakovka, 25.vi.2009, A. Benkovsky. C73: *Maximus subfuscus* (Faust, 1883), ♂ & ♀: Tajikistan, Khatlon reg., Kolob, 31.v.2003, V. Perepechayenko. C74: *Mecaspis alternans* (Herbst, 1795), ♂: Russia, Rostov reg., Nedvigovka, 12.v.2003, D. Popov; ♀: Russia, Rostov-on-Don, vii.2011, S.

Cherednikov. C75: *Mecaspis darwini* (Faust, 1883), ♂: Uzbekistan, Qashqadaryo reg., Nuristan, 9.iv.2014, Ya. Kovalenko; ♀: Turkey, Burlan pass, 24.v.2011, E. Khachikov. C76: *Mecaspis octosignata* (Gyllenhal, 1834), ♂: Uzbekistan, Bukhara, 1.iv.1932, Rodd (ZIN); ♀: Turkey, Burlan pass., 24.v.2011, E. Khachikov. C77: *Mecaspis pallasii* (Fähræus 1842), ♂ & ♀: Turkmenistan, Balkan prov., Garrygala, 12.iv.1953, Gornavskaya (ZIN). C78: *Menecleonus lagopus* (Fähræus 1842), ♂ & ♀: Uzbekistan, Qashqadaryo reg., Nuristan, 9.iv.2014, Ya. Kovalenko. C79: *Menecleonus virgatus* (Schoenherr, 1832), ♂ & ♀: Armenia, Goravan, 9.vi.2003, M. Danilevsky; ♀: Mongolia, Urez-Nur, 8.vii.1973, B. Korotyayev (ZIN). C80: *Microcleonus panderi* (Fischer von Waldheim, 1835), ♂: Mongolia, Kharkhara-Gol, 9.vi.1975, B. Korotyayev (ZIN). C81: *Mongolocleonus gobiensis* (Voss, 1967), ♂: Mongolia, Ömnögovi prov., Khan-Bogdo, 23.vi.1983, G. Medvedev (ZIN); ♀: Mongolia, Shine-Dzhinst, 17.vii.1981, B. Korotyayev (ZIN). C82: *Monolophus praeditus* (Faust, 1883), ♂ & ♀: Mongolia, Ulaanbaatar, 31.vii.1969, L. Arnoldi (ZIN). C83: *Neocleonus sannio* (Herbst, 1795), ♂ & ♀: Africa, Ouagadougou, vii-viii.1927, Olsufiev (ZIN). C84: *Pachycerus madidus* (Olivier, 1807), ♂ & ♀: Russia, Rostov reg., Zavetnoe, 23.vi.2011, K. Artokhin. C85: *Pentatropis formosus* Fähræus, 1842, ♂: Africa (ZMUM). C86: *Pleurocleonus sollicitus* (Gyllenhal, 1834), ♂: Kazakhstan, Kyzylorda reg., Kumzagiz, 28.iv.2014, A. Shapovalov; ♀: Kazakhstan, Kostanay, 3.vi.2013, T. Bragina. C87: *Porocleonus candidus* (Olivier, 1807), ♂ & ♀: Egypt, Cairo, ii.1956. C88: *Prionorhinus canus* Wiedemann, 1823, ♀: "Africa", "Cap" (ZIN). C89: *Pseudoisomerus mangystavicus* (Ter-Minasian, 1976), ♂: Kazakhstan, Barsa-Kelmes, 15.vi.1980, A. Konev (ZIN); ♀: Uzbekistan, Bukhara, 3.vii.1904, G. Suvorov (ZIN). C90: *Pseudocleonus (Asiacleonus) dauricus* (Gebler, 1830), ♂ & ♀: Russia, Ulianovsk reg., Shilovka, 12.vii.2002, A. Zotov. C91: *Pseudocleonus (Asiacleonus) taciturnoides* Arnol'di, 1956, ♂: Kyrgyzstan, Fergana Range, Ak-terek, 29.ix.1937, Kirichenko (ZIN); ♀: Kazakhstan, Almaty reg., Koskelen, 15.v.1996, M. Danilevsky. C92: *Pseudocleonus (Neopseudocleonus) grammicus* (Panzer, 1789), ♂: Russia, Rostov reg., Peskovatka, 20.vi.2005, E. Khachikov; ♀: Russia, Rostov reg., Razdorskaya, 23.v.2003, A. Ponomarev. C93: *Pseudocleonus (Neopseudocleonus) marginicollis* (Fähræus 1842), ♂ & ♀: Armenia, Shorzha, 20.v.1999, M. Nabozhenko. C94: *Pseudocleonus (Phryganocleonus) guldarensis* Arnol'di, 1956; ♀: Tajikistan, Gissar Range, Khan-takhsa, 10.vii.1933, M. Veltishev (ZIN). C95: *Pseudocleonus (Pseudocleonus) cinereus* (Schrank, 1781), ♂ & ♀: Russia, Rostov reg., Nedvigovka, 30.v.1999, Yu. Arzanov. C96: *Pycnodactylopsis tomentosa* (Fähræus 1842), ♂ & ♀: Tunisia, Reitter (ZIN). C97: *Rhabdorrhynchus anchusae* (Chevrolat, 1854), ♂: Iran, Fars, Abadeh, viii.2000, H. Ghahari; ♀: Israel, 1997, D. Simon. C98: *Rhabdorrhynchus echi* (Brahm, 1790), ♂ & ♀: Russia, Rostov reg., Razdorskaya, 7.v.2009, A. Ponomarev. C99: *Scaphomorphus erysimi* (Fall, 1901), ♂ & ♀: USA, California, Santa Barbara Co., 14.viii.1987, Davidson. C100: *Scaphomorphus pallasii* (Faust, 1890), ♂: Mongolia, South Gobi, Somon Bulgan, 1967, Z. Kasab (ZIN); ♀: Russia, Tuva, Ubsanur valley, 10.vii.1961, D. Berman (ZIN). C101: *Scaphomorphus poricollis* (Mannerheim, 1843), ♂ & ♀: USA, Arizona, Cochise Co., 30.vii.1982, R.S. Anderson. C102: *Scaphomorphus vibex* (Pallas, 1781), ♂: Kazakhstan, Atyrau reg., Kulagino, 30.v.2001, A. Zotov; ♀: Kazakhstan, West Kazakhstan, Yanvartsevo, 22.vi.1949, Yarmola (ZIN). C103: *Stephanocleonus (Deracanthopsis) gemellus* Voss, 1967, ♂ & ♀: Mongolia, South Gobi, Bulgan, 6.vi.1972, G. Medvedev (ZIN). C104: *Stephanocleonus (Eremocleonus) costatus* (Gebler, 1832), ♂ & ♀: Mongolia, Dornod prov., Salkhit, 16.vi.1976, E. Gureva (ZIN); ♀: Kazakhstan, Koksengir Mts., Zhana-Arka, 1.vi.1959, Loginova (ZIN). C105: *Stephanocleonus (Eremocleonus) fascicularis* (Gebler, 1833), ♂: Kazakhstan, Taraz, S. Aris (ZIN). C106: *Stephanocleonus (Eremocleonus) gobianus* Suvorov, 1912, ♂ & ♀: Mongolia, South Gobi, Bulgan, 6.vi.1972, G. Medvedev (ZIN). C107: *Stephanocleonus (Sanzia) microgrammus* (Gyllenhal, 1834), ♂ & ♀: Russia, Rostov reg., Morosovsky, 15.v.2015, M. Nabozhenko. C108: *Stephanocleonus (Sanzia) tetragrammus* (Pallas, 1781), ♂ & ♀: Russia, Adygea, Mikhailovka, 11.iv.2007, M. Saprikin. C109: *Stephanocleonus (Stephanocleonus) eruditus* Faust, 1890, ♂ & ♀: Russia, Tuva, Chadan lake, 8.vii.1948, Cherepanov. C110: *Stephanocleonus (Stephanocleonus) favens* Faust, 1884, ♂ & ♀: Mongolia, Uvs prov., Ulangoma, 12.vii.1968, A. Emelianov (ZIN). C111: *Stephanocleonus (Stephanocleonus) fenestratus* (Pallas, 1781), ♂: Mongolia, Ulaanbaatar, 7.vii.1990, A. Anishenko; ♀: Mongolia, Khövsgöl prov., Murena, 23.vii.1975, E. Gureva (ZIN). C112: *Stephanocleonus (Stephanocleonus) fossulatus* (Fischer von Waldheim, 1823), ♂ & ♀: Russia, Tuva, Samagaltay, 15.vi.2004, S. Vashenko. C113: *Stephanocleonus (Stephanocleonus) impressicollis* (Fähræus 1842), ♂ & ♀: Russia, Buryatia, Udunga, 20.vii.2003, N. Kalmykov. C114: *Stephanocleonus (Stephanocleonus) incertus* Ter-Minasian, 1972, ♂ & ♀: Russia, Tuva, Chadan lake, 8.vii.1948, Cherepanov. C115: *Stephanocleonus (Stephanocleonus) mannerheimi* Chevrolat, 1873, ♂: Russia, Tuva, Samagaltay, 10.vi.1948, Cherepanov; ♀: Russia, Tuva, Kyzil, 25.vi.2004, R. Mishustin. C116: *Stephanocleonus (Stephanocleonus) nassiformis* (Goeze, 1777), ♂ & ♀: Mongolia, Tevshruleh, 11.vi.1972, L. Dubeshko. C117: *Stephanocleonus (Stephanocleonus) nubilis* (Fähræus 1842), ♂: Russia, Buryatia, Belozersk, 9.vii.1997, A. Shavrin; ♀: Russia, Buryatia, Shuchie lake, 15.vii.1974, G. Lukina. C118: *Stephanocleonus (Stephanocleonus) paradoxus* (Fähræus 1842), ♂ & ♀: Russia, Tuva, Morek, 23.v.2000, S. Vashenko. C119: *Stephanocleonus (Stephanocleonus) sahlbergi* Faust, 1890, ♂ & ♀: Russia, Tuva, Irbitey, 21.v.1974, B. Korotyayev (ZIN). C120: *Stephanocleonus (Taenioleonus) albofasciatus* Ter-Minasian, 1972, ♂ & ♀: Russia, Tuva, Sheveking-Khem, 10.vii.1990, Molodtsov. C121: *Stephanocleonus (Taenioleonus) excisus* Reitter, 1895, ♂: Mongolia, Erden-e-Santa, 17.vi.1981, L. Borkin (ZIN); ♀: Russia, Chita, ix. 1968, A. Arzanov. C122: *Stephanocleonus (Taenioleonus) helenae* Ter-Minasian, 1972, ♂: Mongolia, South Gobi, Bulgan, 29.vi.1971, A. Emelianov (ZIN); ♀: Mongolia, Shine-Dzhinst, 5.vii.1981, B. Korotyayev (ZIN). C123: *Stephanocleonus (Taenioleonus) korotyayevi* Ter-Minasian, 1979, ♂ & ♀: Russia, Tuva, Soglyi, 1.vi.2003, S. Vashenko. C124: *Stephanocleonus (Taenioleonus) suvorovi* Legalov, 1999, ♂ & ♀: Russia, Tuva, Soglyi, 1.vi.2003, S. Vashenko. C125: *Surchania sijazovi* Lebedev, 1931, ♂: Tajikistan, Garausy, 17.iv.1973, Kh. Nasreddinov (ZIN); ♀: Tajikistan, iv.1959, V. Mikhailov (ZIN). C126: *Temnorhinus (Fabiocleonus) mendicus* (Gyllenhal, 1834), ♂ & ♀: Italy, Sicily, v.1921 (ZIN). C127: *Temnorhinus (Massimocleonus) arabs* Olivier, 1807, ♂ & ♀: Afganistan, Kandahar, Jalalabad, 21.iii.1967, D. Polovny (ZIN). C128: *Temnorhinus (Massimocleonus) elongatus* (Gebler, 1844), ♂ & ♀: Russia, Astrakhan

reg., Baskunchak, 12.v.2011, A. Zotov. C129: *Temnorhinus (Massimocleonus) nasutus* (Hochhuth, 1847), ♂: Armenia, Etchmiadzin (ZIN). C130: *Temnorhinus (Temnorhinus) breviostris* (Gyllenhal, 1834), ♂ & ♀: Israel, Sede Zin, 15.v.2005, E. Groner. C131: *Temnorhinus (Temnorhinus) hololeucus* (Pallas, 1781), ♂ & ♀: Russia, Astrakhan reg., Mayachnoe, 11.ix.2005, Filippov. C132: *Temnorhinus (Temnorhinus) kirghisicus* Chevrolat, 1873, ♂: Russia, Volgograd reg., Elton, 23.iv.1988, A. Kravets; ♀: Kazakhstan, Khar'kin, 30.iv.1951, E.Gureva (ZIN). C133: *Temnorhinus (Temnorhinus) verecundus* (Faust, 1883), ♂: Uzbekistan, Golodnaya step, vii.1968, Kesken (ZIN); ♀: Kazakhstan, Arkalik, 25.vi.1999, M. Danilevsky (ZIN). C134: *Terminasiana granosa* (Zoubkoff, 1833), ♂ & ♀: Russia, Astrakhan reg., Baskunchak, 28.v.2008, A. Zotov. C135: *Tetragonothorax lyali* Alonso-Zarazaga, 1999, ♂ & ♀: R. Congo, Haut-Chari, Fort-Sibut, Le Moul't. C136: *Trachydemus inquinatus* (Olivier, 1807), ♂: Algeria, Oran, P. Mathicuss (ZIN). C137: *Trichocleonus leucophyllus* (Fischer von Waldheim, 1821), ♂: Iran, Esfahan, Aran-va-Bitgol, 26.iv.2007, A. Klimenko; ♀: Turkmenistan, Repetek, 1.iii.1983, A. Krivokhatsky (ZIN). C138: *Whiteheadia brevis* (Fåhraeus, 1842), ♂ & ♀: Ethiopia, D. Dadua, La Moul't. C139: *Xanthochelus cinctiventris* (Fåhraeus 1842), ♂ & ♀: Egypt, Reitter (ZIN). C140: *Xanthochelus ewersmanni* (Fåhraeus 1842), ♂ & ♀: Kazakhstan, Kopchagay, 6.vi.1989, M. Danilevsky. C141: *Xanthochelus major* (Herbst, 1784), ♂: Thailand, Mae Toun Di, 27.vii.2008, A. Pushenko; ♀: Vietnam, Phuc Son, 3.x.2008, V. Zolotuhin. C142: *Xanthochelus miscellanius* Faust, 1892, ♂ & ♀: Egypt, Luksor, Thebes, P. Semenov (ZIN). C143: *Xanthochelus nepotalis* Faust, 1904, ♂ & ♀: Tanzania (ZIN). C144: *Xanthochelus nomas* (Pallas, 1771), ♂: Turkmenistan, Kushka, 20.i.1986 (ZIN); ♀: Azerbaijan, Absheron, Shuveliani, 22.vii.1978, Kazarian (ZIN). C145: *Xenomacrus glacialis* (Herbst, 1797), ♂ & ♀: South Africa (ZIN).