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Morphology-based phylogenetic reconstruction of Cholevinae (Coleoptera: Leiodidae): a new view on higher-level relationships

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Abstract

The current state of knowledge on the suprageneric relationships in Cholevinae is either derived from informal evaluations of putative synapomorphies or based on molecular studies with limited taxonomic sampling. Here we assessed the higher-level relationships in this subfamily based on a phylogenetic analysis of 97 morphological characters scored for 93 terminals, representing all tribes. Both parsimony and Bayesian analyses were used. The monophyletic origin of Cholevinae was corroborated, except for the unexpected inclusion of *Leptinus* in the implied weighting analysis. Eucatopini + Oritocatopini were retrieved as basal branches in the evolution of Cholevinae. The monophyletic origin of all remaining Cholevinae was confirmed, which is consistent with molecular evidence. Anemadini was non-monophyletic, in accordance with earlier hypotheses. Cholevini was rendered non-monophyletic by the uncertain inclusion of *Prionochaeta* and the consistent exclusion of *Cholevinus*. A close affinity of Ptomaphagini to Sciaphyini and Leptodirini was suggested, although the position of *Sciaphyes* remains uncertain. The phylogenetic hypothesis of Cholevinae provided here is the most comprehensive presently available. The list of characters shows that a substantial part of the data was obtained from the ventral side. This is a strong argument for a detailed pictorial documentation of the ventral body parts in taxonomic descriptions, in contrast to the common practice of only illustrating the dorsal habitus of the beetles.

With more than 4100 described species (Newton, 2016) and a worldwide distribution, the staphyliniform family Leiodidae has the second highest species diversity within the megadiverse Staphylinoidea. The eclectic repertoire of habitats and food sources potentially utilized by these beetles is impressive, and difficult to synthesize concisely. According to Newton (2016), however, most leiodids might fit into one of three broad categories: (i) ground-dwelling saprophages or general scavengers of forest leaf litter, deep soil or cave environments; (ii) saprophagous inhabitants of carrion, dung and equivalent concentrated decaying organic matter; or (iii) obligate mycophages relying on various groups of fungi. Some specialized species inhabit nests of social insects including ants, wasps, termites and stingless bees (Jeannel, 1936; Peck and Cook, 2002, 2007; Peck, 2003), while others may be found in nests or burrows of reptiles (e.g. tortoises; Peck and Skelley, 2001), birds (e.g. owls, sparrows, starlings, buzzards; Jeannel, 1936) and mammals (e.g. foxes, moles, shrews and various rodents; Jeannel, 1936; Newton, 1998; Peck and Skelley, 2001). Aditionally, there are a few highly modified ectoparasitic species of aquatic or semi-aquatic mammals (Peck, 1982).

Leiodidae is presently subdivided into six subfamilies. Cholevinae and Leiodinae—informally called small carrion beetles and round fungus beetles, respectively—are by far the most species-rich, with representatives in both tropical and temperate regions. Cholevinae, the most diverse, comprises ca. 2050 species arranged in seven tribes and 17 subtribes (Perreau, 2000; Bouchard et al., 2011). The geographical limits of these subgroups vary substantially: while the

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monogeneric Sciaphyini is only known from a few localities in the East Palearctic region, Anemadini may be found in the Holarctic, Neotropical, Oriental, Australotropical, Australotemperate, Neoguinean, Neozelandic and Andean regions (Newton, 2016). The highly species-rich Leptodirini is mainly restricted to the western Palaearctic, with its greatest diversity found in the north Mediterranean basin (Perreau, 2004; Fresneda et al., 2011). Although not very appealing from an aesthetic perspective (except for the strongly modified cave-adapted leptodirines), cholevine beetles arguably offer a broad array of attractive topics in evolutionary biology, ecology and biogeography.

Intensive investigations have been devoted to the taxonomy of both Leiodidae and Cholevinae in the last decade. Among 674 leiodid species described since 2005, 255 were cholevines (see Newton, 2005, 2016). However, these taxonomic achivements were not paralleled by phylogenetic studies. A robust cladistic investigation explicitly focused on Leiodidae or Cholevinae has not been performed. Within this scenario of limited phylogenetic insights, the molecular analyses of Fresneda et al. (2011) and McKenna et al. (2015) are of great importance, even though these studies were not explicitly designed to investigate the internal relationships throughout Cholevinae or Leiodidae. The study of McKenna et al. (2015) constitutes a large-scale analysis aiming at the phylogeny of Staphyliniformia, and included only about a dozen of selected cholevine representatives. The molecular phylogeny of Fresneda et al. (2011) is the largest for Cholevinae and tentatively sheds some light on its internal relationships. However, as it was targeted at Leptodirini, some cholevine subgroups were not sampled, especially from south temperate faunas.

Whereas the monophyly of Cholevinae was not recovered by Fresneda et al. (2011) and McKenna et al. (2015), this subfamily has been considered as a natural unit by Newton (1998, 2016) based on an informal evaluation of putative synapomorphies. Therefore, the higher level classification of Cholevinae remains an important area of investigation. The aim of the present study was to test the monophyly of Cholevinae on the basis of phylogenetic analyses, and to propose a hypothesis for the higher-level relationships in the subfamily, based on the broadest taxonomic sampling ever conducted.

3 Material and methods

Morphological study and taxonomic sampling

Ninety-seven characters were scored from adult morphology of 93 terminal taxa, mainly using scanning electron microscopy (SEM). Studied character systems were the head, prosternum, meso- and metaventrite, elytra, legs including the pretarsus and distal margin of the terminal tarsomere, and the abdomen including the aedeagus (the last based mainly on data obtained from published descriptions). Other internal characters were not assessed in this study, and data from the literature were not considered sufficiently well documented for a proper interpretation of structures through all the studied taxa. The ingroup included representatives of all currently recognized cholevine tribes and subtribes, with the exception of Baryodirina, a monotypic subtribe proposed on the basis of a single female of *Baryodirus* (Perreau, 2000). This genus, however, was included in the matrix and its characters were coded based on the SEM images of *Baryodirus* provided in the original description of the taxon (Perreau, 2000: figs 1–10). The limited information content of the SEM micrographs concerning the characters utilized here, in addition to the lack of data on males, resulted in a large number of missing entries (~ 46%). We therefore assessed the position of *Baryodirus* employing an additional, separate analysis.

Twelve outgroup taxa were selected from four of the five non-cholevine subfamilies of Leiodidae (representing ten out of 11 non-cholevinae tribes)—Camiarinae: *Agyrtodes labralis* and *Eupelates transversestrigosus* (Agyrtodini), *Camiarus thoracicus* (Camiarini) and *Neopelatops edwarsi* (Neopelatopini); Catopocerinae: *Catopocerus politus* (Catopocerini); Leiodinae: *Colenisia zelandica* (Pseudoliodini), *Decuria* sp. (Agathidiini), *Dietta huanuco* (Estadiini), *Hydnodiaetus* sp. (Sogdini), *Scotocryptus* sp. (Scotocryptini) and *Zeadolopus validipes* (Leiodini); and Platypsyllinae: *Leptinus testaceus*. Only Coloninae (with two genera) and the monotypic Glacicavicolini (Catopocerinae) are not represented. Several cladistic studies based both on molecular data and on morphology have consistently placed Agyrtidae as the sister-taxon of Leiodidae (e.g. Beutel and Molenda, 1997; Beutel and Leschen, 2005; Caterino et al., 2005; McKenna et al., 2015), corroborating the hypothesis of previous taxonomic studies (e.g. Newton, 1997, 1998). The agyrtid *Zeanecrophilus prolongatus* was then used to root the tree. Most species used in the present study were obtained from museums or from private collections. The list of species we examined with their systematic assignment and authorities are provided in Table 1. Most terminal taxa represent single species. Only in three cases was the terminal taxon scored based on two different congeneric species: *Anthroherpon hoermanni* + *A. primitivum*; *Prionochaeta harmandi* + *P. opaca*; and *Platycholeus leptinoides* + *P. opacellus*. It is assumed that these species are more closely related to one another than to any other terminal in the matrix. The character state matrix is shown in Appendix S1.

Table 1
List of the species examined in this study

Systematic assignment				Species	Provenance
Leiodidae					
	Cholevinae	Anemadini	Anemadina	*Anemadus acicularis* (Kraatz)	Monte Vulture, Potenza, Basilicata, Italy
	Cholevinae	Anemadini	Anemadina	*Speonemadus bolivari* (Jeannel)	Complejo del Romeral, Antequera, Málaga, Spain
	Cholevinae	Anemadini	Eocatopina	*Eocatops ophidianus* Szymczakowski	Akdamar Island, Van Gölü, Turkey
	Cholevinae	Anemadini	Eunemadina	*Dissochaetus arizonensis* Hatch	Lincoln County, New Mexico, USA
	Cholevinae	Anemadini	Eunemadina	*Dissochaetus vanini* Gnaspini	Iporanga, São Paulo, Brazil
	Cholevinae	Anemadini	Eunemadina	*Falkocholeva* sp.	Bahía de San Sebastián, Tierra del Fuego, Argentina
	Cholevinae	Anemadini	Eunemadina	*Nargiotes leptocerus* Szymczakowski	Bunya Mountains National Park, Queensland, Australia
	Cholevinae	Anemadini	Eunemadina	*Nargomorphus amplicollis* Szymczakowski	Pemberton, Western Australia, Australia
	Cholevinae	Anemadini	Eunemadina	*Pseudonemadus cheesmani* (Jeannel)	Mount Kaindi, Morobe, Papua New Guinea
	Cholevinae	Anemadini	Nemadina	*Nemadus* sp.	Nymburk, Central Bohemia, Czech Republic
	Cholevinae	Anemadini	Nemadina	*Micronemadus pusillimus* (Kraatz)	Japan
	Cholevinae	Anemadini	Paracatopina	*Paracatops alacris* (Broun)	Kerr Taylor SR, Auckland, Auckland, New Zealand
	Cholevinae	Anemadini	Paracatopina	*Paracatops antipoda* (Kirsch)	Adams Island, Auckland Islands, New Zealand
	Cholevinae	Cholevini	Catopina	*Apocatops monguzzii* Giachino & Vailati	Rezzoaglio, Genova, Liguria, Italy
	Cholevinae	Cholevini	Catopina	*Catops fuliginosus* Erichson	(a) Tossicia, Abruzzo; (b) Matajur, Friuli Venezia Giulia: Italy
	Cholevinae	Cholevini	Catopina	*Catops subfuscus* Kellner	Monte Canin, Sella Nevea, Friuli Venezia Giulia, Italy
	Cholevinae	Cholevini	Catopina	*Cholevinus fuscipes* (Ménétries)	Arzni, Kotayk, Armenia
	Cholevinae	Cholevini	Catopina	*Rybinskiella magnifica* (Rybiński)	Chornohora, Rakhiv, Zakarpattia Oblast, Ukraine
	Cholevinae	Cholevini	Catopina	*Sciodrepoides watsoni* (Spence)	(a) Monti della Laga, Abruzzo; (b) Reggello, Tuscany: Italy
	Cholevinae	Cholevini	Cholevina	*Catopsimorphus orientalis* Aubé	Kastraki, Nemea, Corinthia, Peloponnese, Greece
	Cholevinae	Cholevini	Cholevina	*Choleva agilis* (Illiger)	San Tomio, Malo,Vicenza, Veneto, Italy
	Cholevinae	Cholevini	Cholevina	*Choleva oblonga* Latreille	Cremona, Lombardy, Italy
	Cholevinae	Cholevini	Cholevina	*Nargus badius* (Sturm)	Borghetto di Vara, Liguria, Italy
	Cholevinae	Cholevini	Cholevina	*Prionochaeta harmandi harmandi* Portevin	Omogo Valley, Mount Ishizuchi, Shikoku, Japan
	Cholevinae	Cholevini	Cholevina	*Prionochaeta opaca* (Say)	Natchez Trace, Henderson County, Tennessee, USA
	Cholevinae	Eucatopini		*Eucatops* sp.1	Saint Laurent du Maroni, French Guiana
	Cholevinae	Eucatopini		*Eucatops* sp.2	Puerto Maldonado, Madre de Dios, Peru
	Cholevinae	Leptodirini	Anthroherponina	*Anthroherpon hoermanni* (Apfelbeck)	Bjelašnica, Sarajevo Canton, Bosnia and Herzegovina
	Cholevinae	Leptodirini	Anthroherponina	*Anthroherpon primitivum primitivum* (Absolon)	Kali pećina, Grebci, Ravno, Bosnia and Herzegovina
	Cholevinae	Leptodirini	Anthroherponina	*Hadesia vasiceki* Müller	Vjetrenica, Ravno, Bosnia and Herzegovina
	Cholevinae	Leptodirini	Bathysciina	*Aphaobius milleri springeri* Müller	?
	Cholevinae	Leptodirini	Bathysciina	*Aphaotus jureceki* Breit	Grotta di Costalta, Trento, Trentino-Alto Adige, Italy
	Cholevinae	Leptodirini	Bathysciina	*Bathyscia montana* Schiødte	Zalog, Upper Carniola, Slovenia
	Cholevinae	Leptodirini	Bathysciina	*Oryotus schmidti* Miller	Postojna Cave, Postojna, Littoral, Slovenia
	Cholevinae	Leptodirini	Bathysciina	*Pisidiella kosswigi* Jeannel	Hacı Akif, Beyşehir Gölü, Konya, Turkey
	Cholevinae	Leptodirini	Bathysciotina	*Bathysciotes khevenhuelleri tergestinus* Müller	Trieste, Friuli Venezia Giulia, Italy
	Cholevinae	Leptodirini	Bathysciotina	*Neobathyscia fabianii* (Dodero)	Buso della Rana, Monte di Malo, Vicenza, Veneto, Italy
	Cholevinae	Leptodirini	Bathysciotina	*Ravasinia lonae* (Müller)	Mount Tomorr, Berat, Albania
	Cholevinae	Leptodirini	Bathysciotina	*Speonesiotes* sp.	Pavlova pećina, Trebinje, Bosnia and Herzegovina
	Cholevinae	Leptodirini	Leptodirina	*Antrosedes speluncarius* Reitter	Bjelašnica, Bosnia and Herzegovina
	Cholevinae	Leptodirini	Leptodirina	*Apholeuonus longicollis* Reitter	Bjelašnica, Bosnia and Herzegovina
	Cholevinae	Leptodirini	Leptodirina	*Astagobius angustatus laticollis* Pretner	Ledenica pri Dolu, Trnovski gozd, Littoral, Slovenia
	Cholevinae	Leptodirini	Leptodirina	*Elladoherpon inopinatum* Casale	Seli, Naousa, Imathia, Greece
	Cholevinae	Leptodirini	Leptodirina	*Haplotropidius pubescens* (Müller)	Vrlika, Split-Dalmatia, Croatia
	Cholevinae	Leptodirini	Leptodirina	*Leptodirus hochenwarti* Schmidt	Grotta Noè, Trieste, Friuli Venezia Giulia, Italy
	Cholevinae	Leptodirini	Leptodirina	*Pholeuonidius halbherri* (Reitter)	Campone, Tramonti di Sotto, Friuli-Venezia Giulia, Italy

Table 1
(Continued)

Systematic assignment			Species	Provenance
Cholevinae	Leptodirini	Leptodirina	*Remyella propiformis* Winkler	Dolíće, Pešter Polje, Serbia
Cholevinae	Leptodirini	Leptodirina	*Speoplanes giganteus biocovensis* (Müller)	Ledenica pri Dolu, Trnovski gozd, Littoral, Slovenia
Cholevinae	Leptodirini	Pholeuina	*Albaniola thessalica* (Reitter)	Spiliá, Mount Ossa, Larissa, Greece
Cholevinae	Leptodirini	Pholeuina	*Antrocharis querilhaci* (Lespès)	Grotte de Font Sainte, Ariège, France
Cholevinae	Leptodirini	Pholeuina	*Beskovia bulgarica* Guéorguiev	Cherepishka, Peshtera, Pazardzhik, Bulgaria
Cholevinae	Leptodirini	Pholeuina	*Breuilia triangulum* (Sharp)	Cueva del Escosu, Pelamoru, Asturias, Spain
Cholevinae	Leptodirini	Pholeuina	*Canavesiella lanai* Giachino	Grotta La Custreta, Sparone, Piemonte, Italy
Cholevinae	Leptodirini	Pholeuina	*Dellabeffaella roccae* (Capra)	Grotte di Pugnetto, Alpi Graie, Valli di Lanzo, Piemonte, Italy
Cholevinae	Leptodirini	Pholeuina	*Notidocharis ovoideus* Jeannel	Fonte das Covas, Oballo-Boal, Asturias, Spain
Cholevinae	Leptodirini	Pholeuina	*Parabathyscia (Parabathyscia) ligurica* (Reitter)	Tana do Scovero, Castelbianco, Liguria, Italy
Cholevinae	Leptodirini	Pholeuina	*Paraspeonomus vandeli* Coiffait	Faille de Jouandet, Ariège, France
Cholevinae	Leptodirini	Pholeuina	*Paratroglophyes jeanneli* Coiffait	Grottes d'Anglade, Ariège, France
Cholevinae	Leptodirini	Pholeuina	*Pholeuon knirschi* Breit	Hoanca Apei, Valea Gardei Seci, Bihor Mt, Romania
Cholevinae	Leptodirini	Pholeuina	*Pseudoboldoria robiati* (Reitter)	Crepaccio di Paderno, Paderno d'Adda, Lombardia, Italy
Cholevinae	Leptodirini	Pholeuina	*Quaestus arcanus* Schaufuss	Cueva de la Matona, Comillas, Cantabria, Spain
Cholevinae	Leptodirini	Pholeuina	*Speonomus (Machaeroscelis) infernus* (Dieck)	Haute-Garonne, France
Cholevinae	Leptodirini	Pholeuina	*Troglocharinus ferreri* (Reitter)	(a) Avenc d'en Roca, Cervelló; (b) Vallirana: Barcelona, Spain
Cholevinae	Leptodirini	Pholeuina	*Troglodromus bucheti caussicola* Jeannel	Peille, Alpes-Maritimes, France
Cholevinae	Leptodirini	Platycholeina	*Platycholeus leptinoides* (Crotch)	Pacific House, El Dorado, California, USA
Cholevinae	Leptodirini	Platycholeina	*Platycholeus opacellus* Fall	Stanislaus, Calaveras, California, USA
Cholevinae	Leptodirini	Spelaeobatina	*Spelaeobates kraussi* Müller	Dobra jama, Split-Dalmatia, Croatia
Cholevinae	Oritocatopini		*Afrocatops* sp.	Cathedral Peak Forest Station, KwaZulu-Natal, South Africa
Cholevinae	Oritocatopini		*Chappuisiotes lobeliae* Jeannel	Koitobos, Mount Elgon, Kenya
Cholevinae	Ptomaphagini	Ptomaphagina	*Adelopsis leo* Gnaspini	Iporanga, São Paulo, Brazil
Cholevinae	Ptomaphagini	Ptomaphagina	*Adelopsis rostrata* Gnaspini & Peck	Monteverde, Puntarenas, Costa Rica
Cholevinae	Ptomaphagini	Ptomaphagina	*Amplexella dimorpha* Gnaspini	Rancho Grande, Aragua, Venezuela
Cholevinae	Ptomaphagini	Ptomaphagina	*Parapaulipalpina* sp.	Sipao, 110kmE Caicara, Bolívar, Venezuela
Cholevinae	Ptomaphagini	Ptomaphagina	*Paulipalpina claudicans* (Szymczakowski)	Nova Teutônia, Santa Catarina, Brazil
Cholevinae	Ptomaphagini	Ptomaphagina	*Paulipalpina* sp. *1*	Mérida, Mérida, Venezuela
Cholevinae	Ptomaphagini	Ptomaphagina	*Paulipalpina* sp. *2*	Colonia Tovar, Aragua, Venezuela
Cholevinae	Ptomaphagini	Ptomaphagina	*Paulipalpina* sp. *3*	Leticia, Amazonas, Colombia
Cholevinae	Ptomaphagini	Ptomaphagina	*Ptomaphagus meximontanus* Peck	Pinal de Amoles, Querétaro, Mexico
Cholevinae	Ptomaphagini	Ptomaphagina	*Ptomaphagus sericatus* Chaudoir	Trebnje, Trebnje, Lower Carniola, Slovenia
Cholevinae	Ptomaphagini	Ptomaphaginina	*Ptomaphaginus palpalis* Szymczakowski	Phulchoki, Kathmandu, Nepal
Cholevinae	Ptomaphagini	Ptomaphaginina	*Ptomaphaminus chapmani* (Peck)	Clearwater cave, Gunung Mulu, Sarawak, Malaysia
Cholevinae	Ptomaphagini	Ptomaphaginina	*Proptomaphaginus puertoricensis* Peck	Aguas Buenas Cave, Aguas Buenas, Puerto Rico
Cholevinae	Sciaphyini		*Sciaphyes sibiricus* (Reitter)	Vladivostok, Primorsky Krai, Russia
Camiarinae	Agyrtodini		*Agyrtodes labralis* (Broun)	Matukituki Valley, New Zealand
Camiarinae	Agyrtodini		*Eupelates transversestrigosus* (Fairmaire & Germain)	Alto de Nahuelbuta, Arauco, Bío Bío, Chile
Camiarinae	Camiarini		*Camiarus thoracicus* Sharp	Maraetai Hills, Auckland, New Zealand
Camiarinae	Neopelatopini		*Neopelatops edwardsi* Jeannel	Osorno, Osorno, Chile
Catopocerinae	Catopocerini		*Catopocerus politus* Motschulsky	Witmer, Pendleton County, West Virginia, USA
Leiodinae	Agathidiini		*Decuria* sp.	Puerto Maldonado, Tambopata, Madre de Dios, Peru
Leiodinae	Estadiini		*Dietta huanuco* Peck & Cook	Tingo María, Cordillera Azul, Peru
Leiodinae	Leiodini		*Zeadolopus validipes* (Daffner)	Hunua Ra Mangatangi, Auckland, New Zealand
Leiodinae	Pseudoliodini		*Colenisia zelandica* Leschen	Te Paki, Northland, New Zealand
Leiodinae	Sogdini		*Hydnodiaetus* sp.	Manzanar, Malleco, Araucanía, Chile

Table 1
(Continued)

Systematic assignment		Species	Provenance
Leiodinae	Scotocryptini	*Scotocryptus* sp.	Viçosa, Minas Gerais, Brazil
Platypsyllinae		*Leptinus testaceus* P.W.J. Müller	Giare, Veneto, Italy
Agyrtidae			
Necrophilinae		*Zeanecrophilus prolongatus* (Sharp)	Takitimu, Princhester Hut, Southland, New Zealand

Pictorial documentation

Both dried and alcohol-preserved specimens were examined and documented using SEM. Dissected body parts were immersed in contact lens solution for 24 h to clean the external cuticular structures and then dehydrated in an ethanol series of increasing concentration, air-dried or stove-dried, sputter-coated with gold (Emitech K 500, Sample preparation division, Quorum Technologies Ltd, Ashford, UK) and fixed on a rotatable specimen holder (Pohl, 2010). Most images were taken with an ESEM XL30 (Philips, Amsterdam, the Netherlands) equipped with Scandium FIVE (Olympus, Münster, Germany), but some data were obtained with a Zeiss DSM 940 (Carl Zeiss, Oberkochen, Germany) scanning electron microscope using conventional stubs. Additional morphological observations and documentation were conducted using a Zeiss Discovery V20 stereomicroscope equipped with an AxioCam MRc5 digital camera (Carl Zeiss).

Classification system and terminology

The suprageneric classification of Leiodidae is based on Newton (1998), Perreau (2000) and Bouchard et al. (2011). At the species level, we followed Perreau (2000, 2004). Most of the morphological terms used here are based on Lawrence et al. (2010, 2011). Terms related to the morphology of the pretarsus and distal margin of the terminal tarsomere follow Antunes-Carvalho and Gnaspini (2016).

Cladistic analysis

The data matrix was compiled using MESQUITE 3.10 (Maddison and Maddison, 2016) and analysed under parsimony with TNT v1.1 (Goloboff et al., 2008b). Heuristic searches were performed under both equal and implied weighting (Goloboff, 1993; Goloboff et al., 2008a) using the New Technology algorithms with the following parameters: *sectorial search* (Goloboff, 1999) in default mode, 200 iteractions of *ratchet* (Nixon, 1999), 20 cycles of *drift* (Goloboff, 1999) and ten rounds of *tree fusing* (Goloboff, 1999). This procedure was repeated until the best score was located 100 times. The TNT setk script, developed by Salvador Arias, was used to identify the most appropriate K value through the formula proposed by Goloboff et al. (2008a). A value of 14.7852 was returned and subsequently used in the implied weighting scheme. Nodes were evaluated with Bremer supports (Bremer, 1994) with the Bremer.run script supplied by TNT, and symmetric resampling (Goloboff et al., 2003) expressed as the difference in the CG (contradicted/present groups) frequency (1000 replications). Optimizations were performed with Winclada-ASADO 1.62 (Nixon, 2002). Only unambiguous changes were mapped on the tree. We coded most characters as binary

(88.7%) and treated the multi-state characters as unordered. Parsimony-uninformative characters were deactivated before analysis and therefore do not contribute to tree length nor to other statistics. However, they were optimized onto the tree and were included in the character list and data matrix because they may be of interest for future research.

Bayesian analysis

Bayesian analysis was conducted with MrBayes 3.2 (Ronquist and Huelsenbeck, 2003) using the Mkv model (Lewis, 2001) with a single partition. Two separate runs were conducted, each with one cold and three heated chains, checking for adequate mixing with the statistics provided by the program. To assess convergence and to establish a burn-in fraction, we initially set the analyses to run for an overestimated 25×10^6 generations, sampled every 1000 generations. We then assessed convergence by visual examination of a plot of the standard deviation of the split frequencies between the two simultaneous runs, establishing the burn-in when it reached stable values at ca. 0.005. Once the burn-in was fixed, we let the analyses run until the effective sample size (ESS) reached values above 200 as estimated in Tracer v1.5 (Rambaut and Drummond, 2007), considered to be sufficient for a good sampling of the post-burn-in tree space (Rambaut and Drummond, 2007). The resulting trees were combined in a majority rule consensus topology with posterior probability (pp) of nodes calculated using the sumt command in MrBayes.

Results

External and internal characters were scored for 13 outgroup taxa and 80 ingroup terminals covering all tribes and 16 of the 17 subtribes in Cholevinae. The complete data set comprised 23 characters of the head, six of the prosternum, 22 of the pterothoracic ventrites, seven of the elytra, five of the tarsus and tibial spurs, 28 of the pretarsus and distal margin of the terminal tarsomere, one of the abdomen and five of the male genitalia. Characters 82, 91 and 92 were parsimony-uninformative (autapomorphies of *Ptomaphaminus*, *Leptinus* and *Sciaphyes*, respectively). Traits potentially strongly affected by convergent evolution induced by adaptations to underground life were avoided (e.g. absence of eyes and hindwings).

List of characters

Head.

1. Cuticular surface of gula: (0) reticulated (Fig. 1a); (1) smooth (Fig. 1b). The gular surface is strongly reticulated in all cholevines and some other leiodids. The smooth condition is found on the small gula of *Leptinus*, and in most genera of Camiarinae and Leiodinae examined herein.
2. Hypostomal suture: (0) present, even if very weak (Fig. 1c: hs); (1) absent (Fig. 1d). The gular sutures are anteriorly continuous with the hypostomal sutures, which reach the maxillary grooves in most members of Cholevinae and outgroups. The hypostomal suture is missing in Eucatopini, *Nemadus*, Ptomaphagini, Sciaphyini and a few leptodirines including the basal *Platycholeus*. The hypostomal suture is fissure-shaped in some taxa and clearly recognizable externally, whereas it is more or less obsolete in other groups.
3. Postmandibular ridge: (0) present (Fig. 1e: pmr); (1) absent (Fig. 1f). Present on the ventral face of the head in members of Leiodinae examined. We interpret it tentatively as homologous to the cuticular ridges that form antennal grooves in some species, due to similarities in the position and shape of these structures.
4. Area close to anterior margin of mentum: (0) flat (Fig. 1g); (1) with low transverse ridge (Fig. 1h: arm). A low but recognizable transverse elevation is present close to the anterior margin of the mentum in Eucatopini, Oritocatopini and Sciaphyini. It is also present in *Agyrtodes*, *Eupelates*, *Catopocerus*, *Colenisia*, *Hydnodiaetus* and *Leptinus*. The condition in *Catopocerus*, however, is less distinct than in the other taxa.
5. Lateral margin of mentum: (0) without longitudinal ridge (Fig. 1h); (1) with longitudinal ridge (Fig. 1g: lrm). A narrow longitudinal ridge is present at the lateral margin of the mentum in species of Ptomaphagina, *Eucatops*, *Bathyscia* and *Hadesia*, and apparently in *Baryodirus* (see fig. 5 in Perreau, 2000). This feature also occurs in *Catopocerus*. In *Eucatops* and *Catopocerus* it is anteriorly fused with the transverse ridge of the mentum (see character 4).
6. Ventral surface of prementum (ventral view): (0) without macrosetae (Fig. 2a); (1) with a single macroseta on left side (Fig. 2c); (2) with a single macroseta on right side (Fig. 2d); (3) paramedian pair of macrosetae (Fig. 2b). A pair of macrosetae is present on the exposed part of the ventral premental surface in all outgroup taxa except *Zeanecrophilus*. In some cases additional setae may be present in this area. Two paramedian setae are also inserted on this area in Oritocatopini, Eucatopini, Eunemadina and *Prionochaeta*. Only a single seta is present on the left side of the exposed premental area in *Paracatops*, whereas the seta is placed on the right

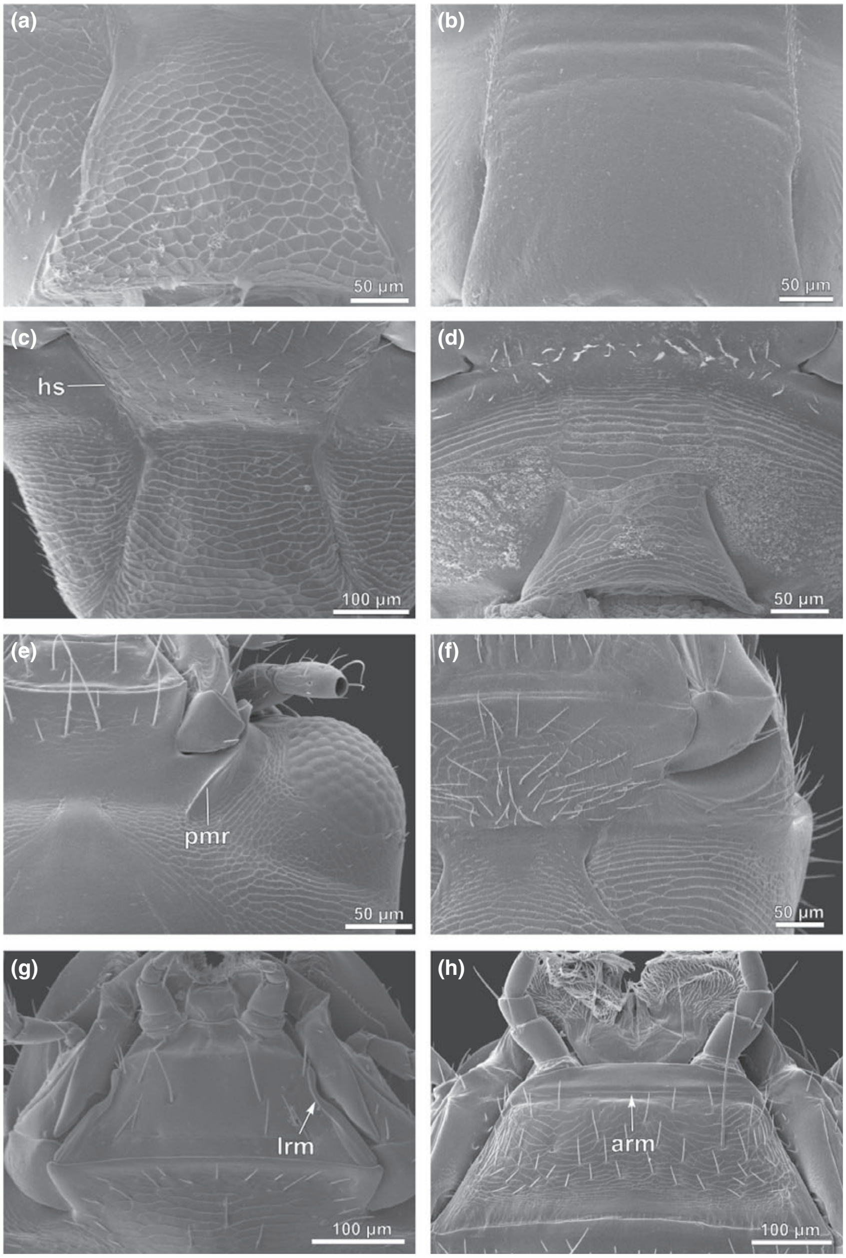

Fig. 1. Head, ventral view. (a) *Anemadus acicularis* (Anemadini). (b) *Camiarus thoracicus* (Camiarinae). (c) *Catops fuliginosus* (Cholevini). (d) *Eucatops* sp. 2 (Eucatopini). (e) *Colenisia zealandica* (Leiodinae). (f) *Paraspeonomus vandeli* (Leptodirini). (g) *Ptomaphagus sericatus* (Ptomaphagini). (h) *Chappuisiotes lobeliae* (Oritocatopini). arm, anterior ridge of mentum; hs, hypostomal suture; lrm, longitudinal ridge of mentum; pmr, postmandibular ridge.

side in *Choleva oblonga*, *Nargus* and *Antrocharis* (in ventral view). The pair of setae is absent in the other cholevine taxa included. In some species, the anterior part of the prementum is completely covered by the mentum, hampering observation of the setae.

7. Apical labial palpomere: (0) without lateral peg-like sensilla (Fig. 2e); (1) with lateral peg-like sensilla (Fig. 2f). In addition to the apical sensorial field, a cluster of peg-like sensilla is present at the outer side of the distal labial palpomere in *Agyrtodes* and *Eupelates*.
8. Size of apical maxillary palpomere: (0) distinctly longer than preapical palpomere (Fig. 2g, i); (1) not longer than preapical palpomere (Fig. 2h, j). The distal maxillary palpomere is approximately as long as or shorter than the subapical one in all Cholevinae except Eucatopini and

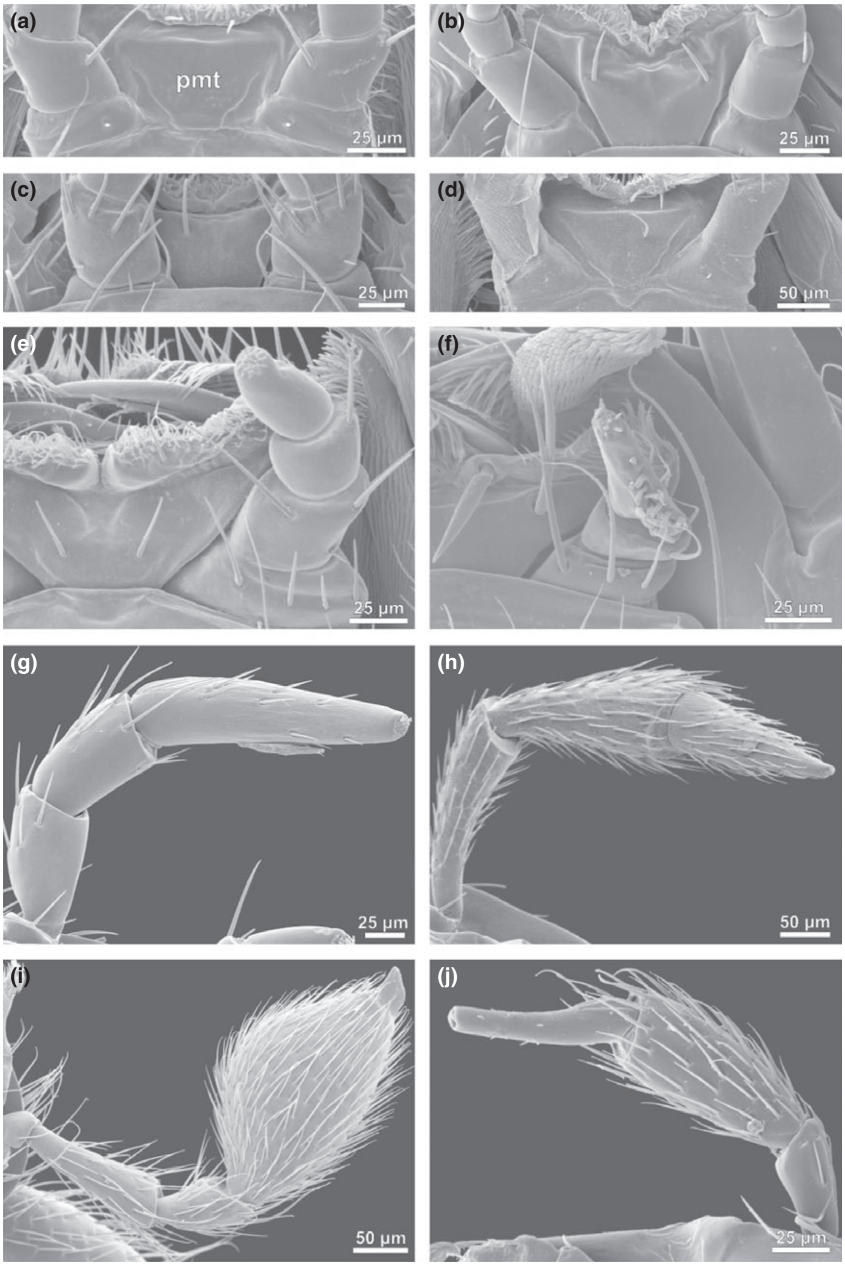

Fig. 2. Mouthparts, ventral view. Ventral surface of prementum of (a) *Eocatops ophidianus* (Anemadini), (b) *Afrocatops* sp. (Oritocatopini), (c) *Paracatops antipoda* (Anemadini), and (d) *Choleva oblonga* (Cholevini). Labial palp of (e) *Prionochaeta harmandi* (Cholevini) and (f) *Agyrtodes labralis* (Camiarinae). Maxillary palp of (g) *Chappuisiotes lobeliae* (Oritocatopini), (h) *Nargus velox* (Cholevini), (i) *Camiarus thoracicus* (Camiarinae) and (j) *Ptomaphaginus palpalis* (Ptomaphagini). pmt, prementum.

Oritocatopini. The same condition occurs in *Scotocryptus* and *Leptinus*.

9. Shape of apical maxillary palpomere: (0) subcylindrical, diameter subequal from base to apex (Fig. 2g); (1) conical (Fig. 2h); (2) subcylindrical and distinctly narrowed just after its base (Fig. 2j); (3) strongly expanded (Fig. 2i). A subcylindrical apical maxillary palpomere, with subparallel sides over the entire length, occurs in *Zeanecrophilus*, some representatives of Leiodinae, and in Eucatopini and Oritocatopini. A conical palpomere is present in the majority of cholevine species. In most Ptomaphagini, however, the distal maxillary palpomere is subcylindrical and thinner just after its base. A thin palpomere is also present in *Spelaeobates*. The distinctly enlarged 4th palpomere of *Camiarus* is probably autapomorphic.

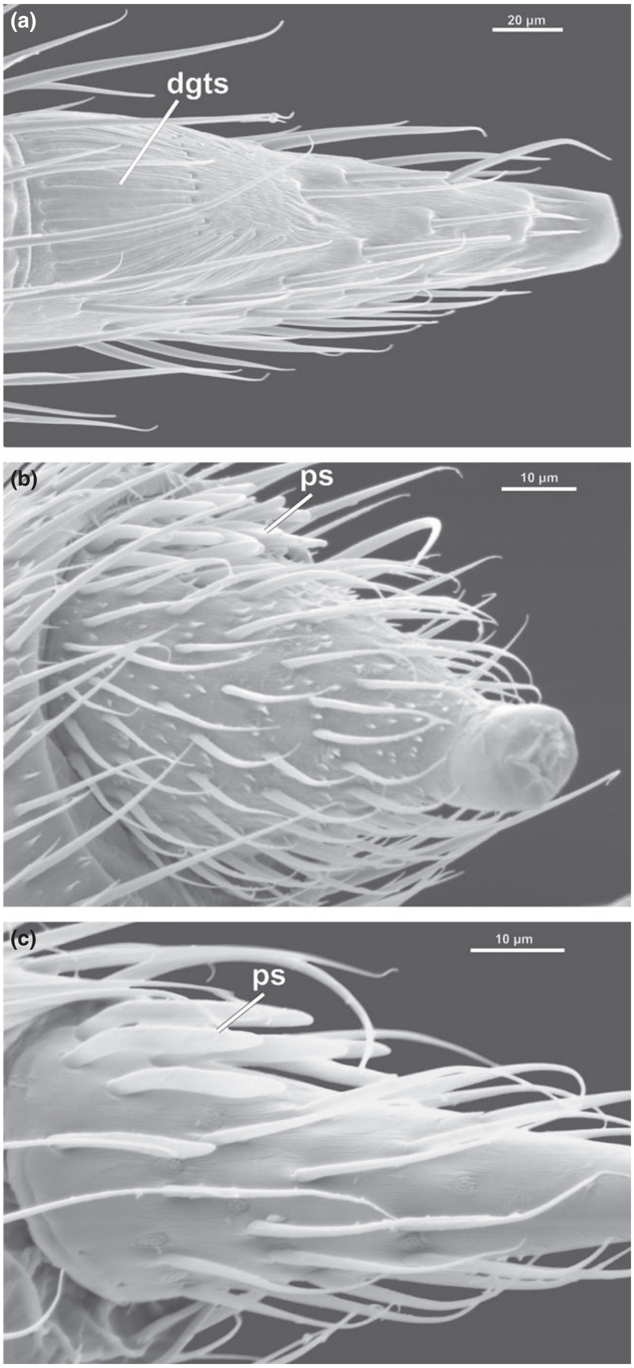

Fig. 3. Apical maxillary palpomere of (a) *Rybinskiella magnifica* (Cholevini), (b) *Platycholeus opacellus* (Leptodirini) and (c) *Quaestus arcanus* (Leptodirini). dgts, digitiform sensilla; ps, projecting sensilla.

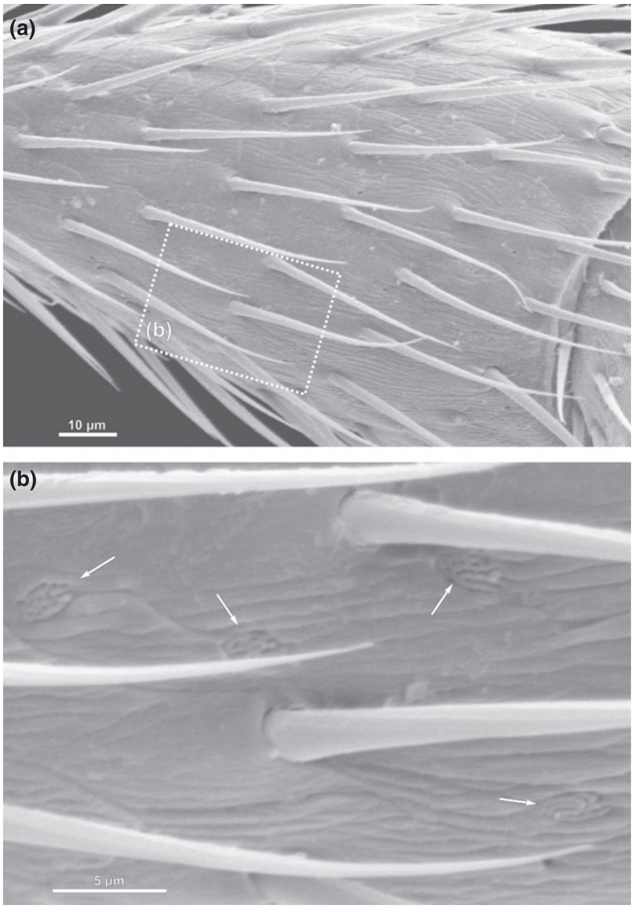

Fig. 4. Subapical maxillary palpomere of *Speonemadus bolivari*. Arrows indicate pore plates.

10. Sensilla of apical maxillary palpomere: (0) digitiform sensilla (i.e. sensilla adpressed to surface; Fig. 3a: dgts); (1) projecting sensilla (i.e. sensilla articulated to surface; Fig. 3b, c: ps). The presence of a set of projecting sensilla on the basal area of the distal maxillary palpomere is an almost unique feature of Leptodirini, except for its occurrence in *Nargomorphus* (and a possible reversal in *Spelaeobates*). These sensilla have already been described in other leptodirines, namely in *Closania*, *Sophrochaeta* and *Tismanella* (Moldova et al., 2004), and in *Anthroherpon*, *Leptomeson* and *Graciliella* (Njunjić et al., 2016). This condition is in contrast to the digitiform sensilla of the apical maxillary palpomere of most Coleoptera. Although Njunjić et al. (2016) do not report the projecting sensilla in *Hadesia*, we confirm its presence in *Hadesia vasiceki*.
11. Vestiture of apical maxillary palpomere: (0) mostly glabrous (Fig. 2j); (1) pubescent (e.g. Figs 2g–i and 3). Setose apical maxillary palpomeres occur in Cholevinae excluding Ptomaphagini. The apical maxillary palpomere is almost glabrous with only minute setae in this tribe, and also in a few species of Leiodinae and in Agyrtidae.
12. Pore plates on the subapical maxillary palpomere: (0) absent; (1) present (Fig. 4). A set of

inconspicuous pore plates on the subapical maxillary palpomere of *Catops* was described and documented (Antunes-Carvalho et al., 2017). These structures are also present in members of most tribes of Cholevinae. The pore plates are generally present on the apical maxillary palpomere (see Antunes-Carvalho et al., 2017: fig. 3f). They are absent in Eucatopini, Oritocatopini and in all outgroup taxa.

13. Setal pits on vertex: (0) without areola or at least absent from most setal pits (Fig. 5d); (1) pits generally with areola (Fig. 5c: sa). A visible areola is present around most setal pits on the vertex of Anemadina, most Eunemadina (absent in *Falkocholeva*), Catopina, *Prionochaeta*, *Chappuisiotes* and *Spelaeobates* (even though less pronounced in this last taxon). Few areola may be also present in some of the taxa coded as (0), but in these cases the absence of setal rings is clearly the predominant pattern on the vertex.
14. Microsculpture of central area of frontoclypeal surface: (0) with inconspicuous irregular strioles (Fig. 5a); (1) with transverse strigae (Fig. 5b); (2) with fine microreticulation (Fig. 5c); (3) smooth (Fig. 5d). Fine, weak strioles characterize the head surface of *Zeanecrophilus*. In *Catopocerus* and *Colenisia*, transverse strigae are distributed over the central area of the frontoclypeal surface, somewhat irregularly in the former taxon. The pattern in most Cholevinae is a fine microreticulation, but several taxa have a smooth frontoclypeal surface including Eucatopini, Oritocatopini, most Ptomaphagini and *Sciaphyes*. The frontoclypeal surface is smooth in most outgroups.
15. Dorsal surface: (0) mostly glabrous (Fig. 5e); (1) pubescent (Fig. 5f). The dorsal surface of the head is densely pubescent in almost all cholevines studied, with few exceptions within the diverse Leptodirini. A dense pubescence is also present in *Leptinus* and most Camiarinae. Only a very short pubescence is present in *Zeanecrophilus*, *Neopelatops*, Leiodinae and Catopocerinae, and it is very sparse in some cases.
16. Anterior margin of clypeus: (0) not delimited by a ridge (Fig. 6a); (1) delimited by a ridge (Fig. 6b: arc). The anterior clypeal border is distinctly demarcated by a ridge in most ingroup taxa. However, this feaure is lacking in almost all Cholevini studied (present in *Sciodrepoides*). It is also missing in Anemadina, *Falkocholeva*, *Eocatops*, *Nemadus* and *Platycholeus*. The ridge is absent in most outgroup taxa (present in *Agyrtodes* and *Zeadolopus*).
17. Anterior portion of clypeus: (0) not truncated (Fig. 6c); (1) truncated (Fig. 6d). In most cholevines the clypeus is prolonged anteriorly, covering part of the dorsal mandibular surface.

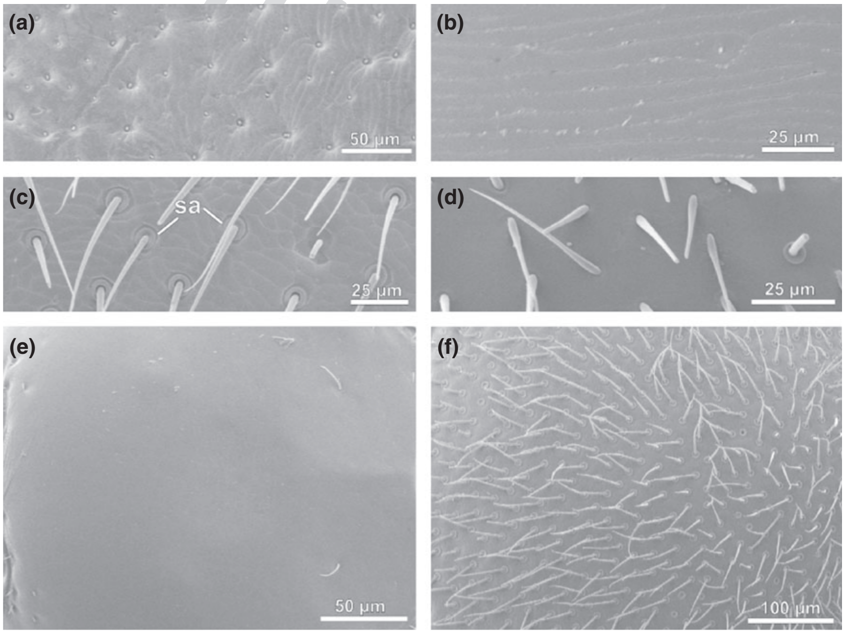

Fig. 5. Central area of the frontoclypeal surface in (a) *Zeanecrophilus prolongatus* (Agyrtidae), (b) *Colenisia zealandica* (Leiodinae), (c) *Rybinskiella magnifica* (Cholevini) and *Eucatops* sp. 2 (Eucatopini). Vertex of (e) *Neopelatops edwarsi* (Camiarinae) and (f) *Pseudonemadus cheesmani* (Anemadini). sa, setal areola.

In contrast, the anterior clypeal portion is truncated in *Eucatops*, *Paracatops antipoda*, Ptomaphagini and *Sciaphyes*, leaving exposed the anterior parts of the dorsal mandibular surface.

18. Frontoclypeal strengthening ridge: (0) visible externally (at least laterally, in some cases weakly impressed) (Fig. 6c: fsr); (1) not visible (Fig. 6d). Not visible in the tribes Oritocatopini, Eucatopini, Ptomaphagini, and some subtribes of Anemadini (Eunemadina, Eocatopina, Nemadina) and Cholevini (Catopina, except *Rybinskiella*). Among outgroups, the frontoclypeal strengthening ridge is not recognizable externally in Catopocerinae and Platypsylliinae, and this condition also occurs within Camiarinae (*Camiarus*) and Leiodinae (*Colenisia* and *Zeadolopus*).
19. Head shape: (0) without transverse border abutting the anterior pronotal edge (Fig. 6e); (1) with transverse border abutting the anterior pronotal edge (Fig. 6f). A characteristic configuration of Cholevinae is the posterodorsal contour of the exposed part of the head abutting with the anterior pronotal edge, both appearing closely connected. In most leptodirines, however, this feature is missing, presumably linked with other morphological changes related to subterranean habits. Platypsyllines display a similar cephalic shape, although with a slight overlapping of the head over the anterodorsal pronotal edge. The condition found in Platypsyllinae probably represents an independent gain.
20. Elevated transverse occipital ridge: (0) absent (Fig. 6g); (1) present (Figs 6h, 7b: or). The posterodorsal border of the head capsule bears a distinct transverse occipital ridge in Anemadini (except *Paracatops antipoda*), Cholevini and Ptomaphagini. It extends posteriorly, partially covering the neck region in dorsal view. The occipital ridge is usually more easily visible in lateral and ventral view. A similar condition is present in *Leptinus*.
21. Posterior face of compound eye: (0) not covered by genal fold, head not abruptly narrowed immediately behind eyes (Fig. 7a); (1) covered by genal fold, head abruptly narrowed immediately behind eyes (Figs 6h, 7b: pogf). A conspicuous genal fold covers the posterior face of the compound eyes in Cholevinae, although it is missing in many eyeless Leptodirini. The postocular genal fold generally distinguishes cholevines from most other leiodid taxa, but a similar condition occurs in Platypsyllinae, even though the eyes are lacking. The co-occurrence of this feature in other staphyliniform groups such as Hydraenidae (Jäch et al., 2000; Beutel et al., 2003) and within Hydrophiloidea (Beutel, 1994; Beutel et al., 2001; Anton and Beutel, 2004) is probably due to parallel evolution.
22. Antennal insertion: (0) visible from above (Fig. 7d); (1) not visible from above (Fig. 7c). The antennal insertion is concealed from above in the Camiarinae and all Leiodinae examined. Newton (1998) considered this feature as a potential synapomorphy uniting both subfamilies. A similar condition was observed in *Leptinus*, although not as distinct as in the other groups.
23. Size of the second club segment in relation to the first and third: (0) subequal; (1) smaller (e.g. Newton, 1998; fig. 7). The interrupted antennal club is characteristic of Leiodidae. It has been used as a morphological argument supporting the monophyly of the family (Newton, 1998, 2016), even though with reversals in some species. The subfamily Coloninae lacks this feature (Newton, 1998). In some cases the reduction of the second club segment may be very subtle, as in *Nargiotes*. The club may be weakly defined in some groups, as in the antennae of some leptodirines. The second club segment generally corresponds with antennomere 8 of the 11-segmented antenna. A periarticular gutter bearing sensilla is usually present on antennomeres 7, 9 and 10, but it is lacking on the reduced antennomere 8 (see Antunes-Carvalho et al., 2017: fig. 2f–i).

Prosternum.

24. Area anterior to procoxal cavities: (0) large (Fig. 8a); (1) strongly shortened (Fig. 8b, c). The prosternal area anterior to the procoxal cavities is strongly reduced in the majority of cholevines. The only exceptions are some highly modified leptodirines, such as *Astagobius*, *Elladoherpon*, *Leptodirus*, *Remyella*, *Speoplanes*, *Anthroherpon* and *Hadesia*. The prosternum is large in *Zeanecrophilus* and other outgroups, but shortened in most Leiodinae.
25. Ventrally directed plate: (0) absent (Fig. 8a); (1) present (Fig. 8b: vdp). A ventrally directed plate protrudes from the anterior prosternal edge in all examined species of Eucatopini, forming a precoxal coverage. This characteristic is probably autapomorphic for the tribe, as it is not recorded in any other taxa examined here.
26. Procoxal cavities: (0) open posteriorly (Fig. 8a); (1) closed posteriorly (Fig. 8b, c). The procoxal cavities are closed posteriorly in all cholevine

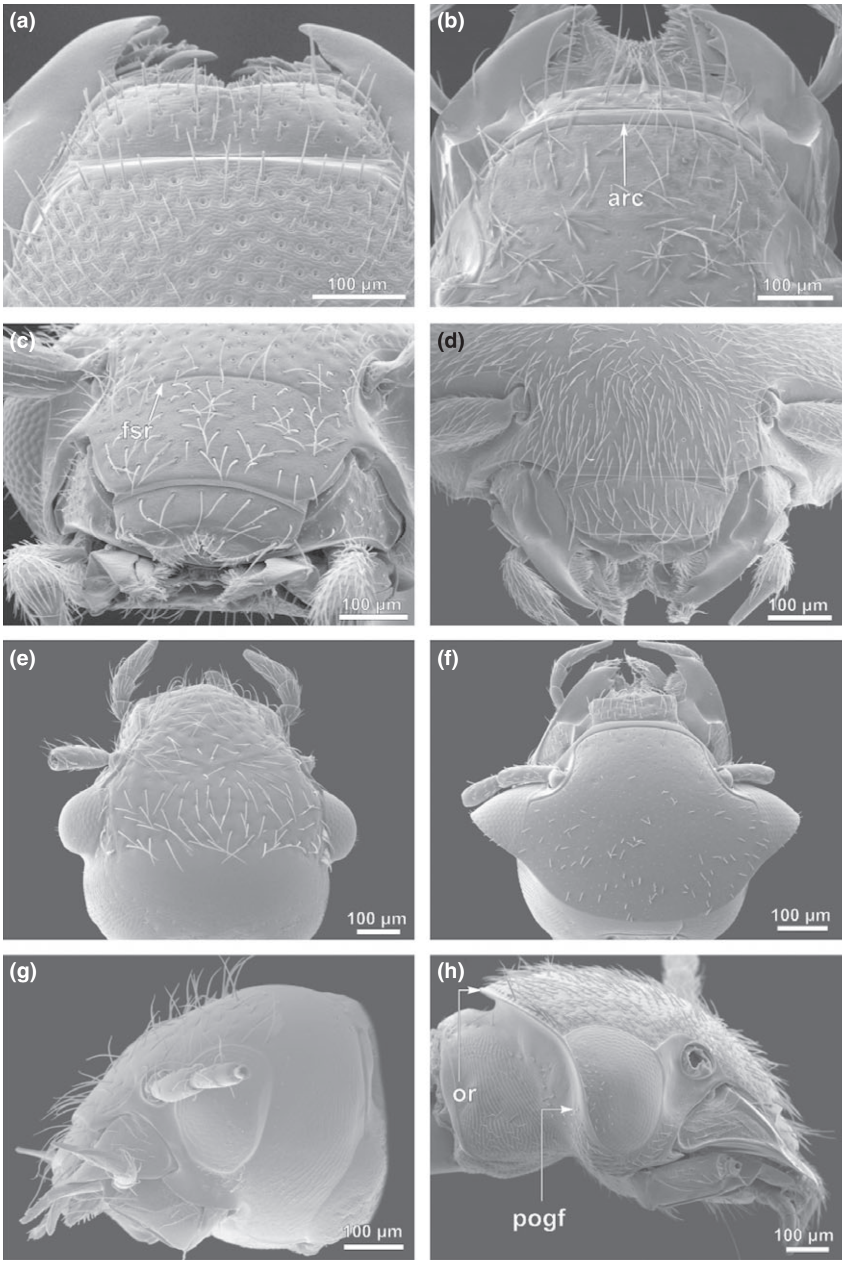

Fig. 6. Dorsal view of anterior margin of clypeus in (a) *Cholevinus fuscipes* (Cholevini) and (b) *Dellabefaela roccae* (Leptodirini). Frontal view of clypeus of (c) *Speonemadus bolivari* (Anemadini) and (d) *Ptomaphagus meximontanus* (Ptomaphagini). Dorsal view of head of (e) *Eupelates transversistrigosus* (Camiarinae) and (f) *Eucatops* sp. 1 (Eucatopini). Lateral view of head of (g) *Agyrtodes labralis* (Camiarinae) and (h) *Catops fuliginosus* (Cholevini). arc, anterior ridge of clypeus; fsr, frontoclypeal strengthening ridge; or, elevated transverse occipital ridge; pogf, postocular genal fold.

taxa, and in most camiarines and leiodines studied.

27. Postcoxal projection of hypomeron (pph): (0) acute (Fig. 8b); (1) broadly rounded or blunt (Fig. 8c). A triangular postcoxal projection of the hypomeron characterizes the prosternum of Eucatopini, in contrast to the rounded or blunt shape of this structure in the other Cholevinae. An acute projection is also present in *Prionochaeta* and, less clearly, in *Ptomaphagus meximontanus*. The acute condition is found in most outgroup taxa.
28. Lateral opening of procoxal cavity: (0) horizontal (Fig. 8c: lopc); (1) oblique (i.e. pointing anterolaterad; Fig. 8b). The lateral slit of the procoxal openings is transversely oriented in the

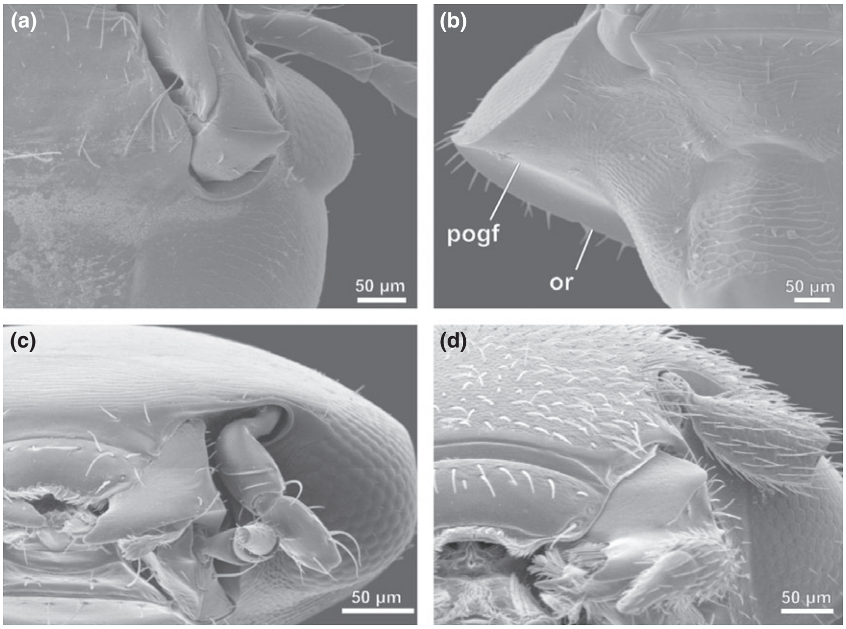

Fig. 7. Partial ventral view of head of (a) *Agyrtodes labralis* (Camiarinae) and (b) *Ptomaphagus sericatus* (Ptomaphagini). Partial frontal view of head of (c) *Colenisia zelandica* (Leiodinae) and (d) *Eocatops ophidianus* (Anemadini). or, elevated transverse occipital ridge; pogf, postocular genal fold.

majority of taxa studied, but not in Eucatopini, Oritocatopini and Ptomaphagini. The procoxal slit is obliquely oriented in all members of these tribes, a characteristic previously not recorded in the literature.

29. Posterior margin of prosternal process: (0) without median notch (Fig. 8c); (1) with acute, short median notch (Fig. 8b: mnp). An acute median notch is present at the posterior prosternal margin of *Eucatops*, Ptomaphagini, most Leptodirini, *Sciaphyes* and some representatives of Anemadini. It is absent in Cholevini and Oritocatopini. This character is not applicable in cases where the procoxal cavity is open posteriorly (Ch26(0)).

Meso- and metaventrite.

30. Mesothoracic anapleural suture [i.e. suture between mesanepisternum (mset) and mesoventrite (msv)]: (0) visible externally on cuticular surface (e.g. Fig. 9a, c, d); (1) not visible externally on cuticular surface (Fig. 9b). Visible on the external cuticular surface between the mesanepisternum and mesoventrite in the majority of cholevine taxa. The suture is indistinct externally in *Afrocatops*, *Astagobius*, *Leptodirus* and *Speoplanes*. It is scarcely visible in some outgroup taxa, and absent in *Catopocerus*, *Leptinus*, and some members of Camiarinae and Leiodinae.
31. Mesothoracic anapleural suture: (0) complete (e.g. Fig. 9a, c, d); (1) incomplete (Fig. 9e, f). Not applicable if the suture is not visible on the cuticular surface (Ch 30(1)). This suture starts at the anterolateral corner of the mesocoxal cavities and usually follows an oblique line until it reachs (or almost) the posterior limits of the prepectus in many studied taxa. However, the suture is incomplete (i.e. shorter, does not extend until the prepectus base) in Ptomaphagini, *Sciaphyes* and Leptodirini examined (with a few exceptions).
32. Mesothoracic pleural suture [i.e. suture between mesanepisternum (mset) and mesepimeron (msp)]: (0) visible externally on cuticular surface (e.g. Fig. 9c, e); (1) not visible externally on cuticular surface (Fig. 9a, b, d). Not visible on the external cuticle in Eucatopini, Oritocatopini, Eunemadina, Paracatopina, Sciaphyini and a few Leptodirini. In some cases the suture is visible as a dark line below the cuticle, but without any external trace. It is also missing as an external furrow in Catopocerinae, Platypsyllinae, and some members of Camiarinae and Leiodinae.
33. Mesothoracic pleural suture: (0) oblique (i.e. pointing anterolaterad; Fig. 9c, f); (1) approximately horizontal (Fig. 9e). The suture starts at the anterolateral corner of the mesocoxal cavities and generally follows a nearly straight oblique line towards the anterolateral corner of the mesothorax. However, it is more laterally

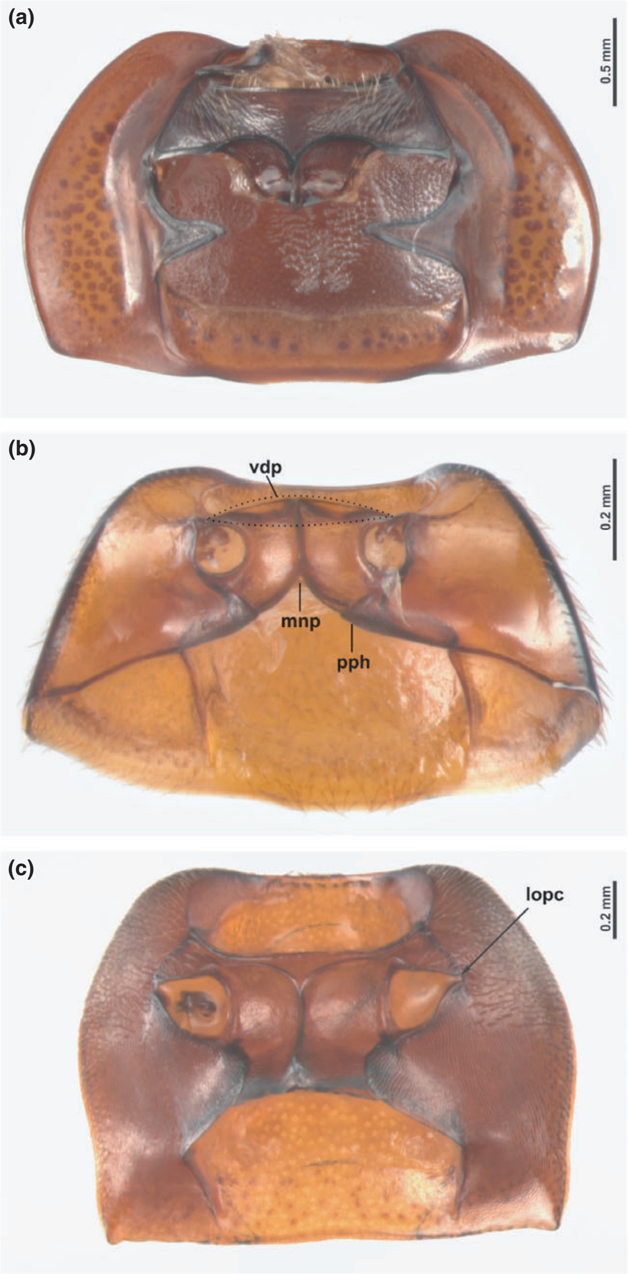

Fig. 8. Protorax, ventral view. (a) *Zeanecrophilus prolongatus* (Agyrtidae). (b) *Eucatops* sp. 2 (Eucatopini). (c) *Rybinskiella magnifica* (Cholevini). lopc, lateral opening of procoxal cavity; mnp, medial notch of the prosternal process; pph, postcoxal projection of hypomeron; vdp, ventrally directed projection of the prosternum.

oriented in Ptomaphagini. The character is not applicable if the suture is not visible externally (Ch32(1)).

34. Posterolateral edge of mesepimeron (msp): (0) not projecting posteriad, lateral portion of the posterior mesepimeral margin slightly curved anterolaterad (Fig. 9d); (1) projecting posteriad, extending to slightly concave posterior mesepimeral margin (Fig. 9f). The posterior margin of the mesepimeron is usually transverse or very slightly concave in Eucatopini, Oritocatopini, Ptomaphagini, Sciaphyini and many Leptodirini. The lateral portion of the posterior mesepimeral margin may be faintly curved downwards in these groups, resulting in a posterolateral corner slightly projecting posteriad. A different condition occurs in Anemadini and Cholevini (except in *Prionochaeta*). In these taxa the posterior mesepimeral margin is generally oblique, with its lateral portion usually curved anterolaterad.
35. Posteromesal corner of mesepimeron (msp): (0) not forming acute angle (Fig. 11a); (1) forming distinct acute angle (Fig. 11b: pcm). The mesal edge of the mesepimeron is often characterized by a distinct narrow plate, usually subtriangular, with an acuminate posterior extension. An acute angle is formed in Oritocatopini, Eucatopini, Ptomaphagini, Sciaphyini and Leptodirini, and is also present in *Speonemadus* and *Colenisia*.
36. Posterior margin of mesepimeron (msp): (0) not bifurcated (Fig. 9e); (1) bifurcated, with two diverging lines (Fig. 9f). A distinct line originates from the posterior mesepimeral margin of some leptodirines. The margin appears bifurcated.
37. Anterior edge of mesoventrite (msv) at midline (Lawrence et al., 2011: Ch163): (0) approximately on same plane as metaventrite (i.e. mesoventral process not projecting ventrad; e.g. Fig. 9); (1) on distinctly different plane than metaventrite (i.e. mesoventral process projecting ventrad; Fig. 10a). On distinctly different plane in *Colenisia*, *Decuria*, *Scotocryptus* and *Zeadolopus*.
38. Median longitudinal carina (i.e. mesoventral keel): (0) absent (e.g. Fig. 9c, d); (1) present (e.g. Fig. 9e, f: mlc). A medial longitudinal carina is found in *Agyrtodes*, *Catopocerus*, *Leptinus*, some leiodines and most subgroups of Cholevinae. It is weakly developed in Anemadini and Sciaphyini, but prominent in Eucatopini, Ptomaphagini and various Leptodirini; in the last-named tribe the structure is lacking only in highly troglobiomorphic members, probably as a consequence of the morphological specialization associated with the subterranean life. The carina is missing in species of Paracatopina and Cholevini under consideration (weakly indicated in *Cholevinus*).
39. Mesocoxal cavities: (0) separated (e.g. Figs 9a, e, 11b); (1) contiguous (Figs 9c, d, 11a). Contiguous mexocoxal cavities occur in all

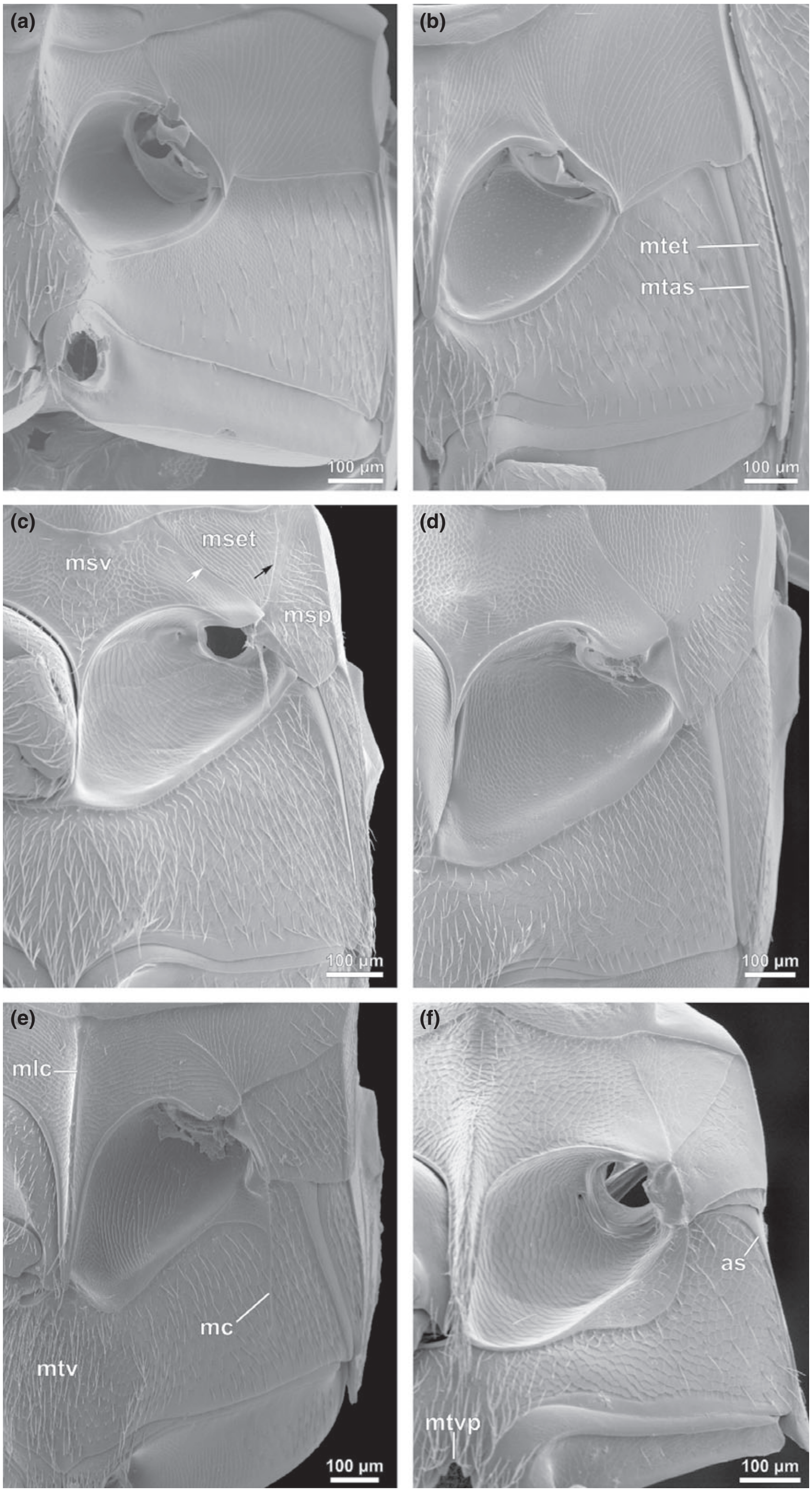

Fig. 9. Pterothorax, ventral view. (a) *Eucatops* sp. 2 (Eucatopini). (b) *Afrocatops* (Oritocatopini). (c) *Sciodrepoides watsoni* (Cholevini). (d) *Paracatops antípoda*. (e) *Ptomaphagus sericatus* (Ptomaphagini). (f) *Oryotus schmidti* (Leptodirini). The white arrow indicates the mesothoracic anapleural suture. The black arrow indicates the mesothoracic pleural suture. mtas, metathoracic anapleural suture; mc, metaventral carina; mlc, median longitudinal carina; mset, mesanepisternum; msp, mesepimeron; msv, mesoventrite; mtet, metanepisternum; mtv, metaventrite; mtvp, metaventral process.

terminals of Anemadini and Cholevini included here, and in few representatives of Leptodirini.

40. Mesoventral process: (0) extending to middle region of mesocoxae (e.g. Fig. 9a); (1) extending beyond middle region of mesocoxae, not reaching posterior edge of mesocoxal cavities (e.g. Fig. 9e); (2) extending beyond posterior edge of mesocoxal cavities but not reaching midlength of metaventrite; (3) extending to or beyond midlength of metaventrite (Fig. 11b). The mesoventral process surpasses the middle region of the mesocoxae but does not reach the posterior limits of the mesocoxal cavities in Oritocatopini, most Ptomaphagini, *Sciaphyes* and some Leptodirini. The same applies to most Camiarinae examined. In *Baryodirus* (Perreau, 2000: fig. 2), *Ptomaphaminus*, *Proptomaphaginus* and different leptodirines, the mesoventral process extends beyond the posterior edge of the mesocoxal cavities but does not reach the midlength of the metaventrite. The mesoventral process is distinctly elongated in *Bathysciotes*, *Breuilia*, *Neobathyscia*, *Pholeuonidius* and *Quaestus*, reaching or surpassing the midlength of the metaventrite. The character is not applicable if the mesocoxal cavities are contiguous (Ch39(1)) or if the mesoventral process is completely fused to the metaventral process or metaventrite (41(3)).
41. Mesoventral and metaventral processes (modified from Lawrence et al., 2011: Ch184): (0) overlapping with metaventrite ventrad of mesoventrite (e.g. Figs 9a and 10b); (1) meeting at point or abutting; (2) fused but with a visible suture or line between them (Fig. 10a); (3) solidly fused without visible suture or line. The mesoventral process overlaps with the metaventral process or metaventrite in most studied taxa. These structures abut one another without overlap in *Scotocryptus* and *Zeadolopus*. The mesoventral process is fused with the metaventral process or metaventrite in the leptodirine genera *Albaniola*, *Speonesiotes* and *Speonomus*, and the same applies to *Dietta* and *Colenisa*, although a transverse line is visible between both structures in these two taxa. The character is not applicable if the mesocoxal cavities are contiguous (Ch39(1)).
42. Distance between mesocoxal cavities (modified from Lawrence et al., 2011: Ch180): (0) up to 1/4 of shortest diameter of coxal cavity (Fig. 9); (1) more than 3/4 of shortest diameter of coxal cavity (Fig. 10a). The mesocoxal cavities are widely separated in *Colenisia* and *Dietta* only.
43. Apex of mesoventral process (modified from Lawrence et al., 2011: Ch173): (0) acute or rounded (e.g. Figs 9a, e, and 10b); (1) truncate (Fig. 10a). Truncate only in some members of Leiodinae. Not applicable if the mesoventral process is fused to the metaventral process or metaventrite (Ch41(3)).
44. Impressions posterior to mesocoxal cavities: (0) absent (e.g. Fig. 10a); (1) present (Fig. 10b). A row of impressions is present on the metaventrite of *Hydnodiaetus* and *Camiarus*, close and parallel to the posterior edge of the mesocoxal cavities.
45. Transverse groove of metaventrite anterior to metacoxal cavity: (0) present (e.g. Fig. 9b, c); (1) absent (e.g. Fig. 9a). A transverse metaventral groove is present in front of the metacoxae of different groups of Coleoptera, including Leiodidae. The groove never crosses the midline of the metaventrite and there is no evidence that this is a remnant of the metakatepisternal suture (see Lawrence et al., 2011). It is absent in Eucatopini, Ptomaphagini, Sciaphyini and many Leptodirini. It is also indistinct externally in *Nargomorphus*, *Nargus* and *Eocatops*. Among the outgroup taxa, this feature was absent in *Leptinus*, *Catopocerus*, and some members of Camiarinae and Leiodinae.
46. Posterior edge of mesocoxal cavity: (0) not widened (e.g. Fig. 9a–e); (1) distinctly widened (Figs 9f and 11). The posterior edge of the mesocoxal cavities is characteristically widened in Leptodirini, with few exceptions. A similar condition is present in *Sciaphyes* and in members of Anemadina examined.
47. Metanepisternum (mtet): (0) distinctly visible in ventral view [i.e. metathoracic anapleural suture (mtas) distinctly visible; e.g. Fig. 9b–e]; (1) very slender or not visible (i.e. metathoracic anapleural suture indistinct or located close to the anterolateral and lateral edge of metaventrite; e.g. Fig. 9f). Very slender or not visible in ventral view in Eucatopini, Sciaphyini and Leptodirini. A similar modification occurs in *Leptinus* and in some Leiodinae.
48. Metaventral suture originating at lateral edge of mesocoxal cavity (Gnaspini, 1996: Ch 1): (0) absent (e.g. Fig. 9a–d); (1) present (Fig. 9e: mc). Present in *Eocatops*, Nemadina and Ptomaphagini, with the metaventral carina extending posteriorly to about half the length between the posterior edge of the metaventrite and the lateral edge of the mesocoxal cavity. This character is possibly linked with character 46. The condition found in *Platycholeus*, *Breuilia*, *Notidocharis*, *Pseudoboldoria, Quaestus* (Fig. 11b) and *Sciaphyes* is presumably a combination of

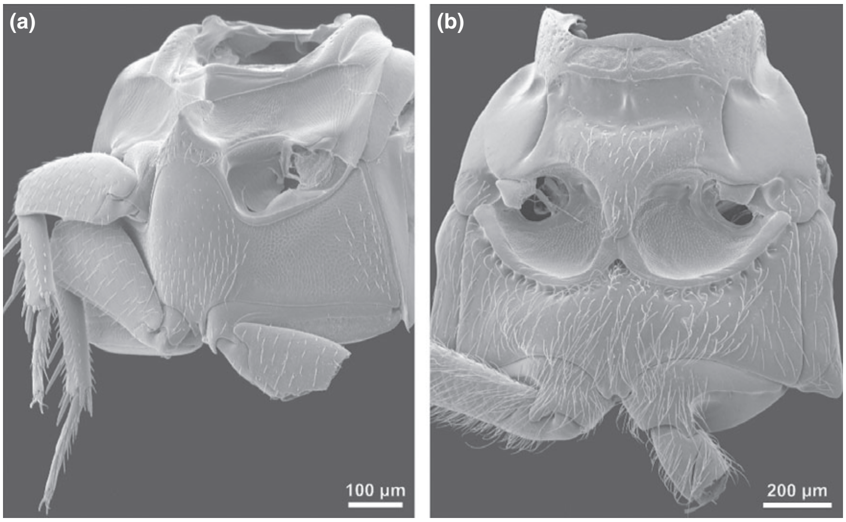

Fig. 10. Pterothorax. (a) *Colenisia zelandica* (Leiodinae), vetrolateral view. (b) *Camiarus thoracicus* (Camiarinae), ventral view.

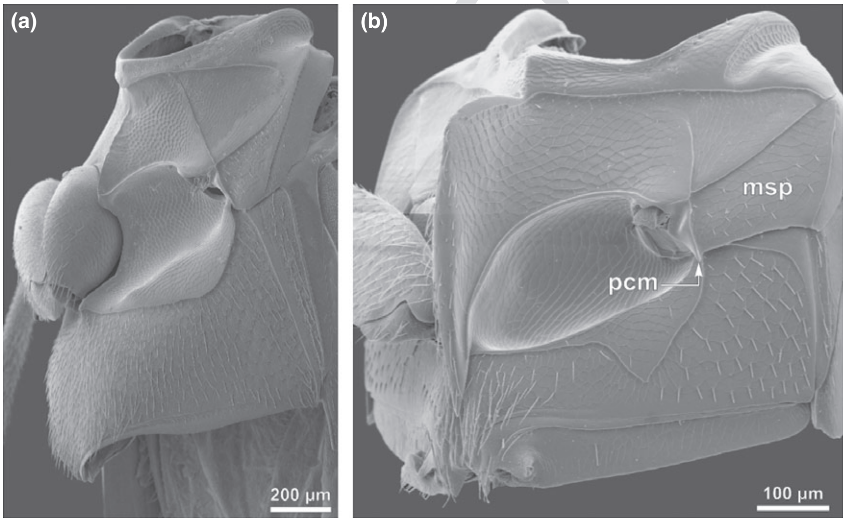

Fig. 11. Pterothorax, ventrolateral view. (a) *Anemadus acicularis* (Anemadini). (b) *Quaestus arcanus* (Leptodirini). pcm, posteromesal corner of mesepimeron.

the presence of a metaventral carina with the widening of the posterior edge of the mesocoxal cavities. This condition was coded as (1) for both characters (46 and 48).

49. Metaventral process (mtvp): (0) bifid (e.g. Fig. 9f); (1) single (e.g. Fig. 9e). The posterior intercoxal process of the metaventrite is undivided in most taxa of Cholevinae. The same condition is present in *Leptinus* and some members of Camiarinae and Leiodinae. The metaventral process is bifid in Sciaphyini and Leptodirini, resulting in a wider separation of the metacoxae. It is weakly developed in *Sciaphyes*, but distinctly elongated in *Albaniola*, *Beskovia* and *Speonesiotes*. It widely separates the metacoxae in *Anthroherpon*, *Antrosedes*, *Astagobius*, *Elladoherpon*, *Leptodirus*, *Pholeuon*, *Remyella* and *Speoplanes*. The condition found in *Hadesia* was interpreted as bifid even though the intercoxal process is very superficially emarginate medially.
50. Metaventral fovea: (0) absent; (1) present. Within our taxonomic sampling, a median setose fovea is only present on the metaventrite of *Decuria* and *Dietta*.
51. Metaventral longitudinal carina: (0) absent; (1) present (e.g. Fresneda et al., 2011: fig. 24). A median longitunidal carina extending along the metaventrite is only present in *Catopocerus* and *Sciaphyes*.

Elytra.

52. Parasutural stria: (0) absent; (1) present. Present in most tribes of Cholevinae, lacking in Sciaphyini and many Leptodirini.
53. Dorsal surface: (0) with impressed and punctate longitudinal striae (Fig. 12a, e); (1) with punctate longitudinal striae (Fig. 12b, f); (2) with transverse strigae (Fig. 12c, g); (3) without distinct striae or strigae (Fig. 12d, h). Within Cholevinae, the dorsal suface of elytra is characterized either by parallel rows of transverse strigae (with the pubescence aligned below them) or distinct striae and strigae are absent. The former pattern is present in several cholevine subgroups including many members of Anemadini, *Eucatops* sp. 1, Oritocatopini, Ptomaphagini, some Leptodirini and Sciaphyini. In Cholevini and most Leptodirini, the elytral surface is devoid of distinct striae and strigae. The same applies to *Eucatops* sp. 2, *Nargiotes* and *Nargomorphus*. This condition does also occur in Catopocerinae, Platypsyllinae and within Leiodinae. Punctate elytral striae are present in some representatives of Camiarinae and Leiodinae, while impressed punctate striae are characteristic for *Zeanecrophilus*.
54. Pubescence: (0) glabrous or with scattered short setae (Fig. 12a, b); (1) densely pubescent (Fig. 12c, d). The dorsal surface of the elytra in Cholevinae is densely pubescent, with a few exceptions within Leptodirini. Pubescent elytra do also occur in Platypsyllinae and most Camiarinae. In contrast, short scattered setae are present on the elytral surface of Catopocerinae and most Leiodinae.
55. Minute setae: (0) absent (e.g. Fig. 13d–f); (1) present (e.g. Fig. 13a–c). In addition to the macropubescence that cover the elytra of Cholevinae, very short setae are present on the elytral surface in almost all studied members of Anemadini and Cholevini; it is absent in *Paracatops antipoda* and *Rybinskiella*. Similar short setae were noticed in *Eupelates*.
56. Distribution of minute setae: (0) irregular (Fig. 13c); (1) arranged in transverse lines (e.g. Fig. 13a, b). Not applicable if the minute setae are absent (Ch55(0)). The minute setae are organized in parallel transverse rows along the elytral surface in *Cholevinus*, *Prionochaeta* and

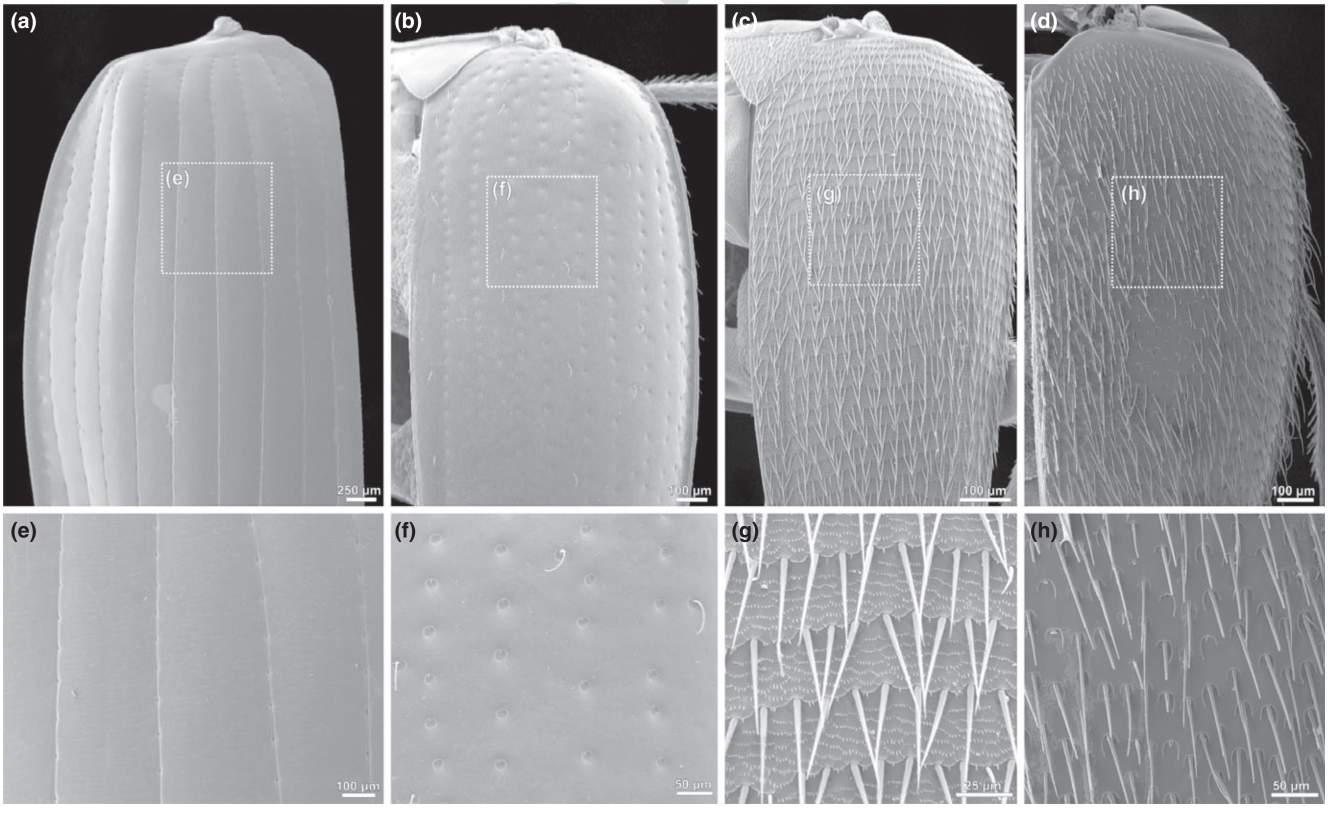

Fig. 12. Elytra, dorsal view. (a, e) *Zeanecrophilus prolongatus* (Agyrtidae). (b, f) *Neopelatops edwarsi* (Camiarinae). (c, g) *Nemadus* sp. (Anemadini). (d, h) *Eucatops* sp. 2 (Eucatopini).

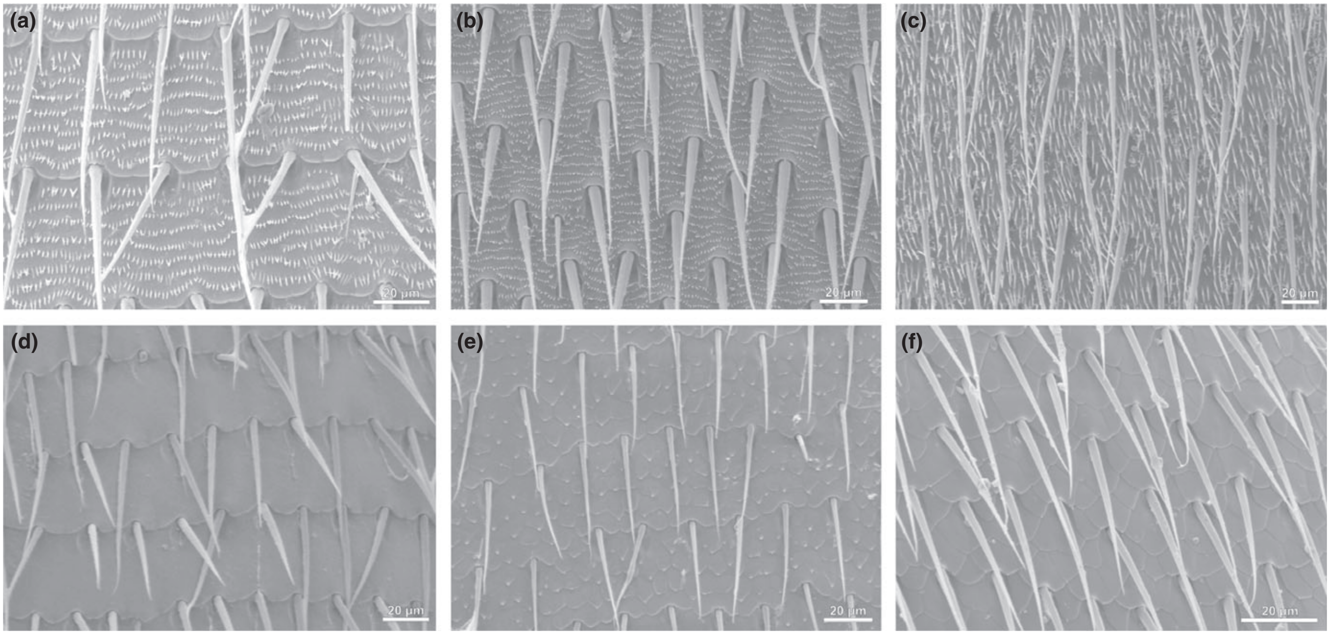

Fig. 13. Detail of elytral surface, dorsal view. (a) *Dissochaetus vanini* (Anemadini). (b) *Prionochaeta harmandi* (Cholevini). (c) *Catops fuliginosus* (Cholevini). (d) *Afrocatops* (Oritocatopini). (e) *Chappuisiotes lobeliae* (Oritocatopini). (f) *Quaestus arcanus* (Leptodirini).

most Anemadini. This condition was recorded by Fresneda et al. (2011) in *Speonemadus clathratus* as ‘transverse strioles’.

57. Minute spine-like cuticular protuberances: (0) absent (e.g. Fig. 13a, d); (1) present (Fig. 13e). Tiny spine-like cuticular protuberances emerge from the dorsal surface of the elytra in *Chappuisiotes* and a few leptodirines.
58. Dorsal surface: (0) smooth (e.g. Fig. 13d); (1) microsculptured (e.g. Fig. 13e, f). An imbricate microsculpture characterizes the dorsal elytral surface in *Chappuisiotes*, Nemadina and various Leptodirini. The elytra of *Leptinus* and *Scotocryptus* also exhibit this feature (less clearly in the latter taxon). In some cases, the microsculpture is very superficial, rendering it difficult to visualize such characteristic.

Legs.

59. Number of protarsomeres in the female (Fresneda et al., 2011: Ch11): (0) five; (1) four; (2) three. The tribe Leptodirini has been morphologically supported as monophyletic based on the reduction of the number of tarsomeres (from five to four) in the female protarsi (Jeannel, 1936; Giachino et al., 1998; Newton, 1998; Fresneda et al., 2011). All other groups of Cholevinae include females with pentamerous protarsi, except for the monotypic Baryodirina, with four protarsomeres in the single female known (Perreau, 2000). *Scotocryptus* has three tarsomeres in the female protarsi (as is the case of all Scotocryptini; e.g. Newton, 1998). Several cases of reduction in the number of tarsomeres are recorded within Leiodidae (e.g. Newton, 1998), but tetramerous protarsi are recorded only in the taxa cited above.
60. Mesotarsus of male (modified from Fresneda et al., 2011: Ch12): (0) expanded (Fig. 14a); (1) not expanded (Fig. 14b). Dilated mesotarsomeres are present in *Zeanecrophilus* and in different taxa of Leiodidae. In Cholevinae, this feature is observed within Anemadini and Cholevini.
61. Meso- and metatibial ventral spurs (modified from Fresneda et al., 2011: Ch13): (0) simple (Fig. 15a–c); (1) pectinate or multi-toothed laterally (Fig. 15d–i). Pectinate or polytoothed ventral spurs occur in most Anemadini and Cholevini, and in all Leptodirini examined except for *Platycholeus* and *Hadesia*. At a first glance, the pectinate spurs seem distinguishable from the multi-toothed condition, but continuous intermediate states occur. The pectinate condition was also documented in *Sciaphyes*.
62. Surface of meso- and metatibial ventral spurs: (0) devoid of spines (e.g. Fig. 15a, f, g, i); (1) densely covered by spines (Fig. 15d, e). In addition to the modifications of the lateral edge (see Ch61), spines along the ventral surface of the meso- and metatibial ventral spurs can occur. This condition is present in a few species within

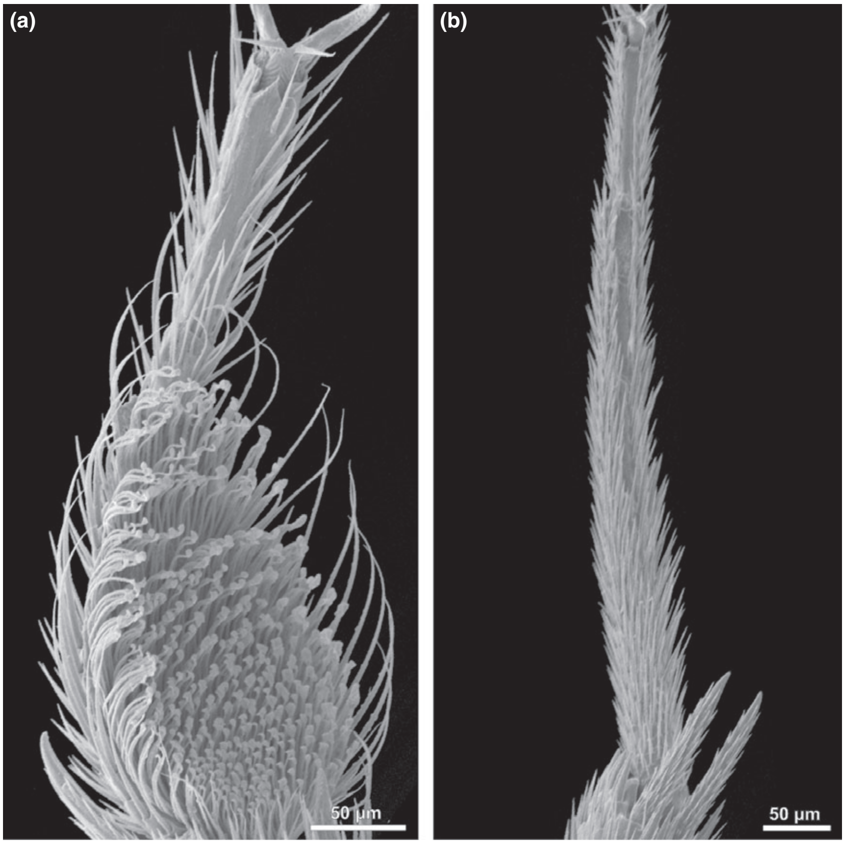

Fig. 14. Mesotarsi of males, ventral view. (a) *Falkocholeva* sp. (Anemadini). (b) *Eocatops ophidianus* (Anemadini).

Anemadini (*Eocatops*, *Falkocholeva* and *Paracatops*) and Cholevini (*Cholevinus* and *Prionochaeta*).

63. Pore plates on terminal tarsomere: (0) absent; (1) present (Fig. 16). A set of minute pore plates is present on the cuticular surface of the terminal tarsomere of Leptodirini. They were found in members of all leptodirine subtribes, except for Platycholeina and Spelaeobatina. The pore plates are mostly arranged on the lateral and dorsal surfaces of the terminal tarsomere, usually close to the base of the setae covering this distal leg segment. Similar structures were documented by Betz (2003) on the tarsi of *Stenus* (Staphylinidae). Betz (2003) showed the association of the pore plates with a unicellular gland of uncertain function, but potentially related to the tarsal adhesive performance. Mainly due to its very small size, the pore plates may be easily overlooked. Its function in leptodirines remains unknown.

Pretarsus and distal margin of the terminal tarsomere.

64. Medial projection of terminal protarsomere (modified from Antunes-Carvalho and Gnaspini, 2016: Ch1): (0) weakly developed (Fig. 17a); (1) trapezoid/triangular (e.g. Fig. 17b); (2) paired (e.g. Fig. 17c: mpp). A pair of distinct triangular projections is present at the ventral margin of the terminal tarsomere of Leptodirini, Ptomaphagini, Nemadina, *Nargomorphus* and *Nargus*. In some species, a few small teeth or a third medial projection are present at the margin between the two main projections. The terminal tarsomere bears a trapezoid/triangular process in the other leiodids examined. In contrast to these patterns, distinct projections are lacking at the distal margin of the terminal tarsomere of *Beskovia* and *Hadesia*, similar to a condition found in *Zeanecrophilus*.
65. Oblique row of spines (rsmp) of medial projection of terminal protarsomere (Antunes-Carvalho and Gnaspini, 2016: Ch2): (0) absent (e.g. Fig. 17a, c); (1) present (Fig. 17b: rsmp). A diagonal row of spines is present on the medial projection of the terminal protarsomere in at least one species of most cholevine tribes. It occurs in *Afrocatops*, *Eucatops*, Paracatopina, most Eunemadina (absent in *Nargiotes*), most Catopina (absent in *Cholevinus* and

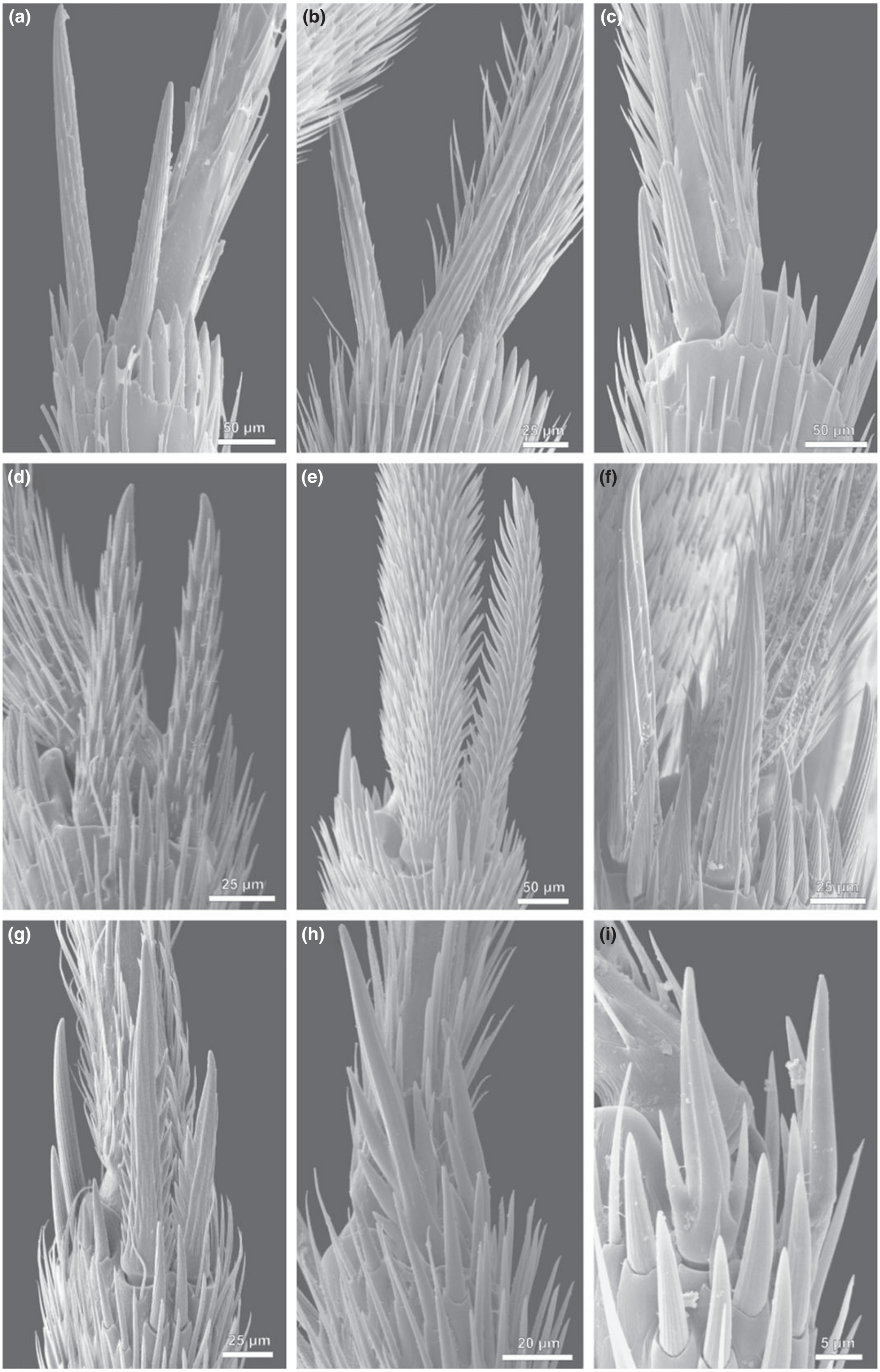

Fig. 15. Mesotibial ventral spurs. (a) *Eucatops* sp. 1 (Eucatopini). (b) *Amplexella dimorpha* (Ptomaphagini). (c) *Platycholeus leptinoides* (Leptodirini). (d) *Eocatops ophidianus* (Anemadini). (e) *Prionochaeta opaca* (Cholevini). (f) *Catops fuliginosus* (Cholevini). (g) *Dellabefaela roccae* (Leptodirini). (h) *Quaestus arcanus* (Leptodirini). (i) *Sciaphyes sibiricus* (Sciaphyini).

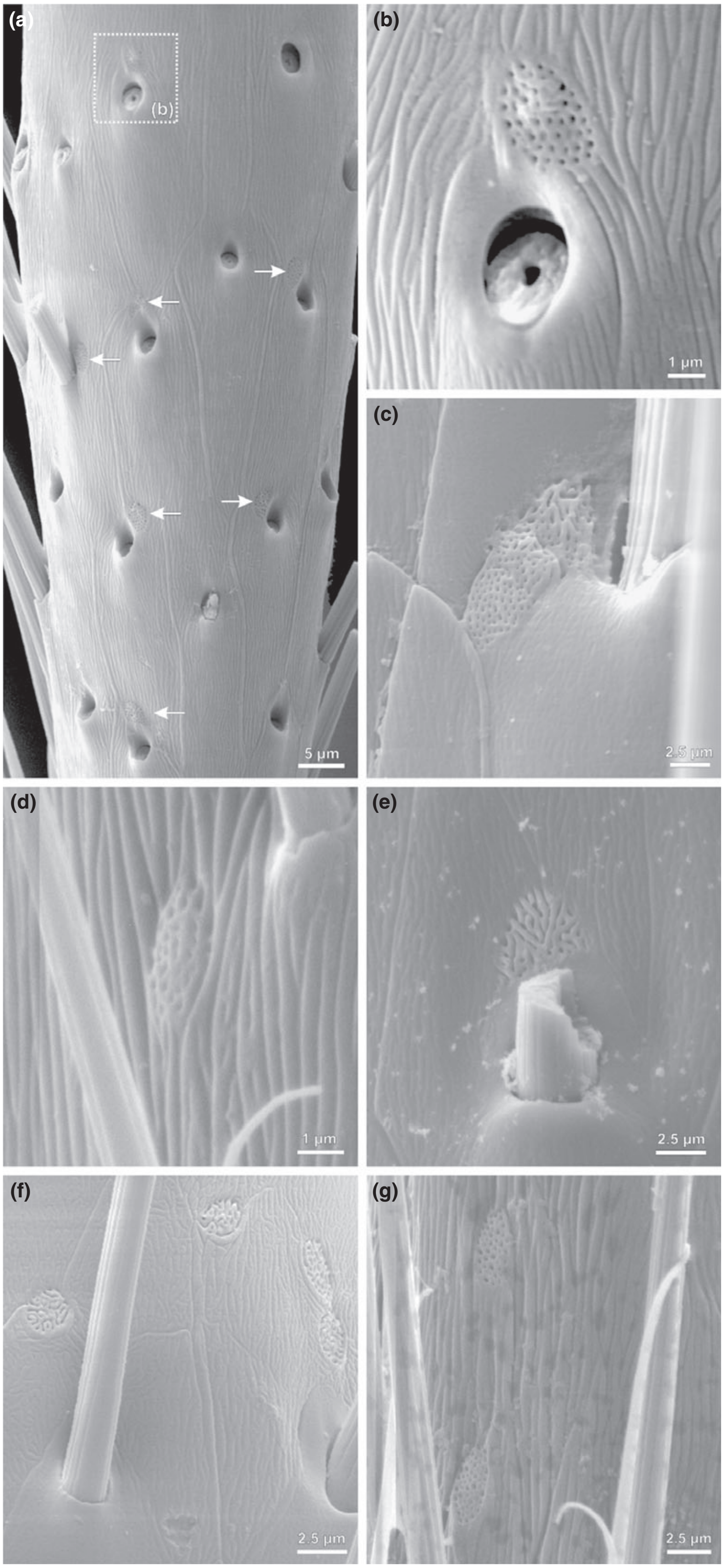

Fig. 16. Pore plates in the terminal tarsomeres of Leptodirini. (a: arrows, b) *Aphaobius milleri*. (c) *Anthroherpon hoermani*. (d) *Ravasinia lonae*. (e) *Apholeuonus longicollis*. (f) *Astagobius angustatus*. (g) *Antrocharis querilhaci*.

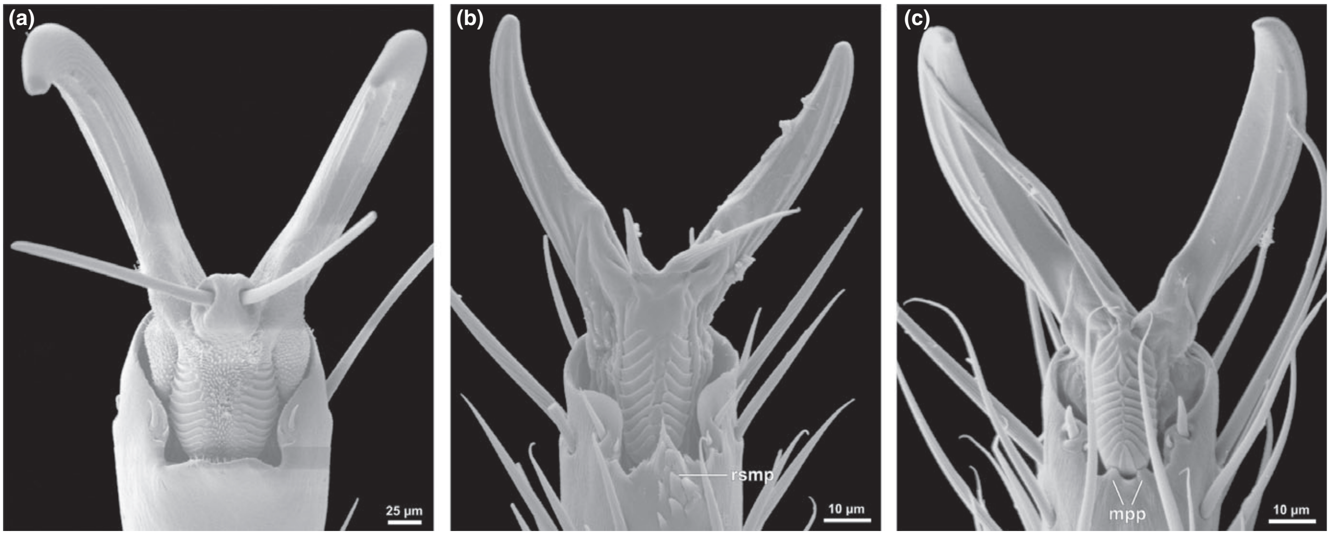

Fig. 17. Pretarsus of foreleg, ventral view. (a) *Zeanecrophilus prolongatus* (Agyrtidae). (b) *Apocatops monguzi* (Cholevini). (c) *Dellabefaela roccae* (Leptodirini). mpp, paired medial projections of the terminal tarsomere; rsmp, oblique row of spines on the medial projection of the terminal tarsomere.

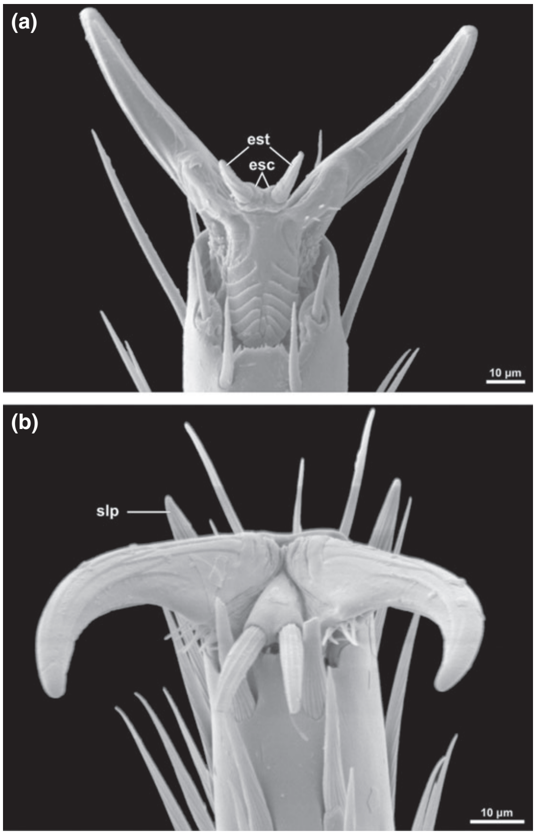

Fig. 18. Pretarsi, ventral view. (a) *Chappuisiotes lobeliae* (Oritocatopini), foreleg. (b) *Afrocatops* sp., hind leg (Oritocatopini). esc, empodial esclerite; est, empodial seta; slp, spine-like projection close to the lateral margin of the terminal tarsomere.

Rybinskiella), *Prionochaeta*, *Nemadus* (spines vertically organized) and *Ptomaphagus sericatus*. This condition also occurs within Camiarinae, in *Neopelatops*, and in *Decuria*, *Hydnodiaetus* and *Dietta* within Leiodinae. The spines are arranged as a cluster in some of these taxa, but more commonly in a row. They are lacking in Leptodirini and Sciaphyini.

66. Medial projection of terminal meso- and metatarsomere (modified from Antunes-Carvalho and Gnaspini, 2016: Ch1): (0) weakly developed; (1) trapezoid/triangular; (2) paired (mpp). The shape of the ventral margin of the terminal meso- and metatarsomere is generally similar to that of the protarsomere, with a few exceptions: the medial projection of the meso- and metatarsomere is paired in *Eucatops* sp. 2 (triangular on the protarsomere), and has a trapezoid shape in *Nargomorphus* and *Nargus* (paired on the protarsomere).
67. Oblique row of spines (rsmp) of medial projection of terminal mesotarsomere: (0) absent; (1) present. A diagonal row of spines is present on the terminal protarsomere of members of many cholevine groups, but only on the terminal mesotarsomere of *Falkocholeva*, Paracatopina and *Apocatops*. This condition is also present in the outgroup taxa *Neopelatops*, *Decuria* and *Dietta*.
68. Oblique row of spines (rsmp) of medial projection of terminal metatarsomere: (0) absent; (1) present. Only present in *Neopelatops*, *Decuria* and *Dietta*.
69. Spine-like projection close to lateral margin of terminal meso- and metatarsomere (Antunes-Carvalho and Gnaspini, 2016: Ch3): (0) absent (e.g. Fig. 19); (1) present (Fig. 18b: slp). *Afrocatops* and *Eucatops* are the only cholevine taxa

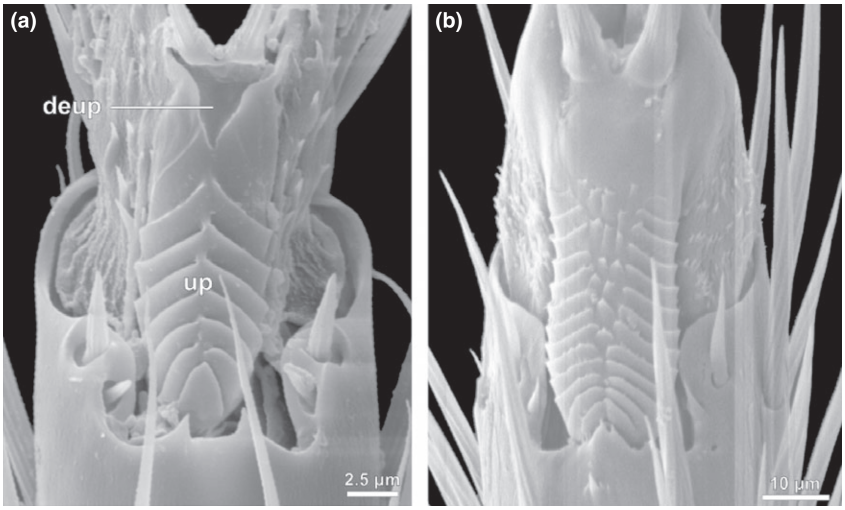

Fig. 19. Unguitractor plate of middle leg, ventral view. (a) *Parapaulipalpina* sp. (Ptomaphagini). (b) *Prionochaeta opaca* (Cholevini). deup, distal extention of unguitractor plate; up, unguitractor plate.

showing this feature. It is also present in *Decuria*, but not in the other outgroup taxa.

70. Dorsal flattened seta in the distal margin of terminal protarsomere: (0) absent; (1) present. Only present in the species of *Paulipalpina* (see Antunes-Carvalho and Gnaspini, 2016: fig. 9H: dfs).
71. V-shaped depression at distal extension of unguitractor plate (Antunes-Carvalho and Gnaspini, 2016: Ch4): (0) absent (e.g. Fig. 19b); (1) present (Fig. 19a). A medial V-shaped depression is present on the distal extension of the unguitractor plate in all members of Ptomaphagini. It extends to the base of the empodial sclerites. The distal extension of the unguitractor plate is smooth in the remaining studied cholevines and in the outgroup taxa, with the exception of *Cholevinus* and *Zeanecrophilus*, where cuticular protuberances are present.
72. Tuft of setae of empodium: (0) absent; (1) present. Only present on the empodium of species of *Paulipalpina* (see Antunes-Carvalho and Gnaspini, 2016: fig. 9J: tf).
73. Median sclerite (ms, Antunes-Carvalho and Gnaspini, 2016: Ch5): (0) not incised medially (e.g. Fig. 20a, b); (1) divided by median incisure (Fig. 20c–e). The pretarsus of Eunemadina and Paracatopina is characterized by a medial incision dividing the median sclerite. The same feature is present in *Nemadus* and *Ptomaphagus sericatus*. The median sclerite is not incised in other leiodids examined.
74. Ventral projection of empodial sclerites: (0) absent (e.g. Fig. 22g); (1) present (Fig. 22h: pesc). A ventrally directed projection is present on the empodial sclerites of *Elladoherpon*, *Parabathyscia* and *Leptinus*, dorsad of the base of the empodial setae. The projection has a pointed tip in *Elladoherpon* and *Parabathyscia*, while it is subtriangular in *Leptinus*.
75. Lateral expansion of empodial sclerites: (0) absent (e.g. Fig. 20a–d); (1) present (Fig. 20e). Laterally expanded empodial sclerites occur only in *Nargiotes* and *Nargomorphus*.
76. Connection between empodial sclerites (esc) and median sclerite (ms) (Antunes-Carvalho and Gnaspini, 2016: Ch6): (0) fused (e.g. Fig. 20b, c); (1) separated by incision (Fig. 20d, e). The empodial sclerites are fused to the median sclerite in all studied taxa, with the exception of Eunemadina and Paracatopina.
77. Connection between empodial sclerites (esc) and empodial setae (est) (Antunes-Carvalho and Gnaspini, 2016: Ch7): (0) articulated (Fig. 18); (1) at least partly fused (e.g. Fig. 20). Within Cholevinae, the pretarsi of Eucatopini and Oritocatopini are easily recognizable by the well-defined articulation between the empodial setae and empodial sclerites. This condition is also present in Agyrtidae and in the leiodid subfamilies Camiarinae, Catopocerinae and Platypsyllinae.
78. Arrangement of empodial setae (est) (Antunes-Carvalho and Gnaspini, 2016: Ch8): (0) side-by-side (e.g. Fig. 21a, b); (1) twisted (e.g. Fig. 21c, d). Two empodial setae are placed diagonally or vertically relative to one another in Old-World-Leptodirini, with the exception of Anthroherponina and *Notidocharis*, where the two empodial setae are arranged side-by-side like in all

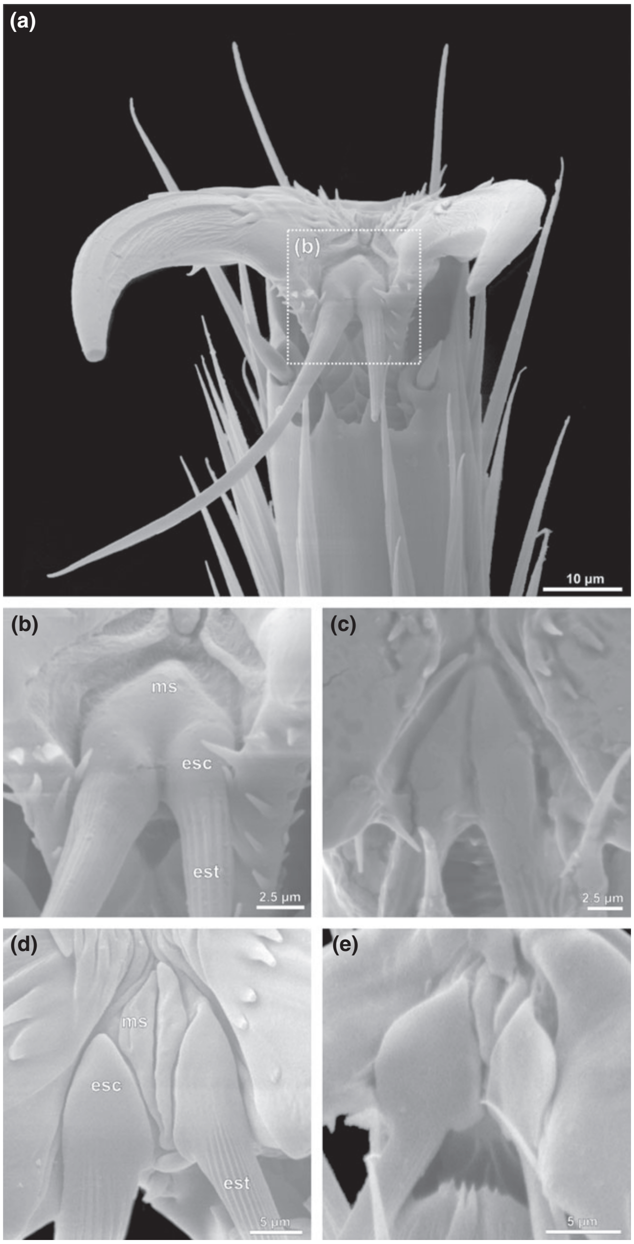

Fig. 20. Empodium. (a, b) *Adelopsis leo* sp. (Ptomaphagini). (c) *Ptomaphagus sericatus* (Ptomaphagini). (d) *Pseudonemadus cheesmani* (Anemadini). (e) *Nargiotes leptocerus* (Anemadini). esc, empodial sclerite; est, empodial seta; ms, median sclerite.

other leiodid groups examined. This character is not applicable when only a single seta is present (Ch80(1)). It is the case of *Beskovia* and the Nearctic *Platycholeus*.

79. Empodial setae (est) (Antunes-Carvalho and Gnaspini, 2016: Ch9): (0) not fused at base (e.g. Fig. 21a, b); (1) fused at base (e.g. Fig. 21c, d). Potentially related to the previous character. The empodial setae are basally fused in all Old-World-Leptodirini, with the exception of members of Anthroherponina, probably due to reversal. This derived condition is exclusively found in Leptodirini, but it is uncertain whether the fusion of the empodial setae has originated in the Palaearctic branch of the tribe, or if it is a ground plan feature of leptodirines with secondary loss of the outer empodial seta in *Platycholeus*. The character is not applicable if only a single seta is present (Ch80(1)).
80. Outer empodial seta (est): (modified from Antunes-Carvalho and Gnaspini, 2016: Ch10): (0) present, in some cases distinctly reduced but recognizable (e.g. Fig. 21); (1) absent (Fig. 22a, b). A pair of empodial setae is present in almost all species examined here. The outer empodial seta is lacking in the leptodirine genera *Platycholeus* and *Beskovia*, and within Camiarinae in *Camiarus*.
81. Outer empodial seta (est): (modified from Antunes-Carvalho and Gnaspini, 2016; Ch10): (0) normally sized (including cases of asymmetry; e.g. Fig. 21); (1) minute (Fig. 22a–h); (2) knob-like structure (Fig. 22i, j). Not applicable if the outer empodial seta is absent (80(1)). A drastic reduction of the outer empodial seta probably took place independently more than once within Cholevinae, reflecting at least two distinct morphological patterns. In Cholevina (excl. *Prionochaeta*), only a small knob-like structure is present, possibly constituting the outer empodial sclerite. Within Pholeuina, a minute, cryptic outer empodial seta occurs in eight of the 16 species studied.
82. Inner empodial seta of foreleg: (0) subcylindrical; (1) strongly flattened. Only present in *Ptomaphaminus* (see Antunes-Carvalho and Gnaspini, 2016: fig. 9L: est). This long and very strongly flattened seta, which is also present on the middle legs of *Ptomaphaminus*, is similar to the one inserted on the middle and hind legs of *Paulipalpina* and on the hind legs of *Baryodirus* (see next characters).
83. Inner empodial seta of middle leg: (0) subcylindrical; (1) strongly flattened. Present in *Ptomaphaminus* and *Paulipalpina*.
84. Inner empodial seta of hind leg: (0) subcylindrical; (1) strongly flattened. Only present in *Paulipalpina* (see Antunes-Carvalho and Gnaspini, 2016: fig. 9I, K: est) and *Baryodirus* (see Perreau, 2000: fig. 10).
85. Dorsal surface of claws: (0) scale-like (Fig. 24a); (1) grooved (e.g. Fig. 24b); (2) smooth (e.g. Fig. 24c, d). Longitudinal grooves are almost generally present on claws of cholevine taxa. However, they are missing in *Sciaphyes* and the Old-World-Leptodirini (excl. *Notidocharis*). The

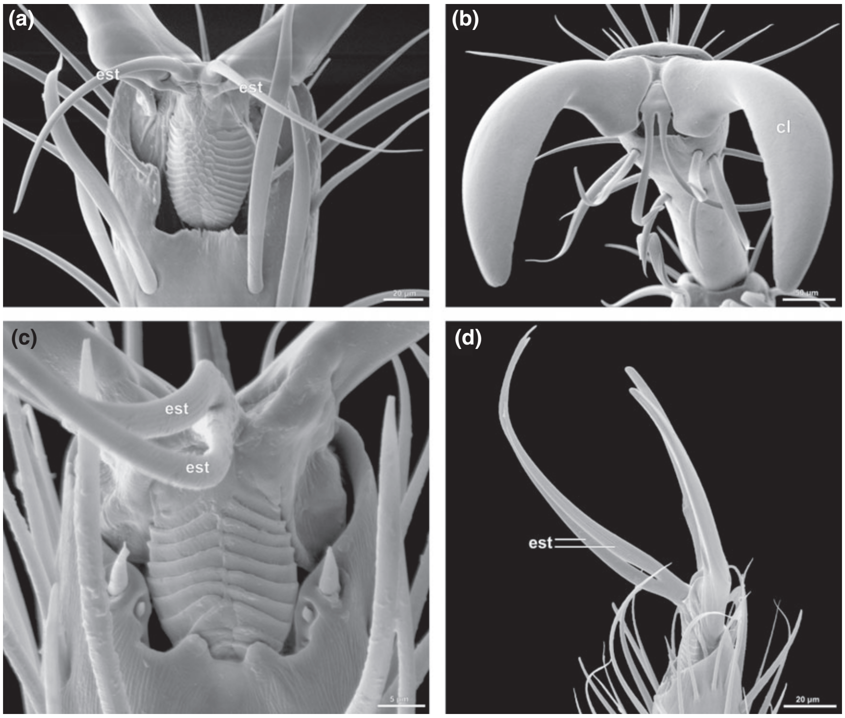

Fig. 21. Pretarsi of Leptodirini. (a, b) Ventral and frontal view of *Hadesia vasiceki*, respectively. (c) *Canavesiela lanai*. (d) *Aphaobius milleri*. cl, claw; est, empodial seta.

same applies to some outgroup taxa, such as *Camiarus*, *Catopocerus* and Leiodinae. The surface is scale-like in *Zeanecrophilus*.

86. Row of strong teeth (tc) at basolateral margin of claw (Antunes-Carvalho and Gnaspini, 2016; Ch11): (0) absent (e.g. Fig. 23b, d); (1) present (e.g. Fig. 23a: tc). The row of teeth is present in *Dissochaetus*, *Pseudonemadus* and Ptomaphaginina. Based on differences in shape and position, we consider these teeth as structures not homologous with the spines on the dorsolateral surface of the claws of Ptomaphagina, despite their superficial similarity. Based on figures provided by Perreau (2000: figs 8–10), the row of teeth also occurs in *Baryodirus*, more distinctly on the forelegs.
87. Long, lateral spines close to base of claws (sbc) (Antunes-Carvalho and Gnaspini, 2016: Ch12): (0) absent (e.g. Fig. 23a, b); (1) present (Fig. 23d: sbc). A long, ventrally projecting spine close to the basolateral margin of the claws was recently described in Cholevina (excl. *Prionochaeta*) by Antunes-Carvalho and Gnaspini (2016). Here we detected the same feature in *Sciaphyes*, possibly independently acquired. The spine is absent in all other species investigated.
88. Set of spines on dorsolateral surface of claws (slc) (Antunes-Carvalho and Gnaspini, 2016: Ch13): (0) absent; (1) present (Fig. 23b: slc). See discussion in character 86. Some thin spines (usually two) protrude from the dorsolateral surface of the base of the claws in members of Ptomaphagina. We found a similar condition in *Micronemadus*.
89. Set of small spines on dorsal surface of base of claws (sdc) (Antunes-Carvalho and Gnaspini, 2016: Ch14): (0) absent; (1) present (Fig. 23c: sdc). Small spines emerge from the dorsomedial surface near the transition zone between claws in Ptomaphagini. Similar spines were encountered in *Micronemadus*, but not in any other species treated here.
90. Transverse groove on claws (tgc) (Antunes-Carvalho and Gnaspini, 2016: Ch15): (0) absent (e.g. Fig. 24a, b); (1) present (Fig. 24c, d: tgc). The claws of *Sciaphyes* and Leptodirini are characterized by an unusual transverse groove on the dorsal surface of the proximal part, extending over about one-fifth to one-third of the entire length. Distally the claws are usually somewhat flattened and have a smooth or (less often) crenulated surface. Sometimes the groove is very shallow and scarcely visible. Among the leptodirines here included, this feature is only missing in *Platycholeus* and *Hadesia*.
91. Paired pad-like structure below claws: (0) absent; (1) present. A membranous, pad-like

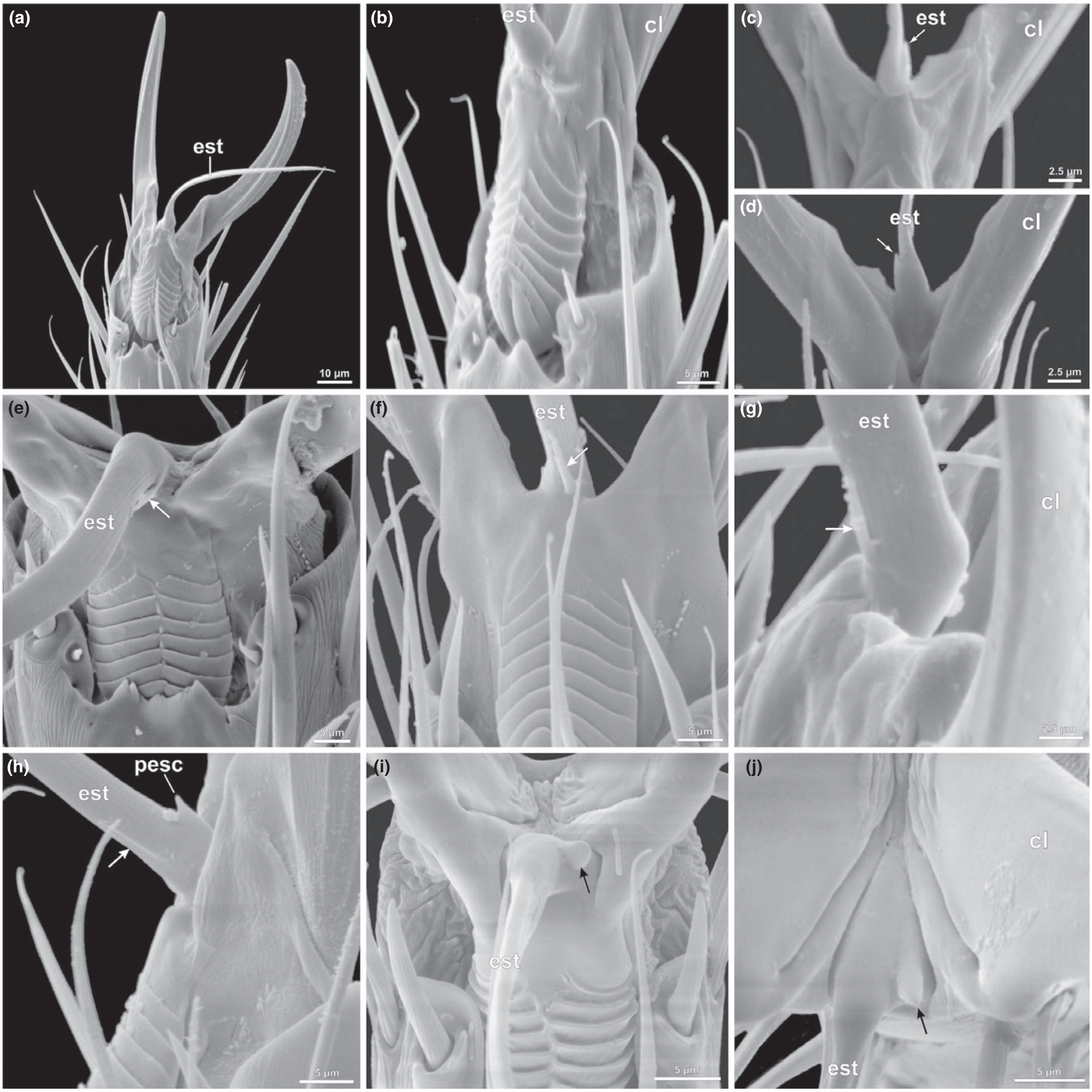

Fig. 22. Pretarsal structures. (a) Pretarsus of middle leg in *Platycholeus leptinoides* (Leptodirini), ventral view. (b) Pretarsus of hind leg in the same species, ventrolateral view. (c) Ventral and (d) dorsal view of empodial setae in *Notidocharis ovoideus* (Leptodirini). (e) Pretarsus of foreleg in *Antrocharis querilhaci* (Leptodirini), ventral view. (f) Pretarsus of foreleg in *Paratroglophyes jeanelli* (Leptodirini), ventral view. (g) Empodial setae of foreleg in *Paraspeonomus vandeli* (Leptodirini), lateral view. (h) Empodial setae of hind leg of *Parabathyscia ligurica* (Leptodirini), frontal view. (i) Ventral and (j) frontal view of pretarsus of hind leg in *Catopsimorphus orientalis* (Cholevini). White arrows (c–h) indicate the minute outer empodial seta found in some species of Leptodirini. Black arrows (i, j) indicate the characteristic knob-like structure present in most members of Cholevina. cl, claw; est, empodial seta; pesc, ventral projection of the empodial sclerite.

structure below the claws is a putative autapomorphy of *Leptinus*. The pad below the outer claw of the middle leg is somewhat reduced and not present below the outer claw of the hind legs.

Abdomen and aedeagus.

92. Longitudinal carina on first abdominal ventrite: (0) absent; (1) present. The median longitudinal carina occurs only in *Sciaphyes* (see Fresneda

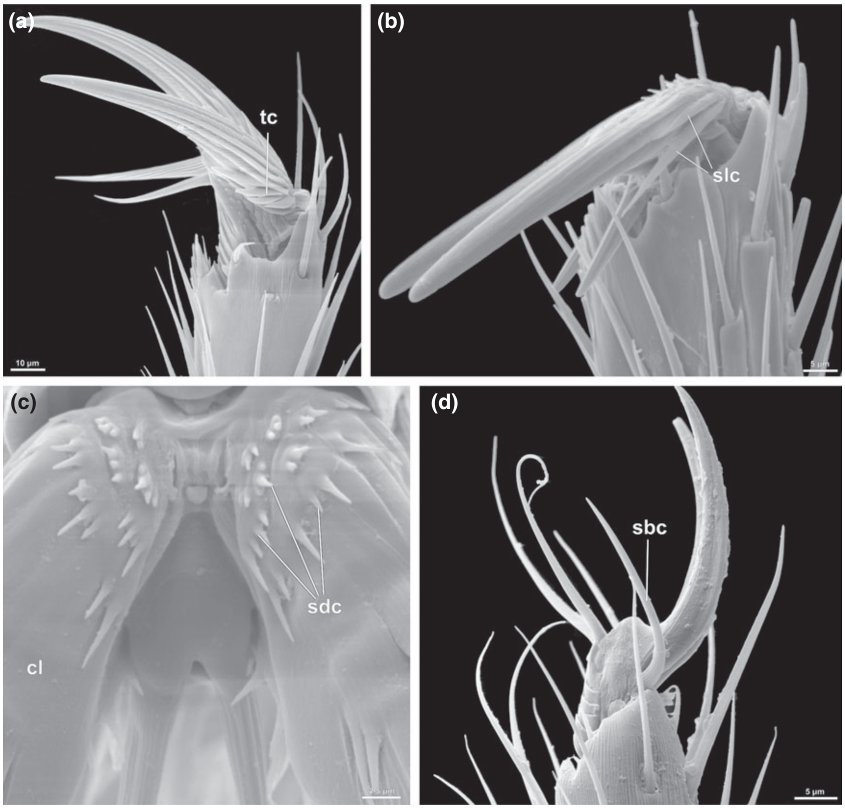

Fig. 23. Armature of claws. (a) *Pseudonemadus cheesmani* (Anemadini), lateral view, foreleg. (b) *Ptomaphagus sericatus*, lateral view, foreleg. (c) *Adelopsis leo* (Ptomphagini), frontal view, middle leg. (d) *Sciaphyes sibiricus* (Sciaphyini), lateral view, hind leg. cl, claw; sbc, lateral spines close to the base of the claws; sdc, spines on the basal dorsal surface of the claws; slc, spines on the basolateral surface of the claws; tc, row of strong teeth at the basolateral margin of the claws.

et al., 2011: fig. 20). It has been used as a diagnostic feature of the genus. The carina is aligned with the median carina extending along the meso- and metaventrite.

93. Symmetry of apical region of penis: (0) symmetric (e.g. Fresneda et al., 2011; fig. 54); (1) asymmetric (e.g. Gnaspini and Peck, 2001; fig. 7; Fresneda et al., 2011; fig. 55). Characteristically asymmetric in ptomaphagines, except *Peckena* (not studied here; see Gnaspini, 1996).
94. Basal lamina of aedeagus: (0) absent (e.g. Fresneda et al., 2011; fig. 56); (1) present (e.g. Fresneda et al., 2011: fig. 54). Present in most cholevines, from poorly to strongly developed. The basal lamina is missing in Ptomaphagini.
95. Apex of parameres (Fresneda et al., 2011: Ch 22): (0) not tapering towards acuminate apex (e.g. Fresneda et al., 2011: fig. 53); (1) tapering towards acuminate apex (e.g. Giachino and Vailati, 1987: fig. 8). The parameres of all members of Catopina are very slender, tapering towards a fine point. Not applicable if parameres are strongly reduced (e.g. *Zeanecrophilus*).
96. Parameres: (0) fused to aedeagus (e.g. Fresneda et al., 2011: figs 55, 56); (1) free, not fused to aedeagus (e.g. Fresneda et al., 2011: figs 53, 54, 57). The male copulatory apparatus of Ptomaphagini is characterized by parameres firmly attached to the entire length of the wall of the aedeagus. The parameres are free in the other species. Not applicable if parameres are strongly reduced (e.g. *Zeanecrophilus*).
97. Ventral lamella of tegmen (modified from Fresneda et al., 2011: Ch 25): (0) present (e.g. Fresneda et al., 2011: figs 8, 10); (1) absent (e.g. Gnaspini, 1996: figs 60, 61). The tegmen of most leiodids is formed by a ventral lamella surrounding the penis as a hyaline band. The length of this structure varies among taxa, from weakly developed (e.g. Anemadina, *Micronemadus* and several leptodirines) to very large (e.g. *Nemadus* and Sciaphyini). It is potentially homologous to the 'basal piece' of *Zeanecrophillus*. The ventral lamella is lacking in Eucatopini, Paracatopina and Ptomaphagini.

Phylogenetic analysis

The heuristic search with equal weights of characters yielded 843 most parsimonious trees of 438 steps, with

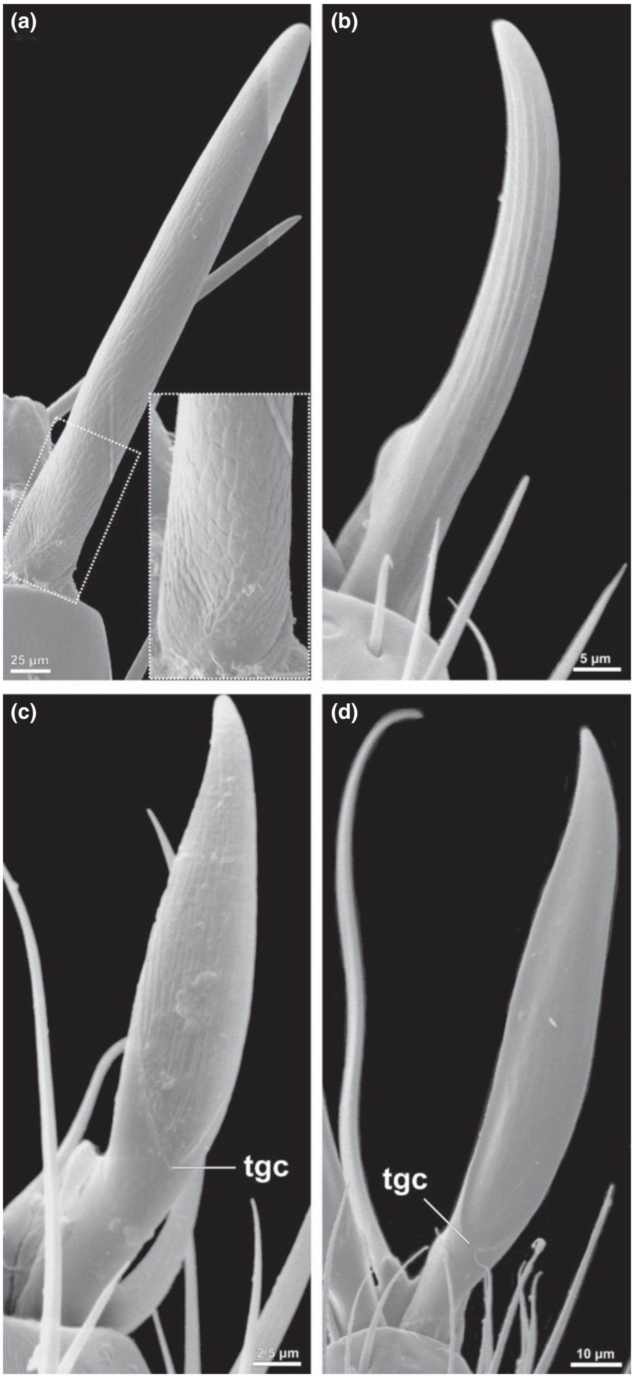

Fig. 24. Claws, dorsal view. (a) *Zeanecrophilus prolongatus* (Agyrtidae), foreleg. (b) *Platycholeus leptonoides* (Leptodirini) middle leg. (c) *Sciaphyes sibiricus* (Sciaphyini), middle leg. (d) *Paratroglophyes jeanelli* (Leptodirini), middle leg. tgc, transverse groove in the claw.

a consistency index (CI) of 0.25 and a retention index (RI) of 0.80. The strict consensus tree (CI 0.21, RI 0.75) with Bremer support values for each branch is shown in Fig. 25. Most nodes received low nodal support. Cholevinae was recovered as monophyletic and sister to *Agyrtodes*. Oritocatopini plus Eucatopini were recovered as sisters to the remaining Cholevinae, with *Eucatops* nested within Oritocatopini. Within Cholevinae minus Eucatopini + Oritocatopini, Eunemadina was recovered as a polyphyletic assemblage of four individual branches placed in a polytomy with the rest of the taxa. Paracatopina was sister to *Falkocholeva*. Anemadina was recovered as a sister group of Cholevini, the latter monophyletic with the exclusion of *Cholevinus*. Catopina and Cholevina were almost mutually monophyletic, except for the exclusion of *Cholevinus* from the former and of *Prionochaeta* from the latter. The grouping of Cholevini (*Cholevinus* excluded) plus Anemadina was placed in a trichotomy containing *Cholevinus* and a broad clade comprising the rest of Cholevinae. Within this clade, Ptomaphagini was monophyletic, as well as its constituent subtribes Ptomaphagina and Ptomaphaginina. Leptodirini was monophyletic except for the inclusion of *Sciaphyes*, which formed a trichotomy with *Platycholeus* and the Old World Leptodirini. The grouping Ptomaphagini + Sciaphyini + Leptodirini was placed in a trichotomy with *Micronemadus* and *Nemadus*, and this entire clade was recovered as sister to *Eocatops*. The additional analysis including *Baryodirus* recovered this genus within Ptomaphagini and close to *Proptomaphaginus* and *Ptomaphaminus* (i.e. inside Ptomaphaginina; see Supporting Information, Appendix S2).

The implied weighting analysis resulted in 76 most parsimonious trees. The strict consensus tree depicted in Fig. 26 is mostly compatible with that obtained with equal weighting. Major topological differences are: (1) the inclusion of *Leptinus* within Cholevinae as sister to the clade comprising all cholevine taxa minus Oritocatopini + Eucatopini; (2) the recovery of Eunemadina as monophyletic (with Paracatopina included); and (3) the change of position of Anemadina, *Prionochaeta* and *Cholevinus*. Furthermore, Sciaphyini was placed as sister to Leptodirini. Therefore, the latter tribe was found to be monophyletic, with *Platycholeus* as the sister taxon of all Old World leptodirines. As in the equal weighthing analysis, most nodes were weakly supported; as a whole, nodes with high support in the previous analysis had similarly strong support under implied weighting.

The overall topology obtained with the Bayesian approach (Fig. 27) was largely in agreement with the results of the parsimony analyses. Main topological changes in relation to the equal weighting analysis include: (1) the placement of *Rybinskiella* and *Prionochaeta* in a polytomy containing Catopina (*Rybinskiella* excluded) and Cholevina (*Cholevinus* and *Prionochaeta* excluded); (2) the collapse of the node that in the parsimony analysis supported the sister-group relationship between Ptomaphagini and Sciaphyini + Leptodirini; and (3) the position of *Sciaphyes*,

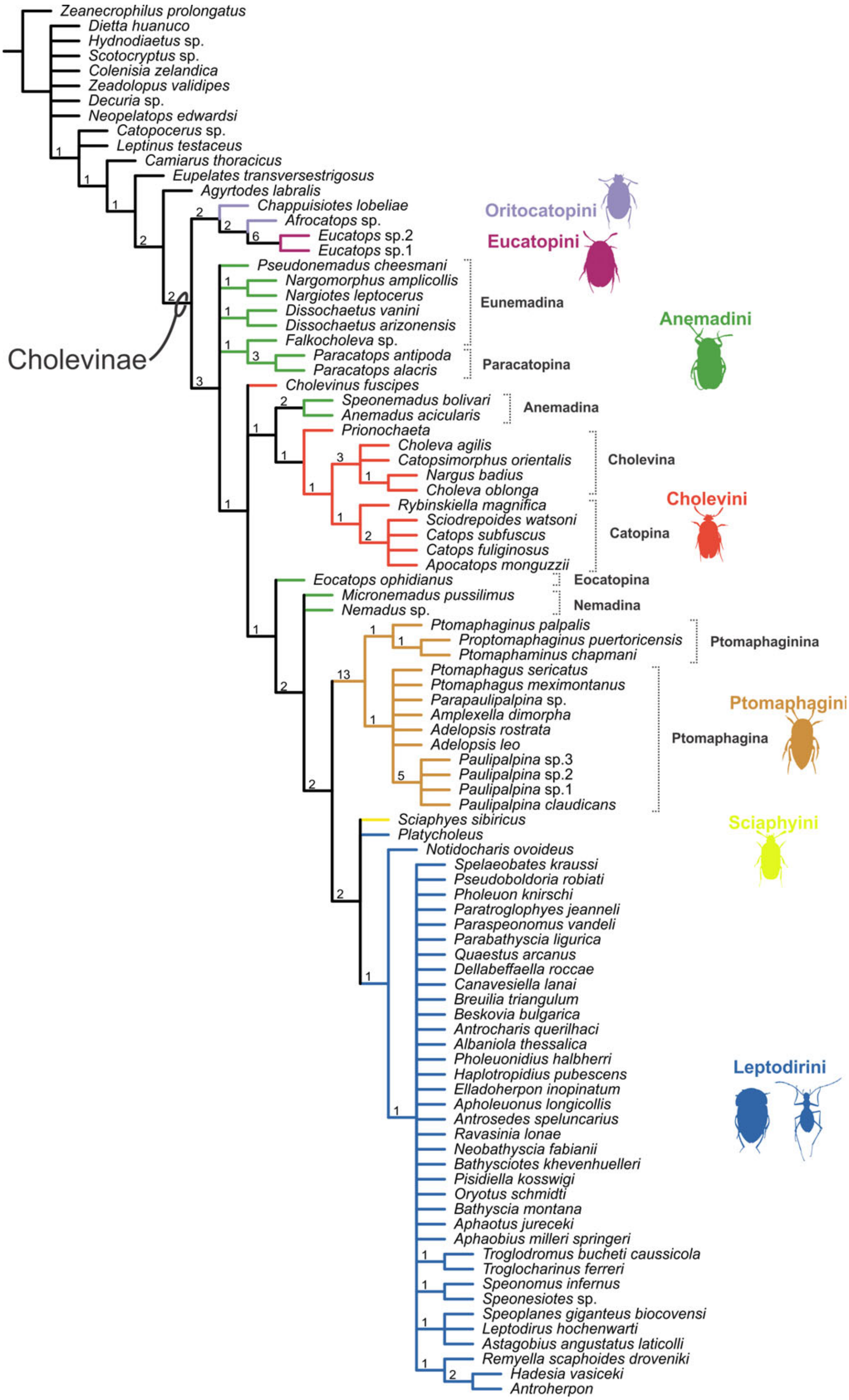

Fig. 25. Strict consensus tree derived from the parsimony analysis with equal weights. Node values represent Bremer support. Colours in tree correspond to tribes of Cholevinae: purple = Oritocatopini, pink = Eucatopini, green = Anemadini, red = Cholevini, brown = Ptomaphagini, yellow = Sciaphyini, blue = Leptodirini.

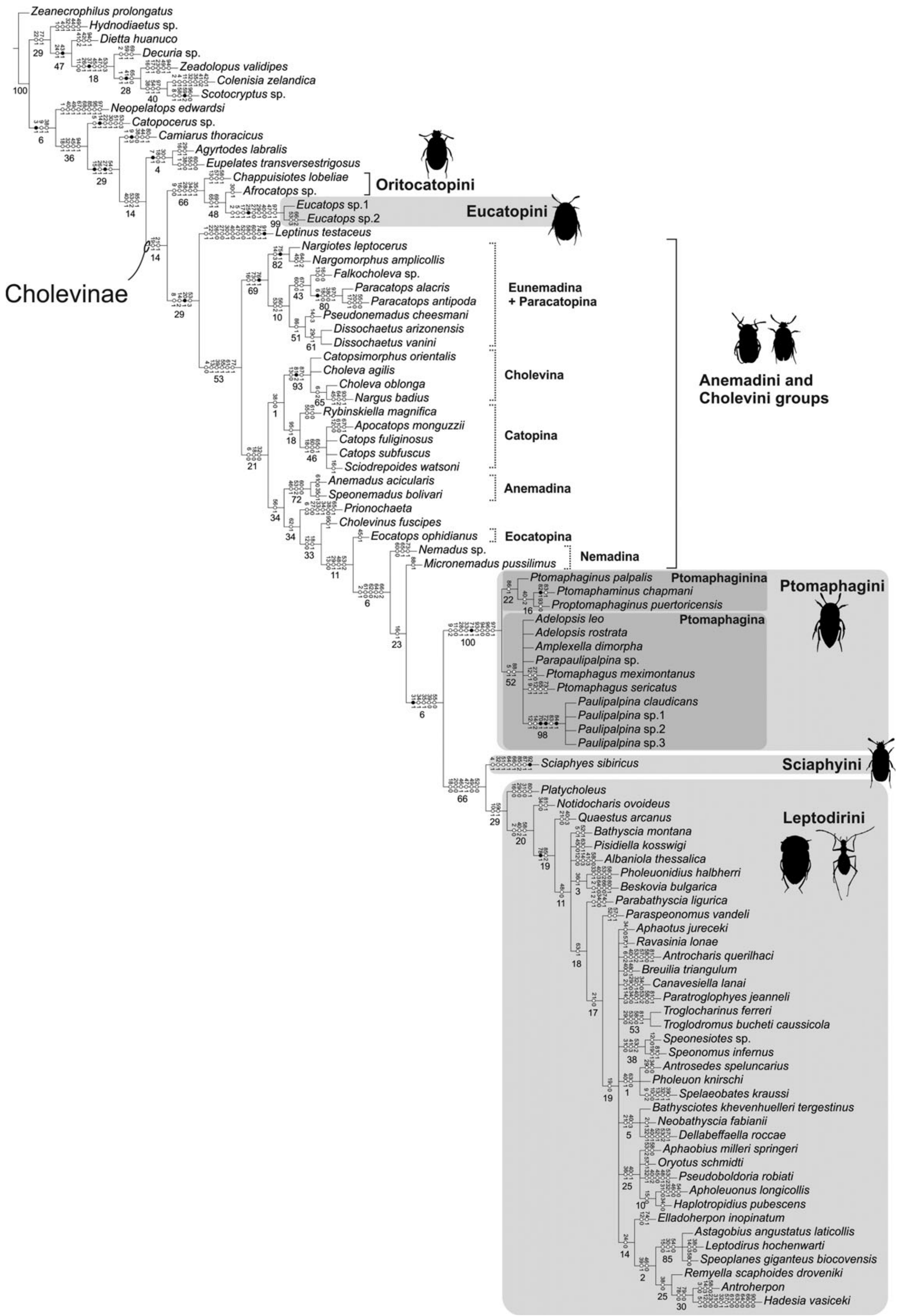

Fig. 26. Strict consensus tree derived from the parsimony analysis with implied weights. Node values indicate the frequency of GC groups derived from symmetric resampling. Non-homoplastic changes in character states are represented with black circles, homoplastic changes with white circles.

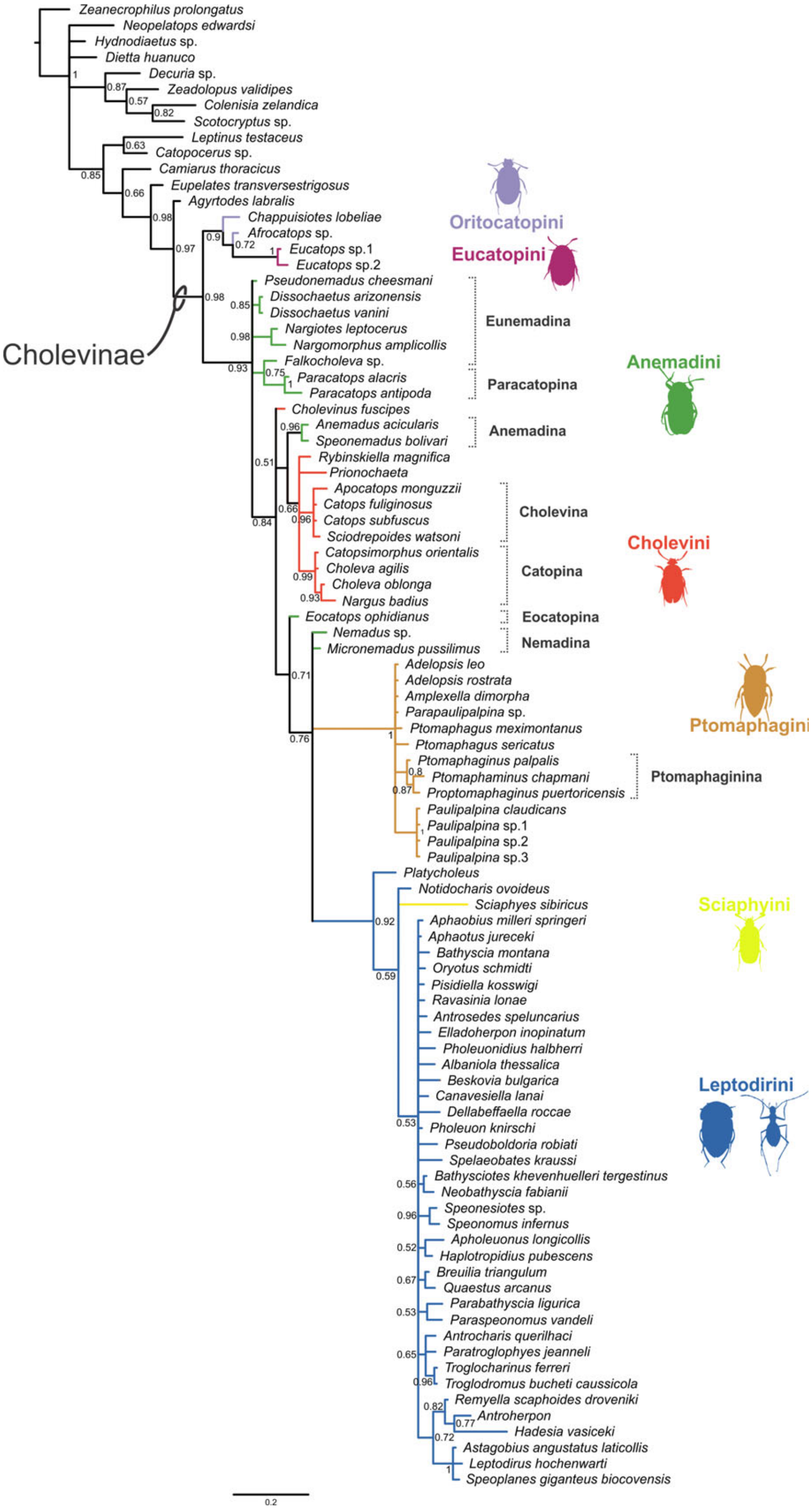

Fig. 27. Majority consensus rule tree obtained in the Bayesian analysis. Numbers on nodes are posterior probabilities (nodes with a $P < 0.5$ are collapsed). Colours in tree correspond to tribes of Cholevinae (as in Fig. 25).

which was retrieved within Leptodirini and placed in a trichotomy containing *Notidocharis* and the rest of the Old World leptodirines. Nodal support values are shown in Fig. 27.

Discussion

The monographic work of Jeannel (1936) was probably the first to address cholevine systematics with a phylogenetic scheme of argumentation. Since then multiple hypotheses of suprageneric relationships have been postulated by different authors (e.g. Perreau, 1989; Giachino and Vailati, 1993; Giachino et al., 1998; Newton, 1998, 2016), in some cases producing contrasting classifications. The presently most widely accepted arrangement of the subfamily was proposed by Newton (1998), who also provided a diagram of inferred relationships using morphological characters. However, none of these efforts was based on a formal, i.e. numerical, cladistic approach. In recent years, higher-level relationships in Cholevinae were addressed in two studies based on molecular data. However, they were either addressing more inclusive taxa (McKenna et al., 2015), thus undersampling several leiodid lineages, or focused on individual tribes (Fresneda et al., 2011).

With the data set presented in our study, with all presently described suprageneric taxa included, a formal phylogenetic investigation of Cholevinae is possible for the first time. Aside from the monophyly of the subfamily, the higher-level interrelationships and the systematic validity of tribes and subtribes are of principal interest. Many of the relationships recovered by our analyses are consistent with recent phylogenetic studies (Fresneda et al., 2011; McKenna et al., 2015) and with the earlier hypotheses based on informal evaluations of morphological characters (e.g. Jeannel, 1936; Giachino et al., 1998; Newton, 1998). However, some findings were unexpected and will be discussed in the following.

Monophyly of Cholevinae

All analyses corroborated Cholevinae as a monophylum, except for the surprising inclusion of *Leptinus* in the topology with implied weights (Figs 25–27). The cholevine clade was weakly supported in the parsimony analyses, but strongly supported in the Bayesian tree. Two potential synapomorphies derived from the head capsule support the monophyly of the subfamily: the posterodorsal border of the exposed cephalic part abutting the anterior pronotal edge, and the presence of a genal fold covering the posterior part of the compound eyes. The monophyly of Cholevinae *s.s.* (i.e. excluding *Leptinus*) implies that these features have evolved independently in *Leptinus*; the second feature also occurs in other staphyliniform lineages (e.g. Hydraenidae: Jäch et al., 2000; Beutel et al., 2003; Hydrophiloidea: Beutel, 1994; Beutel et al., 2001; Anton and Beutel, 2004), also apparently resulting from an independent gain. Both cephalic characteristics are secondarily absent in several species of Leptodirini, presumably as a result of morphological changes related to subterranean habits.

The monophyly of cholevines has been challenged twice in molecular studies, implying the exclusion of *Afrocatops* in McKenna et al. (2015) and of *Eucatops* in Fresneda et al. (2011). In contrast, the monophyly was suggested by Newton (1998, 2016) based on informal evaluations of morphological characters. Potential cholevine synapomorphies pointed out by Newton (1998) are the far-reaching reduction (or even loss) of the abdominal spiracle VIII and the presence of vesicles (‘Hamann’s Organ’) on antennomeres 7, 9 and 10. However, the same features occur in non-cholevine leiodids—the former at least in Camiarinae and Coloninae, while the latter may be found within Coloninae, Leiodinae and Platypsyllinae (see e.g. Peck, 1977; Newton, 1998; Wheeler and Miller, 2005; Park et al., 2014). The elytra lacking striae and the blunt postcoxal hypomeral projection were also assessed as probable synapomorphies by Newton (1998). These interpretations were not confirmed by our analyses. The absence of elytral striae was not treated as a single character state here (see character 53), and the blunt postcoxal hypomeral projection was recovered as a synapomorphy of a more inclusive clade encompassing Cholevinae, Agyrtodini and Camiarini.

Early diverging cholevines: Oritocatopini and Eucatopini

All analyses converged upon a basal dichotomy between Oritocatopini + Eucatopini and the remaining Cholevinae (with *Leptinus* included in the implied weighting analysis; Figs 25–27). *Chappuisiotes* and *Afrocatops* form a grade with respect to *Eucatops*. Potential synapomorphies uniting these genera are the oblique lateral opening of the procoxal cavity, a slightly concave posterior mesepimeral margin and a distinct acute angle formed by the posteromesal mesepimeral corner. A close relationship between Eucatopini and Ptomaphagini was initially proposed by Jeannel (1936), and both have been allied to Oritocatopini in current taxonomic treatments (e.g. Perreau, 1989; Giachino et al., 1998; Newton, 1998, 2016). Characteristics used to group eucatopines and ptomaphagines (in the erstwhile subfamily Eucatopinae; see Jeannel, 1936) include the shared presence of a tibial comb of spines and an incomplete tegmen with parameres inserted directly on the aedeagus. However, both features are weak evidence. The tibial comb of spines occurs in other leiodids and variations in this feature require further investigation (the categorization of varying arrangements of apical tibial spines is not yet fully elucidated). Moreover, the homology between the incomplete tegmen of each tribe is controversial and probably resulted from independent reductions, taking into account the different structural composition of the aedeagus in these groups (Gnaspini, 1994; Newton, 1998). Therefore, our results corroborate the close relationship between Eucatopini and Oritocatopini, and refute the traditional hypothesis of phylogenetic affinities between eucatopines and ptomaphagines (as indicated in Antunes-Carvalho and Gnaspini, 2016), placing the latter as the sister lineage of Sciaphyini + Leptodirini (see below).

Together with Sciaphyini (with only three species), Eucatopini and Oritocatopini are the least diverse tribes of Cholevinae, with 39 and 19 species, respectively (Newton, 2016). These two taxa exhibit a unique combination of plesiomorphies that distinguish them from any other cholevines, such as the retention of an elongate apical maxillary palpomere and the presence of empodial setae distinct from the empodial sclerites. A plesiomorphy added by Newton (1998) is the retained and possibly functional spiracle on abdominal segment VIII, in contrast to its absence in other cholevines. Interestingly, *Eucatops* and *Afrocatops* have been retrieved outside the phylogenetic limits of Cholevinae in the molecular studies of Fresneda et al. (2011) and McKenna et al. (2015). This result could be an artefact due to taxonomic undersampling. In fact, the present phylogenetic analysis is the first to include both Oritocatopini and Eucatopini in a data matrix. Although their phylogenetic proximity has already been suggested in the literature (e.g. Giachino et al., 1998; Newton, 1998), the position of the Neotropical Eucatopini within the African Oritocatopini is unexpected and deserves further attention.

The monophyly of *Eucatops*, the only genus of Eucatopini, is corroborated and strongly supported. Derived characteristics of this monotypic tribe are the absence of a hypostomal suture, the presence of a longitudinal ridge at the lateral margin of the mentum, the truncate anterior clypeal portion, the short medial notch at the posterior margin of the prosternal process, the very slender metanepisternum and the absence of a ventral lamella of the tegmen. All of them also occur in other leiodids, but probably as results of parallel evolution. A unique synapomorphy is the presence of a ventrally directed plate on the prosternum, forming a precoxal coverage.

Within Cholevinae, the tribes Anemadini, Cholevini, Ptomaphagini, Sciaphyini and Leptodirini formed a clade in all analyses. The contiguous mesocoxal cavities, the presence of minute setae on the elytra, and the fusion of the empodial sclerites and empodial setae are some of the characters supporting this group, although reversals occurred multiple times (e.g. nonconfluent mesocoxal cavities in Ptomaphagini, *Sciaphyes* and most leptodirines). The pore plate on the maxillary palp is an unusual character restricted to this group. Pore plates were first described by Antunes-Carvalho et al. (2017) in *Catops*, and have been found in all cholevine tribes except Eucatopini and Oritocatopini (not examined in Sciaphyini). Also in contrast to Eucatopini and Oritocatopini, all other cholevines share the reduced apical maxillary palpomere and the presence of an occipital ridge, even though this structure has been lost in modified leptodirines. It remains unclear, however, if both features have evolved independently in *Leptinus*, or if they constitute synapomorphies of *Leptinus* plus Cholevinae (Eucatopini and Oritocatopini excluded). In Fresneda et al. (2011), both morphological and molecular data placed *Leptinus* outside Cholevinae.

Systematic validity of Anemadini and Cholevini

A clade formed by Anemadini + Cholevini has been suggested based on the broadly contiguous mesocoxal cavities, a single apical tooth on the larval lacinia and a strongly developed larval hypopharyngeal bar, with hypopharyngeal muscle discs reduced or absent, among other traits (Newton, 1998, 2016). However, the sister group relationship of these tribes was refuted in all analyses, as well as their respective monophyly (Figs 25–27).

In this study all subtribes of Anemadini were sampled for the first time in a phylogenetic analysis. Anemadini was consistently recovered as polyphyletic. Under equal weighting and Bayesian inference the genera of Eunemadina were subdivided into four individual lineages, placed in a polytomy with an extensive clade comprising the rest of cholevine taxa (excluding Eucatopini and Oritocatopini). One of the groupings was composed of *Falkocholeva* + Paracatopina. In the analysis with implied weighting, however, the constituents of both Eunemadina and Paracatopina together form a single clade. Characters supporting Eunemadina (with Paracatopina nested within) are the anterior clypeal margin delimited by a ridge and a medial incision dividing the median empodial sclerite. A unique derived trait is the separation of the empodial and median sclerites by an incision. The medial projection of the terminal tarsomere bears an oblique row of spines in all members of this clade, with the exception of *Nargiotes*. However, the same peculiar set of spines also occurs in other leiodids within and outside of Cholevinae. The monophyly of Eunemadina, a taxon erected by Newton (1998), has never been tested. Newton (1998) emphasized that Eunemadina and Paracatopina differ distinctly from the remaining subtribes of Anemadini. This included features of the prosternum, meso- and metaventrite, and antenna, but most of them were not illustrated in his work. The affinity between Eunemadina and Paracatopina was also suggested by McKenna et al. (2015), although in this study *Prionochaeta* was placed between them. McKenna et al. (2015) also recovered this clade as the sister group of all remaining sampled Cholevinae (Oritocatopini excluded), a scenario that agrees with our results.

Unlike all other Anemadini, Eunemadina and Paracatopina have an austral distribution pattern. With the exception of the Neotropical–Nearctic *Dissochaetus*, the species of Eunemadina are scattered throughout the Austral kingdom (*sensu* Morrone, 2002), with most members in the Andean, Neoguinean, Australotemperate and Neozelandic regions, and some species extending into the Indonesian territory (Newton, 1998; Perreau, 2000). Paracatopina, in turn, is restricted to New Zealand and nearby islands. Our results, therefore, seems to mirror the geographic overlap of these groups.

The position of Anemadina remains uncertain. The taxon, here represented by its most diverse genera *Anemadus* and *Speonemadus*, was recovered either as sister to Cholevini (in the equal weighting and Bayesian analyses), or at the base of a clade including members of Cholevini, other Anemadini, Ptomaphagini, Sciaphyini and Leptodirini (in the implied weighting analysis). In both cases node support was low. A derived feature that sustains Anemadina as monophyletic is the distinctly widened posterior edge of the mesocoxal cavities, also present in Leptodirini. The expansion of the mesotarsus in males of Anemadina probably represents a reversal from the apomorphic condition with slender mesotarsomeres, found in most Cholevinae. Fresneda et al. (2011) suggested a sister group relationship of Anemadina and Sciaphyini, and both tribes were placed close to Cholevini. More data are needed to infer the phylogenetic location of Anemadina within Cholevinae.

Eocatopina and Nemadina were recovered close to the clade including ptomaphagines, leptodirines and *Sciaphyes*. *Eocatops* was consistently retrieved as sister to this grouping, albeit with low nodal support. The absence of areolae around the setal pits of the vertex, the acute medial notch at the posterior prosternal margin and the metaventral carina originating at the lateral edge of the mesocoxal cavity are characters that support this node. *Nemadus* and *Micronemadus* were placed at the base of the Ptomaphagini + Sciaphyini + Leptodirini grouping in parsimony analysis, or in a polytomy with Ptomaphagini and Leptodirini (with *Sciaphyes* nested in the latter) with Bayesian inference. Characteristics supporting the clade containing all these taxa include the absence of the hypostomal sutures (reversal in the Old World leptodirines), the non-pectinated meso- and metatibial spurs (reversal in *Sciaphyes* and Old World leptodirines) and the paired medial projection of the terminal tarsomere (reversal in *Sciaphyes*). The set of small spines on the dorsal surface of the claws is only shared by *Micronemadus* and Ptomaphagini, but the optimization is ambiguous in the analysis with implied weights. A sister group relationship between Nemadina and Ptomaphagini was also recovered by McKenna et al. (2015).

Most genera of Cholevini formed a monophylum, but the positions of *Cholevinus*, *Prionochaeta* and *Rybinskiella* were sensitive to the phylogenetic approach. *Cholevinus* was invariably recovered outside Cholevini. The monophyly of Cholevini excluding *Cholevinus* and *Prionochaeta* (implied weighting scheme) is only sustained by the absence of the longitudinal mesoventral carina. If *Prionochaeta* is included (equal weighting and Bayesian analyses), the clade is additionally supported by the absence of distinct striae and strigae on the elytra. *Prionochaeta* was placed outside Cholevini in McKenna et al. (2015).

Catopsimorphus, *Choleva* and *Nargus* formed a clade in all analyses, and also *Apocatops*, *Catops* and *Sciodrepoides*. These two monophyla would be equivalent with Cholevina minus *Prionochaeta*, and Catopina minus *Cholevinus* and *Rybinskiella*, respectively. The former group is strongly supported by two unusual pretarsal characters: the transformation of the outer empodial seta into a knob-like structure and the presence of long spines at the lateral base of the claws. These features were described in Antunes-Carvalho and Gnaspini (2016) and are almost unique to this clade, except for the co-occurrence of lateral spines in *Sciaphyes*. *Catopsimorphus* + *Choleva* + *Nargus* are further supported by the absence of an areola around the setal pits of the vertex. The clade composed by *Apocatops*, *Catops* and *Sciodrepoides* is supported by the absence of the frontoclypeal strengthening ridge and the presence of an oblique row of spines on the medial projection of the terminal protarsomere. The inclusion of *Rybinskiella* in this group, as found in the parsimony analyses, is supported by the presence of very slender parameres tapering towards a fine point.

Cholevina and Catopina were considered as a homogeneous grouping since the extensive study of Jeannel (1936). Their members are usually distinguished from each other by the male mesotarsomeres, expanded in males of Catopina and slender in Cholevina, save for some exceptions (e.g. Jeannel, 1936; Newton, 1998). Although this subdivision received criticism (Iablokoff-Khnzorian, 1975; Perreau, 1989), Newton (1998) retained the two units as separate subtribes, but highlighted the need for further investigation. The close relationship between Cholevina and Catopina has also been suggested by Fresneda et al. (2011) and

McKenna et al. (2015), but with poor generic sampling for both subtribes. Our results show that they can be considered as separate clades after some taxonomic rearrangements.

Monophyly of Ptomaphagini and internal subdivisions

Ptomaphagini was invariably corroborated as monophyletic with high support in all analyses (Figs 25–27). Although the monophyly of the tribe has never been satisfactorily tested, ptomaphagines have been recognized as a natural entity by cholevine taxonomists, even though without any convincing synapomorphies. The monophyly was supported in two previous phylogenetic studies. However, both were based on insufficient ingroup (Fresneda et al., 2011) or outgroup sampling (Gnaspini, 1996).

Derived characters that support the monophyly of Ptomaphagini include the distinctly narrowed apical maxillary palpomere, the oblique lateral opening of the procoxal cavity, the approximately horizontal orientation of the mesothoracic pleural suture, the apical asymmetry of the penis and the absence of a ventral lamella of the tegmen. A unique synapomorphy is the V-shaped depression at the distal extension of the unguitractor plate (Antunes-Carvalho and Gnaspini, 2016). The glabrous apical maxillary palpomere, the absence of the basal lamina of the aedeagus and the fusion of the parameres to the aedeagus are plesiomorphic traits retained by members of this tribe. The set of small spines on the dorsal surface of the base of the claws is an apomorphy almost exclusively found in Ptomaphagini, apart for its occurrence in *Micronemadus*. Ptomaphagini is further characterized by a truncated anterior clypeal portion, a derived condition only observed in *Eucatops*, *Paracatops* and *Sciaphyes* among Cholevinae.

Although the mutual monophyly of the constituent subtribes Ptomaphagina and Ptomaphaginina was retrieved (but see remark about *Baryodirus* below), their support is weak and based on characters with questionable independence. An additional support for Ptomaphagina is the longitudinal ridge on the lateral margin of the mentum, a feature described here for the first time. The division of Ptomaphagini into subtribes was refuted by Gnaspini (1996), although this view was not adopted in subsequent studies, which still recognize Ptomaphagina and Ptomaphaginina (e.g. Newton, 1998; Perreau, 2000, 2004; Bouchard et al., 2011).

Perreau (2000) described Baryodirina as a monotypic subtribe of Ptomaphagini based on a single female of *Baryodirus* collected in Gunung Mulu, Malaysia. Morphological peculiarities of the subtribe include the tetramerous protarsi, a dual setation on the pronotal and elytral surface, and a strongly developed median longitudinal carina (Perreau, 2000). However, the placement of *Baryodirus* in Ptomaphagini has never been tested cladistically. Therefore, we conducted an additional parsimony analysis with Baryodirina added to the data matrix. Both equal and implied weighting analyses corroborated the inclusion of Baryodirina in Ptomaphagini (Appendix S2), even though most synapomorphies of the tribe could not be confirmed for *Baryodirus* due to lack of information. Although a longitudinal ridge is present at the lateral margin of the mentum—a characteristic apparently synapomorphic for Ptomaphagina—the genus was nested inside the Ptomaphaginina clade. This was based on the presence of the row of teeth at the lateral base of the claws, even though less distinct on the middle and hind legs than on the foreleg (see Perreau, 2000: figs 8–10). Morphological similarities of Baryodirina and Ptomaphaginina have already been noted by Perreau (2000), such as the comb of spines along the external edge of the protibia and around its apex. In our analyses, *Baryodirus* was recovered close to *Proptomaphaginus* and *Ptomaphaminus*, supported by the mesoventral process extending beyond the posterior edge of the mesocoxal cavities but not reaching the midlength of the metaventrite.

The sister group relationship between Ptomaphagini and Sciaphyini + Leptodirini was recovered in the parsimony analyses, whereas both clades were retrieved in a polytomy with *Nemadus* and *Micronemadus* with Bayesian inference, but with low nodal support in all cases. Derived features uniting Ptomaphagini with Leptodirini + Sciaphyini are the slightly concave posterior mesepimeral margin, the acute angle formed by the posteromesal mesepimeral corner and the incomplete anapleural suture of the mesothorax, the last representing an unambiguous change. The separation of the mesocoxal cavities and absence of minute setae on the elytra are plesiomorphic traits shared by these tribes. A phylogenetic proximity of Nemadina, Ptomaphagini and Leptodirini was suggested by McKenna et al. (2015), whereas they are not shown as related taxa in the phylogeny of Fresneda et al. (2011).

Controversials around the phylogenetic placement of Sciaphyes

Sciaphyes, the single genus of Sciaphyini, is a poorly known taxon with only three species of small body size, restricted to the Russian Far East (*S. sibiricus* and *S. shestakovi*) and Tsushima Island (*S. kawaharai*) of Japan (Fresneda et al., 2011). The genus has been assigned to Leptodirini for more than a century. The first species was described as a leptodirine (under the name *Bathyscia sibirica* Reitter) until Perreau (2000) allocated it into an individual tribe. The five-segmented protarsi of females, the presence of two empodial setae, and characteristics of the pterothorax and abdominal venter were used by Perreau (2000) as main arguments to exclude *Sciaphyes* from Leptodirini. However, most leptodirines also possess two empodial setae (see Antunes-Carvalho and Gnaspini, 2016).

Different hypotheses on the phylogenetic placement of *Sciaphyes* within Cholevinae were presented. A sister group relationship between Sciaphyini and Leptodirini was proposed by Newton (2005) based on three characters shared by both tribes, a fourth palpomere shorter than the third, non-confluent metacoxae, and a short, ring-like male genital segment. However, none of these features is a strong argument, and the author himself noted the tenuous support of this clade. Shortening of the apical palpomere occurs in most lineages of Cholevinae, except in the basal Eucatopini and Oritocatopini, and separated metacoxae are plesiomorphic in the subfamily. Moreover, the reduction of the male genital segment of *Sciaphyes* is not as pronounced as in Leptodirini. In fact, the typical ring-like shape of the genital segment occurs exclusively in leptodirines (see Fresneda et al., 2011). Hoshina and Perreau [9] (2008) emphasized the 'intermediate' nature of the characters of *Sciaphyes* between Ptomaphagini and Leptodirini, such as the carinae associated with the posterolateral edge of mesocoxal cavities (here subdivided into two individual characters: 46 and 48), and the different degrees of reduction of the male abdominal segment IX. According to Hoshina and Perreau (2008), the absence of eyes and the body depigmentation in both groups are results of convergent evolution associated with a subterranean lifestyle.

In contrast to earlier hypotheses, a sister group relationship between Sciaphyini and Anemadini was recently suggested by Fresneda et al. (2011), based on molecular evidence, although with weak nodal support. Morphologically, the proximity between the tribes was mainly justified by similarities of the male copulatory apparatus. For instance, *Sciaphyes* shares a weakly curved median lobe with Anemadina, and also a strongly delevoped basal lamina with recurved lateral margins almost forming a tube (Fresneda et al., 2011). Parameres longer than the penis and of similar width along their entire length are common to both groups. Similarities in the structure of the aedeagal internal sac were also noted by Fresneda et al. (2011), who considered the internal sac of *Sciaphyes* with two longitudinal bands more similar to that of Eunemadina and Nemadina than to the condition found in Anemadina (although many species of *Anemadus* and *Speonemadus* do also bear two longitudinal bands in the endophallus).

Our study emphasizes the uniqueness of Sciaphyini, but does not resolve its phylogenetic affinities. This uncertainty is at least partly due tp the unusual character combination of *Sciaphyes*, with features irregularly distributed among other cholevine lineages. The shallow, transverse ridge close to the anterior margin of the mentum is a derived feature shared with Eucatopini and Oritocatopini (and some outgroup taxa). In these tribes and in *Sciaphyes*, the mesothoracic pleural suture is not visible externally, a condition also occurring in the clade of Eunemadina and Paracatopina, and also in a few leptodirines. In turn, the long, lateral spine associated with the base of the claws is a characteristic feature shared exclusively with Cholevina (excluding *Prionochaeta*). With leptodirines, *Sciaphyes* share the smooth dorsum of the claws. Finally, the longitudinal carina on the metaventrite is shared with *Catopocerus* (a non-cholevine leiodid), while the carina on the first abdominal ventrite is an autapomorphy of Sciaphyini.

Despite this mixture of phenotypic traits, our analyses retrieved *Sciaphyes* always related to Leptodirini, either in a trichotomy with *Platycholeus* and all remaining leptodirines (equal weighting, Fig. 25), or as sister to monophyletic Leptodirini (implied weighting, Fig. 26), or nested within this group (Bayesian analysis, Fig. 27). Several characteristics support a close affinity between the two tribes. However, they are either homoplastic apomorphies, such as the distinctly widened posterior edge of the mesocoxal cavity and the narrow metanepisternum, or reversals, as in the case of the frontoclypeal strengthening ridge, the absence of an elevated occipital ridge, the bifid metaventral process and the absence of parasutural elytral stria. Additional similarities not recorded before are the pectinate ventral tibial spurs of the middle and hind legs and the transverse groove on the claws. Both characters are present in all leptodirines except *Platycholeus* and *Hadesia*. The latter feature is not found in any other leiodid group. It appears that a combination of extensive morphological and molecular data will be required to assess the phylogenetic affinities of Sciaphyini reliably. Without confirming or refuting alternative hypotheses of relationships, we show that the phylogenetic placement of this enigmatic lineage is problematic and still an unsoved issue.

Basal dichotomies and novel morphological elements in Leptodirini

Leptodirini is an impressive subterranean radiation of beetles. The tribe, the most species-rich and intensively studied of Cholevinae, encompasses seven subtribes and ca. 930 species, mostly distributed in the Palaearctic region (with a single Nearctic genus; Newton, 2016). The restricted distribution of most leptodirine genera and species offers exciting data for biogeographical investigations. The phylogenetic knowledge of Leptodirini has distinctly improved in recent years (Fresneda et al., 2007, 2011; Ribera et al., 2010; Cieslak et al., 2014), even though covering only a fraction of its extraordinary diversity. The monophyletic origin has been demonstrated on the basis of morphological (Fresneda et al., 2007) and molecular evidence (Ribera et al., 2010; Fresneda et al., 2011). Although not covering the entire generic diversity in the tribe, the present contribution is the first to sample representatives from all subtribes and to offer comprehensive information on the external morphology (morphology-based phylogenies are mostly focused on genitalic structures, e.g. Fresneda et al., 2007, 2011). Our data confirm some previous findings, but the poor topological resolution does not allow an in-depth discussion of the internal relationships. Nevertheless, two interesting morphological features of Leptodirini are addressed for the first time: the projecting sensilla on the apical maxillary palpomere, and the pore plates on the terminal tarsomere.

The monophyly of Leptodirini was corroborated, except for the inclusion of *Sciaphyes* in the trees produced by equal weighting analysis and Bayesian inference. Leptodirini *s.s.* is supported by a reduced number of protarsomeres in females (from five to four), also considered an autapomorphy of the tribe in previous investigations (e.g. Fresneda et al., 2007, 2011) and used to charaterize the group by earlier authors (e.g. Jeannel, 1936; Giachino et al., 1998; Newton, 1998). Another characteristic supporting the group is the presence of a set of projecting sensilla on the apical maxillary palpomere, in contrast to digitiform sensilla adpressed to the surface of the palpomere in non-leptodirines. The projecting sensilla are an almost unique apomorphy of Leptodirini, except for its occurence in *Nargomorphus* (Anemadini), and a possible reversal in *Spelaeobates*. This feature has been observed by Moldova et al. (2004) in *Closania*, *Sophrochaeta* and *Tismanella*, and by Njunjić et al. (2016) in *Anthroherpon*, *Leptomeson* and *Graciliella*, but not interpreted phylogenetically. Here we report the broad occurrence throughout Leptodirini and show the phylogenetic relevance of this derived character for the first time. Although the sensilla have not been found in *Hadesia* by Njunjić et al. (2016), we confirm its presence in *Hadesia vasiceki*.

The basal dichotomy between *Platycholeus* and the Old World leptodirines is in agreement with Fresneda et al. (2011), and also with earlier hypotheses (Jeannel, 1924; Newton, 1998). This genus—the only one of Platycholeina—comprises three species and is the single taxon of Leptodirini with well-developed compound eyes and hind wings, in contrast to the remaining flightless species without or with reduced eyes. *Platycholeus* is also unique by its distribution, as the single leptodirine branch in the New World. A possible autapomorphy suggested by our analyses is the loss of the outer empodial seta, but the taxon is also supported by reversals which include the smooth anterior clypeal margin, the missing medial notch at the posterior prosternal margin, and the complete suture between mesanepisternum and mesoventrite. Other plesiomorphies are the simple meso- and metatibial ventral spurs, in contrast to the pectinate spurs of other leptodirines, and the absence of the characteristic transverse groove on the claws. The monophyly of the Old World Leptodirini is sustained by the presence of the hypostomal suture, a mesoventral process extending beyond the posterior edge of the mesocoxal cavities but not reaching the midlength of the metaventrite, and the microsculptured dorsal elytral surface (reversals and other states of these characters occur in different branches within the group). The basal fusion of empodial setae is a derived character exclusive to this clade. However, it is unclear whether this condition has evolved in the common ancestor of the Old World Leptodirini, or whether it is a ground plan apomorphy of the tribe with subsequent loss of the outer empodial seta in *Platycholeus*.

Among the Old World Leptodirini, *Notidocharis* appears as sister to the large and unresolved clade composed by all remaining genera, but with weak support. The basal position of *Notidocharis* was also suggested in other studies (e.g. Fresneda et al., 2007; Cieslak et al., 2014). The minute outer empodial seta is a derived trait of this genus, but with independent origins within Leptodirini. Except for Spelaeobatina (with a single genus) and Anthroherponina (with two genera sampled), all other subtribes were non-monophyletic. This broad assemblage of leptodirines includes several highly modified species, and the unresolved topology probably reflects numerous convergent phenotypic changes related to underground life. The modern subtribal classification is obsolete and requires a profound revision, a herculean task considering the immense diversity of the taxon. The smooth dorsum of the claws and the twisting of the empodial setae are synapomorphies of the Old World leptodirines with the exclusion of *Notidocharis*, the latter representing an unambiguous change. Although a drastic reduction of the outer empodial seta has occurred in some species of Pholeuina, the twisted nature of the setae can be recognized.

Our character survey uncovered a novel structure in Leptodirini: a set of pore plates on the cuticular surface of the terminal tarsomere, probably associated with glands. This structure was identified in members of five of the seven subtribes. Pore plates were not observed in Platycholeina and Spelaeobatina, like in any other leiodids studied here. Under implied weighting, the presence of this feature yielded a potential synapomorphy of a large clade within Leptodirini. In the analysis with equal weights, the presence of this structure turned out as an unambiguous change sustaining all Old World leptodirines with the exception of *Notidocharis*. They are generally distributed on the lateral and dorsal surfaces of the terminal tarsomere of all legs, mostly associated with the base of the tarsal setae. Betz (2003) reported similar structural modifications on the tarsi of *Stenus* (Staphylinidae). He demonstrated their association to a unicellular gland of uncertain function, but possibly related to the tarsal adhesive performance. The function of the maxillary sensilla and tarsal pore plates in leptodirines are unknown. Both structures open new avenues of investigation in functional morphology, ultrastructure and behaviour of Leptodirini.

Conclusion

Our cladistic hypothesis for Cholevinae is the most comprehensive presently available. For the first time an extensive set of morphological characters was scored for a broad taxon sampling and analysed with different approaches. Members from all suprageneric taxa were sampled largely covering the global distribution of the subfamily, including the south temperate regions, which were found to harbour the basal lineages of the Cholevinae.

The monophyly of Cholevinae was confirmed, except for the unexpected inclusion of *Leptinus* in the implied weighting analysis. In contrast to other studies, Eucatopini and Oritocatopini were retrieved as basal branches. The monophyletic origin of all remaining tribes was corroborated, which is congruent with molecular evidence. Anemadini turned out as non-monophyletic, confirming earlier hypotheses. Cholevini was rendered non-monophyletic by the uncertain inclusion of *Prionochaeta* and the consistent exclusion of *Cholevinus*. The affinity of Ptomaphagini with Sciaphyini and Leptodirini was suggested, even though the position of *Sciaphyes* remains not precisely defined. Nemadina was invariably associated with these tribes, and Eocatopina was consistently recovered as the sister taxon of this clade including the three tribes plus Nemadina.

Although genitalic structures have historically played a pivotal role in inferences of relationships among genera, homology hypotheses of various components of the male copulatory apparatus become problematic with increasing phylogenetic distance, namely at the tribal level. This may not be the case for the female abdominal terminalia. Its morphology should be the target of future efforts, from which additional characters may come to light. Our study provided several characters from other body parts and a morphological documentation based on SEM micrographs. Most of the characters have never been used in a phylogenetic context in Cholevinae. Many of them were only described and documented in recent years, such as those from the pretarsus and distal margin of the terminal tarsomere, and were tested for the first time in this study. The list of characters shows that substantial parts of the data were obtained from the ventral side. This is a strong argument for a detailed pictorial documentation of the ventral aspect in taxonomic descriptions, in contrast to the common practice of only illustrating the dorsal habitus of the beetles. In addition to the recent finding of maxillary pore plates in Cholevinae, the discovery of the broad occurrence of tarsal pore plates and projecting sensilla in the maxillary palp of Leptodirini show that even the very well-known cholevines continue to offer valuable reward for careful morphological investigations. The volume of available molecular data for Cholevinae is presently rapidly increasing. The present contribution represents an additional step towards a total evidence analysis of the group and a reconstruction of evolutionary changes on the phenotypic level.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Character matrix. Unapplicable characters are indicated by "-"; missing data are indicated by "?". 13

Appendix S2. Strict consensus tree obtained in parsimony analyses with Baryodirina included in the data matrix. The resultant topologies of both equal and implied weigthing analyses were the same of that depicted in Figs 25 and 26, respectively. Therefore, only the Ptomaphagini clade is shown.