Systematic Entomology

Systematic Entomology (2019), DOI: 10.1111/syen.12338

Comprehensive phylogeny of the Cleroidea (Coleoptera: Cucujiformia)

MATTHEW L. GIMMEL[1,2], MILADA BOCAKOVA[2], NICOLE L. GUNTER[3] and RICHARD A.B. LESCHEN[4]

[1]Invertebrate Zoology Department, Santa Barbara Museum of Natural History, Santa Barbara, CA, U.S.A., [2]Department of Biology, Faculty of Education, Palacky University, Olomouc, Czech Republic, [3]Invertebrate Zoology Department, Cleveland Museum of Natural History, Cleveland, OH, U.S.A. and [4]Manaaki Whenua, New Zealand Arthropod Collection, Auckland, New Zealand

Abstract. The first thorough molecular phylogeny of the superfamily Cleroidea, represented by 377 taxa, and the first with an emphasis on Trogossitidae, was undertaken. Maximum likelihood and Bayesian analyses were performed on a four-gene dataset (*18S*, *28S*, *cox1*, *cytb*) of 395 taxa (along with 18 outgroups), including all 16 currently recognized families of Cleroidea and all current and formerly recognized tribes of Trogossitidae. The superfamily as a whole received strong support in Bayesian analyses. On the basis of phylogenetic results, 18 families in Cleroidea are recognized, including three taxa elevated to family for the first time and two reinstated families. The former tribe Rentoniini (Trogossitidae: Peltinae) was strongly supported as a monophyletic group apart from the remainder of Trogossitidae, and is herein elevated to family status, Rentoniidae **stat.n.** *Protopeltis* was also found to be an isolated lineage and becomes Protopeltidae **stat.n.** Peltini + Larinotini were recovered as a weakly supported sister grouping; Peltini (including only *Peltis*) becomes Peltidae **stat.rest.** The trogossitid subfamily Lophocaterinae, to the exclusion of Decamerini, formed a clade which is here designated Lophocateridae **stat.rest. and sensu n.** The Trogossitinae tribes Calityini, Egoliini (represented by *Egolia*) and Larinotini were recovered apart from core Trogossitidae but showed no strong affinities to other taxa or congruence between analyses; they are here conservatively retained in Trogossitidae as Calityinae **stat.rest.**, Egoliinae **stat.rest.** and Larinotinae **stat.rest.** The genus *Thymalus* of the peltine tribe Thymalini was indicated with moderate to strong support as the sister group of the Decamerini (Trogossitidae: Lophocaterinae); together these represent Thymalidae **stat.n.** and **sensu n.** with subfamilies Decamerinae **stat.rest.** (**new placement**) and Thymalinae **stat.n.** The remainder of Trogossitinae, the tribes Trogossitini and Gymnochilini, formed a well-supported clade which comprises the Trogossitidae: Trogossitinae **sensu n.** The tribe Gymnochilini **syn.n.** is synonymized with Trogossitini. The monotypic family Phloiophilidae was recovered, contradicting a recent placement within Trogossitidae. The melyrid lineage was recovered with moderate (maximum likelihood) to strong (Bayesian analyses) support and includes the families Phycosecidae, Rhadalidae, Mauroniscidae, Prionoceridae and Melyridae (including Dasytidae and Malachiidae). The genus *Dasyrhadus* is tentatively transferred from Rhadalidae to Mauroniscidae. The genus *Gietella*, once proposed as a distinct family but recently placed within Dasytidae, was recovered as strongly sister to Rhadalidae **sensu n.**, and we transfer it to that family as Gietellinae **new placement**. Attalomiminae (formerly Attalomimidae) **syn.n.** is synonymized with Melyridae: Malachiinae: Lemphini **sensu n.** Melyridae **sensu n.** includes only Dasytinae, Malachiinae and Melyrinae. *Metaxina*

Correspondence: Matthew L. Gimmel, Invertebrate Zoology Department, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105, U.S.A. E-mail: mgimmel@sbnature2.org

is returned to the Chaetosomatidae **sensu n.**, of which Metaxinidae **syn.n.** becomes a junior synonym. Resolution within Cleridae was generally poor, but a broadly defined Korynetinae **stat rest.** + Epiclininae received high support (Bayesian analyses). Outside of Trogossitidae, the main focus of this study, major rearrangements of the classification of Cleroidea were not undertaken, despite evidence indicating such changes are needed.

Introduction

With just over 10 000 described species, Cleroidea is the tenth largest superfamily of beetles (Slipinski *et al.*, 2011). Cleroidea is made up of 16 families (Leschen *et al.*, 2010; Bocakova *et al.*, 2012; Robertson *et al.*, 2015; Figs 1–3; Table 1): Acanthocnemidae, Biphyllidae, Byturidae, Chaetosomatidae, Cleridae, Dasytidae, Malachiidae, Mauroniscidae, Melyridae, Metaxinidae, Phloiophilidae, Phycosecidae, Prionoceridae, Rhadalidae, Thanerocleridae and Trogossitidae. More than 20 years ago, Majer (1994a,b) proposed the monogeneric families Attalomimidae and Gietellidae, but these have generally been treated as subfamilies (or tribes) of Malachiidae (=Malachiinae) and Dasytidae (=Dasytinae), respectively, among the coleopterological community (Leschen *et al.*, 2010; Bouchard *et al.*, 2011). Most significantly, the stability and composition of Trogossitidae are problematic and it has been fragmented into as many as three families in previous works (Peltidae, Lophocateridae, Trogossitidae; Crowson, 1970), albeit with unstable composition. Even with this morphology-based three-family system the groups are still quite heterogeneous, each defined by few to no synapomorphies. Trogossitidae is widely presumed to be grossly para- or polyphyletic (see, e.g. McKenna *et al.*, 2015; Robertson *et al.*, 2015). Here we present the first molecular phylogeny to sample all 16 currently accepted families of Cleroidea, plus the four former families proposed by Majer (1994a, b) and Crowson (1970), in order to examine the systematic relationships within the Cleroidea and the various 'trogossitid' groups in particular.

Members of the superfamily exhibit a wide range of natural histories and behaviour, but the most common broad feeding types appear to be predatory (typified by Cleridae and most Trogossitidae: Trogossitinae), pollen- or nectar-feeding (typified by the 'melyrid lineage'), and fungus-feeding (typified by much of the remaining Trogossitidae, and many smaller families). Many of the cleroids in the first two categories are pronouncedly diurnal as adults, some of which have developed bright aposematic coloration and are presumed to be mimics of other, less palatable insects (particularly in Cleridae and Malachiidae; Bocakova *et al.*, 2016). Other groups are much more cryptic and/or nocturnal in their habits (most Trogossitidae and smaller families), and may be found under bark, in fungal fruiting bodies or in rotting wood. Still other groups have odd habits, including scavenging dead animals on bare seashore (Phycosecidae) or being attracted to wood killed in recent fires (Acanthocnemidae).

There has been no cladistics study based on morphology for the whole of the Cleroidea, apart from the inclusion of exemplars in the study by Lawrence *et al.* (2011). To date, there have been three molecular phylogenetic studies with a broad sampling of Cleroidea: that of Gunter *et al.* (2013) (loci used: *28S*, *16S*, *12S*, *cox1*), which focused on relationships within Cleridae; that of Bocakova *et al.* (2012) (loci used: *18S*, *28S*, *16S*, *cox1*), which focused on relationships within the so-called 'melyrid lineage'; and that of Bocakova *et al.* (2016) (loci used: *18S*, *28S*, *16S*, *cox1*), which focused on evolution of aposematism and soft-bodiedness and included primarily melyrid lineage and clerid taxa. The present study includes all of the taxa included in the latter two studies plus many of those in the former, and to improve data congruence *18S* data were generated for taxa of Gunter *et al.* (2013). In addition, we have included a great many critical taxa previously unsampled, including additional genera of Cleridae not in Gunter *et al.* (2013), additional families, subfamilies and tribes of the melyrid lineage not represented in Bocakova *et al.* (2012) and, most critically, a much broader sampling of Trogossitidae and other groups of 'lower Cleroidea'. This is also the first time the Attalomimidae or Gietellidae sensu Majer (1994a, b) have been included in a molecular phylogenetic analysis, and the first time the family Metaxinidae has been analysed in a study focused on Cleroidea. Additionally, all currently and previously recognized subfamilies and tribes (up to 14 in the most fragmented system) of Trogossitidae are represented. Trogossitidae sampled in the current study represent 37 of the 58 described world genera (64%), plus an additional two undescribed genera.

Here we start with a 16-family system based primarily on Bouchard *et al.* (2011), which represents a consensus summary of beetle classifications, with deviations corresponding to subsequent classification changes of Kolibáč & Zaitsev (2010), Kolibáč (2012), Bocakova *et al.* (2012), Gunter *et al.* (2013) and Robertson *et al.* (2015) (see Table 1). Additionally, to explore the validity of a more fragmented classification system, our taxon sampling of Cleridae targets the representatives of the subfamilies within Opitz (2010) rather than the more consolidated system of Kolibáč (1997), the latter having been accepted by Bouchard *et al.* (2011) (see Appendix 1C). The only Cleroidea subfamilies lacking from the present analysis include Platydascillinae (Byturidae; Oriental endemic), Zenodosinae (Thanerocleridae; Nearctic endemic), Anthicoclerinae (Cleridae; western Palearctic and Oriental), Platynopterinae (Cleridae; Neotropical endemic), Amalthocinae and Pagurodactylinae (Malachiidae; Madagascar and subsaharan Africa endemics, respectively).

Taxonomic and phylogenetic history of Cleroidea and Trogossitidae

The concept of Cleroidea is less than 100 years old, having been conceived in roughly its current constitution by Böving &

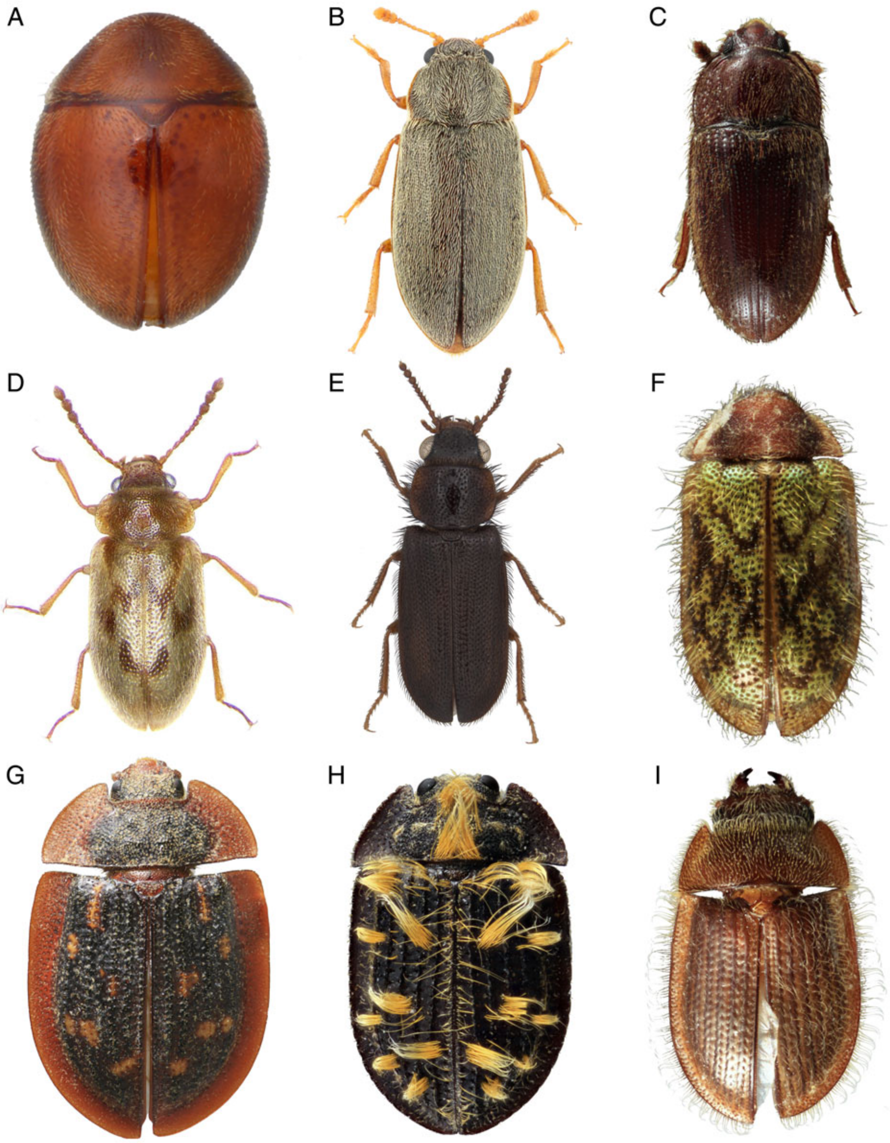

Fig. 1. Habitus photographs of representative Cleroidea. Taxonomy follows newly proposed classification. (A) *Rentonium bicolor* (Rentoniidae; photo by MLG); (B) *Byturus tomentosus* (Byturidae; photo © Kirill Makarov); (C) *Goniocoelus* sp. (Biphyllidae; voucher G0099; photo by Lucie Gimmel); (D) *Phloiophilus edwardsi* (Phloiophilidae; photo © Udo Schmidt); (E) *Acanthocnemus nigricans* (Acanthocnemidae; photo © Her Majesty the Queen in Right of Canada, by Anthony Davies); (F) *Protopeltis viridescens* (Protopeltidae; voucher G0295; photo by Lucie Gimmel); (G) *Peltis pippingskoeldi* (Peltidae; voucher G0016; photo by Lucie Gimmel); (H) *Trichocateres fasciculifer* (Lophocateridae; voucher G0095; photo by Lucie Gimmel); (I) *Ancyrona* sp. (Lophocateridae; voucher G0068; photo by Lucie Gimmel). [Colour figure can be viewed at wileyonlinelibrary.com].

Craighead (1931) based on larval morphology. These authors included a few other groups now placed in various superfamilies, but were the first to formally associate the core groups of Cleroidea: Cleridae, Melyridae, Trogossitidae (see Appendix 1A). During subsequent decades, the concept of Cleroidea was altered multiple times. Cleroidea in essentially the modern sense was first defined by Crowson (1955), who excluded several groups and included two newly split-off families, Chaetosomatidae and Phloiophilidae (as ‘Phloeophilidae’). Few phylogenetic studies have examined the relationships among the Cleroidea. Kolibáč (1999) analysed a small number of adult and larval features, and found nonmonophyly among the informally hypothesized trogossitid group, melyrid group and clerid group. Beutel & Pollock (2000), in another character- and taxon-limited analysis, showed a monophyletic Cleroidea (but Biphyllidae and Byturidae were not examined). Kolibáč (2004), in a review of cleroid classification, described the new family Metaxinidae and divided the Cleroidea into melyrid, trogossitid, clerid and thaneroclerid branches. What follows is a more detailed tracking of the classification of three informally recognized groups of

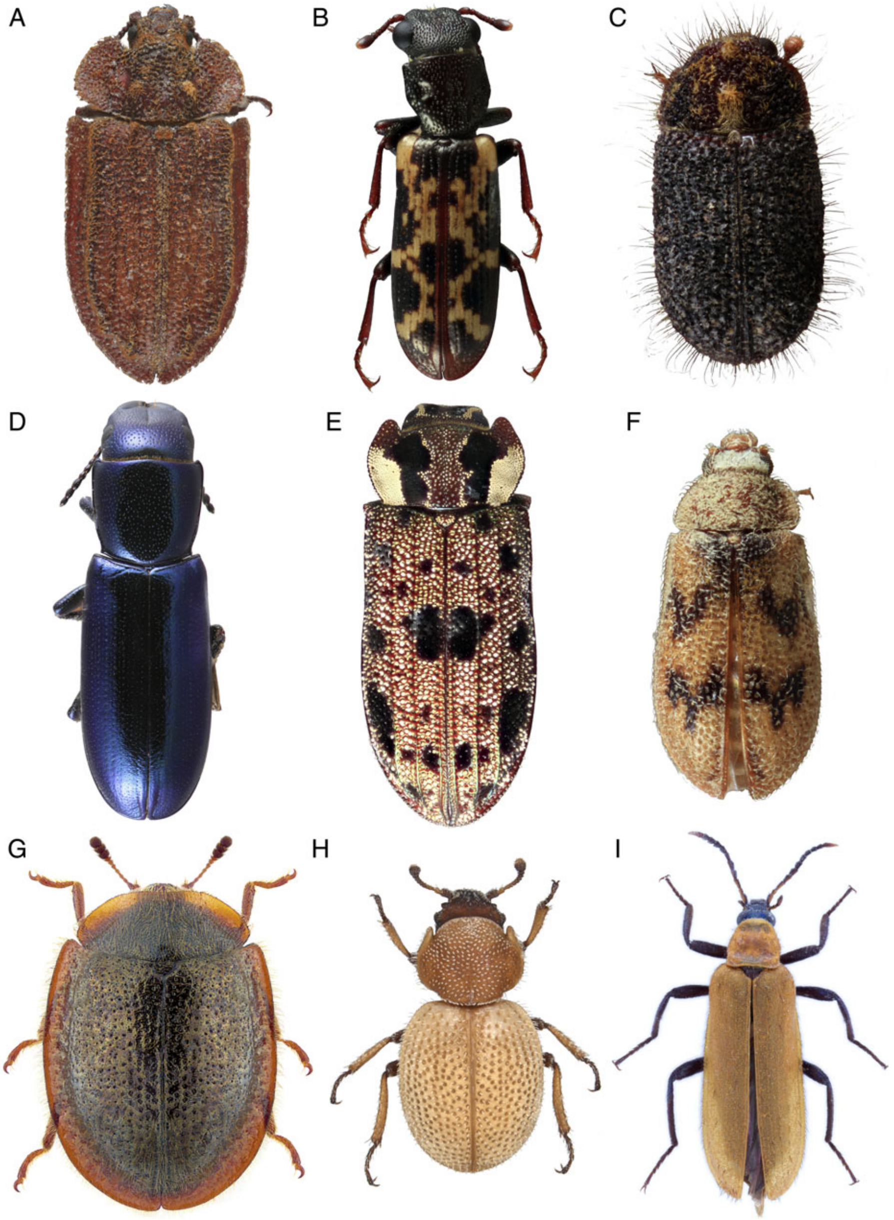

Fig. 2. Habitus photographs of representative Cleroidea, continued. (A) *Calitys scabra* (Trogossitidae: Calityinae; voucher G0015; photo by Lucie Gimmel); (B) *Egolia variegata* (Trogossitidae: Egoliinae; voucher G0121; photo by Lucie Gimmel); (C) *Larinotus umbilicatus* (Trogossitidae: Larinotinae; voucher G0122; photo by Lucie Gimmel); (D) *Temnoscheila chlorodia* (Trogossitidae: Trogossitinae; voucher G0022; photo by Lucie Gimmel); (E) *Leperina decorata* (Trogossitidae: Trogossitinae; voucher G0069; photo by Lucie Gimmel); (F) *Diontolobus punctipennis* (Thymalidae: Decamerinae; photo by Lucie Gimmel); (G) *Thymalus limbatus* (Thymalidae: Thymalinae; photo © Udo Schmidt); (H) *Phycosecis limbata* (Phycosecidae; photo © Her Majesty the Queen in Right of Canada, by Anthony Davies); (I) *Prionocerus bicolor* (Prionoceridae; photo © Chris Wirth). [Colour figure can be viewed at wileyonlinelibrary.com].

Cleroidea in turn: 'Melyrid', 'Trogossitid' and 'Clerid' (including clerid and thaneroclerid branches sensu Kolibáč (2004)).

Trogossitid group. This is the group within Cleroidea with the most taxonomically troubled and erratic history, and comprises the families Phloiophilidae and Trogossitidae. Much of the debate within the trogossitid group concerns the taxonomic status and hierarchy of lineages within the Trogossitidae. Despite this uncertainty, the present constitution of the trogossitid group had been established by the time of Crowson (1955), and supported by both larval and adult character systems. Furthermore, classification problems were compounded by the inclusion of many groups originally described in Trogossitidae that now

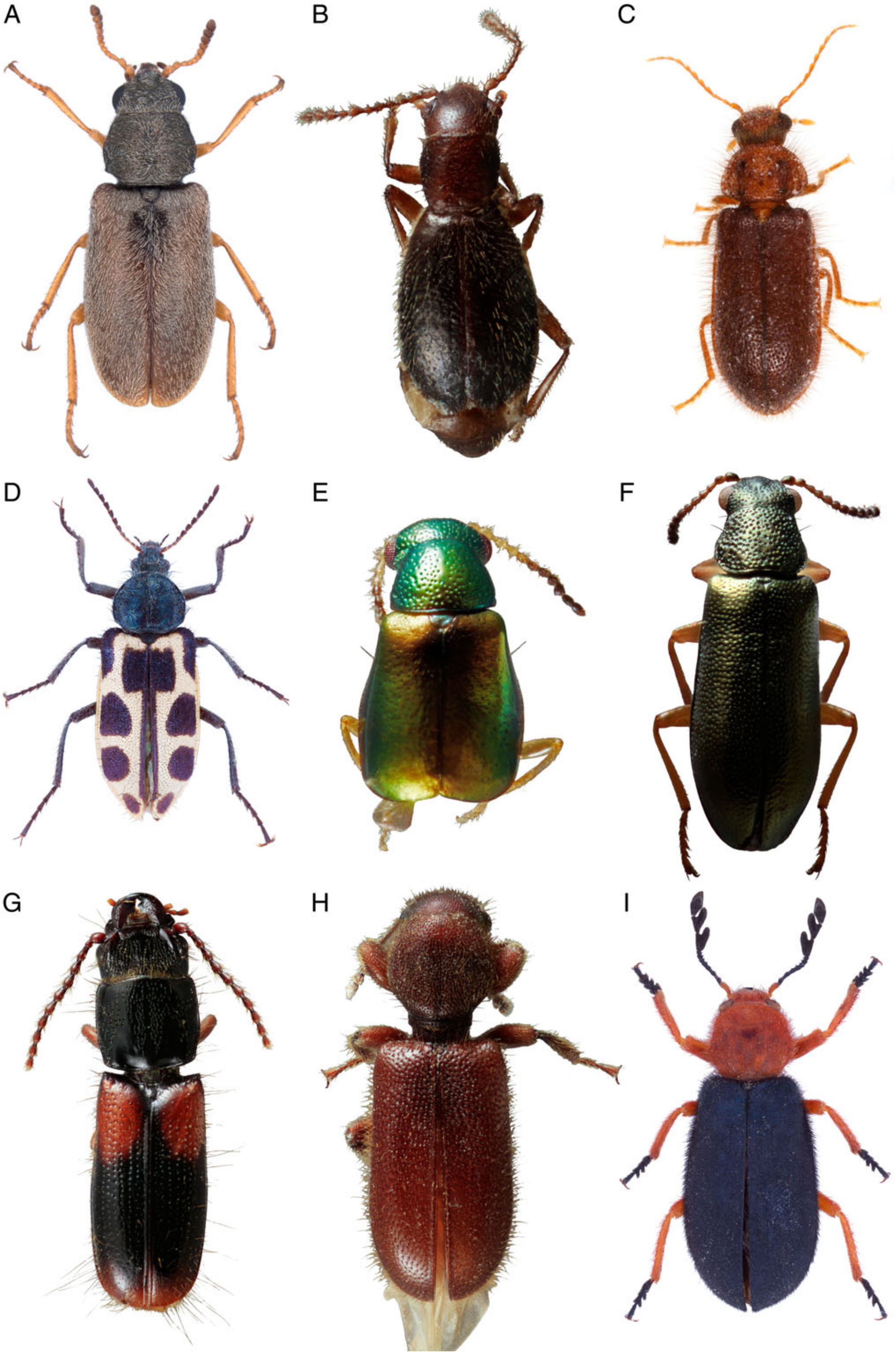

Fig. 3. Habitus photographs of representative Cleroidea, continued. (A) *Mauroniscus maculatus* (Mauroniscidae; photo © Her Majesty the Queen in Right of Canada, by Anthony Davies); (B) *Gietella fortunata* (Rhadalidae: Gietellinae; voucher G0332; photo by Lucie Gimmel); (C) *Rhadalus testaceus* (Rhadalidae: Rhadalinae; photo © Salvador Vitanza); (D) *Astylus atromaculatus* (Melyridae: Melyrinae; photo © Chris Wirth); (E) *Attalomimus* sp. (Melyridae: Malachiinae; voucher G0353; photo by Lucie Gimmel); (F) *Haplamaurus viridimicans* (Melyridae: Dasytinae; voucher G0345; photo by Lucie Gimmel); (G) *Chaetosoma scaritides* (Chaetosomatidae; voucher G0312; photo by Lucie Gimmel); (H) *Thaneroclerus* sp. (Thanerocleridae; photo by Lucie Gimmel); (I) *Chariessa elegans* (Cleridae; photo © Chris Wirth). [Colour figure can be viewed at wileyonlinelibrary.com].

Table 1. Currently recognized 16-family classification of extant family groups of Cleroidea, representing the hypotheses tested in the present work (left column), and new 18-family classification of Cleroidea as a result of this study (right column). The left-hand column is based primarily on Bouchard *et al.* (2011), with deviations from that indicated in superscript.

Old classification scheme		New classification scheme
BYTURIDAE[a]		RENTONIIDAE **stat.n.**
Platydascillinae	[0/4]	BYTURIDAE
Byturinae	[2/3]	**Platydascillinae**
BIPHYLLIDAE[a]	[4/6]	**Byturinae**
PHLOIOPHILIDAE	[1/1]	BIPHYLLIDAE
TROGOSSITIDAE		PHLOIOPHILIDAE
Peltinae		ACANTHOCNEMIDAE
Colydiopeltini	[1/2]	PROTOPELTIDAE **stat.n.**
Peltini	[1/1]	PELTIDAE **stat.rest.**
Thymalini	[8/8]	LOPHOCATERIDAE **stat.rest. and sensu n.**
Lophocaterinae[b]		TROGOSSITIDAE **sensu n.**
Ancyronini	[4/5]	**Calityinae stat.rest.**
Decamerini	[1/3]	**Egoliinae stat.rest.**
Lophocaterini	[6/9]	**Larinotinae stat.rest.**
incertae sedis	[0/1]	**Trogossitinae sensu n.**
Trogossitinae		THYMALIDAE **stat.n. and sensu n.**
Calityini	[1/1]	**Decamerinae stat.rest. and new placement**
Egoliini	[1/5]	**Thymalinae stat.n.**
Gymnochilini	[6/8]	PHYCOSECIDAE
Larinotini	[1/1]	PRIONOCERIDAE
Trogossitini	[7/14]	Lobonychini
CHAETOSOMATIDAE	[1/3]	Prionocerini
METAXINIDAE	[1/1]	MAURONISCIDAE
THANEROCLERIDAE		RHADALIDAE **sensu n.**
Zenodosinae	[0/1]	**Gietellinae new placement**
Thaneroclerinae		**Rhadalinae**
Isoclerini	[1/2]	Aplocnemini
Thaneroclerini[c]	[1/5]	Microjulistini
CLERIDAE[d]		Pelecophorini
Tillinae	[8/67]	Rhadalini
Hydnocerinae		MELYRIDAE **sensu n.**
Callimerini	[3/6]	**Malachiinae**
Hydnocerini	[2/9]	Amalthocini
Lemidiini	[2/8]	Carphurini
Clerinae	[23/113]	Lemphini **sensu n.**
Anthicoclerinae	[0/2]	Malachiini
Epiclininae[e]	[3/4]	Apalochrina
Korynetinae	[3/7]	Attalina
Enopliinae	[2/16]	Colotina
Epiphloeinae	[1/25]	Ebaeina
Orthopleurinae[g]	[4/22]	Illopina
Peloniinae	[1/46]	Malachiina
Platynopterinae[h]	[0/7]	Troglopina
Tarsosteninae	[7/20]	Pagurodactylini
ACANTHOCNEMIDAE	[1/1]	**Melyrinae**
PHYCOSECIDAE	[1/1]	Arthrobrachini
PRIONOCERIDAE		Astylini
Lobonychini	[1/1]	Cerallini
Prionocerini	[2/2]	Melyrini
MAURONISCIDAE	[2/5]	**Dasytinae**
RHADALIDAE[f]		Chaetomalachiini
Aplocnemini	[2/3]	Danaceini
Microjulistini	[0/3]	Dasytini
Pelecophorini	[0/2]	Listrini
Rhadalini	[1/1]	CHAETOSOMATIDAE **sensu n.**
incertae sedis	[1/8]	THANEROCLERIDAE
MELYRIDAE[f]		**Zenodosinae**
Arthrobrachini	[1/1]	**Thaneroclerinae**
Astylini	[1/3]	Isoclerini
Cerallini	[0/3]	Thaneroclerini
Melyrini	[1/8]	CLERIDAE
incertae sedis	[1/1]	**Tillinae**
DASYTIDAE[f]		**Korynetinae stat.rest.**
Chaetomalachiinae	[1/14]	**Epiclininae**
Danaceinae		**Hydnocerinae**
Amauronioidini	[1/5]	Callimerini
Danacaeomimini	[0/5]	Hydnocerini
Danaceini	[6/6]	Lemidiini
incertae sedis	[0/2]	**Clerinae**
Dasytinae		
Dasytini	[6/11]	
incertae sedis	[1/14]	
Gietellinae	[1/1]	
Listrinae	[1/24]	
MALACHIIDAE[f]		
Amalthocinae	[0/1]	
Attalomiminae	[1/1]	
Carphurinae	[1/15]	
Lemphinae	[3/6]	
Malachiinae		
Apalochrini	[5/29]	
Attalini	[4/13]	
Colotini	[2/25]	
Ebaeini	[4/22]	
Illopini	[0/17]	
Malachiini	[5/15]	
Troglopini	[1/19]	
Pagurodactylinae	[0/5]	

[a] Transferred from Cucujoidea by Robertson *et al.* (2015).

[b] Elevated to subfamily by Kolibáč & Zaitsev (2010).

[c] Tribe Viticlerini synonymized with Thaneroclerini by Kolibáč (2012).

[d] Subfamily classification of Cleridae according to Opitz (2010), excluding Thaneroclerideae.

[e] Subfamily created from Clerinae by Gunter *et al.* (2013).

[f] Recognized at the family rank sensu Bocakova *et al.* (2012).

[g] Frequently known as Neorthopleurinae; in fact, Dermestoidinae Jakobson, 1911 has priority.

[h] Subfamily re-elevated by Opitz (2015).

Numbers in square brackets represent the number of genera sampled in this study, followed by number of described extant world genera.

belong to other superfamilies, including current members of Synteliidae, Derodontidae, Monotomidae, Helotidae, Salpingidae, Zopheridae, Chrysomelidae and, more recently, Ciidae (see Gimmel & Leschen, 2014). Appendix 1B summarizes the classification accepted here and alternative classifications proposed through time. In the most fragmented form, up to 14 groups (tribes) have been recognized and supported by morphological hypotheses summarized in the following.

Crowson (1964, 1966, 1970) advocated a classification that recognized Peltidae, composed of mainly the fungus (and flower)-feeding lineages as separate from the remaining predatory groups. Barron (1971) called into question Crowson's splitting of the trogossitid group, which he supposed was based primarily on mouthpart analysis; he tabulated other characters and concluded that peltines and trogossitines were much more closely related to each other than either was to any other cleroid group, and that adult mouthpart characters were too unstable to be relied upon (in particular, he highlighted the variation among peltines, which he surmised was reflective of diverse feeding habits). As a consequence, he recognized all taxa as the single family Trogossitidae. He also moved *Lophocateres* Olliff back to Peltinae based on the mouthparts (protuberant and ridged mola, elongate lacinia with two spines) and the open procoxal cavities. For an excellent summary of character states and feeding habits across families of Cleroidea and subfamilies of Trogossitidae, see Barron (1971: tables 1, 2).

Slipinski (1992) described a new subfamily, Larinotinae, and followed Barron (1971) in recognizing a broadly defined Trogossitidae. He took a fragmented, nonphylogenetic approach based on adult and larval morphological characters, splitting the Trogossitidae into nine subfamilies [Calityinae (as 'Calitinae'), Decamerinae, Egoliinae, Larinotinae, Lophocaterinae, Peltinae, Protopeltinae, Rentoniinae, Trogossitinae].

Kolibáč (2006), in an analysis of adult and larval characters, divided the Trogossitidae into two subfamilies, Trogossitinae [Calityini (as Calityni), Larinotini, Egoliini, Gymnochilini, Trogossitini] and Peltinae (Peltini, Thymalini, Colydiopeltini, Decamerini, Ancyronini, Lophocaterini). This classification was amended by Kolibáč (2008), who included Phloiophilini in Peltinae, and by Kolibáč & Zaitsev (2010) to include a third subfamily, Lophocaterinae (Decamerini, Ancyronini, Lophocaterini) (see Appendix 1B). However, the subsuming of Phloiophilidae into Trogossitidae has not gained general acceptance (see Lawrence & Leschen, 2010a; Bouchard *et al.*, 2011; Kolibáč, 2013; Lawrence *et al.*, 2014).

No phylogenetic analysis has focused on the trogossitid group, but members have either been included as outgroups in studies of other cleroid lineages (Bocakova *et al.*, 2012, 2016; Gunter *et al.*, 2013) or in broad studies of the relationships of higher-level taxa (Lawrence *et al.*, 2011; McKenna *et al.*, 2015; Robertson *et al.*, 2015; Zhang *et al.*, 2018). These preliminary studies have suggested that Trogossitidae is not monophyletic.

Melyrid group. The melyrid group has historically been represented by members of the current families Acanthocnemidae, Phycosecidae, Rhadalidae, Mauroniscidae, Prionoceridae, Melyridae, Dasytidae and Malachiidae. Subsequent to Crowson's works, Majer proposed major classification changes within the melyrid group. Majer (1987) proposed that Prionocerinae were more closely related to Cleridae, but no formal action was taken to transfer it from the Melyridae. In a subsequent work, Majer (1994a) recognized Prionoceridae as a distinct family from Melyridae, along with Attalomimidae, Mauroniscidae (both new families), Dasytidae and Malachiidae. Gietellinae was originally described as a subfamily of Melyridae by Constantin & Menier (1987) but was elevated to family rank as Gietellidae in Majer (1994b). Majer (2002) later provided a new five-subfamily classification for Malachiidae (Carphurinae, Lemphinae, Amalthocinae, Pagurodactylinae, Malachiinae).

The first molecular analysis that focused on any cleroid group analysed the melyrid lineage and found that Rhadalidae, Mauroniscidae, Prionoceridae, Melyridae and Malachiidae were all reciprocally monophyletic (Bocakova *et al.*, 2012; loci used: *18S*, *28S*, *16S*, *cox1*). Dasytidae divided into two clades, one comprising two genera of Danaceinae and the other comprising the remaining sampled genera of Dasytidae (Bocakova *et al.*, 2012). The families Attalomimidae and Gietellidae were not included in that analysis. Those two families have recently been recognized as subfamilies of Malachiidae and Dasytidae, respectively (Lawrence & Leschen, 2010c).

Clerid group. The composition of the clerid group, here considered to include Chaetosomatidae, Metaxinidae, Thanerocleridae and Cleridae, has been relatively stable at the family level compared with the trogossitid and melyrid lineages. Kolibáč (1992) raised Thanerocleridae out of Cleridae to family rank in a revision of the former group, and excluded *Metaxina* Broun from the family, placed there from Chaetosomatidae by Crowson (1964) based primarily on larval characters. Kolibáč (1992) suggested that *Metaxina* was indeed more closely related to Chaetosomatidae, but that it might end up comprising its own family. He later (Kolibáč, 2004) formalized this by recognizing and describing Metaxinidae.

The division of Cleridae into subfamily units has been contentious, with two major classifications dividing the family into either four or 12 subfamilies based on morphological analyses (Kolibáč, 1997; Opitz, 2010); these two systems are compared in Appendix 1C. In the first molecular analysis of the Cleridae, Gunter *et al.* (2013) added another subfamily, the Epiclininae (from Clerinae), and hypothesized that Tillinae were sister to the remaining Cleridae (including Thaneroclerinae). Their results also suggested that Thaneroclerinae and Isoclerinae should be combined, and that Tarsosteninae, Korynetinae, Orthopleurinae (=Neorthopleurinae), Peloniinae and Epiphloeinae should be combined (in a classification system similar to the one of Kolibáč, 1997), though no formal changes were made beyond the new subfamily. Anthicoclerinae were not included in the analysis.

Byturidae and Biphyllidae. Recently, Robertson *et al.* (2015) formalized the transfer of the families Byturidae and Biphyllidae from the superfamily Cucujoidea to the Cleroidea upon a broad molecular phylogenetic study of the classification of the Cucujoidea sensu lato. This relationship had already been suggested in several morpohological studies and by the molecular trees of Hunt *et al.* (2007) and Bocak *et al.* (2014).

Materials and methods

We targeted four genetic markers for this study, *18S*, *28S*, *cox1* and *cytb*, totalling about 3500 bp. Data from *18S*, *28S* and *cox1* loci were available from many previously sequenced Cleroidea, and *18S*, in particular, provides a wealth of character data from a 'slow' genetic locus; *cytb* was included as it was already available for most taxa from a parallel study of mitochondrial genomes and represents a 'fast' genetic locus that prevents data domination at this level by *cox1*.

A total of 395 taxa were sampled in this study, including at least 170 genera (including undescribed) of Cleroidea (Table S1). All Cleroidea samples were extracted and amplified by the authors, with the exception of *Biphyllus lunatus* (Fabricius), which was taken from GenBank (see Table S1 for accession numbers).

Sampling was particularly dense within the Gymnochilini and Trogossitini, providing a robust test of reciprocal monophyly of these large tribes. Our sampling also included all six described genera of the enigmatic group originally described as Rentoniini, plus *Protopeltis* Crowson and *Thymalus* Latreille, which have been associated with the group, plus an additional undescribed rentoniine genus from New Zealand.

Outgroup sampling was not particularly extensive (18 taxa) as most molecular studies (e.g. Hunt *et al*., 2007; Bocak *et al*., 2014; McKenna *et al*., 2015; Robertson *et al*., 2015; Zhang *et al*., 2018) that have sampled extensively within Cucujiformia showed a monophyletic Cleroidea sensu Robertson *et al.* (2015) that includes Biphyllidae and Byturidae. However, we did sample 11 outgroups from Tenebrionoidea (sister group of Cleroidea in Robertson *et al*., 2015 and Zhang *et al*., 2018), three from Cucujoidea, one from Lymexyloidea, one from Derodontoidea, one from Elateroidea and one from Byrrhoidea.

DNA was extracted primarily from metathoracic muscle tissue using a phenol-chloroform method (Vogler *et al*., 1993). Smaller specimens (e.g. Rentoniini) were extracted whole using the blood/tissue protocol of the Qiagen DNAeasy kit (Qiagen, Hilden, Germany). Selected gene fragments were amplified under the following reaction conditions using Bioline taq unless otherwise indicated. *18S* (each of four fragments): 96°C for 5 min; 94°C for 30 s, 50°C for 30 s, 72°C for 1 min (35X); 72°C for 10 min; *28S*: 94°C for 4 min; 94°C for 30 s, 50°C for 45 s, 72°C for 1:45 (39X); *cox1* (Platinum taq): 94°C for 2 min; 94°C for 1 min, 45°C for 1 min, 72°C for 1:30 (39X); 72°C for 10 min; *cytb*: 94°C for 1 min; 94°C for 30 s, 50°C for 30 s, 70°C for 1 min (35X); 72°C for 10 min. Primers used in this study are listed in Table S2; the four *18S* fragments were amplified using the primer pairs 3′I/a2.0 (~700 bp), bi/a1.0 (~430 bp), b2.5/ai (~640 bp), b5.0/5′I (~630 bp) (Shull *et al*., 2001). Amplified products were purified using Millipore MultiScreen plates (Millipore, Burlington, MA, U.S.A.). Cycle sequencing reactions were conducted using BIGDYE TERMINATOR CYCLE SEQUENCING KIT v. 3.1 (Applied Biosystems, Foster City, CA, U.S.A.) before being sequenced using an ABI 377 sequencer in the Institute of Experimental Botany, Olomouc facility.

Sequences of each gene were edited in SEQUENCHER 4.9 (Gene Codes Corporation, Ann Arbor, MI, U.S.A.) and manipulated in GENEIOUS 6.1.8. GenBank accession numbers (MH983862–MH984769) for the newly generated sequences are indicated in Table S1. Of the 377 ingroup terminals, sequences for 228 were newly generated during this study, 36 and 112 were previously generated and published in association with Gunter *et al.* (2013) and Bocakova *et al.* (2012, 2016), respectively, and one ingroup terminal (*Biphyllus lunatus*) was derived from GenBank. Of the 18 outgroup terminals, 15 were derived from GenBank, and three originated with this study (G0042, *Perilopa* Erichson; G0132, *Paracucujus* Sen Gupta & Crowson; G0324, *Rhizonium* Sharp). For voucher G0306 (*Parapeltis australicum* Slipinski), the 18S sequence is a chimera of two specimens from the same collecting event; for terminal G0312 (*Chaetosoma scaritides* Westwood) the *cytb* locus was excised from a published mitochondrial genome (GenBank accession no. EU877951). The total 395-taxon data matrix represented 375 *18S*, 345 *28S*, 353 *cox1* and 280 *cytb* sequences. Only 12 terminals (COL1655, G0039, G0048, G0050, G0066, G0099, G0110, G0133, G0176, G0184, G0314 and UPOL001119) were represented by one locus in the matrix, 39 by two loci, 112 by three loci, and 232 by all four loci. Each gene was aligned separately, with protein-coding genes aligned using default settings of MUSCLE and ribosomal fragments aligned using the E-INS-i algorithm of the MAFFT plugin in GENEIOUS 6.1.8 (http://www.geneious.com; Kearse *et al*., 2012). Protein-coding genes were screened for indels and subsequently checked by translation. The *18S* and *28S* alignments were checked for misalignment and manually edited. All alignments were trimmed, edited to code for missing data and concatenated to produce a total matrix length of 3986 bp.

PARTITIONFINDER 1.1.1 (Lanfear *et al*., 2012) was used to specify the best model and partition scheme for the dataset, which was initially partitioned by codon for protein-coding genes and by gene for ribosomal markers. The analysis was run using the Bayesian information criterion (BIC) and Akaike information criterion (AIC) performed under the greedy search scheme with all models considered. All subsequent analyses were performed under the partition scheme and models suggested by PARTITIONFINDER. The partitioned alignment was analysed using maximum likelihood (ML) and Bayesian analysis (BA) methods hosted on the CIPRES Science Gateway (Miller *et al*., 2010). Maximum likelihood was conducted using RAXML 7.3.1, and bootstrap values from 1000 replicates were calculated under the GTRCAT model. Bayesian analysis was performed in MRBAYES 3.1.2 and the analysis was run for 30 million generations with a random starting tree, two runs with four Markov chains sampled every 1000 generations. The stationarity phase in Markov chains was determined in TRACER 1.5, burn-in was set accordingly at 25% and the posterior probabilities (PPs) were determined from the remaining trees. All trees were visualized in FIGTREE 1.4.2 (available from http://tree.bio.ed.ac.uk/software/figtree/).

Bayesian PP values were deemed to constitute 'high' nodal support if they were in the range 0.95–1.0, 'moderate' support if they were in the range 0.85–0.94 and 'low' if they were in the range 0.75–0.84. Posterior probability values within the range 0–0.74 were considered to constitute no support. For the ML analysis, bootstrap support (BS) was deemed 'high' when in the range 80–100, 'moderate' in the range 60–79 and 'low' if < 60.

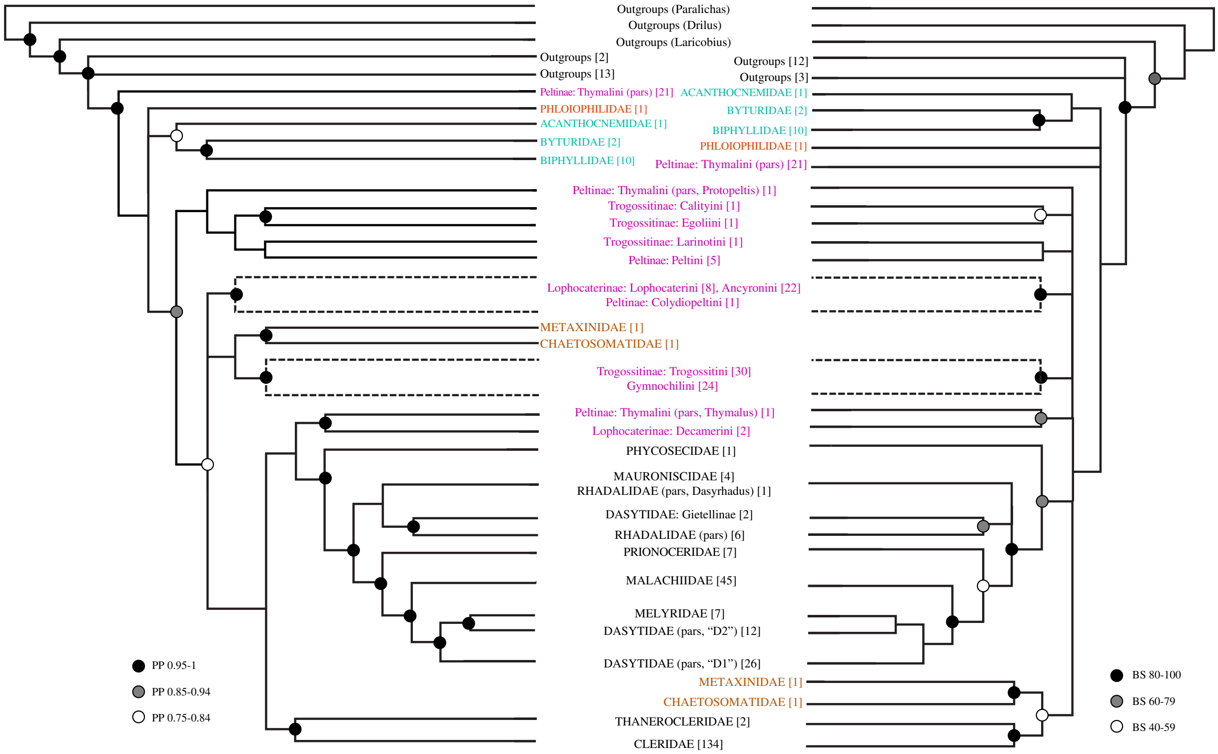

Fig. 4. Mirrored-tree comparison of the higher-level topologies of the Bayesian analysis (left-hand tree) and maximum likelihood analysis (right-hand tree) of 395 terminals representing 377 Cleroidea. Support values for major clades are shown using shaded circles; nodes without circles have support lower than the lowest threshold. Numbers in brackets represent the number of terminals within each collapsed clade. Physically unaligned groups in the mirrored trees are colour-coded for easier visual alignment. Terminals representing the family Trogossitidae before this study are coloured magenta allowing visualization of the polyphyly of the family. Dashed clades represent multiple higher taxa. [Colour figure can be viewed at wileyonlinelibrary.com].

Specimens sequenced are vouchered in the repositories indicated in Table S1. Morphological characters in support of groups defined in the following are based on information contained in the recent literature (e.g. Kolibáč, 2004, 2005, 2006; chapters in Leschen *et al*., 2010), character sets based on Lawrence *et al.* (2011), and an updated key derived from Lawrence *et al.* (2014) (Appendix 3).

Results

The 395-taxa dataset included 2045 constant, 1728 variable uninformative and 1306 parsimony-informative characters (see Table S3 for gene breakdown). On the basis of PARTITIONFINDER results, the dataset was divided into eight partitions: each of three codon positions for the two protein-coding genes, *18S*, and *28S*. A GTR + I + G AIC model was applied to the protein-coding bases, and a SYM + I + G AIC model was applied to the ribosomal-coding bases.

The resultant ML and BA analyses produced superficially similar topologies (Figs 4–10, S1) with long terminal branches and short internodes consistent with the general patterns observed in beetle phylogenies generated from a small number of ribosomal and protein-coding markers (McKenna & Farrell, 2009; McKenna *et al*., 2015; Robertson *et al*., 2015). This general pattern in topology resulted in minimal support on many short internodes comprising the backbone of the tree, particularly in ML analyses; however, major clades were recovered with strong support that provide evidence in favour of a new classification system comprising 18 families within the Cleroidea (Table 1; Appendix 2). Furthermore, the differences in topologies, particularly among poorly supported and unresolved clades, are not unexpected, and are consistent with patterns between BA and ML analyses observed in other systematic studies of beetles (Bocakova *et al*., 2012; Gunter *et al*., 2013; Kim & Farrell, 2015; McElrath *et al*., 2015; McKenna *et al*., 2015; Bocak *et al*., 2016). Given these general trends, particularly in topological support, we refer primarily to the topology of the BA for discussion, although results from both trees are considered.

The overall Bayesian topology was divided into four major clades of Cleroidea with statistical support (Fig. 4) with their interrelations poorly supported. Interrelationships were less clear in the ML analysis; however, BS for monophyly of most family-group clades was obtained (Figs 4, S1). The interrelationships between these major clades were superficially similar with Rentoniidae, Phloiophilidae and the clade containing Acanthocnemidae, Byturidae and Biphyllidae recovered as the earliest branching lineages. However, the support and placement

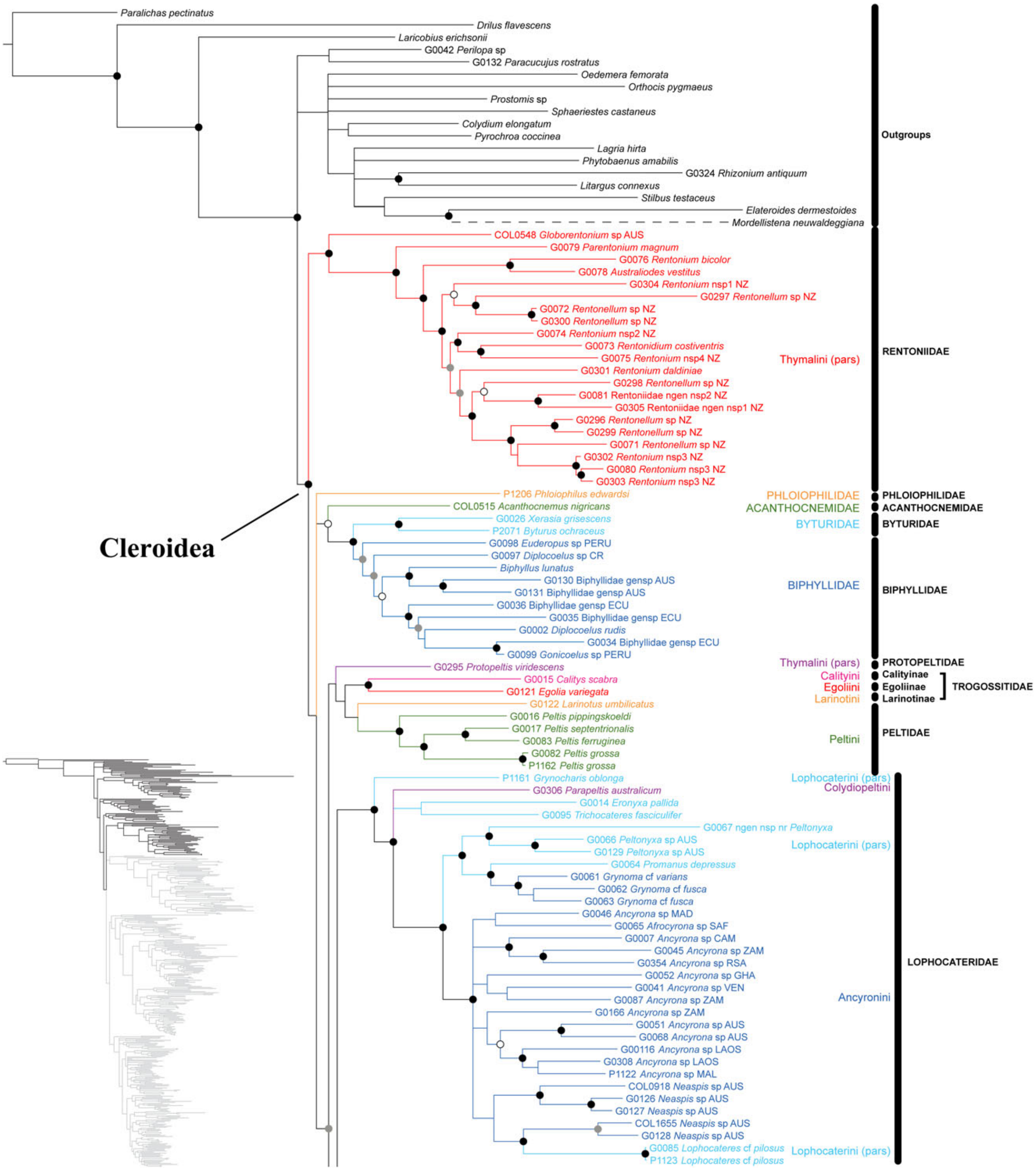

Fig. 5. Consensus tree resulting from Bayesian analysis of Cleroidea taxa (part 1 of 6). The left (coloured) column of names shows the old classification (from left column of Table 1), and the right (black) column shows the new classification (from the right column of Table 1). For names in the old classification, the term 'pars' is given after taxa represented in the tree by more than one nonadjacent clade. Black circles on nodes indicate high (0.95–1.0) posterior probabilities, grey circles indicate moderate (0.85–0.94) posterior probabilities, open circles indicate low (0.75–0.84) posterior probabilities, and the lack of a circle indicates lack of support (0–0.74 posterior probabilities). The dashed branch has been artificially shortened. The small tree in the lower left-hand corner shows the full topology with the currently displayed branches darkened. The root node of Cleroidea is indicated. [Colour figure can be viewed at wileyonlinelibrary.com].

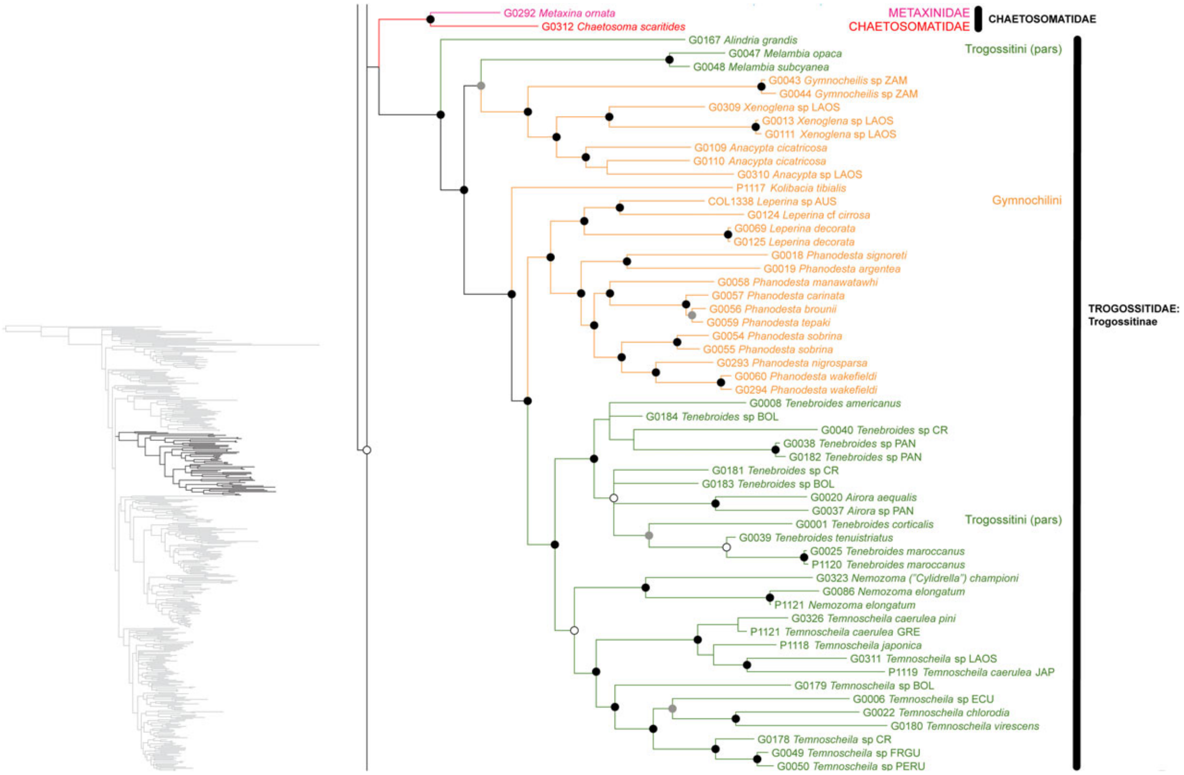

Fig. 6. Consensus tree resulting from Bayesian analysis of Cleroidea taxa (part 2 of 6). [Colour figure can be viewed at wileyonlinelibrary.com].

of these early branching lineages differed. In BA, Rentoniidae was recovered as a supported monophylum separate from an unsupported clade of the remaining Cleroidea, with the position of Phloiophilidae unresolved within the latter clade, whereas in ML the Rentoniidae, Phloiophilidae, Acanthocnemidae and Byturidae + Biphyllidae formed individual clades along the unsupported backbone of Cleroidea (Fig. 4). Given the differing topologies and lack of nodal support across key clades, the earliest diverging lineage of the Cleroidea remains unresolved, although our results indicate that the three clades, Rentoniidae, Phloiophilidae and Acanthocnemidae + Byturidae + Biphyllidae, are candidates for the earliest diverging Cleroidea.

The following relationships were recovered in both BA and ML analyses and form the basis of the proposed updated classification of the Cleroidea presented here: (i) the family Trogossitidae in the present sense was polyphyletic, forming eight distinct monophyletic clades (Fig. 4); (ii) Dasytidae was paraphyletic with respect to Melyridae; and (iii) particular terminal taxa (i.e. genera, some representing monotypic families) were misclassified to natural family-level groups. We take a conservative approach and only propose taxonomic changes based on congruent relationships between both BA and ML and supported by morphological evidence. We found phylogenetic evidence to support additional taxonomic changes, including polyphyletic Danaceini (Melyridae: Dasytinae) and Attalini (Melyridae: Malachiinae), and reciprocally paraphyletic Hydnocerinae and Clerinae (Cleridae). However, given that these groups are some of the richest and most morphologically diverse in the Cleroidea, in the absence of morphological revision, we refrain from making classification changes at this point in time. Additionally, although many rearrangements, elevations, re-elevations and newly defined taxa are proposed, we have not created any new nomina within the Cleroidea.

Discussion

Cleroidea monophyly

The relationships within the superfamily Cleroidea have received limited phylogenetic attention. Although most previous studies supported inclusion of Byturidae and Biphyllidae in Cucujoidea, molecular evidence was the first that highlighted a sister-group relationship between the Byturidae + Biphyllidae clade and Cleroidea (Hunt *et al.*, 2007; Bocak *et al.*, 2014). These families were then formally transferred to the Cleroidea in a major phylogenetic revision of the Cucujoidea undertaken by Robertson *et al.* (2015). Our results (Fig. 5) strongly support the Cleroidea (sensu Robertson *et al.*, 2015) as monophyletic (PP = 0.98) in BA, but the relationship is only recovered with weak support (BS = 30) in ML. Within Cleroidea, a dichotomy was recovered using BA, one branch being the rentoniine trogossitids (Rentoniidae below) and the other (weakly supported, PP = 0.68) representing the remainder of Cleroidea. The hypothesis of trogossitids being part of a grade of 'lower'

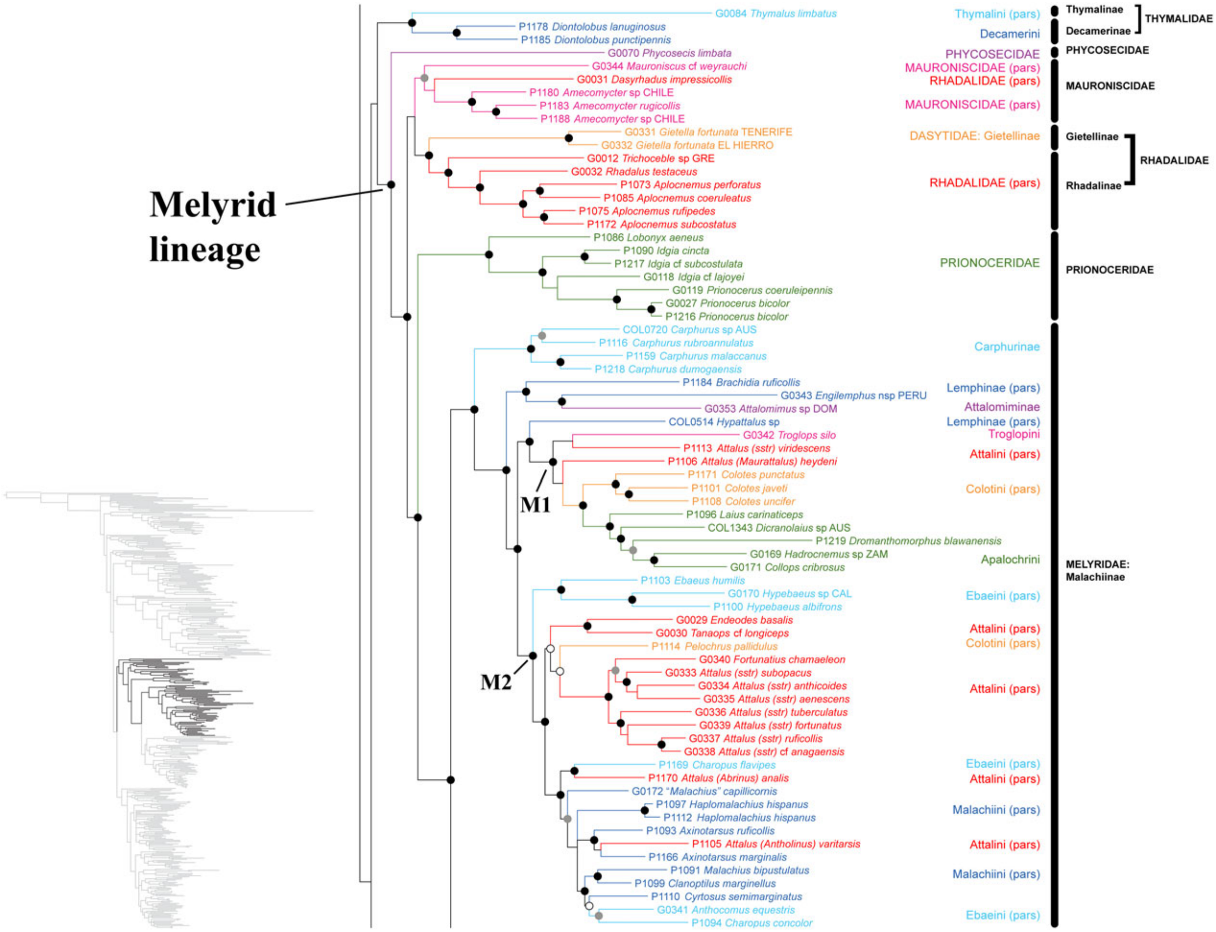

Fig. 7. Consensus tree resulting from Bayesian analysis of Cleroidea taxa (part 3 of 6). The root node of the melyrid lineage is indicated, as are the Malachiinae clades 'M1' and 'M2' (see text). The left (coloured) column of names shows the old classification (from left column of Table 1), and the right (black) column shows the new classification (from the right column of Table 1). For names in the old classification, the term 'pars' is given after taxa represented in the tree by more than one nonadjacent clade. Black circles on nodes indicate high (0.95–1.0) posterior probabilities, grey circles indicate moderate (0.85–0.94) posterior probabilities, open circles indicate low (0.75–0.84) posterior probabilities, and the lack of a circle indicates lack of support (0–0.74 posterior probabilities). The dashed branch has been artificially shortened. The small tree in the lower left-hand corner shows the full topology with the currently displayed branches darkened. The root node of Cleroidea is indicated. [Colour figure can be viewed at wileyonlinelibrary.com].

Cleroidea was expounded by Crowson (1970). However, given the convoluted taxonomic history of family- and subfamily-level groupings within the Trogossitidae (sensu lato) and Crowson's (1964) hypothesis that trogossitids represent multiple lineages among the Cleroidea, the relationship recovered here is only congruent in part with the proposed lineages of Crowson (1964, 1966, 1970).

The topology of the ML tree differed from that of the BA tree; however, the internodes representing deep-level relationships were either weakly supported or unsupported in the former. Regardless of interrelationships between families, topological evidence, including PP of BA and congruent clades, supports the family-level taxonomic changes presented here and our results are consistent with previous molecular studies.

Unsurprisingly, given the heterogeneous morphology of Trogossitidae (sensu lato), the family was recovered as polyphyletic with eight distinctly supported lineages (Fig. 4). These results are congruent with Crowson's proposals to raise Peltidae **stat.rest.** and Lophocateridae **stat.rest.** to family level, and three new families are proposed: Rentoniidae **stat.n.**, Protopeltidae **stat.n.** and Thymalidae **stat.n.** Other taxonomic changes proposed here include elevating the tribe Egoliini to subfamily Egoliinae **sensu n.**; transferring Gietellinae from Dasytidae to Rhadalidae; merging the families Dasytidae, Malachiidae and Melyridae sensu stricto into Melyridae **sensu n.**; and synonymizing the subfamily Attalomiminae **syn.n.** with Malachiinae: Lemphini and the tribe Gymnochilini **syn.n.** with Trogossitini.

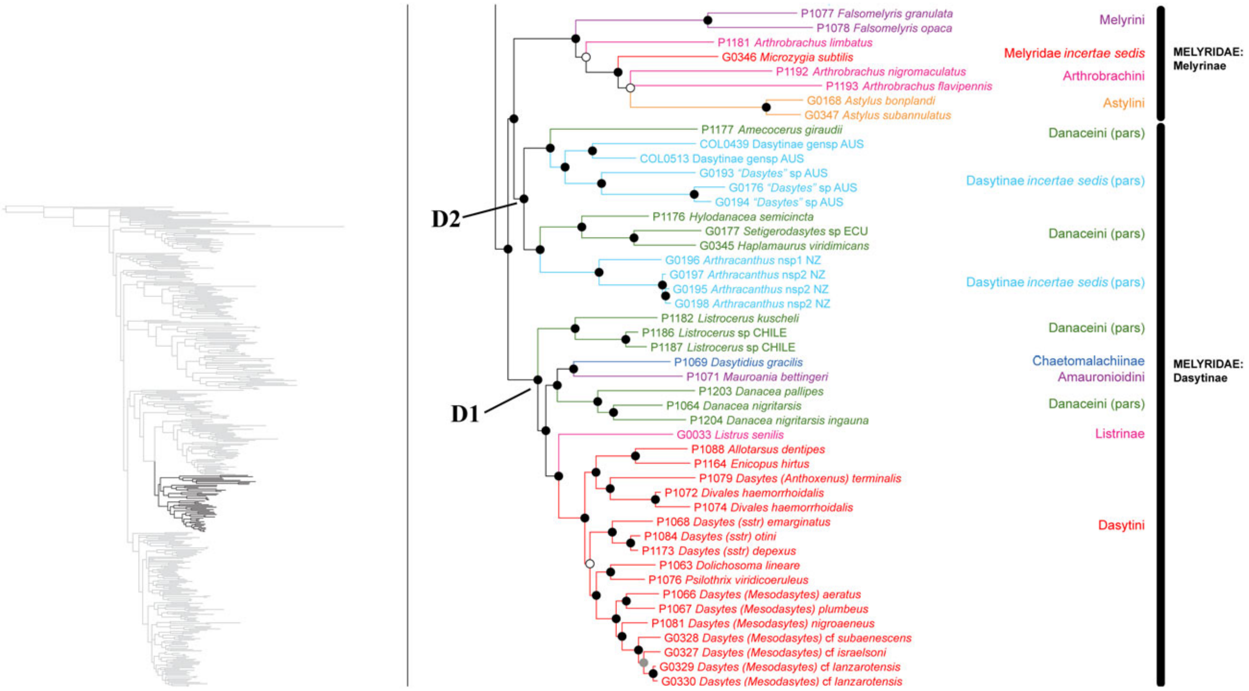

Fig. 8. Consensus tree resulting from Bayesian analysis of Cleroidea taxa (part 4 of 6). Root nodes of Dasytinae clades 'D1' and 'D2' are indicated (see text). The left (coloured) column of names shows the old classification (from left column of Table 1), and the right (black) column shows the new classification (from the right column of Table 1). For names in the old classification, the term 'pars' is given after taxa represented in the tree by more than one nonadjacent clade. Black circles on nodes indicate high (0.95–1.0) posterior probabilities, grey circles indicate moderate (0.85–0.94) posterior probabilities, open circles indicate low (0.75–0.84) posterior probabilities, and the lack of a circle indicates lack of support (0–0.74 posterior probabilities). The dashed branch has been artificially shortened. The small tree in the lower left-hand corner shows the full topology with the currently displayed branches darkened. The root node of Cleroidea is indicated. [Colour figure can be viewed at wileyonlinelibrary.com].

Rentoniidae

The rentoniine trogossitids are a distinctive group of mycophagous small leaf-litter or saproxylic beetles characterized by having a small (about 1–2 mm), strongly globular and convex adult body, an aedeagus with an undivided tegmen (Lawrence *et al*., 2014) and a larva with a single acute lacinial process and urogomphus with a pair of medially adjacent processes or consisting of a single unpaired hook (Gimmel & Leschen, 2014). The group was recovered as monophyletic in both BA (PP = 1) (Fig. 5) and ML (BS = 64) trees. This clade is equivalent to the Peltidae: Rentoniinae: Rentoniini of Crowson (1966), Peltidae: Rentoniinae of Crowson (1970) and Trogossitidae: Rentoniinae of Slipinski (1992). However, this group was not formally recognized in Kolibáč (2013), but subsumed within Trogossitidae: Peltinae: Thymalini along with *Thymalus* Latreille and *Protopeltis* Crowson. In our analysis, all three of these lineages were placed in separate parts of the tree. The rentoniines are a cohesive group of six described genera and at least one undescribed genus occurring in Australia, New Caledonia (undescribed species), New Zealand, Chile and Brazil. Although our taxon sampling is more comprehensive than all previous molecular phylogenies, the distinct relationship of Rentoniinae from other trogossitids was also evident in the phylogenies of Gunter *et al.* (2013), McKenna *et al.* (2015) and Zhang *et al.* (2018).

Within Rentoniidae **stat.n.**, the odd, highly compacted *Globorentonium* Lawrence & Slipinski from Australia was placed strongly sister to the remainder of taxa, all of which represented New Zealand species (PP = 1, BS = 100). Within the New Zealand clade, *Parentonium* Crowson [*P. magnum* (Crowson)] was placed sister to the remainder (PP = 1, BS = 97); *Rentonium bicolor* Gimmel & Leschen and *Australiodes vestitus* (Broun) were strongly (PP = 1, BS = 100) indicated as a monophyletic group sister to a complex clade containing the highly convex and apterous genus *Rentonellum* Crowson, the winged *Rentonidium* Crowson and *Rentonium* Crowson, plus a new morphogenus. Obviously, the generic system of Rentoniidae deserves careful revision, and it appears that an apterous syndrome ('*Rentonellum*') may have evolved multiple times within the family. Unfortunately, Chilean specimens slated for this study were too degraded to be sequenced, but the addition of these and New Caledonian members, plus additional members of the Australian fauna would make for an interesting biogeographical study given the apparent endemic Gondwanan distribution.

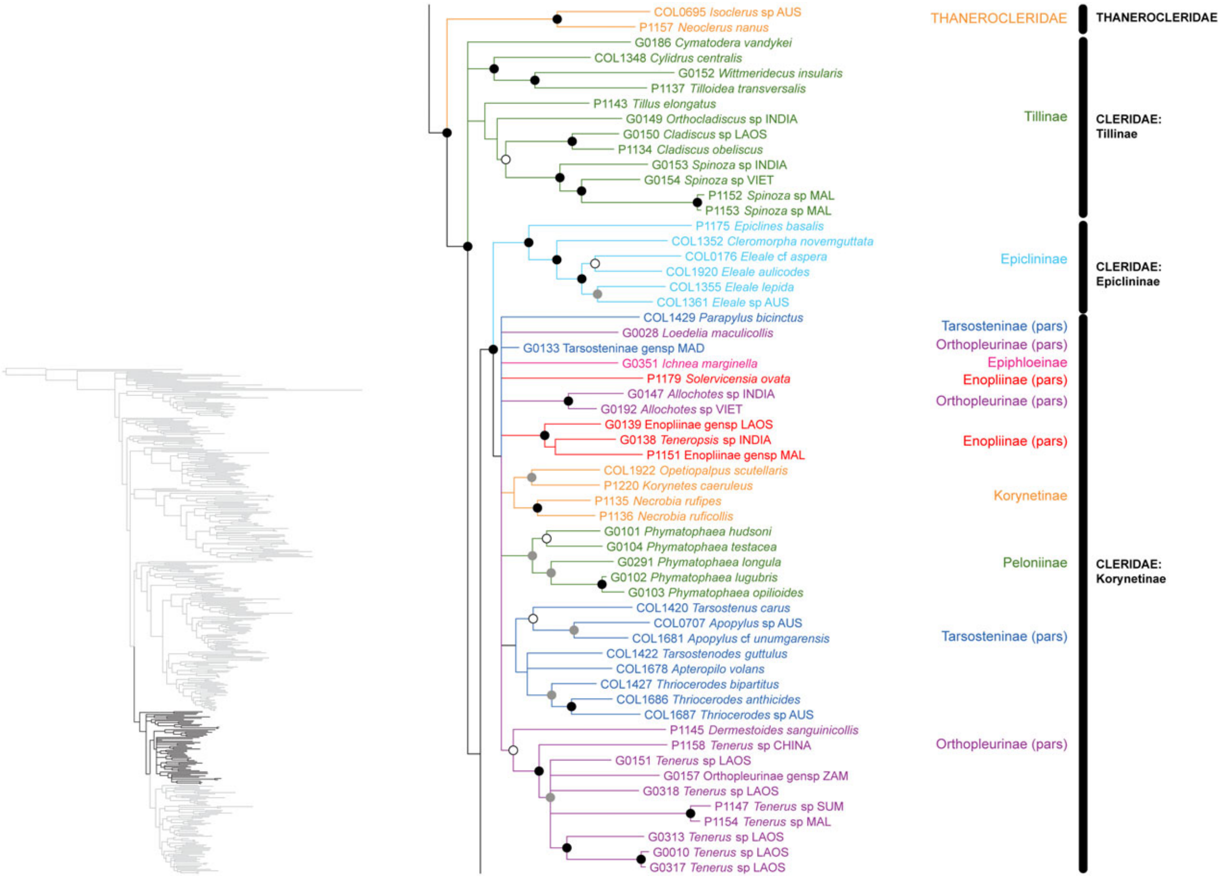

Fig. 9. Consensus tree resulting from Bayesian analysis of Cleroidea taxa (part 5 of 6). The left (coloured) column of names shows the old classification (from left column of Table 1), and the right (black) column shows the new classification (from the right column of Table 1). For names in the old classification, the term 'pars' is given after taxa represented in the tree by more than one nonadjacent clade. Black circles on nodes indicate high (0.95–1.0) posterior probabilities, grey circles indicate moderate (0.85–0.94) posterior probabilities, open circles indicate low (0.75–0.84) posterior probabilities, and the lack of a circle indicates lack of support (0–0.74 posterior probabilities). The dashed branch has been artificially shortened. The small tree in the lower left-hand corner shows the full topology with the currently displayed branches darkened. The root node of Cleroidea is indicated. [Colour figure can be viewed at wileyonlinelibrary.com].

Phloiophilidae

In the BA tree, Phloiophilidae, represented by *Phloiophilus edwardsi* Stephens, were recovered as one branch of an unsupported trichotomy (BS < 50) with Acanthocnemidae + (Byturidae + Biphyllidae) forming another (PP = 0.80), and the remainder of Cleroidea forming the third (PP = 0.88) (Fig. 5). However, the topology of the ML tree recovered Phloiophilidae sister to Rentoniidae, but this relationship was also unsupported. This enigmatic family with one species endemic to Europe was recently transferred as the tribe Phloiophilini to Trogossitidae: Peltinae by Kolibáč (2008), a placement which has not been adopted by subsequent authors (Leschen *et al*., 2010; Bouchard *et al*., 2011; Kolibáč, 2013). Our results reject Kolibáč's (2008) placement in the Peltinae, the core of which are recovered as a distinct monophyletic lineage at the base of the latter clade in our BA tree. Kolibáč's (2008) proposed sister groups to Phloiophilini were Colydiopeltini and Thymalini, which were fragmented into multiple lineages throughout our BA and ML trees.

Acanthocnemidae + Byturidae + Biphyllidae

This clade was recovered as monophyletic in both analyses, albeit weakly supported (PP = 0.80, BS = 30) (Fig. 5). Acanthocnemidae, represented by one species of *Acanthocnemus* Perris, have traditionally been included in the melyrid lineage (Crowson, 1955, 1964, 1970; Majer, 1994a), but our results, which place it as sister to Byturidae + Biphyllidae, suggest that it should be excluded from that strongly supported group (see later); however, our molecular data for *Acanthocnemus* are incomplete. Genitalic characters, particularly the divided or 'double' tegmen, have been suggested as linking the group with Trogossitidae (Crowson, 1964; Lawrence & Leschen, 2010b). The divided tegmen is present in most cleroids (Robertson *et al*., 2015), but is lacking in *Phloiophilus* and Rentoniidae (Lawrence & Leschen, 2010a; Lawrence *et al*., 2014). Byturidae and Biphyllidae have a similar division of the tegmen, each division with a set of struts (Goodrich & Springer, 1992; Leschen *et al*., 2010). Lawrence & Leschen (2010b) noted that the characters of

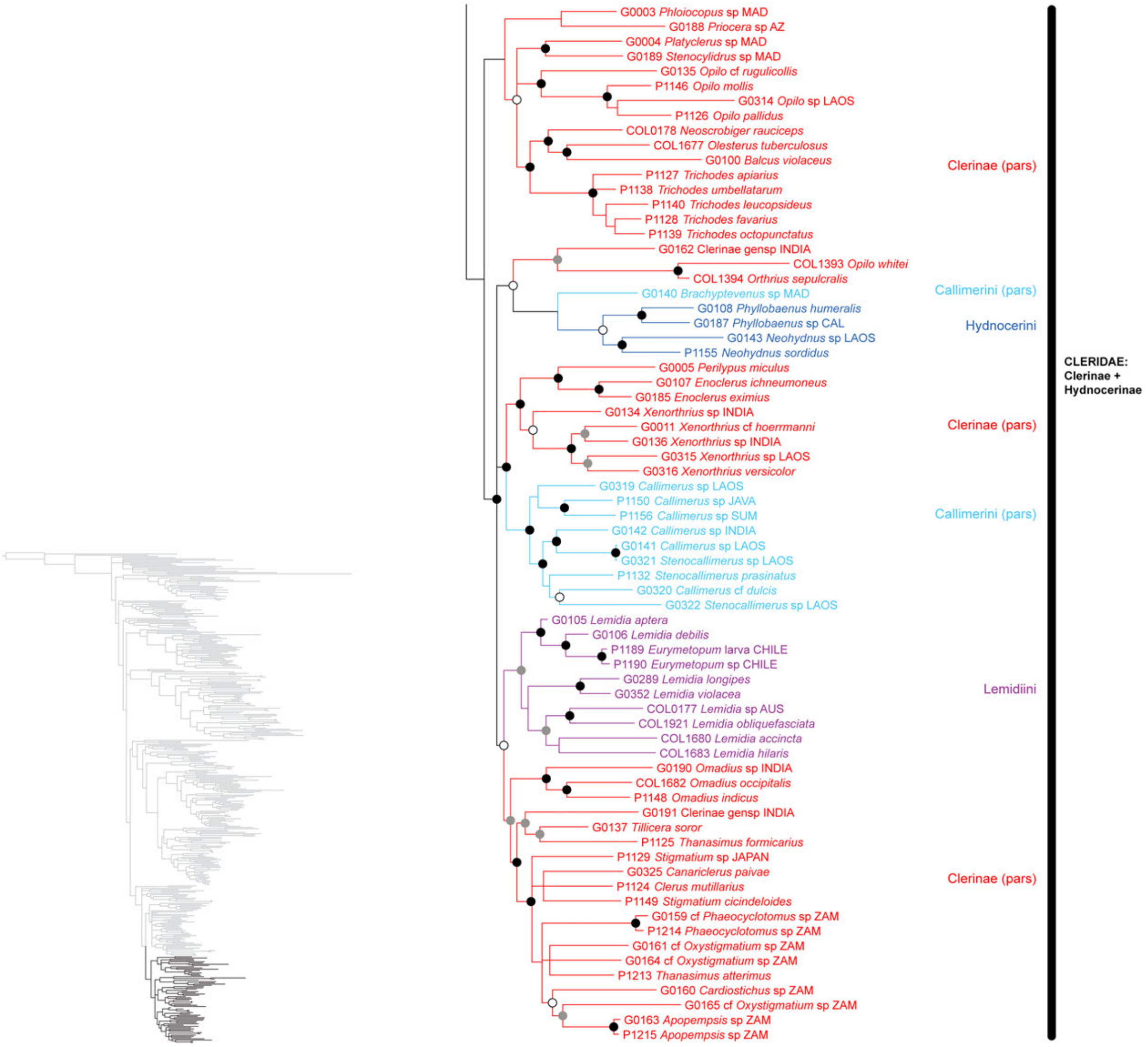

Fig. 10. Consensus tree resulting from Bayesian analysis of Cleroidea taxa (part 6 of 6). The left (coloured) column of names shows the old classification (from left column of Table 1), and the right (black) column shows the new classification (from the right column of Table 1). For names in the old classification, the term 'pars' is given after taxa represented in the tree by more than one nonadjacent clade. Black circles on nodes indicate high (0.95–1.0) posterior probabilities, grey circles indicate moderate (0.85–0.94) posterior probabilities, open circles indicate low (0.75–0.84) posterior probabilities, and the lack of a circle indicates lack of support (0–0.74 posterior probabilities). The dashed branch has been artificially shortened. The small tree in the lower left-hand corner shows the full topology with the currently displayed branches darkened. The root node of Cleroidea is indicated. [Colour figure can be viewed at wileyonlinelibrary.com].

the recently discovered larva of *Acanthocnemus* 'suggest a more basal position within the superfamily' than the melyrid lineage. Interestingly, Pic (1926) recognized the family 'Phloeophilidae' containing *Phloiophilus* Stephens, *Acanthocnemus* and *Xerasia* Lewis (now in Byturidae) and although the position of *Phloiophilus edwardsi* remained unresolved in our study, increased taxon sampling of the Byturidae (including the unsampled subfamily Platydascillinae) and gene sampling of *Acanthocnemus* may improve our understanding of the interrelationships between these four families. The Byturidae and Biphyllidae sister grouping received high support in our BA tree (PP = 1) and our ML tree (BS = 90). Additionally, the groups were recovered as reciprocally monophyletic in our analyses, but only two of seven byturid genera were sampled (PP = 1, BS = 100) whereas six of seven described genera and one undescribed genus of Biphyllidae were sampled (PP = 0.90, BS = 76).

Protopeltidae + Trogossitidae (part) + Peltidae

A lineage containing a heterogeneous group of trogossitids from the genera *Protopeltis* (Peltinae: Thymalini), *Calitys*

Thomson (Trogossitinae: Calityini), *Egolia* Erichson (Trogossitinae: Egoliini), *Larinotus* Carter & Zeck (Trogossitinae: Larinotini) and *Peltis* O.F. Müller (Peltinae: Peltini) was recovered in our Bayesian analysis (Fig. 5). This unsupported clade (PP = 0.58) was recovered as a separate lineage from all remaining Trogossitidae, the melyrid lineage and the clerid group. All of the genera in this clade are currently classified in tribes within the subfamily Trogossitinae or Peltinae. Trogossitinae also includes the tribes Gymnochilini and Trogossitini, which form a distinct, monophyletic clade in our analyses, and Peltinae, represented by the tribes Peltini, Thymalini and Colydiopeltini, is also recovered as polyphyletic in both BA and ML analyses. Our results support taxonomic changes within these subfamilies to reflect more natural groupings.

A taxonomic group including only *Protopeltis*, *Calitys*, *Egolia*, *Larinotus* and *Peltis* would be difficult or impossible to justify on morphological or biological grounds. Furthermore, the topologies between our ML and BA trees were neither congruent nor well supported. In ML, the phylogenetic position of *Protopeltis* was unresolved, forming an independent branch, *Calitys* + *Egolia* were recovered adjacent to the core Trogossitinae, and *Larinotus* + *Peltis* were recovered adjacent to Lophocaterinae (Fig. S1). These alternative relationships observed in ML analysis were unsupported, and the summary tree in Fig. 4 highlights a large polytomy where nodes supported by BS < 30 are collapsed, with only the relationship between *Calitys* + *Egolia* (BS = 59) and *Larinotus* + Peltini (BS = 37) recovered with weak support, *Protopeltis* unresolved, and the remaining trogossitid, melyrid group and clerid group clades recovered with varying support across the large polytomy. Given the limited and alternating phylogenetic support, we refrain from proposing a single taxonomic group for the clade. No clear solution is apparent, and four alternative classifications could be warranted based on the current phylogenetic results. Firstly, in order to create some taxonomic stability that reflects a more natural grouping in the family Trogossitidae, a semiradical approach could be taken that elevates these five tribes each to family ranking. Secondly, a more conservative approach may be taken that (re-)elevates only Protopeltidae and Peltidae to family based on easily distinguishable morphological characters, acknowledging the heterogeneous nature of these former 'Peltinae'; at the same time, Larinotini, Calityini and Egoliini could be re-elevated to subfamily but retained within a possibly polyphyletic Trogossitidae, acknowledging the historically recognized affinities of these groups in the 'Trogossitinae'. Lastly, these groups could be rendered *incertae sedis* among Cleroidea or a combination of these three approaches could be taken. Although no solution is ideal at this early stage, we take a semi-conservative 'middle' approach which is supported by morphology and our phylogenetic results, as follows. It is likely that further taxonomic changes will be made within this lineage with improved taxon sampling, particularly among Egoliini; however, this proposal provides a first step toward more natural groupings within the Cleroidea.

Protopeltis is elevated to family rank as Protopeltidae **stat.n.** *Protopeltis* was previously considered to be related to the rentoniines by Crowson (1966), who subsequently gave it its own subfamily in Peltidae (Crowson, 1970). Most recently, Kolibáč (2006) grouped it (along with rentoniines) into the tribe Thymalini. However, none of our molecular evidence suggests a close relationship between *Protopeltis* and any other cleroid group, including the eight other thymaline genera sensu Kolibáč (2006), which includes *Thymalus* and those in the Rentoniidae clade defined earlier and Lophocaterinae. Because of the mosaic nature of its character states, *Protopeltis* has been difficult to classify within Cleroidea. Adults are similar to those of Lophocaterinae but distinct from many members of this group and other trogossitids by having a membranous prostheca and a submolar lobe on the mandible (Crowson, 1964; Lawrence *et al*., 2014), simple nontuberculate window punctures on the elytra and presence of the transverse metaventral (metakatepisternal) suture that does not cross the midline (J. F. Lawrence & R. A. B. Leschen, unpublished data), aciculate terminal maxillary palpomeres, prosternal process narrow and not expanded at apex, as well as having three lacinial hooks in the larvae (Crowson, 1964), a character absent in trogossitids (Kolibáč, 2006).

Peltidae **stat.rest.** (sensu stricto, containing only *Peltis*) is re-elevated to family. Peltinae formerly comprised the three tribes Peltini, Colydiopeltini and Thymalini. Based on phylogenetic evidence discussed earlier (and also later), only the former Peltini, represented by the single genus *Peltis*, is retained within the family, and no tribes are recognized. Whereas our results suggest a possible sister grouping of *Larinotus* and Peltidae, there are no known adult characters that unite *Larinotus* + *Peltis*. Possible shared larval characters may be presence of minute urogomphi, anterior gular apodemes present (present also in *Thymalus*, *Rentonium* and *Protopeltis*) and absence of dorsal thoracic sclerites (also in Decamerini and some Lophocaterini). *Larinotus* is monotypic and the only genus in the tribe Larinotini (Trogossitinae), and given the lack of unique morphology that links it to Peltidae, coupled with poor support values in ML and BA, we refain from transferring it to the family. Furthermore, based on genetic evidence that it is distantly related from the core Trogossitinae, we take a conservative approach and retain *Larinotus* in subfamily Larinotinae within the narrowed but still heterogeneous and potentially nonmonophyletic concept of Trogossitidae.

Egoliini and Calityini are treated as subfamilies of a restricted concept of Trogossitidae. As with Larinotinae, since these tribes have not been convincingly associated with other higher taxa in this study but are still morphologically coherent, they are conservatively retained in Trogossitidae (=former Trogossitinae) but their rank is elevated to reflect the rank elevation of the parent taxon (Trogossitinae to Trogossitidae). Improved taxon sampling is needed to investigate not only the exact relationship with Trogossitinae, but also the monophyly of Egoliini and to confirm the supported relationship with *Calitys* (Trogossitinae: Calityini) (PP = 1, BS = 59). We considered including Calityini within a broader concept of 'Egoliinae' on the basis of potential larval synapomorphies (i.e. abdominal tergite 9 with a raised rim and a single median pit between bases of urogomphi) and potential adult synapomorphies (i.e. mandibles with a distinct mola accompanied by setal fringe, and the lacinia with a strong hook (derived from Crowson, 1970)). However, the Egoliini are themselves a heterogeneous group containing five genera distributed in Australia and southern South America (but *Calanthosoma* Reitter equatorial, north to at least Venezuela and the Antilles), whereas Calityini contain only the Holarctic genus *Calitys*. Sampling of the additional genera of Egoliini, especially the aberrant *Calanthosoma*, would be highly enlightening for further phylogenetic studies and confirm the relationship between *Calitys* and *Egolia* recovered in our analyses.

There are no known unique and unreversed adult characters to define the new concept of Trogossitidae, but Larinotinae, Egoliinae, Calityinae and Trogossitinae have broadly closed procoxal cavities, a character also present in *Parapeltis* Slipinski.

Lophocaterinae + Colydiopeltini

This group was strongly supported as monophyletic in the BA (PP = 1) (Fig. 5) and ML (BS = 99) trees. Within the clade, the following relationships are consistently recovered: (i) the genus *Grynocharis* Thomson (Lophocaterini) was placed as sister to the remainder of the clade, which received moderate to high support (PP = 0.96, BS = 61); (ii) *Parapeltis* (Peltinae: Colydiopeltini), *Eronyxa* Reitter (Lophocaterini) and *Trichocateres* Kolibáč (Lophocaterini) formed a grade of early branches with various relationships recovered between BA and ML analyses; and (iii) a 'crown group' of Lophocaterinae (PP = 1, BS = 98), represented here by seven genera from the tribe Ancyronini and one genus from the tribe Lophocaterini. Critically, the third tribe of the Lophocaterinae, Decamerini, sampled in our analysis by *Diontolobus* Solier, is not recovered in this well-supported clade containing all Lophocaterini and Ancyronini genera, and *Parapeltis* (see discussion later).

In both analyses, the crown group of lophocaterines was split into two groups, each with high support. The first contained exclusively southern hemisphere genera currently split between Ancyronini (*Grynoma* Sharp) and Lophocaterini (*Promanus* Sharp, *Peltonyxa* Reitter) (PP = 1, BS = 88). Each genus was recovered as monophyletic, but *Promanus* was only sampled by one species. An apparent new genus from Australia, hypothesized to be related to *Peltonyxa*, was recovered as sister to that genus in both analyses (PP = 0.99, BS = 83). The second group (PP = 1, BS = 80) contained the remaining Ancyronini represented by *Ancyrona* Reitter, *Afrocyrona* Kolibáč and *Neaspis* Pascoe, plus *Lophocateres* (Lophocaterini). Our representative of *Lophocateres*, *L.* sp. cf. *pilosus* Olliff, is not mophologically similar to the type species of the genus, *L. pusillus* (Klug), so the actual position of core *Lophocateres* in the tree remains a mystery and future revision may well be necessary. Furthermore, this second clade represents a very large group of Lophocaterinae, containing most of the described species. The largest and most variable genus is the nearly cosmopolitan *Ancyrona*, the limits and composition of which have not been investigated in modern times. Our sampling of that genus was quite broad, including 13 putative morphospecies from Africa, Madagascar, Southeast Asia and South America. Our results suggest that it may be necessary to further divide the genus in the future.

As a result of these congruent phylogenetic relationships and supporting morphological evidence, the following classification changes are proposed. Lophocateridae **stat.rest. and sensu n.** is re-elevated to family and revised to include *Parapeltis* and *Colydiopeltis*, formerly comprising Peltinae: Colydiopeltini, and exclude the Decamerini. Although *Parapeltis* was recovered within the clade representing Lophocateridae in our tree, the relationships of the possibly morphologically convergent *Colydiopeltis* (see Slipinski, 1992: 444) are still open to question, as the latter was not included in our analyses. Given the apparent paraphyly of both Ancyronini and Lophocaterini, we recommend that no subfamilial/tribal system be recognized until further investigation can be conducted within the family. After the exclusion of Decamerini, the following putative larval synapomorphies are proposed for the family Lophocateridae: presence of two stemmata in most taxa (this character is variable, and may be reduced to one, or three may be present, as in *Grynoma*), a plumose lacinia (present outside this group in decamerines), abdominal tergum IX transversely divided (reversed in *Parapeltis*) and median interurogomphal process present (reversed in *Parapeltis*). Kolibáč (2013) suggested that *Eronyxa* should be classified once again with Decamerini, but our results provide strong evidence that it belongs with Lophocateridae, as suggested by Tait *et al.* (1990) in a larval study. *Eronyxa* adults also lack the toothed claws, long postcoxal process of the hypomeron, and membrane between the clypeus and labrum possessed by members of Decamerini.

Trogossitinae: Gymnochilini + Trogossitini

This group was strongly supported as monophyletic in the BA tree (PP = 0.98) (Fig. 6) and ML tree (BS = 98), but did not have a supported sister grouping in either analysis. Members of the tribes Gymnochilini and Trogossitini were recovered reciprocally paraphyletic in both analyses. We sampled six of seven known genera of the former tribe, and seven of 14 known genera of the latter. Characters supporting this group are the strongly asymmetrical antennal club (present in some egoliines) that is usually flattened and always with distinctive sensory fields along the lateral margins, which is a character unique to this grouping. Other characters supporting this group are the adults having the two apical mandibular teeth arranged vertically (present also in *Larinotus* and *Grynoma*), absence of procoxal rests on the mesoventrite (present also in Egoliinae), the larva with paragular sclerites (present in some Egoliinae and Lophocateridae) and pedunculated setae on the lacinia (present also in Lophocateridae; see Kolibáč, 2006; Kolibáč & Zaitsev, 2010). Given the paraphyly of the tribes Gymnochilini and Trogossitini, we synonymize Gymnochilini **syn.n.** with Trogossitini, which comprises the Trogossitidae: Trogossitinae **sensu n.**

Genera currently classified into Gymnochilini were resolved among three separate branches: one branch (PP = 98, BS = 96) comprising the genera *Gymnocheilis* Dejean, *Xenoglena* Reitter and *Anacypta* Illiger (each reciprocally monophyletic); one branch containing only *Kolibacia tibialis* (Reitter), which was strongly (PP = 1, BS = 92) sister to the following clade plus the core Trogossitini; and one branch (PP = 1, BS = 77) containing the genera *Leperina* Erichson and *Phanodesta* Reitter. The latter two genera were strongly recovered as reciprocally monophyletic in the BA tree (PP = 0.99 and 1, respectively), which is consistent with the recent reorganization of the two genera (and creation of *Kolibacia* Leschen & Lackner) by Leschen & Lackner (2013). The ML tree results were less conclusive, with *Leperina* being paraphyletic with weak to moderate branch support with respect to *Phanodesta*.

Within the genera currently classified in Trogossitini, the genus *Alindria* Erichson was recovered as an early-branching member of the Trogossitinae clade, and *Melambia* Erichson was recovered in a sister-group relationship with the *Gymnocheilis/Xenoglena/Anacypta* clade. The large genera *Tenebroides* Piller & Mitterpacher and *Temnoscheila* Westwood were well sampled (11 and 12 morphospecies, respectively). Only the latter genus was shown to be monophyletic (PP = 1, BS = 100). One notable result within *Temnoscheila* was the division into two well-supported clades, one comprising exclusively Old World taxa (PP = 1, BS = 100) and one comprising only New World taxa (PP = 0.99, BS = 81). Weakly indicated (PP = 0.82, BS = 47) as sister to this genus were *Nemozoma* Latreille and the brachelytrous form known until recently as *Cylidrella* Sharp. These latter two genera were synonymized by Kolibáč (2005). Sister to *Temnoscheila* + *Nemozoma* (including *Cylidrella*) was a strongly supported group (PP = 1, BS = 96) containing both *Tenebroides* and *Airora* Reitter. The two sampled *Airora* species were recovered together with high support (PP = 1, BS = 100), but fell out in the middle of a polytomy of *Tenebroides* species. This suggests that the cosmopolitan genus *Tenebroides* deserves to be looked at in greater detail for potential subdivision into several genera, and/or synonymization of *Airora* (and potentially other, unsampled genera). It is interesting to note that, contrary to the key in Kolibáč (2013), many true *Tenebroides* possess the frontal impressed line which also characterizes members of *Temnoscheila*. Based on our sampled morphospecies, a dorsoventrally flattened body shape and straight lateral pronotal carina (when viewed laterally) are more reliable characters for the genus *Tenebroides*. It is likely that many species currently placed in *Temnoscheila* actually belong in *Tenebroides*.

Thymalus + Diontolobus

A small clade containing the highly distinctive and mycophagous genus *Thymalus* (most recently placed in Peltinae: Thymalini) and our two representatives of the Decamerini (most recently placed in Lophocaterinae), *Diontolobus lanuginosus* (Léveillé) and *Diontolobus punctipennis* Solier, was recovered in both topologies with moderate to strong support (PP = 1, BS = 77) (Fig. 7). In both analyses, it was recovered as adjacent to the melyrid lineage, although this sister relationship was not strongly supported (PP = 0.63, BS = 28). *Thymalus* was included in the study of McKenna *et al.* (2015) and was recovered as sister to *Acanthocnemus*; however, Decamerinae were not sampled and total taxon sampling of the Cleroidea was limited to 19 terminals.

The two *Diontolobus* were recovered as the strongly supported sister group to *Thymalus* (PP = 1, BS = 100). The Decamerinae contain two other (unsampled) genera, both more or less parallel-sided flower visitors, *Decamerus* Solier and *Antixoon* Gorham. *Thymalus*, however, is highly modified, cassidine-like in gross morphology, being rounded in outline with highly explanate margins, domed in cross-section, and with the head mostly hidden from above. *Thymalus* and Decamerini lack anterior pronotal angles (a character that is present in Egoliinae and a few Trogossitinae and Lophocateridae), have confusedly punctate elytra (a putative ancestral character for cleroids but not widely present in many other former Trogossitidae) and parameres that are fused to the tegmen (*Thymalus*) or absent (Decamerini). The larval head lacks a dorsal endocarina and ventral epicranial ridges (also absent in many Lophocateridae, Peltidae and Trogossitinae: *Nemozoma*) and antennomere 1 is transverse (shared by *Rentonium*, *Protopeltis* and *Calitys*). The aforementioned larval characters should be accepted with caution, however, because the larval association of *Diontolobus* has not been substantiated (Kolibáč, 2013). Crowson (1970) rhapsodized that, assuming the unusual larva described in Crowson (1964, 1966) as *Diontolobus* was correctly identified, Decamerinae probably deserved its own family. *Eronyxa*, formerly included in Decamerinae (Crowson, 1964, 1966, 1970) prior to its larval description by Tait *et al.* (1990), was not recovered near the decamerines in our analyses but nested firmly within Lophocateridae (see earlier), despite comments to the contrary by Kolibáč (2013: 119–120). McKenna *et al.* (2015) also recovered the sister relationship between *Eronyxa* and Lophocateridae (represented by *Grynoma*).

We conclude that this clade represents a newly defined grouping, the Thymalidae **stat.n. sensu n.**, including two subfamilies, Thymalinae and Decamerinae. The biogeography of the group is interesting to consider. The genus *Thymalus* contains several species, all Holarctic, while the Decamerinae contains three described genera, all occurring in southern South America (*Decamerus*, *Diontolobus*) and Central America (*Antixoon*). In an analogous way to the Egoliini + Calityini clade, the Thymalidae includes two disparate-looking lineages with a primarily amphitropical distribution, with one genus distributed in tropical regions.

Chaetosomatidae and Metaxinidae

This sister grouping of New Zealand taxa was highly supported in both analyses (PP = 1, BS = 100), although its phylogenetic position alternated between the topologies and in each case its placement was weakly supported. In the BA tree (Fig. 6), it was recovered without support (PP = 0.55) as sister to the Trogossitidae (sensu stricto). In the ML tree, it was recovered with weak support (BS = 40) as sister to the Thaneroclerldae + Cleridae, a relationship congruent with the informal clerid group. This latter relationship is relatively congruent with that recovered by McKenna *et al.* (2015), and although taxon sampling among Cleroidea was limited in that study, Chaetosomatidae and

Metaxinidae were recovered as sister to Cleridae (BA) or Cleridae + Thanerocleridae (ML). However, it should be noted that in McKenna *et al.* (2015), this clade was included in a larger clade also containing *Temnoscheila* (Trogossitini), a relationship not supported in our analyses.

Taxa included in Chaetosomatidae and Metaxinidae were historically associated and variously classified in Cleridae (in the original description), Chaetosomatidae (by Crowson, 1952, 1955), Thanerocleridae (by Crowson, 1964, as Cleridae: Thaneroclerinae, along with a larval description) or as Cleroidea *incertae sedis* (by Kolibáč, 1992) until the study of Kolibáč (2004). That morphological analysis included *Chaetosoma* and *Metaxina*, along with other members of the Cleroidea, and based on an unresolved trichotomy along with Chaetosomatidae and Thanerocleridae, Kolibáč (2004) gave *Metaxina* its own family.

In our analyses a strongly supported relationship was recovered between Chaetosomatidae, represented by *Chaetosoma scaritides* Westwood, and the monotypic Metaxinidae, containing only *Metaxina ornata* Broun, differing from the former for its pro- and mesotibiae lacking spines, confused elytral punctation and adult mandibular structure (see Lawrence *et al*., 2014). However, this grouping is strongly supported by adult morphological characters, including filiform antennae, long and bristling setae, simple tarsal claws and gular sutures that are fused or nearly confluent (see Crowson, 1952, 1955; key in Lawrence *et al*., 2014), as well as having the apical labial palpomere slightly expanded, a relatively short prosternal process that does not extend posteriorly beyond the edge of the procoxae, procoxal cavities with anterolateral extensions, hindwing lacking AA_4 and the mesal surface of the larval mandible with two to five hyaline processes (Lawrence *et al*., 2011). We therefore synonymize Metaxinidae **syn.n.** with Chaetosomatidae. Without a sampling of the other two genera of Chaetosomatidae (the New Zealand genus *Chaetosomodes* and the Malagasy *Malgassochaetus*), we refrain from making recommendations on the internal classification of the group.

Melyrid lineage (including Phycosecidae)

The 'melyrid lineage' (Lawrence & Newton, 1982; Bocakova *et al*., 2012), including Phycosecidae but to the exclusion of Acanthocnemidae (see earlier), was recovered with moderate to high support (PP = 0.98, BS = 64) (Fig. 7). Phycosecidae contain one beach-dwelling genus (*Phycosecis* Pascoe) in Australia, New Caledonia, Vanuatu and New Zealand. Crowson (1964) was the first to suggest the relationship of *Phycosecis* with the melyrid lineage, being more 'primitive' than most, while not as 'primitive' as *Acanthocnemus*. He later (Crowson, 1970) created new families for each, despite the latter being based on a misidentified larva (probably representing *Parapeltis* according to Lawrence & Leschen, 2010b). However, our results are consistent with Crowson's general claim that *Phycosecis* is a plesiomorphic melyrid-lineage member, whereas *Acanthocnemus* may be more distantly related. Bocakova *et al.* (2012), although focused on molecular phylogenetics of the melyrid lineage in particular, did not include Phycosecidae or Acanthocnemidae. Our results place Phycosecidae firmly as the first-branching member of the melyrid lineage and are congruent with relationships recovered by McKenna *et al.* (2015). However, the placement of *Acanthocnemus* near Byturidae + Biphyllidae in our analyses differs from the results presented by McKenna *et al.* (2015), which moderately (PP = 0.86) supported an *Acanthocnemus* + *Thymalus* clade within a strongly supported clade of other Trogossitinae and Lophocaterinae. It should be noted that *Acanthocnemus* in our analysis is only represented by two out of four genes sampled in the tree, whereas McKenna *et al.* (2015) included all eight genes sequenced; thus the relationship recovered here may be an artifact of missing data. Alternatively, a placement of *Acanthocnemus* within a moderately supported clade including *Leperina* (Trogossitinae), *Larinotus* (Larinotinae) and *Thymalus* (Thymalidae), and apart from Lophocateridae, was obtained in Zhang *et al.* (2018).

The remainder of the melyrid lineage is represented by two main clades, one poorly supported (PP = 0.70, BS = 28) and containing Mauroniscidae + Rhadalidae, and another weakly to highly supported (PP = 0.97, BS = 46), containing Prionoceridae and Melyridae (including Malachiidae, Melyridae sensu stricto and Dasytidae).

Mauroniscidae

Two of five genera currently classified in the family Mauroniscidae were included in this study. The Mauroniscidae were rendered paraphyletic by the inclusion of *Dasyrhadus* Fall from Rhadalidae (Fig. 7). However, this clade represented by *Amecomycter* Majer, *Mauroniscus* Bourgeois and *Dasyrhadus* was recovered in both analyses with moderate to high support (PP = 0.92, BS = 59). *Dasyrhadus* has been previously recognized as an aberrant member of Rhadalidae (Lawrence & Leschen, 2010c, as Rhadalinae); the adult abdominal ventrites are not connate as in all other known species and the median lobe lacks a dorsal appendage or 'lever'. Crowson (1964) placed it in the Dasytinae, and Peacock (1987: 144) followed this, explaining that '… certainly the example of *Dasyrhadus longior* Fall in the BMNH does not belong to the Rhadalinae [=Rhadalidae]'. Majer (1994a), however, placed it in Rhadalidae, and Mayor (2002) followed this because of the triangular terminal maxillary palpomere and setose eyes, which are traditional rhadalid characters. Our results place *Dasyrhadus* distant from the otherwise strongly monophyletic Rhadalidae clade, although its internal relationships in the Mauroniscidae are not well resolved in our analyses. However, *Dasyrhadus* does not obviously fit in with Mauroniscidae, as it does not share the elongated head and cylindrical pronotum and has well-developed tarsal appendages (like most Dasytinae and some Rhadalidae). The shape of the spiculum gastrale in *Dasyrhadus* resembles that of members of *Amecomycter* in the Mauroniscidae, and the tegmen and penis shape are also fairly similar in gross structure. The relationships of *Dasyrhadus* require more detailed study, but for now we are tentatively transferring it to the Mauroniscidae.

Although monophyly of Mauroniscidae, represented only by three members of the genus *Amecomycter*, was strongly supported in Bocakova *et al.* (2012), its exact placement within the melyrid lineage was ambiguous. In our analyses, monophyly of Mauroniscidae (including *Dasyrhadus*) was moderately to strongly supported (see earlier), and it was recovered adjacent to the Rhadalidae (including *Gietella* Constantin & Menier), but this putative sister relationship had low support in all analyses.

Rhadalidae and Gietella

The family Rhadalidae, to the exclusion of *Dasyrhadus* (transferred earlier in the paper), received high support in both analyses (PP = 1, BS = 90) (Fig. 7). The group was also strongly supported as sister to *Gietella* in BA (PP = 1) and moderately supported as sister in ML (BS = 63). The relationship of *Gietella* with some genera of Rhadalidae (as Rhadalinae) has been discussed before by Constantin & Menier (1990) based primarily on larval characters, including the elongated head with parallel temples, two stemmata on each side, elongate thoracic sclerites, and lack of well-developed urogomphi. However, no adult characters have been suggested as indicating a relationship between the two groups, and they ultimately rejected this hypothesized relationship. One conspicuous character shared by all Rhadalidae (with the exception of *Dasyrhadus*), the connate basal two abdominal ventrites, is not shared by the two species of *Gietella*. The Azorean species of *Gietella*, *G. faialensis* Menier & Constantin, has the first three abdominal ventrites connate, whereas the Canarian species, *G. fortunata* Constantin & Menier, has all abdominal ventrites free. Additionally, the male genitalia of *Gietella* lack a dorsal lever (Constantin & Menier, 1990).

Because of the moderately to strongly supported relationship in our analysis, and the shared larval characters, we hereby transfer the subfamily Gietellinae **new placement** from Dasytidae to Rhadalidae **sensu n.** All previous Rhadalidae (except *Dasyrhadus* – see Mauroniscidae earlier) are to be placed in the subfamily Rhadalinae.

Prionoceridae

Results within Prionoceridae were consistent with the current tribal classification, *Lobonyx* Jacquelin du Val (only representative of Lobonychini) being recovered sister (PP = 1, BS = 100) (Fig. 7) to the remaining Prionoceridae (Prionocerini), including *Idgia* Laporte de Castelnau and *Prionocerus* Perty. However, *Idgia* was recovered as paraphyletic with respect to *Prionocerus*, a topology totally consistent with those of Geiser *et al.* (2016). In our analyses, Prionoceridae are strongly supported as sister to a clade containing Malachiidae, Melyridae sensu stricto and Dasytidae (=Melyridae **sensu n.** in our study), consistent with the results of Bocakova *et al.* (2012) and McKenna *et al.* (2015).

Melyridae

The families Malachiidae, Melyridae sensu stricto and Dasytidae (sensu Bocakova *et al*., 2012) were recovered together as a monophyletic lineage with high support (PP = 0.98, BS = 100). Here we propose a family definition that includes these fragmented family concepts into Melyridae **sensu n.**, equivalent to Melyridae sensu Lawrence & Leschen (2010c) and Bouchard *et al.* (2011), but with Rhadalinae and Gietellini removed to Rhadalidae. We have recognized these three families as one for two reasons. First, the previous study of Bocakova *et al.* (2012) recovered a lineage with the same constitution, but in that study the internal subfamily (= family in that study) nodes presented an alternate topology, including paraphyly of Dasytidae. Secondly, the single-family classification is similar to recently published worldwide treatments of beetle taxa (Lawrence & Leschen, 2010c; Bouchard *et al*., 2011; Lawrence *et al*., 2011). However, establishment of a comprehensive morphological definition of such a broadly defined family will require systematic study of a large number of taxa.

Malachiinae

The family Malachiidae, here recognized as subfamily Malachiinae, was recovered as monophyletic with high support (PP = 0.99, BS = 98) (Figs 7, 8), sister to the Melyridae sensu stricto and Dasytidae (PP = 0.98, BS = 100). This is a contrasting placement to that of Bocakova *et al.* (2012), which indicated Malachiidae as a monophyletic crown group of a grade involving Melyridae sensu stricto and two clades of Dasytidae. The Malachiinae in our analyses were divided into two well-supported clades, the Carphurini (PP = 1, BS = 100), represented by four species of *Carphurus* Erichson in our analyses, and the remaining Malachiinae (PP = 1, BS = 100), represented by Lemphini and Malachiini in our analyses. This topology is consistent with the hypothesis of Majer (2002), but without inclusion of Pagurodactylini or Amalthocini, the earliest branching Malachiinae remain unknown.

Attalomimus *and Malachiinae: Lemphini*

The Lemphini were characterized by Majer (2002, as Lemphinae) as having a reduced tarsomere 4 (shared with the Malagasy endemic Amalthocini) and a pronotum without impressions. *Attalomimus* Wittmer, constituting the monogeneric family Attalomimidae in Majer (1994a), was characterized as having a 4-4-4 tarsal formula and long hairs on intermediate antennal segments. However, it shares with Malachiinae extrusible vesicles and otherwise has a typical malachiine-like habitus. According to Majer (1994a), the genitalia of *Attalomimus* are also quite malachiine-like but differ in the complex apex and divided base of the median lobe. He also stated that ‘the Attalomimidae seem to have common ancestors with the Malachiidae-Lemphinae; the latter group are primitive Malachiidae in which tarsomere 4 is greatly reduced’ (Majer, 1994a: 382). The current molecular results (Fig. 7) go beyond supporting the claim of common ancestry with Lemphini, as *Attalomimus* rests firmly within this group, strongly supported as sister to *Engilemphus* Wittmer (PP = 1, BS = 100) and these, in turn, moderately to strongly

(PP = 0.99, BS = 78) supported as sister to *Brachidia* Solier. However, by our estimation, the Carphurini are sister to the remaining Malachiinae, and the Lemphini are sister to Malachiini (all remaining Malachiinae in our analysis). The most parsimonious conclusion is that the ancestor to Lemphini sensu novo (perhaps plus Amalthocini, unsampled in the present study) evolved a reduced tarsomere 4, which was subsequently lost or fused in *Attalomimus*. From a biogeographic standpoint, the distribution of *Attalomimus* in the West Indies is unsurprising in the context of the known Lemphini. *Brachidia* and *Nemacerus* Solier are Chilean, whereas *Engilemphus*, *Lemphus* Erichson and *Neolemphus* Wittmer are distributed in Central and South America. *Hypattalus* Blackburn, the remaining genus of Lemphini, is distributed in Australia; it is placed apart from the New World Lemphini in the present analysis (see later).

Malachiinae: Malachiini

The weakly to highly supported (PP = 0.98, BS = 48) clade of Malachiini (including *Hypattalus* from Lemphini) was characterized by massive internal polyphyly of the various proposed tribes (Fig. 7). The Australian *Hypattalus* was placed sister to a strongly supported subclade of Malachiini (henceforth ‘M1’) with weak to high support (PP = 0.98, BS = 57). The other subclade of Malachiini (henceforth ‘M2’) was strongly supported in both analyses (PP = 1, BS = 95).

The subtribe Apalochrina, represented here by five genera, was the only subtribe sampled with more than 1 representative that was strongly supported as monophyletic (PP = 1, BS = 99) within our sampled Malachiini; it fell within M1. The Attalina, in particular, were highly polyphyletic, forming five to six separate clades, depending on the analysis. The large cosmopolitan genus *Attalus* Erichson itself appeared in four to five different clades, depending on the analysis, with one to two clades in M1, and four separate clades in M2. *Attalus* was roughly divided by subgenus, but *Attalus* (sensu stricto) was both poly- and paraphyletic, with *A. (sensu stricto) viridescens* Pic falling out in M1, and *Fortunatius* Evers being nested within the main clade of *Attalus* (sensu stricto) in M2. Species of the genus *Colotes* Erichson (Colotina) were found to be sister to Apalochrina (PP = 1, BS = 93) in M1, while the other sampled genus of Colotina, *Pelochrus* Mulsant & Rey, appeared in M2, dividing up the core clade of Attalina there. The Troglopina were sampled by only one species of *Troglops* Erichson and were indicated as weakly sister to *Attalus (sensu stricto) viridescens* in the BA tree (PP = 0.71), but indicated as weakly sister to *Colotes* + Apalochrina in the ML tree (BS = 35) in M1.

In M2, the Ebaeina were strongly divided between *Ebaeus* Erichson + *Hypebaeus* Kiesenwetter on the one hand, forming a strongly supported (PP = 1, BS = 100) sister grouping to the remainder of M2; *Anthocomus* Erichson and *Charopus* Erichson, on the other hand, were recovered in various positions within the Malachiina. The other clade of M2 was weakly to strongly supported (PP = 0.99, BS = 55), and was formed by the non-*Attalus* genera of Attalina (*Endeodes* LeConte*, Tanaops* LeConte), which were strongly sister to each other (PP = 1, BS = 100), *Pelochrus* (Colotina), most *Attalus*, Malachiina and the remainder of Ebaeina. Interestingly, the heavily sampled Canarian species of *Attalus* (sensu stricto) (including the sympatric *Fortunatius*) formed a well-supported clade (PP = 1, BS = 100) to the exclusion of all other sampled taxa of *Attalus* [including the aforementioned *Attalus (sensu stricto) viridescens*]. Representatives of other subgenera (*Abrinus* Mulsant & Rey*, Antholinus* Mulsant & Rey, *Maurattalus* Pardo Alcaide) were recovered with varying support in entirely separate clades. This suggests that these currently recognized subgenera of *Attalus* should probably be elevated to generic rank or combined with other genera. The Malachiina were recovered together in a well-supported clade, but included the *Attalus* subgenera *Abrinus* and *Antholinus*, plus *Anthocomus* + *Charopus* from the Malachiina. The North American representative of *Malachius* Fabricius (*M. capillicornis* Abeille de Perrin) was far removed from the Palearctic representative [*M. bipustulatus* (Linnaeus)]; the many North American species nominally in this genus have previously been considered to represent a distinct genus, but these transfers have not been formally made (A. Mayor, personal communication).

These results suggest that major taxonomic rearrangements are required within the extremely complex and diverse Malachiini. However, as not all tribes, and only a small percentage of genera, have been included, such a reclassification is outside the scope of this study.

Dasytinae + Melyrinae

Dasytidae and Melyridae sensu stricto, henceforth considered as Dasytinae and Melyrinae, were recovered together as a monophyletic group (Fig. 8), subdivided into three clades identical in relationships and constitution in both analyses: Melyrinae were recovered as sister (PP = 0.96, BS = 36) to a clade of southern hemisphere and Andean Dasytinae (henceforth ‘D2’), and this clade sister to the sampled northern hemisphere Dasytinae, plus the South American genus *Listrocerus* Majer (henceforth ‘D1’). This first sister pairing (Melyrinae + D2) was recovered in Bocakova *et al.* (2012), but in that analysis this clade was sister to the remaining Dasytidae + Malachiidae. In our expanded analysis, which includes all taxa from that study, plus a number of additional taxa from Australia, New Zealand and the New World, we recover a weakly to strongly supported (PP = 0.98, BS = 36) clade ((Melyrinae + D2) + D1) sister to Malachiinae.

Tribal relationships within Dasytinae in our analyses differed notably from previous classifications, with the large tribes Dasytini and Danaceini polyphyletic with respect to Melyrinae, Chaetomalachiini (represented by *Dasytidius* Schilsky) and Listrini (represented by *Listrus* Motschulsky). These phylogenetic results strongly suggest that the Dasytinae should eventually be reorganized into at least two newly defined subfamilies. However, formal recognition of these subfamilies is not justifiable within this study because the vast majority of taxa involved have not been properly examined, and a very large proportion are thought to be misplaced at the genus and tribal level (M. L. Gimmel, personal observation).

Melyrinae

In both analyses this group was strongly indicated as monophyletic (PP = 1, BS = 100) (Fig. 8) and divided into two clades, the genus *Falsomelyris* Pic (representing Melyrini) on one hand (PP = 1, BS = 100), and *Arthrobrachus* Solier, *Astylus* Laporte de Castelnau and *Microzygia* Pic on the other (PP = 0.77, BS = 53). *Arthrobrachus*, in particular, was indicated as paraphyletic with respect to both *Astylus* and *Microzygia*.

D1

Sampled Palearctic members of Dasytini (*Allotarsus* Graells, *Dasytes* Paykull, *Divales* Laporte de Castelnau, *Dolichosoma* Stephens, *Enicopus* Stephens, *Psilothrix* Küster) were strongly recovered as a monophyletic group (PP = 1, BS = 100) (Fig. 8), which were weakly to strongly sister to the only North American dasytine sampled and the only representative of Listrini sampled (*Listrus*) (PP = 0.99, BS = 44). This grouping was in turn recovered weakly to strongly (PP = 0.95, BS = 39) sister to the sampled Palearctic members of Danaceini + Chaetomalachiini. Our representative of the latter, *Dasytidius*, was moderately to strongly recovered as sister (PP = 1, BS = 62) to *Mauroania* Majer, our representative of Danaceini: Amauronioidina, which were in turn sister (PP = 1, BS = 44) to the clade of *Danacea* Laporte de Castelnau. All of the foregoing Holarctic representatives were recovered sister with maximal support to *Listrocerus*, a Chilean genus currently placed in Danaceini: Danaceina. This latter genus was included among the other genera of Danaceini (as Danaceinae) in South America by its describer (Majer, 1999), but he noted that it differed considerably from the other genera by its complete prosternal process, partially moniliform antennae, and presence of long, paired basal struts on the median lobe of the aedeagus.

Similar to *Attalus* described earlier, the genus *Dasytes* divided up cleanly along subgeneric lines into three disparate yet monophyletic clades, suggesting these should be raised to generic rank.

D2

The second clade of Dasytinae, recovered as sister to Melyrinae (Fig. 8), consists of a number of Gondwanan and Andean elements, some of which were previously known to be misplaced to genus (e.g. ‘*Dasytes*’ in Australia; see Lawrence & Ślipiński, 2013a). The taxa fell into two main clades, one (PP = 0.99, BS = 99) consisting of *Amecocerus* Solier (‘Danaceini: Danaceina’) plus the Australian ‘*Dasytes*’, and the other (PP = 1, BS = 99) consisting of the South American ‘Danaceina’ *Haplamaurus* Kirsch, *Hylodanacaea* Pic and *Setigerodasytes* Pic plus the New Zealand Dasytinae (represented here by *Arthracanthus* Broun, but also including *Halyles* Broun and undescribed genera).

Based on these results, as well as those described earlier, the classification of the current Dasytinae requires enormous revision, well beyond the scope of this study. For now, we preserve the current concept of Dasytinae (=Dasytidae), while acknowledging the probable paraphyly of this group. Detailed examination of tribal and subfamilial relationships within the Dasytinae, which must include the diverse but currently very poorly understood Nearctic fauna, will be deferred to future study.

Thanerocleridae

The family Thanerocleridae was strongly supported as sister to Cleridae in both analyses (PP = 0.99, BS = 86) (Fig. 9). This contradicts the result of Gunter *et al.* (2013), who found it to be nested within the Cleridae. Three factors may have contributed to this incongruence: (i) our poorer taxon sampling within Thanerocleridae (two species in two genera vs five species in three genera); (ii) our utilization of *18S* data, which were lacking in the Gunter *et al.* (2013) study; or (iii) improved and balanced taxon sampling at the superfamily level within this study, whereas Gunter *et al.* (2013) primarily targeted the Cleridae. Although Kolibáč (1992, 1997, 2004) and Opitz (2010) developed competing classification systems of Cleridae and Thanerocleridae/-inae, both recognized the thaneroclerid/-ine lineage as sister to the remaining lineages of Cleridae (as in our results), but the two authors chose alternate paths of family recognition. Herein we uphold the classification in Leschen *et al.* (2010) and Bouchard *et al.* (2011), retaining Thanerocleridae as a separate family.

Cleridae

There was high support for monophyly of the family Cleridae in both analyses (PP = 0.99, BS = 83) (Fig. 9). Our phylogenetic results demonstrate subdivision of checkered beetles into three major groups: a grade of Tillinae (weak to no support), and clades comprising Korynetinae sensu Kolibáč + Epiclininae (Fig. 9) and Clerinae + Hydnocerinae (Fig. 10); however, the exact relationships within these clades varied between BA and ML analyses particularly within the Korynetinae + Epiclininae clade. Within the latter clade, our BA topology was largely congruent with that of Gunter *et al.* (2013), resolving a grouping of Korynetinae and Epiclininae which was strongly supported (PP = 0.99), but in the ML analysis *Brachyptevenus* Pic (Hydnocerinae) was recovered at the base of the poorly supported clade (BS = 26), and *Phymatophaea* Pascoe (representing Peloniinae sensu Opitz) was recovered as sister to the Epiclininae (BS = 28); this clade was, in turn, adjacent to the remainder of genera (BS = 38).

Opitz’s (2010) fragmented concept of the Cleridae included 12 subfamilies, six of which were considered by Kolibáč (1997) to belong to his broader concept of Korynetinae. In our analysis, only Peloniinae sensu Opitz and Korynetinae sensu Opitz are monophyletic but they are represented in our analysis by a single genus and three genera, respectively. Gunter *et al.* (2013)

had broader taxon sampling of Peloniinae which was recovered as polyphyletic but deep within the larger clade that represented Korynetinae sensu Kolibáč. All other subfamilies of Opitz (2010) in our analysis, the analyses of Gunter *et al.* (2013) and Kolibáč & Huang (2016), were recovered as polyphyletic, thus supporting the classification corresponding to the Korynetinae sensu lato of Kolibáč (1997, 2003, 2010) which groups all clerids with a reduced fourth tarsomere. We considered synonymizing Epiclininae, recently described by Gunter *et al.* (2013), with Korynetinae based on the ML topology; however, support for this broad clade containing *Brachyptevenus* (Hydnocerinae), Epiclininae and Korynetinae, and the relationship between Epiclininae and *Phymatophaea*, was weak (BS = 26 and BS = 28, respectively). Furthermore, this topology was not congruent with our BA, in which the sister relationship of Epiclininae and Korynetinae was strongly supported (PP = 0.99). Epiclininae, here represented by three (of four described) genera and six species, was strongly supported as monophyletic in both analyses (PP = 1, BS = 92), and recognition of the two subfamilies is further justified based on morphology (e.g. fourth tarsomere not reduced in Epiclininae, which is diagnosed on numerous additional characters; see Gunter *et al.*, 2013). Furthermore, members of the Epiclininae were previously classified within Clerinae, indicating their superficial similarity with members of the other major clade. Thus, by broadening the concept of Korynetinae here, we would have rendered almost all clerid subfamilies undiagnosable based on morphology alone. As such, both Korynetinae **stat.rest.** (sensu lato) and Epiclininae are retained as valid subfamilies.

The phylogenetic relationships within the Tillinae also differed depending on analytic method. In BA, the Tillinae split into three clades (one composed of *Cylidrus* Latreille, *Wittmeridecus* Winkler and *Tilloidea* Laporte strongly supported; PP = 1) as part of a tetrachotomy along the backbone of Cleridae, whereas in the ML tree, the Tillinae (seven genera sampled) formed a weakly supported (BS = 24) sister group to the remainder of Cleridae. Gunter *et al.* (2013) recovered Tillinae as a strongly supported monophyletic lineage, and it is well defined based on morphological characters (see Burke & Zolnerowich, 2017). Tillinae is retained as a valid subfamily within the Cleridae.

As for the ‘crown group’ of Cleridae, consisting of the subfamilies Clerinae and Hydnocerinae, support for monophyly of the group as a whole was weak in BA (PP = 0.72) (Fig. 10), and in ML a monophylum was not recovered. Instead *Brachyptevenus* (Hydnocerinae) was recovered at the base of the Korynetinae + Epiclininae clade discussed earlier, and the remaining Clerinae + Hydnocerinae clade was weakly supported (BS = 35). In both analyses, Hydnocerinae and Clerinae were reciprocally paraphyletic, with three clades of the former in both analyses that corresponded to each of the defined tribes (Callimerini, Hydnocerini, Lemidiini; Kolibáč, 1998), and four clades of the latter in both analyses. Support for most of these groups was moderate to strong. Clerinae has never been divided into any formally recognized tribes, and with 113 genera, it is one of the most morphologically diverse lineages of the Cleroidea. To improve the taxonomic stability of the Cleridae and address the paraphyly of Clerinae and Hydnocerinae, two possible changes could be made. First, Hydnocerinae could be synonymized with Clerinae, resulting in an even larger and more morphologically diverse subfamily with 136 genera. Alternatively, the three hydnocerine tribes (morphologically defined by Kolibáč, 1998) could be elevated to subfamily, leaving the Clerinae paraphyletic and in need of future, broad-scale revision. While it is less than ideal to leave both subfamilies paraphyletic, we choose to defer the issue to future studies focused on this clade. Our sampling included approximately one-quarter of clerine genera, which were divided into four lineages; with the current taxon sampling and tremendous diversity of the Clerinae, it is beyond the scope of this project to fully resolve the classification issues within the subfamily.

With the aforementioned classification changes, the Cleridae now comprises the subfamilies Clerinae, Epiclininae, Hydnocerinae, Korynetinae and Tillinae. Additional classification changes will almost certainly be necessary in the future, particularly following a higher-level revision of the Clerinae.

Conclusion

Given the complex taxonomic history of many taxa and the uncertainty expressed in the literature, the many emendations to the classification supported by our study were unsurprising. While the taxonomic rearrangements proposed here certainly do not solve all higher classification issues in Cleroidea, they represent a significant step forward in identifying natural groups and placing the classification on a firmer footing. Previous studies focused on the evolution of Cleroidea suffered from a lack of consideration of these natural groupings, coupled with a dearth of material from odd, primarily southern hemisphere lineages, thus compromising their results relating to the evolution of morphological characters and feeding behaviour within the superfamily. Our results provide a robust framework to further explore systematic relationships and evolution of the Cleroidea.

The evolutionary history among the Cleroidea remains unclear given the limitations in taxa sampled to date. However, the study of McKenna *et al.* (2015) estimated the age of Cleroidea as mid-Jurassic (around 169 Ma), whereas the revised estimate of Toussaint *et al.* (2017) dated the ancestor of Cleroidea near the Permian-Triassic boundary (around 250 Ma). Fossil evidence for many cleroid groups date to mid-Jurassic, including Lophocaterinae (or Decamerini) (Peris *et al.*, 2014; Yu *et al.*, 2014, 2015), Prionoceridae (Liu *et al.*, 2015), Thanerocleridae (Yu *et al.*, 2017) and Cleridae (Kolibáč & Huang, 2016), but as yet no ancient Melyridae fossils have been described. These data, together with branching sequences in our work and previous studies, suggest that the more primitive cleroids were mainly fungus-feeding, like other large groups of Coleoptera (Leschen & Buckley, 2007), and predatory followed by later shifts to flower-feeding, especially in Melyridae.

Although our study cannot contribute to the discussion of age of origin, it is clear that biogeographic structure is evident in many clades. Many isolated antique lineages, including Rentoniidae, Acanthocnemidae, Protopeltidae, Chaetosomatidae and

Phycosecidae, are pronouncedly Gondwanan in distribution. As our study does not provide definitive answers to all issues in evolution and classification of the Cleroidea, four directions are required to further advance our knowledge of these aspects of the superfamily: (i) further refinement of individual clades and their interrelationships, in particular further evaluation of novel groupings we propose [Thymalidae and the clade(s) including Calityinae, Egoliinae, Larinotinae and Peltidae] and assessment of the multiple lineages that remain in a potentially polyphyletic Trogossitidae, as well as Acanthocnemidae; (ii) robust taxon sampling of the two largest families of the Cleroidea, the Cleridae and Melyridae, which were incompletely treated in this study, in order to confidently place the huge diversity of genera into a stable subfamilial and tribal classification; (iii) addition of reliably identified fossils to serve as calibration points for dating the individual lineages within Cleroidea; and (iv) revisionary taxonomic work within many groups, especially the generic limits and species diversity of Melyridae, Cleridae, Trogossitinae and Lophocateridae.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Maximum-likelihood tree. Black circles represent boostrap values > 79, grey circles represent bootstrap values in the range 60–79 and white circles represent bootstrap values in the range 40–59.

Table S1. List of taxa and genetic loci used in this analysis along with GenBank accession numbers. Sequences new to this study are deposited in GenBank under accession numbers MH983862–MH984769. The higher classification given follows that of Cleroidea prior to this study. Collection of origin is indicated in the 'Collection' column with the following codens: ANIC (Australian National Insect Collection, Canberra), ARC (Andrew R. Cline collection, Sacramento, CA), BYUC (Brigham Young University collection, Provo, UT), CGC (Conrad Gillett collection, London), JKC (Jiří Kolibáč collection, Brno, Czech Republic), MLGC (Matthew L. Gimmel collection, Santa Barbara, CA), NZAC (New Zealand Arthropod Collection, Auckland), RCC (Robert Constantin collection, St. Lo, France), RJBC (Rick J. Buss collection, Albuquerque, NM), RRC (Rafał Ruta collection, Wrocław, Poland), SBMNH (Santa Barbara Museum of Natural History, Santa Barbara, CA), UNMC (University of New Mexico collection, Albuquerque, NM), UPOL (Palacký University collection, Olomouc, Czech Republic).

Table S2. Primers used to amplify gene products in this study.

Table S3. Character breakdown of the 3986 bp matrix by gene.

Acknowledgements

We would like to thank the following people for providing specimens for this project: Conrad Gillett (The Natural History Museum, London, U.K.); Adam Ślipiński and Cate Lemann (CSIRO, Canberra, Australia); Andrew Cline (CDFA, Sacramento, CA, U.S.A.); Nathan Lord (Brigham Young University, Provo, UT, U.S.A.); Michael Caterino (Santa Barbara Museum of Natural History, CA, U.S.A.); Robert Constantin (St.-Lô, France); Jiří Kolibáč (Moravian Museum, Brno, Czech Republic); Rafał Ruta (University of Wrocław, Poland); Rick Buss (Albuquerque, NM, U.S.A.); and Shawn Clark (Brigham Young University, Provo, UT, U.S.A.). Roland Gerstmeier (Technische Universität München, Germany), Adriean Mayor (Gatlinburg, TN, U.S.A.), John Leavengood (USDA-APHIS, Tampa, FL, U.S.A.), Weston Opitz (Florida State Collection of Arthropods, Gainesville, FL, U.S.A.) and Michael Geiser (The Natural History Museum, London, U.K.) helped with identifications. MLG specimen vouchers, many of which appear in Figs 1–3, were photographed by Lucie Gimmel. We wish to thank Pat Bouchard, Kirill Makarov, Udo Schmidt, Salvador Vitanza, and Chris Wirth for sharing photographs, and acknowledge Her Majesty the Queen in Right of Canada, as represented by the Minister of Agriculture and Agri-Food Canada (2014) for granting authority to use the copyrighted images in Figs 1E, 2H, and 3A obtained by Anthony Davies (Department of Agriculture and Agri-Food, Government of Canada). Rick Wherley is warmly thanked for enhancing the beetle habitus images. Comments from four anonymous reviewers significantly improved this manuscript. This study has been particularly supported by grants CZ.1.07/2.3.00/30.0004 (MG) and CZ.1.07/2.3.00/20.0166 (MB) from the European Social Fund and the Ministry of Education of the Czech Republic. Furthermore, the project was substantially supported by Palacky University grants PdF_2012_029 (MB), PdF_2013_024 (MLG, MB), and IGA_PdF_2014019 (MLG, MB). RABL was funded in part by the Strategic Science Investment Fund to Crown Research Institutes from the Ministry of Business, Innovation and Employment's Science and Innovation Group and he thanks John Lawrence for lengthy discussions and advice about Trogossitidae during the course of this and prior projects on Cleroidea.

The authors declare that they have no conflict of interest.

References

Arias, E.T., Slipinski, A., Lawrence, J.F. & Elgueta, M. (2009) A review of the Chilean Egoliini (Coleoptera: Trogossitidae) with description of a new species of *Necrobiopsis* Crowson. *Zootaxa*, **2170**, 37–45.

Barron, J.R. (1971) A revision of the Trogositidae[*sic*] of America north of Mexico (Coleoptera: Cleroidea). *Memoirs of the Entomological Society of Canada*, **75**, 1–143.

Beutel, R.G. & Pollock, D.A. (2000) Larval head morphology of *Phycosecis litoralis* (Pascoe) (Coleoptera: Phycosecidae) with phylogenetic implications. *Invertebrate Taxonomy*, **14**, 825–835.

Bocak, L., Barton, C., Crampton-Platt, A., Chesters, D., Ahrens, D. & Vogler, A.P. (2014) Building the Coleoptera tree-of-life for >8000 species: composition of public DNA data and fit with Linnaean classification. *Systematic Entomology*, **39**, 97–110.

Bocak, L., Kundrata, R., Fernández, C.A. & Vogler, A.P. (2016) The discovery of Iberobaeniidae (Coleoptera: Elateroidea): a new family of beetles from Spain, with immatures detected by environmental DNA sequencing. *Proceedings of the Royal Entomological Society of London. Series B*, **283**, 20152350.

Bocakova, M., Constantin, R. & Bocak, L. (2012) Molecular phylogenetics of the melyrid lineage (Coleoptera: Cleroidea). *Cladistics*, **28**, 117–129.

Bocakova, M., Bocak, L., Gimmel, M.L., Motyka, M. & Vogler, A.P. (2016) Aposematism and mimicry in soft-bodied beetles of the superfamily Cleroidea (Insecta). *Zoologica Scripta*, **45**, 9–21.

Bouchard, P., Bousquet, Y., Davies, A.E. *et al.* (2011) Family-group names in Coleoptera (Insecta). *ZooKeys*, **88**, 1–972.

Böving, A.G. & Craighead, F.C. (1931) An illustrated synopsis of the principal larval forms of the order Coleoptera. *Entomologica Americana*, **11**, 1–351, 125 plates.

Burke, A. & Zolnerowich, G. (2017) A taxonomic revision of the subfamily Tillinae Leach *sensu lato* (Coleoptera, Cleridae) in the New World. *ZooKeys*, **179**, 75–157.

Cline, A.R., Goodrich, M.A. & Leschen, R.A.B. (2010) 10.2. Byturidae Jacquelin du Val, 1858. *Handbook of Zoology, Volume 4/39: Coleoptera, Beetles, Volume 2. Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)* (ed. by R.A.B. Leschen, R.G. Beutel and J.F. Lawrence), pp. 286–292. W DeGruyter, Berlin.

Constantin, R. & Menier, J.J. (1987) Étude d'un remarquable Melyridae aptère des Îles Canaries: *Gietella fortunata*, n. gen., n. sp., type d'une sous-famille nouvelle Gietellinae. [Coleoptera, Cleroidea]. *Revue française d'Entomologie*, **9**, 53–63.

Constantin, R. & Menier, J.J. (1990) Description des larves du genre *Gietella* et discussion sur la position systématique du genre [Coleoptera, Melyridae, Gietellinae]. *Revue française d'Entomologie*, **12**, 171–182.

Crowson, R.A. (1952) The classification of the families of British Coleoptera [continued]. *The Entomologist's Monthly Magazine*, **88**, 109–132.

Crowson, R.A. (1955) *The Natural Classification of the Families of Coleoptera*. Nathaniel Lloyd, London.

Crowson, R.A. (1964) A review of the classification of Cleroidea (Coleoptera), with descriptions of two new genera of Peltidae and of several new larval types. *Transactions of the Royal Entomological Society of London*, **116**, 275–327, 1 plate.

Crowson, R.A. (1966) Further observations on Peltidae (Coleoptera: Cleroidea), with definitions of a new subfamily and of four new genera. *Proceedings of the Royal Entomological Society of London. Series B*, **35**, 119–127.

Crowson, R.A. (1970) Further observations on Cleroidea (Coleoptera). *Proceedings of the Royal Entomological Society of London. Series B*, **39**, 1–20.

Geiser, M.F., Hagmann, R., Nagel, P. & Loader, S.P. (2016) A first broad-scale molecular phylogeny of Prionoceridae (Coleoptera: Cleroidea) provides insight into taxonomy, biogeography and life history evolution. *Arthropod Systematics & Phylogeny*, **74**, 3–21.

Gimmel, M.L. & Leschen, R.A.B. (2014) A new species of mycophagous *Rentonium* (Coleoptera: Cleroidea: Trogossitidae) based on larvae and adults, and a catalogue of Rentoniinae. *Journal of Natural History*, **48**, 863–880.

Goodrich, M.A. & Springer, C.A. (1992) A revision of the family Biphyllidae (Coleoptera) for America, north of Mexico. *The Coleopterists Bulletin*, **46**, 361–377.

Gunter, N.L., Leavengood, J.M., Bartlett, J.S., Chapman, E.G. & Cameron, S.L. (2013) A molecular phylogeny of the checkered beetles and a description of Epiclininae a new subfamily (Coleoptera: Cleroidea: Cleridae). *Systematic Entomology*, **38**, 626–636.

Hunt, T., Bergsten, J., Levkanicova, Z. *et al.* (2007) A comprehensive phylogeny of beetels reveals the evolutionary origins of a superradiation. *Science*, **318**, 1913–1916.

Kearse, M., Moir, R., Wilson, A. *et al.* (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, **28**, 1647–1649.

Kim, S.I. & Farrell, B.D. (2015) Phylogeny of world stag beetles (Coleoptera: Lucanidae) reveals a Gondwanan origin of Darwin's stag beetle. *Molecular Phylogenetics and Evolution*, **86**, 35–48.

Klimaszewski, J. & Watt, J.C. (1997) Coleoptera: family-group review and keys to identification. Fauna of New Zealand, **37**, 1–199.

Kolibáč, J. (1989) Further observations on morphology of some Cleridae (Coleoptera) (I). *Acta Scientiarum Naturalium Academiae Scientiarum Bohemoslovacae, Brno*, **23**, 1–50.

Kolibáč, J. (1992) Revision of Thanerocleridae n.stat. (Coleoptera, Cleroidea). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft (Bulletin de la Société Entomologique Suisse)*, **65**, 303–340.

Kolibáč, J. (1997) Classification of the subfamilies of Cleridae (Coleoptera: Cleroidea). *Acta Musei Moraviae, Scientiae naturales*, **81**, 307–361.

Kolibáč, J. (1998) Classification of the subfamily Hydnocerinae Spinola, 1844 (Coleoptera: Cleroidea). *Acta Musei Moraviae, Scientiae biologicae*, **83**, 127–210.

Kolibáč, J. (1999) Comparative morphology of mandible, epipharynx and alimentary canal in larval and adult Cleroidea (Coleoptera). *Acta Musei Moraviae, Scientiae biologicae*, **84**, 11–69.

Kolibáč, J. (2003) A review of Australian genera of Korynetinae (Coleoptera, Cleridae). *Entomologica Basiliensia*, **25**, 41–97.

Kolibáč, J. (2004) Metaxinidae, fam.nov., a new family of Cleroidea (Coleoptera). *Entomologica Basiliensia*, **26**, 239–268.

Kolibáč, J. (2005) A review of the Trogossitidae. Part 1: morphology of the genera (Coleoptera, Cleroidea). *Entomologica Basiliensia et Collectionis Frey*, **27**, 39–159.

Kolibáč, J. (2006) A review of the Trogossitidae. Part 2: larval morphology, phylogeny and taxonomy (Coleoptera, Cleroidea). *Entomologica Basiliensia et Collectionis Frey*, **28**, 105–153.

Kolibáč, J. (2008) Morphology, taxonomy and phylogeny of *Phloiophilus edwardsi* Stephens, 1830 (Coleoptera, Cleroidea). *Entomologica Basiliensia et Collectionis Frey*, **30**, 105–133.

Kolibáč, J. (2010) 9.6. Cleridae Latreille, 1802. *Handbook of Zoology, Volume 4/39: Coleoptera, Beetles, Volume 2. Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)* (ed. by R.A.B. Leschen, R.G. Beutel and J.F. Lawrence), pp. 257–261. W DeGruyter, Berlin.

Kolibáč, J. (2012) *Onerunka longi*, a new genus and species of Thanerocleridae (Coleoptera) from Papua New Guinea, with systematic notes on the tribe Thaneroclerini. *Zootaxa*, **3577**, 71–79.

Kolibáč, J. (2013) Trogossitidae: a review of the beetle family, with a catalogue and keys. *ZooKeys*, **366**, 1–194.

Kolibáč, J. & Huang, D. (2016) The oldest known clerid fossils from the Middle Jurassic of China, with a review of Cleridae systematics (Coleoptera). *Systematic Entomology*, **41**, 808–823.

Kolibáč, J. & Zaitsev, A.A. (2010) A description of a larva of *Ancyrona diversa* Pic, 1921 and its phylogenetic implications (Coleoptera: Trogossitidae). *Zootaxa*, **2451**, 53–62.

Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, **29**, 1695–1701.

Lawrence, J.F. (2010) 9.10. Mauroniscidae Majer, 1994. *Handbook of Zoology, Volume 4/39: Coleoptera, Beetles, Volume 2. Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)* (ed. by R.A.B. Leschen, R.G. Beutel and J.F. Lawrence), pp. 271–273. W DeGruyter, Berlin.

Lawrence, J.F. & Leschen, R.A.B. (2010a) 9.1. Phloiophilidae Kiesenwetter, 1863. *Handbook of Zoology, Volume 4/39: Coleoptera, Beetles, Volume 2. Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)* (ed. by R.A.B. Leschen, R.G. Beutel and J.F. Lawrence), pp. 239–241. W DeGruyter, Berlin.

Lawrence, J.F. & Leschen, R.A.B. (2010b) 9.7. Acanthocnemidae Crowson, 1964. *Handbook of Zoology, Volume 4/39: Coleoptera, Beetles, Volume 2. Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)* (ed. by R.A.B. Leschen, R.G. Beutel and J.F. Lawrence), pp. 262–265. W DeGruyter, Berlin.

Lawrence, J.F. & Leschen, R.A.B. (2010c) 9.11. Melyridae Leach, 1815. *Handbook of Zoology, Volume 4/39: Coleoptera, Beetles, Volume 2. Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)* (ed. by R.A.B. Leschen, R.G. Beutel and J.F. Lawrence), pp. 273–280. W DeGruyter, Berlin.

Lawrence, J.F. & Newton, A.F., Jr. (1982) Evolution and classification of beetles. *Annual Review of Ecology and Systematics*, **13**, 261–290.

Lawrence, J.F. & Ślipiński, A. (2013a) *Australian Beetles: Morphology, Classification and Keys*. CSIRO Publishing, Collingwood.

Lawrence, J.F. & Ślipiński, A. (2013b) *Globorentonium*, a new genus of rentoniine Trogossitidae (Coleoptera: Cleroidea) from Australia and Brazil. *Zootaxa*, **3710**, 257–270.

Lawrence, J.F., Ślipiński, A., Seago, A.E., Thayer, M.K., Newton, A.F. & Marvaldi, A.E. (2011) Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Annales Zoologici*, **61**, 1–217.

Lawrence, J.F., Leschen, R.A.B. & Ślipiński, A. (2014) *Antillipeltis*, a new genus of Antillean Trogossitidae (Coleoptera: Cleroidea) with a key to the Cleroidea. *Zootaxa*, **3794**, 435–454.

Leschen, R.A.B. & Beutel, R.G. (2010) 9.8. Phycosecidae Crowson, 1952. *Handbook of Zoology, Volume 4/39: Coleoptera, Beetles, Volume 2. Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)* (ed. by R.A.B. Leschen, R.G. Beutel and J.F. Lawrence), pp. 265–268. W DeGruyter, Berlin.

Leschen, R.A.B. & Buckley, T.R. (2007) Multistate characters and diet shifts: evolution of Erotylidae (Coleoptera). *Systematic Biology*, **56**, 97–112.

Leschen, R.A.B. & Lackner, T. (2013) Gondwanan Gymnochilini (Coleoptera: Trogossitidae): generic concepts, review of New Zealand species and long-range Pacific dispersal. *Systematic Entomology*, **38**, 278–304.

Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (eds) (2010) *Handbook of Zoology, Volume 4/39: Coleoptera, Beetles, Volume 2. Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)*. W DeGruyter, Berlin.

Liu, Z., Ślipiński, A., Leschen, R.A.B., Ren, D. & Pang, H. (2015) The oldest Prionoceridae (Coleoptera: Cleroidea) from the Middle Jurassic of China. *Annales Zoologici*, **65**, 41–52.

Majer, K. (1987) Comparative morphology and proposed major taxonomy of the family Melyridae (Insecta, Coleoptera). *Polskie Pismo Entomologiczne*, **56**, 719–859.

Majer, K. (1994a) A review of the classification of the Melyridae and related families (Coleoptera, Cleroidea). *Entomologica Basiliensia*, **17**, 319–390.

Majer, K. (1994b) Gietellidae, full family status for Melyridae: Gitetellinae [*sic*] (Coleoptera: Cleroidea). *Entomological Problems*, **25**, 65–72.

Majer, K. (1995) Revision of the family Mauroniscidae (Insecta: Coleoptera: Cleroidea). *Entomologische Abhandlungen*, **57**, 57–89.

Majer, K. (1999) Generic synopsis of Neotropical Danaceinae and a revision of the genus *Hylodanacaea* Pic, 1926 (Coleoptera: Dasytidae). *Boletin del Museo Nacional de Historia Natural, Chile*, **48**, 77–137.

Majer, K. (2002) Subfamilial classification of the family Malachiidae (Coleoptera, Cleroidea). *Entomologica Basiliensia*, **24**, 179–244.

Mayor, A.J. (2002) Melyridae. *American Beetles, Volume 2, Polyphaga: Scarabaeoidea through Curculionoidea* (ed. by R.H. Arnett Jr., M.C. Thomas, P.E. Skelley and J.H. Frank), pp. 281–304. CRC Press, Boca Raton, Florida.

McElrath, T.C., Robertson, J.A., Thomas, M.C., Osborne, J., Miller, K.B., McHugh, J.V. & Whiting, M.F. (2015) A molecular phylogenetic study of Cucujidae s.l. (Coleoptera: Cucujoidea). *Systematic Entomology*, **40**, 705–718.

McKenna, D.D. & Farrell, B.D. (2009) Beetles (Coleoptera). *The Timetree of Life* (ed. by S.B. Hedges and S. Kumar), pp. 278–289. Oxford University Press, New York, New York.

McKenna, D.D., Wild, A.L., Kanda, K. *et al.* (2015) The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology*, **40**, 835–880.

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*. New Orleans, LA, 14 November 2010, pp. 1–8.

Opitz, W. (2010) Classification, natural history, phylogeny, and subfamily composition of the Cleridae and generic content of the subfamilies (Coleoptera: Cleroidea). *Entomologica Basiliensia et Collectionis Frey*, **32**, 31–128.

Opitz, W. (2015) Systematics of the checkered beetle subfamily Platynopterinae Spinola (Coleoptera: Cleridae). *Linzer Biologische Beiträge*, **47**, 1513–1572.

Peacock, E.R. (1987) A review of the Rhadalinae (= Aplocneminae) (Coleoptera: Melyridae). *Bulletin of the British Museum (Natural History), Entomology*, **56**, 129–170.

Peris, D., Kolibáč, J. & Delclòs, X. (2014) *Cretamerus vulloi* gen. et sp. nov., the oldest bark-gnawing beetle (Coleoptera: Trogossitidae) from Cretaceous amber. *Journal of Systematic Palaeontology*, **12**, 879–891.

Pic, M. (1926) Phloeophilidae, Rhadalidae, Prionoceridae. Pars 87. *Coleopterorum Catalogus* (ed. by S. Schenkling), pp. 1–11. W. Junk, Berlin.

Robertson, J.A., Ślipiński, A., Moulton, M. *et al.* (2015) Phylogeny and classification of Cucujoidea and the recognition of a new superfamily Coccinelloidea (Coleoptera: Cucujiformia). *Systematic Entomology*, **40**, 745–778.

Shull, V.L., Vogler, A.P., Baker, M.D., Maddison, D.R. & Hammond, P.M. (2001) Sequence alignment of 18S ribosomal RNA and the basal relationships of adephagan beetles: evidence for monophyly of aquatic families and the placement of Trachypachidae. *Systematic Biology*, **50**, 945–969.

Slipinski, S.A. (1992) Larinotinae – a new subfamily of Trogossitidae (Coleoptera), with notes on the constitution of Trogossitidae and related families of Cleroidea. *Revue Suisse de Zoologie*, **99**, 439–463.

Slipinski, S.A., Leschen, R.A.B. & Lawrence, J.F. (2011) Order Coleoptera Linnaeus, 1758. *Animal Biodiversity: An Outline of Higher-Level Classification and Survey of Taxonomic Richness* (ed. by Z.-Q. Zhang), pp. 203–208. *Zootaxa*, **3148**, 1–237.

Tait, S.M., Dahlsten, D.L., Gill, R.J. & Doyen, J.T. (1990) Life history of the incense cedar scale, *Xylococculus macrocarpae* (Homoptera: Margarodidae), on incense cedar in California with a description of the larvae of one of its common predators, *Eronyxa expansus* Van Dyke (Coleoptera: Trogossitidae). *Hilgardia*, **58**, 1–19.

Toussaint, E.F.A., Seidel, M., Arriaga-Varela, E. *et al.* (2017) The peril of dating beetles. *Systematic Entomology*, **42**, 1–10.

Vogler, A.P., DeSalle, R., Assmann, T., Knisley, C.B. & Schultz, T.D. (1993) Molecular population genetics of the endangered tiger beetle *Cicindela dorsalis* (Coleoptera: Cicindelidae). *Annals of the Entomological Society of America*, **86**, 142–152.

Węgrzynowicz, P. (2015) Catalogue of Biphyllidae (Coleoptera) of the world. *Annales Zoologici*, **65**, 409–471.

Yu, Y., Ślipiński, A., Leschen, R.A.B., Ren, D. & Pang, H. (2014) Enigmatic Mesozoic bark-gnawing beetles (Coleoptera: Trogossitidae) from the Jiulongshan Formation in China. *Annales Zoologici*, **64**, 667–676.

Yu, Y., Ślipiński, A., Leschen, R.A.B., Ren, D. & Pang, H. (2015) New genera and species of bark-gnawing beetles (Coleoptera: Trogossitidae) from the Yixian Formation (Lower Cretaceous) of Western Liaoning, China. *Cretaceous Research*, **53**, 89–97.

Yu, Y., Deng, C., Kolibáč, J., Ślipiński, A., Ren, D., Jin, J. & Pang, H. (2017) The first record of Cretaceous thaneroclerids (Insecta: Coleoptera) from the Burmese amber. *Annales Zoologici*, **67**, 549–554.

Zhang, S.-Q., Che, L.-H., Li, Y., Liang, D., Pang, H., Ślipiński, A. & Zhang, P. (2018) Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. *Nature Communications*, **9**, Article number: 205, 1–11. https://doi.org/10.1038/s41467-017-02644-4.

Accepted 30 October 2018

Appendix 1: Historical classifications of and within Cleroidea

1A. Böving & Craighead (1931) classification of Cleroidea.

Cleroidea family sensu Böving & Craighead (1931)	Current name and constituents	Current superfamily placement
Bothrideridae	Bothrideridae, Teredidae, Zopheridae	Coccinelloidea, Tenebrionoidea
Catogenidae	Passandridae	Cucujoidea
Ciidae	Ciidae	Tenebrionoidea
Cleridae	Cleridae, Thanerocleridae	Cleroidea
Dermestidae	Dermestidae	Bostrichoidea
Melyridae	Dasytidae, Malachiidae, Mauroniscidae, Melyridae, Rhadalidae	Cleroidea
Ostomatidae	Trogossitidae	Cleroidea

1B. Classification of the trogossitid group according to Kolibáč (2013).

Kolibáč (2013)	Alternative modern classifications
Trogossitidae	
Trogossitinae	
Calityini	As subfamily of Trogossitidae (Slipinski, 1992)
Larinotini	With genera of current Colydiopeltini, as subfamily of Trogossitidae (Slipinski, 1992)
Egoliini	As subfamily of Trogossitidae (Slipinski, 1992)
Gymnochilini	
Trogossitini	With Gymnochilini taxa, as subfamily of Trogossitidae (Slipinski, 1992)
Lophocaterinae	As separate family (Crowson, 1970); subsumed within Peltinae (Barron, 1971)
Decamerini	As subfamily of Peltidae (Crowson, 1964, 1966, 1970) or Trogossitidae (Slipinski, 1992)
Ancyronini	
Lophocaterini	With Ancyronini taxa, as subfamily of Trogossitidae (Slipinski, 1992)
Peltinae	As separate family (Crowson, 1964, 1966, 1970)
Peltini	With *Thymalus*, as subfamily of Trogossitidae (Slipinski, 1992)
Thymalini	*Thymalus* included in Peltinae by Slipinski (1992); other genera included in subfamilies Protopeltinae and Rentoniinae of Peltidae (Crowson, 1970) or Trogossitidae (Slipinski, 1992)
Colydiopeltini	Included in subfamily Larinotinae (Slipinski, 1992)
Phloiophilini	As separate family (Crowson, 1964, 1970; Barron, 1971; Slipinski, 1992)

1C. Comparison of the subfamily classifications of Cleridae (and Thanerocleridae) of Kolibáč (1997) and Opitz (2010).

Kolibáč (1997)		Opitz (2010)	
Cleridae	Tillinae	Cleridae	Tillinae
	Hydnocerinae		Hydnocerinae
	Clerinae		Anthicoclerinae
			Clerinae
	Korynetinae		Korynetinae
			Enopliinae
			Epiphloeinae
			Orthopleurinae (as 'Neorthopleurinae')
			Peloniinae
			Tarsosteninae
Thanerocleridae	(No subfamilies recognized)		Isoclerinae
			Thaneroclerinae

Appendix 2: Summary of family groups of Cleroidea

The following is a brief summary of the current family group-level nomenclature, including extant genera and distributional notes for all currently recognized groups of Cleroidea in light of the results of this study.

Rentoniidae Crowson, 1966 , stat.n.
Rentoniinae Crowson 1966

Included genera. *Australiodes* Endrödy-Younga, *Globorentonium* Lawrence & Slipinski, *Parentonium* Crowson, *Rentonellum* Crowson, *Rentonidium* Crowson, *Rentonium* Crowson, two undescribed genera (New Zealand).

Distribution. This family is distributed in the southern hemisphere, members having been recorded from Australia, New Caledonia, New Zealand, Chile and southern Brazil (Gimmel & Leschen, 2014).

Byturidae Gistel, 1848
Byturidae Gistel 1848; Platydascillidae Pic 1914.

Included genera. **Byturinae**: *Byturus* Latreille, *Haematoides* Fairmaire, *Xerasia* Lewis; **Platydascillinae**: *Bispinatus* Springer & Goodrich, *Dascillocyphon* Everts, *Platydascillus* Everts, *Remigera* Springer & Goodrich.

Distribution. This family is known from the Holarctic region, Southeast Asia, and southern South America (Cline *et al*., 2010).

Biphyllidae LeConte, 1861
Diphyllidae LeConte 1861

Included genera. *Althaesia* Pascoe, *Anchorius* Casey, *Biphyllus* Dejean, *Diplocoelus* Guérin-Méneville, *Euderopus* Sharp, *Gonicoelus* Sharp.

Distribution. This family is distributed nearly worldwide (Węgrzynowicz, 2015).

Phloiophilidae Kiesenwetter, 1863
Phloeophilini Kiesenwetter 1863

Included genera. *Phloiophilus* Stephens.

Distribution. The one species of this family, *Phloiophilus edwardsi* Stephens, occurs in Europe (Lawrence & Leschen, 2010a).

Acanthocnemidae Crowson, 1964
Acanthocneminae Crowson 1964

Included genera. *Acanthocnemus* Perris.

Distribution. The one species of this family, *Acanthocnemus nigricans* (Hope), occurs throughout Australia and has been introduced to Europe, Africa and Asia (Lawrence & Leschen, 2010b).

Protopeltidae Crowson, 1966, stat.n.
Protopeltini Crowson 1966

Included genera. *Protopeltis* Crowson.

Distribution. This family is known only from two nominal species distributed in New Zealand (Kolibáč, 2013).

Peltidae Latreille, 1806, stat.rest.
Peltides Latreille 1806; Ostomini Harold 1876

Included genera. *Peltis* O.F. Müller.

Distribution. This family is confined to the Holarctic region.

Lophocateridae Crowson, 1964, stat.rest. and sensu n.
Lycoptini Casey 1890; Lophocaterinae Crowson 1964 [*nomen protectum*]; Ancyronini Kolibáč 2006; Colydiopeltini Kolibáč 2006

Included genera. *Afrocyrona* Kolibáč, *Ancyrona* Reitter, *Antillipeltis* Lawrence, Leschen & Ślipiński, *Colydiopeltis* Slipinski, *Eronyxa* Reitter, *Grynocharina* Reitter, *Grynocharis* Thomson, *Grynoma* Sharp, *Indopeltis* Crowson, *Leptonyxa* Reitter, *Lophocateres* Olliff, *Lycoptis* Casey, *Neaspis* Pascoe, *Parapeltis* Slipinski, *Peltonyxa* Reitter, *Promanus* Sharp, *Trichocateres* Kolibáč, undescribed genus near *Peltonyxa* (Australia).

Distribution. This family occurs nearly worldwide.

Notes. As indicated in the Results section, we recommend that the tribal classification of the former Lophocaterinae be abandoned. Before this study, it consisted of three tribes (Ancyronini, Decamerini, Lophocaterini). Decamerini is transferred to Thymalidae **stat.n.** in this study, and Colydiopeltini is transferred to Lophocateridae **sensu n.** (from Peltinae). Ancyronini and Lophocaterini appear to be reciprocally polyphyletic. Additionally, relationships of the recently described *Antillipeltis* are obscure (Lawrence *et al*., 2014).

Trogossitidae Latreille, 1802, sensu n.
Trogossitarii Latreille 1802; Nemosomida Leach 1815; Égolides Lacordaire 1854; Gymnochilides Lacordaire 1854; Leperini Reitter 1876; Temnochilini Léveillé 1888; Tenebrioidini Ganglbauer 1899; Calityni Reitter 1922; Larinotinae Slipinski 1992

Included genera. **Calityinae stat. rest.**: *Calitys* Thomson; **Egoliinae stat.rest.**: *Acalanthis* Erichson, *Calanthosoma* Reitter, *Egolia* Erichson, *Necrobiopsis* Crowson, *Paracalanthis* Crowson; **Larinotinae stat.rest.**: *Larinotus* Carter & Zeck; **Trogossitinae sensu n.**: *Airora* Reitter, *Alindria* Erichson, *Anacypta* Illiger, *Corticotomus* Sharp, *Dupontiella* Spinola, *Elestora* Pascoe, *Eupycnus* Sharp, *Euschaefferia* Leng, *Gymnocheilis* Dejean, *Kolibacia* Leschen & Lackner, *Leipaspis* Wollaston, *Leperina* Erichson, *Melambia* Erichson, *Narcisa* Pascoe, *Nemozoma* Latreille (including *Cylidrella* Sharp), *Parallelodera* Fairmaire, *Phanodesta* Reitter, *Seidlitzella* Jakobson, *Temnoscheila* Westwood, *Tenebroides* Piller & Mitterpacher, *Xenoglena* Reitter.

Distribution. This family is distributed nearly worldwide. The concepts of the subfamilies outlined here are essentially unchanged from the system of Slipinski (1992).

Thymalidae Léveillé, 1888, stat.n. and sensu n.
Thymalini Léveillé 1888; Decamerinae Crowson 1964

Included genera. **Decamerinae stat.rest.** and **new placement**: *Antixoon* Gorham, *Decamerus* Solier, *Diontolobus* Solier; **Thymalinae stat.n.**: *Thymalus* Latreille.

Distribution. Thymalinae occur in the Holarctic and Oriental regions (Kolibáč, 2013), and the Decamerinae occur in Central and South America.

Phycosecidae Crowson, 1952

Phycosecidae Crowson 1952

Included genera. *Phycosecis* Pascoe.

Distribution. This family, with its four described species, occurs only in coastal areas of Australia, New Zealand, Vanuatu and New Caledonia (Leschen & Beutel, 2010).

Prionoceridae Lacordaire, 1857

Prionocérides Lacordaire 1857; Lobonychini Majer 1987

Included genera. *Idgia* Laporte de Castelnau, *Lobonyx* Jacquelin du Val, *Prionocerus* Perty.

Distribution. This family is distributed in the Palearctic, Afrotropical and Oriental regions (Geiser *et al*., 2016).

Mauroniscidae Majer, 1995

Mauroniscidae Majer 1995

Included genera. *Amecomycter* Majer, *Dasyrhadus* Fall (**new tentative placement**), *Mauroniscus* Bourgeois, *Mecomycter* Horn, *Mectemycor* Majer, *Scuromanius* Majer.

Distribution. Restricted to the New World, occurring from the western United States south to Chile (Majer, 1995; Lawrence, 2010).

Notes. We include here in Mauroniscidae all taxa previously included in the family, plus we tentatively include *Dasyrhadus* (see Results section).

Rhadalidae LeConte, 1861, sensu n.

Rhadalini LeConte 1861; Haplocnémates Mulsant & Rey 1868; Microjulistini Majer 1987; Pelecophorini Majer 1987; Gietellinae Constantin & Menier 1987

Included genera. **Gietellinae new placement**: *Gietella* Constantin & Menier; **Rhadalinae**: Aplocnemini: *Aplocnemus* Stephens, *Kubanius* Majer, *Trichoceble* Thomson; Microjulistini: *Flavojulistus* Majer, *Microjulistus* Reitter, *Semijulistus* Schilsky; Pelecophorini: *Malthacodes* Waterhouse, *Pelecophora* Dejean; Rhadalini: *Rhadalus* LeConte; Rhadalinae *incertae sedis: Anthriboclerus* Schenkling, *Antinea* Peyerimhoff, *Eucymbolus* Champion, *Hemipleurus* Peacock, *Indiodasytes* Pic, *Jelinekius* Majer, *Microcymbolus* Pic.

Distribution. The subfamily Gietellinae occurs only in the Azores and the Canary Islands in the North Atlantic Ocean (Constantin & Menier, 1990), whereas the subfamily Rhadalinae occurs nearly worldwide except for the Australian region (Peacock, 1987).

Melyridae Leach, 1815, sensu n.

(for family-group synonymy see Bouchard *et al*., 2011)

Included taxa. **Malachiinae**: all genera included in the traditional Malachiidae (=Malachiinae of North American authors), including members of Amalthocini (*Amalthocus* Fairmaire); Carphurini, Lemphini **sensu n.** [*Attalomimus* Wittmer (**new placement**), *Brachidia* Solier, *Engilemphus* Wittmer, *Hypattalus* Blackburn, *Lemphus* Erichson, *Nemacerus* Solier, *Neolemphus* Wittmer], Malachiini and Pagurodactylini; **Melyrinae**: all taxa previously included in Melyridae (sensu stricto), including members of Arthrobrachini, Astylini, Cerallini and Melyrini; **Dasytinae**: all taxa previously included in Dasytidae (sensu Bocakova *et al*., 2012), including members of Chaetomalachiini, Danaceini, Dasytini and Listrini.

Distribution. This family occurs virtually worldwide.

Notes. The composition of this family is essentially unchanged from that of Lawrence & Leschen (2010c) and Bouchard *et al.* (2011), except members of Rhadalidae **sensu n.** are excluded. With nearly 6000 species, this is by far the largest group of Cleroidea in terms of species numbers.

Chaetosomatidae Crowson, 1952, sensu n.

Chaetosomatidae Crowson 1952; Metaxinidae Kolibáč 2004, **syn.n.**

Included genera. *Chaetosoma* Westwood, *Chaetosomodes* Broun, *Malgassochaetus* Ekis & Menier (including *Somatochaetus* Menier & Ekis), *Metaxina* Broun (**restored placement**).

Distribution. This family occurs in New Zealand and Madagascar.

Thanerocleridae Chapin, 1924

Thaneroclerinae Chapin 1924; Viticlerini Winkler 1982; Zenodosini Kolibáč 1992; Isoclerina Kolibáč 1992

Included genera. **Zenodosinae**: *Zenodosus* Wolcott; **Thaneroclerinae**: Isoclerini: *Compactoclerus* Pic, *Isoclerus* Lewis; Thaneroclerini: *Meprinogenus* Kolibáč, *Neoclerus* Lewis, *Onerunka* Kolibáč, *Thaneroclerus* Lefebvre, *Viticlerus* Miyatake; Thanerocleridae *incertae sedis: Cleridopsis* Champion, *Cyrtinoclerus* Chapin. NOTE: Opitz (2010) resurrected four of the genera synonymized with *Isoclerus* by Kolibáč (1992).

Distribution. This family is distributed nearly worldwide, though mostly absent from Europe and temperate South America (Kolibáč, 2012).

Cleridae Latreille, 1802

(for family-group synonymy see Bouchard *et al.*, 2011)

Included genera. All genera included in the family sensu Kolibáč (2010) (i.e. excluding Thanerocleridae). Subfamilies are **Tillinae**, **Epiclininae**, **Korynetinae stat.rest.** [including Enopliinae, Epiphloeinae, Dermestoidinae (=Orthopleurinae, Neorthopleurinae), Peloniinae, Platynopterinae, Tarsosteninae], **Hydnocerinae** and **Clerinae** (including Anthicoclerinae).

Distribution. This family is distributed worldwide (Kolibáč, 2010). As a result of this study, we recommend use of the four-subfamily system of Kolibáč (1997, 2010) plus Epiclininae (Gunter *et al*., 2013).

Appendix 3. Key to adults of families and subfamilies of Cleroidea (modified from Lawrence *et al*., 2014)

This key is meant for orientation among the newly outlined families and subfamilies within Cleroidea, and is not a result of comprehensive morphological study of the respective groups. Such an investigation, which will probably turn up additional, more phylogenetically informative characters, must be deferred to a future contribution. Figure references in the key refer to the following: Arias *et al.* (2009) ('AR09'); Crowson (1964) ('C64'); Klimaszewski & Watt (1997) ('KW97'); Kolibáč (1989) ('K89'); Kolibáč (2003) ('K03'); Kolibáč (2004) ('K04'); Kolibáč (2005) ('K05'); Kolibáč (2006) ('K06'); Kolibáč (2008) ('K08'); Kolibáč (2013) ('K13'); Lawrence & Ślipiński (2013a) ('LS13a'); Lawrence & Ślipiński (2013b) ('LS13b'); Majer (1987) ('M87'); Majer (1994a) ('M94'); Majer (1995) ('M95'); Opitz (2010) ('O10'); Slipinski (1992) ('S92').

1 Procoxae not projecting below prosternal process 2

\- Procoxae distinctly, usually strongly, projecting below prosternal process, or IF slightly projecting THEN antennae not capitate and gular sutures more or less confluent 9

2(1) Head ventrally with pair of distinct setose tubular invaginations opening laterally into base of subantennal groove; abdominal ventrite 1 with postcoxal lines that extend to or near the edge of the sclerite .... **Biphyllidae**

Head without tubular invaginations; abdominal ventrite 1 lacking postcoxal lines 3

3(2) Tarsomeres 2 and 3 distinctly lobed, often markedly so .... **Byturidae**

Tarsomeres not distinctly lobed 4

4(3) Procoxae slightly transverse with concealed trochantins; procoxal cavities broadly closed externally (M94, fig. 18; S92, figs 44, 50) 5

\- Procoxae strongly transverse 7

5(4) Procoxal cavities internally closed (S92, fig. 50); metaventrite distinctly longer than abdominal ventrite 1; metanepisterna long and narrow; antenna with 9 antennomeres, with two-segmented club (S92, fig. 49); hindwings present; body densely clothed with long, fine hairs (S92, fig. 46; K13, fig. 3B) .... **Trogossitidae**: **Larinotinae**

\- Procoxal cavities internally open (S92, figs 44); metaventrite not longer than abdominal ventrite 1 (S92, fig. 45); metanepisterna very broad, their combined widths almost equal to width of metaventrite (M94, fig. 19); antenna with one-segmented club; hindwings absent 6

6(5) Antenna with eight antennomeres with one-segmented club (S92, fig. 43); mandible with mola; anterior edge of pronotum truncate; anterior pronotal angles not produced forward; tibial spurs absent; body clothed with expanded setae (S92, figs 36–37; K13, fig. 9F) .... **Lophocateridae**: *Parapeltis*

\- Antenna with ten antennomeres with one-segmented club; mandible without mola; anterior edge of pronotum strongly projecting over head, anterior pronotal angles produced forward and acute (M94, fig. 18); tibial spurs present; body clothed with expanded setae or scales (KW97, fig. 185; LS13a, fig. 82E) .... **Phycosecidae**

7(4) Procoxae with more or less concealed trochantins; procoxal cavities internally closed (S92, fig. 9) 8

\- Procoxae with fully exposed trochantins; procoxal cavities internally open 23

8(7) Body globular and strongly convex, capable of conglobation (KW97, fig. 179; LS13a, fig. 82D; LS13b, fig. 1); sides of pronotum more or less vertically explanate; antenna with ten or 11 antennomeres with one- or three-segmented club (LS13a, fig. 5C); tegmen undivided (LS13a, fig. 6A; K13, fig. 9H) .... **Rentoniidae**

\- Body more or less flattened (S92, fig. 1); sides of pronotum horizontally explanate (S92, fig. 9); antenna with eight antennomeres with one-segmented club (S92, fig. 4; K13, figs 9D–E) .... **Lophocateridae**: *Colydiopeltis*

9(1) Antenna with distinct club; lateral pronotal carinae strongly indicated; tarsi without lobed segments; pretarsal claws simple; gular sutures well separated 10

\- If antenna with well-marked club, tarsi with lobed segments or other characters different 11

10(9) Tibiae with spines on outer edge; pronotal hypomera with pockets near anterior angles of coxal cavities (LS13a, fig. 26G); mesal edge of mandible with membranous lobe and brush of hairs (M94, fig. 28); tegmen divided (M94, fig. 42); male tarsi 4-5-5 (LS13a, fig. 82F) .... **Acanthocnemidae**

\- Tibia without spines on outer edge; hypomera without pockets; mesal edge of mandible with two membranous lobes (K08, fig. 2); tegmen undivided (K08, fig. 16); male tarsi 5-5-5 (K08, p. 121) ... **Phloiophilidae**

11(9) Antenna without distinct club; procoxal cavities widely open externally; tarsomeres rarely lobed beneath and IF SO, THEN eversible lateral glands present on prothorax and at least some abdominal segments 12

\- Antenna more or less capitate OR IF NOT THEN tarsi lobed below and procoxal cavities closed externally; pretarsal claws usually simple, never with membranous appendages; usually at least tarsomere 3 with ventral lobes; prothorax and abdomen never with eversible lateral glands 18

12(11) Gular sutures narrowly separated or more or less confluent (K04, figs 21, 56); antennae filiform or slightly incrassate with all antennomeres longer than wide; scutellar shield elongate (K04, figs 23, 58); body clothed with very long, erect fine hairs (KW97, figs 182–183; K04, figs 1–3); pretarsal claws simple; elytral punctation confused or seriate .... **Chaetosomatidae**

\- Gular sutures well separated; antennae variable; pretarsal claws often more or less cleft, toothed or with membranous appendages beneath (M87, figs 63, 99, 187, 307); elytral punctation confused 13

13(12) Apical antennomere asymmetrical, emarginate or narrowed on one side (M87, fig. 237); head usually rostrate; eyes usually large and anteriorly emarginate; tarsomeres not lobed beneath; male with combs on protarsomeres 1–3 or 2–3 (M87, figs 254, 276); pretarsal claws simple or somewhat thickened at base .... **Prionoceridae**

- Apical antennomere not asymmetrically emarginate or narrowed; male protarsal combs, if present, on tarsomere 1 only; IF tarsomeres lobed beneath THEN eversible lateral glands present on prothorax and at least some abdominal segments; pretarsal claws often cleft, toothed or with membranous appendages beneath (M87, figs 342, 363); without other characters combined (LS13a, figs 83A–B, 83I) 14

14(13) Eversible vesicles present on prothorax and at least some abdominal segments . **Melyridae: Malachiinae**

- Eversible vesicles absent 15

15(14) First two abdominal ventrites connate (Rhadalinae) OR tarsomere 3 strongly lobed beneath (Gietellinae) .... **Rhadalidae**

- All abdominal ventrites free; tarsomere 3 not strongly lobed 16

16(15) Mandible very slender (M94, fig. 48; M95, figs 33, 79); maxilla with fused basistipes and mediostipes (M94, fig. 49; M95, fig. 80); tegmen undivided, 'clerid-like' (M94, fig. 62; M95, fig. 8); pretarsal claws not appendiculate .... **Mauroniscidae**

- Mandible broad; maxilla with divided stipes; tegmen 'melyrid-like'; pretarsal claws usually appendiculate 17

17(16) Tarsomere 1 half as long as tarsomere 2; tentorial cross-bar absent; mandible with ventral dens reduced to absent .... **Melyridae: Melyrinae**

- Tarsomere 1 normal; tentorial cross-bar present or reduced; mandible with well-developed ventral dens. .... **Melyridae: Dasytinae**

18(11) Meso- and metatarsomeres not or only slightly lobed beneath, with tarsomere 1 shorter than 2 and 4 subequal in length to 3 (K89, fig. 6); protarsomeres 1–4 strongly widened and distinctly lobed beneath (LS13a, fig. 71M); empodium prominent, bisetose, projecting between pretarsal claws; gular sutures short and strongly converging anteriorly (K89, fig. 11); metatrochanters not or scarcely protuberant (K89, fig. 16) .... **Thanerocleridae**

- Tarsi almost always with at least tarsomere 3 strongly lobed beneath (K89, figs 51, 98, 114; K03, fig. 17); never with prominent, bisetose empodium; IF gular sutures short and converging, THEN tarsomere 4 much smaller than 3 (K89, fig. 148); metatrochanters usually protuberant (K89, figs 67, 120, 151) 19

19(18) Fourth tarsomere minute .... **Cleridae: Korynetinae**

- Fourth tarsomere not minute 20

20(19) Labrum large, most often not incised mediodistally (O10, figs 6, 10); most species with large bulgy eyes (O10, fig. 7) and relatively short antenna (O10, fig. 9) .... **Cleridae: Hydnocerinae**

- Labrum not particularly large, usually deeply incised (O10, figs 3, 4); eyes not particularly large or bulgy (O10, fig 4); antennae long (O10, fig 40) 21

21(20) Procoxal cavity closed internally and externally (O10, fig 64); pretarsal claws usually multidentated, with (O10, fig 94) or without denticle .... **Cleridae: Tillinae**

- Procoxal cavity never closed interally and almost always open externally (O10, fig 60); pretarsal claws usually not multidentated, but often with a well-developed basal denticle (O10, fig 95) 22

22(21) Pretarsal claws simple, without basal denticle; tarsal pulvillar formula 4-4-4; tibial spur formula 2-2-2; elytral punctation nonseriate . . **Cleridae: Epiclininae**

- Without the above combination of characters .... **Cleridae: Clerinae**

23(7) Procoxal cavities broadly closed externally, the postcoxal processes of hypomera overlapping or interlocking with prosternal process (K05, pl. 68, fig. 11) . . 24

- Procoxal cavities almost always at least narrowly open externally, rarely with postcoxal process of hypomera just reaching intercoxal process 26

24(23) Mandible with distinct basal mola, accompanied by setal fringe; lacinia with strong apical hook; eyes prominent, not flattened or elevated; antennal club less flattened and without sensory fields or with less prominent sensory fields on both anterior and posterior portions of antennomeres 9 and 10 (K05, pl. 14, fig. 5) 25

- Mandible without basal mola; lacinia without apical hook; eyes more or less flattened and sometimes elevated; antennal club strongly asymmetrical and more or less flattened with distinct sensory field occupying anterior portions of antennomeres 9 and 10 (K05, pl. 4, fig. 3; pl. 6, fig. 2; pl. 65, fig. 10) ...... **Trogossitidae: Trogossitinae**

25(24) Antenna with 11 antennomeres, with loose, three-segmented club (K05, pl. 14, fig. 5); mesocoxal cavities not closed laterally by meeting of ventrites; frontoclypeal suture weakly indicated; body broad and flattened; pronotum laterally explanate (K06, pl. 15, fig. 1; K13, fig. 3A) .... **Trogossitidae: Calityinae**

- Antenna with seven to ten antennomeres and compact one- or two-segmented club (AR09; figs 5–6); mesocoxal cavities nearly or quite closed laterally by meeting of ventrites; frontoclypeal suture absent; body narrow and more or less cylindrical; pronotum not laterally explanate (AR09, figs 1–4; K06, pl. 15, fig. 3; K13, figs 3C–G) .... **Trogossitidae: Egoliinae**

26(23) Antennal club symmetrical; mandible with mola; body relatively short and broad with sides of prothorax explanate and elytral epipleura broad and complete OR pretarsal claws cleft or toothed;

scutellar shield sharply raised anteriorly OR gular sutures not converging anteriorly 27

- Antennal club slightly asymmetrical; without other features combined . . . . **Lophocateridae** (greater part)

27(26) Procoxal cavities externally narrowly open or narrowly closed, postcoxal processes of hypomera extending beyond middle of procoxal cavities and sometimes meeting prosternal process; lacinia without apical uncus; scutellar shield not sharply raised; pretarsal claws toothed or cleft . . . . **Thymalidae: Decamerinae**

- Procoxal cavities more broadly open, postcoxal processes of hypomera not extending beyond middle of procoxal cavities; lacinia with apical bidentate uncus; pretarsal claws simple 28

28(27) Mandibular mola accompanied by membranous prostheca and submolar lobe (C64, fig. 10); lateral pronotal carinae denticulate; scutellar shield not sharply raised anteriorly; body more or less flattened, elytra without carinae; length < 4 mm (K13, fig. 9G) . . . . **Protopeltidae**

- Mandibular mola without prostheca or submolar lobe; lateral pronotal carinae smooth; scutellar shield sharply raised anteriorly; body convex or elytral carinae present; length greater than 4 mm 29

29(28) Body convex; postcoxal processes of hypomera absent; elytra without carinae; protibial apex without curved spur; length less than 6 mm (K06, pl. 15, fig. 8; K13, fig. 10A) . . . . **Thymalidae: Thymalinae**

- Body flattened; postcoxal processes moderately long and apically acute; elytra with longitudinal carinae; protibial apex with large curved spur; length at least 7 mm (K06, pl. 15, fig. 7; K13, figs 9A–B) . . . . **Peltidae**