

## Supplementary Information

### **Integrated phylogenomics and fossil data illuminate the evolution of beetles**

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## Taxonomic treatment

SCIRTIFORMIA Lawrence, Ślipiński, Seago, Thayer, Newton and Marvaldi, 2011 / Superfamily SCIRTOIDEA Fleming, 1821 **sensu nov.**

**Type genus:** *Scirtes* Illiger, 1807.

**Diagnosis:** Adult head distinctly declined. Accessory ventral process of mandible present (partim). Ventral side of head with subgenal ridges. Prosternum very short in front of procoxae. Pterothoracic ventrites connected by membranes. Muscles *M. episterno-trochanteralis* 2 (*M. 70*), *M. episterno-coxalis* 3 (*M. 103*), and *M. furca-coxalis posterior* 3 (*M. 109*) absent. Functional spiracles on abdominal segment VIII absent. Hind wing AA<sub>4</sub> joining anal fold posteriorly. Mesothoracic trochantins externally exposed. Metacoxal plates weakly to moderately enlarged. Larva with mandibular mola. Larval galea non-articulated.

**Included taxa:** †Boleopsidae Kirejtshuk and Nel, 2013; Decliniidae Nikitsky, Lawrence, Kirejtshuk and Gratshev, 1994; †Elodophthalmidae Kirejtshuk and Azar, 2008; Scirtidae Fleming, 1821.

**Discussion:** The series Scirtiformia and the superfamily Scirtoidea are herein restricted to only the extant families Scirtidae and Decliniidae, as well as the poorly-known extinct families †Elodophthalmidae from Lower Cretaceous Lebanese amber and †Boleopsidae from lower Eocene French (Oise) amber, whose placement however remains preliminary (Kirejtshuk and Azar 2008; Kirejtshuk and Nel 2013; Lawrence 2019a). The remaining families formerly affiliated with Scirtoidea are removed and placed into a redefined Clambiformia *ser. nov.* (which includes the single superfamily Clamboidea *sensu nov.*).

The basal position of the families Clambidae, Decliniidae, Derodontidae, Eucinetidae, and Scirtidae within Polyphaga was long recognised (Crowson 1955, 1960; Lawrence and Newton 1982; Lawrence et al. 1995b). However, disentangling the relationships among these families has proved challenging. Given that phylogenomic studies (Zhang et al. 2018; McKenna et al. 2019) have now firmly established Scirtidae as the earliest diverging polyphagan lineage, this renders the traditional series Scirtiformia and the superfamily Scirtoidea *sensu* Lawrence et al. (1995b) polyphyletic with the traditional Derodontoidea nested within it, thus mandating a taxonomic change to establish the two as natural groups reflecting evolutionary relationships. Adult Scirtidae are distinguished from Clambiformia *ser. nov.* by an enlarged metacoxal meron and a rounded radial cell of the hind wing, both of which may represent apomorphies of the family. Scirtids further have cone-shaped, distinctly elongated mesocoxae, an elongated metafurcal stalk, and have separated *M. noto-epimeralis* (*L 34*) and *M. epimero-subalaris* (*M. 52*) (Friedrich and Beutel 2006). The larval mandible of Scirtidae bears three putative apomorphies: flattening, suppression of mandibular teeth, and presence of a strong ventral hook at base (Zwick and Zwick 2008).

It should be noted that the position of the rare and monogeneric Decliniidae endemic to eastern Russia and Japan, not sampled in the present analysis, is not fully settled. It was consistently recovered as sister to Scirtidae in morphological (Lawrence et al. 2011) and molecular analyses of six genes (McKenna et al. 2015b). Their sister relationship is supported by the hind wing AA<sub>4</sub> joining anal fold posteriorly, a character otherwise found only in Adephaga. Adults of both families also lack functional spiracles on the eighth abdominal segment (Lawrence et al. 2011). Contrary to this arrangement, Anton et al. (2016) pointed out two potential synapomorphies of Clambidae and Decliniidae: a distinct ventral antennal furrow and a longitudinal carina on the laterodorsal surface of the mandibles. It is clear that the assessment of the systematic position of Decliniidae will require the sequencing of more genes and further morphological studies, especially of adult musculature. For now, the position of the family should be considered as tentative.

CLAMBIFORMIA Cai and Tihelka **ser. nov.** / Superfamily CLAMBOIDEA Fischer, 1821 **sensu nov.**

**Type genus:** *Clambus* Fischer von Waldheim, 1821.

**Diagnosis:** Adult head distinctly declined (prognathous in Derodontidae). Accessory ventral process of mandible present (partim). Ventral side of head with subgenal ridges (lost in Derodontidae). Prosternum very short in front of procoxae. Pterothoracic ventrites connected by membranes. Muscles *M. episterno-*

*trochanteralis* 2 (*M. 70*), *M. episterno-coxalis* 3 (*M. 103*), and *M. furca-coxalis posterior* 3 (*M. 109*) absent. Functional spiracles on abdominal segment VIII present. Hind wing AA4 not joining anal fold posteriorly. Incision between anal field and medial field very deep (in Derodontidae) to moderately deep (in remaining families). Mesothoracic trochantins exposed (except in *Eucinetus*). Metacoxal plates weakly to greatly enlarged. Larva with mandibular mola. Larval galea non-articulated.

**Included taxa:** Clambidae Fischer, 1821; Derodontidae LeConte, 1861; Eucinetidae Lacordaire, 1857; †Mesocinetidae Kirejtshuk and Ponomarenko, 2010.

**Discussion:** The series Clambiformia *ser. nov.* and the superfamily Clamboidea *sensu nov.* as defined herein include Clambidae, Derodontidae, and Eucinetidae, previously placed into the non-monophyletic Scirtiformia / Scirtoidea and Derodontiformia / Derodontoidea *sensu* Lawrence and Newton (1982), Lawrence (1991), Beutel (1996) and Lawrence et al. (2010). When Derodontoidea was defined by Lawrence and Newton (1982), it was understood primarily as a taxon of convenience for Derodontidae and the two other problematic families, Nosodendridae and Jacobsoniidae, and was noted to be “almost certainly paraphyletic”. The taxonomic position of the two above-mentioned families was indeed phylogenetically exceptionally problematic and they were historically placed in a range of positions within Polyphaga, sometimes as *incertae sedis* (reviewed in Lawrence et al. 1995a, 2010). Recent phylogenomic studies have strongly favored the placement of Jacobsoniidae within Staphyliniformia (Zhang et al. 2018; McKenna et al. 2019), which is also supported by morphological characters such as similar hind wing structures and the maxillary galea of adults and larvae (Crowson 1959; 1960). The problematic Nosodendridae represent an isolated lineage sister to Staphyliniformia, Bostrichiformia, and Cucujiformia (Zhang et al. 2018; McKenna et al. 2019).

Because Derodontidae is consistently recovered with high support as sister to Clambidae and Eucinetidae (McKenna et al. 2015b, 2019; Zhang et al. 2018), we herein define the series Clambiformia *ser. nov.* and the superfamily Clamboidea *sensu nov.* to only include the families Clambidae, Derodontidae, and Eucinetidae. This new series is similar in composition to Crowson’s (1981) Eucinetiformia, which included Scirtidae, Eucinetidae, and Clambidae. Morphological similarity between Derodontidae and the abovementioned families, mainly in terms of adult musculature, has been discussed by Kukalová-Peck and Lawrence (2004). Among the important characters uniting Derodontidae with Clambidae and Eucinetidae is the membranous connection of the pterothoracic ventrite. This character is only visible when the mesocoxae are removed from their cavities. It is present in Archostemata (Baehr 1975), but absent in Myxophaga while in Adephaga the two segments are secondarily joined by the interlocking of the meso- and metaventrites. Following Friedrich and Beutel (2006), we consider it to represent a putative shared plesiomorphy of Scirtiformia / Scirtoidea *sensu nov.* and Clambiformia *ser. nov.* / Clamboidea *sensu nov.* It was subsequently gained independently in some polyphagan groups, such as Leiodidae (Friedrich and Beutel 2006; Ge et al. 2007). The absence of *M. episterno-trochanteralis* 2 (*M. 70*) is a feature shared by Scirtoidea and Clamboidea *sensu nov.*, in the sense presented here, although it has also been secondarily lost in some groups of polyphagan beetles such as Nosodendridae, and some groups in Scarabaeoidea, Pyrochroidae, and Dermestidae, while the absence of *M. episterno-coxalis* 3 (*M. 103*) can be considered a derived feature of the two groups (Friedrich and Beutel 2006; Ge et al. 2007). Following Ge et al. (2007), the shared loss of these three muscles, which are otherwise widespread in the remaining Polyphaga, can be considered another potential apomorphy of Scirtiformia / Scirtoidea *sensu nov.* and Clambiformia *ser. nov.* / Clamboidea *sensu nov.*

The remaining diagnostic features of Clambiformia *ser. nov.* are mainly plesiomorphic characters found also in Scirtiformia / Scirtoidea that exclude these taxa from the remaining polyphagan series. Nonetheless, it should be noted that even Scirtiformia / Scirtoidea *sensu* Lawrence et al. (1995b) was difficult to define and its diagnosis was likewise based in a large part on plesiomorphies (Lawrence and Newton 1995; Lawrence 2001). An externally exposed mesothoracic trochantin is also present in some Staphylinidae, Myxophaga, some Adephaga, and most Archostemata (Baehr 1975; Hansen 1997; Larsén 1966; Friedrich and Beutel 2006). Coxal plates are also present in Adephaga, Myxophaga, and some polyphagan groups such as Dascillidae and Ptiliidae (Hansen 1997; Beutel and Leschen 2005; Friedrich and

Beutel 2006). An accessory ventral process of the adult mandible is also present Dascillidae and Scarabaeoidea (Beutel et al. 2018).

The extinct family Mesocinetidae from the Upper Jurassic of Mongolia (Kirejtshuk and Ponomarenko 2010) shares similarities with eucinetids and may be their sister group (Lawrence 2019b). The family is therefore treated as a member of Clambiformia *ser. nov.*, although this placement should be considered as only tentative.

#### RHINORHIPIFORMIA Cai, Tihelka and Engel *ser. nov.*

**Type genus:** *Rhinorhipus* Lawrence, 1988.

**Diagnosis:** As for family Rhinorhipidae (Lawrence 1988, Kusy et al. 2018a): adult head hypognathous, with long temporal regions, lacking transverse occipital ridge or epicranial suture. Cranium with a short, median occipital endocarina and raised antennal insertions. Frontoclypeal region strongly declined and lacking a frontoclypeal suture. Clypeus long and narrow. Corpotentorium very broad. Oral cavity surrounded by setae. Labrum highly reduced, membranous. Mandibles long and with a setose dorsal cavity at base. Maxillae highly reduced, membranous, and setose. Pronotum without lateral carinae, anteriorly constricted and with a pair of elongate, vertical cavities. Procoxae slender and conical, trochantins completely visible, promesothoracic interlocking mechanism weakly developed. Mesothorax with a moderately developed mesoventral cavity reaching to the middle of the ventrite and a pair of well-developed procoxal housings on the mesanepisterna. Mesocoxae greatly projecting, mesotrochantin setose. Metaventrite with a moderately short discrimen. Metendosternite with long, curved lateral arms, anterior process with foramen at its base and a pair of expanded, ear-like, ventrolateral processes. Each elytron with 12 rather complete rows of deep punctures; epipleuron virtually absent, represented by slight thickening without lateral internal locking groove. Hind wing with r-m meeting stub of Rs; CuA3+4 meeting AA3, closing off anal (wedge) cell, cell acute; jugal lobe absent. Legs with enlarged and mesally produced metatrochanters, apically expanded metatibiae; tarsi simple, without pads, brushes, or membranous lobes; pretarsi with a well-developed empodium with two or three setae, and pectinate pretarsal claws (ungues). Abdominal tergite VIII of female dorsally concealed by tergite VII. Six Malpighian tubes. Larvae unknown.

**Included taxa:** Rhinorhipidae Lawrence, 1988.

**Discussion:** The enigmatic family Rhinorhipidae, represented in the modern fauna by a single species known only from northern New South Wales and southern Queensland (Lawrence 1988) is without a doubt one of the most mysterious beetle families. It possesses a suite of unusual characters that make resolving its systematic position difficult. Morphological analyses suggest an affinity to Elateriformia (Lawrence 1988; Lawrence et al. 1995b). As such, it has been included in Elateroidea (Bouchard et al. 2011; Lawrence et al. 2011) or placed as Elateriformia *incertae sedis* (Lawrence and Newton 1995). In a comprehensive morphological analysis, Lawrence (1988) recovered *Rhinorhipus* as sister to Elateroidea, while Lawrence et al. (1995b) recovered it as a sister to Byrrhoidea (all characters) or as sister to Buprestidae + Dascillidae (adult characters). A more recent extensive analysis of adult and larval morphological characters has recovered the family as sister to the elateriform family Rhipiceridae (Lawrence et al. 2011). Kusy et al. (2018a) recovered the family as the earliest diverging group within Elateroidea or as sister to Elateriformia and the rest of the derived Polyphaga. Consequently, the authors erected the superfamily Rhinorhipoidea to accommodate the group. In the more extensive analyses of McKenna et al. (2019) and our own analyses which account for long-branch artifacts, Rhinorhipidae are sister to Elateriformia and the remaining Polyphaga. Because it falls outside of Elateriformia, and would render the group paraphyletic, we erect the new series Rhinorhipiformia Cai, Engel and Tihelka *ser. nov.* for this unique family.

#### BYRRHOIDEA Latreille, 1804 *sensu. nov.*

**Type genus:** *Byrrhus* Linnaeus, 1767.

**Diagnosis:** Adult body strongly sclerotized, highly convex and compact, often possessing mechanisms

for compaction such as cavities for the reception of legs and fitting of hypognathous head against the anterior edge of the prosternum. Head strongly deflexed at base and deeply inserted into prosternum. Mandibles short and broad. Clypeus reduced. Base of labrum on lower plane than apex and usually forming a deep transverse impression between labrum and an abrupt frontal ridge. Eyes small and finely faceted, without interfacetal setae. Pro-mesothoracic interlocking device absent. Prosternum anteriorly not forming a produced chin-piece, but a head rest sometimes present. Procoxal and mescoxal cavities widely separated. Transverse metaventral suture absent. Epipleuron abruptly narrowed. Basal three (less often two) abdominal ventrites connate.

**Included taxa:** Byrrhidae Latreille, 1804.

**Discussion:** Byrrhids have been traditionally regarded as isolated groups within Elateriformia and treated as the sole members of Byrrhoidea (Crowson 1955, 1982; Beutel 2016). Lawrence (1988) subjected Elateriformia to the first cladistic analysis and expanded Byrrhoidea to include buprestids, byrrhids, and dryopoids. Lawrence and Britton (1991) subsequently resurrected Buprestoidea, which is supported by our results and retained in our classification system. The monophyly of Byrrhoidea as defined by Lawrence and Newton (1995) proved challenging to confirm based on adult, larval, and combined morphological datasets (Beutel, 1995; Lawrence et al., 1995, 2011; Costa et al., 1999). Early molecular studies based on a handful of genes have likewise yielded mixed results (Hunt et al., 2007; Bocak et al., 2014; McKenna et al., 2015). Analyses based on 89 (McKenna et al., 2019) and 68 genes (herein) have supported a clade unifying the former Buprestoidea and Byrrhoidea, together forming a sister group to a clade largely consistent with Dryopoidea of Crowson (1960, 1973, 1978, 1982) and Kasap and Crowson (1975). Hence, we herein resurrect the old concept of Byrrhoidea of Crowson (1955).

While different topologies supporting Buprestidae inside the old Byrrhoidea have been recovered by other recent morphological and molecular studies (e.g., Lawrence 1988; Lawrence et al. 2011; Bocakova et al. 2007; Bocak et al., 2014, Kundrata et al. 2014, 2017), it should be noted that the relationships of the ‘byrrhoid-buprestoid complex’ represent a lasting controversy in coleopteran systematics that should be addressed with more complete molecular and taxon sampling in future works.

#### DRYOPOIDEA Billberg, 1820 (1817) **stat. res.**

**Type genus:** *Dryops* A. G. Olivier, 1791.

**Diagnosis:** Adult with frontoclypeal suture mostly distinct. Hind margin of pronotum crenulate or not. Procoxae projecting. Tarsomere 5 often as long as the basal 4 tarsomeres. Functional spiracles on 8th abdominal segment absent. Wing folding of “dryopoid” type. Most larvae with a well-developed and usually setose protheca, short and wide prepharyngeal tube, broad and sclerotised gula, maxilla and labium closely connected, mandibular mola absent, labrum present, and a characteristic abdominal apex formed by tergite IX.

**Included taxa:** Callirhipidae Emden, 1924; Chelonariidae Blanchard, 1845; Cneoglossidae Champion, 1897; Dryopidae Billberg, 1820 (1817); Elmidae Curtis, 1830; Eulichadidae Crowson, 1973; Heteroceridae MacLeay, 1825; Limnichidae Erichson, 1846; Lutrochidae Kasap and Crowson, 1975; Protelmidae Jeannel, 1950; Psephenidae Lacordaire, 1854; Ptilodactylidae Laporte, 1838.

**Discussion:** Dryopoidea was defined by Crowson (1955, 1960, 1973, 1978, 1982) and Kasap and Crowson (1975) as a heterogeneous elateriform group that included beetles whose larvae are often aquatic and adults predominantly terrestrial. This early concept of the superfamily contained the families Chelonariidae, Dryopidae, Elmidae, Eulichadidae, Heteroceridae, Limnichidae, Lutrochidae, Psephenidae, and Ptilodactylidae. Lawrence and Newton (1982) added Callirhipidae which were earlier part of Armatopodea or Rhipicerioidea, and Lawrence (1988) transferred here Cneoglossidae from Cantharoidea. Lawrence (1988) placed dryopoid beetles in a redefined broader concept of Byrrhoidea, which was adopted by subsequent authors (Lawrence and Newton 1995, Beutel 2016). Characters shared by most dryopoid larvae were discussed by Beutel (1995). On the molecular level, the superfamily is characterised by a unique rearrangement of tRNA gene order (Timmermans and Vogler 2012). Dryopoidea was monophyletic in Hunt et al. (2007), McKenna et al. (2015b; 2019), in the mitogenome analyses of Timmermans and Vogler (2012), and Timmermans et al. (2016), Zhang et al. (2018), and the

present study.

#### NOSODENDRIFORMIA Cai and Tihelka **ser. nov.**

**Type genus:** *Nosodendron* Latreille, 1804.

**Diagnosis:** As for the family Nosodendridae (Beutel 1996; Ge et al. 2007; Leschen and Beutel 2010; Lawrence and Ślipiński 2013): Body oval and black, strongly convex dorsally, flattened ventrally. Head prognathous, inserted into the prothorax, with an enlarged mentum concealing the mouthparts. Frontoclypeal suture absent. Eyes large, almost meeting dorsally. Antennal insertions concealed from above by frontal projections. Antennae with a compact three-segmented apical club. All three segments of the thorax shorter than the maximum width of the metaventrite. Prothorax in front of procoxae short. Prosternal process long and wide, extending to mesoventrite. Cavities between hypomeron and prolegs present, further cavities for housing legs present on pterothorax and ventrites. Mesothoracic discriminial line absent. Mesocoxal cavities separated by a broad intercoxal process. Protrochantins concealed. *M. noto-trochantinalis* absent. Procoxae and procoxal cavities transverse. Metacoxal plates well-developed and complete. Metaventrite with more or less complete transverse suture. Radial cross-vein 3 absent, anal field strongly enlarged. Tarsal formula 5-5-5. Larva with labrum and clypeus fused, abdominal apex formed by posterior edge of segment VIII, and anal pads present.

**Included taxa:** Nosodendridae Erichson, 1846.

**Discussion:** The systematic placement of the problematic family Nosodendridae, the wounded-tree beetles, has always represented a persistent problem in systematic coleopterology. Earlier authors placed Nosodendridae into Byrrhoidea and Dascilloidea (Hayes and Chu 1946; Endrödy-Younga 1989), mainly due their gross similarity to byrrhids which also have an adult with a compact and convex body form. Crowson (1959) placed the family into the superfamily Dermestoidea. Lawrence and Newton (1995) considered the family to belong to Bostrichoidea, while Lawrence et al. (2010) placed the family into their Derodontiformia.

Ge et al. (2007) proposed several autapomorphies of Nosodendridae: the three segments of the thorax collectively shorter than the width of the metaventrite; accessory ridge laterally produced into a short, blunt tooth; presence of a hypomeral antennal groove; apical plate of the trochantinopleura distinctly enlarged; strongly shortened precoxal portion of the prosternum; wide prosternal process between procoxae; protrochantins concealed; transverse procoxae and procoxal cavities; mesothoracic discriminial line absent; broad intercoxal process separating mesocoxal cavities; anterior pronotal extension; dentiform process of the pronotal accessory ridge; the extensive apical plate of the trochantinopleura; radial cross-vein 3 absent; anal field strongly enlarged; *M. noto-trochantinalis* absent; and the beetle's strongly reduced flight musculature. The larvae of *Nosodendron* possess the following autapomorphies: labrum and clypeus fused; abdominal apex formed by posterior edge of segment VIII; and anal pads present (Beutel 1996).

#### STAPHYLINIFORMIA Lameere, 1900 **sensu nov.**

**Type genus:** *Staphylinus* Linnaeus, 1758.

**Diagnosis:** Antennae filiform or capitate, rarely serrate or pectinate. Mandibles more-or-less exposed, not concealed under labrum when abducted. Maxillary muscle *M. craniobasimaxillaris* present. Sternite II visible only as a lateral rudiment in nearly all representatives. Aedeagus never of cucujoid type. Metendosternite never of hylecoetoid type. Mesothoracic spiracles concealed under the hypomeron (most representatives). Radial cell primitively eyelet-like but weakened proximally by the obliteration of the base of RA 3+4. Radial bar with a single apical hinge, reinforced by the pinching together of RA 3+4 with the anterior wing margin. RA4 and RP 1 approaching one another and remaining parallel or fused together to form a Y-shaped support for the anterior apical wing margin and large apical field. Posterior coxae with oblique, non-excavate posterior face (absent in some staphylinoids). Protibia often strongly spinose or toothed outwardly. Tarsal formula usually 5-5-5 and simple. Malpighian tubules free, usually four present (Kukalová-Peck and Lawrence 1993; Hansen 1997; Lawrence and Ślipiński 2013).

**Included taxa:** Histeroidea Gyllenhaal, 1808; Hydrophiloidea Latreille, 1802; Scarabaeoidea Latreille, 1802; Staphyloidea Latreille, 1802.

**Discussion:** Staphyliniformia, as presented here in its revised form, roughly corresponds to Kolbe's (1908) concept of Haplogastra, which included superfamilies united by having sternite II visible only as a lateral rudiment and pleural sclerite – Hydrophiloidea, Staphyloidea, Histeroidea and Scarabaeoidea (Grebennikov and Scholtz 2004). The remaining Polyphaga (Kolbe's Heterogastra) has sternite II completely membranous. The Haplogastra concept was subsequently followed, with various modifications, by Peyerimhoff (1933), Jeannel and Paulian (1944), and Crowson (1955, 1960). The concept was later revived in analyses of wing characters (Kukalová-Peck and Lawrence 1993; referred to as the 'hydrophiloid lineage') and combined analysis of adult and larval morphological characters (Hansen 1997) and also appears to be well-supported by molecular data (Caterino et al. 2005; Song et al. 2010; McKenna et al. 2015b, 2019; Zhang et al. 2018).

The constriction of the hypopharynx between the maxillary bases is hourglass-shaped in cross sections in most staphyliniforms, as defined here, although exceptions are known in Silphidae (as Silphinae herein), some Leiodidae, and some Staphylinidae (Beutel and Leschen 2005). The early-diverging scarabaeoid genus *Glaresis* shares its paired ligular lobes, strongly sclerotised and setose anteriorly, with Hydrophiloidea (Anton and Beutel 2004; Beutel and Leschen 2005). In pupae, the presence of a maximum of only four functional abdominal spiracles has been suggested as a possible apomorphy of Staphyliniformia including Scarabaeoidea, or at least a large part of this group since some members such as some Scarabaeoidea, Hydrophilidae, Synteliidae, and Tachyporini have more (Lawrence and Newton 1982, Newton 2020). Anton and Beutel (2012) cited some potential apomorphies supporting Staphyliniformia *sensu nov.* They noted that scarabaeoids share with Hydrophiloidea antenna with asymmetrically widened club segments and discussed the possibility of a shared origin of the deep sensory pouch on the third club segment in Staphyloidea and Scarabaeoidea. Staphyliniformia *sensu nov.* is also characterised by the shared presence of *M. craniobasimaxillaris*, an unusual maxillary muscle apparently found only in members of this group. Scarabaeoidea and some other members of the series also share the sclerotised labrum at least 2.5 times as broad as long, combined length of the scapus and pedicellus exceeding one third of the entire antennal length, and a cupuliform antennal segment VIII preceding three-segmented club. The same condition was suggested as an autapomorphy of Hydrophiloidea. Further characters typical of Staphyliniformia *sensu nov.* were listed by Lawrence and Ślipiński (2013).

#### EROTYLOIDEA Latreille, 1802 **stat. nov.**

**Type genus:** *Erotylus* Fabricius, 1775.

**Diagnosis:** Adults with procoxal cavities internally open or closed by a slender bar. Glandular openings on the body, especially at the fore- and hind angles of the pronotum and prosternum. Tergite VIII in female dorsally concealed by tergite VII. Tarsal formula 5-5-5 in both sexes. Penis not divided into basipenis and distipenis, usually curved in lateral view, anterior edge usually with two penile struts. Adults phytophagous (Boganiidae, many Erotylidae), some pollinivorous, and mycophagous. Larvae with frontal arms lyriform (V-shaped in some Erotylidae), mesal surface of mandible with well-developed mola (some), maxillary articulating area present, hypopharyngeal sclerome present (missing in some Erotylidae). Some characters modified from Robertson et al. (2015).

**Included taxa:** Boganiidae Sen Gupta and Crowson, 1966; Erotylidae Latreille, 1802.

**Discussion:** The large and diverse Erotylidae was confirmed as monophyletic (Robertson et al. 2004; Wegrzynowicz 2002; Leschen 2003), as was the less diverse Gondwanan Boganiidae (Escalona et al. 2015). A close relationship between Erotylidae and Boganiidae was not generally suspected until these groups were recovered as sister taxa by Marvaldi et al. (2009) in an analysis of two rDNA fragments, albeit with considerably limited taxon sampling. In a four-gene analysis, Bocak et al. (2014) recovered Boganiidae as nested within Erotylidae. Genomic analyses have, however, unequivocally recovered Boganiidae and Erotylidae as a clade sister to the remaining Cucujoidea *sensu lato* (Zhang et al. 2018; McKenna et al. 2019; present study).

Boganiidae was not been sampled in many past analyses of Cucujoidea and so the set of characters supporting the superfamily is not extensive. Some Boganiidae (Escalona et al. 2015) and Erotylidae have glandular ducts (Crowson 1990, 1991; McHugh et al. 1997; Leschen 2003), some of which penetrate deep within the body. Similar ducts are present in several other families that are now placed in Coccinelloidea (Discolomatidae) and Cucujoidea (Cryptophagidae), and they also bear resemblance to ducts present in Chrysomeloidea and elsewhere (e.g. Drilling et al. 2013). Tightly bundled glandular ducts, referred to as a microtubulate condition by Leschen (2003), are present in Boganiinae (Boganiidae) and Pharaxonothinae (Crowson 1990, 1991; Leschen 2003). The penis, which is not divided into two parts that characterise several members of the Cucujoidea (e.g., Leschen et al. 2005; Lawrence et al. 2011) is of a single piece and often curved in lateral view, resting in the abdomen on its side. The anterior edge usually bears two elongate struts, which are short in Boganiinae, but elongate in most remaining taxa and fused into a single process. The extent to which aedeagal characters could be considered potential synapomorphies requires additional study.

Both Boganiidae and some phytophagous Erotylidae also share some ecological similarities, even though the ancestral state, at least of Erotylidae, may be fungus feeding. Both contain species that visit cycads in high numbers and probably contribute to their pollination (Crowson 1991; Leschen and Buckley 2007; Suinyuy et al. 2009; Prado et al. 2011). Given the discovery of Cretaceous boganiids preserved alongside cycad pollen, it is likely that the association between Erotyloidea *stat. nov.* and cycads is over 100 Ma old (Cai et al. 2018b).

Some of the families traditionally included in the 'basal Cucujoidea' that lack genetic data may eventually be placed into Erotyloidea; but at present there is no compelling morphological evidence to place them here.

Similarities between the monogeneric *Lamingtonium* and Boganiidae + Erotylidae were discussed by Sen Gupta and Crowson et al. (1969), and the external habitus and fungal feeding behaviour of the group are suggestive. However, the true affinities of the family are difficult to demonstrate conclusively (Lawrence et al. 2011), they lack the glandular ducts present in the families above, and the genitalia differ (Lawrence and Leschen 2003). Lawrence and Leschen (2003) discussed the possible relationship between Erotylidae, Lamingtoniidae, and Cyclaxyridae based on larval characters, and the sister relationship of Tasomosalpingidae and Cyclaxyridae was shown by Leschen et al. (2005). Cyclaxyridae lack glandular ducts and the Tasomosalpingidae have trichome-like structure at the posterior margin of the prothorax that interrupts the pronotal carina but doesn't appear to have the glandular ducts similar to Erotylidae or Boganiinae. Among the aforementioned families, the bipartite penis may not be present, and similar penile struts present in most erotylids also occur in Cyclaxyridae and Tasomosalpingidae, but the former has been placed among Cucujoidea by McKenna et al. (2015b) and Robertson et al. (2015) that placed it as sister taxon to Myraboliidae.

## NITIDULOIDEA Latreille, 1802 **stat. nov.**

**Type genus:** *Nitidula* Fabricius, 1775.

**Diagnosis:** Adults rarely with elongate rostrum. Dorsal part of mandible without setose cavity (except Sphindidae). Subantennal grooves well-developed (except Nitidulidae: Calonecrinae, Smicripidae). Antennae never fully filiform or moniliform, and a club is always present. Gular sutures never confluent (except some Nitidulidae, some Monotomidae). Ventral or lateral portion of prothorax on each side never with incomplete notosternal suture or without sutures (except some Nitidulidae, some Sphindidae, some Monotomidae). Cuticular glands, where present, consist of single ducts. Procoxal cavities internally open (most). Tarsal formula 5-5-5 in female and 5-5-5 or 5-5-4 in male (rarely 4-4-4). Ventricle 1 never much longer than ventricle 2 (except some Nitidulidae and Monotomidae). Abdominal tergite VII exposed in dorsal view and tergite VIII in male with sides curved ventrally forming a genital capsule (in Kateretidae, Monotomidae, Nitidulidae, and Smicripidae). Tergite VIII in female dorsally concealed by tergite VII, tergite X in male completely membranous. Spiculum gastrale present (absent in Sphindidae and some Monotomidae). Larvae with frontal arms lyriform (most), mesal surface of mandible with well-developed mola (most), maxillary articulating area present (most), hypopharyngeal sclerome present (most).



**Included taxa:** Helotidae Chapuis, 1876; Kateretidae Kirby, 1837; Monotomidae Laporte, 1840; Nitidulidae Latreille, 1802; Protocucujidae Crowson, 1954; Smicripidae Horn, 1880; Sphindidae Jacquelin du Val, 1860.

**Discussion:** The former superfamily Cucujoidea *sensu* Crowson (1955) and Lawrence and Newton (1982), more or less corresponding to the old Clavicornia, is a very heterogeneous group containing mostly minute to moderately sized brown to dark beetles that are difficult to place elsewhere (Leschen et al. 2005). As such, the old Cucujoidea has been considered to represent a taxonomically complicated ‘wastebasket group’ that may or may not be monophyletic (Leschen and Ślipiński 2010). There have historically been ample proposals to divide the group, which were reviewed in detail by Lawrence et al. (1995a). Robertson et al. (2015) provided the first step to splitting the traditional Cucujoidea with the use of molecular data, erecting the superfamily Coccinelloidea for ladybird beetles, handsome fungus beetles, and their relatives, and removing the Biphyllidae and Byturidae to Cleroidea. No other divisions of Cucujoidea have been formalised since then. It is notable that in the latter part of his career, Crowson considered the establishment of a separate superfamily for sap beetles and their allies, Nitiduloidea (Audiso 1993; Crowson 1995), although this was never proposed formally. Nonetheless, the group of families surrounding Nitidulidae has been consistently recovered in morphology-based phylogenies and has often been referred to as the ‘nitidulid lineage’, ‘nitidulid series’ or ‘nitidulid assemblage’ (Ślipiński 1998; Leschen et al. 2005; Cline et al. 2014; McKenna et al. 2015b). Genome-scale analyses have unambiguously established the existence of a clade containing the ‘nitidulid lineage’ and the more basal families Helotidae, Sphindidae, Protocucujidae, and Monotomidae (McKenna et al. 2019).

The monophylum consisting of Monotomidae, Nitidulidae, Kateretidae, and Smicripidae is supported by abdominal tergite VII exposed in dorsal view and tergite VIII in males with sides curved ventrally forming a genital capsule (Leschen et al. 2005). LeConte (1861) treated this group as a unified Nitidulidae. Crowson (1955) also considered Monotomidae to belong to the nitidulid group, although he later revised this idea (unpublished, cited in Leschen et al. 2005). The clade containing only Nitidulidae, Kateretidae, and Smicripidae is strongly supported by the frontoclypeal suture present (most), anterior cervical sclerite not contiguous with head capsule or placed in paired emarginations, galea absent (most), anterior pronotal angles absent or not produced forwards, anterior tendons of metendosternite narrowly separated, abdominal tergite VII exposed in dorsal view, tergite VIII in males with sides curved ventrally forming a genital capsule, paired endocarinae absent in the ventral head capsule of larvae, four or fewer stemmata, apex of larval mandible bidentate (most), mesal surface of larval mandible with asperate or tuberculate mola, labial palpi 1-segmented in larva, and larval hypopharyngeal sclerome an irregular molar-like tooth (most) (Leschen et al. 2005). Of these, the absence of a galea is apparently autapomorphic for the group. The basal clade Protocucujidae + Sphindidae has traditionally been well-accepted (Sen Gupta and Crowson 1979; McHugh 1993; Ślipiński 1998) and is supported by the following shared morphological characters: frontoclypeal suture present, apex of mandible tridentate, anterior portion of prosternum at midline as long as prosternal process, procoxal cavity internally open, metendosternal laminae well developed, 5 free veins present in medial area of the hind wing, 5-5-4 male tarsal formula, aedeagus with U-shaped sclerite near apex, loss of articulated parameres, internal sac with basal complex sclerite, labrum of larvae vertical, apex of larval mandible tridentate, and ventral epicranial ridges of larval head capsule absent (Thomas 1984a; Ślipiński 1998; Beutel and Ślipiński 2001; Leschen et al. 2005). Similarities between the two taxa are especially evident in the South American genus *Protosphindus* Sen Gupta and Crowson (1979).

Characters shared by nitidulid families are listed above in the diagnosis section. Identifying characters that support the whole of the eco-morphologically remarkably diverse Nitiduloidea, as defined here, is more difficult. This is not surprising, however, because the same was the case for the old Cucujoidea *sensu* Crowson (1955) and Lawrence and Newton (1982) which likewise lacked a set of unique and widespread apomorphies (Kirejtshuk 2000; Leschen and Ślipiński 2010). Nonetheless, commonalities of the whole Nitiduloidea *stat. nov.* have been noted by coleopterists for over a century. Sharp and Muir (1912) noted similarities of the aedeagus of Helotidae, Monotomidae, and Nitidulidae, although they noted that their taxon sampling was not wide enough to draw definitive conclusions.

Because of the inherent difficulties associated with studying the phylogeny of cucujoid beetles, the division of Cucujoidea *sensu* Robertson et al. (2015) proposed by us into three separate superfamilies leaves several enigmatic families of uncertain placement that were not included in our analyses because of the unavailability of sequences and lack of consensus in morphology-based phylogenies. In the morphological phylogenetic analysis of Leschen et al. (2005), Tasmosalpingidae formed a monophyletic group with Cyclaxyridae but was simultaneously also close to Nitiduloidea based on all characters or adult characters only. When larval characters were analysed alone, it was recovered as sister to Phalacridae. The placement of the fossil families †Parandrexidae and †Wabbelidae has not been formally tested (Kirejtshuk 1994; Escalona et al. 2015; Alekseev, 2017). These fossil taxa are treated as Cucujiformia incertae sedis, as they cannot be placed for sure in either Erotyloidea stat. nov., Nitiduloidea stat. nov., or Cucujoidea *sensu* nov. with certainty.

## CUCUJOIDEA Latreille, 1802 *sensu* nov.

**Type genus:** *Cucujus* Fabricius, 1775.

**Diagnosis:** Adults typically with dorsoventrally flattened bodies (except Cyclaxyridae, some Passandridae, Phalacridae). Head sometimes with elongate rostrum, longer than wide (some Silvanidae, some Laemophloeidae). Dorsal part of mandible without a setose cavity (present in some Silvanidae, some Phloeostichidae). Subantennal grooves weakly developed or absent (except some Passandridae, some Laemophloeidae, Myraboliidae). Antennae filiform or moniliform (some Silvanidae, Cucujidae, some Passandridae, some Laemophloeidae). Tentorium with a medial process (except Myraboliidae, Phalacridae, and Laemophloeidae). Gular sutures at least partly confluent (only in Passandridae). Ventral or lateral portion of prothorax on each side with incomplete notosternal suture or without sutures (some Cryptophagidae, some Silvanidae, some Phloeostichidae, Laemophloeidae). Cuticular glands, where present, consist of single ducts. Procoxal cavities internally open (except some Passandridae, Phalacridae). Ventricle 1 sometimes much longer than ventricle 2 (some Cryptophagidae, some Silvanidae, Myraboliidae). Tergite VIII in female dorsally concealed by tergite VII, tergite X in male completely membranous. Unequal anterior tibial spurs (some, in Passandridae, Phalacridae and Laemophloeidae). Tarsal formula 5-5-5 in female and 5-5-5 or 5-5-4 in male (rarely 4-4-4 or 4-5-4). Penis may be clearly divided into basipenis and distipenis (Leschen, pers. obs.) or undivided with a single, often broad penile strut. Larvae with frontal arms lyriform (most), mesal surface of mandible with well-developed mola (most), maxillary articulating area present (most), hypopharyngeal sclerome present (most).

**Included taxa:** Agapythidae Sen Gupta and Crowson, 1969; Cavognathidae Sen Gupta and Crowson, 1966; Cryptophagidae Kirby, 1826; Cucujidae Latreille, 1802; Cyclaxyridae Gimmel, Leschen and Ślipiński, 2009; Hobartiidae Sen Gupta and Crowson, 1966; Laemophloeidae Ganglbauer, 1899; Lamingtoniidae Sen Gupta and Crowson, 1969; Myraboliidae Lawrence and Britton, 1991; Passandridae Blanchard, 1845; Phalacridae Leach, 1815; Phloeostichidae Reitter, 1911; Priasilphidae Crowson, 1973; Silvanidae Kirby, 1837; Tasmosalpingidae Lawrence and Britton, 1991.

**Discussion:** Cucujoidea, in the strict sense as conceived here, corresponds to the most derived clade of the old Cucujoidea *sensu* Crowson (1955) and Lawrence and Newton (1982) and the ‘basal Cucujoidea’ of Leschen et al. (2005) recovered in our and previous genome-scale molecular studies (Zhang et al. 2018; McKenna et al. 2019). As with the former Cucujoidea *sensu* Crowson (1955) and Lawrence and Newton (1982) or Cucujoidea *sensu* Robertson et al. (2015), finding definitive apomorphies of the group is difficult. The definitions of many of the cucujoid families discussed here have been considerably fluid in the past, often lacking definitive apomorphies, but most concern groups broadly defined in recent decades as Cucujidae and Phloeostichidae. Nonetheless, Cucujoidea *sensu* nov. contains several clades that were strongly suspected to be monophyletic based on morphological studies, in some cases long before the advent of molecular systematics. These include Laemophloeidae, Phalacridae, and Passandridae (Thomas 1984b); Leschen’s (1996) ‘cucujid line’ consisting of Cucujidae, Hobartiidae, Phloeostichidae, Cryptophagidae, Cavognathidae, and Silvanidae, following Thomas (1984a); and the ‘basal Cucujoidea’ of Leschen et al. (2005). Cucujoidea *sensu* nov. is also mostly congruent with the ‘cucujid series’ as recovered in molecular studies by Hunt et al. (2007), Bocak et al. (2014), McElrath et al.

(2015), and Robertson et al. (2015).

The relationships among the family groups and potential synapomorphies for Cucujoidea have been discussed in several papers, but none of the characters are conclusive synapomorphies, as discussed in Leschen (1996), relevant chapters in Leschen et al. (2010), and the study by McElrath et al. (2015) where some salient features of the adults were reconstructed over the Cucujoidea tree. Some characters like the presence or absence of the tentorial spine in the adult or the number of tarsungular setae in the larva (Leschen 1996) are too variable within the group to be identified as a synapomorphy (Leschen 1996). One feature relevant for defining Cucujoidea may be the presence of a bipartite or subdivided penis (Leschen, unpubl.). The penis in Cucujiformia is highly diverse (Lawrence and Slipinski 2013) and many groups have a single or double penile strut. Several members of the Cucujoidea as defined here have a bipartite penis (Cavognathidae, Priasilphidae, Cucujidae, Agapythidae, and Silvanidae; Leschen et al. 2005; Lawrence et al. 2011) and the anterior part could be homologous to the penile strut. Examination of dissections of Hobartiidae and Passandridae and images of Myraboliidae indicate that these may also have a subdivided penis, whereas the remaining families clearly have an undivided penis (Cyclaxyridae, Lamingtoniidae, Phloeostichidae, Phalacridae and Tasmosalpingidae). If we examine this variation in light of our tree and those of Zhang et al. (2018) and McKenna et al. (2019), a bipartite aedeagus is optimised as a synapomorphy, the undivided type (in different forms) as derived. These aedeagal types are similarly optimised on the trees in McElrath et al. (2015) and Robertson et al. (2015).

†ALPHACOLEOPTERA Engel, Cai, and Tihelka **subord. nov.**

**Type family:** †Tshekardocoleidae Rohdendorf, 1944.

**Diagnosis:** Procoxal cavities closed posteriorly; mesothorax shortened and metathorax enlarged; forewings complete, flat over abdomen at rest, with wide epipleura, meeting along and putatively locking along sutural margin except apices acute and typically not meeting along sutural margin (thus, largely but not completely covering metasoma), venation complete, reticulate, longitudinal sectors typically forking (sometimes zigzagged), with multiple cells between veins, small field proximally between Sc and RA (except Permosynoidea), anal vein following sutural margin (posterior trailing margin opposite leading edge), with shoulder placed proximally on A1+2; mesoventrite longer than prosternum; tarsal formula 5-5-5; telescopic ovipositor scarcely sclerotized.

**Included taxa:** Superfamily †Permocupedoidea Martynov, 1932, Superfamily †Permosynoidea Tillyard, 1924, and Superfamily †Coleopseoidea Kirejtshuk and Nel, 2016.

**Etymology:** The name of this suborder is a combination of Greek *álpha* (*ἄλφα*), first letter of the Ancient Greek alphabet and an allusion to “first”, and Coleoptera, itself a combination of Greek *koleós* (*κολεός*), meaning, “sword-sheath”, and *pterá* (*πτερά*, plural of *pterón*, *πτερόν*), meaning, “wings”.

**Discussion:** This group has often been referred to as †Protocoleoptera Tillyard, 1924. Unfortunately, Protocoleoptera was established explicitly for the extinct family †Protocoleidae Tillyard, 1924, a group today known to be a lineage of polyneopteran insects allied to the earwigs (Dermaptera). Another extinct family, †Permophilidae Tillyard, 1924, from the same fossil beds was later established as †Paracoleoptera Laurentiaux, 1953, and also considered a lineage allied to the beetles. †Permophilidae, like †Protocoleidae, are polyneopterans (*e.g.*, Forbes, 1928; Kukalová, 1966). Accordingly, †Protocoleoptera and †Paracoleoptera are objective synonyms of †Protelytroptera, are unrelated to Coleoptera, and, in fact, do not belong to the Eumetabola. Neither †Protocoleoptera nor †Paracoleoptera can be used as suborders of Coleoptera. Similarly, Crowson (1981) established an extinct suborder, †Archecoleoptera, which he considered to exclude the most primitive of beetles but be confined to the Permian. Crowson still considered †Protocoleoptera to be a lineage of early beetles including the †Tshekardocoleidae and others, and therefore excluded them from his ill-defined †Archecoleoptera. †Archecoleoptera were not established on the basis of a specific taxon or characters, but was meant to exclude at the least †Tshekardocoleidae and other early extinct beetles. Thus, the basalmost and extinct suborder of beetles remains without an appropriate name and one is therefore established here.

ZACOLEOPTERA Engel, Cai, and Tihelka **capaxord. nov.**

**Diagnosis:** Procoxal cavities distinct and open; narrow prosternal process present.

**Included taxa:** Suborder Metaxycoleoptera nov. and Hyporder Eucoleoptera nov.

**Etymology:** The name of this capaxorder is a combination of Aeolian Greek *zá* (ζά), meaning, “very”, and Coleoptera.

#### †METAXYCOLEOPTERA Engel, Cai, and Tihelka **subord. nov.**

**Type family:** †Ponomarenkiidae Yan et al., 2017.

**Diagnosis:** Fossil beetles with: antenna moniliform; elytra without window punctures; propleuron exposed; absence of coxal plates; absence of broad contact between meso- and metaventrites; procoxal cavities distinct and open; narrow prosternal process present; internalized metatrochantin; metanepisternum only marginally part of closure of mesocoxal cavity; transverse ridge of mesoventrite; short metacoxae not reaching hind margin of abdominal sternite III. They share with Eucoleoptera open procoxal cavities and a narrow prosternal process.

**Included taxa:** Family †Pronomarenkiidae Yan et al., 2017.

**Etymology:** The name of this suborder is a combination of Greek *metaxú* (μετάξῦ), meaning, “between”, and Coleoptera.

**Discussion:** This extinct group is likely sister to the Eucoleoptera, *i.e.*, the clade comprising all extant beetle suborders.

#### EUCOLEOPTERA Engel, Cai, and Tihelka **hypord. nov.**

**Type family:** Carabidae Latreille, 1802.

**Diagnosis:** Preëpisternal cervical sclerites lacking; procoxal cavities present and distinctly countersunk (secondarily modified in several clades); broad prothoracic postcoxal bridge lacking; narrow prosternal process; mesothoracic discrimen absent (secondarily reversed in various clades); mesothoracic meron absent; mesoscutellar-elytron locking device present; hind wing triangular (pivotal) fold proximal to RA3+4 (*i.e.*, not dividing vein), with vein typically incompletely proximally; mesocoxal cavities deep and completely demarcated mesally and posteriorly by distinct ridge (secondarily reduced numerous times); metascutal fissure present; alacristae present; metapostnotum undivided; metathoracic meron absent; metacoxae transverse, with metacoxal cavities distinct, completely demarcated posteriorly by carina; reduced costal crossvenation; sternite I reduced; female tergite IX divided into paraprocts on either side of tergite X.

**Included taxa:** Adephegata Clairville, 1806, Archostemata Kolbe, 1908, Myxophaga Crowson, 1955, and Polyphaga Emery, 1886.

**Etymology:** The name of this hyporder is a combination of Greek *eû* (εὔ), meaning, “good” or “true”, and Coleoptera.

**Discussion:** This group comprises all extant suborders of Coleoptera, distinct from the exclusively Permian alphacoleopterans.

## Notes on the classification of beetles

†MAGNOCOLEIDAE Hong, 1998 *syn. nov.* – The monotypic fossil family †Magnocoleidae was described by the preeminent Chinese palaeoentomologist Professor Youchong Hong (1998) based on isolated elytra from the Lower Cretaceous Qingshila Formation of China, which were named as *Magnocoleus huangjiapuensis*. No further species belonging to the family have been described since, probably owing to the poorly accessible original description published in Chinese with only a brief English summary in a regional geological bulletin. Hong compared the new family with Permian, Triassic, and Jurassic protocoleopterans and archostematanans, and differentiated it based on elytral venation characters. However, it should be noted that the elytral wing venation pattern of *Magnocoleus* falls well within the range of morphological variation observed in Mesozoic Cupedidae and Ommatidae. Using Ponomarenko's (1969) key to Archostemata *sensu lato*, the presence of five principal elytral veins, together with the shortened ones, and the complete reduction of CuP places *Magnocoleus* into Cupedidae or Ommatidae. Indeed, in a phylogenetic analyses of elytral characters *Magnocoleus* was recovered as sister to Ommatidae and Cupedidae (Lubkin 2007). We thus consider †Magnocoleidae as a junior synonym of Cupedoidea and *Magnocoleus* as *incertae sedis* within that superfamily. The lack of complete body fossils makes it difficult to determine whether the beetles belonged to Ommatidae or Cupedidae, as the two families cannot be reliably distinguished on the basis of elytral venation alone (Lawrence 1999).

HETERO CERIDAE MacLeay, 1825. – The variegated mud-loving beetles were recovered as nested within Limnichidae with moderate support. Heterocerids are characterised by a set of morphological characters that represent extreme adaptations for life in near-water environments, such as fossorial legs and body covered with dense water-repellent setae (Vanin et al. 2016). Historically, the monophyly of Limnichidae, the minute marsh-loving beetles, has been doubted on the basis of both morphological and molecular data (Hinton 1939; Crowson 1978; Beutel 1995; Costa et al. 1999; Bocak et al. 2014). Crowson (1978) regarded Heteroceridae as a sister group to Limnichidae. In a morphological phylogenetic analysis, Beutel (1995) recovered Limnichidae as the sister group to Heteroceridae based on larval morphological characters, while Costa et al. (1999) placed Heteroceridae in a clade with Dryopidae + paraphyletic Limnichidae. Heteroceridae was placed within a paraphyletic Limnichidae in Kundrata et al.'s (2017) analysis of four DNA fragments and the phylogenomic studies of Zhang et al. (2018) and an 89 gene dataset in McKenna et al. (2019). In our analyses, *Heterocerus* was recovered as sister to Limnichinae with full support, although the subfamilies Hyphalinae and Thaumastodinae were not sampled. In the analysis of McKenna et al. (2019), *Heterocerus* was sister to Cephalobyrrhinae.

Regardless of the precise sister group of Heteroceridae it shares with apparently all Limnichidae the presence of a frontoclypeal suture on the adult head, absence of the radial cell in the hindwing, asymmetrical base of the basal piece of the aedeagus, as well as the following larval synapomorphies: head with dense vestiture of long and short setae, presence of accessory anterior tentorial bridge, and a short antenna with a large hyaline sensorium (Crowson 1978; Beutel 1995; Costa et al. 1999). Crowson (1978) furthermore pointed out that the larvae in both families share mandibles with a plumose prosthema and retractable anal tracheal gills in at least some taxa.

We treat Heteroceridae as a separate family, although its incorporation within Limnichidae should be considered if future studies arrive at identical conclusions with increased gene sampling and higher statistical support.

JACOBSONIIDAE Heller, 1926. – The family Jacobsoniidae is herein treated as a member of the superfamily Staphylinoidea. Jacobsoniidae have been placed in a variety of basal polyphagan superfamilies in the past, namely in Bostrichiformia (Lawrence and Newton 1995), Cucujiformia (Sen Gupta 1979) and Derodontiformia (Lawrence and Leschen 2010). Recently, Lawrence (2016) removed Jacobsoniidae from Derodontiformia and treated it as series and superfamily *incertae sedis*.

The placement of some or all of members of Jacobsoniidae within Staphylinoidea is supported by morphological and molecular studies (Lawrence et al. 2011; McKenna et al. 2015b, 2019; Toussaint et

al. 2017; Zhang et al. 2018). The three very different-looking genera have not been included together in any recent analyses, and only two (*Derolathrus* and *Saphophagus*) have genetic data available. Ptiliidae, which together with Hydraenidae formed the sister group to Jacobsoniidae in our analyses, shares with the family reduced hindwing venation and very long fringe hairs forming a “feather-wing”, with a complex folding pattern aided by spicules on the abdominal tergites (Crowson 1960; Yamamoto et al. 2017). The jacobsoniid larval galea also suggests a relationship with Staphylinoidea (Crowson 1960). It should nonetheless be noted that our analyses are only based on the jacobsoniid genus *Derolathrus*; however, *Saphophagus* was placed in the same position in McKenna et al. (2019). Due to the considerable morphological differences between the three genera, it is not certain whether Jacobsoniidae as presently defined is in fact monophyletic (Löbl and Burckhardt 1988), and genetic data for *Sarothrias* (senior synonym of the type genus of the family) would test this hypothesis and settle the superfamily placement of the family.

**COLONIDAE** Horn, 1880 (1859) *stat. nov.* – The leiodid subfamily Coloninae is herein treated as a separate family of Staphylinoidea, in agreement with some historical treatments of Leiodidae and related families (e.g., Jeannel 1936; Perkovsky 1997). In addition to having a brick-wall pattern of abdominal intersegmental membranes, unique outside of Staphylinidae *sensu nov.* as noted below under Silphinae, colonines lack the conspicuous leiodid character of an “interrupted club” with smaller antennomere 8 (e.g., Perkovsky 1997), and have many other characters that are unique or unusual within Leiodidae, including cervical sclerites absent, procoxal cavities closed by fusion of the pronotal and prosternal processes, abdominal spiracles 7-8 absent, and others noted by Newton (1998). Recent molecular phylogenetic studies have also placed Coloninae as an isolated staphylinoid group well outside of an otherwise monophyletic Leiodidae, either as a sister to Hydraenidae+Ptiliidae (McKenna et al. 2015a), or sister to Agyrtidae+Leiodidae (minus Coloninae) (Lü et al. 2020). Recent discovery of mid-Cretaceous fossils (Cai and Huang 2017; Yamamoto and Takahashi 2018) further supports this separation by showing that an unreduced antennomere 8 was already present then and not likely a later secondary development within Leiodidae as previously proposed (e.g., Hansen 1997).

**SILPHINAE** Latreille, 1806 *stat. nov.* – The family Silphidae *sensu* Sikes (2016) is herein treated as a subfamily of Staphylinidae *sensu nov.* Difficulties in clearly distinguishing the two groups were pointed out by coleopterists for almost a hundred years; Hatch (1927) treated the burying beetles as a subfamily of Staphylinidae, but his proposal was not widely accepted. A number of morphological and molecular studies conducted since have firmly established Silphinae *stat. nov.* as either nested within Staphylinidae or at most a sister group to that family, together forming a monophyletic clade (Hansen 1997, Beutel and Molenda 1997; Beutel and Leschen 2005; Caterino et al. 2005; Hunt et al. 2007; Grebennikov and Newton 2009, 2012; Lawrence et al. 2011; McKenna et al. 2015a, 2015b, 2019; Zhang et al. 2018; Lü et al. 2020; Song, et al. 2021). The sister group of Silphinae *stat. nov.* is not resolved, as past studies have suggested a range of topologies often placing the subfamily as sister to the remaining staphylinids (e.g., Grebennikov and Newton 2012) or associated with the subfamily Phloeocharinae (Caterino et al. 2005) or Tachyporinae (McKenna et al. 2015a, 2015b; Lü et al. 2020; Song et al. 2021; Yamamoto 2021). In our analyses, the burying beetles were recovered as sister to a clade containing Osoriinae, Apateticinae, and Scaphidiinae. This rather derived placement within Staphylinidae is consistent with the hypothesis of Lawrence and Newton (1982).

The inclusion of Silphinae *stat. nov.* within Staphylinidae *sensu nov.* is supported by a typical brick-wall pattern of minute sclerites in the abdominal intersegmental membranes, which may represent a synapomorphy of the two groups, although it also occurs in the enigmatic leiodid genus *Colon* Herbst (Hansen 1997) and is not present in many groups (Thayer 2016). The two taxa share a number of morphological characters, most likely correlated with reduced elytra that are abbreviated apically and associated with a more flexible abdomen: a unique wing hinge and asymmetrical folding pattern, aedeagus usually everted asymmetrically and with a large basal bulb and internal muscles for evaginating the internal sac, larvae without labral tormae and mandibular molae but with a modified tentorium whose posterior arms attach directly to the ventral surface of the head and whose bridge is directed posteriorly (Lawrence and Newton 1982; Newton 1997; Sikes et al. 2016). We consider this

evidence, together with the results of molecular phylogenetic studies, as sufficient for formally treating the carrion beetles as members of Staphylinidae *sensu nov.*

The former subfamilies of Silphinae *stat. nov.* are downgraded to tribal level: Silphini Latreille, 1806 and Nicrophorini Kirby, 1837 (both *stat. nov.*).

CLEROIDEA Latreille, 1802. – Gimmel et al. (2019) recently conducted the first in-depth molecular analysis of the relationships within the superfamily Cleroidea, sampling four genes across a wide range of taxa. While the taxon sampling in our study was insufficient to test all their newly proposed classification changes in the superfamily, we did recover their newly proposed Thymalidae, represented by *Thymalus*, nested within Trogossitidae *sensu stricto* of Gimmel et al. (2019). While *Thymalus* was historically placed within the trogossitid subfamily Peltinae (now Peltidae), it does not fit the diagnosis of Trogossitidae in the new, restricted sense, which includes only taxa with broadly closed procoxal cavities (Gimmel et al. 2019). We defer this issue to a subsequent study that includes more taxa of the Trogossitidae (*sensu stricto*) and the other subfamily of Thymalidae, the Decamerinae.

CYBOCEPHALINAE Jacquelin du Val, 1858 *stat. nov.* – The family Cybocephalidae is herein treated as subfamily Cybocephalinae *stat. nov.* within Nitidulidae. The rank and systematic position of this peculiar group was recently discussed by Kirejtshuk and Mantič (2015) and Lawrence (2019c).

MELOIDAE Gyllenhal, 1810. – The family Meloidae *sensu* Bologna et al. (2010) was recovered nested within Anthicidae. Due to their unusual life habits and a similarly unusual morphology, the systematic position of blister beetles has long been considered unresolved. A relationship with the family Anthicidae has been hypothesised by a number of coleopterists in the past (Crowson 1955; Abdullah 1965a, b, 1969; Selander 1966, 1991; Bologna and Pinto 2001). The subtribe Protomeloina has been regarded by Abdullah (1965a, b) as a link between the family and the remaining Anthicidae. The same author also proposed that blister beetles are in fact derived anthicids (Abdullah 1969). Meloidae have been recovered as nested within Anthicidae in the phylogenomic analyses of Zhang et al. (2018) and McKenna et al. (2019) as well as in some analyses of fewer genes (Gunter et al. 2014). Both families share a strongly deflexed head, a somewhat inflated vertex, a narrow neck, and a pronotum lacking lateral carinae (Bologna et al. 2010). Indeed, some meloids and anthicids can be easily confused and unsurprisingly there is a long history of taxa transferred between the two groups. It is interesting to note that some anthicid beetles are attracted to blister beetles and feed on the cantharidin they secrete, which is possibly used for predator defense and/or as a mating attractant, leading Abdullah (1964) to postulate that the production of this substance may have been ancestral to the two groups. This hypothesis seems supported by the fact that some male anthicids have been recorded to secrete cantharidin (Schütz and Dettner 1992). At present, we regard Meloidae as a separate family, but note that the accumulation of further molecular evidence may result into the group being joined within Anthicidae. An alternative treatment may be to divide Anthicidae, which currently contains several subfamilies with apparently disparate morphology, depending on future morphological and molecular evidence.

## Classification of beetles (families and subfamilies)

### Order COLEOPTERA Linnaeus, 1758

†Suborder **ALPHACOLEOPTERA** Engel, Cai, and Tihelka, *nov.*

†Superfamily **Coleopseoidea** Kirejtshuk and Nel, 2016

†Family Coleopseidae Kirejtshuk and Nel, 2016

†Superfamily **Permocupedoidea** Martynov, 1932

†Family Tshekardocoleidae Rohdendorf, 1944

†Family Labradorocoleidae Ponomarenko, 1969

†Family Oborocoleidae Kukalová, 1969

†Family Permocupedidae Martynov, 1932

†Subfamily Permocupedinae Martynov, 1932

†Subfamily Taldycupedinae Rohdendorf, 1961

†Superfamily **Permosynoidea** Tillyard, 1924

†Family Ademosynidae Ponomarenko, 1968

†Family Permosynidae Tillyard, 1924

Capaxorder **ZACOLEOPTERA** Engel, Cai, and Tihelka, *nov.*

Suborder Metaxycoleoptera Engel, Cai, and Tihelka, *nov.*

†Family Ponomarenkiidae Yan, Lawrence, Beattie and Beutel, 2017

Hyporder **EUCOLEOPTERA** Engel, Cai, and Tihelka, *nov.*

Suborder **ADEPHAGA** Claireville, 1806

†Family Tritarsusidae Hong, 2002

†Family Triaplidae Ponomarenko, 1977

Family Haliplidae Aubé, 1836

Family Gyrinidae Latreille, 1810

Subfamily Spanglerogyrinae Folkerts, 1979

Subfamily Gyrinae Latreille, 1810

Subfamily Heterogyrinae Brinck, 1955

†Family Coptoclavidae Ponomarenko, 1961

†Subfamily Timarchopsinae Wang, Ponomarenko and Zhang, 2010

†Subfamily Charonoscapinae Ponomarenko, 1977

†Subfamily Coptoclavinae Ponomarenko, 1961

†Subfamily Coptoclaviscinae Soriano, Ponomarenko and Delclòs, 2007

†Subfamily Hispanoclavinae Soriano, Ponomarenko and Delclòs, 2007

Family Noteridae Thomson, 1860

Subfamily Notomicrinae Branden, 1884

Subfamily Noterinae Thomson, 1860

Family Meruidae Spangler and Steiner, 2005

Family Aspidytidae Ribera, Beutel, Balke and Vogler, 2002

Family Amphizoidae LeConte, 1853

Family Hygrobiidae Régimbart, 1879

Family Dytiscidae Leach, 1815

Subfamily Matinae Branden, 1885

Subfamily Lancetinae Branden, 1885

Subfamily Agabinae Thomson, 1867



Subfamily Colymbetinae Erichson, 1837  
 Subfamily Copelatinae Branden, 1885  
 Subfamily Laccophilinae Gistel, 1848  
 Subfamily Cybistrinae Sharp, 1880  
 Subfamily Dytiscinae Leach, 1815  
 Subfamily Coptotominae Branden, 1885  
 Subfamily Hydrodytinae Miller, 2001  
 Subfamily Hydroporinae Aubé, 1836  
 †Subfamily Palaeogyrininae Schlechtendal, 1894  
 †Subfamily Liadytiscinae Prokin and Ren, 2010  
 Family Trachypachidae Thomson, 1857  
 †Subfamily Eodromeinae Ponomarenko, 1977  
 Subfamily Trachypachinae Thomson, 1857  
 Family Cicindelidae Latreille 1802  
 Family Carabidae Latreille, 1802  
 †Subfamily Protorabinae Ponomarenko, 1977  
 †Subfamily Coniunctiinae Ponomarenko, 1977  
 Subfamily Nebriinae Laporte, 1834  
 Subfamily Carabinae Latreille, 1802  
 Subfamily Loricarinae Bonelli, 1810  
 Subfamily Omophroninae Bonelli, 1810  
 Subfamily Elaphrinae Latreille, 1802  
 Subfamily Migadopinae Chaudoir, 1861  
 Subfamily Hiletinae Schiødte, 1848  
 Subfamily Scaritinae Bonelli, 1810  
 Subfamily Broscinae Hope, 1838  
 Subfamily Apotominae LeConte, 1853  
 Subfamily Siagoninae Bonelli, 1813  
 Subfamily Melaeninae Csiki, 1933  
 Subfamily Gehringiinae Darlington, 1933  
 Subfamily Trechinae Bonelli, 1810  
 Subfamily Patrobinae Kirby, 1837  
 Subfamily Psydrinae LeConte, 1853  
 Subfamily Nototylinae Bänninger, 1927  
 Subfamily Paussinae Latreille, 1806  
 Subfamily Brachininae Bonelli, 1810  
 Subfamily Harpalinae Bonelli, 1810  
 †Family Colymbotethidae Ponomarenko, 1994  
 †Family Parahygrobiidae Ponomarenko, 1977  
 †Family Liadytidae Ponomarenko, 1977

Suborder **ARCHOSTEMATA** Kolbe, 1908

Superfamily **Cupedoidea** Laporte, 1838

= †Family Magnocoleidae Hong, 1998 **syn. nov.**

Family Crowsoniellidae Iablokoff-Khinzorian, 1983

Family Cupedidae Laporte, 1838

Subfamily Priacminae Crowson, 1962

†Subfamily Mesocupedinae Ponomarenko, 1969

Subfamily Cupedinae Laporte, 1838

Family Micromalthidae Barber, 1913

Family Ommatidae Sharp and Muir, 1912

†Subfamily Brochocoleinae Hong, 1982  
Subfamily Ommatinae Ponomarenko, 1969  
Subfamily Tetraphalerinae Crowson, 1962  
†Family Triadocupedidae Ponomarenko, 1966

†Superfamily **Asiocoleoidea** Rohdendorf, 1961  
†Family Asiocoleidae Rohdendorf, 1961  
†Family Tricoleidae Ponomarenko, 1969

†Superfamily **Rhombocoleoidea** Rohdendorf, 1961  
†Family Rhombocoleidae Rohdendorf, 1961

†Superfamily **Schizocoleoidea** Rohdendorf, 1961  
†Family Schizocoleidae Rohdendorf, 1961  
†Family Phoroschizidae Bouchard and Bousquet, 2020  
†Family Catiniidae Ponomarenko, 1968

Suborder **MYXOPHAGA** Crowson, 1955

Superfamily **Lepiceroidea** Hinton, 1936 (1882)  
Family Lepiceridae Hinton, 1936 (1882)

Superfamily **Sphaeriuoidea** Erichson, 1845  
Family Torridincolidae Steffan, 1964  
Subfamily Torridincolinae Steffan, 1964  
Subfamily Deleveinae Endrödy-Younga, 1997  
†Family Triamyxidae Triamyxidae Qvarnström, Fikáček, Wernström, Huld, Beutel, Arriaga-Varela, Ahlberg, and Niedźwiedzki, 2021  
Family Hydroscaphidae LeConte, 1874  
Family Sphaeriusidae Erichson, 1845

Superfamily *incertae sedis*

Suborder **POLYPHAGA** Emery, 1886

Series SCIRTIFORMIA Lawrence, Ślipiński, Seago, Thayer, Newton, and Marvaldi, 2011 **sensu nov.**

Superfamily **Scirtoidea** Fleming, 1821 **sensu nov.**  
Family Decliniidae Nikitsky, Lawrence, Kirejtshuk and Gratshev, 1994  
Family Scirtidae Fleming, 1821  
†Subfamily Mesernobiinae Engel, 2010  
Subfamily Nipponocyphoninae Lawrence and Yoshitomi, 2007  
Subfamily Stenocyphoninae Lawrence and Yoshitomi, 2007  
Subfamily Scirtinae Fleming, 1821  
†Family Elodophthalmidae Kirejtshuk and Azar, 2008  
†Family Boleopsidae Kirejtshuk and Nel, 2013

Series CLAMBIFORMIA Cai and Tihelka **ser. nov.**

Superfamily **Clamboidea** Fischer, 1821 **sensu nov.**  
Family Derodontidae LeConte, 1861  
Subfamily Peltasticinae LeConte, 1861  
Subfamily Derodontinae LeConte, 1861  
Subfamily Laricobiinae Mulsant and Rey, 1864

Family Clambidae Fischer, 1821  
Subfamily Calyptomerinae Crowson, 1955  
Subfamily Acalyptomerinae Crowson, 1979  
Subfamily Clambinae Fischer von Waldheim, 1821  
Family Eucinetidae Lacordaire, 1857  
†Family Mesocinetidae Kirejtshuk and Ponomarenko, 2010

Series RHINORHIPIFORMIA Cai, Engel and Tihelka **ser. nov.**

Superfamily **Rhinorhipoidea** Lawrence, 1988  
Family Rhinorhipidae Lawrence, 1988

Series ELATERIFORMIA Crowson, 1960

Superfamily **Dascilloidea** Guérin-Méneville, 1843 (1834)  
Family Dascillidae Guérin-Méneville, 1843 (1834)  
Subfamily Dascillinae Guérin-Méneville, 1843 (1834)  
Subfamily Karumiinae Escalera, 1913  
Family Rhipiceridae Latreille, 1834  
Subfamily Rhipicerinae Latreille, 1834  
Subfamily Sandalinae Jakobson, 1913

Superfamily **Byrrhoidea** Latreille, 1804 **sensu nov.**  
Family Byrrhidae Latreille, 1804  
Subfamily Byrrhinae Latreille, 1804  
Subfamily Syncalyptinae Mulsant and Rey, 1869  
Subfamily Amphicyrtinae LeConte, 1861  
†Subfamily Lidryopinae Kirejtshuk and Nel, 2016

Superfamily **Buprestoidea** Crowson, 1955  
Family Schizopodidae LeConte, 1859  
Family Buprestidae Leach, 1815  
Subfamily Julodinae Lacordaire, 1857  
Subfamily Polycestinae Lacordaire, 1857  
Subfamily Galbellinae Reitter, 1911  
Subfamily Chrysochroinae Laporte, 1835  
Subfamily Buprestinae Leach, 1815  
Subfamily Agrilinae Laporte, 1835  
†Subfamily Parathyreinae Alexeev, 1994

Superfamily **Dryopoidea** Billberg, 1820 (1817) **stat. res.**  
Family Lutrochidae Kasap and Crowson, 1975  
Family Dryopidae Billberg, 1820 (1817)  
Family Eulichadidae Crowson, 1973  
Family Callirhipidae Emden, 1924  
Family Ptilodactylidae Laporte, 1838  
Subfamily Cladotominae Pic, 1914  
Subfamily Anchytarsinae Champion, 1897  
Subfamily Aploglossinae Champion, 1897  
Subfamily Araeopidiinae Lawrence, 1991  
Subfamily Ptilodactylinae Laporte, 1838

Family Cneoglossidae Champion, 1897  
 Family Chelonariidae Blanchard, 1845  
 Family Psephenidae Lacordaire, 1854  
     Subfamily Afroebriinae Lee, Satô, Shepard and Jäch, 2007  
     Subfamily Eubriinae Lacordaire, 1857  
     Subfamily Psephenoidinae Bollow, 1938  
     Subfamily Eubrianacinae Jakobson, 1913  
     Subfamily Psepheninae Lacordaire, 1854  
 Family Protelmidae Jeannel, 1950  
 Family Elmidae Curtis, 1830  
     Subfamily Larainae LeConte, 1861  
     Subfamily Elminae Curtis, 1830  
 Family Limnichidae Erichson, 1846  
     Subfamily Hyphalinae Britton, 1971  
     Subfamily Limnichinae Erichson, 1846  
     Subfamily Cephalobyrrhinae Champion, 1925  
     Subfamily Thaumastodinae Champion, 1924  
 Family Heteroceridae MacLeay, 1825  
     Subfamily Elythomerinae Pacheco, 1964  
     Subfamily Heterocerinae MacLeay, 1825  
 Superfamily **Elateroidea** Leach, 1815  
     Family Armatopodidae Lacordaire, 1857  
         Subfamily Electribiinae Crowson, 1975  
         Subfamily Allopogoniinae Crowson, 1973  
         Subfamily Armatopodinae Lacordaire, 1857  
     Family Omethidae LeConte, 1861  
         Subfamily Driloniinae Crowson, 1972  
         Subfamily Matheteinae LeConte, 1881  
         Subfamily Omethinae LeConte, 1861  
         Subfamily Telegeusinae Leng, 1920  
     Family Brachypsectridae Horn, 1881  
     Family Throscidae Laporte, 1840  
     Family Eucnemidae Eschscholtz, 1829  
         Subfamily Perothopinae Lacordaire, 1857  
         Subfamily Phyllocerinae Reitter, 1905  
         Subfamily Pseudomeninae Muona, 1993  
         Subfamily Palaeoxeninae Muona, 1993  
         Subfamily Phlegoninae Muona, 1993  
         Subfamily Anischiinae Fleutiaux, 1936  
         Subfamily Melasinae Fleming, 1821  
         Subfamily Eucneminae Eschscholtz, 1829  
         Subfamily Macraulacinae Fleutiaux, 1923  
     Family Cerophytidae Latreille, 1834  
     Family Jurasidae Rosa, Costa, Kramp and Kundrata, 2020  
     Family Elateridae Leach, 1815  
         Subfamily Elaterinae Leach, 1815  
         Subfamily Tetralobinae Laporte, 1840  
         Subfamily Omalisinae Lacordaire, 1857  
         Subfamily Agrypninae Candèze, 1857  
         Subfamily Hapatesinae Kusy, Motyka and Bocak, 2021  
         Subfamily Pityobiinae Hyslop, 1917

Subfamily Lissominae Laporte, 1835  
 Subfamily Thylacosterninae Fleutiaux, 1920  
 Subfamily Campyloxeninae Costa, 1975  
 Subfamily Hypnoidinae Schwarz, 1906  
 Subfamily Dendrometrinae Gistel, 1848  
 Subfamily Negastriinae Nakane and Kishii, 1956  
 Subfamily Cardiophorinae Candèze, 1859  
 Subfamily Oestodinae Hyslop, 1917  
 Subfamily Hemiopinae Fleutiaux, 1941  
 Subfamily Physodactylinae Lacordaire, 1857  
 Subfamily Subprotelaterinae Fleutiaux, 1920  
 Subfamily Morostominae Dolin, 2000  
 Subfamily Parablacinae Kunderata, Gunter, Douglas and Bocak, 2016  
 †Subfamily Protagrypninae Dolin, 1973  
 Family Sinopyrophoridae Bi and Li, 2019  
 Family Lycidae Laporte, 1838  
     Subfamily Dexorinae Bocak and Bocakova, 1989  
     Subfamily Calochrominae Lacordaire, 1857  
     Subfamily Erotinae Leconte, 1881  
     Subfamily Ateliinae Kleine, 1928  
     Subfamily Lycinae Laporte, 1838  
     Subfamily Lyropaeinae Bocak and Bocakova, 1989  
     Subfamily Metriorrhynchinae Kleine, 1926  
 Family Iberobaeniidae Bocak, Kunderata, Fernández and Vogler, 2016  
 †Family Berendtimiridae Winkler, 1987  
 †Family Cretophengodidae Li, Kunderata, Tihelka and Cai, 2021  
 Family Phengodidae LeConte, 1861  
     Subfamily Cydistinae Paulus, 1972  
     Subfamily Phengodinae LeConte, 1861  
     Subfamily Mastinocerinae LeConte, 1881  
     Subfamily Penicillophorinae Paulus, 1975  
 Family Rhagophthalmidae Olivier, 1907  
 Family Lampyridae Rafinesque, 1815  
     Subfamily Luciolinae Lacordaire, 1857  
     Subfamily Pterotinae LeConte, 1861  
     Subfamily Ototretinae McDermott, 1964  
     Subfamily Lamprohizinae Kazantsev, 2010  
     Subfamily Chespiritoinae Ferreira, Keller and Branham, 2020  
     Subfamily Cyphonocerinae Crowson, 1972  
     Subfamily Psilocladinae McDermott, 1964  
     Subfamily Amydetinae Olivier in Wytzman, 1907  
     Subfamily Cheguevariinae Kazantsev, 2007  
     Subfamily Photurinae Lacordaire, 1857  
     Subfamily Lampyrinae Rafinesque, 1815  
 †Family Mysteriomorphidae Alekseev and Ellenberger, 2019  
 Family Cantharidae Imhoff, 1856 (1815)  
     Subfamily Cantharinae Imhoff, 1856 (1815)  
     Subfamily Silinae Mulsant, 1862  
     Subfamily Dymorphocerinae Brancucci, 1980  
     Subfamily Malthininae Kiesenwetter, 1852  
     Subfamily Chauliognathinae LeConte, 1861

Series NOSODENDRIFORMIA Cai and Tihelka **ser. nov.**

Superfamily **Nosodendroidea** Erichson, 1846

Family Nosodendridae Erichson, 1846

Series STAPHYLINIFORMIA Lameere, 1900 **sensu nov.**

Superfamily **Histeroidea** Gyllenhaal, 1808

Family Synteliidae Lewis, 1882

Family Sphaeritidae Shuckard, 1839

†Family Cretohisteridae Zhou, Caterino, Ślipiński and Cai, 2018

Family Histeridae Gyllenhal, 1808

Subfamily †Antigracilinae Zhou, Caterino, Ren and Ślipiński, 2020

Subfamily Niponiinae Fowler, 1912

Subfamily Abraeinae MacLeay, 1819

Subfamily Sapriniinae Blanchard, 1845

Subfamily Dendrophilinae Reitter, 1909

Subfamily Onthophilinae MacLeay, 1819

Subfamily Tribalinae Bickhardt, 1914

Subfamily Histerinae Gyllenhal, 1808

Subfamily Haeteriinae Marseul, 1857

Subfamily Chlamydopsinae Bickhardt, 1914

Superfamily **Hydrophiloidea** Latreille, 1802

Family Hydrophilidae Latreille, 1802

Subfamily Hydrophilinae Latreille, 1802

Subfamily Chaetarthriinae Bedel, 1881

Subfamily Enochrinae Short and Fikáček, 2013

Subfamily Acidocerinae Zaitzev, 1908

Subfamily Cylominae Zaitzev, 1908

Subfamily Sphaeridiinae Latreille, 1802

Family Helophoridae Leach, 1815

Family Epimetopidae Zaitzev, 1908

Family Georissidae Laporte, 1840

Family Hydrochidae Thomson, 1859

Family Spercheidae Erichson, 1837

Superfamily **Scarabaeoidea** Latreille, 1802

†Family Alloioscarabaeidae Bai, Ren and Yang, 2012

†Family Septiventeridae Bai, Ren, Shih and Yang, 2013

Family Lucanidae Latreille, 1804

†Subfamily Protolucaninae Nikolajev, 2007

Subfamily Aesalinae MacLeay, 1819

†Subfamily Ceruchitinae Nikolajev, 2006

Subfamily Syndesinae MacLeay, 1819

Subfamily Lampriminae MacLeay, 1819

Subfamily Lucaninae Latreille, 1804

†Subfamily Paralucaninae Nikolajev, 2000

†Subfamily Litholampriminae Nikolajev, 2015

Family Trogidae MacLeay, 1819

†Subfamily Kresnikinae Tihelka, Huang and Cai, 2019

Subfamily Troginae MacLeay, 1819

Subfamily Omorginae Nikolajev, 2005

Family Glaresidae Prudhomme de Borre, 1886

Family Pleocomidae LeConte-, 1861  
   †Subfamily Cretocominae Nikolajev, 2002  
   †Subfamily Archescarabaeinae Nikolajev, 2010  
   Subfamily Pleocominae LeConte, 1861  
 Family Bolboceratidae Mulsant, 1842  
   Subfamily Athyreinae Lynch Arribálzaga, 1878  
   Subfamily Bolboceratinae Mulsant, 1842  
 Family Diphylostomatidae Holloway, 1972  
 Family Geotrupidae Latreille, 1802  
   Subfamily Taurocerastinae Germain, 1897  
   Subfamily Geotrupinae Latreille, 1802  
 †Family Passalopalpidae Boucher and Bai, 2016  
 Family Passalidae Leach, 1815  
   Subfamily Aulacocyclinae Kaup, 1868  
   Subfamily Passalinae Leach, 1815  
 Family Belohinidae Paulian, 1959  
 Family Ochodaeidae Streubel, 1846  
   †Subfamily Cretochodaeinae Nikolajev, 1995  
   Subfamily Ochodaeinae Streubel, 1846  
   Subfamily Chaetocanthinae Scholtz, 1988  
 Family Glaphyridae MacLeay, 1819  
   †Subfamily Cretoglaphyrinae Nikolajev, 2005  
   Subfamily Glaphyrinae MacLeay, 1819  
   Subfamily Amphicominae Blanchard, 1845  
 Family Hybosoridae Erichson, 1847  
   †Subfamily Mimaphodiinae Nikolajev, 2007  
   Subfamily Anaidinae Nikolajev, 1996  
   Subfamily Ceratocanthinae Martínez, 1968  
   Subfamily Hybosorinae Erichson, 1847  
   Subfamily Liparochrinae Ocampo, 2006  
   Subfamily Pachyplectrinae Ocampo, 2006  
 Family Scarabaeidae Latreille, 1802  
   †Subfamily Lithoscarabaeinae Nikolajev, 1992  
   Subfamily Chironinae Blanchard, 1845  
   Subfamily Aegialiinae Laporte, 1840  
   Subfamily Eremazinae Stebnicka, 1977  
   Subfamily Aphodiinae Leach, 1815  
   Subfamily Aulonocneminae Janssens, 1946  
   Subfamily Termitotroginae Wasmann, 1918  
   Subfamily Scarabaeinae Latreille, 1802  
   †Subfamily Prototroginae Nikolajev, 2000  
   †Subfamily Cretoscarabaeinae Nikolajev, 1995  
   Subfamily Dynamopodinae Arrow, 1911  
   †Subfamily Electrorubesopsinae Bai and Wang, 2019  
   Subfamily Phaenomeridinae Erichson, 1847  
   Subfamily Orphninae Erichson, 1847  
   Subfamily Allidiostomatinae Arrow, 1940  
   Subfamily Aclopininae Blanchard, 1850  
   Subfamily Melolonthinae Leach, 1819  
   Subfamily Oncerinae LeConte, 1861  
   Subfamily Podolasiinae Howden, 1997

Subfamily Rutelinae MacLeay, 1819  
Subfamily Dynastinae MacLeay, 1819  
Subfamily Cetoniinae Leach, 1815

Superfamily **Staphylinoidea** Latreille, 1802

Family Jacobsoniidae Heller, 1926

Family Ptiliidae Erichson, 1845

Subfamily Nossidiinae Sörensson and Delgado, 2019

Subfamily Ptiliinae Erichson, 1845

Family Hydraenidae Mulsant, 1844

Subfamily Orchymontiinae Perkins, 1997

Subfamily Prosthetopinae Perkins, 1994

Subfamily Hydraeninae Mulsant, 1844

Subfamily Ochthebiinae Thomson, 1859

Family Colonidae Horn, 1880 (1859) **stat. nov.**

Family Agyrtidae Thomson, 1859

Subfamily Agyrtinae Thomson, 1859

Subfamily Necrophilinae Newton, 1997

Subfamily Pterolomatinae Thomson, 1862

Family Leiodidae Fleming, 1821 **sensu nov.**

Subfamily Camiarinae Jeannel, 1911

Subfamily Catopocerinae Hatch, 1927 (1880)

Subfamily Leiodinae Fleming, 1821

Subfamily Cholevinae Kirby, 1837

Subfamily Platypsyllinae Ritsema, 1869

Family Staphylinidae Latreille, 1802 **sensu nov.**

Subfamily Silphinae Latreille, 1806 **stat. nov., sensu nov.**

Subfamily Apateticinae Fauvel, 1895

Subfamily Trigonurinae Reiche, 1866

Subfamily Scaphidiinae Latreille, 1806

Subfamily Piestinae Erichson, 1839

Subfamily Osoriinae Erichson, 1839

Subfamily Oxytelinae Fleming, 1821

†Subfamily Protactinae Heer, 1847

Subfamily Omaliinae MacLeay, 1825

Subfamily Microsilphinae Crowson, 1950

Subfamily Glypholomatinae Jeannel, 1962

Subfamily Empelinae Newton and Thayer, 1992

Subfamily Proteininae Erichson, 1839

Subfamily Micropeplinae Leach, 1815

Subfamily Neophoninae Fauvel, 1905

Subfamily Dasycerinae Reitter, 1887

Subfamily Protopselaphinae Newton and Thayer, 1995

Subfamily Pselaphinae Latreille, 1802

Subfamily Mycetoporinae Thomson, 1859

Subfamily Tachyporinae MacLeay, 1825

Subfamily Phloeocharinae Erichson, 1839

Subfamily Trichophyinae Thomson, 1858

Subfamily Habrocerinae Mulsant and Rey, 1876

Subfamily Aleocharinae Fleming, 1821

Subfamily Leptotyphlinae Fauvel, 1874

Subfamily Oxyporinae Fleming, 1821



- Subfamily Megalopsidiinae Leng, 1920
- Subfamily Steninae MacLeay, 1825
- Subfamily Euaesthetinae Thomson, 1859
- Subfamily Solieriinae Newton and Thayer, 1992
- Subfamily Scydmaeninae Leach, 1815
- Subfamily Pseudopsinae Ganglbauer, 1895
- Subfamily Olisthaerinae Thomson, 1858
- Subfamily Paederinae Fleming, 1821
- Subfamily Staphylininae Latreille, 1802

Series BOSTRICHIFORMIA Forbes, 1926

Superfamily **Bostrichoidea** Latreille, 1802

- Family Dermestidae Latreille, 1804
  - Subfamily Dermestinae Latreille, 1804
  - Subfamily Thorictinae Agassiz, 1846
  - Subfamily Orphilinae LeConte, 1861
  - Subfamily Trinodinae Casey, 1900
  - Subfamily Attageninae Laporte, 1840
  - Subfamily Megatomininae Leach, 1815
- Family Endecatomidae LeConte, 1861
- Family Bostrichidae Latreille, 1802
  - Subfamily Dysidinae Lesne, 1894
  - Subfamily Polycaoninae Lesne, 1896
  - Subfamily Bostrichinae Latreille, 1802
  - Subfamily Psoinae Blanchard, 1851
  - Subfamily Dinoderinae Thomson, 1863
  - Subfamily Lyctinae Billberg, 1820
  - Subfamily Euderiinae Lesne, 1934
- Family Ptinidae Latreille, 1802
  - Subfamily Eucradinae LeConte, 1861
  - Subfamily Ptininae Latreille, 1802
  - Subfamily Dryophilinae Gistel, 1848
  - Subfamily Ernobiinae Pic, 1912
  - Subfamily Anobiinae Fleming, 1821
  - Subfamily Ptilininae Shuckard, 1839
  - Subfamily Alvarenganiellinae Viana and Martínez, 1971
  - Subfamily Xyletininae Gistel, 1848
  - Subfamily Dorcatominae Thomson, 1859
  - Subfamily Mesocoelopodinae Mulsant and Rey, 1864

Series CUCUJIFORMIA Lameere, 1938

Superfamily **Cleroidea** Latreille, 1802

- Family Rentoniidae Crowson, 1966
- Family Byturidae Gistel, 1848
  - Subfamily Byturinae Gistel, 1848
  - Subfamily Platydascillinae Pic, 1914
- Family Biphyllidae LeConte, 1861
- Family Acanthocnemidae Crowson, 1964
- Family Protopeltidae Crowson, 1966
- Family Peltidae Kirby, 1837
- Family Lophocateridae Crowson, 1964

Family Trogossitidae Latreille, 1802  
     Subfamily Calityinae Houlbert, 1922  
     Subfamily Egoliinae Lacordaire, 1854  
     Subfamily Larinotinae Slipinski, 1992  
     Subfamily Trogossitinae Latreille, 1802  
 Family Thymalidae Léveillé, 1888  
     Subfamily Thymalidae Léveillé, 1888  
     Subfamily Decamerinae Crowson, 1964  
 Family Phycosecidae Crowson, 1952  
 Family Prionoceridae Lacordaire, 1857  
 Family Mauroniscidae Majer, 1995  
 Family Rhadalidae LeConte, 1861  
     Subfamily Gietellinae Constantin and Menier, 1987  
     Subfamily Rhadalinae LeConte, 1861  
 Family Melyridae Leach, 1815  
     Subfamily Malachiinae Fleming, 1821  
     Subfamily Melyrinae Leach, 1815  
     Subfamily Dasytinae Laporte, 1840  
 Family Phloiophilidae Kiesenwetter, 1863  
 Family Chaetosomatidae Crowson, 1952  
 Family Thanerocleridae Chapin, 1924  
     Subfamily Zenodosinae Kolibáč, 1992  
     Subfamily Thaneroclerinae Chapin, 1924  
 Family Cleridae Latreille, 1802  
     Subfamily Tillinae Fischer von Waldheim, 1813  
     Subfamily Korynetinae Laporte, 1838  
     Subfamily Epiclininae Gunter, Leavengood and Bartlett, 2013  
     Subfamily Hydnocerinae Spinola, 1844  
     Subfamily Clerinae Latreille, 1802

Superfamily **Lymexyloidea** Fleming, 1821  
     Family Lymexylidae Fleming, 1821  
         Subfamily Hylecoetinae Germar, 1818  
         Subfamily Lymexylinae Fleming, 1821  
         Subfamily Atractocerinae Laporte, 1840  
         Subfamily Melittommatinae Wheeler, 1986

Superfamily **Tenebrionoidea** Latreille, 1802  
     Family Ripiphoridae Laporte, 1840  
         Subfamily Pelecotominae Guérin-Méneville, 1857  
         Subfamily Ptilophorinae Gerstaecker, 1855  
         Subfamily Hemirhipidiinae Heller, 1921  
         Subfamily Ripidiinae Gerstaecker, 1855  
         Subfamily Ripiphorinae Laporte, 1840  
     Family Mordellidae Latreille, 1802  
         Subfamily Ctenidiinae Franciscolo, 1951  
         Subfamily Mordellinae Latreille, 1802  
     †Family Apotomouridae Bao, Walczynska, Moody, Wang and Rust, 2018  
     Family Aderidae Csiki, 1909  
     Family Ischaliidae Blair, 1920  
     Family Trictenotomidae Blanchard, 1845  
     Family Scraptiidae Gistel, 1848  
         Subfamily Scraptiinae Gistel, 1848

Subfamily Anaspidinae Mulsant, 1856  
 Family Mycteridae Perty, 1840  
   Subfamily Mycterinae Perty, 1840  
   Subfamily Eurypinae Thomson, 1860  
   Subfamily Hemipeplinae Lacordaire, 1854  
 Family Oedemeridae Latreille, 1810  
   Subfamily Polypriinae Lawrence, 2005  
   Subfamily Calopodinae Costa, 1852  
   Subfamily Oedemerinae Latreille, 1810  
 Family Boridae Thomson, 1859  
   Subfamily Borinae Thomson, 1859  
   Subfamily Synercticinae Lawrence and Pollock, 1994  
 Family Pythidae Solier, 1834  
 Family Salpingidae Leach, 1815  
   Subfamily Othniinae LeConte, 1861  
   Subfamily Prostominiinae Grouvelle, 1914  
   Subfamily Agleninae Horn, 1878  
   Subfamily Inopeplinae Grouvelle, 1908  
   Subfamily Dacoderinae LeConte, 1862  
   Subfamily Aegialitinae LeConte, 1862  
   Subfamily Salpinginae Leach, 1815  
 Family Pyrochroidae Latreille, 1806  
   Subfamily Tydessinae Nikitsky, 1986  
   Subfamily Pilipalpinae Abdullah, 1964  
   †Subfamily Waidelotinae Bukejs, Alekseev and Pollock, 2019  
   Subfamily Pedilinae Lacordaire, 1859  
   Subfamily Pyrochroinae Latreille, 1806  
   Subfamily Pogonocerinae Iablokov-Khnzorian, 1985  
   Subfamily Agnathinae Lacordaire, 1859  
 Family Anthicidae Latreille, 1819  
   Subfamily Eurygeniinae LeConte, 1862  
   Subfamily Macratriinae LeConte, 1862  
   Subfamily Steropinae Jacquelin du Val, 1863  
   Subfamily Copobaeninae Abdullah, 1969  
   Subfamily Lemodinae Matthews, 1987  
   Subfamily Tomoderinae Bonadona, 1961  
   Subfamily Anthicinae Latreille, 1819  
   Subfamily Notoxinae Stephens, 1829  
 Family Meloidae Gyllenhal, 1810  
   Subfamily Eleticinae Wellman, 1910  
   Subfamily Meloinae Gyllenhal, 1810  
   Subfamily Tetraonycinae Böving and Craighead, 1931  
   Subfamily Nemognathinae Laporte, 1840  
 Family Stenotrachelidae Thomson, 1859  
   Subfamily Stenotrachelinae Thomson, 1859  
   Subfamily Cephaloinae LeConte, 1862  
   Subfamily Nematoplinae LeConte, 1862  
   Subfamily Stoliinae Nikitsky, 1985  
 Family Tetratomidae Billberg, 1820  
   Subfamily Tetratominae Billberg, 1820  
   Subfamily Piseninae Miyatake, 1960

- Subfamily Penthinae Lacordaire, 1859
- Subfamily Hallomeninae Gistel, 1848
- Subfamily Eustrophinae Gistel, 1848
- Family Melandryidae Leach, 1815
  - Subfamily Melandryinae Leach, 1815
  - Subfamily Osphyinae Mulsant, 1856 (1839)
- Family Synchronidae Lacordaire, 1859
- Family Prostomidae Thomson, 1859
- Family Ciidae Leach, 1819
  - Subfamily Sphindociinae Lawrence, 1974
  - Subfamily Ciinae Leach, 1819
- Family Ulodidae Pascoe, 1869
- Family Archeocrypticidae Kaszab, 1964
- Family Pterogeniidae Crowson, 1953
- Family Mycetophagidae Leach, 1815
  - Subfamily Esarcinae Reitter, 1882
  - Subfamily Mycetophaginae Leach, 1815
  - Subfamily Bergininae Leng, 1920
- Family Tenebrionidae Latreille, 1802
  - Subfamily Lagriinae Latreille, 1825 (1820)
  - Subfamily Nilioninae Oken, 1843
  - Subfamily Phrenapatinae Solier, 1834
  - Subfamily Zolodininae Watt, 1975
  - Subfamily Pimeliinae Latreille, 1802
  - Subfamily Blaptinae Leach, 1815
  - Subfamily Tenebrioninae Latreille, 1802
  - Subfamily Alleculinae Laporte, 1840
  - Subfamily Diaperinae Latreille, 1802
  - Subfamily Stenochiinae Kirby, 1837
- Family Zopheridae Solier, 1834
  - Subfamily Colydiinae Billberg, 1820
  - Subfamily Zopherinae Solier, 1834
- Family Promecheilidae Lacordaire, 1859
- Family Chalcodryidae Watt, 1974
- Family *incertae sedis*
  - Subfamily Afreminae Levey, 1985
  - Subfamily Lagrioidinae Abdullah and Abdullah, 1968

- Superfamily **Coccinelloidea** Latreille, 1807
  - Family Bothrideridae Erichson, 1845
  - Family Cerylonidae Billberg, 1820
    - Subfamily Ostomopsinae Sen Gupta and Crowson, 1973
    - Subfamily Loeblioryloninae Ślipiński, 1990
    - Subfamily Ceryloninae Billberg, 1820
  - Family Murmidiidae Jacquelin du Val, 1858
  - Family Discolomatidae Horn, 1878
    - Subfamily Notiophyginae Jakobson, 1915
    - Subfamily Discolomatinae Horn, 1878
    - Subfamily Aphanocephalinae Jakobson, 1904
    - Subfamily Cephalophaninae John, 1954
    - Subfamily Pondonatinae John, 1954
  - Family Euxestidae Grouvelle, 1908

- Family Teredidae Seidlitz, 1888
  - Subfamily Teredinae Seidlitz, 1888
  - Subfamily Anommatinae Ganglbauer, 1899
  - Subfamily Xylariophilinae Pal and Lawrence, 1986
- Family Alexiidae Imhoff, 1856
- Family Akalyptoischiidae Lord, Hartley, Lawrence, McHugh, Whiting and Miller, 2010
- Family Latridiidae Erichson, 1842
  - Subfamily Latridiinae Erichson, 1842
  - Subfamily Corticariinae Curtis, 1829
- Family Anamorphidae Strohecker, 1953
- Family Corylophidae LeConte, 1852
  - Subfamily Periptyctinae Ślipiński, Lawrence and Tomaszewska, 2001
  - Subfamily Corylophinae LeConte, 1852
- Family Endomychidae Leach, 1815
  - Subfamily Merophysiinae Seidlitz, 1872
  - Subfamily Pleganophorinae Jacquelin du Val, 1858
  - Subfamily Leiestinae Thomson, 1863
  - Subfamily Xenomycetinae Strohecker, 1962
  - Subfamily Danascelinae Tomaszewska, 2000
  - Subfamily Cyclotominae Imhoff, 1856
  - Subfamily Endomychinae Leach, 1815
  - Subfamily Epipocinae Gorham, 1873
  - Subfamily Lycoperdininae Bromhead, 1838
- †Family Tetrameropsidae Kirejtshuk and Azar, 2008
- Family Mycetaeidae Jacquelin du Val, 1857
- Family Eupsilobiidae Casey, 1895
- Family Coccinellidae Latreille, 1807
  - Subfamily Microweiseinae Leng, 1920
  - Subfamily Monocoryninae Miyatake, 1988
  - Subfamily Coccinellinae Latreille, 1807

Superfamily **Erotyloidea** Latreille, 1802 **stat. nov.**

- Family Boganiidae Sen Gupta and Crowson, 1966
  - Subfamily Paracucujinae Endrödy-Younga and Crowson, 1986
  - Subfamily Boganiinae Sen Gupta and Crowson, 1966
- Family Erotylidae Latreille, 1802
  - Subfamily Cryptophilinae Casey, 1900
  - Subfamily Languriinae Hope, 1840
  - Subfamily Xenoscelinae Ganglbauer, 1899
  - Subfamily Pharaxonothinae Crowson, 1952
  - Subfamily Loberinae Bruce, 1951
  - Subfamily Erotylinae Latreille, 1802

Superfamily **Nitiduloidea** Latreille, 1802 **stat. nov.**

- Family Helotidae Chapuis, 1876
- Family Sphindidae Jacquelin du Val, 1860
  - †Subfamily Libanopsinae Kirejtshuk, 2015
  - Subfamily Protosphindinae Sen Gupta and Crowson, 1979
  - Subfamily Odontosphindinae Sen Gupta and Crowson, 1979
  - Subfamily Sphindiphorinae Sen Gupta and Crowson, 1979
  - Subfamily Sphindinae Jacquelin du Val, 1860
- Family Protocucujidae Crowson, 1954

Family Monotomidae Laporte, 1840  
    Subfamily Rhizophaginae Redtenbacher, 1845  
    Subfamily Monotominae Laporte, 1840  
Family Kateretidae Kirby, 1837  
Family Nitidulidae Latreille, 1802  
    Subfamily Cryptarchinae Thomson, 1859  
    Subfamily Prometopiinae Böving and Craighead, 1931  
    Subfamily Amphicrossinae Kirejtshuk, 1986  
    Subfamily Carpophilinae Erichson, 1842  
    Subfamily Cybocephalinae Jacquelin du Val, 1858 **stat. nov.**  
    Subfamily Calonecrinae Kirejtshuk, 1982  
    Subfamily Epuraeinae Kirejtshuk, 1986  
    Subfamily Meligethinae Thomson, 1859  
    Subfamily Nitidulinae Latreille, 1802  
    Subfamily Maynipeplinae Kirejtshuk, 1998  
    Subfamily Cillaeinae Kirejtshuk and Audisio, 1986  
Family Smicripidae Horn, 1880

Superfamily **Cucujoidea** Latreille, 1802 **sensu nov.**

Family Hobartiidae Sen Gupta and Crowson, 1966  
Family Cryptophagidae Kirby, 1826  
    Subfamily Cryptophaginae Kirby, 1826  
    Subfamily Atomariinae LeConte, 1861  
Family Silvanidae Kirby, 1837  
    Subfamily Brontinae Blanchard, 1845  
    Subfamily Silvaninae Kirby, 1837  
Family Cucujidae Latreille, 1802  
    Subfamily Cucujinae Latreille, 1802  
    Subfamily Pediacinae Jin, Zwick, Ślipiński, Marris, Thomas and Pang, 2020  
    Subfamily Platisinae Jin, Zwick, Ślipiński, Marris, Thomas and Pang, 2020  
Family Phloeostichidae Reitter, 1911  
Family Agapythidae Sen Gupta and Crowson, 1969  
Family Priasilphidae Crowson, 1973  
Family Cavognathidae Sen Gupta and Crowson, 1966  
Family Lamingtoniidae Sen Gupta and Crowson, 1969  
Family Tasmosalpingidae Lawrence and Britton, 1991  
Family Cyclaxyridae Gimmel, Leschen and Ślipiński, 2009  
Family Passandridae Blanchard, 1845  
    †Subfamily Mesopassandrinae Jin, Ślipiński, Zhou and Pang, 2019  
    Subfamily Passandrinae Blanchard, 1845  
Family Myraboliidae Lawrence and Britton, 1991  
Family Phalacridae Leach, 1815  
    Subfamily Phaenocephalinae Matthews, 1899  
    Subfamily Phalacrinae Leach, 1815  
Family Laemophloeidae Ganglbauer, 1899

Series **Cucujiformia** Lameere, 1938 **incertae sedis**

†Family Parandrexidae Kirejtshuk, 1994  
†Family Wabbelidae Alekseev, 2017

Superfamily **Curculionoidea** Latreille, 1802

Family Cimberididae Gozis, 1882  
Family Nemonychidae Bedel, 1882

†Subfamily Aepyceratinae Poinar, Brown and Legalov, 2017  
 Subfamily Rhinorhynchinae Voss, 1922  
 †Subfamily Brenthorrhinae Arnoldi, 1977  
 †Subfamily Distenorrhinae Arnoldi, 1977  
 †Subfamily Eobelinae Arnoldi, 1977  
 †Subfamily Paleocartinae Legalov, 2003  
 †Subfamily Metrioxenoidinae Legalov, 2009  
 †Subfamily Cretonemonychinae Gratshev and Legalov, 2009  
 †Subfamily Selengarhynchinae Gratshev and Legalov, 2009  
 †Subfamily Slonikinae Zherikhin, 1977  
 †Subfamily Eccoptarthrinae Arnoldi, 1977  
 Subfamily Nemonychinae Bedel, 1882  
 Family Anthribidae Billberg, 1820  
   Subfamily Urodontinae Thomson, 1859  
   Subfamily Choraginae Kirby, 1819  
   Subfamily Anthribinae Billberg, 1820  
 Family Belidae Schönherr, 1826  
   †Subfamily Montsecbelinae Legalov, 2015  
   Subfamily Oxycoryninae Schönherr, 1840  
   Subfamily Belinae Schönherr, 1826  
 †Family Mesophyletidae Poinar, 2008  
   †Subfamily Aepyceratinae Poinar, Brown and Legalov, 2017  
   †Subfamily Mesophyletinae Poinar, 2008  
 Family Attelabidae Billberg, 1820  
   Subfamily Attelabinae Billberg, 1820  
   Subfamily Apoderinae Jekel, 1860  
   Subfamily Rhynchitinae Gistel, 1848  
   Subfamily Isotheinae Scudder, 1893  
   Subfamily Pterocolinae Lacordaire, 1865  
 Family Caridae Thompson, 1992  
   †Subfamily Baissorhynchinae Zherikhin, 1993  
   Subfamily Chilecarinae Legalov, 2009  
   Subfamily Carinae Thompson, 1992  
 Family Brentidae Billberg, 1820  
   Subfamily Ithycerinae Schoenherr, 1823  
   Subfamily Brentinae Billberg, 1820  
   Subfamily Microcerinae Lacordaire, 1863  
   Subfamily Eurhynchinae Lacordaire, 1863  
   Subfamily Apioninae Schönherr, 1823  
   Subfamily Nanophyinae Gistel, 1848  
 Family Curculionidae Latreille, 1802  
   Subfamily Brachycerinae Billberg, 1820  
   Subfamily Dryophthorinae Schönherr, 1825  
   Subfamily Platypodinae Shuckard, 1839  
   Subfamily Bagoinae Thomson, 1859  
   Subfamily Hyperinae Marseul, 1863 (1848)  
   Subfamily Entiminae Schönherr, 1823  
   Subfamily Cyclominae Schönherr, 1826  
   Subfamily Curculioninae Latreille, 1802  
   Subfamily Baridinae Schönherr, 1836  
   Subfamily Ceutorhynchinae Gistel, 1848

- Subfamily Conoderinae Schönherr, 1833
- Subfamily Cossoninae Schönherr, 1825
- Subfamily Molytinae Schönherr, 1823
- Subfamily Cryptorhynchinae Schönherr, 1825
- Subfamily Lixinae Schönherr, 1823
- Subfamily Mesoptiliinae Lacordaire, 1863
- Subfamily Scolytinae Latreille, 1804
- Subfamily Oroboidinae Thomson, 1859
- Subfamily Xiphospiidae Marshall, 1920
- †Family Ulyanidae Zherikhin, 1993
- †Family Obrieniidae Zherikhin and Gratshev, 1994
  - †Subfamily Kararhynchinae Zherikhin and Gratshev, 1994
  - †Subfamily Obrieniinae Zherikhin and Gratshev, 1994
  - †Subfamily Pseudobrieniinae Legalov, 2012

Superfamily **Chrysomeloidea** Latreille, 1802

- Family Oxypeltidae Lacordaire, 1868
- Family Vesperidae Mulsant, 1839
  - Subfamily Philinae Thomson, 1861
  - Subfamily Vesperinae Mulsant, 1839
  - Subfamily Anoplodermatinae Guérin-Méneville, 1840
- Family Disteniidae Thomson, 1861
- Family Cerambycidae Latreille, 1802
  - Subfamily Dorcasominae Lacordaire, 1868
  - Subfamily Prioninae Latreille, 1802
  - Subfamily Cerambycinae Latreille, 1802
  - Subfamily Lepturinae Latreille, 1802
  - Subfamily Spondylidinae Audinet-Serville, 1832
  - Subfamily Lamiinae Latreille, 1825
- Family Megalopodidae Latreille, 1802
  - Subfamily Megalopodinae Latreille, 1802
  - Subfamily Palophaginae Kuschel and May, 1990
  - Subfamily Zeugophorinae Böving and Craighead, 1931
- Family Orsodacnidae Thomson, 1859
  - Subfamily Orsodacninae Thomson, 1859
  - Subfamily Aulacoscelidinae Chapuis, 1874
- Family Chrysomelidae Latreille, 1802
  - Subfamily Chrysomelinae Latreille, 1802
  - Subfamily Galerucinae Latreille, 1802
  - Subfamily Synetinae LeConte and Horn, 1883
  - Subfamily Sagrinae Leach, 1815
  - Subfamily Bruchinae Latreille, 1802
  - Subfamily Donaciinae Kirby, 1837
  - Subfamily Criocerinae Latreille, 1804
  - Subfamily Cassidinae Gyllenhal, 1813
  - Subfamily Eumolpinae Hope, 1840
  - Subfamily Lamprosomatinae Lacordaire, 1848
  - Subfamily Cryptocephalinae Gyllenhal, 1813
  - Subfamily Spilopyrinae Chapuis, 1874
  - †Subfamily Protoscelidinae Medvedev, 1968



**INCERATE SEDIS**

Crown **COLEOPTERA** *incerate sedis*

†Subfamily Avitortorinae Nikolaev 2007

Suborder **POLYPHAGA** Emery, 1886 *incertae sedis*

†Family Lasiosynidae Kirejtshuk, Chang, Ren and Kun, 2010

†Family Peltosynidae Yan, Beutel and Ponomarenko, 2018

Family Jurodidae Ponomarenko, 1985

## Phylogenetic and age justifications for fossil calibrations

### **Node 1:** (Megaloptera + Neuroptera) – Coleoptera: **298.75 Ma – 324 Ma.**

**Fossil taxon and specimen:** *Stephanastus polinae* Kirejtshuk and Nel, 2013 [holotype, MNHN.A.49011 (exoskeleton with legs and elytra): Palaeoentomological Laboratory, Muséum national d'Histoire naturelle, Paris, France] from the Commeny Shales Formation in Allier, France (Nel et al. 2013).

**Phylogenetic justification:** Megaloptera and Neuroptera, along with Raphidioptera, form the clade Neuropterida, which is strongly supported by both molecular and morphology-based phylogenies. As discussed in Nel et al. (2013), the extinct *Stephanastus* (family Stephanastidae) is sister to the stem coleopterids, which include the extant Coleoptera. Since the Neuropterida is a sister group to Stephanastidae + coleopterids, the fossil species *Stephanastus polinae* is a crown group of the clade ((Megaloptera, Neuroptera), Coleoptera).

**Minimum age:** 298.75 Ma.

**Soft maximum age:** 324 Ma.

**Age justification:** *Stephanastus polinae* occurs in the Commeny Shales Formation in Allier, France. Although no geochemical dating of the fossil deposit has been carried out, the formation has been regarded as Gzhelian (late Carboniferous) based on stratigraphic evidence. The top of Gzhelian has been dated to  $298.9 \pm 0.15$ , which provides a conservative minimum constraint (298.75 Ma). The soft maximum constraint is based on the earliest occurrence of Archaeorthoptera from the early Carboniferous, which also represents the earliest known Pterygota (including almost all insects (Ectognatha), but not the Archaeognatha or the Zygentoma, two primitively wingless insect orders). This earliest pterygote fossil was described from the Upper Silesian Basin in the Czech Republic (Prokop et al. 2005). The deposit has been dated as the early Carboniferous (Namurian A/E1, ca. 324 Ma) (Jirásek et al. 2013). Regardless the alternative interpretations of the Czech specimen (Dvořák et al. 2019), the other oldest uncontested candidate for the earliest pterygote, is the practically contemporaneous palaeopteran *Delitzschala bitterfeldensis* from near Bitterfeld, Germany (Brauckmann et al. 1994; Brauckmann and Schneider 1996).

### **Node 2:** Crown Coleoptera: **251.878 Ma – 307.1 Ma.**

**Fossil taxon and specimen:** *Ponomarenkium belmonthensis* Yan, Lawrence, Beattie and Beutel, 2018 [holotype, 40278; paratype, 41618 (exoskeletons without legs): Australian Museum, Sydney] from the Tatarian insect beds, Newcastle Coal Measures at Belmont, north of Sydney, Australia (Yan et al. 2018a, b).

**Phylogenetic justification:** This clade comprises four extant beetle suborders Adephaga, Archostemata, Myxophaga, and Polyphaga, their last common ancestor and all of its descendants, but excludes putative stem coleopterans known collectively as Protocoleoptera (Crowson 1975). Yan et al. (2018a) did not provide a formal phylogenetic analysis of *Ponomarenkium* but compared it with related fossil taxa and representatives of four modern suborders. *Ponomarenkium* lacks the ancestral broad and apically truncated prosternal process and a broad prothoracic postcoxal bridge, which suggest it as a crown group Coleoptera (Yan et al. 2018a). Specifically, *Ponomarenkium* may belong to the stem group of either Polyphaga or Myxophaga, or more likely the stem group of a clade comprising more than one of the extant suborders (Yan et al. 2018a).

**Minimum age:** 251.878 Ma.

**Soft maximum age:** 307.1 Ma.

**Age justification:** *Ponomarenkium belmonthensis* was recovered from the late Permian Tatarian insect beds located within the Upper Newcastle Coal Measures of New South Wales, Australia (Yan et al. 2018d). The Belmont insect bed was considered to be Tatarian-aged (late Permian), but no precise dating of the fossil bed has been published. The minimum age for the fossil can be taken from the top of the Changhsingian (dated at  $251.902 \pm 0.024$  Ma), providing a conservative minimum age for *Ponomarenkium*. The earliest definitive beetle, *Coleopsis archaica* is from the early Permian of Germany (Kirejtshuk et al. 2014; Kirejtshuk and Nel 2016). Like most Permian beetles, *C. archaica* belongs to the stem group of Coleoptera. Béthoux (2009) regarded *Adiphlebia lacoana* from the Pennsylvanian (Carboniferous) of Mazon Creek as the oldest beetle, but this hypothesis was rejected based on a critical re-analysis of the anatomy and taphonomy of the fossil.

The original interpretation of *Adiphlebia* as Coleoptera by Béthoux (2009) was based on clay artefacts attached to the wing membrane (Kukalová-Peck and Beutel, 2012). The Mazon Creek Lagerstätte is one of the best records of late Palaeozoic ecosystems, which has yielded diverse insects (11 orders and more than 210 species) preserved within siderite concretions (Clements et al. 2019). Despite the high palaeodiversity of the entomofauna, no beetles, one of most diverse animal group in today's terrestrial ecosystems, have been documented. Palynological and palaeobotanical evidence indicates that the age of the Mazon Creek Lagerstätte equates to the upper part of the Moscovian stage (Clements et al. 2019), the top of which has been dated at  $307.0 \pm 0.1$ . The age 307.1 Ma thus provides a conservative soft maximum constraint.

**Node 3: Gyrinidae – Haliplidae: 251.878 Ma – 293.69 Ma.**

**Fossil taxon and specimen:** *Tunguskagyryrus planus* Yan, Beutel and Lawrence, 2018 [holotype, PIN 5381/32 (exoskeleton without legs): Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia] from the Lebedevskian Horizon at the Anakit locality, which has been correlated with the Kedrovskian layers of the Maltsevo Formation, Krasnoyarsk region, Russia (Yan et al. 2018c).

**Phylogenetic justification:** The placement of *Tunguskagyryrus planus* in the extant family Gyrinidae is supported by numerous derived features of the head, but it bears many ancestral characters, indicating it as a stem group gyrinid (Yan et al. 2018c). *Tunguskagyryrus* demonstrates that the specialised lifestyle of whirligig beetles probably changed little over the past 250 million. As such, *T. planus* is the oldest record of crown group of the Gyrinidae + Haliplidae clade.

**Minimum age:** 251.878 Ma.

**Soft maximum age:** 293.69 Ma.

**Age justification:** *Tunguskagyryrus planus* occurs in the Lebedevskian Horizon. The age of this layer was identified as either Permian or Triassic. In a recent biostratigraphical study by Sadovnikov (2016), it was attributed to the Changhsingian of the uppermost Permian. The minimum age for the fossil can be taken at the top of the Changhsingian, which is currently dated at  $251.902 \pm 0.024$  (International Chronostratigraphic Chart, v. 2018/08). Therefore, the minimum age constraint for this node is 251.878 Ma. The soft maximum constraint is based on the oldest occurrence of a stem group beetle from the early Permian of Germany, as in node 3.

The earliest known beetle, *Coleopsis archaica* (family Coleopsidae), has been reported from the early Permian of Germany (Kirejtshuk et al. 2014). As in many Permian species and some Mesozoic early beetle species, *C. archaica* has well sclerotised elytra with remains of primary venation, which is not developed in crown group beetles. Although *C. archaica* was placed in the extant suborder Archostemata by Kirejtshuk et al. (2014), Beutel et al. (2008) conducted a morphological phylogenetic analysis that supported Tshekardocoleidae as a stem Coleoptera, sister to the other remaining extinct and extant beetles sampled in the study. Permian beetles are largely represented by extinct stem group beetle families, such as Permocupedidae and Tshekardocoleidae (Kirejtshuk et al. 2014). Recently, an intriguing well-preserved fossil beetle, *Ponomarenkia belmonthensis* Yan et al. 2018 (family Ponomarenkiidae), was described from the mid-Permian of Australia that can be excluded from the earliest stem group coleopterans and the four extant suborders. As such, *P. belmonthensis* likely belongs to the stem group of one of the extant suborders or in the stem group of a clade comprising more than one of them (Yan et al. 2018a). Given the discussion above, the age of the oldest beetle, *Coleopsis archaica*, provides a maximum age constraint on the node. *Coleopsis archaica* was recovered from the top of the Meisenheim Formation at Grögelborn, Germany. Schneider and Werneburg (2006, 2012) proposed a Sakmarian age for this horizon based on the occurrence of the biostratigraphically important cockroach *Spiloblattina odernheimensis* Schneider. Therefore, we consider the bottom of the Sakmarian, 293.69 Ma ( $293.52 \pm 0.17$  Ma), as the soft maximum constraint.

**Node 4: Dytiscidae – Noteridae: 155 Ma – 251.878 Ma.**

**Fossil taxon and specimen:** *Palaeodytes gutta* Ponomarenko, 1987 [holotype, PIN2066/2654 (exoskeleton): Paleontological Institute, Russian Academy of Sciences, Moscow, Russia] from the Karabastau Formation of the Karatau Range near the village of Mikhailovka, Chimkent Region, Chayan District, southern Kazakhstan (Ponomarenko 1987).

**Phylogenetic justification:** The extinct genus *Palaeodytes*, currently classified as subfamily *incertae sedis* within Dytiscidae, includes three Mesozoic species: *P. baissensis*, *P. gutta*, and *P. sibiricus* (Prokin et al. 2013). Among them, the Jurassic *P. gutta* represents the oldest unequivocal record for the genus. The phylogenetic position of *Palaeodytes* within Dytiscidae remains untested, but *P. gutta* represents a crown group of Dytiscidae + Noteridae. Ponomarenko (1963) described a dytiscid species, *Angaragabus jurassicus*, from the Lower Jurassic of Irkutsk Oblast (Russia) based on a fossil larva. A re-examination of the fossil confirmed its placement in the superfamily Dytiscoidea, but not necessarily within the extant family Dytiscidae. Instead, *A. jurassicus* probably belongs to the extinct group Liadytidae (Prokin et al. 2013).

**Minimum age:** 155 Ma.

**Soft maximum age:** 251.878 Ma.

**Age justification:** *Palaeodytes gutta* is from the Karabastau Formation in Karatau, Kazakhstan. The precise age of the Karabastau Formation is uncertain within the Late Jurassic, but floras (Doludenko and Orlovskaya, 1976), insects (Rohdendorf, 1968) and stratigraphy (Kirichkova and Doludenko, 1996) suggest a mid–Late Jurassic date, around 155 Ma. Zheng et al. (2018) reported an unnamed beetle belonging to the superfamily Dytiscoidea from the mid-Triassic Tongchuan entomofauna (Shaanxi, central China), which was dated as approximately 237–238 Ma. This dytiscoid fossil, characterised by a streamlined body, smooth elytra, and second abdominal sternite divided by metacoxae, closely resembles some representatives of Noteridae. The soft maximum constraint (251.878 Ma) is based on the oldest occurrence of the suborder Adephaga (a stem group of Gyrinidae) from Late Permian deposits of the Anakit area in Middle Siberia as discussed in node 3.

#### **Node 5: Cupedidae – Torridincolidae: 235 Ma – 293.69 Ma.**

**Fossil taxon and specimen:** *Kirghizocupes cellulosus* Ponomarenko, 1966 [holotype, PIN 2069/107 (exoskeleton): Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia] from the Madygen Formation at the Dzhailyau-Cho locality, Lyailyakskii District, Batken Region, southwest Kyrgyzstan (Ponomarenko 1966).

**Phylogenetic justification:** *Kirghizocupes cellulosus* was originally placed in the extinct family Triadocupedidae (Ponomarenko 1966), which is currently regarded as stem group Coleoptera sister to all four extant suborders or as a member of Archostemata (Yan et al. 2018d). Kirejtshuk et al. (2016) attributed *Kirghizocupes* to the subfamily Cupedinae (= Cupedidae s.s., here adopted, viz Classification of beetles) based on an extensive comparative study of fossil cupedids, representing the earliest known record of the group. Although the systematic position of *K. cellulosus* among Cupedidae s.s. remains untested, it represents a crown group of the Cupedidae + Torridincolidae clade.

**Minimum age:** 235 Ma.

**Soft maximum age:** 293.69 Ma.

**Age justification:** The earliest records of *Kirghizocupes* occur in the Madygen Formation at Dzhailyau-Cho in Kyrgyzstan. The Madygen Formation was dated as Ladinian–Carnian based on the evidence of megafloora (Dobruskina 1995), but the insect assemblage, namely the orders Blattodea, Orthoptera, and Hemiptera, were suggested to be more primitive than the Carnian-aged entomofaunas from South Africa and Australia, which suggests that a Ladinian age is more probable for the Madygen Formation (Shcherbakov 2008). Recent biostratigraphic and radioisotopic data indicated a mid-Triassic age ( $237 \pm 2$  Ma, late Ladinian to early Carnian) of the Madygen Formation (Voigt et al. 2017). Thus, the minimum age constraint on the node is 235 Ma. The soft maximum constraint is based on the oldest occurrence of a stem group beetle from the early Permian of Germany, as in node 3.

#### **Node 6: Crown Polyphaga: 237 Ma – 293.69 Ma.**

**Fossil taxon and specimen:** undescribed taxon of the series Elateriformia [NIGP162053 (exoskeleton without legs): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from the Ladinian Tongchuan entomofauna at Hejiafang, Shaanxi, central China (Zheng et al. 2018).

**Phylogenetic justification:** Although the fossil was not formally named, it is well preserved and displays many features of Elateriformia (e.g., Dascilloidea and Elateroidea), including a robust body with a distinct prosternal intercoxal process and produced hind pronotal angles. The fossil clearly represents a crown group

polyphagan.

**Minimum age:** 237 Ma.

**Soft maximum age:** 293.69 Ma.

**Age justification:** The elateriform beetle originates from the Tongchuan Formation in central China. The insect-bearing layer of this formation was dated to 237 to 238 Ma, providing a minimum age of 237 Ma. The soft maximum constraint is based on the oldest occurrence of a stem group beetle from the early Permian of Germany, as in node 3.

**Node 7: Derodontidae – (Clambidae + Eucinetidae): 165 Ma – 251.878 Ma.**

**Fossil taxon and specimen:** *Juropeltastica sinica* Cai, Lawrence and Huang, 2014 [holotype, NIGP157738 (exoskeleton without legs): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from the Haifanggou Formation at Daohugou, Ningcheng County, Inner Mongolia, northeastern China (Cai et al. 2014a).

**Phylogenetic justification:** *Juropeltastica sinica* from the Middle Jurassic represents the only Mesozoic fossil of the family Derodontidae. Derodontidae currently comprises three subfamilies: Peltasticinae (*Peltastica*), Derodontinae (*Derodontus*), and Laricobiinae (*Laricobius* and *Nothoderodontus*). *Juropeltastica* is placed in the extant subfamily Peltasticinae based on derived characters such as its explanate pronotum and carinate elytra. Additionally, it shares with *Derodontus* the relatively narrow pronotum and densely punctate postgena, prosternum, and meso- and metaventricle. Molecular-based phylogenetic analyses of three genera of Derodontidae by McKenna et al. (2015) indicated *Laricobius* as sister to *Derodontus* + *Nothoderodontus*. As such, *J. sinica* with toothed, explanate pronotum and carinate elytra is a crown derodontid.

**Minimum age:** 165 Ma.

**Soft maximum age:** 251.878 Ma.

**Age justification:** *Juropeltastica sinica* was recovered from the Daohugou beds of the Haifanggou Formation, Inner Mongolia, from northeastern China (Huang 2016). The precise age of the Daohugou beds has been controversial (He et al. 2004; Gao and Ren, 2006; Wang et al. 2005; Zhang 2015). Ar/Ar and SHRIMP U-Pb dating indicated that the age of the intermediate-acid volcanic rock overlaying the Daohugou fossiliferous beds is approximately 164–165 Ma, and so the age of the fossil deposit is older than or equal to 165 Ma, corresponding to the Callovian of the Middle Jurassic (Chen et al. 2004), an age widely adopted by palaeoentomologists (Gao and Ren, 2006). Indeed, the fossil insects from the Daohugou beds may be correlated to those from the slightly younger deposit in Karatau (Kazakhstan) (Zhang 2015), but there is strong evidence indicating that the age of the Daohugou beds may be older (Huang 2016). As such, the most conservative age of the deposit is 165 Ma, providing a minimum age for *Juropeltastica*. The soft maximum constraint, 251.878 Ma, is based on the oldest occurrence of the suborder Adephaga from Late Permian deposits of the Anakit area in Middle Siberia as discussed in node 4.

**Node 8: Clambidae – Eucinetidae: 145 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Mesocinetus aequalis* Kirejtshuk and Ponomarenko, 2010 [holotype, PIN 4270–48, with part and counterpart; paratypes, PIN 4270–1079; PIN 4270–1071, PIN 4270–1078: Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia] from the Upper Jurassic of Shar-Teg, southwestern Mongolia (Kirejtshuk and Ponomarenko 2010).

**Phylogenetic justification:** The extinct genus *Mesocinetus*, along with four other extinct genera, was placed in the extinct family Mesocinetidae, which apparently has close affinity to the extant families Scirtidae and Eucinetidae (Kirejtshuk and Ponomarenko 2010). In particular, *Mesocinetus* strongly resembles extant genera of Eucinetidae, namely *Eucinetus*, in having a characteristic body form with a strongly declined head, and 5-segmented tarsi. The close morphological resemblance indicates that *Mesocinetus* is probably a member of the extant Eucinetidae, rather than Mesocinetidae. Although the phylogenetic position of *Mesocinetus* has not been formally tested, their apomorphies (e.g., declined head and long hind legs) indicate that the genus is a crown group of the Clambidae + Eucinetidae clade.

**Minimum age:** 145 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** *Mesocinetus aequalis* was discovered in the Shar Teg Lagerstätte in southwestern Mongolia. The deposit has not been dated geochemically but its age has been inferred from comparisons of insect assemblages among Middle-Late Jurassic entomofaunas, such as those from Karatau (Late Jurassic) and Daohugou (late Middle Jurassic) (Ponomarenko et al. 2014). The minimum age constraint on the node is thus given by the boundary between the Jurassic and the Cretaceous, ca. 145 Ma. The soft maximum age (ca. 235 Ma) is derived from the age of the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. The entomofauna of the Triassic Madygen fossil locality is dominated by beetles, which constitute one quarter of total insects collected from the Madygen Formation. Among beetles, about 90% of specimens belong to Archostemata, and polyphagans are rare, including the well-known stem group polyphagan beetles belonging to the genus *Peltosyne* Ponomarenko (Ponomarenko 1977; Yan et al. 2018d). *Peltosyne triassica* and *P. varyvrosa* are the earliest-occurring beetles placed in the polyphagan stem group based on specific apomorphies and plesiomorphic features compared to extant lineages.

**Node 9: Rhipiceridae – Dascillidae: 165 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Parelateriformius communis* Yan and Wang, 2010 [holotype, NIGP, nos. 151537a, 151537b (part and counterpart of almost completely preserved beetle; legs missing, antennae partly missing): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from the Haifanggou Formation at Daohugou, Ningcheng County, Inner Mongolia, northeastern China (Yan and Wang 2010).

**Phylogenetic justification:** The genus *Parelateriformius* has been assigned to the extinct polyphagan family Lasiosynidae, a group that apparently shares similarities with Dascillidae. While the most obvious apomorphies of Dascillidae, namely the strongly reduced lacinia and male flabellate antennae (Jin et al. 2013a), are not preserved in the fossil, it shows other important similarities with *Dascillus* (Jin et al. 2013b): presence of a distinct frontoclypeal suture, head lacking a posterior constriction, eyes large and somewhat protuberant, exposed antennal insertions; antenna 11-segmented and serrate, pronotum with a complete lateral carina, prosternum in front of procoxae long, prosternal process complete between coxae, procoxal cavities transverse and with lateral notches exposing protrochantins, mesocoxal cavities narrowly separated, metaventrite with discrien and katepisternal sutures almost complete; hind coxae transverse with large coxal plates, 5-segmented tarsi, simple claws lacking an empodium, and abdomen with 5 ventrites. This would place it within crown Dascilloidea.

**Minimum age:** 165 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** For the minimum age justification of the Daohugou biota, see node 7. The soft maximum age (ca. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

**Node 10: Buprestidae – Byrrhidae: 165 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Sinoparathyrea bimaculata* Pan, Chang and Ren, 2011 [holotype, CNU-COL-NN2010408 (exoskeleton with legs, elytra, and wings): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] from Daohugou Village, Middle Jurassic Jiulongshan Formation, Ningcheng County, Inner Mongolia, China (Pan et al. 2011).

**Phylogenetic justification:** *Sinoparathyrea bimaculata* was described as a member of Buprestidae and placed into the extinct subfamily Parathyreinae (Pan et al. 2011). Cai et al. (2015a), however, pointed out that the characters used to define Parathyreinae (Alekseev 1993), namely the straight katepisternal suture, may be a plesiomorphy. In fact, *Sinoparathyrea* shares a number of characters with members of Schizopodidae, a group that was included as a subfamily within Buprestidae by some authors. These include the relatively short prosternum in front of the procoxae, short and broad prosternal process, and a relatively large radial cell of the hind wing (Cai et al. 2015a). This indicates that *S. bimaculata* belongs to the crown group of Buprestidae – Byrrhidae.

**Minimum age:** 165 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** See node 7 for the minimum age justification of the Daohugou locality. The soft maximum is from the Madygen Formation at the Dzhaikau-Cho locality, Lyailyskii District, Batken Region, southwest Kyrgyzstan, Central Asia, as justified in node 7.

**Node 11: Dryopoidea: 112.6 Ma – 165 Ma.**

**Fossil taxon and specimen:** undescribed taxon of the series family Dryopidae [AMNH SA43296: American Museum of Natural History, New York, USA] from the Lower Cretaceous (Aptian) Crato Formation, northeastern Brazil (Grimaldi and Engel 2005).

**Phylogenetic justification:** The specimen (Fig. 10.35 in Grimaldi and Engel 2005), together with other undescribed material from the deposit, can be placed into the family Dryopidae based on its characteristic habitus, 5-segmented tarsi without lobes, and peculiar antennae with the basal segments expanded.

**Minimum age:** 112.6 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** The oldest fossil dryopid was recovered from the Crato Formation in the Araripe Basin, northeastern Brazil. This unit is generally agreed to date back to around the Aptian/Albian border (Martill et al. 2007). The Crato Formation has been dated using palynomorphs (Pons et al. 1990) to the Aptian. The upper boundary of the Aptian, at 113.0 Ma  $\pm$  0.4 Ma, gives a minimum date of 112.6 Ma. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

**Node 12: Crown Psephenidae: 98.17 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Vetujinbrianax cretaceus* Cai and Huang, 2018 [holotype, NIGP168215 (amber inclusion, male): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] lowermost Cenomanian, from an amber mine located near Noije Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar (Cai and Huang 2018).

**Phylogenetic justification:** *Vetujinbrianax cretaceus* is known from a well-preserved adult from mid-Cretaceous Burmese amber. It can be placed into the family on the basis of the following characters: body apparently soft, antennae pectinate in the males, prothoracitans exposed, maxillary palps relatively long, and tarsi simple and 5-segmented. *Vetujinbrianax* can be placed in the extant subfamily Eubrianacinae based on the presence of plesiomorphic characters such as short prosternal process and paired tibial apical spurs, similar to the extant Oriental genus *Jinbrianax* (Lee et al. 2007; Cai and Huang 2018). *V. cretaceus* represents the oldest fossil record of Eubrianacinae, as well as the first definitive adult fossil of Psephenidae from the Mesozoic. Further specimens of psephenid larvae, also belonging to the subfamily Eubrianacinae from Burmese amber were reported by Bao et al. (2018) and described as *Succinumanax birmaniasis*. They represent the oldest fossil record of Psephenidae, and show a high similarity in morphology with fossils from the Eocene Messel pit, Germany. A phylogenetic analysis demonstrated that *S. birmaniasis* and the Messel specimen can be placed in Psephenidae.

**Minimum age:** 98.17 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** The specimen is preserved in Burmese amber (burmite) mined in the Hukawng Valley, Kachin State, northern Myanmar. Volcanoclastic matrix from the amber-bearing horizon was dated radiometrically at 98.79  $\pm$  0.62 Ma (Shi et al. 2012), although this estimate should be taken as a minimum age (Mao et al. 2018). A mid-Cretaceous age is consistent with paleontological evidence (Grimaldi et al. 2002). The discovery of an ammonite in the amber indicates that it is at most Albian in age (Yu et al., 2019). Here we use 98.17 Ma as the conservative minimum age of Burmese amber from northern Myanmar. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

**Node 13: Elmidae – (Limnichidae + Heteroceridae): 105 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Elmadulescens rugosus* Peris, Maier and Sánchez-García, 2015 [holotype, CES–

567 (amber inclusion): Institut de Recerca de la Biodiversitat (IRBio), Facultat de Geologia, Universitat de Barcelona, Martí i Franquès s/n, 08028 Barcelona, Spain] El Soplao amber outcrop located of the El Soplao Cave, Celis, Cantabria, Spain (Peris et al. 2015a).

**Phylogenetic justification:** *Elmadulescens rugosus* can be placed into Elmidae on the basis of its long, slender and widely inserted antennae, large and protuberant eyes, a pentagonal scutellum abruptly elevated anteriorly, long legs with elongate and simple 5-segmented tarsi, metacoxae with a posterior face, pronotum with complete lateral carinae, the last tarsomere longer than the other four combined, large pretarsal claws, and five abdominal ventrites (Peris et al. 2015a). The holotype is preserved in a transparent amber piece, but is dorsal-ventrally compressed and deformed, making the observation of some characters difficult.

**Minimum age:** 105 Ma

**Soft maximum age:** 165 Ma

**Age justification:** The amber piece was found in Early Albian strata of the Las Peñas Formation, as determined by biostratigraphy (Najarro et al. 2009). The minimum age is derived from the upper Albian. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

#### **Node 14: Crown Heteroceridae: 122.2 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Heterocerites magnus* Prokin and Ren, 2011 [holotype, CNU-COL-LB-2010023 (impression of adult beetle with partly preserved legs and mandibles): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] from the Huanbanjigou of the Yixian Formation, Shangyuan, Beipiao city, Liaoning Province (Prokin and Ren 2011).

**Phylogenetic justification:** The fossil species from the Yixian Formation was placed in the formal genus *Heterocerites* erected by Ponomarenko (1986) for compression fossils of putative heterocerids. While the genus is probably not monophyletic (Li et al. 2020a), *H. magnus* can be placed into Heteroceridae on the basis of having a densely pubescent body, large head with remnants of prominent mandibles and labrum, characteristically modified antennae with the distal half forming a loosely serrated club, a series of spine at the outer edges of the tibiae, short mesosternum, and stridulate ridges on ventrite 1 (Clarke 1973; Vanin et al. 2016). The dark elytra moreover possess tree pairs of light spots, a pattern similar to those found in extant members of the family (Vanin et al. 2016).

**Minimum age:** 122.2 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** Diverse and abundant fossils of the terrestrial Jehol Biota have been discovered from the Yixian Formation and the overlying Jiufotang Formation in Inner Mongolia, Hebei Province and Liaoning Province, northeastern China. The Yixian Formation is Early Cretaceous in age.  $^{40}\text{Ar}/^{39}\text{Ar}$  dating produced a mean age of  $124.6 \pm 0.1$  Ma for sanidine from one tuff interbedded in the fossiliferous horizons of the lower Yixian Formation near Jianshangou village, and  $^{40}\text{Ar}/^{39}\text{Ar}$  single-grain total fusion analyses provided an age of  $124.6 \pm 0.25$  Ma for the same tuff from Sihetun village (Swisher et al. 1999). Chang et al. (2009) provided a high precision  $^{40}\text{Ar}/^{39}\text{Ar}$  dating of the Yixian Formation: the lowest part of the main fossil bed was dated as  $124.1 \pm 0.3$  Ma, while the uppermost part of the bed was dated as  $122.9 \pm 0.7$  Ma. The latter age provides a conservative minimum constraint on the node, 122.2 Ma. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

#### **Node 15: Armatopodidae – Omethidae: 165 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Sinobrevipogon jurassicus* Cai, Lawrence, Ślipiński and Huang, 2015 [holotype, NIGP160704; paratypes, NIGP160705, NIGP160706 (holotype nearly completely preserved adult beetle, with both dorsal and ventral characters visible, including hindwings); paratype NIGP160705 (displays mainly ventral and some dorsal characters); paratype NIGP160706 (shows mainly dorsal and a few ventral characters such as abdominal ventrites): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from the Haifanggou Formation at Daohugou, Ningcheng County, Inner Mongolia, northeastern China (Cai et al. 2015b).

**Phylogenetic justification:** *Sinobrevipogon jurassicus* exhibits a number of defining features of



Artematopodidae, including the presence of paired carinae on the prosternum and an internal apical interlocking tongue on the ventral side of each elytron. However, it differs from modern members of Artematopodidae by having the mesocoxal cavities closed by the mesepimeron and the anterolateral edge of metanepisternum. A morphological phylogenetic analysis nonetheless recovered *Sinobrevipogon* within crown Artematopodidae (Cai et al. 2015b; 2020).

**Minimum age:** 165 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** See node 7 for minimum age justification. The soft maximum age (ca. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

**Node 16: Throscidae – Eucnemidae: 125 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Potergosoma gratiosum* Kovalev and Kirejtshuk, 2013 [holotype, “750” (amber inclusion, probably male): Lebanese University, Faculty of Sciences II, Fanar, Lebanon] from the Early Cretaceous Lebanese amber originating from the outcrop Hammana – Mdeirij, Caza Baabda, Mouhafazet, Jabal Loubnan, central Lebanon (Kovalev et al. 2013; Li et al. 2020b).

**Phylogenetic justification:** *Potergosoma gratiosum* possesses clear diagnostic characters of the Throscidae, some regarded as apomorphies of the family. These are the developed metacoxal plates, exposed and heavily sclerotised labrum, antennae with distinctly enlarged apical antennomeres forming an elongate antennal club, characteristic grooves on the underside for receiving antennae and legs, wide prosternal process, and rather widely separated mesocoxae. The genus also possesses several plesiomorphies: complete lateral pronotal carinae, absence of tarsal grooves, simple tarsomere 4, simple tibiae, poorly developed pro-mesothoracic leg impressions, antennal fossae and distinct serial elytral punctures (Muona 2019).

Morphological phylogenetic analyses recovered *Potergosoma* as a member of stem Throscidae (Muona 2019; Li et al. 2020b), making it suitable for calibrating the split between Throscidae and Eucnemidae.

**Minimum age:** 125 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** Krzemiski et al. (2014) indicated a Barremian age for the amber-bearing outcrop at Hammana – Mdeirij in central Lebanon. A recent biostratigraphic study of Lebanese amber by Maksoud et al. (2017) indicated that the pieces of amber with bioinclusions from the middle and upper intervals may have been reworked from the lower interval, so the age of the amber from “Grès du Liban” could be early Barremian or even older in age. As such, the minimum age for *E. rugidorsum* can be taken from the top of the Barremian, which is currently estimated at 125.0 Ma (International Chronostratigraphic Chart, v. 2018/08), representing the minimum age constraint for this node. The soft maximum age (ca. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

**Node 17: Osseimidae (Elateridae) – Lycidae: 98.17 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Burmolycus compactus* Bocak, Li and Ellenberger, 2019 [holotype, MB.I 7319 (amber inclusion, female): Museum für Naturkunde, Berlin, Germany] lowermost Cenomanian, from an amber mine located near Noije Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar (Bocak et al. 2019).

**Phylogenetic justification:** *Burmolycus compactus* can be placed into the family Lycidae on the basis of having 11-segmented antennae, a ridged pronotum, a very short and transverse prosternum, 5-segmented tarsi, and tarsomeres 2–4 lobed (Bocak and Bocakova 2008, 2010). It can further be assigned to the extant subfamily Dexorinae based on the presence of a prolonged cranium, frontally inserted antennae, antennomere 2 relatively long compared to the antennomere 3, hypognathous head, rounded mouthpart cavity, reduced labium with 1 or 2-segmented labial palpi, and femora obliquely attached to trochanters (Bocak et al. 2019). Other lycids belonging to extant and extinct taxa are known from Burmese amber, making them likewise suitable candidates for calibration of the node (Tihelka et al. 2019; Kazantsev 2019).

**Minimum age:** 98.17 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** See node 12 for minimum age justification. The maximum age constraint is based on the

Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

**Node 18: Lampyridae – Phengodidae + Rhagophthalmidae: 98.17 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Protoluciola albertalleni* Kazantsev, 2015 [holotype, ICM-BU-1687–1 (amber inclusion, male): Insect Centre, Moscow, Russia] lowermost Cenomanian, from an amber mine located near Noiije Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar (Kazantsev 2015).

**Phylogenetic justification:** *Protoluciola albertalleni* can be placed into the extant lampyrid subfamily Luciolinae based on the presence of six ventrites, genital segment apparently absent, the presence of a photic organ on the abdomen, 11-segmented antennae inserted anteriorly to the eyes, and five-segmented tarsi with simple claws (McDermott 1964).

**Minimum age:** 98.17 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** See node 12 for minimum age justification. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

**Node 19: Crown Cantharidae: 105 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Molliberus albae* Peris and Fanti, 2018 [holotype, CES-522 (amber inclusion): laboratory of the El Soplao Cave, Celis-Rábago, Cantabria, Spain) from Early Cretaceous Spanish amber originating from the El Soplao deposit, Celis municipality, Cantabria, Spain (Peris and Fanti 2018).

**Phylogenetic justification:** *Molliberus albae* can be placed into the extant subfamily Cantharinae based on the maxillary palpomeres different in length to the last securiform segment, long elytra, symmetrical last abdominal segments, prothorax without lateral processes, the presence of tibial spurs, and the fourth tarsomere undivided (Peris and Fanti 2018). As such, it represents the earliest member of crown Cantharidae.

**Minimum age:** 105 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** See node 13 for minimum age justification. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

**Node 20: Georissidae – Hydrophilidae: 147.28 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Protochares brevipalpis* Fikáček, Prokin, Yan, Yue, Wang, Ren and Beattie, 2014 [holotype, AMF109568 (exoskeleton preserved in dorsal aspect, with fragments of legs): Department of Earth Sciences, Australian Museum, Sydney, Australia] from Talbragar fossil fish bed, ca. 14 km NNW of Ulan, New South Wales, Australia (Fikáček et al. 2014).

**Phylogenetic justification:** *Protochares brevipalpis* can be assigned to Hydrophilidae based on the unique combination of the following characters: labrum well-sclerotised and largely exposed, clypeus large and with distinct frontoclypeal sutures reaching the lateral margin of the head closely before eyes, scutellum triangular, and head not strongly constricted behind the eyes (Fikáček et al. 2012, 2014).

**Minimum age:** 147.28 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** Dating the Jurassic Talbragar Lagerstätten fish beds has traditionally been contentious because no palynofloras have been recovered from the beds themselves as the rocks are highly oxidised. SHRIMP dating indicated an age of  $151.55 \pm 4.27$  Ma (Bean 2006). This provides a conservative minimum age constraint on the node. The soft maximum age (ca. 235 Ma) is derived from the Madygen Formation at Dzhalayau-Cho, Kyrgyzstan. See node 8 for justification.

**Node 21: Trogidae – Lucanidae: 165 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Juraesalus atavus* Nikolajev, Wang, Liu and Zhang, 2011 [holotype, NIGP 152456 (exoskeleton with legs, preserved in ventral aspect): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from the Haifanggou Formation at Daohugou, Ningcheng County, Inner Mongolia, northeastern China (Nikolajev et al. 2011).

**Phylogenetic justification:** *Juraesalus atavus* can be placed into Lucanidae based on the presence of well-developed and somewhat projecting antennae, a complete prosternal process, concealed trochantins, procoxal cavities strongly transverse, closed externally, open internally, mesocoxal cavities narrowly separated and laterally open, 5-segmented tarsi, and a rather elongate and subglabrous body (Holloway 1960, 1969). Nikolajev et al. (2011) considered the fossil to represent a stem group to the extant subfamily Aesalinae based on the presence of a 3-segmented non-lamellate club, mandibles produced beyond apex of clypeus, eyes not divided by canthus, and abdomen with 5 ventrites. However, Kim and Farrell (2015) pointed out that these characters are not unique to Aesalinae and instead considered *J. atavus* to be the oldest member of Lucanidae s.s. In either way, the fossil would be suitable for calibrating the split between Trogidae and Lucanidae.

**Minimum age:** 165 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** For the minimum age justification of the Daohugou biota, see node 7. The soft maximum age (ca. 235 Ma) is derived from the Madygen Formation at Dzhaibayau-Cho, Kyrgyzstan. See node 8 for justification.

#### **Node 22: Passalidae – Geotrupidae: 122.2 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Parageotrupes incanus* Nikolajev and Ren, 2010 [holotype, CNU-COL-LB2009751 (exoskeleton with partly preserved legs and antennae): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] from the Huanbanjigou of the Yixian Formation, Shangyuan, Beipiao city, Liaoning Province (Nikolajev and Ren 2010).

**Phylogenetic justification:** *Parageotrupes incanus* can be placed into Geotrupidae on the basis of the size and the oval shape of the body, mandibles not hidden by a clypeus, eyes divided by canthus, pygidium hidden by elytra. The clypeus bears a tubercle and is clearly delimited from the vertex, suggesting that the species belongs to the extant subfamily Geotrupinae (Nikolajev and Ren 2010).

**Minimum age:** 122.2 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** For the minimum age justification of the Yixian Formation, see node 14. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

#### **Node 23: Hybosoridae – Scarabaeidae: 155 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Protohybosorus grandissimus* Nikolajev, 2010 [holotype, PIN no. 2335/25 (exoskeleton with fragments of legs and antennae): from Karatau–Mikhailovka, Karabastau Formation of the Karatau Range near the village of Mikhailovka, Chayan District, Chimkent Region, southern Kazakhstan (Nikolajev 2010)

**Phylogenetic justification:** The genus *Protohybosorus*, containing three species, can be assigned to Hybosoridae based on the small size of the species, their developed eyes, labrum and mandibles produced beyond the apex of the clypeus, trapezoidal and convex pronotum with base wider than the elytral base, elytra convex and with well-defined striae, protibia with three teeth, mesotibia and metatibia somewhat dilated at the apex, mesotibia with 2 subequal spurs, mesotibia and metatibia without a transverse carina, and abdomen with five visible sternites (Jameson 2012; Ocampo 2006; Yan et al. 2012).

**Minimum age:** 155 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** For the minimum age justification of Karatau, see node 5. The soft maximum age (ca. 235 Ma) is derived from the Madygen Formation at Dzhaibayau-Cho, Kyrgyzstan. See node 8 for justification.

#### **Node 24: Ptiliidae – Hydraenidae: 182 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Ochtebiites minor* Ponomarenko, 1985 [holotype, PIN 2245/278 (exoskeleton in dorsal and ventral aspect, with fragments of legs): Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia] from trench 82an, Lyagush'ye locality, Kemerovo, Abasheva Formation, Kemerovo

Oblast, Russia (Ponomarenko 1985).

**Phylogenetic justification:** The oldest known representative of the family Hydraenidae is *Ochtebiites minor*. It can be placed in the family based on its small size, elongate body, elongate maxillary palpi, and the presence of an intercoxal sternite between the metacoxae (Jäch et al. 2016).

**Minimum age:** 182 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** The Abasheva Formation appears to be Pliensbachian in age, based on the fossil flora and fauna (Kovalev 1981; Mogutcheva 2009). The top of the Pliensbachian is  $182.7 \pm 0.7$  (International Chronostratigraphic Chart, v. 2018/08), giving a minimum constraint of 182 Ma. The soft maximum age (*ca.* 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

#### **Node 25: Agyrtidae – Leiodidae: 165 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Mesecanus communis* Ponomarenko, 1977 [holotype, PIN 3000/926 (exoskeleton with preserved appendages in dorsal and ventral aspects); paratypes, PIN 3000/915, 3000/913, 3000/909, 2744/12: Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia], from Novospasskoye village, Ichetuy Formation, Buryat, Russia (Ponomarenko, 1977; Perkovsky 1999).

**Phylogenetic justification:** The systematic placement of *Mesecanus communis* has been historically quite unstable. Ponomarenko (1977) placed the species into Agyrtidae, while Perkovsky (1999) assigned the fossil to Leiodidae. It was treated as an agyrtid again by Newton (1997). It nonetheless meets all the diagnostic features of Agyrtidae, and we consider it as a member of this group. It has been compared to the extant genus *Ecanus* by Newton (1997)

**Minimum age:** 165 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** The Novospasskoye locality is usually considered Upper to Middle Jurassic based on biostratigraphy (Ponomarenko 1993). We thus use  $166.1 \pm 1.2$  as a conservative constraint on the node, representing the upper boundary of the Callovian, the last stage of the Middle Jurassic (International Chronostratigraphic Chart, v. 2018/08). The soft maximum age (*ca.* 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

#### **Node 26: Crown Staphylinidae: 165 Ma – 235 Ma.**

**Fossil taxon and specimen:** undescribed member of Silphidae [NIGP 156145a/b (exoskeleton with preserved appendages): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from the Haifanggou Formation at Daohugou, Ningcheng County, Inner Mongolia, northeastern China (Cai et al. 2014b).

**Phylogenetic justification:** The undescribed specimens can be placed into the former family Silphidae, treated here as a subfamily of Staphylinidae *sensu nov.*, based on their general habitus, clubbed antennae, large mesoscutellum, truncate elytra, and well-separated mesocoxae (Cai et al. 2014b). Given that it has been recently demonstrated that the enigmatic *Leehermania prorova* from the Late Triassic Cow Branch Formation on the Virginia-North Carolina border, USA is in fact not a staphylinid as assumed previously, these burying beetles are the oldest candidates for calibrating the node representing crown Staphylinidae (Chatzimanolis et al. 2012; Fikáček et al. 2020).

**Minimum age:** 165 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** For the minimum age justification of the Daohugou biota, see node 7. The soft maximum age (*ca.* 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

#### **Node 27: *Megalopaederus* (Paederinae) – Staphylininae: 122.2 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Megolisthaerus minor* Cai and Huang, 2013 [holotype, NIGP 153697 (amber inclusion): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from the Huanbanjigou of the Yixian Formation, Shangyuan, Beipiao city, Liaoning Province (Cai and Huang

2013).

**Phylogenetic justification:** *Megolisthaerus minor* can be placed into Staphylininae on the basis of its relatively large and elongate body, antennae inserted along the anterior margin of the head, pronotal hypomeron lacking postcoxal processes; pro- and mesotarsi 5-segmented, elytron without epipleural keel, and two pairs of paratergites on abdominal segment III–VI (Cai and Huang 2013).

**Minimum age:** 122.2 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** For the minimum age justification of the Yixian Formation, see node 14. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

**Node 28:** Silphinae – Staphylinidae *partim*: **165 Ma – 235 Ma.**

**Fossil taxon and specimen:** As for node 25.

**Minimum age:** 165 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** As for node 25.

**Node 29:** Staphylinidae: Apateticinae – Osoriinae: **98.17 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Mesallotrochus longiantennatus* Cai and Huang, 2015 [holotype, NIGP157737 (amber inclusion): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] lowermost Cenomanian, from an amber mine located near Noije Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar (Cai and Huang 2015)

**Phylogenetic justification:** *Mesallotrochus* is placed in the extant osoriine tribe Thoracophorini based on its general habitus, the protibia with the inner edge straight, missing ctenidium, exposed protrochantins, open procoxal cavities, and a more or less flattened body (Cai and Huang 2015). As such, *M. longiantennatus* represents the oldest member of Osoriinae and is suitable for calibrating the split between Apateticinae and Osoriinae.

**Minimum age:** 98.17 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** For the minimum age justification of Burmese amber from northern Myanmar, see node 12. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

**Node 30:** Crown Bostrichoidea: **165 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Paradermestes jurassicus* Deng, Ślipiński, Ren and Pang, 2017 [CNU-COL-NN2017001 (exoskeleton) with legs and antennae: Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] from Daohugou Village, Middle Jurassic Jiulongshan Formation, Ningcheng County, Inner Mongolia, China (Deng et al. 2017a).

**Phylogenetic justification:** *Paradermestes* can be placed into Dermestidae on the basis of having a small deflexed head inserted into the prothorax, a developed antennal club, posterior angles of pronotum projecting posteriorly, excavate metacoxae, and simple tarsomeres. Given its age, it is a suitable calibration point for setting the minimum age of Bostrichoidea (Kirejshuk and Azar 2009).

**Minimum age:** 165 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** For the minimum age justification of the Daohugou biota, see node 7. The soft maximum age (*ca.* 235 Ma) is derived from the Madygen Formation at Dzhaibayau-Cho, Kyrgyzstan. See node 8 for justification.

**Node 31:** Crown Bostrichidae: **98.17 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Poinarinius burmaensis* Legalov, 2018 [holotype ISEA no. MA2018/3 (amber inclusion): Institute of Systematics and Ecology of Animals, Novosibirsk, Russia] lowermost Cenomanian, from

an amber mine located near Noije Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar (Legalov 2018)

**Phylogenetic justification:** *Poinarinius* can be placed into Bostrichidae based on its non-pseudotetramerous tarsi, head lacking paired ocelli, mesocoxal cavities closed laterally, short and triangular metatrochanter, and the femur partially separated from the coxa. Based on the protibia with one apical spine and subequal tarsomeres 1 and 2, the fossil was assigned into the extant subfamily Dinoderinae (Legalov 2018).

**Minimum age:** 98.17 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** For the minimum age justification of Burmese amber from northern Myanmar, see node 12. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

### **Node 32: Crown Ptinidae: 105 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Actenobius magneoculus* Peris, Philips, and Delclòs, 2015 [holotype, SJ-10-18, SJ (amber inclusion): San Just amber collection, Fundación Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Spain] from the San Just outcrop, Utrillas, Regachuelo Member, Escucha Formation, Teruel Province, Spain (Peris et al. 2015b).

**Phylogenetic justification:** *Actenobius magneoculus* is placed in the family Ptinidae by its cylindrical body, deflexed head inserted into the prothorax and covered dorsally by the pronotum; antennae with 11 antennomeres and with the last three segments asymmetrically elongated, large compound eyes, reduced prosternum lengthwise and pronotum convex dorsally, ovoid pro- and mesocoxae, transverse and excavated hind coxae for reception of metafemora, slender femora and tibiae, tarsal formula 5-5-5, and tarsomere 1 longer than tarsomere 5 (Lawrence and Britton 1991; Philips and Bell 2010). It can be assigned to Anobiinae based on the metaventrite and first abdominal segment without grooves for the reception of hind legs, complete lateral border of pronotum, and hypognathous head with mandibles not near the metaventrite with the head retracted (Español 1992)

**Minimum age:** 105 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** The amber from San Just is early to middle Albian in age based on palynomorph correlation of the Escucha Formation (Peñalver and Delclòs 2010). We thus use 105 Ma as a conservative minimum on the age of the amber deposit. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

### **Node 33: Thanerocleridae – Cleridae: 165 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Wangweiella calloviana* Kolibáč and Huang, 2016 [holotype, NIGP162533 (exoskeleton with fragments of legs and antennae): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from Daohugou Village, Middle Jurassic Jiulongshan Formation, Ningcheng County, Inner Mongolia, China (Kolibáč and Huang 2016).

**Phylogenetic justification:** *Wangweiella calloviana* can be placed into the clerid subfamily Epiclininae based on its elongate pedicel, absence of paracoxal sutures, basitarsus shortened but not covered from above with the base of tarsomere 2, and tegmen composed of two parts. A morphological phylogenetic analysis recovered the species as sister to the rest of Epiclininae (Kolibáč and Huang 2016), making it suitable for calibrating the split between Thanerocleridae and Cleridae.

**Minimum age:** 165 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** For the minimum age justification of the Daohugou biota, see node 7. The soft maximum age (ca. 235 Ma) is derived from the Madygen Formation at Dzhalylau-Cho, Kyrgyzstan. See node 8 for justification.

### **Node 34: Prionoceridae – Melyridae: 165 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Idgiaites jurassicus* Liu, Ślipiński, Leschen, Ren and Pang, 2015 [holotype: CNU-

COL-NN2010238 (nearly complete exoskeleton in lateral position): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] from Daohugou Village, Middle Jurassic Jiulongshan Formation, Ningcheng County, Inner Mongolia, China (Liu et al. 2015).

**Phylogenetic justification:** *Idgiaites jurassicus* belongs to Prionoceridae based on the general body shape and the 11-segmented antenna with three apical segments flattened and the apical segment enlarged (Liu et al. 2015).

**Minimum age:** 165 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** For the minimum age justification of the Daohugou biota, see node 7. The soft maximum age (ca. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

### **Node 35: Lymexylidae: 112.6 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Cratoatractocerus grimaldii* Wolf, 2011 [holotype SMNS-66534 (exoskeleton with fragments of appendages): Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany] from the vicinity of Nova Olinda, southern Ceará, Nova Olinda Member of the Crato Formation, north-east Brazil (Wolf 2011).

**Phylogenetic justification:** *Cratoatractocerus grimaldii* can be placed into Lymexylidae and the subfamily Atractocerinae based on its long and slender body form, large eyes that occupy almost the entire frons and are narrowly separated, absence of the first radial crossvein, and heavily sclerotised female genitalia (Kurosawa 1985; Wheeler 1986; Wolf 2011).

**Minimum age:** 112.6 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** For the minimum age justification of the Crato Formation, see node 11. The soft maximum age (ca. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

### **Node 36: Crown Tenebrionoidea: 165 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Archaeoripiphorus nuwa* Hsiao, Yu and Deng, 2017 [holotype: CNU-C-NN-2006841 (exoskeleton with fragments of appendages): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] from Daohugou Village, Middle Jurassic Jiulongshan Formation, Ningcheng County, Inner Mongolia, China (Hsiao et al. 2017).

**Phylogenetic justification:** *Archaeoripiphorus* was considered to represent a member of Rhipiphoridae by Hsiao et al. (2017) based mainly on overall morphological similarity. Batelka et al. (2018) reviewed the evidence for the classification of the genus and concluded that it cannot be placed into Rhipiphoridae with certainty. It however clearly is a member of Tenebrionoidea, as indicated by its wedge-shaped body and tarsal formula 5-5-4, and is herein used to calibrate the node representing crown Tenebrionoidea.

**Minimum age:** 165 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** For the minimum age justification of the Daohugou biota, see node 7. The soft maximum age (ca. 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

### **Node 37: Rhipiphoridae – Mordellidae: 98.17 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Protoripidius burmiticus* Cai, Yin and Huang, 2018 [holotype, NIGP166155 (amber inclusion): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] lowermost Cenomanian, from an amber mine located near Noije Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar (Cai et al. 2018a)

**Phylogenetic justification:** *Protoripidius burmiticus* can be assigned to the rhipiphorid subfamily Ripidiinae based on the combination of the following characters: abdominal sternite II visible externally and similar to

sternite III, eyes coarsely faceted, elytra shortened in the male and widely separated, hind wings not folded transversely, tibial spurs completely absent, claws simple, and body densely clothed with short setae (Falın and Engel 2010; Cai et al. 2018a).

**Minimum age:** 98.17 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** For the minimum age justification of Burmese amber from northern Myanmar, see node 12. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

### **Node 38: Ischaliidae – Aderidae: 125 Ma – 165 Ma.**

**Fossil taxon and specimen:** nine undescribed fossils [“JG 204/15”, “96”, “1282”, “AD4A”, “1521”, “1239”, “853-F”, “NBS-2F”, “822” (amber inclusions of various degrees of preservation): Lebanese University, Faculty of Sciences II, Fanar, Lebanon] from the Nabaa Es-Sukkar – Brissa, Hammana – Mdeirij, Ain Dara, Rihane, and Jouar Es-Souss (Bkassine) outcrops, Lebanon (Kirejtshuk and Azar 2013).

**Phylogenetic justification:** Kirejtshuk and Azar (2013) cite nine members of the family Aderidae from Cretaceous Lebanese amber. The presence of aderids in Lebanese amber was also noted by Grimaldi and Engel (2005).

**Minimum age:** 125 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** For the minimum age justification of Lebanese amber, see node 16. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

### **Node 39: Salpingidae – Pythidae: 53 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Eopeplus stetzenkoi* Kirejtshuk and Nel, 2009 [holotype, PA 891/3 (amber inclusion): Laboratoire de Paléontologie, Muséum National d’Histoire Naturelle, Paris, France] from Eocene French amber obtained from the Farm Le Quesnoy locality, Chevrière, region of Creil, Oise department, northern France (Kirejtshuk and Nel 2009).

**Phylogenetic justification:** *Eopeplus stetzenkoi* can be placed into the salpingid subfamily Inopeplinae based on its flattened body, pronotum distinctly narrowing posteriorly, and shortened elytra. It moreover shares with recent representatives of the group the shape of the head, structure of antennae, and others (Kirejtshuk and Nel 2009).

**Minimum age:** 53 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** The age of Oise amber, approximately 53 Ma is indicated by the presence of mammalian fossils corresponding to the MP7 horizon (Kirejtshuk and Nel 2009). The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

### **Node 40: Anthicidae – Meloidae: 125 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Camelomorpha longicervix* Kirejtshuk, Azar and Telnov, 2008 [holotype, “846” (amber inclusion, sex undefinable): Lebanese University, Faculty of Sciences II, Fanar, Lebanon] from the Early Cretaceous Lebanese amber originating from the outcrop Hammana – Mdeirij, Caza Baabda, Mouhafazet, Jabal Loubnan, central Lebanon (Kirejtshuk and Azar 2008).

**Phylogenetic justification:** *Camelomorpha longicervix* can be placed into the anthicid subfamily Macratriinae based on its elongate body, absence of a frontoclypeal suture, elytra with distinct longitudinal sulcus along the lateral margins and parallel to epipleura, mesosternum and mesepisterna fused, without an apparent carina at fusion line (Chandler 2010). It is thus suitable for calibrating the split between Anthicidae and Meloidae.

**Minimum age:** 125 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** For the minimum age justification of Lebanese amber, see node 16. The maximum age



constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

**Node 41: Crown Zopheridae: 98.17 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Paleoendeitoma antennata* Deng, Ślipiński, Ren and Pang, 2017 [holotype, CNU-COL-MA-0312; paratype, CNU-COL-MA-0313 (amber inclusion): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] lowermost Cenomanian, from an amber mine located near Noiye Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar (Deng et al. 2017b).

**Phylogenetic justification:** *Paleoendeitoma* can be placed in Zopheridae, subfamily Colydiinae, based on the antennal insertions concealed by frontal ridges, antennae distinctly clubbed with antennomere 3 as broad as the pedicel, procoxal cavities lacking lateral extensions, procoxae rounded with concealed trochantins, mesocoxae rounded with their cavities externally closed by sterna and the mesotrochantins concealed, abdomen with five ventrites, legs with visible trochanters and 4-segmented tarsi (Deng et al. 2017b).

**Minimum age:** 98.17 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** For the minimum age justification of Burmese amber from northern Myanmar, see node 12. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

**Node 42: Crown Tenebrionidae: 122.2 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Alphitopsis initialis* Kirejtshuk, Nabozhenko and Nel, 2011 [holotype, “A 31966” (exoskeleton with legs and fragments of antennae): Henan Geological Museum, Zhengzhou, China] from the Huanbanjigou of the Yixian Formation, Shangyuan, Beipiao city, Liaoning Province, China (Kirejtshuk et al. 2011).

**Phylogenetic justification:** The species has been assigned to the subfamily Alleculinae and tribe Gonoderini based on its five visible abdominal ventrites, simple tarsomeres without membranous ventral lobes, serrate antennae, and shape of pronotum and the body (Kirejtshuk et al. 2011). It is thus suitable for calibrating the node representing Crown Tenebrionidae.

**Minimum age:** 122.2 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** For the minimum age justification of the Yixian Formation, see node 14. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

**Node 43: Alexiidae – Latridiidae: 125 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Tetrameropsis mesozoica* Kirejtshuk and Azar, 2008 [holotype, “474A” (amber inclusion, sex indeterminate) Lebanese University, Faculty of Sciences II, Fanar, Lebanon] from the Early Cretaceous Lebanese amber originating from the outcrop Hammana – Mdeirij, Caza Baabda, Mouhafazet, Jabal Loubnan, central Lebanon (Kirejtshuk and Azar 2008).

**Phylogenetic justification:** The habitus of the species corresponds to corticariine Latridiidae (Shockley and Alekseev 2014). It was initially placed into its own subfamily, which was later raised to family level by Shockley and Alekseev (2014) where it has been hypothesised to be related to Latridiidae or Latridiidae + Akalyptoischiidae. In either case, the fossil is suitable for calibrating the split between Alexiidae and Latridiidae.

**Minimum age:** 125 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** For the minimum age justification of Lebanese amber, see node 16. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

**Node 44: Crown Endomychidae: 98.17 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Palaeomyces foveolatus* Tomaszewska, Ślipiński and Ren, 2018 [holotype, CNU008072 (amber inclusion): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] lowermost Cenomanian, from an amber mine located near Noiije Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar (Tomaszewska et al. 2018).

**Phylogenetic justification:** *Palaeomyces* can be placed into crown Endomychidae based on having a frontoclypeal suture, lacking antennal grooves, antenna 11-segmented with a club, pronotum with transverse basal and longitudinal paired lateral sulci, visible portion of procoxae globular, procoxae separated by prosternal process, mesocoxal cavities externally open, metaventral paired postcoxal openings usually present, elytral epipleura well-developed, tarsi 4-segmented, abdominal ventrite 1 at least as long as ventrites 2 and 3 combined, and abdominal postcoxal lines absent (Tomaszewska 2000; Robertson et al. 2015)

**Minimum age:** 98.17 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** For the minimum age justification of Burmese amber from northern Myanmar, see node 12. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

#### **Node 45: Crown Coccinellidae: 53 Ma – 125 Ma.**

**Fossil taxon and specimen:** *Rhyzobius antiquus* Kirejtshuk and Nel, 2012 [holotype, MNHN PA 11862 (amber inclusion): Muséum National d'Histoire Naturelle, Paris, France] from Eocene French amber obtained from the Farm Le Quesnoy locality, Chevrière, region of Creil, Oise department, northern France (Kirejtshuk and Nel 2012).

**Phylogenetic justification:** Affinity to Coccinellidae is indicated a broadly rounded body with a convex dorsum and flattened ventral side, clubbed antennae, the presence of a postcoxal line on the first abdominal ventrite, and pseudotrimerous tarsi (Kirejtshuk and Nel 2012).

**Minimum age:** 53 Ma.

**Soft maximum age:** 98.17 Ma.

**Age justification:** For the minimum age justification of Eocene Oise amber, see node 38. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

#### **Node 46: Boganiidae – Erotylidae: 165 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Palaeoboganium jurassicum* Liu, Ślipiński, Lawrence, Ren and Pang, 2018 [holotype, CNU-COL-NN201601PC (exoskeleton with appendages): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] from Daohugou Village, Middle Jurassic Jiulongshan Formation, Ningcheng County, Inner Mongolia, China (Liu et al. 2018).

**Phylogenetic justification:** *Palaeoboganium jurassicum* is the earliest fossil representative of the family Boganiidae, as indicated by the head with an arcuate frontoclypeal suture, labrum not visible externally, mandible with a dorsal tubercle fitting into a depression on lateral edge of clypeus, subantennal grooves absent, antennae short and weakly capitate, pro- and mesocoxae with exposed trochantins, metacoxae narrowly separated and, not extending laterally to meet elytra, and abdomen with five freely articulated ventrites. A phylogenetic analysis of adult external characters recovered *Palaeoboganium* as the sister group of *Paracucujus* and *Metacucujus* (Liu et al. 2018), making it suitable for calibrating the split between Boganiidae and Erotylidae.

**Minimum age:** 165 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** See node 7 for the minimum age justification of the Daohugou locality. The soft maximum is from the Madygen Formation at the Dzhailyau-Cho locality, Lyailyskii District, Batken Region, southwest Kyrgyzstan, Central Asia, as justified in node 7.

#### **Node 47: Helotidae – (Protocucujidae + Spindidae): 125 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Libanopsis poinari* Kirejtshuk, 2015 [holotype, “841 BC” (amber inclusion): Lebanese University, Faculty of Sciences II, Department of Natural Sciences, Beirut, Lebanon] from the Early Cretaceous Lebanese amber originating from the outcrop Hammana – Mdeirij, Caza Baabda, Mouhafazet, Jabal Loubnan, central Lebanon (Kirejtshuk et al. 2015a).

**Phylogenetic justification:** *Libanopsis poinari* can be placed within Sphindidae based on the sparse sculpture of dorsal integument, large coarsely faceted eyes, antennal morphology, undulate lateral pronotal carinas, and small serration in pretarsal claws (Kirejtshuk et al. 2015a).

**Minimum age:** 125 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** For the minimum age justification of Lebanese amber, see node 16. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

**Node 48: Monotomidae – (Kateretidae + Nitidulidae): 165 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Jurorhizophagus alienus* Cai, Ślipiński and Huang, 2015 [holotype, NIGP 161706 (exoskeleton with antennae and partly preserved legs): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from the Haifanggou Formation at Daohugou, Ningcheng County, Inner Mongolia, northeastern China (Cai et al. 2015c).

**Phylogenetic justification:** *Jurorhizophagus alienus* can be placed among monotomids based on its narrowly elongate body, prognathous head with lateral finely faceted eyes, procoxal cavities closed externally, elytra truncate apically and exposing two tergites, and 5-segmented abdomen with relatively long ventrites 1 and 5 (Sen Gupta 1988; Cai et al. 2015c).

**Minimum age:** 165 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** For the minimum age justification of the Daohugou biota, see node 7. The soft maximum age (*ca.* 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

**Node 49: Crown Nitidulidae: 119 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Crepuraea archaica* Kirejtshuk, 1990 [holotype, PIN 3064/7189 (exoskeleton): Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia] Baissa locality situated on the left bank of the Vitim River, 8 km below the mouth of the Baissa River, Buryat Republic, west Transbaikalia, Russia.

**Phylogenetic justification:** As discussed in Kirejtshuk and Ponomarenko (1990) the genus *Crepuraea* has a close affinity to the extant *Epuraea*, which is placed in the subfamily Epuraeinae and tribe Epuraeini (Kirejtshuk 2008). Based on molecular phylogenies of Nitidulidae (Cline et al. 2014), this would place *Crepuraea* well within crown Nitidulidae, making it a suitable candidate for calibrating this node.

**Minimum age:** 119 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** The exact age of the lacustrine sediments of the Zaza Formation at Baissa is disputable. While early estimates suggested an Early Cretaceous (Neocomian–Aptian) age, most palaeoentomologists date them as Valanginian–Hauterivian (Zherikhin et al. 1999). The co-occurrence of *Coptoclava longipoda*, *Ephemeropsis trisetalis* and *Lycoptera* in the Zaza Formation as well as the Jiufotang Formation in western Liaoning, China suggests that the two may be contemporaneous. Given that the latter has been dated to 120 ± 1.0 Ma (unpubl. data; Kirejtshuk and Ponomarenko 1990), we use 119 Ma as the minimum constraint on the clade representing crown Nitidulidae. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

**Node 50: Crown Silvanidae: 98.17 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Protoliota antennatus* Liu, Ślipiński, Wang and Pang, 2019 [holotype, No. CNU008072 (amber inclusion): Key Lab of Insect Evolution and Environmental Changes, Capital Normal

University, Beijing, China] lowermost Cenomanian, from an amber mine located near Noiye Bum Village, Tanaing Town, Hukawng Valley, northern Myanmar (Liu et al. 2019).

**Phylogenetic justification:** The placement of *Protoliota* within Silvanidae is supported by its overall body form, long filiform antennae with long scape and without club, 5-5-5 tarsi, and narrowly open procoxal cavities (Liu et al. 2019). The distinctly lobed tarsomeres and prominent sexual dimorphism manifesting in the presence of male mandibular horns and antennal length (Thomas 2004; Cai and Huang 2019) suggest a placement in Brontinae.

**Minimum age:** 98.17 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** For the minimum age justification of Burmese amber from northern Myanmar, see node 12. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

#### **Node 51: Nemonychidae – Anthribidae: 155 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Protoscelis longicornis* (Medvedev, 1968) [holotype, PIN, no. 2066/3241 (exoskeleton): Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia] from the Karabastau Formation of the Karatau Range near the village of Mikhailovka, Chimkent Region, Chayan District, southern Kazakhstan (Medvedev 1968; Legalov 2013).

**Phylogenetic justification:** The presence of a reduced rostrum, a three-segmented and rather compact antennal club, developed subbasal line on pronotum, and sexually dimorphic antennae place the fossil into Anthribidae (Legalov 2013).

**Minimum age:** 155 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** For the minimum age justification of the Karatau Range, see node 5. The soft maximum age (*ca.* 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

#### **Node 52: Belidae – (Attelabidae, (Brentidae, Curculionidae)): 165 Ma – 235 Ma.**

**Fossil taxon and specimen:** *Sinoeuglypheus daohugouensis* Yu, Davis and Shih, 2019 [holotype, CNU-COL-NN2011122 (exoskeleton with appendages preserved in lateral aspect, sex unknown): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] from the Haifanggou Formation at Daohugou, Ningcheng County, Inner Mongolia, northeastern China (Yu et al. 2019).

**Phylogenetic justification:** The species can be assigned to Belidae on the basis of the irregularly arranged punctures on the elytra, elongated first flagellomere of the antennae, outer longitudinal carina and an apical setal brush on the fore tibiae, wide prothoracic cavity for reception of the procoxa, form of the meso- and metathoracic episterna and epimera, small flange along the elytral basal margin, and lateral carinae on the abdominal ventrites (Yu et al. 2019).

**Minimum age:** 165 Ma.

**Soft maximum age:** 235 Ma.

**Age justification:** For the minimum age justification of the Daohugou biota, see node 7. The soft maximum age (*ca.* 235 Ma) is derived from the Madygen Formation at Dzhailyau-Cho, Kyrgyzstan. See node 8 for justification.

#### **Node 53: Brentidae – Curculionidae: 112.6 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Axelrodiellus raptus* Zherikhin and Gratshev, 2004 [holotype, AMNH 43312 (exoskeleton lacking legs, with fragments of antennae): American Museum of Natural History, New York City, USA] from the Lower Cretaceous (Aptian) Crato Formation, northeastern Brazil (Zherikhin and Gratshev 2004).

**Phylogenetic justification:** The species is placed in Brentidae on the basis of having an unpaired gular suture, narrow and loose antennal club, enlarged trochanters, and fused and strongly enlarged first two abdominal sternites. Assignment to Eurhynchinae is supported by the sloping trochanters and the bases of the femora

reaching the coxae, complete and deep suture between the first two ventrites, gular suture running from the base of the rostrum to the eyes, and striated gular region (Zherikhin and Gratshev 2004).

**Minimum age:** 112.6 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** For the minimum age justification of the Crato Formation, see node 11. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

#### **Node 54: Crown Chrysomelidae: 122.2 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Mesolpinus antennatus* Kirejtshuk, Moseyko and Ren, 2015 [holotype, CNU-COL-LB-2009840 (exoskeleton with fragments of appendages preserved in ventral aspect): Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China] from the Huanbanjigou of the Yixian Formation, Shangyuan, Beipiao city, Liaoning Province, China (Kirejtshuk et al. 2015b).

**Phylogenetic justification:** The genus can be referred to the subfamily Chrysomelinae based on the hypognathous head not narrowed at the base, antennal cavities located in front of eyes and widely separated, frontoclypeus subquadrangular, behind the mandibles and separated from the posterior part of the frons by a wide V-shaped suture, the pronotum laterally margined, all coxae moderately separated, the prosternal process apparently lacking lateral structures for the reception of the procoxae, procoxae distinctly transverse, mesoventrite lacking projections for reception of the mesocoxae, metepisterna simple and lacking projections, the abdomen with ventrite 1 longest and other ventrites subequal in length, not fused, and tarsomere 3 bilobed (Kirejtshuk et al. 2015b).

**Minimum age:** 122.2 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** For the minimum age justification of the Yixian Formation, see node 14. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

#### **Node 55: Crown Cerambycidae: 122.2 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Cretoprionus liutiaogouensis* Wang, Ma, McKenna, Yan, Zhang and Jarzembowski, 2014 [holotype, NIGP154953a, b (exoskeleton with appendages): Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China] from the Huanbanjigou of the Yixian Formation, Shangyuan, Beipiao city, Liaoning Province, China (Wang et al. 2014).

**Phylogenetic justification:** *Cretoprionus liutiaogouensis* can be assigned to Cerambycidae based on its large and robust body, simple mandibular apex, pseudotetramerous tarsi, raised antennal insertions, and long antennae. It can furthermore be placed in Prioninae due to the very large and robust body, absence of a stridulatory plate on the mesonotum, pseudotetramerous tarsi, mouthparts projecting anteriorly, and lateral carinae on the prothorax (Turnbow and Thomas 2002; Wang et al. 2014; Vitali, 2019).

**Minimum age:** 122.2 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** For the minimum age justification of the Yixian Formation, see node 14. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

#### **Node 56: Sagrinae – Bruchinae: 78 Ma – 155 Ma.**

**Fossil taxon and specimen:** *Mesopachymerus antiqua* Poinar, 2005 [holotype, TMP 91.148.771 (amber inclusion): Royal Tyrrell Museum in Drumheller, Alberta Canada] from Cretaceous Canadian amber, obtained from the Grassy Lake amber deposit, Foremost Formation, Alberta, Canada (Poinar 2005).

**Phylogenetic justification:** The widened protarsus 1 reliably places *Mesopachymerus antiqua* among bruchines, making it a suitable candidate for calibrating the split between Sagrinae and Bruchinae (Poinar 2005).

**Minimum age:** 78 Ma.

**Soft maximum age:** 155 Ma.

**Age justification:** The age of Canadian amber has been estimated as approximately 78 – 79 Ma based on biostratigraphic correlation (McKellar et al. 2013). We conservatively use 78 Ma as the minimum age constraint. The soft maximum age is derived from the Karabastau Formation of the Karatau Range, see node 5 for justification.

**Node 57: Galerucinae – Chrysomelinae: 83.4 Ma – 165 Ma.**

**Fossil taxon and specimen:** *Taimyraltica calcarata* Nadein, 2018 [holotype, PIN 3311/1203 (amber inclusion): Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia] from Cretaceous Taimyr amber collected from the right bank of the Maimecha River, Taimyr Peninsula, Kheta Formation, Krasnoyarskiy Krai, Russia (Nadein and Perkovsky 2018).

**Phylogenetic justification:** *Taimyraltica* can be attributed to Galerucinae based on its elongate body, hypognathous head without a constriction behind the eyes, antennal insertions situated between eyes at a distance from anterior margin of frons, eyes without emarginations, pronotum with a lateral margin and not constricted, pronotal base with a transverse furrow, procoxae transverse, elytra regularly punctured, and pygidium not vertical (Nadein and Beždek 2014; Nadein and Perkovsky 2018).

**Minimum age:** 83.4 Ma.

**Soft maximum age:** 165 Ma.

**Age justification:** *Taimyraltica calcarata* occurs in the Late Cretaceous Taimyr amber from the Kheta Formation at the Yantardakh locality, Taimyr Peninsula, Russia. The age of the Kheta Formation is Coniacian-Santonian according to Saks et al. (1959). All amber from the Yantardakh locality has been found in the upper horizons of the formation, and is therefore thought to be Santonian (Zherikhin, 1978) or even upper Santonian based on the presence of marine bivalves of the genus *Inoceramus* in the overlying Mutino Formation (Perkovsky and Makarkin, 2015). As such, the age of Taimyr amber from Yantardakh is late Santonian, the upper boundary of which is dated to  $83.6 \pm 0.2$  Ma (International Chronostratigraphic Chart, v. 2018/08). The minimum age constraint for this node is 83.4 Ma. The maximum age constraint is based on the Daohugou biota, which lacks representatives of the clade. See node 7 for justification.

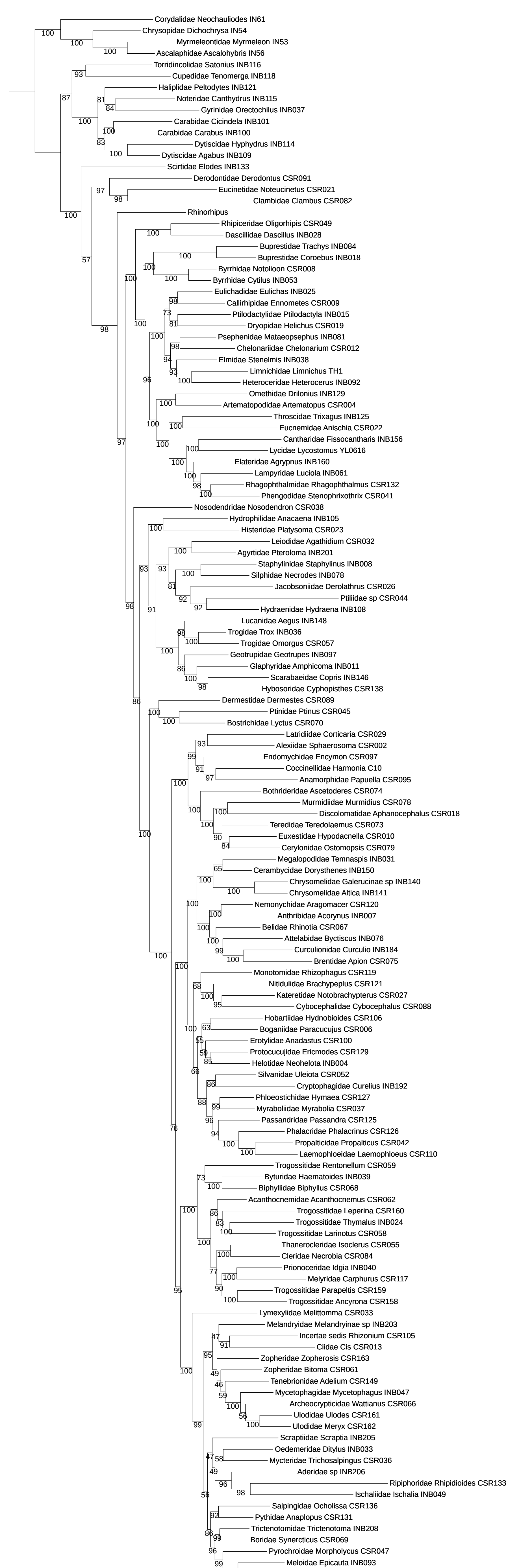
## Beetle phylogeny and evolutionary timescale

**Figure S1.** Test of model-dependent phylogenetic signal on a reduced 138 taxon dataset analysed with the LG model in IQ-TREE.





**Figure S2.** Test of model-dependent phylogenetic signal on a reduced 138 taxon dataset analysed with the WAG model in IQ-TREE.



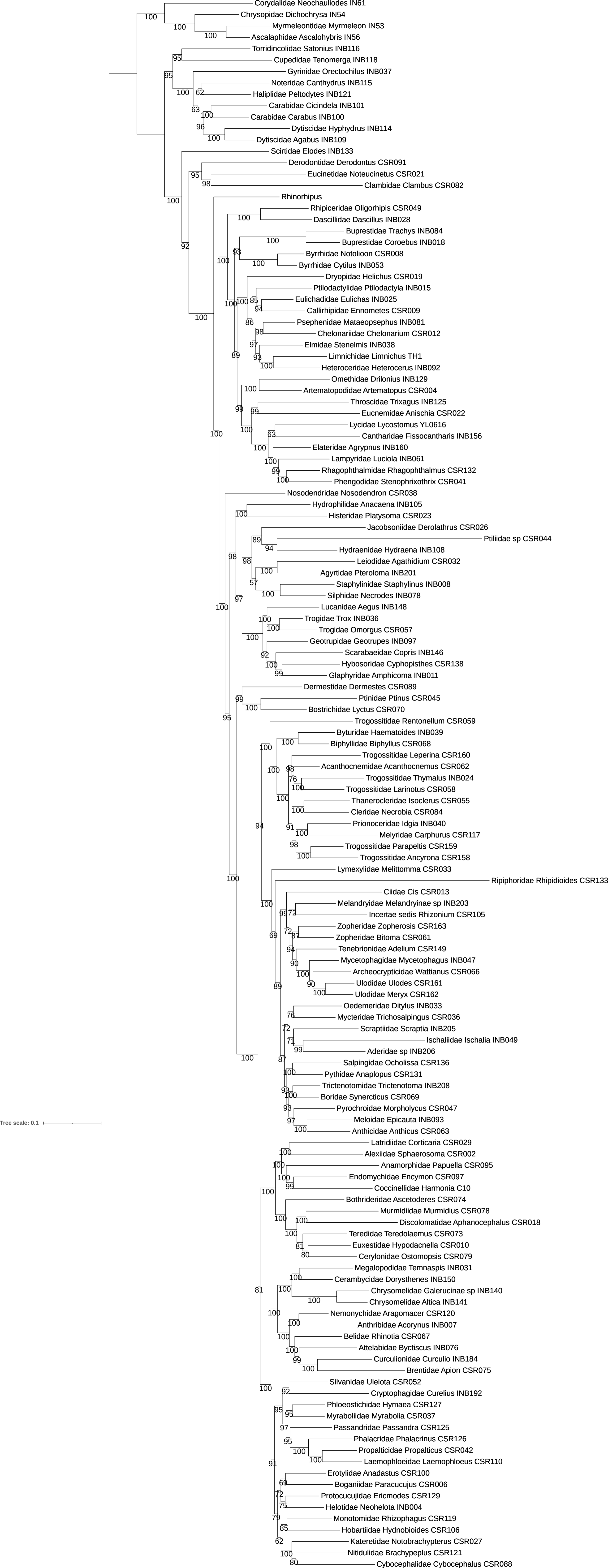
**Figure S3.** Test of model-dependent phylogenetic signal on a reduced 138 taxon dataset analysed with the JTT model in IQ-TREE.



**Figure S4.** Test of model-dependent phylogenetic signal on a reduced 138 taxon dataset analysed with the GTR20 model in IQ-TREE.

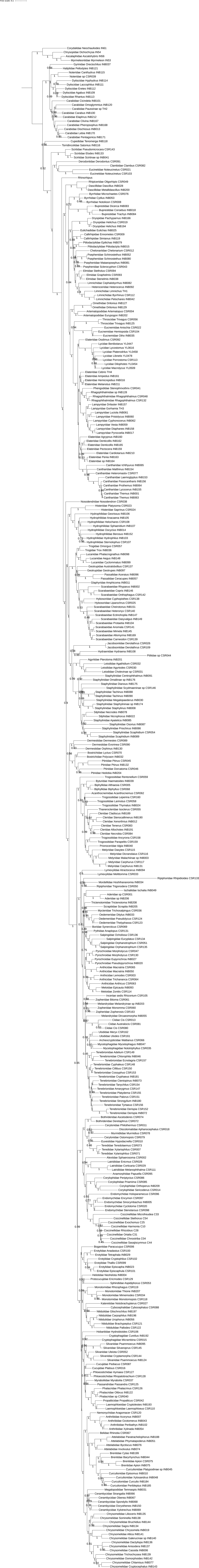


**Figure S5.** Test of model-dependent phylogenetic signal on a reduced 138 taxon dataset analysed with the C10 model in IQ-TREE.

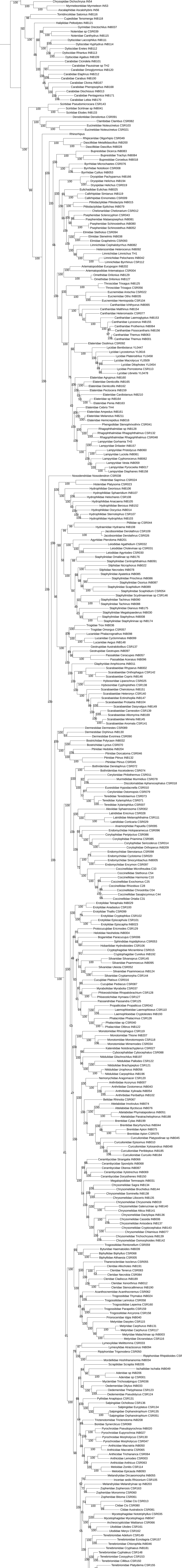




**Figure S6.** Phylogeny of Coleoptera inferred with the site-heterogeneous Bayesian model CAT-GTR+G4 implemented in PhyloBayes.



**Figure S7.** Phylogeny of Coleoptera inferred with the site-homogeneous ML model GTR20 implemented in IQ-TREE.



**Figure S8.** Phylogeny of Coleoptera inferred with the site-homogeneous ML model LG+C20 implemented in IQ-TREE.

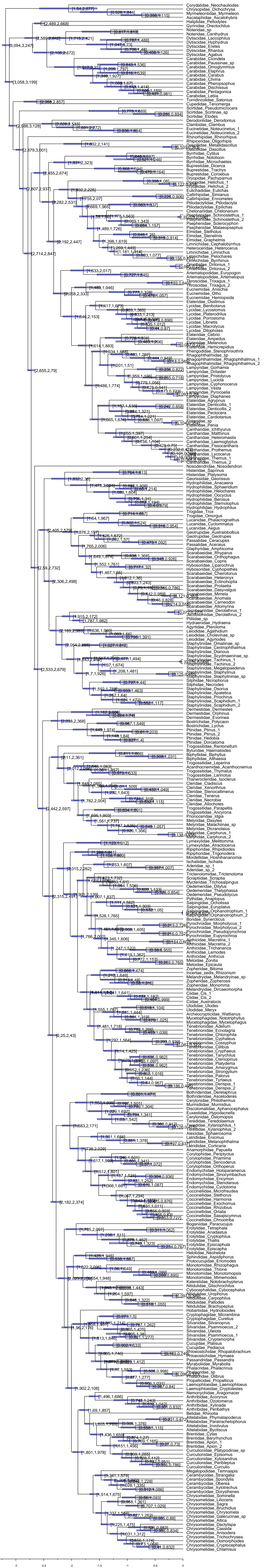


**Figure S9.** Dated phylogenetic tree of Coleoptera; uniform priors, autocorrelated rate clock.

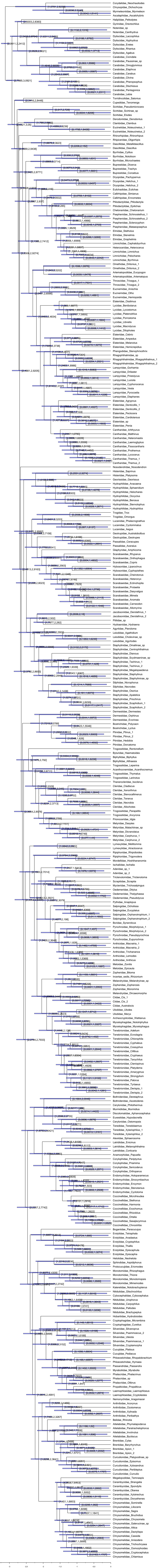




**Figure S10.** Dated phylogenetic tree of Coleoptera; uniform priors, independent rate clock.



**Figure S11.** Phylogenetic tree of Coleoptera displaying the effective priors.



-3 -2.5 -2 -1.5 -1 -0.5 0

**Table S1.** Fit of maximum likelihood (ML) models to the reduced coleopteran dataset for model sensitivity testing, analysed in ModelFinder. Abbreviations: AIC, Akaike information criterion scores.

<b>Model</b>	<b>AIC</b>
C10	1035697.227
GTR20	1210678.781
LG	1211046.717
JTT	1215087.892
WAG	1220238.554

**Table S2.** Overview of fossil calibrations for molecular clock analyses.

Node	Clade	Fossil constraint	Minimum age (Ma)	Maximum age (Ma)
1	(Megaloptera + Neuroptera) – Coleoptera	<i>Stephanastus polinae</i> Kirejtshuk and Nel, 2013	298.75	324
2	Crown Coleoptera	<i>Ponomarenkium belmonthensis</i> Yan, Lawrence, Beattie and Beutel, 2018	251.878	307.1
3	Gyrinidae – Haliplidae	<i>Tunguskagyryrus planus</i> Yan, Beutel and Lawrence, 2018	251.878	293.69
4	Dytiscidae – Noteridae	<i>Palaeodytes gutta</i> Ponomarenko, 1987	155	251.878
5	Cupedidae – Torridincolidae	<i>Kirghizocupes cellulosus</i> Ponomarenko, 1966	235	293.69
6	Crown Polyphaga	undescribed Elateriformia, Ladinian of Tongchuan, China	237	293.69
7	Derodontidae – (Clambidae + Eucinetidae)	<i>Juropeltastica sinica</i> Cai, Lawrence and Huang, 2014	165	251.878
8	Clambidae – Eucinetidae	<i>Mesocinetus aequalis</i> Kirejtshuk and Ponomarenko, 2010	145	235
9	Rhipiceridae – Dascillidae	<i>Parelateriformius communis</i> Yan and Wang, 2010	165	235
10	Buprestidae – Byrrhidae	<i>Sinoparathyrea bimaculata</i> Pan, Chang and Ren, 2011	165	235
11	Dryopoidea – Byrrhoidea + Buprestoidea	undescribed Dryopidae, Aptian Crato Formation, Brazil	112.6	165
12	Crown Psephenidae	<i>Vetujinbrianax cretaceus</i> Cai and Huang, 2018	98.17	165

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13	Elmidae – (Limnichidae + Heteroceridae)	<i>Elmadulescens rugosus</i>	105	165
		Peris, Maier and Sánchez-García, 2015		
14	Crown Heteroceridae	<i>Heterocerites magnus</i>	122.2	165
		Prokin and Ren, 2011		
15	Artematopodidae – Omethidae	<i>Sinobrevipogon jurassicus</i>	165	235
		Cai, Lawrence, Ślipiński and Huang, 2015		
16	Throscidae – Eucnemidae	<i>Potergosoma gratiosum</i>	125	235
		Kovalev and Kirejtshuk, 2013		
17	<i>Osslimus</i> (Elateridae) – Lycidae	<i>Burmolycus compactus</i>	98.17	165
		Bocak, Li and Ellenberger, 2019		
18	Lampyridae – Phengodidae + Rhagophthalmidae	<i>Protoluciola albertalleni</i>	98.17	165
		Kazantsev, 2015		
19	Crown Cantharidae	<i>Molliberus albae</i>	105	165
		Peris and Fanti, 2018		
20	Georissidae – Hydrophilidae	<i>Protochares brevipalpis</i>	147.28	235
		Fikáček, Prokin, Yan, Yue, Wang, Ren and Beattie, 2014		
21	Trogidae – Lucanidae	<i>Juraesalus atavus</i>	165	235
		Nikolajev, Wang, Liu and Zhang, 2011		
22	Passalidae – Geotrupidae	<i>Parageotrupes incanus</i>	122.2	165
		Nikolajev and Ren, 2010		
23	Hybosoridae – Scarabaeidae	<i>Protohybosorus grandissimus</i>	155	235
		Nikolajev, 2010		
24	Ptiliidae – Hydraenidae	<i>Ochtebiites minor</i>	182	235
		Ponomarenko, 1985		
25	Agyrtidae – Leiodidae	<i>Mesecanus communis</i>	165	235
		Ponomarenko, 1977		

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26	Crown Staphylinidae	undescribed Haifanggou China	Silphidae, Formation,	165	235
27	<i>Megalopaederus</i> (Paederinae) Staphylininae	– <i>Megolisthaerus minor</i> Cai and Huang, 2013		122.2	165
28	Silphinae – Staphylinidae <i>partim</i>	<i>Mesecanus communis</i> Ponomarenko, 1977		165	235
29	Staphylinidae: Apateticinae – Osoriinae	<i>Mesallotrochus longiantennatus</i> Cai and Huang, 2015		98.17	165
30	Crown Bostrichoidea	<i>Paradermestes jurassicus</i> Deng, Ślipiński, Ren and Pang, 2017		165	235
31	Crown Bostrichidae	<i>Poinarinius burmaensis</i> Legalov, 2018		98.17	165
32	Crown Ptinidae	<i>Actenobius magneoculus</i> Peris, Philips, and Delclòs, 2015		105	165
33	Thanerocleridae – Cleridae	<i>Wangweiella calloviana</i> Kolibáč and Huang, 2016		165	235
34	Prionoceridae – Melyridae	<i>Idgiaites jurassicus</i> Liu, Ślipiński, Leschen, Ren and Pang, 2015		165	235
35	Lymexylidae	<i>Cratoatractocerus grimaldii</i> Wolf, 2011		112.6	235
36	Crown Tenebrionoidea	<i>Archaeoripiphorus nuwa</i> Hsiao, Yu and Deng, 2017		165	235
37	Rhipiphoridae – Mordellidae	<i>Protoripidius burmiticus</i> Cai, Yin and Huang, 2018		98.17	235
38	Ischaliidae – Aderidae	undescribed Aderidae from Cretaceous Lebanese amber		125	165

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39	Salpingidae – Pythidae	<i>Eopeplus</i> <i>stetzenkoi</i>	53	165
		Kirejtshuk and Nel, 2009		
40	Anthicidae – Meloidae	<i>Camelomorpha</i> <i>longicervix</i>	125	165
		Kirejtshuk, Azar and Telnov, 2008		
41	Crown Zopheridae	<i>Paleoendeitoma</i> <i>antennata</i>	98.17	165
		Deng, Ślipiński, Ren and Pang, 2017		
42	Crown Tenebrionidae	<i>Alphitopsis</i> <i>initialis</i>	122.2	165
		Kirejtshuk, Nabozhenko and Nel, 2011		
43	Alexiidae – Latridiidae	<i>Tetrameropsis</i> <i>mesozoica</i>	125	165
		Kirejtshuk and Azar, 2008		
44	Crown Endomychidae	<i>Palaeomyces</i> <i>foveolatus</i>	98.17	165
		Tomaszewska, Ślipiński and Ren, 2018		
45	Crown Coccinellidae	<i>Rhyzobius</i> <i>antiquus</i>	53	125
		Kirejtshuk and Nel, 2012		
46	Boganiidae – Erotylidae	<i>Palaeoboganium</i> <i>jurassicum</i>	165	235
		Liu, Ślipiński, Lawrence, Ren and Pang, 2018		
47	Helotidae – (Protocucujidae + Sphindidae)	<i>Libanopsis</i> <i>poinari</i>	125	235
		Kirejtshuk, 2015		
48	Monotomidae – (Kateretidae + Nitidulidae)	<i>Jurorhizophagus</i> <i>alienus</i> Cai,	165	235
		Ślipiński and Huang, 2015		
49	Crown Nitidulidae	<i>Crepuraea</i> <i>archaica</i>	119	165
		Kirejtshuk, 1990		
50	Crown Silvanidae	<i>Protoliota</i> <i>antennatus</i> Liu,	98.17	165
		Ślipiński, Wang and Pang, 2019		
51	Nemonychidae – Anthribidae	<i>Protoscelis</i> <i>longicornis</i>	155	235
		(Medvedev, 1968)		

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52	Belidae – (Attelabidae, (Brentidae, Curculionidae))	<i>Sinoeuglypheus daohugouensis</i> Yu, Davis and Shih, 2019	165	235
53	Brentidae – Curculionidae	<i>Axelrodiellus ruptus</i> Zherikhin and Gratshev, 2004	112.6	165
54	Crown Chrysomelidae	<i>Mesolpinus antennatus</i> Kirejtshuk, Moseyko and Ren, 2015	122.2	165
55	Crown Cerambycidae	<i>Cretoprionus liutiaogouensis</i> Wang, Ma, McKenna, Yan, Zhang and Jarzembowski, 2014	122.2	165
56	Sagrinae – Bruchinae	<i>Mesopachymerus antiqua</i> Poinar, 2005	78	155
57	Galerucinae – Chrysomelinae	<i>Taimyraltica calcarata</i> Nadein, 2018	83.4	165

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