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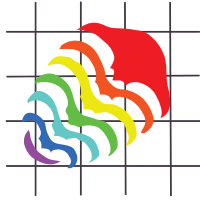
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Catalogue and composition of fossil Anthicidae and Ischaliidae (Insecta: Coleoptera)

Dmitry Telnov and Andris Bukejs

ABSTRACT

Despite the increasing rate of systematic research on extant tenebrionoid Coleoptera of the Anthicidae and Ischaliidae, their fossil records remained largely unrevised. In the current paper we review all hitherto named ant-like flower beetles and false fire-coloured beetles fossils. We suggest 17 fossil species can be reliably assigned to the Anthicidae and three species to the Ischaliidae. We proposed new placements for two fossil Anthicidae taxa: *Petratypus nigri* Kaddumi, 2005 moved from Anthicidae to Cucujiformia Familia incertae sedis and “*Eurygenius*” *wickhami* Cockerell, 1917 is re-described and moved from Eurygeniinae Anthicidae to Tenebrionoidea Familia and Genus incertae sedis. Additionally, three new species are described from Eocene Baltic amber, namely *Nitorus succinius* sp. nov., *Steropes eleticinoides* sp. nov. and *Tomoderus saecularis* sp. nov. An annotated catalogue of fossil Anthicidae and Ischaliidae is provided. We made a qualitative analysis of available data, evaluated the distribution of fossils in the light of current biogeography and geological time. The oldest hitherto known fossil record of the Anthicidae is 130.0–125.5 Ma (same for Macratriinae), of the Anthicinae – 37.2–33.9 Ma, of the Eurygeniinae – 55.8–48.6 Ma, of the Notoxinae, Steropinae and Tomoderinae – 37.2–33.9 Ma. The oldest hitherto know fossil record of the Ischaliidae is 37.2–33.9 Ma.

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INTRODUCTION

Anthicidae (Insecta: Coleoptera), ant-like flower beetles, is a large group of Tenebrionoidea with a cosmopolitan distribution (Chandler, 2010) and over 3500 species (Telnov, 2008) in eight subfamilies (Chandler, 2010). Two groups of uncertain placements, until recently arranged to the Anthicidae, are the Afreminae and Lagrioidinae (Lawrence et al., 2010). There are various fossil records for ant-like flower beetles from around the world.

Ischaliidae (Insecta: Coleoptera), false fire-coloured beetles, is a small monotypic family of nearly 50 species almost exclusively of Northern Hemisphere distribution (Gusakov and Telnov, 2007; Young, 2011), with few fossil records from Eocene Baltic amber (Alekseev and Bukejs, 2017).

There has never been a phylogenetic analysis at the family level for either Anthicidae or Ischaliidae. The Anthicidae has not been formally established as a monophyletic group, and the family, particularly the Steropinae, is morphologically close to the Eleticinae (Meloidae) (Chandler, 2010) and Macratriinae appear closer to Ischaliidae than to Anthicinae (Batelka et al. 2016). Afreminae and Lagrioidinae may not be monophyletic with the Anthicidae (Lawrence and Ślipiński, 2013), and we follow Lawrence et al. (2010) who treated them as Tenebrionoidea incertae sedis (no fossils are known for these two groups). While knowledge of morphological evolution and biogeography of the Anthicidae has grown considerably over the last few decades, their fossils have remained insufficiently studied, with sparse records scattered over numerous publications with the first known records published already 180 years ago (Hope, 1836). In contrast, the first fossil representative of the Ischaliidae was only described a few years ago (Alekseev and Telnov, 2016).

Fossils represent an essential data source for resolving relationships, understanding morphological character evolution and assessing the tempo and mode of diversification (Tarasov et al., 2016). We argue that the minimal age for the Anthicidae should be aligned with the age of *Camelomorpha longicervix* Kirejtshuk, Azar et Telnov in Kirejtshuk and Azar, 2008 (Macratriinae), of which the oldest record is from the Early Cretaceous. Afreminae and Lagrioidinae may not be monophyletic with the Anthicidae (Lawrence and Ślipiński, 2013), and we follow Lawrence et al. (2010) who treated them as Tenebrionoidea incertae sedis (no fossils are known for these two groups). For the Ischaliidae, all known fossil records are from the Eocene.

We plan to catalogue the currently known fossil records of the Anthicidae and Ischaliidae, describe new species and solve nomenclatural uncertainties, provide a preliminary analysis of minimal age of the main subgroups, briefly discuss their morphological features and compile references on the included taxa.

MATERIALS AND METHODS

The published data on fossil Anthicidae and Ischaliidae are summarized from previous reports and supplemented with three new species and additional records described in this paper. The catalogue comprises the following data: full valid taxon name, synonymy (if applicable), list of references and age of fossil records. The nomenclature of the Anthicidae generally follows Chandler (2010), of the Ischaliidae – Gusakov and Telnov (2007), Young (2011). All taxa are listed alphabetically since a phylogenetic arrangement is currently impossible. Authors' comments are placed in square brackets. Specimens were studied using a Leica® S6D stereomicroscope and photographed using a Canon® EOS 450D DSLR camera attached to this stereomicroscope. Multiple photographs were taken at different focal planes and reassembled using CombineZP software.

Institutional Abbreviations

The material examined is deposited in the following collections:

- Center of Natural History (CeNak) (formerly Geologisch-Paläontologisches Institut und Museum, GPIH) of the University of Hamburg, GPIH (Hamburg, Germany);
- Kaliningrad Amber Museum, KAM (Kaliningrad, Russia);
- Latvian Natural History Museum, LDM (Rīga, Latvia);
- Museo de Ciencias Naturales de Álava, MCNA (Vitoria-Gasteiz, Spain);
- Muséum d'Histoire naturelle de Marseille, MHNM (Marseille, France);
- Muséum national d'Histoire naturelle, MNHN (Paris, France);
- Natural History Museum (British Museum, Natural History), BMNH (London, United Kingdom);
- Yale Peabody Museum of Natural History, YPM (New Haven, USA);
- collection of Christel and Hans Werner Hofeins, CCHH (Hamburg, Germany) subsequently will be deposited in the collection of the Senckenberg Deutsches Entomologisches Institut, SDEI (Müncheberg, Germany); and

- collection of Francisco Molino-Olmedo, CMOM (Mancha Real (Jaén), Spain).

SYSTEMATIC PALAEOONTOLOGY

Descriptions of New Taxa

Order COLEOPTERA Linnaeus, 1758
 Suborder POLYPHAGA Emery, 1886
 Superfamily TENEBRIONOIDEA Latreille, 1802
 Family ANTHICIDAE Latreille, 1819
 Subfamily ANTHICINAE Latreille, 1819
 Tribus ANTHICINI Latreille, 1819
 Genus *NITORUS* Telnov, 2007

Remark. The specimen considered here was assigned to the genus *Nitorus* within the tribe Anthicini, based on the following morphological characters: (1) mesosternum simple, laterally curved to the mesocoxal cavities, (2) mesocoxal cavities not isolated from mesepisterna, (3) lateral margins of mesosternum nearly straight, (4) mesepisterna without fringe of setae and glossy, (5) elytra with distinct postbasal transverse impression and (6) dorsal body smooth, glossy and sparsely pubescent.

Nitorus succinius sp. nov.
 Figures 1.1–2, 2.1–4

zoobank.org/6104A725-3B18-405C-B036-7016A9B52484

Type material. Holotype: female ID “SDEI Coleoptera # 301526” [CCHH]: beetle inclusion in a small amber piece embedded in a block of GTS-polyester resin with dimensions 16×7×4 mm, adult female with exposed last visible ventrites. Tarsomeres 2–4 of right metatarsus are missing. No syninclusions present. Specimen provided with two additional printed labels: “HOLOTYPUS” [label red, black framed] and “NITORUS succinius sp. nov. det. D.Telnov and A.Bukejs, 2018”.

Type stratum. Baltic amber, Mid-Eocene to Upper Eocene.

Type locality. Yantarny settlement (formerly Palmnicken), Sambian (Samland) Peninsula, Kaliningrad Region, Russia.

Derivatio nominis. This first fossil representative of the genus *Nitorus* named from Latin “succinius” [amber].

Differential diagnosis. Since no other fossil *Nitorus* are presently known, this new species can be compared with extant taxa only. Few extant *Nitorus* share similar body colouration (uniformly pale forebody, uniformly dark brown elytra) with *N. succinius* sp. nov. *Nitorus acuticollis* (Krekich-Strassoldo, 1914) (E India) and *N. latissimus* (Pic, 1907) (“India” without exact locality) both have dor-

sal forebody densely punctured, opaque (sparsely punctured and smooth in *N. succinius* sp. nov.) and elytra are less strongly punctured in basal half in these species (basal half of elytra covered with dense and deep punctures in *N. succinius* sp. nov.). *Nitorus sensitivus* (Krekich-Strassoldo, 1928) (N India, Nepal) has much longer (extending to mid-length of elytra) and slender antennae, tapered head base (broadly rounded in *N. succinius* sp. nov.), disc of pronotum with very large, irregular, coarse but shallow punctures in basal half (punctures are sparse, deep and not coarse in *N. succinius* sp. nov.). Other extant *Nitorus* species with pale forebody and dark coloured elytra all have pale elytral markings or transverse hair bands. Also in generally paler coloured species (like orange to pale castaneous Indian *N. brevitarsis* (Krekich-Strassoldo, 1931) or Oriental *N. lictor* (Fairmaire, 1896)) a paler (white or almost white) transverse elytral band is present in postbasal transverse impression.

Description. Measurements: Total body length about 2.8 mm [exposed last visible ventrites excluded], maximum combined width across middle of elytra 0.9 mm. Head about 0.6 mm long [not possible to take exact measurements due to the position of head], across eyes 1.03 mm wide, pronotum 0.5 mm long, maximum width 0.9 mm, minimum width in constriction area 0.65 mm, elytra 1.7 mm long, maximum width 0.9 mm.

Colouration: Forebody pale orange with pale castaneous antennae. Elytra dark brown. Legs orange to pale castaneous, pro- and mesocoxae pale orange. Ventral side pale castaneous.

Head dorsally and ventrally smooth, with medium-sized, slightly prominent eyes. Head base very broadly rounded posterior to eyes. Dorsal surface deeply minutely punctate, intervening spaces smooth, about 3–4× as large as punctures. Pubescence sparse, very inconspicuous, appressed. Antennae extending to the postbasal transverse impression of elytra; antennomere 3 slender, 1.3× as long as antennomere 2; antennomeres 3–7 elongate, thickened distally; antennomeres 8–10 shortened, cylindrical and strongly thickened than preceding ones; terminal antennomere in female elongate, broad, tapered distally, about 1.8–2× as long as penultimate antennomere. Terminal maxillary palpomere fusiform, medially widened on inner margin.

Pronotum smooth dorsally, lateral and anterior margins evenly rounded, with strong lateral postmedian constriction. Prebasal area cylindrical, distinctly narrower than anterior portion of pronotum.



FIGURE 1. *Nitorus succinius* sp. nov., holotype female, habitus in dorsal (1), and ventral (2) views. Scale bars equal 1 mm.

Anterior rim narrow. Antebasal sulcus broad. Punctures on disc denser, larger (and of different sizes) and deeper than on head, intervening spaces smooth, about as large as to 2× as large as punctures. Punctures on lateral margins are minute, with wider intervening spaces. Antebasal sulcus area densely, largely, almost coarsely punctured. Pubescence longer and denser than on head, appressed, directed posteriorly. Scutellar shield small, rounded apically, covered with long and dense golden pubescence all along its apical and (partly) lateral margins.

Elytra elongate, smooth and shiny, slightly widened in the middle, with shallow but distinct postbasal transverse impression. Punctures very large, deep and dense in basal half, becoming significantly smaller and sparser in apical half. Inter-

vening spaces smaller than to as large as punctures in basal half, but becoming 2–3× as large as those in apical half of elytra. Each puncture bearing long, appressed and curved seta. A few scattered rather short erect tactile setae in basal half and on sides of elytra. Sutural striae absent. Metathoracic wings apparently fully developed (humeri well developed).

Underside of the body smooth. Metasternum and abdominal ventrites evenly pubescent, setae appressed. Female morphological tergite VII and sternite VII both broadly rounded and densely setose apically.

Legs long and slender, smooth, finely and densely appressedly pubescent. Penultimate tarsomeres narrow, indistinctly bilobate. Claws simple, without appendages or teeth. Female basal

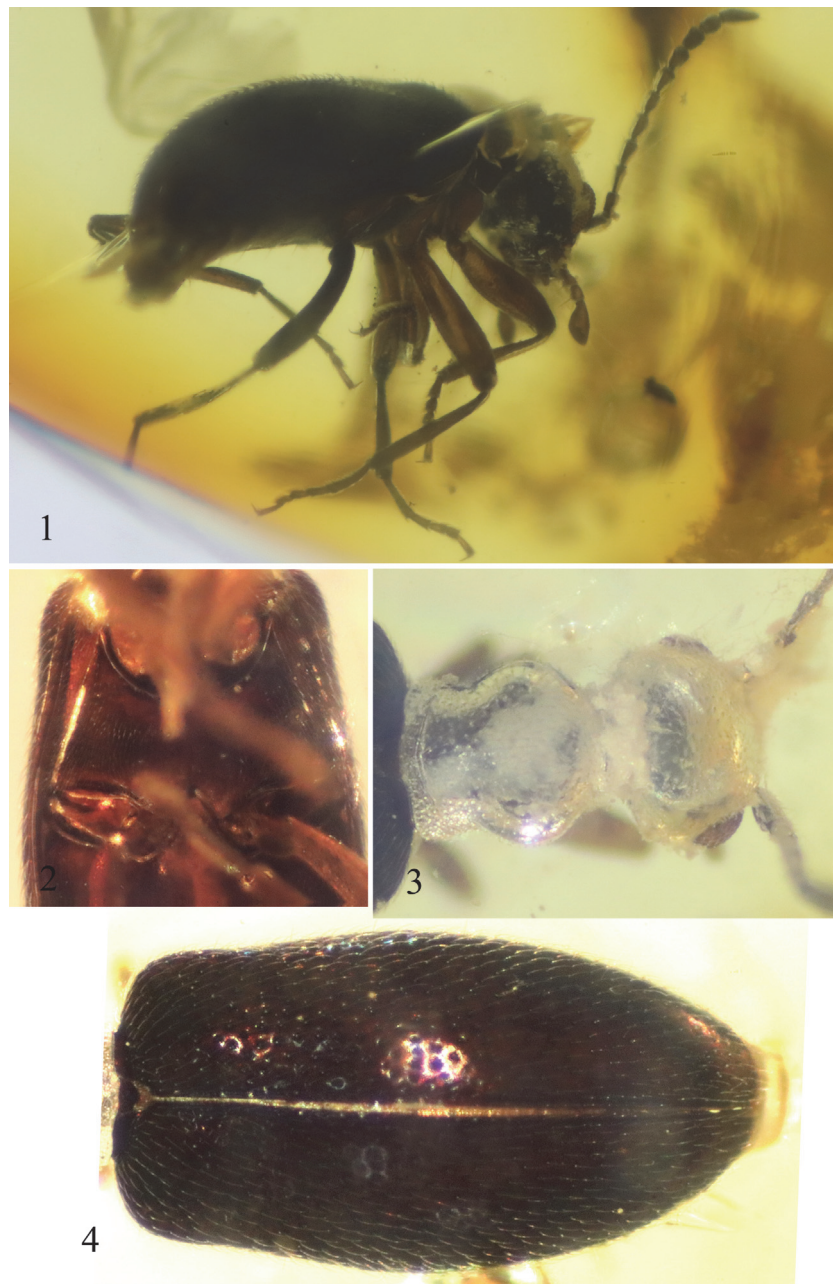


FIGURE 2. *Nitorus succinius* sp. nov., holotype female, habitus in latero-caudal view (1), thorax in ventral view (2), details of forebody in dorsal view (3), and elytra in dorsal view (4). Not reproduced to the same scale. Total body length is 2.8 mm.

metatarsomere as long as combined length of remaining tarsomeres.

Sexual dimorphism. Male is unknown.

Remarks. The present distribution of *Nitorus* is confined to southern and eastern Palaearctic (Central Asia, Far East of Russia, Japanese Archipelago, Korean Peninsula, China, and Himalaya), whole Afrotropical (inclusive Madagascar) and Oriental regions (inclusive insular systems of Greater

Sundas and the Philippines). *Nitorus* is absent from the New World fauna. Its presence in Australia and on New Guinea is not yet confirmed. In Western Palaearctic *Nitorus* is known from southern boundaries, e.g., Egypt and Mauritania (*N. unifasciatus unifasciatus* (Desbrochers des Loges, 1875)). In Central and southern Asia several taxa present nowadays, namely *N. apricans apricans* (Krekich-Strassoldo, 1931) (Afghanistan, Paki-

stan), *N. apricans lindbergi* (Bonadona, 1964) (Afghanistan), *N. petri* (Pic, 1894) (Tian Shan Mountains, Kazakhstan, Turkmenistan), *N. suasum* Telnov, 2010 (Afghanistan), and *N. unifasciatus unifasciatus* (unconfirmed Iran record, see Telnov and Ghahari, 2018). The formerly wider distribution of *Nitorus* correlates with worldwide warmer and more uniform climate of Eocene.

Subfamily STEROPINAE Jacquelin du Val, 1863
Genus *Steropes* Steven, 1806

Remarks. The specimen considered here was assigned to the genus *Steropes* within the subfamily Steropinae on the basis of the following morphological features: (1) procoxal cavities open internally and (presumably, not visible in the holotype) externally, (2) mesoventrite triangular, (3) mesoventrite not completely fused with mesepisterna, suture present in-between, (4) pronotum dorsally without anterior rim, (5) pronotum with complete antebasal sulcus which ends in a pit at some distance from procoxa, (6) neck one-third of head width, (7) palpomeres 2-3 slightly widened and rounded distally, (8) terminal maxillary palpomere scalene-triangular, (9) procoxa elongate, truncate fusiform, (10) apical three antennomeres greatly lengthened, antennomeres 4-8 distally rounded, and (11) tarsal claw with spinose ventral appendage.

Steropes eleticinoides sp. nov.
Figures 3.1–2, 4.1–2

zoobank.org/C6C19F5C-2F14-4121-85D9-E8700D34AA72

Type material. Holotype: female ID “LDM G 404/78” [LDM]: beetle inclusion in a moderate large amber piece of irregular form with dimensions about 40×22×6 mm, adult female with exposed last visible ventrites. Syninclusions are represented by one fungus gnat (Insecta: Diptera: Sciaridae, Gen. sp.), one springtail (Collembola Fam. and Gen. sp.) and four fagacean stellate hairs. Specimen provided with two additional printed labels: “HOLOTYPUS” [red label with black frame] and “*STEROPES eleticinoides* sp. nov. det. D.Telnov and A.Bukejs, 2018”.

Type stratum. Baltic amber, Mid-Eocene to Upper Eocene.

Type locality. Yantarny settlement (formerly Palmnicken), Sambian (Samland) Peninsula, Kaliningrad Region, Russia.

Derivatio nominis. Since a) this is the second known anthicid species with ventral spines (strongly elongate lobes) on the tarsal claws and b) Steropinae are phylogenetically and morphologically similar to Eleticinae Wellman, 1910 of Meloi-

dae (Chandler, 2010), which are known to have spinose tarsal claws (Bologna et al., 2010; Chandler, 2010), this new species is named to indicate its similarity with the Eleticinae subfamily of blister beetles.

Differential diagnosis. This is the only known *Steropes* species and the second taxon among the Steropinae (see also original description of *Australosteropes* in Telnov (2018)) with peculiar, ventrally spinose tarsal claws. Among other tenebrionoid Coleoptera spinose claws currently only known in Meloidae and Stenotrachelidae (Ivie, 2002; Bologna et al., 2010; Lawrence and Ślipiński, 2010).

Description. Measurements: Total body length about 6 mm [exposed last visible ventrites excluded]. Head about 1.15 mm long [not possible to take exact measurements due to the position of head], across eyes 1.03 mm wide, pronotum 1.2 mm long, elytra 3.8 mm long, maximum combined width about 1.3–1.5 mm [impossible to take exact measurements due to the position of the specimen].

Colouration: Dorsum and venter uniformly pale brown, head darker brown with reddish mouthparts. Legs and palps yellow-brown.

Head dorsally subopaque with large and strongly prominent eyes. Eye shortly notched on anterior margin at the insertion of antenna. Head base broadly rounded posterior to eyes. Broad shallow transverse impression at place of frontoclypeal suture. Frons narrow between eyes; in female minimum interocular distance almost half of eye diameter, slightly greater than length of antennomere 1. Dorsal surface deeply punctate, intervening spaces about as large as, to smaller than punctures. Pubescence sparse, inconspicuous, suberect, directed anteriorly. Several longer and erect setae present on vertex and along inner margin of eyes. Antennae extending towards basal third of elytra; antennomeres 3–7 elongate, slightly thickened distally, antennomere 3 the longest; female antennomere 8 shortened, 9–11 greatly lengthened and thickened, antennomeres 9–10 widened distally; female terminal antennomere strongly elongate, broad, tapered distally, about 1.1× as long as combined length of two preceding antennomeres; combined length of antennomeres 1–8 and 9–10 nearly equal [exact measuring not possible due to the position of the specimen]. Maxillary palpomeres 2-3 slightly widened distally. Terminal maxillary palpomere scalene triangular, tapered distally. Neck more than 1/3 of head width, densely and coarsely punctured antennomere 7

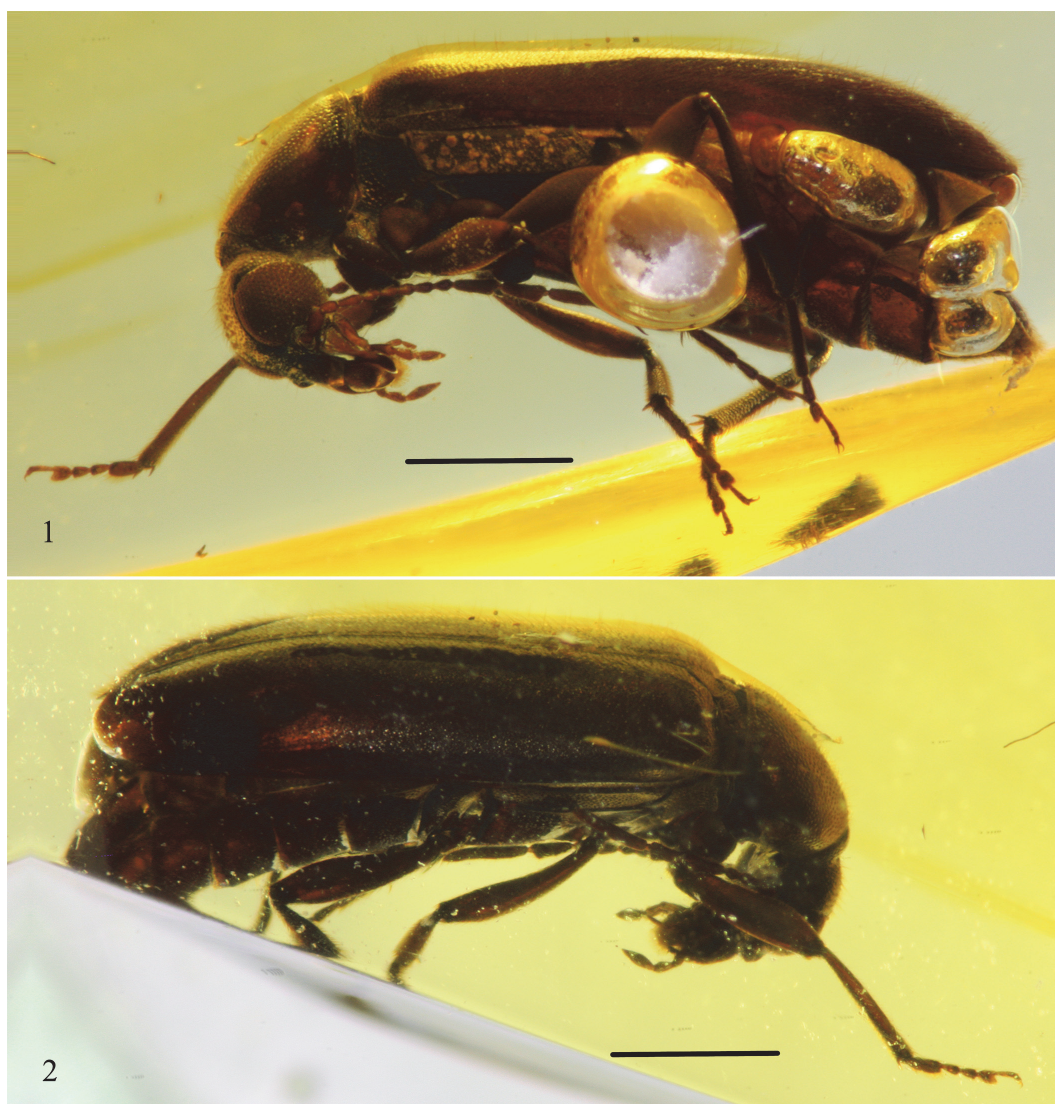


FIGURE 3. *Steropes eleticinoides* sp. nov., holotype female, habitus in left lateral (1), and right dorso-lateral (2) views. Scale bars equal 1 mm.

about as long as wide, 9–10 transverse and shorter than preceding ones; terminal antennomere elongate, asymmetrically triangular, tapered distally, as long as antennomeres 9–10 combined. Terminal maxillary palpomere fusiform, medially angulate on inner margin.

Pronotum smooth dorsally, slightly constricted laterally towards narrower base, its lateral and anterior margins evenly rounded. Anterior rim lacking dorsally, well-defined laterally and ventrally. Pronotal base dorsally with a complete basal bead and antebasal sulcus originating at lateral fovea. Lateral pronotal fovea conspicuous, forming deep and narrow internally closed incision which ends shortly in a pit on both sides. Punctures dense and

uniform (inclusive those of antebasal sulcus area), intervening spaces smooth, about as large as to 2× as large as punctures. Pubescence dense, inconspicuous, suberect, directed posteriorly. Scutellar shield not visible.

Elytra elongate, smooth and shiny, slightly widened around mid-length, with postbasal transverse impression hardly indicated. Humeri obsolete, rounded. Punctures large, deep and dense in basal half, becoming smaller, shallower and sparser in apical half. Punctures arranged into three groups of irregular longitudinal striae on each elytron: the inner one, sutural, initially consists of two irregular rows of punctures of which internal one discontinues in basal third but the outer

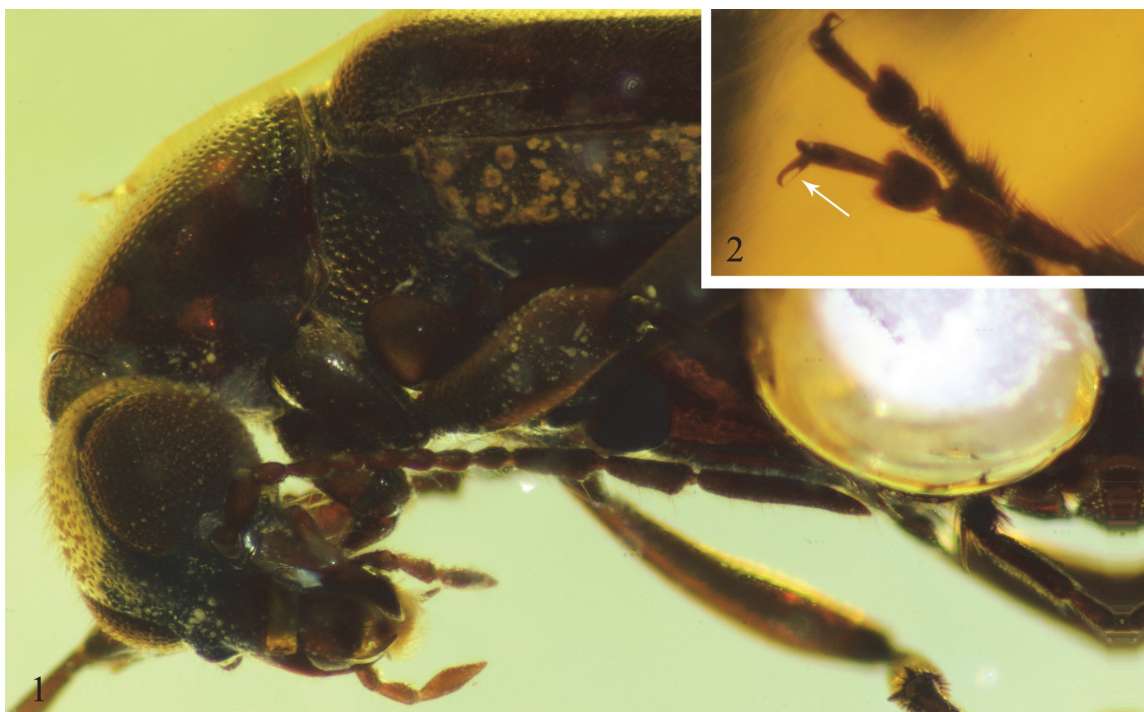


FIGURE 4. *Steropes eleticinoides* sp. nov., holotype female, details of forebody in left lateral view (1), meso- and metatarsus (2), arrow indicates one of ventral blades. Not reproduced to the same scale. Total body length is about 6 mm.

adjoins the suture and continues towards elytral apex; the median one, consists of three irregular rows of punctures becoming irregular postmedium and discontinue in apical third; the outer one, consists of at least four irregular rows of punctures, almost reaching elytral apex. There are narrow unpunctured areas between these three puncture groups (Figure 5.1). Intervening spaces smaller than up to as large as punctures in basal half but becoming larger than those in apical half of elytra. Pubescence yellowish, longer and denser than on forebody (but still sparse), appressed, directed posteriorly. A few scattered long erect tactile setae on disc and sides of elytra.

Metasternum and abdominal ventrites smooth, minutely punctate and with inconspicuous pubescence. Procoxal cavities open externally (presumably also internally). Mesoventrite triangular, mesepisterna almost meeting in front of it [not fully visible because of the position of specimen]. Mesosternum not fused with mesepisterna, with suture present in-between. Metacoxae narrowly separated by acute intercoxal projection. Female morphological tergite VII and sternite VII both broadly rounded on apical margin.

Legs long and slender. Femora broad, finely, sparsely inconspicuously pubescent. Tibiae cov-

ered with long setae which become denser in distal half. Tibial spurs paired, acute; spurs each with 5–6 long microspines on each side. Penultimate tarsomeres widened, indistinctly bilobate. Claws long, curved in distal half and each with a long acute ventral spine of about two-third of claw length. Female basal metatarsomere almost as long as combined length of other tarsomeres.

Sexual dimorphism. Male is unknown.

Remarks. The present distribution of Steropinae is Holarctic (Chandler, 2010), Oriental and Australian (Telnov, 2018). *Steropes* inhabit arid and semiarid areas of the Palaeartic, Nearctic and NE Afrotropical (Arabian Peninsula) regions (Chandler et al., 2008), with single species each in the Oriental (Telnov, 2006) and Australian (Telnov, 2018) regions. Extant *Steropes*, except *S. hercules* Telnov, 2006 from rainforests of Vietnam, seem to avoid forested areas and nowadays occur mostly in open and semi-open landscape. But the Eocene record of *S. eleticinoides* sp.nov. is apparently from ancient pine tree forest. In Western Palaeartic, currently northernmost records of this genus are from Romania, Moldova and Ukraine. The formerly wider distribution of *Steropes* correlate with worldwide warmer and uniform climate of Eocene.

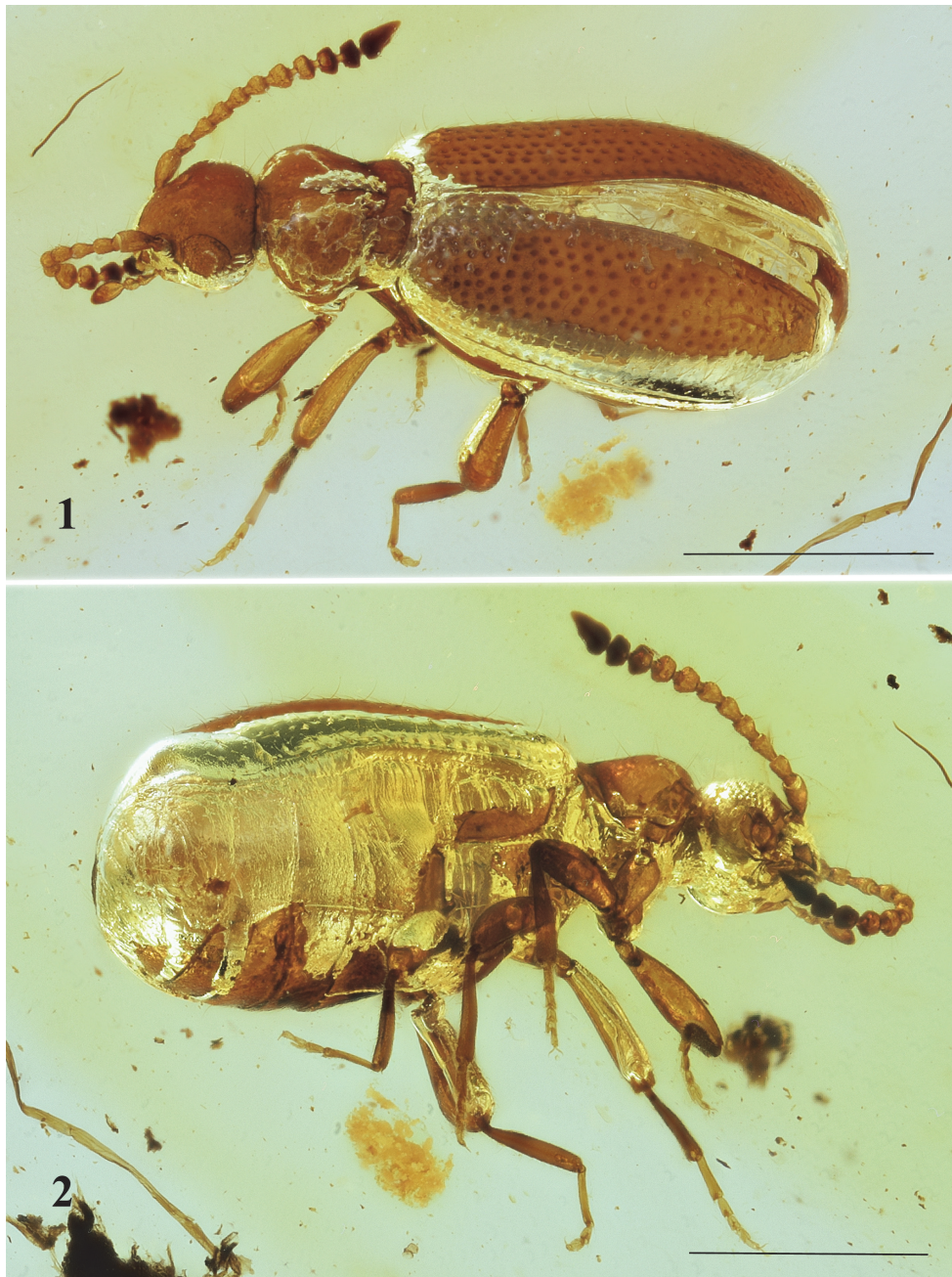


FIGURE 5. *Tomoderus saecularis* sp. nov., holotype, habitus in dorsal (1), and ventral (2) views. Scale bars equal 1 mm.

Subfamily Tomoderinae Bonadona, 1961
Genus *Tomoderus* LaFerté-Sénéctère, 1849

Remarks. The specimen considered here was assigned to the genus *Tomoderus* within the Tomoderinae based on the following morphological characters: (1) pronotum lacking apical rim or collar, (2) distinct lateral antebasal constriction present on pronotum, (3) metacoxae widely separated

and (4) intercoxal process of 1st abdominal ventrite broadly rounded.

Tomoderus saecularis sp. nov.

Figure 5.1–2

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Type material. Holotype: sex unknown, ID "GPIH no. 4958, coll. Gröhn no. 8588" [GPIH]: beetle inclusion in a small amber piece of trapezoidal shape with dimensions 15×10×5 mm, adult speci-

men with all body parts present. Numerous syninclusions present: pieces of soil and plant material. Specimen provided with two printed labels: "HOLOTYPUS" [label red, black framed] and "TOMODERUS saecularis sp. nov. det. D.Telnov and A.Bukejs, 2018".

Type stratum. Baltic amber, Mid-Eocene to Upper Eocene.

Type locality. Yantarny settlement (formerly Palmnicken), Sambian (Samland) Peninsula, Kaliningrad Region, Russia.

Derivatio nominis. This species named from Latin "saecularis" [century, 100 years old] in honour of the 100th anniversary of the Republic of Latvia (1918-2018), where Baltic amber deposits are also known.

Differential diagnosis. Known fossil congeners (*T. balticus* Telnov, 2012a and *T. longelytratus* Telnov, 2013) are both larger and have differently punctured elytra and pronotum. Among extant taxa *T. saecularis* sp. nov. is peculiar primarily in elytral punctures (which are aligned into three groups of irregular punctural rows on each elytron) in combination with roughly punctured pronotal disc and presence of median longitudinal impression on anterior lobe of pronotum, remarkably large eyes and short tempora.

Description. Measurements: Total body length about 2.8 mm [exposed last visible ventrites excluded], maximum combined width across middle of elytra 0.9 mm. Head about 0.5 mm long [not possible to take exact measurements due to the position of head], across eyes about 0.45 mm wide [not possible to take exact measurements due to the position of head], pronotum 0.5 mm long, maximum width about 0.55 mm [not possible to take exact measurements due to the position of pronotum], minimum width at constriction about 0.4 mm [not possible to take exact measurements due to the position of pronotum], elytra 1.3 mm long, maximum combined width about 0.8 mm [not possible to take exact measurements due to the position of elytra].

Colouration: Uniformly brown with paler (yellowish to yellow-brown) legs, maxillary palps and antennomeres 1–9; three terminal antennomeres darkened.

Head dorsally and ventrally smooth. Eyes large, prominent, almost circular, truncate opposite the insertions of antennae. Tempora much shorter than length of an eye, temporal angles broadly rounded. Head base truncate posterior to eyes. Dorsal surface with rather large and very shallow punctures, intervening spaces smooth, up to as

large as punctures. Pubescence very sparse and inconspicuous; few very long erect tactile setae present at base and on tempora. Antennae extending to base of elytra; basal antennomere long, rugulose; antennomere 3 slender, 1.2× as long as antennomere 2; antennomeres 3–6 thickened distally; antennomeres 7 about as long as wide, 9–10 transverse and shorter than preceding ones; terminal antennomere elongate, asymmetrically triangular, tapered distally, as long as antennomeres 9–10 combined. Terminal maxillary palpomere fusiform, medially widened on inner margin.

Pronotum smooth dorsally, wider than head, with strong lateral postmedian constriction, truncate on anterior, evenly rounded on lateral margins. Anterior rim and antebasal sulcus not present dorsally. Posterior lobe of pronotum distinctly narrower than anterior. Anterior lobe with a track of longitudinal median impression, that reaches the postmedian lateral constriction. Punctures on disc of anterior lobe large and dense but shallow, intervening spaces smooth, smaller than punctures; those punctures situated on lateral margins are minute, with wider intervening spaces. Lateral postmedian constriction dorsally largely, coarsely punctured. Pubescence short, sparse and subdecumbent with some long erect tactile setae present on sides and on disc. Scutellar shield transverse, densely punctured, truncate apically.

Elytra elongate, smooth and shiny, slightly widened around mid-length, with postbasal transverse impression hardly indicated. Humeri obsolete, rounded. Punctures large, deep and dense in basal half, becoming smaller, shallower and sparser in apical half. Punctures arranged into three groups of irregular longitudinal striae on each elytron: the first one, sutural, initially consists of two irregular rows of punctures of which internal one discontinues in basal third but the outer adjoins the suture and continues towards elytral apex; the median one, consists of three irregular rows of punctures becoming irregular postmedium and discontinues in apical third; external one, consists of at least four irregular rows of punctures, almost reaching elytral apices. There are narrow unpunctured areas between these three puncture groups (Figure 5.1). Intervening spaces smaller than up to as large as punctures in basal half but becoming larger than those in apical half of elytra. Pubescence yellowish, longer and denser than on forebody (but still sparse), appressed, directed posteriad. A few scattered long erect tactile setae on disc and sides of elytra.



FIGURE 6. “*Eurygenius*” *wickhami* Cockerell, holotype, habitus, dorsal view, in different light racurses (**1**, **2**) (photo courtesy: BMNH). Scale bars equal 1 mm.

Underside of the body smooth, glabrous. Metacoxae broadly separated.

Legs slender, smooth, finely and densely appressedly pubescent on femora, denser pubescent on tibiae. Penultimate tarsomeres narrow, deeply bilobate. Claws simple, without appendages or teeth, rather long. Basal metatarsomere slightly longer than combined length of remaining tarsomeres.

Sexual dimorphism. Unknown.

Systematic Changes

TENEBRIONOIDEA family incertae sedis
“Eurygenius” wickhami Cockerell, 1917 genus
 incertae sedis
 Figure 6.1–2

Cockerell, 1917 (new species, initially assigned to *Eurygenius* (Pedilidae s. lat.), Burmese amber, 99.7–94.3 Ma); Fletcher, 1920; Zherikhin, 1980; Spahr, 1981; Keilbach, 1982; Poinar, 1992; Ross, 1998; Ross and York, 2000; Kirejtshuk, 2002–2013; Kirejtshuk and Azar, 2008; Ross et al., 2010; Wang

and Zhang, 2011; Soriano et al., 2014; Peris et al., 2016 (in Pyrochroidae but without any comments on the placement); Guo et al., 2017; Kirejtshuk et al., 2019 (mentioned Eurygeniinae from Burmese amber but not species).

Remarks. *Eurygenius wickhami* was originally described by Cockerell (1917) as a member of Pedilidae. From the beginning the author was unsure about the placement of his new taxon, which follows from his comment: “It may go in *Eurygenius* as interpreted in the broader sense, though it may hereafter be treated as the type of a distinct genus” (Cockerell, 1917: 325). As a member of the “Pseudo-Anthicides”, *Eurygenius* LaFerté-Sénéctère, 1849 was initially placed in the Pedilidae until relatively recently, when Pedilinae were removed from the Anthicidae to Pyrochroidae by Young and Pollock (1991). Type of this genus is *Eurygenius reichei* LaFerté-Sénéctère, 1849 by monotypy. Presently, *Eurygenius* is a small genus of six New World species distributed from Brazil (where the type species coming from) to the southern United States (Telnov, unpublished data).

After studying the holotype (BMNH) it became evident this species is neither *Eurygenius* nor Eurygeniinae where it was assigned initially. The following basic features of Eurygeniinae are absent in this species: head base truncate or concave except in *Steriphodon* Abeille de Perrin, 1895 (head base either very broadly rounded in "*Eurygenius*" *wickhami*), mandible scooped with wide apex (mandible apice unidentate with tapered apex in "*Eurygenius*" *wickhami*), pronotum anteriorly with dorsal rim flanged (except strongly protruding in *Mitraelabrini* Abdullah, 1969) and ventral rim much narrower (pronotum without anterior dorsal rim in "*Eurygenius*" *wickhami*), antebasal sulcus of pronotum distinct (antebasal sulcus absent dorsally or very inconspicuous in "*Eurygenius*" *wickhami*), elytra coarsely and densely punctured (elytral punctures fine and sparse in "*Eurygenius*" *wickhami*). Moreover, morphological features as visible in "*Eurygenius*" *wickhami* holotype are not sufficient to classify this taxon as the Anthicidae. Considering similarities in external morphology (and phylogenetic relationship) between Mycteridae Blanchard, 1845, Pyrochroidae Latreille, 1807 and Anthicidae, the following characters are crucial to examine prior to assigning this taxon to any of families listed afore (Ivie, 2002; Young, 2005; Chandler, 2010; Pollock, 2010; Young and Pollock, 2010): (1) antebasal sulcus of pronotum extends / not extends laterally onto hypomeron; (2) prothoracic coxal cavities open externally and closed internally / open both externally and internally / procoxal cavities closed internally, open externally; (3) compound eyes conspicuously setose between facets / not setose; (4) metathoracic coxae nearly contiguous mesally / separated; (5) intercoxal process of abdominal ventrite 1 with margins diverging at angle less than 45° / more than 45°; (6) metacoxa extending laterally to body side, completely separating metepisternum and abdominal ventrite 1 / not reaching elytron or side of body, metepisternum and abdominal ventrite 1 in contact laterad metacoxa. These features are not visible in "*Eurygenius*" *wickhami* holotype. Therefore, this taxon cannot be certainly assigned to Anthicidae, Mycteridae, or Pyrochroidae. Until additional material of "*Eurygenius*" *wickhami* Cockerell, 1917 becomes available or technical progress will allow more detailed study of the available inclusion, based on aforementioned facts, we reject the original combination and propose a new placement for "*Eurygenius*" *wickhami* as a *Genus incertus* and *Familia incerta* within the superfamily Tenebrionidea Latreille, 1802.

Type material. Holotype *Eurygenius wickhami* Cockerell, 1917, sex unknown, ID "Swinhoe Collection, NHMUK PI In 19110" [BMNH]: beetle inclusion in a large amber piece of irregular form, adult specimen with metathoracic wings and tip of abdomen (tergite VII) partly exposed from under partly open elytra. The holotype specimen is in a thick slab of dark amber with numerous syninclusions (see the list and inclusion description in Ross and York, 2000), and a ventral view of this specimen is not available.

Type stratum. Burmese amber, Cretaceous.

Type locality. Hukawng Valley, Kachin State, N Burma (now Myanmar).

Re-description. We provide a supplemental description of this species (only dorsal view available, see comment above). Dorsal surface yellowish castaneous, antennomeres 4–11 darker than basal ones. Head smooth dorsally, slightly transverse. Frontoclypeal suture apparently absent. Compound eyes very large and strongly prominent, emarginate (Cockerell (1917: 324) describes the eyes as "apparently not emarginate", which is not correct) at insertions of antennae, occupying whole sides of the head. Minimum interocular distance half of the of eye diameter. Tempora absent. Head base subtruncate or very broadly rounded, with a short median notch. Mandible long and pointed, unidentate apically. Terminal maxillary palpomere elongate, not securiform (exact shape of maxillary palpomeres remains unknown due their position; Cockerell (1917: 324) describes the shape of terminal maxillary palpomere as "elongated, subtriangular", which is of little taxonomical use). Antennal insertions exposed, widely separated. Antenna 11-segmented, filiform, very long, extending over the postbasal transverse impression of elytra. Antennomeres elongate, finely and densely pubescent. Antennomere 3 about 1.3× as long as preceding one; antennomeres 4–8 slightly widened distally; antennomeres 9–10 shorter and distally stronger widened; terminal antennomere tapered, 1.6× as long as preceding one. Neck broad, almost half of the head width.

Pronotum smooth dorsally, about 1.1× as long as head, same width or wider than it (measured at present position of the inclusion), widest at anterior half, strongly constricted laterally at posterior third. Anterior margin rounded, posterior margin straight. Anterior dorsal rim absent. Antebasal sulcus absent dorsally or very inconspicuous. Dorsal sculpture not clearly visible, appears densely and straight longitudinally strigose under certain light conditions, but definitively sparsely punctate (at

least on disc) and not strigose (Cockerell (1917: 324) describes the pronotal sculpture as “consisting of irregular longitudinal grooves”, which is either a result of an optical illusion or structure of the inclusion resin over pronotum; similar but transverse “grooves” appear over basal third of pronotum). Dorsal pubescence inconspicuous, dense. Scutellar shield with broadly triangular posterior edge.

Elytra smooth dorsally, elongate, 2.4× as long as their maximum combined width and 1.5× as long as forebody (head and pronotum), slightly widened apically. Humeral angles widely rounded but distinct. Omoplates not indicated. Postbasal transverse impression shallow, present in basal third. Punctuation irregular, quite dense and shallow. Pubescence uniform, moderately long and dense, suberect (possible that elytral pubescence is complex with setae of two different lengths, but this is not evident in the holotype). Metathoracic wings fully developed.

Legs long and slender. Tibiae straight, densely pubescent. Tibial spurs paired at least of meso- and metatibiae (possible due to the position of the inclusion, only one protibial spur visible), thin, long, not pubescent. Penultimate tarsomeres widened, bilobed. Basal metatarsomere longer than metatarsomeres 2–4 combined. Claws with blunt basal tooth.

CUCUJIFORMIA family incertae sedis

Petratypus nigri Kaddumi, 2005

Kaddumi, 2005 (new genus and species, initially assigned to Cleridae, Jordanian amber, 112.6–99.7 Ma); Kolibáč and Huang, 2016 (moved to Anthicidae).

Remarks. The holotype of this species was not available for our study. In the original description it is clearly stated “All tarsi 5-segmented” (Kaddumi, 2005: 128). There is nothing said in the description about presence or absence of anterior rim and antebasal sulcus on pronotum, but in figure 132 the holotype is depicted without any of them. Each elytron is said to be provided with “... 9-10 longitudinal rows of small punctures”. Tarsal claws as depicted on figure 130 in the original description are basally denticulate. Kolibáč and Huang (2016) proposed new placement for this species in Anthicidae considering “... the shape of the antennomeres and structure of the tarsi”. This proposal should be considered poorly justified since none of significant features of the Anthicidae and its subfamilies were assessed by the aforementioned two authors.

When the type of *Petratypus nigri* Kaddumi, 2005 is re-examined, the missing features have to be described. Based on the original description, tarsal formula of 5-5-5 in particular (tarsal formula is 5-5-4 in the Anthicidae and other Tenebrion-oidea), we propose a new placement for this genus and species as a *Familia incerta* within the infraorder Cucujiformia Lameere, 1938.

New Fossil Record

Macratriinae tribe incertae sedis, genus sp.

Material examined. The examined specimen [ID “LDM G 337/35”] is labelled “MYANMAR Estado Cachin Valle Hukawng” / “MACRATRIINAE Tribe and Gen. sp. det. D.Telnov, 2018”.

One Burmese amber inclusion investigated during our study (kindly provided by F. Molino-Olmedo) contains a specimen of the Macratriinae. Unfortunately, due to the position of this specimen within amber piece and limited clearness of the amber, this specimen cannot be assigned to any of two Macratriinae tribes. Therefore, this species is not named and described here. Nevertheless, this is the oldest known Macratriinae record from Southeast Asia.

The following characters are recognizable on the specimen: eyes very large, round and strongly prominent, entire (not notched at insertions of antennae); tempora much shorter than diameter of an eye; head base rounded to subtruncate; head base shortly notched medially; antennae long with strongly lengthened three terminal antennomeres (terminal one is the longest) and shortened, distally angulate antennomeres 4–8; neck about 1/3 of head width; pronotum short and slightly transverse, anterior margin broadly rounded, laterally strongly constricted towards base, with narrow entire anterior rim and broad, deep antebasal sulcus; elytra elongate and parallel; tibial spurs paired; tibial spurs long, narrow and pointed, protarsi strongly widened; penultimate tarsomeres of all legs strongly widened and distinctly bilobate; tarsal claws simple.

The List of Fossil and Subfossil Records for Anthicidae and Ischaliidae

The list presented below (Table 1) is produced as a result of bibliographical analysis and/or material examination. For each taxon the following information is given: Taxon (name, author(s) and year of description), Holotype depository (see Materials and methods for abbreviations), References, Fossil type and/or Locality information (as specified in cited source), Epoch and Age (according to Beh-

TABLE 1. List of the fossil and subfossil Anthicidae and Ischaliidae records.

Taxon	References	Fossil Type and/ or Locality	Epoch	Age, Ma
Anthicidae Latreille, 1819	Kirejtshuk and Azar, 2013; Peris et al., 2016	Lebanese amber	Cretaceous	130–125.5
	Rasnitsyn and Ross, 2000	Burmese amber	Cretaceous	99.7–94.3
	Kirejtshuk and Nel, 2013	Oise amber: Oise Department (France)	Eocene	55.8–48.6
	Perkovsky et al., 2007, 2010	Rovno amber	Eocene	37.2–33.9
	Berendt, 1845; Menge, 1856: as "Notoxida"; Helm, 1886; Klebs, 1889, 1910; Handlirsch, 1907; Bachofen-Echt, 1949; Abdullah, 1964; Spahr, 1981; Hieke and Pietrzeniuk, 1984; Ritzkowski, 1990; Kulicka and Ślipiński, 1996; Weitschat and Wichard, 2002	Baltic amber	Eocene	37.2–33.9
	Poinar, 1992	Dominican amber	Miocene	20.4–13.6
	Poinar, 1992	Mexican amber	Miocene	20–15
	Schawaller, 1986	lithified, carbonaceous lime mudstone; Randeck Maar formation (Germany)	Miocene	16–13.7
	Bidashko et al., 1995	unlithified lignite and unlithified claystone: Astrakhan (Russian Federation)	Holocene	0.1–0.0
	Anthicinae Latreille, 1819	Kirejtshuk et al., 2019	Isle of Wight Insect Limestone (U.K.)	Late Eocene
Anthicini Latreille, 1819				
<i>Amblyderus</i> sp.	Klebs, 1910; Bachofen-Echt, 1949; Abdullah, 1964; Larsson, 1978; Spahr, 1981; Poinar, 1992; Kirejtshuk, 2002–2013	Baltic amber	Eocene	37.2–33.9
<i>Anthicus neli</i> Arillo et Ortuño, 1997 [MCNA] [(? = <i>Omonadus formicarius formicarius</i> (Goeze, 1777)]. None of features provided in the original description of this taxon are good enough to separate it from extant cosmopolitan <i>Omonadus formicarius formicarius</i> (Goeze, 1777). Considering the fact Hörnschemeyner et al. (2010) pointed on, in certain cases it is not possible to find any morphological features that distinguish the fossils from the extant species on base of morphological characters. We had not examined <i>Anthicus neli</i> holotype, therefore it is not impossible this taxon is conspecific with extant <i>O. formicarius</i> . Authors compared (Arillo and Ortuño, 1997: 295) their new species with <i>Omonadus floralis</i> (Linnaeus, 1758) which is not as similar to it as <i>O. formicarius formicarius</i> .	Arillo and Ortuño 1997; Kirejtshuk 2002–2013	lacustrine claystone: Izarra (Alava, Spain)	Miocene	23–16

TABLE 1 (continued).

Taxon	References	Fossil Type and/ or Locality	Epoch	Age, Ma
<i>Anthicus oustaleti</i> Telnov, 1999 (= <i>melancholicus</i> Oustalet, 1874 nec LaFerté-Sénéctère, 1849) [MHNM]	Oustalet, 1874; Telnov, 1999; Kirejtshuk, 2002-2013	lacustrine shale: Aix-en-Provence (France)	Eocene	28.4–23
<i>Anthicus sepultulus</i> Cockerell, 1926 [BMNH]	Cockerell, 1926, 1936; Kirejtshuk, 2002-2013	lacustrine: Maíz Gordo Formation (Argentina)	Palaeocene	66–55.8
<i>Anthicus</i> sp.	Hope, 1836; Berendt, 1845; Giebel, 1852, 1856a, 1856b; Motschulsky, 1856; Menge, 1856; Scudder, 1885, 1886, 1891; Handlirsch, 1907; Klebs, 1910; Bachofen-Echt, 1949; Abdullah, 1964; Larsson, 1978; Spahr, 1981; Poinar, 1992; Kirejtshuk, 2002-2013	Baltic amber	Eocene	37.2–33.9
<i>Anthicus</i> sp.	Kiselev and Nazarov, 2009	Oler Formation (Russian Federation)	Pleistocene	2.58–0.8
<i>Anthicus</i> sp.	Green et al., 2006	lacustrine; Hackney (United Kingdom)	Pleistocene	0.8 - 0.1
<i>Anthicus</i> sp.	Coope et al., 1961	lacustrine; Worcestershire (United Kingdom)	Holocene	0.1–0.0
<i>Anthicus</i> sp.	Kiselev and Nazarov, 2009	lacustrine; Russian Federation	Holocene	0.1 - 0.0
<i>Cyclodinus efficax</i> Kirejtshuk, 2019 in Kirejtshuk et al., 2019	Kirejtshuk et al., 2019	Isle of Wight Insect Limestone (U.K.)	Late Eocene	37.8-33.9
<i>Nitorus succinius</i> sp. nov. [CCHH]	present paper	Baltic amber	Eocene	37.2–33.9
Endomiini Bonadona, 1958				
<i>Endomia</i> sp. (= <i>Ochthenomus</i> Dejean, 1834)	Klebs, 1910: as <i>Ochthenomus</i> ; Bachofen-Echt, 1949; Abdullah, 1964; Larsson, 1978; Spahr, 1981; Poinar, 1992; Kirejtshuk, 2002-2013	Baltic amber	Eocene	37.2–33.9
Eurygeniinae LeConte, 1862				
Eurygeniini LeConte, 1862				
<i>Oisegenius</i> Kirejtshuk et Nel, 2008	Kirejtshuk and Nel, 2008, 2013; Kirejtshuk, 2002-2013;	Oise amber: Oise department (France)	Eocene	55.8–48.6
<i>Oisegenius antiquus</i> Kirejtshuk et Nel, 2008 [MNHN]	Kirejtshuk and Nel, 2008; Kirejtshuk, 2002-2013; Brasero et al., 2009; Nel and Brasero, 2010	Oise amber: Oise department (France)	Eocene	55.8–48.6
Lemodinae Lawrence et Britton, 1991				
<i>Lemodicarmeria olmedoae</i> Molino-Olmedo, 2017 [CMOM]. This species has general appearance of Tomoderinae. We had not studied the type and therefore follow the original placement.	Molino-Olmedo, 2017	Burmese amber	Cretaceous	99.7–94.3
Macraetriinae LeConte, 1862	present paper	Burmese amber	Cretaceous	99.7–94.3

TABLE 1 (continued).

Taxon	References	Fossil Type and/ or Locality	Epoch	Age, Ma
Camelomorphini Kirejtshuk, Azar et Telnov in Kirejtshuk and Azar, 2008. Most of authors who quoted this taxon ignored the fact the tribe Camelomorphini, genus <i>Camelomorpha</i> and species <i>Camelomorpha longicervix</i> was authored by Kirejtshuk, Azar et Telnov in Kirejtshuk and Azar, 2008 and not by Kirejtshuk et Azar	Kirejtshuk and Azar, 2008, 2013; Kirejtshuk, 2002-2013; Azar et al., 2010; Telnov, 2012b	Lebanese amber	Cretaceous	130–125.5
<i>Camelomorpha</i> Kirejtshuk, Azar et Telnov in Kirejtshuk and Azar, 2008	Kirejtshuk and Azar, 2008, 2013; Kirejtshuk, 2002-2013; Azar et al., 2010; Telnov, 2012b	Lebanese amber	Cretaceous	130–125.5
<i>Camelomorpha longicervix</i> Kirejtshuk, Azar et Telnov in Kirejtshuk and Azar, 2008 [MNHN]	Kirejtshuk and Azar, 2008, 2013; Kirejtshuk, 2002-2013; Penney, 2010; Telnov, 2012b; Soriano et al., 2014; Peris et al., 2016	Lebanese amber	Cretaceous	130–125.5
Macratriini LeConte, 1862				
<i>Macratria</i> Newman, 1838 (= <i>Protomacratia</i> Abdullah, 1964)	Abdullah, 1964, 1969, Telnov, 2012b	Baltic amber	Eocene	37.2–33.9
<i>Macratria alleni</i> Telnov, 2012 [LDM]	Telnov, 2012b; Alekseev, 2013	Baltic amber	Eocene	37.2–33.9
<i>Macratria appendiculata</i> (Abdullah, 1964) [BMNH]	Abdullah, 1964: as <i>Protomacratia</i> , 1975: as <i>Protomacratia</i> ; Larsson, 1978: as <i>Protomacratia</i> ; Spahr, 1981: as <i>Protomacratia</i> ; Kubisz, 2000: as <i>Protomacratia</i> ; Kirejtshuk, 2002-2013: as <i>Protomacratia</i> ; Telnov, 2012b; Alekseev, 2013	Baltic amber	Eocene	37.2–33.9
<i>Macratria gigantea</i> Wickham, 1910 [YPM]	Wickham, 1910; Kirejtshuk, 2002-2013; Telnov, 2011	lacustrine shale: Florissant, Colorado (USA)	Eocene	37.2–33.9
<i>Macratria succinia</i> Abdullah, 1965 [GPIH]	Abdullah, 1965, 1975; Larsson, 1978; Spahr, 1981; Kirejtshuk, 2002-2013: as <i>M. succinea</i> [sic!]; Telnov, 2011, 2012b; Alekseev, 2013: as <i>M. succinea</i> [sic!]	Baltic amber	Eocene	37.2–33.9
<i>Macratria tripunctata</i> (Abdullah, 1964) [BMNH]	Abdullah, 1964: as <i>Protomacratia</i> , 1975: <i>Protomacratia</i> ; Larsson 1978, as <i>Protomacratia</i> ; Spahr, 1981: as <i>Protomacratia</i> ; Kirejtshuk, 2002-2013: as <i>Protomacratia</i> ; Telnov, 2012b; Alekseev, 2013	Baltic amber	Eocene	37.2–33.9
<i>Macratria</i> sp.	Klebs, 1910: as <i>Macratria</i> [sic!]; Bachofen-Echt, 1949; Abdullah, 1964; Larsson, 1978; Spahr, 1981; Poinar, 1992; Kirejtshuk, 2002-2013; Telnov, 2012b; Alekseev, 2017	Baltic amber	Eocene	37.2–33.9
<i>tribus incertus</i> , genus sp.	present paper	Burmese amber	Cretaceous	99.7–94.3
Notoxinae Stephens, 1829				
<i>Notoxus</i> sp.	Hope, 1836; Helm, 1896; Handlirsch, 1907; Larsson, 1978; Spahr, 1981; Poinar, 1992; Kirejtshuk, 2002-2013	Baltic amber	Eocene	37.2–33.9

TABLE 1 (continued).

Taxon	References	Fossil Type and/ or Locality	Epoch	Age, Ma
Steropinae Jacquelin du Val, 1863				
<i>Steropes eleticinoides</i> sp. nov. [LDM]	present paper	Baltic amber	Eocene	37.2–33.9
<i>Steropes</i> sp.	Klebs, 1910; Abdullah, 1964; Larsson, 1978; Spahr, 1981; Poinar, 1992; Kirejtshuk, 2002- 2013	Baltic amber	Eocene	37.2–33.9
Tomoderinae Bonadona, 1961				
<i>Tomoderus balticus</i> Telnov, 2012 [LDM]	Telnov, 2012a; Alekseev, 2013	Baltic amber	Eocene	37.2–33.9
<i>Tomoderus longelytratus</i> Telnov, 2013 [LDM]	Telnov, 2013	Baltic amber	Eocene	37.2–33.9
<i>Tomoderus saecularis</i> sp. nov. [GPIH]	present paper	Baltic amber	Eocene	37.2–33.9
<i>Tomoderus</i> sp.	Klebs, 1910; Bachofen-Echt, 1949; Abdullah, 1964; Larsson, 1978; Spahr, 1981; Poinar, 1992; Kirejtshuk, 2002-2013; Telnov, 2012a, 2013; Alekseev, 2017	Baltic amber	Eocene	37.2–33.9
Ischaliidae Blair, 1920				
<i>Ischalia (Ischalia) youngi</i> Alekseev et Telnov, 2016 [CCHH]	Alekseev and Telnov, 2016	Baltic amber	Eocene	37.2–33.9
<i>Ischalia (Eupleurida) danieli</i> Alekseev et Bukejs, 2017 [GPIH]	Alekseev and Bukejs, 2017	Baltic amber	Eocene	37.2–33.9
<i>Ischalia</i> subg. <i>Eupleurida</i> LeConte, 1862	Alekseev, 2017	Baltic amber	Eocene	37.2–33.9
<i>Ischalia</i> subg. <i>Telnovia</i> Alekseev et Bukejs, 2017	Alekseev and Bukejs, 2017; Alekseev, 2017	Baltic amber	Eocene	37.2–33.9
<i>Ischalia (Telnovia) dohnaturris</i> Alekseev et Bukejs, 2017 [KAM]	Alekseev and Bukejs, 2017	Baltic amber	Eocene	37.2–33.9
<i>Ischalia</i> sp.	Alekseev, 2017	Baltic amber	Eocene	37.2–33.9

rensmeyer and Turner, 2013-2018). In total, three Ischaliidae species of one genus and three subgenera and 17 Anthicidae species of 12 genera belonging to seven subfamilies are known from fossil deposits.

DISCUSSION

Brief Analysis of Known Fossil Records

According to the summarised information (Table 1), fossil records are available for seven of eight Anthicidae subfamilies (88%). This information is detailed in Table 2. The oldest fossil representative of Anthicidae, *Camelomorpha longicervix* Kirejtshuk, Azar et Telnov (Macratriinae: Camelomorphini) was described from Earlier Cretaceous Lebanese amber (130.0–125.5 Ma), while the scarce fossil records of Ischaliidae come only from Upper Eocene Baltic amber (37.2–33.9 Ma).

At present, known fossil records of Anthicidae and Ischaliidae from are most numerous from

Eocene (Figure 7) and mostly originate from Baltic amber. The majority of these fossil records were published in the last two decades (Figure 8).

Biogeographic Analysis

The Ischaliidae, as well as subfamilies and tribes of the Anthicidae, have different distribution patterns in today's zoogeographical regions (this account doesn't includes two Chilean genera of uncertain placement, *Apotominus* Fairmaire et Germain, 1863 and *Heterolobus* Philippi in Philippi and Philippi, 1864 (see Chandler, 2010)). Most widespread and species rich are the Anthicinae (and Anthicini), which occur in all zoogeographical regions (Uhmann, 1976; Chandler, 2010). The Endomiini are restricted to Old World (only one species reaches Australia) as the Formicomini are (with one genus in Chile and several species in Australian and Papuan regions), while the Microhorini are known from the Palaearctic, Afrotropical and Oriental (except insular systems) regions. The

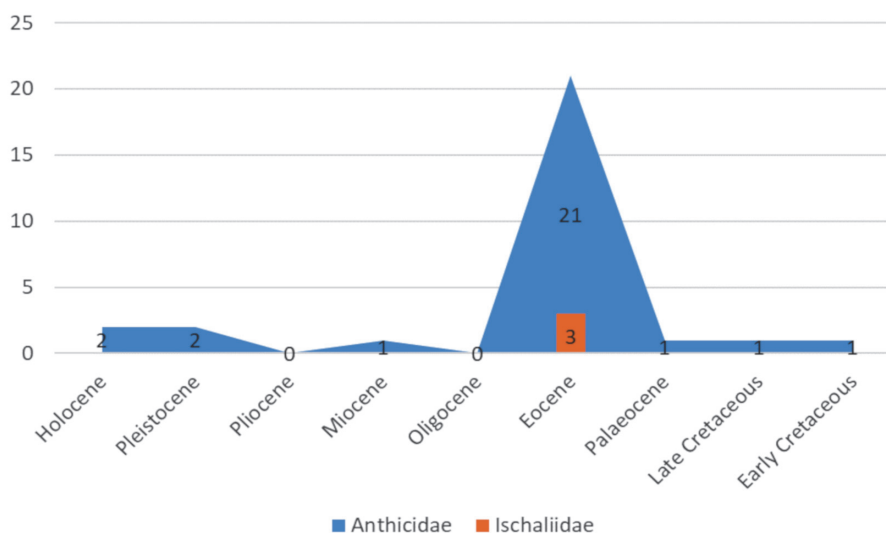
TABLE 2. Fossil records of higher rank Anthicidae taxa.

Subfamily	Tribe	Fossil records (Y / N)
Anthicinae	Anthicini Latreille, 1819	Y
	Endomiini Bonadona, 1958	Y
	Formicomini Bucciarelli, 1980	N
	Microhorini Bucciarelli, 1980	N
Copobaeninae	-	N
Eurygeniinae	Eurygeniini LeConte, 1862	Y
	Ictistygynini Borchmann, 1937	N
	Mitraelabrini Abdullah, 1969	N
Lemodinae	-	Y
Macratriinae	Camelomorphini Kirejtshuk, Azar et Telnov in Kirejtshuk and Azar, 2008	Y
	Macratriini LeConte, 1862	Y
	-	Y
Notoxinae	-	Y
Steropinae	-	Y
Tomoderinae	-	Y

monotypic Copobaeninae is a temperate South American group (Abdullah, 1969; Chandler, 2010). The subfamily Eurygeniinae is less diverse than the Anthicinae in terms of genera and species, but also reveals a cosmopolitan distribution (Chandler, 2010). Within Eurygeniinae, Eurygeniini are presently absent in Western Palaeartic, but known from here in fossil deposits (France). Representatives of Ictistygynini occur in Afrotropical, Australian and Neotropical regions, but the monotypic Mitraelabrini restricted to Chile. The Lemodinae

currently distributed in Australian and Papuan regions and Chile, with fossil record from Oriental Region. The Macratriinae (and Macratriini) are cosmopolitan, while Camelomorphini only known from Western Palaeartic (Lebanese amber, fossil). The Notoxinae and Tomoderinae are cosmopolitan, with just a few genera in each group. Extant Steropinae are of Holarctic, Oriental, and Australian (Telnov, 2018) distribution.

The present distribution of the Ischaliidae is restricted to mild climate areas of the Nearctic, E

**FIGURE 7.** Number of genera and species of the Anthicidae and Ischaliidae reported per epochs.

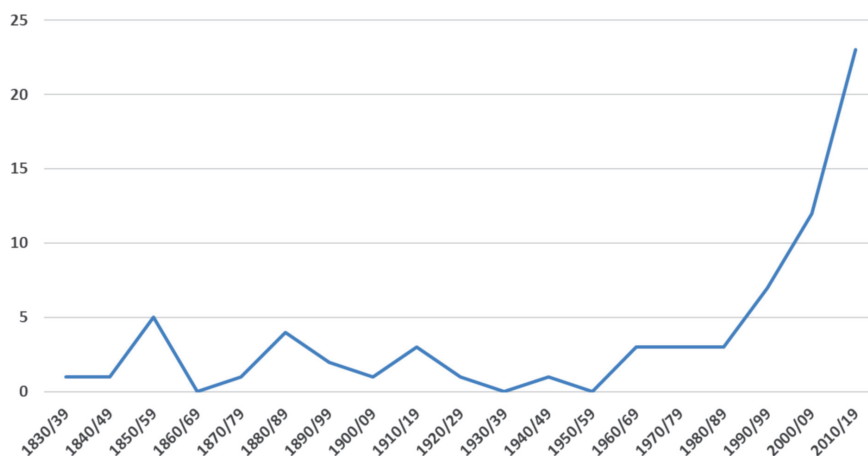


FIGURE 8. Trend of publications containing fossil records on Anthicidae or Ischaliidae.

and S Palaearctic (Himalaya, China except North and West, Far East of Russia, Kurile and Japanese archipelagos, Korean Peninsula, and Taiwan) and Oriental (E India, most of continental Southeast Asia, and Greater Sunda Islands) regions (Gusakov and Telnov, 2007; Young, 2011; Alekseev and Telnov, 2016).

Fossil records illustrate that both ant-like flower beetles and false fire-coloured beetles have fossil representatives occurring outside their contemporary distribution ranges. Several studies have already demonstrated that distribution of numerous extant arthropod taxa differs significantly from their fossil distribution ranges (e.g., Eskov, 1987; 1992). The Western Palaearctic is not in the present distribution for extant Eurygeniini and Ischaliidae, but the Eocene fossil records discussed above (Table 1) illustrate that it was part of their former biogeographical range. The Lemodiinae are not present in the Oriental Region today, but with Late Cretaceous record from this realm. Eskov (2002) already pointed out, that in certain cases, the extant distribution seems to be the relict of a formerly broader distribution, especially concerning arthropods and insects, in particular. The formerly wider distribution ranges of these taxa correlate well with worldwide warmer and uniform climate of Eocene (Frakes et al., 1992; Wedmann et al., 2011). Consequently, we want to emphasize that any interpretations of Coleoptera biogeography based only on extant taxa can be misleading, and therefore we strongly support similar conclusions provided earlier by Wedmann et al. (2011). The known historical biogeography of the Anthicidae and Ischaliidae is summarized in Table 3.

Discussion on Some Critical Features of the Anthicidae Subfamilies

As stated above and noted by earlier authors (e.g., Chandler, 2010), there has never been a phylogenetic analysis at the family level for Anthicidae. Abdullah (1969) presented some (18) of the critical characters and their states in the form of transformation series, dividing them into “primitive” and “derivative”. Nowadays these terms are out of methodology in phylogenetics and lack ground and explanations. We assessed selected morphological features (following Abdullah, 1967; 1969; Chandler, 2010; Telnov, 2018) from extant (text couplets below) and fossil taxa and highlighted minimum age of these features regarding data available from fossil material (Table 4). In the couplets below those features visible (available and fixed) both in fossil and extant taxa are marked with the dagger symbol (†) and enclosed into brackets, but those not yet fixed (e.g., not available or not visible due to the conditions of the fossil specimens) in fossil material but available in extant taxa are not specially marked.

Anthicinae. († head with frontoclypeal suture, which can be represented by an impression) or lacking in some subgroups; († eyes entire); († mandible apice bidentate) or unidentate; († neck narrow, smooth, 1/4 of head width or less); († antenna 11-segmented without modifications in most species); († terminal maxillary palpomere fusiform or triangular); († pronotum anteriorly with rim of equal width dorsally and ventrally); († ante-basal sulcus distinct); († pronotum lacking an apical flange); mesoventrite triangular to transverse; mesepisterna separated from ventrite by distinct suture; procoxal cavities closed externally or inter-

TABLE 3. Matrix of geographical distribution of extant and fossil Anthicidae and Ischaliidae, except incertae sedis groups (according to Chandler 2010; Lawrence et al. 2010). Legends: WP – Western Palaearctic, EP – Eastern Palaearctic, OR – Oriental, AT – Afrotropical and Madagascan, AU – Australian and Papuan, NA – Nearctic, NT – Neotropical, 0 – extant and fossil absence, 1 – extant presence and fossil absence, 2 – fossil presence and extant absence, 3 – fossil and extant presence.

High rank taxa	WP	EP	OR	AT	AU	NA	NT
Anthicidae Latreille, 1819	3	3	3	1	1	3	1
Anthicinae Anthicini Latreille, 1819	3	3	1	1	1	1	3
Anthicinae Endomiini Bonadona, 1958	3	1	1	1	1	0	0
Anthicinae Formicomini Bucciarelli, 1980	1	1	1	1	1	0	1
Anthicinae Microhorini Bucciarelli, 1980	1	1	1	1	0	0	0
Copobaeninae Abdullah, 1969	0	0	0	0	0	0	1
Eurygeniinae Eurygeniini LeConte, 1862	3	1	1	1	1	1	1
Eurygeniinae Ictistygynini Borchmann, 1937	0	0	0	1	1	0	1
Eurygeniinae Mitraelabrini Abdullah, 1969	0	0	0	0	0	0	1
Lemodinae Lawrence et Britton, 1991	0	0	2	0	1	0	1
Macratriinae Camelomorphini Kirejtshuk, Azar et Telnov in Kirejtshuk and Azar, 2008	2	0	0	0	0	0	0
Macratriinae Macratriini LeConte, 1862	3	1	1	1	1	1	1
Macratriinae <i>tribus incertus</i>	0	0	2	0	0	0	0
Notoxinae Stephens, 1829	3	1	1	1	1	1	1
Steropinae Jacquelin du Val, 1863	3	1	1	0	1	1	0
Tomoderinae Bonadona, 1961	3	1	1	1	1	1	1
Ischaliidae Blair, 1920	2	1	1	0	0	1	0

nally; († metacoxae moderately to widely separated by strongly divergent intercoxal projection); († elytra with confused punctures in most subgroups); († tibial spurs small); († tarsal claws simple); († male genitalia usually with phallobase and tegmen distinct); ovipositor coxite 1-segmented or incompletely 2-segmented.

Eurygeniinae. († head lacking frontoclypeal suture); mandible apice usually scooped, broad; eyes emarginate in certain genera; († terminal antennomere not lengthened) or strongly lengthened (in *Bactrocerus* LeConte, 1866); († terminal maxillary palpomere securiform, axeform) or cultriform; († neck broad, 1/3-1/2 of head width); († pronotum anteriorly with dorsal rim strongly protruding / flanged), with ventral rim much narrower (except in *Mitraelabrini* Abdullah, 1969); male metasternum spinous in certain subgroups; procoxal cavities closed externally or internally; metacoxae narrowly separated by acute intercoxal projection; metathoracic wings with radial and anal cells present in some subgroups; († elytra with confused punctures); († abdominal ventrites simple) or with appendages in males of some *Steriphodon* Abeille de Perrin, 1895; tibial spurs long and distinct; tibial

spurs microspinose or not; tibial spur formula 2-2-2; legs with ctenidia present; tarsal claws simple, appendiculate or with blunt basal tooth; ovipositor coxite incompletely 2-segmented.

Lemodinae. Head with frontoclypeal suture variably present, with transverse impression when lacking; († eyes entire); mandible apice bidentate; († antenna 11-) to 12-segmented without modifications; († neck broad, 1/3-1/2 of head width); pronotum with thin anterior rim; antebasal sulcus of pronotum only complete in *Zealanthicus* Werner et Chandler, 1995; procoxal cavities open externally and internally; mesoventrite triangular; mesoventrite discrimen weakly developed or absent; mesosternum and mesepisterna meet at the anterior edge of mesothorax; metacoxae moderately separated by divergent triangular intercoxal projection; († elytra with confused punctures) or arranged into rows; tibial spurs short; tibial spur formula 2-2-2; phallobase short and/or fused to tegmen.

Macratriinae. Peculiar within the Anthicidae primarily due to the mesoventrite fused to mesepisterna; († head lacking frontoclypeal suture); († mandible apice bidentate); († antenna 11-segmented); († 11th or 9-11th terminal antennomeres

TABLE 4. Matrix of selected critical characters of the Anthicidae and their minimum age. Only those critical characters visible and observed in fossil specimens are listed.

Period	Epoch	Age, Ma	Subfamily, tribe	Selected critical characters which appear in fossil taxa
Neogene	Pliocene	5.333-2.58	Anthicinae Anthicini	- [see below]
	Miocene	23.03-5.333	Anthicinae Anthicini	- [see below]
Paleogene	Oligocene	33.9-23.03	-	
	Eocene	56-33.9	Anthicinae	head with frontoclypeal suture or an impression at place of it; eyes entire; mandible apice uni- or bidentate; antenna 11-segmented; terminal maxillary palpomere fusiform or triangular; neck narrow, 1/4 of head width or less; pronotum anteriorly with rim of equal width dorsally and ventrally; ventrite separated from mesepisterna by distinct suture; metacoxae moderately to widely separated by strongly divergent intercoxal projection; elytra with irregular punctures in most subgroups; tibial spurs small; tarsal claws simple; male genitalia with phallobase and tegmen distinct.
			Anthicinae Anthicini	[same as above]
			Anthicinae Endomiini	dorsal setae thickened, scale-like; antennal insertions partly covered by protruding anterolateral margin of frons.
			Eurygeniinae Eurygeniini	head lacking frontoclypeal suture; eyes emarginate in certain subgroups; terminal antennomere not lengthened; terminal maxillary palpomere securiform, axiform or cultriform; neck broad, 1/3-1/2 of head width; pronotum anteriorly with dorsal rim strongly protruding (flanged); elytra irregularly punctate; tibial spurs distinct.
			Macratriinae Macratriini	- [same as subfamily, see below]
			Notoxinae	antenna 11-segmented; neck broad and short, 1/3-1/2 of head width; pronotum with prominent anterodorsal horn; pronotum with cervical notches lateral to neck; antebasal sulcus of pronotum distinct; elytra with irregular punctures; tibial spurs distinct.
			Steropinae	transverse impression at place of frontoclypeal suture; eyes notched anteriorly; maxillary palpomeres 2-3 rounded apically; terminal maxillary palpomere scalene triangular; antenna 11-segmented; three terminal antennomeres strongly lengthened; neck broad, 1/3-1/2 of head width; pronotum dorsally without anterior rim; pronotum lacking an apical flange; antebasal sulcus of pronotum complete; lateral fovea present on pronotum, ends in a pit distantly from procoxae; lateral fovea and pits glabrous; antebasal sulcus of pronotum complete; procoxal cavities open externally (presumably also internally; not visible); procoxa elongate and truncate fusiform; metacoxae nearly contiguous, narrowly separated by acute intercoxal projection; elytra confusedly punctate; tibial spurs distinct; tibial spur formula 2-2-2; tarsal claws with long ventral spine.

strongly lengthened and / or widened); († maxillary palpomeres 2-3 with angular mesal lobes); († terminal maxillary palpomere securiform, axiform) or cultriform; († neck narrow, 1/4 or less of head width); neck smooth; († pronotum with anterior collar of nearly equal width dorsally and ventrally); († antebasal sulcus distinct); († lateral fovea of pronotum extends anteroventrally at lateral margin towards procoxae towards a pit, which is situated

just dorsal of procoxa); († lateral fovea and pits obscured by setation); († mesoventrite triangular, fused to mesepisterna); († procoxa comparatively short, ovoid in lateral view); († procoxal rests contiguous when available); († metacoxae narrowly separated by acute intercoxal projection); († elytra at least with tracks of puncture rows in most species); († tibial spurs long and distinct); tibial spur

TABLE 4 (continued).

Period	Epoch	Age, Ma	Subfamily, tribe	Selected critical characters which appear in fossil taxa
			Tomoderinae	frontoclypeal suture variably present; antennae with a weak club of 3-4 terminal antennomeres; neck narrow, 1/3 of head width or less; pronotum with thin anterior rim; antebasal sulcus only indicated laterally near hypomerion; pronotum strongly constricted laterally postmedium; mesoventrite short, semicircular; mesosternum and mesepisterna meet behind the anterior edge of mesothorax; mesoventrite short, semicircular; metacoxae widely separated; metacoxae widely separated; tibial spurs very short to lacking.
			Ischaliidae	pronotal disc with median carina, sometimes extending beyond posterior edge, or with longitudinal groove; prosternum flat to moderately convex; prosternum in front of coxae shorter than shortest diameter of procoxal cavity; elytral disc always with more or less complete sutural, sublateral and epipleural costae and often with additional, shorter humeral costa.
	Palaeocene	66-56	-	
Cretaceous	Late	100-66	Lemodinae	antenna 11-segmented; neck broad, 1/3-1/2 of head width; elytra irregularly punctate.
	Early	145-100	Macratriinae	frontoclypeal suture not present; mandible apice bidentate; antenna 11-segmented; 1-3 terminal antennomeres strongly lengthened or widened; maxillary palpomeres 2-3 with angular mesal lobes; terminal maxillary palpomere securiform; neck narrow, 1/4 or less of head width; pronotum with anterior collar of equal width dorsally and ventrally; antebasal sulcus distinct; lateral fovea of pronotum extends anteroventrally at lateral margin towards procoxae in a pit, which is situated just dorsal of procoxa; lateral fovea and pits obscured by setation; mesoventrite triangular, fused to mesepisterna; procoxa comparatively short and ovoid; procoxal rests contiguous when available; metacoxae narrowly separated by acute intercoxal projection; elytra at least with tracks of puncture rows; tibial spurs long and distinct; tibial spur formula 2-2-2; tarsal claws deeply cleft; ovipositor coxite 2-segmented.
			Macratriinae Camelomorphini	characters not evaluated (no comparative extant taxa known)

formula 2-2-2); († tarsal claws deeply cleft); ovipositor coxite 2-segmented.

Notoxinae. († head with frontoclypeal suture); († eyes entire in most species); († mandible apice bidentate); († antenna 11-segmented, without modifications); neck broad and short, 1/3-1/2 of head width; († pronotum with prominent anterodorsal horn and cervical notches lateral to neck); († antebasal sulcus of pronotum distinct); mesoventrite triangular; procoxal cavities closed externally or internally; metacoxae moderately to widely separated by divergent triangular intercoxal projection; († elytra with confused punctures); († tibial spurs distinct); tibial spur formula 2-2-2; tarsal claws simple; male genitalia with phallobase and separate parameres; ovipositor coxite 1-segmented or incompletely 2-segmented.

Steropinae. Considered “primitive” member of the Anthicidae by earlier authors (e.g., Abdullah, 1969) this subfamily shares many characters with Pedilinae (Pyrochroidae) and Eleticinae (Meloidae) (Chandler, 2010; Telnov, 2018). († Frontoclypeal suture) variably present, († with transverse impression when lacking); († eyes shortly notched at insertions of antennae) or entire; († maxillary palpomeres 2-3 apically rounded and slightly widened); († terminal maxillary palpomere scalene triangular); († antenna 11-segmented); († three terminal antennomeres strongly lengthened); († neck broad, 1/3-1/2 of head width); († pronotum dorsally without anterior rim; antebasal sulcus of pronotum complete); († lateral fovea present on pronotum, but ends in a pit distantly from procoxae); († lateral fovea and pits glabrous); († pronotum lacking an apical flange); mesepisterna meeting or almost

meeting in front of mesosternite; heart-like sclerite separates procoxal rests; († procoxal cavities open externally) and internally; († procoxa elongate and truncate fusiform); († metacoxae nearly contiguous, narrowly separated by acute intercoxal projection); metathoracic wings with radial and anal cells present; elytra confusedly punctate; male elytra with a spot of very short and dense pubescence in basal third; († tibial spurs distinct); († tibial spur formula 2-2-2); († tibial spurs microspinose in some taxa); († tarsal claws each with long ventral spine) or shallowly toothed or medially lobed; aedeagus with distinct phallobase, penis, and separate parameres; ovipositor coxite 2-segmented.

Tomoderinae. († head with frontoclypeal suture variably present, with transverse impression when lacking); mandible apice bidentate; († antennae with a weak club of 3-4 terminal antennomeres); († neck narrow, 1/3 of head width or less); († pronotum with thin anterior rim); († antebasal sulcus only indicated laterally near hypomeron); († pronotum strongly constricted laterally postmedium), often notched in the constriction; anterior lobe denticu-

late or not on sides; († mesoventrite short, semicircular); († mesosternum and mesepisterna meet behind the anterior edge of mesothorax); († metacoxae widely separated); († tibial spurs very short to absent); male genitalia with phallobase usually fused to tegmen.

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