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First Piestine Rove Beetle in Eocene Baltic Amber (Coleoptera, Staphylinidae, Piestinae)

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ABSTRACT: Fossil piestine staphylinids are extremely rare, with only two definite species known to date. A new rove beetle genus and species, *Eopiestus groehni* Cai & Lü gen. & sp. nov., is described and figured based on an exceptionally well-preserved adult in Eocene Baltic amber from Yantarny in the Kaliningrad region of Russia. The species is the first fossil piestine discovered as an amber inclusion.

KEY WORDS: Coleoptera, Staphylinidae, Piestinae, Eocene, Baltic amber

With 111 species grouped in eight genera (7 extant and 1 extinct), the rove beetle subfamily Piestinae is a small group of Staphylinidae (Caron *et al.*, 2012; Yue *et al.*, 2016). Historically, Piestinae has been an ill-defined dumping ground for Staphylinidae defined by plesiomorphic characters, but the group has gradually been restricted in modern concept (Caron *et al.*, 2012; Grebennikov and Newton, 2012). Piestinae, even after the removal of the tribes Apateticini and Trigonurini as separate subfamilies by Newton and Thayer (1992) based on larval characters indicated in Newton (1982), has not been demonstrated as monophyletic (Grebennikov and Newton, 2012). Together with Scaphidiinae, Oxytelinae and Osoriinae, Piestinae is currently grouped in the newly restricted monophyletic Oxyteline Group of staphylinid subfamilies, but was shown to be paraphyletic with respect to Oxytelinae and Osoriinae (Grebennikov and Newton, 2012; McKenna *et al.*, 2015). A phylogenetic study of Piestinae and its relatives is underway (S. Bortoluzzi, unpublished data).

Piestinae currently includes seven extant genera (Herman, 2001): *Eupiestus* Kraatz, 23 species from the eastern Palearctic and Oriental regions; *Hypotelus* Erichson, 13 species from the Nearctic and Neotropical regions (Bortoluzzi *et al.*, 2017); *Parasiagonum* Steel, one species from New Zealand; *Prognathoides* Steel, 1 species from Australia; *Piestoneus* Sharp, 4 species from the eastern Palearctic region; *Piestus* Gravenhorst, 43 species from the Nearctic and Neotropical regions (Caron *et al.*, 2012); and *Siagonium* Kirby and Spence, 23 species from the Holarctic and northern Neotropical regions. The modern piestine genera are morphologically similar to members of the large subfamily Osoriinae, except for the fact that all members of the latter group lack abdominal paratergites (Newton *et al.*, 2000). Very little is known about the biology of Piestinae. Most species occur under the bark of dead trees (Brunke *et al.*, 2011; Caron *et al.*, 2012), although a minority of species

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Table 1. List of fossil occurrences of Piestinae, Osoriinae, and Oxytelinae of the world (J: Jurassic; K: Cretaceous; Pg: Paleogene; Ng: Neogene; Q: Quaternary; †, extinct genus). Classification of Oxytelinae after Khachikov (2012), age ranges after Cohen *et al.* (2013) except as noted.

Higher taxon	Species	Age (Ma)	Period-age	Locality
Piestinae	† <i>Paleosiagonium adaequatum</i> Yue <i>et al.</i> , 2016	~125	K-Aptian	Chaomidian, China
	† <i>Paleosiagonium brevelytrum</i> Yue, <i>et al.</i> , 2016	~125	K-Aptian	Chaomidian, China
	† <i>Eopiestus groehni</i> Cai & Lü, this study	37.2–33.9	Pg-Priabonian	Kaliningrad, Russia (amber)
Osoriinae	† <i>Mesallotrochus longiantennatus</i> Cai & Huang, 2015	~99	K-Cenomanian	Myanmar (amber)
Thoracophorini	† <i>Paleosorus cambayensis</i> Ortega-Blanco <i>et al.</i> , 2013	56.0–47.8	Pg-Ypresian	Gujarat, India (amber)
	† <i>Lispinomimus atavus</i> Irmler, 2003	20.4–16.0	Ng-Burdigalian	Dominican Republic (amber)
	<i>Nacaeus dominicanensis</i> Irmler, 2003	20.4–16.0	Ng-Burdigalian	Dominican Republic (amber)
	<i>Thoracophorus palaeobrevicristatus</i> Irmler, 2003	20.4–16.0	Ng-Burdigalian	Dominican Republic (amber)
	† <i>Sinolispinodes torosus</i> Zhang, 1989	20.4–16.0	Ng-Burdigalian	Shanwang, China
	<i>Bledius adamus</i> Scudder, 1878	45–53 (Smith <i>et al.</i> , 2008)	Pg (Eocene)	Green River, USA
	<i>Bledius faecorum</i> Scudder, 1900	45–53	Pg (Eocene)	Green River, USA
Oxytelinae	<i>Bledius morsei</i> Scudder, 1900	~34 (Evanoff <i>et al.</i> , 2001)	Pg (Eocene)	Florissant, USA
	<i>Bledius osborni</i> Scudder, 1900	~34	Pg (Eocene)	Florissant, USA
	<i>Bledius primitiarum</i> Scudder, 1900	~34	Pg (Eocene)	Florissant, USA
	<i>Bledius soli</i> Scudder, 1900	~34	Pg (Eocene)	Florissant, USA
	<i>Bledius speciosus</i> Heer, 1862	7.2–5.3	Ng-Messinian	Öningen, Germany
	<i>Bledius glaciatus</i> Scudder, 1890	2.6–0	Q	Scarboro, Canada
	† <i>Mesocoprophilus clavatus</i> Cai & Huang, 2013a	~125	K-Aptian	Chaomidian, China
	† <i>Sinoxytelus breviventer</i> Yue <i>et al.</i> , 2010	~125	K-Aptian	Chaomidian, China
	† <i>Sinoxytelus euglypheus</i> Yue <i>et al.</i> , 2010	~125	K-Aptian	Chaomidian, China
	† <i>Sinoxytelus longisetosus</i> Yue <i>et al.</i> , 2010	~125	K-Aptian	Chaomidian, China
Coprophilini	† <i>Sinoxytelus transbaicalicus</i> Cai <i>et al.</i> , 2013b	145.0–66.0	K	Urey, Russia
	† <i>Pseudanotylus archaicus</i> (Yue <i>et al.</i> , 2012); Cai & Huang, 2013b	~125	K-Aptian	Chaomidian, China
	† <i>Pliosyntomium schmidti</i> Korge, 1967	23.0–2.6	Ng	Willershausen, Germany

Table 1. Continued.

Higher taxon	Species	Age (Ma)	Period-age	Locality
Deleasterini	[†] <i>Protodeleaster glaber</i> Cai <i>et al.</i> , 2013a	~125	K-Aptian	Chaomidian, China
	<i>Deleaster grandiceps</i> Wickham, 1912	~34	Pg	Florissant, USA
Oxytelini	<i>Oxytelus pristinus</i> Scudder, 1876	50.3–46.2	Pg	Chagrin Valley, USA
	<i>Oxytelus subapterus</i> Wickham, 1913	~34	Pg	Florissant, USA
	<i>Platystethus archetypus</i> Scudder, 1900	~34	Pg	Florissant, USA
	<i>Platystethus carcareus</i> Scudder, 1900	~34	Pg	Florissant, USA
	<i>Oxytelus ominosus</i> Förster, 1891	33.9–28.4	Pg	Brunstatt, France
	<i>Oxytelus levis</i> Förster, 1891			
Thinobiini	[†] <i>Dolichoxenus newtoni</i> Engel & Chatzimanolis, 2009	20.4–16.0	Ng-Burdigalian	Dominican Republic (amber)
	<i>Oxytelus proaevus</i> Heer, 1862	7.2–5.3	Ng-Messinian	Önningen, Germany
Incertae sedis	[†] <i>Prajna tiamniaoae</i> Lü <i>et al.</i> , 2017	~99	K-Cenomanian	Myanmar (amber)
	[†] <i>Megalymma gigantea</i> Tikhomirova, 1980	139.8–132.9	K-Valanginian	Manlay, Mongolia
	[†] <i>Megalymma rohdendorfi</i> Tikhomirova, 1980	139.8–132.9	K-Valanginian	Manlay, Mongolia
	[†] <i>Mesoxytelus mandibularis</i> Tikhomirova, 1968	157.3–152.1	J-Kimmeridgian	Karatau-Mikhailovka
	[†] <i>Mesoxytelus parvus</i> Tikhomirova, 1968	157.3–152.1	J-Kimmeridgian	Karatau-Mikhailovka
	[†] <i>Morda mora</i> Ryvkin, 1990	145.0–66.0	K	Chita, Russia
	[†] <i>Turgaphloeus pubescens</i> Ryvkin, 1990	125.0–113.0	K-Aptian	Turga, Russia

occur in other decaying materials including leaf litter; a few have been found with ants or termites. Piestine beetles are nearly all saprophagous (Thayer, 2016), but some may be mycophagous on Ascomycotina (Crowson and Ellis, 1969). It is interesting that the mandibles of *Siagonium* and some other Piestinae possess invaginations similar to the fungal spore-transmitting mycangia of scolytine and cecidomyiid beetles (Crowson and Ellis, 1969).

Fossil piestines are extremely scarce. To date, only two definitive species are known: a genus with two species (*Paleosiagonium brevlytratum* Yue *et al.* and *P. adaequatum*) from the Lower Cretaceous Yixian Formation of Liaoning Province, China (Yue *et al.*, 2016). Caron *et al.* (2012) and Chatzimanolis *et al.* (2012) listed the Mesozoic genus *Abolescus* Tikhomirova, 1968 (Late Jurassic of Karatau, Kazakhstan) in Piestinae, following its original placement in a broader concept of this group where it was compared to *Trigonurus* Mulsant (Tikhomirova, 1968), but it is more plausibly placed in the extant subfamily Trigonurinae, as suggested by Grebennikov and Newton (2012). In contrast, the fossil records of Osoriinae (6 species in 6 genera, Cretaceous through Miocene) and Oxytelinae (31 species in 14 genera, Jurassic through Miocene) are more extensive, as detailed in Table 1.

In this paper, we describe the first fossil species of Piestinae from middle Eocene Baltic amber. The Baltic amber has yielded a great diversity of staphylinids (e.g., Schaufuss, 1890; Klebs, 1910; Larsson, 1978; Spahr, 1981; Pašník and Kubisz, 2002; Puthz, 2010), and representatives of 11 extant subfamilies have been recorded: Aleocharinae, Euaesthetinae, Omaliinae, Oxyphorinae, Paederinae, Proteininae, Pselaphinae, Scydmaeninae, Staphylininae, Steninae and Tachyporinae (see summary in Larsson, 1978; Puthz, 2006, 2008; Chatzmanolis and Engel, 2011).

Material and Methods

The new species described here is known from one adult individual preserved in a clear piece of Baltic amber. The specimen is deposited at the Centrum of Natural History (CeNak) of the University of Hamburg (formerly the Geologisch-Paläontologisches Institut und Museum der Universität Hamburg, GPIH), Germany. Both dorsal and ventral aspects of the beetle are clearly visible. The amber derives from the so-called “Blaue Erde” (blue earth) in Yantarny amber mine in the Kaliningrad region, Russia. A middle Eocene (Lutetian) age has been estimated for the Baltic amber bearing sediments by K-Ar dating (Ritzkowski, 1997), but palynological data supports a younger, upper Eocene (Priabonian) age for the Prussian Formation (Aleksandrova and Zaporozhets, 2008). Photomicrographs were taken using a Canon EOS 450D camera attached to a Zeiss compound microscope with lenses Zeiss Luminar 100 mm, 63 mm, and 40 mm. Measurements (in mm) were taken using a calibrated ocular micrometer in the microscope.

Systematic Paleontology

Order: Coleoptera Linnaeus, 1758
Family: Staphylinidae Latreille, 1802
Subfamily: Piestinae Erichson, 1839
Genus: *Eopiestus* Cai & Lü gen. nov.

Type species. *Eopiestus groehni* Cai & Lü sp. nov., here designated.

Etymology. The genus name is a combination of “*Eo-*” (from Eocene) and “*piestus*” (the extant genus *Piestus*); it is masculine in gender.

Diagnosis. Body small, slender and depressed; head small, with neck narrower than pronotum; antennae long, with each antenniferous longer than wide; pronotum with mid-longitudinal sulcus, prosternum elongate, with anterior margin convex; elytra elongate, slightly widened toward apex, without rows of punctures or striae, epipleural keels complete; legs relatively short, with protrochantins exposed, with femora much stronger than tibiae, with metafemora distinctly inflated; tarsi 5-segmented, metatarsomere 5 longer than 1–4 combined. Abdominal segments III–VII each with a single pair of paratergites, tergites without basolateral ridges; tergite VII longer than VI but less than 1.5 times as long.

Eopiestus groehni Cai & Lü sp. nov.
(Figs. 1, 2 and 4C)

Etymology. The specific epithet is a patronym formed from the surname of Mr. Carsten Gröhn, recognizing his support of this study.

Material. Holotype (sex uncertain): GPIH no. 4563, coll. Gröhn no. 4789; deposited at the Centrum of Natural History (CeNak) of the University of Hamburg (GPIH), Germany.

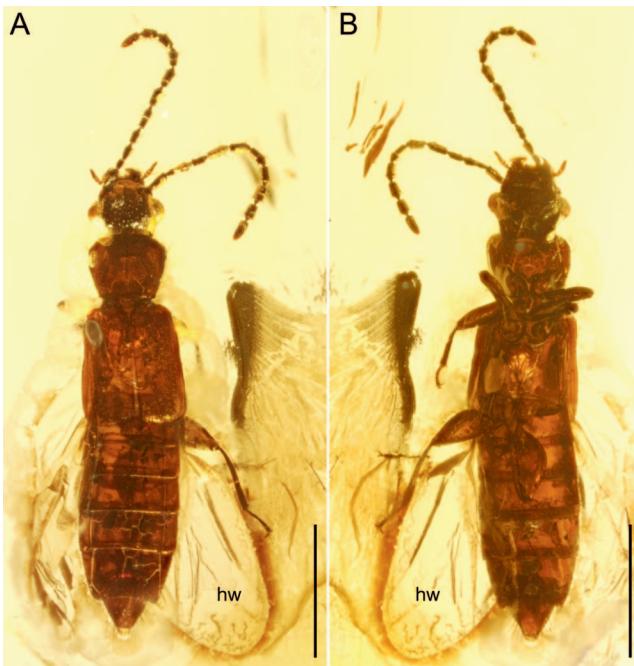


Fig. 1. *Eopiestus groehni* Cai & Lü sp. n., holotype, habitus, under normal reflected light. A. dorsal view; B. ventral view. Abbreviation: hw, hind wing. Scale bars 1 mm.

Occurrence. Baltic amber, upper Eocene Prussian Formation (Priabonian). Estimated age: 37.2–33.9 Ma. Yantarny, Sambian [Samland] peninsula, Kaliningrad region, Russia.

Diagnosis. As for the genus (*vide supra*).

Description. Body small, 3.5 mm long (from mandibular apex to abdominal apex), elongate, depressed, dark brown.

Head (Fig. 2A) subquadrate, as large as pronotum, 0.48 mm long (from mandibular apex to posterior margin), widest across eyes, 0.57 mm wide. Neck constriction absent. Vertex punctate. Eyes (Fig. 2A) large, very prominent and laterally protruding, with two relatively long setae at anterior part of inner margin. Antennae (Fig. 2D) extending to middle of elytra; antennomeres 1 and 2 nearly glabrous except several long setae near apex; antennomeres 5–11 densely pubescent; antennomere 1 elongate, slightly broader than others; antennomere 2 small, about 0.4 times as long as antennomere 1; antennomere 3 longer than antennomere 2; antennomere 4 slightly shorter and narrower than antennomere 3; antennomere 5 distinctly longer than antennomere 4; antennomeres 5–8 successively shorter toward apex; antennomeres 8 and 9 of almost same shape and size; antennomere 10 slightly shorter than antennomere 9; antennomere 11 elongate, bullet-shaped. Antennal insertions (Fig. 2A) concealed under supra-antennal ridges. Mandibles short, stout and simple. Maxillary palpi with palpomere 2 slightly longer than wide, much wider at apex; palpomere 3 transverse, as wide as palpomere 2, but distinctly shorter; palpomere 4 very long, longer than palpomeres 2 and 3 combined, slightly narrowed to rounded apex (Fig. 2A). Galea with a dense brush of setiform projections at apex. Labial palpi with apical

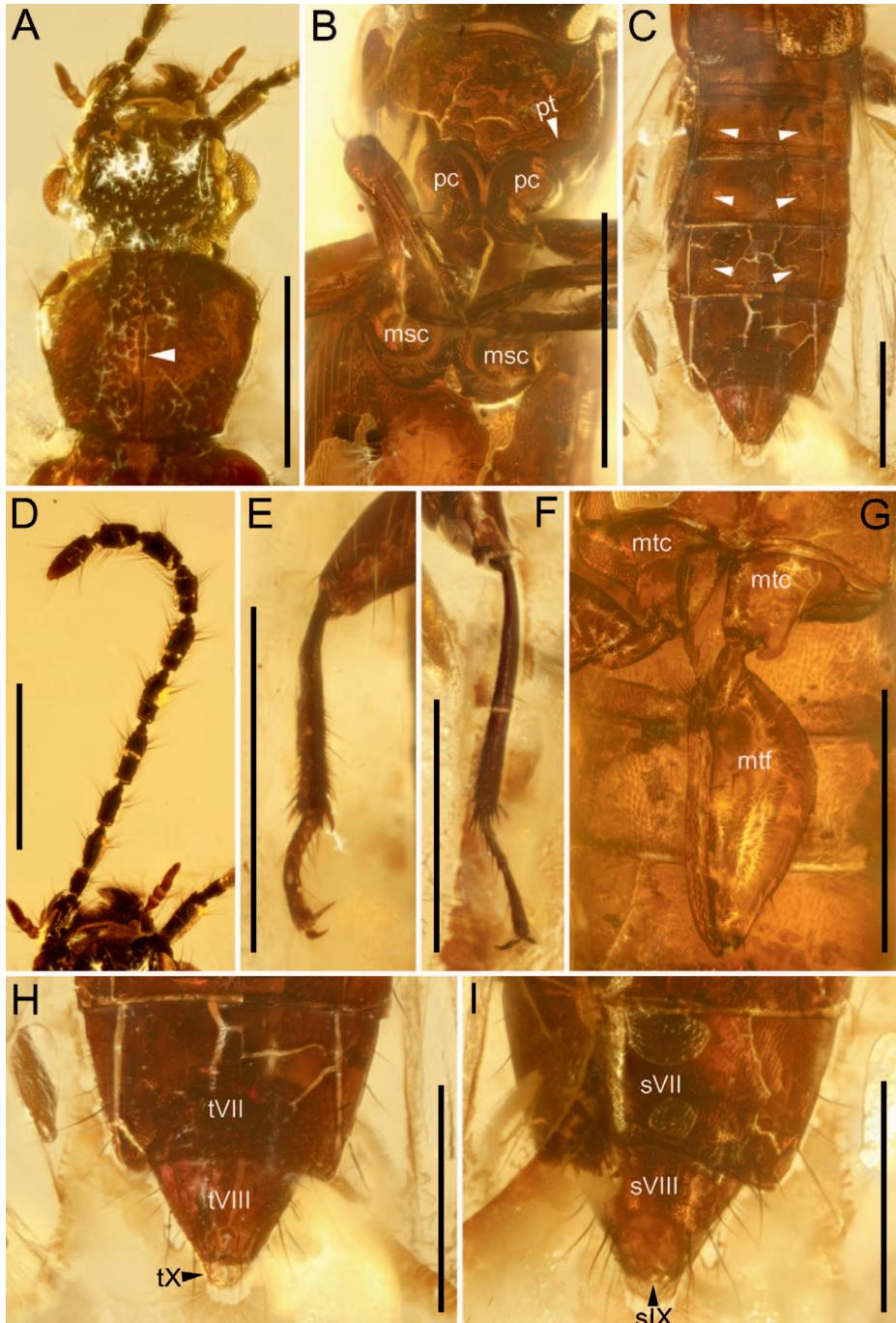


Fig. 2. Details of *Eopiestus groehni* Cai & Lü sp. n., holotype, under normal reflected light. A. head and pronotum, with median longitudinal sulcus on pronotum indicated; B. ventral view of thorax; C. abdomen, with pairs of setae on tergites IV–VI indicated; D. left antenna; E. ventral view of right fore leg; F. dorsal view of right hind leg; G. ventral view of left hind leg, showing dilated metafemur; H. abdominal tergites VII, VIII and X; I. sternites VII–IX. Abbreviations: pc, procoxa; pt, protrochantin; msc, mesocoxa; mtc, metacoxa; mtf, metafemur; tVII/VIII/X, tergite VII/VIII/X; sVII/VIII/IX, sternite VII/VIII/IX. Scale bars 500 μ m.

palpomere elongate and narrow. Gular sutures united at middle, diverging anteriorly and posteriorly.

Pronotum (Fig. 2A) 0.50 mm long and 0.57 mm wide, narrowed posteriorly from anterior fourth. Anterolateral margin with about five setae. Pronotal disc with median longitudinal sulcus. Anterolateral angles broadly rounded; posterolateral angles obtuse. Prosternum (Fig. 2B) well-developed, elongate, longer than procoxae; Prosternal process (Fig. 2B) short, sharp at apex. Anterior prosternal margin bisinuate; pronosternal suture distinct. Procoxal cavities (Fig. 2B) rounded, open behind.

Elytra slightly elongate, partly covering abdominal tergite III, 0.93 mm long and each 0.39 mm wide; surface almost glabrous, without rows of punctures or striae; lateral margin with scattered setae. Epipleural keels developed and complete. Humeral calli developed. Hind wings fully developed, with setae forming fringe along margin. Mesoventrite very short; mesoventral process small and sharp. Metaventrite long and broad, anterior metaventral process rounded (Fig. 2B).

Legs relatively short, slender, setose. Protrochantins large, well exposed; procoxae (Fig. 2B) small, rounded, slightly exserted; protrochanters small, subtriangular; profemora robust; protibiae very slender; protarsi 5-segmented, basal four tarsomeres small and short, together shorter than tarsomere 5; pretarsal claws simple (Fig. 2E). Mesocoxae (Fig. 2B) oblique, oval-shaped, contiguous; mesofemora, mesotibiae and mesotarsi similar to those of fore legs; mesotarsi 5-segmented. Metacoxae (Fig. 2G) transverse, subtriangular and contiguous; metacoxal plates small; metafemora distinctly inflated (Fig. 2G), with outer margins strongly arched; metatibiae slender, longer than those of pro- and mesotibiae, apex with circle of spines; metatarsi 5-segmented, basal four tarsomeres very short, together shorter than tarsomere 5, ventral side of each tarsomere with a few setae (Fig. 2F).

Abdomen (Figs. 1B, 2C) elongate, with six visible sternites. Tergite III partly visible; tergites IV–VI of almost same length, each with pair of short setae near lateral margin (Fig. 2C); tergite VII (Fig. 2H) longest; exposed part of tergite VIII (Fig. 2H) triangular; tergites III–VII without basolateral ridges. Sternites III–V subequal in length; sternite VI slightly longer, sternite VII (Fig. 2I) longest, apical margin slightly concave; sternite VIII (Fig. 2I) triangular, with dense long setae and shallow apical emargination.

Discussion

Based on the overall morphology of this Eocene fossil, it can be placed in the Oxyteline Group of subfamilies. Among the four subfamilies (Osoriinae, Oxytelinae, Piestinae and Scaphidiinae) of the recently restricted Oxyteline Group (Grebennikov and Newton, 2012), the fossil is easily separated from Scaphidiinae by its elongate and slender body form and short elytra. The fossil appears to share characters of the remaining three subfamilies, viz., Osoriinae, Oxytelinae and Piestinae.

The fossil is morphologically close to members of the tribe Eleusinini of Osoriinae; for example, it shares with the extant *Renardia* Motschulsky the general body shape (slender and flat), posteriorly narrowed prothorax, elongate elytra, and relatively broad abdomen (e.g., Grebennikov and Newton, 2012: Fig. 11), but the fossil differs significantly from *Renardia* and all other eleusinines in having well-developed paratergites and lacking the greatly enlarged protrochantins that are a unique synapomorphy of that tribe. In general, piestines are morphologically similar to osoriines, except that all osoriines lack abdominal paratergites (Newton *et al.*, 2000) as a defining characteristic of the subfamily.

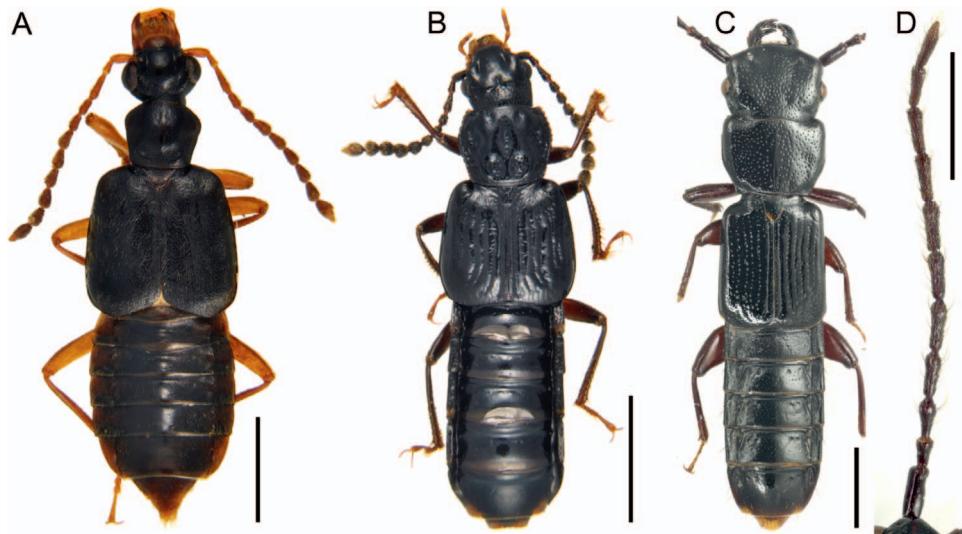


Fig. 3. Two modern basal oxytelines and a modern piestine. A. *Deleaster taiwanensis* Hayashi (Oxytelinae: Deleasterini); B. *Coprophilus formosanus* Shibata (Oxytelinae: Coprophilini); C. *Piestoneus* sp. (Piestinae); D. left antenna of *Piestoneus* sp. Scale bars 2 mm in A and B; 1 mm in C and D.

The fossil also shares characters of some basal groups of Oxytelinae. For instance, it is similar in many respects to the extant genera *Deleaster* Erichson (Fig. 3A; Deleasterini) and *Coprophilus* Latreille (Fig. 3B; Coprophilini), including slender antennae, elongate maxillary palpi with long apical palpomere, laterally protruding eyes, posteriorly narrowed prothorax, broad and apically widened abdomen, and 5-segmented tarsi (e.g., Campbell, 1979; Cuccodoro and Makranczy, 2013). However, the fossil differs from *Coprophilus* by its more slender antennae with each antennomere longer than wide, non-striate elytra, and broad abdominal paratergites and from *Deleaster* by its much more elongate body form, absence of grooves on the head, and unlobed basal tarsomeres. The slender, densely pubescent antennae of the fossil are different from those of *Coprophilus* and *Deleaster*, but typical for most modern Piestinae, such as the genus *Piestoneus* (Fig. 3C and D). More significantly, the subfamily Oxytelinae, as a well-defined monophyletic group, is distinguished from all other staphylinids by the unique presence of paired secretory openings of non-eversible abdominal defensive glands on tergum IX, which is divided by tergum X or nearly so (Herman, 1970; Newton, 1982; Dettner *et al.*, 1985; Czarniawski and Stanić, 1997; Newton *et al.*, 2000; Thayer, 2016), and the presence in most taxa of a fully developed sternite II (Herman, 1970; Newton *et al.*, 2000; Thayer, 2016). The secretory openings of the glands are usually not easy to discern even in modern undissected specimens, and the structure is not visible (probably absent) from the body apex of the fossil, as the last abdominal segment is reduced. In addition, the abdominal sternites of the fossil are well-preserved; there is no trace of a sternite II between sternite III and the metaventrite (Fig. 4C), as is typical for extant piestines (e.g., *Piestoneus*; Fig. 4B). By contrast, in an undissected specimen of *Coprophilus*, sternite II is very short, reduced, and mostly concealed by the metaventrite, but can be seen laterally at the base of the abdomen (Fig. 4A). It is noteworthy that in piestines the metafemora are usually strongly dilated (Fig. 4B), but not in oxytelines,

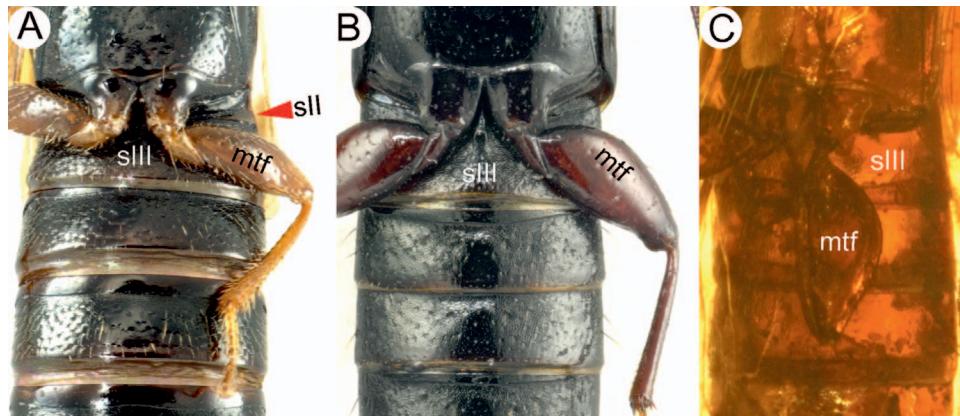


Fig. 4. Comparison of basal abdominal sternites between Oxytelinae and Piestinae. A. *Coprophilus pennifer* (Motschulsky) (Oxytelinae), with reduced sternite II indicated; B. *Piestoneus* sp. (Piestinae); C. *Eopiestes groehni* Cai & Lü sp. n. (Piestinae). Abbreviations: mtf, metafemur; sII/III, sternite II/III.

including *Coprophilus* (Fig. 4A). The metafemora of the fossil (Fig. 4C) are distinctly dilated, more consistent with Piestinae.

Considering the discussion above, the fossil is excluded from the subfamilies Osoriinae and Oxytelinae and therefore also from previously described fossil taxa placed in those subfamilies (see Table 1). The general body form likely resembles the body ground plan for both subfamilies and the allied Piestinae. Adults of Piestinae are diagnosed by the following combination of characters: 1) body elongate and flattened; 2) antennae inserted under shelf-like corners of frons; 3) procoxae small, globose; 4) protrochantins exposed (except in *Eopiestes*); 5) abdomen long and parallel-sided, with six visible sternites and one or two pairs of paratergites per segment; 6) tarsal formula 5–5–5 (Newton *et al.*, 2000; Caron *et al.*, 2012). We place this fossil in Piestinae, because its characters are consistent with this diagnosis, while noting that Piestinae, however, is now considered a paraphyletic group with respect to Oxytelinae and Osoriinae (Grebennikov and Newton, 2012; McKenna *et al.*, 2015). No tribal classification of Piestinae has been established. Among the seven extant piestine genera, the fossil is easily separated from *Siagonium*, *Parasiagonum*, *Piestoneus* and *Prognathoides* by lacking a pair of basolateral ridges on abdominal tergites III–VII (cf. Fig. 3C) and lacking five or more impressed striae or rows of punctures on each elytron (Caron *et al.*, 2012); from *Eopiestes* by lacking three complete longitudinal striae or carinae on each elytron, having exposed protrochantins, and lacking large punctures on head, pronotum and elytra (Caron *et al.*, 2012; Yin and Li, 2016); and from *Piestus* by lacking 5–6 (usually 5) longitudinal striae on each elytron and by the gradually posteriorly-narrowed pronotum (abruptly constricted posteriorly in *Piestus*, e.g., Caron *et al.*, 2012). The new species is most closely related to the extant piestine genus, *Hypotelus*, based on the elongate maxillary palpi with palpomere 3 broader than long, the unmodified head and mandibles, the medially joined gular sutures, the gradually posteriorly-narrowed pronotum, and the glabrous and long non-striate elytra covering tergite III (Caron *et al.*, 2012). However, it differs from *Hypotelus* in several significant ways, including having a single pair of wide paratergites on abdominal segments III–VII (rather than two slender pairs, cf. Caron *et al.*, 2012) and lacking at least four synapomorphies of *Hypotelus* identified in a recently completed revision of that genus (Bortoluzzi *et al.*, 2017): anterior

margin of prosternum straight rather than convex; prosternum projecting posteriorly dorsad to procoxae and visible again behind them; metatarsomere 5 equal to tarsomeres 1–4 combined rather than longer; and tergite VII more than 1.5 times as long as tergite VI. Several other defining characters of *Hypotelus*, such as anterior angles of mentum and setae at the apex of the median sclerotized plate of the ligula, are not visible in the fossil. The observed differences, in our view, justify the placement of the fossil in a new genus.

Yue *et al.* (2016) described a genus of Piestinae with two species (*Paleosiagonium brevityratum* and *P. adaequatum*) from the Mesozoic of northeastern China (Lower Cretaceous Yixian Formation), which represent the first and earliest fossil records for the subfamily. Compared to extant Piestinae, the general body form of *Paleosiagonium* is more suggestive of some members of the tribe Eleusinini (Osoriinae), such as *Eleusis* Laporte. *Paleosiagonium* shares with *Eleusis* short antennae, large head with anteriorly-positioned eyes, bowl-shaped pronotum, short and non-striate elytra, and elongate abdomen. However, the abdominal segments of those fossils bear a pair of broad paratergites, which would exclude them from Osoriinae. (Unfortunately, the condition of the protrochantins is not described nor evident in the illustrations.) *Paleosiagonium* appears to be close to an ancestral form that gave rise to the modern Osoriinae and Piestinae. The Eocene fossil described here is much more modern-looking, and it can be easily separated from the Mesozoic genus by its much more protruding eyes, narrower neck (compared to pronotum), long antennae, and elongate elytra. Given the long history of Piestinae that can be traced back to the Early Cretaceous, the discovery of a new piestine from the mid-Eocene is not surprising. The new species represents the first fossil piestine discovered as an amber inclusion, and is significant for future phylogenetic analysis of relationships among extant Osoriinae, Oxytelinae and Piestinae.

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Literature Cited

- Aleksandrova, G. N., and N. I. Zaporozhets. 2008. Palynological characteristic of the Upper Cretaceous and Paleogene sediments of the western part of the Sambian peninsula (the Kaliningrad Region). Paper 2. Stratigraphy. *Geological Correlation* 16: 75–86. [in Russian]
- Bortoluzzi, S., E. Caron, and C. S. Ribeiro-Costa. 2017. Revision and phylogeny of *Hypotelus* Erichson: a Neotropical genus of minute rove beetles (Coleoptera, Staphylinidae, Piestinae). *Zootaxa* 4273: 451–487.
- Brunke, A., A. Newton, J. Klimaszewski, C. Majka, and S. Marshall. 2011. Staphylinidae of eastern Canada and adjacent United States. Key to subfamilies: Staphylininae: tribes and subtribes, and species of Staphylinina. *Canadian Journal of Arthropod Identification* 12: 1–110.
- Cai, C.-Y., and D.-Y. Huang. 2013a. *Mesocorophilus clavatus*, a new oxyteline rove beetle (Coleoptera: Staphylinidae) from the Early Cretaceous of China. *Insect Systematics & Evolution* 44: 213–220.
- Cai, C.-Y., and D.-Y. Huang. 2013b. Discussion on the systematic position of the oxyteline rove beetle *Anotylus archaicus* Yue, Makranczy & Ren, 2012 (Coleoptera: Staphylinidae). *Insect Systematics & Evolution* 44:

- 203–212.
- Cai, C.-Y., and D.-Y. Huang. 2015. The oldest osoriine rove beetle from Cretaceous Burmese amber (Coleoptera: Staphylinidae). *Cretaceous Research* 52(Special Issue): 495–500.
- Cai, C.-Y., M. K. Thayer, D.-Y. Huang, X.D. Wang, and A. F. Newton. 2013a. A basal oxyteline rove beetle (Coleoptera: Staphylinidae) from the Early Cretaceous of China: oldest record for the tribe Euphamiini. *Comptes Rendus Palevol* 12: 159–163.
- Cai, C.-Y., E. V. Yan, and D. V. Vasilenko. 2013b. First record of *Sinoxystelus* (Coleoptera: Staphylinidae) from Urey locality of Transbaikalia, Russia, with discussion on its systematic position. *Cretaceous Research* 41: 237–241.
- Campbell, J. M. 1979. *Coprophilus castoris*, a new species of Staphylinidae (Coleoptera) from beaver lodges in eastern Canada. *Coleopterists Bulletin* 33: 223–228.
- Caron, E., C. S. Ribeiro-Costa, and A. F. Newton. 2012. Cladistic analysis and revision of *Piestus* Gravenhorst, with remarks on related genera (Coleoptera: Staphylinidae: Piestinae). *Invertebrate Systematics* 25: 490–585.
- Chatzimanolis, S., and M. S. Engel. 2011. A new species of *Diochus* from Baltic amber (Coleoptera, Staphylinidae, Diochini). *ZooKeys* 138: 65–73.
- Chatzimanolis, S., D. A. Grimaldi, M. S. Engel, and N. C. Fraser. 2012. *Leehermania prorova*, the earliest staphyliniform beetle, from the Late Triassic of Virginia (Coleoptera: Staphylinidae). *American Museum Novitates* 3761: 1–28.
- Cohen, K. M., S. C. Finney, P.L. Gibbard, and J.-X. Fan. 2013 (updated). The ICS International Chronostratigraphic Chart. *Episodes* 36: 199–204.
- Crowson, R. A., and I. Ellis. 1969. Observations on *Dendrophagus crenatus* (Cucujidae) and some comparisons with piestine Staphylinidae. *Entomologist's monthly magazine* 104: 161–169.
- Cuccodoro, G., and Gy. Makranczy. 2013. Review of the Afrotropical species of *Deleaster* Erichson, 1839 (Coleoptera, Staphylinidae, Oxytelinae). *Revue suisse de Zoologie* 120: 537–547.
- Czarniawski, W., and B. Staniec. 1997. Notes on the structure of defensive organ openings of some Oxytelinae (Coleoptera: Staphylinidae). *Polskie Pismo Entomologiczne* 66: 33–43.
- Dettner, K., G. Schwinger, and P. Wunderle. 1985. Sticky secretion from two pairs of defensive glands of rove beetle *Deleaster dichrous* (Grav.) (Coleoptera: Staphylinidae): Gland morphology, chemical constituents, defensive functions, and chemotaxonomy. *Journal of Chemical Ecology* 11: 859–883.
- Engel, M. S., and S. Chatzimanolis. 2009. An oxyteline rove beetle in Dominican Amber with possible African affinities (Coleoptera: Staphylinidae: Oxytelinae). *Annals of Carnegie Museum* 77: 425–429.
- Erichson, W. F. 1839. *Genera et Species Staphylinorum Insectorum Coleopterorum Familiae*. F. H. Morin, Berlin, pp. 1–400.
- Evanoff, E., W. C. McIntosh, and P. C. Murphey. 2001. Stratigraphic summary and $^{40}\text{Ar}/^{39}\text{Ar}$ geochronology of the Florissant formation, Colorado. *Proceedings of the Denver Museum of Nature and Science Series* 4: 1–16.
- Förster, B. 1891. Die Insekten des “Plattigen Steinmergels” von Brunstatt. *Abhandlungen zur Geologischen Spezialkarte von Elsass-Lothringen* 3: 333–594 (+ 7 unnn.), pls. 11–16.
- Grebennikov, V. V., and A. F. Newton. 2012. Detecting the basal dichotomies in the monophylum of carrion and rove beetles (Insecta: Coleoptera: Silphidae and Staphylinidae) with emphasis on the Oxyteline group of subfamilies. *Arthropod Systematics & Phylogeny* 70: 133–165.
- Heer, O. 1862. Beiträge zur Insektenfauna Oeningens. Coleoptera. Geodephagen, Hydrocanthariden, Gyriniden, Brachelytren, Clavicornen, Lamellicornen und Buprestiden. *Natuurkundige Verhandelingen van de Hollandsche Maatschappij der Wetenschappen te Haarlem* (2) 16: 1–90, pls. 1–7.
- Herman, L. H. 1970. Phylogeny and reclassification of the genera of the rove beetle subfamily Oxytelinae of the world (Coleoptera: Staphylinidae). *Bulletin of the American Museum of Natural History* 142: 345–454.
- Herman, L. H. 2001. Catalog of the Staphylinidae (Insecta: Coleoptera). 1758 to the end of the second millennium. Parts I–VII. *Bulletin of the American Museum of Natural History* 265: 1–4218 (in 7 vols.).
- Irmler, U. 2003. Osoriinae (Coleoptera: Staphylinidae) from Dominican amber. *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)* 342: 1–16.
- Khachikov, E. A. 2012. To the knowledge of taxonomy of the subfamily Oxytelinae Fleming, 1821 (Coleoptera: Staphylinidae) [in Russian, English abstract]. *Kavkazskii Entomologicheskii Byulleten'*; *Caucasian Entomological Bulletin* 8: 213–231.
- Klebs, R. 1910. Über Bernsteineinschlüsse im allgemeinen und die Coleopteren meiner Bernsteinsammlung. *Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg* 51: 217–242.
- Korge, H. 1967. Ein fossiler Staphylinide aus dem pliozänen Ton von Willershausen im westlichen Harzvorland. *Bericht der Naturhistorischen Gesellschaft zu Hannover* 111: 109–111.

- Larsson, S. G. 1978. Baltic amber – a palaeobiological study. *Entomonograph* 1: 1–192.
- Latreille P.A. 1802: Histoire Naturelle, Générale et Particulière, des Crustacés et des Insectes. F. Dufart, Paris, 467 pp.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata.* Volume 1. L. Salvii, Holmiae, iii + 824 pp.
- Lü, L., C.-Y. Cai, and D.-Y. Huang. 2017. The earliest oxyteline rove beetle in amber and its systematic implications (Coleoptera: Staphylinidae: Oxytelinae). *Cretaceous Research* 69: 169–177.
- McKenna, D. D., B. D. Farrell, M. S. Caterino, C. W. Farnum, D. C. Hawks, D. R. Maddison, A. E. Seago, A. E. Z. Short, A. F. Newton, and M. K. Thayer. 2015. Phylogeny and evolution of Staphyliniformia and Scarabaeiformia: Forest litter as a stepping stone for diversification of nonphytophagous beetles. *Systematic Entomology* 40: 35–60.
- Newton, A. F. 1982. A new genus and species of Oxytelinae from Australia, with a description of its larva, systematic position, and phylogenetic relationships (Coleoptera: Staphylinidae). *American Museum Novitates* 2744: 1–24.
- Newton, A. F., and M. K. Thayer. 1992. Current classification and family-group names in Staphyliniformia (Coleoptera). *Fieldiana: Zoology (N.S.)* 67: 1–92.
- Newton, A. F., M. K. Thayer, J. S. Ashe, and D. S. Chandler. 2000. Staphylinidae Latreille, 1802. In R. H. Arnett and M. C. Thomas (eds.), *American Beetles*. CRC Press, Boca Raton, pp. 272–418.
- Ortega-Blanco, J., S. Chatzimanolis, H. Singh, and M. S. Engel. 2013. The oldest fossil of the subfamily Osoriinae (Coleoptera: Staphylinidae), from Eocene Cambay amber (India). *Coleopterists Bulletin* 67: 304–308.
- Paśnik, G., and D. Kubisz. 2002. A new genus and new species of Staphylinidae (Coleoptera) from Baltic amber. *European Journal of Entomology* 99: 353–361.
- Puthz, V. 2006. Die erste Euaesthetine aus dem Baltischen Bernstein (Coleoptera, Staphylinidae). 90. Beitrag zur Kenntnis der Euaesthetinen. *Entomologische Blätter für Biologie und Systematik der Käfer* 101(2–3): 127–128. [2005]
- Puthz, V. 2008. Über Euaesthetinen aus dem Bernstein (Coleoptera, Staphylinidae). 99. Beitrag zur Kenntnis der Euaesthetinen. *Entomologische Blätter für Biologie und Systematik der Käfer* 103/104: 59–62.
- Puthz, V. 2010. *Stenus* Latreille, 1797 aus dem Baltischen Bernstein nebst Bemerkungen über andere fossile *Stenus*-Arten (Coleoptera, Staphylinidae). *Entomologische Blätter* 106: 265–287.
- Ritzkowski, S. 1997. K-Ar-Altersbestimmungen der bernsteinführenden Sedimente des Samlandes (Paläogen, Bezirk Kaliningrad). *Metalla (Sonderheft)* 66: 19–23.
- Ryvkin, A. B. 1990. Semeystvo Staphylinidae Latreille, 1802, pp. 52–66. In: Rasnitsyn, A. P. (ed.). *Pozdne-mezozoyskie nasekomye Vostochnogo Zabaykal'ya* [Late Mesozoic insects of Eastern Transbaikalia]. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 239: 1–222, 16 pls.
- Schaufuss, L. W. 1890. System-Schema der Pselaphiden, ein Blick in die Vorzeit, in die Gegenwart und in die Zukunft. *Tijdschrift voor entomologie* 33: 101–162.
- Scudder, S. H. 1876. Fossil Coleoptera from the Rocky Mountain Tertiaries. *Bulletin of the United States Geological and Geographical Survey of the Territories* 2: 77–87.
- Scudder, S. H. 1878. The fossil insects of the Green River Shales. *Bulletin of the United States Geological and Geographical Survey of the Territories* 4: 747–776.
- Scudder, S. H. 1890. The Tertiary insects of North America. *Report of the United States Geological Survey of the Territories* 13: 734 pp. [incl. 26 pls.].
- Scudder, S. H. 1900. Adephagous and clavicorn Coleoptera from the Tertiary deposits of Florissant, Colorado with descriptions of a few other forms and a systematic list of the non-rhynchophorous Tertiary Coleoptera of North America. *Monographs of the United States Geological Survey* 40: 11–148, pls. 1–11.
- Smith, M. E., A. R. Carroll, and B. S. Singer. 2008. Synoptic reconstruction of a major ancient lake system: Eocene Green River Formation, western United States. *Geological Society of America Bulletin* 120: 54–84.
- Spahr, U. 1981. Systematischer Katalog der Bernstein- und Kopal-Käfer (Coleoptera). *Stuttgarter Beiträge zur Naturkunde - Serie B (Geology and Palaeontology)* 80: 1–107.
- Thayer, M. K. 2016. Staphylinidae Latreille, 1802. In: Beutel, R. G. & R. A. B. Leschen (eds.). *Handbook of Zoology: Arthropoda: Insecta, Coleoptera, Beetles. Vol. 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim)*. 2nd edition. De Gruyter, Berlin/Boston, pp. 394–442.
- Tikhomirova, A. L. 1968. Staphylinid beetles of the Jurassic of the Karatau (Coleoptera, Staphylinidae), In: B. B. Rohdendorf (ed.), *Jurassic insects of the Karatau* [in Russian]. Akademiya Nauk SSSR, Moskva, pp. 139–154.
- Tikhomirova, A. L. 1980. Rannemelovye zhuki-stafilinidy iz mestonakhzhdeniya Manlay. In: Kalugina, N. S.

- (ed.). Rannemelovoe ozero Manlay. *Trudy Sovmestnoy Sovetsko-Mongolskoy Paleontologicheskoy Eks-peditisii AN SSSR* 13: 57–58.
- Wickham, H. F. 1912. A report on some recent collections of fossil Coleoptera from the Miocene shales of Florissant. *Bulletin from the Laboratories of Natural History of the State University of Iowa* 6: 3–38, pls. 1–8.
- Wickham, H. F. 1913. Fossil Coleoptera from the Wilson Ranch near Florissant, Colorado. *Bulletin from the Laboratories of Natural History of the State University of Iowa* 6: 3–29, pls. 1–7.
- Yin, Z.-W., and L.-Z. Li. 2016. Range extension for *Eupiestus spinifer* Fauvel in China (Coleoptera: Staphylinidae: Piestinae). *Zootaxa* 4114: 64–70.
- Yue, Y.-L., J.-J. Gu, Q. Yang, J. Wang, and D. Ren. 2016. The first fossil species of subfamily Piestinae (Coleoptera: Staphylinidae) from the Lower Cretaceous of China. *Cretaceous Research* 63: 63–67.
- Yue, Y.-L., G. Makranczy, and D. Ren. 2012. A Mesozoic species of *Anotylus* (Coleoptera, Staphylinidae, Oxytelinae) from Liaoning, China, with the earliest evidence of sexual dimorphism in rove beetles. *Journal of Paleontology* 86: 508–512.
- Yue, Y.-L., Y. Zhao, and D. Ren. 2010. Three new Mesozoic staphylinids (Coleoptera) from Liaoning, China. *Cretaceous Research* 31: 61–70.
- Zhang, J.-F. 1989. *Fossil insects from Shanwang*. Shandong Science and Technology Press, Jinan, China, 459 pp.