



Antiquity and long-term morphological stasis in a group of rove beetles (Coleoptera: Staphylinidae): Description of the oldest *Octavius* species from Cretaceous Burmese amber and a review of the “Euaesthetine subgroup” fossil record

Dave J. Clarke^{a,b,*}, Stylianos Chatzimanolis^c

^a Department of Zoology, The Field Museum of Natural History, 1400 S Lake Shore Drive, Chicago, IL 60605, USA

^b Department of Biological Sciences, University of Illinois, at Chicago, 845. Taylor St. M/C 066, Chicago, IL 60607, USA

^c Department of Biological and Environmental Sciences, University of Tennessee at Chattanooga, 615 McCallie Ave., Dept. 2653, Chattanooga, TN 37403, USA

ARTICLE INFO

Article history:

Received 29 May 2009

Accepted in revised form 1 September 2009

Available online 9 September 2009

Keywords:

Bradytely

Euaesthetinae

Euaesthetini

Myanmar

Staphylinine group

Steninae

ABSTRACT

The Staphylinine group of rove beetle subfamilies is a significant animal radiation, and one subordinate monophyletic clade – the ‘Euaesthetine subgroup’ – includes around 3000 species in subfamilies Euaesthetinae and Steninae and has a fossil record dating to the Early Cretaceous. Detailed morphological study of a new well-preserved Cretaceous Burmese amber fossil revealed strong evidence consistent with its taxonomic placement in the euaesthetine genus *Octavius*. We thus describe *Octavius electrospinosus* sp. nov., the first Cretaceous record of the genus and of the tribe Euaesthetini. Previously, the oldest records of *Octavius* and Euaesthetini were from the Eocene (Baltic amber) and discovery of *O. electrospinosus* sp. nov. therefore nearly doubles the minimum lineage age of *Octavius*, increasing it by ~50 million years. We also briefly review the known Euaesthetine subgroup fossil record and tabulate summary data for all previously described fossils. All are placed in extant genera, and have visible diagnostic generic-level characters including some putative synapomorphies as judged by recent phylogenetic work. Including *O. electrospinosus* sp. nov., there are now four known Cretaceous species, all of which belong to either *Octavius*, *Nordenskioldia*, or *Stenus*. To explain the long-term morphological stasis in this group of rove beetles, we suggest that the continuous presence of mesic habitats may have buffered these lineages from strong selection for morphological change. Considering the fossils along with phylogenetic hypotheses we suggest the Euaesthetine subgroup originated in the Late Jurassic–Early Cretaceous and the Staphylinine group in the Early Jurassic. We emphasize the derived status of Cretaceous fossils in assessing possible divergence times and the significance of the pre-Cretaceous taphonomic bias for restricting more robust estimates. Further detailed morphological study of available fossils in a phylogenetic framework is badly needed to clarify the phylogenetic positions of these taxa.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

The beetle family Staphylinidae (rove beetles) is a truly remarkable radiation of animals. With more than 55,000 described species and ~3700 genera placed in 32 subfamilies, the family is now recognized as the most diverse of living organisms (Thayer, 2005; Scydmaenidae added by Grebennikov and Newton, 2009; A.F. Newton unpublished database). Unlike typical beetles, most rove beetles are characterized by extremely reduced wing covers

* Corresponding author. Department of Zoology, The Field Museum of Natural History, 1400 S Lake Shore Drive, Chicago, IL 60605, USA.

E-mail address: dclarke@fieldmuseum.org (D.J. Clarke).

(elytra), an exposed, heavily sclerotized, and often very flexible abdomen, and a highly derived wing folding mechanism (Hammond, 1979; Lawrence and Newton, 1982) – a combination of features purported to have facilitated their diversification into most terrestrial habitats, particularly forest leaf litter, and a wide variety of feeding niches (Hammond, 1979; Hansen, 1997a). According to recent views (summarized in Thayer, 2005) Staphylinidae as traditionally delimited is not monophyletic, but together with the staphylinoid families Silphidae (carrion beetles) and Scydmaenidae (ant-like stone beetles) comprises a well supported monophyletic group (see Thayer, 2005: 322–323 for details). It has long been hypothesized to contain four major lineages (Lawrence and Newton, 1982; Thayer, 2005), and in this paper we focus on the fossil record of a subgroup of one of these lineages (the Staphylinine

group) that we refer to as the 'Euaesthetine subgroup'. This megadiverse monophyletic group (Leschen and Newton, 2003; Clarke and Grebennikov, 2009; Grebennikov and Newton, 2009) consists of the subfamilies Euaesthetinae (~850 species in ~30 genera) and Steninae (~2600 species in 2 genera), which together form a very diverse assemblage of predatory beetles found mostly in moist leaf litter or riparian habitats.

The general staphylinid fossil record, like most other insect groups (Grimaldi and Engel, 2005), is best for the Cenozoic Era. As is typical for other groups known from deposits like the Baltic ambers (e.g., Kulicka and Ślipiński, 1996), the majority of Cenozoic staphylinid fossils belong to extant infrasubfamilial groups. Older fossils from the Mesozoic (Cretaceous and Jurassic) are also known but these are comparatively rare and some are taxonomically problematic. Tikhomirova (1968) described rock fossils from the Jurassic of Kara-Tau representing a number of Recent staphylinid subfamilies from both the Oxytelinae and Tachyporinae groups (Lawrence and Newton, 1982), including the subfamily (then tribe) Piestinae, which Leschen and Newton (2003) considered to be relatively basal within Staphylinidae. The oldest known fossil rove beetles were reported by Gore (1988) and Fraser et al. (1996) from the Triassic (Norian–Carnian, 220–230 Ma), but they have not been formally described and their affinities are unclear. Within the Staphylinine group, three of the ten included subfamilies (Lawrence and Newton, 1982; Grebennikov, 2005; Grebennikov and Newton, 2009) are not yet known as fossils (Leptotyphlinae, Megalopsidiinae, Solieriinae), and another three are known only from Cenozoic deposits (Oxyporinae, Paederinae, Pseudopsinae). Staphylininae are known from the Jurassic (e.g., Zhang, 1988), Cretaceous (e.g., Schlüter, 1978; Ryzkin, 1988), and throughout the Cenozoic (e.g., Scudder, 1900). Scydmaeninae are known from the Cenozoic but now five extinct genera are known from the Cretaceous (e.g. O'Keefe et al., 1997; Newton and Franz, 1998; Poinar and Brown, 2004; Chatzimanolis et al., in preparation). *Stenus* Latreille and several euaesthetine genera are now known from the Cenozoic (Heer, 1856; Wickham, 1913; Benick, 1943; Puthz, 2005; 2008a), but as we will discuss here the Cretaceous Euaesthetine subgroup fossils are a particularly interesting element of the Mesozoic Staphylinine group fossil record.

Amber fossils comprise much of the Staphylinine group and nearly all of the Euaesthetine subgroup fossil record. The remarkably life-like preservation of fossils in amber (Grimaldi, 1996) enables collection of important data for phylogenetic and evolutionary studies (e.g., Cognato and Grimaldi, 2008; see below), particularly in Coleoptera where fine morphological structures necessary for classification are poorly or never preserved in compression fossils (Grimaldi et al., 2002; Kirejtshuk et al., in press). One important and recently highlighted Cretaceous amber deposit is from the Hukawng Valley, northern Myanmar (Burma), dated at 90 Ma (Cenomanian; Zherikhin and Ross, 2000; Grimaldi et al., 2002) or 100–110 Ma (Albian; Cruickshank and Ko, 2003) and most probably was derived from an araucarian tree (Poinar et al., 2007). For the Coleoptera, Burmese amber is noted for a much greater diversity than any other Cretaceous amber and a significantly greater abundance of inclusions than in any other known amber deposit (Grimaldi et al., 2002). Not surprisingly, then, these deposits have yielded numerous rove beetle fossils, most of which are still undescribed but include some interesting new staphylinid records (Chatzimanolis, in preparation).

The taxonomic composition of Burmese and other Cretaceous ambers (see Grimaldi et al., 2002 for citations) suggests that new fossils should belong mostly to primitive species placed in basal higher taxa and mainly extinct infrasubfamilial groups. This is true for most previously studied Burmese amber inclusions. However, Engel and Grimaldi (2002) described the first Cretaceous

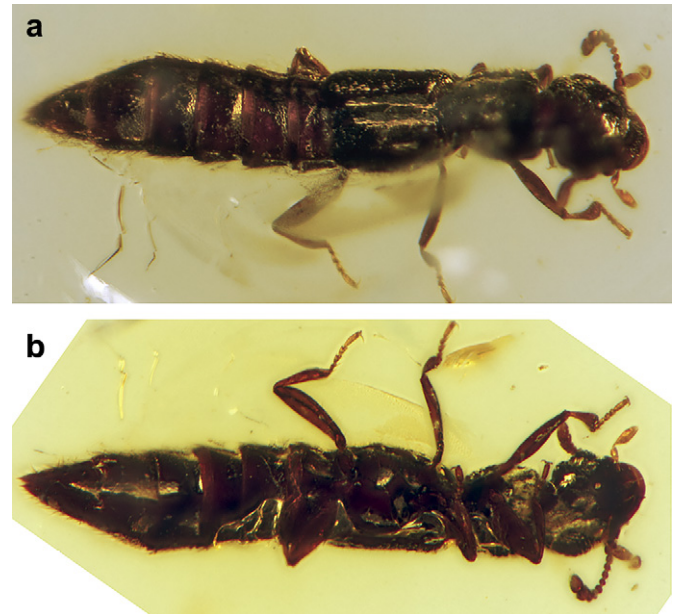


Fig. 1. Photomicrograph of holotype of *Octavius electrospinosus* sp. nov. (AMNH Bu-562). (a), dorsal view; (b), ventral view.

web-spinners (Insecta: Zoraptera), placing three of them in the extant genus *Zorotypus* Silvestri. More recently, Cognato and Grimaldi (2008) reported a new scolytine weevil (Coleoptera: Curculionidae) in the extant genus *Microborus* Blandford. Both sets of authors highlighted the significant period of morphological stasis in these insects implied by the inferred age of the amber (~100 myr), and both genera therefore appear to be bradytelic (with slow rate of morphological evolution). The major goals of the present paper are to describe a new fossil species of Euaesthetinae from Burmese amber, to review the taxonomy of known fossils in the Euaesthetine subgroup, and to discuss the implications of these fossils for divergence times of some lineages within the Staphylinine group. The new species described here (Figs. 1 and 2) strongly resembles some species of *Octavius* Fauvel – an extant genus with ~250 described species broadly distributed mainly in the tropics, Palearctic, and southern Africa (Puthz, 1977; Herman, 2001; A. Newton, unpublished database). Collectively, these fossils suggest that bradytely is widespread within the Euaesthetine subgroup and accumulating phylogenetic evidence is helping to clarify age estimates for some lineages. We therefore discuss implications of the Staphylinine group fossil record and recently published phylogenies (Clarke and Grebennikov, 2009; Grebennikov and Newton, 2009) and outline some speculative arguments regarding the age of origin of this major staphylinid group and several subfamilies within it.

2. Materials and methods

The amber specimen was prepared for examination following protocols outlined in Nascimbene and Silverstein (2000). A polished slab of amber measuring 8.25 mm × 5 mm contained the beetle specimen, which (in dorsal view) was oriented at approximately a 35° angle to the cut surface. Several morphological details of this specimen are obscured by locally collapsed or distorted body regions (Fig. 2, arrows), presumably caused by pressures associated with preservation, and by gas bubbles emitted during decomposition. Areas most strongly affected by these confounding factors include the ventral surface of the head, lateral regions of the prothorax (hypomerall region), metaventrite (particularly around

the mesocoxal acetabula), and abdominal ventrites VI–VIII. Consequently, several systematically important characters are unfortunately obscured. This has resulted in some unavoidable inconsistencies between the descriptive text and what is illustrated in Fig. 2. Where these occur, the text should be considered correct. A Canon D4 camera attached to an Olympus SZX10 dissecting microscope was used to take the color habitus photograph (Fig. 1). A drawing tube attached to a Leica MZ 20.5 C dissecting microscope was used to produce the habitus illustrations (Fig. 2).

To compile literature on rove beetle fossils we consulted A.F. Newton's nearly complete bibliographic database for Staphylinidae housed at the Field Museum of Natural History. Dates and time periods given in Table 1 were standardized to those given in Grimaldi and Engel (2005) if provided there; further details regarding the dating of deposits can be found in citations given by those authors.

3. Systematic placement

3.1. Placement in "Euaesthetine subgroup"

The presence of the following adult synapomorphies visible in our fossil allows definitive assignment of it to the Euaesthetine subgroup (Clarke and Grebennikov, 2009): 1) frontoclypeal suture absent; 2) tips of mandibles concealed beneath labrum when mandibles closed; 3) third maxillary palpomere densely setose and fusiform, without any macrosetae; 4) fourth maxillary palpomere minute and hyaline; 5) second labial palpomere subfusiform; 6) third labial palpomere acicular and hyaline; 7) elytral epipleural keel lacking; 8) metaventrite with mesal posterior lobes (minute in *Octavius*); 7) empodium glabrous (empodial setae absent); and 9) abdominal intersegmental membranes with hexagonal sclerites. Other characters supporting this placement include the clubbed antennae (with 2–3 swollen antennomeres), and the presence of an intercoxal carina on abdominal sternite III and a ctenidium on each side of the apex of each tibia.

3.2. Placement in subfamily Euaesthetinae

Euaesthetinae has usually been circumscribed using various combinations of several non-unique characters (e.g., Hansen, 1997b), including some of those mentioned above and others, e.g., antennal insertions positioned before eyes, distinctly mesad from both sides of head and mandibular articulations (Downie and Arnett, 1996; Newton et al., 2000). The presence of all those characters plus the following synapomorphies (Clarke and Grebennikov, 2009) supports placement of this fossil in Euaesthetinae: 1) serrate or denticulate anterior labral margin; 2) presence of several macrosetae on posterolateral metacoxal margin; 3) apices of gonocoxites produced into spines (specimen is female); and 4) tetramerous tarsi (optimized as three independent synapomorphies by Clarke and Grebennikov (2009)). The suprageneric classification of Euaesthetinae currently in use recognizes six tribes (Scheerpeltz, 1974) but is not likely to be maintained after detailed phylogenetic analyses in progress by one of us (see Clarke and Grebennikov, 2009; D. Clarke, unpublished data). However, the tetramerous tarsi and "marginated" abdomen (i.e., with parasclerites) places it in the tribe Euaesthetini.

3.3. Placement in genus *Octavius* Fauvel

Thirteen valid genera are currently placed in Euaesthetini (Herman, 2001; Makhani, 2007) though three belong in other subfamilies (*Phaenotavius* Pace, belongs to Oxytelinae; *Coiffaitia* Orousset and *Neocoiffaitia* Orousset are of uncertain placement,

possibly in or near Solieriinae – A. Newton, pers. comm.). The genus *Octavius* is morphologically diverse, with included species ranging from fully winged and large-eyed to wingless and blind. The latter are presumably restricted to soil habitats and highly modified for subterranean life (Orousset, 1988). Because of this ecological breadth, *Octavius* is heterogeneous with several likely non-monophyletic species-groups within it. Nevertheless, monophyly is supported (Clarke and Grebennikov, 2009) and our fossil agrees with nearly all broadly distributed "key" characters of *Octavius*. Based mainly on Coiffait (1958), Orousset (1988), and our own observations, these are: 1) Neck present, distinctly narrower than head, with deep dorsal nuchal groove separating it from disc of head; 2) anterior margin of labrum with up to 16 teeth; 3) anterior and posterior pronotal angles rounded; 4) pronotum with medial and/or lateral sulci; 5) mesoventrite with median longitudinal carina at least anteriorly; 6) mesocoxae separated by narrow processes of both the meso- and metaventrites; 7) elytra with epipleural region separated from disc by longitudinal carina (obsolete in our fossil), with shallow furrow medially; 8) mesocoxae globular; 9) metacoxae transverse, subtriangular; 10) tarsi tetramerous; 11) abdominal sternite III with midlongitudinal carina projecting between metacoxae. *Octavius* workers have referred to at least one of these papers for diagnostic characters of this genus.

Other significant characters of most *Octavius* species include: 12) antennomeres 10 and 11 partially fused, therefore not separated by antennal stem; 13) abdomen subpendulous, gradually broadening from segment III to segment VII; 14) abdominal intersegmental membranes attached apically; and 15) abdominal segments III–VII with two pairs of parasclerites. Of these, our fossil agrees with (14) and (15). In characters (12) and (13), however, our fossil appears to be plesiomorphic relative to most extant *Octavius* species: Antennomeres 10 and 11 are separated by an antennal stem and the abdomen is more or less parallel-sided. Clarke and Grebennikov (2009) did not include (13) but recovered (12) as a synapomorphy of *Octavius*. It would seem, though, that at least some species of otherwise typical-looking *Octavius* might not have this derived character state (e.g., *O. confusus* Coiffait). A number of other diagnostic male-specific characters (see Coiffait, 1958; Orousset, 1988) are absent because the specimen is female and some are invisible because of preservation artifacts (see below).

The differences between our fossil and most other genera within Euaesthetini are too numerous to warrant mention here, but three genera may be closely related to *Octavius* and are sufficiently similar to some species-groups to make comparisons with them useful. Our fossil differs from *Euaesthetotyphlus* Coiffait and Decou (monotypic, European) in numerous labile characters (larger eyes, wings, etc.), by lacking papillate setae at the apex of maxillary palpomere III, and in having two pairs of abdominal parasclerites, elongate basal tarsomeres, a simple apex of tergite VIII, and differently shaped gonocoxites (c.f. Coiffait and Decou, 1970, figs. 1, 6, 7, 8, 9); from *Protopristus* Broun (three species, south temperate) in general habitus and numerous characters of the pterothorax (e.g., all described and numerous undescribed species are flightless with elytra fused at suture); and from *Macroturellus* Orousset (monotypic, African) most notably in the structure of antennal scapes, labrum, prothorax, and elytra (Orousset, 1987, figs. 6, 10 and 11).

Based on general habitus and the presence of 13 of at least 15 diagnostic character states for *Octavius* there is both good evidence that it is correctly placed in *Octavius* and insufficient evidence to either erect a new genus for our fossil or place it in any other described one. It seems most similar to some tropical species (e.g., *O. sulcicollis* Bernhauer), *O. mindorensis* Orousset, and *O. neotropicalis* Puthz) rather than any from the more peculiar-looking African or mostly soil-inhabiting Palearctic species-groups.

4. Systematic paleontology

Family: Staphylinidae Latreille, 1802
 Subfamily: Euaesthetinae Thomson, 1859
 Tribe: Euaesthetini Thomson, 1859
 Genus: *Octavius* Fauvel, 1873

Octavius electrospinosus sp. nov. Clarke and Chatzimanolis

(Figs. 1 and 2)

Derivation of name. The specific epithet is an adjective derived from the combination of *electrum* (Latin: “amber”) and *spinosus* (Latin: “with thorns”, referring to the large medial spine of the labrum).

Holotype. Female, AMNH BU-562. Deposited in the amber collection of the Division of Invertebrate Zoology, American Museum of Natural History, NY (USA), and labeled “Myanmar (Burma) Upper Cretaceous, Kachin: Tanai Village (on Ledo Rd. 105 km NW Myitkyna), coll. Leeward Capitol Corp., 2000, AMNH Bu-562”, “Burmese amber: Coleoptera: Staphylinidae” and “HOLOTYPE *Octavius electrospinosus* Clarke and Chatzimanolis.”

Type locality and stratigraphy. The specimen was collected in Tanai Village, Kachin state, Myanmar by Leeward Capital Corp. Stratigraphic details of the amber deposit, including locality maps, are given by Grimaldi et al. (2002) and Cruickshank and Ko (2003), and the age is estimated at between 90–100 myr.

Diagnosis. Distinguishable from all other species of *Octavius* by combination of: Large eyes, approximately one-third head length (measured from frontal margin to nuchal groove); anterior margin of labrum with 13 acute teeth, with single apicomedial tooth approximately twice length of six short paramedial teeth; antennomeres 10 and 11 separated by clear antennal stem; basal tarsomere of each tarsus relatively elongate, longer than second tarsomere; pronotum and elytra each with four elongate sulci; abdomen without rugose sculpture, more or less parallel-sided to segment VI.

Description. General characteristics: Small size, length approximately 1.3 mm. Head, pronotum, and elytra dark brown, strongly

rugosely sculptured, with closely spaced short setae; antennae, legs, and abdomen reddish-brown.

Head: Transverse, widest posteriorly (excluding eyes), with well developed impunctate neck and deep nuchal groove dorsally; epistomal suture absent; dorsal surface without carinae or clear dorsal tentorial pits; eyes large, approximately one-third as long as head (measured from frontal margin to nuchal groove), positioned at approximately middle of side of head, with individual ommatidia distinctly rounded such that eye surface is botryoidal; long interfacetal ocular setae not visible. Antennae inserted at front of head, before an imaginary line drawn between anterior margins of eyes, distinctly mesad from sides of head and mandibular articulations, under weakly developed shelf (condyle of first antennomere not visible in dorsal view), eleven-segmented with distinct two-segmented club; antennomeres 1–2 longer than wide, clavate; second antennomere three times as long as third (appearing two times in Fig. 2), antennomeres 3–6 quadrate, similar in size; antennomeres 8–10 transverse, gradually increasing in width; antennomeres 10 and 11 distinctly separated by antennal stem (i.e., not fused); tenth antennomere 1.5× as wide and 2× as long as ninth; eleventh antennomere subquadrate, as wide and 1.5× as long as tenth. Frontoclypeal-labral junction visible in dorsal view; labrum transverse with at least two pairs of elongate setae (only three individual setae shown in Fig. 2, but these are bilaterally symmetrical), anterior margin moderately convex and denticulate, with single distinctly elongate median tooth at least two times as long as six smaller paramedial angulate teeth on each side. Mandibles closed, with apices completely concealed beneath labrum. Maxillary palps four-segmented; first and second palpomeres elongate; third palpomere 2.5× as long as wide, distinctly fusiform and moderately densely setose; fourth palpomere aciculate and hyaline, minute, and deeply recessed into apex of third palpomere. Insertions of labial palps widely separated; labial palps three-segmented; first palpomere quadrate, short; second palpomere distinctly fusiform, 2× as wide and 3× as long as first; third palpomere as long as second, strongly aciculate and hyaline.

Thorax. Pronotum narrower posteriorly and gradually broadening anteriorly, widest part appearing slightly narrower than head and as wide as elytra, anterolateral and posterolateral angles rounded, with sides finely irregularly toothed; surface undulated, with four elongate sulci, one laterally, and one on each side of midline; lateral pronotal-hypomeral carina faintly discernible, partly obscured from dorsal view by lateral pronotal swelling. Prosternum coarsely sculptured, with anterior margin more or less smooth, not distinctly notched. Mesoscutellum completely hidden by basal pronotal margin. Elytra 1.3× long as wide, with truncate apices, surface finely sculptured, without epipleural or any other discernible carinae but with four shallow elongate sulci. Hindwings presumably present (given elytral length). Mesothorax with mesoventral intermesocoxal process apparently strongly developed, acute, projecting between mesocoxae, and overlapping intermesocoxal process of metaventrite; midlongitudinal mesoventral carina apparently present; metaventrite elongate, smooth, not carinate; mesocoxal acetabula apparently not delimited posteriorly by carina. Legs slender, with femora and tibiae moderately swollen apically; mesocoxae subglobular; metacoxae subtriangular, widely separated, right one with three macrosetae visible along posterolateral margin; trochanters subelongate; tibiae without spines or apical tibial spurs; tarsi each with four discernible tarsomeres (tarsal formula 4–4–4), though basal tarsomeres probably consist of two fused tarsomeres, each with two sets of elongate setae; each of tarsomeres 1–3 with long apicolateral setae; protarsi with length of first tarsomere subequal to combined lengths of second and third tarsomeres; second and third tarsomeres of each leg subequal in length; fourth tarsomere of each leg with greatest length, 1.2–

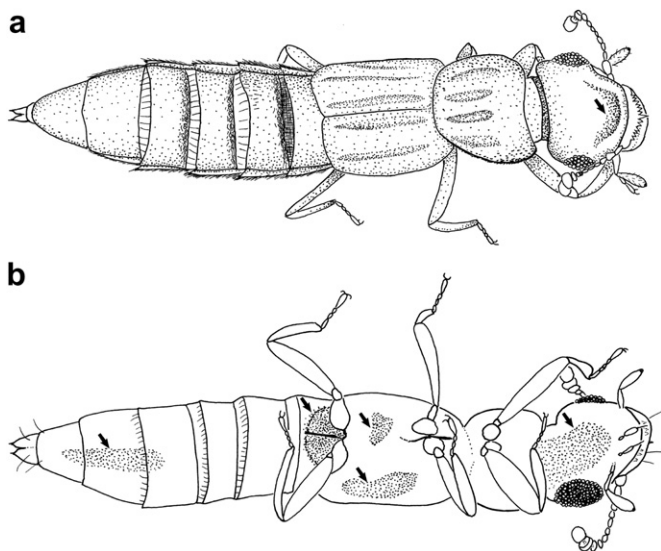


Fig. 2. Habitus of holotype of *Octavius electrospinosus* sp. nov. (AMNH Bu-562). (a), dorsal view; (b) ventral view. Note that in (a) the specimen was drawn close to the horizontal plane whereas in (b) it is oblique to the horizontal plane. Arrows indicate local areas of cuticular distortion or collapse.

1.5 × combined length of second and third tarsomeres, without empodial setae, and with simple latero-obliquely projecting recurved claws.

Abdomen. Abdomen with six visible segments (excluding genital segment), subparallel-sided to segment VI, strongly tapering from segments VII–IX, moderately densely setose; apices of abdominal segments III–VI with moderately long medially curving setae; segments III–VI subequal in length, segment VII slightly longer than preceding segments, with apical margin slightly narrowly convex medially, without apical palisade fringe; segments III–VI each with two pairs of parasclerites (clearly visible only on segment V), segment VII with at least one pair; intersegmental membranes attached apically to preceding segments, with pattern of hexagonal embedded sclerites; bases of segments III–VII with reticulate sculpture; sternite III with distinct medial carina projecting between metacoxae, without discernable lateral carinae on each side of deep metacoxal depressions. Specimen is female, with gonocoxites each produced into distinct apical spine; gonostyles absent.

Remarks. Several areas of deformation (Fig. 2, arrows), gas bubbles, and minute fracture planes prevent a complete view of the specimen. Consequently, the following systematically important characters from several body regions are obscured: 1) dorsum (tentorial pits) and venter (gular sutures, submentum) of head; 2) mouthparts (maxillae, labium, epipharynx, and mandibles); 3) prosternum and hypomerone (pronotosternal suture, prosternal anteprocoxal lobes, intercoxal prosternal process, hypomerone carina); 4) mesoventrite (mesothoracic pleural suture, mesothoracic anapleural carina or suture); 5) metaventrite (widely spaced metacoxae shown in Fig. 2B may reflect cuticular deformation;

Steninae and several euaesthetine genera – but not *Octavius* – do, however, have very widely spaced metacoxae); 6) sternite III (paramedial carinae). Additionally, one other diagnostic *Octavius* character is the distinctly truncate elytral bases but this is obscured by contraction of the pronotum and pterothorax.

5. Review of the “Euaesthetine subgroup” fossil record

Excluding Quaternary subfossils, to date at least 16 fossil specimens have been recorded from the Euaesthetine subgroup. Summary data for these fossils are given in Table 1 and the following sections discuss pertinent features of these fossils.

5.1. Euaesthetinae

A total of seven amber fossils have been referred to Euaesthetinae though one of these is a compression fossil and lacks sufficient detail to confirm its placement. The amber fossil record maximally spans 135 myr, with two of Cretaceous age and the rest from Eocene Baltic amber (Table 1). These fossils collectively represent three of the six tribes (Nordenskiöldiini, Stenaesthetini, and Euaesthetini) introduced by Scheerpeltz (1974), whose suprageneric classification is the one in widespread use, but which probably does not reflect natural (i.e., monophyletic) groups.

5.1.1. Nordenskiöldiini: Genus *Nordenskiöldia* Sahlberg

The Cretaceous species *Nordenskiöldia pentatarsus* (Lefebvre et al.) is the oldest and most comprehensively described euaesthetine fossil originally placed in the new genus

Table 1
Summary data for all known fossils placed in the Euaesthetine subgroup

Taxon	Tribe (Eu.) or Subgenus (St.)	Preservation	Deposit	Time period	Age	Reference
EUAESTHETINAE						
<i>Nordenskiöldia pentatarsus</i> (Lefebvre et al.)	Nordenskiöldiini	Amber	Lebanon	Cretaceous: Neocomian	120–135MYA	Lefebvre et al. (2005)
<i>Stenaesthetus</i> sp. (prope <i>quadrisculatus</i> Cameron)	Stenaesthetini	Amber	Europe: Baltic region	Eocene	44MYA	Puthz 2005
<i>Stenaesthetus</i> sp. (prope <i>quadrisculatus</i> Cameron)	Stenaesthetini	Amber	Europe: Baltic region	Eocene	44MYA	Puthz 2008a
<i>Euaesthetus</i> “sp. A” (prope <i>nitidulus</i> Sharp)	Euaesthetini	Amber	Europe: Baltic region	Eocene	44MYA	Puthz 2008a
<i>Euaesthetus</i> “sp. B” (prope <i>nitidulus</i> Sharp)	Euaesthetini	Amber	Europe: Baltic region	Eocene	44MYA	Puthz 2008a
<i>Octavius</i> sp.	Euaesthetini	Amber	Europe: Baltic region	Eocene	44MYA	Puthz 2008a
<i>Octavius electrospinosus</i> sp. nov.	Euaesthetini	Amber	Myanmar	Cretaceous: Cenomanian/Albian	90–110MYA	present study
Gen. et. sp.	Incertae sedis	Rock, limestone	England, Isle of Wight	Eocene/Oligocene	~38MYA	Kirejtshuk et al. <i>in press</i>
STENINAE						
<i>Stenus prodromus</i> Heer	—	Rock, gypsum marl	France, Aix en Provence	Late Oligocene	?	Heer (1856)
<i>Stenus scribai</i> Heyden and Heyden	—	Brown coal	Germany	Oligocene	?	Heyden and Heyden (1866)
<i>Stenus gypsi</i> Oustalet	—	Rock, gypsum marl	France, Aix en Provence	Late Oligocene	?	Oustalet (1874)
<i>Stenus ornatus</i> Förster	—	Rock, gypsum marl	France	Oligocene	?	Förster (1891)
<i>Stenus morsei</i> (Scudder)	—	Rock, shale	USA, Colorado, Florissant	Late Eocene	36MYA	Scudder (1900), Wickham (1913)
<i>Stenus priscus</i> Benick	<i>Hemistenus</i> (orig. <i>Parastenus</i>)	Amber	Europe: Baltic Region	Eocene	44MYA	Benick (1943)
<i>Stenus inexpectatus</i> Schlüter	<i>Tenusus</i>	Amber	France, Bezonnais	Cretaceous: Cenomanian/Albian	90–110MYA	Schlüter (1978)
<i>Stenus imputribilis</i> Ryvkin	<i>Stenus</i> (orig. <i>Nestus</i>)	Rock	Russia, Magadanskaia obl.	Cretaceous: Cenomanian/Albian	90–110MYA	Ryvkin (1988)

Libanoeuaesthetus. As discussed by Puthz (2008a,b), they provided only superficial characters in support of their new genus and consequently he synonymized *Libanoeuaesthetus* with *Nordenskioldia*. Although *N. pentatarsus* appears very similar to modern *Nordenskioldia* species, this genus appears rather generalized and without any obvious apomorphic characters. All three *Nordenskioldia* species have the ‘key’ character of Euaesthetinae – the toothed anterior labral margin. But within Euaesthetinae at least *N. columbiana* also exhibits several apparently primitive character states: 1) mesothoracic pleural suture present, delimited externally as distinct sulcus, 2) anal lobe of metathoracic hindwing present (though extremely reduced), 3) spiracle of first abdominal segment placed in membrane outside of tergite, 4) pentamerous tarsi, and 5) single pair of abdominal parasclerites. *Nordenskioldia pentatarsus* agrees with characters (4) and (5), but (1) may not be visible and (2) and (3) definitely are not. Extant species are known only from the Russian Far East (*N. glacialis* Sahlberg) and the Canadian Rocky Mountains (*N. columbiana* Puthz), so the type locality of *N. pentatarsus* in Lebanon indicates a previously much wider (or at least different) western distribution for *Nordenskioldia*.

5.1.2. *Stenaesthetini*: Genus *Stenaesthetus* Sharp

The first fossil euaesthetine described (but not named) is by habitus alone very similar to some modern species of *Stenaesthetus*. At least one putative synapomorphy (Clarke and Grebennikov, 2009) is also visible in the published figure (Puthz, 2005, fig. 1): thread-like antennae with antennomeres 9–11 much longer than wide, an antennal form unique within the subfamily. However, the very well-preserved specimen likely has several other visible diagnostic characters (heteromeres 5–5–4 tarsi, elytral epipleural carina, tergite and sternite of abdominal segment III separated by suture, all segments without parasclerites etc.), but the presence of these must unfortunately be inferred from the author’s generic placement. Like *N. pentatarsus*, the record of this genus from Baltic amber demonstrates a wider (or more northern) distribution of *Stenaesthetus* during the Eocene. The most northern records of extant *Stenaesthetus* are from northern China, and the genus for the most part is restricted to tropical regions (Puthz, 2005). This is further indication of the tropical paleoclimate of the Baltic region during the Eocene (Grimaldi and Engel, 2005). Puthz (2008a) recorded a second specimen of presumably the same species and he discusses its taxonomic affinities.

5.1.3. *Euaesthetini*: *Euaesthetus* Gravenhorst and *Octavius* Fauvel

Both of these genera have been reported from Baltic amber (Puthz, 2008a) but with the discovery of *Octavius electrospinosus* sp. nov. the minimum age of *Octavius* is here pushed back ~50 myr (Table 1). In having a pendulous abdomen the Eocene *Octavius* fossil resembles more closely in habitus some extant species; Puthz (2008a) notes a resemblance of this specimen to the African species *O. securifer* Puthz. All Euaesthetini fossils thus show affinities with extant species (Puthz, 2005; 2008a), and at least for the Baltic material this result is consistent with studies of other Baltic amber beetles (Kulicka and Ślipiński, 1996). Although the minimum age of *Euaesthetus* can only be speculated, Clarke and Grebennikov (2009) indicate that a clade comprising *Euaesthetus* + *Edaphus* is sister to another clade comprising the rest of the genera they studied, including *Octavius*. This result therefore implies that that lineage is also at least Cretaceous in age. Unlike *Nordenskioldia* and *Stenaesthetus*, all *Euaesthetus* and *Octavius* fossils have been found within the current distributional limits of these genera, which are both much wider than the known distributions of *Nordenskioldia* and *Stenaesthetus*.

5.2. *Steninae*

5.2.1. Genus *Stenus* Latreille

Eight fossil *Stenus* species have been described and named, and in contrast to Euaesthetinae, most are known from rock fossils (Table 1). The two Cretaceous fossils are of particular interest to systematic problems in the Euaesthetine subgroup. With known contemporaneous fossils of Euaesthetinae and Steninae, Euaesthetinae paraphyly (Hansen, 1997a; Leschen and Newton, 2003) is not strongly supported by the fossil record. The absence of Cretaceous *Stenus* fossils, however, in conjunction with only weak support for Euaesthetinae monophyly (Leschen and Newton, 2003), would have been consistent with that hypothesis.

With many more fossil species of Steninae described and named compared to Euaesthetinae, there have been somewhat greater taxonomic problems. Scudder (1900) described *Bledius morsei* from the Miocene shales of Florissant and considered *S. prodromus* Heer to belong in *Bledius* Leach (subfamily Oxytelinae). But Wickham (1913) disagreed with Scudder’s generic attribution and transferred his species to *Stenus*, providing a description of another specimen of *S. morsei* (both specimens belong to *Stenus*, V. Puthz, pers. comm.). In discussing the stenine fossils known at that time, Benick (1943) doubted that *S. gypsi* Oustalet belonged to *Stenus* but offered no alternative identification. Additionally, some authors have attributed their species to subgenera within *Stenus* but in some cases later authors have not followed these placements (for review of the subgenera of *Stenus* see Puthz, 2008b). These taxonomic issues are important because fossils are frequently used in evolutionary studies of many kinds but because of preservation problems can often not be included directly into phylogenetic analyses. Or, as might be the case in *Stenus*, they may also be misplaced, and it would appear that at least some specimens currently regarded as *Stenus* fossils may be something different. Nevertheless, published descriptions and illustrations suggest that the two Cretaceous species are correctly placed there. Both have very large eyes, a three-segmented club with distinctly bottle-shaped antennomeres (typical of modern stenines), and have at least one visible synapomorphy for Steninae (e.g., Clarke and Grebennikov, 2009): antennal insertions positioned high on frons behind anterior margin of eyes. Outside Steninae this character state occurs only in the distantly related Aleocharinae (Thayer, 2005).

6. Discussion

The Cretaceous record of *Octavius*, and indeed the fossil record of the Euaesthetine subgroup, is significant for several reasons. The most immediately apparent of these being that most extant Euaesthetinae are rarely collected, highly specialized leaf litter and soil dwelling beetles, and so any fossils are rather lucky finds indeed. The only Cretaceous amber deposit preserving a significant litter fauna is from Archingea, SW France (Perrichot, 2004), but so far no Euaesthetinae have been described from there. Below we consider the broader possible implications of these fossils.

6.1. Evolution of *Octavius*

The genus *Octavius*, with around 250 species (and growing), is one of the most diverse in Euaesthetinae. A broadly sampled phylogenetic analysis of *Octavius* is not yet possible, though the genus is probably monophyletic with a sister group hypothesized to be the south temperate (Australia and New Zealand) genus *Protopristerus* (Clarke and Grebennikov, 2009). Puthz (1977) proposed that *Octavius* originated in the tropics, since most Palearctic and temperate species seem to be of the subterranean type, whereas most described tropical species have large eyes

and many are flight-capable. *Octavius electrospinosus* sp. nov., being macrophthalmous, probably fully winged, and from an area thought to have been tropical during the Cretaceous (Grimaldi et al., 2002), is therefore consistent with Puthz's (1977) hypothesis, yet we find no reason to suggest directionality of evolution based on traits now widely known to be evolutionarily labile. Grebennikov and Newton (2009), however, suggest that correlated changes in morphological traits associated with ultra-specialization for subterranean life in Leptotyphlinae may be associated with diversification into previously unoccupied deep soil habitats. A similar trend may have occurred in groups of temperate *Octavius* species, and also in *Protopristus* – all known species of which are wingless and either completely blind or microphthalmous litter/soil dwellers (Clarke, in preparation).

6.2. Bradytely in the “Euaesthetine subgroup”?

Bradytely (Simpson, 1944) or “arrested evolution” refers to apparently slow rates of morphological change exhibited within many groups of “living fossils” – taxa in the fossil record that appear unchanged over millions of years (see Eldredge and Stanley, 1984 for review). Many authors have discussed general hypotheses for bradytely in the fossil record (e.g., see Simpson, 1944; Fisher, 1990; Stanley, 1984; Liow, 2004) and have broadly characterized such taxa as morphologically unspecialized ecological generalists with wide geographic ranges. Several case-specific explanations have also been proposed. Cognato and Grimaldi (2008), for example, attributed bradytely in the scolytine genus *Microborus* to the constraints of a subcortical lifestyle. Citing Grimaldi and Engel (2005: 97) they also noted that some extant tardigrades exhibit cryptobiosis (having a dormant stage), a possible adaptation that may “release tardigrades from the need to evolve elaborate morphological and other adaptations”.

Our taxonomic conclusion is thus not without general precedent, but biological knowledge of extant species in the Euaesthetine subgroup seems partially inconsistent with explanations for bradytely cited above. Although most genera are broadly distributed, they are also morphologically specialized predators and, judging by a diversity of mouthpart and other structures (Clarke, in preparation), are adapted to a diversity of prey and ecological niches. Protection in a “cloistered habitat” has also been suggested as facilitating geological longevity (Stanley, 1984) and most species are found in very mesic habitats or near water sources. We therefore propose that the continuous presence of mesic habitats over geological time explains bradytely in the Euaesthetine subgroup and has buffered these genera from extinction and from strong selection for morphological change.

One notable difference between the Euaesthetine subgroup fossil record and other extant genera reported from the Cretaceous is the relative species diversities. In other purported examples of bradytely, the genera are relatively species-poor compared to *Octavius* and *Stenus*: the genera *Zorotypus* (Insecta: Zoraptera) with 34 species (Engel and Grimaldi, 2002) and *Microborus* (Insecta: Coleoptera) with 8 species (Cognato and Grimaldi, 2008) stand in contrast to the ~250 and ~2400 species of *Octavius* and *Stenus*, respectively. This may indicate differing clade ages or speciation rates, differential fossilization and/or fossil discovery, or lower extinction rates in *Octavius* and *Stenus*. The latter is consistent with our hypothesis.

6.3. Phylogenetic relationships, fossils, and ages of subfamily lineages in the Staphylinine group

Monophyly of the Euaesthetine subgroup, and of Steninae, is strongly supported by morphological (Hansen, 1997b; Leschen and

Newton, 2003; Thayer, 2005; Clarke and Grebennikov, 2009; Grebennikov and Newton, 2009) and 18S rDNA data (Grebennikov and Newton, 2009). Although monophyly of Euaesthetinae has long been doubted (e.g., Hansen, 1997b; Thayer, 2005), Clarke and Grebennikov (2009) recently proposed 19 synapomorphies supporting monophyly of a subset of genera. All recent morphology-based phylogenetic hypotheses concur in placing the Euaesthetine subgroup in a relatively derived position several nodes up from the basal node of the Staphylinine group (Thayer, 2005; Clarke and Grebennikov, 2009; Grebennikov and Newton, 2009). The latter authors proposed a phylogeny of this group indicating two major clades, one including the novel relationship between the Euaesthetine subgroup and the former staphylinoid family Scydmaenidae (ant-like stone beetles), the other with several other subfamilies including the clade Staphylininae + Paederinae as the most derived subgroup (Grebennikov and Newton, 2009, fig. 11, clades A and B, respectively). In addition to rendering polyphyletic Hansen's (1997b) “Stenine group” (Euaesthetinae, Steninae, and Megalopsidiinae), that phylogeny also allows reasonable speculation about *how much* older than the currently known fossils several lineages within the Staphylinine group might be, and possibly the age of the Staphylinine group itself. Below we refer to the aforementioned clades (A) and (B).

Octavius electrospinosus sp. nov. is younger than *Nordenskioldia pentatarsus* (Lefebvre et al., 2005) and most Euaesthetine subgroup fossils are stratigraphically consistent with current hypotheses for the internal phylogeny of the Euaesthetine subgroup (Leschen and Newton, 2003; Clarke and Grebennikov, 2009; D. Clarke, unpublished data). Discovery of *O. electrospinosus* sp. nov. alone therefore does not push back the ages of Euaesthetinae, the Euaesthetine subgroup, or clade (A). But several aspects of these fossils suggest that minimum ages of these clades might be substantially older than the fossils. First, as discussed above, bradytely in these putatively monophyletic extant genera demonstrates the great antiquity of these groups. A related second point concerns the relative ages of *groups* compared to *lineages* (defined and discussed by Norell (1992: 92)). Since minimum lineage ages are always at least as old as subsumed groups and since all Cretaceous Euaesthetine subgroup fossils belong to extant monophyletic groups, the lineages subsuming these fossils are likely *much* older than their included fossils. Third, the *Octavius* + *Protopristus* clade is nested within Euaesthetinae (Clarke and Grebennikov, 2009). Additional phylogenetic research including *N. columbiana* indicates that *Nordenskioldia* may be sister to all other Euaesthetinae (D. Clarke, unpublished data) and indeed it possesses several primitive characters (see Section 5.1.2., above). Although the fossils are stratigraphically consistent with this hypothesis, if the ages of *Octavius* and *Nordenskioldia* are close to maximal then the difference between them – about 20 myr – is small relative to the generic-level lineage diversification and longevity implied by Clarke and Grebennikov's (2009) phylogeny (for example, see Section 5.1.4, above). Finally, since the oldest fossil scydmaenines are also known from Cretaceous amber (O'Keefe et al., 1997; Poinar and Brown, 2004; Chatzimanolis, et al., in preparation), clade (A) renders these fossils partially inconsistent with phylogeny. Although all of them are placed in extinct genera, like Euaesthetine subgroup fossils, these all appear to be derived taxa strongly resembling modern scydmaenines in having secondarily elongate elytra and other characters (Grebennikov and Newton, 2009). Since the minimum group age of Euaesthetinae is Early Cretaceous (~120 myr) the minimum lineage age of Scydmaeninae is also constrained to be at least this old. Moreover, the oldest Staphylinine group fossils are from the Late Jurassic (145–162MYA) and belong to Staphylininae (Zhang, 1988), thus constraining the age of the split between clades (A) and (B) to be at least this old. This further suggests that the

lineage age of Scydmaeninae + Euaesthetine subgroup is at least Early Cretaceous or even Late Jurassic.

The branching order within the Staphylinine group implies substantial diversification both before - and since - the age of the split between clades (A) and (B). A hypothesis of rapid genus-level and subfamily-level diversification within the Staphylinine group in the Late Jurassic–Early Cretaceous would be consistent with lineage ages for these subfamilies that are close to ages of the oldest known fossils, and could also help explain the difficulty in resolving strongly supported basal relationships within several staphylinid groups (Ashe and Newton, 1993; Newton and Thayer, 1995; Ashe, 2005; Clarke and Grebennikov, 2009; Grebennikov and Newton, 2009). But because of the pre-Cretaceous taphonomic bias for amber fossils (Grimaldi and Engel, 2005), there is currently no way to distinguish between this hypothesis and an alternative: Extinction (or lack) of stem group taxa may have preserved combinations of character states important for resolving basal relationships (Blagoderov et al., 2007). Nevertheless, we suggest that more ancient ages for lineages subsuming monophyletic groups and a more gradual evolution of Staphylinine group subfamily lineages (perhaps originating in the Early Jurassic) are distinct possibilities. This view is in line with Engel and Grimaldi's (2002) assessment of the pre-Cretaceous taphonomic bias for Zoraptera. It is also consistent with the observation that much Early Cretaceous and Jurassic insect fossils seem to belong to extinct stem group taxa (Grimaldi and Engel, 2005) but that most Mesozoic Staphylinine group and all Euaesthetine subgroup fossils represent derived taxa belonging to extant monophyletic groups.

7. Conclusions

Lefebvre et al. (2005: 210) suggested that the presence of apparently mostly derived staphylinid taxa in the Mesozoic, including *Libanoeuaesthetus* [now *Nordenskioldia*], “supports the hypothesis of an early division of the different branches of the Hydrophiloid–Staphylinoid lineage ... and the appearance of extant groups in the Triassic and Early Jurassic”. Our review of the Euaesthetine subgroup fossil record supports this view, but their conclusion did not make reference to a phylogenetic hypothesis including groups for which fossils were known. With new hypotheses now available (e.g., Clarke and Grebennikov, 2009; Grebennikov and Newton, 2009) and being further developed for the Euaesthetine subgroup (Clarke, in preparation.), it is now possible to integrate available fossils with phylogeny for a more robust assessment of divergence times. The phylogenetic structure of the Staphylinine group, in conjunction with several features of the Mesozoic Staphylinine group fossil record discussed above, adds further weight to this hypothesis by suggesting an origin of the Staphylinine group, and likely even several Staphylinine group subfamilies (including the Euaesthetine subgroup), much earlier than the Late Jurassic.

More generally, in biogeography there is always a question, especially in the absence of a fossil record, whether a group is old enough to have been affected by relevant geological events. The phylogeny presented by Clarke and Grebennikov (2009) and our extension of the age of *Octavius* back ~50 million years into the mid Cretaceous suggests that several lineages within the subfamily are probably old enough to have been affected by Late Jurassic and later vicariance events. Additionally, our synthesis, though lacking phylogenetic integration of Euaesthetine subgroup fossils, will facilitate careful consideration of several calibration points for future DNA-based evolutionary analyses of the Staphylinine group relying on divergence time estimates. More detailed taxonomic and morphological study of all the above-mentioned fossils is, however, badly needed. Future morphology-based phylogenetic analyses

should, where possible, include these fossils in order to corroborate ideas of their phylogenetic placement mentioned here.

Acknowledgements

We thank David Grimaldi and Michael Engel for access to the already prepared specimen; M.K. Thayer for commenting on the MS; A.F. Newton for providing access to literature and databases; Corrie Moreau for access to her microscope, which we used to create Fig. 2; Thomas Wesener for translating some German literature; and V. Puthz and one anonymous reviewer for providing useful criticism that improved the manuscript. DC was supported by NSF-PEET grant #0118749 to M.K. Thayer and A.F. Newton and a Lester Armour Graduate Fellowship from the Field Museum of Natural History. SC was supported by NSF-DEB 0741475 to S. Chatzimanolis and M.S. Engel.

References

- Ashe, J.S., 2005. Phylogeny of the tachyporine group subfamilies and 'basal' lineages of the Aleocharinae (Coleoptera: Staphylinidae) based on larval and adult characteristics. *Systematic Entomology* 30, 3–37.
- Ashe, J.S., Newton Jr., A.F., 1993. Larvae of *Trichophya* and phylogeny of the tachyporine group of subfamilies (Coleoptera: Staphylinidae) with a review, new species and characterization of the Trichophyinae. *Systematic Entomology* 18, 267–286.
- Benick, L., 1943. Ein *Stenus* aus dem baltischen Bernstein: *St. (Parastenus) priscus* n. sp. (Coleoptera: Staphylinidae). *Arbeiten über Morphologische und Taxonomische Entomologie aus Berlin–Dahlem* 10 (2/3), 101–104.
- Blagoderov, V., Grimaldi, D.A., Fraser, N.C., 2007. How time flies for flies: Diverse Diptera from the Triassic of Virginia and early radiation of the order. *American Museum Novitates* 3572, 1–39.
- Chatzimanolis, S., Engel, M.S., Newton, A., Grimaldi, D. New ant-like stone beetles in mid-Cretaceous amber from Myanmar (Coleoptera: Staphylinidae: Scydmaeninae). *Cretaceous Research*, in preparation.
- Clarke, D.J., Grebennikov, V.V., 2009. Monophyly of Euaesthetinae (Coleoptera: Staphylinidae): phylogenetic evidence from adults and larvae, review of austral genera, and new larval descriptions. *Systematic Entomology* 34, 346–397.
- Cognato, A.I., Grimaldi, D.A., 2008. 100 million years of morphological conservation in a bark beetle (Coleoptera: Curculionidae: Scolytinae). *Systematic Entomology* 34, 1–8.
- Coiffait, H., 1958. Révision du genre *Octavius* Fauvel (Col. Staphylinidae). *Revue Française d'Entomologie* 25, 78–98.
- Coiffait, H., Decou, V., 1970. Recherches sur les Coléoptères endogés des Carpates Roumaines. III Staphylinidae – Euaesthetinae: *Euaesthetotyphlus almajensis*, n.gen., n.sp. *Annales de Spéléologie* 25, 378–382.
- Cruickshank, R.D., Ko, K., 2003. Geology of an amber locality in the Hukawng Valley, Northern Myanmar. *Journal of Asian Earth Sciences* 21, 441–455.
- Downie, N.M., Arnett Jr., R.H., 1996. The beetles of Northeastern North America Volume 1: Introduction; suborders Archostemata, Adephaga, and Polyphaga, thru Superfamily Cantharoidea. Sandhill Crane Press, Gainesville, 880p.
- Eldredge, N., Stanley, S.M. (Eds.), 1984. *Living Fossils*. Springer, New York, p. 291.
- Engel, M.E., Grimaldi, D.A., 2002. The first Mesozoic Zoraptera (Insecta). *American Museum Novitates* 3362, 1–20.
- Fisher, D.C., 1990. Rates of evolution—living fossils. In: Briggs, D.E.G., Crowther, P.R. (Eds.), *Palaeobiology: A Synthesis*. Blackwell Scientific Publications, Oxford, pp. 152–159.
- Förster, B., 1891. Die Insekten des "Plattigen Steinmergels" von Brunstatt. *Abhandlungen zur Geologischen Spezialkarte von Elsass-Lothringen* 3, 333–594.
- Fraser, N.C., Grimaldi, D.A., Olsen, P.E., Axsmith, B., 1996. A Triassic Lagerstätte from eastern North America. *Nature* 380, 615–619.
- Gore, P.J.W., 1988. Paleogeology and sedimentology of a Late Triassic lake, Culpeper Basin, Virginia, USA. *Paleogeography, Paleoclimatology, Paleogeology* 62, 593–608.
- Grebennikov, V.V., 2005. Older-instar larvae of Pseudopsinae (Coleoptera: Staphylinidae): morphological description of three genera and phylogenetic placement of the subfamily. *European Journal of Entomology* 102, 713–724.
- Grebennikov, V.V., Newton, A.F., 2009. Good-bye Scydmaenidae, or why the ant-like stone beetles should become Staphylinidae sensu latissimo (Coleoptera). *European Journal of Entomology* 106, 275–301.
- Grimaldi, D.A., 1996. *Amber: Window to the Past*. Abrams/AMNH, New York.
- Grimaldi, D.A., Engel, M.S., 2005. *Evolution of the Insects*. Cambridge University Press, New York, xv + 755 pp.
- Grimaldi, D.A., Engel, M.S., Nascimbene, P.C., 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity and paleontological significance. *American Museum Novitates* 3361, 1–71.
- Hammond, P.M., 1979. Wing-folding mechanisms of beetles, with special reference to investigations of adephagan phylogeny (Coleoptera). In: Erwin, T.L., Ball, G.E.,

- Whitehead, D.R., Halpern, A.L. (Eds.), *Carabid Beetles: Their Evolution, Natural History, and Classification*. W. Junk, The Hague, pp. 113–180.
- Hansen, M., 1997a. Evolutionary trends in "staphyliniform" beetles (Coleoptera). *Steenstrupia* 23, 43–86.
- Hansen, M., 1997b. Phylogeny and classification of the staphyliniform beetle families (Coleoptera). *Biologiske Skrifter, Det Kongelige Danske Videnskaberne Selskab* 48, 1–339.
- Heer, O., 1856. Ueber die fossilen Insekten von Aix in der Provence. *Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich* 1, 1–40. taf. I, II.
- Herman, L.H., 2001. Catalog of the Staphylinidae (Insecta: Coleoptera). 1758 to the end of the second millennium. IV. Staphylinine Group (Part 1). Euaesthetinae, Leptotyphlinae, Megalopsidiinae, Oxyporinae, Pseudopsinae, Solieriinae, Steninae. *Bulletin of the American Museum of Natural History* 265, 1807–2440.
- Heyden, C., Heyden, L., 1866. Käfer und Polypen aus der Braunkohle des Siebengebirges. In: Meyer, von, H. (Ed.), *Beiträge zur Naturgeschichte der Vorwelt*, vol. 15. *Palaeontographica*, pp. 131–156.
- Kirejtshuk, A.G., Ponomarenko, A.G., Kurochkin, A.S., Alexeev, A.V., Gratshev V.G., Solodovnikov, A.Y., Krell, F.T., Soriano, C. The Beetle (Coleoptera) Fauna of the Insect Limestone (Late Eocene or Early Oligocene), Isle of Wight, South England, Occasional Papers in Palaeontology, Supplementum. In Press.
- Kulicka, R., Ślipiński, S.A., 1996. A review of the Coleoptera inclusions in the Baltic amber. *Prace Muzeum Ziemi* 44, 5–12.
- Lawrence, J.F., Newton Jr., A.F., 1982. Evolution and classification of beetles. *Annual Review of Ecology and Systematics* 13, 261–290.
- Lefebvre, F., Vincent, B., Azar, D., Nel, A., 2005. The oldest beetle of the Euaesthetinae (Staphylinidae) from Early Cretaceous Lebanese amber. *Cretaceous Research* 26, 207–211.
- Leschen, R.A.B., Newton Jr., A.F., 2003. Larval description, adult feeding behavior, and phylogenetic placement of *Megalopinus* (Coleoptera: Staphylinidae). *The Coleopterists Bulletin* 57, 469–493.
- Liow, L.H., 2004. A test of Simpson's "Rule of the survival of the relatively unspecialized" using fossil crinoids. *The American Naturalist* 164, 431–443.
- Makhan, D., 2007. *Hawkeswoodedaphus* gen. nov. from South America (Coleoptera: Staphylinidae: Euaesthetinae). *Calodema Supplementary Paper* 54, 1–7.
- Nascimbene, P., Silverstein, H., 2000. The preparation of fragile Cretaceous ambers for conservation and study of the organismal inclusions. In: Grimaldi, D. (Ed.), *Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey*. Backhuys, Leiden, pp. 93–102.
- Newton, A.F., Franz, H., 1998. World catalogue of the genera of Scydmaenidae. *Koleopterologische Rundschau* 68, 137–165.
- Newton, A.F., Thayer, M.K., Ashe, J.S., Chandler, D.S., 2000[2001]. Staphylinidae Latreille, 1802. In: Arnett Jr., R.H., Thomas, M.C. (Eds.), *American Beetles*. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia, vol. 1. CRC Press, Boca Raton, Florida, pp. 272–418.
- Newton, A.F., Thayer, M.K., 1995. Protopselaphinae new subfamily for *Protopselaphus* new genus from Malaysia, with a phylogenetic analysis and review of the Omaliine Group of Staphylinidae including Pselaphidae (Coleoptera). In: Pakaluk, J., Ślipiński, S.A. (Eds.), *Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson*. Muzeum i Instytut Zoologii PAN, Warszawa, pp. 219–320.
- Norell, M.A., 1992. Taxic origin and temporal diversity: The effect of phylogeny. In: Novacek, M.J., Wheeler, Q.D. (Eds.), *Extinction and Phylogeny*. Columbia University Press, New York, pp. 88–118.
- O'Keefe, S.T., Pike, T., Poinar, G., 1997. *Palaeoleptochromus schaufussi* (gen. nov., sp. nov.), a new antlike stone beetle (Coleoptera: Scydmaenidae) from Canadian Cretaceous amber. *The Canadian Entomologist* 129, 379–385.
- Orousset, J., 1987. Un nouveau genre d'Euaesthetinae africain: *Macrotrellus pulcher* n. gen., n. sp. *Bulletin de la Société Entomologique de France* 91, 219–227.
- Orousset, J., 1988. Insectes, Coléoptères, Staphylinidae, Euaesthetinae. *Faune de Madagascar* 71, 1–208.
- Oustalet, É., 1874. Recherches sur les Insectes Fossiles des Terrains Tertiaires de la France. Deuxième Partie, Insectes Fossiles d'Aix en Provence. *Annales des Sciences Géologiques* 5, 1–347. 6 plates.
- Perrichot, V., 2004. Early Cretaceous amber from south-western France: insight into the Mesozoic litter fauna. *Geologica Acta* 2, 9–22.
- Poinar Jr., G., Brown, A.E., 2004. A new subfamily of Cretaceous antlike stone beetles (Coleoptera: Scydmaenidae: Hapsomelinae) with an extra leg segment. *Proceedings of the Entomological Society of Washington* 106, 789–796.
- Poinar Jr., G., Lambert, J.B., Wu, Y., 2007. Araucarian source of fossiliferous Burmese amber: spectroscopic and anatomical evidence. *Journal of the Botanical Research Institute of Texas* 1, 449–455.
- Puthz, V., 1977. Die Gattung *Octavius* Fauvel (Coleoptera: Staphylinidae) weltweit verbreitet! *Opuscula Zoologica (Budapest)* 14, 105–126.
- Puthz, V., 2005. Die erste Euaesthetine aus dem Baltischen Bernstein (Coleoptera: Staphylinidae) 90. Beitrag zur Kenntnis der Euaesthetinen. *Entomologische Blätter* 101, 127–128.
- Puthz, V., 2008a. Über Euaesthetinen aus dem Bernstein (Coleoptera, Staphylinidae) 99. Beitrag zur Kenntnis der Euaesthetinen[sic]. *Entomologische Blätter* 103/104, 59–62.
- Puthz, V., 2008b. *Stenus* Latreille und die segensreiche Himmelstochter (Coleoptera, Staphylinidae) 300. Beitrag zur Kenntnis der Steninen. *Linzer Biologische Beiträge* 40/1, 137–230.
- Ryvkin, A.B., 1988. *Novye Melovye Staphylinidae [sic] (Insecta) s Dal'nego Vostoka*. *Paleontologicheskii Zhurnal* 1988 (4), 103–106.
- Scheerpeltz, O., 1974. Coleoptera: Staphylinidae. In: Hanström, B.P.B., Brinck, P., Rudebeck, G. (Eds.), *South African Animal Life*, vol. 15. *Swedish Natural Science Research Council*, Stockholm, pp. 43–394.
- Schlüter, T., 1978. Zur Systematik und Palökologie harzkonservierter Arthropoda einer Taphozönose aus dem Cenomanium von NW-Frankreich. A: *Geologie und Paläontologie*. Berliner Geowissenschaftliche Abhandlungen 9, 1–150.
- Scudder, S.H., 1900. Adephagous and clavicorn Coleoptera from the Tertiary deposits at 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, 1–148.
- Simpson, G.G., 1944. *Tempo and Mode in Evolution*. Columbia University Press, New York, 237 pp.
- Stanley, S.M., 1984. Does bradytely exist? In: Eldredge, N., Stanley, S.M. (Eds.), *Living Fossils*. Springer Verlag, New York, pp. 278–280.
- Thayer, M.K., 2005. 11.7. Staphylinidae. In: Beutel, R.G., Leschen, R.A.B. (Eds.), *Handbook of Zoology, Coleoptera. Evolution and Systematics, Archostemata, Adephaga, Myxophaga, Staphyliniformia, Scarabaeiformia, Elateriformia*, vol. 1. De Gruyter, Berlin, pp. 296–344.
- Tikhomirova, A.L., 1968. Staphylinid beetles from the Jurassic of Karatau (Coleoptera: Staphylinidae). In: Rohdendorf, B.B. (Ed.), *Jurassic Insects of Karatau*. *Academiya Nauk SSSR, Moscow*, pp. 139–154. in Russian; Translation via F.M. Carpenter, 1975.
- Wickham, H.F., 1913. Fossil Coleoptera from Florissant in the United States National Museum. *Proceedings of the United States National Museum* 45, 283–303.
- Zhang, J., 1988. The Late Jurassic fossil Staphylinidae (Coleoptera) of China. *Acta Entomologica Sinica* 31, 79–84.
- Zherikhin, V.V., Ross, A.J., 2000. A review of the history, geology and age of Burmese amber (Burmite). *Bulletin of the Natural History Museum. London (Geology)* 56, 3–10.