Gondwana Research 45 (2017) 275–281

Contents lists available at ScienceDirect

Gondwana Research

journal homepage: www.elsevier.com/locate/gr

Evolutionary stasis in enigmatic jacobsoniid beetles

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ARTICLE INFO

Article history:
Received 11 September 2016
Received in revised form 19 December 2016
Accepted 22 December 2016
Available online 12 February 2017

Handling Editor: I. Somerville

Keywords:
Jacobsoniidae
Coleoptera
Bradytely
Evolutionary stasis
Amber

ABSTRACT

Jacobsoniidae is a small but perplexing beetle family, with unknown phylogenetic relationships to other polyphagan Coleoptera. To date, only a single fossil jacobsoniid has been described, from Eocene Baltic amber (~40 Ma). Here, we push back the oldest definitive record of Jacobsoniidae by approximately 60 million years with a new fossil species recovered from mid-Cretaceous (~99 Ma) Burmese amber from Myanmar. Remarkably, exploration of the fossil's morphology with confocal laser scanning microscopy revealed that it belongs to an extant genus, *Derolathrus*. The similarity of the new taxon, *Derolathrus abyssus* n. sp., to modern congeners provides a striking example of morphological stability over deep evolutionary time—a possible outcome of long-term persistence of mesic microhabitats, a hypothesis we argue is supported by a variety of other Recent, litter-inhabiting arthropod taxa now known to be largely unchanged since the Mesozoic. Many such examples belong to the Staphylinoidea—a hyperdiverse beetle superfamily that dominates contemporary mesic habitats, and with which Jacobsoniidae may have a close phylogenetic relationship.

This published work has been registered in ZooBank, http://zoobank.org/urn:lsid:zoobank.org:pub:7C65ACAF-456E-4301-BDD7-0A801768EEB9.

1. Introduction

The recent explosion of work on Mesozoic fossil deposits has yielded numerous cases of modern insect genera that date to the Cretaceous or Jurassic, revealing the potential of some lineages to persist relatively unchanged over very long periods of evolutionary time (Engel and Grimaldi, 2002; Clarke and Chatzimanolis, 2009; Arillo et al., 2009; Cognato and Grimaldi, 2009; Chatzimanolis et al., 2013; Peris et al., 2015; Peris and Háva, 2016; Yamamoto and Solodovnikov, 2016). Within the largest metazoan order, Coleoptera (>390,000 spp.), the polyphagan family Jacobsoniidae represents a minor lineage, comprising only 23 species in three genera: *Sarothrias* Grouvelle, 1918; *Saphophagus* Sharp, 1886, and *Derolathrus* Sharp, 1908 (Háva and Löbl, 2005; Lawrence and Leschen, 2010; Peck, 2010; Bi et al., 2015; Cai et al., 2016). Jacobsoniid beetles are morphologically enigmatic, and consequently their systematic placement within the Coleoptera is controversial. Crowson (1959, 1960) proposed a relationship between Jacobsoniidae and the superfamily Staphylinoidea (infraorder Staphyliniformia), but there has been little agreement among subsequent authors, who have placed the family in various coleopteran infraorders: within Bostrichiformia (e.g., Lawrence and Newton, 1995; Philips et al., 2002), Cucujiformia (e.g., Sen Gupta, 1979) and Derodontiformia (Lawrence and Leschen, 2010). Consistent with Crowson's original hypothesis however, a close affinity with Staphylinoidea has recently been revived by support from both morphological and molecular phylogenetic studies (Lawrence et al., 2011; McKenna et al., 2015; Toussaint et al., 2017). Consequently, in the most recent higher level classification scheme, Lawrence (2016) removed Jacobsoniidae from Derodontiformia but nevertheless treated the taxon as *incertae sedis* ("Series? Superfamily?") within the suborder Polyphaga, reflecting lingering uncertainty over the true systematic position of Jacobsoniidae.

Jacobsoniidae can be recognized by their small-minute size (0.65–2.5 mm) and narrow, elongate body shape (~4 times as long as wide) (Philips et al., 2002; Lawrence and Leschen, 2010), with important characters including an elongate prothorax, lack of a visible scutellum, and a markedly elongate metaventrite (at least 2.5 times as long as the mesoventrite) (Lawrence and Leschen, 2010). The biology of jacobsoniids is poorly known: the beetles are typically found in litter and under bark, but also associate with fungi and bat guano (Philips et al., 2002); one genus (*Sarothrias*) may be myrmecophilous, but this is based purely on an overall morphology that is possibly suggestive of an inquilinous lifestyle (Philips et al., 2002). Until very recently,

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http://dx.doi.org/10.1016/j.gr.2016.12.008

Jacobsoniidae lacked a fossil record, but the discovery of *Derolathrus groehni* Cai et al., 2016 in Lutetian Baltic amber extended the age of the family back to the Middle Eocene (Cai et al., 2016). This fossil was particularly notable because *Derolathrus* is an extant genus. Members of *Derolathrus* can be easily recognized by their minute size (0.65–1.2 mm), yellowish brown body, 3-3-3 tarsal formula, antenna with an apical club composed of two fused segments (antennomeres 10 and 11), and an aciculate apical maxillary palpomere (Sen Gupta, 1979; Philips et al., 2002; Lawrence and Ślipiński, 2013). Recent members of the genus are distributed worldwide, but are particularly well represented in tropical areas and on oceanic islands, in particular Mauritius and Fiji (Dajoz, 1973; Sen Gupta, 1979; Lawrence and Leschen, 2010).

Here, we push the age of Jacobsoniidae back significantly further, with a new extinct species from Upper Cretaceous (earliest Cenomanian; ~99 Ma) Burmese amber from Myanmar. This is the first definitive fossil of the family from the Mesozoic. Remarkably, this species also belongs to *Derolathrus*, demonstrating an extraordinary degree of morphological stability of these beetles over deep evolutionary time.

2. Materials and methods

This study is based on a single jacobsoniid specimen embedded in a transparent piece of Upper Cretaceous Burmese amber. While several localities yield Burmese amber, commercial extraction and scientific studies are focused on only a single site, in the Hukawng Valley, Kachin State of northern Myanmar, located approximately 20 km Southwest of the town of Tanai (Zherikhin and Ross, 2000; Cruickshank and Ko, 2003; Ross et al., 2010). The age of Burmese amber is earliest Cenomanian (98.79 ± 0.62 Ma) based on radioisotopic dating of zircon crystals obtained from the amber matrix (Shi et al., 2012). The amber has a high concentration and diversity of inclusions. Ross et al. (2010) listed 36 orders, 216 families and 228 species of arthropods, and new records are continually being added.

The holotype was originally embedded in an elliptical, medium-sized amber piece (18.1 × 29.9 × 7.5 mm). After cutting and polishing, the amber was prepared as a small, flattened piece (8.92 × 16.10 × 1.24 mm) to allow detailed observation of the beetle. The jacobsoniid is a complete adult specimen and relatively well preserved, although some body parts such as the dorsal surface of the pronotum are deformed, preventing accurate observation. The type specimen is from SY's private collection, currently deposited in the American Museum of Natural History, New York, USA (AMNH), with accession number AMNH Bu-SY6. Compound photomicrographs were produced by making a temporary slide mount of the amber piece in glycerol under a cover slip; a Zeiss Axiocam (Zeiss, New York, NY, USA) mounted on a Zeiss compound microscope was used to make image stacks with Zen software, with LED lighting coming from above. Montages were produced in Zerene Stacker (Richland, WA, USA). For confocal laser scanning microscopy (CLSM), the specimen was mounted in glycerol under a cover slip, and a Leica SP5 confocal with a 488 nm laser and Hybrid detectors was used; confocal sections were taken 1 μm apart through the beetle body, and image stacks were maximally projected to produce the reconstructions in Figs. 2 and 3. Morphological terminology generally follows Philips et al. (2002), Lawrence and Leschen (2010), and Cai et al. (2016).

3. Results

3.1. Systematic palaeontology

Order: Coleoptera Linnaeus, 1758
Suborder: Polyphaga Emery, 1886
Family: Jacobsoniidae Heller, 1926
Genus *Derolathrus* Sharp, 1908
Derolathrus abyssus Yamamoto and Parker, sp. n.

ZooBank LSID: http://zoobank.org/urn:lsid:zoobank.org:act:51DE5FC1-8674-4BAF-8C07-5187E875D4D8

3.2. Material

Holotype, one complete adult specimen, sex undetermined; No. AMNH Bu-SY6, preserved in the collection of AMNH.

3.3. Etymology

The specific epithet refers to the abyss of evolutionary time that separates the new fossil taxon from living species of its genus.

3.4. Age and locality

Earliest Cenomanian (ca. 99 Ma; Shi et al., 2012), Upper Cretaceous; Burmese amber from the Hukawng Valley, Kachin, northern Myanmar.

3.5. Systematic placement

The specimen described here can be readily assigned to the family Jacobsoniidae by its small, narrowly elongate body, elongate prothorax, lack of a visible scutellum, concealed antennal insertions, and markedly elongate metaventrite (Philips et al., 2002; Lawrence and Leschen, 2010). Among the three genera of the family, the new species unambiguously belongs to *Derolathrus* Sharp, based on its combination of a minute body size (0.73 mm), elongate body shape, 3-3-3 tarsal formula, eleven-segmented antenna including an apical club composed of two fused flagellomeres, presence of five free abdominal ventrites, and aciculate apical maxillary palpomeres (Sen Gupta, 1979; Philips et al., 2002; Lawrence and Ślipiński, 2013).

3.6. Diagnosis

Derolathrus abyssus can be separated from its nine described congeners by its less elongate metaventrite, which is slightly shorter than the abdomen (versus metaventrite equal to or longer than the abdomen in congeners). Additionally, while other *Derolathrus* species have elytra covering the entire abdomen, *D. abyssus* has slightly shorter elytra, which leave most of abdominal tergite VII exposed. Further morphological separation from known extant and extinct species is attempted here. Compared to the micropth**t**halmic (small-eyed) and also apterous *D. anophthalmus* (Franz) from the Canary Islands (Cai et al., 2016), *D. abyssus* has fully developed eyes with at least 36 ommatidia and possesses hind wings. *Derolathrus abyssus* can also be distinguished based on its larger eyes from *D. parvulus* (Rücker) (Madeira), *D. troglophilus* (Sen Gupta) (Fiji), and †*D. groehni* Cai et al. from Baltic amber. In contrast to *D. atomus* Sharp (Hawai'i) and *D. insularis* (Dajoz) (Mauritius), which have abdominal ventrites 1–4 subequal in length, *D. abyssus* has a much longer ventrite 1 compared to ventrites 2–4. *Derolathrus insularis* also has a distinctly longer maxillary palpomere 3 (mp3), which is nearly as long as mp2, whereas mp3 of *D. abyssus* is only half as long as mp2. From *D. sharpi* Grouvelle (Guadeloupe), *D. abyssus* can be discriminated by the absence of four longitudinal rows of punctures on the head (Peck, 2010). Furthermore, from *D. cavernicolus* Peck (North America), the new species can be separated by its distinct, unfused metaventrite and abdominal ventrite. Finally, *D. abyssus* can be separated from *D. ceylonicus* (Sen Gupta) (Sri Lanka) by its less elongate prothorax. Because the holotype of *D. abyssus* has a deformed pronotum that prevents us from determining the presence of a longitudinal groove, it is difficult to assess the new species' affinity with other described species of *Derolathrus*. However, considering its large, well-developed eyes, the general structure of the head capsule and elytra, we think *D. abyssus* may be most similar to *D. ceylonicus*.

3.7. Description

Body length 0.73 mm. Shape subcylindrical, dorsoventrally compressed, narrowly elongate (Figs. 1, 2). Color uniformly yellowish-brown (Fig. 1). Surface somewhat glossy, covered with rugose microsculpture on head, pronotum, metaventrite and abdomen (lacking such microsculpture on elytra); dorsal and ventral surfaces with sparsely scattered setae, lacking obvious punctures (Figs. 2, 3).

Head oval, widest across eyes (0.142 mm long, 0.125 mm wide); abruptly constricted behind eyes, forming distinct neck (Fig. 1A–B); eyes large, rounded, somewhat bulging laterally, with at least 36 ommatidia (facets counted in the right eye) (Fig. 3A); temples short, about one-third of eye length (left eye; Fig. 3A); head lacking basal fovea and longitudinal rows of punctures on vertex. Mandibles small, inconspicuous. Maxillary palps consisting of three articles, apical palpomere (mp3) aciculate, short, about half as long as mp2; penultimate palpomere much larger, swollen (Fig. 3A). Gular sutures not visible. Antenna with 11 antennomeres; antennal insertion concealed from above; antennomeres 1–2 distinctly larger than antennomere 3; antennomeres 3–9 moniliform; club composed of two fused segments (10 and 11) as indicated by visible suture, the apical segment globose in shape (Fig. 3A; see Peck, 2010).

Prothorax deformed during preservation (Fig. 2). Pronotum slightly wider than head, only moderately elongate (0.175 mm long, 0.161 mm wide), narrower than elytra, tapering weakly to posterior margin, which is narrower than anterior margin; dorso-lateral margin without carina; discal surface deformed, difficult to assess presence of longitudinal median groove or depression; prosternum broad, not punctate; prosternal process narrow and long, with rounded apex; procoxal cavities posteriorly open (Fig. 3D). Mesoventrite short; mesocoxal process not visible. Mesocoxae only narrowly separated. Metaventrite long, about 0.75 times as long as visible abdomen, gradually widened posteriorly; surface microstrigose. Metacoxae widely separated. Trochanters large, trapezoidal, gradually widened to apex (Fig. 3D–E). Femora slender, slightly shorter than tibiae. Tibiae slender, gradually widened to apex, apical spurs not visible (Fig. 3D–F). Tarsal formula 3-3-3; first and second tarsomeres short, minute, difficult to distinguish (Fig. 3E); third tarsomeres elongate, weakly broadened apically, longer than basal two combined; two tarsal claws long, simple (Fig. 3D, F). Mesoscutellum absent (Fig. 3B). Elytra narrowly elongate (each 0.96 mm long, 0.39 mm wide), nearly entire, but largely exposing abdominal tergite VII (Fig. 3C); elytron broadest around middle, left apex rounded-truncate (apex of right elytron acutely pointed, seemingly during preservation) (Fig. 3C); elytral striae/sulci present only as

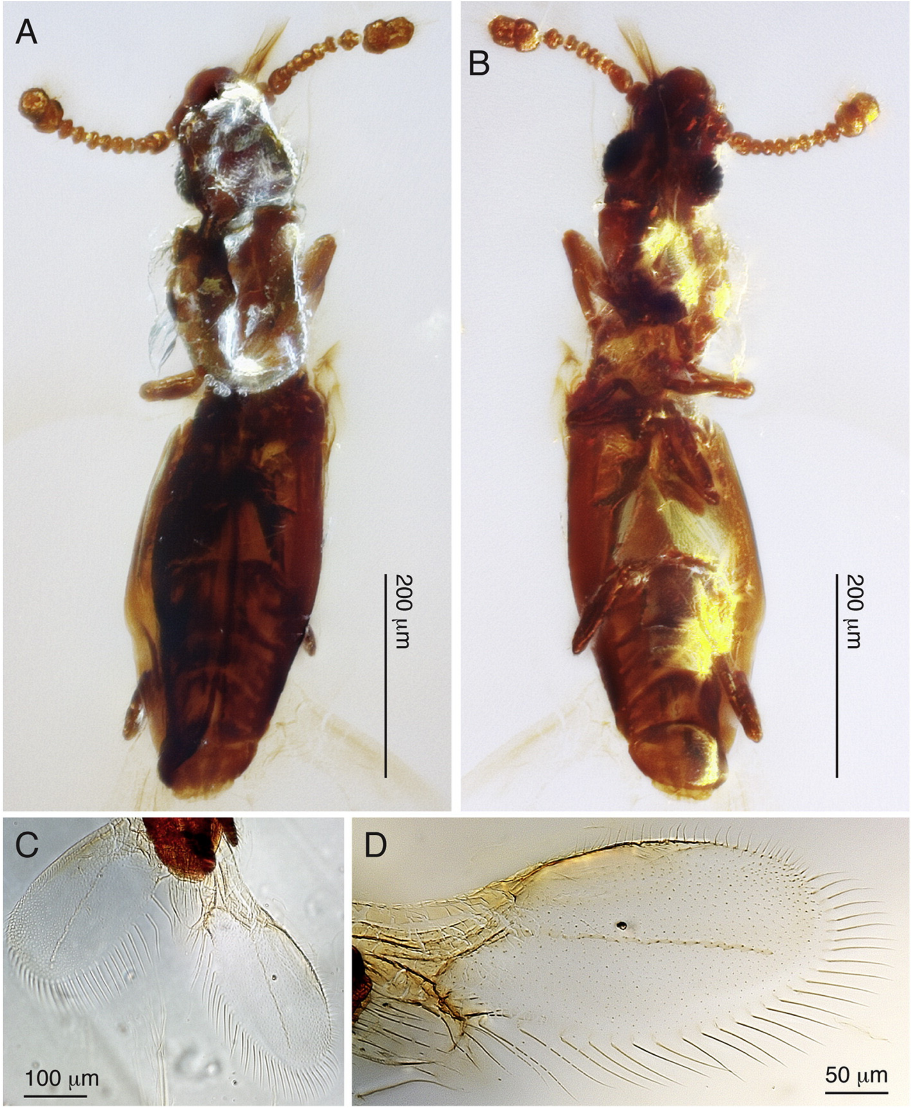

Fig. 1. Photographs of holotype (AMNH Bu-SY6) of *Derolathrus abyssus* Yamamoto and Parker, sp. n., in Upper Cretaceous Burmese amber. A, dorsal habitus; B, ventral habitus; C, D, hind wings in ventral view, showing fringes of hairs along anterior and posterior margins. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

Fig. 2. CLSM images of holotype (AMNH Bu-SY6) of *Derolathrus abyssus* Yamamoto and Parker, sp. n., in Upper Cretaceous Burmese amber. A, dorsal habitus; B, ventral habitus. Scale bars: 150 μm (A, B).

nearly complete sutural sulcus originating from pit near inner apical margin (Fig. 3B, arrow), together with marginal stria extending almost to apex (Figs. 2A, 3B–C); short discal stria absent—mentioned here because it is present in some *Derolathrus* species, e.g., Peck (2010). Elytron surface smooth, with short setae in vague longitudinal rows; elytral epipleura narrow, long, ending at middle of ventrite 4 (sternite VI) (Fig. 3F). Hind wings well developed, longer than pterothorax and abdomen combined; venation highly reduced; anterior margin with ~30 short hairs, posterior margin with at least ~30 longer hairs, forming fringe (based on left hind wing) (Fig. 1C, D).

Abdomen slightly longer than metaventrite, gradually tapered posteriorly (Figs. 2B, 3F). Abdominal ventrites 1 and 5 much longer compared to ventrites 2–4 (Fig. 3F); ventrite 1 not fused with metaventrite, with suture distinct; ventrites 2–4 almost subequal in length.

4. Discussion

4.1. Bradytely in Jacobsoniidae and the long-term persistence of mesic habitats

The general anatomy of *Derolathrus abyssus* is externally very similar to that of extant members of *Derolathrus*, including minute mouthpart characters, hind wing morphology and antennal structures. A comparison with the published description of *D. groehni*, the single known fossil species from Baltic amber (Cai et al., 2016), likewise revealed no substantial differences between these extinct taxa that could warrant creation of a new genus. Hence, we suggest that the genus *Derolathrus* provides a new example of bradytely: long-term morphological stasis of an organismal lineage over deep evolutionary time (Simpson, 1944). In this instance, the morphology of *Derolathrus* appears to have changed little since the mid-Cretaceous. We posit that the primary reason for this >99 million year stasis is the relative stability of the habitat types the genus occupies, as proposed by Clarke and Chatzimanolis (2009) for the euaesthetine group of staphylinid beetles. Presumably, mesic microhabitats such as leaf litter, fungi, rotten wood and underneath bark in which modern *Derolathrus* beetles occur have persisted since the time of Burmese amber production. The discovery in Burmese amber and several other Cretaceous deposits of additional bradytelic beetle taxa with presumed mesic or subcortical palaeoecologies would seem to support this hypothesis. These include *Microborus* bark beetles (Curculionidae: Scolytinae) (Cognato and Grimaldi, 2009), the prostomid *Vetuprostomis* (Engel and Grimaldi, 2008), the dermestid *Attagenus* (Peris and Háva, 2016), the ptinid *Stegobium* (Peris et al., 2015), the palmetto beetle *Smicrips* (Cai and Huang, 2016), and a number of litter-dwelling staphylinids including *Octavius* (Euaesthetinae), *Stenus* (Steninae) (Clarke and Chatzimanolis, 2009), *Phloeocharis* (Phloeocharinae) (Chatzimanolis et al., 2013), *Megalopinus* (Megalopsidiinae) (Yamamoto and Solodovnikov, 2016) *Oxyporus* (Yue et al., 2011) and scydmaenines of the tribes Clidicini, Eutheiini and Cephenniini (Kirejtshuk et al., 2015; Jałoszyński and Peris, 2016; Jałoszyński and Perkovsky, 2016). Outside of the Coleoptera, evolutionary stasis in bryophyte-feeding *Litoleptis* flies (Diptera: Rhagionidae) (Arillo et al., 2009), subcortical microwhip scorpions (Palpigradi) (Engel et al., 2016) and litter-dwelling collembolans (Sánchez-García and Engel, 2016) further attests to the continuity from the mid-Cretaceous (at least) of many lineages that occupy mesic microhabitats in forests, and hence the deep time stability of these habitats. As noted by Chatzimanolis et al. (2013), a further factor promoting lineage survival might be the small body sizes of many of these taxa, although the relationship between size and extinction risk—extensively studied in mammals (Cardillo et al., 2005; Tomiya, 2013)—is poorly understood in terrestrial arthropods (Chown and Gaston, 2010).

Notably however, despite these multiple examples of stasis, the absence thus far of several major Recent groups of litter beetles from Cretaceous deposits implies that the fauna of mesic habitats has nevertheless changed substantially since the Mesozoic. For example, within Staphylinidae, although a number of Cretaceous scydmaenine fossils have now been documented, members of the massively speciose, abundant and widespread Recent genus *Euconnus* have not been recovered (Jałoszyński and Peris, 2016). Similarly, a variety of pselaphines have been found in Cretaceous ambers (Peris et al., 2014; Parker, 2016a), but aside from possible members of the basal-most supertribe, Faronitae, definitive crown-group members of Recent tribes have not been reported, despite being hugely diverse and ecologically abundant today, and also prevalent in Cenozoic ambers (Schaufuss, 1890; Chatzimanolis and Engel, 2013; Parker and Grimaldi, 2014). An analogous situation is seen in Aleocharinae; the small, early-diverging tribes Deinopsini and Mesoporini are known from Burmese amber (Cai and Huang, 2015; Yamamoto et al., 2016), but members of the “higher Aleocharinae” that possess a tergal defensive gland (Steidle and Dettner, 1993; Ashe, 2005), and comprise 99% of the subfamily's contemporary species richness and the majority of its abundance in mesic habitats, are presently unknown prior to the Eocene (Parker, 2016b). If such absences are genuine, or at least indicative of the ecological scarcity of these groups, then mesic habitats appear to have witnessed major radiations of several groups that are predominant today. The causes of such inferred radiations are unknown, but probably the most dramatic change to have occurred in such habitats is the rise to ecological dominance of modern ants and, to a lesser extent, termites during the Cenozoic (Grimaldi and Agosti, 2000; Engel et al., 2009; LaPolla and Dlussky, 2013). Falling under the regulation of social insects may have played an influential role in shaping the beetle composition of modern litter assemblages, selecting for the groups that are abundant today (Parker, 2016b).

4.2. Relationship of Jacobsoniidae to Staphylinoidea

The discovery of *D. abyssus* in Burmese amber reveals that Jacobsoniidae had begun diversifying into crown-group genera by at least the mid-Cretaceous. Recent molecular dating studies of the Coleoptera, which have incorporated a single species of *Derolathrus* and a member of the additional jacobsoniid genus *Saphophagus*, are

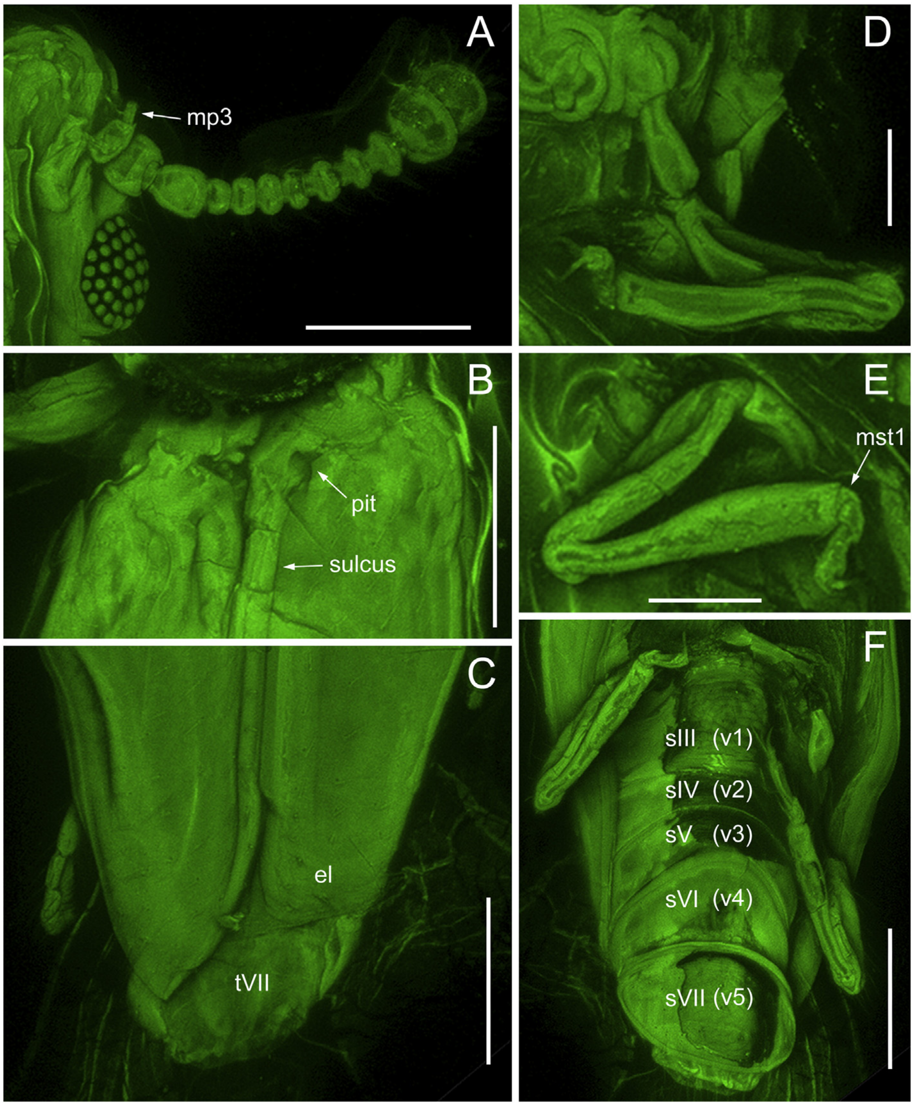

Fig. 3. Close-up CLSM images of holotype (AMNH Bu-SY6) of *Derolathrus abyssus* Yamamoto and Parker, sp. n., in Upper Cretaceous Burmese amber. A, antenna, maxillary palpus, and eye with ommatidia; B, basal area of elytra, showing a pair of small pits (arrow) and sutural stria/sulcus; C, apex of elytra, with slightly exposed abdomen; D, prosternal process and foreleg; E, midleg; F, abdomen, showing elongate ventrite 1. Dorsal view (B, C); ventral view (A, D, E, F). Abbreviations: el, elytron; mp, maxillary palpomere; mst, mesotarsomere; s, sternite, t, tergite; v, ventrite. Scale bars: 75 μm (A, B, C, F), 30 μm (D, E).

consistent with this early, Mesozoic diversification, estimating the split between these two genera to have occurred in the late Jurassic (164.32 Ma in McKenna et al., 2015, and 166.38 Ma in Toussaint et al., 2017). These studies also indicate a close affinity between Jacobsoniidae and Staphylinoidea: under Bayesian analysis, Jacobsoniidae was recovered as sister to Staphylinoidea, while under Maximum Likelihood the family emerged within Staphylinoidea, as sister to a clade formed by Hydraenidae and Ptiliidae (McKenna et al., 2015). In a separate study of the same exemplar taxa, cladistic parsimony analysis of morphological characters similarly recovered Jacobsoniidae as sister to part of Staphylinoidea (Lawrence et al., 2011); in this case, Jacobsoniidae was nested in a grade basal to a clade of four staphylinoid families: Hydraenidae, Ptiliidae, Leiodidae, and Agyrtidae. The hind wings of jacobsoniids, including *D. abyssus*, have reduced venation and very long fringe hairs forming a “feather-wing”, with a complex folding pattern achieved by the aid of spicules on the abdominal tergites (Lawrence and Leschen, 2010). Such wingfolding patches of spicules occur in many groups of Staphylinoidea, in particular Ptiliidae. Indeed, Crowson suggested a possible affinity between these families based on similar hind wing structures, as well as the maxillary galea of adults and larvae (Crowson, 1959, 1960). Evidently, a possible close relationship between jacobsoniids and some staphylinoid taxa, particularly Ptiliidae but also Hydraenidae, should be examined in more detail. The primary feature distinguishing *D. abyssus* from its modern and younger fossil congeners is its slightly shorter elytra (Figs. 2B, 3C), which leave the dorsal tip of the abdomen exposed. Short elytra have evolved repeatedly across the Coleoptera, most notably in Staphylinoidea, and Staphylinidae in particular. In a handful of staphylinid subfamilies there has been secondary development of long elytra from the shorter ancestral condition (Thayer, 2016), and in some of these cases, fossils exist that appear to mark a transitional state in the evolution of long elytra (Chatzimanolis et al., 2010; Cai et al., 2012; Grebennikov and Newton, 2012; Yamamoto, 2016). The antiquity of *D. abyssus* raises the possibility that slightly short elytra might likewise be the ancestral condition within the genus. However, the polarity of this character state change within the genus *Derolathrus* is unknown at present. As we mention in the species diagnosis above, *D. abyssus* may in fact be closest to certain Recent congeners, rather than belonging in the *Derolathrus* stem-group.

5. Conclusions

The discovery of a new jacobsoniid species–*Derolathrus abyssus* sp. n.–in Upper Cretaceous Burmese amber pushes back the definitive oldest record of Jacobsoniidae from the Eocene (~40 Ma) to at least the Upper Cretaceous (~99 Ma). The new species provides yet another example of long-term morphological stasis in mesic habitat-dwelling Coleoptera. Recently, Peris et al. (2016) mentioned an unpublished jacobsoniid fossil in Cretaceous French amber (Cadeuil, uppermost Albian–lowermost Cenomanian). Although no morphological details are available at present, the indication is that jacobsoniid beetles were already widely distributed by the mid-Cretaceous. It is intriguing to speculate how such small beetles can disperse so efficiently; like known flight-capable *Derolathrus* species, our fossil shares a pair of peculiar feather-wing like hind wings (see Discussion). Peck (2010) and Cai et al. (2016) conjectured that jacobsoniids may be capable of long-distance dispersal by "rowing" their wings aided by air currents, rather than flapping, as relatively commonly seen in tiny insects (Walker, 2002). It may be via this form of flight that jacobsoniids, despite their minute size, were able to effectively colonize new tropical/subtropical forest habitats in the Cretaceous and later (Grimaldi et al., 2002).

Competing interests

The authors declare no competing financial interests.

Acknowledgements

SY is grateful to Dr. Toshiya Hirowatari (Kyushu University, Fukuoka) for reading an early version of the manuscript. We also thank Dr. Ron Blakey (Colorado Plateau Geosystems Inc.) for his kind permission to reproduce a palaeogeographic map. This study was supported by a Grant-in-Aid for JSPS Fellows (14J02669) to SY from the Japan Society for the Promotion of Science, Tokyo, Japan. This is a contribution from the Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan (Ser. 7, No. X). JP was supported with funding from the NIH (NIH RO1 GM113000) and is grateful to Gary Struhl (Columbia University) for the freedom to undertake this work in his laboratory.

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