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The first Mesozoic Jacobson's beetle (Coleoptera: Jacobsoniidae) in Cretaceous Burmese amber and biogeographical stasis

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Fossil jacobsoniids are rarely discovered. Here the earliest representative of the enigmatic polyphagan family Jacobsoniidae is described and figured. A new species belonging to the extant genus *Sarothrias* Grouvelle, †*Sarothrias cretaceus* sp. nov., is preserved in the Upper Cretaceous amber from Myanmar, representing the first fossil Jacobsoniidae from the Mesozoic. *Sarothrias cretaceus* is most similar to the Recent species *S. audax* Ślipiński & Löbl from the Tanimbar Islands of East Indonesia, differing from it by the presence of elytral costae bearing squamiform setae, but it appears to retain several ancestral features, including the three-segmented club, non-setose and afoveate abdominal ventrite 1, and well-developed discrimen on the metaventrite. The new discovery indicates antiquity of the genus *Sarothrias* and the family Jacobsoniidae, suggesting that the family probably originated before the breakup of the supercontinent Gondwana, consistent with the hypothesis that the crown-group Staphylinoidea (including Jacobsoniidae) appeared about 193 million years ago. The regional distribution of the modern and fossil *Sarothrias* is indicative of biogeographical stasis, whereby dispersal was limited from the region of origin of the stem group.

<http://zoobank.org/urn:lsid:zoobank.org:pub:93C41362-D78B-4C26-9132-0D56030FB18C>

Keywords: Coleoptera; Jacobsoniidae; *Sarothrias*; fossil; Burmese amber

Introduction

The family Jacobsoniidae (or Jacobson's beetles) is a small group of small-sized (0.65–2.5 mm long) polyphagan beetles, with only 24 described species grouped in three genera (Háva & Löbl 2005; Lawrence & Leschen 2010; Peck 2010). Jacobsoniidae was provisionally included in Bostrichiformia by Lawrence & Newton (1995) and Philips *et al.* (2002). Lawrence *et al.* (2010) placed Jacobsoniidae within the series Derodontiformia, along with the families Derodontidae and Nosodendridae. However, a comprehensive cladistic analysis based on morphological characters of adults and larvae indicated that Jacobsoniidae formed a basal paraphyletic group that is related to part of the Staphylinoidea (Lawrence *et al.* 2011) based on the coding of two genera, *Derolathrus* Sharp and *Saphophagus* Sharp. A recent phylogenetic study based on DNA sequence data revealed that Jacobsoniidae (based on sequences from *Saphophagus*) was within Staphyliniiformia in close relation to

Staphylinoidea (McKenna *et al.* 2015), but the evidence for a monophyletic Jacobsoniidae is lacking, and, critically, the genus *Sarothrias* Grouvelle has not been scored for morphological characters nor sequenced in global phylogenetic studies. Löbl & Burkhardt (1988) and Háva & Löbl (2005) catalogued all species of Jacobsoniidae in the world, and only two extant and one extinct species have been described since (Bi *et al.* 2015; Cai *et al.* 2015; Peck 2010).

Jacobsoniidae includes three extant genera: *Saphophagus* with one species (*S. minutus* Sharp) restricted to New Zealand; *Sarothrias* with 14 species mainly restricted to humid tropical areas (see below; Fig. 1); and *Derolathrus*, with eight described species known from Sri Lanka, North America (Florida) and mainly tropical islands, and one extinct species (*Derolathrus groehni* Cai, Leschen, Liu, & Huang 2015) from middle Eocene Baltic amber. Jacobsoniids can be easily recognized by their minute (0.65–2.5 mm), narrowly elongate (about 2.1–3 times as long as wide), dark to light brown body, an elongate prothorax, lack of a visible

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Figure 1. An extant representative of Jacobsoniidae, holotype of *Sarothrias audax* Ślipiński & Löbl from the Tanimbar Islands of East Indonesia, dorsal view. Scale bar = 500 μ m.

scutellar shield, and markedly elongate metaventrite (at least 2.5 times as long as mesoventrite). All species are poorly represented in museums and little about their biology is known (Philips *et al.* 2002; Lawrence & Leschen 2010), though many collections are from litter and specimens of *Derolathrus* are found in association with bat guano and bird nests.

To date, the species of *Sarothrias* (Pal 1998; Háva & Löbl 2005; Bi *et al.* 2015) are distributed in areas close to the equator except *S. hygrophilus* Pal from north-east India and *S. sinicus* Bi & Chen from Motuo, south-east Xizang of China (Bi *et al.* 2015). Adult *Sarothrias* have been collected in leaf litter and rotten wood, but larvae are as yet unknown (Lawrence & Leschen 2010). *Sarothrias* can be separated from *Saphophagus* by three-segmented tarsi (five-segmented in *Saphophagus*), and from *Derolathrus* by having a three-segmented antennal club (one- or two-segmented in *Derolathrus*) (Burckhardt & Löbl 1990; Lawrence & Leschen 2010).

Fossil jacobsoniids are exceptionally rare. Up to now, only one fossil jacobsoniid belonging to the extant genus *Derolathrus* has been described from the Eocene Baltic amber (Cai *et al.* 2015). Mesozoic jacobsoniids are of great significance for understanding the origin and early diversification of the family and primitive Polyphaga, and

here we describe the first Mesozoic fossil of Jacobsoniidae based on six well-preserved individuals in the Late Cretaceous (earliest Cenomanian) Burmese amber.

Material and methods

The new species is known from two individuals preserved in two pieces of amber from north Myanmar, an amber deposit that is poorly studied. The amber pieces were ground and polished in order to make all of the anatomical features accessible for observation. The holotype (NIGP165261) and paratypes (NIGP165262, NIGP165263, NIGP164024 and SNUC-Paleo-0001) are completely preserved adults. Some parts (meso- and metalegs) of NIGP164024 were ground in order to get a better view of its ventral side. The apex of the body of the paratype (NIGP164025) was not preserved. The type specimens (except SNUC-Paleo-0001) are housed in the Nanjing Institute of Geology and Palaeontology, CAS, Nanjing, China, and one paratype (SNUC-Paleo-0001) is housed in the insect collection of the Shanghai Normal University. Observations and photographs were taken using a Zeiss Axio Imager 2 compound microscope with an AxioCam MRc 5 camera attached. The Zeiss Axio Imager 2 microscope was equipped with a mercury lamp and specific filters for DAPI, eGFP and rhodamine. Photomicrographs with green background were taken under the eGFP mode (Zeiss Filter Set 10; excitation/emission: 450–490/515–565 nm). Extended depth of field images were then digitally compiled using Helicon Focus 3.10 software, and arranged in Adobe Photoshop CS5.

Systematic palaeontology

Order **Coleoptera** Linnaeus, 1758
 Family **Jacobsoniidae** Heller, 1926
 Genus ***Sarothrias*** Grouvelle, 1918

Type species. *Sarothrias eximius* Grouvelle, 1918.

†***Sarothrias cretaceus*** sp. nov.
 (Figs 2–4)

Diagnosis. The new species can be separated from its congeners by the following combination of features: antenna with a three-segmented club; dorsal and lateral portions of pronotum with a few squamiform setae; each elytron with eight rows of large and regularly arranged punctures with a row of squamiform setae developed on elytral costae, presence of four costae (including epipleural ridge) on each elytron; presence of a long metaventral discrimen; and abdominal ventrite 1 devoid of setae and lacking a fovea.

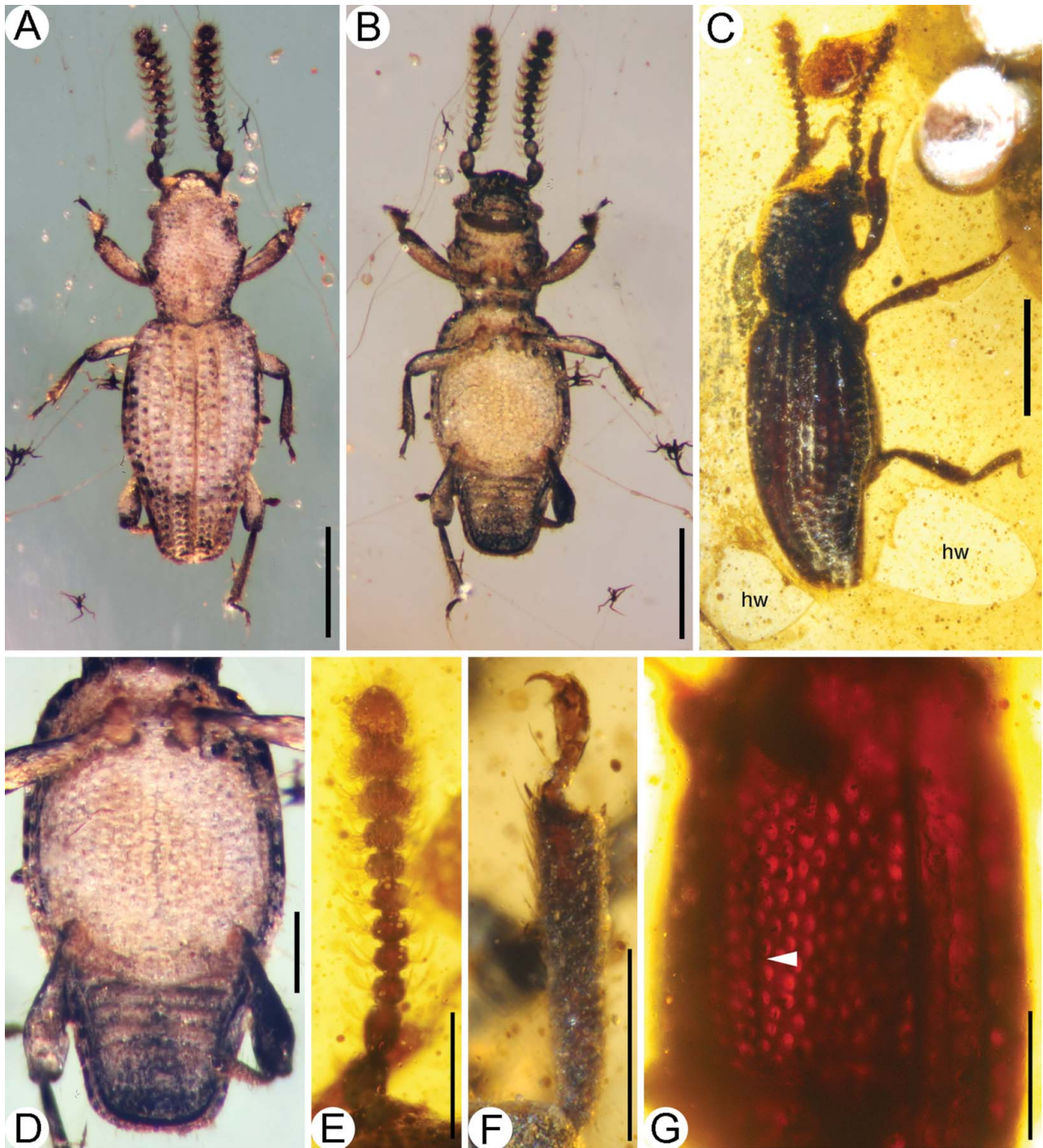


Figure 2. Microphotographs of holotype (NIGP165261) and paratype (NIGP164024) of *Sarothrias cretaceus* sp. nov. in Upper Cretaceous amber from Myanmar; under normal reflected light. **A**, dorsal view of holotype, NIGP165261; **B**, ventral view of holotype, NIGP165261; **C**, dorsolateral view of NIGP164024; **D**, meso- and metathorax and abdomen of holotype, NIGP165261; **E**, left antenna, NIGP164024; **F**, ventral view of left protibia and protarsus, NIGP164024; **G**, ventral view of metaventrite, with arrow indicating discrimen, NIGP164024. Scale bars: A–C = 500 μ m; D–G = 200 μ m.

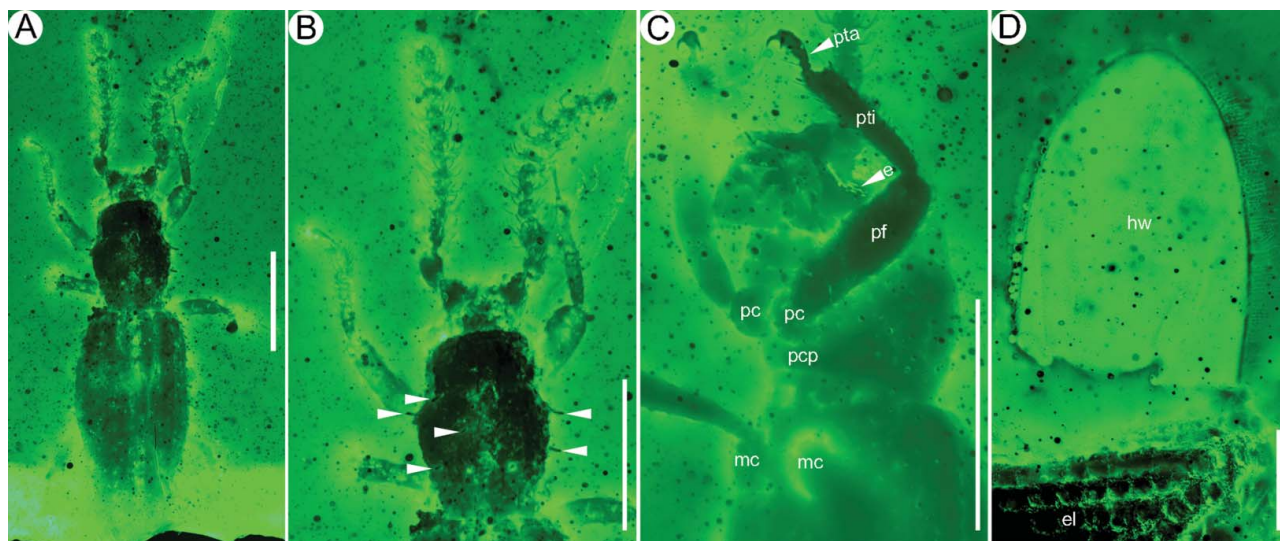


Figure 3. Microphotographs of *Sarothrius cretaceus* sp. nov.; under fluorescence microscopy. **A**, dorsal view of paratype NIGP164025; **B**, forebody of paratype NIGP164025, with arrows indicating squamiform setae; **C**, ventral view of forebody of holotype NIGP164024; **D**, exposed right hind wing of holotype. Abbreviations: e, eye; el, elytron; hw, hind wing; mc, mesocoxa; pc, procoxa; pcp, postcoxal process; pf, profemur; pta, protarsus; pti, protibia. Scale bars: A–C = 500 μ m; D = 200 μ m.

Etymology. Deriving from the Cretaceous age of the fossil. The species is registered under LSID urn:lsid:zoo-bank.org:act:F80C2708-4E05-4471-99ED-46AE93771763.

Material examined. Holotype: NIGP165261. Paratypes: NIGP165262, NIGP165263, NIGP164024, NIGP164025, SNUC-Paleo-0001.

Horizon and locality. Burmese amber, earliest Cenomanian (*c.* 99 Ma) from Hukawng Valley, northern Myanmar.

Description. Body small, 1.82–1.85 mm long, elongate, somewhat convex, dark brown, dorsal surface densely punctate, with whitish (more or less transparent) squamiform setae on pronotum and elytra.

Head slightly declined, distinctly wider than long, widest across eyes, 0.33 mm wide. Eyes protuberant, rounded, coarsely faceted, without interfacetal setae. Antennal insertions concealed from above. Labrum transverse, with slightly convex anterior margin. Antennae (Figs 2B, 3B) long, about as long as head and pronotum combined; densely setose; scape slightly elongate, dilated, distinctly wider than pedicel; pedicel elongate, slightly wider than and about twice as long as antennomere 3; antennomeres 3–8 weakly transverse, similar in shape and size; antennomeres 9–11 form distinct club, antennomeres 9 and 10 transverse, terminal segment conical.

Pronotum elongate, 0.56 mm long, 0.38 mm wide, widest near middle; anterior margin slightly curved; disc with distinct shallow median groove, extending from anterior one-fourth to slightly before base. Punctures on disc small

and dense, similar in size and shape to those on head; pronotal surface with scattered whitish and elongate squamiform setae (0–3 setae along each lateral pronotal margin, and at least six on disc, Fig. 3B). Prosternum in front of coxae slightly longer than diameter of procoxal cavity. Procoxal cavities broadly closed externally (Fig. 3C). Scutellar shield not visible.

Elytra (Fig. 4) complete, 1.16 mm long, combined width 0.57 mm, widest slightly behind middle; surface coarsely punctate (Fig. 4A); each elytron with eight rows of punctures and a row of at least 11 squamiform setae between rows 2 and 3 (Fig. 4B), and several setae between rows 4 and 5, and between rows 6 and 7; secretions or encrustations not visible. Elytral costae present between every two punctate rows (c1, c2 and c3); epipleural ridge (c4) complete, devoid of squamiform setae; costa between rows 7 and 8 (c3) incomplete, developed at apical half (Fig. 4C). Mesoventrite very short; metaventrite very long, covered with dense, rounded and relatively large punctures; discrimen occupying posterior three-fourths of metaventrite (Fig. 2D). Mesocoxal cavities narrowly separated, rounded (Fig. 3C). Hind wings (Fig. 3D) fully developed, long, venation highly reduced; ventral margin and apex with dense and short hairs.

Legs moderately long (Fig. 2C), all tarsi three-segmented (Fig. 2C); basal two tarsomeres very small, subequal; tarsomere 3 elongate, widened towards apex, much longer than basal two tarsomeres combined. Pro- and mesocoxae rounded. Femora robust. Tibiae slightly expanded apically; tibial spurs paired, very short. Pretarsal claws simple.

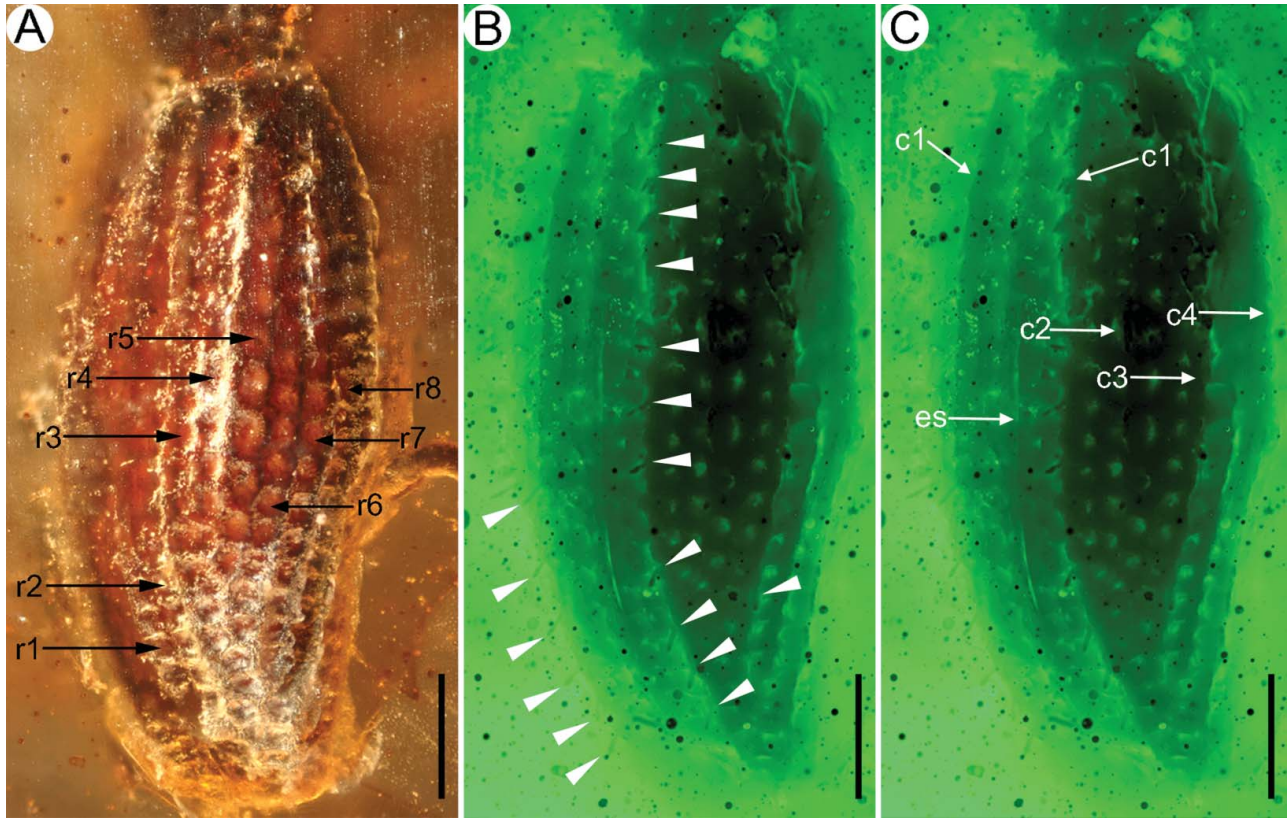


Figure 4. Right elytron of holotype (NIGP164024) of *Sarothrias cretaceus* sp. nov. **A**, under normal reflected light, showing eight rows of punctures; **B**, under fluorescence microscopy, with arrows indicating squamiform setae on elytron; **C**, same as B, with elytral costae indicated. Abbreviations: c, costa; es, elytral suture; r, row. Scale bars = 200 μ m.

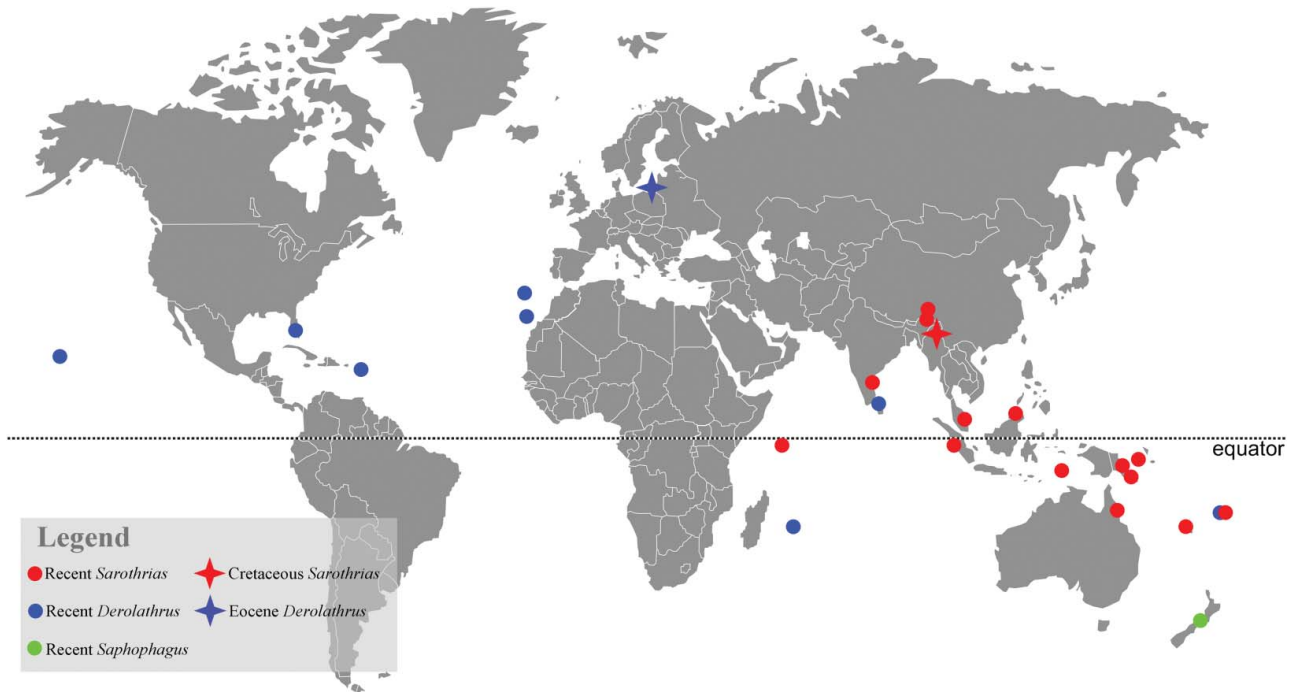


Figure 5. Geographical distribution map of extant and extinct species of Jacobsoniidae.

Abdomen about as long as metaventricle, with five ventrites. Ventrite 1 simple; ventrites 1–3 short; ventrite 4 much longer than ventrite 3; ventrite 5 longest.

Discussion

These fossils can be unambiguously attributed to the enigmatic polyphagan family Jacobsoniidae as supported by their small body size, elongate body shape, and greatly elongated metathorax (or metaventricle) combined with the relatively short abdomen; the last trait is considered a potential synapomorphy of Jacobsoniidae (Lawrence & Leschen 2010). The holotype bears exposed hind wings with reduced venation and a dense fringe of hairs, representing another possible synapomorphy of the family (Lawrence & Leschen 2010), though present in many other groups. Among the three known extant jacobsoniid genera (*Derolathrus*, *Sarothrias* and *Saphophagus*), the fossils are readily excluded from *Saphophagus* by the three-segmented tarsi (tarsal formula 5-5-5 in *Saphophagus*); and from *Derolathrus* by the three-segmented antennal club, densely setose antennae, closed procoxal cavities, and presence of squamiform setae on pronotum and elytra. The fossils are placed in the extant genus *Sarothrias* based on the following combination of characters: (1) body small (less than 2 mm long); (2) antennae setose; (3) procoxal cavities closed externally; (4) lateral pronotal carinae absent; (5) metacoxae globular; and (6) tarsal formula 3-3-3. *Sarothrias cretaceus* is very distinctive by its weak three-segmented antennal club, coarsely punctate elytra, densely punctate metaventricle, presence of a meta-ventral discimen, and absence of a setose fovea on abdominal ventrite 1. Among all known extant *Sarothrias* species, only *S. audax* Ślipiński & Löbl from the Tanimbar Islands of East Indonesia has distinctly well-impressed and regularly punctate elytra; otherwise the punctures are absent or weakly impressed and form well-spaced striae in the remaining species. The elytron of *S. audax* bears eight relatively regular rows of punctures (Ślipiński & Löbl 1995; Fig. 1), resembling those on the elytron of *S. cretaceus*. In addition, as shown in the line drawing of *S. audax* (Ślipiński & Löbl 1995, figs 1–4), at least two squamiform setae (possibly including the apical four setae) are located between elytral rows 2 and 3, a condition very similar to that of *S. cretaceus*. A similar distributional pattern of squamiform setae on the elytron is also found in *S. pacificus* Ślipiński & Löbl (New Caledonia) and *S. amabilis* Ślipiński & Löbl (Malaysia), although these two extant species lack distinct rows of punctures on the elytron (Ślipiński & Löbl 1995). The new species differs from *S. audax* by the presence of squamiform setae on lateral portion of pronotum and the distributional pattern and number of squamiform setae on costae of the elytron.

The new species has several potentially ancestral features. The antenna of the new species bears a weak three-segmented club, while in all extant *Sarothrias* species antennomeres 2–11 are almost moniliform, so that the club is not clearly distinguishable (Lawrence & Leschen 2010). Given that the other two jacobsoniid genera (*Derolathrus* and *Saphophagus*) have a distinct antennal club, it is highly possible that the distinct antennal club in the fossil species represents an ancestral feature. Moreover, all extant *Sarothrias* species have a large setose impression or fovea on abdominal ventrite 1, but this character is not developed in the fossil species. Lastly, the metaventricle of the fossil species bears a longitudinal discimen, which is not developed in other *Sarothrias* species or other jacobsoniids.

Fossil jacobsoniids are very rare. To date, only one species, *Derolathrus groehni* Cai *et al.*, is known from middle Eocene Baltic amber. The discovery of an older Late Cretaceous (c. 99 Ma) representative nearly doubles the age of the oldest fossil record of Jacobsoniidae. It also stands as the first Mesozoic record for the family, and therefore the oldest jacobsoniid fossil known up to now. The new species *S. cretaceus* is morphologically similar to the extant *S. audax*. It probably suggests that the fossil species had a similar life habit to its extant counterparts. The unusual body form of most of the modern *Sarothrias* is reminiscent of social inquiline, which often bear compact moniliform antennae and setose fovea. Unfortunately, nothing is known about the precise feeding behaviour of extant *Sarothrias* species, although they are known to be collected from leaf litter and rotten wood (Lawrence & Leschen 2010), and there are several specimens of *S. lawrencei* taken from ants by H. Escalona (H. Escalona, pers. obs.). Though little can be deduced about the ancient biology of *Sarothrias*, our discovery has significant biogeographical implications for understanding the origin of the genus and the entire family.

The discovery of a 99 million year old *Sarothrias* species from the Cretaceous of Indochina continent may not be surprising because modern *Sarothrias* species are restricted to humid tropical areas close to the equator, with many species found in present day Indonesia and Malaysia. Grimaldi *et al.* (2002) considered that the environment of ancient amber forests was tropical, similar to the environment where extant *Sarothrias* live. Presence in the Cretaceous and the modern distribution of extant *Sarothrias* (Fig. 5) indicate that the genus may be of ancient Gondwanan origin, and that during the course of its long history, *Sarothrias* did not disperse widely from its regional distribution. We refer to this geographical phenomenon as ‘biogeographical stasis’, a feature that occurs in other groups, such as the trogossitid beetle genus *Antillipeltis* Lawrence, Leschen & Ślipiński described from fossils and extant species occurring in a localized area in the Antilles (Lawrence *et al.* 2014). A total of six species of *Sarothrias*

have been discovered from the Australian and Melanesian regions, including three species from Papua New Guinea (*S. bournei* Ślipiński, *S. morokanus* Poggi and *S. papuanus* Ślipiński), one species from Australia (*S. lawrencei* Löbl & Burckhardt), one species from New Caledonia (*S. pacificus* Ślipiński & Löbl) and one species from Fiji (*S. fijianus* Löbl & Burckhardt), all occurring in an area of eastern Gondwana referred to as the Melanesian Arc or Rift (e.g. Michaux 1994; Coleman 1997; Schellart *et al.* 2006). There are three species known from southern Asia (*S. indicus* Dajoz, southern India; *S. hygrophilus* Pal and *S. sinicus* Bi & Chen, southern Tibet), two species from Malaysia (*S. crowsoni* Löbl & Burckhardt and *S. amabilis* Ślipiński & Löbl) and two from Indonesia (*S. dimerus* Heller from Sumatra and *S. audax* Ślipiński & Löbl, from Tanimbar Island of Indonesia, which is located west of the biogeographical boundary known as Lydekker's Line that separates Oriental from Austral species). The only outlier is *S. eximius* Grouvelle, known from the Seychelles located in the Indian Ocean, north-east of Madagascar, but all species are distributed in areas adjacent to or contained within older Gondwanan elements.

A phylogeny of *Sarothrias* would be required to examine its biogeographical history, but we predict that the sharing of characters by *S. audax* and *S. cretaceus* would place these taxa as relatives, and that *S. cretaceus* may be the most primitive member of the group based on its plesiomorphic characters. *Sarothrias eximius*, we predict, would be a more derived species, and its distribution related to dispersal rather than a stem group with wider distribution across Gondwana.

The fossil record of Jacobsoniidae is consistent with the hypothesis that the crown-group Staphylinoidea, including Jacobsoniidae, originated about 193 million years ago (McKenna *et al.* 2015). Older jacobsoniid fossils may be expected in other amber inclusions, especially those like the Early Cretaceous Lebanese amber that was formed in a tropical or subtropical forest (Azar *et al.* 2010). Recently, *Derolathrus groehni* Cai *et al.* was described from middle Eocene Baltic amber (Cai *et al.* 2015), suggesting that *Derolathrus* may have originated long before the middle Eocene. Interestingly, Peris *et al.* (2016) listed a fossil Jacobsoniidae from the Early Cretaceous French amber, which is slightly older than the record we report, but its status cannot be confirmed without formal description. The fossil records (especially from the Mesozoic) and the modern biogeographical pattern of Jacobsoniidae indicate that Jacobsoniidae is a very ancient group and that the group was more diverse than it is in the present.

Conclusions

The discovery and description of a new fossil species of *Sarothrias* is the first from the Mesozoic. The fossil

Sarothrias species from mid-Cretaceous Burmese amber suggests that the genus probably originated before the breakup of the southern supercontinent Gondwana. Some evolutionary questions remain to be solved, mainly whether Jacobsoniidae is monophyletic or not, and if so, we predict that phylogenies would show *Sarothrias* as a sister group to the remaining genera based on our fossil species. Biogeographical stasis as exhibited by *Sarothrias* is a phenomenon that needs to be further examined in other taxa with adequate fossil records.

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