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Carrion beetles from the Lower Cretaceous Yixian Formation of northeastern China (Coleoptera: Staphylinidae: Silphinae)

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Abstract

Recent phylogenetic work has placed the family Silphidae within Staphylinidae as subfamily Silphinae. Despite this taxonomic progress, the early fossil record and the evolution of Silphinae remain incompletely understood. Here I describe *Paracretosaja* **gen. nov.** (type species: *Paracretosaja newtoni* **sp. nov.**) and *Cretosaja thayerae* **sp. nov.**, based on well-preserved compression fossils from the Lower Cretaceous Yixian Formation (Liaoning and Inner Mongolia, northeastern China). Both new taxa possess paired stridulatory files on abdominal tergite V and a distinct, straight frontoclypeal suture that permit confident placement in the extant tribe Nicrophorini. An examination of new specimens of *Cretosaja* Sohn & Nam corrects several earlier character interpretations for *C. jinjuensis* Sohn & Nam. The presence of derived nicrophorines in multiple Early Cretaceous localities, together with slightly younger records from the Jinju Formation of South Korea, indicates a broad geographic distribution of Nicrophorini in eastern Asia. These fossils document that traits associated with communication and parental provisioning were established by the Early Cretaceous, and they imply that carrion-feeding beetles had already assumed important roles in nutrient recycling and terrestrial ecosystem functioning during the Mesozoic.

Key words: burying beetles, fossil, Cretaceous, Jehol Biota, palaeodiversity

Introduction

Silphinae, formerly recognized as an independent family, has been recently classified as a subfamily within the megadiverse family Staphylinidae (rove beetles) (Cai *et al.* 2022, 2024; Sikes *et al.* 2024). This reclassification, supported by both molecular phylogenetic and morphological evidence, has gained widespread acceptance among the taxonomic community; the former subfamilies Nicrophorinae and Silphinae are now formally recognized at the tribal rank as Nicrophorini and Silphini, respectively (e.g., Büchner *et al.* 2024; Haitlinger 2025; Růžička *et al.* 2023). Silphinae is a globally distributed group, absent only from Antarctica (Sikes 2016). It comprises two well-defined tribes, including 14 genera and 206 valid extant species (plus 16 subspecies) (Newton 2025; Sikes & Venables 2013). The tribe Nicrophorini has attracted considerable attention from evolutionary biologists owing to its unique biparental care behaviour among insects (Bartlett & Ashworth, 1988; Kalinová *et al.*, 2009; Scott & Traniello, 1990; Trumbo, 1990; Potticary *et al.* 2024). Although the monophyly of Silphinae is widely accepted (e.g., Sikes 2016), its precise phylogenetic position within Staphylinidae remains unresolved (Cai *et al.* 2022; Sikes *et al.* 2024).

The two tribes differ markedly in their reproductive behaviours. Species of the tribe Silphini exhibit little parental care, typically breeding on larger carrion where larvae feed on maggot masses produced by competing flies. In contrast, Nicrophorini display advanced biparental care: adult pairs bury small vertebrate carcasses underground to form a protected brood chamber, regurgitate pre-digested food to nourish their larvae, and actively defend the resource against competitors (Sikes 2016).

The fossil record of the subfamily Silphinae is poorly known, with the earliest occurrences dating to the Middle Jurassic (Cai *et al.* 2014; Sohn & Nam 2021). Cai *et al.* (2014) documented a diverse assemblage of silphines from

the Mesozoic (Jurassic and Cretaceous) of northeastern China and northern Myanmar, providing important insights into the early evolution of parental care in this group. Silphines from the Middle Jurassic Daohugou Biota (ca. 165 Ma; Li *et al.* 2022, 2023; Lian *et al.* 2021) share many diagnostic characters with the extant tribe Nicrophorini but primitively lack stridulatory files, which are considered important for communication associated with parental care. Although morphologically similar, nicrophorines from the Early Cretaceous Jehol Biota (ca. 125 Ma; Xu *et al.* 2020; Zhou 2014; Zhou *et al.* 2003) possess paired stridulatory files, indicating that a system of parental care had evolved by this time. Notably, burying beetles of the genus *Nicrophorus* Fabricius have their earliest record in mid-Cretaceous Kachin amber, documenting the early evolution of elaborate biparental care and active defense of small vertebrate carcasses for larval development. The rise of Cretaceous Nicrophorini implies a biology broadly comparable to that of their modern counterparts, which typically utilize carcasses of small birds and mammals. More recently, *Cretosaja jinjuensis* Sohn & Nam was described from the Lower Cretaceous Jinju Formation of South Korea. This taxon, closely related to the extant genus *Ptomascopus* Kraatz, was attributed to Nicrophorini (former Nicrophorinae) (Sohn & Nam 2021).

Here, I describe a new genus and two new species of carrion beetles from the Lower Cretaceous Yixian Formation of northeastern China. Both species possess paired stridulatory files and a well-developed, straight frontoclypeal suture, suggesting that they can be confidently placed within the extant tribe Nicrophorini.

Material and methods

The five studied specimens were collected from yellowish tuff of the Jingangshan Member of the Yixian Formation near Huangbanjigou, Beipiao City, Liaoning Province, China (NIGP1561520a, b, NIGP1561521, NIGP1561523, NIGP1561524) and the Yixian Formation at Liutiaogou, Ningcheng County, Inner Mongolia (NIGP156152a, b). Two specimens (NIGP156150 and NIGP156152a, b) are preserved as a compression fossil that was subsequently split along the median plane into two counterparts. The type specimens of the two new species are permanently deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (Nanjing, China) (= NIGP). Photographs under incident light were taken using a Zeiss Discovery V20 stereomicroscope. Image stacks were produced using Helicon Focus 7.0.2 and Zerene Stacker 1.04, and the resulting images were further processed in Adobe Photoshop CC to adjust brightness and contrast.

Systematic palaeontology

Order Coleoptera Linnaeus, 1758

Family Staphylinidae Latreille, 1802

Subfamily Silphinae Latreille, 1806

Tribe Nicrophorini Kirby, 1837

Genus: *Paracretosaja* gen. nov.

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Type species. *Paracretosaja newtoni* sp. nov., here designated.

Etymology. The generic name is a combination of the Latinized prefix *Para-* (meaning ‘near’) and *Cretosaja*, the most closely related genus from the Early Cretaceous; the name is of feminine gender.

Diagnosis. The genus can be distinguished from all other extinct and extant Nicrophorini by the following combination of characters: body relatively small and densely setose (except for head); antennae with relatively short scape and antennomeres 3–11 gradually dilated apically; frontoclypeal (epistomal) suture straight and well developed (not as fine line as in extant Nicrophorini); gular sutures Y-shaped and posteriorly fused; pronotum suborbicular; mesocoxae moderately separated; and abdominal tergite V bearing paired stridulatory files.

***Paracretosaja newtoni* sp. nov.**

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(Figs 1, 2)

Material. Holotype, NIGP156150a, b, male, preserved as part and counterpart. Paratype, NIGP156153, sex unknown.

Etymology. The specific epithet is a patronym honoring Dr. Alfred F. Newton (Field Museum of Natural History, Chicago), a renowned entomologist specializing in the superfamily Staphylinoidea.

Diagnosis. As for the genus.

Type locality and horizon. Lower Cretaceous, Yixian Formation; Huangbanjigou Village, Shangyuan Township, Beipiao City, Liaoning Province, China.

Description. Male. Body length 13.6 mm (from apex of mandible to abdominal apex), moderately elongate, densely pubescent (including pronotum, elytra and abdomen, but not head).

Head distinctly narrower than pronotum, widest across eyes, 1.86 mm wide. Neck constricted behind large and protuberant eyes. Frontoclypeal (epistomal) suture distinct (Fig. 2B). Gular sutures confluent posteriorly, reducing gula to a small piece. Antennal insertions exposed from above. Antenna with 11 antennomeres, with relatively short scape and short pedicel (not fused to antennomere 3), not geniculate; antennomeres 3–11 gradually dilated apically; antennomeres 5–10 each strongly transverse; antennomere 11 oval, largest; antennomeres 9–11 not lamellate (Fig. 2C, D). Mandible simple, without preapical teeth. Maxillary palpus with palpomere 4 distinctly longer than 3; palpomere 4 not reduced.

Pronotum suborbicular, 3.00 mm wide and 2.23 mm long, with lateral edges complete, not explanate; anterior margin slightly concave. Procoxae transverse, contiguous, with exposed trochantins. Procoxal cavities widely open posteriorly and internally. Mesoventrite short and flat, moderately connected with metaventrite between mesocoxae. Mesocoxal cavity laterally bordered by mesepimeron. Mesocoxae moderately separated. Scutellar shield very large, subtriangular, slightly narrower than head.

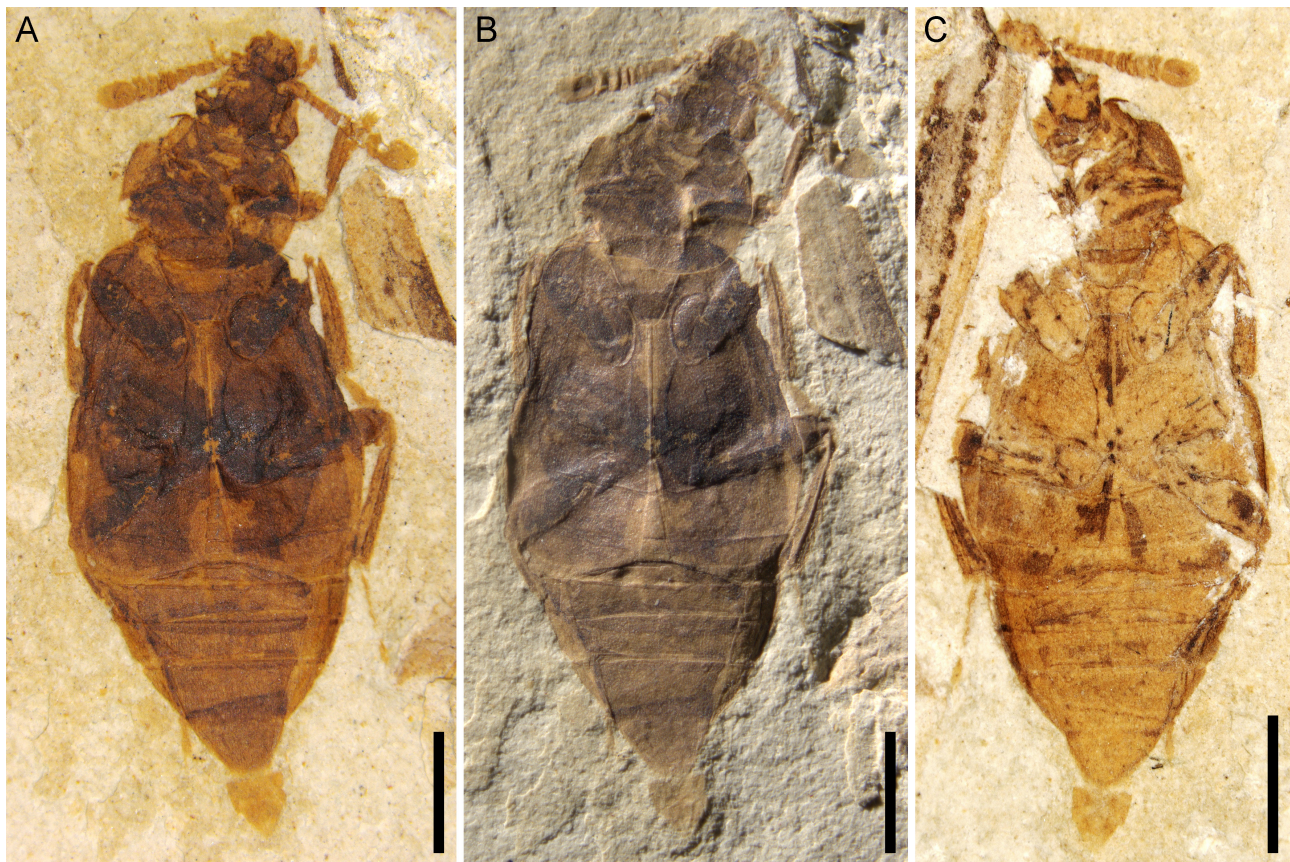


Figure 1. *Paracretosaja newtoni* gen. et sp. nov. from the Lower Cretaceous Yixian Formation of northeastern China. **A**, Dorsal view, under normal light, holotype, NIGP156150a. **B**, Same as **A**, under low-angled light. **C**, Ventral view, under normal light, NIGP156150b. Scale bars = 2 mm.

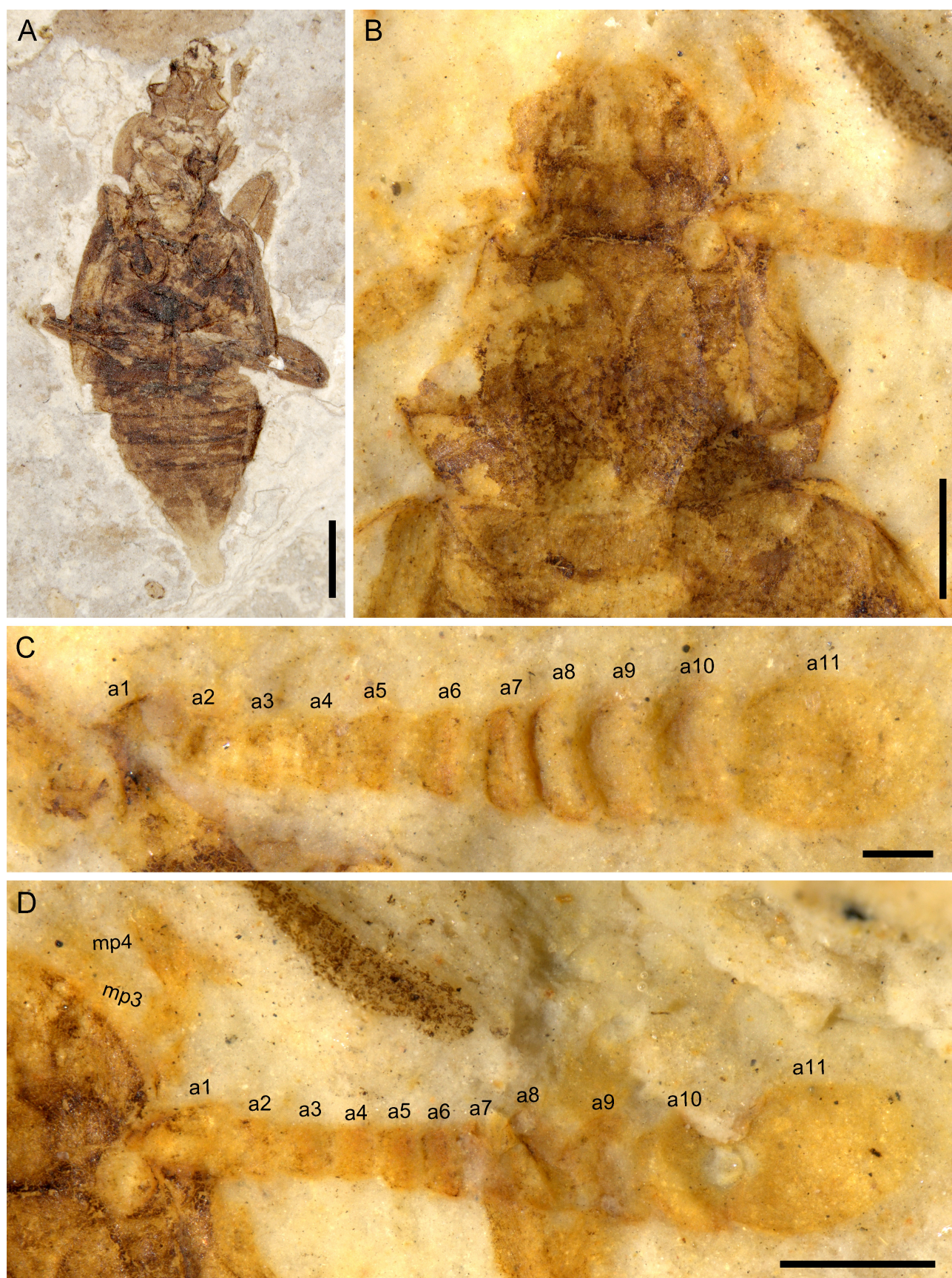


Figure 2. *Paracretosaja newtoni* gen. et sp. nov. from the Lower Cretaceous Yixian Formation of northeastern China. **A**, Ventral view, under normal light, paratype, NIGP156153. **B**, Head of NIGP156150a, moistened with alcohol. **C**, Right antenna of NIGP156150b. **D**, Right antenna of NIGP156150a. Abbreviations: a, antennomere; mp, maxillary palpomere. Scale bars = 2 mm in **A**; 0.2 mm in **C**, 0.5 mm in **B**, **D**.

Elytra truncate, each 5.43 mm long and 2.50 mm wide, exposing 5 abdominal tergites; not striate; without costae or carinae; epipleura well-developed and with epipleural ridge complete; without colored bands or spots. Metaventricle with discrimen. Metacoxae large and contiguous, laterally not reaching elytra. All tibiae carinate, with two enlarged tibial spurs. Metatrochanters small. All tarsi 5-segmented; meso- and metatarsomeres 1 elongate; meso- and metatarsomeres 2–4 each shorter; meso- and metatarsomeres 5 elongate. Pretarsal claws simple.

Abdomen densely setose. Sternites III–VIII visible; sternite VIII rounded apically. Intersegmental membrane with a brick-like pattern of microsclerites.

Remarks. *Paracretosaja* is closely related to *Cretosaja* Sohn & Nam from the Early Cretaceous of South Korea, but differs from it in having a densely setose body and antennae with a relatively short scape and antennomeres 3–11 gradually dilated apically. *Paracretosaja* can be distinguished from extant Nicrophorini by its densely setose body, distinctive antennal morphology, and a well-developed frontoclypeal suture, which is represented only as a fine line in extant members of Nicrophorini.

Subfamily: Silphinae Latreille, 1806

Tribe: Nicrophorini Kirby, 1837

Genus: *Cretosaja* Sohn & Nam, 2021

Type species: *Cretosaja jinjuensis* Sohn & Nam, 2021

***Cretosaja thayerae* sp. nov.**

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(Figs 3, 4)

Material. Holotype, NIGP156151. Paratypes, NIGP156152a, b, NIGP156154.

Etymology. The specific epithet is a patronym honoring Dr. Margaret K. Thayer (Field Museum of Natural History, Chicago), a preeminent entomologist specializing in the family Staphylinidae.

Type locality and horizon. Lower Cretaceous, Yixian Formation; Huangbanjigou Village, Shangyuan Township, Beipiao City, Liaoning Province, China.

Diagnosis. *Cretosaja thayerae* sp. nov. differs from the other fossil species, *C. jinjuensis* Sohn & Nam, primarily by smaller body size (12.4 mm in *C. thayerae* vs 14 mm in *C. jinjuensis*) and narrower pronotum (3.13 mm in *C. thayerae* vs 3.9 mm in *C. jinjuensis*).

Description. Body length 12.4 mm, moderately elongate; head, pronotum and most part of elytra glabrous. Abdomen pubescent.

Head narrower than pronotum, widest across eyes, 2.26 mm wide (Fig. 4D). Neck constricted behind large and protuberant eyes. Frontoclypeal (epistomal) suture distinct. Clypeus straight apically. Gular sutures confluent posteriorly, reducing gula to a small piece. Antennal insertions exposed from above. Antenna with 11 antennomeres, with very elongate scape and short pedicel, not geniculate; antennomeres 4–7 each strongly transverse; antennomeres 8–11 forming a distinct club; antennomere 7 distinctly narrower than antennomere 8; antennomere 11 large (Fig. 4E, F). Mandible simple, without preapical teeth. Maxillary palpus with palpomere 3? distinctly longer than 4; palpomere 4 not reduced.

Pronotum suborbicular, 3.13 mm wide and 2.13 mm long, with lateral edges complete, not explanate; anterior margin slightly concave. Procoxae transverse, contiguous, with exposed trochantins. Procoxal cavities widely open posteriorly and internally. Mesoventrite short and flat, moderately connected with metaventricle between mesocoxae. Mesocoxal cavity laterally bordered by mesepimeron. Mesocoxae moderately separated. Scutellar shield very large, subtriangular, narrower than head.

Elytra truncate, each 4.47 mm long and 2.27 mm wide, exposing 5 abdominal tergites; not striate; with two faint longitudinal carinae; epipleura well-developed and with epipleural ridge complete; without colored bands or spots; lateral margins broadly curved; posterolateral part of elytral disc with dense setae. Metaventricle with discrimen. Metacoxae large and contiguous. All tibiae carinate, with two enlarged tibial spurs. Metatrochanters small. All tarsi 5-segmented; meso- and metatarsomeres 1 elongate; meso- and metatarsomeres 2–4 each shorter; meso- and metatarsomeres 5 elongate. Pretarsal claws simple.

Abdomen densely setose. Sternites III–VIII visible; tergite V with paired stridulatory files (Fig. 5B, C); sternite VIII rounded apically. Intersegmental membrane with a brick-like pattern of microsclerites.

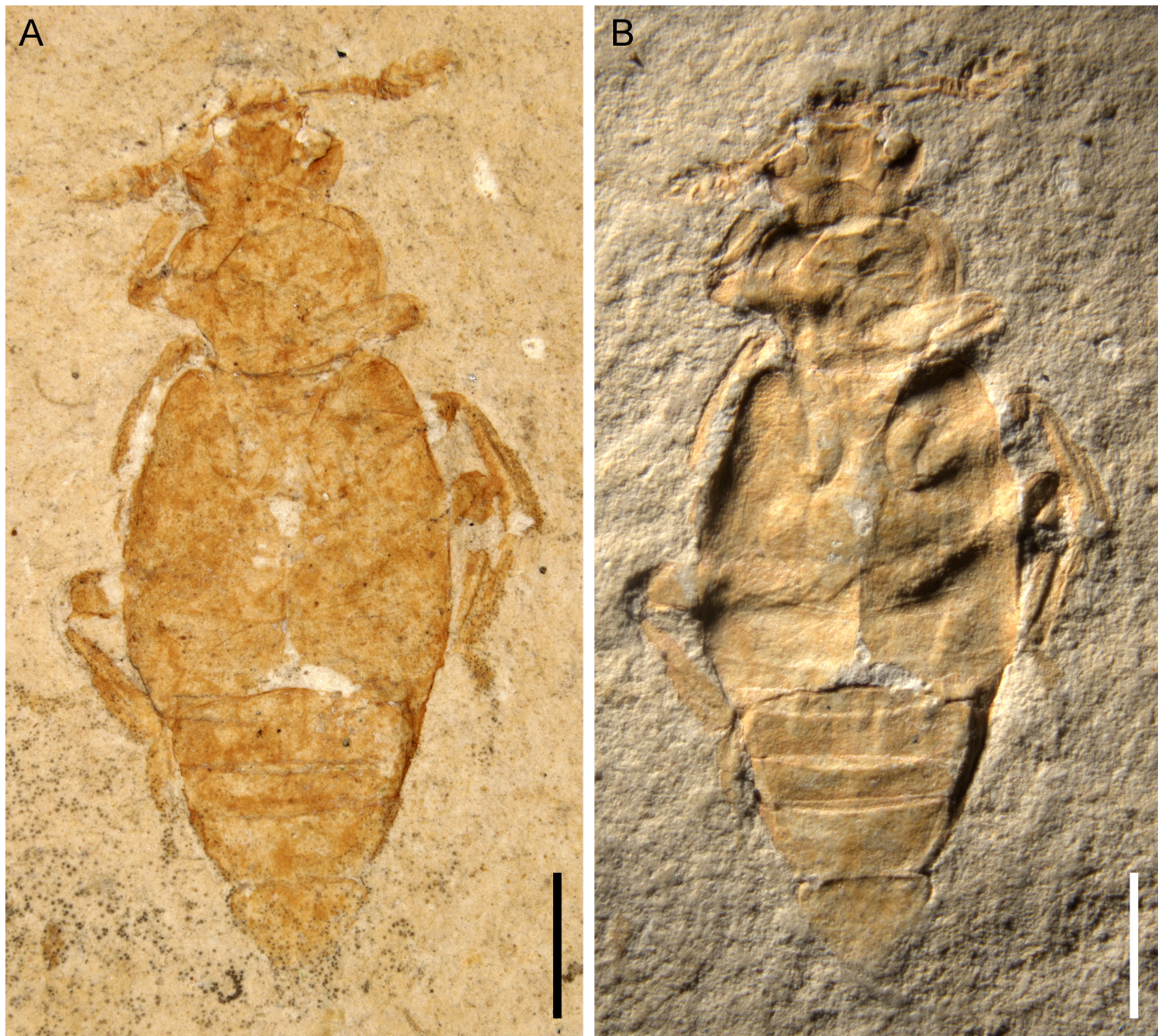


Figure 3. *Cretosaja thayerae* sp. nov. from the Lower Cretaceous Yixian Formation of northeastern China. **A**, Dorsal view, under normal light, holotype, NIGP156151. **B**, Same as **A**, under low-angled light. Scale bars = 2 mm.

Remarks. *Cretosaja* is very similar to the extant genus *Ptomascopus* Kraatz in antennal morphology; however, it was originally distinguished from the latter by an arched anterior margin of the clypeus (transverse in *Ptomascopus*), posteriorly converging frontal sutures, and an orbicular pronotum (Sohn & Nam 2021). Based on a re-examination of new fossil material, I reinterpret several of these characters.

First, the arched anterior margin of the clypeus is probably a taphonomic artefact; in *Cretosaja*, the anterior margin is in fact straight. Second, the structures previously interpreted as posteriorly converging frontal sutures are better interpreted as gular sutures that are confluent posteriorly. This misinterpretation likely resulted from the absence of both part and counterpart for comparison, which can easily lead to confusion in compression fossils. After correction of these character interpretations, *Cretosaja* differs from *Ptomascopus* primarily in having a suborbicular pronotum and broadly curved lateral margins of the elytra. In addition, in the original description and line drawing of *C. jinjuensis*, the scutellar shield was depicted as unusually small because only its posterior portion was illustrated; the basal part of the scutellar shield actually extends to the posterior margin of the pronotum and the scutellar shield should be much larger than originally illustrated. The metacoxae of *C. jinjuensis* were also poorly preserved and were therefore misinterpreted; they are in fact contiguous. Furthermore, the metatrochanters were incorrectly depicted and should be oblique and narrow.

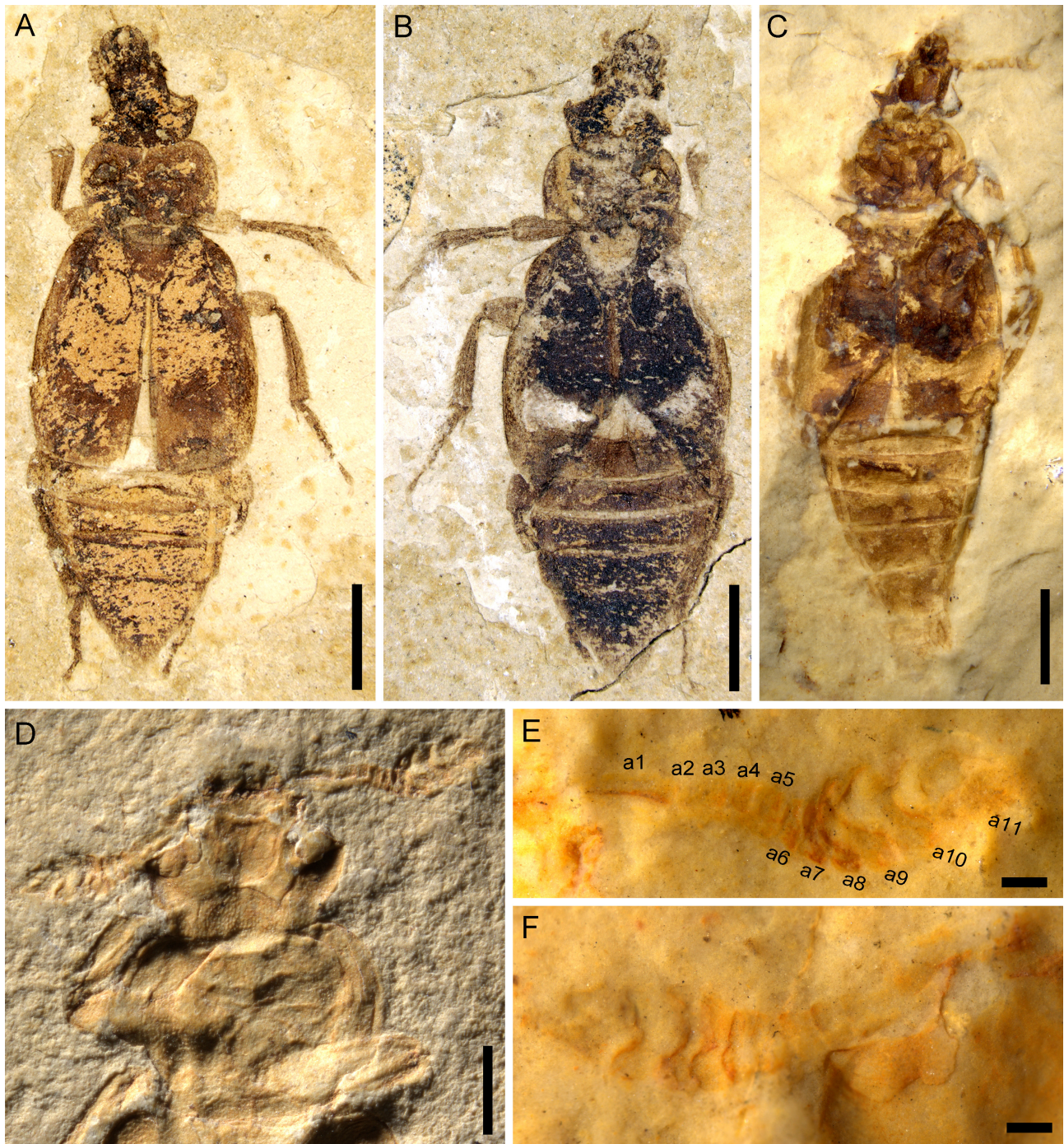


Figure 4. *Cretosaja thayerae* sp. nov. from the Lower Cretaceous Yixian Formation of northeastern China. **A**, Dorsal view, paratype, NIGP156152a. **B**, Ventral view, paratype, NIGP156152b. **C**, Dorsal view, paratype, NIGP156154. **D**, Dorsal of head and pronotum, holotype, NIGP156151, under low-angled light. **E**, Right antenna of holotype, NIGP156151, moistened with alcohol. **F**, Left antenna of holotype, NIGP156151, moistened with alcohol. Abbreviations: a, antennomere. Scale bars = 2 mm in A–C; 1 mm in D; 0.2 mm in E and F.

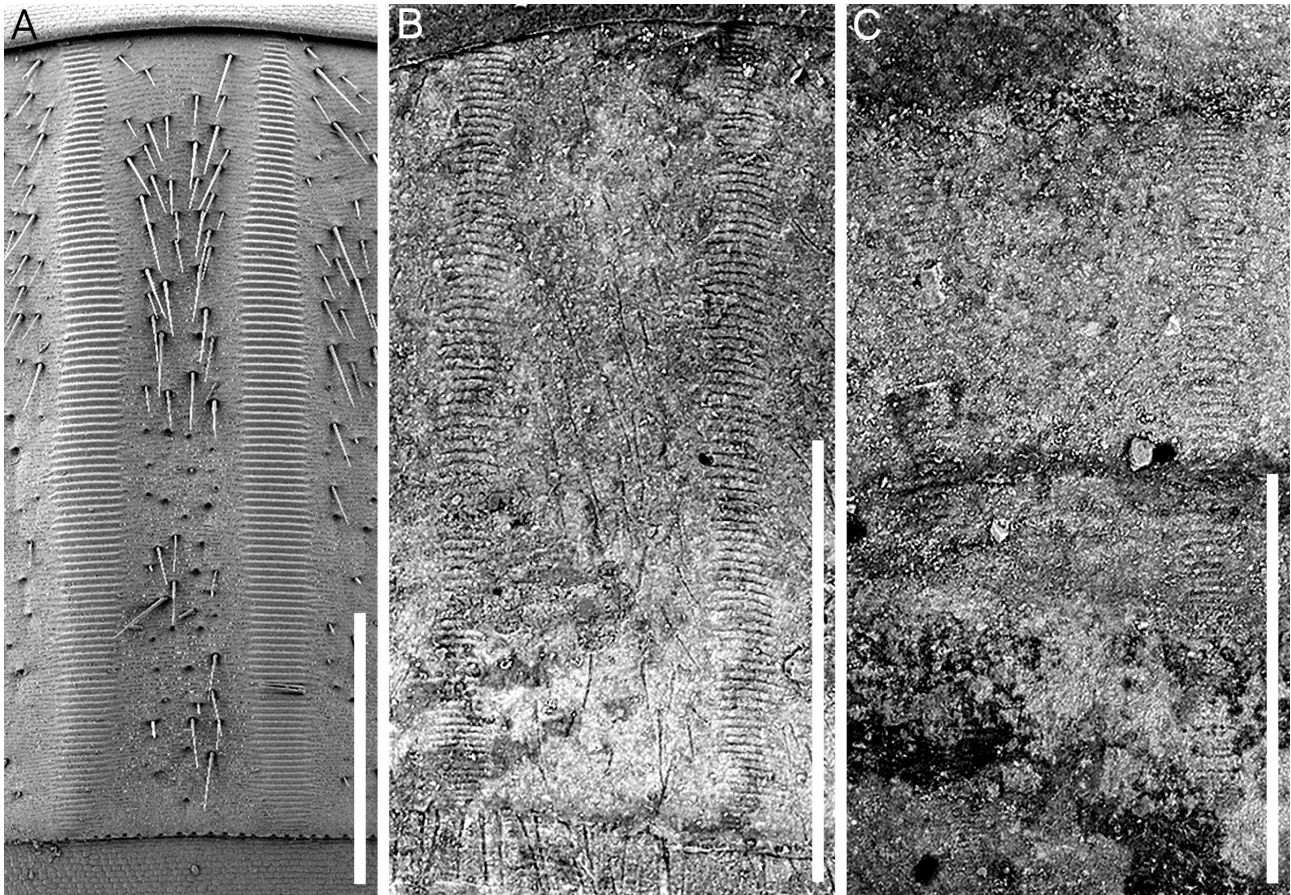


Figure 5. Comparison of stridulatory files between Cretaceous and Recent Nicrophorini carrion beetles, scanning electron micrograph. **A**, Stridulatory files of *Nicrophorus orbicollis*. **B**, Stridulatory files in *Cretosaja thayerae* **sp. nov.**, NIGP156152a. **C**, Stridulatory files in NIGP156154. Adapted from Cai *et al.* (2024). Scale bars = 0.5 mm.

Discussion

As noted in Cai *et al.* (2014), the Early Cretaceous carrion beetles *Paracretosaja newtoni* **gen. et sp. nov.** and *Cretosaja thayerae* **sp. nov.** are superficially similar to the Silphini-looking beetles from the Middle Jurassic Daohugou Biota in their general habitus, body size, and antennal morphology. As in the Jurassic Silphini, the Cretaceous taxa exhibit two antennal types: one gradually dilated apically (*Paracretosaja*), closely resembling one of the Jurassic morphotypes, and the other (*Cretosaja*) characterized by an elongate scape and four distinctly dilated apical antennomeres. In contrast to the Jurassic Silphini, the Cretaceous forms possess Y-shaped, posteriorly fused gular sutures, moderately separated mesocoxae, and, most importantly, paired stridulatory files on abdominal tergite V (Fig. 5). These derived characters indicate that all known Cretaceous forms can be confidently assigned to the extant tribe Nicrophorini.

The occurrence of multiple Early Cretaceous nicrophorine carrion beetles in the Early Cretaceous Jehol biota (Xu *et al.* 2020; Yin *et al.* 2024; Zhou *et al.* 2021) indicates that the tribe Nicrophorini were already diverse and widespread across eastern Asia by this time. Together with previously reported taxa from the Korean Peninsula, the material suggests a broad geographic distribution and an early radiation of the tribe in this region. The discovery of *Cretosaja* and *Paracretosaja* from the Lower Cretaceous Yixian Formation further highlights close entomofaunal similarities between the Lower Cretaceous Jinju Formation of South Korea and the Jehol biota of western Liaoning, China. Both formations preserve exceptionally rich and taxonomically similar insect assemblages, including shared or closely related coleopteran lineages (Lee *et al.*, 2022, 2023, 2024a, 2024b), indicating strong biogeographic connections between these regions. These similarities are consistent with previous studies that have documented overlapping insect faunas and suggest that broadly comparable palaeoenvironmental conditions supported closely related insect communities across eastern Asia during the Early Cretaceous.

Carion-feeding beetles play a crucial role in terrestrial ecosystems by accelerating carcass decomposition, recycling nutrients, and structuring successional communities associated with decaying organic matter (Potticary *et al.* 2024). The presence of nicrophorine beetles in multiple Early Cretaceous deposits indicates that these ecological functions were already well established (Cai *et al.* 2014). In particular, the inferred carcass-utilizing behaviours of basal Nicrophorini suggest that they contributed significantly to nutrient cycling and ecosystem functioning in Mesozoic terrestrial environments, much as their modern descendants do today.

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