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Leehermania prorova, the earliest staphyliniform beetle, from the Late Triassic of Virginia (Coleoptera: Staphylinidae)

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ABSTRACT

The Staphylinidae contain over 57,000 described species, thus comprising one of the largest families in all Insecta. *Leehermania prorova* Chatzimanolis, Grimaldi, and Engel, new genus and species, is described, which is the earliest staphylinid and the oldest definitive polyphagan beetle. The new species is based on a series of well-preserved specimens from the early Norian to late Carnian-aged (Late Triassic) Cow Branch Formation of southern Virginia. It is considered to be subfamily incertae sedis within Staphylinidae, but its possible affinity with the tachyporine group of staphylinids is noted. A summary of all Mesozoic Staphylinidae is provided and the evolutionary history of the lineage briefly discussed.

INTRODUCTION

With more than 360,000 described species, Coleoptera comprise the most diverse order in the 410 million year history of the Insecta. Their success is usually attributed to one hallmark

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feature, which is the pair of elytra, or hardened forewings, that cover and protect the folded hind wings that are used in flight. Indeed, Coleoptera were apparently the first Holometabola to have invaded tight spaces like humus, soil, and wood, while retaining the fundamental adaptation of flight. Many of the morphological features defining the Coleoptera, in fact, are related to the “elytrization” of these insects, and collectively serve in working the insect through substrate (Lawrence and Newton, 1982; Grimaldi and Engel, 2005).

The earliest coleopteran relatives are species in the family Tshekardocoleidae from the Early Permian of Obora, Czech Republic, and Tshekarda, Russia (Rohdendorf, 1944; Ponomarenko, 1963; Kukalová, 1969), which are usually placed into the “Protocoleoptera” (Crawson, 1975; Grimaldi and Engel, 2005), an apparently paraphyletic stem group possessing primitive features like extensive venation on long, pointed, tegminous forewings. Some even possessed a sclerotized, external ovipositor, which all Mesozoic and Recent Coleoptera have lost. Roughly contemporaneous with these tshekardocoleids were also some of the earliest representatives of the “Archecoleoptera” (Lubkin and Engel, 2005; Beckemeyer and Engel, 2008), which still possessed wing veins, though reduced, along with the distinctive rows of square areolae on shorter, more typically rounded elytra. These “Archecoleoptera” became more dominant by the Late Permian (e.g., Martynov, 1932, 1937; Rohdendorf, 1944, 1961; Ponomarenko, 1963, 2000, 2003; Kukalová, 1969; Pinto, 1987; Geertsema and van der Heever, 1996). Béthoux (2009) redefined *Adiphlebia lacoana* Scudder from the Late Carboniferous Mazon Creek Lagerstätten as a stem coleopteran, presumably sister to all other Coleoptera, including the “Protocoleoptera” and “Archecoleoptera.” Under this scenario, Adiphlebioptera represents a stem group to the entire Coleopterida (= “Protocoleoptera,” “Archecoleoptera,” + Coleoptera s. s.), and could not be considered a true beetle without dramatically redefining the order. Recently, Meller et al. (2011) described four new “Protocoleoptera” beetles in the family Permosynidae from the Lunz Formation, Austria (Carnian, Late Triassic), along with the remains of an abdomen putatively belonging to a polyphagan beetle, but without a formal description of the species.

Evidence thus far indicates there was a dramatic change in the coleopteran faunas from the Late Permian to the Triassic. This is attributable to the End Permian Event (EPE) 247 Mya (Erwin, 1993; Bowring et al., 1999), though the stratigraphic sampling is incomplete since fossil insects (including beetles) are essentially lacking from the earliest parts of the Triassic (Induan-Olenekian: 247–241 Mya). Yet the approximately 10 million years after the EPE is evolutionarily a brief interval of time for Coleoptera and many insect groups, since insects in Miocene amber typically reveal very little change from modern ones (Grimaldi and Engel, 2005). Thus, the faunal turnover from the Late Permian to the mid- and Late Triassic probably reflects not sampling bias but a major biotic event (Knoll et al., 1996; Berner, 2002; Huey and Ward, 2005).

The earliest true Coleoptera were diverse by the Anisian (240 Mya), as revealed by 32 “species” or morphotypes, sorted from 584 specimens of primarily elytra in the Grès à Voltzia Formation of the Vosges mountains of northeastern France (Papier et al., 2005). These authors did not propose family classifications for the Grès à Voltzia beetles, stating (as we believe) that “without any visible venation, [it] therefore prevent[s] any systematic study and determination

of their affinities” (Papier et al., 2005: 182). The Madygen Formation (Ladinian-Carnian: 236–220 Mya) from the Fergana Valley, straddling Uzbekistan, Kyrgyzstan, and Tajikistan, has yielded the greatest Triassic diversity: some 65 species assigned to nine families (sorted from 3500 specimens) (Ponomarenko, 1969, 1977, 1995). Coleoptera are scattered amid deposits from the Meride limestone in southern Switzerland and northern Italy (Ladinian: 234 Mya); the Keuper Basin (Norian: 222–209 Ma: Brauckmann and Schlüter, 1993); the Argilliti di Riva di Solto Formation near Bergamo, Italy (Rhaetian: 209 Mya: Whalley, 1986; Bechly, 1997), from deposits of similar age in Britain; and throughout central Asia and Asia Minor (i.e., Tolgoy and Protopivskya Formations: Carnian to Rhaetian). In eastern Asia (including Japan), Triassic Coleoptera predominate in deposits from the Ladinian to the Rhaetian (Lin, 1983, 1986, 1992; Lin and Mou, 1989; Fujiyama, 1973). Two very rich southern deposits harbor diverse Coleoptera, which are the Carnian-aged Ipswich series in Queensland, Australia (e.g., Dunstan, 1923; Riek, 1955), and deposits of similar age in the Molteno beds of South Africa (e.g., Riek, 1974, 1976). Scattered Coleoptera are reported in Late Triassic deposits from South America (e.g., Martins-Neto et al., 2006, 2007, 2008), and other than the Cow Branch Formation fauna (herein, and Grimaldi and Fraser, unpubl. data), the North American fauna of Triassic insects has been extremely depauperate.

In this paper we describe the oldest known staphyliniform beetle, specifically belonging to the family Staphylinidae, from the Late Triassic Cow Branch Formation, and discuss its evolutionary implications. Material examined is deposited in the Virginia Museum of Natural History, Martinsville, Virginia (VMNH), and the Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut (YPM).

GEOLOGICAL SETTING AND PRESERVATION

The deposit is in the Jurassic-Triassic system of rift basins that belong to the Newark Supergroup, which lie along the eastern coast of North America (Olsen, 1986; Olsen et al., 1978, 1991). Insects occur sporadically within Newark supergroup outcrops from Massachusetts to North Carolina (Huber et al., 2003), but only certain outcrops of the Carnian/early Norian-aged Cow Branch Formation consistently yield abundant, diverse, and well-preserved insects and plants (Fraser et al., 1996; Fraser and Grimaldi, 2003). The Cow Branch Formation correlates with the Chinle Formation of the southwestern United States (Olsen et al., 1978; Fraser et al., 1996), and paleomagnetic data as well as the fishes and phytosaurs provide a strong correlation with the Lockatong Formation of Pennsylvania, New Jersey, and New York (Ladinian-Norian: 237–207 Ma) (Olsen and Kent, 1996; Olsen et al., 1996). An abundant, amphibious eosuchian in the Cow Branch, *Tanytrachelos* Olsen, is closely related to mid-Triassic forms from Europe, such as *Tanystropheus* Meyer (Olsen et al., 1978; Fraser et al., 1996).

The main insect-bearing outcrops of the Cow Branch Formation are in quarries of the former Solite Corporation near Cascade, Virginia. These outcrops expose over 30 Van Houten cycles, one of which is particularly fossiliferous (Fraser et al., 1996). The insects occur in a

one-inch-thick layer of very fine-grained, black, microlaminated lacustrine shale, which lies between thick silt layers. It was from this cycle that Olsen et al. (1978) originally reported insects. Taphonomy of the insects is unique because entire specimens are routinely preserved, not just the dissociated wings that are the primary insect remains for the Triassic. Also, the insects and plants are preserved as silvery films of aluminosilicates, the detail in which for insects includes microtrichia on appendages and wings and facets in eyes. Optimal observation of the insects, though, requires either polarized light filters or an intense, diffuse, nondirectional light source such as a fiber optic ring light. Wetting the specimens with ethanol increases the contrast between the fossilized remains and matrix. Specimens can also be examined using scanning electron microscopy, either in backscatter or secondary electron mode, and obviously uncoated (an environmental SEM is not necessary). Here, we used a Hitachi S-4700 field emission SEM and Zeiss Evo-60 variable pressure SEM at 10 kV, which gave good to reasonable results on just two of the four specimens examined, particularly specimen VMNH 1343. There appears to be little correlation between specimen quality as observed using the visible light spectrum, and quality of the electron signal and image using SEM. For example, specimen YPM 1147 has excellent preservation under the stereomicroscope, and despite repeated attempts to image mouthparts, legs, and antennae, there was virtually no signal using the SEM.

Taxonomic papers on other arthropods from this deposit include ones on the oldest araneoid spiders (Selden et al., 1999), the earliest definitive thrips (order Thysanoptera) (Grimaldi et al., 2004), the first Western Hemisphere record of the Mesozoic mecopteridan family Pseudopolycentropodidae (Grimaldi et al., 2005), a cockroach (order Blattaria) (Vršanský, 2003), and a diverse fauna of early Diptera (Blagoderov et al., 2007). Other orders in the Cow Branch Formation besides these and the Coleoptera are Hemiptera, Orthoptera, and Plecoptera (Fraser et al., 1996; Grimaldi, unpubl. data). Autochthonous taxa in the deposit are primarily the waterbugs (Belostomatidae and other Nepomorpha [Hemiptera]), making this one of the earliest aquatic insect faunas (Sinitshenkova, 2002; Grimaldi and Engel, 2005). All the other insects, though, and probably all of the plants are allochthonous. Plants include bennettitaleans, cycads, ferns, ginkophytes, and most commonly, conifers. Most insects preserved in the Cow Branch Formation were probably living amid the vegetation that bordered an ancient lake.

SYSTEMATIC PLACEMENT

PLACEMENT WITHIN COLEOPTERA

A distinctive feature of the family Staphylinidae is the truncated elytra, which occur sporadically in other families but which are distinguishable by the proportions of the elytra and abdomen, and overall body shape. Other families with truncated elytra include the Nitidulidae (especially carophilines), Histeridae, Silphidae, and Melyridae, but these have truncated elytra with only three to four abdominal segments exposed (Staphylinidae typically have six abdominal segments exposed) and the bodies tend to be much broader, flatter, and not at all fusiform. Another key synapomorphy of Staphylinidae (contiguous procoxae) is not visible in the Solite specimens, since none of the specimens have the ventral body surface exposed (all are just dorsal or lateral in preservation).

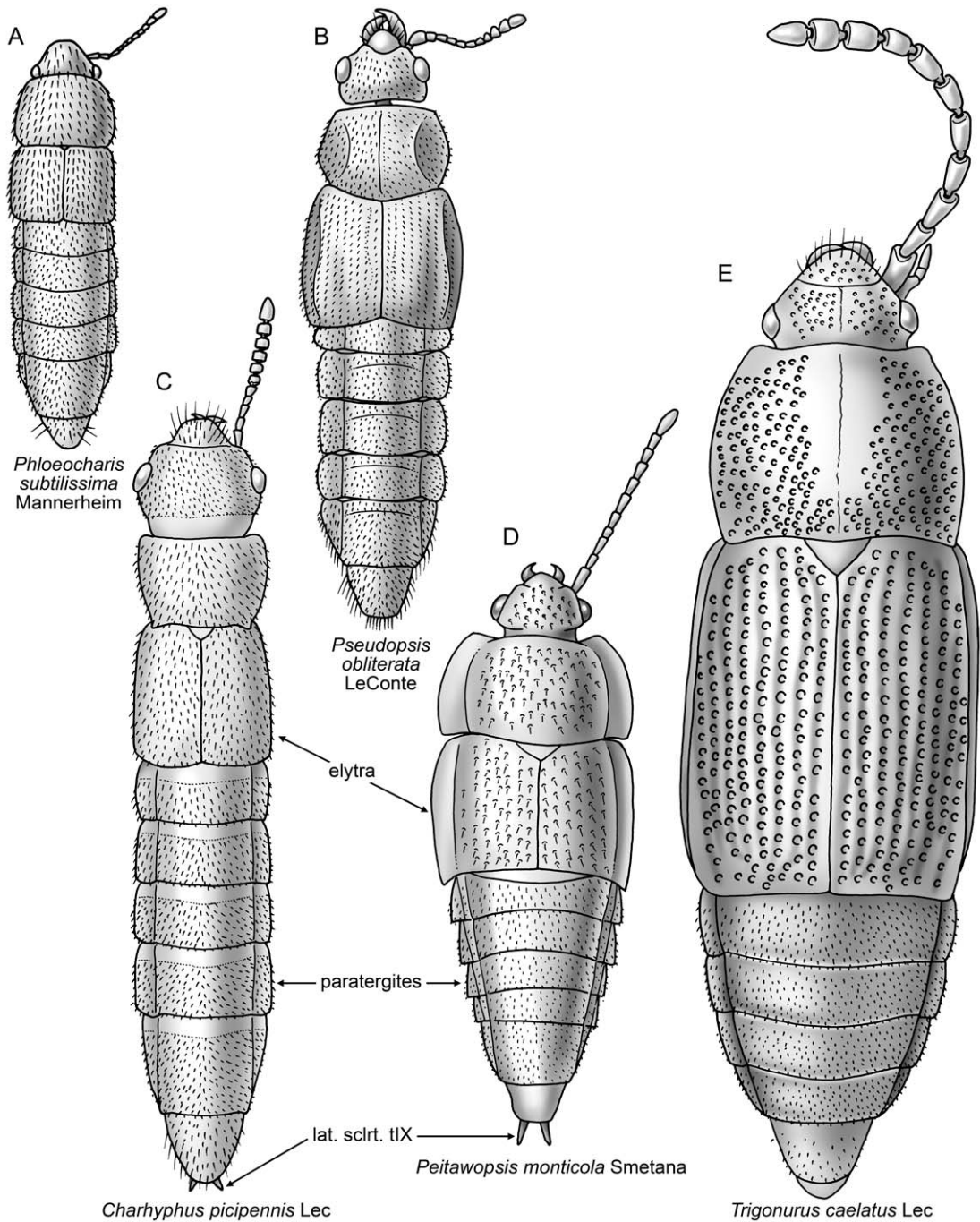


FIGURE 1. Dorsal habitus (without legs) of exemplar Staphylinidae, with labels for structures referred to in the text. **A.** Phloeocharinae. **B.** Pseudopsinae. **C.** Trichophyinae. **D.** Tachyporinae. **E.** Trigonurinae. All to the same scale. Original. Abbreviations: **lat sclrt. tIX**, lateral tergal sclerites of abdominal segment IX.

PLACEMENT WITHIN STAPHYLINIDAE

The placement of this taxon within Staphylinidae is challenging for two reasons: (1) several key morphological features are not preserved (e.g., mouthparts, legs, clear ventral view), and (2) because the phylogenetic relationships of the family are not well understood. Thayer (2005) and Newton (2011) provided a summary phylogeny for the family, but several subfamilies or groups within Staphylinidae are not defined based on synapomorphies. Within Staphylinidae there are four major, presumably monophyletic, informal groups: the Omaliine group, Tachyporine group, Oxyteline group, and Staphylinine group (refer to Thayer, 2005, for more details). Based on the overall body habitus and certain characteristics—antennal insertions exposed, antennae inserted anterior to the eyes, retractable head without distinct neck, and six visible abdominal segments—the taxon newly described herein appears to be a stem group of the Tachyporine group (and thereby more closely related to the subfamily Tachyporinae). However, as stated by several authors (Ashe, 2005; Thayer, 2005), Tachyporinae is probably a group of convenience rather than a monophyletic lineage, and thus there is little point in trying to place this taxon within this assemblage based on specific synapomorphies. Besides the subfamily Tachyporinae, the Tachyporine group includes the subfamilies Aleocharinae, Habrocerinae, Phloeocharinae, Olisthaerinae, and Trichophyinae (Ashe, 2005). Even though characters that would definitely exclude *Leehermania* from Aleocharinae are not visible (e.g., shape of aedeagal parameres, mouthparts), *Leehermania* appears not to belong in Aleocharinae because the posterolateral margins of the elytra are not sinuate (smooth in *Leehermania*) and the antennae are inserted anterior to the compound eyes and not into the vertex between the compound eyes as in most aleocharines. Habrocerinae + Trichophyinae have verticillate antennae that are lacking from *Leehermania*. Lastly, *Leehermania* does not belong in Phloeocharinae because the antennal insertions are not concealed from above (visible in *Leehermania*; fig. 2A, B) or in Olisthaerinae based on the overall shape of the body and because *Leehermania* lacks a pronotal postcoxal process.

Excluding the Tachyporine group, the only other remote membership possibilities for *Leehermania* (based on the habitus) are the subfamilies Trigonurinae, Osoriinae, or Omaliinae. However, these placements seem unlikely for the following reasons: the elytra do not have striae as in the subfamily Trigonurinae (this is not an apomorphy for Trigonurinae but rather for the clade Trigonurinae + Apateticinae: Thayer, 2005); also, the sternites and tergites are not fused but rather separated, unlike the Osoriinae. Finally, *Leehermania* does not possess ocelli, and thus does not seem to belong to Omaliinae (although there are several Omaliinae without ocelli: Thayer, 2005), and because omaliines typically have a much broader shape than seen here.

SYSTEMATIC PALEONTOLOGY

Order COLEOPTERA Linnaeus, 1758

Suborder POLYPHAGA Emery, 1886

Family STAPHYLINIDAE Latreille, 1802

Subfamily incertae sedis

Leehermania Chatzimanolis, Grimaldi, and Engel, new genusTYPE SPECIES: *Leehermania prorova* Chatzimanolis, Grimaldi, and Engel, new species.

DIAGNOSIS: Body sublumiloid, with dorsum of body (especially elytra and pronotum, portions of head and apical tergites of abdomen) with dense vestiture of microsetae. Head prognathous and retractile to compound eye level (as evident in several specimens, e.g., figs. 2, 4, 6); antenna with 11 antennomeres, with narrow antennomeres and slight terminal club; antennal insertions visible from above; neck absent. Pronotum rectangular, with slightly sinuous posterior margin. Elytra rectangular, apical margin flat to slightly convex; elytra long, length $2\times$ length of pronotum, slightly less than $0.3\times$ length of body. Abdomen with six visible segments, tapered apicad to narrow, forked terminal segment (lateral tergal sclerites of abdominal segment IX visible), with sparse stiff macrosetae (fig. 2B); with no paratergites (figs. 2, 4, 5, 6), but tergites and sternites not fused (fig. 8B) (as in most Osoriinae).

ETYMOLOGY: The new genus group name honors Lee Herman, coleopterist at the American Museum of Natural History and world's authority on the Staphylinidae, for his achievements, his expert assistance, and in appreciation of his friendship. The name is feminine.

Leehermania prorova Chatzimanolis, Grimaldi, and Engel, new species

Figures 2–9

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: Body sublumiloid in shape, with lateral margins of pronotum and elytra nearly parallel (slightly wider near middle of elytra), but with abdomen tapered to apical point. Body length (anterior margin of head to apex of abdomen) 2.1–3.1 mm (mean 2.5 mm). Vertex of head, pronotum, entire surface of elytra, and portions of abdominal tergites covered with dense vestiture of long, decumbent microsetae. No color patterns apparent [color patterns are preserved in some other beetles from the Cow Branch Formation]. **Head:** Prognathous; nearly hemispherical in shape but with anterior end slightly narrowed; mandibles pointed. Antennae widely separated, insertions anterior to compound eyes, distance between insertions approximately equal to distance between inner margins of compound eyes; antenna short, length approximately equal to width of head, with sparse macrosetae (e.g., fig. 7); antennomeres 1–8 longer than wide; antennomere 1 (scape) enlarged (fig. 2B); apical three antennomeres slightly thickened into apical club; antenna with at least basal antennomeres having fine setae on anterior surface (few, if any, occur on the posterior surface). Compound eyes of moderate size, greatest diameter approximately one-third length of head (fig. 9B). **Thorax:** Pronotum large, rectangular; anterior margin slightly concave, lateral margins slightly convex, posterior margin slightly sinuate; width $1.6\times$ length; anterolateral angles acute; pronotum slightly wider than head, slightly thinner than greatest width of elytra, with no visible postcoxal process; microsetae near central disk of pronotum pointed toward longitudinal midline, those on lateral sides of pronotum and on elytra pointed posteriad. Elytra long, length approximately $0.31\times$ body length, $2.3\times$ elytron width; lateral margins slightly convex, posterior margins flat to slightly convex. Small, triangular mesoscutellum visible (figs. 2, 6), with microsetae. Legs not clearly visible but in YPM 1147 (fig. 8) with pro-, meso-, and metafemora stout, width ca. $0.5\times$ that of length, tibiae and tarsi thinner; pro- and mesotarsi appearing pentamerous. **Abdomen:** Tapered to narrow apex; apical segment forked, composed of lateral tergal sclerites of segment

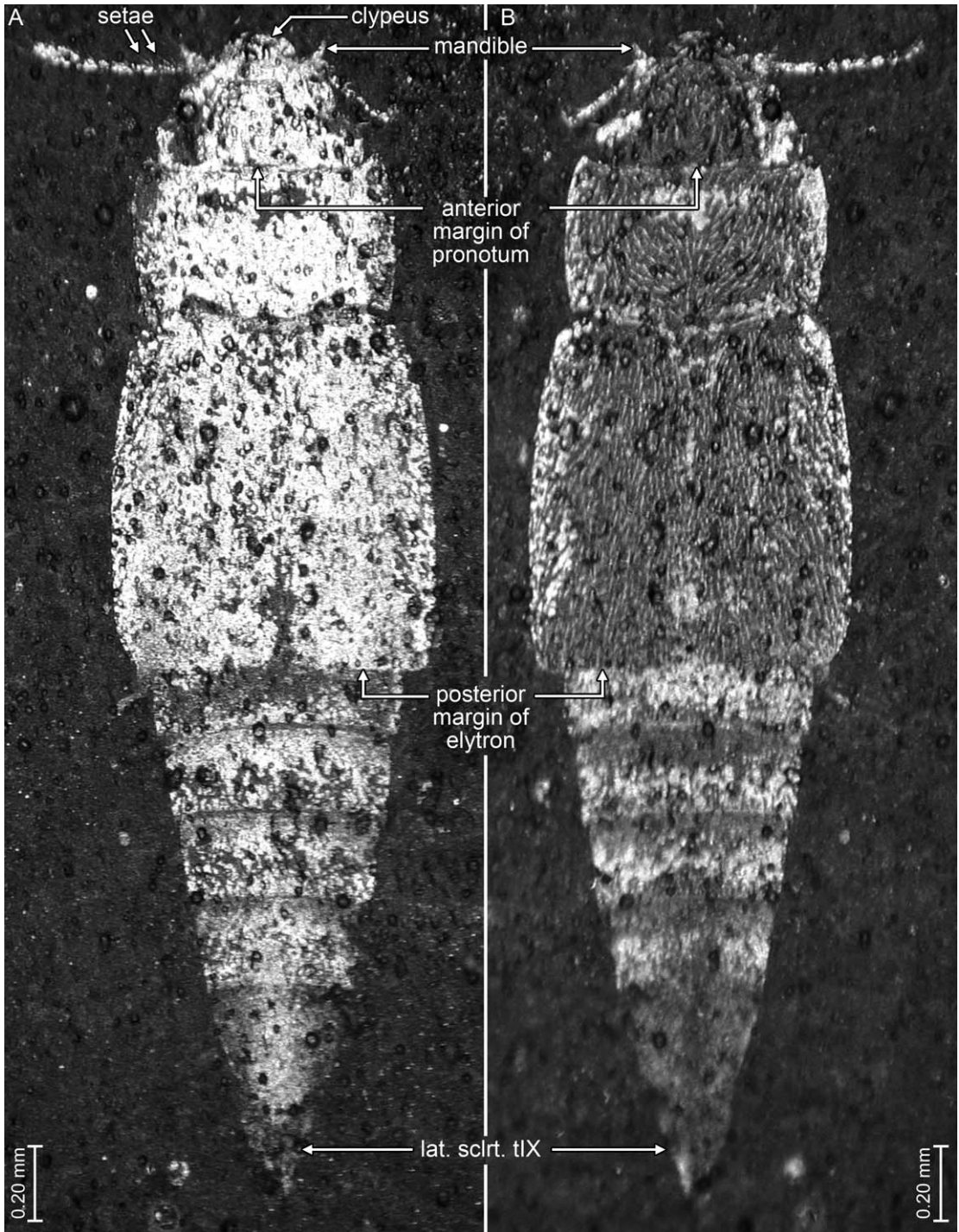


FIGURE 2. Photomicrographs of holotype (VMNH 734) of *Leehermania prorova*, gen. et sp. n., showing dorsal surface. A. Part (VMNH 734a). B. Counterpart (VMNH 734b).

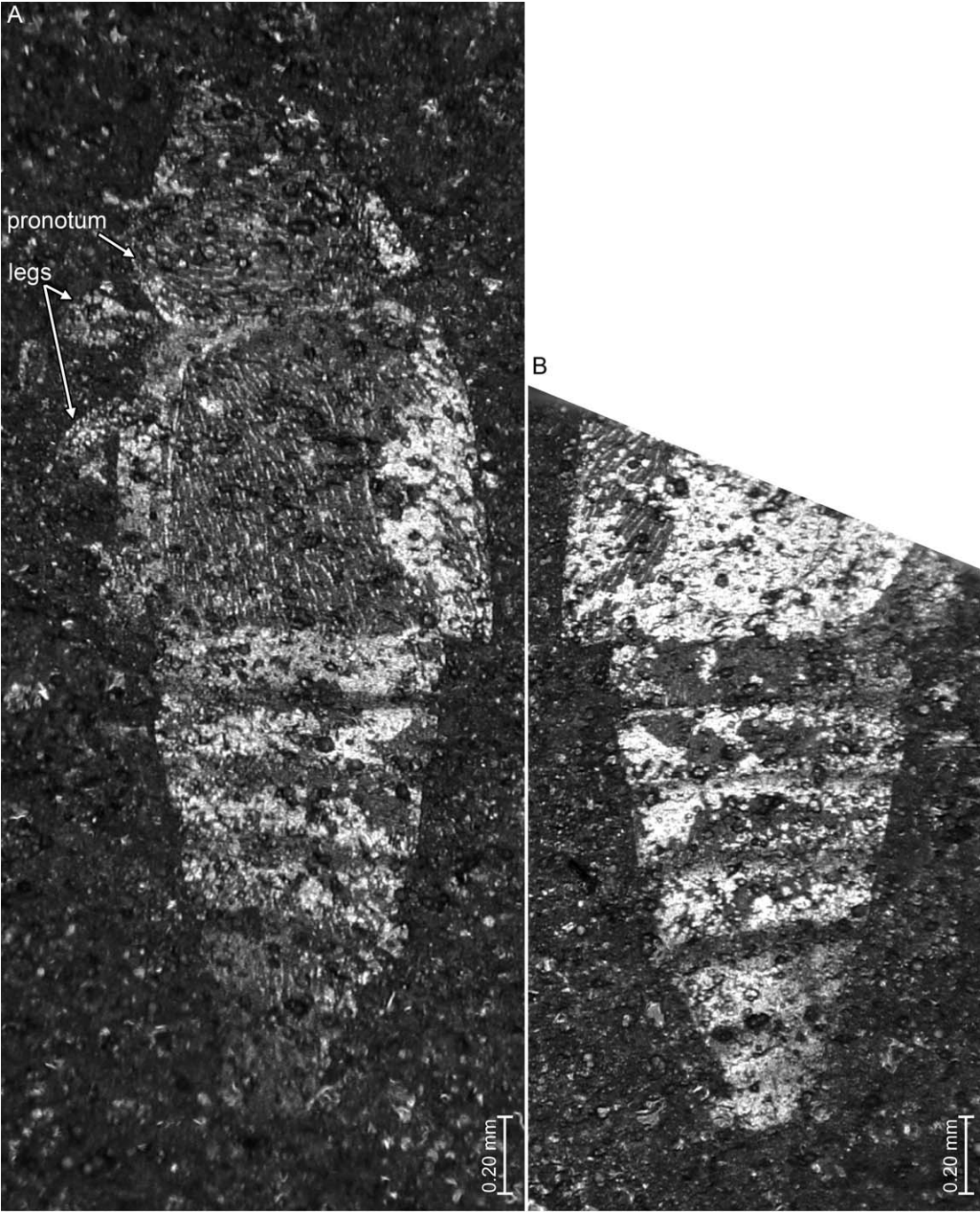


FIGURE 3. Photomicrographs of paratype (VMNH 1233) of *Leehermania prorova*, gen. et sp. n., showing dorsal surface. **A.** Part (VMNH 1233a). **B.** Partial counterpart of posterior half (VMNH 1233b).



FIGURE 4. Photomicrographs of paratypes of *Leehermania prorova*, gen. et sp. n., both showing dorsal surfaces. A. VMNH 1446. B. VMNH FN 442, its left elytron is slightly extended away from body.

IX (i.e., VMNH 1343, figs. 5, 7); six tergites (III–VII) and lateral tergal sclerites of abdominal segment IX visible; tergite VII (5th exposed segment) apparently with fine, irregular striae; lateral tergal sclerites of IX becoming tapered to narrow apex; exposed portion of abdomen $0.44\times$ body length; apex of abdomen with sparse, stiff macrosetae at least on lateral margins and near apex of lateral sclerites of segments IX.

HOLOTYPE: VMNH 734a, b [part and counterpart], sex unknown, from Virginia: Cascade (near Martinsville), Solite Corporation Quarries, Cow Branch Formation (late Carnian–early Norian: Late Triassic); deposited in the Virginia Museum of Natural History, Martinsville.

PARATYPES: (Same locality) VMNH 1233 a, b; VMNH 1343a, b; VMNH 1446; VMNH 1997-174; VMNH FN 442; YPM 1147a, b; YPM 36447; VMNH 2986, VMNH 2805, VMNH 3099.

ADDITIONAL MATERIAL: The following specimens (from the same locality) are not included in the type series due to their incomplete preservation: VMNH C-1; VMNH C-2; VMNH C-3a, b; VMNH C-4a, b; VMNH C-5a, b; VMNH C-6a, b; VMNH C-7a, b; VMNH 1278; VMNH 1341a, b.

ETYMOLOGY: The specific epithet is derived from the words *pro-* (shortened from Greek *prōtos*, “first”) and *-rova*, deriving from the common name of staphylinid (“rove”) beetles.

COMPARISONS AND NOTES: Some specimens (e.g., VMNH 1446, VMNH 1343) appear significantly broader, which is a common taphonomic distortion in Cow Branch specimens, wherein the insect is stretched in one axis. Below we compare *Leehermania* with other Mesozoic Staphylinidae that are possibly related. The first Triassic staphylinid to be reported is a slightly younger specimen also from a Newark supergroup deposit (Gore, 1988). That specimen (NMNH no. 388367) is from the Groveton Section of Culpepper Basin in northern Virginia, which is of Norian age. It was examined by one of us (D.A.G.), and while the body proportions agree with that of *Leehermania*, the coarse grain of the matrix precludes the observation of any details.

Among diverse species of staphylinids described from the Karabastau Formation (Kimmeridgian: Late Jurassic, 155.7–150.8 Mya) of Karatau, Kazakhstan (Tikhomirova, 1968), several resemble *Leehermania*, including the genera *Abolescus* Tikhomirova, *Abscondus* Tikhomirova, *Archodromus* Tikhomirova, *Mesotachinus* Tikhomirova, and *Tachyporoides* Tikhomirova. Tikhomirova (1968) placed the genera *Abolescus* and *Abscondus* in Piestinae, but she used an outdated definition of the subfamily and the taxon should probably be moved to a different oxyteline-group subfamily, while *Archodromus* was placed in Omaliinae. The remaining two taxa (*Mesotachinus* and *Tachyporoides*) were placed in Tachyporinae. *Leehermania* can be distinguished easily from all these genera because it lacks paratergites (present in all others). *Tachyporoides* also has dense microsetae on the elytra, but not on the head or pronotum (as in *Leehermania*), whereas *Mesotachinus* has series of macrosetae on the posterior abdominal segments (*Leehermania* has just a few such setae). *Leehermania* can be distinguished from the species of *Hesterniasca* Zhang, Wang, and Xu (Zhang et al., 1992; Cai et al., 2011; Late Hauterivian–Early Barremian: Early Cretaceous, 132–112 Mya) based on the presence of paratergites in the latter and the dimensions of the pronotum (in *Hesterniasca* the pronotum is much wider than the elytra). Yue et al. (2009a) described *Glabrimycetoporus amoenus* from the Yixian Formation (Late Hauterivian–Early Barremian: Early Cretaceous, 132–112 Mya) and placed it in Tachyporinae and provisionally in Mycetoporini. *Leehermania* differs in the lack of paratergites, the relative proportions of elytra to pronotum (elytra are 1.4× the length of the pronotum in *Glabrimycetoporus* and 2× in *Leehermania*) and the general shape of the abdomen. Gusarov (2000) described *Mesotachyporus puer* from New Jersey amber (Turonian: Late Cretaceous, 93.5– 89.3 Mya), which is similar to *Leehermania* in that it lacks paratergites. However, this species has a glabrous pronotum that is narrowed anteriorly, and long macrosetae on the last



FIGURE 5. Photomicrograph of paratype (VMNH 1343) of *Leehermania prorova*, gen. et sp. n., showing dorsal surface. The specimen is broader than others because of taphonomic distortion. This specimen was imaged also using secondary electron SEM (fig. 7). Part VMNH 1343a.

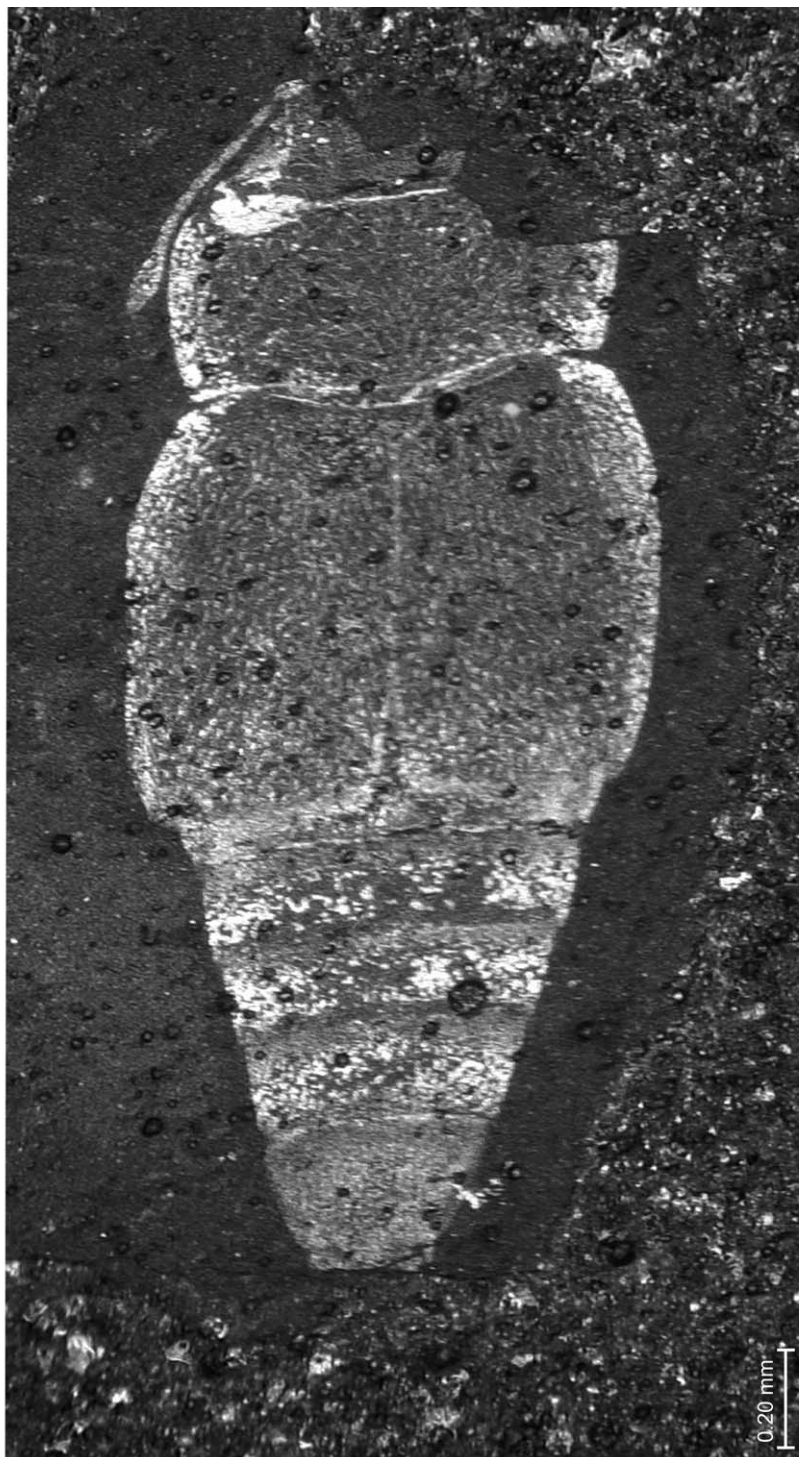


FIGURE 6. Photomicrograph of paratype of *Leehermania prorova*, gen. et sp. n., counterpart of VMNH 1343b.

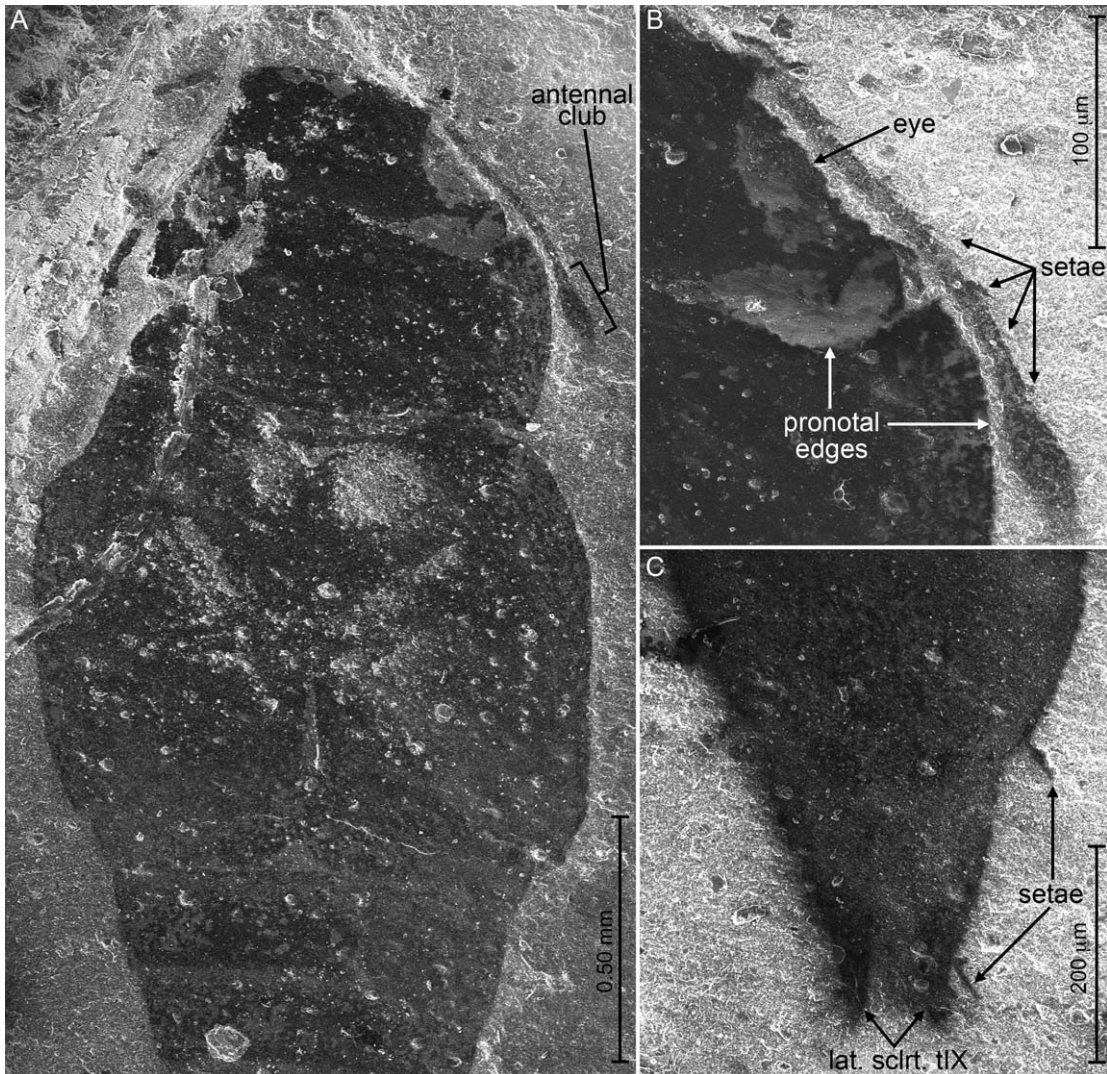


FIGURE 7. Scanning electron micrographs (secondary electron images) of VMNH 1343a. **A.** Anterior portion of body (original magnification 20 \times). **B.** Detail of head, showing some antennal segmentation and setation (original magnification 200 \times). **C.** Detail of posterior end, showing lateral tergal sclerites of abdominal segment IX (lat sclrt. tIX) and scattered stiff setae (original magnification 70 \times).

abdominal segments. *Leehermania* is also morphologically distinct from *Undiatina pilosa* Ryvkin, 1990, *Cuneocharis elongatus* Ryvkin, 1990, and *Ryvkininus gracilis* (Ryvkin, 1990), described originally under the preoccupied name *Mesoporus* Ryvkin, 1990, all placed in Tachyporinae and described from Unda and Daya, Russia, of Early Cretaceous age, 145.5–130 Mya. *Undiatina*, *Cuneocharis*, and *Ryvkininus* have paratergites and their head is conical whereas it is hemispherical in *Leehermania*.



FIGURE 8. Photomicrographs of paratype (YPM 1147) of *Leehermania prorova*, gen. et sp. n., lying in lateral view. A. Part, YPM 1147a. B. Counterpart, YPM 1147b.

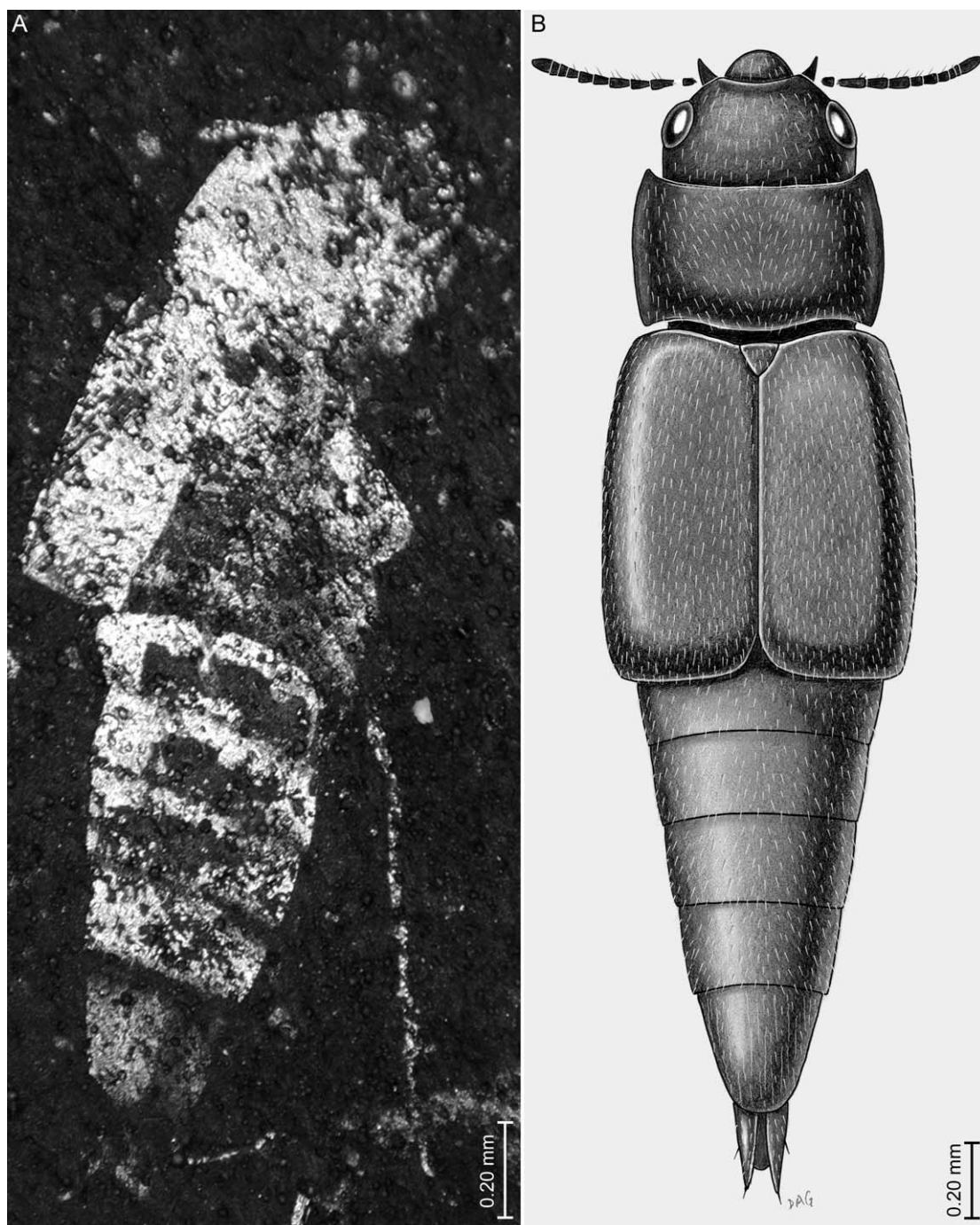


FIGURE 9. **A.** Photomicrograph of paratype, YPM 36447, exposed in a ventrolateral position; its right elytron is slightly lifted away from the body. **B.** Reconstruction of *Leehermania proroa*, gen. et sp. n., based largely on the holotype (VMNH 734) and paratype VMNH 1343.

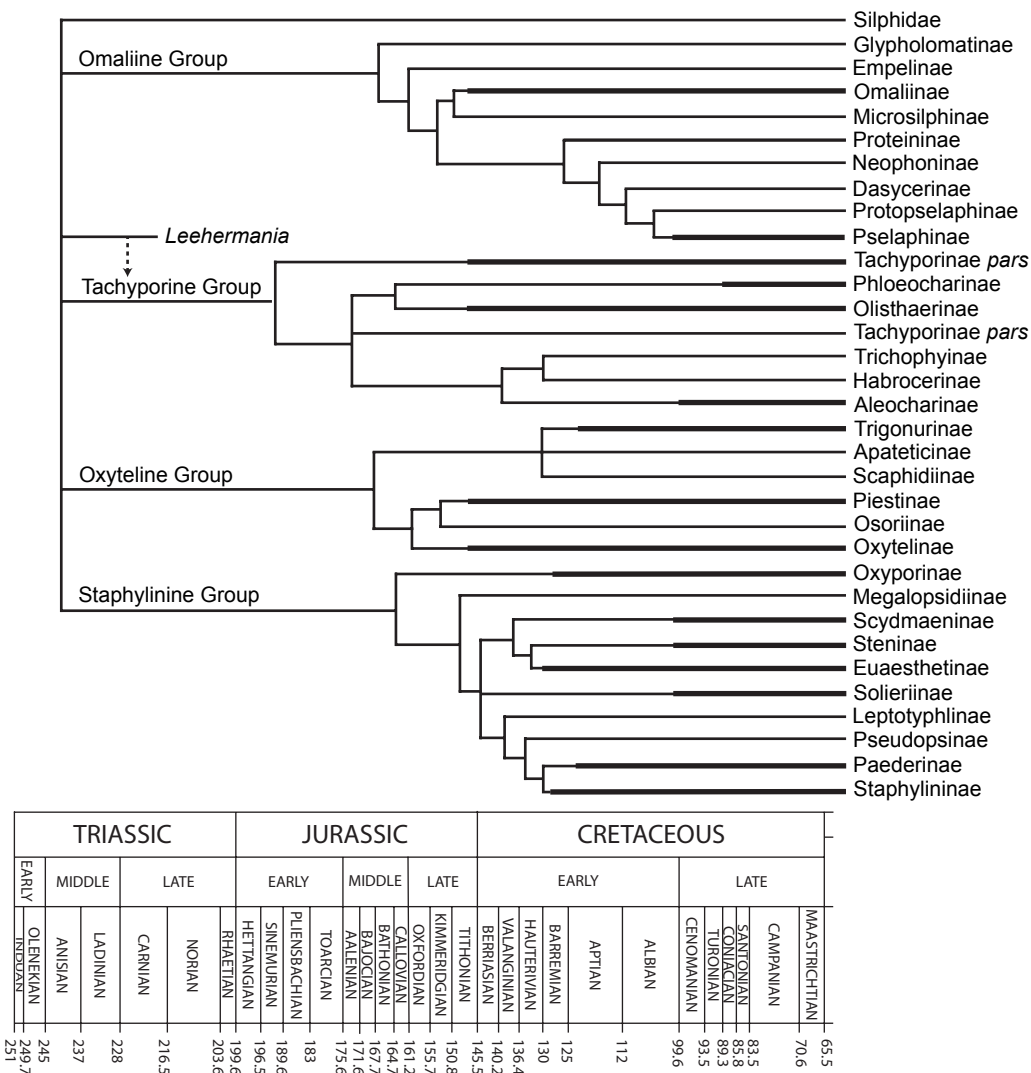


FIGURE 10. Phylogenetic schema of Staphylinidae s.l. after Newton (2011), with placement of *Leehermania* indicated and Mesozoic ranges of subfamilies highlighted based on records summarized in table 1 and personal observations of Pselaphinae and Aleocharinae in Burmese amber, Phloeocarinae in New Jersey amber, and Paederinae in the Crato Formation of Brazil.

DISCUSSION

Based on the morphological characters provided above, *L. prorova* can be placed confidently within Staphylinidae (contra Yue et al., 2010), although it remains unclear whether *Leehermania* is representative of a stem group to the tachyporine lineage or should be placed within one of the existing subfamilies. Regardless, *L. prorova* is the oldest species of the family Staphylinidae, itself numbering more than 57,000 described species today (Herman, 2001b;

A.F. Newton, unpubl. database). Given this Recent diversity, the existence of only one species of Staphylinidae in the Cow Branch Formation contrasts dramatically with that of the order Diptera preserved in this same deposit (Blagoderov et al., 2007).

The Mesozoic record of Staphylinidae is in need of considerable revision, particularly the types of taxa such as *Mesostaphylinus*, *Laostaphylinus*, and Tikhomirova's and Ryvkin's material (observations by one of us [D.A.G.] of Tikhomirova's type material revealed a significant number of inaccuracies in the descriptions). Nonetheless, the available material does shed some light onto the historical diversity of the family. By the Late Jurassic several species of recognizable subfamilies, such as Scaphidiinae, Omaliinae, Tachyporinae, Olisthaerinae, Oxytelinae, and Piestinae, were present in the fauna and, given the phylogenetic placement of these groups, it suggests that a great deal of the higher diversification of Staphylinidae had already taken place (fig. 10). Certainly, the Jurassic staphylinid fauna remains to be better explored and revised (e.g., Cai and Huang, 2010), but the insights currently available support an early diversification of the family into the major "Group" lineages by the Late Triassic. Clarke and Chatzimanolis (2009) argued that the Staphylinine group of subfamilies were established by the Early Cretaceous, and few if any of the subfamilies of Staphylinidae are younger than the Early Cretaceous, although Trichophyinae and Habrocerinae might be of Late Cretaceous, perhaps Early Tertiary, age. Fortunately, attributions of at least six of the families in the Cretaceous are definitive, since they are preserved with fidelity in amber. Regardless, the major radiations of the family, at least at the higher level, seem to predate the rifting of Gondwana. It is therefore not surprising that austral disjunct distributions are not reflected at the subfamily level, although there are certainly much younger tribes or generic clades of Staphylinidae that correlate with such a vicariant pattern (e.g., Newton, 1985; and the Omaliinae genus *Metacorneolabium* Steel: Tayer, 1985).

Implications of a staphylinid of Norian-Carnian age are significant, specifically for timing the radiation of the coleopteran suborder Polyphaga, which comprises at least 85% of all living species and the great bulk of families. As discussed above, the basal suborder of beetles, the Archostemata, has a long, diverse fossil record, with stem-group fossils occurring as early as the Permian. The suborder Adephaga likewise has an excellent fossil record, including definitive Caraboidea (Trachypachidae and Carabidae) in the Triassic, including from the Solite quarries (Ponomarenko, 2002; Grimaldi and Engel, 2005; unpubl.). Definitive Polyphaga from the Triassic, however, have been both elusive and ambiguous. Meller et al. (2011) attributed an isolated abdomen to this suborder, and Papier et al. (2005) reported a possible staphylinid in the Grès-à-Voltzia Formation from France (the unique specimen of which, unfortunately, has the middle portion of the body damaged and obscured). Ponomarenko (2002), in his summary of the fossil record of beetles, mentioned Hydrophilidae, Armatopodidae, Elateridae, and Curculionoidea (Obrienidae) in the Late Triassic. However, the fossils on which these attributions are based either do not belong to these families, or are at best ambiguous. For example, the putative weevil family Obrienidae was later classified as an archostematan (Gratshev and Zherikhin, 2003; Grimaldi and Engel, 2005). Thus, *Leehermania* appears to be the oldest definitive polyphagan, and this underscores a dimension to the exceptional diversity of modern Coleoptera, which is the accrual of taxa through expansive periods of time.

Table 1. Mesozoic Staphylinidae (C = compression; A = amber inclusion).

Taxon	Deposit (Preservation)	Age	References
TRIASSIC			
Subfamily incertae sedis			
<i>Leehermania prorova</i> , n. gen., n. sp.	Cow Branch, VA (C)	Carnian	Herein
Undescribed possible staphylinid	Grès à Voltzia, France (C)	Anisian	Papier et al., 2005
JURASSIC			
Subfamily Olisthaerinae Thomson			
<i>Anicula inferna</i> Ryvkin	Novospassky, Russia (C)	Aalenian?	Ryvkin, 1985
Subfamily Omaliinae MacLeay			
<i>Archodromus brachypterus</i> Tikhomirova	Karatau, Kazakhstan (C)	Kimmeridgian	Tikhomirova, 1968
<i>Archodromus comptus</i> Tikhomirova	Karatau, Kazakhstan (C)	Kimmeridgian	Tikhomirova, 1968
<i>Eophyllodrepa propinqua</i> Ryvkin	Novospassky, Russia (C)	Aalenian?	Ryvkin, 1985
<i>Globoides microps</i> Tikhomirova	Karatau, Kazakhstan (C)	Kimmeridgian	Tikhomirova, 1968
<i>Globoides oculatus</i> Tikhomirova	Karatau, Kazakhstan (C)	Kimmeridgian	Tikhomirova, 1968
<i>Globoides</i> sp.	Neimonggol, China (C)	Bathonian	Zhang, 2002
<i>Morsum abdominale</i> Ryvkin	Kubekovo, Russia (C)	Aalenian	Ryvkin, 1985
<i>Porrhodromus communis</i> Tikhomirova	Karatau, Kazakhstan (C)	Kimmeridgian	Tikhomirova, 1968
Subfamily Oxytelinae Fleming			
<i>Mesoxytelus mandibularis</i> Tikhomirova	Karatau, Kazakhstan (C)	Kimmeridgian	Tikhomirova, 1968
<i>Mesoxytelus parvus</i> Tikhomirova	Karatau, Kazakhstan (C)	Kimmeridgian	Tikhomirova, 1968
Subfamily Piestinae Erichson			
<i>Abolescus glabratus</i> Tikhomirova	Karatau, Kazakhstan (C)	Kimmeridgian	Tikhomirova, 1968
Subfamily Scaphidiinae Latreille			
<i>Scaphidiopsis hageni</i> (Weyenbergh)	Solnhofen, Germany (C)	Kimmeridgian	Weyenbergh, 1869
Subfamily Tachyporinae MacLeay			
<i>Abscondus regularis</i> Tikhomirova	Karatau, Kazakhstan (C)	Kimmeridgian	Tikhomirova, 1968
<i>Abscondus similis</i> Tikhomirova	Karatau, Kazakhstan (C)	Kimmeridgian	Tikhomirova, 1968
<i>Mesotachinus major</i> Tikhomirova	Karatau, Kazakhstan (C)	Kimmeridgian	Tikhomirova, 1968
<i>Mesotachinus medius</i> Tikhomirova	Karatau, Kazakhstan (C)	Kimmeridgian	Tikhomirova, 1968
<i>Mesotachinus minor</i> Tikhomirova	Karatau, Kazakhstan (C)	Kimmeridgian	Tikhomirova, 1968
<i>Tachyporoides villosus</i> Tikhomirova	Karatau, Kazakhstan (C)	Kimmeridgian	Tikhomirova, 1968
Subfamily incertae sedis			
<i>Protostaphylinus mirus</i> Lin	Haifanggou, China (C)	Bathonian	Lin, 1976; Cai and Huang, 2010
<i>Sinostaphylius xiejiajieensis</i> Hong	Jiuda Formation, China (C)	Jurassic?	Hong, 1992
<i>Sulcelytrinus antiquus</i> Tikhomirova	Karatau, Kazakhstan (C)	Kimmeridgian	Tikhomirova, 1968
<i>Tunicopterus sigara</i> Tikhomirova	Karatau, Kazakhstan (C)	Kimmeridgian	Tikhomirova, 1968

Taxon	Deposit (Preservation)	Age	References
CRETACEOUS			
Subfamily Euaesthetinae Thomson			
<i>Nordenskioldia pentatarsus</i> (Lafebvre et al.)	Lebanon (A)	Neocomian	Lefebvre et al., 2005
<i>Octavius electrospinosus</i> Clarke and Chatzimanolis	Myanmar (A)	Albian	Clarke and Chatzimanolis, 2009
Subfamily Omaliinae MacLeay			
<i>Daiodromus umbrosus</i> Ryvkin	Daya, Russia (C)	Neocomian	Ryvkin, 1990
<i>Mesodeliphrum rufulum</i> Ryvkin	Turga, Russia (C)	Neocomian	Ryvkin, 1990
<i>Prodaia inflatas</i> Ryvkin	Daya, Russia (C)	Neocomian	Ryvkin, 1990
Subfamily Oxyporinae Fleming			
<i>Oxyporus yixianus</i> Solodovnikov and Yue	Yixian, China (C)	Barremian	Yue et al., 2011
Subfamily Oxytelinae Fleming			
<i>Anotylus archaicus</i> Yue et al.	Yixian, China (C)	Barremian	Yue et al., 2012
<i>Megalymma gigantean</i> Tikhomirova	Manlay, Mongolia (C)	Valanginian	Tikhomirova, 1980
<i>Megalymma rohdendorfi</i> Tikhomirova	Manlay, Mongolia (C)	Valanginian	Tikhomirova, 1980
<i>Morda mora</i> Ryvkin	Daya, Russia (C)	Neocomian	Ryvkin, 1990
<i>Sinoxytelus breviventer</i> Yue et al.	Yixian, China (C)	Barremian	Yue et al., 2009b
<i>Sinoxytelus euglypheus</i> Yue et al.	Yixian, China (C)	Barremian	Yue et al., 2009b
<i>Sinoxytelus longisetosus</i> Yue et al.	Yixian, China (C)	Barremian	Yue et al., 2009b
<i>Turgaphloeus pubescens</i> Ryvkin	Turga, Russia (C)	Neocomian	Ryvkin, 1990
Subfamily Phloeocharinae Erichson			
<i>Phloeocharis</i> , sp. n.	New Jersey (A)	Turonian	Chatzimanolis et al., submitted.
Subfamily Scydmaeninae Leach			
<i>Ektatotricha paradoxa</i> Chatzimanolis et al.	Myanmar (A)	Albian	Chatzimanolis et al., 2010
<i>Electroatopos castaneus</i> Chatzimanolis et al.	Myanmar (A)	Albian	Chatzimanolis et al., 2010
<i>Hapsomela burmitis</i> Poinar and Brown	Myanmar (A)	Albian	Poinar and Brown, 2004
<i>Kachinus antennatus</i> Chatzimanolis et al.	Myanmar (A)	Albian	Chatzimanolis et al., 2010
<i>Palaeoleptochromus schaufussi</i> O'Keefe et al.	Medicine Hat, Canada (A)	Campanian	O'Keefe et al., 1997
Subfamily Solieriinae Newton and Thayer			
<i>Prosolierius crassicornis</i> Thayer et. al.	Myanmar (A)	Albian	Thayer et al., 2012
<i>Prosolierius mixticornis</i> Thayer et. al.	Myanmar (A)	Albian	Thayer et al., 2012
<i>Prosolierius tenuicornis</i> Thayer et. al.	Myanmar (A)	Albian	Thayer et al., 2012
Subfamily Staphylininae Latreille			
<i>Cretoquedius oculatus</i> Ryvkin	Magadan, Russia (C)	Cenomanian	Ryvkin, 1988
<i>Laostaphylinus fuscus</i> Zhang	Laiyang Formation, China (C)	Barremian	Zhang, 1988

Taxon	Deposit (Preservation)	Age	References
<i>Laostaphylinus nigrtellus</i> Zhang	Laiyang Formation, China (C)	Barremian	Zhang, 1988
<i>Mesostaphylinus fraternus</i> Zhang et al.	Laiyang Formation, China (C)	Barremian	Zhang et al., 1992
<i>Mesostaphylinus laiyangensis</i> Zhang	Laiyang Formation, China (C)	Barremian	Zhang, 1988
Undescribed staphylinids	Bezonais, France (C)	Cenomanian	Schlüter, 1978
Subfamily Steninae MacLeay			
<i>Stenus imputribilis</i> Ryvkin	Magadanskaia obl., Russia (C)	Cenomanian	Ryvkin, 1988
<i>Stenus inexpectatus</i> Schlüter	Bezonais, France (A)	Cenomanian	Schlüter, 1978
Subfamily Tachyporinae MacLeay			
<i>Cuneocharis elongates</i> Ryvkin	Daya, Russia (C)	Neocomian	Ryvkin, 1990
<i>Glabrimycetoporus amoenus</i> Yue et al.	Yixian, China (C)	Barremian	Yue et al., 2009a
<i>Hesterniasca obesa</i> Zhang et al.	Laiyang, China (C)	Barremian	Zhang et al., 1992
<i>Hesterniasca lata</i> Cai et al.	Yixian, China (C)	Barremian	Cai et al., 2011
<i>Mesotachyporus puer</i> Gusarov	New Jersey (A)	Turonian	Gusarov, 2000
<i>Ryvkinus gracilis</i> (Ryvkin)	Daya, Russia (C)	Neocomian	Ryvkin, 1990; Herman, 2001a
<i>Undiatina pilosa</i> Ryvkin	Semyon, Russia (C)	Neocomian	Ryvkin, 1990
Subfamily Trigonurinae Reiche			
<i>Kovalevia onokhoica</i> Ryvkin	Onozhoi, Russia (C)	Valanginian	Ryvkin, 1990
<i>Trigunda lata</i> Ryvkin	Semyon, Russia (C)	Neocomian	Ryvkin, 1990
Subfamily incertae sedis			
<i>Caririderma pilosa</i> Martins-Neto ¹	Crato, Brazil (C)	Aptian	Martins-Neto, 1990, 2005
<i>Megolisthaerus chinensis</i> Solodovnikov and Yue	Yixian, China (C)	Barremian	Yue et al., 2010
<i>Scaphylinus ammanicus</i> Kaddumi	Aarda-Subeihi, Jordan (A)	Neocomian	Kaddumi, 2005
<i>Sinostaphylina nanligezhuangensis</i> Hong and Wang	Yixian, China (C)	Barremian	Hong and Wang, 1990
<i>Apticax volans</i> Schomann and Solodovnikov	Crato, Brazil (C)	Aptian	Schomann and Solodovnikov, 2012
<i>Apticax solidus</i> Schomann and Solodovnikov	Crato, Brazil (C)	Aptian	Schomann and Solodovnikov, 2012
Undescribed staphylinids	Queensland, Australia (C)	Aptian	Jell and Duncan, 1986
Undescribed staphylinids	Las Hoyas, El Montsec, Spain (C)	Barremian	Soriano et al., 2007
Undescribed staphylinids	Álava, Spain (C)	Albian	Alonso et al., 2000
Undescribed staphylinids	Charente-Maritime, France (A)	Albian	Perrichot et al., 2007

¹ Schomann and Solodovnikov (2012) mentioned that *C. pilosa* may not belong in Coleoptera

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