



Remarkable new fossil species of *Schistostoma* Becker (Diptera: Dolichopodidae: Microphorinae) from mid-Cretaceous Burmese amber

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Abstract

Two closely related and distinctive species of *Schistostoma* Becker, *i.e.* *Schistostoma burmanicum* **sp. nov.** and *Schistostoma foliatum* **sp. nov.**, are described from two male specimens preserved in mid-Cretaceous Burmese amber and recorded as the first known fossil representatives of this extant genus of Microphorinae. Both species possess greatly enlarged lamellate fore tibiae and modified leg chaetotaxy that are presumably male secondary sexual features. The generic limits of *Schistostoma* are briefly discussed and a rationale for the inclusion of these new species is provided.

Key words: Empidoidea, Dolichopodidae, Microphorinae, *Schistostoma*, fossils, Burmese amber, new species

Introduction

The subfamily Microphorinae is a small group of empidoid flies classified within the Dolichopodidae *sensu lato*, along with the subfamily Parathalassiinae and the Dolichopodidae *sensu stricto* (Sinclair & Cumming 2006). Adults are small (1.5–3 mm) non-metallic, light grey to black flies, distinguished by the following features: antennal arista-like stylus two-articled, male eyes holoptic, wing with costal vein circumambient, crossvein bm-m complete, wing cell dm usually present (cell dm absent in the extinct genus *Avenaphora* Grimaldi & Cumming) and emitting three branches (Grichanov & Brooks 2017). Microphorines are known from a wide range of habitats including alpine meadows, deserts, sandy sea coasts, lake margins, and various types of riparian zones (*i.e.* large open rivers to small forest streams). Adults are predaceous, but some species are found on flowers feeding on pollen or nectar (Chvála 1986), or sitting on nearby sunlit leaves. The immature stages are unknown, but the larvae are presumed to be predaceous and living in the soil.

Both modern and extinct taxa of Microphorinae are known. The modern taxa include *Microphor* Macquart with 25 described species (14 Nearctic, 9 Palaearctic, 1 Australasian, 1 Oriental) and *Schistostoma* Becker with 22 described species (17 Palaearctic, 4 Afrotropical, 1 Nearctic); however, most of the Nearctic *Microphor* species require formal transfer to *Schistostoma*.

Four extinct species have been assigned to *Microphor*, including the Baltic amber fossils *M. eocenica* (Meunier), *M. putidus* Meunier and *M. rusticus* (Meunier), as well as the Canadian Oligocene compression fossil *M. defunctus* Handlirsch. Of these, only *M. rusticus* seems correctly placed in *Microphor*, whereas *M. eocenica* and *M. putidus* have been referred to *Rhamphomyia* Meigen (Empididae) and *Oedalea* Meigen (Hybotidae), respectively (Hennig 1971). *Microphor defunctus* also appears referable to the Empididae based on its *Rhamphomyia*-like wing venation (see Handlirsch 1910, fig. 33).

The remaining extinct microphorine taxa are fossilized in amber. They include *Avenaphora*, with two described species from Lebanese and French ambers (Grimaldi & Cumming 1999; Nel *et al.* 2017), *Curvus* Kaddumi, with one described species from Jordanian amber (Kaddumi 2005), *Meghyperiella* Meunier, with one described species from Baltic amber (Meunier 1908; Ulrich 2004), and *Microphorites* Hennig with eight described species from Lebanese, French, Spanish and Moravian ambers (Hennig 1971; Grimaldi & Cumming 1999; Nel *et al.* 2004; Arillo *et al.* 2008; Perrichot & Engel 2014; Tkoč *et al.* 2016; Bramuzzo & Nel 2017).

Here we report on two remarkable new fossil species of Microphorinae from the extensive holdings of Burmese amber fossil inclusions housed in the American Museum of Natural History (Grimaldi *et al.* 2002; Grimaldi & Ross 2017). These two new species represent the first microphorines described from Burmese amber, considered to be of Cenomanian age around 99 Ma (Shi *et al.* 2012). Burmese amber contains the most diverse biota known from any of the Cretaceous ambers (Grimaldi & Ross 2017). Although the new species do not belong to any of the fossil Microphorinae taxa mentioned above, they are the first fossils that can be assigned to the modern genus *Schistostoma* as currently defined herein.

Material and methods

This study is based on the examination of two specimens in Burmese amber (AMNH Bu-0029 and AMNH Bu-175) housed in the American Museum of Natural History, New York, USA (AMNH). Both specimens were obtained from amber mines located approximately 32 km southwest of Tanai Village near Noiye Bum, Kachin State, Myanmar, as reported by Grimaldi *et al.* (2002, p. 57, figs 40c, d). Primary type label data are cited verbatim, with data from each label placed in quotation marks and separated from data on other labels by a semicolon. Lines on labels are delimited by a slash (/) with additional information included in square brackets, *i.e.* []. Terms used for adult structures follow Cumming & Wood (2017). Fossil photographs were taken with a Leica camera model DFC5400 using Leica Application Suite X (LAS X). Photo montages were created using LAS X and Zerene Stacker 1.04.

Systematics

Genus *Schistostoma* Becker

Schistostoma Becker, 1902: 46. Type species: *Schistostoma eremita* Becker, by monotypy.

Diagnosis. *Schistostoma* is distinguished from other known microphorine genera by the following combination of features: cell dm of wing present and emitting three branches, anal lobe of wing well-developed and right-angled, scutellum usually with 1–2 pairs of setae, male genitalia with medial hypandrial prolongation, female terminalia with tergite 10 divided and bearing acanthoporous spines or setae.

Remarks. Shamshev & Sinclair (2006) provided key characters to distinguish *Schistostoma* from *Microphor*, the other extant genus of Microphorinae. Two of the features they listed for *Schistostoma*, 1–2 pairs of scutellar setae and female terminalia with acanthoporous spines, are now known to exhibit more variation than they indicated, and this is reflected in the diagnosis of the genus above.

Schistostoma burmanicum sp. nov.

(Figs 1–7)

Type material. HOLOTYPE ♂, AMNH Bu-0029, in Burmese amber with accompanying labels: “AMBER: MYANMAR (BURMA)/ Upper Cretaceous?/ Kachin: Tanai Village (on Ledo Rd./ 105 km NW Myitkyna)/ coll. Leeward Capitol Corp., 1999/ AMNH Bu-0029”; “Burmese amber/ DIPTERA:/ ♂ Microphorinae:/ (raptorial)”; “HOLOTYPE/ *Schistostoma burmanicum*/ Cumming, Brooks & Grimaldi [red label]”.

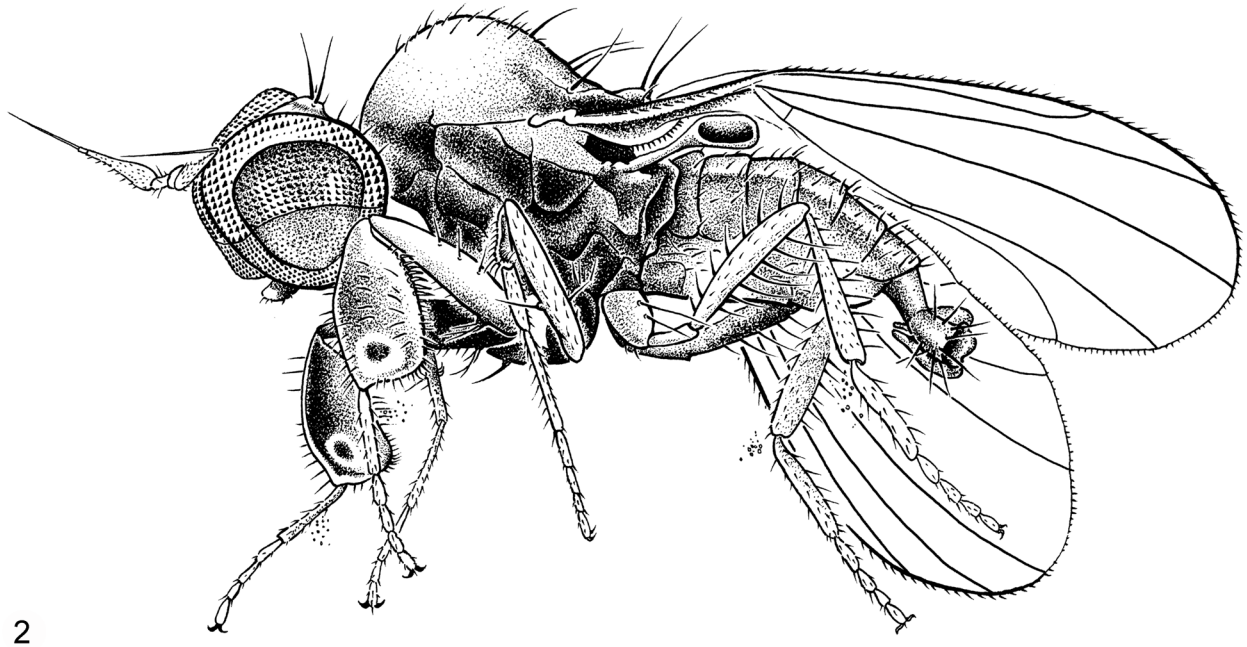
Diagnosis. This species is characterized by its enlarged lamellate apically truncate fore tibia (Fig. 6) with distinctive ‘eye spot’ and laminate setae along upper ventral margin.

Description. Male. Body length 1.8 mm. Wing length 1.4 mm. **Head:** Apparently more or less elliptical in lateral view, but compound eyes, occiput and postgena collapsed. Neck inserted apparently below middle of head, with several short setae adjacent to occipital foramen. Ocellar triangle distinctly protruded with a pair of strong ocellar setae and a pair of weaker postocellar setae. Holoptic with compound eyes contiguous for most of length of frons; compound eye ovoid in lateral view, occupying most of head, bare, dorsal ommatidia distinctly larger than ventral ommatidia, medial edge of eye with emargination slightly below level of antenna giving rise to demarcation

line between larger dorsal and smaller ventral ommatidia. Frons small, triangular, mostly obliterated by eyes. Face and clypeus recessed in oral cavity and obscured from view. Occiput with series of 3–4 visible postocular setae. Gena obscured from view but apparently very narrow. Postgena broad. Antenna (Fig. 5) inserted near middle of head in profile; scape obscured from view, apparently short; pedicel about 2X longer than wide, with several setae; postpedicel elongate subtriangular, about 2.5X longer than wide, clothed in fine hairs; stylus arista-like, terminal, about 2X longer than postpedicel, 2-articled, basal article short. Palpus obscured from view. Proboscis narrow, directed anteroventrally. **Thorax:** Slightly longer than wide in dorsal view. Mesoscutum strongly arched, prescutellar depression present. Proepisternum bare. Postpronotal lobe with 1 strong seta. Acrostichal setae present, apparently biserial; other bristles of thorax well-differentiated, each side with: approximately 9 dorsocentrals, anterior dorso-centrals short and closely spaced, 2 posteriormost dorsocentrals strong and widely separated; 3 apparent supra-alar setae; 2 strong notopleural setae; 1 strong postalar seta. Scutellum with posterior margin rounded, with 2 pairs of setae, outer pair weak, inner pair strong. Mesopleuron apparently bare. **Legs:** Fairly long; foreleg and midleg with specialized morphology and chaetotaxy; tarsal claws, pulvilli and empodium normally developed on all legs. *Foreleg* (Figs 4, 6): Coxa without visible setae; femur with series of 4 visible strong dorsolateral setae, with large basiventral tubercle bearing 4 apical setae, ventral surface immediately distal to basiventral tubercle with series of 7 short setae, each borne on a tiny tubercle; tibia greatly enlarged and lamellate with apical margin truncate, flattened laterally and slightly concave medially, distinctly patterned with ‘eye spot’ on apical third, lateral surface with short setae along dorsal margin as well as two longitudinal series of short setae near middle and adjacent to ventral margin, ventral margin adorned with modified laminate, thickened and curved setae, medial surface with series of short setae along apical margin, otherwise bare; tarsus with short setae, tarsomere 1 as long as combined length of tarsomeres 2–4. *Midleg:* Coxa with strong elongate anterior seta at extreme base and smaller seta immediately below, two weak anterior setae near middle; trochanter with several weak setae; femur with strong basidorsal seta, series of 4 similarly strong anterodorsal setae along basal half, series of short dorsal setae running towards apex, prominent basiventral tubercle bearing thick curved seta and 2 ventral setae near middle (distal seta weaker); tibia with flange on basal half bearing close-set series of short modified setae (some hook-shaped), 1 long erect anterior seta near mid-length; tarsomere 1 as long as combined length of tarsomeres 2–5, with series of erect setae dorsally, otherwise with short setae similar to other tarsomeres. *Hindleg:* Coxa with 1 strong lateral seta at basal third, 2 gradually smaller setae apically, several weak apical setae along anterior margin; femur with series of strong dorsal and ventral setae, ventral setae longer; tibia with series of strong dorsal setae, series of weaker ventral setae along basal half; tarsomere 1 as long as combined length of tarsomeres 2–5, with series of stronger setae dorsally, otherwise with short setae similar to other tarsomeres. **Wing:** Pterostigma absent, membrane entirely covered with minute microtrichia. Anal lobe obscured from view. Costa circumambient. Extreme anterior base of costa with 2 strong setae. Anterior costal section bearing row of short spine-like setae intermixed with fine setae from humeral crossvein to R_{2+3} , posterior part of costa beyond R_{2+3} with only fine setae. Longitudinal veins (except $CuA+CuP$) complete, reaching wing margin. Sc faint apically. R_1 reaching costa beyond middle of wing (or beyond base of M_2). Base of Rs obscured from view. R_{2+3} diverging from R_{4+5} apically. R_{4+5} weakly sinuous. M_1 diverging from R_{4+5} beyond cell dm. M_1 and M_2 strongly diverging beyond cell dm. M_2 and M_4 weakly diverging beyond cell dm. Short r-m crossvein present in basal portion of wing, distal to base of R_{4+5} . Crossvein bm-m apparently complete. Cell dm present, closed by base of M_2 and crossvein dm-m, cell extended to middle of wing. Cells br, bm and cua in basal fourth of wing, partially obscured from view. Cell cua apparently closed, rounded apically with CuA curved. Vein $CuA+CuP$ apparently present and short. Calypter obscured from view. **Abdomen:** Tergites and sternites 1–6 with short setae. Segment 7 tubular, with 1 weak seta visible on sternite. Sternite 8 subrectangular, forming dome-like cap over dorsal region of hypopygium, with several strong marginal setae. *Hypopygium* (Fig. 7): Lateroflexed to right; inverted with posterior end directed anteriorly; small, about 1/5 length of abdomen, apparently symmetrical. Right and left epandrial lamellae rounded basally and oblong in posterior view, each with pair of narrow subequal apical epandrial lobes, cluster of short setae dorsally near base of epandrial lobes, otherwise bare. Hypandrium rounded basally with narrow elongate medial hypandrial process flanked by pair of strong setae. Cercus obscured from view. **Female:** Unknown.

Etymology. The specific epithet refers to Burma, source of the amber.

Remarks. The specimen has clusters of small spheres near the legs (Figs 2, 6), which could be spores, very small pollen grains, or brochosomes (see Suludere *et al.* 2018) that will require higher magnification to ascertain.



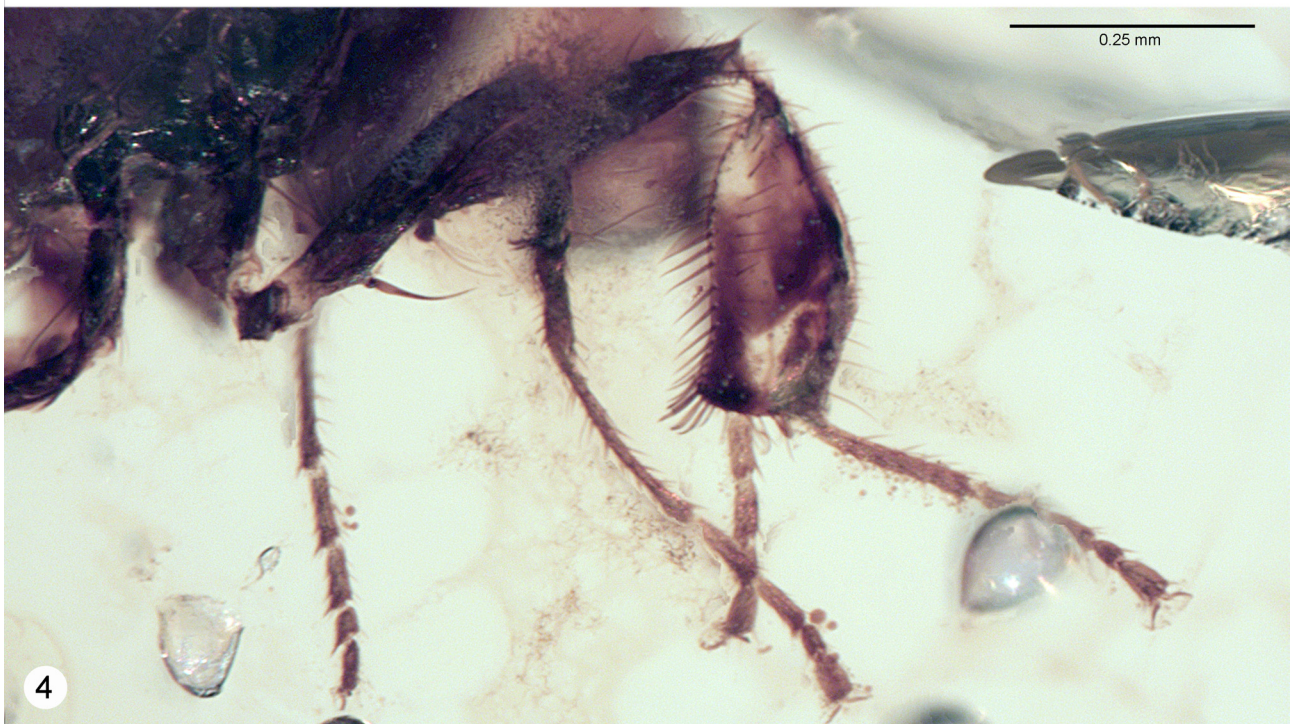
FIGURES 1–2. *Schistostoma burmanicum* sp. nov. male holotype (AMNH Bu-0029). 1. Habitus photograph, left lateral view. 2. Habitus illustration, left lateral view.

***Schistostoma foliatum* sp. nov.**

(Figs 8–12)

Type material. **HOLOTYPE** ♂, AMNH Bu-175, in Burmese amber with accompanying labels: “AMBER: MYANMAR (BURMA)/ Upper Cretaceous/ Kachin: Tanai Village (on Ledo Rd./ 105 km NW Myitkyna)/ coll. Leeward Capitol Corp., 2000/ AMNH Bu-175”; “Burmese Amber/ DIPTERA:/ Microphoridae (raptorial male)*/ 1 ACARINA”; “HOLOTYPE/ *Schistostoma foliatum*/ Cumming, Brooks & Grimaldi [red label]”.

Diagnosis. This species is characterized by its enlarged lamellate apically acute fore tibia (Fig. 8) with distinctive colouration pattern (lacking ‘eyespot’) and fringe-like marginal setae.



FIGURES 3–4. *Schistostoma burmanicum* sp. nov. male holotype (AMNH Bu-0029). **3.** Habitus photograph, right lateral view. **4.** Right foreleg and midleg, right lateral view.

Description. Male. Body length 1.6 mm. Wing length 1.5 mm. **Head:** Elliptical in lateral view. Neck inserted near middle of head, with several short setae adjacent to occipital foramen. Ocellar triangle distinctly protruded with a pair of strong ocellar bristles and a pair of weaker postocellar setae. Holoptic (Fig. 10) with compound eyes contiguous for entire length of frons; compound eye ovoid in lateral view, occupying most of head, bare, dorsal ommatidia distinctly larger than ventral ommatidia, medial edge of eye with emargination slightly below level of antenna giving rise to demarcation line between larger dorsal and smaller ventral ommatidia. Frons entirely obliterated by eyes. Face and clypeus recessed in oral cavity. Face broad, subrectangular. Clypeus weakly bulging, mostly separated from frons, only connected medially by narrow sclerotized bridge. Occiput with series of 8–9 visible postocular setae per side. Gena narrow. Postgena broad. Antenna (Fig. 10) inserted near middle of head in profile; scape short about half length of pedicel; pedicel about 2X longer than wide than wide, with several setae; postpedi-

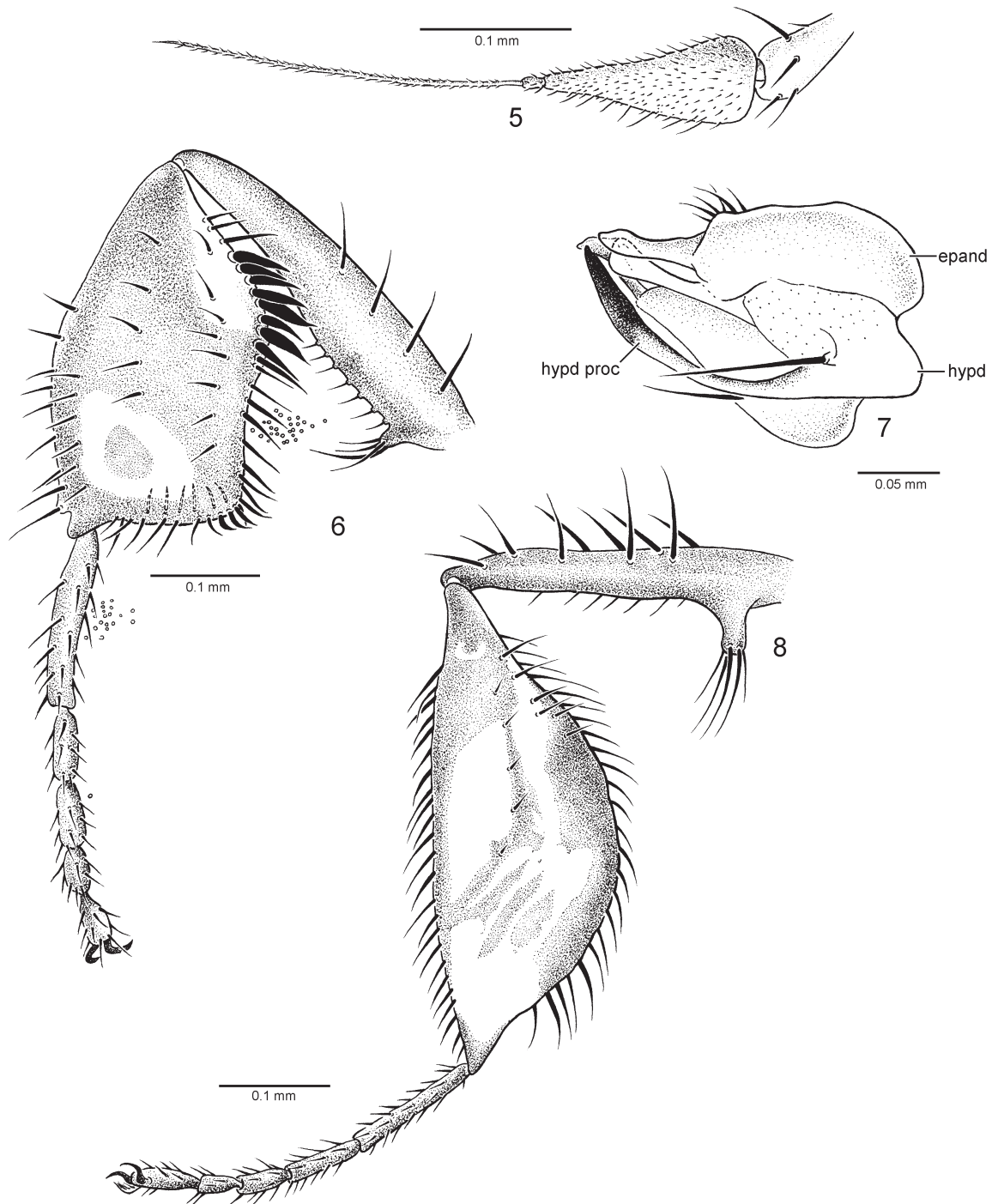
cel strongly narrowing beyond basal third, with dorsal margin concave, about 3X longer than wide, clothed in fine hairs (longer ventrally); stylus arista-like, terminal, about 2.5X longer than postpedicel, 2-articled, basal article short. Palpus digitiform, with short setae. Proboscis narrow, directed anteroventrally, labellum with marginal setae. **Thorax:** Slightly longer than wide in dorsal view. Mesoscutum strongly arched (Fig. 10), prescutellar depression present. Proepisternum bare. Postpronotal lobe with 1 strong seta, with adjacent short seta. Acrostichal setae present, apparently biserial; other bristles of thorax well-differentiated, each side with: apparently 10–11 dorsocentrals, anterior dorsocentrals short and closely spaced, 2 posteriormost dorsocentrals strong and widely separated; several apparent strong supra-alar setae; 2 strong notopleural setae; 1 strong postalar seta. Scutellum with posterior margin rounded, with 2 pairs of setae, outer pair weak, inner pair strong. Mesopleuron apparently bare. **Legs:** Fairly long; foreleg and midleg with specialized morphology and chaetotaxy; tarsal claws, pulvilli and empodium normally developed on all legs. *Foreleg* (Fig. 8): Coxa with a few short subapical setae visible; femur with several strong dorsal and dorsolateral setae, with large strongly projecting basiventral tubercle bearing 5 apical setae, ventral surface immediately distal to basiventral tubercle with series of about 6 short setae (not visibly borne on tubercles); tibia greatly enlarged and lamellate, leaf-shaped with apical margin acute, flattened laterally and very slightly concave medially, distinctly patterned (Figs 8, 12) but lacking discrete ‘eye spot’, lateral surface with longitudinal series of 5 short setae along middle and 6 longer setae basiventrally, dorsal and ventral margins with fringe of setae, medial surface bare; tarsus with short setae, tarsomere 1 as long as combined length of tarsomeres 2–3. *Midleg* (Fig. 12): Coxa with strong elongate anterior seta at extreme base and series of 4 gradually shorter setae towards apex; trochanter with several weak setae; femur with strong elongate basidorsal seta, series of 3 strong anterodorsal setae along basal half (about half-length basidorsal seta), series of short dorsal setae towards apex, prominent basiventral tubercle bearing thick curved seta, 2 ventral setae near middle (of similar size) and several apparent anterior setae; tibia with flange on basal half bearing close-set series of short modified setae (some hook-shaped), 1 long erect anterior seta near mid-length, several hook-shaped setae on distal half; tarsomere 1 with setae somewhat longer than on tarsomeres 2–5. *Hindleg:* Coxal setae obscured from view; femur with series of strong dorsal and ventral setae of similar length, dorsal setae gradually shorter apically, ventral setae gradually shorter basally; tibia with series of strong dorsal setae, gradually stronger distally, series of similar ventral setae, gradually weaker distally; tarsomere 1 slightly shorter than combined length of tarsomeres 2–5, with prominent basiventral seta, otherwise with short setae similar to other tarsomeres. **Wing:** Pterostigma absent, membrane entirely covered with minute microtrichia (Fig. 11). Anal lobe well-developed and right-angled, alula absent. Costa circumambient. Extreme anterior base of costa with 2 strong setae. Anterior costal section bearing row of short spine-like setae intermixed with fine setae from humeral crossvein to R_{2+3} , posterior part of costa beyond R_{2+3} with only fine setae. Longitudinal veins complete reaching wing margin (CuA+CuP obscured from view). Sc faint apically. R_1 weakly sinuous, reaching costa beyond middle of wing (or beyond base of M_2). Base of Rs originating opposite humeral crossvein. R_{2+3} diverging from R_{4+5} apically. R_{4+5} weakly sinuous. M_1 diverging from R_{4+5} beyond cell dm. M_1 and M_2 strongly diverging beyond cell dm. M_2 and M_4 weakly diverging beyond cell dm. Short r-m crossvein present (but nearly indiscernible) in basal portion of wing, distal to base of R_{4+5} . Crossvein bm-m complete. Cell dm present, closed by base of M_2 and crossvein dm-m, cell extended to middle of wing. Cells br, bm and cua in basal fourth of wing. Cells bm and cua broader than br. Cell cua closed, rounded apically with CuA curved. Vein CuA+CuP obscured from view. Calypter obscured from view. **Abdomen:** Tergites and sternites 1–6 with relatively long setae. Segment 7 tubular, surface obscured from view. Sternite 8 ovoid, forming dome-like cap over dorsal region of hypopygium, with several strong marginal setae. *Hypopygium* (Fig 7): Lateroflexed to right; inverted with posterior end directed anteriorly; small, about 1/5 length of abdomen, apparently symmetrical. Right and left epandrial lamellae rounded basally and oblong in ventral view, apices obscured from view. Hypandrium rounded basally with narrow elongate medial hypandrial process flanked by pair of strong setae. Cercus short, subtriangular, setose. **Female:** Unknown.

Etymology. The specific epithet refers to the greatly enlarged leaf-shaped tibia of the male foreleg.

Discussion

Schistostoma as diagnosed above now includes 24 described species and a number of species currently assigned to the genus *Microphor*, as well as several undescribed species. As a result, the concept of the genus is now broader than previously published (see Shamshev & Sinclair 2006; Cumming & Sinclair 2009; Grichanov & Brooks 2017).

Several species groups of *Schistostoma* are apparent within this broader concept of the genus. The two fossil species described here appear to represent another species group in the genus, defined primarily by the fore femur with a basiventral tubercle bearing several apical setae, a greatly enlarged patterned lamellate fore tibia, and the midleg with a basiventral femoral tubercle bearing a single curved seta and a tibial flange. Although distinctive, these new species are assigned to *Schistostoma* based on possession of the characteristic medial hypandrial prolongation of the male genitalia (a putative generic synapomorphy) and a well-developed right-angled anal lobe of the wing. They are the first species of *Schistostoma* known from the Oriental Region and the earliest known members of the genus. Appearance of *Schistostoma* as far back as the mid-Cretaceous is not unreasonable given the number of microphorine fossil taxa already described from both the Early and Late Cretaceous periods.

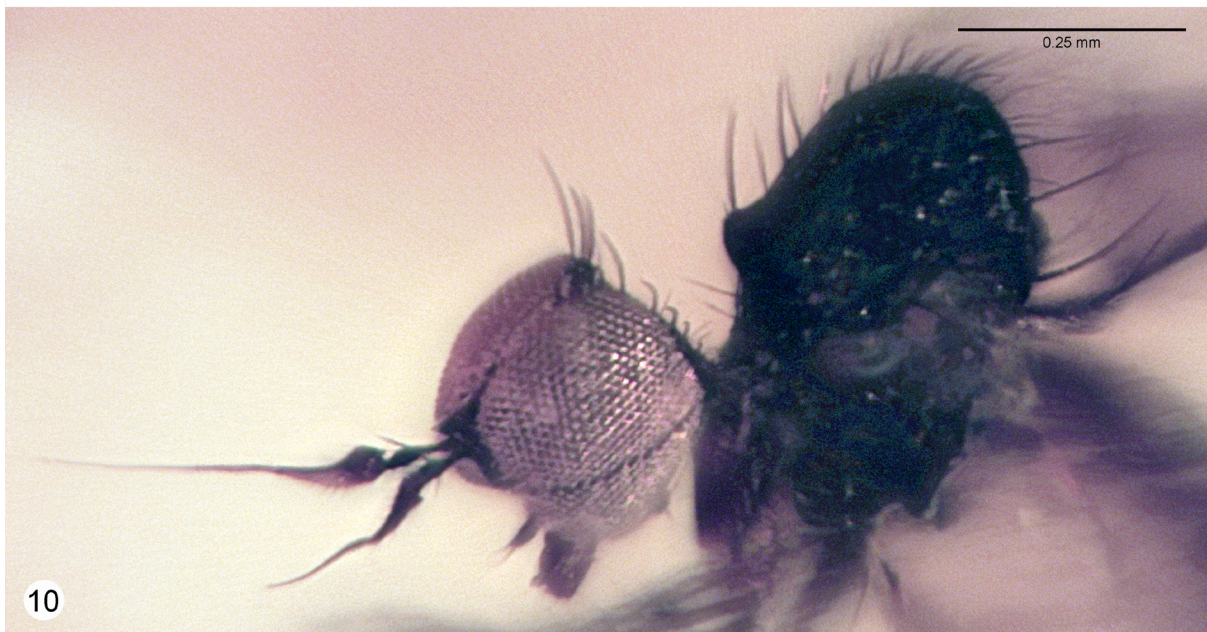


FIGURES 5–8. *Schistostoma burmanicum* sp. nov. and *Schistostoma foliatum* sp. nov. **5.** Right antenna of *S. burmanicum*, left medial view. **6.** Left foreleg of *S. burmanicum*, left lateral view. **7.** Hypopygium of *S. burmanicum*, ventral view. **8.** Left foreleg of *S. foliatum*, left lateral view. Abbreviations: epand—epandrium; hypd—hypandrium; hypd proc—hypandrial process.

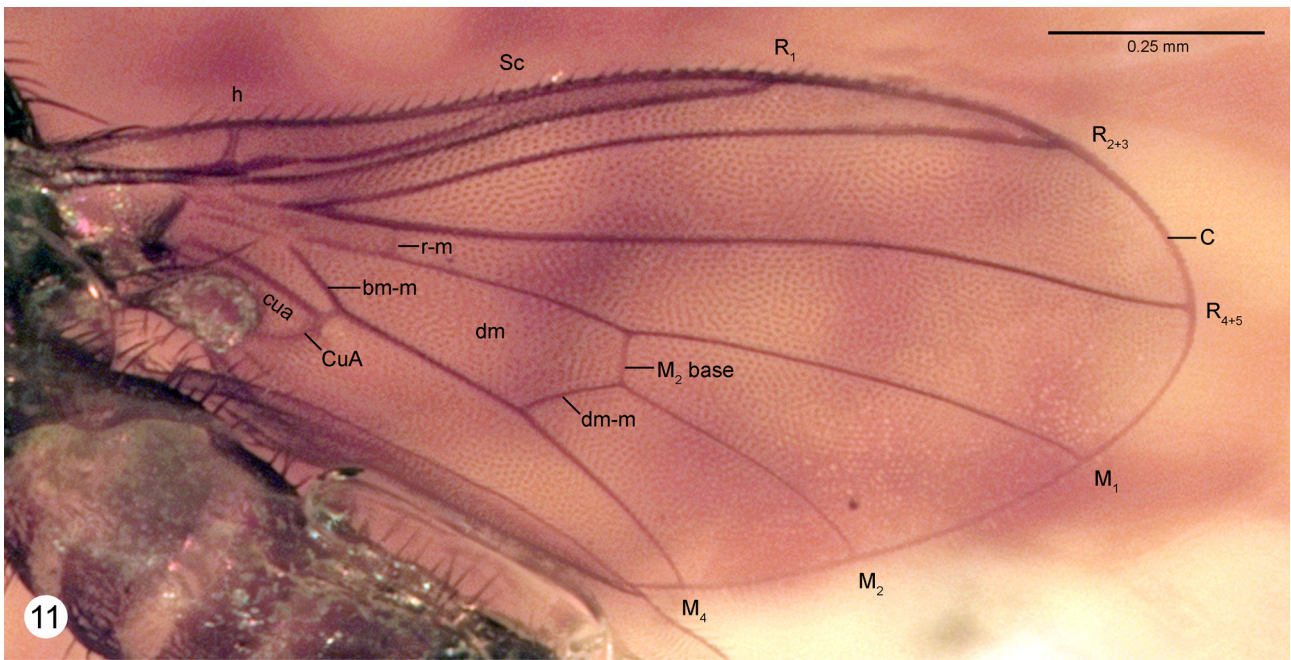
The highly modified enlarged fore tibiae of both species are presumably male secondary sexual features. Enlarged fore tibiae are unknown in other Microphorinae. The lamellate fore tibiae appear to bear diagnostic patterning, suggesting that they were probably used for both sexual signalling and clasping during mating. Signalling may have been involved in courtship displays with females, or competitive displays towards other males, although mating behaviour of any kind has not been reported for Microphorinae.

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FIGURES 9–10. *Schistostoma foliatum* sp. nov. male holotype (AMNH Bu-175). **9.** Habitus, right lateral view. **10.** Head and thorax, left dorsolateral view.



FIGURES 11–12. *Schistostoma foliatum* **sp. nov.** male holotype (AMNH Bu-175). **11.** Wing. **12.** Legs, right lateral view. Abbreviations: C—costal vein; CuA—anterior branch of cubital vein; cua—anterior cubital cell; dm—discal medial cell; dm-m—discal medial crossvein; h—humeral crossvein; M₁, M₂, M₄—medial veins; R₁, R₂₊₃, R₄₊₅—radial veins; r-m—radial-medial crossvein; Sc—subcostal vein.

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