Revision of the bizarre Mesozoic scorpionflies in the Pseudopolycentropodidae (Mecopteroidea)

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The Mesozoic family Pseudopolycentropodidae presently consists of seven described species from the mid-Triassic to the Late Jurassic of Europe and Asia. *Pseudopolycentropus prolatipennis* Whalley, from the Early Jurassic of England, is revised based on re-examination of the type. Four new species are described herein that add significant distributional and stratigraphic extensions to the family. *Pseudopolycentropodes virginicus* Grimaldi and Fraser, gen. n., sp.n. from the Late Triassic (Carnian) of Virginia USA is the first species of the family from the Western Hemisphere. *Pseudopolycentropus daohugouensis* Zhang, sp. n. from the Late Jurassic of China is very similar to *P. latipennis* Martynov, 1927 from the Late Jurassic of Kazakhstan. Four specimens belonging to two very similar species in mid-Cretaceous amber from northern Burma (Myanmar), *Parapolycentropus burmiticus* Grimaldi and Rasnitsyn, gen. n., sp.n. and *P. paraburmiticus* Grimaldi and Rasnistyn, sp.n., are the only specimens of the family from the Cretaceous. The amber species are exceptional, with the hind wing reduced to a minute lobe, the antennal flagellum modified into an arista, labial palps are lost, and – like the Late Jurassic species — the laciniae and what are probably mandibles are modified into a long, stylet-like proboscis. What the species with long proboscides fed upon is ambiguous, but it was doubtfully blood. Complete preservation in amber of morphological details, particularly the female terminalia, confirms previous views that this unusual group is phylogenetically basal to Recent Mecoptera.

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Introduction

Fossils traditionally classified in the Mecoptera are extremely diverse, numbering some 400 species and 16-25 families from the Late Permian to the Recent, depending on the system of classification (Willmann, 1978; 1989; Carpenter, 1992; Novokshonov, 2002). There are only approximately 600 Recent species of Mecoptera, classified into nine families. If all of these fossil taxa were indeed true Mecoptera, such high proportions of extinct taxa would indicate that this order is relict – reduced by extinction – more than any other group of Holometabola. But, current concepts indicate that Permian and early Mesozoic fossils are stem groups to true Mecoptera, the latter of which definitively appeared first in the Jurassic. To complicate matters, some families, like the "Orthophlebiidae," are extensively paraphyletic (Willmann, 1989; Novokshonov, 2002). Certainly among the most distinctive, homogeneous, and natural groups of fossil mecopteroids, though, is the Pseudopolycentropodidae, a small family that until now consisted of just seven described species from the mid-Triassic to Late Jurassic, which we review below.

© *Insect Systematics & Evolution* (Group 6)

The Pseudopolycentropodidae was placed by Tillyard (1919) into a separate order (the Paratrichoptera) with another family, the Mesopsychidae. As other families were gradually added to the Paratrichoptera, thoughts on their relationships became more confused, ranging from their being close relatives of Diptera, of Mecoptera, Trichoptera, and even to Lepidoptera (reviewed by Willmann, 1989; Schlüter, 1997; Novokshonov and Sukatscheva, 2001). Some families were pruned from the Paratrichoptera, notably several that are in fact closely related to the Diptera (Permotanyderidae, Permotipulidae, Robinjohniidae), leaving essentially just three families: Aneuretopsychidae, Mesopsychidae, and Pseudopolycentropodidae (Novokshonov, 2002). The relationships of the former two of these families among mecopteroids remains uncertain, but significant new light is cast on the Pseudopolycentropodidae because of the remarkable preservation of several new species in amber.

Amber is renowned for the myriad life forms preserved in it with life-like fidelity, but one inadequacy often cited is that fossils in amber are no older than the Early Cretaceous, specifically 125-130 mya. The evolutionary history of insects, by contrast, is more than three times this age. Actually, amber, or globules of fossilized resin, occurs as early as the Late Triassic, ca. 220 mya, but arthropods and other larger organisms first occur in amber only from the Neocomian of Austria, England, Japan, and especially Lebanon (reviewed in Grimaldi, 1996; Grimaldi and Engel, 2005). Occasionally, though, insects are found in Cretaceous ambers that belong to archaic, pre-Cretaceous groups. Such discoveries provide a unique window for observing the anatomy of archaic groups, and therefore discerning their relationships – groups that would otherwise be known mostly just as compressions or impressions of wings in rocks. Recent discoveries of this sort include two extinct families, mesoraphidiid snakeflies (Raphidioptera) and protopsyllidiid hemipterans, both preserved in Cretaceous amber from New Jersey and Myanmar (Grimaldi, 2000, 2003; Engel, 2002). Mesoraphidiidae occurred in rocks from the Early Jurassic to the Early Cretaceous (reviewed in Engel, 2002), and Protopsyllidiidae from the Late Permian to the Early Cretaceous (Grimaldi, 2003). To these archaic insect groups in Cretaceous amber can now be added the Pseudopolycentropodidae, new specimens of which provide remarkable new details for evaluating the phylogenetic position of this interesting family. We take this opportunity to likewise report two other new species of the family, one from the Triassic of North America (the first record of the family from the Western Hemisphere) and an Upper Jurassic species from China.

Material and Methods

The Triassic specimens derived from the Solite Corporation quarries in Cascade, near Martinsville, Virginia, USA, which is on the Virginia-North Carolina border near the middle of the state. These quarries contain fossiliferous outcrops of black, very fine-grained shale belonging to the Cow Branch Formation (Carnian/Norian: Late Triassic, ca. 230-220 myo). Diverse insects derive from a shallow stratum of this formation, along with abundant conchostracans, plants, and the amphibious reptile *Tanytrachelos* (reviewed in Fraser et al., 1996). This formation, moreover, is one of the earliest definitive freshwater insect faunas (Sinitschenkova, 2002). The fossil insects and plants are preserved entirely as two-dimensional silvery images, often with very fine details preserved, such as microtrichia on wing membranes. The fossils, though, can be very obscure unless the matrix is wet with alcohol and observed under strong, diffuse light, preferably using a fiber optic ring light. All of the specimens are housed in the Virginia Museum of Natural History, Martinsville VA, USA (VMNH) and the Peabody Museum of Natural History, Yale University, New Haven CT, USA (YPM).

The specimen from the Upper Jurassic of China derives from the Daohugou Formation, age of which is debatable but which is interpreted here as being near the J/K boundary, 150-145 myo. Some Chinese researchers consider the lacustrine rocks that bear animal and plant fossils from this formation to be the Yixian Formation, which is approximately Barremian (Early Cretaceous) (Wang et al., 2000; Wang, 2000). Later, views changed slightly that this formation belonged to a basal portion of the Yixian Formation or Dabeigou Formation, which is an underlying stratigraphic unit of the Yixian Formation (Wang et al, 2002). Others yet have argued that this formation belongs to the Late Aalenian or Early Bajocian Jiulongshan Formation (Ren and Jin, 2002; Ren and Oswald, 2002). Based on new biostratigraphic data it appears that

the Daohugou Formation is correlated with the Karabastau Formation in Karatau, Kazakhstan, the latter of which is Kimmeridgian in age, ca. 150 myo (Zhang, 2002, 2003). Based on the Hymenoptera fauna, the Daohugou Formation appears to be mid-Jurassic in age (A. Rasnitsyn, unpubl), but the dipteran fauna appears to be very close to the Jurassic-Cretaceous boundary (D. Shcherbakov and E. Lukashevich, unpubl.). The new scorpionfly described here supports an age contemporaneous with that of the Karabastau Formation. Detailed discussion of the stratigraphy of the Daohugou Formation is provided elsewhere (Zhang, 2002; 2003).

The amber specimens derived from the state of Kachin in northern Myanmar (Burma), approximately 100 km southwest of the village of Tanai. The age of Burmese amber has been obscure for nearly 100 years, and up until approximately five years ago it was considered as young as Miocene. Detailed study of the inclusions, though, indicate it is Cretaceous (reviewed by Zherikhin and Ross, 2000), and even as old as mid-Cretaceous, approximately Cenomanian (ca. 100 myo) (Grimaldi et al., 2002). Modest evidence from an ammonite and some pollen suggests an age that is even Late Albian (115-112 myo) (Cruikshank and Ko, 2003). The Natural History Museum, London has a collection of Burmese amber, containing approximately 1,200 insect inclusions (Rasnitsyn and Ross, 2000), but no pseudopolycentropodids occur in this collection. All of the amber specimens from the present study are in the American Museum of Natural History (AMNH); they were prepared according to the protocols described in Nascimbene and Silverstein (2000).

Taxonomy

Family PSEUDOPOLYCENTROPODIDAE Handlirsch, 1925

Genus *Pseudopolycentropus* Handlirsch, 1906

Type species. – *Phryganidium perlaeformis* Geinitz, 1884.

Diagnosis. – (Emended) Mesozoic mecopteroids with generally a broad, triangular fore wing and smaller to highly reduced hind wing; fore wing with simplifed venation: Sc short, R_1 simple, Rs with 4 branches, M with 5 branches, a central discal cell present, CuA and CuP simple, vein A very small or absent, and few crossveins (as figured).

The venation of some species in the genus is shown in Figure 1. Previously described species of *Pseudopolycentropus* and their stratigraphic distributions are the following (Willmann [1978] gave a complete list of synonyms for the older binomials):

JURASSIC:

P. latipennis Martynov, 1927: Late Jurassic (Kimmeridgian) of Karatau, Kazakhstan. Redescribed in detail by Novokshonov (1997) based on additional, better-preserved material. Wings and body.

P. obtusus Bode, 1953: Upper Lias (Toarcian) of Braunschweig, Germany. This species needs to be restudied. Fore wing only.

P. perlaeformis (Geinitz, 1884): Upper Lias (Toarcian) of Dobbertin, Germany. Fore wing only.

P. prolatipennis Whalley, 1985: Early Jurassic (Sinemurian) of Dorset, England. Fore wing only.

P. triangularis Handlirsch, 1925: Upper Lias (Toarcian) of Dobbertin, Germany. Redescribed in detail by Ansorge (1996) based on additional, well-preserved material. Fore and hind wings only.

TRIASSIC:

P. madygenicus Novokshonov, 1997: Late Triassic (Carnian?) of Fergana Valley, Kyrgyzstan. Fore wing only.

P. triasicus Papier, Nel, and Grauvogel-Stamm, 1996: mid-Triassic (Ladinian) of France. Fore wing only.

Pseudopolycentropus prolatipennis Whalley

(Fig. 1)

P. prolatipennis Whalley, 1985: 155. By original designation.

Material examined. – Holotype, NHM In. 53915, which is part and counterpart of a fore wing preserved in rock from the mid-Lias (Sinemurian) of Charmouth, Dorset, England.

Redescription. – A revised version of the fore wing venation is shown in fig.1, based on the first author's re-examination of the type specimen in the Natural History Museum, London. Deciphe-

ring the fine veins against the grain of the matrix requires constant tilting, lighting adjustment, and comparison to the venation of better preserved species of the family. Whalley (1985) essentially included too many crossveins in the Cu and A region, among more subtle inaccuracies, as follows: R_1 has no small apical fork; the apical fork of R_{2+3} is slightly deeper than originally depicted; a very faint r-m crossvein appears to be present; there are 3 small crossveins at the base of the Cu and A veins, not the 11 indicated by Whalley, with positions as redrawn (fig.1).

Comments. – As revised, the fore wing venation of *P. prolatipennis* is very similar to that of *P. latipennis*. The latter species, from the Late Jurassic (Kimmeridgian, ca. 152 mya) of Kazakhstan, was accurately redescribed and figured by Novokshonov (1997) and re-examined by the senior author (fig. 1). *Pseudopolycentropus prolatipennis* differs

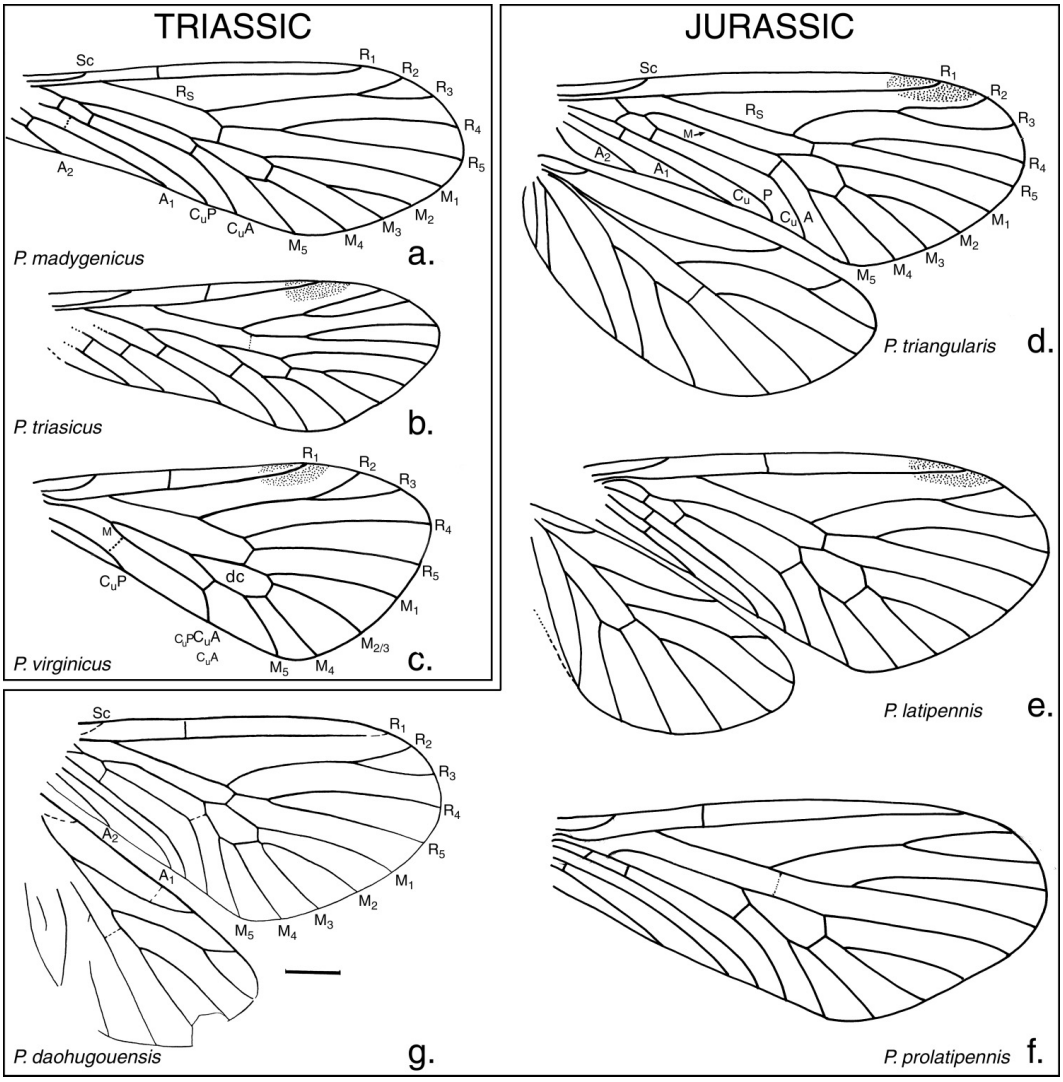

Fig. 1. Wings of Pseudopolycentropodidae, redrawn from the original or best sources (not to the same scale). That of *P. prolatipennis* Whalley is revised from the original description, based on re-examination by the senior author.

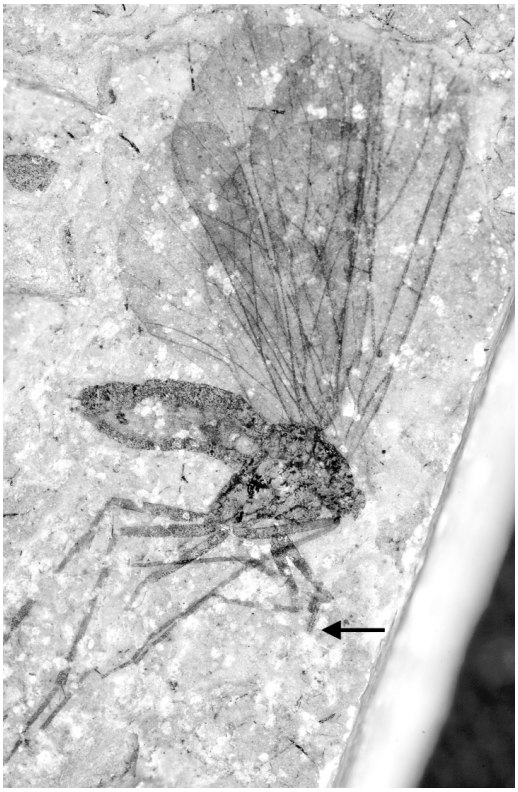

Fig. 2. *Pseudopolycentropus latipennis*, from the Late Jurassic of Kazakhstan (Paleontological Institute, Moscow). Arrow indicates the tip of the proboscis. The basal part of the proboscis is preserved in the counterpart. Photo by D. Grimaldi.

from *P. latipennis* by the following subtle venational features: a slightly longer and more slender discal cell in *P. prolatipennis*, R_{2+3} fork slightly longer, and base of M without a noticeable kink. The body of *P. prolatipennis* is unknown, but *P. latipennis* is virtually complete and it possessed a long, thin proboscis (fig. 2). This species is also very similar to *P. daohugouensis* sp. n., but differs from it based on the wing venation diagnosed for the new species.

Genus *Pseudopolycentropodes* Grimaldi and Fraser, NEW GENUS

Type species. – *P. virginicus*, sp. n.

Diagnosis. – Distinguished from all other species of the family based on the distinctive fore wing shape and venation, specifically: wing broad and virtually triangular; base of R_5 connected to r-m crossvein, instead of branching directly off R_4; M_2 or M_3 lost (these veins not forked); anal portion highly reduced, with CuP reaching only slightly distal to fork of M-CuA, and A veins either lost or extremely reduced [not visible]. Long proboscis lacking.

Pseudopolycentropus daohugouensis Zhang, sp. n.

(Figs 1, 3)

Material examined. – Holotype, DHG200301, in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. From the Upper Jurassic Daohugou Formation, China.

Etymology. – in reference to the type deposit, the Daohugou Formation.

Diagnosis. – Differs from all other Jurassic species of the genus by r-m crossvein being oblique, not perpendicular to R and M veins or nearly so; by the short stem of M_2 –M_3; the curved, distal portions of CuA and CuP being slightly longer and more angled. Like *P. triangularis* it possesses only one crossvein at the base (cup-a_1), versus 2-3 such crossveins.

Description. – A very well preserved, virtually complete specimen, body length (exclusive of proboscis) approximately 7.5 mm. HEAD: antenna long, greater than 2.8 mm, filamentous, moniliform, with >33 flagellomeres. Eye deep, depth ~1.75x the width. Mouthparts comprise a very long and thin proboscis, composed of 3 discernable stylets. THORAX: short, fore femur ~1.8mm long; tibia slightly longer, with two short apical spurs. Wings with venation as depicted (fig. 1), with defining features as indicated in diagnosis. Forewing length ~7 mm, hindwing length ~5.5 mm. ABDOMEN: large, ~5.5 mm long, with 8 large tergites; sex unknown but pair of small, oval structures lying near segment 7 that appear to have been heavily sclerotized, which presumably were spermathecae.

Comments. – This species is morphologically and chronologically most similar to *P. latipennis* (Figs 1, 2) and among all known Jurassic species it is geographically closest to *P. latipennis* as well. Both species have similar body size, wing and proboscis proportions, and venation.

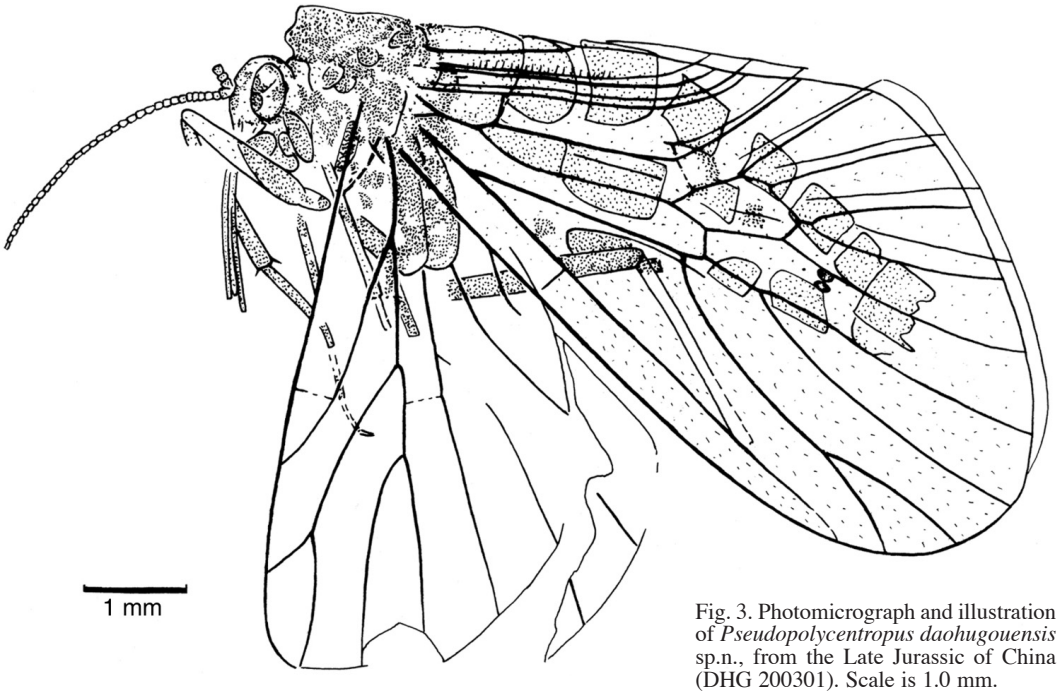

Fig. 3. Photomicrograph and illustration of *Pseudopolycentropus daohugouensis* sp.n., from the Late Jurassic of China (DHG 200301). Scale is 1.0 mm.

Pseudopolycentropodes virginicus Grimaldi and Fraser, sp. n.

(Figs 1, 4, 5)

"Trichoptera" Fraser et al., 1996: 616, 617 [misidentification].

Material examined. – Holotype, VMNH 730; Paratypes YPM 35982, YPM 35986. All are from the Cow Branch Formation (Carnian: Late Triassic) exposed at the Solite Quarries, Martinsville, Virginia USA (Fraser et al., 1996).

Etymology. – In reference to the state of origin.

Diagnosis. – as for genus.

Description. – Body length 3.2 (VMNH 73), 3.3 mm (YPM 359822). HEAD: Eyes large, widely separated; antennae multiarticulate, with numerous segments [no other details observable]. Long proboscis lacking. THORAX: Pronotum small; mesothorax large, with large scutum and scutellum. Fore wing broad and virtually triangular, length 3-3.3 mm; membrane covered in macrotrichia; Sc very short, apex not reaching to level of M-Cu fork; R_1, R_{2+3} are thickest veins; forked ends of R_{2+3} turned anteriad; r-m crossvein connected to distal half of dc cell, base of R_5 connected to r-m crossvein; vein M_2 or M_3 lost (these veins not forked); apex of CuA turned strongly posteriad; crossvein m-cua near middle of dc cell, not near proximal end of cell; anal portion highly reduced, with CuP reaching only slightly distal to fork of M-CuA, and A veins either lost or extremely reduced [not visible]. Hind wing small [observed in VMNH 730], length ca. 0.7x that of fore wing. At least some tibiae, probably all, with pair of very large apical spurs, their lengths ca. 2-3x the width of tibia. Fore tibia 0.6 mm); fore tibial spurs 0.3 mm (VMNH 730). Femur and tibia with fine annuli of microtrichia [uncertain which pairs of legs]. Abdomen long and slender, with at least eight large tergites, terminal tergite apically pointed.

Comments. – VMNH 730 was chosen as the holotype specimen since it has more features preserved than the other two specimens. Indeed, the other two Triassic species of the genus are known only from wings, so *P. virginicus* is the best preserved of the three species from this geological period. The species is similar to *P. triasicus*, from the mid-Triassic of France (Papier et al., 1996), by crossvein m_5-cua being near the middle of the discal cell instead of close to the proximal end. The broad, triangular fore wing with smaller hind wing, and large mesothorax, indicate that this species was probably a strong, agile flier that mostly used just its fore wings in flight. The Virginia Triassic specimens reveal for the first time that thick, multiarticulate antennae and large tibial spurs occurred in early Pseudopolycentropodidae, with which it differs considerably compared to the Cretaceous species (below). Large stiff setae on the body agree with those seen in the

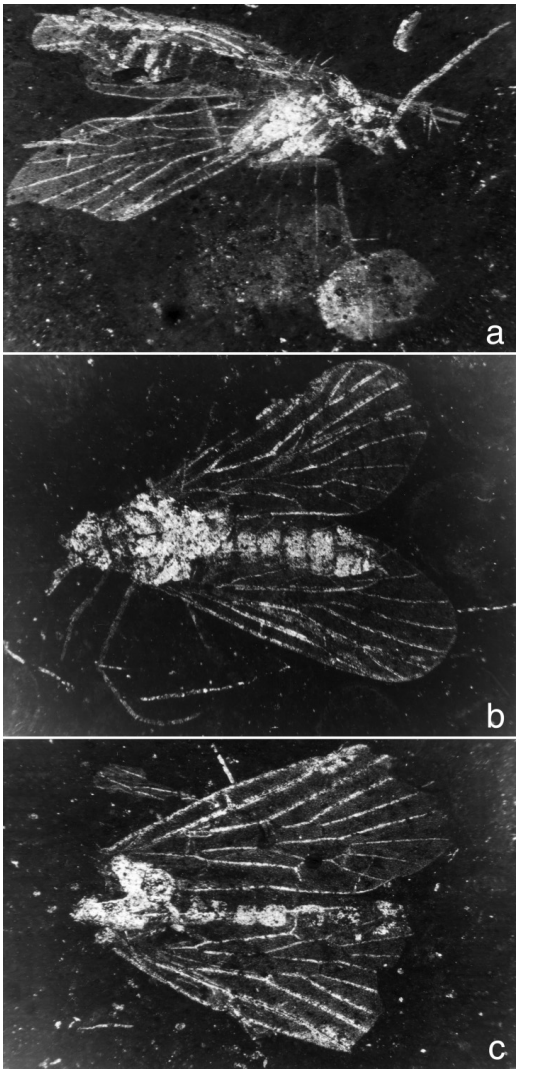

Fig. 4. Photomicrographs of *Pseudopolycentropodes virginicus*, gen. n., sp.n., from the Late Triassic of Virginia. (a) holotype, VMNH 730; (b) paratype YPM 35982; (c) paratype, YPM 35986.

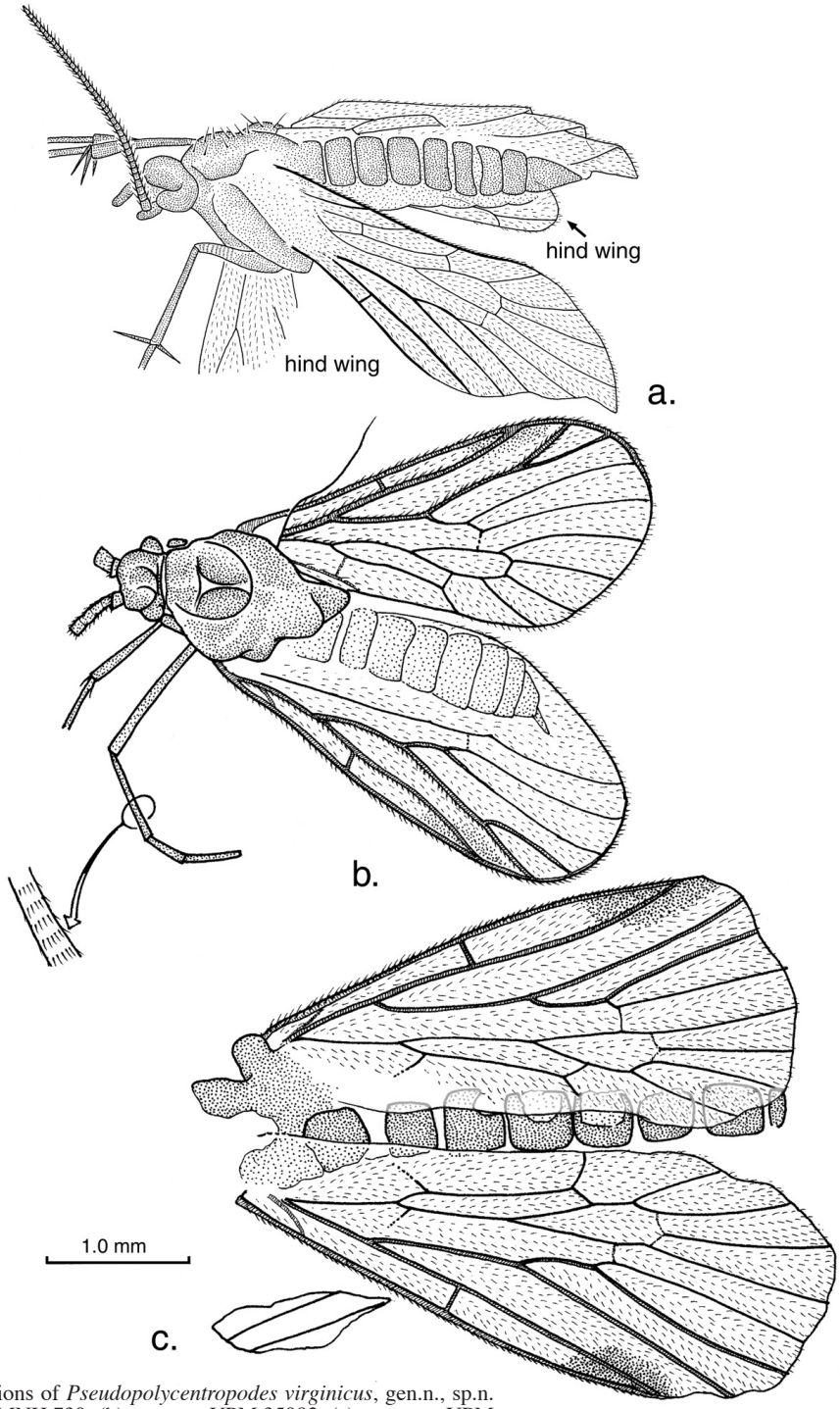

Fig. 5. Illustrations of *Pseudopolycentropodes virginicus*, gen.n., sp.n. (a) holotype, VMNH 730; (b) paratype YPM 35982; (c) paratype, YPM 35986. a, c: counterparts to photos of specimens in figs. 3a, 3c.

Cretaceous species, but there is no indication that similar setae occurred on the head as in the Cretaceous species. Lastly, the fine annuli of microtrichia on the legs confirm this feature occurs elsewhere in the family besides the Jurassic species *P. latipennis* (see Novokshonov, 1997), though such annuli do not occur in the best preserved species (in amber). Preservation of the head in two specimens indicates that this species did *not* have a proboscis like *P. latipennis*, *P. daohuguoensis*, and the species in Burmese amber.

Genus *Parapolycentropus* Grimaldi and Rasnitsyn, NEW GENUS

Type Species. – *P. burmiticus*, sp. n.

Diagnosis. – Proboscis very long and fine, length 2.6x depth of head capsule, distinguished from compression fossil genera also by the wings: fore wing shape ovoid, not triangular; hind wing reduced to a minute lobe; only 4 branches of M present (vs. 5); 2 distal crossveins present (vs. none), between r_2-r_3 and between r_5-m_1; anal vein highly reduced, joined to base of CuP for 2/3 of its length; thick r+m-cu and cua-cup crossveins virtually in line with each other.

Parapolycentropus burmiticus Grimaldi and Rasnitsyn, sp. n.

(Figs 6 - 8a, b)

Material examined. – Holotype, male, AMNH Bu694, in mid-Cretaceous amber from northern Myanmar, Kachin state. Collected by Leeward Capital Corp., 1999, from mines approximately 100 km sw of Tanai (Grimaldi et al., 2002; Cruikshank and Ko, 2003). Paratype, female, AMNH Bu134, with same provenance as holotype. The amber is considered to be between Turonian to latest Albian in age, approximately 90-105 myo.

Etymology. – From the former name of the country of origin.

Diagnosis. – *P. burmiticus* distinguished from *P. paraburmiticus* by venation and female terminalia: *burmiticus* with apical forks of R_2-R_3 and M_1-$M_{2/3}$ slightly more symmetrical, M_5 shorter, crossveins r_{4+5}-m_{1+2} and $m_{2/3}$-m_4 lacking; female terminalia of *burmiticus* with GSVIII much larger, GSIX with complete (vs. incomplete) median suture, and tXI present (vs. absent)

Description. – Body length 3.0 mm. HEAD (based mostly on paratype female): With long thin rostrum. Eyes large, occupying virtually entire lateral surface of head, well separated (frons, face, and vertex wide). Vertex with thick, stiff setae; lateral row of 6 setae near margin of eye, inclined anteriad, medial row of 5 longer setae, projecting upward; pair of thick setae in middle of frons, projected anteriad. Ocelli on a raised mound, with several pairs of small, thick setae. Frons with pair of distinctive, rounded carinae between ocelli and antennal bases. Antenna with funnel-shaped scape, scoop-shaped pedicel; flagellum with 16 flagellomeres, basal 5 segments tapered in size, apical 11 segments very fine, forming an arista. Clypeus narrow and apically pointed. Maxillary palp slender, length approximately equal to that of clypeus; with 3 or 4 segments, but not 5 (a minute basal segment may be present). Long, fine, stylet-like mouthparts, length approximately 3 times depth of head. Proboscis length 1.3 mm. Proboscis formed from laciniae, which have fine annuli of microtrichia, and very fine central stylet formed from pair of joined structures (probably the mandibles, possibly galeae). Paired mandibles discernable from tip of central stylet, which is bifid. No fine teeth or serrations apparent on laciniae or central stylet. Labium probably highly reduced; labial palps either minute or lost. THORAX: Deep in lateral view, with pronotum small and strap-like. Mesothorax large, notum with scattered, thick, stiff setae; katepisternum large. Legs long and slender, with slender, articulated, spine-like spur at apex of tibiae and tarsomeres. Fore legs with long, slender coxae (0.4 mm); no distinctive setae on femora or tibiae except on hind tibiae. Fore femur 0.7 mm; fore tibia 0.65 mm, tarsi 0.09 mm. Hind tibia with row of 9 thick, sharp, slightly curved setae along distal 2/3, alternate with smaller setae. Claws bifid, with small tooth in middle of longer portion of claw. Wings: Only fore wings developed, 4.0 mm length. No nygmata or thyridia present. Hind wing reduced to a minute, suspended lobe, with tegula remaining; hind wing lobe with 3 thick, stiff setae at apex. Fore wing very long, extended beyond tip of abdomen about 0.4x its entire length. Pterostigma present, edges bounded by apex of R_1 and C; with dense macrotrichia. Distal half of wing with macrotrichia, arranged in more regular rows towards apex of wing. Sc very short, apex extended only slightly past basal fork of R. R_1 with short crossvein joined to C near its middle; apex of R_1 extended to nearly 0.75x length of wing. Rs with four apical branches; crossvein join-

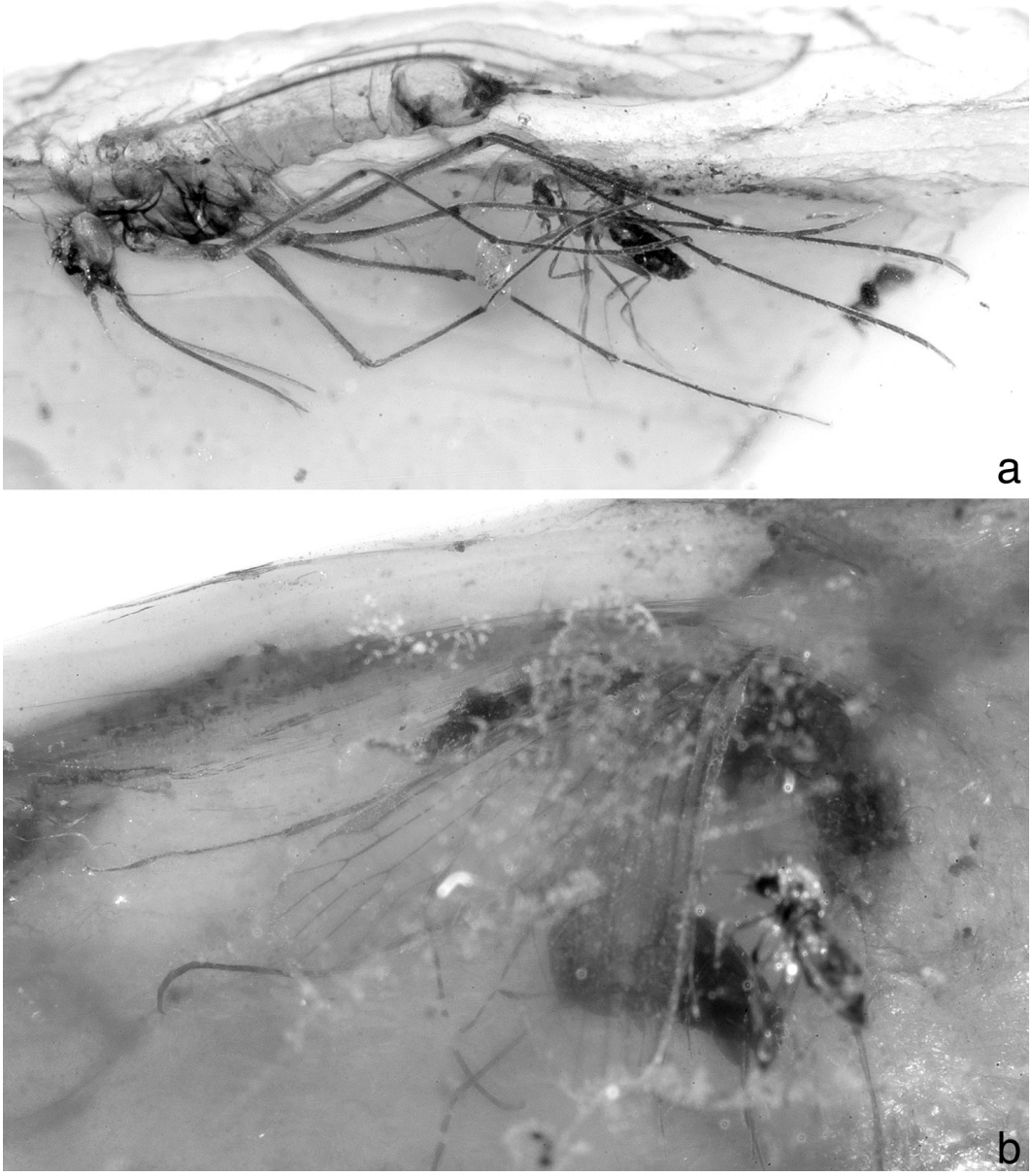

Fig. 6. Photomicrographs of *Parapolycentropus burmiticus*, sp.n., in Burmese amber. Above, paratype female (AMNH Bu134). Below, holotype male (AMNH Bu694).

ing apex of R_1 and stem of R_{2+3}. Crossvein between R_3 and R_4 and between R_5 and M_1 very faint. Crossveins r_{4+5}-m_{1+2} and $m_{2/3}$-m_4 lacking. Apical forks of R_2-R_3 and M_1-$M_{2/3}$ slightly asymmetrical. Base of M diverges from R near base of wing. Four branches of M present: M_1, $M_{2/3}$, M_4, M_5. CuP vein short, length slightly more than half that of CuA. Anal vein highly reduced, joined to base of CuP for 2/3 of its length; thick r+m-cu and cua-cup crossveins virtually in line with each

other. ABDOMEN: Long and slender, with base membranous. Basal tergite (1?) reduced to thin lateral strap. Spiracles not visible. Female terminalia with bulbous GSVIII; small tIX; short, tubular tX; and short tXI, divided longitudinally. Cerci with 2 long, slender segments each. Gonocoxosternites IX a pair of short valves ventrally; invaginated near is pair of sclerites, probably the laterotergites. Male terminalia with bulbous segment IX(?), small gonocoxites and gonostyli.

Comments. – Since the holotype male has a body that is poorly preserved, the species identity of the paratype female is largely based on the fragmentary wing venation. Other than the incomplete wing, the body of the female paratype is very well preserved. The body of the holotype male is considerably compressed and distorted, such that no details of the head and few details of the terminalia are discernable. The wings are the best preserved portion of the holotype specimen. The holotype is in a piece of amber that is a deep, cloudy red, also containing a mordellid beetle and ceratopogonid midge.

Parapolycentropus paraburmiticus Grimaldi and Rasnitsyn, sp. n.

(Figs 6; 8c, d)

Material examined. – Holotype, female, AMNH Bu1558, in Burmese amber with same age and provenance as for specimens of *P. burmiticus*.

Etymology. – Similar to *burmiticus*.

Diagnosis. – Distinguished from the very similar species *P. burmiticus*, from the same deposits, as given above in the diagnosis for that species.

Description. – HEAD: not preserved. THORAX: Wing as for *P. burmiticus*, with differences as given in the diagnosis for that species. Wing length 4.3 mm. Female terminalia: tVIII small and flat, tIX scoop-shaped and narrowed apicad; tX small, apparently cylindrical; cerci two-segmented, with slender segments; GSVIII large, with small laterotergite just anterolateral to it; GSIX a scoop-shaped shelf posteroventral to GSVIII, with narrow median notch on apical half.

Comments. – The holotype specimen is incompletely preserved, and the numerous inclusions prevent preparation very close to the mecopteran. The abdomen, terminalia, thorax, wings, and four legs are preserved. Lost are the head and what appear to be the forelegs. The amber piece is 17 x 14 x 7 mm, deep red in color, and with a suspension of particulate debris and flows. It contains, besides the mecopteran, two Coleoptera (Rhipiphoridae), one Diptera (Hilarimorphidae), remains of a large centipede, and the partial remains of a roach.

Discussion

Pseudopolycentropodes virginicus extends the geographic distribution of the family to the Western Hemisphere; previously, all species of the family were known only from the Mesozoic of Europe and Asia. This would be expected on the basis of Pangean reconstructions, during which time Laurasian and even Gondwanan landmasses were contiguous. Oddly, Pseudopolycentropodidae are as yet unknown from the vast Triassic deposits in Queensland, Australia and the Molteno Formation of South Africa, the former of which contains diverse mecopteroids. Discovery of the species in Burmese amber extends the age of the Pseudopolycentropodidae to nearly 50 million years from the previously youngest age (which was the Late Jurassic of Kazakhstan, or Kimmeridgian, ca. 155 mya, and *Pseudopolycentropus daohugouensis* from China). Thus, known duration for the group is now from the mid-Triassic Grés-a-Voltzia Formation of Vosges, Alsace, France (Anisian: ca. 240 mya) to the mid-Cretaceous of northern Myanmar, ca. 100 mya.

It is reasonable to assume that the Cretaceous species in amber would be a reliable exemplar of the family. The mouthparts, antennae, and hind wings of *P. burmiticus* and *P. paraburmiticus* are highly modified, but the female terminalia appear conservative in structure like the venation, and it is on the basis of the former of these that significant inference on relationships to Recent Mecoptera can be made (Mickoleit, 1978; Willmann, 1989). Important plesiomorphic features of female terminalia in the amber species are the following. GSIX is present and is a well-developed, protruding lobe as is found in the basal-most Recent mecopteran, *Nannochorista* (Nannochoristidae: monogeneric); GSIX is otherwise hidden between GSVIII and tIX (Eomeropeidae [monogeneric: *Notiothauma*]) or it is lost (most other Recent mecopterans). Also, GSVIII is large and undivided, and is situated below tVIII, again as in Nannochoristidae. In all other Recent mecopterans GSVIII is usually divid-

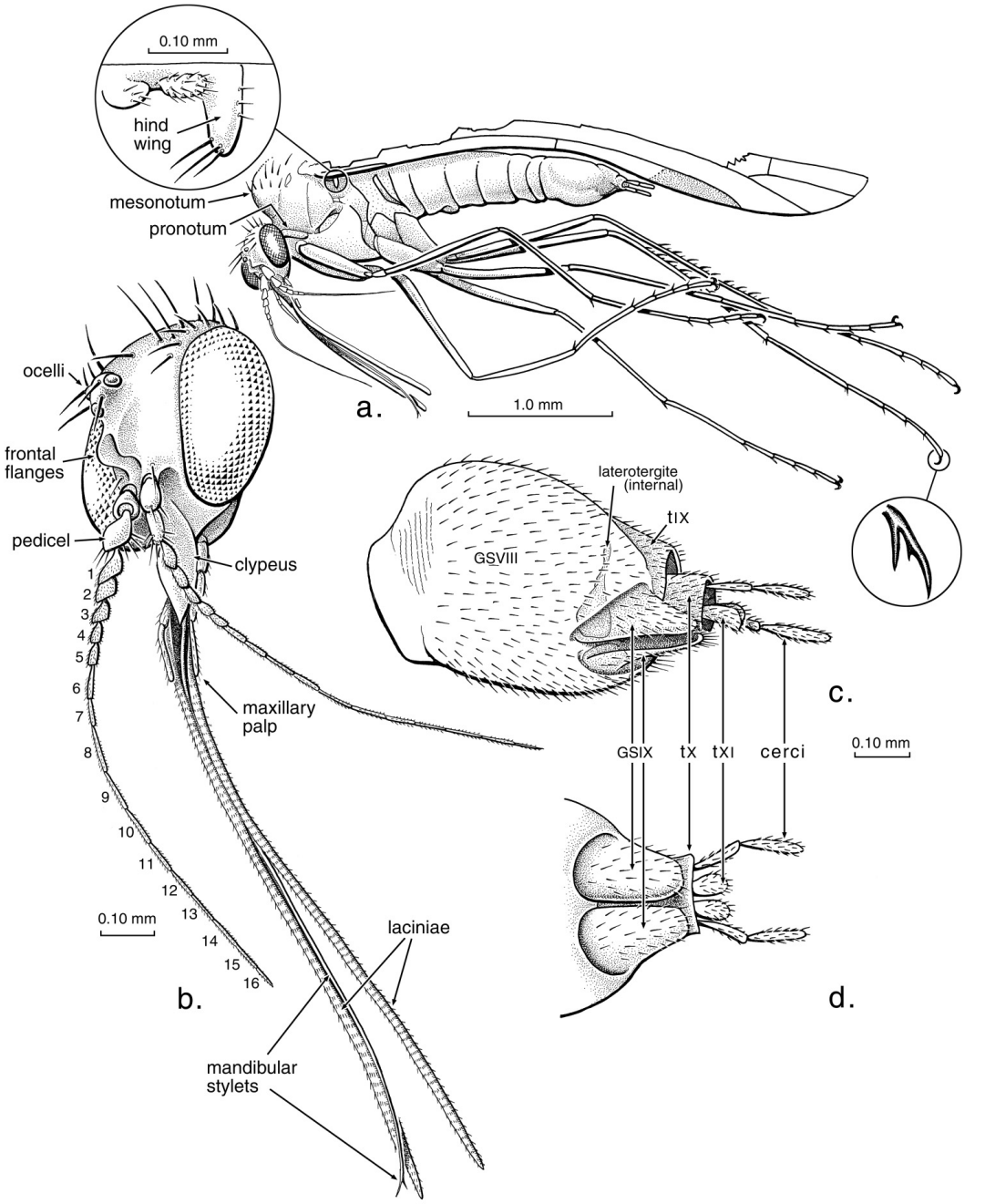

Fig. 7. *Parapolycentropus burmiticus*, sp. n., paratype female in Burmese amber (AMNH BU134). (a) Left lateral view of entire specimen, also showing detail of claw and hind wing. (b) Detail of head, oblique frontal view. (c, d) Female terminalia. (c) Ventrolateral view. (d) Full ventral view.

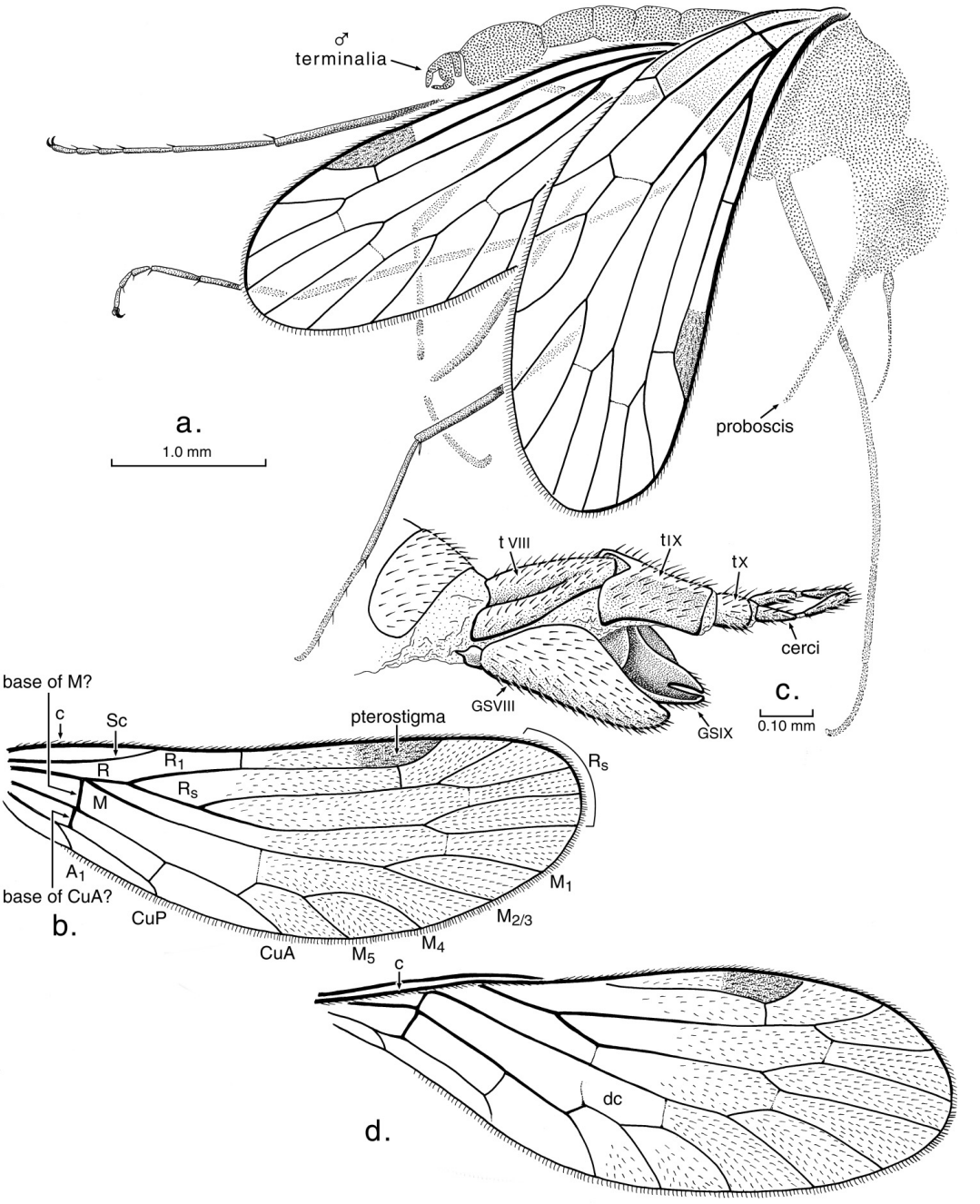

Fig. 8. *Parapolycentropus burmiticus*, n.sp. (a, b) and *P. paraburmiticus* n.sp. (c, d) in Burmese amber. (a, b): *P. burmiticus*, holotype male (AMNH Bu694). (a) Right lateral view of entire specimen. (b) Fore wing, reconstructed from different angles. (c, d): *P. paraburmiticus*, holotype female (AMNH Bu1558). (c): Terminalia, oblique lateral view. (d). Fore wing. The costal section near the wing is folded over the wingbase and could not be reconstructed.

ed and situated beneath tVIII and tIX, or just undivided and situated below just tIX. Also, tX is tubular in the amber species, as in *Nannochorista* and most other mecopterans, not incomplete and saddle-shaped as in *Bittacus*. Lastly, tXI is present in *P. burmiticus*, but is not apparent (perhaps lost) in *P. paraburmiticus*. This tergite is plesiomorphically present in *Nannochorista* and Bittacidae, but lost in other Recent mecopterans or at least reduced to narrow lateral straps ("Circumapikalsklerit" [Mickoleit, 1978; Willmann, 1989]), which are situated just ventral to the most basal segment of the cercus. Oddly, in *P. burmiticus* tXI is medially divided, but where it occurs in true Mecoptera it is entire.

Autapomorphically, the amber species appear to have two-segmented cerci (vs. three in most Recent mecopterans). Though the bases of the cerci in *P. burmiticus* are obscured by tX, in *P. paraburmiticus* the cerci are completely exposed and definitely two-segmented. Interestingly, cerci with two segments are in the ground plan of the Diptera, as they occur in most nematocerans and basal Brachycera.

Preservation of the amber species provides refined details even of the wings of Pseudopolycentropodidae. For example, the faint distal crossveins r-rs, r_3-r_4, and r_5-m_1 occur in the amber species, which are widespread in Mecoptera and even occur in some basal Diptera. This suggests that they were too obscure in the compression/impression fossil wings to be preserved or observed. Also, the tiny nygmata and thyridia are absent from the fore wing of the amber specimens. Nygmata are small sensory spots that occur in typical locations among several holometabolous orders (i.e., neuropteroids, Trichoptera, Mecoptera). In Mecoptera there are typically three nygmata, two in the long cells separated by crossvein r-m, and another basal one. Thyridia are areas of cuticular weakness and desclerotization, through which runs the median flexion line, or the line of weakness on which the wing folds and flexes during flight. Like nygmata, the thyridia occur in various Holometabola, but sporadically. In Recent Mecoptera a thyridium occurs very consistently at the basalmost fork of vein M. Its definitive absence in the amber species may be plesiomorphic or autapomorphic. Given the functional significance of the thyridium, it plausibly can be easily modified depending on the flight of the insect, including whether it has one or two pairs of wings.

Disregarding the autapomorphies of the Burmese amber *Parapolycentropus* as phylogenetically uninformative, the plesiomorphic features of the female terminalia and wings support Willmann's (1989) hypothesis of a basal position of the Pseudopolycentropodidae among Mecopteroidea, followed later by Novokshonov (2002). Willmann (1989) specifically hypothesized that the Pseudopolycentropodidae is one of four stem-group families to the Antliophora (Diptera + Mecoptera), but given the great similarity of the female terminalia of Pseudopolycentropodidae and *Nannochorista* it is likely that the former of these is closer to the Mecoptera than previously proposed. This makes stratigraphic sense as well. Apparent stem groups to the Diptera and Mecoptera appeared in the Late Permian, so these two Recent orders appear to have diverged prior to the first appearance of the Pseudopolycentropodidae in the mid- and Late Triassic. It is proposed that Pseudopolycentropodidae is a specialized lineage derived from some stem-group Mecoptera, which evolved remarkably parallel with Diptera.

The most striking aspect of the new fossils is the proboscis of *Parapolycentropus burmiticus* and *P. paraburmiticus*, and the detail of the structures. Among insects, fine, long proboscides occur in Hemiptera, one Coleoptera, a genus of Trichoptera, in glossatan Lepidoptera, and various Diptera. In Diptera such a proboscis has evolved at least 20 times: in Lygistorrhinidae, Sciaridae (*Rhynchosciara*), Mycetophilidae (*Gnoriste*), Blephariceridae, Tipulidae (*Elephantomyia*, etc.), *Culicoides yoosti* (Ceratopogonidae), Culicidae, various empidine Empididae, and numerous lower Brachycera (some Acroceridae, Apioceridae, various Bombyliidae, Nemestrinidae, pangoniine Tabanidae). A long proboscis also occurred in the extinct mecopteroid family Aneuretopsychidae (Late Jurassic to Early Cretaceous), which is purportedly closely related to the Pseudopolycentropodidae. In all of the Recent groups a slender proboscis functions for probing flowers, for predation, for piercing skin and sucking blood, or combinations of these. Also, the components of the proboscis in these groups are usually quite different, such that mouthparts are modified in different ways among the groups, but diets can also vary dramatically even within a species. For example, the males of many blood-feeding culicomorphan midges, including mosquitoes, will typically feed only on nectar. Empidine empidids are predatory,

and pangoniine tabanids are vicious biters, but some strictly flower-feeding species occur in each of these. For blood-feeders, though, the apices of the stylets, whether they are modified mandibles, laciniae, or even the labrum or labium, almost always have fine serrations or teeth (McAlpine et al., 1981, 1986). No such teeth occur in *Parapolycentropus burmiticus* and *P. paraburmiticus*. This fact, plus the age of these species suggest that they may have been flower-feeders. The earliest angiosperms are from the Hauterivian-Valanginian of the Early Cretaceous (ca. 135 mya), and by the Turonian (ca. 90 mya) many major clades and even specialized pollinator syndromes of flowers had appeared (reviewed in Wing, 2000; Crepet, 1996). The problem with this hypothesis is that *Pseudopolycentropus latipennis*, *P. daohugouensis*, and *Aneuretopsyche rostrata* from the Late Jurassic also had long proboscides. Though the fine structure of the proboscides in these three species is not preserved, a long proboscis clearly occurred too early for flower feeding. It could be argued that the proboscis of the Jurassic species was used to probe the reproductive structures of gnetaleans or bennettitaleans for pollen or whatever rewards they offered, but that would be pure speculation.

Two other remarkable structures of the Cretaceous amber *Parapolycentropus* are the extremely vestigial hind wings (with the concomitant enlargement of the mesothorax), and the aristate antennae. These probably are all functionally related. In Antliophora, an aristate antenna occurs in most Brachycera and in a species of the extinct nematoceran (sciaroid) family Archizelmiridae (Grimaldi et al., 2003). In that species, *Burmazelmira aristica*, the basal flagellomeres are very compact and bulbous, and just the apical flagellomere is whip-like (incredibly, that species too is known just from Burmese amber). Thus, the mecopteroid is the third antliophoran group wherein the antenna is modified as an arista. Reduction in the size of the hind wing or its coupling to the fore wing is strongly correlated with a maneuvered flight in diverse insects. Among Diptera, two-winged flight is most maneuvered in the Brachycera, particularly those that hover, and their aristate antennae may be involved in the detection of air movement and speed. The flight of *P. burmiticus* and *P. paraburmiticus* was probably agile and maneuvered, and with such large eyes the insect was probably quite active. Given the feeding habits of Recent Mecoptera it is safest to assume that *Pseudopolycentropus* and *Parapolycentropus* from the Late Mesozoic used their long proboscides for preying on other insects and scavenging. For species that evolved in the mid-Cretaceous, the function of this remarkable structure may then have been co-opted for feeding from flowers as well, or even exclusively.

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