The long-tongued Cretaceous scorpionfly Parapolycentropus Grimaldi and Rasnitsyn (Mecoptera: Pseudopolycentropodidae): New Data and Interpretations

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The long-tongued Cretaceous scorpionfly *Parapolycentropus* Grimaldi and Rasnitsyn (Mecoptera: Pseudopolycentropodidae): New data and interpretations

DAVID GRIMALDI[1] AND M. ANDREW JOHNSTON[1,2]

ABSTRACT

The genus *Parapolycentropus*, originally described for two species in 99 myo Burmese amber, is unique among Mecoptera for its long, thin proboscis and possession of just the mesothoracic pair of wings. A new series of 19 specimens with excellent preservation allows description and redescription of virtually all morphological details. Male terminalia are very similar to those of the Holarctic Recent family of "snow fleas," the Boreidae. Thoracic sclerites are highly convergent with nematocerous Diptera in the expansion of the mesothorax and great reduction of the pro- and metathoraces. The metathoracic wing vestige appears to be just the tegula; axial sclerites are lost. Details of the pretarsal claws are described; in *P. paraburmiticus* Grimaldi and Rasnitsyn the outer claw of the meso- and metathoracic pretarsi is elongate and the inner claw reduced. The proboscis is comprised not of a labial tube and "pseudolabellum" (contra Ren et al., 2009), but is mostly maxillary in origin, with the outer valves probably being galeae and the central, serrated stylet probably the hypopharynx. Abdominal sternites are greatly reduced (more so in females), suggesting that the abdomen was distensible, a feature that is common in some fluid-feeding insects. The proboscis, claw, and sternite modifications indicate that *Parapolycentropus* fed on the hemolymph of small insects, not the blood of vertebrates.

KEY WORDS: Myanmar, amber, mouthparts, predation, hematophagy.

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INTRODUCTION

Within the complex 250-million-year history of Mecoptera, few extinct groups have attracted as much attention and interest as the Mesozoic family Pseudopolycentropodidae and their long-tongued relatives Mesopsychidae and Aneuretopsychidae (Tillyard, 1919; Novokshonov, 1997, 2002; Grimaldi and Engel, 2005; Grimaldi et al., 2005; Ren et al., 2009; 2010a, 2010b; Shih et al., 2011). Late Jurassic and Early Cretaceous species of these fascinating insects possessed a long, thin proboscis, hypothesized to have functioned in probing the recesses of reproductive structures of extinct gymnosperms (Labandeira et al., 2007; Ren et al., 2009). As such, they may have served as specialized pollinators well before the radiation and even advent of angiosperms.

The Pseudopolycentropodidae existed for at least 130 million years. The oldest records are from the mid- to Late Triassic of Kyrgyzstan, France, and Virginia (reviewed in Grimaldi et al., 2005); the youngest records are in 99 myo amber from Myanmar, the subject of this paper. In all, there are four genera and 14 species (most of them *Pseudopolycentropus*); nine of these species are known as compression fossils from the Middle Jurassic to Early Cretaceous of Europe and Central Asia. A wealth of beautifully preserved specimens is being recovered from the late Middle Jurassic Jiulongshan Formation (Bathovian-Callovian) of Mongolia (Ren et al., 2009, 2010a, 2010b; Shih et al., 2011).

The initial impetus for our study was discovery of a series of male *Parapolycentropus* in Burmese amber (figs. 1–3), allowing for the first time a detailed study of the male terminalia, and thus providing more data on the phylogenetic position of this enigmatic family. In the course of the work we realized that in the original paper on *Parapolycentropus* (Grimaldi et al., 2005) various morphological details were insufficiently described (particularly regarding the mouthparts and thorax), the original descriptions based on four incomplete to poorly preserved specimens. The present paper also seems an appropriate occasion to address conclusions about mouthpart homologies of the genus and family (Ren et al., 2009). Insect mouthpart structure highly reflects diet, and in the case of *Parapolycentropus,* Ren et al. (2009) suggested that these distinctive, gracile insects fed on blood (presumably of vertebrates), either exclusively or along with nectar, evidence of which is assessed here.

MATERIALS AND METHODS

The basis of this paper is a series of newly discovered specimens of *Parapolycentropus* preserved in mid-Cretaceous amber from northern Myanmar. One of the new specimens is in the AMNH; all others comprise a series of 18 specimens residing in the collection of Burmese amber fossils belonging to James Zigras (JZC Bu numbers). Burmese amber derives from the northern province of Kachin (localities and history summarized by Zherikhin and Ross, 2000; Grimaldi et al., 2002; Cruikshank and Ko, 2003). This amber was stratigraphically dated as Late Albian (Cruikshank and Ko, 2003), and its age radiometrically refined to ca. 99 myo (Albian-Cenomanian boundary), using U-Pb isotopes (Shi et al., 2012). Since structures critical for study are minute (e.g., details of mouthparts, terminalia), it was necessary to meticulously

prepare the specimens. Polished cabochons of amber containing specimens were trimmed into thin slabs using a fine (1 mm thick) diamond-edged, water-fed trim saw, generally to maximize a lateral view of the scorpionfly. These amber chips were further thinned and polished using a series of wet Buehler® emory papers from coarse to fine (400, 600, 800, 1200, 2500 grits), on a Buehler Ecomet® variable-speed, flat lapidary wheel. Preparations were typically between 1.5–3 mm in thickness, and critical structures were often just microns beneath the surface. Specimens were then applied to a glass microscope slide using a drop of glycerine, and a coverslip was applied using another drop on the opposite surface. This allows observation with finer resolution since it obscures fine surface scratches. Slide-mounted preparations were then studied using a Nikon SMZ1500 stereomicroscope, and measured and photographed using Nikon DIS Elements software (including Z-stacked photos, as indicated in figure legends). Structures requiring highest magnification used a Nikon Eclipse compound microscope with bright field illumination at 100× or 200× magnification, and photographed using a Nikon D1 camera and the Z-stacking software program HeliconFocus (e.g., figs. 4D, E; 9A, C).

MORPHOLOGY

Head and Mouthparts

Recent Mecoptera. With the exception of a distended rostrum in many species, the head and mouthparts of Recent Mecoptera is quite generalized for Holometabola. Head morphology is elegantly surveyed by Otanes (1922) for Mecoptera in general, and for particular genera by Beutel and Baum (2008) and Friedrich et al. (2013). The clypeus and labrum are either fused or nearly so, the latter condition having a very fine suture demarcating the boundary (e.g., in *Apterobittacus*, *Bittacus*, *Merope*, *Panorpodes*, and *Nannochorista*). A hallmark feature of many mecopterans is the elongation of the ventral/anterior portion of the head into a rostrum, which is specifically formed by elongation of the clypeolabrum, gena, stipes, galeae, and sometimes the submentum. The remaining mouthparts (palps, mandibles, glossae) are of normal positions and relative proportions at the end of the rostrum. In some taxa with a short rostrum (e.g., *Apterobittacus*, some *Bittacus*), the mandible is long and slender, with a single large tooth at the apex. The labial palps in Mecoptera are commonly reduced to two or even one palpomere (vs. three labial palpomeres primitively in insects). With exception of the elongation of the stipes, the cardo-stipital elements are relatively unspecialized; the most modified and specialized element of the maxilla is the pair of galeae, the bases of which articulate with the apices of the stipes. Not only are the galeae elongate in many Mecoptera, but each one is often split into a pair of lobes covered with microtrichia, the inner (more mesal) lobe commonly bearing a brushy tip. In *Merope*, the galeae are modified into a pair of broad brushes (Otanes, 1922; Friedrich et al., 2013).

Parapolycentropus. One of the most striking features of *Parapolycentropus* concerns its long, thin proboscis (figs. 4, 5). Ren et al. (2009) referred to it as "stylate," in reference to its needlelike structure and apparent function in puncturing (vs. "siphonate," a functional type of proboscis that sucks up surface fluids and which all other long-tongued pseudopolycentropo-

TABLE 1. Proportions in *Parapolycentropus* Specimens (measurements in mm).

Specimen	BL	ThL	WL	FF	MF	HF	FT	MT	HT	PL
Males										
P. paraburmiticus										
Bu273	3.15	0.59	3.71	0.99	0.92	1.14	0.77	1.05	1.32	0.62
Bu80	3.22	0.65	3.79	0.75	0.67	0.98	0.79	1.12	1.31	0.65
Bu81	3.03	0.69	3.31	0.91	0.78	0.88	0.74	1.02	1.30	0.65
Bu82	2.72	0.62	3.40	0.83	0.78	0.96	0.74	0.97	1.32	0.67
Bu148	2.69	0.67	3.45	0.93	0.87	1.03	0.78	1.05	1.30	0.75
Bu542A	2.88	0.58	3.27	0.85	0.82	0.94	—	1.01	1.14	0.64
Bu1433A	1.79	0.42	3.15	0.85	0.82	0.85	0.68	0.86	1.19	0.77
Bu1433B	2.43	0.57	3.52	0.79	0.96	0.92	0.84	—	1.20	0.74
Females										
P. burmiticus										
Bu134*	2.62	0.89	3.78	0.89	0.87	1.00	0.73	1.04	1.34	1.28
Bu1268	3.48	0.74	4.02	1.00	0.93	1.07	0.83	1.12	1.45	1.26
P. paraburmiticus										
Bu274	3.43	0.88	4.08	0.99	0.95	1.14	0.80	1.10	1.34	0.70
Bu525	2.82	0.61	3.80	1.02	0.90	1.09	0.77	1.15	1.43	0.89
Bu590	3.20	0.66	—	0.99	0.95	1.12	0.84	1.07	1.36	0.96
Bu no #	3.91	1.11	4.38	0.99	1.14	1.28	0.90	1.14	1.42	0.93
Bu1192	3.12	0.85	4.34	1.00	1.01	1.18	0.83	1.25	1.59	0.95
P. paraburmiticus?										
Bu1121	2.36	0.80	—	—	0.89	1.07	—	1.16	1.46	0.77
Bu1329	2.01	0.86	—	0.93	0.91	1.08	0.69	—	—	0.85

*AMNH, all others JZC

Abbreviations: **BL**, body length; **ThL**, thorax length; **WL**, wing length; **FF**, fore femur length; **MF**, midfemur length; **HF**, hind femur length; **FT**, fore tibia length; **MT**, midtibia length; **HT**, hind tibia length; **PL**, proboscis length.

dids possess). Indeed, the proboscis of *Parapolycentropus* is significantly thinner than other taxa in the family. There is considerable variation in length of the proboscis among species of *Parapolycentropus*, with the rarer species *P. burmiticus* Grimaldi and Rasnitsyn having a particularly long one (fig. 2C; table 1). In the two specimens of *P. burmiticus* that were measureable (which were females) proboscis length was an average of 1.27 mm, or 0.32× the wing length; in females of *paraburmiticus* Grimaldi and Rasnitsyn the proboscis length was 0.93 mm, or 0.22× the wing length ($N = 4$) (table 1). Interestingly, males of *P. paraburmiticus* have a slightly shorter proboscis, approximately 0.19× the wing length ($N = 6$) (table 1).

The anterodorsal portion of the head, anterior to the antennal sockets, is slightly projected and narrowed, which is the clypeus (fig. 5A). The boundary between the clypeus and smaller

labrum is demarcated by a very fine, transverse suture, so these sclerites are partly fused. The labrum is small, apically rounded (its length approximately equal to the width), appearing barely moveable against the clypeus, and it lies over the bases of the mouthparts, including the palps. Maxillary palps are short, setose, and 3-segmented, the apical segment being narrow and tapered. In some specimens (e.g., JZC Bu81, JZC Bu82; figs. 4A, 5B), the ventral surface of the head is visible, which is membranous for essentially the entire anterior half. Within this membrane lies a pair of parallel sets of sclerites, a smaller posterior sclerite (the cardo) and a long, slender anterior one (the stipes). There is a distinct separation between the ipsilateral cardo and stipes, and further evidence of their independent articulation is indicated by the fact that in some specimens they are folded slightly into two planes. Attached to the narrow apex of the stipes is a very thin connection to the maxillary palps. Lying approximately in the same plane as the cardo-stipes but anterior to them is a narrow sclerite, apparently the mentum (and the sole remnant of the labium). The apex of the mentum is slightly (JZC Bu81) to significantly (JZC Bu82) V-shaped.

Lying immediately dorsal to the mentum and near its distal end are the narrowed bases of a pair of long, lateral, annulated valves of the proboscis (figs. 4A, B; 5A, B). These were originally interpreted as laciniae (Grimaldi et al., 2005), but which may in fact be the galeae. Ren et al. (2009: 843–844), in their examination of one poorly preserved specimen (AMNH Bu1444), described the proboscis as bearing "at least one protruding, robust stylet above two, elongate lobes that form pseudolabellae (type 4)" and that *Parapolycentropus* has "stylate mouthparts within a labial tube." In the specimen Ren et al. examined these galeal valves are slightly separated at the proboscis apex, giving the appearance of two narrow labellar lobes like that seen in some long-tongued brachyceran flies. This preservation may have led to their conclusion that the valves are labial in origin, along with the fact that the proboscis tip in compression-fossilized, Jurassic *Pseudopolycentropus* is swollen.

In fact, the galeae in *Parapolycentropus* can be "unzipped" their entire length (figs. 1A–C; 2A, C, D; 3C). Along the entire length of the galea is a series of approximately 40 thin, transverse, cuticular bands, separated by thinner bands of membrane (figs. 4A–D; 5A–E). Each cuticular band has a whorl of microtrichia (contra Ren et al., 2009: 843, "prominent setae arising from interannular sulci"). This structure is highly convergent with the galeae of Lepidoptera, which are also elongate, form a siphonate proboscis, and are composed of cuticular bands that allow the proboscis to coil in glossatan Lepidoptera. In these Lepidoptera, the median edges of each cuticular band have lamellae that interlock to "zip" the galeae together. Although the unzipped galeae of *Parapolycentropus* can curve significantly (but not coil) (e.g., figs. 1A, 2D), there appears to be no intrinsic or extrinsic musculature in the galeae. Musculature is often viewable through the cuticle of insects in amber. There is undoubtedly an interlocking mechanism for the *Parapolycentropus* galeae, though it was not observable in this study.

There are several lines of evidence for homologizing the long, annulated proboscis valves as galeae. First, they are inserted *dorsal* to the mentum, and connected by a fine ligament to the apex of the stipes (seen in several specimens through the partly cleared cuticle of the mentum). If these valves were labial palps they would articulate apically (i.e., at the distal end) with

FIGURE 1. Photomicrographs of male *Parapolycentropus paraburmiticus*. **A.** JZC Bu81. **B.** JZC Bu82. **C.** JZC Bu148. **D.** JZC Bu273. All to the same scale.
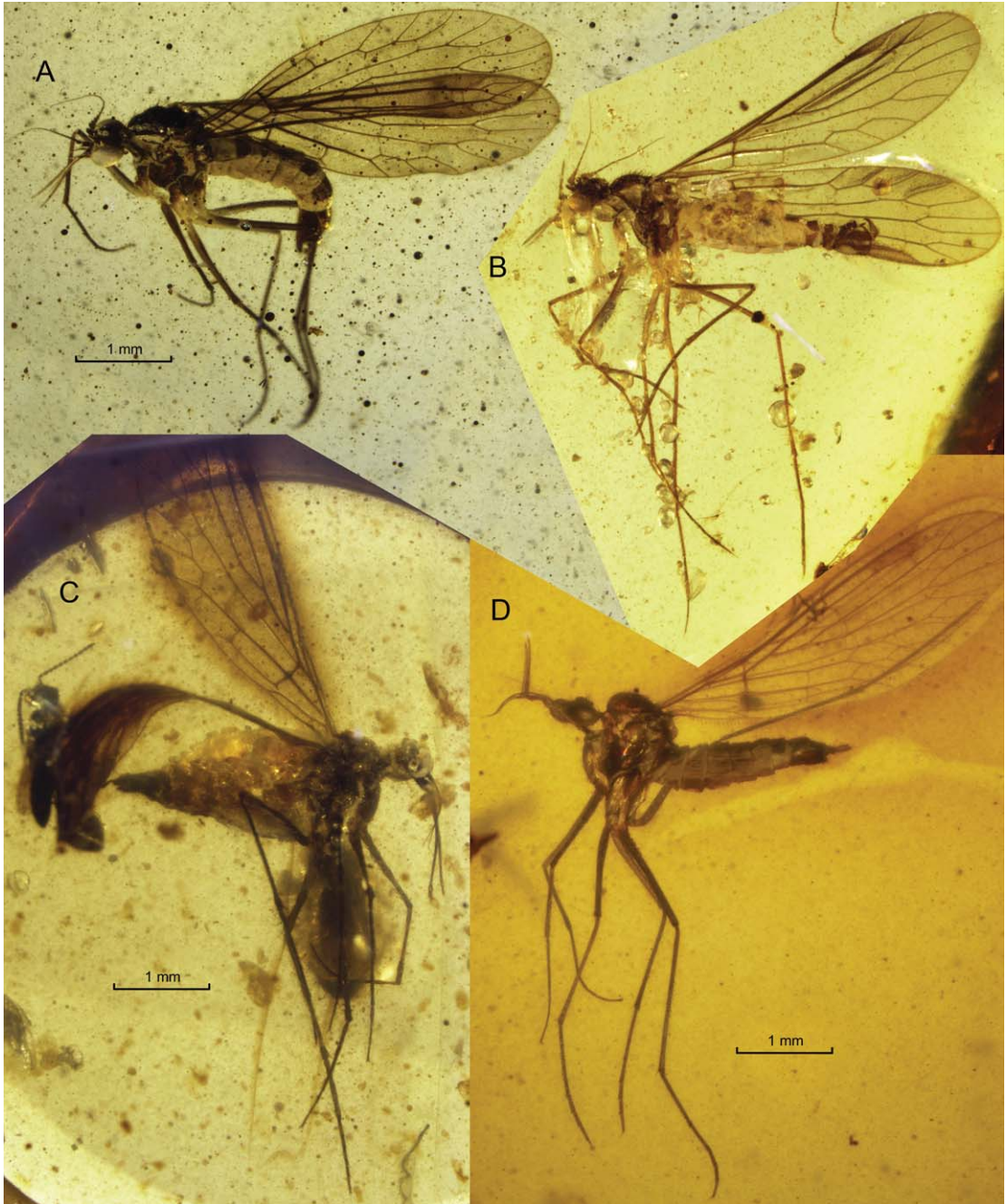
FIGURE 2. Photomicrographs of *Parapolycentropus* species. **A, B, D,** *P. paraburmiticus;* **C,** *P. burmiticus*. **A.** Female, JZC Bu274. **B.** Male, JZC Bu542A. **C.** Female, JZC Bu1268. **D.** Female, JZC Bu1192.

the mentum. Second, there is no evidence of any primary segmentation in the proboscis valves. If the valves were, again, labial palps, there would be at least one suture present (between a palpomere and palpifer). Third, the galeae in Recent Mecoptera are commonly elongate lobes, and they are always covered with a dense vestiture of microtrichia. Some Mecoptera in fact (e.g., *Apterobittacus*) have the galeal microtrichia also arranged into transverse bands.

Lying *between* the galeae (not above, contra Ren et al., 2009) is a fine, unpaired, apically pointed element that is nearly as long as the galeae; this is probably the hypopharynx (figs. 4, 5). Its diameter is approximately equal to that of the galea. Ren et al. (2009) referred to it simply as the "stylet," a general term for any needlelike structure. Its base lies immediately ventral to the labrum and between the bases of the palps, and significantly more proximal than the bases of the galeae. The hypopharynx lacks microtrichia, but has a series of fine, transverse grooves and serrations on the ventral surface. The serrations are flattened (not pointed or toothlike), with the long axis inclined slightly distad, approximately 24 per 100 μm section (or 4 μm in length each) (figs. 4E; 5D, F). The dorsal surface of the hypopharynx has a very fine, longitudinal, median groove along its entire length, which is the food channel (figs. 5A, E). The thin, sharp structure of the hypopharynx, its apparent rigidity, presence of a feeding canal, and the ventral serrations are suggestive of a piercing function, although it is possible that the serrations serve in a locking mechanism for the galeal valves. No sexual dimorphism was observed in the hypopharyngeal serrations of *P. paraburmiticus*; in the mandibles of blood-feeding flies well-developed serrations usually occur just in females.

A schematic of the proboscis structure of *Parapolycentropus* is shown in figure 5. Essentially, when the galeae interconnect to form a tube around the hypopharynx, the fine dorsal longitudinal groove on the hypopharynx is sealed off to form a closed tube through which food passes. In order for the hypopharynx to pierce, the galeal valves would need to either separate or push back and fold, like the tubular labium of mosquitoes. Hypotheses on diet and feeding behavior are presented below, under Discussion.

Thorax

Recent Mecoptera. The thoracic structure of Recent Mecoptera is remarkably conservative, even that of highly specialized taxa. Comparing, for example, *Nannochorista* (Nannochoristidae) (Friedrich and Beutel, 2010: fig. 2; redrawn here, fig. 6A) and *Panorpa* (Panorpidae) (e.g., Snodgrass, 1935: 179, fig. 99), which are at opposite ends of the mecopteran phylogenetic tree, the proportions and arrangements of thoracic sclerites are extremely similar. In general, the mecopteran pronotum is reduced and the propleuron is a small, nearly isolated sclerite ventral to it that articulates anteriorly with the lateral cervical sclerite and ventrally with the procoxa. The prothoracic spiracle always occurs near the posterolateral margin of the pronotum. The mesothorax is only slightly larger than the metathorax. The mesoscutum partly covers the dorsal surface of the mesothorax and does not extend laterally; the metascutum is slightly shorter and less arched. A small, elongate subalare sclerite is isolated within a large membranous space in both the meso- and metathorax. The mesopleural suture is well developed and bisects the mesopleuron into a nearly equivalent mesepimeron and mesepisternum (which are

slightly more developed in *Nannochorista* than *Panorpa*). A scutellum and postnotum are well developed for both the meso- and metathorax. Membrane separates the metanepisternum from the mesopleuron; an anapleural cleft is well developed and partly separates the metathoracic preepisternum and anepisternum. Meso- and metathoracic coxae are nearly twice the size of procoxae, with the mesomeron and metameron clearly delineated from their respective coxa by a sulcus.

The thorax of *Merope* (e.g., Mickoleit, 1967: 316, fig. 2) is more modified than that of *Nannochorista* and *Panorpa*, because this scorpionfly is flattened and roachlike, scuttling among leaves and logs in the forest understory. Like roaches, the pleural sclerites and sutures of *Merope* are significantly oblique to the longitudinal axis of the body. Also convergent with roaches, the pronotum of *Merope* is well developed, dorsally shielding a portion of the head. Its meso- and metathoracic pleurae are shortened, as are the coxae of these segments, which are adpressed to the thorax. The mesocoxal sclerites of *Merope* are reduced, surrounded dorsally and ventrally by extensive membrane. Otherwise, the relative positions of thoracic sclerites do not fundamentally differ from those of *Nannochorista* and *Panorpa*.

Parapolycentropus. The thorax of *Parapolycentropus* (figs. 6B, 7B) differs radically from Recent Mecoptera and in fact is extremely similar to that of basal Diptera (e.g., Tipulomorpha: McAlpine, 1981: 24, fig. 2.64; herein fig. 7A), in its dramatic expansion of the mesothorax and great reduction of pro- and metathoraces. This is clearly a functional and structural convergence related to the dipterous condition; the slightly different terminology used for the dipteran mesopleural sclerites are in brackets below. Moreover, the thoraces of *Parapolycentropus burmiticus* and *paraburmiticus* differ significantly. In both species the thorax is comprised almost entirely of mesothoracic sclerites, the prothorax is virtually lost and the metathorax highly reduced; pleural sutures and coxae are either vertically oriented (*burmiticus*) or nearly so (*paraburmiticus*). The prothorax is reduced to two or three small, slender sclerites, including the pronotum (which articulates with the mesoanepisternum just above the mesoanapleural cleft). The propleuron is a small, slender sclerite just ventral to the pronotum. In *Limonia* the prothorax is actually larger and the pronotum and propleuron largely fused (fig. 7A). All coxae of *Parapolycentropus* are long with a significant portion of each free from the thorax, much like that of sciaroid fungus gnats. The procoxa in *P. burmiticus* is longer than the meso- and metacoxa, and may serve to extend the reach of the prolegs. The mesoscutum is a very large, dome-shaped sclerite with several well-defined dorsal sutures; it covers approximately 70% of the dorsal surface of the thorax, not unlike that of *Limonia*. A mesopleural suture is well defined in both species of *Parapolycentropus*, and in *P. burmiticus* it is perfectly vertical to the longitudinal axis of the body (slightly oblique in *P. paraburmiticus*). However, the mesopleuron is also divided by a transverse suture that originates either just above the mesoanapleural cleft (*paraburmiticus*) or significantly dorsal to this (*burmiticus*). There is a very large mesoepisternum in *P. burmiticus*, which possesses a well-developed, sinuous premesocoxal suture (which is lacking in *P. paraburmiticus*). Thus, the mesopleuron in *P. paraburmiticus* is essentially divided into quarters by sutures: an anterodorsal mesoanepisternum, a posterodorsal mesoanepimeron (which is largely absent in *P. burmiticus*), an anteroventral mesopre-episternum [mesokatepi-
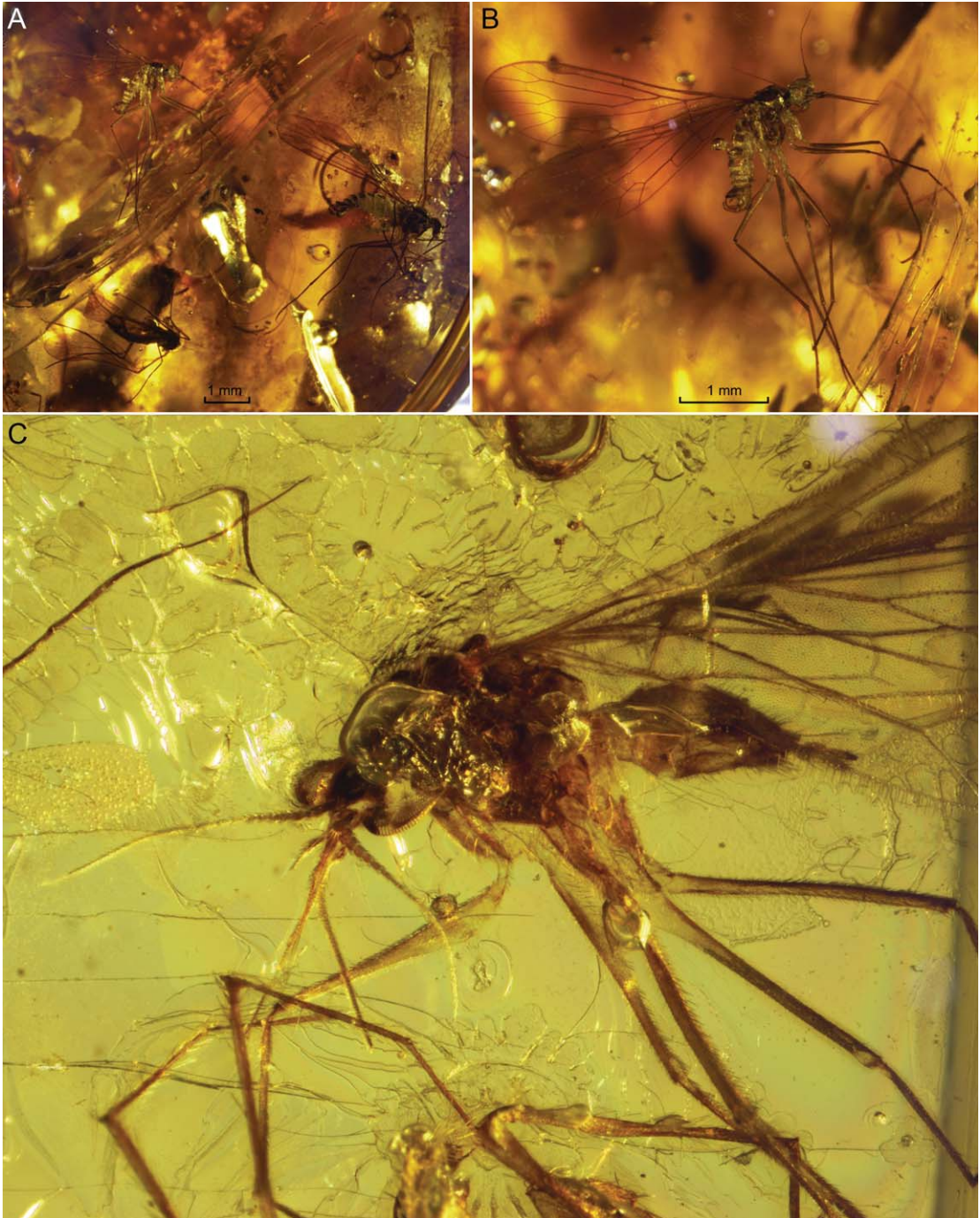
FIGURE 3. Photomicrographs of *Parapolycentropus* sp., a small, possibly new species. **A.** Small aggregation (swarm?) of 3 males, JZC Bu433; **B.** Detail of one male in aggregation. **C.** Female, JZC Bu1329.
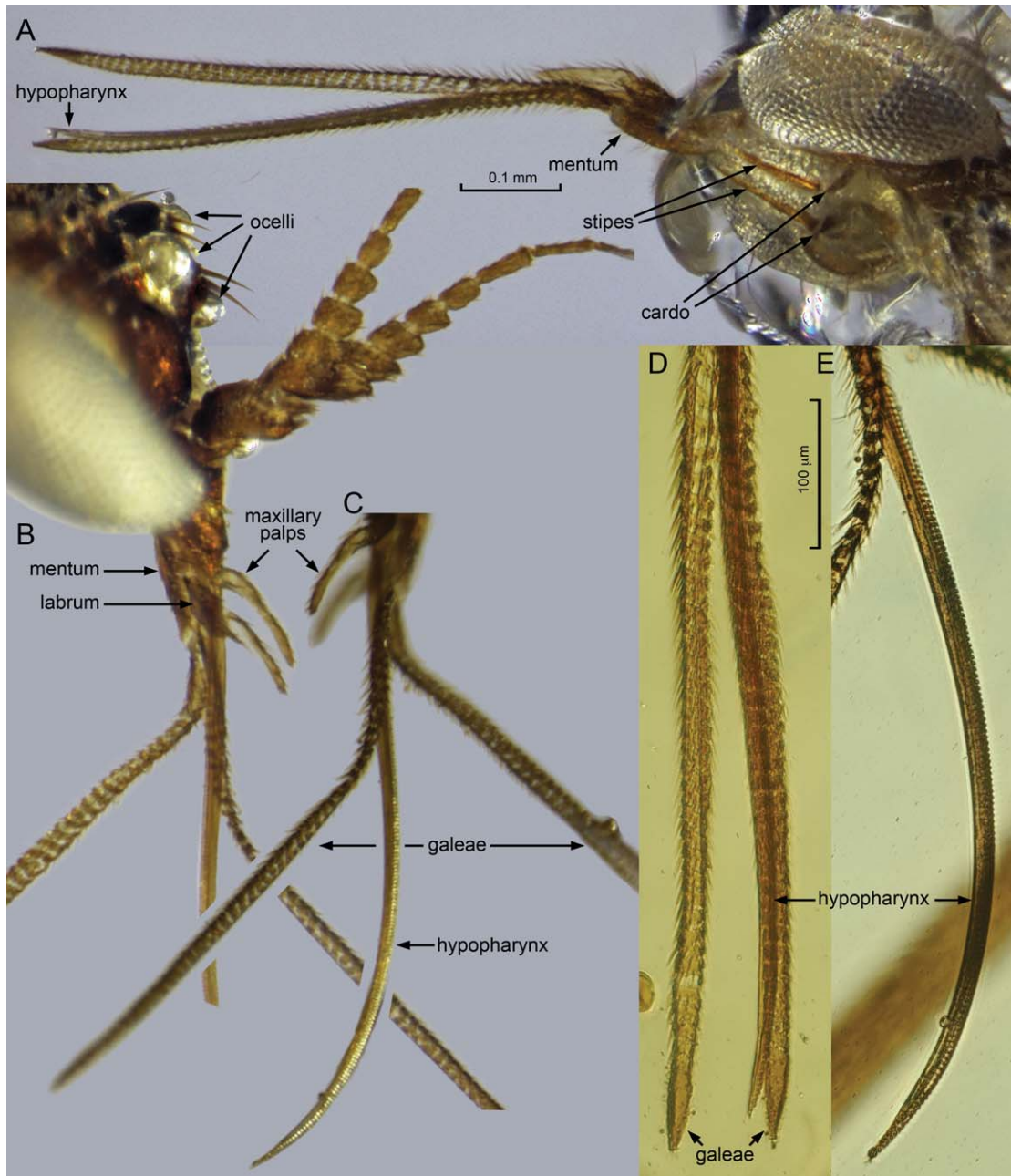
FIGURE 4. Photomicrographs of heads and/or mouthparts of *Parapolycentropus*. **A.** Oblique ventral view of head and proboscis, JZC Bu81. **B, C,** Opposite views of JZC Bu82: **B.** Dorsolateral view, showing frons and base of mouthparts, **C.** ventral view of mouthparts. **D.** Proboscis, JZC Bu148. **E.** Hypopharynx, JZC Bu82. **A, D, E,** Fully Z-stacked photos; **B, C,** partially Z-stacked. **D, E,** Photographed at 200× using compound microscope.

sternum in Diptera], and a posteroventral mesepimeron [mesokatepisternum in Diptera]. The anapleural cleft is wide and occurs only on the mesopleuron; it is suturelike and occurs on this segment plus the metapleuron of Recent Mecoptera. *Limonia* lacks the extensive membranous area beneath the mesothoracic wings, as well as the mesoanapleural cleft. There is a triangular sclerite above the mesocoxa in *Parapolycentropus*, which is subdivided by a short transverse suture; the lower sclerite may be the mesotrochantin (which is normally a small, thin, free sclerite). Very interesting are the meso- and metathoracic merons. The mesothoracic meron is contiguous with only the dorsal half of the coxa and is almost free in *Parapolycentropus*, the two separated by a deep fissurelike sulcus very similar to the situation in basal Diptera. In Recent Mecoptera the merons are integrated with the coxa, defined by a fine suture. The metathoracic meron is very small in *P. burmiticus* and lost altogether in *P. paraburmiticus*. The membranous space between the meso- and metapleura is more extensive in *Parapolycentropus* than in extant Mecoptera (and there is virtually no such membrane in Diptera). The mesoscutellum is well developed, as in both Mecoptera and Diptera, and the mesopostnotum [the "mediotergite" in Diptera] is much larger than in Recent Mecoptera and protruding well beyond the scutellum, very similar to that in the tipulomorphan *Limonia* (fig. 7A). The metathorax of *Parapolycentropus* is highly reduced compared to Recent Mecoptera, but not to the extreme seen in Tipulomorpha (where the remnant of this segment is just a thin, transverse strip of sclerite anterior to abdominal tergite one) (fig. 7A). A metapleural suture and small metanotum is apparent in *P. burmiticus* but not in *P. paraburmiticus*; other elements of the metathorax are not apparent.

The wing and venation of *Parapolycentropus* was described earlier (Grimaldi et al., 2005), but the wing base observed much more closely for the present study (fig. 6C). The base of the forewing possesses the full complement of axillary sclerites, largely unmodified from other Mecoptera. The hind wing, as originally described, is a small, digitate lobe with a pair of stout apical setae. Similar setae occur on the forewing tegula, so it appears that the vestige of the hind wing is largely comprised of the tegula. There are no axillary sclerites remaining with the hind wing. Another interesting aspect of the forewing base of *Parapolycentropus* is a lobe (lost in the hind wing) that bears a row of thickened setae along the margin, very similar to the calypter of flies.

The legs of *Parapolycentropus* are long and slender, as for Bittacidae and most nematocerous Diptera, the most interesting aspect involving the claws. In the females of *P. burmiticus* (well-preserved males being unavailable) there is little or no discernable differentiation among the pairs of pretarsal claws. In this species the outer claw is slightly larger and both claws on a pretarsus have a large, pointed basal tooth (fig. 9B). The prothoracic pretarsal claws of both sexes of *P. paraburmiticus* are like those of *P. burmiticus*, but in this species the meso- and metathoracic pretarsi have the outer claw elongate, slender, linear, and with a small basal tooth; the inner claw is approximately 1/3 the length and comprised of two, sharp, curved teeth (fig. 9B). These large claws have microtrichia over much of the surface (fig. 9A), and an extremely minute preapical tooth occurs on the ventral edge near the claw tip (figs. 9A, B). An arolium, an empodium, and pulvilli do not appear to be present on any pretarsi in *Parapolycentropus*. There does not appear to be any sexual dimorphism in claw size or structure.
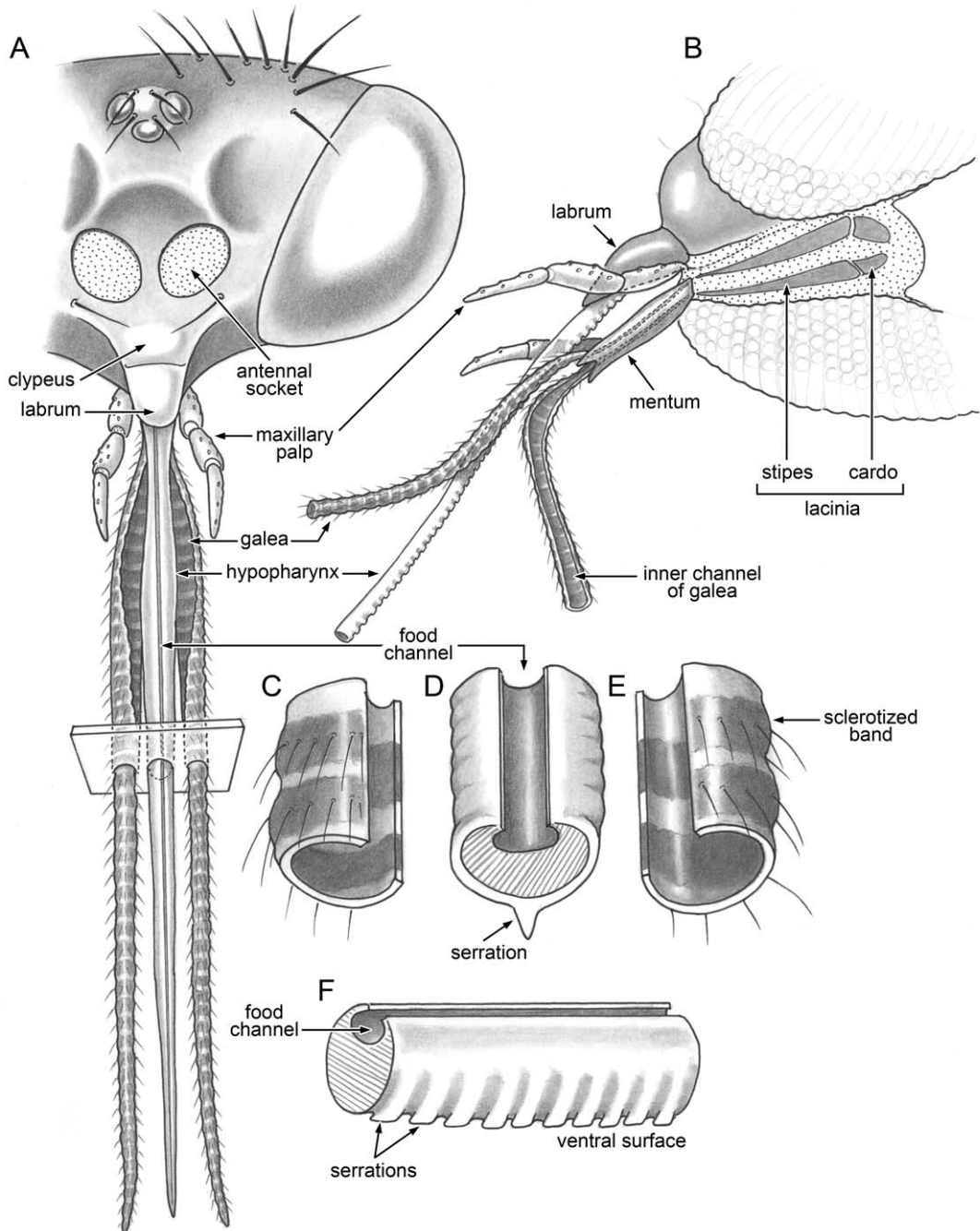
FIGURE 5. Head and mouthparts of *Parapolycentropus*. **A, C–F,** Diagrammatic representations of proboscis. **A.** Head and proboscis, dorsal view. **B.** Ventral view of proximal regions of mouthparts, based on JZC Bu82, JZC Bu274. **C–E.** Diagrammatic representation of adjacent sections of galeae and hypopharynx. **F.** Diagrammatic representation of a section of hypopharynx, lateral view.
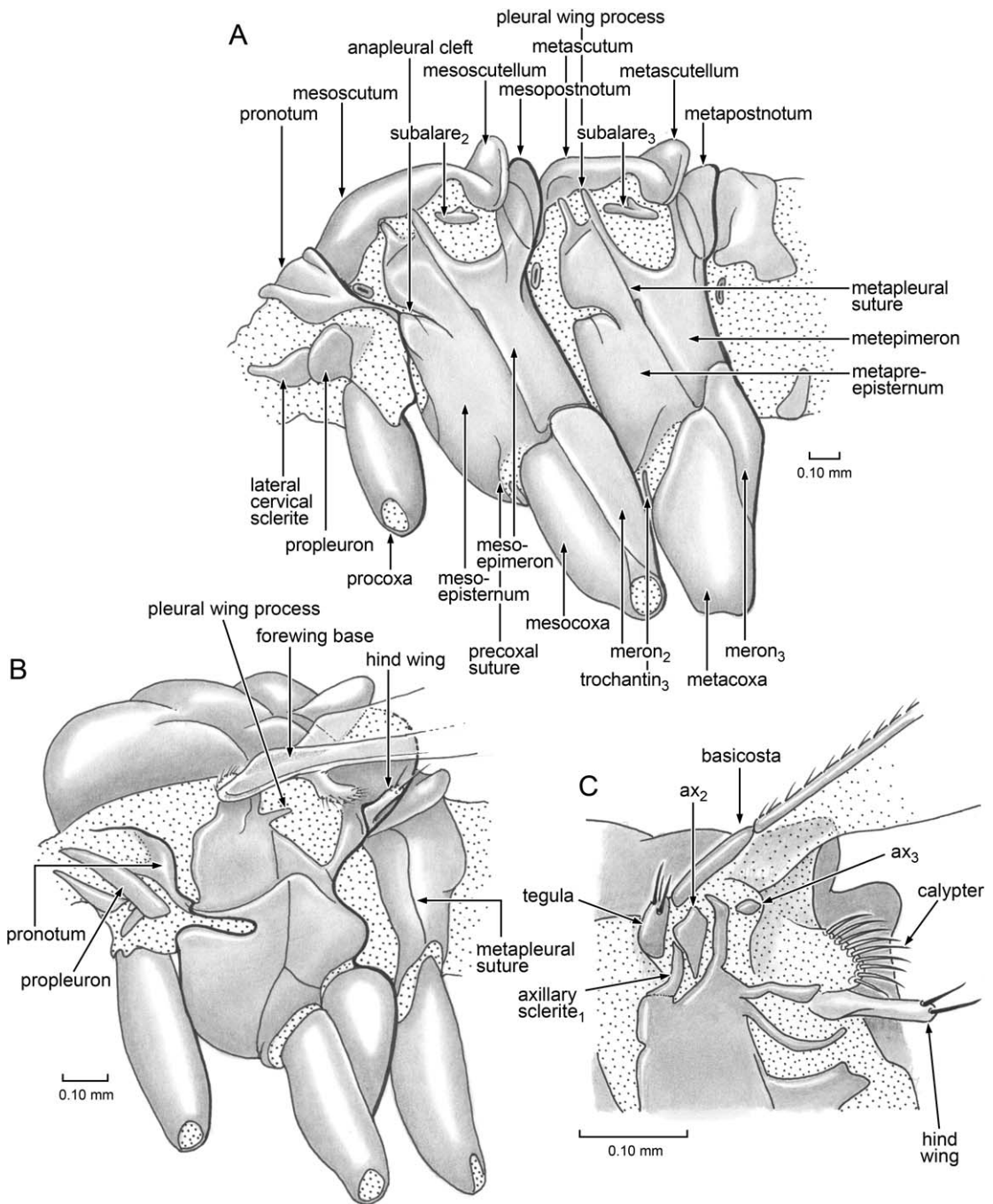
FIGURE 6. Thoraces of Mecoptera. **A.** *Nannochorista* (Nannochoristidae) (redrawn from Friedrich and Beutel, 2010). **B.** *Parapolycentropus paraburmiticus* (original). **C.** Detail of wing base, based on specimen JZC Bu542A. Note differences in scale. Bold lines indicate divisions between pro-, meso-, and metathoraces.
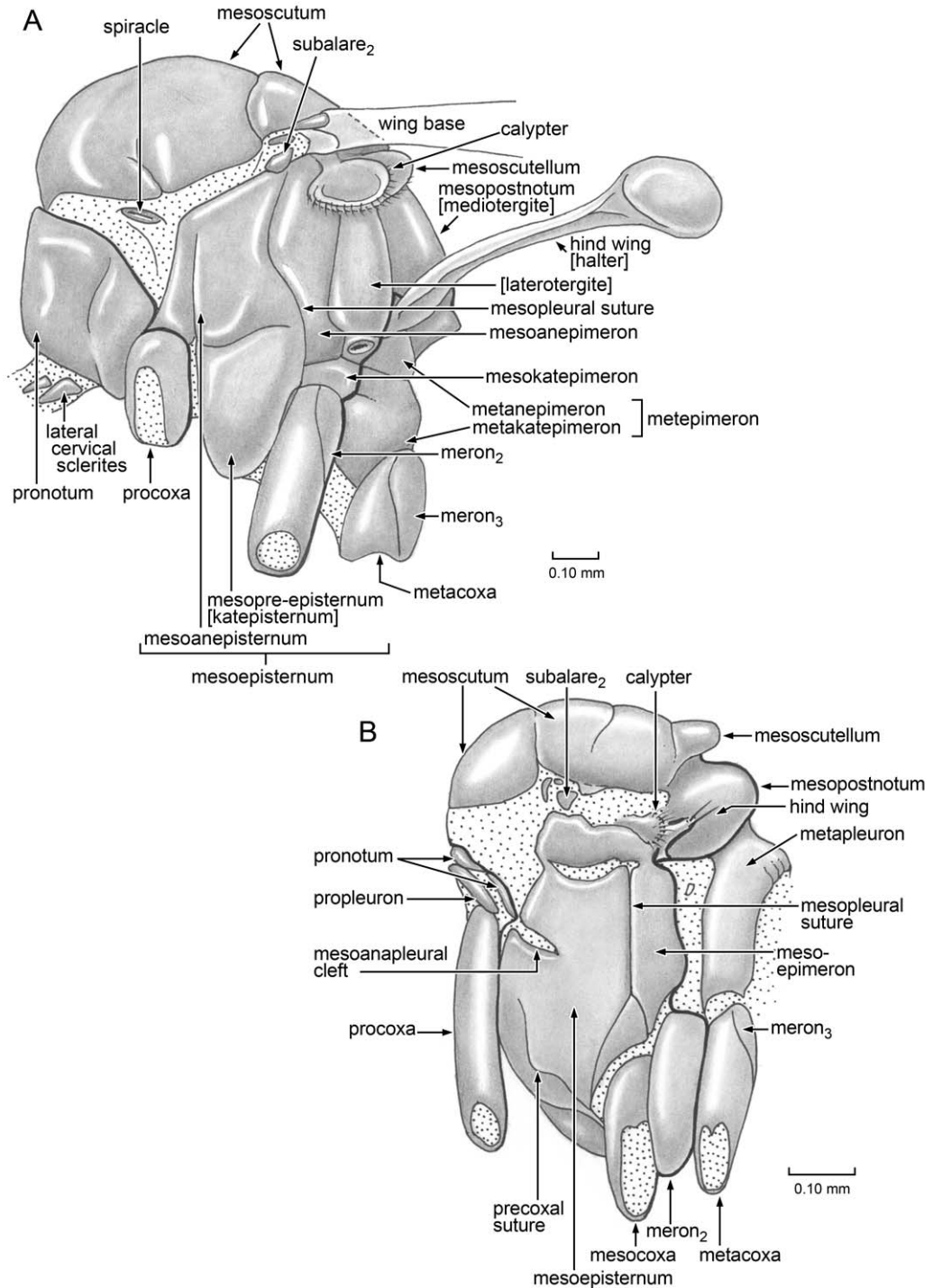
FIGURE 7. Thoraces of Diptera (A) and *Parapolycentropus burmiticus* (B). **A.** *Limonia* sp. Words in brackets are terms alternatively used in dipterology. **B.** *Parapolycentropus burmiticus.* Note differences in scale; bold lines indicate divisions between pro-, meso-, and metathoraces.

Abdomen and Terminalia

Abdomen. This body tagma is long and slender in *Parapolycentropus*, but may have been capable of significant distension. As reported earlier (Grimaldi et al., 2005), the tergites of this genus are fairly typical for Mecoptera, but the sternites are highly reduced. Moreover, we can now report that there is sexual dimorphism in the reduction of the sternites and some tergites. In females, abdominal segments I and II lack both tergites and sternites; segments III–VI lack just sternites; and segment VII has a small sternite. In males, there is a small, narrow sternite on each of segments I–V; the long axis of these sternites is aligned with the length of the abdomen (fig. 8A). Sternite VI in males is a narrow transverse sclerite, and sternite VII is either lost or concealed by a very large, V-shaped sclerite that is either stVIII or the basistylus, or both (fig. 8A). Spiracles were observable in JZC Bu148, lying in the membrane at the anterolateral edges of tergites II–V (they are probably present on more distal segments, but were not observable). The extensive membrane covering the ventral half of the abdomen is suggestive of considerable distension, though none of the specimens we have seen had an abdomen distended to the extent one might find, for example, in a replete mosquito. In *P. paraburmiticus* the lateral surfaces of the abdominal membrane have minute, sclerotized, setigerous spots.

Female Terminalia. These structures were described in detail for *Parapolycentropus* by Grimaldi et al. (2005), with some additional details and comments provided here based on several new specimens that are extremely well preserved (figs. 8C–E). Essentially, the cercus segmentation and position of tergite XI in *Parapolycentropus* does not correspond to any basic structure found in Recent Mecoptera, as presented by Mickoleit (1975, 1978). Specifically, *Parapolycentropus* has a small tXI separated from and lying between the bases of the cerci, as in the basal family Nannochoristidae, but the cerci of *Parapolycentropus* are only 2-segmented (vs. 3-segmented in Nannochoristidae). In Apteropanorpidae, Choristidae, Meropeidae, *Notiothauma*, and Panorpidae + Panorpodidae, the pair of basal cercomeres are either partly or completely fused into a basodorsal sclerite that lies over and obscures tergite XI (Mickoleit, 1975, 1978). The plesiomorphic condition in Diptera is the possession of two cercomeres; no Diptera have three such segments, and higher Brachycera have just one cercomere. The most interesting aspect of *Parapolycentropus* female terminalia concerns the modifications of the preapical segments. In *P. paraburmiticus* (JZC Bu274), segments VIII and IX almost form a capsule. Abdominal tergite VIII is fairly standard (somewhat smaller than ones anterior to it); tergites IX and X are significantly smaller, tX actually forming a ring of approximately 270°. Sternite IX has a posterior margin that is formed into a deep, V-shaped incision. A complete proctiger is present, formed by small, opposing tXI and sXI.

Male Terminalia. These structures are newly reported here (e.g., fig. 8B), since in the original report (Grimaldi et al., 2005) well-preserved males of *Parapolycentropus* were not available. The genus possesses many generalized genitalic features common throughout Mecoptera: Tergite IX is large, flattened, and shieldlike, lying dorsally over other portions of the terminalia; a pair of 1-segmented cerci are present, as is a complete but small epi- and hypoproct (tXI and sXI); the cerci and epi/hypoprocts are attached to extensive membrane; the gonostylus is well developed, strongly upturned, and divided into a stout, large, V-shaped basistylus and
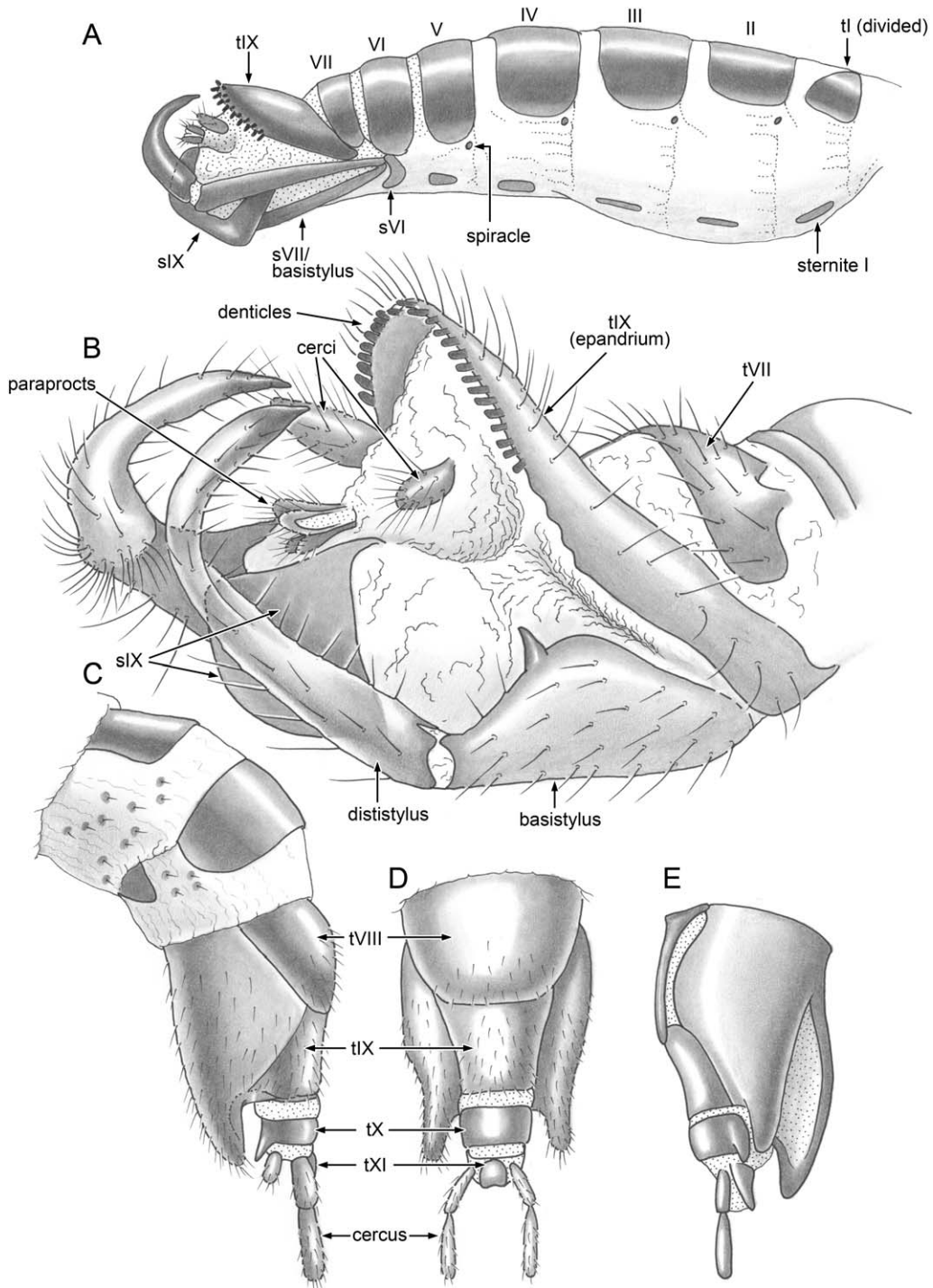
FIGURE 8. Abdomens and terminalia of *Parapolycentropus paraburmiticus*. **A.** Abdomen with male terminalia, based largely on JZC Bu148. **B.** Male terminalia of JZC Bu81. **C–E,** Female terminalia of JZC Bu274, three views. **C.** Left lateral. **D.** Dorsal. **E.** Ventrolateral.
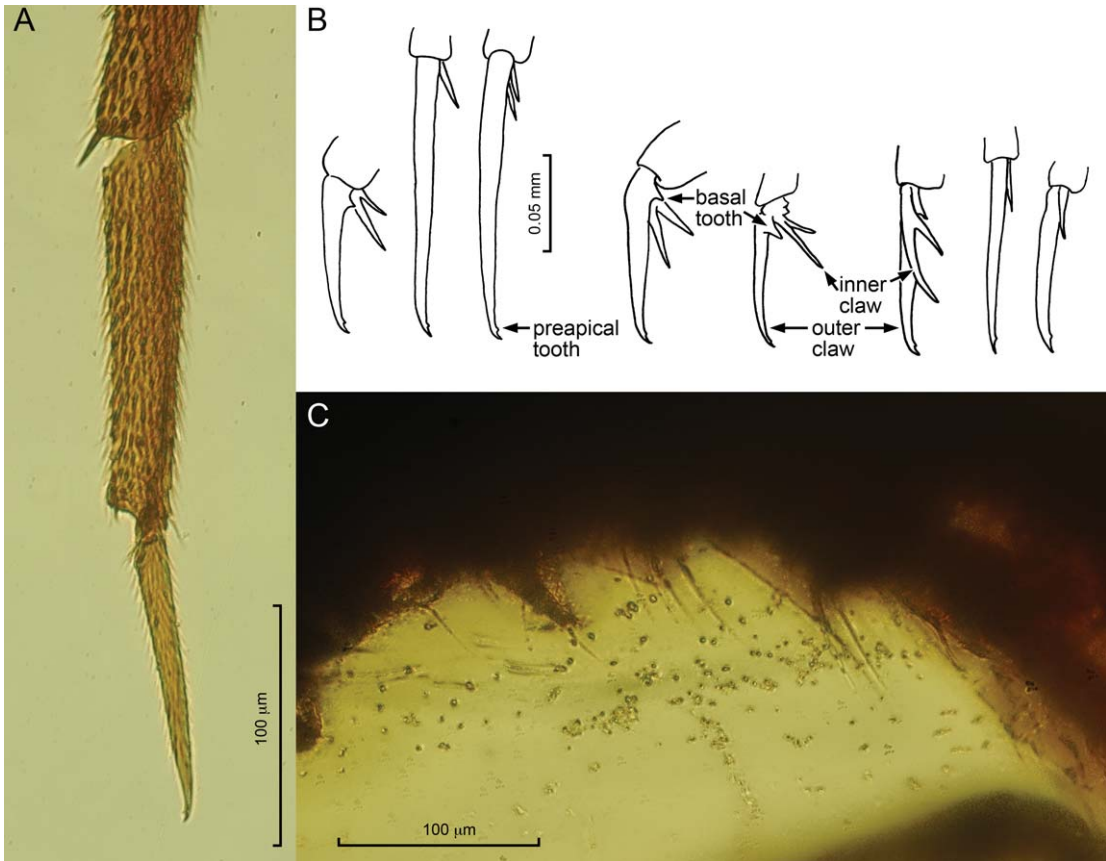
FIGURE 9. Assorted details of *Parapolycentropus paraburmiticus*. **A.** Distitarsus and pretarsal claw of JZC Bu148, lateral view (Z-stacked compound photomicrograph, 200×). **B.** Drawings of pretarsal claws of representative specimens: pro-, meso-, and metathoracic claws of JZC Bu273; prothoracic claws of JZC Bu80 and JZC Bu81, showing basal tooth; and pro-, meso-, and metathoracic claws of JZC Bu542A. **C.** Ventral margin of middle of abdomen showing small grains, JZC Bu148 lateral view (Z-stacked photo using compound microscope at 200×).

more slender dististylus; and sIX is large and rounded apically. Specialized features of the *Parapolycentropus* terminalia include a row of nearly 30 peglike denticles along the posterior margin of tIX, a spine on the basistylus on the dorsomesal surface, reduced size of the cerci, and long, recurved dististyles (fig. 8B).

DISCUSSION

Relationships. The male terminalia of *Parapolycentropus* are surprisingly similar in many respects to those of the specialized Recent family Boreidae (see, e.g., Crampton, 1931; Penny, 1977; Willmann, 1981). In Boreidae, the posterior margin or portion of tIX also possesses black denticles, though they occur only sometimes in a row along the posterior edge, otherwise they are clustered near this edge. The dististyles of Boreidae are also

upturned (but not as long as in *Parapolycentropus*, nor recurved), and they are lobed and often dentate (in *Parapolycentropus* they are simple). In both groups sIX is large and forms a shallow cup to dorsal structures. Male cerci are reduced in size in *Parapolycentropus*; they are lost in Boreidae. Lastly, and quite significant, the aedeagus in the Boreidae and in *Parapolycentropus* is a bulbous, membranous, eversible structure with a small dorsolateral sclerite. This is clearly seen in the everted aedeagus of specimen JZC Bu273 (fig. 1D). In a taxon that is otherwise highly modified, the male terminalia of *Parapolycentropus* provide rare evidence of relationships. Despite their highly specialized morphology, the Boreidae are generally considered to have a basal position among the extant, crown-group families of Mecoptera (Grimaldi and Engel, 2005). They have been hypothesized to be either a sister group to the Siphonaptera (Whiting, 2001), or near the base of Mecoptera after the Nannochoristidae (Willmann, 1989; Friedrich et al., 2013).

Stylate Mouthparts. Given the very fine, rigid, styletiform structure of the proboscis, there is little doubt that *Parapolycentropus* fed on fluids, which it obtained partly or wholly by piercing. A diet of animal fluids and nectar is hardly contradictory, since in many species of insects with styletiform mouthparts they feed on hemolymph or blood as well as nectar, the best-known example involving mosquitoes. In Culicidae the females typically feed on vertebrate blood (required for vitellogenesis), and males feed on nectar. Other examples of hematophagous or hemolymph-feeding Diptera that also feed on nectar include some Ceratopogonidae, some Empididae (especially long-tongued taxa), and long-tongued Tabanidae (especially pangoniines). In such cases, the sexual differences in diet are also manifest in the fine structure of the piercing structures, but other than a slightly shorter proboscis in *P. paraburmiticus* (table 1), *Parapolycentropus* males and females have no differences in hypopharynx serrations. The question is: Did these scorpionflies feed on insect hemolymph or vertebrate blood? Evidence from other body structures is suggestive of an insectivorous diet.

Thoracic and Wing Structure. The overall body structure of *Parapolycentropus* is extremely similar to that of many nematocerous Diptera: a generally gracile body with a slender abdomen; long, thin legs; a compact thorax comprised almost entirely of mesothorax; and great reduction of the hind wings. In Diptera, the halteres are commonly viewed as gyroscopic organs that help stabilize the insect against pitch and roll, but these largely serve as sophisticated sensory organs that detect slight changes in body orientation (Nalbach and Hengstenberg, 1994; Dickinson, 1999). Halteres and halterlike structures have evolved convergently in male Coccoidea (Hemiptera) and male Strepsiptera. In Strepsiptera the halteres are the reduced forewings, and they too serve in equilibrium reflexes (Pix et al., 1993); male coccoids have the hind wing reduced to a hamulohaltere, so-named for the minute apical hamuli that couple this structure to the fully developed forewing (the setae at the apex of the vestigial hind-wing lobe in *Parapolycentropus* are not hooked; almost certainly they did not couple with the forewings). In most groups of insects where the hind wing is reduced it is usually coupled to the forewing by hooks (e.g., the hamuli in Hymenoptera), but in very few other insects is one pair of wings fully developed and the other pair almost entirely lost as

in *Parapolycentropus*. Two such groups are minute parasitoid Hymenoptera, the extant family Mymaridae and an extinct family known only in Cretaceous amber, the Spathiopterygidae. The flight mechanics of *Parapolycentropus* is an interesting consideration.

The complete loss of an anal and jugal lobe of the forewing, and the extent of membranous area of the pteropleuron is suggestive of substantial thoracic distortion and wing-base mobility. We suggest that *Parapolycentropus* could probably fly with considerable maneuverability. Moreover, these scorpionflies may have swarmed, as based on specimen JZC Bu1433, a piece that contains three males in close proximity (the piece also contains seven small nematocerans [prey?]) (fig. 3A). *Parapolycentropus* is somewhat rare in Burmese amber, a specimen found in approximately every 500 inclusions, so the probability of finding three individuals (males) based on chance alone is rather remote. While mecopterans can be found in large aggregations, they do not engage in male mating swarms as do many nematocerans (Downes, 1969). *Parapolycentropus* may have been a nematoceran analogue in more than just morphology. It should be noted that the specimens in amber piece JZC Bu1433 are distinctively small, similar in body size and proportions to specimens JZC Bu1121 and JZC Bu1329 (table 1). However, male terminalia of JZC Bu1433 show no differences with that of *P. paraburmiticus*, and all of these may just be individuals at the smallest end of the size distribution.

Large Claws. In the postmortem condition of many of the *Parapolycentropus* specimens (e.g., figs. 1–3), the mid and hind legs are held slightly forward and curved slightly upward, which would seem adaptive for the aerial capture of insect prey. However, many gracile, long-legged nematocerans in amber have this posture, including ones that are not insectivorous (e.g., Lygistorrhinidae: Sciaroidea). The large, single claw found on the mid and hind tarsi in *Parapolycentropus paraburmiticus* is quite distinctive (figs. 9A, B), and it may reflect an insectivorous diet. Indeed, the only Recent family of Mecoptera that is truly predatory is the Bittacidae (all other families are either saprophagous, phytophagous, or scavengers [Byers and Thornhill, 1983; Penny, 2006]), and in this family there is also a single, large pretarsal claw, but on the metatarsus. The common name of bittacids, "hanging flies," derives from their habit of hanging from a stem by their fore- and midlegs and using the hind tarsi to snag passing insects. The bittacid hind tarsus is curled against itself, making it prehensile. While none of the *Parapolycentropus* specimens have the tarsi curled, this does not preclude that the large pretarsal claw could not fold, like a jackknife, against the distitarsus.

Evidence that best supports an insectivorous diet of *Parapolycentropus* lies in a group nosee-um midges (Ceratopogonidae) that has convergently developed large claws, specifically the more derived subfamily Ceratopogoninae (e.g., Borkent, 1995, 2000). Basal lineages of Ceratopogonidae feed on vertebrate blood, but in ceratopogonine females that have large claws they are predators of small midges and other insects of approximately similar size (e.g., Downes and Wirth, 1981: figs. 28.71–28.97) (an exception is *Palpomyia*, which feeds on small Ephemeroptera). In all cases, the female ceratopogonid feeds on the hemolymph of its prey (sometimes even of its mate), using styletiform mandibles and laciniae to puncture the body and siphon hemolymph. The enlarged claws of insectivorous ceratopogonines are usually strongly curved, have a sharp basal tooth, and occur in pairs (though one claw of the pair can be reduced in size), a condition that *Parapolycentropus* shares.

Reduced Sternites, Distensible Abdomen. With little question, the highly reduced sternites in *Parapolycentropus* allowed the abdomen to distend considerably. Such sternite reduction is unique in Mecoptera, and so would seem to be related functionally to other unique features of the genus, particularly the claws, proboscis, and two-winged flight. In perhaps all cases of gross enlargement of the abdomen in arthropods it occurs in groups that feed on blood or hemolymph. Notable examples include ticks (Acari: Ixodida); cimicid bugs; some fleas (i.e., Tungidae); some hematophagous midges such as Phlebotominae (Diptera: Psychodidae) and assorted Culicomorpha, like mosquitoes (Culicidae); Hippoboscidae; and *Carnus* flies. A particularly instructive and perhaps analogous example concerns, again, Ceratopogonidae, this time of the subfamily Forcipomyiinae, which feed on the hemolymph of large insects like dragonflies, mantises, and stick insects. Female forcipomyiines attach to a membranous area of their host, or a wing vein, their abdomens bloating to several times the original size with hemolymph (which is the origin of their common name "stick ticks"). While sternite reduction is not a necessary condition for abdominal distension (many of the groups above have unmodified sternites, including forcipomyiines), the degree of sternite reduction seen in *Parapolycentropus* signifies significant capability of distension.

Other Evidence. In the male specimen JZC Bu148 there are numerous minute, rounded particles in the amber that were captured while wafting away from the ventral portion of the abdomen (fig. 9C). These are suggestive of pollen or spores since they are rounded and uniform in diameter (whereas small bubbles and debris particles in amber vary in size). However, the grains are approximately 2–3 μm in diameter, which is about half the size of the smallest known angiosperm pollen (that of *Myosotis* spp., or forget-me-not flowers [Proctor et al., 1996]), and too small for high magnification (e.g., 400×) observation, so detailed structure could not be determined. Angiosperm and gymnosperm pollen grain size is most commonly in the 30–40 μm size (Cruden and Lyon, 1985; Proctor et al., 1996; Kirk, 1993). The small plume of grains in the amber adjacent to the scorpionfly apparently came from the insect, since the grains are denser near the insect and many grains are still attached to fine setae on the abdomen. It is possible that these grains are minute crystals of pyrite, which is often observed adjacent to amber inclusions in incipient stages of pyritization. This could eventually be tested using microanalytic chemical methods.

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REFERENCES

Beutel, R., and E. Baum. 2008. A longstanding entomological problem finally solved? Head morphology of *Nannochorista* (Mecoptera, Insecta) and possible phylogenetic implications. Journal of Zoological Systematics and Evolutionary Research 46: 346–367.

Borkent, A. 1995. Biting midges in the Cretaceous Amber of North America (Diptera: Ceratopogonidae). Leiden: Backhuys Publishers.

Borkent, A. 2000. Biting midges (Diptera: Ceratopogonidae) from Lower Cretaceous Lebanese amber with a discussion of the diversity and patterns found in other ambers. *In* D. Grimaldi (editor), Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey: 355–451. Leiden: Backhuys Publishers.

Byers, G.W., and R. Thornhill. 1983. Biology of the Mecoptera. Annual Review of Entomology 28: 203–228.

Crampton, G.C. 1931. The genitalia of male Diptera and Mecoptera, compared with those of related insects, from the standpoint of phylogeny. Transactions of the American Entomological Society 48: 207–225.

Cruden, R.W., and D.L. Lyon. 1985. Correlations among stigma depth, style length, and pollen grain size. Do they reflect function or phylogeny? Botanical Gazette 146: 143–149.

Cruikshank, R.D., and K. Ko. 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. Journal of Asian Earth Sciences 21: 441–455.

Dickinson, M.H. 1999. Haltere-mediated equilibrium reflexes of the fruit fly, *Drosophila melanogaster.* Philosophical Transactions of the Royal Society of London Series B Biological Sciences 1385: 903–916.

Downes, J.A. 1969. The swarming and mating flight of Diptera. Annual Review of Entomology 14: 271–298.

Downes, J.A., and W.W. Wirth. 1981. Ceratopogonidae. *In* J.F. McAlpine et al. (editors), Manual of Nearctic Diptera, vol. 1: 393–421. Ottawa: Research Branch Agriculture Canada Monograph 27.

Friedrich, F., and R.G. Beutel. 2010. The thoracic morphology of *Nannochorista* (Nannochoristidae) and its implications for the phylogeny of Mecoptera and Antliophora. Journal of Zoological Systematics and Evolutionary Research 48: 50–74.

Friedrich, F., H. Pohl, F. Beckmann, and R. G. Beutel. 2013. The head of *Merope tuber* (Meropeidae) and the phylogeny of Mecoptera (Hexapoda). Arthropod Structure and Development 42: 69–88.

Grimaldi, D.A., and M.S. Engel. 2005. Evolution of the insects. New York: Cambridge University Press.

Grimaldi, D.A., M.S. Engel, and P.C. Nascimbene. 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. American Museum Novitates 3361: 1–72.

Grimaldi, D.A., J.-F. Zhang, N.C. Fraser, and A. Rasnitsyn. 2005. Revision of the bizarre Mesozoic scorpionflies in the Pseudopolycentropodidae (Mecopteroidea). Insect Systematics and Evolution 36: 443–458.

Kirk, W. D. 1993. Interspecific size and number variation in pollen grains and seeds. Biological Journal of the Linnean Society 49: 239–248.

Labandeira, C.C., J. Kvaček, and M.B. Mostovski. 2007. Pollination drops, pollen, and insect pollination of Mesozoic gymnosperms. Taxon 56: 663–695.

McAlpine, J.F. 1981. Morphology and terminology – adults. *In* J.F. McAlpine et al. (editors), Manual of Nearctic Diptera, vol. 1: . 9–63. Ottawa: Research Branch Agriculture Canada Monograph 27.

Mickoleit, G. 1967. Das Thoraxskelet von *Merope tuber* Newman (Protomecoptera). Zoologisches Jahrbucher für Anatomie 84: 313–342.

Mickoleit, G. 1975. Die Genital- und Postgenitalsegmente der Mecoptera-Weibchen (Insecta, Holometabola). 1. Das Exoskelett. Zeitschrift für Morphologie der Tiere 80: 97–135.

Mickoleit, G. 1978. Die phylogenetischen Beziehungen der Schnabelfliegen-Familien aufgrund morpologischer Ausprägungen der weiblichen Genital- und Postgenitalsegmente (Mecoptera). Entomologica Germanica 4: 258–271.

Nalbach, G., and R. Hengstenberg. 1994. The halteres of the blowfly *Calliphora*. II. Three-dimensional organization of compensatory reactions to real and simulated rotation. Journal of Comparative Physiology A 175: 695–708.

Novokshonov, V.G. 1997. Early evolution of scorpionflies (Insecta: Panorpida). Moscow: Nauka Press. [in Russian]

Novokshonov, V.G. 2002. Order Panorpida Latreille, 1802. The scorpionflies. *In* A. Rasnitsyn and D.L.J. Quicke (editors), History of insects: 194–198. Dordrecht, Netherlands: Kluwer Academic Publishers.

Otanes, F.Q. 1922. Head and mouth-parts of Mecoptera. Annals of the Entomological Society of America 25: 310–322.

Penny, N.D. 1977. A systematic study of the Boreidae (Mecoptera). University of Kansas Science Bulletin 51: 141–217.

Penny, N.D. 2006. A review of our knowledge of California Mecoptera. Proceedings of the California Academy of Sciences 57 (9): 365–372.

Pix, W., G. Nalbach, and J. Zeil. 1993. Strepsipteran forewings are halterelike organs of equilibrium. Naturwissenschaften 80: 371–374.

Proctor, M., M. Yeo, and A. Lack. 1996. The natural history of pollination. Portland, OR: Timber Press.

Ren, D., et al. 2009. A probable pollination mode before angiosperms: Eurasian, long-proboscid scorpionflies. Science 326: 840–847 (+ online supporting material).

Ren, D., C.-K. Shih, and C.C. Labandeira. 2010a. New Jurassic pseudopolycentropodids from China (Insecta: Mecoptera). Acta Geologica Sinica 84 (1): 22–30.

Ren, D., C.C. Labandeira, and C.-K. Shih. 2010b. New Mesozoic Mesopsychidae (Mecoptera) from northeastern China. Acta Geologica Sinica 84 (4): 720–731.

Shi, G., et al. 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Research 37: 155–163.

Shih, C.-K., X. Yang, C.C. Labandeira, and D. Ren. 2011. A new long-proboscid Pseudopolycentropodidae (Insecta: Mecoptera) from the Middle Jurassic of China and its gymnosperm associations. Zookeys 130 (suppl.): 281–297.

Snodgrass, R.E. 1935. Principles of insect morphology. New York: McGraw-Hill.

Tillyard, R.J. 1919. Mesozoic insects of Queensland. 5. Mecoptera, the new order Paratrichoptera, and additions to Planipennia. Proceedings of the Linnean Society of New South Wales 44: 194–212.

Whiting, M.F. 2001. Mecoptera is paraphyletic: Multiple genes and a phylogeny for Mecoptera and Siphonaptera. Zoologica Scripta 31: 93–104.

Willmann, R. 1981. Das Exoskelett der maennlichen Genitalien der Mecoptera (Insecta). I. Morphologie. II. Die phylogeneticschen Beziehungen der Schnabelfliegen-Familien. Zeitschrift für Zoologische Systematik und Evolutionsforschung 19: 96–150.

Willmann, R. 1989. Evolution und phylogenetisches System der Mecoptera (Insecta, Holometabola). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 544: 1–153.

Zherikhin, V.V. and A. J. Ross. 2000. A review of the history, geology and age of Burmese amber (burmite). Bulletin of the Natural History Museum, Geological Series 56: 3–10.

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