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Collembola (Arthropoda, Hexapoda) from the mid Cretaceous of Myanmar (Burma)

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Abstract

A prior study involved 78 Collembola specimens preserved in Upper Cretaceous (Campanian) amber from Canada. This work deals with 109 specimens from the mid Cretaceous (Cenomanian or possibly slightly lower) of Myanmar, 37 of which have been identified to the generic level; 14 new species are described. Two species of the family Isotomidae are placed in previously described genera. One is placed in the Late Cretaceous genus *Protoisotoma* (*burma*), and one in the extant genus *Proisotoma* (s.l.) *pettersoni*. The remaining specimens are placed in 11 newly erected genera or as ''Incertae sedis'' taxa in the broadly construed families Sminthuridae, Isotomidae, and Neanuridae. The new genera are Sminthuridae (s.l.): *Grinnellia*, *Sminthuricinus*, *Mucrovirga*, and *Sminthurconus*; Isotomidae: *Villusisotoma* (two species, *V. brevis* and *V. longa*), *Burmisotoma*, *Propachyotoma*, and *Protodesoria*; Neanuridae (s.l.) *Protodontella*. Two new genera (*Praentomobrya* and *Cretacentomobrya*) are placed in a new family (Praentombryidae), which is similar to the modern family Entomobryidae. Most of the extinct genera are very similar to modern genera. This similarity, along with the occurrence of an extant genus, suggests that a greater proportion of the Collembola of Myanmar (Burma) survived the end-Cretaceous than did taxa in Canada, even though the former are approximately 30 Ma older.

Keywords: Collembola; Springtail; Cretaceous; Myanmar, Burma; Taxonomy; Taphonomy; Amber; Cenomanian-Turonian; Isotomidae; Neanuridae; Sminthuridae; Entomobryidae

1. Introduction

The fossil history of the Collembola (springtails) extends from the Early Devonian (Hirst and Maulik, 1926) to the Pleistocene (Yosii, 1974). Unfortunately, there are remarkably few fossil records of Collembola over this long interval (Christiansen and Pike, 2002). Due to their small size and lightly sclerotized cuticle, Collembola do not readily fossilize as compression fossils in rock, even though their predilection for moist environments should facilitate preservation in lacustrine sediments. Their fossilization requires encapsulation in such materials as chert and amber. Christiansen and Pike (2002) described eight new genera and one new family in Campanian Canadian amber and redescribed the single previously known Mesozoic specimen. The senior author is presently studying a small collection by Dany Azar from the Lower Cretaceous of Lebanon. From the Cenozoic only four fossil deposits that bear Collembola have been recorded: the mid-Eocene Baltic amber; lower Miocene amber from Chiapas, Mexico, and from the Sierra Septentrional of the Dominican Republic; and Pleistocene amber from Mizunami, Japan.

The present study involves 122 specimens from the Mid Cretaceous amber of Myanmar (Burma): 12 specimens were fragments identifiable only as probable Collembola; 62 specimens were identifiable only to family or superfamily level (see Table 1); 34 specimens could be identified, at least tentatively, to genus, and 8 of these could be placed in previously described genera (1 extinct, 1 extant). The remaining specimens were placed in one of 11 undescribed extinct genera; 2 of these could not be placed in any family, and so a new family is created for these genera.

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Table 1
Specimens and genera: Myanmar Cretaceous Collembola examined

Specimens seen	Specimens identifiable to genus	New genera	Upper Cretaceous genera	Extant genera	
Sminthuridae					
36	11	4	0	0	
Isotomidae					
33	16	5	1	1	
Poduromorpha					
36	4	1	0	0	
Entomobryomorpha					
4	3	2	0	0	
Tomoceridae					
1	0	0	0	0	
Identifiable only as Collembola					
12	0	0	0	0	
122	34	12	1	1	totals

2. Material and methods

All except three of the specimens examined were from the paleoentomological collections of the American Museum of Natural History, and were recovered by David Grimaldi and the junior author from that institution. These specimens were mined from lignitic seams near the village of Tanai on the Ledo Road in the Hukawng Valley in Kachin State, Myanmar (Grimaldi et al., 2002). The age of these deposits remains in question. They have been considered to be of Cenomanian-Turonian age based on a comparison of their insect inclusions to those in other Cretaceous amber deposits that are better studied stratigraphically. A recent study based on minimal palynological samples and one ammonite indicates a late Albian age (Cruickshank and Ko, 2003). The location, nature, history of exploitation and significance of these deposits is extensively discussed in Grimaldi et al. (2002).

The specimens were recovered from bags of crude amber purchased from the Leeward Corporation (Grimaldi et al., 2002). The pieces were first washed with hydrochloric acid to dissolve calcite seams and coatings found on many samples. They were then lightly polished to create ''windows'' for observation, after which they were embedded in an epoxide resin under vacuum for better viewing and conservation (following the protocols set forth in Nascimbene and Silverstein, 2000); the treated pieces were trimmed and polished. The junior author further trimmed each sample into even smaller, thinner sections, and finely polished the specimens, because our study indicated a need for exceptionally close viewing. Two specimens, also from the Hukawng Valley, were from Edward Pike. All specimens were examined with two different phase contrast microscopes, normal light microscopy, a phase-interference microscope, and a confocal microscope, as well as a dissection microscope. It is a remarkable feature of the amber Collembola that any specimen looks different under each microscope we used. Thus, it was impossible to include all observed features in any one drawing, since these were observed using multiple microscopy techniques. Our choice of microscope used for drawing was limited by the fact that only one phase contrast microscope had a drawing tube. Drawings of features visible but unclear under this microscope were altered based on what was visible under other microscopes. Features not visible under the drawing arm microscope but seen with other microscopes were included in the descriptions. This state of affairs indicates that it is important in studying amber Collembola not to limit examination to a single microscopic technique. All measurements are in millimeters. Photomicrography was done with a Nikon D-1 digital camera attached to a Nikon compound microscope.

Many inclusions in Burmese amber typically are distorted by compression, sometimes extremely so, and even disarticulated. Much compression and distortion was evident in these small, soft-bodied specimens in Burmese amber, likely due to specific taphonomic factors. Compression and disarticulation are common artifacts of arthropods in Burmese amber. This was shown by the fact that only 36% of the specimens here studied were identifiable to genus (see Table 1), in contrast to 80% of those in the Canadian Cretaceous amber. Even the specimens identifiable to genus left many important anatomical structures unseen or questionable. One result has been the placement of many specimens as Incertae sedis.

3. Systematic descriptions

Note: In our descriptions, the terms $1+1$, $4+4$, etc., are used to indicate bilaterally symmetrical organs.

Family: Sminthuridae s.l. Lubbock, 1862

Remarks. The family Sminthuridae as defined by Lubbock remained constant for over 100 years although a number of subfamilies were subsequently created. Many of the subfamilies have been raised to family status or otherwise treated but we prefer to use the traditional classification to make placement easier and more readily comparable to other studies of fossil Collembola. In addition, many of the criteria used to distinguish these subfamilies are not visible on the Burmese amber specimens.

This family is well represented in the Burmese material. We examined 37 members of this family. Regrettably, only 11 of these were identifiable to genus; the remaining 26 specimens are discussed under ''Incertae sedis''. The specimens we have seen are quite similar to Sminthuridae recovered from Eocene and younger rocks. This similarity contrasts with the few Sminthuridae seen in the Upper Cretaceous Canadian amber. A comparison of the salient measurements of the described genera is shown in Table 2.

All specimens are deposited in the American Museum of Natural History.

Genus *Grinnellia* gen. nov.

Derivation of name. *Grinnellia* after Grinnell College, which has supported this and much other Collembola research.

Table 2
Myanmar Cretaceous Sminthuridae other than sample 1079 (measurements in mm)

Sample and specimen	Cephalic diagonal	Antennal segment 4	Antennal segment 3	Antennal segment 2	Antennal segment 1	Body	Hind tibiotarsus	Hind femur	Hind trochanter	Manubrium	Dens	Mucro
Grinnellia holotype	0.240	0.152	0.034	0.026	0.018	0.435	0.073	0.038	0.027	0.110	0.195	0.057?
Grinnellia?	?	?	?	?	?	?	0.23	0.10	0.075	0.13	0.20	0.070
Mucrovirga holotype	0.250	0.195	0.105	0.050	0.030	0.365	0.11	0.07?	?	0.10	0.190	0.065
Mucrovirga paratype	0.25	?	0.095	?	?	0.525	0.24	?	?	0.15	0.20	0.045
Sminthuricinus holotype	0.255	0.290	0.100?	?	?	0.62	0.24	0.102	0.077	0.125	0.190	0.073
Sminthuricinus paratype	0.225?	0.290?	0.098	0.07	0.055	0.525	0.24	0.10	0.072	0.115	0.215	0.070
Sminthuricinus? 1452C specimen 1	0.240	0.275	0.150	0.070	?	0.475	0.225	0.082	0.064	0.115	0.175	0.065
Sminthuricinus? 723 specimen 6	0.35	0.30?	0.13?	?	?	0.515	0.310	0.130	0.103	0.165	0.250	0.104
Sminthuricinus? 810B	0.240	0.20	0.07	?	?	0.61	0.195?	0.117?	0.065?	0.11	0.19	0.08
Sminthurconus holotype	0.31	0.325	0.156	0.086	0.073	0.60	0.208	0.107	0.088	0.125	0.210	0.068
Sminthurconus paratype	0.240	0.275	0.150	0.070	?	0.475	0.225	0.082	0.064	0.115	0.175	0.065
Sminthurconus? 853	0.210?	?	?	?	?	0.40?	0.185	0.095	0.065?	?	0.135?	0.050
Incertae sedis other than sample 1079												
027	0.29	?	0.125	0.085	?	0.50	0.225	0.105	0.09?	0.15	0.19	0.057
071	?	0.285	0.095	0.060	0.045	?	?	?	?	?	0.18	0.08
151	0.25?	?	?	?	?	0.475?	0.235	0.09	0.107	?	0.195	0.068
457 A	0.270?	0.20?	0.125	0.055	0.04	0.45?	0.20?	0.095	0.065	?	0.20	0.055
474 specimen 1	0.225	0.160	0.065	0.045	?	0.30?	0.15	?	?	?	0.165	0.048
474 specimen 2	?	?	?	?	?	?	?	?	?	?	0.20?	0.075
818A1 specimen 2	?	?	?	?	?	?	?	0.100	0.075	0.20	0.23	0.105
854 B	?	~0.31	0.109	?	?	?	0.260	0.143	0.078	?	?	?
992	0.20	?	0.105	0.050	0.030	0.30	?	?	?	0.10	0.180	0.060
1069	0.250	0.215	0.100	0.065	?	0.34	?	?	?	?	0.185	0.050

Type species. *Grinnellia ventis* sp. nov., mid Cretaceous, Myanmar (Burma).

Diagnosis. The genus *Grinnellia* can be distinguished from all other extant or extinct Symphypleona by the combination of a trochanter more than 60% as long as the femur and by the large cephalic and body spines and absence of clavate tenent hairs.

Included species. Type species only.

Remarks. This genus bears a remarkable superficial similarity to the extant genus *Pararrhopalites* Bonet and Tellez (1947). The distribution of the cephalic and body spines, the antennal structure, and the foot complex are all very similar to species of *Pararrhopalites* illustrated by Betsch (1980) and others. *Grinnellia* also has the entire mucronal apex and long bothriotrix A of this genus but differs in the absence of numerous anterior dental setae characteristic of the tribe Sminthurini. The large trochanters and the peculiar cheek pouches distinguish it from *Pararrhopalites* as well as most other Sminthurini. The large hind trochanters are most similar to the genus *Spatulosminthurus* Betsch and Betsch-Pinot (1983), but *Grinnellia* lacks the spatulate tenent hairs characteristic of *Spatulosminthurus*. The legs are much too obscured by the body to determine whether or not a trochanteral spine is present with transmitted or confocal microscopy; however, under the highest magnification of the reflected light microscope a trochanteral spine can be vaguely seen in the distal part. This, along with the presence of a well-developed spine of the putative second specimen, makes it likely that this spine is present in *Grinnellia*. Unfortunately, the ommatidia are not clearly visible under any microscope but under the highest magnification of reflected light, it appears that the ommatidium patch is larger than that seen in *Pararrhopalites*.

Grinnellia ventis sp. nov.
Figs. 1A, 2–4

Derivation of name. Named for Summer Ventis, who prepared Fig. 1 and whose assistance in this and earlier amber studies has been very valuable.

Holotype. AMNH Bu 0117A specimen 2. American Museum of Natural History.

Type locality and stratigraphic horizon. Myanmar (Burma), Kachin State, Tanai Village (on Ledo Road, 105 km from Miyitkama); collected by Leeward Capitol Corp.; mid Cretaceous.

Material. Holotype and one possible fragment, same data as specimen 3.

Diagnosis. As for the genus.

Description. Body length 0.435 mm, and cephalic diagonal 0.24 mm. Organ sizes are shown in Table 2. The fourth antennal segment has ten subsegments (Fig. 3A). These subsegments have one whorl of large, slender, curved, acuminate

setae (which are ~ maximum width of subsegments), and some smaller setae. The second and third segments have scattered, somewhat shorter, acuminate setae. The vertex of head has 4 + 4 large, anteriorly curved spines (Fig. 2), which are associated with 3 + 3 heavy, less curved acuminate setae. Ommatidia are unclear but at least 2 + 2. The anterior face of head with numerous slender acuminate setae (Fig. 3A), ranging from 0.05 to 0.01 mm. The head has two lateral cheek-like bulging pouches (Fig. 2), which bear very small acuminate microsetae and are separated by a broad median ridge. The legs are mostly obscured by an opaque body mass and thus only clearly visible under a reflecting or dissecting microscope. The left side of the specimen has the best exposure of the legs (Fig. 3C) but the anterior leg of the right side is twisted underneath the body and over to the left side. Thus the only leg structures clearly visible are the distal ends of the tibiotarsus and the foot complex for all legs and the distal four-fifths of the tibiotarsus of the hindleg. The fore tibiotarsus appears to have numerous slender acuminate straight to slightly curved setae, the longest about as long as the widest width of the tibiotarsus. The anterior foot complex has a long slender unguis with no tunica and a narrow unguiculus with an apical filament exceeding the apex of the unguis. The distal inner end of the tibiotarsus bears a strongly inwardly curved acuminate seta, slightly thicker than the remaining setae. Only the outline of the mid-leg is visible and this is so angled that measurements are not possible. The mid-foot complex is unclear but appears to be similar to that of the foreleg. The hind trochanter is 68% as long as the longest measure of the hind femur and is clearly flexed at the joint between the two. The unguis is untoothed and with a basal tunica. The unguiculus is broad with a well-developed apical filament, which arises from its apex and reaches the level of the apex of the unguis. The distal part of the hind tibiotarsus has long slender acuminate setae, the longest of which are ~ twice as long as width of tibiotarsus. The greater abdomen and thorax are not clearly separated; both are equipped with large heavy spines. On the thoracic region, there are two pairs of spines, with an unpaired median spine between them. On the greater abdomen, there are long spines in three irregular transverse rows of four but spines are more irregularly distributed and vary in size on the posterior portion of the greater abdomen. Only one dorsal bothriotrix can be seen on the greater abdomen (Fig. 2). The lesser abdomen is sharply demarcated from the greater abdomen and projects upward, with an anterior (pair?) of bothriotricha (Fig. 2) and a few slender scattered dorsal slender setae. The ventral surface is equipped with numerous curved acuminate setae and a (pair?) of short, posterior bothriotricha. No subanal appendage is clearly seen on the holotype. The dentes have 8 dorsal but no ventral setae (Fig. 2B). The mucrones have a pair of narrow and weakly dentate lamellae.

Remarks. The only other possible specimen of this genus is specimen 3 in the same amber piece. Unfortunately, specimen 3 consists only of the posterior part of the abdomen (Fig. 3), several legs and the furcula. All save the furcula are cleared. This partial specimen shares with *Grinnellia* the weakly dentate mucronal lamellae and is one of two other specimens of Sminthuridae in all the samples studied that has this condition. It is also similar in having the hind trochanter about 70% as long as the femur, in having a similarly shaped fore foot complex and hind unguis, and by having a few large abdominal spines. It differs from the holotype of *Grinnellia* in having a possible small subanal appendage and in lacking an apical posterior unguiculus filament. It also has a clear distal trochanteral spine (Fig. 4A), not visible on the holotype. This specimen is somewhat larger than the holotype (mucro and dens 1.2 times as large). It is possible that the holotype is a subadult male, and that the spines seen on it are sexually dimorphic. Yet, since there is no evidence of a genital swelling on the holotype, this seems unlikely. The one hind unguiculus seen in specimen 3 appears to be truncate, but the apical filament could be broken off. The shared mucronal shape, the large abdominal spines, as well as the proximity of the specimens in the same amber piece, all make it seem likely that they represent the same taxon, but this remains unresolved.

Genus *Sminthuricinus* gen. nov.

Derivation of name. After the similarity to both Sminthurini and Sphyrothecini.

Type species. *Sminthuricinus decepta* sp. nov., mid Cretaceous, Myanmar (Burma).

Diagnosis. The presence of a heavy trochanteral spine places the genus in the subfamily Sminthurinae. The long antennae and symmetrical mucro apex are characteristic of the tribe Sminthurini. The weak separation between the greater and lesser abdomen, plus the and extremely elongate hind trochanter; distinguish the genus from most genera of the subfamily. The latter feature is similar to some species of the genus *Spatulosminthurus* and to the herein described *Grinnellia*. The new genus lacks the strongly clavate tenent hairs and crenulate mucro found in *Spatulosminthurus* and the heavy, large cephalic and body spines of *Grinnellia*.

Included species. Type species only.

Remarks. There are peculiar mushroom-shaped structures on the head of the holotype that are almost certainly taphonomic artifacts. An identical structure can be seen on the holotype of a new genus of the superfamily Entomobryoidea. A second artifact close to one of the mushroom-shaped structures, at first appears to be an antenna but closer examination shows that it lacks all structures characteristic of antennae (Fig. 5C). They may represent some fungal growth not seen on modern Collembola. This genus has characteristics of both the Tribes Sminthurini and Sphyrothecini, such as long antennae, the symmetrical mucro apex characteristic of the former, and an elongate trochanter found in some members of the Sphyrothecini. While it has no anterior dental setae, it possesses something similar to the mesothoracic tubercle typically found in many genera of Sphyrothecini, as well as the

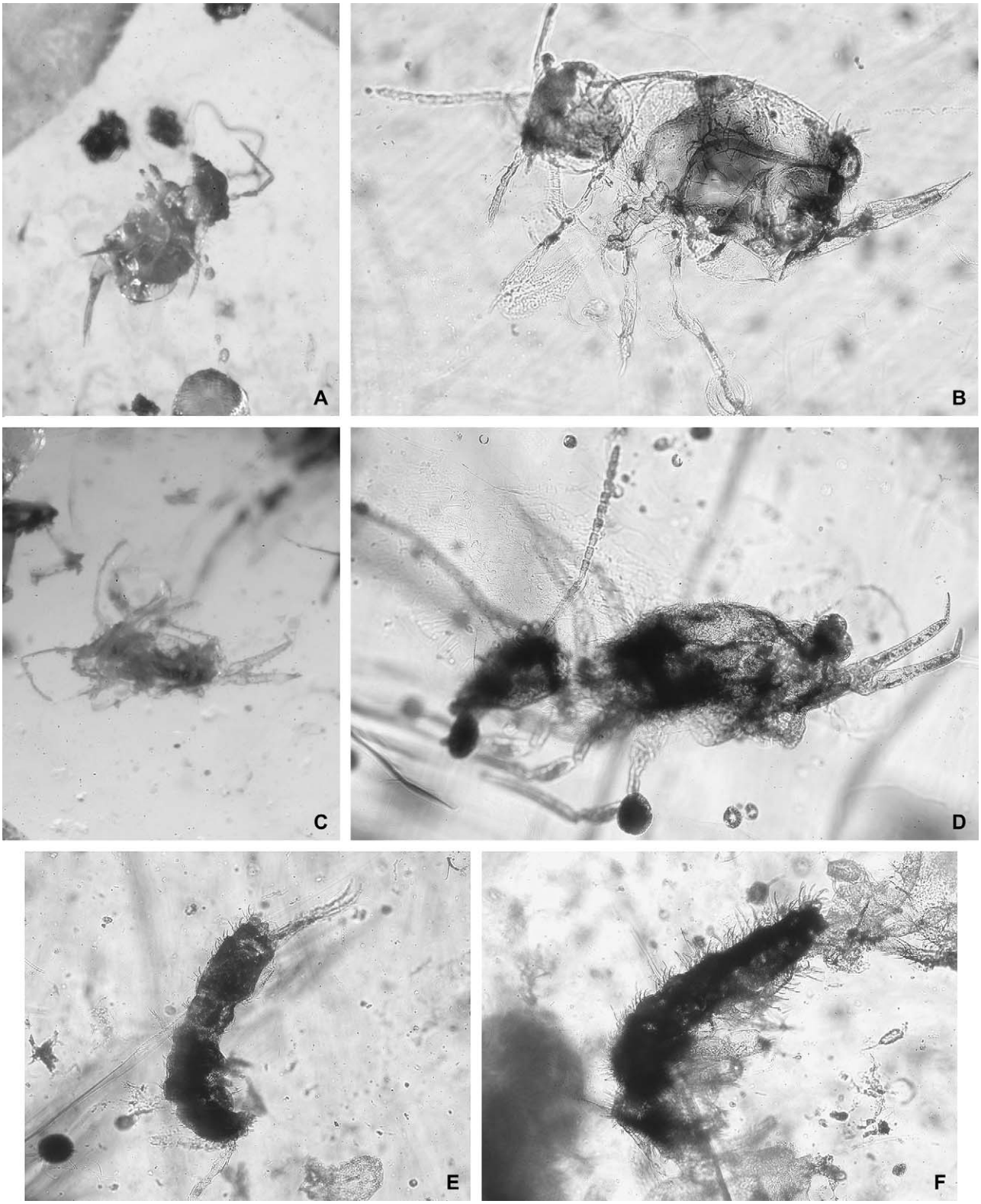

Fig. 1. Habitus of holotypes (total length of specimen exclusive of appendages in mm). A, *Grinnellia ventis* sp. nov. (0.61 mm). B, *Sminthuricinus decepta* sp. nov. (0.78 mm). C, *Mucrovirga incompleta* sp. nov. (0.35 mm). D, *Sminthurconus grimaldi* sp. nov. (0.90 mm). E, *Villusisotoma brevis* sp. nov. (0.565 mm). F, *Villusisotoma longa* sp. nov. (0.961 mm).

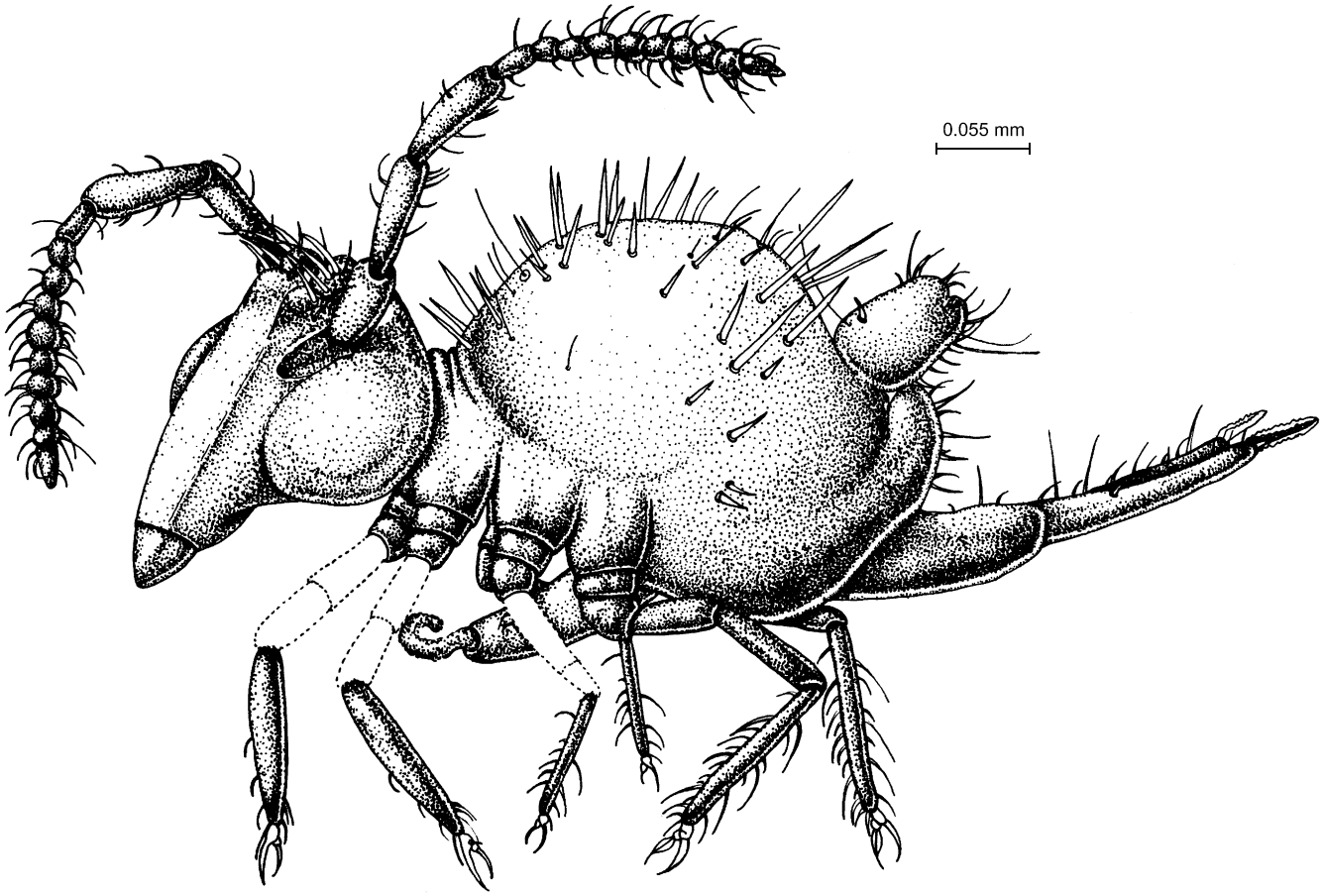

Fig. 2. *Grinnellia ventis* sp. nov. Probable appearance in life (most setae omitted).

small number of short outer tibiotarsal setae that are also associated with Sphyrothecini. The weakly demarcated lesser abdomen and posterior bothriotricha are found in neither tribe. The inability to see a clear subanal appendage may be a result of the condition of the specimens; however, the lateral view presented by the lesser abdomen in the holotype would appear to be ideal for seeing a subanal appendage and many acuminate setae can be seen in the area. There is a slender, truncate seta in the appropriate position for a subanal appendage but it lacks any swollen socket or other feature characteristic of this organ.

Sminthuricinus decepta sp. nov.
Figs. 1B, 5, 6

Derivation of name. Referring to the deceptive mushroom-like artifacts.

Holotype. AMNH Bu 810 A, American Museum of Natural History.

Type locality and stratigraphic horizon. Myanmar (Burma), Kachin State, Tanai Village (on Ledo Road, 105 km from Miyitkama); collected by Leeward Capitol Corp.; mid Cretaceous.

Material. Holotype plus three possible congeneric specimens: AMNH Bu 145A, AMNH Bu 723C specimen 6 and AMNH Bu 810 B. All have the same locality and stratigraphic horizon as the holotype.

Diagnosis. As for the genus.

Description. Body length 0.6 mm, head length 0.27 mm. Organ sizes are shown in Table 2. The body and at least posterior parts of head have short, blunt spines (Fig. 5B). Only bothriotricha C and D can be seen, and both are on the greater abdomen. In addition, only the fourth antennal segment can be seen clearly on the holotype (Fig. 5C), but the apex of the third segment has no setae or other features clearly visible. The fourth antennal segment bears 11–12 subsegments with about 15 (ca. 0.03 mm long) straight to slightly curved, smooth acuminate setae, that are either attached or in the immediate vicinity of the segment. The segment is distinctly longer than the cephalic diagonal. At least five ommatidia can be seen on one side. The prothorax has a small fleshy projection with no setae and a slightly swollen apex attached to the coxal region of one foreleg. The greater abdomen bears numerous short, apically rounded, cylindrical spines. Bothriotrix C is in the normal position, but D is attached to the posterior margin of the greater abdomen. The lesser abdomen is 20% as

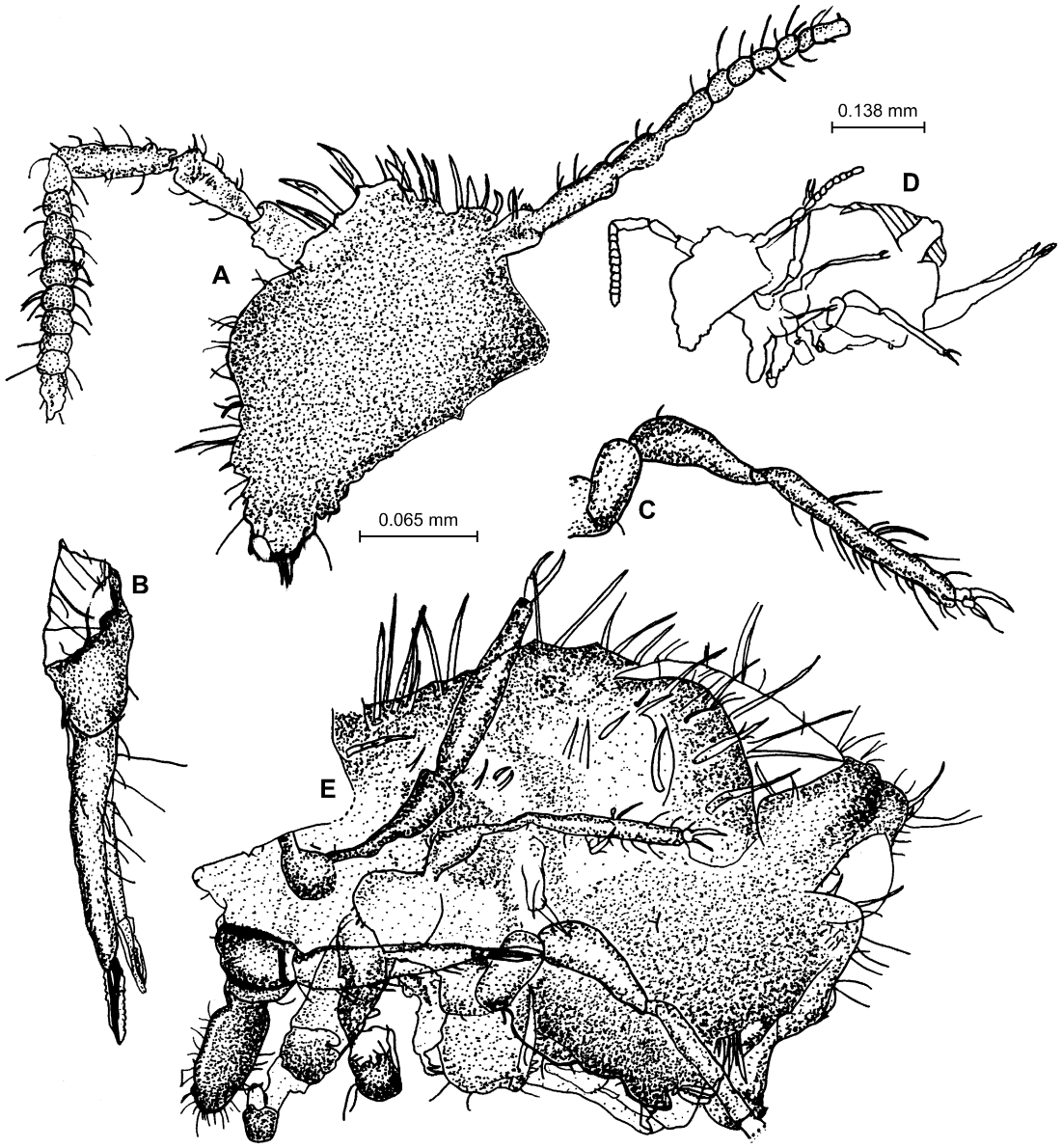

Fig. 3. *Grinnellia ventis* sp. nov. All figures of holotype. A, head and antennae. B, furcula. C, hindleg. D, habitus. E, body and legs.

long as the greater abdomen and the two are separated only by a shallow groove. There is no clear demarcation between the fifth and sixth segments, but the sixth bears a peculiar slightly hooked dorsal projection near its anterior margin. The lesser abdomen has several ca. 0.07-mm-long cylindrical truncate setae and two bothriotricha like the one setae attached near the end of the sixth segment. The manubrium and dens on the holotype are decayed and have no visible setae. The mucro is relatively long (38% the length of the dens) and narrow, with a narrow lamella and an entire rounded tip. The legs project on only one side of the holotype. The mid- and hindlegs on the other side are partly obscured by the body mass, and the foreleg is missing. The foreleg on the projecting side has thick subapical setae at the distal end of the tibiotarsus. The projecting mid-leg has heavy subapical acuminate setae near the end of the tibiotarsus. The foot complex is not seen in plain view in the holotype, but has a slender, slightly basally swollen unguiculus with a short apical filament. The end of the mid tibiotarsus on the other side of the holotype has one very weakly clavate tenent hair. A bubble distorts the foot complex of the hind foot as well as the distal end of the tibiotarsus. One weakly clavate tenent hair is present, along with a cluster of setae near the end of the tibiotarsus (Fig. 6A, B). The unguis lacks teeth or tunica and has an unguiculus with an apical filament almost reaching the level of the apex of the unguis. The tibiotarsus is equipped with numerous short, acuminate smooth setae, mostly upon the inner surface. The hind trochanter is 71–72% as long as the femur (Fig. 6A) and has a blunt cylindrical spine.

Remarks. There are three specimens, which may be congeneric. The first of these is AMNH Bu 145A. This specimen

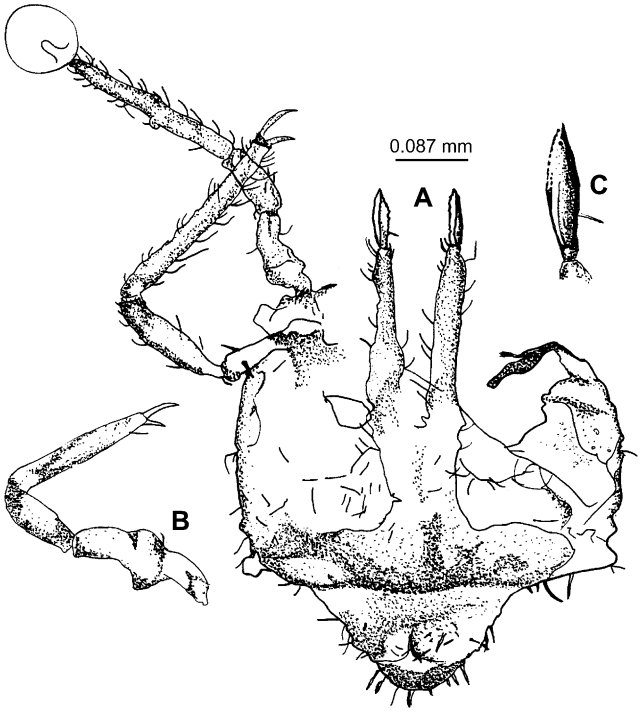

Fig. 4. Probable *Grinnellia*, Sample Bu 0117 specimen 3. A, posterior part of body from below. B, mid-leg from below. C, enlargement of right mucro from above.

has many features similar to *Sminthuricinus*, and initially we considered it as a paratype; however, closer examination led us to question it as a member of the genus. It has antennal structure (Fig. 6H), short blunt spines, leg and furcula ratios, as well as a trochanteral spine (Fig. 6E) similar to the holotype. In addition, there is a cluster of short stout setae at the end of the tibiotarsus (Fig. 6J) similar to that seen on one hindleg of the holotype; however, the position of these on NMNH Bu 145A appears to be different. This could be the result of the distortion on the holotype caused by a bubble on the leg. The biggest problem in ascertaining the identity of specimen 145A is the extreme deformation of the body, which makes it impossible to develop a good habitus image. In addition, a bubble covers much of the dorsum of the body of this specimen. Thus the nature of the separation between the greater and lesser abdomen is unclear. The mid-leg of the specimen is seen in plain view and shows the apical filament of the unguiculus to arise from below the apex. There are 12–13 dorsal, slender, acuminate, smooth setae on the dens, but no ventral setae. The antennae have 1–2 whorls of setae ranging from 0.01 to 0.03 mm in length. 145A also differs from the *Sminthuricinus* holotype in having a wider lamella on the mucro. The conclusion we make is that it likely belongs to the genus *Sminthuricinus*, but is probably a different species.

The second possible *Sminthuricinus* is AMNH Bu 723 C specimen 6 which has some short cephalic spines and a trochanter ca. 70% as long as the femur, and has a few short spines on the body. There is a clear twisted distal trochanteral spine. The tibiotarsus is unclear. There is a thoracic tubercle larger than that seen in the holotype. The abdomen is badly decayed. A large projection from the dorsum appears to be extruded body contents. The furcula has a mucro somewhat longer than that of the holotype (Fig. 6F). There are clear dorsal but no ventral dental setae. The mucronal lamellae are faint, and thus the mucrones appear pointed on first glance. The antennae are missing.

AMNH Bu 810 B specimen 3 may be *Sminthuricinus*, but it is only fragmentary and is distorted by a bubble. It has a number of blunt spines of different sizes, most appearing slightly longer than those seen on the greater abdomen of the holotype. The specimen is so distorted that the position of these spines is difficult to ascertain. Two things are clear on this specimen: the first is that the fourth antennal segment on one side has 10–11 subsegments. The second is that the lesser abdomen is short and compressed (Fig. 6D) with a few body spines, a bothriotrix D and a pair of distal bothriotricha on the sixth segment as well as a number of pseudobothriotricha-like setae. A possible subanal appendage can be seen; however, this is so obscured by the bubble and corresponding distortion that its nature remains problematic.

Genus *Mucrovirga* gen. nov.

Derivation of name. Latin *virga*, referring to the peculiar rod-like structure of the mucro.

Type species. *Mucrovirga incompleta* sp. nov., mid Cretaceous, Myanmar (Burma).

Diagnosis. This genus is characterized by a mucro consisting of a very thick rachis with a subapical tooth and no lamella. Another distinguishing feature is the third antennal segment, which is about 70% as long as the fourth segment, which is divided into ten subsegments.

Included species. Type species only.

Remarks. The mucrones on the two type specimens are unlike those seen on any extant or extinct genus of Sminthuridae. The thickened rachis is similar to that seen in species of the tribe Sminthuridinae, but these are always accompanied by well-developed lamellae and lack the blunt tip and teeth seen in this genus. We at first thought there might be a mucronal lamella but examination with the confocal microscope showed this to be an artifact. In addition, the antennal structure is quite unlike that seen in the Sminthuridinae. The holotype is badly distorted and with considerable debris attached. A mushroom-like growth on the head of the holotype, similar to that of *Sminthuricinus*, caused confusion until we were able to ascertain its taphonomic nature. An apparent basal mucronal spine was shown to be an artifact by examination with the confocal and phase-interference microscopes. In spite of the condition of the specimens their unique visible characteristics, particularly the mucro with a thick dentate rachis lacking lamellae, made us feel secure in describing them as a new genus.

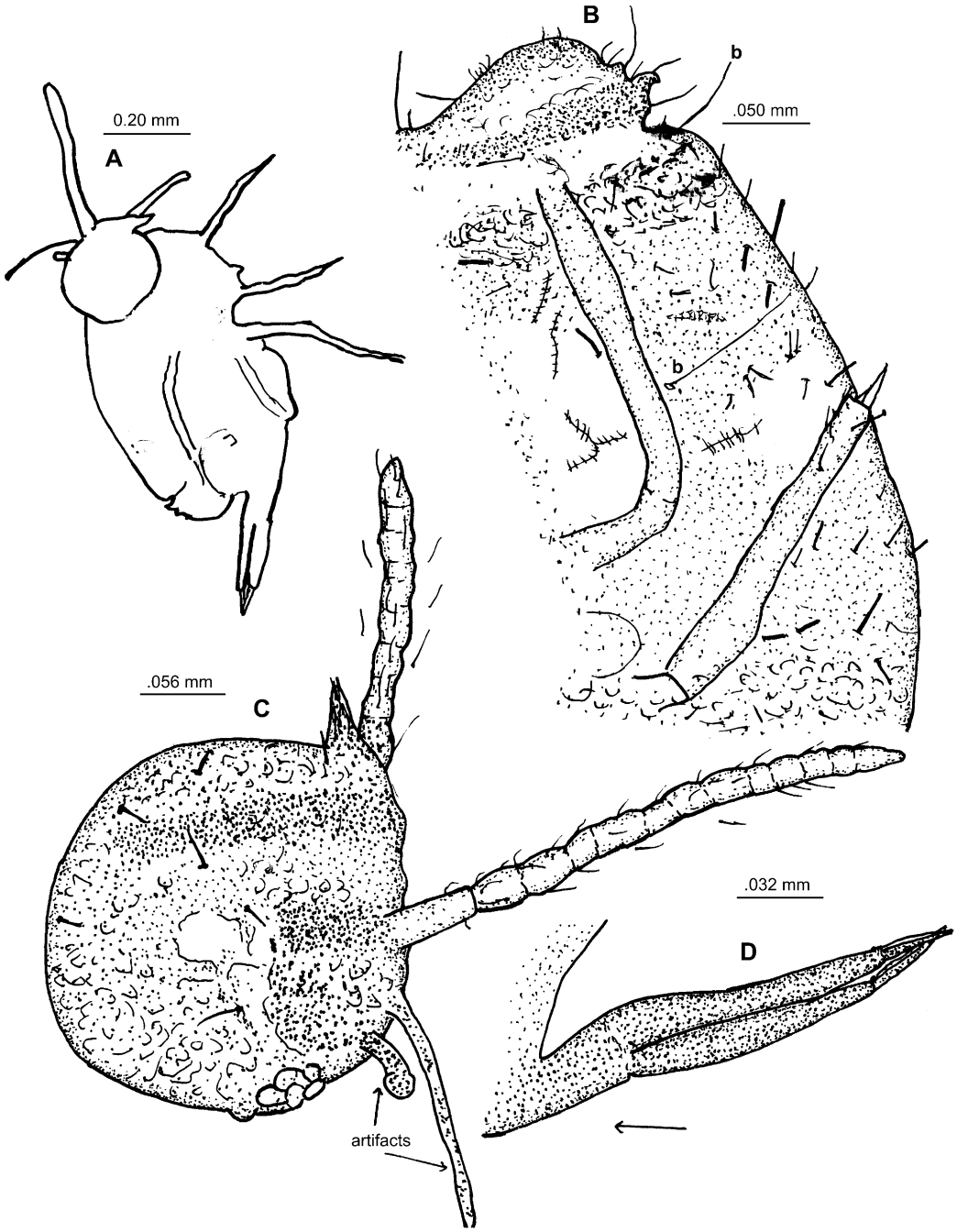

Fig. 5. *Sminthuricinus decepta* sp. nov. All figures of holotype. A, habitus outline. B, dorsum of abdomen leg setae omitted (b, bothriotricha). C, head. D, furcula.

Mucrovirga incompleta sp. nov.
Figs. 1C, 7

Derivation of name. Referring to the number of features not visible on the specimens.

Holotype. Amber AMNH Bu 168. American Museum of Natural History.

Type locality and stratigraphic horizon. Myanmar (Burma), Kachin State, Tanai Village (on Ledo Road, 105 km from Miyitkama); collected by Leeward Capitol Corp.; mid Cretaceous.

Material. Holotype and paratype Bu 0117B specimen 1, same locality and horizon.

Diagnosis. As for the genus.

Description. Body length is 0.365 mm, and cephalic diagonal 0.255 mm. Antennal sizes are shown in Table 2. The fourth antennal segment has 9–10 subsegments (Fig. 7B), each with a single whorl of acuminate, smooth, curved, 0.013–0.021-mm-long setae. The third segment has only a few such setae and none can be seen on segments one or two. The head is badly distorted and mostly opaque with

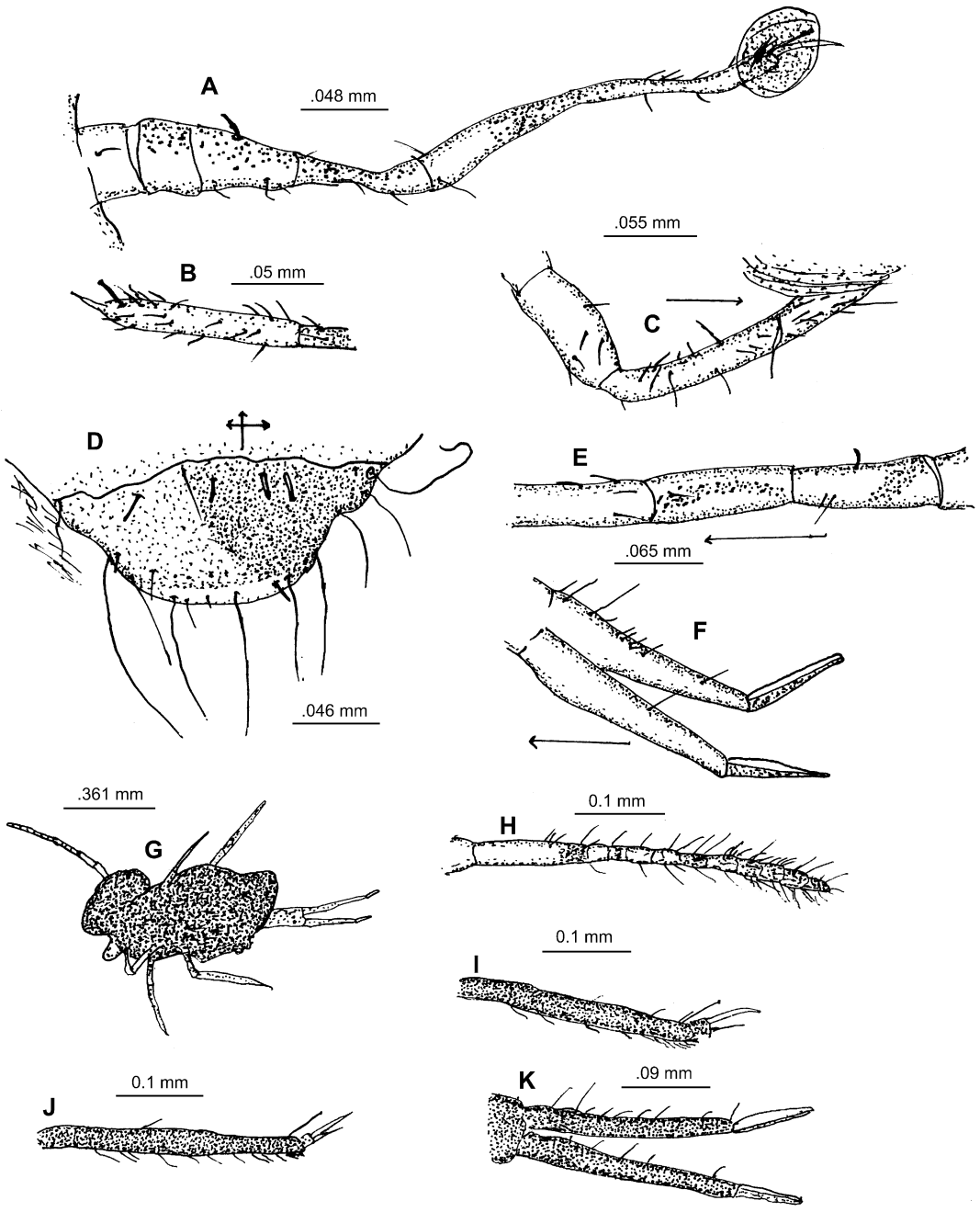

Fig. 6. *Sminthuricinus decepta* sp. nov. A–C, holotype. A, left hindleg. B, mid tibiotarsus and unguis. C, detail of right tibiotarsus and femur. D–K, probable specimens of *Sminthuricinus*. D, end of abdomen, sample Bu 810-B. E, hind trochanter, and femur and base of tibiotarsus. F, dentes and mucrones, sample Bu-723C specimen 6. G–K, sample Bu-145A. G, habitus. H, third and fourth antennal segments. I, hind tibiotarsus and foot complex. J, mid tibiotarsus and foot complex. K, dentes and mucrones.

only two ommatidia seen on one side and no setae. The greater abdomen is also distorted and mostly opaque but a few (ca. 0.018 mm long) blunt, straight, slender setae are present. The lesser abdomen has a deep groove separating it from the greater abdomen, and a few acuminate smooth setae are attached to or near it. A short, straight, blunt, thick probable subanal appendage is seen on one side. The manubrium surface is unclear, but probably has a number of small dorsal setae. The dens has 3–4 dorsal and three ventral setae (Fig. 7E). The mucro consists of a thick rachis, bearing a subapical spine, 4–5 very small, low, intermediate teeth and an upcurved blunt tip. No lamella is present. The legs are unclear, but one foot complex bears a simple unguis and three clavate tenent hairs (Fig. 7D).

Remarks. The paratype specimen, Bu 0117 specimen 1, has a similar mucro, and the single surviving antenna, while unclear, appears to have a similarly long third antennal segment and a lesser abdomen sharply divided from the greater. It also has a clear short, straight subanal appendage with a small hooked apex. One possible tenent hair (Fig. 7K) can be seen on one foot complex.

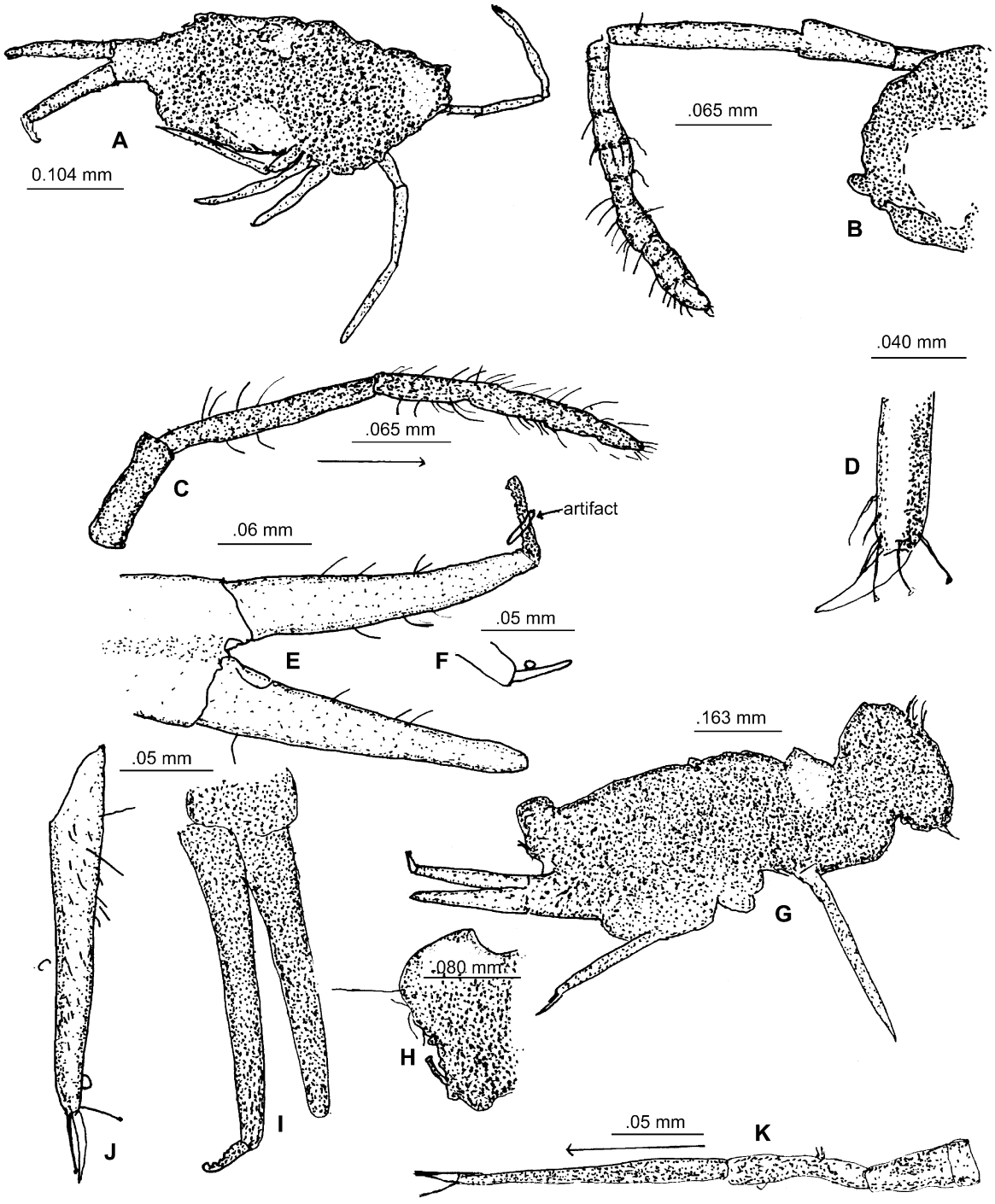

Fig. 7. *Mucrovirga incompleta* sp. nov. A–F, holotype. A, habitus. B, right antenna. C, left antenna. D, end of tibiotarsus and unguis, mid-leg. E, furcula. F, mucro seen from below. G–K, paratype. G, habitus. H, enlargement lesser abdomen. I, furcula. J, hind tibiotarsus and foot complex. K, foreleg.

Genus *Sminthurconus* gen. nov.

Derivation of name. After the peculiar conical integumentary decoration.

Type species. *Sminthurconus grimaldi* sp. nov., mid Cretaceous, Myanmar (Burma).

Diagnosis. The conical integumentary structures plus the very large trochanter and the basal mucronal ventral tooth distinguish this from all genera of the family Sminthuridae s.l.

Included species. Type species only.

Remarks. Circular mound-like structures bearing median short spines are clearly visible on the abdomen of the paratype, where one portion of this part of the body is both translucent and well preserved. These structures are not clear on the holotype, where the areas in question are opaque and badly

decayed; however, some hints of these structures can be seen under the phase-interference and high-powered dissecting microscopes. A few blunt spines can be clearly seen under all microscopes. The smaller similar mound-like structures seen in the interocular areas on the paratype are not seen clearly on the holotype, but the protruding ocelli and antennae block this region. The conical cuticular projections also appear to occur on the mid-portion of the vertex, but are more minute than those seen on the body. In spite of the good condition of the lateral cuticle on the greater abdomen of the paratype, no setae, sockets, or bothriotricha were seen. It is possible that two species are represented; however, the general agreement between the two specimens is so great that we feel it unwise to consider them as such.

This genus has features of a number of tribes. The protruding ommatidia are similar to those seen in some species of the Bourletiellinae genus *Heterosminthurus*, but more prominent. The large saddle before the sixth abdominal segment (obscured by a bubble in the paratype) is also similar to *Heterosminthurus* Stach (1955); however, there are no tenent hairs or sockets showing their loss. The base of the mucro is similar to that seen in a number of species of the Katianninae genus *Sminthurinus* Börner (1901). The large trochanter and trochanteral spine is similar to subfamily Sminthurinae. The projecting ommatidia, concomitant angled vertex and conical integumentary structures are all unique. The presence of a trochanteral spine would seem to place it in the Sminthurini but its placement there is problematic. Thus, the genus can only be placed in the family Sminthuridae s. l.

Sminthurconus grimaldi sp. nov.
Figs. 1B, 8, 9

Derivation of name. Named in honor of David Grimaldi, whose work made this study possible.

Holotype. AMNH Bu 854A specimen 2. American Museum of Natural History.

Type locality and stratigraphic horizon. Myanmar (Burma), Kachin State, Tanai Village (on Ledo Road, 105 km from Miyitkama); collected by Leeward Capitol Corp.; mid Cretaceous.

Material. Holotype and paratype, same locality, AMNH Bu 1452C, specimen 1.

Diagnosis. As for the genus.

Description. Maximum body length is 0.71 mm and cephalic diagonal 0.36 mm. The antenna is more than twice the length of the cephalic diagonal. The organ sizes are shown in Table 2. The fourth segment has 12 subsegments (Figs. 8E, 9C). Most antennal setae are straight, slender, smooth and acuminate. The head has cheek pouches similar to those of *Grinnellia*, but much less prominent. The ommatidia are eight per side with cornea large and protruding prominently (Figs 1D, 8F). The expansion of these ommatidia distorts the head so that the vertex is at right angles to the dorsum of the head. The vertex has three slender thin spines, two slightly curved and one (the shortest) straight. These spines are probably paired in life (Fig. 8F). The interocular area is equipped with several small mounds bearing short spines (Fig. 9C) while the hind trochanter is 78–82% as long as the femur (Fig. 8B), and has a very slender blunt spine. The unguis is slender and untoothed. The hind unguiculus is ca. 0.5 mm as long as the inner unguis and has a narrow base and no apical filament. The fore unguiculus has an apical filament almost reaching the apex of the unguis. No tenent hairs can be seen, and few setae remain on the legs. Those that exist are slender, straight, smooth and acuminate. The greater abdomen is devoid of setae, but has short blunt spines. On the lateral posterior portions, these are borne on separated small mounds (Fig. 9B). A major portion (possibly all) of the body is covered with densely packed (0.002–0.011 mm long) conical cuticular projections (Fig. 8G). The fifth abdominal segment and a small part of the greater abdomen are depressed dorsally, making a large saddle between the rest of the greater abdomen and the sixth abdominal segment. The sixth segment has a number of slender, smooth acuminate setae, the longest of which are ca. 0.025 mm in length. The furcula is without setae. The mucro has a smooth lamella and a basal ventral tooth (Figs. 8I, 9D). The rachis of the mucro contains 3–4 extremely minute toothlets (Fig. 9D).

Remarks. Sample AMNH Bu 853 (same locality) may be a member of this genus; however, the small specimen is so badly distorted it is impossible to tell. The body appears to have appropriate conical integumentary decorations. The ommatidia may be projecting and the trochanter may be unusually long but none of this is clear.

Sminthuridae incertae sedis

Remarks. Most of the specimens of Sminthuridae s.l. we saw were too fragmentary or badly preserved to ascertain whether they belonged to any described genus. Many of these taxa have an unusually large hind trochanter (see Table 2) that would serve to separate them from most extant genera; however, they are not well enough preserved and therefore lack unique features to allow us to describe them as a new genera. We are placing these species in ‘‘Incertae sedis’’ but describing and illustrating visible features of some specimens where this might make it possible for future workers to determine whether their new taxa are probably the same as ours. In other cases, the specimens are merely listed so that other researchers can locate them when new tools for study become available enabling better analysis.

Only the AMNH Bu number and specimen location are given in bold face below for all the AMNH materials:

027 smaller piece: Labrum with two short, lateral, heavy rod-like projections. Hind tibiotarsus with one cylindrical tenent hair.

071: 12 fourth-antennal subsegments, narrow mucro, small and sharply demarcated sixth abdominal segment.

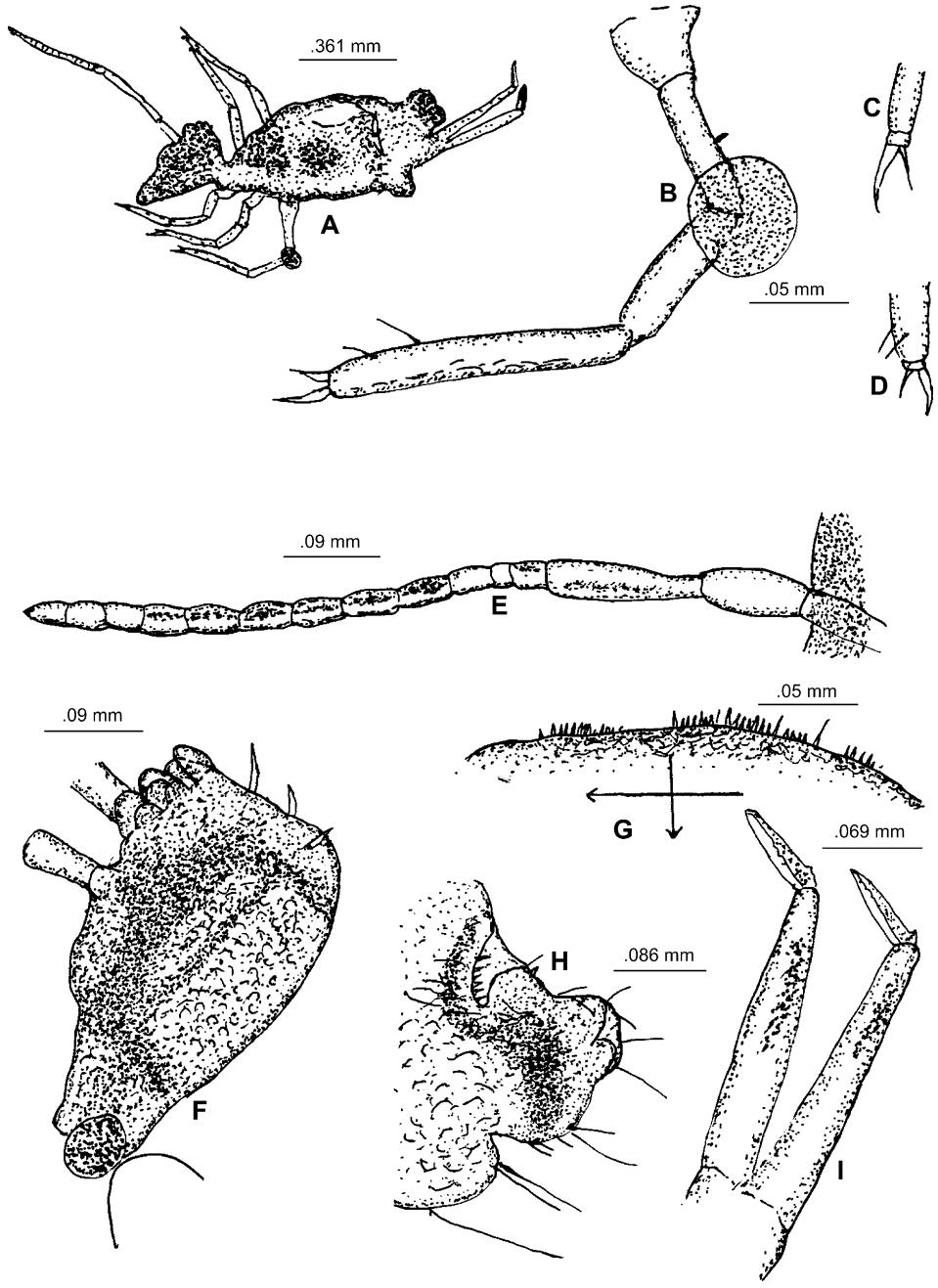

Fig. 8. *Sminthurconus grimaldi* sp. nov. All figures of holotype. A, habitus. B, hindleg. C, fore foot complex. D, hind foot complex. E, left antenna. F, Head, lateral view. G, lateral profile mid two-thirds of greater abdomen. H, end of abdomen, lateral view. I, mucro and dens and mucro lateral–dorsal view.

151: This shows some similarities to *Sminthuricinu*s. It has short spines similar to the holotype, and a hind trochanter with spine and trochanter apparently 77% as long as the femur. One foreleg has a cluster of distal tibiotarsal setae as in the type specimen and AMNH Bu 145A. A different leg shows a possible slightly clavate tenent hair. The antennae are not visible. The mucro lamella is relatively broader than that seen in *Sminthuricinus*.

457A specimen 3 (Fig. 10A–D): The fourth antennal segment has ten subsegments (Fig. 10A) and one or two whorls of smooth acuminate setae on each subsegment. The largest of these is ca. 1.5 times as long as subsegment width. The third antennal segment is unusually long, ca. 63% as long as the fourth segment. There is at least one row of six dorsal cephalic spines directly behind the antennal base. The hindleg trochanter is ca. 70% as long as the femur. The fore unguiculus has an apical filament almost reaching the apex of the unguis. The mid-foot lacks an apical filament. A possible thoracic appendage is present. The body has a few small to medium spines. The specimen is badly decayed but this has made the body transparent. Bothriotricha A and B are clear on the greater abdomen, but bothriotricha C and D (Fig. 10B) are less clear. Nevertheless, all these appear to display the inverted pattern of the genus *Termeritas*, except for the fact that putative

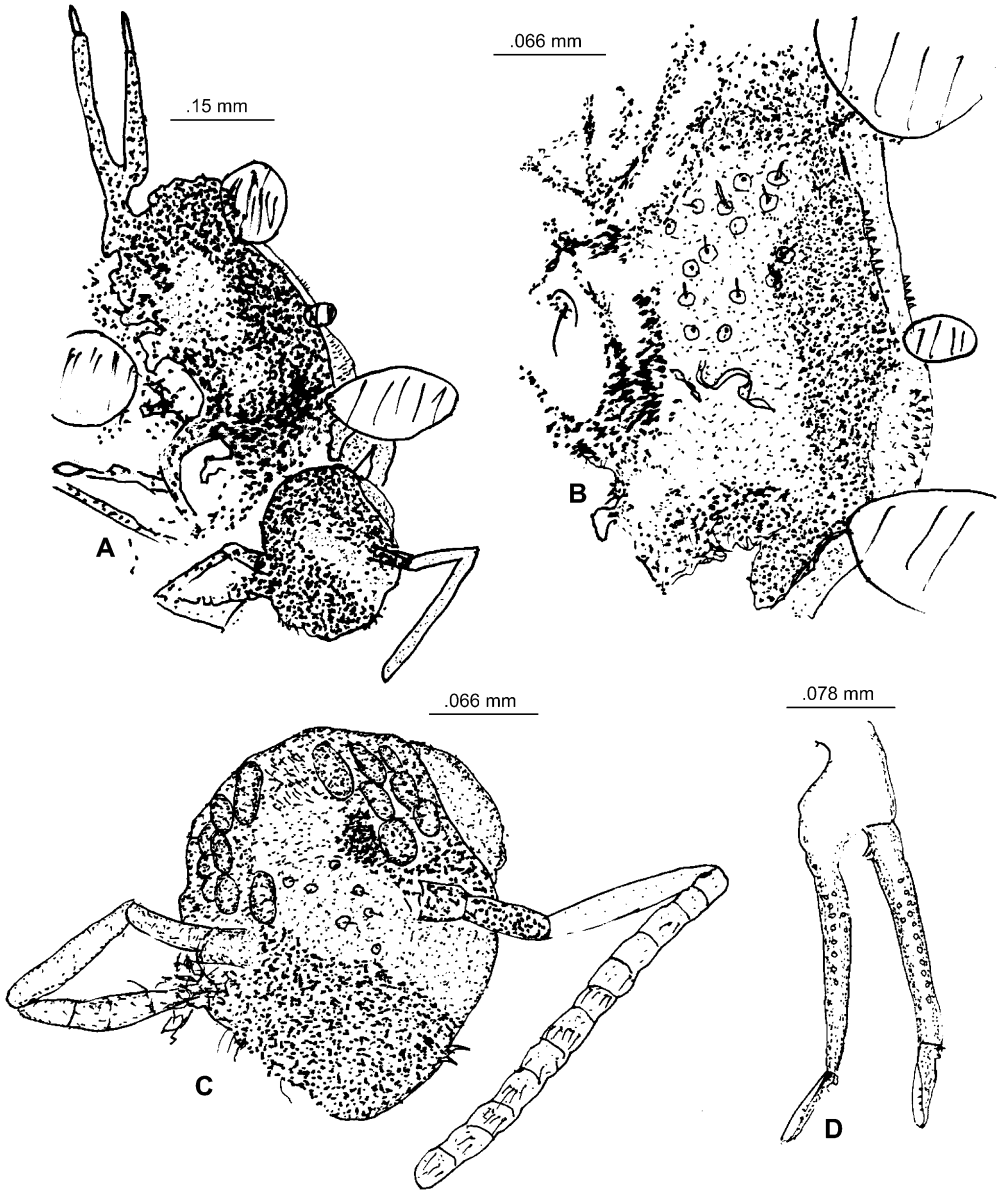

Fig. 9. *Sminthurconus grimaldi* sp. nov. All figures of paratype. A, habitus. B, dorsal and lateral portions of middle of greater abdomen. C, head and antennae. D, dentes and mucrones.

bothriotrix D appears to be on the posterior margin of the greater abdomen. There is a fifth uncertain bothriotrix that fits into no known pattern. The mucro is lamellate with smooth edges. The furcula lacks visible setae. This specimen may belong to the genus *Sminthuricinus* but has a relatively much longer third antennal segment and lacks any cluster of distal tibiotarsal setae. In addition, the mucronal lamella is broader (Fig. 10C) and the unguis is shorter and broader (Fig. 10D).

818-1A1 specimen 2 (Fig. 10E, F): The well-preserved furcula shows setae (Fig. 10F) and one hindleg (Fig. 10E). The remainder is missing, except for a fragment of the posterior abdominal cuticle and two other legs, partly obscured by debris. The visible portions are not enough to place it to any genus; however, the mucronal lamella is weakly dentate as in *Grinnellia*, and is unlike any other Burmese amber Sminthuridae; but it lacks any other features of *Grinnellia*. There is a possible trochanteral spine on the third leg, but the darkening of the segment obscures this.

854A specimen 1 (Fig. 11A): The sixth abdominal segment is evocative of that seen in the Late Cretaceous genus *Keratopygos*, but the horn is shorter and extends backward (see Fig. 11A). The body is devoid of setae and shows no cuticular structures. The hind trochanter is unclear but appears to be more than half as long as the femur. The mucro is narrow, with a slightly upturned tip and a very narrow lamella. The base of the mucro has a ventral expansion in some small circular areas on the abdominal cuticle. Both are somewhat similar to structures seen on *Sminthurconus*.

992: This cleared, badly decayed fragmented specimen has a narrow, smoothly tapered mucro. The lesser abdomen has a deeply grooved separation from the greater abdomen.

1069: Two specimens, both in very poor condition, but each with 12 fourth-antennal subsegments as in *Sminthurconus*. Only one specimen (Fig. 11B) shows any other detail, having a head with slightly protruding ocelli; however, the lack of conical cuticular decorations and the absence of trochanters about half as long as the femurs, separate these specimens from *Sminthurconus*. The specimens are badly contorted.

1079 (divided into 3 pieces) (Fig. 11C–I): all the specimens came from the same small piece of amber. There are 16 Sminthuridae in this sample, including fragments. In spite of this large number, none is adequate to serve as a holotype for a genus. The prolonged study of these specimens was frustrating in the extreme. It is very unlikely that these specimens belong to the same taxon. All attempts at lumping specimens together into clusters failed. We tried doing this on the basis of morphological features such as narrow versus broad mucronal lamellae, subanal appendages, organ sizes, or ratios. Every grouping we made came in conflict with some other groupings (see Tables 3 and 4). Furthermore, no features could be seen on all specimens and some on very few. This has made it impossible to develop any composite identities. Some of this variation can be seen in Tables 3 and 4. The specimens are badly decayed and most are clearly early instars. They are all characterized by long trochanters, which vary widely from 62–89% as long as their femurs. Where the trochanter is clearly visible, a spine is present. The foot complex shows a clear elongate apical filament on one specimen. 8 + 8 ommatidia (Fig. 11E), and a well-developed subanal appendage can be seen on several specimens;

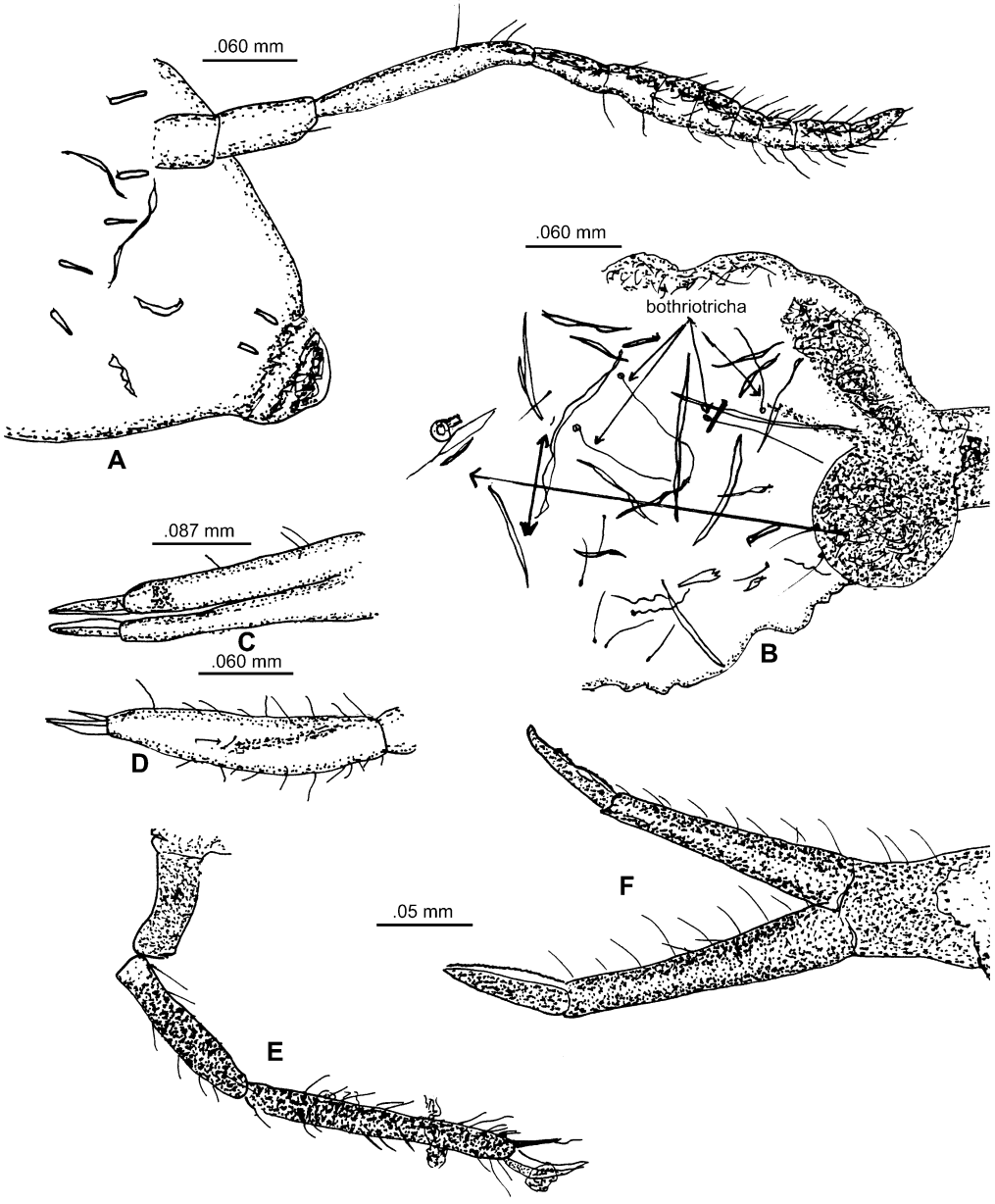

Fig. 10. Sminthuridae incertae sedis. A–D, sample 457A specimen 3. A, apex of head and left antenna. B, distal third of abdomen. C, dentes and mucrones. D, hind tibiotarsus and foot complex. E, F, 818A1 specimen 2. E, hindleg. F, dentes and mucrones.

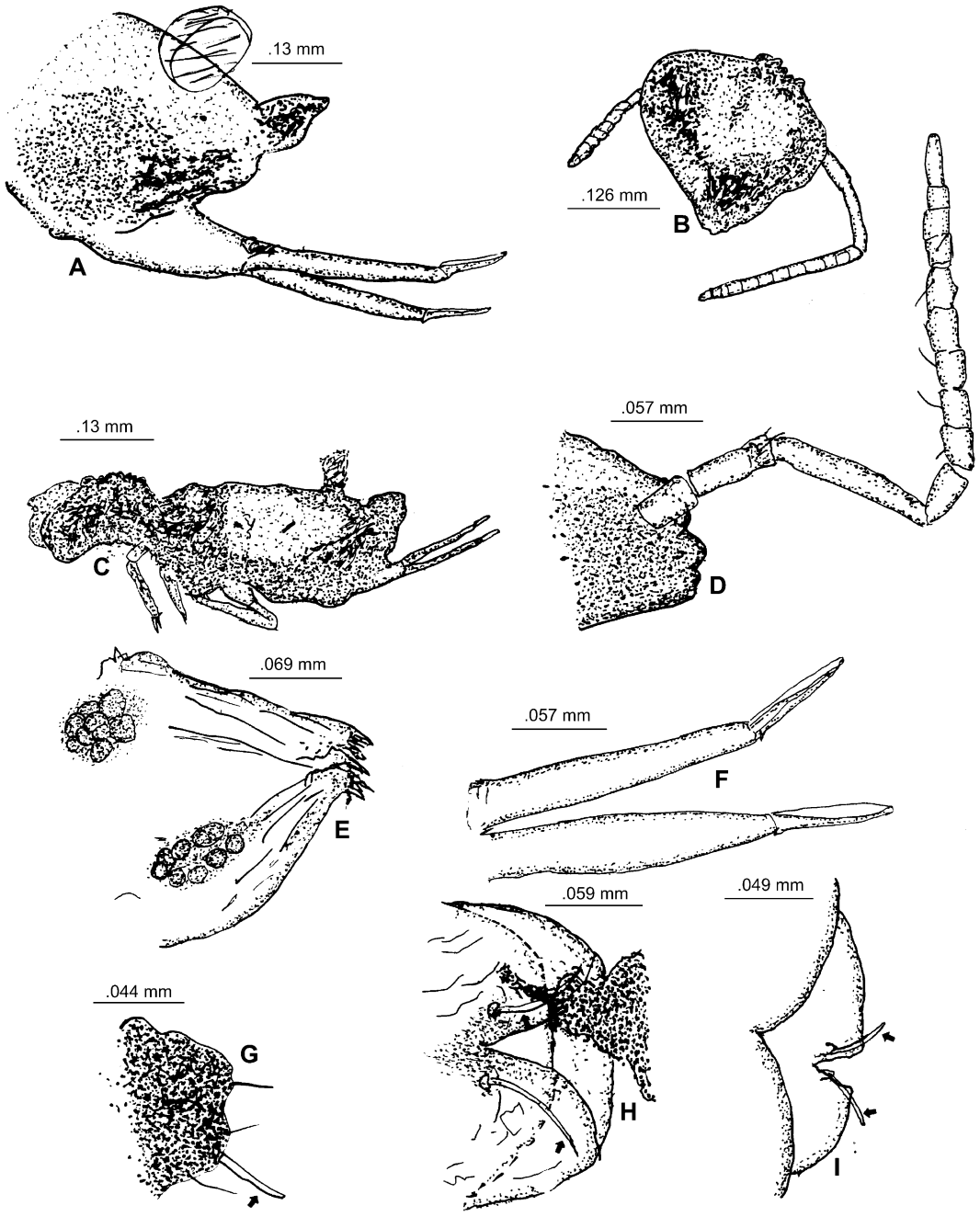

Fig. 11. Sminthuridae incertae sedis. A, sample 854A specimen 2, posterior half of abdomen and furcula. B, sample 1069, head and antennae, frontal view. C–I, sample 1079. C, subsample A specimen 2, habitus. D, subsample C specimen 5, right antenna and side of head seen from above. E, subsample A specimen 6, anterior part of head, frontal view. F, subsample C specimen 4, furcula. G-I, subanal appendages (arrows). G, subsample B specimen 2. H, subsample C specimen 6. I, subsample B specimen 7.

however, these appendages vary from straight and blunt (Fig. 11G) to curved and acuminate (Fig. 11H), or to blunt and curved (Fig. 11I). While some of this may be due to the orientation of the specimen, it seems more likely that several types are represented. Acuminate slender spines of moderate length occur on the abdomen or part of the abdomens of most specimens. The lesser abdomen is sharply smaller than the greater abdomen, but usually without a clear separating indentation. The mandibles protrude from the head in several specimens. The mucro has a lamella but this varies from broad to very narrow and always has smooth edges. One edge usually appears to have a thick base, tapering to a narrow apex. In almost all specimens with a lateral view of the mucro, it is expanded slightly at the ventral base. No specimen has well preserved setae and only one specimen has setae on the furcula (but its mucro is unclear). Many specimens show what could be thoracic or cervical vesicles. These forms are clearly members of the Sminthurini and different from *Grinnellia* in the absence of large spines on the body

Table 3
Morphologic features of specimens of Myanmar Cretaceous Sminthuridae in sample 1079

Specimen	Antenna 4 subsegments	Mucro lamella	Trochanter/ femur	Trochanteral spine	Thoracic appendage	Unguiculus filaments	Dental setae	Cephalic spines	Body spines	Sub-anal appendage
A2	?	?	80%	?	?	?	?	2	2	−?
A3	10	Narrow edge smooth?	74%	?	+?	1,2 reach tip unguis	?	?	?	?
A4	10	?	85%	+?	?	?	?	Few short	few medium	?
A5	10	?	77%	?	?	?	?	?	Few medium	?
A6	?	?	?	?	+??	?	?	Few short	1 medium	?
A7	?	edge smooth	?	?	+?	?	1 dorsal	?	?	+ straight acuminate
A8	?	? tapered	?	?	+	?	1 dorsal	?	?	+ curved acuminate
B1	10–11	?	70%	+	?	2–	?	1 short	1 large 12 medium	?
B2	10?	+ faint	73%	+	?	?	–	–	2 large	+ straight
B3	?	?	?	+	?	?	?	1 medium	?	Male?
B4	10	+ narrow	?	?	+??	?	?	?	3 medium	?
B5	10–11	Smooth broad	89%?	+	+	?	?	?	2 medium	?
B6	10–11	?	62%?	+?	?	?	?	3	1	+?
B7	?	smooth	79%	+	?	?	?	2 small	2 medium 1 large	+ blunt curved
C3	?	+ edge smooth	86%	?	?	?	1 dorsal	?	4 +?	?
C4	11	+	71%	+?	+??	1,2 reach apex unguis	?	2	1	?
C5	10	+ edge smooth	?	?	+?	+	–	1	?	?
C6	10–11	?	70%	+	?	?	?	1 small	?	+

and head as well as the absence of cheek pouches. None displays features that would allow them to be considered as members of *Grinnellia*, *Sminthuricinus*, *Mucrovirga*, or *Sminthurconus.*

Family: Isotomidae Börner, 1913

Remarks. We examined 32 both complete specimens and fragments that could be placed in this family and 16 were identifiable to genus. The most abundant of the specimens assignable to genera (seven) belong to a new species of *Protoisotoma*, the dominant genus in the Late Cretaceous Canadian material. In addition, one extant genus is represented. The other nine generically assignable specimens are put into four new genera. The remaining specimens are discussed under ''Incertae sedis''. None of the specimens have many clear features. No genital areas were clear so nothing definitive could be determined concerning instar of any of these specimens; however, the relatively small mucrones suggest adult or subadult stages. Most genera have head–body ratios larger than is typical in extant genera but similar to those in the genus *Isotomurus* Börner (1903). It is also interesting that the commonest specimens clearly belong to the Late Cretaceous genus *Protoisotoma*. Half of the genera have some features (long slender ungues and/or tuberculate dentes) suggestive of an aquatic or subaquatic habitat (see Table 5).

Genus *Villusisotoma* gen. nov.

Derivation of name. Latin, *villus*, furry, with reference to the furry appearance of the animals.

Type species. *Villusisotoma brevis* sp. nov., Mid Cretaceous, Myanmar (Burma).

Diagnosis. This genus is characterized by having all segments of the furcula clear but the mucro small (6–14% as long as the dens), bidentate, with a minute apical tooth and lacking lamellae. The dentes are long and tapered with the dorsal surface tuberculate and the ventral and dorsal surface having ten or more setae. The unguis and unguiculus are simple but clavate tenent hairs are present. The clothing consists of numerous curved cylindrical, rugose or very finely ciliate setae and longer slender smooth, straight, acuminate setae. The genus is pleurochaetotic with setae so densely packed that rows cannot be determined. It has six clear abdominal segments, at least four ommatidia per side, and the ventral surface of the manubrium has 1 + 1 seta or no setae. The dorsal surface has eight or more setae.

Included species. Type species and *Villusisotoma longa* sp. nov.

Remarks. This genus shows some similarities to the modern proisotomine genera *Pachyotoma* Bagnall (1949), *Ballistura* Börner (1906) and *Jestella* Najt (1978); however, the extremely small bidentate mucrones lacking lamellae serve to distinguish it from all of these genera. In addition there is no occurrence of cylindrical, truncate setae like those found in *Villusisotoma* in any of these genera. The largest setae are somewhat similar to the male setae seen in *Dimorphotoma* Grinbergs (1975) but the genus bears little other resemblance to *Dimorphotoma*. The small mucrones of *Villusisotoma* are similar to but somewhat larger than those seen in the Cretaceous genus *Protoisotoma*; but the furcula of these genera are otherwise quite different, being dorsally knobbed or humped in the former and crenulate or smooth in the latter. In addition, the greatly expanded fourth antennal segment of

Table 4
Myanmar Cretaceous Sminthuridae of sample 1079 (measurements in mm)

Specimen	Eyes seen	Bothriotricha	Cephalic diagonal	Antenna 4	Antenna 3	Antenna 2	Antenna 1	Body	Hind tibiotarsus	Hind femur	Hind trochanter	Manubrium	Dens	Mucro
A2	6		0.21	0.19	?	?	?	0.36	0.175	0.075	0.06	?	?	?
A3			0.25	0.24	?	?	?	0.42	0.25	0.090	0.065	?	?	?
A4	4	1D?	0.245	0.240	0.115	0.065	?	0.40	0.24	0.09	0.074	?	?	?
A5	5–6		0.235					0.32		0.095	0.070			
A6	8 + 8		0.250											
A7												0.10	0.195	0.075
A8												0.11	0.20	0.050
B1	8	1	0.375	0.285	0.150	?	?	?	0.205	0.104	0.073	?	?	?
B2	6+		0.30					0.65	0.240	0.095	0.070	0.155	0.205	0.075
B3								0.675	0.470	0.125				
B4	3+		0.240	0.225	0.075	0.055	?	0.45	0.20	0.09		0.10?	0.175	0.050
B5		1		0.195	0.083				0.112	0.073	0.065?			
					0.073									
B6	8	1(D)						0.359	0.143	0.104	0.065?			
B7	6–7		0.221					0.369	0.169	0.057	0.045	0.075	0.124	0.042
C3									0.239	0.104	0.090	0.156	0.195	0.075
C4	8		0.255	0.205	0.125	0.076	0.039	?	0.246	0.115	0.078	?	0.153	0.060
C5	4		0.255	0.247	0.107	0.055	0.046	0.45					0.261	
C6	8		0.340	0.351	0.177		0.046	0.60	0.275	0.150	0.105		0.221	0.078

Protoisotoma is absent in the *Villusisotoma*. It is likely that the holotypes of both species of *Villusisotoma* are subadults or late instar young. This would mean that some features, most notably the ventral manubrial setae, would be different in adults. Thus there may be a number of other genera that are similar; however, the numerous truncate body setae, the pleurichaetotic condition and the relatively small bidentate simple mucro with a minute apical tooth would separate *Villusisotoma* from any of the others.

Villusisotoma brevis sp. nov.
Figs. 1E, 12

Derivation of name. Latin, *brevis*, short, referring to the relatively short cylindrical setae.

Holotype. AMNH Bu 818A2, specimen 6, American Museum Natural History.

Type locality and stratigraphic horizon. Myanmar (Burma), Kachin State, Hukawng Valley, 32 km southwest of Tanai, near Noije Bum (hill), approx. 250 m; mid Cretaceous.

Material. Holotype and one paratype: AMNH Bu 818A2 specimen 10.

Diagnosis. With characteristics of genus and differentiated from the other species of the genus by its short cylindrical body setae (longest posterior setae ca. 0.026 mm), normal shorter setae ca. 0.017 mm plus cylindrical setae on the dorsum of the manubrium and small bumps or knobs on the dorsum of the dentes. The clavate tenent hairs are 1-1-2 on the fore–hindlegs.

Description. Maximum length, exclusive of appendages, is 0.71 mm. Lengths of organs are shown in Table 6. Antennae are four-segmented with the first segment about half as long as the second and second segment about 1.2 times as long as the third. Total length of the antennae is ca. 1.2 times as long as the head. Fourth antennal segment is about as wide as third segment; it is densely setaceous with numerous curved setae, some of which appear to be cylindrical, truncate and rugose while others are acuminate, slender and smooth. Somewhat longer straight setae are common and these are almost all acuminate. The third antennal segment has many fewer setae, (no more than 17 seen) which are mostly acuminate. The second antennal segment has about the same number of setae as on the third segment, all acuminate. A simple post-antennal organ was seen on the paratype. Ommatidia are not visible on the holotype, but six were seen on one side of paratype (Fig. 12F). The head is clothed with numerous short curved, truncate setae (Fig. 12C) and a few somewhat longer straight, acuminate setae. The labium has long lateral curved setae projecting well beyond its margin. The prelabrum with an unusually long (0.02 mm) projecting acuminate smooth seta. The dorsum of thorax and abdomen are clothed with numerous short curved cylindrical setae (Fig. 12E) ranging from 0.009 to 0.02 mm long. The largest of these appear to be rugose and are seen on posterior part of the abdomen. Long slender pseudobothriotricha are seen on the abdomen. The ventral surface of the abdomen is clothed with short curved acuminate setae. Legs have numerous stout curved acuminate setae. The hind trochanter and coxae each have two strongly curved truncate setae. The hindlegs have two weakly clavate tenent hairs, one longer and more slender than the other. The midleg has one clavate tenent hair. The unguis is without teeth. The unguiculus is about one-half as long as the inner unguis, acuminate and basally moderately expanded and without a corner tooth. Clavate tenent hairs are present: 1-1-2 from fore to hind foot (Fig. 12D). The separation between the dens and manubrium is difficult to determine. The mucro has a strong subapical tooth and a small forward projecting apical one. There are no lamellae. The manubrium has a maximum of two distal

Table 5
Characteristics of described genera of Myanmar Cretaceous Isotomidae

Genus	C.D. %body	Mucro/dens	Cylindrical setae	Clavate tenent hairs	Dens dorsal surface	Dorsal dens setae	Ventral dental setae	Ventral manubrial setae	Pseudobothriotricha	Integument decoration	Abdomen 3/4	Mucro
Villusisotoma	37–47	0.06–0.10	Antenna head body	All feet	tuberculate	10–15	12–30	0–2	+	smooth	0.76–0.95	Bidentate minute apical tooth
Proisotoma	44	0.10	-	All feet	tuberculate	5	7	0	-	smooth	1.22	Bidentate straight apical tooth
Burmisotoma	36	0.12	antenna legs + end abdom.	All feet	tuberculate	~12	10–13	0	-	smooth	1.34–1.43	Bidentate lamellate
Propachyotoma	32–41	0.05–0.07	-	-	Conical projections	0	many	0	-	granulate	1.18	Bidentate minute apical tooth 12% dens
Protoisotoma	34–44	0.02	-	-	crenulate	many	many	many	+	smooth	1.2–2.5	Bidentate minute
Protodesoria	31–35	0.05–0.07	-?	-	crenulate	many	many	many	+?		1.09 1.17	Tridentate
Incertae sedis taxon 2	39	0.05	-	-	crenulate	many	many	many	-	smooth	1.26	Bidentate?
Incertae sedis taxon 1	34	0.05	-	?	tuberculate	many	many	many	+	Finely granulate	1.54	Tridentate + minute apical tooth

ventral setae and nine dorsal setae, the distal three or four being curved cylindrical and truncate while the others are acuminate. The dens are dorsally equipped with numerous small knobs or conical projections (Fig. 12B) and they also have 11 dorsal setae and 12–14 ventral acuminate, stout, curved setae on the distal half. The integument of head and body smooth or very finely granulate.

Remarks. The drawings do not reflect this rugosity of the cylindrical setae since the greatest magnification with which we could use the drawing arm was 40×, and when drawn with this magnification, the rugosity fails to show up. Additional setae were visible with the confocal microscope and here the rugosity was sometimes clear. The holotype is mostly opaque due to body contents. While the paratype is transparent, it is badly decayed.

Villusisotoma longa sp. nov.
Figs. 1F, 13

Derivation of name. Latin *longus*, long, referring to the long body setae.

Holotype. AMNH Bu 8181-A2, specimen 8. American Museum Natural History.

Type locality and stratigraphic horizon. Myanmar (Burma), Kachin State, Hukawng Valley, 32 km southwest of Tanai, near Noije Bum (hill), approx. 250 m; mid Cretaceous.

Material. Holotype and paratype, same sample, specimen 11.

Diagnosis. With the characteristics of the genus and differentiated from the other species of the genus by the long cylindrical body setae (longest posterior setae ca. 0.052 mm) and normal shorter setae ca. 0.017–0.039 mm in length. It lacks cylindrical setae on the dorsum of the manubrium and has broad humps on the dorsum of the dentes. The clavate tenent hairs are 1-2-3 or 4 on the fore–hindlegs.

Description. Maximum length, exclusive of appendage, is 0.9 mm. Organ lengths are shown in Table 6. Total length of antennae not seen on holotype, but on the paratype it is about 1.4 times as long as the head. Fourth antennal segment about as wide as the third segment, densely setaceous (Fig. 13F) with numerous curved setae, a few of which appear to be cylindrical and truncate while others acuminate. Somewhat longer straight setae are common and these are all acuminate. The third antennal segment has many (over 30) setae, all acuminate and smooth. The chaetotaxy of the first and second antennal segments is not clear. The ommatidia are not visible on the holotype, but four were seen on one side of the paratype. The labial palp is clear and has six smooth setae (Fig. 12B). A ca. 0.04-mm-long seta occurs between the labrum and labium and a series of these occur at the base of the labrum. Whether the latter are in a row or not is unclear. No post-antennal organ can be seen on the holotype, but

Table 6
Myanmar Cretaceous Isotomidae, described species (measurements in mm)

Specimen	Cephalic diagonal	Antenna 1	Antenna 2	Antenna 3	Antenna 4	Thorax 2	Thorax 3	Abdomen 1	Abdomen 2	Abdomen 3	Abdomen 4	Abdomen 5	Abdomen 6	Hind tibiotarsus	Hind femur	Manubrium	Dens	Mucro	Head + body
Villusisotoma brevis																			
Holotype	0.152	0.02	0.05	0.03	0.06	0.05	0.06	0.05	0.06	0.065	0.072	0.03	0.025	?	?	0.094	0.10	0.010	0.565
Paratype	0.226	0.03	0.077	0.05	0.11	0.052	0.074	0.04	0.064	0.076	0.090	0.048	0.038	0.066	0.048	0.126	0.126	?	0.708
Villusisotoma longa																			
Holotype	0.265	?	?	0.078	0.130	0.156	0.065	0.062	0.078	0.104	0.138	0.060	0.041	?	?	0.136	0.312	0.026	0.961
Paratype	0.172	0.022	0.056	0.047	0.095	0.076	0.047	0.048	0.043	0.082	0.078	0.043	0.038	0.077	0.068	?	?	?	0.611
Proisotoma s.l. *petersonae*																			
Holotype	0.228	?	?	?	?	0.073	0.062	0.060	0.078	0.081	0.099	0.049	0.039	0.078	0.054	0.198	0.238	0.023	0.769
Burmisotoma lamellifera																			
Holotype	0.224	0.026	0.065	0.047	0.082	?	?	0.042	0.050	0.060	0.086	0.040	0.036	0.107	0.077	0.086	0.151	0.018	0.847
Propachyotoma conica																			
818A1–3	0.200	0.026	0.056	0.050	0.094	0.08	0.05	0.051	0.056	0.073	0.065	0.043	0.030	0.086	?	?	0.202	0.010	0.648
Paratype	0.180	?	0.04	0.03	0.068	?	?	?	?	?	?	?	0.026	?	?	0.110	0.140	0.010	?
Holotype	0.154	?	0.044	0.045	0.072	0.070	0.05	0.044	0.066	0.080	0.068	0.045	0.032	0.070	0.050	0.129	0.194	0.014	0.529
Protoisotoma burma																			
Holotype	0.221	0.018	0.055	0.047	0.114	0.091	0.065	0.034	0.057	0.096	0.080	0.080	0.030	0.117	?	?	0.208	0.005	0.754
Paratype 2	0.225	?	?	0.035	0.100	0.125		0.035	0.055	0.100	0.090	0.105		0.115	?	0.115	?	?	0.735
Paratype 1	0.234	?	0.060	0.050	0.124	?	?	?	?	?	0.098	0.052	0.031	?	?	0.143	0.208	0.005	~0.78
Paratype 3	0.190	?	0.052	0.043	0.112	0.091	0.065	0.039	0.065	0.123	0.079	0.078		?	?	?	?	?	0.730
Protodesoria granda																			
Holotype	0.290	0.045	0.119	0.132	0.171	0.132	0.138	0.053	0.105	0.158	0.125	0.078	0.052	0.158	0.132	0.185	0.329	0.025	1.12
Paratype	?	?	?	?	?	0.095	0.10	0.050	0.085	0.125	0.115	0.050	0.035	0.115?	0.090	0.104	0.247	0.013	?

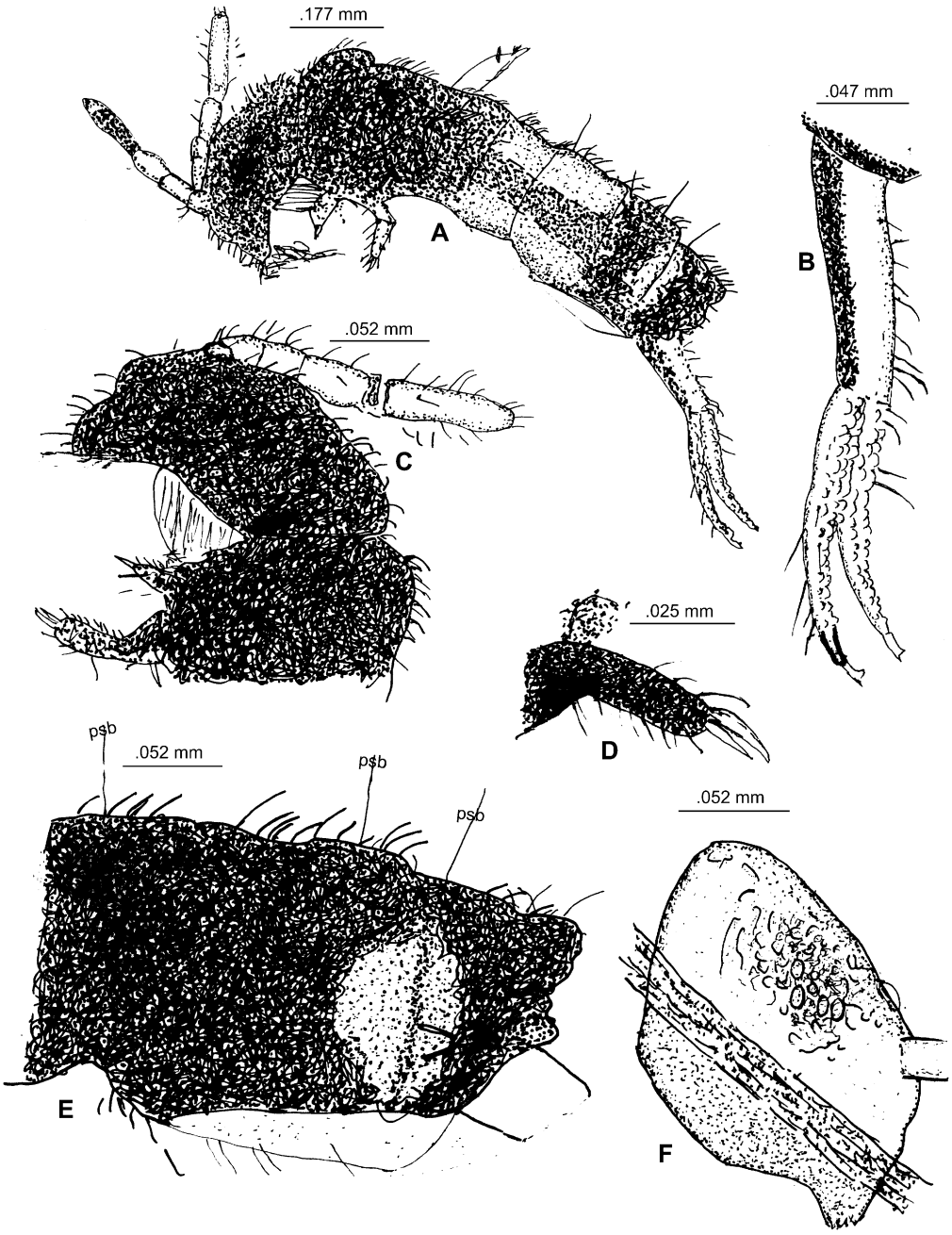

Fig. 12. *Villusisotoma brevis* sp. nov. A–E, holotype. A, habitus. B, furcula. C, detail of left antenna, head and mesothorax. D, hind foot complex and tibiotarsus. E, detail of abdominal segments 2–6 (psb, pseudobothriotricha). F, paratype, head seen from right side.

a simple one is seen on one side of the paratype. The head is clothed dorsally with a few short curved, cylindrical setae and many short, curved, smooth, acuminate setae (Fig. 13C). The ventral and lateral surfaces have only acuminate setae. The setae on the vertex of the head are much longer than the other cephalic setae. The thorax (Fig. 13D) and abdomen (Fig. 13A) have numerous curved, cylindrical rugose or very finely ciliate setae ranging from 0.017 to 0.052 mm in length with the longer setae on the posterior part of the abdomen (Fig. 13F). Interspersed among these are straight, smooth, acuminate setae ranging from 0.04 to 0.08 mm in length plus many 0.013–0.018-mm-long curved acuminate setae. One pseudobothriotrichum was seen on each segment. The tibiotarsal setae are unclear, but are apparently acuminate and smooth on the basal portions while curved and truncate on the distal portions of the leg. The unguis is slender and without teeth. The unguiculus is angulate, with a minute corner tooth on the fore foot. Tenent hairs are clavate and 1-2-3 or 4 on the fore–hindlegs, with two of the posterior tenent hairs much longer than the others. In addition to the typical tenent hairs, the mid- and hindlegs have two heavy curved slightly clavate setae just above the tenent hairs. The furcula is about half as long as the body. The manubrium about 70% as long as the dentes and equipped dorsally with at least 20 short (ca. 0.02 mm long) stout, smooth acuminate setae and possibly

two straight long setae. The anterior (pair?) ca. 0.038 mm and the posterior (pair?) ca. 0.085 mm. The ventral surface is not clear and no clear setae were seen. The dens has 10–15 straight, or slightly curved smooth, acuminate setae dorsally, ranging from 0.025 to 0.047 mm in length (Fig. 13G). The ventral surface has about 25 very short (0.006–0.008 mm long) slightly curved, smooth, acuminate setae. The ventro-lateral surface has a row of about twelve (ca. 0.01 mm long) slightly curved, smooth, acuminate setae. The measurements are shown in Table 6. The integument of the head and body is smooth or very finely granulate.

Remarks. The body and the head of the holotype are almost entirely opaque and can thus be seen only in profile. The density of the setae is so great that it is difficult to make out individual setae. The long setae on the manubrium are questionable. In neither case can an appropriate paired socket be seen and the position does not indicate unpaired setae. The paratype is both much smaller than the holotype and very decayed. A portion of the paratype's posterior abdominal cuticle is torn away from the rest and cleared. This appears to show a series of humps, most of which bear setae at their apices. This is never clear on the rest of the animal or on the holotype.

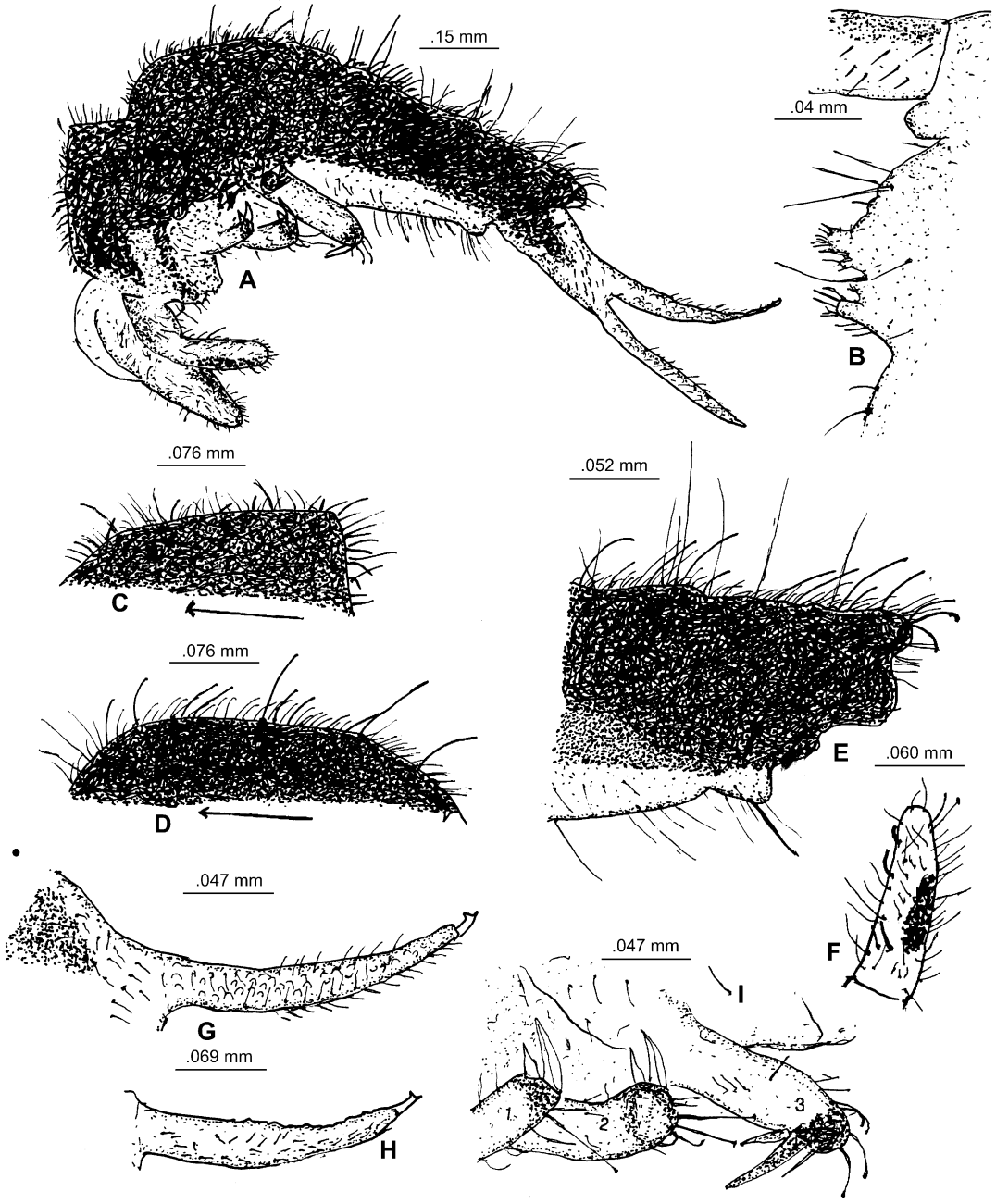

Fig. 13. *Villusisotoma longa* sp. nov. All figures of holotype. A, habitus. B, apex of head. C, dorsum of head. D, dorsum thoracic segments two. E, posterior of abdomen. F, left fourth antennal segment. G, dorsum right dens. H, venter of same. I, foot complexes (1, prothoracic; 2, mesothoracic; 3, metathoracic).

The tenent hairs are difficult to distinguish from neighboring smaller truncate setae.

Genus *Proisotoma* Börner, 1901

Type species. *Isotoma minuta* Tullberg, 1871.

Remarks. This genus has generally been defined as containing all species of Isotomidae with ommatidia, five or six abdominal segments, fully developed furcula and having six or fewer ventral manubrial setae. It has been subdivided into a number of subgenera, which are often raised to generic status.

Proisotoma pettersonae sp. nov.
Figs. 14A, 15

Derivation of name. In honor of Stephanie Peterson, whose work on this manuscript was very valuable.

Holotype. AMNH Bu 818-A1 specimen 1. American Museum of Natural History.

Type locality and stratigraphic horizon. Myanmar (Burma), Kachin State, Hukawng Valley, 32 km southwest of Tanai, near Noije Bum (hill), approx. 250 m; mid Cretaceous.

Material. Holotype only.

Diagnosis. Distinguished from other members of the genus by the small dorsal tubercles on the dentes combined with the very small non-lamellate mucro.

Description. Length, exclusive of appendages, is 0.75 mm. Lengths of organs are shown in Table 6. Four antennal segments are badly disoriented so that the relative lengths are not determinable. The fourth antennal segment has numerous small (0.007–0.015 mm long) smooth acuminate setae (Fig. 15A); the third segment has numerous curved ca. 0.03-mm-long acuminate smooth setae. The second segment distally has similar setae and basally has straight, smooth, ca. 0.02-mm-long, acuminate setae. The first segment has a few such straight setae. The head has at least 6 + 6 ommatidia, but no post-antennal organ was seen. The head is clothed with straight smooth, acuminate 0.01–0.02-mm-long setae. The thoracic segments are clothed mostly with short straight 0.015–0.03-mm-long smooth acuminate setae. At each posterior lateral margin there is a larger (0.05 mm) heavy, curved smooth acuminate seta. The abdomen is clothed with a mixture of straight and weakly curved 0.03–0.10-mm-long setae. Small blunt sensory setae are visible on the fourth abdominal segment (Fig. 15C, D). On the dorsal surface these are positioned before the posterior row of setae. At the tip of the sixth segment there are several 0.05-mm-long thicker setae. The furcula is well developed with one or possibly two pairs of ventral and at least five dorsal manubrial setae. The dens is tapered and has numerous small tubercles dorsally (Fig. 15B), with at least six ventral setae on the distal half and at least five dorsal setae. The mucro is small (0.023 mm long), bidentate, and without lamellae. One hindleg is the only one with all parts visible. Its coxa has at least five setae of varying lengths. The longest of these is a thick, curved, 0.03-mm-long, truncate seta. Distal of this is a thick curved, acuminate seta. A pair of these is present on the trochanter. The femur bears at least nine curved, acuminate setae (0.015–0.05 mm long) and a single thick 0.05-mm-long acuminate seta on the anterior median face. The tibiotarsus has numerous straight, to slightly curved acuminate setae ranging from 0.015 to 0.05 mm in length. The unguis is simple and untoothed with an acuminate unguiculus about half as long as the inner unguis. The hindleg has a pair of clavate tenent hairs (Fig. 15E), one longer than the other. The anterior legs, so far as can be seen, appear to be clothed similarly to the hindlegs, but have only a single truncate tenent hair. The angle of viewing of these makes it impossible to say if the prominent setae mentioned above are present. The manubrium is devoid of setae and the dentes is dorsally tuberculate with five dorsal and seven ventral short acuminate setae.

Remarks. This genus keys out to *Proisotoma* in both the Potapov (2001) key and the Christiansen and Janssen World Wide Web (WWW) key. The mid-tergal position of the sensory setae on the dorsum of the fourth abdominal segment and long furcula would place this species close to putative primitive subgenera such as *Scutisotoma*, *Dimorphotoma*, and *Rhodanella* in recent splitting of the genus into smaller genera or subgenera. This is the only species of known Cretaceous Collembola ascribable to an extant genus. Even so, the inability to see the region of the post-antennal organ makes the placement in this genus somewhat tentative.

Genus *Burmisotoma* gen. nov.

Derivation of name. After the former name of the country of discovery, Burma.

Type species. *Burmisotoma lamellifera* sp. nov., mid Cretaceous, Myanmar (Burma).

Diagnosis. The genus belongs to the subfamily Anurophorinae of Potapov (2001) or the subfamily Proisotominae of Stach (1947). It is distinguishable from other genera of these taxa by the combination of having a well-developed furcula with no ventral manubrial setae, a strongly tapered dentes with ten or more ventral setae, numerous dorsal setae, and many small dorsal tubercles. The mucrones are bidentate and lamellate. The genus is also distinguishable by the presence of stout, cylindrical truncate setae and ommatidia.

Included species. Type species only.

Remarks. This genus and species key out to either *Clavisotoma* or *Ballistura* in both the Potapov (2001) key and the Christiansen and Janssen WWW key. However, it differs

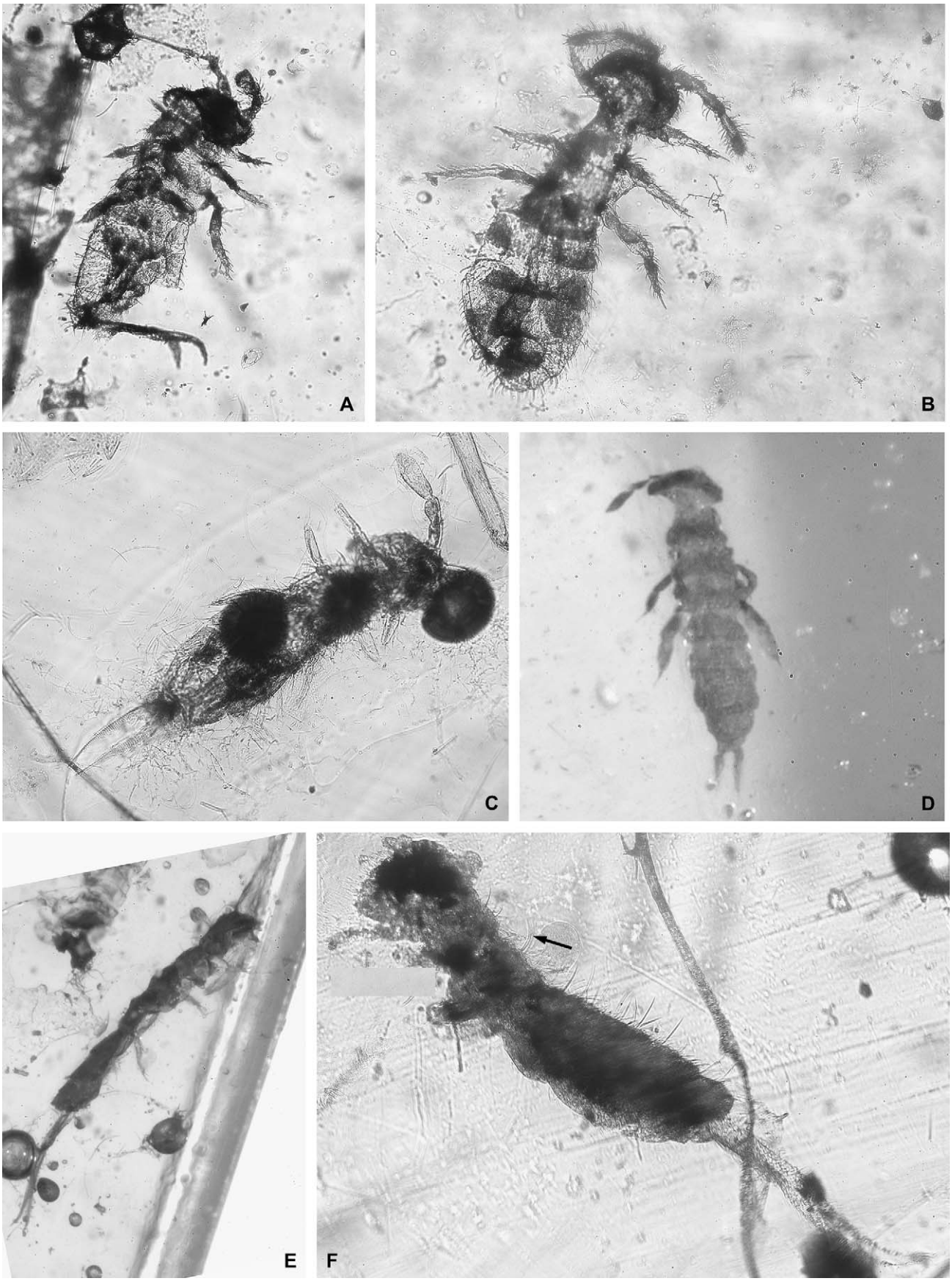

Fig. 14. Habitus of holotypes (total length of specimen exclusive of appendages in mm). A, *Proisotoma pettersonae* sp. nov. (0.76 mm). B, *Burmisotoma lamellifera* sp. nov. (0.840 mm). C, *Protoisotoma burma* sp. nov. (0.75 mm). D, *Propachyotoma conica* sp. nov. (0.60 mm). E, *Protodesoria granda* sp. nov. (1.13 mm). F, Isotomidae incertae sedis, taxon 1 (0.91 mm).

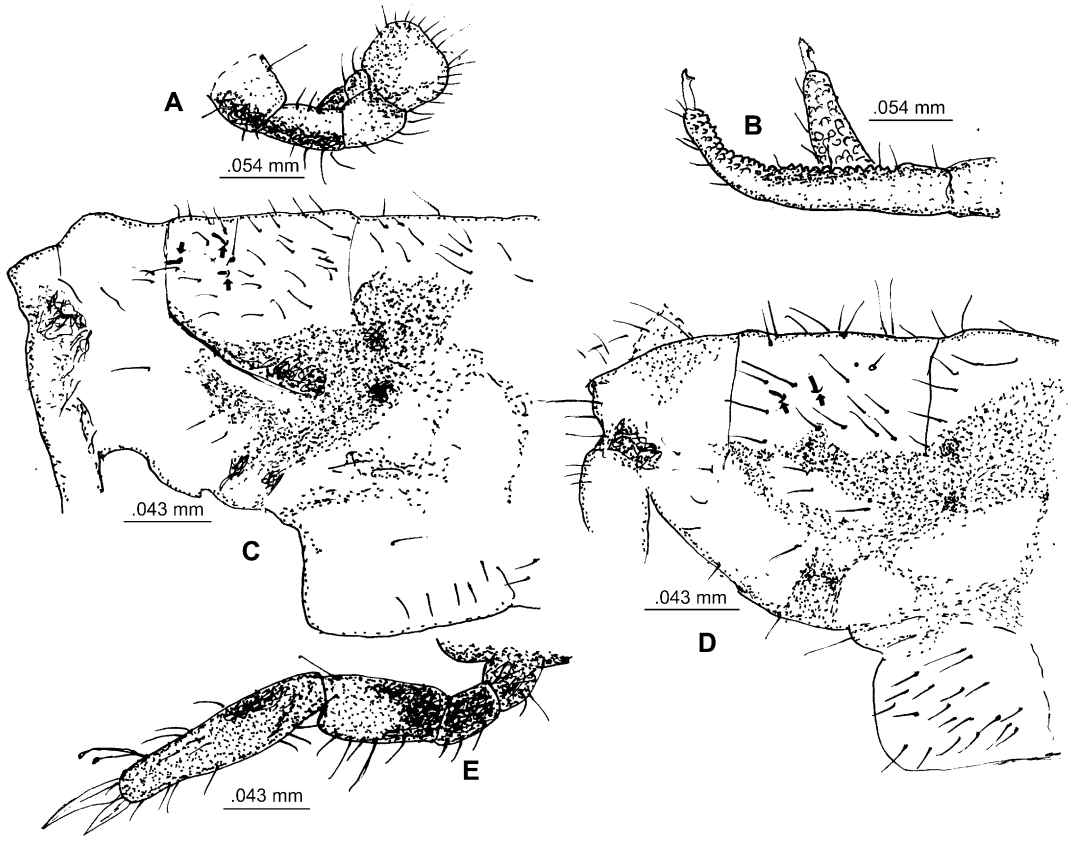

Fig. 15. *Proisotoma petersonae* sp. nov. All figures of holotype. A, right antenna. B, dentes and mucrones. C, posterior abdomen, left side, arrows show sensory setae. D, posterior abdomen, right side, arrows show sensory setae. E, hindleg.

from both by: (1) having cylindrical blunt or truncate setae on the antennae and legs; (2) the dentes being strongly tapered; and (3) having the mucro much shorter (12%) than the dens. It is similar to *Villusisotoma*, but differs in not being pleurochaetotic, lacking the numerous cylindrical setae over the head and anterior body and by having lamellate mucrones lacking pseudobothriotricha.

Burmisotoma lamellifera sp. nov.
Figs. 14B, 16

Holotype. AMNH Bu 818 A 2 specimen 7. American Museum of Natural History.

Type locality and stratigraphic horizon. Myanmar (Burma), Kachin State, Hukawng Valley, 32 km southwest of Tanai, near Noije Bum (hill), approx. 250 m; mid Cretaceous.

Material. Holotype only.

Diagnosis. As for genus.

Description. Length, exclusive of appendages, is 0.85 mm. Organ lengths are shown in Table 6. The fourth antennal segment is densely setaceous with setae mostly weakly curved and acuminate, varying from 0.007 to 0.04 mm long (Fig. 16B). A number of these setae are cylindrical and truncate including several 0.025–0.03-mm-long thick truncate setae on the apical half of the segment. The second and third segments have a similar range of setae, but lack the thick shorter truncate ones. The ommatidia are at least 6 + 6 (Fig. 16A). No post-antennal organ was seen. The head is densely clothed with 0.007–0.018-mm-long, mostly curved, acuminate setae. The first thoracic segment is membranous, without setae. The second and third segments are highly distorted and with most setae being lost. The setae remaining are short, weakly curved and acuminate. The first abdominal segment is obscured by body contents. Abdominal segments 2–6 (Fig. 16C, D) are sparsely setaceous with smooth, mostly acuminate, straight to weakly curved setae ranging from 0.015 to 0.040 mm long. The sixth abdominal segment with a few cylindrical blunt, 0.04-mm-long curved setae. The legs are mostly clothed with 0.015–0.020-mm-long, weakly curved acuminate smooth setae. The hind- and mid-trochanters each has one 0.05-mm-long curved cylindrical blunt seta, and hind tibiotarsus has several shorter (ca. 0.03 mm long) such setae. The hind femurs (Fig. 16E) have a peculiar cluster of curved acuminate setae near the inner apex, giving the appearance of a spine under low magnification. The unguis and unguiculus are unclear from dorsal or ventral views, but from a frontal angle the unguis is seen in plan view to be simple, without teeth while the unguiculus is acuminate and about half as long as the inner unguis. Each foot has one tenent hair, strongly clavate on the hind foot and weakly clavate

(Fig. 16F) or truncate on the others. The furcula has all segments well developed. The manubrium has no ventral setae and numerous, curved, short, acuminate dorsal setae. The dentes are strongly tapered with 10–13 ventro-lateral setae, which are short, weakly curved to straight, acuminate (Fig. 16G). The dens has numerous small tubercles along whole dorsal surface and 3–4 short acuminate setae. The mucrones are lamellate with two teeth. The cuticle is smooth.

Remarks. The holotype has the furcula appressed to the body and some features are thus difficult to see, it is possible that a single large seta occurs near the base of ventral surface of the dens, but is also possible that this has been displaced from elsewhere. This is one of the better specimens we saw, being well cleared, with many setae preserved and not badly distorted. The fact that the furcula was drawn up and had to be seen appressed to the body created some problems in interpreting this structure. It is possible to see the head from an angled frontal view in the amber in which it is imbedded. This allowed us to see the ommatidia better than from the top view. They are still somewhat obscured, but appear to be at least six per side. No clear post-antennal organ could be seen but the area where it would occur is somewhat obscured.

Genus *Protoisotoma* Christiansen and Pike, 2002

Type species. *Protoisotoma micromucra* Christiansen and Pike, 2002.

Remarks. This extinct genus is characterized by having a greatly swollen fourth antennal segment, a post-antennal organ, and a minute mucro. The dens is elongate and clearly crenulate dorsally, with or without setae. The body is densely covered with curved, acuminate, smooth setae plus erect pseudobothriotricha on the abdomen.

Protoisotoma burma sp. nov.
Figs. 14C, 17

Derivation of name. After the former name of the country from which the sample was collected.

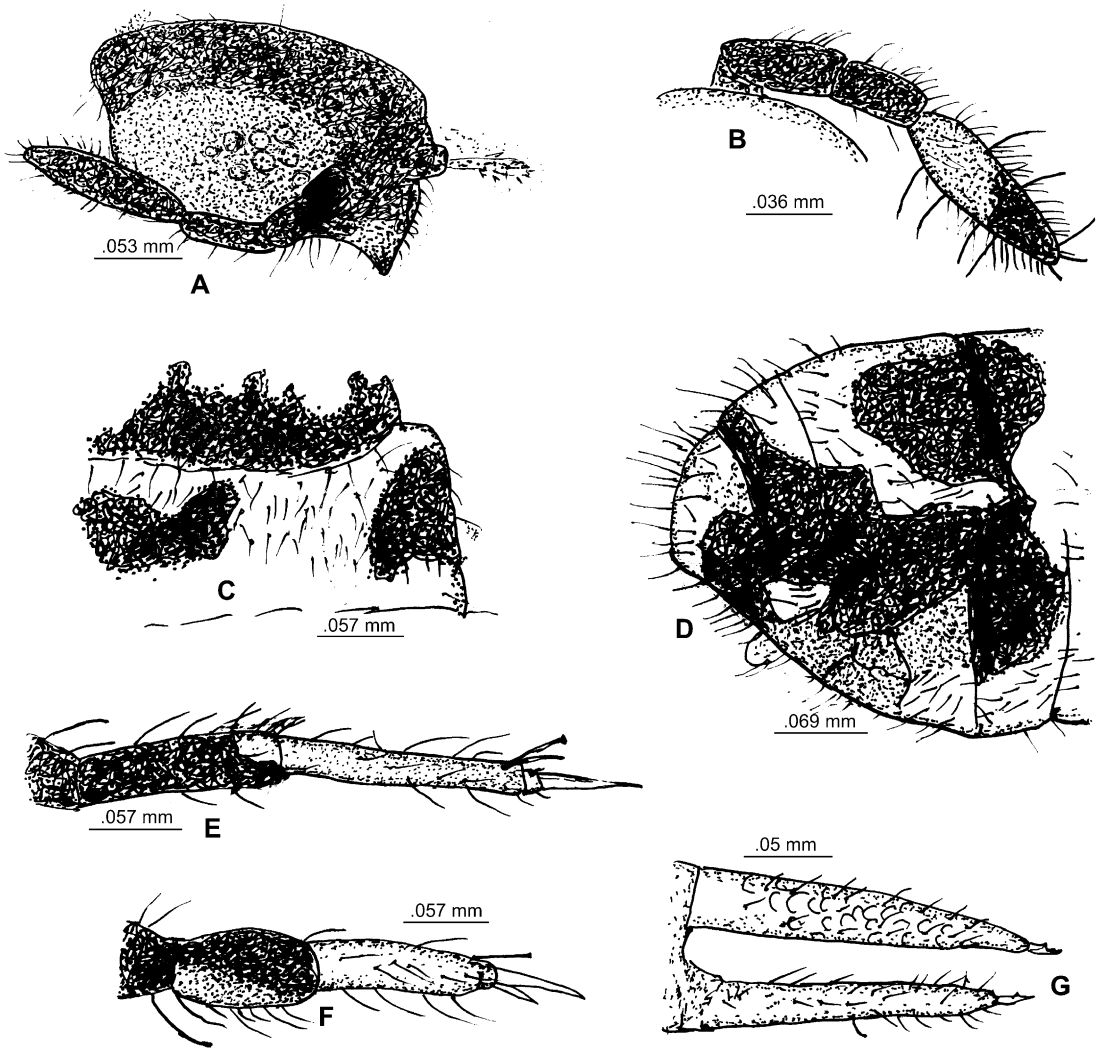

Fig. 16. *Burmisotoma lamellifera* sp. nov. All figures of holotype. A, head seen from front. B, right antenna. C, right side second abdominal segment. D, abdominal segments 3–6. E, hindleg. F, mid-leg. G, dentes (above, dorsal surface; below, ventral surface).

Holotype. AMNH Bu 1074A1 specimen 1. American Museum of Natural History.

Type locality and stratigraphic horizon. Myanmar (Burma), Kachin State, Hukawng Valley, 32 km southwest of Tanai, near Noije Bum (hill), approx. 250 m; mid Cretaceous.

Material. Holotype plus six paratypes: AMNH Bu 1074A1, specimens 3 and 4; AMNH Bu 1074A2, specimens 2 and 3; and AMNH Bu 1074A3 specimens 1 and 2.

Diagnosis. This species can be distinguished from other species of *Protoisotoma* by its somewhat longer fourth antennal segment setae and by the total absence of truncate setae. In this characteristic it resembles Form 2 of *Protoisotoma*, but differs from this form in lacking long dental setae, and having the fifth and sixth abdominal segments together measuring longer the fourth.

Description. Maximum length, exclusive of appendages, is 0.75 mm. There are four antennal segments with the fourth segment swollen and 2.42–2.85 times as long as the third. Organ measurements as shown in Table 6. The fourth antennal segment (Fig. 17C) is clothed with small (ca. 0.017 mm long), smooth, acuminate setae. The second and third segments are similarly clothed, but have a few longer (0.03 mm) setae. At least 6 + 6 ommatidia are present as well as a small, possibly lobed, post-antennal organ (Fig. 17E). The head has numerous smooth acuminate setae (Fig. 17A) ranging from 0.013 to 0.03 mm in length. The thorax (Fig. 17A) and abdomen (Fig. 17B) have numerous similar setae, which are somewhat longer (0.078–0.085 mm), which are scattered in the holotype but abundant in one paratype. There are four pairs of longer (0.15 mm) pseudobothriotricha, two on the second and third abdominal segments and four on the fourth segment. The legs cannot be seen clearly on any specimen except for the hind tibiotarsus on the holotype and two paratypes. Here setae are absent and the unguis is simple and untoothed. The manubrium has at least six dorsal setae and numerous small, acuminate, smooth ventral setae (Fig. 17D). The dentes are long and slender, dorsally crenulate, with numerous very small dorsal and lateral setae and few or no ventral setae, limited to the basal third of the organ. The mucrones are minute (0.005 mm or less) and bidentate.

Remarks. This species displays the characteristics of the genus *Protoisotoma*, i.e., a swollen fourth antennal segment, minute mucrones, at least 6 + 6 ommatidia, numerous ventral manubrial setae and a post-antennal organ. Overall, the species is remarkably similar to specimens of the same genus from Late Cretaceous Canadian amber, previously described as Form 2. The genus was previously known only from the Canadian material. The post-antennal organ cannot be seen clearly on any specimen, but appears to be complex with lobes or subdivisions. Pseudobothriotricha appear to be much less numerous in this species than in other species, but the small nature of the samples combined with the fragility of these setae makes it impossible to be certain that other pseudobothriotricha do not exist. The manubrium can be seen clearly on only one paratype, but here the numerous small ventral setae are highly visible. The dental setae are seen clearly only on the holotype and two paratypes. None of the specimens shows the claws clearly.

Genus *Propachyotoma* gen. nov.

Derivation of name. After the most similar extant genus, *Pachyotoma*.

Type species. *Propachyotoma conica*, mid Cretaceous, Myanmar (Burma).

Included species. Type species only.

Diagnosis. This genus is distinguished from other genera of the Anurophorinae or Proisotominae by the combination of six well-developed abdominal segments and, a long, slender furcula with peculiar small, dorsal triangular projections on the dens. The manubrium and dorsal surface of the dens lack setae and there is a body clothing of numerous very fine, small, acuminate, smooth setae. There are at least six ommatidia per side and a simple post-antennal organ. The unguis is simple and clear; clavate or truncate tenent hairs are lacking.

Propachyotoma conica sp. nov.
Figs. 14D, 18

Derivation of name. Latin, *conica*, for the conical dental projections.

Holotype. AMNH Bu 818A2, specimen 12. American Museum of Natural History.

Type locality and stratigraphic horizon. Myanmar (Burma), Kachin State, Hukawng Valley, 32 km southwest of Tanai, near Noije Bum (hill), approx. 250 m; mid Cretaceous.

Material. Holotype and paratype AMNH Bu 818A1, specimen 4.

Diagnosis. As for the genus.

Description. Length, exclusive of appendages, is 1.1 mm (Fig. 18A). The lengths of organs as shown in Table 6. Antennae are slightly longer than the cephalic diagonal. The fourth antennal segment with a small apical bulb, slightly less than twice as long as the third, which is subequal to or slightly shorter than the second segment. The antennae are clothed with a number of short (0.003–0.009 mm) smooth, slender acuminate setae (Fig. 18D, H). The ommatidia are unclear but 5–6 ommatidia were seen with a reflected light microscope on the holotype as well as a simple post-antennal organ about twice as large as the largest ommatidia. The head and body are mainly clothed with slender, smooth, acuminate setae, 0.005–0.009 mm long. A few longer such setae

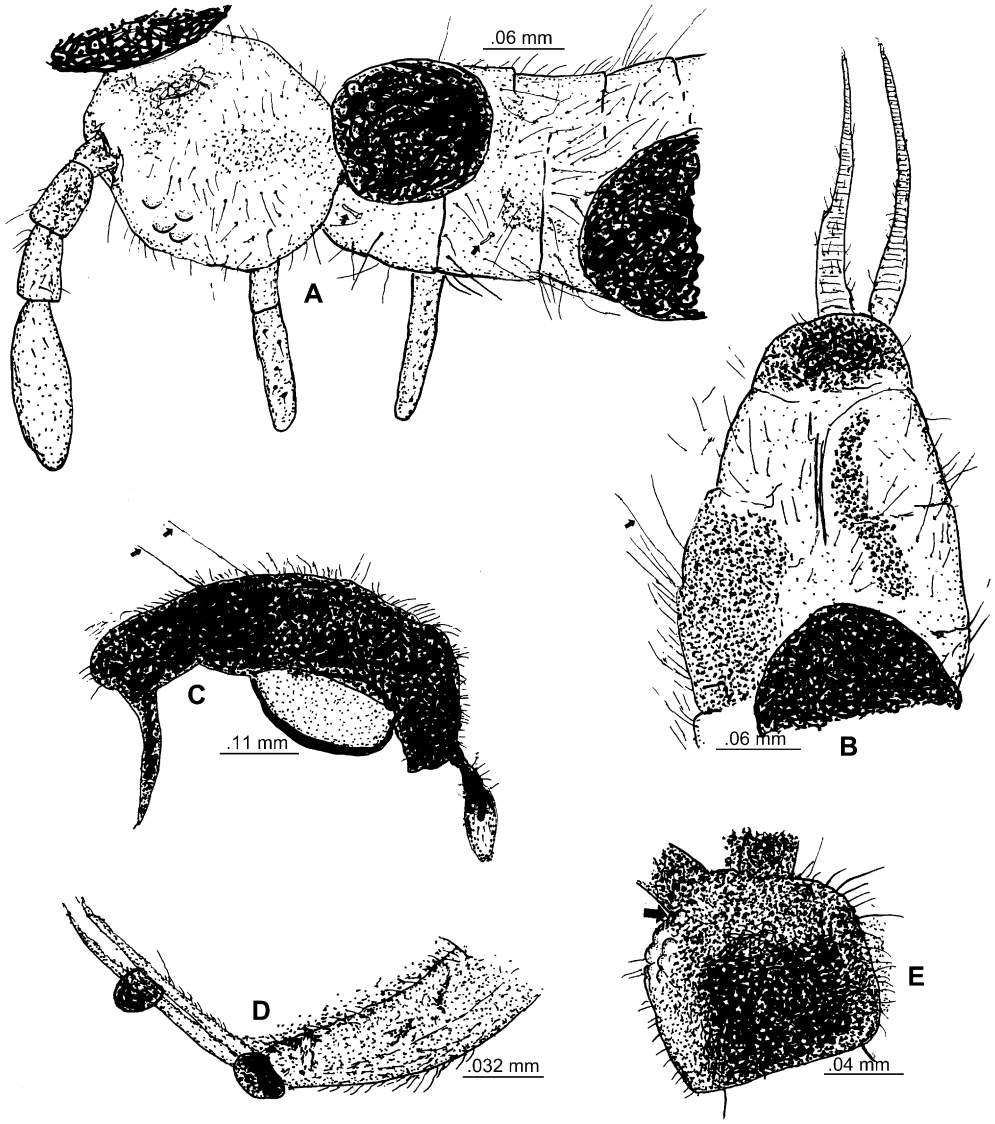

Fig. 17. *Protoisotoma burma* sp. nov. A, holotype, dorsal surface head, thorax and anterior abdomen (arrows, ''sensory'' setae). B, holotype, posterior abdomen and furcula (arrow, pseudobothriotrichum). C, paratype 1074A1 specimen 4, habitus (arrows, pseudobothriotricha). D, paratype 1074A1 specimen 3, furcula. E, sample 1074A2 specimen 3, head from above (arrow, post-antennal organ).

(0.02–0.024 mm) are found on the thorax and abdomen. Curved (ca. 0.02 mm long) truncate, cylindrical setae (Fig. 18B, C) are scattered over the head and body. Few setae are seen on the legs but those visible are similar to the smaller body setae. No tenent hairs are present. The unguis is simple and untoothed. The unguiculus is untoothed, acuminate, and with the slope on the inner edge only. The furcula is 1.1–1.4 times as long as the cephalic diagonal, with the dens 1.3–1.5 times as long as the manubrium. No setae were seen on the venter of the manubrium, but the dorsal surface has several acuminate setae and two distal curved truncate setae (Fig. 18E). There are four acuminate setae on the basal half of the dorsal side of the dentes; the ventral side has six smooth, curved, acuminate setae. The dentes have 8–9 dorsal small conical projections (Fig. 18E, G). The mucro is small (0.010–0.016 mm in length) with a distal clear subapical tooth and a minute apical tooth projecting back. The integument is finely granulate (Fig. 18I, J).

Remarks. The paratype is devoid of setae. In the Christiansen and Janssen WWW key this genus keys out to *Pachyotoma*. In Potapov's key it keys out to *Pachyotoma* or *Archisotoma* Linnaniemi (1912). The genus is easily separable from both. The long slender dentes, the presence of small triangular projections and few setae on the dorsum of the dentes as well as the granulate integument unlike *Pachyotoma*. The dentes and the mucrones separate genus 4 from *Archisotoma*. On the mid-leg of one specimen of *Propachyotoma* there appear to be two 0.012-mm-long curved blunt setae, but their absence on the other specimen leads us to believe they are artifacts. AMNH Bu 818A1 specimen 3 is almost certainly another member of this genus; however, it differs from the holotype in lacking head and body setae (Fig. 18F) but this is a probable taphonomic phenomenon. It also has somewhat larger integumentary granulations. It may represent a separate species, but it is possible that there is sexual dimorphism within one species.

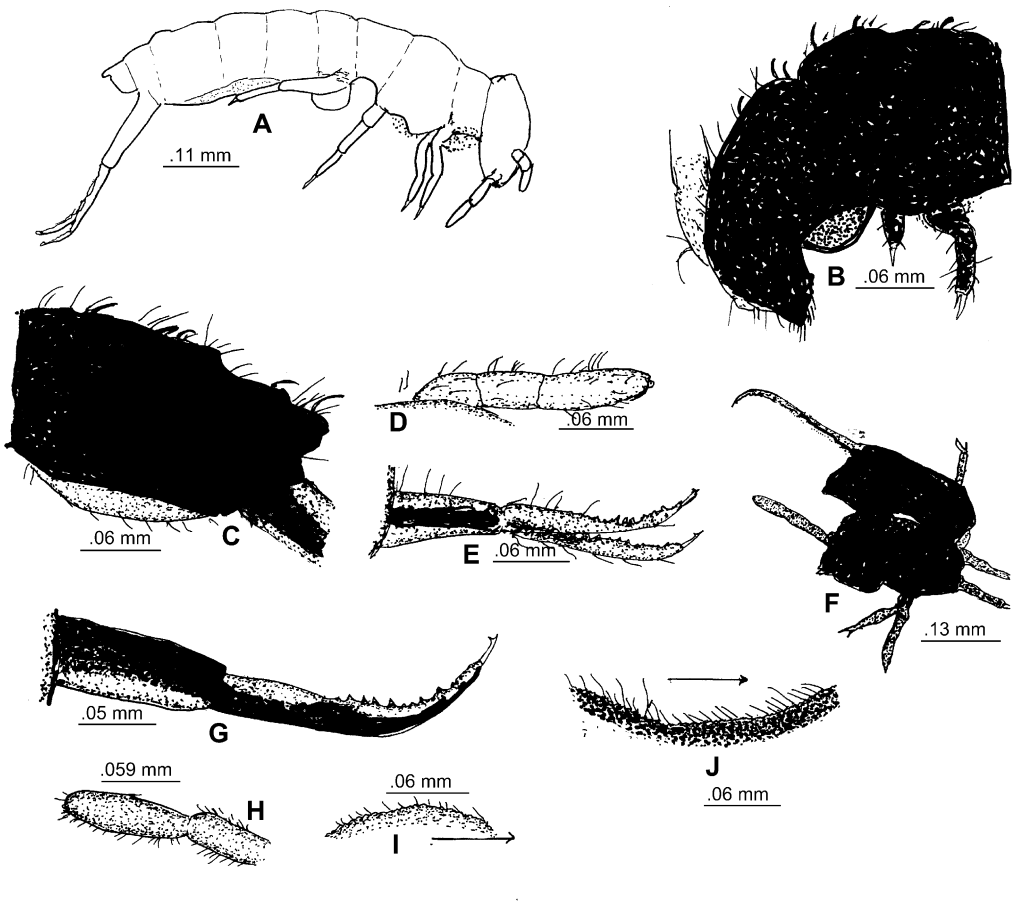

Fig. 18. *Propachyotoma conica* sp. nov. A–E, holotype. A, outline habitus showing segmental margins. B, detail of head and thorax. C, detail of abdominal segments 3–6. D, right antenna. E, furcula. F, habitus, paratype. G, furcula, paratype. H, antennal segments 3 and 4, sample 818A1 specimen 3. I, outline of dorsum of head, same specimen. J, outline of dorsum of abdominal segments 2–4.

Genus *Protodesoria* gen. nov.

Derivation of name. After the most similar extant genus, *Desoria* Nicolet, 1841.

Type species. *Protodesoria granda* sp. nov., mid Cretaceous, Myanmar (Burma).

Diagnosis. Six clear abdominal segments, at least six ommatidia per side, and a manubrium with numerous small ventral setae, crenulate dens and a small mucro without lamellae as well as three teeth all characterize the genus. The fourth antennal segment is slightly swollen and the body is equipped with cylindrical rugose or finely ciliate setae and spine-like heavy setae. Bothriotricha and pseudobothriotricha are absent. Clavate tenent hairs are lacking.

Included species. Type species only.

Remarks. This genus is similar to the extant genus *Desoria* but differs from the latter in possessing cylindrical rugose or finely ciliate setae. *Protodesoria* is like *Villusisotoma* (described herein) in this respect, but these are much less numerous in than those in *Villusisotoma*. *Protodesoria* also differs from *Desoria* in possessing multilaterally ciliate setae as well as in the presence of one or more thoracic spines. The enlarged fourth antennal segment is similar to the genus *Protoisotoma*; however, it differs from the latter genus in having a larger and tridentate mucro, no pseudobothriotricha and in having abundant ventral dental setae. The genus is of interest since the head-to-body ratio more nearly approaches that seen in most extant genera than does this ratio in the majority of Cretaceous Burmese Isotomidae.

Protodesoria granda sp. nov.
Figs. 14E, 19

Derivation of name. Latin, *granda*, referring to its relatively large size.

Holotype. AMNH Bu 1452C specimen 9. American Museum Natural History.

Type locality and stratigraphic horizon. Myanmar (Burma), Kachin State, Tanai Village (on Ledo Road, 105 km from Miyitkama); collected by Leeward Capitol Corp.; mid Cretaceous.

Material. Holotype and paratype same sample specimen 11.

Description. Holotype length, exclusive of appendages, is 1.32 mm; lengths of organs are shown in Table 6. There are four antennal segments with segmental ratios 1–4 as 1-2.6-2.9-3.8. The third (Fig. 19B and C respectively) have numerous short smooth setae ranging from 0.003 to 0.005 mm in length. The fourth segment is slightly swollen and has a clear pin seta on its apex. The second segment is less densely setaceous, with mostly 0.03-mm-long acuminate smooth setae. The second segment has a few longer (0.04 mm) cylindrical truncate setae. The head has a number of curved, acuminate, smooth (ca. 0.03 mm long) setae on the dorsum and a number of longer (0.04 mm) such setae (Fig. 19A). The labrum is projecting and has clear ridged papillae such are characteristic of the genus *Isotomurus*. A prominent (0.055 mm long) forward projecting seta can be seen on one side of the labrum. There is probably one on each side. No labral ciliations were seen. The labial appendage has eight setae ranging from 0.005 to 0.02 mm in length. There are at least 6 + 6 ommatidia. An unclear but probable simple post-antennal organ was seen. Most of the body setae are smooth, 0.03–0.04 mm long, acuminate and weakly curved. There are a number of 0.08-mm-long spine-like setae, which are either curved or straight and acuminate (Fig. 19I), or cylindrical (Fig. 19D, M); several of these setae are still attached to the specimen, but most are nearby. The integument is smooth. The largest cylindrical setae have a rugose or finely ciliate surface. Also in the immediate vicinity are a number of acuminate multilaterally ciliate setae (one of which is possibly still attached). None of these setae resembles bothriotricha or pseudobothriotricha. The hind femur and tibiotarsus are densely clothed with straight to very slightly curved, heavy, smooth, acuminate (0.02–0.03 mm long) setae (Fig. 19E, F). The inner face of the femur also has two ca. 0.05-mm-long, straight prominent basal setae. The unguis is long, slender and toothless. The unguiculus is lanceolate (Fig. 19H), without any corner tooth. Clavate or clearly distinguished tenent hairs are absent. The manubrium has many small, smooth ventral setae and a pair of heavier (0.02 mm long) setae distally. The dorsum of the manubrium is unclear, but has a few slender acuminate smooth setae on both surfaces. The dens is densely setaceous on all surfaces, with short, smooth acuminate setae (Fig. 19J). The dorsal surface is clearly crenulate distally, but not basally. However, it is partly obscured by a bubble basally. The mucro is small (0.025 mm long), but bears three clear teeth with no lamellae or basal setae. The holotype bears an extremely minute basal toothlet, but this is missing from the smaller paratype.

Remarks. Because the holotype is fairly large, a number of features that could not be drawn with the arm on the compound microscope can nevertheless be clearly seen under the reflecting microscope. These include the ommatidia and the body segmentation. The post-antennal organs are seen only on the holotype, and are not very clear there. The paratype may be a different species, but a number of its features can only be seen on the confocal microscope, due to a large occluding bubble. In addition, the paratype does not show the head or antennae, so these cannot be compared. The only visible significant difference between the two specimens is the absence of the minute apical mucronal toothlet in the paratype. The occurrence of the two specimens close together in the same sample makes it seem unlikely that they are different species.

Isotomidae incertae sedis

Remarks. Like the specimens of the family Sminthuridae we examined, many specimens belonging to the Isotomidae could neither be placed in previously described genera, nor be reasonably excluded from it. Some of them, which are possible members of species described in this study, are mentioned in the remarks concerning the appropriate species. Most of the remainder are listed below by sample and specimen number, with some brief notes; however, the first two such taxa listed have specimens that are sufficiently well preserved to merit a description.

Incertae sedis taxon 1 (723C, specimen 3; Fig. 14F). Length, exclusive of appendages, is 0.94 mm; lengths of organs are shown in Table 6. Antennae are missing. At least 6 + 6 ommatidia can be seen. The head is badly decomposed, and little else is visible. The body, except for setae, is also badly decomposed, so the segmental margins are hard to determine. The first thoracic segment appears to be much more distinct than is normal for the Isotomidae. Legs are missing. The thorax and abdomen are clothed in numerous, mostly slightly curved, smooth, acuminate setae, ranging from 0.02 to 0.07 mm in length. In addition, there are numerous pseudobothriotricha and a few abdominal bothriotricha, all of which are ca. 0.1 mm long. On the metathorax, there is one heavy, rugose, curved acuminate spine. The manubrium and dens are both clothed with numerous slightly curved, smooth, acuminate (ca. 0.03 mm long) setae on all surfaces. The dentes is dorsally tuberculate, while the mucrones are slender and tridentate, with a minute ventral, apical toothlet.

Remarks. The poor preservation of this specimen makes it very difficult to place. Its general form and visible features would seem to place it in the Isotomidae; however, if the prothorax (not clearly visible) was well developed, such placement would be erroneous. The mucronal structure and presence of bothriotricha appear similar to *Isotomurus*, but the peculiar thoracic spine is quite distinct, as are the presence of bothriotricha and pseudobothriotricha. While the features just mentioned make it likely that this specimen is distinct from all extant and known extinct genera, we think it best not to describe it based on the poor material at hand. Another specimen, 1074D, may be congeneric; it is large and badly decayed, with numerous small, smooth acuminate body setae.

Incertae sedis taxon 2 (1452A 1, specimen 5; Fig. 20A). Length, exclusive of appendages, is 0.86 mm. Lengths of organs are shown in Table 6. Antenna 4 is four-segmented: the second segment is about twice as long as the first, the third segment is slightly shorter than the second, and the fourth segment is about

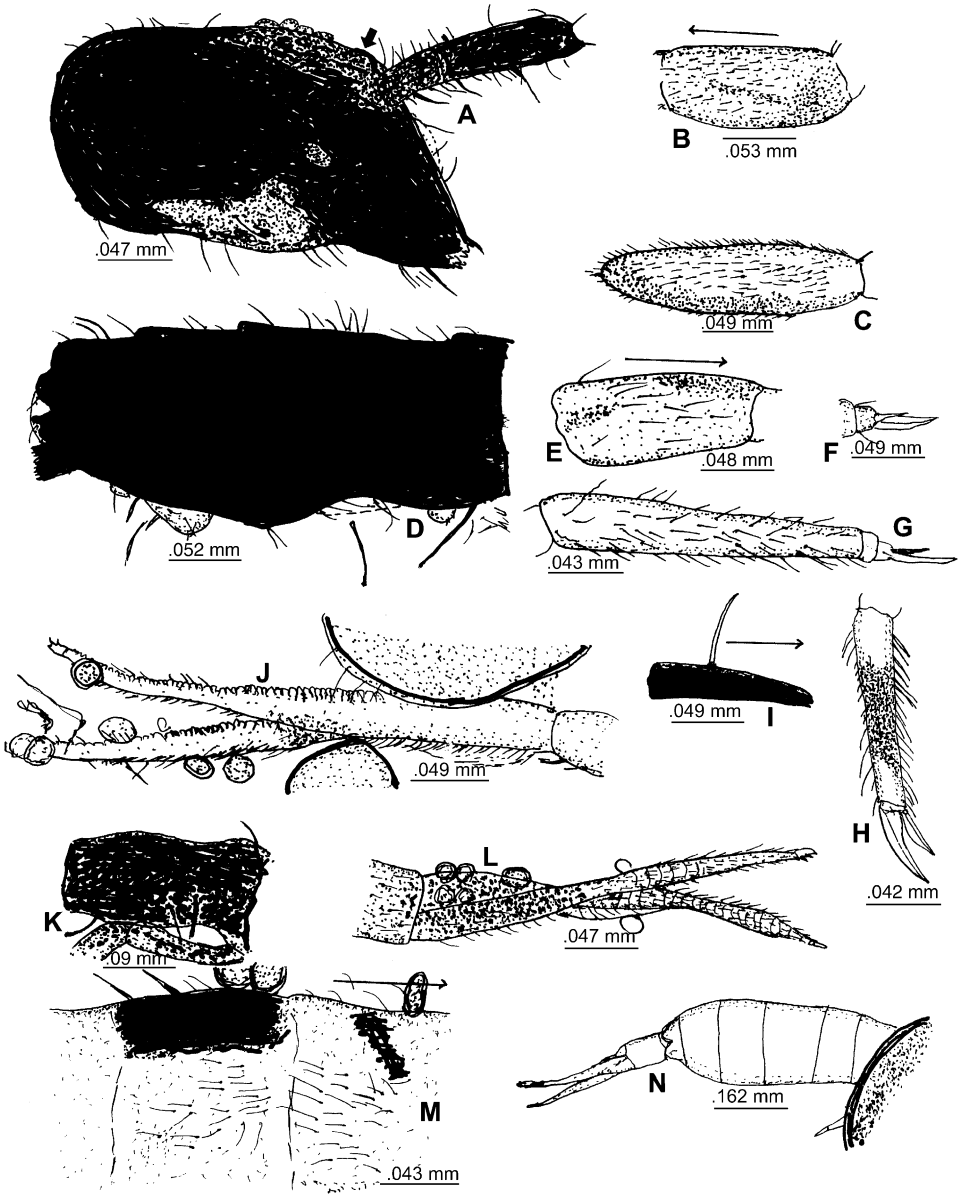

Fig. 19. *Protodesoria granda* sp. nov. A–K, holotype. A, head (arrow, post-antennal organ). B, flattened third antennal segment. C, flattened fourth antennal segment. D, posterior part of abdomen. E, outer face, hind femur. F, fore foot complex. G, hind tibiotarsus and foot complex. H, mid tibiotarsus and foot complex. I, dorsum of second thoracic segment showing spine-like setae. J, dentes and mucrones. K, spine-like setae of second abdominal segment. L, M, paratype. L, dentes and mucrones. M, chaetotaxy of second and third abdominal segments. N, posterior end in outline as seen in phase contrast microscope.

twice as long as the third. The fourth segment has numerous smooth acuminate (0.008–0.011 mm long) setae. The apex has a small, clear pin seta. The third and second segments are similarly clothed with a few 0.018 long setae. The head is similarly clothed with a few 0.031 long cylindrical smooth setae laterally. There are at least seven ommatidia on one side. A simple, almost circular post-antennal organ appears to occur at the base of the antenna, on one side. Thoracic segments are distorted greatly and unclear. Most tibiotarsi are sparsely clothed with (ca. 0.015 mm–0.025 mm long) straight, smooth, acuminate setae; one seta is ca. 0.04–ca. 0.05 mm in length. The femur is similarly clothed, but several of the setae are longer.

The unguis is short and stout, without teeth. Tenent hairs are absent. The unguiculus is untoothed and basally enlarged. The abdomen is sparsely clothed with straight to slightly curved (0.010–0.050 mm long) smooth, acuminate setae. The manubrium has numerous setae on both faces, but only the sockets are visible on the posterior face. The dens is crenulate, with numerous short, smooth, acuminate setae on both faces. The mucro is not clearly seen, but is ca. 0.015 mm long and probably bidentate.

Remarks. There is a peculiar fleshy projection on the right hind trochanter, but its absence on the other hindleg makes it probable that it is an artifact. While this genus is readily separable from all other known Cretaceous genera, its incomplete condition makes it impossible to separate it from the extant genus *Isotoma* s.l., yet at the same time impossible to place it

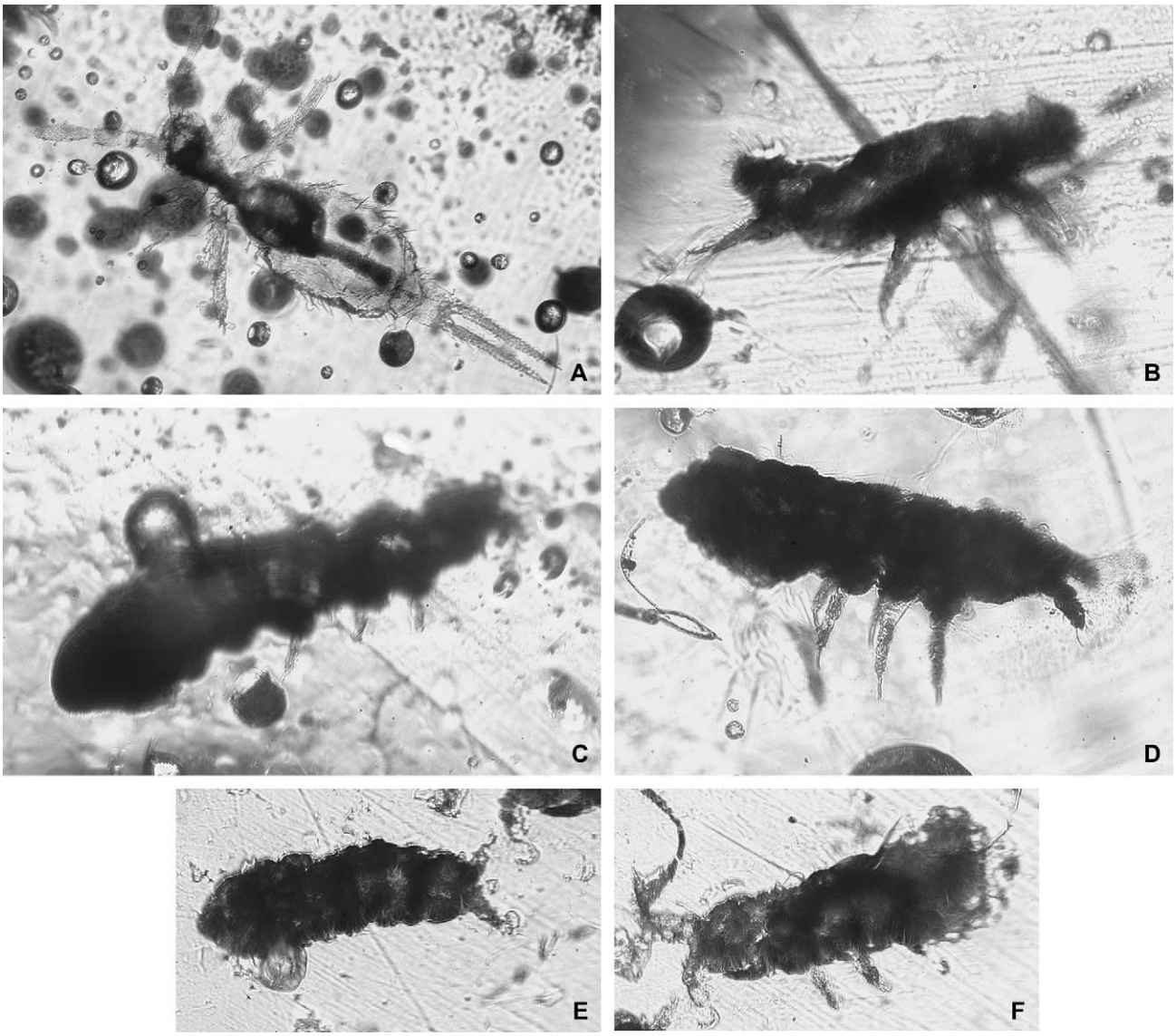

Fig. 20. Habitus of specimens (total length of specimen exclusive of appendages in mm). A, Isotomidae incertae sedis, taxon 2 (0.65 mm). B, *Protodontella minicornis* sp. nov. holotype (0.67 mm). C, Neanuridae s.l. incertae sedis, taxon 1 specimen 1452B-3 (0.71 mm). D, Neanuridae s.l. incertae sedis, taxon 2 specimen 723C-4 (0.60 mm). E, Neanuridae s.l. incertae sedis, taxon 3 specimen 723A-12a (0.46 mm). F, Poduroidea s.l. taxon 4 (0.53 mm).

within that genus with any certitude. Therefore, we choose to place it in ''Incertae sedis''.

Fourteen additional specimens have too little visible detail to enable assignment to distinct taxa. 087A1: This specimen is obscured by artifacts, but may be a *Protoisotoma*; 318: This specimen has the minute mucro and large fourth antennal segment of *Protoisotoma*, but no other features are visible; 346B: Contains three Isotomidae specimens, which show some similarities to *Propachyotoma*; however, the body setae and furculas are missing. In addition, one specimen shows two very large setae, which are absent in *Propachyotoma*; 818B: Has an unusually long mucro (ca. 35% as long as dens). Antennae and feet are missing. Little else is visible; 1074A2: Specimen 1 appears to be *Protoisotoma*, having an ommatidium and post-antennal organ identical to several paratypes; however, neither the antennae, furcula, nor chaetotaxy are visible, making placement questionable; 1074D: A single specimen, very decayed, with chaetotaxy similar to *Protoisotoma*, but mucro not visible and fourth antennal segment not swollen. No tenent hairs can be seen; 1452B: Specimen 2 shows some features of *Protodesoria*, but lacks the spines seen in that genus and is a very young specimen. All setae have been lost; 1452B: Specimen 4 appears to be Isotomid, but neither furcula, legs, nor antennae can be seen. It appears to be shorter and stouter than any other Isotomidae have seen in this material; 1452A1: Specimens 7 and 8. Both have heads missing; they have minute mucrones, and are possible *Protoisotoma*; 1452B: Specimen 2 is a possible *Protoisotoma*, but the fourth antennal segment is smaller than usual; 1452C: Specimen 11 is badly decayed, and has a very small mucro, as well as a long slender dentes. Possible *Protoisotoma*.

Family: Neanuridae Cassagnau, 1955

Remarks. Most of the specimens that appear to be members of the Poduromorpha do not have sufficient characters visible to ascertain whether they belong to some described genus. No furcula can be seen on most of these specimens, but due to the opaque bodies and angle of viewing, it is not possible to be certain in most cases. All lack an unguiculus. We are placing these species in ''Incertae sedis'', but describing and illustrating the visible features. This might make it possible for future workers to determine whether their taxa are probably the same as ours. None of these specimens has mouthparts clearly visible, but in a number of them, it is clear that no molar plate occurs. This fact, combined with the habitus of all the species, and the clear buccal cone in many, leads us to believe that almost all these specimens can be placed in the family Neanuridae s.l. The specimens of one taxon have sufficient features visible to make us feel confidant that they belong to no previously described genus.

Genus *Protodontella* gen. nov.

Derivation of name. After its similarity to extant members of the Odontellinae.

Type species. *Protodontella minicornis*.

Diagnosis. This genus is characterized by 5 + 5 ommatidia, a simple post-antennal organ, the absence of an unguiculus or swollen setae on the antennae, a rod-like, bidentate maxilla, a reduced or absent mandible, small anal horns and a well-developed furcula, with all segments well developed, and a long simple slender mucro.

Included species. Type species only.

Remarks. This genus is in some respects similar to the Late Cretaceous genus *Bellingeria* (Christiansen and Pike, 2002). The body form, antennae, 5 + 5 ommatidia, and foot complex are all similar, but genus 1 differs from *Bellingeria* in having a reduced maxilla, lacking a post-antennal organ, having a furcula with all segments well developed, and not having the third and fourth abdominal segments fused. The habitus, anal spines, antennal shape, furcula and ommatidia number recall the genus *Friesea*; however, the mouthparts are entirely different. The furcula is similar to that of some genera of the Odontellinae, but relatively longer.

Protodontella minicornis sp. nov.
Figs. 20B, 21

Derivation of name. Latin, *minicornis*, referring to small anal horns.

Holotype. Bu 723C, specimen 2. American Museum of Natural History.

Type locality and stratigraphic horizon. Myanmar (Burma), Kachin State, Tanai Village (on Ledo Road, 105 km from Miyitkama); collected by Leeward Capitol Corp.; mid Cretaceous.

Material. Holotype and three paratypes, from sample 723A: specimens 12, 15 and 20.

Diagnosis. As for genus.

Description. Maximum length, exclusive of appendages, is 0.67 mm. Lengths of organs are shown in Table 7. The body is broadly elliptical, with segments from thoracic segment two to abdominal segment four laterally bulging, but without tubercles (Fig. 21A). The sixth abdominal segment, seen from above (Fig. 21B), is sharply narrower than the fifth, roughly pyramidal, with a blunt apex and two small anal horns. The integument is finely granulate, with granules conical. The antennae are four-segmented (Fig. 21C), with the fourth segment 1.1–1.3 times as long as the third, and clothed with some straight to slightly curved, acuminate or truncate, slender (0.01–0.04 mm long) setae, and numerous ca. 0.005-mm-long-acuminate setae. The setae were also seen on other segments, but all are similar to those of the fourth segment. No thick setae are present. Mouthparts project into a short buccal cone. The maxilla is a single slender rod with a bidentate apex (Fig. 21G). No mandible was seen. Ommatidia are 5 + 5. The head has a few slightly curved, slender, cylindrical (0.03 mm long) setae similar to those on the antennae, as well as numerous (0.012 mm long) straight, acuminate, smooth setae. The body has some slender, straight to slightly curved (0.01–0.08 mm long), acuminate smooth setae laterally, but with only a few setae seen on the dorsum (except for the fifth and sixth abdominal segments). The posterior dorsum of the fifth and sixth segment has at least six slightly curved (0.034–0.05 mm long), cylindrical, smooth, slender, blunt setae, plus numerous (0.025–0.030 mm long) smooth slender acuminate setae (Fig. 21A). The dorsal apex of the sixth segment has a pair of short, seta-like anal horns. Femurs and tibiotarsi are subequal, with numerous (0.005–0.013 mm long) acuminate, smooth setae, and one long, weakly clavate tenent hair. The unguiculus is absent, and the unguis is long, slender and untoothed. All segments of the furcula are well developed dorsally (Fig. 21A, E, H), with at least four manubrial and eight dental (0.008–0.021 mm long) smooth acuminate setae. No ventral setae can be seen. The mucro is slender, more than two-thirds as long as the dens, without lamellae, with an apical tooth and a few extremely minute dorsal teeth on the basal half.

Remarks. Paratype 1 shows what appears to be a simple circular post-antennal organ; however, the head is so badly distorted that it is difficult to ascertain. No other specimen shows any post-antennal organ. Only the holotype and paratypes 2 and 3 show clavate tenent hairs, while the others appear to have lost most or all of their setae. Paratype 3 is badly decayed, but the mouthparts are more visible than elsewhere. The maxilla is clear, but no mandible can be seen.

Table 7
Myanmar Cretaceous Neanuridae s.l. *Protodontella* and related specimens (measurements in mm)

Specimen	Cephalic diagonal	Antennal segment 1	Antennal segment 2	Antennal segment 3	Antennal segment 4	Thoracic segment 1	Thoracic segment 2	Thoracic segment 3	Abdominal segment 1	Abdominal segment 2	Abdominal segment 3	Abdominal segment 4	Abdominal segment 5	Abdominal segment 6	Hind femur	Hind tibiotarsus	Manubrium	Dens	Mucro
Holotype	0.125	?	?	?	0.026	0.023	0.031	0.031	0.024	0.025	0.034	0.052	0.031	0.031	0.042	0.057	0.054	0.047	0.039
Paratype2	0.156	0.023	0.037	0.033	0.039	0.039	0.060	0.055	0.057	0.057	0.065	0.070	0.036	0.026	?	0.054			
Paratype3	?	?	?	?	?	?	?	?	?	0.042	0.052	0.062	0.039	0.028	?	0.044	?	0.057	0.024
Paratype1	0.112	?	0.021	0.025	0.036	?	?	?	?	?	?	?	0.052	0.039	?	0.034	?	0.043	0.029
Related specimens																			
087A-1	0.109	?	?	?	?	?	0.03?	0.049	0.026	0.031	0.042	0.052	0.026	0.023	0.021	0.026	0.042	0.031	0.023
1452C-2	0.107	0.016	0.021	0.018	0.026	0.037	0.047	0.049	0.042	0.052	0.073	0.052	0.044	0.036	?	0.047	.?	0.036	0.026

There is one short rod-like structure in the appropriate position for a mandible, but this is partly obscured. No other mouthpart-associated structures can be seen, so that it is impossible to tell whether the cardo is present or absent. Paratypes 2 and 3 reside in a large sample, and can be seen clearly only on dorsal view; nevertheless, an edge-on view of the sample shows the furcula sufficiently well to determine that it is similar to those of the other type specimens. Sample 1452C, specimen 2, may belong to the same genus; however, it probably represents a different species. It has five ommatidia on one side, but no mouthparts can be seen, and it shows a similar dens and body form, as well as the conical cuticular sculpturing and other general features of the genus; however, the fifth abdominal segment is somewhat longer than that of the others, the unguis shorter and the anal horns larger (Fig. 21H). Sample 087A1 is similar to the types in most observable features; however, setae are absent and the mucro is bilamellate (see Fig. 21I), as in *Odontella* Schaeffer (1897) and *Superodontella* Stach (1949). Thus, 087A1 may belong to a distinct, related genus.

There are a number of specimens that are probably congeneric, but for which a lateral view is not obtainable, and thus no furcula can be seen. Sample 723A, specimen 18, has a habitus, anal spines, $5 + 5$ ommatidia, a simple post-antennal organ, and some bulging segments of the genus. Specimen 1452B-5 has unclear ommatidia, but which are apparently $5 + 5$. No post-antennal organ is visible. The organ ratios are generally similar to those of the holotype. The mouthparts are unclear, and no molar plate or large-toothed structures are visible. Specimen 1452C-4 is opaque, but the general appearance and body segments are very similar to the genus. Only a few setae remain, but these are all on the sixth abdominal segment, acuminate, slender (0.013–0.021 mm long). No legs are visible. The body ratios are different from those of the holotype.

Superfamily: Poduroidea incertae sedis

Remarks. Almost all the specimens that appear to be members of the Poduroidea do not have sufficient characters visible to ascertain whether they belong to some previously described genus, or, in some cases, whether they belong in Neanuridae s.l. or Hypogastruridae s.l. Only one of these species shows a definite furcula; it is uncertain in most cases whether or not a furcula is present. All of the specimens, where legs are visible, lack an unguiculus, making it much more likely that they belong to Neanuridae s.l. than to Hypogastruridae. We are placing these species in ''Incertae sedis'', but describing and illustrating some of the visible features. The measurements of these specimens are shown in Table 8. These descriptions might make it possible for future workers to determine whether their taxa are similar to ours. Although none of these specimens has mouthparts clearly visible, it is clear that no molar plate occurs in some of them. This combined with the fact that there is a habitus in all the species, as well as a clear buccal cone many, leads us to believe that a significant number can be placed in the family Neanuridae s.l.

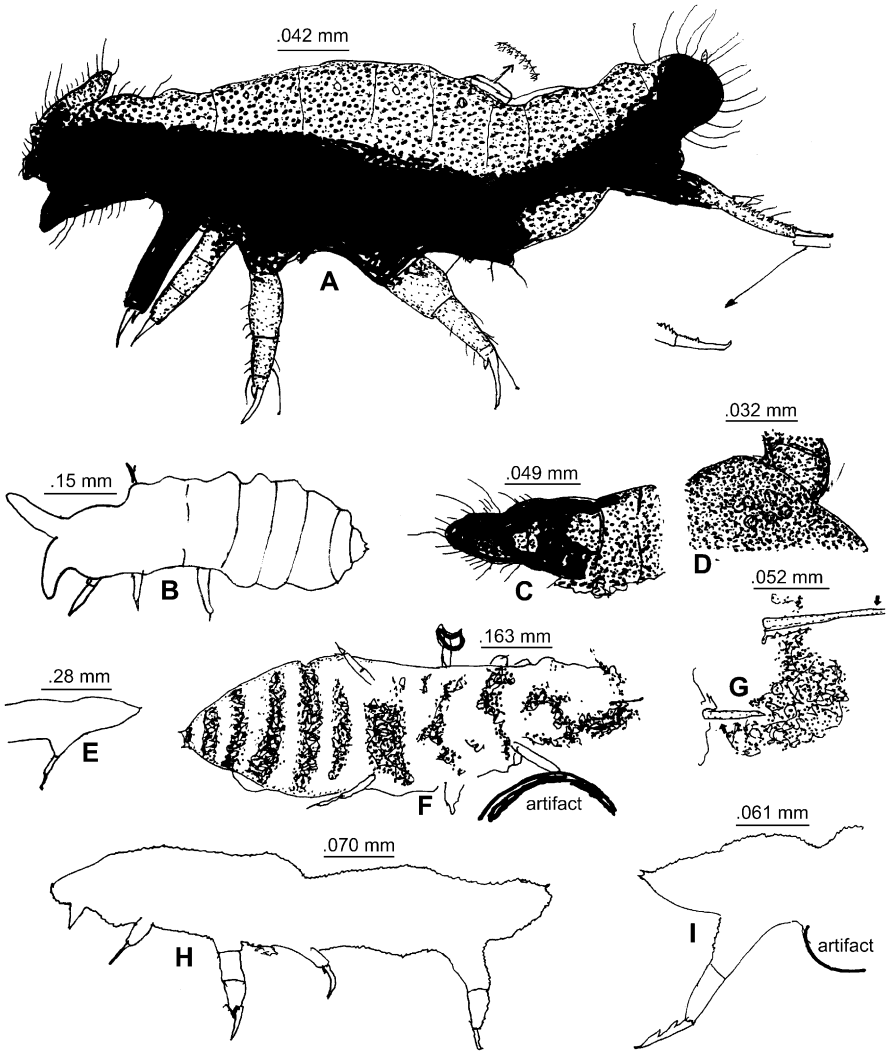

Fig. 21. *Protodontella minicornis* sp. nov. A, holotype (arrows: above, enlargement of cuticle; below, mucro). B–D, paratype 2. B, outline of habitus. C, right antenna. D, left eye patch. E–G, paratype 3. E, outline posterior end seen from side. F, habitus. G, anterior head region (arrows: upper, maxilla; lower, possible mandible). H, outline lateral view, related form, specimen 1452C-2. I, rear end, related genus, sample 087A1.

Family Neanuridae s.l.

Incertae sedis taxon 1 (Fig. 20C). This genus (with two specimens: 723B, specimen 1, and 1452B, specimen 3) resembles *Pseudofriesea* in body form but has no bulging segments, furcula or other features of that genus. The lengths of organs are shown in Table 8. The specimens have a prominent buccal cone and almost certainly belong to the family Neanuridae s.l. They have no anal spines and lack large abdominal setae. The ommatidia cannot clearly be seen, but on specimen 723B, there appear to be at least four ommatidia on one side. Specimen 723B also has a weak transverse line on the tibiotarsi, which at first led us to believe these were subsegmented. Examination under the confocal microscope showed this to be incorrect. The paucity of visible characteristics makes it possible that these specimens could belong to one of a number of genera of the tribe Anuridini or Friesini.

Incertae sedis taxon 2 (723 B, specimen 13, and 723C, specimen 4; Fig. 20D). This genus has a blunt sixth abdominal segment. Lengths of organs are shown in Table 8. The cuticle is decorated with large (ca. 0.003 mm long) knobs. Mouthparts are unclear, but 723C, specimen 4, lacks a molar plate, and is thus placed in the Neanuridae s.l. There are 7–8 ommatidia per side and no post-antennal organ. There are no bulging segments, and a peculiar large curved cylindrical seta occurs on the outer margin of the last antennal segments. Two other specimens, 723A specimen 12A and 11, may be the same genus. Both have a large cuticular ornamentation and a single large seta, similar to those seen on the antennae of the other specimens. They also both have $7 + 7$ or $8 + 8$ ommatidia. The latter specimen is badly decayed, and it appears to have an opening where the post-antennal organ would be, while the former specimen has a poorly visible, four-lobed post-antennal organ in a similar site. Such an organ is not visible on the other two specimens. 723C, specimen 5, is similar in habitus to Incertae sedis taxon 1. The specimen is in very poor condition, but at least four ommatidia can be seen on one side. The antennae are unclear, but the integumentary ornamentation is like taxon 1.

Table 8
Myanmar Cretaceous Poduroidea incertae sedis s.l. (measurements in mm)

Specimen	Cephalid diagonal	Antennal segment 1	Antennal segment 2	Antennal segment 3	Antennal segment 4	Thoracic segment 1	Thoracic segment 2	Thoracic segment 3	Abdominal segment 1	Abdominal segment 2	Abdominal segment 3	Abdominal segment 4	Abdominal segment 5	Abdominal segment 6	Hind femur	Hind tibiotarsus
Incertae sedis taxon 1																
723B-1	0.156	?	?	?	?	0.060	0.083	0.078	0.260				0.039	0.031	0.034	0.039
1452B-3	0.104	?	?	?	0.021	0.029	0.062	0.062	0.030	0.070	0.065	0.165			?	?
Incertae sedis taxon 2																
723C-4	0.170	?	0.038	0.05		0.034	0.058	0.057	0.048	0.047	0.052	0.064	0.031	0.034	0.031	0.039
723B-13	0.085	0.018	0.023	0.049		0.029	0.036							0.026	?	?
								0.182								
723A-11	0.088	0.013	0.016	0.013	0.016	0.026	0.039	0.036	0.029	0.036	0.039	0.026	0.018		?	?
Incertae sedis taxon 3																
1452C-3	0.125	?	?	?	0.034	0.031	0.049	0.049	0.042	0.047	0.060	0.130			?	?
723A-12a	0.073	0.008	0.013	0.016	0.016	0.026	0.039	0.039	0.041	0.042	0.042	0.047	0.039	0.026	?	?
Increate sedis taxon 4																
723A-10	0.117	0.013	0.026	0.026	0.042	0.016	0.052	0.047	0.031	0.039	0.034	0.049	0.029	0.016	0.039	0.047
Incertae sedis taxon 5																
723C-5	0.117	?	?	?	?	0.028	0.034	0.057	0.052	0.065	0.073	0.097	0.034	0.029	0.030	0.074
Incertae sedis taxon 6																
818A2-9	0.275	?	?	?	?	0.65									?	?
346A	0.221	?	?	?	?	0.50									?	?
Incertae sedis taxon 7																
723C-7	0.117	0.020	0.023	0.015	0.018	0.034	0.073	0.078	0.068	0.060	0.044	0.052	0.029	0.027	0.023	0.027
723B-14	0.100	?	?	?	?	0.030	0.045	0.045	0.045	0.045	0.060	0.065	0.025	0.020	0.030	0.045
1452A-3	0.130	0.021	0.021	0.016	0.026	0.031	0.072	-065	0.083	0.052	0.057	0.047	0.031	0.029	0.036	0.043
Incertae sedis taxon 8																
723A-16	0.130	?	?	?	?	0.046	0.07?	0.07	?	?	0.046	0.052	0.052	0.041	?	?
Unplaced specimens																
723A-18	0.143	0.013	0.018	0.020	0.026	?	?	?	?	?	?	0.049	0.034	0.026	?	?
1452B-5	0.104	0.016	0.023	0.021	0.028	0.020	0.040	0.030	0.225	0.035	0.025	?	?			
1452B-8	0.101	?	?	?	?	0.029	0.042	0.059	0.036	0.024	0.032	0.041	0.026	0.029	0.018	0.029
1452C-5	0.112	0.013	0.016	0.026	0.031	0.030	0.044	0.057	0.033	0.033	0.044	0.052	0.026	0.018	?	?
1452C-4	0.130	0.013	0.208	0.208	0.260	0.034	0.047	0.081	0.039	0.042	0.047	0.049	0.031	0.026	?	?

Incertae sedis taxon 3 (1452C, specimen 3, and 723A, specimen 12A; Fig. 20E). The abdomen has a rounded end, the unguis is simple, no setae are seen, and the antennae are unclearly seen. Ommatidia are at least five per side. Lengths of organs are shown in Table 8. No setae can be seen. There are circular 7–8 lobed post-antennal organs larger than any ommatidium. No molar plate exists.

Incertae sedis taxon 4 (723A, specimen 10; Fig. 20F). This specimen is badly decayed and mostly opaque. Lengths of organs are shown in Table 8. No mouthparts are visible. The abdomen is blunt, and no anal spines or setae can be seen. There is a simple post-antennal organ and at least three ommatidia on one side. The unguis is simple and untoothed. Antennae are four-segmented with a peculiar projection beyond the apex. This does not appear to be a bulb, but looks like a solid, more or less semicircular mass.

Incertae sedis taxon 5 (723C, specimen 5; Fig. 22A). This is similar in habitus to Incertae sedis taxon 1, but has a sixth abdominal segment much smaller than any seen elsewhere (less than one-half the length of the fifth). Lengths of organs are shown in Table 8. The specimen is in very poor condition, but at least four ommatidia can be seen on one side. The antennae are unclear.

Incertae sedis taxon 6 (818A2, specimen 9, and 346A; Fig. 22B). These unfortunately incomplete specimens are the only ones showing a weakly blobbed sixth abdominal segment. Lengths of organs are shown in Table 8. The head is missing on 818, and only one, untoothed unguis can be seen from a side view (and this poorly). The anterior body parts on specimen 346A are very badly decayed, and the head is not decipherable. The body is densely clothed with slender cylindrical smooth setae, particularly on the posterior segments of the abdomen. These range from 0.003 to 0.18 mm in length. The integument has very small conical projections, similar to those seen in genus 2, but no large knobs or tubercles are present. The absence of the head makes it impossible to place this species in the tribe Enamoring.

Incertae sedis taxon 7 (723C specimen 7; 723B specimen 14 and 1452A specimen 3; Fig. 22C). Similar in body form to *Pseudofriesea*, but lacks a furcula. Lengths of organs are shown in Table 8. They can be seen in profile on one side, in both specimens 723C and 1452A. They are slightly protruding and at least five in number. The mouthparts can be seen in a lateral view on 723B, but all that can be certain is that there is no molar plate.

Incertae sedis taxon 8 (723A, specimen 16; Fig. 22D). This is the only specimen of the family (other than *Pseudofriesea*) that has a furcula. The single specimen is in very poor condition, so that it is impossible to be certain of any details; however, the furcula is short, and the mucro appears to have an upwardly-curved median lamella similar to those seen in *Odontella*. Lengths of organs are shown in Table 8. There appear to be six or more ommatidia, located more posteriorly on the head than is normal, as well as a complex lobed post-antennal organ. The midpart of the abdomen appears to have lateral projecting knobs on two segments. The tip of the abdomen is broadly blunt.

Superfamily: Poduroidea, family unknown

723 A, specimen 18: This may be a specimen of *Pseudofriesea*, but it is impossible to tell whether a furcula is present. There are 5 + 5 ommatidia, but no post-antennal organ; 1074A1, specimen 5: This specimen has a broadly blunt (but not indented or bilobed) sixth abdominal segment. It is impossible to tell if it has a furcula, or find other useful details of anatomy; 1452A2, specimen 2: Bubbles cover most of the posterior half of this specimen, making it impossible to place; 1452B, specimen 4: It is only visible from above and below. Densely opaque, possible taxon 1, but not clear; 1452C, specimen 2: Also only visible from above or below. Possible taxon 8. Has a blunt abdomen similar to taxon 8, and a possible furcula, but this is appressed to body and not clearly visible; 1452C, specimens 4 and 5: These have rounded sixth abdominal segments and no anal spines. Legs are not visible and body is opaque. They are visible only from the dorsal surface. Extremely opaque. Possibly taxon 1, but no prominent buccal cone or legs are visible; 1452B, specimen 8. Similar to taxon 8, but the furcula is unclear; Eight additional specimens have too little visible detail to merit distinct taxa or description.

Family: Praentombryidae, fam. nov.

Type genus. *Praentomobrya* gen. nov.

Diagnosis. These entomobryomorph Collembola have a reduced first thoracic segment, and a fourth abdominal segment more than twice as long as the third, lacking scales and abdominal bothriotricha, or normal trochanteral organs. Ommatidia are present, post-antennal organs and scales are absent, and type 1 setae (Christiansen, 1958) are present. The body is equipped with a few ciliate setae, and numerous short smooth acuminate setae. The mucro is bidentate with a basal spine. Antennae are four-segmented, but lack apical bulbs or pin setae.

Remarks. The body shape, large fourth abdominal segment, presence of type 1 setae, and bidentate mucro with a basal spine, would all seem to place these genera in the family Entomobryidae s.l.; however, the absence of abdominal bothriotricha and the rudimentary trochanteral organ with few (four or five) setae, and none of these short and straight, as is typical of trochanteral organs, differentiate these genera from all extant genera. As was pointed out by Szeptycki (1979), the family Entomobryidae is remarkably constant in the presence of abdominal bothriotricha, and also in their distribution 2-3-2 on abdominal segments 2–4. The new family is most similar to the genera *Capbrya* Barra (1999) and *Corynothrix* Tullberg (1876), but differs in the paucity of ciliate or serrate setae, and in the absence both of abdominal bothriotricha and a typical trochanteral organ with straight smooth setae. The long fourth abdominal segment makes it unlikely that this family represents a group ancestral to modern Entomobryidae, since it would appear unlikely that such an organism would give rise to the Orchesellinae. Because only the habitus is known

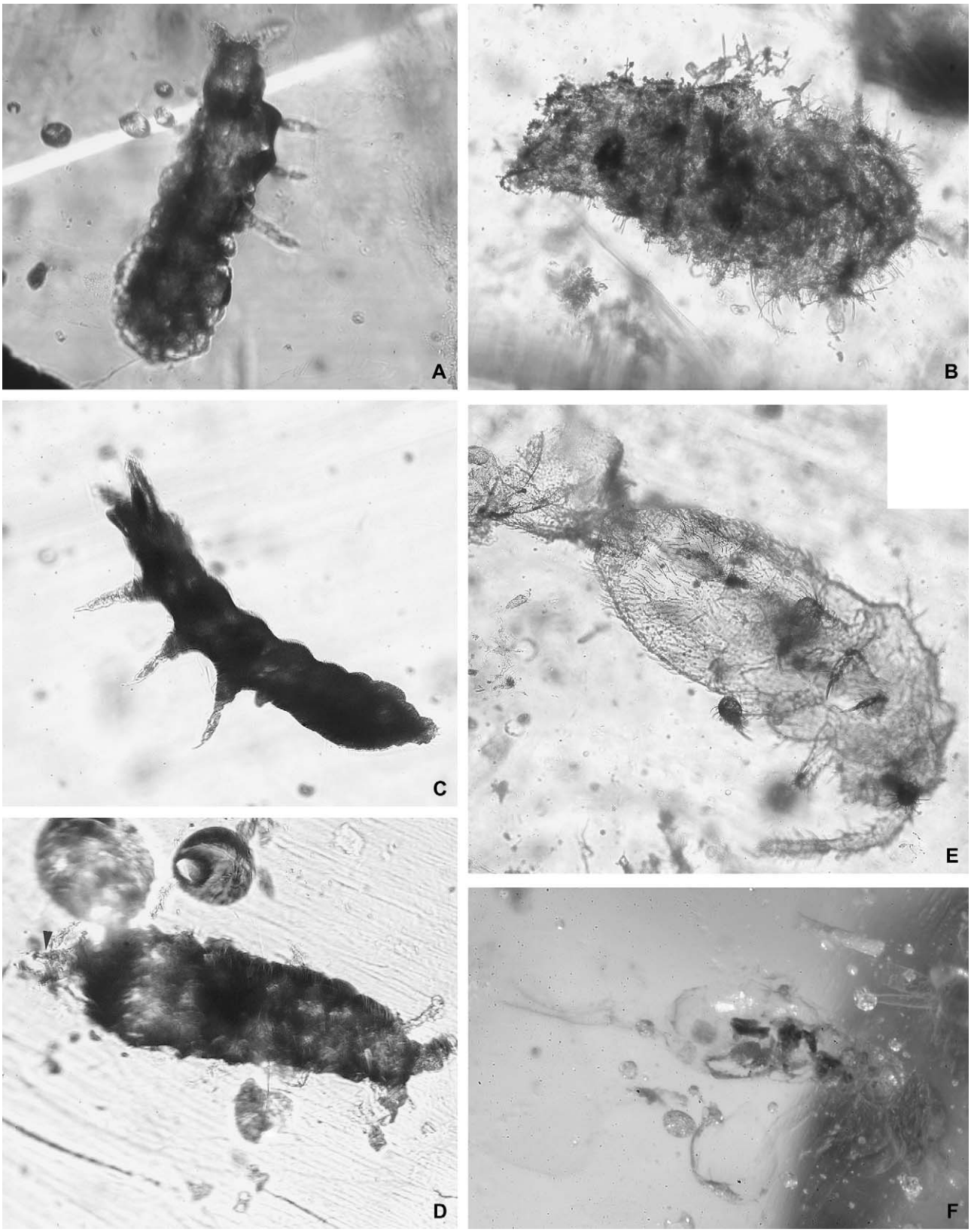

Fig. 22. Habitus of specimens (total length of specimen exclusive of appendages in mm). A, Neanuridae s.l. incertae sedis, taxon 5 (0.59 mm). B, Neanuridae s.l. incertae sedis, taxon 6 specimen 818A2-9 (0.93 mm). C, Neanuridae s.l. incertae sedis, taxon 7 specimen 723C-7 (0.58 mm). D, Poduroidea s.l., taxon 8 (0.50 mm). E, *Praentomobrya avita* sp. nov., holotype (1.50 mm). F, *Cretacentomobrya burma* sp. nov., holotype (1.15 mm).

for the sole Permian Collembola (*Permobrya* Riek, 1976), it is quite possible that this *Permobrya* belongs to Praentombryidae.

There are two known genera: *Praentomobrya* gen. nov. and *Cretacentomobrya* gen. nov.

Genus *Praentomobrya* gen. nov.

Derivation of name. Latin *prae*, before, and *Entomobrya*, referring to most similar extant group.

Type species. *Praentomobrya avita* sp. nov., mid Cretaceous.

Diagnosis. This genus is distinguished by the characteristics of the family, which are an oval-elliptical body, a fourth abdominal segment more than three times as long as the third, some type 1 setae (Christiansen, 1958), as well as the lack of bothriotricha or a normal trochanteral organ. It is distinguished from the other genus of the family by the presence of crenulations on the dentes, and by the presence of clavate tenent hairs.

Included species. Type species only.

Remarks. This is probably the best specimen of Arthropleona recovered thus far from Burmese amber. The habitus (see Fig. 22E) is typical of Entombryini in having the fourth abdominal segment at midline more than three times as long as the third. The stunning problem is that the specimen has no bothriotricha. This could mean that they were lost, but this specimen has almost no missing setae, and in a few places, there is a thick cylindrical seta in a position similar to that of bothriotricha in some genera of Entomobryidae. It is unlikely that these represent pre-bothriotricha, since they display none of the characteristics of these setae; it is much more likely that the pseudobothriotricha seen in many Isotomidae represent this condition.

Praentomobrya avita sp. nov.
Figs. 22E, 23

Derivation of name. Latin, *avita*, very old.

Holotype. 818A2, specimen 5, American Museum Natural History.

Type locality and stratigraphic horizon. Myanmar (Burma), Kachin State, Hukawng Valley, 32 km southwest of Tanai, near Noije Bum (hill), approx. 250 m; mid Cretaceous.

Material. Holotype only.

Diagnosis. As for genus, plus clavate tenent hairs and crenulate dens.

Description. Length, exclusive of appendages, is ca. 1.5 mm, with organ measurements shown in Table 9. The

Table 9
Myanmar Cretaceous Entomobryoidea (measurements in mm)

Specimen	Cephalic diagonal	Antennal segment 1	Antennal segment 2	Antennal segment 3	Antennal segment 4	Thoracic segment 2	Thoracic segment 3	Abdominal segment 1	Abdominal segment 2	Abdominal segment 3	Abdominal segment 4	Abdominal segment 5	Abdominal segment 6	Hind tibiotarsus	Hind femur	Manubrium	Dens	Mucro	Body + head total
Praentomobrya avita																			
Holotype	0.375	0.065	0.085	0.095	0.195	0.208	0.148	0.130	.114	0.099	0.309	0.068	0.041	0.19	0.135	0.15	0.175	0.026	1.12
Cretacomobrya antiqua																			
Holotype	0.260	0.040	0.078	0.088	0.117?	0.120	0.11	0.089	0.105	0.085	0.202	0.10	0.039	?	0.109	0.24	0.425	0.020	0.90
Paratype	0.114	0.016	0.021	0.018	0.052	0.039	0.036	0.013	0.028	0.043	0.088	0.026	0.021	0.044	0.039	0.059?	0.143	0.009	0.30
Incertae sedis																			
1452C-7	0.18	0.018	0.022	0.019	0.055	0.052	0.091	0.073	0.078	0.117	0.156	0.048	?	0.044	0.039	?	0.137	0.013	0.60

body is oval-elliptical (Fig. 22E). The fourth antennal segment is ca. twice as long as the third, which is slightly longer than the second. The fourth antennal segment is clothed dorsally with mostly curved or apically hooked (0.02 mm long) cylindrical setae (Fig. 23D). In addition, there are smooth, straight (5.05 mm long) acuminate setae. Laterally, there are numerous cylindrical (ca. 0.009 mm long) setae, and several smooth (0.025 mm long), acuminate setae. Ventrally, there are numerous smooth (0.03–0.05 mm long) acuminate setae (Fig. 23C). Scattered over the whole segment are blunt, curved (ca. 0.008 mm long) ''sensory'' setae. There is an apical retractile bulb, and pin setae are absent. The third segment ventrally has one smooth, straight (0.068 mm long) acuminate seta, while the dorsal surface has ca. six (0.026–0.055 mm long) acuminate setae, and about six slender, strongly curved (ca. 0.025 mm long) cylindrical setae. The inner and outer faces have slender straight (0.025–0.04 mm long) setae, and short stout ca. 0.01 ones (Fig. 23B). Second segment is clothed mostly with straight to weakly curved (0.02–0.05 mm long) acuminate setae. In addition, there are two short, straight spines on the inner face. The labral and prelabral setae are 4-4-4-4, all smooth, with row 2 shorter than others and curved (Fig. 23A). Labral papillae are minute and simple. There are at least seven ommatidia per side. No post-antennal organ can be seen. The head is clothed with numerous stout, curved (0.01–0.03 mm long) acuminate setae. Along the posterior margin of the head capsule, there are straight (6.04 mm long) acuminate setae, and on either side of these is a curved (0.05 mm long) pointed spine-like seta. The body is abundantly covered with smooth or rugose (0.05 mm long) mostly curved, weakly tapered acuminate type 5 setae. Scattered among these are very slender cylindrical setae of similar length. On the abdomen, there are a few thicker straight or very slightly curved (ca. 0.08 mm long), finely ciliate, type 2 acuminate setae. Type 1 setae are not as large as those seen in most Entomobryidae, and are similar to those seen in *Capbrya*. They are few in number, and limited to the thorax, with a few narrower similar setae at the end of the abdomen (Fig. 23G). Bothriotricha are absent. The hind trochanter (Fig. 23K) lacks the short straight smooth setae typical of trochanteral organs. In place of these are five normal curved setae, similar in position to the trochanteral organ setae seen in *Capbrya*. Femurs and tibiotarsi are densely clothed with short, curved (0.018–0.04 mm long) acuminate setae. The hind femurs (Fig. 23I) each have an outstanding, straight (0.055 mm long) acuminate seta on the inner surface. The unguis and unguiculus are simple, without teeth. A single clavate tenent hair is present on all feet. The manubrium and dentes are densely clothed with smooth (0.013–0.05 mm long) acuminate setae. The dens is dorsally crenulate (Fig. 23J), and the mucro is bidentate.

Remarks. *Praentomobrya* is very similar in some respects to *Cretacentomobrya*, and the possible bothriotricha in that genus are found only on the second thoracic segment. Since this segment in *Praentomobrya* is obscured, it is possible that such bothriotricha also exist in this genus. The hind trochanter is clear on one side, and it lacks a trochanteral organ, but the setae present are very similar in position and number to those seen in the trochanteral organ in Barra's *Capbrya*, and are not like that seen in the small species of *Isotoma* we have examined. They are also five in number as are those seen on *Cretacentomobrya*. Finally, while there are some setae present that are similar to the type 1 setae (Lasiotrichia) of Entomobryidae seen in *Capbrya*, as well as some that are similar to the type 2 setae, the majority of setae (type 5) are small, smooth or rugose, more characteristic of Cretaceous Isotomidae than Entomobryidae. The claws are simple and untoothed, but have clavate tenent hairs. The dentes show clear dorsal crenulations.

Genus *Cretacentomobrya* gen. nov.

Type species. *Cretacentomobrya burma* sp. nov.

Derivation of name. After Cretaceous and *Entomobrya*, the most similar extant genus.

Diagnosis. This genus is separable from other entomobryomorph genera by the characters of the family. It is separable from the other genus of the family by the absence of clavate tenent hairs and dorsal dental crenulations.

Included species. Type species only.

Remarks. There is a remarkable disconnection between one's initial impression of this specimen, based on overall appearance, and close examination. At first glance, the holotype would appear to be a species of *Entomobrya* or one of the closely related genera. Its habitus, the presence of a clear patterned pigment, the strongly curved posterior margin of the third abdominal segment and parafucular lobe, long slender dentes and a bidentate mucro, as well as its antennal structure, are all very similar to *Entomobrya*. Quite different are the chaetotaxy, with its relatively uniform distribution of straight smooth simple acuminate setae, the lack of abdominal bothriotricha or a trochanteral organ, the lack of dorsal crenulations on the dens, and the absence of tenent hairs.

Cretacentomobrya burma sp. nov.
Figs. 22F, 24

Derivation of name. After the country of origin.

Holotype. Bu 1452B, specimen 9. American Museum of Natural History.

Type locality and stratigraphic horizon. Myanmar (Burma), Kachin State, Hukawng Valley, 32 km southwest of Tanai, near Noije Bum (hill), approx. 250 m; mid Cretaceous.

Material. Holotype and one paratype: sample 1452C, specimen 10.

Diagnosis. As for genus.

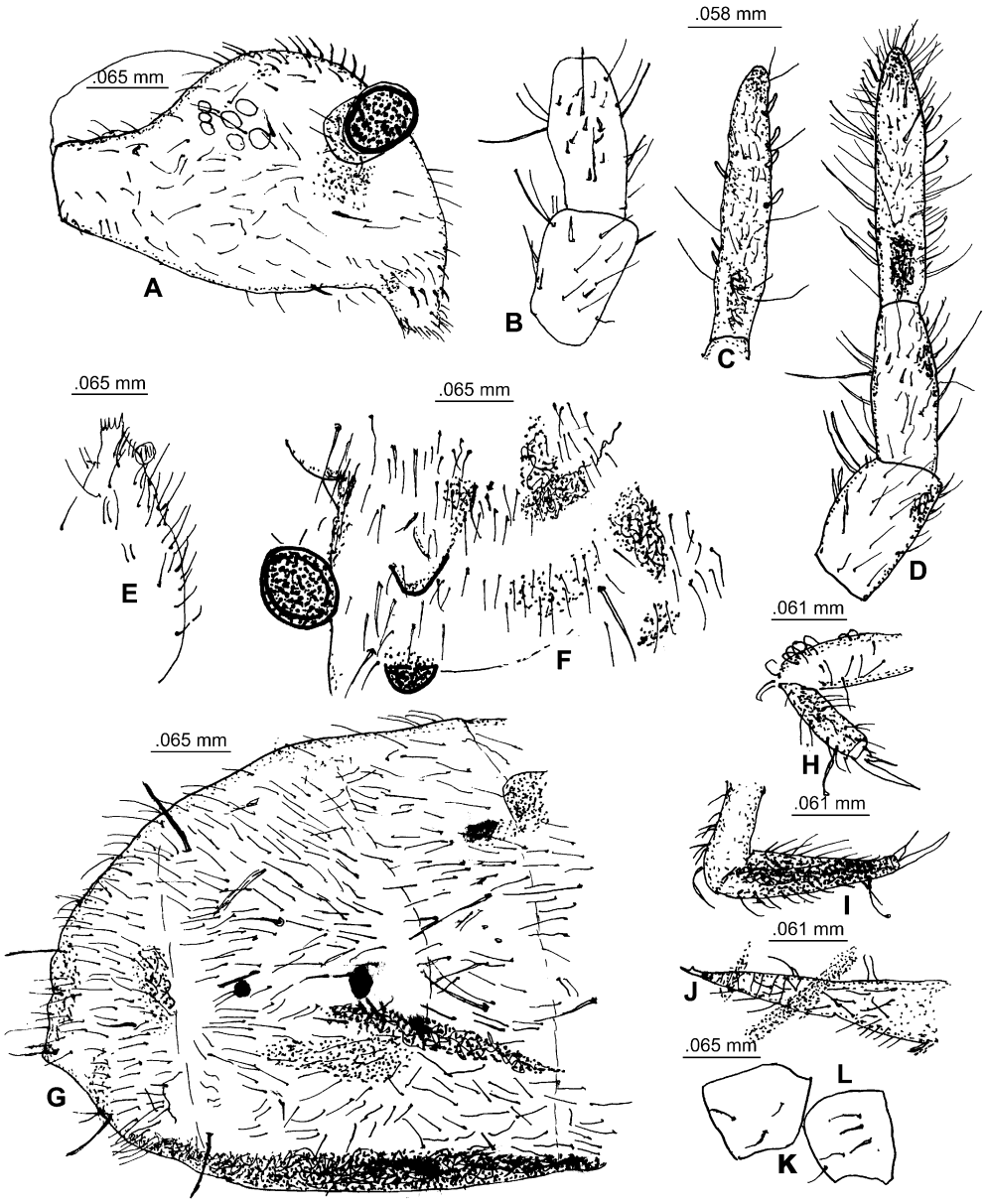

Fig. 23. *Praentomobrya avita* sp. nov. All figures of holotype. A, head lateral view. B, left antenna, inner face segments 2 and 3. C, same, segment 4. D, outer face segments 2–4. E, ventral surface, left half of head. F, chaetotaxy, left half abdominal segments 1 and 2. G, chaetotaxy posterior abdomen. H, mid-leg. I, hindleg. J, dorsal surface of dens. K, outer face hind trochanter. L, Inner face hind trochanter.

Description. Length, exclusive of appendages, is ca. 1.15 mm, with organ measurements shown in Table 9. The body is typically entomobryid oval-elliptical (Fig. 22F). Blue pigment remains on the lateral and extreme lateral anterior portions of abdominal segment 4, and most of the intact portion of abdominal segment three. The second antennal segment is shorter than the third (Fig. 24C, D). The fourth segment is ca. 1.3 times as long as the third (Fig. 24I), without an apical bulb or pin seta. All setae, unless otherwise indicated, are smooth, straight and acuminate. Antennae are densely clothed with 0.013–0.02-mm-long setae. The apical organ on the third segment has two minute pegs in separate grooves. Labral setae are in four rows of 0.002-mm-long curved acuminate setae. Prelabral setae are similar, but ca. 0.013 mm long. The ventral surface of the head is badly torn and distorted, but clothed with numerous 0.013–0.02-mm-long setae. The dorsal surface of the head (Fig. 24B) has very few setae remaining; most of these are similar to those on the ventral surface, with a few somewhat longer (0.03 mm). In addition, there are three straight, slender, cylindrical (ca. 0.05 mm long) truncate setae. Between the two antennae, there are a series of small circles, which may be macrochaetae bases. Ommatidia are at least $7+7$ (Fig. 24P). The first thoracic segment is reduced and largely hidden by the head. The second segment is torn and distorted (Fig. 24E), with few setae remaining. Most of these setae are typical, but a few are narrow and cylindrical, all resembling those seen on the head and antennae. In addition, there is

a single bothriotrichum-like seta that lacks the minute ciliations normally seen on these. In this respect, it resembles the pseudobothriotricha found in Isotomidae, but lacks the slight taper characteristic of these setae. Furthermore, there is a single thick, typical 0.05-mm-long type 1 seta on the right lateral margin. Thoracic segment 3 and abdominal segments one and two are largely obscured by debris. Where the view is clear, there are scattered ca. 0.025-mm-long setae; however, on the pigmented portion of the fourth abdominal segment, it can be seen that these setae are more numerous than those shown on the remaining clear spaces. The setae of abdominal segments 3–5 are mostly lost on the left side, but the right side has numerous setae such as are common on the rest of the body (Fig. 24F). Also observed is one straight smooth (ca. 0.065 mm long) acuminate seta on the posterior lateral part of the third segment. The legs are only partly visible, and appear to have lost some setae. The remaining setae are similar to most of those seen elsewhere. There are no short straight smooth setae typical of trochanteral organs (Fig. 24J). There are instead four normal curved smooth setae similar to those on the body. Three feet were seen, but none on the holotype had any unguiculi (although what appear to be vestiges were seen on two feet). One foot on the paratype was intact (Fig. 24N). The unguiculus is normal for Entomobryids. The ungues are simple and untoothed. No tenent hairs were seen. The manubrium has been mostly lost, but the remaining part has typical setae, from 0.02 to 0.03 mm in length. The dentes are slender and about 18 times as long as the manubrium (Fig. 24G). They lack crenulations or knobs, and are densely clothed with ca. 0.02-mm-long setae. The mucro is bidentate with a basal spine.

Remarks. Some of the features of this species resemble those of *Corynothrix* and *Capbrya*, but it has many differences from these, including the lack of abdominal bothriotricha, the relatively much longer fourth abdominal segment, the minute labral setae, the absence of either apical bulbs or pin setae on the antennae, and the absence of ciliated setae other than those of type 1. The mouthparts could only be seen in lateral view; thus, no molar plates or other distinguishing features could be observed; however, there is a peculiar blunt lobe, which appears to project outward from the tip of the mandible (see Fig. 24K). This genus is similar to *Praentomobrya* in many respects, but differs in the elongate slender dentes, lack of clavate tenent hairs, lack of cylindrical antennal and body setae, lack of dental crenulations, and very different antennal chaetotaxy. The dentes in some respects resemble those of the Late Cretaceous genus *Protoentomobrya*, in being long and slender, lacking crenulations, and having setae on all surfaces; however, these dentes lack the telescoping subdivisions on the dentes characteristic in *Protoentomobrya*. The single bothriotrichum seen on the holotype may be an artifact, since the basal socket cannot be seen clearly, and it is unusually straight for a bothriotrichum, lacking any ciliations.

The paratype, sample 1452C, specimen 10, is a much smaller specimen (see Table 9), and probably represents a very early instar. The head is considerably larger relative to the body, and the overall size is about half that of the holotype. It has long slender dentes without clear crenulations, and with dense short smooth setae, as well as heavy curved spine-like set on the first antennal segment. The body setae are all smooth and acuminate, but it does not have the cylindrical setae seen on genus 2, nor any sign of a bothriotrichum. In addition, while the acuminate body setae have the same range of sizes seen in the type specimen, the smaller size specimen would be expected to have smaller setae. The important feature is that this specimen shows clear lanceolate unguiculi, which makes it likely that their vestigial nature in the holotype is a taphonomic artifact.

Superfamily: Entomobryoidea incertae sedis

Specimen 1452C-7 has the general habitus of Entomobryoidea. The specimen is badly distorted, but would appear to differ from all known Entomobryoidea by having the second thoracic segment much smaller than the third. Setae have almost all been lost, but the dentes are well preserved and densely covered with very small acuminate, smooth setae on all surfaces. The mucro can only be seen from above, and may be tridentate. The fourth abdominal segment appears to be only one and one-half times as long as the third. Little other detail can be seen.

Family: Tomoceridae Börner, 1913

Remarks. Unfortunately, there is only a single poor specimen of this family (sample 1452A2, specimen 1). The antennae are well preserved and typical of the subfamily Tomocerinae, with an elongate highly subdivided third antennal segment and a small subdivided fourth segment. Ommatidia can be seen, but not clearly enough to determine their number. Under the confocal microscope, five ommatidia can be observed on one side. The legs are fragmentary, and some are broken off from the body. What appears likely to be the hind trochanter has six to seven smooth straight setae visible; this could be a trochanteral organ, but it is impossible to determine which face the setae are on. Only a badly distorted manubrium and the base of the dens can be seen on the furcula. There are no spines or setae remaining, but many scales can be observed in the immediate vicinity of the specimen. What can be seen is very similar to modern Tomocerinae.

4. Discussion

4.1. Implications for Collembola communities and evolution

This work, combined with the recent study of Late Cretaceous Collembola in Canadian amber by Christiansen and Pike (2002), enables us to take a broader perspective concerning the changes through time in the worldwide Collembolan fauna (see Table 10). Any comparison of the Cretaceous amber fauna with other arthropod fossil faunas or extant Collembola faunas is hindered by the fact that while the majority of

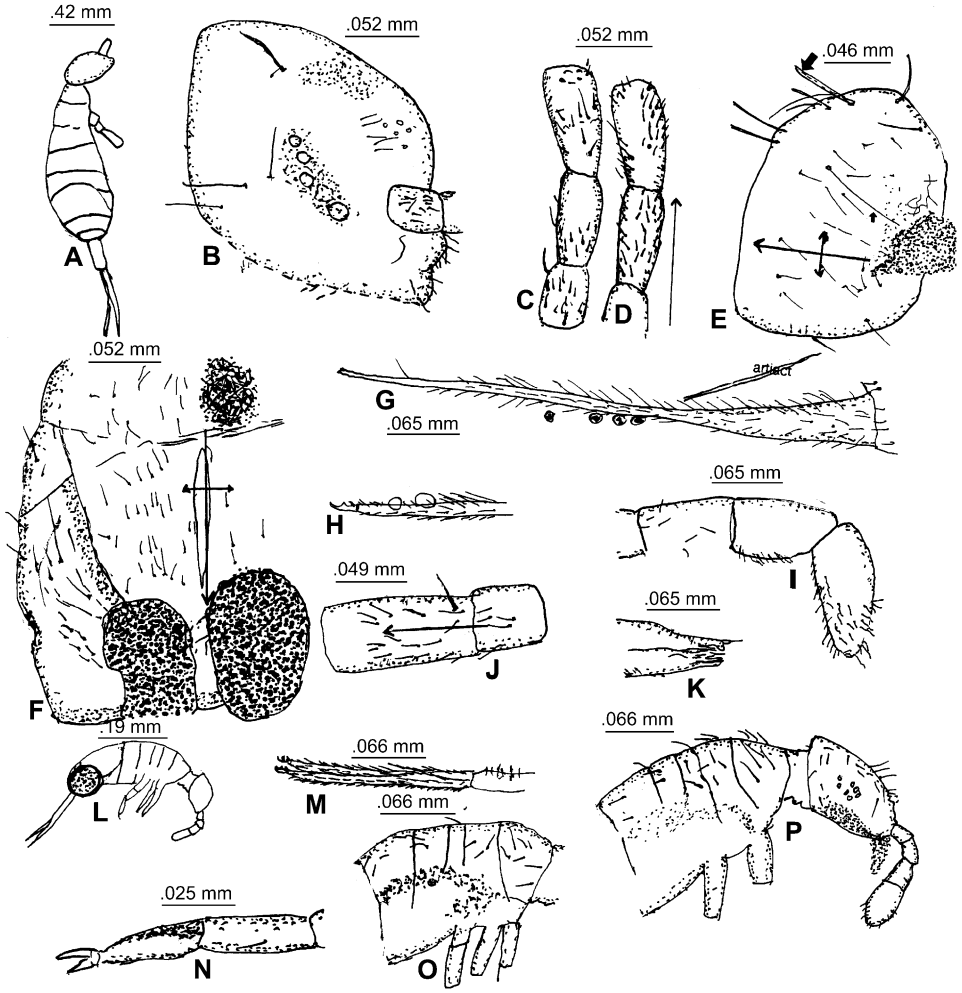

Fig. 24. *Cretacentomobrya burma* sp. nov., holotype. A, outline of habitus showing apparent segmentation. B, seen from right side. C, first three right antennal segments seen from outer side. D, same from inner side. E, second thoracic segment (small arrow, possible bothriotichum; large arrow, type one seta). F, fourth and fifth abdominal segments, chaetotaxy. G, right dentes and mucro. H, apex left dentes and mucro. I, left antenna. J, inner face hind trochanter and femur. K, mandible and maxilla seen from side. L–P, paratype. L, outline of habitus showing apparent segmentation. M, furcula. N, hindleg. O, left side of thorax and first three abdominal segments. P, head thorax, and first three abdominal segment right side.

Collembola are soil, microcavernicole, or subsurface litter forms, the amber faunas are typically arboreal forms with a few surface litter forms. Thus it is better to compare the amber Collembola with extant arboreal faunas than with soil and litter faunas. Compendia of such extant faunas are lacking, necessitating our examination of 11 studies of arboreal Collembola involving both tropical and temperate forests. A total of over 120,000 specimens were identified in these studies. In the studies of extant arboreal Collembola, the family Entomobryidae s.l. was always dominant and represented over 70% of the total fauna varying from 58% to 98% in different studies. The next most abundant family was Sminthuridae s.l., which represented 12.2% of the total fauna, varying from 6% to 40% in different studies. None of the remaining groups represented more than 5% of the total and all varied greatly in the different studies. Table 10 shows a comparison between these studies and the known fossil Collembola faunas. The most striking feature of this examination is the enormous change in the contribution of the superfamily Entomobryoidea. During the Cretaceous Period this clade represented a minor element, and furthermore fossil forms from this interval are not assignable to modern families of the superfamily. In all Eocene and more recent faunas the Entomobryoidea are dominant and assignable to the family Entomobryidae s.l.

Four possible hypotheses explain this trend. First, the modern Entomobryidae s.l. had not evolved by the Cretaceous. Second, they had evolved but had not yet colonized trees and thus were not part of the arboreal fauna. Third, no discovery of Cretaceous Entomobryidae s.l. has been made because of the small number of Collembola recovered from the Cretaceous. Fourth, while the Entomobryidae had evolved in the Cretaceous they were extremely rare. The third option seems highly improbable when we consider that Entomobryidae dominate every extant arboreal Collembola study whether the samples are large or small, tropical (Christiansen and Bellinger, 1992; Palacios-Vargas et al., 1999; Guilbert et al., 1995) or temperate (Uchida, 1969; Bowden et al., 1976; Thunes et al., 2003). In addition, they dominated in the two Miocene studies where samples were very small (Christiansen, 1971; Mari-Mutt, 1983). Entomobryidae have been the most

Table 10
Identifiable specimens of Collembola of different suprageneric categories found in different intervals of geologic time (*Number*, percentage)

Group	Mid Cretaceous	Late Cretaceous	Eocene	Miocene	Pleistocene	Average recent arboreal
Poduroidea	*26*, 25%	*13*, 15%	*5*, 1%	0	*2*, 13%	5%
Sminthuridae	*36*, 35%	*6*, 7%	*60*, 14%	*2*, 2%	*1*, 7%	14.4%
Entomobryoidea	*4*, 4%	*1*, 1%	*284*, 65%	*95*, 78%	*6*, 40%	73.9%
Isotomidae	*36*, 35%	*58*, 69%	*13*, 3%	*25*, 20%	*4*, 27%	3.9%
Tomoceridae	*1*, 1%	*3*, 4%	*36*, 8%	0	*1*, 7%	2.8%

prevalent Collembola recovered from the much more extensive Baltic Eocene amber specimens (Handschin, 1926). The first hypothesis is supported by the presence of three genera of Entomobryoidea during the Cretaceous that belong to two extinct families, whereas all the amber and arboreal Entomobryoidea from the Eocene to the present are placed in the family Entomobryidae s.l. Furthermore, while there is a single Entomobryomorph fossil from the Upper Permian, the nature of the preservation shows no detail and it is attributable to Entomobryoidea solely on the characteristic body form. It could belong to one of the extinct families described from the Cretaceous. However, in genetic phylogenetic analyses of Collembola, none places the Entomobryidae among the more recently evolved families (d'Haese, 2002; Lee et al., 1995). The second option is inconsistent with the basic morphological and dietary features distinguishing the Entomobryidae from most other Collembola, which are adaptations for life above ground. From their origin, one would expect Entomobryidae to be abundant in arborescent vegetation and vulnerable to entrapment in amber. The fourth explanation has no supporting evidence. Paleocene deposits might shed light upon this question, but given the competitive abilities of members of the Entomobryidae and the apparent antiquity of their origin this explanation does not seem likely. Therefore, none of the available explanations for the absence of Entomobryidae s.l. in Cretaceous amber is satisfactory.

4.2. Implications concerning the distribution of Collembola

The extant genera most similar to *Protoisotoma* are currently limited to Australia, New Zealand, and sub-Antarctic islands. That *Protoisotoma* is the dominant genus in Canadian amber and is numerous in the mid Cretaceous of Myanmar argues for it being very widespread in Mesozoic times. On the other hand, Tertiary genera recovered from the Eocene Baltic and tropical American Miocene ambers are still extant in the same regions. The situation regarding Collembola appears to differ from that described by Ross et al. (2000, p. 294) for a large number of hexapods, in which he states "…many modern insects have a more restricted distribution than their Tertiary predecessors…".

4.3. Implication concerning K/T extinction

Except for the genus Protoisotoma, extant Canadian Collembola are considerably more similar to the mid Cretaceous species in Burmese amber than they are to the Late Cretaceous fauna in Canadian amber. This suggests that the latter were largely eradicated east of the northern Rocky Mountain regions by the end of the Cretaceous and replaced by migrants from elsewhere, probably Laurasia. It is very likely that some event between the end of the Cretaceous and now had a devastating effect on the arboreal Collembola of eastern Alberta. Many authorities (Tschudy et al., 1984; Wolbach et al., 1988; Johnson, 1992; Labandeira et al., 2002) have provided disparate evidence supporting the statement that: "… North American land plants were devastated from Alberta to New Mexico at the K-T boundary" (Cowen, 1994, p. 293). This devastation could have largely extirpated the arboreal Collembola of the region.

Considering this scenario, it is likely that the Collembola may have been affected by paleoecological events in a different way than most other hexapod groups. While both Jarzembowski and Ross (1996) and Ross et al. (2000) indicate that there was little change in the number insect families across the K-T boundary, three out of eight Collembola families did not survive into the Eocene, when the fossil record of Collembola next appears. It is notable that all of these were in the Entomobryomorpha and two were in the superfamily Entomobryoidea (vide supra).

4.4. Implications for the environment of the Burmese amber

A number of the genera described herein display features suggestive of a neustonic or subaquatic habitat. Six genera (*Grinnellia*, *Sminthuricinus*, *Protodesoria*, *Villusisotoma*, *Praentomobrya*, and *Protodontella*) display the long, slender ungues characteristic of such habitats (Christiansen, 1961), and in the Isotomidae four of the eight taxa showing dens features clearly (see Table 5) have tuberculate dentes, which we and other Collembolists (Michael Potapov, pers. comm. 2004) have noticed is characteristic of subaquatic species. The subaquatic nature of many Collembola would agree well with the suggestion of Cruickshank and Ko (2003, p. 452) concerning the depositional environment "… A near shore marine setting (bay lagoon, or estuary) proximal to a river outlet may be the best explanation…." These environmental conditions are probably very common in amber producing sites (Grimaldi, 1996).

5. Collembola in amber

The rarity of Collembola in amber deposits remains a mystery. In studies with extant arboreal arthropod faunas, Collembola are usually found in both temperate and tropical

forests and typically in great abundance. Strangely, no Collembola have been found in the insect-rich Siberian Cretaceous amber (Zherichin and Sukatcheva, 1973) or Cretaceous New Jersey amber (Grimaldi, pers. comm. 2004), or the Tertiary Arkansas amber (Santiago-Blay, pers. comm. 2004). Only four specimens have so far been found in the Lebanese Lower Cretaceous amber. There are approximately ten (unidentified) from the Cretaceous amber of Álava Spain and 11, mostly fragments, from the Lower Cretaceous of France (Perrichot, 2004). The latter samples are unusual because, while the Collembola are not identified, the identified forms indicate mostly litter organisms, a habitat where Collembola are a dominant group.

In spite of this, as of the last compilation, the number of known extinct genera of Collembola found in the Cretaceous (19) is quite comparable to most groups of insects and is larger than many (Carpenter, 1992). A more recent compilation might show a different picture. The status of the amber Collembola is anomalous in that there presently are more genera known from the Cretaceous than from the mid-Eocene to the Oligocene (15). This is almost certainly is a reflection of the fact that there has been no recent comprehensive work on the latter, and not an actual feature of the Collembolan fossil record.

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