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An Unusual, Primitive Piesmatidae (Insecta: Heteroptera) in Cretaceous Amber from Myanmar (Burma)

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ABSTRACT

Cretopiesma suukyiae, new genus and species, is described, based on a unique female specimen in mid-Cretaceous (c. 100 myo) amber from northern Myanmar. Features of *C. suukyiae* unique for the small Recent family Piesmatidae include a long, protrudent clypeus, a dorsal carina of the head, lack of “jugal” lobes/appendices, widely separated coxae, very large scutellum, and the venation of the corium; some of these are plesiomorphic and shared with Aradidae. *C. suukyiae* possesses the cuticular areolation and propleural cavities distinctive to Piesmatidae. Phylogenetic analysis of Recent and fossil genera of piesmatids resulted in a cladogram with *Cretopiesma* as sister group to the remainder of the family. Relationships of this unusual species and of Piesmatidae within Pentatomomorpha are discussed.

INTRODUCTION

The Piesmatidae is a small family of approximately 40 Recent species and three genera, which are rather small in size (generally 2–4 mm long) and have extensive areolation of the head, thorax, and corium of the hemelytra. The distinctive microsculpture initially led hemipterists to classify these bugs within or near the cimicomorphan family

Tingidae (see the historical reviews by Drake and Davis, 1958; Heiss and Péricart, 1983). Not until the work of Tullgren (1918), Leston et al. (1954), and Drake and Davis (1958) was the position of the family within the Pentatomomorpha established, though relationships within this infraorder are still obscure. Piesmatids have been considered to have an isolated position in the Pentatomomorpha (Štys, 1967), to be within the “malcid line”

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(Malcidae, Colobathristidae, Berytidae) of the Lygaeoidea (Schaefer, 1972, 1981), or closely related to the rare, coleopteriform lygaeoids, the Psamminae (Henry, 1997). Later we will discuss the evidence for family-level relationships of the Piesmatidae, in light of the primitive new fossil we describe here. Major works on the family are the following: Drake and Davis (1958) on the morphology, an overview of genera, and treatment of the American species; Heiss and Péricart (1983), also on morphology, but also with detailed information on life histories, development, and the Palearctic species; Narisu (2000) on a review of their biology; and two papers by Schaefer (1972, 1981) on relationships.

The Recent genera are *Piesma* Lepeletier de Saint Fargeau and Audinet-Serville, *Miespa* Drake, and *Mcateella* Drake. The rare Asian genus *Thaicoris* Kormilev was originally (Kormilev, 1969) and later (e.g., Schaefer, 1972, 1981) placed in the Piesmatidae, but it has recently been shown to belong to the Thaumastocoridae (Heiss and Popov, 2002). *Piesma* is the largest genus with approximately 31 species, and is largely Holarctic but with some African species. One common Western Hemisphere species, *Piesma cinereum* (Say), extends from North America into tropical regions of Central and South America. Péricart (1974) classified the genus into three subgenera, but most recently Heiss and Péricart (1997) elevated two of these (*Afropiesma* Péricart and *Parapiesma* Péricart) to generic rank. *Miespa* is a monotypic genus known only from Chile; *Mcateella* contains four described species from Australia, although numerous undescribed species exist (G. Cassis, personal commun., 2006). Thus, the family is essentially bipolar, occupying mostly the temperate regions of the northern and southern hemispheres.

Host plants of the few piesmatid species where feeding habits are known have been reviewed by Schaefer (1981). The Chenopodiaceae is the family that is most commonly exploited as hosts, species of which are common in salt marshes (the family also includes beets and spinach). Some species in the family Caryophyllaceae ("pinks," including carnations) are also common hosts. The widespread species *Piesma cinereum* is known

to feed on three genera of chenopods, an amaranth (*Amaranthus*), and even a sedge (Cyperaceae). Several species feed on *Acacia* (Leguminosae), which are *P. limnavouri* Štys in Africa, and *Mcateella* in Australia. The hosts of *Miespa* are unknown.

Until now only two fossil species have been known. *Heissiana serafini* Popov in Eocene Baltic amber is considered to be closely related to the two small austral genera (Popov, 2001). *Eopiesma trimerus* Nel, Waller and De Ploëg, in lowermost Eocene (Sparnacian-aged) amber from the Paris basin is considered to be the sister group to all other piesmatids including *Heissiana* (Nel et al., 2004). Thus, the fossil we report here is only the third one documented for this interesting family of true bugs, and it extends the known geological age of the family to approximately twice what was known.

MATERIALS AND METHODS

Burmese amber derives from the northern province of Kachin, near Myitkyina. The specimen reported here was specifically derived with thousands of other pieces from near the villages of Huangpa and Tanai, collected by R. Cruickshank of Leeward Capital Corp. (reviewed in Grimaldi et al., 2002). Age of the amber is estimated to be Cenomanian to Late Albian. The Cenomanian age (ca. 98 mya) is based on the geological occurrence of 21 Mesozoic insect taxa that occur as inclusions in Burmese amber (Grimaldi et al., 2002). The Albian age (ca. 105–100 mya) is based on one ammonite specimen and a modest sample of spores from one site (Cruickshank and Ko, 2003). Thus, a reasonable estimate of the age of Burmese amber is approximately 100 myo. The piece of amber was prepared according to the protocols described in Nascimbene and Silverstein (2000). Critical observation of the minute specimen (body length 1.45 mm) required high resolution and magnification to view features such as scent glands, trichobothria, etc. Reflected fiber optic illumination was used to study the specimen at 144× with a Leitz Wetzlar stereoscope and also with a Zeiss compound scope at magnifications from 100 to 400×. We examined two specimens of *Heissiana serafini* Popov (nos. GPIH 4490, and paratype GPIH 2208), loaned to us by Dr.

Wolfgang Weitschat of the Geologisch-Paläontologisches Institut und Museum at the University of Hamburg. This allowed us to score several characters not mentioned in the original description of that species.

SYSTEMATICS

Family PIESMATIDAE Amyot and Audinet-Serville, 1843

Piesmides Amyot and Audinet-Serville, 1843: 300. Type genus: *Piesma* Lepeletier de Saint-Fargeau and Audinet-Serville, 1825.

Zosmenidae Dornh, 1859: 41. Type genus: *Zosmenus* Laporte, 1833.

DIAGNOSIS: Small (2–4 mm in length) pentatomomorphan bugs, some without trichomorphan synapomorphies. Integument and corium densely areolate-punctate. Head roughly transverse; compound eyes positioned posteriorly, roughly contiguous with pronotum; ocelli present in macropterous forms, absent in brachypterous and submacropterous forms; “jugal” appendices/lobes present and elongate (primitively absent in *Cretopiesma*); four antennomeres; mandibular plates strongly produced, reaching apex of clypeus in modern genera (unknown for Tertiary genera, not produced in *Cretopiesma*); labium four-segmented; bucculae present at base of rostrum. Pronotum subquadrate and explanate, with distinct longitudinal carinae (absent in the Eocene genus *Eopiesma*), without collar, calli distinct; propleura with distinct cavities beneath paranota; prosternum with depression for reception of rostrum. Mesoscutellum greatly exposed and generally small except primitively greatly enlarged in *Cretopiesma*; mesosternum with depression for reception of rostrum except in *Miespa* and *Cretopiesma*. Metapleural scent gland ostiole present (primitively so in *Cretopiesma*) or vestigial (all other genera). Hemelytral corium areolate; membrane reduced, nearly absent, or present with three or four nebulous veins and no cells; venation of corium (when present or discernable) variable. Hing wing (when present) with Sc absent; R and M separated distally. Legs unarmed; coxae close together, except widely separated in *Cretopiesma*; coxal cavities open; tarsi dimerous (trimerous in *Eopiesma*); pretarsus with paired, leaflike pseudopulvilli (i.e.,

arising from unguitactor plate, not the claws). Abdomen of nymphs and adults with dorsal abdominal glands on terga 3–4 or 4–5 (glands remain functional in adults); spiracles 2–6 in dorsal position (pair 6 sometimes in submarginal position); sternum V and VI with trichobothria anterior to spiracle, except absent or very highly reduced in *Miespa*, *Mcateella*, and *Cretopiesma* (and perhaps also *Heissiana* and *Eopiesma*); female sternum VII completely divided into hemisternites; ovipositor lanceolate; second gonocoxopodites in inverted U position; spermatheca median, unpaired; male genitalia symmetrical.

Cretopiesma, new genus

DIAGNOSIS: Distinguished from all other genera of piesmatids, Recent and extinct, by the following features: clypeus long, protruding, with a prominent median carina that extends to middle of frons; lack of “jugal” appendices/lobes; rostrum about as long as head, inserted far from clypeal apex, enclosed by bucculae at base; pronotum with pair of paramedian carinae, posterior margin slightly concave; mesoscutellum very large (length $0.21 \times$ the body length); coxae of each pair widely separated; corium venation distinctive, where veins Sc, R+M, and Cu are not fused in a vein that runs parallel and proximal to the margin of the membrane and corium, instead with two transverse veins; membrane without “sutural area”.

TYPE SPECIES: *Cretopiesma suukyiae*, new species.

ETYMOLOGY: From *Piesma*, the type genus of the family; and from the Latin *creta*, meaning “white earth” or “chalk”, which refers to deep, chalky deposits in England that originally defined the Cretaceous Period (145–65 mya).

Cretopiesma suukyiae, new species

Figures 1–3

Piesmatidae sp.: Grimaldi et al., 2002: 41, fig. 25e.

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: Based on unique female specimen; small, body flattened, length

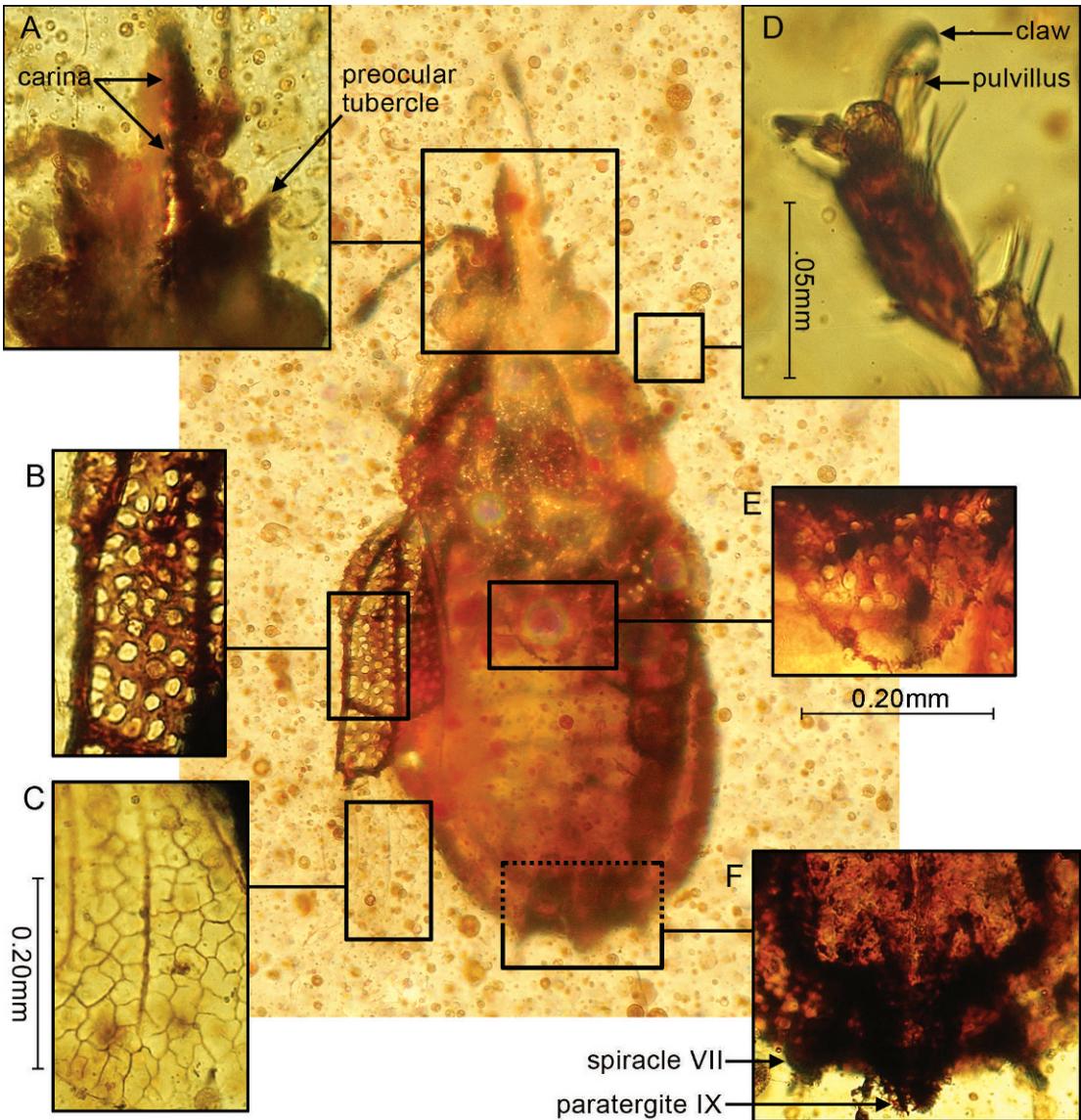
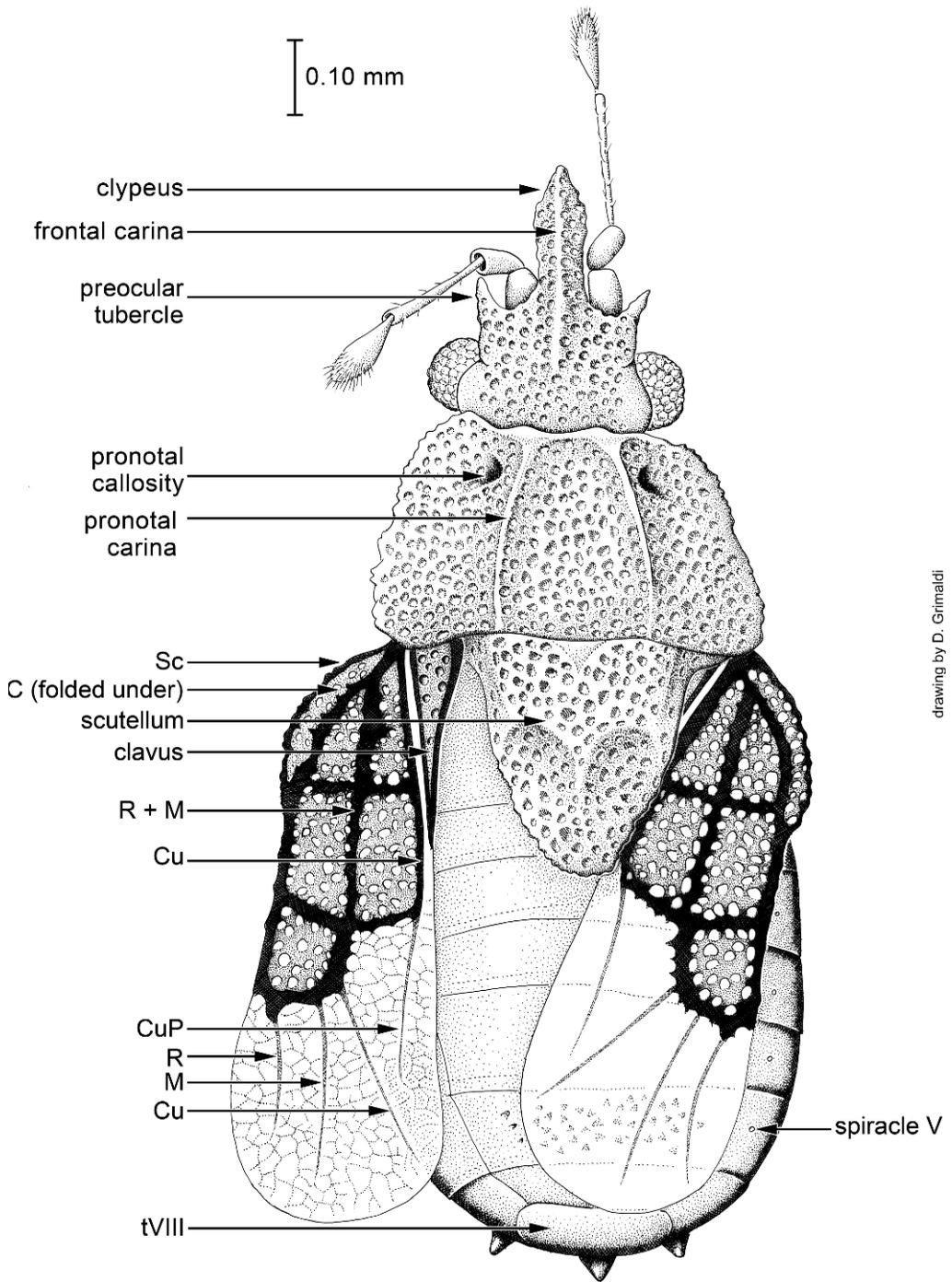


Fig. 1. Photomicrographs of holotype (AMNH Bu958) of *Cretopiesma suukyiae*, new genus and species, with dorsal habitus in center. **A.** Head, dorsal view. **B.** Detail of corium. **C.** Detail of wing membrane. **D.** Protarsus. **E.** Tip of scutellum. **F.** Terminalia, ventral view. A, B, C, E, F to same scale.

1.45 mm. **Head:** Wide, inserted into prothorax up to ventral margin of eyes; dorsally areolate; prognathous. Eyes extremely convex, bare of setulae; width across eyes 0.36 mm. Ocelli absent, typical of submacropterous forms. Clypeus long, protrudent, tip extended to level of middle of 3rd antennomere. Clypeus with median carina, extending from tip to middle of frons. Jugal appendices absent. Ventral sur-

face of head areolate. Bucculae short, extended from approximately middle of clypeus to anterior margin of preocular tubercles. Pair of large, conical preocular tubercles present, tips extend nearly to distal end of first antennomere. Antenna with four antennomeres; two basal antennomeres short and wide, relative lengths: (1) 1.0: (2) 1.1: (3) 2.9: (4) 1.5. Antennomere 3 long and thin, antennomere



drawing by D. Grimaldi

Fig. 2. Dorsal habitus of holotype of *Cretopiesma suukyiae*, new genus and species.

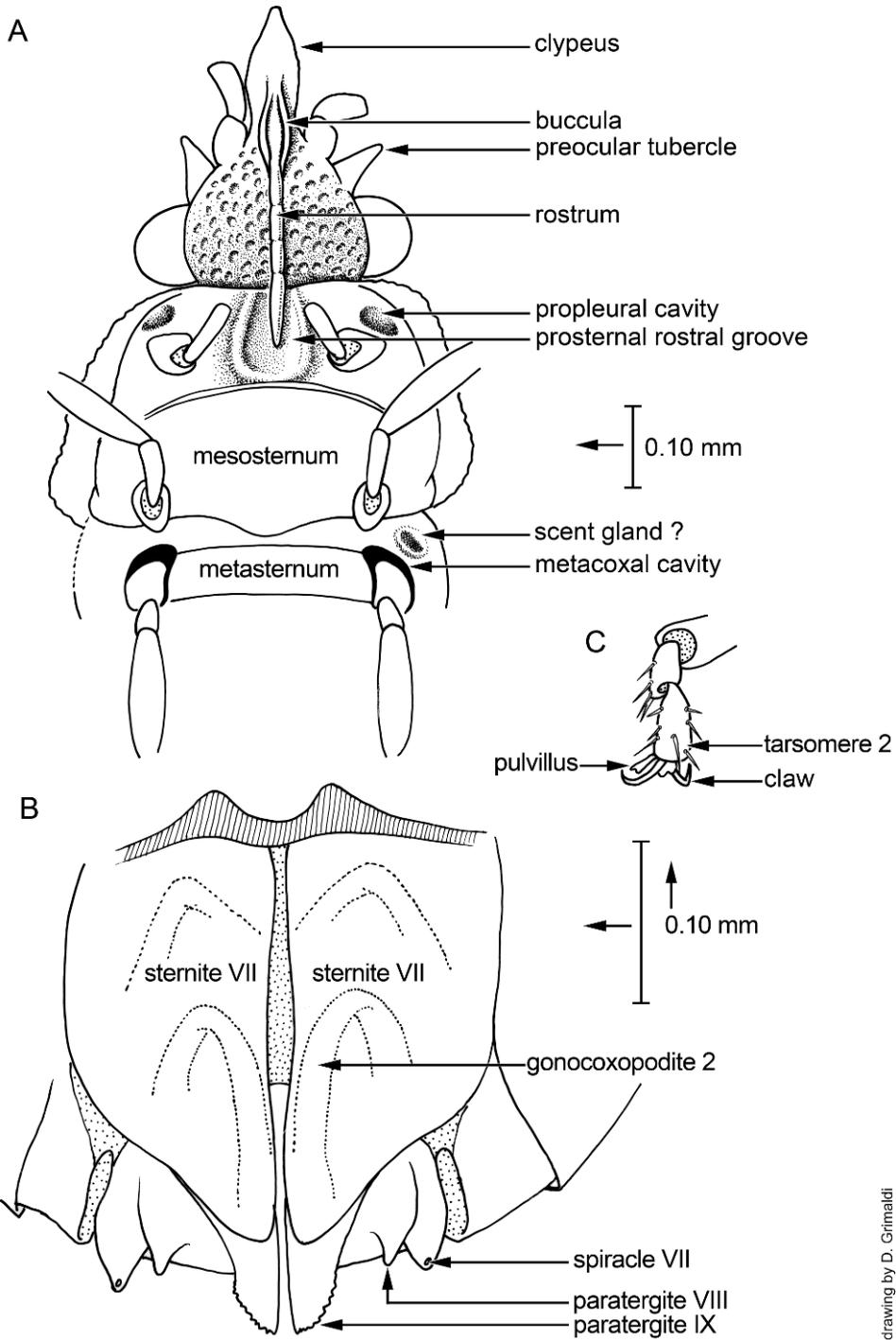


Fig. 3. Details of holotype of *Cretopiesma sukyiaie*, new genus and species. **A.** Ventral view of head and thorax. **B.** Apex of abdomen (ventral view). **C.** Mesothoracic tarsus.

4 fusiform, with dense, long setulae at apex. Antennal insertion between preocular tubercle and clypeus. Rostrum extended to level of fore coxae (segmentation obscure).

Thorax: Pronotum broad (length at middle 0.28 mm, greatest width 0.52 mm), explanate; trapezoidal in shape, with lateral margins diverging caudad, posterior margin slightly concave (vs. slightly convex or flat). Pronotum areolate over entire dorsal surface, with two large paramedial carinae extended full length of pronotum. Carinae tapered in thickness and slightly divergent caudad; anteriorly fused with thick transverse carina on anterior margin of pronotum. Pronotum with pair of callosities lateral to carinae and in slightly recessed areas. Mesoscutellum very large, 0.31 mm in length, 0.37 mm width; dorsal surface completely areolate, with apical margin broadly rounded. Posterior half of scutellum with paramedial pair of rounded depressions. All sternites smooth, not areolate or punctate. Prosternum with very broad rostral groove; no mesosternal groove. Propleural cavities present, just anterior to fore coxae. Metasternum very broad; no scent gland channel present, but apparently with small ostiole (scent gland opening?) anterolateral to metacoxa. All coxae widely separated in each pair. Legs short, femur thickest podite; all podites devoid of spines, but femur and tibia covered with numerous, fine tubercles. Tarsi with two short tarsomeres, apical tarsomere slightly longer; pretarsal claws apparently simple, rather long; pulvilli large, slender, flat, slightly shorter than claws.

Wings: Hemelytra short (submacropterous form?), apices extend to apex of abdomen but not beyond; length 0.76 mm, greatest width 0.28 mm. Apex of hemelytron broadly rounded, not narrowed. Corium occupies approximately half the hemelytral surface; entire corium areolate, except veins. Veins thickened, heavily sclerotized. Vein C short, occupies 2/3 basal half of hemelytron. Sc very short, branches off main stem of Cu, meets C (not R+M), length ca. $0.25 \times$ wing length. Two thick transverse veins present, one connecting apex of Sc and Cu (near apex of clavus); another a slightly V-shaped crossvein near middle of wing connecting C and Cu. Clavus narrow, apex very slender and acute, mem-

brane areolate; distinct commissure between clavus and rest of corium. Membrane of hemelytra with fine reticulations, four faint longitudinal veins with apices evanescent and not meeting distal margin of wing. Membrane veins interpreted here as R, M, Cu, and PCu; latter two veins convergent but not actually intersecting. Hind wing unapparent or absent.

Abdomen: Flat, broad; length 0.85 mm, width 0.55 mm. Ventral trichobothria not apparent, or absent. Spiracles situated dorsally on paratergites II–V. Tergite VII with numerous small spicules. Pair of spiracles on segment VII situated on small tubercles. Paratergites VIII a pair of small lobes flanking paratergites IX, which are apicalmost appendages. Paratergites IX apparently flat, with outer margins finely dentate. Sternite VII divided, pair of gonocoxopodite 2 visible beneath sternite VII, \cap -shaped.

MATERIAL EXAMINED: Holotype (unique specimen), female, AMNH Bu958, from Kachin Province, northern Myanmar, near the town of Tanai in the Hukwang Valley. In the amber fossil collection, Division of Invertebrate Zoology, American Museum of Natural History.

ETYMOLOGY: Matronym in honor of Aung San Suu Kyi from Burma, the 1991 laureate of the Nobel Peace Prize. Ms. Suu Kyi has spent 18 years isolated in house confinement (from 1989–95, 2000–02, and 2003 to present) for her promotion of democracy in Myanmar. It is fitting that a Burmese species, seemingly delicate but which has beautifully endured for so long, be named in her honor.

DISCUSSION

On the surface, the many unique or highly unusual features of *Cretopiesma* listed in the generic diagnosis might suggest its placement in a family other than Piesmatidae. However, at least some of these features are plesiomorphic for the family and others autapomorphic. More importantly, features of *Cretopiesma* that are diagnostic for Piesmatidae are the following: head, thorax, and corium with the same, distinctive form of areolation (e.g., fig. 4A); a short, stout second antennomere (cf. figs. 2, 4C); pronotum explanate and with dorsal carinae; presence of propleural cavities (figs. 3,

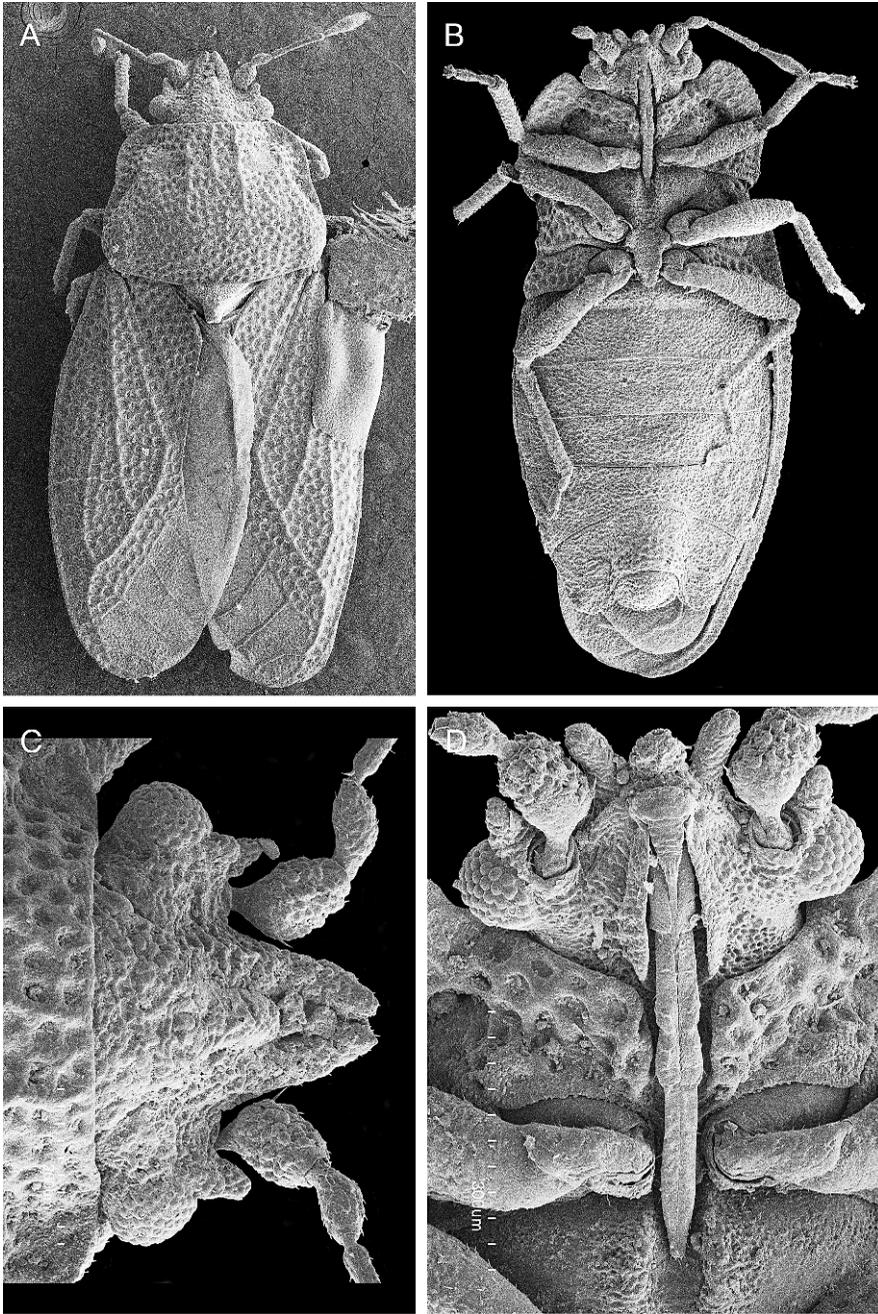


Fig. 4. Scanning electron micrographs of *Piesma* spp. (A, C: Arizona; B, D: South Africa). A. Habitus, dorsal view. B. Habitus, ventral view. C. Head and anterior pronotum, dorsal view. D. Head and anterior thorax, ventral view.

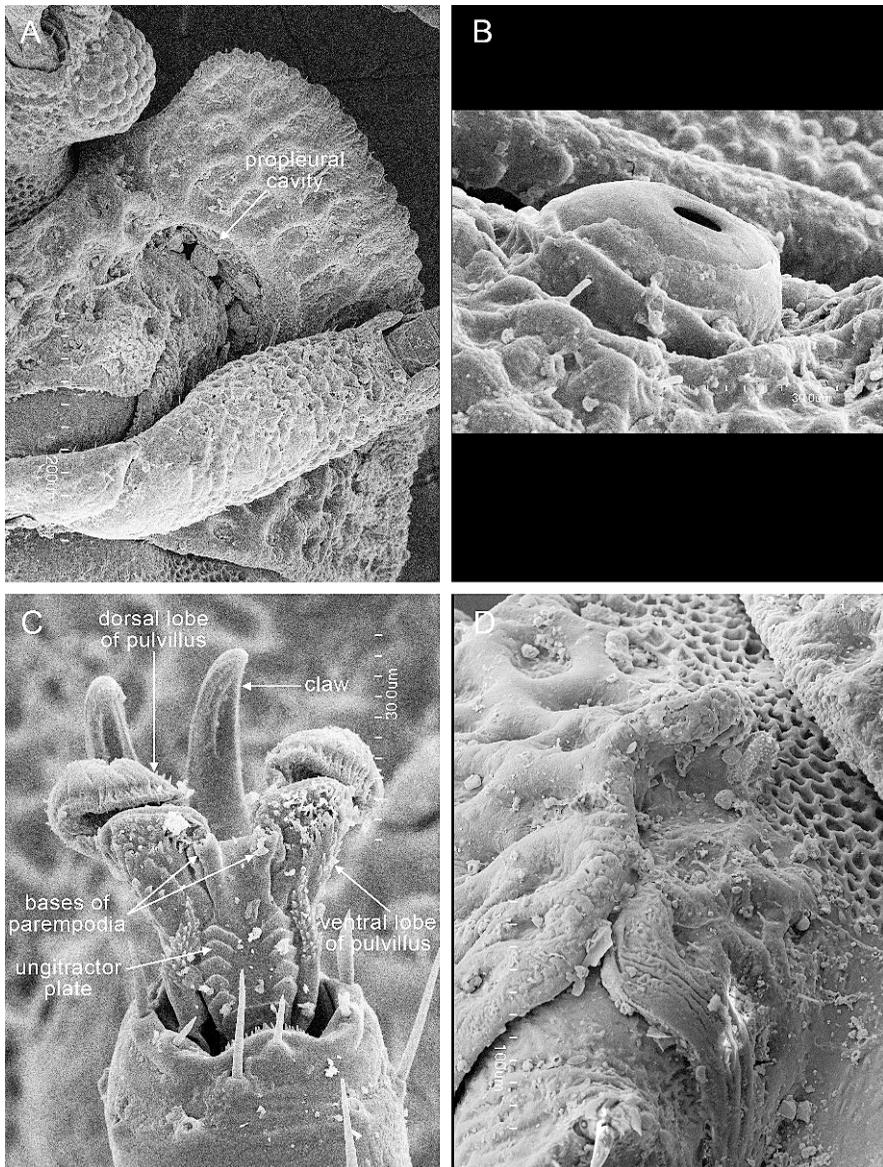


Fig. 5. Scanning electron micrographs of *Piesma* sp. (South Africa). **A.** Left anterior portion of thorax (ventral view), showing propleural cavity. **B.** Trichobothrial pad. **C.** Pretarsus, showing well-developed pulvilli. **D.** mesopleural fold near coxa.

5A); and the structure of the female terminalia, where sternum VII is entirely divided into hemisternites, the ovipositor lanceolate, and the second pair of gonocoxopodites are an inverted U (fig. 3). Further features of *Cretopiesma* that are consistent with *Piesmatidae* (though not exclusive to this family) are the

small, flattened body; proportions of the four antennomeres; preocular tubercles large and protuberant; hemelytron with basal half coriaceous, apical half membranous with four light veins (fig. 2); two tarsomeres present, with pretarsus having a pair of large, leaflike pulvilli (fig. 1D).

RELATIONSHIPS WITHIN PIESMATIDAE

An attempt was made to investigate relationships among living and fossil genera by expanding upon and revising those characters employed by Schaefer (1972, 1981). In addition, several new characters were included to accommodate the features found in the one Cretaceous (herein) and two Eocene (Nel et al., 2004; Popov, 2001) fossils. Twenty-three characters were identified and coded for cladistic analysis. In the following list apomorphies are described first (coded as 1 in the matrix: table 1), succeeded by brief notes on the distribution of the trait and its plesiomorphic condition. Outgroups included the basal pentatomomorphan family Aradidae.

HEAD:

1. Clypeus reduced, not projecting. This feature is found in all Recent piesmatid species and in the Tertiary fossils. *Cretopiesma* plesiomorphically has a strongly projecting clypeus similar to that of many Aradidae (cf. figs. 2, 6A).
2. Preocular tubercles bifid, with small secondary pair lateral to the large pair found in Recent and extinct species. This feature is autapomorphically present in *Piesma* (*Paropiesma*); all other species have the single large pair.
3. Rostrum short, apex extending no farther than the level of procoxae. Plesiomorphically, the rostrum extends well beyond this level, a condition found in the fossil genera *Heissiana* and *Eopiesma*, and in *P. (Paropiesma) kolenatii* (Fieber), *P. pupula* Puton, and *P. tenellum* Horvath.
4. "Jugal" lobes³ absent, which is a feature found in *Cretopiesma*. All other piesmatids have well-developed jugal lobes (figs. 4C, D).
5. "Jugal" lobes long, projecting well beyond the clypeus in adults, which is found in *Piesma* s.l. Plesiomorphically, the apices of the jugal lobes are at the same level as the apex of the clypeus.

³This is an adjectival form of the "juga" (extensions lateral to the clypeus) and should not be confused with the more widespread application of this term for the membranous lobe formed by the jugum in the posterior base of the insect wing.

TABLE 1
Data Matrix for Phylogenetic Analysis of
Piesmatidae
(see text for description of characters)

taxa	characters
	11111111112222
	12345678901234567890123
<i>Piesma</i>	
(<i>Piesma</i>)	10111110\$11111111011111
(<i>Paropiesma</i>)	1111111021111111011111
(<i>Afropiesma</i>)	1011111001111111011111
<i>Miespa</i>	10110000201101?11011011
<i>Mcateella</i>	10110000201111011211011
<i>Heissiana</i>	10010000101111?1111?011
<i>Eopiesma</i>	10010001?01??0011?0111
<i>Cretopiesma</i>	00100110010000010000011
Outgroup*	00000000000000000000000

* The outgroup was generated from plesiomorphic states inferred by comparison across basal pentatomorphs.

\$ subset polymorphism (= 0/1)

6. Third antennomere very slender and significantly longer than second antennomere, which is a feature found in *Piesma* and *Cretopiesma* (figs. 2, 4B). In the plesiomorphic condition the third antennomere is barely longer or even shorter than antennomere 2, which is found in the austral and Tertiary fossil genera.
7. Position of head porrect (apomorphic) versus declivant, the apomorphic state occurring in *Piesma* and *Cretopiesma*.

THORAX:

8. Absence of pronotal callosities (or calli): this state is hypothesized to be apomorphic (i.e., a loss), since the presence of callosities is widespread in Heteroptera. This presumably occurs just in the fossil *Eopiesma*, but the structure can be difficult to discern even in amber fossils (and the bubble above the pronotum in the unique holotype [Nel et al., 2004: 46, fig. 1] might obscure this feature). Like all other features of *Eopiesma* that we scored, we relied on the observations by Nel et al. (2004).
9. Pronotum with short, median carina (e.g., fig. 4A): Plesiomorphically this structure is absent (0); apomorphically with small or faint carina (1), or with a well-developed, longer carina (2). This feature

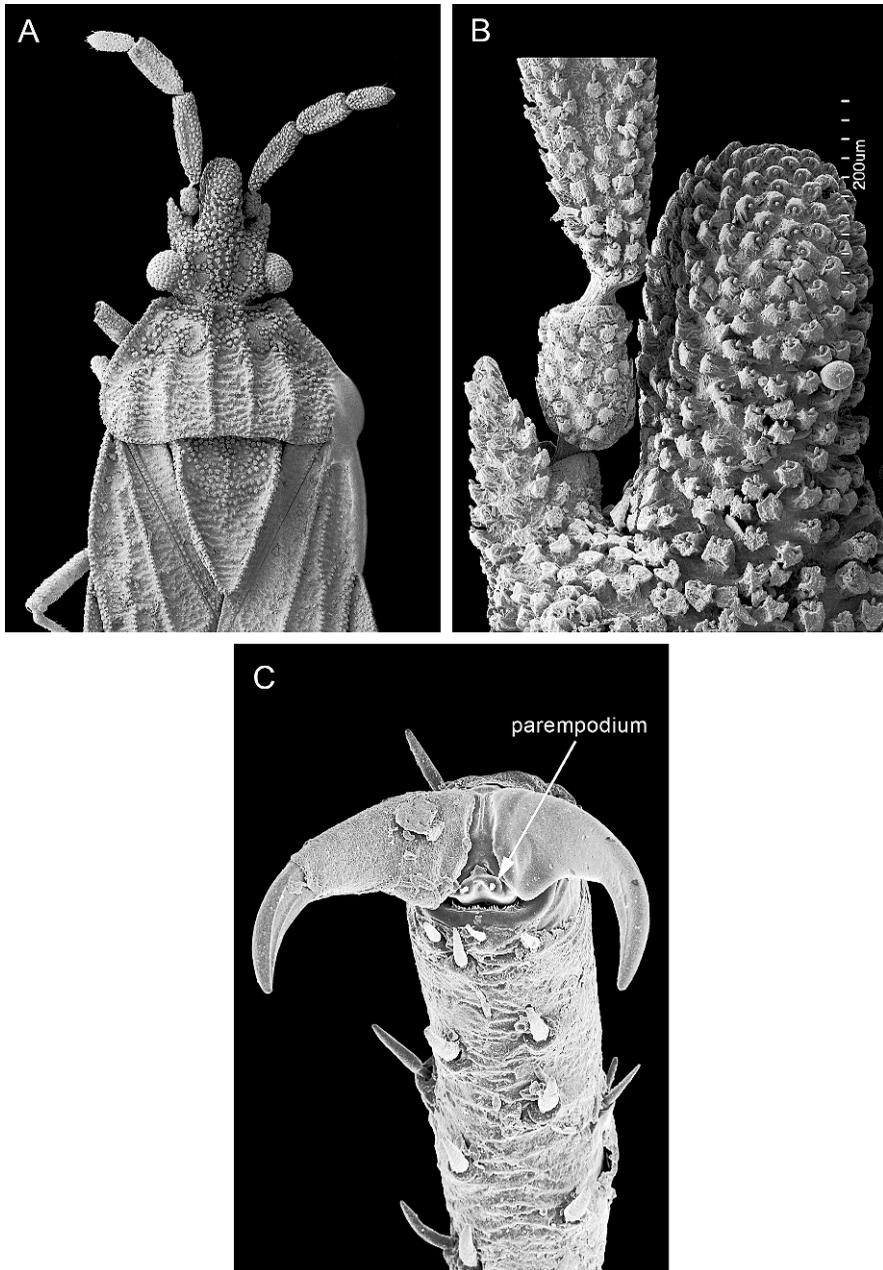


Fig. 6. Scanning electron micrographs of *Aradus brasiliensis* Usinger (Aradidae). A. Dorsal habitus, anterior half. B. Detail of clypeus, jugal lobe and antennal base (dorsal view). C. Detail of pretarsus (terminal view).

was coded as “?” in the matrix for *Eopiesma*, even though this genus was reported to lack carinae. A bubble obscures the relevant area of the pron-

tum in the unique type of *Eopiesma*, so if it is present and as cryptic as it is in *Heissiana* (personal obs.) then it would not be noticeable in *Eopiesma*.

10. Pronotum with paired, paramedian carinae (usually incomplete [fig. 4A], but complete in *Cretopiesma* [fig. 2]). The absence of the paramedian carinae is interpreted as primitive. Note that the complete absence of pronotal carinae in *Eopiesma* is enigmatic as all piesmatids have some combination of carinae—either paramedian carinae or a median carina (character 9). The bubble above the pronotum in the unique holotype of *E. trimerus* (Nel et al., 2004: 46, fig. 1) might obscure this feature.
11. Mesoscutellum small: it is uniformly and apomorphically small in Recent and Tertiary Piesmatidae (fig. 4A), generally half or less the clavus length. *Cretopiesma* plesiomorphically has a very large scutellum (widespread throughout Pentatomomorpha [fig. 6A]), which is longer than the clavus.
12. Pair of mesopleural tubercles present laterally (apomorphic). The absence of these tubercles is a notable plesiomorphy of *Cretopiesma*.
13. Mesosternum and prosternum with labial depressions (fig. 4D), a state apomorphic to that in which the labial depression occurs only on the prosternum (fig. 3).
14. Pleural lamina (“coxal lobes”) are apomorphically present on all living piesmatids, as well as in the Eocene *Heissiana*, but absent in *Cretopiesma*.
15. Metathoracic scent gland channels present, and apomorphically in the form of a pair of narrow, transverse troughs (fig. 4B). These occur in all Recent genera except *Mcateella* (unknown for *Miespa*), and do not occur in the fossil genera in which this area is visible.
16. Tarsomere number reduced to two, which occurs in all genera except *Eopiesma*, which has three. Three tarsomeres is almost certainly the plesiomorphic state. Since Nel et al. (2004: 47, fig. 2) have photographs of the trimerous tarsi of *Eopiesma*, the condition is unambiguous for that genus.
17. Corium venation with what are presumed to be veins R+M (Cu in Heiss and Pericart, 1983) and Cu (Br, *ibid.*) meet in a vein that runs parallel and proximal

to the distal edge of the corium. Corium venation is very conservative in piesmatids, the exception being *Cretopiesma*. In that genus, and apparently the plesiomorphic condition, these veins extend directly to the proximal edge of the corium, with nebulous extensions into the membrane (fig. 2).

18. Hemelytral membrane veins reduced (*Eopiesma* and *Heissiana* to three veins: state 1) or absent (*Mcateella*: state 2). All other piesmatids have four nebulous veins in the membrane.
19. Coxal bases are apomorphically close to each other in each pair, generally separated by a distance no greater than the diameter of the coxal base (fig. 4B). This is apomorphically found in all piesmatids including *Heissiana*, but plesiomorphically not in *Cretopiesma*, which has the coxae of each segment very widely separated by a distance of 3–4× the coxal diameter (fig. 3). Widely separated coxae are found in some basal pentatomomorphs, such as Aradidae.

ABDOMEN:

20. Abdominal spiracles 2–5 or 2–6 are dorsally situated apomorphically. Plesiomorphically spiracles 2–5 are situated dorsally, and pair 6 ventrally, as in *Eopiesma*, *Cretopiesma*, and *Piesma* s.l.
21. Trichobothria are present as a single pair laterally on sternites V and VI (fig. 5B), but plesiomorphically absent in *Heissiana*, *Miespa*, *Mcateella*, and *Cretopiesma*. The ground-plan condition of the Pentatomomorpha would seem to be the presence of abdominal trichobothria, but this pertains to the Trichophora (i.e., all pentatomomorphs except Aradoidea).
22. Female sternum VII divided medially into lateral hemisternites. This notable apomorphy is found in all Recent Piesmatidae and in *Cretopiesma* (unknown for the other fossils), and probably supports monophyly of the family.
23. Second gonocoxopodites in an inverted-U (i.e., \cap) configuration (fig. 3B). Like character 22, this feature may support monophyly of the family.

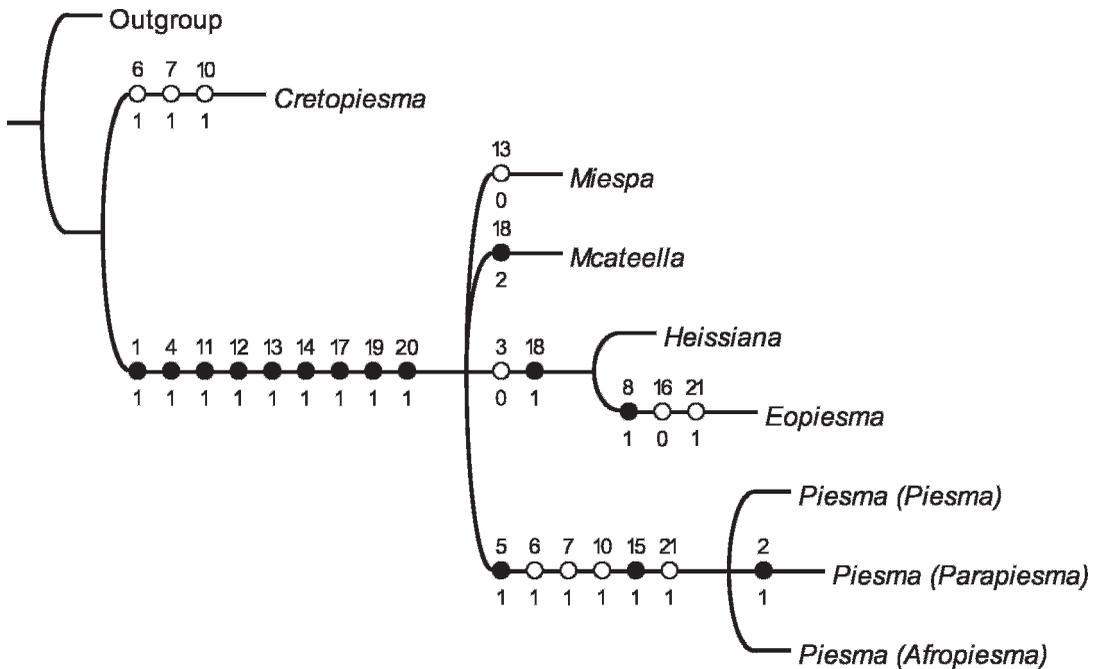


Fig. 7. Strict consensus tree (L 33, C.I. 72, R.I. 75) of four cladograms of Recent and extinct genera of Piesmatidae, based on the matrix in table 1. Characters on the cladogram are listed in the text. Open circles are homoplasious characters; solid circles are unambiguous synapomorphies.

The matrix is provided in table 1. All characters were considered nonadditive and of equal weight. The matrix was analyzed using the *wh**; *max** commands in *NONA* (Goloboff, 1997) and the resultant topologies visualized with *WinClada* (Nixon, 2002). The analysis revealed a single topology with 33 steps, a consistency index of 0.72 and retention index of 0.75. There were four equally most parsimonious trees, with the consensus cladogram presented in fig. 7. This cladogram, and the meager diversity of the family, suggest that the recognition of higher groups within Piesmatidae is unwarranted. Popov (2001) established the tribe Heissianini for *Mcateella*, *Miespa*, and the Baltic amber genus *Heissiana*. As the cladistic analysis demonstrates, Heissianini is paraphyletic and should be retained for *Heissiana* and *Eopiesma* only. Interestingly, these two genera are approximately contemporaneous in the Eocene.

Also interesting is that the austral genera, *Miespa* and *Mcateella*, appear not to be sister taxa (contrary to Popov, 2001), but form a

paraphyletic stem group to the living piesmatids and thus cast different light on the supposed gondwanan vicariance of these two genera. Instead, the piesmatids were likely widespread in the past and have dwindled in diversity, undergoing differential extinction across the Northern Hemisphere (perhaps at the Eocene-Oligocene transition), leaving *Mcateella* and *Miespa* isolated in the southern temperate regions of South America and Australia. Though *Miespa* and *Mcateella* are austral relicts in a modern bipolar distribution the family was likely widespread as recently as the Early Tertiary and long after the rifting of Gondwana. Paleontological data has revealed that many apparent Recent austral disjunctions were previously widespread (Grimaldi and Engel, 2005), a pattern to which piesmatids can be added.

PHYLOGENETIC POSITION OF PIESMATIDAE

As mentioned in the Introduction, identifying the living sister group of the Piesmatidae

has been challenging. The earliest classifications placed Piesmatidae with the cimicomorphan family Tingidae or in various positions among the Lygaeoidea. Henry (1997) considered piesmatids as lygaeoids and included *within* the family the rare and unusual Psammidae.

While *Cretopiesma* is very likely a piesmatid, it is also quite aradoid in character, which is a grouping of the two families that was first proposed by Spinola (1852), though on a superficial basis. Similarities that *Cretopiesma* plesiomorphically shares with Aradoidea include the very large mesoscutellum; coxae widely separated in each pair; and the absence of trichobothria. They apomorphically share a long, jutting clypeus. It is interesting that the Burmese amber fauna also contains a remarkably primitive aradid, *Archearadus burmensis* Heiss and Grimaldi (2001, 2002), which possesses the plesiomorphic features of pseudopulvilli on the pretarsus, dimerous tarsi, and metapleural scent gland ostioles, but which in all other respects is a typical aradid. Indeed, primitive for aradids are a rostrum arising far from the clypeal apex, basally enclosed by bucculae and about as long as the head, and a prosternal furrow for reception of the rostrum—all features similarly possessed by *Cretopiesma*. *Cretopiesma* differs from all living and extinct aradids in several striking respects: 1. It is far smaller than any known aradid; 2. it has well developed pseudopulvilli (cf. figs. 1D, 3C, 5C, 6C), while most living aradids have lost these; 3. the antennal structure and proportions are very similar to those of piesmatids, and are not stout and papillate as in aradids (fig. 6A); and, 4. the cuticular microsculpture of *Cretopiesma* is completely unlike that of aradids. Most aradids have a granular cuticle, which under SEM magnification (fig. 6B) reveals the granules to have a distinctive irregular to stellate form, with a small papilla recessed at the apex.

Despite these striking differences, one reviewer maintained that *Cretopiesma* was actually an aradid, and that the subordinate placement of Piesmatidae within Lygaeoidea in Henry's (1997) phylogeny precluded Piesmatidae from being closely related to Aradidae or being at the base of the Pentatomomorpha. In fact, there are several aspects of that paper

that reveal that caution should be used in interpreting the proposed pentatomomorph relationships. One, the terminal taxa in the analysis were not exemplar species, but subfamilies and families, so terminal taxa were coded as ground plans. Secondly, several of the more inclusive synapomorphies proposed by Henry (1997) do not apply to the Piesmatidae, such as his characters 5-0, 20-1, 28-1, 47, and 48. Third, we re-analyzed the original matrix in Henry (1997) using NONA, and a strict consensus of the raw data (no weighting) produced a tree with 12 unresolved basal branches, seven of which were groupings of 2–7 terminals ($L = 175$ steps based on 12 trees, $CI = 41$, $RI = 67$). While the smaller groupings of taxa in this strict consensus tree and in Henry's preferred tree (his fig. 3) entirely coincided, the basal relationships were completely different. A strict consensus tree based on 11 *ordered* multistate characters (Henry [1997] mentioned there were nine, but there are actually 11 in the matrix) produced a tree in NONA of 190 steps (from 24 trees total), or $CI = 38$ and $RI = 69$, which is shorter than the one in Henry (1997). The cladograms with ordered characters were largely similar, except for significant differences among basal lygaeoids—precisely the area of the tree where Piesmatidae supposedly fit. This similarity, however, is what one would expect by constraining character evolution, particularly when 20% of the characters are ordered. Fourth, for nine nodes and 38 steps, seven characters involved a loss from basal nodes (4, 5, 19, 32, 35, 46, 47) and/or their re-appearance (4, 12). Interpreting the absence of features in such cases is ambiguous. In Henry's (1997) hypothesis, a piesmatid-psammine relationship (the “most well-supported grouping”) was specifically based on the loss of ocelli, presence of “hemelytral punctures or areoles”, two-segmented tarsi, loss of trichobothria on abdominal sternites IV and V, very short second antennomere, and a “scutellar process”. Reduction of the tarsus to two tarsomeres, as for all characters of loss, is difficult to homologize. Also, most adult macropterous piesmatids have ocelli, as well as trichobothria on sternum V (abdominal trichobothria are absent or very highly reduced in *Miespa*, *Mcateella*, and *Cretopiesma*). Furthermore,

the cuticular microsculpture of psammides and piesmatids is distinctively different—the former has punctures and rugosities, the latter irregular areoles. Lastly, the position of the Psammidae in Henry (1997) is based partly on three characters that are inferred, and actually unknown, for this rare group (57-1: structure of egg eclosion fracture; 42-2: karyology; and 52-1: number of salivary gland lobes).

While we recognize the contributions brought to the confusing classification of Lygaeoidea by Henry (1997), we don't believe that on the basis of this study one could dismiss the possibility of a close relationship between Piesmatidae and Aradoidea, as *Cretopiesma* suggests.

GEOLOGICAL HISTORY OF PENTATOMORPHA

The confusing phylogenetic position of Piesmatidae highlights the difficulty of placing some higher Panheteroptera, even with full suites of data using modern species. Thus, the consistent lack of critical details in fossils, particularly compressions, seriously compromises the placement of fossils. This must be kept in mind with any consideration of the geological history of Pentatomorpha.

Abundant compression fossils from the Mesozoic have been ascribed to the Pentatomorpha, and to modern superfamilies and families thereof (e.g., Popov, 1968, 1980, 1986, 1990; Popov and Pinto, 2000). In contrast, the record of pentatomorphs in Cretaceous ambers is exceedingly sparse, while modern superfamilies of Cimicomorpha (e.g., Tingoidea) are fairly diverse in Cretaceous amber (e.g., Golub and Popov, 2000, 2003; Perrichot et al., 2006). Indeed, the only documented Cretaceous amber Pentatomorpha are the aforementioned aradid *A. burmensis* and *Cretopiesma suukyi*, both in Burmese amber and both significantly plesiomorphic. While it is reasonable to assume that Aradoidea and Piesmatidae originated in the Early Cretaceous, ca. 140–120 Ma, definitive Trichophora are not known until the Tertiary. Trichophorans (as are commonly defined and understood based on modern representatives) no doubt were probably present during the Late Cretaceous, and Pentatomorpha probably originated in the Late Jurassic, since

definitive cimicomorphs do occur as compressions in such deposits (e.g., Zhang et al., 2005). However, the Jurassic and Early Cretaceous taxa that are assigned to modern trichophoran superfamilies may actually be stem-group trichophorans or pentatomorphans. The discovery of additional pentatomorphans in Cretaceous ambers will contribute significant information on the age and phylogeny of these bugs.

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