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The oldest fossil piesmatid bug in the Lowermost Eocene amber of the Paris Basin (Heteroptera: Lygaeoidea: Piesmatidae)

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⊢ ABSTRACT ⊢

The oldest fossil Piesmatidae, *Eopiesma trimerum* n. gen., n. sp. is described from the Lowermost Eocene amber of Paris Basin (France). It is considered as the sister group of all other Piesmatidae. This family probably diversified during the Lower Cenozoic.

KEYWORDS | Insecta. Heteroptera. Piesmatidae. n. gen., n. sp. Eocene French amber. Phylogeny.

INTRODUCTION

The Piesmatidae is a small family of Lygaeoidea, with 6 known modern genera (Schuh and Slater, 1995; Heiss and Péricart, 1997). It is poorly represented in the fossil record, except for a citation of an undescribed specimen from the Upper Cretaceous Burmese amber (Grimaldi et al., 2002) and a fossil genus and species *Heissiana serafini* POPOV 2001 from the Upper Eocene Baltic amber. Thus, the present discovery of a Lowermost Eocene Piesmatidae is of great importance for the phylogeny and chronology of the family.

SYSTEMATIC PALEONTOLOGY

Order: Hemiptera LINNAEUS, 1758 Suborder: Heteroptera LATREILLE, 1810 Family: Piesmatidae AMYOT and SERVILLE, 1843

GENUS Eopiesma n. gen.

Type species: Eopiesma trimerum n. sp.

Diagnosis: This new genus is characterized by a combination of the following characters: the 3-segmented tarsi; abdominal spiracle 6 ventral; preocular tubercle simple; 3 strong veins on well-developed membrane; and pronotum without carinae.

Etymology: After the Eocene period and Piesma.

Eopiesma trimerum n. sp. Figures 1 and 2

Material: Female holotype specimen PA 2306, mounted in Canada balsam, in collection De Ploëg and Indivision Langlois-Meurine, deposited in the Muséum National d'Histoire Naturelle, Paris. Specimens collected in Le Quesnoy all bear the letter PA for Paris (meaning Paris Basin).

Locality deposit: Le Quesnoy, Chevrière, region of Creil, Oise department, France.



FIGURE 1 *Eopiesma trimerum* n. gen., n. sp., female holotype specimen PA 2306. A) Photograph in dorsal view. B) drawing in dorsal view. Scale bar: 1 mm.

Geological age: Lowermost Eocene, Sparnacian, level MP7 of the mammal fauna of Dormaal. We have demonstrated that the amber is autochthonous and very different from the Baltic amber in age, chemical composition and origin (Feugueur, 1963; De Ploëg et al., 1998; Nel et al., 1999).

Etymology: Named after the 3-segmented tarsi, a diagnostic characteristic of this fossil species.

Diagnosis: That of the genus.

Description: Dorsal surface of body and hemelytra finely to rather coarsely lacy, veinlets forming limits of areolae slightly raised.

Head: compound eyes normal, with many ommatidia; 2 very small well-separated ocelli; antennal segment I, 0.1 mm long, segment II, 0.12 mm, segment III, 0.14 mm, segment IV clavate, 0.12 mm and bearing some rather long setae; thus segment II slightly longer than segment I; segment III longest; head slightly produced in front of eyes, but not surpassing antennal segment I; bucculae long, punctuate but without any areolae, and not protruding below or before the head; no clypeal spine; preocular tubercle simple and very small (*sensu* Heiss and Péricart, 1983); jugal appendices small and well separated with a large clypeus between them; 4-segmented rostrum, very long, reaching mesothoracic coxae.

Thorax: lacking visible channel of metathoracic scent gland; anterior pronotal carina absent; paranota well developed, 0.16 mm wide, with one row of areolae; disc of pronotum strongly gibbous, anteriorly produced, covering basal half of head; collar absent; no visible callosities; hind pronotal margin slightly curved, not triangularly prolonged backwards; scutellum small but clearly visible, without outgrowth at its apex. Abdomen: abdominal sternites II reduced to 2 lateral sclerites; sternites III and IV fused (i.e. the sutures between these sternites without any intersegmental membrane), unlike the sutures between the following abdominal sternites; abdominal sternites VIII and IX cannot be distinguished (possible because of poor preservation); 2 lateral trichobothria on both abdominal segments V and VI; spiracles II to V dorsal (visible in ventral view through transparent cuticle); spiracle VI ventral, very close to the dorso-ventral sulcus; spiracle VII not visible; genital appendages hardly visible, but specimen may be a female.

Fore wings: macropterous; costal fracture absent; hemelytral clavus well developed, with 5 rows of areolae in its broadest part; clavo-corial suture present; sutural area with 3 rows of areolae; hyaline membrane large, crossed by 3 veins distally evanescent and without any areolae, the hemelytra are broadly overlapping; hemelytra areolae small and rather regular, of the same size and covering all surface except membrane; subcostal vein present only on distal half, basally vanishing in fused cubital + subcostal area; subcostal area with 2-3 rows of areolae at widest part; cubital area with 4 rows of areolae at widest part; costal lamina present, with one row of areolae; brachial vein weak but long parallel to clavus; brachial area narrow, with one row of areolae.

Hind wing: not visible under the hemelytra, although the abdomen is clearly visible; apparently absent or greatly reduced.

Legs: tarsal claw without basal tooth; parempodia present but very small; pulvillus present, in the form of a small sclerotized basipulvillus and a distipulvillus having a smooth margin under the tarsal claw (*sensu* Goel and Schaefer, 1970); trochanter free, well separated from coxa; femora and tibiae densely granulated by 'microtubercles', each bearing a short bristle; femora slightly swollen; tarsi very clearly three-articulated, the second tarsomere being shortest and third tarsomere the longest.

Discussion: The Dipsocomorpha: Hypsipterygidae, the Tingoidea, some Thaumastocoridae (both Cimicomorpha) and the Piesmatidae (Pentatomomorpha) have the dorsal surface of body and hemelytra areolate. We assign *Eopiesma* n. gen. to the Pentatomomorpha on the basis of the presence of distinct corium, clavus and membrane (Panheteroptera *sensu* Wheeler et al., 1993), the absence of the costal fracture in forewing, the presence of trichobothria on the abdominal sternites 5-6, and the presence of a basipulvillus and a distipulvillus (Leston et al., 1954; Wheeler et al., 1993). The xylastodorine Thaumastocoridae have 'pentatomomorphan-like pulvilli' (Schuh and Stys, 1991). Tingidae lack abdominal trichobothria (Péricart, 1983) and pulvilli (Drake and Davis, 1960; Goel and Schaefer, 1970; Péricart, 1983). Nevertheless, the Upper Cretaceous vianaidid genus *Vianagramma* GOL-UB and POPOV 2000 has pulvilli on the ventral surface of claws, but apparently not separated from the claws (Golub and Popov, 2000). The exact structure of the pulvilli of this taxon remains somewhat uncertain. It could be interesting to compare them to the pulvilli of the Thaumastocoridae: Xylastodorinae (Schuh and Slater, 1995). Golub and Popov (2000) also indicated that *Vianagramma* differs from the modern Vianaididae in the 'ocelli absent', but Kormilev (1955) and Drake and Davis (1960) indicated that the ocelli are also absent in modern Vianaididae and Tingoidea. The exact affinities of the genus *Vianagramma* remain somewhat uncertain.

The placement of *Eopiesma* n. gen. in Piesmatidae is based on the following character states (after Henry,



FIGURE 2 *Eopiesma trimerum* n. gen., n. sp., female holotype specimen PA 2306. A) Photograph of lateral view of the three hind tarsi. B) Photograph of dorsal view of the three mid tarsi. Scale bar: 0.25 mm.

1997): presence of only 3 simple and distally vanishing veins in the membrane (synapomorphy of Lygaeoidea); abdominal spiracles 2-5 dorsal and 6 ventral; antennal segment 4 clubbed; buccula long and narrow; ocelli present; and hemelytra areolate. Furthermore, *Eopiesma* n. gen. shares with the Piesmatidae the presence of ocelli unlike tingid bugs (= [Vianaididae + (Tingidae + Cantacaderidae)] *sensu* Lis, 1999).

Nevertheless, Eopiesma n. gen. differs from the modern Piesmatidae in having clearly 3-segmented tarsi. The modern Piesmatidae (+ Lygaeidae: Psamminae) have 2segmented tarsi (derived state character after Henry, 1997). Henry (1997) grouped together the Piesmatidae and Psamminae on the basis of: (1) 'loss of ocelli'. This is a partial error of Henry, as the Piesmatidae have ocelli (Drake and Davis, 1958; Heiss and Péricart, 1983), 'though there is a tendency in the group to go from a reduction to complete absence of ocelli in certain taxa' (Henry, pers. comm. 2002); (2) 'presence of hemelytra puncture or areoles'. This character is clearly subject to homoplasy within the Heteroptera as it is without doubt convergently present in Tingoidea. Furthermore, it is not clear that the punctured hemelytra of the Psamminae are homologous with the areolate hemelytra of the Piesmatidae (Schuh and Slater, 1995); (3) '2-segmented tarsi'. The presence of 3-segmented tarsi in a Piesmatidae suggests that this character was convergently acquired by the Piesmatidae and the Psamminae; (4) 'loss of trichobothria on abdominal segments IV and V'. If the Piesmatidae and Psamminae have no trichobothria on segment IV, some have a pair of trichobothria on segment V (Drake and Davis, 1958; Heiss and Péricart, 1983; Schuh and Slater, 1995). Thus, the clade (Piesmatidae + Lygaeidae: Psamminae) proposed by Henry (1997) seems more weakly supported than supposed by this author and suggests more study is needed. The Psamminae lack ocelli and hemelytral membrane, and have a habitus very different from piesmatids. Thus, it is an opinion that Eopiesma n. gen. is more Piesmatinae than Psamminae, regardless if the latter is considered a piesmatid subfamily or if it is relegated to family status.

The '3-segmented tarsi' of *Eopiesma* n. gen. is a character state present in numerous other Lygaeoidea (including Lygaeidae non Psamminae, among others) and should be considered plesiomorphic, as treated by Henry (1997). Based on this character state, *Eopiesma* n. gen. would assume a basal position within the Piesmatidae.

Schaeffer (1972, 1981) proposed a cladistic analysis of the genera of Piesmatidae with a character polarization not based on a real outgroup but on a hypothetical ancestor. No other phylogenetic analysis is available. Following Schaeffer's study, the character state 'abdominal spiracle 6 ventral' is shared by *Eopiesma* n. gen. and *Piesma* and absent in the genera *Miespa* DRAKE 1948, *Mcateella* DRAKE 1924 and *Thaicoris* KORMILEV 1969. Heiss and Popov (2002) transferred *Thaicoris* from the Piesmatidae into the Thaumastocoridae. Henry (1997) considered this state plesiomorphic in the basal clades of the Lygaeoidea but with a homoplasious distribution in more advanced clades. Thus, it is difficult to establish if it is a plesiomorphy for the Piesmatidae.

A simple preocular tubercle (antennal tubercle *sensu* Schaeffer, 1981) is present in *Eopiesma* n. gen. and all Piesmatidae, except in *Parapiesma* PÉRICART 1974 (considered as a subgenus of *Piesma* LE PELETIER and SERVILLE 1825 by Heiss and Péricart, 1983, but later given generic status by the same authors in 1997). The character 'presence of 3 veins in membrane area' would exclude *Mcateella* and *Thaicoris*.

Popov (2001) erected the tribe Heissianini for the fossil genus *Heissiana* and the two modern genera *Miespa* and *Mcateella* on the basis of the following characters: (1) 'subcostal vein not developed'; (2) subcostal and cubital area presented by a single common area'; (3) 'sutural area well developed' (in macropterous forms); (4) 'juga subequal to clypeus'; (5) 'antennal tubercle always simple'; and (6) 'pronotum without or with one median carina'.

Hemelytra characters have to be considered carefully because of possible strong modifications in vein structures related to more or less important brachyptery. Characters (1) and (2) are clearly correlated. The subcostal vein is well developed in *Eopiesma* n. gen., at least in its distal half. Popov (2001) noted that a similar situation occurs in Parapiesma quadratum (FIEBER 1844) (Heiss and Péricart, 1983). Thus, some intermediate states can occur for this character between the presence and the complete reduction of subcostal vein. Character (3) was already proposed by Schaefer (1981) as a synapomorphy to support his clade (Miespa + Mcateella). Eopiesma n. gen. has a less well-developed sutural area than Heissiana, Miespa and Mcateella. Eopiesma n. gen. has jugal lobes distinctly smaller than clypeus and the antennal tubercles simple, a probable plesiomorphy.

Drake and Davis (1958) and Péricart (1974) indicated that the genus *Piesma* has a pronotum bi- or tri-carinate, unlike *Eopiesma* n. gen. that lack carinae on the pronotum. *Heissiana*, *Miespa*, and *Mcateella* have none or only one carina. *Thaicoris* has very long preocular tubercles, jugal appendices, and clypeus (Kormilev, 1969).

Eopiesma n. gen. has no particular affinities to one of the two subgroups of modern Piesmatidae proposed by Schaeffer (1981) and no particular affinities with the tribe Heissianini, suggesting that it probably represents the sister group of all the other Piesmatidae. The presence of a partially reduced subcostal vein in *Eopiesma* n. gen., together with its complete reduction in Heissianini and its presence in *Piesma*, suggest that the reduction of this structure occurred at least two or three times in *Eopiesma* n. gen., *Parapiesma* and the Heissianini. If so, this character is very homoplasious, as already indicated by Popov (2001). Popov (2001) also suggested that the presence of a long rostrum in piesmatids is plesiomorphic. The presence of a long rostrum in *Eopiesma* n. gen. supports this hypothesis.

The discovery of Eopiesma n. gen. demonstrates that the Piesmatidae were present during the Lowermost Eocene. After the preliminary description proposed by Grimaldi et al. (2002), the unnamed Upper Cretaceous 'Piesmatidae' would have a 'dorsal crest on the head' that should be 'distinctive of the family', but there is no dorsal crest in the piesmatid heads (Heiss and Péricart, 1983). Also, Grimaldi et al. (2002) indicated that there are no ventral trichobothria on the abdomen. All known Piesmatidae have abdominal trichobothria, as do other Pentatomomorpha. Thus, its attribution to the Piesmatidae needs confirmation. Nevertheless, if it is exact, this Burmese fossil has two very distinct long preocular tubercles and two long jugal lobes, apparently very similar to those of a Recent Piesma (compare Heiss and Péricart, 1983, fig. 1 to the photograph of Grimaldi et al., 2002, fig. 25e). Concerning these features, this older fossil seems to be more closely related to Piesma than to Eopiesma n. gen. It suggests that the separation between the lineage of *Eopiesma* n. gen. and that of recent genera could have occurred during the Upper Cretaceous.

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