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Original article

Phylogenetic relationships of the Mesozoic paraneopteran family Archipsyllidae (Insecta: Psocodea)

Relations phylogénétiques de la famille paranéoptère mésozoïque Archipsyllidae (Insecta : Psocodea)

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Abstract

The Middle Jurassic *Archipsylla sinica* sp. n. is the first record of the enigmatic Mesozoic family Archipsyllidae from China. This well-preserved Chinese material bears several apomorphies allowing an attribution of this family to the Psocodea. The presence of four-segmented tarsi in Archipsyllidae suggests that the reduction in number of tarsomeres occurred independently at least two times in the modern paraneopteran lineages Psocodea (''Psocoptera'' + Phthiraptera) and Condylognatha (Thysanoptera + Hemiptera).

Résumé

Archipsylla sinica nov. sp. du Jurassique moyen est le premier fossile chinois connu de la famille énigmatique mésozoïque Archipsyllidae. Ce matériel chinois, très bien conservé, montre plusieurs apomorphies qui permettent l'attribution de cette famille aux Psocodea. La présence de tarses avec quatre articles chez les Archipsyllidae suggère que la réduction du nombre de tarsomères s'est produite indépendamment chez les deux lignées modernes de Paranéoptères (Psocodea et Condylognatha).

Keywords: Paraneoptera; Psocodea; Archipsyllidae; Nov. sp.; Evolution; Middle Jurassic; China

Mots clés : Paranéoptère ; Psocodea ; Archipsyllidae ; Nov. sp. ; Évolution ; Jurassique moyen ; Chine

1. Introduction

Although several Permian to Liassic fossils have been attributed to the Psocoptera, Mockford (1993, p.2) considered that the earliest unquestionable fossil psocids known are from Cretaceous amber. These pre-Late Jurassic fossils are currently considered as representatives of the paraneopteran stem group, but resembling Psocoptera. Their position is uncertain because their delicate body structures that could reveal synapomorphies of the Psocodea have not been fossilised. The oldest records of the living groups of this last clade are from the Late Jurassic of Karatau and/or the Early Cretaceous ambers (Baz and Ortuño, 2000; Grimaldi and Engel, 2005; Azar and Nel, 2004). These last authors considered the Liassic to Early Cretaceous family Archipsyllidae Handlirsch, 1906 as one of the enigmatic paraneopteran groups, but Rasnitsyn (2002) put them in Psocoptera. Their position is debatable. The present description of new and well-preserved fossils of this family from China is of great interest for improving the knowledge of the psocodean and paraneopteran evolution. We follow the wing venation and body terminology of Mockford (1993).

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2. Systematics

Clade PSOCODEA
Family ARCHIPSYLLIDAE Handlirsch, 1906
Genus ***Archipsylla*** Handlirsch, 1906

Archipsylla sinica nov. sp.
Fig. 1(A–I)

Material: Holotype NIGP 142194 (Fig. 1(A)), paratypes NIGP 142195 (Fig. 1(B)), 142196 (Fig. 1(C D), part and counterpart), 142197 (Fig. 1(E)), stored in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Age and outcrop: The Middle Jurassic Jiulongshan Formation at the locality near the Daohugou Village, Ningcheng County, Inner Mongolia, China.

Etymology: After the Latin name for China.

Diagnosis: Head with filiform, ca. 11-segmented annulated flagellomeres. Forewing with pterostigma sclerotized, relatively short but distinctly longer than wide and not posteriorly angled, related to Rs by a cross-vein. Cross-vein rs-m ending on anterior branch of M. M4 present. Areola postica elongate and free. No nodulus and 1A closer to Cu2 than to 2A. Hind wing with nearly the same size and venation structures as fore wing.

Description: Head 1.5 mm long; compound eyes 0.25 mm wide; antenna filiform 7.5 mm long, with about 13 segments, scape and pedicel bulbous and short; a rupturing mechanism at the bases of the basal flagellomeres; flagellomeres annulate, long, first one 1.0 mm long; frons rather reduced compared to the bulbous and protruding postclypeus; mandibles elongate, lacinia present, narrow and elongate, with a strong apical tooth (Fig. 1(F, I)); last segments of the labial and maxillary palps are visible, very elongate, but their exact number cannot be determined. Thorax 2.0 mm long. Legs long and slender, tarsi four-segmented, first hind tarsomere cylindrical and very elongate, 0.85 mm long, second cylindrical but shorter, 0.3 mm, third triangular at base, 0.1 mm, fourth rounded at base and cylindrical, 0.25 mm long; claws symmetrical, with a large secondary tooth and a rather large modified pulvillus at its base, a rather large arolia (Fig. 1(H)). Abdominal segment number unknown; at apex of abdomen of the holotype, two poorly sclerotized structures probably correspond to the arms of phallosome, and an enigmatic strongly sclerotized structure bearing five strong curved setae (?) (Fig. 1(G)).

Wings hyaline, fore wing 7.8 mm long, 2.5 mm wide (holotype), fore wing of paratype NIGP 14295 is 7.0 mm long and 2.2 mm wide; NIGP 142196: fore wing is 7.7 mm long and 2.3 mm wide, hind wing is 7.2 mm long, 2.3 mm wide; NIGP 142197: fore wing is 6.5 mm long and 2.1 mm wide. Other dimensions concern the holotype only. Sc consisting of three parts, entering C 1.5 mm from wing base, appearing as an oblique cross-vein between C and R, ending on R 1.5 mm distally, and closing pterostigma basally; R and M basally fused, M emerging from R 1.5 mm from wing base; Rs separating from R 0.5 mm distally; pterostigma Pt sclerotized, dark, rounded, not very elongate, 1.1 mm long, 0.45 mm wide, with a cross-vein r-rs ending in it; Rs with an apical fork; a cross-vein rs-m 0.7 mm basal of cross-vein r-rs, on anterior branch of M; M with two main branches, each apically divided into two branches; Cu1 with two apical branches defining the areola postica cell, free narrow and elongate, 1.5 mm long, 0.5 mm wide; Cu2 very weak, hardly visible on nearly all specimens, well separated from 1A at their apices (nodulus wanting); 1A closer to Cu2 than to 2A, but not strongly approximate, i.e. distance between Cu2 and 1A 0.35 mm, between 1A and 2A 0.55 mm, along posterior wing margin; 1A and 2A simple, subparallel, and weakly curved.

Hind wing (visible in paratype NIGP 142196) very similar to the fore wing in shape and venation, especially in the sclerotized pterostigma, but slightly shorter, with apices of fore and hind wings at the same point when wings are at rest (Fig. 1(C)).

Discussion: We attribute all these fossils to the same species on the basis of their identical wing venation, despite of the rather large range in their wing sizes. Similar intraspecific variation in the wing size can be observed in the recent Psocoptera. The head, thorax, wing venation and leg structure of these fossils support their attribution to the Jurassic family Archipsyllidae Handlirsch, 1906–1908 (Vishniakova, 1976). This last author attributed *Eopsylla* Vishniakova, 1976 to this family, but Rasnitsyn (2002; p. 129) indicated that it belongs to the Psocidiidae Tillyard, 1926 because of its complete Sc. *Archipsylla sinica* sp. n. can be distinguished from it with this character but also in its rather short pterostigma and cross-vein rs-m ending on anterior branch of M. *A. sinica* differs from *Archipsyllopsis* Vishniakova, 1976 in its 1A closer to Cu2 than to 2A, not equidistant. *A. sinica* differs from *Archipsyllodes* Vishniakova, 1976 in its more elongate pterostigma. Differences with representatives of *Archipsylla* Handlirsch, 1906 are compatible with an attribution to this genus. The Liassic type species *A. primitiva* Handlirsch, 1906 and *A. similis* Vishniakova, 1976 differ from *A. sinica* in the posteriorly angled pterostigma (Vishniakova, 1976; Ansorge, 1996). *A. lata* Vishniakova, 1976 differs from *A. sinica* in the Cu2 and 1A strongly approximate. Note that Vishniakova (1976) indicated that *Archipsylla* has a hyaline pterostigma, unlike *A. sinica*, but this character is dubious as the sclerotization of this structure is frequently absent or badly preserved among different specimens of a same psocopteran species.

3. Position of the Archipsyllidae

The phylogenetic relationships of the Archipsyllidae currently are very uncertain, as Grimaldi and Engel (2005, p 269) considered them as a ‘‘paraneopteran stem group that resembles Psocoptera’’. Nevertheless, the bulbous and protruding clypeus (character already indicated by Vishniakova, 1976 for the Archipsyllidae), and the presence of a rupturing mechanism at the bases of the basal flagellomeres currently are considered as apomorphies of the Psocodea present in *A. sinica* (Seeger, 1975; Grimaldi and Engel, 2005, p. 262), although Yoshizawa and Saigusa (2003) hypothesized that the enlargement of the clypeus could be an autapomorphy of the Paraneoptera. Within this clade, Grimaldi and Engel (2005, p. 262) considered the presence of an areola postica as an apomorphy of Psocodea only present in the Psocoptera, and reduced in other Psocodea (Liposcelidae and

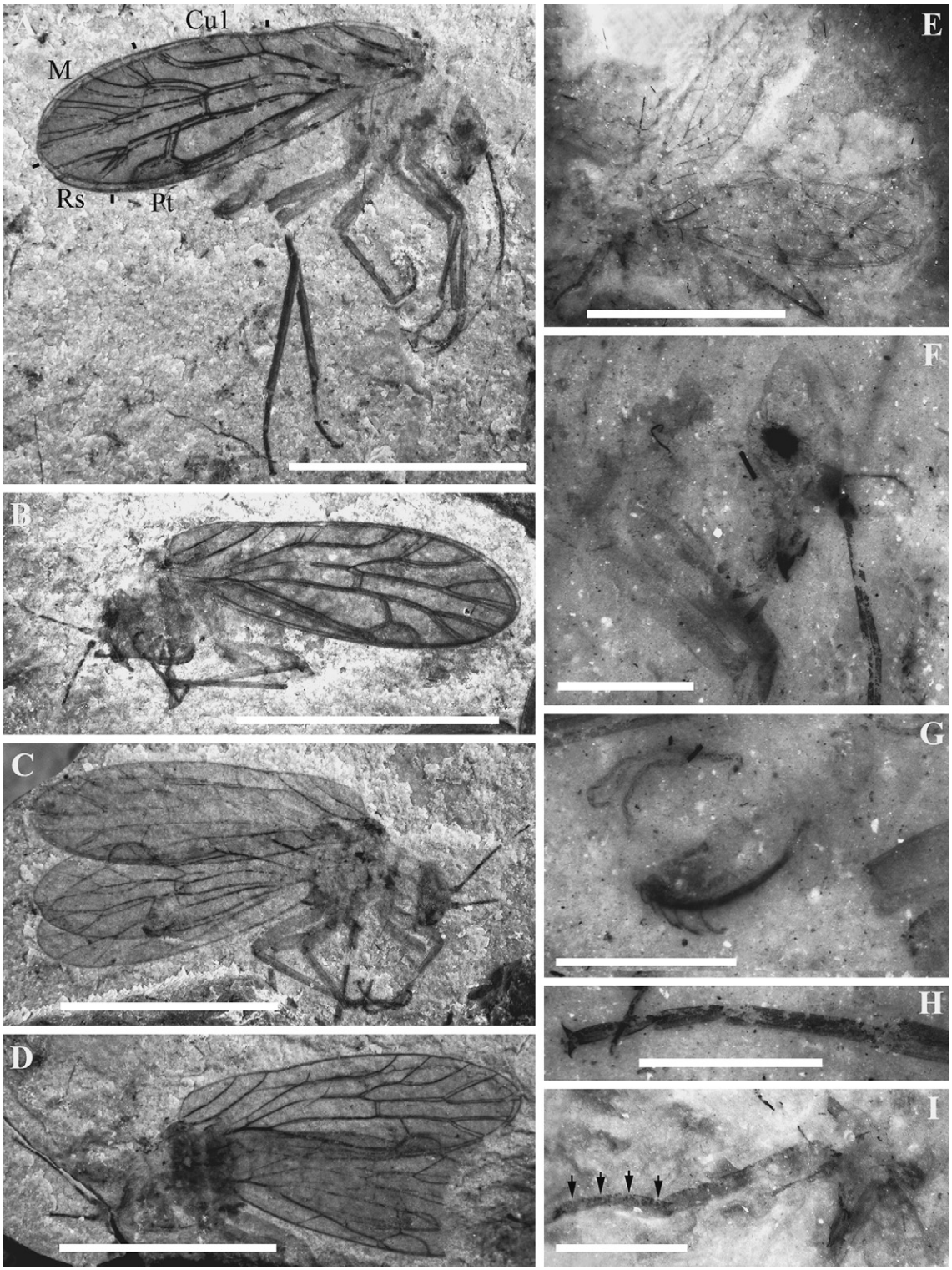

Fig. 1. *Archipsylla sinica* nov. sp., photographs. **A**. Habitus of holotype NIGP 142194. **B**. Habitus of paratype NIGP 142195. **C**. Habitus of paratype NIGP 142196 (part). **D**. Habitus of paratype NIGP 142196 (counterpart). **E**. Habitus of paratype NIGP 142197 (scale bars represent 5 mm). **F**. Mouthparts and bases of antennae of holotype. **G**. Genital appendages of holotype. **H**. Hind tarsus of holotype. **I**. Mouthparts and fore leg of paratype NIGP 142197 (arrows indicate the tarsomeres) (scale bars represents 1 mm).

Archipsylla sinica *nov. sp., photographies. **A**. Habitus de l'holotype NIGP 142194. **B**. habitus du paratype NIGP 142195. **C**. Habitus du paratype NIGP 142196 (part). **D**. habitus du paratype NIGP 142196 (contrepartie). **E**. Habitus du paratype NIGP 142197 (les échelles représentent 5 mm). **F**. Pièces buccales et bases des antennes de l'holotype. **G**. Appendices génitaux de l'holotype. **H**. Tarse postérieur de l'holotype. **I**. Pièces buccales et patte antérieure du paratype NIGP 142197 (les flèches indiquent les tarsomères) (les échelles représentent 1 mm).*

Phthiraptera) which have no areola postica. This character can be found also in other paraneopteran clades viz. the hemipteran Psyllidae.

The four-segmented tarsus of the Archipsyllidae is a plesiomorphic character first reported by Vishniakova (1976). It suggests an inclusive position of this family in the psocodean stem group. The present attribution of the Archipsyllidae to this clade implies that the reduction in the number of tarsal segments (three or less) is not an apomorphy of the modern lineage of the Paraneoptera, but occurred independently in the two clades Psocodea and Condylognatha (Thysanoptera + Hemiptera), a conclusion not supported by Grimaldi and Engel (2005).

The Archipsyllidae have several plesiomorphic characters in their wing venation compared to the more advanced Psocodea, namely fore and hind wings of nearly the same size and venation, no nodulus (but homoplastic in recent Psocodea), and median vein and Rs completely separated. The structure of the subcosta in the Archipsyllidae is very similar to those of some recent taxa, with Sc strongly approximating costal margin, then distally posteriorly bent and fused with radial vein, and emerging again distally along basal margin of pterostigma. This pattern is visible in Empheriidae, Archaeatropidae, Prionoglaridae and Compsocidae, among others. The only difference with Archipsyllidae is that Sc is fused with costal margin instead of being strongly approximate in the latter group. This character can be considered as an apomorphy of the Archipsyllidae.

A. sinica has a troctomorphan character, namely flagellomeres annulated, but another character currently considered as psocomorphan, particularly a sclerotized pterostigma (Mockford, 1993). This suggests that at least some of the characters currently used to separate the major psocopteran subgroups are plesiomorphies or homoplastic, and that a major reconsideration of the whole classification of the Psocoptera must be done, but only after including fossil data.

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