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A new Archipsocidae (Psocodea: Psocomorpha) from the middle Miocene Zhangpu amber, China

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Abstract

A new species of Archipsocidae, *Archipsocus palaeosinicus* n. sp., is described and illustrated from the middle Miocene Zhangpu amber. This taxon possesses all the synapomorphies of the Archipsocidae family and can be confidently classified within the genus *Archipsocus* due to its exceptional preservation, which allows for the detailed examination of the morphological traits used to define the genus and its species. *Archipsocus palaeosinicus* n. sp. is distinguished from other species of *Archipsocus*, *inter alia*, because of the first flagellomere that is shorter than the pedicel, a relatively flat antennal diagram, a unique arrangement of marginal setae on its fore- and hindwings, distinct venation patterns in both wings, and hindlegs with the first tarsomere longer than the second. The discovery of this species indicates that the genus *Archipsocus* likely had a broad distribution, with representatives in both China and Mexico during the Miocene.

Keywords: Archipsocetae; *Archipsocus*; diversity; Cenozoic; new species

1. Introduction

The order Psocodea, which includes barklice, booklice, and parasitic lice, originated during the early Carboniferous (e.g., Johnson et al., 2018; Yoshizawa et al., 2019). Historically, Psocodea comprised two distinct groups: ‘Psocoptera’ (free-living barklice and booklice) and Phthiraptera (parasitic lice), which were previously classified as separate orders (de Moya et al., 2021). ‘Psocoptera’ traditionally includes three suborders — Trogiomorpha, Psocomorpha, and Troctomorpha (Lienhard and Smithers, 2002), while Phthiraptera has four suborders: Amblycera, Ischnocera, Rhynchophthirina, and Anoplura (Price et al., 2003).

The order Psocodea includes species with diverse feeding preferences. Barklice and booklice members primarily feed on detritus, plant material (such as pollen and decaying leaves), and microflora (including cyanobacterial films, fungi, and lichens) (Broadhead and Wapshere, 1966; New, 1970, 1987; Broadhead and Richards, 1982). In contrast, lice are obligate ectoparasites feeding on birds and mammals, deriving nutrients from skin debris, feathers, and blood or skin secretions (Price et al., 2003; Clayton et al., 2015).

The fossil record of Psocodea is rich, with numerous species identified from amber deposits (Baltic, Oise, and Kachin), thanks to the focused efforts of a few

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paleoentomologists (e.g., Azar and Nel, 2004; Nel et al., 2004, 2005; Azar et al., 2009, 2014). However, the Psocodea fossil record remains spatially and temporally heterogeneous, with most species documented from only a few deposits (Álvarez-Parra et al., 2020). Additionally, there is a notable imbalance in fossil species numbers between 'Psocoptera' and Phthiraptera, with 'Psocoptera' accounting for nearly all fossil records (157 versus 2 species; https://paleobiodb.org, accessed 31/10/2024). This discrepancy is likely not only due to behavioral differences: parasitic lice, which spend most of their time on hosts, are less likely to become trapped in resin flows compared to free-living 'Psocoptera', but also because of a fossilization bias that tends to favor Psocodea living in resiniferous forests (Álvarez-Parra et al., 2022). Furthermore, fossil diversity across suborders of 'Psocoptera' Trogiomorpha, Psocomorpha, and Troctomorpha also shows disparity, with 65, 38, and 50 fossil species respectively (https://paleobiodb.org, accessed 31/10/2024). This contrasts sharply with the extant diversity in these groups, comprising 478, 5,478, and 6,067 species, respectively (Hopkins et al., 2024). Given these numbers, one might question why the less speciose suborder Trogiomorpha is the best documented in the fossil record. Does this indicate a genuine pattern, suggesting that Trogiomorpha was more diverse in the past, or does it reflect a scarcity of fossil material for the other two suborders? To address this question, further research is necessary to more accurately assess the past diversity of the other suborders, particularly that of Psocomorpha.

The suborder Psocomorpha has its crown group estimated to be around 104 million years old, indicating a rapid diversification during the Cenozoic era (de Moya et al., 2021). Within Psocomorpha, the family Archipsocidae consistently emerges as the earliest diverging family, based on both morphological and molecular data, and is classified within its own infraorder, the Archipsocetae (e.g., Yoshizawa and Johnson, 2014; de Moya et al., 2021). The Archipsocidae include over 80 valid extant species, divided into two subfamilies: Archipsocinae (which includes *Archipsocopsis* Badonnel, 1948, and *Archipsocus* Hagen, 1882) and the Pararchipsocinae (which includes *Notarchipsocus* Mockford, 1991, *Pararchipsocus* Badonnel, Mockford and García-Aldrete, 1984, and *Pseudarchipsocus* Mockford, 1974). To date, two fossil species from this family have been described: *Archipsocus puber* Hagen, 1882, from Eocene Baltic amber, and *Archipsocopsis antigua*, from Miocene Mexican amber (Hagen, 1882; Mockford, 1969). Additionally, a specimen determined as *Archipsocus* cf. *puber* has been described from Ypresian Oise amber, one specimen attributed to *A. puber* was described from Rovno amber, one specimen from Študlov amber (Czech Republic) was determined as *Archipsocus*? sp., and one specimen of *Archipsocus* sp. was documented from Miocene Mexican amber (Mockford, 1969; Nel et al., 2005; Engel and Perkovsky, 2006; Solórzano Kraemer, 2007; Škorpíková, 2020). It is likely that more fossil specimens are preserved in institutional collections and remain undescribed. Given the origin of the family in the Late Cretaceous (de Moya et al., 2021) and its widespread distribution across North and South America, Africa, Asia, and Australia, it is probable that additional fossil specimens will be discovered in amber deposits from these regions.

In this study, we describe the first *Archipsocus* species from the recently discovered Miocene Zhangpu amber, as evidence supporting the above speculation for an occurrence in Asia.

2. Material and methods

Zhangpu amber is found alongside plant impressions within two sandy mudstone layers interbedded with coal seams in the Fotan Group, a geological unit widely distributed in Zhangpu County, Fujian Province, southeastern China (Wang et al., 2021, fig. 1). Dating of the amber is tightly constrained by underlying and overlying basalt layers, placing it between 14.8 ± 0.6 Ma and 14.7 ± 0.4 Ma, corresponding to the middle Miocene (Langhian; Zheng et al., 2019).

This study is based on a complete female specimen, generously provided by Prof. Bo Wang (Nanjing, China) and housed in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China. The piece of amber was polished using thin silicon carbide papers on a Buehler Metaserv 3000 polisher. The specimen was examined with a Zeiss Axio Zoom V16 stereomicroscope with an attached Zeiss AxioCam 512 color camera. All images are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using Helicon Focus 6.7. The figures were composed with Adobe Illustrator CC2018 and Photoshop CC2018. The terminology of the thorax follows Yoshizawa (2005, fig. 9), that of the wing venation is adapted from Yoshizawa (2005, fig. 17), and the genitalia terminology follows Yoshizawa (2005, fig. 24A).

This published work and its included nomenclatural acts are registered in ZooBank (https://www.zoobank.org, accessed 22/12/2024), with the following LSID: urn:lsid:zoobank.org:pub:F4B4115A-0A13-489B-9F8C-E57293973CDB.

3. Systematic paleontology

Order Psocodea Hennig, 1966
Suborder Psocomorpha Weber, 1936
Infraorder Archipsocetae Yoshizawa, 2002
Family Archipsocidae Enderlein, 1903

Subfamily Archipsocinae Enderlein, 1903

Remarks: Species within Archipsocidae are primarily distinguished by subtle morphological traits, with features such as the lacinia, wing venation, and genital structures often regarded as having limited taxonomic value (New, 1973). In fossil specimens, many of these diagnostic characters can be challenging, if not impossible, to interpret clearly. In this case, however, the amber preservation of the specimen enables the observation of several of these key traits. For species delimitation, a combination of specific characteristics is used: (1) body size and coloration, (2) absolute lengths of antennal segments and their relative proportions, (3) wing ciliation, (4) the extent and shape of the sclerotized region of the subgenital plate, including the pilosity and contour of its posterior edge (rounded or tapered), and (5) relative lengths of the hind tarsomeres (New, 1973; Mockford, 1977).

Genus *Archipsocus* Hagen 1882

Type species: *Archipsocus puber* Hagen, 1882 by original designation; Priabonian, Baltic amber, Russian Federation.

Archipsocus palaeosinicus n. sp.

(Figs. 1–4)

LISD: urn:lsid:zoobank.org:act:6D15BD6B-E8BA-4427-91C0-FBE8E790E27E.

Etymology: The species name combines ‘*palaiós*’, meaning ‘ancient’ in Greek and ‘*sinicus*’, in reference to the Chinese geographic origin of Zhangpu amber.

Material: Holotype female, NIGP206616, no syninclusions, housed in the NIGP, Nanjing, China.

Type locality: Zhangpu County, Zhangzhou City, Fujian Province, China.

Horizon: Sedimentary layer II, Fotan Group; middle Miocene, Langhian, 14.7 Ma.

Diagnosis (female): Minute species, body about 1 mm long. Antennae short, with first flagellomere shorter than pedicel, lengths of flagellomeres III to X relatively constant, antennal diagram relatively flat (no sawtooth pattern). Forewing with setae along anterior margin extremely long (about 0.08 mm long), shortening along apex and posterior margin; pterostigma present; R+M long (versus short in *A. puber*; see Enderlein, 1911, fig. G or Nel et al., 2005, fig. 11). Hindwing with short setae along anterior margin (up to 0.42 of wing length), no setae from slightly after apex of basi-radial cell to apex of R along anterior margin, long setae present after apex of R and along apical and posterior wing margin; Sc short, present as a sclerotized stub basally (somewhat similar to *Archipsocus floridanus* Mockford, 1953: fig. 1b), then spectral, reaching middle of basi-radial cell; basi-radial cell long, about 3× longer than wide, shorter than R+M. Hindlegs with tibia shorter than femur (T/F±tr index: ≈0.75), first tarsomeres (t1) longer than second tarsomere (t2). Subgenital plate triangular, with posterior margin covered with setae, without slight median inflection, lateral margin with a slight median inflection (resembling that of *Archipsocus cervinoides*; see Badonnel, 1987, fig. 17), distal third covered with setae; external valves with posterior margin covered with long setae; paraprocts, clunium and epiproct setose.

Description: Female. Body length about 1 mm (Fig. 1).

Head (Fig. 2A): As long as wide, 0.36 mm long, 0.36 mm wide (measure just after eyes in dorsal view); vertex covered by setae; epicranial suture absent; ocellar triangle developed, distance between posterior ocelli about 0.025 mm; compound eye circular, about 0.07 mm wide and long, in dorsal view bulging from cephalic capsule; distance between antenna base and eye about 0.05 mm long; malar space about 0.07 mm long; antennae complete with 11 flagellomeres (Fig. 2B), about 0.43 mm long; setae present on all flagellomeres; scape 0.04 mm long, pedicel (p) 0.06 mm long; approximate lengths of flagellomeres of left antenna: f1 0.05 mm, f2-6 0.03 mm, f7-10 0.02 mm, f11 0.05 mm; f11 with a nipple-like apex; flagellomeres lacking secondary annulations (Fig. 2A, B); clypeus bulging; maxillary palps clavate, four-segmented, two apical palpomeres (maybe first and second too) covered by short setae (Fig. 2A, B); lengths of maxillary palpomeres: I at least 0.04 mm, II 0.05 mm, III 0.02 mm, IV 0.06 mm; distal maxillary palpomere longer than wide, widening toward apex, apex clavate; labial palps seemingly two-segmented; lacinia not visible.

Thorax: About 0.3 mm long (Fig. 2C); pronotum bulging, covered by a few setae; mesothorax transverse; anterior lobe of scutum triangular, about 0.07 mm long, 0.1 mm wide anteriorly, not reaching scutellum; distance between bases of forewings about 0.20 mm; scutellum triangular, about 0.05 mm long; postnotum long, about as long as scutellum (maybe due to deformation during fossilization); metathorax well preserved, dorsally obscured by wings. — Wings: membrane hyaline with setae; forewing much longer than hind wing, greatly surpassing the distal p1art of the abdomen (Fig. 1), margin covered by two rows of long setae (Fig. 3A); hind wing membrane setose (Fig. 3B). Forewing much longer than wide, 1.09 mm long and 0.28 mm wide (although slightly folded); Sc+R straight, forking at about 0.45 mm from wing base; nodus slightly anteriad R+M origin; free section of Sc short, faint, joining anterior margin at level of 1-R and M meeting point; R1 joining anterior margin at level of 2-R midpoint; pterostigma about 0.25 mm long; M+CuA well-defined, fork aligned with Sc+R fork; first section of M slightly curved, about 0.1 mm long; R+M nearly straight about 0.14 mm long, ending at about 0.65 mm from wing base; M1+2 faint, slightly sigmoidal, disappearing in wing membrane, joining wing margin at about 0.95 mm from wing base; 2-R about as long as R+M, ending at about 0.80 mm from wing base; R2+3 and R4+5 faint, disappearing in wing membrane; CuA slightly arched inward, about 0.12 mm long, fork at about 0.55 mm from wing base; CuA1 and CuA2 reaching wing margin at about 0.75 mm and 0.60 mm from wing base, respectively; triangular areola postica; A1 slightly arched and reaching margin at about 0.40 mm from wing base; nodulus present (Figs. 3A, 4A). Hind wing about 3.5× longer than wide, about 0.80 mm long and 0.22 mm wide (Figs. 2B, 4C); basi-radial cell elongate, triangular, anterior side strongly arched, posterior side slightly arched, distal side straight

Fig. 1. Holotype (NIGP206616) of *Archipsocus palaeosinicus* n. sp., female specimen, Langhian Zhangpu amber. Scale bar = 0.2 mm.

and inclined, cell about 0.15 mm long, 0.04 mm wide, terminating at about 0.30 mm from wing base; CuA emerging from postero-apical corner of basi-radial cell, reaching wing margin at about 0.38 mm from wing base; R+M straight, 0.18 mm long, ending at about 0.48 mm from wing base; R and M respectively reaching wing margin at about 0.57 and 0.62 mm from wing base, disappearing in wing membrane (in Fig. 3B the membrane was impregnated by water, which blurs the path of the vein). — Legs: femora thick, and covered by setae; tibiae thin, with at least two spines, and covered by setae; tarsi two-segmented, with both tarsomere covered by a few short setae (Fig. 2D, E); fore- and midlegs with femora about 0.16 mm long, tibiae about 0.19 mm long, tarsi about 0.09 mml long; hindleg with trochanter (tr) about 0.05 mm long, femur (F) 0.24 mm long, tibia (T) 0.22 mm long, t1 about 0.06 mm long, t2 about 0.05 mm long; tarsal claws lacking preapical tooth (i.e., simple), arolium if present extremely reduced, and pulvillus setiform if present (or corresponding to ‘parempodia’).

Abdomen apex slightly twisted (i.e., the median axis of the subgenital plate misaligned relative to the rest of the genitalia) (Fig. 2F). Genitalia well visible; in posteroventral view subgenital plate wide (Fig. 2G); visible part of external valves large, subtriangular, overlapping clunium (cl), left external valve (e) slightly overlapping right one (Fig. 2H); clunium boarding paraprocts (pa); paraprocts lobe-shaped; tip of epiproct (ep) discernible.

Remarks: The presence or absence of a pterostigma is a diagnostic feature in certain extant *Archipsocus* species (Georgiev, 2024). In the current amber-preserved specimen, identifying the pterostigma is challenging due to the faintness of the enclosing veins. However, by adjusting the angle of the light illuminating the amber, the vein pattern becomes slightly discernible, and the narrow pterostigma is visible.

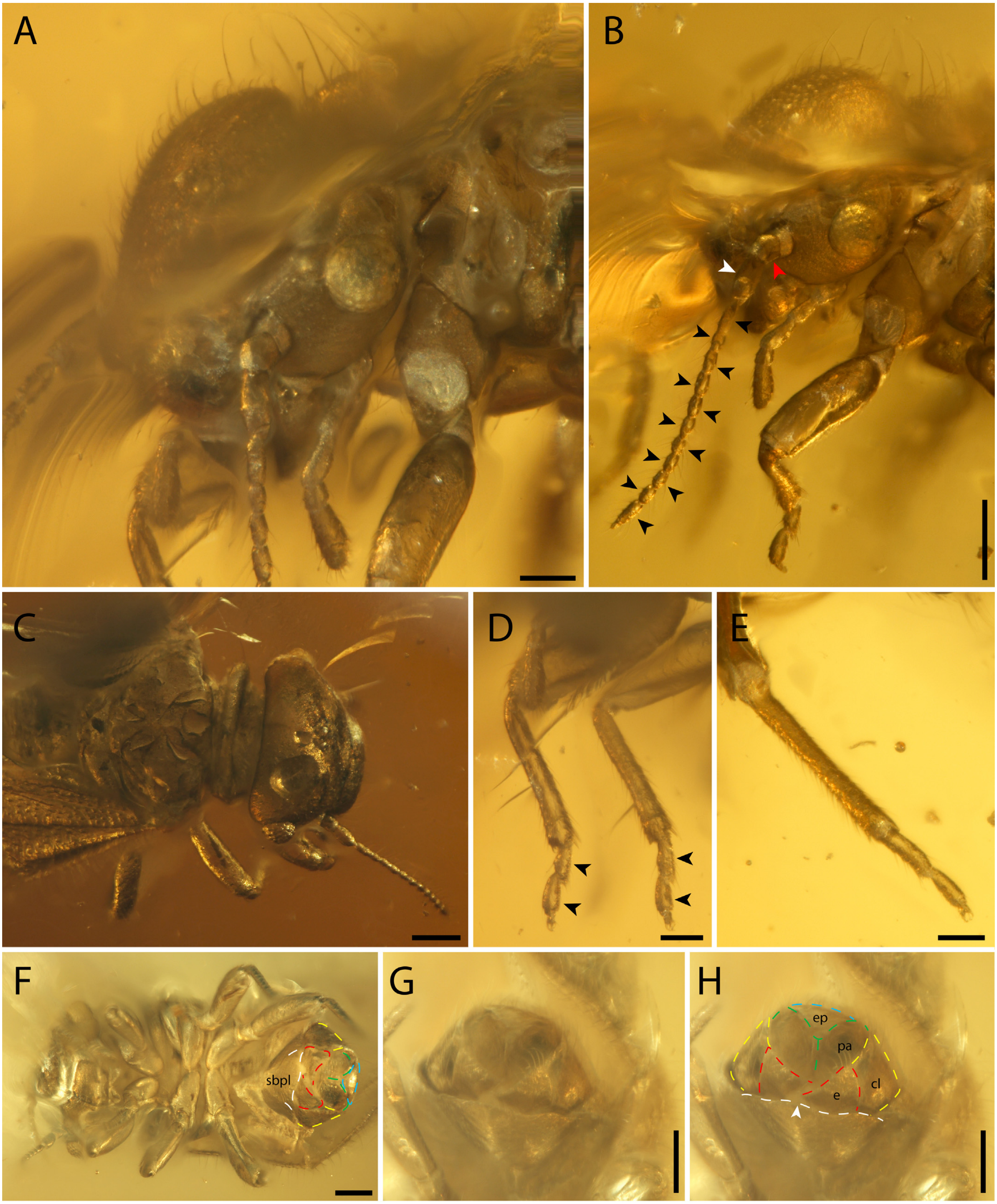

Fig. 2. Holotype (NIGP206616) of *Archipsocus palaeosinicus* n. sp. (A) Detailed left lateral view of the head. (B) Left lateral view of the head; red arrow pointing to scape; white arrow pointing to pedicel; black arrows pointing to flagellomeres. (C) Dorsal view of the head and thorax. (D) Detailed view of the right fore- and midlegs; black arrows pointing to tarsomeres. (E) Detailed view of right hindleg. (F) Habitus in ventral view with limits of genitalia parts highlighted (sbpl: subgenital plate). (G) Detailed view of genitalia. (H) Detailed view of genitalia with limits of genitalia parts highlighted (cl: clunium; e: external valve; ep: epiproct; pa: paraproct); white arrow pointing to the tip of the subgenital plate. Scale bars = 0.05 mm for (A, D, E), 0.1 mm for (B, C, F–H).

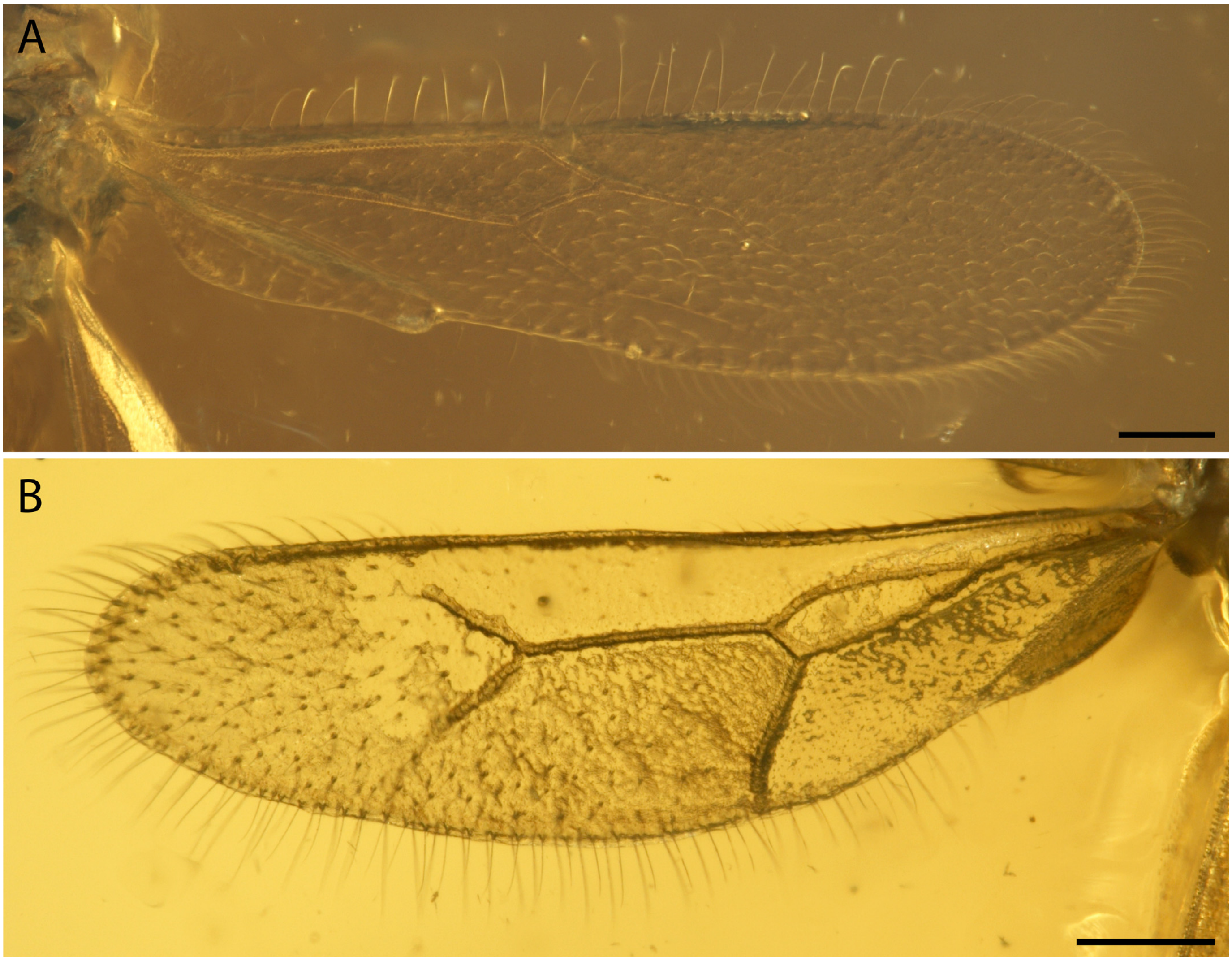

Fig. 3. Holotype (NIGP206616) of *Archipsocus palaeosinicus* n. sp. (A) Detailed view of left forewing. (B) Detailed view of left hindwing. Scale bars = 0.1 mm.

When examining the illustrations (Fig. 2D) of the specimen, one might question whether there is a single long seta present on both the fore- and mid-tibiae. However, these features are not setae, instead they are cracks within the amber matrix.

4. Discussion

4.1. Systematic placement

This fossil has the synapomorphies of Archipsocidae, as proposed by Yoshizawa (2002): precoxal bridge broad, marginal setae of forewing crossing on apical margin, forewing veins reduced in apical part (autapomorphy), ventral setae of forewing present, preapical tooth of claws absent. Its classification within Archipsocidae is further supported by the following characters: macropterous, tarsi two-segmented, no preapical tooth on claws, forewing venation evanescent in distal part (Badonnel, 1966; Smithers, 1972, 1990; Mockford, 1993). Further, the presence of a large closed basi-radial cell in the hind wing places this fossil in the subfamily Archipsocinae, rather than Pararchipsocinae (Badonnel et al., 1984). Characteristics supporting its placement in the genus *Archipsocus* Hagen, 1882, include an elongate, broad and large basal cell of the hind wing, two broad external valves of the gonapophyses, and antennomeres 6–10 with discoidal sensilla bearing a long filament (Badonnel, 1966, 1978).

Badonnel (1987) proposed several species-groups in *Archipsocus*, but the specimen does not fall in any of them. It does not fall in the species-group ‘A’, characterized by t1 < t2 of hindlegs, and f1 < p (Badonnel, 1983, figs. 1–5), because its t1 > t2 (Fig. 2A, B). Similarly, it cannot be placed in the species-group ‘B’, characterized by t1 < t2 and f1 > p, because its t1 > t2 and its f1 < p (Badonnel, 1987).

The fore- and hindwing venations of the new specimen resemble those of *Archipsocus puber* Hagen, 1882 (upper Eocene Baltic and Rovno ambers) and *Archipsocus* cf. *puber* (lower Eocene Oise amber). However, it can be readily

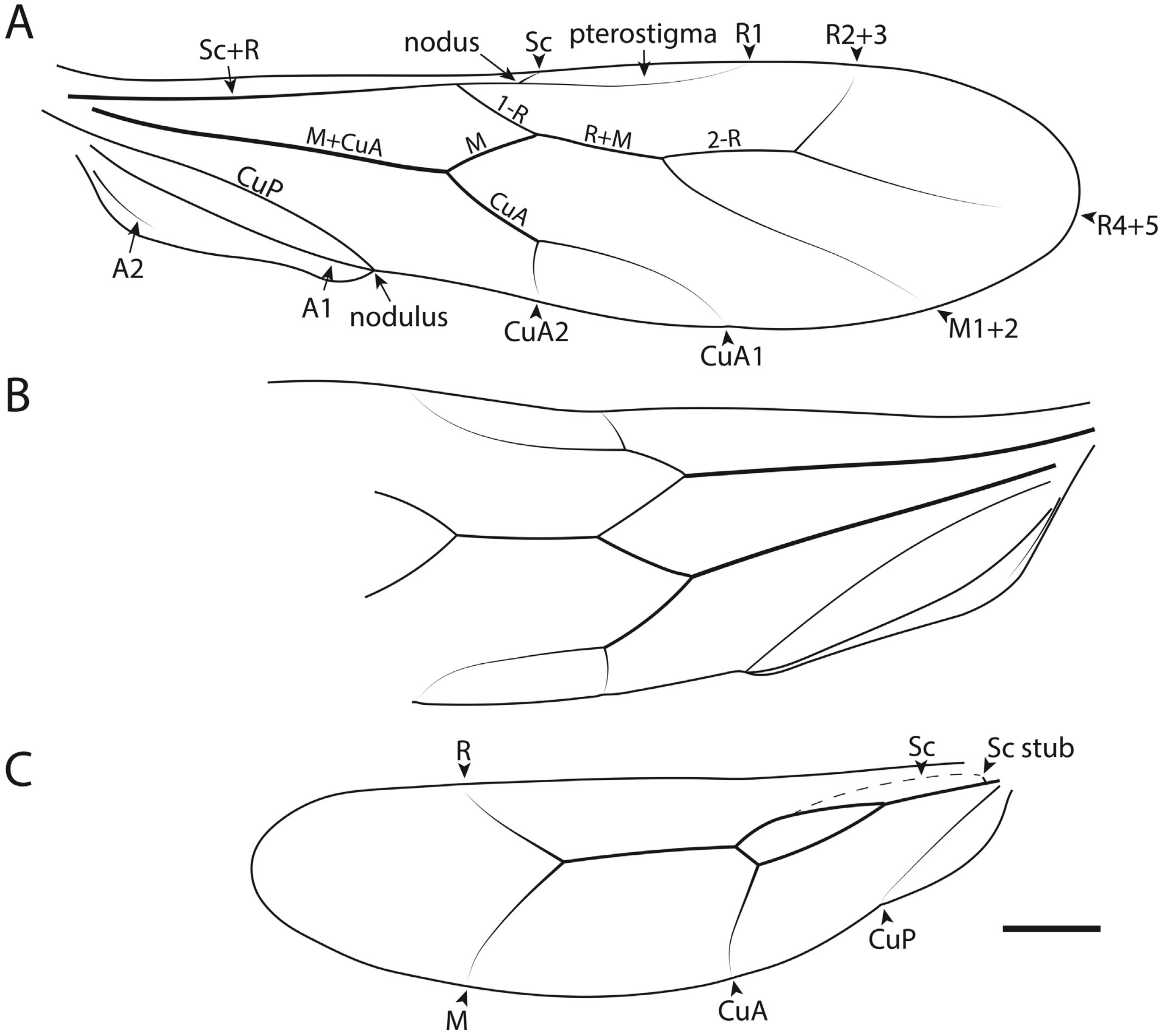

Fig. 4. (A) Interpretative drawing of left forewing with names of veins labeled; setation omitted. (B) Interpretative drawing of the basal part of right forewing; setation omitted. (C) Interpretative drawing of left hindwing with names of veins labeled; setation omitted. Scale bar = 0.1 mm.

distinguished from this species by several characteristics: the forewing with a long R+M (about as long as 2-R), the much narrower and shorter basi-radial cell in the hind-wing (shorter than R+M versus longer in *A. puber*), the comparatively longer R+M stem, the presence of a short sclerotized stub of Sc, Sc is then spectral and reaches the middle of the basi-radial cell (versus long, reaching the anterior wing margin slightly before the apex of R), and the hindtibia shorter than the femur (Enderlein, 1911, fig. G; Nel et al., 2005, fig. 11D). The subgenital plate of *A. puber* was re-illustrated using a well-preserved specimen, as the apex of the abdomen of the type specimen was deformed (Badonnel, 1966, figs. 1–5). However, the new specimen differs from *A. puber* by having a slight lateral concavity or inflection on each side, a characteristic more closely resembling *A. cervinoides* Badonnel, 1987 (Badonnel, 1987, figs. 17).

A specimen of *Archipsocus* sp. and the species *Archipsocopsis antigua* (Mockford, 1969) were previously described from Chiapas Miocene amber (Mexico) (Mockford, 1969). Mockford noted the similarities in wing venation between *A. antigua* and *Archipsocus frater* Mockford, 1957 (Mockford, 1969). He later elaborated on the species' life history and illustrated differences between macropterous and brachypterous females (Mockford, 1962, figs. 1, 2). Our new specimen combines forewing venation characteristics of the macropterous form with hindwing venation of the brachypterous form of *A. frater*. However, it can be distinguished from *A. antigua* by its antennal diagram relatively flat (more similar to *Archipsocus cervinoides*

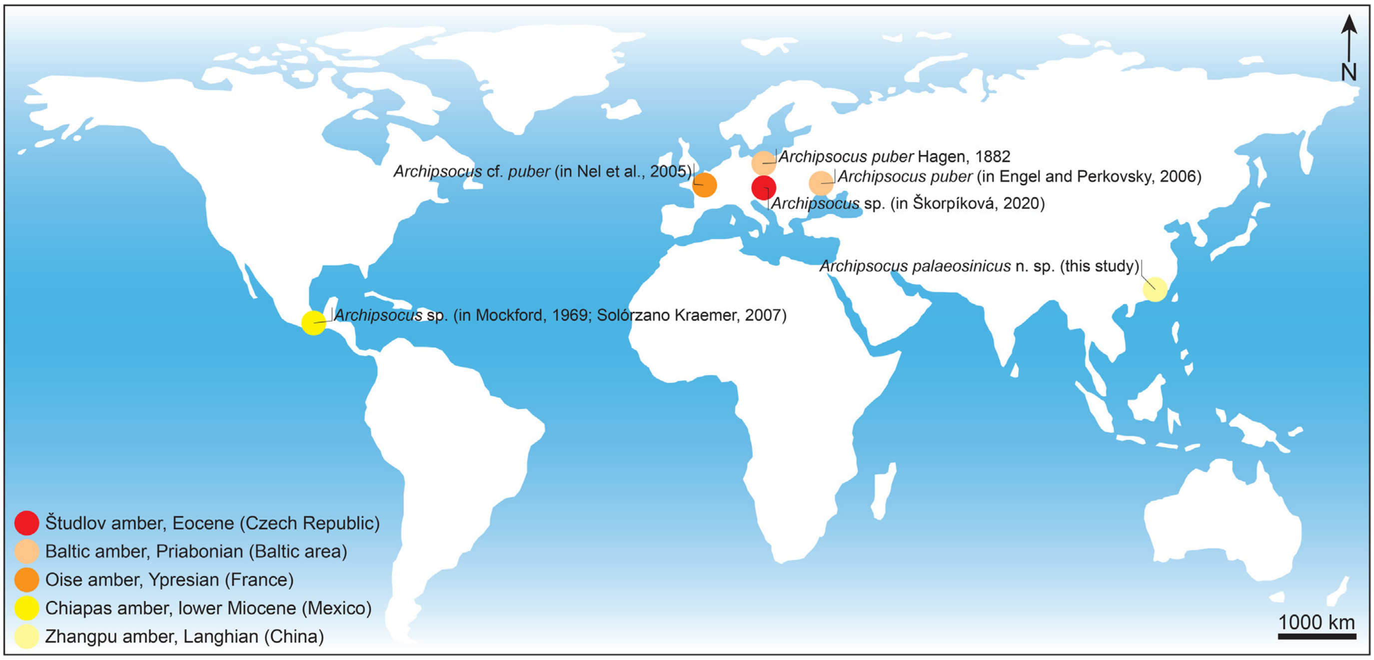

Fig. 5. Distribution of fossil *Archipsocus* (map modified from Jouault et al., 2023).

Badonnel, 1987 than *Archipsocus jaliscoensis* Badonnel, 1987; see Badonnel, 1987, figs. 34, 35), a forewing with 2-R (versus absent; Mockford, 1962, figs. 1, 2), and its t1 longer than t2 (versus shorter; Mockford, 1969, p. 1272).

In the fossil record, the maximum lifespan of an invertebrate species is estimated to be around 11 million years (Raup, 1978). However, Grimaldi and Engel (2005) adjusted this estimate specifically for insects, suggesting a considerably shorter average species lifespan of roughly 2 million years. Based on these estimates, it is highly improbable that the new specimen belongs to any Eocene or extant species.

4.2. *Comment on the biogeography of* Archipsocus

The genus *Archipsocus* is today distributed across sub-Saharan Africa, the New World tropics, Southeast Asia, and northeastern Australia. Fossil evidence suggests that its presence in the New World, within the same region it inhabits today, dates back to at least the early Miocene, based on specimens from Mexican amber (Fig. 5). In Asia, the newly discovered specimen represents the northernmost record of the genus. This finding likely reflects the impact of climate and biome changes between the Miocene and the present, which may have driven the genus' retreat to the more favorable tropical regions of Southeast Asia. Broadly, this hypothesis aligns with the entomofauna preserved in Zhangpu amber, which reflects an ecosystem resembling modern tropical forests of Southeast Asia or New Guinea (Wang et al., 2021). The disappearance of the genus from Europe between the Eocene and the present is likely attributable to similar factors, namely changes in climate and biome shifts over time.

5. Conclusion

The description of *Archipsocus palaeosinicus* n. sp. suggests that the genus had a wide distribution during the Miocene. This new taxon also implies that the diversity of Psocomorpha in the fossil record is likely significantly underestimated, despite the presence of crown group representatives in various amber deposits. The morphology of *Archipsocus palaeosinicus* n. sp. demonstrates that the synapomorphies proposed for the Archipsocidae family, as well as the characteristics used to differentiate between extant archipsocid genera, are also applicable to fossil specimens. Ultimately, the discovery of this new taxon opens avenues for further studies on the psocodean fauna found in Zhangpu amber.

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