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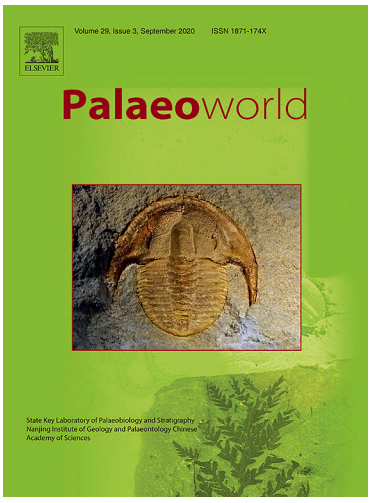

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The first fossil *Parascleroderma* (Hymenoptera: Bethylidae): a new species in mid-Miocene Zhangpu amber

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Abstract

The recently discovered amber biota from Zhangpu, China, offers a unique window into the tropical ecosystem of an Asian rainforest during the Mid-Miocene Climatic Optimum (MMCO). Here, the first flat wasp (Bethylidae) from this deposit is documented: *Parascleroderma palaeosinica* n. sp. is described and figured from a single male, and is the first fossil *Parascleroderma* known to date. The new extinct species is characterized by its minute size, the pedicel longer than the flagellomeres, the posterior ocelli inserted much posteriad on head, the notauli not impressed on anterior third of anteromesoscutum, and the hypopygium simple, with posterior margin slightly incurved medially. *Parascleroderma* is a cosmopolitan genus within the Pristocerinae and it is therefore not surprising to find its record in the Zhangpu biota, simultaneously with the northern expansion of the southeastern Asian tropical forest during the MMCO.

Keywords: Chrysidoidea; Bethylidae; Pristocerinae; Cenozoic; Miocene; China

1. Introduction

With up to 3000 current species arranged in 96 valid genera (Azevedo et al., 2018), the Bethylidae form the largest family among the Chrysidoidea. This family of wasps displays its greatest diversity in tropical regions but is cosmopolitan in its

global distribution. Bethylid wasps are generally considered as external parasitoids of lepidopteran and coleopteran larvae that they paralyze and drag into cracks (Evans, 1964; Rubink and Evans, 1979).

Within Chrysidoidea, Bethylidae are generally retrieved as the sister-group of Chrysididae in phenotypic studies (Brothers and Carpenter, 1993; Carpenter, 1999; Brothers, 2011; Brothers and Melo, 2021), but sister to Plumariidae in phylogenomic studies (Branstetter et al., 2017; Peters et al., 2017). Grimaldi and Engel (2005) indicate that the narrowly transverse and nearly completely hidden metanotum would be the synapomorphy of the clade (Bethylidae + Chrysididae). However, in the bethylid subfamily Pristocerinae, the metanotum is developed medially and tends to overlap the mesoscutellum (Azevedo et al., 2018). Bethylids are recognizable by the prognathous head, the antennae with the same number of antennomeres in males and females (11 or 10, rarely 8 or 7 flagellomeres), the pronotum with anterior flange, the prosternum small, transverse, and the six or seven exposed metasomal terga (Finnamore and Brothers, 1993). The flattened body, evolved to sneak into their host habitats, is also retained as a characteristic feature of the family, hence their nickname 'Flat wasps'. Nine subfamilies were recently recognized in the Bethylidae (Colombo et al., 2020): the extant Bethylinae, Epyrinae, Mesitiinae, Pristocerinae and Scleroderminae, and the extinct Elektroepyrinae, Holopsenellinae, Lancepyrinae and Protopristocerinae. Since then, however, *Holopsenella* Engel et al., 2016, type genus of the Holopsenellinae, has been removed from Bethylidae and elevated to a family left as *incertae sedis* in the Aculeata (Lepeco and Melo, 2022).

With more than 90 species in seven of the eight subfamilies (no fossil Mesitiinae has been described yet), the fossil record of Bethylidae spans nearly 130 million years from the Lower Cretaceous to the Holocene (see Martynova et al., 2019; and the posterior discoveries of: Engel, 2019; Falières and Nel, 2019a, 2019b, 2019c, 2020; Colombo et al., 2020, 2021a, 2021b; Jouault et al., 2020, 2021; Colombo and Azevedo, 2021; Jouault and Brazidec, 2021; Tribull et al., 2021). Despite this relatively high richness compared to other chrysidoid lineages (e.g., Chrysididae), lots of new species are likely to be described from Cretaceous or Cenozoic deposits, particularly from the recently discovered Miocene amber of Ethiopia and China (Bouju and Perrichot, 2020; Wang et al., 2021). Even from the long-surveyed deposits such as Baltic amber, new taxa may be recovered, as exemplified by the recent discovery of a new pristocerine genus (Tribull et al., 2021).

Here, we report the first Bethylidae from the rich mid-Miocene amber biota of Zhangpu, in Fujian Province, China, and we discuss its taxonomic affinities.

2. Material and methods

Zhangpu amber is found with plant impressions in two layers of sandy mudstone interbedded with coal seams that belong to the Fotan Group, a geological unit that occurs widely in Zhangpu County, Fujian Province, southeastern China (Wang et al., 2021, fig. 1). Under- and overlying basalt layers allow constrained dating of the amber between 14.8 ± 0.6 Ma and 14.7 ± 0.4 Ma, which corresponds to the middle Miocene (Langhian; Zheng et al., 2019).

This study is based on a complete male specimen kindly lent by Prof. Bo Wang (Nanjing, China) to the authors for study, and housed in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China. The fragile amber piece was embedded in a block of epoxy resin (Araldite® 2020) for consolidation and posteriorly polished to facilitate the observation of the specimen, using thin silicon carbide sanding papers on a grinder polisher (Buehler EcoMet 30). The examination and photographs were conducted with a Leica DMC4500 camera attached to a Leica M205C stereomicroscope. All images are digitally stacked photomicrographic composites of several focal planes, which were obtained using Helicon Focus 6.7 software. Adobe Illustrator CC2019 and Photoshop CC2019 software were used to compose the figures and ImageJ 1.53 for measurements. The description of the characters follows the nomenclature of Lanes et al. (2020).

This published work and its new nomenclatural act are registered in ZooBank with the following LSID (reference): urn:lsid:zoobank.org:pub:570AA2F6-4E8D-4DD0-B01A-9D824F8CD4F6.

3. Systematic palaeontology

Superfamily Chrysidoidea Latreille, 1802

Family Bethylidae Haliday, 1839

Subfamily Pristocerinae Mocsáry, 1881

Genus *Parascleroderma* Kieffer, 1904

Parascleroderma palaeosinica n. sp.

(Figs. 1, 2)

LSID: urn:lsid:zoobank.org:act:1E0E3362-9053-47AA-A6A2-457880270E5E.

Etymology: The species name combines '*palaiós*', meaning 'ancient' in Greek and '*sinica*', in reference to the geographic origin of Zhangpu amber.

Material: Holotype male, NIGP178180.

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

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

Diagnosis (male): Body minute-sized, 1.67 mm long, pale brown; pedicel longer than each flagellomere (Fig. 1C); posterior ocelli inserted much posteriad on head (Fig. 1D); notauli not impressed on anterior third of anteromesoscutum, well-marked on posterior two-thirds (Fig. 1D); hypopygium simple with posterior margin slightly incurved medially (Figs. 1A, 2).

Description: Male. Body flattened and narrow, not visibly sculptured, pale brown. Head prognathous, longer than high, longer than wide, oval in dorsal view; frons smooth, concave, with faint median sulcus originating from anterior ocellus, frons with sparse long setae; compound eye oval, longer than high, without visible setae, located in anterior part of head; mandibles only slightly overlapping at tip; maxillary palpus with at least 4 palpomeres and long apical setae; 13 antennomeres, all antennomeres bearing numerous long setae at most as long as one third of flagellomere length; scape elongate, 2.5 times longer than wide, slightly curved, pedicel as long as apical flagellomere; all flagellomeres cylindrical, longer than wide, flagellomeres I–X subequal in length, only slightly shorter than flagellomere XI; anterior ocellus located at back of frons, posterior ocelli pushed at extreme posterior of frons and widely separated from each other; occipital carina present, forming ridge extending from occipital foramen to mandibles.

Mesosoma shorter than metasoma; propleuron elongate, slightly exposed dorsally, 'neck-shaped'; pronotal flange developed, dorsal pronotal area longer than anteromesoscutum, narrowed anteriorly; prosternum reduced between procoxae; mesoscutum with notauli impressed on posterior two thirds, slightly converging posteriorly, absent anteriorly; parapsidal signum not marked; mesoscutellum with blunted apex; metanotum large, overlapping mesoscutellum posteriorly, transversally carinate; metapectal-propodeal complex longer than wide, without posterolateral spines, smooth, without sharp longitudinal carinae. Forewing with only costal [C], radial [R] and cubital [1Cu] cells closed by tubular veins; C, Sc+R, M+Cu, A, Rs, cu-

a, basal segment of M and Cu tubular; basal segments of Rs and M forming contiguous line; cu-a angled at junction with Cu; Cu nebulous posteriorly to junction with 1m-cu then completely fading; 1m-cu nebulous; pterostigma reduced in length, rapidly vanishing after 2r-rs; R1 not apparent after pterostigma; 2r-rs and Rs continuously arched, without marked angles between sections, distal segment of Rs tubular for much of its length, then reaching wing margin as nebulous vein, thus not closing radial cell [2R1]; distal segment of M completely spectral. Hind wing slightly shorter than forewing; C only pigmented vein; Rs originating from C in anterior half of wing, nebulous to spectral; no closed cells. Legs sparsely pubescent; profemur swollen; first tarsomere longer than combined length of following tarsomeres; pro- and mesotibiae with two spurs, metatibial spurs not visible; metafemur enlarged, without spines.

Metasoma sparsely setose; metasomal tergites without modifications; metasomal tergite I as long as wide; metasomal tergite II shorter than I; hypopygium not divided, with outer surface flat and posterior margin weakly incurved medially; genital structures not visible.

Measurements (in mm): Body length 1.67; head length 0.34, width 0.26; scape length 0.10, width 0.04; pedicel length 0.06; flagellomeres I–X length ca. 0.04–0.05; flagellomere XI length 0.06; mesosoma length 0.63; forewing length ca. 1.10; hind wing length 0.98; mesosoma length 0.70.

4. Discussion

Following the key to the subfamilies of Bethylidae of Azevedo et al. (2018), the new fossil keys out in Pristocerinae because of the following characters: macropterous species, forewing with Rs+M vein absent, metanotum developed medially and overlapping mesoscutellum posteriorly. This last character is usually considered as a synapomorphy of the Pristocerinae.

Following the keys to pristocerine genera of Azevedo et al. (2018), the new fossil keys near *Parascleroderma* because of the following characters: body smaller than 15 mm, hypopygium not deeply divided into two lobes, outer surface of hypopygium flat, dorsal pronotal area short, forewing with intersection of Rs&M far from pterostigma, profemur narrow, metafemur without spines, hypopygium slightly incurved. Among the diagnostic characters provided by Azevedo et al. (2018) for the genus *Parascleroderma*, the fossil clearly possesses the body flattened and elongated,

the propleuron elongated, the pronotum elongated and anteriorly narrowed, the intersection of Rs&M and Sc+R far from pterostigma and the metafemur enlarged. Because of the preservation in amber, characters on the clypeus, genitalia, and internal features of hypopygium cannot be observed. *Parascleroderma* is closely related to *Afgoiogfa* Argaman, 1988, *Dissomphalus* Ashmead, 1893, *Foenobethylus* Kieffer, 1913, *Protisobrachium* Benoit, 1957, and *Pseudisobrachium* Kieffer, 1904 (Alencar et al., 2018). These genera differ from our fossil as follows (Azevedo et al., 2018): pterostigma comma-like, maxillary palpus with 3 palpomeres and a long apical seta or 6 palpomeres with only short setae, notauli large and poorly impressed (*Afgoiogfa*); body robust, metasomal tergum II with process (*Dissomphalus*); posterior hypopygial margin abruptly v-incurved, metatrochanter and metafemur usually with spines (*Foenobethylus*); eyes with long erect setae, R1 present and long after the pterostigma, posterior hypopygial margin strongly incurved (*Protisobrachium*); forewing with intersection of Rs+M and Sc+R close to pterostigma (*Pseudisobrachium*). Therefore, our new species is excluded from these genera and, instead, displays features that are all diagnostic of *Parascleroderma*.

Parascleroderma was erected by Kieffer (1904) based on a species from Italy: *P. nigriceps* Kieffer, 1904. In the following years, the same author subsequently described species from Hungary, Italy, France and the Seychelles (e.g., Kieffer, 1908, 1912): *P. fulviceps* Kieffer, 1906, *P. fuscipennis* (Kieffer, 1905) (synonymized from *Ceratepyris* Kieffer, 1905 by Argaman, 1988), *P. remota* (Kieffer, 1912) (transferred from *Apenesia* by Azevedo et al., 2018), *P. seychellensis* (Kieffer, 1912) (transferred from *Sclerodermus* Latreille, 1809 by Evans, 1964) and *P. sulcatifrons* (Kieffer, 1908) (synonymized from *Ceratepyris* by Argaman, 1988). The genus currently includes 32 extant species and has a cosmopolitan distribution (Fig. 3), but was hitherto undocumented from the fossil record. Among major contributors to the knowledge of *Parascleroderma*, Evans (1963, 1964, 1967, 1978) described four new species from America North of Mexico: *P. arivaca* Evans, 1978, *P. carinata* Evans, 1964, *P. insolita* (Evans, 1963) (transferred from *Apenesia* by Evans, 1964), *P. minima* Evans, 1978; and one from Peru: *P. pucallpa* Evans, 1967. Argaman (1988) summarized the known species and erected six new ones from Europe, Turkey, Israel, and Iran: *P. cisnora* Argaman, 1988, *P. fiturcata* Argaman, 1988, *P. hindola* Argaman, 1988, *P. norcasta* Argaman, 1988, *P. oriana* Argaman, 1988 and *P. varlinda* Argaman, 1988. Terayama (1998, 2006), Xu et al. (2002), and Lim et al.

(2011) described new species from the Oriental region (i.e., Korea, China, Taiwan, and Japan): *P. atayal* Terayama, 1998, *P. ishama* Terayama, 2006, *P. jinmo* Terayama, 2006, *P. maae* Xu, He and Terayama, 2002, *P. okajimai* Terayama, 1998, *P. renaiensis* Terayama, 1998 and *P. tetradentica* Lim and Lee in Lim et al., 2011. The vast majority of the known *Parascleroderma* species have been collected in the northern hemisphere but six species occur in the southern hemisphere: one from Peru and two from the Seychelles, mentioned above, *P. neounicolor* Alencar and Azevedo in Azevedo et al., 2018 (Marquises Islands), *P. nigra* Brues, 1910 (South Africa) and *P. azevedonis* (New Zealand). Alencar et al. (2018) also indicate potential new species in Thailand, Australia and South Africa.

The Zhangpu amber originated from a tropical rainforest with abundant Dipterocarpaceae (Wang et al., 2021) in the greenhouse context of the Mid-Miocene Climatic Optimum (Kasbohm and Schoene, 2018). Thus, the presence of *Parascleroderma* in Thailand nowadays is interesting because southeast Asian dipterocarp forests are the closest extant relatives of the mid-Miocene Zhangpu amber forest in terms of floral assemblage and climate (Wang et al., 2021, fig. 2). This further supports our attribution of the new species to *Parascleroderma*, whose extant species are present in tropical biomes. Therefore, it is not surprising to discover an extinct species of *Parascleroderma* northward in the Zhangpu biome (24.2°N), simultaneously with the megathermal climate of the MMCO that allowed the tropical forest to expand toward higher latitudes.

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Figure captions

Fig. 1. *Parascleroderma palaeosinica* n. sp., holotype, NIGP178180; (A) habitus in lateroventral view; (B) habitus in dorsal view; (C) head in dorsal view; (D) line drawing of head and mesosoma in dorsal view; scale bar = 0.5 mm.

Fig. 2. Line drawing of *Parascleroderma palaeosinica* n. sp. in lateroventral view; scale bar = 0.5 mm.

Fig. 3. Distribution map of extant and extinct species of *Parasclerodermа* showing type localities.