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A second cuckoo wasp species from the mid-Miocene Zhangpu biota (Hymenoptera: Chrysididae)

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Abstract

The Miocene history of the aculeate family Chrysididae is poorly known, with only two species described for that time interval. Here, a third species is introduced, the second from the rich middle Miocene Zhangpu amber, southeastern China. †*Trichrysis perrichoti* n. sp. is described and illustrated based on a nearly complete female specimen. The new species displays characters of the *cyanea* species group, which is today the most common for *Trichrysis* Lichtenstein, 1876 in China. This discovery further strengthens the affinities between the Zhangpu entomofauna and the modern Southeast Asia entomofauna.

Keywords: Systematics; palaeoentomology; Chrysidoidea; Chrysidinae; parasitoid wasp

1. Introduction

The Chrysididae are the second most speciose chrysidoid family after the Bethylidae, with approximately 3000 described species (Kimsey and Bohart, 1991). Despite having been well surveyed in the European and North American regions (Kimsey and Bohart, 1991), the fauna is still understudied in other regions of the world, such as Southeast Asia, sub-Saharan Africa or South America, where new taxa keep being described (e.g., Lucena et al., 2016; Kimsey and Copeland, 2017; Kimsey, 2019; Rosa et al., 2021a; Rosa, 2024). Chrysidid females exhibit a parasitoid behaviour on different insect groups. The Cleptinae use sawfly larvae as hosts, the Amiseginae and Loboscelidiinae parasitize phasmid eggs, and the Chrysidinae are parasitoids or cleptoparasites of solitary bees and aculeate wasps, hence the nickname "cuckoo wasps", which was later used for the entire family (Kimsey and Bohart, 1991).

To this date, about 30 fossil species of Chrysididae have been described (e.g., Lucena and Melo, 2018; Brazidec et al., 2024), mostly in the late Eocene and Late Cretaceous deposits. Moreover, only two species are known from the Miocene, although this is the most recent period with abundant fossil material. The Chrysidini †*Ceratochrysis dominicana* Engel, 2006 was described from Dominican amber, and the Amiseginae †*Atoposega rosai* (Brazidec and Perrichot, 2023) was described from Zhangpu amber (Engel, 2006; Brazidec and Perrichot, 2023). The recent discovery of the latter deposit, in the southeast of China, in Langhian (middle Miocene) sediments (Wang et al., 2021)

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has offered new opportunities to investigate the recent evolution of the family.

In this contribution, we describe a new species of Chrysididae from Zhangpu amber which represents the second record of the family in this deposit, and the first fossil record of *Trichrysis* Lichtenstein, 1876.

2. Material and methods

Zhangpu amber occurs within two sandy mudstone layers interbedded with coal seams, which are part of the Fotan Group in Zhangpu County, Fujian Province, southeastern China (Wang et al., 2021: fig. 1). The amber-yielding layer is dated of the Langhian stage, middle Miocene, between 14.8 ± 0.6 Ma and 14.7 ± 0.4 Ma (Zheng et al., 2019).

This study is based on an almost complete female 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 sticky 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 MetaServ 3000). The examination and photographs were made using a Zeiss Axiocam 705 color camera attached to a Zeiss Axio Zoom V16 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 Adobe© Photoshop CC2019 were used to compose the figures, while ImageJ 1.53 was used for measurements. The description of the characters follows the terminology of Kimsey and Bohart (1991); the wing venation follows Azevedo et al. (2018). Abbreviations are used as follows: F1, F2, F3, etc. = flagellomeres 1, 2, 3, etc.; MOD = median ocellus diameter; P = pedicel; PD = puncture diameter; S = scape; T1, T2, T3 = metasomal tergite 1, 2, 3; TFC = transverse frontal carina.

This published work and its new nomenclatural act are registered in ZooBank with the following LSID: urn:lsid:zoobank.org:pub:23C1E88F-0437-4FAC-8186-F2C1AE25CCEE.

3. Systematic palaeontology

Order Hymenoptera Linnaeus, 1758
Superfamily Chrysidoidea Latreille, 1802
Family Chrysididae Latreille, 1802
Subfamily Chrysidinae Latreille, 1802
Tribe Chrysidini Latreille, 1802
Genus *Trichrysis* Lichtenstein, 1876

Trichrysis perrichoti n. sp.
(Figs. 1, 2)

LSID: urn:lsid:zoobank.org:act:98F5DA1C-A43C-4C73-8754-E8FDB836C100.

Etymology: We dedicate this species to Dr. Vincent Perrichot (Université de Rennes), specialist on fossil insects, in gratitude for the supervision of the first author's PhD. The specific epithet is to be treated as a noun in a genitive case.

Type material: Holotype female, NIGP208750, an almost complete specimen, lacking the left posterolateral part of the metasoma.

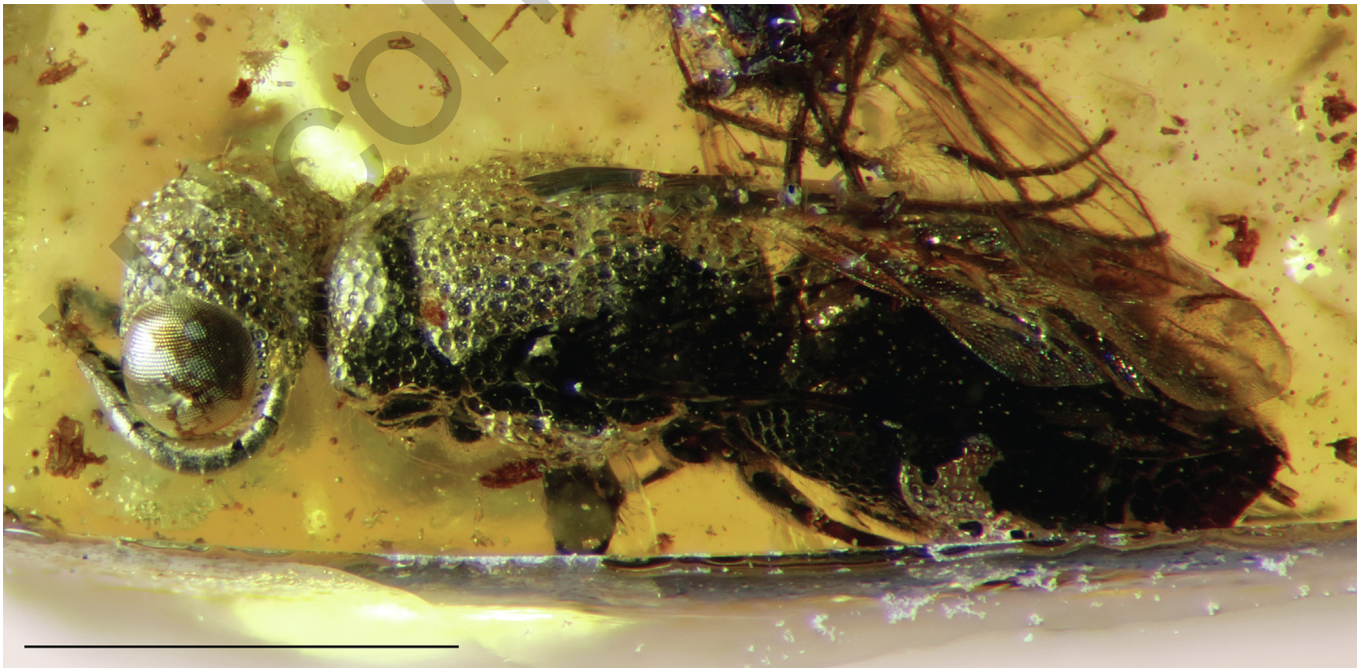

Fig. 1. *Trichrysis perrichoti* n. sp., holotype female, NIGP208750, habitus in dorsolateral view. Scale bar = 1 mm.

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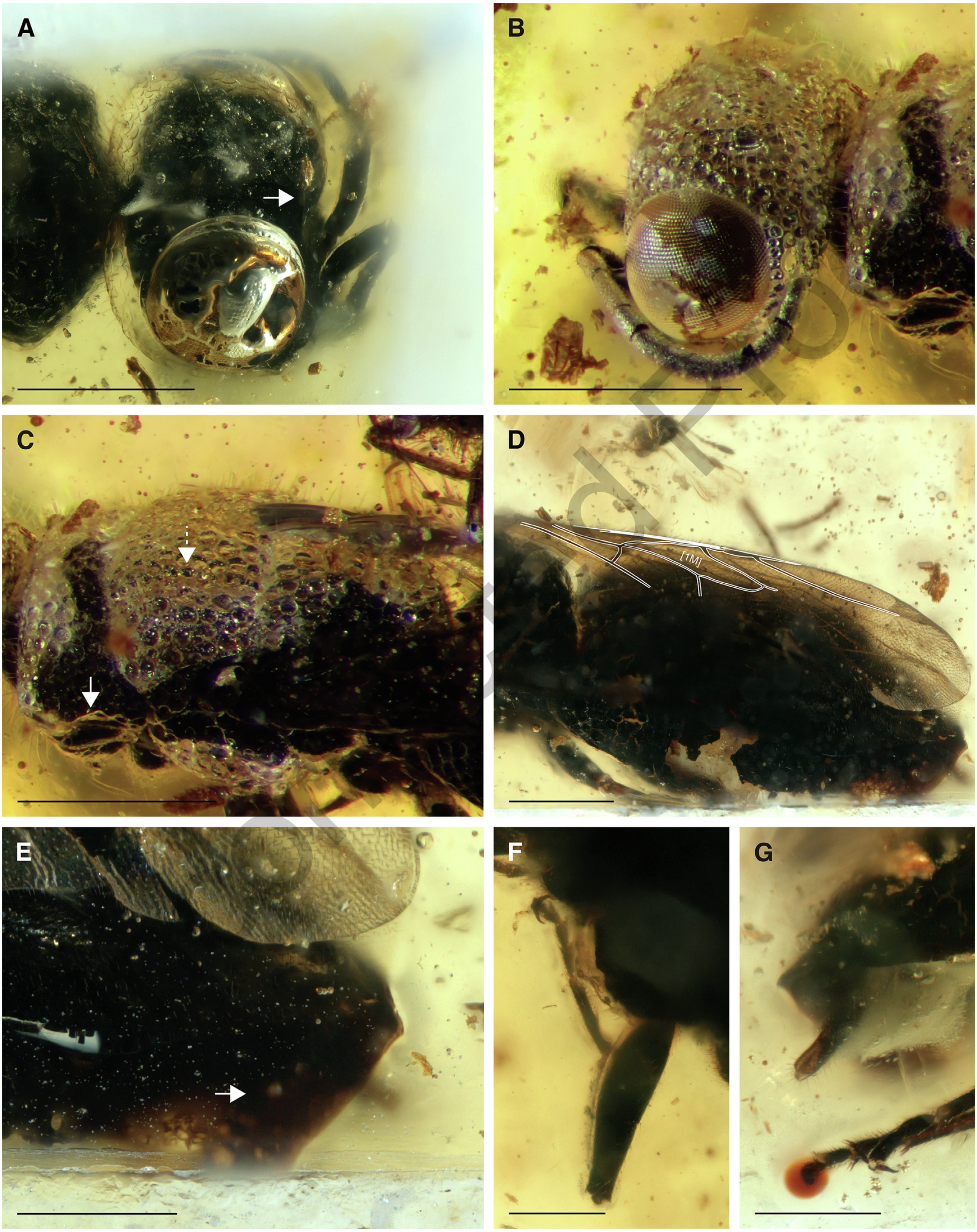

Fig. 2. *Trichrysis perrichoti* n. sp., holotype female, NIGP208750. (A) Head in right dorsolateral view (white arrow = TFC); (B) head in left dorsolateral view; (C) mesosoma in dorsal view (solid line arrow = sublateral pronotal carina; dotted line arrow = notaulus); (D) detail of fore wing with underlined pigmented veins; (E) detail of T3 (white arrow = pit row); (F) fore tarsal claws; (G) detail of apex of ovipositor. Scale bars = 0.5 mm (A–D) or 0.25 mm (E–G).

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Type locality: Zhangpu County, Zhangzhou City, Fujian Province, China.
Horizon: Sedimentary layer II, Fotan Group; Middle Miocene: Langhian, 14.7 Ma.
Diagnosis (female): Body punctures with narrow interspaces, at most 0.2 PD (Fig. 1); TFC forming upcurved crescent (Fig. 2A); F1 length 2.0 × median width (Fig. 2B); sublateral pronotal carina distinct (Fig. 2C); [1M] cell fully enclosed by pigmented veins (Fig. 2D); T3 posteriorly with longitudinal median elevation directed to median tooth and forming blunt crest, three angular teeth, with intervals slightly outcurved (Fig. 2E).
Description: Body length 3.2 mm. Head globose, higher than long (length 0.6 mm); integument mostly with metallic reflections (see "Remarks" section), pubescence sparse and short. Frons and vertex roughly punctate, punctures about 0.5 × MOD, subcontiguous, separated by less than 0.2 PD, postero-lateral area of posterior ocellus impunctate; vertex convex. TFC present, forming simple upcurved crescent reaching about two-thirds of eye height, medially smoothly curved, distant from middle ocellus by about 1.0 × MOD. Compound eye glabrous, oval, covering 0.8 × head length. Scapal basin present, sculpture not visible. Scape 4.1 × longer than median width; relative length of S:P:F1:F2:F3 = 4.3:1:1.8:1.3:1.3; F1 2.0 × longer than median width.

Mesosoma stout (length 1.0 mm); integument with metallic reflections; pubescence sparse. Pronotum shorter than mesoscutum (length of pronotum dorsally 0.2 mm), punctate, punctures about 0.5 × MOD, separated by about 0.2 PD; dorsal pronotal area convex; anterolateral pronotal corner angulate; sublateral pronotal carina distinct; lateral pronotal depression deep; mesoscutum about 2.0 × dorsal pronotal length (length 0.4 mm), punctured like pronotum; notauli fully developed, converging posteriorly. Mesoscutellum 0.5 × mesoscutum length (mesoscutellum length 0.2 mm), as long as and punctured like pronotum; metanotum as long as mesoscutellum (metanotum length 0.2 mm). Mesopleuron punctate, punctures separated by about 0.2 PD; episternal sulcus present; scrobal sulcus present. Tegula covering fore wing base. Propodeal angle triangular, broad, apex blunt.

Legs with uniform short semi-decumbent pubescence; tibial spur formula 1–2–2; pretarsal claws slightly curved, simple.

Fore wing hyaline (length 1.6 mm), uniformly micropubescent; C, Sc+R, M+Cu, A, 1Rs, 1M, cu-a, Rs+M, 1Cu, 2Cu, m-cu, R1, 2r-rs&Rs veins pigmented; 1Rs much shorter than 1M; 1M posteriorly curved, aligned with cu-a; [1M] cell fully closed by pigmented veins; pterostigma thin, longer than 1Rs; R1 length about 1/3 × 2r-rs&Rs length; 2r-rs&Rs evenly curved towards wing apex, vein apex at less than 2 × MOD from wing apex. Hind wing hyaline, uniformly micropubescent; venation reduced; three hamuli visible.

Metasoma longer than mesosoma (length 1.2 mm) with three tergites visible externally; T1 length 0.3 mm, T2 length 0.6 mm, T3 length 0.3 mm; tergites with uniform medium-sized punctures; T3 medially elevated longitudinally, with distinct pit row, posterior rim with three short angular blunt teeth, intervening margin slightly outcurved.

Remarks: Between the first and second series of photographs (e.g., Fig. 2B, versus Fig. 2A), the cuticle of the specimen suffered from exposure to fluids and darkened. In the cephalic region, the cuticle has shrunk, leaving only its imprint in the amber. Therefore, the coloration and measurements indicated here correspond to the original state of the specimen.

4. Discussion

Based on the propodeum not developed dorsally, the fore wing venation, the regularly sized tegula (i.e., not reduced or covering both fore and hind wing bases), the edentate tarsal claws, the three visible metasomal tergites, and the pit row on T3, the new fossil is firmly placed in the subfamily Chrysidinae, and in the tribe Chrysidini. The specimen displays all diagnostic characters of *Trichrysis* Lichtenstein, 1876: the scapal basin concave, the TFC present, the distinct sublateral pronotal carina, the episternal and scrobal sulci, the mesoscutum not expanded laterally, 2r-rs&Rs (= Rs in Kimsey and Bohart, 1991) less than 2 × MOD from fore wing margin, [1M] cell (= discoidal cell) veins tubular, propodeal angle triangular, T3 with three teeth (Rosa et al., 2016, 2022).

The presence of the sublateral pronotal carina and the fully pigmented veins excludes the specimen from *Chrysidea* Bischoff, 1913, a genus with which *Trichrysis* is often confused (Rosa et al., 2022). *Caenochrysis* Kimsey and Bohart, 1981 is very similar to *Trichrysis*, and differs primarily in the presence of a pair of facial foveae, the visibility of which is difficult to assess here. However, in many *Caenochrysis* species, the dorsoposterior margin of the head is marked by a deep medial depression (Lucena and Almeida, 2022) which is absent in our specimen (Fig. 2B). Several *Caenochrysis* species also display a mucronate-shaped and medially depressed metanotum (Lucena and Almeida, 2022: fig. S18D), unlike what is observed in our current new species (Fig. 2C). Additionally, extant *Caenochrysis* are only known from the Nearctic and Neotropical regions (Linsenmaier, 1984; Kimsey and Bohart, 1991) whereas *Trichrysis* is widely distributed throughout the Palearctic, Afrotropical, Australian, and Oriental regions (Rosa et al., 2022). Therefore, we attribute the specimen to *Trichrysis* and propose the new species †*Trichrysis perrichoti* n. sp.

Trichrysis is a rather speciose genus within the Chrysidini tribe, comprising approximately 40 extant species distributed in the Old World (Bohart, 1988; Rosa et al., 2016, 2021b, 2022; Wiśniowski et al., 2020). The genus exhibits particularly diverse faunas in China (Rosa et al., 2016; Nguyen et al., 2022), India (Rosa et al., 2022), Vietnam, Indonesia, and the Philippines (Wiśniowski et al., 2020), and South Africa (Kimsey and Bohart, 1991). Fourteen species have been recorded in China (Rosa et al., 2016; Nguyen et al., 2022), most belonging to the *cyanea* species group, to which †*Trichrysis perrichoti* n. sp. belongs. The *cyanea* species group is characterized by a combination of the following characters: T3 tridentate, the sublateral pronotal carina, and TFC present. †*Trichrysis perrichoti* n. sp. shows conservative features with minimal differences compared with modern species. Besides its sculpture with overall subcontiguous and large body punctuation, it can be separated from modern species with short, angular apical teeth (as opposed to species with larger teeth, e.g., *Trichrysis tridensnotata* Rosa, Wei and Xu in Rosa et al. 2016) by combination with other characters. It can be separated from *Trichrysis cyanea* (Linnaeus, 1758) by the sharp sublateral pronotal carina and strong longitudinal keel on third tergum (not so distinctly sharp and without keel in *T. cyanea*); from *Trichrysis secernenda* (Mocsáry, 1912) by the sharp sublateral pronotal carina and notauli formed by a series of deep punctures (sublateral pronotal carina less expanded and notauli as a fine line in *T. secernenda*); from *Trichrysis triacantha* (Mocsáry, 1889) by the shape of the head, with short distance between frontal carina and anterior ocellus (about 1.0 × MOD) (> 2.0 × MOD in *T. triacantha*); from *Trichrysis sinica* Rosa, Nguyen and Wiśniowski, 2022 in Rosa et al. (2022) and *Trichrysis tonkinensis* (Mocsáry, 1914) by the simple third tergum (prepit bulge slightly convex). Other differences may lie in the shape of the black spots of the second sternum, an important diagnostic character (Rosa et al., 2016: figs. 96–107; Rosa et al., 2022), which are not visible in the holotype of our new species.

Trichrysis species have been identified as nest parasites of various apoid genera (e.g., Sphecidae, Pemphredonidae, Crabronidae; Tormos et al., 1996; Abitha et al., 2022). Recently it was also confirmed that *T. cyanea* parasitizes nests of the pompilid genera *Auplopus* Spinola 1841 (Theunert, 1997) and *Deuteragenia* Šustera 1912 (e.g., Pärn et al., 2015; Paukkunen et al., 2015) and not only Crabronidae. *Trichrysis cyanea* is therefore a kleptoparasite whose larvae gain nourishment from the hosts' provisions. A switch from apoid wasps (the presumed ancestral condition) to spider wasps has been an evolutionary step that is still to be studied and allocated in time. The specific diversity of the genus and data on its biology are expected to increase as new discoveries continue to be made, particularly in the Oriental region (Nguyen et al., 2022).

Zhangpu amber offers a unique window into the palaeoenvironment of Southeast Asia during the Miocene. Other important insect faunas for that period are found in Dominican Republic (Arillo and Ortuño, 2005), Mexico (Solórzano Kraemer, 2010), Ethiopia (Bouju et al., 2021), New Zealand (Kaulfuss et al., 2015), Australia (McCurry et al., 2022), or France (Engel and Nel, 2024). A similar deposit in terms of age and latitude is known in the southeastern Yunnan Province (e.g., Engel et al., 2018), although the latter was dominated by Fagaceae and Fabaceae, whereas Zhangpu amber was formed in a Dipterocarpaceae megathermal rainforest (Wang et al., 2021). The Zhangpu palaeoentomofauna shows close affinities with the modern Chinese or more generally continental Southeast Asian faunas in generic composition (e.g., Brazidec and Perrichot, 2023; Perrichot, 2023; Xu et al., 2023). The exceptions to this pattern are the presence of the bee genus *Austroplebeia* Moure, 1961 (Engel et al., 2021) and the barklouse genus *Belaphotroctes* Roesler, 1943 (Engel and Wang, 2022), the latter case being explained by the poor phylogenetic resolution of the genus and its probable paraphyly or polyphyly. The discovery of †*Trichrysis perrichoti* n. sp. is another indication that the modern Southeast Asian dipterocarp forest insect community was already in place during the Miocene.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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