

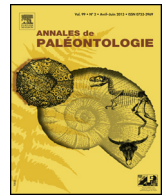


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Original article

The first fossil record of the cuckoo wasp genus *Primeuchroeus* in Eocene Baltic amber, with revision of two fossil Chrysididae (Hymenoptera: Chryridoidea)



Le premier fossile de guêpe coucou du genre Primeuchroeus dans l'ambre éocène balte, avec révision de deux Chrysididae fossiles (Hymenoptera : Chryridoidea)

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ABSTRACT

Chrysididae fossils are rare and understudied compared to their extant diversity, with an overwhelming proportion of genera found in Cenozoic fossiliferous deposits currently thought to be extinct. Here, we document the oldest known representative of the extant genus *Primeuchroeus* Linsenmaier, 1968 based on a specimen from Priabonian (upper Eocene) Baltic amber, and described as *Primeuchroeus groehni* sp. nov. This finding is the oldest Chrysididae fossil indisputably attributed to an extant genus and refutes the hypothesis that modern genera are not older than Neogene in age, as hitherto believed. Additionally, we propose the reallocation of a recently described fossil genus and fossil species. The genus *Sphaerocleptes* Cockx et al. (2016), described in the subfamily Cleptinae from Cenomanian French amber, is transferred to Chrysidinae, tribe Elampini; this is the first temporal occurrence for the tribe, previously not known earlier than the upper Eocene. The fossil species *Hedychridium rosai* Brazidec and Perrichot, 2023 is transferred from the subfamily Chrysidinae to Amiseginae and we propose the new combination *Atoposega rosai* (Brazidec and Perrichot, 2023) comb. nov. These findings provide deep insights into the evolution of Chrysididae: within the Chrysidinae subfamily, established by the mid-Cretaceous, some of the modern generic lineages had already diverged by the upper Eocene, and the Miocene Chrysididae fauna was likely similar to the extant fauna, pending further discoveries. Based on our observations, the fossil record of Chrysididae shows more similarities to that of other diverse hymenopteran families than was previously thought.

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RÉSUMÉ

Les fossiles de Chrysididae sont plutôt rares et sous-étudiés par comparaison à leur diversité actuelle, avec une proportion importante de genres fossiles dans les gisements cénozoïques. Dans cette étude, nous décrivons le plus ancien représentant connu du genre *Primeuchroeus* Linsenmaier, 1968 : *Primeuchroeus groehni* sp. nov., sur la base d'une femelle préservée dans l'ambre balte (Priabonien, Éocène supérieur). Ce spécimen est le plus ancien Chrysididae incontestablement attribuable à un genre actuel et réfute l'hypothèse que les genres modernes n'ont pas divergé avant le Néogène. De plus, nous proposons la réallocation d'un genre et d'une espèce récemment introduits. Le genre *Sphaerocleptes* Cockx et al. (2016),

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décrit dans la sous-famille Cleptinae de l'ambre cénomanien de France, est transféré dans les Chrysidinae, tribu Elampini ; il s'agit de la plus ancienne occurrence temporelle de la tribu, jusqu'ici inconnue avant l'Éocène supérieur. L'espèce *Hedychridium rosai* Brazidec et Perrichot, 2023, de l'ambre miocène de Chine, est transférée des Chrysidinae aux Amiseginae et nous proposons la nouvelle combinaison *Atoposega rosai* (Brazidec et Perrichot, 2023) comb. nov. Ces découvertes permettent de mieux comprendre l'évolution des Chrysididae : au sein de la sous-famille Chrysidinae, déjà établie au Crétacé moyen, certaines des lignées génériques modernes avaient déjà divergé à l'Éocène supérieur ; en termes de distribution et de composition, la faune miocène semble similaire à la faune actuelle. Sur la base de nos observations, le registre fossile des Chrysididae présenterait plus de similitudes avec celui d'autres familles d'hyménoptères qu'on ne le pensait auparavant.

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1. Introduction

Among the aculeate wasps Chrysoidea, Chrysididae are the second largest family with about 3000 valid species, arranged in 93 valid genera (e.g., Kimsey and Bohart, 1991; and subsequent studies of Antropov, 1995; Kimsey, 2005, 2014a; Kurzenko and Lelej, 1994; Rosa et al., 2016a,b). They are distributed worldwide, though they show a pattern of greater diversity in temperate areas (Finnamore and Brothers, 1993), and often referred to as jewel wasps because of the metallic reflection of their integument or cuckoo wasps for their brood-parasitic behavior (Kimsey and Bohart, 1991).

However, chrysidid fossils are far more poorly known than those of Bethyloidea and Dryinoidea, the two other largest families of Chrysoidea. Less than 30 fossil chrysidid species have been described so far, while more than 90 fossil species are known for these two comparison families (Martynova et al., 2019). The first described fossil chrysidids originated from Cenozoic deposits, viz. the Eocene of Florissant (Cockerell, 1907), Eocene Baltic amber (Brues, 1923, 1933) and Oligocene of Brunstatt (Förster, 1891). Subsequent studies during the second half of the 20th century, and in the last few years, described taxa from Cretaceous amber (e.g., Krombein, 1986; Lucena and Melo, 2018; McKellar and Engel, 2014), which represent half of the known fossil chrysidids. Among this scattered record, Amiseginae and Chrysidinae are the richest subfamilies with eleven and nine fossil species, respectively, from Cretaceous and Cenozoic deposits (Brues, 1923; Engel, 2006; Krombein, 1986; Lucena and Melo, 2018; Martynova and Perkovsky, 2017). Five Cleptinae are known from Cretaceous ambers only (Evans, 1973; McKellar and Engel, 2014; Cockx et al., 2016), whereas five fossils from Kachin amber and Lower Cretaceous Transbaikala compressions were classified as *incertae sedis* (Lucena and Melo, 2018).

In this study, we describe the first fossil species of *Primeuchroes* Linsenmaier, 1968 from Baltic amber. *Primeuchroes* is an extant genus comprising 33 species, distributed in the Afrotropical, Oriental, Australian and East Palearctic regions (Kim, 2013), which has been reared from the nest of Crabronidae (Apoidea) (Kimsey and Bohart, 1991). We also discuss the correct placement of an extinct genus known from Cenomanian French amber, *Sphaerocleptes* Cockx et al. (2016), and of a species from the rich mid-Miocene biota of Zhangpu, China, *Hedychridium rosai* Brazidec and Perrichot, 2023.

2. Material and methods

2.1. Age of deposits

2.1.1. Baltic amber

The main Baltic amber-bearing layer is the Blue Earth Formation, which occurs throughout northern Europe just under the sea-level around the Baltic shore (Weistchat and Wichard, 2010;

fig. 1). Palynological data indicate an upper Eocene age, late Bartonian to Priabonian, (ca. 34–38 Ma; Aleksandrova and Zaporozhets, 2008). An older Lutetian age (44.1 ± 1.1 Ma: Ritzkowski, 1997) has been proposed for this formation but was probably an overestimate (Clauer et al., 2005). Small amounts of amber occasionally occur in older layers (Weistchat and Wichard, 2010) as well as in Oligocene sediments, that may be redeposited Eocene material (Standke, 2008). In this paper, we assume a Priabonian age for Baltic amber, following Seyfullah et al. (2018).

2.1.2. Archingeay amber

The specimen studied herein derived from the uppermost of two amber strata of the Font de Benon quarry, between Archingeay and Les Nouillers villages, Charente-Maritime, southwestern France (Perrichot et al., 2007; fig. 2; Perrichot et al., 2010). As opposed to the lower stratum from sub-unit A1sl-A (uppermost Albian), the upper stratum from sub-unit A2sm1-2 has yielded fewer arthropods (Perrichot et al., 2010; Saupe and Selden, 2009; Vršanský, 2009). The amber is found in a clay lens with locally abundant plant remains, dated from the lowermost Cenomanian (Néraudeau et al., 2002).

2.1.3. Zhangpu amber

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 occurring 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).

2.2. Repository of specimens

The Baltic specimen GPIH 5201 (CCGG n° 3751) was found in the collection of Carsten Gröhn (Glinde, Germany) and is now deposited in the public amber collection of the Leibniz Institute for the Analysis of Biodiversity Change, Hamburg, Germany (GPIH, Carsten Gröhn coll. CCGG).

The Archingeay specimen IGR.ARC-419.1 is housed in the amber collection of the Geology Department and Museum of the University of Rennes, France (IGR), and was examined directly.

The Zhangpu specimen NIGP200741 is housed in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China, and was examined directly following the original loan by Prof. Bo Wang.

2.3. Preparation and examination of specimens

The amber piece containing the specimen GPIH 5201 has been trimmed and polished to facilitate the study of the specimen under different views, using thin silicon carbide sanding papers

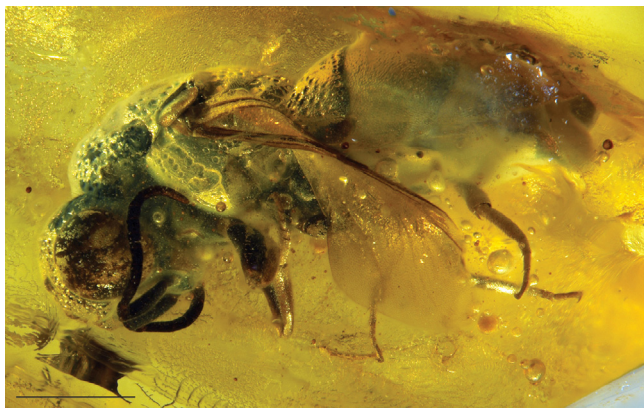


Fig. 1. *Primeuchroeus groehni* sp. nov., holotype GPIH 5201, habitus in lateral view. Scale bar = 2 mm.

Primeuchroeus groehni sp. nov., holotype GPIH 5201, habitus en vue latérale. Barre d'échelle = 2 mm.

on a grinder polisher (Buehler MetaServ 3000). The examination and photographs were conducted with a Leica DMC4500 camera attached to a Leica M205C stereomicroscope. Images of the specimen are digitally stacked photomicrographic composite of several focal planes, which were obtained using Helicon Focus 6.7.

Adobe Illustrator CC2019 and Photoshop CC2019 software were used to compose the figures and ImageJ 1.53 for measurements.

The description of morphological characters follows Kimsey and Bohart (1991), except for the wing venation, which follows the system of Azevedo et al. (2018: fig. 7). The following abbreviations are used throughout the text: F1, F2, F3, etc. = flagellomeres 1, 2, 3, etc.; MOD = middle ocellus diameter; MS = malar space, the shortest distance between base of mandible and compound eye; OOL = oculo-ocellar line, the shortest distance between lateral ocellus and compound eye; P = pedicel; PD = puncture diameter; POL = shortest distance between posterior ocelli; T1, T2, T3 = metasomal tergite 1, 2, 3; TFC = transverse frontal carina.

The published work and nomenclatural acts are registered in ZooBank with the following LSID: <https://zoobank.org/E7E47BA7-B17A-4281-85AB-77A15BF9AC29>.

3. Systematic palaeontology

Order Hymenoptera Linnaeus, 1758
 Superfamily Chrysoidea Latreille, 1802
 Family Chrysididae Latreille, 1802
 Subfamily Chrysidinae Latreille, 1802
 Tribe Chrysidini Latreille, 1802
 Genus *Primeuchroeus* Linsenmaier, 1968

Primeuchroeus groehni sp. nov.

(Figs. 1 and 2)

<https://zoobank.org/1594A6EF-32BC-43DF-AF28-14AF29F57597>

Material. Holotype GPIH 5201 a complete female; housed in the Carsten Gröhn amber collection (under CCGG no. 3751) of the Leibniz Institute for the Analysis of Biodiversity Change, Hamburg, Germany.

Type locality. Baltic region.

Age. Late Eocene: Priabonian, 34–38 Ma.

Etymology. The specific epithet is a patronym honoring Carsten Gröhn, a renowned amber enthusiast and co-founder and current president of the German amber work group ('Arbeitskreis Bernstein'), who generously made the specimen from his collection available for study. The specific epithet is a noun in genitive case.

Diagnosis. Body mainly metallic blue, except black clypeus, antenna (Fig. 1); head, mesosoma and T1 with large punctures (Fig. 2A); T2 and T3 with fine dense punctures (Fig. 2C). TFC medially strongly arched toward middle ocellus; scapal basin with transverse medial line complete (Fig. 2E); F1 3.1 × longer than wide. Mesopleuron with V-shaped enclosure below scrobal sulcus. Fore wing with Rs+M and Cu tubular, m-cu spectral; 2r-rs&Rs fading near wing margin (Fig. 2F). T3 posterior margin unmodified, continuous, evenly outcurved with a sub basal smooth angle (Fig. 2D).

Description. Body length 11.2 mm. Head globose, about as long as high (length 2.1 mm); integument with uniform light blue metallic reflections, except black non-metallic clypeus, antenna and legs. Frons and vertex roughly punctate (punctures ca. 0.4 × MOD); vertex convex. TFC with posterior branches, forming two down-curved crescents, medially joining at acute angle distant from middle ocellus by 1.0 × MOD. Compound eye glabrous, round, covering 0.7 × lateral surface of head. Scapal basin hollowed medially, finely striate to wrinkled; medial line complete from median pit of scapal basin to clypeal margin. Clypeus wide, polished with sparse, fine punctures, apical margin slightly incurved. OOL = 1.8 × MOD; POL = ca. 3.4 × MOD; MS = 0.9 × MOD. Scape 3.0 × longer than median width; relative length of P:F1:F2:F3 = 1:1.8:1.1:1.1; F1 3.1 × longer than median width.

Mesosoma stout (length 3.7 mm); integument with metallic reflections. Pronotum with large punctures, 0.5–0.8 × MOD, sublateral pronotal carina weak but present. Mesoscutum striate rugose, punctured like pronotum but with sparser larger punctures; notauli fully developed, converging posteriorly. Mesopleuron anteriorly with two longitudinal rows of large punctuations and posteriorly with sparse large punctures; episternal sulcus present; scrobal sulcus evident; V-shaped enclosure below scrobal sulcus evident. Metanotum with sparse, large foveae. Propodeal declivity with transverse row of foveae; propodeal teeth not visible.

Fore wing hyaline (length 6.2 mm), uniformly micropubescent. Veins C, Sc+R, M+Cu, A, Cu, 1Rs, 1M, cu-a, Rs+M and 2r-rs&Rs tubular; m-cu spectral, leaving [1M] cell widely open; 2r-rs&Rs evenly curved toward wing apex, fading about 1–2 MOD before reaching margin.

Metasoma longer than mesosoma (length 5.5 mm); T1 length 1.3 mm, T2 length 1.7 mm, T3 length 2.4 mm. T1 anteriorly with 3–4 transverse rows of punctures, punctures large, separated by less than 1 PD; posteriorly with a transverse row of subcontinuous punctures; rest of T1 covered with fine, dense punctures; T2 uniformly covered with fine punctures; T3 punctured like T2, pit row distinct; lateral margin with small angle antero-laterally, posterior margin evenly outcurved, without teeth, notch or angle.

Remarks. The holotype belongs to the genus *Primeuchroeus* due to the distinctive shape of the TFC (Kimsey and Bohart, 1991: fig. 136; Wei et al., 2014: fig. 30), the elongate T3 which is rounded and continuous with a small angle antero-laterally (Kimsey and Bohart, 1991: fig. 136; Wei et al., 2014: fig. 36), and the distinctive sculpture of T2 and T3 compared to T1 (Kim, 2013: figs 1–2; Wei et al., 2014: figs 1–2). The fossil mainly differs from extant species of *Primeuchroeus* by its fully developed and enlarged episternal sulcus, ventrally with large fovea, similar to relict mesopleural sulcus, and with enlarged V-shaped substanding area formed by omaulus and verticaulus. Some extant species have evident episternal sulcus (e.g., *Primeuchroeus kansitakuanus* (Tsuneki, 1970), see Wei et al., 2014: figs. 19–20) but none are known that present a scrobal sulcus, according to Bohart (1988) and Kimsey and Bohart (1991). Actually, some species of *Primeuchroeus* not examined by the latter authors have scrobal sulci [e.g. *Primeuchroeus adelaianus* (Linsenmaier, 1982) and *P. pentapromotus* (Linsenmaier, 1982)], both erroneously synonymised with *P. kriechbaumeri* (Gribodo, 1879), but none also present the V-shaped area that is expanded in a similar manner to other related genera such as *Spinolia* Dahlbom,

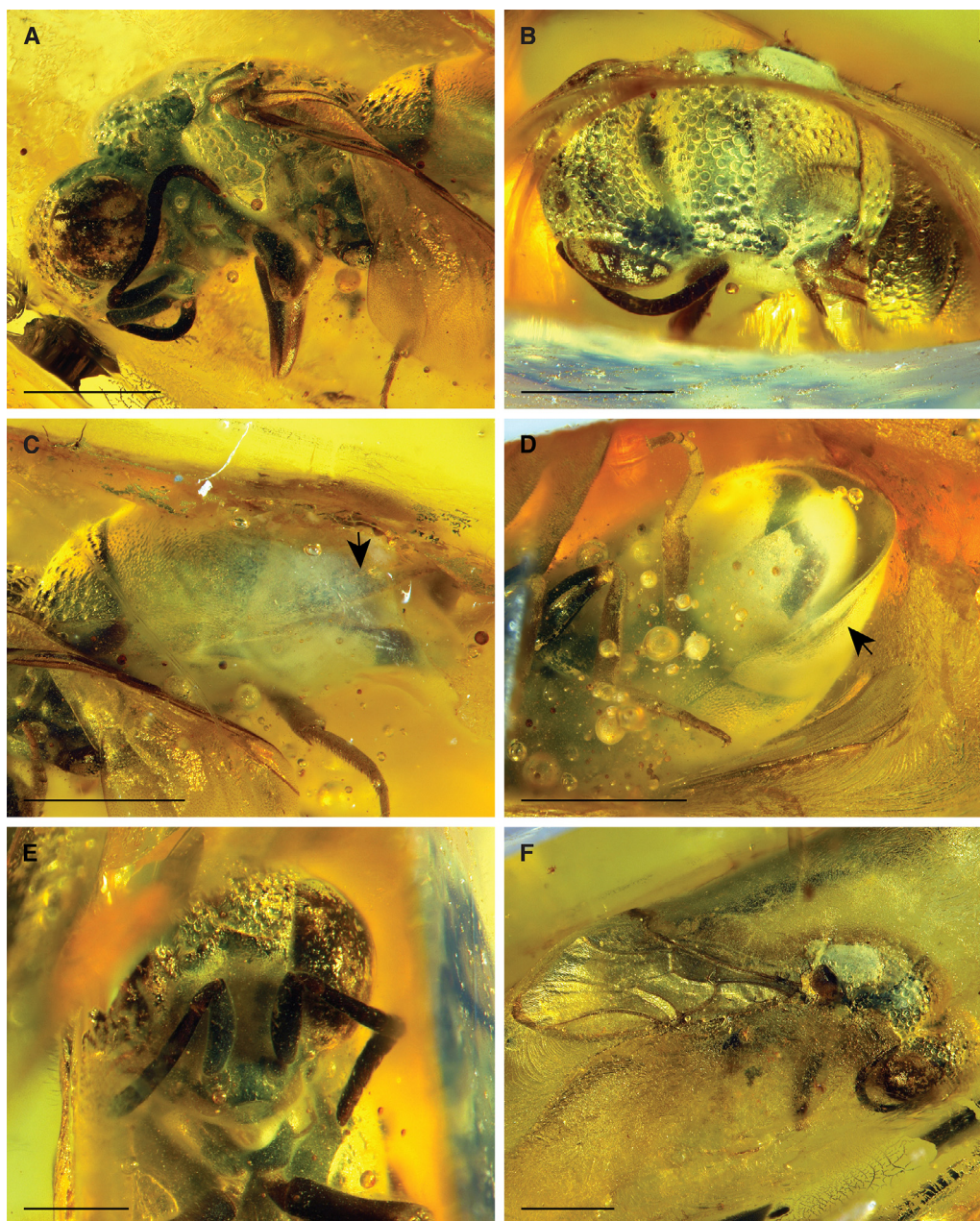


Fig. 2. *Primeuchroeus groehni* sp. nov., holotype GPIH 5201. A. Head, mesosoma and T1 in lateral view. B. Head, mesosoma and T1 in dorsal view. C. Metasoma in lateral view (black arrow pointing pit row). D. Metasoma in ventrolateral view (black arrow pointing pit row). E. Head in frontal view. F. Fore wing and part of head and mesosoma in lateral view. Scale bars: A–D, F=2 mm, E=1 mm.

Primeuchroeus groehni sp. nov., holotype GPIH 5201. A. Tête, mésosome et T1 en vue latérale. B. Tête, mésosome et T1 en vue dorsale. C. Métasome en vue latérale (flèche noire : rangée de fosses). D. Métasome en vue ventro-latérale (flèche noire : rangée de fosses). E. Tête en vue frontale. F. Aile antérieure et portion de la tête et du mésosome en vue latérale. Barres d'échelle : A–D, F=2 mm, E=1 mm.

1854 and *Pseudochrysis* Semenow, 1891 (P.R., pers. obs.).

Species transferred to Chrysidinae

Tribe **Elampini** Dahlbom, 1854

Genus ***Sphaerocleptes*** Cockx et al., 2016

Type species. *Sphaerocleptes neraudeaui* Cockx et al., 2016 by original designation.

Emended diagnosis. Head spherical; scapal basin depressed, medial line extending from clypeus to top of scapal basin; flagellomeres 2–10: $0.5 \times$ pedicel length; mandibles with three teeth; pronotum short, $0.4 \times$ length of mesoscutum; notaulus complete; scutellum $0.5 \times$ length of mesoscutum; fore wing with [1 M] and [1R1] cells widely opened; A vein present distad cu-a; 1 M evenly

outcurved; 2r-rs&Rs almost reaching anterior margin; R1 half-length of [2R1 cell]; Cu entirely tubular; probasitarsomere longer than combined length of protarsomeres 2–4; tarsal claws with one subsidiary tooth; metasoma with three tergites.

Remarks. Cockx et al. (2016) assigned *Sphaerocleptes* to the subfamily Cleptinae. Nevertheless, based on the morphological features of *Sphaerocleptes neraudeaui*, a re-assignment to the subfamily Chrysidinae, tribe Elampini is supported by the following characters: scapal basin present, pronotum very short and transverse, mesoscutum larger than pronotum, propodeum short and not elongate, and wing venation with long Rs vein.

The pronotum of Cretaceous Cleptinae was already bell-shaped (=campanulate) and their propodeum elongate, aligned to the



Fig. 3. *Sphaerocleptes neraudeaui* Cockx et al., 2016, holotype IGR.ARC-419.1. A. Line drawing of habitus in dorsal view. B. Habitus in dorsal view. Scale bars = 1 mm. *Sphaerocleptes neraudeaui* Cockx et al., 2016, holotype IGR.ARC-419.1. A. Dessin de l'habitus en vue dorsale. B. Habitus en vue dorsale. Barre d'échelle = 1 mm.

metanotum in lateral view (see *Procleptes* Evans, 1969 and *Hypocleptes* Evans, 1973; McKellar and Engel, 2014). Therefore, the mention 'Metanotum broad and projecting posteriorly over propodeum, with low dorsal convexity' (Cockx et al., 2016: 3) is not a diagnostic character for Cleptinae. Additionally, the ventrally convex metasoma described is also found in living Elampini (e.g., *Adelopyga* Kimsey, 1988) but could be a post-mortem modification. After re-examination of the specimen, we confirm the presence of three metasomal terga instead of four, as previously interpreted, which further support the attribution to the Chrysidinae. The metasoma, and the general habitus "globular" and "spherical" suggest that this species is a primitive member of the subfamily Chrysidinae and not Cleptinae, which have a typical slender habitus. We here transfer *Sphaerocleptes* to the subfamily Chrysidinae.

Sphaerocleptes neraudeaui Cockx et al., 2016
(Fig. 3)

Material. Holotype IGR.ARC-419.1 of unknown sex; housed in the amber collection of the Geology Department and Museum of the University of Rennes, France (IGR).

Type locality and horizon. Font de Benon quarry, near Archingeay, Charente-Maritime, southwestern France. Lithological sub-unit A2sm1-2.

Age. Late Cretaceous: earliest Cenomanian.

Diagnosis. As for genus.

Description. Body length 4.0 mm. Head largely spherical (length 0.7 mm, width 1.0 mm), hypognathous; integument sculpture hardly distinguishable, apparently rugose. Ocelli poorly preserved, apparently situated behind posterior margin of compound eye. Scapal basin present, depressed, with narrow median line extending from clypeus top of scapal basin. Scape elongate, 2.5 × longer than median width, subcylindrical; pedicel longer than flagellomeres; 11 flagellomeres, poorly visible because of orientation and clouding of amber, compact, half-length of pedicel; F11 slightly

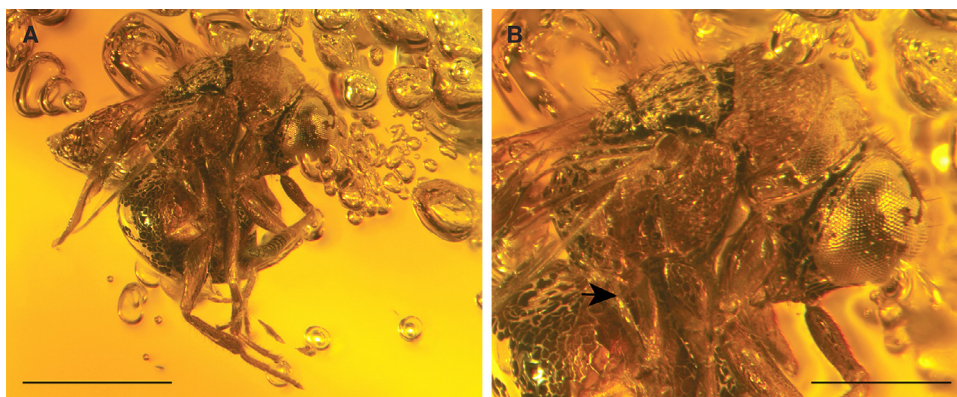


Fig. 4. *Atoposega rosai* (Brazidec and Perrichot, 2023) comb. nov., holotype NIGP 200741. A. Habitus in lateral view. B. Head, mesosoma and T1 in lateral view (black arrow pointing metacoxal dorso-basal carina). Scale bars: A = 1 mm, B = 0.5 mm.

Atoposega rosai (Brazidec et Perrichot, 2023) comb. nov., holotype NIGP 200741. A. Habitus en vue latérale. B. Tête, mésosome et T1 en vue latérale (flèche noire : carène métacoxale dorso-basale). Barres d'échelle : A = 1 mm, B = 0,5 mm.

longer than F10, apex rounded; antenna bearing short and sparse sensillae. Maxillary palpus with four visible articles; labial palpus with three visible articles. Mandibles short and thick, bearing three apical teeth. Occipital carina apparently faint.

Mesosoma shorter than metasoma (length 1.6 mm). Pronotum preserved as translucent surface, short (length 0.3 mm), gradually sloping anteriorly. Mesoscutum bulbous (length 0.7 mm), with strongly impressed notaulus throughout length. Scutellum with translucent preservation, about half-length of mesoscutum. Metanotum broad and projecting posteriorly over propodeum, with low dorsal convexity. Propodeum short, with rounded postero-lateral corners and steep posterior declivity. Legs bearing abundant setae; probasitarsomere longer than combined length of protarsomeres 2–4; one wide and curved protibial spur; two mesotibial spurs, one half-length of second; two metatibial spurs, one long and thick, second much shorter (about one-sixth length of first spur); tarsal claws bearing perpendicular medial tooth.

Fore wing hyaline (length 2.3 mm), uniformly micropubescent; C; Sc + R, M + Cu, A, 1 M, cu-a, Cu and Rs tubular; A extending distad cu-a; 1 M evenly outcurved; intersection of 1 M and 1Rs anterior (1 M much longer than 1Rs); 1Cu strongly curved toward posterior margin; 2Cu angled with respect to 1Cu, slightly curved and reaching apical margin; 2r-rs&Rs evenly curved, almost reaching anterior margin; R1 extending on half-length of [2R1] cell. Hind wing venation reduced to Sc + R.

Metasoma smooth (length 1.7 mm) and globular. Three tergites; T2 longest.

Species transferred to Amiseginae

Subfamily Amiseginae Mocsáry, 1889

Genus *Atoposega* Krombein, 1957

Atoposega rosai (Brazidec and Perrichot, 2023) comb. nov. *Hedychridium rosai* Brazidec and Perrichot, 2023: 702.

(Fig. 4)

Material. Holotype NIGP 200741, a complete female; housed in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China.

Type locality and horizon. Zhangpu County, Zhangzhou Prefecture, Fujian Province, China. Sedimentary layer II, Fotan Group.

Age. Middle Miocene: Langhian, 14.7 Ma.

Emended diagnosis. Pronotum, mesopleuron, metapleuron, legs, scape, pedicel, flagellomeres 1–3 and back of head metallic red; scapal basin, mesoscutum, mesoscutellum, metanotum, propodeum, metasoma and flagellomeres 4–11 black with metallic

reflections; vertex, frons, mesoscutum, scutellum and metanotum coarsely punctate; pronotal disc with larger punctuations. Scapal basin slightly depressed, deeply striate; F1 4.7 × P; compound eyes with sparse setae. Propodeum areolate; postero-lateral surface of propodeum without spine (Fig. 4B). Profemur ventrally carinate; metafemur enlarged dorsoventrally. Fore wing cu-a distad M. Metasoma smooth and impunctate.

Description. Body length 3.2 mm. Head as long as wide (length and width 0.7 mm), integument with metallic reflections. Vertex and frons coarsely punctate (punctuations ca. 0.7–1 × MOD). Vertex with a few long setae. Ocellar triangle isosceles, posterior ocelli separated by about 1.5 × MOD. Compound eye large, covering most of head length, bulging, with some sparse setae, inner ocular margin rather diverging downward. Scapal basin deep, wide, black with parallel golden striations extending from median longitudinal ridge to lateral margin of scapal basin. Distance between eye and scapal basin ca. 1.0 × MOD. Clypeus short and wide. OOL = ca. 1 × MOD; POL = 1.9 × MOD; MS = ca. 2 × MOD. Scape elongate, 3.6 × as long as median width; pedicel shorter than flagellomeres; 11 flagellomeres; relative length of P:F1:F2:F3 = 1:4.7:1.1:1.1; F1 4 × longer than median width; F1–3, reddish, lighter than F4–11, darker to blackish; antennal pubescence shorter than one third the length of the apical flagellomere.

Mesosoma shorter than metasoma (length 1.2 mm); black with pronotum, mesopleuron and metapleuron metallic red to golden. Dorsal area of pronotum punctate (punctures ca. 0.5 × MOD), box-like (length 0.3 mm), with long setae along lateral margins, divided by thin median sulcus; pronotal lateral lobe close to tegula, but not reaching it; pronotum anteriorly expanded, this apparent expansion two-thirds as long as rest of pronotum (length 0.2 mm). Mesoscutum longer than scutellum (length 0.3 mm), coarsely punctate (punctuation ca. 0.5–0.7 × MOD), notaulus complete and convergent posteriorly. Mesopleuron punctate, ventrally rounded, scrobal sulcus absent, omaulus indistinct but present. Scutellum punctate similarly to mesoscutum. Metanotum about 0.7 × scutellum length, with triangular medial enclosure. Propodeum as long as metanotum, dorsal surface of metapostnotum areolate; postero-lateral angle truncate. Legs bearing erect long setae; protibial spur long and curved; probasitarsomere basally curved; metacoxa elongate with dorso-basal carina; metafemur enlarged dorsoventrally; tarsal claws curved, with one small subsidiary tooth; arolium present.

Fore wing hyaline with preserved darkened patterns (length 1.3 mm), uniformly micropubescent; C, Sc + R, M + Cu, A, 1 M, cu-a and Rs tubular; cu-a slightly distad 1 M; Cu nebulous; Rs + M spectral; 2r-rs&Rs evenly curved toward wing margin, fading far

from wing margin, distal remnant indistinct; pterostigma poorly defined, shorter than M; R1 as long as pterostigma. Hind wing without visible venation.

Metasoma (length 1.3 mm) smooth and impunctate. Four external terga. T2 longest. Ovipositor exerted, curved and well-sclerotized (length 0.52 mm). Sternum convex.

Remarks. After re-examination of the type specimen, we re-evaluated the generic placement of *Hedychridium rosai*, originally included within the Chrysidinae by Brazidec and Perrichot (2023). The four metasomal terga as well as the structure of head and antennae preclude the assignment to this subfamily. The correct placement of this fossil in the Amiseginae is the only option based on morphological observations, further supported by the cross-ridged scapal basin, bicolored flagellum, pronotum with a median sulcus, and needle-like ovipositor. The unusual anterior shape of the pronotum, previously interpreted as an expansion of the pronotal collar is here interpreted as an artefact. Such structure is not known in any Chrysididae and, despite its apparent symmetry, it is most probably the result of an extrusion of an internal membrane during the effort of the insect to escape the resin or later during its desiccation.

Hedychridium rosai shows close affinities with the Indo-Malayan genus *Atoposega* Krombein, 1957 by displaying scapal basin wide and coarsely cross-ridged, eyes with sparse setae, eye encircled by carina; female flagellum fusiform, with short flagellomeres F2–F11, flattened on one surface; pronotum with posteromedial groove; notauli deep and fully developed, omaulus faint and scrobal sulcus absent, female wings fully developed, metanotum with triangular medial enclosure, cu-a vein distad 1 M, R1 present, 2r-rs&Rs short and fore wing membrane with dark patterns (Kimsey, 2014b). Other Amiseginae genera can be excluded as follows: females of *Afrosega* Krombein, 1983, *Alieniscus* Benoit, 1951, *Baeosega* Krombein, 1983, *Exopapua* Krombein, 1957, *Exova* Riek, 1955, *Leptosega* Krombein, 1984, *Mahinda* Krombein, 1983, *Microsega* Krombein, 1960, *Myrmecomimesis* Dalla Torre, 1987, *Obenbergerella* Strand, 1929, *Reidia* Krombein, 1957, *Saltasega* Krombein, 1983, *Serendibula* Krombein, 1980 are apterous or micropterous; *Adelphé* Mocsáry, 1890, *Amisega* Cameron, 1888, *Anachrysis* Krombein, 1986, *Duckeia* Costa Lima, 1936 and *Nesogyne* Krombein, 1957 have the metanotum less than 0.5 × scutellum length; *Bupon* Kimsey, 1986, *Cladobethylus* Kieffer, 1922, *Colocar* Krombein, 1957, *Indothrix* Krombein, 1957, *Isegama* Krombein, 1983 and *Kryptosega* Kimsey, 1986 lack the omaulus; *Magdaliium* Kimsey, 1986 and *Rohweria* Fouts, 1925 have the scrobal sulcus present; *Imasega* Krombein, 1983 lacks the dorso-basal metacoxal carina; *Perissosega* Krombein, 1983 has a frontal carina framing the scapal basin (Kimsey and Bohart, 1991). The two main differences between *H. rosai* and the extant *Atoposega* are the configuration of the distal remnant of 2r-rs&Rs which is not visible, where it should be spectral and abruptly bent towards the anterior wing margin, and the absence of the acute spine-like propodeal angle (Kimsey, 2014b: figs. 8–11). However, given that wing venation is not very informative for Chrysididae and that *Atoposega* is an obscure genus, we opt for a more conservative approach and attribute *H. rosai* to *Atoposega*, pending the discovery of additional material (fossil or living). Following this transfer, we propose the new combination *Atoposega rosai* (Brazidec and Perrichot, 2023) comb. nov.

4. Discussion

The Chrysididae fossil record is particularly unusual within the Hymenoptera. What is generally observed in families with similar or greater species richness is the emergence of modern generic lineages during the Paleogene (Grimaldi and Engel, 2005). The first temporal occurrence for many modern hymenopteran genera is

often recorded from upper Eocene Baltic amber, thanks to the richness of its deposits or earlier in smaller deposits (e.g., lower Eocene French and Chinese ambers; Azevedo et al., 2018; Colombo et al., 2021; Falières and Nel, 2018). This is observed for closely related groups (e.g., Bethyliidae: Colombo et al., 2021; Scolebythidae: Perkovsky and Rasnitsyn, 2013) or more distant ones (e.g., ants: Perkovsky, 2016; bees: Engel, 2001; Siricidae: Fidalgo and Smith, 1987; Diapriidae: Buhl, 2002). Early representatives can occur synchronously with extinct genera (e.g., Bethyliidae: Tribull et al., 2021; ants: Radchenko and Perkovsky, 2020; bees: Engel, 2001). Later, the proportion of extinct genera vs. extant tends to decrease throughout the Neogene (e.g., Bethyliidae: Barbosa and Melo, 2023; ants: Durán-Ruiz et al., 2013; bees: Engel et al., 2021). No extant genera of Chrysididae have to date been confirmed from deposits of Paleogene age. Three Eocene and Oligocene rock specimens have been attributed to the extant *Chrysis* Linnaeus, 1761 but this type of fossilization preserves far fewer morphological characters than amber, preventing a definitive identification of the fossils described by Förster (1891), Cockerell (1907) and Rowher (1909) that we cannot confidently place in any extant genus. In any case, the absence of modern genera in the early fossil records may be a bias due to under sampling or lack of identification of chrysidid specimens in collections. Nevertheless, Chrysididae are apparently not rare in upper Eocene ambers of Baltic and Ukraine (Martynova and Perkovsky, 2017; Martynova et al., 2019), in particular specimens of the extinct *Palaeobethylus* Brues, 1923 are rather abundant in collections (Martynova et al., 2019; M.B., pers. obs.). This supports the hypothesis of Lucena and Almeida (2021) that extant generic lineages have diverged and diversified only very recently, during the Neogene.

Primeuchroes groehni sp. nov. becomes the oldest Chrysididae indisputably attributed to an extant genus. *Primeuchroes* is currently absent from the Western Palaeartic (Kim, 2013), although it was probably more globally distributed during the Paleogene before regressing. Geographic regressions during the Cenozoic have been already observed in other groups (e.g., ants: Perkovsky, 2016; Bethyliidae: Ramos et al., 2014; Megalyridae: Poinar and Shaw, 2007), and even at a more important scale (e.g. *Eupsenella* Westwood, 1874, known from lower Eocene French amber and upper Eocene Rovno amber and now restricted to Australia and New Zealand; De Ploëg and Nel, 2004; Ramos et al., 2014; Ramos and Azevedo, 2012).

Extant species of *Atoposega* are known from southeastern Asia: Myanmar, Thailand, Malaysia, and the island of Borneo (Kimsey, 2014b). One additional species, *Atoposega decorata* Kimsey, 1995 has also been recorded in New Caledonia but probably belongs to a distinct genus (Kimsey, 2014b). Based on available data, the distribution of the genus does not extend northward to China, stopping at around 20°N. However, the specimen found in Zhangpu amber (24°N) was originally living in a tropical rainforest, whose vegetation was dominated by Dipterocarpaceae (Wang et al., 2021) during the Mid-Miocene Climatic Optimum (Kasbohm and Schoene, 2018), thus confirming the occurrence of this genus in a tropical or subtropical area. Megathermal rainforests of similar floral composition are today found in the lower latitudes of continental southeastern Asia, typically central Thailand, having regressed since the Miocene following the global cooling of the climate (Wang et al., 2021: fig. 1). Two modern species, *Atoposega striata* Kimsey, 2014b and *Atoposega rufithorax* Kimsey, 2014b, have been collected in this forest habitat (Kimsey, 2014b). *Atoposega rosai* is the second known chrysidid species from the Miocene period, after *Ceratochrysis dominicana* Engel, 2006, from Dominican amber, both belonging to extant genera. For this reason, we can infer that the chrysidid Miocene fauna was probably similar to the extant in terms of generic composition and biogeographical patterns as observed in

other Hymenoptera families (Brazidec and Perrichot, 2022; Engel and Aber, 2022; Perrichot et al., 2022).

The discovery of a new *Primeuchroeus* fossil species and the reevaluation of the genus *Sphaerocleptes* sheds new light on the timing of Chrysididae evolution. The presence of *Primeuchroeus* in the Baltic amber indicates that at least some modern generic lineages within Chrysidinae had already diverged by the upper Eocene. This is a new observation compared to what we previously knew from the scarce fossil record (e.g., Brues, 1933; Martynova and Perkovsky, 2017) and from what was retrieved based on a phylogenetical perspective (Lucena and Almeida, 2021: figs. 3–5). The inclusion of *Sphaerocleptes* in Elampini also pushes back the divergence ages found by Lucena and Almeida (2021). The latter inferred tip dating phylogenetic study suggested that the Elampini diverged from the rest of the Chrysidinae *stricto sensu* during the Upper Cretaceous (highest posterior density 95% interval for the age: 101–71 Ma; mean: 85 Ma). *Sphaerocleptes* was retrieved as *incertae sedis* within the Chrysididae, and outside of the Cleptinae. Therefore, inclusion of the genus within the Elampini implies that the divergence of the tribe from the [Parnopini + [Allocoeliini + Chrysidini]] clade occurred not later than the Lower Cretaceous. This discrepancy can be explained by the poor temporal calibration of the tribe, based on *Paleochrum diversum* Krombein, 1986 from upper Eocene, the only known elampine fossil.

5. Conclusions

Contrary to what was previously thought, the fossil record of Chrysididae has more parallels with that of other hymenopteran lineages. Two subfamilies were established during the Upper Cretaceous (Chrysidinae and Cleptinae), an extant genus is confirmed as occurring in the upper Eocene (*Primeuchroeus*), and two extant genera were present during the Miocene (*Ceratochrysis* and *Atoposega*). This is similar to what is known in closely related families such as Bethylinidae or Scolybythidae or more distant but diverse families such as Formicidae or Diapriidae. It is crucial to document additional fossil occurrences, even in some apparently well-studied deposit, as exemplified by the discovery of *Primeuchroeus groehni* sp. nov. in Baltic amber, in order to trace the evolution of the Chrysididae with greater certainty.

Disclosure of interest

The authors declare that they have no competing interest.

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