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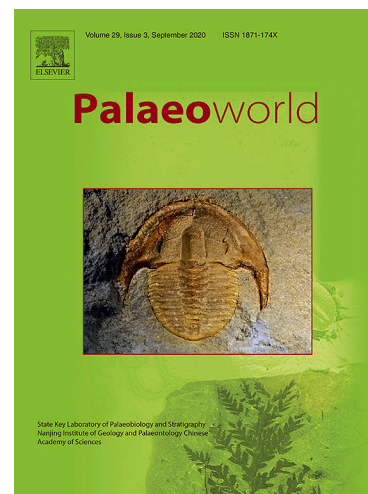
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## Two new chrysidoid wasps (Hymenoptera: Bethylidae, Chrysididae) from mid-Miocene Zhangpu amber

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### Abstract

The Miocene fossil record of Chryridoidea is particularly scarce despite numbers of insect-bearing deposits available. This record is here summarized, highlighting the overwhelming proportion of fossils from Dominican Republic amber while other deposits, e.g., Zhangpu, Mexican or Ethiopian ambers, seem promising for the study of the group but suffer from the lack of interest for this period. We describe and figure two new species from Zhangpu, China, a rich amber biota that formed in the Asian rainforest during the Mid-Miocene Climatic Optimum (MMCO): *Sierola colomboi* n. sp. (Bethylidae, the second from Zhangpu amber) and *Hedychridium rosai* n. sp. (Chrysididae). *Sierola* currently has a circum-pacific distribution with two fossils from European Eocene deposits. Four species have been recorded from China but *Sierola colomboi* n. sp. is the first fossil species from the country. *Hedychridium* is a cosmopolitan genus, the second largest within its family and *Hedychridium rosai* n. sp. represents its first known fossil species.

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## Abstract

The Miocene fossil record of Chrysidoidea is particularly scarce despite numbers of insect-bearing deposits available. Their record is here summarized, highlighting the overwhelming proportion of fossils from Dominican Republic amber while other deposits, e.g., Zhangpu, Mexican or Ethiopian ambers, seem promising for the study of the group but suffer from the insufficient interest in this period. We describe and figure two new species from Zhangpu, China, a rich amber biota that formed in the Asian rainforest during the Mid-Miocene Climatic Optimum (MMCO): *Sierola colomboi* n. sp. (Bethylidae, the second from Zhangpu amber) and *Hedychridium rosai* n. sp. (Chrysididae). *Sierola* currently has a circum-pacific distribution with two fossils from European Eocene deposits. Four species have been recorded from China but *Sierola colomboi* n. sp. is the first fossil species from the country. *Hedychridium* is a cosmopolitan genus, the second largest within its family and *Hedychridium rosai* n. sp. represents its first known fossil species.

**Keywords:** Chrysidoidea; Bethylinae; Chrysidinae; Cenozoic; Miocene; China

## 1. Introduction

The Chrysidoidea are the basalmost superfamily within stinging Hymenoptera (Aculeata). They are composed of six extant and two extinct families, their oldest representative dating back to the Lower Cretaceous (early Barremian) of the Isle of Wight, UK (Perkovsky et al., 2020a). Even with disparities between each family, Chrysidoidea are not infrequent in the fossil record, with about 270 formally named species (Martynova et al., 2019, and later summaries of Brazidec and Perrichot, in press for Bethylidae; Lucena and Almeida, 2021 for Chrysididae; Martynova et al., 2020 for Dryinidae; Perkovsky et al., 2020a for Embolemidae; Perkovsky et al., 2020b for Sclerogibbidae; Lepeco and Melo, 2022 for Scolebythidae; and Rasnitsyn and Brothers, 2020 for Plumalexiidae). The extant Bethylidae, Chrysididae and



Dryinidae are much more speciose than the rest of chrysidoid families and are more commonly encountered in the fossil record.

The Bethylidae, dubbed ‘flat wasps’, are the most diverse of all chrysidoid families, with 3000 species described (Azevedo et al., 2018). The bethylids for which biology is known are external parasitoids of lepidopteran and coleopteran larvae in cryptic habitats (Evans, 1964; Rubink and Evans, 1979). Nine subfamilies are recognized within the Bethylidae (Colombo et al., 2020), four of them being exclusively fossil.

The 2500 valid species of Chrysididae display a greater diversity in temperate desert but are distributed worldwide (Finnamore and Brothers, 1993). Chrysidids are sometimes referred to as ‘gold wasps’ because of the predominantly metallic coloration of the body, which makes them highly appreciated by collectors, or ‘cuckoo wasps’ because of the cleptoparasitic habits of some species (Kimsey and Bohart, 1991). The current consensus on the chrysidid taxonomy acknowledges four main subfamilies: the Cleptinae, parasitic on prepupal larvae of sawfly wasps; the Amiseginae and Loboscellidinae, which oviposit into previously nipped stick-insects (Phasmatodea) eggs; and the Chrysidinae, the true cuckoo wasps, specialized cleptoparasites attacking aculeate wasp nests (Kimsey and Bohart, 1991; Lucena and Almeida, 2021).

In this contribution, one new species of Bethylidae and another of Chrysididae are described from the recently-discovered amber deposit of Zhangpu, in Fujian Province, China, where paleobiota is for now largely unknown.

## 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, B. et al., 2021, fig. 1). Under- and overlying basalt layers allow constrained dating of the amber between  $14.8 \pm 0.6$  Ma and  $14.7 \pm 0.4$  Ma, which corresponds to the middle Miocene (Langhian; Zheng et al., 2019).

This study is based on two individuals in separate pieces 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 pieces were embedded in a block of epoxy resin (Araldite® 2020) for consolidation and posteriorly polished to facilitate the observation of the specimens, using thin silicon carbide papers on a grinder polisher (Buehler MetaServ 3000). The examination and photographs

were conducted with a Leica DMC4500 camera attached to a Leica M205C stereomicroscope or a Canon EOS 250D camera attached to a Leica M80 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 surface sculpturing follows the nomenclature of Harris (1979); bethylid and chrysidid morphological characters respectively follow the nomenclatures of Lanes et al. (2020) and Kimsey and Bohart (1991). Main measurements and indices used are as follows: the maximum length of fore wing from the apex of the axillary sclerite to the wing apex (LFW); the length of the head capsule excluding the mandibles, measured from posteriormost point of vertex to anteriormost point of clypeus (LH); the width of the head measured immediately behind the eyes in dorsal view (WH); the width of frons measured in dorsal view (WF); the maximum width of eye in lateral view (HE); ocello-ocular line, the minimum length from the posterior ocellus to the ocular margin (OOL); the maximum width of the ocellar triangle, measured in dorsal view (WOT); the maximum diameter of anterior ocellus (DAO); vertex-ocular line, the minimum length from the vertexal margin to posteriormost eye margin, measured in lateral view (VOL).

This published work and its new nomenclatural acts are registered in ZooBank with the following LSID (reference): [urn:lsid:zoobank.org:pub:BB079D89-C9FE-4F27-AF99-E94506E891E5](https://zoobank.org/pub:BB079D89-C9FE-4F27-AF99-E94506E891E5).

### 3. Systematic palaeontology

Superfamily Chrysoidea Latreille, 1802

Family Bethyloidea Haliday, 1839

Subfamily Bethyloinae Haliday, 1839

Genus *Sierola* Cameron, 1881

*Sierola colomboi* n. sp.

(Figs. 1, 2)

**LSID:** [urn:lsid:zoobank.org:act:2786F41D-6B8E-440D-A7EE-8CDBF3FECAE0](https://zoobank.org/act:2786F41D-6B8E-440D-A7EE-8CDBF3FECAE0).

**Etymology:** We dedicate this species to Dr. Wesley D. Colombo, specialist on living and fossil Bethyloidea. The specific epithet is to be treated as a noun in a genitive case.

**Material:** Holotype, NIGP200740, a complete male with some features hidden by small bubbles.

**Diagnosis:** Body stout (Fig. 2A); head globose; frons coriaceous with sparse long setae; median clypeal lobe obtuse triangular; mandibles large, ventral margin outcurved; posterior ocelli very close to occiput; dorsal pronotal area 2.3 times wider than long, transverse pronotal carina raised, humeral angles sharp; anteromesoscutum 0.78 length of dorsal pronotal area (Fig. 2B); fore wing uniformly micropubescent (Fig. 1); [C], [R], [1Cu], [1M] and [2R1] cells closed by tubular veins (Fig. 2D); meso- and metafemora thick (Fig. 2A, C).

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

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

**Description:** Body not especially flattened (length 1.90 mm). Head prognathous, globular, slightly longer than wide; LH: 0.42 mm, WH: 0.43 mm; WF: 0.26 mm; HE: 0.23 mm; OOL: 0.16 mm; WOT: 0.06 mm; DAO: 0.04 mm; VOL: ca. 0.12 mm; frons slightly convex, bearing sparse long setae, longer than flagellomere width; compound eyes almond-shaped, longer than high, glabrous; frons and vertex finely coriaceous; clypeus short with median lobe obtuse triangular, clypeal carina extending on frons for short distance; mandibles large, ventral margin outcurved, four short teeth along masticatory margin; antenna short, not extending beyond pronotum; scape 3.6 times longer than pedicel (length 0.18 mm); pedicel longer than flagellomere 1 (length 0.05 mm versus 0.03 mm); 11 flagellomeres hardly longer than wide, cylindrical; vertex crest rounded; ocellar triangle compact, posteriad on head, posterior ocelli distant from occiput by less than their diameter; occipital carina absent.

Mesosoma shorter than metasoma (length 0.66 mm), dorsum sparsely pubescent; dorsal pronotal area wider than long (length 0.14 mm; width 0.32 mm), transverse pronotal carina protruding, forming sharp humeral angles, posterior margin straight medially; anteromesoscutum 0.78 length of dorsal pronotal area; notauli absent; parapsidal signum present; mesopleuron not prominent, barely visible dorsally; mesoscutellum with posterior margin blunted, not contacting propodeum; metanotum reduced; dorsal area of metapectal-propodeal complex coriaceous, bordered by marginal carinae; median metapostnotal and metapostnotal-propodeal suture absent; propodeal declivity without carina. Fore wing hyaline and without particular patterns of micropubescent (LFW: 1.53 mm); C, Sc+R, M+Cu, A, Rs&M and cu-a tubular; Rs&M curved; Rs+M tubular; prestigma triangular; pterostigma rounded; 2r-rs&Rs contiguous, widely arched toward anterior wing margin distally and reaching it; [C], [R], [1Cu], [1M] (areolet) and [2R1] cells closed by tubular veins; [2R1] cell

wider distally than basally. Legs slightly pubescent; meso- and metafemora thick; tarsal claws angled.

Metasoma fusiform (length 0.82 mm), smooth.

Family Chrysididae Latreille, 1802

Subfamily Chrysidinae Latreille, 1802

Tribe Elampini Dahlbom, 1854

Genus *Hedychridium* Abeille de Perrin, 1878

*Hedychridium rosai* n. sp.

(Figs. 3–5)

**LSID:** urn:lsid:zoobank.org:act:9589AF1B-BE56-4DC3-B69E-FB7195148F65.

**Etymology:** We dedicate this species to Dr. Paolo Rosa, specialist on Chrysididae. The specific epithet is to be treated as a noun in a genitive case.

**Material:** Holotype, NIGP200741, a complete female.

**Diagnosis:** Body metallic gold except metallic black mesoscutum, mesoscutellum, metanotum, propodeum and flagellomeres 4–10 (Fig. 3); vertex and frons punctate; scapal basin flat, not depressed, with minute, continuous and parallel striations (Fig. 5B); scape 5.5 times longer than pedicel; first flagellomere 4 times longer than second flagellomere (Fig. 4B); compound eyes with sparse setae (Fig. 5A); pronotal collar distinct and two-thirds as long as rest of pronotum, swollen, foveolate; pronotum with median sulcus; propodeum areolate (Figs. 3, 4C, 5C); metafemur enlarged dorsoventrally (Fig. 4D); fore wing cu-a postfurcad M (Fig. 5D).

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

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

**Description:** Body length 3.20 mm; integument shining; body mostly metallic gold except mesoscutum, mesoscutellum, metanotum, propodeum and flagellomeres 4–10, black with metallic reflections.

Head as long as wide (length and width 0.64 mm), hypognathous; vertex and frons punctate; vertex with a few long setae, without median ridge; ocellar triangle compact, on top of head; scapal basin flat, not depressed, with minute, continuous and parallel striations; clypeus short and wide; scape elongate, 5.5 times longer than pedicel (length 0.33 mm); pedicel shorter than flagellomeres (length 0.06 mm); 11 flagellomeres; flagellomere 1

elongate, 4 times longer than following flagellomeres (length 0.28 mm versus 0.07 mm); antennae bearing numerous short sensilla, shorter than one third the length of the apical flagellomere; compound eye large, covering most of head length, bulging, with some sparse setae, inner ocular margin rather diverging downward; malar space shorter than one third of eye length, convergent.

Mesosoma shorter than metasoma (length 1.25 mm); pronotal collar swollen, easily distinguishable from pronotum, two-thirds as long as rest of pronotum (dorsal length 0.21 mm), minutely foveolate, posteriorly delimited by transverse groove; dorsal area of pronotum box-like, punctate with long setae along lateral margins, (length 0.32 mm), divided by thin median sulcus, lateral lobe nearly contacting tegula but not reaching it; mesoscutum punctate (length 0.33 mm), notauli present and deep; mesopleuron punctate, rounded, scrobal sulcus and omaulus indistinct; propodeum short, dorsal surface areolate. Legs bearing erect long setae; protibial spur long and curved; probasitarsomere basally curved; metacoxa elongate; metafemur enlarged dorsoventrally; tarsal claws curved, with one small subsidiary tooth; arolium present. Fore wing hyaline, uniformly micropubescent (length 1.31 mm); C, Sc+R, M+Cu, A, M, cu-a and Rs tubular; cu-a slightly postfurcad M; Cu nebulous; Rs+M spectral; Rs curved toward wing margin, tubular on half length of marginal cell; pterostigma poorly defined, shorter than M; R1 as long as pterostigma. Hind wing without visible venation; 4 hamuli.

Metasoma smooth (length 1.31 mm); three external segments visible; sternum concave; tergite 2 longest; tergite 3 without apical row or pits or posterior denticulate margin; ovipositor exerted, curved and well-sclerotized (length 0.52 mm).

#### 4. Discussion

The Bethyridae specimen can confidently be identified as a Bethylinae, given the presence of numerous features reminiscent of the subfamily: the clypeal carina extending on frons, the tarsal claws angled, the fore wing with Rs+M tubular and Rs&M angled. Following the key to the genera of Bethylinae by Azevedo et al. (2018), the specimen keys in *Sierola* Cameron, 1881 for the following characters: antennae with 11 flagellomeres, dorsal pronotal area regularly long, posterior margin outcurved medially, fore wing with five closed cells, metapectal-propodeal complex without metapostnotal-propodeal suture and mesopleuron not prominent, fore wing with [2R1] cell closed. The absence of notauli and median propodeal carina, the [1M] cell closed and the [2R1] cell 'triangular' (distalmost part of the cell wider than basalmost part) are additional diagnostic characters of *Sierola*, which strengthen the

attribution of the fossil to this genus. However, *Sierola colomboi* n. sp. also displays some unusual features for a Bethylinae. The anterior part of the dorsal pronotal area is bordered by a raised carina, known as the transverse pronotal carina, producing the anterior pronotal corners into sharp humeral angles. This configuration is similar to what is known in the epyrine genus *Anisepyris* Kieffer, 1905 in Kieffer and Marshall, 1904–1906 (Barbosa and Azevedo, 2018, fig. 1J, K) while *Sierola* usually has more rounded corners (Wang, C. et al., 2021, figs. 1D, 2F, 3F). The presence of the transverse pronotal carina is a novel pattern for *Sierola* although some species possesses more or less produced anterior pronotal corners. Nevertheless, it does not question the generic position of the fossil.

*Sierola* is the largest genus within its subfamily, with 249 species, but no less than 232 have been described from Hawaiian Islands (Fullaway, 1920; Azevedo et al., 2018; Magnacca, 2020). It has a circum-pacific distribution, with species recorded from Marques Islands, Fiji (Fullaway, 1920), California (Evans, 1978), Australia (Gordh, 1998), Thailand, India (Terayama, 2004) and Japan (Terayama, 2006). Gordh (1998) assumed that *Sierola* originates from continental Asia, before invading Hawaiian Islands, and rapidly radiated in a few million years while Magnacca (2020) proposed an Australian origin of the genus. Four species are known from China (Zhejiang Province and Macao, Wang, C. et al., 2021). Despite being apparently endemic of the circum-Pacific belt, two species have been described from the Upper Eocene Baltic and Rovno ambers: *Sierola hastata* Sorg, 1988 and *Sierola rovniana* Ramos and Azevedo in Ramos et al., 2014. This pattern of regression toward tropical latitudes of Australasia (maybe correlated to Cenozoic global climate cooling) is also found in the extant Australian *Eupsenella* Westwood, 1874 (Ramos and Azevedo, 2012; Ramos et al., 2014). *Sierola colomboi* n. sp. differs from the two other fossil species as follows: clypeus obtuse rather than angulate, notauli absent, [R], [1Cu] and [1M] cells formed by tubular veins rather than nebulous (*S. rovniana*; Ramos et al., 2014); [1M] cell pentagonal rather than hexagonal; distal segment of 2r-rs&Rs strongly angulate rather than gently bent toward anterior wing margin (*S. hastata*; Sorg, 1988).

*Sierola* species for which the biology is known mainly parasitize microlepidopteran caterpillars (e.g., Gelechiidae, Batrachedridae, Tortricidae, Gracillariidae, Magnacca, 2020 and references therein), which is considered to be the ground plan for the genus. Some species would also present unusual habits such as attacking insects in non-lepidopteran-induced galls (Ashmead, 1901; Santosh, 2017) or beetle larvae (Swezey, 1954; Magnacca, 2020) but these records are yet to be confirmed. The extant *Sierola mawarajo* Terayama, 2004 was reared in the tropical rainforest of the Khao Yai National Park (Thailand), where vegetation is



dominated by members of the Dipterocarpaceae (Smitinand, 1968). Today's southeast Asian dipterocarp forests are the closest extant relatives of the mid-Miocene Zhangpu amber forest in terms of floral assemblage and climate (Wang, B. et al., 2021, fig. 2). Furthermore, the lepidopteran families mentioned above occur widely in these environments (e.g., Ujiye et al., 1996; Park and Ponomarenko, 1999, 2004; Brown et al., 2019). Therefore, both for biogeographical and biological reasons, it is not surprising to discover *Sierola* in the Zhangpu biome, simultaneously with the megathermal climate of the Mid-Miocene Climatic Optimum that allowed the tropical forest to expand toward higher latitudes (Kasbohm and Schoene, 2018).

Following the key to the subfamilies of Chrysididae by Kimsey and Bohart (1991), the chrysidid specimen keys in the Chrysidinae for the gaster with three external segments, the sternum rather concave and the propodeum short dorsally. Chrysidinae are further divided in four tribes: the Allocoeliini, Parnopini, Chrysidini and Elampini. The specimen keys in the latter tribe due to the gaster with three terga, the body partly metallic, the tegula not covering both fore and hind wing bases and the tergite 3 without pit row. Following the key to the genera by Elampini of Kimsey and Bohart (1991), it keys in *Hedychridium* Abeille de Perrin, 1878 because of the following characters: hind tarsal claws with one tooth, scutellum anteriorly without tubercles, fore wing Rs more than half as long as M, face flat with at least a narrow zone of fine cross-ridging in scapal basin. *Hedychridium rosai* n. sp. is easily recognizable within the genus for the hypertrophied pronotal collar, which differs from the rest of the pronotum by its sculpture.

*Hedychridium* is the second largest genus of the Chrysididae and the largest within its tribe with more than 300 species described (Rosa et al., 2022). This genus occurs in all zoogeographic regions except the Australia, its diversity being highest in arid parts of the Holarctic and southern Africa (Kimsey and Bohart, 1991). Seven species are known in China, exclusively from the Palearctic part of the country: Xinjiang, Inner Mongolia, Gansu, Shanxi, Hebei and Heilongjiang regions (Rosa et al., 2014). Chrysididae are scarcer than Bethyridae or Dryinidae in the fossil record (Martynova et al., 2019), for current equivalent diversity. Thus, even if *Hedychridium* contains numerous species, *Hedychridium rosai* n. sp. is its first fossil species reported to date.

Little is known about the *Hedychridium* biology, the few records suggesting a parasitic behavior on ground-nesting bees and Sphecidae (e.g., Mocsáry, 1889). *Hedychridium monochroum* Buysson, 1888 is the only representative of the genus in southeast Asia, from Lamphun, North Thailand (Tsuneki, 1961), where the vegetation is partly composed of

dipterocarp forests (Maxwell et al., 1995). Additionally, this species has been reported to lay eggs into nests of Crabronidae (Martynova, 2017). It is not possible to evaluate the possible hosts for *Hedychridium rosai* n. sp., as no aculeate wasps other than Bethylidae, ants (Perrichot, in press) and stingless bees (Engel et al., 2021) have been described from this deposit. However, similar to *Sierola colomboi* n. sp., the presence of *Hedychridium* in the Zhangpu amber does not denote with what is known of the tropical palaeoenvironment.

The Miocene Chrysoidea are poorly known, possibly because of the increasing interest for Cretaceous material that has become much more accessible in the past few years. *Hedychridium rosai* n. sp. is only the second formally described Chrysididae from this period, after *Ceratochrysis dominica* Engel, 2006 and the second unambiguous fossil species belonging to an extant genus. A few non-amber fossils have been attributed to *Chrysis* Linnaeus, 1761 but without enough characters preserved to ensure their generic attribution (e.g., Förster, 1891; Rohwer, 1909). The Bethylidae are more common, with eight species previously named, *Sierola colomboi* n. sp. being the ninth one. Thanks to the work of Olmi (1989, 1995, 2005a), the Dryinidae received more consideration, with 17 species reported in amber. Finally, the less diverse Sclerogibbidae and Scolebythidae are both known by two species while only two indetermined Embolemidae are mentioned in the literature (Table 1). However, the vast majority of the chrysidoid wasps from this period have been described from Dominican Republic. This is not surprising, considering that Dominican amber has drawn attention for at least six decades (Sanderson and Farr, 1960) but it is much less than in Burmese amber, where renewed interest is more recent (e.g., Olmi et al., 2014; Melo and Lucena, 2019; Martynova et al., 2020). Several fossiliferous sites worldwide, notably Zhangpu, Mexican, Ethiopian or New Zealand ambers, could enrich the knowledge on Miocene Chrysoidea (Solórzano Kraemer et al., 2015; Schmidt et al., 2018; Bouju and Perrichot, 2020; Wang, B. et al., 2021). With more than 25000 inclusions identified in Zhangpu amber, this deposit is very likely to reveal some additional chrysidoid wasps in the upcoming years.

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### Figure captions

Fig. 1. *Sierola colomboi* n. sp., holotype, male, NIGP200740, habitus in dorsal view. Scale bar = 0.5 mm.

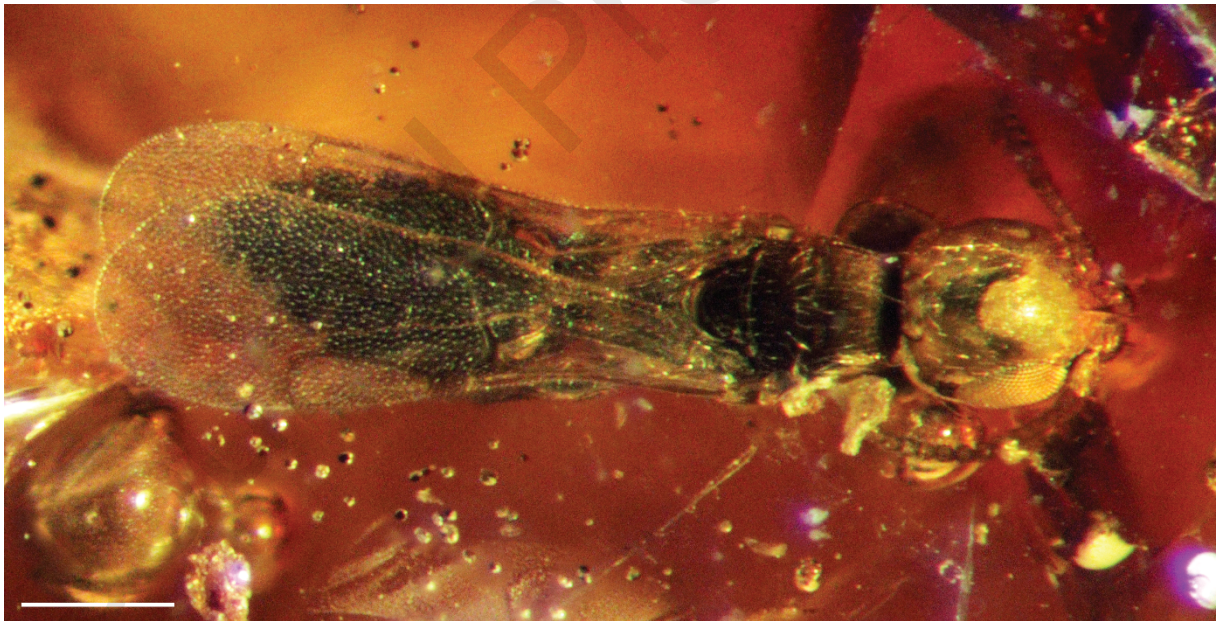


Fig. 2. *Sierola colomboi* n. sp., holotype, male, NIGP200740. (A) Habitus in lateral view. (B) Head and mesosoma in dorsal view. (C) Propodeum in laterodorsal view. (D) Line drawing of fore wing. Scale bar: 0.5 mm for (A, D); 0.25 mm for (B, C).

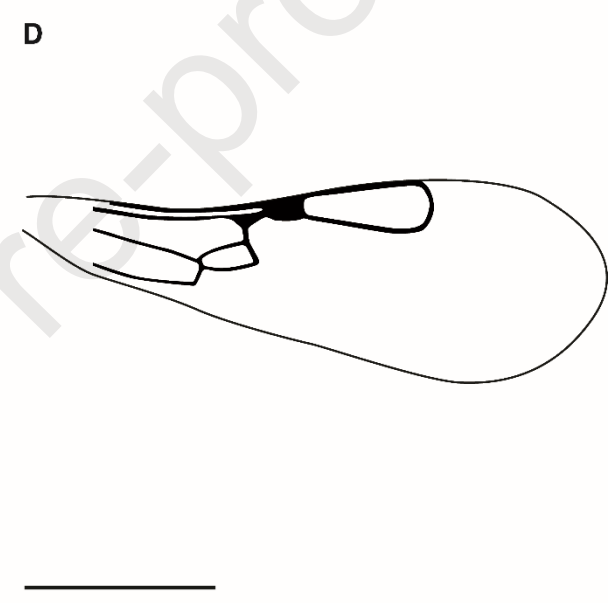
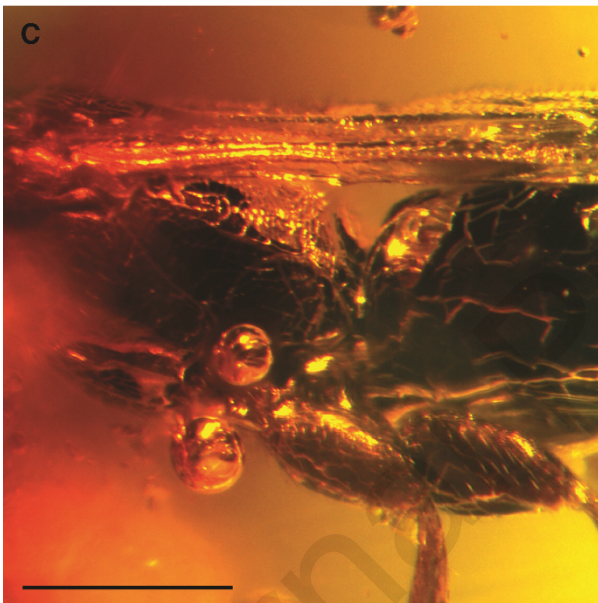
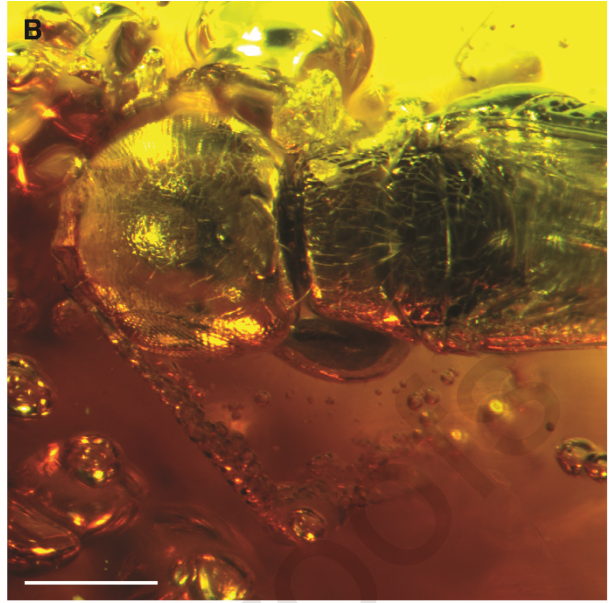
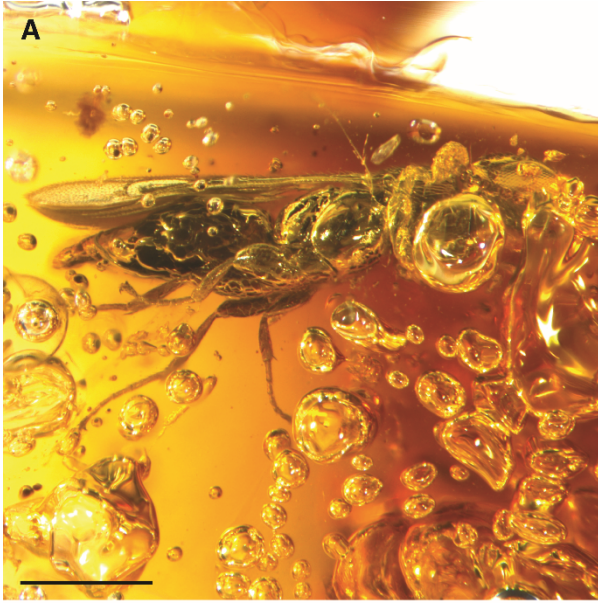
Fig. 3. *Hedychridium rosai* n. sp., holotype, female, NIGP200741, habitus in right lateral view. Scale bar = 1 mm.

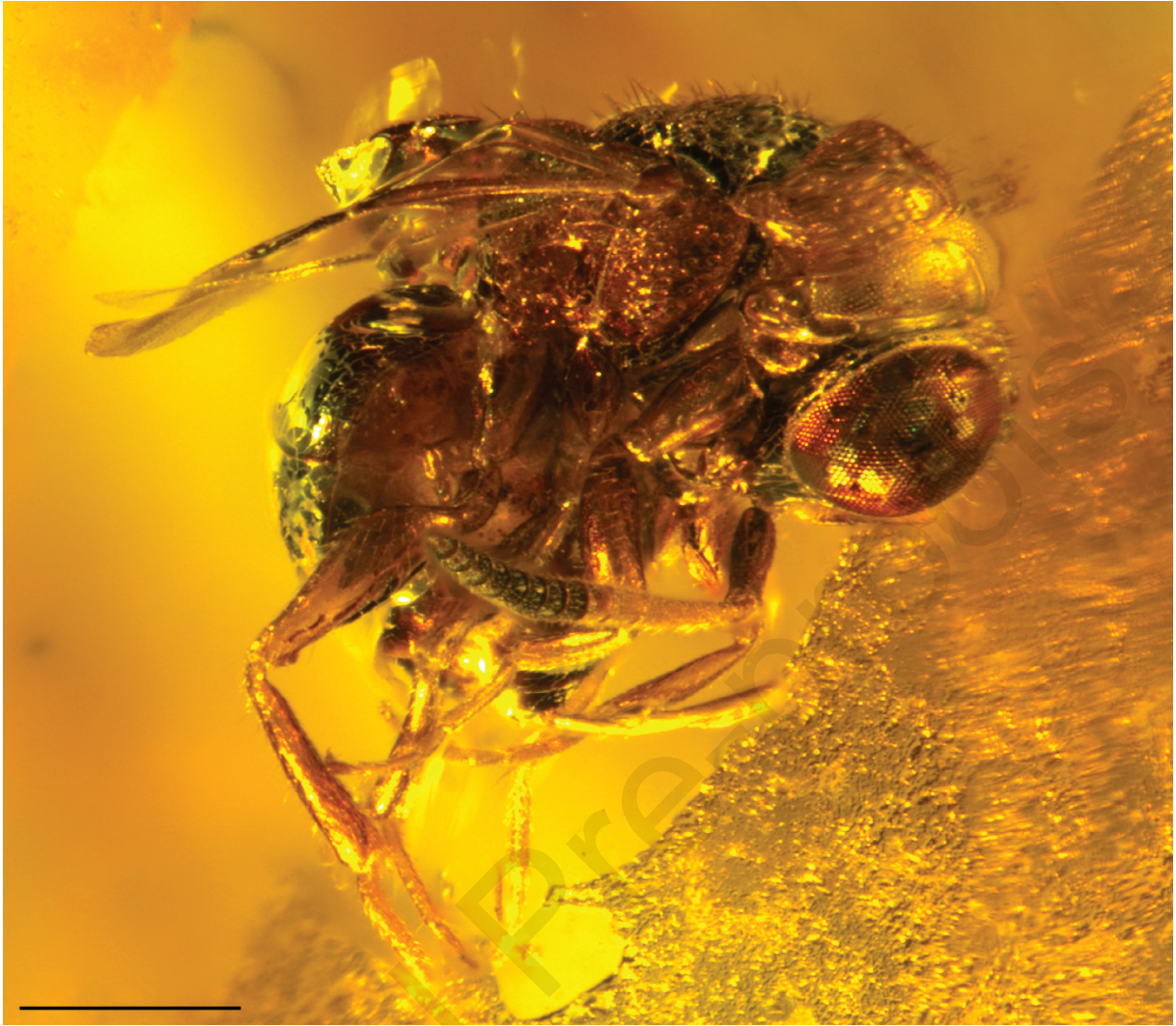
Fig. 4. *Hedychridium rosai* n. sp., holotype, female, NIGP200741. (A) Habitus in left lateral view. (B) Habitus in ventral view. (C) Habitus (centred on mesosoma) in dorsal view. (D) Habitus (centered on anterior metasoma) in dorsal view. Scale bar = 1 mm.

Fig. 5. *Hedychridium rosai* n. sp., holotype, female, NIGP200741. (A) Head and mesosoma in left lateral view. (B) Head in frontal view. (C) Mesosoma in dorsal view (white arrows: hamuli). (D) Line drawing of fore wing. Scale bar = 0.5 mm.



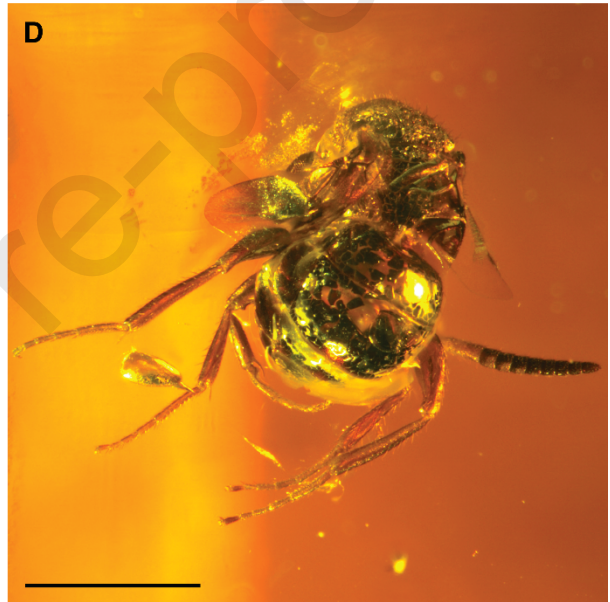
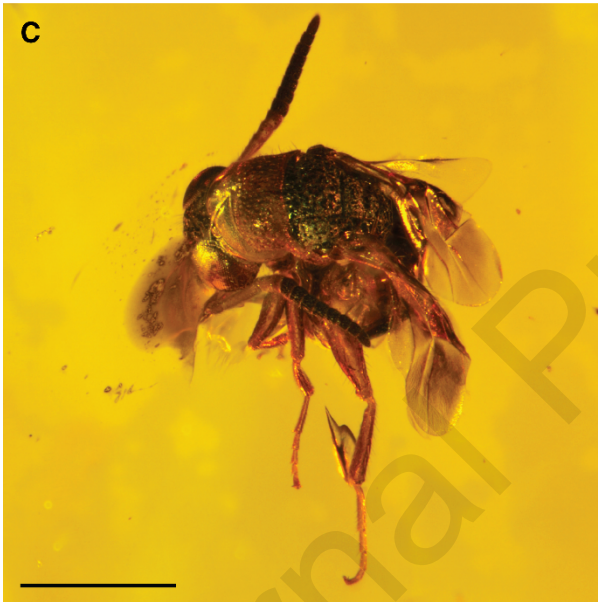
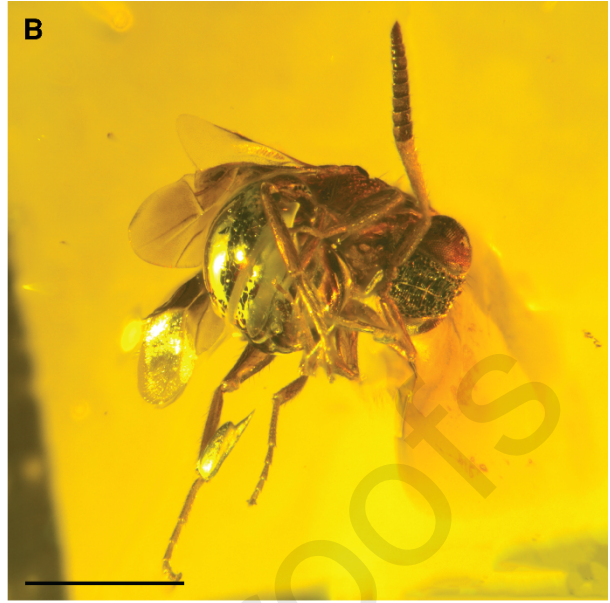






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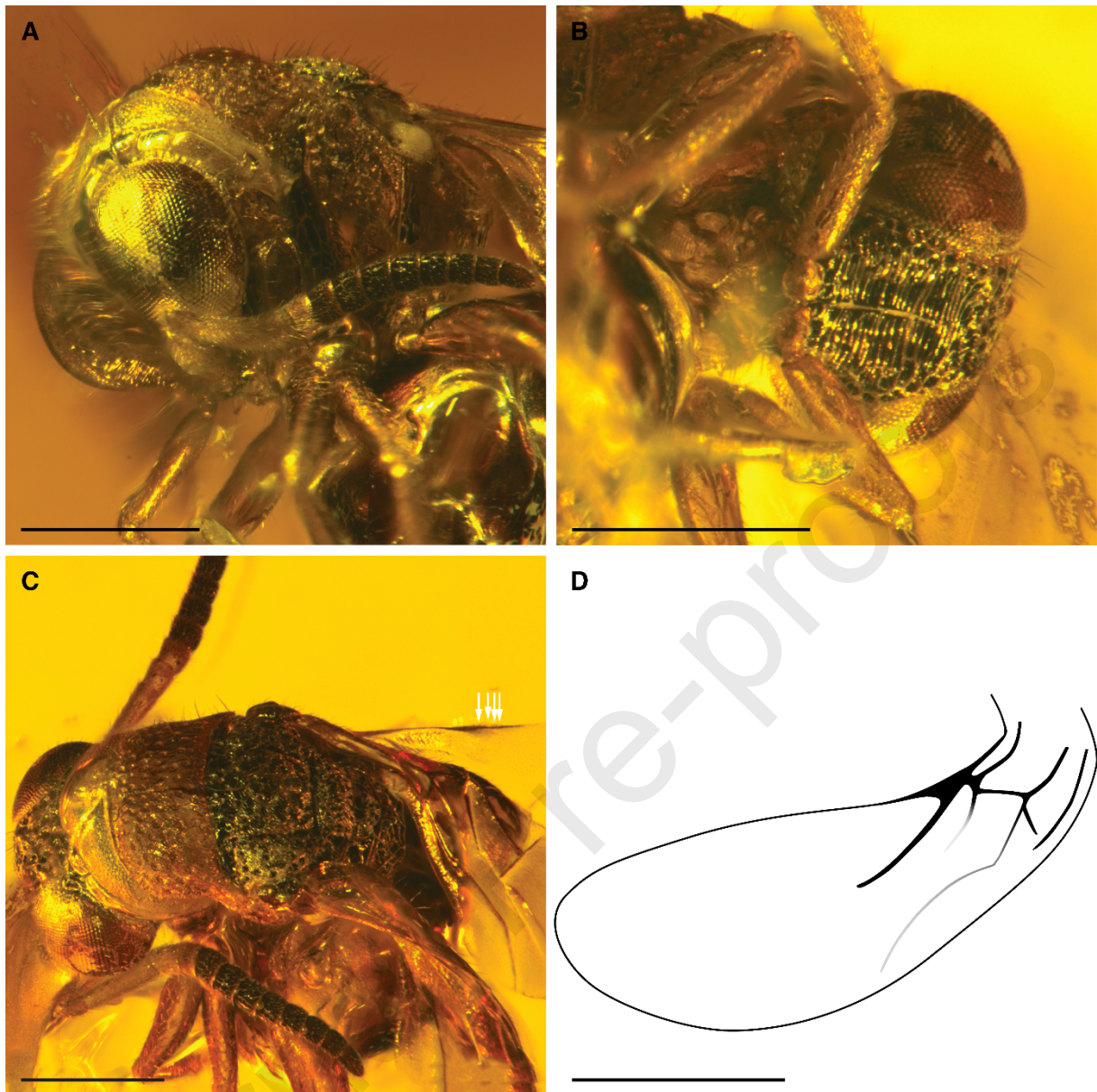


Table 1. Summary of the Miocene record of Chrysidoidea.

Taxon	Deposit	Reference
<b>Bethylidae</b>		
<i>Apenesia miki</i> (Terayama, 2004)	Dominican Republic amber	Terayama, 2004
<i>Alongatepyris pedrocai</i> Colombo and Azevedo, 2022	Dominican Republic amber	Colombo et al., 2022
<i>Anisepyris gradatus</i> Sorg, 1988	Dominican Republic amber	Sorg, 1988
<i>Goniozus respectus</i> Sorg, 1988	Dominican Republic amber	Sorg, 1988
<i>Bakeriella nanyhelae</i> Brazidec and Perrichot, 2022	Mexican amber	Brazidec and Perrichot, 2022
<i>Goniozus cotyi</i> Brazidec and Perrichot, 2022	Mexican amber	Brazidec and Perrichot, 2022

<i>Solepyris electromexicanus</i> Brazidec and Perrichot, 2022	Mexican amber	Brazidec and Perrichot, 2022
<i>Goniozus</i> sp.	Rubielos de Mora, Spain	Peñalver-Mollá, 1998
<i>Parascleroderma palaeosinica</i> Brazidec and Perrichot	Zhangpu amber, China	Brazidec and Perrichot, in press
<i>Sierola colomboi</i> n. sp.	Zhangpu amber, China	This paper
<b>Chrysididae</b>		
<i>Ceratochrysis dominica</i> Engel, 2006	Dominican Republic amber	Engel, 2006
Chrysididae indet.	Tállya, Hungary	Sziráki and Dulai, 2002
<i>Hedychridium rosai</i> n. sp.	Zhangpu amber, China	This paper
<b>Dryinidae</b>		
<i>Aphelopus poinari</i> Olmi, 1998	Dominican Republic amber	Olmi, 1998
<i>Bocchus vetustus</i> Olmi, 1989	Dominican Republic amber	Olmi, 1989
<i>Dryinus alamellatus</i> Olmi and Guglielmino, 2011	Dominican Republic amber	Olmi and Guglielmino, 2011
<i>Dryinus grimaldii</i> Olmi, 1995	Dominican Republic amber	Olmi, 1995
<i>Dryinus hymenaeophilus</i> Olmi, 1995	Dominican Republic amber	Olmi, 1995
<i>Dryinus palaeodominicanus</i> Currado and Olmi, 1983	Dominican Republic amber	Currado and Olmi, 1983
<i>Dryinus poinari</i> Olmi, 1998	Dominican Republic amber	Olmi, 1998
<i>Dryinus priscus</i> Olmi, 1998	Dominican Republic amber	Olmi, 1998
<i>Dryinus pristinus</i> Olmi, 1998	Dominican Republic amber	Olmi, 1998
<i>Dryinus rasnitsyni</i> Olmi and Guglielmino, 2011	Dominican Republic amber	Olmi and Guglielmino, 2011
<i>Dryinus vetustus</i> Olmi, 1995	Dominican Republic amber	Olmi, 1995
<i>Harpactospecion scheveni</i> Olmi, 2005	Dominican Republic amber	Olmi, 2005a
<i>Harpactospecion sucinum</i> (Olmi, 1987)	Dominican Republic amber	Olmi, 1987
<i>Thaumatodryinus fuscescens</i> Martins and Melo, 2020	Dominican Republic amber	Martins and Melo, 2020
<i>Thaumatodryinus miocenicus</i> Olmi, 1995	Dominican Republic amber	Olmi, 1995
<i>Thaumatodryinus priscus</i> (Olmi, 1998)	Dominican Republic amber	Olmi, 1998
<i>Dryinus palaeomexicanus</i> Olmi, 1995	Mexican amber	Olmi, 1995
<b>Embolemidae</b>		
Embolemidae indet.	Dominican Republic amber	Rasnitsyn, 1996
<b>Sclerogibbidae</b>		
<i>Probethylus poinari</i> Olmi, 2005	Dominican Republic amber	Olmi, 2005b



<i>Pterosclerogibba antiqua</i> Olmi, 2005	Dominican Republic amber	Olmi, 2005b
<b>Scolebythidae</b>		
<i>Clytopsenella mirabilis</i> Engel, 2015	Dominican Republic amber	Engel, 2015
<i>Pristapenesia inopinata</i> (Prentice and Poinar, 1996)	Dominican Republic amber	Prentice et al., 1996