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A new epyrine wasp (Hymenoptera: Bethylidae) from the late Eocene of Europe

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Abstract. The aculeate family Bethylidae is represented in Baltic amber by about 40 species. We here describe and figure a new species in the subfamily Epyrinae from this late Eocene deposit: †*Gracilepyris carsteni* sp. nov., based on a complete male specimen. This is the first fossil species of *Gracilepyris* Colombo, Tribull & Azevedo, 2022, a recently discovered genus, comprising five extant species from the northern Neotropical, Nearctic, and Palaearctic regions. *Gracilepyris* is characteristic of the *Epyris* complex, a group of genera possessing individualized foveae at the mesoscuto-mesoscutellar suture. The finding of †*Gracilepyris carsteni* sp. nov. in Baltic amber is consistent with the estimated Late Cretaceous–Paleogene radiation of this derived group. Finally, we revive the name *Risepyris dubius* (Kieffer, 1904) for an extant European bethylid species which was unnecessarily renamed *Holepyris neodubius* Azevedo, 2018; we also propose the new name †*Risepyris bruesi* Brazidec nom. nov. for the Eocene fossil †*Risepyris dubius* (Brues, 1933), which was objectively invalid as a junior homonym.

Keywords. Insecta, Chrysidoidea, Priabonian, Baltic amber, taxonomy.

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Introduction

The Bethylidae Haliday, 1839 are a cosmopolitan and highly speciose family of Chrysidoidea Latreille, 1802, comprising more than 3300 species (Colombo & Azevedo 2023; Santos *et al.* 2024). Bethylid wasps are generally small-sized insects, rarely exceeding one centimetre in length, and are typically brown to dark brown in coloration. They are characterized by a pronounced prognathism, a reduced fore wing venation, the metapostnotum extending into the propodeum, and often, though not invariably, a flattened body, hence their common name “flat wasps” (Azevedo *et al*. 2018; Lanes *et al*. 2020). The majority of Bethylidae are endoparasitoids of xylophagous coleopteran larvae, pupae, and adults (e.g., Batchelor *et al*. 2006; Amante *et al*. 2018; Azevedo *et al*. 2018; Honsberger *et al*. 2024), whereas members of the Bethylinae Haliday, 1839 and some Epyrinae Kieffer, 1914 instead parasitize lepidopteran larvae (e.g., Azevedo *et al*. 2018; Polaszek *et al*. 2019; Staude *et al*. 2020). Several species are of economic importance, such as *Goniozus legneri* Gordh, 1982, which has been employed as a biological control agent against the lower navel orangeworm (Lepidoptera) (van Lenteren 2011; Brock *et al*. 2021).

The fossil record of the Bethylidae extends back to the Early Cretaceous, and representatives of the family have been recovered from most major Cretaceous and Cenozoic amber deposits worldwide (e.g., Azevedo & Azar 2012; Martynova *et al*. 2019; Colombo *et al*. 2021a; Brazidec & Perrichot 2022a, 2023). To date, more than 100 fossil species have been described, providing valuable insights into the co-occurrence of extinct and extant subfamilies during the Cretaceous (e.g., Ortega-Blanco & Engel 2013; Engel 2019; Colombo *et al*. 2021b; Jouault *et al*. 2026), the emergence of modern genera throughout the Cenozoic (e.g., Barbosa *et al*. 2013; Colombo *et al*. 2021a; Barbosa & Melo 2023; Brues 1923), and the progressive geographic regression of tropical lineages since the Eocene (Ramos *et al*. 2014; Brazidec & Perrichot 2022b). Nevertheless, the fossil record of the family is markedly uneven, with two pronounced peaks in species richness during the Cenomanian and the late Eocene, which together account for approximately 70% of all described fossil Bethylidae. These peaks largely reflect the exceptional diversity and preservation quality of the Myanmar and Baltic amber deposits, respectively (e.g., Martynova *et al*. 2019). Baltic amber, in particular, has been known since the 18th century (Sendel 1742) and has yielded more than 3000 described species (Penney & Jepson 2014). Hymenoptera Linnaeus, 1758 constitute roughly 10% of the arthropod inclusions in this deposit (Perkovsky *et al*. 2007), with some extensively studied groups such as bees (Engel 2001) and ants (Dlussky & Rasnitsyn 2009).

The Baltic amber Bethylidae have also received particular attention, especially during the first half of the 20th century (Brues 1923, 1933) and since 2010 (Ramos *et al*. 2014; Colombo *et al*. 2021a, 2021b). As of today, approximately 40 fossil bethylid species have been described from this deposit (Table 1). At the subfamilial level, the Bethylinae and Epyrinae are the most diverse, with 13 and 17 species, respectively. In contrast, the Pristocerinae Mocsáry, 1881 are represented by only a few species, despite being the most speciose subfamily in the extant fauna (Azevedo *et al*. 2018). Similarly, the Scleroderminae Kieffer, 1914, Glenoseminae Azevedo & Colombo, 2024, and the extinct †Protopristocerinae Nagy, 1974 are only sparsely represented, the latter being the sole extinct bethylid subfamily known from Baltic amber. Most Baltic amber species are assigned to genera that persist in the extant fauna (e.g., Brues 1933; Ramos *et al*. 2014; Colombo *et al*. 2021a), although a small number belong to extinct genera restricted to this deposit, within the Pristocerinae, Scleroderminae, and †Protopristocerinae (e.g., Brues 1923; Colombo & Azevedo 2021; Tribull *et al*. 2021).

In this contribution, we describe a new species of Bethylidae from the late Eocene Baltic amber, assigned to the Epyrinae subfamily, representing the first record of the genus *Gracilepyris* Colombo, Tribull & Azevedo, 2022 in Baltic amber.

Material and methods

The main Baltic amber-bearing layer is the Upper Blue Earth Member of the Prussian Formation which occurs throughout northern Europe just under the sea-level around the Baltic shore (Weistchat & Wichard 2010: fig. 1). Palynological data indicate a Priabonian age (Late Eocene) for this member, (ca 34–38 Ma; Aleksandrova & Zaprozhets 2008; Iakovleva *et al*. 2022; Iakovleva 2023). An older Lutetian age (44.1 ± 1.1 Ma: Ritzkowski 1997) has also been proposed but this was likely an overestimate (Clauer

Table 1 (continued on next page). Synopsis of species of Bethylidae Haliday, 1840 discovered in Eocene Baltic amber.

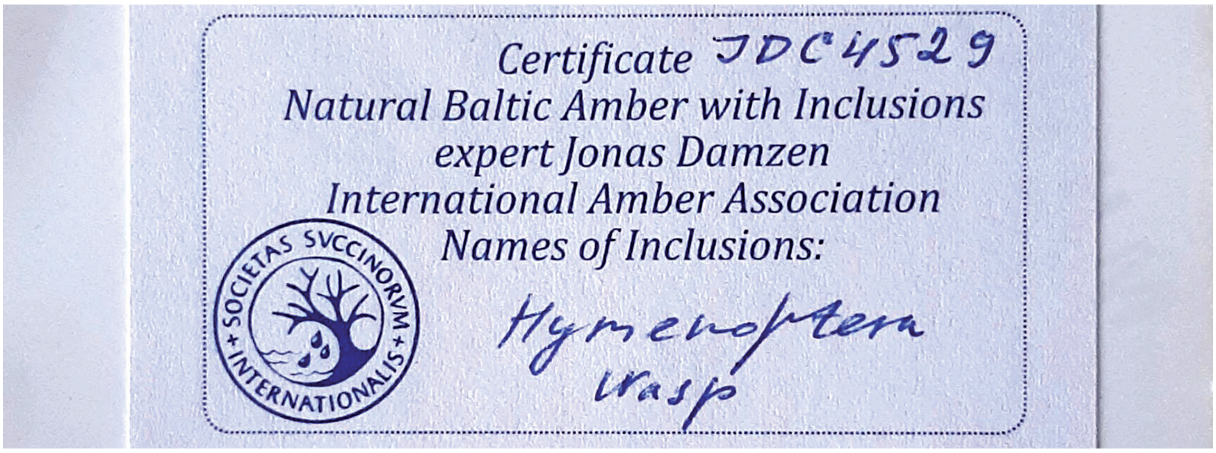
Subfamily	Species	Reference
Bethylinae	†*Eupsenella aulax* Ramos & Azevedo, 2014	Ramos *et al*. (2014)
Bethylinae	†*Eupsenella rossica* Ramos & Azevedo, 2014	Ramos *et al*. (2014)
Bethylinae	†*Eupsenella yantarnica* Ramos & Azevedo, 2014	Ramos *et al*. (2014)
Bethylinae	†*Goniozus contractus* (Brues, 1933)	Brues (1933)
Bethylinae	†*Goniozus definitus* Ramos & Azevedo, 2014	Ramos *et al*. (2014)
Bethylinae	†*Lytopsenella baltica* Ramos & Azevedo, 2014	Ramos *et al*. (2014)
Bethylinae	†*Lytopsenella crastina* Brues, 1923	Brues (1923)
Bethylinae	†*Lytopsenella kerneggeri* Ohl, 1995	Ohl (1995)
Bethylinae	†*Lytopsenella maritima* Ramos & Azevedo, 2014	Ramos *et al*. (2014)
Bethylinae	†*Lytopsenella setigera* Brues, (1933)	Brues (1923)
Bethylinae	†*Lytopsenella simplex* Brues, (1933)	Brues (1923)
Bethylinae	†*Prosierola submersa* Brues, (1933)	Brues (1923)
Bethylinae	†*Sierola hastata* Sorg, 1988	Sorg (1988)
Epyrinae	†*Chlorepyris concaptus* (Brues, 1933)	Brues (1933) Colombo *et al*. (2021a)
Epyrinae	†*Chlorepyris engeli* Colombo & Azevedo, 2021	Colombo *et al*. (2021a)
Epyrinae	†*Chlorepyris hopei* Colombo & Azevedo, 2021	Colombo *et al*. (2021a)
Epyrinae	†*Chlorepyris invelatus* (Brues, 1933)	Brues (1933) Colombo *et al*. (2021a)
Epyrinae	†*Chlorepyris meunieri* Colombo & Azevedo, 2021	Colombo *et al*. (2021a)
Epyrinae	†*Chlorepyris neli* Colombo & Azevedo, 2021	Colombo *et al*. (2021a)
Epyrinae	†*Chlorepyris perrichoti* Colombo & Azevedo, 2021	Colombo *et al*. (2021a)
Epyrinae	†*Chlorepyris setosus* (Brues, 1933)	Brues (1933) Colombo *et al*. (2021a)
Epyrinae	†*Epyris kiefferi* Brues, 1910	Brues (1910); Colombo *et al*. (2021a)
Epyrinae	†*Gloxinius bifossatus* (Brues, 1939)	Brues (1939) Colombo *et al*. (2021a)
Epyrinae	†*Gracilepyris carsteni* sp. nov.	This study
Epyrinae	†*Laelius pallidus* Brues, 1933	Brues (1933); Colombo *et al*. (2021a)
Epyrinae	†*Rysepyris bruesi* nom. nov.	Brues (1933); Colombo *et al*. (2021a, 2022); this study
Epyrinae	†*Rysepyris minor* (Brues, 1939)	Brues (1939); Colombo *et al*. (2021a, 2022)
Epyrinae	†*Rysepyris planiceps* (Brues, 1933)	Brues (1933); Colombo *et al*. (2021a, 2022)
Epyrinae	†*Rysepyris precursor* (Brues, 1933)	Brues (1933); Colombo *et al*. (2021a, 2022)
Epyrinae	†*Rysepyris rasnitsyni* Colombo & Azevedo, 2021	Colombo *et al*. (2021a, 2022)
Epyrinae	†*Rysepyris robustus* (Brues, 1933)	Brues (1933); Colombo *et al*. (2021a; 2022)

Table 1 (continued).

Subfamily	Species	Reference
Glenoseminae	†*Glenosema electrum* Colombo & Azevedo, 2021	Colombo & Azevedo (2021)
Pristocerinae	†*Archeonesia eocena* Tribull, Pankowski & Colombo, 2021	Tribull *et al*. (2021)
Pristocerinae	†*Cleistepyris baryonyx* Colombo, Gobbi & Azevedo, 2021	Colombo *et al*. (2021b)
Pristocerinae	†*Pristocera skwarrae* (Brues, 1933)	Brues (1933); Colombo *et al*. (2021b)
Pristocerinae	†*Pseudisobrachium elatus* (Brues, 1933)	Brues (1933); Colombo *et al*. (2021a)
Pristocerinae	†*Pseudisobrachium inhabilis* (Brues, 1923)	Brues (1923); Colombo *et al*. (2021a)
†Protopristocerinae	†*Bethylopteron ambiguum* Brues, 1933	Brues (1933)
†Protopristocerinae	†*Protopristocera succini* Brues, 1923	Brues (1923)
Scleroderminae	†*Allobethylus bei* Colombo & Azevedo, 2021	Colombo & Azevedo (2021)
Scleroderminae	†*Archaeonoxus scintillatus* Colombo & Azevedo, 2021	Colombo & Azevedo (2021)
Scleroderminae	†*Mael longiceps* (Brues, 1923)	Brues (1923); Colombo *et al*. (2021a)
Scleroderminae	†*Nothepyris pretiosus* Colombo & Azevedo, 2021	Colombo & Azevedo (2021)
Scleroderminae	†*Plastanoxus atrescens* Colombo & Azevedo, 2021	Colombo & Azevedo (2021)

et al. 2005). Small amounts of amber occasionally occur in older lower layers (Weistchat & Wichard 2010; Iakovleva 2023) as well as in Oligocene sediments; the latter may be redeposited Eocene material (Standke 2008). In this paper, we assume a Priabonian age for most of the Baltic amber available on the market, following Seyfullah *et al*. (2018).

The amber piece containing the specimen studied here originated from a mine in Yantarny on Sambia Peninsula, Kaliningrad Region, Russia. It was purchased by Carsten Gröhn (Glinde, Germany) from Jonas Damzen (Vilnius, Lithuania), and was accompanied with a certificate of Natural Baltic amber delivered by the International Amber Association (https://www.amber.org.pl/; Fig. 1). The specimen



Certificate JDC4529
Natural Baltic Amber with Inclusions
expert Jonas Damzen
International Amber Association
Names of Inclusions:
Hymenoptera
Wasp

Fig. 1. Certificate of Baltic origin for the amber, delivered by the International Amber Association.

is deposited in the amber collection of the Leibniz Institute for the Analysis of Biodiversity Change, Hamburg, Germany (GPIH), under collection number GPIH 5021 (Carsten Gröhn coll. CCGG 9223).

The amber was prepared using thin silicon carbide sanding papers on a grinder polisher (Buehler MetaServ 3000). The examination and photographs of the specimens were conducted with a Zeiss Axiocam 512 color camera attached to a Zeiss Axio Zoom.V16 stereo microscope. All images are digitally stacked photomicrographic composites of several focal planes, which were obtained using HeliconFocus ver. 6.7. Adobe Illustrator CC2019 and Photoshop CC2019 software were used to compose the figures and ImageJ ver. 1.53 for measurements. The description of morphological characters follows Lanes *et al*. (2020), except the fore wing venation nomenclature, which follows Azevedo *et al*. (2018: fig. 7); the surface sculpturing follows Harris (1979).

Main measurements (Brazidec *et al*. 2024: fig. 1) and indices used are as follows throughout the text and figures:

DAO = diameter of anterior ocellus
f1, f2, f3 = flagellomere of respective number
HE = height of eye
LFW = length of fore wing
LH = length of head, measured from vertex to apex of clypeus
OOL = ocello-ocular line, the shortest distance between posterior margin of eye to the anterior margin of the anterior ocellus
p = pedicel
s = scape
VOL = vertex-ocular line, the shortest distance between posterior margin of eye to the vertex crest
WF = width of frons
WH = width of head above eyes
WOT = width of ocellar triangle, the shortest distance between posterior ocelli

Results

Class Insecta Linnaeus, 1758
Order Hymenoptera Linnaeus, 1758
Superfamily Chrysidoidea Latreille, 1802
Family Bethylidae Haliday, 1840
Subfamily Epyrinae Kieffer, 1914
Genus *Gracilepyris* Colombo, Tribull & Azevedo, 2022

†***Gracilepyris carsteni*** sp. nov.

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Figs 2–4

Diagnosis

Male

Frons protruding anteriorly into medial projection hiding antennal foramina and lateral clypeal lobe (Figs 2A, 3A–B); lateral clypeal lobe inconspicuous; malar space much reduced (Fig. 3A–B); mandible tridentate, basally with laminar expansion (Fig. 3A); antennal foramen directed anteroventrally (Fig. 3B); scape length 3.0 × medial width (Fig. 3C); pedicel longer than flagellomere 1 (Fig. 3C); flagellomere 1 as long as wide (Fig. 3C); scape bearing sparse long setae (Fig. 3C); lateral pronotal area concave, pronotal lobe small (Fig. 3E); anteromesoscutum half as long as dorsal pronotal area, as long as mesoscutellum (Fig. 3D); notaulus drop-shaped, deeply impressed posteriorly, faint anteriorly (Fig. 3D); parapsidal signum present on half anteromesoscutum length (Fig. 3D); foveae of mesoscuto-mesoscutellar suture separated by 6.0 × fovea width (Fig. 3D); mesoscutellum not contacting metapectal-propodeal complex (Fig. 3D); transepisternal line connecting with mesopleural pit (Fig. 3E); metapostnotal median carina present (Fig. 3D); metapostnotal-propodeal suture slender; 2r-rs&Rs curved towards wing tip (Figs 3F, 4); profemur strongly swollen, flattened (Fig. 3E, G); mesotibia with longitudinal rows of spines (Fig. 3H); mesotibial spurs longer than mesotibia diameter (Fig. 3H).

Etymology

The specific epithet is a patronym honouring Carsten Gröhn, who generously made the specimen available for study. The specific epithet is to be treated as a noun in the genitive case.

Type material

Holotype

RUSSIA • ♂ (complete specimen in amber); Yantarny, Sambia Peninsula, Kaliningrad region; GPIH 5021 (CCGG 9223).

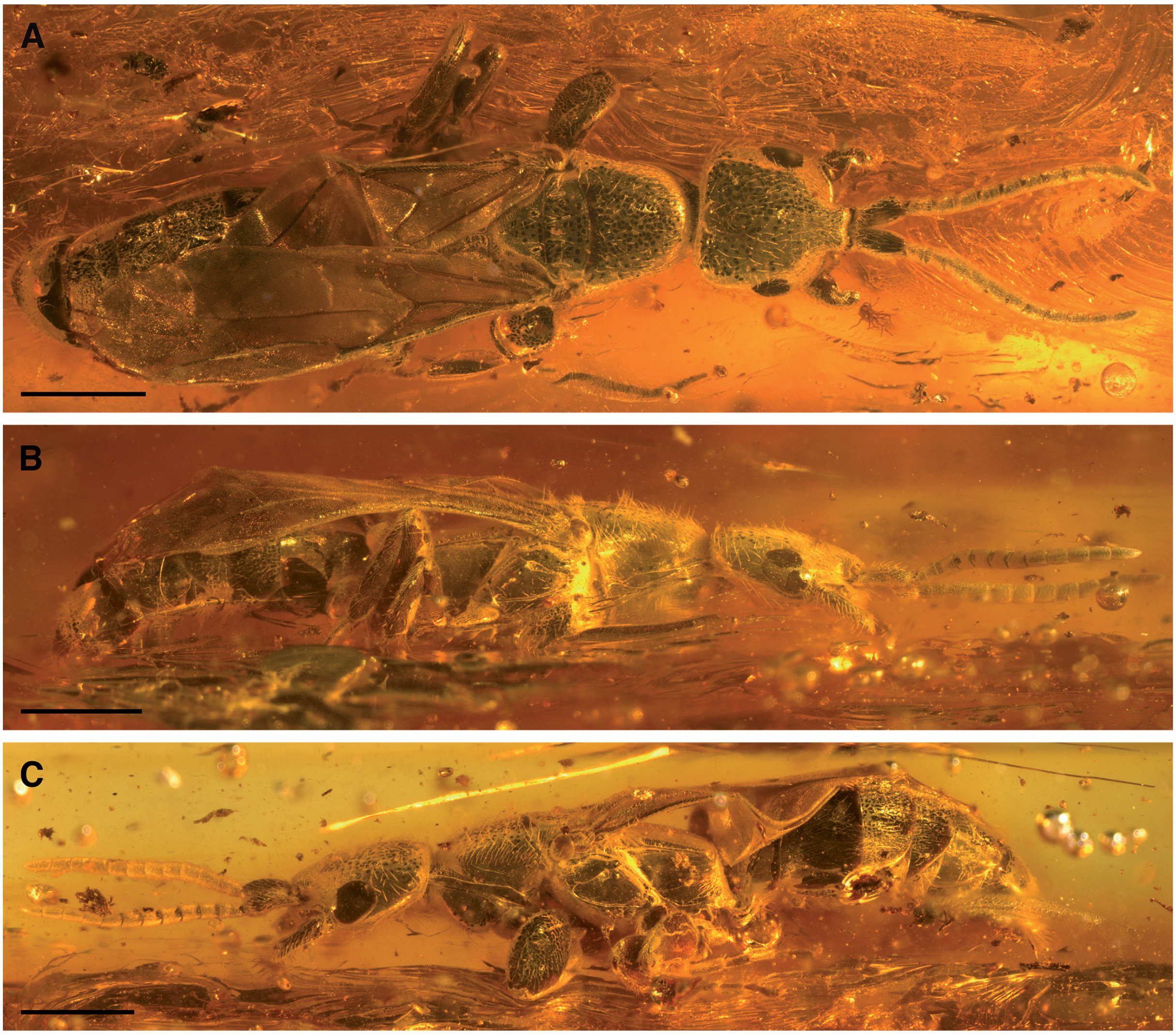

Fig. 2. †*Gracilepyris carsteni* sp. nov., holotype, ♂, GPIH.5021 (CCGG 9223). **A**. Habitus in dorsal view. **B**. Habitus in right lateral view. **C**. Habitus in left lateral view. Scale bars = 1 mm.

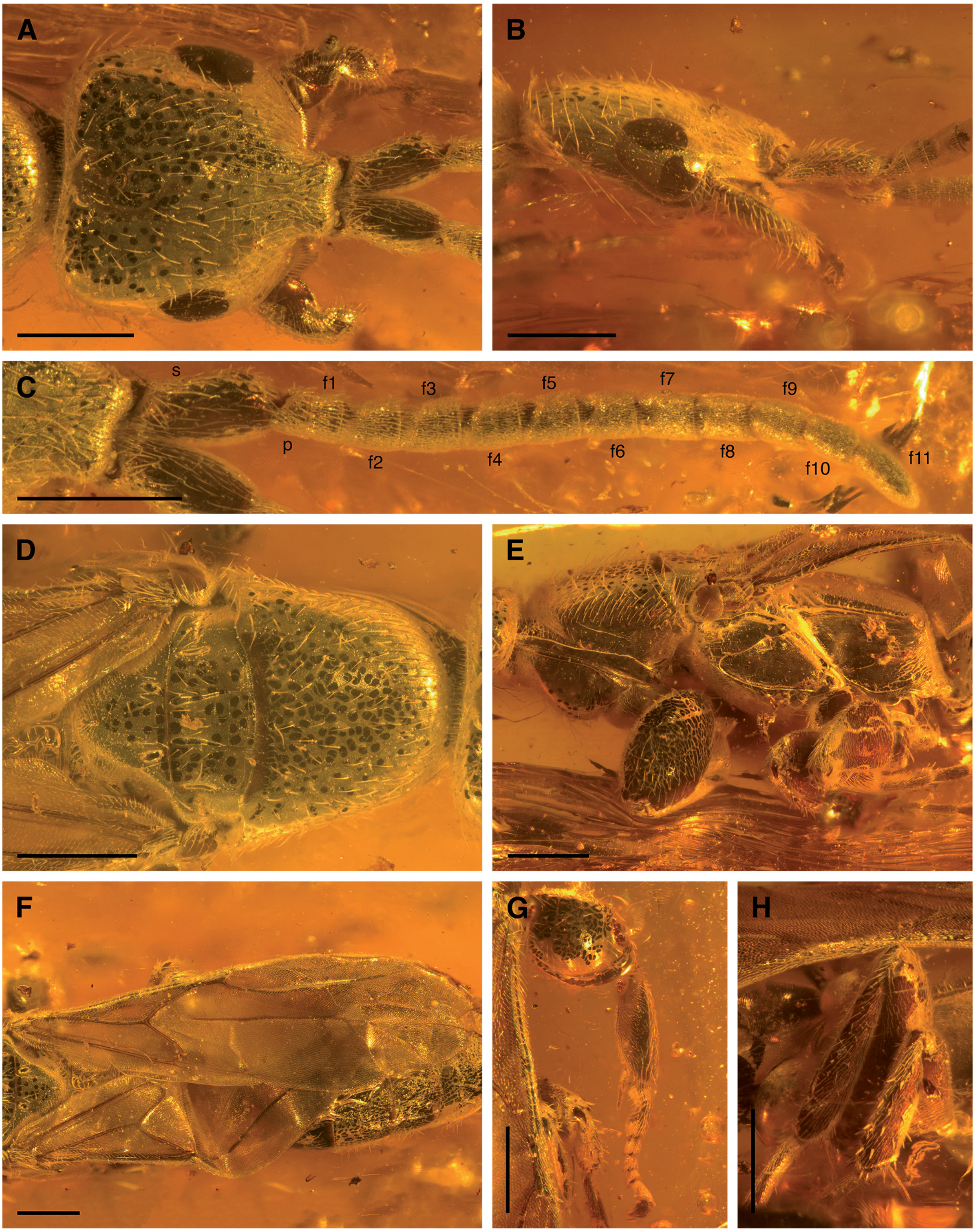

Fig. 3. †*Gracilepyris carsteni* sp. nov., holotype, ♂, GPIH.5021 (CCGG 9223). **A**. Head in dorsal view. **B**. Head in right lateral view. **C**. Antenna. **D**. Mesosoma in dorsal view. **E**. Mesosoma in left lateral view. **F**. Fore wings. **G**. Fore leg. **H**. Middle and hind femora and tibias. Abbreviations: see Material and methods. Scale bars = 0.5 mm.

Type locality and age

Yantarny, Sambia Peninsula, Kaliningrad region, Russia. Late Eocene: Priabonian, 34–38 Ma.

Description

Body. Stout, length 6.67 mm.

Head. Slightly longer than wide, flattened, prognathous; LH = 1.27 mm, WH = 1.12 mm, WF = 0.90 mm, HE = 0.44 mm, OOL = 0.49 mm, VOL = 0.45 mm, WOT = 0.24 mm, DAO = 0.07 mm; frons flat to slightly convex in lateral view, imbricate, bearing sparse long setae, protruding anteriorly into medial, not elevated, frontal projection overlapping antennal foramina; frontal line absent; vertex flat to slightly convex in lateral view, imbricate, bearing sparse long setae dorsally; vertex crest bluntly angulate as seen in dorsal view; compound eye developed, barely protruding from side of head, located anteriorly on head, closer to mandible than to vertex crest, covering ca 0.3 × side of head, glabrous; gena with sparse long setae, genal setae longer than frontal setae; lateral clypeal lobe inconspicuous, median clypeal lobe outcurved, much hidden under frontal projection and scape; malar space inconspicuous, shorter than basal mandibular width; mandible curved, basally with laminar expansion, bearing setae longer than basal mandibular width, tridentate; labial palp as long as mandible; antennal foramen directed anteroventrally; antenna filiform; radicle and scape axes distinct; scape length 3.0 × medial width (length 0.44 mm), wider medially than basally and distally, basally forming flangelike expansion hiding radicle; pedicel pyriform, as long as wide (length 0.11 mm), longer than flagellomere 1; flagellomere 1 shortest flagellomere, wider than long (length 0.09 mm); flagellomeres 2–10 longer than wide (length ca 0.15–0.20 mm); flagellomere 11 longest flagellomere (length 0.25 mmº), tapering apicad; scape bearing sparse long setae, setae length about 0.5 × scape width; pedicel and flagellum bearing uniform short setae, setae length shorter than 0.5 × flagellomere width; ocellar triangle much posterad on head; anterior ocellus posterad supra-ocular line; occipital carina present.

Mesosoma. Shorter than metasoma (length 2.44 mm); propleuron not visible in dorsal view; propleural epicoxal sulcus circular; dorsal pronotal area slightly convex (length 0.77 mm), bearing sparse long setae, ecarinate, anterior and lateral margins outcurved, humeral angle not pronounced, posterior margin incurved; lateral pronotal area concave; pronotal lobe small, reaching tegula; anteromesoscutum flat to slightly convex, length 0.5 × dorsal pronotal area length (length 0.38 mm); notaulus present, drop-shaped, deeply impressed and wide posteriorly, faint and present only as line anteriorly, notauli posteriorly separated by less than distance between foveae of mesoscuto-mesoscutellar suture; parapsidal signum present as conspicuous sulcus, effaced anteriorly and posteriorly; mesoscuto-mesoscutellar suture with foveae not connected by sulcus, foveae oval, separated one to another by 6.0 × fovea width; mesoscutellum as long as anteromesoscutum (length 0.38 mm); metanotum reduced, distinct

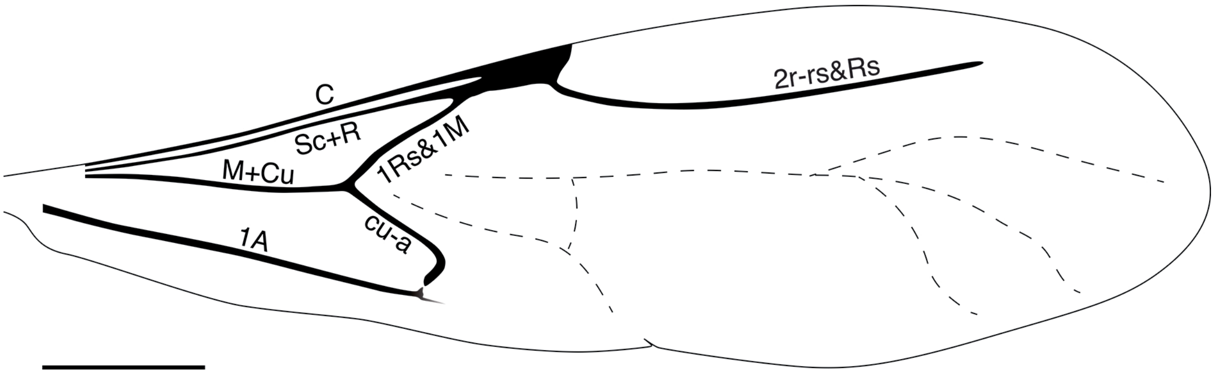

Fig. 4. †*Gracilepyris carsteni* sp. nov., line drawing of fore wing. Scale bar = 0.5 mm.

medially (i.e., mesoscutellum not contacting metapectal-propodeal complex); mesopleuron convex, with transepisternal line deeply impressed, anteriorly connecting with mesopleural pit, mesopleural pit separated from mesepimeral sulcus by about its diameter; metapectal-propodeal disc longer than wide, flat to slightly convex; metapostnotum rugulose; metapectal-propodeal disc with sculpture indistinct, anteriorly margined by transverse anterior carina of metapectal-propodeal complex, laterally margined by lateral marginal carina of metapectal-propodeal complex, posteriorly margined by transverse posterior carina of metapectal-propodeal complex; propodeum laterally slightly concave, thinly striated; metapostnotal median carina present, complete, strong; metapostnotal-propodeal suture present at least anteriorly, slender; lateroposterior propodeal angle angulate.

WINGS. Fore wing developed (LFW = 3.73 mm), hyaline, uniformly micropubescent; veins C, Sc+R, M+Cu, 1A, 1Rs&1M, cu-a, 2r-rs&Rs tubular; M+Cu shorter than A and Sc+R, forming obtuse angles with 1Rs&1M and cu-a; 1Rs&1M and cu-a confluent; 1Rs&1M slightly incurved medially; cu-a strongly bent toward A posteriorly; 1A not tubular distad cu-a, only thin spectral segment of 2A visible; 2r-rs&Rs without angulation, curved towards wing tip, distalmost section almost straight, fading before reaching margin, at distance subequal to pterostigma length; pterostigma distinct, slightly thickened; no other veins present but patterns of flexion lines visible in medial and distal sections of wing. Hind wing shorter than fore wing (length 1.72 mm), hyaline, micropubescent, posteriorly bordered by long setae; anal lobe delimitated by distinct incision, length ca 0.2 × hind wing length.

LEGS. Profemur much swollen, length ca 1.8 × width, flattened, almost paddle-shaped, bearing sparse long setae; protibia fusiform, bearing uniform short setae and sparse long setae; strigil present; protarsomeres bearing uniform short setae; probasitarsomere longest, distal protarsomere longer than 0.5 × probasitarsomere length; mesofemur fusiform, length ca 2.7 × width, bearing uniform short setae; mesotibia fusiform, bearing uniform short setae and sparse spines on every faces and along distal rim, spines as long as setae, apparently organized in longitudinal rows; mesotarsomeres bearing uniform short setae; mesobasitarsomere longest; metafemur fusiform, length ca 3.5 × width, bearing uniform short setae; metatibia bearing uniform short setae; metatarsomeres bearing uniform short setae; metabasitarsomere longest; tibial spur formula 1–2–2; protibia with calcar; mesotibial spurs longer than mesotibia diameter; tarsal claws evenly curved, edentate; arolium small.

METASOMA. Fusiform (length 2.96 mm), imbricate, bearing sparse long pubescence, especially near posterior margin of sternites; tergite 2 longest tergite, length 1.6 × tergite 3 length.

Genus *Rysepyris* Kieffer, 1906

Rysepyris dubius (Kieffer, 1904)

Holepyris dubius Kieffer, 1904: 394.
Holepyris neodubius Azevedo in Azevedo *et al*., 2018: 172 [unnecessary replacement name].

Rysepyris dubius – Colombo *et al*. 2022: table S18.

Remarks

Azevedo *et al*. (2018: 172) proposed the replacement name *Holepyris neodubius* Azevedo, 2018 for *Holepyris dubius* Kieffer, 1904 rather than †*Holepyris dubius* (Brues, 1933) (Azevedo *et al*. 2018: 9, 171). However, this action was based on a misunderstanding of the homonymy: *H. dubius* Kieffer, 1904 is the senior homonym, and †*H. dubius* (Brues, 1933) is the junior homonym. Therefore, *Holepyris neodubius* Azevedo, 2018 is an unnecessary replacement name for *H. dubius* Kieffer, 1904. Furthermore, †*H. dubius* (Brues, 1933) was incorrectly named †*Holepyris neodubius* Azevedo, 2018 in Colombo *et al*. (2021a) and †*Rysepyris neodubius* (Azevedo, 2018) in Colombo *et al*. (2022: table S18).

To resolve the homonymy correctly, we here propose a new replacement name for the junior homonym:

†***Rysepyris bruesi*** Brazidec nom. nov., replacement name for †*Rysepyris dubius* (Brues, 1933)

†*Misepyris dubius* Brues, 1933: 135.

†*Holepyris dubius* – Evans 1964: 140. — Azevedo *et al*. 2018: 171
†*Holepyris neodubius* – Colombo *et al*. 2021a: 64 [incorrect species name].
†*Rysepyris neodubius* – Colombo *et al*. 2022: table S18 [incorrect species name].

Etymology

The replacement name is a patronym honouring Charles T. Brues, who originally described this Baltic amber species.

Type material

Holotype

RUSSIA • ♂ (specimen in amber); housed in the University of Königsberg; specimen without code (lost).

Locality and age

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

Discussion

The fossil specimen studied here is confidently assigned to the Bethylidae, subfamily Epyrinae, based on the following characters: winged form, fore wing with Rs+M vein absent, metanotum not developed medially or overlapping mesoscutellum, metapectal propodeal-complex not depressed and without pronounced posterolateral projection, C vein tubular, and transepisternal line present (Azevedo *et al*. 2018). Based on the key to the epyrine genera of Brazidec *et al*. (2024), the specimen falls between *Muellerella* Saussure, 1892 and *Gracilepyris* as follows: mesoscuto-mesoscutellar suture with foveae not connected by sulcus (Fig. 3D), posterior ocelli distant one to another by more than their diameter (Fig. 3A), dorsal pronotal area without anterior elevation, incurved anterior margin, and angulate humeral angle (Fig. 3D), antennae not pectinate, flagellomere 1 reduced but not ring-shaped (Fig. 3C), mesoscuto-mesoscutellar foveae distant by more than 4.0 × fovea width (Fig. 3C), and eye flat (Fig. 3A). *Gracilepyris* and *Muellerella* are closely related and morphologically similar genera, having long been treated as synonyms of *Epyris* Westwood, 1832 (Colombo *et al*. 2022). Nevertheless, the specimen exhibits a series of characters that more closely aligns it with *Gracilepyris*. These include the fore wing anterobasally regularly setose, with cu-a vein strongly bent posteriorly and 2r-rs&Rs vein long and tubular, as in *Gracilepyris* (Meidani *et al*. 2024: figs 2b, 3b, 6b) but unlike in *Muellerella* (Ito *et al*. 2022: fig. 7; Singh *et al*. 2021: fig. 37j); and the protarsi without specialized spines as in *Gracilepyris* (Meidani *et al*. 2024: figs 5d, 6i) but unlike in *Muellerella* (Ito *et al*. 2022: fig. 6; Singh *et al*. 2021: fig. 37g). Additional characters of the specimen are also found in various species of *Gracilepyris*, albeit in different combinations. The reduced flagellomere 1 is present in *Gracilepyris malakae* Meidani & Khayrandish, 2024 (Meidani *et al*. 2024: fig. 7f), the indistinct malar space occurs in *Gracilepyris rufipes* (Say, 1824) (Meidani *et al*. 2024: fig. 9d), the ventrally-directed antennal foramina are observed in *Gracilepyris brachypterus* (Ashmead, 1893) (Meidani *et al*. 2024: fig. 5a), and the relative proportions of the pronotum, anteromesoscutum, and mesoscutellum closely match those of *G. brachypterus* and *G. rufipes* (Meidani *et al*. 2024: figs 5c, 9g, 11f). However, the specimen also exhibits several distinctive features not known in any described species of *Gracilepyris*, including the mandible with a basal laminar extension (Fig. 3A), the pronounced frontal projection that hides the medial clypeal lobe in dorsal view (Fig. 3A–B), the lateral clypeal lobes inconspicuous (Fig. 3B), and the mesotibial spines (Fig. 3H).

Despite these differences, the overall morphological evidence supports placement within *Gracilepyris*. Accordingly, we describe †*Gracilepyris carsteni* sp. nov. to accommodate this specimen with characters that place it outside of any other species of *Gracilepyris*. The generic concept of *Gracilepyris* was initially established based on the female morphology (Colombo *et al*. 2022) and later complemented by the description of the male (Meidani *et al*. 2024), which revealed a slight sexual dimorphism, as observed in other epyrine genera (e.g., Colombo *et al*. 2022). †*Gracilepyris carsteni* does not conflict with the current generic diagnosis, as most of its characters are also present in other species of *Gracilepyris* (e.g., antennomere proportions, malar space length, mesosoma proportions, and fore wing venation). Although the fossil exhibits some additional features not reported in extant species, such as the mandibular basal extension, the pronounced frontal projection, and the presence of mesotibial spines, these differences are not sufficient to justify the erection of a separate genus. Instead, †*Gracilepyris carsteni* suggests that certain morphological characters may exhibit a broader range of variation within *Gracilepyris* than previously recognized.

Gracilepyris is a recently erected genus, established to accommodate a Nearctic and Neotropical species previously placed in *Epyris* but recovered outside that genus by Colombo *et al*. (2022). Until recently, *G. rufipes* was the sole species included in the genus and was known only from the female morph. Çan (2022) subsequently reported the occurrence of this taxon in Turkey; however, this identification was later questioned by Meidani *et al*. (2024), who revised the genus, described additional species as well as the male morphology, and synonymized several bethylid taxa under *G. rufipes*. To date, *Gracilepyris* comprises five extant species and one extinct species with a combined Nearctic, northern Neotropical, and Palaearctic distribution (Fig. 5). With the exception of *Gracilepyris longicollis* (Kieffer, 1906), the American species exhibit broad distribution ranges, occurring along both the Atlantic and Pacific margins of Canada, the United States, and Mexico. The specimen of *G. rufipes* reported from Turkey may instead represent a distinct, undescribed species or reflect a human-mediated introduction, possibly linked to agricultural trade between western Asia and North America (Meidani *et al*. 2024). In contrast, *G. longicollis* and *G. malakae* are currently only known from their respective type localities, although expanded sampling may reveal wider distributions and additional species, particularly in the Palaearctic region. As observed in several other bethylid genera (Ramos *et al*. 2014; Colombo & Azevedo 2021; Colombo *et al*. 2021b), the presence of †*Gracilepyris carsteni* sp. nov. in late Eocene Baltic amber indicates that the genus formerly occupied a broader geographic range than it does today.

Gracilepyris belongs to the *Epyris* complex, a clade of Epyrinae genera characterized by individualized mesoscuto-mesoscutellar foveae (Colombo *et al*. 2022: fig. 3), contrasting with the plesiomorphic sulcate condition in which the foveae are connected by a distinct sulcus (Colombo *et al*. 2022: fig. 6g). The sulcate epyrine genera do not form a monophyletic assemblage but instead comprise two distinct lineages within the subfamily, with the (*Rysepyris* + (*Holepyris* + *Disepyris*)) lineage recovered as sister to the *Epyris* complex. Sulcate genera account for approximately 72% of extant epyrine species (Colombo *et al*. 2022), a disparity that is also reflected in the fossil record, where most fossil Epyrinae are assigned to genera exhibiting this morphology (Colombo *et al*. 2021a), particularly in Baltic amber (Table 1). The earliest record of Epyrinae dates back to the early Cenomanian and consists of species with a sulcate mesoscuto-mesoscutellar suture (Brazidec *et al*. 2024; Jouault *et al*. 2026). In contrast, representatives of the non-sulcate lineage are first documented from the early to late Eocene (Brues 1910; Cockerell 1921; Falières & Nel 2018), with several species historically attributed to *Epyris*. However, these assignments have been questioned due to preservation or illustration issues (but see Colombo *et al*. 2021a: 58–61) for comments on †*Epyris deletus* Brues, 1910, †*Epyris kiefferi* Brues, 1910, †*Epyris moulyi* Falières & Nel, 2018, and †*Epyris rectinervis* (Cockerell, 1921)). The discovery of †*Gracilepyris carsteni* sp. nov. in the late Eocene Baltic amber confirms that the *Epyris* complex had already diversified by that time. This finding is consistent with the divergence-time estimates of Santos *et al*. (2024), who inferred that the *Epyris* complex originated during the second half of the Late Cretaceous and diversified into the

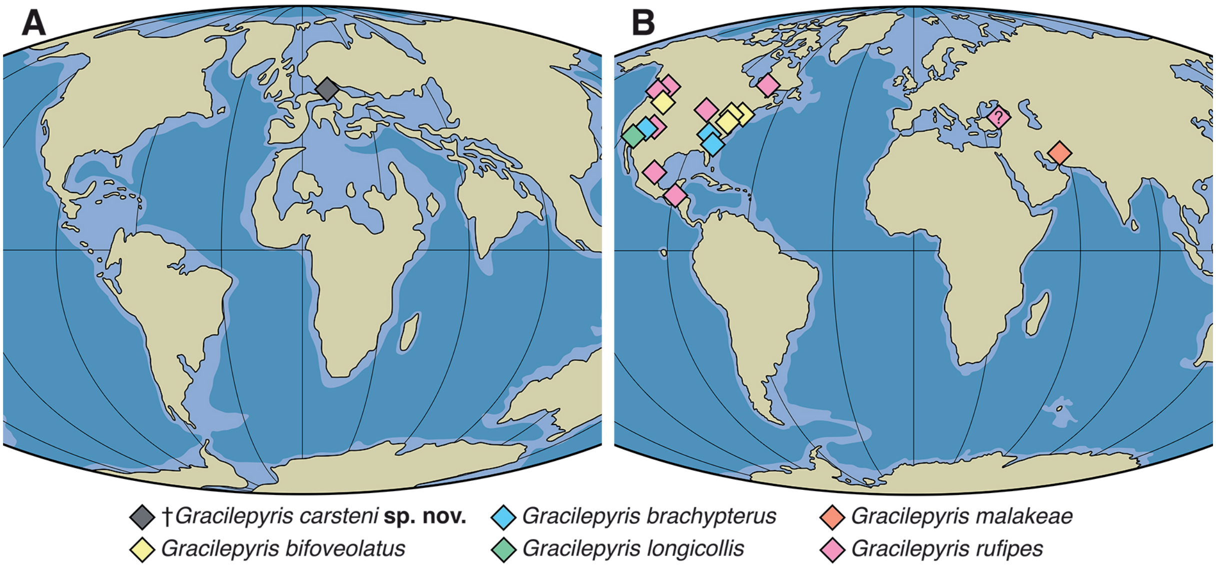

Fig. 5. Distribution maps of species of *Gracilepyris* Colombo, Tribull & Azevedo, 2022. **A**. Eocene. **B**. Modern day.

early Paleogene, with *Gracilepyris* itself estimated to have arisen in the early Eocene. Taken together, these data suggest that a substantial portion of epyrine morphological and phylogenetic diversity was already established before the Eocene. Nevertheless, the scarcity of Cretaceous Epyrinae hampers a more precise reconstruction of the early evolutionary history of the group, highlighting the need for further investigations of Cretaceous bethylid assemblages.

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