

# A new genus and species of *Pristocerinae* (Hymenoptera, Bethylidae) from upper Eocene Baltic amber with a review of conspecific association from insect fossils

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Academic editor: Michael Ohl | Received 14 May 2021 | Accepted 15 June 2021 | Published 31 August 2021

<http://zoobank.org/9D5B00CA-75F0-4E1F-B847-11D490F769CD>

**Citation:** Tribull CM, Pankowski MV, Colombo WD (2021) A new genus and species of *Pristocerinae* (Hymenoptera, Bethylidae) from upper Eocene Baltic amber with a review of conspecific association from insect fossils. *Journal of Hymenoptera Research* 85: 119–133. <https://doi.org/10.3897/jhr.85.68658>

## Abstract

A new extinct genus and species of *Pristocerinae*, †*Archeonesia eocena* Tribull, Pankowski & Colombo, **gen. et. sp. nov.**, are described from upper Eocene Baltic amber from the Yantarny amber mine in the Kaliningrad region, Russia. Descriptions, remarks, illustrations, and comparisons to all extinct and extant *Pristocerinae* are provided. †*Archeonesia* is described as a new genus because neither the male nor the female can be placed in any previously described genera, although the female is most similar to *Acrenesia* and the male is most similar to *Cleistopyris*. Rare for Bethylidae, and Hymenoptera in general, this fossil contains both a male and female specimen that we are describing as conspecifics. A brief review from the paleoentomological literature is provided to describe how insect fossils containing evidence of reproductive behavior have been used to associate conspecifics in extinct species.

## Keywords

Amber, Bethylidae, Eocene, fossil, *Pristocerinae*

## Introduction

Bethylidae are a family of parasitoid wasps within the aculeate superfamily Chrysi-doidea that have a cosmopolitan distribution and are known for attacking lepidopteran and coleopteran hosts, including agricultural pests like the navel orangeworm, pink bollworm, and coffee berry borer (Gordh et al. 1983; Abraham et al. 1990; Azevedo et al. 2018). Currently, the family contains nearly 3,000 species in about 100 genera within five extant subfamilies (Bethylinae, Epyrinae, Mesitiinae, Pristocerinae, and Scleroderminae) and four extinct subfamilies (†Elektroepyrinae, †Lancepyrinae, †Holopsenellinae, and †Protopristocerinae) (Azevedo et al. 2018; Colombo et al. 2020a, b). There are about 90 flat wasps fossil species described, with the oldest known extinct Bethylidae coming from early Cretaceous amber deposits (Engel et al. 2016). However, the greatest number of fossil bethylids comes from the Eocene, specifically Oise, Rovno, and Baltic amber deposits (Colombo et al. 2020a, 2021).

With over 1,000 species in 26 genera, Pristocerinae are the most speciose subfamily within Bethylidae and are found worldwide (Azevedo et al. 2018; Colombo et al. 2020a, 2021). The subfamily is known for its remarkable sexual dimorphism, with males possessing robust bodies, wings, and conspicuous eyes and ocelli while females are wingless, lack ocelli, and have eyes that are extremely reduced or missing (Alencar et al. 2018). The vast majority of Pristocerinae species are known from ‘males-only’ or ‘females-only’ and conspecific associations between males and females are rare, typically the result of collecting specimens copulating or rearing them from the same host (Azevedo et al. 2016; Alencar et al. 2018; Chen and Azevedo 2020).

There are 15 extinct species of Pristocerinae in 10 genera, with the oldest species, †*Foenobethylus electriphilus* (Cockerell) known from mid-Cretaceous Burmese amber (Cockerell 1920; Falières and Nel 2019, 2020; Colombo et al. 2020a). Of these species, 11 are known from males only, three are known from females only, and only one species, *Pristocera skwarrae* (Brues), was described from a fossil that contained both a male and female. Additionally, Brues (1933) does not include any illustrations of the species and it was presumed to be lost during World War II (Colombo et al. 2021).

About 50% of extinct Bethylidae come from Baltic amber deposits dated to the late Eocene, including four of the 15 extinct Pristocerinae from the genera *Pseudisobrachium* Kieffer, *Cleistepyris* Kieffer, and *Pristocera* Klug (Colombo and Azevedo 2019; Colombo et al. 2021). Here we present a new extinct genus of Pristocerinae from Baltic amber, †*Archeonesia* Tribull, Pankowski & Colombo, gen. nov. with the type species †*A. eocena* Tribull, Pankowski & Colombo, sp. nov. Like the lost *Pristocera skwarrae*, this amber fossil shows both a male and female together, granting us the rare opportunity to describe both sexes for a new extinct bethylid genus.

## Materials and methods

The specimens are embedded in Baltic amber sourced from the Yantarny mine in the Kaliningrad region. The piece was acquired from, trimmed, and polished by Marius

Veta and has clear dorsal and ventral views, although the lateral views are obscured by bubbles. The type material is deposited in the American Museum of Natural History, USA (AMNH, curator: David Grimaldi) with the specimen catalogue number AMNH\_IZC 00361788.

The specimens were studied with an Olympus SZX-10 stereomicroscope and photomicrographs were acquired with a DP27 digital camera, using Olympus's Cellsens software. Multiple Z-stacks were compiled using Helicon Focus. The drawings were scanned and vectorized into Adobe Illustrator CS6 version 23.0.3, and images were edited and combined into a single plate using Adobe Photoshop CC.

Terminology for the integument and sculpturing follows Harris (1979) and general terms follow Lanes et al. (2020).

## Systematic palaeontology

Family Bethylidae Haliday, 1839

Subfamily *Pristocerinae* Mocsáry, 1881

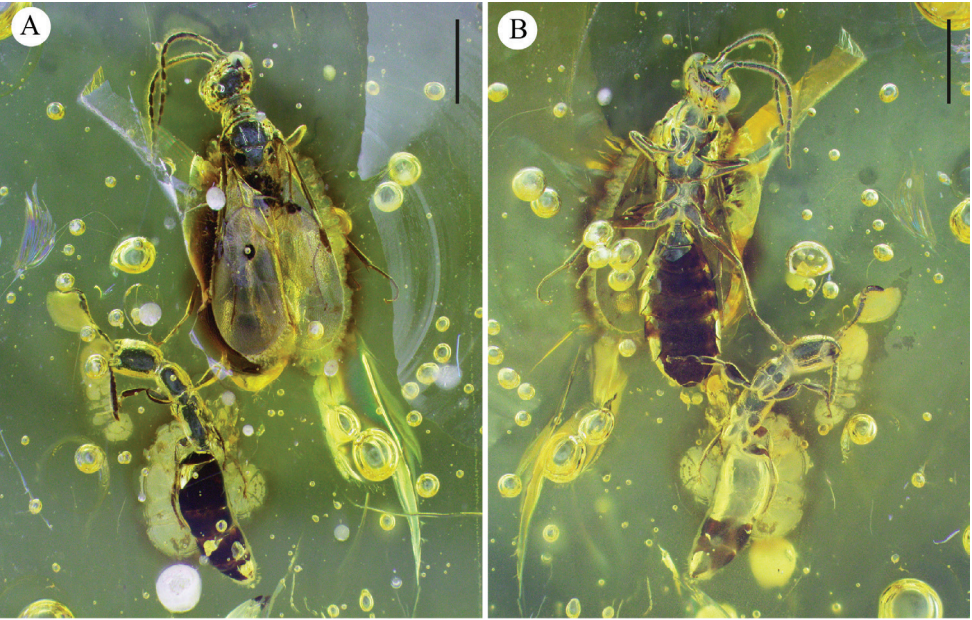
Genus †*Archeonesia* Tribull, Pankowski & Colombo, gen. nov.

<http://zoobank.org/6764DE3C-095F-4067-B96D-79706FF609C5>

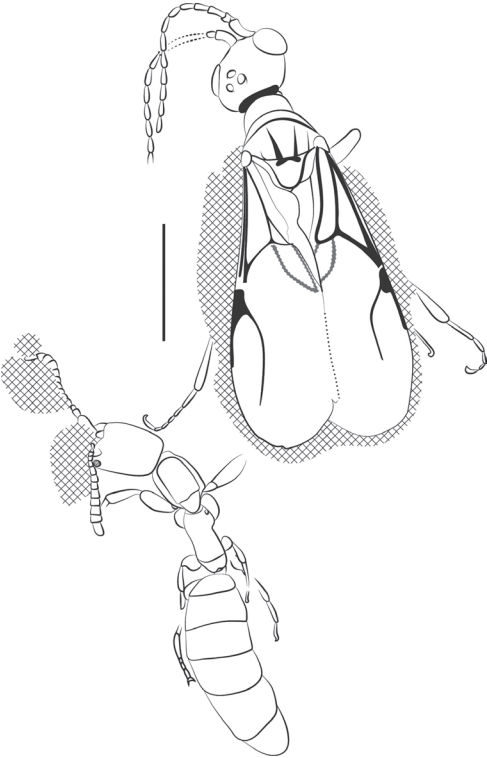
**Type-species.** †*A. eocena* Tribull, Pankowski & Colombo, sp. nov. by original designation.

**Description. Male** (Figs 1–4). Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma dark castaneous to black; wings hyaline. Head as long as wide and subquadrate, not globoid in lateral view. Clypeus with triangular median lobe, visible dorsally, lateral lobe reduced. Median clypeal carina delimited, lower than frons. Flagellomere longer than wide, with first flagellomeres larger than distal ones; flagellar pubescence erected; pedicel shorter than flagellomere I, apex dilated. Eye located touching mandibular base, glabrous, bulging. Frons weakly coriaceous, punctures large and sparse. Frontal line not visible. Ocellus large, salient. Frontal angle of ocellar triangle in obtuse angle. Anterior ocellus posterior to supra-ocular line. Occipital carina present. Dorsal pronotal area wider than long, weakly coriaceous, punctures small and sparse. Metafurcal pit oval. Posterior mesofurcal pit crown-shaped. Notaulus present, large, converging posteriorly, smooth. Parapsidal signum shorter than notauli. Forewing with three cells closed (C, R, 1Cu), distal flexion line visible, 2r-rs&Rs vein tubular, long, well pigmented, angled, not converging posteriorly to anterior margin, R1 vein tubular, long. Pterostigma enlarged, lanceolate. Mesoscutum-mesoscutellar sulcus present, posterior margin strongly incurved medially. Metanotum well-developed medially. Metapectal-propodeal disc not visible. Mesotibia without spines. Metasoma polished. Ninth abdominal segment with margin weakly incurved, undivided.

**Female** (Figs 1–3, 5). Head, pronotum, mesoscutum, metapectal-propodeal complex, petiole, antenna, and metasoma light to dark brown. Head longer than wide and rectangular, not globoid in lateral view. Clypeus with median lobe trapezoidal,



**Figure 1.** †*Archeonesia eocena* Tribull, Pankowski & Colombo, gen. et. sp. nov. **A** dorsal habitus of male holotype and female allotype **B** ventral habitus of male holotype and female allotype. Scale bars: 1 mm (**A**, **B**).



**Figure 2.** †*Archeonesia eocena* Tribull, Pankowski & Colombo, gen. et. sp. nov. Illustration of dorsal habitus of male holotype and female allotype. Scale bar: 1 mm.



**Figure 3.** †*Archeonesia eocena* Tribull, Pankowski & Colombo, gen. et. sp. nov. Illustration of ventral habitus of male holotype and female allotype. Scale bar: 1 mm.

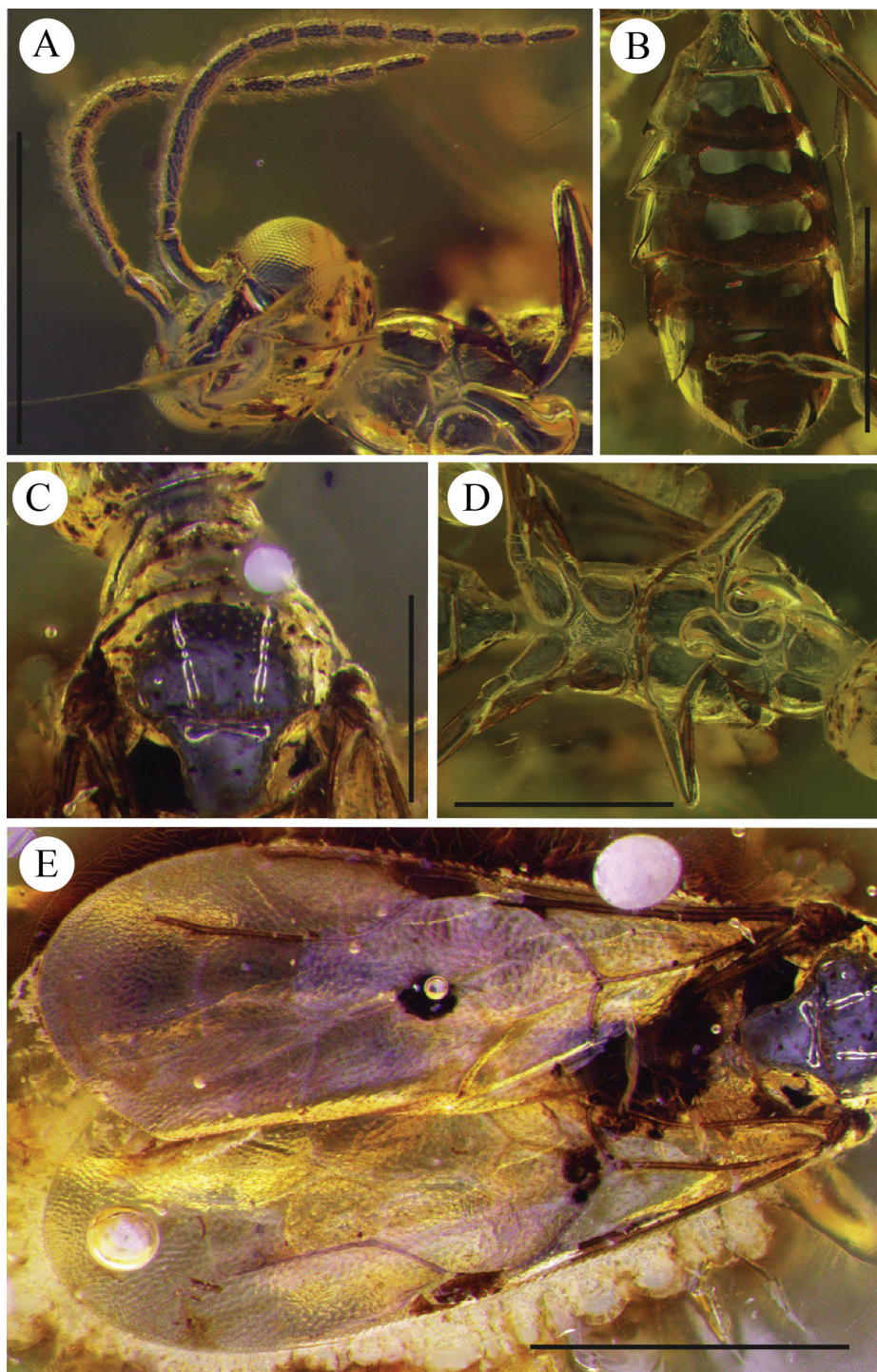
visible dorsally, lateral lobe reduced. Median clypeal carina not visible. Flagellomere as long as wide, with first flagellomeres wider than distal ones; flagellar pubescence appressed; pedicel barrel shaped, as long as flagellomere I. Eye located almost touching mandibular base, glabrous, reduced, flat. Frons weakly coriaceous, punctures small and sparse. Frontal line not visible. Ocelli absent. Dorsal pronotal area smooth, longer than mesoscutellum medially. Metafurcal pit oval. Posterior mesofurcal pit oval. Anteromesoscutum with anterior margin straight. Notaulus absent. Parapsidal signum absent. Mesoscutum-mesoscutellar sulcus absent. Mesopleuron visible dorsally, broad. Apterous. Mesotibia spinose. Metapectal-propodeal disc long, broadly in contact with anteromesoscutum, anterior margin wider than posterior one, lateral margin almost parallel in dorsal view, weak constriction at spiracles present. Second abdominal segment without flap expanded laterally.

**Etymology.** The name †*Archeonesia* comes from the genus *Acrenesia*, which the female is closest to. The prefix 'Archeo' represents the extinct nature of the genus. Gender feminine.

**Included species.** †*A. eocena* sp. nov.

**Distribution.** Baltic amber, Russian Federation.





**Figure 4.** †*Archeonesia eocena* Tribull, Pankowski & Colombo, gen. et. sp. nov., male holotype **A** head, ventro-frontal view **B** metasoma, ventral view **C** prothorax and mesothorax, dorsal view **D** mesosoma, ventral view **E** wings, dorsal view. Scale bars: 500 μm (**C**); 1 mm (**A**, **B**, **D**, **E**).





**Figure 5.** †*Archeonesia eocena* Tribull, Pankowski & Colombo, gen. et. sp. nov., female allotype **A** habitus, dorsal view **B** habitus, ventral view **C** head, ventro-lateral view **D** eye, with red arrow pointing to lower margin. Scale bars: 650  $\mu$ m (**D**), 1 mm (**A–C**).

†*Archeonesia eocena* Tribull, Pankowski & Colombo, sp. nov.

<http://zoobank.org/DD4A55F3-1F38-4415-A91D-C9FD28E8B287>

**Description.** Male holotype (Figs 1–4). Same as the genus, except for the following features: body length 4.0 mm. Mandible pentadentate. Palpal formula 5:3. Genitalia not visible.

Female allotype (Figs 1–3, 5). Same as the genus, except for the following features: body length 3.30 mm. Mandible not unidentate, either bidentate or tridentate, but obscured by bubbles in resin. Palps obscured. Metasoma polished.

**Type material.** Holotype, deposited at the AMNH Invertebrate Zoology Collection (specimen catalogue number AMNH\_IJC 00361788). Two complete flat wasps are embedded in amber measuring about 21 mm × 11 mm. There are numerous bubbles, but no other syninclusions.

**Etymology.** The species epithet *eocena* represents the geological epoch the species is known from.

**Stratigraphic horizon.** Priabonian, 33.9 to 37.7 million years ago (Cohen et al. 2020), upper Eocene.

## Discussion

The specimens considered here were assigned to the subfamily Pristocerinae based on the following character states, in the key from Azevedo et al. (2018), for males: (1) the forewings without Rs+M veins, (2) the metanotum is well-developed medially; and for females: (1) the wings are absent, (2) the eyes are very reduced, and (3) the ocelli are absent.

The male specimen studied here does not have visible important morphological characters, mainly from the genitalia, which does not allow the correct identification of the genus. We performed comparisons with males of all 23 known pristocerine genera, excluding *Anisobrachium* Kieffer, †*Ekaterina* Colombo & Azevedo (in Colombo et al. 2020a) and *Scaphepyris* Kieffer, because these genera are known only from females.

The male of this species has the ninth abdominal segment undivided and with the posterior margin weakly concave. For this reason, this species does not belong to †*Eopristocera* Falières & Nel, *Pristocera* Klug, *Prosapenesia* Kieffer, *Propristocera* Kieffer and *Pristonesia* Alencar & Azevedo (in Alencar et al. 2018), because the males of *Pristocera* have the ninth abdominal segment divided into two lobes and the males of †*Eopristocera*, *Prosapenesia*, *Propristocera* and *Pristonesia* have the ninth abdominal segment with the posterior margin strongly concave.

The male of this species does not belong to *Dissomphalus* Ashmead, *Protisobrachium* Benoit and *Trichiscus* Benoit, because those males have the clypeus with median and lateral lobes not well outlined, whereas †*A. eocena* sp. nov. has the clypeus with median lobe clearly defined and lateral lobes reduced.

Additionally, the median clypeal lobe of †*A. eocena* sp. nov. is projected forward, triangular, and the median clypeal carina is lower than frons, and for this reason, this



species does not belong to *Acrenesia* Alencar & Azevedo (in Alencar et al. 2018), *Dracunesia* Alencar & Azevedo (in Alencar et al. 2018), *Eleganesia* Alencar & Azevedo (in Alencar et al. 2018), *Epynesia* Alencar & Azevedo (in Alencar et al. 2018), *Pristepyris* Kieffer and †*Uniceratops* Colombo & Azevedo (in Colombo et al. 2020), because the males of *Pristepyris* have the median clypeal lobe short and truncate; the males of *Eleganesia* also have the median clypeal lobe short and with apical margin outcurved; males of *Acrenesia* and *Dracunesia* have the median clypeal lobe trapezoidal; males of *Epynesia* have the median clypeal lobe very projected and sharply angulated, and the male of †*Uniceratops* has the median clypeal carina higher than frons, horn-shaped.

†*A. eocena* sp. nov. has the dorsal pronotal area with the lateral and anterior margins distinct and for this reason, this species does not belong to *Apenesia* Westwood, *Afgoiogfa* Argaman, *Foenobethylus* Kieffer and *Parascleroderma* Kieffer, because the males of these genera have the dorsal pronotal area with the lateral and anterior margins barely distinct. Additionally, the males of the last three genera, together with *Austranesia* Alencar & Azevedo (in Alencar et al. 2018), have the prepectus very large, about 0.25× mesopectus length, whereas the male of this species has the prepectus reduced, about ~0.15× mesopectus length.

The male of this species does not belong to *Caloapenesia* Terayama, *Calobrachium* Gobbi & Azevedo and *Pseudisobrachium* Kieffer, because these males have the eyes very setose, and the median clypeal lobe is usually trapezoidal, whereas †*A. eocena* sp. nov. has the eyes glabrous and the median clypeal lobe triangular, as aforementioned.

The last possible genus is *Cleistepyris* Kieffer. However, males of *Cleistepyris* have the forewings with the junction of 2r-rs and Rs veins almost indistinct, pterostigma triangular, and the R cell as wide as 1Cu cell, and for this reason, this species does not belong to *Cleistepyris*, because the male of this species has the forewings with the junction of 2r-rs and Rs veins distinct, pterostigma lanceolate, and the R cell wider than 1Cu cell. Finally, due to the male morphological differences aforementioned, we are allocating this species to a new genus.

We concluded that the female is the same species as the male (see below), and we studied the female morphology to support the allocation of this species in a new genus. The female specimen studied here does have important morphological characters visible and because of this, we used the key proposed by Azevedo et al. (2018, p. 57–58). Following the key, it would go to the genus *Acrenesia*, because of the following characters: (1) the head is longer than wide; (2) the clypeus with the median lobe trapezoidal; (3) the eyes with more than one facet; (4) the mesonotum is triangular, short, transverse, and much wider than long; (5) the mesopleuron is quite large and is reaching at least the anterior third of metapectal-propodeal complex, in dorsal view; (6) the anterior portion of the metapectal-propodeal complex is slightly narrower than posterior one; (7) the metapectal-propodeal complex with inconspicuous constriction near the spiracles; and (8) the second abdominal segment without flap expanded laterally. However, †*A. eocena* sp. nov. has the pronotum as wide as the metapectal-propodeal complex, in dorsal view; and anteromesoscutum with anterior margin straight; whereas *Acrenesia* has the pronotum wider than the metapectal-propodeal complex, in

dorsal view; and anteromesoscutum with anterior margin incurved. Only †*Ekaterina* is not included in the pristocerine key of Azevedo et al. (2018, p. 57–58), because this genus was published later by Colombo et al. (2020a). †*Ekaterina* has the mesonotum somewhat diamond-shaped and metapectal-propodeal disc with strongly evident constriction; however, †*A. eocena* sp. nov. has the mesonotum triangular and metapectal-propodeal disc with weakly evident constriction. So, this female does not belong to any known pristocerine genera, and we are describing it as a new genus.

The amber fossil contains both a male and female specimen of *Pristocerinae*, an occurrence of conspecifics in the subfamily that has only previously been recovered in *Pristocera skwarrae*, which was never photographed or drawn, and was lost in World War II (see Colombo et al. 2021). While the two specimens were not preserved copulating, we have chosen to assign them to the same species as conspecifics. To justify this decision, we reviewed the paleoentomological literature concerning the association of conspecifics in fossils and found three main reasons why authors choose to associate specimens in the same fossil as conspecifics: 1) The specimens were preserved during copulation, 2) the specimens present evidence that copulation just occurred or was about to occur, and 3) knowledge of reproductive and/or social behavior of extant relatives was used to justify the association.

When previously undescribed insects are preserved during copulation, authors describe them as the same species – examples have been found in both rock impressions and amber fossils from a variety of different terrestrial arthropods. For example, in Li et al. (2013), a rock compression fossil from the middle Jurassic of China shows two froghoppers copulating with the male's aedeagus inserted into the female. In Klimov and Sidorchuk (2011) and Sidorchuk and Klimov (2011), a pair of copulating mites were redescribed from upper Eocene Baltic amber. Although there are other records of insects (especially Diptera) being preserved while mating in amber or as rock compressions, these publications broadly focus on describing behavior instead of acting as new species records (Grimaldi and Engel 2005; Takahashi et al. 2017).

Taxonomic records written from insects preserved while unequivocally copulating are rare, and more common are examples in which specimens are presumed to have already mated or were engaged in mating behavior. Evidence provided by the authors typically relies on the close proximity of supposed conspecifics, evidence of reproductive behaviors (like grasping), or evidence of exposed genitalia. For example, in Fischer and Hörnig (2019), the authors describe a new species of *Tineidae* from a male and female preserved in Baltic amber, arguing that the orientation of abdomens and genitalia, plus the rarity of moths in Baltic amber (less than 1% of all inclusions), means that it is unlikely the fossil represents a random co-occurrence. In Andersen and Poinar (1998), a new species of water strider was described from a Dominican amber piece that contained a male grasping a female, a position that suggests that they were trapped just before, during, or after mating. From Burmese amber, Chen and Su (2019) described a new species of *Zoraptera* in which copulation was suspected based on the identification of the male's intromittent organ.

Finally, authors also rely on knowledge of extant relatives' behavior to suggest that male and female conspecifics were preserved before, during, or just after mating. From

Mexican amber, Macadam and Ross (2016) describe two mayfly imagos (a male and female) as the same species, suggesting that it's unlikely the pair would have been caught in the same amber if not during a mating swarm given the short lifespan of extant adult Ephemeroptera. From mid-Cretaceous Burmese amber, a new species of dance fly was described from possible conspecifics with the justification that extant dance flies only form aggregations during courtship and mating. The authors also rely on possible evidence of the consumption of a nuptial meal by the female and sexual dimorphism in the inflated antennae of the male (Zhang et al. 2021). Gregarious mating behavior is also used as a justification for conspecific association of a whitefly species, especially given that all previous extinct Aleyrodidae were only known from individual specimens (Szwedo and Drohojowska 2016). From Upper Cretaceous Burmese amber, Cockx and McKellar (2018) described a new genus and species of Crabronidae from two males and a female, noting that the co-occurrence of the three could be due to either social behavior (as seen in extant relatives) or evidence of mating. It should also be noted that there are examples in the taxonomic literature in which no justification is given to support the association of conspecifics beyond the preservation of a male and female together (Szadziewski and Grogan 1998; Fanti and Kupryjanowicz 2017). Similarly, there are instances where authors do not assign potential conspecifics to the same species, but instead place them in the same genus (Wichard et al. 2020). Within Bethyilidae, there have only been two other instances of sexual association entirely from fossils – the aforementioned †*Pristocera skwarrae* and †*Lytopsenella maritima* Ramos and Azevedo (from the subfamily Bethylinae). Beyond being found in the same amber piece, Brues (1933) does not provide justification for the former, and Ramos et al. (2014) cite shared anatomical features (sexual dimorphism is low in the species) and preservation in the same piece.

Herein, we associate the male and female syninclusions as conspecifics based on our knowledge of the reproductive behavior of extant *Pristocerinae*. Female *Pristocerinae* are apterous and rarely collected by the same methods that commonly capture winged males. Occasionally, males and females will be captured attached (in copula) from Malaise traps and yellow pan traps as a result of phoretic copulation, in which the male transports the female while mating (Azevedo et al. 2016; Chen and Azevedo 2020). Phoretic copulation is observed in several Hymenopteran families with extreme sexual dimorphism, such as Tiphiidae, Mutillidae and Bethyilidae, and is hypothesized as a method to aid in the dispersal of apterous females in need of hosts or food sources (Azevedo et al. 2016; Vivallo 2021). The male and female described here might have been trapped in resin millions of years ago, much in the same way that an extant male *Pristocerinae* occasionally transports his mate to her demise.

In addition to †*A. eocena* sp. nov., four other species of *Pristocerinae* are known from Baltic amber deposits – †*Pristocera skwarrae*, †*Cleistepyris baryonyx* Colombo, Gobbi & Azevedo, †*Pseudisobrachium elatus* (Brues), and †*Pseudisobrachium inhabilis* (Brues) (Colombo et al. 2020a, 2021). Besides Baltic amber, Rovno amber deposits are also linked to the upper Eocene and contain extinct *Pristocerinae* – †*Pseudisobrachium megalosaurus* Colombo, Gobbi & Azevedo, †*Pseudisobrachium stegosaurus* Colombo, Gobbi & Azevedo, and †*Cleistepyris allosaurus* Colombo, Gobbi & Azevedo (Colombo



et al. 2020a). Given that Baltic amber from the Kaliningrad region has been extracted for more than a century and averages much greater yields than Rovno amber from Ukrainian mines in recent years, it's possible that †*A. eocena* sp. nov., might also be recovered from Rovno amber (Colombo et al. 2021). This possibility is reinforced by the finding that 50% of Rovno amber Hymenoptera fauna are also found in Baltic amber (Perkovsky 2018).

Of the upper Eocene Pristocerinae, *Cleistepyris*, *Pristocera*, and *Pseudisobrachium* are known from both extant and extinct species, while †*Archeonesia* is only known from the extinct species described here. From lower Eocene Oise amber, there is also the extinct monotypic genus *Eopristocera*. While extant *Pristocera* are known from the Palearctic (as well as other parts of the world), extant *Cleistepyris* are known only from Nearctic and Neotropical regions, and extant *Pseudisobrachium* are primarily found in southern distributions and common in the neotropics, which demonstrates how the biogeography of Pristocerinae has changed since the Eocene (Azevedo et al. 2018; Colombo et al. 2020a). The end of the Eocene marked the start of a cooling period, which likely drove the extinction of thermophile bethylids like †*Archeonesia* and †*Eopristocera*, as well as the local extinction of *Cleistepyris* in Europe (Bogri et al. 2017).

## Conclusion

Compared to other Bethyridae families like Epyrinae (30 species) and Bethylinae (20 species), there are fewer records of extinct Pristocerinae (Ramos et al. 2014; Azevedo et al. 2018; Colombo et al. 2021). With the description of †*Archeonesia eocena*, there are now 16 extinct species of Pristocerinae. Given that Pristocerinae are the most speciose and abundant subfamily of Bethyridae, it is interesting that it would rank third in extinct diversity. However, this could be due to the extreme sexual dimorphism within the subfamily reducing the number of individuals that were captured in resin – unlike Pristocerinae, most females of Bethylinae and Epyrinae can fly. In Epyrinae and Bethylinae, more than 65% of fossil records are from females, but in Pristocerinae, the opposite is seen with more than 70% of fossil records from males, suggesting that when the female is winged in Bethyridae, the chances are greater that a specimen will be preserved as a fossil.

Finally, extinct Bethyridae known from both sexes are extremely rare. In addition to †*Pristocera skwarrae*, one other extinct species of Bethyridae is known from both sexes. In Bethylinae, one species (representing 5% of extinct bethylines), †*Lytopsenella maritima*, is known and the association was justified by the weak sexual dimorphism and proximity of the specimens in the amber. In Epyrinae, one species (representing 3% of all extinct epyrines), *Epyris staphylinoides* (Hope), is known for only one extinct male and other extant males and females, so the association was not performed by representatives in the same fossil. While we hope for the discovery of more fossils that have preserved both sexes of a species together, it is likely that their occurrence will continue to be rare in Bethyridae.

## Acknowledgements

We thank the subject editor Dr. Michael Ohl, Dr. Evgeny Perkovsky and one anonymous reviewer for their valuable suggestions. The authors are thankful for the resources and support from their home institutions and research departments. CMT thanks the biology department and office of the provost at Farmingdale State College (State University of New York), as well as the American Museum of Natural History for accessioning the fossil. WDC thanks CAPES – Demanda Social for its Ph.D. scholarship. Additionally, we are thankful for the generosity of the Pankowski family in supporting paleontological research through their donation of fossils to research institutions.

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