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A new fossil genus near *Meghyperus* Loew from Baltic amber (Diptera: Atelestidae)

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The Atelestidae are a small family of empidoid flies (Diptera: Empidoidea), including 15 recent species in five genera (Sinclair & Grimaldi, 2020). In contrast, they have a rather high fossil diversity (Table 1), with 28 species in nine genera. These fossil taxa are almost entirely from Cretaceous ambers (Canadian, Lebanese, Myanmar, New Jersey, Spanish), and prior to this study only a single described species from Baltic amber (*Nemedina eocenica* Sinclair & Arnaud, 2001) was known. The extant species are widespread, with two Afrotropical, three Neotropical, two Nearctic and eight Palaearctic species. This family is recognized within the Empidoidea on the basis of their well-developed anal lobe of the wing, distinct alula, R_{4+5} unforked, M_{1+2} usually unforked or forked beyond cell dm, cell cua long, at least as long as cell bm, female tergite 10 absent, male terminalia symmetrical and unrotated, with elongate gonocoxal apodemes and shortened hypandrium (Chvála, 1983; Grimaldi & Cumming, 1999; Sinclair & Cumming, 2006).

As far as known, extant adult Atelestidae are flower visitors, feeding on nectar and pollen (Sinclair & Cumming, 2006). *Meghyperus* Loew, 1850 has been collected on flowers in western North America and pollen grains have been found in the abdomen of *Acarteroptera* Collin, 1933. Recent systematic collecting activities in southern Germany have shown that *Meghyperus* species are rare and similar to other atelestids (*e.g.*, *Atelestus pulicarius* (Fallén, 1816)), are restricted to primeval forests or to those with old trees (D. Doczkal, pers. comm. to AS).

A new genus and species of Atelestidae was found together in the same amber piece with the holotype of *Panorpodes weitschati* Soszyńska-Maj & Krzemiński, 2013 (Mecoptera) and the fly is partially visible in the habitus image of this species (Soszyńska-Maj & Krzemiński, 2013: fig. 9). This new taxon is described and illustrated, together with a key to extant and extinct European genera of Atelestinae.

Material and methods. This study is based on a single inclusion in Baltic amber, based on pollen and dinoflagellate dated upper Eocene, 41.2–33.9 Ma, Bartonian/Priabonian (Kasiński *et al*., 2020), deposited in the collection of the Geological and Paleontological Institute and Museum (GPIH), Museum of Nature, Leibniz Institute for the Analysis of Biodiversity Change, Hamburg, Germany. Photographs were made with a Leica M205 C stereomicroscope equipped with a Leica DMC5400 camera. Focus stacks were acquired and processed in Leica Application Suite X (LAS X). The terminology follows Sinclair & Cumming (2006) and Cumming & Wood (2017).

Systematic palaeontology

Meghyperites Sinclair & Stark **gen. nov.**
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Type species. *Meghyperites balticus* **sp. nov.**

Diagnosis. Readily differentiated from all other empidoid genera by the absence of cell dm with loss of crossvein dm-m, alula distinct and anal lobe well developed, M_{1+2} branched and petiolate, CuA arched, forming rounded apex of cell cua, postpedicel broadly conical with short one-articled stylus and slightly longer apical sensillum, hind tibia clavate, with hind tarsomere 1 broader than remaining tarsomeres, male terminalia with semi-circular epandrium and subapical surstyli.

Etymology. From *Meghyperus* (an extant genus of Atelestidae) + the suffix *-ites*, Greek for "like" in reference to the similarity of the two genera. The gender is masculine.

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Remarks. This new fossil genus is assigned to the subfamily Atelestinae of the family Atelestidae on the basis of the following characters: wing with well-developed anal lobe, alula distinct, R_{4+5} unforked, M_{1+2} forked; cell dm absent, cell cua longer than cell bm, fore tibial gland absent, male terminalia symmetrical and unrotated, surstylus subapical. It is clearly most closely related to the extant genus *Meghyperus* on the basis of wing venation (petiolate M_{1+2}, Fig. 2A) and male terminalia, with semi-circular epandrium (Fig. 2C). It is distinguished by wing with the open cell dm with the loss of crossvein dm-m and antenna with broadly elongate postpedicel with very short, one-articled apical stylus.

Meghyperites balticus Sinclair & Stark **sp. nov.**
(Figs 1, 2)
urn:lsid:zoobank.org:act:6D2146C5-74AD-4EC1-A090-047C927418DF

Type material. Holotype male, GPIH-3687 [syninclusion of holotype of *Panorpodes weitschati* Soszyńska-Maj & Krzemiński, 2013; Mecoptera], very well preserved and complete, eyes collapsed, otherwise all body parts present and clearly visible (GPIH).

Diagnosis. The species appears distinct by the spine-like projection on the inner apex of the epandrial lamella.

Description. Male. Holoptic, upper facets enlarged. Ocellar triangle slightly raised with pair of short, divergent ocellar setae. Antenna (Fig. 2B) with postpedicel broadly conical, tapered [unable to view laterally], densely pubescent; stylus very short with single terminal basal article and slightly longer apical peg-like sensillum. Proboscis retracted within head.

Thorax with postpronotal lobe with 2 long setae. Scutum with acrostichal setae not visible in available views; dorsocentrals forming uniserial row of setae [based mostly on sockets], ending with strong prescutellar seta; 2 presutural and 2–3 postsutural supra-alar setae; 2 notopleural setae, upper seta stronger; 1 postalar seta; 3 pairs of marginal scutellar setae. Laterotergite obscured by milky froth. Legs: length moderate, with distinct rows of setulae, mostly lacking large setae, except for subapical tibial setae and marginal dorsal setae on tarsomeres; mid tarsomere 1 possibly with cluster of strong preapical ventral setae. Femora similar in width. Fore and mid tibiae slender, slightly longer than length of corresponding femur; hind tibia clavate (Fig. 1A), shorter than corresponding femur. Hind tarsomere expanded, narrower than apex of tibia, shorter than remaining tarsomere, combined; tarsal claws well developed, pulvilli slender, two-thirds length of claw.

Wing length 1.7 mm (Fig. 2A). Hyaline with fine microtrichia over entire membrane. Pterostigma overlapping apex of R_1. Vein C fading beyond apex of R_{4+5}; Sc apically evanescent, ending well before costal margin; Rs arising well distant from level of humeral crossvein; R_1 ending slightly beyond medial fork; R_{2+3} straight, gently curved to C apically, ending equal-distance between apex of R_1 and R_{4+5}; R_{4+5} parallel to M_1 apically; cell dm absent, crossvein dm-m absent; M_{1+2} weakened, forked slightly proximal to apex of R_1; M_4 extending straight to wing margin; CuA curved, arched slightly beyond apex of cell bm; apex of cell cua rounded; CuA+CuP weak, ending before wing margin. Anal lobe well developed, broad, with alular incision obtuse; alula distinct.

FIGURE 1. *Meghyperites balticus* **gen. et sp. nov. A**, Habitus, scale bar = 1.0 mm (wing of *Panorpodes weitschati* on left). **B**, Male terminalia, dorsal view scale bar = 0.1 mm. **C**, Head and antennae, scale bar = 0.1 mm.

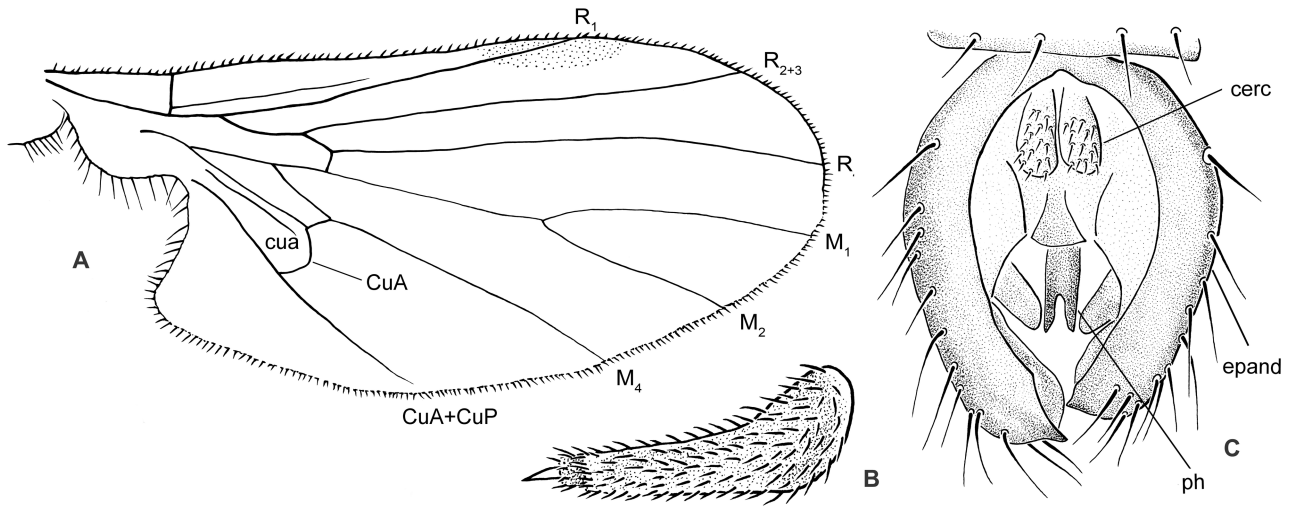

FIGURE 2. *Meghyperites balticus* **gen. et sp. nov. A**, Wing. **B**, Antenna, postpedicel. **C**, Male terminalia, dorsal view. Abbreviations: cerc, cercus; CuA, anterior branch of cubital vein; cua, anterior cubital cell; CuA+CuP, anterior branch of cubital vein + posterior branch of cubital vein; epand, epandrium; M, medial veins; ph, phallus; R, radial veins.

Abdominal sclerites well sclerotized. Terga 1–7 broad, well developed, with long lateral and marginal setae. Tergum and sternum 8 not visible. Terminalia (Figs 1B, 2C): symmetrical, unrotated, held at apex of abdomen. Cercus small, flat, subrectangular. Epandrium semi-circular, with narrow dorsal bridge anterior to cerci; inner apical margin concave; apex of tooth-like projection. Surstylus subapical, subrectangular. Hypandrium subtriangular. Phallus cylindrical, straight; apex forked.

Female. Unknown.

Etymology. Named after the origin of the amber.

Key to extant and extinct genera of the subfamily Atelestinae (Atelestidae)

1 Apex of cell bm modified with inclusion of short vertical Rs, recurrent r-m, radial veins and M_{1+2} closely approximated; cell bm usually absent.....Nemedininae
- Apex of cell bm unmodified with inclusion of long, curved Rs, vertical r-m, radial veins and M_{1+2} well separated; cell bm present.....Atelestinae.....2
2 Cell dm absent due to absence of crossvein dm-m (Fig. 2A).....3
- Cell dm present.....4
3 M_{1+2} forked and petiolate (Fig. 2A)..... .....*Meghyperites* **gen. nov.**
- M_{1+2} unforked.....*Atelestus* Walker
4 Three veins (M_1, M_2, M_4) branching separately off apex of cell dm.....*Atelestites* Grimaldi & Cumming
- Two veins (M_{1+2}, M_4) branching separately off apex of cell dm.....5
5 M_{1+2} forked and petiolate.....6
- M_{1+2} unforked.....7
6 R_{2+3} forked..... .....*Dianafranksia* Coram, Jarzembowski & Mostovski
- R_{2+3} unforked.....*Meghyperus* Loew
7 Cell dm subtriangular, with crossvein r-m inserted at or distal to middle of cell.....*Alavesia* Waters & Arillo
- Cell dm subrectangular, with crossvein r-m inserted near base of cell.....*Acarteroptera* Collin

Discussion. The new fossil taxon, *Meghyperites balticus* **gen. et sp. nov.** is represented by an extremely well preserved specimen. This taxon represents the second described Baltic amber species of Atelestidae and first Baltic amber taxon of the subfamily Atelestinae. This new fossil was found together with a completely preserved male scorpionfly of the family Panorpodidae (*Panorpodes weitschati*). It is extremely rare that two such scientifically valuable (holotypes) and perfectly preserved insects are found in one piece of amber. Imagoes of Mecoptera are extremely rarely preserved in amber due to their large size. It is interesting to note that extant species of the genus *Panorpodes* MacLachlan, 1875 occur only in the region of western North America and eastern Asia; whereas extinct species have been found only in present day Europe. This overall distribution is similar to the extant genus *Meghyperus* (Sinclair & Grimaldi, 2020).

Meunier (1908) described another (monotypic) genus of empidoid flies, *Meghyperiella* from Baltic amber. Based on the similarity of the name, Meunier (1908: 87) was suggesting a close relationship with the extant genus *Meghyperus*, but they differ in wing venation. This relationship was rejected by Ulrich (2004) who transferred the genus to the subfamily Microphorinae (Dolichopodidae *s. lat.*). Shamshev & Perkovsky (2022) recently redescribed this genus, based primarily on new specimens from Rovno amber.

As can be seen in Table 1, all but one genus of fossil Atelestidae are based on remnants of dipterans preserved in amber. The genus *Dianafranksia* is based on a wing preserved in a mudstone; therefore, nothing is known about characters of the head, thorax and abdomen of that genus, but the wing venation is unique among Atelestidae, as it has a forked R_{2+3}.

The description of this new genus in the subfamily Atelestinae helps to fill in some of the missing fossil record between the Cretaceous fossils and extant taxa. Knowledge gaps still remain and further studies and exploration on the diversity of this family need to continue.

TABLE 1. Fossil taxa of the family Atelestidae, arranged by geological age.

Bartonian/Priabonian (41.2–33.9 Ma)	
Nemedina Chandler, 1981 *eocenica* Sinclair & Arnaud, 2001 ***Meghyperites* gen. nov.** *balticus* **sp. nov.**	BALTIC AMBER
Campanian (83.6–72.1 Ma)	
Cretodromia Grimaldi & Cumming, 1999 *glaesa* Grimaldi & Cumming, 1999 ***Nemedromia*** Grimaldi & Cumming, 1999 *campania* Grimaldi & Cumming, 1999 *telescopica* Grimaldi & Cumming, 1999 ***Prolatomyia*** Grimaldi & Cumming, 1999 *elongata* Grimaldi & Cumming, 1999	CANADIAN AMBER
Turonian (93.9–89.8 Ma)	
Nemedromia Grimaldi & Cumming, 1999 *turonia* Grimaldi & Cumming, 1999 ***Neoturonius*** Grimaldi & Cumming, 1999 *asymmetrus* Grimaldi & Cumming, 1999 *cretatus* Grimaldi & Cumming, 1999 *vetus* Grimaldi & Cumming, 1999	NEW JERSEY AMBER
Cenomanian (100.5–93.9 Ma) [continuation]	
Alavesia Waters & Arillo, 1999 *angusta* Sinclair & Grimaldi, 2020 *brevipennae* Sinclair & Grimaldi, 2020 *hadroceria* (Poinar & Vega, 2020) *lanceolata* Sinclair & Grimaldi, 2020	MYANMAR AMBER
Cenomanian (100.5–93.9 Ma) †	
Alavesia Waters & Arillo, 1999 *latala* Sinclair & Grimaldi, 2020 *longicornuta* Sinclair & Grimaldi, 2020 *longistylata* Zhang & Wang, 2020 *magna* Sinclair & Grimaldi, 2020 *myanmarensis* Jouault, Ngô-Muller & Nel, 2020 *pankowskiorum* Sinclair & Grimaldi, 2020 *spinosa* Sinclair & Grimaldi, 2020 *tripudii* Zhang & Xie, 2021 *wimpala* Stark, Hoffeins, Hoffeins & Arillo, 2020 *zigrasi* Sinclair & Grimaldi, 2020	MYANMAR AMBER
Albian (113.0–100.5 Ma)	
Alavesia Waters & Arillo, 1999 *prietoi* Peñalver & Arillo, 2007 *subiasi* Waters & Arillo, 1999	SPANISH AMBER
Lower Cretaceous, Neocomian (145.0–121.4 Ma)	
Atelestites Grimaldi & Cumming, 1999 *senectus* Grimaldi & Cumming, 1999 ***Phaetempis*** Grimaldi & Cumming, 1999 *lebanensis* Grimaldi & Cumming, 1999	LEBANESE AMBER
Border of Jurassic age to Cretaceous age (146.0–141.0 Ma)	
Dianafranksia Coram, Jarzembowski & Mostovski, 2000 *fisheri* Coram, Jarzembowski & Mostovski, 2000	PURBECK LIMESTONE group, compression fossil

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