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Wasp mimicry among Palaeocene reduviid bugs from Svalbard

TORSTEN WAPPLER, ROMAIN GARROUSTE, MICHAEL S. ENGEL, and ANDRÉ NEL

The enigmatic Svalbard Palaeocene fossil taxon *Hymenopterites deperditus* is revised, and is neither a wasp nor a plant seed, but turns out to be a bug hemelytra corresponding to the oldest described reduviid bug. It can be attributable to the “emesine-saicine clade”. The presence in the Svalbard Palaeocene of this insectivorous bug, showing possible mimicry of a wasp model, confirms the presence of diverse entomofauna and of rather warm palaeoclimatic conditions.

Introduction

The attribution of fossils to some bug families can be rather delicate due to their frequent mimicry of other insects. Heteropteran (adults and nymphs) are involved in many mimetic complexes, including often with hymenopteran models, particularly ants and wasps, sometimes bees, but also spiders or even other Heteroptera (Schuh and Slater 1995; Zrzavy 1994; Santiago-Blay and Maldonado-Capriles 1988; Ambrose-Dunston 2003; Wignall and Taylor 2011). One of the characteristics of these cases of mimicry concerns the general habitus, wing coloration and shape, and venation including the presence of “pterostigmata” on the costal margin of the hemelytra. This is especially the case for some Emesinae (Reduviidae) that are considered probable spider mimics (Santiago-Blay and Maldonado-Capriles 1988; Wignall and Taylor 2011). Reduviid mimicry with wasps is well documented (Maldonado-Capriles and Robles 1992; Hogue 1993) and sometime spectacular (RG personal observation). The reduviid bugs seem to have hemelytral morphology and venation that sufficiently resemble wasp wings as to result in confusions among the palaeo-entomologists who have described them. For example, Nel (1992) noted a case with *Manevalia* Piton, 1940 that was originally attributed to Reduviidae but is in fact a hymenopteran wing.

A particularly interesting and remarkable case of such misidentification is *Hymenopterites deperditus* Heer, 1870 from the Palaeocene of the Svalbard Archipelago (Norway). This species was originally described as the forewing of an unknown wasp species, but upon recent examination it is actually the hemelytra of an assassin bug. Herein we provide a new description of the fossil and discuss its correct placement among the Reduviidae along with its concomitant implications for biogeography and the age of the family.

Abbreviations.—NRM, Swedish Museum of Natural History, Stockholm; PETM, Paleocene-Eocene Thermal Maximum; veins: Cu, cubitus; M, media; Pcu, postcubitus; R, radius; Rs, radial sector; cells: (M), cell between Cu and M; (t), triangular cell between Pcu and Cu.

Material and methods

The type specimen was collected from the *Taxodium* layer from Kapp Starostin (earlier spelled Cap Staratchin or Kap Staratschin). Kapp Starostin itself is made up of Permian rocks, but the section from there towards Grønfjorden ends in a small outcrop of lower Palaeocene conglomerates, and continues on the eastern side of Grønfjorden upsection into the Eocene. The closest place that exists in the vicinity of the Palaeocene occurrence west of Grønfjorden is Festningsodden (Winfried K. Dallmann personal communication, December 2011). Precise ages of Palaeocene sedimentary rock formations on Spitsbergen are still not entirely settled but no younger rocks than Eocene occur in the entire Isfjorden area (Dallmann et al. 1993, 1999). Vonderbank (1970) and Schweitzer (1980), based on plant and animal fossils, suggested that the lowermost Firkanten Formation should be dated as Palaeocene. Older biostratigraphic work also assigned a Palaeocene age to the Firkanten Formation (Ravn 1922; Manum 1962; Livšić 1974). Dallmann et al. (1999), although assigning a conservative Palaeocene age to the Firkanten Formation, considered the overlying Basilika Formation to be of Late Palaeocene age. This would suggest an Early to middle Palaeocene age for the Firkanten Formation. More recent data suggest that most of this formation was deposited after the Early Palaeocene thus clearly before the PETM (e.g., Cepek 2001; Dypvik et al. 2011; Wappler and Denk 2011). The specimen was examined using a Leica MZ 9.5 Stereomicroscope. Photographs were made with a Leica MZ 16 Stereomicroscope, and either JVC (model KY-F70B) or Nikon D100 digital camera and processed using image editing software (Adobe CS5®). For the descriptions we follow the wing venation nomenclature of Wygodzinski (1966) and Weirauch (2008).

Systematic palaeontology

Class Insecta Linnaeus, 1758

Order Hemiptera Linnaeus, 1758

Family Reduviidae Latreille, 1807

Genus *Hymenopterites* Heer, 1870

Type species: *Hymenopterites deperditus* Heer, 1870; Grønfjorden NW (SE of Festningsodden), Spitsbergen, Norway; Early Palaeocene.

Emended diagnosis.—Based on hemelytral characters only. Two distal cells between M, Rs and R, an ambient vein along distal margin of wing, cell (M) between Cu and M very long and broad; cell (t) rhomb in shape with acute distal angle.

Hymenopterites deperditus Heer, 1870

Fig. 1E, F.

Material.—Holotype specimen, NRM Ar. 46 (impression in a piece of black shale), leg. A.E. Nordenskiöld, 1868 (Stockholm, Sweden).

Description.—An incomplete hemelytra, membraneous and apparently hyaline except along the darker costal margin, elongate and very narrow, preserved part 7.10 mm long and 1.70 mm wide, probable complete length 8.0 mm; a dark broad area along costal margin from wing base to wing apex, 0.25 mm wide in widest part and 0.10 mm wide in narrowest part, near wing apex; M+Cu parallel to posterior wing margin near wing base, forming a strong angle and reaching R, then R+M+Cu parallel to costal margin more distally, only apical part of vein R present as a short vein reaching M+Cu just basal to point of separation between Cu and M; second longitudinal vein Pcu straight and closely parallel to posterior wing margin; short vein cu-pcu between M+Cu and Pcu, aligned with basal part of M+Cu and distal part of Pcu, emerging from M+Cu 5.50 mm from wing apex and 0.20 mm long; Cu emerging from M+Cu 0.30 mm distal of point of fusion of R with M+Cu, straight, 1.0 mm long; cell (t) formed by cubital and postcubital veins in membrane of forewing is rhomb in shape, with apex acute and oriented posteriad; M separating from R 2.70 mm distal of base of Cu and 2.60 mm from wing apex; a very large and broad cell (M) between Cu, Pcu, and M, 4.50 mm long and about 1.10 mm wide; Rs emerging from R and directed posteriorly towards M; R, M, and Rs defining a triangular cell, 1.3 mm long, 0.60 mm wide, a second cell distal to this first cell, distally limited by an ambient vein formed by R, M, and Pcu fusing together.

Discussion.—This fossil was originally described as a wasp under the name of *Hymenopterites deperditus* by Heer (1870: 96, pl. 16: 45). It was later revised by Birket-Smith (1977: 34, fig. 21) suggested that it was perhaps not an insect wing at all but a winged seed similar to that of an *Acer* sp. We disagree with both opinions because this fossil has not enough cells and veins to be a membrane of a winged seed and has not the venation of any living or fossil Hymenoptera, especially in the presence of an ambient vein in the apical part of the structure. In fact it corresponds in all visible details to the hemelytron of a reduviid bug, particularly those of the subfamily Saicinae in which the wing is also very narrow in its basal half and more rounded apically, with two main more-or-less parallel longitudinal veins, with three more-or-less oblique veins between them (cu-pcu, Cu, and M) that define large cells, and an ambient vein in the apical half of the wing (see Blinn 1994; Ishikawa and Yano 2002; Weirauch 2008). Some other heteropteran groups also have hemelytra with large cells (especially in the Enicocephalomorpha and Gerromorpha), but none have a similar pattern of organization of the veins R, M, and Cu in the basal half of wing, proper to the Reduviidae. Thus, we consider that the fossil belongs to the Reduviidae. Few subfamilies have a hemelytral venation showing some similarities with this fossil. More precisely, the nearly completely membraneous hemelytra (with reduced corium to basal part of the wing) is an apomorphy present in the subfamilies Ectrichodiinae, Emesinae,

Holoptilinae, Saicinae, Tribelocephalinae, and Visayanocorinae. The median and cubitus form a combined vein, an apomorphy present in the Ectrichodiinae, Saicinae, Tribelocephalinae, Vesciinae, and Visayanocorinae, while the shape of cell (t) is a specialized character present in Saicinae and in Visayanocorinae (Weirauch 2008). Thus *Hymenopterites* can be attributed to a bug closely related to the Saicinae because its wing venation strongly differs from those of the Visayanocorinae, in the narrower costal area (Miller 1952; Malipatil 1990). Ectrichodiinae, Tribelocephalinae, and Vesciinae have also hemelytra distinctly broader than in *Hymenopterites*. Nevertheless the dark “pterostigma” of *Hymenopterites* goes close to the wing apex, which is unlikely in modern Saicinae. It is quite possible that it can turn out to be a representative of some specific tribe or even subfamily (Yuri Popov, personal communication 2011). The fragmentary state of preservation of this fossil prevents a precise attribution as to subfamily except to note that it probably belongs to the complex of subfamilies of the “emesine-saicine clade” sensu Weirauch (2010).

Reduviidae have had a checkered history over the last few centuries, and even today there is little agreement on how many subfamilies Reduviidae contain. Since no study on the phylogeny of extant and extinct Reduvidae has been done so far, the divergence times of most scarab families remain widely uncertain (Weirauch and Schuh 2011). For Reduviidae, Weirauch (2008) has tested hypotheses of subfamily-level relationships within assassin bugs that corroborate the nesting of phymatine or ambush bugs within Reduviidae, establish a sister-group relationship between Ectrichodiinae + Tribelocephalinae, show Reduviinae to be polyphyletic, and recover Triatominae as monophyletic.

The only described Mesozoic taxon that has been attributed to the Reduviidae is *Liaoxia longa* Hong, 1987, based on a body compression from the Early Cretaceous of China. Except for the rostrum that seems to be more or less curved, there is no clear argument supporting this family assignment (Hong 1987). Yao et al. (2006) transferred Hong’s species into their Mesozoic family Vethanthorcoridae. Putshkov and Moulet (2009: 110) indicated the presence of undescribed compressions of Reduviidae from the Cretaceous of Mongolia, but these have not been described formally. Other fossil reduviids are all Cenozoic in origin, the oldest described being the harpactorine *Amphibolus disposi* Kinzelbach, 1970 from the middle Eocene Messel Formation (Germany) (Kinzelbach 1970; Forero et al. 2004). As already mentioned, *Manevalia pachyliformis* Piton, 1940 from the Palaeocene of Menat (France), was attributed originally to the Reduviidae but is in fact the hind wing of a symphytan wasp (Piton 1940; Nel 1992). Thus, *H. deperditus* can be considered as one of the oldest definitive record of the Reduviidae. Its attribution to the “emesine-saicine” group, which is one of the most derived clades in the lineage, strongly supports the conclusion that the Reduviidae diversified much earlier, during at least the Cretaceous (Patterson and Gaunt 2010). According to current opinion, the emergence of the predatory reduviids during the early Cretaceous period (135–70 Ma) is consistent with their current wide diversity in continents then connected as Gondwanaland. The calculated time for the separation of Gondwanaland is

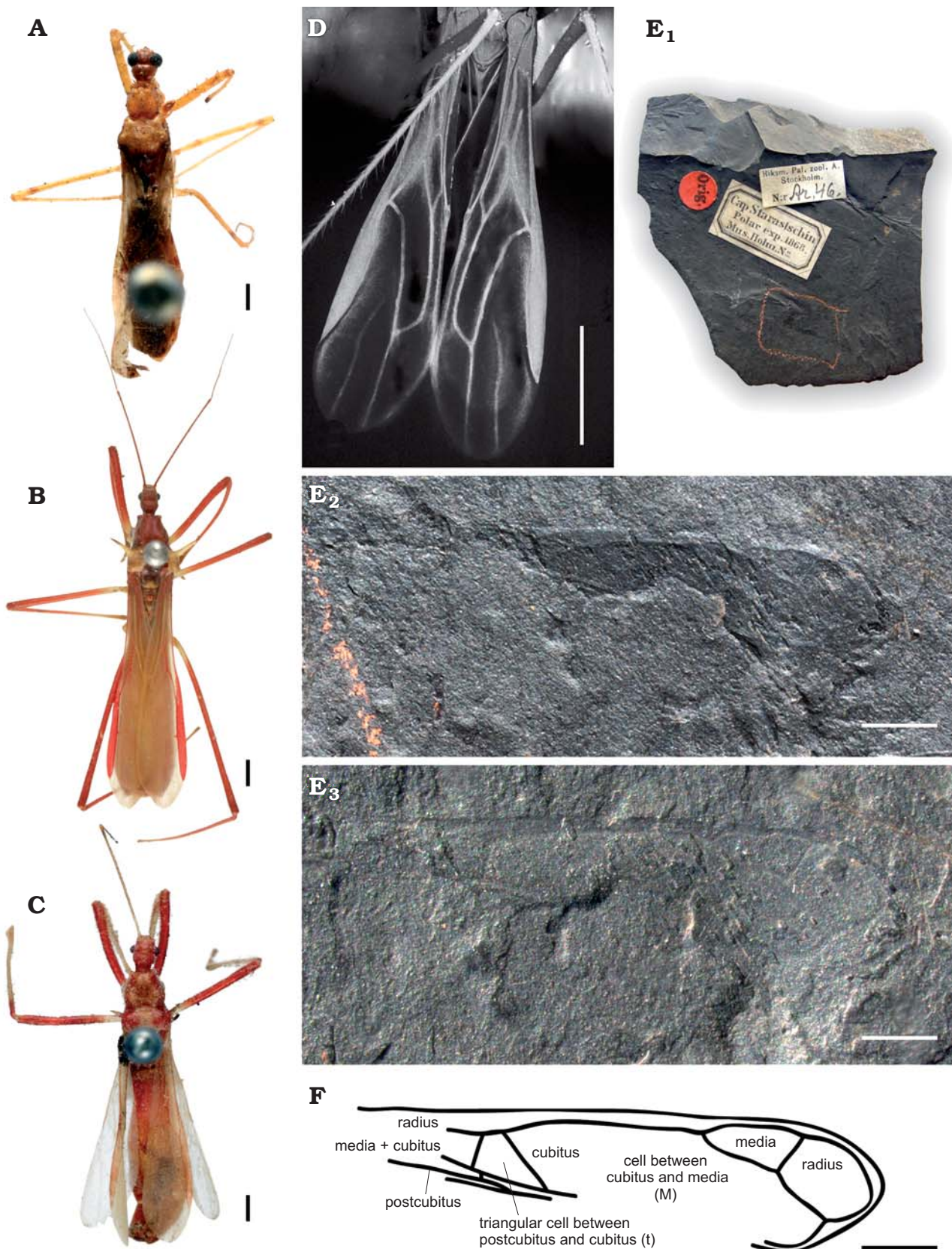


Fig. 1. Representative assassin bugs of the subfamily Saicinae (Reduviidae), Recent (A–D) and fossil (E) specimens. **A.** *Tagalis inornata* Stål, 1860. **B.** *Polytoxus wahlbergi* Stål, 1855. **C.** *Saica tibialis* Stål, 1862. **D.** Uncoated ESEM on the wings of *Tagalis* sp. (det. Christiane Weirauch). **E.** *Hymenopterites* Heer, 1870, coll. No. Ar 46. Holotype specimen with original labeling from Alfred Erik Nordenskiöld (E₁). Specimen photographed under normal light conditions (E₂) and under alcohol (E₃). **F.** Line drawing of forewing. Scale bars 1 mm.

about 100–90 Ma (Pitman et al. 1993). Africa and South America began to divide at their southern end about 120 Ma but did not become completely separated until less than 100 Ma (Smith et al. 1981). Divergence of the ancestors of the Triatomini and Rhodniini is then put at the time when South America was already separated from Africa.

Hymenopterites deperditus belongs to a group of insectivorous bugs, and its presence in the Palaeocene high latitudes of Svalbard demonstrates the presence of a complex insect ecosystem, revealed and confirmed by the 19th century discoveries of terrestrial and aquatic carnivorous, phytophagous, and detritivorous beetles (Heer 1870; Birket-Smith 1977). Modern Reduviidae of the “emesine-saicine group” are mainly pantropical, living in rather warm climate regimes, at least of the Mediterranean type (Putshkov and Moulet 2009). Thus, *H. deperditus* also suggests a similar climate for Svalbard during the Palaeocene (Greenwood et al. 2010; Harrington et al. 2011; Harding et al. 2011; Wappler and Denk 2011).

It is perhaps not a coincidence that this bug was of a gracile form given that these insects are transported easily to isolated islands by wind (analogous with the modern fauna from the Pacific area; Putshkov and Moulet 2009).

Lastly, Palaeocene mimicry of a heteropteran bug based on a hymenopteran model implies a relative long coevolution between the model and its mimic, and probably a relative diversity of the model lineage in the surrounding environment, or at least an obvious ecological importance or abundance which would drive the evolution of such a mimetic association. If Müllerian mimicry is supposed (both mimic and model are vulnerable for predators), this also implies the presence of at least one aculeate harmful wasp species and supports the hypothesis that the insects were an important component of the forests thriving in the higher latitudinal ecosystems.

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