A New Fossil Genus of Small-Headed Flies (Diptera: Acroceridae: Philopotinae) from Baltic Amber

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ABSTRACT A new genus of philopotine Acroceridae in Baltic amber is described from both sexes. *Archaeterphis hennigi* gen. et sp. nov. is easily diagnosed from all other acrocerid genera by the deeply emarginate hind margin of the eye, short mouthparts, reduced wing venation, modified hind femora, and the large postpronotal lobes being proximate but not touching. The new genus is closely related to the extant genus *Africaterphis* Schlinger from southern Africa, which accords with a common biogeographic pattern in insects.

ZUSAMMENFASSUNG Eine neue Gattung philopotiner Acroceriden aus dem Baltischen Bernstein wird von beiden Geschlechtern beschrieben. *Archaeterphis hennigi* gen. et sp. nov., ist eindeutig von allen anderen Acroceriden anhand des tief eingeschnittenen Augenhinterrands, des kurzen Rüssels, des reduzierten Flügelgeäders, der modifizierten Hinterschenkel und der grossen postpronotal Loben, welche sich naehern aber nicht berühren, zu unterscheiden. Die neue Gattung ist eng mit der rezenten Gattung *Africaterphis* Schlinger aus dem südlichen Afrika verwandt. Die nahe Verwandschaft zwischen fossilen Taxa des Baltischen Bernsteins und rezenten Taxa aus der Ethiopis, stellt ein häufig beobachtetes biogeographisches Muster dar.

KEY WORDS Diptera, Acroceridae, Baltic amber, fossil, Nemestrinoidea

Small-headed flies (Diptera: Acroceridae) are a distinctive group of true flies whose larvae develop as internal parasitoids of spiders. There are presently >500 described species worldwide with at least 50 genera divided among three subfamilies: Panopinae, Acrocerinae, and Philopotinae (Schlinger 2003). Acrocerids are often considered to be the sister group to Nemestrinidae, in the superfamily Nemestrinoidea. Evidence for the monophyly of this group is not conclusive, because it is based on a shared parasitoid life history of the two families (Woodley 1989), a biology derived in at least 21 different families through the entire Diptera (Eggleton and Belshaw 1992). Nemestrinoidea are numerous in the fossil record, although the bulk of these flies belong to Nemestrinidae described from Lower Jurassic- to Tertiary-aged compression fossils (Evenhuis 1994, Ansorge and Mostovski 2000, Mostovski and Martínez-Delclòs 2000). The origin of the superfamily likely occurred during the Lower Jurassic (Ansorge and Mostovski 2000), with the oldest definitive fossils of both Nemestrinidae and Acroceridae described from the Jurassic (Ussatchov 1968, Mostovski 1998). Evidence supporting a Jurassic divergence of Nemestrinidae and Acroceridae also comes from Bayesian-based dating methods of DNA sequence data (Wiegmann et al. 2003, Winterton et al. 2007), placing the age of the Nemestrinoidea within at least the Lower Jurassic.

Relatively few acrocerid fossils are described, and there is disparity among their ages (Grimaldi 1995, Grimaldi and Engel 2005). The oldest described fossils, *Juracyrtus kovalevi* Nartshuk and *Archocyrtus gibbosus* Ussatchov, are described from Upper Jurassic-aged (≈150 myo) Karatau deposits in Russia (Ussatchov 1968, Nartshuk 1996, Grimaldi et al. 2002). Based on the figures in Nartshuk (1996), both *Juracyrtus* and *Archocyrtus* are very similar in appearance, and these two specimens are probably congeneric, if not conspecific. The elongate mouthparts of *Juracyrtus* figured by Nartshuk (1996) are, however, probably misinterpretations of extraneous vegetative material, and the mouthparts are more probably very short like other *Acrocera*-like species (Grimaldi 1999, Grimaldi et al. 2002). The next oldest fossil is an undescribed species of Acroceridae from Burmese amber (Grimaldi et al. 2002, Grimaldi and Engel 2005) from the Upper Cretaceous (≈100 myo) (Zherikhin and Ross 2000). Hennig (1966) revised the Baltic amber fauna (mid-Eocene, ≈45 myo), describing two of the three species then known from this deposit. Of these species, one species belongs in the subfamily Acrocerinae and two species belong in

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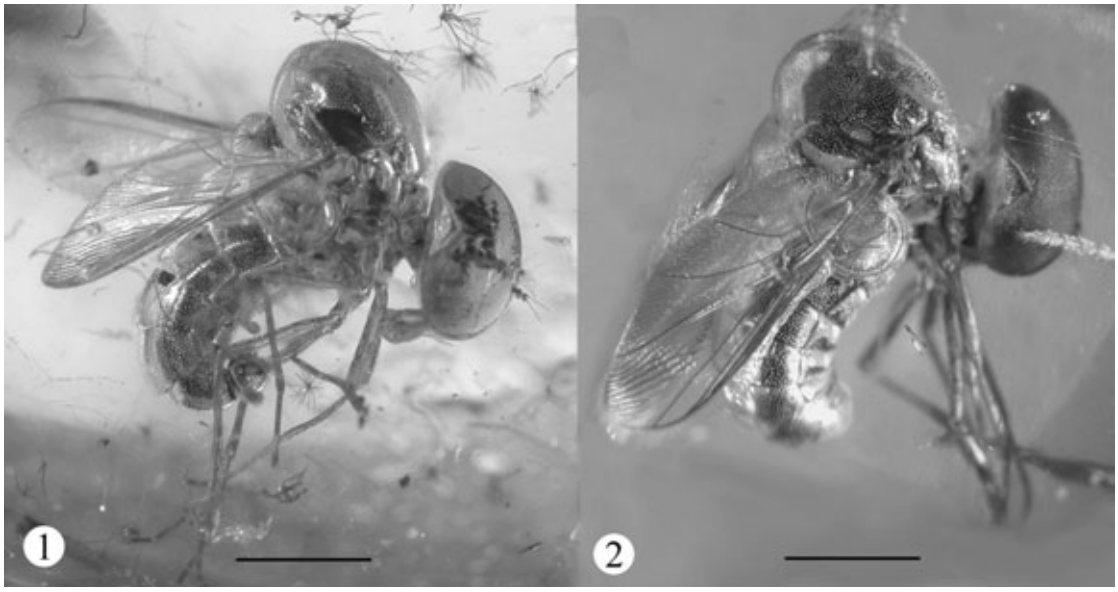


Figs. 1–2. Photomicrographs. (1) Male holotype of *A. hennigi* gen. et sp. nov., lateral view. Scale line = 1 mm. (2) Female paratype of *A. hennigi* gen. et sp. nov., lateral view. Scale line = 1 mm.

the subfamily Philopotinae. Hennig (1968) described a fourth species of Acrocerinae from Baltic amber. The geologically most recent fossil is known from the Dominican amber (Miocene) (Grimaldi 1995). The fossil acrocerid, *Archaeterphis hennigi* gen. et sp. nov., is described herein from two Baltic amber inclusions, represented by a male and a female. This new species is placed in the subfamily Philopotinae, and seems to be closely related to the extant southern African genus *Africaterphis* Schlinger.

Materials and Methods

Photographs of fossils were captured using a Nikon Coolpix 4500 digital camera mounted on a Nikon SMZ-1500 stereomicroscope. Terminology follows that of Schlinger (1981). Abbreviations are as follows: SMNS, Staatliches Museum für Naturkunde, Stuttgart (Germany); and AMNH, American Museum of Natural History, NY.

Archaeterphis gen. nov.
(Figs. 1–8)

Diagnosis. This genus is recognized by the reduced wing venation (only one single wing cell present), the reduced proboscis (Fig. 3), eyes being continuous above and below the antennae (Fig. 4) and deeply emarginate along the posterolateral margin (Fig. 3), the postocellar ridge and gena of head not raised into collar (raised collar characteristic of most philopotine genera) and by the postpronotal lobes being proximate but not touching.

Etymology. *Arche* (Gr.) = beginning; *Terphis* = an acrocerid genus; referring to the hypothesized close relationship to the extant sub-Saharan genus *Africaterphis* Schlinger and the New World genus *Terphis* Erichson.

Type Species. *Archaeterphis hennigi* sp. nov., by monotypy.

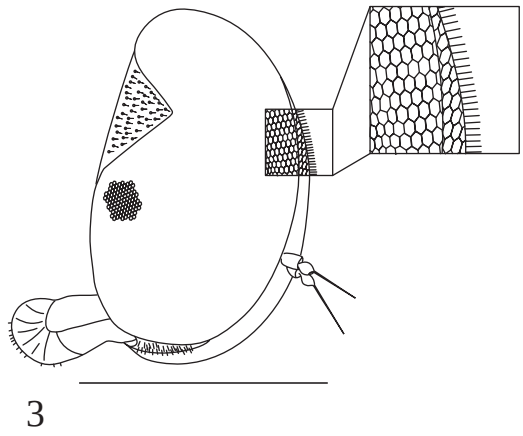
Description. See species description.

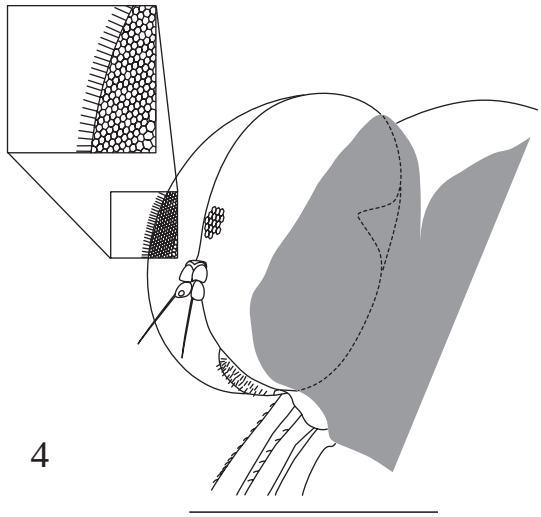
Archaeterphis hennigi sp. nov.
(Figs. 1–8)

Diagnosis. Characteristic for this species is the spine-like (male) (Fig. 7) or peg-like (female) (Fig. 8) extension on the base of the hind femur.

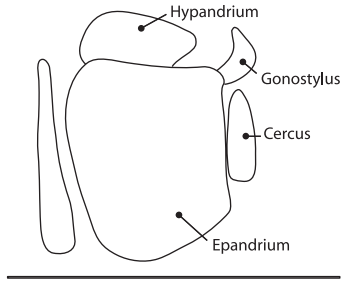
Etymology. This species is named in honor of Willi Hennig, whom besides laying down the foundation for modern phylogenetics also published the most comprehensive papers on fossil acrocerids in amber.

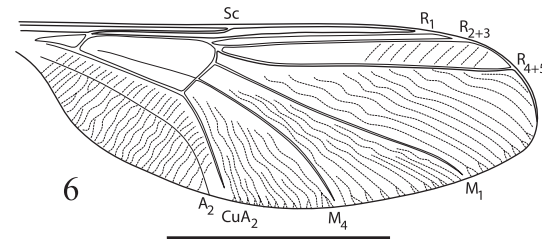
Description of male holotype (deposited in AMNH, type # Ba 13-17). Body length: 3.1 mm; wing length: 2.5 mm. *Head* ovate, higher than long; eyes holoptic (Fig. 3), covered with erect minute setae, meeting above and below antennal base; frontal ommatidia larger than marginal ones and extended across entire frons; frontal tubercle absent, eyes deeply emarginate along posterolateral margin; antenna inserted on lower half of head, closer to mouthparts than to ocellar tubercle; scape very small, hardly discernable; pedicel short, quadrate; flagellum ovate basally with long arista-like process, total length of flagellum more than four times the length of pedicel, anterobasally with round sensory pit on oval-shaped portion; ocellar tubercle small, raised; mouthparts short but not vestigial; maxillary palpus absent. *Thorax* with scutum distinctly raised and bulbous ('hump-backed'), covered with sparse short setae (Fig. 1); postpronotal lobes enlarged, proximate medially but not touching; scutellum relatively large, covered with short setae; wing

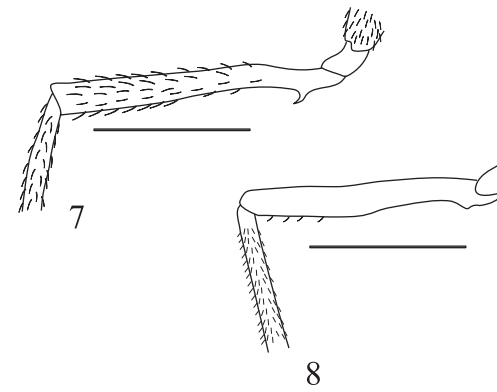




Figs. 3–4. *A. hennigi* gen. et sp. nov. (3) Male head, anterolateral view. Scale line = 1 mm. (4) Female head, lateral view. Scale line = 1 mm.







Figs. 5–8. *A. hennigi* gen. et sp. nov. (5) Male terminalia, lateral view. Scale line = 0.5 mm. (6) Female right wing, dorsal view. Scale line = 1 mm. (7) Male right hind femur, lateral view. Scale line = 0.5 mm. (8) Female right hind femur, lateral view. Scale line = 0.5 mm.

hyaline, relatively narrow; wing venation reduced with few cross-veins; membrane with numerous corrugations (rippled) (Fig. 6); costal vein terminating at wing apex; subcostal and radial veins closely grouped in anterior portion of wing, all joining costal margin before wing apex; vein A2 represented by a crease; *br* and *bm* cells separated by a crease in the wing membrane, thus forming a large combined cell basally in wing, which is the only wing cell present; legs covered with small setae, hind femur with distinctive spine-like process basally on ventral surface (Fig. 7). *Abdomen* long, curved ventrally with terminal segments constricted; setae short and sparse on all segments; sclerites of genitalia well defined (Fig. 5) with elongate gonostylus and hypandrium visible.

Comments. The amber matrix is reddish and darker than the matrix in which the female is preserved. Syninclusions are several mites, two nematoceran Diptera and one small parasitic wasp. A photograph of the male specimen was originally published by Janzen (2002) (fig. 377).

Description of paratype (coll Hauser, for deposition in SMNS).

Female (Figs. 2 and 4, 6, 8). As in male except for the following: Body length 3.0 mm. Scutum not as bulbous as in male; hind femur with only a small rounded peg basally on ventral surface (Fig. 8). The amber is clear yellow and transparent. The left side of the inclusion has some mold, which covers all of the left side of the body except parts of the legs, the wing and part of the eye. Syninclusions are fragments of a leg and antennae of a nematoceran fly.

Discussion

Archaeterphis gen. nov. is placed in the subfamily Philopotinae based on the enlarged postpronotal lobes and the humpbacked appearance. Enlarged postpronotal lobes that meet medially is a synapomorphy for the subfamily. In *Archaeterphis* gen. nov., the post-

pronotal lobes are closely proximate medially but are not contiguous. This condition is also found in one extant genus, *Africaterphis* from southern Africa (Schlinger 1968).

Philopotine acrocerids typically have elongate mouthparts that extend between the legs along the ventral surface of the body. By contrast, *Africaterphis* has short, but still functional mouthparts, as apparently does *Archaeterphis.* Compared with most philopotine acrocerids, *Archaeterphis hennigi* gen. et sp. nov. is small, approximately half the body length of most other philopotine acrocerids. Similar sized acrocerids in that subfamily include *Eulonchiella eocenica* Meunier, also from Baltic amber (Hennig 1966), an undescribed Burmese amber species (Grimaldi et al. 2002) and an undescribed extant genus from New Caledonia. Philopotinae form two distinctive groups based on wing venation; genera that have more complete venation include *Helle* Osten-Sacken, *Parahelle* Schlinger, *Thyllis* Erichson, *Dimacrocolus* Schlinger, *Megalybus* Philippi, and *Eulonchiella* Hennig. Those with relatively reduced wing venation include *Oligoneura* Bigot, *Philopota* Wiedemann, *Terphis*, *Africaterphis*, the aforementioned undescribed New Caledonian genus, and *Prophilopota* Hennig (Baltic amber). *Archaeterphis* gen. nov. fits within the latter group with venation similar to that of *Terphis* and *Africaterphis. Archaeterphis hennigi* gen. et sp. nov. shares some rather unique characteristics with *Africaterphis acroceroides* (Sabrosky) (e.g., short mouthparts, wing venation, proximate but noncontiguous postpronotal lobes), but erection of a new genus is proposed for these fossil specimens based on the very different head shaped (i.e., nonspherical and head lacking raised postocular and genal margins), recurved abdomen and emarginate posterior margin of the eye. *Archaeterphis hennigi* gen. et sp. nov. is the first acrocerid, extant or extinct, with cuticular spines or pegs on the femora.

Remarkable are the similarities of *Archaeterphis hennigi* gen. et sp. nov. with an undescribed Acrocerid from Burmese amber (Grimaldi et al. 2002). Both species have enlarged pronotal lobes, reduced mouthparts, eyes being continuous above and below the antennae, and deeply emarginate along the posterolateral margin as well as the small body size. An important difference is the wing venation, which is strongly reduced in *Archaeterphis hennigi* gen. et sp. nov., with only one cell present, but relatively complete in the undescribed Burmese fossil. A further comparison and a phylogenetic reclassification of these fossils have to await the description of this interesting fossil.

In conclusion, Schlinger (1971) divided the genera of Philopotinae into four genus groups, of which *Archaeterphis* gen. nov. would be placed in Group A along with *Terphis* and *Africaterphis.* There is a clear relationship between *Archaeterphis* gen. nov. and *Africaterphis* based on reduced wing venation, short mouthparts and only briefly contiguous postpronotal lobes. The relationship between extinct Baltic amber groups and recent sub-Saharan groups is a common pattern. The climate conditions of the amber forest must have been sub-tropical and therefore much warmer than the climate in this region today. Engel (2001) described the strong relationships of the Baltic amber bee fauna with the extant fauna of sub-Saharan Africa and Asia. Also, Hennig (1966) suggested a close relationship between the fossil *Eulonchiella* and the genus *Thyllis* from southern Africa. The same pattern is found in the recently described order Mantophasmatodea, which was first discovered as a Baltic amber fossil and only later extant species were found in southern Africa (reviewed by Grimaldi and Engel 2005). Therefore, the putative relationship between the Eocene *Archaeterphis* from Baltic amber and the recent *Africaterphis* from southern Africa corresponds to a well-documented zoogeographic pattern.

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