

First record of the Strepsiptera genus *Caenocholax* in Baltic amber with the description of a new species

Jeyaraney Kathirithamby & Hans Henderickx

Abstract. A new species of Strepsiptera, *Caenocholax groehni* sp. n., in Baltic amber (44 myo) is described. This might prove morphological stasis and the existence of a largely recent New World lineage in the Baltic region more than 40 million years ago. It also supplies evidence concerning the ancient origin of Strepsiptera, and shows that species of this genus were in existence throughout most of the Tertiary. A revised diagnosis of the genus *Caenocholax* is also provided.

Samenvatting. Eerste vermelding van het genus *Caenocholax* (Strepsiptera) in Baltische barnsteen en beschrijving van een nieuwe soort.

Een nieuwe soort Strepsiptera, *Caenocholax groehni* sp. n., uit Baltische barnsteen (44 miljoen jaar oud) wordt beschreven. Deze soort kan eventueel morfologische stasis bevestigen en het bestaan aantonen van een tamelijk recente verbinding van de Baltische streek met de Nieuwe wereld iets meer dan 40 miljoen jaar geleden. Het biedt tevens bewijs voor het oeroude ontstaan van de Strepsiptera en toont verder aan dat de soorten uit dit genus voorkwamen gedurende het Tertiair. Een aangepaste diagnose voor het genus *Caenocholax* wordt gegeven.

Résumé. Première mention du genre *Caenocholax* (Strepsiptera) dans l'ambre baltique avec description d'une espèce nouvelle.

Une espèce nouvelle de Strepsiptère, *Caenocholax groehni* sp. n., provenant de l'ambre baltique (44 millions d'années) est décrite. Cette découverte pourrait confirmer le stasis morphologique et l'existence d'une relation entre la région baltique et le Nouveau Monde d'il y a plus de 40 millions d'années. De plus, l'origine très ancienne des Strepsiptera est ainsi confirmée ainsi que la présence des espèces de ce genre pendant la période tertiaire. Une diagnose révisée du genre *Caenocholax* est présentée.

Key words: Strepsiptera – Baltic amber – *Caenocholax* – new species.

Kathirithamby, J.: Department of Zoology, South Parks Road, Oxford OX1 3PS, UK.
jeyaraney.kathirithamby@zoo.ox.ac.uk (author for correspondence).

Henderickx, H.: Department of Biology, University Antwerp, Groenenborgerlaan 171, 2020 Antwerpen, Belgium.

Introduction

Since the description of the first strepsipteran by Rossi in 1793, morphological stasis has been observed in Strepsiptera, mainly from extant species. However, in the present study we report that fossil Strepsiptera display stasis for 40 million years, and we describe a new species of *Caenocholax* (Myrmecolacidae) from Baltic amber.

The sexes in Strepsiptera exhibit extreme dimorphism: adult males are morphologically highly specialized and free-living, while females are neotenic, endoparasitic (except in the family Mengenillidae), and devoid of most recognizable insect features. The extreme sexual dimorphism in Strepsiptera extends in the members of the family Myrmecolacidae even to their hosts which are disparate: the sexes parasitize hosts belonging not only to different species, but to different orders of insects. Heteronomy is found in only two lineages of insects: the strepsipteran family Myrmecolacidae (Kathirithamby 1991) and the hymenopteran subfamily Aphelinidae (Walter 1982), both of which are parasitic

insect groups. Males of Myrmecolacidae parasitize Hymenoptera (ants) and females parasitize Orthoptera (grasshoppers and crickets) and Mantodea (Ogloblin 1939, Kathirithamby 1991, Kathirithamby & Hamilton 1992, Kathirithamby & Johnston 2004). The here described new myrmecolacid appears to belong to *Caenocholax*, a genus with extant members that are morphologically remarkably similar but genetically very divergent.

Materials and Methods

The specimen is fossilized in a clear yellow piece of Baltic amber (14×5×2 mm) showing a trace of the original crust and stellate hairs which are typical of this amber.

FTIR analysis was conducted. In the graphic of the sample (Fig. 1) the typical 'Baltic shoulder curve' is clear (Y. Sashoua, personal communication).

After examination, the amber was coated for preservation on a rotating device in viscoused Epoxy (Araldite 2020). Examinations and measurements have been carried out with a Leitz microscope and Optika Photolib software, additionally with a Zeiss measuring ocular and object plate. Pictures were taken with a Fuji Finepix S2 camera, combined when necessary with Helicon Focus software.

All measurements are in mm.

Family Myrmecolacidae Saunders

Myrmecolacides Saunders, 1872

Genus *Caenocholax*

Caenocholax Pierce, 1909

Type species: male *Caenocholax fenyesi* Pierce, 1909, from Cordoba, Veracruz, Mexico: USNM type 10081, originally part of the Fenyés collection at the Californian Academy of Sciences, San Francisco.

Diagnosis of *Caenocholax*: The following are the general characteristics of the *Caenocholax* complex:

Aedeagus: dorsally curved prong, with anchor-shaped dorsal terminal plate with a long medial and two lateral spines (Kathirithamby & Johnston 1992, Kathirithamby & Grimaldi 1993), or with median spine only.

Abdominal segment X: enlarged lobate plate overhanging abdominal segment IX (Kathirithamby & Johnston 1992).

Wing: R₂ short, R₃ absent; MA slightly longer than CuA, CuP absent (Kathirithamby & Johnston 1992).

Description

Caenocholax groehni sp. n. (Fig. 2)

Male fossil material: Type specimen in a clear piece of Baltic amber from Kaliningrad, Russia, ex coll. Gröhn 1500, deposited at the Geologisch-Paläontologisches Institut und Museum, Hamburg (GPIH 4495).

Etymology: named after the collector Carsten Gröhn.

Diagnosis:

Head: Mandibles short, 0.11 mm (L), 0.02 mm (W); maxilla 0.25 mm (L), 0.02 mm (W); eyes large with about 20 eyelets.

Antennae: 7-segmented; antennomere III (0.39 mm) lamellate; antennomere IV (0.03 mm), V (0.18 mm) and VI (0.11 mm) almost half the length of antennomere VII (0.20 mm).

Wing venation similar to *C. fenyesei* sensu lato: R₂ short, R₅ ending considerably distant from wing margin; MA slightly longer than CuA; CuP absent.

Tarsi: 4-segmented without pretarsal claws; sensory spots visible on basitarsus.

Aedeagus: only the large and curved basal part is visible.

Abdominal segment X: large lobate plate, which narrows apically overhanging abdominal segment IX.

Body length: 1.35 mm.

Caenocholax groehni **sp. n.** differs from the other three extant genera of Myrmecolacidae in the absence of R₃, CuA₁ and CuA₂ veins (*Lyncholax* Bohart, 1951), absence of CuP (which is long in *Myrmecolax* Westwood, 1861), and absence of MA₁ (which is long in *Stichotrema* Hofeneder, 1910). The wing venation (short R₂, absence of MA₁ and CuP) and short mandibles in the new fossil species are typical of *Caenocholax*. It differs from *C. fenyesei* sensu lato in the proportions of the antennae. Antennomere III plus flabellum is shorter (0.39 mm) in *C. groehni* **sp. n.** than in the two fossil specimens from Dominican amber, *C. dominicensis* (, 1993) and *C. brodzinskyi* (Kathirithamby & Grimaldi, 1993). The antennomeres VI and VII are not equal in length (VII twice that of VI) in *C. groehni* **sp. n.**, whereas they are equal in length (VI 0.19–0.24 mm, VII 0.19–0.28 mm) in *C. fenyesei* and in both Dominican fossil species (*C. dominicensis* VI, VII 0.71 mm; *C. brodzinskyi* VI, VII 0.56 mm in DR-10-3 and 0.68 in DR-10-5). The large Xth abdominal segment, typical of *C. fenyesei* sensu lato, narrows apically in *C. groehni* **sp. n.** whereas it is broad with a straight posterior margin in *C. fenyesei texensis* Kathirithamby & Johnston, 2004 and *C. fenyesei waloffi* Kathirithamby & Johnston, 2004 and distinctly narrowed and notched apically in *C. brodzinskyi*.

Caenocholax groehni **sp. n.** differs from the fossil *Palaeomyrmecolax succineus* (Kulicka, 2001) by the shape of the maxilla (which is round and narrow, rather than wide and flat as in *P. succineus*) and the antennomere VII is three times as long as VI in *P. succineus*. The R₃ and CuP veins are present in *P. succineus*, *P. giecewiczi* Kulicka, 2001 and *P. gracilis* Kulicka, 2001, but are absent in *C. groehni* **sp. n.**; the MP and CuA veins extend to the wing margin in *P. succineus*, *P. giecewiczi* and *P. gracilis* but not in *C. groehni* **sp. n.**

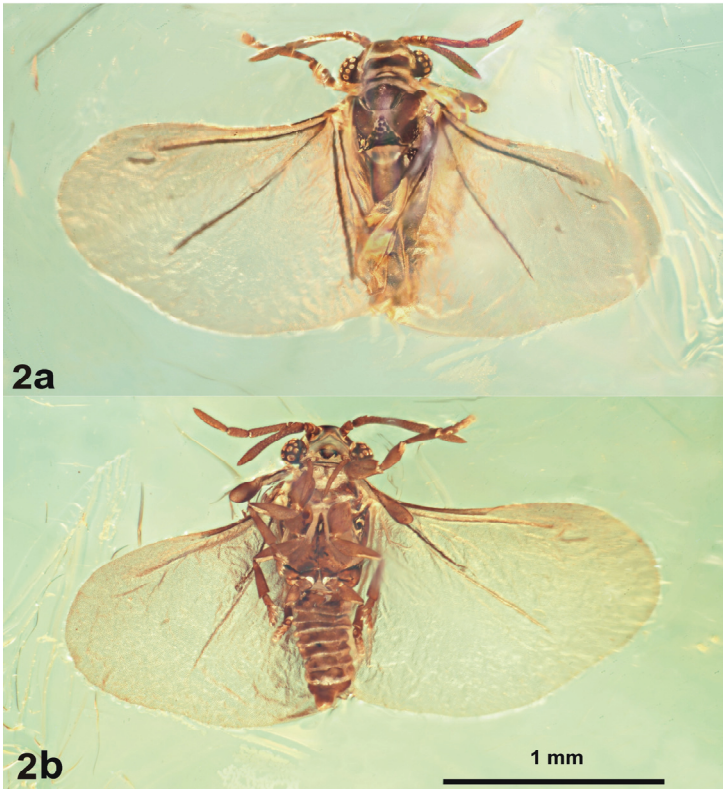
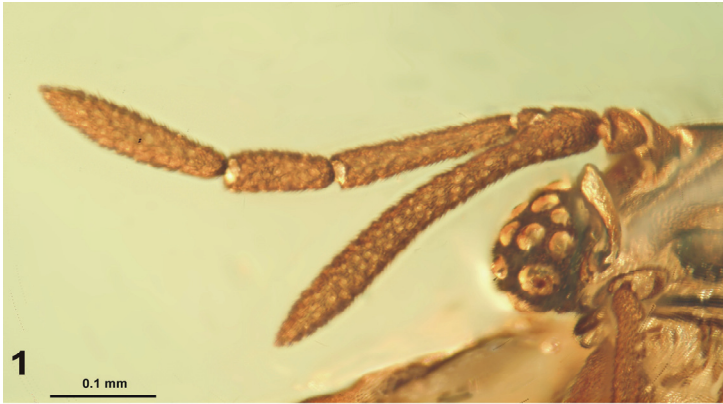


Fig. 1. *Caenocholax groehni* sp. n., holotype; ventral view of head with right antenna and right mandibula.

Fig. 2. *Caenocholax groehni* sp. n., holotype; a: dorsal view, b: ventral view.

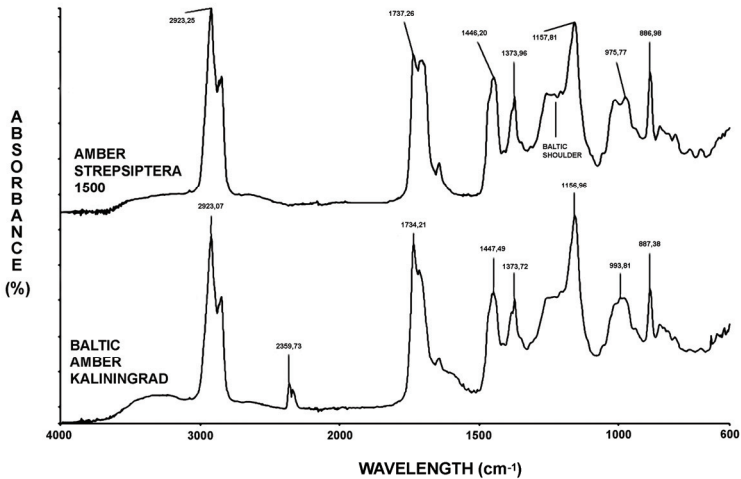


Fig 3. FTIR analysis of *Caenocholax groehni* sp. n. holotype amber matrix, graphic, Baltic shoulder indicated.

Based on the morphology of the striking wing venation similar with *Caenocholax fenyesi* sensu lato, the shape of the Xth abdominal segment and the antennal proportions this specimen appears to be closest to the genus *Caenocholax*, and is therefore described in this genus.

Discussion

The hypothesis is that Strepsiptera originated in the Early Cretaceous or Late Jurassic (Grimaldi *et al.* 2005, Grimaldi & Engel 2005). Fossil records of Strepsiptera have shown punctuated change in extinct species (Grimaldi *et al.* 2005, Pohl *et al.* 2005). A primitive extinct strepsipteran, *Cretostylops* (Grimaldi *et al.* 2005), was described from the Cretaceous Burmese amber while the Eocene Baltic amber contained the most primitive strepsipteran *Protoxenos*, a sister group to all other strepsipterans (Pohl *et al.* 2005), and the extinct primitive genus *Menge* (Menge 1866). Myrmecolacids *Stichotrema* and *Palaeomyrmecolax* have been found in the Baltic amber (Kinzelbach & Pohl 1994, Pohl & Kinzelbach 1995, Kulicka 2001), and 1st instar larvae are known from Eocene brown coal (Kinzelbach & Lutz 1985) but no *Caenocholax* has so far been reported from this age. From the Miocene Dominican amber the extant families Myrmecolacidae (Kinzelbach 1983, Kathirithamby & Grimaldi 1993, Kinzelbach & Pohl 1994, Pohl & Kinzelbach 1995), Elenchidae (Kinzelbach

1979, Kinzelbach & Pohl 1994) and Bohartillidae (Kathirithamby & Grimaldi 1993, Kinzelbach & Pohl 1994) have been described. These findings suggest that the Eocene was probably a transitional period between archaic and modern Strepsiptera faunas (Grimaldi *et al.* 2005). Stasis has been observed in Dominican amber in the case of *Bohartilla megalognatha* (Kathirithamby & Grimaldi, 1993), two species of *Caenocholax* and three species of *Stichotrema* (Kathirithamby & Grimaldi 1993, Kinzelbach & Pohl 1994). *Caenocholax groehni* **sp. n.**, however, is the first extinct species to indicate such an extensive period of morphological stasis in Strepsiptera.

The discovery of the genus *Caenocholax* in Baltic amber offers a possible explanation of the biogeography of the *C. fenyesei* species complex: the ancestors were possibly widespread during the globally tropical/subtropical Eocene. Recent males of *Caenocholax* have a general similarity in morphology and secondary sexual characters through out their range from southern United States, through Central America to South America, and from Vietnam (East Asia). The present report of a myrmecolacid from Baltic amber, close to recent males of the *fenyesei* complex, establishes even with more certainty that Strepsiptera undergo long periods of morphological stasis. The extreme sexual dimorphism in Strepsiptera allows stasis to be observed prominently only in one sex – the male.

Molecular genetic studies are revealing that there is cryptic speciation in Strepsiptera. Recent male *C. fenyesei* are similar morphologically but show dramatic underlying genetic divergence (Kathirithamby & Johnston 2004, Kathirithamby *et al.* 2007). Speciation in this group of bizarre entomophagous parasitoids might entail gradual Darwinian microevolutionary changes in genetic divergence.

Morphological stasis in Strepsiptera has been observed over a wide geographical range in recent taxa (Kathirithamby *et al.* 2007), and we here show that it is also observed over a long time span. Morphological stasis is recognized as one of the striking aspects of fossil records (Williamson 1981), and the geological time of morphological stasis varies greatly between taxa. Morphological stasis is seen here for the first time in Strepsiptera to be more than 40 million years.

There are only two fossil records of parasitized ants. Pohl & Kinzelbach (2001) describe a possible female myrmecolacid parasitic in a now extinct ant subfamily Prionomyrmecinae, *Prionomyrmex* sp., from the Baltic amber. But the photograph provided in the paper is not very convincing that it is a female myrmecolacid. A more convincing suggestion that males of myrmecolacids parasitized ants in the Eocene was advanced by Lutz (1990), who reports of a find of a *Camponotus* sp. with two male puparia of *Stichotrema* in Middle Eocene oil slate. Males of *C. fenyesei* have so far been found to parasitize the ant subfamilies Dolichoridinae, Formicinae and Myrmicinae in the Nearctic, Central and South America (Kathirithamby 2009, in press). All three subfamilies of ants have also been found in Eocene Baltic amber (Grimaldi & Engel 2005). Only two records of female strepsipterans are found in fossil records: one in an ant

(doubtful if female, Pohl & Kinzelbach 2001) and a delphacid with a female with 1st instar larvae (Poinar 2004).

All fossil Myrmecolacidae are from the Eocene, and that they parasitized ants in the Eocene is indicated by the parasitized *Camponotus* in the Eocene brown coal. The age of the host-relations of the female myrmecolacids are more difficult to estimate, as no specific records have been found. This may be because stylopized hosts, especially those with endoparasitic female strepsipterans exhibit a change in behaviour (Kathirithamby 2005). Hence more fossil free-flying male strepsipterans are found than females which remain endoparasitic in hosts (except in the family Mengenillidae).

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