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A putative twisted-wing parasitoid planidium (Insecta: Strepsiptera) in Taimyr Upper Cretaceous amber

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ABSTRACT

A planidium is newly recorded from Upper Cretaceous (Santonian) amber of the Taimyr Peninsula, Krasnoyarsk Territory, Siberia. This peculiar fossil is tentatively attributed to the order Strepsiptera, representing the first record of this lineage from these deposits. Planidia of a similar conicocephalate form are known from the slightly younger amber of western Canada (Campanian) as well as in the earlier (Cenomanian) amber of Myanmar, and comparisons are made with those fossils, as well as with living Strepsiptera and the beetle family Ripiphoridae (Tenebrionoidea). Given recent debate concerning the strepsipteran attribution of these planidia, we provide some discussion about the available and expected character evidence, and tend to believe assignment to Ripiphoridae is untenable. While placement with Strepsiptera remains difficult to state conclusively, the current limited evidence still tends to prefer the strepsipteran hypothesis.

1. Introduction

The Strepsiptera, or twisted-wing parasitoids, are one of the more remarkable of insect orders. While seemingly miniscule in proportions and diversity compared to their titanic relatives among the Holometabola, they more than compensate in their considerable biological, physiological, morphological, and life-history specializations (Kinzelbach, 1971a, 1971b, 1978; Kathirithamby, 1989, 2009; Grimaldi and Engel, 2005). All of the approximately 613 species (Kathirithamby, 2015) of living Strepsiptera are parasitoids of other insect lineages, and in all but one family the adult females are obligate endoparasitoids that have lost their appendages (inclusive of the mouthparts and antennae), wings, compound eyes, genitalia, and other typically mature structures. The free-living females of Mengenillidae, which are obligate parasitoids on silverfish (Zygentoma), are still neotenic, but they are exceptional in that they primitively retain their appendages, compound eyes, and more clearly defined body segmentation. Further, it is solely within the Mengenillidae that late instar females emerge from the host and pupate externally (as do the males). Females of all forms are viviparous. Males, while appearing as more typical free-living adult insects, possess many unusual features. The males are novel for their reduction of the forewings (resembling the hind wing halteres of Diptera), their unique hind wings (and the associated expanded metathorax resulting from posteromotorism), largely reduced mouthparts, distinctive compound eyes with large eyelets separated by microtrichiate integument, and a remarkably small genome (Johnston et al., 2004), among other unique attributes (Kinzelbach, 1971b, 1978; Kathirithamby, 1989, 2009). Associated with these many specializations are diverse life histories and host associations, ranging from the aforementioned silverfish to Orthoptera, Dictyoptera (Blattaria and Mantodea), Hemiptera, Diptera, and particularly aculeate Hymenoptera (Kathirithamby, 1989, 2009).

The early larval instars of Strepsiptera. Strepsipterans exhibit hypermetamorphosis and the first instars are free-living planidia.

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The planidia are highly active and seek out new hosts or become phoretic on transient hosts that carry them back to their nests where they victimize the brood. Once on the host they secrete enzymes that permit them to invade the host's body, and then quickly molt to an apodous larval form, inducing the host's tissues to produce a chamber in which the parasitoid feeds and continues its development (Kathirithamby, 2009). The highly mobile planidium is perhaps key to the diversification of the Strepsiptera across a broad array of host taxa. Mobility allows the larvae to locate and parasitize one of a potential range of suitable hosts in a variety of microhabitats.

Not surprisingly for a lineage of endoparasitoid insects, there is a less than robust fossil record. Further, many fossil deposits lack sufficient fidelity to permit ready recognition and comparison with extant relatives of such small insects (most adults are around 1.5–5 mm in total body length). Accordingly, most fossils are preserved in amber and largely comprise the free-living adult males, because as they are the most conspicuous dispersal form. Males of various families have been recorded in lower Miocene Dominican amber (Kinzelbach, 1979, 1983; Kathirithamby and Grimaldi, 1993; Pohl and Kinzelbach, 1995) and Eocene Baltic amber (e.g., Menge, 1866; Kulicka, 1978, 1979, 2001; Kinzelbach and Pohl, 1994; Pohl and Kinzelbach, 1995, 2001; Pohl et al., 2005; Kathirithamby and Henderickx, 2008; Henderickx et al., 2013; Kogan et al. 2015) with one male recorded from lower Eocene Fushun amber (Wang et al., 2014, 2016) and three described males in the Upper Cretaceous amber of Myanmar (Grimaldi et al., 2005; Engel et al., 2016; Pohl and Beutel, 2016). Two pupae of male Myrmecolacidae parasitic in an ant, a female cephalothorax in an ant host, a planidium, and two adult males were also recorded from Middle Eocene oil slate, Baltic amber, Eocene brown coal of the Geiseltal, and compression deposits in thinly bedded limestone, respectively (Kinzelbach and Lutz, 1985; Lutz, 1990; Pohl and Kinzelbach, 2001; Pohl, 2009; Antell and Kathirithamby, 2016). Quite fascinatingly, putative planidia have also been documented from Cretaceous amber (Grimaldi et al., 2005), although the latter have been disputed (Beutel et al., 2016; *vide etiam* Discussion).

Here we record the presence of a putative strepsipteran planidium for the first time from Santonian-aged Taimyrian amber of the Kheta Formation. If true, this larva represents the first account of the order for these deposits. The planidium is similar in some important details with the instar described from the Upper Cretaceous (Campanian) Foremost Formation in western Canada (Grimaldi et al., 2005). It also shares some features of a planidium reported from Upper Cretaceous Burmese amber (Beutel et al., 2016), with all three differing in seemingly the same details from modern strepsipteran planidia. Most notably the Cretaceous forms have a pronouncedly conical head, whereas conicocephalate forms are unknown even in the most primitive of crown-group strepsipterans (Pohl, 2002), nor are they indicative of planidia occurring in any other order. Here we describe the present fossil and provide a brief discussion as to its potential affinities with Strepsiptera in favor over alternative hypotheses.

2. Material and methods

A single planidium was identified in a piece of relative clear, yellow retinite from the Kheta Formation (Santonian) in 2012 by A.G. Ponomarenko. The retinites originated from the Yantardakh locality of a cliff ca. 200 m long, 30 m high: 71°18′26.54″N 99°33′46.51″E, just northeast from the tiny settlement of Katyryk, right bank of the Maimecha River, 3 km upstream from its confluence with the Kheta River (Rasnitsyn et al., 2016: their figure 3). Pieces were collected by the expedition of Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN) in 2012 by E.A. Sidorchuk, D.S. Kopylov, and D.D. Vorontsov. The Kheta Formation has been dated by Saks et al. (1959) biostratigraphically as Coniacian-Santonian, with most of the retinite at Yantardakh originating from the upper horizons, leading Zherikhin (1978) to ascribe a Santonian age to the amberiferous layer. The Mutino Formation conformably overlays, without breaks, the amber layer (Rasnitsyn, 1980), and includes the mollusc genus *Inoceramus* Sowerby 1814, (Bivalvia: Praecardioida: Inoceramidae), of late Santonian to early Campanian age (Zherikhin and Eskov, 1999). The amber itself is likely from the upper Santonian, but a more precise assignment cannot be made at this time. The environment has been inferred as warm-temperate, but this is reconstructed for the Mutino Formation (Golovneva, 2012), and is only presumed for the underlying horizons. Certainly the known insect inclusions do not contradict such a conclusion, with the general biota of Taimyrian amber summarized by Zherikhin (1978). The locality of the amber-bearing strata has been detailed and mapped by Perkovsky and Makarkin (2015: their figure 1).

The amber piece was trimmed and polished into a thin chip approximately 1.26 mm wide and 1.64 mm long, with the inclusion situated near the center and with its long axis parallel to the amber's length. The specimen is situated with its legs outstretched from the body. Although there are some minor fractures and distortions within the amber, there are no major obstacles obscuring dorsal and ventral views of the inclusions, although its exceedingly small size makes some of its microscopic structural details difficult to resolve. Lateral views are not possible through the thin edge of the amber chip. No syninclusions were present with the planidium.

Photographs of the inclusion were taken with a Zeiss Axioimager M1, in Kiev and Leica M165 with attached Leica DFC 425 digital camera (PIN). The format and general morphological terminology for the description are modeled after Grimaldi et al. (2005), particularly given the remarkable similarity of the planidia. The description is provided in the context of preparing a comparative account of Cretaceous strepsipterans as such work is the first step toward broader explanations of diversity through time (Grimaldi and Engel, 2007). We have adopted here the term 'planidium' for the mobile, first instar, rather than the often used terms 'triungulin' or 'triungulinid' (the latter are specialized descriptors applicable only to the three-clawed first instars of Meloidae, 'triungulin' by definition refers to the three-clawed condition, which is not applicable for these larvae or, in fact, any larva outside of Meloidae). Thus, 'planidium' is a more general term for the kind of larvae observed in other insect groups, including Strepsiptera, and avoids unintended connotations tied to 'triungulin'.

3. Systematic palaeontology

Order Strepsiptera Kirby, 1813
Family Indeterminate

Planidium (Fig. 1)

Material. Planidium (first instar), PIN 3311/3243, Paleontological Institute of the Russian Academy of Sciences, Moscow. Deposited in the Paleontological Institute, Russian Academy of Sciences, Moscow.

Locality and horizon. Russia: Krasnoyarskiy Krai, Taimyrsky (Dolgano-Nenetsky) District, Taimyr Peninsula, right bank of the Maimecha River 3 km upstream from its confluence with the Kheta River (a left tributary of the Khatanga River), Yantardakh Hill. Upper Cretaceous, Santonian (Kheta Formation).

Description. Total length (from apex of head to apex of abdominal sclerites, not including styli) 528.4 μm; integument generally brown and slightly translucent (gut can be seen running length of