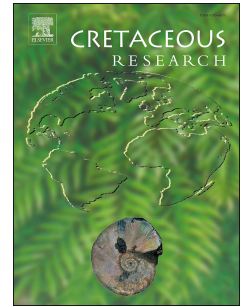# Accepted Manuscript

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Cretaceous Research

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

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ASTRACT

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.

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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 posteromoterism), 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).

Of particular interest here are the early larval instars of Strepsiptera. Strepsipterans exhibit hypermetamorphosis and the first instars are free-living planidia. 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

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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; Kogan, et al. 2015) 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), 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, in press). 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.

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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, consisting 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, and although there are some minor fractures and distortions within the amber, there are no major obstacles obscuring dorsal and ventral views of the inclusion (although its exceedingly small size places 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 body as a lighter area, widening in abdomen and narrow through thorax); integumental surface relatively smooth although apparently microscopically textured (finely imbricate or coriaceous?) on thoracic nota and abdominal terga.

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Head prognathous, conical, tapering anteriorly to acutely rounded point, shorter than pronotum, median cephalic length 47.8 µm, maximum posterior width 83.3 µm; no sutures evident; head separated from pronotum by distinct membranous cervix. Apical part of head in ventral view apparently with small set of mandibles situated in a ventral groove along apical cone; mandibles close together, positioned to move horizontally, with apex curved, apparently without subapical teeth. Presumably two stemmata present at posterolateral area of head dorsum (circular lighter patches that are presumably stemmata anterior and posterior to area where material is being extruded from head capsule on either side). Two coarse ctenidia on ventral posterior surface, anterior row composed of 4–5 teeth on either side of a broad gap, with gap between each lateral part about one-half width of row, and posterior row composed of 8–9 teeth on either side of midline, without prominent medial gap and spanning full posterior width of head.

Pronotum large, broad, median length 54.4 µm, median width 84.5 µm, lateral borders straight and parallel, anterior margin weakly convex, posterior margin faintly concave; apicolateral angles each with a prominent, stiff, elongate seta extending outward from body, setal length 65.6 µm; surface with scattered, minute, appressed setae. Mesonotum large, median length 67.5 µm, maximum width (posteriorly) 89.2 µm, lateral borders straight, converging anteriorly, anterior width 61.6 µm; anterior border apparently straight, posterior margin distinctly concave, giving posterolateral corners a broadly rounded, lobed appearance; apicolateral angles each with two prominent, stiff, elongate setae extending outward from body, setal length 48.9 µm; surface with minute, appressed, posteriorly-directed setae scattered over surface. Metanotum large (largest of thoracic segments), median length 78.5 µm, maximum width (posteriorly) 94.5 µm, lateral borders straight, converging anteriorly, anterior width 62.8 µm; anterior border apparently straight, posterior margin faintly concave; apicolateral angles each with two prominent, stiff, elongate setae extending outward from body, setal length 48.9 µm; surface with scattered, minute, appressed setae although sparser than those on pronotum or mesonotum. Legs well-developed and laterally extended; coxae not fused to thorax, comparatively large, articulated posterolaterally on each thoracic venter, ventrally separated by at least 2x coxal length on prothorax and ca. 1x coxal length on meso- and metathoracic segments, each coxa with some short, stiff, preapical setae; trochanters absent, apparently completely fused to femora; femora strongly crassate, profemur length 45.3 µm, maximum width 24.3 µm, mesofemur length

52.9 µm, maximum width 28.0 µm, metafemur length 63.7 µm, maximum width 25.3 µm; femora with some minute setae present at least basally on dorsal margin; tibiae slender, each shorter than corresponding femur, protibia length 41.6 µm, mesotibia length 55.8 µm, metatibia length 61.1 µm; tarsus slender, undivided (with a single tarsomere), each tarsus shorter than corresponding tibia, protarsus length 20.5 µm, mesotarsus length 31.7 µm, metatarsus length 25.1 µm; pretarsal claws absent; large pretarsal bladder present (as preserved, bladders are slightly deformed and it is difficult to determine conclusively whether observed form on the meso- and metapretarsi are double lobed or if their condition is merely postmortem distortion), bladder lengths as preserved: 2.7 µm (pro-pretarsus), 3 µm (meso-pretarsus), 3.5 µm (meta-pretarsus).

Abdomen slightly narrower than meso- and metathoracic segments, lateral margins slightly widening toward midlength, not tapering strongly posteriorly; tergum IX greatly reduced, strongly transverse; tergum X narrow, short, broadly rounded apically; tergum XI apparently present as small, lateral, sclerotized lobes each bearing each terminal style connected by thin band of integument; terminal styli elongate, bristle-like, length 205 µm. Tergum I length 41.4 µm, width 86.2 µm; tergum II length 33.5 µm, width 93.4 µm; tergum III length 28.0 µm, width 98.9 µm; tergum IV length 31.9 µm, width 102.6 µm; tergum V length 31.0 µm, width 100.9 µm; tergum VI length 26.7 µm, width 90.6 µm; tergum VII length 31.5 µm, width 82.3 µm; tergum VIII length 33.8 µm, width 65.9 µm. Terga with prominent, bristle-like setae posteriorly, with at least one a pair laterally, extending obliquely from body, lengths 61.2 µm; paramedian pair of setae extending posteriorly; sterna without ctenidia of any kind; spiracles apparently absent (the abdominal segments can be discerned remarkably well and there is no evidence of spiracles).

4. Discussion

As noted, the record here of a planidium from Taimyrian amber is potentially the first report of a strepsipteran for these deposits. It is the third account of the conicocephalate form of these instars, the others being from Canadian and Burmese amber (Grimaldi et al., 2005; Beutel et al., 2016), although the condition of the latter fossil marginally qualifies as it is apparently much more broadly rounded, albeit still narrowing. Like the planidium reported from Canadian

amber (Grimaldi et al., 2005), the head tapers anteriorly to an acute point giving it a cone-shaped appearance (conicocephalate); there is a distinct, coarse, ventral ctenidium posteriorly on the head (two rows in the Taimyrian planidium); the pronotum is large and almost square; the coxae are large and free from the thorax; the femora are greatly swollen; and there are numerous, long, stiff setae all over the body. If the Canadian specimen has only a single tarsomere (as we suspect), then this would also represent a further similarity between the two specimens. It is tempting to consider all of these features as symplesiomorphies between the two Cretaceous planidia owing simply to their antiquity relative to modern forms. In the absence of a resolved phylogenetic position for these larvae and ideally a broader sampling of material and diversity from the Cretaceous and Palaeogene, there is no justification for *a priori* assuming these species embody plesiomorphies in all traits. The long, bristle-like setae, the conicocephalate heads, and the ctenidia could well be considered apomorphic, while the free coxae could be more readily argued to be a retained primitive feature. Of course, the polarity of all of these traits requires testing.

Naturally, there are some distinct differences between the Taimyrian, Canadian, and Burmese planidia. The abdomen is narrower and of comparatively uniform width along its length in the Taimyrian fossil (Fig. 1), versus the broader abdomen that strongly tapers posteriorly in the Canadian and Burmese species (Grimaldi et al., 2005; Beutel et al., 2016). In addition, the apical-most abdominal segment is elongate in the Canadian and Burmese species, while this same segment is short and much broader than long in the present fossil, in this regard better approximating that condition present in crown-group Strepsiptera (e.g., Pohl, 2009). The dorsal bristles of the abdomen are more elongate in the Taimyrian species, at least those paramedian on the individual terga. In the Canadian species the lateral margins of the head are comparatively straight, converging anteriorly to an acute apical point and giving the head a strongly triangular appearance in dorsal view (Grimaldi et al., 2005). This is analogous to the condition observed in the present fossil, while the Burmese amber specimen has the head more rounded anteriorly (Beutel et al., 2016), better approximating the condition observed in modern Strepsiptera (Pohl, 2000). The mesonotum is the longest thoracic segment in the Canadian species versus the metanotum being longest in the Taimyrian planidium. In general, the meso- and metathoracic segments are more elongate in the latter species rather than broad in the former. The posterior margin of the mesonotum in the Canadian species is straight, while it is distinctly concave in the

one from Taimyr. If these are strepsipterans, as we tend to suspect (*vide infra*), then it would be fascinating to know what the corresponding adults might have been like for these species, and whether they were anything like the adults of the primitive, stem-group fossil genera *Cretostylops* Grimaldi and Kathirithamby, *Phthanoxenos* Engel and Huang, *Kinzelbachilla* Pohl and Beutel, or *Protoxenos* Pohl et al. (Grimaldi et al., 2005; Pohl et al., 2005; Engel et al., 2016; Pohl and Beutel, 2016). Of course, and quite unfortunately, adult strepsipterans have not yet been recovered from either Canadian or Taimyrian ambers, but the discovery of these planidia reinforces the hope that in time males shall be recovered and shed further light on the Cretaceous diversity of Strepsiptera.

Earlier, Pohl (2009) excluded the Canadian planidium from Strepsiptera, concluding it represented a nymph of Tubulifera, specifically noting the putatively dimerous tarsi and elongate apical tergum. The presence of two tarsomeres in the Canadian species was not conclusive (Grimaldi et al., 2005), and there very well may be only a single tarsomere, as in the present fossil. Moreover, the Canadian and Taimyrian specimens differ from thysanopteran nymphs in the reduced mouthparts, more strongly sclerotized bodies, lack of well-developed eyes, stiff body bristles (characteristic for parasites), presence of ctenidia, absence of antennae, and presence of elongate terminal styli. As to the elongate apical tergum IX in the Canadian species, it would appear that this is merely an autapomorphy of that taxon as the tubular segment in Phlaeothripidae is tergum X (in fact, seemingly in this respect similar to the Burmese amber specimen: Beutel et al., 2016). The segment in the fossil furthermore resembles little the condition in Thysanoptera. Given these realities we believe a thysanopteran or even paraneopteran attribution is not supported, and more recently Beutel et al. (2016) have also argued that these forms must be holometabolan larvae.

Recently, Beutel et al. (2016), when describing the Burmese amber specimen (of which there are actually several such planidia known from these deposits: pers. obs.), rightly noted that many of the features observed in these planidia are unknown among crown-group Strepsiptera, and attributed the fossils to the beetle family Ripiphoridae (Tenebrionoidea). While the absence of traits of crown-group Strepsiptera is important, this does not exclude such a relationship and, more importantly, the differences could represent features of the stem group. One would not expect a stem-group strepsipteran planidium to be entirely like those of crown-group clades. By their very nature they should lack some, or potentially many, synapomorphies of the latter; have

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symplesiomorphies with other groups; as well as unique apomorphies of their own. Indeed, only adult Mesozoic Strepsiptera are known for stem groups (Grimaldi et al., 2005; Engel et al., 2016; Pohl and Beutel, 2016), and so the traits embodied by their associated planidia are entirely unknown, but would have assuredly differed to some degree from modern strepsipteran larvae. Thus, the present fossil larvae could just as easily belong to Cretostylopidae, Phthanoxenidae, Kinzelbachillidae, or even the younger Protoxenidae. Merely the presence of unique features does not refute the strepsipteran hypothesis. Conversely, one cannot make the same argument for planidia of Mesozoic Ripiphoridae as all of the known fossils of this family belong to the crown group (Perrichot et al., 2004, 2007; Falin and Engel, 2010; Batelka et al., in press), and therefore should, by definition, have those features known for their respective subordinate clades. Most importantly, the basal lineage of Ripiphoridae, the Pelecotominae (Batelka et al., 2016), lacks planidial larvae and contains parasitoids of wood-boring beetles (Lawrence et al., 2010). Thus, basal ripiphorids, and therefore also likely the stem group to the entire family, are not expected to have planidia. So, while one expects a Cretaceous strepsipteran planidium to be quite different, perhaps strikingly so, from their crown group, we expect precisely the opposite for Cretaceous ripiphorids. Namely, if ripiphorid planidia were discovered from the Cretaceous, then they would correspond only to a higher clade within the crown group. In this context, the cavalier assignment of these fossils to Ripiphoridae is less tenable than an association with Strepsiptera, because none of them are like the primary larvae of Ripiphorinae or Ripidiinae, despite assertions (*vide infra*).

There are any number of features peculiar to these Cretaceous larvae. As we note however, these traits cannot exclude them from the strepsipteran stem group, and instead only serve to denote that they are different from the crown group. For example, the absence of three, peg-like, stiff spines on the ventral surfaces of the coxae does not preclude a placement as a stem-group strepsipteran, particularly if these structures are a synapomorphy for only the clade that circumscribes Mengenillidae + Stylopidia, to the exclusion of the more basal families. The presence of these, and in fact *any* larval traits, in all of the more basal lineages of Strepsiptera is unknown and it cannot, therefore, be used as evidence for exclusion until such time as there is positive evidence that this trait is indicative of a more inclusive clade. This same line of reasoning applies to the conicocephalate form of the head, the coarse ventral ctenidia, the absence of large stemmata (yet, the fossil under study appears to have stemmata represented,

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albeit they are small), the laterally protruding coxae, the absence of rows of spines and setae on the abdominal sterna, and the elongate stiff setae of the Cretaceous taxa. As to the putatively dimerous tarsi, the tarsus of the present fossil is clearly not dimerous, and this is likely the same for the Canadian amber fossil. We cannot speak to the condition of the specimen reported by Beutel et al. (2016), and apparently neither could these authors as they merely refer in the description to the tarsus and not to a specific number of tarsomeres. But their figure tends to indicate that it is undivided and, in fact, more similar to Strepsiptera (Pohl, 2000) than those of the Canadian or Taimyrian specimens. The putative absence of sternal plates in the Burmese specimen seems to be a taphonomic artifact, as the present planidium clearly has sternal plates (e.g., the prosternum can be seen in Fig. 1B). Accordingly, the above characters do not constitute an argument for the exclusion of the fossils from stem-group Strepsiptera, nor do they support placement anywhere else.

Returning specifically to Ripiphoridae, the characters used to attribute these fossils to the family are questionable and there are many points that require clarification. The ripiphorid hypothesis rests in essence on the following features: presence of 'pad-like distal leg modifications', 'head shape similar to ripidiine and ripiphorine larvae', and effectively the presence of ripiphorids in Cretaceous amber (Beutel et al., 2016). With regards to the last of these three lines of evidence, this hardly constitutes evidence of any kind, because strepsipterans are similarly known from Cretaceous amber. Furthermore, the known strepsipterans are stem groups to the Mengenillidae+Stylopidia clade, whereas those known ripiphorids are members of crown-group Ripidiinae, or a single species of Pelecotominae which have no planidia (Batelka et al., in press). Regarding head shape, the head shape of ripiphorid larvae and strepsipteran planidia are actually nearly the same (e.g., Besuchet, 1956; Pohl, 2000, 2002; Lawrence et al., 2010), and both are different from the head shape of the fossils, particularly the one specimen described here and the Canadian species. Thus, this does not constitute evidence of attribution to Ripiphoridae so much as it merely emphasizes, once again, that the fossils are peculiar with respect to both groups. In the present fossil, the 'distal-leg modification' appears to be a modification of the pretarsus, forming what we believe is analogous to a pretarsal bladder. Here, we do admit some similarity to the fleshy pulvillus of some Ripidiinae and Ripiphorinae (Lawrence et al., 2010). However, given the current absence of any other features indicative of crown-group Ripiphoridae, particularly Ripidiinae, we are forced to consider this as convergent.

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Moreover, if the rounded and expanded tarsal lobe found in Strepsiptera results from unification of the pretarsus and tarsus, then this could well represent an early development of the strepsipteran trait. This feature remains speculative and we do not consider it as evidence for placement in Strepsiptera, but only note it to highlight that the differences between the two are rather subtle, particularly when one realizes that similarities with ripiphorids are elusive.

Since we expect a Cretaceous ripiphorid planidium, based on available information from the known Cretaceous adults, to have characters of the crown group, one can immediately note that crown-group ripidiines (and, in fact, all ripiphorids) are entirely without analogs to these fossil larvae (Besuchet, 1956; Lawrence et al., 2010). For example, crown-group ripiphorids lack ctenidia as observed in the fossils, possess well-developed antennae with a long setiform sensorium, well-developed stemmata, a gula, distinct spiracles on the thoracic and at least some abdominal segments, and a trochanter, while in ripidiines (to which all previously described Cretaceous ripiphorids can be assigned without hesitation: Batelka et al., in press), members possess an elongate tibiotarsus. None of these features are present in these fossils, and to consider these larvae as ripiphorids would require a long list of *ad hoc* reversals or modifications in order to squeeze them into the crown group, particularly for Ripidiinae (Besuchet, 1956; Lawrence et al., 2010). It is particularly revealing that the larva described here lacks a gula, a trochanter, and pretarsal claws, structures present in crown-group ripiphorid larvae but absent in Strepsiptera (e.g., Pohl, 2002); and at least the latter two characters are apparently apomorphic, tending to suggest some kind of relationship.

Indeed, as in modern Strepsiptera, the Taimyrian fossil has a single tarsomere (which is acutely rounded apically, albeit bluntly attached to a pretarsal bladder), fused trochanters, 11 abdominal segments, horizontally-moving mandibles, what appear to be two stemmata, and lacks abdominal spiracles and pretarsal claws (Pohl, 2000, 2002). This combination of features serves to distinguish this planidium from an early-instar ripiphorid, as well as other clades with planidial larvae (Pohl, 2002). Interestingly, the mandibles situated anteriorly on the head and in a ventral groove of the apical cone could be considered a precursor to the reduced, preoral mandibles situated within a small cavity in modern strepsipteran planidia. There is some form of material extruded from either side of the head, the position of the stemmata. On the one side it appears as though this is being extruded from a slightly ventral position, while on the other side it is from a more dorsal position, and while these extrusions are along the same transverse

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tangent, they are therefore asymmetrical in point of origin. The nature of this material is entirely unclear. Perhaps examination using synchrotron-radiation μ-CT might aid any further inquiry into this matter.

We certainly agree with Beutel et al. (2016) that these miniscule fossils are peculiar and challenging to place with confidence. Nonetheless, and in the spirit of collegial scientific discussion, we respectfully disagree with the totality of their argument and believe that their assertions have been made from a line of reasoning that reads as an almost *a priori* decision that these must be beetles. We believe the matter requires further careful consideration, but that for the time being and with all other evidence being equal, there seems to be more slightly in favor of an attribution to stem-group Strepsiptera than to Ripiphoridae or any other known beetle clade. Of course, a thoroughly conclusive decision as to the identity of these remarkable plandia must await the discovery and documentation of further material, and an enriched source of character information. Fine resolution of the anatomy of these animals is needed in order to better resolve our understanding of their phylogenetic affinities, and certainly more is required before they may be finally placed among the Coleoptera.

5. Concluding remarks

The present discovery provides a significant new record for the Santonian fauna of Taimyr amber, indicating the potential presence of Strepsiptera. The fossil further provides greater information and possibly further clarification as to the identity of these enigmatic fossils, tending to refute the possible association with beetles of the family Ripiphoridae. Admittedly, the placement as planidia of Strepsiptera is not overwhelmingly supported, but the limited evidence suggests this is more likely than the specimens representing beetle larvae. We believe the most solid position is to admit such doubts. Regardless, these tiny fossils reveal the wonderful diversity of insects during the Cretaceous, with its many significant varieties that existed and perished long before the fauna as we understand it today came into form.

Acknowledgments

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Figure Captions

Figure 1. Microphotographs of planidium in Taimyrian Upper Cretaceous amber (PIN 3311/3243). A, Dorsal habitus of specimen as preserved. B, Detail of ventral surface of head (rmd = right mandibular apex, a-ct = anterior ctenidial teeth, p-ct = posterior ctenidial teeth). C, Detail of midleg (cx = mesocoxa, fm = mesofemur, mn seta = mesonotal seta, tib = mesotibia, ts = mesotarsus, pt = mesopretarsus).