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Fossil lice (Insecta: Phthiraptera) reconsidered

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Abstract. Five papers describing fossils considered to be Phthiraptera (lice) by their authors are reviewed. We place the specimens described in three papers in the Acari (mites) and regard them as probably not fossils. A fourth paper describes what appears to be a fossil insect. However, we do not consider it to be a louse. The fifth paper describes a more recent fossil that differs little from extant lice.

Introduction

Prior to 1999, no postembryonic fossil louse (Insecta: Phthiraptera) had been described. At that time, Phthiraptera was the only extant insect order lacking a fossil record. Although Voigt (1952) had described and illustrated eggs of sucking lice (Phthiraptera: Anoplura) attached to mammal hair imbedded in Baltic amber, fossil nymphs or adults were unknown. Since 1999, five papers describing fossils, considered to be lice by their authors, have been published (Kumar & Kumar, 1999, 2001; Rasnitsyn & Zherikhin, 1999; Kumar, 2004; Wappler *et al*., 2004). Here we discuss and review the systematic status of the taxa described in those five publications.

Discussion

In 1999, Kumar & Kumar described but did not name '... three different fossilized microscopic wingless parasitic insects...' from India – one of these was a complete specimen from sandy clay overlying Bagra Conglomerates exposed at the Khatama caves and two were from subsurface Denwa clay bands exposed in an artesian well cutting at the village of Anhoi. From the stratigraphy, associated pollen and other characteristics, these specimens were dated as from the Upper Triassic. Four photomicrographs of the specimens were included in one plate.

The Khatama specimen, shown here in Fig. 1(A), was subsequently described and named by Kumar (2004) as the new species *Amblyceropsis indica*, for which he erected a new genus and a new family. The diagnosis of *A. indica* (Phthiraptera: Amblycera: Mammalophagidae) is as follows:

> The chewing mouthparts consist of three pairs of vertically arranged mandibles. They are sclerotized, cone shaped and each with anteriorly directed tooth (Pl. I, Fig. 8). There is one pair of maxillary palp. These mouthparts are underside the head, but are slightly projected anteriorly outside (Pl. I, Fig. 6).

The species is further defined in the description as:

> ... One pair of clubbed, many segmented exposed antennae (Pl. I, Figs 2, 3, 6, 8) are present which arise from sockets or grooves and their three parts flagellum, pedicellus and scarpus can be clearly demarcated (Pl. I, Fig. 8).
>
> ... Abdomen bears comb shaped lateral setae (Css) (Pl. I, Fig. 7).
>
> ... The male genitalia is simple and is partially extruded posteriorly from the abdomen (Pl. I, Figs 4, 5 and 7, 8).

No dimensions are given, although fig. 1a and plate I, part 1 in Kumar (2004) contain a scale. These same photomicrographs are included in fig. 1 of Kumar & Kumar (1999: 1539), whose legend gives the dimensions of the specimen as '230 μm long, 105 μm broad'. The significance of the above diagnosis and description is discussed in the Remarks by Kumar (2004: 160) as follows:

> It is included in Amblycera because of its flat shape, minute size, prognathus head, which is wider than long, and other characters that resemble with living Amblycera which parasitize mammals (see Emerson & Price, 1975). Presence of comb-shaped setae on this specimen is the primitive feature of Amblycera (Bedford, 1932). An extruded genitalia (Pl. I, Fig. 7) as observed in this specimen is generally found in living Amblycera. Two flap-like structures present near genitalia have resemblance with living chewing lice, *Eicono-lipeurus inexpectatus* (see Emerson, 1967). Due to its some primitive characters, e.g. cone-shaped mandible, simple male genitalia, it is considered to be the earliest Amblycera and may be called as Protoamblycera.

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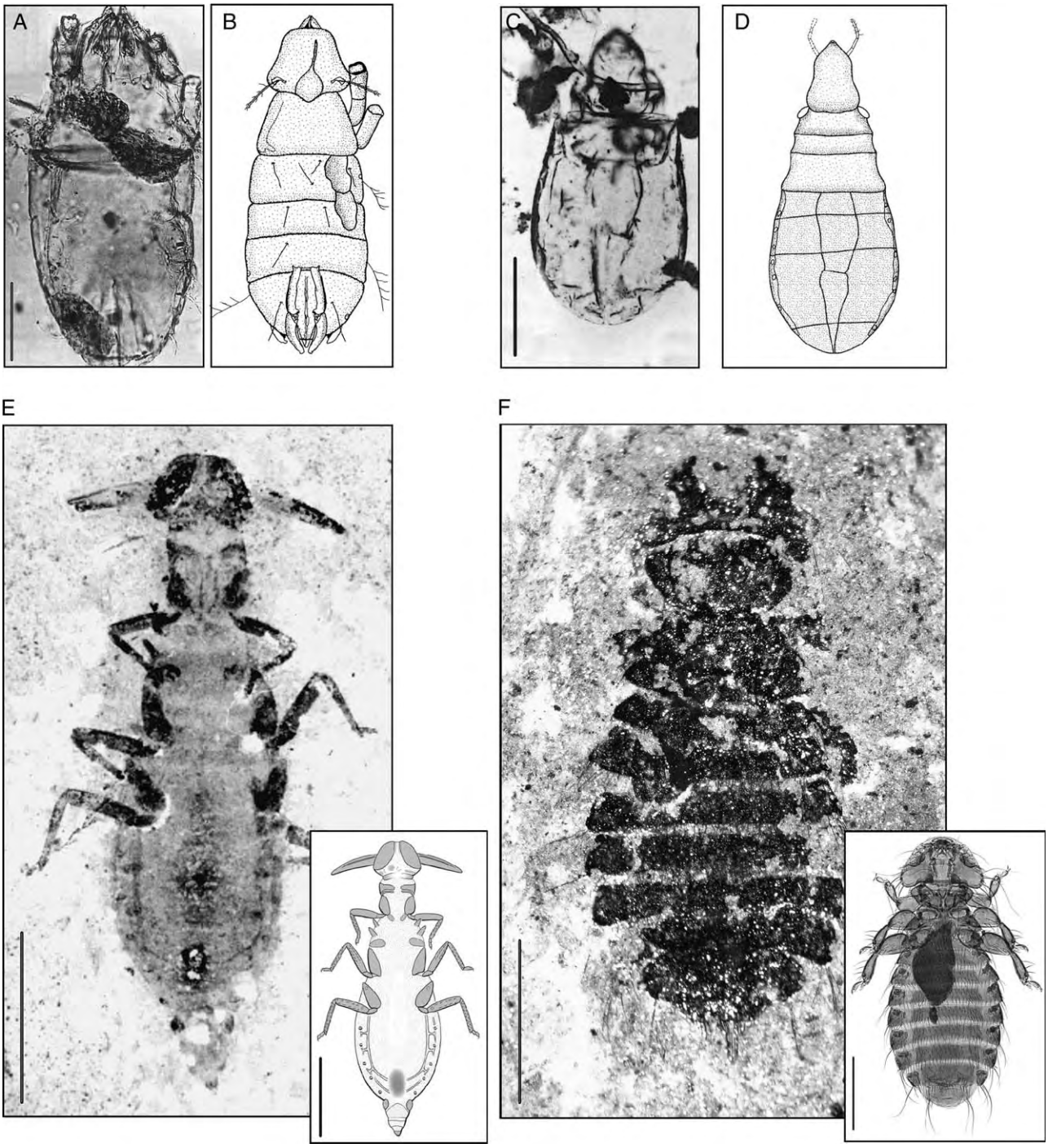

Fig. 1. Putative fossil lice. A, *Amblyceropsis indica*, regarded by Kumar (2004) to be a fossil amblyceran louse, herewith considered to be a mite (Acari); B, Kumar's (2004) 'reconstruction' of *Amblyceropsis indica*; C, *Anopluropsis khatamaensis*, regarded by Kumar (2004) to be a fossil anopluran louse, herewith considered to be an oribatid mite (Acari); D, Kumar's (2004) reconstruction of *Anopluropsis khatamaensis*; E, *Saurodectes vrsanskyi* and its schematic illustration (inset), considered by Rasnitsyn & Zherikhin (1999) to be an ischnoceran louse of pterosaurs, herewith considered to be an insect of uncertain ordinal affinities; F, *Megamenopon rasnitsyni* and its extant close relative *Holomenopon brevithoracicum* (Piaget) (inset), considered by Wappler *et al.* (2004) to be an amblyceran menoponid louse and herewith considered to be the only known fossil that can be placed without reservation within the insect order Phthiraptera. A–D are reproduced with permission from the *Journal of the Palaeontological Society of India*; E and the inset are reproduced with permission from the authors and publisher of Grimaldi & Engel (2005); and F and the inset are reproduced with permission from the Royal Society. Scales bars: A = 0.05 mm; C = 0.2 mm; E and inset = 5.0 mm; F = 2.0 mm; F inset = 0.5 mm (no scale given for B and D).

None of the described or illustrated structures is consistent with the placement of this specimen in Amblycera, Phthiraptera, or even Insecta. No louse or insect has three pairs of mandibles, whether 'saw-like' (Kumar & Kumar, 1999: 1540), or 'cone-shaped' (Kumar, 2004: 160). No lice have 'comb-shaped' setae, nor is there any 1932 publication by Bedford as listed by Kumar (2004: 168). Some lice have setae in rows, which are commonly referred to as setal combs or ctenidia, but none has branched or comb-shaped setae. Extrusion of the genitalia is a common artefact of mounting specimens on microscope slides and is found throughout slide-mounted Phthiraptera. Whatever the 'flap-like' (Kumar, 2004: 160) structures may be, their resemblance to those of *Eiconolipeurus* (= *Oxylipeurus* Mjöberg, 1910) would place it in the suborder Ischnocera, not Amblycera. In addition, the body length of this specimen is exceedingly small. The dimensions of the smallest louse [the anopluran *Microphthirus uncinatus* (Ferris, 1916)] is almost twice that given by Kumar & Kumar (1999: 1539) for *Amblyceropsis*, and even this is atypically small for Phthiraptera. The combination of these features, in addition to the fused head and thorax (cephalothorax), are diagnostic of an arachnid rather than an insect. From the available images, the specimen strongly resembles an acariform mite, probably of the suborder Prostigmata. Kumar's (2004) reconstruction, shown here as Fig. 1(B) is difficult to reconcile with the available images and adds little to the interpretation of the specimen. Furthermore, the structural details reported, together with the characterization of the yellowish brownish, leathery exoskeleton, strongly suggest this is not a fossil, but rather a modern contaminant.

Kumar & Kumar (2001) reported another specimen, shown here in Fig. 1(C), which was described and named by Kumar (2004: 163) as the new genus and new species, *Anopluropsis khatamaensis*, placed in the new family Khatamamammalophagidae (Phthiraptera: Anoplura). The diagnosis and description of this new taxon is devoid of any taxonomically significant characters or comparisons with similar or related taxa, as recommended by the International Commission on Zoological Nomenclature (1999: 17, Recommendation 13A). As with his previous description, Kumar (2004: 163) does not provide dimensions. However, the scale accompanying plate II, fig. 1 allows calculation of the specimen length as 600 μm. That figure, a photomicrograph, clearly shows a mite – probably belonging to the Oribatida, based on its shape and the presence of a scutum (reduced dorsal shield) – not an insect. Therefore, we agree with the statement made by Grimaldi & Engel (2005: 275) that 'Cuticular remains of a microscopic arthropod from the Triassic of India (Kumar & Kumar, 2001) cannot be phthirapteran but appear to be that of an oribatid mite'. The details reported on the fine structure of the mouthparts, if indeed visible, again point to this specimen not being a fossil, but rather a contaminant modern mite. Kumar's (2004) reconstruction of this specimen (Fig. 1D) is based on the premise that the thorax (inferred here to be the scutum) has sunken into the abdomen of the original specimen. Kumar illustrates divisions between the thoracic segments, although these segments are indivisibly fused in all extant Anoplura.

Saurodectes vrsanskyi Rasnitsyn & Zherikhin, 1999 was described as the 'First fossil chewing louse…'. It is from marls of the Zaxa Formation of the Baissa, Transbaikalia, Russia, and dated as Lower Cretaceous. The authors place this new genus and species in the new family Saurodectidae, and inferred that *Saurodectes* was an ectoparasite of pterosaurs, based on its unusual morphology, which they considered to be an adaptation to the dense fur on pterosaur wing membranes (Rasnitsyn & Zherikhin, 1999: 254). They follow the Rohdendorf (1962) concept of codified higher taxon names, thus ascribing the new family to Insecta: Pediculida: Philopterina. The new taxon is then tentatively placed in the superfamily Philopteroidea, with the acknowledgement that: 'Numerous unique characters known for no other lice question the ischnoceran attribution seriously'. No other specialist currently working in louse taxonomy follows Rohdendorf's scheme; thus, for clarification, not criticism, the following more widely used higher classification is given here: Insecta: Phthiraptera: Ischnocera: Saurodectidae: *Saurodectes*. We concur with Rasnitsyn & Zherikhin (1999) in questioning the attribution of *S. vrsanskyi* to the suborder Ischnocera. We go further in questioning its placement within the Phthiraptera and its dubious host association with pterosaurs. However, in the absence of a more appropriate placement or any direct evidence of a parasitic association with a host, we refrain from speculative placement in another insect order. More productive is highlighting the characters that appear inconsistent with the placement of this fossil within any suborder of extant lice.

The actual fossil has not been examined. However, the senior author (RCD) is indebted to Professor Rasnitsyn for his discussion of questions raised regarding the interpretation of characters, and for providing a digital image of the fossil that is superior to the original published as fig. 2 in Rasnitsyn & Zherikhin (1999). This image and its reconstruction from Grimaldi & Engel (2005) are reproduced here, with permission, in Fig. 1(E). In that discussion, but not in the original paper, Rasnitsyn describes the fossil's preservation as 'very good', adding that 'both sides of the fossil are discernible'. Rasnitsyn & Zherikhin (1999) determined that the fossil was a louse by a process of elimination. The presence of chewing mandibles, complete loss (absence) of wings, and the one-segmented tarsus excluded the orders Gryllones (= Polyneoptera), Hemiptera, Thysanoptera, Odonata, Ephemeroptera and Coleoptera. The absence of caudal appendages eliminated the Thysanura and the 'Far lateral position of the coxae distinguishes the fossil in comparison from the Psocida'. The legs are not '… at all characteristic of the larval holometabolas'. 'This leaves us only with the Pediculida s.l. (= Anoplura + Mallophaga), and particularly with the latter subgroup that retains the chewing mandibles'. … 'Within the chewing lice, mandibles directed vertical are the diagnostic character of the ischnocerans, and the absence of apparent impression for short, clavate antenna, as characteristic of the amblycerans, could

support this inference if proved correct' (Rasnitsyn & Zherikhin, 1999: 253–254). The presence of mandibles is an essential and primary diagnostic character in reaching the determination that this fossil is a chewing louse. However, in the generic diagnosis they are described as: 'Mandibles short, looking rather irregular in outline (probably because of incomplete preservation)'. In the family diagnosis they are described as: 'Mandibles at rear of head margin, short, orientated mediocaudad, probably vertical in life position (no palps preserved)'. In correspondence with Rasnitsyn, regarding the mandibles, he wrote that: 'Structures termed mandibles in the description are not very typical mandibles indeed, and they are not very well seen, particularly because the head displays various sclerotized structures partly overlapping each other and so not easy to outline and interpret. However, the insect should have mandibles, and these structures look the best candidates. Nothing like [a] proboscis or stylets are seen in or around the head'. Engel (pers. comm.) reports that he has examined the specimen and '. . . could not make out the mandibles at all on the specimen, they are either not preserved or not present'. The presence and location of mandibles are crucial to the diagnosis of this fossil as a louse. They are described as being at the 'rear of head margin', thus distinguishing them from all extant lice. This feature alone would eliminate the inclusion of *S. vrsanskyi* within the Phthiraptera, as effectively as other characters were used to eliminate other insect orders. Although it is undeniable that we do not know what lice of the Lower Cretaceous looked like, neither do we know the full range of variation of structures within other orders of that period, which were eliminated on the basis of less significant characters. The large 'lateral head processes (trabeculae?)' observed are also absent from the Phthiraptera and no similar cephalic structures are known from any other insect order. Rasnitsyn is confident (pers. comm. to RCD) that the lateral head processes are an integral part of the fossil and not an artefact. Neither are they segmented to suggest that they are antennae. The large total length of *S. vrsanskyi* (18.5 mm), the position of its mouthparts, and the strong possibility of having ommatidia, all suggest that this species is not a louse, considering the present definition of Phthiraptera. A similar conclusion was reached by Grimaldi & Engel (2005: 275) when they wrote that 'Its placement in the Phthiraptera was largely based on a process of elimination of other orders, particularly since *Saurodectes* has several features highly unusual for lice'.

Wappler *et al*. (2004) described *Megamenopon rasnitsyni* (Insecta: Phthiraptera: Amblycera: Menoponidae) as 'what appears to be the first bird louse fossil', and is shown here in Fig. 1(F). This is an extremely well-preserved fossil from an oil shale, reliably dated at 44.3 ± 0.4 million years before present from the crater of the Eckfeld maar near Manderscheid, Germany [not Grube Messel, as erroneously reported by Grimaldi & Engel (2005: 275)]. The affinities of this specimen to the amblyceran louse family Menoponidae were verified by phylogenetic analysis (Wappler *et al*., 2004), based on characters derived from a cladistic study of amblyceran generic-level phylogeny (Marshall, 2003). This analysis placed *Megamenopon* within the *Austromenopon*-complex sensu Marshall (2003). All observed morphological characters appear similar to those of extant menoponid taxa and, were it not for its size (*M. rasnitsyni* is twice the length of known closely related living species such as *Holomenopon* Eichler, 1941 shown inset in Fig. 1F), and some autapomorphies of the thorax, it could easily have been placed in a modern genus.

We conclude that, of the five papers reporting the discovery of a 'fossil louse', only one (Wappler *et al*., 2004) describes a specimen that can be placed without reservation in the Phthiraptera. The specimens reported in three papers are not even insects. Another paper (Rasnitsyn & Zherikhin, 1999) describes a very interesting insect fossil whose placement is uncertain, but it no better fits in the Phthiraptera than in any other insect order.

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