

Scratching an ancient itch: an Eocene bird louse fossil

Torsten Wappler¹, Vincent S. Smith^{2*}
and Robert C. Dalgleish³

¹Department of Geology, Palaeontology and Mineralogy, Hessisches Landesmuseum Darmstadt, Friedensplatz 1, 64283 Darmstadt, Germany

²Institute of Biomedical Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK

³Department of Entomology, San Diego Natural History Museum, PO Box 121390, San Diego, CA 92112, USA

* Author for correspondence (v.smith@bio.gla.ac.uk).

Recd 16.11.03; Accptd 10.12.03; Published online

Out of the 30 extant orders of insects, all but one, the parasitic lice (Insecta: Phthiraptera), have a confirmed fossil record. Here, we report the discovery of what appears to be the first bird louse fossil: an exceptionally well-preserved specimen collected from the crater of the Eckfeld maar near Manderscheid, Germany. The 44-million-year-old specimen shows close phylogenetic affinities with modern feather louse ectoparasites of aquatic birds. Preservation of feather remnants in the specimen's foregut confirms its association as a bird ectoparasite. Based on a phylogenetic analysis of the specimen and palaeoecological data, we suggest that this louse was the parasite of a large ancestor to modern Anseriformes (swans, geese and ducks) or Charadriiformes (shorebirds). The crown group position of this fossil in the phylogeny of lice confirms the group's long coevolutionary history with birds and points to an early origin for lice, perhaps inherited from early-feathered theropod dinosaurs.

Keywords: coevolution; lice; fossils; Phthiraptera; Eckfeld maar

1. INTRODUCTION

Obligate interactions such as those between birds or mammals and their parasitic lice provide some of the classically cited examples of coevolution and cophylogeny (Page 2002). Genera of lice are often restricted to single families or orders of birds and mammals. This tight host-specificity might suggest that lice and their hosts have a long coevolutionary history. There has been much debate over the age of lice and the origins of parasitism in this group (Lyal 1985). However, until now, to our knowledge there has been no direct evidence available regarding the age of the host-parasite association between lice and their vertebrate hosts. Here, we provide the first direct evidence on the antiquity of this association in the form of what appears to be the first bird louse fossil: an exceptionally preserved specimen in which bird feather remnants can be seen preserved within the specimen's foregut.

Although the fossil record is replete with examples of mammals and birds, the fossilized remains of their parasite fauna are virtually unknown. In this regard lice are no exception. There are three previous reports of fossil lice,

two of which are based on fragmentary fossils that are much too small to be lice (Kumar & Kumar 1999, 2001), while the third (Rasnitsyn & Zherikhin 1999) is ambiguous and shares characters in common with several insect orders. The former describe specimens with a total length of 0.23 mm, have a cephalothorax (a fused head and thorax) and branched setae. By comparison the smallest extant louse is 0.33 mm, all lack a cephalothorax (a character restricted to arachnids and crustaceans) and do not have branched setae. We concur with Price *et al.* (2003) in the suggestion that these specimens are most probably mites (Acari). The latter report (Rasnitsyn & Zherikhin 1999) is of a specimen 18.7 mm in length (almost twice that of the largest extant louse), with structures unlike Phthiraptera or any known insect order. Without evidence these authors postulate that this taxon parasitized pterosaurs. On the basis of morphology and this dubious host association this insect lacks all affinity with extant lice from mammals or birds and we conclude it is not a phthirapteran within the current concept of the order. Although there are no other reports of fossilized lice, a report of eggs attached to mammal hair preserved in Baltic amber (Voigt 1952) are clearly those of an ectoparasite and perhaps those of sucking lice (Anoplura).

The parasite described here is extraordinary in several respects. Few fossils are preserved with the contents of their last meal *in situ*. While the level of feather preservation within the specimen's foregut is insufficient for us to deduce a likely host from its morphology, phylogenetic analysis of the louse allows us to infer candidate hosts. Avian lice exhibit a high level of host specificity and the fossil can be unambiguously assigned to a modern louse group. Its discovery completes the representation of all insect orders in the fossil record.

2. MATERIAL AND METHODS

The specimen was collected from the Eckfeld maar near Manderscheid, Eifel, Germany. This volcanic crater formed a freshwater lake with an original diameter of 900 m and a depth exceeding 110 m (Pirrung *et al.* 2001). Rapid sedimentation over a 250 000 year period combined with anoxic alkaline conditions (no bioturbation) explain the perfect preservation of fossils within the lamination of the oilshale (Mingram 1998). As a consequence, coloration and minute structural details are present in many of the 30 000 plus macrofossils recovered from this site, which document a diverse Eocene terrestrial flora and fauna. Argon^{40/39} dating of basalt from the diatreme breccia underlying the lake sediments establishes an age of 44.3 ± 0.4 million years (Myr) ago for Eckfeld (Mertz *et al.* 2000). The fossil and surrounding matrix were preserved by immersion in glycerine to prevent oxidation. Photographs were taken digitally with the aid of a dissection microscope and compared with related extant specimens taken from the collections of R.C.D. Morphological nomenclature follows Clay (1970) and Marshall (2003).

Louse phylogeny was determined from a cladistic analysis of 147 morphological characters and 45 extant taxa using a dataset modified from Marshall (2003) (TREEBASE accession SN1027; <http://www.treebase.org/>). A heuristic search with PAUP* (Swofford 2003) using tree bisection-reconnection (TBR) branch swapping yields six equally parsimonious trees from which a strict consensus was constructed and used as a backbone constraint to determine the phylogenetic placement of the fossil taxon. This constrained search was restricted to 24 of the 147 morphological characters that could be scored from the fossil.

3. RESULTS

(a) Classification

Class Insecta, Linnaeus 1758; order Phthiraptera, Haeckel 1896; suborder Amblycera, Kellogg 1896; family Menoponidae, Mjöberg 1910; genus *Megamenopon*, gen. nov.; type species *Megamenopon rasnitsyni*, sp. nov.

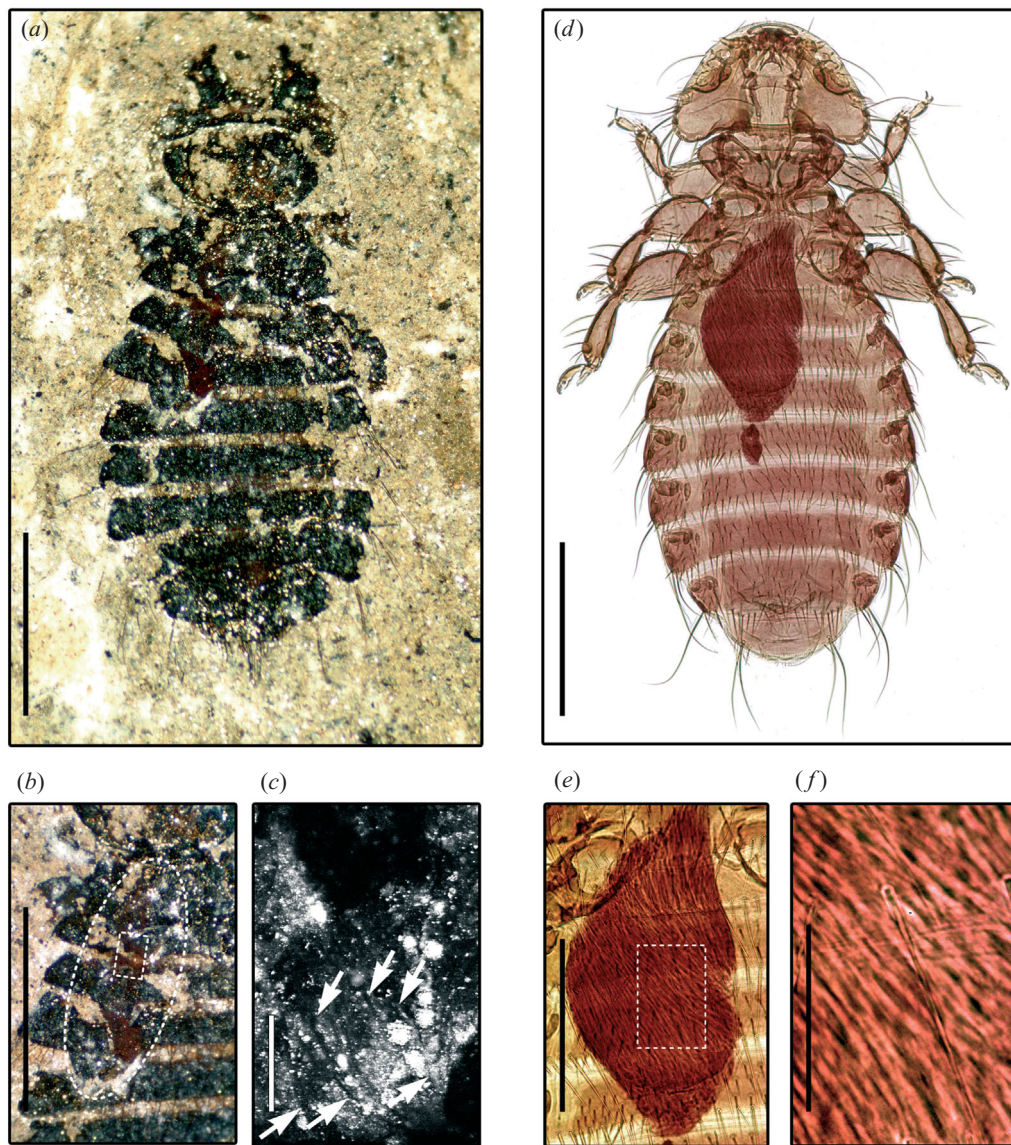


Figure 1. *Megamenopon rasnitsyni* gen. et sp. nov. and its extant close relative *Holomenopon brevithoracicum* (Piaget). (a) Complete exoskeleton of *Megamenopon rasnitsyni*. (b) Enlargement of the crop (encircled), part of the foregut visible within the abdomen. (c) Enlargement of the rectangular section highlighted in (b) showing feather barbules preserved within the crop. Examples are highlighted with arrows. (d) *Holomenopon brevithoracicum* from a mute swan (*Cygnus olor* (Gmelin)). (e) Enlargement of the *Holomenopon* crop. (f) Enlargement of the section highlighted in (e) showing feather barbules within the *Holomenopon* crop. Scale bars: (a–b) 2 mm, (c) 0.125 mm, (d) 0.5 mm, (e) 0.3 mm, (f) 0.1 mm.

(b) *Etymology*

The generic name is based upon ‘menopon’ the root of the family to which it belongs, and the prefix references its large size. The species name is in recognition of the contribution of Alexander P. Rasnitsyn of the Palaeontological Institute, Russian Academy of Sciences, Moscow, towards our understanding of fossil insects.

(c) *Holotype*

PE1997/33.LS, Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz, Germany (figure 1a–c).

(d) *Generic and specific diagnosis*

Temples narrowly lobed extending beyond median posterior margin of head, bounded by dorsal head setae (DHS) 21–27; DHS 23 close to DHS 22 and alveoli of DHS 26 and 27 separate; DHS 29–31 present; prothorax

enlarged, longer than head bearing episternal carina running the length of the segment; transverse pronotal carina expanded medially; division between meso/metathorax marked by an indentation in the lateral margin; posterior margin of metathorax convex; lateral tergal thickenings of abdomen absent; abdominal tergites comprising single plates per segment bearing single rows of setae extending across posterior margin of preceding segment; abdominal spiracles open onto tergites; margin of lateral ventral plate square, not extending into a medial protuberance; subgenital plate (segments VIII + IX) present and anal margin fringed with setae.

4. DISCUSSION

The holotype is a female 6.74 mm long that is almost complete, showing sections of most dorsal and some protruding ventral features, in addition to a discoloured portion of the foregut corresponding to the crop or ‘feather

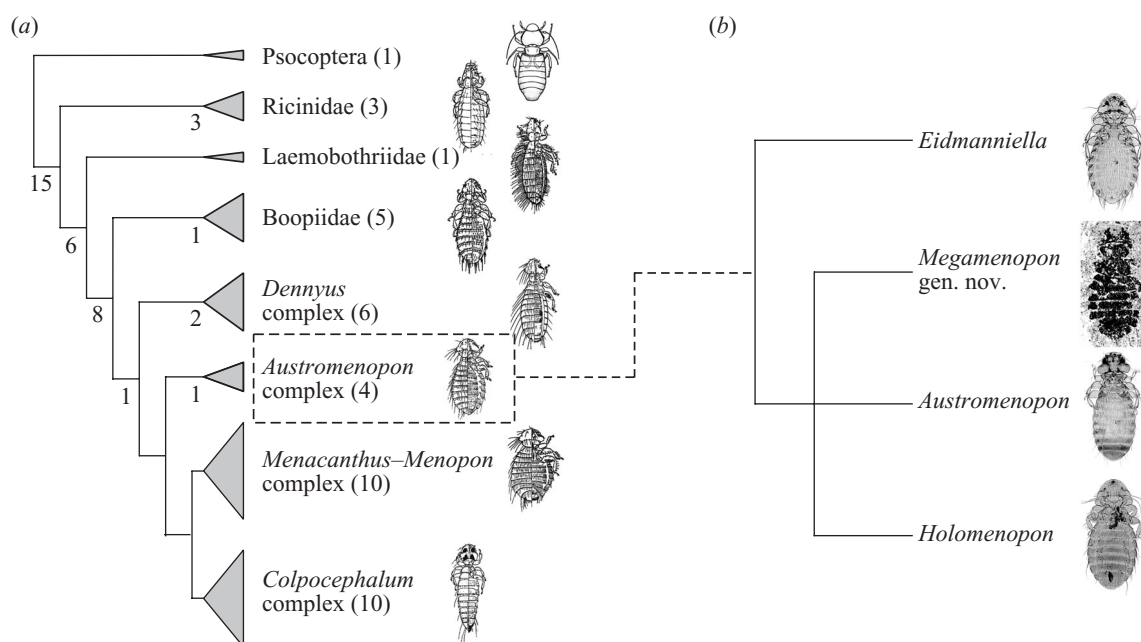


Figure 2. Phylogenetic position of *Megamenopon* gen. nov. within the phylogeny for amblyceran lice of birds and mammals. Decay indices are indicated below the nodes (TBR branch swapping, 1000 replicates). (a) Phylogeny of the principal amblyceran louse clades. The number of terminal taxa are given in parentheses. *Megamenopon* is placed within the *Austromenopon* complex that are parasites of aquatic birds. (b) Strict consensus of two most parsimonious trees for the *Austromenopon* complex. *Megamenopon* is either placed in a trichotomy with *Austromenopon* and *Holomenopon* as shown here or as sister taxon to a *Austromenopon*–*Holomenopon* clade. These lice parasitize anseriform, charadriiform and procellariiform birds.

sac' (figure 1a–c). The specimen closely resembles extant menoponid lice (Insecta: Phthiraptera: Amblycera: Menoponidae). This was verified by subjecting the specimen to a cladistic analysis using characters of Marshall (2003) (figure 2). Using characters that could be scored from the fossil the constrained heuristic search generates two equally parsimonious trees, a strict consensus of which is shown in figure 2b. The head lacks any pattern of thickened chitin as found in some contemporary menoponid lice. The prothorax is enlarged relative to the head with a smooth lateral margin. This readily distinguishes *Megamenopon* from extant menoponid genera. The abdomen is widest at segment V with lateral tergal thickenings absent. Within the anterior third of the abdomen between the tergites a large oval structure is visible that contains the partly digested feathers of the specimen's last meal (figure 1b,c). This part of the alimentary canal corresponds to the crop, and is identical in size, position and discolouration to that of extant feather lice (figure 1d–f). The lower portion of the fossilized crop is partly covered by the displaced femur and tibia of the left third leg. However, the anterior portion (figure 1c) contains structures similar to those present in the crop of contemporary menoponid feather lice (figure 1f). These are too small to be setae and we conclude that these are feather barbules.

Avifauna from this period and locality is poorly known, and *Megamenopon* was not found in direct association with fossil remains of any host material. Despite this the shared phylogenetic history of many lice and their hosts coupled with their host specificity (Price *et al.* 2003) allows us to identify candidate hosts for *Megamenopon*. Phylogenetic analysis places the fossil within a crown group clade corresponding to the *Austromenopon* complex (*Austromenopon*–*Holomenopon*–*Eidmanniella*; figure 2) *sensu* Marshall

(2003). Its closest extant relatives are louse genera restricted to seabirds (Procellariiformes), shorebirds (Charadriiformes) or ducks (Anseriformes). Based on Eocene palaeogeography Eckfeld lies 100–150 km from the sea (Harms & Schaal 2000), ruling out Procellariiformes as likely hosts. However, representatives of both Charadriiformes and Anseriformes have been found at the Messel Lagerstätte near Darmstadt, Germany (Mayr 2000), located close to Eckfeld maar. These sites share a similar palaeoecology and biostratigraphy (Messel is *ca.* 5 Myr older than Eckfeld), suggesting that representatives of these host orders were in the vicinity of Eckfeld at this time.

Our specimen indicates that avian lice had at least a Lower Eocene origin: a time when many modern bird lineages had already diversified (Cooper & Penny 1997). The crown group position of *Megamenopon*, combined with the recent discovery of fossil eggs (probably mites) on a Cretaceous feather (Martill & Davis 1998), confirms a coevolutionary history between parasites and birds that spans more than 120 Myr. This raises the possibility that the ancestral host for parasitic lice was not a modern bird or mammal as is generally accepted, but an early-feathered dinosaur.

Acknowledgements

Finance and assistance with the excavations at Eckfeld were provided by the federal state government of Rheinland-Pfalz, the local administration and municipal authorities of Eckfeld and Manderscheid, and RWE Aktiengesellschaft, Essen. We thank H. Lutz for loan of the specimen. This research was supported by a grant from the German Science Foundation (DFG) (LU 794/1-1, 1-2) to T.W. and a Wellcome Trust junior biodiversity fellowship (063734/Z/01/Z) to V.S.S.

Clay, T. 1970 The Amblycera (Phthiraptera: Insecta). *Bull. Br. Mus. (Nat. Hist.) Entomol.* **25**, 75–98.

- Cooper, G. W. & Penny, D. 1997 Mass survival of birds across the Cretaceous–Tertiary boundary: molecular evidence. *Science* **275**, 1109–1113.
- Harms, F. J. & Schaal, S. 2000 Die Geologie der Grube Messel. In *Fenster zur Urzeit: Weltnaturerbe Grube Messel* (ed. E. R. Kächler), pp. 16–23. Wiesbaden, Germany: Hessisches Ministerium für Wissenschaft und Kunst.
- Kumar, P. & Kumar, P. 1999 Insect remains from Upper Triassic sediments of Satpura Basin, India. *Curr. Sci.* **76**, 1539–1541.
- Kumar, P. & Kumar, P. 2001 Phthirapteran insect and larval Acanthocephala from the Late Triassic sediments of the Satpura basin, India. *J. Palaeontol. Soc. India* **46**, 141–146.
- Lyal, C. H. C. 1985 Phylogeny and classification of the Psocodea, with particular reference to lice (Psocodea: Phthiraptera). *Syst. Entomol.* **10**, 145–165.
- Marshall, I. K. 2003 A morphological phylogeny for four families of amblyceran lice (Phthiraptera: Amblycera: Menoponidae, Boopidae, Laemobothriidae, Ricinidae). *Zool. J. Linn. Soc.* **138**, 39–82.
- Martill, D. M. & Davis, P. G. 1998 Did dinosaurs come up to scratch? *Nature* **396**, 528–529.
- Mayr, G. 2000 Die Vögel der Grube Messel: ein Einblick in die Vogelwelt Mitteleuropas vor 49 Millionen Jahren. *Nat. Mus.* **130**, 365–378.
- Mertz, D. F., Swisher, C. C., Franzen, J. L., Neuffer, F. O. & Lutz, H. 2000 Numerical dating of the Eckfeld maar fossil site, Eifel, Germany: a calibration mark for the Eocene time-scale. *Naturwissenschaften* **87**, 270–274.
- Mingram, J. 1998 Laminated Eocene maar-like sediments from Eckfeld (Eifel region, Germany) and their short term periodicities. *Palaeogeogr. Palaeoclimatol.* **140**, 289–305.
- Page, R. D. M. (ed.) 2002 *Tangled trees: phylogeny, cospeciation and coevolution*. University of Chicago Press.
- Pirrung, M. G., Büchel, G. & Jacoby, W. 2001 The Tertiary volcanic basins of Eckfeld, Enspel and Messel (Germany). *Z. Deut. Geol. Ges.* **152**, 27–59.
- Price, R. D., Hellenthal, R. A., Palma, R. L., Johnson, K. P. & Clayton, D. H. 2003 *The chewing lice: world checklist and biological overview*. Champaign-Urbana, IL: Illinois Natural History Survey.
- Rasnitsyn, A. P. & Zherikhin, V. V. 1999 First fossil chewing louse from the Lower Cretaceous of Baissa, Transbaikalia (Insecta, Pediculida=Phthiraptera, Saurodectidae fam. n.). *Russian Entomol. J.* **8**, 253–255.
- Swofford, D. L. 2003 *PAUP*. Phylogenetic analysis using parsimony (*and other methods)*, v. 4. Sunderland, MA: Sinauer.
- Voigt, E. 1952 Ein Haareinschluß mit Phthirapteren: Eiern im Bernstein. *Mitt. Geol. Staatsinst.* **21**, 59–74.