A new opilioacarid mite in Baltic amber

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Abstract

The second fossil opilioacariform mite (Acari: Anactinotrichida: Opilioacarida) is described as ?*Opilioacarus aenigmus* sp. nov., from Baltic amber (Palaeogene: Eocene). Compared to the previously described amber opilioacarid, the new fossil reveals more of the genital region, as well as an unusual pattern of long setae towards the distal end of the first leg. Unlike the previous species, the new fossil bears only two pairs of eyes and the fourth pair of legs are shorter in relation to the body. This clearly indicates a new fossil taxon. Recent work on the phylogenetic position of the mites – and their constituent subgroups – is briefly reviewed, together with a summary of the fossil record of anactinotrichid mites in general.

INTRODUCTION

Opilioacarids (Acari, Anactinotrichida, Opilioacarida) are a rather rare group (ca 20 species) of mites, sometimes referred to by the alternative names Opilioacariformes or Notostigmata. In older literature opilioacarids were often treated as 'primitive' mites, largely because they retain a number of plesiomorphic characters, such as multiple lateral eyes and externally visible opisthosomal segmentation. They have even on occasions (e.g. Reuter 1909) been excluded from Acari *sensu stricto*. Their current placement within the Anactinotrichida mite lineage (Parsitiformes *s. l.* in some schemes) is now strongly supported (see below). Valuable morphological accounts of opilioacarids include With (1904), Grandjean (1936), van der Hammen (1968, 1976, 1977, 1989), Lehtinen (1980), Klompen (2000) and Vázquez & Klompen (2002). The first, and so far only, fossil opilioacarid

to be described is *Paracarus pristinus* Dunlop, Wunderlich & Poinar, 2004 from Eocene Baltic amber. The well-preserved holotype (and only known specimen) was assigned to a recent genus with a Central Asian distribution today. Here, we describe only the second fossil example of an opilioacarid mite (Figs 1–5), a fossil again originating from Baltic amber. The ventral surface of this new specimen is particularly well preserved, including some details not observed in Dunlop et al.'s (2004) original study. The new specimen also expresses a prominent group of very long setae towards the distal end of the first pair of legs. This, and other characters – such as eye number and leg proportions – differ substantially from the condition seen in *P. pristinus* and indicate that the present fossil represents a new taxon, which we tentatively assign here to the Recent Mediterranean genus *Opilioacarus* With, 1902.

MATERIAL AND METHODS

The fossil described here derives from the Wunderlich collection (F1882/BB/AC/CJW) and will eventually be transferred either to the Senckenberg Museum (Frankfurt am Main) or the Görlitz Museum. It was photographed using a Leica Systems camera arrangement attached to a stereomicroscope, which generates a series of images through the specimen at different focal planes. The ca 20 individual images per picture were combined into final composites (Figs 1, 2) using the software package Auto Montage©. A Canon Eos Digital Camera attached to a Nikon compound microscope was used for close-up work (Fig. 5). The specimen was drawn by CS using a stereomicroscope with a camera lucida attachment. (Figs 3–4) Morphological terminology was adopted from the literature, principally van der Hammen (1976), but also Klompen (2000). The precise locality from which the specimen was recovered is not recorded, but much of the recently collected Baltic amber originates from the Kaliningrad area on the coast of the Baltic sea. It is generally dated at Palaeogene (Eocene), with an approximate age of 45–50 Ma.

MORPHOLOGICAL INTERPRETATION

The specimen is a largely complete inclusion, preserved at the base of a subtriangular piece of translucent, yellow amber with maximum dimensions of ca 12 x 6 mm. The specimen is best seen in ventral view. A hole in the posterior dorsal part of the body, together with a thin, white emulsion over the entire upper body makes interpretation of the dorsal surface more difficult. Limbs and mouthparts are preserved in some detail (see below) and in general the fossil closely resembles living opilioacarid species. All measurements are in mm.

Dorsal surface. The mite body is traditionally divided into a gnathosoma (i.e. the pedipalps and mouthparts) and the idiosoma comprising the remainder of the body. The idiosoma is broadly oval in outline. Dorsally there is a subtriangular 'anterior area' (cf. Klompen 2000), alternatively called the prodorsum (*sensu* van der Hammen 1976, 1989) and perhaps equivalent to the carapace of other arachnids. Due the emulsion film, details such as setae are largely equivocal (Fig. 1). However, on the right side two eye lenses can be resolved (Fig. 3), suggesting that the animal had two pairs of eyes (see chap. Systematic Palaeontology). The anterior area is delimited posteriorly by a transverse disjugal furrow. Behind this, further furrows hint at up to four additional, short dorsal segments on the remainder of the idiosoma. However, expected details (setae, lyrifissures, spiracles, etc.) are indistinct due to the emulsion film and the fact that much of the posterior part of the dorsal idiosoma has collapsed to leave a large hole in the dorsal surface.

Gnathosoma. In ventral view (Figs 2, 4, 5a) the ventral surface (infracapitulum) of the gnathosoma is quite well preserved and partly overlain by the sternapophyses (see below) which cover the expected position of the subcapitular gutter. Laterally, the dark, sclerotised rutella insert on this infracapitulum. As in modern taxa, the rutella are dentate on their inner (mesal) surface and we were able to resolve five teeth in total. We could not identify either With's organ – expected immediately mesal of each rutellum – or the adjacent lateral lips and regard these as equivocal for the fossil. Between the rutella, the anterior margin of the infracapitulum is slightly recurved and presents a series of quite elongate, anteriorly-projecting setae (Figs 4–5a). In van der Hammen's terminology these probably comprise circumbuccal and paralabial setae; whereby the rutella and With's organ are often interpreted as modified paralabial setae. Specific patterns of setae position on the infracapitulum could not be resolved. The bases of the chelicerae are hidden in the ventral view, but as in modern opilioacarids there are three articles, the dis-

tal two forming a small chela. The fixed finger is slightly dentate, the free (movable) finger is smooth. The pedipalps are fairly short and pediform. The proximal articles are largely concealed above the gnathosoma, but the terminal tarsus can be seen more clearly. It is covered distally with fine setae and bears a pair of very fine claws (the apotele).

Ventral idiosoma. The ventral idiosoma reveals more detail. At the anterior end, a pair of slender, elongate sternapophyses project forwards and underlie the gnathosoma (Figs 2, 4, 5a). Setal patterns on the sternapophysis can be useful taxonomically, but the presence of any particular pattern in the fossil is difficult to resolve. We found evidence for at least one lateral seta on each sternapophysis; possibly the latero-ventral, antaxial one *sensu* van der Hammen (1989). Flanking the sternapophyses are the sternal verrucae; rounded, wart-like valves of uncertain function. Genital structures are detailed below. The post-genital ventral idiosoma preserves few features of interest; only a couple of isolated setae. A series of eight weakly defined transverse furrows, which do not extend all the way across the ventral surface, probably indicate segment boundaries, but patterns of lyrifissures (slit sense organs), which can also indicate segmentation, could not be resolved. At the posterior end of the idiosoma, a distinct anal tubercle is present, closely resembling that figured by, e.g., van der Hammen (1989, fig. 122). The opilioacarid anal tubercle is essentially retractable and consists of a pair of valves, covering a soft, expandable, membranous region. Compared to illustrations of extant species the anal tubercle in the fossil is quite large, is clearly preserved in its open, expanded state, and we consider it plausible that the whole structure has been forced outwards during fossilisation.

Genital region. Behind the sternapophyses, the pregenital area of the idiosoma (Fig 5a) contains an approximately 'V'-shaped depression. A number of setae can be re-

solved in this area, but a distinct pattern is absent. The pregenital area is bordered posteriorly by a small sclerite – segment VII *sensu* van der Hammen – which is procurved anteriorly, but has a more or less straight posterior margin. Further lineations, or sulci, within segment VII can also be resolved. Segment VII is flanked by the genital verrucae, a prominent pair of raised, wart-like structures bearing three setae. In juvenile instars this plate-like structure is absent (e.g. van der Hammen 1966, fig. 5B), thus we interpret this fossil as an adult. Determining gender is more difficult. In some extant taxa there are differences in the number of pregenital papilliform setae: typically five or more in males as compared to two in females. These pregenital setae should occur directly in front of segment VIII (van der Hammen 1966, fig. 5B) and are *not* the longer hairs more widely distributed pregenitally as alluded to above. We were not able to observe any papilliform pregenital setae in the fossil. However, we should note Grandjean's (1936) observation that females of *Opilioacarus segmentatus* lack pregenital setae altogether; thus we favour the possibility that this specimen could be a mature female. Internal features such as a female ovipositor or male accessory glands are equivocal.

Legs. The legs are moderately long and robust (Figs 1–4). Leg I is longest, followed by leg IV. Legs II and III are shorter, but it is difficult to obtain an accurate comparative measure of total leg length due to their position bent around the body within the matrix. The pattern of articles (*sensu* van der Hammen, 1966) matches that of Recent opilioacarids, beginning with a coxa and trochanter; including two trochanters in legs III and IV. This is followed by the femur, divided into a basi- and telofemur in leg I, and the genu (= patella in arachnological terminology) and tibia; subdivided into a basi- and telotibia in leg I. The tarsus is divided into a basitarsus, a telotarsus and, in legs II–IV, additionally an acrotarsus. The legs end in the

Fig. 1. *Opilioacarus aenigmus* n. sp., an opilioacarid mite from Palaeogene (Eocene) Baltic amber. Dorsal overview. Scale bar equals 0.5 mm.

pretarsus in the form of a fleshy pulvillus, plus the apotele consisting of a small pair of claws or ungues.

The legs are largely covered with distinct rows of robust, perpendicular, papilliform setae, but towards their distal ends ordinary setae (*sensu* van der Hammen, i.e. unmodified hairs or setae) come to dominate, especially on leg IV. These ordinary setae are not so outstanding and tend to lie flatter against the article along its length. On the proximal articles the papilliform setae tend to be club-shaped, while on more distal podomeres they are often thinner, more pointed and resemble the ordinary setae. On the proximal podomeres of legs II–IV, the papilliform setae largely occur in four discrete rows – i.e. dorsal, ventral and two lateral – although additional rows of shorter papilliform setae can be seen as in, e.g., the distal half of the femur of leg IV. This regularity breaks down towards the distal end. It is also worth noting that on the dorsal side at least one proximal article, probably a trochanter of leg 2, the setae are small and slightly fan-shaped and may be notched distally (see also illustrations in van der Hammen's papers). Leg I in the fossil is slightly different in that the papilliform setae are less perpendicular and are more angled towards the limb articles and they persist in regular rows at least up to the end of the tibia.

Of particular note here are additional long, slender, presumably sensory, setae originating from the distal end of the tibia and the proximal end of the basitarsus of leg 1 (Figs 1, 3). Up to twelve individual hairs, at least as long as the basitarsus, can be resolved (Fig 5b); some of which actually recurve backwards from their insertion point. We have been unable to find a matching description for such setae in the opilioacarid literature and this character does not seem to be known from modern species (Hans Klompen, pers. comm. 2008). The possibility that these hairs could be fungal in nature – and thus not part of the animal – was considered, but examination courtesy of Alexander Schmitt (pers. comm. 2008) who has much experience with amber microorganisms (e.g. Schmitt et al. 2007) did not support a fungal origin. The hairs seem to originate directly from the body and to be preserved in an identical manner to the mite's other setae. The long hairs thus appear to be genuine and a convincing diagnostic character for the fossil species.

PALAEOECOLOGY

In recent years a number of amber arachnids have been published which imply the presence of dry, well-lit habitats within the original Baltic amber forest environment. These potential indicator taxa include the opilioacarids, like the one described here, camel spiders (Solifugae) and certain spiders (Ara-

neae) for example in the family Plectreuridae (Wunderlich 2004). All of these taxa are very rare in amber and typically known only from isolated specimens. Their modern relatives have a tendency to be found in dry habitats; i.e. not deep in forests. Assuming that the amber species had a similar ecology to their recent counterparts, one could conceive of them inhabiting 'dry islands' within the larger Eocene forest – similar environments being known even in the modern Amazon rainforests. According to Bachofen-Echt (1949: 33–35) certain plants have also been recorded in Baltic amber, which today show a preference for dry and sunny habitats: namely members of the Ericaceae, Euphorbiaceae, Santalaceae, Thymeliaceae and Urticaceae. Conceivably the arachnids mentioned above may have undergone some sort of passive transport – the mechanism of which remains unclear – to reach the sap-secreting trees. This might explain the extreme rarity of these animals.

SYSTEMATIC PALAEONTOLOGY

Acari Nitzsch, 1818

Comments. Mites can be broadly divided into two major lineages; see e.g. Alberti (2006) for details and a recent review. The anactinotrichids (Parasitiformes *sensu lato* in some schemes) include opilioacarids (see below), gamasids, holothyrids and ticks. The actinotrichids (Acariformes in some schemes) include the remaining mite groups: such as velvet mites, water mites, gall mites, oribatids and the astigmatids such as fur, food or dust mites, etc. The question of whether mites form a single, monophyletic lineage – as favoured by, e.g., Lindquist (1984) and assumed in most cladistic studies of arachnid relationships – has recently come back into focus. Dunlop & Alberti (2008) offered a summary of developments in this field. Interestingly, Shultz (2007) recovered mites as paraphyletic with respect to the species-poor arachnid order Ricinulei, at least under

Fig. 2. *Opilioacarus aenigmus* n. sp., an opilioacarid mite from Palaeogene (Eocene) Baltic amber. Ventral overview. Scale bar equals 0.5 mm.

some parameters of analysis. This is the first time that an explicit test of parsimony has favoured diphyletic mite origins. Klompen et al.'s (2007) molecular results found weak support for a monophyletic Acari and further studies in this direction with a wider taxon sampling would be welcome. Key to resolving this monophyly question are further integrative approaches to mites and non-mite arachnids. An almost independent literature has developed in both camps, often with inconsistent terminologies for probably homologous structures which mask potentially synapomorphic features. Indeed, despite decades of morphological study, Dunlop & Alberti (2008: table 1) could identify surprisingly few unique and unequivocal characters which could be used to support a
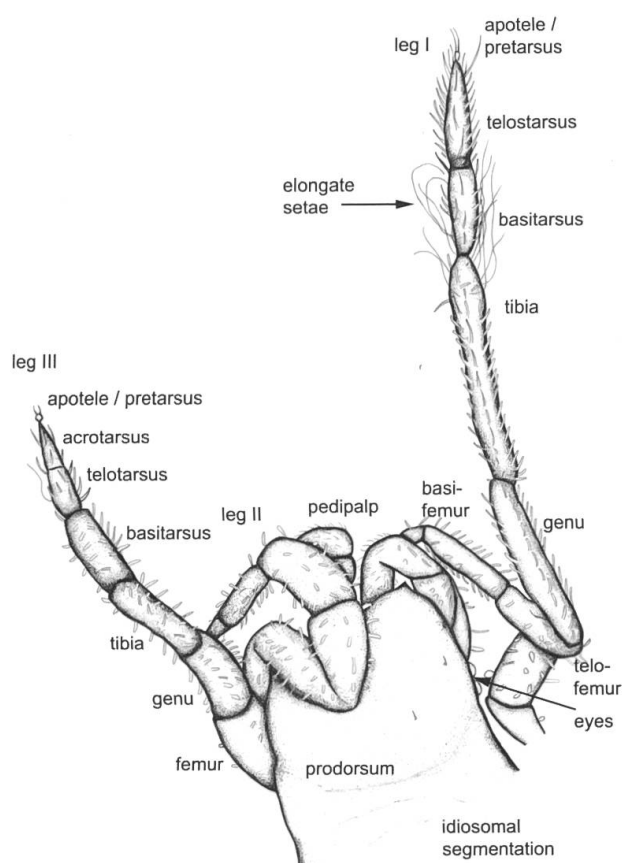
Fig. 3. *Camera lucida* drawing of the specimen shown in Fig. 1. Scale bar equals 0.5 mm.

particular arachnid order being sister-group of either all mites, or of one of their two major lineages.

Anactinotrichida Grandjean *in* van der Hammen, 1961

Remarks. Historically, opilioacarids have been treated as non-mites, 'primitive' mites (see above), or as Grandjean's (1936) "acarien synthétique"; the latter view finding reflection in the recognition of three lineages of equal rank in combinations such as Opilioacarida, Anactinotrichida and Actinotrichida (cf. Harvey 2002). More recently, there has been fairly unanimous cladistic support for grouping opilioacarids *within* Anactinotrichida (Murrell et al. 2005; Klompen et al. 2007) and lists of explicit characters shared by opilioacarids and other members of this group, can be found in, e.g., Alberti (2006) and Dunlop & Alberti (2008) and references

therein. The sister-group of Opilioacarida is in dispute. The more traditional view (e.g. Lindquist 1984) – also recovered from the molecular data of Klompen et al. (2007) – places opilioacarids as sister-group of the Parasitifomes *sensu stricto,* i.e. Holothyrida, Gamasida (= Mesostigmata) and Ixodida (ticks). By contrast Murrell et al. (2005), also using molecular data, did not recover parasitiforms *s. s.* as monophyletic; instead resolving opilioacarids as sister-group to holothyrids and ticks only, with gamasids now forming the outgroup. Further discussion can be found in these publications.

Opilioacarida With, 1902
Family Opilioacaridae Vitzthum, 1931
Genus ?*Opilioacarus* With, 1902

Comments. Only a single opilioacarid family is currently accepted. Harvey (1996, fig. 2) recognised nine genera plus two undescribed Australian ones. Of these, our new fossil can be excluded from *Paracarus* Chamberlin & Mulaik, 1942 from Central Asia and *Siamacarus* Leclerc, 1989 from Thailand, since both genera are characterised by three pairs of eyes. The new fossil has only two pairs. Significantly, this also shows that the new fossil is *not* conspecific with the previous record from Baltic amber, *Paracarus pristinus,* which also has three pairs of eyes (Dunlop et al. 2004, fig. 2a). A further notable difference is in the length of the fourth leg. In *P. pristinus* this is distinctly elongate – about 2.1 times the length of the body and similar in length to the first pair of legs – while in the new fossil the fourth leg is about 1.6 times body length and a little shorter than the first leg. This relatively long fourth leg was noted by van der Hammen (1968, p. 67) as diagnostic for *Paracarus.*

Of the remaining seven genera, Harvey (1996) recognised a clade containing *Vanderhammenacarus* Leclerc, 1989 from Thailand, *Salfacarus* van der Hammen, 1977 from southern Africa and Madagascar and *Panchetes* Naudo, 1963 from West Africa, plus the

undescribed Australian forms. These were defined by the putative apomorphy of dorsal setae on segments XV–XVII. This character cannot be tested here adequately due to the broken and emulsion-covered posterior dorsal surface. However, a second feature was also mentioned for these taxa (Harvey 1996, p. 157), namely the presence of two or more ventral setae on segment XVIII; i.e. the segment preceding the anal tubercle. While body hairs are generally not easy to resolve in our new fossil we found no evidence for hairs in front of the anal tubercle (Figs. 2, 4) and thus tentatively use this feature to exclude the three genera listed above.

Four genera remain under consideration. *Phalangiacarus* Coineau & van der Hammen, 1979 from West Africa was defined by a very long and pale (depigmented) first pair of legs, ca 2.8 times as long as the body. The first leg of our new fossil is only about 1.8 times body length and shows no evidence of depigmentation. For this reason we exclude it from *Phalangiacarus*. We were only able to discern at most five teeth in the rutellum which, according to van der Hammen (1969, p. 125), would exclude *Adenacarus* van der Hammen, 1966 from Yemen which has six. However, Lehtinin (1980) cautioned that the armature of the rutellum may only be of value for defining species. The two remaining genera, *Neocarus* Chamberlin & Mulaik, 1942 from America and *Opilioacarus* With, 1902 from the Mediterranean region, have historically proved problematic and were treated by some authors (see especially van der Hammen 1966, 1989) as synonyms. Authors such as Lehtinen (1980) recognised characters such as a strong basal tooth on the rutellum and two setae on the sternapophyses as potentially diagnostic for *Neocarus*. Yet when compared to illustrations in the original description of the *Opilioacarus* type species, *O. segmentatus* With 1902 (cf. pl. 4, fig. 4), the basal tooth of the rutellum appears quite large too, while Grandjean (1936, fig. 3B) figured two hairs on the sternapophysis of the same *Opilioacarus* species!
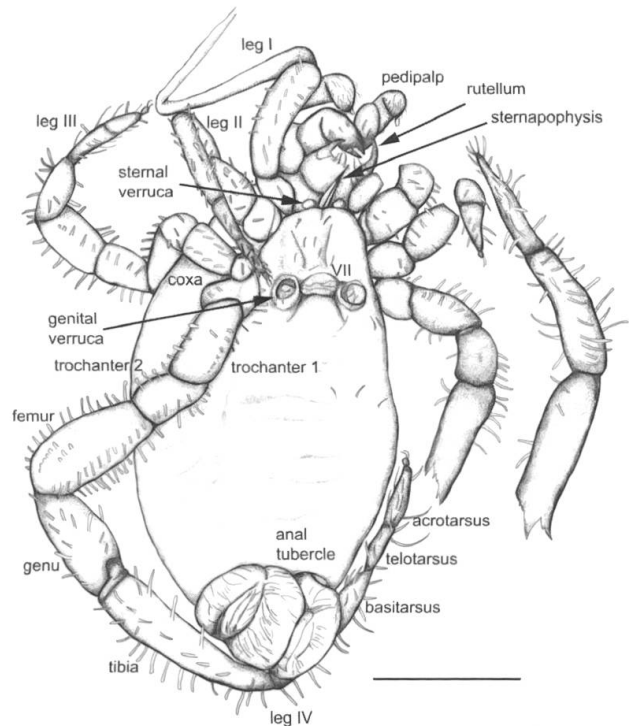

Fig. 4. Camera lucida drawing of the specimen shown in Fig. 2. Scale bar equals 0.5 mm.

In summary, we favour affinities with *Opilioacarus* based on a combination of morphology (see above) and geographical affinities with the Mediterranean. However, we concede that we have mostly had to exclude taxa based on negative characters and that the features available in the fossil are not as extensive as those used in the taxonomy of living opilioacarids and thus do not permit an unequivocal assignment. The long setae on the first leg of the fossil (see above) appear to be a unique feature compared to living opilioacarids. Conceivably, the new fossil could be raised to a new genus, but we prefer to adopt a cautious approach given that there are unresolved questions about the taxonomy of the living species as per the *Opilioacarus/Neocarus* problem alluded to above.

?*Opilioacarus aenigmus* sp. nov. (Figs 1–5)

Material. Wunderlich collection no. F1882/ BB/AC/CJW. Baltic amber, exact locality not recorded, but probably from the vicinity of
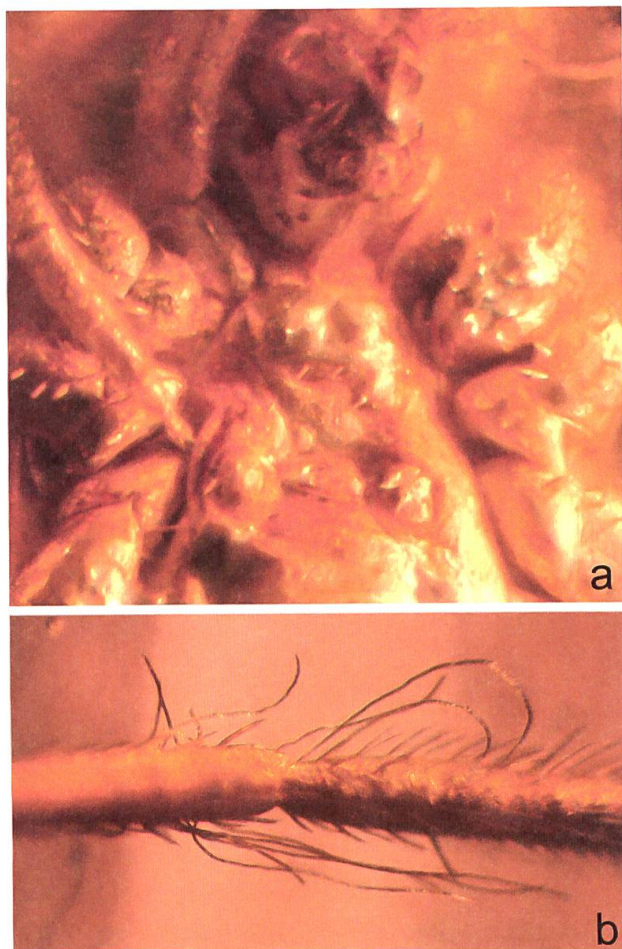
Fig. 5. a. Close-up of the gnathosomal and genital region. b. Close-up of the putative long setae on the tibia and basitarsus of the first leg. Such setae are not known from any living species.

Kaliningrad, Baltic coast of Russia. Palaeogene (Eocene).

Diagnosis. Fossil *Opilioacarus* uniquely with ca 12 elongate hairs on the distal tibia and proximal basitarsus of leg I.

Description. Body oval, total length (without gnathosoma) 1.6, maximum width 0.85. Anterior area (prodorsum) of idiosoma 0.52 long, bearing two eye lenses on right side. Corresponding eye position on left side obscured. Prodorsum demarcated by transverse groove and followed by four further transverse grooves demarcating at least four short, length ca 0.1, segments. Spiracular openings here and remainder of dorsal idiosoma equivocal. Gnathosoma compact, includes chelicerae formed from three articles.

Distal articles chelate; fixed finger dentate, free finger smooth. Infracapitulum with semicircle of fine, forward-projecting setae at its recurved anterior margin. Margin flanked laterally by rutella. Each rutellum dentate, with five teeth. With's organ and lateral lips equivocal and further gnathosomal details obscure. Pedipalps pediform, distally setose, with fine, hair-like claws. Sternapophyses project together in parallel beneath the gnathosoma, length 0.37, flanked by small, rounded (diameter 0.03) paired sternal verrucae. Pregenital area with sparse setae; no explicitly pregenital setae observed. Segment VII small, procurved, sclerotised; flanked by rounded paired genital verrucae (diameter 0.09), bearing 3 setae. Postgenital region of idiosoma largely featureless, but up to eight furrows hint at segmentation.

Article lengths of leg I: coxa 0.12, trochanter 0.4, basifemur 0.29, telofemur 0.28, genu 0.54, tibia 0.7, basitarsus 0.25, telotarsus 0.33. Article lengths of leg II: proximal articles equivocal, basitarsus 0.31, telotarsus 0.16, acrotarsus 0.12. Lengths of leg III: coxa 0.06, trochanter 1 0.17, trochanter 2, 0.10, femur and genu equivocal, tibia 0.20, basitarsus 0.20, telotarsus 0.16, acrotarsus 0.11. Article lengths of leg IV: coxa 0.1, first trochanter 0.32, second trochanter 0.17, femur 0.45, genu 0.3, tibia 0.65, basitarsus 0.5, telotarsus 0.17, acrotarsus 0.22. All legs end in pulvillus (pretarsus) and paired claws (ungues).

DISCUSSION

Mites actually have a richer fossil record than might be expected, but there are important and significant differences between the two main groups. Actinotrichids potentially go back as far as the Early Ordovician (ca 480 Ma) (Bernini et al. 2002) and they are unequivocally present by the Early Devonian (ca 410 Ma). Their fossil record is quite good compared to other that of other arachnids and second only in species number to spiders; particularly in terms of oribatids from amber and as subfossils assignable to modern species from Holocene peat deposits. 292

TAXON	AGE	LOCALITY	LITERATURE
Opilioacarida			
Paracarus pristinus	Eocene	Baltic amber	Dunlop et al. (2004)
?Opilioacarus aenigmus	Eocene	Baltic amber	this study
Gamasida			
Sejus bdelloides	Eocene	Baltic amber	Koch & Berendt (1854)
*Aclerogamasus stenocornis	Eocene	Baltic amber	Witaliński (2000)
Dendrolaelaps fossilis	Miocene	Chiapas (Mexican) amber	Hirschman (1971)
Paleozercon cavernicolus	Miocene	New Mexico Cave	Blaszak et al. (1995)
Holothyrida			
no fossil record			
Ixodida			
Compluriscutula vetulum	Cretaceous	Myanmar amber	Poinar & Buckley (2008)
Cornupalpatum burmanicum	Cretaceous	Myanmar amber	Poinar & Brown (2003)
Carios jerseyi	Cretaceous	New Jersey amber	Klompen & Grimaldi (2001)
Ixodes succineus	Eocene	Baltic amber	Weidner (1964), Weitschat (2004)
Ixodes tertiarius	Oligocene	Wyoming, USA	Scudder (1885)
Ornithodoros antiquus	Miocene	Dominican amber	Poinar (1995)
**Amblyomma near *argentinae*	Miocene	Dominican amber	Lane & Poinar (1986)
**Dermacentor near *reticulatus*	Pliocene	auditory canal of a rhino	Schille (1916)

Table 1 Summary of fossil anactinotrichids described in the literature, arranged by suborder and then by stratigraphy (oldest records first).

*Joel Hallan's online mite catalogue <http://insects.tamu.edu/research/collection/hallan/acari/Family/Parasitidae.htm> flagged two further *Aclerogamasus* species from Romania as fossils, but when checked against the original citation (Juvara-Balş 1977) these are in fact Recent species described from caves.
**Recent species: described as "*A.* near *testudinus*"; a species which has subsequently been treated as a synonym of *A. argentinae* (cf. Camicas et al. 1998, p. 103).

fossil actinotrichid species (including Recent forms found as subfossils) have been recorded (Dunlop et al. 2010). By contrast, there are – including our new find – only fourteen fossil species of anactinotrichids (Table 1) and their record goes back no further than the Cretaceous (e.g. Poinar & Buckley 2008). Fossil anactinotrichids now include two opilioacarids, four gamasids, no holothyrids and eight ticks (both hard and soft). The rather young and markedly less diverse anactinotrichid fossil fauna is probably a sampling artefact and may also reflect the fact that relatively little effort has been devoted to the study of non-oribatid mites in amber in gen-

eral. Nevertheless, gamasids are an extremely diverse and abundant group in modern soil ecosystems and the fact that only four have been formally identified – and only as far back as the Eocene – remains puzzling.

REFERENCES

Alberti, G. 2006. On some fundamental characteristics in acarine morphology. *Atti della Accademia Nazionale Italiana di Entomologia.* Rendiconti LIII-2005: 315–360.

Bachofen-Echt, A. 1949. *Der Bernstein und seine Einschlüsse.* [Reprinted in 1996 by Publishing House Jörg Wunderlich. Straubenhardt, Germany.]

Bernini, F., Carnevale, G., Bagnoli, G. & Stouge, S. 2002. An early Ordovician mite (Acari: Oribatida) from the island of Öland, Sweden. In: Bernini, F., Nannelli, R., Nuzzaci, G., Lilo, E. de (eds): *Acarid Phylogeny and Evolution: Adaption in Mites and Ticks*, pp. 45–47, Kluwer Accademic Publishers, Dordrecht.

Błaszak, J., Cokendolpher, J.C. & Polyak, V.J. 1995. *Paleozercon cavernicolous*, a new genus and new species of fossil mite from a cave in the southwestern U.S.A. (Acari, Gamasida: Zerconidae). *International Journal of Acarology* 21: 253–259.

Camicas, J.-L., Hervy, J.-P., Adam, F., Morel, P.-C. 1998. *Les Tiques du monde. Nomenclature, stades décrits, hôtes, répartition.* Institut Français de Recherche Scientifique pour le Développement en Coopération, Paris.

Chamberlin, R.V. & Mulaik, S. 1942. On a new family in the Notostigmata. *Proceedings of the Biological Society of Washington* 55: 125–32.

Dunlop, J.A. & Alberti, G. 2008. The affinities of mites and ticks: a review. *Journal of Zoological Systematics and Evolutionary Research* 46: 1–18.

Dunlop, J.A., Wunderlich, J. & Poinar jr., G.O. 2004. The first fossil opilioacariform mite (Acari: Opilioacariformes) and the first Baltic amber camel spider (Solifugae). *Transactions of the Royal Society of Edinburgh: Earth Sciences* 94: 261–273.

Dunlop, J.A., Penney, D. & Jekel, D. 2010. A summary list of fossil spiders and their relatives. In Platnick, N. I. (ed.) The world spider catalog, version 11.0 American Museum of Natural History, online at http://research.amnh.org/entomology/spiders/catalog/index.html

Grandjean, F. 1936. Un acarien synthétique: *Opilioacarus segmentatus* With. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* 27: 413–444.

Hammen, L. van der 1961. Description of *Holothyrus grandjeani* nov. spec., and notes on the classification of the mites. *Nova Guinea, Zoology* 9: 173–194.

Hammen, L. van der 1966. Studies on Opilioacarida (Arachnida) I. Description of *Opilioacarus texanus* (Chemberlin & Mulaik) and revised classification of the genera. *Zoologische Verhandelingen* 86: 1–80.

Hammen, L. van der 1968. Studies on Opilioacarida (Arachnida) II. Redescription of *Paracarus hexophthalmus* (Redikorzev). *Zoologische Mededelingen* 43: 57–76.

Hammen, L. van der 1976. *Glossaire de la terminologie acrologique. Vol. 2. Opilioacarida.* Dr. W. Junk bv Publishers, The Hague.

Hammen, L. van der 1977. Studies on Opilioacarida (Arachnidea) IV. The genera *Panchaetes* Naudo and *Salfacarus* gen. nov. *Zoologische Mededelingen* 54: 43–78.

Hammen, L. van der 1989. *An introduction to comparative arachnology.* SPB Academic Publishing bv, The Hague.

Harvey, M. 2002. The neglected cousins: what do we know about the smaller arachnid orders. *Journal of Arachnology* 30: 357–372.

Hirschmann, W. 1971. A fossil mite of the genus *Dendrolaelaps* (Acarina, Mesostigmata, Digamasellidae) found in amber from Chiapas, Mexico. *University of California Publications in Entomology* 63: 69–70.

Juvara-Balş, I. 1977. Quelques remarques sur les *Aclerogamasus* de Roumanie, *A. bicalliger* Athias et *A. motasi* n. sp. (Acarina: Gamasida: Parasitidae). *Travaux de l'Institut de Spéologie "Émile Racovitza"* 16: 37–45.

Klompen, H. 2000. Prelarva and larva of *Opilioacarus* (*Neocarus*) *texanus* (Chamberlin and Mulaik) (Acari: Opilioacarida) with notes on the patterns of setae and lyrifissures. *Journal of Natural History* 34: 1977–1992.

Klompen, H. & Grimaldi, D. 2001. First Mesozoic record of a parasitiform mite: a larval argasid tick in Cretaceous amber (Acari: Ixodida: Argasidae). *Annals of the Entomological Society of America* 94: 10–15.

Klompen, H., Lekveishvili, M. & Black IV, W.C. 2007. Phylogeny of parasitiform mites (Acari) based on rRNA. *Molecular Phylogenetics and Evolution* 43: 936–951.

Koch, C.L. & Berendt, G.C. 1854. Die im Bernstein befindlichen Myriapoden, Arachniden und Apteren der Vorwelt. In: Berendt, G.C., *Die im Bernstein befindlichen organischen Reste der Vorwelt*. 1. Berlin, Nicolai.

Lane, R.S. & Poinar, G.O. 1986. First fossil tick (Acari: Ixodidae) in New World amber. *International Journal of Acarology* 12: 75–78.

Leclerc, P. 1989. Considérations paléobiogéographiques a propos la découverte en Thailande d'Opilioacariens nouveaux (Acari – Notostigmata). *Compte Rendu des Séances, Société de Biogéographie, Paris* 65: 162–74.

Lehtinen, P.T. 1980. A new species of Opilioacarida (Arachnida) from Venezuela. *Acta biologica Venezuelica* 10: 205–214.

Lindquist, E.E. 1984. Current theories on the evolution of major groups of Acari and on their relationships with other groups of Arachnida with consequent implications for their classification. In: Griffiths, D.A. & Bowman, C.E. (eds), *Acarology, Vol. 1.*, pp. 28–62, Ellis Horwood Ltd., Chichester.

Murrell, A., Dobson, S.J., Walter, D.E., Campbell, N.J.H., Shao, R. & Barker, S.C. 2005. Relationships among the three major lineages of the Acari (Arthropoda: Arachnida) inferred from small subunit rRNA: paraphyly of the Parasitiformes with respect to the Opilioacarifomes and relative rates of nucleotide substitution. *Invertebrate Systematics* 19: 383–389.

Naudo, M.H. 1963. Acariens Notostigmata de l'Angola. *Publicações Culturais da Companhia de Diamantes de Angola, Lisboa* 63: 13–24.

Nitzsch, C.L. 1818. In: Ersch, J.S. & Gruber, J.G., *Allgemeine Encyclopaedie der Wissenschaften und Künste* 1, Leipzig.

Poinar, G.O. 1985. First fossil soft tick, *Ornithodoros antiquus* n. sp. (Acari: Argasidae) in Dominican amber with evidence of their mammalian host. *Experientia Basel* 51: 384–387.

Poinar, G.O. & Brown, A. 2003. A new genus of hard ticks in Cretaceous Burmese amber (Acari: Ixodida: Ixodidae). *Systematic Parasitology* 54: 199–205.

Poinar, G.O. & Buckley, R. 2008. *Compluriscutula vetulum* (Acari: Ixodida: Ixodidae), a new genus and species of hard tick from Lower Cretaceous Burmese amber. *Proceedings of the Entomological Society of Washington* 110: 445–450.

Reuter, E. 1909. Zur Morphologie und Ontogenie der Acariden mit besonderer Berücksichtigung von *Pediculopis graminum*. *Acta Societatis Scientiarum Fennica* 36: 1–288.

Schille, F. 1916. Entomologie aus der Mammut- und Rhinoceros-Zeit Galiziens. *Entomologische Zeitschrift* 30: 42–43.

Schmidt, A.R., Dörfelt, H. & Perrichot, V. 2007. Carnivorous fungi from Cretaceous amber. *Science* 318: 1743.

Schultz, J.W. 2007. A phylogenetic analysis of the arachnid orders based on morphological characters. *Zoological Journal of the Linnean Society* 150: 221–265 .

Scudder, S.H. 1885. Arachnoidea. Spinnen. Skorpione. In: Zittel, K.A. (ed.), *Handbuch der Palaeontologie. I. Abteilung. Palaeozoologie. II. Band. Mollusca und Arthropoda*, pp. 732–746. Verlag von R. Oldenbourg, München & Leipzig.

Vázquez, M.M. & Klompen, H. 2002. The family Opilioacaridae (Acari: Parasitiformes) in North and Central America, with descriptions of four new species. *Acarologia* 42: 299–322.

Vitzthum, H. Graf 1931. 9: Ordnung der Arachnida: Acari=Milben. In: Kükenthal, W. (ed.), *Handbuch der Zoologie, Vol. III*, 2. (3), pp. 1–160, Walter de Gruyter & Co., Berlin.

Weidner, H. 1964. Eine Zecke, *Ixodes succineus* sp. n. im Baltischen Bernstein. *Veröffentlichungen aus dem Überseemuseum Bremen* 3: 143–151.

Weitschat, W. 2004. Zecken im Bernsteinwald – wahre Raritäten. *ImpfDialog* 2004 (1): 11–12.

Witaliński, W. 2000. *Aclerogamasus stenocornis* sp. n., a fossil mite from the Baltic amber (Acari: Gamasida: Parasitidae). *Genus* 11: 619–626.

With, C.J. 1902. A new acaride *Opilioacarus segmentatus. Comptes Rendus du Congrès des Naturalistes et Médicins du Nord* 20: 4–5.

Wunderlich, J. 2004. Fossil spiders (Araneae) of the superfamily Dysderoidea in Baltic and Dominican amber, with revised family diagnoses. In: Wunderlich, J. (ed.), *Beiträge zur Araneologie* 3: 633–746.