

Acarologia

A quarterly journal of acarology, since 1959
Publishing on all aspects of the Acari

All information:

<http://www1.montpellier.inra.fr/CBGP/acarologia/>
acarologia-contact@supagro.fr



**Acarologia is proudly non-profit,
with no page charges and free open access**

Please help us maintain this system by
encouraging your institutes to subscribe to the print version of the journal
and by sending us your high quality research on the Acari.

Subscriptions: Year 2021 (Volume 61): 450 €

<http://www1.montpellier.inra.fr/CBGP/acarologia/subscribe.php>

Previous volumes (2010-2020): 250 € / year (4 issues)

Acarologia, CBGP, CS 30016, 34988 MONTFERRIER-sur-LEZ Cedex, France

ISSN 0044-586X (print), ISSN 2107-7207 (electronic)

The digitalization of Acarologia papers prior to 2000 was supported by Agropolis Fondation under the reference ID 1500-024 through the « Investissements d'avenir » programme (Labex Agro: ANR-10-LABX-0001-01)



Acarologia is under **free license** and distributed under the terms of the Creative Commons-BY.

A putative fossil sejid mite (Parasitiformes: Mesostigmata) in Baltic amber re-identified as an anystine (Acariformes: Prostigmata)

Jason A. Dunlop^a, David E. Walter^b, Jenő Kontschán^c

^a Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstrasse 43, D-10115 Berlin, Germany.

^b Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada; Queensland Museum 4101 and University of the Sunshine Coast, Queensland, Australia, 4556.

^c Plant Protection Institute, Centre for Agricultural Research, Hungarian Academy of Sciences, H-1525 Budapest, P.O. Box 102, Hungary.

ABSTRACT

The Acari (mites) is currently interpreted to consist of two superorders. In contrast to the relatively rich history of the mite superorder Acariformes, fossils of the Parasitiformes are extremely rare. This is especially true of the most diverse order, Mesostigmata, with only nine families recorded, including four named species, having been described so far. As part of a wider effort to clarify the diversity of Baltic amber Mesostigmata the historically oldest fossil, *Sejus bdelloides* Koch & Berendt, 1854, is re-examined. While clearly a mite, it is not a mesostigmatan, but a member of the Prostigmata (Acariformes), referable to the Anystina. Thus of the three main mesostigmatan lineages currently recognised both Sejida and Trigynaspida lack a fossil record. Monogynaspida can be traced with confidence back to the Eocene (ca. 44 – 49 Ma).

Keywords Sejida, Sejus, Anystina, fossil record, Mesostigmata

Zoobank <http://zoobank.org/77E87B16-2E25-45C4-942B-A9211E7C4BCB>

Introduction

Although there are around 11,400 living species of mesostigmatian mites (Acari: Parasitiformes: Mesostigmata) (Beaulieu *et al.* 2011), this impressive diversity is not reflected in their fossil record. As noted by Dunlop *et al.* (2014), a possible reason for this is that few mesostigmatan lineages currently inhabit tree bark which, if current ecology reflects ancient ecology, reduced the chance of them becoming preserved as inclusions in amber. Only four fossil species have been formally named: *Sejus bdelloides* Koch and Berendt, 1854 from Eocene Baltic amber, *Dendrolaelaps fossilis* Hirschmann, 1971 from Miocene Chiapas (or Mexican) amber, *Palaeozercos cavernicolus* Błaszczak *et al.*, 1995 from a subfossil cave deposit in the USA, and *Alecrogamasus stenocornis* Witaliński, 2000, again from Baltic amber. In addition to this, there are further examples of fossil mesostigmatans in the literature (see citations in Table 1). Several of them were discovered in association with other arthropods (Lyubarsky and Perkovsky 2012; Dunlop *et al.* 2013, 2014), but could not be identified beyond the family or genus.

Fossil arachnids are proving to be of increasing importance in calibrating molecular phylogenies by, for example, constraining minimum ages for cladogenesis and offering divergence times between the appearance of stem-group members of a given lineage and crown-group taxa typically assignable to modern genera. Recent examples include Dabert *et al.* (2010) for acariform mites, Giribet *et al.* (2009) and Hedin *et al.* (2012) for harvestmen and

Received 30 January 2018

Accepted 16 April 2018

Published 25 July 2018

Corresponding author

Jason A. Dunlop:

jason.dunlop@mfn-berlin.de

Academic editor

Ekaterina Sidorchuk

DOI

10.24349/acarologia/20184263

© Copyright

Dunlop J.A. *et al.*

Distributed under

Creative Commons CC-BY 4.0



How to cite this article Dunlop J.A. *et al.* (2018), A putative fossil sejid mite (Parasitiformes: Mesostigmata) in Baltic amber re-identified as an anystine (Acariformes: Prostigmata). *Acarologia* 58(3): 665-672; DOI 10.24349/acarologia/20184263

Wood *et al.* (2013) for spiders. Yet before fossils can be used in this way it is important to check the reliability of published attributions. In this context, three principal clades of Mesostigmata are currently recognised: Sejida, Monogynaspida and Trigynaspida. Most of the published mesostigmatan fossils are monogynaspids (Table 1), while Trigynaspida currently lacks a fossil record.

The third group, Sejida is uniquely represented by the historically oldest species: *Sejus bdelloides*. However, there are several problems associated with this record. In the mid-19th century when this fossil was described the concept of *Sejus* – sometimes spelled *Seius*; see synonymy list – was rather loose, the genus name being used for a variety of mesostigmatans. Also, the original line drawings in Koch and Berendt's (1854) monograph consist of somewhat idealised reconstructions (Figure 1), and are not always reliable guides to the appearance of the actual specimens in the matrix. Thus to clarify whether sejid mites were present in the fossil record, we re-examined the holotype of *S. bdelloides* (Figures 1, 2) and suggest here that it is neither a Sejida, nor even a Mesostigmata.

Materials and methods

The holotype of *Sejus bdelloides* originates from Baltic amber and lies within a fairly large piece of dark orange (*i.e.* partially oxidised) amber, with dimensions of ca. 35 x 15 mm. Two fragments have split off from the main amber piece, but do not contain any inclusions. The specimen is part of the scientifically, and historically, valuable Berendt collection held in the palaeontology section of the Museum für Naturkunde Berlin (MfN). The holotype has the modern repository number MB.A.1634 (for Museum Berlin, Arthropoda). The original label also bears the older collection numbers “117” and “7279”. The amber piece is quite complicated in that it contains numerous syninclusions – most of which are also type and figured specimens – including a cheyletid mite (Acariformes: Prostigmata: Cheyletidae), a clubionid spider and two archaeognath hexapods. Baltic amber is thought to have been deposited in a warm forest environment and is conventionally dated at Eocene (Lutetian), or about 44 – 49 Ma. For a recent overview of this amber deposit and its geological setting see Weitschat and Wichard (2010).

Recognising *S. bdelloides* from within this diverse assemblage was thus challenging, but we believe it to be the mite towards the middle of the amber piece, tucked in close to the antennae of one of the archaeognaths (Figure 1A). In support of this assertion is the fact that the mite in question bears a small pair of posterior setae, whereby similar setae are indicated both in the original text description “am Hinterrande zwei kurze Borsten”. Furthermore, the notes (“Anmerkungen”) to the original description in Koch and Berendt (1854) state: “Das einzige Exemplar liegt tief in einem etwas dunkelfarbigem Steine und ist überdies noch an der Spitze des Kopfes mit einer undurchsichtigen Blase bedeckt, in welcher auch Rüssel und Taster versteckt sind. Dieses Thierchen gehört bestimmt in die Familie der Gamasiden und den Beinen nach zu gegenwärtiger Gattung.” We translate this as: “The only specimen lies deep in a rather dark stone and is covered from the tip of the head with an opaque bubble which conceals the snout and palps. This little animal certainly belongs in the gamasid family and based on the legs to a living genus.” The specimen figured here has a smooth prodorsal shield, which could appear like a bubble (Figures 1B), and the gnathosoma cannot be seen, thus it fits quite well with Koch and Berendt's comments. Koch and Berendt (1854) also noted that the first pair of legs was the thickest, which also corresponds well (Figure 1B, 2B) with the specimen we presume to be their holotype.

The specimen was studied and drawn under a Leica stereomicroscope and a Zeiss Axioscope compound microscope; both with a *camera lucida* attachment. Since the specimen is deeply buried in the now darkened amber, several details in the drawing were visualised with the *camera lucida* on the compound microscope allowing minute variations in the depth of field to yield more details (e.g. setae); however photographing all of these details with the

Table 1 Summary of the fossil record of the Mesostigmata and the nine families recorded so far. All families with a fossil record belong to the Monogynaspida clade. Both Trigynaspida and now also Sejida (this study) lack a fossil record. Sequence and nomenclature of higher taxa follow Beaulieu *et al.* (2011).

Infra- / Hyporder	Superfamily	Family	Range	Reference(s)
Mesostigmata indet.	?	?	Cretaceous–Recent	Poinar (1998); Peñalver <i>et al.</i> (2017)
UROPODINA				
	Microgynioidea			
		uncertain	Eocene–Recent	Dunlop <i>et al.</i> (2013)
	Uropodoidea			
		(1) Trematuridae	?Eocene–Recent	Lyubarsky and Perkovsky (2012); Ramsay (1960)
		(2) Urodinychidae	Eocene–Recent	Dunlop <i>et al.</i> (2013)
GAMASINA				
		“Gamasina indet.”	Eocene–Recent	Perkovsky <i>et al.</i> (2007)
EPICRIIAE				
	Zerconoidea			
		(3) Zerconidae	Quarter.–Recent	Błaszak <i>et al.</i> (1995)
PARASITIAE				
	Parasitoidea			
		(4) Parasitidae	Eocene–Recent	Witaliński (2000); Dunlop and Falkenhagen (2014)
DERMANYSSIAE				
	Rhodacaroidea			
		(5) Digamasellidae	Eocene–Recent	Perkovsky <i>et al.</i> (2007); Hirschmann (1971)
	Eviphidoidea			
		(6) Macrochelidae	Quarter.–Recent	Ramsay (1960)
	Ascoidea			
		(7) Ascidae	Eocene–Recent	Dunlop <i>et al.</i> (2013)
	Phytoseioidea			
		(8) Podocinidae	Quarter.–Recent	Aoki (1974)
	Dermanyssoidea			
		(9) Laelapidae	Eocene–Recent	Dunlop <i>et al.</i> (2014)

equipment available was not possible. The specimen was photographed (Figure 1) under a stereomicroscope via the Leica Application Suite software which enables stacks of images to be combined into a final picture. Since the specimen is part of a series of types all within one – now rather fragile – amber piece, it was not permitted to carry out tomographic scans which might have revealed further anatomical details.

Trombidiformes Reuter, 1909

Prostigmata Kramer, 1877

Cohort (=Infraorder) Anystina sensu Krantz & Walter, 2009

?Anystoidea Oudemans, 1936, *incertae sedis*

***Sejus bdelloides* Koch and Berendt, 1854 *nomen dubium* (Figures 1, 2)**

Sejus bdelloides, Koch and Berendt, 1854: 110, pl. 15, fig. 115; Nec *Sejus bdelloides* [as *Seius*] Bronn, 1849; Giebel, 1856: 484; Scudder, 1891: 288; *nomen nudum* according to Oudemans, 1937: 376) Vitzthum, 1943: 730 [as *Seius*]; Petrunkevitch, 1955: 97 [as *Seius*]; Selden, 1993: 310 [as *Seius*]; Walter and Proctor, 1999: 16 [as *Seius*]; Dunlop *et al.*, 2010: 67; Dunlop *et al.*, 2013: 338.

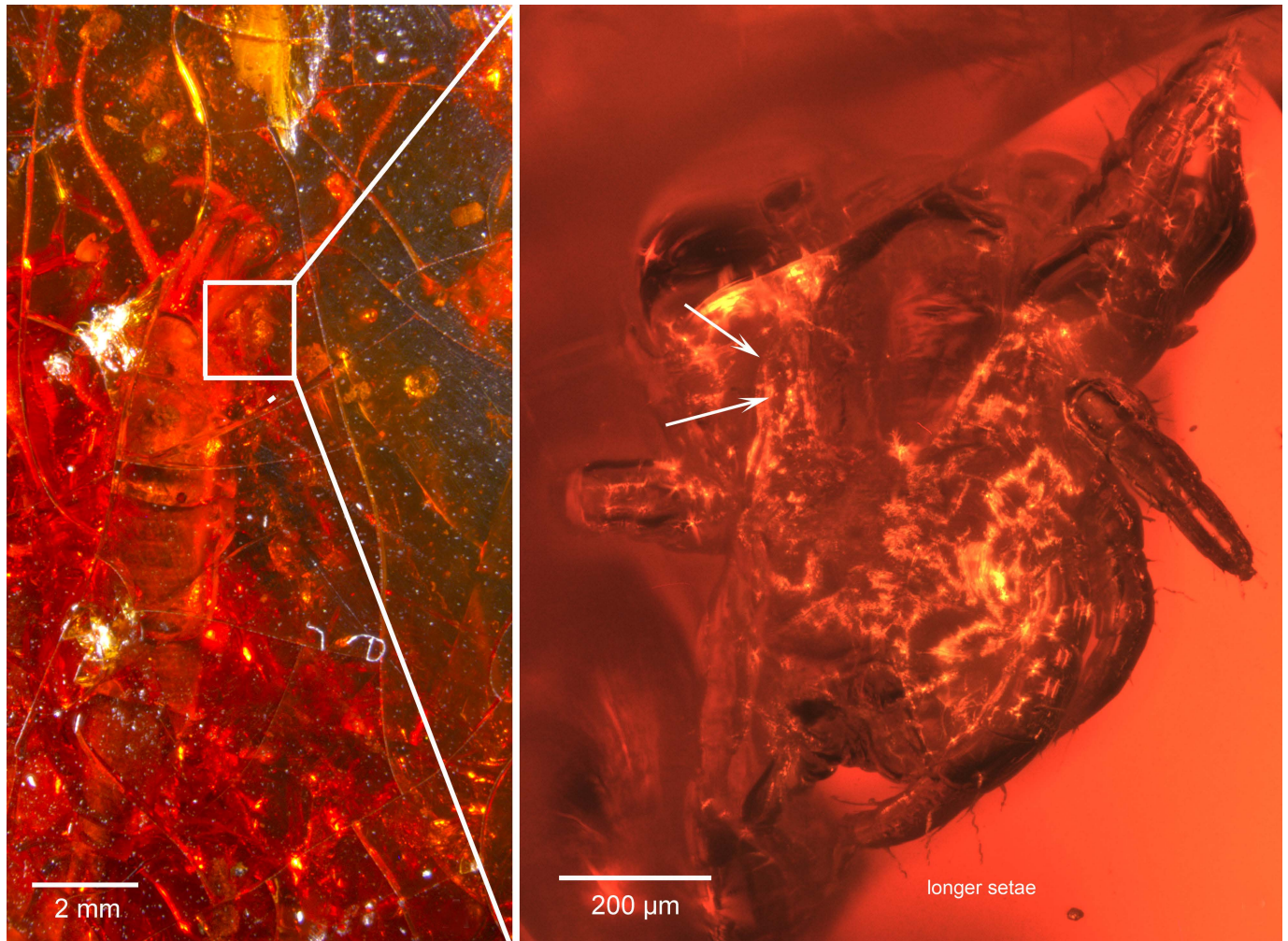


Figure 1 MB.A.1634, the presumed holotype of *Sejus bdelloides* from Eocene Baltic amber; at present the only fossil assigned to the suborder Sejida within the Mesostigmata. A – Overview of the mite inclusion in close proximity to an archaeognath insect; B – detail of the mite. The darkened and fractured amber matrix surrounding this historical specimen renders details hard to resolve. Possible ocelli arrowed and longer setae towards the back of the animal indicated. Photograph 1B by Ekaterina Sidorchuk.

Material examined — MB.A.1634 (*ex* Berendt collection no. 7279). Baltic amber, precise locality not recorded. Palaeogene: Eocene: Lutetian.

Description — Total body length 656 µm; maximum width ca. 460 µm. Dorsum: Prodorsal shield oval, 364 µm long and 241 µm wide, surface smooth. Prodorsal shield with four pairs of smooth and needle-like setae (potentially representing setae *vi*, *ve*, *sci* and *sce*), in which case *ve* and *sce* are longer (ca. 100 µm) than *ve* and *sce* (ca. 50 µm). Two putative pairs of ocelli situated on membranous cuticle, lateral to prodorsal shield and at level of *sce*. Four pairs of setae (potentially representing *c1*, *d1*, *e1* and *f1*) presented posterior to prodorsal shield. Setae *c1* and *d1* short (ca. 30 µm) and needle-like, *e1* three times longer (ca. 90 µm) and needle-like. Setae *f1* absent, only their insertion visible. Setae *c2* longer (ca. 130 µm) than other setae on membranous cuticle and situated anterior to *c1*. Setae *h2* or *ps1* and not visible. Legs with smooth and simple setae, but all setae and solenida not visible. Claws visible only on tip of leg II, large and with median fleshy pad (empodium).

Remarks — The original description of *Sejus bdelloides* does not provide sufficient

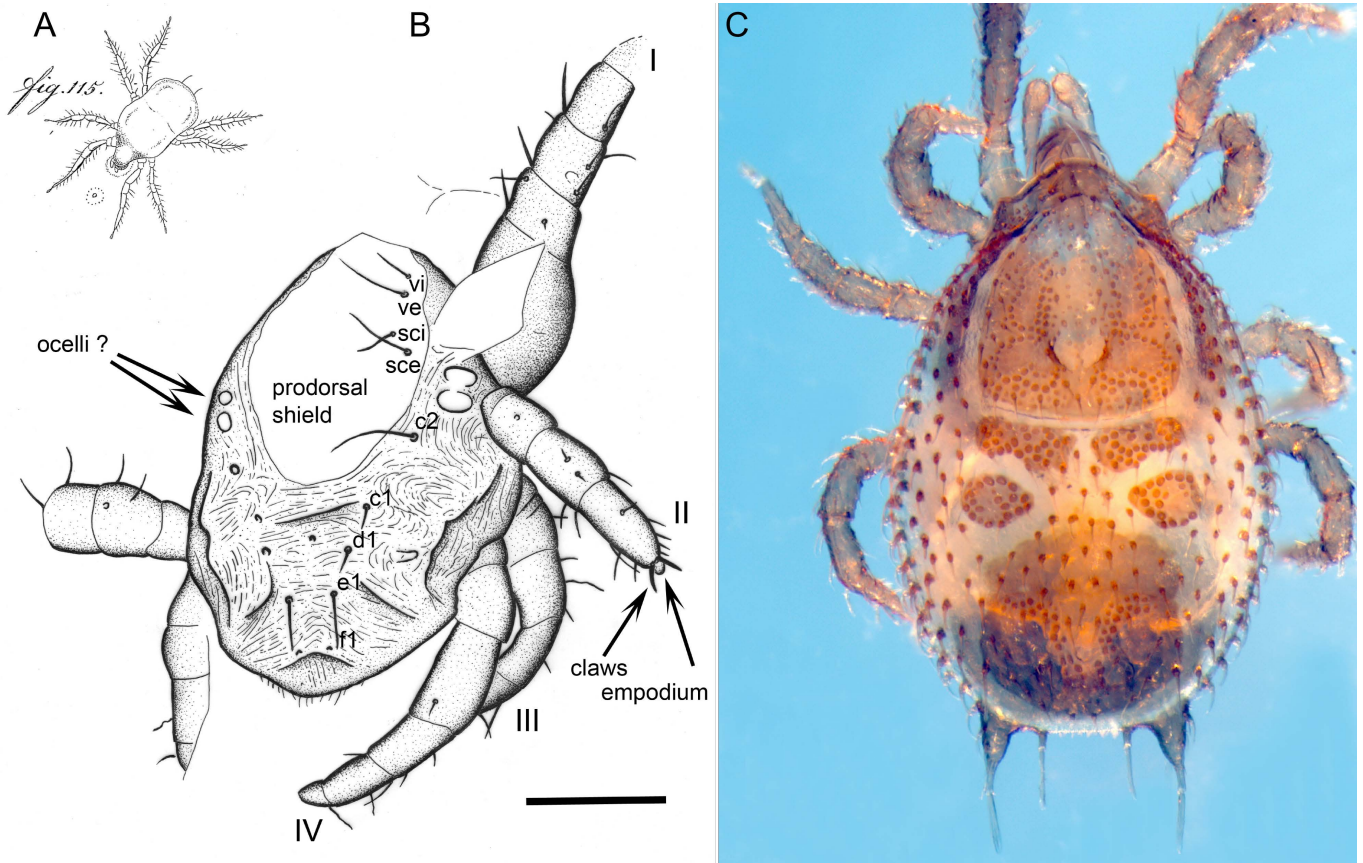


Figure 2 A – Facsimile copy of the original drawing of *Sejus bdelloides* Koch and Berendt, 1854. Note that it includes features such as the gnathosoma and leg claws which are not obvious in the specimen we interpret as their holotype; B – *Camera lucida* drawing of the holotype of *S. bdelloides*; here regarded as a *nomen dubium* which can nevertheless be referred to ?*Anystoidea incertae sedis* (Acariformes: Prostigmata). Legs numbered from I to IV. Note the two pairs of putative lateral ocelli adjacent to the prodorsal shield. Tentative identifications for the setae (or their sockets) are provided. Base of leg I partly obscured by a crack in the amber. Scale bar equals 200 μ m; C – Comparative image of a female belonging to the modern species *Sejus americanus* (Banks) (Sejidae) – see also Walter (2013, figs 36–37) – which differs markedly in habitus to the putative amber sejid. Photograph by David E. Walter.

characters to unequivocally place the fossil in Sejida as it is understood today, simply stating (as noted above) that it's a gamasid and that, based on the legs, it belongs in the modern genus. Interestingly, *Sejus* Koch, 1836 was created a few years earlier by one of the describers of the amber inclusion, whereby Carl Ludwig Koch may have been influenced by the apparent posterior setae in the amber specimen (Figure 2B). These are vaguely reminiscent of the condition seen in his (living) type species *Sejus togatus* Koch, 1836 (see e.g. figures in Hirschmann *et al.* 1991), although several other mites can show paired posterior setae. However, unlike the dorsally rather setose and pustulate *S. togatus*, the amber fossil is uniformly plicate except for a prodorsal shield and reveals little in the way of structures consistent with – or diagnostic for – any of the known families of Sejida. A comparative image of *Sejus americanus* (Banks, 1902) is also included here for reference (Figure 2C) and again the pattern of sclerites and setae here differ markedly from the habitus of the amber inclusion. *Sejus bdelloides* must therefore be excluded from both Sejida, which now lacks a fossil record entirely, and we see no characters justifying its referral to Mesostigmata in general. The median empodium on leg II also rules out Mesostigmata.

We suspect that this amber mite in fact belongs to the acariform suborder Prostigmata. A prodorsal shield with four pairs of setae is visible (Figures 1B, 2B), flanked by what appear to be two pairs of ocelli. This character would also rule out mesostigmatan affinities, as all

of these mites should be blind. Note that Koch and Berendt (1854) did not record the eyes, stating “Die Augen sind nicht sichtbar”. We are not sure why this discrepancy exists, but the putative eyes are quite hard to see even with modern microscopes (Figure 1B). The legs are relatively stout and tarsus II on the right ends in a pair of claws and empodium (Figures 1B, 2B). Unfortunately the gnathosoma is hidden and the form of the chelicera and palps cannot be determined, but the idiosomal setation is not consistent with any Parasitiformes.

That said, *Sejus bdelloides* does resemble extant members of the cohort Anystina (Walter *et al.* 2009) and could even be a member of the Anystoidea. Extant Anystoidea are often arboreal, have a similarly shaped body, an anterior dorsal plate with 4 pairs of setae and flanked by two pairs of ocelli (Figure 2B), and similar idiosomal setation. The obscuration of the gnathosoma precludes a definitive identification, but extinct members of Anystoidea have been previously recorded in both Late Cretaceous amber (see Walter and Proctor 2013, Figure 2.12a), Cretaceous and Paleogene Russian amber (Zacharda and Krivolutsky 1985) and Baltic amber by Koch and Berendt (1854) and Sayre *et al.* (1992). What we interpret as a pair of eyes laterad on the dorsal plate and anteriormost seta (possibly *vi*) remote from a naso (Figure 2B) is reminiscent of some modern Teneriffiidae, see e.g. Bernardi *et al.* (2012). The general habitus is similar to some extant *Austroteneriffia* Womersley, 1935 species (e.g. Khanjani *et al.* 2014: Figure 1), but the fossil does differ in the leg chaetotaxy and the absence of pectinate claws.

Since the available material in its current state of preservation does not allow a clear resolution of its familial or generic affinities we prefer to treat *Sejus bdelloides* as a putative Anystina and refer the material to ?Anystoidea *incertae sedis*. Given that *S. bdelloides* cannot be meaningfully placed in a known genus – and raising an extinct genus defined on an incomplete character set would be unhelpful – we consider it best to be to formally treat the species name as a *nomen dubium*. It is not a *nomen nudum* (*sensu* Oudemans 1937) as Koch and Berendt’s name is clearly associated with a (brief) description and a figure.

Discussion

The principal conclusion of our study is that neither Sejida nor Trigynaspida have a demonstrable fossil record. A handful of putative mesostigmatans have been reported from the Cretaceous. Poinar (1998: fig. 1C) figured a specimen from New Jersey amber (90 – 94 Ma), while Peñalver *et al.* (2017) mentioned their presence in the slightly older Burmese (ca. 99 Ma) and Lebanese (ca. 130 Ma) ambers respectively. However none of these Cretaceous records have been formally described, confirmed as Mesostigmata, or assigned to a higher group. Thus only Monogynaspida is unequivocally represented as fossils; whereby nine of the 77 known families (*sensu* Beaulieu *et al.* 2011) have now been recorded (Table 1). Both of the two main monogynaspid clades (*i.e.* Uropodina and Gamasina) can be traced back to the Eocene (44 – 49 Ma), although this rather young age remains a puzzle given that there are mid-Cretaceous records of two of the other three parasitiform clades, namely Opilioacarida (Dunlop and Bernardi 2014) and Ixodida (ticks) (Poinar and Brown 2003; Poinar and Buckley 2008; Chitimia-Dobler *et al.* 2017; Peñalver *et al.* 2017). The final parasitiform group, Holothyrida, lacks a fossil record. By contrast, acariform mites go back over 410 million years to the Early Devonian (Hirst 1923). We hope that Mesozoic ambers will begin to yield further fossil Mesostigmata, and we expect that most of the major parasitiform lineages will prove to be considerably older than their present record indicates. The Late Jurassic origins implied by Peñalver *et al.* (2017: fig 10) are almost certainly an underestimate, given that most orders of arachnids have Palaeozoic representatives.

Acknowledgements

We thank Christian Neumann for access to the Berendt collection in Berlin, two anonymous reviewers for valuable comments on a previous version of the typescript and Ekaterina Sidorchuk for editorial comments and assistance with producing one of the figures during a visit to Berlin.

References

- Aoki J. 1974. [On the fossil mites in Mizunami amber from Gifu Prefecture, Central Japan]. Bulletin of the Mizunami Fossil Museum, 1: 397-399 [in Japanese with English summary].
- Beaulieu F., Dowling A.P.G., Klompen H., Moraes G.J. de, Walter D.E. 2011. Superorder Parasitiformes Reuter, 1909. In: Zhang Z.-Q. (Ed.). Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. Zootaxa, 3148: 123-128.
- Bernardi L.F. de O., Pellegrini T.G., Ferreira R.L. 2012. New species of *Neoteneriffiola* (Acari: Trombidiformes: Teneriffiidae) from Brazilian caves: geographical distribution and ecological traits. International Journal of Acarology, 38: 410-419. doi:10.1080/01647954.2012.662246
- Błaszak J., Cokendolpher J.C., Polyak V.J. 1995. *Paleozercion 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. doi:10.1080/01647959508684068
- Chitimia-Dobler L., De Araujo B.C., Ruthensteiner B., Pfeffer T., Dunlop J.A. 2017. *Amblyomma birmutum* a new species of hard tick in Burmese amber. Parasitology, 144: 1411-1448. doi:10.1017/S0031182017000853
- Dabert M., Witalinski W., Kazmierski A., Olszanowski Z., Dabert J. 2010. Molecular phylogeny of acariform mites (Acari, Arachnida): strong conflict between phylogenetic signal and long-branch attraction artifacts. Molecular Phylogenetics and Evolution, 56: 222-241. doi:10.1016/j.ympev.2009.12.020
- Dunlop J.A., Bernardi L.F. de O. 2014. An opilioacarid mite in Cretaceous Burmese amber. Naturwissenschaften, 101: 759-763. doi:10.1007/s00114-014-1212-0
- Dunlop J.A., Falkenhagen R. 2014. Raubmilbe in Aragonit. Fossilien, 2014(3): 53-55.
- Dunlop J.A., Kotschán J., Zwanzig M. 2013. Fossil mesostigmatid mites (Mesostigmata: Gamasina, Microgyniina, Uropodina), associated with longhorn beetles (Coleoptera: Cerambycidae) in Baltic amber. Naturwissenschaften, 100: 337-334. doi:10.1007/s00114-013-1031-8
- Dunlop J.A., Kotschán J., Walter D.E., Perrichot V. 2014. An ant associated mesostigmatid mite in Baltic amber. Biology Letters, 10(9): 20140531. doi:10.1098/rsbl.2014.0531
- Dunlop J.A., Sempf C., Wunderlich J. 2010. A new opilioacarid mite in Baltic amber. In: Nentwig W., Schmidt-Entling M., Kropf C. (eds). European Arachnology, 2008: 59-70.
- Giebel C.G. 1856. Die Insekten und Spinnen der Vorwelt mit steter Berücksichtigung der lebenden Insekten und Spinnen; monographisch dargestellt. Leipzig, 511 pp
- Giribet G., Vogt L., Pérez González A., Sharma P., Kury A.B. 2009. A multilocus approach to harvestman (Arachnida: Opiliones) phylogeny with emphasis on biogeography and the systematics of Laniatores. Cladistics, 25: 1-30.
- Hedin M., Starrett J., Akhter S., Schönhofer A.L., Shultz J.W. 2012. Phylogenomic resolution of Paleozoic divergences in harvestmen (Arachnida, Opiliones) via analysis of next-generation transcriptome data. PLoS ONE, 7(8): e42888. doi:10.1371/journal.pone.0042888
- 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.
- Hirschmann W., Wisniewski J., Kaczmarek S. 1991. Gangsystematik der Parasitiformes Teil 530. Weltweite Revision der Ganggattung *Sejus* C.L. Koch 1836 (Trichopygidina). Neubeschreibung von 26 *Sejus*-Arten. Wiederbeschreibung der Typenart. Acarologie, 38: 136-214.
- Hirst S. 1923. On some arachnid remains from the Old Red Sandstone (Rhynie Chert bed, Aberdeenshire). Annals and Magazine of Natural History, (9)12: 455-474. doi:10.1080/00222932308632963
- Khanjani M., Hoseini M.A., Asali Fayaz B. 2014. *Austroteneriffia kohrrambadiensis* n. p. (Acari: Teneriffiidae): a new species from southwestern Iran, with a description of the male. Acarologia, 54: 69-79. doi:10.1051/acarologia/20142116
- Koch, C.L. 1836. Deutschlands Crustaceen, Myriapoden und Arachniden, Herausgegeben von Herrich-Schäffer, Regensburg, Fasc. 1.
- Koch C.L., Berendt G.C. 1854. Die im Bernstein befindlichen Myriapoden, Arachniden und Apteren der Vorwelt. In: Berendt G.C. (Ed.) Die in Bernstein befindlichen organischen Reste der Vorwelt gesammelt in Verbindung mit mehreren bearbeitet und herausgegeben 1. Berlin, Nicolai, 124 pp.
- Kramer, P. 1877. Grundzüge zur Systematik der Milben. Archiv für Naturgeschichte, 43: 215-247.
- Lindquist E.E., Krantz G.W., Walter D.E. 2009. Order Mesostigmata. In: Krantz G.W., Walter D.E. (Eds) A Manual of Acarology. Third Edition. Texas Tech University Press, Lubbock, Texas, pp. 124-231.
- Lyubarsky G.Y., Perkovsky E.E. 2012. The first Eocene species of the genus *Cryptophagus* (Coleoptera, Clavicornia, Cryptophagidae). Vestnik zoologii, 46: 36-40.
- Oudemans 1937. Kritisch Historisch Overzicht Der Acarologie, 3de Gedeelte, band C, 1937
- Peñalver E., Arillo A., Delclòs X., Peris D., Grimaldi D.A., Anderson S.R., Nascimbene P.C., Pérez-de la Fuente R. 2017. Ticks parasitized feathered dinosaurs as revealed by Cretaceous amber assemblages. Nature Communications, 8: 1924.

- Perkovsky E.E., Rasnitsyn A.P., Vlaskin A.P., Taraschuk M.V. 2007. A comparative analysis of the Baltic and Rovno amber arthropod faunas: representative samples. *African Invertebrates*, 48: 229-245.
- Petrunkevitch A.I. 1955. Arachnida. 42-162. In: Moore R.C. (Ed.) *Treatise on invertebrate paleontology, Part P, Arthropoda 2*. Geological Society of America, Boulder, and University of Kansas Press, Lawrence, xvii + 181 pp.
- Poinar Jr G.O. 1998. Fossils explained 22: Palaeontology of amber. *Geology Today*, July–August 1998: 154-160. doi:10.1046/j.1365-2451.1998.014004154.x
- Poinar Jr G.O., Brown A.E. 2003. A new genus of hard ticks in Cretaceous Burmese amber (Acari: Ixodida: Ixodidae). *Systematic Parasitology*, 54: 199-205. doi:10.1023/A:1022689325158
- Poinar Jr 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. doi:10.4289/07-014.1
- Ramsay G.W. 1960. Sub-fossil mites from the Hutt Valley. *Transactions of the Royal Society of New Zealand*, 88: 575-576.
- Sayre R.M., Smiley R.L., Walter, D.E. 1992. Report of a teneriffiid mite (Acari) in Baltic amber and notes on recent discoveries. *International Journal of Acarology*, 18: 303-305. doi:10.1080/01647959208683964
- Scudder S.H. 1891. Index to the known fossil insects of the world including myriapods and arachnids. *Bulletin of the United States Geological Survey*, 71: 1-744.
- Selden P.A. 1993. Arthropoda (Aglaspidida, Pycnogonida and Chelicerata). Pp. 297-320. In: Benton M.J. (Ed.) *The Fossil Record 2*. Chapman & Hall, London. xvii + 845 pp.
- Vitzthum H. 1943. Acarina. Bronns Klassen und Ordnung der Tierreichs, Band 5, I Abteilung. Arachnoidea, 1. Lieferung. Akademische Verlagsgesellschaft, Leipzig.
- Walter D.E. 2013. A new genus and family of sejine mites (Acari, Parasitiformes, Mesostigmata, Sejoidea) based on new species from Lord Howe Island and Brazil, and a redescription of *Sejus americanus* (Banks, 1902). *Zootaxa* 3691: 301-323. doi:10.11646/zootaxa.3691.3.1
- Walter D.E., Proctor H. C. 1999. *Mites. Ecology, Evolution and Behaviour*. CABI Publishing, Wallingford.
- Walter D.E., Proctor H.C. 2013. *Mites: Ecology, Evolution and Behaviour*. 2nd Edition – Life at a Microscale. Springer, Amsterdam. 494 pp.
- Walter D.E., Lindquist E.E., Smith I.M., Cook D.R., Krantz G.W. 2009. Order Trombidiformes. In: Krantz G.W., Walter D.E. (Eds) *A Manual of Acarology*. Third Edition. Texas Tech University Press, Lubbock, Texas. Pp. 233-420.
- Weitschat W., Wichard W. 2010. Baltic amber. In: Penney D. (Ed.) *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester, pp. 80-115.
- Witaliński W. 2000. *Aclerogamasus stenocornis* sp. n., a fossil mite from the Baltic amber (Acari: Gamasida: Parasitidae). *Genus*, 11: 619-626.
- Wood H.M., Matzke N.J., Gillespie R.G., Griswold C.E. 2013. Treating fossils as terminal taxa in divergence time estimation reveals ancient vicariance patterns in the palpimanoid spiders. *Systematic Biology*, 62: 264-284. doi:10.1093/sysbio/sys092
- Zacharda M., Krivolutsky D.A. 1985. Prostigmatic mites (Acarina: Prostigmata) from the Upper Cretaceous and Paleogene amber of the USSR. *Věstník Československé společnosti zoologické*, 49: 147-152.