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Adding to the few: a tomocerid collembolan from Baltic amber

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Abstract

We describe a fossil collembolan specimen preserved in Baltic amber. The single specimen is interpreted as a representative of Tomoceridae; more precisely, the specimen is tentatively assigned to *Tomocerus* cf. *taeniatus* (Koch & Berendt, 1854). Although the systematic ascription remains not completely resolved, the description of collembolan specimens from amber is seen as an important task. While there are numerous reports of specimens preserved in amber, only few species have been formally described; for example, only two valid fossil species of Tomoceridae have been erected. Describing fossil collembolans with modern documentation and description tools for providing data for a larger-scale comparative approach is thus necessary.

Keywords: Tomoceridae, Collembola, springtail, fossil resin, descriptive matrix.

1. Introduction

Among entognathan hexapods, Collembola (springtails) is the best known and most diverse group (Grimaldi & Engel 2005). Yet, due to their minute size (they do not exceed 17 mm in total length), they are often simply overlooked. Currently nearly 8000 described species are known in the modern fauna (Christiansen et al. 2009). They are distributed over all zoogeographical regions and can even be found in Antarctica (McGaughran et al. 2011).

This extensive distribution has been interpreted as reflecting an ancient origin (Rapoport 1971). The oldest fossil remains of hexapods are known from the Devonian, ca. 400 million years ago (Mya), especially from the famous Rhynie chert and the nearby Windyfield chert. Besides a putative pterygote, *Rhyniognatha hirsti* Tillyard, 1928 (Engel & Grimaldi 2004) and a possible zygentome or archaeognathan, *Leverhulmia mariae* Anderson & Trewin, 2003, a collembolan, *Rhyniella praecursor* Hirst & Maulik, 1926, has been described from these deposits (though the fossil remains of *Rhyniella praecursor* may in fact belong to different, not even closely related collembolan species; see discussion in D´Haese 2003). Edwards et al. (1995) described possible collembolan fossil faeces (coprolites) in approximately 412 million years old strata, i.e., Silurian. Yet, this ascription needs to be corroborated. Another fossil species was described from South African deposits of upper Permian age (ca. 270 Mya); *Permobrya mirabilis* Riek, 1976 shows more similarities with extant representatives of Collembola than *Rhyniella praecursor* (Riek 1976).

Tab. 1. Fossil collembolan specimens and their occurrence in different amber deposits.

Deposits	Number of specimens	Age	Reference
Alava amber (Spain)	80 specimens	Early Cretaceous	Delclòs et al. (2007)
Baltic amber	1063 specimens	Eocene	Zherikhin et al. (2009)
Bitterfeld amber (Germany)	1213 specimens	Eocene	Zherikhin et al. (2009)
Burmese amber (Myanmar)	122 specimens	Late Cretaceous	Christiansen & Nascimbene (2006)
Buzinie amber (France)	2 specimens	Late Cretaceous	Perrichot et al. (2007)
Cedar Lake amber (Canada)	70 specimens	Late Cretaceous	Christiansen et al. (2009)
Charente-Maritime amber (France)	11 specimens	Early Cretaceous	Perrichot (2004)
Chiapas amber (Mexico)	70 specimens	Miocene	Christiansen (1971)
Dominican amber	408 specimens	Oligocene–Miocene	Zherikhin et al. (2009)
Ethiopian amber	5 specimens	Cretaceous	Schmidt et al. (2010)
Lebanese amber	7 specimens	Early Cretaceous	Azar (2000), cited in Perrichot (2004)
Mizunami amber (Japan)	16 specimens	Pleistocene	Yosii (1974)
Rovno amber (Ukraine)	89 specimens	Eocene	Zherikhin et al. (2009)

While there are only two Palaeozoic collembolan fossils, the majority of collembolan fossils were found in amber ranging from the Cretaceous to the Pliocene (CHRISTIANSEN et al. 2009). Thus, there is a huge gap in the fossil record from the Permian until the Cretaceous. Approximately 3000 specimens are known from different amber deposits (Table 1). Among these specimens, a peculiar feature concerning the fossil record of Collembola becomes obvious. HANDSCHIN (1926) already pointed out: "Die Collembolen des Bernsteins sind den unseren gleichwertig und können keinesfalls als ancestral angesehen werden." ("The collembolans in amber (Baltic) are equivalent to ours and can in no way be classified as being ancestral"; translated by the authors). Indeed, the fossils from the Cretaceous and more recent periods share many morphological features, e.g., ventral tubus, distinct furca shape, with modern representatives of Collembola (e.g., *Protentomobrya walkeri* FOLSOM, 1937; see, e.g., CHRISTIANSEN & PIKE 2002).

At least all Eocene and more recent fossil specimens appear so similar to modern forms that they have been ascribed to extant genera or have even been considered conspecific to modern species (CHRISTIANSEN et al. 2009; for details see CHRISTIANSEN & PIKE 2002).

More differences have been identified in some pre-Eocene collembolans, which led to the recognition of extinct "higher" taxonomic units, some genera and one family (see CHRISTIANSEN & PIKE 2002). But, this seems to be more a phenomenon of taxonomic practice than of true evolutionary relevance.

Precise determination of specimens preserved in amber is often difficult. Only a few species have been described among the few thousand known specimens. This low ratio is based on several reasons:

1) Incomplete preservation.
2) Specimens covered or concealed by secretions and/or excretions.
3) Specimens covered by other inclusions.
4) Distortions of surrounding resin due to movement of the specimen during the embedding process.
5) Layering of amber due to different chemical composition because of gases or fluids originating in the decay process (ZAWISCHA 1993).
6) Whitish clouding caused by fluids or gases (e.g., sea water, see BUCHBERGER et al. 1997; decay fluids, see ZAWISCHA 1993).
7) Cracks caused by inflation of the inclusion during decay or mechanical damage (ZAWISCHA 1993).
8) Deterioration (e.g. crazing, darkening) due to ageing (caused by, e.g., UV light, chemicals, or other disadvantageous storing conditions; for additional details, see WADDINGTON & FENN 1998 and BISULCA et al. 2012).

A group of collembolans rarely found in amber is Tomoceridae. The extant fauna comprises 115 species of Tomoceridae (HOPKIN 1997). Fossil representatives of Tomoceridae are known from the following deposits:

1) Baltic amber (WEITSCHAT & WICHARD 2002), one species.
2) Burmese amber (CHRISTIANSEN & NASCIMBENE 2006); one undet. species.
3) Canadian amber (CHRISTIANSEN & PIKE 2002); one species and one undet. species,
4) Rovno amber (PERKOVSKY et al. 2007); one undetermined species.

Additional specimens of Tomoceridae might be present in other deposits, but were not separately described by previous researchers. Hence, only two fossil species of Tomoceridae are currently known, *Entomocerus mirus* CHRISTIANSEN & PIKE, 2002 from Canadian amber of Cedar Lake and *Tomocerus taeniatus* (KOCH & BERENDT, 1854) from Baltic amber.

We describe here a new tomocerid specimen from Baltic amber considered to be of Eocene origin (34–42 Mya; WEITSCHAT & WICHARD 2010). We discuss possible affinities and stress the necessity to bring more well-documented specimens of fossil collembolans into the scientific public.

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2. Material and methods

We investigated a single specimen preserved in Baltic amber, which is considered to be Eocene in age. Additional information on the specimen is unavailable. The specimen is part of the collection of the Field Museum of Natural History in Chicago (FMNH) and registered under the collection number PE 61069. The specimen was documented on a Leica DM 2500 P geological compound microscope

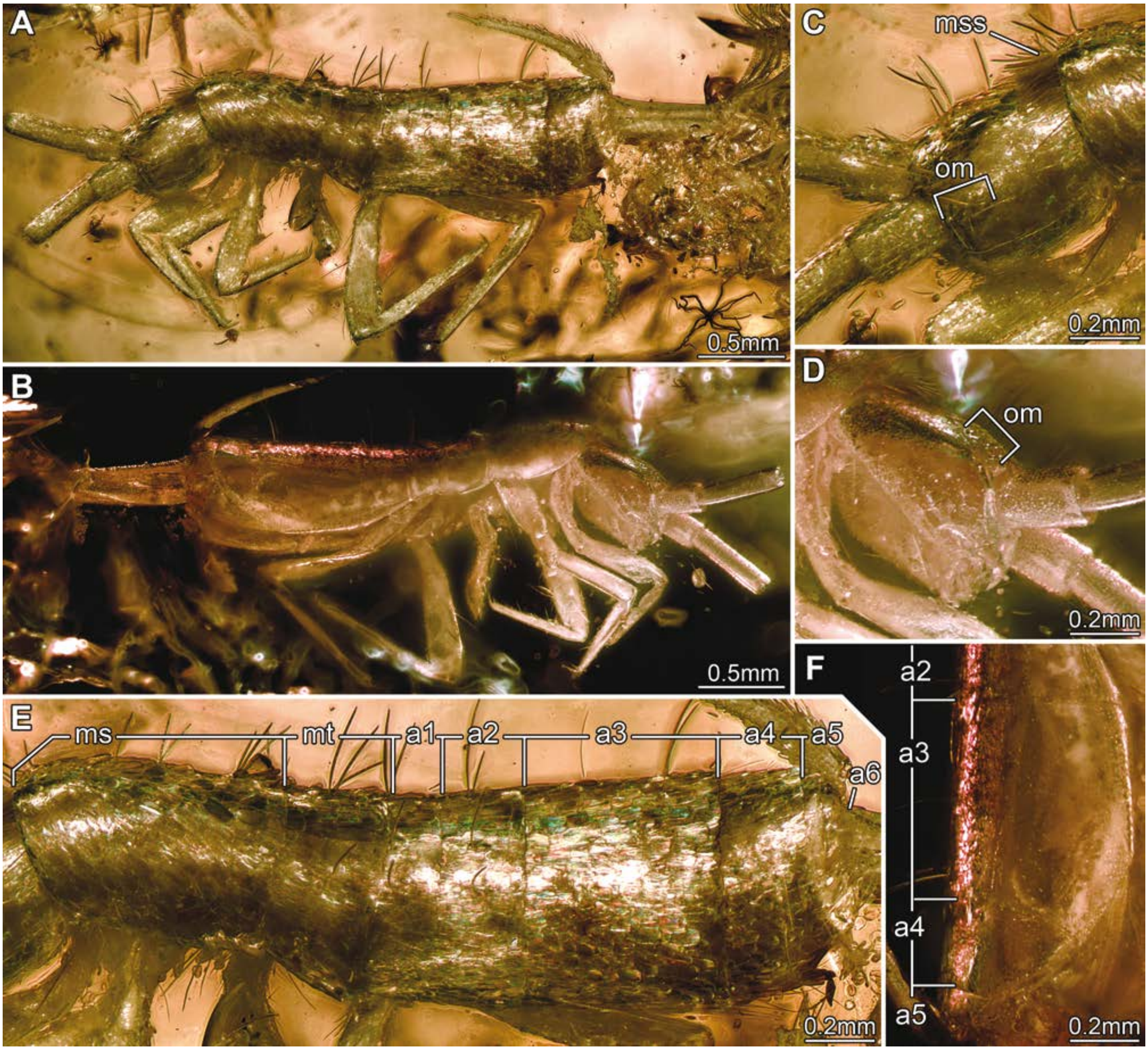

Fig. 1. Overview and tagmatization of PE 61069; **A:** left side; **B:** right side; **C:** close up on head capsule from left side; **D:** close up on head capsule from right side; **E:** entire segmentation of the trunk; note preserved details such as scales and setae of varying sizes and diameters; **F:** segmentation of the posterior trunk; abbreviations: a1–a6: abdomeres 1–6, ms: mesonotum, mss: mesanotal setae, mt: metanotum, om: ommatidia.

with a SkopeTec DCM 510 ocular camera. For reducing optical deformations caused by oblique surfaces of the amber piece, a drop of glycerol was put onto the region of interest and covered with a cover slip, resulting in a flat surface. For illumination we used external fiber light sources. Light was distributed as evenly as possible from a low angle. Fiber lights were equipped with polarization filters that were crossed-polarized to a polarizer in the microscope. In this way, most of the reflections were reduced, yet, some internal reflections within the amber could not be eliminated. A 4 x objective was used, resulting in an approximately 40 x magnification.

To compensate the limited depth of field, stacks were recorded, i.e., several images (frames) of the same image detail were taken in different focal planes. The focus was shifted manually in steps of 20 micrometers. The stacks were fused with the software Image Analyzer. A virtual surface based on the unsharpness of the images was calculated (see Haug et al. 2013). Even though this method may produce certain artifacts due to the transparency of the amber, it provides additional topological information of the specimen, provided as stereo-images.

Measurements were obtained directly from the images. Descriptive terminology is kept general and follows, as far as possible, neutral arthropod terminology to make it also understandable for the non-specialist. As the tagmata in different arthropod groups are not homologous among each other (see, e.g., discussion in Walossek & Müller 1997), terms such as 'thorax' and 'abdomen' are used according to the standard hexapod terminology. The description is given as a descriptive matrix as proposed in Haug et al. (2012, see supplement).

3. Results

Systematic placement:

Collembola
Entomobryomorpha
Tomoceridae
Tomocerus
Tomocerus cf. *taeniatus* (Koch & Berendt, 1854)

Description (extracted from descriptive matrix):

Habitus. – Total length about 3 mm. Body with (presumably) 15 segments, the ocular segment and 14 post-ocular segments. Dorso-lateral regions of ocular segment and post-ocular segments 1–5 form a head-capsule. Post-ocular segments 6–8 with walking appendages; 'thorax'. Post-ocular segments 9-15 without walking appendages; 'abdomen' (Figs. 1A, B, 2A, B).

Head. – Head capsule drop shaped, longer (0.65 mm) than high (0.35 mm). Surface of capsule densely covered with scales and setae of different lengths (Fig. 1C, D). Few prominent setae of up to 0.18 mm length. Dorsally on head capsule at least seven ommatidia are present on each side (Fig. 1C, D; for comparison see Fig. 3B). Diameter of single ommatidium about 0.03 mm. Antenna (deutocerebral appendage, antennula of Arthropoda sensu stricto) arising anteriorly from the head capsule (Fig. 2C). Putatively with four antennomeres. Antennomere 1 about 0.25 mm long (proximo-distal dimension) and about 0.2 mm wide (diameter), densely covered with small scales and hairs. Antennomere 2 about 0.45 mm long (proximo-distal dimension) and about 0.15 mm wide (diameter), densely covered with small scales and hairs. Antennomeres 3 and 4 unknown due to preservation. Other head appendages (mouth parts) small, concealed in cephalic pouch, not accessible.

Thorax. – Pronotum (tergite of thoracomere 1; post-ocular segment 6) presumably small in size, concealed by the mesonotum. Appendage of post-ocular segment 6 (propodium or fore leg) with 5 distinguishable elements, coxa, trochanter, femur, tibiotarsus, and distal claw (Fig. 2D). Coxa about 0.3 mm long (proximo-distal dimension) and about 0.15 mm wide (diameter). Trochanter about 0.18 mm long (proximo-distal dimension) and about 0.12 mm wide (diameter). Femur about 0.54 mm long (proximo-distal dimension) and about 0.14 mm wide (diameter) at the middle, tapering towards both ends. Tibiotarsus about 0.5 mm long (proximo-distal dimension) and about 0.1 mm wide (diameter), tapering towards distal end (Fig. 2D–F). Distal claw small, spine-like, about 0.08 mm long; less than 0.01 mm at the base. Mesonotum (tergite of thoracomere 2; post-ocular segment 7) large, about 0.75 mm long. Anterior rim of mesonotum armed with numerous long setae (estimated two dozens, longest about 0.18 mm long), covering the posterior third of the head capsule (Fig. 2E). Surface of mesonotum densely covered with scales and setae of various lengths. Scales of varying sizes; largest scale about 0.1 mm long, 0.05 mm wide. Few prominent setae arranged in groups of two or three, up to 0.2 mm long. Appendage of post-ocular segment 7 (mesopodium or mid leg) with 5 distinguishable elements, coxa, trochanter, femur, tibiotarsus, and distal claw (Fig 2D, F). Coxa about 0.43 mm long (proximo-distal dimension) and about 0.2 mm wide (diameter). Trochanter about 0.15 mm long (proximo-distal dimension) and about 0.12 mm wide (diameter). Femur about 0.50 mm long (proximo-distal dimension) and about 0.12 mm wide (diameter) at the middle, tapering towards both ends. Tibiotarsus about 0.54 mm long (proximo-distal dimension) and about 0.1 mm wide (diameter), tapering towards distal end. Distal claw small, spine-like, about 0.1 mm long; less than 0.01 mm at the base. Metanotum (tergite of thoracomere 3; post-ocular segment 8) shorter than mesonotum, about half the length; 0.3 mm. Surface of metanotum densely covered with scales and setae of various lengths (Fig. 1E). Scales of varying sizes; smaller than scales on mesonotum. Few prominent setae arranged in groups of two or three, up to 0.25 mm long. Appendage of post-ocular segment 8 (metapodium or hind leg) with 4 distinguishable elements, trochanter, femur, tibiotarsus, and distal claw (Fig. 2F); the coxa is concealed. Trochanter about 0.22 mm long (proximo-distal dimension) and about 0.12 mm wide (diameter). Femur about 0.61 mm long (proximo-distal dimension) and about 0.18 mm wide (diameter) at the middle, tapering towards both ends. Tibiotarsus about 0.92 mm long (proximo-distal dimension) and about 0.1 mm wide (diameter), tapering towards distal end. Distal claw small, spine-like, about 0.1 mm long; less than 0.01 mm at the base.

Abdomen. – Hexapod-type abdomen, not homologous to abdomina of other arthropods. Abdomere 1 (post-ocular segment 9) relatively short, about 0.15 mm

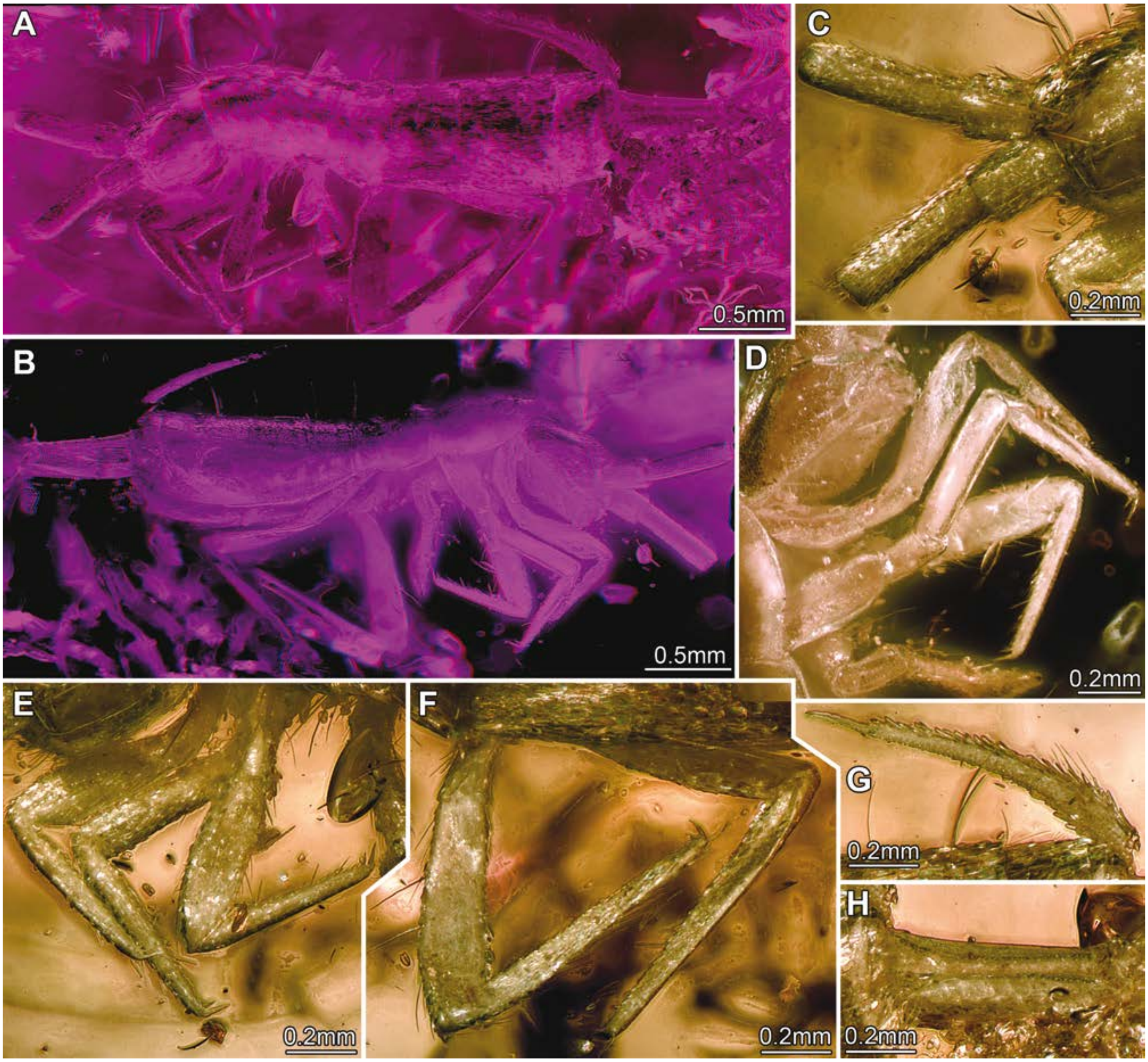

Fig. 2. Stereo images and details of PE 61069; **A:** stereo-anaglyph of left side; **B:** stereo-anaglyph of right side; **C:** details of the antennae; **D:** details of anterior two thoracic appendages, left side; **E:** details of anterior two thoracic appendages, right side; **F:** details of third thoracic appendages; **G:** distal, dislocated part of the furca; **H:** proximal part of the furca.

long. Surface of abdomere 1 densely covered with scales and setae of various lengths. Few prominent setae arranged in groups of two, up to 0.25 mm long. Abdomere 2 (post-ocular segment 10) about twice as long as preceding segment, about 0.25 mm. Surface of abdomere 2 densely covered with scales and setae of various lengths. Few prominent setae arranged in groups of two, up to 0.27 mm long. Abdomere 3 (post-ocular segment 11) slightly less than twice the length of the preceding segment, 0.5 mm. Longest segment of abdominal series. Border to next succeeding segment indistinct. Surface of abdomere 3 densely covered with scales and setae of various lengths. Few prominent setae arranged in groups of two, up to 0.2 mm long. Abdomere 4 (post-ocular segment 12) about one third of the length of the preceding segment, about 0.2 mm. Surface of abdomere 4 densely covered with scales and setae of various lengths. Appendages of post-ocular segment 12, furca, mostly concealed (Fig. 2H). Distal part of furca (dislocated) about 0.95 mm long (Fig. 2G). Maximum diameter (close to the base) about 0.12 mm, tapering towards the end. Sides of furcal branch equipped with about 22 soft bulbous structures extending into setae. Distal part of furcal branch about 0.19 mm long. At the base 0.04 mm wide, tapering towards the distal tip. Possibly with two teeth, one apical, one proximal. Abdomere 5 (post-ocular segment 13) about half of the length of the preceding segment, about 0.1 mm. Abdomere 6 (post-ocular segment 14) about one third of the length of the preceding segment. Small indistinct, about 0.03 mm.

4. Discussion

Preservation. – With some exceptions, most structures are well preserved and the specimen can be examined from different directions. Unfortunately, the distal elements of the antennae are not preserved. Also the furca is not well accessible; it is covered by some gas bubbles and a diffracting film or layer; especially the manubrium was not identifiable. Here it is fortunate that one mucro and dentes of the furca appears to have become dislocated, lying directly adjacent to the abdomen and pointing anteriorly. The preservation of details is relatively good with numerous distinct scales and setae of different sizes on body segments and appendages.

Although all legs are present, not all of them are equally well recognizable. This is particularly the case for the right mesopodium, which is orientated orthogonal to the body axis. Hence, specific features are difficult to examine. Certain restrictions also limit the examination of the other legs, but to a lesser extent. Especially the proximal podomeres are only visible from the right side of the body. Moreover, the limited resolution allows only a vague description of further details. Some features are recognizable (e.g., scales, setae, claws), but mainly their presence can be stated.

The same applies for the abdominal appendages. Here, neither retinaculum (sometimes also termed tenaculum) nor a ventral tubus are visible. Furthermore, most parts of the furca are unrecognisable. Besides the above mentioned dislocated furcal branch of the furca, the posterior portion of the abdomen provides a confusing image. Covered with a semi-translucent film, there seem to be two posterior appendages arising from the end of the abdomen. A distinct dark line appears to separate two different appendages. The lower one tapers towards the abdomen. Furthermore, the upper portion reaches only two thirds the length of the dislocated furcal branch.

Likely, the dentes and mucro of both furcal branches broke off, while the manubrium remains attached to the abdominal tip perpendicularly. One furcal branch lies above the abdomen, while the other one folds toward the abdomen and rests below the manubrium. This view is supported by the minor length of this furcal branch in respect to the dislocated one, and by the tapering of the lower portion.

Systematic placement. – A small pronotum concealed by the mesonotum, as observed in the here described specimen, as well as the presence of pronounced scales suggest an affiliation to Entomobryomorpha (see, e.g., Schaller 1970) (for comparison see Fig. 3A). A more precise ascription of the here described specimen within this monophyletic group is more complicated. Scales are found in Isotomidae, Entomobryidae, Oncopoduridae, Tomoceridae and certain Paronellidae. Among these groups the specimen's habitus is best comparable with Entomobryidae, Paronellidae and Tomoceridae (cf. e.g., Greenslade 1991; Hopkin 1997). The length ratio of the third and fourth abdominal segment can also be observed in Oncopoduridae and Tomoceridae. This feature makes a close affiliation of the specimen to Entomobryidae and Paronellidae highly unlikely, since both monophyletic groups differ in the arrangement of the respective abdominal segments.

At last, the extensive covering with scales makes it most likely that the specimen is a representative of Tomoceridae. Unfortunately, the most significant feature of Tomoceridae, the presence of an annulated and elongate third antennomere (Hopkin 1997), cannot be evaluated in our specimen.

Comparison with described fossil species. – There are only two formally described species of fossil tomocerid collembolans. *Tomocerus taeniatus* was

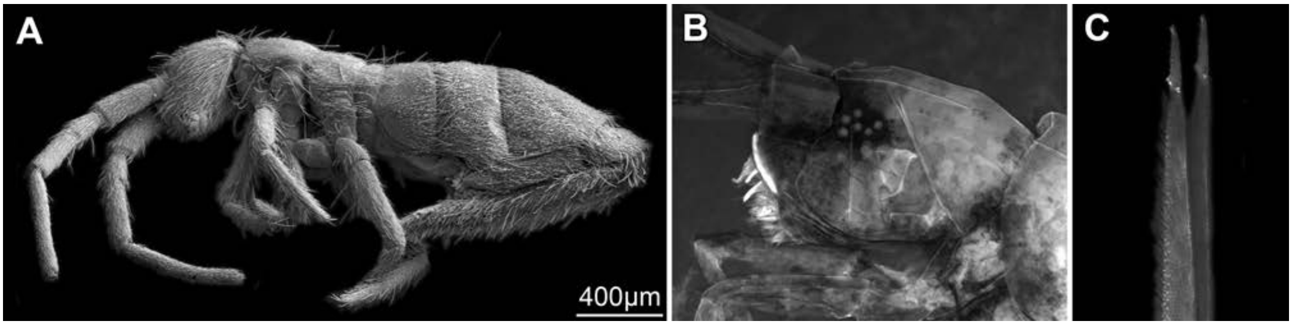

Fig. 3. Examples of extant collembolans for comparison; **A:** overview of an entomobryoid collembolan; **B:** close-up on head; **C:** close-up on mucro and dentes.

originally described by Koch & Berendt (1854) as *Podura taeniata*. This original description remains very vague. The re-examination of Handschin (1926) provides the most suitable basis for a comparison. Furthermore, Handschin (1926) established close affinities to the extant species *Tomocerus vulgaris* (Tullberg, 1871). *Entomocerus mirus* was established by Christiansen & Pike (2002).

Both species share some features with the here described specimen, especially the structure of the scales and the collar consisting of setae arising from the anterior margin of the mesonotum. *E. mirus* differs in some aspects from the specimen described here. Scales are differentiated into two types in *E. mirus*, small striated ones and larger ones with rough ridges. Although it is slightly difficult to evaluate, we could not observe such a differentiation in the specimen described in this paper. The mucro is small in *E. mirus*, but pronounced in our specimen. Also the overall body size differs significantly. *E. mirus* reaches only 1.18 mm and is thus only about one third of the total length of the specimen described in this paper.

These differences do not apply for *T. taeniatus* and our specimen. Scales are not differentiated in this species, the mucro is well developed with an apical tooth and an additional one (possibly three teeth in the specimen described here). Also the body size of about 4 mm is comparable to the 3 mm in the here described specimen. The here presented specimen appears thus very similar in many aspects to *T. taeniatus*. Both are known from Baltic amber. We therefore assign the here described specimen tentatively to *Tomocerus* cf. *taeniatus*.

5. Outlook

We hope that subsequent comparative investigations will allow a more reliable ascription. Although the systematic ascription is not completely resolved in this case, providing a precise documentation and description is seen as important. The large number of available specimens of collembolans in amber and the low number of formally described species demands for a rigorous comparative investigation. Amber fossils have the potential to provide important additional information about the evolutionary history of Collembola, and this potential should be exploited.

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