

New data on fossil Archaeognatha from Baltic amber and the origin of the insect ovipositor

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Abstract

The primary wingless insect group Archaeognatha (=Microcoryphia) is the sister group of dicondylid insects (Zygentoma + Pterygota). Therefore knowledge of character states in Archaeognatha is essential for the discussion of insect evolution as a whole. The incorporation of data from the fossil record is necessary for evolutionary biology as well as systematics, to introduce possible more ancestral character states. In the last years, fossil archaeognathans were described from amber deposits around the world, yet most data from Baltic amber dates more than hundred years back. In this paper we describe two new specimens of fossil Archaeognatha from Baltic amber. The ovipositor of one specimen, hence a female, is well-preserved showing four valves each representing an elongate multi-annulated structure distantly resembling the cerci. In pterygote insects the valves, as the name suggests, are usually solid simple structures. We therefore take the morphology of the aracheognathan ovipositor as a starting point to discuss potential homologies of the insect ovipositor also in comparison to non-insect arthropods.

Key words: Amber, Baltic, *Petrobius*, ovipositor.

1. Introduction

Archaeognathans (=Microcoryphia) are considered to exhibit numerous plesiomorphic characters or characters states. Among Insects, they are the sister group of Dicondylia (Zygentoma + Pterygota) and therefore of major interest for inferring for systematics and reconstructing the evolution of Hexapoda and its ingroups. As such it is an important task to reconstruct the ground pattern of Archaeognatha, i.e. the morphology of the ancestor (stem-species) of archaeognathans. As fossil species can possess plesiomorphic traits no longer found in modern representatives (e.g., DONOGHUE et al. 1989; RUST 2006; EDGECOMBE 2010; HAUG JT et al. 2010) they are especially valuable for such an approach.

STURM & BACH (1993) provided the first attempt to phylogenetic relationships in Archaeognatha using principles of phylogenetic systematics (e.g., SUDHAUS & REHFELD 1993), but this study was exclusively based on extant species. BITSCH & NEL (1999) investigated the relationships among Archaeognatha including fossil representatives. The authors group extant Machilidae together with Meinertellidae as sister group of extinct *Triassomachilis uralensis*. Yet, RASNITSYN (2002) considered *T. uralensis* as mayfly nymph (see also SINITSHENKOVA 2000). STURM & MACHIDA (2001) considering only extant representatives, resolve *Ditrigoniophthalmus* as the sistergroup of Machilidae (restr.) + Meinertellidae. Besides *Ditrigoniophthalmus*, the authors mention additional ‘palaeoforms’ (*Mesomachilis* and *Charimachilis*). The analysis of KOCH (2003) supports *Ditrigoniophthalmus* as sister group of other extant archaeognaths. Furthermore, he proposes the

extinct Dasyleptidae (=Monura sensu SHAROV 1957; Carboniferous to Triassic according to BECHLY & STOCKAR (2011) as sister group of *Ditrigoniophthalmus* + extant Archaeognatha.

Apart from describing archaeognathan ichnofossils GETTY et al. (2013, see also MENDES & WUNDERLICH 2013) gave a detailed summary of fossil Archaeognatha (imprints and amber inclusions). The most diverse fossil archaeognathan fauna (so far) can be found in Baltic amber.

First note on Archaeognatha preserved in Baltic amber was given by KOCH & BERENDT (1854). Some additional inclusions were described by v. OLFERS (1907). Together these authors described 36 fossil species, but SILVESTRI (1912) revised the specimens leaving only 11 species. Recent authors (WEITSCHAT & WICHARD 2002; MENDES & WUNDERLICH 2013) demand a revision of archaeognathan fossils in Baltic amber.

We describe two fossil representatives of Archaeognatha from Baltic amber, deposited at the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We use modern imaging techniques to document all available aspects of morphology and discuss the most important characters in the context of the insects’ ovipositor evolution.

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2. Material and methods

2.1. Material

We examined two inclusions in Baltic amber assigned to the Eocene (40–50 mya). Both specimens are deposited in the Bayerische Staatssammlung für Paläontologie und Geologie, Munich, with the collection number BSPG 1967 XX 4 and BSPG 1995 I 53.

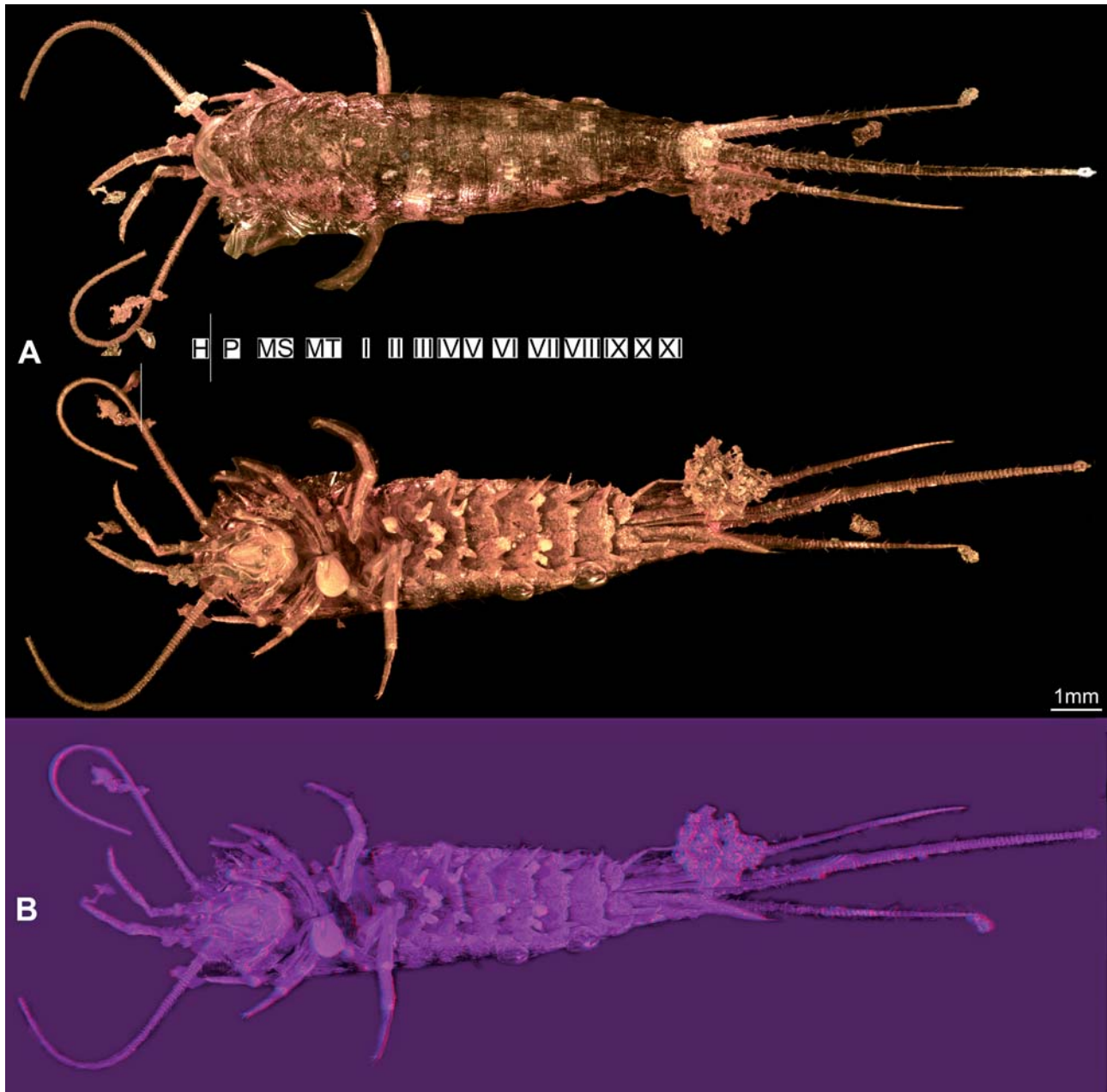


Fig. 1. Habitus of BSPG 1995 I 53 **A:** dorsal and ventral view. Background cleared manually **B:** red-blue stereo anaglyph of a virtual surface reconstruction in ventral view. Please use red-cyan glasses to view. Abbreviations: H: Head, P: prothorax, MS: mesothorax, MT: metathorax, I-XI: abdominal metameres 1-11.

BSPG 1967 XX 4 was part of the collection “SCHEELE”, with the origin given as “Samland”. BSPG 1995 I 53 was donated in 1995 by MIKE BÄÄTJER (Hamburg) and originated from the Tertiary of Poland. Further aspects remain unknown.

2.2. Documentation methods

Overview and close-up images were taken with a Zeiss Axiophot compound microscope equipped with a Scopetek DCM 510 ocular camera. 2.5x and 4x objectives were used, which equals a magnification of 25 respectively 40 times. Light was cross-polarised to reduce reflexions (e.g., HAUG C et al. 2011, 2012; HAUG JT et al. 2012, 2013a; HÖRNIG et al. 2013). To compensate surface irregularities of the amber, glycerine was applied and covered by a cover slip (e.g., HAUG JT et al. 2013b; HÄDICKE et al. 2013). To generate consistently sharp images in all arrays, stacks up to 60 images along the z-axis were taken and fused with Image Analyzer (<http://loginet.dk/Analyzer/>). Fused single images were stitched with the Photomerge function of Adobe Photoshop CS3.

Stereo images (red/blue) of specimen BSPG 1967 XX 4 were processed with ImageAnalyzer (<http://loginet.dk/Analyzer/>), based on the image stacks (HAUG JT et al. 2012, 2013b; HAUG C et al. 2013).

For stereo images of specimen BSPG 1995 I 53, we used a Canon Eos Rebel T3i camera equipped with a Canon MP-E 65 mm macro objective and a Canon Macro Twin Lite MT-24 EX flashlight with polarisation filters. Two images from different angles were taken and arranged and edited with Adobe Photoshop CS3.

2.3. Method of descriptions

Morphological descriptions follow the concepts presented by HAUG JT et al. (2012). Hence first the general

body organisation is mentioned, then each body segment is described strictly from anterior to posterior. Each appendage is described from proximal to distal, element for element. Terminology is kept in a neutral way, to allow also non-specialists to understand it, but specialist terms are additionally given. This is thought to enhance communication also beyond the archaeognath community. Additionally for this case measurements are given also for “non-standard” structures as these might be relevant in a broader comparisons. Measurements were taken on the images. As a remark this also applies to names of larger monophyletic groups. While *Microcoryphia* VERHOEFF, 1904 seems now to be used within the specialists’ community, we use here *Archaeognatha* BÖRNER, 1904 as it seems to be the more generally known term.

3. Results

3.1. Description of BSPG 1995 I 53

Habitus: Total length approximately 17 mm (body with terminal filament), female. Body with (presumably) 20 segments (or metameres), the ocular segment and 19 post-ocular segments (Fig. 1). Ocular segment and post-ocular segments 1–5 form the head capsule. Post-ocular segments 6–8 with walking legs; ‘thorax’. Post-ocular segments 9–16 with a pair of lateral styli and median eversible vesicles. Post-ocular segments 17 and 18 with a pair of valves. Post-ocular segment 19 with paired lateral cerci (approx. 5 mm long) and median terminal filament (approx. 7.6 mm long) (Fig. 1).

Head (ocular segment + post-ocular segment 1–5): Head capsule ellipsoid, broader

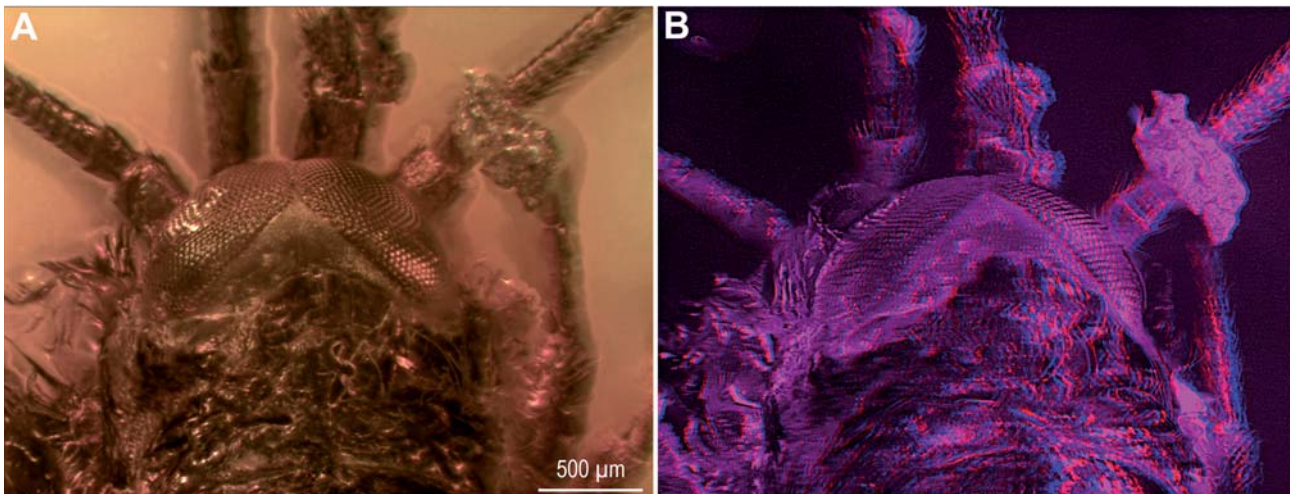


Fig. 2. Dorsal view of the head of BSPG 1995 I 53. **A:** Colour image, **B:** stereo anaglyph of the same region. Please use red-cyan glasses to view.

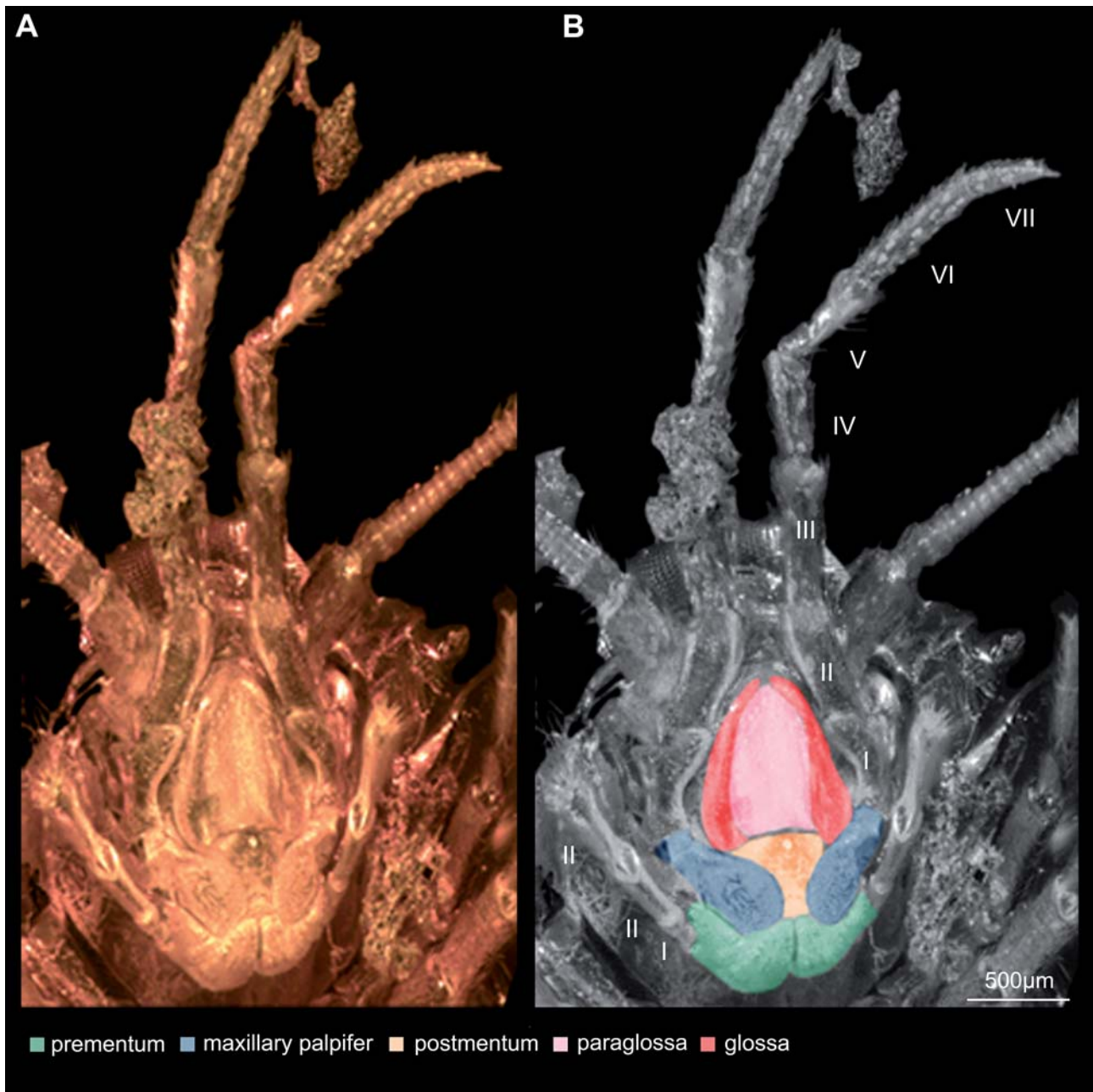


Fig. 3. Ventral site of the head of BSPG 1995 I 53. **A:** colour image. **B:** Topological mapping of identified structures. Italic numbers refer to elements of labial and maxillary palp.

(1.4 mm) than long (0.5 mm) (Fig. 2). Dorsal site occupied by large compound eyes, which meet medially. Ocelli not visible. Antennae and maxillary palps visible. Antennae (deutocerebral appendage, antennula of Arthropoda sensu stricto) consist of two proximal elements (scapus, pedicellus) and a distal flagellum. Scapus longer (0.5 mm) than broad (0.4 mm) (Fig. 2). Covered with setae. Pedicellus broader (210 µm) than long (170 µm). With a tuft of distal

setae. Flagellum consists of numerous small ringlets (flagellomeres, all together approx. 4.6 mm long), partly covered with debris, distal most flagellomeres are most likely lost. Setae are evident on both antennae, in dorsal view scapus and proximal flagellomeres of the left antenna appear to lack bristles. Mouthparts (appendages of postocular segment 3–5) partly known (Fig. 3). Mandibles concealed, maxillae partly and labium completely visible.

Maxilla only known by the maxillary palp. Maxillary palp consists of seven elements (palpomeres). All but the first maxillary palpomere with setae and scales. Maxillary palpomere 1, proximally articulated to stipes, club-shaped, 0.4 mm long, proximally 0.2 mm and distally 0.4 mm broad. Maxillary palpomere 2 tube-shaped, 0.5 mm long and 0.2 mm broad. Maxillary palpomere 3 tube-shaped, 0.7 mm long and 0.2 mm broad. Maxillary palpomere 4 tube-shaped, 0.5 mm long and 0.2 mm broad. Maxillary palpomere 5 tube-shaped, 0.5 mm long and 0.2 mm broad. Maxillary palpomere 6 tube-shaped, 0.7 mm long and 0.2 mm broad. Maxillary palpomere 7 peg-like, 0.4 mm long and 0.2 mm broad. Labium (medially conjoined appendages of post-ocular segment 5) known with, distal central part (prementum), bearing three antero-median, shovel-like enditic protrusions (unpaired glossa and paired paraglossae) and distally with two labial palps. Labial palp consists of three elements (palpomeres), setae are evident on the 3. palpomere labial palpomere 1, proximally articulated to prementum tube-shaped, 150 μ m long and 125 μ m broad. Labial palpomere 2 tube-shaped, 0.3 mm long and 0.1 mm broad. Labial palpomere 3 tube-shaped, 0.5 mm long and 0.2 mm broad.

Thorax (post-ocular segments 6–8): Dorsally each of the three segments with a sclerotised tergite (pronotum, mesonotum, metanotum). Pronotum broader (1.6 mm) than long (0.6 mm), except for a lateral patch of scales no details are visible due to distortion of the amber. Appendages of post-ocular segment 6 (propodia) consist of six elements (coxa, trochanter, femur, tibia, tarsus, pretarsus) (Fig. 4). All covered with setae, scales are not visible. Procoxa tube-shaped, 0.8 mm long and 0.2 mm broad. Protrochanter covered by debris (left one)

or concealed due to orientation. Profemur tube-shaped, 0.7 mm long and 0.2 mm broad. Left one partly covered with debris. Protibia tube-shaped, 0.5 mm long and 0.1 mm broad. Left one partly covered with debris. Protarsus consists of three elements (tarsomeres): 1st tarsomere: 0.3 mm long and 0.1 mm broad, 2nd tarsomere: 0.4 mm long and 0.1 mm broad, 3rd tarsomere: 0.2 mm long and 0.1 mm broad. The propretarsus bears paired claws, together they are 0.1 mm long. Mesonotum broader (2 mm) than long (0.6 mm) dorsally. No details but laterally located scales are visible. Appendages of post-ocular segment 7 (mesopodia) consist of six elements (coxa, trochanter, femur, tibia, tarsus, pretarsus). All covered with setae, scales are not visible. Mesocoxa tube-shaped, 0.6 mm long and 0.2 mm broad. Mesotrochanter: right one covered with secretion (Verlumung) and left one only partly visible due to orientation. Mesofemur tube-shaped, 0.6 mm long and 0.2 mm broad. Mesotibia tube-shaped, 0.6 mm long and 0.2 mm broad. Mesotarsus with three elements (tarsomeres), 1st tarsomere: 0.3 mm long and 0.1 mm broad, 2nd tarsomere: 0.2 mm long and 0.1 mm broad, 3rd tarsomere: 0.3 mm long and 0.1 mm broad. The mesopretarsus bears paired claws, together about 0.1 μ m long. Metanotum broader (2.4 mm) than long (1.2 mm), except for a lateral patch of scales no surface features are visible. Metapodia consist of coxa, trochanter, femur, tibia, tarsus, pretarsus. Occupied by setae, scales are not visible. Metacoxa tube-shaped, 0.8 mm long and 0.4 mm broad and bearing a coxal stylet. Metatrochanter tube-shaped, 0.7 mm long and 0.2 mm broad. Metafemur tube-shaped, 0.8 mm long and 0.3 mm broad. Metatibia tube-shaped, 0.8 mm long and 0.3 mm broad. Metatarsus consists of three elements (tarsomeres), 1st tarsomere: 0.3 mm long and 0.1 mm broad, 2nd tarsomere: 0.3 mm long and

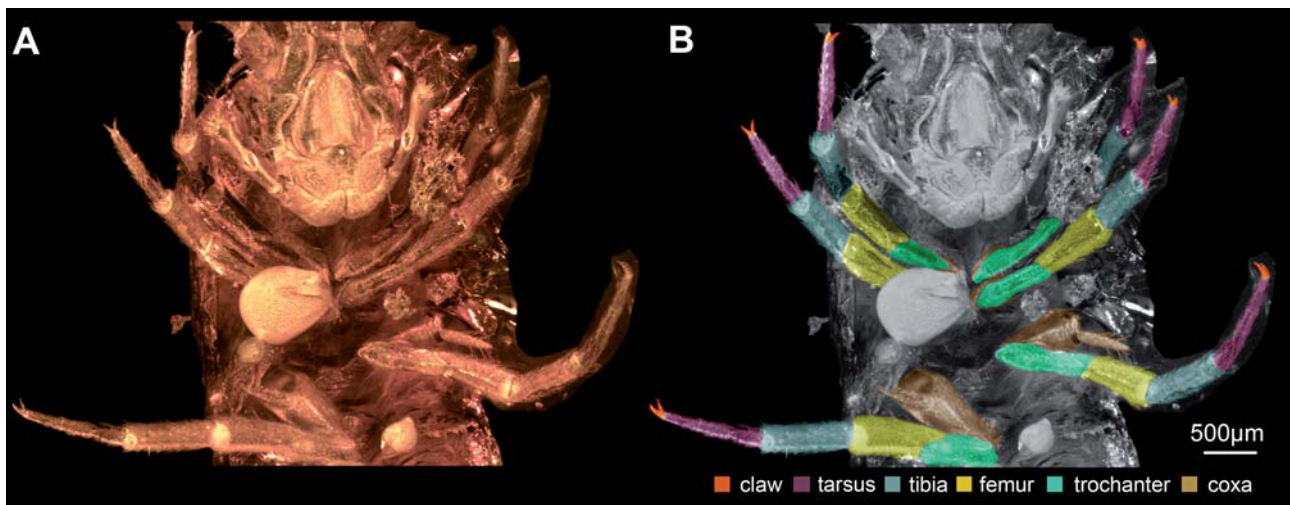


Fig. 4. Ventral view of the thorax of BSPG 1995 I 53 **A:** colour image. **B:** Topological mapping of identified structures. Proximal elements of right pro- and mesopodia are covered by escaped body fluid.

0.1 mm broad, 3rd tarsomere: 0.3 mm long and 0.1 mm broad. Metapretarsus equipped with paired claws, together 0.2 mm long.

Abdomen (post-ocular segments 9–19): Abdomen consists of eleven metameres (Figs. 5, 6). Abdominal metamere 1, dorsally with a well-sclerotised tergite (notum). Notum broader (2.4 mm) than long (0.7 mm), covered with scales (visible laterally) and setae.

Abdominal metamere 1 ventrally partly concealed by metapodia, with a median pair of coxopodal vesicle, stylus visible on the right margin. Abdominal metamere 2 dorsally with a well sclerotised tergite (notum). Notum broader (2.4 mm) than long (0.4 mm), covered with scales and setae. Abdominal metamere 2 ventrally with median and lateral pair of coxopodal vesicles as well as left stylus are evident. Coxopodites not visible. Abdominal metamere 3, dorsally with a well sclerotised tergite (notum). Notum broader

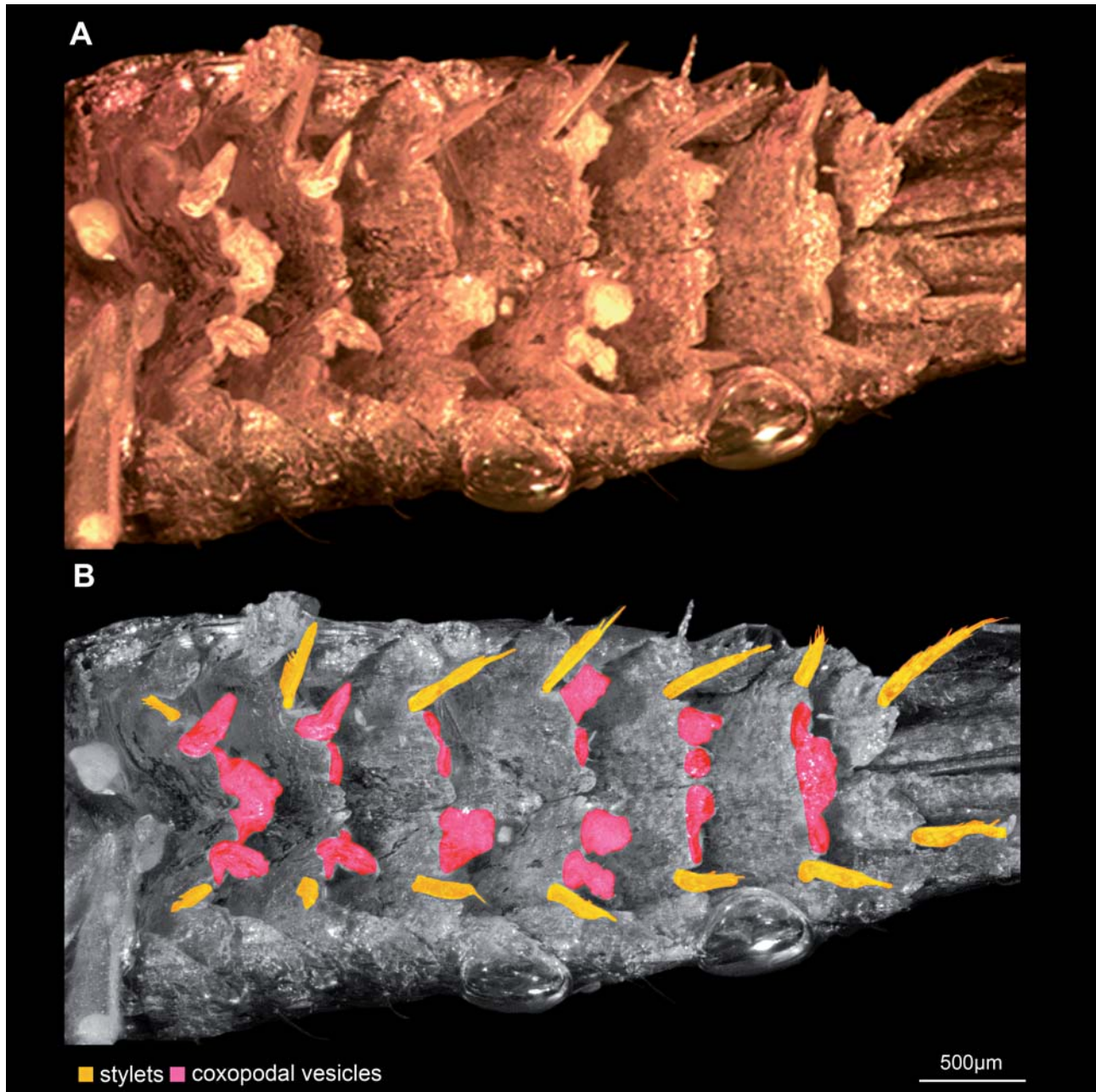


Fig. 5. Ventral view of the abdomen of BSPG 1995 I 53 **A:** colour image. **B:** Topological mapping of identified structures. Retracted coxopodal vesicles are difficult to ascertain, so maybe not all are marked.

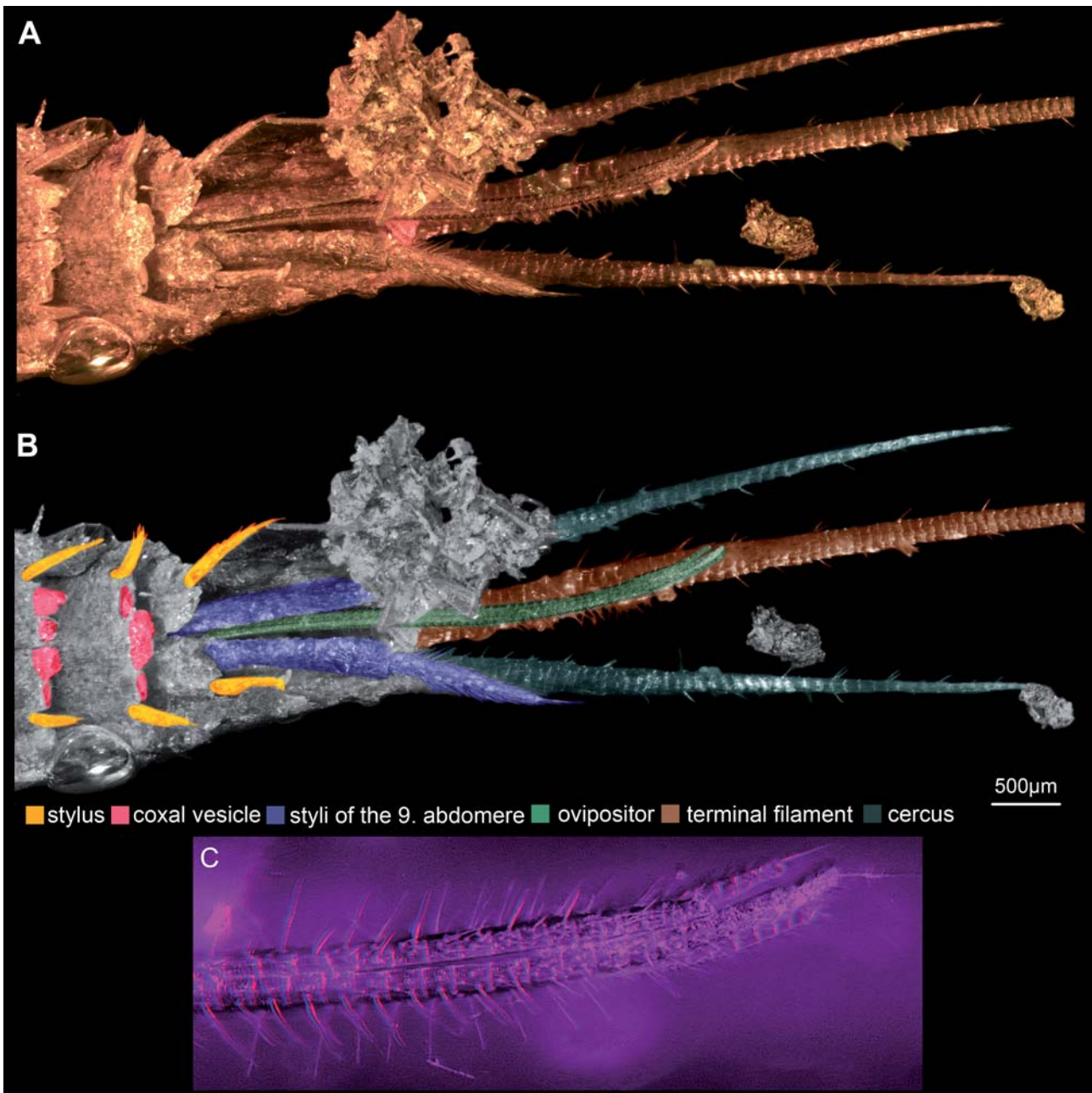


Fig. 6. Ventral view of the terminal portion of the abdomen in BSPG 1995 I 53 **A:** colour image. **B:** Topological mapping of identified structures. **C:** Stereo image of the distal portion of the ovipositor.

(2.3 mm) than long (0.5 mm), covered with scales and setae. Abdominal metamere 3, ventrally with median coxopodal vesicles perhaps collapsed, lateral pair of coxopodal vesicles and right stylus visible. Distal portion of coxopodites recognizable. Abdominal metamere 4, dorsally with a well sclerotised tergite (notum). Notum broader (2.4 mm) than long (0.4 mm), covered with scales and setae. Abdominal metamere 4, ventrally with one median coxopodal vesicle evaginated, two visible styli, coxopodites distinctly

separated. Abdominal metamere 5, dorsally with a well-sclerotised tergite (notum). Notum broader (2.3 mm) than long (0.5 mm), covered with scales and setae. Abdominal metamere 5 ventrally with one median coxopodal vesicle evaginated, lateral coxopodal vesicle and both styli visible. Abdominal metamere 6 dorsally with a well-sclerotised tergite (notum). Notum broader (2.2 mm) than long (0.6 mm), covered with scales and setae. Abdominal metamere 6 ventrally with only median coxopodal vesicles

are evident, both styli are recognizable, coxopodites distinct distally. Abdominal metamere 7 dorsally with a well-sclerotised tergite (notum). Notum broader (2 mm) than long (0.7 mm), covered with scales and setae. Abdominal metamere 7 ventrally with only median coxopodal vesicles, both styli are recognizable, coxopodites indistinct. Abdominal metamere 8, dorsally with a well-sclerotised tergite (notum). Notum broader (1.9 mm) than long (0.7 mm), covered with scales and setae. Abdominal metamere 8 ventrally with styli inserted on the distal tip of then coxopodites, both coxopodites separated from base to tip. Abdominal metamere 9 dorsally with a well sclerotised tergite (notum) notum broader (1.7 mm) than long (0.6 mm), covered with scales and setae. Abdominal metamere 9 ventrally with styli are evident, coxopodites not visible. Abdominal metamere 10 dorsally with a well sclerotised tergite (notum). Notum broader (1.3 mm) than long (0.5 mm), covered with scales and setae. Abdominal metamere 11 dorsally with a well-sclerotised tergite (notum). Notum broader (1.1 mm) than long (0.4 mm), bears terminal filament (7.5 long, 78 presumably elements) and cerci (5 mm long, presumably 45 elements), covered with scales and setae.

Genitalia: Ovipositor consists of four valves; valves 1 3.5 mm long; valves 2 3.7 mm; annulated bearing several setae; number of annuli not detectable due to resolution (Fig. 6).

3.2. Description of BSPG 1967 XX 4

Habitus: Total length approximately 12.8 mm (body with broken terminal filament), perhaps male (no ovipositor visible) (Fig. 7). Ventral side of the abdomen largely covered by secretion (Fig. 7 B). Body with (presumably) 20 segments, the ocular segment and 19 post-ocular segments. Numerous scales are located around the specimen. Ocular segment and post-ocular segments 1–5 form the head capsule. Post-ocular segments 6–8 with walking legs; ‘thorax’ Post-ocular segments 9–16 with a pair of lateral styli and median eversible vesicles. Post-ocular segment 19 with paired lateral cerci (approx. 4.1 mm; likely broken) and median terminal filament (approx. 3.2 mm long; broken).

Head (ocular segment + post-ocular segment 1–5): Head capsule ellipsoid, broader (1.7 mm) than long (0.6 mm). Dorsal site occupied by large compound eyes, which meet medially (Fig. 7 C). Left compound eye collapsed. Both eyes partly covered distortions of the amber. Ocelli not visible. Antennae and maxillary palps visible. Antennae (deutocerebral appendage, antenna of Arthropoda sensu stricto) consists of scapus, pedi-

cellus and flagellum. Scapus longer (1.9 mm) than broad (1 mm). Scales visible but no setae (Fig. 7 C). Pedicellus broader (0.8 mm) than long (0.6 mm). Neither setae nor scales visible. Flagellum right one lost. Left one consist of numerous elements (flagellomeres). Setae are evident on the flagellum, scales are visible. Mouthparts concealed by whitish clouding (Fig. 7 D). Mandibles not visible. Maxilla represented by the maxillary palp, ventrally. Maxillary palp consists of seven elements (palpomeres). At least the distal palpomeres equipped with setae. Scales are not visible. Maxillary palpomere 1: left one concealed by right one visible, club-shaped. Approx. 400 µm long and 216 µm broad, distally. Maxillary palpomere 2 tube-shaped, 0.8 mm long and 0.2 mm broad. Maxillary palpomere 3 tube-shaped, 0.6 mm long and 0.2 mm broad. Maxillary palpomere 4 tube-shaped, 1.4 mm long and 0.3 mm broad. Maxillary palpomere 5 tube-shaped, 0.6 mm long and 0.3 mm broad. Maxillary palpomere 6 tube-shaped, 0.9 mm long and 0.2 mm broad. Maxillary palpomere 7 peg-like, 0.4 mm long and 0.1 mm broad. Labium represented by labial palps only. Left one covered by whitish clouding. Labial palp consists of three elements (palpomeres), setae are evident on the palpomere 2 and 3. Labial palpomere 1 both not visible. Labial palpomere 2 tube-shaped, 0.5 mm long and 0.2 mm broad. Labial palpomere 3 poorly clavate, 0.2 mm broad length not measurable due to orientation.

Thorax (post-ocular segments 6–8): Pronotum broader (1.7) than long (1 mm), likely covered with scales (conceal by distortions of the amber). Dark coloured with a pair of pale bands (Fig. 7 A). Propodia with femur, tibia, tarsus and pretarsus visible. Covered with setae and scales. Left propodium completely and the proximal podomeres of the right propodium covered by white clouding and dislocated. Profemur tube-shaped, 0.8 mm long and 0.3 mm broad. Protibia tube-shaped, 0.7 mm long and 0.2 mm broad. Protarsus no segmentation visible, is tube-shaped, approx. 0.8 mm long and 0.1 mm broad. The propretarsus bears paired claws, together they are 0.1 mm long. Mesonotum broader (1.9 mm) than long (0.5 mm) dorsally. Covered with scales, Dark coloured with four pale bands. Mesopodia consists of femur, tibia, tarsus and pretarsus. Covered with setae and scales. Left propodium completely and the proximal podomeres of the right propodium covered by white clouding. Mesotrochanter tube-shaped, 1 mm long and 0.4 mm broad. Mesofemur tube-shaped, 0.3 mm broad and length not measurable due to orientation. Mesotibia tube-shaped, 0.2 mm broad and length not measurable due to orientation. Mesotarsus no segmentation visible, tube-shaped, approx. 0.7 mm long and 0.2 mm broad. Mesopretarsus bears paired claws, together about 0.2 mm long. Metanotum broader (3 mm) than long (1.1 mm), Covered with scales. Six longitudinal

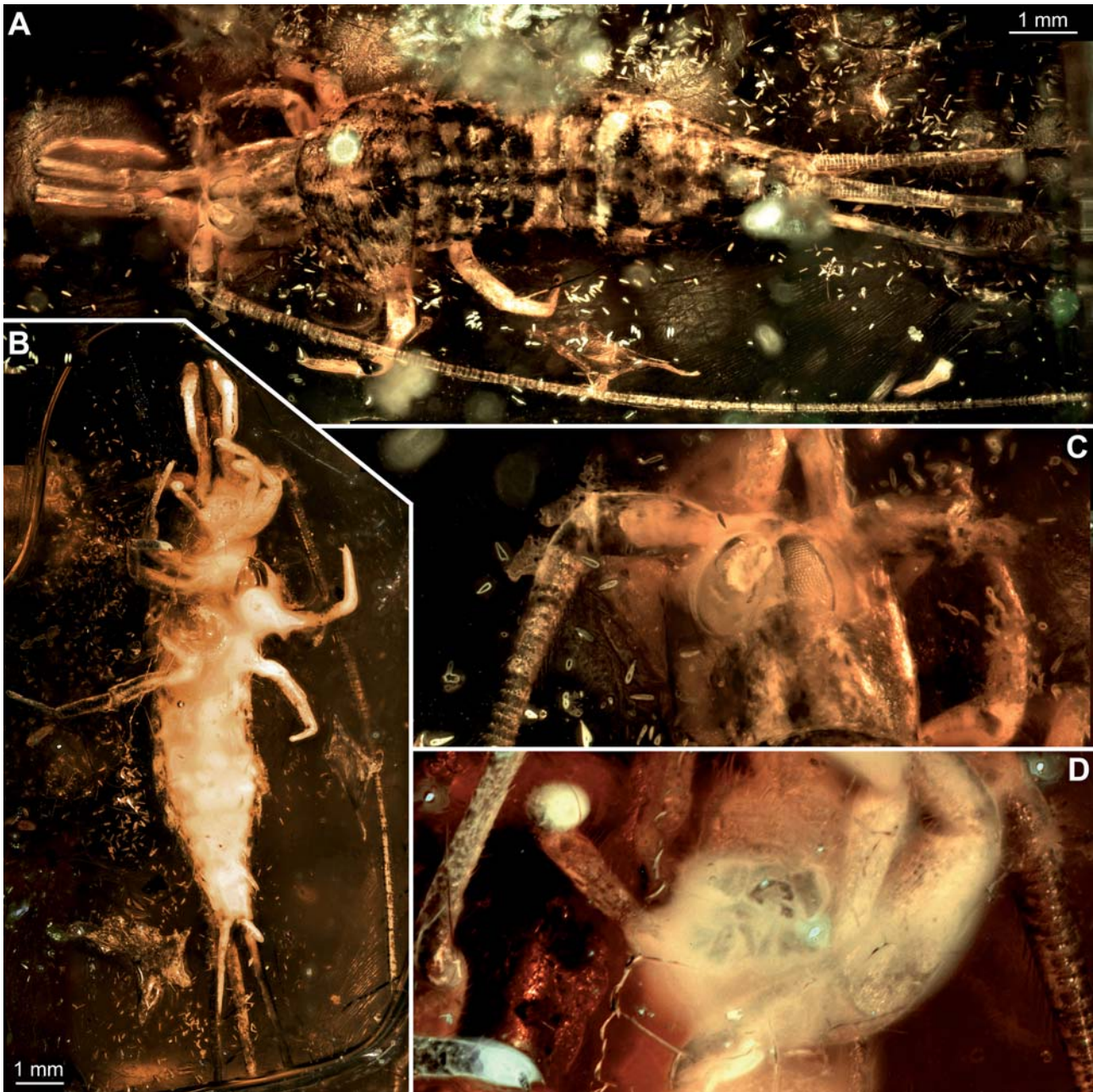


Fig. 7. Habitus and details of BSPG 1967 XX 4. **A:** Dorsal view, note the detached scales. The anterior portion is blurry due to distortions of surrounding resin and the thorax is partly covered by other inclusions. **B:** Ventral view, note the massive *Verlumung* (whitish clouding) of the ventral portion and appendages. **C:** Dorsal portion of head. Note left antenna equipped with scales. **D:** Ventral side of the head.

pale bands are evident on a dark background. Metapodia consist of coxa, trochanter, femur, tibia, tarsus, pretarsus. Pretarsus not visible. Left podomere and proximal right podomeres largely covered by white clouding. Metacoxa tube-shaped, 0.3 mm broad and bearing a stylus. Length

not measurable due to orientation. Metatrochanter tube-shaped, 1.1 mm long and 0.4 mm broad. Metafemur tube-shaped, 1.1 mm long and 0.3 mm broad. Metatarsus and metatibia are not separable. Tube-shaped and together 1 mm long and 0.1 mm broad.

Abdomen (post-ocular segments 9–19): Abdomen consists of eleven metameres. Clouding covers the right margins of abdominal nota 3–5 and the left margin of abdominal nota 10 and 11 (Fig. 7A). Abdominal metamere 1 notum broader (2.4 mm) than long (0.6 mm), covered with scales. The notum exhibits alternating dark and pale longitudinal bands. Abdominal metamere 2 notum broader (2.2 mm) than long (0.4 mm), covered with scales. The notum exhibits alternating dark and pale longitudinal bands. Abdominal metamere 3 notum broader (2 mm) than long (0.4 mm), covered with scales. The notum exhibits alternating dark and pale longitudinal bands. Abdominal metamere 4 notum broader (2 mm) than long (0.4 mm), covered with scales. The notum exhibits alternating dark and pale longitudinal bands. Abdominal metamere 5 notum broader (1.9 mm) than long (0.4 mm), covered with scales. The notum exhibits alternating dark and pale longitudinal bands. Abdominal metamere 6 notum broader (2.1 mm) than long (0.5 mm), covered with scales. The notum exhibits alternating dark and pale longitudinal bands. Abdominal metamere 7 notum broader (2.3 mm) than long (0.5 mm), covered with scales. The notum exhibits alternating dark and pale longitudinal bands. Setae are evident on the right margin. Abdominal metamere 8 notum broader (2.3 mm) than long (0.6 mm), covered with scales. The notum exhibits alternating dark and pale longitudinal bands. Abdominal metamere 9 notum broader (1.8 mm) than long (0.5 mm), covered with scales. The notum exhibits alternating dark and pale longitudinal bands. Abdominal metamere 10 notum broader (1.5 mm) than long (0.5 mm), covered with scales. The notum exhibits alternating dark and pale longitudinal bands. Setae are evident on the right margin. Abdominal metamere 11 notum broader (1.1 mm) than long (0.7 mm), covered with scales. The notum exhibits alternating dark and pale longitudinal bands. Setae are evident on the right margin. Bearing an unpaired terminal filament (3.2 mm long; broken) and lateral cerci (approx. 3.9–4.2 mm, distally broken).

4. Discussion

Knowledge of fossil Archaeognatha preserved in Baltic amber stagnated for more than hundred years. With the present study we provide detailed descriptions of hitherto undescribed specimens assigned to Archaeognatha.

4.1. Phylogenetic interpretation of BSPG 1995 I 53

The long maxillary palps, consisting of seven palpomeres, places this fossil within Archaeognatha. Large eyes, touching each other at the median axis of the head is a synapomorphy with the sister group *Ditrigoniophthalmus*

+ (“Machilidae” + Meinertellidae). Other apomorphies quoted by KOCH (2003) are not visible. Meso- and metacoxae with styli, head and appendages covered with scales etc. suggest affinities with Machilidae. Scales on the flagellum are absent, suggesting a placement in Petrobiinae (STURM & MACHIDA 2001).

The doubled pair of coxal vesicles, occurring also on the abdominal coxopodites 2 to 5, as observed in this specimen is in favour of a close affinity to *Machilis macrura*, *M. corusca* or *M. diastatica* of SILVESTRI (1912).

Although the terminal filament is damaged, the cerci are likely more than half of the length of the terminal filament. Therefore, the specimen is perhaps a representative of *M. corusca* or *M. diastatica*. Yet, as outlined above this specimen most likely belongs to Petrobiinae. Descriptions for the last two species are given by v. OLFERS (1907, *M. diastatica* as *Machilodes diastatica*), KOCH & BERENDT (1854, *M. corusca* as *Petrobius coruscus*) and SILVESTRI (1912, both species). Both species are smaller than this specimen (but it is not clear, whether the measurements of other studies also include the terminal filament). They share the presence of two pairs of coxopodal vesicles on the abdominal coxopodites 2–5 with our specimen. There are some more similarities between the larger (9–10 mm long) *M. diastatica* and the present specimen, ovipositor longer than gonostyli of the ninth abdominal coxopodites and meso- and metacoxae with styli. In the smaller (7.5 mm) *M. corusca*, the ovipositor is as long as the gonostyli. However, according to previous description scales are present on the antennae, thus both species do not belong to Petrobiinae. STURM & MACHIDA (2001) distinguish four genera groups in Petrobiinae, among these only representatives of *Petrobius* occur in Europe, thus a comparison with this group is obvious. The present specimen shares the following characters with *Petrobius*: flagellum without scales, two pairs of coxal vesicles on abdominal coxopodites 2–5, styli on meso- and metacoxae (?). But these features are also shared by other representatives of Petrobiinae (MENDES 1990). The primary ovipositor observed in these specimens, however, suggests close affinities to the *Petrobius* group of STURM & MACHIDA (2001). This group comprises *Petrobius* and *Parapetrobius azoricus*, the later exhibits only one pair of coxopodal vesicles on the abdominal coxopodites. Therefore, the present specimen likely belongs to *Petrobius*. In particular two extant species are known from Northern Europe: *P. brevistylis* and *P. maritimus*. The ovipositor of *P. brevistylis* is quoted to be as long as the styli of the ninth abdominal coxites (CARPENTER 1913).

Hence the specimen exhibits a mosaic of characters. It quite likely represents a new species, based on the distinctly longer ovipositor which distinguishes it from other known representatives of *Petrobius*. Yet, a clear differential diagnosis would demand a revision of all known archaeognathan species known from Baltic amber. As

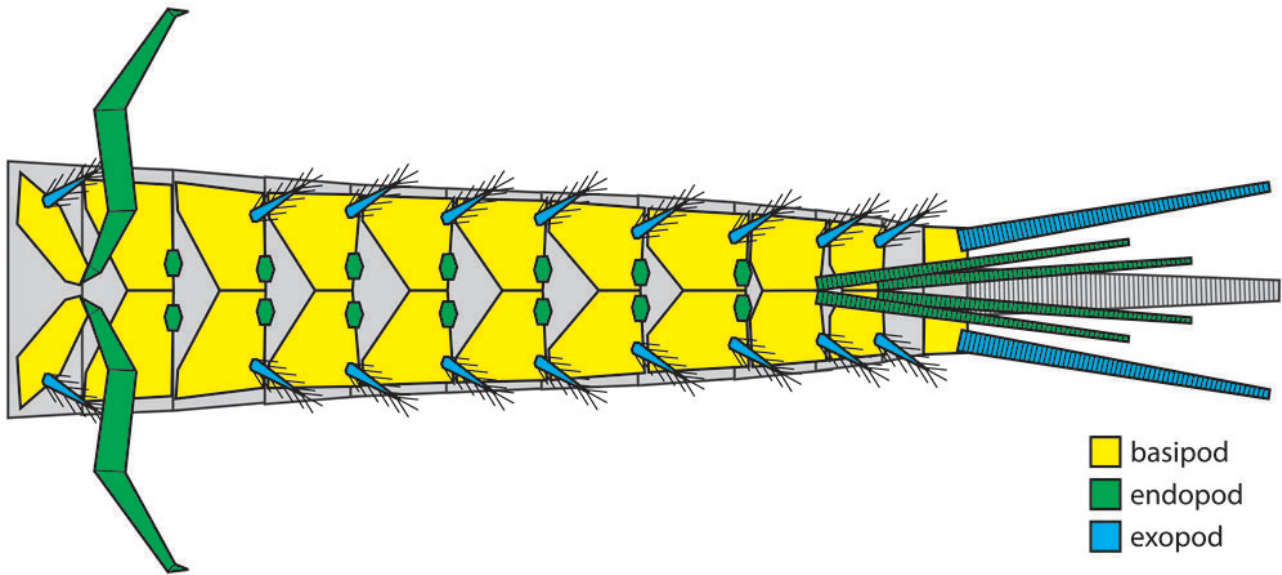


Fig. 8. Schematic drawing of an archaeognathan abdomen, showing possible homologies of insect appendages to those of other crustaceans as proposed in this paper. Colour scheme following WALOSSEK (1993).

such an approach is clearly beyond this study, we can currently not erect a new species.

4.2. Phylogenetic interpretation of BSPG 1967 XX 4

In this specimen, scales are present in the antennae. It thus is undoubtedly a representative of Machilinae. Further details are difficult to observe due to the state of preservation. This demonstrates a general problem with Archaeogatha in amber. Although, the specimen appears well-preserved, most taxonomically important characters are not available. Therefore we hope that the exhaustive description given here for both specimens will facilitate a future recognition of new diagnostic characters which are more easily accessible also in fossil specimens.

5. Evolutionary origin of the ovipositor

A key character of insects (Ectognatha of most German authors) well exhibited in one of the specimens is the ovipositor, consisting of two pairs of so-called gonapophyses or valves. This apomorphy of the Insects (BEUTEL et al. 2014) is maybe another feature responsible for the profound success of this group. The evolution of this structure is coupled to the behaviour to lay the eggs inside a substrate (e.g., soil, plants, animals) instead of onto a surface. This strategy appears to be coupled to the following advantages:

1) More stable environmental conditions for the eggs. Within the substrate external factors such as temperature

and humidity are likely more stable or at least less variable than on a surface.

2) Protection from predators and parasitoids. If the egg is laid within a substrate the possible predators will have more difficulties in locating it compared to an egg on the surface.

Usually a long posteriorly extending structure should also be a disadvantage, hence have evolutionary costs (see e.g. discussion in HÖRNIG et al. 2013). Yet, as archaeognathans also possess the terminal filament which extends even further, there seems to be virtually no costs in this case.

While the function of an oviposition “tool” can readily be reconstructed the exact origin of this structure remains partly problematical. The available data still give a very incomplete picture, different authors interpret these more or less scarce data differently and also the present authors do not share a common opinion on this issue. Hence it seems to be worthwhile to briefly discuss two opposing views on the ovipositor origin.

5.1. Ovipositor origin: an entomologist’s view by CWH

5.1.1. Ovipositor morphology: historical sketch

The evolutionary origin of the insect ovipositor is controversially discussed for more than hundred years. Originally a sternal origin of external genitalia in insects was proposed by LACAZE-DUTHERIERS (1849, 1850, 1853) based on comparative morphology.

This interpretation was questioned by subsequent embryological and morphological studies (WEISMANN 1866; GANIN 1869; WOOD-MASON 1879; WHEELER 1893), in which the ovipositor was interpreted as deviated appendages without sound arguments (ZANDER 1899).

HEYMONS (1876, 1897) revived LACAZE DUTHERIES' hypothesis by outlining that anlagen abdominal podia differ from genitalia ones in spatial and time origin. This view was again opposed by VERHOEFF (1896, 1903), who based on comparative morphology favoured an appendicular origin (but see MATSUDA 1958).

The idea that gonapophyses are homologous of coxal vesicles was introduced by SILVESTRI (1905); evidences were given by GUSTAFSON (1950), WYGODZINSKY (1961) and BITSCH (1974). Coxal vesicles were considered to be homologous with legs by several authors (SHAROV 1966; SNODGRASS 1933). However, the interpretation of homologous structures varies. SMITH (1969) summarised four views regarding the evolutionary origin of insect external genitalia:

- 1) Derived from appendages;
- 2) derived from parts of appendages;
- 3) derived from sternal surface as outgrowth.

The main problem for sound conclusions on the evolution of the insect ovipositor arises from the embryological paradox, that in many insect representatives putative appendicular anlagen on the sternum disappear during subsequent developmental phases (MATSUDA 1958, 1976). The relevance of this reflects in used terminology, for example, the term 'gonapophyses' is only appropriate in case of a sternal origin, while, if originated from appendages, the term 'gonopods' should be used (ESCHERICH 1905). In the subsequent sections we will explore that the evolutionary origin of insect genitalia (or coxopodal vesicles) is still open for debate.

5.1.2. Ovipositor morphology: comparative morphology with other arthropods

MATSUDA (1976) stated: "... any theory that derives the whole genitalia in insects from apparent counterparts in other arthropods is invalid." This fundamental position presupposes a sternal origin of insect genitalia. In Archaeognatha, however, anlagen of styli and putative valves are situated on a coxopodite, offering a different starting point for evolutionary hypotheses.

1) Proximal appendage region. The proximal part of the thoracopods is termed 'coxa', and 'coxopodite' in abdominal appendages of Hexapoda. There has been accumulating support for the hypothesis that the insect coxa is homologous to the basipod of crustaceans (SHAROV 1966; HENNIG 1969):

– Based on motoneuron innervation (WIENS & WOLF 1993);

– homology of the insect sub-coxa with the coxa of crustaceans (BÄCKER et al. 2008).

The position and shape of the insect coxa and coxopodite suggest serial homology (MACHIDA 1981; UCHIFUNE & MACHIDA 2005). Consequently, the coxopodite are also homologous to the crustacean basipod. Observations on the cerci (LARINK 1969; MACHIDA 1981) suggest the same for the proximal elements of these structures.

In conclusion, the proximal elements of thoracopods and abdominal appendages can be interpreted as serially homologous and as representing the basipod.

2) Latero-distal appendage parts and medio-distal appendage parts. In euarthropods, the postantennal appendages are biramous, the basipod distally carries two rami: the endopod medio-distally, and the exopod latero-distally (e.g., BOXSHALL 2004; HAUG JT et al. 2013c). Due to position alone, the walking legs represent the endopod, and styli the exopod.

This arrangement is evident in Eucrustacea (e.g., BOXSHALL 2004, fig. 5C) and machilid Archaeognatha. In Myriapoda, structures similar to thoracic styli occur in Symphyla (EISENBEIS & WICHARD 1985, fig. 103) and Pauropoda (BOXSHALL 2004, fig. 7E and 'Keulenhaar' on panel 74 in EISENBEIS & WICHARD 1985). Conditions of the endopod will be discussed in details in the subsequent sections, thus we here focus on lateral appendages.

In Symphyla, the styli-like structures, however, are located medially, suggesting a homology to the endopod due to the positional criterion alone. Yet, significant differences in shape of endopod and styli clearly falsify this interpretation (structural criterion), but this example shows, that position alone is not enough to postulate homology. Indeed, thoracic and abdominal styli in machilid Archaeognatha exhibit structural differences. KLASS & KRISTENSEN (2001; compare BOXSHALL 2004, 2013 for recent discussions of the annuli vs. 'true' segments) distinguished two categories of styli:

1) Abdominal, (perhaps) long multi-segmented in Carboniferous groups (KUKALOVÁ-PECK 1983 1991) otherwise unsegmented, intrinsic muscles only in Archaeognatha (BRIKET-SMITH 1974), otherwise supported by muscles of the coxopodite,

2) Thoracic, unsegmented (compare STURM & MACHIDA 2001, fig. 8.15), without musculature, in extant hexapoda only Machiloidea (Archaeognatha) possess this type of styli, probably present in fossil Diaphanopteroidea (KUKALOVÁ-PECK 1983).

While this as well as the separation of podomere and annulus bases on typological reasoning, they encourage asking, how reliable a homology of styli and coxopodal vesicles (or insect genitalia) with either exo- or endopod is.

Styli also show external similarities with other lateral structures in crustaceans (exites, epipods; see BOXSHALL &

JAUME 2009; MAAS et al. 2009). In particular for a non-carcinologists the use of these terms is bewildering, assigned to structures locating lateral on the protopod (coxa and basis). Thus, homology of styli and these structures can be postulate based on the positional and structural criterion (external shape). Furthermore, these structures share the absence of intrinsic muscles with thoracic styli. Thus based on primary homology either exopod, exites or epipod can be hypothesized as homologues of styli in machilid Archaeognatha. In contrast to exopods, thoracic styli as well as exites and epipods lack intrinsic muscles. Assume homology of thoracic styli and exopods, an additional evolutionary step (reduction of intrinsic muscle) needs to be considered. According to the congruence criterion it is parsimonious to assume homology between exopod and abdominal styli, while thoracic styli are homologous to other propodial structures. An evolutionary novelty of thoracic styli as proposed by BOUDREAUX (1979) is possible, but not likely.

5.1.3. Ovipositor morphology: comparative morphology and serial homology within Hexapoda

The presence of appendicular remnants in different Hexapoda (AX 1999), leaves no doubt, that abdominal limbs occur in ancestral Hexapoda. The ovipositor has been argued to be derived from coxopodal vesicles (WYGODZINSKY 1961; BITSCH 1974) or styli (DURDEN 1978). The presence of styli and ovipositor valves on the same metameres, clearly indicates, that styli are not the ovipositor's origin. Among Hexapoda, only insects and Protura possess external genitalia (CHAPMAN 1998), while the remaining groups (Collembola and Diplura) lack external genitalia. External genitalia in Protura and insects are located on different metameres (e.g., JANETSCHKE 1970), contradicting their homology. So-called eversible sacs can be found in:

- Archaeognatha (coxopodal vesicles of this study),
- *Zygentoma* (including *Tricholepideon gertschi*) (coxopodal vesicles on abdominal metameres 2 to 7; WYGODZINSKY 1961; AX 1999),
- Diplura (on intersegmental membrans of 2. to 8. abdominal metamere, DENIS 1949),
- Protura (coxopodal vesicles on either 1st to 3rd, 1st and 2nd or 1st abdominal metamere only, JANETSCHKE 1970).

Potential homology to abdominal appendages in Collembola (ventral tube, tenaculum) is difficult to ascertain due to the highly deviated state of these structures. Diplura and Collembola devoid separated coxopods. That makes it difficult to seek for potential evolutionary precursors. In Protura, abdominal appendages consist of two element or three elements (RUSEK 1974). The proximal element resembles the insects' coxa (i.e. basis of Crustacea) due to intrinsic muscles. Distally, the coxa bears a so-called terminal article and in some proturan repre-

sentatives a second element (without intrinsic muscles). The terminal article bears coxopodal vesicles, but styli are absent. In conclusion, the arrangement observed in Archaeognatha is likely closer to the hexapod ground pattern than those in other basal hexapods, while conditions in Ellipura (Protura+Collembola) and Diplura are potential apomorphies, respectively.

For statements on serial homology please consult the section of JTH below. Here, I will encourage to question an obvious serial homology of thoracic and abdominal styli (already proposed by VERHOEFF 1903), in light of the above discussion.

5.1.4. Ovipositor morphology: embryonic development in extant Archaeognatha

A 300 days old embryo of *Petrobius brevistylis* exhibits anlagen for styli on the 3rd to 10th abdominal metameres, while coxopodal vesicles are only present on the 3rd to 5th abdominal metamere (LARINK 1969, fig. 18). Subsequently, anlagen for coxopodal vesicles ('rundlichen Wulst') appear on the remaining abdominal metameres (1st to 9th; LARINK 1969, fig. 19). In contrast to these findings, MACHIDA (1981) described single anlagen (his fig. 14), which differentiate into anlagen of styli and coxopodal vesicles (his figs. 18 and 26) in *Pedetontus unimaculatus* ("biramous appendages"). However, MACHIDA (1981) also quoted that anlagen of the 8th and 9th abdominal metameres do not separate and only differentiated into styli (compare his figs. 26, 29, 34 and 35). In summary, contradicting statements on the ontogeny of abdominal appendages in Archaeognatha occur. Appearance of styli und coxopodale vesicles can either be spatially and temporally different (*P. brevistylis*) or not (*P. unimaculatus*). Observations on the brachiopod *Orchestia cavimana* (WOLF & SCHOLZ 2008) correspond to MACHIDA'S (1981) interpretation of "biramous" abdominal appendages, but differ from descriptions of LARINK (1969). Thus we cannot decide which conditions represent the archaeognathan ground pattern. Notwithstanding, it is apparent that the ontogenetic origin of the genitalia in Archaeognatha is temporally (and spatially?) different from the ontogeny of previous abdominal metameres.

This brings us back to the embryological paradox introduced above. Seemingly, conditions in Archaeognatha mirror the dispute on insect genitalia in small scales. While adult morphology supports an appendicular origin (compare section of JTH), ontogeny does not support this position. In my view, the disagreement with the principle of "congruence with developmental patterns" sensu SZUCSICH & WIRKNER (2007), if not refutes an appendicular origin of insects genitalia, at least cause 'reasonable' doubts. First steps to solve this causal gap are additional studies on the embryonic development in Archaeognatha,

with special reference to the contradicting observations introduced above.

5.2. Ovipositor origin: the carcinologists' view by JTH

Insects are an ingroup of Crustacea sensu lato (e.g., ZHANG et al. 2007; HAUG JT et al. 2010). Hence the origin of certain structures in insects, in this case the ovipositor can also be discussed in the light of their wider relationships. As a kind of "first try" this will be outlined in the following.

5.2.1. Ovipositor morphology: phylogenetic consideration

At first the morphology of the ovipositor valves is partly surprising with all of them being annulated, occurring in Archaeognatha (STURM & MACHIDA 2001; KLASS & MATUSHKINA 2012) and different Zygentoma (ESCHERICH 1905). Annulated valves therefore seem to be plesiomorphic (apomorphic for insects) while solid valves are apomorphic for Pterygota and an ingroup of Zygentoma.

5.2.2. Interpretation of proximal appendage region

The proximal part of insect thoracopods is termed 'coxa', and 'coxopodite' in abdominal appendages. There has been accumulating support for the hypothesis that the insect coxa (of the thoracopods) is homologous to the basipod of crustaceans (as outlined above).

As, based on position and shape and ontogeny, the insect coxa and coxopodite appear to be serially homologous (see above), coxopodites represent basipods of the abdominal appendages (including ovipositor forming appendages). Based on observations on the late embryos and early larvae of archaeognathans (MACHIDA 1981) cerci also arise from such a proximal portion, also representing the basipod. Hence all the proximal elements of thoracopods and abdominal appendages, including the genitalia and cerci are interpreted as being serially homologous and as representing the basipod. An appendicular origin of the genitalia is therefore seen as unequivocal.

5.2.3. Latero-distal appendage parts

The basipod distally carries two rami (e.g., HAUG JT et al. 2013c and references therein): endopod (medio-distally), and exopod (distally). The best candidates to represent the exopod are the styli, based on their position (also proposed by HENNIG 1994). Yet, among insects, only archaeognathans possess these structures on the thoracopods, all other insects seem to lack these. Alternative views put forward by KUKALOVÁ-PECK have been questioned (e.g., BÉTHOUX & BRIGGS 2008; HAUG JT et al. early view). Hence one could argue that these structures are a specialisation of Archaeognatha.

Different crustaceans usually possess an exopod in that very position. Therefore, it seems more parsimonious to assume a loss of these structures two times, in Entognatha (here possibly coupled to paedomorphosis?) and Dicondylia.

Based on position and shape also the serial homology of thoracic styli and abdominal styli is proposed. There have been arguments against this homology based on muscle innervations (see above). Yet, differences are not an exclusion of homology. Both structures occur in the corresponding position and are extremely similar in outer appearance. An independent (non-homologous) evolution of two structures in exactly corresponding position with similar outer morphology seems very unlikely. Both structures, thoracic and abdominal styli, were likely more similar ancestrally but became altered during further evolution. The shape and position of the cerci in the embryonic stages (MACHIDA 1981) furthermore clearly indicate a serial homology with the styli.

Exopods of malacostracan crustaceans are often elongate in shape and annulated (HAUG JT et al. 2013a, b) hence distantly resembling cerci, demonstrating that exopods in principle can acquire such a shape. While a relative elongate shape and annulated condition could well represent a plesiomorphic state (depending on the outgroup of Hexapoda), the extreme elongation of these structures is most likely an apomorphy.

It should also be considered for the styli if these could be derived from a multi-annulated condition via paedomorphosis. In fact, they very much appear like undeveloped precursors of a multi-annulated exopod. Undeveloped cerci which still lack subdivision into separate elements are indeed very similar to styli in appearance.

It seems unlikely that the styli, thoracic and abdominal represent the epipod. Epipods are usually rather soft, do not bear setae and, most importantly, represent exites. Exites arise laterally and abaxially. Styli appear to arise latero-distally and hence can be best interpreted as being in the orientation of the main axis. The split into endopod and exopod (WOLFF & SCHOLTZ 2008) has not been observed. Yet, this split has been observed in amphipod crustaceans only based on stainings, not on external structures of the embryo. Hence we cannot know whether such a split occurs in Archaeognatha as such types of stainings have not yet been performed.

5.2.4. Medio-distal appendage parts

As styli most likely represent exopods, the further median structures are likely derivatives of the endopod. For the thoracopods the morphology of the distal part of the leg (starting from the trochanter) is perfectly compatible with such an assumption. More problematic is the condition of the anterior abdominal appendage. Here only the

so-called coxopodal vesicles occupy a position that could be identified as the insertion area of the endopod. Therefore, we must consider it as likely that these tiny structures are remains of the endopod or possibly only of the membrane between the former endopod and the basipod. Serially homologous position in the abdominal appendage 8 and 9 is occupied by the valves. Hence, these should be considered as representing the endopod.

Annulated endopods of elongate shape are also known from different malacostracan crustaceans. Hence, the morphology of the valves fits also well the interpretation that these represent endopods. The elongate shape and the annulation could therefore be a retained feature (depending on the outgroup of insects), while the use as an ovipositor is a novelty of insects. We would need to assume a single loss of annulated, elongate endopods at abdominal appendages 8 and 9 in Entognatha. Yet, again depending on the outgroup, such a loss should be more likely than the re-evolution of a functional endopod. It is therefore also not likely that the valves evolved from coxopodal vesicles. It is more likely that coxal vesicles are reduced endopods and valves are specialised endopods.

To conclude the carcinologist's view: The here presented homologisation has to remain a working hypothesis. Yet it must be seen as a plausible explanation of the available data.

To speculate a bit further on this: The insect ancestor might have had abdominal appendages with two branches (endopod and exopod) which were elongate and multi-annulated. This should be true at least for the very posterior segments, but might well apply for the entire abdominal segments (compare Fig. 8).

5.3. Ovipositor origin: a solution in sight?

As can be seen by the two opposing views outlined above the exact evolutionary origin of the insects ovipositor must currently remain unclear. A larger-scaled comparison with discrete bit-by-bit comparisons will be necessary to resolve this issue more reliably.

6. Conclusions

To briefly summarise: We presented two exceptionally preserved specimens of Archaegnatha found in Baltic amber. One specimen is preserved perfectly with all details of the ventral morphology including abdominal appendages and genitalia. The evolutionary origin of these structures appears currently not resolvable unequivocally even when incorporating fossil and embryological evidence. We still lack a lot of details of the early evolution of insects and of the early insect groups. Hence, finding exceptionally preserved fossils like the here presented

ones add significant new pieces to the still ongoing reconstruction of these groups.

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