Available online at www.sciencedirect.com
ScienceDirect
Organisms, Diversity & Evolution 9 (2009) 215–231
ORGANISMS DIVERSITY & EVOLUTION
www.elsevier.de/ode

Devonohexapodus bocksbergensis is a synonym of *Wingertshellicus backesi* (Euarthropoda) – no evidence for marine hexapods living in the Devonian Hunsrück Sea

Gabriele Kühl*, Jes Rust

Steinmann Institute, Division of Palaeontology, University of Bonn, Nussallee 8, 53115 Bonn, Germany

Received 11 December 2008; accepted 12 March 2009

Abstract

The Devonian Hunsrück Slate fossil *Devonohexapodus bocksbergensis* Haas, Waloszek & Hartenberger, 2003 has been interpreted as a stem-lineage representative of the Hexapoda, implying their marine origin and independent terrestrialisation within the 'Atelocerata'. *Devonohexapodus bocksbergensis* was based on a single specimen embedded in a lateral position. Reinvestigation of that holotype and of all known specimens of the Hunsrück Slate arthropod *Wingertshellicus backesi* Briggs & Bartels, 2001 demonstrates that all this material represents a single species. The latter is redescribed, its taxonomic diagnosis is emended, and the name *Devonohexapodus bocksbergensis* is treated as a junior synonym of *Wingertshellicus backesi*. The phylogenetic position of *W. backesi* neither is that of a stem-lineage representative of Hexapoda, nor does it fall within the crown group Mandibulata. The Hunsrück Slate provides no evidence of an independent terrestrialisation within the 'Atelocerata' or of a marine origin of the Hexapoda.

Keywords: *Devonohexapodus bocksbergensis*; *Wingertshellicus backesi*; Hexapoda; Euarthropoda; Terrestrialisation; Lower Devonian

---

Introduction

The Lower Devonian Hunsrück Slate (Rhenish Massif, Germany; Lower Emsian, age about 405 Ma) is known for its unique fauna and remarkable preservation of pyritised fossils. The arthropods in particular are highly diverse. Several of them are known only from that Lagerstätte, e.g. the herein reinterpreted *Devonohexapodus bocksbergensis* Haas, Waloszek & Hartenberger, 2003 and *Wingertshellicus backesi* Briggs & Bartels, 2001, as well as *Cambronatus brasseli* Briggs & Bartels, 2001.

Devonohexapodus bocksbergensis was interpreted by Haas et al. (2003) as a stem-lineage representative of Hexapoda. Their investigation was based on a single specimen embedded in a lateral position. According to Haas et al. (2003) the fossil is characterised by a small head with large eyes and long antennae, by a three-segmented thorax, including three pairs of long and slender thoracopods, and by an abdomen with 35–40 segments bearing uniramous limbs. Because *D. bocksbergensis* occurs in a marine deposit, the phylogenetic interpretation of Haas et al. (2003) implied that the Hexapoda evolved in a marine environment as surprisingly large organisms, considering the small size of all living basal hexapod taxa, and that terrestrialisation took place independently in the myriapod and the

---

*Corresponding author.
E-mail address: gkuehl@uni-bonn.de (G. Kühl).

1439-6092/$ - see front matter
doi:10.1016/j.ode.2009.03.002

hexapod lineage of ‘Atelocerata’ (independent terrestrialisation in these taxa has been inherent anyway in the currently dominating Tetraconata hypothesis of arthropod relationships). This controversial issue was discussed in several subsequent works, e.g. Nardi et al. (2003), Harzsch (2004), Pisani et al. (2004), Regier et al. (2004), Fayers and Trewin (2005), Grimaldi and Engel (2005), Haas (2005), Willmann (2005), Glenner et al. (2006), Klass (2007), and Rust (2007). This debate focused mainly on aspects of the interpretation of morphological characters within the framework of different phylogenetic hypotheses, on the process of terrestrialisation, the early evolution of the myriapods and hexapods, as well as on the monophyly of Hexapoda.

Wingertshellicus backesi and *Cambronatus brasseli*, both described by Briggs and Bartels (2001), were also considered by Haas et al. (2003). The latter authors mentioned the similarity of *Devonohexapodus bocksbergensis* to *Wingertshellicus backesi*, and postulated a close phylogenetic relationship between the two perceived taxa, but had not re-examined the available material of *W. backesi*. Haas et al. (2003) also interpreted *Cambronatus brasseli* as a representative of the hexapod stem lineage, and placed it in an even more derived position than *D. bocksbergensis* and *W. backesi*. However, an ongoing reinvestigation of *C. brasseli* by the present authors shows that its morphology is strikingly different from that of *D. bocksbergensis* and *W. backesi*. There is no evidence of a phylogenetic affinity of *C. brasseli* as a stem-lineage representative of Hexapoda.

Because of the significance of the interpretation of *D. bocksbergensis* by Haas et al. (2003) for the origin of hexapods, a detailed re-examination of all available fossil specimens *of W. backesi*, *D. bocksbergensis* and *C. brasseli* was carried out. Here, we focus on the interpretation of the important morphological characters, their preservation, and the systematic position of *D. bocksbergensis*. The results of the re-investigation of *C. brasseli* will be the subject of a future publication.

Material and methods

The holotype of *Wingertshellicus backesi* (specimen NMPWL 1993/354-LS) as well as the specimens NMPWL 1999/4-LS and NMPWL 1998/150-LS are held at Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz (Germany). Specimen SUE WB is the property of Wouter Suedkamp (Bundenbach, Rheinland-Pfalz, Germany), and was at our disposal during the reinvestigation. Specimen SMNS 64880, the holotype of *Devonohexapodus bocksbergensis*, carries an inventory number from the State Museum of Natural History in Stuttgart (Baden-Württemberg, Germany). For the sake of clarity, this specimen is referred to as ‘SMNS 64880 (*D.b.*)’ below, the term in parenthesis indicating *Devonohexapodus bocksbergensis*.

The complete fossils were photographed with a Nikon D1 and Nikon D100 by Georg Oleschinski (Steinmann Institute, Division of Palaeontology, University of Bonn). Additional pictures were made with a Nikon Coolpix 4500 through the ocular of a Leica Stereomicroscope MZ125. All specimens were X-rayed with a Radiflor 120 from Philips, also by Georg Oleschinski. Drawings were made by the first author using a Leica MZ75 stereomicroscope including a camera lucida. All photographs, radiographs and drawings were edited with Adobe Photoshop® CS3 and Adobe Illustrator® CS3.

For the terminology used to describe and discuss the various appendages and other body parts, see Table 1 and the text section “Interpretation of morphological characters” below.

Taphonomy and preservation

Although the Hunsrück Slate fossils are famous for their exceptional state of preservation, some details are often missing. Sometimes isolated fine and thin structures are pyritised in every detail, whereas more consolidated and formerly heavily sclerotised structures are more heavily pyritised, often concealing important morphological details. In spite of the rich fossil record for some of the arthropods of the Hunsrück Slate, e.g. for *Vachonisia rogeri* Lehmann, 1955 and *Mimetaster hexagonalis* Stürmer & Bergström, 1976, detailed preservation of important structures such as limb bases almost never occurs (Kühl et al. 2008). This is also true for the material studied here, as the bases of the limbs, especially in the head region, are almost never preserved. The ommatidia of the compound eyes are also often concealed by pyritisation. Several species of the crustacean *Nahecaris* are known from numerous specimens none of which show preserved ommatidia, but in some cases these structures are well documented. The eyes of the specimens reinvestigated here are considered as compound eyes, even though ommatidia are not preserved.

The degree of fragmentation and disarticulation depends on the former state of decay and the transport of the animal (Allison and Briggs 1991). This implies that even if the organisms were transported only over short distances, decay could cause fragmentation and disarticulation as in the available material. Compared to the remaining material studied here, the specimens NMPWL 1998/150-LS, SUE WB, and SMNS 64880 (*D.b.*) are quite poorly preserved. In each case the anterior part of the head carrying the antenna, the stalked compound eyes and the head appendages is bent dorsally, and therefore separated from the remainder of the body. Due to the anterior head portion being bent to

Table 1. Overview of the different labelling and interpretation of head appendages and anterior body units of *Wingertshellicus backesi* (specimen PWL 1993/354-LS) in three published studies.

	Briggs and Bartels (2001)			Haas et al. (2003)		Present study	
Antenna	rh1/lh1			ant		ha1	
Post-antennal appendages	–/lh2		head app.	lab	head app.	ha2	head app.
	rh2/–		head app.	–	–	ha3	head app.
	rh3a/lh3a	1 of 3 rami	head app.	thp1	head app.	ha4	head app.
	rh3b + c/lh3b	2 of 3 rami	head app.	thp2 (r)	thoracic app.	ha5	head app.
	rh4a/lh4a	1 of 2 rami	head app.	thp2 (l)	thoracic app.	ha6	head app.
	rh4b/lh4b	1 of 2 rami	head app.	thp3	thoracic app.	ha7	head app.
	trunk			abdomen		trunk	

Abbreviations: ant = antenna; app. = appendage; ha = head appendage; lab = labium; rh/lh = right/left head appendage (a, b, c = separate rami); thp = thoracopod (r = right, l = left).

dorsal in specimen SUE WB, the latter is lacking the antenna and the stalked eyes, which may have been lost already before the organism was finally embedded. The posterior trunk region of specimen NMPWL 1998/150-LS is not present, because the slab is not complete. In each specimen (except SUE WB), one member of the head appendage pair ha2 and ha3 is not preserved.

At first sight it seems that *W. backesi* had only small and slender post-antennal appendages (SMNS 64880 (*D.b.*), NMPWL 1998/150-LS, NMPWL 1999/-LS). On the other hand, Briggs et al. (1996) have verified from trilobites that the pyrite preservation of appendages in specimens from the Hunsrück Slate is often only the infill of the former cuticle. Additionally, the thickness of the preserved appendage infill is very variable due to the orientation of the fossil relative to bedding, which is evident especially in some of the pycnogonid specimens from the Hunsrück Slate (Bartels et al. 1998, p. 153, fig. 130). The orientation and thickness of the post-antennal head appendages of the holotype (NMPWL 1993/354-LS) and of SUE WB show that these appendages were originally quite robust; in these specimens the appendages are probably preserved with their original outlines rather than as infill.

Generally, it is important to consider that the interpretation of morphological characters of Hunsrück Slate fossils and their special pyrite preservation has to be made very carefully in order to avoid misidentifications. Furthermore, it is absolutely necessary to study and compare all available material, so that different modes of embedding can be considered as much as possible. The reinvestigation and new interpretation of the morphology of *Bundenbachiellus giganteus* (Moore et al. 2008) is a striking example.

Results

Based on re-examination of all known specimens of *Devonohexapodus bocksbergensis* (holotype only) and *Wingertshellicus backesi* (one new and three previously known specimens) we conclude that all this material belongs to the same species. Therefore, we treat the name *D. bocksbergensis* as a junior synonym of *W. backesi*.

Figs. 1–3 illustrate all available material of *W. backesi*, including the holotype of *D. bocksbergensis*.

Wingertshellicus backesi Briggs & Bartels

Wingertshellicus backesi Briggs & Bartels, 2001. – Briggs and Bartels (2001, pp. 282–293, figs. 4–10). See also Bartels (1995, p. 47, fig. 2); Bartels and Blind (1995, p. 94, figs. 15–16); Bartels et al. (1997, p. 66, figs. 86–87).

Devonohexapodus bocksbergensis Haas, Waloszek & Hartenberger, 2003; syn. nov. – Haas et al. (2003, p. 39–54, figs. 2–4). See also Grimaldi and Engel (2005, p. 111, fig. 3.27); Rust (2007, p. 77, fig. 3A).

Material examined

Wingertshellicus backesi. Holotype, NMPWL 1993/354-LS (Briggs and Bartels 2001, p. 284–293, figs. 4–6). Additional specimens: NMPWL 1999/4-LS, NMPWL 1998/150-LS, SUE WB.

Devonohexapodus bocksbergensis. Holotype, SMNS 64880.

Diagnosis

(emended after Briggs and Bartels 2001)

The body is divided into two tagmata: head and trunk. The head bears up to seven pairs of appendages (including one pair of antennae), a triangular structure with a small circular mouth, and large, stalked eyes. The trunk comprises up to 40 segments with biramous appendages. Its rear end carries specialised, large and laterally projecting, fluke-like terminal appendages with distal flagellate structures.

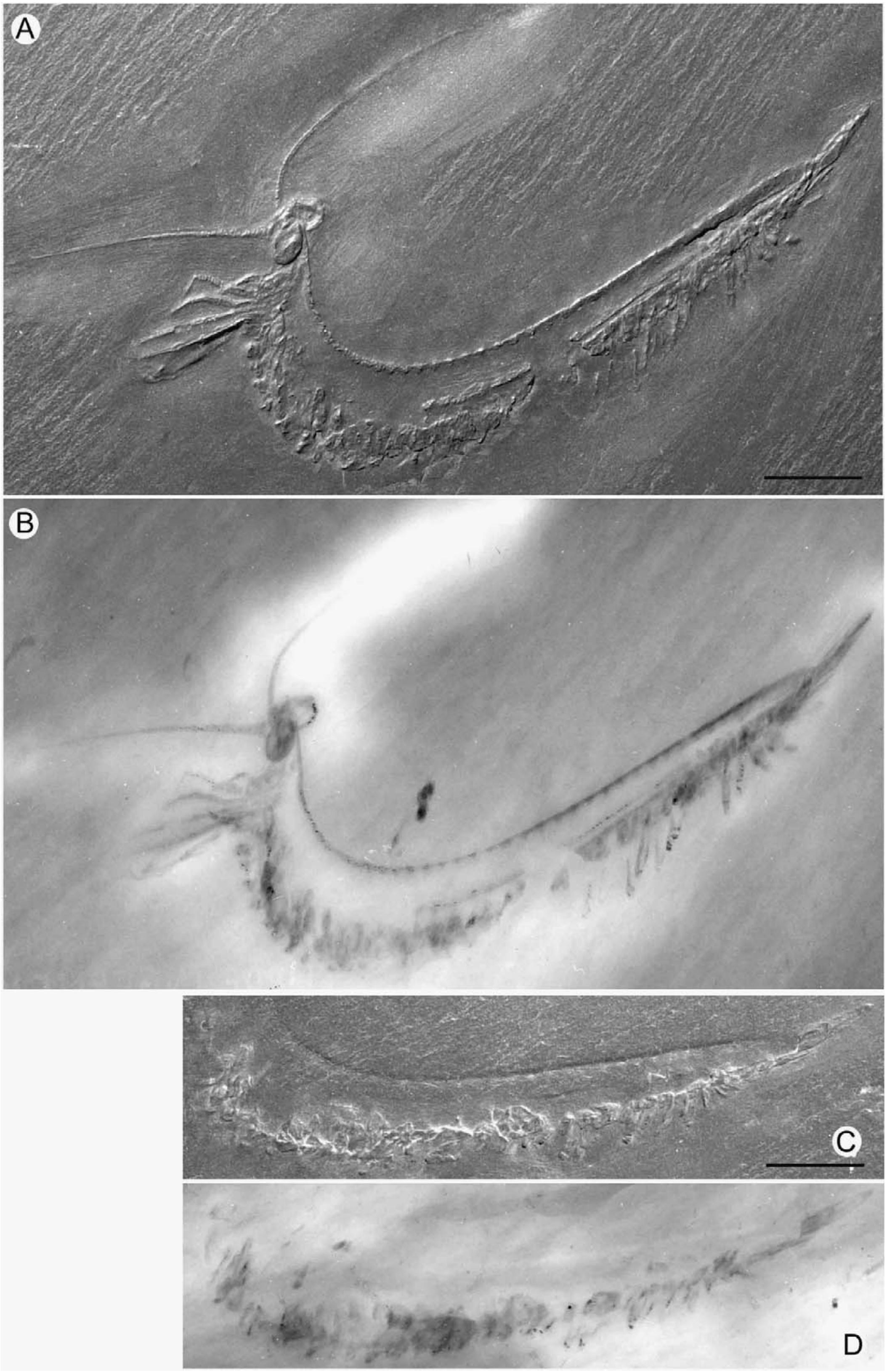

Fig. 1. *Wingertshellicus backesi*, lateral view, specimen SMNS 64880 (*D.b.*). (A) Photograph. (B) Radiograph. (C) Counterpart; photograph. (D) Counterpart; radiograph. Scales 10 mm.

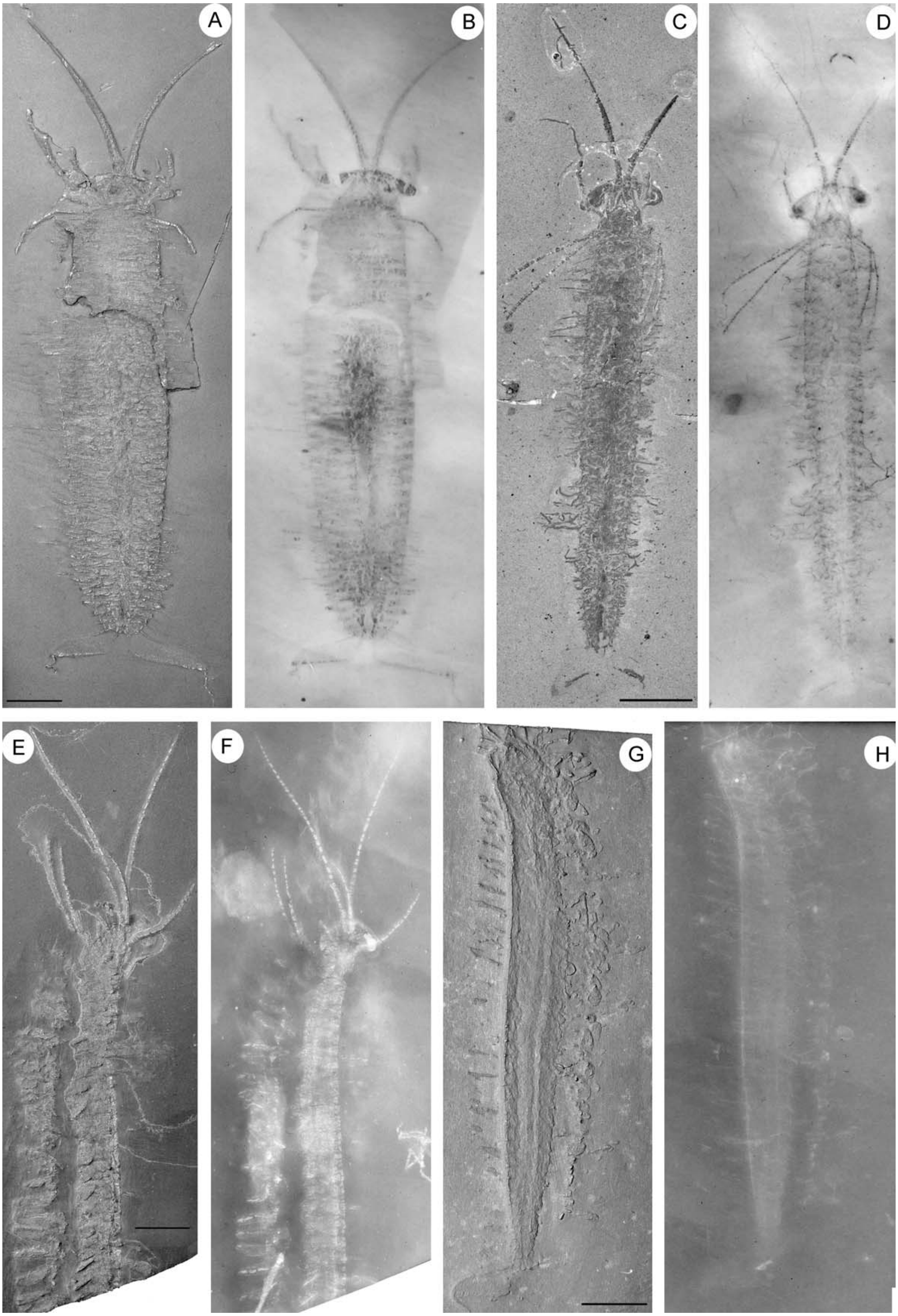

Fig. 2. *Wingertshellicus backesi*, ventral (A–F) and dorsal (G, H) views in photographs (A, C, E, G) and radiographs (B, D, F, H). (A, B) Specimen NMPWL 1993/354-LS. (C, D) NMPWL 1999/4-LS. (E, F) NMPWL 1998/150-LS. (G, H) SUE WB. Scales 10 mm.

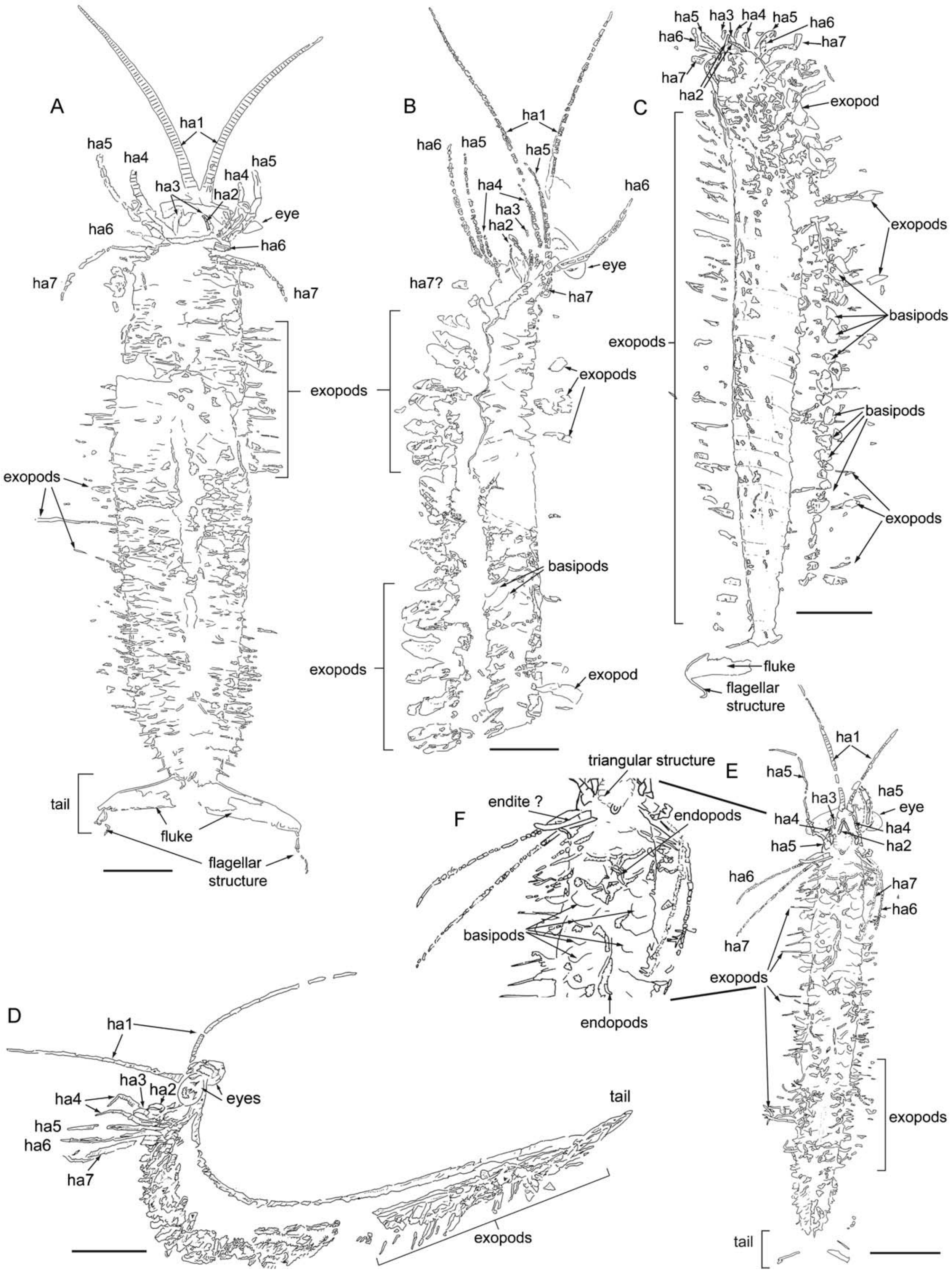

Fig. 3. *Wingertshellicus backesi*, explanatory drawings of specimens. (A) NMPWL 1993/354-LS. (B) NMPWL 1998/150-LS. (C) SUE WB. (D) SMNS 64880 (*D.b.*). (E, F) NMPWL 1999/4-LS; full view and enlarged detail of anterior trunk region. Abbreviation: ha = head appendage. Scales 10 mm.

Redescription

Head. The head is defined here as a functional unit of the anterior body parts comprising the uniramous antenna, one pair of eyes, the mouth, which is a posterior terminal opening of a triangular structure, and six pairs of post-antennal appendages specialised for feeding and/or locomotion (Fig. 3A–E). The eyes are considered as compound eyes, even though no ommatidia are preserved (see text section "Taphonomy and preservation" above).

The evidence of a head shield is unclear due to poor preservation. Specimen SUE WB shows a delicate line (Fig. 4A, dotted line) presumably indicating the presence of a weakly sclerotised head shield, similar to that in certain crustaceans such as Copepoda or Anostraca. That line is distinguished from the segmental trunk borders by having a different angle. In specimen SMNS 64880 (*D.b.*), neither the radiograph nor the specimen exhibits segmentation of the dorsal margin anterior to ha7 (Fig. 5B, C); this fact is an indirect indication for the presence of a head shield. Specimen NMPWL 1999/4-LS at least shows a line that could be interpreted as the lateral margin of a head shield in ventral view (Fig. 6).

Eyes are preserved in the specimens NMPWL 1993/354-LS, NMPWL 1998/150-LS, NMPWL 1999/4-LS, and SMNS 64880 (*D.b.*) (Figs. 1A–F; 2A, B; 3A, B, D, E). As already described by Briggs and Bartels (2001) and Haas et al. (2003), the eyes are large and positioned distally on an eye bridge. On the left eye of NMPWL 1999/4-LS, a delicate line might indicate the margin of a dorsal covering of the eye.

The antenna (ha1) inserts on the ventral side of the head, close to the midline (Figs. 3E; 5B, C; 6B); it has one large basal segment, followed by numerous small antennomeres that taper distally. The basal segment is preserved in NMPWL 1993/354-LS, NMPWL 1999/4-LS, and SMNS 64880 (*D.b.*). Specimens NMPWL 1999/4-LS and SMNS 64880 (*D.b.*) especially show that the insertion of the antenna is ventral (Figs. 6B and 5B, C, respectively).

The mouth is a very small roundish opening (Figs. 4A, 6B), preserved in two specimens: SUE WB and NMPWL 1999/4-LS. In NMPWL 1999/4-LS it is the termination of a triangular structure (Fig. 6A, B). Morphological details and function of this structure are unclear, due to weak preservation.

All specimens have the same number and sequence of post-antennal head appendages (ha2–ha7) (Fig. 3A–E). Appendages ha2 and ha3 are short and stout compared to appendages ha4–ha7. Segmentation for ha2 is preserved in NMPWL 1999/4-LS (Fig. 6), for ha3 in SMNS 64880 (*D.b.*) (Fig. 5C). Head appendage ha4 is twice as long as those preceding it (Figs. 3A, B, D; 5C). The following head appendages ha5–ha7 are longer than ha4, but subequal in length to each other (Fig. 3A, B, D, E).

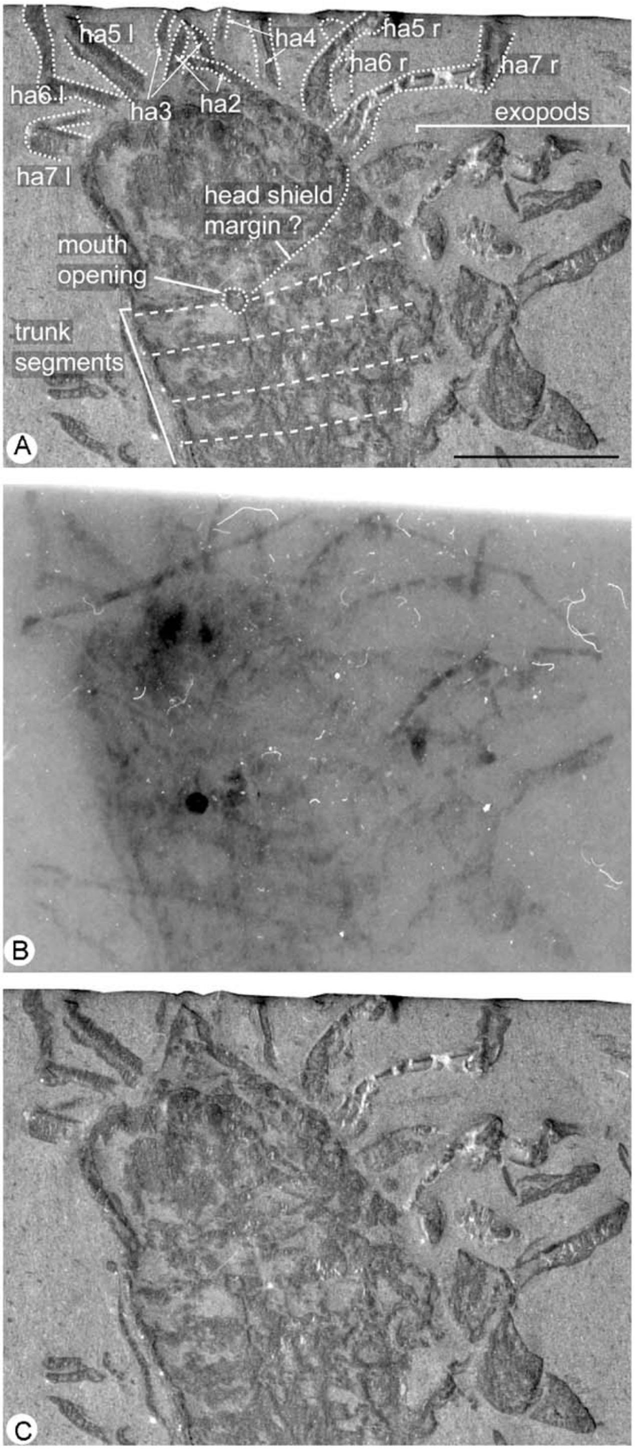

Fig. 4. *Wingertshellicus backesi*, specimen SUE WB, anterior regions. (A) Photograph with head shield and margins of head appendages (ha) indicated by dotted lines, segmental borders marked by dashed lines. (B) Radiograph. (C) Photograph without explanatory labelling. Scale 5 mm.

Due to the incomplete preservation especially of appendage bases it is difficult to determine whether the post-antennal head appendages are uniramous or

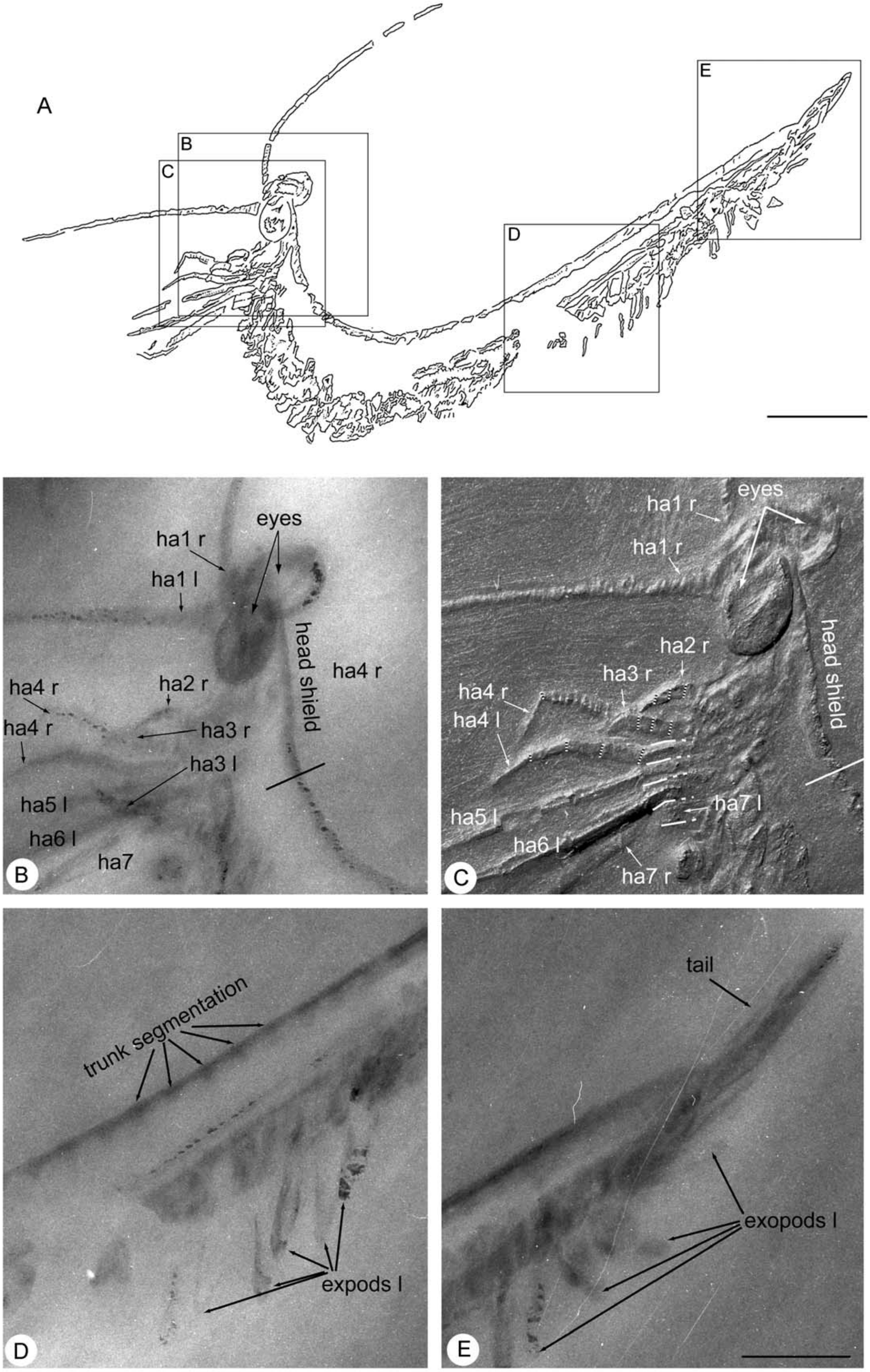

Fig. 5. *Wingertshellicus backesi*, specimen SMNS 64880 (*D.b.*). (A) Overview drawing indicating respective positions of details B–E. (B) Radiograph and (C) photograph of antennae, eyes, head shield and head appendages (ha); in C podomeres marked by dashed lines, posterior end of head shield by a white line. (D) Radiograph of middle trunk region with marked trunk segmentation and trunk exopods. (E) Radiograph of posterior region with marked trunk exopods and lateral 'tail'. Scales 5 mm.

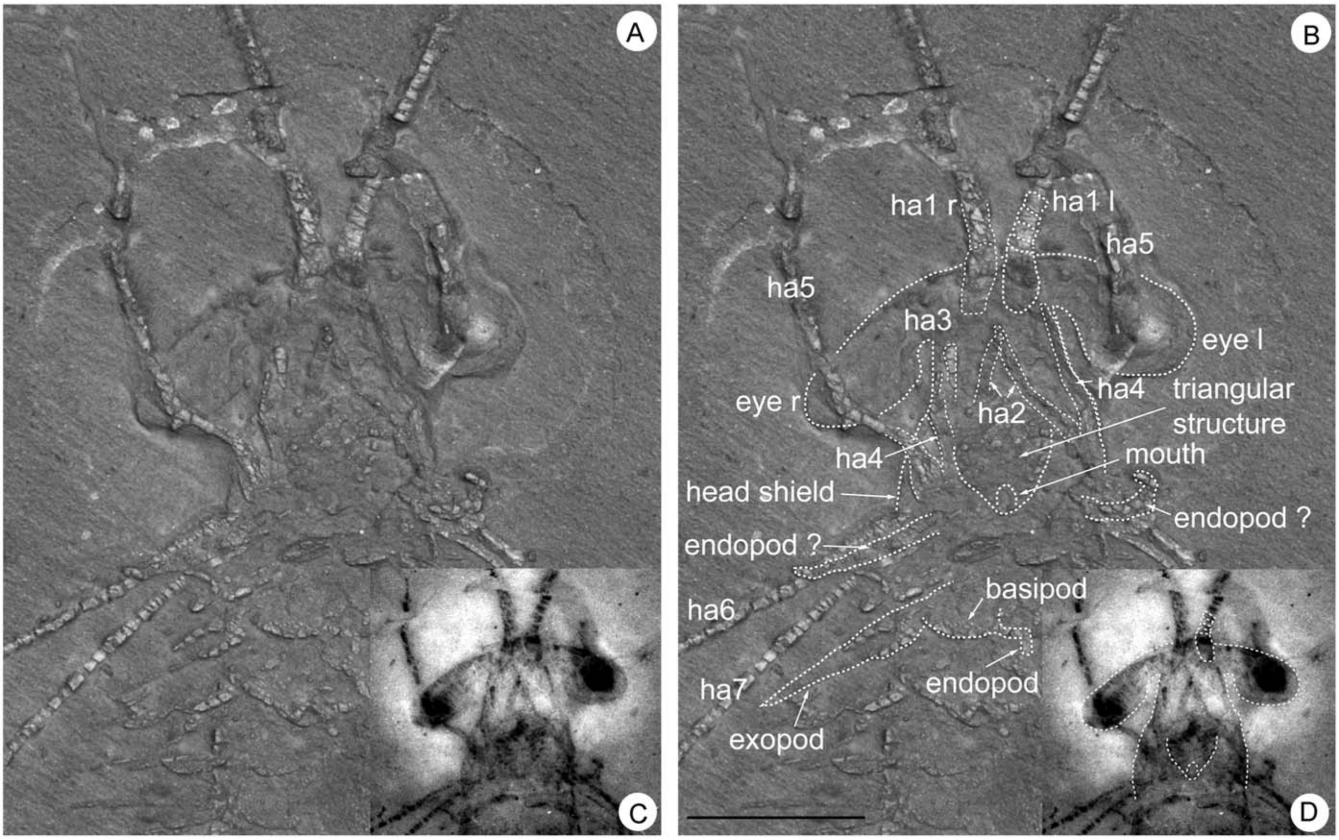

Fig. 6. *Wingertshellicus backesi*, anterior regions of specimen NMPWL 1999/4-LS in photographs (A, B) and radiographs (C, D). (A, C) Without explanatory lines. (B, D) Dotted lines mark margins of some important head and trunk structures; ha = head appendage. Scale 5 mm.

biramous. Our terminology (ha2–ha7; Table 1) is based on the assumption that all those appendages are uniramous; should any of them prove to be biramous, the numbering would have to be modified accordingly. We do not follow Briggs and Bartels (2001) in seeing ha3–ha5 as the rami of a triramous appendage, because ha4 and ha5 have clearly separate bases (Fig. 6B). Considering NMPWL 1999/4-LS (Fig. 6B), however, the existence of a shared basal podomere of ha2 and ha3 cannot be excluded. These appendages are also annulated, but the podomere borders are hard to distinguish from pyrite annulations, as they are elsewhere. Specimen NMPWL 1998/150-LS is heavily pyritised, so that the podomere boundaries are not clearly visible. Only NMPWL 1993/354-LS and SMNS 64880 (*D.b.*) have the podomere boundaries on ha5 preserved, but the total number is uncertain. In SMNS 64880 (*D.b.*) the overlying appendage ha4 shows at least the basal segment plus three segments. There is no hint that this appendage could be combined with one of the flanking appendages to form a biramous appendage (Fig. 5C). This specimen was not part of the investigation by Briggs and Bartels (2001), thus provides new evidence. In specimen NMPWL 1999/4-LS the last head appendage ha7 has a short endite (Figs. 3F, 6B). No endites are preserved in any of the other specimens, which might be due simply to their embedding positions.

Trunk. The trunk of all specimens is clearly segmented. Some of the segmental borders are obscure, which leads to a final segment number of 36–40 segments. Though the specimens differ considerably in size, the number of trunk segments is basically identical, as already recognised by Briggs and Bartels (2001).

The preservation of the trunk appendages is extremely poor; therefore their interpretation is difficult. The trunk appendages are biramous, consisting of a short endopod and a long flap-like exopod, which both originate from an enlarged basipod (Fig. 6B). The endopod is only poorly preserved in NMPWL 1999/4-LS, and SUE WB (Fig. 3C, E). The basipods are evident in specimens NMPWL 1999/4-LS and NMPWL 1998/150-LS (Fig. 3B, E, F). In NMPWL 1999/4-LS they can be traced from the first to the twenty-ninth segment. The exopods are the most prominent structures and usually extend beyond the lateral margins. They are preserved in all specimens (Fig. 7). No annulation of the exopod was found in any specimen.

Terminal fluke-like appendages (tail). The tail of *W. backesi* includes a pair of fluke-like appendages. On both sides the distal tips of the flukes continue into a flagellar structure, which is preserved in specimens NMPWL 1993/354-LS and SUE WB (Figs. 1A, B, G, H; 3A, C–E). Specimen SMNS 64880 (*D.b.*) shows the tail embedded in a lateral position. In specimen NMPWL 1999/4-LS, only remains of the posterior margin and of one side of the anterior margin are preserved. Part of the flagellate structure is also preserved on one side only.

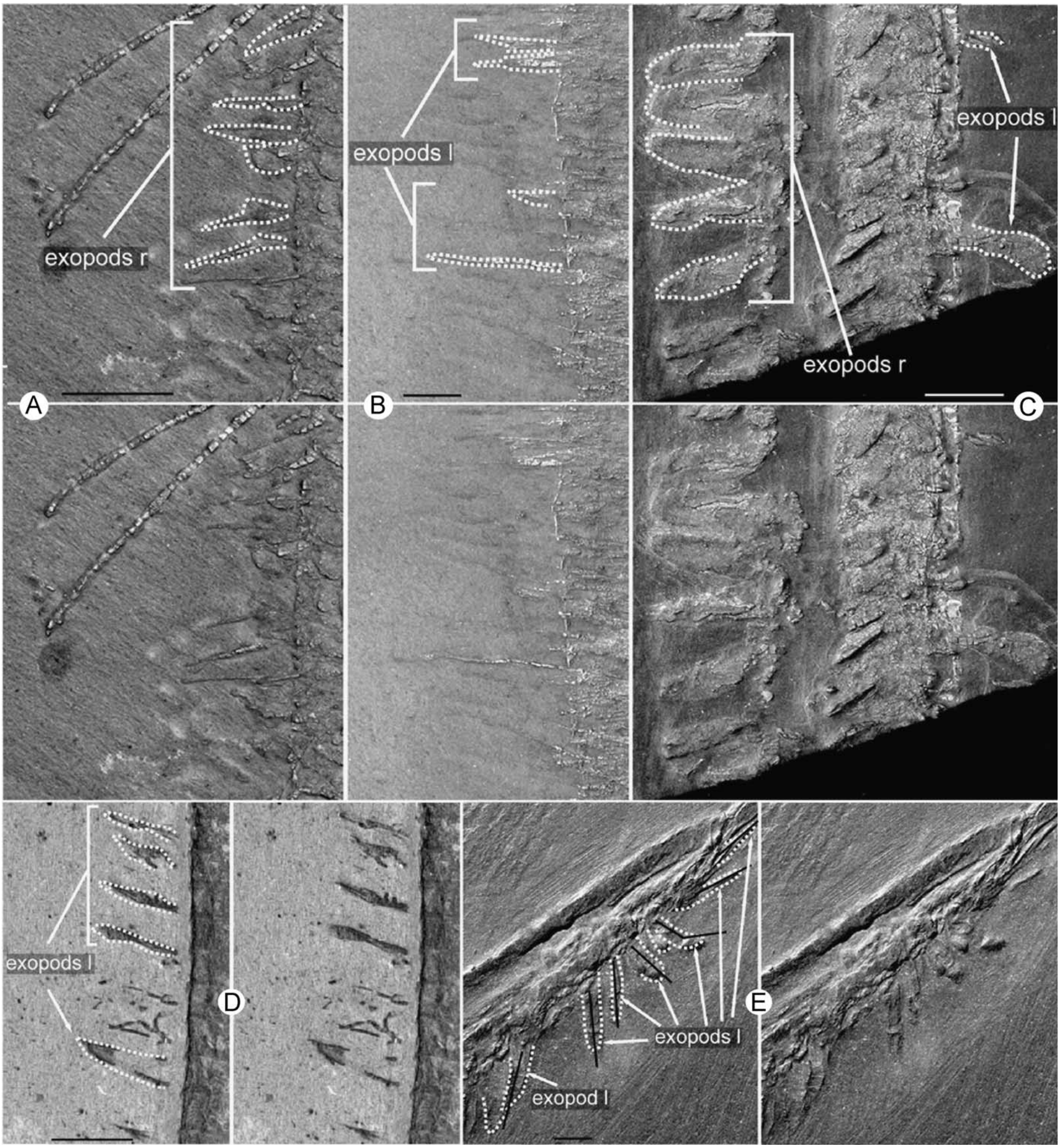

Fig. 7. *Wingertshellicus backesi*, exopods (l = left, r = right), photograph pairs with and without explanatory labelling, respectively; dashed lines mark examples of trunk exopods. (A) Specimen NMPWL 1999/4-LS. (B) NMPWL 1993/354-LS. (C) NMPWL 1998/150-LS. (D) SUE WB. (E) SMNS 64880 (*D.b.*). Scales 5 mm.

Mode of life

The long and streamlined body, the terminal fluke-like tail, and the large exopods of the trunk appendages demonstrate that *W. backesi* was well adapted to swimming, as already suggested by Briggs and Bartels (2001). The huge eyes of *W. backesi* obviously indicate excellent visual capability, which could have been useful to escape from predators such as other arthropods or fishes. The long and slender antennae clearly had sensory functions.

The head appendages have been interpreted in different ways. Briggs and Bartels (2001) postulated a primarily sensory function, with the possibility of prey-catching. Haas et al. (2003) also considered that these appendages might have been used to catch prey. Additionally, they suggested that the long head appendages (ha4–ha7) could have been used for walking on the substrate, or for clinging to stones. In our view, the locomotion of *W. backesi* was dominated by swimming. Use of the long head appendages (ha5–ha7) for walking is highly unlikely, because the original substrate was very soft and fine-grained (there is no evidence of hard substrates). Such fine sediment does not offer suitable surfaces for walking legs without any specialised terminal structures such as the ‘snow shoe’ tips of the appendages in xiphosurans in general, but also in other Hunsrück Slate arthropods like the trilobite *Chotecops* (see Seilacher 1962) and *Nahecaris stuertzi* (see Bergström et al. 1987). Use of the appendages for prey-catching is unlikely as well, because *W. backesi* was hardly able to feed on any prey. The organism only had a very small and roundish mouth (Figs. 4, 6) without any evidence of gnathobases, which rather suggest feeding on suspended material. The head appendages might have had mainly sensory function (Briggs and Bartels 2001).

We follow the latter authors in considering that the stable number of trunk segments in the variously sized specimens indicates that the full number of segments was reached already at an early ontogenetic stage.

Comparison and taxonomic identity of *Devonohexapodus bocksbergensis* with *Wingertshellicus backesi*

Taking the special mode of preservation of the Hunsrück arthropods into account, *Devonohexapodus bocksbergensis* (SMNS 64880 (*D.b.*)) and *Wingertshellicus backesi* (remaining specimens studied here) undoubtedly belong to the same species; therefore, the two names are synonymous. The conclusion of species identity is based on the fact that no morphological differences between the specimens could be demonstrated. All differences we observed are interpreted as either resulting from the respective individual state of decay, or from preservational peculiarities or differences in the embedding position. Species identity is confirmed by the same tagmosis pattern (head and trunk), identical antennae and one pair of large, stalked compound eyes, by corresponding numbers and identical design and position of the post-antennal head appendages, corresponding numbers of trunk somites, the evidence of identical trunk exopods as parts of biramous appendages as well as by identical terminal, fluke-like trunk appendages (tails).

The head and appendages of specimen SMNS 64880 (*D.b.*) do not show striking differences to any of the *W. backesi* specimens (Fig. 3). In each case (except in SUE WB, the antennae and eyes of which are not preserved) the antennae have a large basal segment, which inserts close to the midline of the ventral side of the head, and numerous smaller antennomeres (Fig. 8). The ratio between the length of the antenna and the body length is 1/3 in specimens SMNS 64880 (*D.b.*), NMPWL 1993/354-LS, and NMPWL 1999/4-LS (the remaining two specimens are too incomplete for that ratio to be calculated). The large, compound and stalked eyes likewise do not show any striking differences among the available specimens on which eyes are preserved (Figs. 3, 8).

The tail appendages are positioned on the terminal trunk segment, and are specialized for swimming. In specimen SMNS 64880 (*D.b.*) these appendages are embedded in a lateral position, in contrast to conditions in the other specimens in which tail appendages are preserved.

The numbers of head appendages are identical, as are their respective relative lengths. In specimen SMNS 64880 (*D.b.*), appendages ha2 and ha3 are half the length of ha4, and ha5–ha7 are the longest head appendages. This condition can also be observed in specimen NMPWL 1999/4-LS. It is also partly evident in specimens NMPWL 1993/354-LS and NMPWL 1998/150-LS, as far as these are preserved (Fig. 3).

Although there is some uncertainty concerning the total number of trunk segments, segment number is not obviously different between SMNS 64880 (*D.b.*) and other specimens. The trunk appendages are not easy to compare, because only specimen NMPWL 1999/4-LS shows nearly complete preservation. In specimen SMNS 64880 (*D.b.*), only the exopods are preserved.

Due to the numerous concordances of morphological characters among the available specimens, and to the lack of any striking differences, specimen SMNS 64880 (*D.b.*) must be interpreted as a representative of *W. backesi*. Therefore the two species names are formally synonymised here. There are several examples from other arthropods of the Hunsrück Slate that show similar patterns of taphonomically induced variation in a single species, e.g. *Vachonisia rogeri* Kühl et al., 2008; *Bundenbachiellus giganteus* Moore et al., 2008;

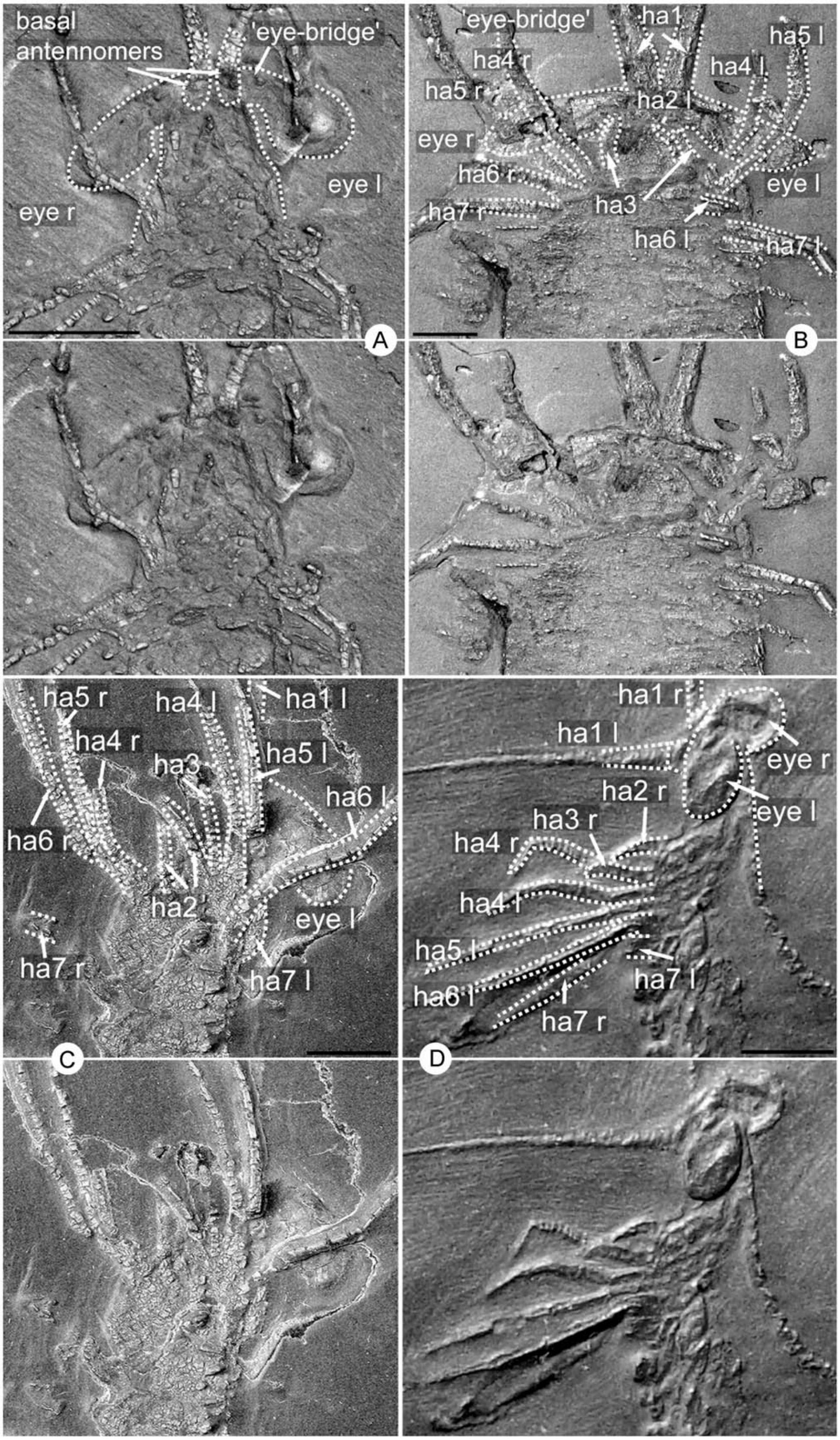

Fig. 8. *Wingertshellicus backesi*, eyes and antennae, photograph pairs with and without explanatory labelling. respectively; dashed lines mark margins of relevant structures; ha = head appendage; l = left, r = right. (A) Specimen NMPWL 1999/4-LS. (B) NMPWL 1993/354-LS. (C) NMPWL 1998/150-LS. (D) SMNS 64880 (*D.b.*). Scales 5 mm.

Dilophaspis lata Hahn, 1990; *Chotecops* (Bartels et al. 1998, p. 133).

Interpretation of morphological characters

Some morphological characters of SMNS 64880 (*D.b.*) are interpreted differently here compared to Haas et al. (2003).

In the five *Wingertshellicus* specimens we studied (including *D.b.*) we found a corresponding series of anterior appendages of the body, ha1–ha7, without any signs of regular postmortal detachment of any additional pair. This provides a reliable basis that the evident set of anterior appendages is the complete one. This stands in contrast to Haas et al.'s (2003) hypothesis of one appendage pair (''mandibles'') and perhaps a second one (''1st maxilla'') having been lost in SMNS 64880 (*D.b.*). Haas et al. (2003) described ha2 as the labium, an interpretation we do not follow. The labium should be placed posterior to the mouth, whereas ha2 in specimen NMPWL 1999/4-LS is positioned a clearly anterior to the mouth opening (Fig. 6D).

None of the specimens shows any remnants or even insertion traces of a monocondylic mandibulatan mandible as postulated in Haas et al. (2003). The gap between the antenna and the remaining head appendages is not a consequence of destruction (Haas et al. 2003); on the contrary, it is a natural 'open space' between those appendages (see specimen NMPWL 1999/4-LS; Figs. 3E, 6B). The suggestion by Haas et al. (2003) that the mandible could have been lost by taphonomic processes is extremely unlikely, as Willmann (2005) has pointed out already. Therefore we conclude that no mandibulatan mandible in a hexapod-like differentiation ever existed.

Haas et al. (2003) postulated a three-segmented thorax with one pair of thoracopods per segment (Table 1). These appendages are reinterpreted as head appendages here, as evidenced by specimens SUE WB (Fig. 4), NMPWL 1999/4-LS (Fig. 6), and indirectly also by SMNS 64880 (*D.b.*) (Fig. 5B, C). In specimen NMPWL 1999/4-LS the appendages are arranged circum-orally. A separation between a head and 'thorax' is not evident, as in specimens SUE WB and SMNS 64880 (*D.b.*) (Figs. 4–6). Therefore, any similiarity in number and length of the appendages in *Devonohexapodus* and Hexapoda is superficial and accidental, and does not allow the postulation of a close phylogenetic relationship between those taxa.

The appendages described by Haas et al. (2003) as uniramous segmented leglets (Fig. 5D, E) are now interpreted as exopods (outer rami of biramous appendages). Segmentation of those 'leglets' is not evident, e.g. in the radiograph of that specimen (Fig. 5D, E). On the other hand, these exopods are evident on every other available specimen (Fig. 7).

Two posterior exopods were described as clearly different and more specialised (gonopods) compared to the other trunk appendages (Haas et al. 2003). Figs. 3D, 5E and 7 show that no specialisation of these appendages is evident. The posterior direction of these appendages is an accidental consequence of the transport and embedding process of the individual, rather than evidence of any kind of morphological specialisation. Moreover, the preceding exopods point in different directions (Fig. 7E). Due to their embedding position the last two exopods appear more slender than the others.

The terminal, fluke-like trunk appendages (tail) of SMNS 64880 (*D.b.*) were interpreted as hexapod cerci in Haas et al. (2003). This interpretation is not supported by the fossil. As in all other specimens, the tail is divided to form a paired, fluke-like appendage, which shows no sign of segmentation (Fig. 9). The wrinkled surface, as described in Haas (2005), does not provide any indication of segmentation, which is also evident in specimen SMNS 64880 (*D.b.*) (Fig. 5E). The surface structure is a result of compression and probably slight torsion during the lateral embedding of the animal, whereas the currently visible surface originated when the slab was split. The flagellate structures are not preserved in specimen SMNS 64880 (*D.b.*).

Discussion

Wingertshellicus backesi – a stem lineage representative of the Hexapoda?

The discussion of the origin of the Hexapoda has been highly controversial, which is on the one hand related to the phylogenetic relationships and monophyly of the Hexapoda, on the other hand linked to the question of their marine or terrestrial origin. The oldest fossil insects are of Devonian age, known from three different fossil Lagerstätten. The Lower Devonian Rhynie Chert (Pragian; older than Hunsrück Slate) is famous, among other reasons, for the oldest springtails (Collembola) *Rhyniella praecursor*, Hirst & Maulik, 1926 and bristletails (Archaeognatha) *Leverhulmia mariae*, Fayers & Trewin, 2005. Engel and Grimaldi (2004) redescribed Ectognatha from the Lower Devonian Rhynie Chert. Archeognatha have been described also from the Lower Devonian Gaspé Lagerstätte in Québec, Canada (Labandeira et al. 1988). In each case the depositional environment was identified as terrestrial.

The origin of hexapods in the marine realm indicated by a fossil specimen was first postulated by Haas et al. (2003). These authors discussed the phylogenetic

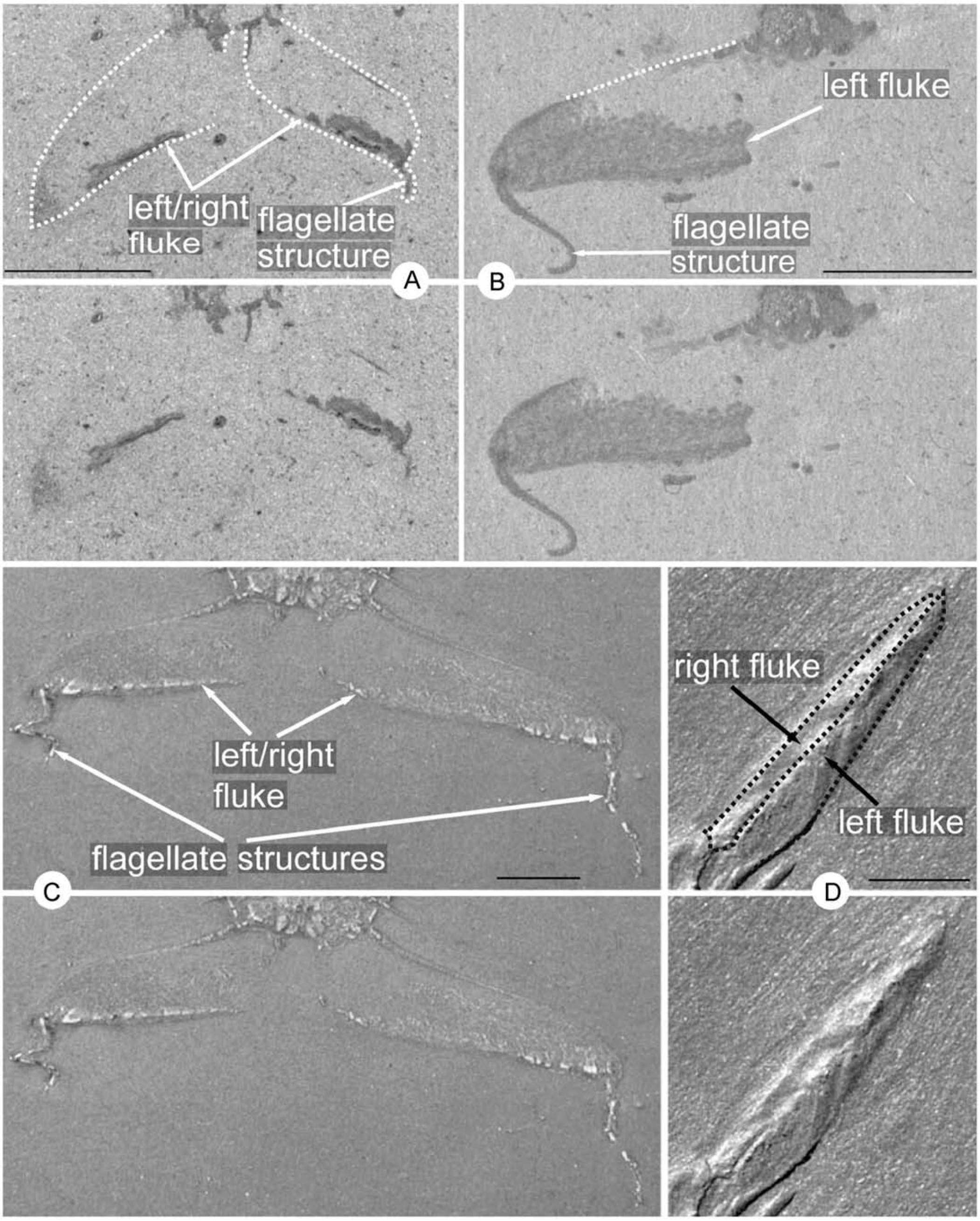

Fig. 9. *Wingertshellicus backesi*, terminal trunk appendages ('tails'), photograph pairs with and without explanatory labelling. respectively; dashed lines mark margins of relevant structures. (A) Specimen NMPWL 1999/4-LS. (B) NMPWL 1993/354-LS. (C) SUE WB. (D) SMNS 64880 (*D.b.*). Scales 5 mm.

position of *Wingertshellicus backesi* as a stem-lineage representative of hexapods only in the light of the 'Atelocerata' or 'Tracheata' concept, following the traditional opinion of most morphologists that the Hexapoda are either the sister group of the Myriapoda or a myriapod subgroup (for summaries, see Willmann 2003 and Bitsch and Bitsch 2004). Haas et al. (2003) did not consider other hypotheses such as the Pancrustacea or Tetraconata concept that suggest a monophyletic Crustacea and Hexapoda clade excluding the Myriapoda, based on morphological, developmental, and molecular evidence (e.g. Zrzavý and Stys 1997; Dohle 2001; Schram and Jenner 2001; Richter 2002; Nardi et al. 2003; Mallatt et al. 2004; Klass 2007). But not only are the phylogenetic relationships of Hexapoda still a matter of discussion, their monophyly (discussed by, e.g., Hennig 1969; Kristensen 1998; Willmann 1998; Ax 1999; Klass and Kristensen 2001; Willmann 2003; Bitsch and Bitsch 2004; Mallatt et al. 2004) also has been doubted repeatedly (e.g. Regier and Shultz 1997, 2001; Giribet et al. 2001; Nardi et al. 2001, 2003; Carapelli et al. 2005; see Klass 2007). Particularly the morphological evidence for monophyly of Hexapoda is weak (Klass 2007), not least because the taxon's sister-group relationships remain unclarified.

According to Haas et al. (2003), the main synapomorphies which led these authors to characterise *W. backesi* as a stem-lineage representative of the 'Atelocerata' (1) or Hexapoda (2–7) are: (1) The reduction of the second antenna; (2) the presence of a labium; (3) the subdivision of the post-cephalic trunk into thorax and 'abdomen'; (4) slender and stenopodial thoracopods with no more than six podomeres; (5) an 'abdomen' with short, stout leglets; (6) terminal structures similar to cerci; and (7) a specialisation of the posterior trunk appendages into gonopods.

Apart from the fact that there is no consensus on whether these characters are important enough to substantiate the monophyly of Hexapoda or generally too weak (e.g. Klass and Kristensen 2001; Willmann 2003, 2005; Bitsch and Bitsch 2004; Klass 2007), the reinvestigation of the fossil material presented here shows that these presumed 'hexapodan' auapomorphies either do not exist or are over- or misinterpretations of poorly preserved fossil structures. The absence of the second pair of antennae (1) need not be a consequence of reduction in the light of the 'Ateloceratan' concept (Haas et al. 2003). The existence of only one pair of antennae is a basic character of most stem-lineage representatives of the Euarthropoda. The presence of a labium (2), mandibles or maxillae in a Hexapoda- or even Mandibulata-like differentiation is not evident in the available fossil material described here, nor is a subdivision of the trunk in thorax and abdomen (3). Three pairs of slender and stenopodial legs (4) are identified in the present investigation as additional head appendages with an unclear number of podomeres. The uniramous leglets (5) are now identified as unsegmented exopods of the biramous trunk appendage, which is a plesiomorphic character state again, already developed in stem-lineage representatives of the Euarthropoda (e.g. Budd 2001, 2002; Waloszek et al. 2007; Zhang and Briggs 2007). The terminal structures (6) are not interpreted as similar to hexapodan cerci here. Within the Hexapoda cerci are appendages of the eleventh abdominal segment (the tenth in Diplura; missing in Collembola and Protura) (Willmann 2003; Klass 2007). In *W. backesi* the terminal structures are appendages of approximately the fortieth trunk segment. Even if a reduction in trunk segment number from 40 to 11 is assumed, these terminal, fluke-like structures are clearly locomotory appendages for swimming in a marine environment. Moreover, cerci are probably not an equivocal ground plan character of the Hexapoda (e.g. Willmann 2003; Klass 2007). Terminal 'tail' structures are common in early euarthropods already. A specialisation of two posterior trunk appendages into gonopods (7) again is not evident in the reinvestigated fossil material. These appendages are interpreted in the present work as exopods of the biramous trunk appendages.

Hence, the phylogenetic position of *W. backesi* as a stem-lineage representative of the Hexapoda or even of the 'Atelocerata' is rejected, and all implications derived from that assumption (e.g. independent terrestrialisation and marine origin of Hexapoda, large body size of stem-lineage hexapods) are considered as unfounded, but independent terrestrialisation in Hexapoda and Myriapoda would be the consequence, if the Tetraconata concept is followed.

Phylogenetic position of *Wingertshellicus backesi*

As pointed out above, *W. backesi* can be ruled out as a member of the 'Atelocerata' or even of the crown group Mandibulata. Additionally, no character supports close relationship to the Chelicerata or their crown group.

It is not clear whether the head appendages are truly uniramous, some uncertainty about the number of head appendages remains, and the presence of a head shield also is equivocal. *Wingertshellicus backesi* has (1) an organisation of the body in two tagmata (head and trunk), (2) one pair of stalked compound eyes, (3) one pair of uniramous and slender antennae, (4) a ventral mouth opening, (5) undifferentiated head appendages, (6) about 40 trunk segments with (7) homonomous biramous appendages, and (8) a specialisation of the terminal trunk appendage as a fluke-like tail.

Compound stalked eyes (2), tail appendages (8), and biramous trunk appendages (7) are plesiomorphic characters that developed before the stem lineage of the Euarthropoda (sensu Zhang and Briggs 2007, and Budd 2002). The ventral position of the mouth opening (4), another plesiomorphic character, already developed in anomalocarid-like taxa (Zhang and Briggs 2007), but has also been regarded as a basic euarthropod character (Budd 2001, 2002). The high number of segments (6) and the 'long' body, the tagmosis into head and trunk (1), as well as the uniramous pair of antennae (3) are features that were most probably already characteristic for the arthropod ground pattern (Bergström and Hou 2003; Waloszek et al. 2005, 2007).

Wingertshellicus backesi has no special characters that allow a solid conclusion as to its phylogenetic affinities at this time. All we can gather at the moment is that this organism displays a series of plesiomorphic characters that do not contradict a position as a stem-lineage representative of the Euarthropoda, or at least exclude it from the crown groups of Chelicerata and Mandibulata.

Acknowledgements

The specimens studied were kindly lent to us by the Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz, the State Museum of Natural History in Stuttgart, and by Wouter Suedkamp in Bundenbach. We thank Dr. Klaus-Dieter Klass (Museum für Tierkunde, Dresden) for fruitful suggestions on an earlier draft of the manuscript, Prof. Derek E.G. Briggs (Yale University, New Haven) and PD Dr. Andreas Maas (Ulm University) for helpful comments on the manuscript, and Georg Oleschinski (Institute for Palaeontology, Bonn) for photographs and radiographs. Funding was provided by the DFG (project No. RU 665/5-1).

References

Allison, P.A., Briggs, D.E.G., 1991. The taphonomy of soft-bodied animals. In: Donovan, S.K. (Ed.), The Processes of Fossilisation. Columbia University Press, New York, pp. 120–140.

Ax, P., 1999. Das System der Metazoa, Bd. II. Gustav Fischer, Stuttgart.

Bartels, C., 1995. Die unterdevonischen Dachschiefer von Bundenbach. In: Weidert, W.K. (Ed.), Klassische Fundstellen der Paläontologie, Vol. 3. Goldschneck, Weinstadt, pp. 38–55.

Bartels, C., Blind, W., 1995. Röntgenuntersuchung pyritisch vererzter Fossilien aus dem Hunsrückschiefer (Unter-Devon, Rheinisches Schiefergebirge). Metalla 2, 79–100.

Bartels, C., Briggs, D.E.G., Brassel, G., 1998. The Fossils of the Hunsrück Slate – Marine Life in the Devonian. Cambridge University Press, New York.

Bartels, C., Lutz, H., Blind, W., Opel, A., 1997. Schatzkammer Dachschiefer. Die Lebenswelt des Hunsrückschiefer-Meeres. Landessammlung für Naturkunde Rheinland-Pfalz, Mainz und Deutsches Bergbau-Museum, Bochum.

Bergström, J., Briggs, D.E.G., Dahl, E., Rolfe, W.D.I., Stürmer, W., 1987. *Nahecaris stürtzi*, a phyllocarid crustacean from the Lower Devonian Hunsrück Slate. Paläont. Z. 61, 273–298.

Bergström, J., Hou, X.-G., 2003. Arthropod origins. Bull. Geosci. 78, 323–334.

Bitsch, C., Bitsch, J., 2004. Phylogenetic relationships of basal hexapods among the mandibulate arthropods: a cladistic analysis based on comparative morphological characters. Zool. Scr. 33, 511–550.

Briggs, D.E.G., Bartels, C., 2001. New arthropods from the Lower Devonian Hunsrück Slate (Lower Emsian, Rhenish Massif, Western Germany). Palaeontol. 44, 275–303.

Briggs, D.E.G., Raiswell, R., Bottrell, S.H., Hatfield, D., Bartels, C., 1996. Controls of the pyritization of exceptionally preserved fossils: an analysis of the Lower Devonian Hunsrück Slate of Germany. Am. J. Sci. 296, 633–663.

Budd, G.E., 2001. Tardigrades as 'stem-group arthropods': the evidence from the Cambrian fauna. Zool. Anz. 240, 265–279.

Budd, G.E., 2002. A palaeontological solution to the arthropod head problem. Nature 417, 271–275.

Carapelli, A., Nardi, F., Dallai, R., Boore, J.L., Liò, P., Frati, F., 2005. Relationships between hexapods and crustaceans based on four mitochondrial genes. In: Koenemann, S., Jenner, A. (Eds.), Crustacea and Arthropod Relationships. Taylor and Francis, New York, pp. 295–306.

Dohle, W., 2001. Are the insects terrestrial crustaceans? – A discussion of some new facts and arguments and the proposal of the proper name 'Tetraconata' for the monophyletic unit Crustacea + Hexapoda. In: Deuve, T. (Ed.), Origin of the Hexapoda. Ann. Soc. Entomol. Fr. 37, 85–103.

Engel, M.S., Grimaldi, D.A., 2004. New light shed on the oldest insect. Nature 427, 627–630.

Fayers, S.R., Trewin, N.H., 2005. A hexapod from the Early Devonian Windyfield Chert, Rhynie, Scotland. Palaeontol 48, 1117–1130.

Giribet, G., Edgecombe, G.D., Wheeler, W.C., 2001. Arthropod phylogeny based on eight molecular loci and morphology. Nature 413, 157–161.

Glenner, H., Thomson, P.F., Hebsgaard, M.B., Sørensen, M.V., 2006. The origin of insects. Science 314, 1883–1884.

Grimaldi, D., Engel, M.S., 2005. Evolution of the Insects. Cambridge University Press, New York.

Haas, F., 2005. *Devonohexapodus bocksbergensis* is a stem group hexapod – a reply to R. Willmann. Org. Divers. Evol. 5, 315–316.

Haas, F., Waloszek, D., Hartenberger, R., 2003. *Devonohexapodus bocksbergensis*, a new marine hexapod from the Lower Devonian Hunsrück Slate, and the origin of Atelocerata and Hexapoda. Org. Divers. Evol. 3, 39–54.

Harzsch, S., 2004. Phylogenetic comparison of serontonin-immunoreactive neurons in representatives of the Chilopoda, Diplopoda, and Chelicerata: implications for arthropod relationships. J. Morphol. 259, 198–213.

Hennig, W., 1969. Insect Phylogeny. Academic Press, New York.

Klass, K.-D., 2007. Die Stammesgeschichte der Hexapoden: eine kritische Diskussion neuerer Daten und Hypothesen. Denisia 66, 413–450.

Klass, K.-D., Kristensen, N.P., 2001. The ground plan and affinities of hexapods: recent progress and open problems. Ann. Soc. Entomol. Fr. 37, 265–298.

Kristensen, N.P., 1998. The groundplan and basal diversification of the hexapods. In: Fortey, R.A., Thomas, R.H. (Eds.), Arthropod Relationships. Assoc. Spec. Vol. 55. Chapman and Hall, London, pp. 281–293.

Kühl, G., Bergström, J., Rust, J., 2008. Morphology, palaeobiology and phylogenetic position of *Vachonisia rogeri* (Arthropoda) from the Lower Devonian Hunsrück Slate (Germany). Palaeontogr. B 286, 123–157.

Labandeira, C.C., Beall, B.S., Hueber, F.M., 1988. Early insect diversification: evidence from a Lower Devonian bristletail from Québec. Science 242, 913–916.

Mallatt, J.M., Garey, J.R., Shultz, J.W., 2004. Ecdysozoan phylogeny and Bayesian inference: first use of nearly complete 28S and 18S rRNA gene sequences to classify the arthropods and their kin. Mol. Phyl. Evol. 31, 178–191.

Moore, R.A., Briggs, D.E.G., Bartels, C., 2008. The arthropod *Bundenbachiellus giganteus* from the Lower Devonian Hunsrück Slate, Germany. Paläont. Z. 82, 31–39.

Nardi, F., Boore, J.L., Carapelli, A., Dallai, R., Frati, F., 2003. Response to comment on "Hexapod origins: monophyletic or paraphyletic?". Science 302, 1482.

Nardi, F., Carapelli, A., Fanciulli, P.P., Dallai, R., Frati, F., 2001. The complete mitochondrial DNA sequence of the basal hexapod *Tetrodontophora bielanensis*: evidence for heteroplasmy and tRNA translocation. Mol. Biol. Evol. 18, 1293–1304.

Pisani, D., Poling, L., Lyons-Weiler, M., Hedges, S.B., 2004. The colonialization of land by animals: molecular phylogeny and divergence times among arthropods. BMC Biol 2, 1–10.

Regier, J.C., Shultz, J.W., 1997. Molecular phylogeny of the major arthropod groups indicates polyphyly of crustaceans and a new hypothesis for the origin of hexapods. Mol. Biol. Evol. 14, 902–913.

Regier, J.C., Shultz, J.W., 2001. Elongation Factor-2: a useful gene for arthropod phylogenetics. Mol. Biol. Evol. 20, 136–148.

Regier, J.C., Shultz, J.W., Kambic, R.E., 2004. Phylogeny of basal hexapod lineages and estimates of divergence times. Ann. Entomol. Soc. Am. 97, 411–419.

Richter, S., 2002. The Tetraconata concept: hexapod-crustacean relationships and the phylogeny of Crustacea. Org. Divers. Evol. 2, 217–237.

Rust, J., 2007. Die Bedeutung von Fossilien für phylogenetische Rekonstruktionen. Species Phylog. Evol. 1, 75–87.

Schram, F.R., Jenner, R.A., 2001. The origin of Hexapoda: a crustacean perspective. Ann. Soc. Entomol. Fr. 37, 243–264.

Seilacher, A., 1962. Form und Funktion des Trilobiten-Dactylus. Paläont. Z., H. Schmitz Festband, 218–227.

Waloszek, D., Chen, J., Maas, A., Wang, X.-Q., 2005. Early Cambrian arthropods – new insights into arthropod head and structural evolution. Arthropod Struct. Devel. 34, 189–205.

Waloszek, D., Maas, A., Chen, J., Stein, M., 2007. Evolution of cephalic feeding structures and the phylogeny of Arthropoda. Palaeogeogr., Palaeoclimatol., Palaeoecol. 254, 273–287.

Willmann, R., 1998. Advances and problems in insect phylogeny. In: Fortey, R., Thomas, R.H. (Eds.), Arthropod Relationships. Chapman and Hall, London, pp. 269–281.

Willmann, R., 2003. Entstehung und Grundplanvertreter der Insecta. In: Dathe, H.H. (Ed.), Wirbellose Tiere – 5. Teil: Insecta. Spektrum Akademischer Verlag, Heidelberg, pp. 9–14.

Willmann, R., 2005. Reinterpretation of an alleged marine hexapod stem-group representative. Org. Divers. Evol. 5, 199–202.

Zhang, X.-L., Briggs, D.E.G., 2007. The nature and significance of the appendages of *Opabinia* from the Middle Cambrian Burgess Shale. Lethaia 40, 161–173.

Zrzavý, J., Stys, P., 1997. The basic body plan of arthropods: insights from evolutionary morphology and developmental biology. J. Evol. Biol. 10, 353–367.