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Devonohexapodus bocksbergensis, a new marine hexapod from the Lower Devonian Hunsrück Slates, and the origin of Atelocerata and Hexapoda

Fabian Haas^{1,*}, Dieter Waloszek¹, Rolf Hartenberger²

¹ Section for Biosystematic Documentation, University of Ulm, Germany

² Oberbrombach, Germany

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Abstract

We describe a new arthropod (approximately 75 mm long) from the Lower Devonian (Lower Emsian) Hunsrück Slates near Bundenbach, western Germany. The specimen is from an isolated piece of rock found on the quarry dump, precluding precise resolution of stratigraphic age. The Hunsrück Slates are marine sediments with a rich fauna of exclusively marine taxa, suggesting that our fossil was also marine. The animal has a small head with large compound eyes and long, filiform, myocerate antennae. Its trunk is divided distinctly into a thorax with three segments and three pairs of slender legs, and a post-thoracic domain composed of 35–40 limb-bearing segments of which the anteriormost are paired, stout, and ventrally-oriented leglets; the three ultimate limb-bearing segments bear longer, posteriorly-oriented and apparently specialised appendages. The overall appearance of the new form is reminiscent of Archaeognatha or Odonata. It is interpreted as a representative of the Hexapoda because of the possession of a three-segmented thorax and three pairs of legs that are clearly distinct from the posterior set. The large number of leg-bearing post-thoracic segments discriminates it from the Insecta, which possess 11 “abdominal” segments maximally, originally also leg-bearing. The formal systematic classification of the organism is: (Hexapoda (*Devonohexapodus bocksbergensis* + Insecta (“entognaths” + Ectognatha))). The morphology of the fossil and its environment suggest that the hexapody of hexapods did not evolve as an adaptation to terrestrial locomotion, but was already developed in the marine habitat. No terrestrial arthropods have changed their original tagmosis for biomechanical reasons, for example, no “myriapods” have reduced their leg numbers or modified their trunk to evolve a thorax and abdomen similar to insects. Walking exclusively on uniramous prosomal legs in the Chelicerata also occurred well before terrestrialization of this other euarthropodan group. It is not unlikely that the last common ancestor of the Hexapoda was large and that the small size of extant “entognaths” evolved due to reduction in their stem lineage. Being marine, the new fossil also has considerable impact on hypotheses about the early evolution of Atelocerata (“myriapods” + Hexapoda). For example, if their last common ancestor was aquatic, terrestrialization took place at least twice and tracheal breathing probably evolved independently in both taxa after terrestrialization.

Key words: phylogeny, evolution, Insecta, tagmosis, palaeo-environment, habitat

Introduction

The approximately 390 million years old, Lower Devonian (Lower Emsian) Hunsrück Slates are deposits of marine, fine-grained mudstones that occur in the Hunsrück area near Bundenbach, Gemünden and Kaub (Dachstein-Schiefer), western Germany (Fig. 1). These slates have yielded beautifully preserved fossils of more than 200 species. The range spans from ichnofossils,

protists, plants and spores to a wide range of Metazoa including poriferans, cnidarians, molluscs, arthropods, brachiopods, echinoderms and vertebrates. Most of these species have not been recorded elsewhere.

Accordingly, Hunsrück Slate has become one of the most important fossil Lagerstätten of the Palaeozoic and has attracted many authorities in this field (particularly Bartels et al. 1998, and references therein). The deposits indicate a shallow-water environment of deposi-

*Corresponding author: Fabian Haas, Section for Biosystematic Documentation, University of Ulm, Helmholtzstraße 20, D-89081 Ulm, Germany; e-mail: haas.smns@naturkundemuseum-bw.de

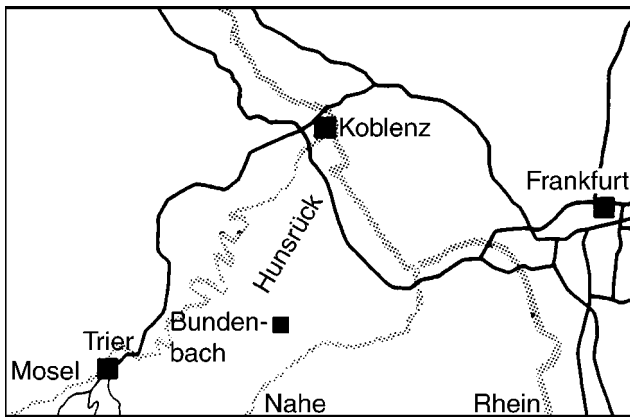


Fig. 1. Map of the Hunsrück area, Germany, with locality of the find.

tion, but in an offshore habitat, closer to the shelf margin of the northern continent (Bartels 1994). At least in part, preservation has been interpreted as being caused by occasional submarine landslides (turbiditic events) that buried benthic organisms under thick layers of mud (similar to the interpretation of sites of “Burgess Shale” type preservation, Briggs & Bartels 2001). Microbes may have mediated decay, while pyritisation caused the delicate preservation of the fossils. This has made it possible to study Hunsrück fossils using X-rays, first introduced around 1906, and extensively adopted as a research technique by W. M. Lehmann in the early 1930s and, later, by W. Stürmer (Blind 1995). Famous examples include pictures of trilobite legs and belemnite bodies (Stürmer 1969, Stürmer & Bergström 1973). Most of the fossils have been collected from residues of the excavation process, such as on quarry dumps, which makes stratigraphy, dating and palaeo-ecology difficult. A large part of the fossiliferous interval of the Hunsrück Slate has been dated as Lower Emsian (*Anetoceras* and *Mimagoniatites* genozones; see Struve 1985 and Weddige 1996).

With respect to Euarthropoda (sensu Waloszek 1999), the Hunsrück Slate has hitherto yielded the only fossil representative of Pycnogonida (for a much older, Cambrian pycnogonid from the Swedish “Orsten” see Waloszek & Dunlop 2002). Many trilobite species have also been described, some with exceptionally well-preserved limbs (Bergström & Brassel 1984), as well as representatives of the Eurypterida and Xiphosura (e.g., *Weinbergina opitzi* Richter & Richter 1929; redescription of soft parts in Stürmer & Bergström 1981) and the phyllocarid crustacean *Nahecaris stuertzi* Jaekel, 1921 (redescription in Bergström et al. 1987). Several species have also been found whose assignment to any larger euarthropod clade is still questionable. These include *Cheiloniellon calmani* Broili, 1932, *Mimetaster hexagonalis* (Gürich, 1931) (Birenheide 1971), *Vachonisia rogeri* (Lehmann, 1955) (redescriptions of soft parts in Stürmer

& Bergström 1976, 1978) and, recently, four new one-centimetre-long forms (Briggs & Bartels 2001).

Two decades of collecting effort and preparation experience in the Hunsrück Slates (RH) (see also Hartenberger 1995) have led to the discovery of a single specimen of a new unknown arthropod from one of the slate dumps. Herein we describe the specimen as a new arthropod genus and species. Its similarities with insects are striking, and affinity to the Hexapoda is discussed in the light of its marine habitat and the four new arthropods of questionable assignment described by Briggs & Bartels (2001; two of them formerly reported briefly by Bartels 1995 and Blind 1995). Together, these fossils have considerable impact on existing hypotheses about the early evolution and terrestrialization of Atelocerata and Hexapoda/Insecta.

Two taxa of (at least) disputed monophyly, the Myriapoda versus “myriapods” and Entognatha versus “entognaths”, are mentioned throughout the text. As our description of the new fossil does not contribute any new information on the systematic status of either taxon, we use “myriapods” and “entognaths” for convenience. For a discussion of the relationships of the “myriapods” we refer the reader to recent papers by Ax (1999), Edgecombe & Giribet (2002), Kraus (2001), and citations therein; the relationships of “entognaths” are discussed in Bitsch & Bitsch (1998), Koch (2001), Kristensen (1998) and Kukulová-Peck (1991).

Material and methods

Geology and preservation

The Hunsrück Slates were deposited during the Devonian, from the end of the Pragian Series to the start of the Lower Emsian, and are therefore approximately 350 million years old. They are composed of mudstones deposited in offshore but rather shallow marine conditions. During deposition the area was subdivided into various basins and ridges. Occasional evaporites indicate temporary and localised dry or mudflat conditions with changing currents and tidal activity (Bartels 1994). The Hunsrück Slates are the product of erosion of the Old Red continent, the coast of which ran approximately 150–200 km north of the area of deposition. Hunsrück Slates were mined extensively in the past. Until recently, one quarry, Eschenbach-Bocksberg, was still active and produced new finds, but this was closed at the end of 1999.

During the Carboniferous, sediments in the Hunsrück area were subject to severe folding and faulting due to the Variscan orogeny (a consequence of the collision of northern Europe with the African plate). Sediment was metamorphosed, leading to the formation of slaty cleavage. In general, fossils are scarce in slates and occur only, if at all, in characteristic layers. Usually the cleavage planes along which the slates split have a more or less pronounced angle to the original sedimentary surface. Only in rare cases do the slates split parallel to the origi-

nal sedimentary surface. Such slabs are called “Plattenstein” and occur in the Bundenbach area where the new fossil was found (Fig. 1).

The sediments are indicative of a soft-bottom environment that differed locally, offering a wide variety of habitats, particularly for benthic and mud-dwelling organisms. Hunsrück Slates are broadly similar to the slates of the Rheinisches Schiefergebirge where hard-part preservation is predominant.

For at least some of the Hunsrück Slates, a taphonomic situation similar to the Canadian Burgess Shale “konservat-lagerstaetten” has been proposed: burial of the organisms by submarine turbidites. Under low-oxygen to anoxic conditions, a change of organic matter into pyrite occurred, while formation of sulphuric acid may have been responsible for a decalcification of skeletal hard parts. Plant fossils are very rare, with the exception of spores which are assumed to have drifted far offshore and are not integral to understanding the environment and habitats of the Bundenbach Sea (for details see Bartels 1994). Thus, there is no basis to assume a terrestrial origin of any of the Hunsrück Slate animals or terrestrial environmental conditions from the plant fossil record. The species probably lived in a brackish (indicated by some pisciform vertebrate fossils) to fully marine environment (indicated by poriferans, cnidarians, molluscs, arthropods, worm-like forms, other pisciform vertebrates). Most of the taxa are known exclusively from marine environments, such as brachiopods and echinoderms.

Preparation and documentation

The material consists of a single specimen and its counterpart on two slabs cut from a larger piece of slate. The surrounding parts have regrettably been lost, thus no further splitting of shale close to the animal could be undertaken. The rock was

prepared (RH) using fine needles, steel tools and a scalpel, under water where details are best seen due to differences in colour. Ground material was periodically removed with a wet cloth.

The specimen was examined using stereo microscopy and camera lucida equipment, and digitally imaged using a 24-bit flatbed scanner at resolutions ranging from 600 to 1200 dpi to permit image enhancement in the computer. Additional details were photographed using a Polaroid IMC digital camera mounted on a Leica photo stereomicroscope. Occasionally, the fossil was submerged in alcohol for photography. X-ray images were taken at the Palaeontological Institute, University of Bonn, with a Radifluor 120 radiographic inspection system on AGFA Strukturix D2 FW film at 70 kV, 3 mA, and exposed for 30 seconds, at a working distance of 25 cm. X-ray stereo pairs were obtained by tilting the fossil through approximately 5° about its long axis.

Terminology and nomenclature

In general, we apply standard entomological terminology but also use a more general crustacean-arthropod terminology (mainly as introduced by Waloszek 1993) in cases where it facilitates wider comparability. For example, the “abdomen” of insects is composed of the segments that follow the three-segmented thorax. It has long been recognised that the insect abdomen originally bore legs and the present legless condition is clearly secondary. Thus, the “abdomen” (i.e. the post-thoracic trunk) of Hexapoda is not homologous to the primarily apodous “abdomen” of entomostracan Crustacea (for a detailed discussion of tagmosis in Crustacea see Waloszek & Müller 1998, Ax 1999). Indeed, leglets are known from most early palaeopteran insects, such as Diaphanopteroidea (Kukalová-Peck & Brauckmann 1990). Owing to the differ-

Table 1. Abbreviations used in figures and text

Abbreviation	Full spelling
ABD	“abdomen” (traditional term for the post-thoracic body of Hexapoda)
abdl	“abdominal” limbs = leglets = limbs of post-thoracic trunk
ant	antenna = first limb of euarthropod head = 1 st antenna of Crustacea; antennula (not to be mismatched with the antenna) = second limb = 2 nd antenna of Crustacea
ce	cercus / cercopod(s) = limb(s) of the last ‘abdominal’ segment, irrespective of its specific segment number (in extant insects on their 11 th segment)
gop	gonopods = modified leglets of 3 rd and 4 th penultimate “abdominal” segment, resp. 8 th and 9 th in Ectognatha
H	head, cephalon
lab	labium = 5 th head limb of Insecta and Eucrustacea, but developed as a maxilla = 2 nd maxilla (mx2) only in certain in-group Eucrustacea, otherwise unspecialised; also = 1 st trunk limb of Euarthropoda (which have only 4 head limbs: antennae + 3 pairs of limbs)
mx2	see labium
TH	thorax (= anterior part of trunk, composed of three leg-bearing segments in Hexapoda)
thp	thoracopods (= uniramous legs) of the three thoracomeres in Hexapoda
TR	post-thoracic body = “abdomen” of insects (originally leg-bearing); more generally: trunk = all of post-cephalic body of arthropods (whether uniform or tagmatized)

ence of meaning between Hexapoda and other Arthropoda, the term “abdomen” is used informally and set in single quotation marks. Furthermore, we prefer the taxon name *Atelocerata* Heymons, 1901, over *Tracheata* Lang, 1888, because the latter originally included some arachnids, onychophorans, “myriapods” and insects (Edgecombe, pers. comm. 2000).

Systematics

Devonohexapodus bocksbergensis n. gen. n. sp.

Etymology

The generic name combines “Devono”, referring to the geological age of the specimen, and “hexapodus”, referring to the distinctive three-segmented post-cephalic body domain with three pairs of long legs that are indicative of close relationships to the Hexapoda. The species name is derived from Bocksberg hill in the area where the fossil was found.

Type locality and stratum

Found in a piece of rock (“Iesestein”) collected from a slate dump at the Eschenbach-Bocksberg quarry, “Eschenbacher Zug” stratum.

Type material

Limited to the holotype specimen, consisting of the part (the more completely preserved side, described below in detail) and counterpart (with few remains of the fossil attached; Fig. 2). Both slabs are in the collections of the Staatliches Museum für Naturkunde Stuttgart, Baden-Württemberg, Germany, deposited under catalogue number SMNS64880.

Combined diagnosis

Body differentiated into three tagmata, the head, thorax and post-thoracic trunk (“abdomen”). Head small with large, globular, sub-oval (most likely faceted) eyes leaving little of the remaining head visible. Antennae long, filiform, myocerate, multi-annulate and originating rostrally of the eyes. Thorax comprising three segments, each with a pair of long, slender, uniramous legs, first pair two-thirds the length of the posterior two. Post-thoracic trunk consisting of approximately 35 segments, cigar-shaped and gently tapering towards posterior. All tergites smooth and lacking lateral epimeric extensions; no overlapping of tergites. Each “abdominal” segment bears a pair of stout leglets, less than one third the length of, and much thicker than, the thoracopods. Last three pairs of “abdominal” appendages differentiated and orientated to posteri-

or. First two pairs spine-like, ultimate pair thick, directed to posterior, elongate. Length of body: 75 mm; length of head: 5 mm; length of thorax: 10 mm; length of “abdomen” without caudal leglets: 60 mm.

Description

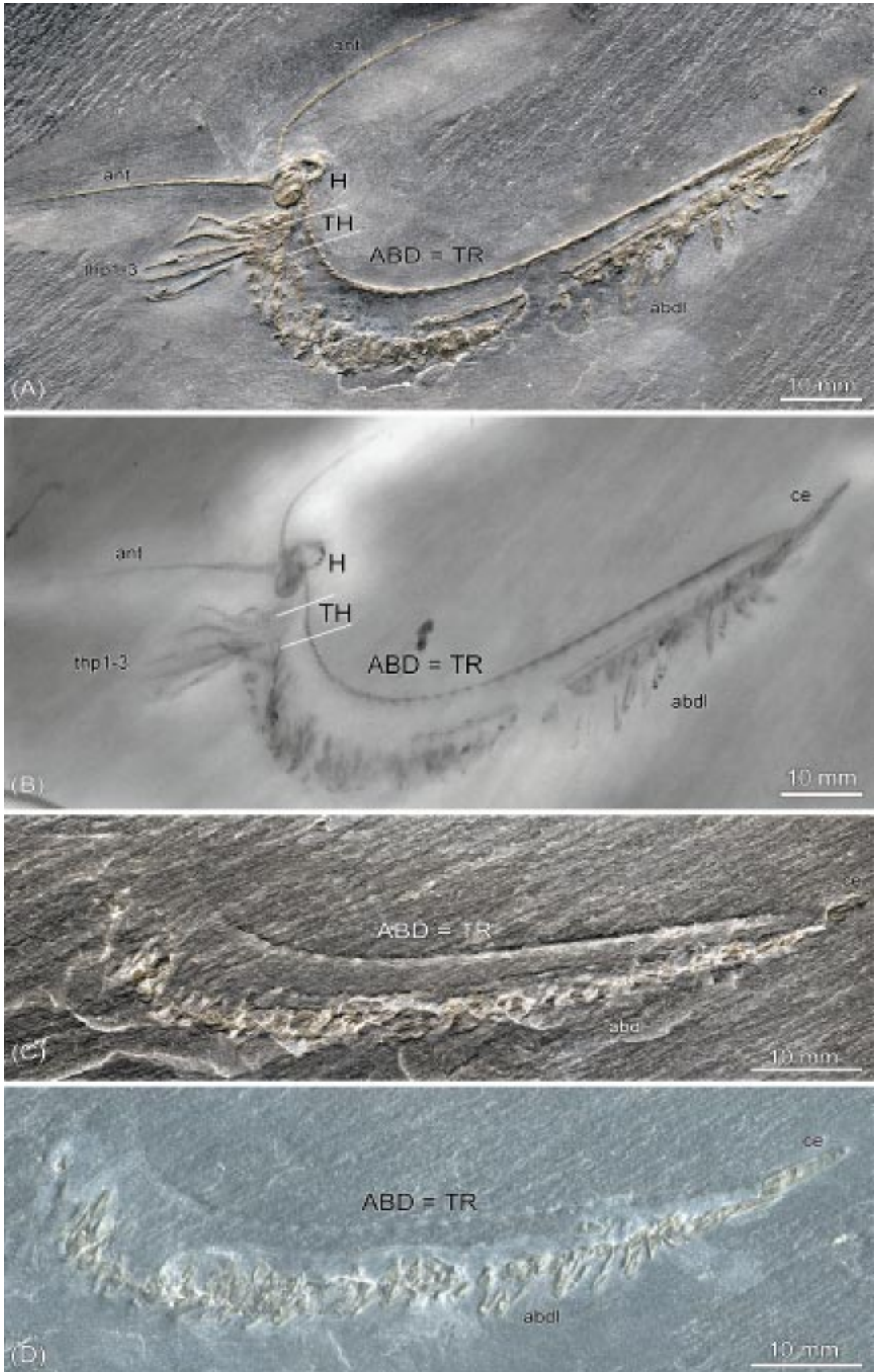
Preservational aspects: The holotype reflects the complete animal in left-lateral view, but part and counterpart differ in their presentation of details. The part depicts most of the left side of the animal from the antennae to the caudal appendages (Fig. 2); this appears to be the original top, cuticular layer. Initially, the counterpart was interpreted as an imprint of the animal (Fig. 2C, D) with only a few cuticular remains adhering, such as a few proximal parts of the leglets and caudal appendages. Further preparation (RH) revealed these structures better than x-ray images.

The anterior end is preserved at a higher level in the sediment than the rest of the body and, at first, this was attributed to post-mortem, taphonomic effects. However, this might also be due to the function of the thoracopods, as discussed below.

Although almost all of the body is preserved in lateral aspect (Fig. 2), the head appears to be directed into the slab and is preserved in a dorso-lateral aspect; the thorax may also be preserved in a similar orientation. The post-thoracic trunk has collapsed laterally in the region of the tergites, most likely due to internal shrinkage and, as a result, loss of volume. Thus, it is difficult to resolve the proximal ends of the leglets. The posterior “abdominal” segments are less affected by shrinkage and show segmental boundaries more clearly (Fig. 3F). Segmental boundaries are hidden by rock in the anterior portion of the “abdomen”. Preparation revealed a second (presumably right) row of leglets and the right cercus, which exhibits some striking wrinkles (Fig. 2C, D). Nevertheless, several of the appendages are well preserved, including the finely segmented myocerate antennae and the labium (mx2), the three pairs of long, uniramous thoracopods, and some of the “abdominal” leglets. The position and orientation of the posteriormost legs is clear, but their shape is poorly resolved (Fig. 2).

Head (Figs 2A, B; 3A, B; 4): No significant head capsule visible behind or between the large eyes. From the preservation of a narrow, unsegmented, cuticular bridge between the eyes and between eyes and trunk, it seems that the ventral head region embracing the mouthparts was destroyed at or after death. The ovoid compound eyes are the largest elements of the head (5 x 3 mm; facets not visible; Fig. 4) and appear to have extended

Fig. 2. *Devonohexapodus bocksbergensis* n. gen. n. sp., full specimen. (A) Part. (B) X-ray image of part. (C), (D) Counterpart, before (C) and after (D) additional preparation. Abbreviations see Table 1. ▶





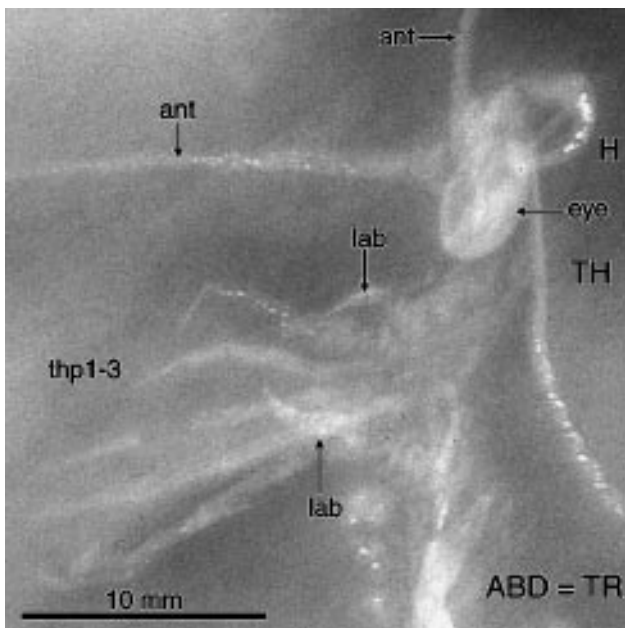


Fig. 4. *Devonohexapodus bocksbergensis* n. gen. n. sp., x-ray image of head, thorax and thoracopods. Abbreviations see Table 1.

latero-dorsally from the body. The myocerate antennae are inserted rostro-ventrally of the eyes, and were possibly positioned in close proximity. The long distal end of the antenna arises from a broad, conical peduncle. About 30 mm of the antennae are preserved in the holotype, consisting of probably more than 40 segments that decrease in diameter only very slightly. The X-ray images (Figs 2C, 4) clearly demonstrate that the head is twisted in such a way that the peduncle of the left antenna has shifted to the right. The eyes and peduncles obscure the pre-oral area. Further ventral cephalic details are not visible on the holotype. One appendage lies in close vicinity of the thorax, is approximately 3 mm long, tapered, and consists of several podomeres the most distal of which is directed inwards like on a grasping leg. X-ray images confirm the presence of at least one pair of legs in the head region, but these are displaced so that they came to lie one behind another. Thus, we interpret this pair of legs as the maxillary head legs (i.e. the labium of hexapods). X-ray images support the view that the ventral part of the head is not preserved.

Thorax (Figs 3A, C, D; 4): Partially laterally compressed, much higher than long. Lateral sclerotic components difficult to discriminate and interpret, most likely very short, smooth tergites without lateral extensions.

There appears to be an increase in height towards the third thoracomere. The bases of the three pairs of thoracopods are located in very close proximity, but their detailed segmentation is obscured proximally. All three legs are uniramous and very slender, increasing in length from 9 mm in the first leg to 11 mm in the two posterior legs. All appear to possess six podomeres. Limb bases seem to be short, with at least three slender tubular podomeres and no tarsomeres. The posteriormost two legs seem to be even thinner than the anterior thoracopods (distinct joints marked in Fig. 3C). The sharp margins of these legs may be an artefact of preservation resulting from collapse of the carcass and accumulation of sediment on either side; this interpretation is confirmed by the x-ray images.

Post-thoracic region (Figs 2; 3D, F): Proximally, the short post-thoracic segments have the same size as the posteriormost thoracic segments. However, they decrease in height caudally to about 5–6 mm, and increase in length to about 2–3 mm; the caudalmost post-thoracic segments are comparable in height and length. Accordingly, the trunk has an overall cigar-shaped profile, though slightly wider anteriorly and with a maximum width between thoracomere 3 and the first few post-thoracic trunk segments. The posteriormost segments slope toward the caudal appendages, giving the outline of the trunk a blunt posterior margin. The segments are easily discerned only in the posterior section where lateral collapse is least pronounced. There are two alternative interpretations for the structures visible along the trunk. One is that the visible depression filled with sediment (Fig. 3F, thick white arrow) is mainly tergal. Accordingly, the ridge running caudally above the limb bases would represent the ventro-lateral tergal margins. The sternites would be seen as overturned with both limb series exhibited. Alternatively, the tergites may have collapsed into the sediment dorso-laterally, and then the trunk would be preserved with the latero-dorsal side up and the left set of limbs uppermost, with the sternite region and the right set of appendages obscured underneath. The weakly preserved structures along the midline of the trunk would thus be interpreted as sternites, and the right limbs as compressed through the tergal cuticle. Following this interpretation, the tergal margin would be close to the base of the limbs, as it is most apparent in the caudal trunk region. The white lines in Figure 3F delimit the segment margins. Derived from the correlation of dorsal humps along the right edge of the fossil and the opposite leglets, *D. bocksbergensis* had no less than 35 post-thoracic segments.

Fig. 3. *Devonohexapodus bocksbergensis* n. gen. n. sp., details. (A) Head and thorax. (B) Eyes and antenna. (C) Thoracopods or legs. (D) Terminalia. (E) Thoracopods and their podomeres. (F) Posterior portion of "abdomen". Abbreviations see Table 1.

The legs associated with the post-thoracic trunk segments are shorter and stouter than those of the thorax, and accordingly are referred to as leglets. These are about the same shape, uniramous, lack claws, and consist of (probably) five to six podomeres. The leglets are approximately 7 mm long, with a maximum diameter of 4 mm. As in the thoracopods, there are no clearly discernible limb bases. The visible joints (Fig. 3F) indicate an inward-outward swing of the distal podomeres. It may be that the distal podomere tapered to a pointed tip, not unlike the distal ends of the legs of proturans or collembolans. However, the distal ends of the legs appear to point into the rock and thus the tips are not visible.

The three terminal pairs of leglets are clearly different from the foregoing series and appear to be more specialised. All are directed to posterior, the ultimate is oriented straight back. The anterior two leglets are spine-like with poorly-developed segmentation; details and size are difficult to detect (Figs 3D, F). The ultimate leglet is approximately 9 mm long, longer than the anterior leglets, considerably thicker and shaped like an elongate cone. The ultimate leglet is paired (Fig 2C and D). Subdivision into podomeres is unclear, although nodes and fine stripes on the surface suggest at least 4–5 subdivisions. X-ray images reveal at least one subdivision at about the middle of the appendages (Fig. 2B). This leglet was probably soft, and so taphonomic collapse caused the wrinkled appearance. The dark central strand apparent on the x-ray images is interpreted as the remains of an internal cavity filling, suggesting that the leglets were rounded in cross-section but collapsed during compaction. The possibility of a flat lateral margin on the ultimate leglet is unlikely.

Discussion

Interpretation and homology of structures

Apart from the prominent eyes there are few features of the head of *Devonohexapodus bocksbergensis* preserved well enough for a detailed comparison. Structures such as the triplet of median eyes seem to be missing on the narrow cuticular bridge between antennal bases and lateral (compound) eyes, as are the clypeus and labrum more ventrally. The ventral head area was twisted and expanded relative to the dorsal region; mouthparts are lost, except for the maxillae (i.e. labium). The maxillae were displaced somewhat during compaction so that one leg in the pair lies in front of the first thoracopod (Fig. 3A), while the other one came to lie between the anterior thoracopods (Fig. 4). The maxillae consist of a few rod-shaped podomeres and are considerably shorter than the three subsequent legs. Their distal ends are curved medially, as in grasping legs (compare Kukalová-Peck's 1991

reconstruction of long and segmented leg-like palps for the maxillae/labium of fossil *Monura* and *Archaeognatha*). Our findings support this reconstruction and long, leg-like palps probably represent the plesiomorphic condition in the Atelocerata. It follows that the mouthparts of *D. bocksbergensis* were ectognathous, in contrast to the only other Devonian hexapod found thus far, the collembolan *Rhyniella praecursor* Hirst & Maulik, 1926 (complete description in Scourfield 1940).

The myocerate antennae are long, slender, and feeler-like (Fig. 3B). Posteriorly there are no traces of a further pair of appendages, suggesting the presence of homologues of the so-called 2nd antennae (appendages of the insect intercalary segment). This contrasts with the structure in the ground pattern of Crustacea where the uniramous first antennae, or antennulae (ant1), have a low number of tubular and seta-bearing articles (setae oriented significantly towards the posterior and used for locomotion and feeding). The biramous second antennae, or antennae (ant2), are composed of a five-segmented endopod and a multi-annulate swimming exopod in the ground pattern, both arising from a common basis, or basipod (Waloszek & Müller 1990; Waloszek 1993, 1999). In fact, the second antennae (ant2) are the most important organs for feeding and locomotion in crustaceans, with a coxa-basis subdivision of the limb base later in the stem lineage of the eucrustaceans. The second antennae retain their original locomotory function in the ground pattern of entomostracan adult crustaceans, a feature best seen in clam shrimps and water fleas (Waloszek 1999; also discussing other crustacean features and establishing the monophyly of Entomostraca). These are the largest appendages in the early feeding entomostracan nauplii, often accompanied by reduced functionality of antennulae (ant1, anterior) and mandibles (posterior). Malacostracan eucrustaceans have non-feeding free-living nauplii and metanauplii (if developed at all), although the second antennae (ant2) are also very prominent. Subsequently, in ontogeny and evolution, the eucrustacean antennae may become multi-functional (including sensorial) and assume different shapes. However, they are very rarely reduced, as in female anostracan Branchiopoda, or even completely lost, as in terrestrial isopods.

"Myriapod" atelocerates have no appendages between their feeler-like, multi-annulate (first) antennae and their mandibles. Thus, it seems more likely and more parsimonious to assume an ateloceratan affinity for *D. bocksbergensis* than to assume repeated loss of antennae and reappearance of feeler-like antennulae. This assumption is particularly necessary if a close relationship of Hexapoda and some crustacean taxa is postulated.

The post-cephalic trunk of *Devonohexapodus bocksbergensis* is separated into two tagmata, recognisable by clear differences in the shape of the legs, both in the part

and counterpart. As in the Hexapoda, and nowhere else among arthropods, the anterior part is composed of three leg-bearing segments, which we refer to as the thorax. The thorax has narrow segments but its exact structure is unclear due to distortion. The very slender and clearly uniramous legs may have been locomotory, although it is difficult to determine how the body could have been orientated such that both thoracopods and leglets could have walked together (see below). The number of podomeres appears to have been limited to six in each leg. The distalmost podomere is arcuate, but neither tarsomeres nor claw-like structures are seen in *D. bocksbergensis*. Thoracopod 1 is more finely annulate, superficially resembling true podomeres, but this is very likely due to pyritisation (a preservational artefact resulting from the cleavage of pyrite). Only distinct joints can be used to unequivocally identify podomeres, as in the middle part of the legs (Fig. 2C). Kukalová-Peck (1991) described Carboniferous representatives of the Monura, the sister group to Cercofilata, within the Dicondylia (Fig. 5), with more thoracic leg podomeres. Consequently, she assumed 11 podomeres for the ground pattern of Hexapoda. The maximum number of 6 podomeres in *D. bocksbergensis* does not support her view (see Bitsch 2001, for a review of hexapod leg structure). The high podomere

number in Kukalová-Peck's Carboniferous monurans might well be a preservational artefact or, if supported by further study, an autapomorphy of these monurans.

The post-thoracic trunk of *D. bocksbergensis* has approximately 35 segments, all bearing pairs of short leglets. No known extant insect has more than 11 "abdominal" segments. Kukalová-Peck (1991) has reconstructed the leg-bearing condition for various Carboniferous insects, revealing that their legs were rather shorter and composed of a limited number of podomeres. The situation in *D. bocksbergensis* and in Kukalová-Peck's reconstructions implies that the number of "abdominal" segments was reduced before the "abdominal" leglets. Accordingly the plesiomorphic condition was present in the stem lineage of insects, and leglets became modified to various structures such as ventral tube, retinaculum and furca in Collembola, and styli, cerci and various genital structures in other Hexapoda. Structurally, the leglets of *D. bocksbergensis* resemble the walking legs of some Collembola (Neanuridae), Diplopoda, Symphyla and Pauropoda, demonstrating the usefulness of these leglets for walking. More comparative studies are required to clarify this intriguing observation which has relevance to understanding the use and evolution of these leglets in the insect lineage. In the marine environ-

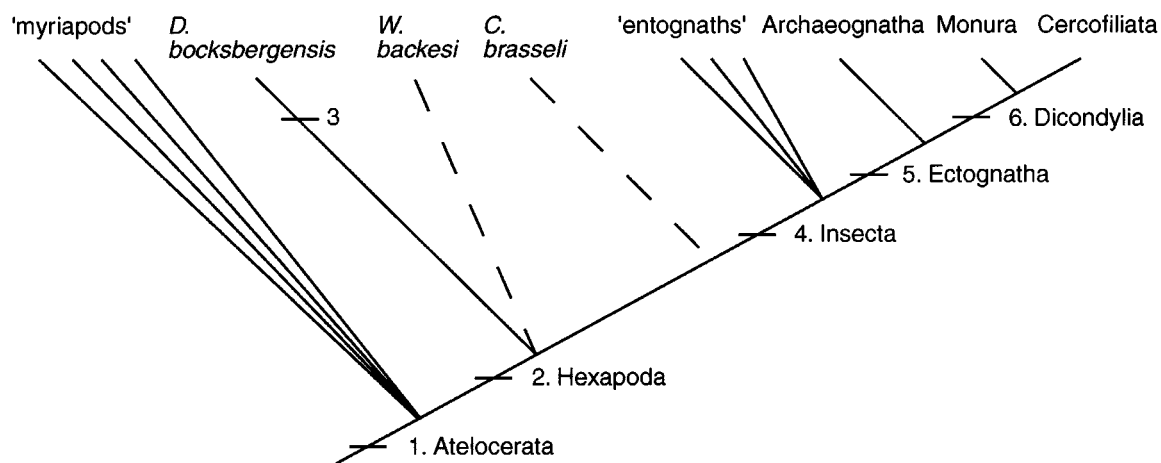


Fig. 5. Suggested relationships of *D. bocksbergensis* n. gen. n. sp. within Hexapoda, including autapomorphies of the named taxa. C. = genus *Cambrohexapodus*, D = *Devonohexapodus* n. gen., W. = genus *Wingertshellicus*, other abbreviations see Table 1.

Set 1 Atelocerata sensu Heymons (1901). Two tagmata: head and trunk; head with one pair of antennae followed by an appendage-less "intercalary" segment, a segment bearing jaw-like uniramous appendages (so-called mandibles), and two pairs of leg-like uniramous mouthparts (so-called maxilla and labium); head enclosed within a sclerotic capsule; eyes arise dorsally; Tömösvary organs. Other proposed synapomorphies relate to the assumption of a terrestrial habitat of the last common ancestor and are not listed here.

Set 2 Hexapoda. Three tagmata; head with dorsally inserted antennae, thorax with three segments each with a pair of slender thoracopods, thoracopods with six podomeres; last three pairs of "abdominal" legs modified, the other "abdominal" legs short; caudal appendages developed as cerci.

Set 3 *Devonohexapodus bocksbergensis* n. gen. n. sp. Large eyes on small head.

Set 4 Insecta (sensu Hennig 1969, Ax 1999). Eleven "abdominal" segments, the tenth without appendages.

Set 5 Ectognatha (sensu Kukalová-Peck 1991, Ax 1999). Flagellar antenna; Johnston's organ; three ocelli; paired claws; segmented tarsus; gonapophyses of female on "abdominal" segments 8+9; terminal filament.

Set 6 Dicondylia (Kukalová-Peck 1991). Mandible dicondyllic; "abdominal" tracheal systems with longitudinal and transverse trunks; gonangulum.

ment such leglets might have had functions other than those acquired on land (see below). In marine forms, such as *D. bocksbergensis*, the leglets appear to have functioned as locomotory legs. This raises the question of function of the thin thoracopods. This cannot be resolved at present because the body of the holotype of *D. bocksbergensis* is bent dorsally in the thoracic and anterior “abdominal” region. It remains possible that this is natural and may have enabled the animal to cling to substrates or to catch prey while walking on the leglets.

The anterior two of the three posteriormost leglets of *D. bocksbergensis* appear to be modified on the basis that they are directed posteriorly and appear rather spine-like (Fig. 2). The structure of the leglets raises the question of whether these appendages were used for egg deposition in the marine environment, or in a context of reproduction similar to insect terminalia. However, we explicitly deny any homology with the gonopods of Crustacea. The posteriormost pair of leglets is even much broader and longer than any of the other “abdominal” leglets. They are considered as cerci because their structure, situation and orientation closely resemble the cerci of extant insects. The proposed homology is discussed further below.

In summary, *Devonohexapodus bocksbergensis* shares with the Atelocerata the following characters (character set 1 in Fig. 5):

- lack of a limb corresponding to the first post-antennal appendages of Euarthropoda
- trunk with uniramous legs.

The presence of uniramous, myoerate, sensory first antennae corresponds to the situation in the ground pattern of Euarthropoda and is thus regarded as a symplesiomorphy. The same is true for a trunk with a continuous series of legs. However, uniramy (without differentiation of coxa and basipodite) and small size of a pygidial portion as the ultimate, unsegmented trunk part (i.e., the telson of Crustacea?) are probably synapomorphies for these taxa,

Insecta and *Devonohexapodus bocksbergensis* share several synapomorphies (character set 2 of Hexapoda in Fig. 5), including:

- subdivision of the post-cephalic trunk into thorax and “abdomen”
- three pairs of uniramous thoracic legs
- thoracopods slender and stenopodial
- thoracopods with no more than six podomeres
- an “abdomen” with short, stout leglets.

Concerning the segment number of the post-thoracic trunk and homology of the terminalia, several explanations are possible:

A) in the ground pattern of Hexapoda (*D. bocksbergensis* + Insecta) there are 11 “abdominal” segments and the “abdomen” of *D. bocksbergensis* was secondarily elongated by the addition of segments anterior to the ultimate three;

B) in the ground pattern of Insecta the “abdomen” was shortened to 11 segments by losing terminal segments;

C) in the ground pattern of Insecta the “abdomen” was shortened to 11 segments by losing segments anterior to the ultimate three segments.

We favour hypothesis C and thus the homology of the terminal segments of *D. bocksbergensis* with those in Hexapoda. In extant insects the cerci are the modified leglets of the eleventh “abdominal” segment, and so the structures called cerci in *D. bocksbergensis* are only homologous if hypothesis A or C are true, while hypothesis B requires convergent evolution of terminalia including cerci. Hypotheses A and C further imply that cerci were lost in Ellipura and thus cerci constitute an autapomorphy of Hexapoda and not a synapomorphy of Diplura + Insecta. Current knowledge on the developmental biology of arthropods does not contradict any possibilities of increase or decrease in “abdominal” segment number. Increase in trunk segment number with conservation of the terminalia is exemplified in scolopendromorph and geophilomorph Chilopoda. Therefore, the terminalia in *D. bocksbergensis* are seen as homologous to those in Insecta, particularly the cerci-like structures, thus representing an autapomorphy of Hexapoda and a synapomorphy of *D. bocksbergensis* and Insecta (see below). Otherwise, convergent origin of the terminalia would have to be assumed, which seems much less parsimonious to us. Other terminal structures, such as the telson and anus, are not visible in the holotype of *D. bocksbergensis* and cannot contribute to this discussion.

Additional autapomorphic characters of Hexapoda (character set 2 in Fig. 5) would thus be:

- “abdominal” appendages short (leglets)
- terminal three pairs of “abdominal” appendages modified and pointing posteriorly
- posteriormost pair of “abdominal” appendages modified into cerci.

The small head, large compound eyes, and the conspicuous slender thoracopods are considered to be autapomorphies of *D. bocksbergensis* (character set 3 in Fig. 5). We suggest, therefore, that the Hexapoda includes the sister taxa *D. bocksbergensis* and Insecta (“entognaths” + Ectognatha). *D. bocksbergensis* is clearly set apart from its sister taxon by a plesiomorphically large number of “abdominal” segments versus the 11 post-thoracic segments in the ground pattern of Insecta (character set 4 in Fig. 5).

New arthropods from the Hunsrück Slates

From the same strata as *Devonohexapodus bocksbergensis*, two arthropod fossils of uncertain affinity have preliminarily been reported by Bartels (1995) and have recently been formally described, together with two addi-

tional fossils, by Briggs & Bartels (2001). From their figures, X-ray images and drawings, *Cambronatus brasseli* and *Wingertshellicus backesi* show certain similarities to *D. bocksbergensis* in several aspects, that in our view indicate a close relationship. Our opinion, derived from the illustrations presented in Briggs & Bartels (2001), strikingly contrasts with the authors' morphological and systematic interpretations. Although this has a strong bearing on the discussion of early hexapod phylogeny exposed by Hunsrück Slate evidence, we hesitate to go into more detail and to reinterpret these fossils without first studying the original material.

Remarkably, all four fossils are in the range of several centimetres body length, and *Cambronatus brasseli* and *Wingertshellicus backesi* both have prominent antennae. Both species possess only one pair of long, slender antennae, although *C. brasseli* was not described like this. Briggs & Bartels (2001) emphasise that the proximal parts of the antennal rami are not visible, and so it remains unclear if they have a single stem, although these authors did add this feature to the diagnosis of *C. brasseli*. There are several other problems with this article. For example, the interpretation of the anterior body region (head and its appendages according to their interpretation) led Briggs & Bartels (2001) to consider these fossils as "crustaceanomorphs". However, this taxon does not exist and the characters mentioned do not support this statement. The overall similarities (body size, approximately 35 appendage-bearing segments) between *Wingertshellicus backesi* and *D. bocksbergensis* may be superficial. However, the 11 appendage-bearing segments ("abdominal") of *Cambronatus brasseli* support our hypothesis of a close relationship between these organisms and Hexapoda. Briggs & Bartels (2001) state that a forthcoming cladistic analysis will clarify the systematic position contended, and we keenly await the publication of this study.

In this context, we draw attention to another possible stem lineage representative of Hexapoda. *Tesnusocaris goldichi* Brooks, 1955, from the Carboniferous, was re-described by Emerson & Schram (1991) as a fossil representative of the Remipedia. Although it is stated in their diagnosis for the Remipedia that the first antennae (ant1) are biramous, the authors on several occasions describe the antennae as poorly preserved or not preserved at all, and thus no definite statement on this character can be made. From the descriptions and figures given (no original material was available to us) the (first) antennae seem long, unbranched and filiform and, thus, ateloceratan-like in our view. Most striking to us are the long and filiform caudal appendages, which are most extraordinary for Crustacea, but rather common for Hexapoda. Along with body shape, size and eyes, these give a strong archaeognathan appearance to the reconstruction of *Tesnusocaris goldichi* in Emerson & Schram

(1991: fig. 28). Clearly, this question needs more attention and a redescription addressing these problems should be considered.

Biology and environment of *Devonohexapodus bocksbergensis*

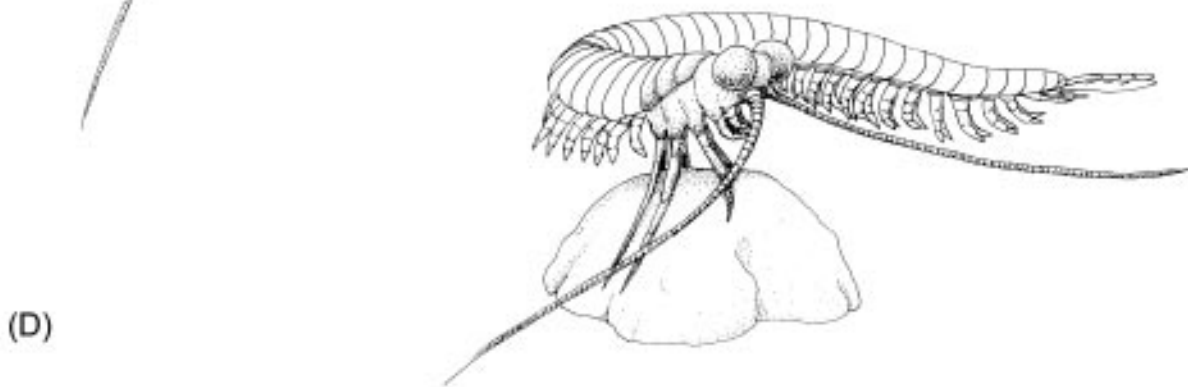
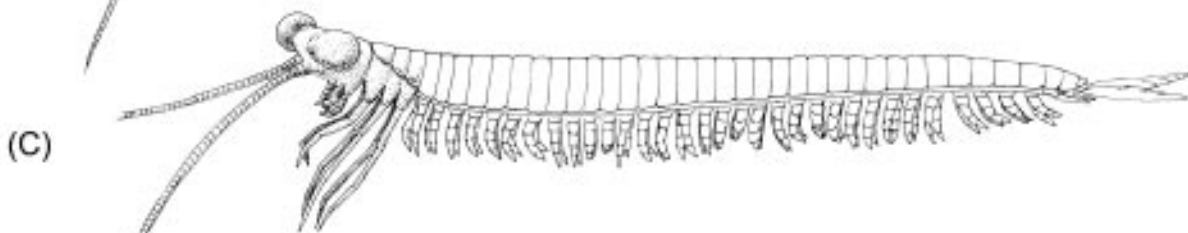
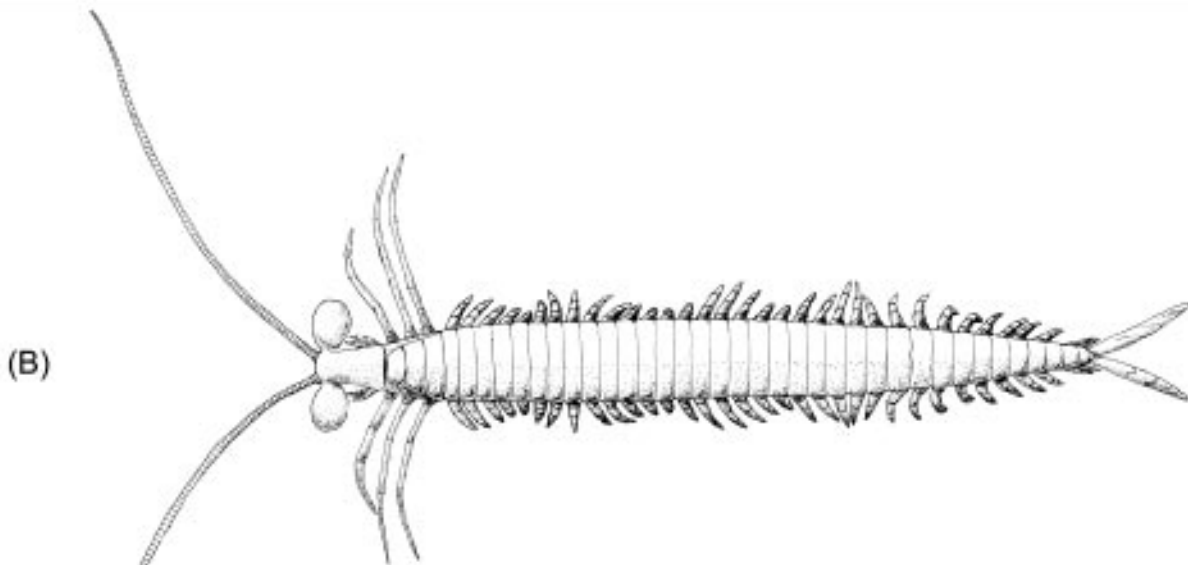
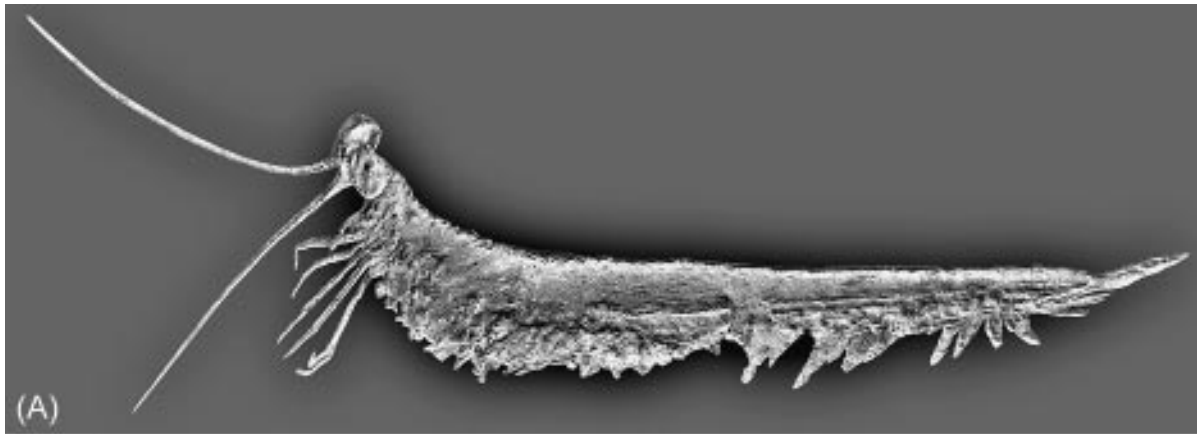
The biology of a partly known fossil is, of course, difficult to infer and the same applies to the associated fauna and environment. The specimen is from an isolated rock slab and has been found in a quarry dump. The strata and sediments of the Hunsrück Slate (Bartels 1994) suggest that *Devonohexapodus bocksbergensis* was fossilised in a strictly marine milieu. No evidence is available for a near-shore environment. The occurrence of exclusively marine taxa, such as echinoderms and placoderms, indicates an open-sea regime. Accordingly, we assume a marine habitat for *D. bocksbergensis* and reject the idea that it was simply washed into the sea from land.

The three pairs of long thoracic legs are not paddle-like, but very long and slender. *D. bocksbergensis* might have used them for walking on the sediment surface, in addition to the shorter post-thoracic trunk limbs, though the former are rather long for this purpose. Alternatively, *D. bocksbergensis* might have walked mainly on the "abdominal" leglets and used the thoracic legs to catch prey or hold on to substrate (Fig. 6D). The bending of the anterior thoracopods suggests this. The animal might also have swum along by holding the thoracopods laterally and additionally paddling with the stout leglets. For stability, it could have used its caudal appendages as steering aids (Fig. 6B, C). The modified terminal pairs of leglets suggest that these were possibly used as in extant Ectognatha: *D. bocksbergensis* may have deposited eggs by using the penultimate two pairs of spike-like legs for laying into the substrate or onto water plants. This would be in clear contrast to a release of eggs into the free water, as has been reconstructed for the ground pattern of Euarthropoda, Crustacea and Eucrustacea (*sensu* Waloszek 1999).

Phylogenetic and evolutionary implications

With its unique body structure, *Devonohexapodus bocksbergensis* provides important new information on the early evolution of tagmosis and body parts in Hexapoda and Insecta. We propose that the tagmotic split of an originally uniform trunk into thorax and "abdomen" evolved before the final number of "abdominal" segments was reached.

D. bocksbergensis – possibly along with the taxa described by Briggs & Bartels (2001), if their hexapod affinity is confirmed – appears to contradict the views of Kraus & Kraus (1994), Kraus (2001) and Hilken (1998) that stem lineage insects were small (a few millimetres



long) and that the major impetus for terrestrialization was the presence of fungi, as a food source, on land. The new fossils with their significant size (larger than most Recent insects), together with the large Carboniferous Diplura, Monura and Zygentoma (Kukalová-Peck 1987), suggest that stem-lineage hexapods and stem-lineage insects were large (assuming that there is no sampling bias towards large hexapods). The hypothesis raised by Kraus and others implies that hexapod size was reduced to a few millimetres prior to terrestrialization, and subsequently increased again. We consider this improbable and find an autapomorphic reduction of body size in Collembola and Protura the more plausible explanation. Stem-lineage hexapods might have resembled the large dipluran, *Heterojapyx evansi* Womersley 1945, which was about 50 mm in length. Early aquatic “myriapods” were also large, and *Arthropleura* reached sizes in the decimetre to metre range (Briggs et al. 1984; Hahn et al. 1986). The (autapomorphic) small size of Collembola and Protura is probably linked to their special feeding strategies. The primary impetus to leave the aquatic habitat may not necessarily have been to access new food resources, but instead to escape predatory pressure or to enhance egg survival. This hypothesis is in accordance with the special terminal leglets of *D. bocksbergensis*. Accordingly, access to the new food resources may have been gained only later in the evolution of hexapods and insects. The numerous examples of medium- to large-sized amphibious to terrestrial Crustacea also contradict Kraus & Kraus’ (1994) and Kraus’ (2001) view that small size is a prerequisite of terrestrialization.

Kraus & Kraus (1994), Kraus (2001) and Hilken (1998) also suggest multiple origins of the tracheal system in several “myriapod” taxa and the Hexapoda. No tracheae are visible in *Devonohexapodus bocksbergensis*. Assuming that tracheae are only useful for breathing, the marine habitat of *D. bocksbergensis* suggests that the last common ancestor of the Tracheata had no tracheae. Thus a convergent development of tracheae in “myriapods” and Hexapoda has to be assumed. If, however, the tracheal system was useful in an aquatic environment, then the aquatic habitat of *D. bocksbergensis* does not imply multiple origins of tracheae. “Usefulness” rests with oxygen distribution through the gaseous phase. This is about 10,000 times faster than diffusion in the haemolymph (Chapman 1998: 452, 461, 464; Eckert 1988: 512). Hence, an efficient oxygen transport system becomes more and more relevant in larger organisms, such as *D. bocksbergensis* and the known fossil “myriapods”, and may well have been developed in the aquatic environment.

The Devonian fossil record of early Hexapoda is very scanty, consisting only of *Devonohexapodus bocksbergensis* and, if a hexapod affinity is assumed for these, *Wingertshellicus backesi* and *Cambronatus brasseli*. The structure of the latter two animals suggests that in the marine habitat, and at roughly the same geological time, the hexapod abdomen was reduced to 11 segments. Their large body size suggests that *D. hexapodus* is not exceptional in body dimensions. Concerning the fossil record of insects, primitively wingless forms are known to have existed since the Lower Devonian. The oldest described insect is the collembolan *Rhyniella praecursor* Hirst & Maulik, 1926. This fossil, found in the famous Rhynie Chert of Scotland, is derived and resembles extant Collembola, thus providing no indication of the morphology in stem-lineage Hexapoda, Insecta or the other fossil taxa discussed herein. The same applies to the mandibular bodies of (possibly) monurans, diplurans and zygantomans in the same strata (Kukalová-Peck 1991: 143). In some Carboniferous and Permian pterygotan insects (Kukalová-Peck 1991) at least five or six “abdominal” segments seem to have borne leglets, representing the plesiomorphic character state also found in *D. bocksbergensis*. This suggests that a seemingly legless “abdomen” has evolved convergently in “entognaths” and Pterygota, if not several times in the Pterygota. Retention of modified legs in these taxa also points in this direction (tube and furca in collembolans, genital legs and cercopods in insects).

Functional differentiation of limbs on land and in water

If we are right, hexapod body division into three tagmata evolved before terrestrialization. Consequently, hexapods were walking on three pairs of thoracic legs (and a set of “abdominal” appendages). Possibly, morphological modifications for egg-laying had also evolved. The following observations support this view. There is considerable variation in the number and structure of segments in the trunk of “myriapod” taxa. Segment numbers vary from 10 to almost 200, and some segments may be specialised, like those bearing the gonopods (on segments 8 and 9) in protandrian Diplopoda, the poison claw (first trunk segment) in Chilopoda, and also the terminal segments in these groups. In spite of this variation, segment number increased without fundamental change in morphology and locomotion pattern and, thus, tagmosis did not change. There is no species of “myriapod” that shows any tendency to evolve an insect-like “ab-

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Fig. 6. *Devonohexapodus bocksbergensis* n. gen. n. sp., computer-generated view (A) and tentative reconstructions in dorsal (B) and lateral views (C) and in a life position (D) resting on a stone at the bottom of the sea.

domen”, i.e. a tripartite body. In Insecta and Chelicerata, tagmosis does not change either, although Protura among Insecta, and Uropygi and Amblypygi among Chelicerata, have modified their locomotory pattern by devoting the first leg to a sensory function. Other secondary modifications include larvae with “abdominal” legs, or completely apodous larvae, for example in Hymenoptera and Lepidoptera, among Insecta (in-group autapomorphies). However, no terrestrial arthropod seems to have modified a larger part of its body into a new tagma, as suggested by the hypothesis of a terrestrial last common ancestor of Atelocerata.

The situation is different in aquatic arthropods, mainly Crustacea. Tagmata with different segment numbers are common amongst entomostracan Crustacea and clearly evolved independently several times in this taxon. For example, in Branchiopoda the segment numbers vary from six limb-bearing thoracomeres among cladocerans to 13 in anostracans, some 30 in spinicaudate conchostacans, and more than 70 in notostracans (for an account of the morphology and phylogeny of the Branchiopoda see Waloszek 1993).

In contrast to this enormous variation, terrestrial arthropods seem to be constrained in the development of tagmata. We suggest biomechanic reasons, as terrestrial locomotion has complex requirements for neural and muscular coordination of walking, preventing a functional change. As studies have shown (e.g. Martinez et al. 1998), underwater walking is less demanding for co-ordination because of the water’s support and lift. According to Martinez et al. (1998), locomotory studies of amphibious decapod Crustacea show much more variable locomotion and movement of legs in water than on land. The same applies to human locomotion when gravity is counteracted or reduced, in water or on the moon, respectively. Many more locomotory patterns are possible when gravitational constraints are loosened. Hence differentiation in tagmosis and segment numbers is less constrained in an aquatic environment, and probably evolved several times.

Apart from *D. bocksbergensis*, these functional reasons give further support to the assumption that hexapods did not evolve from a terrestrial ancestor with a homonomous “myriapod” body and evolved an “abdomen” only later, from an aquatic ancestor already supplied with three tagmata, as seen in the new fossil presented herein.

Conclusions

With a head bearing long myocerate antennae and large eyes, resembling that of Odonata or Archaeognatha, a three-segmented thorax with long, slender locomotory legs, and a post-thoracic trunk end with short leglets (Fig. 6), *Devonohexapodus bocksbergensis* shares a set

of characters with the Hexapoda not found in any “myriapods” or other euarthropods. Furthermore, the posterior three trunk legs appear to be specialised and are directed to posterior, a character seen exclusively in insects. These morphological characteristics are considered synapomorphies of *D. bocksbergensis* and Hexapoda, ruling out closer relationships of *D. bocksbergensis* with any other Atelocerata or Euarthropoda, particularly Crustacea or Eucrustacea (sensu Waloszek & Müller 1990 and Waloszek 1999). The high number of “abdominal” segments with leglets is a striking feature of *D. bocksbergensis*, which it shares with *Wingertshellicus backesi* (Briggs & Bartels 2001).

Not surprisingly, a large number of “abdominal” leglets characterises the ground pattern of Hexapoda. The rudimentary or modified leglets on various “abdominal” segments of insect taxa are referred to differently: styli, ventral tube, cerci, retinaculum, or furca (furcula). Our new fossil, together with *Wingertshellicus backesi* and *Cambronatus brasseli*, points to the evolution of Hexapoda from an ancestor with a multi-segmented trunk, to forms with 11 “abdominal” segments. These recent finds from Hunsrück Slates demonstrate that stem-lineage Insecta coexisted during the Devonian with early 11-segmented insects and with more derived taxa such as collembolans (the Rhynie Chert collembolan, *Rhyniella precursor*, is an example). All of these early hexapods had leglets throughout the trunk, and this should terminate discussion over the homology of the insect and crustacean “abdomen”. These body parts are clearly not homologous; whereas the situation is uncertain for the trunk end in the stem lineage of Crustacea, the abdominal segments of Entomostraca clearly do not bear limbs. Malacostraca have a trunk subdivided into two sets of segments, of which the posterior set traditionally has been interpreted as an “abdomen”. In fact this part, the pleon, bears legs on all segments, and must be reinterpreted as the second set of thoracomeres (thorax I and II sensu Waloszek & Müller 1998; see also Olesen & Waloszek 2000). Any modification of the hexapod post-thoracic trunk is derived from a stem taxon with serial leglets on this body part.

In the remaining stem lineage of Insecta the terminal “abdominal” leglets were specialised as gonopods. The similarity of the penultimate two pairs of leglets in *Devonohexapodus bocksbergensis* with those of insects suggests that the leglets of this fossil taxon were already pre-adapted to possible gonopod function. The assumed sister-group relationship of *Devonohexapodus bocksbergensis* with the Insecta has several evolutionary implications. One is that gonopods are a plesiomorphy of the ground pattern of the Insecta. Again, Hexapoda and “myriapods” have conquered the land in separate events of terrestrialization. This implies that specific adaptations, such as the tracheae (if an adaptation to terrestrial

life), have evolved several times, as was proposed by Hilken (1998; for a contrasting view see Ax 1999). The same applies to the Malpighian tubules, the Tömösvary (post-antennal) organ, and the indirect transfer of the spermatophore (Ax 1999). If considered as directly linked to a terrestrial habitat, these assumed synapomorphies appear as convergences in “myriapods” and Hexapoda. The appearance of similar structures in derived taxa of the Arachnida demonstrates that convergent evolution is possible and has taken place. This in itself does not, of course, exclude the possibility that these structures are synapomorphies of Atelocerata but, rather, increases the probability of convergence. The alternative assumption is that these structures are indeed not related to terrestrial life but had some functional significance, as yet unknown, in the marine environment. However, this seems doubtful for tracheae and Malpighian tubules.

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References

- Ax, P. (1999): Das System der Metazoa II. 384 pp., G. Fischer, Stuttgart.
- Bartels, C. (1994): Weltberühmt: Die “Bundenbacher Fossilien” des Hunsrückschiefers. Schriftenr. Schiefer-Fachverband in Deutschland e. V. (SVD) 3: 11–85.
- Bartels, C. (1995): Bundenbachs fossile Schätze. Kosmos 1/95: 36–37.
- Bartels, C., Briggs, D. E. G. & Brassel, G. (1998): The Fossils of the Hunsrück Slate – Marine Life in the Devonian. Cambridge Paleobiology Series 3, 323 pp., Cambridge University Press, Cambridge.
- Bergström, J. & Brassel, G. (1984): Legs in the trilobite *Rhenops* from the Lower Devonian Hunsrück Slate. Lethaia 17: 67–72.
- Bergström, J., Briggs, D. E. G., Dahl, E., Rolfe, W. D. I. & Stürmer, W. (1987): *Nahecaris stuerzi*, a phyllocarid crustacean from the Lower Devonian Hunsrück Slate. Paläont. Z. 61: 273–298.
- Birenheide, R. (1971): Beobachtungen am “Scheinstern” *Mimetaster* aus dem Hunsrück-Schiefer. Senckenb. Lethaea 53: 77–91.
- Bitsch, C. & Bitsch, J. (1998): Internal anatomy and phylogenetic relationships among apterygote insect clades (Hexapoda). Anns Soc. Entomol. Fr. (N. S.) 34: 339–363.
- Bitsch, J. (2001): The hexapod appendage: basic structure, development and origin. Anns Soc. Entomol. Fr. (N. S.) 37: 175–193.
- Blind, W. (1995): Die Lebewelt der Hunsrückschiefer im Röntgenlicht. Katzensgold macht Weichteilstrukturen sichtbar. Spiegel der Forschung 12: 22–27.
- Briggs, D. E. G., Plint, A. G. & Pickerill, R. K. (1984): *Arthropleura* trails from the Westphalian of eastern Canada. Palaeontology 27: 843–855.
- Briggs, D. E. G. & Bartels, C. (2001): New arthropods from the Lower Devonian Hunsrück Slate (Lower Emsian, Rhenish Massif, western Germany). Palaeontology 44: 275–303.
- Chapman, R. F. (1998): The Insects: Structure and Function. 4th edition. 770 pp., Cambridge University Press, Cambridge.
- Eckert, R. (1988): Animal Physiology: Mechanisms and Adaptations. 3rd edition, 683 pp., Freeman, New York.
- Edgecombe, G. D. & Giribet, G. (2002): Myriapod phylogeny and the relationships of Chilopoda. Pp. 143–168 in: Llorente B. J. & Morrone, J. J. (eds.) Biodiversidad, Taxonomía y Biogeografía de Artrópodos de México: Hacia una Síntesis de su Conocimiento, Volumen III. Prensas de Ciencias, Universidad Nacional Autónoma de México, México D.F.
- Emerson, M. J. & Schram, F. R. (1991): Remipedia, part 2, paleontology. Proc. San Diego Soc. Nat. Hist. 7: 1–52.
- Hahn, G., Hahn, R. & Brauckmann, C. (1986): Zur Kenntnis von *Arthropleura* (Myriapoda; Ober-Karbon). Geol. Palaeontol. 20: 125–137.
- Hartenberger, R. (1995): *Palaeoisopus problematicus* Broili, 1928 (Arthropoda) aus dem Hunsrückschiefer (Devon) mit behaartem Abdomen. Paläont. Z. 69: 121–123.
- Hennig, W. (1969): Die Stammesgeschichte der Insekten. 436 pp., Kramer, Frankfurt a. M.
- Heymons, R. (1901): Die Entwicklungsgeschichte der Scolopender. 244 pp.+8 pls, Biblioth. Zool. 13, Stuttgart.
- Hilken, G. (1998): Vergleich von Tracheensystemen unter phylogenetischem Aspekt. Verh. naturwiss. Ver. Hamburg 37: 5–94.
- Koch, M. (2001): Mandibular mechanisms and the evolution of hexapods. Anns Soc. Entomol. Fr. (N. S.) 37: 129–174.
- Kraus, O. (2001): “Myriapoda” and the ancestry of the Hexapoda. Anns Soc. Entomol. Fr. (N. S.) 37: 105–127.
- Kraus, O. & Kraus, M. (1994): Phylogenetic system of the Tracheata (Mandibulata): on “Myriapoda”-Insecta relationships, phylogenetic age and primary ecological niches. Verh. naturwiss. Ver. Hamburg 34: 5–31.
- Kristensen, N. P. (1998): The groundplan and basal diversification of the hexapods. Pp. 281–293 in: Fortey, R. A. & Thomas, R. H. (eds) Arthropod Relationships. Syst. Assoc. Spec. Vol. Ser. 55, Chapman & Hall, London.
- Kukulová-Peck, J. (1987): New Carboniferous Diplura, Monura, and Thysanura, the hexapod ground plan, and the

- role of thoracic side lobes in the origin of wings (Insecta). *Can. J. Zool.* 65: 2327–2345.
- Kukalová-Peck, J. (1991): Fossil history and the evolution of hexapod structures. Pp. 141–179 in: CSIRO (ed.) *The Insects of Australia*. 2nd edition, Vol. 1. Cornell University Press, Ithaca.
- Kukalová-Peck, J. & Brauckmann, C. (1990): Wing folding in pterygote insects, and the oldest Diaphanopteroidea from the early Late Carboniferous of West Germany. *Can. J. Zool.* 68: 1104–1111.
- Martinez, M. M., Full, R. J. & Koehl, M. A. R. (1998): Underwater punting by an intertidal crab: a novel gait revealed by the kinematics of pedestrian locomotion in air versus water. *J. Exp. Biol.* 201: 2609–2623.
- Olesen, J. & Waloszek, D. (2000): Limb ontogeny and trunk segmentation in *Nebalia* species (Crustacea, Malacostraca, Leptostraca). *Zoomorphol.* 120: 47–64.
- Scourfield, D. J. (1940): The oldest known fossil insect (*Rhyniella praecursor* Hirst & Maulik) – further details from additional specimens. *Proc. Linn. Soc.* 152: 113–131.
- Struve, W. (1985): Phacopinae aus den Hunsrück-Schiefern (Unterdevon des Rheinischen Gebirges). *Senckenb. Lethaea* 66: 392–432.
- Stürmer, W. (1969): Pyriterhaltung von Weichteilen bei devonischen Cephalopoden. *Paläontol. Z.* 43: 10–12.
- Stürmer, W. & Bergström, J. (1973): New discoveries on trilobites by X-rays. *Paläontol. Z.* 47: 104–141.
- Stürmer, W. & Bergström, J. (1976): The arthropods *Mimetaster* and *Vachonisia* from the Devonian Hunsrück Shale. *Paläontol. Z.* 50: 78–111.
- Stürmer, W. & Bergström, J. (1978): The arthropod *Chelonielon* from the Devonian Hunsrück Shale. *Paläontol. Z.* 52: 57–81.
- Stürmer, W. & Bergström, J. (1981): *Weinbergina*, a xiphosuran arthropod from the Devonian Hunsrück Slate. *Paläontol. Z.* 55: 237–255.
- Waloszek, D. (1993): The Upper Cambrian *Rehbachella kinnekullensis* and the phylogeny of Branchiopoda and Crustacea. *Fossils & Strata* 32: 1–202.
- Waloszek, D. (1999): On the Cambrian diversity of Crustacea. Pp. 3–27 in: Schram, F. R. & von Vaupel Klein, J. C. (eds) *Crustaceans and the Biodiversity Crisis, Proceedings of the Fourth International Crustacean Congress*, Vol. 1. Brill Academic Publishers, Leiden.
- Waloszek, D. & Dunlop, J. (2002): A larval sea spider (Arthropoda: Pycnogonida) from the Upper Cambrian “Orsten” of Sweden, and the phylogenetic position of pycnogonids. *Palaeontol.* 45: 421–446.
- Waloszek, D. & Müller, K. J. (1990): Upper Cambrian stem lineage crustaceans and their bearing upon the monophyletic origin of Crustacea and the position of *Agnostus*. *Lethaia* 23: 409–427.
- Waloszek, D. & Müller, K. J. (1998): Cambrian “Orsten”-type arthropods and the phylogeny of Crustacea. Pp. 139–153 in: Fortey, R. A. & Thomas, R. H. (eds.) *Arthropod Relationships, Syst. Assoc. Spec. Vol. Ser. 55*. Chapman & Hall, London.
- Weddige, K. (1996): Devon-Korrelationstabelle. *Senckenberg. Lethaea* 76: 267–286.