

A Cambrian micro-lobopodian and the evolution of arthropod locomotion and reproduction

Andreas Maas^{1†}, Georg Mayer², Reinhardt M. Kristensen³ & Dieter Waloszek¹

¹Section for Biosystematic Documentation, University of Ulm, Helmholtzstrasse 20, D-89081 Ulm, Germany;

²Department of Anatomy and Cell Biology, University of Melbourne, Victoria, Australia 3010;

³Zoological Museum, University of Copenhagen, 15 Universitetsparken, DK-2100 Copenhagen, Denmark

The evolutionary success of arthropods, the most abundant and diverse animal group, is mainly based on their segmented body and jointed appendages, features that had evolved most likely already before the Cambrian. The first arthropod-like animals, the lobopodians from the Early Cambrian, were unsclerotized and worm-like, and they had unjointed tubular legs. Here we describe the first three-dimensionally preserved Cambrian lobopodian. The material presented of *Orstenotubulus evamuelleræ* gen. et sp. nov. is the smallest and youngest of a lobopodian known. *O. evamuelleræ* shows strikingly detailed similarities to Recent tardigrades and/or onychophorans in its cellular-structured cuticle and the telescopic spines. It also shows similarities to other, longer known lobopodians, but which are ten times as large as the new form. These similarities include the finely annulated body and legs, which is characteristic also for Recent onychophorans, and paired humps continuing into spines situated dorsally to the leg insertions, a feature lacking in the extant forms. The morphology of *O. evamuelleræ* not only elucidates our knowledge about lobopodians, but also aids in a clearer picture of the early evolution of arthropods. An example is the single ventral gonopore between a limb pair of *O. evamuelleræ*, which indicates that a single gonopore, as developed in onychophorans, tardigrades, pentastomids, myriapods and insects, might represent the plesiomorphic state for Arthropoda, while the paired state in chelicerates and crustaceans was convergently achieved. Concerning life habits, the lateral orientation of the limbs and their anchoring spines of the new lobopodian imply that early arthropods were crawlers rather than walkers.

lobopodians, Arthropoda, evolution, phylogeny, reproductive system, locomotion

Evolution of animals with segmented bodies, dorsal subdivisions into tripartite, sclerotized tergites, compound eyes, and articulated appendages can be traced back to more than 520 million years into the Early Cambrian. Forms with such a design can be regarded as arthropods *sensu stricto*^[1,2]. Coeval worm-like forms, the so-called lobopodians, had segmental but unjointed uniramous appendages and are of fundamental interest because they can provide a model of the “pre-jointed” stage of body design in arthropod evolution. Likewise, their legs can serve as a model for pre-cursor arthropod appendages prior to the development of jointed articles. Fossil lobopodians known hitherto are 1–20 cm long,

from the Lower and Middle Cambrian^[3–10]. Some had long legs, such as species of *Hallucigenia* and *Paucipodia*, and others had short legs, such as species of *Aysheaia* and *Onychodictyon*. None of them are preserved three-dimensionally and therefore the true body shape and posture of the legs remained unknown and ideas about the lifestyle of these extinct forms and about the evolution and function of limbs in the early phase of arthropod evolution are speculative.

Among Recent arthropod-like animals, Onychophora

Received April 25, 2007; accepted July 24, 2007

doi: 10.1007/s11434-007-0515-3

†Corresponding author (email: andreas.maas@uni-ulm.de)

(‘velvet worms’) and Tardigrada (‘water bears’) resemble lobopodians in having, e.g., a tubular body with tubular, uniramous legs with distal claws. These two extant groups are sometimes considered as pre-cursors of arthropods or as the most basal living arthropod groups, and occasionally referred to as ‘living fossils’^[11]. Phylogenetically onychophorans (Figure 1(a)), tardigrades, lobopodians and Arthropoda sensu stricto (i.e. Arthropoda sensu lato) have a chitinous cuticle and segmented body and appendages, while features such as sclerotization, joints between segments and limb articles, compound eyes and more^[2] are exclusive for Arthropoda sensu stricto (including several fossil taxa such as trilobites and the crown group Euarthropoda such as chelicerates, crustaceans, myriapods and insects). Evolution of arthropod locomotion has been a contentious issue^[10,12–14]. The mode of locomotion of marine fossil lobopodians has been largely deduced from the Recent terrestrial velvet worms. Likewise, lobopodian legs have been reconstructed as hanging more or less downwards,

lifting the body far above the substrate^[3,13,15,16]. Even long-legged forms are assumed to have walked on limbs rather than creeping on the ground, although there is some evidence that at least in some lobopodians legs were not oriented ventrally^[17]. On the basis of a three-dimensionally preserved new lobopodian from the uppermost Middle Cambrian of Sweden, *Orstenotubulus evamuelleræ* gen. et sp. nov.^[18], we propose a model of long-legged lobopodian locomotion that can also serve as a model for the “pre-stage” of true arthropod appendages. Furthermore, we propose a model for gonad evolution in arthropods based on the gonopore observed in the new species.

1 Systematic paleontology

Arthropoda s. l. (sensu ref. [1])

Orstenotubulus gen. nov. (type species: *Orstenotubulus evamuelleræ* gen. et sp. nov.)

Orstenotubulus evamuelleræ gen. et sp. nov. (Figure 1(b)–(d); Figure 2(a), (b), and (d); Figure 3(a) and (b);

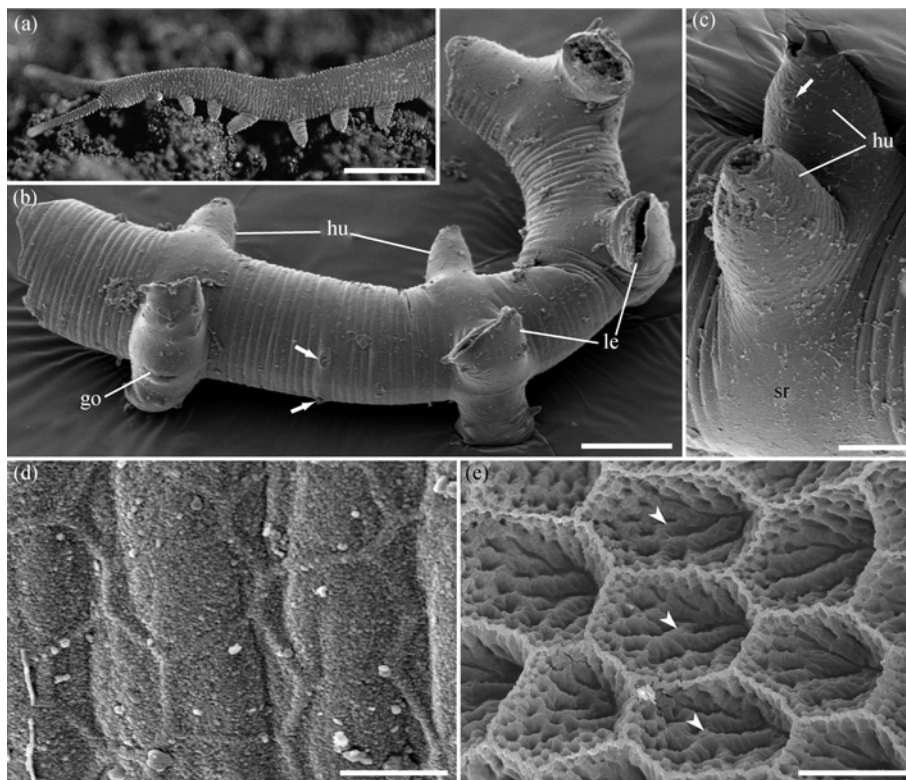


Figure 1 Comparison of *Orstenotubulus evamuelleræ* with Onychophora. (a) *Metaperipatus blainvillei* (Onychophora, Peripatopsidae) from Chile; (b)–(d) scanning electron micrographs of *O. evamuelleræ*. (b) Holotype (UB W 126), slightly ventral view; (c) Dorsal humps (specimen UB W 126), dorso-lateral view, spines broken off; (d) Hexagonal pattern on the body surface (specimen UB W 127). (e) Scanning electron micrograph of the hexagonal pattern in the molted cuticle of *Metaperipatus inae* (Onychophora, Peripatopsidae) viewed from inside. go, genital opening (Figure 2(d)); hu, dorsal humps; le, legs; sr, smooth, vaulted ring bearing paired dorsal humps. White arrows in (b) and (c) indicate the position of dermal papillae. Arrowheads in (e) show micro-texture within hexagons of onychophoran cuticle. Scale bars for (a)–(e): 10 mm, 150 µm, 50 µm, 10 µm, and 10 µm.

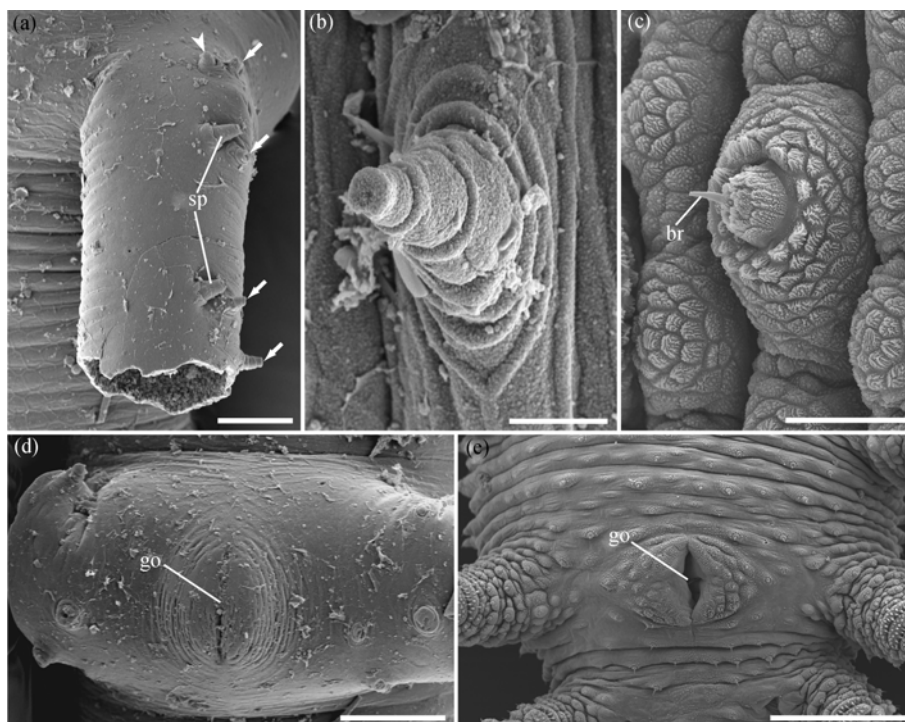


Figure 2 Comparison of *Orstenotubulus evamuelleriae* with onychophorans (scanning electron micrographs). (a) Longest preserved leg fragment in *O. evamuelleriae* (specimen UB W 127). Ventrolateral view. Note the fine annulation of leg surface at left. (b) Dermal papilla from an annulated inter-pedal body region of *O. evamuelleriae* (specimen UB W 127). (c) Dermal papilla from the body surface of *Epiperipatus biolleyi* (Onychophora, Peripatidae). (d) Genital opening of *O. evamuelleriae* (holotype specimen: UB W 126) in ventral view. (e) Genital opening of a juvenile of *E. biolleyi* (Onychophora, Peripatidae) in ventral view. br, sensory bristle; go, genital opening; sp, retractable spines. White arrows in (a) indicate the dermal papillae on the ventral leg surface, the arrowhead points to a spine in a retracted condition (Figure 4(a) and (b)). Scale bars for (a)–(e): 50 μ m, 10 μ m, 50 μ m, 50 μ m, and 500 μ m.

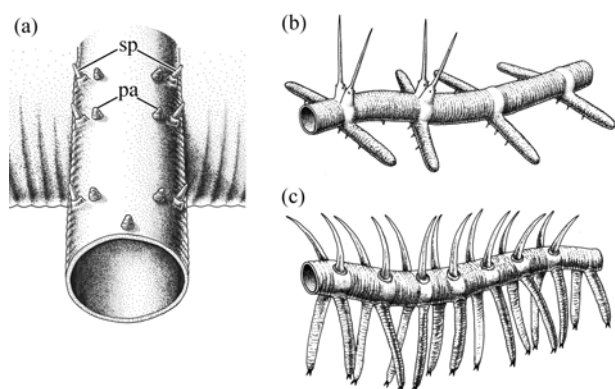


Figure 3 Schematic representation of *Orstenotubulus evamuelleriae* and the morphologically related Cambrian *H. fortis*. Anterior left. (a) Illustration of proximal leg part in *O. evamuelleriae* in ventral view; (b) illustration of the body trunk of *O. evamuelleriae*, with dorsal spines complemented; (c) body trunk of the lobopodian *Hallucigenia fortis* (redrawn and modified from fig. 1C in ref. [12]). pa, sensory dermal papillae; sp, retractable spines.

Figure 4(a) –(c)

2001 “new fossil supposedly lobopod” (Maas & Waloszek^[10], p. 457, Figure 12).

2003 “Upper Cambrian ‘Orsten’ lobopodian” (Waloszek^[18], p. 83, Figures 4 and 5).

2006 “Hitherto undescribed lobopodian stem arthropod from the Upper

Cambrian” (Maas et al.^[19], p. 275, Figure 5(d)).

Etymology. From the fossil preservational type ‘Orsten’ and the tubular body and appendages; in honor of Eva Müller, the late wife of Klaus Müller, the discoverer of the Swedish ‘Orsten’-type fossils.

Holotype. A fragment consisting of four segments (University of Bonn no. UB W 126, specimen 4157, sample 6760; Figures 1(b) and 2(d)).

Locality and horizon. Gum, Kinnekulle, Västergötland, Sweden, *Agnostus pisiformis* Biozone (formerly zone 1 of the Upper Cambrian succession in Sweden).

Other material. One leg-bearing portion consisting of two halves of successive segments (UB W 127, specimen 4166, sample 6734; Figure 1(c) and (d), Figure 2(a) and (b), Figure 4(a)–(c)) from NNE Backeborg, Kinnekulle, Västergötland, Sweden, *Agnostus pisiformis* Biozone; and a fragment consisting of two segments (UB W 128, specimen 4167, sample 6760) from type locality. The three specimens differ in preservation, completeness and size but are strongly similar to each other morphologically. Therefore they seem to belong to

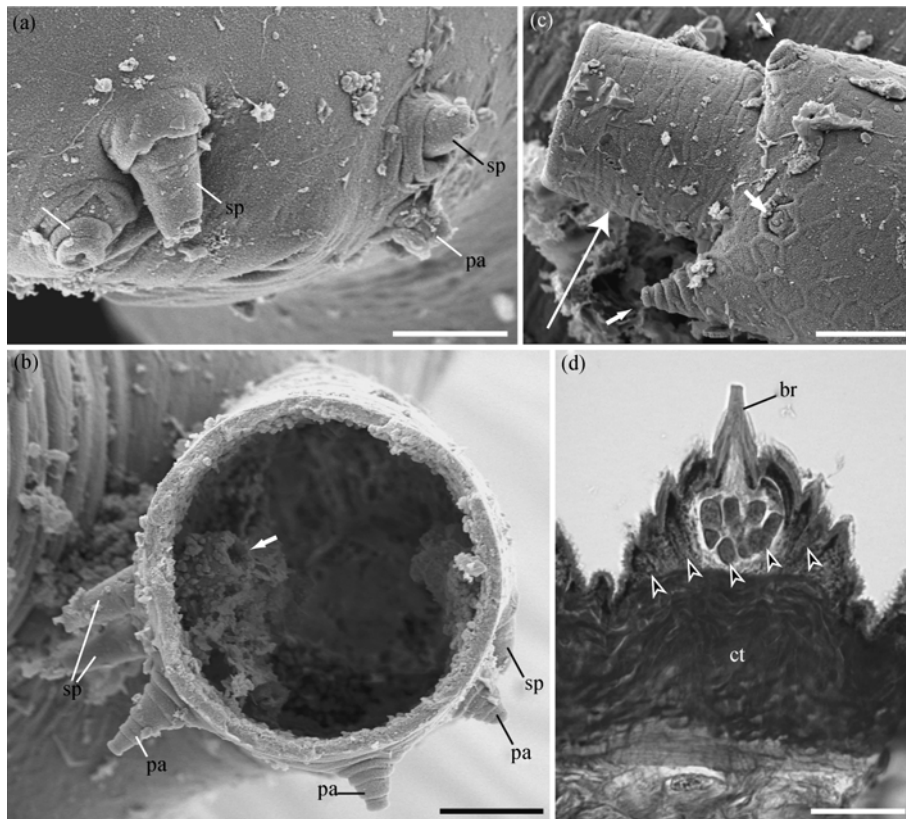


Figure 4 (a) Retractable spines on the ventral leg surface of *Orstenotubulus evamuellerae* (specimen UB W 127). The spine on the right is in a retracted condition. sp, retractable spines; pa, sensory dermal papillae. Scale bar: 20 μm . (b) View inside a leg of *O. evamuellerae* (specimen UB W 127). Dorsal is up. The white arrow points to a retracted spine inside the leg. pa, sensory dermal papillae; sp, retractable spines. Scale bar: 30 μm . (c) Posterior view of a dorsal hump displaying the base of the basally broken terminal spine (large arrow) (specimen UB W 127). Small arrows indicate the position of dermal papillae. Note the hexagonal surface pattern. Scale bar: 20 μm . (d) Histological section (Azan staining) through a dermal papilla of *Metaperipatus blainvillei* (Onychophora, Peripatopsidae), which is composed of several cells. The arrowheads point to the cell nuclei within the dermal papilla. br, sensory bristle; ct, connective tissue. Scale bar: 30 μm .

the same ontogenetic stage. Whether the material presented herein represents the adult or a juvenile stage cannot be stated with certainty.

Sizes. Diameter of body 120 μm (UB W 128) to 205 μm (UB W 126, 127), diameter of legs 80–100 μm ; estimated total body length (expecting 9–10 leg-/spine-bearing segments) 4–5 mm.

Diagnosis. Minute, finely annulated ‘lobopodian’ with possibly 9–10 leg-bearing segments, characterized by paired conical dorsal humps (domes, lacking in at least two body segments) extended into long spines and two distinct types of short extensions on body and legs: dermal papillae made of several epidermal cells, and conical sockets with retractable spines.

Description. Small, micro-annulated with a worm-like, elongate cylindrical body (Figure 1(b)), with tapering anterior and posterior ends; diameter 120–205 μm . All segments show a smooth area bearing laterally ori-

ented legs ventrally and micro-annulated inter-pedal regions. At least two kinds of segments: with and without paired dorsal humps. The strongest humps with spines were most likely located in the mid-body while towards the anterior and posterior end of the animal, the humps/spines were less conspicuous or even absent. Dorsal spines arose from the humps and had a basal diameter of 40 μm (Figures 1(c) and 4(c)). A pair of ventrolateral dermal papillae occurs in the micro-annulated inter-pedal regions (Figures 1(b) and 2(b)). Papillae are absent between those smooth rings that lack conical humps. The body surface shows a micron-scale hexagonal pattern (Figure 1(d)), which is independent of the micro-annulation and becomes less distinct ventrally on the smooth areas. This hexagonal pattern of the surface is also present on the dorsal humps and their spines (Figure 4(c)). Only the proximal parts of the legs are preserved, with the largest fragment being ca. 250 μm (Figure 2(a)). The diameter of legs ranges between 80

and 100 μm . The preserved portions of the tubular legs do not decrease in diameter distally, so the legs must have been rather long. Anteroventrally and posteroventrally, they bore at least three pairs of retractable spines (Figure 2(a), Figure 4(a) and (b)) on short, soft bases (Figures 2(a) and 4(a)) and such spines were most likely distributed ventrally along the entire leg. All spines are accompanied by a set of six dermal papillae (Figures 2(a), 3(a), and 4(a)). In addition a median papilla occurs towards the distal part of the leg (Figures 3(a) and 4(b)). Similarly-sized papillae, one median and two lateral ones also occur on each dorsal hump, near the bases of missing spines (Figures 1(c) and 4(c)). In the holotype, one of the ventral bars bearing legs has an unpaired, axially oriented slit-like opening (Figures 1(b) and 2(d)), interpreted as the genital opening.

2 Comparisons

O. evamuelleriae had a cylindrical, segmented body with a diameter of 120–205 μm , being the smallest known lobopodian and most likely a member of the benthic meiofauna. Its preservation is detailed with cellular structures visible. The largely micro-annulated surface (Figure 1(b)) alternating with smooth regions (Figure 1(c)) and the bent posture (Figure 1(b)) indicate that the cuticle was rather thin and the body flexible. The cuticle shows a regular, micron-scale hexagonal pattern (Figures 1(d) and 4(c)). Among extant arthropods, such an annulated cuticle with a similar sized hexagonal texture is present only in onychophorans (Figure 1(d) and (e)). In onychophorans, the hexagons correspond to the epidermal cells and the same might also be assumed for the fossil. The surface of the onychophoran epicuticle is hydrophobic^[20], probably due to an additional micro-texture within the hexagons (Figure 1(e)), perhaps reflecting their terrestrial lifestyle. Such micro-texture is absent in the marine *O. evamuelleriae*.

The pattern of micro-annulated regions alternating with smooth regions also occurs in the Cambrian Chengjiang biota lobopodians *Cardiodictyon catenulum* and *Microdictyon sinicum*^[6,7,12]. The micro-annulation indicates that the body of *O. evamuelleriae* was flexible only in the limbless, inter-pedal regions whereas the smooth regions were most likely sclerotized. The smooth zones give rise to tubular legs that insert on both sides of ventral, elevated abaxial bars (Figures 1(b), 2(a) and (d), 3(a) and (b)). Hence, the legs are pointed later-

ally. In some segments, the smooth zones of *O. evamuelleriae* are dorsally drawn out into paired, conical humps or domes (Figure 1(c)). Each dome bore a spine (Figures 1(c) and 4(c)), possibly protecting the animal from predators^[6, 12, 21]. The Lower Cambrian *Xenusion auerswaldae*^[21] and the Middle Cambrian lobopodians *Hallucigenia sparsa*^[22], *H. fortis*^[12], and *Miraluolishania haikouensis*^[23] show spines similar to those of *O. evamuelleriae* presumably possessing telescopic movability^[3]. *H. sparsa* even had similar domes, from which the spines arose^[22]. Comparable dorsal outgrowths and telescopic spines are absent in extant Onychophora (Figure 1(a))^[20], but do occur in some Tardigrada^[24,25].

Like the inter-pedal regions of the body, the legs of *O. evamuelleriae* are micro-annulated, but their annuli are narrower (Figure 2(a)). The distal leg parts are missing, but the legs must have been much longer than the length preserved, since the longest preserved leg does not taper towards its distal end (Figure 2(a)). On the anteroventral and posteroventral sides of the legs, spine-like outgrowths (Figures 2(a) and 3(a)) occur on short, soft bases (Figures 2(a) and 4(a)). They were probably distributed ventrally along the entire leg and were, most likely, capable of being telescopic and retractable (Figures 2(a), 3(a), 4(a) and (b)). Comparable spine-like outgrowths seem to occur on the legs of other lobopodians, such as *Aysheaia pedunculata*^[15], *X. auerswaldae*^[21], and possibly *Miraluolishania haikouensis*^[23] and *Jianshanopodia decora*^[17], but tardigrades and onychophorans lack such structures^[20,25].

Towards the ventral midline of each leg, the spine-like outgrowths are accompanied by sets of outgrowths, here named dermal papillae (Figures 2(a), 3(a), and 4(a)). The texture of the cuticle indicates that the papillae were composed of several compartments referred to as cells (Figure 2(b)). These papillae might have had a sensory function, such as coordinating the retraction of spines during locomotion. There is a single median papilla towards the distal part of the leg (Figures 3(a) and 4(b)). Similarly-sized papillae, one median and two lateral ones also occur on each dorsal hump, near the bases of the spines (Figures 1(c) and 4(c)), and on the micro-annulated body region of certain segments ventrolaterally, halfway between two subsequent leg bars (Figures 1(b) and 2(b)). There are no such papillae on the smooth areas and on those smooth rings lacking conical humps. Among extant arthropod-like animals, similar dermal

papillae only occur in onychophorans, but they are much more abundant and have more cells and a sensory bristle at their tip (Figures 2(c) and 4(d)). In fossil lobopodians, Whittington^[15] described the so-called ‘tubercles’ scattered over the body surface of *A. pedunculata*. Based on their size and distribution, these ‘tubercles’ might also represent dermal papillae. We cannot exclude the possibility that the dermal papillae of *O. evamuelleriae* also had apical bristles originally (their absence may be a preservational or preparational artifact). The structural similarity of dermal papillae in *O. evamuelleriae* and extant onychophorans might indicate their homology. This type of sensory structures was possibly a feature common to the earliest arthropods.

One specimen of *O. evamuelleriae* shows an unpaired opening on one of the elevated bars connecting a limb pair (Figures 1(b) and 2(d)). Its mid-ventral position and axially oriented slit-like appearance strongly suggest that it is equivalent to the gonopore of the onychophorans (Figure 2(e)), where it is placed between either the last or the penultimate limb pair^[20,26]. Similarly, in the tardigrade group Heterotardigrada, the single gonopore is located pre-anally. Eutardigrada, by contrast, has a cloaca, i.e. the gonad opens into the end gut. If the orientation of the fossil specimen is as given in Figure 3(b), the gonopore of *O. evamuelleriae* was located in the fourth-last segment or even further anteriorly.

3 Discussion and phylogenetic implications

Paleontological records^[4–8,12–17] and the new species establish that marine lobopodians existed for at least almost 30 million years, from the Lower to the upper Middle Cambrian. Recent onychophorans are terrestrial, and their unknown lobopodian ancestors presumably existed at least until the development of anatomies suitable for life on land.

The overall anatomy of *O. evamuelleriae* is comparable to that of other lobopodians and extant onychophorans in having a soft, micro-annulated body and unjointed legs^[6,12,20,22], and is, like that of many other lobopodians^[8,9,13,16,22], of the long-legged type. One of the key morphologic innovations in arthropod history is the acquisition of segmentally arranged limbs^[1,10]. We propose in our model of arthropod evolution that the early legs not only were uniramous and tubular but also bore supporting structures, such as retractable or tele-

scopic spine-like outgrowths and probably even sensory papillae, as recognized in the new lobopodian. Equipped with such a limb design, early arthropods could accomplish complex movement patterns, although not operated and controlled by segmental ganglia (which are also absent in onychophorans). In Euarthropods, however, one pair of nerve ganglia is responsible for the limbs and all sensory structures of one segment. Locomotion in early arthropods presumably occurred by snaking of the body, and the limbs were alternatingly used to push the body forward using the spines as anchors on the soft substrate. The abaxial ventral bars served to stretch the limbs in a horizontal plane, and prevented them from dangling ventrally. As demonstrated in our specimens, ‘ventral dangling’ might not even occur after death. Preservation of the legs of other lobopodians, in two dimensions, seems to imply such a mode, but in such cases, not only the animals are lying on their sides, but also their leg pairs are pressed together. The possible existence of bars in these forms too is evident in images of *Paucipodia inermis*^[6] and *Miraluolishania haikouensis*^[23], with the latter being preserved with laterally extended limbs. This suggests that the lateral preservation of specimens is artificial and does not reflect life position. This might hold true also for at least some short-legged forms, as in *Jianshanopodia decora* whose limbs insert ventrolaterally^[17]. Consequently, walking on long, unsclerotized and unjointed limbs, as previously suggested for all lobopodians (Figure 3(c))^[3,13,16,27], is hardly conceivable. Subsequent changes in locomotory mechanisms followed in different arthropod lineages, i.e. Onychophora, Tardigrada, and the Arthropoda sensu stricto^[2,10].

Other taxa such as *Aysheaia* might indeed have walked on their legs, so it remains unclear which one of the two sets—legs hanging down or horizontally oriented—represents the plesiomorphic state. Thus, uncertainty remains as to whether early Arthropoda locomoted by walking or creeping. Though it is perhaps more compelling to have the horizontal-legs model to be plesiomorphic, we have only evidence for the Arthropoda sensu stricto^[2], clearly having lateroventrally oriented appendages. Their long limb rods, which consisted of about 20 articles, seem to favor the ‘horizontal-legs’ model. This would imply that the short length of legs in lobopodians is derived. Another uncertainty remains in that the limb rod of Arthropoda sensu stricto has no distal claw, while this is a common structure among lobopodians, onychophorans and tardigrades. The limb of

Arthropoda sensu stricto also possesses a flap (exopod) at the outer lateral edge of the limb rods, which represents a novel feature in arthropod evolution. These new characters of the limbs in Arthropoda sensu stricto indicate that they have been rather strongly modified from the original legs that evolved in the Arthropoda sensu lato. Hence, any assumption regarding the original state, no matter whether 'long-legged' or 'short-legged', is premature, since the morphological gap is too wide.

O. evamuelleriae also furnishes, uniquely for fossil lobopodians, details of the integument at cellular level and of the reproductive system. Some lobopodians, including *O. evamuelleriae*, were armed segmentally with paired dorsal spines^[6,9,15], possibly for protection. Domes with spines represent a feature that characterizes a possible (unnamed) taxon comprising the lobopodian species *Hallucigenia sparsa*, *H. fortis*, *Xenusion auerswaldae*, *Miraluolishania haikouensis*, possibly *Jianshanopodia decora* and *O. evamuelleriae* (comparable structures are unknown from other lobopodians, Onychophora, Tardigrada and Euarthropoda). However, this possible interpretation is too simple. *O. evamuelleriae* shows that in one individual, spines may occur on some body segments but not on the others, and this may represent a kind of tagmatization, the specialization of specific body parts. Other lobopodians such as *Onychodictyon ferox* and *Microdictyon sinicum* have paired dorsal plates that could potentially be drawn out into spines. The homology of all these structures and the direction of their evolution (character polarization) are uncertain.

Details of a gonopore in an arthropod fossil are demonstrated for the first time (Figures 1(b) and 2(d)), being single and ventrally pre-terminal. This gonopore also allows us a statement on the individual age of the presented material. The gonopore as exhibited by the lobopodian fossil presented herein is as differentiated as that of subadult to adult onychophorans. In onychophorans, the gonopore develops as a pair of simple pores lateroventrally on the posterior end of the embryo^[28]. During further embryogenesis, the pores migrate toward the ventral midline of the body. They fuse and appear as a differentiated opening as illustrated in Figure 2(e) not before a subadult stage already in cm range^[28]. Again, also in tardigrades, the gonopore appears not before at least a subadult stage^[25,29]. We therefore conclude that the material we presented of *O. evamuelleriae* represents at least a subadult stage. If lobopo-

dians are a reliable model for early arthropod design prior to sclerotization of body segments and appendages, the implication is that an unpaired genital opening represents the plesiomorphic character state within Arthropoda. Of significance for the ground pattern of this taxon, it may be one of the newly evolved (i.e. autapomorphic) characters of the stem species of this taxon. Thus, a single gonopore and paired gonads are assumed to be basal for all arthropods and plesiomorphically retained in onychophorans, chelicerates, myriapods and insects. Remarkably, the ground pattern of eucrustaceans includes paired gonads and a pair of gonopores. This situation must be derived among arthropods and is quite different from that in the ground pattern of annelids, where it is assumed that paired gonads and gonopores occurred in every segment. The cycloneuralians, the sister group of Arthropoda within Ecdysozoa, have a paired gonad and an unpaired gonopore. In this respect, arthropods clearly resemble other ecdysozoans rather than annelids, indicating that the situation in arthropods is a plesiomorphy.

4 Methods

(1) Specimen recovery. Specimens of *Orstenotubulus evamuelleriae* gen. et sp. nov. were recovered from limestone using acetic acid techniques^[10,18,30]. The onychophoran species *Metaperipatus blainvillei* (Gervais, 1853), *Metaperipatus inae* Mayer, 2007, and *Epiperipatus biolleyi* (Bouvier, 1902) were obtained from cultures (G.M.).

(2) Scanning electron microscopy (SEM). The onychophorans were fixed either in 7% formaldehyde or Bouin's fluid, dehydrated in an ethanol series, automatically dried in a critical-point dryer (BALTEC, CPD 030), coated with gold in a sputter coater (BALZERS, SCD 040) and examined in a Philips Quanta 200 SEM. The fossils were gold-coated, glued to SEM stubs and studied under a Zeiss DSM 962 SEM.

(3) Histology and light microscopy. Specimens of *M. blainvillei* were fixed in Bouin's fluid, dehydrated in an ethanol series, methylbenzoate, and butanol and embedded in paraplast (Kendall). Series of 5 μm thin sections were made on a microtome (Reichert-Jung, 2050 Supercut) with steel blades. The sections were stained with an Azan staining method and analyzed with a light microscope (Olympus BX2) equipped with a color digital camera (Colour view II, SIS).

This publication results from a participation in the COBICE project (Copenhagen Biosystematics Centre), which offered the use of facilities of the Zoological Museum Copenhagen to D.W. and A.M. The work of G.M. was supported by DFG grants BA 1520/8-2 and MA 4147/1-1. We gratefully

acknowledge the help of David Siveter, Leicester, UK, for reading the draft and giving valuable suggestions. Dong Xiping, Beijing, Xiao Shuhai, Blacksburg and an anonymous reviewer gave helpful comments.

- 1 Maas A, Waloszek D, Chen J Y, et al. Phylogeny and life habits of early arthropods — predation in the early Cambrian sea. *Prog Nat Sci*, 2004, 14: 1–9
- 2 Waloszek D, Chen J Y, Maas A, et al. Early Cambrian arthropods—new insights into arthropod head and structural evolution. *Arthr Str Dev*, 2005, 34: 189–205
- 3 Conway Morris S, Whittington H B, Briggs D E G, et al. Atlas of the Burgess Shale. London: The Palaeontological Association, 1982
- 4 Ramsköld L, Hou X G. New early Cambrian animal and onychophoran affinities of enigmatic metazoans. *Nature*, 1991, 351: 225–228
- 5 Ramsköld L. Homologies in Cambrian Onychophora. *Lethaia*, 1992, 25: 443–460
- 6 Chen J Y, Zhou G Q, Ramsköld, L. A new Early Cambrian onychophoran-like animal, *Paucipodia* gen. nov., from the Chengjiang fauna, China. *Trans R Soc Edinb, Earth Sci*, 1994, 85: 275–282
- 7 Hou X G, Bergström, J. Cambrian lobopodians—ancestors of extant onychophorans? *Zool J Linn Soc*, 1995, 114: 3–19
- 8 Budd G E, Peel J S. A new xenusiid lobopod from the Early Cambrian Sirius Passet fauna of north Greenland. *Palaeontology*, 1998, 41: 1201–1213
- 9 Ramsköld L, Chen J Y. Cambrian lobopodians: morphology and phylogeny. In: Edgecombe G D, ed. *Arthropod Fossils and Phylogeny*. New York: Columbia University Press, 1998. 107–150
- 10 Maas A, Waloszek D. Cambrian derivatives of the early arthropod stem lineage, pentastomids, tardigrades and lobopodians—an ‘Orsten’ perspective. *Zool Anz*, 2001, 240: 449–457
- 11 Monge-Nájera J, Hou X G. Disparity, decimation and the Cambrian ‘explosion’: comparison of early Cambrian and present faunal communities with emphasis on velvet worms (Onychophora). *Rev Biol Trop*, 2002, 48: 333–351
- 12 Bergström J, Hou X G. Cambrian Onychophora or xenusians. *Zool Anz*, 2001, 240: 237–245
- 13 Dzik J. Early Cambrian lobopodian sclerites and associated fossils from Kazakhstan. *Palaeontology*, 2003, 46: 93–112
- 14 Bergström J, Hou X G. Chengjiang arthropods and their bearing on early arthropod evolution. In: Edgecombe G D, ed. *Arthropod Fossils and phylogeny*. New York: Columbia Univ Press, 1998. 151–184
- 15 Whittington H B. The lobopod animal *Aysheaia pedunculata* Walcott, Middle Cambrian, Burgess Shale, British Columbia. *Phil Trans R Soc London, B*, 1978, 284: 165–197
- 16 Hou X G, Aldridge R J, Bergström J, et al. The Cambrian fossils of Chengjiang, China — The Flowering of Early Animal Life. Malden: Blackwell, 2004
- 17 Liu J, Shu D G, Han J, et al. A large xenusiid lobopod with complex appendages from the Lower Cambrian Chengjiang Lagerstätte. *Acta Pal Pol*, 2006, 51: 215–222
- 18 Waloszek D. The ‘Orsten’ window—a three-dimensionally preserved Upper Cambrian meiofauna and its contribution to the understanding of the evolution of Arthropoda. *Pal Res*, 2003, 7: 71–88
- 19 Mass A, Braun A, Dong X P, et al. The ‘Orsten’ — More than a Cambrian Konservat-Lagerstätte yielding exceptional preservation. *Palaeoworld*, 2006, 15: 266–282
- 20 Storch V, Ruhberg H. Onychophora. In: Harrison F W, Rice M E, eds. *Microscopic Anatomy of Invertebrates*. New York: Wiley, 1993. 11–56
- 21 Dzik J, Krumbiegel G. The oldest ‘onychophoran’ *Xenusion*: a link connecting phyla? *Lethaia*, 1989, 22: 169–181
- 22 Conway Morris S. A new Metazoan from the Cambrian Burgess Shale of British Columbia. *Palaeontology*, 1977, 20: 623–640
- 23 Liu J, Shu D G, Han J, et al. A rare lobopod with well-preserved eyes from Chengjiang Lagerstätte and its implications for origin of arthropods. *Chin Sci Bull*, 2004, 49(9): 1063–1071
- 24 Kristensen R M. Sense Organs of Two Marine Arthrotardigrades (Heterotardigrada, Tardigrada). *Acta Zool*, 1981, 62: 27–40
- 25 Kristensen R M, Higgins R P. Revision of *Styraconyx* (Tardigrada: Halechiniscidae), with Description of Two New Species from Disko Bay, West Greenland. *Smith Contr Zool*, 1984, 391: 1–40
- 26 Mayer G. Origin and differentiation of nephridia provide no support for the Articulata. *Zoomorphology*, 2006, 125: 1–12
- 27 Budd G E. Why are arthropods segmented? *Evol Dev*, 2001, 3: 332–342
- 28 Walker M H, Tait N N. Studies of embryonic development and the reproductive cycle in ovoviviparous Australian Onychophora (Peripatopsidae). *J Zool*, 2004, 264: 333–354
- 29 Bertolani R, Grimaldi De Zio S, D’Addabbo Gallo M, et al. Postembryonic development in heterotardigrades. *Monitore Zoologico Italiano (N.S.)*, 1984, 18: 307–320
- 30 Waloszek D, Müller K J. Upper Cambrian stem-lineage crustaceans and their bearing upon the monophyletic origin of Crustacea and the position of *Agnostus*. *Lethaia*, 1990, 23: 409–427