

Possible Ediacaran ancestry of the halkieriids

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ABSTRACT

Diverse faunas with mollusks, brachiopods, and possible annelids are known from the earliest Cambrian. No doubt, body plans of these spiralian phyla diversified and probably originated well within the Ediacaran. The Ediacaran fossils of soft-bodied animals, although rather bizarre taphonomically and ecologically, remain virtually the only source of paleontological evidence on these events. Among the most controversial trochozoan spirilians of the Cambrian are halkieriids (interpreted as early mollusks or annelids). Their possible relative among the ediacarans is *Kimberella*, believed to be a mollusk. The anatomy of *Kimberella*, as currently understood, is rather distant from typical mollusks and this introduces some uncertainty regarding its widely accepted identity as a pre-Cambrian member of the Spiralia. It is suggested here that the gap in the stratigraphic succession and morphological series of forms may be filled with the Namibian *Ausia*, an undescribed specimen of which shows some similarity to the halkieriids and to *Kimberella* in the distribution of dorsal cuticular protuberances. The molluscan affinity of the mid-Cambrian *Wiwaxia* and *Odontogriphus*, which are at least superficially similar to the halkieriids, is another question. Their jaw apparatuses resemble molluscan radulae rather remotely, instead showing more similarity to ancient eunicid polychaete jaws, as for example the Ordovician *Archaeoprion*.

RÉSUMÉ

Depuis le Cambrien le plus reculé on connaît des faunes diverses avec des mollusques, des brachiopodes et des annélides possibles. Il n'y a aucun doute que les schémas d'organisation anatomique de ces phyles spiraliens se sont diversifiés et ont eu leur origine probablement pendant l'Ediacara. Les fossiles d'animaux à corps mou édiacariens, bien qu'ils soient assez bizarres taphonomiquement et écologiquement, restent en fait la seule source d'évidence paléontologique de ces événements. Parmi les spiraliens trochozoaires les plus controversables du Cambrien sont des halkieriids (qu'on interprète comme de premiers mollusques ou comme des annélides). Leur parent possible parmi les édiacariens est *Kimberella*, qui on croit était un mollusque. L'anatomie de *Kimberella*, comme nous la comprenons couramment, ressemble peu aux mollusques typiques; et ceci présente quelque incertitude au sujet de son identité, généralement acceptée, comme un membre précambrien des Spiraliens. On suggère ici que le vide dans la succession stratigraphique et les séries morphologiques de formes peut être rempli par l'*Ausia* namibien, duquel un spécimen inédit montre quelque ressemblance aux halkieriids et à *Kimberella* quant à la distribution de protubérances de cuticule dorsales. L'affinité molluscoïde de *Wiwaxia* et *Odontogriphus* du Cambrien moyen, qui sont au moins superficiellement semblables aux halkieriids, est une autre question. Leurs appareils de mâchoire ressemblent très peu à des radulae molluscoïdes, ayant plutôt une plus grande ressemblance à des mâchoires des polychètes eunicides anciens, comme par exemple l'*Archaeoprion* de l'Ordovicien.

INTRODUCTION

Recent development in molecular phylogenetics of the Metazoa, initiated by the seminal paper of Aguinaldo et al. (1997), imposed new and unexpected demands on paleontology. It has to mediate between conflicting views derived from analysis of either morphological characters or nucleotide sequences, because the emerging pictures of high rank groupings of animal phyla is not quite consistent with their traditional classification. This discrepancy has resulted from a loss of information on ancient evolutionary stages, which is usually preserved in some traits of Recent animals, during a half billion years of their transformations. Also the difficulties with distinguishing the original simplicity from secondary simplification contribute to distortion of the morphology-based phylogenetic tree. No doubt that it is the duty of paleontologists to find and present evidence on lost characters and extinct ancestors.

In respect to evolutionary unity of animals shedding their cuticle, the Ecdysozoa, the fossil evidence supporting this taxonomic unit was available already before the molecular data emerged (Dzik and Krumbiegel, 1989; Harvey et al., 2010). Also the early emergence of chordates in respect to other deuterostomes, as well as the basal position of ctenophores, seem consistent with the fossil record (Conway Morris and Collins, 1996; Dzik, 2002). What is much more problematic, is the ability of paleontology to decipher early evolution of the large branch of protostomes characterized by planktonic larva and spiral cleavage, that is the Spiralia (or Lophotrochozoa).

The Spiralia comprise the most terminal branch in recently proposed molecular phylogenetic trees of the Metazoa (Helmkamp et al., 2008; Paps et al., 2009). It is now widely acknowledged that their few shared unique morphological characters, mainly the trochophora-like pelagic larva and capillary setae secreted by microvilli-bearing cells, are true evolutionary novelties. More problematic are hypotheses on the evolution of their body plan, and there is no convincing theory proposing what exactly the ancestral status was. Among speculative scenarios are ideas such as derivation of the spiralian annelids from the ecdysozoan nematomorphs, which cite similarity in the mode of locomotion and structure of integument (with the early Cambrian problematic *Myoscolex* as a connecting link; Dzik, 2004), or derivation of lophophorates from mollusks, represented by the Cambrian *Halkieria*, proposed to be another connecting link, by bending in half its body with two dorsal shells (Conway Morris and Peel, 1995).

This alone calls for more evidence on possible pre-Cambrian relatives of these organisms. This is not so easy because of a rather fundamental disparity between the Cambrian and Vendian fossil record, preventing direct tracing of lineages across the boundary. At least three factors contribute to difficulties with finding comparable sources of fossil

evidence across the Vendian-Cambrian boundary (e.g., Dzik, 1994, 2005): (1) invention of peristaltic burrowing near the end of the Ediacaran resulted in subsequent destruction of microbial mats, which dramatically reduced the extent of the biota living on them and ceased their Ediacaran-style fossilization; (2) invention of mineral skeletons (having probably the same cause—selective pressure from macroscopic predators) secured abundance of skeletal fossils; and (3) probably climate-controlled extensive phosphatogenesis resulted in abundance of microscopic phosphatized mineral debris and delicate organic structures (including eggs with embryos inside).

As a result, about sixty million years separate the Early Cambrian abundance of phosphatized fossils from the preceding, taphonomically similar, Doushantuo phosphorites. Thus, virtually all the animal lineages traced back to near the base of the Cambrian (owing to their phosphatized fossil remnants) truncate at its boundary with the Vendian. Also the halkieriids, almost certainly belonging to the Spiralia, are among high-rank taxa suffering from this discrepancy in taphonomic conditions between the periods.

No doubt that body plans of the spiralian and other main animal phyla originated in, or at least not much before, the Vendian. The Ediacaran faunas, although both taphonomically and ecologically rather bizarre, remain virtually the only source of fossil evidence on such events. Unfortunately, metazoan affinities of the Ediacarans are still only weakly supported. Thus, indirect trace fossil evidence suggests that the priapulid body plan emerged near the end of the Ediacaran, and this is the oldest record of the Ecdysozoa (Dzik, 2005, 2007). Although consistent with molecular expectations, possible relationship between the Ediacaran petalonamean ‘sea pens’ and the ctenophores (Dzik, 2002) awaits convincing connecting links before it is accepted. Some putative anatomical homologies between the dickinsoniid dipleurozoans and chordates were also suggested (Dzik, 2000). *Kimberella* is believed to represent mollusks in the Ediacaran (Fedonkin and Waggoner, 1997; Fedonkin et al., 2007), but there is hardly any Cambrian mollusk with apparent resemblance to it. This introduces some uncertainty regarding affinities of this widely accepted pre-Cambrian member of the Spiralia.

It is suggested here that, despite taphonomic impediments, the gap in the stratigraphic succession of fossil Spiralia may be filled with *Ausia fenestrata* Hahn and Pflug, 1985 from the latest Precambrian of Namibia. I present below some new information on the morphology of this controversial enigmatic fossil and propose its provisional interpretation as a cuticular structure with serially arranged weakly sclerotized protrusions. If true, such organization would make *Ausia* similar to the Early Cambrian sachtids (halkieriids) and the alleged limpet-like Precambrian mollusk *Kimberella*. Reinterpretation of the anatomical restoration of the latter is also forwarded here.

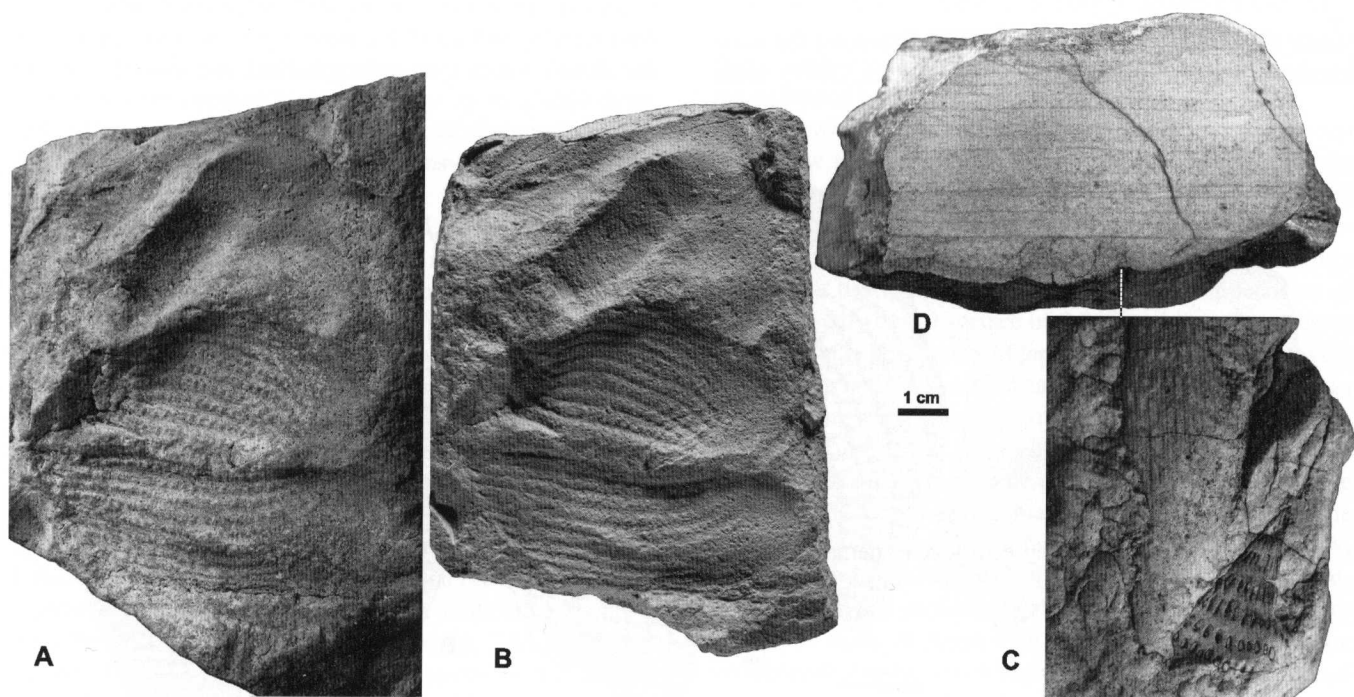
MATERIAL AND METHODS

I studied the specimens from the Ediacaran of Namibia referred to in this paper when they were in the care of the late Hans Pflug at his home in Lich near Gießen. Most of them were subsequently transferred to the National Earth Science Museum in Windhoek, Namibia (abbreviated NESM). Such is the present location of the holotype of *Ausia fenestrata* Hahn and Pflug, 1985, labeled GU Pf 393 at the time of my examination (originals were prefixed with the acronym GU Pf, as being temporarily at the University of Gießen, whatever their final placement) but now NESM F542. It was collected on the Aus field of the Plateau farm from the Kliphoek Member of the Dabis Formation, Nama Group. The strongly folded fossil is preserved near the inferred base of a white sandstone bed. The matrix of the fossil is unstratified and full of randomly distributed rolls of probable microbial mat (Text-fig. 1C), but the bed above is distinctly laminated and composed of pure quartz sand. This is consistent with Jenkins' (1985, p. 338) interpretation of the Nama group fossil assemblages as preserved in storm-produced beds of sandy

sediment. Apparently, conditions of the sand sedimentation stabilized after the catastrophic deposition event.

The current whereabouts of the second small-size specimen, GU Pf 131, are unclear. It has not been traced in the collection of Windhoek Museum (Helke Mocke, Geological Survey of Namibia, personal communication, 14/12/2007). Silicone and plaster casts of it are housed at the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw; I took also photographs of the original. It is preserved in gray non-laminated sandstone on the surface of a relatively large block.

In 2001 I had an opportunity to participate in an expedition, organized by Andrey Y. Ivantsov from the Paleontological Institute of the Russian Academy of Sciences, to the Zimnie Gory locality of Vendian fossiliferous strata at the White Sea shore in northern Russia. I assisted there in collecting *Kimberella* fossils and did a taphonomic study, results of which were used to interpret anatomy of other Vendian organisms (Dzik, 2003). It appears that the surface morphology of fossils such as *Kimberella*, preserved as depressions on the basal surface of sandstone lenses, was stabilized by early



Text-fig. 1. *Ausia fenestrata* Hahn and Pflug, 1985 in sandstone blocks of the Kliphoek Member of the Dabis Formation, Nama Group, collected on the Aus field of Plateau farm in Namibia. **A–B.** Specimen GU Pf 131 as preserved in gray sandstone (**A**) and its plaster cast (**B**). **C–D.** Strongly folded membrane of the holotype NESM F542 (formerly GU Pf 393) as seen on the inferred lower surface of white sandstone (**C**) and in cross section (**D**); broken line connects the same part of the specimen in different views; note non-stratified rock matrix surrounding the fossil compared with the laminations above it.

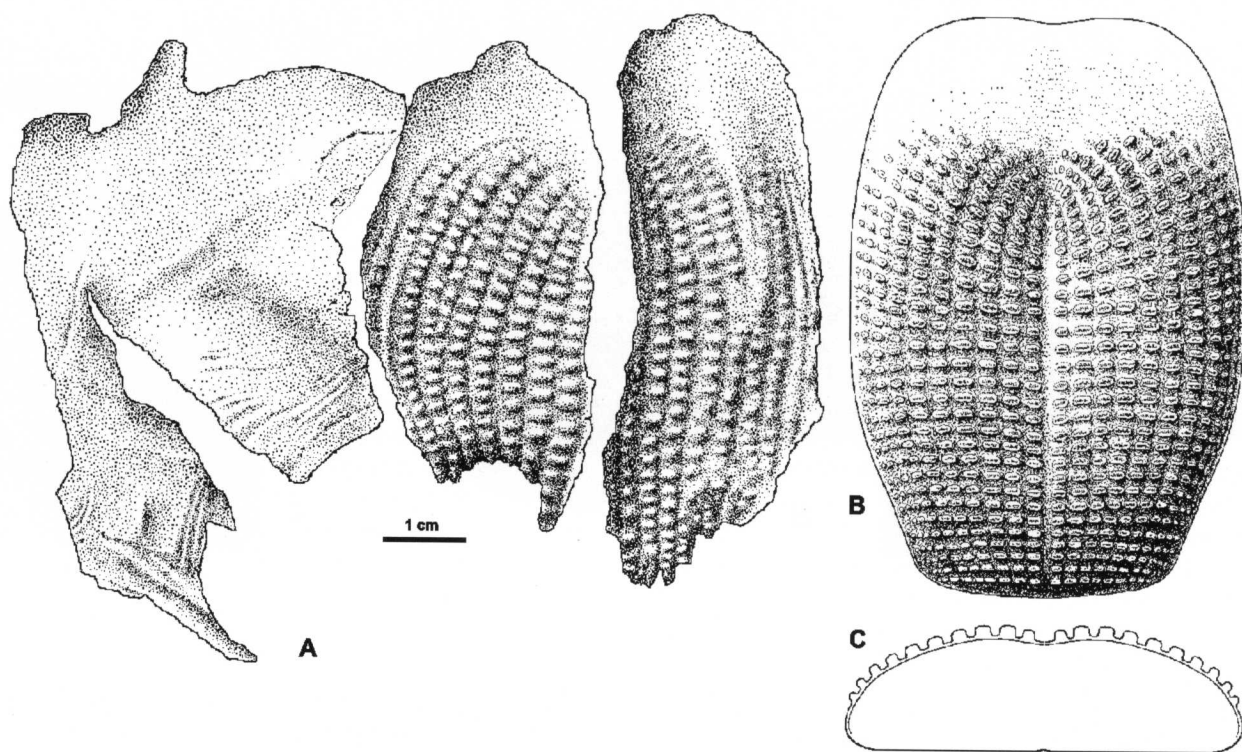
cementation of the rock with iron sulfides. The presence of pyritic cement only in close proximity to the rock sole suggests that the decaying body and microbial mat were the source of sulfur ions, whereas the suddenly deposited sand provided iron (Dzik, 2003). 'Stretch marks' penetrated with fluidized sand together with concave bedding of sandstone lenses indicate that their deformation was synsedimentary (load structures). The sediment was non-consolidated and organic structures remained intact even after cementation of the boundary surface took place (Dzik, 2003; contrary to Fedonkin et al., 2008b, who interpret sandstone lenses as sediment-filled canals in the underlying clay, despite their concave bedding). These taphonomic peculiarities enabled preservation of the dorsal surface of Ediacaran soft-bodied organisms at various stages of their decay and compression under the sand load. This reasoning is used below to re-interpret published data on *Kimberella*. Examination of original specimens housed at the Paleontological Institute of the RAS in Moscow (PIN) and plaster casts of some specimens from that collection given to me by Andrey Y. Ivantsov were of much help in these efforts.

REINTERPRETATION OF *AUSIA*

Ausia fenestrata Hahn and Pflug, 1985 is among the least known of the Namibian fossils (Vickers-Rich, 2007). Both

the holotype GU Pf 393 (Text-figs. 1C, D) and the other probably conspecific specimen NESM F542 (Text-figs. 1A, B) represent a discontinuity within the sandstone bed presumably corresponding to an organic wall embedded in the suddenly deposited sand. No signs of collapse of any associated soft tissue are recognizable.

My examination of the holotype slab supports the suggestion by Hahn (*in* Hahn and Pflug, 1985, p. 4) that this is a complexly rolled continuous membrane rather than two separate individuals. The membrane may have been torn into pieces but this cannot be determined with certainty because the sandstone slab is broken and the fossil is incomplete. Most of it is represented in the form of a flattened cylinder. Its exposed convex surface is covered with regular rows of elongated oval protuberances. They are worn and do not show tips, but their nature is revealed in the conical portion exposed from the concave side. Seen as dimples in the original description (Hahn and Pflug, 1985), they were incorrectly interpreted as openings (each leading to a small polyp); this was apparently followed by Fedonkin (1996), who proposed an archaeocyath affinity of *Ausia*, and by Fedonkin et al. (2008a), who suggested a relationship to ascidians. Some dimples are completely free of sediment and show gently concave, smooth, oval bottoms leaving no doubt that they were closed. Each dimple is up to 4.0 mm long and about 1.2 mm wide at its base; their bases are about 1.8 mm apart in longitudinal, and about 0.8 mm in



Text-fig. 2. *Ausia fenestrata* Hahn and Pflug, 1985, drawing of the preserved parts of the exfoliated membrane (cuticle?) possibly representing four units of the body covers in specimen GU Pf 131 (A) and tentative restoration of its appearance in dorsal view (B) and cross section (C).

transverse rows (orientation of the rows is discussed below in connection with the other specimen).

The conical part of the holotype shows significant deformation that probably originated when the sand bed was deposited and the enclosing membrane became folded. Near their tips, the dimples are laterally constricted into fissures but their longitudinal distribution remained regular and distances are like those in the non-deformed portion of the membrane. This indicates some flexibility but also certain stiffness of the original membranous organic skeleton. Unlike other Namibian fossils (Vickers-Rich, 2007) similarly preserved within the sandstone beds (*Ernietta* or *Pteridinium*), deformations that could result from elastic extensions of the membrane are not so apparent. The membrane behaved rather like external cuticle, not like collagenous basement membrane of internal organs (e.g., Dzik, 1999, 2003).

Fragmentary preservation of the holotype of *Ausia fenestrata* prevents any reasonable restoration of its original shape and arrangement of the membrane. This is partially enabled by the second specimen GU Pf 131. It is significantly smaller than the holotype and of more complex organization. Despite the difference in size and imperfect preservation, its species identity is supported by the presence of regular rows of transversely elongated, elevated structures. Their tips are worn but it seems likely that they correspond to dimples in the holotype. Their exact shape cannot be determined, but their tips were apparently separated by up to a little more than 3.0 mm in longitudinal rows (instead of almost 5 mm in the holotype) and about 1.5 mm in transverse rows (instead of about 2 mm).

On the surface of slab GU Pf 131, there are two well delimited tongue-like membrane units in a mirror image arrangement. The rows of transversely arranged protuberances cover most of their surface, about ten on each unit, at least thirty protuberances in each row. A significant portion of each unit remains smooth. Behind this presumably anterior portion of the membrane, the rows of protuberances curve towards the symmetry axis separating the units. Some of the rows seem to furcate and at least one additional row developed in the mid-length. The rows are parallel to each other up to the transversely truncated, presumably posterior end. Lateral margins of the units are somewhat raised. Imprints of similarly paired but smooth membrane units are associated with the paired ornamented ones (Text-fig. 2A). That they belonged to the same individual is suggested by the similarity of the medial elevation separating each pair, the rounded appearance of one end, and the transverse truncation of the opposite, with indistinct transverse wrinkles nearby. The mode of deformation of the completely smooth units is suggestive of some elasticity. If the correspondence between them is real, the fossil would represent four units, each in a mirror-image symmetrical relationship. The prominently ornamented and stiffer pair of the units may have been protective, and thus dorsal, whereas the smooth units with deli-

cate transverse wrinkles may have been the ventral portion of the body. The elevated medial belts separating both pairs of units seem to have originated as a result of folding and tearing. This suggests the presence of mechanically weaker zones along the midline of the body, on both the dorsal and ventral sides. One may interpret such a disposition of units as an expression of modified tetrameric and possibly originally biradial organization (like the priapulid larva). Such organization could have been a modification of biradial tetrameric symmetry, known in some other Ediacarans, e.g., *Ernietta* (Dzik, 1999), and perhaps also in the frondose petalonameans (Dzik, 2002), but also in cuticle-covered larvae of the priapulid worms. Whether the suggested separation of dorsal and ventral sets of cuticular units is a result of exuviation or rather post-mortem decomposition cannot be decided with the material in hand.

If correctly interpreted, the original form of the body of *Ausia* would be oval sac-like, with the dorsal and ventral sides different and opening obliquely at one end (presumably posterior). This makes it possible that the fossil from the same locality, named *Kuibisia glabra* by Hahn and Pflug (1985) and suggested to be synonymous with *Ernietta* (Runnegar and Fedonkin, 1992) or *Namalia* (Grazhdankin and Seilacher, 2005), represents a poorly preserved but more complete *Ausia* seen from the side with tuberculation. This is further supported by the conical appearance of this fossil and the deformed portion of the *Ausia* holotype.

Somewhat confusingly, the holotype and smaller specimen show the membrane either convex or concave on the tuberculated side. In the holotype, the membrane was rolled transversely to the body axis. In the other specimen the central parts are slightly convex, but marginal areas are slightly concave. It has to be decided what the actual appearance of the supposedly dorsal surface of the animal was. The present condition may be a matter of taphonomy of Ediacaran fossils preserved within unstratified sandstone beds, presumably as a result of instantaneous deposition from suspension, together with a sand matrix. In such preserved membranous fossils, the lower side tends to be convex. This factor may have controlled distortion of the smaller specimen. Folding of the holotype, which shows no preferential orientation in the rock, seems to express predisposition of the cuticle to bend according to its original geometry. Following this assumption, I restored the body of *Ausia* with each unit externally convex and separated in pairs by a slight concavity along both dorsal and ventral midlines (Text-figs. 2B, C).

A completely different interpretation, which cannot be rejected at present, would be that the membrane was originally covered with a series of depressions. They could have held bases of some serially arranged organs. Their transverse extension may suggest that these were comb- or scale-like units (perhaps setae?). The fossil would then represent not a cuticle, but the basement membrane underlining externally located muscular structures. In such an interpretation, the el-

evated bands separating the rows of dimples, being rounded in cross section, may have covered canals of nourishing functions, perhaps forming a network penetrating the spaces between depressions. Although possible, such anatomy has no analogues in other organisms known to me and seems unlikely. The main difficulty with the model of depressions holding unpreserved organs is the supply of nourishment from the interior of the body which was separated by an imporous membrane.

As typical for the ediacarans, not much information is offered by fossils of *Ausia*, and its biological interpretation is further hampered by the lack of close zoological analogues. Thus, any anatomical restoration remains conjectural at best. Along with its inferred stiffness, yet another reason to suggest that the membrane of *Ausia* represents a cuticular structure (perhaps an exuvium) is some similarity of the proposed body plan to that of the halkieriids, especially in the distribution of probable dorsal cuticular protuberances.

MOLLUSCAN AFFINITIES OF THE HALKIERIIDS

Isolated halkieriid sclerites (classified in the order Sachitida) are among the most common phosphatized Cambrian fossils but their actual nature remained unknown until the discovery of articulated fossils in the Early Cambrian of Greenland (Conway Morris and Peel, 1995). It appeared that sclerites of different morphology may belong to the same animal. Most of them are arranged in regular rows (Text-fig. 3). A surprising aspect of the morphology of *Halkieria* is the presence of two incrementally growing shells at opposite ends of the body. The anterior one resembles Cambrian conchs traditionally attributed to the helcionellid monoplacophorans. The meaning of this similarity, despite various attempts to interpret it in evolutionary terms, remains puzzling. Interestingly, the recently discovered, apparently more derived halkieriid relative *Orthrozanclus* from the mid-Cambrian Burgess Shale fauna, bears only one conch-like sclerite near the anterior end of its body (Conway Morris and Caron, 2007).

Because of their early geological age and bizarre morphology, the halkieriids attract attention as possible basal-most Spiralia, that is, lophotrochozoans. Conway Morris and Peel (1995) proposed that the body plan of brachiopods can be derived from that of *Halkieria* by bending it in half and making the oval terminal sclerites the ventral and dorsal brachiopod shell valves. Many isolated brachiopod-like Cambrian shells were attributed to the halkieriids since that proposal, but the diagenetically flattened shells of the originals are of too indifferent morphologically to support such identifications reliably.

The dorsal skeleton composed of numerous sclerites and surrounding more than one mineralized and accretionary growing plates makes the halkieriids at least remotely similar

to the amphineuran mollusks, including polyplacophorans. They are traditionally believed to be closer than conchiferans to the ancestral mollusk, but this is not well supported by the fossil evidence. Contrary to expectations, unquestionable fossils of isolated plates of the polyplacophoran armor are unknown from before the Late Cambrian (Vendrasco and Runnegar, 2004). The oldest articulated chitons bear the same number of plates as their extant relatives, that is eight, although their morphology is much simpler. Apart of the main lineage leading to Recent chitons, there are polyplacophorans of basically different morphology and mode of life in the early Paleozoic (Text-fig. 3). Of these, probably the most unusual morphology developed in the lineage that includes the oldest, known from the mid Ordovician (Blackriveran), namely *Echinochiton*. This genus is characterized by the main row of eight plates, which are backed from each side by two additional rows of large plates and numerous small lateral sclerites (Pojeta et al., 2003; Pojeta and DuFoe, 2008). Most probably, the Silurian *Hercolepas* represents the same lineage that continues to the mid-Devonian *Strobilepas* and Early Carboniferous *Polysacos*, in which plates of the medial row are greatly reduced in size (Vendrasco et al., 2004). These polyplacophorans resemble halkieriids in having several rows of dorsal sclerites, but these are robust calcareous plates, not thin sclerotic covers of flap-like soft tissue protuberances.

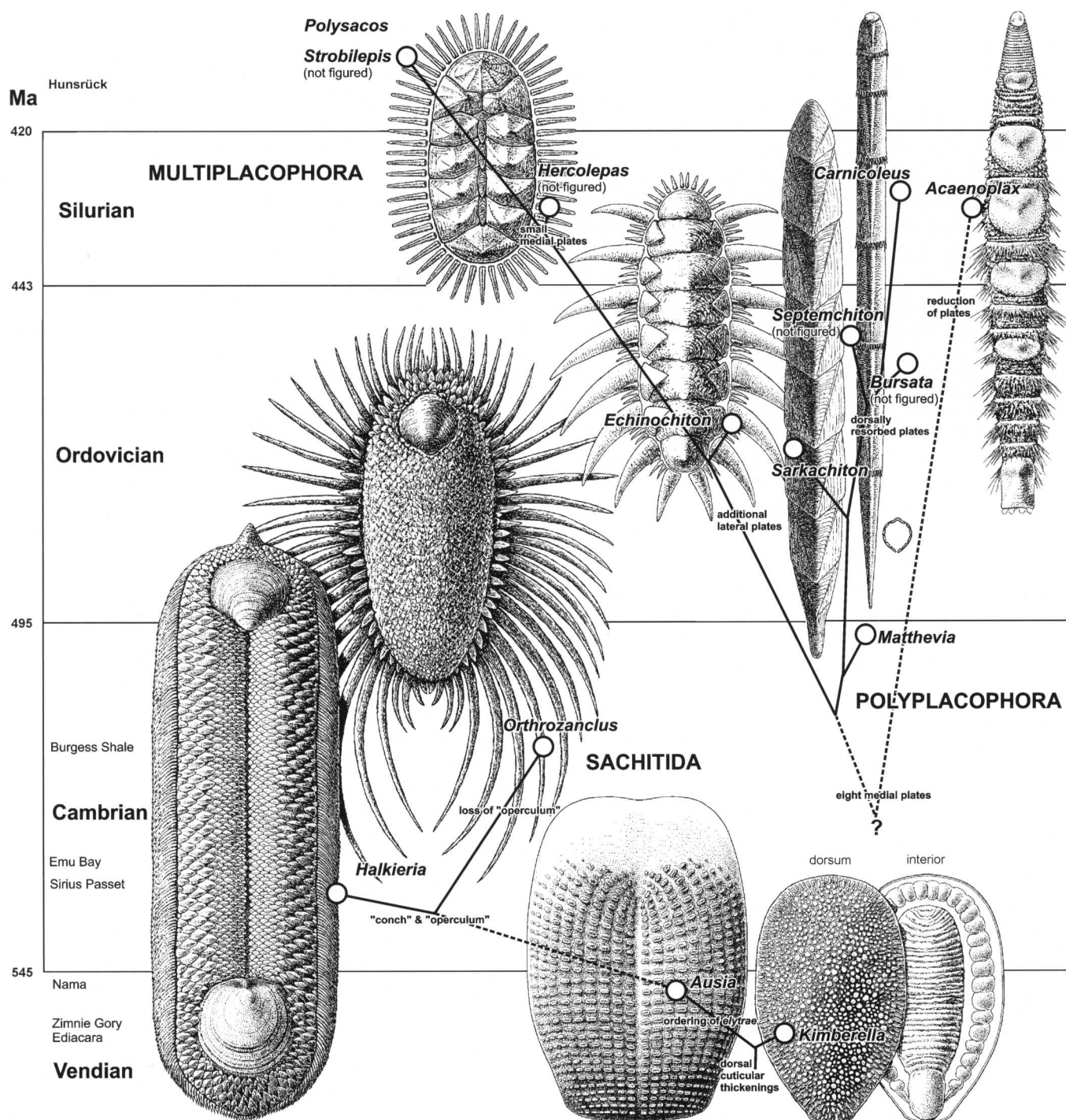
In yet another lineage of early polyplacophorans, the main attribute of mollusks, the foot, underwent gradual reduction. The final result of this trend, the Silurian *Carnicoleus*, had ventral margins of most of its plates merging along the midline. Their growth in size required resorption along the dorsal 'hinge' (Dzik, 1986) in the same way as in the rostroconch mollusks. A similarly reduced foot, replaced with a ventral furrow, characterizes Recent naked amphineurans, the Solenogastres. This may be a homology, but caution is suggested by somewhat similar organization of the skeleton developed independently in the Ordovician machaeridian polychaetes discussed below.

Thus it seems that if even the halkieriids were mollusks, there is no clear evidence of their direct relationship to any known class of this phylum. Similarities to the conchiferan (anteriorly located strongly convex 'conch' and rather flat posterior 'operculum') or amphineuran (minute sclerites, but of basically different origin) mollusks are too general and superficial to provide reliable phylogenetic information.

Whatever the systematic position of the halkieriids, it is almost certain that their roots should be looked for in the Vendian (Ediacaran). The expected body plan of their pre-Cambrian ancestor can be inferred from data on the anatomy of two relatively well known halkieriid relatives (the Sirius Passet *Halkieria* and Burgess Shale *Orthrozanclus*), but also from morphology of the least derived isolated halkieriid sclerites of Early Cambrian age. Among the

stratigraphically oldest (Tommotian) findings of this kind, probably the most informative are sclerites of *Sachites*.

These are relatively large sclerites; two kinds can be attributed to the same organism, as suggested by rather specific



Text-fig. 3. Stratigraphic distribution and suggested relationships of the halkieriids, *Ausia*, *Kimberella*, and earliest amphineuran mollusks; data compiled from sources reviewed in the text; lines connecting particular findings denote course of evolutionary transformations most parsimonious in respect to both morphological and time distances.

scale-like surface ornamentation (Dzik, 1994, fig. 9). Of these two, the sclerite type more typically halkieriid in its morphology is tubular, bent near its base, and transversely oval in cross section. In fact, it resembles morphologically particular 'rays' of composite sclerites of the associated problematic Chancelloriida. The other kind is hat-like, with a paraboloidal central tip and a wide rim. The earliest and generalized 'coeloscleritophorans', like *Sachites*, are of more conoidal appearance than more advanced flat sclerites of *Halkieria*. If one extrapolates backward this morphological series, the result would be similar to relatively low, transversely elongated protuberances on the membrane of *Ausia*. Also their arrangement seems to be consistent with the halkieriid body plan.

The next question, which emerges immediately, is: how did the regular distribution of protuberances in *Ausia* develop? Is it metamery resulting from serial arrangement of internal organs, or rather a secondary regularity, developed independently of the anatomical ground plan? There are some irregularities in the distribution of rows of protuberances in *Ausia*, but it is unclear whether they resulted only from the convexity of the body surface and whether a complete set of these structures was growing together with the body, possibly shed out as a continuous cuticular cover. If true, this would suggest some correspondence to underlying anatomical structures. An alternative would be that new protuberances were inserted during growth and thus growing individually (then actually representing sclerites). The most likely candidate for affinity with *Ausia* that may help in solving this question seems to be *Kimberella* from probably slightly older strata of Australia and northern Russia.

REINTERPRETATION OF *KIMBERELLA*

Kimberella quadrata (Glaessner and Wade, 1966) has a complex history of systematic attributions, originally described as a medusa from the classic Rawnsley Quartzite at Ediacara, Flinders Range of South Australia. Following description of much more informative materials from the Yorgia Beds of the Mezen Formation at Zimmie Gory, White Sea shore, Russia (Fedonkin and Waggoner, 1997), its interpretation as an early mollusk is widely accepted. Description of an extremely rich collection of over 8000 specimens (Fedonkin et al., 2007; Ivantsov, 2009) makes it one of the best-known Vendian (Ediacaran) fossils.

The basic premise in the reasoning of Fedonkin et al. (2007; e.g., caption of fig. 11) is that the surface of the fossil directly reproduces morphology of the ventral side of the body, that is morphology of a molluscan foot surrounded with a ribbon-like fringe of respiratory function, analogous to ctenidia. This results in some inconsistencies of interpretation: for instance, how is it that some specimens show morphology of the stomach and dorsal 'shell' at the same

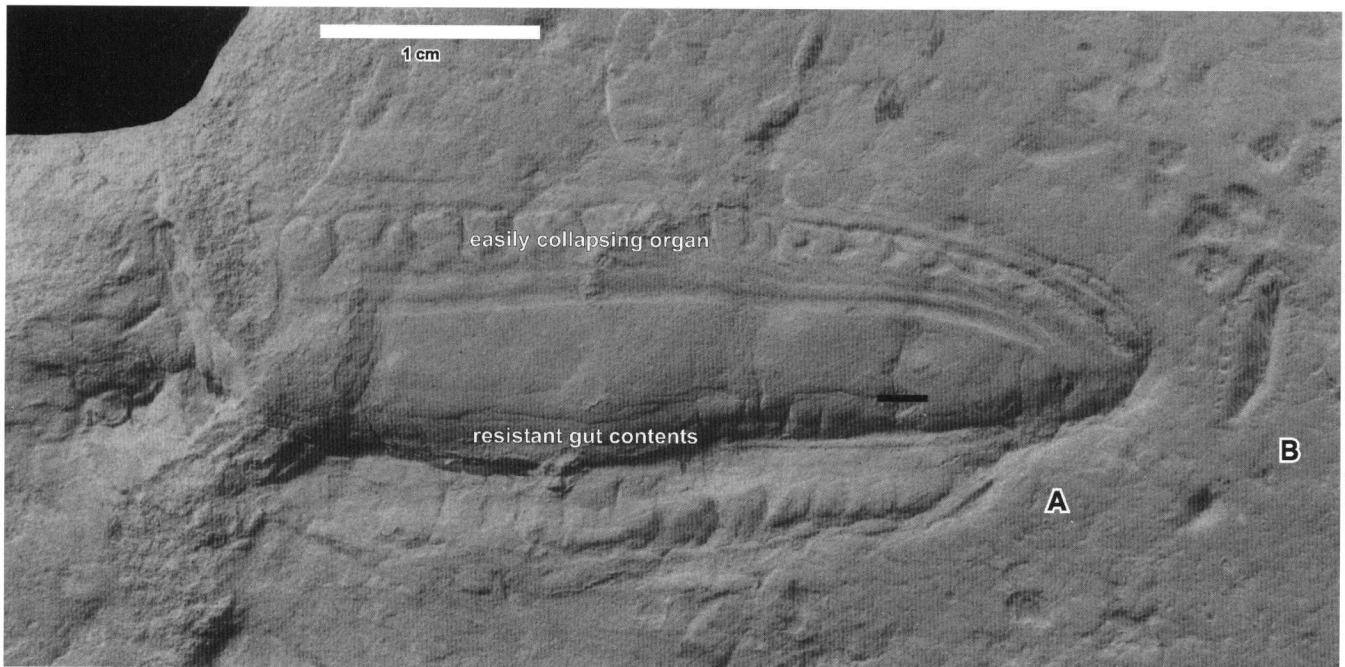
time? Because of assumed analogy (or even homology) with the sole of the molluscan foot and the allegedly limpet-like shape of the animal, the narrower part of the gut (overlooked by Fedonkin and Waggoner, 1997) was interpreted as a proboscis by Fedonkin et al. (2007) and Ivantsov (2009).

I propose to apply a different way of reasoning, which was originally invented for interpretation of *Dickinsonia*-like fossils from other beds at the Zimmie Gory locality (Dzik, 2003) and briefly described above under MATERIALS AND METHODS. If a sequential collapse of the body and preservation of its various stages by pyrite cementation is accepted, then interpretation of *Kimberella* would be dramatically different (Ivantsov, 2009). No one specimen would represent an imprint of the foot; this would require positive relief representation on the sandstone bed sole! Also the lateral irregularly crenulated zone can hardly represent any basally extending structure but is instead just an impression of an internal, easily collapsing organ, perhaps gonads or glands with a spacious internal cavity (Text-figs. 5A–F). The central part of the body is invariably represented by a deep depression because it corresponds to the clay-rich gut contents resistant to compression, occasionally displaced to one side (Text-fig. 4A).

Only in rare specimens, covered with sand cemented early enough to reproduce an intact surface of the body, is the dorsal surface covered with preserved tubercle-like protuberances. Such fossils are usually black with pyrite. In numerous specimens partially preserving the dorsum, it is more or less folded and the tubercles are of uneven size and shape. Commonly, minute tubercles occur in-between larger ones (e.g., Fedonkin et al., 2007, fig. 7). This suggests that they were inserted during growth of the body. Whether the whole structure was increasing its size only by insertion of permanent sclerite-like tubercles or whether it was periodically shed out as a whole, cannot be decided with the available evidence. In any case, it was not a molluscan periostracum, contrary to claims by Fedonkin et al. (2007), because its growth was definitely not incremental.

The restoration obtained in this way (Text-figs. 5G, H) shows an animal externally not unlike *Ausia*, but with irregular distribution of tubercles. It is also similar to halkieriids. Not being constrained by the alleged outline of the foot, I propose that the narrower part of the gut is actually posterior and the head region was located below the rounded, proposedly anterior part of the gut. This removes problems with scratch marks located behind the end of the body with an alleged proboscis, which forced Fedonkin et al. (2007, p. 174) to propose that "during the feeding process, the animal periodically moved backward."

The inferred presence of a radula-like feeding apparatus in *Kimberella* invokes the question of homology of the feeding apparatus in the mid-Cambrian putative halkieriid relatives *Wiwaxia* and *Odontogriphus*. Their size relative to body dimension and number of teeth roughly corresponds to scratches associated with *Kimberella*.



Text-fig. 4. *Kimberella quadrata* Glaessner and Wade, 1966, plaster cast from slab PIN 3993-4004 from the Yorga Beds of the Mezen Formation at Zimmie Gory, White Sea shore, Russia. Two specimens preserved on the sandstone lens sole; the large one (A) shows laterally displaced gut contents and completely collapsed internal organ surrounding the gut (gonad?); small specimen (B) shows outline of the gut.

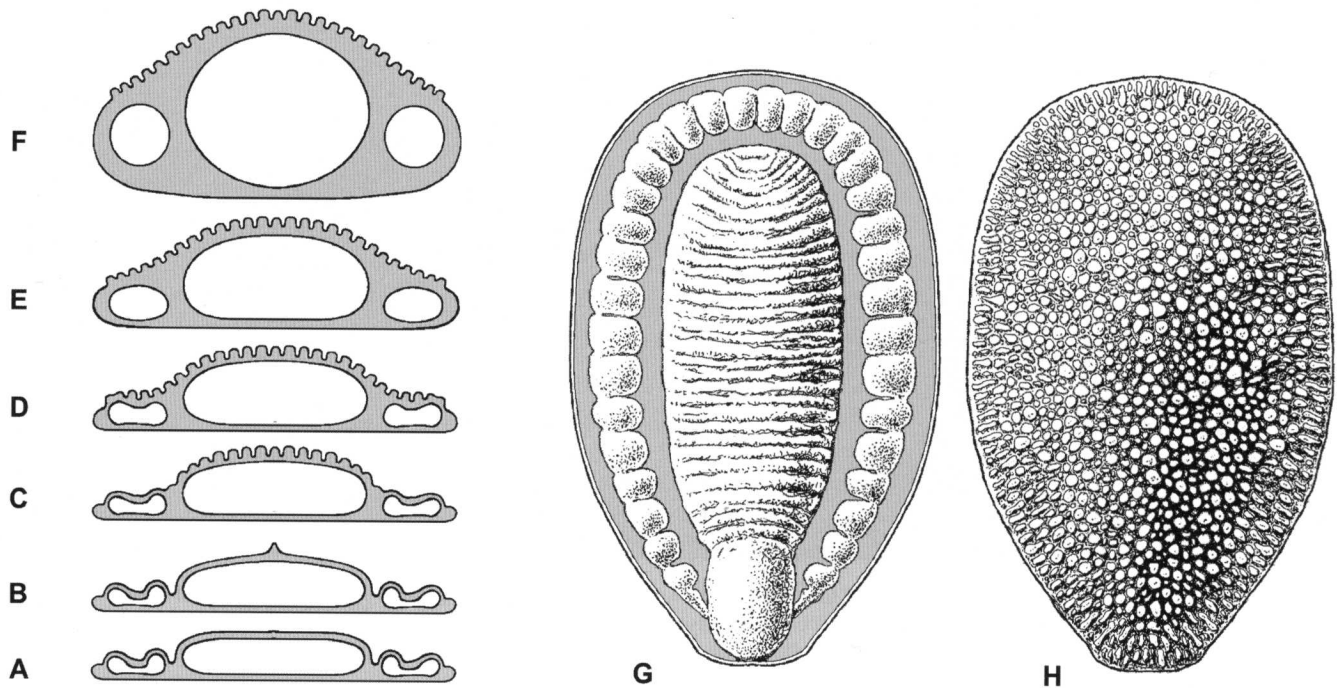
HOMOLOGY OF MOUTH APPARATUS

Halkieriid affinities of the Burgess Shale *Wiwaxia* were originally proposed because of alleged similarities in shape and arrangement of its large scale-like dorsal sclerites (Text-fig. 6), which represent three distinct morphologic groups (Conway Morris, 1985). This was challenged by Butterfield (1990, 2003, 2006) who identified internal capillary structures of these sclerites, which are closely similar to those of the associated polychaete *Canadia* but unknown in sclerites of undoubted halkieriids. He insisted on homologizing the *Wiwaxia* sclerites with setae of polychaetes, not with their elytrae.

Mineralized elytrae of polychaetes are common fossils in the Early Paleozoic and document evolution of the group classified as the Machaeridia. Their true nature was rather unexpectedly clarified by fossils with preserved soft parts (Vinther et al., 2008). Calcitic walls of advanced machaeridian elytrae developed significant thickness, with a deep muscle attachment scar (e.g., Dzik, 1986). Originally there were four rows of elytrae but the marginal rows gradually reduced their size and disappeared in some forms. Their evolution led towards a ‘segmented bivalve’ body plan that characterizes the most advanced members. Although advanced machaeridian calcified scales are very different from Recent polychaete elytrae or the sclerites of *Halkieria*, their underived form clearly shows that they developed as sclerotized covers of a flap-like extension of soft tissue (Dzik, 1986). The large

time gap between the earliest occurrence of the machaeridians and the last reported halkieriids call for caution in suggesting homology of their sclerites, but there is another kind of anatomical evidence that suggests an evolutionary connection between *Wiwaxia* and Early Palaeozoic polychaetes.

This evidence may be offered by the most intriguing aspect of the anatomy of *Wiwaxia*: its jaws, which are composed of two pairs of transverse series of strong teeth, sometimes with an additional pair behind (Conway Morris, 1985; Butterfield, 2006). Such jaws occur also in the mid-Cambrian *Odontogriphus* (Caron et al., 2006). *Odontogriphus* was originally classified as a lophophorate, and denticles in the jaws were suggested to represent ‘paraconodonts’ (Conway Morris, 1976). This resulted in a rather misleading attribution of this fossil to chordates (where ‘paraconodonts’ belong). Jaws of both *Wiwaxia* and *Odontogriphus* are generally believed homologous with the molluscan radula (Caron et al., 2006; Butterfield, 2006). Although some mollusks have radulae composed of small number of units, generally this organ is tape-like, with numerous transverse rows of chitinous teeth, and thus unlike the situation in *Wiwaxia* or *Odontogriphus*. But there is an alternative that should probably be considered (Butterfield, 2006): these jaws are more similar to some underived polychaete jaws as for example the Ordovician *Archaeoprion* (Mierzejewski and Mierzejewska, 1975), than to a radula. The eunicids, to which such fossil jaws (scolecodonts) probably belonged, occupy a rather basal position on the molecular tree of polychaetes (Struck et al., 2007), and



Text-fig. 5. *Kimberella quadrata* Glaessner and Wade, 1966. **A–F.** A series of diagrammatic cross sections showing succession of decay and collapse of internal body structures, with the most common representing only internal structure (**A**, similar to that shown in Text-fig. 4 or fig. 2 in Fedonkin et al., 2007) to almost perfect representation of the dorsal body surface (**F**, as in Text-fig. 5 in Fedonkin et al., 2007). **G.** Internal organs in dorsal view; it is suggested that the mouth opening was ventrally oriented and located under the center of the anterior (upper on the figure), rounded portion of the gut. **H.** Restoration of the dorsal surface of the body, with irregular distribution and variability in size of tubercles, suggestive of their insertion during growth.

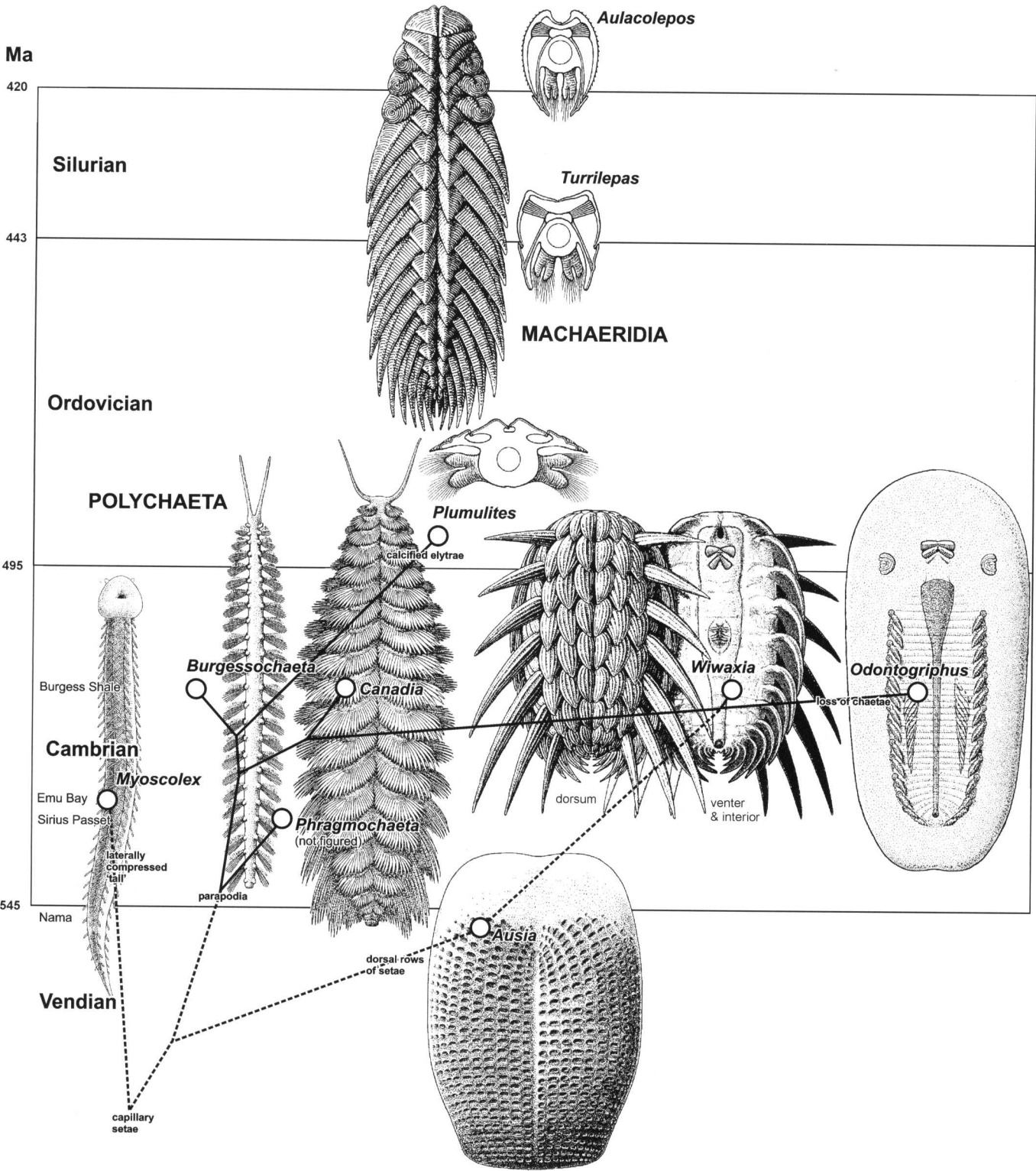
it is not unlikely that such morphology of a jaw apparatus is rooted deeply in the Cambrian.

Isolated Early Cambrian structures at least resembling the jaws of *Wiwaxia* are known (Butterfield, 2008). They were compared with molluscan radulae but, knowing the complexity of jaws of early polychaetes, one can hardly reject this alternative interpretation. Also the organic late Vendian fossil *Redkinia* may belong to this class of jaws (e.g., Sokolov, 1998, pls. 3:1 and 13:4). The zoological meaning of these fossils remains mysterious, however. The fossil record of unquestionable polychaetes, supported by soft part preservation, can be traced to the Early Cambrian Sirius Passet fauna (Conway Morris and Peel, 2008), but no jaw structures have been reported in Cambrian polychaetes.

This posits a problem not easily solved. The ideas of either a radular or a scolecodont nature for the *Wiwaxia* and *Odontogriffus* (perhaps also *Kimberella*) oral apparatuses cannot be married, because radulae and polychaete jaw apparatuses have different locations in the mouth. Whereas the radula is a ventral organ and has its denticles oriented upwards, the serial polychaete jaws (maxillae) develop on

the dorsal wall of the stomodeum (Dales, 1962). Interestingly, in some amphinomid polychaetes the ventral part of the pharynx, bearing transverse ridges, is everted to scrap food (thus working in the same way as a radula) (Tzvetlin and Purschke, 2005). The amphinomids are the most basal of extant polychaetes (Struck et al., 2007). Perhaps they preserved an ancestral status preceding evolutionary divergence of these two distinct kinds of oral apparatuses. The anatomy of the common ancestor of mollusks and annelids remains completely unknown.

There is a wide morphological gap between the polyplacophoran mollusks and polychaete annelids to be filled, if they are truly related. However, some Early Paleozoic fossils are difficult to place in either of these phyla and in several aspects they are anatomically transitional. Such is the Silurian worm-like *Acaenoplax* (Sutton et al., 2001). Its chaetation and annulation of the body are similar to those of annelids, but it bears seven chiton-like dorsal plates (note that in the Ordovician septemchitonids, the anteriormost plate is greatly reduced in size and tends to disappear). The geological age of *Acaenoplax* is too late to make retention of ancestral traits



Text-fig. 6. Stratigraphic distribution and suggested relationships of the earliest polychaete annelids known after complete body fossils; and *Ausia* interpreted as a fossilized basement membrane; data compiled from sources reviewed in the text.

self-evident. Another putative annelid, the problematic Early Cambrian *Myoscolex*, would merge annelids rather with the nematomorph ecdysozoans than with mollusks, if its anatomy is truly underived (Dzik, 2005). Layers of oblique, transversely oriented collagen cords in the integument (Harvey et al., 2010) and lateral waving of the body are possible synapomorphies of polychaetes and nematomorphs.

Placing the halkieriids with *Ausia* and *Kimberella* somewhere between annelids and mollusks is tempting but the available evidence is too scarce to take such phylogenetic interpretation seriously. Although limited, the new evidence on *Ausia* may have some bearing on the relationships of the enigmatic Cambrian group of the cancelloriids. These were sessile organisms, long classified as sponges because of superficial similarity of their cuticular sclerites to spicules. Despite the close similarity in sclerite structure between cancelloriids and halkieriids, they fundamentally differ in their body plan: the halkieriids are bilaterally symmetrical, whereas the cancelloriids are of radial organization. Rudimentary traits of tetra- or biradial organization of *Ausia* offers a hint as to how such a disparity could have originated in the course of evolution, providing some support to the concept of the Coeloscleritophora connecting halkieriids with cancelloriids (Bengtson and Hou, 2001; Janussen et al., 2002; Porter, 2008). One may speculate that strictly bilateral organization is an adaptation to crawling over the sediment surface, full radiality is an expression of sedentary mode of life, and both originated from a biradial free-living ancestor.

CONCLUSIONS

An earlier undescribed specimen of *Ausia fenestrata* from the late Vendian (Ediacaran) of Namibia shows that this was a bilaterally symmetrical organism with a morphologically complex dorsal side, whereas the venter was smooth. If the fossilized membrane was a cuticle with rows of transversely elongated protuberances (instead of basement membrane with dimples), *Ausia* is transitional morphologically between the Cambrian halkieriids and Ediacaran *Kimberella*. The latter organism, if its fossils are interpreted in terms of the 'Ediacaran death mask', had a cuticularized dorsum covered with irregular tuberculation, and a spacious gut filled with clay-rich contents, which was surrounded laterally and frontally by probable gonads that open near the posterior end of the body to a narrow proctodeum. The mouth was presumably located ventrally, under the anterior portion of the gut. The body plan shared by *Kimberella*, *Wiwaxia*, and probably the halkieriids, does not allow discrimination between their possible molluscan or annelidan affinities; however, the mouth apparatus of *Wiwaxia* and the feeding marks left by *Kimberella* better fit their interpretation as annelids armed with jaws on the dorsal wall of the stomodeum than as mollusks with a ventrally located radula.

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