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CHAPTER 13

Evolutionary Origin of Asymmetry in Early Metazoan Animals

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Introduction

In inanimate world, symmetry is uncommon and implies some order (information) to be introduced. It is probably why so much importance has been given to studies on symmetry in organisms. However, contrary to intuition, anatomical symmetry requires relatively little information to be involved and symmetric organisms are usually those of the simplest and most archaic anatomy. This is because the anatomical symmetry results from a rather trivial interactions of simple developmental mechanisms of morphogenetic field and cell clone. Although there is little doubt that the earliest animals were not asymmetric, it is far from being settled which kind of symmetry was ancestral for them and which of the extant organisms preserved it.

For a long time it was generally believed that Recent coelenterates, and especially the anatomically simplest hydroids among them, provide the clue to understanding the earliest stages in the evolution of the Metazoa (metazoans are multicellular animals characterised by some of their cells being underlined by collageneous basal membrane). Their radial symmetry would then represent the beginning of the story. However, most of the characters used to define the phylum Coelenterata are related to their anatomical simplicity that does not necessarily need to be primitive for the group. This especially refers to their allegedly original radiality, which seems to be contradicted by the presence of vestigial bilateral symmetry in the most primitive fossil members of the group [1]. Their present radiality can be interpreted as a consequence of their being sessile as polyps and/or passive planktonic drifters as medusae [2]. A secondary trend towards radiality on becoming sessile is very common among undoubtedly originally bilateral metazoan groups. Such interpretation of the evolutionary origin of the coelenterates is also consistent with the palaeontological evidence [3]. It appears thus that all Recent animals with a well developed radial organisation achieved it secondarily (the early evolutionary history of sponges remains obscure and is not considered here). Their anatomy cannot be directly used to restore the ancestral body plan of the Metazoa.

Anyway, even if the Recent coelenterates are most probably secondarily simplified, some kind of symmetry definitely characterised the initial stages of the metazoan evolution, as it is repeated today in their embryonic development. The development of antero–posterior polarity was probably the first step in the evolution of the anatomical organisation of the Metazoa [4]. An axial organisation, with identical body organs repeated radially around the body axis was probably the next step, as an expression of a polarity generated by the axial organs of the body. Resulting gradient of a morphogenetic factor presumably controlled activation of homeotic genes and creation of secondary morphogenetic fields around the body axis. Geometrically, the axial organisation means that several planes of sectioning can produce similar halves of the body. The more sophisticated biradial symmetry occurs where only two planes of sectioning can divide the animal into similar halves. Most interestingly, biradial symmetry superimposed on some signs of octoradial symmetry is recognisable in Recent animals which are known to have a very ancient evolutionary history. It is expressed in the priapulid larvae, loricae of the Rotatoria, and the internal anatomy of the ctenophorans. This kind of symmetry characterised already the early Cambrian problematic hexaconulariids [5,6]. The octoradial symmetry is partially preserved in the anatomy of the aschelminthan worms, with their body covers frequently showing octomeric organisation, it is recognisable also in the echiuroid worms.

Usually, bilateral symmetry expressed primarily in the position of the main ventral nerve cord is superimposed on the basic pattern of radial symmetry. This is because in benthic organisms gravity-related dorso–ventral morphological gradient developed, obliterating the other planes of symmetry than the sagittal one. This apparently happened very early in the evolution of the Metazoa [7]. Strictly bilateral symmetry is a manifestation of the proximo-distal locomotion-related gradient along the longitudinal axis (see [8]), of the same kind as in radial symmetry but restricted to just two lateral body units which have became a mirror-image pair.

Segmentation along the body axis is probably the last stage in the evolutionary succession of symmetry types. The repetition of the same organs along the body axis (translational symmetry) seems to be controlled by closely similar mechanisms as the distribution of serially homologous units around the axis, that is by an externally stimulated localised expression of homeotic genes sets [9]. In all cases a divergent evolution of gene sets responsible for organisation of particular of the units (organs differentiation or tagmation) may follow.

The evolutionary appearance of asymmetry was not a trivial phenomenon. In its simplest form this may be just fluctuation in the developmental program (fluctuating asymmetry of Van Valen [10] which will not be dealt with further). When clearly heritable but without a strict control of right–left polarity it results in equally frequent left- and right-hand forms (antisymmetry; [11]). Directional asymmetry requires additional mechanism to connect it with laterally polarised developmental program. Although some genes which are resposible for anatomical asymmetry have been identified [12], the way in which it is executed remains unknown. It is possible that this is rooted in a chirality of particular cells cytoskeleton (especially that of the egg) and cytoskeleton dyneins may play there a role [13] although not necessarily directly controlling the polarity of asymmetry. The asymmetric pattern of transport through gap junctions of early embryos and influence of endogenous electric field on embryonic development of asymmetry points to connexins as another class of proteins involved in the process [13], again not necessarily as primary determinants but possibly rather involved in execution of the inheritance program. Geometrically the simplest case of asymmetry is perhaps the spiral cleavage of the embryo. Its geometry results from obliquity of the cell division spindle. In effect the originating cell cycles lie somewhat offset to each other, so their convexities fit depressions separating cells of the other [2]. The main cause for the cleavage to be spiral instead of radial may be the lack of egg membrane, which enables particular cells to attain the geometrically most stable positions [14]. Even if cleavage is not completely determinate, the orientation of the spindle obliquity may influence the fate of developing organs and eventually control their asymmetry.

This knowledge of general mechanisms of the physiologic control of symmetry and asymmetry in animal's development is not enough to infer the exact course of evolutionary events which have led to their present anatomical diversity. The evolution is a historical, unpredictable process and the fossil evidence remains decisive in establishing its course. The present review is restricted to those evolutionary events in the early history of the Metazoa which are relatively well documented palaeontologically. This refers mainly to the geological time span from about 560–400 Ma (Vendian to Silurian). The three main kinds of asymmetry expression will be discussed:

1. Anatomical asymmetry which may concern the whole body plan, the main internal organs of the body or just the feeding apparatus;
2. Asymmetry caused by a spatial differentiation of secretion rates of the external skeleton, eventually resulting in asymmetry of internal body organs which have to accommodate in their packing to the shape of the shell; and finally
3. The most sophisticated results of behavioural asymmetry, which requires that organisms were able to recognise left and right sides while feeding or constructing their shelters.

To illustrate those early expressions of asymmetry, particular cases of the evolution of fossil animals groups will be commented on. These will be the Cambrian carpoid echinoderms as an example of the body plan asymmetry (with an alleged relationship to the anatomical asymmetry in chordates), the Vendian dipleurozoans which show the hydraulic skeleton asymmetry, the asymmetry in the feeding apparatus of the conodont chordates, the origin of shell asymmetry in the gastropods, and finally the evolution of behaviour in the graptolite hemichordates. This will start from some introductory comments on the background at which those expressions of asymmetry developed. The recently emerging picture of relationships among the earliest metazoans is so different from the textbook views that it requires a brief review.

Anatomy of the ancestral Metazoa

The traditional view that the tetraradial symmetry was primitive for the coelenterates and, by implication, to the earliest metazoans, is contradicted by both zoological and palaeontological evidence. The Scyphozoa and Hydrozoa, which show this kind of symmetry, cannot be evolutionarily primitive because they share linear mitochondrial DNA which remains primitively circular in the Anthozoa, as well as in other primitive metazoans [15]. This means that the scyphozoan-hydrozoan stock split postdates its derivation from the anthozoans. Ironically, the Recent Anthozoa are thus nearest to the primitive stock of cnidarians [16], being anatomically the most complex. In fact, the nematocysts structure in Recent corals is much more primitive structurally than in hydroids [17]. The octocoral nematocyte host cell bears a regular flagellum surrounded by seven stereocilia (like in sponge choanocytes), instead of specialized tactile hair organ, there is no specialized lid or harpoon-like sting [18]. Also nucleotide sequences on 5S rRNA [19] support such relationships among coelenterate classes.

Phylogenetic position of the cnidarians

Quite contrary to earlier expectations, the pre-Ordovician coelenterate fossil record is poor and mostly questionable. The majority of textbook examples of the oldest polyps and medusae turned out, after closer examination, to have nothing to do with the coelenterates [3]. The allegedly early appearance of the chondrophorans is inconsistent also with zoological evidence. The chondrophoran morphology is highly derived but otherwise close to advanced athecate hydroids. Their origins should thus be rather recent. In fact, Petersen [20] classifies all the chondrophorans within the single family Velellidae and gives them the rank of superfamily within the suborder Zancleida of capitate hydroids!

The only more or less reliable pre-Ordovician coelenterates are the conulariids and the earliest rugose corals. Undoubted conulariids (for review of recent literature see [21] and [22]) are known beginning with the Ordovician but possibly ancestral forms with a thick cylindrical phosphatic tests, showing tetraradial symmetry only in the distribution of internal septa, are known from the Early Cambrian fossils [23]. Their tests were laterally flattened, exhibiting thus biradial symmetry which disappeared in later forms [24]. Traces of originally biradial symmetry point to the morphologically simple tubes of the Cambrian to Permian *Torellella-Sphenothallus* clade as possibly related. Moreover, the Early Cambrian hexaconulariids may appear also the member of the same group. Although even embryonic stages of the hexaconulariids are known, owing to extremely fine secondary phosphatisation of organic cuticle [25], there is not enough anatomical evidence to establish zoological affinities of these organisms. Apparently, they had either U-shaped intestine with the anus opened close to the mouth or the anal opening was missing at all. The very fine ornament on their surface resembles ciliary cones (see e.g. [17]: Fig. 38) covered with a thin cuticle. Coelenterate affinities are thus possible but the presence of a distinct larval stage and biradial symmetry make them unlike the Recent cnidarians.

The presence of protective devices in the oldest coelenterates ('origami' closure in the conulariids and opercula in the Middle Cambrian coral *Cothonion*; [1,26,27]) is puzzling. They are suggestive of nematocysts being either inefficient as a protection against predators or perhaps even missing. The acquisition of the nematocysts may thus appear to be relatively late in the evolution of coelenterates and connected with the appearance of predators with exposed soft tissues (cephalopods and fishes) in the early Palaeozoic [1]. From the Ordovician to Devonian the large arthropods were replaced by molluscs and vertebrates as the major predators on coelenterates. A gene transfer that could result in independent acquisition of nematocysts by particular groups of the coelenterates was proposed by Buss & Seilacher [28], not necessarily immediately after formation of the coelenterate clade.

The oldest clonal coelenterate-like fossil is the enigmatic Middle Cambrian *Tretocylichne*, with secondary calyces budding laterally from the parental one [29], similarly as in poorly preserved *Lipopora* [26] associated with *Cothonion*. Both *Lipopora* and *Tretocylichne* show an octomeric symmetry, which makes them similar to some early tabulate corals (e.g. *Billingsaria*). The interior of the conical calyx of *Tretocylichne* bears two ribs at each of its eight corners. What makes this fossil truly enigmatic and unlike any known coelenterate, is the presence of growth lines inside (sic!) the calyx [29]. Some skeletal fossils from the Early Cambrian which are believed by some authors to be clonal cnidarians (e.g. [30]) hardly provide any conclusive evidence of the coelenterate and non-sponge or algal relationship and are separated from superficially similar unquestionable Ordovician corals by a long time gap. The similarity of the Ediacaran *Rangea* and other Petalonamae to the pennatulaceans is completely superficial, as more extensively discussed below.

It may thus be inferred that the oldest coelenterates were at least as complex anatomically as Recent anthozoans, with a muscular body, complex organisation of the gastric cavity, and elaborated tentacular apparatus. Their ancestors were bilateral or biradial organisms of unknown morphology.

Possible benthic ancestry of the ctenophores

The newly emerging evidence on the early evolution of the ctenophores makes them likely relatives of the earliest coelenterates. They appear to be highly diverse already in the Cambrian (Fig. 1). An unnamed Early Cambrian species from the Chengjiang locality of China and the Middle Cambrian *Ctenorhabdotus* from the Burgess Shale both have distinctly octomeric organisation and longitudinally arranged comb rows [31–33]. The comb rows in the Recent ctenophores are arranged in pairs ([34]: p. 361), which may suggest their original tetrameric organisation. The Middle Cambrian ctenophore *Fasciculus* had clearly biradial symmetry with comb rows [31,35,36] in a feather-like arrangement. If restored in 'interradial' view these organs

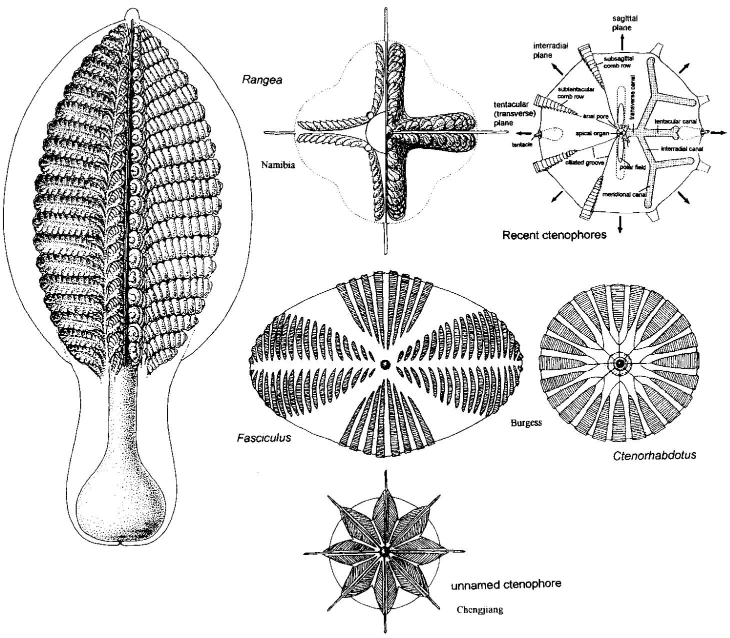

Fig. 1. Expression of biradial, tetrameric, and octomeric symmetry in fossil ctenophores and their possible Precambrian relatives. In the frond of *Rangea schneiderhoehni* [37], on the left side internal structures are restored as they are represented in three-dimensionally preserved specimens in the Kliphoek Member of the Dabis Formation, Nama Group of Namibia, collapsed under the sand load; right half of the drawings shows possible shape of the organs before collapse (based on examination of original specimens). The apical view of *Rangea* is compared with similar diagrammatic presentations of the Middle Cambrian Burgess Shale ctenophorans *Fasciculus vesanus* [35] and *Ctenorhabdotus capulus* [31] (based on reconstructions in [31]) and the Early Cambrian unnamed ctenophoran from Chengjiang, Yunnan, China (based on illustrations in Chen et al. [33] and examination of original specimens). Body plan of a generalised Recent ctenophoran slightly modified after Hernandez-Nicaise [34].

would exhinbit a closely similar organisation to that of the petaloids of the late Precambrian (Vendian) petalonamean *Rangea*, except for having a much wider 'rhachis' region.

A ctenophoran affinities for *Rangea* were suggested already by Gürich [37,38], the discoverer of the Namibian Precambrian metazoans. His interpretation, after being abandoned for a long time in favour of the coelenterate one [39], has found support in recent discoveries of Cambrian ctenophores in the Burgess Shale [31] and

Chengjiang ([31]: p. 287; [32]: Fig. 5.9F). *Rangea* is the only Namibian fossil which provides a relatively complete information about its body form and internal organisation (Fig. 1). It seems reasonable to assume that the petaloid modules developed phylogenetically from a non-metameric ancestral pattern. What we actually see in the post-Vendian fossil record, however, is the reverse course of the evolution of the frond. This refers to the morphocline, being to some degree a chronologically arranged series, formed by the feather-like Vendian relatives of *Rangea*, the Early to Middle Cambrian ancestral Ctenophora, and the Recent members of the phylum. It is thus likely that the pelagic Ctenophora are direct successors of the benthic Precambrian to Cambrian Petalonamae.

The anatomy of the Middle Cambrian petalonamean *Thaumaptilon* may be helpful in understanding the relationships between anatomies of those organisms. Particular fusiform units of the petaloid of *Thaumaptilon* show irregularly distributed pustules (interpreted as zooids by Conway Morris [40]) instead of the transverse striation typical of comb organs of the coeval ctenophores [31]. If they are homologous, which seems likely, than the difference would be that in *Thaumaptilon* the ciliated cells were not arranged in regular transverse bands but irregularly distributed. In *Fasciculus*, there are deeply located metamerically arranged internal organs with 'a feathery appearance' (lobate organ of Conway Morris & Collins [31]: p. 291) which may be homologous with the petaloids of *Rangea*. They occupied a position on the frond roughly corresponding to that of the paired meridional canals in the ctenophores (see [34]). The common canal, from which all the petaloid units originate (or to which they merge) would then correspond to the interradial canal. Along with their digestive function, the meridional canals of the Ctenophora hold also gonads. The 'folded margin' of *Thaumaptilon* [40] resembles the marginal radial membranes of both *Rangea* [41] and the unnamed Chengjiang ctenophore [32]. The apex of its rachis, separated morphologically from the frond, corresponds closely to the apical organ of the Cambrian ctenophores. The rachis itself is darker than the rest of the frond which may mean that this is a gastric cavity filled with organic-rich matter. The specimen may thus be a medially split body of an organism different from *Rangea* only in its more elongated body.

Despite the relatively complex anatomical organisation of the ctenophores, nucleotide sequences of 18S rRNA suggest their branching off the main stock of the Metazoa even earlier than the cnidarians [42,43]. The Recent Ctenophora is a compact morphologically group and even if some among them are benthic, these certainly developed their mode of life secondarily from pelagic ancestors. The most parsimonious interpretation of the ctenophoran phylogeny by Harbison [44] implies that the ancestral pelagic ctenophore had radially symmetrical arrangement of canals with anastomosing diverticula in large specimens, spacious gastric cavity and large mouth. The beroid ctenophores, active predators lacking tentacles but searching for the prey, may be close to the ancestor of all Recent ctenophores; passive feeding with tentacles would then be a secondary achievement. This is not unlike what can be seen in the Cambrian [31].

Exuviation as an ancient trait

The aschelminthan worms and articulates share the presence of external chitinous cuticle which has to be periodically shed off to allow growth of the body volume. Owing to works on the Cambrian priapulids from the Burgess Shale and other North American Middle Cambrian faunas by Conway Morris [45,46], it is now well known that the priapulids are the most ancient of the Nemathelminthes, being one of the most important phylogenetically stocks of the early Metazoa. The biradial symmetry of the priapulid larvae makes also their relationships to the petalonamean-ctenophore-cnidarian stock likely. It seems possible that a chitinous cuticle was present also in the ancestor of the cnidarians. The Early Cambrian *Markuelia* known from an embryo preserved inside egg covers [25] may possibly belong to the palaeoscolecids, another Early Palaeozoic group of the nemathelminthan worms. The priapuloids and/or palaeoscolecids may have been ancestral to a great division of metameric metazoans with bodies covered with periodically shed chitinous cuticle (Fig. 2). The lobopodian Xenusia link them with the articulates [47].

Some signs of octoradial symmetry can be identified in the body plan of the Echiura, which may be an ancient group of worms. In the Carboniferous they were already represented by forms of quite modern aspect [48]. Traces of life activity from the Cambrian left by organisms with anatomical organisation resembling the echiurans suggests their great diversity. These are permanently inhabited burrows of the Cambrian *Trichophycus* and *Treptichnus* with characteristic fecae [49] and tubular tracks of *Plagiogmus* (=*Psammichnites*), an organism peristaltically propelled within the sediment and collecting detritus above the sediment with a long proboscis [50,51]. Perhaps some sediment filled probably chitinous body covers from the Vendian of Namibia (*Protechiurus* and *Aussia*; [52,53]) represent also the echiurids.

The origins of the deuterostomians

Although it is generally accepted that the echinoderms, hemichordates, and chordates form a monophyletic clade, its origin remains difficult to be traced. Molecular evidence fails to provide reasonable solutions to the problem, both in respect to the real sequence of anatomical transformations or even dating of divergences [54] which are unrealistically high (see comments by Conway Morris [55]). The peculiar way of embryogeny is not unique for them, being known also in the nemathelminthan worms (nematomorphs). Probably the most ancient traits shared by the deuterostomes, which can be used to identify their relatives, is the enterocelic origin of the coelom and their inability to secrete cuticle (Fig. 2). Whereas the skeletal structures of animals of the nemathelminthan-articulate-molluscan stock are based on or derived from chitinous cuticle, the nemerteans and deuterostomians have to rely on other kinds of skeletal materials. They share with the ctenophores the lack of chitin synthase [2,56]. This is probably why the skeleton in many of them is internal, formed of intracellularly secreted calcite (echinoderms), modified keratinous cytoskeleton (horny tissue of the vertebrates), or phosphatic tissues secreted

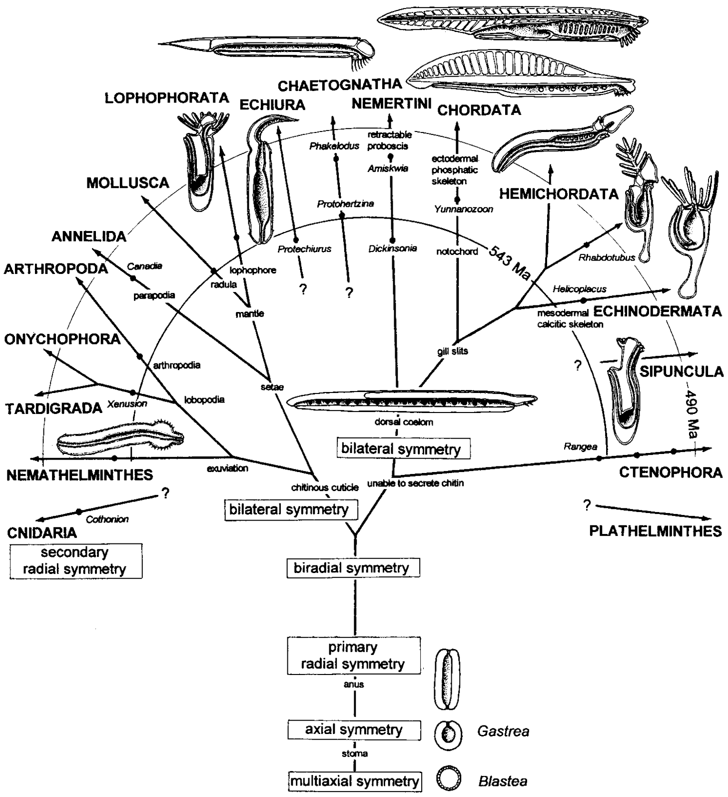

Fig. 2. Possible relationship among metazoan phyla as suggested by the Precambrian and Early Palaeozoic fossil evidence. Extreme body plans are schematically presented and ages of the oldest Precambrian and Cambrian fossil representatives indicated (543 million years is the age of the Vendian–Cambrian boundary, 490 corresponds to the base of the Ordovician). Note that Conway Morris and Peel [152] attempted to resolve the mollusc-annelid-lophophorate relationship on the basis of fossil evidence in somewhat different way; the apparently secondary reduction of skeletal plates in the Solenogastres and possibly the conch at the origin of the polyplacophorans [112] makes the original presence of a shell- or tube-secreting mantle in this stock likely.

extracellularly but internally by derivatives of the ectoderm (ectodermal vertebrate enamel, ectomesenchymal dentine, and bone). This split in secreting abilities was definitely very early as the vertebrate-like phosphatic tissue is known from the very early Cambrian (Tommotian; [57]) and the echinoderm-like skeleton appeared not much later (Atdabanian, Fig. 5; [58]).

The lack of abilities to secrete any external water-proof skeleton made adaptation of the deuterostomians to terrestrial life very difficult. Although some skeletal polysaccharides are produced by chordates, they form only an internal skeleton and their correspondence to chitin remains controversial [56,59]. When finally the vertebrates overcame the problem, they developed an analogue of the cuticle using dead keratinised cells of the epithelium. Eventually, the horny tissue is now exuviated like a cuticle (by snakes) and forms segmented, arthropod-like armors (in armadillos) or even rigid carapaces (in turtles).

Anatomical asymmetry

The above review of the early differentiation of body plans (formation of phyla; Fig. 2) show that the origin of anatomical asymmetry in early Metazoa took place in already rather complex phylogenetic context. The most apparent and best-documented geologically early cases of the evolution towards asymmetry are to be commented below. The oldest of them is the asymmetry expressed in at least some body organs of the dipleurozoans, numerous poorly preserved fossils of which are known from the classic Precambrian locality of Ediacara in Australia. A new material from northern Russia [60] provides completely new insight in the problem of their anatomy and relationships. Even more important from the evolutionary point of view is the meaning of the body plan asymmetry in the early Palaeozoic carpoid echinoderms, believed to be ancestral to the chordates by some authors. It is widely speculated that he carpoid ancestry may solve the question how old is anatomical asymmetry of the vertebrates [61,62]. These two problems will form the core of this chapter.

Asymmetry of the muscular body unit in the Ediacaran Dipleurozoa

Perhaps the most controversial issue in today's palaeontology is the relationship and biology of the late Precambrian macroscopic organisms usually referred to as the Ediacaran biota. Their time range remains rather poorly dated but they seem to be mostly restricted to the Vendian period, defined as the time between the Laplandian glaciations and the base of the Cambrian, with a good geological record on the East European Platform (Ediacaran is sometimes used as its equivalent or as an epoch of the late Vendian when the Ediacaran biota were especially abundant). Radiometric datings in Namibia show that the Ediacaran biota were represented up to above the Vendian–Cambrian boundary [63] with several lineages continuing to the Middle Cambrian [40] although the Ediacaran type of preservation seems to disappear within the Early Cambrian [64]. Virtually all the Ediacaran organisms show some degree of asymmetry [65] but this refers mostly to an alternate distribution of paired anatomical units, which seems to be rather an effect of simple geometric packing. However, there are some cases of unquestionable anatomical asymmetry.

Until quite recently, the main source of evidence on the anatomy and faunal diversity of the Ediacaran biota was their nominal locality in Australia. The Ediacara fossils are preserved in the relatively coarse Pound Quartzite sandstone as imprints on the basal surface of the beds. Their origin remained a mystery until similar modes of fossilisation have been identified in fine-grained rocks of the late Precambrian of the White Sea shore in northern Russia. It appears that the imprints represent various stages of decay of organic tissues covered with sediment deposited on sand penetrated with cyanobacterial filaments. Owing to cyanobacterial mucopolysaccharide the sandy sediment had apparently gelatinous appearance which protected its surface from being worn out during deposition of subsequent portions of the sediment. Moreover, the high organic content promoted early diagenesis in the overlying bed (mostly pyritisation) which precisely replicated the morphology of the surface with imprinted and deposited macroscopic organisms [66].

Dickinsonia is among the most intriguing organisms of the Ediacara fauna. Although preserved in coarse sediment, which makes details of morphology difficult to observe, numerous specimens of this fossil organism provide a lot of information which can be used to restore its original anatomy. Owing to observations and interpretations by Seilacher [65,67] it is known that in the body of *Dickinsonia* there was a segmented unit composed of a series of chambers separated from each other by walls and filled with a liquid under pressure during life. Some specimens show changes in the diameter of the body, apparently a result of loosing internal pressure by the fluid inside the chambers, others show wrinkles parallel to the margin providing evidence of concentric muscle action [68]. The *Dickinsonia* body increased in size by adding new metameric units at its posterior end [69]. The anteriormost chamber was unpaired, and at early ontogenetic stages it was rounded triangular in outline (Fig. 3). Some *Dickinsonia* specimens show the presence of a sediment-filled cylindrical gut under the segmented unit [39]. An internal sediment fill shows the presence of metameric intestinal caeca, not connected in their distribution with the metameric dorsal chambers [70].

In the White Sea Precambrian fauna an unnamed *Dickinsonia*-like organism occurs, possibly congeneric with the Podolian *Valdainia*. In its body, the anterior medial unpaired unit is expanded laterally and drawn to the left, presumably because of a weaker tension from the concentric fibrous and muscular skeleton. In fact, the transverse wrinkles at the surface of chambers which are interpreted as being a result of muscle contraction do not parallel the body margin in its anterior part. Moreover, the whole metameric chambered unit seems to be shifted backward, in respect to the situation present in *Dickinsonia*. This exposes anteriorly a belt with branched caeca, which in *Dickinsonia* are completely covered by the unit (Fig. 3). Although only a few specimens preserved well enough to show clearly the morphology of the anteriormost chamber are known, in all cases the unit is bent to the left. This strongly suggests directional asymmetry.

The anatomy of the White Sea animal helps to understand relationships among significant part of the members of the Ediacaran biota. Ramified tubular structures in the anterior part of the body and posteriorly arched segments make the Ediacara

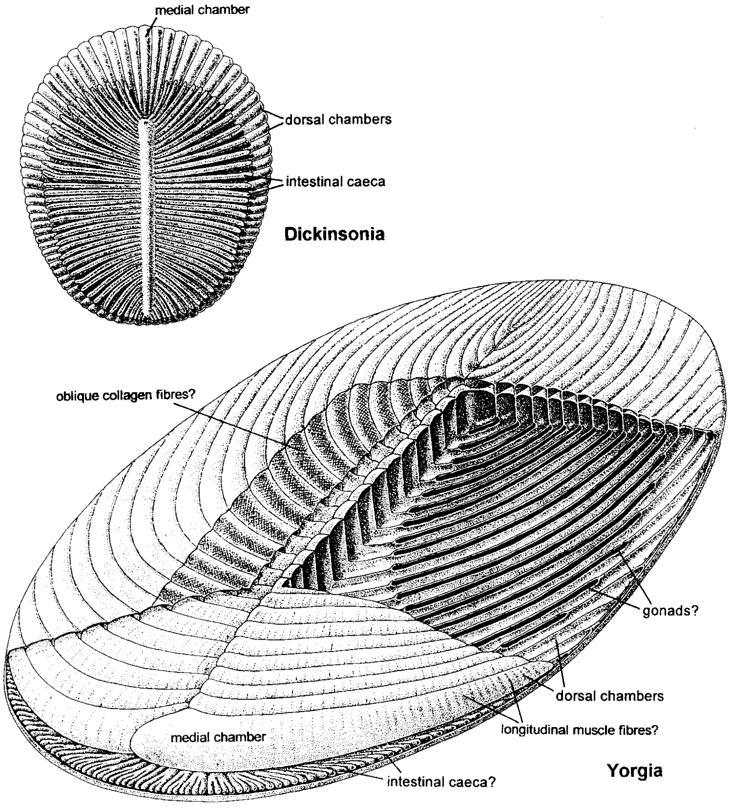

Fig. 3. Restoration of the anatomy of the Vendian dipleurozoans. Preserved internal organs of *Dickinsonia costata* [153] from the Pound Quartzite of Ediacara, Australia in ventral view (modified after Dzik [101]). *Yorgia waggoneri* [60] from the Yorga Beds of the Mezen Formation at Zimnie Gory near Verkhnia Zolotica, Arkhangelsk District, northern Russia, is shown in oblique view with part of the body covers 'cut off'.

Marywadea, *Praecambridium*, and *Spriggina* closely similar to the new animal. It appears that the same body plan is shared by the Vendian organisms ranging from the oval *Dickinsonia* to elongated *Spriggina*, with the White Sea animal in the middle of the series. This body plan consists of dorsally located segmental fluid-filled units, a straight gut with metameric caeca, and external body covers repeating segmental organisation and with transversely arranged oblique fibres. Elongate organs attached to septa of the chambers in the posterior part of the body seem to represent gonads.

A hint regarding possible zoological affinities of this group of Ediacaran animals is provided by their dorsal hydraulic skeleton. The hydraulic function of dorsal chambers implies some contribution from muscular cells to their walls and connection to an osmoregulatory system to keep a constant pressure of the fluid during life. Functionally similar hydraulic structures occur widely among Recent animals, the most similar being the coelomic chambers of the chaetognaths and the rhynchocoel of the nemerteans. The rhynchocoel is a dorsal muscular coelomic chamber, being thus at least an analogue of the *Dickinsonia* dorsal organ. The oldest possible nemertean is the Middle Cambrian *Amiskwia*, although Conway Morris [71] doubted its relationship directly to the nemerteans because neither rhynchocoel nor intestinal caeca are preserved in the Burgess Shale fossils. Typical nemerteans are known from the Carboniferous Mazon Creek fauna, identified on the basis of everted proboscis but do not showing details of their internal anatomy [72,73]. Some metamery of the body interior is apparent in co-occurring with them bizarre *Tullimonstrum* which had a long, but probably not retractable, proboscis armed with strongly skeletised teeth (stylets?) and a pair of stalked eyes(?). Also the coelomic cavities of the chaetognaths develop as muscular units with their walls composed of myoepithelial cells. The basement membrane forms there a sort of exoskeleton with a layer of collagenous fibers which are obliquely oriented in alternating directions.

Among the Cambrian animals, the only one showing at least remote similarities to the White Sea metazoan is *Odontogriphus* from the Burgess Shale [74] and the Early Cambrian chordate *Yunnanozoon* from the Chinese locality of Chengjiang [70]. The presence of metameric gonads in *Yunnanozoon* is a trait shared not only with the enteropneusts but also with the nemerteans, which makes it a likely primitive (plesiomorphic) feature. The Dipleurozoa may thus appear ancestral to both those phyla with dorsally developed coelom of locomotory hydraulic functions. Perhaps it gave rise to the rhynchocoel of the Recent Nemertini (perhaps in effect of secondary simplification), coelomic body chambers of the chaetognaths and enteropneusts (by reduction in number and ventral expansion), and myomeres of the chordates [70]. Such relationship would explain the mentioned above peculiar distribution of the inability to secrete chitin, shared by the nemerteans with sipunculans, hemichordates, echinoderms, and chordates.

Asymmetric body plan of the carpoid echinoderms

The nemertean-chordate relationship is in conflict with generally held phylogenetic interpretations. For instance, much phylogenetic importance is given by many authors to the internal anatomical asymmetry which characterises a large group of early Palaeozoic echinoderms usually referred to as the Carpoidea. They developed mobile benthic mode of life laying on the soft bottom with their flattened body side and moving slowly by an action of their modified stem or arm. Jefferies [75] proposed that the carpoid asymmetry was original, that they originated directly from the pterobranch hemichordates and gave rise to various lineages of the chordates. The anatomical symmetry of Recent larval amphioxus was used as an important argument in forwarding this hypothesis whereas the differences in the organisation of the skeleton was considered of secondary importance. The carpoids had an internal calcareous trabecular skeleton structurally indistinguishable from that of other echinoderms, thus apparently mesodermal and intracellularly secreted, therefore the name Calcichordata was proposed for them to fit the alternative phylogenetic affiliation. The main resulting difficulty is that the skeleton of the undoubted early Palaeozoic chordates was phosphatic and, similarly as that of Recent primitive fishes, extracellularly secreted by ectodermal epithelium or ectomesenchyme. The carpoid-chordate transition would thus require that the calcitic echinoderm-type skeleton was secondarily lost in the course of evolution to be replaced by a newly formed phosphatic skeleton [61]. In fact, the oldest chordates with the phosphatic skeleton (conodonts) are as old as the carpoids or even (if the problematic earliest Cambrian *Fomitchella* belongs there; [57]) significantly older, older even than all the echinoderms.

This is not the only problem with the concept of 'calcichordates'. Even more serious are difficulties with homology of particular body organs as restored by Jefferies [61,75,76]. Owing to their internal calcitic skeleton, easily fossilised and providing a lot of information on their soft part anatomy, the evolution of echinoderms is relatively well understood [77–79]. The oldest known articulated echinoderm fossils are middle Early Cambrian in age. They represent two basic body plans. The main distinction seems to be the presence *versus* absence of extrathecal extensions of the ambulacral apparatus (Fig. 4). In the gogiid eocrinoids, the presumed ancestors of the later cystoids and related groups [80], the five bifurcating ambulacral furrows extend in long brachioles with well developed internal skeleton. In the course of evolution, the basal part of the originally sac-like body narrowed and the platy cover was transformed into rings (columnals) independently at least in the cystoids and crinoids. In the other branch, represented by the edrioasteroids and some related, exclusively Cambrian groups, the ambulacra run over the body surface. In both clades the ambulacral furrow was covered with movable platelets [78].

The carpoids as early as in the Middle Cambrian developed at least three separate clades. The crucial role in the 'calcichordate' theory play members of the Cornuta, with their skeletal anatomy thoroughly restored by Jefferies [76,81]. Their lobate body bears an appendage at its end opposite to where a pyramid composed of numerous elongated sclerites is located. Such associations of sclerites are interpreted as the anal pyramid in primitive echinoderms and in the other carpoid group, Soluta, which precede the cornutans stratigraphically ranging back to the late Early Cambrian (Kinzers Formation; [78,82]). In the solutans, the pyramid is located close to the base of the undoubted stem, and the opposite part of the body is armed with a single appendage structurally indistinguishable from ambulacral appendages of primitive pelmatozoan echinoderms. If then

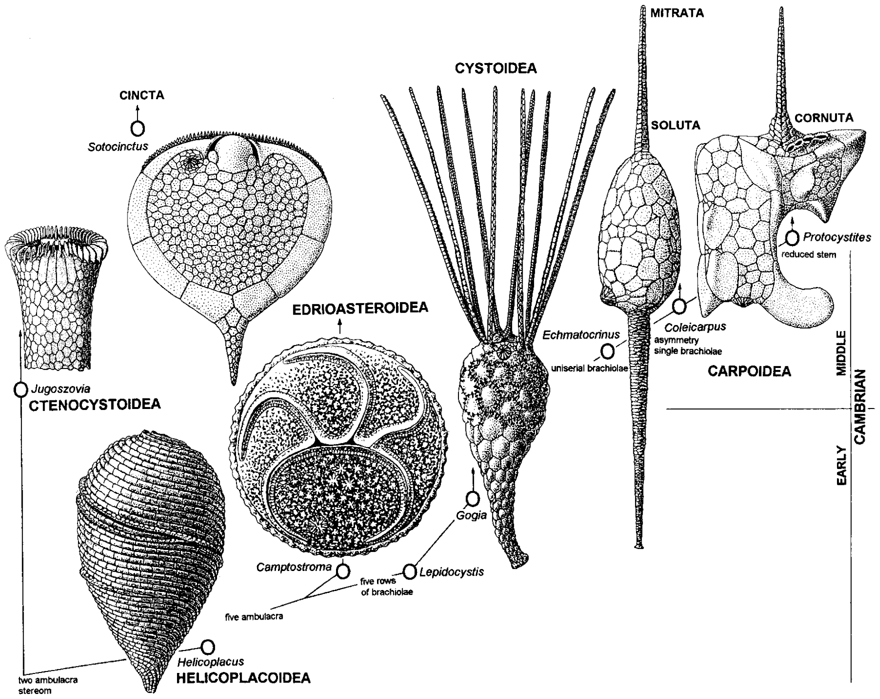

Fig. 4. Probable relationships among the earliest know Cambrian echinoderms. Note that pentameric symmetry developed gradually and relatively late in the evolution (compilation from numerous sources cited in the text).

the single appendage of the cornutans is actually of ambulacral nature, the whole internal anatomy restoration offered by Jefferies [75], allegedly homologous in details to that of the chordates, is wrong [83]. The question of homology of the cornutan appendage is thus of a crucial importance and its solution depends on how the organisation of ambulacral appendages (brachiolae) of the most primitive pelmatozoan echinoderm is interpreted.

The appendage (alleged calcichordate stem) in the Early Ordovician cornutans *Cothurnocystis* and *Lyricocarpus* bears wing-like cover plates, which are frequently preserved in gaping position, oriented to sides of the appendage [84,85]. Isolated plates of this kind ([86]: Pl. 67:9) show a wide rounded distal end and basal attachment, hardly suggesting any permanent articulation, which would be the case if these were parts of the skeleton of a stem. In fact, these are comparable with the brachiolar cover plates in the Early Cambrian gogiids, the most primitive typical pelmatozoans (Fig. 4). When preserved in articulated position (Fig. 6) they are either closed, protecting ambulacral tentacles (feet), or opened laterally. The only difference between the gogiid brachiolae and the carpoid appendages is in that the main sclerites are biserially arranged in the gogiids instead of being uniserial. However, uniserial arms are common among later pelmatozoans and such is the anatomy of the controversial early Middle Cambrian *Echmatocrinus* from the Burgess Shale [87,88]. What may be meaningful in the case of *Echmatocrinus*, the number of appendages is reduced from that typical for the gogiids (7 or 8 instead of 10) and departs from the pentaradial symmetry.

Unlike the ambulacral appendages, very well preserved sclerites of the proximal part of the true stem in the Late Ordovician *Girvanicystis* [89] represent semicircular units, together forming strong ridges transverse to the stem axis. This leaves little doubt regarding homology of this organ in the solutes and other echinoderms. Most interestingly, the oldest known early Middle Cambrian (*Ptychagnostus gibbus* Zone) solute *Coleicarpus* shows also the most distinct echinoderm traits being attached to the hard substrate with holdfasts (Fig. 4) in the same way as relatively advanced Cambrian eocrinoids [90]. It shows also the most primitive plating of the stem among the carpoids. Closely related and geologically younger (*Ptychagnostus punctuosus* Zone) *Castericystis* had its stem subdivided into two parts covered by different plates and remained attached only at juvenile stages [91,92]. The ancestor of the solutans was thus a regular pelmatozoan echinoderm (Fig. 4).

The third Cambrian 'carpoid' branch is represented by the exclusively Middle Cambrian lineage of the Ctenocystoidea. Its oldest and most primitive member, the early Middle Cambrian *Jugoszowia*, shows a relatively large, vermiform body covered with small, irregular plates (Fig. 5). During the Middle Cambrian, the Ctenocystoidea evolved towards a smaller mature size while their plating was becoming increasingly robust and regular [93]. They had no appendage or stem and probably originated from the ancestral echinoderms lacking not only ambulacral appendages and stem (both structures originated in the late Early Cambrian with *Lepidocystis*; [78,79]) but even pentameric symmetry. They had thus a common ancestry with the oldest known echinoderms, the Early Cambrian helicoplacoids, being directly not related to the true carpoids (Fig. 4).

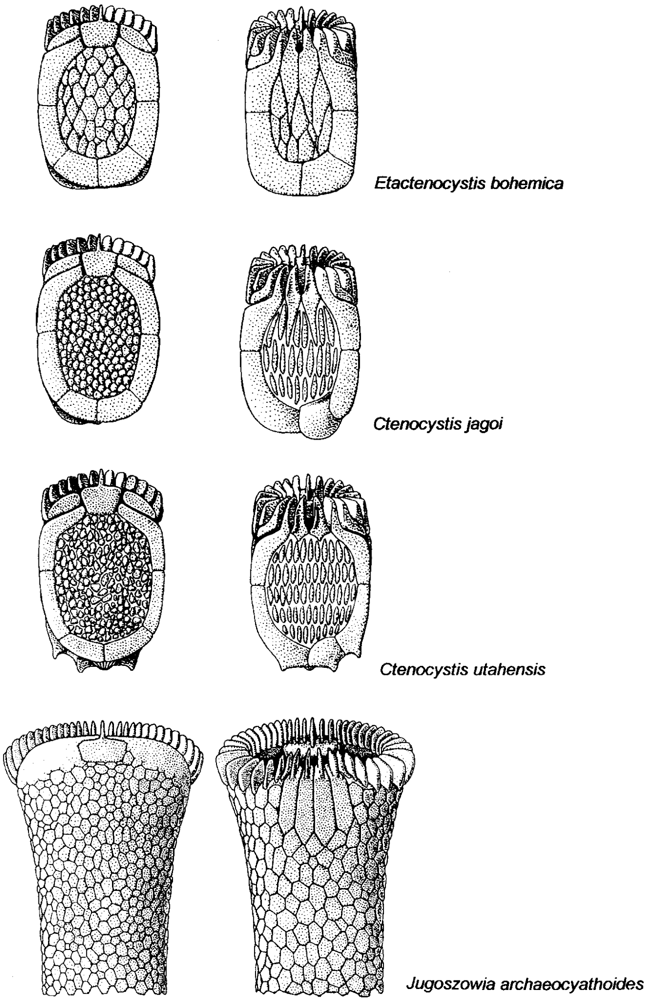

Fig. 5. Middle Cambrian ctenocystoid thecae (ventral and dorsal views) shown in stratigraphic succession (see [93] for details and other sources); note gradual development of the 'carpoid' morphology, bilaterally symmetric perioral region of the body, and asymmetry of posterior end.

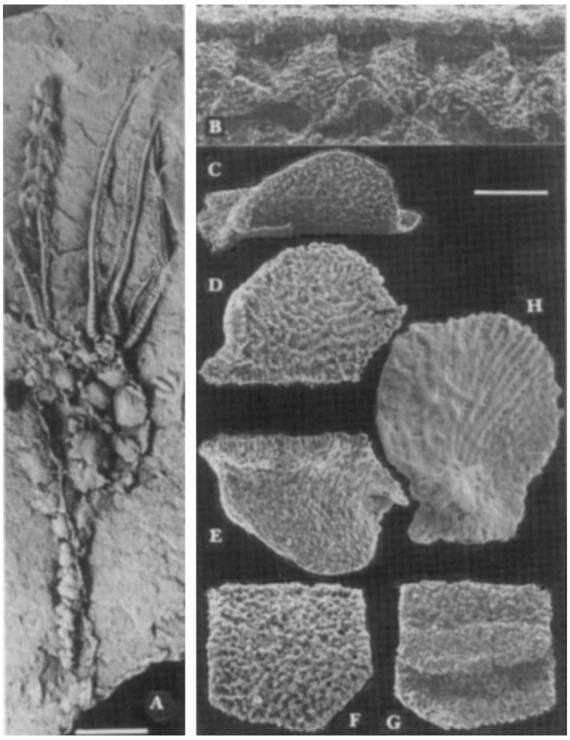

Fig. 6. Morphology and location of ambulacral cover plates in the most primitive Cambrian pelmatozoan echinoderms compared with those of the carpoids. A–B. Middle Cambrian gogiid pelmatozoan *Sineocrinus lui* [154] from the Kaili formation (bed 18) at Gedong, Guizhou province, South China; articulated skeleton and upper view of a fragmentary brachiola showing alternate distribution of cover plates. C–G. Isolated gogiid cover (C–E, oblique upper, external and internal views, respectively) and brachiolar plates (F–G, external and internal lateral views) from the Early Cambrian Pestrotsvetnaya Formation (3.4 m below the top, middle Atdabanian) at Uluchan Kyyry Taas, Yakutia, Siberia, possibly conspecific with *Sibirecystis reticulata* [155]. H. Cover plate of an undetermined cornutan ([86]: Pl. 67, Fig. 6) from the Caradoc of the Mójcza Limestone (sample Ma-87) at Mójcza in the Holy Cross Mountains, Poland. Photographs of Chinese specimens show latex casts coated with ammonium chloride (A) and under SEM (B), Siberian specimens are calcitic plates, extracted from a micritic limestone with buffered acetic acid, Polish carpoid plate is a phosphate coating extracted with formic acid from limestone. *Sibirecystis* is probably the oldest echinoderm known; scale bar is 5 mm (A), 200 μm (C–G), and 120 μm (H).

It appears thus that the carpoids were secondarily asymmetrical echinoderms with no relationships to the chordates. Their asymmetry was an adaptation to sessile mode of life on the soft bottom, several times repeated in the evolution of the pelmatozoan echinoderms in the Palaeozoic.

Asymmetry of the feeding apparatus

Skeletal elements performing the function of a jaw tend to have opposing (occluding) surfaces different. This is perhaps the best expressed in the organisation of mammal teeth. The teeth of the upper jaw are there not a mirror image of those of the lower jaw. The opposing orientation of tubercles and crests arranged in triangles developed already in jaws of the Cretaceous mammals. In the case of the gnathostome vertebrates such difference between two parts of the jaw does not disturb the bilateral symmetry. Other jaw-like organs, for instance the mandibles of the crustaceans, work in sagittal plane and the difference between the left and right working surface results in a deviation from the bilateral symmetry. A pattern of reversed triangles on the working surfaces of mandibles in the Silurian archaeostracan crustaceans gave thus a clear anatomical asymmetry [94].

Bilaterally symmetrical cuticular armament of the evertible proboscis occurs also in many polychaete annelids. In the eunicid polychaetes they form a complex apparatus with units opposed in sagittal plane. In its evolution originally numerous cuticular teeth arranged in symmetrically opposing transverse rows [95] differentiated already within the Early Ordovician into a series of units (scolecodonts) of very different size. A clear asymmetry was expressed in the presence of an additional 'basal plate' which fits an indentation of the right 'first jaw' [96]. The basal plate underwent a gradual reduction during the early Palaeozoic and most of the late Palaeozoic and later forms show virtually symmetrical organisation of the apparatus [97]. The functional meaning of this complex course of the evolution remains unsolved.

The most unusual kind of asymmetry is known among Devonian and Carboniferous conodont chordates, some elements of the oral apparatus of which seemingly do not form pairs. When identified in loose fossil material they appear to be represented only by one morphologic type of elements. This is a case of the axial symmetry (reviewed in Dzik [98]: p. 302). What is perhaps meaningful, this kind of geometrical symmetry (but asymmetry from functional point of view) developed several times in the evolution of a rather small clade of the ozarkodinid conodonts (Sweet [99]: p. 96, 120–122). Perhaps the elements of the apparatus in this particular group acted in deeper contact [100] (note that according to the 'horny cup' model of the conodont apparatus there was additional tissue in between the phosphatic elements [101]), which stimulated this kind of symmetry. The way, in which apparently the same developmental program was executed in elements on both sides of the apparatus, is an interesting biological question.

Accretional asymmetry

The unique for palaeontology opportunity to observe evolutionary development of asymmetry in the real geological time is easiest to achieve in the case of mollusc conchs, having generally good fossil record. It is now evident that asymmetry in both bivalved and spirally coiled molluscs originated many times. Both the coiling and asymmetry of any skeleton secreted around the body margin, whether it is a mollusc conch or a worm tube, results from differences in rates of secretion of the skeleton by the mantle (or its analogue). Several ways to express the resulting geometry in simple formulas were proposed, the closest approximation to the mechanisms of secretion being included in the tube model of Okamoto [102]. Even the superficially most complex conch morphology can be then generated in a relatively simple way. Those quantitative methods were most extensively used to show the development of conch asymmetry in the phylogeny of cephalopods, where it is best documented.

Trochoidally coiled conchs developed in several lineages of the Silurian and Devonian nautiloids (reviewed in [103]) and at least three times in the evolution of ammonoids: in the Late Triassic cochloceratids [104] and the Early Cretaceous ancyloceratids [105]. In all those cases the loss of symmetry in favour of antisymmetry usually transformed into directional asymmetry was probably connected with a change of the mode of life from nectonic to planktonic (passively floating). The conch's hydrodynamic properties no longer were of significance, at least at some stages of ontogeny. Virtually no data on the soft anatomy of the ammonoids is available, it thus remains unknown whether this was connected with any deeper transformations in the distribution of body organs. In bivalve molluscs numerous cases of the evolutionary development of asymmetry have been documented, the most important being that one which marks the origin of the pterioid bivalves in the Middle Ordovician (for review of current ideas see Johnston [106]). From some reason antisymmetry is relatively rare among bivalves. Antisymmetric shapes developed also in brachiopods, being there rather ephemeral and no large clade with asymmetric shells developed in the long evolutionary history of those invertebrates. Most of those cases have much better zoological than palaeontological documentation and were recently reviewed by Palmer [107].

In the Recent gastropods, asymmetry is inherited maternally [108], which is interpreted as an evidence for its cytoskeletal determination [13]. The conch asymmetry does not necessarily imply an asymmetry of the body organs. The most primitive of Recent gastropods preserved size of most of their originally paired organs similar. In the course of the evolution the anatomy accommodated to the asymmetry and elongation of the interior of the conch, in a similar way as the abdomen of hermit crabs adapted to their conchs. Palaeontological material rarely provides any direct evidence on the internal anatomy of fossil molluscs, and it can be only indirectly inferred from the muscle attachment scars. The following review will thus refer only to the external shell morphology, which was geometrically rather simple in the oldest gastropods.

Origin of the gastropods

The most important evolutionary change from bilateral symmetry to asymmetry in the evolution of molluscs was that at the origin of the gastropods. The picture offered by palaeontological evidence is in this case rather complicated. The main problem with interpretation of the data is that the adult conch morphology alone does not provide enough information to identify zoological affinities of early molluscs.

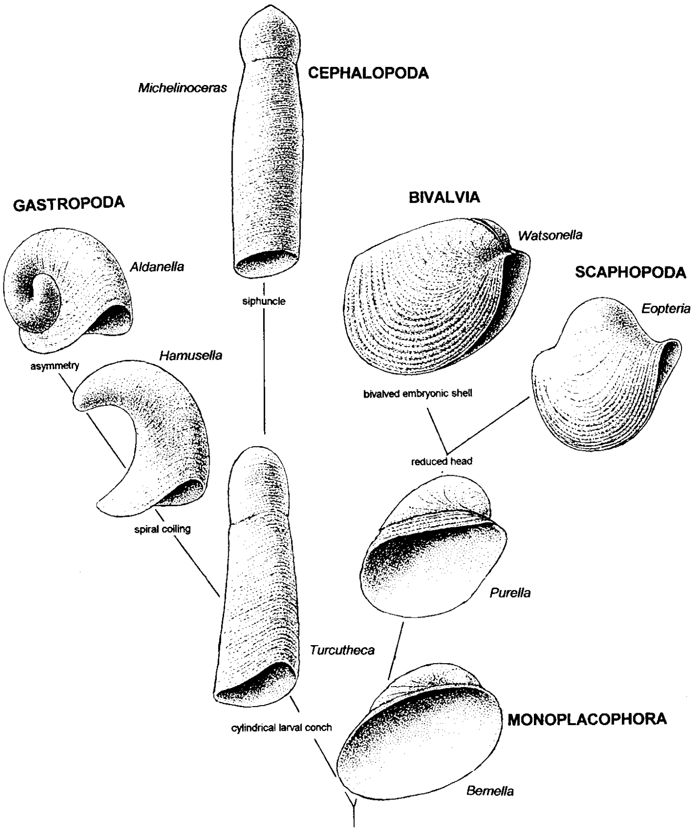

Fig. 7. Diversification of the larval conch morphology in the early evolution of molluscs (except for the cephalopods and rostroconch ancestors of the scaphopods, which are Ordovician, all illustrated specimens come from the Cambrian; see [1] for details); note the basic difference in the larval conch form between the monoplacophorans and gastropods.

A complete series of early Cambrian conch forms connects straight coniform *Turcutheca* via *Ceratoconus* and *Hamusella* with the spirally coiled monoplacophorans (Fig. 7). The series continues further, to the pelagiellids. Whether these molluscs represent already gastropods is highly questionable, however. Muscle attachments scars in *Pelagiella* are paired, which is suggestive of a pre-torsional anatomy with the conch coil being oriented anteriorly, hanging over the head [109]. These were minute animals, with the conch diameter of a few millimetres, and its shape was widely conical with hardly more than one coil developed.

In the lack of other anatomical evidence, the protoconch morphology remains the main set of characters which can be used to resolve relationships of the earliest gastropods. Well preserved protoconchs are known in *Pelagiella* from the Atdabanian Parara Limestone of Australia [110] and closely related *Costipelagiella* from the Middle Cambrian Exsulans Limestone of Bornholm. In the latter the protoconch is clearly different in its weakly developed growth lines from the teleoconch [111]. It is relatively large, about 150 μ in length and almost hemispherical in shape. In this respect it closely resembles protoconchs of the probable early Palaeozoic ancestors of Recent scaphopods, the rostroconch molluscs [112] and sinistrally coiled mimospirine gastropods [113]. Anatomically dextral gastropods with sinistrally coiled conchs (hyperstrophic) were common in the early Paleozoic but the mimospirines show sinistral asymmetry already at the embryonic stage. These were thus neither hyperstrophic nor secondarily sinistral but, instead, originally sinistrally coiled gastropods or gastropod-like monoplacophorans. To which class the pelagiellids and mimospirines are attributed, is a matter of convention. The pelagiellid protoconch is similar both in shape and size to the most primitive bellerophontids (*Protowenella* [114]; *Modestospira* [115,116]), molluscs with tightly coiled conchs and paired muscle scars but the course of larval development closely similar to coeval gastropods. A strong increase in mortality at the conch diameter of about 0.6–0.7 mm suggests metamorphosis [115] in both the Ordovician bellerophontids and associated pleurotomariid gastropods. This finds support in a similar increase of mortality at the metamorphosis in the Early Palaeozoic bivalves, where the presence of the veliger stage is apparent [70]. This is not consistent with the view held by most zoologists that the ancestral gastropods did not have separate protoconch I and II stages [117] but definitely the protoconch morphology of all the early Palaeozoic was different than their Mesozoic and Recent successors. Anyway, if the larval morphology of the oldest known gastropods is taken into account, the bellerophontids and pelagiellids appear more similar to them than to the tryblidiid monoplacophorans. The protoconch morphology is known in the Silurian monoplacophorans [70] and it was similar to that in their Recent relatives. The external surface of the embryonic shell was rather smooth, with delicate, regularly distributed growth increments — probable result of stable conditions of development, as up to the stage of creeping juvenile they are brooded in oviducts [118]. Similar protoconch morphologies characterise also the Early Cambrian helcionellids and the rostroconch molluscs [70], although there the protoconch had a hemispherical shape intermediate between the tryblidiids and the pelagiellids.

The protoconch morphology suggests that the tryblidiid monoplacophorans, now represented by *Neopilina* and other closely related forms, are rather distant anatomically from the symmetrical ancestors of the gastropods. The elongated conical appearance of the earliest gastropod protoconch, although spirally coiled, is not much different from that of the extinct hyoliths, which are generally of slightly larger size, or even cephalopods, significantly larger in size. The curved earliest Cambrian *Ceratoconus* and *Hamusella* were similar to the ancestral hyolith *Turcutheca* which allows to arrange all those early molluscs in a single morphocline. The gastropods seem thus to be related closer to the ancestors of cephalopods than bivalves and scaphopods.

No single dextral specimen has been found among several hundred specimens of the sinistrally coiled Ordovician *Mimospira* [113]. Sinistrally coiled specimens in populations of dextral Ordovician gastropods were definitely not more common than in Recent ones. This may mean that determination of the adult asymmetry took place very early in the phylogeny and embryogeny, possibly being causally connected with the inclination of spindle at the beginning of spiral cleavage. When this connection was established remains unknown. Among the Early Cambrian gastropods there are both sinistral and dextral forms, mostly known on the basis of phosphatic nuclei or, at the best, phosphate coated larval conchs. Such specimens exhibit the general geometry of the shell but the evidence on the morphology of adult teleoconch and muscle attachments is missing. Even the size of teleoconchs remain unknown and, although it is commonly assumed that the phosphatised specimens represent adults [119], adult shells of some earliest Cambrian molluscs reached more than 2.5 cm in diameter [3]. The most common Cambrian probable gastropods, pelagiellids, are dextrally coiled. Some sinistral forms, for instance *Yangtzespira* [120], closely resemble symmetrical *Anabarella* in the flattened conch form and ornamentation, and may be related to it. Virtually circular section of the coils and relatively large apex characterise sinistral Early Cambrian forms attributed to *Nomgoliella* [121], *Xinjispira* [122], or *Barskovia* [123]. The fossil evidence seems thus to show that the conch asymmetry of the ancestral gastropods developed in connection with its being rotated backward while dragged by the animal (Fig. 8). The conch asymmetry enabled then a better packing of the body without any enlargement of the aperture being necessary. This allowed to preserve the protective function of the operculum.

The main gastropod diversification of the gastropods took place in the late Cambrian and the Early Ordovician [109]. The early Palaeozoic gastropod embryonic and larval conchs are relatively well known owing to secondarily phosphatised fossils with fine details visible under the scanning electron microscope [70,113,115]. They are similar to those of the bellerophontids in having only slightly curved and distinctly separated embryonic stage (protoconch I), the first coil showing a smaller or larger umbilical perforation. This makes both those groups of early molluscs different from later gastropods, which virtually always have their protoconchs tightly coiled from the beginning. Remarkably, *Aldanella*, the oldest known gastropod from the Early Cambrian, shows a rather advanced morphology of the initial parts of the conch, with a very small in size apex of the protoconch [108]. A secondary uncoiling of the larval conch characterises the early pleurotomariid gastropods. In some cases the larval conch had initially straight conical shape (*Eccyliomphalus*, *Subulites*; Fig. 9).

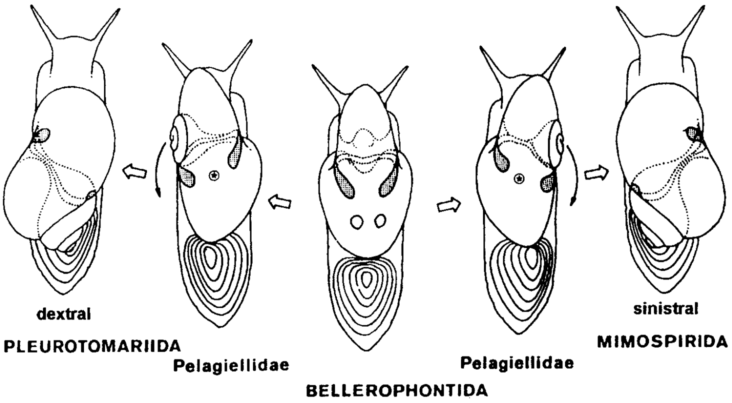

Fig. 8. Schematic presentation of the origin of sinistrally and dextrally coiled gastropods from bilaterally symmetrical bellerophontids with backward rotation of originally planispiral conch [32].

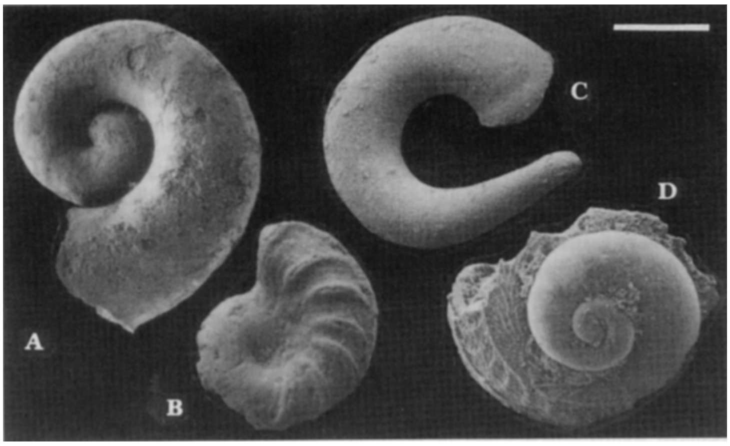

Fig. 9. Larval conchs of early gastropods. A–B. Ordovician bellerophontid *Modestospira* (A, phosphatic nucleus of a complete larval conch; B, incomplete phosphate coating; ([116]: Pl. 55, Fig. 1,2) from the Caradoc of the Mójcza Limestone at Mójcza in the Holy Cross Mountains, Poland. C. Ordovician *Subulites*? (phosphatic nucleus; [112]: Fig. 22A) with high adult but loosely coiled larval conch from a glacial erratic of Baltic origin, Llanvirn. D. Devonian pleurotomariid *Mourlonia*? (apex of a shell replaced with pyrite; [112]: Fig. 35G) from the Famennian Łagów Beds of Łagów in the Holy Cross Mountains, Poland. Scale bar is 200 μm.

Among the known Ordovician gastropod larvae, those of the trochonematids are the most similar to the modern gastropod protoconchs. Their first half-coil is smooth, relatively tightly coiled, with a very small umbilical perforation and relatively large apex. The plane of coiling is slightly oblique to the following whorls. The spiral ornamentation, when present, appears suddenly, together with distinct growth lines [116]. This may suggest an early development within the egg covers. The early stages of the Ordovician pleurotomariids were apparently similar to those of the coeval holopeids, assumedly members of the trochid branch. All this is in contradiction with ontogenetically late calcification of gastropod protoconchs proposed to be phylogenetically ancient by Bandel [117]. In the Silurian, very narrow, almost fusiform larval shells are known which probably represent the branch of the loxonematids, as suggested by the morphology of the Carboniferous and Triassic members of the group illustrated by Herholz [124] and Bandel [125,126]. The protoconchs typical of more advanced Recent gastropod groups developed during the late Palaeozoic and Mesozoic [127].

There is an interesting analogy between the evolutionary history of gastropod asymmetry and the phylogeny of the charophyte oogonia (Soulie-Märsche, this volume). There also at the very beginning, in the late Silurian and Devonian, dextral (*Trochiliscus*), symmetrical (*Sycidium*) and sinistral (*Eochara*) forms developed. The radially symmetric forms had several (about ten) cortical filaments with several cells involved in calcification of the oogonium wall (gyrogonite). Both the dextral and sinistral forms preserved the originally high number of filaments but with only one elongated cell in each filament involved in building the oogonium wall. In the lineage of sinistral forms the number of filaments was reduced to five during its evolution in the Devonian, and all later charophyceans developed from this single lineage. Similarly as in the case of gastropods, it is unlikely that sinistrality alone gave them superiority over dextral and radial relatives, so it seems reasonable to assume that the survival of sinistrality was a result of other characters being by chance connected with this kind of chirality.

Behavioural asymmetry

Behaviour is better known than anatomy in many primitive metazoans of the latest Precambrian and early Palaeozoic. This happens owing to the abundance of marks left in the sediment by benthic organisms during their feeding activity (trace fossils) as well as remnants of their shelters built of collected sediment particles or of secreted organic matrix.

Perhaps the oldest case of ordered behaviour in respect to the left and right sides is that represented by the Late Cambrian burrows of *Treptichnus* [49]. These organisms produced U-shaped tubular cavities within the mud with walls stiffened with mucus. Faecal pellets occurring at the bottom of some burrows indicate that they were empty during life of the animal. Scratches on their walls approximately in the middle of their length show the presence of about 16 hooks arranged around the body. Its probable earliest Cambrian ancestor *Trichophycus* had much less regular mode of burrowing, with densely packed particular burrows [128] whereas the Devonian *Treptichnus* shows even more regular pattern of burrows branching. This is suggestive of a very slow directional evolution of behaviour.

The early Palaeozoic graptolites offer an opportunity, unique in the whole living world, to study the evolution of a complex behaviour in a long geological time span. These extinct organisms were shown to be pterobranch hemichordates by Kozłowski [129,130] who pointed out that the fusiform units (fuselli) of their colony skeleton imply the same mode of secretion as in Recent *Rhabdopleura*, that is with the glandular preoral lobe. For a long time the nature of the additional layered tissue (proven to be collagenous by Towe and Urbanek [131]), which gave graptolite colonies (rhabdosomes) their strength owing to secondary thickening, remained enigmatic. Eventually, Crowther [132,133] documented irregularly meandering 'bandages' which cover the rhabdosome surface, apparently corresponding in width to the graptolite animal preoral lobe. Finally, fossilised zooid bodies [134] confirmed their hemichordate affiliation. The pterobranch model seems thus fully consistent with the available evidence [135], which means that all the complexity of the rhabdosome organisation depends solely on the behavioural activity of the animals forming the colony (clone).

Carbonised collagenous skeletons of the graptolite colonies are common fossils in Palaeozoic rocks. Of special interest are pelagic graptolites, being widely distributed geographically and thus suitable for evolutionary studies. Their phylogeny is well known [136] and they are traditionally believed to be the fastest evolving fossils organisms of the Ordovician and Silurian and are used as guide fossils for the standard stratigraphic subdivision of those periods. Unfortunately, evolutionary studies are rarely performed at the species level and available quantitative data on the morphologic evolution are very sparse.

Evolution of collagenous pterobranch 'nests'

The evolution from the oldest Middle Cambrian *Rhabdopleura*-like benthic pterobranchs [137] to pelagic graptoloids was the most dramatic at the early postlarval stages of the colony development (astogeny). Originally, the larva produced a dome-shaped skeleton (prosicula) immediately after settling over the substrate. After the metamorphosis was completed, the first zooid perforated its wall and started to secrete a collagenous tube (metasicula) with its pre-oral disc. Zooids of subsequent generations perforated the creeping base of the tubes forming the network of the colony (Fig. 10).

In the course of the evolution leading from the rhabdopleurids to the benthic graptolites, a strong size dimorphism developed among zooids, expressed in the diameter of their tubes (thecae). The dimorphism was apparently sexual and the smaller tubes (bithecae) are assumed to belong to males. Advanced benthic graptoloids developed erect coniform colonies [138] by gradually reducing the creeping stage in their astogeny, until the first perforation developed at the top of cylindrical prosicula. At this stage in the latest Cambrian lineage of *Rhabdinopora* the development of protosicula ceased to be preceded by settlement of the larva and

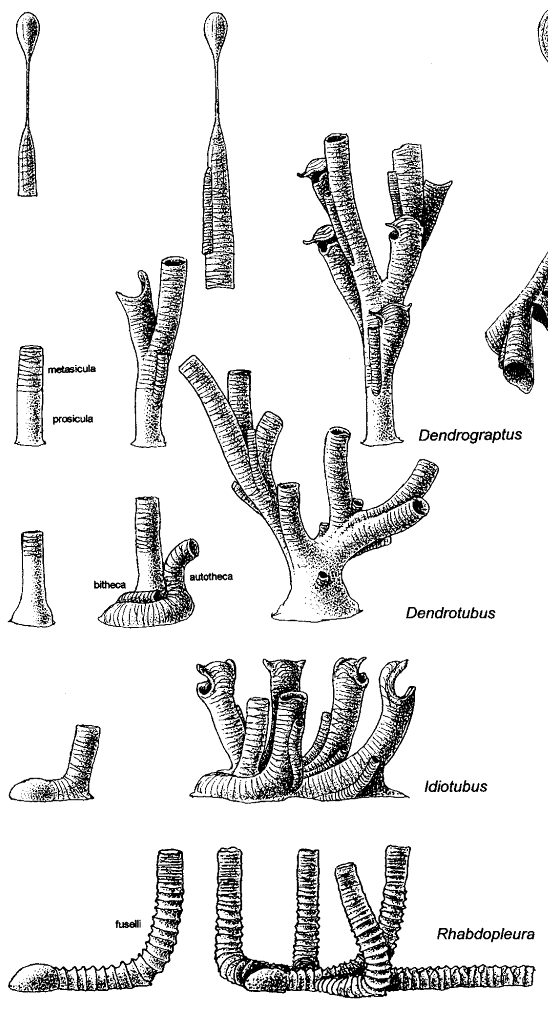

Fig. 10. Diagrammatic presentations of the transformation of astogeny in the evolution from the rhabdopleurid pterobranchs, through benthic graptolites with dimorphic thecae to pelagic graptoloids; three subsequent stages in the colony development are shown.

the whole astogeny proceeded in the water. How this was executed, remains a mystery [139]. With the transition to the pelagic mode of life the male tubes (bithecae) became restricted to the few first generations (frequently they opened into the female tubes) and finally disappeared. This is suggestive of a far-reaching reduction in size of male zooids, unable to produce their own thecae, or their complete disappearance. In any case this would mean the lack of gene flow between graptolite colonies, thus the biological species concept does not apply to them! The lack of a common gene pool apparently did not have any influence on the rate of evolution of the graptolites. The alternative, that formerly female zooids became hermaphroditic, seems less likely and cannot be supported by the irregular pattern of variability in graptolite fossil assemblages [140] which is to be expected when interbreeding is lacking.

However, what is the most important for the topics of this review, in the course of the evolution the astogeny became progressively more and more ordered. The form of the colony, which was apparently of much hydrodynamic importance, was determined already at the beginning of the astogeny, by the direction of budding of the first few generations of zooids. Despite numerous reversals of the evolution, the main trend in the evolution of the pelagic graptoloids, as nicely shown by Mitchell [141] and Melchin [142], was a reversal in the orientation of the thecae in respect to the probably stabilising fin (nematularium) and progressing reduction in number of thecal rows (stipes). During this evolution, the zooids which initially built their tubes parallel to the sicula, did it in the opposite direction, starting from the distal part of the stipes and reaching the stage when already the single tube of the first generation was opposite to the sicula and produced only a single stipe. In a lineage of the graptoloids with extremely thin colony skeleton with two rows of tubes connected together along the mid-line, the number of zooids was reduced and became finite in the astogeny (*Holoretiolites*). In extreme cases there was actually only a single fully developed zooid in the colony (*Corynites*), which means that coloniality was secondarily lost in a very sophisticated way [143].

An interesting question thus emerges, how precise was the behavioural control of the early astogeny and how it developed in the evolution. Unfortunately, data on the population variability of the early astogeny in benthic erect graptolites (dendroids) are missing. This is understandable, as their earliest astogenetic stages being covered with the collagenous cortical tissue, require sophisticated and time consuming techniques to be revealed [144]. It is much easier to study early stages of astogeny in pelagic graptolites, as thousands of juvenile colonies can easily be obtained from a single sample. In the higly ordered early astogeny of the Middle Ordovician graptolites with biserial colonies, the first post-sicular generation zooid perforated the wall of the sicula in location which was presumably determined by the mode of budding, thus developmentally controlled. In contrast, the sinuous course of the theca was a result of the graptolite animal peculiar behaviour, as the structure was built-up by the organism with fusellar collagenous units secreted by its preoral lobe glands. The following succession of alternate left and right directions of budding of new zooids and construction of their thecae was apparently a mixture of developmental and behavioural controls. Very few specimens departed from the precisely determined order of budding direction ([145]: p. 266). The final morphology of particular thecae and the whole rhabdosome depended solely on the behavioural mechanisms, although some morphologic gradients are typical for the earliest parts of the colony, suggestive of sicula-born physiologic control [146,147] or accumulation of morphogenetic factors during the colony growth [148,149]. The available evidence is thus suggestive of an extremely precise control of the early astogeny of the graptolites, including the left–right side recognition by the zooids constructing the collageneous colony skeleton with the secretion of their preoral discs.

Behavioural asymmetry had its expression not only in the mode of establishing ('budding') new colony tubes (thecae). In several cases asymmetry of apertural structures developed in the evolution of graptolites, the best documented being the Late Silurian lineages of *Lobograptus*, *Cucullograptus*, and *Neocucullograptus*. In a series of samples from the borehole Mielnik in eastern Poland, with a very good stratigraphic control, Urbanek [150,151] documented a gradual development of

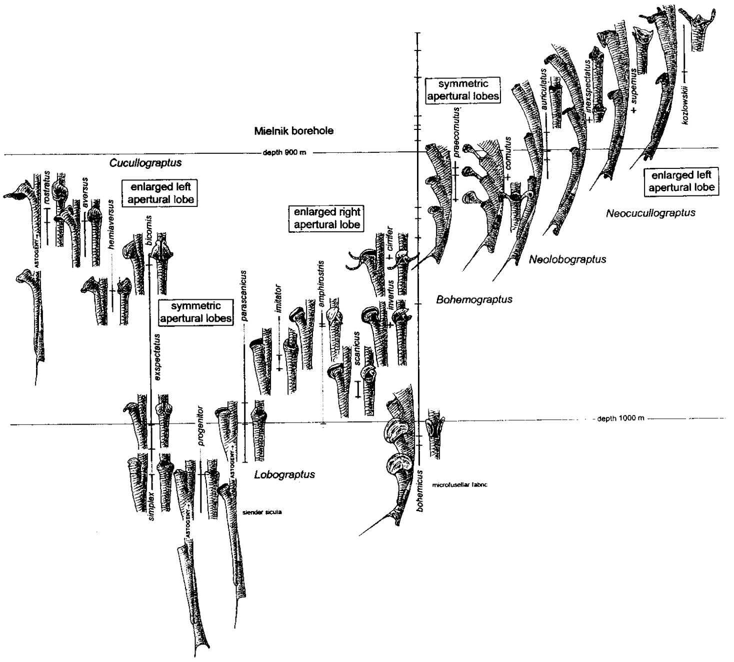

Fig. 11. Recurrent development of asymmetric apertural structures in thecae of Late Silurian monograptids (based on [150,151]).

asymmetry in hood-like apertural modifications of those graptolites (Fig. 11). In each of the three cases asymmetry developed independently from a bilaterally symmetric ancestral status. Moreover, the lineage of *Neocullograptus* developed asymmetry in apertural structures which were built in basically different way, as indicated by a different microstructure of the collagenous tissue (microfusellar fabric). The control of asymmetry was precise from the beginning and practically all specimens in samples of *Cucullograptus* and *Neocucullograptus* have their left apertural lappet enlarged, whereas in the lineage of *Lobograptus* this was the right lappet which was larger (Fig. 11). Urbanek ([150]: p. 337) interpreted the asymmetry of apertural structures as an expression of an anatomical asymmetry of the lophophore. However, as the fuselli were apparently deposited by an animal crawling over the colony skeleton it was a result of its behaviour that the hood was asymmetric, even if truly an asymmetric anatomy was fit into it after construction.

Conclusions

Despite the generally held view that strictly radiate animals were ancestral to those showing bilaterally symmetrical bodies, no convincing fossil evidence is available that radially organised coelenterates were present either in the Vendian or Cambrian. Instead, biradially organised ctenophores and their possible ancestors, the Petalonamae, as well as the nemathelminthan worms, seem to play a crucial role in the early phylogeny of the Metazoa. There is also no fossil evidence which could substantiate the basal position of the turbellarian flatworms in the animal phylogenetic tree. Both the body fossils and traces of life activity preserved in the Vendian and Cambrian rocks indicate that among the earliest bilaterians there were also forms similar in their body organisation to the echiurans, nemerteans, and molluscs. Asymmetry developed in those relatively advanced groups of organisms several times but generally did not persist for long. There was no case of continuity of an asymmetric body plan across a phylum boundary.

In the evolution of asymmetry in the early metazoan, antisymmetry is missing or at least insignificant as the initial stage. This suggests that the rooting of polarity of asymmetry in the early embryogenesis proceeded rather easily. As the early evolution of anatomical and behavioural asymmetry shows no preference in respect to handedness, the transmission of asymmetry from molecular to organismal levels (if occurred) could not be straightforward.

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