

The Early Cambrian medusiform metazoan *Eldonia* from the Chengjiang Lagerstätte

CHEN JUN-YUAN, ZHU MAO-YAN, and ZHOU GUI-QING



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The alleged Chengjiang scyphozoans *Stellostomites eumorphus* and *Yunnanomedusa eleganta* are conspecific. Because of the strong resemblance to the Burgess Shale type species of *Eldonia*, the Chinese species is relocated to this genus. *Eldonia*, originally described as a holothurian, on anatomical grounds may as well be interpreted as a lophophorate. The superficial resemblance to jelly-fish is apparently a result of adaptation to pelagic life. Although the extant lophophorates are without exception sedentary, their pelagic relatives were probably abundant in the Early Paleozoic.

Key words: Early Cambrian, *Eldonia*, lophophorate, Chengjiang, China.

Chen Jun-yuan, Zhu Mao-yan and Zhou Gui-qing, Nanjing Institute of Geology and Palaeontology, Academia Sinica, Chi-Ming-Ssu, Nanjing, 210008, People's Republic of China.

Introduction

Medusiform animals were a significant component of Cambrian marine communities. Among the fossils from the Early Cambrian Chengjiang Lagerstätte, such abundantly occurring medusiforms were first described by Sun & Hou (1987) and assigned to four species: *Heliomedusa orientalis* interpreted to be a hydroid, allegedly chondrophoran *Rotadiscus grandis*, and alleged scyphozoans *Stellostomites eumorphus* and *Yunnanomedusa eleganta*. Although they were all classified in the Cnidaria, none of them have been proved to bear a real cnidarian affinity. As a result of subsequent revision, *H. orientalis* has appeared to be an inarticulate brachiopod with well-preserved mantle setae (Conway Morris & Robinson 1988; Chen & Erdtmann 1989; Jin Yugan & Wang Huayu 1992). Although *Stellostomites eumorphus* and *Yunnanomedusa eleganta* do have a soft-bodied

'umbrella', very similar to medusae, their anatomical organization is very different from that of the cnidarians.

The Chengjiang fossil Lagerstätte is of Early Cambrian age, located stratigraphically in the lower part of the *Eoredlichia* Zone within the Yu'an-shan Member, the upper unit of the Qiongzhusi (Chiungchussu) Formation (Zhang 1987; Chen & Erdtmann 1989). Most of the fossils examined were collected from the quarry (labelled MQ1) on the western slope of the Mt. Maotian in a single mudstone layer. They are also numerous in several thin mud layers above and below in an interval of about 30 meters. A few of them came from Xiaolantian, Ma'an hill and Daputou, roughly representing the same stratigraphical horizon.

In the present study we will show that *Stellostomites eumorphus* and *Yunnanomedusa eleganta* are conspecific, showing a strong resemblance to the Burgess Shale type species of *Eldonia*, *E. ludwigi* Walcott 1911. The *Eldonia* species is one of the most abundant components of the Chengjiang Lagerstätte fossil assemblage, being represented by at least two thousand specimens. Eight hundred of them were examined and form the basis of the following detailed description of the internal anatomy of the *Eldonia* animal and discussion on its taxonomy and biological affinities.

Most of the specimens used in this study were collected by the authors during several separate field seasons since the winter of 1990 and are housed in the Museum of Early Life Research Centre (prefix ELRC), Nanjing Institute of Geology & Palaeontology (prefix NIGP). Most fossils retain part (postfix a) and counterpart (postfix b). In specimens with catalogue numbers without postfix counterparts are missing.

Preservation

The fossils are reddish or dark yellow after weathering, while the matrix is yellowish. The color contrast is assumed to be due to differences in iron or kerogen contents. *Eldonia* was apparently soft-bodied and thus should be flattened into a thin film unless the mud was injected into the body cavities. Actually, there were some such hollow spaces in the body of *Eldonia* which vary in their accessibility to the mud. Usually fine mud filled one or several of the cavities, the others remaining empty. The degree of compression depends on the amount of mud which was introduced into the body cavity. The mode of preservation varies thus considerably both in different parts of an individual and between individuals.

Split of the rock may cross several stacked structures in *Eldonia* discs (Fig. 1). The dorsal radial canals generally provide a preferable route for the split, except in the area of coiled sac where the split usually follows the route along the ventral surface of the sac rather than the dorsal radial canal. In rare cases the lobe-like structures and associated ventral radial canals was a preferable route for the split.

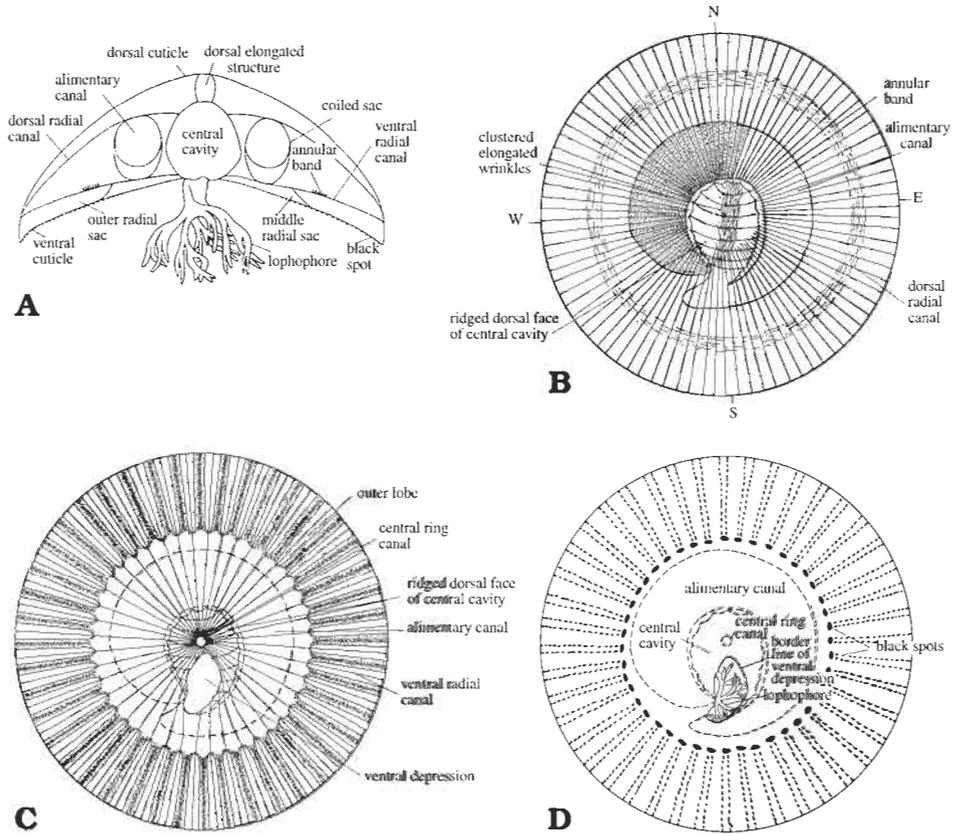


Fig. 1. Diagrammatic reconstruction of *Eldonia eumorpha* (Sun & Hou 1987) from the Early Cambrian (Atdabanian) of Chengjiang, China. □A. Vertical cross section of the disc. □B. Dorsally located transverse section of the disc; letters denote conventional sectors. □C. Ventrally located transverse section of the disc. □D. Ventral surface of the disc.

Sediment filling. — The concave side of the disc of *Eldonia* formed a depression. It readily accumulated a large amount of mud while the animal floated within a suspended mud flow. Because of the thick mud load, the major part of the depression is usually buried within the rock matrix. The body cavity of *Eldonia* was subdivided into numerous compartments. The major hollow compartments in *Eldonia* include the central cavity, coiled sac (the term introduced by Duncan Friend), and the structure interpreted as the alimentary canal. The injected fine mud within these compartments supported and separated the delicate structures and probably inhibited biodegradation by absorbing enzymes (Butterfield 1990). The central cavity easily accepted sediment, and is usually preserved three-dimensionally, with the thickness of mud filling ranging from 0.5 mm to 1.5 mm.

The tentacles appear to be hollow and their commonly three-dimensional preservation suggests that their internal cavities usually were accessible for the suspended mud. The ventral radial canals are usually

flattened, which means that they were closed and inaccessible to the sediment.

Orientation. — The original orientation of slabs is known in almost 200 specimens, being marked in the field. In other specimens of *Eldonia*, it can be determined from sediment grain gradation in their host slabs.

Eldonia was of low bell shape, and mostly preserved in the hydrodynamically most stable position with their concave surface in parallel orientation with respect to the plane of bedding. The specimens are usually imbricated, apparently an effect of unidirectional transportation by channel currents. Few specimens are reversed with the convex surface facing down, suggesting that they deposited from suspension.

Pattern of deformation. — Commonly the discs were buried in an oblique orientation. As an effect of subsequent compression, the outline of the body has become oval. The tilted angle of each specimen can be counted as the cosine of the ratio of short to long axis. In a few cases, the two opposite margins of the body penetrate into deeper sediment layers. Also in this case compaction resulted in an oval disc shape. About twenty per cent of the specimens under present study exhibit a major modification of the body shape.

Deformation of the *Eldonia* discs occurred preferentially. If sectors of the disc are conventionally denominated with geographic directions (Fig. 1B), the mouth and anus being located at S, deformations tend to occur in their SE and SW sectors. Among 362 specimens with known orientation, 32.6% are deformed on SW, 29.3% on SE, 14.6% on NE, 12% on NW, 4.4% on W, 4.1% on S, 3.9% on E, and 1.5% on N.

Taphonomy

All the specimens of the 'medusoids' *Eldonia* were entombed in groups within fine mud layers, 95% of them being preserved in a one centimetre thick single mudstone bed. It shows evidence of a grading structure in its lower part, suggestive of continuous transport by turbidity currents flowing downward and deposited on the distal prodeltaic environment.

Benthic organisms such as the priapuloid worms *Maotianshania*, linguloids (Chen *et al.* 1995a), brachiopods *Heliomedusa*, and arthropods inhabited also this area and usually embedded together in the same bed. Both the animals living in the mud (*Maotianshania* and linguloids) and at

Fig. 2. *Eldonia eumorpha* (Sun & Hou 1987) from the Early Cambrian (Atdabanian) of Chengjiang, China (locality M2): specimen NIGP 100323a. partial disc buried subparallelly, with the plane tilted to S: explanatory drawing (A) and photograph (B; light from NNW, low angle), both $\times 1.4$. Note (1) trace of clockwise coiled sac, (2) ridged dorsal wall of the central cavity, (3) ventral canals radiating from the centre and passing the coiled sac ventrally; lobe-like structures are present, each associated with primary and auxiliary canals; lobes are bilaterally symmetrical except for the SW sector where they are asymmetrical with anticlockwise sides steeper.

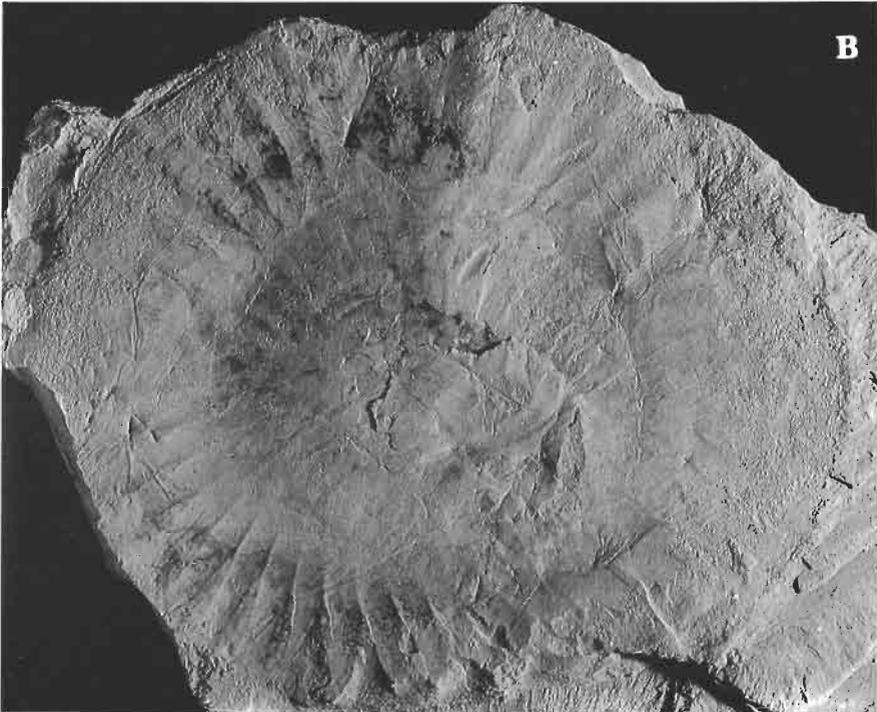
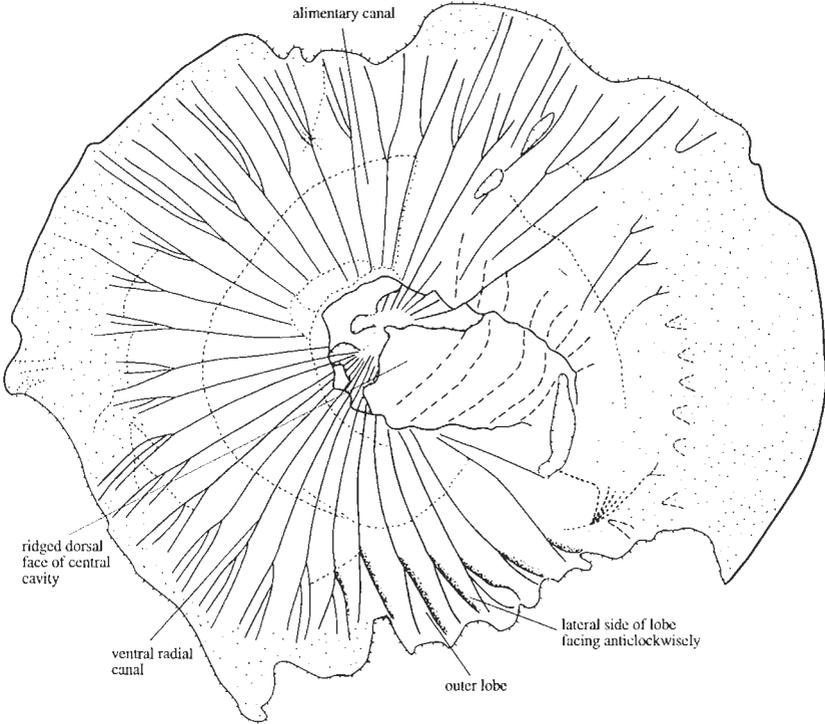


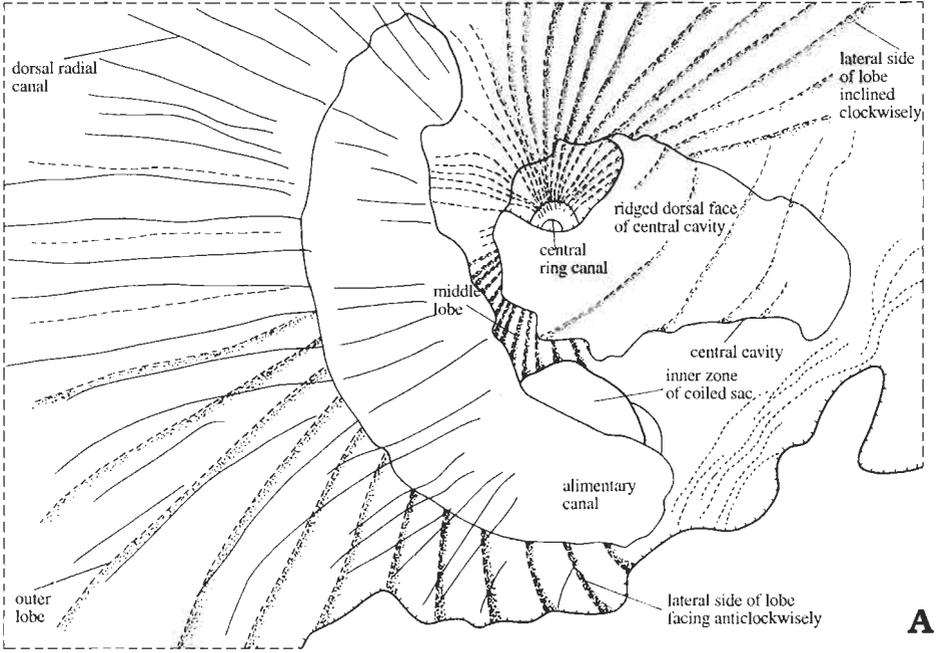


Fig. 3. *Eldonia eumorpha* (Sun & Hou 1987) from the Early Cambrian (Atdabanian) of Chengjiang, China (locality M2): enlarged portion of NIGP 100323a (Fig. 2), light from N, low angle; $\times 3$.

its surface or above (*Heliomedusa* and arthropods) were carried by the down-slope low density flows. Thus the transportation distance of most benthic components in the *Eldonia*-layers appears to be only minimal. A careful preparation (by Zhou Gui-qing) of the specimen ELRC 01063 revealed that the *Maotianshania* priapulid worm had penetrated upwards through the *Eldonia* carcass, which is suggestive of utilization as a trophic source. Presumably, the *Eldonia* disc was buried by a microturbidite event and then scavenged by the infaunal *Maotianshania*.

Eldonia external covers were non-mineralized; the survival time of its carcass in sea water was thus probably short. As the fossils found are all

Fig. 4. *Eldonia eumorpha* (Sun & Hou 1987) from the Early Cambrian (Atdabanian) of Chengjiang, China (locality MQ1), part of specimens ELRC 02034 buried obliquely with disc inclined toward S (judging from the dislocation of the radiating centre between dorsal and ventral canals) in top view, explanatory drawing (A) and photograph (B, light from NE, low angle), both $\times 3$. Note (1) three dimensionally preserved coiled sac with alimentary canal largely exposed to surface and the sac proper only partially exposed, (2) dorsal radial canals above the coiled sac, (3) lobe-like structures which pass ventrally through the coiled sac being bilaterally symmetrical in N sector and asymmetrical in W and E sectors, with the a steeper and narrower side facing to the inclination of the disc, and (4) three-dimensionally preserved central cavity with a convex and ridged dorsal face.



whole animals, it is reasonable to believe that the death of the animals occurred either during transportation or shortly after burial. The fossil specimens are oriented downward with their concave surfaces, mostly parallel to the bedding plane, and the convex aboral surface penetrating the overlying laminae, rarely they show oblique burial or overturned position. This orientation is interpreted here as physiological. The pattern of burial orientation suggests that most of the animals were still alive not only in the cohesive 'nepheloid clouds', but also while sinking in the sediment.

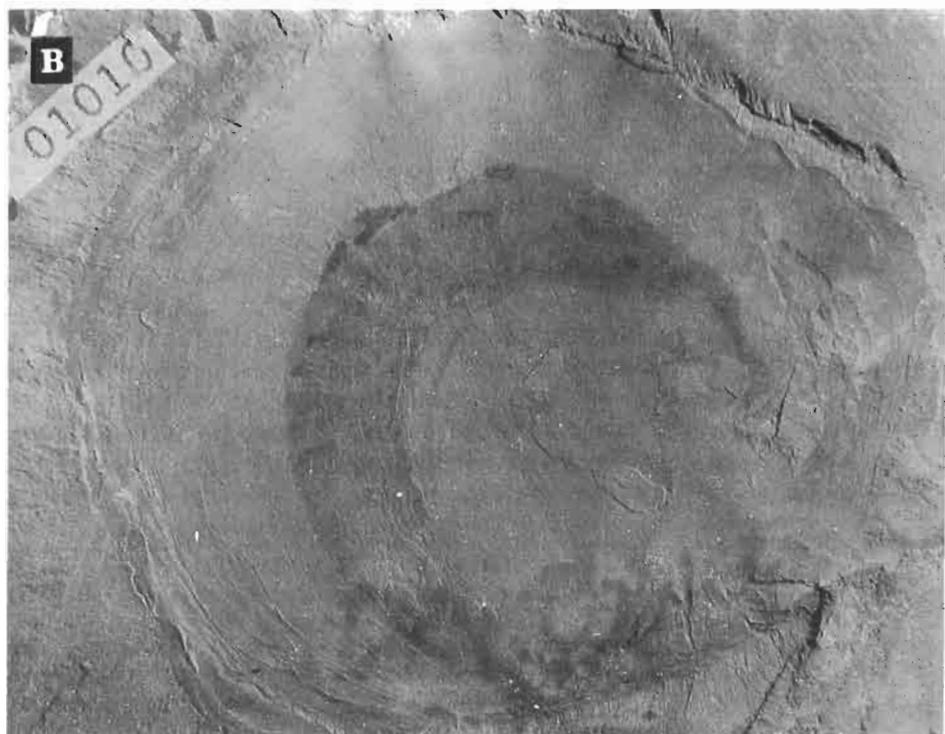
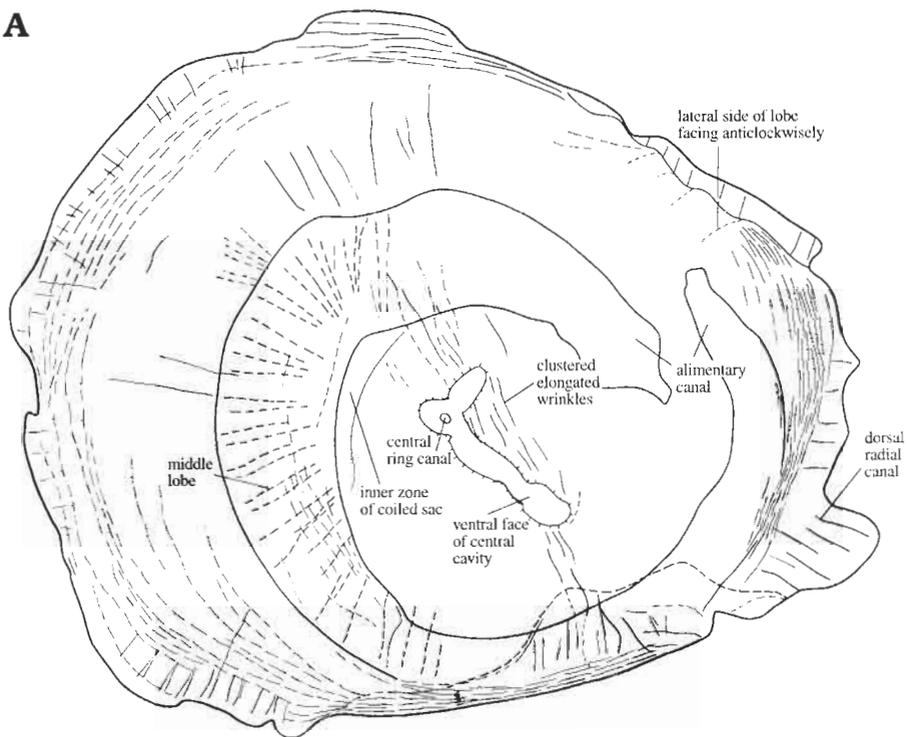
Paleoecology

The present Chengjiang area was part of the shallow epicontinental sea bordering the Kan-Dian land to the east. Paleomagnetic data suggest that this area was in the tropical climatic zone (Qiao *et al.* 1988; Liang *et al.* 1990). A high proportion of clay minerals in the mudstones, together with quartz being the dominant constituent of coarse-grained sediments, indicates a wet tropical climate, which might have controlled the type of sedimentation. Due to inferred discharge of fresh water from the river (or rivers), probably a shallow layer of relatively warm water developed there with a markedly lower salinity than that of sea-water. The water column was thus stratified into the upper warm brackish water and the lower cold marine water of higher density, with rapid changes of temperature and salinity at the boundary. The pycnocline (or thermocline) zone tends to be rich in nutrient, thus with a high productivity. Influx of the fine terrigenous material was partly emplaced by the nepheloid clouds flowing preferably along the pycnocline zone probably resulting in periodical mass mortality of organisms living there.

Eldonia is traditionally regarded as a pelagic organism, because its external morphology is basically the same as that of the extant cnidarian medusae. The medusiform shape of *Eldonia* seems to be an example of adaptation to a pelagic mode of life. This was, however, challenged by the recent study of Dzik (1989), who took a radical view of the animal as sedentary benthos for the reason that related forms were heavily sclerotized (Masiak & Żylińska 1994). He interpreted the central structure,

Fig. 5. *Eldonia eumorpha* (Sun & Hou 1987) from the Early Cambrian (Atdabanian) of Chengjiang, China (locality MQ1); specimen ELRC 01010b buried subparallelly to the plane of bedding; explanatory drawing (A) and photograph (B, bottom view of a slab, light from NW, low angle), both $\times 1.7$. Disc modified by formation of a pair of veils (on SE and SW margins of disc) which were ascending subvertically and converge horizontally toward S; judging from accentric disposition of central ring canal, body was inclined to N; coiled sac buried obliquely, with a inner zone of lower sac appearing in middle length of the coiled sac; lobe-like structures only represented by middle lobes; velum-like structure seen on NE area of the disc (view from top).

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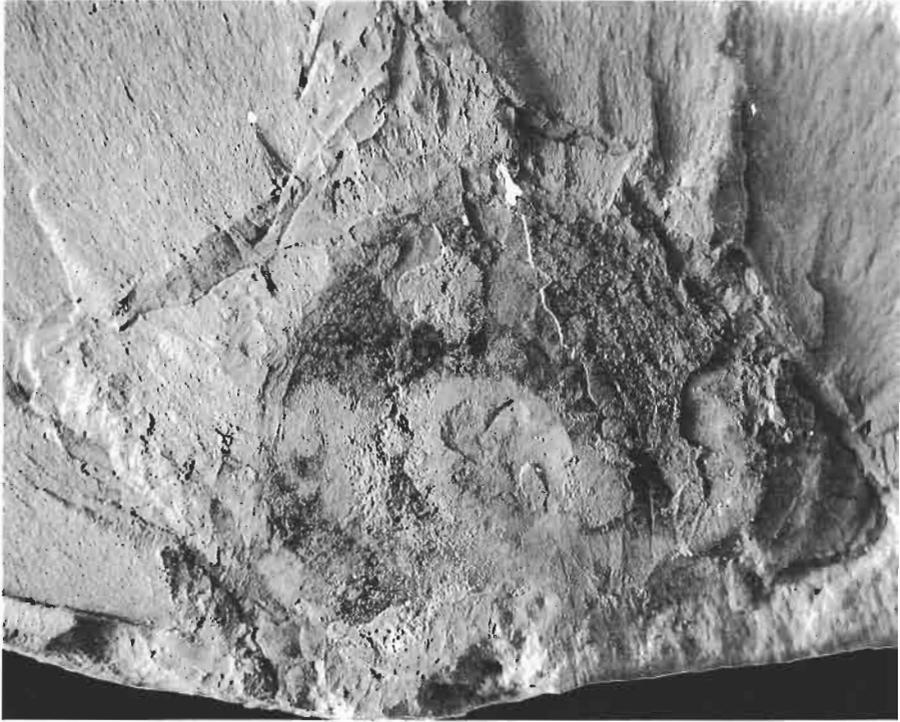


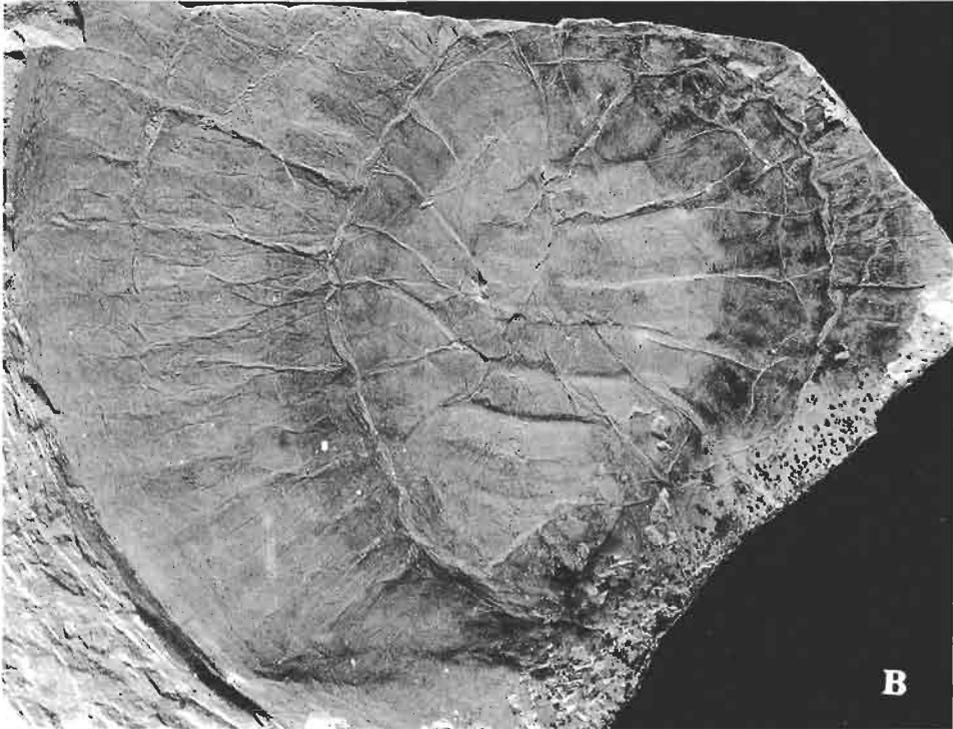
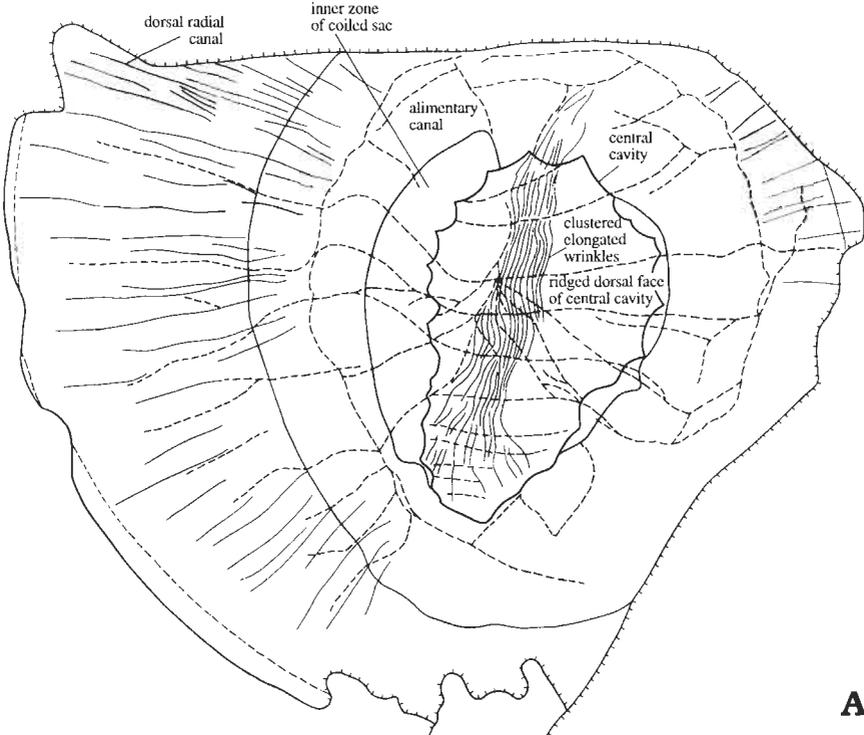
Fig. 6. *Eldonia eumorpha* (Sun & Hou 1987) from the Early Cambrian (Atdabanian) of Chengjiang, China (locality MQ1); specimen ELRC 01336, light from W, low angle, top view; $\times 3$. Disc bears two pairs of 'erected veils'.

which was incorrectly interpreted as a mouth by Sun & Hou (1987), as an attachment organ.

Eldonia population dominated the Chengjiang community, contributing one sixth of the entire number of soft bodied fossil macrofauna in the Chengjiang Lagerstätte. They show mass occurrence, almost 1,000 individuals being collected from a thin single event mud layer in an area of a few dozens square meters. The mass occurrence indicates that *Eldonia* animal concentrated in flocks that were caught or redeposited by mud flows.

In a number of cases lobopodians *Microdictyon* (Chen *et al.* 1989; pl. 3: 6) and *Paucipodia* (Chen *et al.* 1995b) directly attached to *Eldonia* discs have been found. One specimen of *Eldonia eumorpha* bears eight *Microdic-*

Fig. 7. *Eldonia eumorpha* (Sun & Hou 1987) from the Early Cambrian (Atdabanian) of Chengjiang, China (locality MQ1); specimen ELRC 01011; explanatory drawing (A) and photograph (B, light from NE, low angle), view from the base of the slab; both $\times 2$. Note a velum-like structure on the periphery of disc, coiled sac with the inner zone of the sac proper, ventral view of ridged dorsal membrane of the central cavity, clustered elongated wrinkles extending from N to S across entire length of the central cavity; velum-like structure on E margin of the disc.



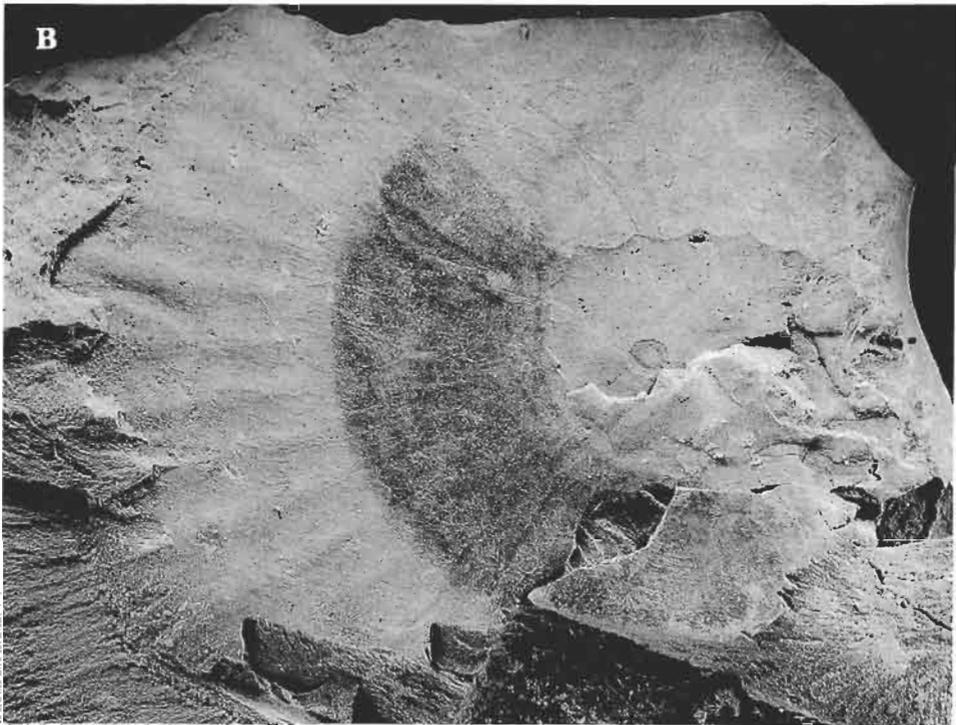
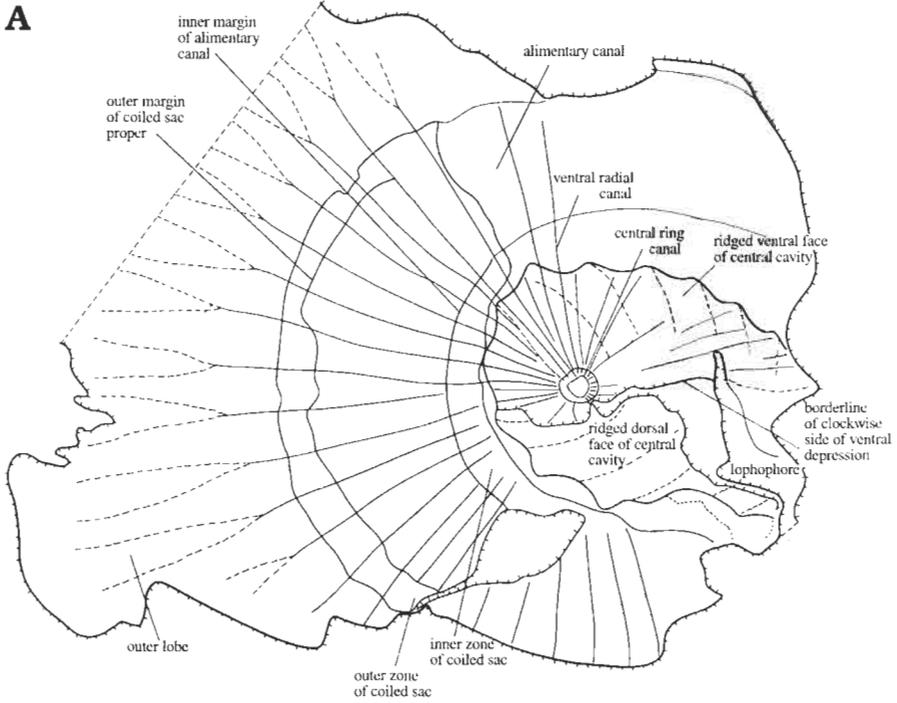
tyon juveniles upon it, indicating either symbiotic or scavenging behavior. An entire specimen of *Paucipodia* is preserved in presumably life position on the top of another *Eldonia* disc, also suggesting a scavenging behavior (Chen *et al.* 1995b).

Restoration

As restored (Fig. 1) *Eldonia* is low bell-shaped, with the convex upper surface, a concave lower surface, and its outer margin usually forming a circular shelf projecting inward. The internal anatomy of *Eldonia* is by no means radial but asymmetric, with a subhorizontally clockwise (as seen from above) coiled sac. The coiled sac possesses a well defined internal elongated structure in a number of specimens in the Burgess species (Duncan Friend, personal communication) and an identical structure has also been identified in a number of specimens from Chengjiang. The internal elongated structure situated dorsally within the coiled sac is interpreted as an alimentary canal. The alimentary canal ends with mouth and anus openings ventrally, both off the centre on one side of the disc and close to each other. The lophophore bears a semi-circular extended base that surrounds the mouth. If this interpretation is accepted, the sac itself cannot represent any alimentary canal but rather a kind of peritoneum. The sac is enclosed, and thereby suspended both by the dorsal and ventral sets of radial canals.

The body cavity of *Eldonia* is subdivided into a central cavity and radial sacs. The radial sacs were closed completely as they invariably are preserved without any mud filling being flattened completely into a thin film. The films in a number of cases are preserved as dorsally convex radial structures which were recently identified by Duncan Friend (oral communication) in the Burgess Shale species, referred to as lobe-like structures. Identical structures are also present in a number of specimens in Chengjiang. They are arranged radially, bearing 44 equally-shaped and sized sacs within each of the concentric areas referred to as inner, middle and outer circle of the disc correspondingly. Each of the three radially-aligned ventral canals within each sac shared a primary ventral canal which provided a link between them and the central ring canal. All the inner, middle and outer sacs as indicated by the lobe-like structures, were wedge-like in outline, expanding in width toward the disc margin.

Fig. 8. *Eldonia eumorpha* (Sun & Hou 1987) from the Early Cambrian (Atdabanian) of Chengjiang, China (locality MQ1); specimen ELRC 01049; explanatory drawing (A) and photograph (B, light from NE, low angle); both $\times 2.5$. This is a top view of disc buried subparallelly, inclined toward NNW, both outer and inner margin of the membrane of sac are preserved, the central cavity preserved dorsally with ridged convex face and ventrally with a ridged imprint at the top of the inner lobe-like structures; radial lobe-like structures and associated ventral canals radiate from the central ring canal to periphery of the disc through the coiled sac ventrally.



Below detailed evidence is provided for the proposed restoration of particular organs of the *Eldonia* body.

External morphology. — The wall of the convex, proposedly dorsal surface of the *Eldonia* disc is distinctly defined, gray or reddish color in contrast to the yellowish weathered rock matrix. A number of specimens (ELRC01019ab, ELRC02653, and others) show the presence of fine concentric lines (Fig. 11) which are evenly spaced, about 0.1 mm, throughout the entire dorsal surface. These are probably growth lines. The wall of the ventral, concave surface of the body was thinner but also bears fine concentric lines, interpreted as growth lines, which are densely spaced at the same distance as the dorsal epidermis. This indicates that a cuticular skeleton that covered both dorsal and ventral surfaces of the body was secreted by epidermis at the margin of the disc (see also Dzik 1989).

In a number of specimens the disc rim forms a velum-like structure, ranging 2–4 mm in width, projecting inward at the lower surface (Figs 5, 7).

Coiled sac and enclosed alimentary canal. — Almost all of the examined specimens have a well defined coiled sac located about midway between the center and margin of the disc and surrounding intestine. The sac was spacious. Mud injection penetrated separately the alimentary canal and a cavity of the sac below of it. The alimentary canal can be arbitrarily subdivided into esophagus, stomach, and intestine. Except for its anterior and posterior extremities, that may have been curved downward, the intestine is spiral, generally in the same plane. The proposed anus opens at a point about midway between the centre and outer margin with the anterior or oral end located more centrally. The esophagus narrows rapidly anteriorly and ends with a terminal constriction. The stomach (Figs 4–5, 7–8, 12, 14, 16) is the most prominent part of the alimentary canal, being strongly curved, and occupies the broadest portion of the alimentary canal. It diminishes in width both posteriorly and anteriorly. A conspicuous feature of this structure is its black stain, usually absent in its adjacent parts of the intestine and in underlying sac. The posterior end shows an abrupt contraction, usually the black stain terminates there. The posterior portion of the digestorial tract is elongate, roughly as long as the stomach, with its width equal to about one-half the maximum diameter of the stomach. The lower compartment of the sac, referred to here as the coiled sac proper seems to be a vascular organ

Fig. 9. *Eldonia eumorpha* (Sun & Hou 1987) from the Early Cambrian (Atdabanian) of Chengjiang, China (locality MQ1); specimen ELRC 01067 buried parallel to the plane of bedding in top view. Explanatory drawing (A) and photograph (B, light from NE, low angle); both $\times 1.5$. Note (1) exposed dorsal face of the digestive tract, in its midlength the spit steps down to a deeper level of the sac proper, (2) dorsal radial canals, (3) central cavity filled with mud, with convex dorsal and flat ventral face, (4) ventral depression with apex in subcentral position, (5) inner part of the ventral canals originating from the central ring canal, (6) imprint of clustered elongated wrinkles on the raised dorsal face of the central cavity.

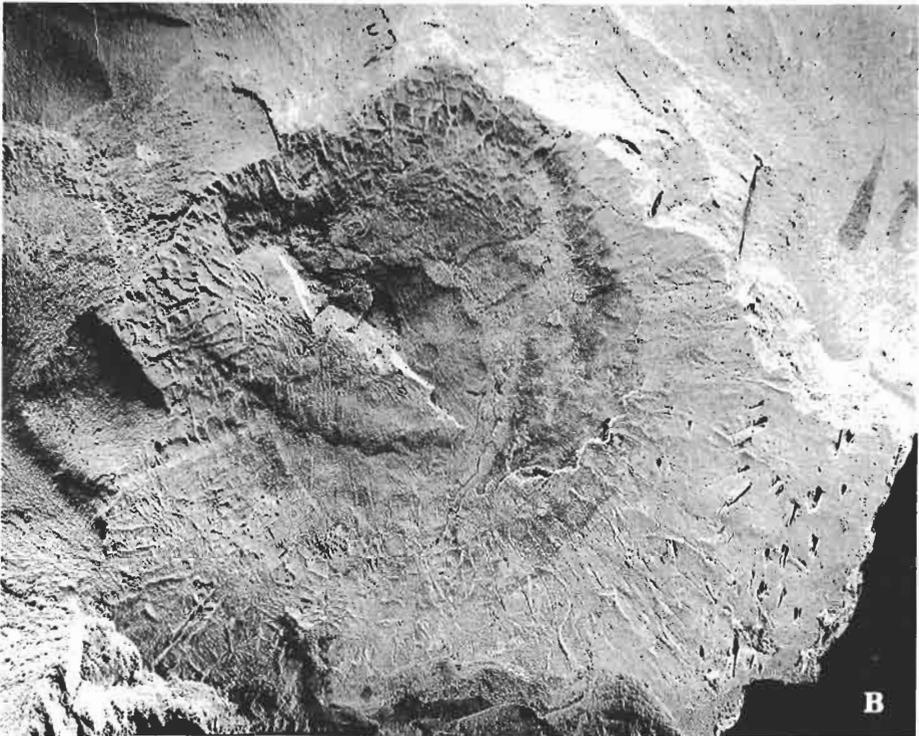
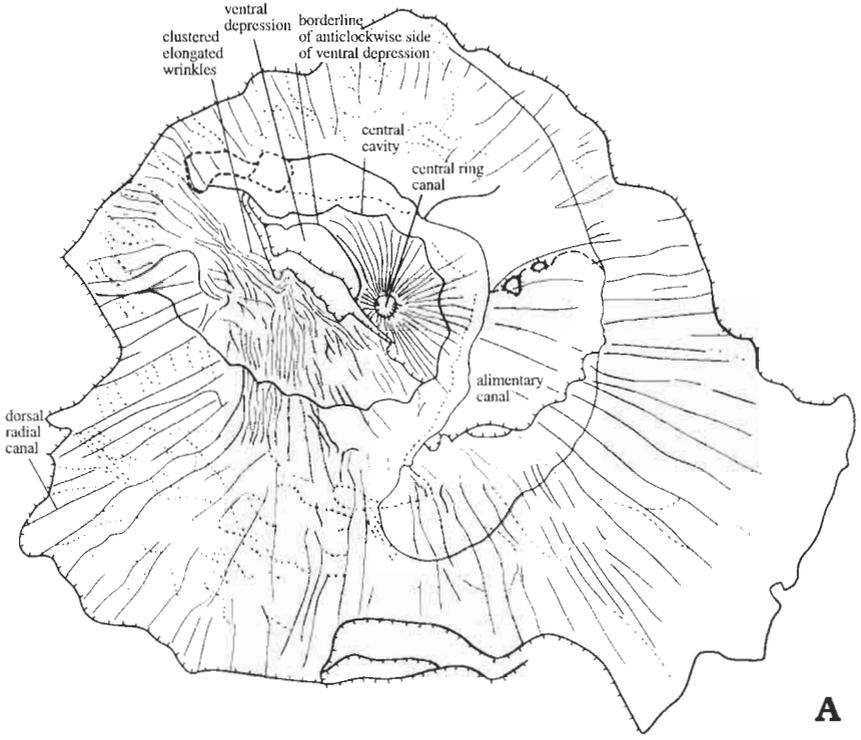




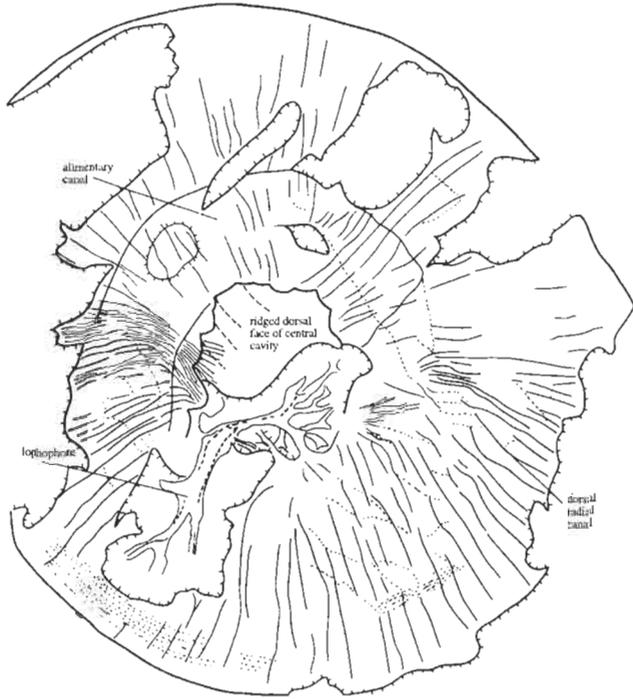
Fig. 10. *Eldonia eumorpha* (Sun & Hou 1987) from the Early Cambrian (Atdabanian) of Chengjiang, China (locality MQ1); enlarged part of specimen ELRC 01067 (Fig. 9) prepared to expose inner lobe-like structure and associated ventral radial canals, ridged ventral face of the central cavity, triangular ventral depression, and lophophore (light from E, low angle); $\times 3$.

enclosed ventrally by radial sacs. The coiled sac is preserved as a yellowish structure without any indication of black stain.

The alimentary canal and the coiled sac proper appear to be of similar sizes. In result of vertical compaction, they overlap one other completely at their entire length, only one of them being exposed to the surface. However, in a number of cases the split revealed both structures (Figs 4, 10, 11, 14). When compaction was in an oblique direction, the two structures are only partially overlapped, showing an elongated zone of overlap within the outline of the sac (Figs 5, 7, 8, 14). The border lines are well defined and probably represent mesenteria of the alimentary canal.

Elongated wrinkled structure. — A large number of specimens show linearly arranged wrinkles in the centre. They seem to correspond to an

Fig. 11. *Eldonia eumorpha* (Sun & Hou 1987) from the Early Cambrian (Atdabanian) of Chengjiang, China (locality MQ1); specimen ELRC 01001a with dorsal side within a micro-turbidite mud layer, basal surface of the slab: explanatory drawing (A) and photograph (B, light from NW, low angle); both $\times 1.2$. Note gently convexed dorsal surface with trace of growth lines, dorsal radial canals which step dorsally across the coiled sac, lateral borders of ventral depression, and lophophore (arrowed in B).



internal structure extended horizontally and dorsally at the top of the central cavity and connecting oral or anal ends of the alimentary canal with its centre (Figs 7, 9). Its length equals one third of the diameter of the disc. The structure is usually slightly wider in its mid-length, narrowing towards the ends (Fig. 7). The structure in all known specimens is preserved as a wrinkled film.

Radial canals. — Inside the body there were two sets of radial canals. The dorsal radial canals 88 in number are well visible in outer part of the disc in most specimens. They radiate straight to the periphery which suggests they were rather stiff. No signs of deformation that would indicate they occupied different planes have been identified, except for the middle part where they seem to ascend to the top of the coiled sac. A few canals are recognizable at the top of the central cavity (Figs 9–11). It remains unknown how they terminate. The radial canals were probably circular in cross section, of diameter about 0.1–0.2 mm.

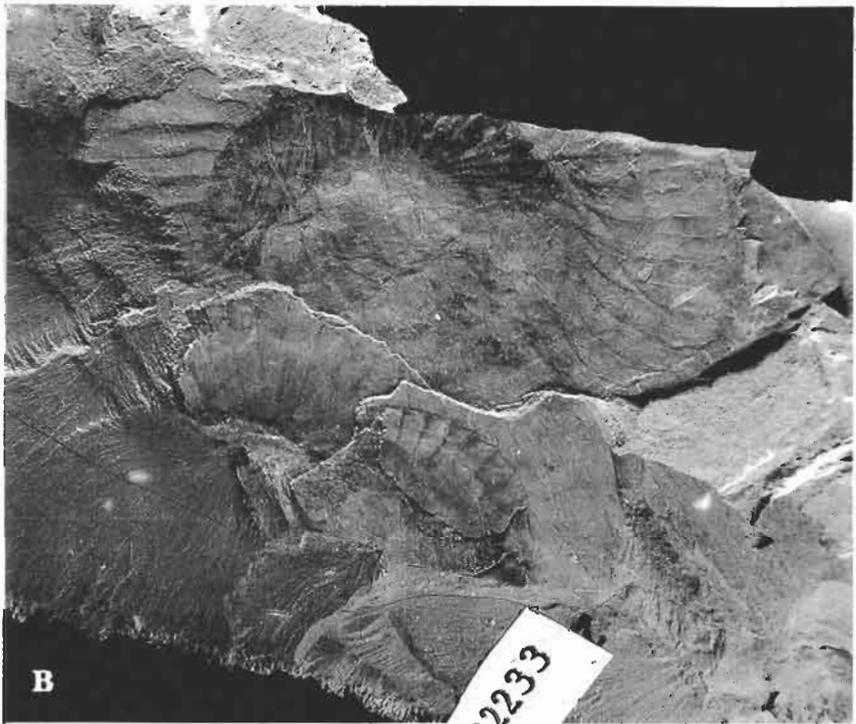
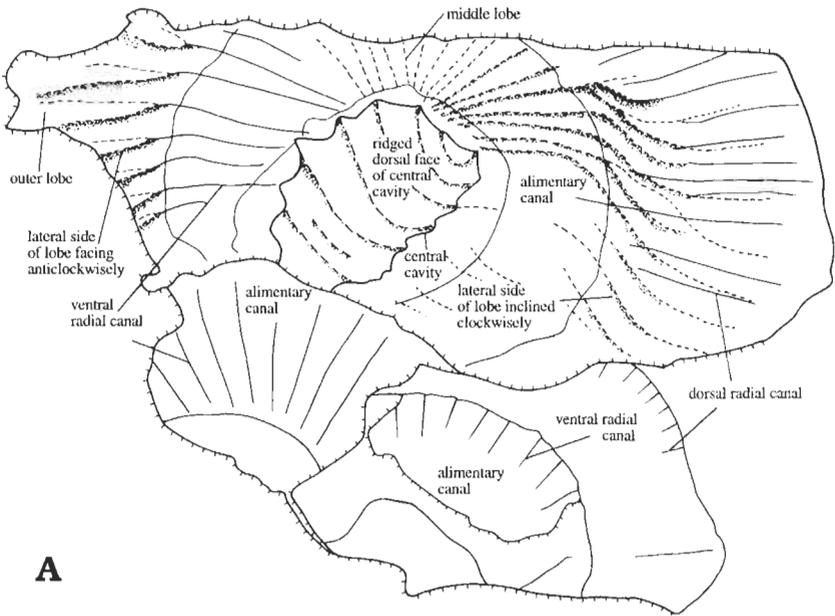
The ventral radial canals, 44 in number, extend from a central ring canal horizontally outward to the periphery of the disc (Figs 2–4, 8, 10, 14–15). They cross the coiled sac being probably attached to its ventral surface. Their course, which is strictly radial otherwise, tends to deflect from radially in the area adjacent to the ventral depression (Figs 9–10). To each of the primary canal a pair of auxiliary canals is added at its mid-length, approximately at the outer margin of the coiled sac (Figs 2–3).

The ventral radial canals are considered here as water vascular structures, radiating from the central ring canal to the periphery generally on the same plane throughout the body.

Ventral radial sac. — Well-defined lobe-like structures at the ventral disc surface correspond to ventral radial sacs. The sacs were built of a soft tissue and closed as they show complete compression into a thin film. In most of cases their dorsal surface was supported from below by ventral canals and tended to maintain a positive relief while the original shape of their ventral surface was completely obliterated. The lobe-like structures can be subdivided into inner, middle and outer lobes, which corresponds to respective circles in the disc. The three radially-aligned canals appear to be independent but linked each to other by a primary ventral canal. The full number of the canals is thus 132.

The inner lobe-like structures (see Figs 4, 12) are slightly convex, extending radially from the central ring canal and widening outward. They cover most parts of the inner circle except for the ventral depression. The

Fig. 12. *Eldonia eumorpha* (Sun & Hou 1987) from the Early Cambrian (Atdabanian) of Chengjiang, China (locality MQ1); three specimens (ELRC 02233, ELRC 02234, and ELRC 02235a) buried in an imbricated stack, ELRC 02235a being at the deepest horizon, inclined to S; explanatory drawing (A) and photograph (B, light from W, low angle); A \times 2; B \times 1.5. Note (1) a clockwise coiled sac. (2) well defined middle lobes, asymmetric with clockwise face steeper on E and anticlockwise on W, their longitudinal axes bent with concave side facing toward steeper side on W and gentle side on E. (3) central cavity represented by a ridged dorsal surface.



boundaries of the lobes are generally straight although several of them in S sector tend to deflect in order to avoid passing over the ventral depression. The middle sacs are represented by gently to moderately convex lobe-like structures (Figs 2, 4–5, 8, 12, 14), with narrow end located above the outer margin of the central cavity.

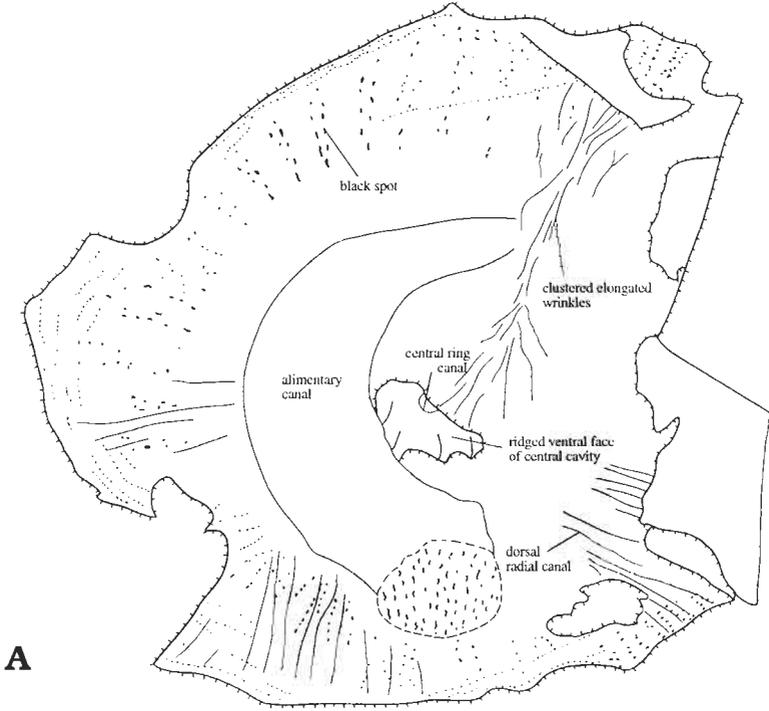
The outer sacs are prominently expressed (Figs 2–4, 8, 12, 14). In addition to the primary canal each sac bore a pair of auxiliary canals which originated at mid-length of the primary canal, diverging under a narrow angle (see Figs 2–3, 12).

In specimen ELRC 02235a (Fig. 12), which was buried obliquely with its S side underneath another *Eldonia*, the sacs both in W and E sectors were buried obliquely with sagittal plane tilted toward N side. The sacs lying both in the E and W sectors are preserved as asymmetrical with their steeper and narrower slopes arranged clockwise on E side and anticlockwise on W side. Their longitudinal axes show a conspicuous curvature; the depth of curvature measures 4 mm, which indicates that the longitudinal axis of the sacs was convex longitudinally. In W side area the longitudinal axis of the lobes has its concave side facing toward the steeper face, suggesting that the axis was concave instead of convex.

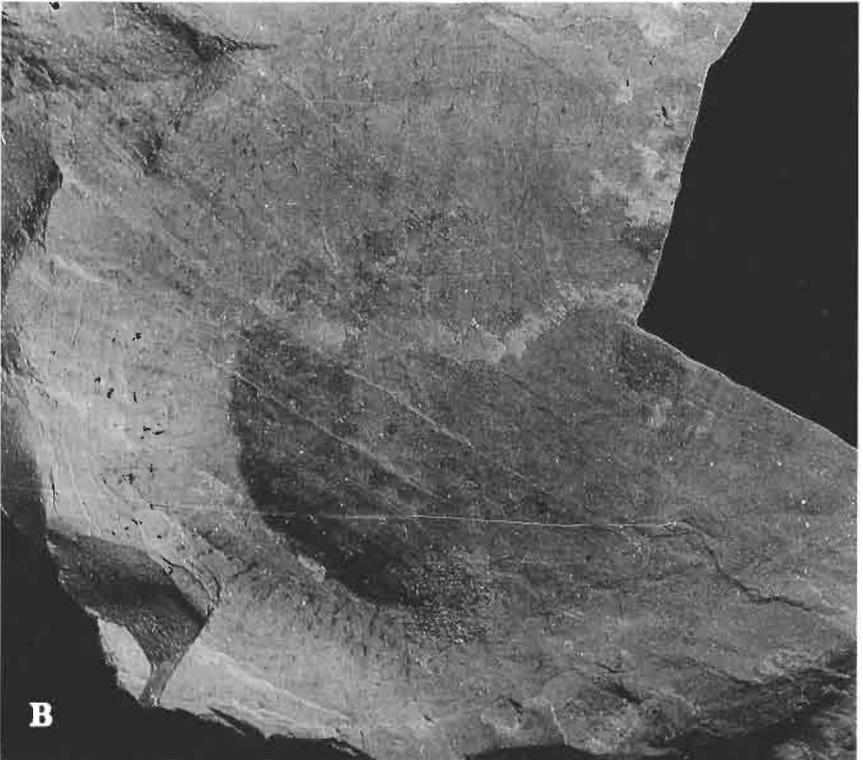
The radial sacs lack any mud filling and on this basis are inferred to be completely closed. As a result of compaction, they are flattened into a thin film which is either convex or smooth. The convex preservation suggests that the sac resisted compaction. An upward drift of the ventral face resulted in formation of a lobe-like convex areas (Figs 2–4 show a view from above). In obliquely deformed specimens the sagittal plane of sacs usually tends to be inclined (Figs 2, 4–5, 12). As an effect of compaction, some sacs are asymmetrical, with one side (opposite to the slope of the sagittal plane) being narrower and steeper than the other. As an effect of post-burial compaction, some sacs are preserved as lobe-like structures, while others are flattened into an evenly-extended film.

Sclerites. — Black small objects form spots which had both concentric and radial arrangement (see Figs 1, 13–14) within an area relating to the outer circle of the concave area of the disc. The objects are exceptionally black, in sharp contrast with other parts of the body. This indicates their different composition. They probably were highly sclerotized or mineralized, as they were resistant to diagenetic compaction and show positive relief even on top of the disc. The sclerites apparently were external structures, attached to the outer surface of the ventral cuticle. They were usually detached after the death of the animal. In most cases

Fig. 13. *Eldonia eumorpha* (Sun & Hou 1987) from the Early Cambrian (Atdabanian) of Chengjiang, China (locality MN5), specimen ELRC 01145, basal view. Explanatory drawing (A) and photograph (B, light from W, 40°); both $\times 1.4$. Note (1) anticlockwise coiled sac, (2) black spots appearing ventrally in outer part of the disc, (3) velum-like structure, (4) dorsal canals running across the velum-like structure to its outermost margin, (5) partially preserved ventral wall of the central cavity, and (6) elongated cluster of wrinkles extending at a N–S direction.



A



B

they are either entirely absent or only partly preserved. Details of their morphology are not clearly recognizable. They appear to have a subcircular base and an elongated distal spine, of about the same size, 0.2 mm wide and 0.35 mm long except for the innermost one which is considerably larger.

Concentric rows of the sclerites are roughly 1 mm apart; radial rows correspond in distribution to the ventral radial canals.

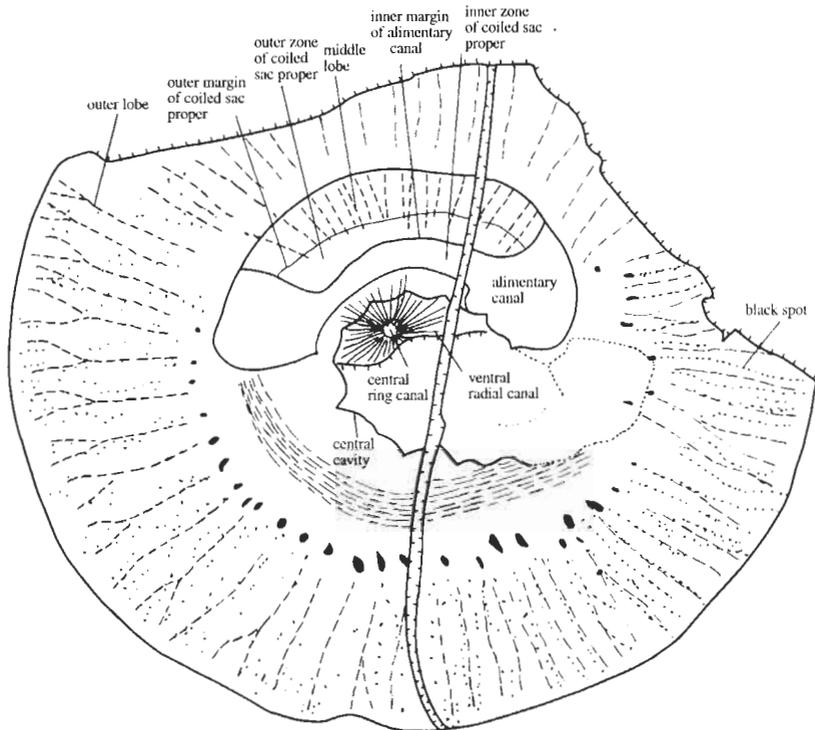
Central cavity. — In the central part of the body an elongate dome-shaped cavity is present within the outline of the coiled alimentary canal. The cavity was enclosed from all sides within a rigid ridged membrane. Its convex dorsal face was strengthened with 7–8 transverse ridges (Figs 2–4, 7–12, 16). They are parallel to each other, extending diagonally in the NW to SE direction throughout the cavity. The ridges were sharp, separated by broadly rounded troughs in between. The ridges tend to be flattened into smooth or slightly projected surfaces in their mid-length, being better recognizable toward the sides of the cavity. On lateral margins of the cavity the ridges tend to incline subvertically, partially preserving original presumably vertical orientation.

The ventral face of the central cavity appears largely to be enclosed by a rigid ridged membrane except for its S side area where the membrane appears to be soft, tending to be lowered ventrally to form a triangular depression (Figs 1, 9). The ridged ventral face is usually represented as an imprint of linear structures on the top of the inner lobe-like structures (see Figs 8, 15). The structures run horizontally from NE to SW on top of the inner lobe-like structures and within the outline of the central cavity, with a direction normal to the extension of the dorsal ridges. In rare cases (see Fig. 16) the ventral surface of the central cavity is exposed, showing a ridged membrane and a wrinkled triangular structure.

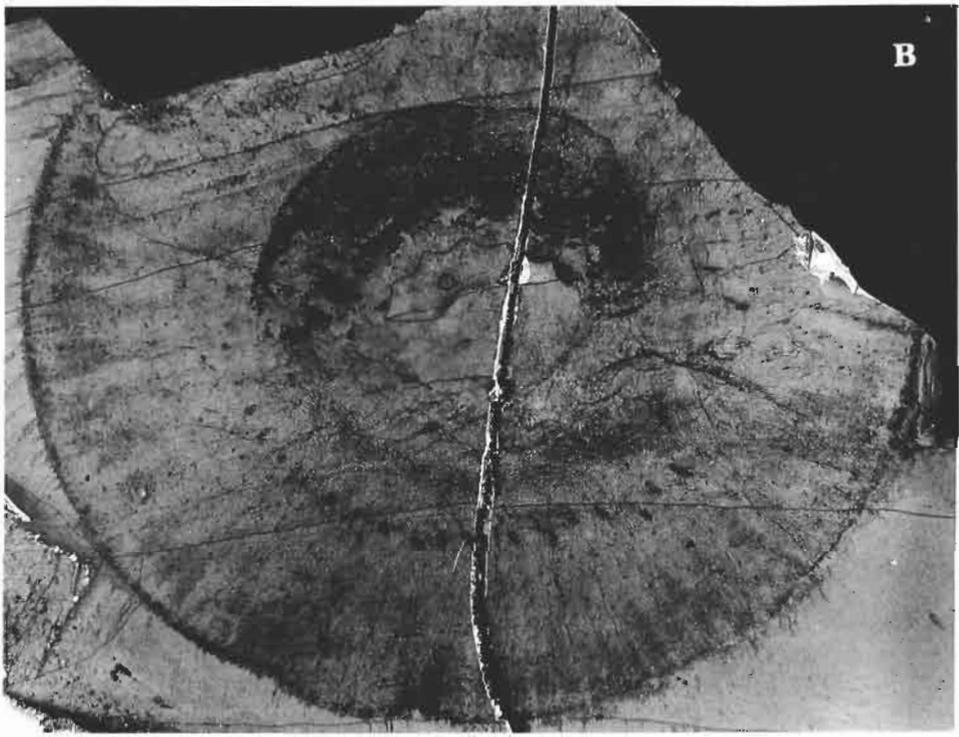
Ventral depression. — The ventral depression is defined laterally by a pair of black borderlines which are diverging from an apex situated subcentrally, but S to the central ring canal (Figs 8–10). They diverge outward to join to the coiled sac terminals. The borderlines appear to be rigid, presumably providing for muscle attachment. Their dark coloration suggest that their composition differ from adjacent parts of the body. The depression usually encloses a substantial amount of the mud, therefore being three-dimensional. When without mud-filling, the depression is completely compressed into a film, being unrecognizable (see Fig. 16).

Lophophore. — Lophophore is preserved in 44 specimens. It is always observed on the ventral surface and in continuity with the alimentary

Fig. 14. *Eldonia eumorpha* (Sun & Hou 1987) from the Early Cambrian (Atdabanian) of Chengjiang, China (locality MQ1); specimen ELRC 01059a in ventral view; explanatory drawing (A) and photograph (B, light at high angle and alcohol wetted); A \times 1.3; B \times 1.5. Note central ring canal and inner portion of the ventral radial canals radiating from inner margin of the central ring canal (see Fig. 15), anticlockwise coiled intestine, central cavity represented by partially preserved ridged ventral face, and black spots arranged both radially and concentrically in the outer circle of the disc.



A



B



Fig 15. *Eldonia eumorpha* (Sun & Hou 1987) from the Early Cambrian (Atdabanian) of Chengjiang, China (locality MQ1); enlargement of specimen ELRC 01059a (light from N, low angle), showing details of the proximal part of the ventral radial canals which originate from inner margin of the central ring canal; $\times 5$.

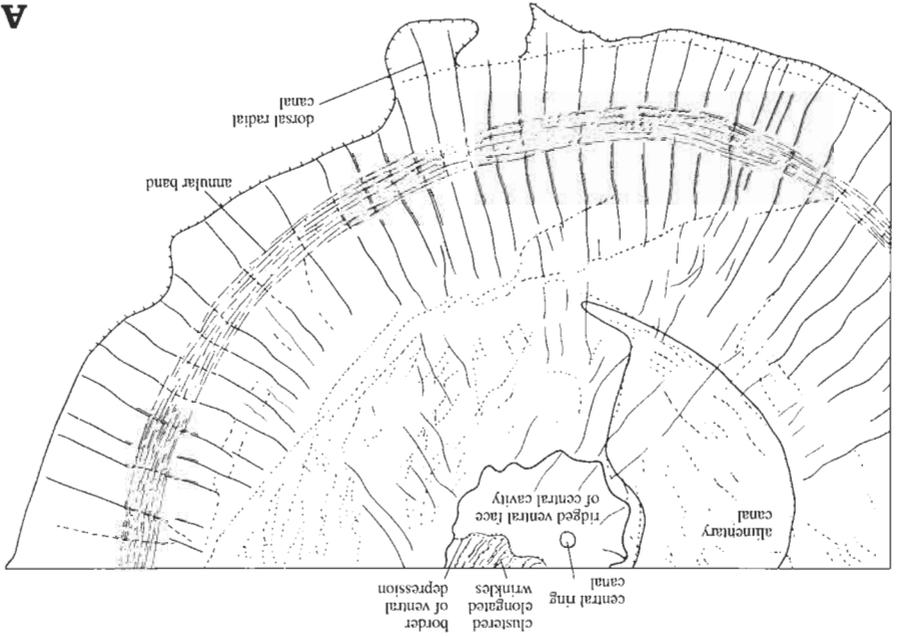
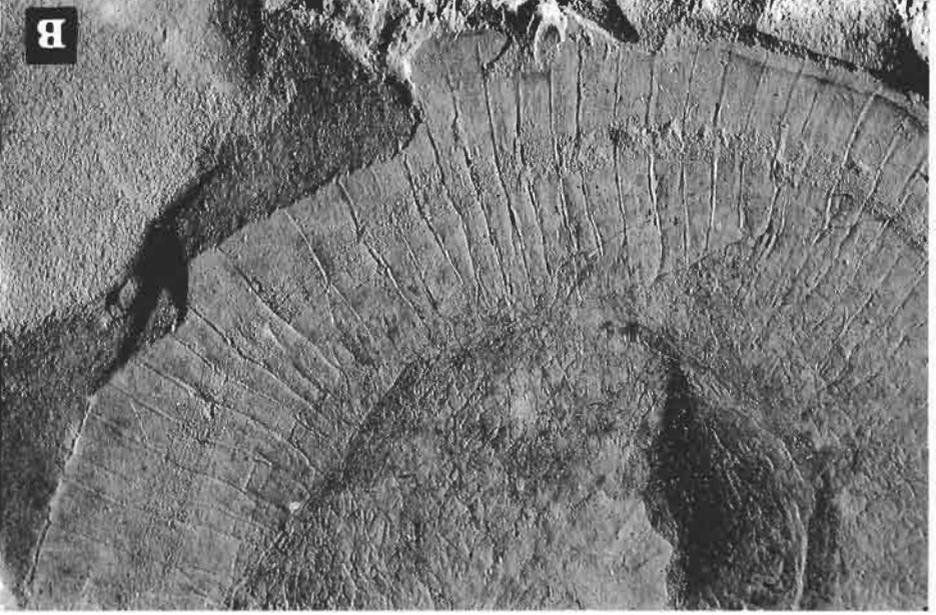
canal, usually concealed either by the disc or by matrix, although preserved in most specimens. The interior of the lophophore appears to be hollow as it is filled with mud in some specimens. Due to resistance to diagenetic compaction, the lophophore usually penetrates into the matrix in the three-dimensional specimens, leaving no trace on the overlying disc. In the overturned specimen (Figs 10–11) the three-dimensionally preserved lophophore shows a conspicuously upward extension with the rock matrix laminae separating the structure from the ventral surface of the disc. It consists of two arm-like ridges, interpreted as the tentacle-carrying organs, which are curved and semi-circular in outline. Tentacles are 4 in number, each with numerous finer branches in its distal part. The three-dimensionally preserved main part of lophophore was revealed also in another specimen (Fig. 8) with the tentacle-carrying organ extending inward, its distal margin being covered by the body. The other end, however, exposes two tentacles, each with several finer dichotomous branches. In a number of vertically compressed specimens, lophophore structures are observable as obscure darker traces.

In a few specimens instead of pro-oral position the lophophore is situated within the triangular depression. This departure from its normal place suggests that the lophophore was flexible and could be retracted.

The lophophore of the Burgess Shale species of *Eldonia* was originally interpreted by Walcott (1911) as the 'peltato-digitate' oral tentacles, later proposed to be two in number by Durham (1974).

Annular band. — This is represented by a group of concentric, raised riblets about 2–4mm wide, located at one fifth of the disc radius from its outer margin. It is ventral to the radial canals but dorsal to the lobe-like structures. The riblets of the annular band appear to be rigid and rough, yellowish in coloration. They (Fig. 16, view from lower surface) ventrally cross the dorsal radial canals. In some specimens the band passes dorsally over the ventral radial canals (NIGP 100320; Sun & Hou 1987).

Fig. 16. *Eldonia eumorpha* (Sun & Hou 1987) from the Early Cambrian (Atabanian) of Chengjiang, China (locality M2), paratype (NIGP 100309) in ventral view; explanatory drawing (A) and photograph (B, light from NW, low angle); both $\times 2$. Note (1) dorsal radial canals and annular band consisting of concentrically extended lines which pass ventrally through the dorsal radial canals, (2) central ring and ridged ventral face of the central cavity, (3) ventral depression flattened into a wrinkled structure.



Variability

Altogether 1075 vertically compressed specimens of *Eldonia* were measured, mostly collected from the quarries in Mt. Maotian, few from Ma'an hill, Xiaolangtian, and Dapotou. Some of them apparently derived from populations which had probably undergone catastrophic extermination, among them 477 specimens being collected by the authors from a single mud layer at quarry MQI on the western slope of the peak of Mt. Maotian. They thus correspond to a life assemblage either of a single flocks or numerous populations and can be subjected to a census (Hallam 1972). Size frequency distribution in both homogenous sample from a single (Fig. 17A), as well as in the bulk sample comprising numerous populations (Fig. 17C), exhibits a moderately positive skewing that indicates a stable population. The size-survivorship curve (Fig. 17B, D) shows mortality declining up to the size of 55–60 mm, and then increasing at later stage corresponding to sizes ranging from 60 to 110 mm.

Relationships

The systematic position of *Eldonia* has evoked much controversy since 1911 when it was originally described by Walcott (1911) as a holothurian. Also, A.H. Clark (1912, 1913), A.L. Clark (1912), and Croneis & McCormack (1932) considered it an echinoderm. Madsen (1956, 1957, 1962) and Seilacher (1961) proposed it was a siphonophore. Lemche (1960) and Sun & Hou (1987) interpreted the creature as representing coelenterate medusa and scyphozoans, respectively, while Dzik (1989) suggested it was a sedentary lophophorate. As *Eldonia* does not fit well morphologies known among members of recent phyla, its biological affinities were regarded as problematic by Conway Morris & Robison (1988) and by Chen & Erdtmann (1989).

The interpretation of *Eldonia* as a holothurian introduced by Walcott (1911) remained prevalent for a long time (Durham 1974). Recently Duncan Friend (personal communication) evoked it again pointing to similarities with a group of extant deep-sea pelagic holothurians (see Gee 1992). However, the echinoderm affinity of *Eldonia* has been doubted by other authors (Paul & Smith 1984). No sign of pentamerous symmetry, typical for primitive echinoderms, has been identified in *Eldonia*. The endoskeleton in the Echinodermata is represented by calcareous, mesodermally secreted trabeculae; nothing like that exists in *Eldonia*. The pelagic Holothurioidea, although having a weakly developed calcareous skeleton, are highly derived eleutherozoans and their mouth and anus open at opposite ends of the body. Marginally accreted external skeleton in *Eldonia* and related forms remains unknown in any echinoderm. For these reasons, *Eldonia* can not be attributed to the Echinodermata, but rather to a pre-echinoderm deuterostomes (Conway Morris 1993).

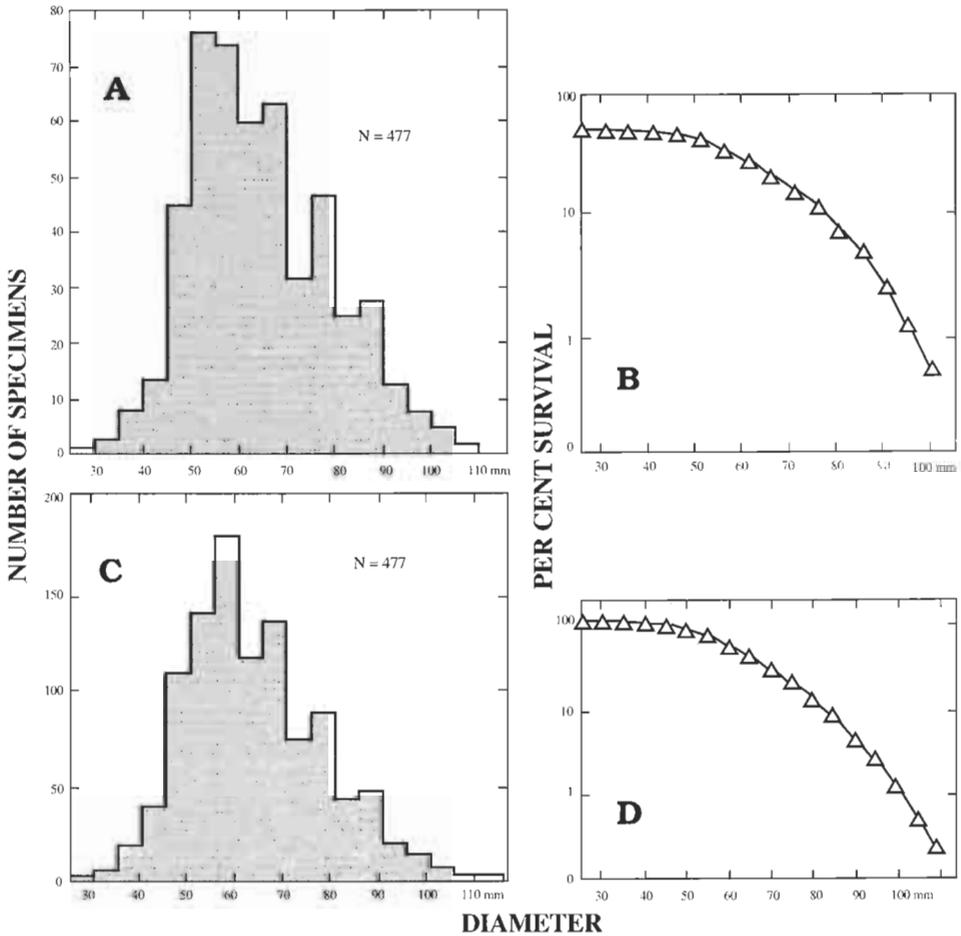


Fig. 17. □A. Size-frequency distribution of a homogenous population of *Eldonia eumorpha* collected from a single thin microturbidite mud layer in MQ1. □B. Size-survivorship curve for the same sample of A. □C. Size-frequency distribution in bulk sample of C taken from different localities and layers. □D. Size-survivorship curve for the same sample.

Recently Dzik (1989) interpreted *Eldonia* as a lophophorate. He based his evidence on the original presence of an external skeleton with growth lines in some Cambrian organisms related to *Eldonia* and the presence of U-shaped gut and tentacular apparatus. This interpretation appeared to be highly speculative but the results of the current study of the Chengjiang medusiform fossils provide new evidence consistent with it.

The extant lophophorates, which include the phoronids, bryozoans, and brachiopods, all are provided with a lophophore, a tentacle-bearing organ surrounding the mouth. All these groups are probably closely related. The lophophorates share adult features such as reduced preoral parts, secretion of protective coverings, and a U-shaped gut with anus placed near the mouth, all of which are probably related to adaptation to

the sessile life. A new reconstruction of *Eldonia eumorpha* proposed in the present study shows notable resemblance to lophophorate animals. This resemblance is expressed by having a lophophore and U-shaped alimentary canal with anus placed near mouth, the lack of any prominent preoral lobe, and the organization of vascular system. However, there are some significant differences. In *Eldonia* the alimentary canal is coiled horizontally instead of vertically. The oral surface faced ventrally instead of dorsally; this is an expected result of the shift from a sedentary to a pelagic life style.

Eldonia eumorpha bore an unique pallial(?) vascular system including a central ring canal and 44 radial ventral canals which are radially-extended to the periphery of the disc. There is a clockwise coiled sac which surrounds the digestive tract and is encircled with ventral vascular sacs on the ventral side and a large internal body cavity on dorsal and lateral sides. With such a unique body plan, *Eldonia* can not fit in with any recognized classes of the lophophorate phylum. Alternatively, it may be interpreted either as one of the forerunners of the deuterostomes (Conway Morris 1993) or a representative of an extinct separate lophophorate branch that developed a medusiform pelagic mode of life.

The forms that may be related to *Eldonia*, include Early to Middle Cambrian *Rotadiscus* (Sun & Hou 1987; Zhao & Zhu 1994; Masiak & Żylińska 1994; Chen *et al.* in preparation). They share the disc shape, oral tentacles which are present on the ventral surface and contiguous with an internal alimentary canal, inside the body there is at least one set of radial canals and lobe-like structures. We regard these features as synapomorphies defining a monophyletic group. To this group of eldonioids may be added the poorly known Newfoundland early Cambrian *Hullingia* (Narbonne *et al.* 1991), Polish middle Cambrian *Velumbrella* (Stasińska 1960; Dzik 1989; Masiak & Żylińska 1994) and New York middle Ordovician *Paropsonema* (Ruedmann 1916). The eldonioids, therefore, appear to have been widespread in the Early Palaeozoic oceans.

Taxonomy

Class Eldonioidea Dzik 1989 (emended herein)

Emended diagnosis. — Medusiform lophophorates with radially-symmetrical disc either soft-bodied or sclerotized. U-shaped alimentary canal coiled subhorizontally. Mouth placed near anus, both facing ventrally. The mouth surrounded by a lophophore. Vascular system consisting of numerous radially-extended sacs, radially-extended vascular canals radiating from central ring canal to periphery.

Genus *Eldonia* Walcott 1911

(= *Stellostomites* Sun & Hou 1987, *Yunnanomedusa* Sun & Hou 1987)

Type species: *Eldonia ludwigi* Walcott 1911.

Emended diagnosis — Weakly sclerotized, low bell-shaped eldonioids, with convex upper and concave lower surface. Subhorizontally clockwise (from above) coiled sack enclosed alimentary canal. Lophophore bearing at least four elongated tentacles. Vascular system consisting of numerous dorsal radial sacs and ventral canals radiating from the central ring canal. Dorsal radial canals curved to enclose the coiled sac dorsally.

Eldonia eumorpha (Sun & Hou 1987)

Stellostomites eumorphus sp. n.; Sun & Hou 1987: pp. 264–266, pl. 4: 1–6; pl. 5: 1a–f, 2a,b.

Yunnanomedusa eleganta sp. n.; Sun & Hou 1987: pp. 266–267, pl. 6: 1–2; text-fig. 7.

Stellostomites eumorphus Sun & Hou, 1987; Chen & Erdtmann 1991: pl. 2: 2.

Holotype: NIGP 100307, pl. 4: 1a in Sun & Hou (1987).

Type horizon and locality: Chengjiang Lagerstätte, Atdabanian.

Emended diagnosis. — Body low bell-shaped, strictly circular in outline, 50–70 mm in diameter at adult growth stage. The anus and mouth located at one-third the length off the centre of disc. Dorsal radial canals 88 in number. Ventral radial canals 44 in number. Lophophore consisting of 4 tentacle-bearing branches. Ventral surface concave, provided with numerous black spots arranged both radially and concentrically. A triangular ventral depression extends from the centre of the body to the oral and anal ends of the alimentary canal.

Material. — Holotype NIGP 100307 is an incomplete specimen without counterpart. It is dorsally flattened, showing ridged dorsal face of the central part of the membrane, radial canals, and muscle band which extended throughout and underneath the radial canals.

Other material figured by Sun & Hou (1989), includes (1) NIGP 100308 (Sun & Hou 1987: pl. 4: 1b), part of which is concealed underneath the holotype, (2) NIGP 100320 (Sun & Hou 1987: pl. 5: 2a), NIGP 100321 (Sun & Hou 1987: pl. 5: 2b), and NIGP 10032 (Sun & Hou 1987: pl. 5: 2c), all imbricated one under another, retaining only a part of muscle-band in ventral view that extends across the radial canals, (3) NIGP 100313 (Sun & Hou 1987: pl. 4: 6), a specimen in ventral view with its margin folded inward giving an irregularly polygonal outline, the muscle band extends ventrally across the radial canals. Seven specimens occur on a single slab (6) NIGP 100314 (Sun & Hou 1987: pl. 5: 1a), NIGP 100315 (Sun & Hou 1987: pl. 5: 1b), NIGP 100316 (Sun & Hou 1987: pl. 5: 1c), NIGP 100317 (Sun & Hou 1987: pl. 5: 1d), NIGP 100318 (Sun & Hou 1987: pl. 5: 1e) and NIGP 100319 (Sun & Hou 1987: pl. 5: 1f). Three specimens (NIGP 100315, NIGP 100317 and one unfigured) show only minor portions of the disc exposed. Three other specimens (NIGP 100314, NIGP 100316, and NIGP 100318) show the ventral surfaces. The specimen NIGP 100312 (Sun & Hou 1987: pl. 4: 5) presents a top view of the radial canals extending across the dorsal surface of the coiled sac. Specimens NIGP 100309 (Sun & Hou 1987: pl. 4: 2) and NIGP 100310 (Sun & Hou 1987: pl. 4: 3), present ventral views of the muscle band (adjacent to the outer margin of the alimentary canal) and the mode of coiling of the alimentary canal. Spe-

cimen NIGP 100311 (Sun & Hou 1987: pl. 4: 4) is stained with blue ink which shows a well defined, broad muscle band (2.5 mm wide).

The holotype of *Yunnanomedusa eleganta* (Sun & Hou 1987: pl. 6: 1, 2) is represented by part and counterpart. The split extends parallelly and largely along the upper surface of well-defined, radial lobe-like structures.

The specimen NIGP 108503 figured by Chen & Erdtmann (1989: pl. 2: 2), shows a ventral view of the body, with indication of ventral depression structure, ventral view of the lobe-like structures which radiate from the central part of the body underneath the alimentary canal. In part of the specimen three finer canals are visible in between the regular radial canals. Most of the body was buried parallel to the bedding plane but some part of the lateral margin is folded in form of a sharp triangular extension.

Remarks. — *Eldonia ludwigi* differs from *E. eumorpha* in number of internal lobe-like structures, and radial canals, as well as in shape of lophophore tentacles (Duncan Friend, personal communication).

Examination of the type specimens of *Eldonia eumorpha* has revealed that the allegedly circular mouth structure actually represents a dorsal view of the central cavity within the body. This internal structure was erroneously regarded as an attachment organ by Dzik (1989). In their reconstruction, Sun & Hou (1987) proposed the presence of a circular gastrovascular structure which is another erroneous interpretation for the outer margin of the alimentary canal.

Yunnanomedusa eleganta was erected by Sun & Hou (1987), as a soft-bodied medusiform animal which differs from *E. eumorpha* in having radial canals which bifurcated and radiated from the 'mouth' instead of the outer margin of the 'gastrovascular cavity'. These features are actually results of different rock split. The split of the rock occasionally provides a false impression of canals radiating outward either from the outer margin of the sac, which results in 'Stellostomites' morphology, or from the central cavity, which results in 'Yunnanomedusa' morphology. *Y. eleganta* is apparently a synonym of *E. eumorpha*, with the name chosen for the revised species according to page order.

The new reconstruction of the animal, however, displays a striking resemblance to the Middle Cambrian Burgess Shale species *Eldonia ludwigi* in: (1) the disc-shaped soft body, (2) the clockwise coiled sac, (3) the ventral radial canals radiating outward from the central ring canal, (4) the presence of lophophore, and (5) the anus being placed near the mouth and both the anus and the mouth facing ventrally off one side from the centre of the disc (Walcott 1911; Durham 1974). Therefore, they are considered generically identical, with the name *Eldonia* having priority.

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Streszczenie

W sławnym stanowisku Chengjiang w południowych Chinach, gdzie wczesnokambryjskie zwierzęta zachowane są wraz z wewnętrznymi organami, najpospolitszymi skamieniałościami są kapeluszowate formy opisane niegdyś pod nazwami *Stellostomites eumorphus* Sun & Hou 1987 i *Yunnanomedusa eleganta* Sun & Hou 1987. Zgromadzony przez autorów materiał ośmiuset okazów dowodzi, że w istocie jest to jeden gatunek, pokrewny *Eldonia ludwigi* Walcott 1911 ze środkowego kambru Kolumbii Brytyjskiej, określony więc nazwą *Eldonia eumorpha* (Sun & Hou 1987). Ukształtne jelito, dwudzielny aparat czułkowy przy otworze gębowym i złożony system kanałów płaszczowych potwierdzają przynależność *Eldonia* do typu czułkowców Lophophorata, w którym wraz z *Rotadiscus* i świętokrzyską *Velumbrella* tworzy gromadę Eldonioidea.