Yunnanozoon and the ancestry of chordates

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Dzik, J. 1995. *Yunnanozoon* and the ancestry of chordates. *Acta Palaeontologica Polonica* **40**, 4, 341–360.

The oldest known chordate, *Yunnanozoon lividum* Hou *et al.* 1991, from the Chengjiang Lagerstätte of Yunnan shows several features in its anatomy that had not been expected to occur at this stage of evolution. Its metameric dorsal myomeres were separated by straight myosepta. The notochord was located ventrad of the muscular blocks instead of being bordered by them. The pharynx did not contain any filtratory basket but had only seven pairs of branchial arches. These were composed of rows of minute scleritic segments that connected the notochord with a rigid ventral trough. The head region was rather complex in organization and bore a specialized ring-like mouth apparatus. The presence of sensory organs, perhaps large eyes with sclerotic rings, is probable. Only in the remarkable elongation of the notochord and metameric arrangement of oval gonads this early chordate is similar to *Branchiostoma*. The anterior part of the muscular blocks of *Yunnanozoon* resembles a little the proboscis and collar of the enteropneusts and may perhaps be homologous with these structures, although in *Yunnanozoon* they are displaced much behind the mouth. The whole metameric muscular unit is proposed to correspond to the 'quilted pneu structure' of the Ediacaran problematic fossil *Dickinsonia*. Monotypic Yunnanozoa classis n., Yunnanozoida ordo n., and Yunnanozoidae fam n. are proposed for this early chordate.

Key words: Cambrian, Precambrian, chordates, conodonts, cephalochordates, *Dickinsonia*, origins, phylogeny.

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Introduction

The chordate origin remains an unresolved problem despite all the improvements in research techniques of zoology and prolific paleontological evidence. Instead, the discrepancy between paleontological and zoological views on this subject even seems to increase with each new finding. The recent identification of a chordate in the early Cambrian Chengjiang Lagerstätte of Yunnan may appear to be the turning point in the discussion. This fossil provides a completely new set of data on the soft anatomy of the earliest chordates and makes some basic rebuilding of the phylogenetic tree of early chordates and vertebrates necessary.

Yunnanozoon lividum Hou *et al.* 1991 had originally been described as a problematicum (Hou *et al.* 1991). Its affinities remained unclear until the autumn of 1993 when, while studying in Nanjing two specimens of this species newly collected at the type locality by Chen Junyuan, I identified in them branchial arches, notochord, and metameric gonads. These basic chordate features enabled reinterpretation of the earlier recognized internal structures, that is metameric muscular blocks and scleritic rings in the head region, in terms of chordate anatomy. Results of that research, supplemented by observations by Lars Ramsköld and Gregory D. Edgecombe on later collected more numerous specimens, have been published recently (Chen *et al.* 1995). The purpose of the present study is to discuss in more detail the available evidence on the anatomy of *Yunnanozoon* and to attempt an evolutionary interpretation of the data.

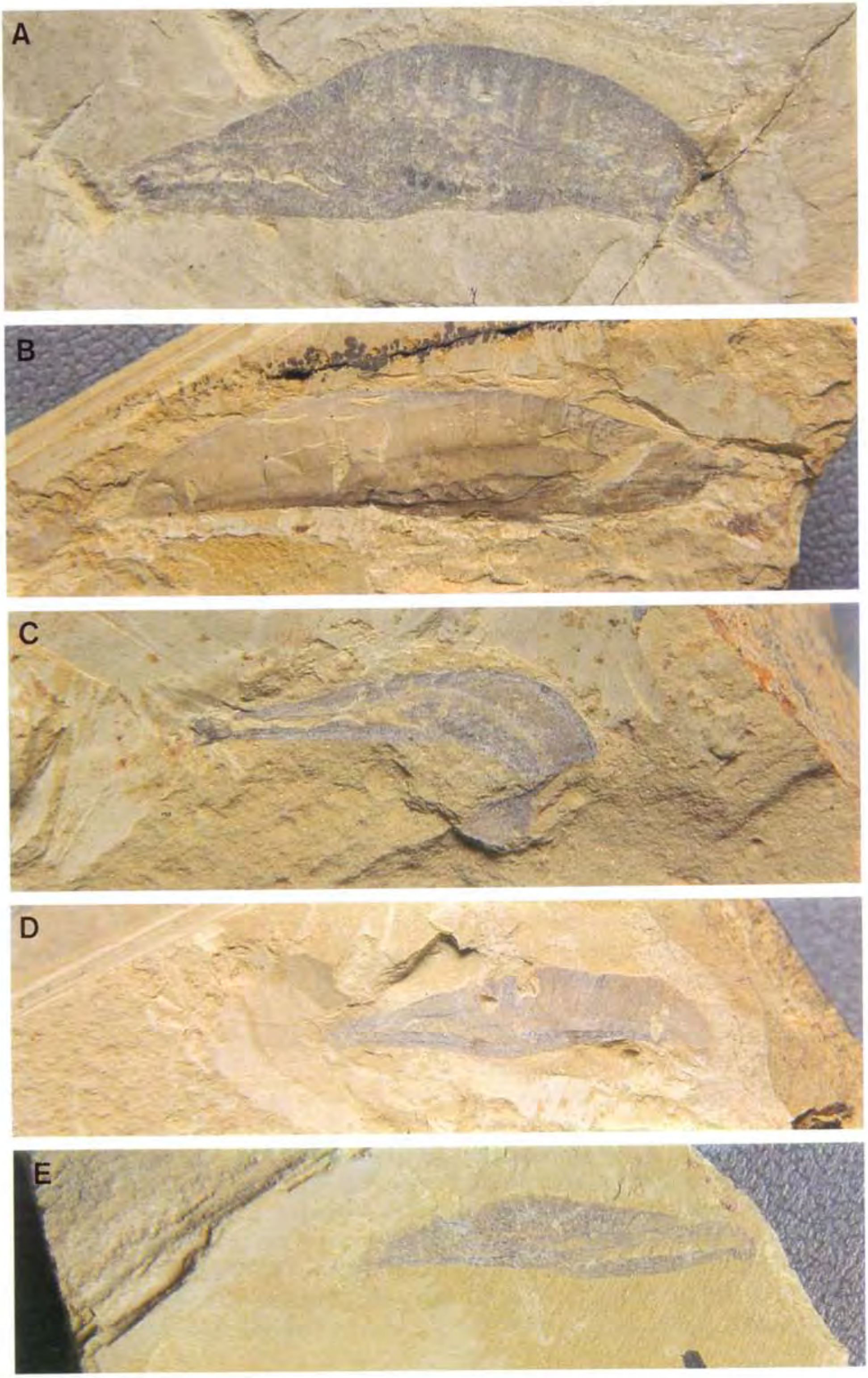
Material

Yunnanozoon is one of the rarest Chengjiang fossils. Still, about sixty specimens have been identified among more than 10,000 fossils of soft-bodied or lightly scleritized organisms collected at the Chengjiang site (Shu *et al.* 1995). They all come from the lower part of the *Eoredlichia* Zone within the Yu'anshan Member, the upper unit of the Qiongzhusi (Chiungchussu) Formation (Chen & Erdtmann 1989). The three specimens on which the original description of the species was based were collected by Hou Xianhuang from the level M2 on the west slope of the mountain Maotian (locality MQ 1). The two of them which were illustrated show well-preserved posterior parts of the body but their anterior parts are missing (in the paratype the ventral structure is laterally folded and recurved) or strongly deformed (Hou *et al.* 1991).

The main conclusions of the present paper have been reached on the basis of two further specimens ELRC 52001 and 52002 collected by Chen Junyuan from another exposure of approximately the same lithologic unit on the NW slope of the same mountain (locality MN) and available to study in 1993. In these specimens the preservation of dorsal musculature is not so good, but details of the anterior part of the body are well recognizable. The larger one is 37 mm long (Figs 2A, 3A), being thus slightly larger than the holotype, the second is 24 mm (Figs 2B, 3B) long.

More than twenty additional specimens have been collected from the same locality in the last few years (reviewed in Chen *at al.* 1995). They all

Fig. 1. *Yunnanozon lividum* Hou *et al.* 1991; Early Cambrian Chengjiang fauna, locality MN, Yunnan, China; specimens ELRC 52001 (A), ELRC 52003 (B), ELRC 52013 (C), ELRC 52004 (D), and ELRC 52002 (E); all × 4.


A
B
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E

show more or less the same preservation of anatomical structures. In two of them, ELRC 52013 and 52015, discussed below (Fig. 4A, B), a dark dorsal band within the muscular blocks, unknown earlier has been identified. Some additional data on the head structure have been provided by another specimen ELRC 52004 examined by myself in 1995 (Fig. 4C, see also Chen *et al.* 1995).

Interpretation of the fossils

Only the axial part of the *Yunnanozoon* body (interpreted below as the pharynx and intestinum) was penetrable by the sediment. This allowed, with a high degree of confidence, the restoration of spatial relationships among structures interpreted as the branchial arches, gonads, ventral trough and notochord.

The rest of the body was not accessible to the mud and completely collapsed under the weight of the sediment which effected its subsequent compaction. However, the collapse was not uniform; particular regions of the body behaved in different ways during post-mortem compression. This enables some inference on their original nature. Usually, the specimens are almost completely flattened but some are convex in their central part. Presumably, these are basal bedding planes that reproduce the pattern of deformation of the underlying sediment surface by parts of the body having different susceptibility to compaction. The areas of what is interpreted as the notochord, the dorsal part of the ventral trough, and the head region appear thus to be most rigid.

Another way of reasoning on the original anatomy of *Yunnanozoon* refers to differences in coloration of particular organs of the body. Whatever was the taphonomic history of these fossils (possibly early diagenetic phosphatization is the reason for their impressive preservation but Butterfield 1995 advocates a purely organic preservation of the Chengjiang fossils), it can be assumed that darker regions were richer in organic matter while paler regions represent probably organs with a vacuolarized, water-rich tissue.

Myomeres. — The dorsal metameric unit is composed of blocks, 23 in number (Hou *et al.* 1991), that are preserved as a thin film, unusually dark stained in respect to co-occurring fossil soft-bodied and sclerotized animals. This indicates a high original content of organic matter, suggestive of the originally muscular nature of the blocks (Hou *et al.* 1991). All the studied specimens of *Yunnanozoon* are preserved lying on one side — the body was evidently laterally compressed. In specimen ELRC 52004 the lines representing presumably contacts (sutures) of myosepta with the external body wall are arched in their dorsal parts in the middle of the body length (Fig. 4C). This can be interpreted as an effect of oblique compression with the corresponding part of the body dipping into the sediment under some angle. A shortening of a few myomeres behind that zone (Fig. 4C)

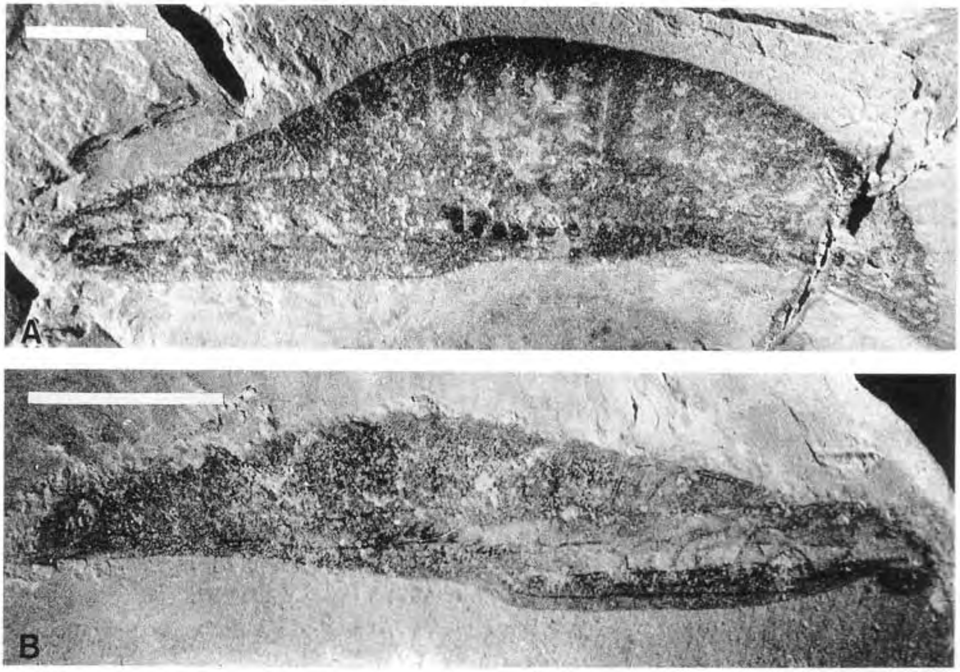

Fig. 2. *Yunnanozon lividum* Hou *et al.* 1991; Early Cambrian Chengjiang fauna, locality MN, Yunnan, China. ❑A. Probably adult specimen ELRC 52001, level 6; note dark bodies in the middle. ❑B. Juvenile specimen ELRC 52002, level 5; note notochord and ventral trough, well delimited with dark lines, segmented branchial arches, and laterally compressed mouth apparatus of sclerites arranged in a ring (here laterally compressed). Scale bar equals 5 mm.

indicates that the specimen was bent there within the sediment before compaction.

It remains unclear whether the muscular blocks were paired, each pair being separated by a medial membrane, or not. Presumably only the external surface morphology of the muscular blocks, with myoseptal sutures delimiting them, is represented by the dark stain. Oblique dark lines in the smallest of the studied specimens – ELRC 52002, in the posterior part of ELRC 52004, and on the dark dorsal zone in ELRC 52015 (Figs 3B, 4B, C) – seem to represent wrinkles on the surface of collapsed muscular blocks. Their distribution may reflect the arrangement of collagen fibres in the body covers. The most prominent of these lines may correspond to myosepta, which are displaced from their normal transverse position on one side of the body.

In two specimens (ELRC 52015 and 52013; Fig. 4A, B) along the dorsal part of the body there is a darker zone in which myosepta are not visible. This can be the medial wall exposed by the split of the rock that passed exactly medially, separating the lateral myomere sets. This would require that the wall is by chance preserved only dorsally. More likely, this is a wall produced by dorsal invagination of the body covers that reached about one third of the depth of the muscular block. Being of double thickness it produced a darker stain. In specimen ELRC 52015 (Fig. 3B) oblique irregular dark lines probably represent wrinkles of the external body covers collapsing over the medial dark zone. This does not exlude medial separation of the lateral myomere sets below this zone by a less organic-rich tissue that was not stained being deeply inside the body. In several other specimens the apparently external myomere sutures reach the dorsal margin of the body without any marginal zone and with no space left between the dorsal ends of myosepta and the clearly delimited body margin. This again suggests that the marginal zone was located between the lateral myomere sets, not above.

Notochord. — Immediately below the presumed myomeres there is a paler smooth structure, which is of a rather uniform width in the main middle part of the body but smoothly tapering in the posterior half. At its anterior end it is slightly curved ventrally and ends parabolically. The structure is apparently a remnant of a cylindrical organ that collapsed during sediment compaction (without allowing sediment to enter inside). As it does not contain sediment or organic-rich fecal content it probably had no connection with the gut. Its preservation is closely similar to that of the stalk of the associated probable lophophorate *Dinomischus*, also interpreted as a fluid-filled hydraulic organ (Chen *et al.* 1989). Other tubular structures in similarly preserved fossils (for instance the gut of associated *Eldonia*, filled with a dark organic-rich content, or the rachis in Burgess Shale 'sea pen' *Thaumaptilon*, which is also darker than the rest of the frond; Conway Morris 1993) do not show any resemblance to the axial tube of *Yunnanozoon*. It was probably a hydrostatic axial skeleton — the notochord. The *Yunnanozoon* notochord extended to the anterior end of the body (Chen *et al.* 1995), as in *Branchiostoma*. The transverse striation reported to occur in the type specimen (Hou *et al.* 1991) may possibly correspond to transverse collagenous fibers of the sheath (see Briggs & Kear 1994).

Pharynx and branchial arches. — In at least the anterior part of the body, there is a narrow zone below the proposed notochord with no apparent lateral walls except for thin transverse segmented arches, seven in number, and external to them oval dark-stained bodies (interpreted as gonads). Both these kinds of structures are paired and in both specimens the left and right sets are separated by a relatively thick sediment layer.

The curvature of the arches, opposing in sets, suggests that before compaction they were convex laterally and somewhat inclined anteriorly in dorsal parts (Fig. 5). The dorsal end of each arch seems to touch the lateral surface of the notochord. Ventrally they can be traced only to the boundary of the ventral trough. Arches are composed of very dark minute segments, about 20 in number (see Chen *et al.* 1995).

The sediment-filled zone, interpreted as the digestive tract, continues posteriorly behind the ventral trough (see below), but the anal opening has not been traced. In the specimen ELRC 52004, behind the pharynx and

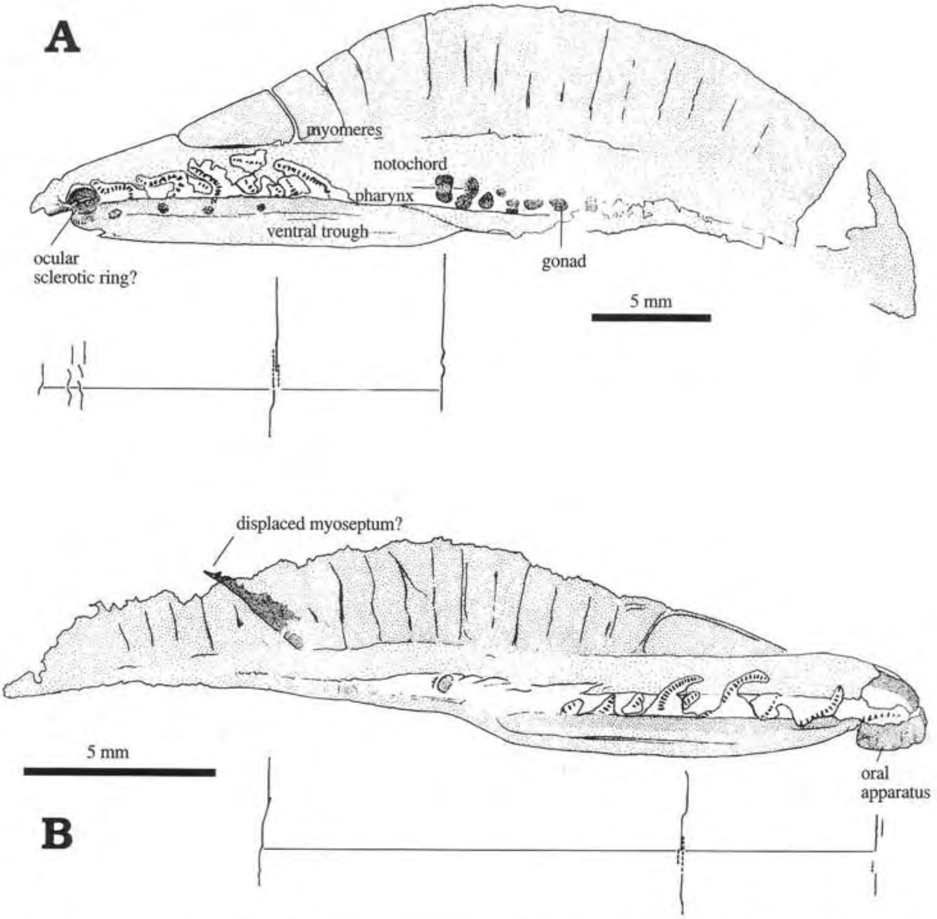

Fig. 3. Camera lucida drawings of the specimens of *Yunnanozon lividum* Hou *et al.* 1991 from the Early Cambrian Chengjiang fauna with diagrammatic cross sections below showing relative positions of particular structures within the rock matrix (horizontal line shows position of the lower margin of notochord), both strictly laterally compressed (see also Fig. 2). A. Specimen ELRC 52001. B. Specimen ELRC 52002.

below the notochord, there is a narrow darker zone subdivided into segments by oblique bands (Fig. 4C). This may be a helically constricted fecal content of the gut. The end of the pharyngeal cavity may be only indirectly inferred from the position of an angular bend, recognizable in all specimens approximately at the 14th myomere. The anus was located further behind, possibly in a position similar to that in *Branchiostoma*.

Gonads. — The paired oval bodies, regularly distributed along the body and perhaps of similar number to that of the myomeres, follow the lower margin of the presumed notochord and extend backwards to approximately the 14th myomere (Fig. 5; Hou *et al.* 1991). They are poorly visible in the anterior part of the pharynx where gill arches occur. Only in specimen ELRC 52001 was a dark body also traced between the arches, deeply imbedded in the sediment and apparently external to the arches. Perhaps the bodies continued up to the anterior end of the pharynx. If spacing of the bodies is extrapolated from the posterior part of the body to the anterior one, two pairs of them correspond to each pair of branchial arches. There is no evidence of any original mineralization of the bodies. In their oval shape, an evidently high content of organic matter, and metameric distribution restricted to the proposed pharynx they resemble the gonads of *Branchiostoma* (see Briggs & Kear 1994).

Ventral trough. – In the anterior part of the darker band located ventrally of the pharynx, two zones are clearly marked by a difference in color. The dorsal one is darker, with parallel and straight boundaries. Each branchial arch ends there in a darker depression and arches were probably fixed there (Fig. 3A). The lower zone is ventrally convex in outline, at least at the ends, and less darkly stained. The preservation of this part of the body in *Yunnanozoon* closely resembles that of the ventral part of the Carboniferous 'conodontochordate' *Typhloesus* (Conway Morris 1990). The specimen ELRC 52013 is slightly torted along the axis and shows the venter in oblique compression (Fig. 4A). Even stronger tortion of the anterior part of the body in the holotype (Hou *et al.* 1991: fig. 9A) provides a similar view of the area. In both cases longitudinal lines demarcate folds of the ventral band.

In the paratype specimen (Hou *et al.* 1991: fig. 9B) the ventral band is posteriorly recurved. This indicates that it was more resistant to decay than the body integuments located superficially and dorsally to it. The ventral band had similar properties in this respect to the head region and the muscular blocks. In decaying specimens the muscular blocks and ventral band happen to be preserved almost completely apart except for the short, probably post-anal, zone close to the end of the body (this led Shu *et al.* 1995 to consider all other specimens to be folded in mid-length of the body, the original shape of the body being vermiform).

Similarly as in the *Typhloesus*, the dark ventral band of *Yunnanozoon* apparently had a trough-like shape with angular ventro-lateral margins, possibly equipped with ribs that may correspond to the paler ventral zone of the band. A few less prominent ribs run parallel to and along the venter as suggested by the ventral appearance of the trough provided by the torted specimen ELRC 52003 (Fig. 4A). Perhaps the endostyle was located inside the trough (Chen *et al.* 1995) but there is no direct evidence for this and no reason to assume a filtratory mode of feeding.

Head organs. – In the large-sized specimen ELRC 52001, close to the anterior end of the body, there is a dark-stained structure, which is strongly concave, larger than the proposed gonads, and separated from the branchial arch underneath by a thick layer of sediment (Fig. 3A). The structure is thus located at the same level as the gonads behind. Although incomplete and deformed in shape, it seems to have had a ring-like original appearance. It resembles thus in position and appearance the scleritic ocular rings of the conodonts (Aldridge & Theron 1993). The specimen

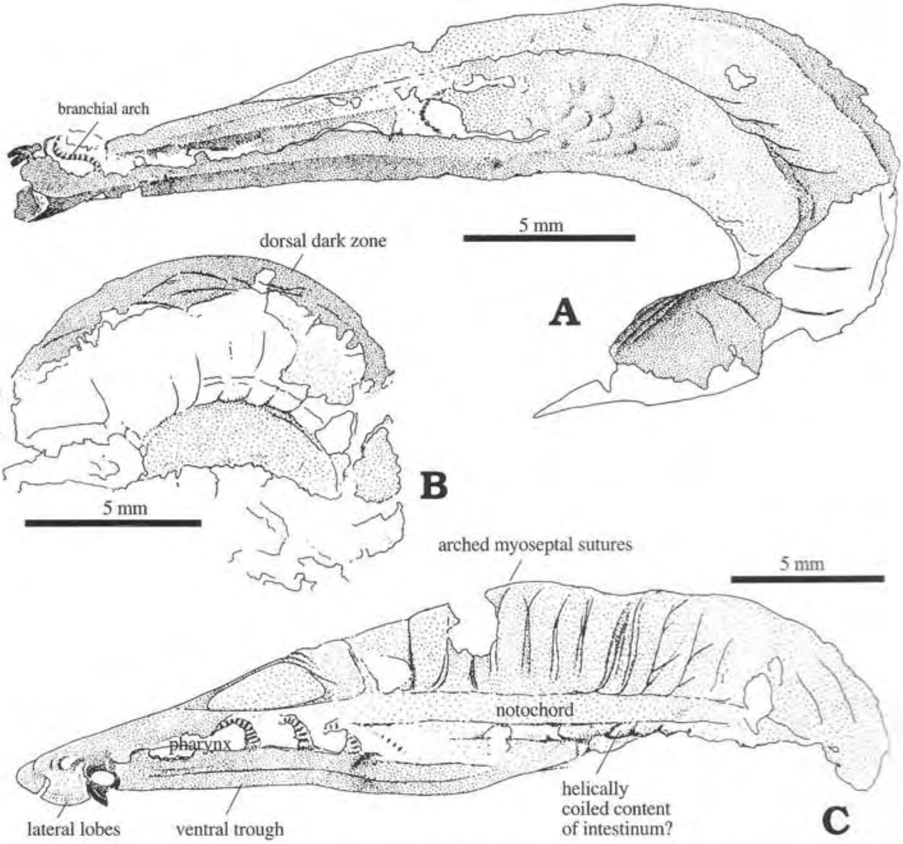

Fig. 4. Camera lucida drawings of the specimens of *Yunnanozoon lividum* Hou *et al.* 1991 from the Early Cambrian Chengjiang fauna. □A. Somewhat obliquely compressed specimen ELRC 52013 in basal view, with the tail folded above the trunk; the unshadowed part of the tail taken from the counterpart; gonads visible only as deeper imbedded impressions (in this case elevated as this is probably the basal view), only the posterior margin of the head preserved. The narrow appearance of the anterior end of the body results from its rotation, the first myomeres are covered by the ventral trough. □B. Partially preserved specimen ELRC 52015 showing the dark dorsal band with wrinkles. □C. Laterally compressed (but with some undulations) specimen ELRC 52004; note arched sutures of myosepta in the central part and relatively complete head region.

ELRC 52004 provides good evidence that the head was bearing two large ventro-lateral lobes with semicircular lateral margins and probably with holes in the center of each of them (Fig. 4C), in the position corresponding to that of the ring-like structure of the specimen ELRC 52001. The exact nature of the dorsolateral area of the head remains poorly known, however.

In the small specimen ELRC 52002, the head region is not well preserved externally, but another dark-stained structure of much larger size is exposed (Fig. 3B). It is subdivided into several sclerotic units, apparently forming together a ring. Their number cannot be precisely established, but probably it was more than twelve. This seems to represent a lateral compression of a circular structure of the same kind as that represented in the holotype (Hou *et al.* 1991) in ventral view, having there an apparent ring-like organization. Unlike the much smaller ring-like structure discussed above in connection with the specimen ELRC 52001, this one is oriented ventrally rather than laterally. Also in the specimen ELRC 52004 some remnants of a very dark ventrally oriented structure occurs in the medial area of the head and slightly behind the lateral lobes. It is bordered both by the lobes and lateral walls of the trough. All these could be remnants of a circular mouth apparatus, antero-ventrally oriented and possibly protrusible. Some longitudinal striation recognizable in the darkest regions of the mouth area in specimens ELRC 52004 and 52013 (Fig. 4A, C) may suggest paired spines or denticles.

Anatomy of *Yunnanozoon*

As the body of *Yunnanozoon* was laterally compressed, apparently the tail was waved laterally while propelling the animal, as in most Recent primitive chordates. Such movement requires separate muscular units on both sides of the body and this was probably the case at least in the main part of the muscular unit — that with the relatively short myomeres. The first triangular segment of the unit is of strangely antero-posteriorly elongated shape. There is some gradient in shape and elongation of the first few myomeres. This may be connected developmentally with the apparent elongation of the anterior part of the body.

The exact homology, and by inference the function, of the branchial arches in *Yunnanozoon* is difficult to trace. The branchial arches of the agnathans, fish, and cephalochordates are probably not homologous with each other (Mallatt 1984), even if their gills may be (although there are some arguments in favor of the opposite; see Schaeffer & Thomson 1980). The apparent external position of the arches in *Yunnanozoon* is suggestive of their gill rays being oriented towards the pharynx. This requires that the branchial apparatus of *Yunnanozoon* was not similar in its organization to the branchial basket of the cephalochordates (Drach 1966) or tunicates, but rather to that of the agnathans. Nor is it similar to the branchial skeleton of the eneteropneusts. One may guess that the branchial openings were located in between the arches, being perhaps slit-like (Fig. 6). Each segment of the arches may have supported its own gill blade.

The gonads of *Yunnanozoon* were located immediately below the skin and outside the gills. This closely resembles the organization of the branchiogenital region in the enteropneusts (Dawydoff 1966). Probably the gonads opened outside, like in enteropneusts.

The pharynx was a spacious cavity in *Yunnanozoon*, perhaps expanding laterally into gill pouches between arches (Fig. 6) and it definitely continued at least to the last gill slit. Behind the gill arches and up to the level of 14th myomere, the ventral trough enclosed a space of relatively large

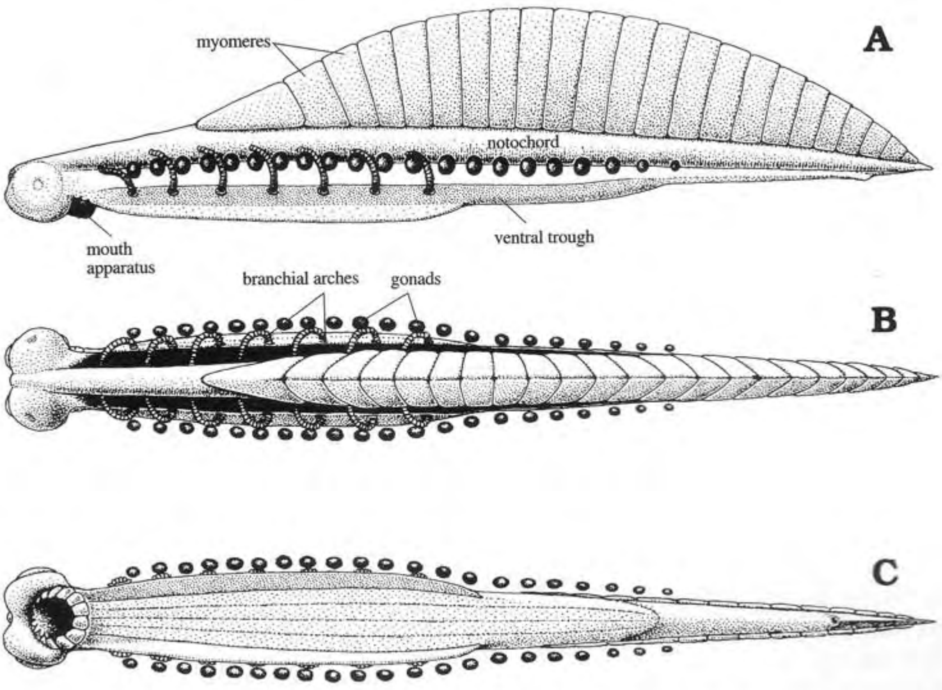

Fig. 5. Diagrammatic reconstruction of spatial relationships between the body organs of *Yunnanozon lividum* Hou *et al.* 1991 preserved in fossils from the Early Cambrian Chengjiang fauna in lateral (A), dorsal (B), and ventral (C) views.

diameter that probably contained some kind of stomach, intestine, and liver. In the following narrower part of the digestive tract the fecal content was probably packed in helically coiled bodies.

The ventral trough and the notochord were the main skeletal structures in *Yunnanozoon*. Their walls were rather rigid but flexible, as documented by the observed pattern of deformation, especially in decaying specimens. One may guess that they were collagenous in composition.

The interpretation of structures preserved in studied specimens of *Yunnanozoon* (Fig. 5) is tentative and may prove incorrect in detail when better material is found. Nevertheless, several aspects of its anatomy are rather well documented and others highly probable. No doubt the head region of *Yunnanozoon* was of complex organization, probably with mouth apparatus and sophisticated sense organs. Ocular sclerotic rings are known in the Ordovician and Carboniferous conodonts (Aldridge *et al.* 1993; Aldridge & Theron 1993; Gabbott *et al.* 1995) as well as the early Silurian anaspid *Jamoytius*, where the mouth was also armed with a sclerotic ring (Ritchie 1968). It would not be surprising if those organs correspond to the dark structures in the head of *Yunnanozoon*.

The unexpectedly high organization of the head in *Yunnanozoon*, with possible presence of eyes and a mouth apparatus requires that the neural system was accordingly advanced. No clear remnants of any structure that could be interpreted in this way are preserved in Chengjiang specimens. It is reasonable to expect that such a tube ran in between the myomeres more or less in the middle of their height. This would correspond approximately to the lower boundary of the dorsal dark zone (Fig. 4B, 6).

Relationships to Recent chordates

The body plan of *Yunnanozoon*, although typically chordate, is not the same as that of Recent *Branchiostoma* (see Drach 1966). In having strictly transverse myosepta, robust myomeres, as well as a small number and probably direct openings of particular gill slits, it seems more primitive than any known Recent or fossil chordate (see Blieck 1992). The possible presence of eyes with sclerotic rings, which makes it similar to the conodonts, may appear to be an ancient chordate trait and not a vertebrate acquisition, as generally assumed (i.a. Holland *et al.* 1994). The large size of the notochord and strictly dorsal position of the muscular blocks is difficult to reconcile with presently accepted views of the early phylogeny of the chordates. Paradoxically, the extreme anterior extension of the notochord, listed as a derived feature by Lövtrup (1977) may appear a reversal to the ancestral state in *Branchiostoma*. Only the low number of gill-slits is confirmed to be a really old trait.

It seems thus that *Yunnanozoon* belongs to a completely extinct group of the earliest chordates and that their main traits (dorsal position of myomeres, complex head structure, and peculiar branchial skeleton) are not recapitulated in the ontogeny of Recent chordates, being supressed by later anatomical acquisitions. The embryological evidence does not seem to be matched by paleontological data deeper than the Middle Cambrian *Pikaia*, except for the earliest embryonic stages, when the myocoel developes as metamerically arranged vesicles dorsal to the long notochord. They merge enclosing the neural tube in a way similar to that in the collar region of enteropneusts.

Relationships to other fossil chordates

The conodonts represent the only larger group of fossil organisms with well-established chordate affinities (Dzik 1986) that ranges back to the Cambrian. Their evolution is known mostly due to the presence of well mineralized oral denticles that form complex apparatuses (see review in Sweet 1988 and Dzik 1991). The soft anatomy of the conodonts is well documented only in the early Carboniferous *Clydagnathus* (Aldridge *et al.* 1986, 1993) but there is evidence that some late Ordovician conodonts had well developed ocular scleritic rings, suggestive of a similar anatomy (Aldridge & Theron 1993; Gabbott *et al.* 1995). The most important

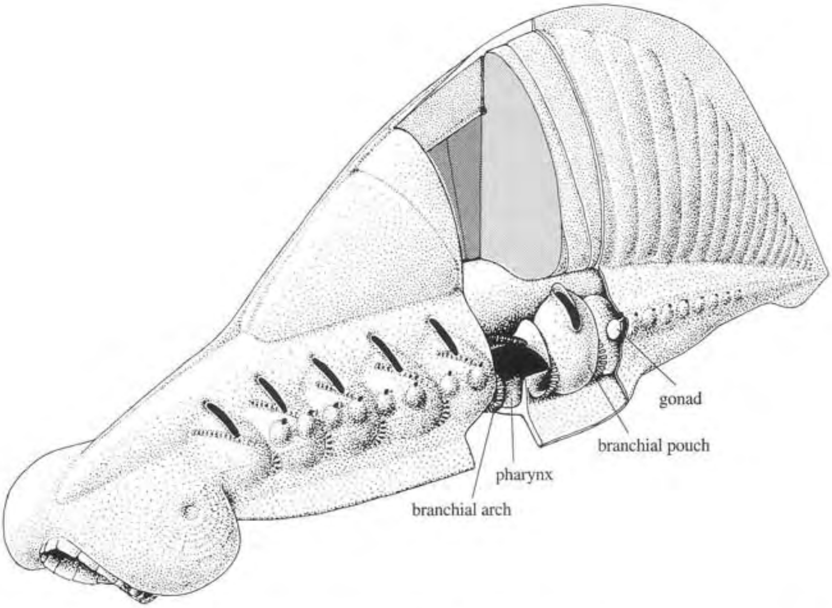

Fig. 6. Diagrammatic presentation of reconstructed anatomy of *Yunnanozoon lividum* Hou *et al.* 1991 from the early Cambrian Chengjiang fauna of Yunnan. Part of the left side of the body has been 'sectioned'.

chordate feature of *Clydagnathus* is the V-shaped arrangement of numerous myomeres (Briggs *et al.* 1983). This is the feature which relates conodonts anatomically to *Branchiostoma* and other primitive chordates but makes them basically different from *Yunnanozoon*.

Some of the Middle Cambrian Burgess Shale fossils have also been proposed to represent early chordates. Among them *Pikaia* is considered the most convincing (Conway Morris & Whittington 1979) although its full description has not yet been published. *Pikaia*, as well as *Metaspriggina* from the same locality (Simonetta & Insom 1993), shows the V-shaped arrangement of myomeres (Conway Morris & Whittington 1979; Whittington 1985), which is so typical for Recent primitive chordates and fossil conodonts. The notochord has been proposed to be located dorsally, like in Recent *Amphioxus*, which is another difference with respect to *Yunnanozoon*. The Chengjiang chordate is thus, in the notochord-myomere spatial relationship, rather apart not only from Recent but even from Cambrian chordates, presumably being much more primitive in its anatomical organization.

Relationships to hemichordates

The only non-chordate Recent animals that have metameric branchial slits are the enteropneusts. However, the branchial skeletal rods of the enteropneusts do not resemble the branchial arches of *Yunnanozoon* and the architecture of their branchial apparatus seems to be derived (see Dawydoff 1966).

The only parts of the enteropneust body that may be comparable to the muscular blocks (or perhaps rather bladders) of *Yunnanozoon* is the proboscis and collar. In fact, there is some resemblance in shape between the first, antero-posteriorly elongated and possibly unpaired, muscular block in *Yunnanozoon* and the proboscis and between the following block and the collar. The proboscis coelom in the enteropneusts constitutes an unpaired cavity but the collar coelom developes by invagination from two lateral pouches and, at least in the simply organized *Protoglossus*, it is separated in two parts by both dorsal and ventral mesenteria. Both the proboscis and collar coelom open outside by pores (Hyman 1959).

The collar is the only part of the enteropneusts where the nervous system is internal. In some species the collar neural cord has a continuous lumen that opens to the exterior at each end by neuropores. The collar cord developes in early ontogeny either by invagination (*Glandiceps*) or delamination (*Saccoglossus*) (see Hyman 1959; Dawydoff 1966). This does not contradict the suggested homology of the collar with the muscular blocks of *Yunnanozoon*. Even if the interpretation of the dorsal dark zone as an invagination separating medially the muscular blocks in *Yunnanozoon* is weak, their homology with myomeres of later chordates (as well as functional reasons) implies that the nerve cord was located in between them.

The only anatomically preserved fossil enteropneust is *Megadereion* from the early Jurassic of Italy. It already shows the basic anatomical features of the class, connected with adaptations to burrowing in the muddy substrate (Arduini *et al.* 1991). There is no evidence that enteropneusts were hydraulic burrowers already in the Cambrian; so the possibility remains that their proboscis and collar developed from structures more similar to *Yunnanozoon* myomeres, present in the common ancestor of these organisms. However, in lack of any good fossil evidence, the opposite — that the myomeres of *Yunnanozoon* are modified structures that originated as an adaptation to burrowing of their enteropneust-like ancestors, remains plausible as well.

Possible ancestry of *Yunnanozoon*

There is another Cambrian organism that shows a metameric dorsoventrally compressed body with metameric structures resembling those in *Yunnanozoon*. The middle Cambrian *Odontogriphus* from the Burgess Shale of British Columbia, known from a single, poorly preserved specimen (Conway Morris 1976a) had a bilaterally symmetrical elongated body with distinct segmentation at least in its adaxial part. The specimen is dorsoventrally compressed, probably corresponding to the original

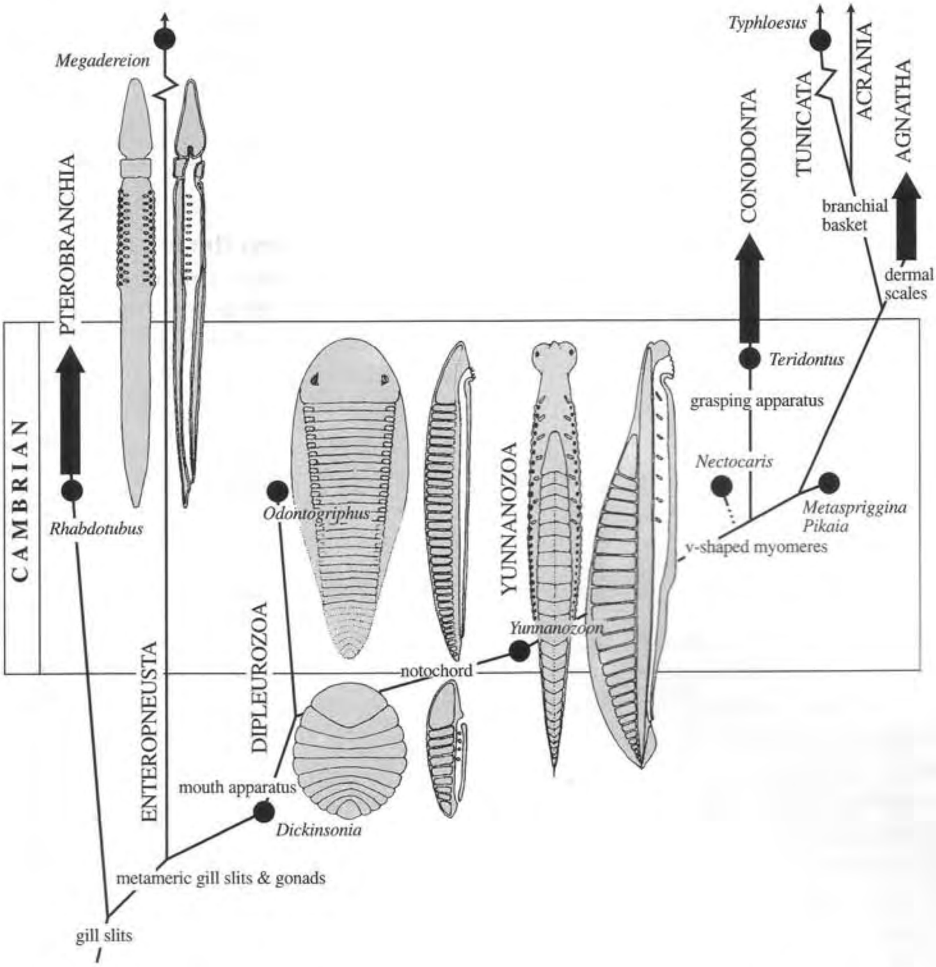

Fig. 7. Proposed evolutionary relationships of *Yunnanozoon* with other most primitive chordates and hemichordates. Restored anatomy of *Dickinsonia* refers to juvenile specimens as interpreted by Runnegar (1980, data also from Glaessner & Wade 1966 and Jenkins 1985).

compression of the body. The body segments are very short, with clear, strictly transverse boundaries; in this respect they resemble the myomeres of *Yunnanozoon*. Oval dark structures, resembling the gonads in the Chengjiang species, border the segmented axial zone of the body of *Odontogriphus*. Lateral to the dark body belts there are unsegmented fields that may correspond to lateral fins or the ventral trough of *Yunnanozoon*. The intestine runs along the midline under the segments and ends in a bilobate mouth apparatus, apparently ventral in position. The mouth apparatus was armed with denticles resembling westergaardodinid conodont elements ('paraconodonts'). The head region was not segmented and was equipped with a pair of sensory organs ('palps') that remotely resemble, in their preservation, the eyes of the Carboniferous conodont.

Chordate affinities of *Odontogriphus*, proposed long ago (Dzik 1976, 1993) may find support in the anatomy of *Yunnanozoon*. The dorsoventrally compressed oval body of this Middle Cambrian organism may be a trait connecting it with some fossils even older and more primitive than *Yunnanozoon*.

If one accepts the idea that *Yunnanozoon* and *Odontogriphus* are the most primitive chordates (Fig. 7), some expectations can be formulated regarding the anatomy of the common ancestor of these organisms. It should bear metamerically arranged muscular bladders with internal cavities separated from each other by transverse myosepta. A cylindrical intestine, with several branchial slits or pouches in the anterior part, should run below this metameric vesicular unit. The notochord may have been an evolutionary novelty connected with the chordate style of locomotion (by lateral undulations of the body), not necessarily present in *Odontogriphus* and its common ancestor with *Yunnanozoon*.

The only known pre-Cambrian organism that shows the presence of metamerically arranged bladders with muscular walls that were located anatomically above the intestinum is, somewhat surprisingly, Ediacaran *Dickinsonia*.

In the 'quilted pneu structure' of *Dickinsonia* (Seilacher 1989, 1992) there is an anterior medially elongated unpaired unit followed behind by transversely elongated modules that seem to be at least subdivided medially by a kind of mesenterium in the center of the body. The *Dickinsonia* body increased in size probably by adding new metameric units at its posterior end. At early ontogenetic stages with a low number of muscular units the anteriormost one was much more elongated and rounded triangular in outline (Runnegar 1982).

The convincing evidence that particular modules of *Dickinsonia* were liquid-filled bladders has been offered by Seilacher (1989) but some additional specimens that were torn across the modules prior to burial show that this was a cellular tissue rather than fluid which would have leaked from the fractured body (Runnegar & Gehling 1995). Runnegar (1982) has shown that the modules were contractible and provided evidence that some muscle fibres run longitudinally (parallel to the body margin: Runnegar 1982: fig. 1E). The ventral and dorsal sides of the 'quilted structure' of *Dickinsonia* were apparently of the same morphology; so it hardly can be compared with any complete known organism. However, some specimens show a presence of sediment-filled medial canals, apparently under the 'quilted structure' (Runnegar 1982: fig. 1C; Jenkins 1985). This is a spatial relationship between muscular blocks and the alimentary tract of the same kind as in *Yunnanozoon* and, proposedly, in *Odontogriphus*. The main difference in respect to the latter is that in adult specimens of *Dickinsonia* the body was very strongly dorso-ventrally flattened. In the anterior part of yet another specimen of *Dickinsonia* there are sediment-filled canals running from the medial area to both sides of the body but slightly oblique to the module boundaries. They were interpreted as intestinal caeca by Glaessner & Wade (1966: pl. 101: 4) but in such strongly dorsoventrally compressed organisms branchial pouches would look the same.

Classification

It follows from the phylogenetic interpretation presented here (Fig. 7) that *Yunnanozoon*, with its laterally compressed body but dorsally located 'pneu' myomeres, occupies a transitional position between the branch leading from *Dickinsonia* to *Odontogriphus* and that leading from *Pikaia* to all the later chordates, including conodonts, agnathans, cephalochordates and tunicates, characterized by V-shaped myomeres backing the notochord. The body plan of the tunicates is the most derived; but it has been suggested that the Carboniferous *Typhloesus*, that shows some relationships to the anaspid agnathans, can be an ancestor of Recent salps (Dzik 1986, 1993). This implies rooting of the tunicate evolutionary branch in more advanced chordates than usually assumed.

Several high rank taxonomic units are available to enclose *Dickinsonia* and *Odontogriphus*. The class Dipleurozoa Harrington & Moore 1955, as well as the order Dickinsoniida Harrington & Moore 1955 and family Dickinsoniidae Harrington & Moore 1955, can serve for this purpose. The mouth denticles of *Odontogriphus* were originally compared with those of the 'paraconodonts', the ordinal unit for which is Westergaardodinida Lindström 1970. *Pikaia* is generally believed to be a cephalochordate, despite the pair of long tentacles and a series of shorter paired appendages following it, which make it somewhat similar rather to coeval Burgess Shale *Nectocaris pteryx* Conway Morris 1976, also having its body subdivided in numerous V-shaped segments. Chordate affinities of this organism have been rejected because of large eyes and preoral scleritized 'appendages' (Conway Morris 1976b) both now known to be typical for conodonts. Perhaps the 'shield' of *Nectocaris* can be compared with the branchiogenital region of *Yunnanozoon*, the general proportions of the body in this species being otherwise similar to *Pikaia*. The exact affinities of these fossils have to be proven by more detailed description than those yet published, but allow at least provisional placement of the family Pikaiidae Walcott 1911 in the Acrania Bleeker 1859 or Cephalochordata Owen 1846.

It remains thus to establish taxonomic units of corresponding rank for *Yunnanozoon*. Its transverse myosepta and the organization of the pharyngeal region of the body, with unnumerous gill arches, allow diagnosing a new class for it, with the proposed name Yunnanozoa. Probably the ring-like mouth apparatus and annulated branchial arches are specializations deserving recognition in diagnosing lower rank taxa, Yunnanozoida ordo n. and Yunnanozoidae fam n.

Conclusions

Although there are still controversies regarding time correlation of the basal Cambrian strata in low and high latitudes of that epoch (Vidal *et al.* 1995), the base of the Cambrian is definitely older than 534.6 ± 0.6 Ma (middle Tommotian) or even 543.9 ± 0.24 Ma (middle Manykayan) (Isachsen *et al.* 1994; Tucker & Mc Kerrow 1995). The presence of a chordate in the Chengjiang fauna, of late Atdabanian or early Botomian (see Hou *et al.* 1991; Chen & Erdtmann 1991; Butterfield 1995) age, thus probably almost 530 Ma, extends the fossil record of chordates several million years back in time in respect to earlier (but still inadequately) known *Pikaia* and *Metaspriggina* from the Burgess Shale. It also gives an insight into the anatomy not expected to occur earlier within the chordates or even at the transition from hemichordates to chordates. This completely new anatomical information opens again to further enquiry into the old problem of how to root the chordate phylogenetic tree within the invertebrates.

Acknowledgments

My two research stays in Nanjing in 1993 and 1995 were possible due to a travel grant from the Comittee of Scientific Research (Warsaw, Poland) and the exchange program between the Polish Academy of Sciences and Academia Sinica.

This paper owes much to discussions on the subject with my Institute colleague Magdalena Borsuk-Białynicka and to her very thorough review of the final manuscript. I also appreciate reviews of earlier versions of the manuscript by Simon Conway Morris (University of Cambridge) and anonymous reviewers. Adolf Seilacher and Wolf-Ernst Reif (both University of Tübingen) have read and commented the final version of the manuscript.

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Streszczenie

Wśród tysięcy skamieniałych zwierząt nie mających mineralnego szkieletu z wczesnokambryjskiego stanowiska Chegjiang w prowincji Yunnan znalazły się też szczątki pierwszych strunowców. *Yunnanozoon lividum* Hou *et al.* 1991, opisany jako problematyk przed kilku laty, ukazuje wypełnioną osadem gardziel z łukami skrzelowymi i gonadami po bokach, a nad nią cylindryczną strukturę ubogą w substancje organiczne i z wnętrzem niedostępnym dla mułu — zapewne wypełniony płynem lub zwakuolizowanymi komórkami osiowy szkielet a więc struna grzbietowa. Zaskakującymi cechami *Yunnanozoon* są prostopadłościenne bloki miomerów, zapewne mające postać umięśnionych, wypełnionych płynem worków oraz rozbudowana głowa z aparatem gębowym o pierścieniowej nierozpoznanej dokładnie strukturze i zapewne z dużymi organami zmysłowymi (oczami?).

Dowodzi to, że cechy uważane za osiągnięcia kręgowców charakteryzowały już pierwsze strunowce. Poszukując krewniaków i przodka *Yunnanozoon* wśród innych kambryjskich i prekambryjskich organizmów (powinni się cechować metamerycznymi workami mięśniowymi ponad jelitem z bocznymi wypustkami otwartymi na zewnątrz) wskazać można na przypuszczalnego konodonta *Odontogriphus* ze środkowego kambru Burgen i *Dickinsonia* z prekambru Ediacara i Morza Białego.