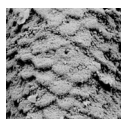


Early Cambrian eodiscoid trilobite *Hupeidiscus orientalis* from South China: ontogeny and implications for affinities of *Mongolitubulus*-like sclerites

GUOXIANG LI, MICHAEL STEINER, MAOYAN ZHU & XIN ZHAO



Delicately phosphatized specimens of the eodiscoid *Hupeidiscus orientalis* were documented from the lower Cambrian Shuijingtuo Formation through acetic acid maceration of limestone samples. The material enables us to better understand the meraspid to holaspid ontogenetic development of *H. orientalis*, and to evaluate its relations with other eodiscoid taxa occurring in South China. The development of its pygidium and thoracic segments is very similar to that of “*Shizhudiscus*” *longquanensis*, suggesting that *Shizhudiscus* is a junior synonym of *Hupeidiscus*. However, the synonymization of *Hupeidiscus* with *Tsuniyidiscus* remains open as little is known about the ontogeny of the latter genus. The spines of *H. orientalis* are of particular importance. Like the enigmatic sclerite taxon *Mongolitubulus*, its spines are ornamented with a distinctive scaly sculpture, shedding new light on the origin and affinities of *Mongolitubulus*-like sclerites. The squamose ornament was gradually transformed from granules on the exoskeletal surface at the base of the spines. Other strands of evidence, *e.g.*, the outline, exuviating growth, and the spatio-temporal distribution, also suggest that some isolated sclerites previously assigned to *Mongolitubulus* are possibly related to the spines of eodiscoid trilobites. This finding implies that such morphologically similar spines may be essentially of multiple pan-arthropod origins (bradoriids, eodiscoids, *etc.*), and they may be of morphologic analogues rather than homologues, suggesting that *Mongolitubulus* shall be cautiously used as a generic name unless the circumstance of its type specimens from Mongolia gets clarified. • Key words: eodiscoid, *Hupeidiscus*, sclerite, *Mongolitubulus*, Lower Cambrian, South China.

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The apparent abundance of sclerite-bearing metazoans is a conspicuous aspect of the early Cambrian skeletal faunas (Conway Morris & Chen 1997), and lots of the so-called small shelly fossils represent only disarticulated sclerites, which are elements of more complex skeletons (scleritomes) (Bengtson 1985). Although the scleritomes and zoological affinities of some isolated sclerites, such as *Hadimopanella*-like sclerites (Hinz *et al.* 1990, Conway Morris 1997), *Microdictyon* (Chen *et al.* 1989), *Halkieria* (Conway Morris & Peel 1990), and *Paterimitra* (Skovsted *et al.* 2009), have been well documented by discovery of extraordinarily preserved material, overall configurations of the scleritomes of many groups still remain enigmatic. In most of the above cases, previous scleritome reconstructions based on disarticulated sclerites have been shown to be inappropriate, though some analyses may provide general guidelines for studying assemblages of disarticulated

sclerites or searching for more complete fossils (Bengtson & Conway Morris 1984, Conway Morris & Chen 1997, Dzik 2003). Discoveries of exceptionally preserved specimens have been hitherto the most convincing approach for documenting scleritomes from isolated sclerites, and the search for articulated or well phosphatized fossils continues to be an essential impetus in better understanding the biology of isolated sclerites.

The difficulties in studying early Cambrian isolated sclerite fossils could be exemplified by *Mongolitubulus*-like spines. The small ‘phosphatic’ fossil *Mongolitubulus* was first described by Missarzhevsky (1977) on the basis of material from the lower Cambrian of Mongolia. It is characterized by a tubular or spiniform outline with a prominent scaly ornamentation on the outer surface. This kind of spines has been widely reported from the lower Cambrian, *e.g.* in Mongolia (Missarzhevsky 1977),

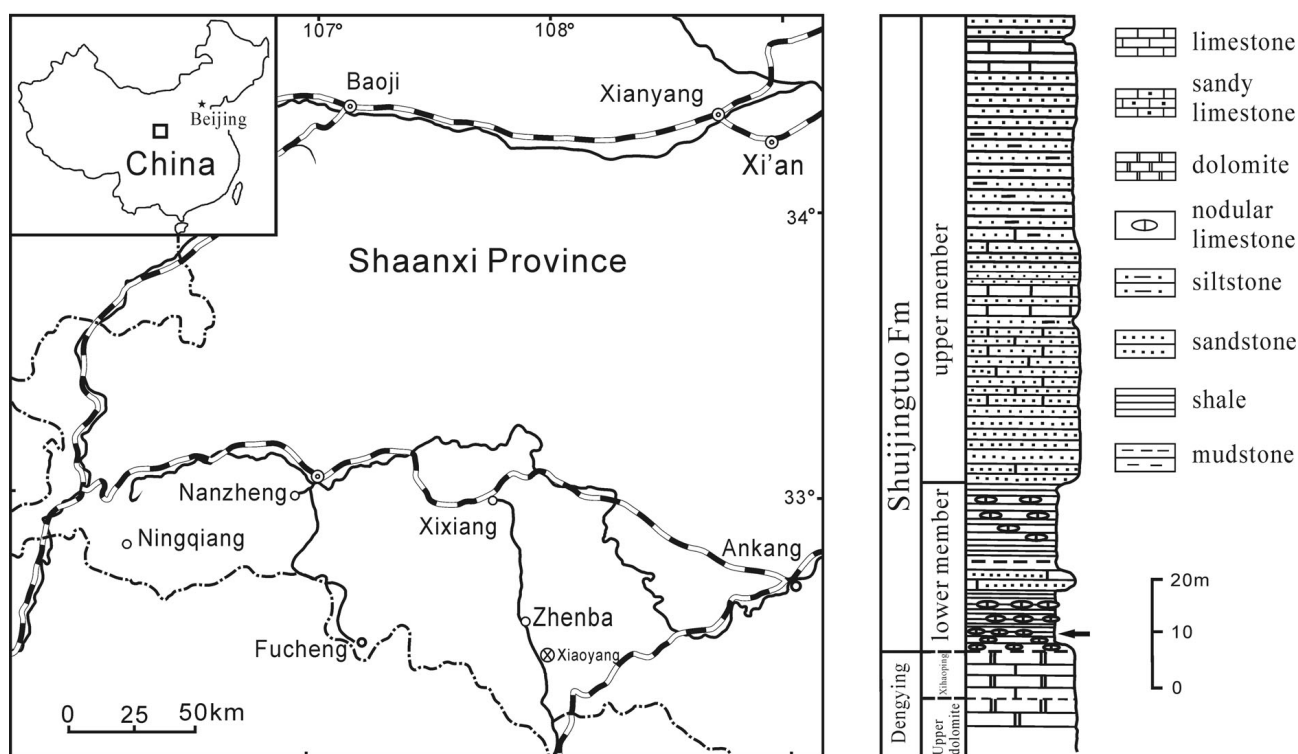


Figure 1. Geographic location and stratigraphic column of the Xiaoyang section. Level with specimens illustrated in Figs 2 to 4 is indicated by arrow.

Kazakhstan (Dzik 2003), Antarctica (Gazdzicki & Wrona 1986), Greenland (Peel & Blaker 1988, Skovsted & Peel 2001), and Australia (Topper *et al.* 2007). Since *Mongolitubulus* was described mainly on the basis of isolated sclerites, its scleritome and affinities remained unresolved, being assigned to protoconodonts (Missarzhevsky 1977, Esakova & Zhegallo 1996), or interpreted as carapace spines of bivalved arthropods (Melnikova 2000, Skovsted & Peel 2001) or as lobopodian spines (Dzik 2003). The discovery of bradoriid specimens with scaly ornamented spines from Australia provides definitive evidence for a bradoriid affinity, at least for some *Mongolitubulus*-like spines (Topper *et al.* 2007), though it could not conclude that all scaly ornamented spines are related to bradoriids. Actually, some scaly spines somewhat resemble trilobite spines. Especially the small isopygous eodiscoid trilobites, occurring worldwide in the Lower and Middle Cambrian (Jell 1997), have an approximately coincident distribution with *Mongolitubulus*-like sclerites, and some of them bear genal, occipital and axial spines. Therefore, a detailed study on eodiscoid spines can possibly provide important hints for documenting the affinities of *Mongolitubulus*-like sclerites.

The purpose of the present paper is to document delicately phosphatized specimens of the eodiscoid *Hupeidiscus orientalis* from basal limestones of the Lower Cambrian Shuijingtuo Formation at the Xiaoyang section, Zhenba County, Shaanxi Province, China. The specimens

were recovered from limestone samples through acetic acid (3–5%) maceration, and were examined and photographed under SEM. The marked scaly ornamentation of the genal, occipital and axial spines of *H. orientalis* suggests that some *Mongolitubulus*-like sclerites can be related to eodiscoids, implying that such morphologically similar spines may have multiple pan-arthropod origins, and suggesting that *Mongolitubulus* shall be cautiously used as a generic name unless the circumstance of its type specimens from Mongolia can be clarified. This finding is a new paradigm of sclerites (spines) identified with body (skeleton) fossils, and indicates that some enigmatic sclerites could be related to familiar animal groups. The abundant phosphatized material also provides significant insights into the ontogenetic development of *Hupeidiscus* and evaluation of its relationship to other eodiscoid taxa.

Locality and stratigraphy

The specimens studied here were collected from limestones of the basal Shuijingtuo Formation at the Xiaoyang section, Zhenba County, southern Shaanxi Province (Fig. 1). The section is situated on the present-day northern margin of the Yangtze Platform. A sequence of upper Neoproterozoic to lower Cambrian stratigraphic strata well crops out along the road cut and riverbank. In an ascending order, the lower Cambrian succession consists of the Xihaoping

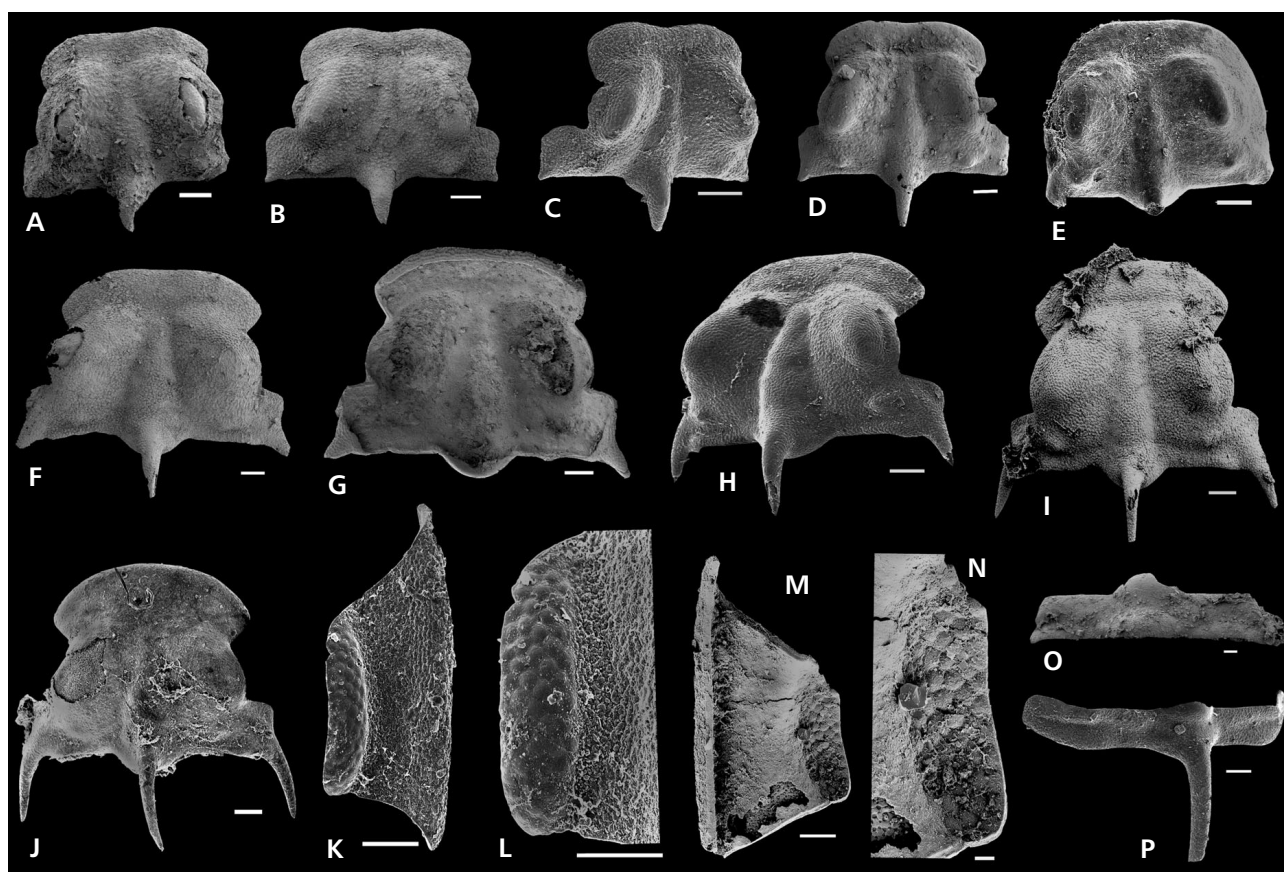


Figure 2. *Hupeidiscus orientalis* from the basal Shuijingtuo Formation in the Xiaoyang section. A–J showing the series changes of cranidia, K–N librigena with eyes. • A – NIGP153721, dorsal view of M0b. • B – NIGP153722, dorsal view of M0c. • C – NIGP153723, oblique posterodorsal view of M0c. • D – NIGP153724, dorsal view of M1a. • E – NIGP153725, dorsal view of a cephalon of M1b. • F – NIGP153726, dorsal view of M1b. • G – NIGP153727, ventral view of M1b. • H – NIGP153728, oblique posterodorsal view of M2. • I – NIGP153729, dorsal view of M3. • J – NIGP153730, dorsal view of H0. • K – NIGP153731, dorsal view. • L – close-up of K. • M – NIGP153732, ventral view. • N – close-up of N. • O – NIGP153733, dorsal view of the first thoracic segment. • P – NIGP153734, dorsal view of a spine-bearing thoracic segment (second or third). Scale bars 100 μ m, except in L (70 μ m) and N (20 μ m).

Member of the Dengying Formation, and the Shuijingtuo and Shipai formations. Similar lithostratigraphic units are widely distributed in southeast Shaanxi and northwest Hubei region (Qian 1999, Steiner *et al.* 2007). The 8.37 m thick Xihaoping Member, which unconformably overlies the upper dolomite member (Ediacaran) of the Dengying Formation, consists of light dolomites and dolomitic or phosphatic limestones with abundant skeletal fossils, including phosphatic brachiopods, sponge spicules, molluscs, cambroclaviids, hyolithelminths, *etc.* Due to the sedimentary architecture, the Xihaoping Member was deposited in peritidal, high-energy environments (Li *et al.* 2004). The Shuijingtuo Formation, unconformably overlying the Xihaoping Member, can be subdivided into two members. The 31 m thick lower member consists of dark or black, thin-bedded siltstones, mudstones and argillaceous limestones with abundant skeletal fossils, including trilobites (eodiscoids and polymerids), lingulate brachiopods, protoconodonts and the conodont-like fossil *Rhombocor-*

niculum cancellatum, microdictyonid plates, sponge spicules, *etc.* The lower Shuijingtuo Formation is interpreted as deposited in subtidal, low-energy environments (Li *et al.* 2004). The 85 m thick upper member consists of fine sandstones and siltstones with a few intercalated thin limestone beds, and only contains scarce skeletal fossils.

Previously, the Xihaoping Member was inappropriately correlated with the Shiyantou Formation (upper Meishucunian) of eastern Yunnan (Xie 1988). Based on the occurrence of *Microcornus*, *Cambroclavus*, *Ninella*, *etc.*, the Xihaoping Member has recently been considered as the middle Qiongzhusian in age (Qian 1999, Li *et al.* 2004, Steiner *et al.* 2007). Although no complete trilobite cranidia or pygidia have been collected, a great number of librigenal and occipital spines of trilobites were recovered through etching of the carbonate samples with acetic acid (Li *et al.* 2004). The occurrence of trilobite spines also suggests an early or middle Qiongzhusian age for the Xihaoping Member, and indicates the presence of a

protracted hiatus at least spanning the Meishucunian between the Xihaoping and upper dolomite members. The lower Shuijingtuo Formation contains *Hupeidiscus*, *Zhenbaspis*, *Eoredlichia* (trilobites), and *Kunmingella* (a bradoriid), all of which indicate the lower Shuijingtuo Formation is of the late Qiongzhusian age (Li *et al.* 2004, Steiner *et al.* 2007). The occurrence of the cosmopolitan index fossil *Rhombocorniculum cancellatum* (Li *et al.* 2003) provides important information for global correlation of the late Qiongzhusian. The absolute time spanning the hiatus between the Xihaoping Member and the Shuijingtuo Formation is unclear. Although the upper Shuijingtuo Formation is routinely interpreted as representing the lower Canglangpuan Stage, it is difficult to draw the boundary horizon between the Qiongzhusian and Canglangpuan at the Xiaoyang section since the upper member contains only scarce fossils.

The phosphatized eodiscoid *Hupeidiscus orientalis* from the basal Shuijingtuo Formation co-occurs with *Microdictyon* spp., *Rhombocorniculum cancellatum*, *Kunmingella douvillei*, *Dabashanella hemicyclica*, *Palaeobolus liantuoensis*, and *Lingulellotreta malongensis* (Li & Holmer 2004), indicating a late Qiongzhusian age (approximately equivalent to the late Atdabanian to early Botomian Siberian stages), or Stage 3 of Series 2 in the new subdivision scheme for the Cambrian System (Zhu *et al.* 2006).

All specimens illustrated in this paper are housed in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Ontogeny of *Hupeidiscus orientalis*

General features

All specimens studied herein were collected from limestone samples of the basal Shuijingtuo Formation. The phosphatized preservation of *H. orientalis* enabled us to obtain three-dimensionally preserved specimens through acetic acid maceration in laboratory, and could add more knowledge for elucidating the ontogeny than crack-out specimens. Most of the specimens of *H. orientalis* recovered herein are disarticulated exuviae, and include hundreds of cranidia, librigenae with eyes (Fig. 2K–N), (transitory) pygidia and thoracic segments of meraspid and holaspid, allowing us to describe its ontogenetic development, despite that no protaspid and hypostomes were recovered.

The moult stages and growth instars of *H. orientalis* studied herein are very similar to those of '*Shizhudiscus*' *longquanensis* described by Zhang & Clarkson (1993), and hence the terminology for describing the ontogeny and discriminating growth stages follows that of Zhang & Clarkson (1993). As in '*S.*' *longquanensis*, the ontogeny of *H. orientalis* includes three periods: protaspid (no speci-

mens recovered herein), meraspid and holaspid periods. The most distinct ontogenetic changes took place in the morphogenesis of the transitory pygidia during the meraspid period, and four meraspid degrees (stages) (M0, M1, M2 and M3), defined by the progressive release of thoracic segments from the transitory pygidia, can be recognized. Seven meraspid substages or stages (M0a, M0b, M0c, M1a, M1b, M2 and M3) are subdivided according to the number of developing new rings (axial segments) in the rachis of the pygidia (Zhang & Clarkson 1993). The holaspid period (H) begins after the third thoracic segment being liberated from the transitory pygidium. The ontogenetic changes of the eodiscoid cranidia were fairly gradual and could not be tracked by such an evident developmental marker as was present throughout the whole growth series of the transitory pygidia (Cederström *et al.* 2009). Scatter diagrams of previous bivariate (length vs width) analyses of eodiscoid cranidia (*e.g.*, Zhang & Clarkson 1993, Cederström *et al.* 2009) show a nearly isometric increase, and there are no distinct clusters of growth stages. Thus, bivariate analysis could not help to define growth stages of the cranidium since overlapping size ranges between adjacent instars may be generally a common feature for eodiscoids (Cederström *et al.* 2009). Although the cranidium and pygidium of a same individual is nearly equal in size (especially width) in isopygous eodiscoids (Zhang & Clarkson 1993), it is difficult to refer disarticulated cranidia exactly to the corresponding growth stages of the pygidia simply on the basis of size comparison. However, a series of gradual development changes for the cranidium and discovery of complete enrolled and outstretched specimens (Zhang & Clarkson 1993, Cederström *et al.* 2009) could facilitate allocation of disarticulated cranidia approximately to the growth stage defined by the transitory pygidia.

Since the ontogeny of *H. orientalis* studied herein is quite similar to that of '*S.*' *longquanensis*, which was described and illustrated in detail by Zhang & Clarkson (1993), the following paragraphs will just give a brief description of the ontogeny of *H. orientalis* with special notes on their ontogenetic differences.

Meraspid period

The majority of the disarticulated pygidia and cranidia investigated herein belong to the meraspid period. As in all trilobites, the meraspid period starts with the appearance of an articulation hinge between the cephalon and the proto-pygidium. Articulated trilobites lacking thoracic segment are assigned to meraspid stage 0 (M0). M0 can be subdivided into 3 substages (M0a, M0b and M0c) according to the number of axial rings in the transitory pygidium of *H. orientalis*. In substage M0a, the axis of the transitory

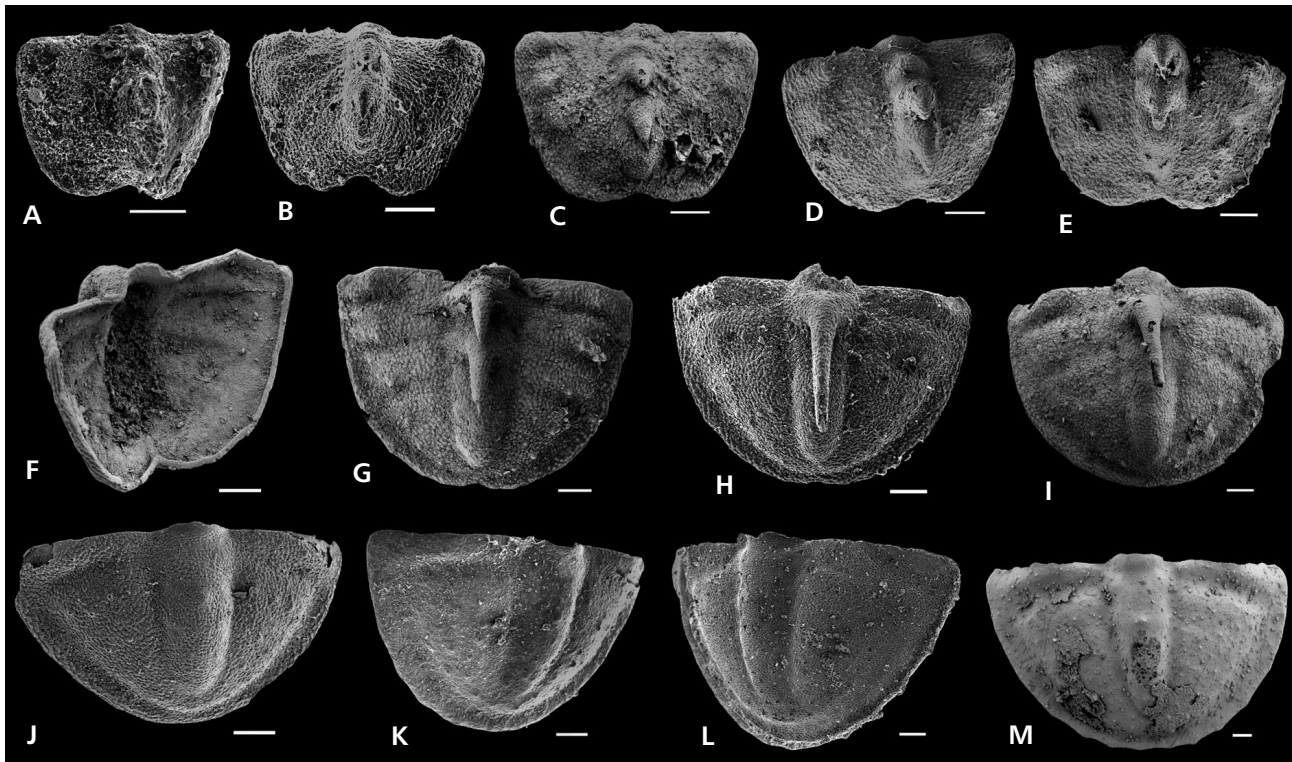


Figure 3. Pygidia of *Huupidiscus orientalis* from the basal Shuijingtuo Formation in the Xiaoyang section. • A – NIGP153735, oblique posterodorsal view of M0b. • B – NIGP153736, dorsal view of M0b. • C – NIGP153737, dorsal view of M0c. • D – NIGP153738, dorsal view of M0c. • E – NIGP153739, dorsal view of M1a. • F – NIGP153740, oblique lateroventral view of M1a. • G – NIGP153741, dorsal view of M1b. • H – NIGP153742, dorsal view of M2. • I – NIGP153743, dorsal view of M2b or M3? • J – NIGP153744, dorsal view of H0. • K – NIGP153745, oblique laterodorsal view of H1. • L – NIGP153746, oblique lateroventral view of H1. • M – NIGP153747, dorsal view of H1. Scale bars 100 μ m.

pygidium consists of three segments, and the two posterior axial rings bear two strong axial spines (Zhang & Clarkson 1993). In substage M0b, an additional axial ring was added at the rear of the axis, and the transitory pygidium has four axial rings and three pleural ribs (Fig. 3A, B). In substage M0c, the pygidium bears five axial rings and four pleural ribs (Fig. 3C, D). Stage 1 (M1) has one free thoracic tergite (Fig. 2O), which was the first spineless segment released from the transitory pygidium. The transitory pygidium of M1a has five axial rings and four pleural ribs (Fig. 3E), whereas the pygidium of M1b has six axial rings and five pleural ribs (Fig. 3G). In stage M2, the first spine-bearing segment had been released from the transitory pygidium, and the trilobite has two free thoracic segments [a spineless one and one with a long axial spine (Figs 2P, 4I, K)], and the transitory pygidium of M2 bears only one axial spine and has six axial rings and five pleural ribs (Fig. 3H). Before the third thoracic segment was released from the transitory pygidium, the pygidium gained a new axial ring and a pair of pleural ribs and bears seven axial rings and six pleural ribs (Fig. 3I). This stage was designated as M3 by Zhang & Clarkson (1993, text-fig. 2), but actually it may also be considered as a substage of M2 according to the release of the thoracic segments.

Along with the size increase and moulting, the following gradual changes in morphology can be distinguished. The size of meraspid cranidia ranges from 0.40 to 1.06 mm in length and from 0.61 to 1.50 mm in width. The meraspid cranidia of stage M0 are subtrapezoidal in outline with the anterior margin curved backwards medially. During ontogenetic development, the cranidial anterior margin progressively becomes curved forwards, and the cranidia are approximately semi-circular in outline. The anterior border becomes wide and moderately convex. The fixigenal lobes are strongly convex in early meraspid stages, and become moderately convex in later ontogenetic stages. The paired bacculae posterior to the fixigenal lobes are distinctly convex in stage M0 (Fig. 2A–F), but they progressively disappear and are fused into the fixigenal lobes in holaspides (Fig. 2J). The posterior border furrows appear in late meraspid stages, and become distinct in the holaspid period (Fig. 2J). The genal and occipital spines undergo a progressive expansion during the ontogenetic development.

The transitory pygidia are 0.37–1.00 mm long, 0.51–1.60 mm wide. The transitory pygidium of stage M0 is also subtrapezoidal in outline, and has a pronounced larval notch (a w-shaped posterior margin) (Fig. 3A–F)

(cf. Cederström *et al.* 2009). The larval notch becomes progressively indistinct in late meraspid stages (Fig. 3H), and the w-shaped posterior margin becomes semicircular (Fig. 3I) with some microscopic serrations along the posterior margin (Fig. 4O). In the early meraspid stages (M0), the axis consisting of 3 to 5 strongly elevated axial rings, which are separated by indistinct axial furrows. The second and third axial rings bear a prominent spine with the apex pointing backwards. The lateral and posterior borders are moderately convex, and separated from the pleural areas by shallow border furrows. A few tubercles, arranged in rows, occur on each pleural rib in late meraspides (Fig. 4M, O). The tubercles are not apparent on the rachis. The pleural furrows become more indistinct during the ontogeny. The number of axial rings in the transitory pygidium increases throughout meraspid development until the third thoracic segment is liberated. The cephalon and pygidia become progressively more convex during meraspid ontogeny.

Early holaspid period

The holaspid period begins after the third thoracic segment has been liberated from the transitory pygidium (Zhang & Clarkson 1993). The pygidium of H0 bears six axial rings and five pairs of pleural ribs (Fig. 3J). With further growth, the pygidium develops a new and final axial ring and a pair of pleural ribs, and the mature pygidium (H1) bears seven axial rings and six pairs of pleural ribs (Fig. 3K–M). The cranidia of the early holaspides (Fig. 2J) are very similar to those of later meraspides in morphology. As the cranidia increase progressively in size, the anterior border furrow becomes wide and deep, and the anterior border widens. The palpebral lobe becomes distinct, and the glabella becomes tapered forwards and less elevated but with the occipital ring and the posterior lobe of the glabella much swollen. The transverse glabellar furrows become visible and the axial furrows get wide and deep. The occipital and posterior furrows get deep and more evident (Fig. 2J). The occipital and genal spines progressively become elongated and more prominent.

The spineless holaspid pygidium is semicircular with a rounded posterior margin, and is moderately convex with axis raised high above the pleural areas. Both the rachis and the pleural regions are strongly fused. The ring furrows and pleural and interpleural furrows are nearly effaced. The distinct tubercles (Fig. 3K, M) arranged in rows on the pleural regions provide means for distinguishing the pleural ribs, though only the anterior pleural furrow is evident. The axial and border furrows become deep and narrow. The border slopes laterally and becomes relatively narrow with a weakly serrated margin.

Thoracic segments

The present material includes dozens of isolated thoracic segments, but most of them are fragmentary. The width variation of size indicates that these thoracic segments belong to different meraspid and holaspid stages. The holaspid thorax of *H. orientalis* consists of three segments. All segments have an arched articulating half-ring anteriorly and a larger axial ring posteriorly, which is slightly broader and longer than the articulating half-ring (Fig. 4I, K). The spineless thoracic segment represents the first of the three thoracic segments (Fig. 2O) (Zhang & Clarkson 1990), while the second and third ones each bear a very long axial spine (Figs 2P, 4I, K) though the differentiation of these two thoracic segments is difficult because of their strong morphological similarities. The posterior segments have prominent articulating facets anterolaterally (Fig. 4K). Both the anterior and posterior edges of the thoracic segments are virtually straight with a moderately deep pleural furrow. The abaxial parts of the pleura slope downwards.

Librigena and eyes

The material has yielded dozens of isolated librigena with the eyes preserved. The size, outline and course of the facial suture indicate that these librigena belong mainly to the holaspid period. Only one cephalon (Fig. 2E), which was identified as a meraspis of substage M1b, was found with both librigena intact. It possibly represents the remains of a dead individual rather than an exuvium (Zhang & Clarkson 1993). The eye development of '*Shizhudiscus longquanensis*' has been studied by Zhang & Clarkson (1990, 1993) in detail. They showed that a holochroal type of eye developed from a single lens through a pattern of hexagonal close packing as more lenses are emplaced. The eye development of *Hupeidiscus orientalis* as illustrated herein (Fig. 2K–N) is essentially identical to that of '*S. longquanensis*', and will therefore not be reiterated. The cephalon of substage M1b might provide supplementary data for analyzing the eye development, but the lenses are too poorly preserved to be described.

Ornamentations of exoskeletons and spines

The phosphatization of eodiscoids in South China is related to the early Cambrian phosphate concentration episode (Zhang 1989; Zhang & Clarkson 1990, 1993). The diagenetic phosphatization resulted in the delicate preservation of exoskeletons (including the surficial sculpture). The exoskeleton of *Hupeidiscus orientalis* consists of an outer layer and an inner one. The external surface of the outer

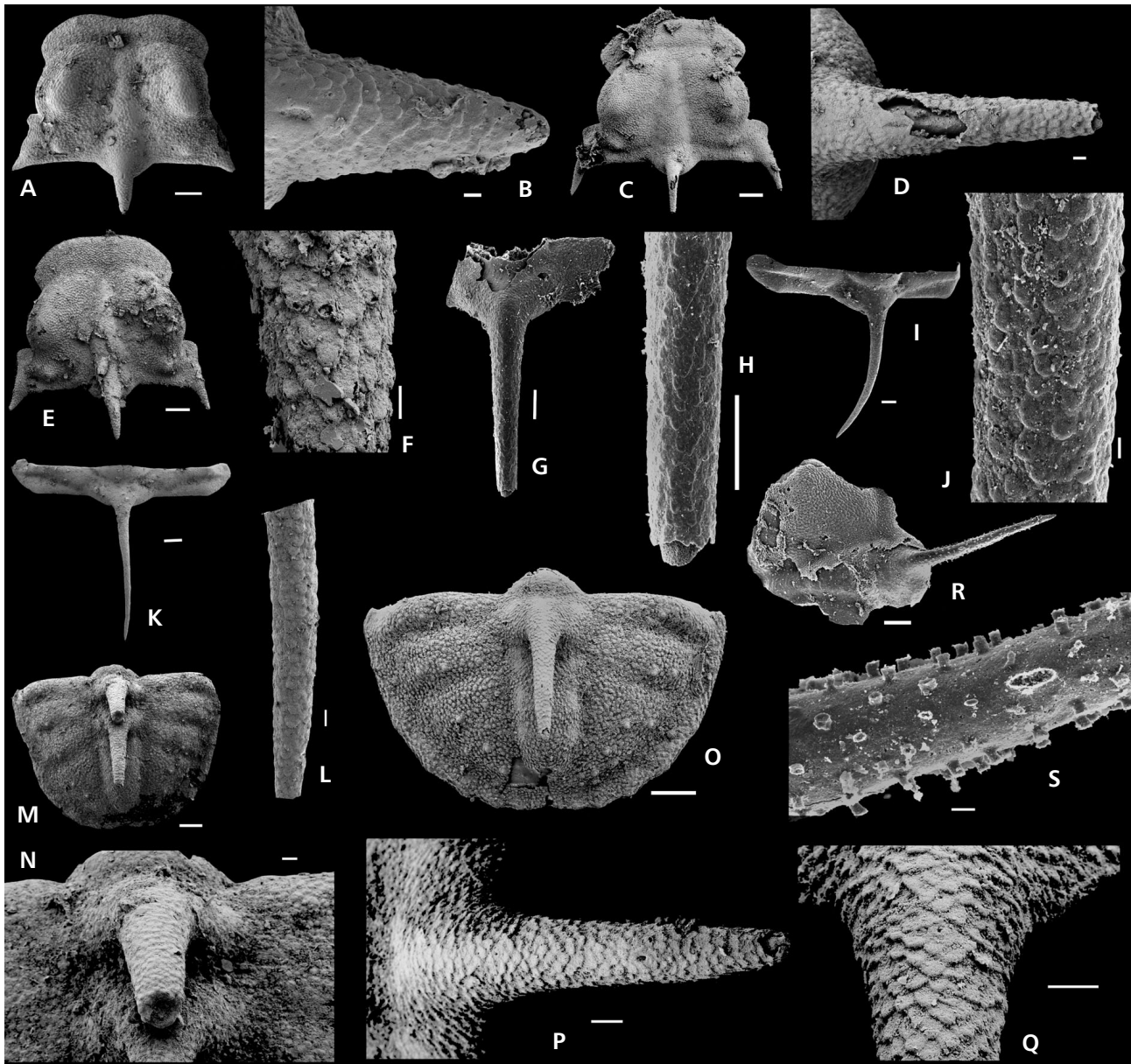


Figure 4. *Huheidiscus orientalis* from the basal Shuijingtuo Formation in the Xiaoyang section, showing the ornamentation variation of the spines. • A – NIGP153748, dorsal view of a cranidium (M0c). • B – close-up of the occipital spine in A; scale bar 20 μ m. • C – NIGP153749, dorsal view of a cranidium (M3). • D – close-up of the occipital spine in C; scale bar 10 μ m. • E – NIGP153750, dorsal view of a cranidium (M2). • F – close-up of the occipital spine in E; scale bar 10 μ m. • G – NIGP153751, an axial spine. • H – close-up of G. • I – NIGP153752, a spine-bearing thoracic segment. • J – close-up of the spine in I; scale bar 10 μ m. • K – NIGP153753, a spine-bearing thoracic segment. • L – close-up of the spine in K; scale bar 20 μ m. • M – NIGP153754, dorsal view of a pygidium (M1b). • N – close-up of the spine in M; scale bar 20 μ m. • O – NIGP153755, dorsal view of a pygidium. • P – close-up of the spine in O; scale bar 20 μ m. • Q – close-up of P; scale bar 20 μ m. • R – NIGP153756, a fragmentary cranidium. • S – close-up of the spine in R; scale bar 20 μ m. Scale bars 100 μ m, if not otherwise indicated.

layer is ornamented with fine granules. The size of the granules (5–7 μ m in diameter) does not much change during growth (M1b to H1). The outer surface of the inner layer is nearly smooth except for some tubercles (Fig. 3M). Some specimens are covered with diagenetic coatings or encrustations, and hence, the sculpture could not be examined (Figs 2A, 3H). Occasionally, some pyrite crystals can be

observed on the surface (Fig. 2D, E). The granules are more or less even distributed on the cranidia except that there are relatively fewer granules in the axial furrows. Compared with the granular outer layer, the outer surface of the inner layer is more or less smooth but covered with scattered tubercles. Occasionally, some pygidia can be examined with only the outer layer preserved (Fig. 3L), and

the internal surface of the outer layer is full of small pits (corresponding to the granules) with scattered larger pits (corresponding to the tubercles). The tubercles (15–18 µm in diameter) are most common on the pygidia. They scarcely occur on the cranidia and the thoracic segments. The tubercles first appear during substage M0b on the new developing pleural ribs. The anterior three pairs of pleural ribs usually lack tubercles.

The axial spines of late meraspid and holaspid stages are slender, slightly curved posteriorly towards the body, and taper gradually to a pointed apex. In contrast to the granular ornamentation of the major exoskeleton, the axial, occipital and genal spines are usually characterized by a prominent scale-like ornamentation on the outer surface. The ornamentation often consists of densely-spaced, ovoid to diamond-shaped scales arranged in regular rows (Fig. 4M–Q). Individual scales merge with the general surface at their abapical margin and have a raised apical end pointing towards the spine tip. Actually, the scaly ornamentation is just a transformation of the external granules on the exoskeletal surface, and the transformation occurs at the base of the spine (Fig. 4N, P). The specimens illustrated herein exhibit a substantial variation in the morphology of the scales. In some specimens, the scales are much subdued and irregular both in morphology and arrangement (Fig. 4G–J). On the surface of the inner layer (outer layer partly peeled off) (Fig. 4R, S), the spine bears some micro-spines.

Discussion

Taxonomic implications

The eodiscoids are a group of diminutive miomerid trilobites and a common element in many Cambrian faunas (Zhang *et al.* 1980, Jell 1997). Its systematic position, especially its relation with agnostids, has been extensively discussed in literatures. There are two major views about the systematic feature of the eodiscoids: they are either traditionally classified together with the agnostoids, which were thought to be derived from the eodiscoids (Fortey 1990), or they are considered to have evolved from polymerid trilobites by paedomorphosis (Shergold 1991, Jell 1997). A cladistic analysis showed that the eodiscoids were derived from polymerids through progenetic heterochrony (Babcock 1994). The ontogenetic development (*e.g.* morphological changes, hypostomal development and the presence of calcified protaspides) provides important evidence for analyzing the systematic position of the eodiscoids, supporting the view that they are related to polymerid trilobites (Cederström *et al.* 2009).

Eodiscoids have been recovered in abundance from the lower Cambrian of South China, especially from the black

shale or siltstone units, *e.g.*, the Yu'an-shan Formation in eastern Yunnan, the Niutitang Formation in Guizhou, the Jiulaodong Formation in western Sichuan, and the Shuijingtuo Formation in northwestern Hubei and southern Shaanxi (Lu 1974, Li 1980, Zhang *et al.* 1980, Zhang 1987, Zhang & Clarkson 1993, Yuan & Zhao 1999, Lin *et al.* 2004). Many genera and species have been established on the basis of material from these regions, and the taxonomic proliferation is quite obvious since the ontogenetic development and morphological variation were not sufficiently evaluated in many taxonomic studies. In reviewing these eodiscoid genera, Zhang (1987) considered *Shizhudiscus* Zhang & Zhu in Zhang *et al.*, 1980 and *Guizhoudiscus* Zhang in Zhang *et al.*, 1980 to be junior synonyms of *Hupeidiscus* Chang in Lu *et al.*, 1974, and *Mianxiandiscus* Zhang & Zhu in Zhang *et al.*, 1980 and *Emeidiscus* to be junior synonyms of *Tsuniyidiscus* Chang, 1966. Jell (1997) further regards *Shizhudiscus*, *Guizhoudiscus*, *Hupeidiscus*, *Mianxiandiscus*, and *Emeidiscus* as junior synonyms of *Tsuniyidiscus*.

Amongst these genera, *Hupeidiscus* and *Shizhudiscus* are most closely related and distinguished largely on the basis of differences in the morphology of the pygidium (with pleural furrows or not). Zhang & Clarkson (1993) kept the synonymization open and cautiously retained *Shizhudiscus* as a valid generic name since the ontogeny of *Hupeidiscus* was poorly known. The present study shows that the ontogenetic developments of '*S.*' *longquanensis* and *H. orientalis* are quite similar, especially with respect to the development of the pygidium, suggesting that *Shizhudiscus* is a junior synonym of *Hupeidiscus*. There are, however, some differences between *H. orientalis* and '*S.*' *longquanensis*. During growth, the short genal spikes of *H. orientalis* progressively increase and develop into long fixigenal spines, whereas the short genal spikes of '*S.*' *longquanensis* become reduced and the genal angles are rounded in holaspides (no fixigenal spines). In early meraspides of '*S.*' *longquanensis*, the anterior border bears two distinct tubercles anteriorly (Zhang & Clarkson 1993), whereas the anterior border of *H. orientalis* lacks the tubercles. In contrast to the smooth holaspid pygidium of *H. orientalis*, the holaspid pygidium of '*S.*' *longquanensis* bears distinct pairs of pleural furrows. These differences show that they shall belong to two separate species.

The relationship between *Hupeidiscus* and *Tsuniyidiscus* is much unclear. The cranidium of *Tsuniyidiscus* is mainly characterized by having a row of nodes on the anterior border. The ontogeny of *Tsuniyidiscus* is not well known for lack of three-dimensionally preserved specimens. In addition, *Hupeidiscus* usually occurs in younger strata than *Tsuniyidiscus* (Steiner *et al.* 2001, Yang *et al.* 2003), and they rarely co-occur. Hence, we suggest that *Hupeidiscus* should be retained as a valid genus until more is known about the ontogeny of *Tsuniyidiscus*.

Implications for affinities of the *Mongolitubulus*-like sclerites

Mongolitubulus Missarzhevsky, 1977 was established on the basis of isolated tube (spine)-like fossils with prominent scale-like external ornamentation, and it was originally described as a protoconodont. As mentioned above, the affinities of these tube- or spine-like fossils have been controversial. Recently, *Mongolitubulus* has been tentatively considered to represent the detached spines of phosphocopiids or bradoriids (Skovsted & Peel 2001, Melnikova 2000) or lobopodians (Dzik 2003). The discovery of bradoriid specimens with *Mongolitubulus*-like spines from Australia provides definitive evidence for a bradoriid affinity for some of these spines (Topper et al. 2007).

Eodiscoid trilobites have a global distribution during early and middle Cambrian times. Phosphatized specimens show that their external skeleton surfaces are usually covered with granules. Little attention has been paid to the surface sculpture of the spines in eodiscoids since the micro-spines of crack-out specimens are usually not well preserved for examination of their ornament. The specimens obtained from acid maceration are usually three-dimensionally preserved, and enable a detailed examination of the spine ornamentation. Specimens of *H. orientalis* from southern Shaanxi illustrated herein show that the spines have a distinct scale-like sculpture, which resemble that of the *Mongolitubulus*-like spines. Generally, eodiscoids have two kinds of spines, fixigenal spines and axial (occipital and thoracic) spines. The recognition of two kinds of *Mongolitubulus* spines from the Lower Cambrian of Kazakhstan (Dzik 2003) is somewhat consistent with the two kinds of eodiscoid spines (genal and axial). The palaeogeographic and stratigraphic distribution patterns of eodiscoids and *Mongolitubulus* are fairly similar: worldwide occurrence in the lower and middle Cambrian (Zhu et al. 2004). *Mongolitubulus* spines show no evidence of incremental growth but growth following moulting (Skovsted & Peel 2001, Dzik 2003). These pieces of evidence indicate that at least some *Mongolitubulus*-like spines can represent spines of eodiscoids. An integration of prior studies and the present finding implies that morphologically similar sclerites may have essentially of multiple origins among the ecdysozoans (eodiscoids, bradoriids, other bivalved arthropods, lobopodians, etc.). These discoveries reveal that those spines with scale-like ornaments may actually be of morphologic analogues of convergent evolution, and the similarity may be just of functional significance with less value for taxonomy. Hence, *Mongolitubulus* shall be cautiously used as a generic name unless the circumstance of its type specimens from Mongolia gets clarified. Furthermore, the spines of the eodiscoids described herein preserve a wide spectrum of ornamentation patterns, indicating that the ornamentation is an unreliable feature for discriminating taxa.

Conclusions

The well preserved, phosphatized specimens of *H. orientalis* from the Shuijingtuo Formation permit us to better understand its meraspid to holaspid ontogenetic development and to study the zoological affinities of *Mongolitubulus*-like sclerites. The most distinct ontogenetic changes of *H. orientalis* occur in the morphogenesis of the transitory pygidia during the meraspid period. Seven meraspid substages (stages) (M0a, M0b, M0c, M1a, M1b, M2 and M3) can be distinguished on the basis of the progressive release of thoracic segments from the transitory pygidia and by the number of new developing rings (axial segments) in the pygidial rachis. The holaspid period (H) begins when the third thoracic segment has been liberated from the transitory pygidium. Only the anterior pair of interpleural furrows is distinct in the holaspid pygidium of *H. orientalis*.

The ontogeny of *H. orientalis* is closely comparable to that of '*S. longquanensis*' in many aspects, supporting the view that *Shizhudiscus* can be regarded as a junior synonym of *Hupeidiscus*. During ontogeny, short genal spines of *H. orientalis* progressively increase in length and develop into long fixigenal spines, whereas those of '*S. longquanensis*' become reduced and holaspides have rounded genal angles. The holaspid pygidium of *H. orientalis* is almost smooth except for the anterior pair of pleural furrows, whereas the holaspid pygidium of '*S. longquanensis*' bears distinct pairs of pleural furrows. These differences show that *H. orientalis* and '*S. longquanensis*' belong to two separate species. Since the ontogeny of *Tsuniyidiscus* is not well known, and *Hupeidiscus* usually occurs in younger strata than *Tsuniyidiscus* (Steiner et al. 2001, Yang et al. 2003), synonymization of *Hupeidiscus* with *Tsuniyidiscus* shall be cautious.

The spines of *H. orientalis* are ornamented with a distinct scale-like sculpture, which just resemble the sculpture of *Mongolitubulus*-like sclerites. The recognition of two kinds of *Mongolitubulus* spines from the Lower Cambrian of Kazakhstan is consistent with two kinds of spines of eodiscoids (genal and axial spines). The temporal and spatial distribution of both eodiscoids and *Mongolitubulus* are quite similar. *Mongolitubulus* shows no evidence of incremental growth but growth following moulting. These pieces of evidence indicate that *Mongolitubulus*-like spines may be essentially of multiple pan-arthropod origins (bradoriids, eodiscoids, etc.), and they may be of morphologic analogues rather than homologues, suggesting that *Mongolitubulus* should be cautiously used as a generic name until the circumstance of its type specimens is clarified. This study shows that some problematic sclerites of many early Cambrian small shelly fossils with a bizarre appearance may have affinities with familiar animal groups.

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