CAMBRIAN PHOSPHATIZED FOSSILS FROM SOUTHERN CHINA AND THEIR BEARING ON EARLY METAZOAN EVOLUTION

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ABSTRACT

Richly fossiliferous nodular and thin-bedded limestones of Lower and Middle Cambrian age are widespread in southern China, and contain abundant, diverse, and exceptionally well preserved fossils. By acid digestion of the limestones, numerous phosphatized shells displaying detailed three-dimensional characters have been isolated. The univalved ostracode larvae, displaying a univalved-bivalved transition, argue that univalved form may be a primitive larval character for shell-secreting crustaceans. The arthropod (possibly eodiscid trilobite) embryos with preserved blastomeres belong to two embryonic stages; the basic embryonic development of arthropods seems unchangeable with time. Cuticles of three palaeoscolecid worms display unique ornaments and body structures; their discovery reveals that wormlike organisms have achieved a high taxonomic diversity and a wide geographic distribution during the Early Cambrian. The description of redlichiid trilobite larvae and ontogenetic stages of Ichangia ichangensis Chang is of potential interests in recognizing the relationships among the oldest trilobite faunas. Morphological and fuctional analysis on especially long genal and axial spines of some rodiscids provodes key evidence to deduce their locomotion and life mode. Early instars of bradoriid ostracodes and eodiscid trilobites exhibit apparent morphological diversity, which seems to contrast with the traditional view that regards early development as conservative. However, a complex silicified sponge spicule assemblage associated with the Early Cambrian phosphatized fauna in Zhenping demonstrates that their conservative styles of body architecture were established quickly in the earliest Phanerozoic. These fossil Lagerstätten , as representatives of early skeletal metazoans, have displayed their

primitive features without 'modification' relevant to adaptive radiation's of later times. Their morphological and ontogenetic data are therefore essential in evaluating the rapid diversification of early skeletal organisms and the phylogenetic relationships among major metazoan groups.

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TABLE OF CONTENTS

CHAPTER 1

INTRODUCTION

One of the most dramatic events in the geological record is the abrupt proliferation of skeletal invertebrates at the beginning of the Cambrian. At least until the Atdabanian stage, most of the extant phyla and classes of marine metazoans, including possible Chordata, were already in place (Valentine, 1994; Chen et al, 1995; Shu et al., 1996), and the rapidity of skeletal metazoan diversification is constrained by U-Pb zircon data (Bowring et al., 1993). Associated with this evolutionary event is a global phosphogenic event (Cook and Shergold, 1984), which might have been a driving mechanism for the Cambrian explosion and the initiation of biomineralization (Cook, 1992).

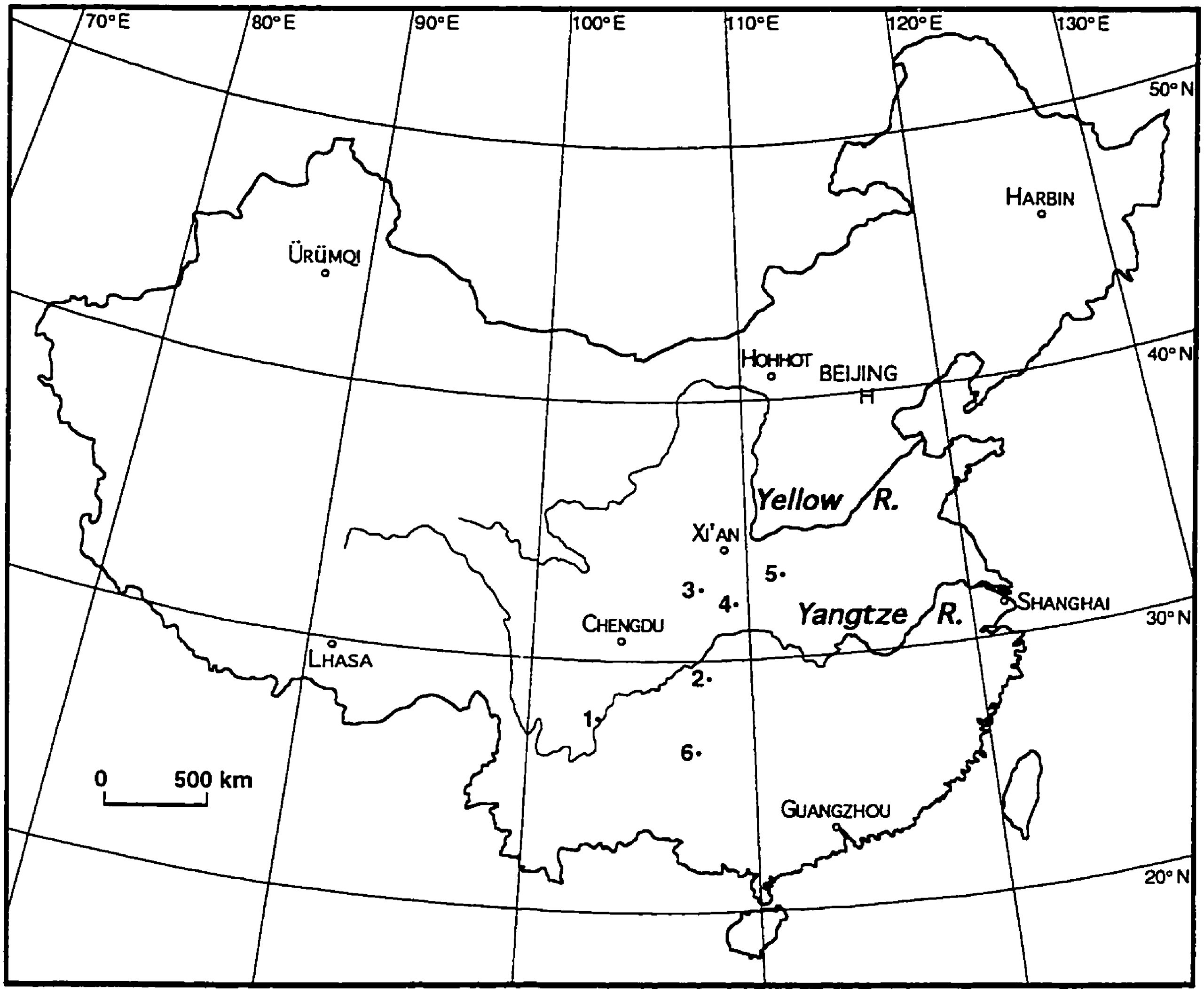
It is well known that all major skeletal materials -- calcite, magnesian calcite, aragonite, apatite and opal -- were involved in the earliest invertebrate skeletons (Runnegar and Bengtson, 1990). Some of these initial invertebrates have had their original calcite or aragonite skeletons replaced by apatite without their external morphology being affected, thus exhibiting the highest quality of preservation. Although the origin of the phosphorus content in metazoan skeletons remains poorly understood, diagenetic phosphatization occurs mainly in association with phosphate deposits in natural environments (Prévôt and Lucas, 1990). Probably for this reason, many Cambrian phosphatized fossil-bearing strata are found associated geographically with phosphate depositional sites. For instance, all phosphatized fossil-bearing sequences reported here are scattered within or nearby some well known big Cambrian phosphate ores in southern China; the Middle Cambrian Georgina Basin in Australia is also rich in both phosphate deposits and phosphatized fossils.

Historical Outline

In China, acid etching technique was not widely applied to extract Cambrian fossils until extensive studies on Precambrian/Cambrian boundary and associated small shelly fossils e.g., Jiang, 1980; Luo et al., 1984). With the search extending to younger strata, phosphatocopid ostracodes from the Lower Cambrian Shuijingtuo Formation in Shaanxi were first described by Huo and Shu (1985). As a result of subsequent extensive acid extraction, more and more Cambrian phosphatized shell-bearing invertebrates were discovered, including bradoriid ostracodes (Zhang, 1987; Cui et al., 1987; Huo et al., 1991; Shu, 1990; Zhang and Pratt, 1993), eodiscid trilobites (Zhang, 1989; Zhang and Clarkson, 1990, 1993; Zhang and Pratt, 1994b; Pratt and Zhang, 1995), onychophoran Microdictyon (Hao and Shu, 1987; Shu and Chen, 1989; Tong, 1989), worm-like palaeoscolecid sclerites (Zhang and Pratt, 1996), and many sclerites of uncertain affinities (Qian and Bengtson, 1989). In addition, silicified sponge spicules are found associated with these phosphatized fossils (Zhang and Pratt, 1994a).

Localities

The collections considered here originate from localities widespread in southern China (Text-fig. 1.1). Of the six successions, five (the Laozizhai section in Xichuan, the Longquanxi section in Pengshui, the Xiaoyang section in Zhenba, the Qingmingtian



TEXT-FIGURE 1.1. Location of six Cambrian successions in southern China where phosphatized fossils were collected for this study. 1: Jinyang, 2: Pengshui, Sichuan; 3: Zhenba, 4: Zhenping, Shaanxi; 5: Xichuan, Henan; 6: Duyun, Guizhou.

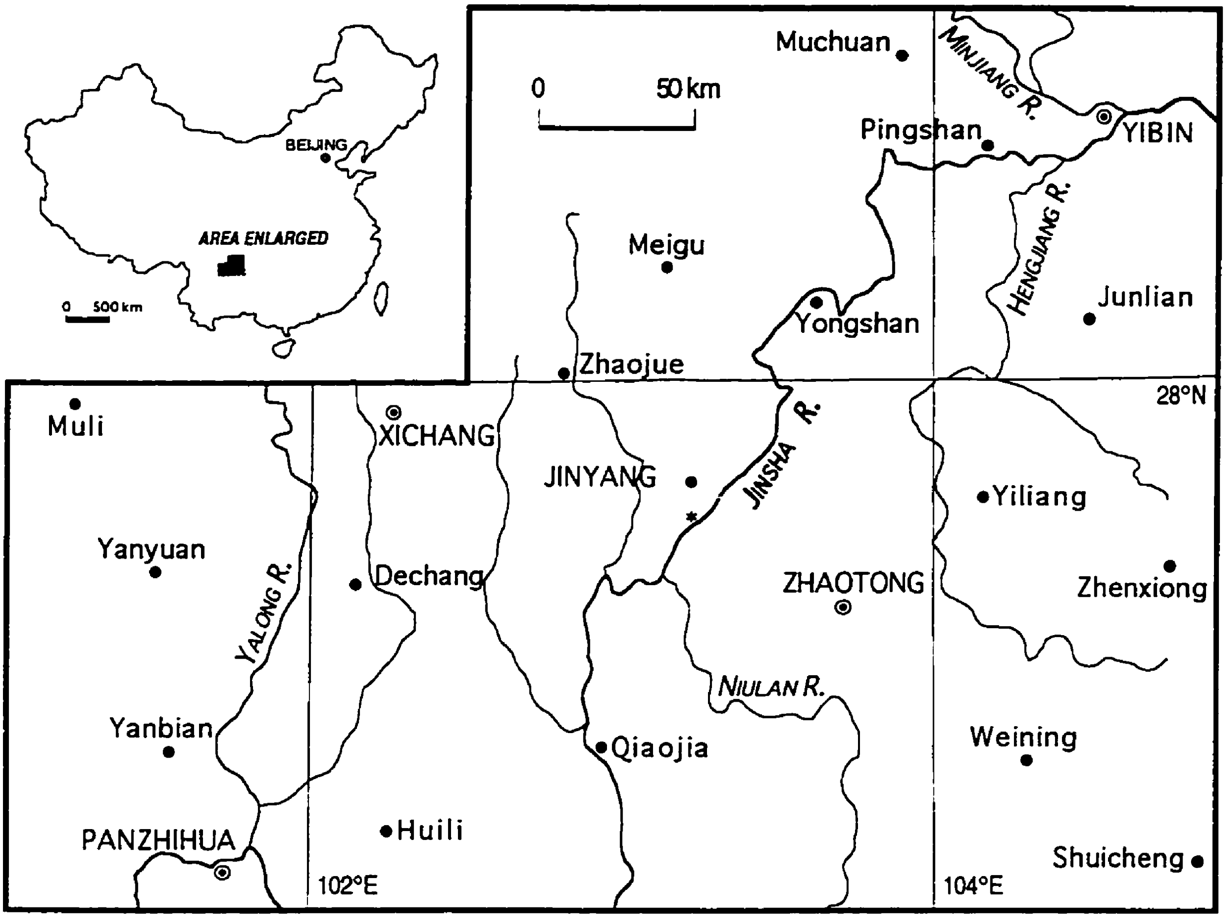
exposure in Zhenping, and the Balang section in Duyun) have been separately reported (see Zhang, 1987; Zhang and Clarkson, 1991; Shu, 1990; Zhang and Pratt, 1993, 1994b). One new locality is the Mocaowan section (27°35'N, 102°40'E) approximately 18 km south of Jinyang, Sichuan Province (Text-fig. 1.2). 74 m of Lower Cambrian Qiongzhusi Formation were measured along north bank of the Jinsha River (a local name for Yangtze River within Sichuan and Yunnan provinces). Except being metioned in an unpublished geological survey report, this section has received little attention.

Geological Setting

The four fossil assemblages from Pengshui, Zhenping, Zhenba and Jinyang come from dark grey nodular or thin-bedded limestones sandwiched between black shales of the Lower Cambrian Qiongzhusi or Shuijingtuo Formation. These strata contain some redlichiid trilobites belonging to the Lower Cambrian trilobite Eoredlichia-Wutingaspis Zone in southern China (Chang, 1980). Below this zone occurs the oldest redlichiid trilobite Parabodiella (=Abodiella), which has also been found as a pioneer trilobite in South Australia (Jell, 1990).

According to associated trilobites (see Chapter 3), the fossil assemblage in the Laozizhai section of Xichuan is somewhat younger than the four mentioned above.

The fossil assemblage in the Balang section of Duyun contains the eodiscid Pagetia (Pl. 7, figs. 6-11), and was collected from the basal part of the Middle Cambrian Gaotai Formation.

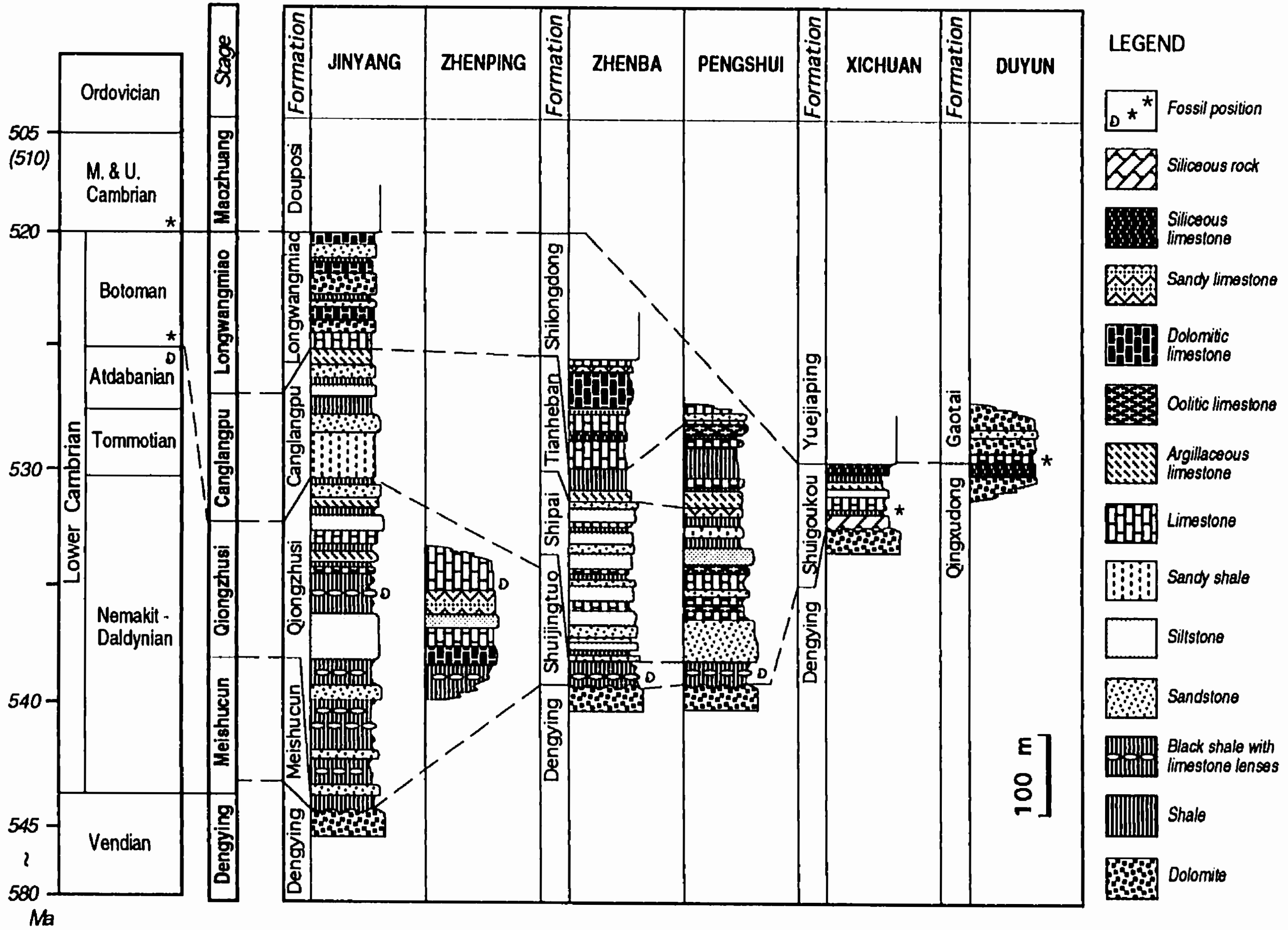


TEXT-FIGURE 1.2. Location map for the Mocaowan section (asterisk) in Jinyang, Sichuan, where bradoriid ostracodes described in this paper were collected.

The lithostratigraphy and correlation of the six Cambrian successions are given in Text-figure 1.3. The strata containing phosphatized faunal elements exhibit features suggestive of deeper water, low-energy depositional surroundings. However, their detailed sedimentology has not yet been worked out.

Because of co-occurrence with Parabodiella (Huo and Shu, 1985; Chang, 1987; Hou, 1987), bradoriid ostracodes represent another group of oldest fossil arthropods. However, many taxa of these initial bradoriids, such as Shensiella, Hanchiangella and Nanchengella, share general similarities with Kunmingella. These genera, in my opinion, are synonyms. Their assignment to separate genera is due to either flexible carapaces which were deformed to some extent when preserved in shales, or immature instars exhibiting pronounced morphological variations. Despite this unsolved taxonomic problem, it seems apparent that some kunmingellids studied in Chapters 2 and 4 are representatives of, or closely related to, the oldest fossil ostracodes hitherto known from China.

The initial trilobites are distributed worldwide but seem to belong to isolated evolutionary lineages, whose endemic taxa raise questions about international biostratigraphical correlations. To alleviate this situation, ichnofaunas of uncertain affinities were recommended to mark the base of the Lower Cambrian (Narbonne et al., 1987; Brasier et al., 1994), but I am convinced that this will turn out to be an unfortunate solution. At least for the present, even if some traces could be reliably attributed to trilobites or other metazoans, direct information regarding the type of animal responsible for a given trackway or burrow mostly remains speculative. It becomes increasely evident that the first appearance of



TEXT-FIGURE 1.3. Lithostratigraphy and correlation of the six Cambrian successions in southern China. The geochronological time scale after Bowring et al. (1993).

Cambrian skeletal invertebrates is diachronous (Brasier et al., 1997). Likewise, the ichnofossils left by even earlier metazoans might be diachronous as well. It seems doubtful that these never-to-be determined animals can provide more precise biostratigraphic control. There are no correlations between the Chinese sequences and the global stratotype section in Newfoundland. However, because the Cambrian trilobite assemblages found in Australia are comparable to those in both southern China and Siberia (Bengtson et al., 1990), fossils in this study from the Eoredlichia Zone are best considered to be late Atdabanian and early Botoman in age.

Material and Methods

Fossiliferous nodular or thin-bedded limestones were dissolved in 5% acetic acid, which is replaced at intervals of one or two days, when insoluble residues are carefully collected. Testing indicates that long-term etching (even with very dilute acid) may cause damage of certain delicate parts of shells that are only partially phosphatized.

In order to mount tiny specimens that need to be subsequently removed and turned over for additional SEM photography of the reverse side, dilute glue solution is prepared by dissolving about 10 cm SCOTCH double sided tape in 2 ml of the organic solvent xylene in a vial. After the evaporation of xylene from the solution which has been evenly brushed on the surface of an aluminium stub, the remaining film of glue is very thin but sticky. Meanwhile, the fixed specimen can be easily picked up after the film is dissolved by a drop of xylene. This procedure is only applicable to minute specimens: the bigger the sample, the thicker the glue film should be, by brushing the solution twice. For big and heavy specimens, double-coated tape is used directly.

Because of the advantage of the SEM photographs in depth of field, an oblique view can vividly show a three-dimensional sample well, and has been adapted in many fossil photographic illustrations, instead of traditionally supplying both dorsal and anterior (or lateral) views.

Phosphatization and Preservation

Phosphatized specimens obtained from etched residues have three apparent advantages: First, they are mostly preserved displaying detailed three-dimensional morphological features on both exterior and interior of their shells, which provide more taxonomic credence to fossil identification. Secondly, numerous isolated skeletal remains representing different growth stages (including tiny larvae) from a single species enable precise measurement and a thorough understanding of its morphological variation through ontogeny. Lastly, phosphatized fossil assemblages also show taxonomic variation with geological time and with geographical distribution within the particular paleoenvironments conducive to their preservation.

Nevertheless, such excellently preserved fossils are rare; not all skeletal animals buried in a horizon within a phosphate-rich region are phosphatized. For instance, phosphatized sclerites of the eodiscid trilobite Tsunyidiscus are abundant in the Lower Cambrian Shuijingtuo Formation in the Xiaoyang section, Zhenba, but sclerites of Tsunyidiscus collected from the same interval in the Maoergou section, Xixiang, about 160 km northeast of Zhenba (see Shu, 1990a), are still calcite. This is why for a long time nobody working in this area had discovered the phosphatized Lagerstätten even though lots of fossils, including phosphatized ones visible on hand-specimens, were collected. Locally, eodiscid trilobites and bradoriid ostracodes with phosphatized skeletons occur together with calcite redlichiid trilobites which appear to be chemically resistant to diagenesis, while the eodiscids or bradoriids obtained phosphate through the phosphatization process. This phenomenon indicates selective phosphatization, which was most likely related to primary differences in the nature of the exoskeletons.

Recent investigation shows that some originally phosphatic fossil skeletons (i.e. lingulate brachiopods and small shelly fossils) of the Chengjiang fauna no longer retain their phosphate, whereas bradoriid ostracodes still contain high phosphorus composition (Leslie et al., 1996). Observation of this fossil Lagerstätte suggests that many of these exceptionally preserved organisms are actually only thin layers or impressions, most of their original material having disappeared. Electron microprobe WDS (wavelength-dispersive spectrometer) analysis indicates that some Cambrian ostracode carapaces are multilamellar, of which only one or two lamellae were phosphatized. This may be another example of selective phosphatization. Further geochemical investigations on these Cambrian fossil assemblages will enlarge our understanding of Cambrian skeletal phosphatization.

Faunal Associations

These phosphatized fossils provide insights into the composition of Lower and Middle Cambrian benthic communities in relatively deep, low-energy environments. As an example, the four Lower Cambrian Qiongzhusian assemblages (see Table 1.1) are characterized by:

(1) Each assemblage contains either Eoredlichia or Zhenbaspis, trilobites typical of the Eoredlichia-Wutingaspis Zone, from which approximate contemporaneity can be inferred. However, these redlichiids are still all calcite.

(2) Eodiscid trilobite exoskeletons are dominant in fossil assemblages from Pengshui and Zhenba, and buried with many lingulate brachiopods and bradoriid ostracodes, a few small shelly fossils, and rare hexactine and pentactine sponge spicules. However, in Zhenping and Jinyang, bradoriid ostracodes are the dominant element, whereas no eodiscids have been found.

(3) Trilobite assemblages from Zhenba and Pengshui contain some seemingly endemic genera, such as Shizhudiscus and Tsunyidiscus, but share no common species. The specimens in the Zhenba collections are left under open nomenclature, but they are certainly not conspecific with those from Pengshui. Most bradoriid ostracodes appear to be endemic species too, except the widely distributed phosphatocopid Dabashanella. That genus may include some cosmopolitan species, but the extreme simplicity of their shells hinders a convincing taxonomy.

			JINYANG Mocaowan Section	ZHENPING Qingmingtian Section	ZHENBA Xiaoyang Section	PENGSHUI Longquanxi Section
QIONGZHUSIAN, LOWER CAMBRIAN	*Eoredlichia-Wutingaspis* Zone	Trilobites	*Eoredlichia intermedia*	*Eoredlichia intermedia* *Eoredlichia zhenpingensis*	*Eoredlichia angusta* *Zhenbaspis lata* *Shizhudiscus* sp. *Tsunyidiscus* sp. *Guizhoudiscus hepingensis*	*Zhenbaspis similis* *Shizhudiscus longquanensis* *Tsunyidiscus tuberculata*
		Ostracodes	*Kunmingella douvillei* *Kunmingella typica* *Dabashanella* sp. *Kunyangella dactylica* *Prealutella minuta*	*Tsunyiella zhenpingensis* *Jixinlingella clithrocosta* *Zhenpingella steatocula* *Eoduibianella reticula* *Spinella blackwelderi* *Retialuta rara*	*Kunmingella bulbosa* *Houlongdongella elevata* *Dabashanella retroswinga*	*Tsunyiella luna* *Houlongdongella elevata* *Dabashanella retroswinga* *Beyrichona longquanensis*
		Other fossils	*Obolus* sp. *Microdictyon* sp. *Protospongia* sp. Pentactine, hexactine *Rhombocoruiculum* sp.	*Obolus* sp. *Microdictyon* sp. various sponge spicules Palaeoscolecidae *Lapworthella* sp.	*Obolus* sp. *Microdictyon anus* Pentactine *Hyolithes* sp.	*Lingulella* sp. *Microdictyon* sp. *Protospongia* sp. *Hyolithes* sp.

TABLE 1.1. Phosphatized faunal association of four Lower Cambrian sections from southern China.

(4) The eodiscids and bradoriids tend to form some subzones within the Eoredlichia-Wutingaspis Zone. These subzones may contain only one eodiscid or bradoriid species, which in most cases does not extend to other adjacent subzones.

(5) Small shelly fossils are common in the phosphatized assemblages as survivors of their once highly diversified ancestors. They never comprise the majority of skeletal elements recovered. Net-like sclerites of Microdictyon are widely found in the Lower Cambrian of southern China, but variation in their morphology suggests that species composition differs from place to place. The assemblages also contain some problematic taxa that have not been studied.

CHAPTER 2

CAMBRIAN FOSSIL LARVAE AND EARLY METAZOAN EVOLUTION

Abstract

With exceptionally well-preserved larvae and diverse early instars, phosphatized eodiscid trilobites and bradoriid ostracodes from the Lower Cambrian of southern China exhibit their ontogenetic sequences in detail. These extraordinary fossils, as representatives of early skeletal metazoans, have displayed their primitive features without 'modification' relevant to adaptive radiations during later times. Their ontogenetic data should therefore bear crucial criteria for evaluating their own early evolutionary diversification -- a new approach to the phylogeny of some major clades of Arthropoda. An undescribed new genus and species of eodiscid trilobite with especially strong genal and axial spines and relatively small librigenae may relate to a floating mode of life. A consideration of its functional morphology suggests that such eodiscids may have adopted jet locomotion for escaping from predators, a specialized adaptation that may be reasonable in light of the ecologically complex surroundings in the Early Cambrian.

Larval Diversity

Early instars of bradoriid ostracodes

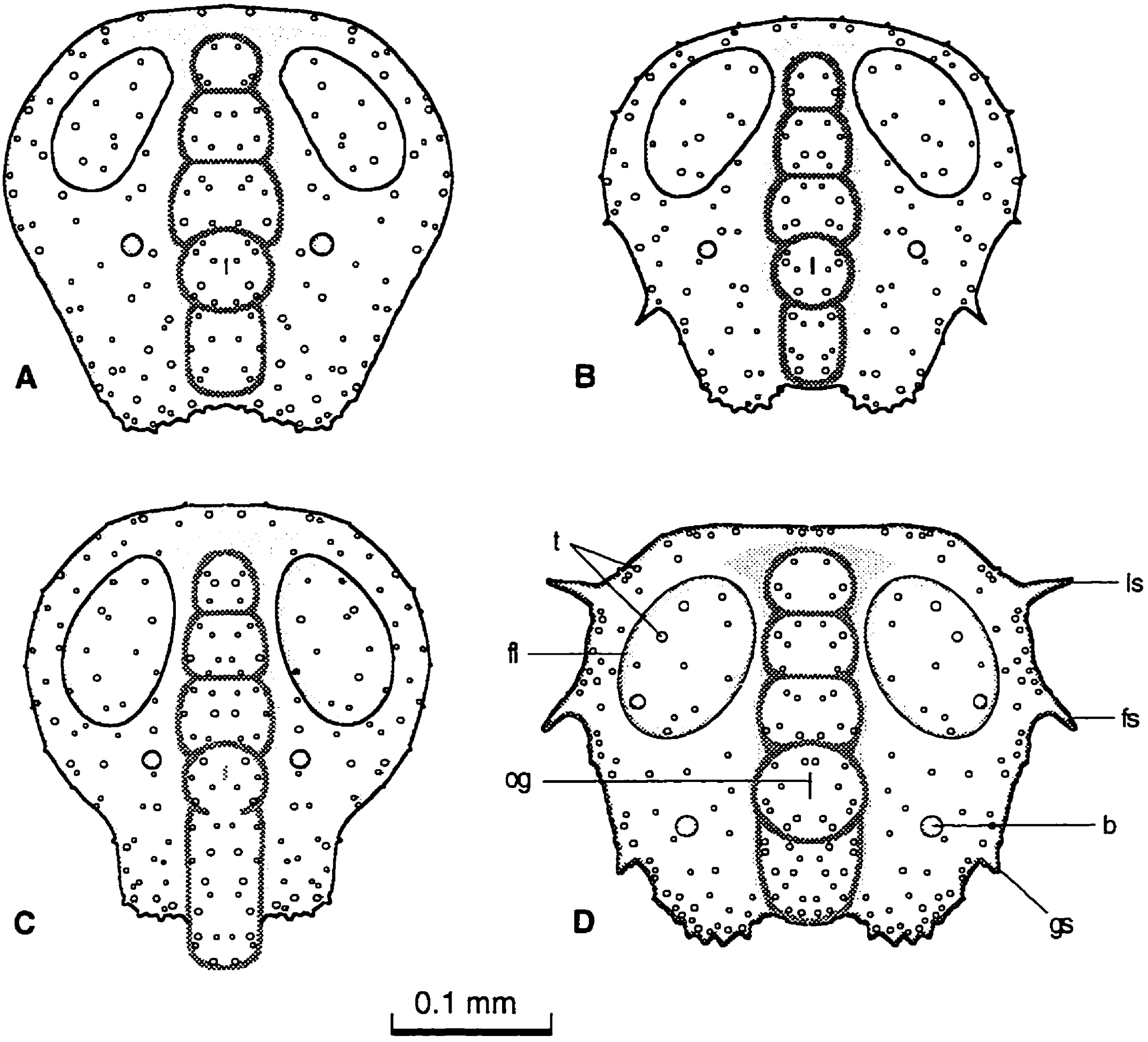
Usually, the ontogenetically younger the larvae of closely related taxa, the more similar in morphology are their body plans. This seems the case for some bradoriid ostracodes whose early developmental phases are known. The univalved carapaces of *Duibianella* sp. and *Kunmingella douvillei* (Mansuy 1912) show rough similarities (Pl. 1, figs. 1-7; Pl. 3, figs. 1-3). However, their subsequent instars are gradually marked by their own specialized features (Pl. 1, figs. 8, 9; Pl. 2, figs. 1-15; Pl. 3, figs. 4-12; Pl. 4, figs. 1-18). *Kunmingella* (*Spinokunmingella*) *typica* Huo and Shu, is characterized by its especially long ventral spine. Although no univalved carapace of this species has been found, the smallest bivalved one (Pl. 5, fig. 1) bears similar fine reticulate ornament and narrow marginal rim that are seen on both the univalved and the smallest bivalved carapaces of *K. douvillei*. Because of incomplete preservation, the paired posterior spines are missing on the smallest bivalved carapace of *K.* (*S.*) *typica*, but are well preserved among somewhat bigger ones of later instars (Pl. 5, figs. 2, 3). There are further more distinct characters shared by the early instars of *K. douvillei* and *K.* (*S.*) *typica*: anterior node, posterior lobe, paired dorsal gland (or sensory hair) openings (Pl. 3, figs. 1, 5, 8, 12; Pl. 4, figs. 17, 18; Pl. 5, figs. 4, 15; Pl. 6, fig. 13), and possible muscle scar (Pl. 3, figs. 8, 11; Pl. 5, figs. 4, 7, 15). In general, the young instars of both species keep a resemblance to each other until the posterior lobe displays prominent differentiation: the lobe is always as an elevated ridge in *K. douvillei* (Pl. 4, figs. 4-8, 15), but becomes a strong ventral spine in *K.* (*s.*) *typica* (Pl. 6, figs. 1-13).

Kunmingella (*Spinokunmingella*) *typica* geologically existed earlier than *K. douvillei*; both kunmingellids define two mutually exclusive subzones within the *Eoredlichia-Wutingaspis* Zone. That is, *K. douvillei* has not been found co-existing with *K.* (*S.*) *typica*.

The presence and absence of both kunmingellids in the strata seem unlikely related to selective preservation, but indicate a relatively short time span for the existence of either kunmingellid species.

Diverse eodiscid trilobite larvae

Because of their relatively small adults, eodiscid trilobites comprise the smallest protaspides (<0.2 mm). Like other known protaspides, the single shield of eodiscid larvae bears no articulating joints, but the basic traits of its protocephalon and protopygidium are distinct. These early instars are similar to each other, in having pear-shaped outline, paired elevated fixigenal lobes, paired bacculae, three glabellar lobes, dome-like occipital ring with a occipital gap, and net-like prosopon of fine ridges and tubercles. Juvenile and adult features clearly unite the Eodiscidae. On the other hand, the eodiscid protaspides in my collections display striking variation that was never reported from previous studies. For example, protaspides of Tsunyidiscus sp. (Pl. 7, figs. 4, 5) and T. longispinus S. G. Zhang (Text-fig. 2.4B; Pl. 9, figs. 1, 2) bear paired lateral genal spines; the paired spines are more prominent on the protaspis of an unidentified eodiscid (Text-fig. 2.4D; Pl. 11, figs. 1-3), but seem absent among protaspides of Neocobboldia chilinensis Lee (Text-fig. 2.4A; Pl. 7, figs. 1, 2). In addition, the long spine-bearing, new eodiscid genus and species (Text-fig. 2.4C; Pl. 10, fig. 1) displays a unique elevated protopygidial axis, which may contain the embryonic occipital and axial spines. The major morphological variations among these eodiscid trilobites seem to arise abruptly in the larval phase. This obviously



TEXT-FIGURE 2.1. Various eodiscid trilobite larvae (protaspides) from the Lower Cambrian in southern China. A, Neocobboldia chinlinica Lee. B, Tsunyidiscus longispinus S. G. Zhang. C, eodiscid new genus and species with especially long genal and axial spines. D, eodiscid new genus and species with three paired genal spines. b: baccula, fl: fixigenal lobe, fs: fixigenal spine, gs: genal spine, ls: librigenal spine, og: occipital gap, and t: tubercle.

contrasts with the traditional evolutionary view that regards early development as conservative. Presumably, eodiscids may have developed through a series of embryonic stages, either prior to hatching or as 'pre-protaspides' without calcified exoskeletons. Perhaps only these early instars displayed close morphological similarities.

In tending to form subzones within the Eoredlichia-Wutingaspis Zone as previously noted, the striking replacement of some eodiscid and bradoriid taxa within the upper Atdabanian, an interval that lasted only a few million years (Bowring et al., 1993) argues that these early arthropods existed for relatively short periods. The rapid diversification of such early skeletal arthropods seems to have duplicated the rapid turnover rates of Cambrian polymeroid trilobites in general (Foote, 1988).

With numerous well preserved skeletons representing various growth stages of eodiscid trilobites, ostracodes, and lingulate brachiopods, certain parameters such as growth ratio and variation in geometry (Alberch et al., 1979; Kluge, 1988) can be quantitatively worked out. A comparison of the ontogenetic data derived from eodiscid trilobites and other trilobites of later times, along with the growth rate of coeval lingulate brachiopods as well as their modern representatives may reveal what the rapid evolution means. However, this is a significant but time-consuming task awaits future fulfilment.

Ontogeny Data and Phylogenetic Divergence

Preserved appendages of Kunmingella maotianshanensis Huo and Shu, 1983 from the Chengjiang Lagerstätte raise more problems about the systematic position of

Bradoriida, which were recently regarded as neither being Ostracoda, nor closely related to Phosphatocopida (Hou et al., 1996). Morphological variation (including arrangement) in arthropod appendages is often interpreted as adaptive innovation, which may simply reflect phylogenetic divergence. Therefore, appendages have been successfully used for classification of modern ostracodes. On the other hand, ostracode appendages appear to be an easy part to be modified, and appendages of modern ostracodes should have undergone a series of serious changes in morphology through time. Not surprisingly, younger ostracodes possess quite different appendages as compared with older ones, particularly with their Cambrian ancestors. According to cladistics, an ancestor belongs within a larger, paraphyletic group, and only symplesiomorphies (shared primitive characters) can reveal the phylogenetic links among clades of the paraphyletic group. Certain derived characters (synapomorphies) defined descendant ostracodes must be totally missing in their ancestors (Paul, 1992; Smith, 1994). Differentiations in appendages in this case mean nothing in recognizing their ancestry. There is no biological or cladistic reason to believe that the arrangement of the cephalic appendages is the only reliable character available for fossil arthropod classification, and this confusion of logic leads to more difficulties in phylogenetic analysis of ostracodes and arthropods in general.

Examination of numerous crustaceans, including embryos and larvae, has demonstrated that cephalic carapace folds may never develop among some major crustacean groups, and the carapaces carried by various other crustaceans are heterogeneous (Dahl, 1991). There is little doubt that the multi-origin of cephalic carapace folds of modern crustaceans recorded by embryos and larvae resulted from divergent evolution, which is likely to have been rampant even in strongly divergent lineages. Each modern clade is therefore a unique combination of historical constraints and adaptive innovations. Comparative biological study has provided infinitely detailed morphological evidence, which is critical in extant arthropod taxanomy but of limited potential in the rooting of the arthropod cladogram. Natural processes are often so complex to defy complete, rigorous treatment. Our poor knowledge about the variability of arthropod Baupläne through time prevents us from recognizing their very early ancestors.

Nevertheless, it is the initial divergence of biota that has defined high-level classification based theoretically on cladistics. Thus, fossils, particularly oldest ones, are crucial to understanding the sequences of early divergence. In addition, initial shelly fossils also display some of the most primitive characters we can employ for cladistic analysis. The rapid proliferation of skeletal organisms representing major invertebrate groups approximately co-occurred with the beginnings of biomineralization. The variation shown by ontogenetic processes of Early Cambrian metazoans should reflect the initial innovation and diversification of shelly metazoans. In other words, these Early Cambrian representatives, merely constrained by their previous history without extensive morphological diversity resulting from adaptive radiations during later times, should contain unique information concerning the relations among major Cambrian invertebrate groups. This approach, reliant as it is on available Cambrian fossils and their ontogenetic processes, has received relatively little attention. Recently, molecular sequence data suggest a long evolutionary history of metazoans preceding the Cambrian (Runnegar, 1982; Wray et al., 1996). This phylogenetic hypothesis also emphasizes the initial metazoan diversification beyond fossil evidence, because Precambrian animals might lack the shells and exoskeletons, or they might have existed as microscopic organisms (Davidson et al., 1995; Wray et al., 1996).

Somewhat like the univalved larvae of Early Cambrian ostracodes (Zhang and Pratt, 1993) are the phaselus (Fortey and Morris, 1978) and the ontogenetically younger trilobite exoskeletons (protaspides), and similar single shields have also been found from some Upper Cambrian <u>orsten</u> arthropods (Müller and Walossek, 1986; Walossek, 1993; Walossek and Müller, 1990). These larval shields of Early Cambrian arthropods should bear features of direct and critical phylogenetic meaning. Although there is no mechanistic justification for Haeckel's recapitulation theory in its pure sense, it has a measure of truth in it. By means of symplesiomorphies we can trace back from a modern clade to its fossil ancestors, or vice versa. However, as this attempt is usually hindered by an incomplete fossil record, ontogeny can supply decisive information. Previous ontogeny studies have demonstrated how sagittally articulated carapaces of bradoriids and transversely segmentary tergites of trilobites were formed. Because the univalved carapace of bradoriids is comparable to that of the crustacean nauplius, the univalved instar, as a symplesiomorphy, would infer a common ancestor for bradoriids and coeval crustaceans. Nevertheless, it remains obscure how far back in geological time the single-shield ancestor would go: around, or deeply beyond, the Precambrian/Cambrian boundary? Trilobites also originated from a single shield with a cephalon of fused anterior segments, but during subsequent development, their transversely articulated tergites would arise with the segmentation of the soft body. Nauplius and nauplius-like larvae of crustaceans and bradoriids display fused anterior segments, but the subsequent segmentation of the abdomen is always achieved without recognizable effects on their carapaces. This ontogenetic difference in early arthropods highlights derived characters and tends to infer a unique common ancestor for bradoriids and crustaceans. The ancestor most likely existed in the Precambrian, and the bradoriids should be a branch of Crustacea instead of an isolated arthropod group as Hou et al. (1996) suggested.

Podocopid ostracodes have a long geological range from Ordovician to Recent, but the earliest representatives have been identified merely on carapace morphology. Without fossil evidence, little is known about whether the appendages of the Recent podocopids are similar to their putative, direct Ordovician ancestors, or the latter turn out to be comparable to Cambrian ancestors and/or other closely related crustacean clades. Nevertheless, more characters recognized from phosphatized bradoriid carapaces may yield important taxonomic criteria, which might favour a true ostracode relationship. For instance, all bradoriids in my collection possess possible muscle scars except for phosphatocopids whose smooth carapaces are too structurally simple to record the presumed scar. A distinct duplicature is always found along the free margin in bivalved carapaces of various taxa. Fine dorsal gland (or sensory hair) openings, which are comparable to the crustacean dorsal organ (Martin and Laverack, 1992), have been well preserved in a few kunmingellids. Of the various ornaments on the outer surface of carapaces, some are very complex, resembling those of ostracodes of later times. Although ornamentation is too unstable within populations to apply to phylogenetic analysis, the appearance of ostracode-style ornaments among Early Cambrian bradoriids presents another puzzle to us. These bradoriid carapace morphological characters appear to be diagnosable traits among some Ordovician ostracodes, which may indicate a closer relationship with bradoriids rather than other post-Cambrian ostracode groups.

Eodiscid Trilobites and Jet Swimming

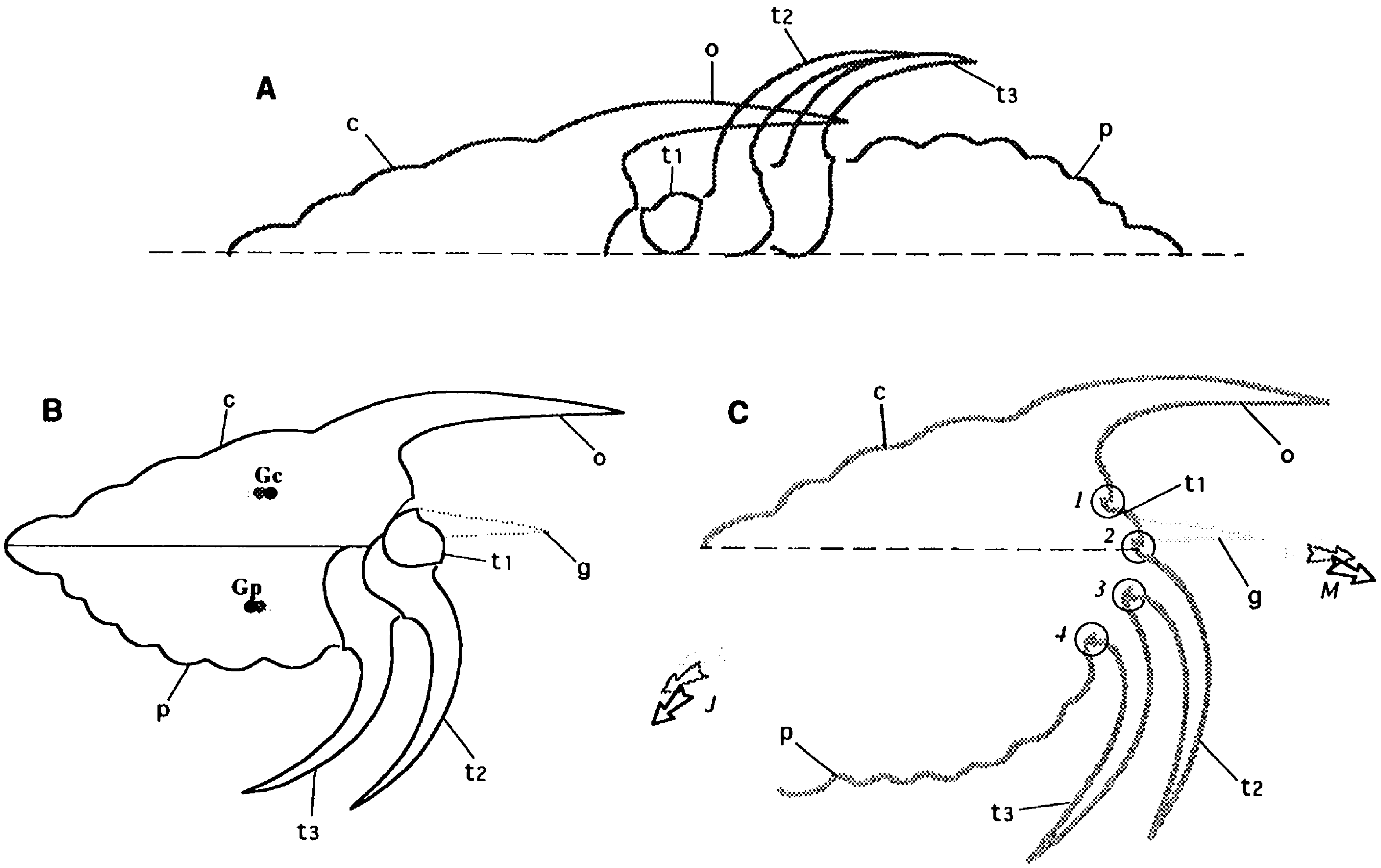
Long spines and enrolment

Trilobites bear various spines, whose functions are evaluated on the basis of the trilobite body plans and relevant life habits. For example, genal and occipital spines of the Silurian odontopleurids are believed to function as protection, and their thoracic spines probably also as stabilizers (Clarkson, 1969). Fine spines of tiny trilobite protaspides were assumed to have been relevant to movement, buoyancy and sensory perception (Speyer and Chatterton, 1989). The genal and ophthalmic spines of horseshoe crab Euproops danae were interpreted as adapting for steady fall during passive settling away from predators (Fisher, 1977). The body plan of long spine-bearing eodiscids is roughly comparable to that of E. danae except for its small size, although this does not preclude the possibility that eodiscids were also adapted to such a passive manner of protection. In addition, tubular external spines of the Jurassic brachiopod Acanthothiris were suggested to have played a role as an 'early warning' system (Rudwick, 1965). All long genal and axial spines of eodiscid trilobites are hollow, but it also needs further evidence to confirm the 'early warning' protection or sensory perception for these structures.

Enrolled agnostid and eodiscid trilobites are relatively common, and it is generally accepted that enrolment of their exoskeletons served for protection. The agnostid trilobite Agnostus pisiformis Wahlenberg is believed to have exhibited adaptation for half-enrollment by keeping a gap between cephalon and pygidium when feeding or swimming (Müller and Wallossek 1987). Eodiscids may have adopted the same mode of life because they exhibit a similar body plan. Moreover, some early meraspides of eodiscid trilobites have fully developed occipital, thoracic, and pygidial axial spines (Pl. 8, figs. 1-7; Pl. 10, figs. 2-4), which may interfer with each other and prevent the whole body from stretching straight out (Text-fig. 2.5A), even since the segmentation of the trilobite tergite.

Morphology and locomotion

Predation has been assumed an essential factor controlling the evolution of animal skeletons (Vermeij, 1990; Bengtson and Zhao, 1992). However, mineralized skeletons would not always gain advantage, because skeletons might become clumsy for some vagile organisms, hindering escape movement. Jet swimming is well known among cephalopods and scallops for evading their predators. By shutting its half-enrolled shell, an eodiscid or agnostid trilobite would be propelled in a direction opposite to the gap from



TEXT-FIGURE 2.2. Sagittal sections of an eodiscid trilobite with long spines. A, an impossible situation of an outstreched exoskeleton. B, exoskeleton enrolled; C, in swimming position. Arrow J indicates the direction of water pushed out when cephalon and pygidium are 'clapped' together. Arrow M indicates the direction of the movement of the eodiscid trilobite. c: cephalon; g: genal spine; o: occipital spine; p: pygidium; t1-t3: 1st-3rd thoracic segments; 1-4: 1st-4th articulating joints (circled); Gc, Gp: shifting centres of gravity of cephalon and pygidium.

which the water ejected. The more abruptly the shutting, the quicker the movement. Possibly, some agnostid and eodiscid trilobites may have achieved quick, spasmodic and 'bouncing' movement through the use of jet propusion.

The mode of locomotion of any swimming animal is constrained by its size and architecture. For young eodiscid instars (protaspides and early meraspides), they are most likely to rely on passive buoyancy because of their tiny bodies. These eodiscid larvae could also have move independently through water or stay suspended like the crustacean nauplius and many other planktonic larvae of marine invertebrates (Chia et al., 1984), when their appendages and antennules were used for locomotion (Gauld, 1959).

The essential requisite for jet swimming is a body form which is sufficiently deformable to take in a considerable amount of water and then expell it outside (Trueman, 1975). With growth, both cephalon and pygidium of an eodiscid trilobite became markedly more convex, favouring not only the growing soft body, but also a potentially larger volume of water intake.

Some eodiscids, such as Shizudiscus longquanensis S. G. Zhang and Zhu (Pl. 8, figs. 1-7), Tsunyidiscus sp. (Pl. 8, figs. 8-13), and eodiscid new genus and species (Pl. 10, figs. 2-10), had extremely long spines since the early meraspid instars, and the elongation of these spines with growth would have drastically changed the centre of gravity of the whole body. There are two corresponding effects:

(1) The two backward-curving axial spines on the pygidium would somewhat lower the centre of gravity of the whole body, perhaps providing stablization for swimming.

(2) With elongation of long spines on both cephalon and pygidium, the centre of gravity of each shield would shift. As a result, the new centre of gravity either in the cephalon or in the pygidium would be a negative force in shutting the shell but a positive one for the opening (Text-fig. 2.5B). That is, the anterior margin of the cephalon would go faster than the corresponding edge of the pygidium. Thus, the body's free margins would close around the articulate joint until a complete shutting of the articulated exoskeleton. In this way, the animal would propelled 'backwards' along a curved line because the water pressed out of the shell is always changing its direction (Text-fig. 2.5C). Some enrolled individuals clearly show a small gap at the extreme of the pygidium (Pl. 9, figs. 8, 9, 13), which would result in a slightly downwards ejection when water is pushed out. Correspondingly, the angled current would also affect the body's movement. Although we cannot exactly describe the jet swimming, it is most likely that the eodiscid trilobite might be propelled along an irregular, 'bouncing' rather than a straight path -- a significant escape movement.

Like other previously known spiny trilobites, the long genal and axial spines of eodiscid trilobites, may have also acted basically as protection, as well as buoyancy and sensory perception while adapted to a floating mode of life. In addition, the forward-pointing occipital and paired genal spines may provide further protection, when the animal is propelled by shutting its shields, not away from but towards the predator.

Cephalic suture and ecdysis

The relatively small librigena of eodiscid new genus and species outlines its poorly developed facial suture, which, in general, conforms to proparian pattern (Pl. 10, figs. 2, 4). From some fragments of holaspid cephala, it is seen that the librigena remains small with growth, and the suture on the ventral side goes underneath the genal angle and along the posterior margin (Pl. 10, figs. 8, 9). If the cephalic suture of the new eodiscid functioned in ecdysis as that of most other trilobites, what are the special functional features relevant to the small librigena and short facial suture? Agnostids and some eodiscids are believed to have been blind, because of the lack of convincing visual structures or cephalic suture. Is there any link between the poorly developed librigena of the new eodiscid and its absence in other blind trilobites which lack a facial suture, or just have it along the margin or virtually on the ventral side? Or this is merely some sort of a specialized adaptation for a planktonic mode of life. Perhaps, because the acquisition of dorsal and genal spines is likely related to a floating mode of life, the small librigena with poorly developed compound eyes may also be a corresponding adaptation to this life style.

Systematic Paleontology

The terms used here generally follow Harrington (1959), Edgecombe et al., (1988), Speyer and Chatterton (1989), and Fortey (1990).

Specimens used for this study are deposited at the Chengdu Institute of Geology and Mineral Resources.

Class Trilobita Walch, 1771

Order Agnostida Kobayashi, 1935

Suborder Eodiscina Kobayashi, 1939

Family Eodiscidae Raymond, 1913

New genus

Diagnosis.--A genus of Eodiscidae with gently convex cephalon. Glabella narrow, conical, defined by shallow axial furrow. Librigena very small, crescent-shaped. Occipital spine long, slightly curved ventrally. Genal angle curved with genal spine fixed to lateral border. Three thoracic segments, posterior two bearing extremely long axial spine.

Discussion.--This new genus and species, with extremely long axial spines and very small librigena, are unique among known eodiscid trilobites.

New genus and new species

Pl. 10, figs. 1-10

Material.--Two protaspides, two meraspid cranidia, eight incomplete holaspid cranidia, five meraspid pygidia and four meraspid-holaspid thoracic segments. Without a complete holaspis, the generic diagnosis is based mainly on holaspid fragments and meraspides.

Occurrence.--Eoredlichia-Wutingaspis Zone of the Lower Cambrian Shuijingtuo Formation in Pengshui, Sichuan, China.

Protaspid Period

Stage 0 (Pl. 10, fig. 1, Text-fig. 2-4C)

Material.--Two complete protaspides.

Description.--Exoskeleton ovoid in outline, gently convex, tapering slightly rearwards, 0.19 mm long and 0.18 mm wide, flexed ventrally. Rear part of protopygidium sagittally strongly convex. Axis conical and depressed anteriorly but strongly inflated behind occipital ring. Axial furrow and three transglabellar furrows shallow; protopygidial axis lacking axial furrows. Prosopon of fine ridges and granules.

Discussion.--The protaspis of this new genus and new species is distinguishable from any known eodiscid protaspides by it prominently elevated protopygidial axis and the way the protopygidium coils ventrally.

Meraspid Period

Stage 0 (Pl. 10, figs. 2, 3)

Material.--One cranidium and two pygidia.

Description.--Cranidium subquadrate in outline, 0.35-0.40 mm long (excluding occipital spine), 0.37-0.43 mm wide. Anterior margin almost transverse; posterior margin transverse. Glabella conical, narrow, defined by shallow axial furrows. Palpebral lobe weakly defined. Occipital furrow and three transglabellar furrows very shallow. Occipital spine very strong, long, curved slightly ventrally. Sinus on lateral margin of cranidium conforming to very small librigena. Pygidium wide, bilobate with broad median indentation and curved posterolateral margin. Pygidial axis with three axial rings: the second, as well as terminal piece, bearing long spine. Pleura gently convex, pleural and interpleural furrows invisible.

Stage 1 (Pl. 10, fig. 4)

Material.--One cranidium.

Description.--Cranidium gently convex, semicircular in outline. Glabella conical, weakly elevated, defined by shallow axial furrows. Librigena small, crescent-shaped. Palpebral lobe weakly defined. Occipital spine very strong. Genal spine short; posterior margin curving anteriorly.

Stage 2 (Pl. 10, figs. 5, 6)

Material.-- Two transitory pygidia.

Description.--Transitory pygidium moderately convex, semicircular in outline. Border and doublure narrow, border furrow wide, shallow. Pleural or interpleural furrows absent. Pygidial axis elevated, bearing long axial spine.

Holaspides (Pl. 10, figs. 7-10)

Material.--Eight incomplete cranidia and four thoracic segments.

Description.--Cranidium convex, semicircular in outline (?). Glabella defined by shallow axial furrows; occipital spine long. Genal spine slightly curved, lengthening with growth. Librigena small, crescent-shaped. Posterior margin curving anteriorly. Three thoracic segments with shallow pleural furrows; each of two posterior ones bearing long, slightly curved axial spine.

Discussion.--The holaspis of this new genus and new species is characterised by its extremely small librigena and long axial and genal spines.

CHAPTER 3

EARLY CAMBRIAN TRILOBITE LARVAE AND ONTOGENY OF ICHANGIA ICHANGENSIS (REDLICHIIDA) FROM HENAN, CHINA[1]

ABSTRACT--The Lower Cambrian Shuigoukou Formation of Xichuan, Henan province, China, yielded phosphatized instars belonging to the redlichiid species Ichangia ichangensis Chang and two undetermined, but probably also redlichiid, taxa. With relatively simple body plans, the three larval forms resemble to each other to some extent, and protaspides of I. ichangensis show general similarities to those of the redlichiid Palaeolenus lantenoisi Mansuy. However, their early ontogenetic processes exhibit subtle yet distinct taxonomical differences. One group of unassigned protaspides possesses a sagittal glabellar furrow and protopygidial spines with branching extremities. The other unassigned protaspides bear especially long genal and protopygidial spines. The detailed preservation of these trilobite larvae reveals delicate structural variations that help provide a framework for evaluating relationships among Early Cambrian redlichiid trilobites as well as other contemporaneous trilobite groups.

INTRODUCTION

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[1] Chapter 3 is a manuscript submitted to ***Journal of Paleontology***.

ONE OF the puzzles in trilobite studies is the abrupt appearance in the Early Cambrian of two partially overlapping trilobite provinces (or realms) which are defined by the primitive families Redlichiida and Olenellida. Although these families displayed quite a high early diversity, they are presumed to comprise a monophyletic group (Fortey and Whittington, 1989), yet this assumption lacks direct paleontological evidence because the fossil record tells us little about their prior evolutionary history. Documentation of trilobite larvae is vital because they demonstrate phylogenetic links between taxa that are often morphologically disparate as adults, or point to different evolutionary histories of convergent groups. Clearly, then, study of the ontogenies of these Early Cambrian species will provide critical data concerning their origins and phylogenetic relationships.

The first appearance of articulation in the shield, via a transverse joint, has been considered as distinguishing the meraspid from the protaspid (Whittington, 1959), with the subdivision of meraspid growth stages corresponding to the number of thoracic segments (Barrande, 1852; Raw, 1925). The episodic release of thoracic segments in most cases corresponds to the increase in the number of axial rings of the transitory pygidium, although a few trilobites may form two or more thoracic segments after a single molting (Whittington, 1957, 1959; Feist, 1970; Pabian and Fagerstrom, 1972). Moreover, the segmentation of the axis posterior to the occipital ring in the protaspis, i.e. in the protopygidium has also been employed as a criterion in dividing discrete growth stages, or ecdysis events, of the protaspid period (Šnajdr, 1981; Tripp and Evitt, 1983). This may be suitable for description of many trilobite protaspides, but may not be applicable to all. For example, protaspid instars of genus and species indet. 2 described here display rather large variations in size and morphology prior to the segmentation of their protopygidia. Nevertheless, subtle developmental variation within the protaspid stages may be the harbinger of dramatic morphological differences in subsequent instars.

Dilute (5%) acetic acid dissolution of about 20 kg of thin-bedded micritic limestone from the Lower Cambrian Shuigoukou Formation from the Laozizhai section in Xichuan, Henan Province, China (Figure 3.1), yielded abundant delicately phosphatized fossils, including bradoriid ostracodes (Zhang, 1987), the eodiscid trilobite Neocobboldia chinlinica Lee, 1963 (Zhang, 1989), as well as lingulate brachiopods, sponge spicules, hyoliths, some enigmatic taxa, and the redlichiid trilobite Ichangia ichangensis Chang, 1957 which is widely distributed in southwestern China (Zhou and Yuan, 1980). Because the Xichuan fossil assemblage was found immediately above the late Qiongzhusian Sinodiscus Zone and below Palaeolenus, it is probably from the latest Atdabanian or early Botoman (Figure 3.2).

In previous studies, only separate holaspid cranidia and pygidia of I. ichangensis were described (Chang, 1957; Zhang et al., 1980). However, originally articulated trilobites are so rarely found in acid-etched residues, and disaggregated exoskeletons coming from different taxa are mixed. This makes identification more complex, especially for the smallest trilobite protaspides with simple and similar body plans. Only by examining ontogenetic variations of certain traits can the links be made between these larvae and their corresponding later instars. On this basis, immature instars of I.

ichangensis co-occurring with their non-phosphatized adults are recognized, which permit a more detailed description of their growth history, although the assignment of pygidia and hypostomes to this taxon is tentative. We also describe early instars of two other co-occurring trilobites, which are of uncertain identity because no adult trilobites of other taxa have been recovered from the assemblage. Furthermore, a group of hypostomes, although well preserved, is also of uncertain affinity.

SYSTEMATIC PALEONTOLOGY

The terms used here generally follow Palmer (1957), Harrington (1959), Edgecombe et al. (1988), Speyer and Chatterton (1989), Chatterton et al. (1990), Fortey (1990), and Lee and Chatterton (1996, 1997).

In this paper, the four glabellar lobes and one occipital ring are distinct even in the earliest protaspid of the three trilobite taxa, such that there is no reason to infer an earlier instars with fewer glabellar lobes. The dorsal shield of a larval trilobite, without visible segmentation posterior to the occipital ring is considered as a stage 0 protaspis. A stage 1 protaspis bears one axial ring posterior to the occipital ring (with or without a pair of protopygigial spines), but no transverse joint. Meraspid stages are defined by the progressive release of thoracic segments, one by one. Because of their relatively small size, most of the disarticulated cranidia and pygidia in the collection are considered to be meraspides. Only the few bigger specimens are tentatively assigned to the holaspid period.

Specimens used for this study are deposited at the Chengdu Institute of Geology and Mineral Resources (CIGM prefix) and the Department of Geology, Northwest University, Xi'an (Hti prefix).

Order REDLICHIIDA Richter, 1933

Family PROTOLENIDAE Richter and Richter, 1948

Subfamily ICHANGIIDAE Zhu, 1980

Discussion.--According to Zhu (in Zhang et al., 1980, p.237), this subfamily consists of ten genera that have been found only in southern China: Ichangia Chang, 1957, Pseudichangia Chu and Zhou, 1974, Proichangia Zhang and Zhu, 1980, Shifangia Chien and Yao, 1974, Shiqihepsis Chien and Yao, 1974, Hsueaspis Chang, 1957, Changyangia Chang, 1965, Wangzishia Sun, 1977, Zhuxiella Zhang and Zhu, 1980, Hupeia Kobayashi, 1944. Not all these taxa may be sustainable, as some are based on limited material and some are monospecific. Hsueaspis and Proichangia may be synonymous, as may be Shifangia and Pseudoichangia. However, it is beyond the scope of this paper to attempt a revision of the subfamily.

Genus ICHANGIA Chang, 1957

Type species.--Ichangia ichangensis Chang, 1957 from the Lower Cambrian Canglangpu Formation in Ichang, Hubei province, China.

Diagnosis.--A genus of Ichangiidae with anteriorly slightly expanding glabella defined by shallow axial and lateral glabellar furrows. Anterior border short, moderately convex; preglabellar field long, gently convex, without preglabellar median ridge. Fixigena wide. Pygidium with two or three pairs of posterior border spines.

Ichangia ichangensis Chang, 1957

Figures 3.3.1, 3.3.2, 3.5.1-3.5.16, 3.6.11-3.6.15, 3.7.11-3.7.16

Ichangia ichangensis CHANG, 1957, p. 145, fig. 2; LU ET AL., 1965, p. 88, Pl. 13, fig. 7; ZHANG ET AL., 1980, p. 238, Pl. 76, figs. 4-8; ZHANG, 1987, p. 9, fig. 3F; 1989, p. 28, fig. 12A.

Ichangia oblonga Zhang and Zhu. ZHANG ET AL., 1980, p. 239, Pl. 76, fig. 9.

Ichangia aspinosa Zhang and Zhu. ZHANG ET AL., 1980, p. 239, Pl. 76, figs. 10, 11.

Material.-- 73 cephala shields of protaspides or cranidia of meraspides and holaspides are assigned to I. ichangensis, including 27 protaspides, 39 meraspides, and 7 holaspides. In addition, 26 pygidia and 11 hypostomes are believed to come from meraspides and holaspides of this taxa.

Protaspid Period

Stage 0 (Figure 3.3.1, 3.5.1-3.5.4)

Description.--Shield circular in outline with even convexity and two pairs of border spines: lateral pair short, posterior pair (protofixigenal spines) long. Shield (exclusive of posterior spines) 0.26-0.35 mm long, 0.33 to 0.44 mm wide. Axial furrows shallow. Axis convex, extends nearly the entire length of shield, divided into five lobes by faint transverse glabellar and occipital furrows; anterior glabellar lobe distinctly longer and wider than remaining lobes. Border defined by shallow border furrow, which connects to pair of prominent fossulae adjacent to anterior glabellar lobe. Behind fossulae, pair of palpebral lobes poorly developed. Librigenae probably on the ventral side. Doublure developed along the lateral and posterior margins, approximately same width as border. Prosopon fine pattern of polygonal ridges.

Stage 1 (Figure 3.3.2, 3.5.5-3.5.9)

Description.--Shield suboval in outline and convex, 0.35-0.38 mm long (exclusive of posterior fixigenal spines), 0.44-0.52 mm wide. Axis with strongly expanded anterior glabellar lobe. Fossulae and anterior border furrow well impressed. Palpebral lobe distinct, gently arcuate; connected to distinct palpebral ridge. Facial suture located at anterior and lateral part of the shield. Protopygidial axis as small lobe behind occipital ring; pair of protopygidial spines between posterior fixigenal spines.

Meraspid period

Stage 0 (Figure 3.5.10, 3.6.11, 3.6.12)

Description.--Cranidia subcircular, 0.39-0.46 mm long, 0.50-0.57 mm wide. Fossulae adjacent to expanded anterior glabellar lobe and anterior border furrow moderately impressed. Palpebral lobes and palpebral ridge well defined. Occipital ring semicircular in outline, defined by deep occipital furrow, bearing small axial node. Smallest transitory pygidium rectangular in outline, bearing two axial rings and two pairs of long, thick pygidial spines, first pair longer than second. In larger pygidia, axis with three to four axial rings and three to four pairs of pygidial spines.

Discussion.--So far only protaspides of I. ichangensis with one or two pairs of short protopygidial spines have been found (Figure 3.5.6-3.5.10). Probably, the initial transverse joint occurred with the development of the second pair of pygidial spines. By definition, during meraspid stage 0 there were no thoracic segments being released. However, transitory pygidia with two and three axial rings have indeed been collected (Figure 3.6.11, 3.6.12). These discontinuous changes in morphology within the earliest meraspid growth stage therefore suggests it can be subdivided into two substages: Stage 0_2 and Stage 0_3. Because there was no release of thoracic segments, the width of disarticulated pygidia of this stage should match the width of the posterior margin of the cephalon. This seems the case for the smallest pygidia with two or three axial rings (Figure 3.6.11, 3.6.12), whose width is 0.31 mm, whereas the posterior margin of an early cranidium (Figure 3.5.11) is 0.28 mm. It should be noted that the width of posterior margin of the cephalon increases quickly during this growth stage (see Figure 3.5.10, 3.5.11), although the width of cephalon increases at a constant rate.

Stage 1, 2, ... (Figure 3.5.11-3.5.13, 3.6.13-3.6.15, 3.7.11-3.7.16)

Description.--Cranidia subcircular in outline. Glabella moderately inflated; anterior glabellar lobe still expanded. Short anterior border defined by shallow border furrow; paired fossulae faint. Anterior fixigenal spine disappeared; posterior fixigenal spine larger. In progressively larger cranidia, glabella rectangular in outline; posterior glabellar lobes widening and glabella becoming increasingly convex. Three shallow transglabellar furrows gradually transforming into lateral glabellar furrows. Axial and occipital furrows narrower, deeper. Posterior border transverse; posterior border initially shallow, becoming deeper. Palpebral lobe long, well defined; palpebral ridge well defined. Fixigena increasingly convex. Occipital ring changing from subcircular to subtriangular in outline. Posterior fixigenal spine reducing to nubs or absent.

Hypostomes of different growth stages varying in size. Anterior wing long, projecting laterally. Anterior margin slightly curved, connected to subrectangular rostral plate. Median body strongly convex; anterior lobe long, width increasing with growth. Lateral and posterior borders relatively wide. Posterior margin semicircular in outline, along which ten marginal spines extend radially. Anteriormost pair of spines straight or slightly curved inward; rest somewhat shorter, extending initially laterally before flexing posteriorward, with heel-like expansion at the bend. Prosopon granulate, with fine anastomosing terrace lines on lateral and posterior borders and marginal spines. Width (trans.) of rostral plate about 3 times length (sag.).

Discussion.-- With growth pygidium increased in width and released thoracic segments, and long pygidial spines became progressively shorter. Thoracic segments presumably were released 13 times, because some ichangiid holaspides have 13 thoracic segments (Zhang et al., 1980). For late meraspides and holaspides, the width of the pygidium is no longer equal to the width of the posterior border of the cephalon, and becomes relatively shorter and shorter with the formation of more thoracic segments. According to their size, all hypostomes and some pygidia have been assigned to meraspid and holaspid instars, but it is not possible to assign them to specific growth stages. Of the two groups of hypostomes, the more common one displays a curved anterior margin that is comparable to the anterior margin of the cephalon, and has a similar prosopon.

Holaspid period (Figure 3.5.14-3.5.16)

Cranidium moderately convex, semicircular in outline. Anteriorly slightly expanding glabella defined by deep axial furrows, with three pairs of lateral glabellar furrows. Anterior border short ridge, separated by shallow anterior border furrow from long, gently convex preglabellar field. Occipital ring extending backward, forming short, broad spine. Palpebral ridge and lobe well defined. Pygidium transverse, semi-elliptical in outline. Axial rings poorly defined by shallow axial furrows. Two or three pairs of flat pygidial spines situated along pygidial border. Thoracic segment bears pleural spine and fine granules (Zhang, 1989, fig. 7C).

Discussion.--The number of holaspides and meraspides recovered is insufficient to prove a clear-cut size division of growth stages (Figure 3.4). The protaspid and early meraspid stages obviously show overlap, this probably because their variation is greater than the average increase in size of each instar. The overlapping in size of early instars is not rare among trilobites and may be typical. Olenellus gilberti Meek, 1874 (Palmer, 1957) and Neocobboldia chinlinica (Zhang, 1989) are two unrelated trilobites, yet the protaspides and early meraspides of both show the same overlapping in size.

Abrupt morphological modifications are known to occur during certain ontogenetic phases because of metamorphosis that accommodate ecological changes (e.g. Chatterton, 1980; Speyer and Chatterton, 1989). There seem to be no dramatic morphological changes during the ontogeny of Ichangia ichangensis. The co-occurrence of both larvae and adults of this species *in situ* indicates that they were once living in the same environment and growth may not have involved a major transformation of mode of life.

In general, ontogenetic trends exhibited by I. ichangensis can be summarized as follows:

1. Cephalon

Glabella.--The protaspis bears an expanded anterior glabellar lobe, but with growth, the posterior glabellar lobes and occipital ring widened. The convexity of the glabella increased.

Axial, glabellar, and occipital furrows.--All these furrows deepened with growth, and the three shallow transverse glabellar furrows became lateral glabellar furrows as the glabella inflated.

Palpebral ridge and palpebral lobe.--Even the smallest protaspis bears weakly elevated palpebral ridges, which extend horizontally to connect the palpebral lobes located on the lateral border. The palpebral lobes became slightly more elevated during late meraspid or early holaspid periods, but the palpebral ridge is always prominent.

Anterior border, preglabellar field, and fossula.--The anterior border is ridge-like and defined by short anterior border furrow. Two deep fossulae on either side of the anterior glabellar lobe merge with the anterior border. With the disappearance of fossulae during late meraspid stages, the anterior border furrow widened and flattened to become the preglabellar field, which became longer than the anterior border during the holaspid period.

Facial suture and librigena.--The facial suture and librigenae are invisible in all small protaspides. Probably they are located on the lateroventrol sides. With increasing size, the facial suture moved dorsally to adopt an anterolateral to posterolateral trace.

Fixigenal spines.--The smallest protaspis possesses two pairs of fixigenal spines, the anterior pair reducing in size gradually and finally disappearing during the late meraspid period; the posterior pair became short nubs on the posterior border in the early holaspid period.

2. Pygidium

The protaspis has no pygidium. Rather it seems to develop from the narrow border between two posterior fixigenal spines and behind the occipital ring. It may include a corresponding doublure on the ventral side. A pair of protopygidial spines developed with the addition of a new axial ring behind the occipital ring. Appearance of the transverse joint coincided with the development of the second axial ring and second pair of protopygidial spines. During subsequent growth stages, the transitory pygidium assumed more axial rings and corresponding paired border spines. It seems when the pygidium achieved four axial rings, the anterior part of the pygidium began to release the first thoracic segment. The pygidium became wider with growth, but the axial furrows defining the newly added axial rings shallowed. The conical pygidial spines became flat and short, and in mature holaspides only the anterior two or three pairs of spines remained.

3. Thoracic segments

Because no complete exoskeletons have been collected, the number and morphology of the thoracic segments are unknown. However, both Hsueaspis and Zhuxiella have 13 thoracic segments, and incomplete specimens of Wangzishia have at least 9 (Zhang et al., 1980, p. 237). Thus, it is likely that I. Ichangensis has 13 thoracic segments as well.

4. Prosopon

The protaspis bears fine polygonal ridges with tiny granules. Similar prosopon has been seen on some meraspides, but the holaspis is mainly smooth. Probably this is due to flaking off of the outermost integument. Terrace lines are present on the doublure of some of the smallest protaspides (Figure 3.5.2, 3.5.3), and similar lines were also found on hypostomes (Figure 3.7.11, 3.7.13-3.7.15).

GENUS AND SPECIES INDET. 1

Trilobite larva, ZHANG, 1989, p. 28, fig. 12C.

Figure 3.3.3, 3.3.4, 3.6.1-3.6.10

Material.--Of 40 shields, 24 are early protaspides, which bear no axial ring behind the occipital ring. Subdivision of three early protaspid substages (P0a, P0b, and P0c) is based on body size, development of sagittal glabellar furrow, and addition of third pair of fixigenal spines between anterior and posterior fixigenal spines. 16 larger shields are assigned to protaspid Stage 2 (P2), because their protopygidia bear two axial rings and two pairs of protopygidial spines. Neither protaspis of Stage 1, which is assumed characterized by one pygidial axial ring and pair of protopygidial spines, nor meraspis or holaspis of this species has been found.

Protaspid period

Stage 0a (Figure 3.3.3, 3.6.1, 3.6.2)

Description.--Shield subcircular in outline and moderately convex, about 0.35 mm long (excluding posterior fixigenal spines), and 0.40 mm wide (excluding anterior fixigenal spines). Glabella with five lobes poorly defined by shallow axial furrow, crossed by complete transverse furrows. Anterior glabellar lobe slightly expanded extending to short anterior border, with pair of deeply impressed fossulae on each side. Posteriormost axial lobe is occipital ring located close to posterior margin. Sagittal glabellar furrow very poorly impressed. Pair of faint palpebral ridges connected to palpebral lobes. Posterolateral border narrow, posterolateral border furrow shallow. Anterior pair of fixigenal spines short, situated at lateral border; posterior pair of fixigenal spines strong, at posterior extremity of the posterior border.

Stage 0b (Figure 3.3.4, 3.6.3, 3.6.4)

Description.--Shield transversely oval in outline, 0.38 mm long (excluding posterior fixigenal spines) and 0.43 mm wide (excluding anterior fixigenal spines). Axis relatively wide, defined by well incised axial furrows. Sagittal glabellar furrow moderately impressed, dividing three central axial rings into paired lobes. Palpebral ridge moderately well defined. Fossulae visible. Paired fixigenal spines lengthening markedly.

Stage 0c (Figure 3.6.5, 3.6.6)

<u>Description</u>.--Shield circular in outline, 0.57 mm long (excluding anterior fixigenal spines) and 0.65 mm wide (excluding anterior fixigenal spines). Sagittal glabellar furrow running from rear part of anterior glabellar lobe to occipital furrow. Palpebral ridge and palpebral lobe prominent. Librigenae located on anterior lateral border. Paired mid-fixigenal spines located between the anterior and posterior fixigenal spines.

Stage 2 (figure 3.6.7-3.6.10)

<u>Description</u>.--Shield subcircular in outline, 0.62-0.75 mm long (excluding posterior fixigenal spines), and 0.64-0.80 mm wide (excluding anterior fixigenal spines). Occipital ring strongly convex, behind which are two axial rings. Two pairs of protopygidial spines located between posterior fixigenal spines, first pair possessing branched extremities. Sagittal glabellar furrow faint. Prosopon fine network with fine granules.

<u>Discussion</u>.--Protaspides assigned to genus and species indet. 1 differ from those of <u>Ichangia ichangensis</u> because they have a sagittal glabellar furrow, a wider axis, three pairs of fixigenal spines, and branched protopygidial spines. This feature cannot be related to pygidia with short marginal spines assigned to <u>I. ichangensis</u> (Figure 3.6.13-3.6.15).

Sagittal glabellar furrows have been found in some small protaspides of redlichiids, ptychopariids, phacopinids, and calymenines (Hu, 1971; Fortey and Chatterton, 1988; Chatterton et al., 1990), and this feature disappeared during the growth in the late protaspid period. The possible function of this structure is obscure. Because sagittal furrows are obviously present among such widely disparate trilobite groups from various ages and regions, it seems that this character has no importance for high-level phylogenetic analysis. Although previously described Chinese redlichiid larvae vary greatly in morphology, their preservation seems too poor to show this furrow (Lu, 1940; Kobayashi and Kato, 1951; Zhang et al., 1980; Yi, 1988). The sagittal glabellar furrow-bearing protaspis of genus and species indet. 1 is the oldest known example from the Lower Cambrian in the Yangtze Platform, where the fossil assemblage is dominated by redlichiids at that time. Thus, a redlichiid affinity for these larvae is most likely.

GENUS AND SPECIES INDET. 2

Ichangia ichangensis Chang, ZHANG, 1989, p. 28, fig. 12B.

Figure 3.3.5, 3.3.6, 3.7.1-3.7.8

Material.--Of 62 shields, 2 are early protaspides (stage 0), 29 late protaspides (stage 1), and 31 meraspid cranidia.

Protaspid period

Stage 0 (Figure 3.3.5, 3.7.1, 3.7.2)

Description.--Shield transversely oval in outline, moderately convex. About 0.30 mm long (excluding posterior fixigenal spines), and 0.39 mm wide (excluding anterior fixigenal spines). Axis with five lobes defined by well-incised transglabellar and axial furrows. Anterior glabellar lobe expanded laterally, with fossula at each side. Posteriormost axial lobe is occipital ring located almost at posterior margin. Two pairs of fixigenal spines thin; anterior pair located near middle of lateral margin, and posterior pair at posterior margin.

Stage 1 (Figure 3.3.6, 3.7.3-3.7.5)

Description.--Shield transversely subhexagonal in outline, moderately convex. 0.30-0.38 mm long (excluding the posterior fixigenal spines), and 0.42-0.48 mm wide. Axis slightly elevated. Anterior glabellar lobe expanding slightly. Occipital ring distinct as raised lobe, behind which is protopygidial axial ring. Fossulae shallow. Faint palpebral ridge extending laterally to palpebral lobe. Anterior border nearly straight or curved gently backward. Anterior pair of fixigenal spine disappeared, posterior pair markedly longer. Pair of strong, irregularly curved pygidial spines between two posterior fixigenal spines.

Meraspid period

(Figure 3.7.6-3.7.8)

Description.--Cranidium subcircular in outline. Glabella moderately convex, defined by deep axial furrows. Anterior glabellar lobe expanding slightly; three glabellar lobes defined by shallow transverse glabellar furrows and occipital furrow. Occipital ring semicircular in outline. Anterior border wide; anterior border furrow shallow. Posterior border narrow. Fixigena increasingly convex. Palpebral lobe well defined; palpebral ridge prominent, long. Anterior pair of fixigenal spines disappearing and posterior pair of fixigenal spines reducing in length with growth.

Discussion.--The protaspis of genus and species indet. 2 is similar to that of Ichangia ichangensis of Stage 0, but the latter is subcircular rather than transversely oval, and possesses a more expanded anterior glabellar lobe and two pairs of relatively strong fixigenal spines.

One specimen that had been misidentified previously as protaspis of I. ichangensis (Zhang, 1989, fig. 12B) is Stage 1 instars of this indeterminate trilobite species. These protaspides possesse one axial ring posterior to the occipital ring, and a pair of pygidial spines which vary in length from specimen to specimen. This indicates a continued growth of the first pair of spines prior to the appearance of second pair. These instars with long or short pygidial spines may result from more than one protaspid molt stage.

Protaspides of Stage 0 of this species are distinguished from those of I. ichangensis by their extremely long, paired protopygidial spines. These protaspides conceivably represent an aberrant or special developmental phase of I. ichangensis, rather than another species. However, it is hard to explain why the trilobite would have possessed two kinds of similarly sized protaspid morphologies.

The protaspis with long, paired protopygidial spines may have been adapted to a planktonic mode of life. The paired spines likely disappeared during growth, because no adult trilobite bearing such long pygidial spines has been found from the Lower Cambrian. This could suggest a dramatic modification during the early ontogenetic period, a metamorphosis which led to the adults of this species being adapted to another mode of life in different surroundings, rather than co-occurring with these larvae.

GENUS AND SPECIES INDET. 3

Figure 3.7.9, 3.7.10

Material.--2 meraspid hypostomes.

Hypostome

Description.--Anterior wing conical, spine-like, projecting laterally horizontally. Median body moderately inflated; anterior lobe long. Anterior margin transverse. Posterior margin gently curved with 5 pairs of border spines; first three pairs short; fourth pair long, gently curved; anterior pair short, extending dorsally. Width (trans.) of rostral plate 6 times length (sag.).

Discussion.--The two meraspid hypostomes probably belong to one of the other indetermenite redlichiids described above, on the basis of the transverse anterior margin and general resemblance to those assigned to Ichangia ichangensis. The pair of long posterior border spines might favor genus and species indet. 2 because of the long spines on the posterior margin of the protaspis of that taxon.

COMPARISON WITH PROTASPIDES OF OTHER GROUPS

Because of generally poor preservation, the smallest of previously described redlichiid protaspides from China provide limited morphological information. Only those somewhat bigger (about 0.7 mm long) of later protaspid stages share some common characters to what is documented here in I. ichangensis: (1) the anterior border is a thin ridge; (2) the palpebral ridge is strong; and (3) the facial suture is moved to the dorsal side (Zhang et al., 1980). Protaspides of Palaeolenus lantenoisi Mansuy, 1912 (Yi, 1988) share some common features with that of I. ichangensis, such as the expanded anterior glabellar lobe and elevated fixigenal lobe. They probably possess marginal spines and weak palpebral ridges, but preservation is insufficient to show these.

As compared to trilobite dorsal exoskeletons, hypostomes are very rare in our collection. Hypostomes of closely related taxa are commonly indistinguishable, but major differences are preserved in some higher level groups or of different geological ages (Whittington, 1988). Hypostomes described here are somewhat similar to those of olenellids (Palmer, 1957) in the presence of the convex anterior lobe of the median body and the posterior marginal spines. Parallel ecological influences may have been responsible for their superficial resemblance.

By Fortey's (1990) proposal, conterminant is the primitive hypostomal attachment, from which natant evolved. Among many ptychparioid trilobites, such as Ehmaniella, Crassifimbra, and Sao, the hypostomal attachment condition changed from conterminant to natant with the lengthening of the preglabellar field during ontogeny. Both types of meraspid hypostomes in this study are connected to a rostral plate (Figure 3.7.9, 3.7.15). However, for some larger hypostomes of of I. ichangensis, there is no rostral plate attached (Figure 3.7.11). Since the width of the cephalic doublure is approximately the same as the cephalic border, and the sagittal length of the rostral plate is equal to the cephalic doublure, which itself appeared in the meraspid period, the hypostome of I. ichangensis became natant with the lengthening of the preglabellar field during the late meraspid and holaspid stages.

The protaspis of Olenellus gilberti bears a pair of prominent intergenal spines (Palmer, 1957), which are comparable to the long protopygidial spines on genus and species indet. 2, and may indicate adaptation to a planktic life style. However, they are not homologous, since in O. gilberti they are always fixed to the cephalon as intergenal spines, whereas in the redlichiid they formed the first pair of pygidial spines with the appearance of the transverse joint. The development of these spines in the olenellids separate them from all other trilobite groups. The redlichiid protaspides described here resemble more closely generalized ptychoparioid counterpacts (Palmer, 1958; Hu, 1971). Their morphological differences could imply that the olenellid and redlichiid-ptychoparioid clades diverged prior to the skeletonization of early trilobites.

Cephalon of fused anterior segments is one of apomorphies shared by arthropods, and each body segment may bear a pair of jointed appendages. Nauplius -- the first larval stage of crustaceans -- possesses three pairs of appendages but shows no external signs of body segments. The fused cephalon of trilobite larvae seems various in segmentation: most earliest protaspides have five glabellar lobes (like that of I. ichangensis), but four lobes are also known. For example, protocephala of the eodiscids Neocobboldia chinlinica (Zhang, 1989), Shizhudiscus longquanensis S. G. Zhang, 1980 (Zhang and Clarkson, 1993), and Tsunyidiscus longispinus S. G. Zhang, 1980 (see Chapter 2) contain three glabellar lobes and one occipital ring. These glabellar lobes are likely primary segments formed from the mesodermal germ band before hatching. On the other hand, the posteriormost axial lobe of some phacopoid protaspides displaying four glabellar lobes was named as Lp to indicate its non-homology with the occipital ring (L0), and Lp was believed to have budded off both glabellar lobes and protopygidial axial rings (Lee and Chatterton, 1996, p. 439). However, this assumption lacks convincing biological support, because the proliferation of new segments is controlled apparently by genetic system(s) rather than any particular body segment. Secondly, if a segment is budded off from the posteriormost axial lobe, a logical confusion results: what formed the last pygidial segment? It should be noted that Lp is always relatively large among phacopid larvae of protaspid stage 1 (Chatterton et al., 1990; Lee and Chatterton, 1996, 1997). The Lp of stage 1 of Rossaspis pliomeris may have been composed of L1 and L0, because the newly formed L1 of stage 2 is obviously smaller than Lp of stage 1. (see Lee and Chatterton, 1996, fig. 1). Unfortunately, available specimens of the earliest cheirurid instars (stage 1s) do not show details of the glabellar lobes or furrows, and the segmentation of stage 2s and stage 3s of this taxon is obscure (see Lee and Chatterton, 1997, fig.4.1-4.3). Like other arthropods, newly hatched trilobite larvae may consist of certain number of primary segments, and a pygidial growth zone (rather than Lp) gives birth to additional segments. This is enhanced by the fact that the occipital (or axial) ring would never reduce in size with the growth of a new axial ring posterior to it. The size variation of phacopid axial lobes during the ontogenetic process may suggest the presence of L1 and L0 as 'fused' primary segments because the occipital furrow (S0) might be too faint in tiny early protaspides.

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FIGURE CAPTIONS

FIGURE 3.1--Location map. The asterisk (*) shows the position of the Laozizhai section in Xichuan, Henan Province, China, where the trilobites were collected. The section is about 2 km east of Xichuan.

FIGURE 3.2--Stratigraphic column measured from the Laozizhai section in Xichuan, Henan province. The numerical time scale is after Bowring et al.(1993). Black points and bars to right of lithologic column indicate the occurrences and ranges of fossils so far known.

FIGURE 3.3--Reconstructions of Early Cambrian protaspides from Xichuan. 1, 2: Ichangia ichangensis Chang. 1, dorsal view of protaspid stage 0; 2, oblique lateral view of protaspid stage 1. 3, 4: genus and species indet. 1 with sagittal glabellar furrow. 3, dorsal view of protaspid stage 0a; 4, oblique lateral view of protaspid stage 0b. 5, 6: genus and species indet. 2 with long pygidial and genal spines. 5, dorsal view of protaspid stage 0; 6, oblique lateral view of protaspid stage 1. Abbreviations: afs=anterior fixigenal spine; b=baccula; L0=occipital ring; L1-L4=protoglabellar glagellar lobes; pfs=posterior fixigenal spine; ps1=first protopygidial spine; P1=first pygidial axial ring.

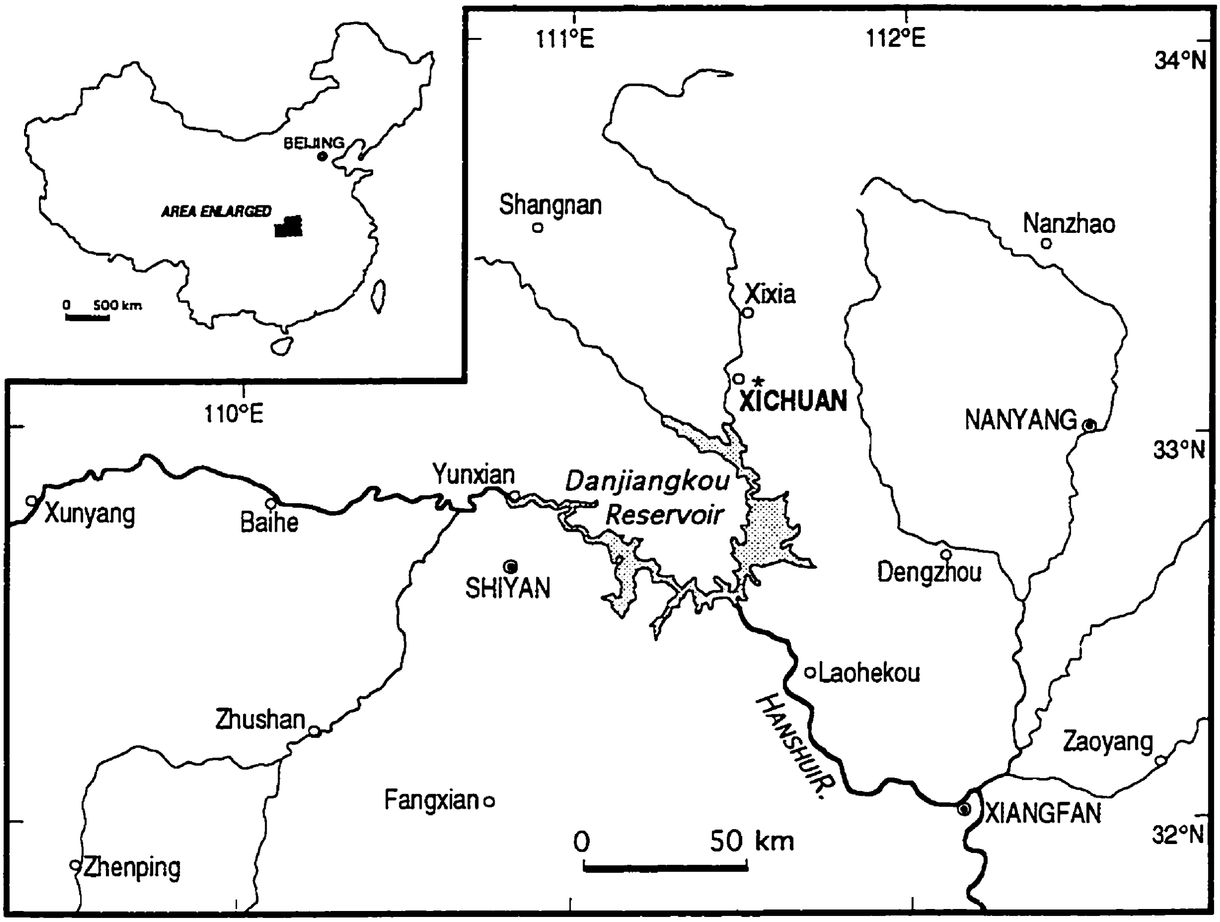
FIGURE 3.4--Plot of cephalic/cranidial length versus width of 73 specimens of Ichangia ichangensis Chang. Each of the 12 specimens illustrated in Figure 5 is labeled with a corresponding number on the plot.

FIGURE 3.5--1-16: Ichangia ichangensis Chang from the Lower Cambrian Shuigoukou Formation in Xichuan. 1 CIGM-XC1001, Oblique lateral view of protaspis of stage 0, X135. 2 CIGM-XC1002, oblique ventral view of protaspis of stage 0, X145. 3, Detail of 2, showing doublure with no sign of librigena, X415. 4, CIGM-XC1003, dorsal view of protaspis of stage 0, X117. 5, CIGM-XC1004, oblique lateral view of protaspis of stage 1 (?), X120. 6, CIGM-XC1005, dorsal view of protaspis of stage 1, X125. 7, detail of 6, showing protopygidium with one axial ring and a pair of protopygidial spines, X280. 8, CIGM-XC1006, dorsal view of protaspis of stage 1, X122. 9, detail of 8, showing tuberculate prosopon and network of fine terrace lines on anterior border (arrowed), X235. 10, CIGM-XC1007, dorsal view of meraspis of stage 0 with two pairs of protopygidial spines, X115. 11, CIGM-XC1008, dorsal view of early meraspid cranidium, X100. 12, CIGM-XC1009, oblique lateral view of meraspid cranidium, X80. 13, CIGM-XC1010, oblique dorsal view of meraspid cranidium, X45. 14, HTi-14, dorsal view of early holaspid cranidium, X12. 15, 16, Hti-20, HTi-13, dorsal views of later holaspid cranidia, X6.

FIGURE 3.6--Protaspides and pygidia from the Lower Cambrian Shuigoukou Formation in Xichuan. 1-10: protaspides of genus and species indet. 1. 1, CIGM-XC1011, oblique dorsal view of protaspis of stage 0a, X152. 2, CIGM-XC1012, dorsal view of protaspis of stage 0a, X139. 3, 4, CIGM-XC1013, dorsal and oblique dorsal views of protaspis of stage 0b, X115. 5, CIGM-XC-1014, dorsal view of protaspis of stage 0c, X70. 6, CIGM-XC1015, dorsal view of protaspis of stage 0c, X95. 7, CIGM-XC1016, dorsal view of protaspis of stage 2, X78. 8, detail of 7, showing small tubercles on outermost thin layer of the skeleton, X380. 9, CIGM-XC1017, dorsal view of protaspis of stage 2, X93. 10, CIGM-XC1018, dorsal view of protaspis of stage 2 with branched posterior protopygidial spines, X95. 11-15: dorsal views of pygidia of Ichangia ichangensis Chang. 11, CIGM-XC1019, meraspis stage 0_2, with two axial rings and two pairs of marginal spines, X124. 12, CIGM-XC1020, meraspis of stage 0_2, X138. 13, CIGM-XC1021, meraspis of uncertain stage, with four axial rings and four pairs of marginal spines, X120. 14, HTi-30, meraspis of uncertain stage, with four axial rings and four pairs of marginal spines, X93. 15, Hti-31, early holaspis, X93.

FIGURE 3.7--Trilobite instars and hypostomes from the Lower Cambrian Shuigoukou Formation in Xichuan. 1-8: protaspides and meraspides of

genus and species indet. 2. 1, 2, CIGM-XC1022, dorsal and oblique lateral views of protaspis of stage 0, X150. 3, CIGM-XC1023, oblique lateral view of protaspis of stage 1, X100. 4, CIGM-XC1024, posterodorsal view of protaspis of stage 1, X115. 5, detail of 4, showing granules on protopygidial spine, X240. 6, CIGM-XC1025 dorsal view of broken meraspis, X98. 7, CIGM-XC1026, dorsal view of more advanced meraspis, X79. 8, CIGM-XC1027, oblique dorsal view of meraspis, X62. 9, 10: hypostomes of genus and species indet. 3. 9, CIGM-XC1028, dorsal view, with rostral plate still attached, X148. 10, CIGM-XC1029, ventral view, X138. 11-16: hypostomes of *Ichangia ichangensis* Chang. 11, CIGM-XC1030, ventral view, X100. 12, detail of 11, showing granules on anterior lobe of the median body, X400. 13, detail of 11, showing granules on posterior lobe and terrace lines on marginal spines, X190. 14, CIGM-XC1032, ventral view, X120. 15, CIGM-XC1031, dorsal view of hypostome with rostral plate still attached, X115. 16, detail of 15, showing anastomosing terrace lines on marginal spines, X480.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Yunxian
Danjiangkou Reservoir
Xunyang
Baihe
SHIYAN
Dengzhou
Laohekou
HANSHUIR.
Zhushan
Zaoyang
Fangxian
XIANGFAN
0 50 km
Zhenping

Figure 3.1.

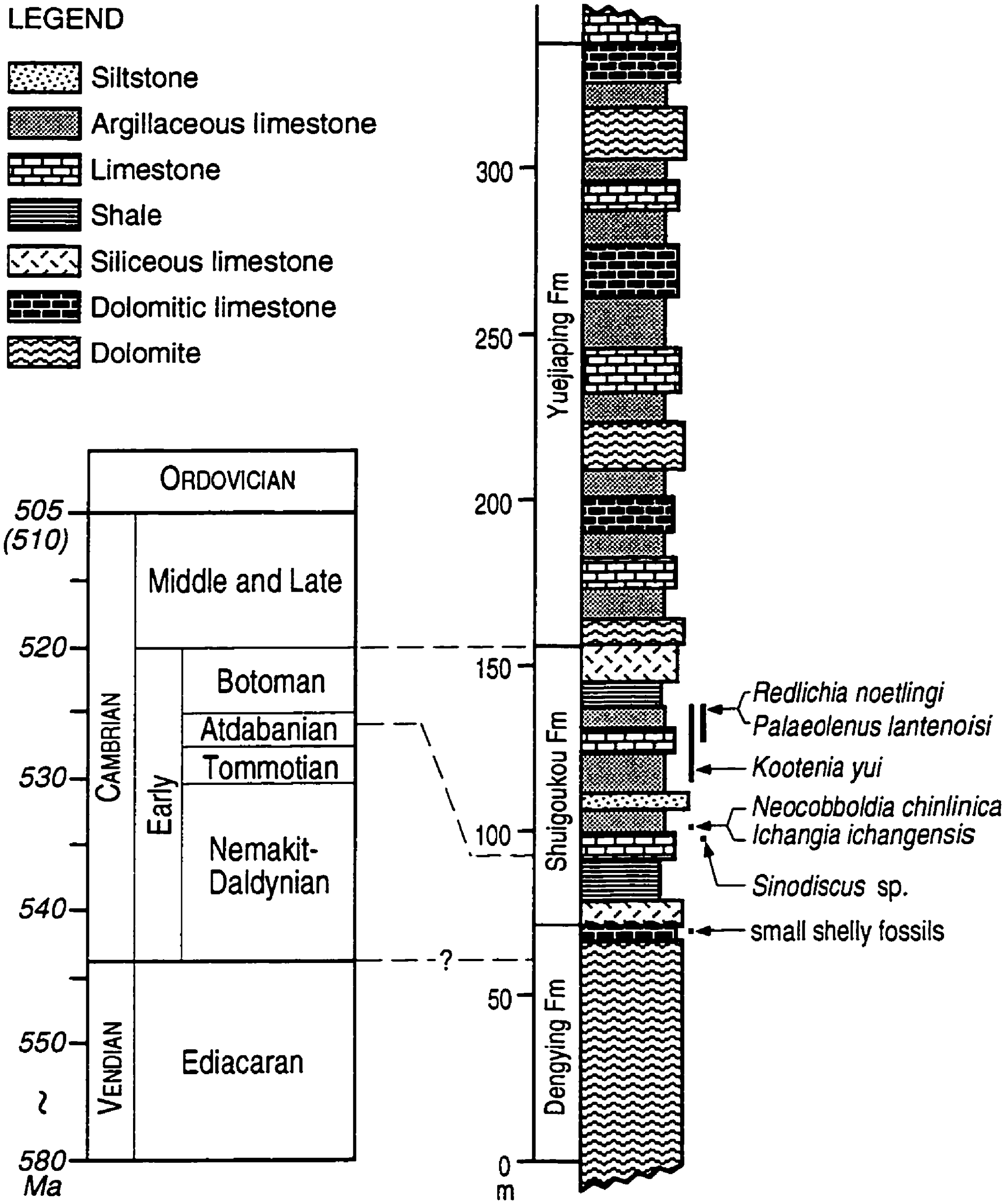
LEGEND
Siltstone
Argillaceous limestone
Limestone
Shale
Siliceous limestone
Dolomitic limestone
Dolomite
ORDOVICIAN
505
(510)
520
530
540
550
580
Ma
CAMBRIAN
VENDIAN
Middle and Late
Early
Botoman
Atdabanian
Tommotian
Nemakit-Daldynian
Ediacaran
?
300
250
200
150
100
50
0
m
Yuejiaping Fm
Shuigoukou Fm
Dengying Fm
Redlichia noetlingi
Palaeolenus lantenoisi
Kootenia yui
Neocobboldia chinlinica
Ichangia ichangensis
Sinodiscus sp.
small shelly fossils

Figure 3.2.

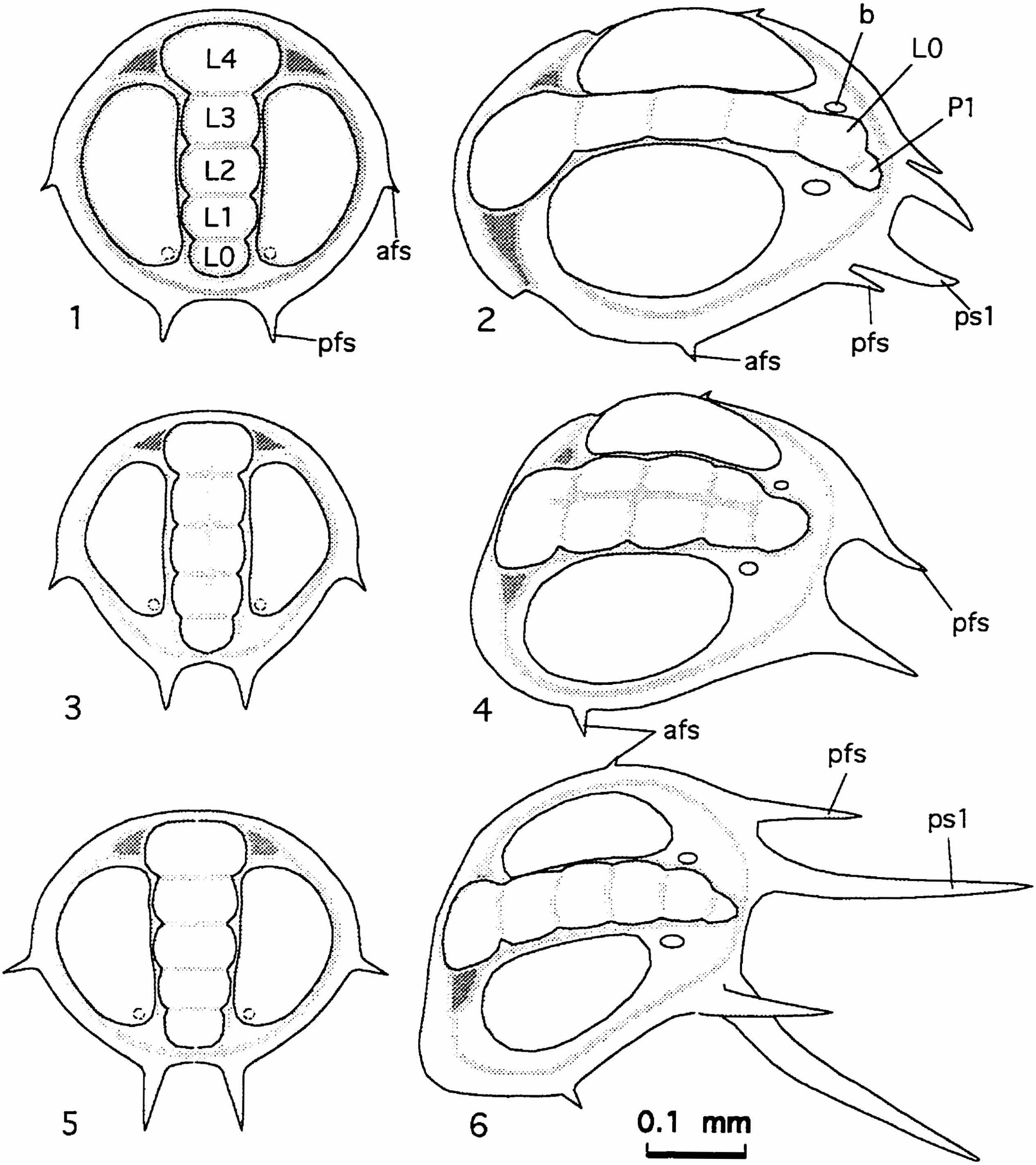
L4
L3
L2
L1
L0
afs
1
pfs
b
L0
P1
2
ps1
pfs
afs
3
4
pfs
afs
pfs
ps1
5
6
0.1 mm

Figure 3.3.

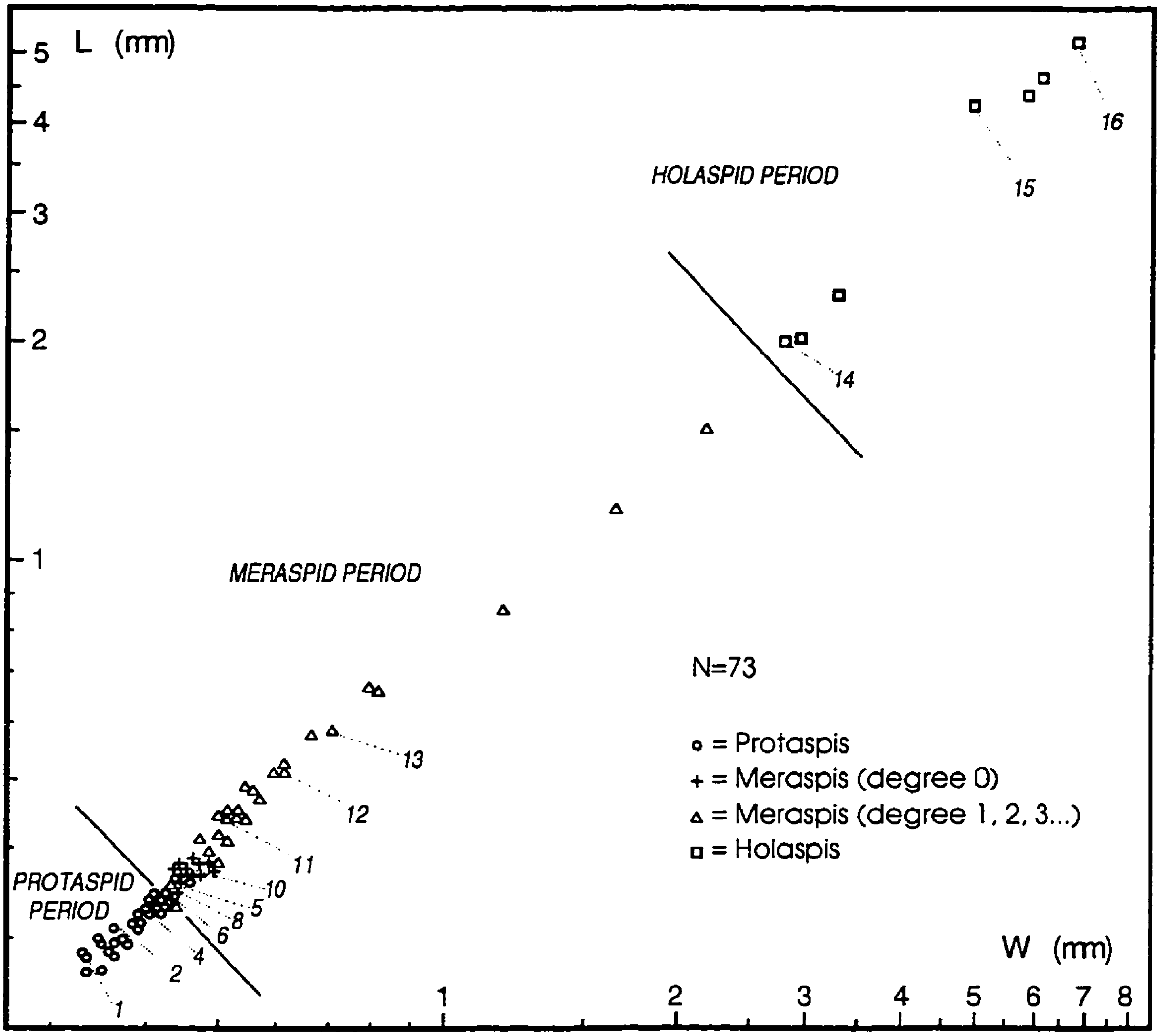
L (mm)
5
4
3
2
1
W (mm)
1
2
3
4
5
6
7
8
HOLASPID PERIOD
MERASPID PERIOD
PROTASPID PERIOD
N=73
o = Protaspis
+ = Meraspis (degree 0)
△ = Meraspis (degree 1, 2, 3...)
□ = Holaspis
1
2
4
6
8
5
10
11
12
13
14
15
16

Figure 3.4.

CHAPTER 4

EARLY CAMBRIAN OSTRACODE LARVAE WITH A UNIVALVED CARAPACE[2]

Phosphatized univalves, recovered from the Lower Cambrian (~530 million years old) Qiongzhusi Formation in southern China, are recognized as early instars belonging to bradoriid ostracodes whose later instars are bivalved. The univalved form is the primitive larval character for shell-secreting crustaceans, although most post-Cambrian ostracodes bypassed this developmental phase. The univalved-bivalved transition during early ontogeny represents an important evolutionary event in ostracodes, with implications for crustacean classification, and implies that the ostracode ancestor achieved this bivalved capacity before the appearance of mineralized skeletons during the "Cambrian explosion".

The Ostracoda are small crustaceans that widely inhabit marine, brackish, hypersaline and fresh-water environments. As fossils, the earliest bradoriid ostracodes are associated with the oldest redlichiid trilobites near the base of the Cambrian in China (1). Phosphatized Cambrian Bradoriida and Phosphatocopida that have preserved delicate appendages and soft body parts show no departure from the basic ostracode Bauplan (2-5). However, such extraordinary preservation is confined to just a few Lagerstätten within the long geological range of this group. Most fossil ostracodes are merely calcareous or phosphatized carapaces, which show a

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[2] Chapter 4 is the manuscript published in ***Science***, v. 262, p. 93-94 (1993).

greater diversity than all other crustacean groups but shed little light on their early ontogeny, especially how they developed from an egg through the nauplius larval stage to a bivalved juvenile. This lack of information is likely a result of the tiny size of the initial larvae and the fact that the juvenile carapaces were too poorly mineralized to withstand post-ecdysial disintegration. Nonetheless, it has long been accepted that a bivalved nauplius is common to both fossil and extant ostracodes (5-7). Here, we show that at least some Early Cambrian bradoriid ostracodes had univalved larval and juvenile instars before the youngest bivalved ones.

By dilute (~5%) acetic acid digestion of thin-bedded limestones of the Qiongzhusi Formation from two sections exposed 760 km apart in Zhenping, Shaanxi (8) and Jinyang, Sichuan, China, we extracted secondarily phosphatized carapaces that represent rare univalved instars of two bradoriid taxa and abundant bivalved later instars. The rocks are fine-grained and were deposited in a deep-water environment. The two ostracode assemblages consist of different bradoriid taxa: Kunmingella douvillei (Mansuy, 1912) occurs in Jinyang and many other places in southern China but not in Zhenping, whereas Duibianella sp. nov. is restricted to Zhenping. In addition, both assemblages contain inarticulate brachiopods, sponge spicules, and small shelly fossils but have so far yielded neither trilobite protaspides nor meraspides. Many adult redlichiid trilobites, preserved in the same strata with their original calcareous exoskeletons, indicate that both faunas belong to the Lower Cambrian Eoredlichia-Wutingaspis Zone, Qiongzhusi (=Chiungchussu) Stage, approximately equivalent to the upper Atdabanian of Siberia.

The small univalved carapaces recovered from Zhenping (Figs. 4.1 and 4.2) and Jinyang (Fig. 4.3) can be linked to co-occurring larger bivalved bradoriid carapaces that belong to subsequent ontogenetic stages; they each represent at least one of the earliest instars preceding the youngest bivalved ones. The univalved instar may therefore be equivalent to the nauplius or metanauplius larva of extant Crustacea.

The purported pre-protaspid larva of a Lower Ordovician trilobite (9) is similar in shape and ornament to our bradoriid larvae. However, the early protaspis of trilobites commonly bears paired border spines, and although some taxa may be domical (10), most exhibit variably distinct furrows as evidence of the axial lobe. The axial furrows and paired eye ridges develop during subsequent growth, but no such furrows and ridges could be seen on the external surfaces of the univalved carapaces we isolated (Figs. 4.1, A to C, and 4.3A). These basic features are the main criteria that distinguish univalved ostracode instars from trilobite protaspides.

The first naupliar instar of almost all extant ostracodes, whose ontogenies are known, is bivalved and resembles the adult form (11-12). The only known exception to this is the punciid Manawa staceyi Swanson, 1989, whose nauplius and metanauplius carry single carapaces. In this species, the univalved-bivalved transformation results from the development of the sagittal hinge during early ontogeny (13), which thus indicates that this species exhibits a growth history similar to that of our Cambrian bradoriids. The transition shown by bradoriid and punciid ostracodes is more or less a progressive, gradual process rather than one involving abrupt changes. This development history argues against the possibility that the transition from univalves to bivalves is a metamorphosis linked to changes in life habit. Adult carapaces of Lower Cambrian Phaseolella dimorpha Zhang, 1987 from China (14) and Middle Cambrian Svealuta sp. A from Australia (15) vary from this process in that they achieved an overall bivalved shape but retained the single shell and never developed a hinge at all. Therefore, we regard the univalved phase as the primitive character, an inheritance from a single-shelled ancestor, rather than as a special feature that arose in early instars as an adaptation to unusual ecological conditions. The primitive nature of the univalved phase is supported by other crustacean groups like the Cirripedia and Branchiopoda, whose larvae also carry a single carapace regardless of whether it originated from the naupliar head, akin to a specialized head shield (16), or from the thoracic region (17).

The transition from a univalved to a bivalved shape represents an important event in ostracode evolution, because it may have been motivated by the need of the ancestor of bradoriids to adapt to complex surroundings. For example, one of the selection pressures that is thought to have played an important role in the earliest phases of evolution of animal skeletons is predation (18). Because this transition during ontogeny is displayed by some of the earliest known bradoriids, the advantage of a bivalved carapace may have been realized before the onset of mineralization near the beginning of the Cambrian.

The smallest bivalved instars of those Recent ostracodes that have been studied, as well as those of phosphatized Cretaceous Pattersoncypris micropapillosa Bate, 1972 from Brazil (4), are considerably larger than their corresponding egg cases. The smallest bivalved instar of Upper Cambrian Falites sp. from Sweden is spheroidal in shape like the first instar of Recent cyprid ostracodes (11) and was therefore interpreted as the first moult stage (2). Nevertheless, it remains possible that other young instars of extant and fossil ostracodes with a univalved shell might be present but still await discovery.

The absence of the univalved phase in most post-Cambrian ostracodes suggests that development of the organism was accelerated while it was still in the egg stage. If so, the bivalved ostracode nauplius can then be regarded as an autapomorphy that unites members of this class as a divergent arthropod group, whereas bradoriid and punciid ostracodes bearing univalved carapaces would be separate branches within the class. However, the phylogenetic relationship between Recent punciid and Cambrian bradoriid ostracodes is uncertain, because the univalved naupliar stage is only a symplesiomorphic (shared primitive) character and the geological interval between the known occurrences of the two groups is very long. It is still unknown whether the bradoriids formed the stem group for all later ostracodes or a sister group derived from a generalized crustacean ancestor. Bradoriids may comprise a polyphyletic group (1, 15). The classification of ostracodes is further unsettled because of the possibility that the Phosphatocopida were secondarily phosphatic in composition; their limb structure differs from that of other ostracodes and suggests a closer affinity to barnacles (6, 19), but this may simply be the result of convergence.

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FIGURE CAPTIONS

Fig. 4.1. Duibianella sp. nov. from the Lower Cambrian Qiongzhusi Formation of Zhenping, Shaanxi, China. Scale bars, 0.1 mm. (**A**). Dorsal view of a univalved carapace (ZP 0001), which is circular in outline, moderately convex, and surrounded by a narrow rim along which developed fine denticles and a pair of backward-directed posterior spines. The exterior surface of the carapace is covered with a reticulate network of fine ridges that produce an ornament of irregular but equant polygons. (**B**). Dorsal view of a later univalved instar (ZP 0002). The carapace extends more laterally than sagittally, becoming strongly convex transversely. The posterior spines become more prominent and separated from the rim/ The reticulate ornament has more polygons, and several symmetrically paired tubercles appear on either side of the carapace (arrows). (**C**). Dorso-laterior view of a later univalved instar (ZP 0003). The carapace becomes more curved transversely and expands ventrally to develop a nascent bivalved shape, leaving a gape along the free margin. The hinge is still invisible, and the dorsal margin remains moderately arched. The dorsally directed posterior spines increase in size and advance farther from the margin, and more fine tubercles appear in the reticulate surface. (**D**). Lateral view of a pre-adult left valve (ZP 0004), showing the appearance of the truly bivalved structure. The paired posterior spines shift somewhat toward the anterior.

Fig. 4.2. Reconstruction of Duibianella sp. nov. showing the transformation from a univalved carapace (**A** through **C**) to a bivalved one (**D**); d, duplicature; r, marginal rim; s, posterior spine; and t, tubercle. Scale bars, 0.1 mm.

Fig. 4.3. Kunmingella douvillei (Mansuy, 1912) from the Lower Cambrian Qiongzhusi Formation of Jinyang, Sichuan, China. Scale bars, 0.1 mm. (**A**) Dorso-lateral view of the only univalved carapace (JY 0006), which resembles the univalved instar of Duibianella sp. nov. but is more convex transversely and bears a straighter anterior margin. We assign it to K. douvillei, whose bivalved juveniles and adults are common in the same bed. Its youngest bivalved instar shares certain features that appear to have been derived from the domical univalved form: (I) The smallest bivalved carapace bears a pair of posterior spines that still project from the narrow marginal rim; and (ii) the exterior surface is similarly covered with a reticulate ornament. (**B**). Right view of a juvenile bivalved carapace (JY 0007). The appearance of a hinge made it possible for the carapace to close tightly along the free margin, but the dorsal margin is still arched. (**C**). Right view of a further growing juvenile carapace (JY 0008), showing the straightened hinge, posterior spine, and indistinct anterior node and posterior lobe. (**D**). Dorso-lateral view of a bivalved pre-adult carapace (JY 0009) with a prominent anterior node and posterior lobe. In

addition, a pair of dorsal pores (possible gland exits) is present in all instars (arrows).

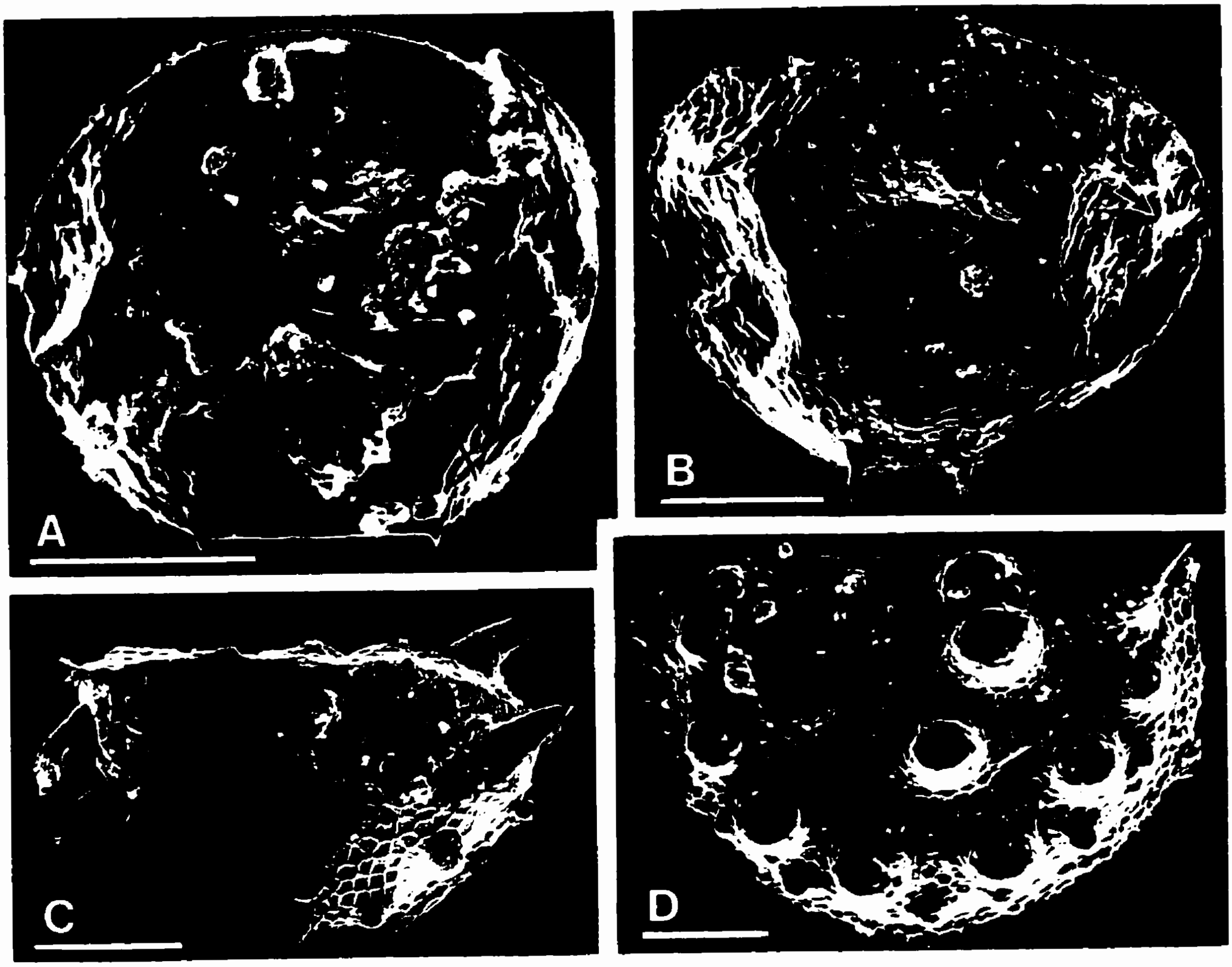

FIGURE 4.1.

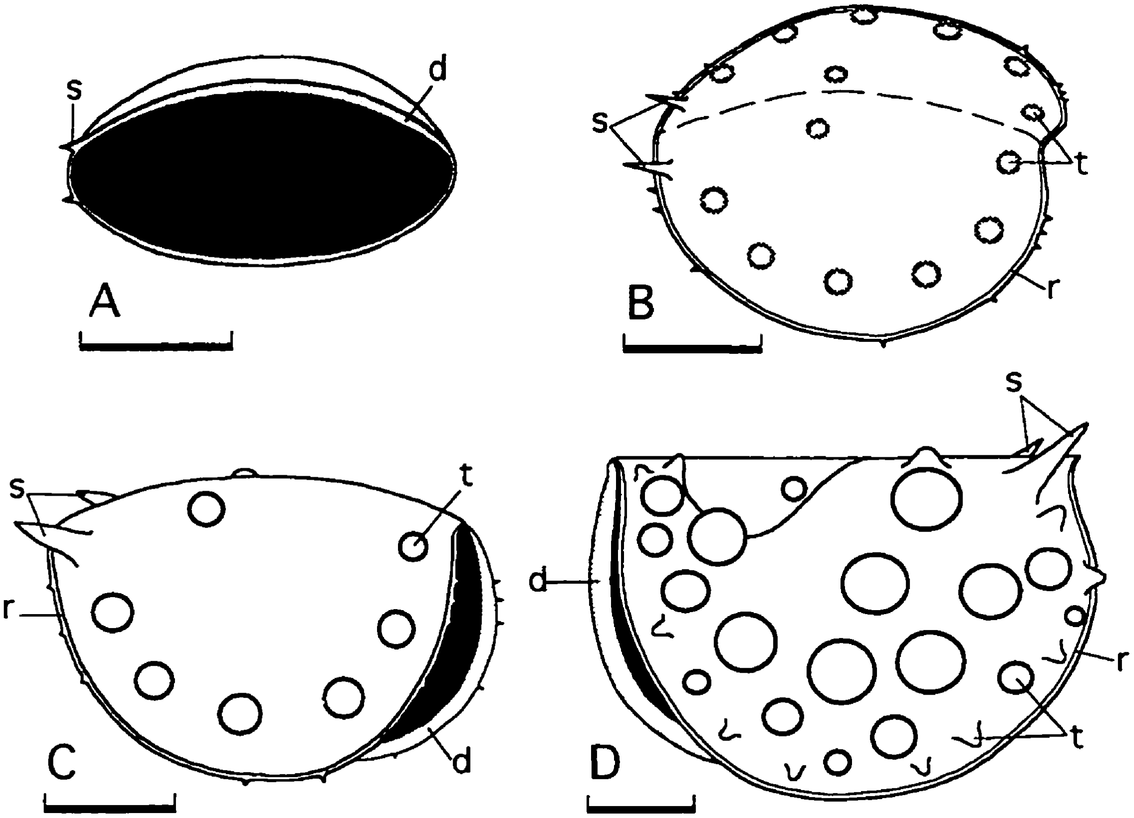

Figure 4.2.

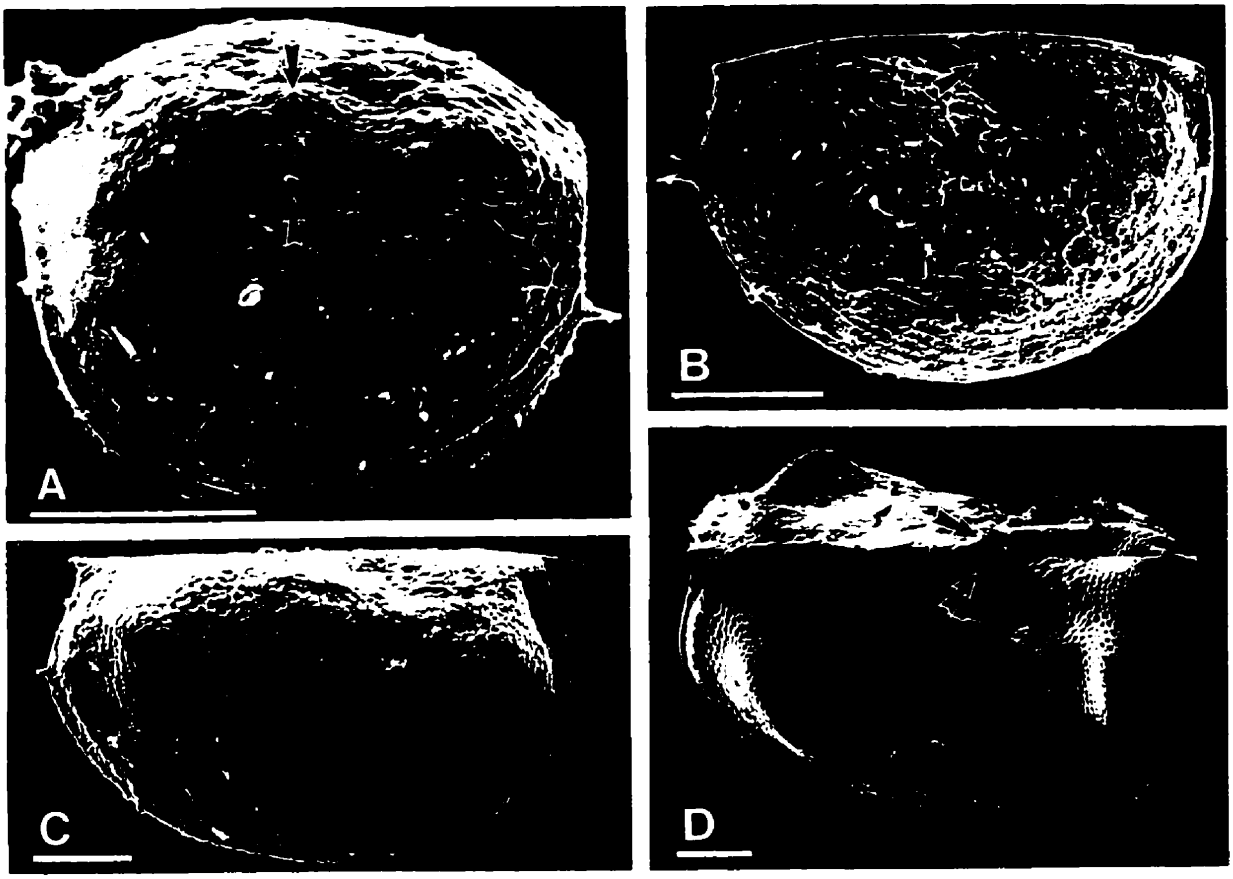

FIGURE 4.3.

CHAPTER 5

NEW AND EXTRAORDINARY EARLY CAMBRIAN SPONGE SPICULE ASSEMBLAGE FROM CHINA[3]

ABSTRACT

The fossil record of siliceous sponges, compared with that of other skeleton-secreting Metazoa, is poorly known, based as it is on disarticulated spicules and sporadically preserved body fossils. Abundant spicules recovered from Lower Cambrian strata in Shaanxi, China, essentially double the known morphological diversity of siliceous sponges for that interval of geologic time. These fossils, along with a comparable coeval fauna from South Australia, have a remarkably modern aspect, thereby demonstrating that the principal siliceous sponge groups and styles of body architecture were established quickly in the earliest Phanerozoic as part of the Cambrian "explosion" and that they inhabited a variety of low-energy, relatively deep water settings. The similarity of spicule shape and variation to that of younger assemblages reflects a conservative architecture for the siliceous sponges.

INTRODUCTION

Sponges have been a highly successful group throughout the Phanerozoic, colonizing most marine and some freshwater environments. Siliceous sponges have been

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important constituents in reefs since the Early Ordovician (Pratt and James, 1982), and calcareous sponges -- as archaeocyathans and stromatoporoids -- were primary reef builders even in the Early Cambrian (Pratt, 1990; Wood, 1991). Knowledge of the fossil record of siliceous sponges is based on whole, relatively rigid skeletons, compressed molds, casts or films of once-flexible spicular networks, or isolated spicules seen in thin section or recovered as insoluble residues. Sponge body fossils with simple spicular morphology and architecture preserved in the Chengjiang and Burgess Shale faunas (Lower and Middle Cambrian, respectively) provide the only reliable foundation for classification for these early taxa, and show their rapid diversification in nonreefal environments (Rigby, 1986; Chen et al., 1989). However, such outstanding fossil Lagerstätten are mere glimpses, and the most common evidence of past sponges is isolated spicules.

Most Cambrian siliceous sponges were composed of relatively simple spicules, such as monaxons, stauractines, hexactines, or pentactines (Sdzuy, 1969; Mostler and Mosleh-Yazdi, 1976; Ding and Qian, 1988; Wrona, 1989; Mehl, 1991). However, an Upper Cambrian spicule assemblage from Queensland (Bengtson, 1986), and the recently described Early Cambrian spicules from South Australia (Bengtson, 1990) indicate a much higher diversity and complexity than previously recognized and provide evidence that early siliceous sponges are comparable to some extent to Mesozoic and Cenozoic lithistids and hexactinellids. We report a somewhat similar but even more diverse sponge spicule assemblage from approximately coeval Lower Cambrian strata in Zhenping, southern Shaanxi, China.

STUDY AREA

Spicules were recovered by dilute (5%) acetic acid digestion of a thin-bedded, black argillaceous limestone of the Qiongzhusi (Chiungchussu) Formation in Zhenping, Shaanxi (Chon-p'ing-hien, Shensi) (Fig. 5.1), where Blackwelder (1907) visited during 1903-1904 and conducted the first stratigraphic study. This limestone was deposited in relatively deep water in a slope setting. The area is structurally complex, however, and no continuous section can be measured. The associated fauna, including bradoriid ostracodes, inarticulate brachiopods, and redlichiid trilobites, belongs to the Early Cambrian Eoredlichia-Wutingaspis Zone, Qiongzhusi Stage (Xiang et al., 1981), which is roughly equivalent to the upper Atdabanian of Siberia.

The Qiongzhusi Formation is widespread in southwestern China, but only the single unit at this locality has so far yielded such a spicule assemblage. The spicules are disorganized but concentrated in thin layers and mixed with other bioclasts (Fig. 5.2), indicating that, although derived from many disintegrated sponge skeletons, they underwent minimal transport. The variety of spicules present argues that the benthic sponge community consisted of several coexisting species. Petrographic observations of the limestone indicate that only some of the spicules retain their primary silica mineralogy. Most of the others are found as calcite cement-filled molds because of the tendency of opaline silica to dissolve in seawater and during early burial (Land, 1976; Brasier, 1992). The Shaanxi siliceous sponge spicule assemblage thus represents fortuitous preservation, and we suspect that siliceous sponges were more widely distributed than the current fossil record would suggest.

SPONGE SPICULES

The spicule network of some sponges is constructed of only one spicule type, but most contain more, either interlocked or fused into networks. Spicule form in many extant and fossil sponges is complex and variable, difficult to use by itself in classification (Bergquist, 1978). Most isolated stauractines or hexactines from Cambrian rocks, which have been traditionally identified as Protospongia, for example, also exist in many other taxa (Rigby, 1981). In most circumstances, it is impossible to reconstruct the network or even recognize the assemblage belonging to an individual taxon on the basis of isolated spicules. We therefore consider it premature to apply formal taxonomy to the Shaanxi spicules.

Because classificatory terms for spicule morphology are many and no common scheme has been agreed to, we have attempted to use the simplest terms plus descriptors and have grouped the Shaanxi sponge spicules into seven categories.

1. Oxeas (monaxons pointed at both ends) are the simplest elements. Acanthoxeas resemble oxeas but are covered with fine spines, and hexactine forms bear four short rays (Fig. 5.3A).

2. Some smooth spicules resemble tylostyles -- long, thin rhabdomes with a globular swelling at one end -- but with a cladome of three to nine, slightly curved clads at the other (Fig. 5.3, B-D). Triaenes with three clads (Fig. 5.3C) are common in the fossil sponge record. A second type in this group bears a series of cladlike but short spines arranged in rings along the end of the rhabdome opposite the terminal knob (Fig. 5.3D).

3. A series of smooth spicules possesses a primary ray and four to nine rays radiating in a common plane from a central focus, forming orthopolyaenes (Fig. 5.3E). Some have rays that are slightly curved in an irregular manner (Fig. 5.3F).

4. Triactines have three smooth rays diverging from a central focus (Fig. 5.3G).

5. Oxyasters bear many rays which also diverge from a central focus (Fig. 5.3, H and I).

6. Two kinds of smooth spicules exhibiting forked rays are particularly common in this assemblage. Dichopentactines have four straight rays with one short projection orthogonal to them (Fig. 5.3J); dichostauractines lack the short ray, and the forked rays are both straight and curved (Fig. 5.3K). Rays may have one to four degrees of splitting independent of size and, therefore, probably independent of spicule growth.

7. Many spicules are ornamented with short spines. Acanthopentactines have five rays (Fig. 5.3, L and M) and, although variable, may be roughly subdivided into two kinds: one bearing a short rhabdome and four rays approximately equal in size but curved and extending irregularly (Fig. 5.3L), the other with short rays on one plane and a very

long rhabdome (Fig. 5.3M). Acanthohexactines have six rays but the primary one is markedly thicker (Fig. 5.3N).

DISCUSSION

The seven spicule groups belong to the Hexactinellidae and Lithistidae. Some of them seem unique and probably represent new taxa. The high degree of diversity and size variation of these sponge spicules confirms Bengtson's (1990) suggestion that some taxa were structurally advanced, with spicules arranged into inner and outer walls. Varying spicule size in the skeletal framework can be attributed in part to progressive growth.

The Shaanxi spicule fauna bears some similarities to a coeval assemblage from South Australia (Bengtson, 1990) but lacks representatives of the Calcarea, presumably because the Shaanxi fauna lived in a deeper water setting. Our tylostyles resemble Nabaviella from South Australia and from the Upper Cambrian of Iran (Mostler and Mosleh-Yazdi, 1976) but the Australian one lacks the terminal swelling present on the primary rays; clavules from the Upper Ordovician of New South Wales are also similar (Webby and Totter, 1993, Figs. 3.11, 3.12). Our orthopolyaene form may correspondingly belong to Heterostella from approximately coeval strata in Siberia (Fedorov, 1987) and questionably from South Australia. It is also similar to Taraxaculum but in this taxon the tip of the primary ray may be pointed or split into short processes (Bengtson, 1990). Our curved-ray hexactine may belong, or be related, to Inflexiostella, also from Siberia. Our acanthopentactines and acanthohexactines are similar to forms from the Upper Cambrian of Queensland (Bengtson, 1986), the Upper Silurian of Arctic Canada (de Freitas, 1991) and the Upper Triassic of Austria (Mostler, 1986), although in the South Australia Lower Cambrian fauna only hexactinellid spicules developed acanthose surfaces (Bengtson, 1990, Fig. 15). Our dichopentactines and dichotetractines appear to be new.

CONCLUSIONS

Hexactinellid sponges made their first appearance in the Tommotian as isolated stauractines in Siberia (Rozanov and Zhuravlev, 1992) and as hexactines and pentactines in South China (Ding and Qian, 1988), and possibly appeared even earlier (Brasier, 1992, Fig. 4). By the Atdabanian, siliceous sponges seem to have become fairly widespread in low-energy, offshore marine environments in China, Australia, and Siberia. This supports Webby's (1984) suspicion of a deep-water origin for these sponge groups, but more sampling is needed. Laurentian strata, for example, have so far yielded no such assemblages.

The Shaanxi sponge spicule assemblage is complex and strikingly modern in appearance, and therefore suggests not only a rapid diversification of the siliceous sponges during the Cambrian "explosion," but that they achieved quickly an architecture that remained stable during their subsequent evolutionary history.

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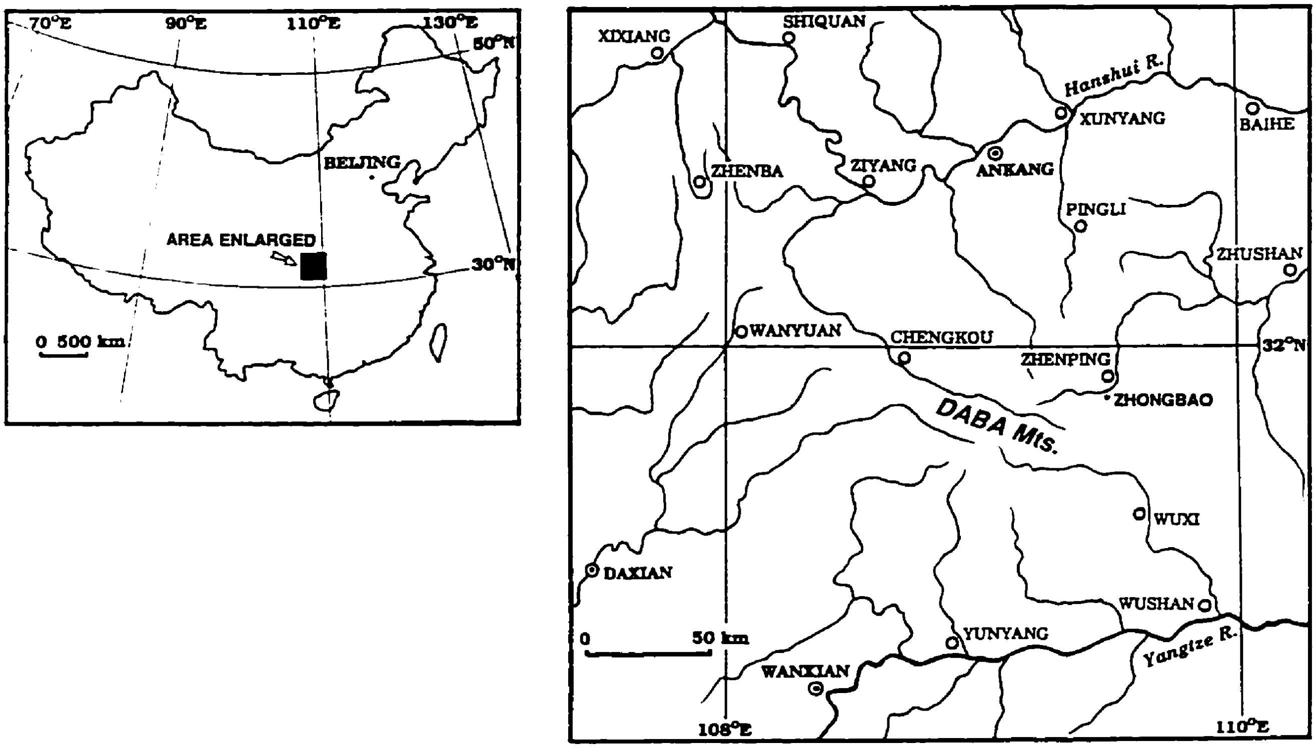
FIGURE CAPTIONS

Figure 5.1. Location map. Fossils for this study were collected from Lower Cambrian Qiongzhusi Formation in Zhongbao (asterisk), a small town 10 km south of Zhenping, southern Shaanxi, China.

Figure 5.2. Partially acid digested limestone from Lower Cambrian Qiongzhusi Formation in Zhenping, southern Shaanxi, China, showing varied sponge spicules densely accumulated (ZP 0010). White arrows indicate two bradoriid ostracodes; black arrow indicates inarticulate brachiopod. Scale bar (middle bottom)=1 mm.

Figure 5.3. Isolated sponge spicules from Lower Cambrian Qiongzhusi Formation in Zhenping, southern Shaanxi, China. A: Hexactine oxea (ZP 0011). B: Tylostyle (ZP 0012). C: Triaene tylostyle (ZP 0013). D: Modified tylostyle (ZP 0014). E: Orthopolyaene (ZP 0015). F: Curved-clad hexactine (ZP 0016). G: Triactine (ZP 0017). H, I: Oxyasters (ZP 0018, ZP 0019). J: Dichopentactine (ZP 0020). K: Dichostauract (ZP 0021). L: Curved-clad acanthopentactine (ZP 0022). M: Swollen-rhabdome acanthopentactine (ZP 0023). N: Acanthohexactine (ZP 0024). Scale bar (bottom right)=0.4 mm for A-F and K; 0.3 mm for H-J, M, and N; 0.2 mm for G and L.


70°E
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BEIJING
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XIXIANG
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Hanshui R.
XUNYANG
BAIHE
ZHENBA
ZIYANG
ANKANG
PINGLI
ZHUSHAN
WANYUAN
CHENGKOU
ZHENPING
32°N
ZHONGBAO
DABA Mts.
WUXI
DAXIAN
WUSHAN
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YUNYANG
Yangtze R.
WANXIAN
108°E
110°E

Figure 5.1.

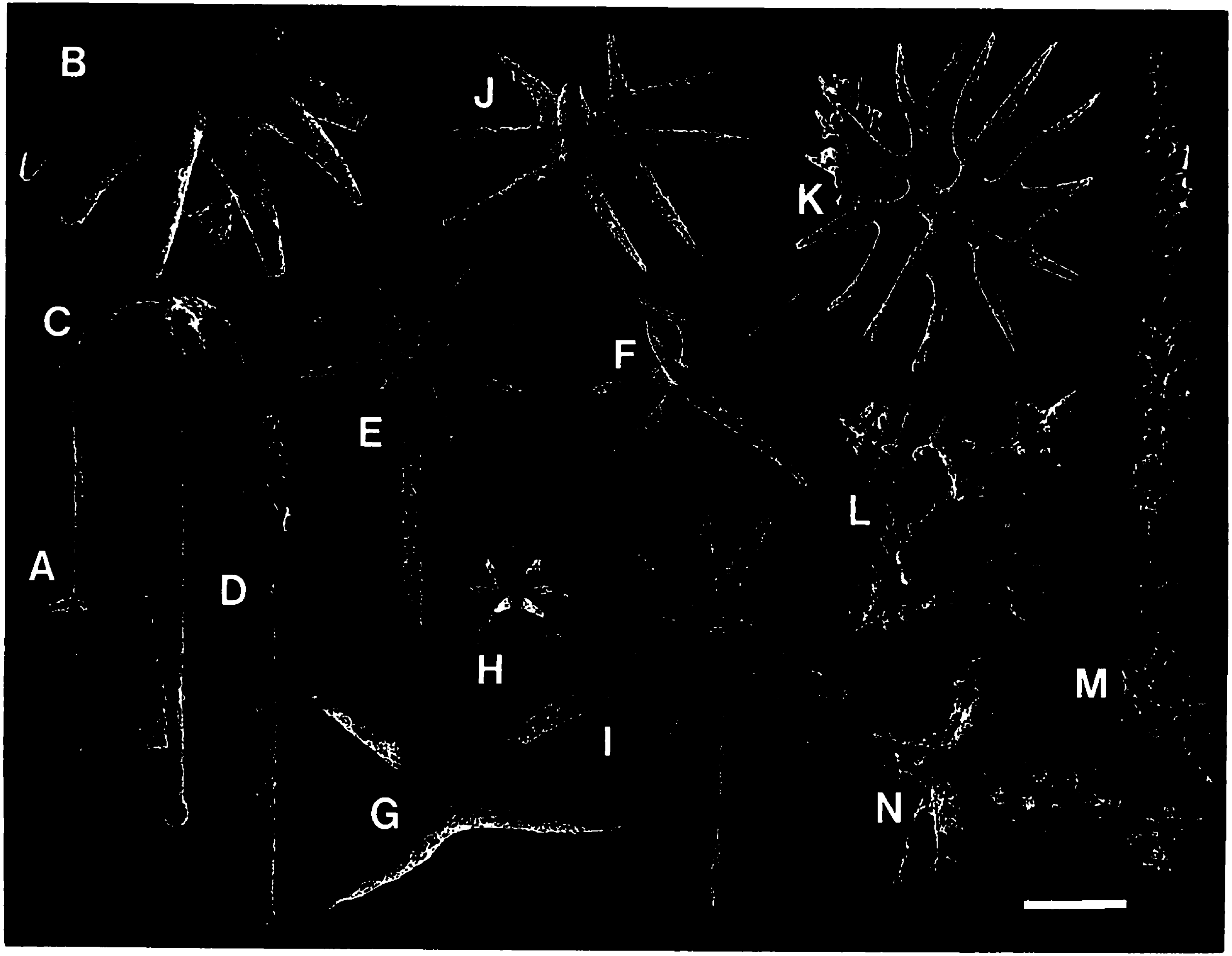

FIGURE 5.3.

CHAPTER 6

MIDDLE CAMBRIAN ARTHROPOD EMBRYOS WITH BLASTOMERES[4]

A phosphatized Middle Cambrian (~510 Myr ago) fauna from Duyun, southern China has yielded fossil eggs that may be of arthropod affinity, and could belong to the co-occurring eodiscid trilobite Pagetia sp. The eggshell was most likely flexible and possessed at least two thin layers. Four eggs reveal blastomeres, and two embryonic stages are represented. These eggs demonstrate that the basic paradigm for the growth of the invertebrate embryo has not altered in more than half a billion years.

A unicellular zygote (fertilized egg) is converted into a multicellular organism by successive cleavages during embryonic development. Lacking mineralized tissues, however, invertebrate eggs are unlikely to escape breakdown. Fossil examples are therefore exceedingly scarce, and none reveals embryonic stages. Among the Echinodermata, for instance, only a single blastoid from the Lower Pennsylvanian of Oklahoma contains probable eggs (1). Fossil trilobite eggs were mentioned in several nineteenth-century publications, but were not conclusive (2). The trilobite embryo and the suspected pre-protaspis stage have been unknown (3). Possible ostracode eggs from the Lower Cambrian of China (4) and Lower Cretaceous of Brazil (5), as well as shrimp eggs

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[4] Chapter 6 is the manuscript published in ***Science***, v. 266, p. 637-639 (1994).

similarly from the Cretaceous of Brazil (6), are non-descript spheres (7). Possible Middle Cretaceous insect eggs from Brazil (8) have not been substantiated, but a single, Upper Cretaceous moth eggshell from Massachusetts does possess a well-preserved lepidopteran sculpture (9). In this report, we describe the first example of fossil eggs bearing delicate blastomeres.

These eggs are phosphatized and co-occur with many trilobite juveniles (protaspides and meraspides) of the eodiscid *Pagetia* sp. and an unidentified polymeroid trilobite, a few adult bradoriid ostracodes, and lots of inarticulate brachiopod valves. We liberated these fossils by dilute (~5%) acetic acid digestion of 7 kilograms of a thin, bioclastic limestone bed sandwiched between grey dolomites within the lower part of the Middle Cambrian Gaotai Formation in Duyun, Guizhou, China.

The five eggs are ovoid (Figs. 6.1 and 6.2). The lengths range from 0.30 to 0.35 mm, and the widths from 0.24 to 0.27 mm (10). The eggshell, being about 1.5 Fm thick and seemingly composed of two layers (11), was probably slightly flexible in that it was evidently bent down (Fig. 6.1B) or pushed in (Fig. 6.1E) before lithification. Polygonal structures are visible beneath the shells of two eggs under reflected light: one has its entire surface under the eggshell fully occupied by about 60 tightly packed polygons (mainly hexagons with a few pentagons and heptagons) of varying size (Fig. 6.2B); the other only has a patch of the polygon pattern preserved. We interpret the polygonal structures as blastomeres comprising the blastoderm around the yolk. Under the SEM, because of the obstruction of the eggshell only where the outermost thin shell layer is partially flaked off do its surviving parts defined in positive relief roughly outline polygonal blastomeres beneath (Fig. 6.1, A and B; Fig. 6.2A). In a third egg (Fig. 6.1C) apatite replaced polygonal blastomeres which are visible as many tightly packed convex surfaces where the eggshell has been peeled away. The fourth egg is broken (Fig. 6.1D), but where the eggshell is flaked off, polygonal holes also appear to outline blastomeres underneath. In this egg some of the cell walls are visible at the broken side, no recognizable structure is evident in the center of the egg. Fine dimples on the exterior of a fifth egg (Fig. 6.1E) may reflect some of the underlying blastomeres (12).

The number of blastomeres can be estimated from the average length of the sides of some well-defined polygons (13). Both the third and fourth eggs (Fig. 6.1, C and D) exhibit smaller polygons, and thus contain approximately twice as many cleavage cells than do each of the first two eggs (Fig. 6.1A). Presumably, these eggs belong to two successive (64-cell and 128-cell) cleavage stages. Unfortunately, no evidence is available to ascertain if gastrulation had started.

In general, the ovoid shape of the five eggs, their flexible eggshell, tightly packed blastomeres, and cleavage stages are all typical embryonic phenomena among modern invertebrates. These eggs can not be assigned unequivocally to a particular Middle Cambrian taxon. The egg morphology, the cleavage cells, and possible cleavage stages do closely resemble these features of extant arthropods more than any other invertebrate group (14, 15). We therefore infer that these Middle Cambrian eggs have an arthropod affinity. Because the assemblage does not contain juvenile ostracodes, we suggest that populations of this group hatched and reached adulthood elsewhere in the sedimentary basin. On the other hand, co-existing eodiscid and polymeroid trilobite protaspides and meraspides are abundant, indicating that these trilobites did complete their life cycles in this depositional setting. Thus, the evidence is in favor of a trilobite affinity for these eggs (16). They more likely belong to the eodiscid Pagetia sp., on the basis of their size (17). However, we cannot rule out the possibility that they might belong to a soft-bodied arthropod whose later instars were not preserved.

Early replacement of soft tissues by calcium phosphate--apatite--before substantial degradation is probably the most important taphonomic means by which soft bodies and even cellular details of tissues can be fossilized (6, 18). The fossilization of these eggs at certain stages indicate that they died during their initial embryonic development and were almost immediately replaced by apatite. However, we do not understand why this early apatite mineralization seemingly affected so few eggs, despite the multitudes probably laid, and did not lead to any soft tissue preservation for other fossils even though there was widespread phosphatization of calcitic skeletons in the Duyun fauna. These eggs preserve no obvious microbes, so we cannot ascertain whether bacterial activity was involved in the phosphatization process, as has been suggested (6, 18, 19).

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7. Cambrian spheres *Archaeooides* and *Olivooides* found from several localities in China were all described as fossils of uncertain systematic position because of their simple, non-diagnostic morphology. Some of them are oval-shaped [X. Yang, Y. He and S. Deng, *Bull. Chengdu Inst. Geol. Miner. Resour. Chinese Acad. Geol. Sci.* **4**, 91 (1983); P. Chen, *Professional Papers Strat. Palaeont.* **13**, 49 (1984)] and may be eggshells, but published illustrations are insufficient to demonstrate this.
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10. Egg size and morphology may vary within genera and species ofsome living crustaceans [G. Mura, *Crustaceana* **61**, 241 (1991); *ibid.* **63**, 225 (1992)], and chelicerates (14).

11. The thickness of the eggshell is measurable under SEM in three of the eggs. An outermost layer, 0.5 Fm thick, is determined in three eggs (Fig. 1, A to C, and E).

12. Dimples on part of the surface of the fifth egg resemble those on the blastomeres of extant crayfish eggs [J. D. Celada, P. de Paz, V. R. Gaudioso, R. Fern<ndez, The Anatomical Record **219**, 304 (1987); J. D. Celada, J. M. Carral, J. Gonz<lez, Crustaceana **61**, 225 (1991)] and may reflect partial collapse of these cells.

13. During the embryonic process, the surface area of an egg can be considered as a constant even though the number of blastomeres inside increases with growth.

$$A = \frac{3\sqrt{3}}{2}(s_1^2 + s_2^2 + s_3^2 + \ldots s_n^2) \approx \frac{3\sqrt{3}}{2} nS^2,$$

Considering, in the simplest case, polygons on the outer surface of an eggshell to be all hexagons, the surface area (A) of the egg is:

where s is the length of a side of a hexagon, S is the average length of all measured

$$\frac{3\sqrt{3}}{2} n_1 S_1^2 = \frac{3\sqrt{3}}{2} n_2 S_2^2,$$

sides, and n is the total number of hexagons. Therefore, for any two eggs, their equal surface areas can roughly be expressed as:

or $n_1/n_2=S_2^2/S_1^2$. If the number of blastomeres would double in the subsequent division stage, that is $n_1/n_2=2$, then, S_1/S_2=%2/2. The average length (S_1) of the third egg is approximately 0.008 mm, and (S_2) for the first two eggs showing blastomeres is 0.011 mm. S_1/S_2.0.7.%2/2.

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16. Trilobita are closely related to Crustacea and Chelicerata [D. E. G. Briggs and R. A. Fortey, *Science* **246**, 241 (1989); G. Budd, *Nature* **364**, 709 (1993)]. The four fossil eggs exhibiting blastomeres are much smaller but otherwise appear comparable to stage 2 and stage 3 eggs of modern horseshoe crabs (14), and their eggshells are similarly laminated.

17. Of the associated youngest trilobite instars, the protaspis of the unidentified polymeroid trilobite is about 0.50 mm long and wide, while the protaspis of *Pagetia* sp. is about 0.25 mm in our collection and 0.28-0.35 mm in previously reported specimens [J. H. Shergold, *Alcheringa* **15**, 65 (1991)]. On the basis of size, the five eggs are more likely eodiscid trilobite eggs.

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20. Work was supported by the Natural Sciences and Engineering Research Council of Canada. We thank D. M. Lehmkuhl and D. M. Martill for criticizing an earlier version of the manuscript, and Y. Yano for assistance with SEM photography.

FIGURE CAPTIONS

Fig. 6.1. Phosphatized (possibly eodiscid trilobite) eggs from the Middle Cambrian Gaotai Formation in Duyun, Guizhou, southern China. (**A**), A complete egg (DY 0002) with blastomeres, of which only a few are defined by polygons of surviving parts of the outermost thin shell layer (arrows indicate three adjacent sides shared by three polygons). (**B**), Different view of **A** showing other polygons (arrows indicate a pair of opposite sides of a polygon). Shell is bent down beside a crack at the lower left side. (**C**), An incomplete egg (DY 0003) whose other half opposite this surface has broken off. Part of its eggshell is missing so that some blastomeres beneath are visible. (**D**), A broken egg (DY 0004), whose blastomeres are visible (arrows indicate surviving normal walls of polygonal cells). (**E**), An entire egg (DY 0001) with its eggshell caved in on the right side and partially ornamented with fine depressions on the outer surface (arrowed). Scale bars, 0.1 mm. Specimens are deposited in the Chengdu Institute of Geology and Mineral Resources, Chengdu, China.

Fig. 6.2. Drawings of a Middle Cambrian arthropod (possibly eodiscid trilobite) egg with blastomeres, based on specimen in Fig. 6.1, A and B (DY 0002). (**A**), Sketch showing the surviving outermost thin layer of the eggshell (fine dotted areas) corresponding to the blastomeres beneath. d: minute debris fixed on the eggshell. (**B**), Reconstruction of the same egg.

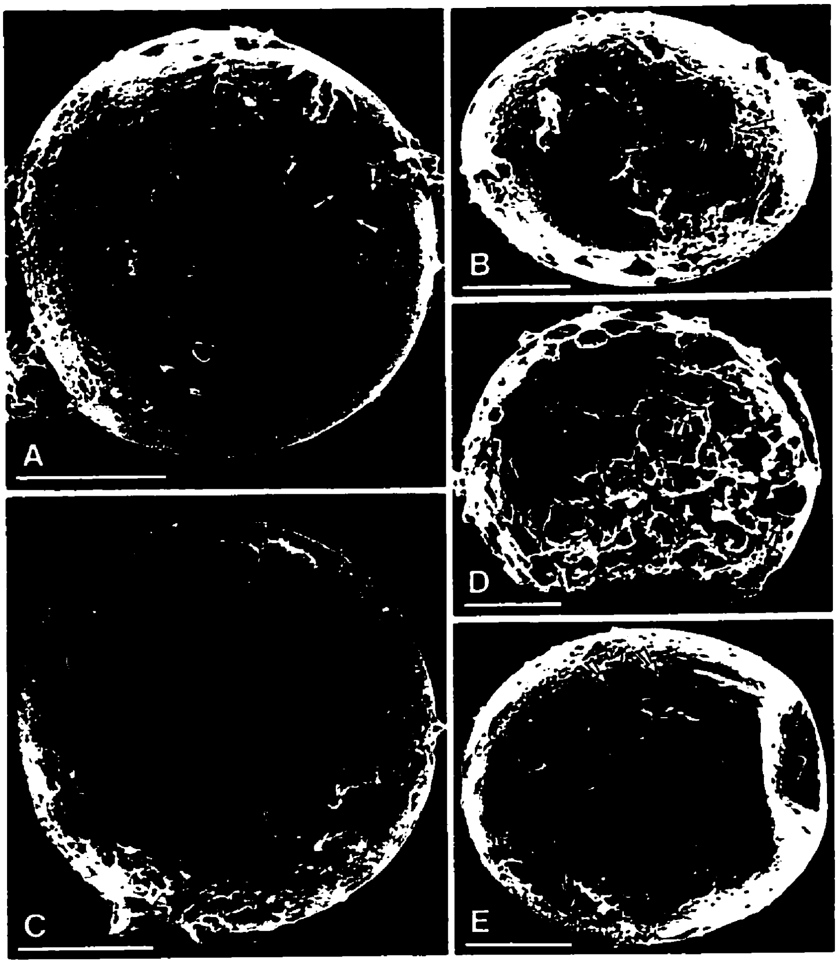

Figure 6.1.

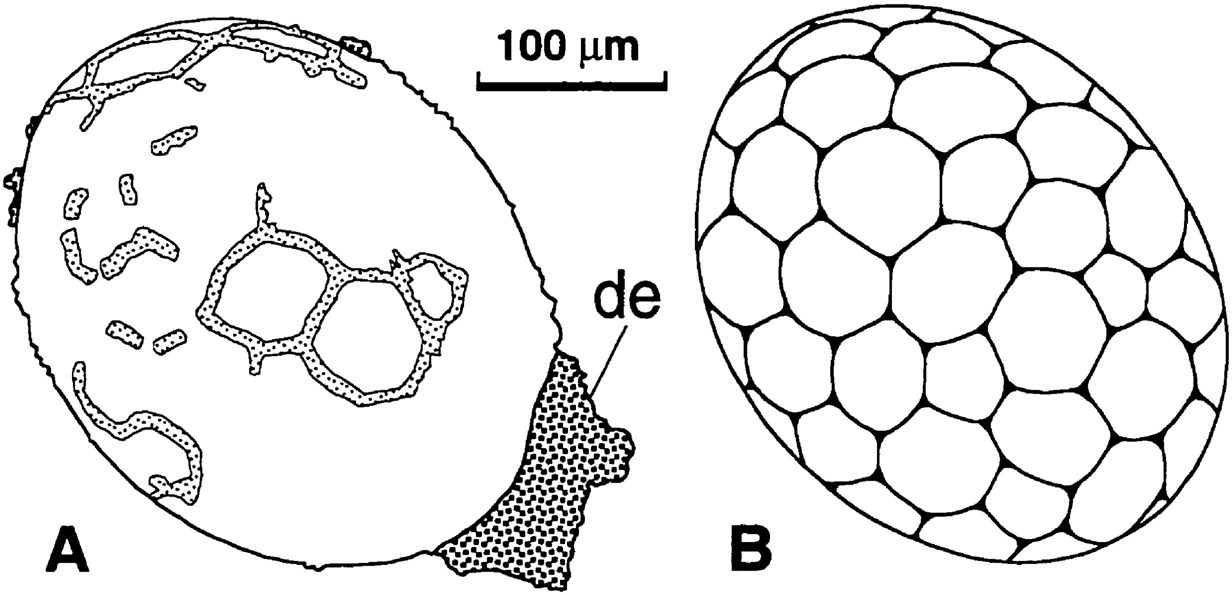

Figure 6.2.

CHAPTER 7

EARLY CAMBRIAN PALAEOSCOLECID CUTICLES FROM SHAANXI, CHINA[5]

ABSTRACT--Phosphatized, three-dimensional cuticle fragments of the palaeoscolecids Houscolex lepidotus new genus and new species, Houscolex species indeterminate, and an unidentified form are described from the Lower Cambrian Qiongzhusi Formation of Shaanxi, China. These segmented worms, characterized by regularly arranged simple plates and platelets, small circular pores and fine pits, and irregularly distributed nipplelike protuberances, are unique among known palaeoscolecids. The occurrence of such cuticles as seemingly persistent elements of phosphatized faunas suggests that wormlike organisms achieved a fairly high diversity and widespread geographic distribution during the Early and Middle Cambrian.

INTRODUCTION

WORMLIKE ORGANISMS are extremely rarely preserved as fossils by comparison with skeleton-secreting metazoans. Trace fossils are the common geological evidence for soft-bodied animals, and they record the presence of wormlike organisms in strata as old as late Vendian (Crimes, 1992). Convincing body fossils have been described from the

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Lower Cambrian (Glaessner, 1979; Sun and Hou, 1987; Hou and Sun, 1988; Hou and Bergström, 1994) and possibly the Neoproterozoic (Sun et al., 1986). Extraordinary Lagerstätten, such as the Early Cambrian Chengjiang fauna (Ramsköld and Hou, 1991; Hou and Bergström, 1994) and Middle Cambrian Burgess Shale (Conway Morris, 1977), reveal that wormlike organisms belonging to separate systematic groups underwent extensive independent, adaptive radiations at the beginning of the Phanerozoic.

Secondary phosphatization before substantial biodegradation is a crucial taphonomic mechanism whereby soft tissues and non-mineralized cuticles can be preserved in detail. With this in mind, several problematical Cambrian and Ordovician microfossil taxa have now been assigned to Palaeoscolecida (Hinz et al., 1990). Likewise, Stoibostrombus crenulatus Bengtson from the Lower Cambrian of Australia (Bengtson, et al., 1990) may also be sclerites of a wormlike organism (Conway Morris, personal commun, 1994). A comprehensive association of palaeoscolecid worms preserved in three dimensions from the Middle Cambrian of Queensland (Müller and Hinz-Schallreuter, 1993) attests to the early diversity and complexity of wormlike organisms. In this paper we describe several further phosphatized palaeoscolecid cuticles from the Lower Cambrian of China. These were recovered during sampling for phosphatized bradoriid ostracodes and therefore point to the possibility of further discoveries with more systematic collecting.

The material was extracted by weak (5 percent) acetic acid digestion of about 18 kg of limestone from a single bed, 8 cm thick, in the Qiongzhusi Formation at Qingmingtian. This is a geologically unmapped site along the Zhenping-Wuxi road, 1.2 km south of

Zhongbao, in Zhenping, southern Shaanxi, China (Figure 7.1). A complete Lower Cambrian section cannot be measured because of structural complexity and discontinuous exposure. However, from the same locality Li (1975) reported bradoriids co-occurring with *Eoredlichia (Eoredlichia)* aff. *intermedia* Lu, and Huo and Shu (1982) described 4 new bradoriid taxa. The Zhenping fauna thus belongs to the Early Cambrian *Eoredlichia-Wutingaspis* Zone, Qiongzhusi Stage, which is roughly equivalent to the upper Atdabanian of Siberia. Besides the trilobite *Eoredlichia*, the bradoriids *Zhenpingella* Lee and *Jixinglingella* Lee, the bed also yielded the univalved bradoriid *Duibianella* Shu (Zhang and Pratt, 1993) and siliceous sponge spicules (Zhang and Pratt, 1994). The dark grey, thin-bedded, plane-laminated limestone was deposited in a low-energy, relatively deep-water setting.

The palaeoscolecid cuticles described here are fragments, which prevent a complete reconstruction of these creatures, but they display some delicate ornaments, such as buttonlike plates, fine polygonal platelets, nipplelike structures, and a possible seta. Yet, these Early Cambrian ornaments are different from the wide variety documented from younger phosphatized palaeoscolecids (Kraft and Mergl, 1989; Brock and Cooper, 1993; Müller and Hinz-Schallreuter, 1993).

All previous, acid-liberated wormlike fossils are preserved as incomplete trunk fragments or isolated annuli. Infestation by possible fungal hyphae (Müller and Hinz-Schallreuter, 1993, Text-fig. 4A) and crumpling of fragments before phosphatization argues that the worms were already dead. Although co-occurring with ostracodes and siliceous sponges that were likely in situ faunal elements, our palaeoscolecid worms may have been swept from a different environmental setting, especially if the cuticles were broken mechanically. However, breakage by predators or scavengers cannot be ruled out either. Palaeoscolex is thought to have been infaunal because no distinction between the dorsal and ventral sides is apparent (Robison, 1969; Conway Morris and Robison, 1986; Kraft and Mergl, 1989). The trunk fragment of Houscolex lepidotus new genus and new species exhibits differentiated sides, so that it is conceivable that this palaeoscolecid worm was adapted for an epifaunal mode of life.

SYSTEMATIC PALEONTOLOGY

All specimens described in this paper are deposited at the Chengdu Institute of Geology and Mineral Resources, Chengdu, China.

Class PALAEOSCOLECIDA Conway Morris and Robison, 1986

Order and Family uncertain

Genus HOUSCOLEX new genus

Type species.--Houscolex lepidotus new genus and new species

Diagnosis.--Segmented worm whose annulation defined by deep intersegmental furrows. Outer surface of cuticle covered with buttonlike concave projections (plates) and fine, polygonal tubercles (platelets). Some annuli bear nipplelike projections and possibly setae.

Etymology.--After Xian-guang Hou for his contributions on palaeoscolecid worms and other soft-bodied fossils from the Chengjiang Fauna.

HOUSCOLEX LEPIDOTUS new genus and new species

Figure 7.2.1-7.2.13

Diagnosis.--As for genus.

Description.--Seven broken, curved, twisted, or folded cuticle fragments available for this new species. Distinctly arched annuli, uniform in length in individuals but varying between specimens from 40 to 130 μm, separated by deeply incised intersegmental furrows. One specimen not segmented. Outer surface of cuticle covered with tightly packed, fine polygonal platelets 2-5 μm in diameter, and offset rows of plates 9-22 μm in diameter with gently concave upper sides, either scattered among platelets, or tightly packed but separated by rows of platelets exhibiting hexagonal "sutures". All plates distributed within a longitudinal band with wavy boundaries. Inner surface of cuticle ornamented with tubercles corresponding to the plates on the outer surface. Hollow, conical, nipplelike projections of various size (50-90 μm wide at base) exhibiting irregular concentric wrinkles on outer surface, located irregularly on some annuli. One possible seta found.

Cuticle fragments exhibit distinct variation in length of segments. Those with longer segments bear more plates and platelets than fragments with shorter segments whose plates occur only along the intersegmental furrows or scattered among fine platelets. Size of plates increases with growth, but size of platelets remains the same.

Holotype.--CIGM-ZP026.

Discussion.--Houscolex lepidotus new genus and new species is distinctly annulated like other palaeoscolecids, and variations in length of the metameres (or segments) and size of plates (Figure 7.2.1-7.2.3 and 7.2.7-7.2.9) suggest that these specimens belong to different growth stages. However, it is uncertain if there is a continued increase in size of plates with growth, because one large cuticle fragment (Figure 7.2.5) bears slightly smaller plates than some of the other cuticles (Figure 7.2.7 and 7.2.10); the difference in the average diameter of plates, 17 µm versus 20 µm, may not be significant. The large fragment shows the same ornaments that other segmented cuticles possess, i.e. tightly packed buttonlike plates separated by fine platelets on the outer surface, and tubercles on the inner side (Figure 7.2.6), and we assume it belongs to H. lepidotus but comes from either a portion of the trunk without annuli, or some extremely long segment. The buttonlike plates with smooth upper surface, characteristic of H. lepidotus, have not been observed in previously described palaeoscolecids. These plates, surrounded by fine circular furrows (Figure 7.2.7-7.2.9) were probably originally small bumps or nodes, but variation in their shapes suggests that this tissue was "frozen" by phosphatization at various stages of shrinkage and degradation. Circular pores on the cuticles (Figure 7.2.10-7.2.13) are places where the plates decomposed and vanished before phosphatization. The location of the plates along one side (Figure 7.2.1, 7.2.3, 7.2.7 and 7.2.10) suggests that the ventral and dorsal sides of H. lepidotus exhibited different ornament, but we are uncertain which side is which. An increase in size and density of plates and platelets in specimens with larger annuli has been reported in Kaimenella dailyi Brock and Cooper, and argues that this occurs during growth. The plates and platelets of H. lepidotus, however, only increase in density with growth, their size remaining almost the same.

Nipplelike protuberances have been reported from Schistoscolex species indet. and aff. Hadimopanella oezguli form species I, and some were considered as paired appendages (Müller and Hinz-Schallreuter, 1993), though the arrangement of these nipples, with respect to the number of annuli between each, seems irregular. Nipplelike projections in Houscolex lepidotus similarly vary in size and do not appear to be paired (Figure 7.2.7). While these nipples are unlikely to be parapodia or appendages, their function is uncertain. Only one of them has a spine or bristle (Figure 7.2.13) which may be a seta. These nipples are concentrically wrinkled probably because they suffered some contraction before phosphatization.

Etymology.--Lepidotus (Greek), scaly.

HOUSCOLEX species indet.

Figure 7.3.1-7.3.4

Description.--Two specimens recovered, one gently curved, exhibiting fourteen ridge-like annuli defined by shallow intersegmental furrows 60 μm apart; the other with belts defined by variation in the cuticle ornament rather than furrows. The outer surface of one side covered with tightly packed spheroidal knobs about 10 μm in diameter, regularly arranged in rows with platelets 1-2 μm wide in between, whereas only platelets cover the other side. Inner surface of cuticle smooth, without ornament.

Discussion.--This species exhibits two kinds of ornament (knobby plates and fine platelets) arranged in distinct, longitudinal bands that may correspond to ventral and dorsal sides (Figure 7.3.1). It resembles Houscolex lepidotus new genus and new species but differs by having shallower furrows, ridgelike rather than arched segments, and knobby plates rather than gently concave plates. In addition, no tubercles have been observed on the inner surface.

Figured specimens.--CIGM-ZP029, CIGM-ZP053.

PALAEOSCOLECIDA genus and species indet.

Figure 7.3.5, 7.3.6

Description.--One flattened, cylindrical cuticle fragment about 0.9 mm long and 1.2 mm wide, with four complete annuli defined by narrow, relatively shallow intersegmental furrows. Each annulus 0.12 mm long with flat to gently depressed median belt containing tightly packed polygonal or circular pits 2-3 μm in diameter. Belts on either side of median belt and adjacent to each furrow bear close-packed ranks of 3-4 circular pores 14 μm in diameter, separated by some irregularly polygonal pits. Slightly sunken central part of larger pores display thin membrane with 3-5 fine holes, each about 1.5 μm in diameter. No differentiation of ornament that might refer the dorsal and ventral sides.

Discussion.--The cuticle resembles a typical palaeoscolecid in which each segment possesses one plain (unornamented) belt sandwiched between two ornamented ("papillate") belts of identical width. The belts with larger pores and finer pits, expressed as a 2121 repeat pattern (see Conway Morris and Robison, 1986), may be equivalent to the papillate and unornamented belts, respectively. However, the pores of the cuticle are too small to have housed setae and are much smaller than the regularly arranged tubercles and papillae characteristic of other palaeoscolecids. The pores, pits, and pitted membranes inside each pore may represent contracted and partially degraded tissue. We cannot give this specimen a generic assignment because of our uncertainties about how taphonomic artefacts affect cuticle structures.

Figured specimen.--CIGM-ZP025.

DISCUSSION AND CONCLUSIONS

Palaeoscolecid worms found in shales (Whittard, 1953; Robison, 1969; Glaessner, 1979; Conway Morris and Robison, 1986; Hou and Bergström, 1994) are preserved as compressed films, whereas three-dimensional examples preserved by phosphate (Kraft and Mergl, 1989; Hinz, et al., 1990; Brock and Cooper, 1993; Müller and Hinz-Schallreuter, 1993) reveal more details of the cuticle. Our palaeoscolecids occur with similarly phosphatized trilobites and ostracodes, but this assemblage is the only example so far known from South China. The compressed body fossils in the Chengjiang Fauna are approximately contemporaneous, but consist of different palaeoscolecid taxa.

Nevertheless, along with isolated sclerites of Palaeoscolecida that were previously considered problematic (e.g., Bengtson, 1977; Hinz et al., 1990), our fauna and that from Australia demonstrate a worldwide distribution for the group as a whole, and a fairly conservative morphology over a geologically long time span; they have potential biostratigraphical application (Müller and Hinz-Schallreuter, 1993). The known palaeoscolecid, annelid, and onychophoran taxa, taken together, appear to reflect the achievement of a reasonably high diversity in the Early Cambrian (Atdabanian), approximately coinciding with the diversity maximum exhibited by the ichnofauna (Crimes, 1992), part of which was no doubt due to wormlike organisms.

The Early Cambrian wormlike fossils reported here display general similarities with previously described palaeoscolecids, especially with Middle Cambrian ones from Australia. The Australian worms in general bear more complex plates and platelets, and fewer rows of plates on each annulus. In fact, our palaeoscolecid cuticles possess microstructures hitherto unknown in this group--simple buttonlike or knobby plates. The nipplelike projections may be common among these palaeoscolecids, although their function is uncertain. In addition, the fragmentary cuticle lacking segmentation (Figure 7.2.5) may come from either an especially wide annulus or a non-segmented portion of the body, but this feature has not been reported from any known phosphatized palaeoscolecid. It has the same ornaments, as the segmented fragments, but it is possible that it belongs to an unknown animal that is not a worm at all. Such quandaries emphasize the difficulties in assessing the affinity of these wormlike organisms.

A relationship between palaeoscolecid worms and nematomorphs is suggested by compressed examples in the Chengjiang Fauna exhibiting the spiny proboscis on the anterior end and hooks on the posterior (Hou and Bergström, 1994). However, no such spines and hooks have been recovered associated with cuticles in acid residues. Nothing is known about the anterior end, but the posterior end of palaeoscolecids from Australia (Müller and Hinz-Schallreuter, 1993) has four nipples seemingly unlike nematomorphic structures. It is clearly premature to assign these wormlike organisms to separate groups.

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FIGURE CAPTIONS

FIGURE 7.1--Location maps. The asterisk (*) shows the locality where the fossil worm cuticles were found.

FIGURE 7.2--Phosphatized cuticle fragments of palaeoscolecid Houscolex lepidotus new genus and new species from the Lower Cambrian Qiongzhusi Formation of Zhenping, Shaanxi, China. 1-3, paratype, CIGM-ZP027, 1, twisted and folded cuticle fragment with plates only along deeply incised furrows, is about 0.5 mm in width, suggesting that the undeformed trunk of the worm was about 0.3 mm wide, x140; 2, detail of 1, showing concave plates and fine platelets, x810; 3, opposite side of 1, tubercles on the inner surface are indicated by arrow, x140. 4, paratype, CIGM-ZP028, inner surface of fragmentary cuticle, showing tubercles along intersegmental furrows corresponding to concave plates on outer surface, x60. 5, 6, paratype, CIGM-ZP054, 5, a folded and non-segmented fragmentary cuticle, x86; 6, detail of 5, showing the densely packed plates (one of which is indicated by a white arrow), and tubercles (one is indicated by a black arrow), x270. 7-9, holotype, CIGM-ZP026, 7, cuticle fragment showing eight incompletely preserved annuli, deep intersegmental furrows, three nipplelike projections, and two longitudinal bands of different ornaments, x89; 8, 9, detail of 7: 8, showing annulated nipple, and

ornament of platelets and concave plates in circular pits, x265; *9*, a small annulated nipple, x265. *10-13*, paratype, CIGM-ZP052, *10*, a flattened cuticle fragment with nipplelike projections and a possible seta (arrowed), x137; *11-13*, detail of *10*: *11*, showing a compressed nipple (arrowed), x660; *12*, an intersegmental furrow bearing no plates but only tightly packed platelets across the lower part of the illustration, x1,080; *13*, a possible seta, x680.

FIGURE *7.3*--Phosphatized cuticle fragments of Palaeoscolecida from the Lower Cambrian Qiongzhusi Formation of Zhenping, Shaanxi, China. *1-4*, *Houscolex* species indet. *1*, CIGM-ZP029, bent cuticle fragment with the presumed ventral side starting along the lower edge (arrowed), x83; *2*, detail of *1*, showing small, knoblike plates and irregular polygonal platelets on outer surface of presumed dorsal side, x840; *3*, detail of *1*, showing outer surface of presumed ventral side with only platelets, x840; *4*, CIGM-ZP053, a fragmentary cuticle with small plates packed in belts and indistinct intersegmental furrows that are suggested by fine pits, x165. *5*, *6*, Palaeoscolecida genus and species indet.: *5*, CIGM-ZP025, flattened fragmentary cylindrical cuticle, x52; *6*, annulus of *5*, showing detail of circular pores regularly arranged in offset ranks and separated by finer pits, x490.

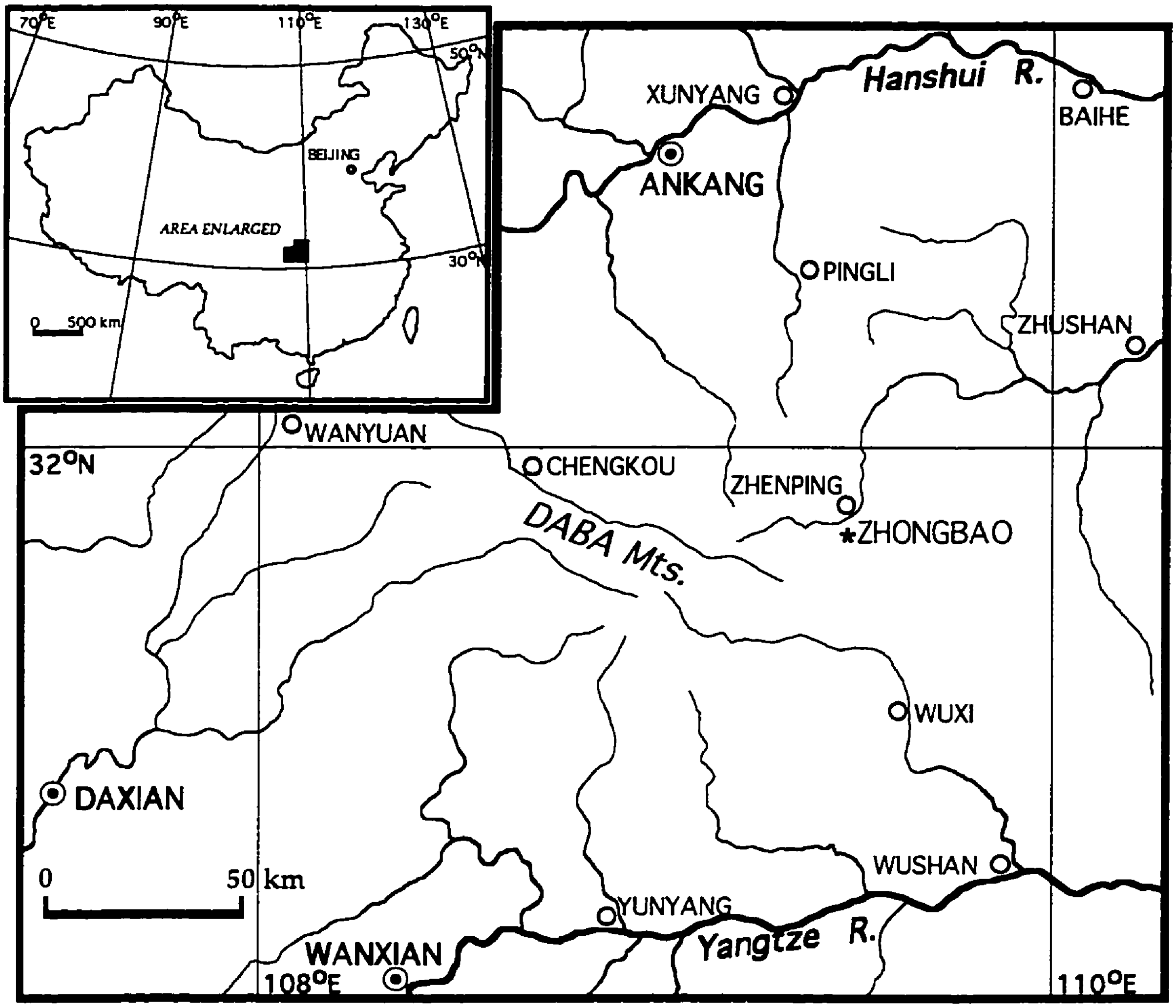
70°E
90°E
110°E
130°E
50°N
30°N
BEIJING
AREA ENLARGED
0 500 km
Hanshui R.
XUNYANG
ANKANG
BAIHE
PINGLI
ZHUSHAN
WANYUAN
32°N
CHENGKOU
ZHENPING
ZHONGBAO
DABA Mts.
WUXI
DAXIAN
0 50 km
WUSHAN
YUNYANG
Yangtze R.
WANXIAN
108°E
110°E

Figure 7.1.

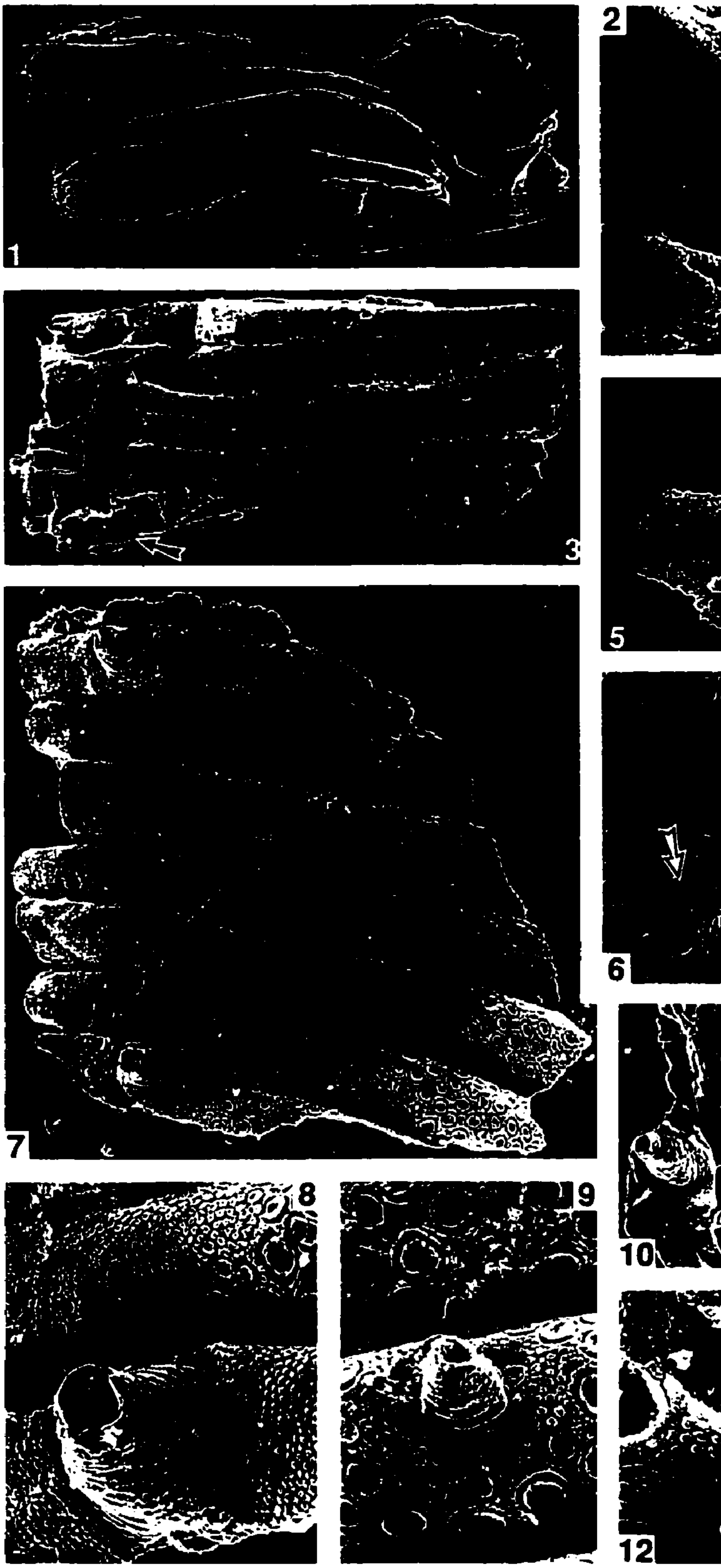

Figure 7.2.

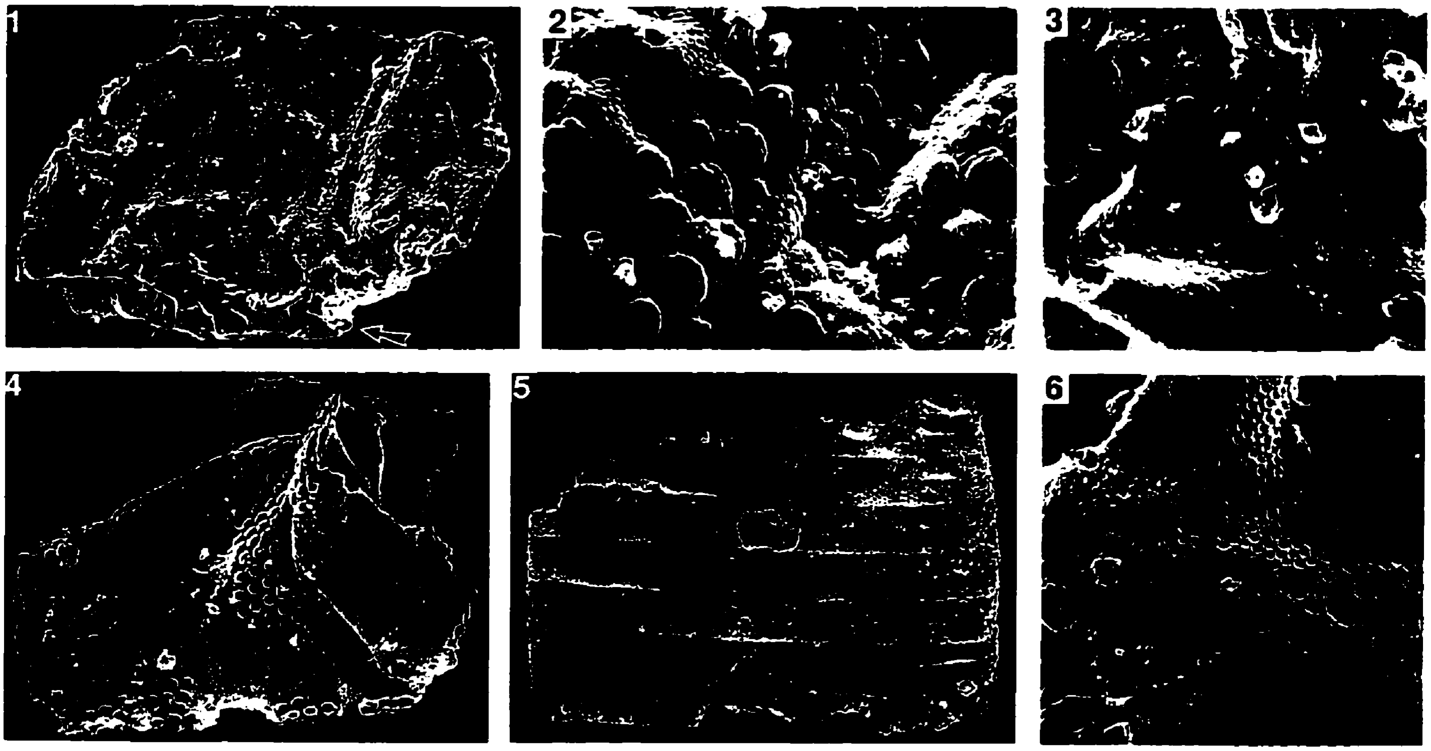

Figure 7.3.

CHAPTER 8

PROBLEMS AND PERSPECTIVES

The relatively rapid appearance of skeletal marine invertebrates at the base of the Cambrian has puzzled workers for over a century. The basic problem of the origin of life is partly constrained by limited geological and paleontological data. Yet the discovery of Burgess shale-like soft bodied faunae have provided us with a deep insight about the Early Cambrian marine invertebrates (e.g. Conway Morris et al., 1987; Ramsköld and Hou, 1991; Chen et al., 1995). Through this thesis I have tried to show that the phosphatized specimens are also an important source for the study of early metazoans and their early evolution. More importantly, phosphatized fossils, characterized by detailed three-dimensional preservation of delicate structures and ornaments of their carapaces, tiny embryos and larval instars, supply more reliable data for morphological, taxonomic, and geochemical studies. Below I outline briefly some future research directions making use of this kind of fossil preservation.

Revision of Chinese bradoriid ostracodes

Hinz-Schallreuter (1993) pointed out that the majority of known Cambrian bradoriids were described from China. However, many of these published bradoriid taxa are based on rare or ill-preserved specimens, and carapaces coming from the same locality and horizon were often assigned to different species and genera (Hou et al., 1996).

Phosphatized fossil assemblages reveal that shells belonging to a population consist of instars of different growth stages with striking variation in morphology, and some of them have been deformed to some extent during the fossilization. For example, different species of Kunmingella coming from the same horizon may be synonyms (Huo et al., 1991). A major taxonomic study is neccessary to re-examine these Chinese bradoriids, and phosphatized specimens will supply key morphological criteria. Because some phosphatized fossils were contemporaneously living with the soft-bodied Chengjiang animals, examination of material exhibiting both styles of preservations will play an important role in the revision of Chinese bradoriid ostracodes.

Molting stages and ontogenetic pattern of agnostid and eodiscid trilobites

The ontogenetic pattern of the Ordovician agnostid trilobite Trinodus elspethi Raymond, 1925 showing a series of distinct instars (Hunt, 1967) has been widely quoted (e.g. Raup and Stanley, p. 50, 1978; Robison, 1987) as providing a model or paradigm for recognizing trilobite growth stages. Hunt's work had indicated that the growth between successive instars was great enough and instar variability sufficiently low for the instars to be separated on the basis of size. In my previous studies of eodiscid trilobite ontogeny, all specimens were measured under a microscope with a precision of ±0.025 mm. However, although the early instars (including protaspides and early meraspides) can be roughly defined by measurement, later instars (including some late meraspides and all holaspides) overlapped one another (Zhang, 1989, Fig. 2; Zhang and Clarkson, 1993, Text-fig. 2).

Therefore, the eodiscid molting pattern contrasts with that seen in Hunt's agnostids. Do eodiscids possess their own unique ontogenetic process compared to agnostids so that the two trilobite groups are not as closely related as originally thought (see Walossek and Müller, 1990)? Or, might the variation in morphology shown by ontogenetic processes be an example to support Hughes' (1991) suggestion that genetic systems were less strongly canalized during the Cambrian than in later times? On the other hand, the eodiscid and agnostid patterns may not reflect a real ontogenetic process, in that specimens coming from the same bed are actually derived from mixed populations, each exhibiting slight environmentally or genetically induced variability.

Investigation of ontogenetic patterns shown by other agnostid and eodiscid trilobites will provide insight into the evolutionary relationships and exact growth patterns of these trilobite groups.

Stable isotopes in organic skeletons and secular $\delta^{13}C$ variation

The covariant carbon isotope records for both carbonate and organic carbon, and similar large-scale $\delta^{13}C$ variations observed worldwide in Vendian strata are believed to record primary secular oscillations, when combined with correlated changes of trace elements and $\delta^{18}O$ values, stratigraphic, and sedimentologic data in order to try to distinguish secular from local signals in the $\delta^{13}C$ composition (Knoll et al., 1986; Pelechaty et al., 1996). Nevertheless, the reliability of whole-rock $\delta^{13}C$ values remains questionable, because altered isotopic values have been recognized in Cambrian synsedimentary cements (Whittaker et al., 1994), and the localized depletion of $\delta^{13}C$ in seawater measured from modern carbonate platforms argues that cautious interpretation on ancient $\delta^{13}C$ variation is neccessary (Patterson and Waiter, 1994).

The rapid proliferation of skeletal organisms has made the geochemical cycling of carbon isotopes more complex since the Cambrian explosion. However, because biochemical precipitates can retain information on ancient oceanic chemistry, a comparison of carbon isotopes preserved in carbonate sediments and invertebrate skeletons should shed light on primary secular $\delta^{13}C$ variations, but such investigation on the Lower Paleozoic seems rather rare. Articulate brachiopods with low-Mg calcite shells are widely employed for stable isotopic analysis (e.g. Popp et al., 1986; Wadleigh and Veizer, 1992; Grossman et al., 1993; Qing and Veizer, 1994), despite the possibility of 'vital effects' and diagenesis (Carpenter and Lohmann, 1995). Where the trace elements Mn, Fe, Sr, and Na and $\delta^{18}O$ values suggest possible modification of whole-rock $\delta^{13}C$ data in a normal carbonate succession, do brachiopod values shift in the same direction as the whole-rock variations and at the same rate (covariantly)? Or do they just display a unique variation that may represent original signatures?

With primary low-Mg calcite skeletons, trilobites should house important $\delta^{13}C$ data for assessing Paleozoic secular variations, but the measured isotopic values have been assumed to have been modified to some extent by the fillings in their exoskeletons which were sometimes porous (Wilmot and Fallick, 1989). Recently, improved microsampling and laser techniques provide a powerful tool for isotope analysis upon extremely small samples (Dettman and Lohmann, 1995; Sharp and Cerling, 1996). By means of these new techniques, sampling trilobite skeletons without touching canal fillings may become available when basic structures and molting processes of trilobites and ostracodes are well known. Locally, phosphatized and partially phosphatized exoskeletons of eodiscid trilobites and/or ostracodes co-occur with calcite redlichiid trilobites, which may have been chemically resistant to burial diagenesis. In this case, could the calcite redlichiid skeletons contain near-pristine isotopic data, while their host carbonates have altered isotopic compositions; what are the differences housed in these organic and inorganic material? It is common that trilobites were buried with articulate brachiopods in Paleozoic strata, how would the trilobite isotopic data compare with that of brachiopods?

Future studies could select several carbonate formations within individual Ordovician to Devonian basins that contain abundant, well-preserved brachiopods and trilobites and other invertebrates originally with high-Mg calcite shells, as well as Cambrian units yielding both phosphatized and calcite trilobites. Then are could:

(1) Determine $\delta^{13}C$ and $\delta^{18}O$ values from these fossils and their coeval carbonates in continuous sequences, trying the microsampling method on trilobite skeletons and ostracodes which are likely of original calcite;

(2) Determine trace elements Mn, Sr, Na, Mg, Fe etc. from the strata and examining the trends of their variations;

(3) Analyze the alterations in carbon isotopes thought to have resulted from depositional effects, such as paleo-depth and temperature of seawater, hiatuses etc. within the strata; and

(4) Combine all data to compare the $\delta^{13}C$ excursions derived from whole-rock carbonates and organic skeletons.

Phosphatized soft-bodied fossils in southern China

Finally, It should be pointed out that all fossils described in this study were extracted from the most fossiliferous limestones within the six successions in southern China (Text-fig. 1.2), where there are still many phosphatized fossil-bearing horizons lacking thorough study. In addition, more materials will be available elsewhere in southern China. With economic development, more new roads through mountainous areas will not only make it easy to access these areas, but also provide new roadcuts through Cambrian strata containing phosphatized fossils.

Although we do not know exactly under what situations it took place, phosphatization can preserve soft bodies and appendages of marine animals. Such miraculous preservation is mainly known from Orsten limestones in Sweden (Walossek and Müller, 1992). Somewhat semilar but rare examples have also been reported from Georgina Basin of Australia (Walossek et al., 1993) and Newfoundland (Kaustuv and Fåhraeus, 1989). These soft-bodied fossils always seem to co-occur with lots of phosphatized empty shells. So far there are lots of empty shells but no soft bodied fossils found in all known phosphatized fossil assemblages in southern China. Much further work is neccessary to find the extraordinary horizons, and the recent discovery of Early Cambrian metazoan embryos in southern China (Bengtson and Zhao, 1997) indicates the great possibility of finding phosphatized soft-bodied fossils there -- a dream I really hope would become true soon.

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FIGURE CAPTIONS

Plate 1

Figs. 1-9: Duibianella sp. from the Lower Cambrian Qiongzhusi Formation in Zhenping, Shaanxi. 1, 2, ZP 0001, dorsal and ventral views of univalved carapace, X250, X475. 3, ZP 002, dorsal view of univalved carapace showing paired gland openings (black arrows) and paired small nodes (white arrows), X210. 4-7, CIGM-ZP1001, laterally bent (univalved) carapace, 4-6, oblique dorsal, posterior, and dorsal views, all X245. 7, detail of anterior marginal rim, X345. 8, CIGM-ZP1002, right view of bivalved carapace, X108. 9, CIGM-ZP1003, dorsal view of bivalved carapace showing newly developed hinge line with U-shaped posterior extremity (arrowed), X220.

Plate 2

Figs. 1-15: Duibianella sp. from the Lower Cambrian Qiongzhusi Formation in Zhenping, Shaanxi. 1, CIGM-ZP1004, right valve with relatively short posterior spine (arrowed), X82. 2, 3, CIGM-ZP1005, lateral and anterior views of right valve showing node-like posterior spine (arrowed), both X60. 4, 5, CIGM-ZP1006, lateral and anterior views of left valve, both X63. 6, CIGM-ZP1007, slightly deformed carapace showing duplicature (arrowed), X78. 7-10, CIGM-ZP1008, mature right valve, 7-9, lateral, posterior, and anterior views, all X56. 10, detail of anterior node, X195. 11, CIGM-ZP1009, detail of muscle scar on immature left valve, X280. 12, detail of 1, showing muscle scar and fine polygonal ridges, X280. 13, CIGM-ZP1010, detail of nodes under anterior dorsal margin, X200. 14, detail of 2, showing conical nodes, X141. 15, CIGM-ZP1011, detail of domal nodes, X280.

Plate 3

Figs. 1-12: *Kunmingella douvillei* (Mansuy) from the Lower Cambrian Qiongzhusi Formation in Jinyang, Sichuan. 1-3: JY0006, univalved carapace with a pair of posterior marginal spines (right one broken) and gland openings (arrowed). 1, dorsal view, X292. 2, 3, oblique left and posterior views, both X250. 4, CIGM-JY0010, left view of bivalved carapace, X162. 5, JY0007, right view of bivalved carapace with gland opening (arrowed), X196. 6, JY0008, right view of bivalved carapace, X110. 7, CIGM-JY0011, detail of posterior marginal spine and reticulate ornament, X410. 8, CIGM-JY0012, detail of posterior part of right valve with reticulate ornament, X465. 9, CIGM-JY0013, detail of anterior part of right valve with paired gland openings (arrowed), X253. 10, CIGM-JY0014, right view of squashed carapace, X58. 11, JY0009, oblique dorsal view of bivalved carapace, X78. 12, detail of 11 showing paired gland openings (arrowed) and muscle scar behind anterior node, X160.

Plate 4

Figs.1-18: *Kunmingella douvillei* (Mansuy) from the Lower Cambrian Qiongzhusi Formation in Jinyang, Sichuan. 1, CIGM-JY0015, detail of posterior lobe on left valve, X112. 2, CIGM-JY0016, left view of bivalved carapace whose two valves are partially separated along posterior dorsal margin, X43. 3, CIGM-JY0017, detail of posterodorsal part of right valve, X115. 4, CIGM-JY0018, right valve, X37. 5, CIGM-JY0019, posterolateral view of left valve, X28. 6, 7, CIGM-JY0020, lateral and dorsal views of right valve, both X21. 8-11, CIGM-JY0021, mature left valve, 8, lateral view, X15. 9, detail of the posterior lobe, X42. 10, 11, detail of fine reticulate ridges and tubercles, X207, X550. 12, CIGM-JY0022, detail of reticulate ornament on anterior margin, X210. 13, 14, CIGM-JY0023, left valve, 13, inside view, X21. 14, detail of laminated carapace, X127. 15, 16, CIGM-JY0024, right valve, 15, lateral view, X15. 16, detail of healed scar, X61. 17, CIGM-JY0025, detail of paired gland openings (black arrow) and small nodes (white arrows) above muscle scar, X57. 18, CIGM-JY0026, detail of paired gland openings (black arrow) and small nodes (white arrows) above muscle scar, X57.

Plate 5

Figs. *1*-*17*: *Kunmingella* (*Spinokunmingella*) *typica* Huo and Shu from the Lower Cambrian Qiongzhusi Formation in Jinyang, Sichuan. *1*, CIGM-YS0001, right view of bivalved carapace, X180. *2*, *3*, CIGM-YS0002, right and dorsal views of bivalved carapace, both X140. *4*-*6*, CIGM-YS0003, lateral, anterolateral, and oblique dorsal views of right valve with paired gland openings (arrowed), all X87. *7*, CIGM-YS0004, detail of anterior part of right valve showing muscle scar, X130. *8*, CIGM-YS0005, left view of bivalved carapace, X103. *9*, CIGM-YS0006, dorsal view of opened carapace, X250. *10*, CIGM-YS0007, ventral view of bivalved carapace, X110. *11*, *12*, CIGM-YS0008, squashed carapace, *11*, left dorsal view, X114. *12*, detail of posterior articulate suture and ornament of fine tubercles, X490. *13*, *14*, CIGM-YS0009, bivalved carapace, *13*, dorsal view, X67. *14*, detail of bifurcated dorsal spines, X460. *15*, CIGM-YS0010, detail of anterior part of right valve showing paired gland openings (arrowed) and muscle scar, X240. *16*, CIGM-YS0011, detail of anterior node and muscle scar, X147. *17*, CIGM-YS0012, opened carapace, X63.

Plate 6

Figs. *1*-*15*: *Kunmingella* (*Spinokunmingella*) *typica* Huo and Shu from the Lower Cambrian Qiongzhusi Formation in Jinyang, Sichuan. *1*-*3*, CIGM-YS0013, left valve, *1*, *2*, lateral dorsal and anterolateral views, both X46. *3*, detail of posterior lobe, X213. 4, 5, CIGM-YS0014, left valve, 4, posterolateral view, X46. 5, detail of posterior lobe, X258. 6, CIGM-YS0015, right valve, X55. 7, 8, CIGM-YS0016, lateral dorsal and anterolateral views of left valve, both X42. 9, CIGM-YS0017, left valve with bent ventral spine, X31. 10, CIGM-YS0018, posterolateral view of mature right valve, X34. 11-13: CIGM-YS0019, mature right valve, 11, 12, lateral and dorsal views, both X25. 13, detail of anterior part showing paired gland opening (arrowed), X63. 14, CIGM-YS0020, detail of fine reticulate ridges and tubercles, X188. 15, detail of the reticulate ornament on margin of 14, X192.

Plate 7

Figs. 1-3: *Shizhudiscus longquanensis* S. G. Zhang from the Lower Cambrian Shuijingtuo Formation in Pengshui, Sichuan. 1, CIGM-PS1001, dorsal view of protaspis of stage 0, X250. 2, CIGM-PS1002, lateral ventral view of protaspis of stage 0, X250. 3, PSO 5718, oblique dorsal view of meraspid stage 0 cranidium, X102. Figs. 4, 5: *Tsunyidiscus* sp. from the Lower Cambrian Shuijingtuo Formation in Zhenba, Shaanxi. 4, CIGM-ZB0001, ventral view of protaspis of stage 0, X200. 5, CIGM-ZB0002, dorsal view of protaspis of stage 0, X200. Figs. 6-11: *Pagetia* sp. from the Middle Cambrian Gaotai Formation in Duyun, Guizhou. 6, 7, CIGM-DY0005, dorsal and oblique lateral views of protaspis, both X185. 8, CIGM-DY0006, lateral dorsal view of early meraspid pygidium, X152. 9, CIGM-DY0007, lateral dorsal view of meraspid pygidium, X100. 10, 11, CIGM-DY0008, dorsal and lateral dorsal views of meraspid cranidium, both X140.

Plate 8

Figs. 1-7: Shizhudiscus longquanensis S. G. Zhang and Zhu from the Lower Cambrian Shuijingtuo Formation in Pengshui, Sichuan. 1, PSO 5610, left view of early meraspid (M0) pygidium, X175. 2, CIGM-PS1003, right view of later stage of early meraspid (M0) pygidium, X130. 3, CIGM-PS1004, left dorsal view of meraspid (M1) pygidium, X112. 4, PSO 5617, left view of early holaspid (H0) pygidium, X113. 5, CIGM-PS1005, dorsal view of meraspid cranidium, X92. 6, PSO 5718, left dorsal view of meraspid cephalon, X118. 7, CIGM-PS1006, dorsal view of early holaspid second or third thoracic segment, X74. Figs. 8-13: Tsunyidiscus sp. from the Lower Cambrian Shuijingtuo Formation in Pengshui, Sichuan. 8, CIGM-PS1007, dorsal view of meraspid cranidium, X117. 9, CIGM-PS1008, ventral view of meraspid cranidium, X106. 10, CIGM-PS1009, dorsal view of early meraspid (M0) pygidium, X170. 11, CIGM-PS1010, dorsal view of early holaspid (H0) pygidium, X78. 12, CIGM-PS1011, dorsal view of broken holaspid second or third thoracic segment, X52. 13, CIGM-PS1012, dorsal view of holaspid first thoracic segment, X52.

Plate 9

Figs. *1*-*3*, *7*-*14*: *Tsunyidiscus longispinus* S. G. Zhang from the Lower Cambrian Shuijingtuo Formation in Zhenba, Shaanxi. *1*, CIGM-ZB2001, dorsal view of protaspis, X200. *2*, CIGM-ZB2002, oblique dorsal view of protaspis, X200. *3*, CIGM-ZB2003, dorsal view of meraspid cranidium, X60. *7*, ZB9Ca001, oblique ventral view of enrolled meraspis of stage 1, X162. *8*, CIGM-ZB2004, oblique dorsal view of enrolled meraspis of stage 1, X162. *9*, CIGM-ZB2005, oblique ventral view of enrolled meraspis of stage 0, X147. *10*, *11*, CIGM-ZB2006, enrolled meraspis, *10*, ventral view, X100. *11*, detail of partially fused joint, X196. *12*, CIGM-ZB2007, posterior view of enrolled meraspis, X100. *13*, CIGM-ZB2008, anterior view of enrolled meraspis, X106. *14*, CIGM-ZB2009, detail of partially developed joint between first thoracic segment and rest of pygidium, X270. Figs. *4*-*6*: *Shizhudiscus* sp. from the Lower Cambrian Shuijingtuo Formation in Zhenba, Shaanxi. *4*, *5*, CIGM-ZB2010, right dorsal and dorsal views of meraspid cranidium, *both* X127. *6*, CIGM-ZB2011, right dorsal view of holaspid cranidium, X51.

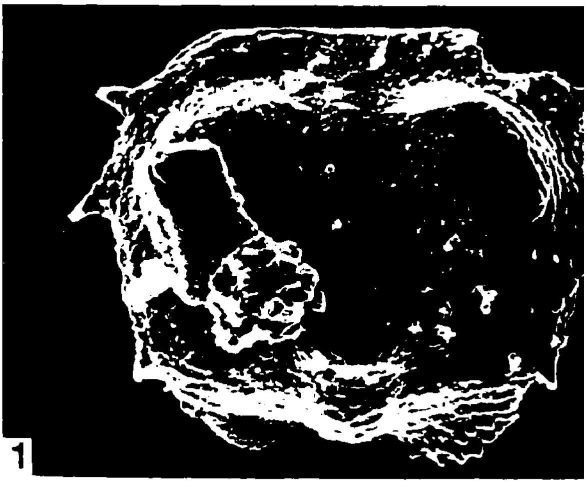
Plate 10

Figs. *1*-*10*: Eodiscid new genus and species from the Lower Cambrian Shuijingtuo Formation in Pengshui, Sichuan. *1*, CIGM-PS1013, ventral view of protaspis, X210. *2*, CIGM-PS1014, left dorsal view of early meraspid cranidium, X137. 3, CIGM-PS1015, dorsal view of early meraspid pygidium, X158. 4, CIGM-PS1016, dorsal view of late meraspis, X86. 5, CIGM-PS1017, lateral ventral view of meraspid stage 2 pygidium, X84. 6, CIGM-PS1018, lateral dorsal view of meraspid stage 2 pygidium, X62. 7, CIGM-PS1019, dorsal view of articulated first and second thoracic segments, X78. 8, CIGM-PS1020, ventral view of partially preserved left fixigena and occipital spine, X92. 9, CIGM-PS1021, ventral view of right genal spine, X100. 10, CIGM-PS1022, anterior dorsal view of second or third thoracic segment, X84. Figs. 11-14: Tsunyidiscus longispinus S.G. Zhang from the Lower Cambrian Shuijingtuo Formation in Zhenba, Shaanxi. 11, CIGM-ZB2012, ventral view of second and third thoracic segments articulated to pygidium, X75. 12, CIGM-ZB2013, lateral dorsal view of holaspid cranidium, X53. 13, CIGM-ZB2014, lateral dorsal view of holaspid pygidium with third thoracic segment attached, X67. 14, CIGM-ZB2015, lateral dorsal view of second and third thoracic segments, X45.

Plate 11

Figs. 1-13. Eodiscid new genus and species from the Lower Cambrian Shuijingtuo Formation in Pengshui, Sichuan. 1, CIGM-PS1023, dorsal view of protaspis, X220. 2, 3, CIGM-PS1024, dorsal and lateral dorsal views of protaspis, both X220. 4, CIGM-PS1025, dorsal view of meraspid cranidium, X150. 5, CIGM-PS1026, ventral view of meraspid cranidium, X126. 6-8, CIGM-PS1027, dorsal, oblique dorsal, and posterior dorsal views of meraspid cranidium, all X100. 9, CIGM-PS1028, dorsal view of late meraspid cranidium, X100. 10, CIGM-PS1029, dorsal view of early meraspid pygidium, X120. 11-13, CIGM-PS1030, meraspid pygidium, 11, dorsal view, X85. 12, detail of marginal spines, X270. 13, detail of axial rings, X320.

PLATE 3.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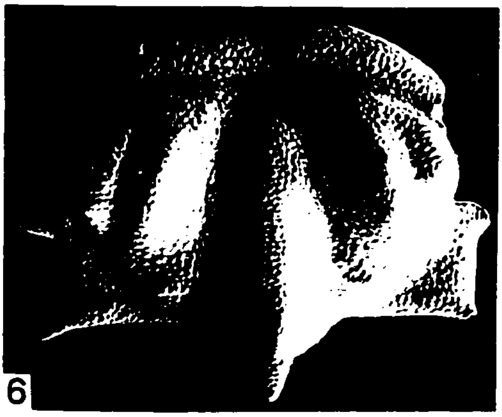
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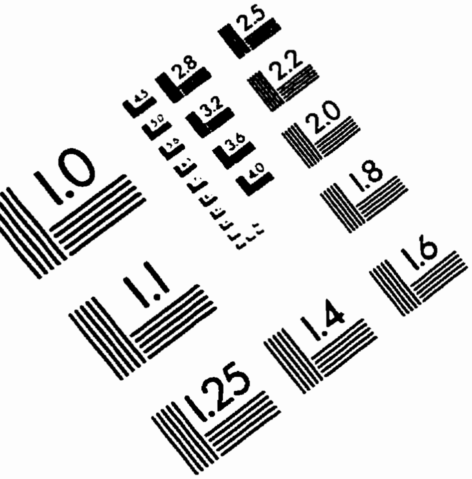
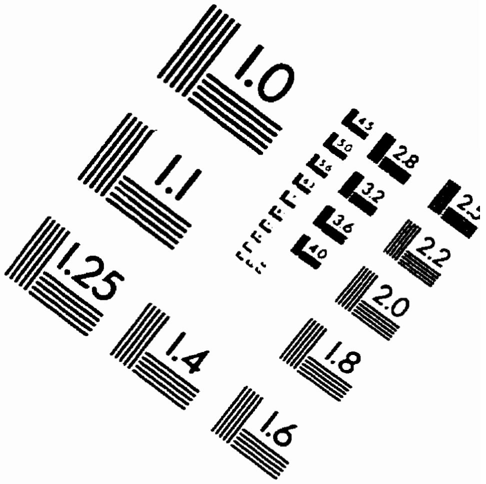
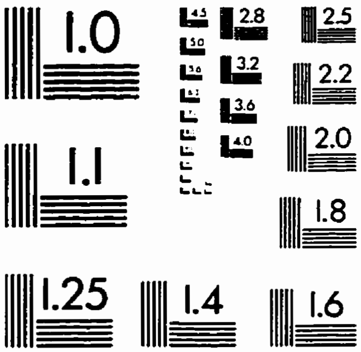
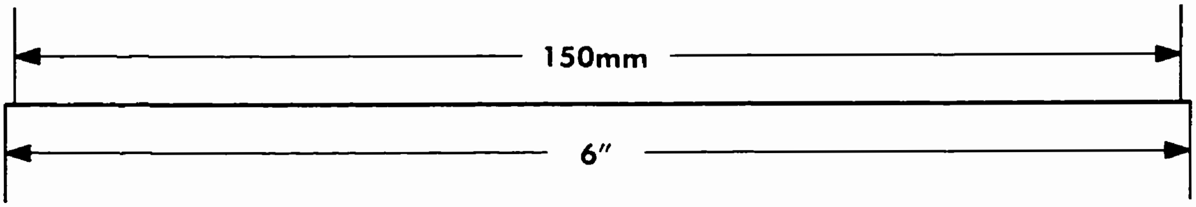
PLATE 11.

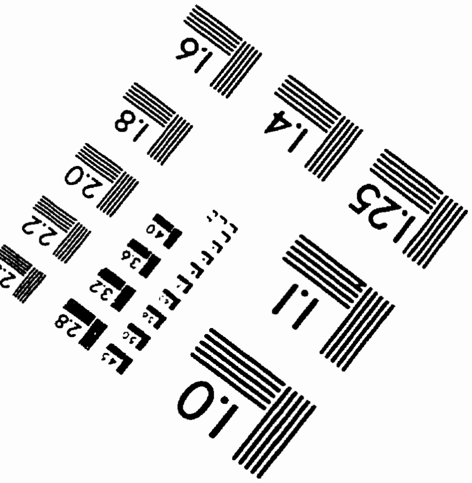
IMAGE EVALUATION TEST TARGET (QA-3)

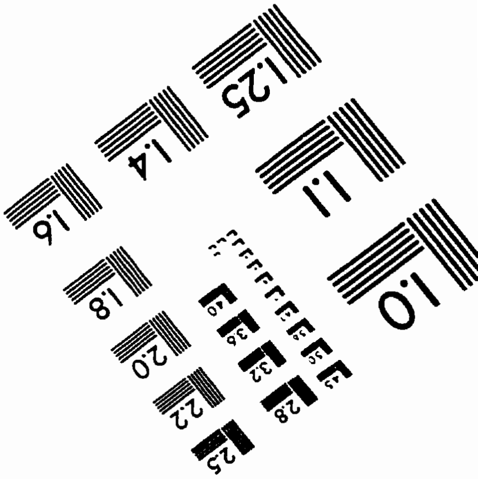












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