CAMBROCLAVES AND PARACARINACHITIDS, EARLY SKELETAL PROBLEMATICA FROM THE LOWER CAMBRIAN OF SOUTH CHINA

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ABSTRACT. Cambroclaves are a major group of sclerite-bearing metazoans, known from the Lower Cambrian of China (south China, Xinjiang), USSR (Kazakhstan) and Australia. *Zhijinites longistriatus* Qian is redescribed on the basis of abundant material from the Hongchunping Formation at Maidiping, Sichuan. Sclerites show extensive morphological variability and have a taphonomic history of endolithic infestation and diagenetic phosphatization, the latter leading to replication of wall ultrastructure. *Deiradoclavus trigonus* gen. et sp. nov. and *Deltaclavus graneus* gen. et sp. nov. are younger cambroclaves recovered from the Guojiaba Formation near Kuanchuanpu, Shaanxi, and the Shuijingtuo Formation at Taishanmiao, Hubei. Both taxa bore a cataphract scleritome, composed of interlocking sclerites. In *Deltaclavus* articulated series of sclerites include 'arm-like' structures. Paracarinachitids may be related to cambroclaves, and are described on the basis of isolated sclerites of *Paracarinachites spinus* Yu from the Yuhucun Formation of Meishucun, Yunnan. *Protopterygotheca leshanensis* Chen from the Hongchunping Formation of Maidiping is included in the paracarinachitids, and is described on the basis of isolated sclerites bearing prominent flanges on either side of the spatulate axis. The primary function of the scleritomes of cambroclaves and paracarinachitids may have been protective, but in the absence of intact scleritomes both the palaeoecology and affinities of these groups are uncertain. The new class Cambroclavida is proposed.

THE irruption of skeletal faunas close to the Precambrian–Cambrian boundary (Conway Morris 1987, 1989*a*) has attracted wide attention on two principal counts. First, there is debate as to whether the acquisition of skeletons (*a*) was mediated by extrinsic factors, such as changes in ocean chemistry, and/or (*b*) represents a biological response such as providing a defensive cover against durophagous predators and offering greater support to soft tissues. The second point of discussion is the part these early skeletal faunas played in the major adaptive radiations that are often referred to as the 'Cambrian explosion'. Evidence for metazoan diversification is readily apparent from both the record of trace fossils (Crimes 1989) and Burgess Shale-type soft-bodied assemblages (Conway Morris 1989*b*), but by taphonomic necessity the bulk of the evidence must come from skeletal remains. It has become apparent that many of the earliest of these forms are of problematic affinity, bearing no clear relationship to known phyla. Although some taxa continue to languish in a taxonomic limbo, recent work has demonstrated the presence of several major groups. All are extinct, but their status probably deserves the cognomen, in terms of orthodox taxonomy, of phylum on account of their distinctive body-plans (but see Conway Morris 1989*c*). Such groups now include the tommotiids, coeloscleritophorans, anabaritids, cambroclaves and the possibly related paracarinachitids, the last two of which are the subject of this paper. With the exception of the tubicolous anabaritids, all these groups share a skeletal arrangement of sclerites that presumably coated the exterior body to form the scleritome. Reconstruction of the original scleritome ideally relies on articulated material such as might occur in a Konservat-Lagerstätte. With the halkieriids (Coeloscleritophora) comparisons with the Burgess Shale *Wiwaxia* allowed the latter to act as a model for scleritome reconstruction (Bengtson and Conway Morris 1984), and this may now be tested further on account of the discovery of articulated halkieriids in the Lower Cambrian of north Greenland (Conway Morris and Peel 1990). In the remaining cases, however, sclerite arrangement must be inferred from either rare specimens showing fusion or functional analysis of areas of articulation between adjacent sclerites.

[Palaeontology, Vol. 34, Part 2, 1991, pp. 357–397, 9 pls.]

CAMBROCLAVES

Cambroclaves are represented by a distinctive group of sclerites that consist of a circular to oval base that bears a spine, usually elongate. They are recorded from the Lower Cambrian of China (Text-fig. 1), Kazakhstan, and Australia. However, they appear to be unknown from other parts of the world, including the equivalent-aged sections in Mongolia, the Siberian platform, and Canada. In the past, it has been found useful to make a distinction between sclerites with a sub-circular base bearing a prominent spine (zhijinitid morph) and those with a more elongate base, often having a dumb-bell shape, with the spine arising from the anterior half (cambroclavid morph). The orientation of cambroclaves follows that outlined by Mambetov and Repina (1979, fig. 8), with the prominent spine assumed to arise from the anterior end of the dorsal surface. In the absence of any articulated scleritomes, overall sclerite attitude with respect to the entire animal, assumed to be a bilaterally symmetrical metazoan, is not known.

Scleritomes that appear to have consisted of either entirely zhijinitids or predominantly cambroclavids with a small proportion of zhijinitids are both known. The former type is documented in some detail here on the basis of Chinese material of *Zhijinites longistriatus* Qian, while cambroclavids have received extensive study on the basis of well-preserved material of a new species of *Cambroclavus* from South Australia (Bengtson *et al.* 1990). Reconstructions of cambroclave scleritomes may also be inferred with varying degrees of confidence from descriptions in the literature. However, the wide morphological variability of the sclerites has resulted in excessive use of form-taxa by some authors, and one aim of the extensive synonymy list proposed here for *Z. longistriatus* is to encourage a classification designed to lead to more reliable scleritome reconstructions. In addition to the two basic sclerite types mentioned above, two other variants are reported on the basis of scleritomes inferred to have consisted of (*a*) oval sclerites bearing a ridge-like spine (*Deiradoclavus* gen. nov.), and (*b*) sclerites with a predominantly triangular outline (*Deltaclavus* gen. nov.).

The first report of cambroclaves was by Zhong [Chen] (1977), who mentioned and illustrated material from Guizhou and Sichuan provinces as *Zhijinites* sp. However, as none of the formalities of his taxonomic description accords to those laid down by the International Commission for Zoological Nomenclature, this reference to *Zhijinites* must be taken as a nomen nudum. Formal descriptions of *Zhijinites* (*Z. longistriatus*, *Z. minutus*), on the basis of material from near the town of Zhijin, west of Guiyang in Guizhou Province (Text-fig. 1), were made available shortly afterwards by Qian (1978*a*, see also 1978*b*). This and adjacent localities in Guizhou have continued to provide abundant material of *Zhijinites* (Chen 1979; Qian and Yin 1984*a*, *b*; Wang *et al.* 1984*a*, *b*), as have other localities (Text-fig. 1) in Sichuan (Chen 1979; Yin *et al.* 1980*a*, *b*; Yang *et al.* 1983; He *et al.* 1984), Yunnan (Jiang 1980, 1982; Luo *et al.* 1984*a*) and Hubei provinces (Chen 1979; Qian *et al.* 1979). Numerous species of *Zhijinites* have been erected, most of which are probably synonymous (see below). In addition the genera *Heterosculpotheca* Jiang, 1982 and *Parazhijinites* Qian and Yin 1984*b*, are both regarded as junior synonyms of *Zhijinites*. Furthermore, what are evidently specimens of *Zhijinites* have been referred to the conodont-like *Fomitchella* (Yin *et al.* 1980*a*), the halkieriid *Sachites* (Yin *et al.* 1980*a*) and the hyolith *Allatheca* (Yang *et al.* 1983).

Notwithstanding the taxonomic confusion that appears to accompany our existing understanding of *Zhijinites* from south China, in the majority of samples it seems that the sclerites are derived from the dispersal of a scleritome composed exclusively of zhijinitid morphs. There is, however, evidence

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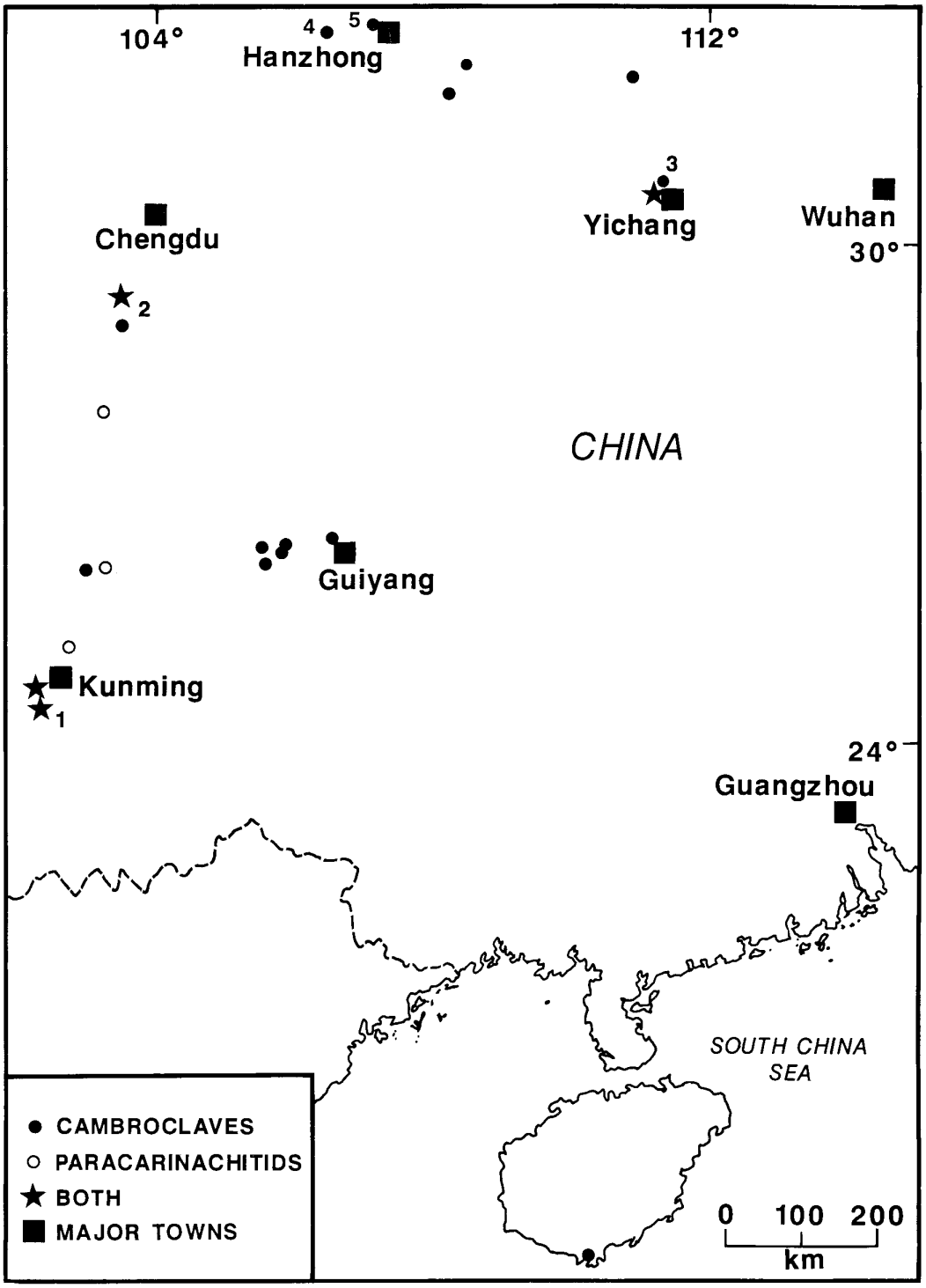
TEXT-FIG. 1. Distribution of cambroclaves and paracarinachitids in China. The numbers refer to localities from which material described herein has been recovered: 1, Meishucun, Yunnan (see Text-fig. 6); 2, Maidiping, Sichuan (see Text-fig. 3); 3, Taishanmiao, Hubei (see Text-fig. 5); 4, Xuanjiangping, Shaanxi; 5, Liangshan, Shaanxi (for both see Text-fig. 4). In addition to these occurrences cambroclaves are reported also from Xinjiang province, China (Qian and Xiao 1984), Kazakhstan, USSR (Mambetov and Repina 1979) and Australia (Bengtson *et al.* 1990). Paracarinachitids are reported also by Kerber (1988) from southern France.


104°
112°
Hanzhong
4
5
3
Yichang
Wuhan
Chengdu
30°
2
CHINA
Guiyang
Kunming
1
24°
Guangzhou
SOUTH CHINA SEA
CAMBROCLAVES
PARACARINACHITIDS
BOTH
MAJOR TOWNS
0 100 200
km

that in some stratigraphically higher cambroclaves such morphs persisted as a minor component in a scleritome otherwise composed of cambroclavid sclerites. For example, in reconstructing an Australian cambroclave the occasional zhijinitid morphs were regarded as an integral part of the scleritome (Bengtson *et al.* 1990). This decision was based on the presence of intermediate forms which showed a progressive reduction of the posterior end, general similarities of ornamentation, and consistent co-occurrence with the more abundant cambroclavid morphs. It is for this reason that a number of Chinese species placed in *Zhijinites* are regarded tentatively as more probably being derived from a cambroclavid scleritome, rather than once constituting a scleritome composed of only zhijinitids. One such instance might be *Z. intermedius*, and perhaps *Z. claviformis*, from the Lower Cambrian Yurtus Formation of Xinjiang Province (Qian and Xiao 1984) that could be attributable to the same scleritome that yielded elements referred to *Cambroclavus* (= *Sugaites*) *bicornis*. Similarly, zhijinitid morphs (*Z. claviformis*, *Z. cordiformis*) co-occurring with cambroclavid sclerites in the upper Lower Cambrian (Damao Group) of Yaxian County, Hainan Island (Text-fig. 1) (Jiang and Huang 1986) may all be derived from the same scleritome. Duan (1984) described zhijinitid-morphs, which he attributed to *Tanbaoites* (*T. porosus*, *T. spiculosus*) from the Xihaoping Formation of Hubei Province (Text-fig. 1). However, they co-occur with a plethora of cambroclavid taxa (nine species placed in *Cambroclavus*, *Sinoclavus* and *Phyllochiton*) that may all be derived from a single scleritome. What may be similar cambroclavids have also been recorded from strata of Atdabanian age from a section at Xiaoyangba in Zhenba County, Shaanxi (Text-fig. 1) (Xie 1988, fig. 1).

It is clear, therefore, that until a more rigorous approach to scleritome reconstruction in Chinese cambroclaves is undertaken, little headway can be expected in draining the swamp of form-taxonomy that mires present efforts to introduce a degree of order. This is also exemplified in the interpretation of cambroclaves from Maly Karatau and Talassky Ala-Too, Kazakhstan (Mambetov *in* Mambetov and Repina 1979; see also Missarzhevsky and Mambetov 1981). Mambetov provided the first description of the cambroclave morph in the form of *Cambroclavus antis*. In addition a zhijinitid-morph was distinguished as *C. undulatus*, which both Jiang (1982) and Duan (1984) transferred to *Zhijinites*. As the stratigraphic range of *C. antis* and *Z. undulatus* only partly overlap, it is possible that each was derived from a separate scleritome. It is also conceivable, however, that the concept of *Z. undulatus* is incompletely understood. Zhijinitid-morphs that co-occur with *C. antis* (Mambetov *in* Mambetov and Repina 1979, pl. 13, figs 2, 10, 13) appear to differ from those collected from a separate horizon (Mambetov *in* Mambetov and Repina 1979, pl. 13, figs 1, 4, 11, 12), and it may be that only the latter belong to *Zhijinites* s.s., having been derived from a scleritome composed solely of zhijinitids. Yet another type of cambroclave, *Pseudoclavus singularis* (Mambetov *in* Mambetov and Repina 1979, pl. 14, figs 5, 7, 10, 11) represents a distinctive variety of cambroclave, apparently unique to Kazakhstan. The status of the remaining taxon, *C. clavus*, described by Mambetov *in* Mambetov and Repina (1979, pl. 13, figs 3, 5, 7–9), is somewhat uncertain, but it seems to be a zhijinitid-like morph with a conspicuous spine and diminished base.

Although sclerites are almost invariably found isolated owing to both post-mortem decay of any intervening soft tissue and the exigencies of the extraction technique of acid digestion and sieving, their original arrangement may be preserved in rare instances as fused associations. These were noted first by Mambetov (*in* Mambetov and Repina 1979, pl. 14, figs 6, 8, 9) who depicted sclerites of *C. antis* deployed in orderly rows. Amongst the well-preserved cambroclavids from the Atdabanian Ajax Limestone of South Australia rare examples of two sclerites fused in a longitudinal direction were noted (Bengtson *et al.* 1990). Such specimens confirm the function of the anterior ventral and posterior dorsal facets. In addition, outline shape of these Australian cambroclavids shows how they would have interlocked to form a cataphract (chainmail-like) arrangement (Text-fig. 11B), and this lends credence to the idea that the sclerites might have formed a protective coating on a metazoan. Analogies to the wiwaxiids and halkieriids, where entire specimens are known, might suggest that cambroclaves were also worm or slug-like. However, unusual examples of articulated series of sclerites in *Deltaclavus graneus* gen. et sp. nov. (see below) and lack of knowledge of associated soft parts makes these analogies distinctly tentative.

The analysis of the new Australian species of *Cambroclavus* also revealed the sclerites to have a very wide degree of morphological variability, encompassing not only radical differences in typical cambroclavid types, but also reduction towards a zhijinitid condition of sub-circular base surmounted by prominent spine (Bengtson *et al.* 1990). While the possibility cannot be dismissed that any one individual bore a restricted range of sclerite morphs, it is considered more likely that mutual accommodation in shape between adjacent sclerites would have led to extensive variation across the body. For the most part, published illustrations of cambroclaves are insufficient to gauge reliably the extent of morphological variability. However, the likelihood of extensive synonymies within suites of sclerites, ostensibly belonging to a plethora of nominal taxa, from localities such as Hubei (Duan 1984; Qian and Yin 1984*b*) and Xinjiang provinces (Qian and Xiao 1984) argue for morphological variability being widespread in cambroclaves.

PARACARINACHITIDS

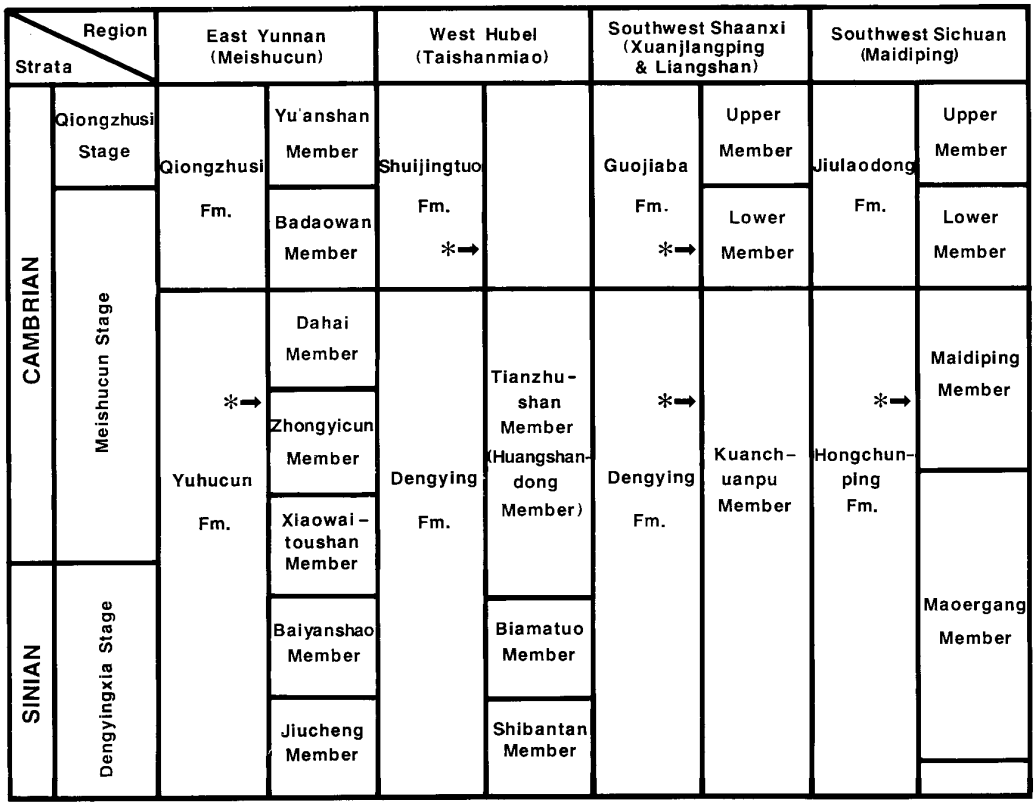
These distinctive sclerites have been reviewed critically by Qian and Bengtson (1989), who recognized four species (the type species *Paracarinachites sinensis*, and also *P. columellatus*, *P. parabolicus* and *P. spinus*). Paracarinachitids have a narrow spatula-like form with a median row of spines, and evidently grew incrementally. Although best known from South China (Qian and Bengtson 1989), sclerites from the Montagne Noire of southern France are important because they show also a flange (Kerber 1988). Here, we describe material probably attributable to *P. spinus*, but differing in occurring as single sclerites rather than articulated associations where the sclerites are arranged in a row. In *Protopterygotheca leshanensis* Chen in Qian *et al.*, 1979 sclerite form is especially clear on account of well-developed flanges, but the diagnostic paracarinachitid spines are only seldom evident. Ultimately it may transpire that *Protopterygotheca* Chen, 1979, should be taken as a senior synonym of *Paracarinachites* Qian and Jiang, 1982 (see Qian and Bengtson 1989), but this is premature on existing evidence. Qian and Bengtson (1989) proposed that paracarinachitids and zhijinitids are closely related. This may well be correct for *P. spinus*, but the remaining three species of *Paracarinachites* (and the related sclerites of *Protopterygotheca* and *Scoponodus*) may be better treated as a group distinct from the cambroclaves. In addition, the possibility that *Ernogia* (see Qian and Bengtson 1989, pp. 100–102, figs 64 and 65) be included in the roster of paracarinachitids may also bear further consideration. Qian and Bengtson (1989) considered this option briefly, on account of both overall shape and growth incrementation. The nodular ornamentation on the exterior of *Ernogia* stands in contrast to the median spines of *Paracarinachites*, but this difference may be of relatively minor importance given the more or less smooth appearance of most sclerites of *P. leshanensis* described herein.

STRATIGRAPHY AND LOCALITIES

The material described herein comes from the following horizons and localities:

1. *Zhijinites longistriatus*. All the material illustrated here was obtained from Beds 36 and 37 of the Maidiping Member, Hongchunping Formation (Text-fig. 2), exposed at the Maidiping section near to Emei, Sichuan Province (Text-fig. 3). This section is one of many Precambrian–Cambrian Boundary sections located around Emei Mountain (see He *et al.* 1984, fig. 4-1), but its stratigraphy and fossil content have received particularly detailed attention by several workers (e.g. Yin *et al.* 1980*a*, *b*; He and Yang 1982; He *et al.* 1984). Zhijinitids were reported by Zhong [Chen] (1977, p. 123), Chen (1979, p. 281), and Yin *et al.* (1980*a*, pp. 178–179; see also synonymy list for apparently erroneous assignments to *Fomitchella* and *Sachites hastatus*).

Comparable material was obtained from the Dananguo section, Liangshan (Text-fig. 4), located 3 km from the Oriental Instrument Plant factory and 10 km north-west of Hanzhong (Fu 1983, fig. 1; Ding *et al.* 1983, fig. 2). Here the Yangjiakon member of the Dengying Formation (Text-fig. 2) (Fu's placement of this part of the section in the Guojiaba Formation is less likely, because correlations suggest it to be equivalent to the deeper water Kuanchuanpu Member exposed west of Hanzhong in the Ningqian area (see Xing and Yue 1984; Conway Morris and Chen 1989)) is composed near its top of sandy glauconitic limestones. It yields abundant zhijinitids (Fu 1983; Ding *et al.* 1983) which, however, are generally somewhat smaller than those recovered

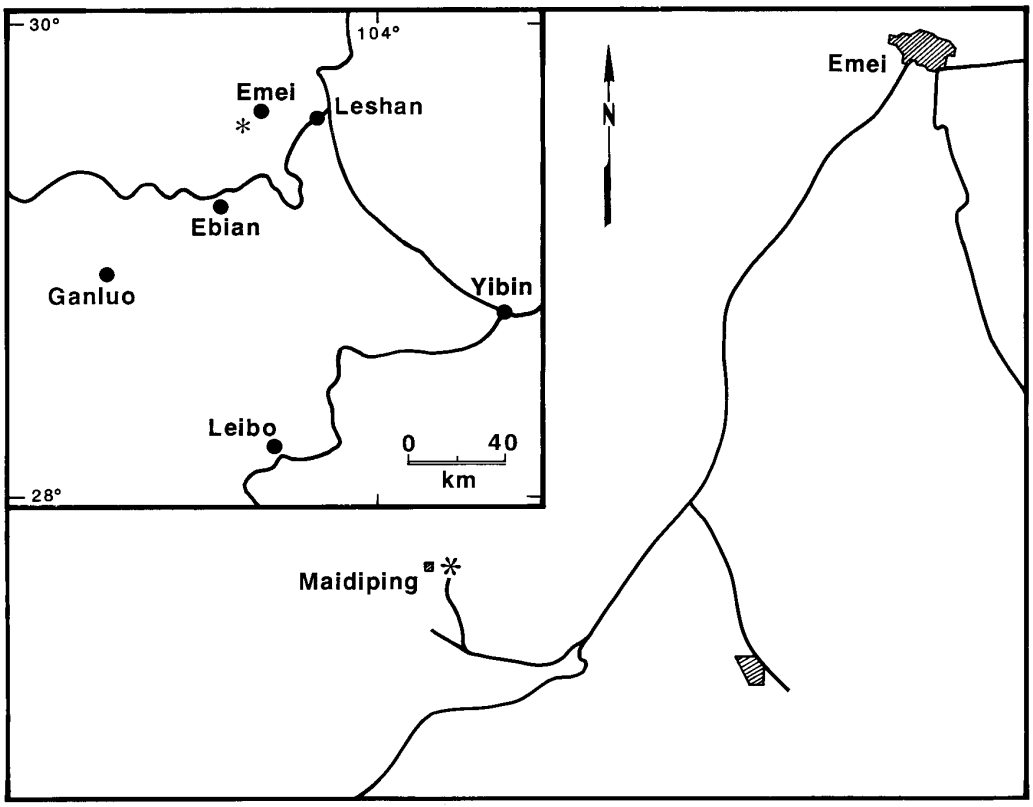


TEXT-FIG. 2. Summary stratigraphic chart for the Sinian–Cambrian boundary sequence in South China (see Text-fig. 1 for position of localities). Asterisked arrows refer to stratigraphic horizons of occurrence of cambroclaves and paracarinachitids, see text for further details. Based on table 8-1 of Ding *et al.* (1984).

from Maidiping. In addition to zhijinitids the productive sample yielded also abundant *Hyolithellus*, rare *Protohertzina* (cf. Fu 1983) and spicules. From the overlying shales of the Guojiaba Formation (equivalent to the Qiongzhusi Formation) at Liangshan Chen (1985) has described trilobites.

2. *Deiradoclavus trigonus* gen. et sp. nov. Abundant specimens were recovered from a calcareous horizon (thin limestones overlying beds with calcareous concretions) in the otherwise largely clastic Guojiaba Formation (Text-fig. 2) (see Chen *et al.* 1975, fig. 2). The outcrop forms part of the Xuanjiangping section, and is located in a stream about 1500 m southeast of the hamlet of Xuanjiangping (Text-fig. 4). The underlying strata, especially of the Kuanchuanpu Formation, have received extensive attention on account of their abundant small skeletal fossils and proximity to the Precambrian–Cambrian Boundary (e.g. Shizhonggou section, Xing and Yue 1984; Xing *et al.* 1984; Piaojiaya section (Text-fig. 4), Conway Morris and Chen 1989). However, apart from reports of *Tommotia* (Qin and Yuan 1984), the small skeletal fossils of the Guojiaba Formation appear to have received little attention. In addition to *Deiradoclavus* the sample yielded *Tannuolina zhangwentangi* (Conway Morris and Chen 1990*b*; Qin and Yuan's (1984) report on *Tommotia* may refer to this taxon), *Pelagiella* sp., *Actinotheca*, bradoriids, unidentified tubes, and other problematica.

3. *Deltaclavus graneus* gen. et sp. nov. Abundant material was recovered from the lower Shuijingtuo Formation (Text-fig. 2; see also Zhou and Xu 1987), exposed in the Taishanmiao section, near the village of Taishanmiao, Hubei Province (Text-fig. 5). The sample was a fallen block in a roadside quarry about 250 m south of the Precambrian–Cambrian Boundary as locally defined within the Tianzhushan member of the

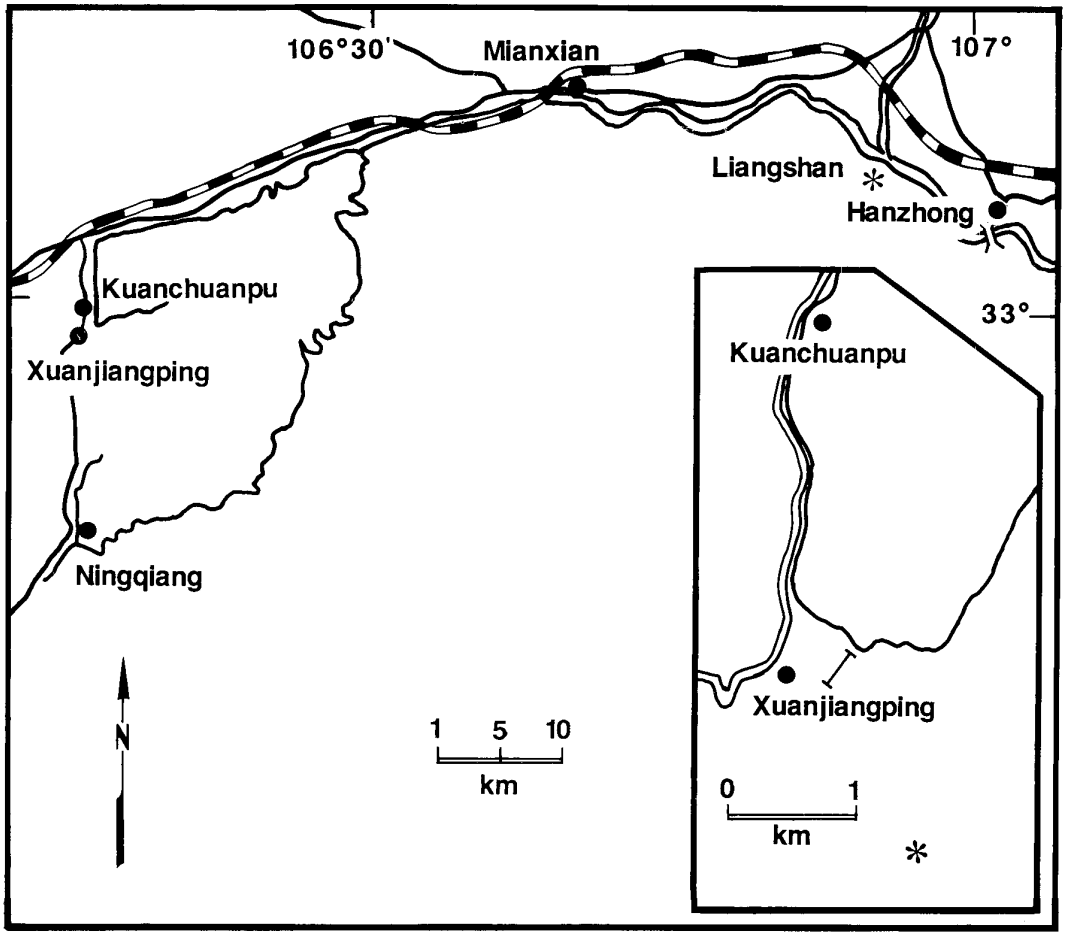


TEXT-FIG. 3. Locality map of region around Emei (Sichuan), showing location of Maidiping section (asterisked). Based on fig. 1 of Yin *et al.* (1980*b*) and fig. 4.1 of He *et al.* (1984).

Dengying Formation (see Conway Morris and Chen (1990*a*) for further details of locality and associated fauna, including the problematic *Blastulospongia*).

Despite a variety of stratigraphic terms, for the most part correlation of the Lower Cambrian around the Yangtze platform of South China (Text-fig. 2) is reasonably straightforward (e.g. Xing *et al.* 1984). Accepting the existing scheme of correlations it would appear that the zhijinitids from Maidiping (Sichuan) and Meishucun (and Liangshan, Shaanxi) are of approximately the same age, falling into the lower part of the *Paragloborilus–Siphogonuchites* assemblage. *Deiradoclavus* gen. nov. from the lower Guojiaba Formation (Shaanxi) and *Deltaclavus* gen. nov. from the lower Shuijingtuo Formation are somewhat younger, and about the same age as one another. These two genera appear to be closely related, and it is to be expected that similar cambroclaves will be found in due course in equivalent strata such as the Badaowan member of the Qiongzhusi Formation (Yunnan) and the Jiulaodong Formation (Sichuan) (Text-fig. 2). These are predominantly clastic units, but so far investigation of carbonate horizons in both formations (Conway Morris and Chen, 1990*b*; see also Qian and Bengtson 1989) has not revealed any material.

4. *Paracarinachites spinus*. Numerous specimens were recovered from dolomites of Bed 7 of the Zhongyicun member, Yuhucun Formation (Text-fig. 2) exposed at the Xiawaitoushan section of the Kunyang Phosphorite Mine, at Meishucun, Yunnan Province (Text-fig. 6) (Luo *et al.* 1980, 1982, 1984*a*, *b*). The Meishucun locality has attracted widespread interest on account of it being the Chinese stratotype candidate for the Precambrian–Cambrian Boundary. To date, this taxon has been chiefly documented from articulated series of sclerites from this horizon and the overlying Bed 8 of the Dahai Member (Text-fig. 2) (see Qian and Bengtson



TEXT-FIG. 4. Locality map of region near Hanzhong (Shaanxi), showing locations of section near Liangshan (asterisk on main map) and near Xuanjiangping (asterisk on inset map), and also Piaojiaya section (see Conway Morris and Chen 1989). Based on fig. 6-1 of Xing and Yue (1984).

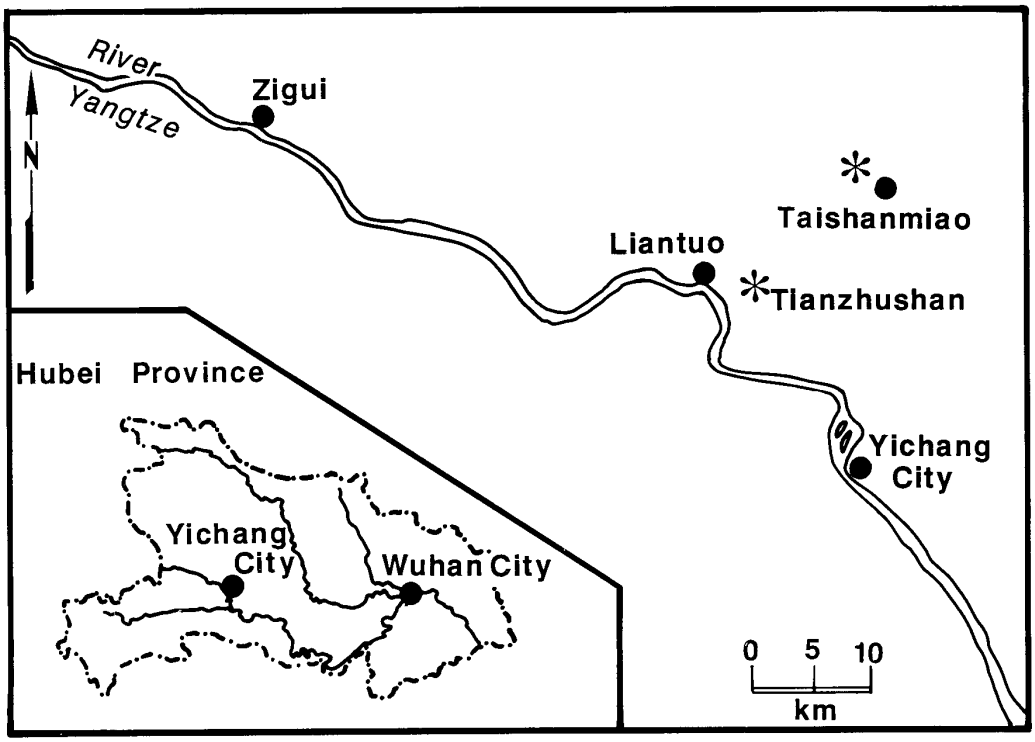
1989; He and Xie 1989), and the abundant isolated sclerites are less well known (He and Xie 1989, pl. 1, figs 20 and 22).

5. *Protopterygotheca leshanensis*. This material, which only seldom has the median spines diagnostic of other paracarinachitids present, was obtained from the same horizons at Maidiping, Emei (Text-fig. 3) as the specimens of *Z. longistriatus* (see above). The type material of this taxon comes from the Tianzhushan section in Hubei (Text-fig. 5).

SYSTEMATIC DESCRIPTIONS

Class CAMBROCLAVIDA nov.

Diagnosis. Calcareous(?) sclerites with variously shaped base bearing an elongate spine, forming a scleritome that ranged from articulated cataphract array to individual sclerites studding surface, apparently separated by unmineralized tissue.



TEXT-FIG. 5. Locality map of region around Yichang (Hubei), showing location of Taishanmiao and Tianzhushan sections (asterisked). Based on fig. 2-1 of Chen *et al.* (1984).

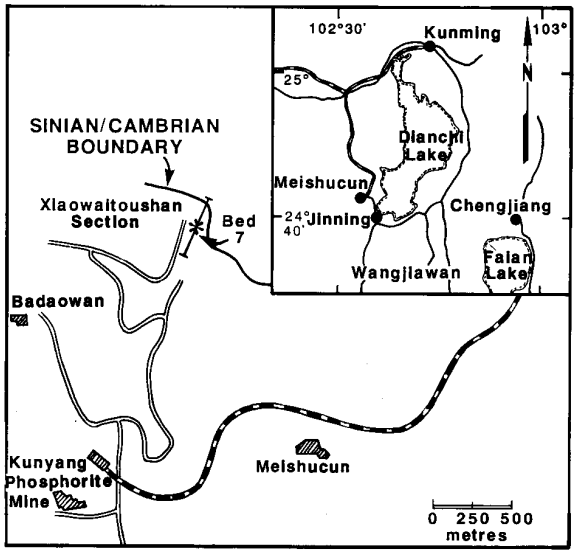
Family ZHIJINITIDAE Qian, 1978*a*

Emended diagnosis. Sclerites composed of base and elongate spine, now hollow, formerly filled with soft tissue? Base may be subcircular to elongate. In the latter case it may have prominent constriction imparting dumb-bell shape, and usually articulatory facets. Dorsal surface ornamentation frequently of radiating low ridges. Spine elongate, usually recurved posteriorly, transverse section varies from circular to elongate. Original composition probably calcareous.

Component genera. (1) *Zhijinites* Qian, 1978*a* (junior synonyms include *Sachites* sensu Yin *et al.*, 1980*a*, *non* Meshkova, 1969; *Fomitchella* sensu Yin *et al.*, 1980*a*, *non* Missarzhevsky *in* Rozanov *et al.*, 1969; *Heterosculpotheca* Jiang, 1982; *Parazhijinites* Qian and Yin, 1984*b*). (2) *Cambroclavus* Mambetov *in* Mambetov and Repina, 1979 (junior synonyms include *Phyllochiton* Duan, 1984; *Sinoclavus* Duan, 1984; *Sugaites* Qian and Xiao, 1984; and probably *Isoclavus* Qian and Zhang, 1983; *Tanbaoites* Duan, 1984; *Wushichites* Qian and Xiao, 1984; and *Zhijinites* (in part) sensu Qian and Xiao, 1984; and Jiang and Huang, 1986; see above). (3) *Deiradoclavus* gen. nov. (4) *Deltaclavus* gen. nov.

ZHIJINITES Qian, 1978*a*

Type species. Zhijinites longistriatus Qian, 1978*a*.



TEXT-FIG. 6. Locality map of region around Meishucun (Yunnan), showing location of Bed 7 of the Xiaowaitoushan section (asterisked). Based on figs 1 and 2 of Luo *et al.* (1984*b*).

Diagnosis. Sclerite base subcircular to somewhat elongate, ventral base gently concave, dorsal surface convex. Margin usually entire, occasionally with prominent cleft that may be enclosed to leave perforation. Spine elongate, inclined, more or less straight. Transverse section of spine variable from subcircular to concavo-convex, ornamentation variable, including prominent transverse ridges, longitudinal ribbing to more or less smooth.

Zhijinites longistriatus Qian, 1978*a*

Plates 1–3; Text-figs 7 and 11*a*

1977 *Zhijinites* sp. Zhong [nomen nudum], p. 123, pl. 3, fig. 7; pl. 4, figs 22–27.
1978*a* *Zhijinites longistriatus* Qian, p. 34, pl. 2, fig. 5*a*, *b*.
1978*b* *Zhijinites longistriatus* Qian, p. 350, pl. 142, fig. 5*a*, *b*.
1978*a* *Zhijinites minutus* Qian, p. 34, pl. 2, fig. 6*a–c*.
1978*b* *Zhijinites minutus* Qian, p. 350, pl. 142, fig. 4*a–c*.
1979 *Zhijinites annae* Chen [nomen nudum], p. 281, fig. 3*d*.
1979 *Zhijinites costatus* Chen [nomem nudum], p. 281, fig. 3*b*.
1979 *Zhijinites dictyoformise* Chen [nomen nudum], p. 281, fig. 3*e*.
?1979 *Zhijinites lubricus* Qian *et al.*, p. 225, pl. 4, figs 14 and 15.
1979 *Zhijinites minutus* Lu, pl. 1, figs 6 and 7.
1979 *Zhijinites longistriatus* Lu, pl. 1, figs 19 and 20; pl. 2, figs 2 and 11.
?1980 *Zhijinites lubricus* Zhao *et al.*, p. 49, pl. 3, fig. 21.
?1980*a* *Zhijinites lubricus* Yin *et al.*, p. 178, pl. 19, figs 11 and 12.
1980*a* *Zhijinites longistriatus* Yin *et al.*, p. 179, pl. 19, figs 8 and 10.
1980*a* *Zhijinites minutus* Yin *et al.*, p. 179, pl. 19, fig. 9.
?1980*a* *Fomitchella* sp. Yin *et al.*, pl. 19, fig. 7.
1980*a* *Sachites hastatus* Yin *et al.*, p. 195, pl. 18, fig. 9 (?non pl. 18, fig. 30).
?1980*b* *Zhijinites lubricus* Yin *et al.*, p. 65.
1981 *Zhijinites minutus* Xiang *et al.*, pl. 1, fig. 15.
1982 *Zhijinites longistriatus* Yin *et al.*, pp. 287, 291.

1982 *Zhijinites minutus* Yin *et al.*, pp. 287, 291.
1982 *Zhijinites longistriatus* Jiang, p. 181, pl. 17, figs 8, 9, 19.
?1982 *Zhijinites lubricus* Jiang, p. 182, pl. 17, fig. 13.
1982 *Zhijinites minutus* Jiang, p. 182, pl. 17, figs 6, 7, 20.
?1982 *Zhijinites undulatus* Jiang, p. 182, pl. 17, fig. 11 (non fig. 12, 12*a* ? = *Paracarinachites spinus*).
?1982 *Zhijinites umbelletes* Jiang, p. 182, pl. 17, fig. 10, 10*a*.
1982 *Heterosculpotheca pheneres* Jiang, p. 166, pl. 13, figs 23, 23*a*, 24, 25.
?1983 *Zhijinites lubricus* Fu, p. 416, pl. 1, figs 12 and 13.
?1984 *Zhijinites lubricus* Qian, pl. 3, fig. 8.
1984 *Zhijinites minutus* Qian, pl. 3, fig. 7.
?1984 *Zhijinites* sp. Qian, pl. 3, fig. 16.
?1983 *Allatheca nanjiangensis* [nomen nudum] Yang *et al.*, p. 95, pl. 1, fig. 14.
1984*a* *Zhijinites longistriatus* Qian and Yin, pl. 4, fig. 14.
1984*a* *Zhijinites minutus* Qian and Yin, pl. 5, fig. 14.
1984*b* *Zhijinites longistriatus* Qian and Yin, pp. 215, 218, pl. 1, figs 12–15.
1984*b* *Zhijinites cordiformis* Qian and Yin, pp. 215, 219, pl. 1, figs 20–23.
1984*b* *Zhijinites minutus* Qian and Yin, pp. 215, 218, text-figs 1.3 and 3*c*.1, 2; pl. 1, figs 1–11.
1984*b* *Zhijinites panduriformis* Qian and Yin, pp. 215, 218, 219, pl. 1, figs 16–19.
1984*b* *Zhijinites triangularis* Qian and Yin, pp. 215, 219, pl. 2, figs 14–21.
?1984*b* *Parazhijinites quizhouensis* [sic] Qian and Yin, p. 220, text-fig. 3.3; pl. 2, figs 1–8.
1984*a* *Zhijinites longistriatus* Wang *et al.*, pl. 22, figs 13 and 14.
1984*a* *Zhijinites minutus* Wang *et al.*, pl. 22, figs 1–4.
1984*a* *Zhijinites panduriformis* Wang *et al.*, p. 177, pl. 22, figs 9–12.
?1984*a* *Parazhijinites guizhouensis* Wang *et al.*, p. 177, pl. 22, figs 5–8.
1984*b* *Zhijinites longistriatus* Wang *et al.*, pl. 4, fig. 9.
1984*b* *Zhijinites minutus* Wang *et al.*, pl. 5, fig. 14.
1984*a* *Zhijinites minutus* Luo *et al.*, pl. 10, fig. 24.
1984 *Heterosulpotheca* [sic] *phaneres* [sic] Jiang, fig. 4.3.
1984 *Heterosulpotheca* [sic] *phoneres* [sic] Jiang, pl. 2, fig. 8.
1984 *Zhijinites minutus* Jiang, pl. 3, fig. 11.
?1987 *Parazhijinites quizhouensis* [sic] Liu, fig. 3A.
?1987 *Zhijinites triangularis* Liu, fig. 3B.
1989 *Zhijinites* sp. Chen, pl. 1, fig. 1.

Diagnosis. As for the genus.

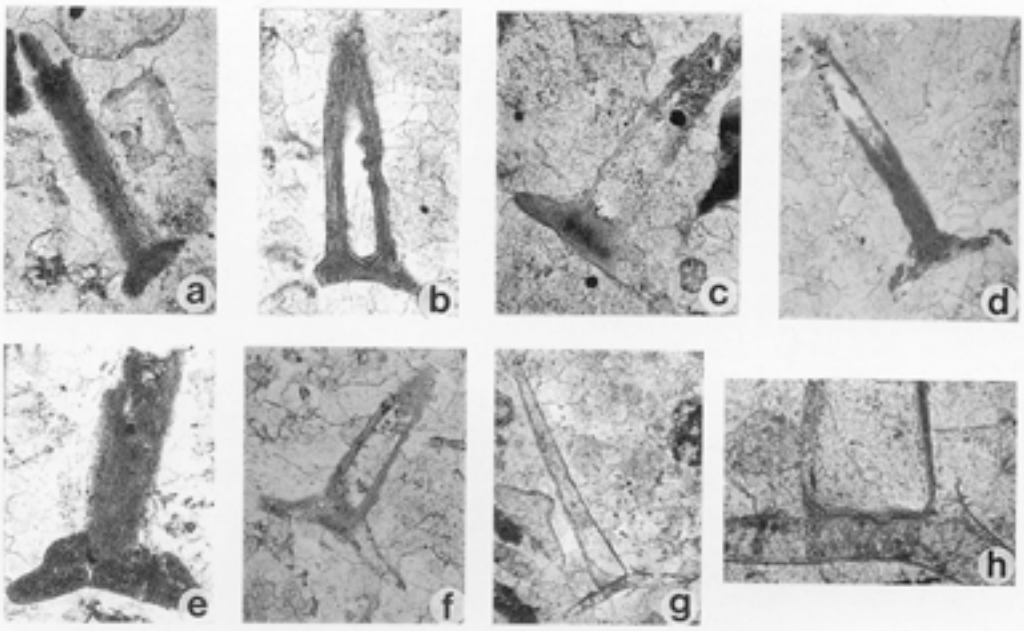
Holotype. Institute of Geology and Palaeontology, Academia Sinica, Nanjing, ASN 33676 (Qian 1978*a*, pl. 2, fig. 5).

Material illustrated here. Institute of Geology (Beijing), Academia Sinica IGAS-BC-88-30079-30112.

Stratigraphic horizon. Beds 36 and 37, Maidiping Member, Hongchunping Formation, Meishucun Stage, Lower Cambrian (see Yin *et al.* 1980*a*, *b* and He *et al.* 1984 for further details).

Locality. Maidiping section, Emei, Sichuan.

Preservation. The majority of specimens consist of sclerites with a phosphatized wall enclosing a central cavity (Text-fig. 7). Petrographic sections demonstrate that the extent of phosphatization varies quite widely, and may include obvious spherulitic ingrowths on the interior of the spine cavity (Text-fig. 7*b*). The dorsal side of the base is, apart from radial furrows, often relatively smooth (e.g. Pl. 1, figs 1, 3, 16, 17; Pl. 2, figs 4, 8, 13). It is frequent on the spine, however, for surfaces to be more irregular, consisting of a fibrous ultrastructure running parallel to the long axis of the spine (Pl. 1, figs 5, 11–14, 16; Pl. 2, figs 1 and 10). This fibrosity is interpreted as diagenetic phosphatization of an originally calcareous wall. In addition, endolithic borings are also abundant in some specimens. These may be visible as openings on the surface of the base (Pl. 1, figs 8 and 9), or as steinkerns of tubes that run along the spine (Pl. 3, figs 1–3, 9, 12). The tubes consist of two distinct size classes (*c.* 3 μm and 7 μm diameter respectively). The larger category possesses a series of swellings, sometimes locally pronounced, that impart a beaded appearance (Pl. 3, figs 10 and 13) and may end blindly



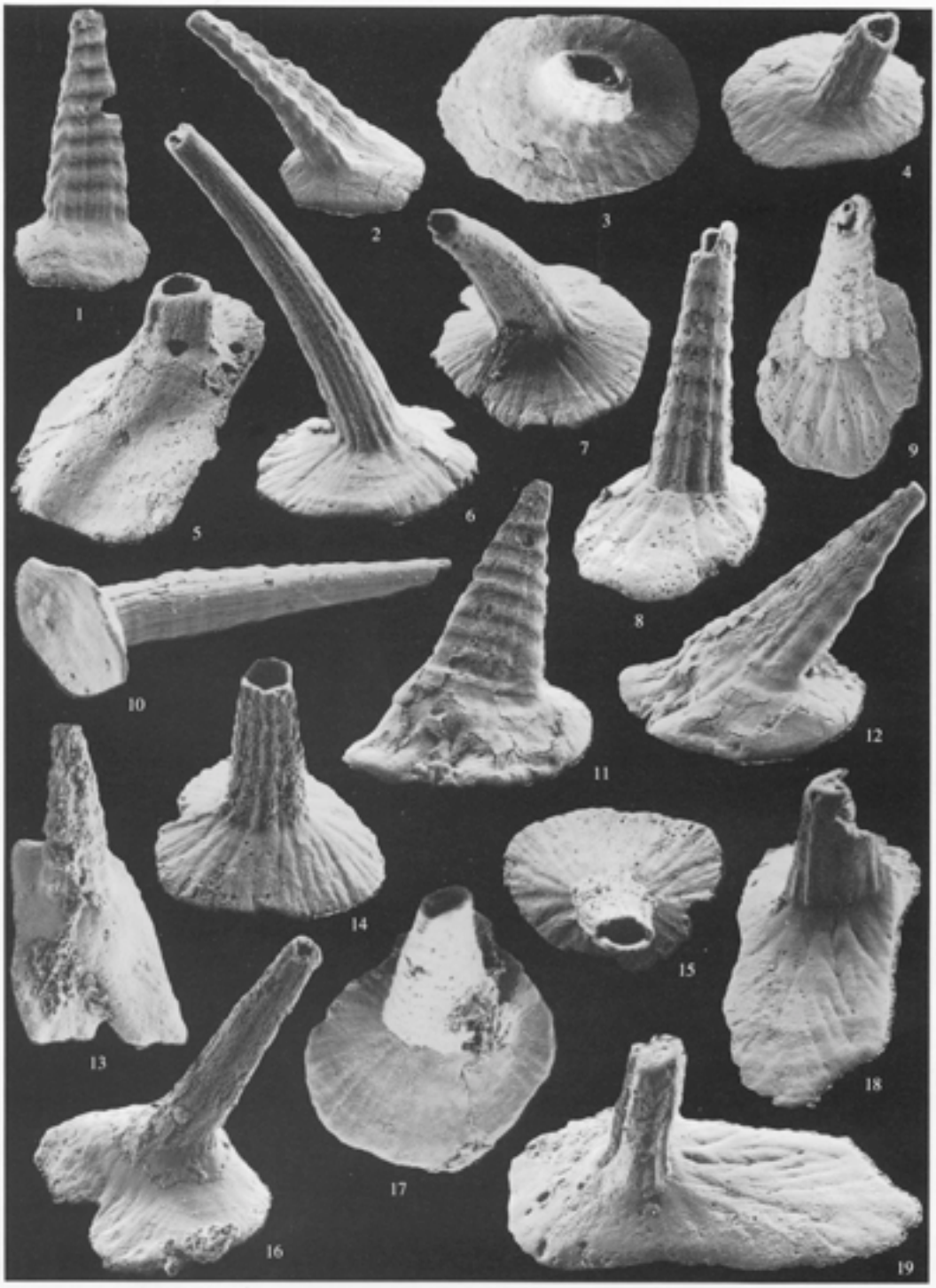
TEXT-FIG. 7. Petrographic thin sections of *Zhijinites longistriatus* Qian, 1978 from Beds 36 (*a–c*, *e*, *g* and *h*) and 37 (*d*, *f*), Maidiping Member, Hongchunping Formation at Maidiping section, Emei, Sichuan, China, to show varying degrees of diagenetic phosphatization. *a*, IGAS-BC-88-30199, distal portion of spine abraded, ×66. *b*, IGAS-BC-88-30200, note spherulitic growths into central cavity, ×66. *c*, IGAS-BC-88-30201, note abraded tip and incomplete phosphatization, ×45. *d*, IGAS-BC-88-30202, ×38. *e*, IGAS-BC-88-30203, ×22. *f*, IGAS-BC-88-30204, note incomplete phosphatization of base, ×43. *g* and *h*, IGAS-BC-88-30205; *g*, note restricted degree of phosphatization, ×33; *h*, detail of proximal area with septum between cavities of spine and base respectively, ×135.

(Pl. 3, fig. 7). The borings run sub-parallel, but may recurve or arch over each other near points of contact (Pl. 3, fig. 11). The smaller tubes are generally more filiform (Pl. 3, figs 10 and 11), may show branching and only locally possess swellings in diameter.

The other principal type of preservation is as steinkerns of the spine (Pl. 2, fig. 16; Pl. 3, figs 4–6). These were regarded as a separate taxon, referred to as *Heterosculpotheca pheneres* by Jiang (1982, pl. 13, figs 23, 23*a*, 24, 25), which is taken here as a junior synonym of *Zhijinites longistriatus*. Their origin can be confirmed, both from Jiang's (1982) illustrations (especially his pl. 13, figs 23*a* and 25) which show the characteristic transverse ornamentation of the spines, and the identical ultrastructure of the steinkern surface as seen in isolated specimens and in exposed patches beneath the wall of more complete individuals (see Runnegar 1985 for similar examples of ultrastructural replication). The ultrastructure consists of longitudinal lineations that have a stepped appearance along irregular re-entrants (Pl. 2, fig. 17; Pl. 3, figs 8, 10, 13). In addition the surface bears elongate pores (Pl. 3, fig. 4) that mark the course of tubes that enter the steinkern at shallow angles.

EXPLANATION OF PLATE 1

Figs 1–19. *Zhijinites longistriatus* Qian, 1978. 1 and 2, IGAS-BC-88-30079. 3 and 4, IGAS-BC-88-30080. 5, IGAS-BC-88-30081. 6 and 7, IGAS-BC-88-30082. 8 and 9, IGAS-BC-88-30083. 10, IGAS-BC-88-30084. 11 and 12, IGAS-BC-88-30085. 13, IGAS-BC-88-30086. 14 and 15, IGAS-BC-88-30087. 16, IGAS-BC-88-30088. 17, IGAS-BC-88-30089. 18 and 19, IGAS-BC-88-30090. All isolated sclerites from Bed 36, Maidiping Member, Hongchunping Formation at Maidiping section, Emei, Sichuan, China. Magnification all ×70.



CONWAY MORRIS and CHEN, *Zhijinites*

Description. The overall form of a circular base bearing an elongate spine is subject to considerable degrees of morphological variation (Pl. 1, figs 1–19; Pl. 2, figs 1–9, 11–15). The basal unit is concave–convex, and in the majority of specimens more or less circular. However, elongate and more irregular forms (Pl. 1, figs 5, 18, 19; Pl. 2, figs 7 and 15) are also known. A more persistent trait is the presence of an embayment or notch on the anterior/posterior margin (Pl. 1, figs 13 and 16). In most specimens there is only a single embayment, but occasionally several occur adjacent to one another in one sclerite. In some individuals this feature is open, but in others it is tightly incised so that ultimately it consists of a perforation through the base, connected to the margin by a ligatural line (Pl. 2, fig. 6).

The concave ventral side of the base appears to have been smooth (Pl. 1, fig. 10; Pl. 2, fig. 5), but the dorsal surface characteristically bears an ornamentation of irregular furrows (Pl. 1, figs 3, 4, 6–9, 14–19; Pl. 2, figs 4, 10, 11). Where the base is circular these furrows have a radial disposition, whereas in more elongate sclerites the ornamentation shows a corresponding linearity.

The elongate spine generally arises eccentrically, although whether nearer to the anterior or posterior margin depends on possible homologies with the cambroclavid sclerites. If the spine is anterior, as in cambroclavids (Mambetov *in* Mambetov and Repina 1979; Bengtson *et al.* 1990), then in contrast to the cambroclavids the zhijinitid spine was sometimes inclined anteriorly (e.g. Pl. 1, figs 4, 9, 16; Pl. 2, figs 3, 8, 12, 13). If the spine is posterior, then the marginal notch (when present) would be consistently located on the anterior margin (Pl. 1, figs 13 and 16; Pl. 2, fig. 6), whereas in cambroclavids it is usually on the posterior margin (e.g. Qian and Zhang 1983, pl. 3, figs 9, 11, 12, 14, 16; Duan 1984, pl. 5, figs 16*a*, *b* and 17*a*, *c*; Qian and Xiao 1984, pl. 1, figs 7 and 13; pl. 3, figs 11, 16, 18; see Bengtson *et al.* 1990 for proposed synonymies of the taxa erected by these Chinese workers).

In the majority of sclerites the area of insertion of the spine occupies a relatively small proportion of the dorsal surface (Pl. 1, figs 3, 4, 6, 15; Pl. 2, figs 4 and 11). In a few individuals the ratio between spine and base is greatly increased (Pl. 2, figs 1 and 9), although incomplete margins often make it difficult to determine the exact proportions. The spine arises from the base at varying angles, ranging from more or less right angles (Pl. 1, fig. 19; Pl. 2, figs 9 and 15) to about 45°, the latter being more common. The distal end of the spine is almost invariably absent, but it is clear that the length varied and bears no simple relationship to diameter of the base. In a longitudinal direction the spine is usually more or less straight, but recurved instances are also known (Pl. 2, fig. 14). In transverse section the spine varies between circular (e.g. Pl. 1, figs 6 and 16) to distinctly elongate (at right angles to the antero-posterior axis), sometimes with a more or less prominent groove on one margin. Most typically the ornamentation of the spine consists of prominent transverse welts that impart a ribbed appearance (Pl. 1, figs 1, 2, 8, 11). In some sclerites a subsidiary longitudinal ornamentation gives a more nodular appearance to the spine (Pl. 2, figs 3, 7, 8, 12), while in some spines the surface bears only longitudinal lineations (Pl. 1, figs 6, 10, 14). In this last case, care must be exercised between recognizing an original ornamentation and a spine where loss of the outer layers (Pl. 1, figs 5 and 16) has affected the original pattern and imparted a subdued longitudinal fibrosity that stems from exposure of the wall ultrastructure (see above).

Discussion. The wide morphological variation of the sclerites has been interpreted by previous workers as representing several discrete taxa, which have been distinguished principally upon the criteria of spine ornamentation and spine length. The co-occurrence of morphs ascribed to a number of nominal species in our samples and the continuity of variation suggest that many, if not all, these sclerites were derived from a single species, here recognized on grounds of priority as *Z. longistriatus*. Specimens with spines bearing longitudinal ribbing have been attributed by previous workers mostly to either *Z. longistriatus* or *Z. costatus*, while those with transverse folds have been

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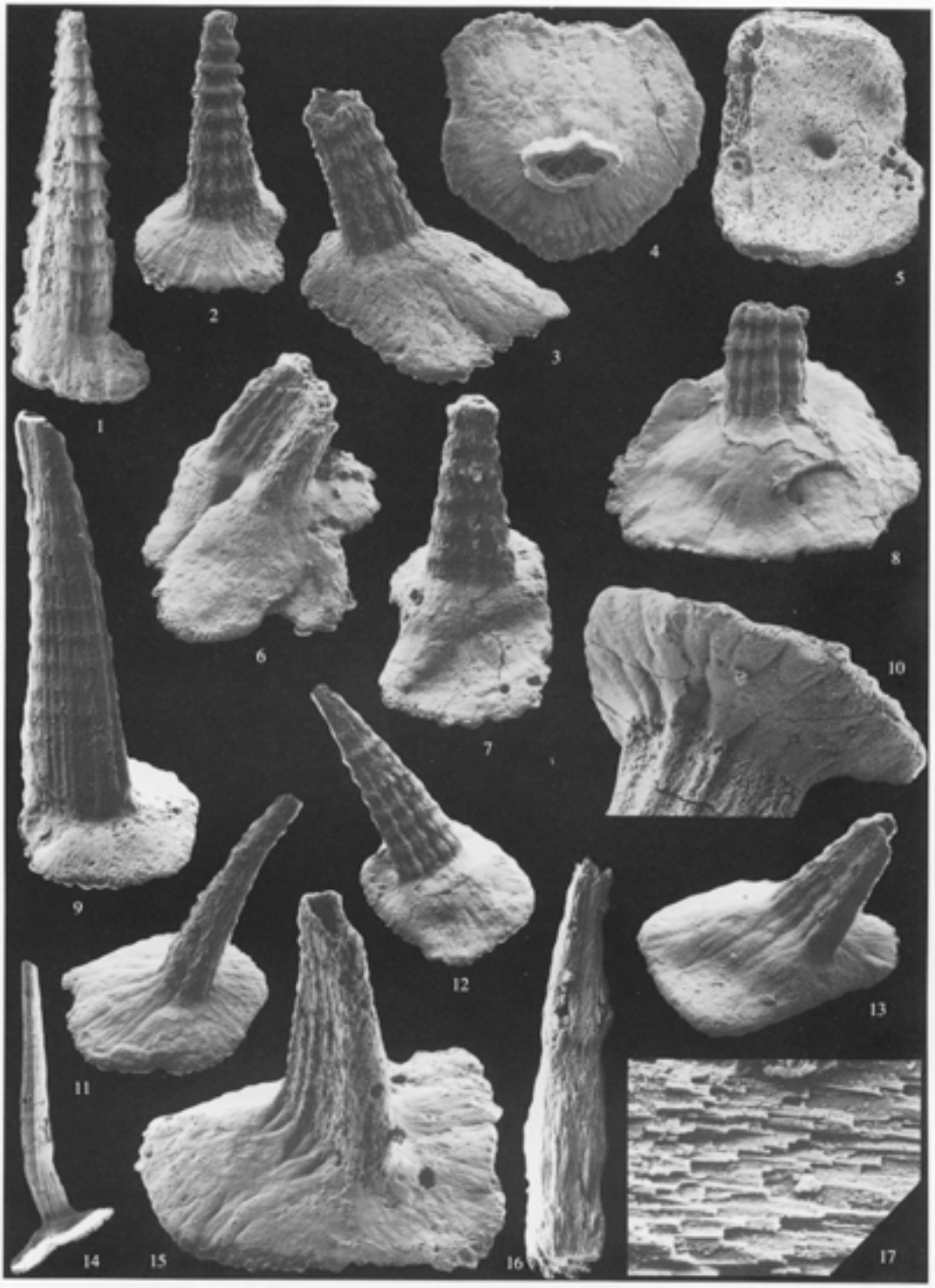
EXPLANATION OF PLATE 2

Figs 1–17. *Zhijinites longistriatus* Qian, 1978. 1, IGAS-BC-88-30091. 2, IGAS-BC-88-30092. 3, IGAS-BC-88-30093. 4, IGAS-BC-88-30094. 5, IGAS-BC-88-30095, ventral surface. 6, IGAS-BC-88-30096. 7, IGAS-BC-88-30097. 8, IGAS-BC-88-30098. 9, IGAS-BC-88-30099. 10, IGAS-BC-88-30100. 11, IGAS-BC-88-30101. 12, IGAS-BC-88-30102. 13, IGAS-BC-88-30103. 14, IGAS-BC-88-30104. 15, IGAS-BC-88-30105. 16 and 17, IGAS-BC-88-30106; 16, steinkern of spine cavity; 17, detail of steinkern surface showing possible replication of wall ultrastructure. All isolated sclerites from Bed 37, Maidiping Member, Hongchunping Formation at Maidiping section, Emei, Sichuan, China. Magnifications all × 70, except Fig. 10 (× 100), Fig. 14 (× 35), and Fig. 17 (× 700).



CONWAY MORRIS and CHEN, *Zhijinites*

placed in at least four nominal species (*Z. annae* [nomen nudum], *Z. dictyformise* [nomen nudum], *Z. minutus* and *Z. triangularis*). The synonymy of certain other species with *Z. longistriatus* remains less certain. Sclerites with more or less smooth spines have been placed mostly in *Z. lubricus*, while sclerites with a slipper-like base and very elongate spine have been named as *Parazhijinites guizhouensis* (sometimes misspelt *quizhouensis*).

If the extensive synonymies proposed above are accepted, albeit some being provisional, then it remains to be decided whether an individual possessed a corresponding range of sclerite types or whether the variability was greater between animals, with any one individual showing a more restricted degree of variation. In the absence of either articulated individuals or fused sclerites (see below), these alternatives remain unresolved. However, as a working hypothesis it is proposed that morphological variability of sclerites in any one individual was pronounced.

If it was possible to provide an adaptive explanation for the different sclerite types, especially with respect to spine angle and spine ornamentation, then one might hypothesize further about the possible distribution of the sclerites over the body. In discussing cambroclaves from the Lower Cambrian of Australia, Bengtson *et al.* (1990) suggested the sclerites were used to grip the sediment, as well as providing a protective function. If *Zhijinites* had a similar mode of life, then it seems possible that the inclined spines served to provide anchors on the sediment during locomotion. It is suggested further that the transverse corrugations (Pl. 1, figs 1, 2, 11; Pl. 2, figs 1–3, 7–9, 12) acted as a ratchet-like device to increase frictional contact with the sediment grains. In this context those spines with a more subdued ornamentation may have occupied regions of the body that were not directly involved with acting as anchors. Concerning the varying angles the spines make with the basal unit, and by implication the surface of the body, this could be linked to local configurations of the epithelium.

DEIRADOCLAVUS gen. nov.

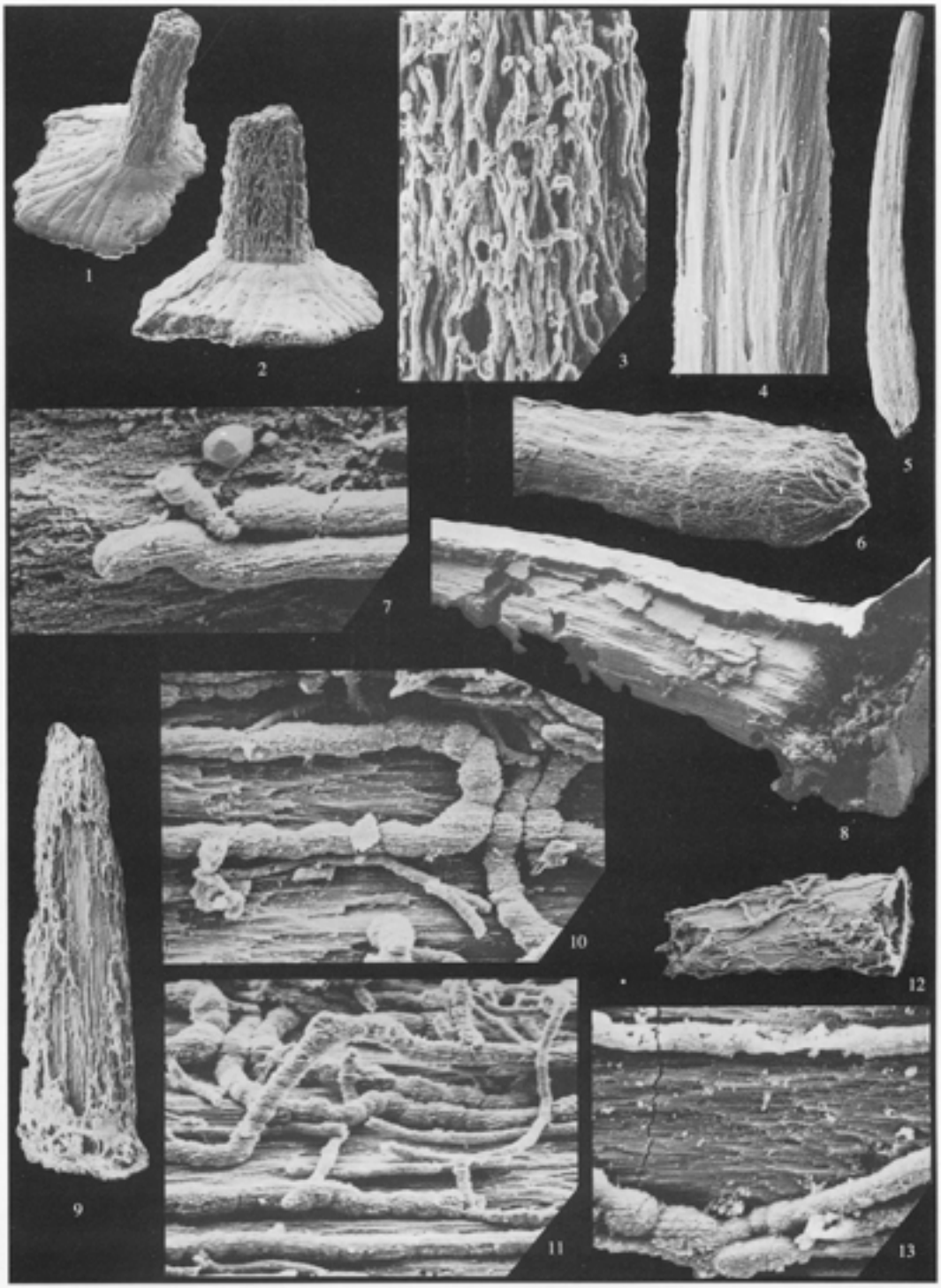
Type species. Deiradoclavus trigonus gen. et sp. nov.

Derivation of generic name. From the Greek *deirados*, meaning ridge, in reference to prominent ridges on both upper and lower surfaces.

Diagnosis. Small sclerites with variably subcircular outline, occasionally tending to quadrate. Dorsal surface bearing tri-radiate ridge, delimiting anterior embayment and paired postero-lateral embayments. Anterior embayment bears transversely elongate spine. Ventral surface bearing tri-radiate ridge in opposite orientation to that of dorsal surface, so delimiting posterior embayment and paired antero-lateral embayments.

EXPLANATION OF PLATE 3

Figs 1–13. *Zhijinites longistriatus* Qian, 1978. 1–3, IGAS-BC-88-30107; 1 and 2, entire sclerite; 3, detail of steinkerns of endolith borings. 4–6, IGAS-BC-88-30108; 4, detail of steinkern surface showing possible replication of wall ultrastructure; 5, steinkern of spine cavity; 6, detail of basal region of steinkern. 7, IGAS-BC-88-30109, detail of steinkerns of endolith borings showing blind terminations and imprint of wall ultrastructure. 8, IGAS-BC-88-30110, steinkern and partial preservation of outer wall. 9–11, IGAS-BC-88-30111; 9, steinkern of spine cavity; 10 and 11, detail of steinkern surface showing wall ultrastructure and endolith borings, note variation in thickness. 12 and 13, IGAS-BC-88-30112; 12, steinkern of spine cavity; 13, detail of steinkern surface showing wall ultrastructure and endolith borings. All isolated sclerites from Bed 36, Maidiping Member, Hongchunping Formation at Maidiping section, Emei, Sichuan, China. Magnifications: ×70 (Figs 1, 2, 5, 9, 12); ×500 (Fig. 3); ×350 (Fig. 4); ×140 (Figs 6, 8); ×700 (Figs 7, 10); ×600 (Fig. 11); ×1000 (Fig. 13).



CONWAY MORRIS and CHEN, *Zhijinites*

Deiradoclavus trigonus gen. et sp. nov.

Plates 4 and 5; Text-fig. 11*c*

Derivation of specific name. On account of the three-angled (*gonia*, Greek for angle) arrangement of the ridges.

Diagnosis. As for the genus.

Holotype. IGAS-BC-88-30114 (Pl. 4, fig. 2).

Paratypes. IGAS-BC-88-30113, 30115–30136.

Stratigraphic horizon. Guojiaba Formation.

Locality. Xuanjiangping section, near Xuanjiangping village, Kuanchuanpu, Shaanxi.

Taxonomic comparisons. With one possible exception, no published descriptions of cambroclaves can be closely compared to *Deiradoclavus*. The exception is specimens from the Yurtus Formation of Xinjiang, referred to *Wuschichites polyedrus* by Qian and Xiao (1984, pl. 3, figs 12 and 13). Here the ventral surface appears to bear a tri-radiate ridge, while the opposite surface is described as having a tri-radiate groove. However, while the tri-radiate pattern recalls *Deiradoclavus*, in this new genus both sides bear ridges. It remains conceivable that *W. polyedrus* should be transferred to *Deiradoclavus*, but synonymy of the genera would not be necessary because of the distinctive status of the type species, *W. minutus* (Qian and Xiao 1984, pl. 1, fig. 7; pl. 3, fig. 11). Although the ventral surface bears a tri-radiate ridge, the sclerites of *W. minutus* differ from *Deiradoclavus* in having a prominent posterior notch and bulbous anterior. Indeed, in the Xinjiang material similar features are also visible in some co-occurring sclerites of *Cambroclavus* (see Qian and Xiao 1984, pl. 3, figs 16, 18, 19); these supposedly distinct sclerites may represent end-members of a single cambroclavid species, so making *Wushichites* a junior synonym of *Cambroclavus* (see Bengtson *et al.* 1990).

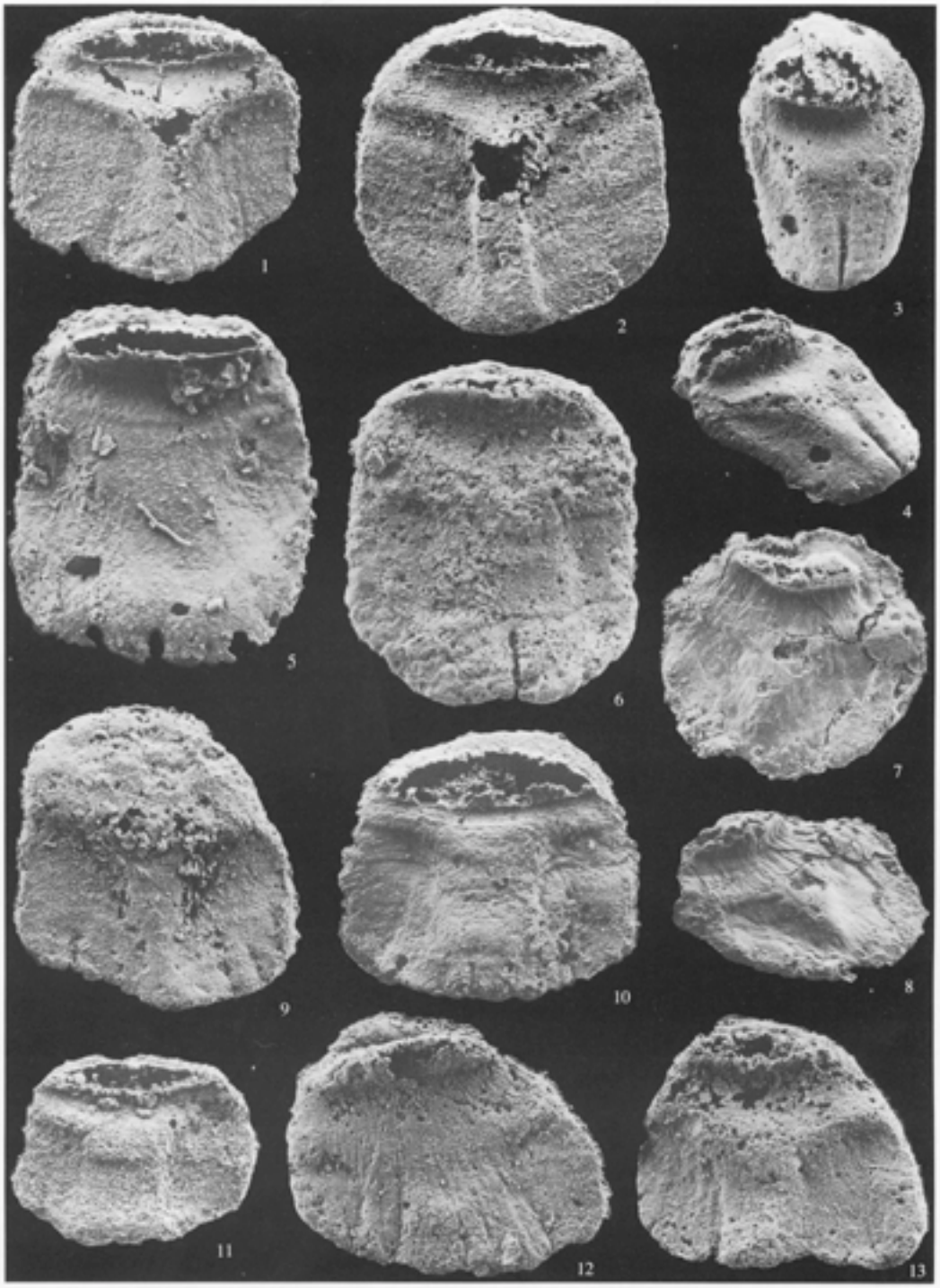
Preservation. In common with other cambroclaves, the sclerites of *Deiradoclavus* (Pls 4 and 5) appear to have had their originally calcareous walls replaced and/or partly coated with diagenetic phosphate, leaving the interior of the sclerite hollow. The quality of replication varies, but in some specimens a fibrous arrangement (e.g. Pl. 5, fig. 2) may represent an original ultrastructure of the wall. A similar ultrastructure has been noted in both cambroclaves (Bengtson *et al.* 1990) and zhijinitids (see above).

Description. The sclerites may be sub-circular in outline (Pl. 4, figs 1, 2, 7, 12), but the range of variation is very considerable; many sclerites approach a quadrate shape (Pl. 4, figs 5, 6, 10; Pl. 5, figs 1, 3, 8, 9, 12), while others are relatively elongate (Pl. 4, figs 3 and 4) or more irregular in shape (Pl. 4, figs 12 and 13; Pl. 5, fig. 2). Orientations are based on comparisons with other cambroclaves (Mambetov *in* Mambetov and Repina 1979; Bengtson *et al.* 1990; see also discussion above of zhijinitid orientation); in particular the spine is taken to be anterior and to arise from the dorsal surface.

Notwithstanding wide morphological variation, the dorsal surface of most sclerites bears a tri-radiate ridge that has a point of divergence located slightly anterior to the mid-line (Pl. 4, figs 1, 2, 10, 11, 13; Pl. 5, figs 1 and 3). The posterior arm, so named because it extends to that margin, is relatively broad and sometimes flares towards its termination. The pair of anterior arms are narrower, and usually diverge from the midline at an angle of about 60°. Variation in development of these ridges, however, is considerable. In some specimens the

EXPLANATION OF PLATE 4

Figs 1–13. *Deiradoclavus trigonus* gen. et sp. nov. 1, IGAS-BC-88-30113. 2, IGAS-BC-88-30114, holotype. 3 and 4, IGAS-BC-88-30115. 5, IGAS-BC-88-30116. 6, IGAS-BC-88-30117. 7 and 8, IGAS-BC-88-30118. 9, IGAS-BC-88-30119. 10, IGAS-BC-88-30120. 11, IGAS-BC-88-30121. 12, IGAS-BC-88-30122. 13, IGAS-BC-88-30123. All isolated sclerites, dorsal surface, from the Guojiaba Formation at Xuanjiangping section near Kuanchuanpu, Shaanxi, China. Magnifications all ×90.



CONWAY MORRIS and CHEN, *Deiradoclavus*

posterior arm is very broad and may bear either a median furrow (Pl. 4, figs 3 and 4; Pl. 5, fig. 3) or a series of grooves (Pl. 4, figs 10 and 12) that are irregularly disposed and extend from the posterior margin by variable amounts. Similarly, the strength of development of the anterior arms varies, but usually at least some trace is perceptible (Pl. 4, fig. 5). The tri-radiate nature of the ridge defines three gently concave depressions, termed here embayments, that open towards the anterior margin (1) and postero-lateral margins (2, 3) respectively. The anterior embayment houses a narrow, transversely elongate ridge (Pl. 4; Pl. 5, figs 1–3) whose distal termination is not known owing to incomplete phosphatization. This structure is referred to as the anterior spine, a term that, while not precisely descriptive, emphasizes its presumed homology with comparable structures in other cambroclaves.

The ventral surface also bears a tri-radiate ridge (Pl. 5, figs 4–15), although its sense of branching is reversed (i.e. rotated through 180°), in comparison to the Y-shaped ridge on the upper surface. Accordingly, an anterior ridge diverges from the paired postero-lateral ridges, with the point of divergence located more or less at the mid-point of the sclerite. Although the anterior arm is sometimes a single crest, more often it forms a pair of ridges that are separated by a median depression (Pl. 5, figs 4–6, 14). On occasions this furrow is bisected by yet another ridge (Pl. 5, figs 10 and 11). The postero-lateral arms are usually simple and diverge at an angle that is controlled by the shape of the sclerite and varies from about 125°, in sclerites which are broader than long (Pl. 5, fig. 5), to about 100° where the sclerite is more quadrate (Pl. 5, fig. 12). The embayments defined by the tri-radiate ridge on the ventral surface are broadly concave. This is particularly noticeable in the posterior embayment (Pl. 5, figs 4, 11, 13) that is flanked by the postero-lateral arms. The anterior embayments occasionally bear subsidiary ridges (Pl. 5, figs 10 and 11) and may also be traversed by subdued grooves (Pl. 5, fig. 15).

Palaeoecology. Evidence from fused sclerites (Mambetov *in* Mambetov and Repina 1979; Bengtson *et al.* 1990), articulatory facets, and outline shapes that allow for mutual accommodation and interlocking in *Cambroclavus* all suggest that the animal was originally coated by a scleritome (Text-fig. 11*b*). Fused sclerites have not been recognized in *Deiradoclavus*, but the paired postero-lateral embayments on the dorsal surface are interpreted as acting as points of articulation with the anterior corners of the two adjacent sclerites (Text-fig. 11*c*). In this schema the anterior depression, defined by the two ridges on the ventral surface of most sclerites, would act to accommodate the posterior arm on the dorsal surface of the next sclerite to the anterior. Such an interlocking pattern would have provided a more or less continuous cover of the body, providing an effective armour, especially with the added complement of spines projecting from the anterior of each sclerite.

Relationships. *Deiradoclavus trigonus* is regarded as a cambroclave because of its broad similarity to *Cambroclavus* spp, including an anterior spine and median ridge flanked by embayments. Indeed, rare sclerites approach quite closely *Cambroclavus* (Pl. 4, figs 3 and 4), but the great majority differ in three principal ways: they are more or less sub-circular to quadrate rather than elongate, they bear prominent tri-radiate ridges on both dorsal and ventral surfaces, and the anterior spine is elongately transverse rather than a simple conical extension.

Mention was made above concerning possible comparisons between *Deiradoclavus* and *Wushichites*, especially *W. polyedrus* (Qian and Xiao 1984). With the available illustrations and lack of information on scleritome variability of co-occurring cambroclaves, objective comparisons are not easy, and the possible inclusion of *W. polyedrus* in *Deiradoclavus* must be regarded as tentative. Although *Zhijinites* has a more or less circular base, it is surmounted by an eccentrically located spine and is less similar to *Deiradoclavus* than *Cambroclavus*. Indeed the transition between

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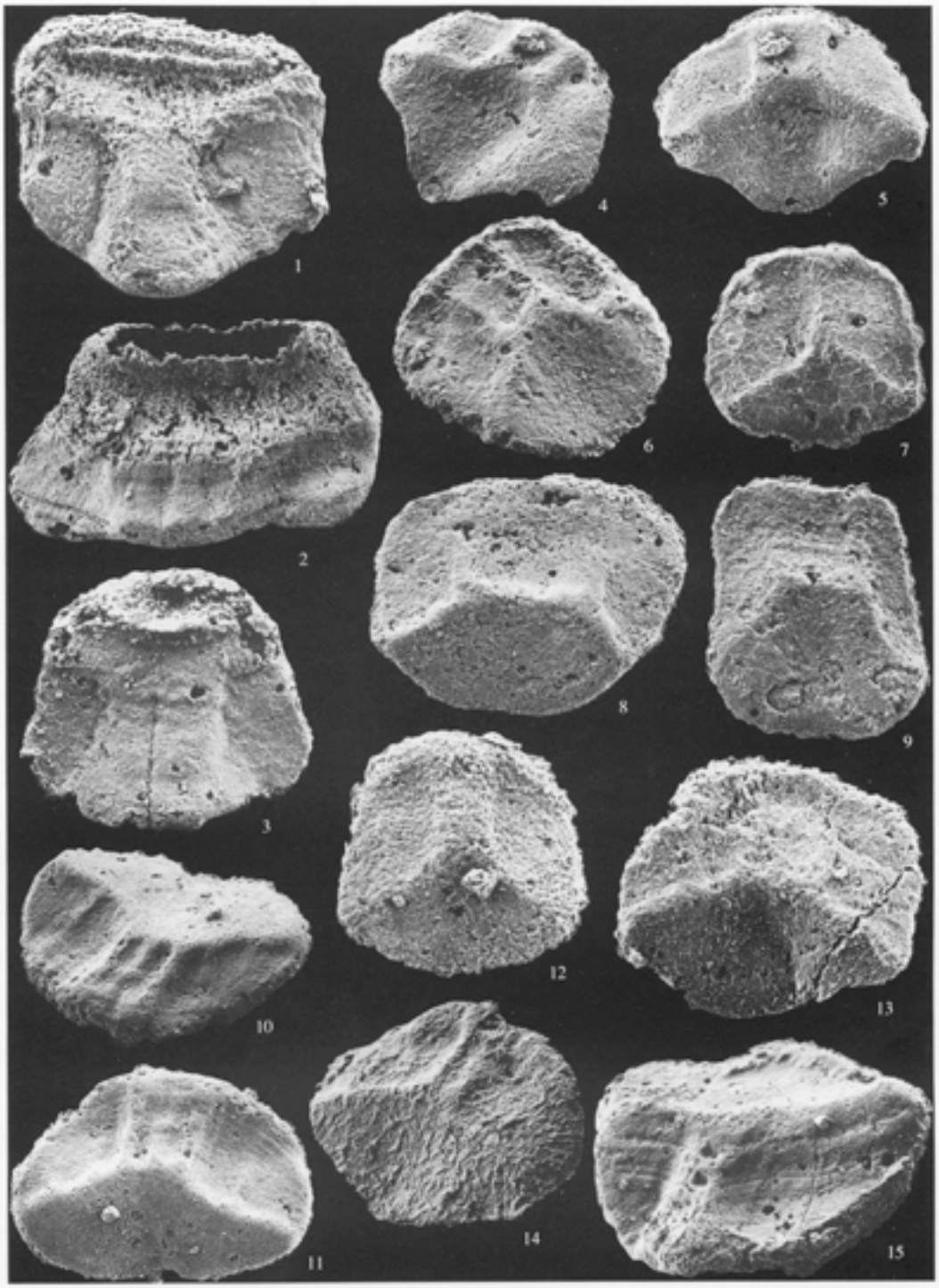
EXPLANATION OF PLATE 5

Figs 1–15. *Deiradoclavus trigonus* gen. et sp. nov. 1, IGAS-BC-88-30124. 2, IGAS-BC-88-30125. 3, IGAS-BC-88-30126. 4 and 5, IGAS-BC-88-30127. 6, IGAS-BC-88-30128. 7, IGAS-BC-88-30129. 8, IGAS-BC-88-30130. 9, IGAS-BC-88-30131. 10 and 11, IGAS-BC-88-30132. 12, IGAS-BC-88-30133. 13, IGAS-BC-88-30134. 14, IGAS-BC-88-30135. 15, IGAS-BC-88-30136. All isolated sclerites, dorsal (Figs 1–3) and ventral (Figs 4–15) surfaces, from Guojiaba Formation at Xuanjiangping section near Kuanchuanpu, Shaanxi, China. Magnifications all ×90.



CONWAY MORRIS and CHEN, *Deiradoclavus*

Zhijinites and *Cambroclavus* may be envisaged as arising from an extension of the posterior region and the development of a closely interlocking scleritome. *Deiradoclavus* would be derived in turn from a cambroclavid by decreasing the length to width ratio, which would also explain the transversely elongate spine.

Genus DELTACLAVUS gen. nov.

Type species. Deltaclavus graneus gen. et sp. nov.

Derivation of the generic name. On account of the triangular or delta shape of the sclerites.

Diagnosis. Sclerites with broad anterior edge, and lateral edges converging to posterior point, imparting triangular outline. Dorsal surface with longitudinal median ridge, terminating anteriorly in subdued spine. Lateral portions of dorsal surface gently concave. Ventral surface with prominent anterior facet, sometimes bounded by subdued ridges. Remainder of ventral surface gently rounded and more or less smooth.

Deltaclavus graneus sp. nov.

Plates 6 and 7; Text-figs 8, 9, 11*d*

Derivation of specific name. From the Latin *graneus*, in reference to the seed or pip-like appearance of the individual sclerites.

Diagnosis. As for the genus.

Holotype. IGAS-BC-88-30180 (Text-fig. 9*a–c*).

Paratypes. IGAS-BC-88-30154-30179, 30181.

Stratigraphic horizon. Lower Shuijingtuo Formation, Lower Cambrian.

Locality. Taishanmiao section, near the village of Taishanmiao, Hubei.

Preservation. The style of preservation, with secondary phosphatization of the sclerite wall and limited infill of the central cavity, is comparable to that described above for the type material of *Deiradoclavus trigonus* gen. et sp. nov.

Description. The majority of specimens are isolated sclerites (Pls 6 and 7), but rare examples of fused assemblages (Text-figs 8 and 9) are of considerable importance for partial scleritome reconstruction. In comparison with other cambroclave species, isolated sclerites are relatively small, typically about 350–400 μm in length. In dorso-ventral view the sclerites have a triangular shape, defined by a gently convex arcuate anterior margin and lateral margins that converge posteriorly to a pointed termination (Pl. 6, figs 1, 4, 5, 7, 11, 14; Pl. 7, figs 1, 5, 6, 8, 11, 13). The outline shape varies from relatively narrow (Pl. 6, fig. 5) to rarer broader sclerites (Pl. 6, fig. 13; Pl. 7, figs 3 and 8). In lateral view, the sclerite is highest at the anterior, and declines posteriorly (Pl. 6, figs 3, 6, 12, 13; Pl. 7, figs 2 and 3). The dorsal surface bears a prominent median ridge that at the anterior end expands into a broader area, surmounted by a knobbly spine (Pl. 6, figs 1, 8, 14; Pl. 7, figs 1 and 4). In narrower sclerites this latter structure is more or less circular, but in broader ones it is transversely

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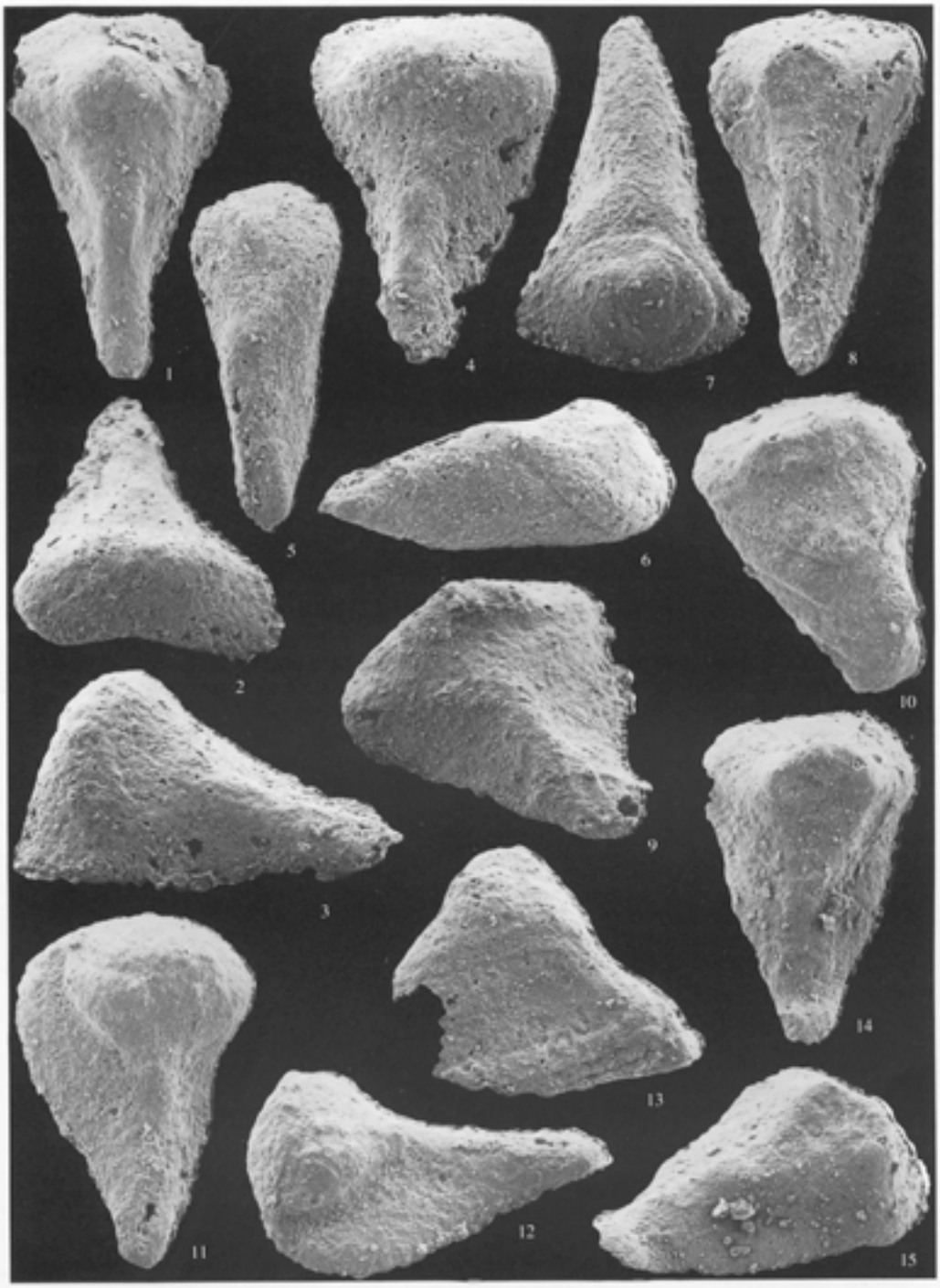
EXPLANATION OF PLATE 6

Figs 1–15. *Deltaclavus graneus* gen. et sp. nov. 1, IGAS-BC-88-30154. 2–4, IGAS-BC-88-30155. 5 and 6, IGAS-BC-88-30156. 7, IGAS-BC-88-30157. 8, IGAS-BC-88-30158. 9, IGAS-BC-88-30159. 10, IGAS-BC-88-30160. 11 and 12, IGAS-BC-88-30161. 13, IGAS-BC-88-30162. 14 and 15, IGAS-BC-88-30163. All isolated sclerites, dorsal surface, from the Shuijingtou Formation at the Taishanmiao section, near Taishanmiao, Hubei, China. Magnifications all × 150.



CONWAY MORRIS and CHEN, *Deltaclavus*

expanded. Although this projection is more nodose than spinose, the term spine is employed here (as with *Deiradoclavus trigonus* gen. et sp. nov., see above) because of its inferred homology with other cambroclavid spines. The lateral regions on either side of the dorsal ridge are gently concave. Apart from occasional sclerites with subdued ridge-like developments, the dorsal surface is more or less smooth. The ventral surface is also more or less smooth, and gently rounded, except at the anterior end where there is a distinct concave facet that may be flanked by subdued ridges (Pl. 7, figs 6–14).

Fused assemblages of sclerites occur as two variants. The first type consists of a longitudinal file of three, four or five sclerites with the posterior dorsal surface in juxtaposition to the ventral facet of the anterior region (Text-figs 8*a*, *b* and 9*a–c*). The second variant consists of fused rows, that also articulate via their ventral surface with another row such that the posterior ends of opposite sclerites touch one another. Two such examples of sclerite rows running 'back to back' have been recognized. One consists of a single file (Text-fig. 8*c–f*) on each side, and the other of a double file (Text-fig. 9*d–h*). In the latter case the interlocking of adjacent sclerites of each file on either side is seen to alternate. The sclerites of the second type of fused assemblage are broader, with the posterior termination more distinctly demarcated from the remainder of the sclerite whose lateral edges tend to be wing-like.

Remarks. The significance of the fused assemblages of *D. graneus* in scleritome reconstruction of cambroclaves is discussed below. Specimens of sclerites comparable to *Deltaclavus* appear not to have been recognized previously, although in this context attention should be drawn to problematical fossils from the Lower Tal Formation of Uttar Pradesh, India. In particular a specimen illustrated by Bhatt *et al.* (1983, pl. 2, fig. 2) seems to be comparable to *D. graneus*, and in any event their attribution to *Sachites* seems unlikely. It should be noted that the stratigraphic position of the Indian occurrence at present is correlated with substantially older sequences (Brasier and Singh 1987) than the Shuijingtuo Formation from which *D. graneus* derives.

Family PARACARINACHITIDAE Qian, 1984

Diagnosis (emended from Qian 1984). Sclerites concavo–convex, more or less bilaterally symmetrical. Elongate spatula-like axis, tapering to blunt apex, usually bearing median row of spines but sometimes smooth. Lateral flanges, wing-like, sometimes present, smooth except for occasional furrows. Incremental growth. Calcareous composition.

Discussion. Qian and Bengtson (1989, p. 48) only referred to this family in passing, but noted that *Paracarinachites* might be related to *Scoponodus* Jiang, 1982. They drew attention to possible similarities to *Ernogia* Jiang, 1982, and as noted below it may transpire that both these genera should be accommodated in Paracarinachitidae.

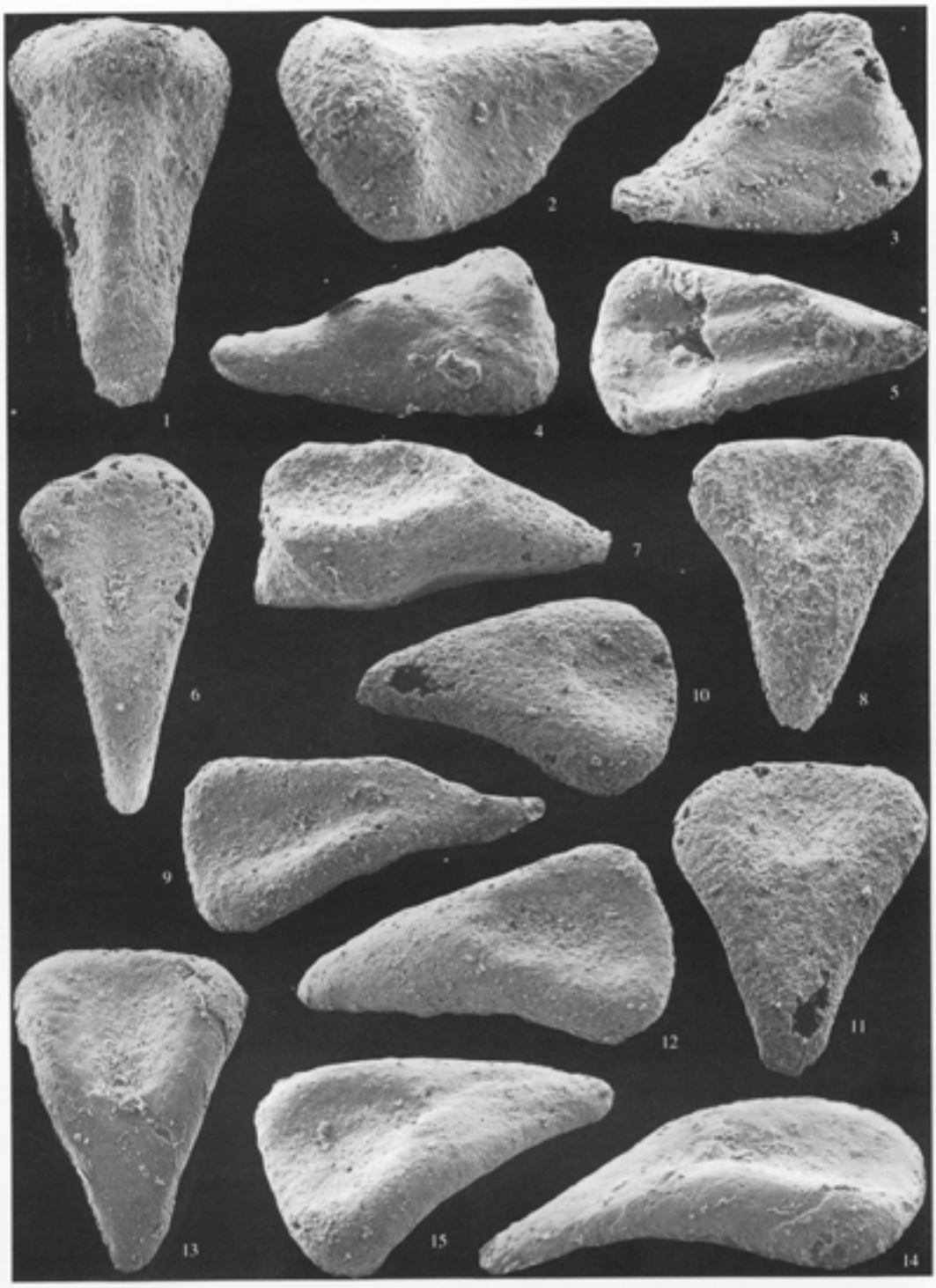
PARACARINACHITES Qian and Jiang, 1982

Type species. Paracarinachites sinensis Qian and Jiang, 1982.

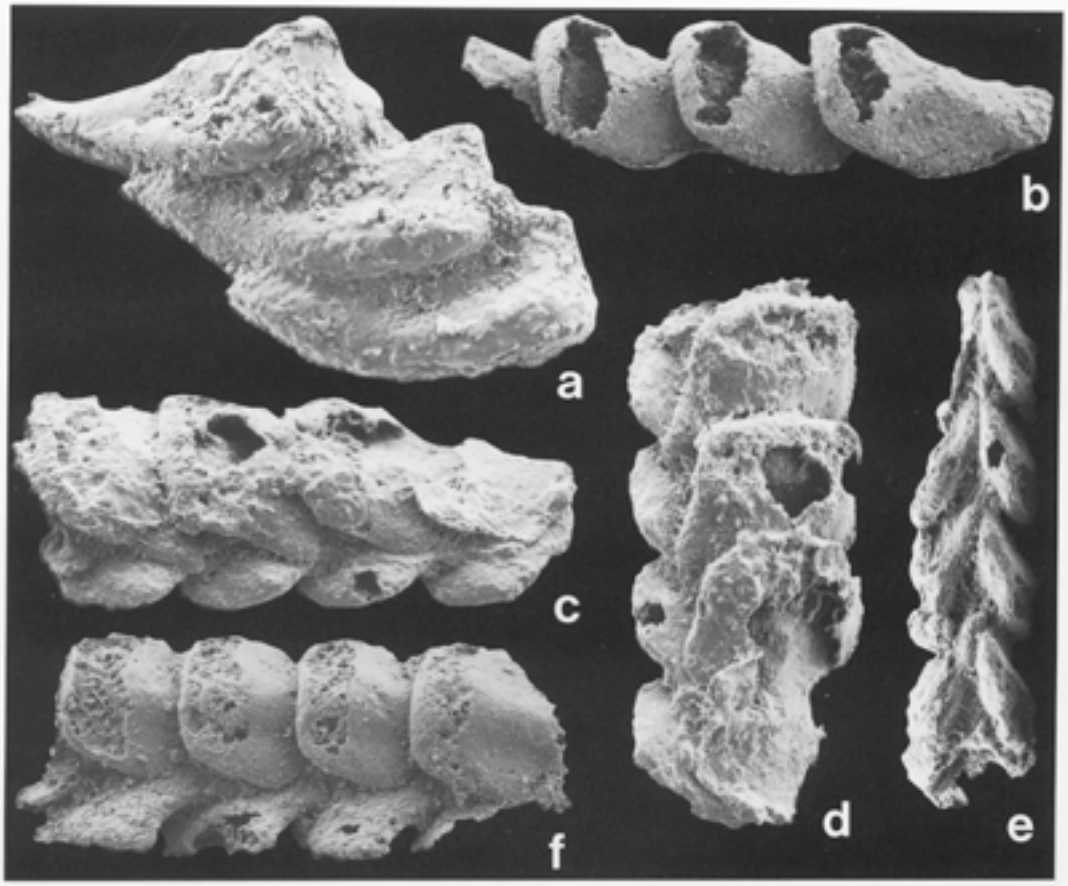
Diagnosis. See Qian and Bengtson (1989, p. 49).

EXPLANATION OF PLATE 7

Figs 1–15. *Deltaclavus graneus* gen. et sp. nov. 1, IGAS-BC-88-30164. 2, IGAS-BC-88-30165. 3, IGAS-BC-88-30166. 4, IGAS-BC-88-30167. 5, IGAS-BC-88-30168. 6, IGAS-BC-88-30169. 7, IGAS-BC-88-30170. 8, IGAS-BC-88-30171. 9, IGAS-BC-88-30172. 10 and 11, IGAS-BC-88-30173. 12, IGAS-BC-88-30174. 13 and 14, IGAS-BC-88-30175. 15, IGAS-BC-88-30176. All isolated sclerites, dorsal (Figs 1–4) and ventral (Figs 5–15) surfaces, from the Shuijingtou Formation at the Taishanmiao section, near Taishanmiao, Hubei, China. Magnifications all × 150.



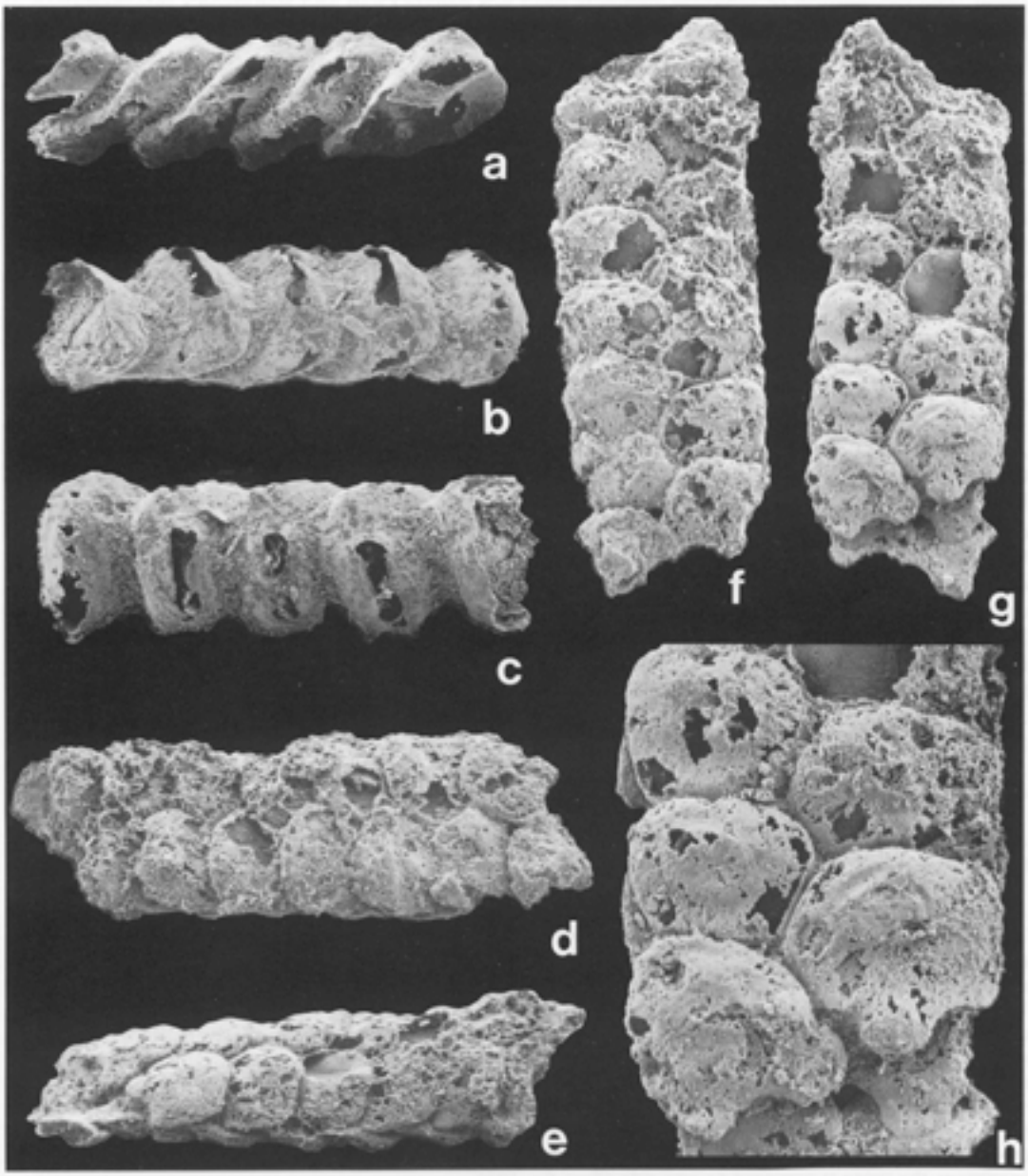
CONWAY MORRIS and CHEN, *Deltaclavus*



TEXT-FIG. 8. *Deltaclavus graneus* gen. et sp. nov. *a*, IGAS-BC-88-30177. *b*, IGAS-BC-88-30178. *c–f*, IGAS-BC-88-30179; *c* and *d*, 'lower' surface; *e*, lateral view; *f*, 'upper' surface. All articulated series of sclerites, from the Shuijingtou Formation at the Taishanmiao section, near Taishanmiao, Hubei, China. Magnifications: *a*, ×150; *b–f*, ×100.

Discussion. An extensive discussion of *Paracarinachites* (junior synonyms include *Yangtzechiton* Yu 1984*a*, *Luyanhaochiton* Yu 1984*a*) is provided by Qian and Bengtson (1989) who recognised four species (*P. sinensis*, *P. columellatus*, *P. parabolicus* and *P. spinus*; whether the species erected by He and Xie (1989, pl. 1, figs 13–15) as *Paracarinachites bispinosus* can be included in this genus seems to be more questionable). In each case the available specimens consist of elongate, bilaterally symmetrical sclerites composed of a series of growth increments that are usually marked by denticles arising from the outer side. In *P. spinus* the incremental nature of the sclerites is particularly clear on account of the prominent divisions that convey the impression of units overlapping in an abapical direction (see Qian and Bengtson 1989, fig. 29; He and Xie 1989, pl. 1, figs 17–19, 21). Qian and Bengtson (1989) emphasized, however, that the sclerite was a single unit, citing evidence of lateral fusion on the outer side and a seamless appearance on the lower side that they interpreted as resulting from the adpression of successive lamellae during growth.

Here we report also zhijinitid-like denticles that are strikingly similar to the increments that go to make up the sclerites of *P. spinus* as reported by Qian and Bengtson (1989; see also He and Xie



TEXT-FIG. 9. *Deltaclavus graneus* gen. et sp. nov. *a–c*, IGAS-BC-88-30180, holotype; *a*, lateral view; *b*, oblique view; *c*, dorsal view. *d–h*, IGAS-BC-88-30181; *d*, *f*, 'lower' surface; *e*, *g*, 'upper' surface; *h*, detail of 'upper' surface. All articulated series of sclerites, from the Shuijingtou Formation at the Taishanmiao section, near Taishanmiao, Hubei, China. Magnifications: *a–c*, ×100; *d–g*, ×75; *h*, ×150.

1989). The recognition of separate elements need not negate Qian and Bengtson's interpretation of an incremental assemblage and the significance of these observations on the affinities of *Paracarinachites* are returned to below.

Paracarinachites spinus (Yu, 1984*a*)

Plate 8; Text-fig. 10

Diagnosis. For isolated sclerites: base semi-circular to oval with concave ventral surface, dorsal surface bearing prominent curved spine, inserted towards anterior side. Dorsal surface variously ornamented, including concentric ridge and towards margin radial ridges. For fused sclerites, see Qian and Bengtson (1989).

Holotype. ASN 84135 (see Yu 1984*a*, pl. 1, figs 8 and 9).

Material illustrated here. IGAS-BC-88-30137–30153.

Remarks. A synonymy and discussion of the taxonomic status of these sclerites are provided by Qian and Bengtson (1989), to which may be added illustrations of fused and isolated sclerites from Meishucun by He and Xie (1989, pl. 1, figs 16–22) who continued to refer to it as *Yangtzechiton elongatus*. In addition, it seems conceivable that one specimen identified as *Zhijinites* sp. from the top of the Zhongyicun Member at Meishucun (Jiang 1980, pl. 4, fig. 17; the other specimen illustrated in pl. 4, fig. 18 may not be a cambroclave) is an isolated sclerite comparable to material described here. The status of *Z. undulatus* in this context is more uncertain. One sclerite, from near Leibo, Sichuan (Jiang 1982, pl. 17, fig. 12, 12*a*) might be tentatively referred to *P. spinus*. However, the other specimens illustrated by Jiang (1982, pl. 17, fig. 11), from the Dahai section near Huize, are assigned provisionally to *Z. longistriatus* (see above).

Stratigraphic horizon. Bed 7, Zhongyicun Member, Yuhucun Formation, Meishucun Stage, Lower Cambrian.

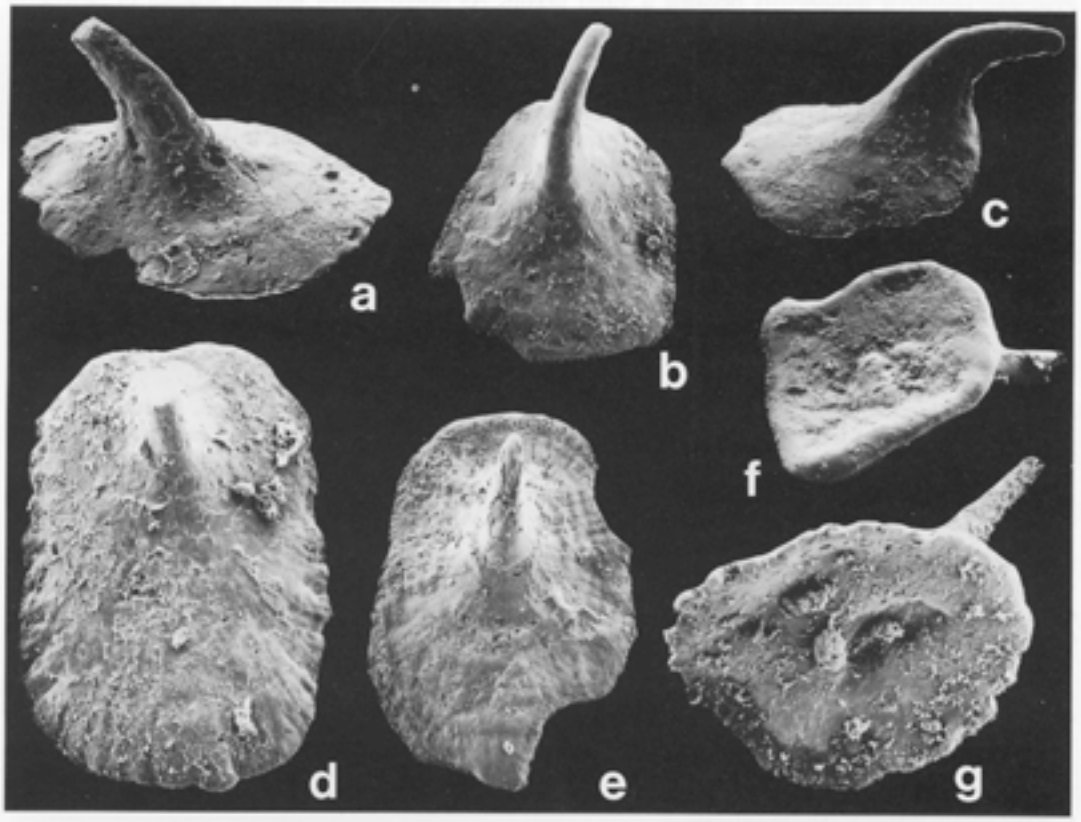
Locality. Xiaowaitoushan section, Kunyang Phosphorite Mine, Meishucun, Yunnan.

Preservation. The sclerites are replaced with massive phosphate, which in etched and polished material is seen to replace not only the walls but also the internal cavity.

Description. The sclerites are divisible into a sub-circular to oval base and elongate spine (Pl. 8; Text-fig. 10). The former unit has a concave lower surface, that is more or less smooth (Pl. 8, fig. 6; Text-fig. 10*f, g*). The opposite surface of the base usually bears subdued ornamentation, which may include a series of concentric ridges (Pl. 8, figs 2, 3, 17; Text-fig. 10*e*) or more occasionally a more pronounced furrow (Pl. 8, figs 14 and 15). A finer-scale ornamentation of radial ridges, that tends to be most accentuated near the margins, is characteristic (Pl. 8, figs 1, 4, 5, 7, 8, 10, 15, 17; Text-fig. 10*e*). The margins themselves are often more or less smooth, but on occasion they show indentations or more developed scallops, especially on the posterior margin.

The spine is conspicuous, usually stout, and terminates in a simple point. Its insertion is eccentric, towards the presumed anterior side and it may even arise from the anterior margin (Text-fig. 10*c*). The degree of curvature is variable, and although in most sclerites the spine inclines towards the posterior mid-point, in some specimens the spine is recurved to one side (Text-fig. 10*b*).

Discussion. If a series of these sclerites was aligned in an imbricated file parallel to their antero-posterior axes they would appear to be almost indistinguishable from the fused assemblages described by earlier workers (Qian and Bengtson 1989; see also Yu 1984*a*, *b*, 1989). Qian and Bengtson (1989) presented evidence for the fused assemblages to be primary rather than diagenetic, although in either case juxtaposition of the sclerites presumably reflects a life orientation. Unless the fused assemblages are teratological, then it seems likely that they derived from one or more specific



TEXT-FIG. 10. *Paracarinachites spinus* (Yu, 1984). *a*, IGAS-BC-88-30148. *b* and *c*, IGAS-BC-88-30149. *d*, IGAS-BC-88-30150. *e*, IGAS-BC-88-30151. *f*, IGAS-BC-88-30152. *g*, IGAS-BC-88-30153. All isolated sclerites, dorsal (*a–e*) and ventral (*f* and *g*) surfaces, from Bed 7, Zhongyicun Member, Yuhucun Formation at Xiaowaitoushan section, Kunyang Phosphorite Mine, Meishucun, Yunnan, China. Magnifications all ×90.

regions of the body, while the isolated sclerites described here (see also He and Xie 1989) come from other regions.

Apart from occurrences of fused assemblage of *Paracarinachites spinus*, the sclerites of this taxon differ from those of *Zhijinites longistriatus* in several respects. These include relative proportions of base to spine, and ornamentation of spine. However, as noted below, *P. spinus* may be considerably more closely related to the zhijinitids (see also Qian and Bengtson 1989, p. 56) than other species of *Paracarinachites* (including the type species, *P. sinensis*), so that inclusion in the Zhijinitidae may be a preferred option. If this transpires to be the case then the similarity between the serial row of fused sclerites in *P. spinus* and the spinose row in other paracarinachitids would be convergent.

Protopterygotheca leshanensis Chen in Qian, Chen and Chen, 1979

Plate 9; Text-figs 12 and 13

1977 *Protopterygotheca leshanensis* (nomen nudum) Zhong [Chen], p. 122, pl. 3, figs 16–18.
1979 *Protopterygotheca leshanensis* Chen in Qian *et al.*, pp. 221–222, pl. 3, figs 18 and 19.

Discussion. Although fossils attributable to this taxon were illustrated by Zhong [Chen] (1977), the formalities necessary for a proper description were not met until 1979 (Qian *et al.* 1979) when

Protopterygotheca leshanensis became a valid taxon. As noted below several species of *Solenotia* may also be compared to *Protopterygotheca*.

Diagnosis. Sclerite broadly trilobate with elongate central axis flanked by marginal flanges. Strongly convex axis, apex bluntly pointed and increasing width abapically. Axis usually smooth, but occasionally with transverse furrows, and more rarely subdued denticles in median row. Lateral zones slope from axis, outline more or less triangular. Lateral zones usually smooth, but may bear transverse or more occasionally longitudinal folds. Sclerite edges marked by doublure, sometimes showing growth increments. Interior of sclerite usually smooth, occasionally irregular furrows on marginal zone.

Holotype. ASN 51764.

Paratypes. IGAS-BC-88-30183-30198.

Stratigraphic horizon. Beds 36 and 37, Maidiping Member, Hongchunping Formation, Meishucun Stage, Lower Cambrian (see also Zhong [Chen] 1977; note that the holotype is recorded as coming from the Tianzhushan section, near Yichang, Hubei (see Qian *et al.* 1979, p. 222)).

Locality. Maidiping section, Emei, Sichuan.

Preservation. The sclerites are preserved as fine-grained phosphate, densely interwoven with abundant vermiform tubules (Pl. 9, fig. 15). This texture appears to have resulted by diagenetic phosphatization, possibly of an originally calcareous skeleton. The tubules are believed to represent endolithic organisms, possibly algae, that infested disassociated sclerites after the death of the animal.

Description. Sclerites show wide morphological variability about a basic deltoid shape that consists of a central axis flanked by marginal zones (Pl. 9, figs 1, 2, 4–14; Text-fig. 12*a*, *b*, *d*, *g*, *h*). Sclerites appear to have been more or less bilaterally symmetrical, although differences in outline and furrow development on each lateral zone leads to slight departures in symmetry. The sclerites are orientated with respect to the beak-like apex of the central axis, arbitrarily regarded as anterior, and the convex dorsal surface being distinguished from the corresponding concave ventral surface.

The central axis is strongly convex. Its angle of cross-section may exceed 180°, so that the furrow between the axis and lateral flanges forms a recessed overhang (Text-fig. 12*g*). The axis tapers anteriorly to a blunt apex, while its expansion in the opposite direction is relatively even (Pl. 9, figs 1, 5–8, 11; Text-fig. 12*h*). The posterior edge may be largely occupied by this expanded central axis, which tends to have a more flattened convexity than adapically. In longitudinal section the axis tends to be gently arcuate about a mid-point, with both anterior and posterior sections curving downwards (Pl. 9, fig. 4; Text-fig. 12*d*, *i*). In most sclerites the central axis is more or less smooth. More occasionally, especially when the axis is relatively broad, it is traversed by furrows (Pl. 9, fig. 13). These are relatively subdued, and while some are irregularly developed others can be traced across the entire axis and on the midline form an anterior cuspate extension. In such cases the midline also bears an associated series of subdued tubercles inclined abapically (Text-fig. 12*e*, *f*).

The extent of the lateral flanges appears to be controlled in part by preservation, but also reflects original variation. The angle the flanges make with the axial zone varies widely so they may be more or less flat or contribute significantly to the overall convexity of the sclerite. Along the anterior edges the lateral extension

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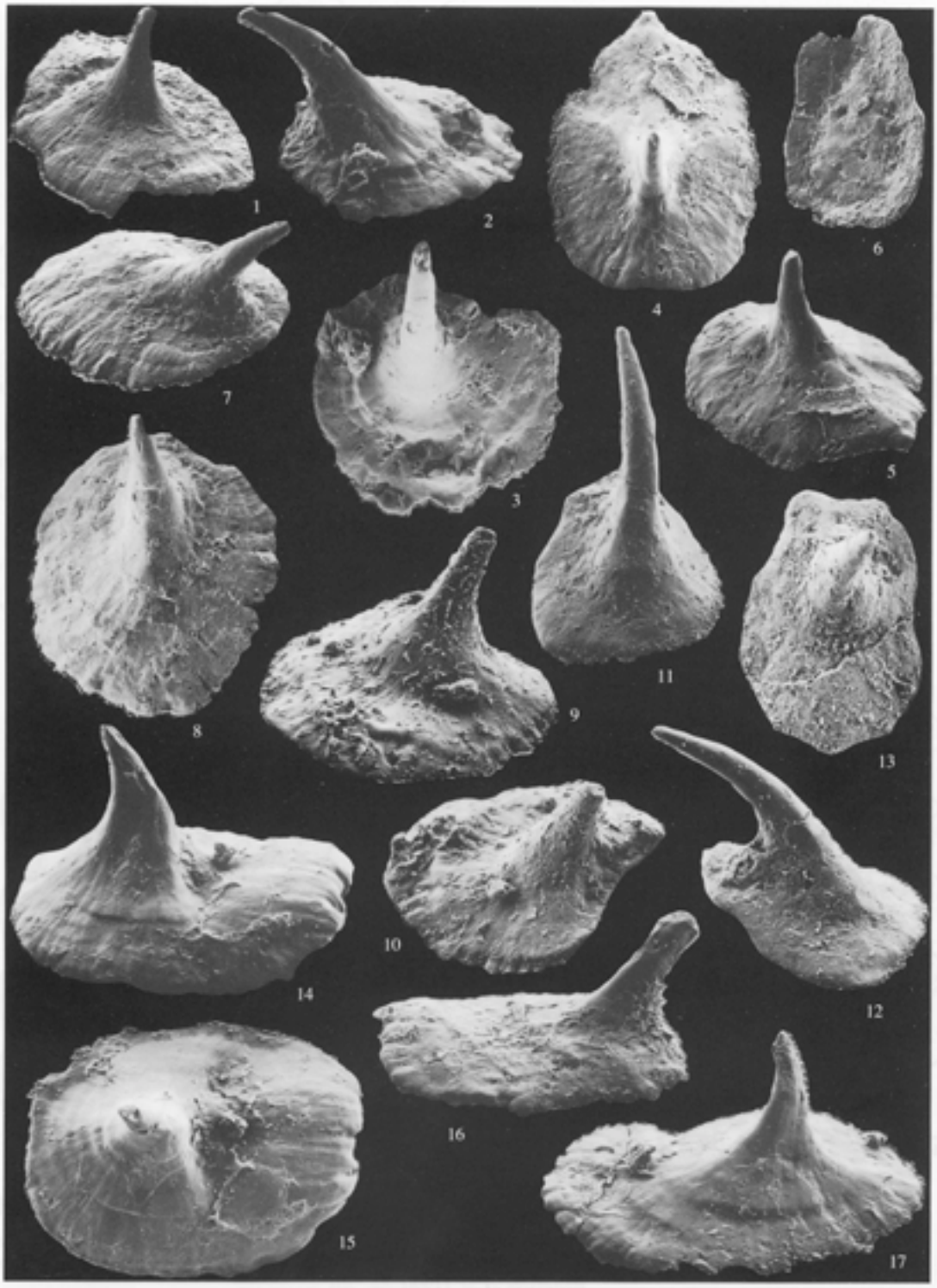
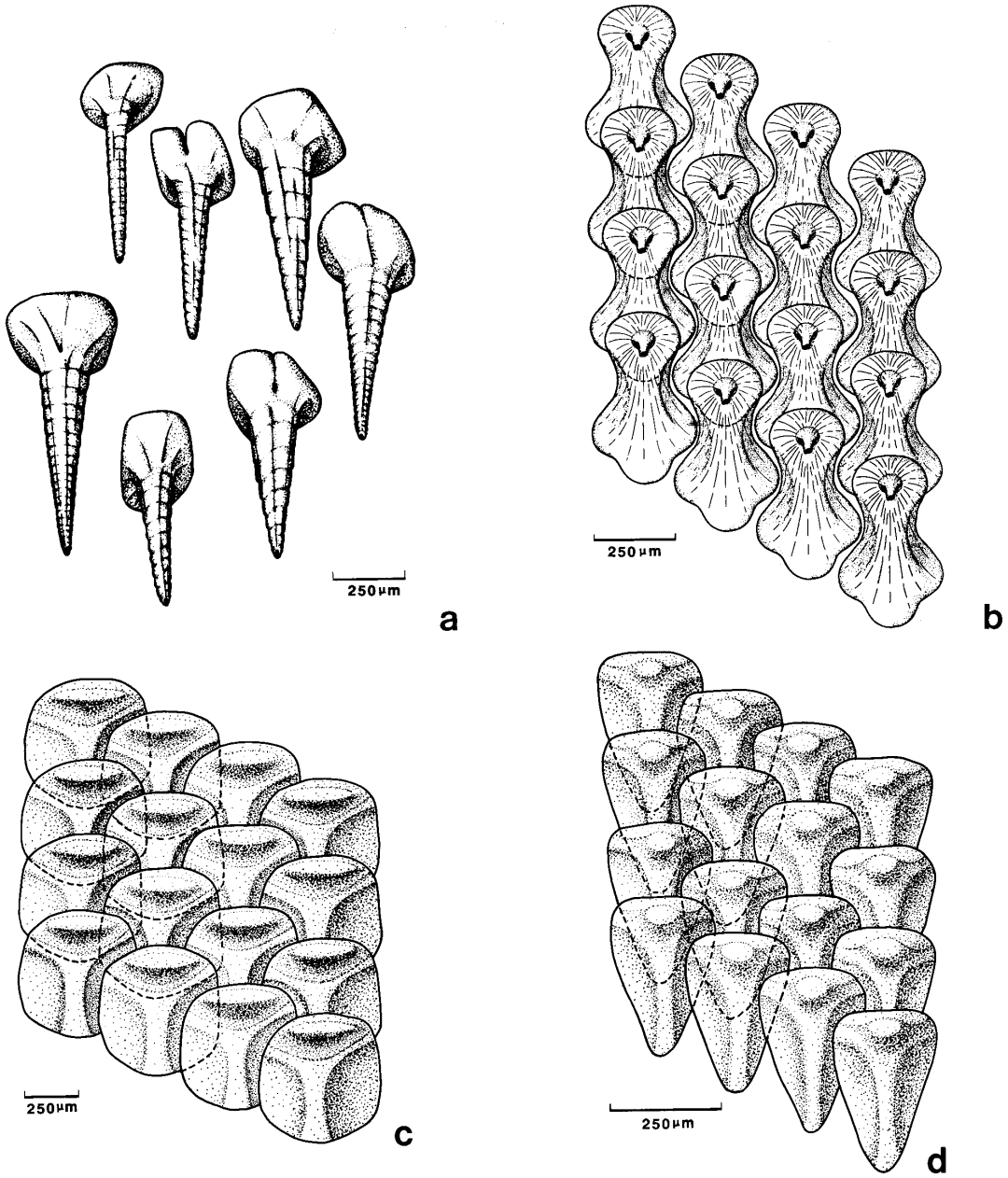
EXPLANATION OF PLATE 8

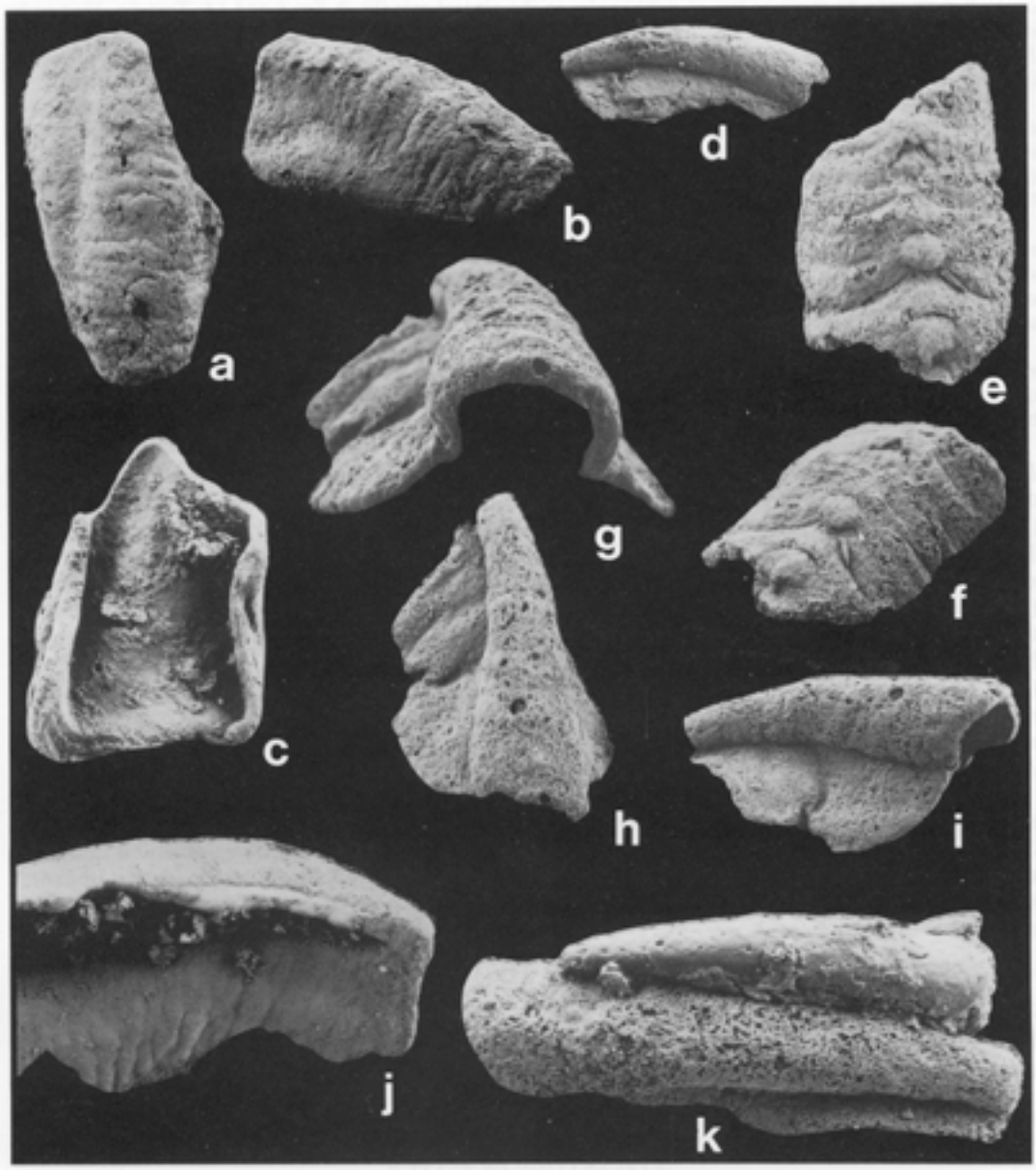
Figs 1–17. *Paracarinachites spinus* (Yu 1984). 1, IGAS-BC-88-30137. 2 and 3, IGAS-BC-88-30138. 4 and 5, IGAS-BC-88-30139. 6, IGAS-BC-88-30140. 7 and 8, IGAS-BC-88-30141. 9 and 10, IGAS-BC-88-30142. 11 and 12, IGAS-BC-88-30143. 13, IGAS-BC-88-30144. 14 and 15, IGAS-BC-88-30145. 16, IGAS-BC-88-30146. 17, IGAS-BC-88-30147. All isolated sclerites, dorsal (Figs 1–5, 7–17), and ventral (Fig. 6) surfaces, from Bed 7, Zhongyicun Member, Yuhucun Formation at Xiaowaitoushan section, Kunyang Phosphorite Mine, Meishucun, Yunnan, China. Magnifications all ×90.



CONWAY MORRIS and CHEN, *Paracarinachites*



TEXT-FIG. 11. Hypothetical reconstructions of partial portions of the scleritome of (*a*) *Zhijinites longistriatus*; (*b*) *Cambroclavus absonus*; (*c*) *Deiradoclavus trigonus*; (*d*) *Deltaclavus graneus*. Text-figure 7*b* is based on Bengtson *et al.* (1990, fig. 70).



TEXT-FIG. 12. *Protopterygotheca leshanensis* Chen in Qian *et al.*, 1979. *a* and *b*, IGAS-BC-88-30192; *a*, dorsal view; *b*, oblique view. *c*, IGAS-BC-88-30193, ventral view. *d*, IGAS-BC-88-30194, lateral view; *e* and *f*, IGAS-BC-88-30195; *e*, dorsal view; *f*, oblique view. *g–i*, IGAS-BC-88-30196; *g*, posterior view; *h*, dorsal view; *i*, lateral view. *j*, IGAS-BC-88-30197, ventral view with internal furrows. *k*, IGAS-BC-88-30198, fused specimen. Isolated sclerites from Bed 37 (*a–c*) and Bed 36 (*d–k*), Maidiping Member, Hongchunping Formation at Maidiping section, Emei, Sichuan, China. Magnifications: *a–d*, ×30; *e*, *f*, *h–k*, ×60; *g*, ×100.

of the flanges may be more or less at right angles to the central axis (Pl. 9, figs 6 and 14; Text-fig. 12*a*) or be inclined posteriorly so that the maximum width is nearer the transverse mid-line (Pl. 9, figs 7 and 11; Text-fig. 12*h*). The flanges, therefore, form wing-like extensions of widely variable shape according to the angles of insertion towards the anterior and posterior ends of the central axis.

Each lateral flange of a sclerite is similar, but minor differences can exist by the asymmetrical development of furrows on one flange (Pl. 9, figs 6, 8, 9, 11, 12; Text-fig. 12*h*). Typically these furrows are transverse, and if they extend to the sclerite margin may disrupt the outline. The furrows grade from fairly open folds to more deeply incised structures. Often the folds are grouped, sometimes radiating outwards. In addition, a few flanges bear longitudinal folds.

In the majority of sclerites the margins are simple, but this may be an artefact of preservation because in some specimens the sclerite edge forms a simple doublure (Text-fig. 12*c*). However preserved, the edge seldom shows internal structure, although rarely incremental units are visible (Pl. 9, figs 4 and 10). The internal surface of the sclerite is normally smooth (Pl. 9, fig. 3), but on occasion a series of transverse furrows that increase in strength towards the margin (Text-fig. 12*f*) have been noted.

With one exception, the sclerites occur isolated. In one individual, however, part of a central axis (and a specimen of *Zhijinites longistriatus*) appears to have fused to another sclerite, the respective axes pointing in opposite directions (Text-fig. 12*k*). It is argued below that the sclerites may have formed an imbricated series, but this particular association seems to be one of post-mortem fusion during phosphatization.

Discussion. In isolation the central axis of these sclerites strongly resembles in overall shape and dimensions specimens of *Paracarinachites sinensis* (Qian and Bengtson 1989). In addition Kerber (1988) noted traces of lateral extensions in his paracarinachitid material from the Montagne Noire, France, but it is difficult to decide whether the absence from the Chinese material is preservational or an original difference that justifies taxonomic separation between it and the French examples (Qian and Bengtson 1989). While the specimens described here from Maidiping can be referred to the paracarinachitids, the precise taxonomic status is somewhat uncertain. Principally, this is because the median row of spines, a diagnostic feature of *Paracarinachites*, is only rarely expressed (Text-fig. 12*e*, *f*). Given the quality of preservation, including the survival of the lateral flanges, it seems implausible that the median spines are lost because of poor preservation. Accordingly, there seems to be reason to retain the genus *Protopterygotheca* at the moment as separate from *Paracarinachites*, and refer to both informally as paracarinachitids.

Attention should be drawn also to problematical fossils from Guizhou that Qian and Yin (1984*a*; see also Wang *et al.*, 1984*b*) referred to as *Solenotia* (type species *S. lata*, also *S. lobata* and *S. elongata*; note *S. incurva* (Wang *et al.* 1984*a*, pl. 21, fig. 17) appears to be a nomen nudum). The material is fragmentary and details are difficult to discern in the published photographs, but some specimens may be comparable to *P. leshanensis* (see in particular Qian and Yin 1984*a*, pl. 5, figs 1 and 4).

DISCUSSION

Scleritome reconstruction

In *Cambroclavus* (Mambetov *in* Mambetov and Repina 1979; Bengtson *et al.* 1990) and *Deltaclavus* gen. nov. fused assemblages suggest that the cataphract scleritome in these taxa was

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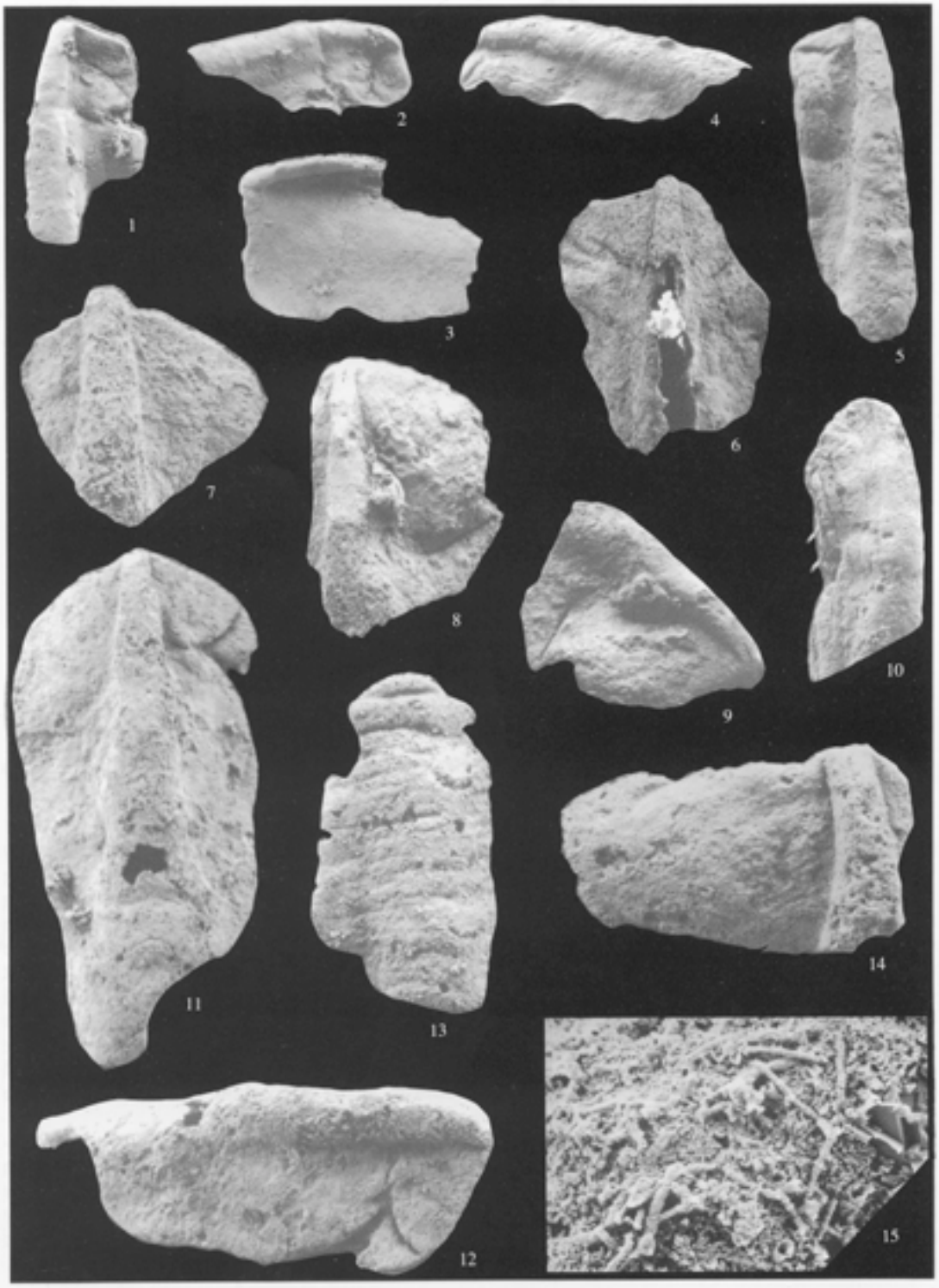
EXPLANATION OF PLATE 9

Figs 1–14. *Protopterygotheca leshanensis* Chen in Qian *et al.* 1979. 1 and 2, IGAS-BC-88-30182; 1, dorsal view; 2, oblique view. 3, IGAS-BC-88-30183, ventral view; 4 and 5, IGAS-BC-88-30184; 4, oblique view; 5, dorsal view; 6, 15, IGAS-BC-88-30185; 6, dorsal view; 15, wall ultrastructure showing diagenetic phosphatization and endolithic borings; 7, IGAS-BC-88-30186, dorsal view. 8 and 9, IGAS-BC-88-30187; 8, dorsal view; 9, oblique view. 10, IGAS-BC-88-30188, dorsal view. 11 and 12, IGAS-BC-88-30189, holotype; 11, dorsal view; 12, lateral view. 13, IGAS-BC-88-30190, dorsal view. 14, IGAS-BC-88-30191, dorsal view. All isolated sclerites from Bed 37, Maidiping Member, Hongchunping Formation at Maidiping section, Emei, Sichuan, China. Magnifications: ×30 (Figs 1–6, 8–12); ×60 (Figs 7, 13, 14); ×400 (Fig. 15).



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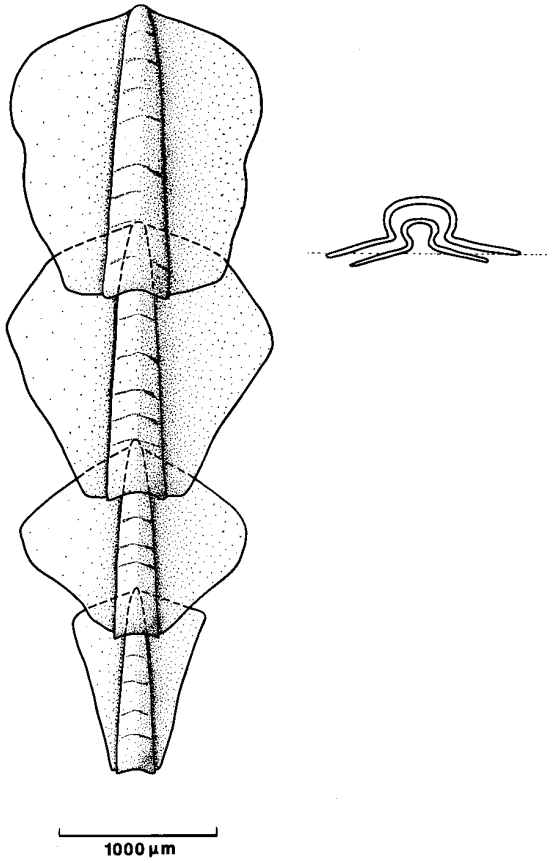

TEXT-FIG. 13. Hypothetical reconstruction of a partial portion of the scleritome of *Protopterygotheca leshanensis*.

closely integrated with longitudinal files articulating via facets and transverse files interlocking by virtue of congruent shapes (Text-fig. 11*b*, *d*). A reconstruction of the sclerites providing a coating to a worm-like animal thus seems reasonable, in a manner analagous to Recent spicule-bearing animals such as aplacophorans and certain turbellarians (Rieger and Sterrer 1975). In at least some species of *Cambroclavus*, such as a new species from Australia (Bengtson *et al.* 1990), the morphological variation of the sclerites is very wide, and includes many sclerites that depart conspicuously from a bilaterally symmetrical shape. In this new Australian species it was postulated that variability of sclerites occurred within single scleritomes, and that mutual accommodation between differently shaped sclerites could lead to changes in sclerite appearance across the scleritome. Similarly, in *Deiradoclavus* it is supposed that the variability of sclerite shape was typical of individuals, and relatively rapid changes in sclerite shape across the scleritome could be accommodated by a series of minor adjustments.

However, the recognition of articulated series of sclerites in double layers in *Deltaclavus* (Text-fig. 9*d–h*) hints at previously unexpected complexities of anatomy in this taxon, although the morphological similarities and comparable age (Text-fig. 2) of *Deltaclavus* and *Deiradoclavus* suggest that their scleritomes did not differ radically from one another. Given the orderly appearance and sense of articulation it seems unlikely that these fused assemblages are taphonomic

artefacts, formed for instance by folding together of a single layer. Granted that they are original features, then one interpretation would be to regard them as arm-like extensions, analagous for example to the feeding arms of various pelmatozoan echinoderms. *Deiradoclavus* gen. nov. is known only from isolated sclerites. However, reconstruction as a tightly integrated scleritome (Text-fig. 11*c*) is plausible given the distribution of concave facet-like areas on the dorsal and ventral surfaces.

In contrast to all the above genera, the circular outline of sclerites of *Zhijinites* suggests that they were separate, possibly studding the body surface and isolated by areas of non-mineralized cuticle (Text-fig. 11*a*). What may represent an intermediate case, with some sclerites articulated and others isolated, occurs in *Paracarinachites spinus*. In this taxon some sclerites occur in fused longitudinal rows, whose life association was cogently argued for by Qian and Bengtson (1989). Co-occurring isolated sclerites in part may have been derived by disarticulation of less welded portions of the scleritome, but other sclerites lack any obvious zones of articulation and abutment.

It is questioned whether the remaining species of *Paracarinachites* and *Protopterygotheca* (see above) are either closely related to *P. spinus* or to the zhijinitids (see also Qian and Bengtson 1989, p. 56). One reason to propose this is the distinctive morphology of *P. leshanensis* whose similarity to the type species *P. sinensis* is clear, but whose derivation from any cambroclave morph seems forced. In *P. leshanensis*, where sclerite form is arguably more complete, it is hypothesized that they could have formed an imbricated row (Text-fig. 13). In contrast Qian and Bengtson (1989, p. 56) suggested that 'Several *Paracarinachites* sclerites were positioned close to each other in a cone-like structure, so that the apical ends met in the centre', while similar remarks were also addressed to the possibly related *Scoponodus*.

Biomineralization and mode of secretion

The original composition of the sclerite wall of cambroclaves appears to have been calcareous, with evidence surviving from steinkerns and phosphatic replacement for an originally fibrous ultrastructure. In life the hollow within the sclerites is believed to have been occupied by soft tissue, presumably including secretory epithelia. Such an arrangement is thought more likely than having the sclerites covered with secretory tissue. However, if the calcareous wall was laid down by internal tissue, it seems that initial formation or additions to the scleritome must have entailed patches of secretory tissue that formed a template whose precise expression was governed by the bounding nature of the adjacent sclerites. In this manner accommodation between sclerites to produce a well-integrated scleritome would not need to be under precisely specified genetic control, and would be responsive to local morphology and possibly damage repair.

The relationship between the tissue enclosed in the sclerite and any surrounding tissue is rather problematic. A crude analogy might be drawn with echinoderm ossicles, which contain stereom tissue but are embedded in mesoderm. Although pores are observed on the inner walls of the spinose portion of *Zhijinites* sclerites (Pl. 3, fig. 4) it is not clear if soft tissue extended to the outer margin, especially as the spines are envisaged as projecting free of the body wall.

In *P. spinus* heavy diagenetic phosphatization appears to have obliterated all traces of original mineralogy. However, granted that the fused series described by Qian and Bengtson (1989) represent a primary association, then it is necessary to postulate secretory tissue that lay beneath the sclerite series. In the remaining paracarinachitids the clear distribution of growth lamellae (Kerber 1988; Qian and Bengtson 1989; see also Pl. 9, figs 4 and 10) suggests that secretory tissue formed a mantle-like layer responsible for production of mineralized increments.

Palaeoecology

Scleritome reconstruction of a new species of *Cambroclavus* from Australia (Bengtson *et al.* 1990) was taken to indicate a primarily defensive role, presumably against predators and physical abrasion. The elongate spines arising from the anterior region of each sclerite would be an important contributory factor, but it was also noted that their recurved nature could have assisted in grasping substrates. However, if *Cambroclavus* was a burrowing organism, then one might predict an allometric change in spine size to compensate for increase in body size in comparison with

habitation of a substrate of fixed grain size (see Aller 1974 for an analagous example in bivalve molluscs). Tentative evidence from the Australian material, however, did not support such an allometric response.

Systematic position

The relationships of cambroclaves to other major groups remain problematic. Mambetov's (*in* Mambetov and Repina 1979) comparison of the cambroclaves to the protoconodont *Protohertzina* and conodont-like *Rhombocorniculum* seems to be without foundation. Various Chinese workers (e.g. Qian and Yin 1984*b*) have placed the cambroclaves in the Acanthocephala, an endoparasitic group of worms with no known fossil record (Conway Morris and Crompton 1982). This supposition is based on the similarities between cambroclave sclerites, especially of *Zhijinites*, with the proboscis hooks of acanthocephalans (see also Qian and Xiao 1984, p. 79). However, differences in composition, mode of secretion, and recognition in cambroclaves of an integrated scleritome, that at least in *Deltaclavus* includes 'arm-like' structures, all suggest that cambroclaves are unlikely to be related to acanthocephalans. However, in the absence of complete scleritomes and associated soft-part preservation, the wider affinities of this group remain uncertain.

No further light can be thrown either on the wider affinities of the paracarinachitids, other than the tentative proposal that *P. spinus* be regarded as belonging to the cambroclaves, while the remaining species of *Paracarinachites*, possibly together with *Scoponodus* and even *Ernogia* (see above), be regarded as a distinct group. What is clear, however, is that comparisons between paracarinachitids and polyplacophorans (e.g. Yu 1989) are without foundation, a point already cogently made by Qian and Bengtson (1989, pp. 48–49).

Acknowledgements. Samples from Shaanxi and Sichuan provinces were collected during a Royal Society–Academia Sinica Exchange Scheme in 1986. Field trips to Hubei and Yunnan provinces in 1987 were possible thanks to the organizers of an International Symposium on the Terminal Precambrian and Cambrian Geology, Yichang, Hubei. S.C.M. acknowledges support for attendance from a Royal Society–China Agreement on Science and Technology (CAST) Exchange Scheme. A Royal Society–USSR Academy of Sciences Exchange Scheme allowed S.C.M. to examine relevant material from Kazakhstan, and I am most grateful to Dr V. V. Missarzhevsky for his generosity in allowing access to collections. Laboratory work was supported by the Nuffield Foundation (One Year Science Research Fellowship) and NERC (research grant GR3/6456), to whom grateful acknowledgement is made. Fossil picking by Zoë Conway Morris, technical assistance by Liz Harper, Ken Harvey, David Newling, Sarah Skinner and Sarah Palmer, and extensive typing by Sandra Last are all warmly appreciated. Valuable reviews by Stefan Bengtson and Adrian Rushton are also appreciated. Cambridge Earth Sciences Publication 1645.

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Typescript received 19 December 1989
Revised typescript received 11 May 1990