LOWER CAMBRIAN CAMBROCLAVES (*INCERTAE SEDIS*) FROM XINJIANG, CHINA, WITH COMMENTS ON THE MORPHOLOGICAL VARIABILITY OF SCLERITES

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ABSTRACT. Four species of cambroclave, an enigmatic group whose position within the Metazoa is unresolved, are described from the Lower Cambrian Yurtus Formation of western Xinjiang, China. *Cambroclavus bicornis* is similar to a number of previously described species, including *C. absonus* from approximately equivalent age strata of South Australia. As in many cambroclave taxa, morphological variability of individual sclerites appears to be considerable. Morphometric analysis of four populations of *C. bicornis*, using elliptic Fourier shape analysis (EFA), demonstrates that this technique offers considerable discriminatory power. Two samples from the upper parts of one section (Sugaitbulak) show morphological stasis. They are also readily distinguishable from two other samples, which although from near-equivalent horizons in adjacent sections on Yurtus Mountain differ significantly from one another. *Zhijinites claviformis* is a robust sclerite, with a strongly ribbed spine. In contrast, *Parazhijinites* cf. *guizhouensis* has a remarkably slender spine, arising from a much reduced base. Finally, *Wushichites minutus* is more reminiscent of other Chinese cambroclaves, notably *Deiradoclavus trigonus*, with a sclerite with a sub-circular base indented by a posterior notch, and a much reduced spine. Although the overall morphology of cambroclaves appears to be related to protection from predatory attack, the wide variation in basic sclerite types lacks convincing ecological explanations.

THE most obvious manifestation of the rapid diversification of metazoans close to the Vendian-Cambrian boundary is the relatively abrupt appearance of skeletal parts. Many have been long familiar, such as the remains of trilobite exoskeletons, brachiopod valves, and echinoderm ossicles. Others were once enigmatic, but are now recognized as dispersed units of scleritomes. An example of the latter are the halkieriids, slug-like metazoans with a cataphract armour of sclerites (Conway Morris and Peel 1995). There remains, however, a considerable number of Cambrian taxa which are of very uncertain systematic position. They have no obvious affinity to any known major group, and often show at least a moderate diversity of form. The cambroclaves exemplify this problem: they are represented by a variety of sclerite morphs, typically phosphatized during diagenesis but with good evidence of an original composition of calcium carbonate. The sclerites have the common form of a basal unit and projecting spine. The interior of the sclerite is hollow, and originally was presumably filled with soft tissue and/or fluid. A somewhat crude sub-division recognizes four types of sclerites. Zhijinitids and paracarinachitids have an approximately oval base and prominent spine. Cambroclavids have a 'dumb-bell' shape, with the spine located at the anterior (arbitrarily defined) end. Deiradoclavids (and the similar wushichitids) are approximately circular and the spine may form a transverse ridge. Finally, deltaclavids are approximately tear-drop-shaped with the short spine located at the expanded anterior end.

The great majority of sclerites are found isolated. Rare examples of fused assemblages, combined with analysis in single sclerites of congruent outlines and articulatory facets, demonstrate, however, that at least some areas of the scleritome could have formed interlocking arrays, if not sheets. Of particular significance was the independent recognition of relatively extensive fused clusters in

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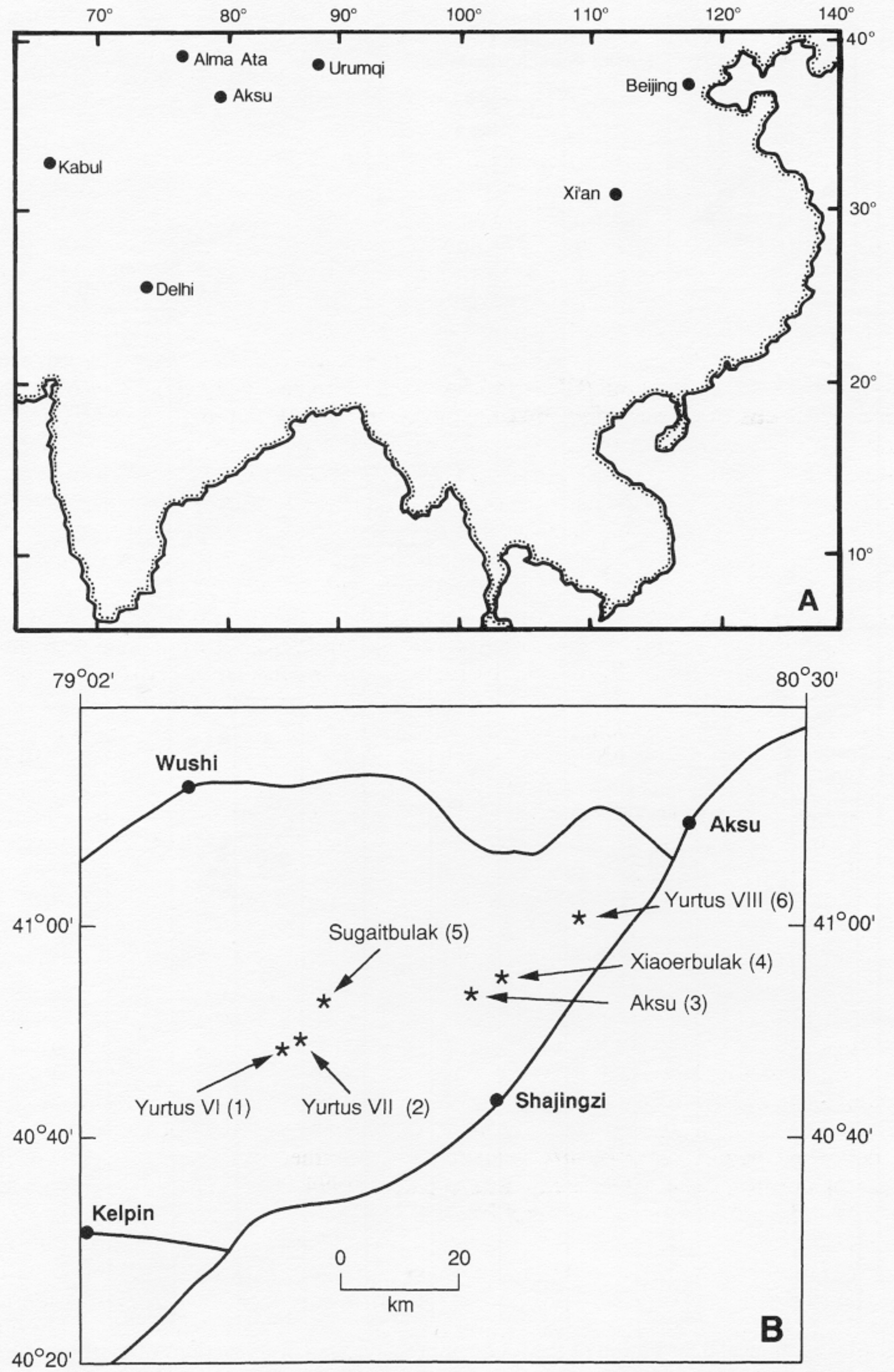
Chinese material by Conway Morris and Chen (1991) and Yue (1991). Of equal interest was the observation that the sclerites can form two layers, back-to-back. This suggests that, unless this configuration arose by some sort of post-mortem folding, which seems rather unlikely, the scleritome arrangement was not a simple cataphract armour covering the surface of a slug-like animal. A further observation is that in a fused assemblage of four parallel rows, the two central ones are notably smaller than those flanking on either side (Yue 1991, fig. 1.5).

The affinities of cambroclaves remain enigmatic. Comparisons between the zhijinitids and the hooks of parasitic worms such as the Acanthocephala (e.g. Qian and Yin 1984) are considered unlikely (Conway Morris and Chen 1991). The apparent arm-like nature of some assemblages allows a very tentative comparison with the echinoderms (Conway Morris 1993), but the sclerites do not show the characteristic stereom ultrastructure of this phylum. Another possibility should also be noted. One of the priapulid worms (*Cricocosmia jinningensis*) from the Lower Cambrian Konservat-Lagerstätte of Chengjiang, Yunnan province, China, has a double row of sclerites that extend along almost the entire trunk (Hou and Sun 1988; Hou and Bergström 1994). These sclerites have received only cursory description, but examination of material in Nanjing (courtesy of Hou Xianguang and Chen Junyuan) indicates that they have a distinctive structure. Each sclerite is somewhat elliptical in outline, and concavo-convex. The upper surface is traversed by a low ridge at the anterior. The lower concave surface bears a doublure-like structure on its anterior margin. There are also a number of undescribed worms from the Chengjiang biota that carry other types of discoidal and conical sclerites. None of these is directly comparable to known cambroclaves but an affinity with the priapulids or some other group of protostome worms cannot be ruled out. Finally, it might be noted that the gastrotrichs, a phylum of microscopic animals that are usually placed in the aschelminths, sometimes have cuticular spines that have quite striking similarities to cambroclaves (e.g. Evans 1992; Balsam and Fregni 1995). Nevertheless, at the moment no other evidence appears to support a phylogenetic connection between these two groups.

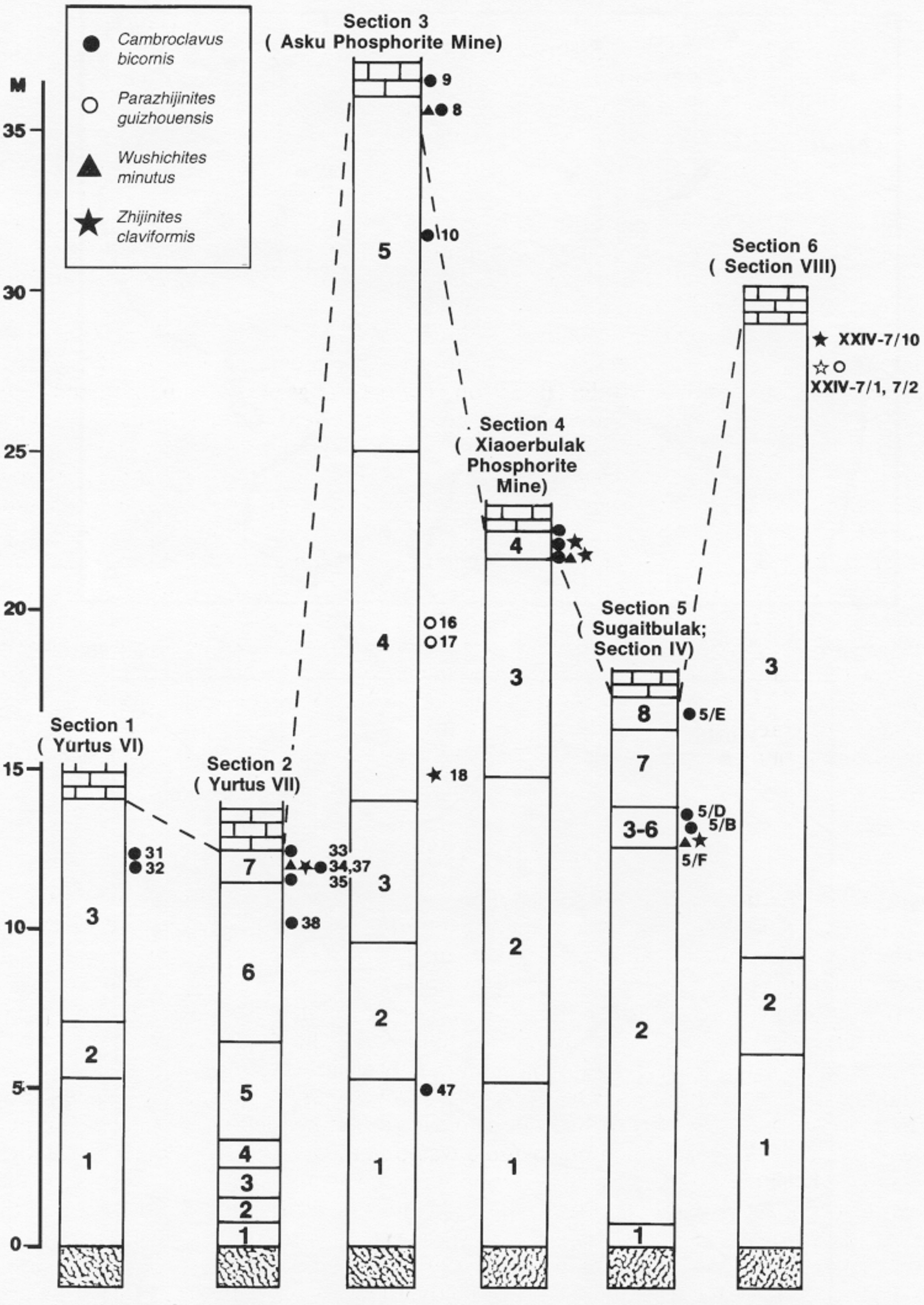
While a position with the Metazoa still seems more plausible, it may also be worth speculating whether cambroclaves could be some type of algae. In particular Dzik (1994, fig. 19) illustrated isolated meroms of an Ordovician receptaculitid, which resemble cambroclavid sclerites. They also have a fibrous ultrastructure that resembles that documented in cambroclaves (e.g. Bengtson *et al.* 1990, figs 64S, 65P, S, W, 67O), and was interpreted by Dzik (1994) as a replacement of an acicular aragonite ultrastructure. Receptaculids are widely regarded as algal, perhaps related to the dasycladeans (e.g. Nitecki 1986), but Dzik (1994) has reiterated the possibility of a sponge relationship.

The history of research into cambroclaves and their palaeobiology were both reviewed at some length by Conway Morris and Chen (1991), and will not be repeated here. Since then, however, several items require discussion. First, relatively few new reports on cambroclaves have been issued. An important record, however, is from sections in Shaanxi province that have a number of faunal similarities to the equivalent-aged strata in Xinjiang (Ding *et al.* 1991). The taxonomy of the Shaanxi cambroclaves requires some revision, but in particular the material ascribed to *Zhijinites* sp. (Ding *et al.* 1991, pl. 2, figs 29–31, 36) from sections near Xixiang approaches quite closely the material described herein as *Zhijinites claviformis*. Another new report is from the upper Atdabanian of Görlitz, eastern Germany where Elicki (1994, fig. 6.17–6.20; see also Elicki and Schneider 1992, pl. 16, figs 10–11; Geyer and Elicki 1995) documents *Cambroclavus ludwigsdorfensis*. More information is also available on the cambroclaves from the Yurtus Formation of western Xinjiang (e.g. Duan and Xiao 1992; Xiao and Duan 1992; Yue and Gao 1992), but as these form the main point of this paper these reports are assessed in more detail below. Considerably more doubt surrounds fossils, from the Lower Cambrian of Cape Breton Island, that Landing (1991, p. 591) described as *Samsanoffoclavus matthewi* and proposed tentatively might be 'a zhijinitiid or zhijinitiid relative'. *S. matthewi* consists of hollow sclerites, with a pointed apical region extending into a much broader base, which defines a wide aperture. Although zhijinitids have a spine and base, the demarcation is generally much stronger and the base is usually closed.

Another area of confusion that remains unresolved is the appropriate taxonomy for



TEXT-FIG. 1. Locality maps. A, central Asia showing the position of the town of Aksu. Urumqi is the capital of Xinjiang. Alma Ata is in Kazakhstan. The localities that yield the cambroclaves in this region (see text) are situated to the east of Alma Ata. B, detailed locality map of the Aksu-Wushi area, showing the position of the six stratigraphical sections that yielded cambroclaves.



TEXT-FIG. 2. Stratigraphical distribution of the four cambroclave taxa in six sections of the Yurtus Formation, Aksu-Wushi, Xinjiang, China. The underlying unit is the Qigebulak Formation, the overlying unit is the Xiaoerbulak Formation. The numbers 9–10, 16–18, 31–35, 37–38, 42–44 and 47 refer to field numbers of samples collected in 1991. Other samples were collected earlier by one of us (XB): 5/B, 5/D–5/F are from Sugaitbulak; XXIV-7/1, 7/2 and 7/10 are from Section VIII. See Text-figure 1 for geographical locations of these sections. Stratigraphical sections are based on Figure 2.6 of Gao *et al.* (1985*a*).

cambroclaves, especially at the generic and specific levels. Despite discussions of morphological variability (see also below), which in at least some populations is marked (Bengtson *et al.* 1990; Conway Morris and Chen 1991), and the reiterated need to consider larger sample sizes than is current practice, more recent reports tend to document material or even erect new taxa on limited appraisal of scleritome variability (e.g. Xiao and Duan 1992; Yue and Gao 1992; Elicki 1994). In addition, the status of a number of cambroclave genera is unresolved. Duan (1984) erected *Phyllochiton*, *Sinoclavus* and *Tanbaoites* for cambroclave material recovered from the Xihaoping Formation of Shennongjia, Hubei province. He also described a number of new species of *Cambroclavus*. Duan's (1984) actions were reviewed by Bengtson *et al.* (1990, p. 103) who tentatively proposed that all three genera were junior synonyms of *Cambroclavus*. For the most part, the nominal species of cambroclave from the four sections documented in Shennongjia by Duan (1984) overlap (see his Table 1), and they may all derive from a single species. Yue (1991), however, continued to recognize *Phyllochiton*, following Duan's (1984) discrimination of sclerites bearing lateral spurs. Such structures, however, are variably present in species of *Cambroclavus*, such as *C. absonus* from South Australia (Bengtson *et al.* 1990, figs 64A–B, R, 65G, T) and *C. bicornis* from Xinjiang (see below). There is, however, a danger of over-enthusiastic forays into synonymy. In particular, a distinctive type of cambroclave, with a small base and a very elongate, narrow spine, is referred to as *Parazhijinites guizhouensis* (Qian and Yin 1984, pl. 2, figs 1–8). It was first described from Guizhou province, and subsequently was tentatively synonymized with *Zhijinites longistriatus* by Conway Morris and Chen (1991, p. 367). In this paper, however, it is now restored as a separate taxon, with possible new records from western Xinjiang (see below). Finally, it should be noted that the palaeobiogeography of the cambroclaves has received little attention, although Jiang (1992, fig. 8) invoked a diachronous migration across central and south Asia.

The purpose of this paper is two-fold. First, it redescribes and reassesses the cambroclave fauna of Xinjiang with detailed descriptions of *Cambroclavus bicornis* (Qian and Xiao, 1984), *Zhijinites claviformis* Qian and Xiao, 1984, *Parazhijinites* cf. *guizhouesis* Qian and Yin, 1984, and *Wushichites minutus* Qian and Xiao, 1984. Secondly, a quantitative consideration of cambroclave variability is provided, using elliptic Fourier shape analysis (EFA) of outlines from selected populations of *C. bicornis*.

STRATIGRAPHY AND LOCALITIES

The geographical locations of the studied sections in the Yurtus Formation are shown in Text-figure 1. A summary of the Vendian–Cambrian stratigraphy of this area and the sections sampled is given by Conway Morris and Chapman (in press), and only a few comments will be given here. The Yurtus Formation (Text-fig. 2) is of variable thickness, and consists of a mixture of calcareous clastics and impure limestone, although the basal unit is a siliceous phosphorite that has been mined quite extensively. Text-figure 2 depicts the distribution of the cambroclave taxa, and further comments for each species are given below. In general, occurrences tend to be concentrated near the top of the Yurtus Formation, where there is evidence for sedimentary condensation and phosphatization, prior to the abrupt transition to the ribbon-bedded limestones of the overlying Xiaoerbulak Formation (from which one sample was obtained). The abundance of cambroclaves in these horizons is, therefore, mostly taphonomically enhanced, and the occurrence of *Cambroclavus bicornis* low in the section at Aksu phosphorite mine (Text-figure 2) shows that this species of cambroclave at least has a relatively long range. Of the six sections that yielded one or more species of cambroclave, five were visited in 1991. The sixth, at Sugaitbulak, was inaccessible owing to deterioration of the track, and the productive samples were obtained earlier by one of us (XB).

The age of the Yurtus Formation and its inferred correlation with other Precambrian–Cambrian units is not entirely resolved. Recovery of *Rhombocorniculum cancellatum* from the Yurtus Formation (Yue and Gao 1992) indicates, however, that the bulk of this unit is Atdabanian. The most secure correlations appear to exist with the sequences in Kazakhstan, especially the Maly

Karatau region, on account of the general faunal similarities. Much of the Yurtus Formation appears to correlate with Chulaktau Formation and the lower part of the overlying Shabakty Formation. These correlations and the general faunal aspect of the Yurtus Formation also support this age assignment. A more detailed discussion of these topics is given by Conway Morris and Chapman (1996, in press).

SYSTEMATIC PALAEONTOLOGY

Class CAMBROCLAVIDA Conway Morris and Chen, 1991
Family ZHIJINITIDAE Qian, 1978
Genus CAMBROCLAVUS Mambetov *in* Mambetov and Repina, 1979

Cambroclavus bicornis (Qian and Xiao, 1984)

Plate 1; Plate 2, figures 1–9

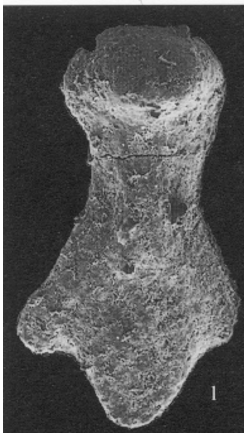
1984	*Sugaites bicornis* Qian and Xiao, p. 79, pl. 1, figs 9, 12–13; pl. 3, figs 16–19.
1984	*Sugaites soleiformis* Qian and Xiao, p. 80, pl. 1, figs 10–11; pl. 3, figs 14–15.
1984	*Sugaites sicyojdeus* Qian and Xiao, p. 80, pl. 3, fig. 23.
1984	*Sugaites hastatus* Qian and Xiao, p. 81, pl. 3, figs 20–22.
1984	*Sugaites saccatus* Qian and Xiao, p. 81, pl. 3, figs 24–26.
1984	*Cambroclavus paradoxus* Qian and Yin, p. 220, pl. 2, figs 9–12.
1985*a*	*Sugaites bicornis*; Gao *et al.*, pl. 5, figs 9–11; pl. 8, figs 9–11.
1985*a*	*Sugaites soleiformis*; Gao *et al.*, pl. 5, figs 12–13; pl. 8, figs 12–14.
1985*a*	*Sugaites saccatus*; Gao *et al.*, pl. 8, figs 6–8.
1985*a*	*Sugaites hastatus*; Gao *et al.*, pl. 8, figs 15–18.
1985*b*	*Sugaites bicornis*; Gao *et al.*, pl. 34, fig. 21.
1985*b*	*Sugaites soleiformis*; Gao *et al.*, pl. 34, fig. 22.
1985	*Cambroclavus bicornis*; Wang *et al.*, pl. 3, fig. 13.
1992	*Cambroclavus* sp.; Yue and Gao, pl. 4, fig. 4.
1992	*Sinoclavus* Xiao and Duan, p. 225, pl. 3, figs 24–25.
1992	*Cambroclavus bicornic* [*sic*]; Xiao and Duan, pl. 4, fig. 35.
1992	*Cambroclavus* spp.; Xiao and Duan, pl. 4, figs 27, 32, 37.
1992	*Cambroclavus soleiformis*; Xiao and Duan, pl. 4, figs 14–15.
1992	*Cambroclavus hastatus*; Xiao and Duan, pl. 4, figs 13, 24–26, 30.
1992	*Phyllochiton vescus* [*nomen nudum*]; Xiao and Duan, pl. 4, figs 3–4.
1992	*Phyllochiton tubercularis* [*nomen nudum*]; Xiao and Duan, p. 225, pl. 4, figs 1–2, 8.
1992	*Phyllochiton tubercularis*; Duan and Xiao, p. 343, pl. 1, figs 17–18.
1992	*Phyllochiton vescus*; Duan and Xiao, p. 343, pl. 2, figs 17–18.
1992	*Cambroclavus hastatus*; Duan and Xiao, pl. 3, figs 1, 15.
1992	*Cambroclavus soleiformis*; Duan and Xiao, pl. 3, fig. 2.
1992	*Cambroclavus* sp.; Duan and Xiao, pl. 3, fig. 20.
1992	*Sinoclavus*; Duan and Xiao, pl. 3, fig. 21.
1992	*Cambroclavis bicornis*; Jiang, figs 8, 8a, 13.
1992	*Cambroclavus soleiformis*; Jiang, figs 5, 7, 7a, 12.
?1994	*Zhijinites*; Yue and Gao, pl. 12, fig. 11.

Holotype. Xinjiang Institute of Geology 10583.

EXPLANATION OF PLATE 1

Figs 1–12. *Cambroclavus bicornis* (Qian and Xiao, 1984). 1, SM X.26167. 2, SM X.26168. 3, SM X.26169. 4, SM X.26170. 5, SM X.26171. 6, SM X.26172. 7, SM X.26173. 8, SM X.26174. 9, SM X.26175. 10, SM X.26176. 11, SM X.26177. 12, SM X.26178. All isolated sclerites, dorsal (1–2, 4, 8–12) and ventral surfaces (3, 5–7), from the Yurtus Formation, Yurtus Mountain; section 1 (sample XI/91/31), 1–3; section 2 (sample XI/91/35), 4–12, Aksu-Wushi, Xinjiang, China. Magnifications are × 100 (1–2), × 110 (3), × 150 (4–6, 9, 11), × 175 (7–8), × 200 (10, 12).

PLATE 1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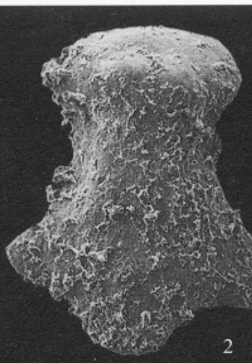
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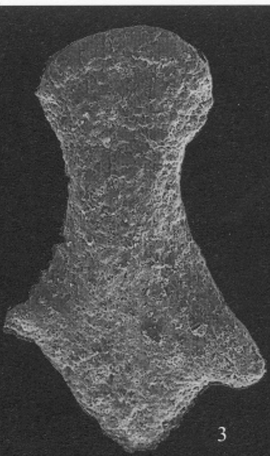
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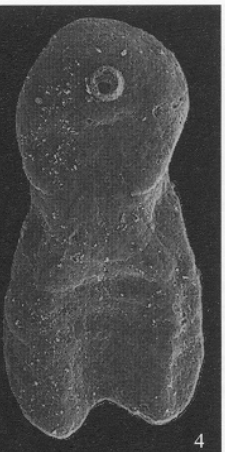
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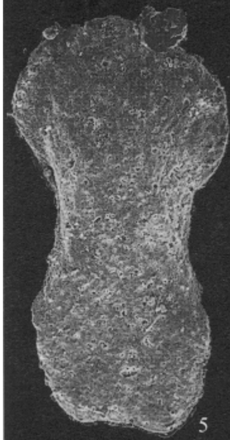
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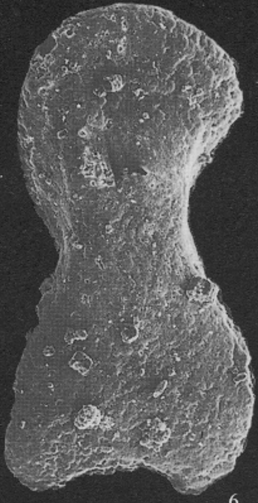
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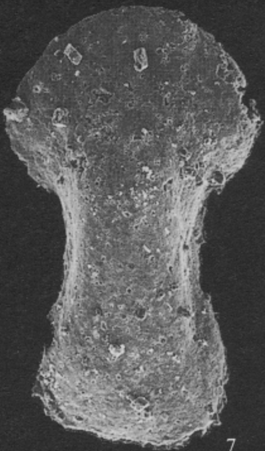
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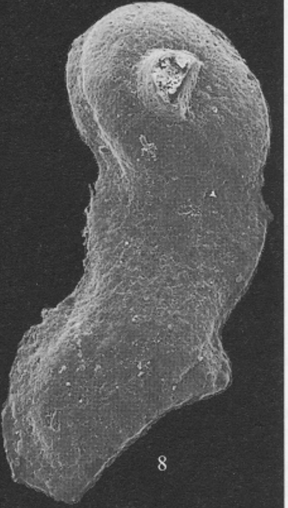
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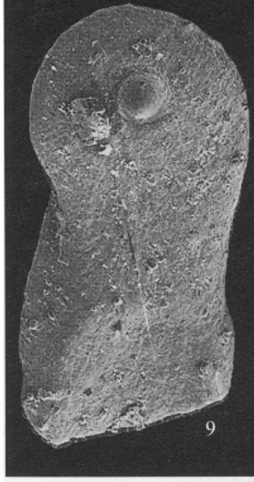
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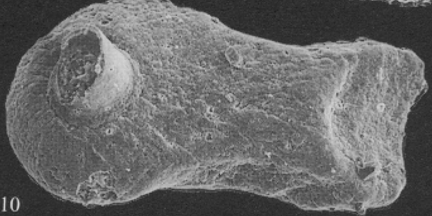
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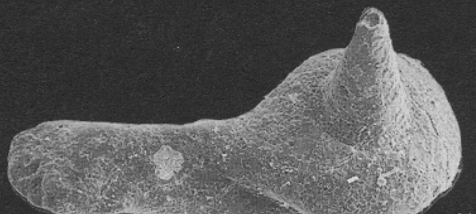
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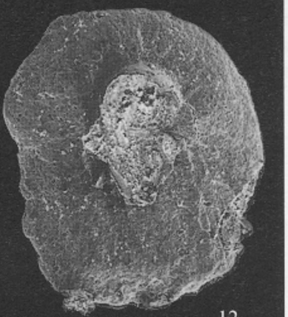
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CONWAY MORRIS *et al.*, *Cambroclavus*

Material illustrated here. Sedgwick Museum (University of Cambridge) SM X.26167–X.26187.

Stratigraphical horizon. Yurtus Formation (and basal-most Xiaoerbulak Formation), Atdabanian Stage, Lower Cambrian.

Localities and sections. Mountains south-west of Aksu, western Xinjian, China. *C. bicornis* has been recovered from all sections, except for Section VIII. As Text-figure 2 shows, in some samples it co-occurs with one or more of the other cambroclave taxa, but in other instances it is the only taxon to be recovered.

Preservation. The phosphatic composition of the sclerites is evidently diagenetic, after an originally calcareous composition (Bengtson *et al.* 1990; Conway Morris and Chen 1991). In most of the Xinjiang specimens the fidelity of overgrowth is moderately good, although the spine is usually incomplete. In a few cases original ultrastructure appears to be preserved, most notably as radiating fibres in the anterior section (Pl. 2, figs 1–2). Similar ultrastructure has also been observed in cambroclaves from Australia (Bengtson *et al.* 1990, figs 65s, 67o, 69p).

Diagnosis. Sclerites variable in shape, but most are 'dumb-bell' in outline with waist-like mid-region separating expanded anterior section and a posterior area of variable configuration that ranges from relatively expanded to tapering. Anterior spine relatively stout. Posterior of some sclerites bears prong-like extensions. Concave facet-like structures variably developed on lateral edges of mid-region, and in some sclerites also at posterior.

Description. As has been documented elsewhere, populations of cambroclave sclerites show considerable morphological variation (e.g. Bengtson *et al.* 1990; Conway Morris and Chen 1991). This is also the case for *C. bicornis* (e.g. cf. Pl. 2, figs 3 and 6), although overall many sclerites approximate to a dumb-bell-like shape. In general the sclerites are approximately symmetrical (e.g. Pl. 1, figs 1–2, 7; Pl. 2, figs 1, 3, 6–8), but some sclerites show a considerable degree of asymmetry (e.g. Pl. 1, fig. 8; Pl. 2, fig. 9). The great majority of sclerites consist of an anterior region, more or less circular in outline, that extends posteriorly as a broad shaft. Very often this posterior region is also expanded in width. Variations on this arrangement are common. In some specimens (e.g. Pl. 2, fig. 3) the posterior region shows a more pronounced taper, whereas in others (e.g. Pl. 1, fig. 9; Pl. 2, fig. 9) there is little change in width towards the posterior. In at least one sclerite (Pl. 1, fig. 12) the posterior is strongly truncated, so that it approaches a zhijinitid-like condition. This does not appear to be due to breakage, and a similar condition is more common in *Cambroclavus absonus* from the Lower Cambrian of South Australia (Bengtson *et al.* 1990).

The anterior spine is generally truncated (e.g. Pl. 1, figs 4, 8–9; Pl. 2, figs 4, 9), but this is evidently a result of incomplete fossilization and in well-preserved sclerites the spine is stoutly conical (Pl. 1, fig. 11; Pl. 2, fig. 5). The mid-section of the sclerite tends to consist of a central ridge with flanking edges, that form variably defined arcuate embayments (e.g. Pl. 1, fig. 10; Pl. 2, figs 2, 4, 7–8) whose original function is inferred to have been articulatory facets to accommodate the expanded ends of adjacent sclerites (see Bengtson *et al.* 1990, fig. 70; Conway Morris and Chen 1991, text-fig. 11). Occasionally, the central ridge has a lobe-like development (Pl. 1, fig. 4). The central region of the posterior end is sometimes excavated to form a shallow facet (e.g. Pl. 1, figs 4, 9; Pl. 2, figs 4, 8). As with the lateral facets this embayment presumably housed the arcuate lower surface of the next-posterior sclerite in the longitudinal file. In some specimens this facet is also associated with a variably developed notch which thereby defines lobe-like extensions (Pl. 1, figs 4, 6, 10; Pl. 2, fig. 8). In one sample (XI/91/31; section 1, Yurtus Mountain; Text-fig. 2) the population has a conspicuous number of

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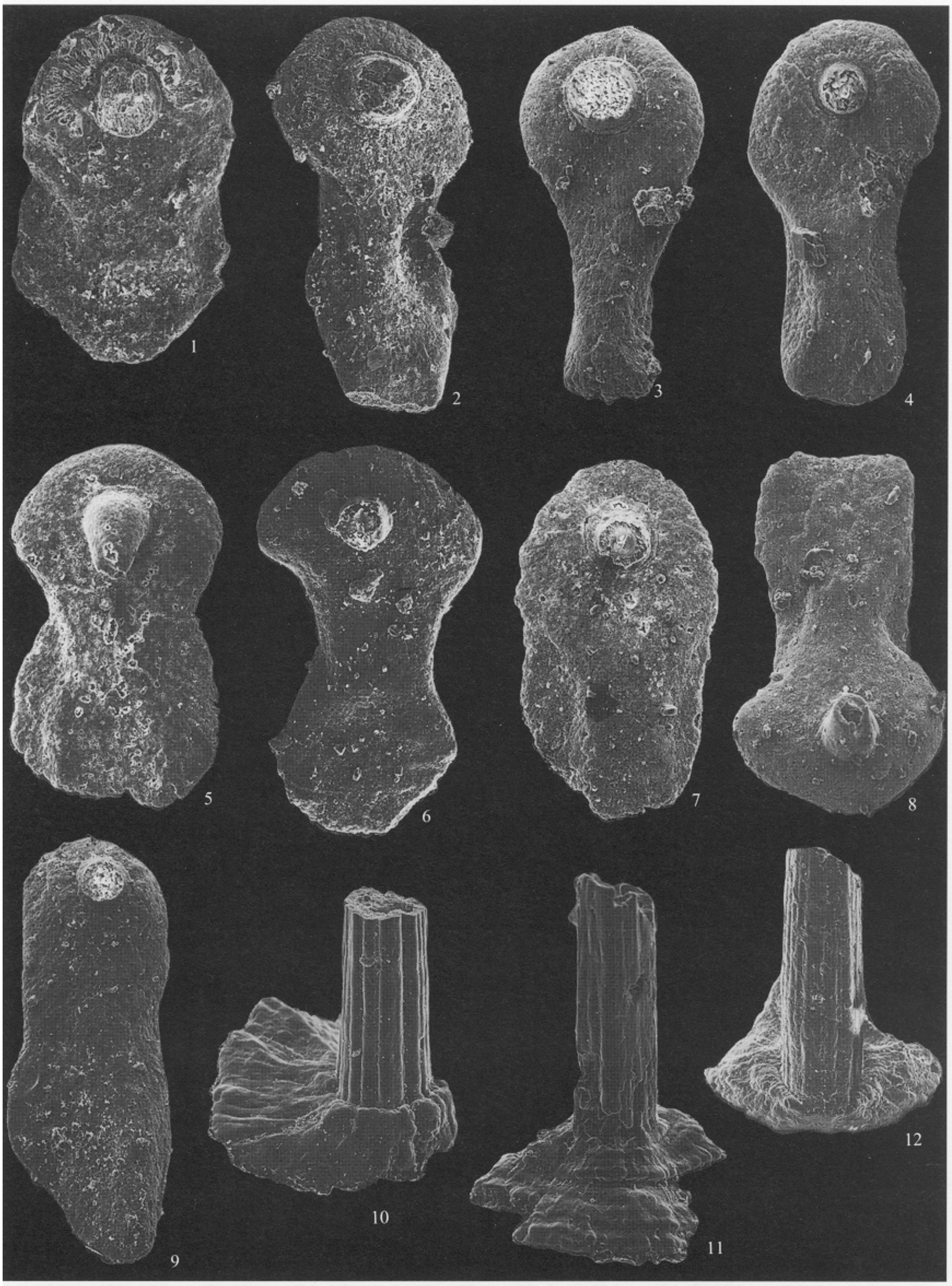
EXPLANATION OF PLATE 2

Figs 1–9. *Cambroclavus bicornis* (Qian and Xiao, 1984). 1, SM X.26179. 2, SM X.26180. 3, SM X.26181. 4, SM X.26182. 5, SM X.26183. 6, SM X.26184. 7, SM X.26185. 8. SM X.26186. 9, SM X.26187.

Figs 10–12. *Zhijinites claviformis* (Qian and Xiao, 1984). 10, SM X.26188. 11, SM X.26189. 12, SM X.26190. All isolated sclerites, dorsal (1–9) and lateral (10–12) surfaces, from the Yurtus Formation, Yurtus Mountain section 2 (sample XI/91/35), 1–9; section 6 (sample XXIV-7/2), 10–12, Aksu Wushi, Xinjiang, China. Magnifications are × 150 (1–4, 9), × 200 (4), × 175 (5–6, 8, 10–11), × 125 (12).



CONWAY MORRIS *et al.*, *Cambroclavus*, *Zhijinites* sclerites with the posterior region bearing a pair of rather prominent prong-like extensions (Pl. 1, figs 1–3). The significance of the morphometric variation in *C. bicornis* is discussed below.

Remarks. The synonymy list given above, where a number of species is subsumed within *C. bicornis*, is based on the reasonable assumption that, as in many other cambroclaves, the sclerites of this species show considerable morphological variation and more importantly cannot be easily divided into species. Many of the features described here have already been illustrated by Chinese workers, albeit without detailed comment. Thus, features such as prominent posterior prongs (Xiao and Duan 1992, pl. 4, figs 1–4) and posterior notch (Qian and Xiao 1984, pl. 3, figs 16, 18–19) are already known, but used for interspecific distinctions that we prefer to interpret as variability within a single species (but see below).

Comparisons with previous descriptions of cambroclaves are for the most part difficult because few workers have adopted scleritome-based interpretations. It is evident, however, that close similarities exist between *C. bicornis* and *C. absonus* from the Lower Cambrian of Australia. While synonymy remains possible, the Australian taxa appears to differ in terms of the relative abundance of zhijinitid-like morphs (Bengtson *et al.* 1990, figs 69B–C, E–F, H–P). In addition, although the morphological variability of both species is very wide and counterparts between nearly all types of sclerite shape can be found, in *C. absonus* there seems to be a greater tendency towards sclerites with a flared posterior section (Bengtson *et al.* 1990, figs 64O, X; 65A, T–U, 65X, 67D), whereas in *C. bicornis* such morphs are rare (Xiao and Duan 1992, pl. 4, fig. 37).

In general, the strongest faunal similarities of the Xinjiang assemblages are with Kazakhstan and to a lesser extent South China, as is evident for example from a comparison of the halkieriids (Conway Morris and Chapman in press). In the case of the cambroclaves, however, matters are somewhat more complicated. As documented below in terms of zhijinitid morphs, there appears to be a significant similarity between Kazakhstan and Xinjiang faunas in the form of *Zhijinites undulatus* and *Z. claviformis* respectively. Unfortunately, the type species of *Cambroclavus*, *C. antis* from Kazakhstan, is relatively poorly documented, although it is known from articulated arrays (Mambetov and Repina 1979). *C. antis* is broadly similar to *C. bicornis*, but appears to differ in an accentuated anterior section with characteristic radial furrows on its underside, and relatively pronounced longitudinal ridges on upper and lower surfaces.

In terms of the Lower Cambrian sequences on the South China platform, the most extensive documentation of *Cambroclavus* is by Qian and Zhang (1983) and Duan (1984), both of whom illustrated material from Hubei Province. The latter publication erects what we regard as a plethora of form-taxa. In apparent contrast, Qian and Zhang (1983) place all their material in a single species (*C. fangxianensis*), but the morphological variability of the sclerites they illustrate is considerably less. Overall, the similarities between *C. bicornis* and the material from Hubei do not seem to be very pronounced. There is, however, an indication of a stronger resemblance between material placed in various species of *Sinoclavus* (Duan 1984, pl. 5, figs 11–15) and *C. antis* from Kazakhstan, most notably in the shared possession of the ridges radiating across the lower surface of the anterior unit.

Accompanying the sclerites of *Cambroclavus* in the Hubei samples is a distinctive deiradoclavid form that Qian and Zhang (1983) assign to *Isoclavus*, and Duan (1984) placed in *Tanbaoites*. These

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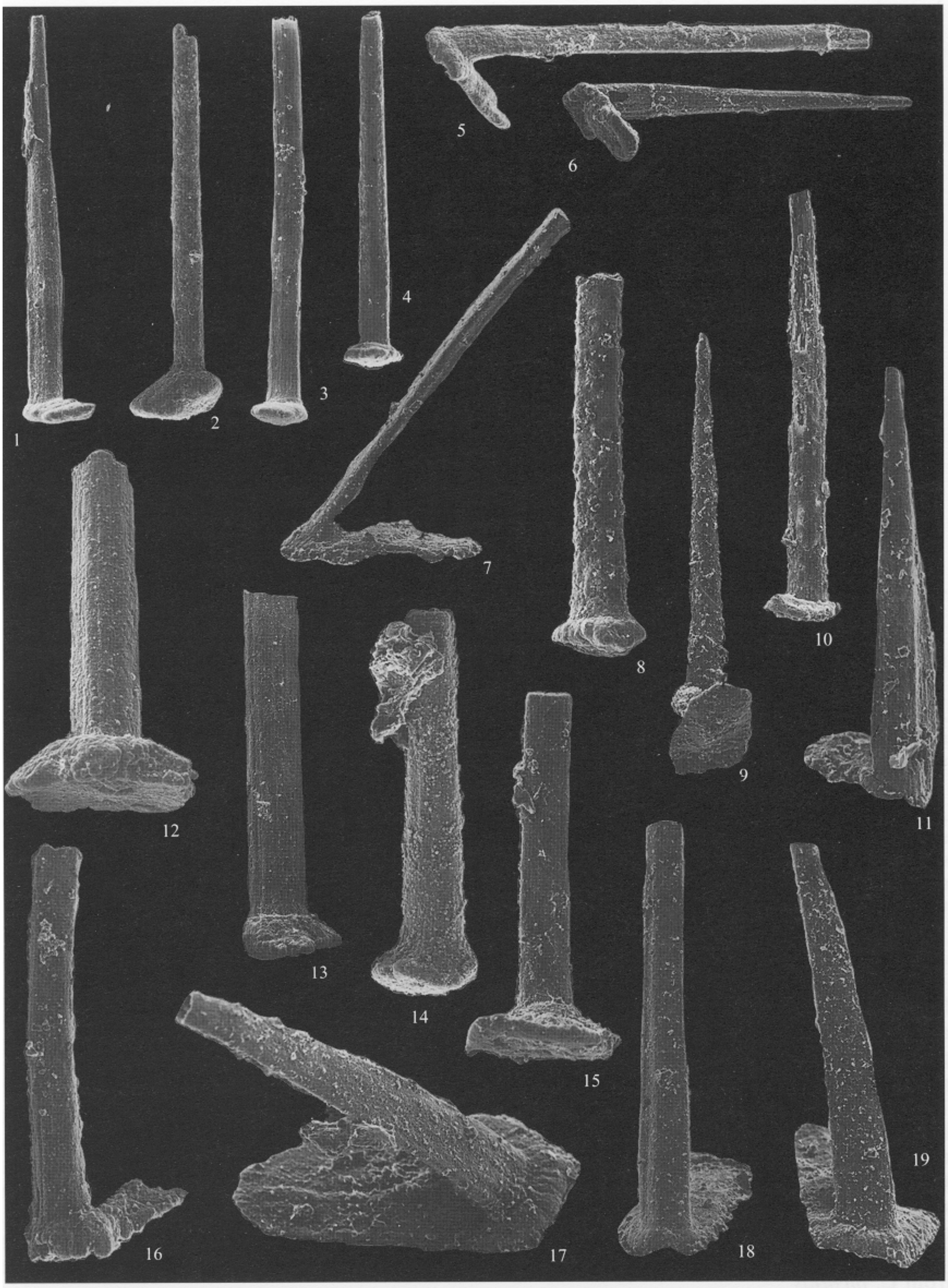
EXPLANATION OF PLATE 3

Figs 1–19. *Parazhijinites guizhouensis* Qian and Yin, 1984. 1, SM X.26191. 2, SM X.26192. 3, SM X.262193. 4, SM X.26194. 5, SM X.26195. 6, SM X.26196. 7, SM X.26197. 8, SM X.26198. 9, SM X.26199. 10, SM X.26200. 11, SM X.26201. 12, SM X.26202. 13, SM X.26203. 14, SM X.26204. 15, SM X.26205. 16, SM X.26206. 17, SM X.26207. 18, SM X.26208. 19, SM X.26209. All isolated sclerites from the Yurtus Formation, Aksu phosphorite mine; section 3 (sample XI/91/17), 1–6, 8, 10, 15–16; (sample XI/91/16), 7, 9, 11, 17–19; section 6 (sample XXIV-7/2), 12–14; Aksu-Wushi, Xinjiang, China. Magnifications are × 125 (1, 4, 6–7, 13, 18), × 175 (2, 10), × 150 (3, 5, 19), × 200 (8, 11, 14–15, 17), × 100 (9), × 225 (12), × 250 (16).

PLATE 3



CONWAY MORRIS *et al.*, *Parazhijinites* latter two genera are evidently synonymous. The sclerites are sub-circular in outline, apart from a rather prominent posterior notch. The spine is relatively robust, and tends to be transversely elongated. Bengtson *et al.* (1990, pl. 115) proposed that these sclerites may derive from the same scleritome as *C. fangxianensis*. *Wushichites*, described below, is quite similar to *Isoclavus*, but its distribution in the Xinjiang samples appears to be more consistent with it forming a separate taxon.

Zhijinites claviformis Qian and Xiao, 1984

Plate 2, figures 10–12

1984 *Zhijinites claviformis* Qian and Xiao, pl. 81, pl. 2, fig. 14; pl. 3, fig. 27.
1985*a* *Zhijinites claviformis*; Gao *et al.*, pl. 5, fig. 14; pl. 8, figs 1–3.
1985*b* *Zhijinites claviformis*; Gao *et al.*, pl. 34, fig. 20.
1985 *Zhijinites claviformis*; Wang *et al.*, pl. 3, figs 11–12.
?1991 *Zhijinites* sp.; Ding *et al.*, p. 103, pl. 2, figs 29–31, 36.
?1992 *Zhijinites longistriatus*; Yue and Gao, pl. 3, fig. 8.
1992 *Zhijinites deltatus*; Xiao and Duan, p. 225, pl. 3, figs 17, 19–20.
1992 *Zhijinites clavus*; Xiao and Duan, p. 224, pl. 3, fig. 18.
1992 *Zhijinites planispinosus*; Xiao and Duan, p. 225, pl. 3, fig. 23.

Holotype. Xinjiang Institute of Geology 03109.

Material illustrated here. SM X.26188–X.26190.

Stratigraphical horizon. Yurtus Formation, Atdabanian Stage, Lower Cambrian.

Localities and sections. This species occurs in all sections, except for section 1 on Yurtus Mountain, but it is found in fewer of the sampled horizons than *C. bicornis* (Text-fig. 2).

Diagnosis. Robust zhijinitid morph. Base sometimes quite steep with prominent radial and sometimes annular ornamentation. Stout spine eccentrically located, towards presumed anterior, with prominent longitudinal ribbing.

Description. In contrast with most cambroclaves, the sclerites consist of a relatively small base and a massive spine. The spine is located towards the presumed anterior end of the base. The base typically bears pronounced, somewhat irregular, radial ornamentation. In addition, there may be annular structures that give the base a stepped appearance (Pl. 2, fig. 11). For the size of the sclerite the spine is remarkably robust, when compared with other zhijinitids. It bears prominent longitudinal ribbing.

Remarks. This species has been illustrated by a number of Chinese workers (e.g. Qian and Xiao 1984; Xiao and Duan 1992), but as the synonymy list indicates there seems to be little justification for the recognition of so many nominal species. In terms of other cambroclaves, *Z. claviformis* appears to approach most closely *Z. undulatus* from Kazakhstan (Mambetov and Repina 1979, p. 123, pl. 13, figs 1, 4, 6, 11–12; note that there is some evidence that the specimen illustrated in pl. 13, figs 2, 10, 13 is distinct and may derive from the co-occurring *C. antis*, see Bengtson *et al.* 1990, p. 113). The principal points of difference between *Z. claviformis* and *Z. undulatus* appear to be that in the latter taxon the base tends to be more raised and the spine, while robust and strongly ribbed, tapers much more abruptly. As Bengtson *et al.* (1990) also noted in discussing the Kazakhstan cambroclaves there is reasonable evidence that *Z. undulatus* derives from a different scleritome than *C. antis*. Of the 16 horizons in the Yurtus Formation that have yielded *C. bicornis*, only in four does it co-occur with *Z. claviformis*, and the latter taxon occurs in three other horizons (Text-figure 2). This supports the likelihood that *Z. claviformis* derives from a scleritome separate from *C. bicornis*.

Parazhijinites cf. *guizhouensis* Qian and Yin, 1984

Plate 3

1984	*Parazhijinites quizhouensis* [*sic*] Qian and Yin, p. 220, text-fig. 3.3; pl. 2, figs 1–8.
1984	*Parazhijinites quizhouensis* [*sic*]; Wang *et al.*, p. 177, pl. 22, figs 5–8.
?1984	*Zhijinites intermedius*; Qian and Xiao, p. 82, pl. 3, figs 28–29.
?1985	*Zhijinites intermedius*; Gao *et al.*, pl. 8, figs 4–5.

Holotype. Nanjing Institute of Geology and Palaeontology 68238 (Qian and Yin 1984, pl. 2, fig. 2).

Material illustrated here. SM X.26190–X.26208.

Stratigraphical horizon. Yurtus Formation, Atdabanian Stage, Lower Cambrian. Also known from the Gezhongwu member of the Niutitang Formation, Guizhou Province (see Wang *et al.* 1984).

Localities and sections. Mountains south-west of Aksu, western Xinjiang, China. *P.* cf. *guizhouensis* has been recovered from two adjacent samples in the mid-section of Aksu Phosphorite Mine and from a sample close to the top of the Yurtus Formation in Section VIII (Text-fig. 2). At the Aksu Phosphorite Mine *P.* cf. *guizhouensis* does not occur with any other taxon of cambroclave, whereas in Section VIII it co-occurs with *Zhijinites claviformis*.

Diagnosis. Zhijinitid sclerite with small base, sometimes very reduced. Radial ornamentation on base, reduced on smaller bases to more nodular appearance. Spine exceptionally elongate, circular to transversely compressed. Subdued longitudinal ribbing, occasionally central ridge on anterior side.

Description. The most noticeable feature of this species is the elongate spine arising from a small base. The degree of reduction of the base is quite variable, ranging from a relatively elongate posterior section (Pl. 3, figs 7, 17–19) to ones that are reduced to little more than the diameter of spine (Pl. 3, figs 8, 14). On the larger bases the ornamentation consists of a subdued structure, whereas in the reduced bases the ornamentation is more nodular (e.g. Pl. 3, figs 8, 12–13). In comparison with most other cambroclaves the spine is exceptionally elongate, and its tip is almost invariably missing. Where the base is fairly well developed the angle between it and the spine is relatively oblique, at about 55°. Where the base is reduced, however, the spine is almost vertical. The cross sectional shape of the spine also appears to be related to the size of the spine relative to its base. Thus, in sclerites with a reduced base the spine has a circular cross section, whereas when the base is better developed the spine is more flattened in the transverse plane. Many spines bear a subdued longitudinal ribbing, but in the more compressed spines the anterior side may bear a central ridge (Pl. 3, figs 11, 18).

Remarks. In an earlier discussion of cambroclaves from the South China platform it was tentatively proposed that *Parazhijinites guizhouensis* was synonymous with *Zhijinites longistriatus* (Conway Morris and Chen, 1991, p. 366). The distinctiveness of comparable material from Xinjiang and the likelihood that these sclerites are not associated with any of the other cambroclave taxa indicate that *P. guizhouensis* is best treated as a distinctive and separate species. The poor quality of many earlier illustrations and the lack of reinvestigations still leave a number of uncertainties concerning the taxonomy of Chinese cambroclaves. One taxon that is somewhat similar to *P. guizhouensis* is *Z. lubricus* (see Conway Morris and Chen 1991 for the latter's tentative synonymy with *Z. longistriatus*).

In terms of other cambroclave taxa the material from Xinjiang resembles at least some sclerites of *C. clavus* from Kazakhstan (Mambetov and Repina 1979, p. 122, pl. 13, figs 3, 5, 7–9). This taxon remains rather poorly known, but although Bengtson *et al.* (1990, pp. 37, 112) questioned its place in the cambroclaves, drawing attention to fossils from the Lower Cambrian of South Australia which they referred to as Spicule A, it now seems likely that at least some of the material from Kazakhstan is genuinely cambroclave, but should be referred to as *Zhijinites clavus*.

Wushichites minutus Qian and Xiao, 1984

Plate 4

1984	*Wushichites minutus* Qian and Xiao, p. 76, pl. 1, fig. 7; pl. 3, fig. 11.
1984	*Wushichites polyedrus* Qian and Xiao, p. 77, pl. 3, figs 12–13.
1985*a*	*Wushichites minutus*; Gao *et al.*, pl. 8, figs 19–20.
1985*a*	*Wushichites polyedrus*; Gao *et al.*, pl. 8, figs 21–22.
1985*b*	*Wushichites minutus*; Gao *et al.*, pl. 34, fig. 17.
1985*b*	*Wushichites polyedrus*; Gao *et al.*, pl. 34, fig. 18.
1985	*Wushichites minutus*; Wang *et al.*, pl. 3, fig. 25.
1985	*Wushichites polyedrus*; Wang *et al.*, pl. 3, fig. 26.
1989	*Isoclavus minutus*; Qian, p. 236, pl. 61, figs 4–10.
1992	*Wushichites minutus*; Duan and Xiao, pl. 1, fig. 13.
1992	*Wushichites minutus*; Jiang, figs 5, 9–10.
1992	*Wushichites minutus*; Xiao and Duan, pl. 1, figs 27–28.

Holotype. Xinjiang Institute of Geology 10455.

Material illustrated here. SM X.26209–X.26220.

Stratigraphical horizon. Yurtus Formation, Atdabanian Stage, Lower Cambrian.

Localities and sections. *Wushichites minutus* is relatively uncommon in the Xinjiang sections, but occurs in section 2 of Yurtus Mountain, Aksu Phosphorite Mine, Xiaoerbulak Phosphorite Mine, and the Sugaitbulak section (Text-fig. 2). It often co-occurs with *C. bicornis* and *Z. claviformis*.

Diagnosis. Sub-circular sclerites, more or less bilaterally symmetrical. Anterior region may bear a subdued dome and in at least some sclerites a narrow cleft. Posterior almost invariably with prominent notch. Upper surface with radial ornamentation.

Description. As noted above the sclerites of *W. minutus* are notable, with few exceptions (Pl. 4, figs 11–13), for a rather thick overgrowth of phosphate that tends to obscure many of the finer details. In outline the sclerites are almost bilaterally symmetrical, and vary from sub-circular to oval. A posterior notch is almost invariably present, but it may be only slightly developed (Pl. 4, figs 5–6, 9) or be variably prominent, sometimes to the extent of defining distinct lobes (Pl. 4, fig. 8). The area equivalent to the anterior spine of other cambroclaves is represented by a low dome (Pl. 4, figs 3, 7), and there is no clear evidence that a discrete spine was present.

The phosphatic coating normally obscures the surface details. In well-preserved specimens, however, the ornamentation of the upper surface is seen to consist of fine radial striae on the upper surface (Pl. 4, fig. 12).

Remarks. *Wushichites* is most similar to *Isoclavus* (and the synonymous *Tanbaoites*), described from Lower Cambrian sections in Hubei province (Qian and Zhang 1983; Duan 1984; Qian 1989). In this latter taxon there is also a variably developed posterior notch (Qian and Zhang 1983, pl. 3, figs 9, 11–16), but the spine is prominent. Qian (1989) synonymized *Wushichites* and *Isoclavus*. The apparently more prominent spine in the latter genus is our criterion for keeping these two genera separate. While the absence of a spine in many specimens of *Wushichites* could be diagenetic

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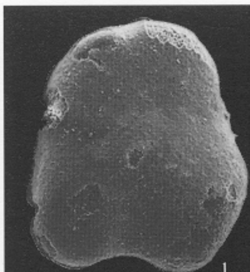
EXPLANATION OF PLATE 4

Figs 1–13. *Wushichites minutus* Qian and Xiao 1984. 1, SM X.26210. 2, SM X.26211. 3, SM X.2612. 4, SM X.26213. 5, SM X.26214. 6, SM X.26215. 7, SM X.26216. 8, SM X.26217. 9, SM X.26218. 10, SM X.26219. 11–12, SM X.26220. 13, SM X.26221. All isolated sclerites from the Yurtus Formation, Yurtus Mountain; section 1 (sample $81K_2$ H′-V-6/1), 1–9; Yurtus Mountain; section 2 (sample XI/91/34), 11–13; (sample XI/91/35), 10; Aksu-Wushi, Xinjiang, China. Magnifications are × 110 (1), × 125 (2, 6, 9, 11, 17), × 100 (3–5, 7–8), × 150 (10), × 250 (12).



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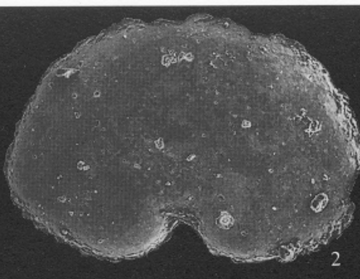

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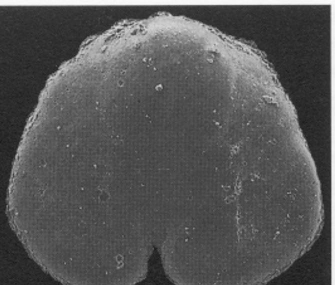

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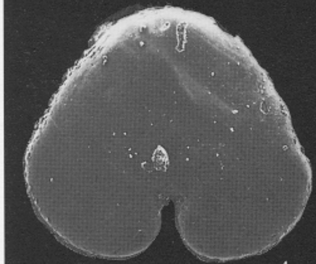

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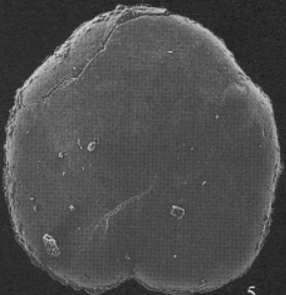

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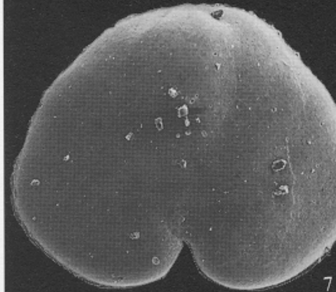

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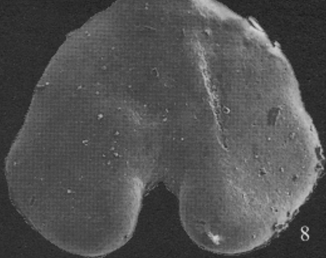

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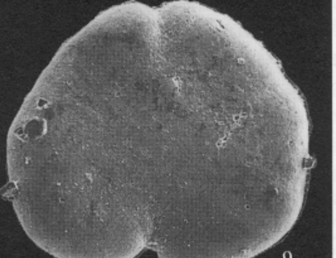

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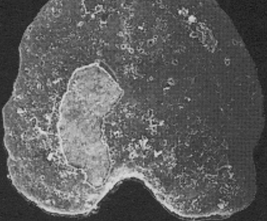

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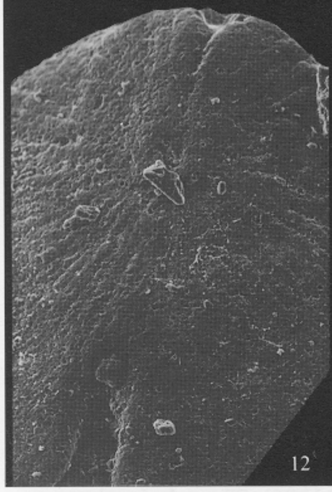

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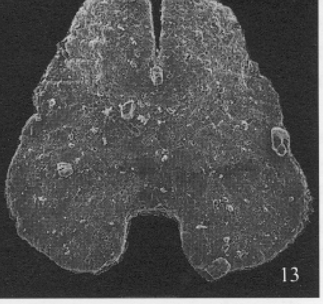

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CONWAY MORRIS *et al.*, *Wushichites*

and linked to the overcoat of phosphate, in well preserved specimens (Pl. 4, figs 11–13) the spine is not apparent. *Wushichites* is somewhat less similar to *Deiradoclavus*, the latter genus having a well-defined triradiate ridge on its upper surface. In addition, the spine is transversely elongate, and overall the sclerites of the latter appear to show a wide degree of morphological variation.

The possibility that *Isoclavus* actually derives from the same scleritome as co-occurring cambroclaves (see above) raises the same possibility for *Wushichites minutus* and *Cambroclavus bicornis*. Of the four horizons that have yielded *Wushichites*, in three of them there occurs also *C. bicornis*. This latter genus, however, is found at substantially more horizons without *Wushichites* (Text-fig. 2). On balance, therefore, it seems preferable to keep these two taxa separate.

SHAPE ANALYSIS OF CAMBROCLAVES

The morphological variability of cambroclaves is pronounced (e.g. Bengtson *et al.* 1990; Conway Morris and Chen 1991). With so little known about the original nature of the scleritome, one avenue of enquiry is to document the degree of variability in terms of morphospace occupation by the sclerites. More specifically, the aim of this section is to see the manner in which populations of sclerites from particular samples in the Yurtus Formation occupy morphospace. Do such populations occupy discrete 'clouds' within morphospace? If so, does such a pattern represent a species with polymorphism in terms of sclerite types, or alternatively could it indicate separate taxa?

Outline shape and size of the cambroclave sclerites were examined using a technique known as elliptic Fourier shape analysis (EFA). EFA, first described by Kuhl and Giardina (1982), is a biometric technique particularly suited to the description of fossils lacking many homologous landmarks (Crampton 1995). The method mathematically 'decomposes' a digitized, two dimensional outline into a series of harmonically related trigonometric (sine and cosine) curves. For any harmonic these curves define an ellipse in the x–y plane, and successive harmonics describe progressively smaller features of the outline. The size, shape and orientation of each harmonic ellipse are represented using four Fourier coefficients. These coefficients were computed using a modified version of program EFA written by F. J. Rohlf and S. Ferson (1985–1991; kindly made available by F. J. Rohlf), and modified by one of us (JSC, in association with A. Buckley and J. Sloan). An earlier, unmodified version of this program is available in Rohlf and Bookstein (1990). Coefficients from many outlines are compared using standard multivariate statistical techniques. Computational details of EFA are given in Kuhl and Giardina (1982) and Ferson *et al.* (1985), and some of the methodological considerations are discussed in Crampton (1995). Hitherto, EFA has been applied quite widely, including the study of bivalves (Ferson *et al.* 1985; Crampton in press), insect wings (Rohlf and Archie 1984) and plant leaves (White *et al.* 1988).

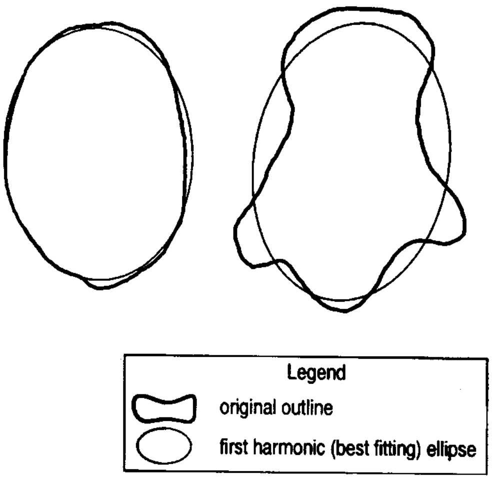
Methods

In the present study, outlines were digitized using a video camera attached to a binocular microscope and the image analysis software VIDS-IV (Synoptics Cambridge, formerly Ai, Cambridge). Specimens were orientated in a standard fashion, upperside visible with the spine towards the top. The sclerites were then traced in a clockwise sense from the spine, using a hand-held cursor. Previous experience indicates that errors introduced during hand digitization are negligible when compared with the morphological variation between specimens.

In any EFA it is necessary to estimate the number of harmonics required to describe an outline with a given degree of precision; this can be done in a number of ways (see Crampton 1995). In the case of the cambroclaves 99·9 per cent. of the variance or 'shape information' is captured by the first nine harmonics. Exploratory statistical analyses revealed, however, that harmonics seven to nine contribute little to the discrimination of groups, and hence our subsequent interpretation was based on the first six harmonics.

Using parameters of the first harmonic it is possible to make several normalizations to the outlines during computation of the Fourier coefficients (Ferson *et al.* 1985). The sclerite data were normalized for starting position and orientation of the outline trace for two reasons. First, EFA is rather sensitive to variations in these factors. Secondly, it was difficult to define exactly homologous orientations and starting positions during digitization. In addition, it is possible to normalize outlines for size. In a study of shape *per se* it is clearly desirable to eliminate the effects of size, even though we acknowledge that this information could carry some biological significance. Hence in this study shape data were normalized for size, and this information was extracted and examined separately.

Size itself was examined using univariate analysis of the first harmonic amplitude, based on non-normalized data. For any outline the first harmonic represents the 'best-fitting' ellipse, and the amplitude of this harmonic can be taken as a proxy for outline size (Text-fig. 3). The amplitude is given by the square root of the sum of the squared Fourier coefficients. Amplitude data were compared both graphically and in an analysis of variance (ANOVA). The ANOVA was performed using the pc-based software SYSTAT v. 5.0.



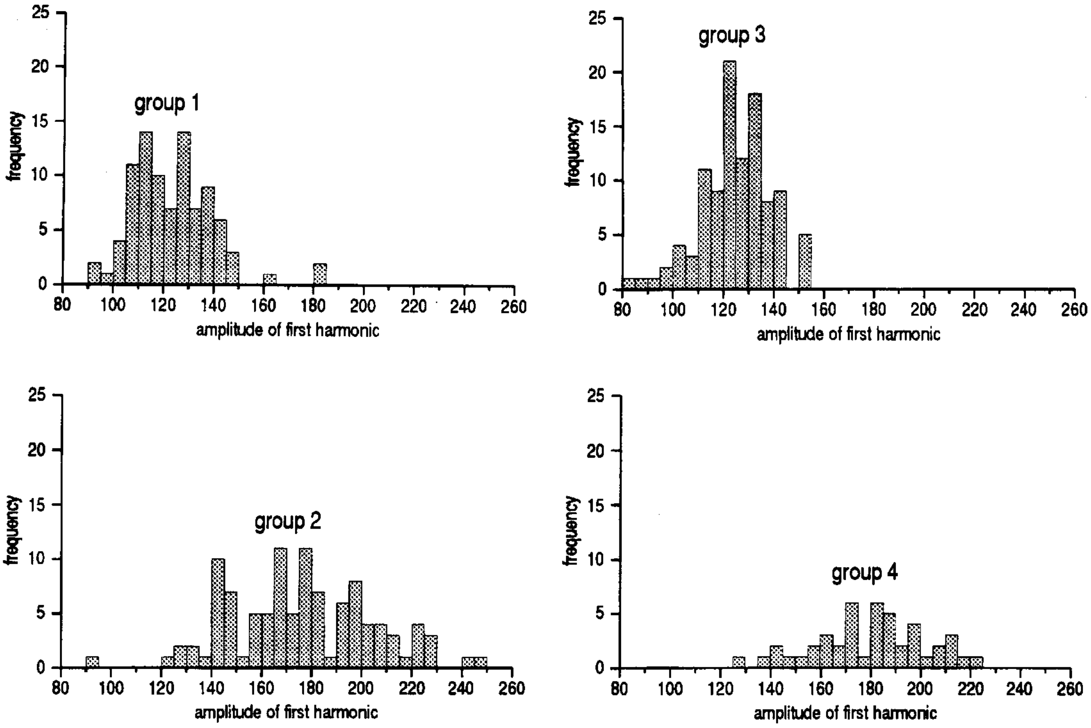
TEXT-FIG. 3. Three representative outlines of cambroclave sclerites, showing first harmonic ('best-fitting') ellipses generated during EFA. The size, or amplitude, of these ellipses can be taken as a proxy for outline size.

Shape was examined using multivariate analyses of Fourier coefficients for harmonics two to six, based on size-normalized data. Arguments for the elimination of the first harmonic in an analysis of this sort were discussed in Crampton (1995). Coefficients for many outlines were interpreted using principal components (PCA) and canonical variates (CVA) analyses calculated using the pc-based program NTSYS-pc v. 1.80 (Rohlf 1993).

Four samples (1–4) of cambroclaves were chosen for this study. The details of their location are as follows: 1, Sample 5/B from Bed 4 of the Sugaitbulak section (91 specimens; not illustrated here, but practically indistinguishable from 3 (sample 5/E), see below); 2, Sample XI/91/34 from Bed 7 of section 2 on Yurtus Mountain (105 specimens; see Text-fig. 3, left); 3, Sample 5/E from Bed 8 of the Sugaitbulak section (250 specimens; see Text-fig. 3, right); and 4, Sample XI/91/3 from Bed 3 of section 1 on Yurtus Mountain (45 specimens; see Pl. 1, figs 1–3 and Text-fig. 3, central). Note that the specimens mentioned here cannot be taken as 'average' because the shapes are so disparate in each group. Their relative positions in the stratigraphy are given in Text-figure 2. This demonstrates that samples 2 and 4 come from similar horizons in adjacent sections on Yurtus Mountain. Samples 1 and 3 derive from the same section, but the former is from a stratigraphically lower horizon.

Results

Frequency histograms of first harmonic amplitudes for each of the four groups are shown in Text-figure 4. Means and standard deviations are shown in Table 1. The data clearly fall into two major



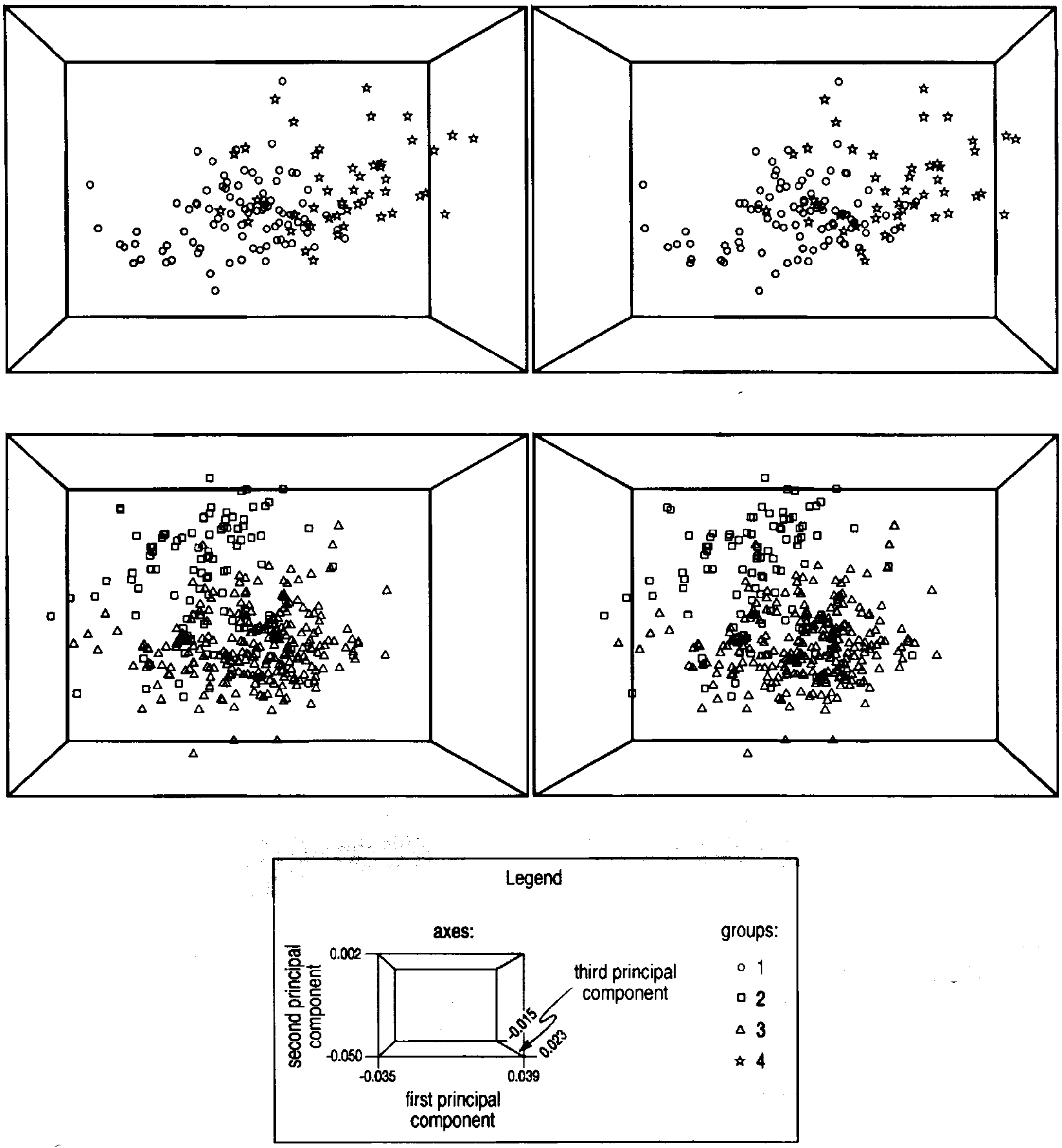
TEXT-FIG. 4. Histogram of first harmonic amplitudes, derived from the elliptic Fourier coefficients, for each of the four *a priori* groups of sclerites. Relationships between these four groups were studied further using an ANOVA (see text). Group means and standard deviations are presented in Table 1.

TABLE 1. Means and standard deviations for first harmonic amplitudes derived from the elliptic Fourier coefficients for each of the four *a priori* groups of sclerites. Relationships between these four groups were studied further using an ANOVA (see text).

	1	2	3	4
Mean	123·47	176·32	121·89	179·73
Standard deviation	16·20	28·81	14·01	22·47

groups, the amplitudes of groups 2 and 4 being substantially larger than those of 1 and 3. An ANOVA demonstrated that some of the group means are indeed significantly different from others (degrees of freedom = 3, 486; *f*-statistic = 253·9; probability = 0·000). This result was explored further using a post-hoc Tukey's test. This confirmed that the amplitudes of groups 1 and 3 are not significantly different from each other, those of groups 2 and 4 are also not significantly different from each other, and that all other comparisons are significant at the > 99·9 per cent. level of confidence. Note that group variances are strongly heteroscedastic, a condition which contravenes one assumption of the ANOVA. Hence data were transformed prior to analysis using Taylor's power law model (Green 1979).

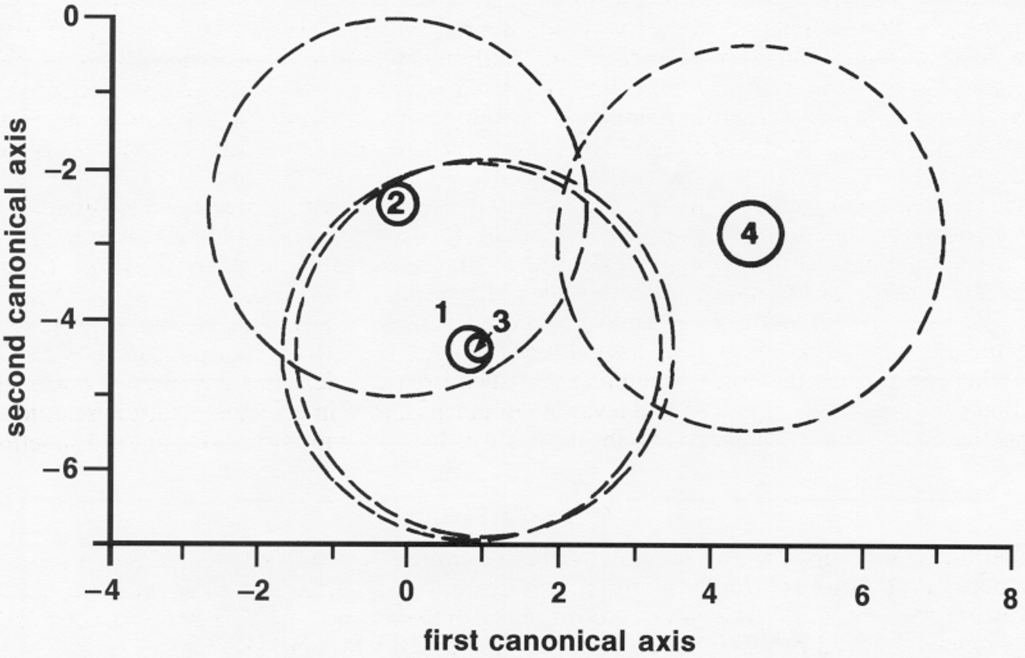
Shape data were examined initially using PCA (Text-fig. 5). These data are displayed as a stereo-plot of the first three principal components designed for viewing with a pocket stereoscope. The x- and y-axes (first and second principal components) may be read without recourse to stereoscopy although interpretation is enhanced by three-dimensional viewing. This plot reveals that the four groups are clustered in morphospace and that there is a greater or lesser degree of overlap between



TEXT-FIG. 5. Principal components analysis of elliptic Fourier coefficients (harmonics two to six) derived from sclerite outlines. Stereoplots of the first three principal components, which account for 69 per cent. of the total variance. For clarity the data are displayed on two plots. Note that groups are clustered in morphospace, and that all overlap to a greater or lesser extent.

all groups. These results were studied in more detail using CVA (Text-fig. 6). This analysis demonstrates very clearly that groups 1 and 3 are indistinguishable on the basis of shape, whereas mean shapes of groups 2 and 4 are significantly different from each other and also from groups 1 and 3.

A number of conclusions can be drawn from these results. First, in terms of groups 1 and 3 overlap is almost complete so that they are indistinguishable on the basis of size and shape. This



TEXT-FIG. 6. Canonical variates analysis of elliptic Fourier coefficients (harmonics two to six) derived from sclerite outlines. Plot of first two canonical axes, which account for 97 per cent. of the within- to between-groups variance. Note that groups 1 and 3 are indistinguishable on the basis of shape, whereas the mean shapes of groups 2 and 4 are clearly distinguished from each other and from groups 1 and 3. The numerals 1–4 represent the position of the group means of TF4. Circles with solid outlines indicate the 90 per cent. tolerance regions for group populations, and those with dashed outlines the 95 per cent. confidence regions on positions of group means.

indicates that in Section 5 (Sugaitbulak), from which these groups were collected, there is morphological stasis through the upper part of the Yurtus Formation (Text-fig. 2). Second, groups 2 and 4 are clearly discriminated from each other on the basis of shape. This is largely due to the predominance of sclerites in group 4 with prominent posterior prongs (Pl. 1, figs 1–3). Moreover, groups 2 and 4 are also discriminated from groups 1 and 3 on the basis of size and shape. In part, this is probably because in the latter two groups the posterior region tends to be reduced in width. The separation in morphospace of these samples, most notably group 4, raises the question of whether all the sclerites should be accommodated in *Cambroclavus bicornis* or should be split into two or more separate taxa. For the moment the former option is preferred, for the following reasons. The distinctiveness of the sclerites in group 4 is due largely to the prong-like extensions. Although very abundant, not every sclerite from this sample possesses this feature, which also occurs sporadically elsewhere in the Yurtus Formation. Moreover, in the cambroclave assemblages from South Australia (Bengtson *et al.* 1990) the presence of prongs is scattered amongst sclerites from different samples.

It is clear that the morphometric methods used here have considerable discriminatory power and that a more extensive survey of cambroclave morphospace would be highly desirable. Several areas stand out as potentially interesting in this regard. For example, the nature of interlocking between adjacent sclerites presumably places constraints on form. Thus in the sclerites of *Cambroclavus* their dumb-bell shape and presumed articulatory facets are evidently largely determined by the requirements for congruent margins. Further morphometric analysis could be used to generate artificial shapes corresponding to points not filled by real data. Such artificial shapes can help in the visualization and understanding of morphological variation, including the creation of extreme morphologies that exaggerate axes of variation defined by the real data. Our existing data would allow such an exercise in 'reverse engineering', although it would be necessary to retain the first harmonic, which in the study reported above was used as a proxy for size. Such a PCA analysis does not give such good shape discrimination between the groups, does not relate to the existing axes of variation, and might be of questionable relevance when so little is yet known about cambroclave palaeobiology.

Indeed, even existing palaeontological data may question the utility of such an approach. In the only known examples of relatively extensive sheets of articulated material, which are from Kazakhstan (Mambetov and Repina 1979, pl. 14, figures 6, 8–9), the sclerites appear to have a rather uniform shape. In material from China, however, the most extensive array (Yue 1991, fig. 1.5) consists of two central rows flanked by a row of larger sclerites, but each set appears to show little morphological variability. In assemblages of disarticulated sclerites wide morphological variability seems to be the norm. Assuming that such isolated sclerites derive from a single species and that each individual organism had a variety of morphs, then in principle a shift in sclerite shape across the body could be managed in short distances by minor modifications at each junction.

CONCLUSIONS

Further understanding of the palaeobiology of the cambroclaves will be hindered until one or more specimens of the entire scleritome are found in a Lower Cambrian Konservat-Lagerstätten, such as the Chengjiang or Sirius Passet biotas. Nevertheless, in the meantime an extensive survey of sclerite morphometrics would probably help to identify more natural groupings.

The functional significance of the different shapes of sclerite are largely speculative. At present it is envisaged that the sclerites of zhijinitids (*Parazhijinites*, *Zhijinites*) were separately embedded in a tegument, in contrast to the other cambroclaves which formed closely articulated scleritomes (Bengtson *et al.* 1990; Conway Morris and Chen 1991). A protective role seems to be the most probable function and this presumably would be accentuated by the anterior spines. Nevertheless, the ecological context in which the very slender spines of *P. guizhouensis* were employed in contrast to the shorter spines of other cambroclaves is speculative.

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