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The earliest Cambrian Polyplacophorans from China

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Abstract – Restudy of *Yunnanopleura, Tchangsichiton, Runnegarochiton, Meishucunchiton, Yangtzechiton* and *Luyanhaochiton* from the earliest Cambrian in the Yangtze Region of China confirms the appearance of the Polyplacophora in the earliest Cambrian. It also suggests an origin for the class in late Proterozoic. *Yangtzechiton* and *Luyanhaochiton*, represented in the study material, are typical polyplacophorans having head, intermediate and tail valves, each with a tegmentum and an articulamentum. These morphologic features establish their distinction from the non-molluscan genus *Paracarinachites.* The polyplacophoran character of species of the genera *Yunnanopleura, Tchangsichiton, Meishucunchiton* and *Gotlandochiton?* is demonstrated by the presence of discrete areas (central or jugal, lateral) on the intermediate valves. *Yunnanopleura* is probably ancestral to the Early Ordovician *Chelodes* Davidson and King. *Runnegarochiton* appears to be closely related to the Middle Ordovician *Priscochiton* Dall.

INTRODUCTION

The Yangtze Region is one of the areas in China where the Lower Cambrian is most developed. It has been studied in great detail, with the location of type sections for series division and stages established. During the past 30 years, as a result of ongoing research on the Proterozoic-Cambrian boundary strata, a great number of molluscs have been discovered from the Meishucun Stage of eastern Yunnan, western Sichuan, western Hubei and southwestern Shaaxi. They are especially significant from the Meishucun section of Jinning and the Baizai section of Xundian, Yunnan (Figure 1).

The Meishucun Stage of the Yangtze Region is dominated by a micromolluscan fauna. The fauna contains a diversity of primitive forms of polyplacophorans, merismoconchs, bivalves, stenothecoids, rostroconchs, hyoliths, tergomyans, helcionellids and gastropods. Among these fossils, the appearance of primitive Polyplacophora in the pre-trilobite and pre-archaeocyathid stage is particularly significant (Figure 2).

The writer has described two polyplacophorans from the earliest Cambrian, *Yangtzechiton elongatus* Yu (1984a, plate 1, figures 1–7; Yu 1984b, text-figure 4a–e) and *Luyanhaochiton spinus* Yu (1984a, plate 1, figures 8, 9; Yu 1984b, text-figure 4f–g). In 1987, the writer reported further earliest Cambrian polyplacophorans, including *Yunnanopleura biformis* Yu (1987b, plate 17, figures 1–8; plate 18, figures 1–9; text-figure 43), *Tchangsichiton notabilus* Yu (1987b, plate 4, figures 1–10; text-figure 33), *Sinuconus clypeus* Yu (1979, plate 1, figures 10–13; 1987b, plate 5, figures 1–11), *Runnegarochiton modestus* Yu (1987b, plate 6, figures 1–6; text-figures 13, 35), *Meishucunchiton vulgarus* Yu (1987b, plate 15, figures 4–10; text-figures 36, 37), *Postestephaconus tentes* Jiang (1980, plate 1, figures 10–13; Yu 1987b, plate 7, figures 1–11; text-figure 38), *Stoliconus vomeres* Jiang (1980, plate 1, figure 2; Yu 1987b, plate 5, figures 12–13; plate 6, figures 7–10; text-figure 39) and *Gotlandochiton? minimus* Yu (1987b, plate 15, figures 1–3; plate 16, figures 1–8; text-figure 42). Smith and Hoare (1987: 3) listed *Yangtzechiton elongatus* Yu and *Luyanhaochiton spinus* Yu as representatives of the Early Cambrian Polyplacophora. Haszprunar (1988: 402) has pointed out, "It is argued that the fossil record of the Polyplacophora starts much later than that of the Conchifera. However, in the light of recent findings of tiny Polyplacophora from the lowest Cambrian (Yu, 1987), this argument must be abandoned".

Some scholars have lumped *Yangtzechiton* and *Luyanhaochiton* under *Paracarinachites* (Kerber, 1988: 187). Qian and Bengtson (1989: 48) have stated: "We cannot accept Yu's (1984a, 1984b, 1987) interpretation of *Yangtzechiton* and *Luyanhaochiton* as polyplacophorans. As shown below, both of these generic names are junior synonyms of *Paracarinachites*...".

On the other hand, He and Xie (1989: 126) considered that *Paracarinachites* has a long plate with spines, possibly representing the dorsal shield

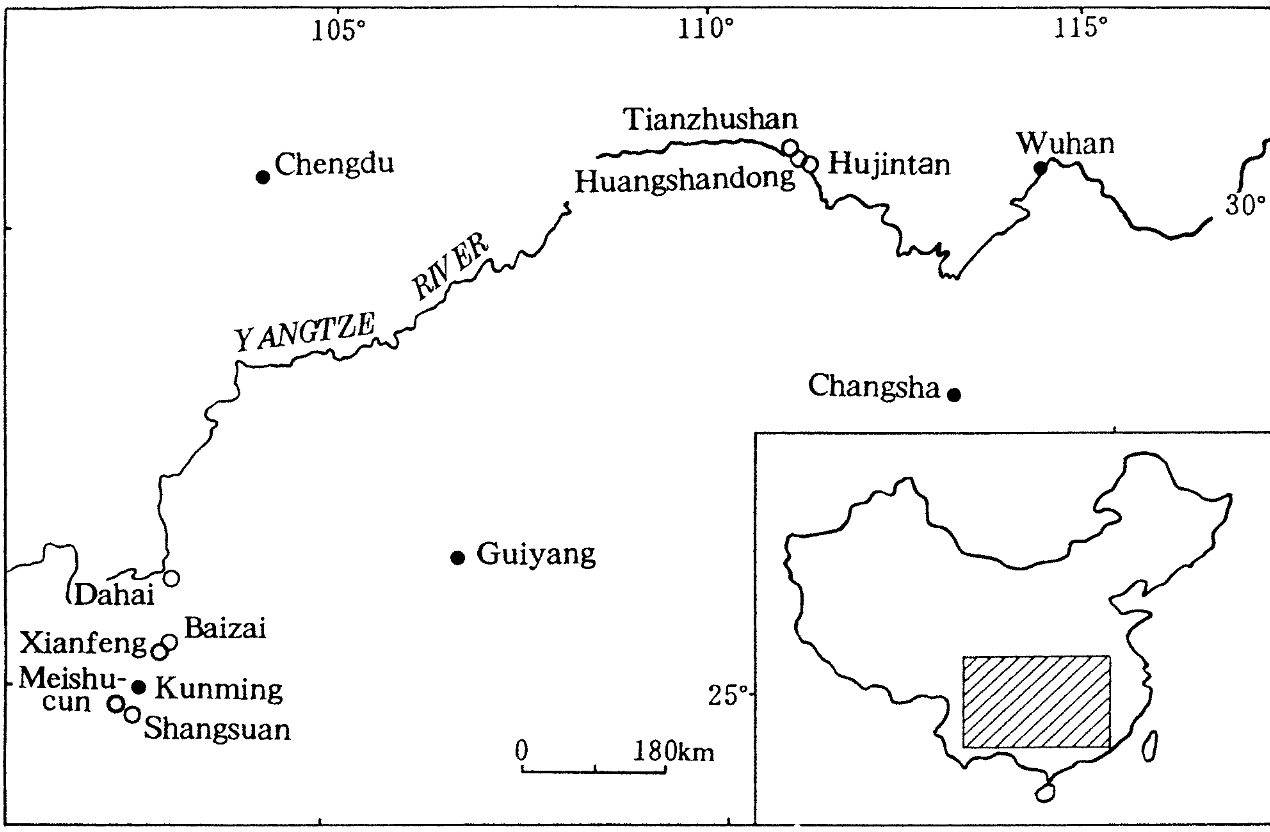


Figure 1 Map showing important localities of the earliest Cambrian polyplacophorans in Yangtze Region of China.

of an animal. It was their view that *Yangtzechiton* might be the shells of primitive animals belonging to the Polyplacophora. Salvini-Plawen (1990: 2) wrote: "Moreover, the Precambrian and Early Cambrian Placophora described by Yu (1987) from China were like-wise small (1.2 mm–5 mm) ...". Morris (1990: 76) clearly stated that the Meishucunian contains a rich fauna of chitons, equal to any locality today. Peel (1991: 5) stated: "During the last decade fused associations of minute sclerites have been described from the earliest Cambrian of China and interpreted as microchitons (Yu, 1987, 1990). These have been seized upon as the missing early polyplacophoran link in molluscan evolution (e.g. Haszprunar, 1988; Yu, 1990)".

In the same year, Conway Morris and Chen (1991: 384, plate 8; text-figure 10) agreed with Qian and Bengtson's viewpoint. Runnegar (1996: 82) stated "the earliest known chitons are not *Runnegarochiton* and its associates but instead are species of *Matthevia* from the latest Cambrian of the United States".

The writer is firmly of the view that *Yangtzechiton* and its related genera belong to the Class Polyplacophora, and that the affinities of *Paracarinachites* remain to be clarified (Yu, 1987b, 1990, 1993, 1996). During the last few years, there have been some exciting contributions on Cambrian fossils. *Triplicatella disdoma* Conway Morris, 1990 from the Lower Cambrian Parara Limestone and Ajax Limestone of South Australia (Bengtson *et al.* 1990) was reinterpreted as the earliest known polyplacophoran by Yates, Gowlett-Holmes and McHenry (1993: 71). Chen *et al.* (1995) recognized *Yunnanozoon lividum* Hou, Ramsköld and Bergström, 1991 as the oldest chordate recorded from the Maotianshan Shale Member of the Lower Cambrian Yu'anshan Formation of Chengjiang, Yunnan, China (Chen *et al.*, 1995).

There has also been new work on the Precambrian. Molecular test results of Wray *et al.* (1996) suggested that invertebrates including echinoderms, arthropods, annelids and molluscs diverged from chordates about a billion years ago, about twice as long as the Phanerozoic. One of the non-mineralized Ediacaran fossils, *Kimberella quadrata* (Glaessner and Wade 1966), from the Ust'-Pinega Formation of the Winter Coast of the White Sea in northern Russia, was reinterpreted by Fedonkin and Waggoner (1997) as a mollusc-like fossil. Zhang *et al.* (1998) indicated that permineralized fossils from the terminal Proterozoic Doushantuo Formation of South China, including the large animals, radiated into a world rich in prokaryotic, protistan and even multicellular diversity which existed just before the Ediacaran radiation. The origin of shelled chitons within the late Proterozoic is in accord with the likely

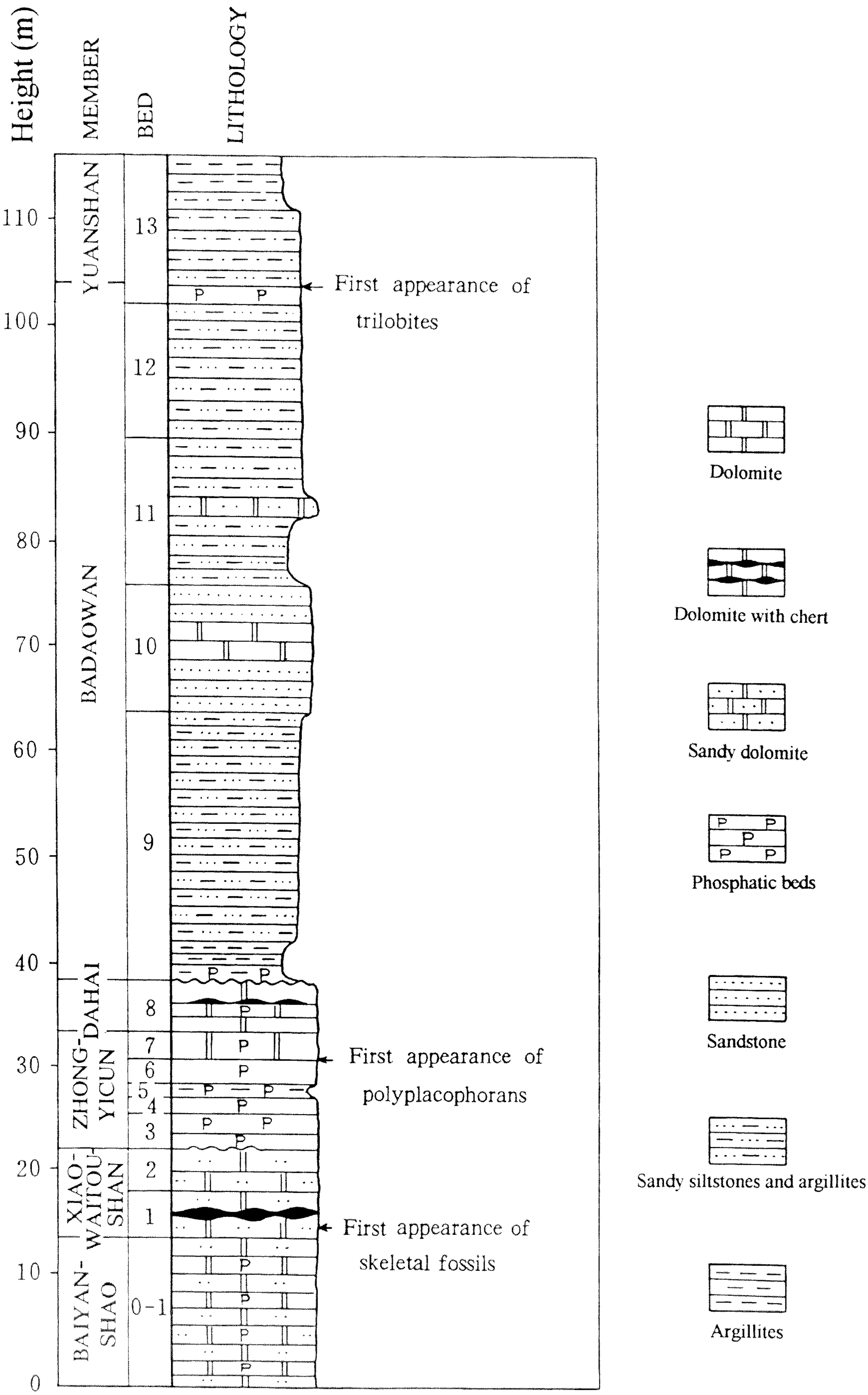
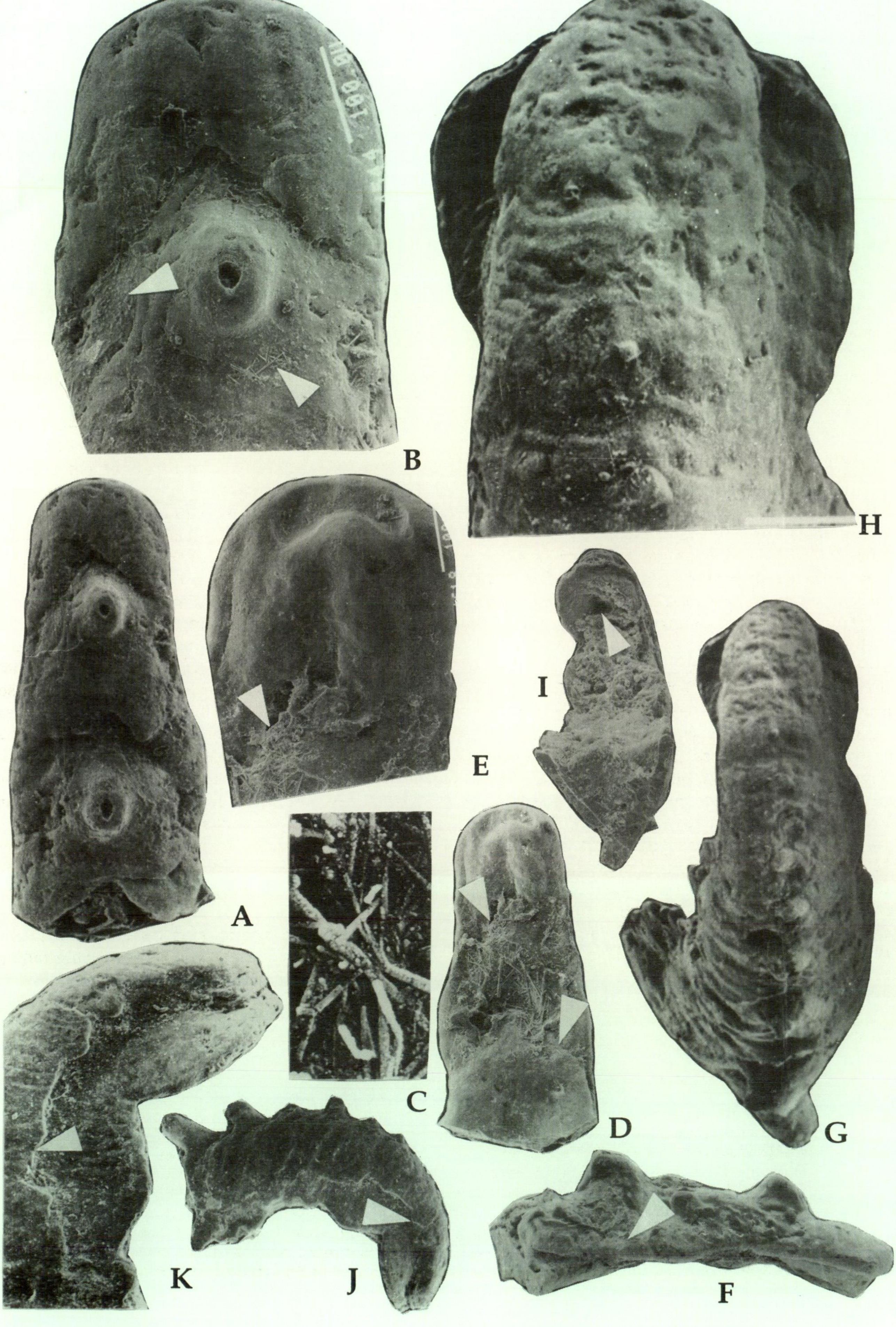


Figure 2 Sketch map showing possible occurrence position of the three earliest Cambrian biotas (with the Meishucun section, Kunyang phosphorite mine, Yunnan, reproduced from Brasier *et al.* (1990) and revised by the writer).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evolutionary history of the Phylum Mollusca.

Early Cambrian *Yangtzechiton* and related genera possess some peculiar structures and they bear a very close evolutionary relationship to younger chitons.

What has been mentioned above indicates that polyplacophorans had already begun to diversify by the beginning of the Early Cambrian. However, Qian and Bengtson placed these polyplacophorans in synonymy with other small shelly fossils, and they are jumbled together with their taxa (Qian and Bengtson, 1989, 1992a, b; Qian, 1989, 1993;). The aim of this paper is to discuss how to distinguish early polyplacophorans from other small shelly fossils in the earliest Cambrian.

Illustrated specimens are housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, People's Republic of China.

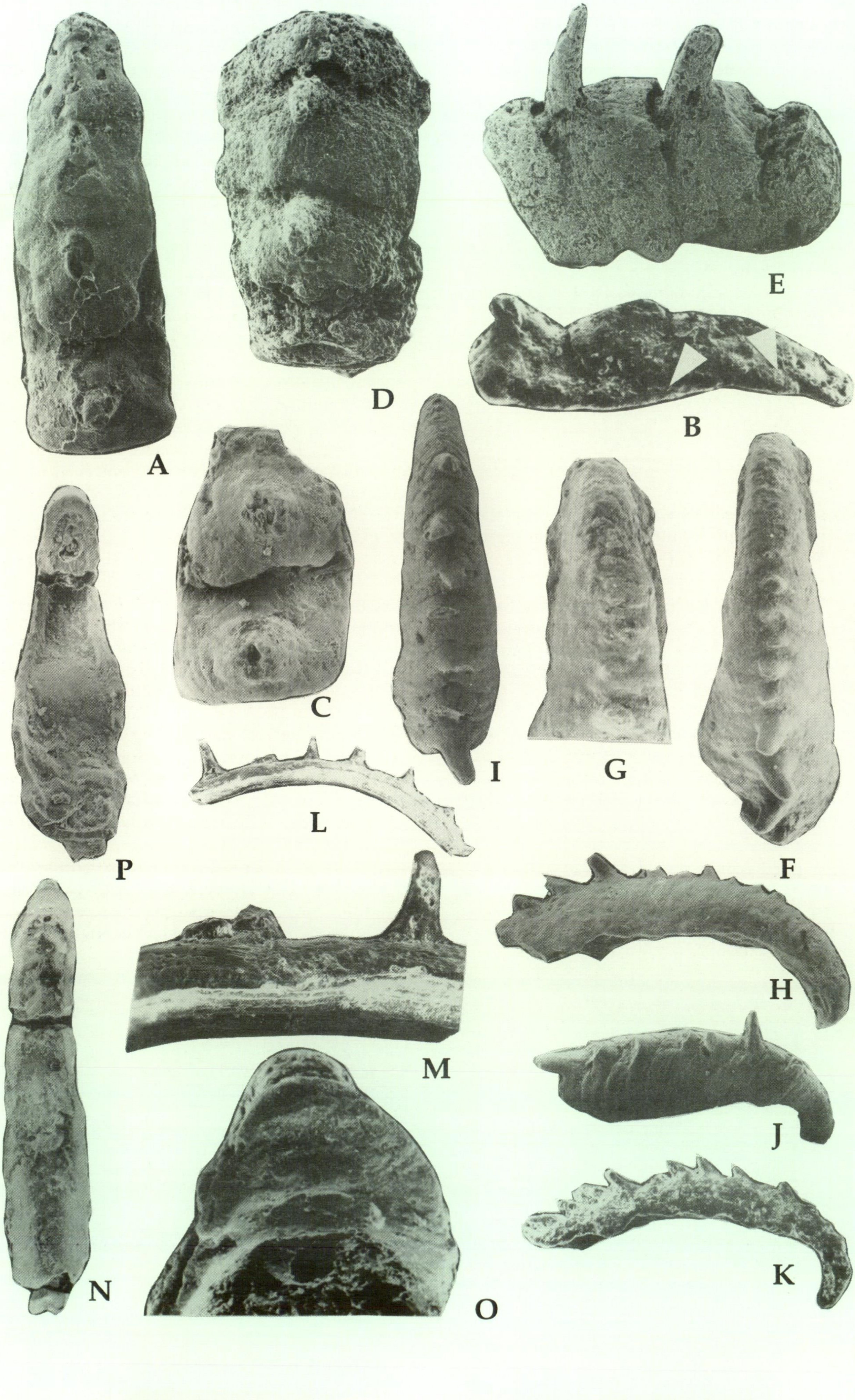
WHY *YANGTZECHITON* AND RELATED GENERA ARE POLYPLACOPHORANS

Qian and Bengtson (1989: 49) concluded that there is no basis for the claim to polyplacophoran affinities of '*Yangtzechiton*' or '*Luyanhaochiton*', and that both are synonyms of *Paracarinachites*. The present writer finds Qian and Bengtson's conclusion to be incorrect for the following reasons:

The polyplacophorans, or chitons, generally have a series of eight overlapping plates or valves, situated dorsally, and held in place by a tough muscular girdle, which may be either naked or variously ornamented with spicules, scales, bristles, or hairy protuberances (Smith, 1960). In *Yangtzechiton elongatus* Yu, the holotype comprises a head valve and two intermediate valves (Yu, 1984a, plate 1, figures 1–5; 1987a, plate 1, figures 1–4; 1987b, plate 8, figures 1–4, plate 9, figures 1–3, plates 10–12; 1990, plate 2, figures 1–3, plate 3, figures 1–5; 1993, plate 1, figures 1–2; Figures 3A–F); the paratype is composed of four intermediate valves and one tail valve (Yu, 1984a, plate 1, figures 6–7; 1987b, plate 8, figures 5–7, plate 14, figures 1–4; 1990, plate 2, figures 4–5; 1993, plate 1, figures 3–4; Figure 4A–B), and the third figured specimen has two intermediate valves (Yu, 1987a, plate 1, figure 5; 1987b, plate 9 figure 4; Figure 4C). In the other specimens there are six overlapping valves (Qian and Bengtson, 1989, figure 29A; Qian, 1993, plate II, figure A; Figure 5). In *Luyanhaochiton spinus* Yu, the holotype is composed of a head valve and three intermediate valves (Yu, 1984a, plate 1, figures 8–9; 1987a, plate 1, figures 6–7; 1987b, plate 13, figures 1–5, plate 14, figures 5–6; 1990, plate 2, figures 6–8; 1993, plate 1. figures 5–6; Figure 4D–E) and the figured specimen has two intermediate valves (Yu, 1987a, plate 1. figure 8; 1987b, plate 13, figure 6). So far as I know, no other chitons with such well preserved shells have been recorded from the Cambrian. The earliest hitherto fossil polyplacophoran remains (generally separate valves) occur in the Upper Cambrian and have been found sparingly in rocks of all geological ages (Smith, 1960). In most, the full complement of head, intermediate, and tail valves has not been found (Smith and Hoare, 1987).

The shells of polyplacophorans are generally 25–75 mm in length and occasionally up to 43 cm in the largest one known. However, the shells of those discovered from the earliest Cambrian of the Yangtze Region are only 3–5 mm in length, and just over 5 mm in the largest one. Although these primitive chitons are very tiny, they possess the basic features of the Class Polyplacophora. Smith (1960) indicated that head and tail valves usually differ in shape from each other and from the six intermediate valves, the latter commonly being much alike in contour. Like modern chitons, the shell of *Yangtzechiton elongatus* is composed of three different shapes of valves: the head valve is nearly as long as wide, without a raised hole (Figure 3A–B), anterior margin broadly rounded, posterior margin with a broad and deep sinus; the intermediate valve is longer than wide, with one-half of the valve overlapped by the preceding one, the middle of the anterior part has an elliptical hole, which may be the result of a hollow spine falling

◀ **Figure 3** A–F. *Yangtzechiton elongatus* Yu, A. Dorsal view of shelly fossil, showing head and intermediate valves, x 90. B. Enlargement of the head and intermediate valves, showing the granules and spicules (white arrow) x 195. C. Enlargement of spicules on the dorsal side of the intermediate valve, x 900. D. Ventral view, showing the contiguous fissures between individual valves (white arrow), x 70. E. Ventral view of the head valve, showing the nephroid depression, contiguous fissure and other structures (white arrow), x 135. F. Right lateral view, showing the one-half of an intermediate valve overlapped by the preceding one (white arrow), x 110. Holotype. NIGP 84131. Coll. no. KM-7. Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Meishucun of Jinning, E. Yunnan. G–K. *Paracarinachites sinensis* Qian and Jiang, G. Dorsal view, showing alternately arranged spines and nodular projections, x 120. H. Enlargement of nodular projections and expansively overturned ventral margin in adapical curved part, x 250. I. Ventral view, showing a subcircular dish with an opening in its subcentre (white arrow), x 80. J. Lateral view, showing many thin lamellae arranged parallel to each other (white arrow), x 65. K. Enlargement of thin lamellar (white arrow), x 170. NIGP 101908. Coll. no. XB-40. Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Baizai of Xundian, E. Yunnan.



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off; and the tail valve is long and arched, rectangular, with subcentrally located mucro (Figure 4A–B). In *Luyanhaochiton spinus* the head valve is much wider than long, the anterior margin is semicircular, and there is no hollow spine; the intermediate valves differ from the head valve in the presence of a hollow spine, the basal part of the spine is broadly rounded and extends toward and inserts into the preceding valve, connecting the anterior valve with the posterior one (Figure 4D–E). The tail valve is unknown.

The surface of the intermediate valves is usually marked off by a diagonal line or rib into three triangular areas, one median and two lateral (Hyman, 1967). *Yunnanopleura biformis* Yu is distinctly divided into three areas: a large central area, roundly convex, occupying most of the dorsum and ornamented with coarse to fine transverse ribs; and two lateral areas which are small, subtriangular, distinct in its dividing line from the central area, ornamented with 10–12 stout oblique ribs, and with one of the ends intersecting the transverse ribs in the central area at 40° (Yu, 1987b, plates 17–18; 1990, plate 4; Figure 8 H–N). *Gotlandochiton*? *minimus* is obviously divided into jugal and lateral areas. Jugal area rounded and convex, jugal sinus broadly concave, U-shaped; lateral area separated from jugal area by a stout, rounded ridge extending from near the apex to anteriolateral margin (Yu, 1987b plate 15, figures 1–3; plate 16, figures 1–8; Figure 9 L–P). The intermediate valves of the *Tchangsichiton notabilus* Yu (Figure 8 A–G), *Postestephaconus tentes* Jiang (Figure 8 O–R) and *Meishucunchiton vulgarus* Yu (Figure 9E–I), are weakly divided into three areas.

Although *Yangtzechiton* and related genera are provided with some peculiar structures, they bear a very close evolutionary relationship to younger taxa. *Yunnanopleura* having a long valve and an apical hole, probably gave rise to *Chelodes* Davidson and King (1874), frequently found from the Early Ordovician (Bergenhayn, 1960; Runnegar *et al.*, 1979) to Silurian (Figure 6D–F). *Meishucunchiton* is similar to *Eochiton* Smith (1964) from the Lower Ordovician of southern Oklahoma; *Runnegarochiton* is closely related to *Priscochiton* Dall (1822) from the Middle Ordovician of Canada in the outline of the intermediate valve and in the presence of a recurved tegmentum (Figure 6J–L). *Yangtzechiton* bears some resemblance to the genus *Glyptochiton* de Koninck (1883) from the Lower Carboniferous of Belgium (Figure 6P–Q), in the possession of a broad sinus at the posterior margin of the head valve, the intermediate valves are longer than wide and bearing a concave hole, though they are rather far from each other in geological age. *Luyanhaochiton* is analogous to the chitons of the later Paleozoic in the morphology of the shell, but in this genus, the anterior end of the intermediate valve is possessed of an obliquely backwardly directed hollow spine which makes it different from other known genera. Finally, *Gotlandochiton*? *minimus* Yu is similar to *Gotlandochiton troedssoni* Bergenhayn from the Silurian of Sweden (Bergenhayn, 1955, plate I, figure 9; plate II, figure 7; Figure 6N).

These examples demonstrate that *Yangtzechiton* and related genera not only represent primitive forms of the major polyplacophoran groups that evolved after the Early Cambrian, but they also represent the initial diversification of the Class Polyplacophora. This discussion on the evolutionary relationships of polyplacophorans further confirms that C.R. Stasek's prediction has been realised in the Chinese fossil collections: "The

◀ **Figure 4** A–C. *Yangtzechiton elongatus* Yu, A. Dorsal view of shelly fossil, showing intermediate valves and tail valve, x 120. B. Right lateral view, showing the one-half of an intermediate valve overlapped by the preceding one, x 105. NIGP 84132 Coll. no. KM-7. Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Meishucun of Jinning, E. Yunnan. C. Dorsal view of two intermediate valves, x 60. NIGP 84133. Coll. no. XB-28. Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Baizai of Xundian. E. Yunnan. D–E. *Luyanhaochiton spinus* Yu, D. Dorsal view of shelly fossil, showing head and intermediate valves, x 80. E. Left lateral view, showing the anterior part of the spine extending and inserting into the preceding valve, x 80. Holotype. NIGP 84135. Coll. no. KM-7. Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Meishucun of Jinning, E. Yunnan. F–P. *Paracarinachites sinensis* Qian and Jiang, F. Dorsal view, showing nodular projections and expansively overturned ventral margin in the adapical part and alternately arranged spines in the posterior part, x 50. G. Enlargement of the adapical part, showing the nodular projections, x 80. H. Lateral view, x 40. NIGP 101902. Coll. no. XB-40. I. Dorsal view, x 55. J. Lateral view, x 30. NIGP 101901. Coll. no. XB-28. K. Lateral view, x 24. Cat. no. 10362 (Chengdu Institute of Technology, Sichuan). Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Yulu of Huize, E. Yunnan. L–M. Longitudinal sections, showing the thin lamellar arranged parallel to each other, x 30, and x 120. Cat. no. 10356 (Chengdu Institute of Technology, Sichuan). Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Meishucun of Jinning, E. Yunnan. N. Ventral view, showing adapical curved part with a subcircular dish and widely concave posterior part, x 35. O. Enlargement of subcircular dish, x 150. NIGP 101909. Coll. no. XB-28. P. Ventral view, showing adapcial part with a subcircular dish and widely concave posterior part, x 70. NIGP 101916. Coll. no. XB-28. Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Baizai of Xundian, E. Yunnan.

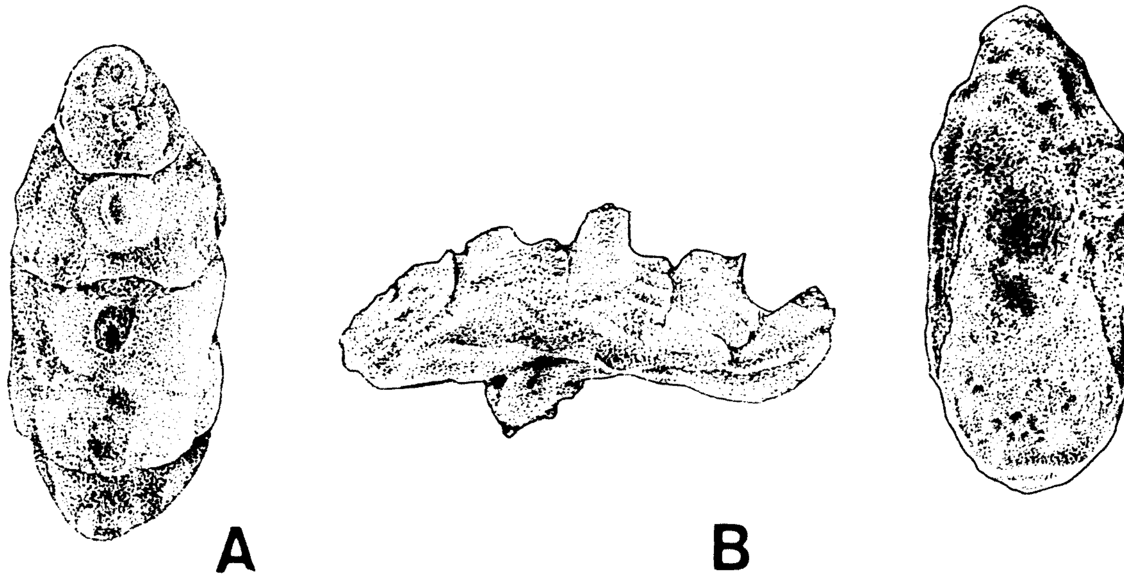


Figure 5 *Yangtzechiton elongatus* Yu, A. Dorsal view of shelly fossil, showing intermediate valves. B. Left lateral view, showing the one-half of each intermediate valve overlapped by the preceding one. C. Ventral view, showing the continguous fissues between individual valves, x 50, NIGP 106887, (after Qian and Bengtson, 1989: 53).

chiton fauna of the Upper Cambrian was probably the result of a very early and separate trend from much smaller ancestral forms whose remains have not yet been found or recognised" (Stasek, 1972: 12).

A COMPARATIVE STUDY OF *YANGTZECHITON* YU AND *PARACARINACHITES* QIAN AND JIANG

Comparisons were made between a great number of samples (more than five hundred specimens) were collected by the writer and his colleagues from the Baizai section in Xundian and the Meishucun section in Jinning, Yunnan in 1980. On the 11th June, 1981, the writer picked for the first time from an acid-residual sample, an earliest Cambrian polyplacophoran with the head valve and intermediate valves overlapping together. This came from the Lower Cambrian Zhongyicun Member of Tongying Formation of the Meishucun section of Jinning. The writer gave this information to Liu Di-rong and Qian Yi and introduced to them the locality, horizon and the morphological features of the Lower Cambrian Polyplacophora, as well as outlining the essential significance of the research on these fossils.

In 1984, Qian published on the Lower Cambrian polyplacophorans *Carinachites spinatus* and *Paracarinachites sinensis.* However, Qian's published descriptions and illustrations of presumed Early Cambrian polyplacophorans were not molluscs; he mistakenly regarded *Carinachites spinatus* Qian (1977: 265, plate III, figures 17–19) and *Paracarinachites sinensis* Qian and Jiang 1982 (in Luo *et al.*, 1982: 183, plate 17, figure 17) as members of the Class Polyplacophora (Qian, 1984a: 93, plate I, figures 26–28; plate II, figures 14–16, 23–24; 1984b: 18, figures 1, 37–1, 38).

As previously noted (Yu, 1987b, 1990, 1993), the shell of *Yangtzechiton elongatus* is composed of a head, intermediate and tail valves. The intermediate valves consist of tegmentum and articulamentum, longer than wide, with one-half of the valve overlapped by the preceding one, and with an elliptical hole in the middle of anterior part, while *Paracarinachites* is an elongately curved sclerite, the whole composed of many thin lamellae arranged parallel to each other, and with 15–20 nodular projections and spines alternately arranged on the outer side.

The description of *Paracarinachites sinensis* (Qian and Bengtson, 1989: 49) centres around the sclerite formed by growth increments overlapping each other on the inner surface towards the abapical end. From the description and illustrations in He and Xie (1989, plate 1, figures 11–12); Qian and Bengtson, (1989, figures 27–28), and Yu (1993, plate 1, figures 10–11), it is clear that *P. sinensis* is composed of many thin lamellae arranged parallel to each other.

Along the middle of the dorsal surface of chitons, there extends a longitudinal series of eight, usually overlapping valves (Hyman, 1967). Overlapping refers, in particular, to the form of the shell in the Polyplacophora. In general, the posterior valve is usually overlapped by the preceding one. Sclerites, on the other hand, have been described by Qian and Bengtson (1989: 51): "The sclerites have a clearly laminated structure (Figure 27A3), suggesting that they are built up of superimposed

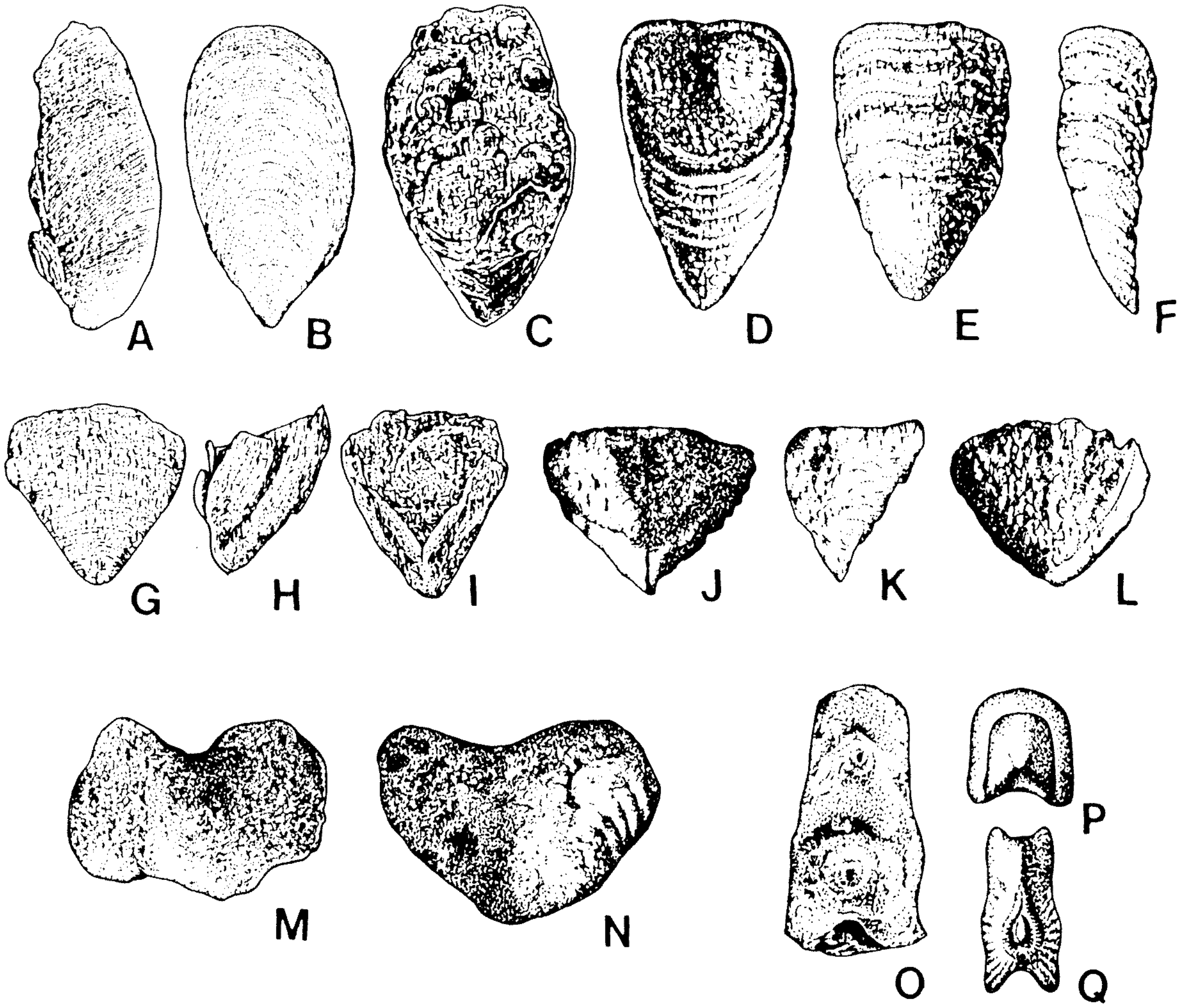


Figure 6 Diagrams showing that the earliest Cambrian Polyplacophorans bear a very closely evolutionary relationship to younger taxa. A–C. *Yunnanopleura biformis* Yu, x 20. NIGP 84173. Zhougyicun Member of Lower Cambrian Tongying Formation, Baizai of Xundian, E. Yunnan. D–F. *Chelodes bergmani* Davidson and King, x 2. Middle Silurian of Gotland, Sweden (after Davidson and King, 1874). G–I. *Runnegarochiton modestus* Yu, x 20. NIGP 84161. Zhongyicun Member of Lower Cambrian Tongying Formation, Meishucun of Jinning, E. Yunnan. J–L. *Priscochiton canadensis* (Billings), x 4. Middle Ordovician of Ottawa River, Canada (after Smith, 1960). M. *Gotlandochiton? minimus* Yu, x 32.5. NIGP 84155. Zhongyicun Member of Lower Cambrian Tongying Formation, Meishucun of Jinning, E. Yunnan. N. *Gotlandochiton troedssoni* Bergenhayn, x 4.6. Silurian of Gotland, Sweden (after Smith, 1960). O. *Yangtzechiton elongatus* Yu, x 35. NIGP 84131. Zhongyicun Member of Lower Cambrian Tongying Formation, Meishucun of Jinning, E. Yunnan. P–Q. *Glyptochiton cordifer* de Koninck, Lower Carboniferous of Belgium (after Smith, 1960).

growth layers. The apical end of several specimens has a characteristic build-up of laminae (Figure 28) that also appear to represent successive growth increments". In fact, *P. sinensis* is built-up of six or more parallel arranged lamellae (Qian and Bengtson, 1989, figure 28; Figures 4L–M, 7B–C). Therefore, the present writer concludes that these authors have not distinguished between the meaning of the words 'overlapped' and 'superimposed'.

In *Yangtzechiton elongatus*, the ventral side of the head valve has a nephroid depression near the anterior margin, with a series of W-shaped curved striae in the posterior part of the depression; the intermediate valves are slightly concave on the ventral side, with contiguous fissures between individual valves clearly visible (Yu, 1984a, plate 1. figure 3; 1987a, plate 1, figure 2; 1987b, plate 8, figure 2; 1990, plate 2, figure 2; 1993, plate 1, figure 2; Figure 3D–E). In *Paracarinachites sinensis,* the lower side of the sclerite is divided into two parts: the adapical curved part with a subcircular dish bearing an opening in its subcentre, and posterior part widely concave (Qian, 1984a, plate I, figure 27; Yu, 1993, plate 1, figures 8–9, 12–14; Figure 3I, 4N–P).

The number and arrangement of the spines or denticles also serve to distinguish between *Yangtzechiton* and *Paracarinachites.* In *Yangtzechiton elongatus*, the head valve is small, without a raised

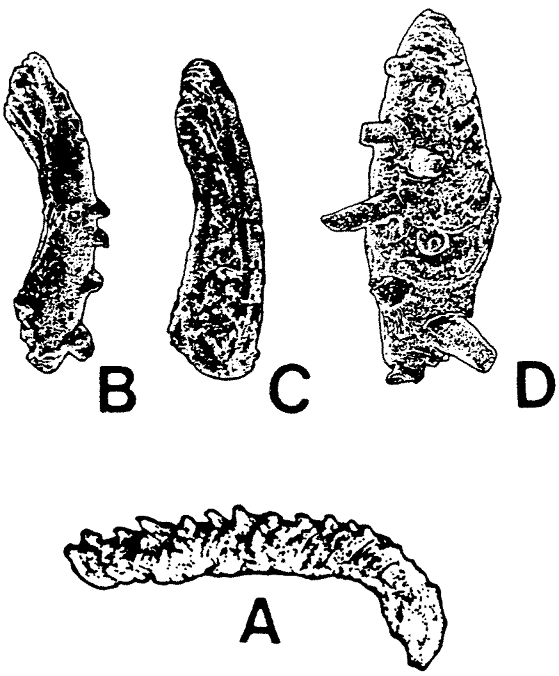


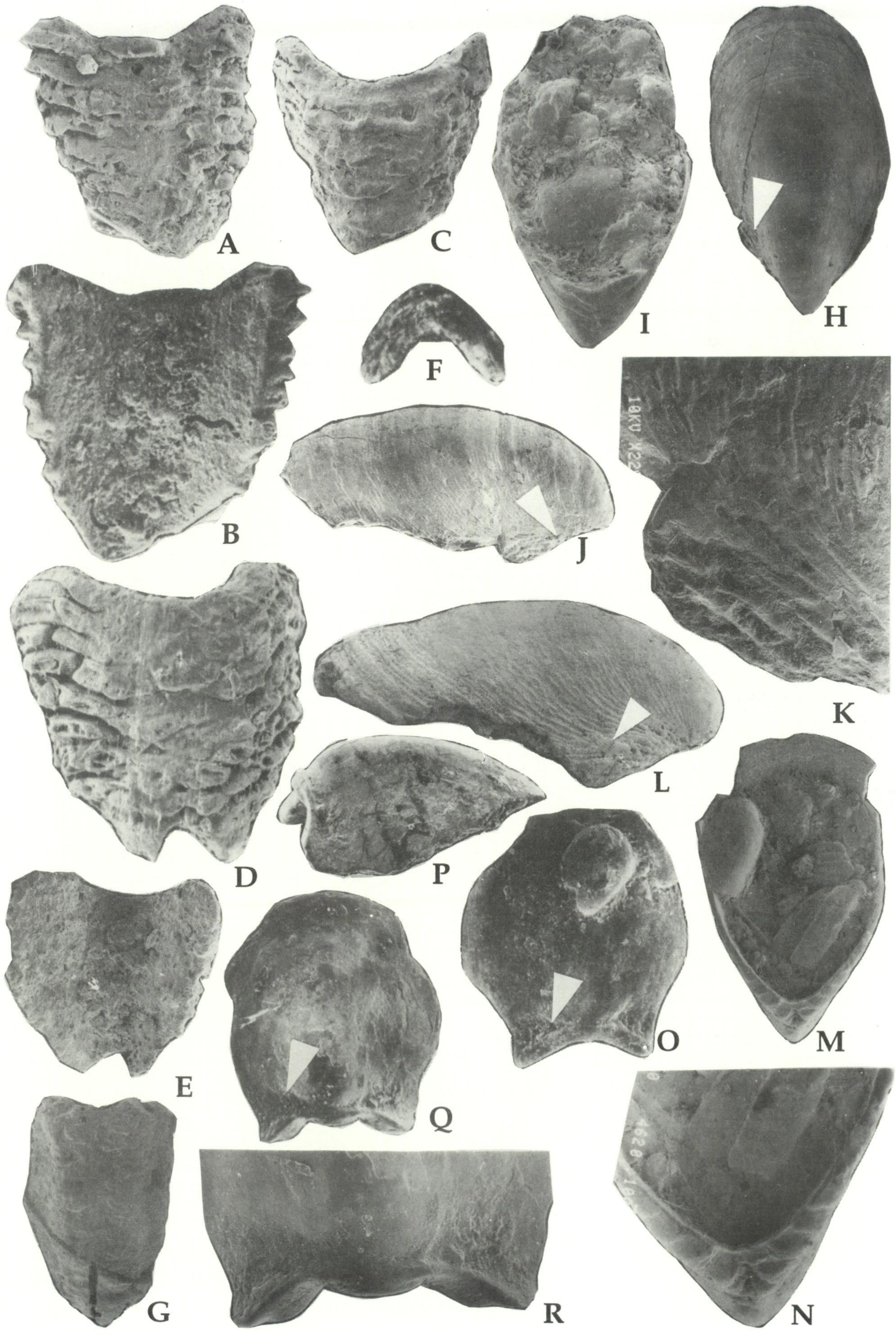
Figure 7 A–C. *Paracarinachites sinensis* Qian and Jiang, A. Lateral view, x 30, NIGP 70939 (after Qian, 1984a). B–C. Lateral and ventral views, x 60, NIGP 106886 (after Qian and Bengtson, 1989). D. *Paracarinachites bispinosus* He and Xie, dorsal view, x 37.5, NIGP 106896 (after Qian and Bengston, 1989).

has a raised hole, which may be the result of a hollow spine falling off (Yu, 1984a, plate 1, figures 1, 4, 6–7; 1987a, plate 1, figures 1, 3, 5; Figure 3A–B; 4A–C), while in *P. senensis*, the outer surface of the sclerite bears 5–6 nodular projections in the adapical curved part and 10–15 alternately arranged spines in the posterior part (Yu, 1987b, 1990, 1993; He and Xie, 1989; Figure 3G–H, 4F–K). But Qian and Bengtson (1989: 51) considered that "The largest number of denticles observed is 10". In their illustration the denticles usually number 10 or less, due to the incomplete specimens. However, years earlier Qian described a well-preserved specimen of *P. sinensis*, which has at least fifteen spines alternately arranged on the dorsal side (Qian, 1984a, plate 1, figure 28, NIGP 70939; Figure 7A).

In the diagnosis of the genus *Paracarinachites*, Qian and Bengtson (1989: 49) stated: "Outer surface with regularly spaced denticles, usually inclined towards the abapical end of the sclerite". The published illustrations of many specimens of *P. sinensis* (He and Xie, 1989, plate 1 figures 8–10; Qian and Bengtson, 1989, figure 27: Yu, 1993, plate 1, figures 7, 10, 15–18) clearly show the denticles alternately arranged on the dorsal side with their tips obliquely backward and inclined leftward (or rightward). In 1989, a new species *Paracarinachites bispinosus* He and Xie (1989, plate 1, figures 13–15) (=*P. parabolicus* Qian and Bengtson, 1989, figures 30–31) was described from the Lower Cambrian Dahai Member of the Tongying Formation of Huize, Yunnan. This species has two rows of spines on the dorsal side, their tips aligned obliquely leftward (or rightward) and backward (Figure 7D), similar to those of *P. sinensis*. These characteristics fully demonstrate that the diagnosis of the genus *Paracarinachites* and the description of *P. sinensis* provided by Qian and Bengtson (1989) does not fully reflect the precise features of the species, *P. sinensis*.

In this monograph, Qian and Bengtson claim that *Yangtzechiton* Yu and *Luyanhochiton* Yu, are both junior synonyms of *Paracarinachites* Qian and Jiang (Qian and Bengtson 1989: 48–54, 102–103). Conway Morris and Chen (1991: 382–385, 393–394), Bengston (1992b: 408), Bengston and Conway Morris (1992: 461, 467) and Qian (1989: 265; 1993) repeated the same view. From the above comparisons, it is clear that *Yangtzechiton* and *Luyanhaochiton* are both valid taxa and that they belong to the Class Polyplacophora. *Paracarinachites* is no more than a single sclerite. The multivalved and univalved form is a major

Figure 8 A–G. *Tchangsichiton notabilus* Yu, A. Dorsal view of an intermediate valve, showing the central and lateral areas and broadly U-shaped jugal sinus, x 65. B. Ventral view, showing the deep concave central area, x 80. Holotype. NIGP 84140. Coll. no. TF-1. C. Dorsal view of an intermediate valve, showing aesthetes, x 60. NIPG 84141. Coll. no. TF-1. D. Dorsal view, showing the sculptures, x 70. E. Ventral view, x 55. F. Posterior view, x 40. NIGP 84142 Coll. no. TF-1. G. Dorsal view of the tail valve, x 60. NIGP 84143. Coll. no. TF-1. Upper part of Huangshandong Member of Lower Cambrian Tongying Formation. Tianzhushan of Yichang, W. Hubei. H–N. *Yunnanopleura biformis* Yu, H. Dorsal view of an intermediate valve, showing the central and lateral areas (white arrow), x 30. I. Ventral view, showing the apical area with several rows of nodular projections, x 35. J. Left lateral view, showing the lateral and central areas (white arrow) x 35. K. Enlargement of the central and lateral areas, showing different kinds of the sculptures in the central and lateral areas, x 80. Holotype. NIGP 84173. Coll. no. XB-52. L. Left lateral view, showing lateral and central areas (white arrow), x 35. NIGP 84172 Coll. no. XB-52. M–N. Ventral views, showing the V-shaped apical area and other structures, x 30 and x 60. NIGP 84174. Coll. no. XB-52. Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Baizai of Xundian, E. Yunnan. O–R. *Postestephaconus tentes* Jiang, O. Dorsal view of an intermediate valve, showing the central and lateral areas (white arrow), x 90. NIGP 84206. Coll. no. XB-28. Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation, Baizai of Xundian, E. Yunnan. P. Right lateral view, x 85. Q. Dorsal view, showing bluntly rounded apex and lateral area (white arrow), x 90. R. Enlargement of apex and lateral areas x 180. NIGP 84209. Coll. no. KM-7. Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Meishucun of Jinning, E. Yunnan.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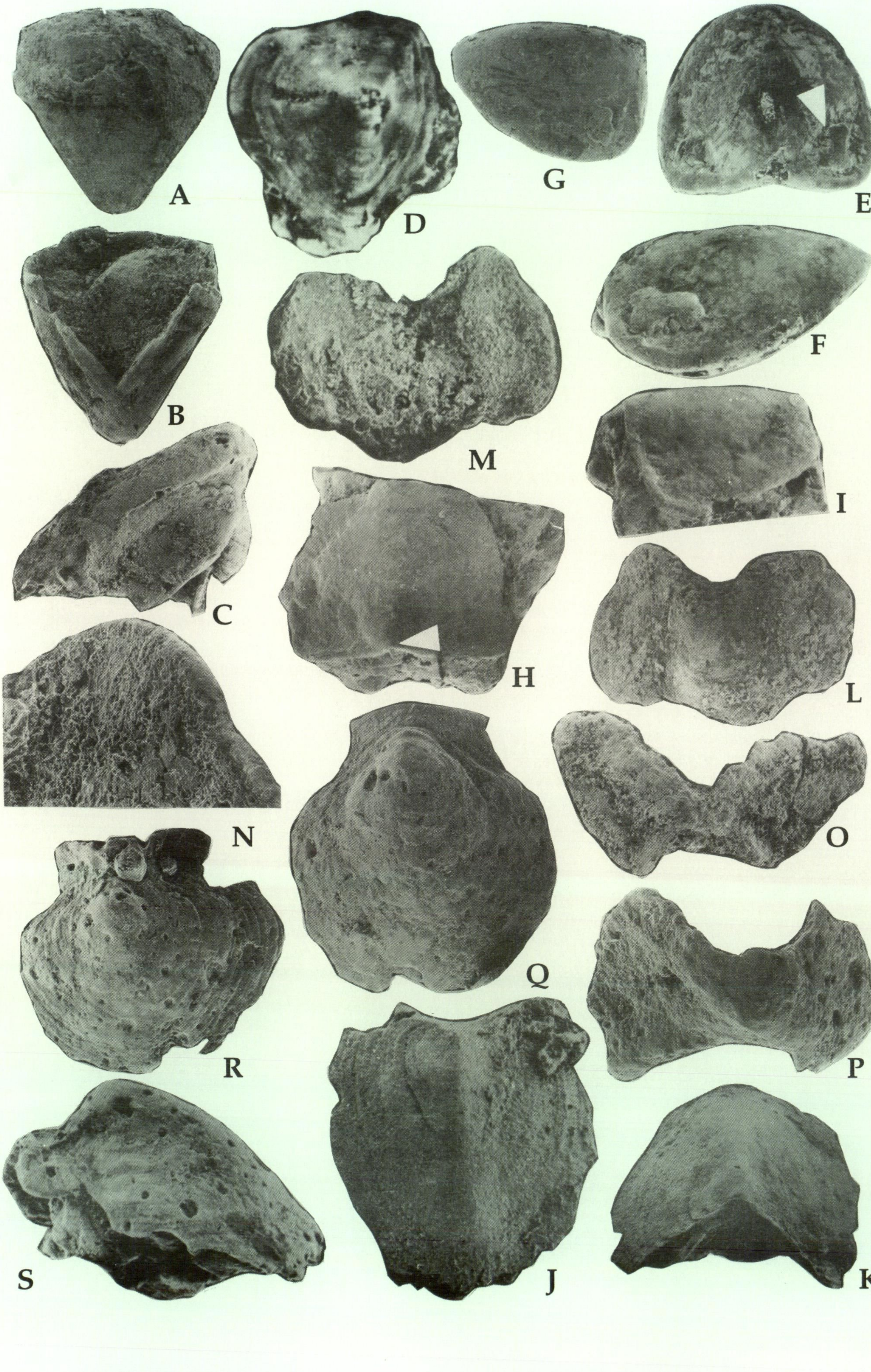
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character used in high level classification. Qian and Bengtson's treatment of *Yangtzechiton* and *Luyanhaochiton* as junior synonyms of *Paracarinachites*, is at variance with the basic concepts of biological taxonomy.

ON THE DIFFERENCES BETWEEN *OCRURANUS* LIU AND *RUNNEGAROCHITON* YU

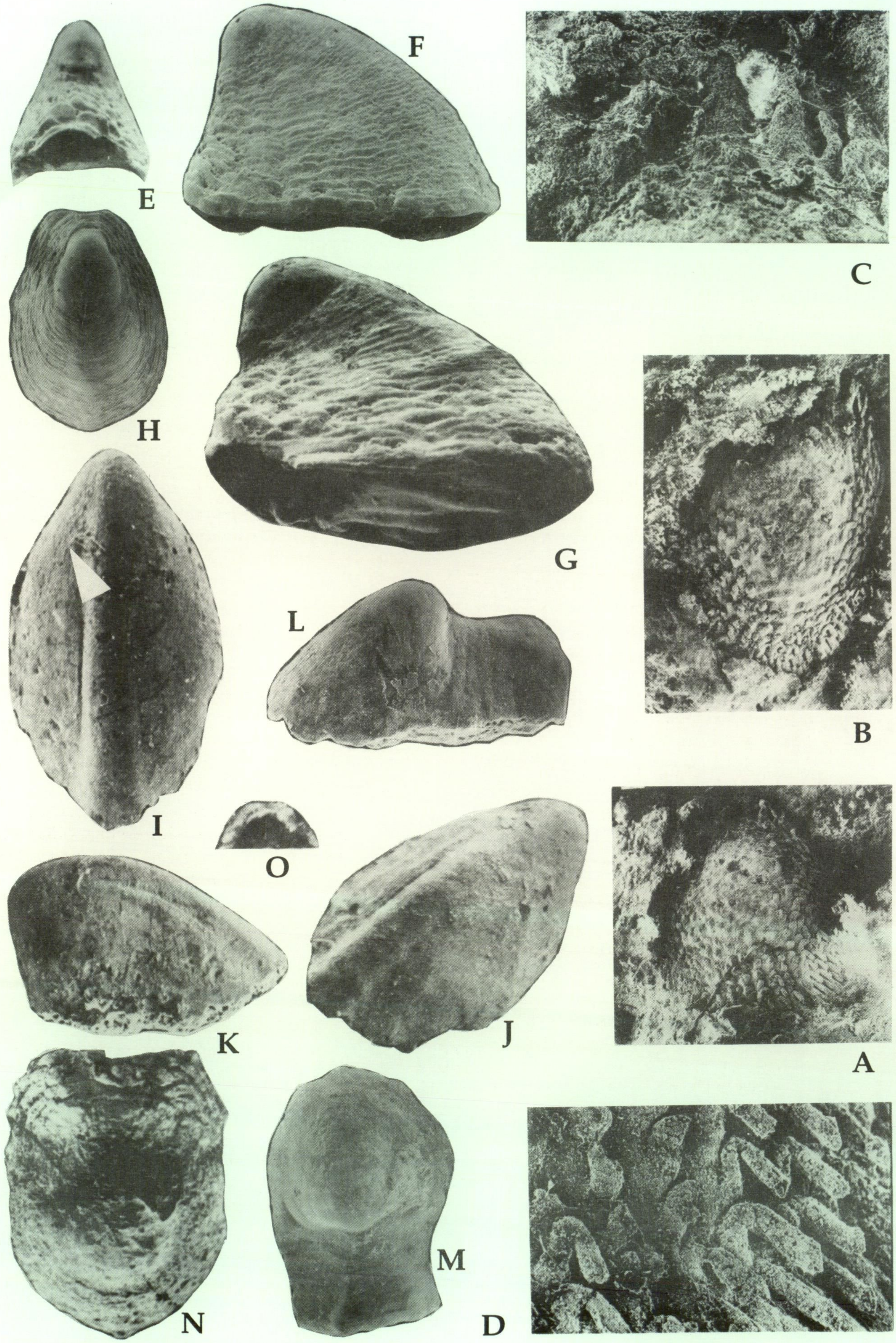
Qian and Bengtson (1989) discuss some other polyplacophorans from the Meishucun Stage, in which certain genera and species of the genus *Ocruranus* Liu are lumped together. However, before discussing the classification of these fossils, it is necessary to make clear the generic characteristic of *Ocruranus*. The genus was erected in 1979 by Liu, taking *Ocruranus finial* Liu as the type species (Liu, 1979, plate 1, figure 3; Figure 9D). The generic diagnosis given (Liu, 1979: 506) as follows: "Outline nearly conical; hinge line straight and wide; pseudointer area high, nearly procline; pseudodelthyrium round-convex and complete, without foramen pedicle. Surface with concentric growth striates".

Liu (1987: 376–377) later supplemented the generic characteristics of *Ocruranus* as follows: "Shell small, slightly bilaterally asymmetrical, with semiconical ventral and dorsal valves in rough mirror symmetry; ventral interarea procline, while dorsal one small, nearly catacline; homeodeltidium convex and well-developed, but with no foramen seen; surface with only a small number of concentric bands; shell microstructure consisting of alternate sparse and dense thin layers of flakes". The amended generic diagnosis of *Ocruranus* is used for discussion of the problems with in Qian and Bengtson's taxa.

Runnegarochiton Yu, 1987 is a polyplacophoran with *R. modestus* Yu as the type species. A comparison of *R. modestus* with the *Ocruranus finial* Liu shows their essential difference. In *R. modestus* (Yu, 1987b, plate 6, figures 1–6, Text-figures 13, 35; 1990, plate 1, figures 3–6; Figure 9A–C), the intermediate valve is subtriangular in dorsal view; the tegmentum is recurved onto the ventro-posterior portion of the valve, forming a V-shaped hole below the apex, with its margin extending downward and then inversely curved outward, forming a recurved plate (Figure 9B–C). In *Ocruranus finial* (Liu, 1979, plate 1, figure 3; Figure 9D), the shell is subcircular, ventral valve semiconical, pseudointer area high and procline, pseudodelthyrium roundly-convex, but with no visible foramen; dorsal valve low-conical, apex rounded and slightly curved, situated posteriorly, interarea low (Liu, 1979: 506).

Runnegarochiton modestus is also easily distinguished from *Ocruranus subpentaedrus* (Jiang) (1980: 117, plate 1, figures 6, 9, 14), because the shell of *O. subpentaedrus* is generally rounded to ovoid in outline and has a more or less straight proximal edge. The apex is situated close to the proximal margin. The subapical field is set off by a more or less pronounced furrow. A characteristic feature is the re-entrant at the proximal margin, which may form an acute angle and extend to the apex, or be less pronounced, resulting in a higher subapical field. The apical part together with the thickened rim of the subapical re-entrant are commonly preserved as isolated fragments (Qian and Bengtson, 1989: 106).

◀ **Figure 9** A–C *Runnegarochiton modestus* Yu. A. Dorsal view of an intermediate valve, x 30. B. Ventral view, showing the V-shaped apical area and recurved plate, x 30. C. Left lateral view, showing the recurved plate on the ventral side, x 50. Holotype. NIGP 84161. Coll. no. KM-7. Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Meishucun of Jinning, E. Yunnan. D. *Ocruranus finial* Liu, ventral valve, external view, x 30. Holotype. NIGP 57926. Coll. no. AB-21. Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Meishucun of Jinning, E. Yunnan. E–I. *Meishucunchiton vulgarus* Yu, E. Dorsal view of an intermediate valve, showing the central and lateral areas (white arrow) x 50. F. Right lateral view, x 85. G. Left lateral view, x 60. Holotype. NIGP 84191. Coll. no. XD-2. H. Dorsal view, showing the slightly raised apex (white arrow), x 50. NIGP 84193. Coll. no. XD-2. Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Xianfeng of Xundian, E. Yunnan. I. Right lateral view, showing the slightly raised apex, x 50. NIGP 84194. Coll. no. XB-40. Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Baizai of Xundian, E. Yunnan. J–K. *Eohalobia diandongensis* Jian, J. Dorsal view, x 60. K. anterior view, x 55. NIGP 84233. Coll. no. XB-28. Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Baizai of Xundian, E. Yunnan. L–P. *Gotlandochiton? minimus* Yu, L. Dorsal view of an intermediate valve, showing broadly arched jugal area, narrow lateral area and broadly U-shaped jugal sinus. x 50. M. Ventral view, x 55. N. Enlargement of the ventral valve, x 185. Holotype. NIGP 84155. Coll. no. KM-7. O. Dorsal view of an intermediate valve, x 40, NIGP 84145. Coll. no. KM-7. P. Dorsal view, x 100. NIGP 84158. Coll. no. KM-7. Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Meishucun of Jinning, E. Yunnan. Q–S. *Ocruranus subpentaedrus* (Jiang), Q. Dorsal view, x 65. NIGP 101918. Coll. no. S-7. Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Shangsuan of Jinning, E. Yunnan. R. Dorsal view, x 50. S. Lateral view, x 70. NIGP 101917. Coll. no. XB-28. Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Baizai of Xundian, E. Yunnan.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OTHER POLYPLACOPHORANS

As to the classification of *Stoliconus vomeres* Jiang (1980, plate 1, figure 2; Figure 10L–M) and *Postestephaconus tentes* Jiang (1980, plate 1, figure 13; Figure 8O–R) the problem is not as simple as Qian and Bengtson (1989: 103–106; Bengtson, 1992a: 416–417) suggested. It cannot be solved by attributing these taxa respectively to the species *Ocruranus finial* Liu and *O. subpentaedrus* (Jiang). The specimens of *O. subpentaedrus* obtained from the Zhongyicun Member of the Shangsuan Phosphorus Mine section in Jinning, Yunnan are abundant and are preserved relatively intact. More research is necessary to understand the classification of these groups.

Meishucunchiton Yu, 1987 was established with *M. vulgarus* Yu (1987b, plate 15 figures 4–10: Figure 9E–I) as the type species. Its generic diagnosis is as follows: "Shell very small, elongate, possibly belong to vermiform polyplacophorans. Intermediate valves heart-shaped, slightly wider than long. Anterior margin narrowly rounded. Latero-posterior corner obtusely rounded; posterior margin with a median sinus. Tegmentum weakly divided into central and lateral areas; central area widely convex, occupying most part of the dorsum, with a slightly raised apex; lateral areas small, subtriangular. Margin of valve with a narrow marginal edge. Head and tail valves unknown." (Yu 1987b: 110–111). This genus somewhat resembles *Eochiton* Smith (1964) from the Lower Ordovician of southern Oklahoma. It is easily distinguished from the latter by the heart-shaped intermediate valves and smaller lateral areas.

At a glance, *Meishucunchiton vulgarus* Yu (Figure 9E–I) appears similar to *Eohalobia diandongensis* Jiang (Jiang in Luo *et al.*, 1982, plate 21, figures 5–6; Yu, 1987b, plate 66, figures 1–11; Figure 9J–K) in dorsal view, but the differences are: (1) In *Meishucunchiton vulgarus*, the intermediate valve is nearly heart-shaped in dorsal view, while in *Eohalobia diandongensis*, it is elongately round or subovate. (2) In *Meishucunchiton vulgarus*, the dorsal side is divided into central and lateral areas, while in *Eohalobia diandongensis* it is undifferentiated. (3) In *Meishucunchiton vulgarus*, the apex is slightly protruding, while in *Eohalobia diandongensis*, it is bluntly rounded. Here the intermediate valve, with its dorsal side divisible into different areas as observed in *Meishucunchiton vulgarus*, indicates an essential characteristic of the Polyplacophora.

It must be pointed out that the writer (Yu, 1987b) established *Meishucunchiton vulgarus* Yu, but it is misspelt as "*Meishucunconus*" *vulgarus* Yu, in Qian and Bengtson's monograph (1989: 108). *Meishucunconus* was established by Jiang (1980) with *Meishucunconus campylurus* Jiang as the type species. It represents another group entirely different from *Meishucunchiton*, and therefore they should not be lumped together.

Gotlandochiton? minimus Yu (1987b, plate 15, figures 1–3; Figure 9L–P), an element frequently seen in Bed 7 of the Meishucun section, is regarded by some authors as mere fossil fragments. However, the specimens are similar to the intermediate valves of extant Polyplacophora, because in these valves the dorsal side is obviously divided into the jugal and lateral areas, with jugal sinus broadly concave and U-shaped, indicating that these valves are undoubtedly polyplacophorans and unrelated to *Ocruranus subpentaedrus* (Jiang) (Qian and Bengtson, 1989; Bengtson, 1992a).

JINKENITES – A WONDERFUL FOSSIL

Yu (1988, plates 1–2; Figure 10A–D) described the well-preserved earliest Cambrian fossil *Jinkenites zhaoi*. However, in Qian and Bengtson's monograph, *Jinkenites zhaoi* Yu is also attributed to the genus *Canopoconus* Jiang, 1982 (Jiang in Luo *et al.*, 1982: 193; Qian and Bengtson, 1989: 89; Bengtson, 1992a: 403). In fact, *Jinkenites* represents a fossil animal with several anterior marginal spines and peculiar spines on the dorsal side and is entirely different from the genus *Canopoconus* Jiang.

Noting that Bengtson (1992a: 403–404) reconsidered *Canopoconus* Jiang 1982 as a junior

◀ **Figure 10** A–D. *Jinkenites zhaoi* Yu, A. Apical view, showing anterior marginal spines and different kinds of dorsal spines, x 40. B. Oblique apical view, x 50. C. Enlargement of anterior marginal spines, x 180. D. Enlargement of geniculate spines in the posterior part of the body, x 300. Holotype NIGP 83999. Coll. no. HF-1. Upper part of Huangshandong Member of Lower Cambrian Tongying Formation. Huangshandong of Yichang, W. Hubei. E–H. *"Purella" squamulosa* Qian and Bengtson, E. Anterior view, x 30. F. Lateral views, x 75. NIGP 101919. Coll. no. XB-28. G. Lateral view, x 60. H. Apical view, x 40. NIGP 101920. Coll. no. XB-40. Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Baizai of Xundian, E. Yunnan. I–K. *Purella tianzhushanensis* Yu, I. Dorsal view, showing a strongly elevated dorsal ridge and the cancellated sculptues (white arrow), x 75. J. Oblique dorsal view, showing the dorsal ridge, x 80. K. Lateral view, x 55. Holotype NIGP 54453. Coll. no. TF-1. Upper part of Huangshandong Member of Lower Cambrian Tongying Formation. Tianzhushan of Yichang, W. Hubei. L–M. *Stoliconus vomeres* Jiang. L. Lateral view, x 75. M. Dorsal view, x 75. NIGP 84225. Coll. no. KM-7. Upper part of Zhongyicun Member of Lower Cambrian Tongying Formation. Meishucun of Jinning, E. Yunnan. N–O. *Sinuconus clypeus* Yu, N. Dorsal view of an intermediate valve, x 72. O Posteral view, x 40. NIGP 54408. Coll. no. HF-2. Upper part of Huangshandong Member of Lower Cambrian Tongying Formation. Huangshandong of Yichang, W. Hubei.

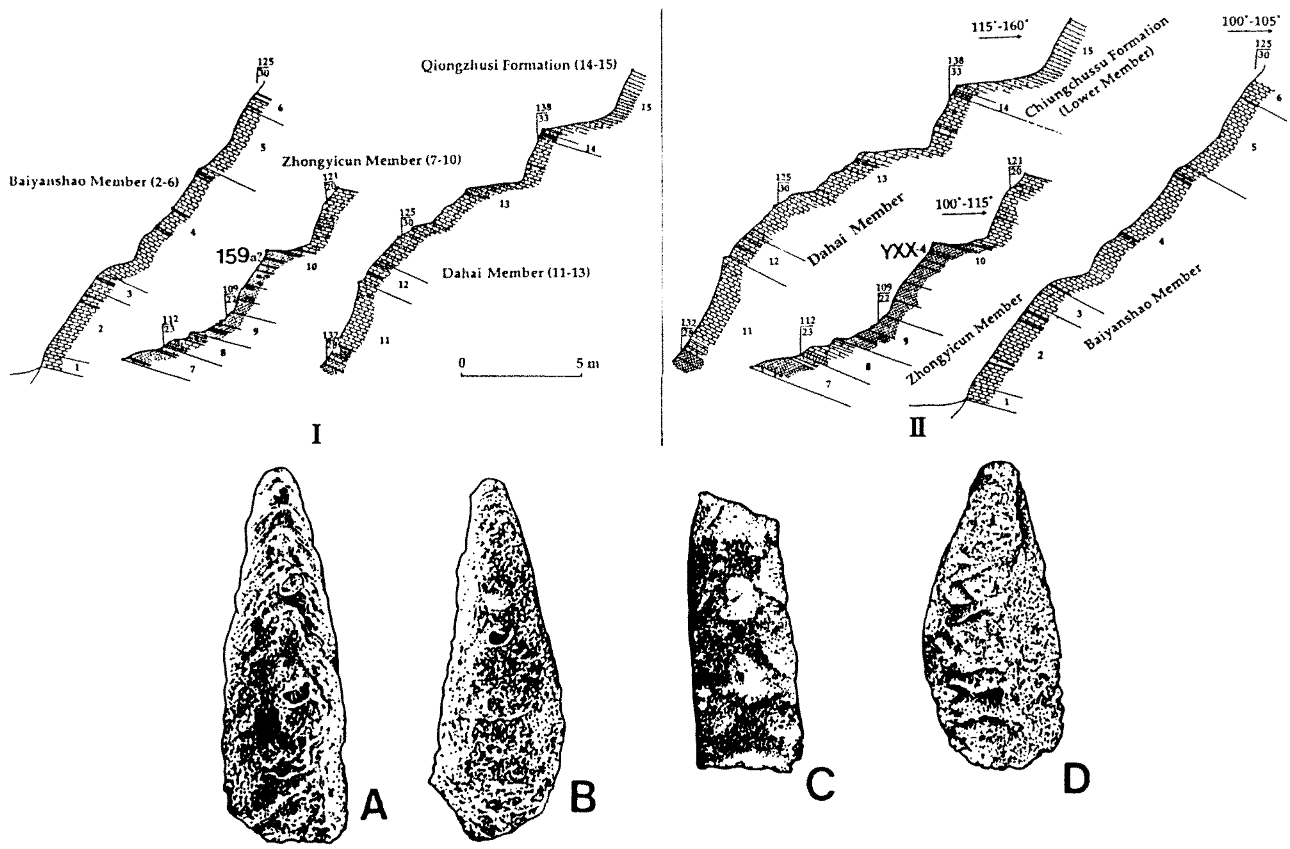

Figure 11 *Paracarinachites sinensis* Qian and Jiang. The collection number of Sample A, x 27 (NIGP 106878) and B, x 30 (NIGP 106882) are 159a. They are collected from Section I (after Qian and Bengtson, 1989, p. 8). The collection number of sample C, x 40 (NIGP 89505) and sample D, x 20 (NIGP 89575) are YXX-4. They are collected from Section II (after Qian, 1989, p. 11).

synonym of *Maikhanella* Zhegallo (Zhegallo in Voronin *et al*., 1982), then a further likely synonym of *Maikhanella calvata* (Jiang) (Jiang in Luo *et al*., 1982: 193, plate 21, figure 1; Qian and Bengtson, 1989: 91, figure 57) is *"Purella" squamulosa* Qian and Bengtson (1989, figure 61; Bengtson, 1992a: 410; Figure 10E–H). Judging from the smooth, rounded apical region and the scaly-surface pattern, there is no great difference between *"Purella" squamulosa* and *Maikhanella calvata* (Jiang). A great number of specimens indicate that they belong to the same genus and possible species, and are different from *Purella*. The latter was established by Missarzhevsky (1974: 184), with *Purella cristata* Missarzhevsky as the type species. The Chinese species *Purella tianzhushanensis* Yu (1979: 253, plate 3, figures 18–19; 1987a, plate 3, figures 14–15; 1987b: 189, plate 37, figures 6–9, Text-figure 56; Figure 10I–K) is closely related to *P. cristata* Missarzhevsky (1974, plate 23, figures 3–5) from the Lower Cambrian Tommotian Stage of Siberian Platform, but differs from the latter in the more bluntly rounded dorsal ridge, in the steeper subapical surface and in having spiral lines. However, in the undeveloped dorsal ridge, smooth and rounded apex and the imbricating scale-like protrusions, *"Purella" squamulosa* is quite different from *Purella cristata* and *P. tianzhushanensis*, but closely resembles these features of the genus *Maikhanella*.

SOME COMMENTS ABOUT THE FOSSIL LOCALITIES AND HORIZONS IN QIAN AND BENGSTON'S 1989 MONOGRAPH

All the fossils described in Qian and Bengtson's monograph were provided by Qian alone. The fossils were collected from the Meishucun section of Jinning and Baizai section and Xianfeng section of Xundian by Yu, Qian and others in 1980. However, in the collection, those fossils from the Meishucun section are labelled from beds 3–13, while all of the specimens from bed 10 of the Xianfeng section bear only one collection number 159a in their monograph. Among the 57 species under their description, 36 species were collected from the Meishucun section, while the remaining 21 species are from only the Xianfeng section. The 36 species from Meishucun section include 9 species, such as *Archiasterella* cf. *pentactina* Sdzuy, *Allonnia*? *tetrathallis* (Jiang), *A. erromenosa* Jaing, *A.? simplex* Jiang, *Halkieria stenobasis* (Jiang), *Sinosachites flabelliformis* He, *Lapworthella rete* Yue, *Tannuolina zhangwentangi* Qian and Bengtson and *Coleoloides typicalis* (Walcott) which have also been found in the Yu'anshan Member of the Chiungchussu Formation. The remaining 27 species separately yielded from the Zhongyicun, Dahai and Badaowan Members of the Tongying Formation. The 21 species from Xianfeng section bearing the collection number 159a are all collected from the Zhongyicun Member of the Xianfeng section (Figure 11, section I). The present writer has some doubts about the locality and horizon of the collection number 159a specimens.

The Xianfeng section, one of the important sections in eastern Yunnan, is near the Damaidi village, about 23 km west of Xundian County. There the writer and Qian together systematically collected the samples (Coll. No. XD 1–4; X = Xundian, D = Damaidi village), based on the study of previous authors, without personally measuring the section. The section has been measured by many people, who collected much material, using glacial acetic acid treatment on the matrix. Some fossils have been extracted from the ore, but only a few are well preserved. This is because the massive phosphorites in the Zhongyicun Member are medium-bedded, compact and solid. However, fine fossils from number 159a are shown in Qian and Bengtson's monograph.

The Baizai section is located about 1 km west of Baizai village which is about 10 km north of Xundian county. This section is a test pit numbered TC 101, where the slopes on both sides are covered with dense vegetation, and the outcrops are very poor. The basal part is composed of argillaceous dolomite; the dolomitic massive phosphorus rocks of the Zhongyicun Member are extremely loose due to strong weathering. Among the material, which was collected by the writer and Qian, and accompanied by Wang Chong-wu and Xu Chong-jiu of the First Geological Survey Team, Geological Bureau of Yunnan Province in December 1980 (Coll. No. XB 1–52; X = Xundian, B = Baizai village), some samples are rather porous, from which very well preserved fossils can be obtained simply by soaking and washing with water, especially specimens of *Yunnanopleura biformis* Yu, *Archaeospira ornata* Yu, *Yangtzespira exima* Yu *and Paracarinachites sinensis* Qian and Jiang. As far as I know, the specimens from the Baizai section are the best preserved ones in eastern Yunnan and in the Yangtze Region.

Qian (1989) published another monograph in which he described 117 species of small shelly fossils. Among them, 19 species were collected from the same section of Xianfeng Phosphorite Quarry in Xundian (Figure 11, Section II). Qian (1989, p. 11) wrote: "The Xianfeng section (Text-figure 5) is located at the Xianfeng Phosphorite Quarry, 23 km. west of Xundian, Yunnan was mapped out in 1981 by Wang Zhao-bi *et al.* and revised by the writer". Huang Zhao-bi (1986), however, is misspelt as Wang Zhao-bi by Qian in Qian and Bengtson's (1989) and Qian's monographs (1989). Most small shelly fossils also occur in the bed 10, the collection number is YXX-4 (Y = Yunnan, X = Xundian, X = Xianfeng phosphorite Quarry, it may be equal to Yu's XD-4) but not collection number 159a in Xianfeng section. The contrast of the fossils between the labelled 159a and those labelled YXX-4 is obviously different, especially as some of the same species were collected from the same horizon in the same section; the features of the fossils are not alike. For example, the species *Paracarinachites sinensis*, with collection number 159a are very beautiful and well-preserved (Qian and Bengtson, 1989, figures 27–28; Figure 11A–B), while the collection number YXX-4 is very poor in preservation (Qian, 1989, plate 44, figures 1–3; plate 45, figures 9–10; plate 48, figures 1–3; Figure 11C–D). In addition, the same results show clearly in the species *Scoponodus renustus* Jiang, *Paragloborilus subglosus* He and *Cyrtochites pinnoides* Qian, etc. What is more, among the plentiful specimens studied by the writer, *Yunnanopleura biformis* Yu, *Archaeospira ornata* Yu, *Yangtzespira exima* Yu and *Paracarinachites sinensis* Qian and Jiang are mainly found in the upper part of the Zhongyicun Member in the Baizai section while those specimens obtained from other sections are poor. Judging from the preservation of the fossils and other aspects, it is reasonable for the writer to consider that Qian's 159a specimens represent a mixed fauna, which comprises not only those fossils from Xianfeng section, but also more specimens probably from the Baizai section.

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