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Early Devonian Conodonts from the Kuan Tung Formation, Thailand: Systematics and Biogeographic Considerations

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ABSTRACT. A small conodont assemblage, obtained from a limestone marking the boundary between the middle and upper units of the Kuan Tung Formation, Satun Province, South Thailand, contains *inter alia* *Pandorinellina steinhornensis steinhornensis*, *Polygnathus labiosus mawsonae* n.subsp., and *Pseudooneotodus kuangtungensis* n.sp., indicating an Emsian age (*perbonus-serotinus* Zones). Studies on ontogenetic variation in Pa elements of *Polygnathus labiosus mawsonae* n.subsp. show that smaller Pa elements have fewer transverse ridges on the posterior third of the platform, more distinct marginal denticulation on the platform and a proportionately smaller basal cavity. The basal cavity lips may break off in mature specimens; this gives an appearance of a small basal cavity. The distribution of *P. labiosus*, *P. pseudoserotinus*, *P. perbonus* and *Pseudooneotodus kuantungensis* n.sp., in the Shan-Thai and South China Terranes, together with supporting evidence from thelodontid and placoderm fishes, suggests that these terranes were in close proximity to the eastern margin of Gondwana at the end of the Early Devonian.

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Little is known of the Devonian conodont faunas from south-east Asia compared to the vast amount of data from Europe, America and Australia. Conodont faunas from Thailand have been listed by Baum *et al.* (1970) and Bastin *et al.* (1977) for isolated localities in the north of the country. Most of these are of Early Devonian age, except for two sites yielding Givetian and Famennian conodonts. None of the localities are from specifically named lithological units, and their stratigraphic relationships are uncertain. Burrett *et al.* (1987) described a limited conodont fauna from the Mae Ping Formation, south of Chiang Mai, establishing a Siluro-Devonian age for a sequence previously thought to be Ordovician. Fortey (in press) reports that a few conodonts including *Icriodus* sp. and *Polygnathus* sp. were recovered from chippings of limestone from preparation of trilobites from Satun Province in the south of Thailand. These come from the same stratigraphic section as the fauna described herein. No icriodids were recovered from

our samples.

The Shan-Thai Terrane (*sensu* Burrett & Stait, 1987) incorporates the eastern side of Burma, the western half of Thailand, parts of Malaysia, the west of Yunnan Province, China, and the small area of Laos between these regions (Fig. 1). Our knowledge of Devonian conodonts from within these boundaries is still small but information from all known assemblages collectively builds up a scenario of the Shan-Thai Devonian conodont fauna. Lane *et al.* (1979, also Alexander & Müller 1963) documented Early-Late Devonian conodont faunas from Batu Gajah, near Perak, Malaysia (Fig. 1), and Metcalfe (1983) described one element of *Polygnathus linguiformis* s.s. from near this area. To date, no conodonts have been described from Burma or the Shan-Thai region of Laos. Recently Wang *et al.* (1986) described Middle Devonian thelodont scales from Shidian, Western Yunnan (Fig. 1) and listed the major conodont species occurring in the section, from Lower Devonian (*serotinus* Zone) to the base of the Upper Devonian (*asymmetricus* Zone) in age.

Conodonts studied in this paper were obtained from a limestone horizon in the Kuan Tung Formation, Satun Province during fieldwork by Burrett & Wongwanich in 1987. The complete stratigraphic section, with precise locality details for measured stratigraphic sections, has been described by Wongwanich *et al.* (in press), and has been designated a type section for the Devonian in South Thailand. Many samples have been taken for detailed biostratigraphic work, but the results of these studies will not be available for some time. This work describes a limited conodont fauna of some 114 elements collected from the Kuan Tung Formation and discusses the biogeographic implications of the fauna. The precise locality of the sample is from an exposure of the Kuan Tung Formation in a pararubber plantation 10 km north of Langu (grid ref. 7000, 8500, Amphoe Langu 1:50,000 sheet).

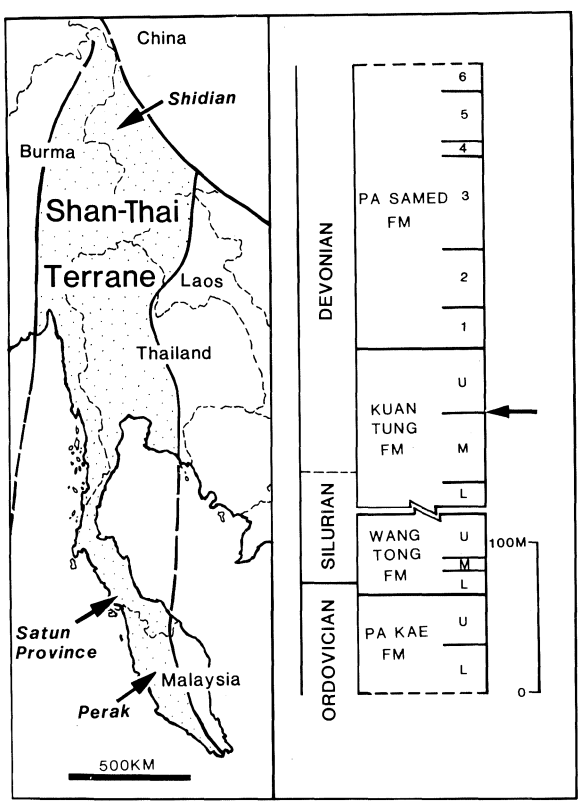

Fig.1. Map showing boundaries of Shan-Thai Terrane and localities mentioned in text. Part of the stratigraphic column of Satun Province is shown on the right with an arrow indicating the horizon where the conodont sample was collected.

Systematic Palaeontology

Only the Pa elements of polygnathids are described. Specimens are housed in the collections of the Geology Department, University of Tasmania (UTGD). All material was photographed by the Scanning Electron Microscope with tilt adjustments correcting optical distortions.

Belodella (Pander, 1856)

Belodella devonica Stauffer

Figs 2.4, 2.6

Remarks. Few specimens are well preserved, but all of them show the biconvex cross-section and gently tapering shape characteristic of this species.

Material examined. 9 specimens (UTGD 123739-123747).

Belodella resima (Philip 1965)

Figs 2.1

Remarks. This species is identified by the triangular cross-section and well-defined crista bordering the outer margin. The illustrated specimen shows the characteristic strongly incurved tapering point.

Material examined. 3 specimens (UTGD 123748 - 123750).

Drepanodus Pander, 1856

Drepanodus sp.

Figs 2.2, 2.3, 2.5

Remarks. These drepanodiform elements are characterised by their compressed basal cross-section and slightly flared base.

Material examined. 5 specimens (UTGD 123713-715; 123753-754).

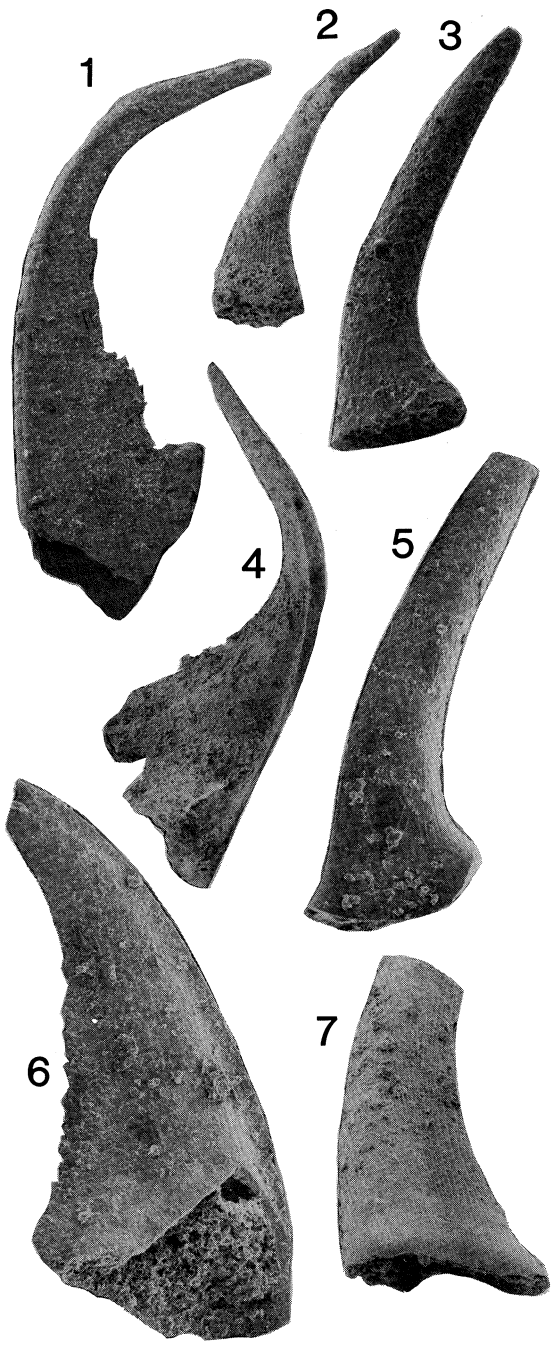

Fig.2. 1, *Belodella resima* (Philip), UTGD 123478, x57. 2, 3, 5, *Drepanodus* sp. 2, UTGD 123753, x70; 3, UTGD 123713, x143; 5, UTGD 123714, x131. 4, 6, *Belodella devonica* Stauffer. 4, UTGD 123739 x50; 6, UTGD 123740, x126. 7, *Panderodus* sp., UTGD 123756, x140.

Panderodus Ethington, 1959

Panderodus sp.

Fig. 2.7

Remarks. The few, incomplete specimens in the material resemble *P. acostatus* in the cusp being gently recurved and lacking the longitudinal carina seen in *P. unicostatus*. The lateral faces are somewhat rounded and the base of the unit is compressed in cross-section.

Material examined. 2 specimens (UTGD 123755-756).

Pandorinellina Müller & Müller, 1957

Pandorinellina steinhornensis steinhornensis (Ziegler, 1956)

Fig. 3, Fig. 4.1, 4.2, 4.5, 4.6, 4.10.

Remarks. This species is readily identified by the even denticulation of the blade and the widely flared, asymmetric basal cavity located closer to the posterior half of the unit. Lane *et al.* (1979) noted a new subspecies of *P. steinhornensis* from Perak, Malaysia, occurring in the *gronbergi-dehiscens* Zones. Our specimens, however, differ from the Malaysian subspecies in having a broader basal cavity in an off-central position along the blade. One specimen (Fig. 4.5, 4.6) has a more rounded basal cavity outline than all others, but in other respects falls within the normal range of variation for the species. In Australia *P. steinhornensis steinhornensis* has been recorded from the Lilydale Limestone (Philip & Pedder 1967); however these specimens have a large basal cavity which extends to the posterior end.

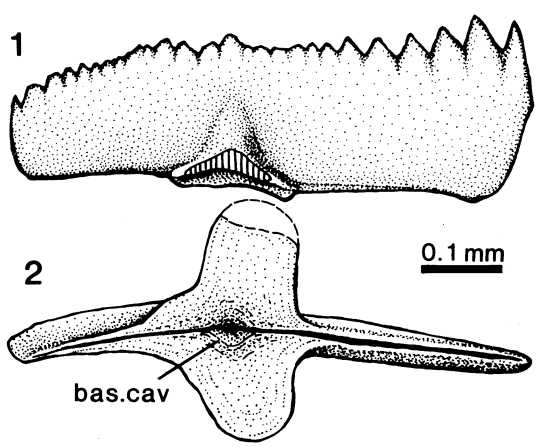

Fig.3. *Pandorinellina steinhornensis steinhornensis*, typical morphotype from Kuan Tung Fm, UTGD 123680. bas.cav - basal cavity.

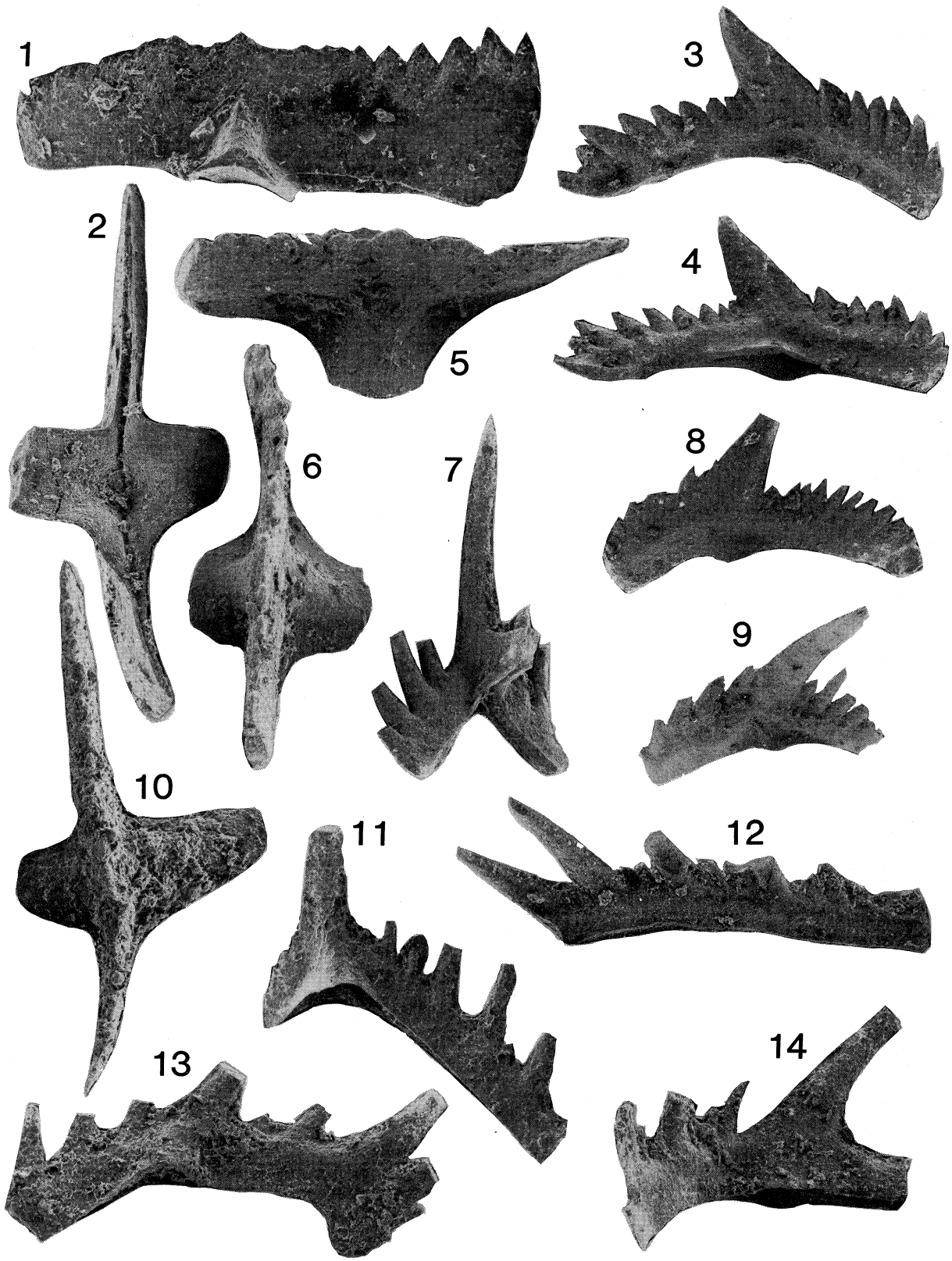

Fig.4. 1, 2, 5, 6, 10. *Pandorinellina steinhornensis steinhornensis*. 1, 2, UTGD 123680, x 150. 5, 6, UTGD 123682, x 170. 10, UTGD 123679, x 170. Unassigned polygnathid and ozarkodinid elements: Pb elements -3, 4, UTGD 123697, x 140; 8, UTGD 123698, x 140; 9, UTGD 123699, x 140. Sa element - 7, UTGD 123702, x 140. M element - 11, UTGD 123706, x140. Sc element - 12, UTGD 123705, x 140. Sb elements - 13 (polygnathid), UTGD 123701, x 150; 14 (ozarkodinid), UTGD 123707, x 140.

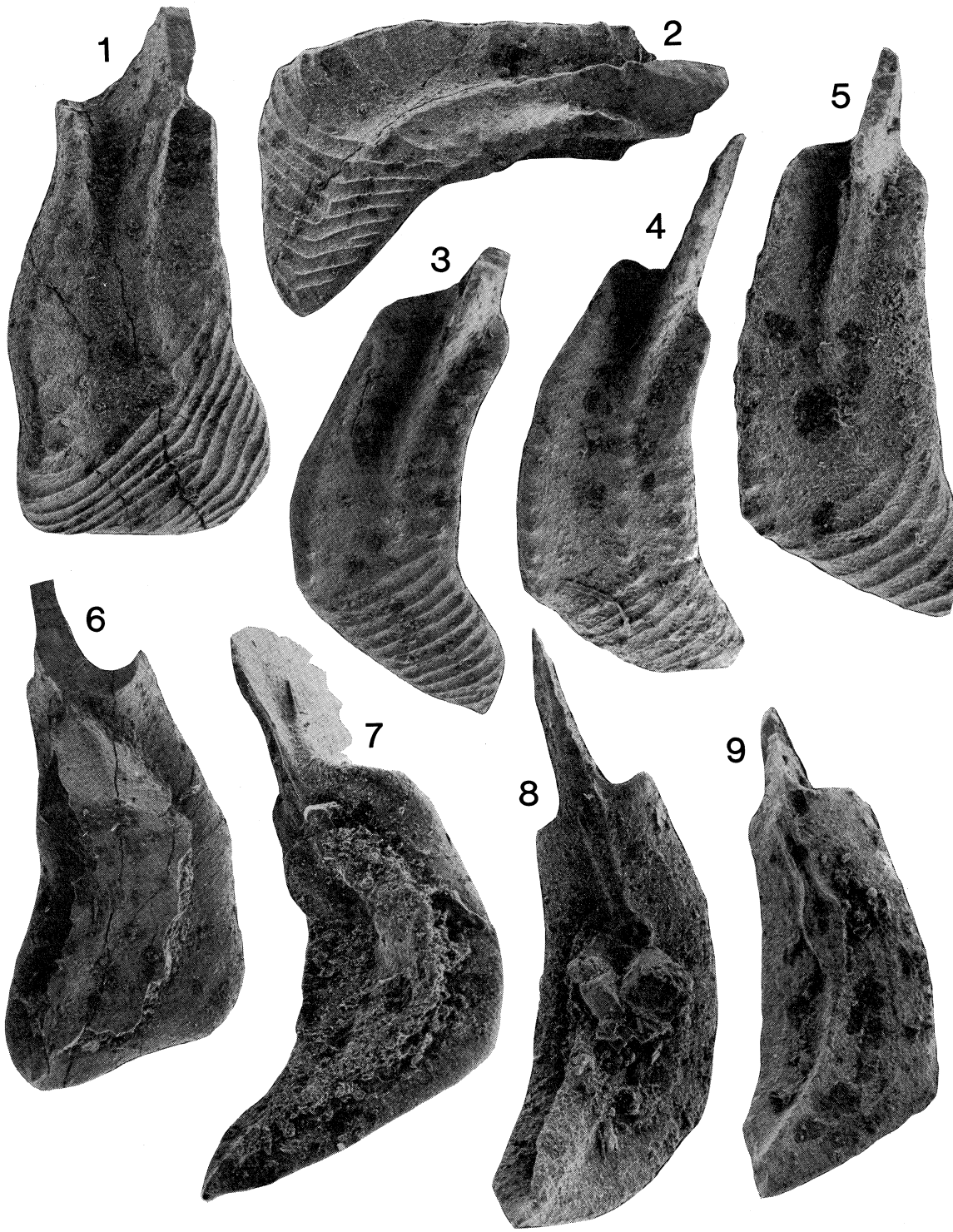

Fig.5. *Polygnathus labiosus mawsonae* n.subsp. 1, 2, 6, paratype UTGD 123643, x 76 (lips of basal cavity well preserved). 3, 7, holotype UTGD 123642, x 78 (anterior region of free blade damaged during handling: absent in 3); 4, 8, paratype UTGD 123644, x 78 (lips of basal cavity partially broken off); 5, 9, paratype UTGD 123645, x 101 (lips of basal cavity completely broken away).

Material examined. 11 specimens (UTGD 123672-682).

Polygnathus Hinde, 1879

Remarks. Klapper (*in* Ziegler, 1973) discussed the genus, and Mawson (1987a) reviewed the Australian Lower Devonian species.

Polygnathus labiosus Mawson 1987a

Polygnathus labiosus mawsonae n.subsp.

Figs 5, 6, 7

Etymology. For Dr Ruth Mawson, Macquarie University, Sydney.

Diagnosis. Pa elements of *P. labiosus* in which the posterior third of the platform is particularly broad and is ornamented with closely-spaced parallel transverse ridges which rarely bifurcate; the anterior margin of the platform is narrower than the broadest part of the posterior end of the platform; and the inner and outer margins have weak denticulation. The basal cavity has a rounded anterior margin.

Material examined. 30 specimens. HOLOTYPE: UTGD 123642 [Fig. 5(3,7); Fig. 6(1,2)]. PARATYPES: UTGD 123643 [Fig. 5(1,2,6); Fig. 6(3)], UTGD 123644 [Fig. 5(4,8)], UTGD 123645 [Fig. 5(5,9)], UTGD 123646. Other material UTGD 123647-123671, plus several unregistered broken Pa elements.

Remarks. The Pa elements of this species are identified by the flaring lips on the large relatively flat to concave basal cavity with the basal aperture situated well anterior of the strong inward deflection of the platform. The flared lips are not basal filling but true extensions of the basal cavity rims.Close examination of the lips shows that the surface is smooth and lacking the spongiose texture of basal filling, and that when a specimen is dissected the cross-section shows the outward extension of the rims of the basal cavity.The outer margin is strongly convex.The carina (car, Fig. 6) is weakly developed on the platform and ends about halfway along the the platform. The posterior half of the platform has gently convex margins. The outer platform anterior margin is lower than that of the inner platform. The ornamental ridges on the inner and outer platform margins are weakly developed, and there is a broad smooth area between the end of the carina and the posterior region of the outer platform.

Our specimens differ from those figured from the type

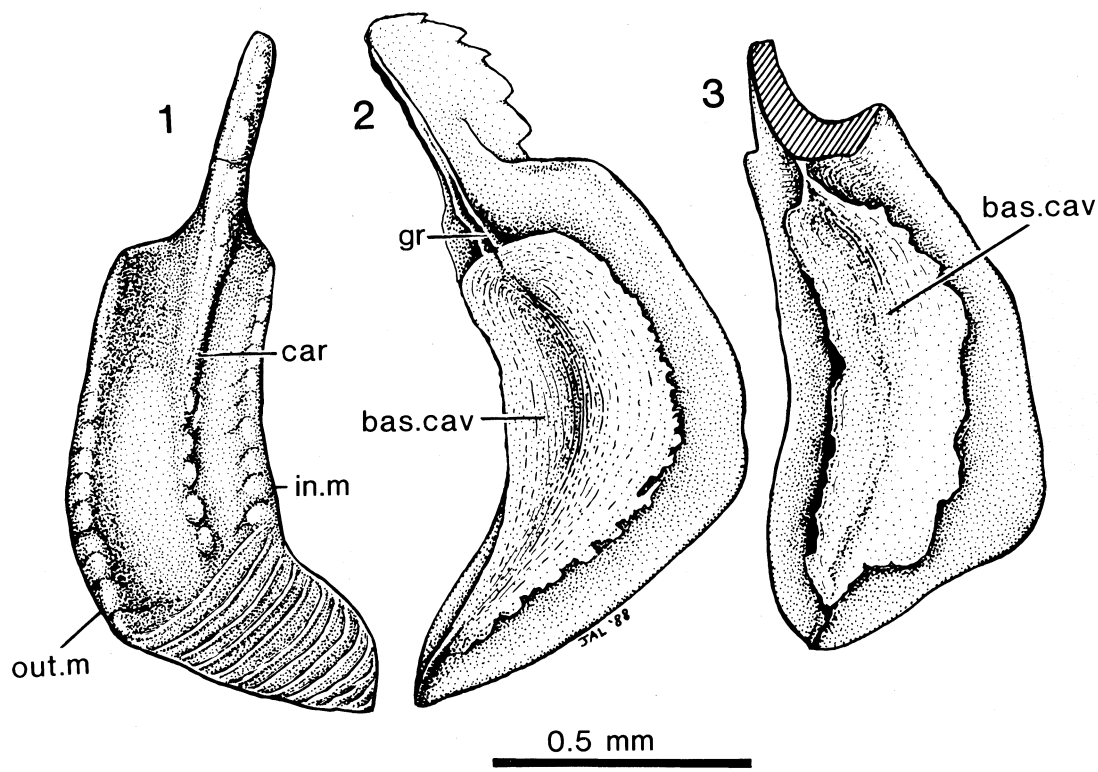

Fig.6. *Polyganthus labiosus mawsonae* n.subsp., large Pa elements. 1, 2, Sketch of holotype UTGD 123642 showing main features, basal cavity partially restored to full shape (note: the anterior region of free blade was present when this sketch was done). 3, basal view of paratype UTGD 123643. bas.cav - basal cavity; car - carina; gr - basal groove; in.m - inner margin; out.m - outer margin.

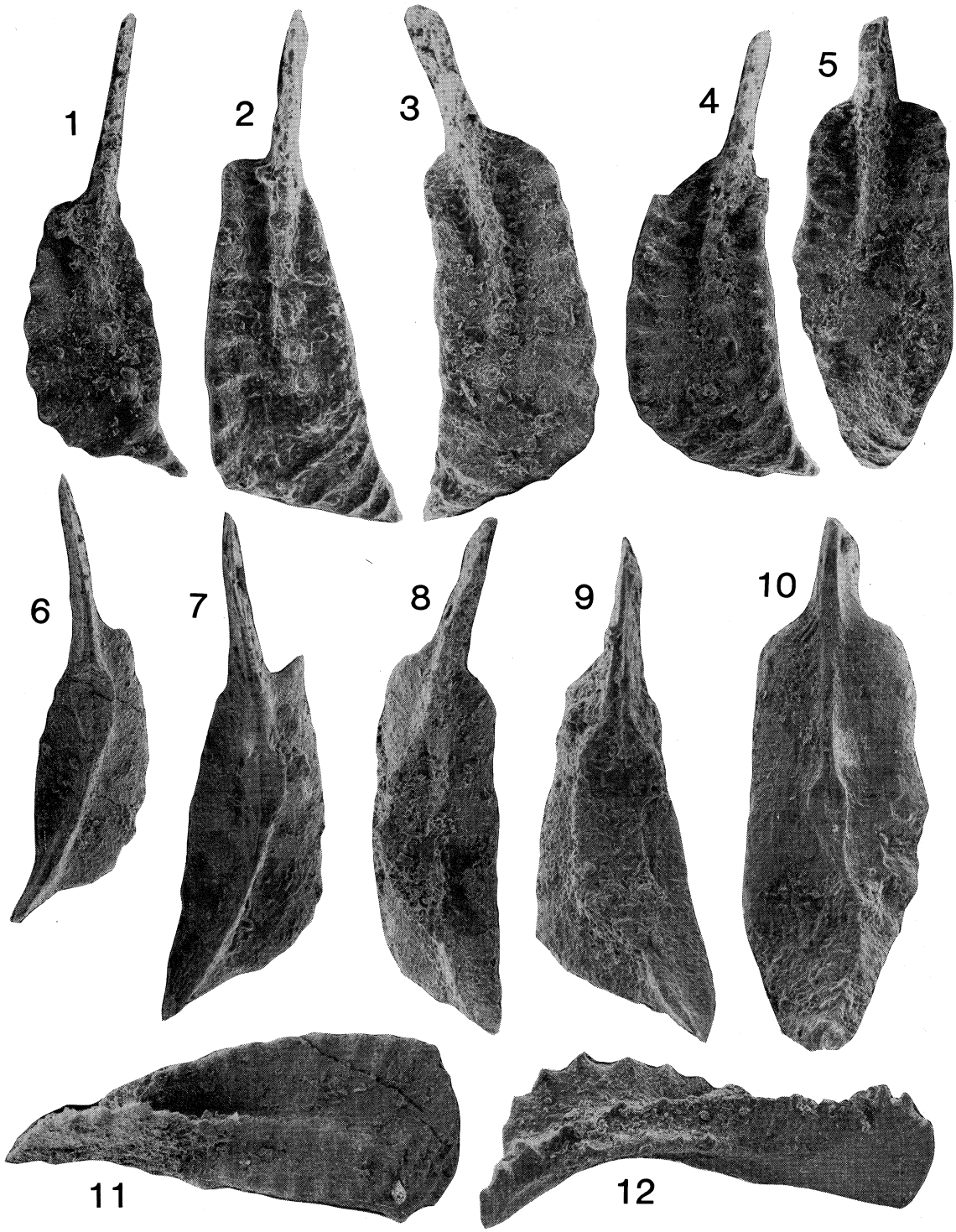

Fig.7. *Polygnathus labiosus mawsonae* n.subsp. Small specimens of Pa elements. 1,2,12, UTGD 123647, x 131; 2, 7, UTGD 123648, x 120; 3, 8, UTGD 123649, x 131; 4, UTGD 123650, x 130; 5, 10, UTGD 123651, x 101; 9, UTGD 123652, x 130; 11, UTGD 123653, x 101.

locality, Buchan, eastern Victoria, in the posterior third of the platform having a broader shape and being considerably broader than the anterior margin of the platform, generally having a larger basal cavity in the biggest elements, and a weaker development of the marginal denticulation. In addition, the anterior margin of the basal cavity is more rounded in the Thai specimens, whereas in *P. labiosus* s.s. the basal cavity tapers anteriorly (Figs 10-12). Most of the Thailand specimens have a strongly deflected platform which has many fine transverse ridges, and only one specimen (Fig. 5.1) has bifurcation of the transverse ridges on the posterior third of the platform. None of the specimens illustrated by Mawson (1987a, pl.35, figs 1-9, pl.36, figs 3,4) show the posterior half of the platform being as broad as the anterior margin, which is the reverse of the case in the Thailand specimens.

The range of variation seen in *P.labiosus mawsonae* n.subsp., is shown in Figures 5, 6, 7 and 10, and ontogenetic variation in the subspecies is discussed below. One specimen (Fig. 5.1, 5.2, 5.6) is particularly broad across the posterior half of the platform and shows an irregular pattern of transverse ridges, some of which are not continuous accross the breadth of the platform. Specimens which appear to have a small basal cavity similar to *P. linguiformis* s.s., but resemble *P. labiosus mawsonae* in all other features have breakage of the flared margins of the basal cavity away from the platform. This was demonstrated by manual dissection of a specimen (UTGD 123671) which displayed a well-preserved basal cavity with flared margins.

Initial examination of our polygnathid Pa elements indicated that perhaps two species were present: a large form with broad flared basal cavity and numerous ridges on the posterior third of the platform, and a smaller form with small basal aperture and fewer ridges on the platform. However, measurements of the platform size versus the basal cavity size indicates that we are dealing with only one species, and the observable differences in form is attributable to either ontogenetic variation or post mortem damage. Juvenile forms show a proportionately smaller basal cavity and the outline of the Pa element is broader and more rounded (Fig. 10). With increased growth the tongue acquires more transverse ridges and projects posteriorly, whilst the marginal denticulation becomes less distinct. The basal cavity develops as a broad posterior expansion of the lips which seam together in the posterior half of the element (Fig. 10.9, 10.10). Large specimens show either good preservation of the broad basal cavity (Fig. 5.6, 5.7, 5.8) or have the lips broken off, leaving a small basal aperture visible (Fig. 5.9, Fig. 7.10). Statistical representation of this phenomenon is shown in Figure 11 which plots the length of the basal cavity/length of the platform versus the platform length, and shows the morphological development of transverse ridges on the platform in parentheses. The bottom line on this graph shows elements in which the flared lips have broken off, whereas the top line represents well-preserved specimens with basal cavity rims intact. Examination of these specimens shows coarse sediment between the flared lips and the aboral surface of the platform (Fig. 5.7).

Such studies have implications to conodont taxonomy. For example, some of our smaller specimens fall within the morphological range of *Polygnathus linguiformis bultyncki* (e.g. Fig. 7.1, 7.2, 7.6, 7.7) or other *P. linguiformis* morphotypes. If growth sequences were not identified we could have assigned these elements to different taxa, and this indicates the need for further studies of growth

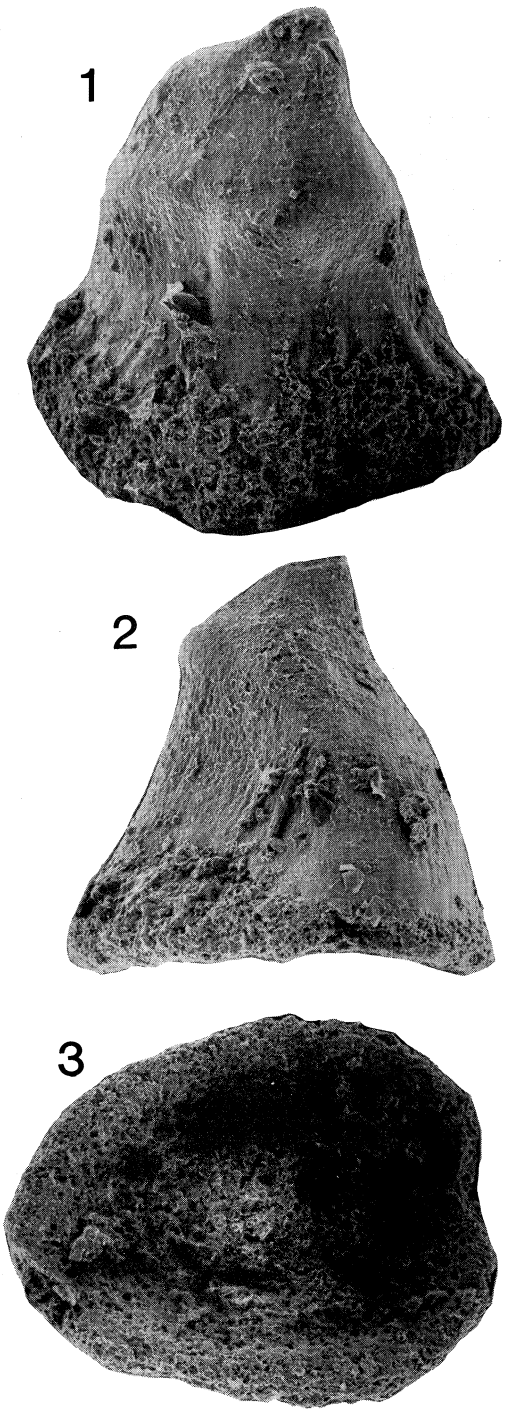

Fig.8. *Pseudooneotodus kuantungensis* n.sp. 1, holotype UTGD 123730, x 160; 2, paratype UTGD 123729 x 160; 3, paratype UTGD 123731, basal view, x 160.

sequences in polygnathid taxa to evaluate their taxonomic status. The changes in number of ridges and different development of the carina in *P. linguiformis linguiformis* morphotypes (Ziegler, 1977) would indicate some degree of heterochronic change, such as paedomorphosis (McNamara, 1986), in the evolution of such lineages.

Pseudooneotodus Barrick & Klapper, 1977

***Pseudooneotodus kuangtungensis* n.sp.**

Figs 8, 9

Gen. et sp. indet. A... Philip, 1965: 113, pl.1, figs 1-4.

Etymology. After the Kuan Tung Formation, the type stratum.

Diagnosis. Small (0.3-0.7mm) conoidal elements having an expanded elliptical concave base which is broader than long, tapering to a pointed crown which is separated from the base by a thickened rim. In profile the denticles have gently concave sides.

Material examined. 23 specimens. HOLOTYPE UTGD 123730 (Fig. 8.1). PARATYPES UTGD 123729 (Fig. 8.2), UTGD 123731 (Fig. 8.3). Others UTGD123716-123738 (123735-738 are thin-sections).

Remarks. Philip (1965) described and figured similar elements from the Tyers Limestone, Victoria, but was not sure whether they were conodonts. He referred to other occurrences of these enigmatic cones from the Upper Silurian and Lower Devonian of Europe (Bischoff & Sanneman 1958, Jentzsch 1962). Bischoff & Sanneman (1958) regarded their specimens as detached basal cones of an oistodid conodont, but Philip pointed out that they are composed of a similar substance as the outside surface of conodonts, so cannot be basal cones. Jentzsch tentatively referred the cones to the conodont *Oneotodus* (now *Drepanodus*, Hass 1962) but expressed doubts as to their conodont nature. Uyeno & Mason (1975) described similar cone-like structures which were identified as acodiniform elements of a a new conodont species, *Pelekysgnathus pedderi*. These differ morphologically from *Pseudooneotodus kuantungensis* by their more elongate shape and absence of a well-defined rim marking off the crown from the base, and their occurrence with other elements recognisable as icriodiform. Despite having over 20 elements of this shape, there are no icriodiform elements associated with these in our samples. Thin-sections of our specimens confirm that they are conodonts rather than the dermal denticles of primitive placoderm or elasmobranch fishes. The walls thicken apically and have a multilaminate structure, thus agreeing with the generic diagnosis of Clark *et al.* (1981) - "...stout cones with a deep basal cavity; walls thicken apically, relatively smooth surface". Our elements agree in all respects with this definition, and as they differ morphologically from the two established species, *P. bicornis* and *P. tricornis*, we here erect a new species.

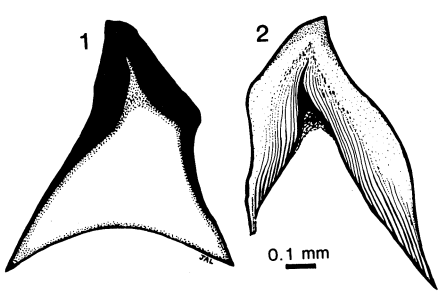

Fig.9. *Pseudoneotodus kuantungensis* n.sp. Sketch of thin-sections of UTGD 123735 (1) and UTGD 123736 (2) showing walls thickening apically and multilaminate structure of apex.

Pseudooneotodus kuantungensis n.sp., which has only one point on the apex, differs from the type species *P. bicornis*, which has two apices, and from *P. tricornis*, which has three apices, mainly by the well defined neck which separates the pointed apex from the stout sides. This feature is clearly visible in the specimens figured by Philip (1965, pl.1, figs 1-4).

It is probable that *P. kuantungensis* (Lochovian-Emsian) is derived from the twin-pointed form *P. bicornis* (Wenlockian), which is probably derived from the stratigraphically younger triple-pointed form, *P. tricornis* (Llandoverian-Wenlockian; Barrick & Klapper 1976; Barrick, 1977).

Biogeographic Implications

Although many conodont species have cosmopolitan distributions, there is a high degree of endemism exhibited by groups of species for specific time periods (Fåhraeus, 1976; Telford, 1979; Charpentier, 1984). Klapper & Johnson (1980) found that the Early Devonian was a time of high endemism for certain conodont species, and this endemism continued until late in the Middle Devonian, when cosmopolitan species start to outnumber the endemic species. Mawson (1987a) revised the taxonomy of certain Early Devonian polygnathids with large basal cavities, and in her review of *P. perbonus* found that most non-Australian occurrences of this species could be referred to her new species, *P. nothoperbonus*. The closely related species *P. perbonus*, *P. labiosus* and *P. pseudoserotinus* are thought to be derived from *P. dehiscens abyssus*, which occur mainly in Australia (Mawson, 1987a). Another new species, *P. pugiunculus* from Queensland, is probably derived from *P. pseudoserotinus* (Mawson, 1987b). The only occurrences of any of these species outside Australia are of *P. perbonus* from the South China Terrane (Wang, 1981, Wang & Ziegler, 1983) and from central Tadzhikstan (Karakum Terrane, Bardashev, 1986), and

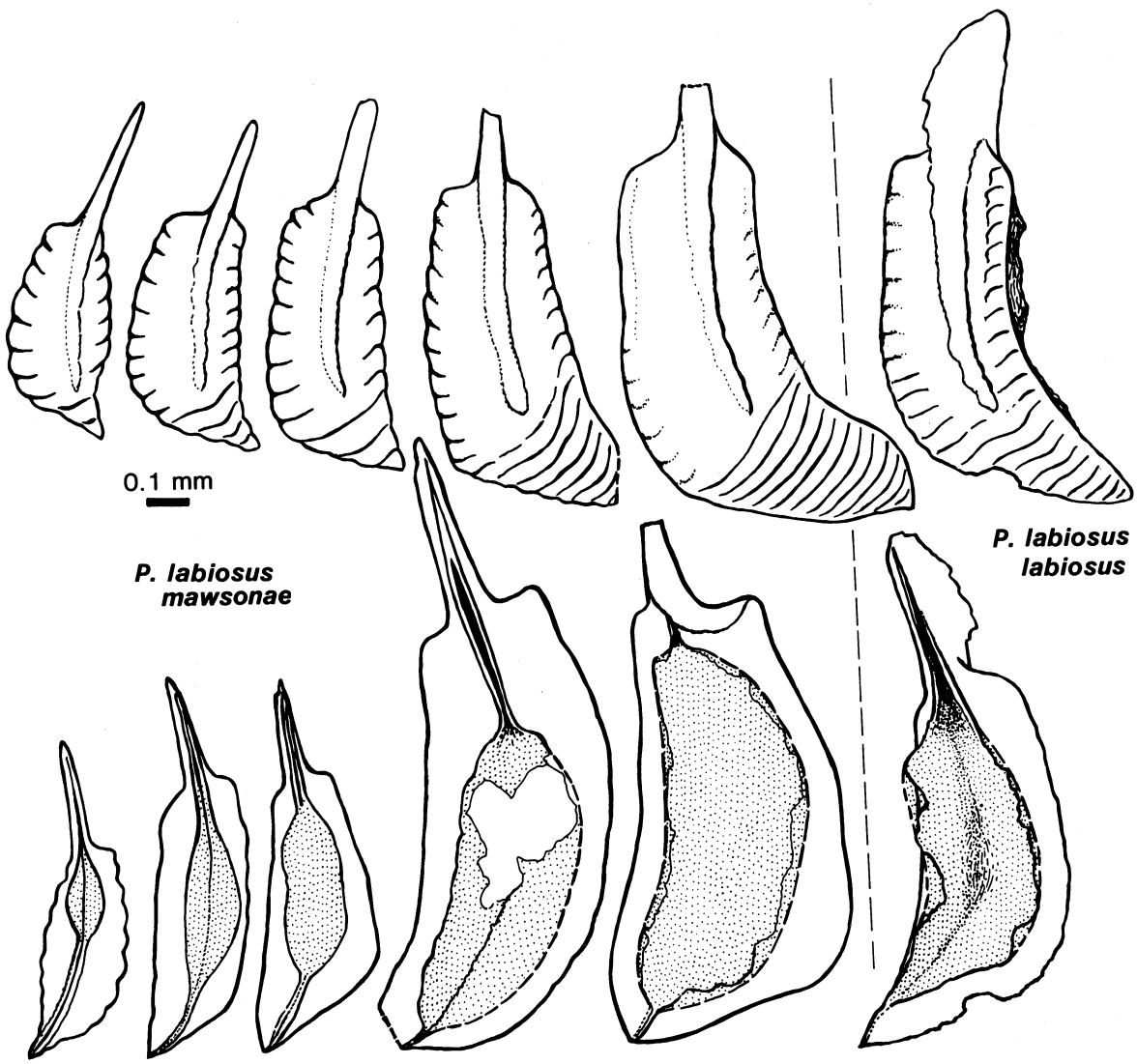

Fig.10. 1-10, ontogenetic variation in *Polygnathus labiosus mawsonae* n.subsp. showing oral and aboral surfaces, basal cavities stippled. 11, 12, an early form of *P. labiosus labiosus* (after Mawson, 1987a: pl.35, figs 1, 2). Note that upper and lower sketches do not correspond to the same specimens (see photos for specimen numbers).

P. pseudoserotinus from Perak, Malaysia by Lane *et al.* (1979; Mawson, 1987a: 277). *Polygnathus declinatus* (Wang, 1979) from the Lower Devonian of South China is either synonymous with *P. pseudoserotinus* or may be a transitional form of *P. inversus* (Mawson, 1987a: 278). *Polygnathus declinatus* would have priority over *P. pseudoserotinus* if there is no 'seaming-up' of the basal cavity. The lineage or clade of polygnathids including *P. dehiscens abyssus* through to *P. pseudoserotinus* most probably originated in the East Gondwana Province, and the only other outside occurrences are from the South China Terrane, the Karakum Terrane (*P. perbonus*; uncertain Devonian palaeoposition), and the Shan-Thai Terrane (*P. pseudoserotinus*). Furthermore, *Pseudooneotodus kuangtungensis* n.sp. is also known only from the Lower Devonian of Thailand and Australia. In a diverse group with generally cosmopolitan distribution, such as polygnathids, the regional restriction of a major clade probably has biogeographic significance. Either these species have not been recognised in other samples, which is highly unlikely given the amount of conodont sampling which has been going on; or alternatively, the group of species in question were restricted to an area encompassing the East Gondwana Province and the Shan-Thai and South China Terranes.

A further test of this hypothesis is to examine the distribution of other groups of taxa showing widespread distribution to see if the pattern of their Early Devonian or later distributions corroborates that of the polygnathids. One such group, the thelodontid agnathans, demonstrates a similar distribution. The species *T. pagoda* (Wang *et al.*,

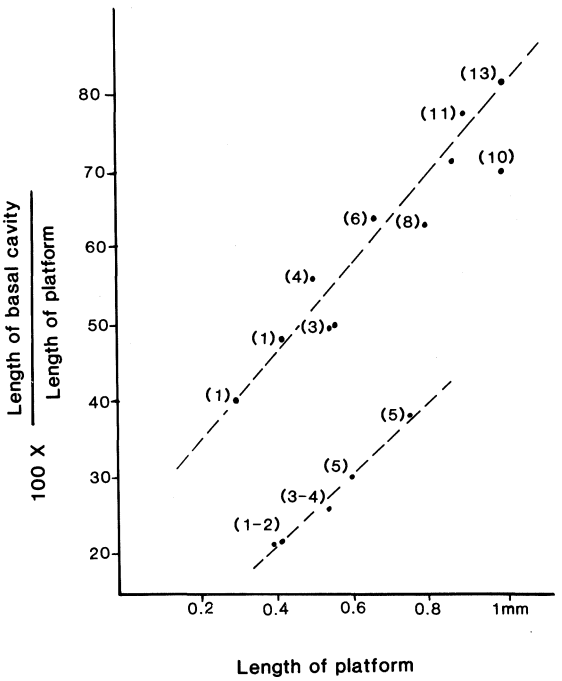

Fig.11. Graphical representation of increasing size of basal cavity with growth for *Polygnathus labiosus mawsonae*. The top line shows specimens preserved with basal cavity complete; the bottom line shows specimens with basal cavity lips broken off, giving the appearance of a smaller basal aperture. Numbers in parentheses refer to number of transverse ridges on the posterior third of the platform. Length of platform measured from ocular of microscope.

1986) occurs in Shidian, west Yunnan (Shan-Thai Terrane, there is good evidence that the Chinese and Shan-Thai Terranes were attached to Gondwana during the Early Palaeozoic (Burrett & Stait 1986, 1987) these Devonian occurrences lead us to suggest that the Shan-Thai Terrane was still in close contact with the eastern margin of Gondwana during the Early and Middle Devonian, as proposed by Bunopas (1981). The South China Terrane was close to these Terranes, and remained so until at least the end of the Devonian as evidenced by the distributions of Late Devonian terrestrial fish, e.g. sinolepids in the Late Devonian of Australia (Hunter Siltstone, NSW), South China and Ningxia (Young, 1987; Pan Jiang, 1987). Further Late Devonian evidence of proximity between the Shan-Thai, East Gondwana and South China Terranes comes from recent new finds of microvertebrates from Northern Thailand. This fauna contains similar species of the chondrichthyan *Phoebodus* from Queensland, Thailand and South China, as well as a peculiar new shark genus only known from South China and Thailand (Long, in press). Figure 12 shows the distribution of endemic polygnathids with large basal cavities on a modified Devonian base map in which the Shan-Thai, North and South China Terranes are located within the palaeolatitudinal controls indicated by Heckel & Witzke (1979), but placed closer to the eastern margin of East Gondwana, as suggested by faunal comparisons. Further descriptions of Shan-Thai Devonian faunas are needed to refine this model and delineate the relationships between East Gondwana, Shan-Thai and the Chinese Terranes (North and South China, Tarim, Quaidam etc.) for stages in the Devonian.

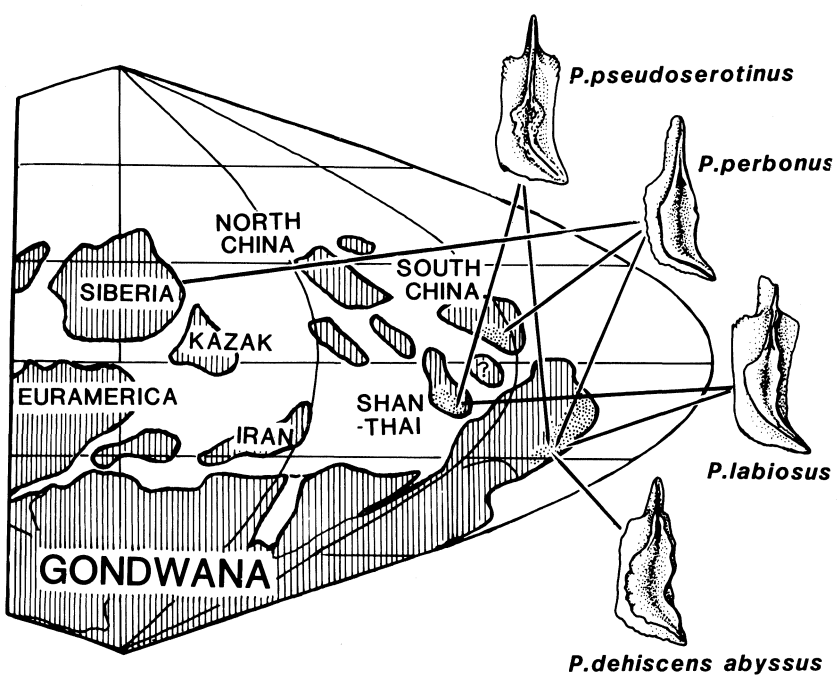

Fig.12. Distribution of certain endemic polygnathid species shown on a modified palaeogeographic base map for the Devonian (after Heckel & Witzke, 1979). Placement of South China, North China, Shan-Thai Terranes is closer to East Gondwana than for previous reconstructions, based on faunal comparisons discussed in text. The small terrane with a question mark between Shan-Thai and South China is the Indo-China Terrane. Polygnathid sketches after Mawson (1987a).

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