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The musculature and vascular systems of two species of Cambrian Paterinide (Brachiopoda)

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Two species of Paterinide brachiopod preserving details of the musculature and vascular systems have been studied. Their dorsal valves are shown to have a large quadripartite muscle field not unlike that of the articulates with further scars located on the inner face of the apex of the homeochilidium. The dorsal vascular system is possibly saccate (apocopate). The ventral muscle field has two short subtriangular scars divided from one another by the proximal portions of main vascular canals. The location of other scars is uncertain. The ventral vascular system is probably saccate.

Introduction

The paterinides are an enigmatic group of brachiopods that have customarily been assigned to the Inarticulata because they lack tooth and socket articulation and possess phosphatic shells. Their relationship to other brachiopod groups has long been problematical, a dilemma partly caused by the paucity of knowledge of their musculature and vascular systems.

During a study of Early and Middle Cambrian faunas from central Australia two species of paterinide exhibiting relatively well-preserved interiors were recovered from acid residues. Their internal structures are described herein.

Acknowledgements

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Localities

Two groups of specimens are studied herein. The first is referable to *Paterina* sp. and comes from locality H583 in the Middle Cambrian Arthur Creek Formation of the southwest Georgina Basin (136°07′00″E, 22°35′45″S, Huckitta 1:250 000 Sheet SF53-11). The second belongs to a new genus and species, here referred to aff. *Dictyonina* sp., and was found at locality NT600 in the late Atdabanian (Laurie & Shergold, 1985) Todd River Dolomite of the northeast Amadeus Basin (134°18′40″E, 24°2′00″S, Rodinga 1:250 000 Sheet SG53-2).

Previous work

Walcott (1912, p. 333) noted meagre details of the interiors of several species of paterinide, with the dorsal valve of one species (*Micromitra* (*Iphidella*) *pannula ophirensis*) exhibiting 'a median ridge, the base of the main vascular sinuses and two central muscle scars.'

Bell (1941, p. 211), in discussing the species *Iphidella hexagona*, noted that the pattern of internal callosities in the species 'remotely resembled the distribution of muscle attachment sites in the most primitive calcareous 'articulates''. He suggested that, in the ventral valve, the median callosity may have been the site of 'adductor' attachment with the pair of callosities anterior to it bearing the 'diductors'.

Williams & Rowell (1965, p. H127) and Rowell (1965, p. H294) reviewed knowledge of the internal structure of members of the group. They concluded that all the scars were narrowly triangular and radiated from the apices of their respective valves. In the ventral valve, two narrow slightly divergent tracks extended from the beak to near the valve mid-length, whereas in the dorsal valve two pairs of tracks radiated from the beak, a longer pair extending to near the valve mid-length, forming a single median depression, and a shorter pair diverging anterolaterally.

More recently, Rowell (1980, p. 18), in studying etched material of *Dictyonina pannula* (White), generally reiterated the view that the ventral muscle field is elongate triangular, but noted that it was divided into three sectors by long, slightly divergent troughs, which he suspected were mantle canals.

Descriptions and interpretations

***Paterina* sp.** (Plate 1, figs 1–14, Plate 2, figs 1–11)

The ventral interior has a low broad median ridge that bifurcates anteriorly and a pair of very low indistinct submedian ridges that, a short distance anterior to the umbo, curve abruptly to become subparallel to the median ridge or ridges. These ridges are interpreted as bounding a pair of broad subparallel vascular canals, as advocated by Rowell (1980, p.18). Anteriorly, these canals appear to curve laterally, becoming concentric (see Plate 1, figs 12, 13; Plate 2, figs. 2, 9), subsequently giving rise to many radially disposed terminal branches (see Plate 1, figs. 13, 14; Plate 2, figs. 1, 6–9).

Lateral to the submedian ridges in the posterior fifth (or less) of the valve are two short, triangular areas, which, in some specimens, are thickened (Plate 1, fig. 13; Plate 2, fig. 2), and, in others, have a well-developed concentric growth lineation (Plate, 1, fig. 12; Plate 2, figs. 2, 3, 8) or are bounded anterolaterally by low ridges (Plate 2, figs. 4, 6, 7, 11). These triangular areas are interpreted as the major ventral muscle scars, possibly homologous with the diductors of the articulates.

Indications of other scars are less clear. Possible candidates are found as depressions inserted between the branches of the median ridge (Plate 1, fig. 13; Plate 2, fig. 2) or as thickenings in the same area (Plate 2, fig. 5). It is also conceivable that the area between the major muscle scars in the apex of the valve was occupied by muscle attachment sites. In some specimens, this area is quite deeply impressed (Plate 1, figs. 12, 13; Plate 2, figs; 2, 3, 7, 8) and occasionally appears to be separated from the proximal parts of the main vascular canals by low transverse ridges (Plate 1, figs. 12, 13; Plate 2, figs. 3, 6, 7).

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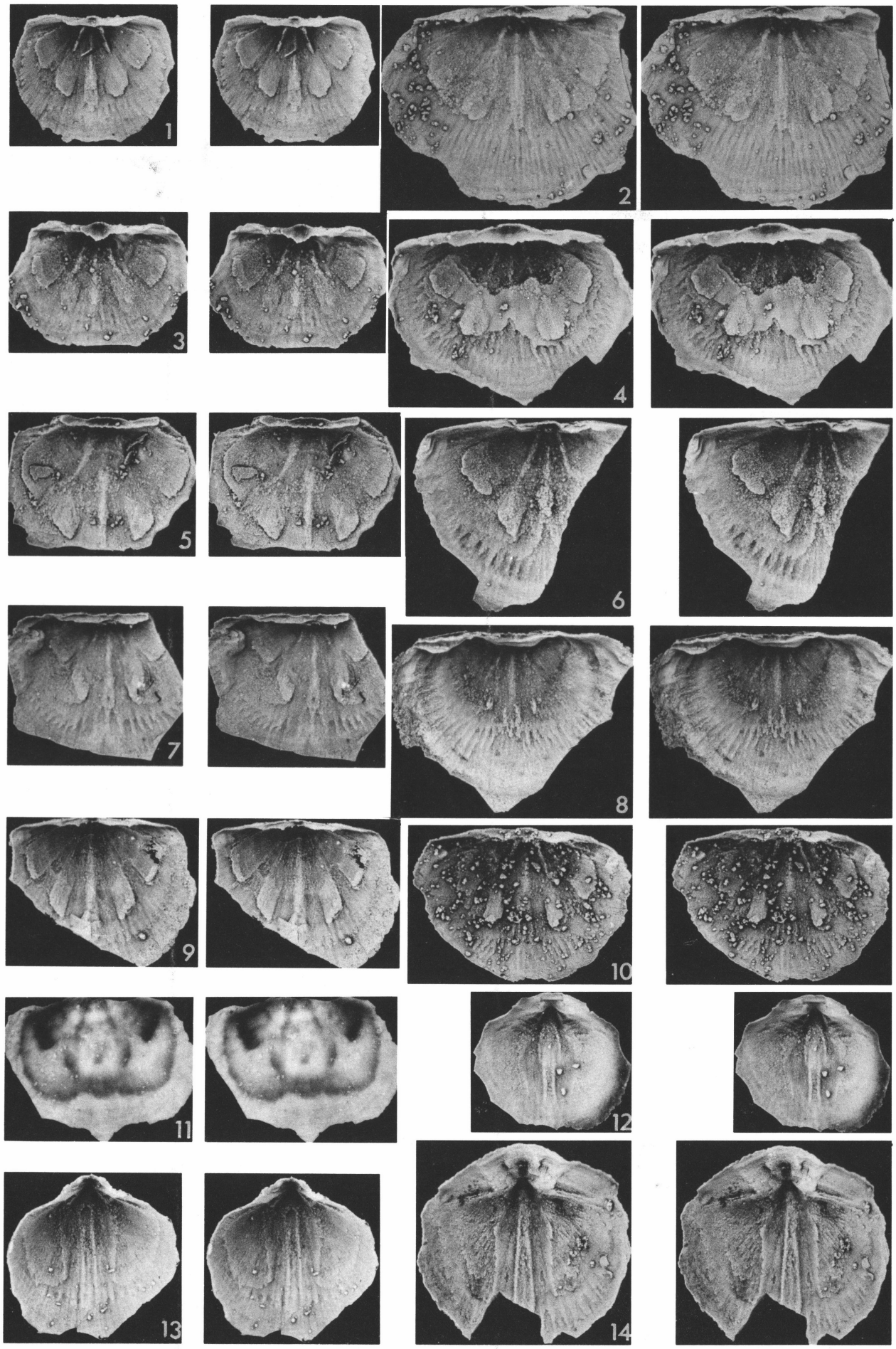

Plate 1. *Paterina* sp.
All stereo pairs; all ×10; all coated with ammonium chloride except where noted. Figs. 1–11, Dorsal valve interiors: 1, CPC25016; 2, CPC25024; 3, CPC25017; 4, CPC25014; 5, CPC25015; 6, CPC25011; 7, CPC25010; 8, CPC25022; 9, CPC25013; 10, CPC25012; 11, CPC25023, uncoated. Figs. 12–14, Ventral valve interiors. 12, CPC24990; 13, CPC25000; 14, CPC24989.

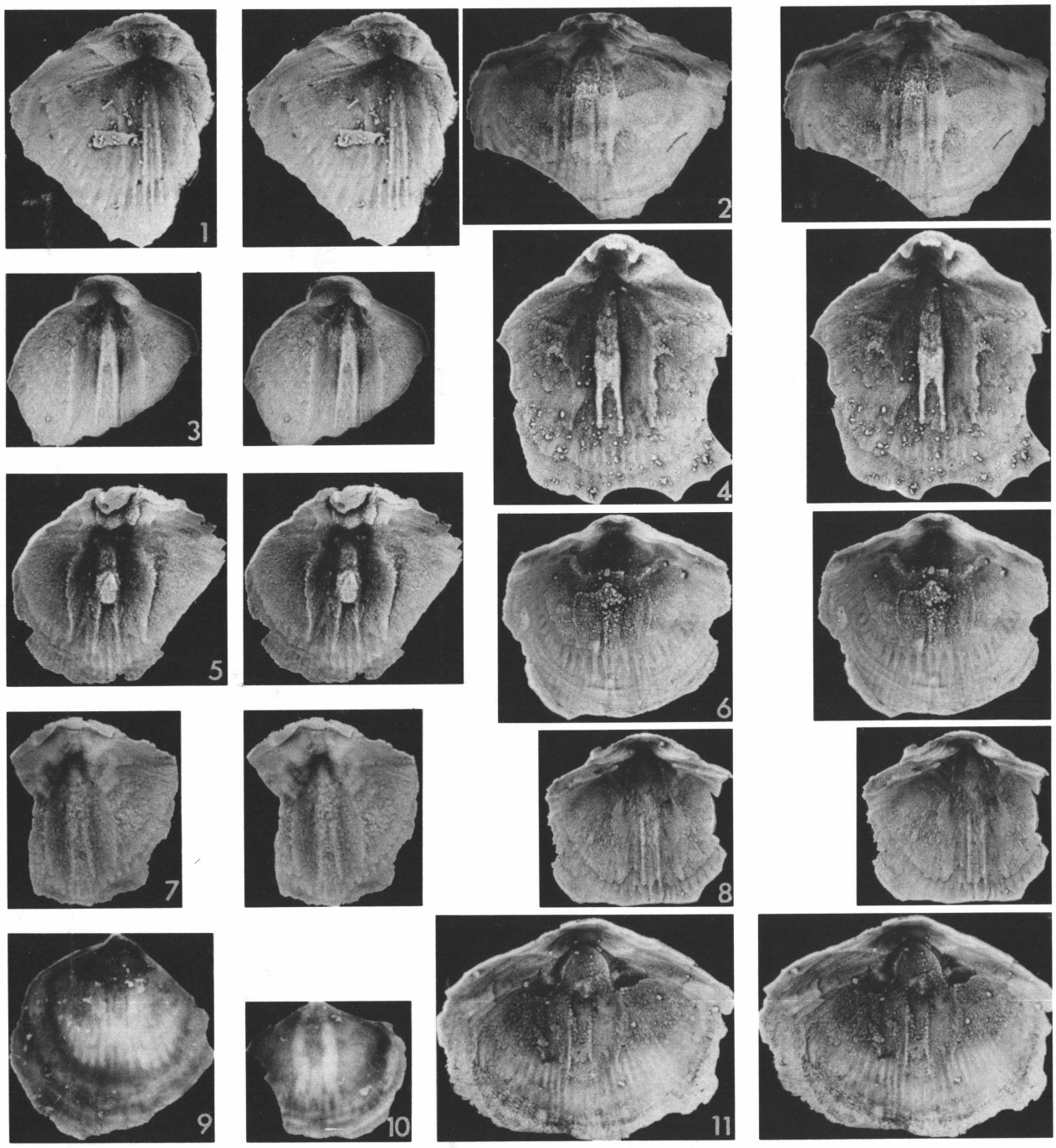

Plate 2. *Paterina* sp.
All stereo pairs except where noted; all ×10; all coated with ammonium chloride except where noted; all ventral valve interiors: 1, CPC24992; 2, CPC25004; 3, CPC24999; 4, CPC24988; 5, CPC24996; 6, CPC24997; 7, CPC25006; 8, CPC25007; 9, CPC25001, not stereo pair, uncoated; 10, CPC25002, not stereo pair, uncoated; 11, CPC25003.

Also present in several ventral valves are large reniform areas located laterally to the main vascular canals (Plate 1, figs. 12, 13, 14; Plate 2, figs. 1, 3, 5, 8). These have, in some cases, a pustulose ornamentation, and resemble the saccate vascula genitalia of some orthides.

The interior of the homeodeltidium is quite variable in its structure, but generally seems to consist of a median trough bounded by variably developed ridges (Plate 1, figs. 12, 13, 14; Plate 2, figs. 1, 2, 4, 5) with occasional thickening of the distal margin (Plate 2, figs. 2, 4, 5, 6).

The dorsal interior has a low median ridge, commonly extending to or beyond the valve mid-length, and two submedian ridges, which rarely extend very far from the umbonal region. Two pairs of muscle scars are located on the floor of the valve: one pair being located at about valve mid-length, a short distance laterally to the median ridge; the other pair being located about midway between the anterior scars and the posterolateral extremities of the valve, a short distance laterally to the anterior extremities of the submedian ridges (Plate 1, figs. 1–11).

Passing between the median ridge and the anterior pair of muscle scars is a pair of large vascular canals, whose anterior ends curve abruptly laterally to become concentric (Plate 1, figs. 4, 6, 7), subsequently giving rise to many radially disposed terminal branches (Plate 1, figs. 2, 4, 6, 7). The

posterolateral extent of these main canals is uncertain, but they appear to extend at least one third of the distance from the midline to the posterolateral margin. Other markings on the valve floor are unclear or ambiguous.

The interior of the homeochilidium has a variably developed transverse pit, which in some specimens is weakly bilobate (Plate 1, figs. 4, 8). It is very tempting to suggest that this is a muscle attachment site homologous with the dorsal diductor attachment sites of the articulates.

Aff. *Dictyonina* sp. nov.

The ventral interior has two well-developed broad submedian ridges diverging anteriorly at about 10–15 degrees, commonly with a low narrow ridge between them. One further pair of ridges (lateral ridges), found in several specimens, extends anterolaterally from the lateral margins of the pedicle callist(?) (see Plate 3, fig. 3). The lateral and submedian ridges bound a pair of subtriangular to semicircular muscle scars (Plate 3, figs. 1–4). No other attachment areas are apparent. Anterior to the muscle scars, the submedian ridges become lower and less regular, and appear to laterally bound a pair of principal vascular canals. These canals apparently branch at about two-thirds valve length, then become obscure (Plate 3, fig. 1). A further series of vascular markings arises from the anterolateral margins of the muscle scars, trends anterolaterally for a short distance, then curves abruptly but not very strongly towards the anterior, whereupon they disappear (Plate 3, fig. 1). These may be impressions of the radial structure of the vascula genitalia.

The dorsal interior has a transversely ovate to subquadrate, slightly depressed posteromedial area that is divided into roughly equal quarters by a low narrow median ridge and two oblique ridges or groups of ridges diverging anteriorly from the median ridge at about 45 degrees (Plate 3, figs. 5–7). In one specimen, faint impressions of muscle scars can be seen (Plate 3, fig. 7). One pair of scars (anterior pair) are rounded triangular to longitudinally ovate and bounded laterally by the oblique ridges, and the two scars are separated from one another by the median ridge. The other pair (posterior pair) are posterolateral to the oblique ridges and are narrow, rounded triangular in shape. As in *Paterina* sp., some specimens have a small pit on the inner surface of the apex of the homeochilidium. No traces of the vascular system have been observed.

Comparisons

Each of the above species has a short ventral muscle field with the scars lateral to the submedian ridges, which in turn laterally bound major mantle canals, proximally separated from one another by the usually low median ridge. It is these mantle canals and their bounding ridges that Rowell (1980) assumed to be the ventral muscle field. In aff. *Dictyonina* sp. nov. these mantle canals are obscure distally, but in *Paterina* sp., at about two-thirds valve length, they curve abruptly laterally to become concentric. In so doing they apparently encircle, at least in part, somewhat reniform fields, herein interpreted as impressions of saccate vascula genitalia. Laterally disposed radial markings in the ventral valve of aff. *Dictyonina* sp. nov. are interpreted similarly.

Both species have a large quadripartite dorsal muscle field with the slightly smaller anterior pair of scars located a short distance laterally to the median ridge and the posterior pair located posterolaterally to the anterior pair. Only *Paterina* sp. shows any trace of the vascular system. In this species one median pair of canals passes between the median ridge

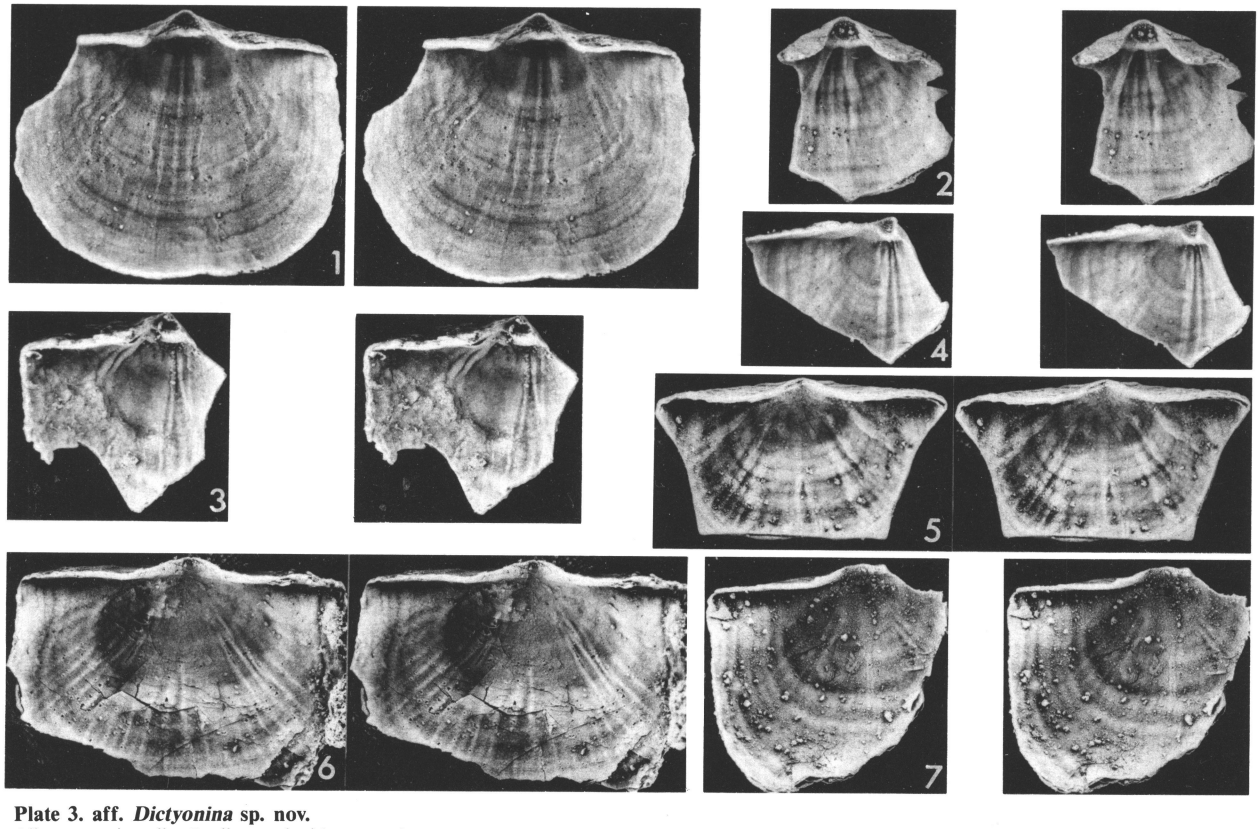

Plate 3. aff. *Dictyonina* sp. nov.
All stereo pairs, all ×7; all coated with ammonium chloride. Figs. 1–4, Ventral valve interiors: 1, CPC23642; 2, CPC23648; 3, CPC23644; 4, CPC23649; Figs 5–7, Dorsal valve interiors: 5, CPC23655; 6, CPC23654; 7, CPC23656.

and the anterior muscle scars, then curves laterally to become concentric. Their extent towards the posterolateral margins is unclear, but the pattern has similarities with the saccate (apocopate) condition.

Both species commonly have a small pit or depression on the inner face of the apex of the homeochilidium. It is suggested that this too is a site of muscle attachment.

Concluding remarks

The striking feature of the internal structure of the species studied herein is its similarity to that of articulate brachiopods, particularly the orthides. Although it is not clear how the valves of paterinides opened and closed, the general similarity in musculature to representatives of the Articulata suggests a similar system operated. For the paterinides to use such a lever action, a suitable axis of rotation and a line of action for one set of muscles posterior to this axis must exist. The broken nature of the specimens of *Paterina* sp. prevent the examination of such geometric considerations, but the specimens of aff. *Dictyonina* sp. nov. exhibit a wide, straight hingeline, a feature that suggests coincidence with the rotational axis. If this is the case, then one set of muscles necessarily occurs posterior to this hinge. For this to occur in a species with an apsacline (nearly catacline) ventral pseudointerarea and an anacline (nearly catacline) dorsal pseudointerarea, the muscles must be close to the posterior margin of either or both valves. For such a muscle arrangement to occur in a species with a procline ventral interarea (e.g. *Dictyonites perforata* Cooper 1956), the dorsal valve must extend posteriorly to the hinge axis, with the dorsal and ventral attachment sites of the 'diductors' tending to be more posterior than in an apsacline-anacline species. Such is the case when comparing the ?procline-?anacline species discussed above as *Paterina* sp. with the apsacline-anacline aff. *Dictyonina* sp. nov. A more detailed geometric analysis of these functional possibilities must await the availability of more specimens of a less fragmented nature that I have at my disposal.

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