EVALUATION OF A THECIDEIDINE BRACHIOPOD FROM THE MIDDLE JURASSIC OF THE COTSWOLDS, ENGLAND

by P. G. BAKER

ABSTRACT. The discovery of sources of material of Aalenian (Middle Jurassic) age has enabled restudy of *Moorellina dundriensis* (Rollier). Although in general morphology the species resembles other monoseptate moorellinins, the absence of brachial lobes, together with the characteristically thickened shell and distinctive skeletal shell fabric, clearly separates it from all other contemporaneous representatives of *Moorellina*. On this basis it is assigned to a new genus *Pachymoorellina*. The shell microstructure, with its suppressed secondary fibrous mosaic, resembles that of the polyseptate *Mimikonstantia sculpta* Baker and Elston with which it is associated. The microstructure of the pedicle valve indicates a phylogenetic link with the Lower Cretaceous *Thecidiopsis tetragona* (Roemer). Furthermore, correlation of the microstructure of certain tubercles in the brachial valve of *Pachymoorellina dundriensis* with almost identical structures in the Recent *Thecidellina barretti* (Davidson) suggests a more rectilinear evolutionary pattern for the *Thecidellina* group than has previously been supposed.

THE phylogenetic importance of the suppressed (Williams 1973) secondary fibrous shell mosaic found in a recently described (Baker and Elston 1984) upper Aalenian micromorphic polyseptate genus prompted the search for possible ancestral stock. Study of the ontogeny (Baker and Elston 1984, p. 784) of *Mimikonstantia sculpta* Baker and Elston clearly showed the development of the polyseptate condition from an early juvenile monoseptal phase, indicating derivation from a monoseptate ancestor. Further, the absence of brachial lobes suggested the possibility of descent via a *bouchardi* or *dundriensis*-type moorellinid ancestral line. A normal (*sensu* Williams 1973, p. 465) secondary shell layer has been identified in the Liassic *Moorellina bouchardi* (Davidson) and, although this does not completely rule out *bouchardi* stock, the simultaneous acquisition of a suppressed secondary mosaic and polyseptate condition in *Mimikonstantia sculpta* is thought to be unlikely. Serial sectioning of micromorphic *dundriensis*-type specimens associated with *M. sculpta* in loosely consolidated marly horizons overlying hardgrounds in the Pea Grit at Crickley Hill (N.G.R. SO 928 163), near Cheltenham, yielded startling results. They were found to have a strongly suppressed secondary fibrous mosaic totally unlike that of any associated *Moorellina* species and a pedicle valve skeletal fabric which, in part, parallels that exhibited by certain Lower Cretaceous thecideidines. The Crickley specimens are morphologically identical with the Bajocian specimens assigned to *Moorellina dundriensis* (Rollier) from the Inferior Oolite of Dundry Hill, near Bristol. The Dundry material also shows the same suppressed secondary fibrous mosaic. *M. dundriensis*, with its empty brachial cavities and enormously thickened pedicle valve, has always been noticeably different from the associated Dundry species *M. granulosa* (Moore) and *M. duplicata* (Moore) with their characteristically developed brachial lobes. The differences in morphology, together with a fundamentally different shell secretory regime, clearly separate *M. dundriensis* from all other known moorellinin genera. In view of this and the phylogenetic implication discussed later, it is proposed to assign *M. dundriensis* to a new genus and to include the Crickley specimens therein. The confusion surrounding the identity, description, and location of Moore's original type specimens and the selection of hypotypes from the Crickley material necessitates emendation of the previous diagnoses.

Registration of material. The paratypes (M2848) and the hypotypes figured in this paper (PB3250-3256) are housed in Bath Geology Museum. Other hypotypes are located in the Institut de Paléontologie (Natural History), Paris (MNHN IP B44600 and B44601). The specimen of *Thecidiopsis tetragona* is housed in the Musée Géologique, Lausanne (42533).

Preparation of material. The techniques used for the recovery and preparation of the specimens were fully described by Baker and Elston (1984, p. 777) and require no further elaboration here.

SYSTEMATIC PALAEONTOLOGY

Order SPIRIFERIDA Waagen, 1883
Suborder THECIDEIDINA Elliott, 1958
Superfamily THECIDEACEA (Gray, 1840) H. and G. Termier, 1949
Family THECIDEIDAE Gray, 1840
Subfamily MOORELLININAE Pajaud, 1966
Genus PACHYMOORELLINA gen. nov.

Etymology. From the Greek *pakhus* (thick) after the greatly thickened free ventral wall of the pedicle valve.

Diagnosis. Endopunctate, monoseptate moorellinin having a strongly suppressed secondary fibrous shell mosaic, brachial valve with a fragile, very wide peripheral flange and a high median septum separating brachial cavities devoid of brachial lobes, and pedicle valve with a large area of attachment and characteristically thickened free ventral wall.

Type species. Thecidea (Davidsonella) Dundriensis Rollier, 1915 *nom. subst.* [*pro Thecideum Bouchardii* Moore, 1854 (*non* Davidson, 1851)].

Pachymoorellina dundriensis (Rollier, 1915)

Plates 9 and 10; Plate 11, figs. 1-6; text-figs. 1-3

1854 *Thecideum Bouchardii* [*non* Davidson] Moore, p. 116, pl. 1, figs. 11-13.
1854 *Thecideum Bouchardi* Davidson, p. 79.
1876 *Thecideum Bouchardii* Davidson, p. 106, pl. 13, figs. 1-3.
1915 *Thecidea (Davidsonella) Dundriensis* Rollier, p. 53.
1963 *Moorellina dundriensis* (Rollier); Pajaud, p. 996.
1966 *M. (Moorellina) dundriensis* (Rollier); Pajaud, p. 633, figs. 4 and 6.
1970 *Moorellina (Moorellina) dundriensis* (Rollier); Pajaud, p. 164, pl. 3, fig. 4; pl. 8, figs. 1 and 2; text-figs. 66Dc and 67.


EXPLANATION OF PLATE 9

Figs. 1-8. *Pachymoorellina dundriensis* (Rollier). Stereoscan photomicrographs of specimens from the Aalenian (Middle Jurassic) Pea Grit of Crickley Hill, near Cheltenham, Gloucestershire; all specimens were coated with evaporated gold before photography. 1 and 2, PB3250, brachial and posterior views of hypotype brachial valve in which the delicate endopunctate marginal flange is almost intact, × 22. 3 and 4, PB3251, brachial and posterior views of a hypotype to show the morphology typical of separated brachial valves in which the marginal flange is broken away and the median septum usually damaged, × 20. 5, three-quarters profile view of same specimen (rotation, 40°; tilt angle, 45°), showing the form of the brachial cavities and the remains of the ridges uniting the posterior of the median septum with the bridge abutments, × 20. 6, PB3254, three-quarters profile view (rotation, 45°; tilt angle, 35°) of an immature hypotype pedicle valve showing the large area of attachment, the characteristic marginal crest, and the precursor of the enormously thickened free ventral wall, × 17. 7, PB3250, enlarged portion of the lateral margin of a brachial valve showing the terminal faces of a small patch of secondary fibres (lower centre) at the point where the marginal flange unites with the sub-peripheral rim, × 1200. 8, PB3250, enlarged view of part of the outer margin of the sub-peripheral rim of a brachial valve showing the tubercles composed of granular calcite, × 1000.
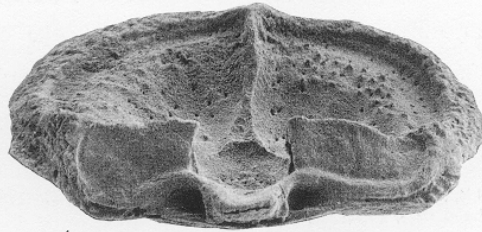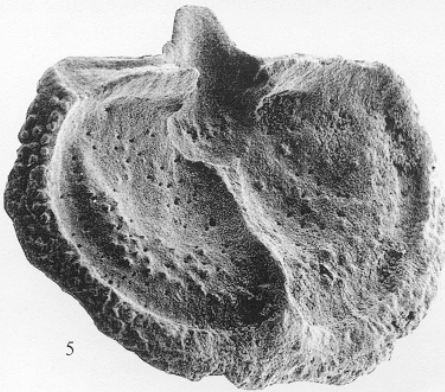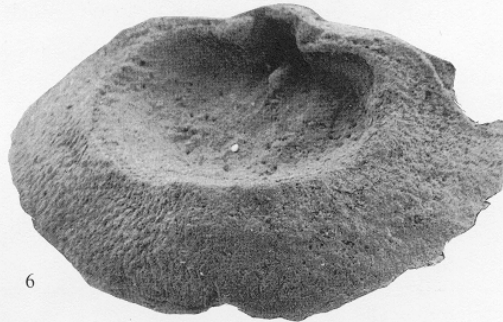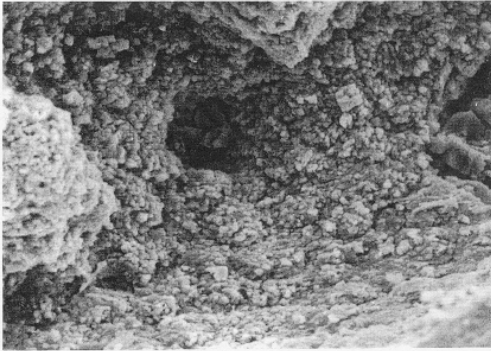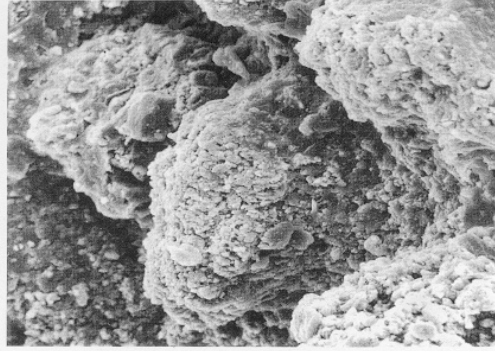
PLATE 9
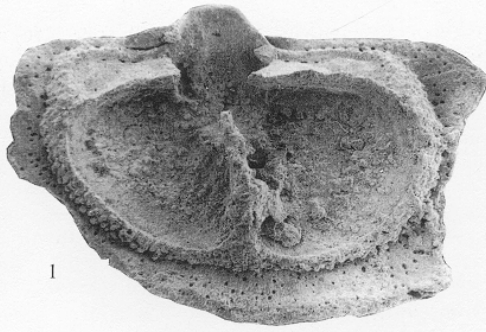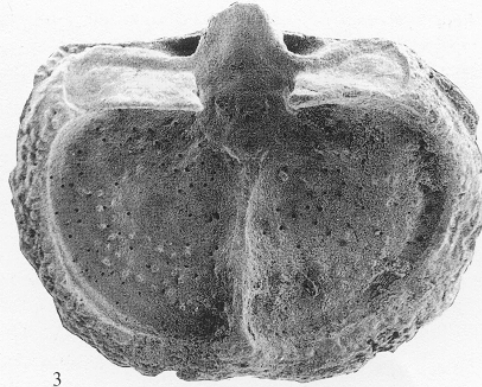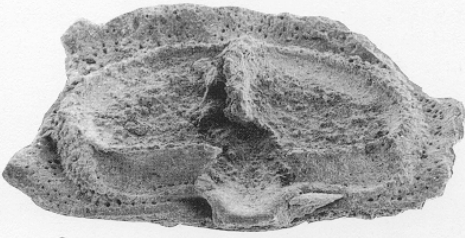
BAKER, *Pachymoorellina*

Type specimens. No holotype designated. Four paratypes on M2848; hypotypes PB3250–3256 and MNHN IP B44600–44601.

Original diagnosis (Moore 1854). Shell inequivalve, flattened, subcircular; attached by the principal portion of the ventral valve; deltidium large, elevated, triangular; area large and extended showing lines of growth; hinge line depressed in centre, leaving a small flat area under the deltidium; dorsal valve much smaller than the ventral. The interior of the ventral valve shows a slight middle septum, on either side of which are two large scars, due to the attachment of the cardinal muscle, on the outer edge of which are two small depressions, which received the adductor muscles; interior rugosely striated; the cavity of the valve in adult shells surrounded by a broad margin, having a wavy appearance, due to lines of growth. Interior of the dorsal valve has a broad granulated margin, within which is a very high central septum, nearly reaching the surface of the opposite valve from whence proceeds a granulated ridge, united by a bridge over the visceral cavity; within this ridge is a smooth slightly concave space, between which and the granulated interior is a small granulated ridge.

Emendation of original diagnosis (Pajaud 1970). Coquille de taille moyen (L = 6·5 mm; l = 8 mm), légèrement transverse, très inéquivalve et à surface de fixation relativement peu étendue. Grand valve subcirculaire, à cavité distincte, peu dévelopée, avec pseudodeltidium bombé; bord cardinal long. Petite valve subcirculaire, mégathyride; processus cardinal saillant, aires articulaires étendues; limbe marginal granuleux. Septe médian long, haut et mince; formation en V très visible. Aires lophophoriennes lisses ou légèrment granuleuses.

Emended diagnosis. Moderate sized *Pachymoorellina*, up to about 5·5 mm in length, 6·5 mm in width, and 3·5 mm in thickness. Outline transversely elliptical; weakly dorsiconvex up to the point at which the free ventral wall of the pedicle valve begins to develop, after which the lateral profile becomes flattened triangular. Pseudodeltidium large, transversely convex, and elevated above the surface of the ventral interarea, with a flattened exposed anterior terminal face. Hinge line long, only slightly shorter than the maximum width of the shell. The undamaged brachial valve is characterized by a wide, very thin, peripheral flange which, in complete shells, conceals the disproportionately thickened rim of the pedicle valve.

Description. A moderate sized moorellinin with a large attachment scar and a variably developed free ventral wall, giving a range from dorsiconvex to flattened triangular lateral profile. The ventral interarea is clearly developed with a large, well-defined, transversely convex pseudodeltidium. There is never more than a trace of an interarea in the rather weakly convex brachial valve. In articulated shells the delicate peripheral flange of the brachial valve is almost invariably broken away, producing a marked inequivalve appearance with the characteristically thickened free ventral wall of the pedicle valve exposed.

Distribution. Geographical distribution unknown but probably more widespread than its recorded occurrence. Although the precise details remain unknown, the locality from which Moore collected his original material is given (Moore 1854, p. 110) as a small quarry in the lower part of the Dundry Freestone situated above the village of Bishport, near Dundry (Avon). As far as can be ascertained this would approximate stratigraphically to a *parkinsoni* Zone, *truelli* Subzone position. The new material was obtained from near the top of the Pea Grit (Aalenian, *murchisonae* Zone, *murchisonae* Subzone) at Crickley Hill (Grid Ref. SO 928 163), near Cheltenham, Gloucestershire, indicating a range of at least Aalenian to Bajocian for the species.

MORPHOLOGY, GROWTH AND SHELL MICROSTRUCTURE

Valve characters

Pedicle valve (Pl. 9, fig. 6; text-fig. 1E, F). Hemispondylium sessile with the elongate diductor muscle scars deeply impressed into the floor of the valve and united posteriorly to form a characteristic inverted V; the median myophragm is prominent, bifurcating, and grooved anteriorly to accommodate the median adductor muscle scars. The lateral adductor muscle scars are large and widely separated with a narrow groove along their dorsal margin. The teeth are weakly to moderately developed.

Brachial valve (Pl. 9, figs. 1–5; text-fig. 1A–D). The cardinal process is relatively small and obscurely bilobed. The lateral adductor muscle scars are large, rounded rectangular, and erect (almost perpendicular to the commissural plane), occupying most of the posterior border. The inner socket ridges are extended laterally
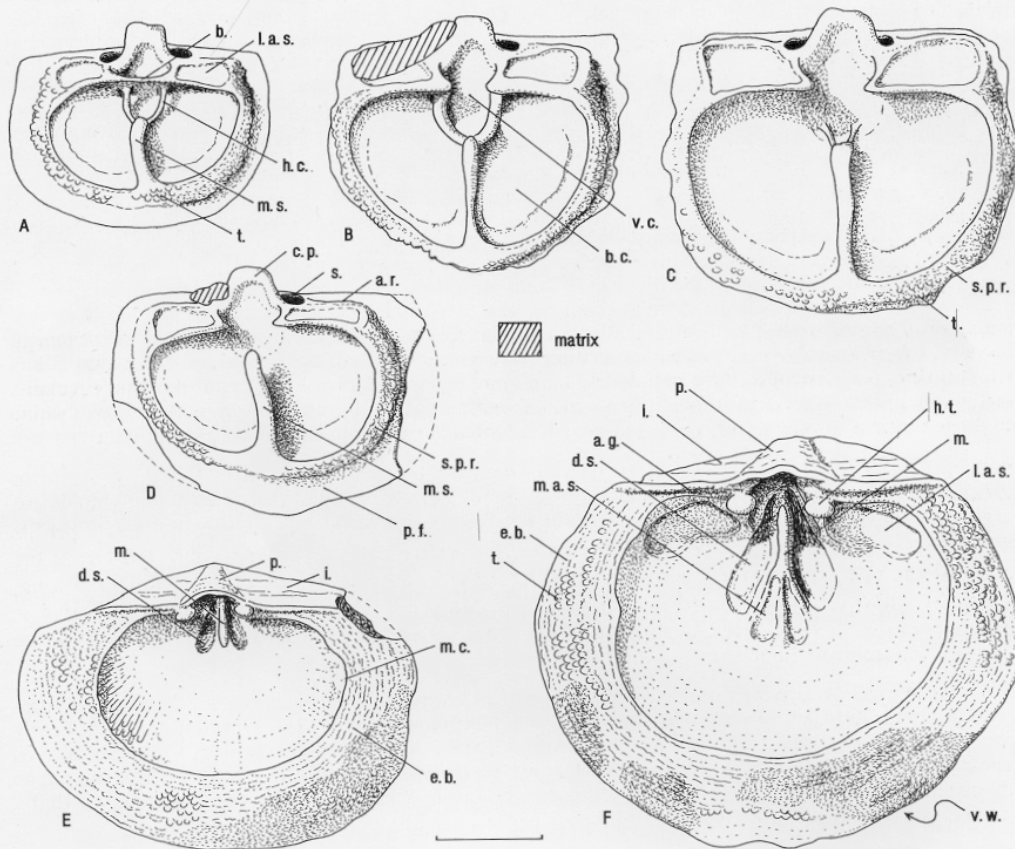
TEXT-FIG. 1. 'Wild' stereomicroscope traces (except A) to show the essential morphology of *Pachymoorellina dundriensis* (Rollier). A, PB3252, reconstruction of the juvenile brachial valve, based on three specimens, to show the form of the 'horn-like' connections between the posterior of the median septum and the bridge abutments. B, PB3253, immature brachial valve showing fusion of the connections between the median septum and the bridge abutments with the floor of the valve; the peripheral flange is missing in this specimen. C, M2848, interior view of a paratype brachial valve showing the morphology typical of mature brachial valves in which the peripheral flange is missing. D, PB3250, interior view of a hypotype brachial valve showing the almost intact peripheral flange. E, PB3254, immature pedicle valve showing the large area of attachment (entire ventral surface of the valve as figured) and the characteristic marginal crest with its very wide externally inclined border. F, M2848, interior view of a paratype pedicle valve showing the morphology typical of mature pedicle valves; note the similarity in the appearance of the tuberculate margin, in dorsal view, both before (E) and after the development of the free ventral wall. Abbreviations: *a.g.*, articulatory groove; *a.r.*, articulatory ridge; *b.*, bridge; *b.c.*, brachial cavity; *c.p.*, cardinal process; *d.s.*, diductor muscle scar; *e.b.*, externally sloping finely tuberculate border; *h.c.*, horn-like connection; *h.t.*, hinge tooth; *i.*, ventral interarea; *l.a.s.*, lateral adductor muscle scar; *m.*, median myophragm; *m.a.s.*, median adductor muscle scar; *m.c.*, marginal crest; *m.s.*, median septum; *p.*, pseudodeltidium; *p.f.*, peripheral flange; *s.*, dental socket; *s.p.r.*, sub-peripheral rim; *t.*, tubercle; *v.c.*, visceral cavity; and *v.w.*, free ventral wall. Scale bar represents 1·00 mm.

along the dorsal margin of the lateral adductor muscle scars to form low, narrow ridges which articulate with the complementary grooves in the pedicle valve. The median septum is thin and blade-like, extending over the body cavity. Posteriorly, two ridges diverge from the base of the median septum. These ridges may extend across the floor of the valve for only a short distance or, in some cases, form low ridges extending round the perimeter of the visceral cavity to unite with the bridge abutments. The brachial cavities are smooth or weakly granulose. The outer surface of the sub-peripheral rim is ornamented with small tubercles. A wide but very thin and fragile endopunctate peripheral flange (Pl. 9, figs. 1 and 2) is present. This invariably shows some damage and in separated valves is usually broken away altogether (Pl. 9, figs. 3 and 4; text-fig. 1c).

Ontogeny

Pedicle valve. All the characters of the pedicle valve are present in the smallest valves available. Ontogenetic development involves the development of the hinge line, slight changes in the relative proportion of the pseudodeltidium, the muscle scars, the hinge teeth, and, most noticeably, the development of the free ventral wall. Up to the point at which the valve is about 5·0 mm long, attachment is effected by the whole surface (Pl. 9, fig. 6). The precursor of the free ventral wall is present, however, even during this phase of development. It is represented by a clearly defined marginal crest demarcating the limit of the internal cavity and falling away laterally and anteriorly (Pl. 9, fig. 6; text-fig. 1E) to form a very wide, finely tuberculate, externally sloping border. As development proceeds, the outer edge of the valve begins to grow away from the substrate but shell material continues to be accreted to the whole area external to the marginal crest so that, in relative terms, an enormously thickened free ventral wall is developed (text-figs. 1F and 3G).

Brachial valve. The juvenile valve, apart from being slightly more circular, with less erect lateral adductor muscle scars, differs from the adult valve only in the presence of two posteriorly directed horn-like processes (text-fig. 1A) extending from near the base of the posterior edge of the median septum. These structures often extend backwards to unite with the bridge abutments. Initially they remain separated from the valve floor but as growth proceeds, accretion of material along their dorsal edges eventually unites them with the floor of the valve (text-fig. 1B). Evidently, in the adult valve shell resorption activity outstrips accretion as the structures are eliminated altogether or reduced to low ridges bounding the visceral cavity (Pl. 9, fig. 5).
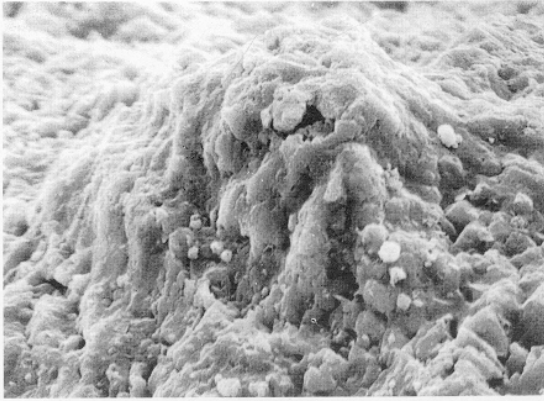
Microstructure

In contrast with all other described monoseptate moorellinins, the shell of *P. dundriensis* shows strong suppression of the secondary fibrous layer. Significant differences in the microstructure of the brachial and the pedicle valve necessitate description of the two valves separately.
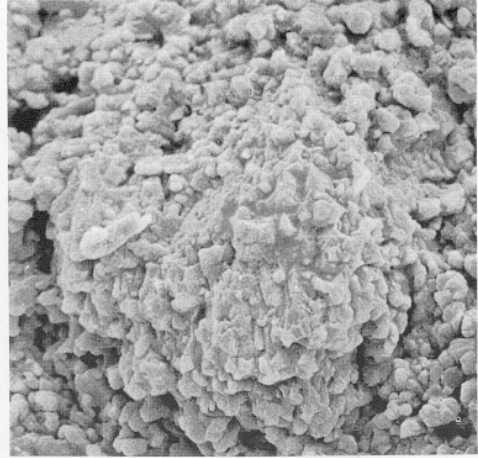
Pedicle valve. A thin, granular primary layer is present, composed of approximately equant granules about 1 μm across. Orthodoxly stacked secondary fibres (*sensu* Williams 1973, p. 454) are restricted to the hinge teeth, tooth ridges, and occurrence as occasional strands (Pl. 11, fig. 1) along the posterior and posterolateral margins of the valve. The lateral, anterolateral, and anterior sectors of the valve are characterized by tracts
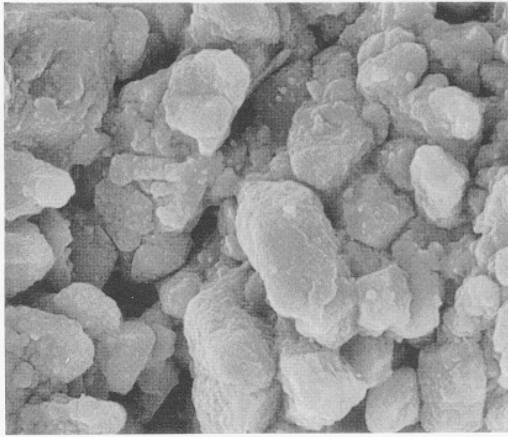
EXPLANATION OF PLATE 10

Figs. 1–6. *Pachymoorellina dundriensis* (Rollier). Stereoscan photomicrographs of specimens and cellulose acetate peels of sectioned specimens; all specimens were coated with evaporated gold before photography. 1, PB3251, enlargement of a tubercle on the floor of the right brachial cavity showing its component secondary fibres arranged into a low cone, × 1500. 2, PB3254, enlargement of a pedicle valve tubercle showing the terminal surface of an acicular crystallite tract emerging from a matrix of finely granular calcite to form a tubercle; seen end-on, the acicular crystallites are virtually indistinguishable from granules, × 1000. 3, PB3254, floor of pedicle valve adjacent to the marginal crest, showing detail of the much coarser granular calcite which is deposited as the valve thickens in association with the developing free ventral wall, × 3000. 4, PB3255, acetate peel section (3255/4) through a pedicle valve showing the general appearance of the acicular crystallite tracts which form the tubercle cores (section orientation—parallel with the area of attachment; section location—anterolateral sector), × 750. 5, enlargement of the area outlined in fig. 4 to show the splayed relationship of the terminal crystallites, × 1250. 6, detail of acicular crystallite tracts in longitudinal section showing the characteristic splayed arrangement of the component crystallites along their entire length (section orientation and location as in fig. 4), × 1250.
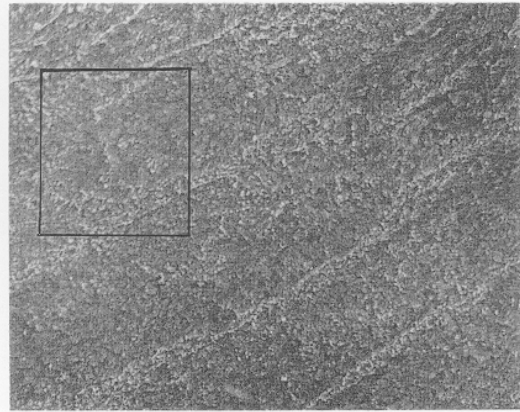
PLATE 10

BAKER, *Pachymoorellina*

Legend:
- granular primary shell layer
- acicular crystallite tracts (outline only)
- secondary fibrous shell
- coarse granular calcite shell
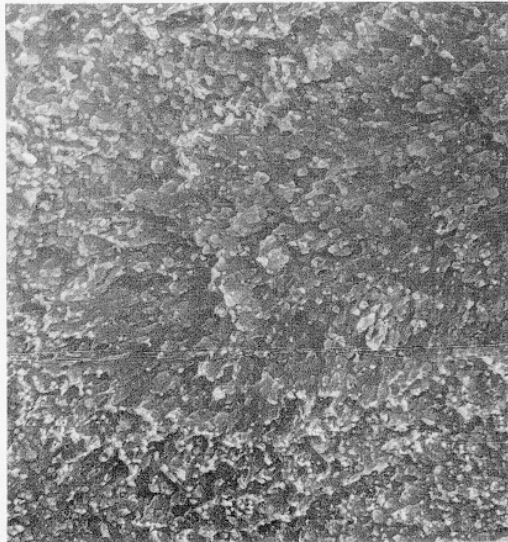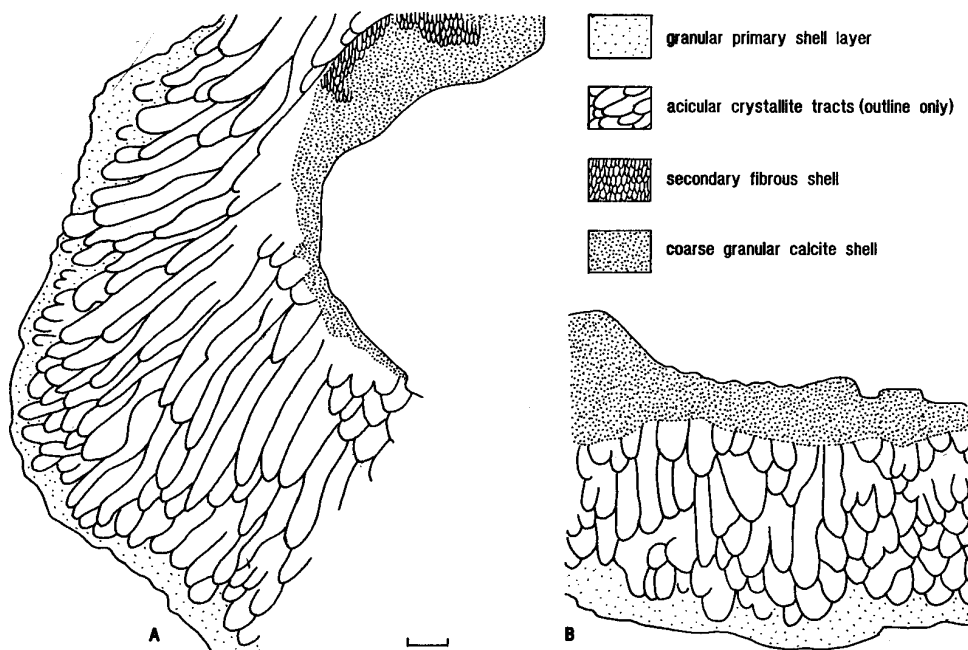
TEXT-FIG. 2. 'Wild' stereomicroscope traces of cellulose acetate peels of horizontal sections through the pedicle valve of *Pachymoorellina dundriensis* (Rollier). A, PB3255/6, posterolateral to anterolateral sector of specimen showing the arrangement and distribution of the acicular crystallite tracts in longitudinal section, relative to the granular calcite shell. B, PB3255/14, part of the anterior sector of the specimen showing the arrangement and distribution of acicular crystallite tracts close to the rim of the valve; note the relative thickening of the granular shell layer in the free ventral wall. Scale bar represents 100 μm.

(Pl. 10, fig. 4) of acicular crystallites, about 1 μm wide and about 10 μm long, aggregated into series that exhibit a typically splayed (Pl. 10, fig. 5) relationship. The characteristic grouping and arrangement of the crystallites creates an overlapping series of large apparent megafibres up to 100 μm wide and up to 0·8 mm long (Pl. 10, fig. 6; text-fig. 2). In many cases the aggregates appear to be almost contiguous (Pl. 11, fig. 2) or separated only by narrow strips of granular calcite. The tracts of acicular crystallites form a thick wedge almost totally comprising the marginal crest (text-fig. 3F) of the immature pedicle valve. Because of the peculiarity of the ontogenetic development of the immature pedicle valve, sections orientated parallel with the plane of the attachment scar (text-fig. 2A) enable the path of these crystallite aggregates to be traced through to the external surface of the sloping border. Their tips are seen to emerge as small tubercles (Pl. 10, fig 2; text-fig. 3F). In reality, therefore, the apparent megafibres are revealed as a series of closely packed tubercle cores. As the growth pattern of the valve changes and the shell begins to grow away from the substrate to form a free ventral wall, granular primary shell forms the outer layer. As the free ventral wall develops and increases in height, it is thickened by the deposition of granular calcite on its inner surface (text-figs. 2B and 3G). This inner layer may be up to 0·3 mm thick and the component granules are much coarser (Pl. 10, fig. 3) than the granules of the primary layer. The shell substance is apparently impunctate as no endopunctae have been observed in any of the material studied.

Brachial valve. A thin granular primary layer is present. Fibrous secondary shell is well represented in the cardinal process, inner socket ridges, and posterior border. Elsewhere it occurs as thin sheets, only a few fibres thick, providing almost continuous cover in posterolateral sectors (Pl. 11, fig. 5; text-fig. 3D) and appearing as intermittent patches in lateral sectors (Pl. 9, fig. 7; text-fig. 3E) of the valve. Additionally, sporadic secretion of small aggregates of about fifty secondary fibres (Pl. 10, fig. 1) forms low conical mounds
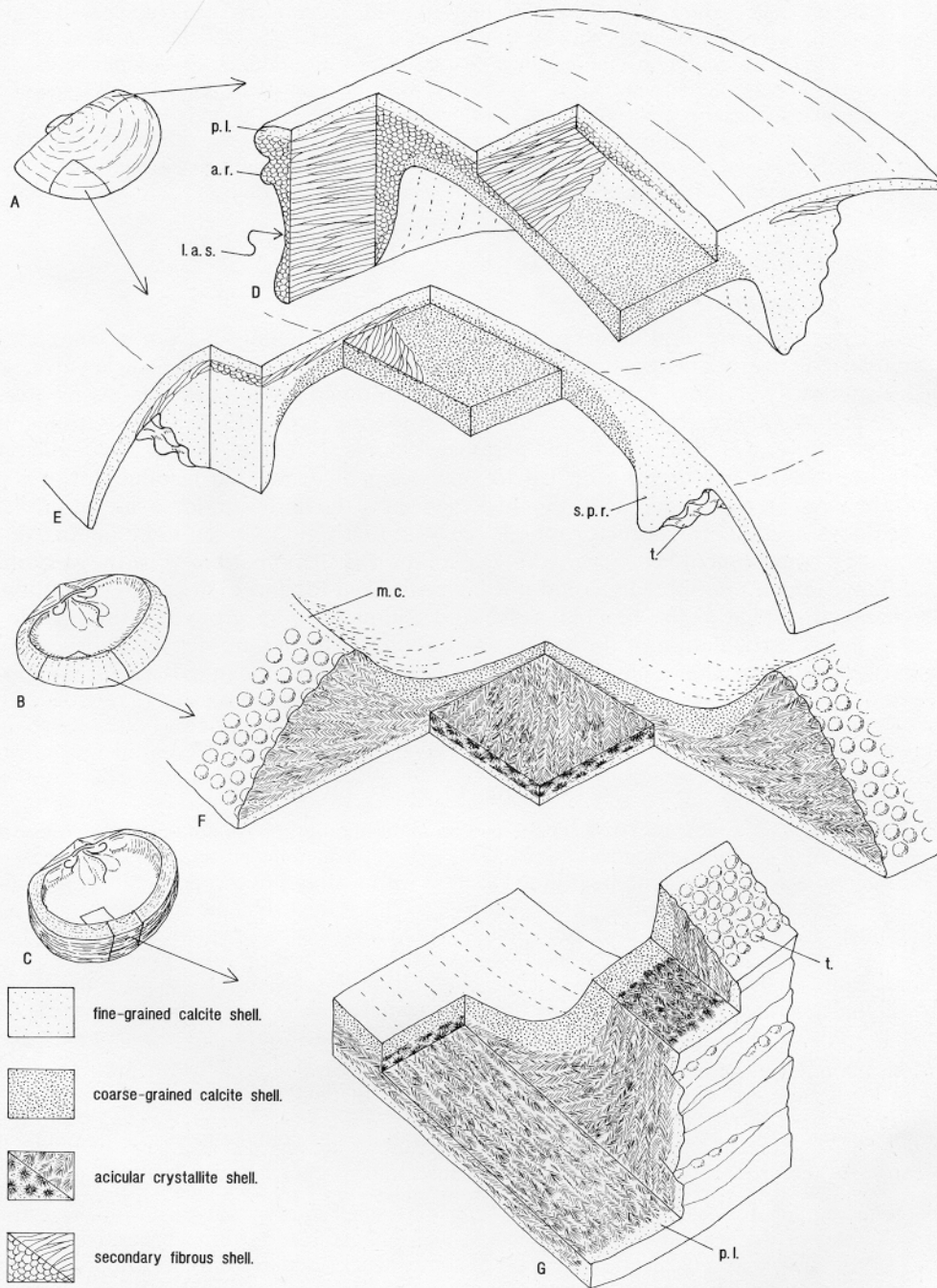
TEXT-FIG. 3. Diagrammatic reconstruction of the shell microstructure of *Pachymoorellina dundriensis* (Rollier). A–C, locational diagrams. D–G, block diagrams showing the varying microstructure of brachial and pedicle valves. D, posterolateral and E, anterolateral sectors of the brachial valve. F, anterolateral sector of the immature pedicle valve. G, anterior sector of the mature pedicle valve. Abbreviations: *a.r.*, articulatory ridge; *l.a.s.*, lateral adductor muscle scar; *m.c.*, marginal crest; *p.l.*, primary layer; *s.p.r.*, sub-peripheral rim; and *t.*, tubercle.

on the floor of the brachial cavities. With these exceptions, the remainder of the shell is composed of granular calcite. This occurs in two principal layers: an outer, fine-grained layer including the tuberculate sub-peripheral rim (Pl. 9, fig. 8; Pl. 11, fig. 3); and an inner, much coarser layer with granules up to 5 μm across flooring the brachial cavities (Pl. 11, fig. 4; text-fig. 3D, E). Clearly, as in the case of the pedicle valve, the accretion of the coarse granular material is associated with the thickening of the shell underlying the brachial cavities as they increase in size through resorptive activity around the inner margin of the sub-peripheral rim (Baker 1970) as the valve increases in size. In contrast to the pedicle valve, the brachial valve is clearly endopunctate, with the peripheral flange in particular being penetrated by numerous endopunctae.

DISCUSSION

Relationship with substrate

In almost all cases the peripheral flange of the brachial valve is damaged. Even in complete shells the brachial valve is nearly always slightly impressed into the interior of the pedicle valve, so that the flange is split away and lost, leaving the erroneous impression of a markedly inequivalve shell. As noted, the pedicle valve margin slopes from the crest to the exterior (Pl. 9, fig. 6). This inclination is paralleled by the ventral deflection of the peripheral flange (Pl. 9, fig. 2). The few pedicle valves which have been found in situ are attached to shells cemented into hardground surfaces. In P. dundriensis the large area of attachment, the thickened shell, the flattened dorsoventral profile, and the very well-developed lateral adductor muscle scars, at first sight all seem to be indicative of life in a high energy environment. However, this explanation is incompatible with the very delicate peripheral flange which undoubtedly could not have survived long in high energy conditions. On the other hand, the ridge in the brachial valve and complementing groove in the pedicle valve suggests that precise articulation of the valves was essential. The organo-detrital debris associated with the hardground may offer a clue. Together with broken shells, the matrix encloses gaping but


EXPLANATION OF PLATE 11

Figs. 1-6. *Pachymoorellina dundriensis* (Rollier). Stereoscan photomicrographs of gold-coated cellulose acetate peels (except fig. 6) of sectioned specimens. 1, PB3255, section through the posterolateral margin of pedicle valve showing an acicular crystallite tract in association with a strand of secondary fibres (*left*) (section orientation—parallel with the area of attachment), × 1000. 2, high oblique section through acicular crystallite tracts showing detail of their contiguous relationship (section orientation—horizontal, almost perpendicular to the shell surface; section location—anterior sector, pedicle valve, close to the base of the free ventral wall), × 1400. 3, PB3256, low oblique section through brachial valve showing the distribution of coarse granular calcite in the brachial cavity (*left*), fine granular calcite in the sub-peripheral rim (*centre*), and contact with the thin layer (*right*) of secondary fibrous shell which, in places, separates it from the primary granular layer (section orientation—parallel with the plane of the commissure; section location—posterolateral sector), × 600. 4, section showing detail of the junction between the fine granular calcite of the sub-peripheral rim and the coarse granular calcite flooring the brachial cavities (section orientation and location as in fig. 3), × 1600. 5, section showing detail of the fine granular calcite of the sub-peripheral rim and the junction with the almost continuous layer of secondary fibrous shell in the posterolateral sectors of the brachial valve (section orientation and location as in fig. 3), × 1300. 6, PB3255, transmitted light photomicrograph of a cellulose acetate peel (3255/14) through a pedicle valve showing the distribution and gross mosaic of the acicular crystallite tracts in high oblique section through the free ventral wall; because of their splayed arrangement, small areas of component crystallites will be sectioned transversely, appearing as darker patches (arrowed) (section orientation as in fig. 2; section location as in fig. 2, but approximately 0·5 mm below the lip of the valve), × 75.

Fig. 7. *Thecidiopsis tetragona* (Roemer). Musée Géologique, Lausanne, 42533. Transmitted light photomicrograph of a cellulose acetate peel (42533/12) of a section through the free ventral wall of a pedicle valve showing the gross mosaic of the acicular crystallite tracts in high oblique section and its close resemblance to the gross mosaic of P. dundriensis (section orientation—parallel with the commissural plane; section location—anterior sector, close to the attachment scar), × 70.

PLATE 11
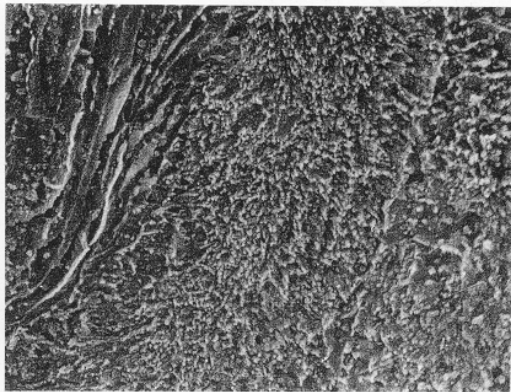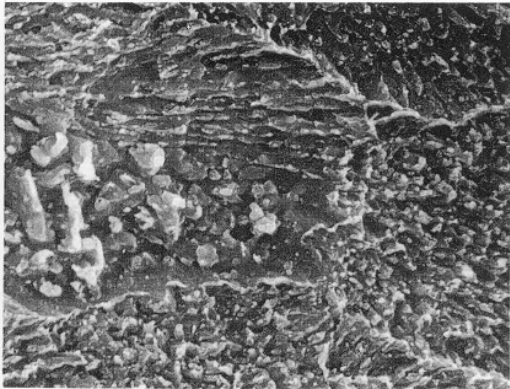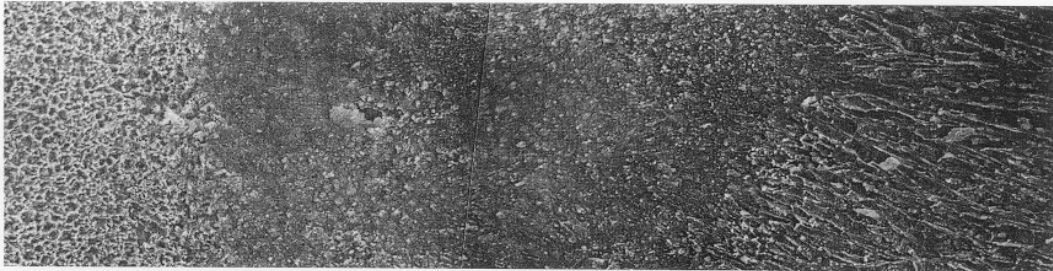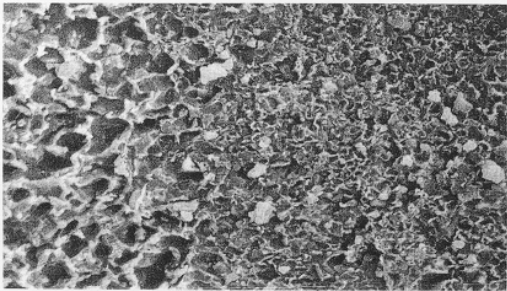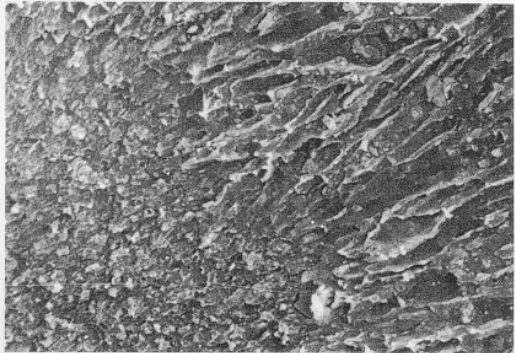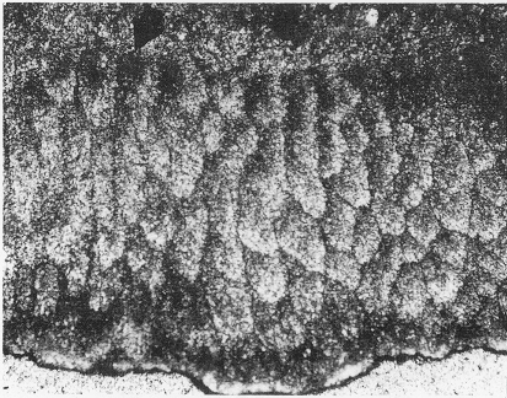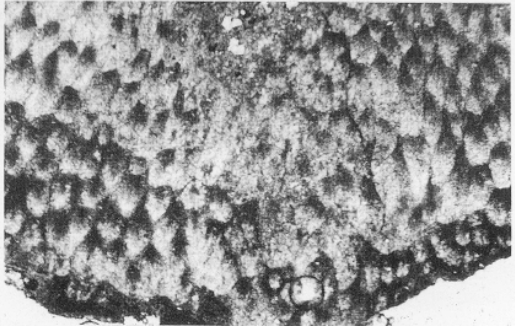

BAKER, *Pachymoorellina*, *Thecidiopsis*

still articulated bivalves and unbroken juvenile echinoid coronas. The assemblage indicates rapid accumulation with limited transport and little sorting, possibly as a result of storm activity, followed by quiet conditions. It seems probable that *P. dundriensis* subsequently colonized suitable niches. The growth profile and the inclination of the peripheral flange relative to the commissural plane is such that any 'snapping' action of the brachial valve would ensure the expulsion of a water current downwards towards the substrate. In this way the extraordinary development of the adductor muscle field can be reconciled with a functional requirement. It is envisaged that *P. dundriensis*, once established in fortuitous niches, employed a snapping valve action to waft away fine sediment or to discourage the unwelcome spatfall of competitors in the vicinity of the shell. The anterior wall of mature pedicle valves often shows exposed segments of border (text-fig. 3G) indicating mantle retraction. This is followed by accretion of granular primary shell on to the exposed tuberculate surface until the valve profile has been re-established. Such discontinuities may reflect minor damage to the edge of the brachial valve's peripheral flange.

Relationship with other species

Jurassic. As is the case with so many other micromorphic species described in the mid-nineteenth century, confusion exists regarding type specimens. Careful comparison of Bath Geology Museum material with the figures in Moore's (1854) paper leaves no room for doubt that Moore based his original description on four paratypes comprising a complete shell, a pedicle valve, and two brachial valves. Although Moore identified most of the essential morphological characters of the species, he unfortunately confused his specimens with the Liassic *Thecidea Bouchardi* Davidson, 1851. The error was later noticed (Rollier 1915) and the species *T. (D.) Dundriensis* Rollier, 1915 was erected to separate the Bajocian specimens. The distinctive 'lame circumpalléale papilleuse' (Rollier 1915) may now be identified as the granulose sub-peripheral rim, clearly seen on some Crickley specimens. Subsequently (Pajaud 1963) the species was assigned to *Moorellina dundriensis* (Rollier). In his comprehensive monograph, Pajaud (1970) overlooked the existence of the Moore paratypes in Bath. He concluded correctly that a holotype had never been designated and selected a brachial valve from the Paris Museum collections to serve as a neotype. Unfortunately, since the type material was never lost and Moore was in error only over the name, the neotype designation must be regarded as invalid and the registered specimen (MNHN IP B44600) relegated to hypotype status.

In comparison with contemporaneous Middle Jurassic monoseptate forms, *P. dundriensis*, with its large empty brachial cavities (without brachial lobes) and grossly thickened pedicle valve, has always rested uncomfortably alongside the more conventional morphologies of *M. granulosa* (Moore), *M. duplicata* (Moore), and *M. dubia* (D'Orbigny). These species, with their well-developed brachial lobes, reduced areas of attachment, and relatively thin-walled pedicle valves, also show a marked distinction at the level of shell microstructure. Investigation (Baker 1970) of the shell microstructure of *M. granulosa* revealed the presence of a secondary layer of normally fashioned fibres. Although the secondary shell fabric was modified by the presence of tubercle cores and the effects of shell resorption, it was found (Baker 1970, text-fig. 6, p. 91) to form a complete lining in both valves. A similar, fully developed secondary fibrous layer was subsequently identified (Williams 1973) in the Liassic *M. bouchardi*, *M. deslongchampsi* (Davidson), *Eudesella mayensis* (Eudes-Deslongchamps), and the Oxfordian *Rioultina ornata* (Moore). Recently (author's unpublished work), fully developed secondary fibrous shell layers have been found in the Aalenian *M. duplicata* and *M. dubia*, and also in the Bathonian *R. triangularis* (D'Orbigny). Nothing remotely resembling the microstructure of *P. dundriensis* has been discovered in any of the above species. The fibrous tubercle cores (Baker 1970, pl. 21, fig. 5) seen in the free ventral wall of the pedicle valve of *M. granulosa* are composed of conically arranged aggregates of normal fibres. The microstructure of *M. prima* Elliott has not been investigated owing to the unavailability of material for sectioning. In addition to the moorellinin species, the monoseptate Lower Jurassic davidsonellin *Davidsonella* must be considered. As Williams's comprehensive (1973) survey has shown, *Davidsonella sinuata* (Eudes-Deslongchamps), in addition to its concavo-convex adult profile and

well-developed brachial lobes, also has a fully developed secondary fibrous shell layer in both valves.

On morphological and microstructural evidence, therefore, a genetic link between *P. dundriensis* and any described monoseptate species is not easily established. As mentioned earlier, the detailed investigation of *P. dundriensis* was prompted by the discovery that the polyseptate *Mimikonstantia sculpta* developed from an early juvenile monoseptal phase and, by implication, was descended from a monoseptate ancestor. However, although both species are without brachial lobes and possess an inner granular shell layer, the suppression of the secondary fibrous shell is much more pronounced in *P. dundriensis* where, as described, secondary fibrous shell is restricted in its occurrence in the brachial valve and even more localized in its distribution in the pedicle valve. In *M. sculpta*, the secondary fibrous layer, although reduced in thickness and penetrated by granular calcite tubercle cores (Baker and Elston 1984, pl. 71; text-fig. 4) is retained as a continuous layer in both valves. Nothing resembling the acicular crystallite tracts of *P. dundriensis* has been seen in *M. sculpta*, although a capability apparently enjoyed by both species was thickening of the shell by rapid deposition of granular calcite, around the anterior of the juvenile median septum in *M. sculpta* and near the base of the free ventral wall in *P. dundriensis*. Clearly, although close to the same line of descent, the contemporaneous occurrence of the two species and the higher degree of suppression of secondary fibrous shell precludes the possibility of *P. dundriensis* being ancestral to *M. sculpta*. However, the view that they share a common plexus of descent is strengthened by the evidence obtained from certain Lower Cretaceous species.

Lower Cretaceous. The relationship between the Aalenian *M. sculpta* and the Lower Cretaceous *Thecidiopsis tetragona* (Roemer) was considered by Baker and Elston (1984, p. 789). A phylogenetic link was postulated on the basis of morphology, ontogeny, and shell microstructure. The elucidation of the shell microstructure of *P. dundriensis* enables a remarkable similarity in the microstructure of the pedicle valve of *P. dundriensis* and *T. tetragona* to be demonstrated. In both species the anterior and anterolateral sectors of the pedicle valve are characterized by acicular crystallite tracts (Pl. 11, figs. 6 and 7) which are barely distinguishable from each other. The only discernible difference is that in *T. tetragona* the tracts, or so-called 'Fir-tree structures' of Smirnova (1979), often have a central axis containing much larger crystallites. It is not proposed to offer a detailed comparison here as a critical revision of the microstructure of the shell of *T. tetragona* is to be published separately. Additionally, in *P. dundriensis* the distal splaying of the acicular crystallites (Pl. 10, fig. 5) is almost identical (Baker and Laurie 1978, pl. 62, *cf.* fig. 8) with the pattern seen in the Aptian *Bifolium faringdonense* (Davidson).

Recent. The very detailed investigation (Williams 1973) of the monoseptate *Thecidellina barretti* (Davidson) revealed the presence of tubercles in the brachial valve which showed (Williams 1973, pl. 43, fig. 25) the characteristic development of ten to twelve secondary fibres. Larger but otherwise almost identical structures (Pl. 10, fig. 1) composed of thirty to fifty fibres are found in the brachial cavities of *P. dundriensis*.

Phylogeny

In considering thecideidine phylogeny, Pajaud (1970) noted a rectilinear evolutionary pattern with offshoots in the *Lacazella* clan and a discontinuous zigzag progression in the *Thecidellina* clan. Although the database needs further extension, a more rectilinear pattern of evolution in the *Thecidellina* group *sensu* Williams (1973, fig. 100, p. 468) is beginning to emerge. Essentially, it seems that two plexi of descent are involved: one, including *Moorellina*, *Eudesella*, and *Rioultina* exhibits retention of a fully developed secondary fibrous layer in both valves; the other, with its early representatives as yet little known but including *Pachymoorellina*, *Bifolium*, *Mimikonstantia*, *Thecidiopsis*, and *Thecidellina*, exhibits a secondary fibrous layer suppressed to a greater or lesser extent and a continuity of organization of microstructural features (such as acicular crystallite tracts and characteristic secondary fibre segregations) traceable over long periods of time.

CONCLUSIONS

The present study further illustrates the recognized (Nekvasilová 1967, p. 128) inherent weakness of thecideidine taxonomy based on the morphology of separated valves in which delicate structures such as brachial lobes and peripheral flanges are so easily damaged, particularly as convergent evolution (Baker 1984) appears to have played such an important role in the emergence of representatives of the suborder.

It is remarkable to find the shell microstructure of an Aalenian monoseptate species so closely paralleled in a polyseptate species of early Cretaceous age. Also, the discovery of a suppressed secondary fibrous shell mosaic in *M. sculpta*, its correlation with *T. tetragona*, and, via ontogeny, the probability of its descent from a monoseptate ancestor now assumes greater significance. It appears that the *Thecidellina* group had its origin in a *Pachymoorellina*-type ancestor in the Lias. The search for this must continue, however, since all the described contenders have a fully developed secondary fibrous shell layer. It is concluded that the *Moorellina* plexus, already diverged from the main line of descent by the Lias, did not survive the Jurassic. Also, the new evidence substantiates the view that the main line of descent of the *Thecidellina* plexus, via *Pachymoorellina*-type stock, probably followed a rectilinear trend similar to that exhibited by the *Lacazella* group.

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