MORPHOLOGY AND SHELL MICROSTRUCTURE OF CRETACEOUS THECIDEIDINE BRACHIOPODS AND THEIR BEARING ON THECIDEIDINE PHYLOGENY

by PETER G. BAKER

ABSTRACT. New morphological and microstructural information from *Bifolium faringdonense* (Davidson, 1874), *Bosquetella campichei* (de Loriol, 1872), *Thecidiopsis tetragona* (Roemer, 1839) and *Thecidiopsis bohemica imperfecta* Nekvasilová, 1967 indicates that the specimens assigned to *T. bohemica imperfecta* do not belong to *Thecidiopsis*. The organization and microstructure of the brachial valve, place *T. bohemica imperfecta* close to thecidellinids such as the Recent *Thecidellina blochmanni* Dall, 1920. In comparison with other Cretaceous monoseptate forms, differences in morphology and shell microstructure clearly separate *T. bohemica imperfecta, B. faringdonense* and *B. campichei*, and are considered to be distinctive enough to allow *T. bohemica imperfecta* to be assigned to a new genus, *Eothecidellina*. The discovery of canopied brachial lobes in *B. faringdonense* and rudimentary canopies in the Middle Jurassic *Moorellina dubia* (d'Orbigny, 1850), together with the clarification of the systematic position of *Eothecidellina imperfecta* (Nekvasilová), provides a much clearer picture of thecidellinid evolution. The correlation of the morphology and shell microstructure of *T. tetragona* with basal Middle Jurassic genera and the narrowing of the thecidein plexus of descent, enables a revised thecideidine phylogeny to be presented.

DISCOVERY of a Middle Jurassic thecideidine with a partially suppressed fibrous secondary shell mosaic (Baker and Elston 1984), recognition of shell microstructural features traceable over long periods of time (Baker 1989), and studies on ontogeny (Smirnova 1969, 1984) pointed to weaknesses in existing taxonomic and phylogenetic frameworks for thecideidines. The evidence indicated that conclusions about thecideidine evolution based on brachial lobe morphology (Pajaud 1970) and the time of onset of the suppression of fibrous secondary shell secretion (Williams 1973) had been premature. Smirnova's (1984) contention that *Thecidellina* arose from Upper Aptian *Bifolium* stock, prompted the restudy of Upper Cenomanian monoseptate forms previously assigned (Nekvasilová 1967) to *Thecidiopsis*, and renewal of the search (Baker and Laurie 1978) for better-preserved specimens of *Bifolium*. The further suggestion that *Thecidellina* might be traced back to a Jurassic moorellinid ancestor (Smirnova 1984) revived interest in the smaller species of *Moorellina*. When it was shown (Baker and Elston 1984; Baker 1989) that the Lower Cretaceous (Upper Valanginian) *Thecidiopsis tetragona* (Roemer, 1839) could also be traced back to Middle Jurassic (Aalenian) roots, a restudy of *T. tetragona* became necessary. Although the general *Thecidiopsis* shell succession had been established (Williams 1973; Smirnova 1979, 1984), the requirement for a clearer understanding of the detailed shell microstructure of *T. tetragona* was increased following the discovery by Baker (1989) of a parallel shell development pattern in the early Middle Jurassic *Pachymoorellina dundriensis* (Rollier, 1915).

MATERIAL AND METHODS

Specimens of *Eothecidellina imperfecta* (Nekvasilová, 1967) from Zbyslav, Czechoslovakia, were obtained from Dr O. Nekvasilová, Academy of Sciences Prague. Specimens of *Bosquetella campichei* (de Loriol, 1872) and *Thecidiopsis tetragona* (Roemer, 1839) from Château du Marais, Auberson, were loaned from the Campiche Collection, housed in the Musée Géologique, Lausanne.

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Specimens of *Bifolium faringdonense* (Davidson, 1874) were selected from material previously collected from the Faringdon Sponge Gravels (Baker and Laurie 1978) and *Moorellina dubia* (*d'Orbigny, 1850*) from material collected from Crickley Hill, near Cheltenham (Baker 1989).

The holotype of *Eothecidellina imperfecta* (ON-3) and paratypes ON-1, ON-2, ON-4 to ON-8 and ON-2661 to ON-2664 are housed in the Geological Institute of the Czechoslovak Academy of Sciences in Prague. The specimens of *E. imperfecta*, *Bifolium faringdonense* and *Moorellina dubia* figured in this paper (BD9023–BD9028) are housed in the British Museum (Natural History). The specimens of *Bosquetella campichei* (reg. no. 42530) and *Thecidiopsis tetragona* (reg. nos 42531–42533) are housed in the Musée Géologique, Lausanne.

The techniques used for the recovery and preparation of *E. imperfecta* were fully documented by Nekvasilová (1967, p. 117) and require no elaboration here. Similarly, for the recovery and preparation of *B. faringdonense* specimens see Baker and Laurie (1978, p. 557), and for *M. dubia* see Baker and Elston (1984, p. 777).

SYSTEMATIC PALAEONTOLOGY

Order SPIRIFERIDA Waagen, 1883
Suborder THECIDEIDINA Elliott, 1958
Superfamily THECIDEACEA Gray, 1840
Family THECIDELLINIDAE Elliott, 1958
Subfamily THECIDELLININAE Elliott, 1953
Genus EOTHECIDELLINA gen. nov.

Etymology. From the Greek *eos* (dawn) after the very early appearance of canopied intrabrachial cavities of thecidellinid type.

Type species. *Thecidiopsis* (*Thecidiopsis*) *bohemica imperfecta* Nekvasilová, 1967.

Age. Upper Cretaceous, Upper Cenomanian.

Diagnosis. Small endopunctate thecidellinin, pedicle valve typically with a flat, well defined ventral interarea, shallow anterior sulcus and relatively large, rounded-triangular attachment scar, brachial valve with intrabrachial cavities roofed by perforate canopies and a long, straight, median septum onto which the characteristic pustulose ornament of the subperipheral rim is extended.

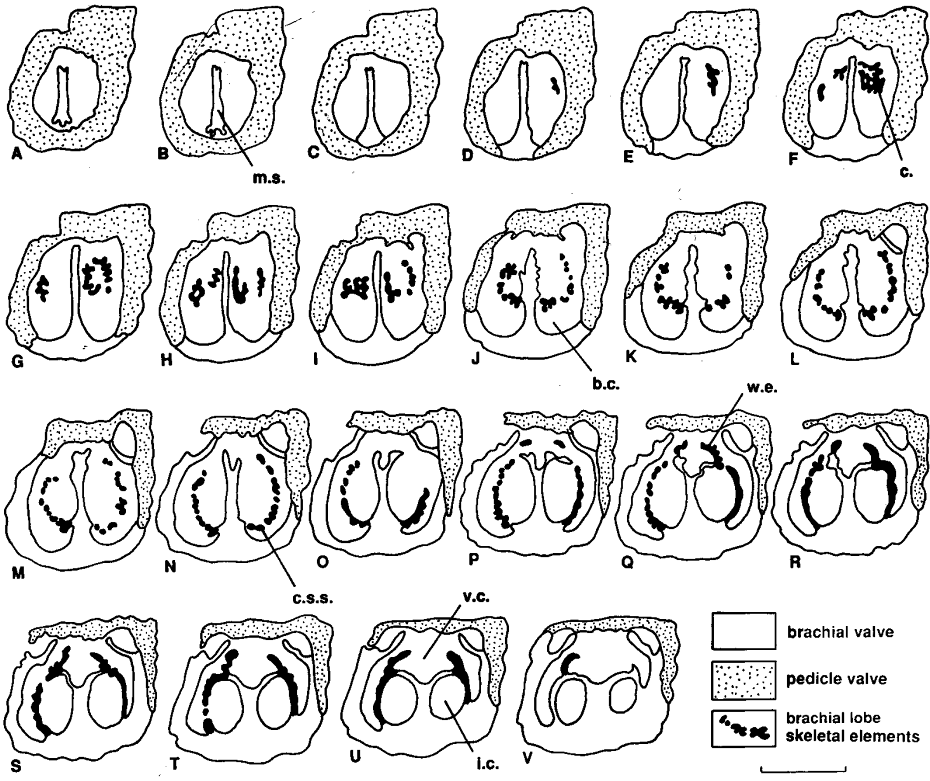
Eothecidellina imperfecta (Nekvasilová, 1967)

Plate 1, figs 1–6; Plate 3, figs 1–3; Plate 4, figs 1–7;
Text-figs 1, 4A–C, 5A–C, 6C

1868	*Thecidium* sp.; Schloenbach, p. 156, pl. 5, fig. 9
1959	*Thecidiopsis* (*Thecidiopsis*) *bohemica* Backhaus; Nekvasilová, p. 147; pl. 11, figs 1–4.
1967	*Thecidiopsis* (*Thecidiopsis*) *bohemica imperfecta* Nekvasilová, p. 115–136, pls 1–8; text-figs 1–11.
1968	*Thecidiopsis bohemica imperfecta* Nekvasilová; Pajaud, p. 45.
1968	*Thecidiopsis bohemica imperfecta* Nekvasilová; Smirnova and Pajaud, p. 143.
1970	*Thecidiopsis bohemica imperfecta* Nekv.; Pajaud p. 208, pl. 4, fig. 2.
1972	*Thecidiopsis* (*Thecidiopsis*) *bohemica* Backhaus; Smirnova, p. 123.

Type specimens. Holotype ON-3, paratypes ON-1, ON-2, ON-4 to ON-8, ON-2661 to ON-2664, hypotypes BD9023–BD9025.

Distribution. The locality from which the type material was obtained is given as Zbyslav, near Čáslav, Bohemia, Czechoslovakia. The species has, however, been recorded from a number of other Bohemian localities, namely



TEXT-FIG. 1. *Eothecidellina imperfecta* (Nekvasilová). A–V, 'Wild' stereomicroscope traces of cellulose acetate peels (8–25, out of series 1–49) of serial sections through the median septum and brachial lobes of specimen BD 9024. Plane of section horizontal, relative to the surface of the brachial lobes; intersecting the commissural plane with an angle of about 5° ventral deflection. Abbreviations: b.c., brachial cavity; c., brachial lobe canopy; c.s.s. canopy skeletal support; i.c., intrabrachial cavity; m.s., median septum; v.c., visceral cavity; w.e., wing-like extension. Peel interval approximately 20 μm. Scale bar represents 1·0 mm.

Kamajka and Starkoč near Čáslav, Kank near Kutná Hora, Vitězov near Velim, Skalka near Zehušice and Předboj near Prague. At all the recorded localities the material was collected from sediments of Upper Cenomanian age, approximating stratigraphically to a *plenus* Zone position.

Diagnosis. Eothecidellina up to about 2·5 mm in length, 1·9 mm wide and 2·00 mm thick. Outline roughly pyriform; dorsiconvex initially, but developing a characteristically triangular lateral profile after the appearance of the free ventral wall. Pseudodeltidium flat, parallel with the surface of the ventral interarea, demarcated only by indistinct grooves. Hinge line straight with a ratio of length to shell width of approximately 0·5. Brachial valve moderately convex with a small hypercline dorsal interarea.

Description. Small, roughly pyriform thecidellinid, with a relatively large attachment scar and well developed free ventral wall giving rise to a characteristically triangular lateral profile. The ventral interarea is clearly developed with a flat indistinct pseudodeltidium. The moderately convex brachial valve has a small but well defined hypercline dorsal interarea.

MORPHOLOGY, GROWTH AND SHELL MICROSTRUCTURE OF *EOTHECIDELLINA IMPERFECTA*

Valve characters

Pedicle valve. Hemispondylium raised, with clearly defined dental ridges, hemispondylial plate and supporting septum, rising from a weakly developed median ridge. The teeth are clearly cyrtomatodont and not widely separated. The inner surface of the valve is ornamented by scattered tubercles. In the anterior sector the tubercles are arranged in more linear series and many coalesce to form low ridges on the inner surface of the free ventral wall.

Brachial valve. (Pl. 1, figs 3–6; Text-figs 1, 4B, 5A–C, 6C). The cardinal margin is straight, extending for slightly more than half the maximum width of the valve. The cardinal process is relatively large, faintly trilobed, and with a characteristic dorsal deflection. The sides diverge anteriorly to form well developed inner socket ridges. The lateral adductor muscle scars are erect (orientated almost perpendicular to the commissural plane) and asymmetrically pyriform as a result of constriction by the cardinal process. The brachial bridge is well developed. The outer surface of the subperipheral rim is ornamented by up to four rows of small tubercles, with the tubercles of each row usually offset by one half phase relative to adjacent rows. The inner margin of the subperipheral rim is characterized by a row of elongate impressed areas which have been identified by Williams (1973, p. 48, fig. 10) as lophophore muscle scars. The tuberculate ornament of the subperipheral rim extends onto the median septum which is typically long and prominent, relatively thick anteriorly and, posteriorly, arching over the visceral cavity. The brachial cavities are occupied by medium-sized brachial lobes which are developed as perforate canopies over intrabrachial cavities. The brachial lobes are invariably broken in separated valves, so that the intrabrachial cavities are exposed as two shallow, roughly oval depressions, characteristically ringed by the damaged canopy skeletal supports (Pl. 1 fig. 3; Pl. 3, fig. 3). Each complete brachial lobe, therefore, represents a sort of posteriorly open, perforate calcareous sac (Text-fig. 6C), situated on either side of the median septum and slightly contiguous with it posteriorly. A previously unrecorded feature of the brachial lobes is the development of a pair of wing-like extensions (Text-fig. 1R) arching backwards into the visceral cavity. The broken remains of these structures can be identified (Pl. 1, figs 4 and 5), even in brachial valves in which the brachial lobes have been substantially damaged.

Ontogeny

The early ontogeny of *E. imperfecta* is not known. All the characters of pedicle and brachial valves are present in the smallest valves available. In the pedicle valve, the beginning of the development of the free ventral wall is thought to coincide with the onset of sexual maturity (Nekvasilová 1967,

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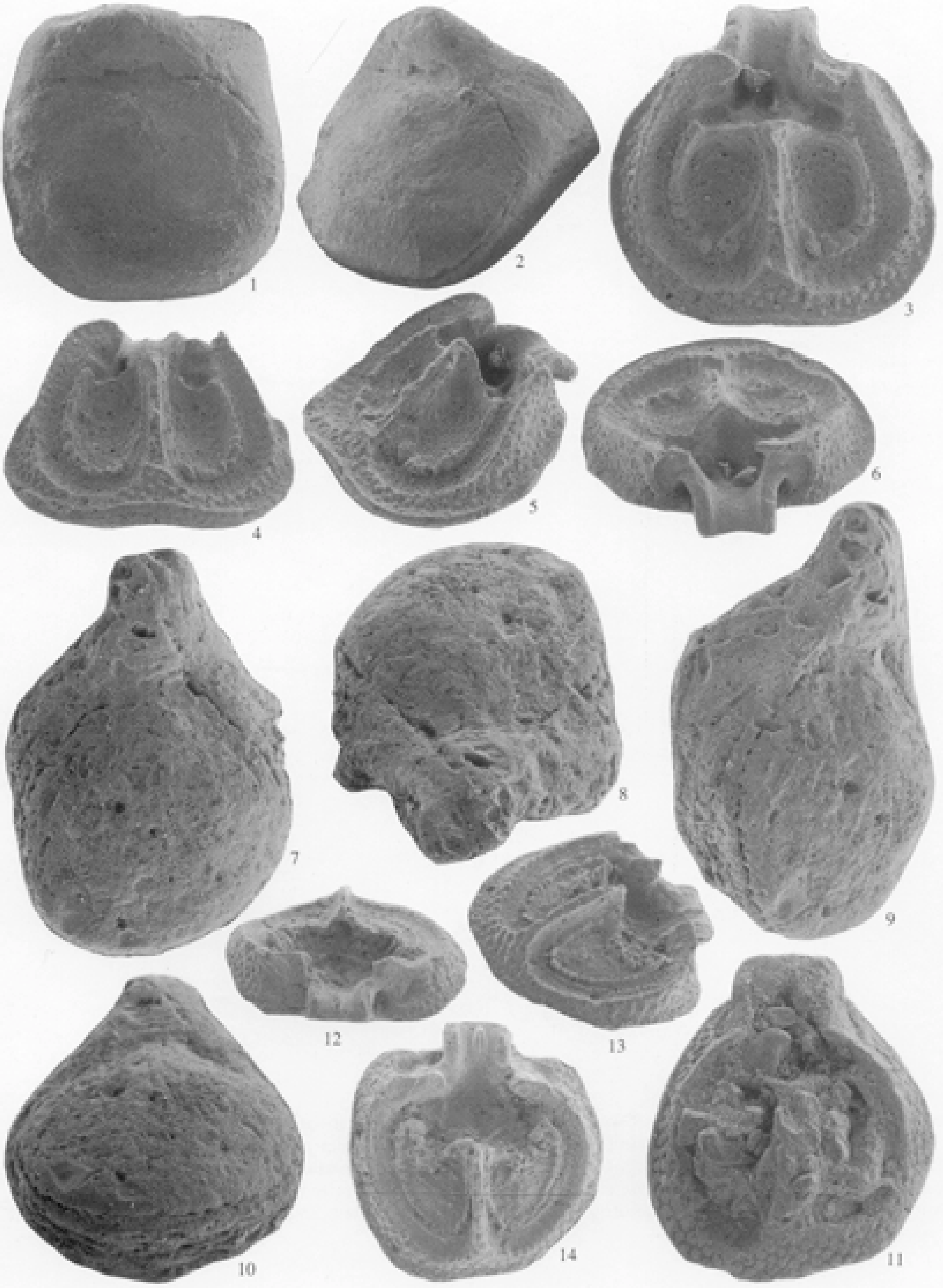
EXPLANATION OF PLATE 1

Figs 1–6. *Eothecidellina imperfecta* (Nekvasilová). Upper Cenomanian of Zbyslav, Czechoslovakia. 1 and 2, BD 9023; brachial and three-quarters profile views, photographic record, of hypotype sectioned complete shell, × 18. 3–6, BD 9025; brachial anterior, three-quarters profile and posterior views of a hypotype to show the morphology typical of separated brachial valves in which the brachial canopies have been destroyed, exposing the intrabrachial cavities, × 20.

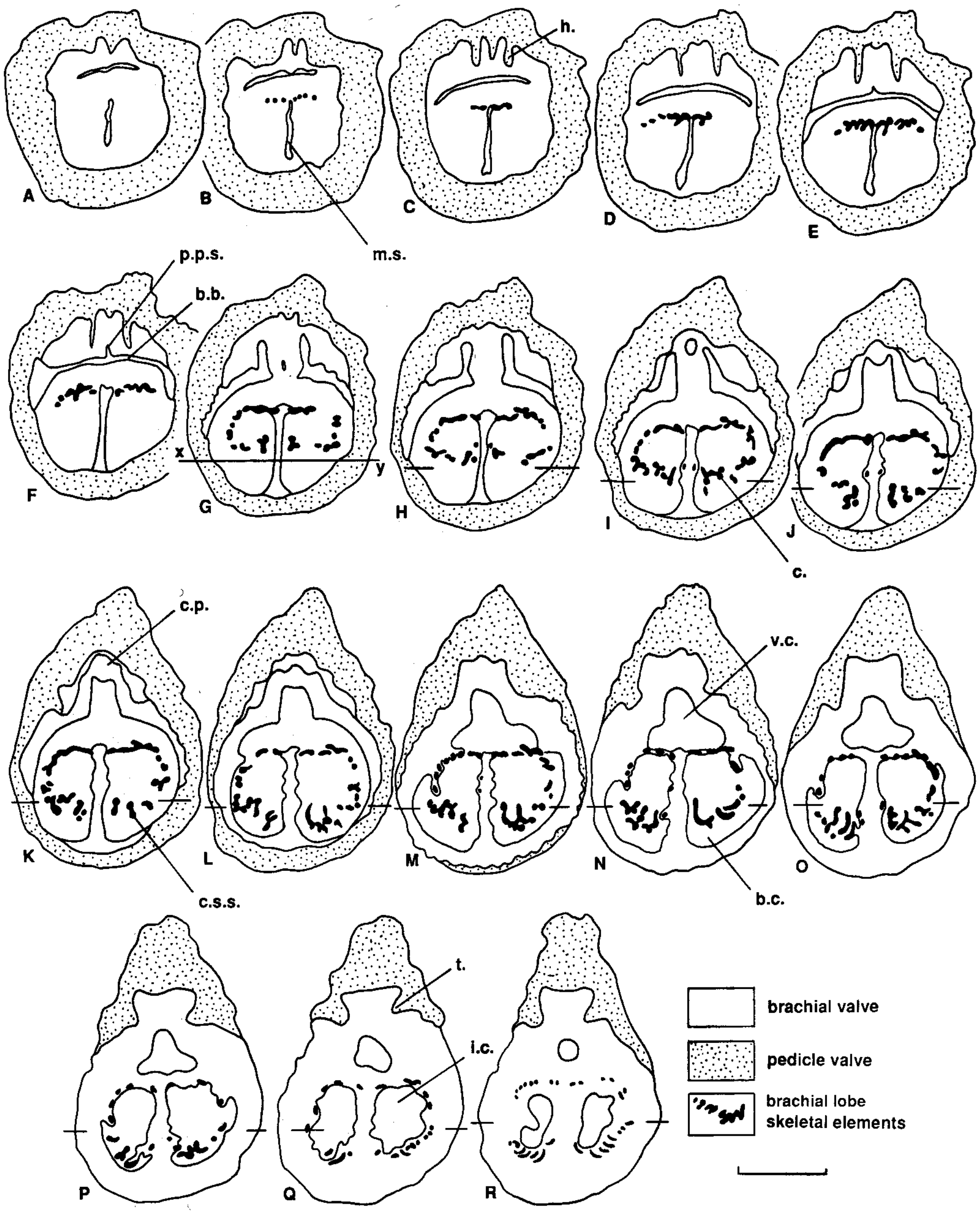
Figs 7–11. *Bifolium faringdonense* (Davidson). Upper Aptian; Faringdon, Oxfordshire. 7–10, BD 9026; brachial, posterior, lateral and anterior views, photographic record, of hypotype sectioned complete shell, × 20. 11, BD 9027; interior of hypotype brachial valve showing the remains of brachial canopies and the intrabrachial cavities filled with quartz grain matrix, × 18.

Figs 12–14. *Bosquetella campichei* (de Loriol). Upper Valanginian; Auberson; Musée Géologique, Lausanne, 42530; posterior, three-quarters profile and brachial views, photographic record, of hypotype sectioned brachial valve, × 12.

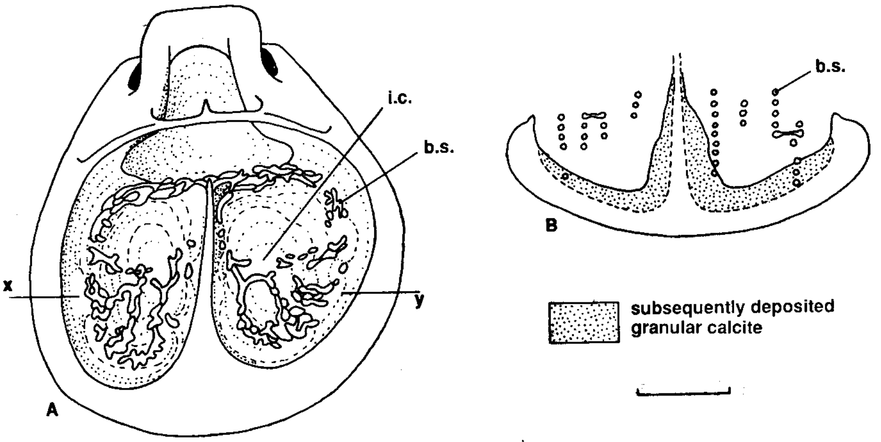
All scanning electron micrographs of gold-coated material.



BAKER, *Eothecidellina, Bifolium, Bosquetella*



TEXT-FIG. 2. *Bifolium faringdonense* (Davidson). A–R, 'Wild' stereomicroscope traces of cellulose acetate peels (13–30, out of series 1–36) of serial sections through the median septum and brachial lobes of specimen BD 9026. Plane of section horizontal, approximately parallel with the commissural plane. Abbreviations as in Text-figure 1, plus: b.b., brachial bridge; c.p., cardinal process; h., hemispondylium of pedicle valve; p.p.s., posteriorly projecting spur; t., hinge tooth. Peel interval approximately 25 μm. Scale bar represents 1·0 mm.



TEXT-FIG. 3. *Bifolium faringdonense* (Davidson). Partial reconstruction of the brachial lobes of serially sectioned specimen BD 9026, with no attempt to hypothesise the nature of the connection of the skeletal elements between successive peels. A, brachial view. B, vertical plot of peel data along x–y (Text-figs 2 and 3A) for acetate peels 19–33 (Text-fig. 2G–R inclusive), to show the brachial lobe skeletal elements in tranverse location, forming a canopy over the intrabrachial cavities. Abbreviations; b.s., brachial lobe skeletal elements; i.c., intrabrachial cavity. For ease of correlation of peel traces with original acetate peels, left is plotted as viewed, not anatomically. Scale bar represents 0·5 mm.

p. 125). In the brachial valve, ontogenetic development is characterized by slight changes in the relative proportion of the median septum and the brachial lobes, and also by increasing dorsal deflection of the cardinal process. The median septum, initially quite stubby, becomes increasingly blade-like. The immature brachial lobe canopies are characterized by relatively large, more irregular perforations which are reported to be gradually sealed as the brachial lobes mature (Nekvasilová 1967, p. 126).

Microstructure (Text-fig. 4A–C)

Although the shell shows the suppression of fibrous secondary shell typical of Cretaceous thecideidines, *E. imperfecta* is unusual among Upper Cretaceous species in that fibrous secondary shell remains a major component of the pedicle valve.

Pedicle valve. A thick granular primary layer is present, underlain by fibrous secondary shell. The fibrous secondary shell layer appears to be partially suppressed and is absent from the attachment scar area. It is, however, present as a continuous thin sheet over the entire area of the free ventral wall (Text-fig. 4C). In this region the granular calcite layer is approximately 75 μm thick, almost half the thickness of the shell wall. Sections (Pl. 4, figs 1–5) show that, at its inner boundary, the granular layer is longitudinally invaginated into the fibrous layer and eventually may become pinched off to form flattened tubercle cores surrounded by fibrous secondary shell. The development pattern seems to restrict the formation of tubercles to a single row in antero-lateral sectors of the valve. However, the thickened median ridge (Pl. 4, fig. 7) can clearly be seen to have originated from a succession of such structures, sandwiched between sheets of fibrous secondary shell. A normal orthodoxly stacked fibrous secondary shell succession (Williams 1973) is also seen in the hinge teeth.

Brachial valve. The secretion of fibrous secondary shell is almost completely suppressed, secondary fibres only occurring on the sides of the cardinal process and the inner socket ridges (Pl. 3, fig. 2). The remainder of the shell (Text-fig. 4B) is composed of granular calcite (Pl. 3, fig. 1; Pl. 4, fig. 6) in which the mainly equant granules are up to 3·0 μm in diameter.

MORPHOLOGY AND SHELL MICROSTRUCTURE OF OTHER CRETACEOUS THECIDEIDINES

Bifolium faringdonense (*Davidson*), *Upper Aptian*

Morphology. The morphology of *B. faringdonense* has been described by Elliott (1948) and Pajaud (1970) with additional comments by Baker and Laurie (1978). The form of the brachial lobes has always been interpreted from their morphology as seen in separated brachial valves. The indequacy of this approach was noted by Nekvasilová (1967), but the weakly coherent matrix of complete shells frustrated attempts (Baker and Laurie 1978, p. 557) to obtain reliable evidence from Faringdon specimens.

Recently, however, a brachial valve with partially preserved brachial lobes was discovered (Pl. 1, fig. 11; Pl. 2, fig. 6), and also a complete shell (Pl. 1, figs 7–10) filled with crystalline calcite. The latter when serially sectioned (Text-fig. 2) enabled the first full description of the brachial apparatus of *B. faringdonense*. The previously described auriform structures (Pajaud 1970, p. 193; Baker and Laurie 1978, p. 563) are identified as the damaged supports of a network of skeletal strands almost 40 μm thick, anastomosing to form perforate canopies, partially roofing the intrabrachial cavities (Text-figs 3 and 6B). The posteriorly projecting spur, first observed in juveniles (Baker and Laurie 1978, p. 568) is confirmed by the current study (Text-figs 2F and 3A).

Microstructure. Previous studies of shell microstructure (Williams 1973, p. 465; Baker and Laurie 1978, p. 569) have shown that, with the exception of the teeth and inner socket ridges, fibrous secondary shell is replaced by granular calcite in *B. faringdonense*. Splayed acicular crystallites are associated with the development of tubercles in the subperipheral rim. The current study reveals the presence of secondary fibres in the sides of the cardinal process. Also, in (presumably aged) adults the brachial valve is so thickened by the subsequent deposition of granular calcite, that the skeletal supports of the brachial lobe canopies become substantially buried (Text-figs 2Q, R and 3B).

Bosquetella campichei (*de Loriol*), *Upper Valanginian* (Pl. 1, figs 12–14)

Microstructure

Pedicle valve. No pedicle valve was available for study from the Campiche Collection, but Smirnova (1984) described pedicle valves from Solovevka, Crimea, in which tubercle cores of granular calcite are pinched off from the primary layer and enveloped by secondary fibres in a manner very similar to that seen in *E. imperfecta*. In *B. campichei*, however, unlike *E. imperfecta*, fibrous shell is underlain by granular calcite (Smirnova 1984, pl. 23, fig. 1).

Brachial valve. Fibrous secondary shell is strongly suppressed so that, with the exception of the

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EXPLANATION OF PLATE 2

Figs 1–5. *Thecidiopsis tetragona* (Roemer). Upper Valanginian; Auberson; Musée Géologique, Lausanne. 1 and 2, 42531; brachial and three-quarters profile view, photographic record, of a sectioned young adult complete shell, × 12. 3–5, 42532; brachial, tilted lateral and posterior views showing the morphology typical of separated brachial valves and the interdigitation of brachial lobes (all damaged) and lateral septa, × 15.

Fig. 6. *Bifolium faringdonense* (Davidson). Angled view (rotation, 45°; tilt angle, 50°) of the right brachial cavity of specimen BD 9027, showing the remains of the brachial canopy (arrowed) in more detail, × 30.

Figs 7–9. *Moorellina dubia* (d'Orbigny). Aalenian; Crickley Hill, near Cheltenham; BD 9028; three-quarters profile, posterior and brachial views of a hypotype showing the almost intact brachial lobes in the form of rudimentary canopies; the external surface of this specimen (especially figure 8, lower) is encrusted by a bryozoan, × 30.

All scanning electron micrographs of gold-coated material.

PLATE 2


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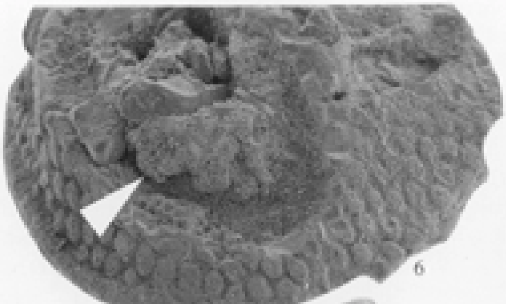
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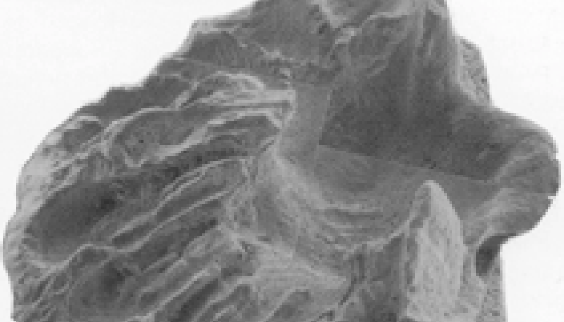
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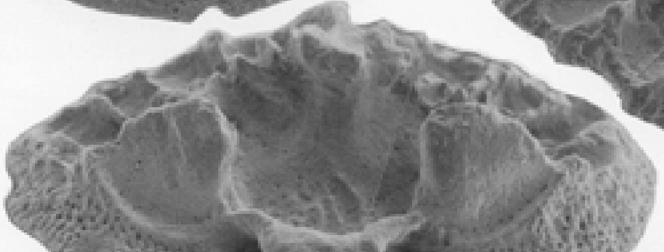
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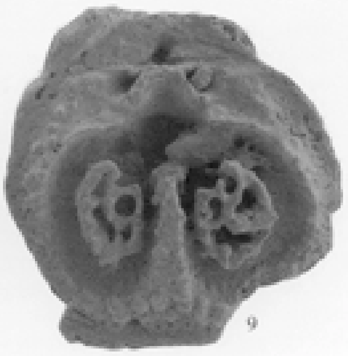
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BAKER, *Thecidiopsis*, *Bifolium*, *Moorellina* cardinal process and inner socket ridges, the brachial valve consists of a single layer of microcrystalline calcite. This consists of equant grains about 3·5 μm in diameter (Pl. 3, fig. 7) but, in the subperipheral rim and areas close to it where resorption has occurred, tubercle cores are formed from acicular crystallites which show the same splayed orientation (Pl. 4, fig. 8) as that found in *Bifolium faringdonense*.

Thecidiopsis tetragona *(Roemer), Upper Valanginian* (Pl. 2, figs 1–5)

Microstructure

Smirnova's (1979, 1984) studies revealed that in *T. tetragona* fibrous secondary shell is strongly suppressed. She identified a primary layer of granular or acicular calcite underlain principally by granular calcite, with or without the presence of fibrous secondary shell. Secondary fibres are restricted to the hinge teeth and the hemispondylium, and to occurrence as irregular bundles in the wall of the pedicle valve. In the brachial valve, secondary fibres are only to be found in the inner socket ridges. Additionally in *T. tetragona*, the secondary shell mosaic was reported (Smirnova 1979, p. 340) to be complicated by the inclusion of 'rod-like' bodies and 'fir-tree' structures.

Pedicle valve. (Text-fig. 4F). Detailed investigation of serially sectioned specimens from the Campiche Collection, confirms the presence of a thin granular primary layer and enables the so-called, rod-like bodies, to be identified as acicular crystallite tubercle cores (Baker 1989, p. 62) of the type found in *Pachymoorellina*. Sections parallel with the boundary of the primary layer show that the tubercle cores are initiated through 'seeding' acicular crystallites on to its inner surface (Pl. 5, fig. 1). Initially, the tubercle cores remain separated by granular calcite (Pl. 5, fig. 2) but as they develop, this is gradually excluded and the tubercle cores come into lateral contact with their neighbours (Pl. 5, fig. 7). Each generation is usually offset by a half-phase so that, in oblique section, a very characteristic overlapping 'fish-scale' effect is produced (Pl. 5, fig. 8). In high oblique or transverse section (Pl. 5, fig. 4) the tubercle cores often appear to have a centre column of granular calcite. This is usually a consequence of the splayed arrangement of acicular crystallites forming the tubercle core. Crystallites in near axial orientation will be sectioned transversely (Pl. 5, fig. 3) and give the appearance of being granular. Some tubercle cores, however, do appear to have an axial structure in which scalenohedra-like bodies (Pl. 5, fig. 5) are mixed with the axially orientated acicular crystallites. Away from the hinge teeth and hemispondylium, where it is well represented, fibrous secondary shell is restricted to the inner margin of the free ventral wall. It occurs as irregular, attenuated strands (Pl. 5, figs 3 and 6), pinched and deflected by the development of the acicular

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EXPLANATION OF PLATE 3

Figs 1–3. *Eothecidellina imperfecta* (Nekvasilová). All BD 9025. 1, granular calcite shell and endopuncta (top left) in the floor of the left brachial cavity, × 2000. 2, right inner socket ridge (socket, lower centre) showing the development of fibrous secondary shell, × 150. 3, left brachial cavity showing detail of the broken canopy supports, ringing the intrabrachial cavity (upper right), × 100.

Figs 4 and 5. *Thecidiopsis tetragona* (Roemer). 4, 42531; granular primary layer, × 4000. 5, 42532; coarser secondarily deposited granular calcite (cf. Fig. 4) in the floor of the brachial cavity, associated with the development of the brachial lobes, × 2000.

Figs 6 and 7. *Bosquetella campichei* (de Loriol). 6, 42530; enlarged view of the brachial cavities showing the asymmetrically pyriform brachial lobes and absence of intrabrachial cavities, × 35. 7, fracture surface on the median septum of the same specimen; showing the granular calcite shell, × 3000.

Figs 8 and 9. *Moorellina dubia* (D'Orbigny). 8, BD 9028; enlarged view of the right brachial cavity showing detail of the canopy and the nature of the canopy skeletal supports, × 130. 9, same specimen; showing the typical partially resorbed moorellinid fibrous secondary shell, × 3000.

All scanning electron micrographs of gold coated material.


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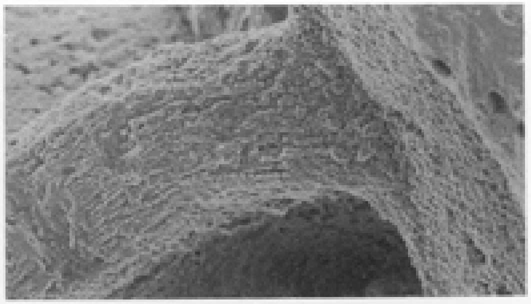
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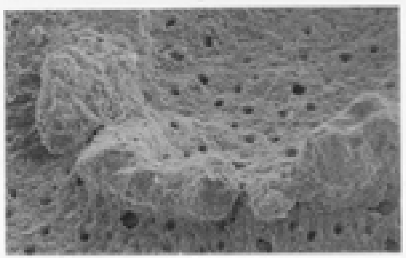
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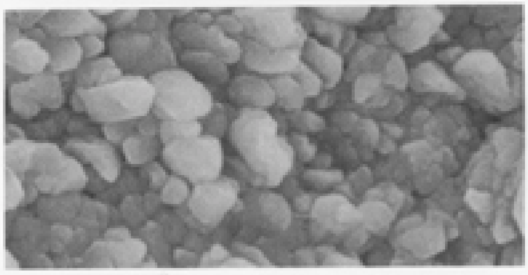
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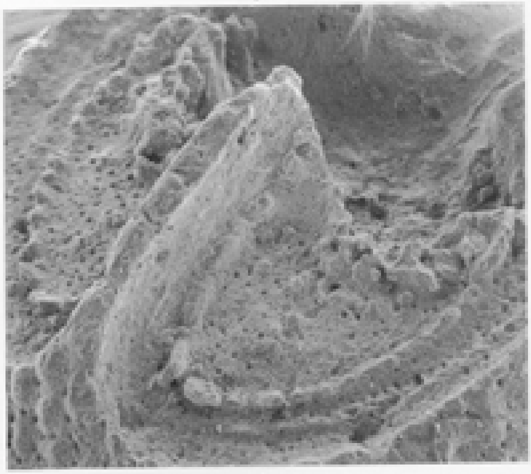
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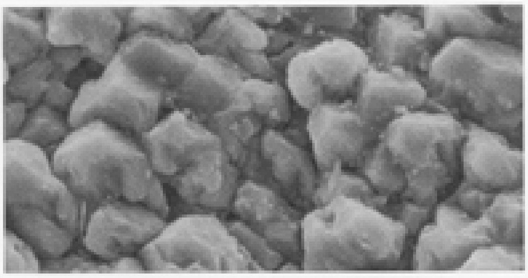
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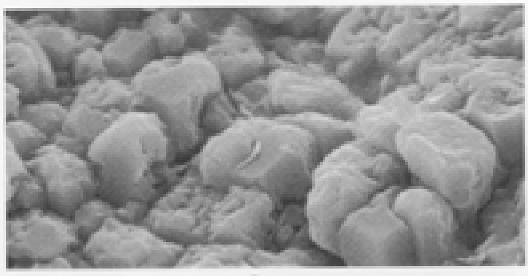
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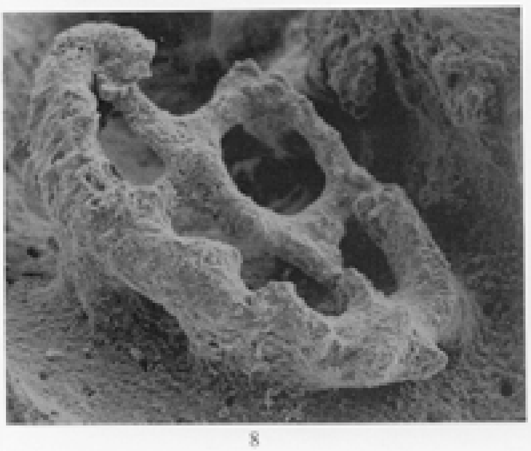
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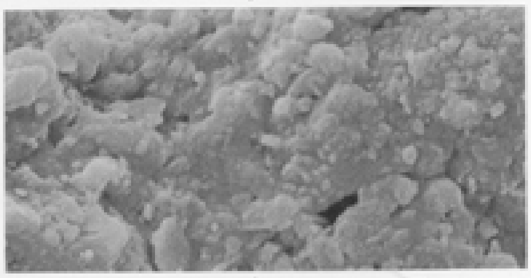
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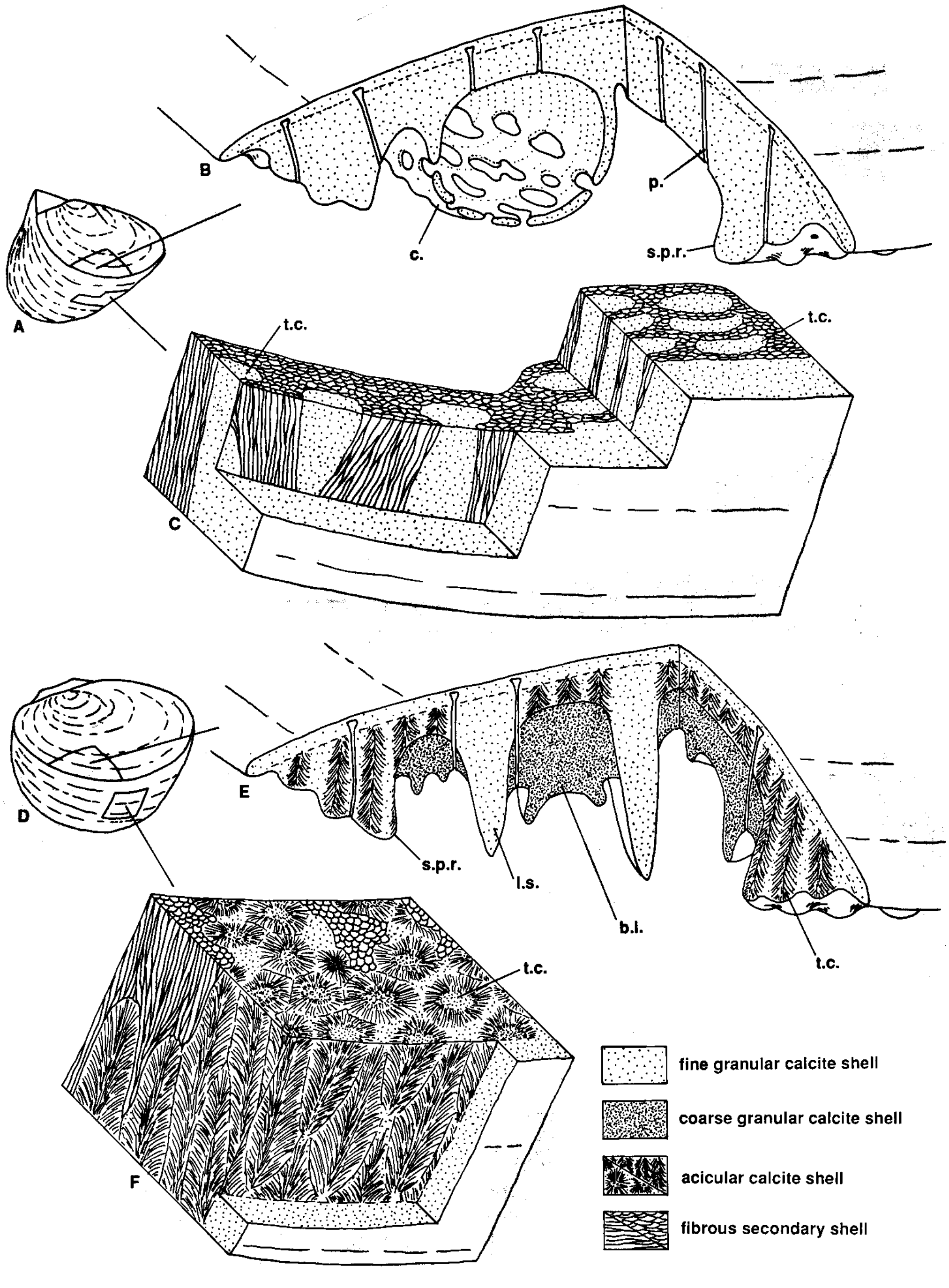
BAKER, *Eothecidellina*, *Thecidiopsis*, *Bosquetella*, *Moorellina*



TEXT-FIG. 4. Diagrammatic reconstruction of the shell microstructure of A–C, *Eothecidellina imperfecta* (Nekvasilová) and D–F, *Thecidiopsis tetragona* (Roemer). A, D, locational diagrams. B, E, block diagrams showing the microstructure of brachial valves. C, F, block diagrams showing the microstructure of pedicle valves. Abbreviations: b.l., brachial lobe interdigitation; c., brachial lobe canopy; l.s., lateral septum; p., endopuncta; s.p.r., subperipheral rim; t.c., tubercle core.

crystallite tubercle cores. In view of their abrupt appearance close the inner surface of the shell wall, these groups of secondary fibres must, presumably, originate from epithelial cells which had previously been secreting acicular calcite. Somehow the 'memory' of certain cells is triggered and fibrous secondary shell is secreted.

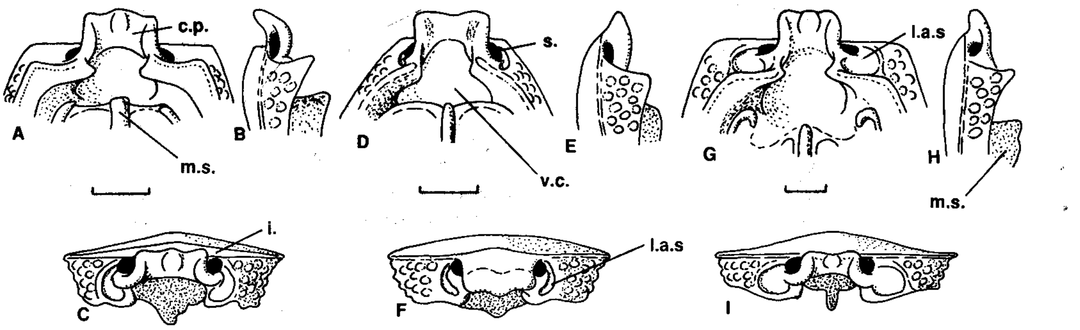
Brachial valve. (Text-fig 4E). Smirnova (1979, p. 340) described the brachial valve as double layered, with an outer crystalline layer containing 'fir-tree' structures, aligned nearly perpendicular to the external surface of the valve. The fir-trees were reported to be abruptly cut off from the granular calcite inner layer. Serially sectioned Campiche specimens show that the fir-trees (subsequently called 'herring-bone' patterns by Smirnova (1984)) are the equivalent of the acicular crystallite splays (Baker and Laurie 1978, p. 564, text-fig. 5D) found in the tubercle cores of *Bifolium*. In *T. tetragona* the wall of the brachial valve is thickened as a result of the increasing development of the brachial lobes and their interdigitation with the lateral septa. The inner layer described by Smirnova is the product of deposition of granular calcite in areas where shell resorptive activity had previously been operative. The cut-off, therefore, as in *Pachymoorellina dundriensis* is really the trace of the transgression across an older resorption surface. As in *P. dundriensis* the secondarily deposited granular calcite is coarser (Pl. 3, fig. 5) than the granular calcite underlying the transgression surface (Pl. 3, fig. 4). Clearly, the so-called third layer (Smirnova 1979, p. 340) associated with the development of the hemispondylium in the pedicle valve of *T. tetragona* has the same origin. Similar transgression surfaces have been identified in *Thecidellina barretti* (Davidson, 1864) by Williams (1973, p. 452, fig. 26).

DISCUSSION

Eothecidellina imperfecta may be distinguished from *Bifolium faringdonense* and *Bosquetella campichei* through differences in morphology and shell microstructure. Brachial, posterior and lateral views of the dorsal cardinalia (Text-fig. 5) show that the lateral adductor muscle scars differ in shape, orientation and disposition. In *E. imperfecta* the cardinal margin is straight and slightly more than one-half the width of the valve (Text-fig. 5A), whereas in *B. faringdonense* it is very short, usually not extending beyond the boundary of the dental sockets (Text-fig. 5D). *B. campichei* also has a straight cardinal margin but the cardinal process is relatively, much smaller (Text fig. 5G) than that of *E. imperfecta*. The cardinal process differs in attitude (Text-fig. 5B, E, H). *E. imperfecta* has a small hypercline dorsal interarea (Text-fig. 5C), a feature not seen in *B. faringdonense* or *B. campichei* (Text-fig. 5F, I). The configuration of the brachial lobes as indicated by their skeletal elements is oval in *E. imperfecta* and *B. faringdonense* (Pl. 1, figs 3 and 11) and the canopies overarching the intrabrachial cavities are more completely developed in *E. imperfecta* than in *B. faringdonense*. In *B. campichei* the brachial lobes are asymmetrically pyriform (Pl. 1, fig. 14). There are no intrabrachial cavities (Pl. 3, fig. 6) and, as far as is known, the skeletal elements of the brachial lobes are not overarching.

With the exception of the inner socket ridges and sides of the cardinal process, the brachial valve of *E. imperfecta* appears to be composed entirely of granular calcite. There is no differentiation into acicular crystallites as seen in *B. faringdonense* and *B. campichei*. In the pedicle valve, the tubercle cores clearly originate in the same way in *E. imperfecta* and *B. campichei*, but in *B. campichei*, the tubercle cores are not stacked to form a median ridge. In *E. imperfecta* fibrous secondary shell forms a complete inner lining, whereas, in *B. campichei* the inner shell layer is composed of granular calcite. No tubercle cores have been seen in the pedicle valve of *B. faringdonense* and, except in the hinge teeth, there is no development of fibrous secondary shell.

The brachial lobe canopies of *E. imperfecta* are very similar to those of thecidellinids such as *Thecidellina blochmanni* Dall. *T. blochmanni* may be distinguished by its much smaller, incipiently trilobed cardinal process. In *Eothecidellina* the posterior projecting spur (Text-fig. 6C) may be the precursor of the much more prominent posterior extension of the *Thecidellina* brachial lobe skeleton (Text-fig. 6D). *E. imperfecta* has a brachial valve microstructure which is closely comparable with the strongly suppressed fibrous secondary shell succession of *Thecidellina barretti* (Davidson),



TEXT-FIG. 5. Drawings to show brachial, lateral and posterior views of dorsal cardinalia. A–C, *Eothecidellina imperfecta* (Nekvasilová). D–F, *Bifolium faringdonense* (Davidson). G–I, *Bosquetella campichei* (de Loriol). Abbreviations: c.p., cardinal process; i., interarea; l.a.s., lateral adductor muscle scar; m.s., median septum; s., dental socket; v.c., visceral cavity. Scale bars represent 0·5 mm.

mapped by Williams (1973). In *T. barretti* the secretion of fibrous secondary shell is also strongly suppressed in the pedicle valve, in marked contrast to the well developed fibrous secondary layer found in *E. imperfecta*.

It is probable that the specimens alleged to be juveniles of *Backhausina schlueteri* (Lundgren) and *Backhausina groenwalli* (Nielsen) figured by Pajaud (Pajaud 1970, p. 221, figs A*a* and C*b*) are assignable to *E. imperfecta*. However, because of their different age (*B. schlueteri*, Campanian; *B. groenwalli*, Danian) and geographical occurrence, they are not included in the synonymic list. In view of what is now known about ontogeny the specimens are, nevertheless, clearly separable from *Backhausina*, which destroys the argument for the neotenous derivation of *Thecidellina* from *Backhausina* (Pajaud 1970).

The differences in morphology, microstructure and stratigraphic occurrence are thought to be indicative of the taxonomic separation of *Eothecidellina* and *Thecidellina*, but similarities, particularly in the development of the brachial lobes (Text-fig. 6C, D), are thought to imply a close phylogenetic relationship. Similarly, the new evidence indicates that *Eothecidellina* and *Bifolium* are phylogenetically related. Although morphologically distinct, the similarity of the brachial lobes is

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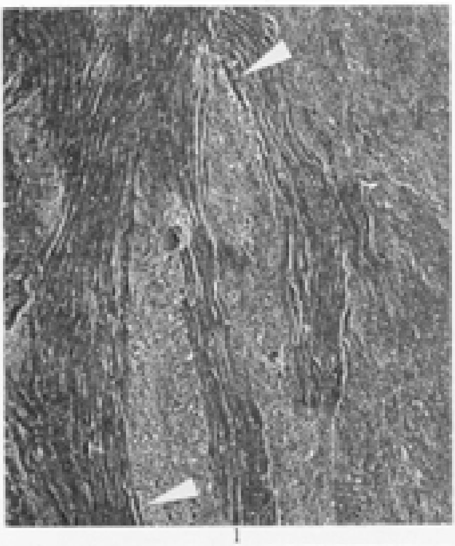
EXPLANATION OF PLATE 4

Figs 1–7. *Eothecidellina imperfecta* (Nekvasilová). 1, BD 9024/4; section through the free ventral wall of the pedicle valve, showing the general shell fabric and invaginated granular calcite in longitudinal section (section orientation – horizontal, almost parallel with the shell surface; section location – anterior sector), ×200. 2, BD 9023/33; section through the free ventral wall, showing the fibrous secondary shell and invaginated granular calcite in transverse section (section orientation – parallel with the plane of the commissure; section location – anterior sector), ×700. 3, same specimen; showing invaginated granular calcite almost pinched off to form a tubercle core, ×1000. 4, enlarged portion of figure 1, as indicated; to show the junction between granular calcite and fibrous secondary shell in detail, ×1200. 5, as figure 4; but showing detail of the convergence of fibrous secondary shell to pinch off granular calcite in the formation of a tubercle core, ×400. 6, uniform granular calcite in the median septum of the brachial valve, ×3000. 7, BD 9023/48; transverse section through the free ventral wall showing the succession of tubercle cores, stacked to form a median ridge (section orientation – parallel with the plane of the commissure; section location – anterior sector, mid-line of shell), ×250.

Fig. 8. *Bosquetella campichei* (de Loriol). 42530/23; section through the brachial valve showing acicular calcite tubercle cores in transverse section (section orientation – parallel with the plane of the commissure; section location – antero-lateral sector), ×700.

All scanning electron micrographs of gold-coated cellulose acetate peels of sectioned specimens.

PLATE 4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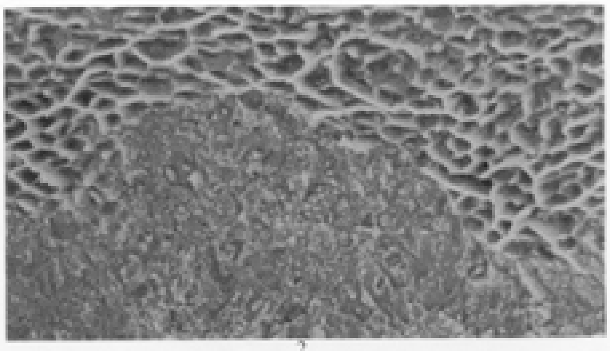
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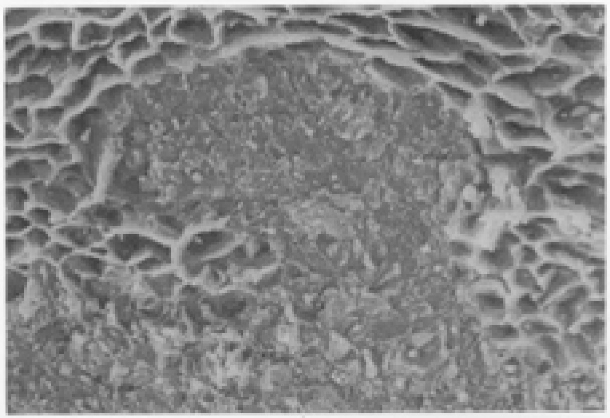
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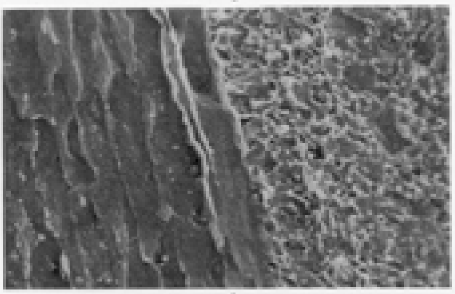
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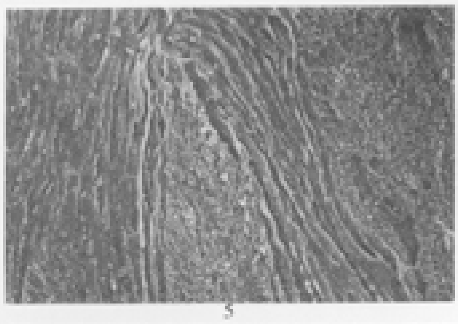
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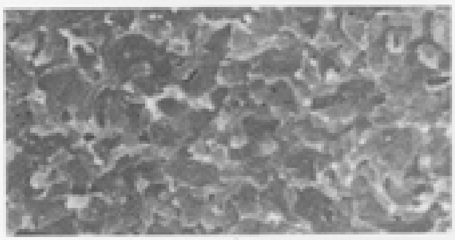
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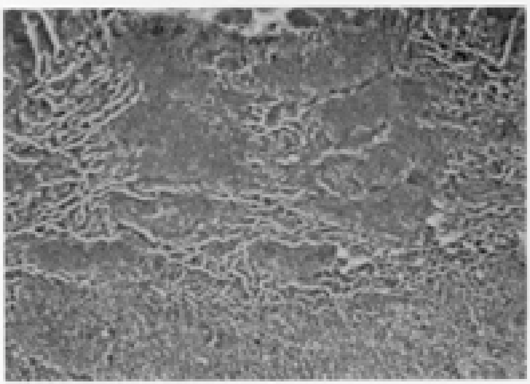
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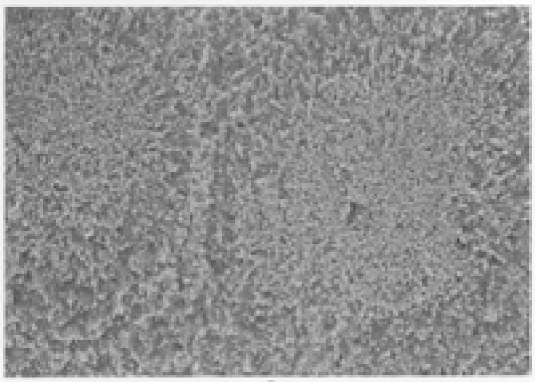
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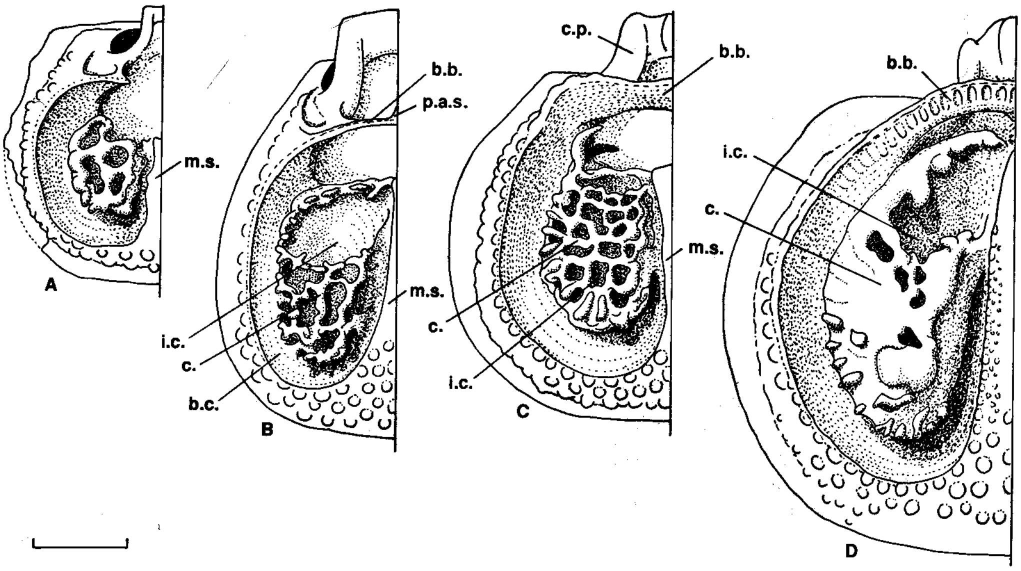
BAKER, *Eothecidellina*, *Bosquetella*



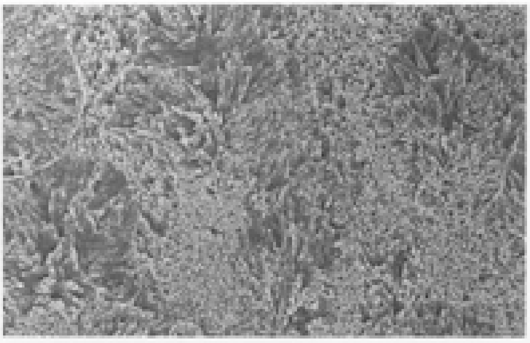
TEXT-FIG. 6. Diagrams to show the possible sequence (A–D) in the development of canopied brachial lobes. A, *Moorellina dubia* (d'Orbigny), Aalenian, drawn from specimen BD 9028. B, *Bifolium faringdonense* (Davidson), Upper Aptian, reconstructed from specimen BD 9026. C, *Eothecidellina imperfecta* (Nekvasilová), Upper Cenomanian, reconstructed from specimen BD 9024. D, *Thecidellina blochmanni* Dall, Recent, after Nekvasilová (1967, pl. 6, fig. 1). Abbreviations: b.b, brachial bridge; b.c., brachial cavity; c., brachial lobe canopy; c.p., cardinal process; i.c., intrabrachial cavity; m.s., median septum; p.a.s., posteriorly arching spur. Scale bar represents 0·5 mm.

again striking. Its earlier occurrence (Upper Aptian) and the less complete development of the canopies of the brachial lobes (Text-fig. 6B) places *Bifolium* in an attractive position from an evolutionary point of view. However, the heavily suppressed fibrous secondary mosaic of the pedicle valve seems to rule out *Bifolium* from a direct ancestral position. Pajaud (1970) regarded *Rioultina* as being ancestral to *Bifolium*. Smirnova (1984) considered *Rioultina* to be close to, but, slightly off the main line of *Bifolium* descent from *Moorellina* stock. Smirnova's interpretation is probably more accurate, since it can now be demonstrated that the small, Middle Jurassic (Aalenian) *Moorellina*

EXPLANATION OF PLATE 5

Figs 1–8. *Thecidiopsis tetragona* (Roemer). 1, 42532/3; inner surface of the primary layer showing acicular crystallites of future tubercle cores 'seeded' on to granular calcite (section orientation – parallel with the external shell surface; section location – antero-lateral sector), × 350. 2, same specimen; showing acicular crystallite tubercle cores developed but still separated by granular calcite, × 350. 3, 42533/49; transverse section through the free ventral wall showing the attenuated fibrous strands at the inner boundary (lower margin) and transversely sectioned tubercle cores (section orientation – parallel with the plane of the commissure; section location – as fig. 1), × 375. 4, same specimen; showing tubercle core in greater detail, × 800. 5, enlarged portion of figure 4; showing the development of scalenohedra-like bodies (lower left) in the axial region, × 4000. 6, 42533/49; attenuated strand showing detail of fibrous secondary shell in transverse section (section orientation and location as in figure 3), × 400. 7, 42533/7; oblique section through the free ventral wall showing the acicular crystallite tubercle cores in lateral contact (section orientation and location as in figure 3), × 325. 8, same specimen; showing the characteristic 'fish-scale' overlap of acicular crystallite tubercle cores in oblique section, × 250.
All scanning electron micrographs of gold-coated cellulose acetate peels of sectioned specimens.

PLATE 5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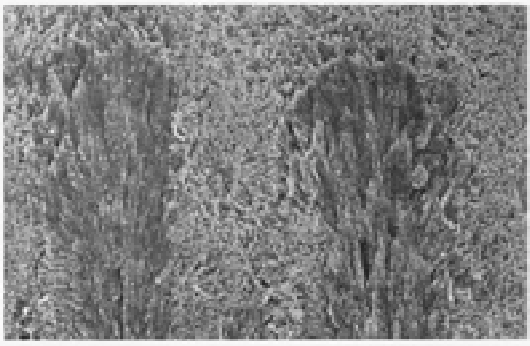
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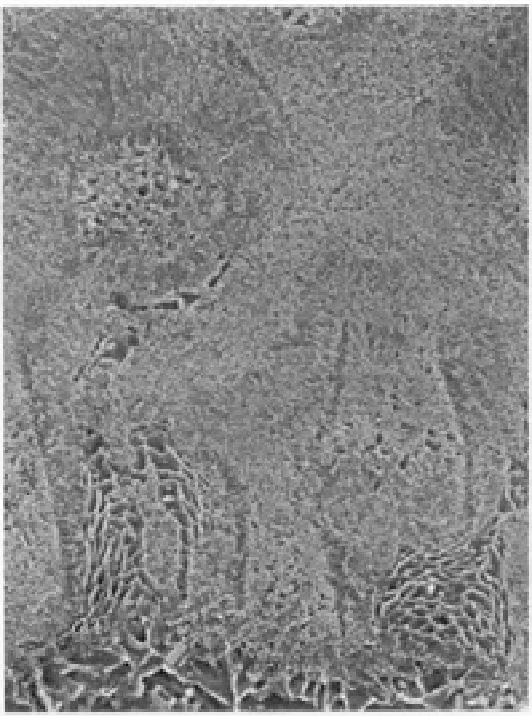
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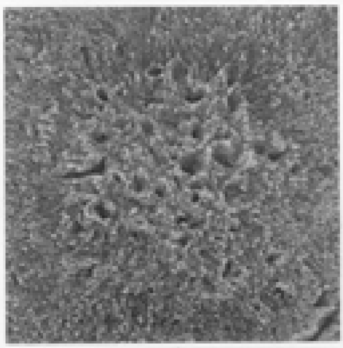
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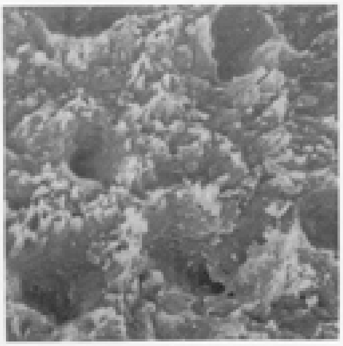
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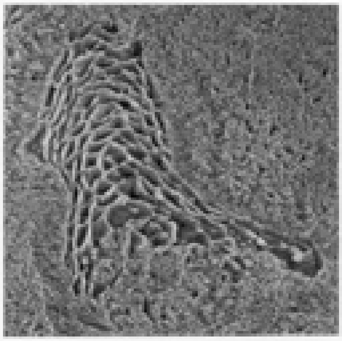
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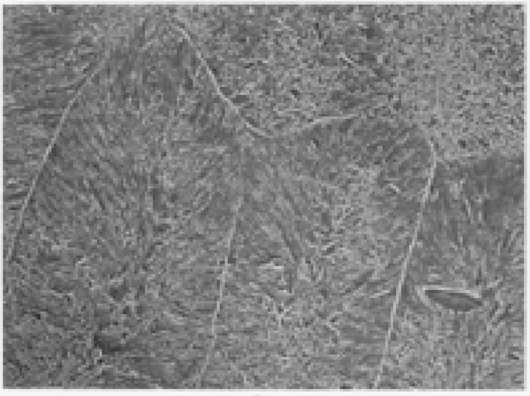
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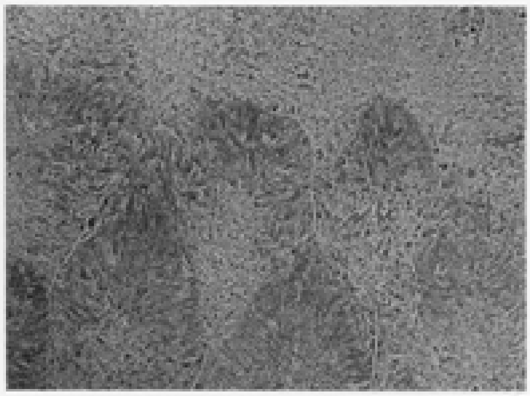
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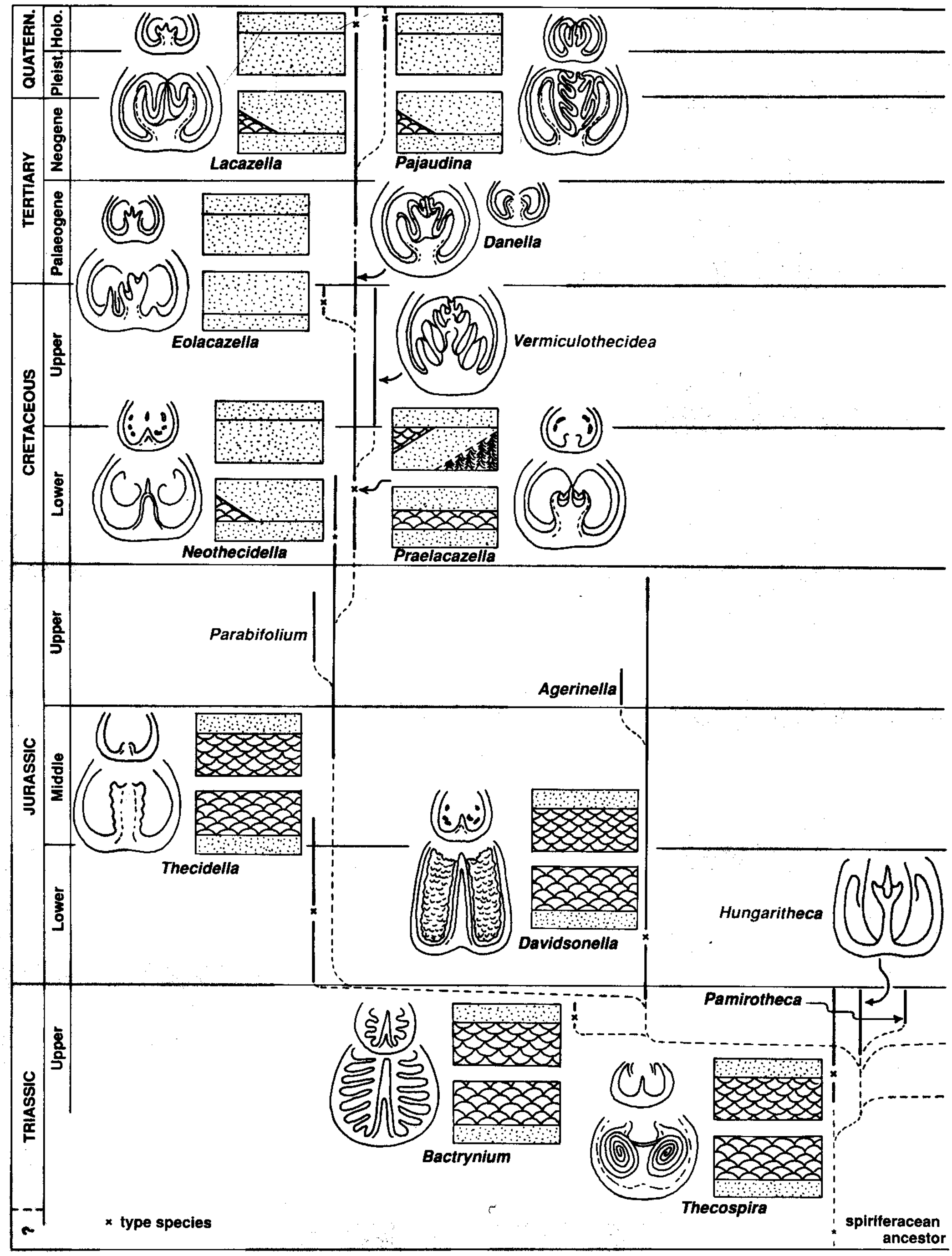
BAKER, *Thecidiopsis*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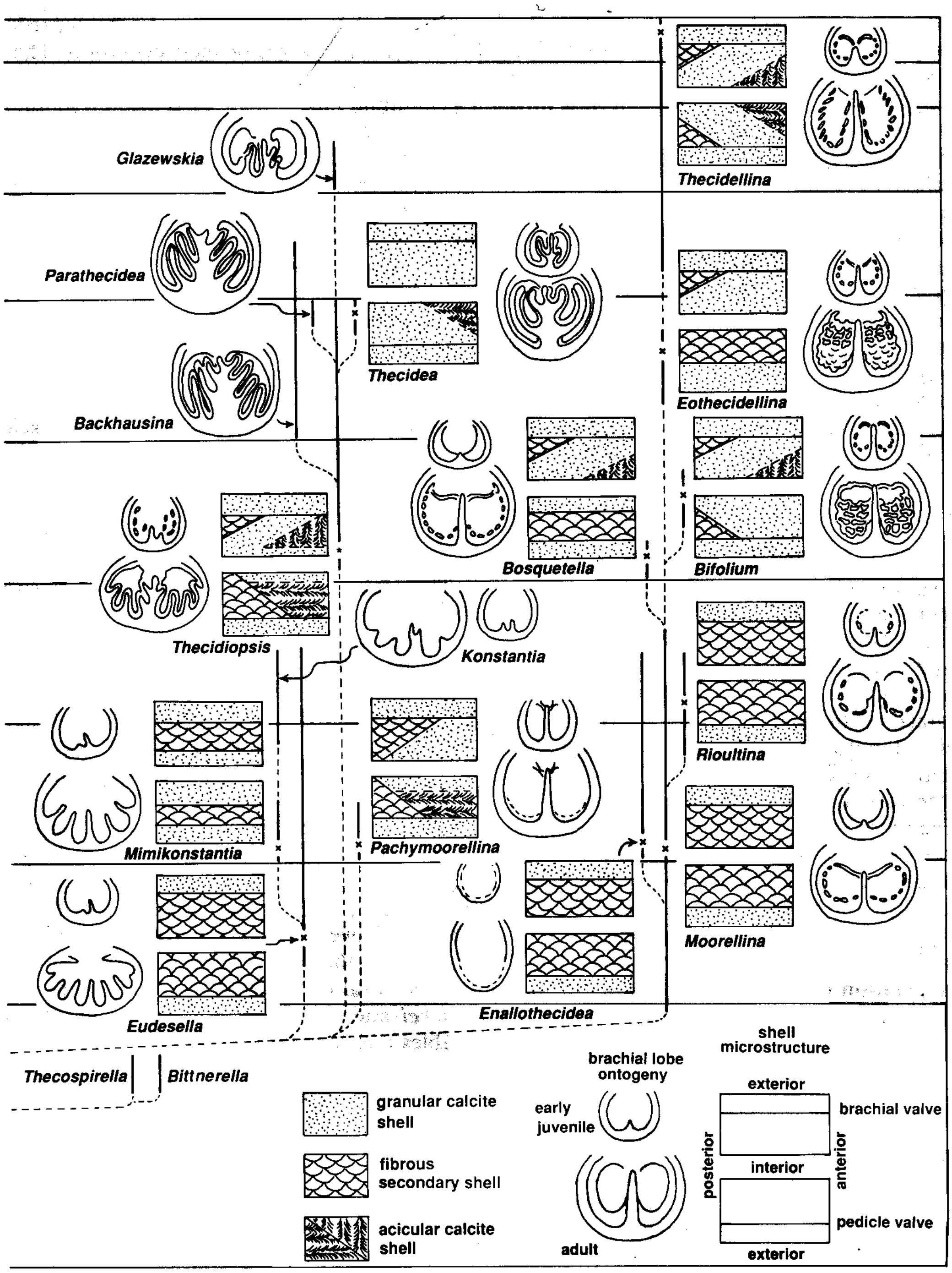

TEXT-FIG. 7. Phylogenetic reconstruction, showing, where known, the essential ontogeny of the brachial supports, and, shell microstructure of thecideidine genera. In the diagrammatic illustrations of shell microstructure, horizontal lines indicate continuous layers, diagonal lines indicate restricted distribution. The presence of periostracum is assumed in all genera.

dubia possessed brachial structures (Pl. 2, figs 7–9; Text-fig. 6A) which may be regarded as rudimentary canopied brachial lobes (Pl. 3, fig. 8), in the early stages of their evolution. The shell microstructure of *M. dubia* is typically moorellinid (Pl. 3, fig. 9). Smirnova's (1969) discovery that the ontogeny of *Thecidiopsis* did not pass through a rioultinid phase (undivided median septum and auriform brachial lobes (Pajaud 1966, p. 630)) clearly separates *Eothecidellina* from *Thecidiopsis*.

The distribution of secondary fibrous shell in *E. imperfecta* and *T. tetragona* is instructive. Although fibrous secondary shell forms a continuous thin sheet in the pedicle valve of *E. imperfecta*, its appearance coincides with the beginning of the development of the free ventral wall. In *T. tetragona* the residual strands of fibrous secondary shell appear at the inner boundary of the free ventral wall, after substantial deposition of acicular calcite. The diagram of *T. tetragona* shell microstructure in Smirnova's (1979) paper is misleading because the fibrous secondary layer is depicted as a well-differentiated, continuous internal layer. The seeding of patches of acicular crystallites on to the inner surface of the primary layer is very reminiscent (see Williams 1968, p. 7, text-fig. 4) of the initiation of normal secondary fibres. In both genera the sudden appearance of fibrous secondary shell, suggests a latent ability of the epithelial cells to switch from the secretion of acicular crystallites, to the secretion of normal secondary fibres. As already noted, the acicular crystallite tracts discovered in *Pachymoorellina*, and well established in *T. tetragona*, equate with the rod-like bodies of Smirnova (1979, 1984) not, as previously stated (Baker 1989, p. 67), with the fir-tree structures.

Thecideidine phylogeny

The various phylogenetic models proposed for the Thecideidina have been thoroughly reviewed in a recent paper (Baker 1990) and need only brief further mention here. The earlier interpretations of Elliott (1948, 1953) and Backhaus (1959) were modified by Rudwick (1968), Smirnova (1969) and Pajaud (1970). Although the rectilinear evolutionary pattern of the Lacazellinae had been well understood for some time (Pajaud 1970) the evolution of the Thecidellinidae and Thecideinae had remained problematical. Smirnova's (1969) demonstration of the distinctiveness of thecidellinid and thecideid ontogenetic development patterns revived interest in Backhaus's (1959) idea of two phyletic groups, and introduced the notion of parallel lineages within the groups. Smirnova's (1969) interpretation, with additional refinement (Smirnova 1984), was much more satisfactory, since it avoided most of the problems (Baker 1990, pp. 177, 180) of heterochronous expression, mutation, neoteny and undiscovered adults attendant to the other schemes. Williams's (1973, p. 468, fig. 100) phylogenetic chart of thecideidine shell structure variation had been modelled on the phylogenetic framework proposed by Pajaud (1970). Subsequent studies (Baker and Elston 1984; Smirnova 1984; Baker 1989) showed that Pajaud's phylogeny was flawed. Also, the suppression of fibrous secondary shell occurred much earlier in the history of the group than Williams envisaged. Interpretation of the new morphological and microstructural evidence obtained from the current study of *E. imperfecta*, *B. faringdonense*, *B. campichei* and *M. dubia*, not only strengthens the lineages identified by Smirnova (1984), but also enables a clearer understanding of the phylogeny of thecidelliniform genera to be reached. Similarly, the new interpretation of the shell microstructure of *T. tetragona*, allied to the evidence from study of *Mimikonstantia sculpta* Baker and Elston, 1984, and *P. dundriensis* (Baker 1989), gives a much clearer picture of lineage within the Thecideinae.

My review of existing taxonomic and phylogenetic models (Baker 1990) clearly stated the case for including thecospiraceans and *Bactrynium* in the Thecideidina and supported the view of Dagis (1973) that early thecospiraceans were very close to thecideidine ancestral stock. I concluded that sufficient information was available to enable a reliable taxonomic and phylogenetic framework to be established. A revised classification was presented, including the Thecospiracea and the Bactryniidae in the Thecideidina which, in turn, was included in the Spiriferida. A recent study (Benigni and Ferliga 1989), assigning Carnian thecospirids from Italy to the Strophomenida, failed to address the arguments advanced by Williams (1973) and Baker (1984) in favour of removal of the Thecospiracea to the Spiriferida. In content, if not conclusion, the study confirms the very close relationship between thecospiracean and thecideacean shell microstructure and strengthens the argument for inclusion of the Thecospiracea in the Spiriferida, because the microstructure of the so-called taleolae of *Thecospira semseyi* Bittner, 1912, is so close to the microstructure of the denticles of juvenile spiriferaceans (compare Benigni and Ferliga 1989, p. 527, fig. 9*b*, with Baker 1984, pl. 77, fig. 3) as to almost be interchangeable.

Proposals about phylogeny were deferred (Baker 1990, p. 183; research in progress) pending the interpretation of new morphological and microstructural evidence. The evidence from the current study, incorporated into the existing framework, now enables a revised phylogeny to be presented (Text-fig. 7). Shell microstructure must not be regarded as diagnostic in every case. For example, although uniformity of shell microstructure is characteristic of the various species of *Moorellina*, shell microstructure varies in *Thecidiopsis*. Williams's (1973, p. 465) study of *T. essenensis* indicated a more heavily suppressed fibrous secondary mosaic than that found in *T. tetragona*. In *T. essenensis*, fibrous shell is found in the hinge teeth and base of the outer wall of the hemispondylium but, unless overlooked, is absent from the free ventral wall. Therefore, although considerable variation of shell structure may be found among species assigned to a particular thecideidine genus, the status of observed differences remains uncertain. It is clear, however, that the range of shell microstructure differences reflects the operation of biologically distinct physiological processes, which are probably no less diagnostic than differences in morphology. Nevertheless, in the absence of quantifiable morphological variation, it would be premature to identify morphogenera solely on the basis of shell microstructure. Therefore, in the current study shell microstructure of the genera is illustrated in so far as is possible by that of the type species (Text-fig. 7).

CONCLUSIONS

It is clear that ideas about morphology of the brachial lobes of species such as *E. imperfecta* and *B. faringdonense*, based solely on interpretation of broken skeletal supports as seen in separated brachial valves, may lead to confusion over the systematic arrangement of taxa. The current study further emphasises the critical importance of the study of serially sectioned whole shells in the determination of the form of thecideidine brachial lobes, because the often distinctively sculptured structures, arising from differential shell accretion and resorption, are almost invariably destroyed in separated valves.

As for shell microstructure, the essential limitation of morphogeneric taxonomic or phylogenetic frameworks remains the inability to incorporate distinctions which may be perfectly valid biogenerically, but remain undifferentiated at morphogeneric level. However, in the Thecideidina, chronologically arranged changes in shell microstructure and microstructures persistent over long periods become important indicators of lineage, especially when allied to morphological and ontogenetic evidence.

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