

REVISION OF APTIAN THECIDEIDINE BRACHIOPODS OF THE FARINGDON SPONGE GRAVELS

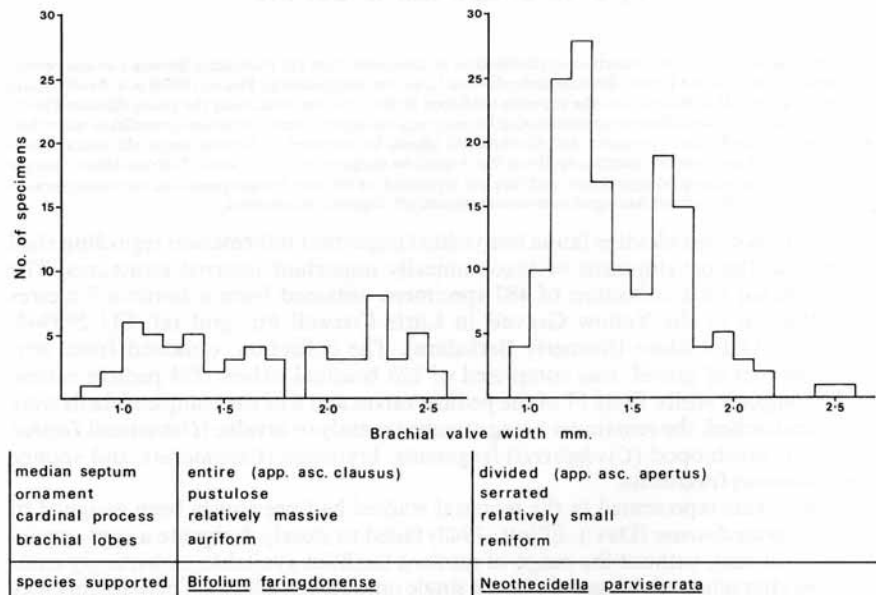
by P. G. BAKER and K. LAURIE

ABSTRACT. The study of a new collection of thecideidine brachiopods from the Faringdon Sponge Gravels reveals the presence of two distinct forms, *Bifolium faringdonense* (Dav.) as interpreted by Pajaud (1970) and *Neothecidella parviserrata* sp. nov. It is believed that the previous confusion in the literature concerning the genus *Bifolium* Elliott, stems from Elliott's (1948) failure to appreciate that his proposed ontogenetic series embraced juveniles of more than one species. Despite Pajaud's proposal that *Neothecidella* should be restricted to Jurassic usage, the characters of the new species are so obviously neothecidelliform that it must be assigned to *Neothecidella*. It is considered that the ornament has some ecological significance and that the separation of the two Aptian genera on microstructural as well as morphological evidence has significant taxonomic and phylogenetic implication.

THE Faringdon thecideidine fauna has yielded important information regarding shell growth and the development of taxonomically important internal structures. The paper is based on a collection of 487 specimens obtained from a horizon 2 metres below the top of the Yellow Gravels in Little Coxwell Pit, grid ref. SU 285943, Faringdon, Oxfordshire (formerly Berkshire). The collection, obtained from wet-sieved samples of gravel, was comprised of 228 brachial valves, 224 pedicle valves, and 35 complete shells. Only 17 of the pedicle valves and 6 of the complete shells were found unattached, the remainder being attached mainly to bivalve (*Ostrea* and *Lopha*) fragments, brachiopod (*Cyclothyris*) fragments, bryozoan (*Cardioecia*), and sponge (*Raphidonema*) fragments.

All the forms represented in the material studied had previously been assigned to *Bifolium faringdonense* (Dav.). Elliott (1948) failed to clearly designate a type species of the genus and, without the range of modern facilities available, unwittingly combined the characters of two genera into a single ontogenetic plexus. This explains why Elliott, at the end of his description found it necessary to note so many aberrant forms. Principal amongst these was a form in which the median septum 'Instead of being a single solid feature, is double-walled, shallow or hollow within, of varying width and, when well developed widens slightly to a rounded posterior termination'. Elliott (1953, p. 694) subsequently referred a stratigraphically higher form, with a divided septum and reniform brachial lobes to *B. lacazelliforme*, obviously associating it with the Faringdon specimens which he himself regarded as variants. Both Backhaus (1959) and Pajaud (1970) have reviewed the problem. Backhaus, stating that *Bifolium* was invalidly designated, reassigned *B. lacazelliforme* to *Lacazella* Munier-Chalmas and, acting upon the evidence provided by the *apparatus ascendens apertus* (Backhaus 1959, p. 12) forms, reassigned *B. faringdonense* to *Lacazella* also. Smirnova and Pajaud (1968), seemingly ignoring Backhaus, continued to refer forms with a divided (*apertus*) median septum to *B. faringdonense*. Publication of Pajaud's (1970) monograph clarified the situation considerably. He formally established the genus *Bifolium*,

properly citing the type species, emending Elliott's possibly ambiguous diagnosis and, equally important, limiting the species to the *app. asc. clausus* (Backhaus 1959, p. 12) specimens which Elliott had described (1948, pp. 7-9, pl. 1, figs. 1-5, 10; pl. 2, figs. 11-15, 18-20) in the 'normal' ontogenetic series. Pajaud (1970, p. 193) although referring specifically to forms such as *L. lacazelliformis*, suggested that the further attribution of species with the *app. asc. apertus* to the genus *Bifolium* should no longer be justified. He then proceeded to reassign forms such as *L. lacazelliformis* and *L. wetherelli* to *Praelacazella* Smirnova but left the *B. faringdonense* variants in limbo.



TEXT-FIG. 1. Histograms to show the size distribution of the two series of brachial valves collected from Little Coxwell Pit. For the reasons outlined in Baker (1969) the width of the brachial valve is adopted as the parameter for determining the approximate population structure within each series. The tabulated characters, fully discussed in the text, form the basis for separation of the two species.

A sample of 215 brachial valves was studied on the basis of the form of the median septum, ornamentation of the sub-peripheral rim, the form of the dorsal cardinalia, and the development of the brachial lobes. The valves were found to fall into two groups (text-fig. 1) one showing the typical *B. faringdonense* morphology *sensu* Pajaud, the other showing the morphology of a *Neothecidella*. Both groups showed an ontogenetic series. As the organization of the two groups is so distinct and the form of the median septum, currently of such high taxonomic importance, there is every justification for assuming that the Faringdon material contains the ontogenetic series of two distinct species. The sequence of ontogenetic events described by Elliott

(1948, pp. 7-9) clearly defines the *app. asc. clausus* forms. Unfortunately he then (1948, p. 10) proceeded to relate 'variants from the normal pattern' to the series previously described. Restudy of these so-called variants shows quite clearly that Elliott's material (British Museum (Natural History) Reg. nos. BB 9468-BB 9479) represents a combination (specified later) of the ontogenetic stages in the development of two species.

In view of the considerable confusion regarding the status of *Bifolium*, the authors consider it necessary to designate the new species prior to discussion of the characters which demonstrate that its differences are systematic rather than random and, therefore, require its separation from *B. faringdonense*.

Thecideidine brachiopods are notoriously difficult to identify on the evidence of their external morphology. The authors therefore do not feel justified in selecting a complete shell to serve as the holotype, since confirmation of its validity could only be achieved through destruction of the specimen. Accordingly, a brachial valve, supported by three paratypes, has been selected to serve as the holotype.

Registration of material. The holotype, paratypes, and topotypes, together with sectioned material are housed in the British Museum (Natural History) under Reg. nos. BB 76260-BB 76271. Specimens of *B. faringdonense* used for comparative studies and figured in this paper are also registered under numbers BB 76272-BB 76277.

Preparation of material. Bulk samples of gravel were washed through a nest of 1.0 cm, 2.5 mm, 1.0 mm, 600 μ m, and 350 μ m aperture sieves. The macrofragments and dried residues were then hand-picked under a binocular microscope. The thecideidines were collected and transferred to glass tubes for further cleaning by weak sonication for periods of five to fifteen seconds. Specimens selected for sectioning were embedded in Araldite and processed in the manner described in Baker (1969). The nature of the matrix, i.e. quartz grains in a weakly coherent haematitic cement, makes detailed investigation of the internal morphology of complete shells virtually impossible. Slight movement of quartz grains during grinding down, quickly destroys any delicate internal structures. A technique which has met with some success is vacuum impregnation of the matrix of partially sectioned or breached shells.

The drawings in text-figs. 2-4 represent traces of actual specimens (registration numbers as specified) made with the aid of a Wild stereomicroscope fitted with drawing tube. Specimens selected for stereoscanning were coated with evaporated aluminium before photography.

SYSTEMATIC PALAEOLOGY

Order uncertain

Suborder THECIDEIDINA Elliott, 1958

Superfamily THECIDEACEA (Gray, 1840) H. and G. Termier, 1949

Family THECIDEIDAE Gray, 1840

Subfamily LACAZELLINAE (Backhaus, 1959) Pajaud, 1966

Genus NEOTHECIDELLA Pajaud, 1970

Neothecidella parviserrata sp. nov.

Plate 60, figs. 1-4, 6, 8; Plate 61, figs. 1, 4, 7; text-figs. 2H, 3K-M, 4E.

Derivation of name. From the weakly serrated sub-peripheral rim.

Diagnosis. Small *Neothecidella* up to about 2.7 mm in length, 2.5 mm in width, and 1.6 mm in thickness. Rounded-triangular in outline, with a variable area of attachment. Ventral interarea not well defined. The anterior commissure is marked by

a slight invagination of the brachial valve, opposite a complementary sulcus in the pedicle valve.

Type specimens. Holotype, Reg. no. BB 76260, and three paratypes, Reg. nos. BB 76261–BB 76263 housed in the British Museum (Natural History).

Distribution. Geographic distribution unknown. All the material studied was collected from the Yellow Sponge Gravels, Upper Aptian, Nutfieldensis Zone, in Little Coxwell Pit, grid ref. SU 285943, Faringdon, Oxfordshire.

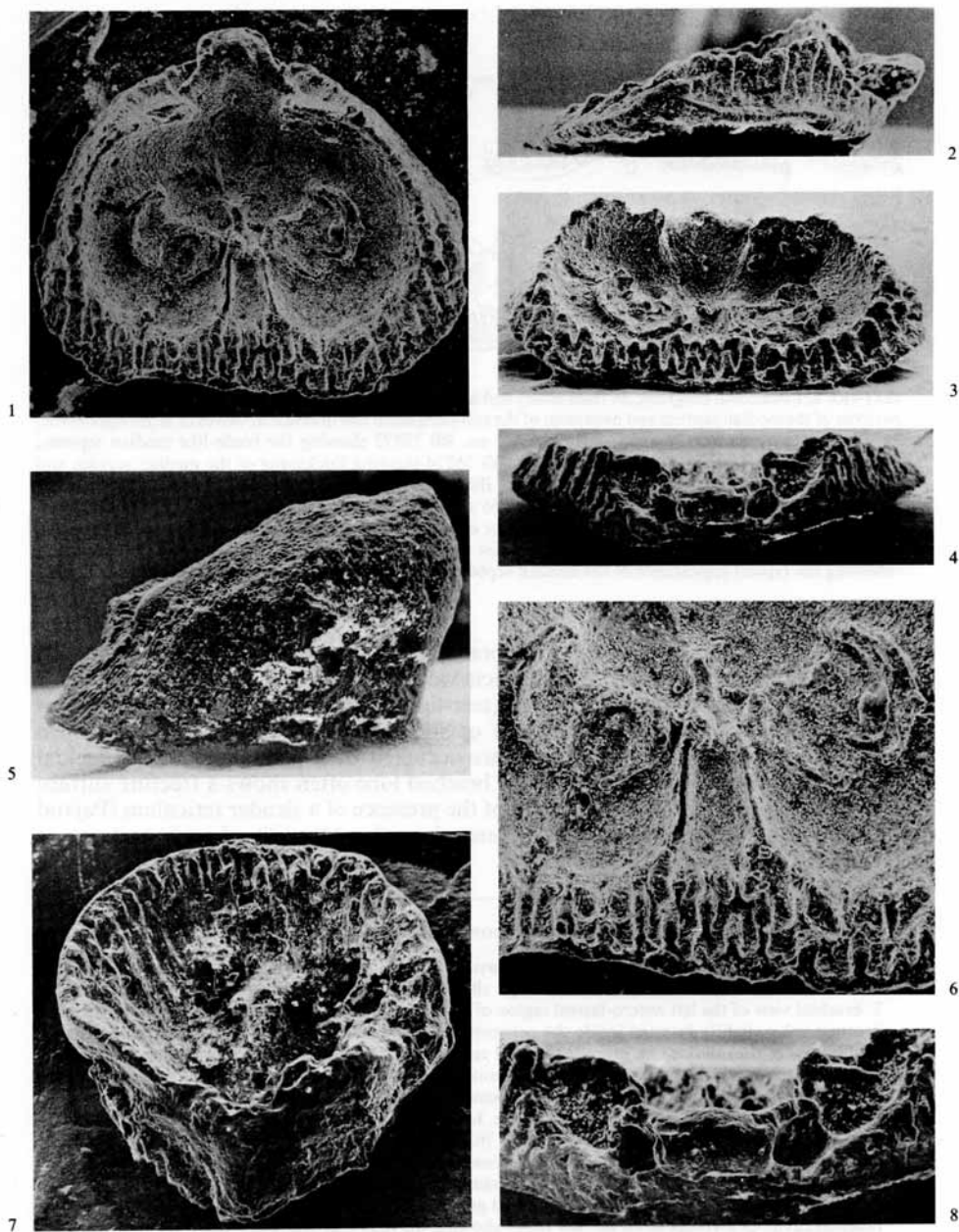
Description. External characters. Study of complete shells and pedicle valves shows that the lateral profile is typically triangular (Pl. 60, fig. 5) with a relatively large area of attachment and well-developed free ventral wall. The dorsal surface of the pseudodeltidium runs parallel with the contour of the ventral interarea and is not convex as in *Bifolium*. There is no evidence of an interarea in the brachial valve, although the brachial umbo is usually prominent. The growth lines are usually clearly defined in well-preserved specimens.

Internal characters. Pedicle valve. The pedicle valve (Pl. 60, fig. 7) differs only in detail from that of *Bifolium*. A sessile or raised hemispondylium is present, as are the characteristic pollicial thecideidine hinge teeth. A ring of ribs and grooves runs round just inside the perimeter of the valve. These correspond with the serration of the brachial valve and often extend right down the interior surface of the ventral wall to the point at which it merges with the area of attachment. In *B. faringdonense* this ornament is beaded or pustulose.

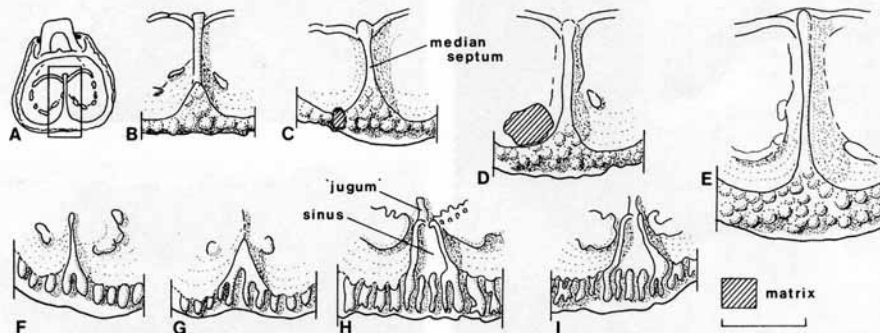
Brachial valve. Slightly wider than long, reaching a maximum width in the order of 2.5 mm, although the adult characters are present by the time the valve has attained a width of approximately 1.6 mm. The median septum (Pl. 60, fig. 6; text-fig. 2) is of the *app. asc. apertus* type, consisting of a central shallow sinus, flanked by two high anteriorly diverging ridges. The floor of the sinus is at approximately the same level as the floor of the brachial cavities. It is terminated anteriorly by a row of ridges and grooves, indistinguishable from the ornament of the sub-peripheral rim. Posteriorly, the sinus opens into the body cavity via a narrow channel (text-fig. 2H, I). Immediately posterior to this opening is a lobe of material interpreted as a primitive jugum. The cardinal process is relatively small compared with that of forms such as *B. faringdonense* and is more dorsally placed (Pl. 60, fig. 8; text-fig. 3M). The sides curve downwards and diverge to form the inner socket ridges, uniting with the postero-medial area towards the base of the bridge abutments. The cardinal process often shows a faint trilobation. The border is almost non-existent and the serration of the outer boundary of the sub-peripheral rim runs down fairly steeply, almost to the valve

EXPLANATION OF PLATE 60

Figs. 1–8. Stereoscan photomicrographs of *N. parviserrata*. 1–4, brachial, lateral, anterior, and posterior views of the holotype, $\times 40$. 5, lateral view of a paratype no. BB 76263 showing the characteristic triangular lateral profile, $\times 50$. 6, enlargement of the anterior region of the holotype showing the divided median septum with the central sinus and rudimentary jugum and the form of the adult brachial lobes, $\times 70$. 7, posterior view, tilt angle 35° , of a paratype no. BB 76262 pedicle valve showing the serrated rim and poorly defined interarea, $\times 42$. 8, posterior view of the holotype enlarged to show the relatively small cardinal process, the dental sockets, and lateral adductor muscle scars, $\times 70$.



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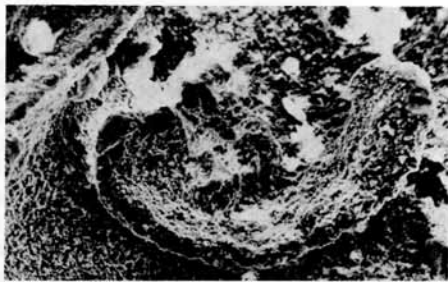
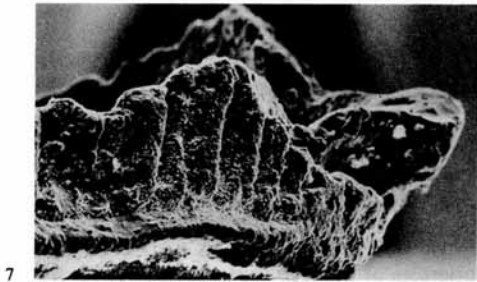
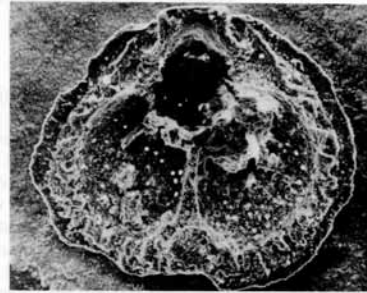
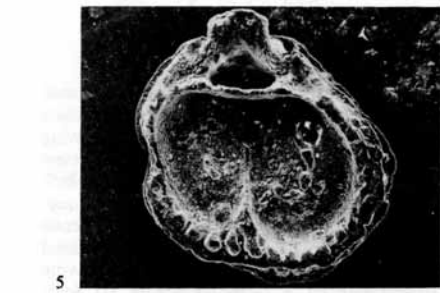
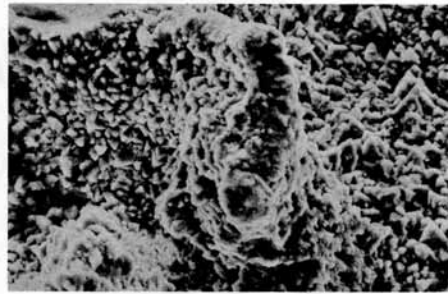
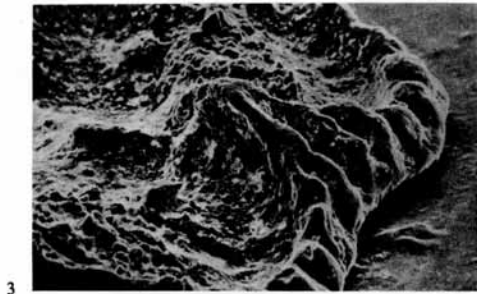
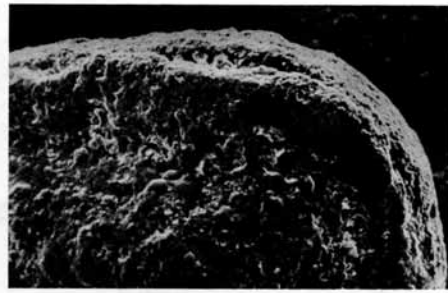
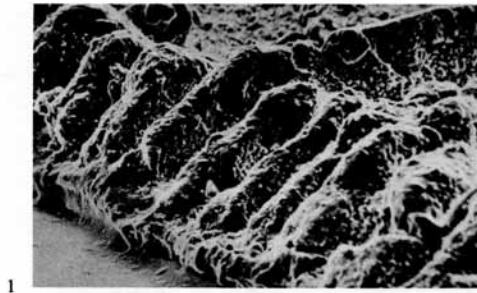


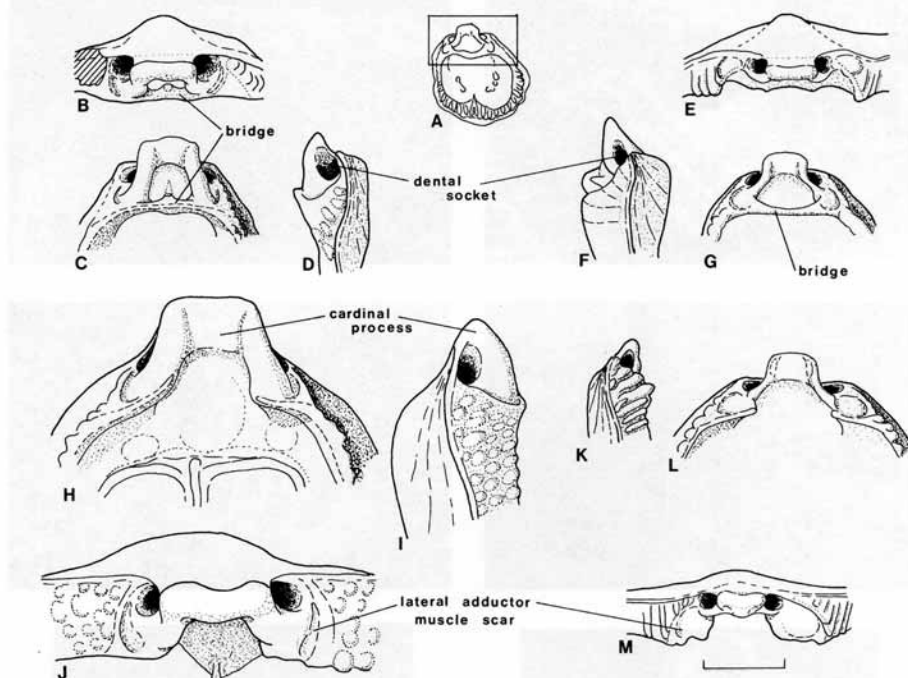
TEXT-FIG. 2. Locational diagram, 2A (half scale) and a series of drawings to show the different development patterns of the median septum and ornament of the sub-peripheral rim in brachial valves of *B. faringdonense*, 2B-E and *N. parviserrata*, 2F-I. 2B, early juvenile no. BB 76272 showing the blade-like median septum; 2C, juvenile no. BB 76273; 2D, young adult no. BB 76274 showing thickening of the median septum and increase in the pustulose ornament; 2E, adult no. BB 76275 showing the median septum and ornamented rim fully developed. 2F, early juvenile no. BB 76265 showing the low ridge-like median septum, bifurcated anteriorly; 2G, juvenile no. BB 76266 showing the endotomous branching at the anterior of the median septum and the initiation of the sinus; 2H, I, adult no. BB 76260 (holotype) and unregistered specimen showing the typical appearance of the median septum and serrated ornament. Scale represents 0.5 mm.

edge (Pl. 61, fig. 1; text-fig. 2G-I). The brachial valve normally fits slightly inside the rim formed by the perimeter of the pedicle valve (Pl. 61, fig. 2). The lateral adductor muscle scars are large, almost circular (text-fig. 3M) and not constricted by the root of the cardinal process. The brachial cavities are shallow, with well-developed resorption fronts (Pl. 61, fig. 3), and are occupied by a pair of reniform brachial lobes. The posterior termination of the brachial lobe often shows a fracture surface (Pl. 61, fig. 4; text-fig. 4D, E) indicative of the presence of a slender reticulum (Pajaud 1970, fig. 8C). Some juveniles show precocious development of such a structure (Pl. 61, fig. 6; text-fig. 4H).

EXPLANATION OF PLATE 61

Figs. 1-8. Stereoscan photomicrographs of *N. parviserrata*. 1, three-quarters profile view of the anterior border of the brachial valve of the holotype showing the characteristic serrated ornament, $\times 150$. 2, brachial view of the left antero-lateral region of a complete shell, unregistered specimen, showing the brachial valve slightly inserted inside the perimeter of the pedicle valve, $\times 70$. 3, near three-quarters profile view of the interior of a juvenile brachial valve no. BB 76266 showing the resorption fronts at the anterior of the brachial cavities, $\times 100$. 4, posterior termination of the right brachial lobe of the holotype showing the apparent fracture surface (centre) possibly indicative of a reticulum, $\times 370$. 5, early juvenile brachial valve no. BB 76265 showing the bridge, low median septum, and clusters of brachial tubercles, $\times 45$. 6, early juvenile brachial valve no. BB 76270 showing the development of horn-like processes (right process obscured by matrix) curving backwards and inwards to unite with the posterior end of the median septum, $\times 54$. 7, lateral view of the postero-lateral region of the brachial valve of the holotype showing the well-developed serration ridges and grooves, $\times 90$. 8, three-quarters profile view of the left brachial cavity of a young adult no. BB 76269 showing the reniform brachial lobe, $\times 130$.

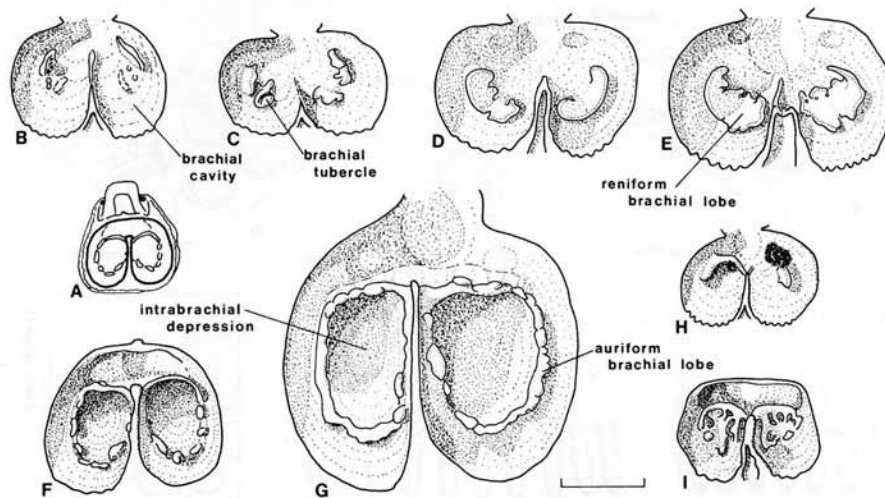




TEXT-FIG. 3. Locational diagram, 3A (half scale) and a series of drawings to show the differences in the dorsal cardinalia and postero-lateral ornament of *B. faringdonense* and *N. parviserrata*. 3B-D, posterior, brachial (spur restored), and lateral views of an early juvenile *B. faringdonense* brachial valve no. BB 76272, showing the relatively massive cardinal process and its insertion into the postero-medial border; 3H, brachial view of an adult (possibly gerontic) brachial valve of *B. faringdonense* no. BB 76277 showing the apparent lack of bridge remnants; 3I, J, lateral and posterior views of an adult specimen no. BB 76276 showing the characteristic insertion of the cardinal process. 3E-G, posterior, lateral, and brachial views of an early juvenile *N. parviserrata* brachial valve no. BB 76265 showing the relatively small and more dorsally inserted cardinal process; 3K-M, lateral, brachial, and posterior views of the holotype *N. parviserrata* no. BB 76260 showing the insertion of the cardinal process and lateral adductor muscle scars (cf. *B. faringdonense* fig. 3J). Scale represents 0.5 mm.

Microstructure. Investigation of transverse and horizontal sections through shells shows that the secretion of secondary shell is neotenously suppressed. Although the gross mosaic of the morphological elements of the shell is discernible using transmitted light, in cellulose acetate peels of etched surfaces (Pl. 62, fig. 4) stereoscan photomicrographs show that almost all of the elements are composed of granular calcite, indistinguishable from primary shell (Pl. 62, fig. 5).

In the pedicle valve secondary fibres are only found in the hinge teeth, occurring as bundles of fibres situated towards the ventral side of the tooth (Pl. 62, fig. 6) and extending back into the tooth ridges. The tubercles of the free ventral wall appear as



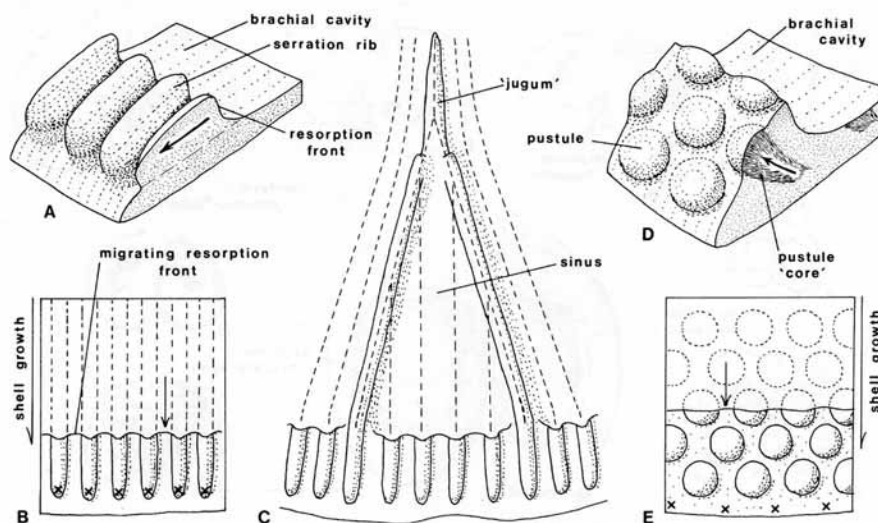
TEXT-FIG. 4. Locational diagram, 4A (half scale) and series of drawings to show the development of the brachial lobes in *N. parviserrata* and *B. faringdonense*. 4B-E, *N. parviserrata* ontogenetic sequence; 4B, early juvenile no. BB 76267 showing the initial brachial tubercle cluster; 4C, juvenile no. BB 76268 showing coalescence of the brachial tubercles; 4D, young adult no. BB 76269 showing the development of the reniform shape of the brachial lobes; 4E, holotype no. BB 76260 showing the fully developed brachial lobes (possibly with broken reticulum) and primitive jugum. 4F, G, juvenile, 4F (no. BB 76272) and adult, 4G (no. BB 76276) *B. faringdonense* showing the development of the brachial lobes from a tuberculate ring, leading to the formation of auriform lobes with deep intrabrachial cavities. 4H, I, aberrant juveniles of *N. parviserrata*, specimen no. BB 76270 showing the development of horn-like processes, 4H, and specimen no. BB 76271 showing the development of reticulate lobes, 4I. Scale represents 0.5 mm.

cylindrical cores of granular calcite (Pl. 62, fig. 7) with their axes inclined dorsally, at a low angle from the external surface of the shell. They are partially enveloped by subsequently deposited material, also granular in texture, in such a way that their exposed surfaces coincide with complementing grooves in the serrated sub-peripheral rim of the brachial valve.

In the brachial valve secondary shell appears to have been suppressed completely, as no trace of secondary mosaic has been found, even in the inner socket ridges. The axes of development of the serration ribs run approximately parallel (text-fig. 5A) with the external surface of the shell. They are less deeply enveloped than the tubercle cores of the pedicle valve, but are resorbed posteriorly as the brachial cavities increase in size.

Ontogeny. Pedicle valve. All the characters of the pedicle valve are present in the smallest valves available. Ontogenetic development is therefore concerned with the spread of the ornament and slight changes in the relative proportion of the pseudodeltidium, the hinge teeth, and the hemispondylium.

Brachial valve. The smallest valves available for study (Pl. 61, fig. 5) have a width of approximately 0.9 mm. The median septum is already present, represented by



TEXT-FIG. 5. A, reconstruction of a portion of the margin of a brachial valve of *N. parviserrata*, showing the shell microstructure, the position of the resorption front, and the relationship of the axis (arrowed) of development of the serration, with the shell surface. B, model to illustrate the extension of the serration shown in A as the shell increases in size, by addition of material at the primary accretion points (X) and by resorption posteriorly (resorbed tracts dotted). C, model to illustrate the mode of development of the median septum and sinus in *N. parviserrata*, by endotomous branching (dotted lines) of two diverging serration ribs in which the posterior tracts remain unresorbed. D, reconstruction of a portion of the margin of a brachial valve of *B. faringdonense* showing the microstructure, the position of the resorption front, and the relationship of the axis (arrowed) of development of the pustule, with the shell surface. E, model to illustrate the extension of the pustulose ornament shown in fig. D as the shell increases in size, by initiation of new pustules (X) and resorption of previously formed pustules (dotted).

a low ridge with an indentation at the anterior end (text-fig. 2F). Ornament consists of a single row of elongate tubercles. The cardinal process shows all the adult characters. The bridge is intact (text-fig. 3E-G) and the brachial lobes are represented by a small cluster of tubercles on the floor of the brachial cavities (text-fig. 4B). Ontogenetic development is essentially concerned with the changes occurring in the sub-peripheral rim, the median septum, and the brachial lobes as the brachial cavities increase in size.

Development of the sub-peripheral rim and median septum (text-fig. 2F-I). As the brachial cavities develop, the sub-peripheral rim migrates, by the simultaneous accretion and resorption of material, in the manner described in Baker (1970). The elongate tubercles are extended radially as ridge-like structures or serrations, undergoing continuous resorption posteriorly, so that the serrated margin (Pl. 61, fig. 1) typical of the species is developed. As the valve increases in size the indentation at the anterior of the median septum deepens to form a trough-like sinus. Pajaud (1970, p. 26) uses the term *median ramus* for this structure. Sinus is considered to be a more

descriptive term and is adopted here. The divergent ridges bounding the sinus on either side appear to have been formed from the unresorbed posterior tracts of two developing serrations (text-figs. 2F, G, 5C). The integrity of the ornament ring appears to be maintained by a form of endotomous branching of the serrations as they extend anteriorly. Further development of the sinus is accomplished by the establishment of a resorption front at its anterior end, which operates in the same manner as in the brachial cavities. At, or near, maturity the resorption regime is modified slightly so that a narrow channel is formed posteriorly, connecting the sinus with the body cavity.

Development of the brachial lobes (text-fig. 4B-E). The brachial tubercles of the initial cluster increase in size (text-fig. 4C) and coalesce to form low incomplete, irregularly reniform (Pl. 61, fig. 8; text-fig. 4D) lobes. These subsequently increase in size as a result of peripheral accretion of material (text-fig. 4E). As noted earlier, the posterior edge of the adult lobes often shows a fracture surface, indicating the presence of an extension, no longer preserved. Often, in juveniles, the two posterior tubercles of the initial group develop a horn-like process which curves backwards and inwards to unite with the posterior end of the median septum (Pl. 61, fig. 6; text-fig. 4B, H). More rarely, outgrowths from other tubercles unite with this process to form reticulate structures (text-fig. 4I). The presence, therefore, of a reticulum *sensu* Pajaud, although suspected, is not confirmed in the separated adult brachial valves studied.

DISCUSSION

It has been suggested by Pajaud (1970, p. 195) that the forms studied by Elliott were juveniles. This suggestion is not accepted as valid. Arguments previously advanced (Baker 1969) for regarding the largest specimens in *Moorellina* Elliott populations as adults are equally applicable to this study.

The similarity in size and general morphology of *B. faringdonense* and *N. parviserrata* may have masked some of the more fundamental differences in organization. In *N. parviserrata* the median septum prior to the development of the sinus, is usually a low structure, often no more than a longitudinal median ridge. In *B. faringdonense*, however, the septum is always high and blade-like (text-fig. 2B-E). In *N. parviserrata* the brachial lobes develop essentially from peripheral expansion of a skeletal framework of coalesced brachial tubercles. In *B. faringdonense* the brachial lobes develop forwards from two posteriorly situated ridges, in the manner described by Elliott (1948, p. 9), ultimately forming circular ridges (auriform lobes of Pajaud) round deep intrabrachial depressions (Pl. 62, fig. 2; text-fig. 4F-G). In *N. parviserrata* the lateral adductor muscle scars in the brachial valve are almost circular and inserted ventral to the root of the cardinal process but in *B. faringdonense* they are more crescent-shaped as a result of constriction by the cardinal process (text-fig. 3B-D, H-J).

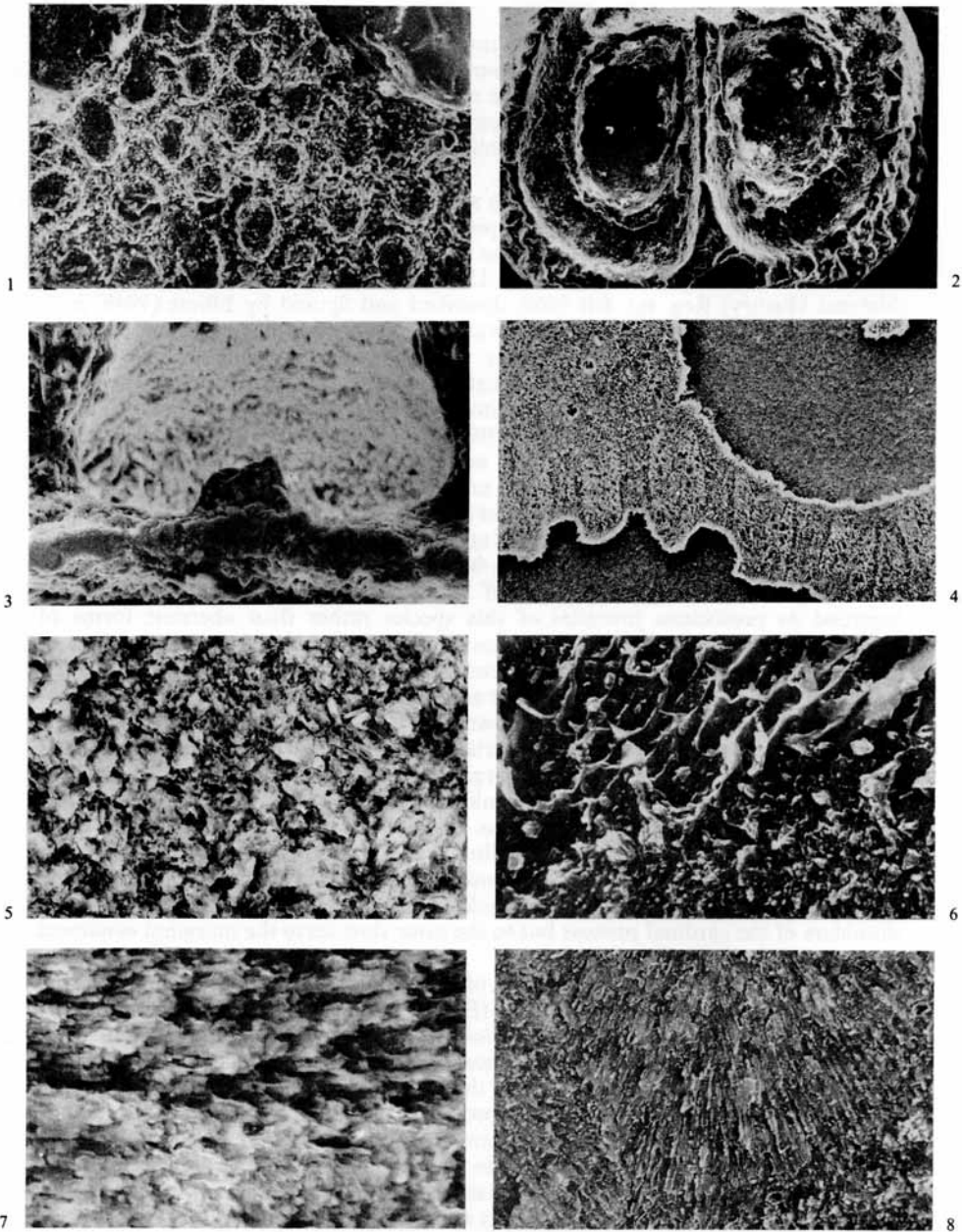
Although the difference in the ornament might seem trivial, the authors regard it of critical significance, as the ornament represents the expression of quite distinct secretory regimes (text-fig. 5) and appears to have some taxonomic significance when considered in dynamic (Rudwick 1968) rather than in static terms. Comparison of the ornament in anterior, antero-lateral, and postero-lateral regions of the brachial valve (text-figs. 2, 3) shows that in *B. faringdonense* the tubercles are discrete pustules

(Pl. 62, fig. 1) whereas in *N. parviserrata* the secretory system produces an essentially serrated margin ornamented by radially arranged ridges with intervening grooves (Pl. 61, fig. 1). This feature provides the only firm basis for differentiation between the pedicle valves of the two species. In the *Bifolium* type ornament the pustules are round and, collectively, represent the product of a discontinuous secretory regime. The axis of a pustule is perpendicular to the terminal face and new pustules are initiated into the succession usually offset by one half phase (Pl. 62, fig. 1; text-fig. 5). In the *Neothecidella* type ornament the tubercles are rib-like and are the product of a continuous secretory regime, accreting anteriorly and resorbing posteriorly, so that the resulting serrated ornament is really the unresorbed portion of a series of radially arranged ridges (Pl. 60, fig. 6; text-fig. 5). Their relationship with the median septum has already been discussed. The significance of the ornament merits some consideration as such an elaborate arrangement must have evolved in response to specific environmental pressure. As suggested previously for Middle Jurassic thecideidines (Baker 1970) the series of interlocking tubercles round the edge of the valves probably increased the stability of the brachial valve in the closed position, possibly indicative of a high-energy environment. *Praelacazella baltoviensis* Barczyk offers indirect support for this view (Pajaud 1974). Examination of the postero-lateral areas shows quite clearly (Pl. 61, fig. 7) that the serration ridges and grooves acted as accessory teeth and sockets when the valves were gaping. Possibly *N. parviserrata* was capable of colonizing the organo-detrital debris poured into the Lower Greensand trough (Krantz 1972). The preservation of fine detail on some of the separated valves requires some such explanation, particularly in view of the coarse nature of the enclosing sediment. The associated *B. faringdonense* has a relatively thick brachial valve with pustulose ornament and usually shows a greater degree of abrasion, possibly indicating transportation over a greater distance and a different source for the material, hence the difference in the population structure (text-fig. 1). Modern forms such as *Thecidellina barretti* (Davidson) are also ornamented by several rows of pustules

EXPLANATION OF PLATE 62

All figures are stereoscan photomicrographs.

Fig. 1. Anterior of a brachial valve of *B. faringdonense* no. BB 76275 showing the characteristic pustulose ornament of the sub-peripheral rim, $\times 115$. 2, interior of a brachial valve of *B. faringdonense* no. BB 76276 showing the blade-like median septum and deep intrabrachial depressions surrounded by auriform brachial lobes, $\times 40$. 3, enlarged view of the bridge of an early juvenile *B. faringdonense* brachial valve no. BB 76272 showing the posteriorly directed spur (damaged during cleaning), $\times 225$. 4, cellulose acetate peel of a horizontal section through a brachial valve of *N. parviserrata* no. BB 76264A showing the gross mosaic of the floor of the median sinus, upper left, and the serration ribs, lower margin, $\times 140$. 5, etched surface of a horizontal section through a brachial valve of *N. parviserrata* no. BB 76264A showing the granular structure of the secondary shell, $\times 800$. 6, cellulose acetate peel of a horizontal section through a pedicle valve of *N. parviserrata* no. BB 76264A showing the bundle of normal secondary fibres, upper left, developed in the tooth ridges, $\times 1420$. 7, etched surface of a horizontal section through the free ventral wall of a pedicle valve of *N. parviserrata* no. BB 76264A showing the similarity of the shell structure in an enveloped tubercle, upper, and the shell wall, lower, tubercle axis running left to right almost parallel with the plane of section, $\times 1800$. 8, cellulose acetate peel of a horizontal section through a brachial valve of *B. faringdonense* no. BB 76264B showing the typical splay of crystallites forming the pustules, pustule axis running top to bottom inclined at approximately 40° to the plane of section, $\times 625$.



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which may now be performing a sediment-straining role in the cryptic habitat (Jackson *et al.* 1971) occupied by the animal.

Probably in the course of thecideidine evolution, the role played by certain structures, has been modified in a number of ways. It certainly seems that in *N. parviserrata* the sinus arose fortuitously from the establishment of a resorption front at the anterior of an otherwise normal median septum.

Despite an exhaustive search through sieved residue down to 350 μm mesh size, it has not been possible to isolate any specimens with a brachial valve width of less than 0.8 mm so the authors are unable to comment on the earliest ontogenetic stage of *Bifolium* as interpreted by Elliott. Unfortunately, specimen British Museum (Natural History) Reg. no. BB 9468, described and figured by Elliott (1948, p. 7, Pl. 1, fig. 1) is no longer available for study. A substitution has been made but the only specimen available was a slightly more advanced juvenile which supports Elliott's description with the exception that incipient septum formation may be noted. Of the remaining Elliott material, specimen BB 9469 is an early juvenile *N. parviserrata*, specimen BB 9474 is an adult, BB 9475 an aberrant juvenile, and BB 9478 a suspected *N. parviserrata*. The tubed material BB 9480 and BB 9482 contains a mixture of specimens of *N. parviserrata* and *B. faringdonense*.

Elliott (1948, p. 10) mentioned aberrant forms in which the brachial lobes appeared as two horn-like processes. These forms are also encountered in the material studied in this paper. It will be noted (text-fig. 4h) that with the exception of the brachial lobes, they possess all the characters of *N. parviserrata* and should, therefore, be regarded as precocious juveniles of this species rather than aberrant forms of *B. faringdonense*. In some early juveniles of *B. faringdonense* the posterior face of the bridge is armed with a short, backwardly projecting spur (Pl. 62, fig. 3; text-fig. 3b, c). The purpose of this structure and whether it is associated with sexual dimorphism (Elliott 1948) remains unknown.

It is curious that in both Elliott's material and the material considered in this paper the bridge is invariably missing in the larger brachial valves of *B. faringdonense*. The areas where the bridge attachments would have been located become progressively more rounded. In the largest specimens available for study these areas are quite smooth (text-fig. 3h). This may be attributed to abrasion but the authors consider that in gerontic forms of *B. faringdonense* the bridge was probably resorbed. It is difficult to envisage a process which would abrade areas relatively protected by the shoulders of the cardinal process but at the same time leave the marginal ornament untouched (Pl. 62, fig. 1).

With regard to the systematic position of *N. parviserrata*, it is not far removed from the form assigned to *P. lacazelliformis* (Elliott) from the Chalk Marl, Cambridge. It also resembles juveniles of *P. valangiensis* but this species is far removed stratigraphically (Hauterivian) and geographically (Crimea). The sinus is much narrower than that of *Praelacazella* and without the characteristic ramuli, also there are no lanceolate minor lobes. Pajaud (1970) proposed the genus *Neothecidella* to include Upper Jurassic forms with a divided septum without ramuli and without a lacazelliform jugum or lanceolate component in the brachial lobes. The lobe of material posterior to the median septum is very similar to the structure seen in *N. ulmensis* and interpreted by Pajaud (1970, p. 112) as an early representative of the *Lacazella*

jugum. The new species is obviously attributable to *Neothecidella* and represents a continuation of the stock up into the Lower Cretaceous. On morphological grounds Pajaud placed *Neothecidella* in the plexus of descent culminating in the Lacazellinae and *Bifolium* in the plexus of descent culminating in the Thecideinae. Pajaud's phylogenetic reconstruction was supported by Williams (1973) in his critical survey of thecideidine shell structure. The difference illustrated in the present study, in the secretory regimes of *N. parviserrata* and *B. faringdonense* confirms a fundamental physiological difference between the two species. A preliminary survey of the development pattern of the ornamented borders of other representatives (*Moorellina*, *Rioltina*, and *Thecidiopsis*) of the *Thecidellina* group and a representative (*Praelacazella*) of the *Lacazella* group, support this view and reinforce the argument so ably advanced by Williams (1973, p. 468) on the evidence of shell structure. Both *B. faringdonense* and *N. parviserrata* show suppressed secondary shell mosaics. However, differences do occur. Williams (1973, p. 465) has identified secondary fibres in the inner socket ridges of *B. faringdonense*, a feature not seen in *N. parviserrata*. The ultrastructure of the sub-peripheral rim also differs. In *N. parviserrata* the serration ribs are composed of uniformly granular calcite but in *B. faringdonense* the pustules in section, appear as a fan-shaped splay (Pl. 62, fig. 8) of acicular crystallites in which the crystallite axes are aligned perpendicular to the pustule surface (text-fig. 5D).

The suppression of secondary shell secretion in *N. parviserrata* confirms the suspicion (Williams 1973, p. 469) that a drastic reduction in secondary shell secretion, paralleling that of the *Thecidellina* group, took place in the *Lacazella* group during the late Jurassic or early Cretaceous. The evolution of the ultrastructure of the thecideidine skeleton does therefore appear to be an example of synchronous, parallel neoteny. With regard to the origin of *Neothecidella*, Pajaud has suggested that it may be derived from *Thecidella* of Lower to Middle Jurassic age. The authors consider that the median septum of *Thecidella* shows a higher degree of sophistication than that of *Neothecidella* and that *Thecidella* should be regarded as a specialization just off the main line of descent. This would eliminate the need for regression from *Thecidella* to *Neothecidella* and more satisfactorily conform to the pattern of a neothecidelliform stage in the ontogenies of *Thecidella* and other later genera such as *Praelacazella*, *Danella*, and *Eolacazella*. The new understanding of the mode of development of the median septum and serration in *Neothecidella* removes any objection to the derivation of the genus from more conventional monoseptal forms of *Moorellina* type. Although no structural study has been made, it may be significant that a serrated moorellinid, *M. serrata* occurs in the Bajocian deposits of Dundry Hill.

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