

THE CLASSIFICATION, ORIGIN AND PHYLOGENY OF THECIDEIDINE BRACHIOPODS

by P. G. BAKER

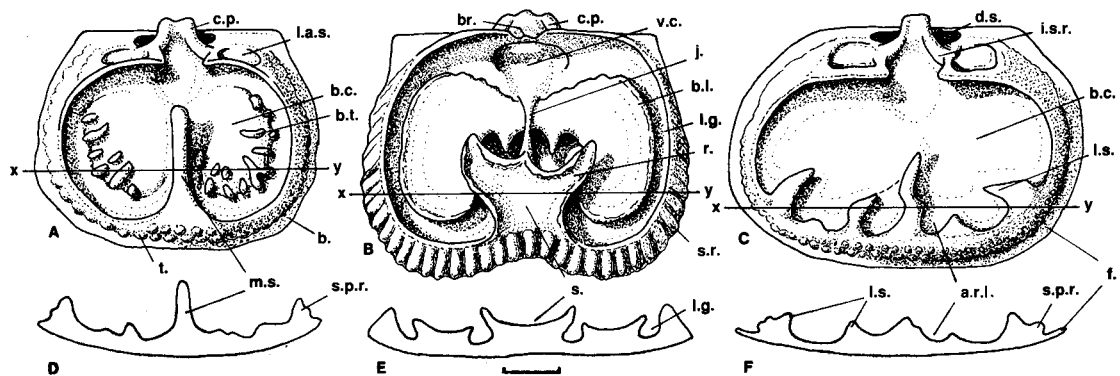
ABSTRACT. Recent studies on ontogeny and shell microstructure enable recognition of the inherent weakness of basing thecideidine taxonomy and phylogeny on morphological characteristics of separated brachial valves. Some previous assumptions are invalidated. The more robust components of lophophore supports are useful in determining relationships, but the form of the brachial lobes, because of their fragility, is less easy to establish, and, without the supporting evidence from sectioned complete shells, their value as taxonomic indicators is questionable. General evolutionary trends may be established through increasing complexity of lophophore supports, but for a clear understanding of thecideidine phylogeny detailed investigation of ontogeny and shell microstructure is required. Neotenus origin and the masking effects of convergent evolution have combined to obscure the line of thecideidine descent. However, shell microstructural evidence now points clearly to a spiriferacean ancestor. The high degree of external morphological similarity makes it essential to consider evidence compiled from studies of morphology, ontogeny and shell microstructure. A revised taxonomy assigning the Thecideidina, Thecospiracea and Bactryniidae to the Spiriferida is proposed.

THECIDEIDINE brachiopods have the dubious distinction not only of having previously been assigned to three articulate orders within the Brachiopoda but to the Mollusca also. Although some of the important early contributions must be mentioned, this paper is not an attempt to chronicle the many publications on thecideidine brachiopods. Much of the content of studies prior to 1965 was synthesized by Pajaud: his monograph (Pajaud 1970) is especially useful in providing fuller details of earlier works on the taxonomy and systematics of the group. Williams's (1973) review of the origin of the thecideidines provided an important summary of previous opinions about the systematic position of the group. The essential purpose of this review, therefore, is to consider the status of arguments advanced in the early 1970s in the light of further developments of the past twenty years. Although obviously interconnected, investigations relevant to this paper can broadly be grouped into studies aimed at the elucidation of taxonomy, ancestry and evolution using morphological, ontogenetic or microstructural evidence. This arrangement broadly reflects the chronological order of the major landmarks in the study of the group and thus serves as a useful framework around which to order the content of the paper.

THECIDEIDINE TAXONOMY

Although shells had been described earlier (Faujas 1798; Schlotheim 1813), the earliest use of 'thecidean' apparently dates from the introduction of the term by Defrance (1822) to refer to the distinctive morphological characters of representatives of a newly designated genus *Thecidea*. It was, however, another eighteen years before the group emerged (Gray 1840) as a taxon of family rank containing six species, all assigned to *Thecidea*. After the establishment of the Thecideidae Gray, 1840, a series of classic descriptive works followed, notably those of Davidson (1851, 1854, 1874, 1876), D'Orbigny (1847), Eudes-Deslongchamps (1853), Lacaze-Duthiers (1861) and Moore (1854). These studies, although varying the generic spelling between *Thecidea*, *Thecidium* and *Thecideum*, introduced many new species. At about this time the expanding family attracted the interest of systematists (e.g. Dall 1870). Munier-Chalmas (1880, 1887) began the task of differentiating the taxa at generic level and, in view of the small size of many of the representatives,

it is perhaps a tribute to his observation and interpretative skills that the genera he created remain unmodified to the present day. At higher level, Waagen (1882) assigned the thecideans to the Terebratulacea, whereas Schuchert (1896) transferred them to the Strophomenacea. With only minor adjustments (Rollier 1915; Thomson 1915), this steady state persisted for half a century. However, beginning with the combination (Termier and Termier 1949) of thecideids and lytoniids into a new superfamily Thecideacea, the next twenty years saw more changes than had been witnessed during the previous one hundred and fifty.

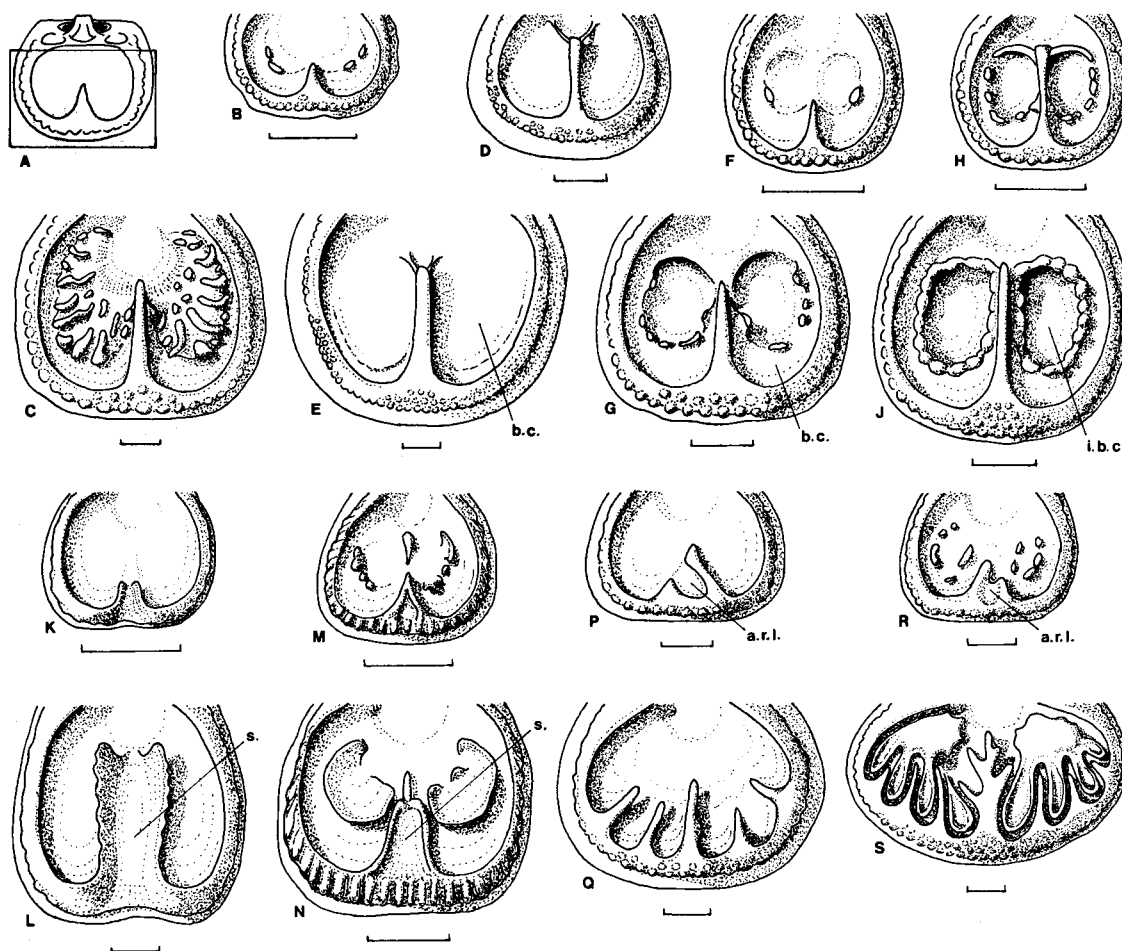


TEXT-FIG. 1. Drawings to show the internal morphology, typical of the principal types of thecideid brachial valve. A, monoseptate form cf. *Moorellina* with blade-like median septum, brachial bridge broken. B, median septum with well-developed sinus cf. *Praelacazella*. C, polyseptate form cf. *Mimikonstantia*, bridge broken, lateral septa damaged. D-F, transverse sections, x-y, through brachial valves A-C respectively. Abbreviations: a.r.l., auxiliary resorption lobe; b., border; br., bridge; b.c., brachial cavity; b.l., brachial lobe; b.t., brachial tubercle; c.p., cardinal process; d.s., dental socket; f., flange; i.s.r., inner socket ridge; j., jugum; l.a.s., lateral adductor muscle scar; l.g., lophophore groove; l.s., lateral septum; m.s., median septum; r., ramulus; s., sinus; s.p.r., sub peripheral rim; s.r., serration rib; t., tubercle; v.c., visceral cavity. Scale bar represents 0.5 mm.

Elliott (1948) recognized two groups of thecideidines: (i) a thecideiform group, in which numerous septa (text-fig. 1C, F), supporting a multilobed lophophore, arose either from the valve margin or as lateral branches of a median septum; (ii) a thecidelliniform group, characterized by a single median septum and a bilobed lophophore (text-fig. 1A). In the latter group, Elliott (1948, p. 26) detected the incomplete record of a continuous line of descent, *Thecidella* (Lias)—*Bifolium* (Cretaceous)—*Thecidellina* (Recent). Subsequently, Elliott (1953) assigned all the monoseptate forms to the new subfamily Thecidellinae. He conceded that the classification of the heterochronous thecideiform branches was more difficult, as most of the stocks, with the exception of *Eolacazella*—*Lacazella*, were divergent. He recognized that *Davidsonella* was technically thecidelliniform, but argued that the very long brachial lobes showed the same functional attainment as the later thecideiform ptycholophe and included the genus, together with *Eudesella*, *Thecidiopsis*, *Thecidea*, *Eolacazella*, *Lacazella* and *Vermiculotheceida*, in the subfamily Thecideinae. Later, Elliott (1958) considered that intermediate forms between thecideidines and strophomenides or terebratulides were unlikely to be identified and proposed the elevation of the Thecideacea, as understood by Termier and Termier (1949), to subordinal rank to emphasize their distinctiveness. Pajaud's (1970) criticism of Elliott's classification was unjustified. His assertion that Elliott regarded *Thecidella*, *Moorellina*, *Bifolium* and *Thecidellina* as the trunk of a phyletic tree from which the ptycholophous forms branched was incorrect. Elliott clearly understood that two plexi of descent were involved, one rectilinear (Thecidellinae) and the other discontinuous (Thecideinae).

Although incorrect in several respects, e.g. the systematic position of *Thecidella* and *Lacazella*, Elliott's reasoning has stood the test of time (and an enlarged database) remarkably well and in it can be identified the root of all modern classification of the group. However, an important oversight on Elliott's part was his failure to recognize that in genera such as *Thecidella* the median septum was divided by the development of a trough-like depression (text-fig. 1B) or sinus (Baker and Laurie 1978, p. 564). Backhaus equated the median septum with ascending lophophore supporting elements. He coined the terms (Backhaus 1959, p. 12) *apparatus ascendens apertus* to describe the divided median septum (text-fig. 1E) as in *Lacazella*, and *apparatus ascendens clausus* to describe the blade-like median septum (text-fig. 1D) as in *Thecidellina*. Backhaus, like Elliott, also perceived two groups (= tribes of Backhaus 1959) but, unlike Elliott, noted that the *Praelacazella* species showed a progressive passage between the *Thecidella* species of the Lias and the *Lacazella* species of the Tertiary. A further problem stemmed from Elliott's (1948) account of the ontogeny of *Bifolium faringdonense*. Subsequent studies (Baker and Laurie 1978) showed that Elliott had unknowingly combined the ontogeny of the thecidellin *B. faringdonense* with that of the lacazellin *Neothecidella parviserrata*. The earlier failure to recognize this mixed assemblage had led Backhaus (1959), Pajaud (1966a) and Smirnova and Pajaud (1968) to assign forms with an 'open' ascending apparatus to *Bifolium*. Worse, the authors shared a common view that a juvenile 'closed' ascending apparatus (i.e. undivided median septum) could give way to an open (divided median septum) form in the adult, thus paving the way for important misconceptions about thecidiidine phylogeny. It was only later that Pajaud and Smirnova (1971) showed that the form of the median septum is established very early and remains unaltered throughout ontogeny (text-fig. 2). They removed the 'open' *Bifolium lacazelliforme* types to *Praelacazella*.

Having established a marker (Pajaud 1963), and having published a series of short communications on preliminary notes and problems (Pajaud 1966a, 1966b), new genera (Pajaud 1966c, 1966d; Pajaud and Glazewski 1964; Pajaud and Patruilius 1964; Termier, Termier and Pajaud 1966), mutation (Pajaud 1968a), neoteny (Pajaud 1968b), and ontogeny (Smirnova and Pajaud 1968), Pajaud then embarked on the monumental task of monographing all known thecidiidines. The monograph (Pajaud 1970) continued to include the Permian *Cooperina* Termier, Termier and Pajaud, 1966, despite the clear indication (Cooper and Grant 1969, p. 18) that *Cooperina* should be regarded as a productidine assigned to the Strophalosioacea. In view of the, then current, controversy surrounding thecidiidine ancestry, one can sympathize with the authors' eagerness (Termier, Termier and Pajaud 1966) to reveal to the scientific community the first Palaeozoic thecidiidine with such obvious links with the Strophomenida. Cooper and Grant were not to be denied, however, and had, understandably, retained the finest specimens in their own collections. The description and illustration of this material (Cooper and Grant 1975) closely following the systematic dismantling (Dagis 1973, p. 367; Williams 1973, p. 470) of Pajaud's (1970) arguments, dispelled any further doubt about the genus's productidine identity, although reassigned (Cooper and Grant 1975) to the Aulostegacea. Pajaud's reluctance to abandon the identification of *Cooperina* as a thecidiidine (Pajaud 1974; Patruilius and Pajaud 1974) succeeded only in casting a shadow over a study (Pajaud 1970) which remains the most comprehensive statement on matters other than thecidiidine shell microstructure. Pajaud's (1970) proposal to elevate the Thecididina to a taxon of ordinal rank received little support from other workers, probably because it would have contributed nothing towards a better understanding of thecidiidine systematics, but would merely have frozen the uncertainty within the broader framework of ordinal relationships. Pajaud (1970, p. 74) constructed a taxonomy based on the philosophy that the recognition of genera should be based principally on the morphology of the brachial system. By comparing plans of the brachial structure he was able to identify what appeared to constitute natural groups with a high level of internal coherence. The scheme worked reasonably well up to subfamily level, but encountered difficulties when the phyletic relationship between subfamilies was considered. The principal source of the problems lay in the belief that polyseptate genera such as *Eudesella* arose from monoseptate genera such as *Moorellina* by simple mutation, that monoseptate juveniles of *Bosquetella*-type somehow metamorphosed into polyseptate adults of *Thecidiopsis*-type, and that *Thecidellina*-like



TEXT-FIG. 2. Drawings to show juvenile and adult phases in the brachial valve ontogeny of representative species of monoseptate (*apparatus ascendens clausus*), B–J, and polyseptate (*apparatus ascendens apertus*), K–S, thecideidine genera. A, locational diagram. B, C, *Moorellina granulosa* (Moore). D, E, *Pachymoorellina dundriensis* (Rollier). F, G, *Riultina ornata* (Moore). H, J, *Bifolium faringdonense* (Davidson). K, L, *Thecidella rustica* (Davidson). M, N, *Neothecidella parviserrata* Baker and Laurie. P, Q, *Mimikonstantia sculpta* Baker and Elston. R, S, *Thecidiopsis tetragona* (Roemer). Abbreviations: a.r.l., auxiliary resorption lobe; b.c., brachial cavity; i.b.c., intra-brachial cavity; s., sinus. Scale bar represents 0.5 mm.

morphology arose neotenuously from *Backhausina*. It is now accepted (O. Nekvasilová, pers. comm. 1985) that the monoseptate specimens figured as juveniles of *Thecidiopsis bohémica* (Nekvasilová 1964, pl. 11, figs. 1–4) are in fact wrongly assigned to that species. Conversely, the detailed study of the ontogeny of *Thecidiopsis tetragona* revealed (Smirnova 1969) that brachial valves as little as 2.5 mm long already showed the development of lateral septa (text-fig. 1F) and confirmed that Pajaud was incorrect in the belief that the early ontogenetic development of *Thecidiopsis* passed through an auriform (entire median septum and auriform brachial lobes) phase. Although critical of the systematic schemes of Elliott and Backhaus, two thinly disguised groups (= clans) also emerged in Pajaud's (1970) classification. Pajaud's idea of a loose grouping into six subfamilies failed to appeal to Smirnova (1972, 1984) who, on the basis of detailed studies of ontogeny and comparative morphology, decided (Smirnova 1984, p. 109) that the fundamental shortcoming of all

existing classifications was the underrating of the importance of the type of lophophore. Smirnova, in resurrecting Elliott's (1965) family grouping, ascertained that the thecidellinid forms with their schizolophous lophophore (text-fig. 2A-J) differed sharply in ontogeny from the thecideid forms (text-fig. 2K-S) with their ptycholophous or thecidolophous (Pajaud 1970) lophophore. Members of the Thecidellinidae Elliott, 1958 are characterized by a schizolophous lophophore and an undivided median septum which remained a stable character through the Mesozoic to Cenozoic history of the group. The taxon embraces the subfamilies Moorellinae Pajaud, 1966 and Thecidellinae Elliott, 1958. In the Thecideidae Gray, 1840, a complexly divided thecidolophous lophophore is inherent, but it always originates as a concave plate dividing into separate lobes. The taxon embraces the subfamilies Thecideinae Gray, 1840, Davidsonellinae Pajaud, 1968, and Lacazellinae Backhaus, 1959. Arising from the more precise understanding of the various ontogenies, Smirnova (1972) recommended a certain amount of inter-subfamilial rearrangement of taxa, namely that *Eudesella* and *Konstantia* be transferred from the Moorellinae, as understood by Pajaud (1970), to the Thecideinae, and that the monoseptate genera *Bifolium* and *Bosquetella* be removed from the Thecideinae. *Bosquetella* was reassigned to the Moorellinae, *Bifolium*, along with *Rioltina* and *Elliottina*, being reassigned to the Thecidellinae. The only other important subsequent move (Smirnova 1984) was the transfer of *Glazewskia* from the Lacazellinae to the Thecideinae. Discovery of new sources of material enabled the restudy (Baker 1983) of the minute *Enallothecidea pygmaea* (Moore). The absence of a median septum and the incomplete sub-peripheral rim placed the genus close to the most primitive thecideidines. Other discoveries (Baker and Elston 1984) revealed that *Eudesella* was not the sole Early Jurassic polyseptate representative. Detailed study of the ontogeny of *Mimikonstantia* Baker and Elston, 1984 showed that, in its basic expression, it differed little from the development pattern described for *Thecidiopsis* by Smirnova (1969). The conclusion that *Mimikonstantia* was also related to *Konstantia* greatly strengthened Smirnova's (1972) argument for reassignment of *Eudesella* and *Konstantia* to the Thecideinae.

THECIDEIDINE ANCESTRY

A major problem posed by the study of the Thecideidina has always concerned the affinities of the suborder. The group has been identified as having originated from various articulate groups, with the Terebratulida (Elliott 1965), Spiriferida (Williams 1968, 1973) and, in particular, several strophomenide taxa (Rudwick 1968; Baker 1970; Pajaud 1970; Grant 1972; Dagens 1973) emerging as the main contenders. Clearly, their neotenous origin and the influence of palaeogenetic and proterogenetic processes have clouded the image of the line of thecideidine descent. Ideas in the late 1960s and early 1970s had been hampered by uncertainty regarding the Triassic spire-bearing *Thecospira*. Williams (1968, p. 48) revised an earlier opinion that the genus should be identified as a davidsoniacean (Williams 1953, p. 12) in favour of reassignment to the Spiriferida. This proposal was contested by Rudwick (1968, 1970), Baker (1970) and Dagens (1973), who favoured a strophomenide affinity for the genus. Williams, however, remained unconvinced by any counter arguments and reiterated (Williams 1973, p. 475) his earlier view that *Thecospira* should be regarded as a spiriferide, a view supported by Mackinnon (1974). Additionally, it was shown by Hölder (1975) that the brachial supports of complex thecideidines were anatomically different from strophalosiacean productidines. In rejecting the views of other authors, Williams (1973, p. 441) declared that any attempt to identify the ancestor of the thecideidines must take account of the shell microstructure and the likelihood that the thecideidines arose neotenously or paedomorphically. After refuting the arguments in favour of a strophomenide ancestor, Williams was less certain about choosing between spiriferides and terebratulides as the probable ancestral stock. However, after citing cementation in *Thecospira* and recalling differences in the structure of the mantle edge in the thecideidines and terebratulides, Williams (1973, p. 475) finally emerged in favour of descent from a punctate spiriferide. The earlier identification of the Permian *Cooperina* as a thecideidine (Termier, Termier and Pajaud 1966) had sparked off similar controversy (Cooper and Grant 1969; Dagens 1973) before its productidine identity was finally confirmed (Cooper and Grant 1975).

An important development, however, had been the demonstration (Dagis 1973) that the shell microstructure of thecospirids is practically the same as that of early thecideidines and that, in the Thecospiracea, the hungarithecidids were probably ancestral to the thecideidines. Dagis perceived a similarity between plectambonitacean and thecospiracean shell microstructure but, because of the time gap, rejected any idea of a genetic link. However, after evaluation of other characters he considered that, although morphological resemblance to the davidsoniaceans may have been largely convergent, the thecospiraceans were descended from strophomenide ancestors which, by lineage therefore, were also ancestral to thecideidines.

Williams's (1973) meticulously detailed defence of his argument for spiriferide affinity left counter arguments difficult to sustain. The single weakness in Williams's thesis was his inability to demonstrate, other than at general level, any microstructure in the shells of spiriferides and thecideidines which represented unequivocal evidence of a genetic relationship. Because of the profound influence of neoteny in thecideidine evolution (Elliott 1953; Pajaud 1970; Williams 1973, 1984), I concluded (Baker 1984) that study of the characters of potentially ancestral adult shells would be unlikely to provide the key to the identification of the thecideidine ancestor. Also, within the Thecideidina the effects of neoteny suppression of some shell secretion processes were so dramatic that it became difficult to identify characters of phylogenetic significance. Eventually, cyrtomatodont teeth (Jaanusson 1971), secondary fibrous shell, and tubercles came to be recognized as characters which were sufficiently stable to survive all but the most drastic changes affecting the shell microstructure of later representatives of the group. It was perceived that such stable characters should be a feature of at least juveniles of the ancestral stock. The results of examination of the shell microstructure of juvenile representatives of potentially ancestral stock (Baker 1984) confirmed Williams's (1973) opinion and were positive enough to make his arguments in favour of spiriferide affinity virtually unassailable. The circle was closed, therefore, on the earlier demonstration (Dagis 1973) that the shell microstructure of thecospiraceans was almost identical with the microstructure of the majority of Early Jurassic thecideidines, since the confirmation of a genetic link between the thecideidines and spiriferides (Baker 1984) also established a genetic relationship for the thecospiraceans and spiriferides. The identification of the thecideidine tubercle as a structural homologue of the spiriferacean denticle pointed to a spiriferacean, rather than the suessiacean ancestor envisaged by Williams. Contrary to the opinion of Smirnova (1984, p. 115), I have never considered that the thecideidines might be descended from a terebratulide ancestor.

THECIDIIDINE PHYLOGENY

Elliott (1948, 1953) may be credited with the first attempt to elucidate the phylogeny of the, by then, numerous described species. Elliott envisaged, within the suborder, a palingenetic progression from a schizolophous monoseptate form to a ptycholophous polyseptate condition. He considered that the monoseptate genera like *Bifolium* and *Thecidellina*, appearing later, represented the heterochronous expression of the palingenetic trend. Backhaus (1959) rejected Elliott's views, making the important observation that thecideidine lophophore supports developed from the two basic, *apparatus ascendens clausus* and *apparatus ascendens apertus*, patterns. On this basis, Backhaus conceived the idea of two phyletic groups (tribes). He seems to have extrapolated from a thorough knowledge of Cretaceous thecideidines to a much more tenuous understanding of pre- and post-Cretaceous representatives of the suborder. Thus, his proposed phylogeny identifying *Moorellina*, despite its stratigraphic range, as a juvenile *Eudesella*, *Bosquetella* as a juvenile *Thecidiopsis*, and *Thecidellina* as the juvenile of some undiscovered ptycholophous adult, was manifestly suspect.

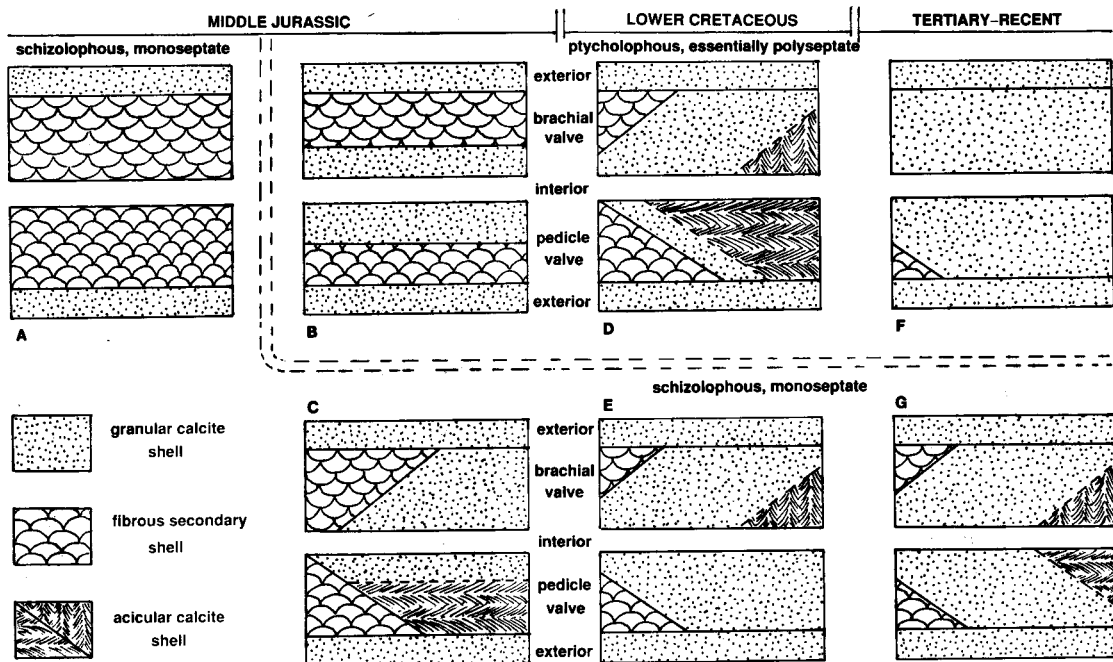
Rudwick's study of food-gathering mechanisms (Rudwick 1968) brought the problematical Triassic genera *Bactrynum* Emmrich, 1855, and *Thecospira* Zugmayer, 1880 into the picture, introducing the concept of the 'functional zone' as a measure of the phyletic relationship between the Thecideacea, Davidsoniaceae and Lyttoniaceae. Rudwick (1968, p. 353) included *Bactrynum* in the Thecideacea, arguing that the strophic hinge and articulation was quite unlike the aberrant

structures of the lytoniaceans and that the lophophore lay in lobed grooves like those found in polyseptate thecideidines.

Work on a very large collection of 2700 Early Cretaceous thecideid shells from Valanginian and Hauterivian bioherms in the Crimea (Smirnova 1969) enabled detailed study of the ontogeny of species of the thecidellinid genera *Bifolium* and *Bosquetella*, and the thecideid genera *Thecidiopsis* and *Praelacazella*. Close similarities in development suggested (Smirnova 1969, p. 64) that *Moorellina* was probably ancestral to *Bosquetella*. More important, the earliest stages in the development of both *Praelacazella* and *Thecidiopsis* were characterized by a broad median septum with a central sinus. In *Praelacazella* the structure was retained throughout all growth stages, whereas in *Thecidiopsis* it was quickly translated, though the development of a split in the median septum near the hinge-line, into the precursor of a polyseptate condition. The distinctiveness of the thecidellinid and thecideid ontogenetic development patterns provided interesting confirmation of Backhaus's (1959) idea of two phyletic groups. Additionally, within the groups, lineages showing parallel development were beginning to appear. *Moorellina*—*Bosquetella* and *Elliottina*—*Bifolium*—*Thecidellina* lineages were identified in the Thecidellinidae, and *Thecidella*—*Praelacazella*—*Lacazella* and *Eudesella*—*Thecidiopsis*—*Glazewskia* lineages were recognized in the Thecideidae. Smirnova's important contribution probably appeared too late to allow Pajaud (1970) the opportunity for comment. He was unenthusiastic about Rudwick's (1968) views on thecideidine phyletic relations, in which he saw the resurrection of Elliott's ideas. However, Pajaud (1970, p. 79) did feel able to support the location of *Bactrynum* near to the Thecideidae in the Thecideacea. He appreciated the phyletic significance of Backhaus's two tribes and, with some modification of Backhaus's ideas, introduced a new phylogeny based on the concept of *Lacazella* and *Thecidellina* 'clans', embracing five subfamilies. Despite the weight of evidence against it, the Permian *Cooperina* was still identified at the base of the main trunk from which the two branches separated. Pajaud considered that the *Lacazella* clan, including the Davisonellinae and Lacazellinae, arose from a *Davidsonella*-type ancestor and that the evolution from the Lias to Recent followed a rectilinear pattern. The *Thecidellina* clan which included the Moorellininae, Thecideinae and Thecidellininae was also believed to have arisen from a *Davidsonella*-type ancestor. The evolution of the latter group was more complicated, and mutation was invoked (Pajaud 1968a) to explain the recurrent appearance of Jurassic and Cretaceous polyseptate forms, whereas neoteny was invoked (Pajaud 1968b) to account for the return to a monoseptate condition in the Tertiary.

Through his comprehensive survey of characteristically thecideidine features, Williams (1973, p. 466) was able to identify a range of unifying characters in strong contrast to the profound evolutionary changes suffered by the shell microstructure and lophophore supports. In consideration of the ptycholophe as opposed to the thecidolophe (Pajaud 1970, p. 33), Williams concluded that both conditions could be regarded as equipotential adult elaborations of an immature schizolophe and may, therefore, have recurred many times in thecideidine history. Unfortunately, although ignoring *Cooperina*, his chart showing the phyletic variation in thecideidine shell microstructure (Williams 1973, fig. 100, p. 468) was based on Pajaud's phylogenetic reconstruction (Pajaud 1970, fig. 31, p. 82) and was, therefore, constrained by the same misconceptions which characterized Pajaud's phylogeny.

In a more recent contribution, Smirnova (1984) has shown that the early juveniles of the Lower Cretaceous *Bifolium mica* are very similar to adults of the Middle Jurassic *Rioulina* and *Elliottina* which, in their adult morphology approach *Bifolium* and *Thecidellina*. On this basis, Smirnova detected a genetic relationship and rejected Pajaud's (1970) view that *Thecidellina* arose neotenuously from a Cretaceous thecideid which, instead of having a blade-like median septum, would be characterised by a concave median septum, quickly opening out to form lobes. It is now clear (author's unpublished work) that the adult *Bifolium faringdonense* has canopied brachial lobes like *Thecidellina*, offering further support for Smirnova's view. Although the development of the polyseptate condition from a concave triangular plate (Smirnova 1984) is a unifying character in the Thecideidae, representatives of the Thecideinae are characterized by lobes which are differentiated in a lateral direction, whereas representatives of the Lacazellinae are characterized by lobes which



TEXT-FIG. 3. Diagrammatic representation of the chronological succession of the principal events in the evolution of thecideidine shell structure. Posterior and postero-lateral sectors of valve, left, anterior and antero-lateral sectors of valve, right. Horizontal lines indicate continuous layer, diagonal lines indicate restricted distribution. A, *Moorellina*, continuous fibrous secondary shell layer in both valves. B, *Mimikonstantia*, partially suppressed fibrous secondary shell. C, *Pachymoorellina*, partially suppressed fibrous secondary shell and introduction of acicular calcite tracts. *Thecidiopsis*, D, more strongly suppressed fibrous secondary shell, acicular calcite well-developed. E-G, fibrous secondary shell vestigial, restricted mainly to teeth and inner socket ridges, acicular calcite often well-represented but the shell is composed principally of granular calcite. E, *Bifolium*, F, *Lacazella*. G, *Thecidellina*. No lineage is implied.

are differentiated in a front to rear direction. In this respect, Pajaud's (1970) assignment of *Bactrynum* to a position near the Thecideidae seems reasonable. The two subfamilies of the Thecideidae appear to have showed parallel evolutionary development, expressed through a small number of lophophore lobes in the Lower Jurassic, becoming increasingly complex during the Upper Jurassic and Lower Cretaceous, with the maximum complexity reached simultaneously in both groups during the Upper Cretaceous. Changes at the Cretaceous/Palaeocene boundary led to the extinction of the specialized forms. The survival of thecideidines was attributed (Smirnova 1984) to the existence of 'primitive' forms able to adapt to life in various conditions and continue the existence of simply-organized genera in modern basins. Smirnova also studied the evolution of thecideidine shell microstructure and reached essentially the same conclusion as Williams (1973, 1984), namely that the continuous fibrous secondary lining (text-fig. 3A) characteristic of early Jurassic shells had been reduced to vestigial patches on the teeth and sockets (text-fig. 3E) by the Early Cretaceous. Williams (1973, p. 469) envisaged that suppression of the fibrous secondary layer was accomplished rapidly, and placed the onset of the trend in late Jurassic time. Williams (1984, p. 739) regarded the suppression of fibrous secondary shell as an expression of neoteny. Smirnova (1984) was able to identify three stages to the suppression process which affected the brachial and pedicle valves differentially. Jurassic representatives were found to have a fibrous secondary layer in both valves. In the Lower Cretaceous, Berriasian to Hauterivian species showed a reduction (text-

fig. 3D) in the fibrous secondary layer in the brachial valve. The suppression of fibrous secondary shell was then extended to the pedicle valve also (text-fig. 3E-G), so that from the Barremian to the Present both valves were characterized by the complete reduction of the fibrous secondary layer, the end product being a granular calcite shell, with or without acicular calcite aggregations, in which the occurrence of fibrous secondary shell, if present at all, was restricted to the teeth and inner socket ridges. Study of a newly-discovered basal Middle Jurassic species (Baker and Elston 1984) cast some doubt on opinions about the timing of the onset of the evolutionary changes in shell microstructure. The shell microstructure of *Mimikonstantia* revealed that the onset of the neotenous suppression of fibrous secondary shell could be traced back at least as far as the beginning of the Middle Jurassic. Also, the shell microstructure resembles that of the Lower Cretaceous species *Thecidiopsis tetragona* and *T. lata*. The conclusion that *Mimikonstantia* and *Thecidiopsis* were phylogenetically linked (Baker and Elston 1984) offered indirect support for Smirnova's belief in a phylogenetic link between Jurassic and Cretaceous polyseptate forms. Consideration of the mechanical requirement for the multiplication of lateral septa suggested a possible sequence (Baker and Elston 1984, fig. 5, p. 790) in the development of a thecidiolophous form from a ptycholophous ancestor and thus, by implication, linked *Mimikonstantia*, *Thecidiopsis*, *Backhausina* and *Thecidea*, again supporting Smirnova's (1984, fig. 64, p. 110) ideas. The evidence indicated that Pajaud's (1970) tentative derivation of *Konstantia* and *Thecidiopsis* from monoseptate *Rioulina* stock was no longer tenable as *Mimikonstantia* pre-dates *Rioulina*. Recent studies (Baker 1989) also enable the origin of *Thecidiopsis* to be traced back to basal Middle Jurassic roots, although analysis of the shell microstructure of a newly designated genus indicates that both *Mimikonstantia* and *Eudesella* are slightly diverged from the main line of descent.

DISCUSSION

Ideas about thecideidine taxonomy, origin and phylogeny have been developed through consideration of morphological, ontogenetic and, more recently, shell microstructural evidence. The review would be incomplete without consideration of the value of the contribution made by each of these aspects.

The value of morphology

Because of their external morphological similarity and because their abnormally wide gape facilitates post-mortem liberation of brachial valves, the taxonomy of thecideidine brachiopods has traditionally relied heavily on the internal morphology of separated pedicle and brachial valves. Particular attention has always been paid to the skeletal supports for the lophophore. Although septa are usually sufficiently robust to provide reliable evidence of their location and general form, other structures, especially brachial and interbrachial lobes, are often fragile and finely sculptured and are almost invariably broken in separated brachial valves. Reservations about the reliability of the evidence as seen in separated brachial valves were expressed as early as the beginning of this century (Upton 1905, p. 91). Nekvasilová, after careful study of the Lower Turonian *Thecidiopsis (T.) bohémica imperfecta*, reached the conclusion (Nekvasilová 1967, p. 130) that, in thecideidines, determination based on the so-called brachial ridges as seen in detached brachial valves was quite inadequate, since such ridges may be a relic of structures whose complete shape may only be studied through sectioning of complete shells. She remarked on the similarity between the reconstructed brachial lobes of the Lower Turonian specimens and those of the Recent *Thecidellina blochmanni* Dall. Work on the ontogenetic development of *Moorellina granulosa* (Moore) showed that the brachial tubercles were the broken remains of much more elaborate structures (Baker 1969) which overarched the intra-brachial cavities. Perforate canopies have subsequently been identified (research in progress) in the Aalenian *M. dubia* and the Aptian *Bifolium faringdonense*. Clearly therefore, the development of the brachial lobes in the *Moorellina*—*Thecidellina* plexus of descent, as envisaged by Smirnova (1984), conformed to a more coherent pattern than became apparent from the study of separated brachial valves. Similarly, the radially disposed septa (Baker and Elston

1984) of the polyseptate *Mimikonstantia sculpta* are almost invariably broken in separated brachial valves.

Over-reliance on morphological evidence has been responsible for some of the most heated controversy surrounding the probable origin and systematic position of the Thecideidina. Termier, Termier and Pajaud's (1966) introduction of *Cooperina* as the first Palaeozoic thecideidine is a case in point. The authors' selective recognition of 'thecideidine' morphological characteristics prompted the omission of the obviously non-thecideidine aspects of the genus. Their arguments were systematically dismantled by Cooper and Grant (1969, p. 18) and finally refuted (Cooper and Grant 1975) through the description and figuring of the superb *Cooperina* specimens to which they had access. A similar selective approach was required to enable Grant (1972) to 'force' the conclusion (see Hölder 1975) of a genetic relationship between thecideidines and strophalosiacean productidines such as *Falafer*.

Rudwick (1968) recognized that in polyseptate thecideidines such as *Thecidiopsis* the primary lophophore lobe is that furthest from the mid-line in a postero-lateral position, and that in *Bactrynum* the primary lobe is located close to the median septum in an anterior position. In this respect the antero-postero extension of the lophophore lobes of *Bactrynum* resembles the development pattern of the lacazellins rather than the lateral extension pattern seen in the thecideidines. Rudwick's error lay in the assumption that, in polyseptate thecideidines, growth without shell resorption was able to translate the juvenile arrangement into the adult complement of lateral septa. Study of the development of septa in relation to shell growth in polyseptate thecideacean species (Baker and Elston 1984) has shown that as the brachial valves increase in size, the zones of maximum growth acceleration (Baker 1970) become increasingly separated from the median septum. Therefore, in a shell which is increasing in width more rapidly than it is increasing in length, lateral migration of septa relative to the principal growth vectors is required, and a precisely-controlled process of shell accretion and resorption is necessary for this to be accomplished. On the other hand, if the brachial valve is increasing in length more rapidly than it is increasing in width, as in *Bactrynum*, zones of maximum growth acceleration will remain aligned essentially parallel with the median septum, and the antero-postero development pattern described by Rudwick (1968) will represent the optimum for the circumstances appertaining. This implies, therefore, that septal (and lophophore lobe) development patterns are a strategic response to shell growth requirements and present no real obstacle to the postulation of a genetic relationship between *Bactrynum* and thecideidines. The observation, in addition to the more general morphological considerations, that the shell succession in *Bactrynum* included a normally developed fibrous secondary layer and impersistent tubercles (Williams 1973, p. 475) further substantiated the view that the genus might reasonably be included in the Thecideidina. Although Rudwick was able to accept convergent evolution as the explanation for the morphological similarity between *Bactrynum* and lytoniacean genera, he firmly resisted the idea (Rudwick 1968, p. 329) that the morphological similarity between *Thecospira* and the davidsoniaceans could be similarly explained. By concentrating on cementation, lobed brachial grooves, pseudodeltidium and absence of pedicle foramen as prime evidence, Rudwick was able to assign the thecideidines (including *Bactrynum*) to the Davidsoniacea along with *Thecospira*. Williams (1973) was critical of Rudwick's selective approach and, as subsequent studies have shown (Baker 1984), convergent evolution in reef-associated faunas is probably common. Also, brachial grooves are not characteristic of all early thecideidines (Baker and Elston 1984). Cementation and a pseudodeltidium are also not as exclusive as Rudwick believed (Cooper and Grant 1975). Additionally, there is some evidence that very early thecideidines may have possessed a transient apical pedicle foramen (Baker 1983) and that, initially at least, the pseudodeltidium was located apically in the delthyrium. The accumulated evidence, reinforced by the discovery that the thecideidine tubercle should be regarded as homologous with the spiriferide denticle rather than the strophomenide taleola (Baker 1984) led to abandonment of the notion that the ancestors of the thecideidines were to be found among the strophomenides.

The value of ontogeny

Although some of the palingenetic and neotenous processes thought to have been operative during thecideidine evolution subsequently proved to be questionable, it is probable that as many issues have been resolved through the interpretation of ontogeny as have been clouded by misinterpretation of morphology. It is unfortunate, therefore, that one of the earliest detailed studies (Elliott 1948) combined events in the ontogenies of *Bifolium* (text-fig. 2H, I) and *Neothecidella* (text-fig. 2M, N) into a single sequence, resulting in considerable taxonomic confusion until the error was noted and rectified (Baker and Laurie 1978). Similarly, it is now clear that the rioultnid (undivided median septum and auriform brachial lobes) brachial valves (text-fig. 2G) figured as juveniles of *Thecidiopsis bohémica* (Nekvasilová 1964, pl. 11, figs. 1–4) were wrongly identified (O. Nekvasilová, pers. comm. 1985). After a detailed study of available ontogenetic records, Pajaud (1970) concluded that the evolution of the lophophore supports followed a more complex pattern than the palingenetic (Elliott 1953, p. 698) or neotenously-induced (Backhaus 1959, p. 77) progressions previously favoured. The real key to understanding phyletic relationships, however, was provided by Smirnova's (1969, 1984) correlation of the development of the lophophore supports in the various groups. The very large collections of material from the Crimea enabled considerable progress to be made in the detailed interpretation of the ontogeny (Smirnova 1969) of *Thecidiopsis*, *Praelacazella*, *Bosquetella* and *Bifolium*. The discovery that the ontogeny of *Thecidiopsis* (text-fig. 2R, S) did not pass through a rioultnid phase (Smirnova 1969) came too late, however, to prevent Pajaud (1970) from deriving *Thecidellina* neotenously from *Thecidiopsis* stock. But, it was not until much later, that Smirnova formally rejected (Smirnova 1984) the citation of monoseptal forms such as *Bosquetella* as initial stages in the evolution of *Thecidiopsis tetragona* (Backhaus 1959) and *T. bohémica* (Nekvasilová 1964). Smirnova considered thecidellinin ontogenetic changes as being exemplified by the ontogenetic development of *Bifolium mica*. The ontogeny of *Bifolium* was traced via genetic links with *Elliottina* and *Thecidellina* and *Bosquetella* with *Moorellina*, thereby vindicating Elliott's remarkably perceptive observation (Elliott 1948) that although some species may have become extinct there is little doubt that most of the monoseptate, schizolophous species known, represent the broken record of a continuous series of thecidellinins from the Mesozoic to the present day. With allowance for a tachygenetic element, the correlation of the mechanics of shell growth with septal development pattern (Baker and Elston 1984) reveals a remarkable similarity between the early ontogeny of *Mimikonstantia* and *Thecidiopsis*, even down to the thickened triangular structure from which the lateral septa develop (text-fig. 2P, Q). According to Smirnova (1984) this triangular element could be correlated with the primitive divided median septum of some davidsonellins which was considered to link the Davidsonellinae with the Thecideinae and Lacazellinae in the Thecideidae. Evidence from ontogenetic studies has proved useful in the resolution of other taxonomic problems. Because Pajaud (1966b) had queried the validity of the species designation, Barczyk (1970, p. 653) was uncertain about the status of specimens of *Moorellina septata* (Moore) from the Upper Jurassic of Poland. Study of juveniles of a newly-designated Middle Jurassic genus (Baker 1989) shows that the specimens of *M. septata* queried by Pajaud as juveniles of *M. dundriensis* (Pajaud 1966b) in no way correspond to the latter.

The value of shell microstructure

The use of shell microstructure as an indicator of thecideidine relationships entered the arena relatively late, and for a variety of reasons (Grant 1972, p. 244; Williams 1973, p. 441), its potential value continued to be underestimated (Smirnova 1984). With the exception of three investigations of *Lacazella* shell microstructure (Davidson 1887, Oehlert 1887; Thomson 1927), thecideidine shell microstructure remained virtually unknown until Elliott's (1953, 1955) studies. The early studies were hampered by the difficulty of preparing sections and certain resolution deficiencies of optical microscopes. Also, by chance selection for study (Williams 1955) of a species in which fibrous secondary shell had been almost completely suppressed, it was not discovered that, in the majority of thecideidines, the shell microstructure differs in brachial and pedicle valves. Although Elliott

(1953, p. 695) observed 'the dark-coloured elements of typical pseudopunctuation are seen against clearer lamellar shell, but never so clearly as good examples of pseudopunctuation in certain Palaeozoic brachiopods', neither the resolution of the instruments nor the current state of knowledge enabled the observers to differentiate between taleolae and tubercle cores. Resolution problems were subsequently eliminated (Williams 1968) with the advent of scanning electron microscopy facilities, and the problems of section preparation were considerably alleviated by the use of cold-setting transparent embedding resins and the development of techniques (Baker 1970) for serially sectioning the very small shells at intervals of approximately 20 μm . The demonstration that the shell (text-fig. 3A) of the Middle Jurassic *Moorellina granulosa* was lined by a continuous layer of fibrous secondary shell (Baker 1970) caused Williams (1973) to modify his earlier conclusion (Williams 1968) that the shell microstructure (text-fig. 3F) of *Lacazella* was typical of the thecideidine model. Appreciation of the critical importance of precise location and orientation of section (Baker 1970) no doubt informed the ensuing study, of thecospiracean shell microstructure (Dagis 1973) the very detailed investigation of the Recent thecideidines *Thecidellina barretti* (Davidson) and *Lacazella mediterranea* (Risso) by Williams (1973), and studies of the shell microstructure of Lower Cretaceous species (Smirnova 1979, 1984). Even after the thecideidine structures had been identified as the cores of tubercles (Baker 1970), the pseudopunctuation signal was still so strong that it was easy to continue to regard them as being homologous with taleolae and, through association, perceive a relationship with strophomenides. Although concluding that thecospiraceans were closer to thecideidines than any other group, Dagis's opinion (1973) about the systematic position of the thecospiraceans and their relationship with thecideidines was also coloured by the strength of the historical association of both groups with the Strophomenida. It is unfortunate that, after demonstrating the genetic relationship, he then went on to parallel in thecospiraceans my misconception (Baker 1970) of the thecideidine tubercle as structurally homologous with the strophomenide taleola. Williams (1973), prompted by the discovery of fibrous secondary shell in early Middle Jurassic representatives of the group, undertook a critical survey of the shell microstructure of the majority of the described thecideidine genera. This study established that a continuous lining of fibrous secondary shell was the standard Lower to Middle Jurassic condition (text-fig. 3A) and the indications were that the onset of its neotenus suppression was not effected until the Upper Jurassic or Early Cretaceous (text-fig. 3D, E). Smirnova (1979), in pursuit of Williams's (1973) idea of a Late Jurassic to Early Cretaceous date for fibrous secondary shell suppression, studied the shell microstructure of three Lower Cretaceous species, *Thecidiopsis tetragona* (Roemer), *Thecidiopsis lata* Smirnova and *Praelacazella valangiensis* (de Loriol) in an attempt to find out if the change was abrupt or gradual. The differences in the microstructure of *T. tetragona* and *T. lata* and the similarity of *P. valangiensis* to both, helped to convince her that microstructure was of limited taxonomic value, but useful in dating the important steps in the structural evolution of the shell. This conviction was strengthened by a later study (Smirnova 1984) in which she deduced that, although the structural changes of the shell proceeded steadily, the disappearance of the fibrous secondary layer was quick and probably occurred in the first half of the Lower Cretaceous. Smirnova concluded that the degree of plasticity of microstructural changes in the thecideidine shell rendered shell microstructure almost valueless in the comparison of Mesozoic thecideidines and Triassic thecospirids with ancient Palaeozoic groups, and virtually useless for drawing conclusions about their hypothetical relationship. She felt that shell microstructure was only of value when its use was confined to the study of successive groups in time. The situation was envisaged as being most complicated from the Upper Cretaceous to Recent, as a consequence of the relative uniformity of shell microstructure (Smirnova 1984), when, the extreme difficulty of determining the relationship between layers of granular and acicular calcite rendered it of little use for systematization purposes. Work by Baker and Elston (1984) on newly-discovered Middle Jurassic material demonstrated, contrary to the view of Williams (1973) and Smirnova (1979, 1984), that although the fibrous secondary layer was still continuous, the trend towards its suppression (text-fig. 3B) was already established by the early Middle Jurassic. Subsequent investigations (Baker 1989) revealed that *Mimikonstantia sculpta* was not the only species affected.

In the contemporaneous *Pachymoorellina dundriensis*, fibrous secondary shell had already disappeared (text-fig. 3C) from the anterior and antero-lateral sectors of both valves.

CONCLUSIONS

The conjectural nature of some of the identifications of brachial lobe morphology has created taxonomic and phylogenetic problems. Until about the mid-1960s, interpretation was made more difficult because the size of most thecideacean representatives of the suborder fell outside the optimum resolution range for both conventional photography and reflected light photomicrography, so that the quality of plate figures was modest by current standards. Study of the detail of thecideidine morphology, and especially their shell microstructure was revolutionized by the advent of the scanning electron microscope. Considerable emphasis has been placed on the relative value of shell microstructure as a distinctive character. Although general shell fabric may not be diagnostic, structures such as tubercle cores, from a unifying point of view, show a remarkable continuity of expression throughout the history of the group. Also, it was only the demonstration that the thecideidine tubercle was probably the structural homologue of the spiriferacean denticle, rather than the strophomenide taleola, that enabled the link between thecideidines and strophomenides to be severed with confidence. The thecideidines represent a group whose classification is aided by the recognition of genera showing a high level of coherence from a genetic relationship point of view. Clearly, much remains to be discovered about the stratigraphic and geographical range of this still comparatively little-known group. Also, much more work is required on the detailed mapping of the various successions of shell microstructure, which is emerging as a taxonomic indicator of far greater potential than has hitherto been appreciated. However, in my opinion, sufficient information is now available to enable a reliable taxonomic and phylogenetic framework to be established.

RECOMMENDATIONS

Revised classification

Excluding the aulostegacean *Cooperina*, for the reasons given by Cooper and Grant (1969, 1975), Dągis (1973) and Williams (1973), the Thecideidina, as understood by Pajaud (1970, pp. 82–83) included twenty two genera distributed among five subfamilies. Apart from some rearrangement of genera and the resurrection of older family grouping (Smirnova 1984), Pajaud's framework has persisted, largely unaltered, to the present time. A further, subfamily Enallothecideinae Baker, 1983 and four additional genera *Enallothecidea* Baker, 1983, *Mimikonstantia* Baker and Elston, 1984, Pajaudina Logan, 1988 and *Pachymoorellina* Baker, 1989 may now be added. The general organization and shell microstructure of *Enallothecidea* is similar to that of early juvenile moorellinins prior to the full differentiation of the median septum. It is proposed, therefore, to reassign the Enallothecideinae to the Thecidellinidae. In view of the perceived relationship between *Bactrynum* and thecideidines, and the weight of evidence about the genetic relationship between thecospiraceans and thecideidines and their affinity with spiriferides a revised classification is proposed as follows:

- Order SPIRIFERIDA Waagen, 1883
- Suborder THECIDEIDINA Elliott, 1958
- Superfamily THECOSPIROIDEA Bittner, 1890
- Family THECOSPIRIDAE Bittner, 1890
- Genus THECOSPIRA Zugmayer, 1880
- Family THECOSPIRELLIDAE Dągis, 1973
- Genus THECOSPIRELLA Bittner, 1900

Family HUNGARITHECIDAE Dagens, 1973

Genus HUNGARITHECA Dagens, 1973

Superfamily THECIDEOIDEA Gray, 1840

Family THECIDELLINIDAE Elliott, 1958

Subfamily ENALLOTHECIDEINAE Baker, 1983

Genus ENALLOTHECIDEA Baker, 1983

Subfamily MOORELLININAE Pajaud, 1966

Genera MOORELLINA Elliott, 1953; PACHYMOORELLINA Baker, 1989; BOSQUETELLA Smirnova, 1969

Subfamily THECIDELLININAE Elliott, 1953

Genera RIOULTINA Pajaud, 1966; BIFOLIUM Elliott, 1948; THECIDELLINA Thomson, 1915

Family BACTRYNIIDAE Williams, 1965

Genus BACTRYNIUM Emmerich, 1855

Family THECIDEIDAE Gray, 1840

Subfamily DAVIDSONELLINAE Pajaud, 1966

Genera DAVIDSONELLA Munier-Chalmas, 1880; AGERINELLA Patruilius, 1964

Subfamily LACAZELLINAE Backhaus, 1959

Genera THECIDELLA Oehlert, 1887; NEOTHECIDELLA Pajaud, 1970; PARABIFOLIUM Pajaud, 1966; PRAELACAZELLA Smirnova, 1969; VERMICULOTHECIDEA Elliott, 1953; DANELLA Pajaud, 1966; EOLACAZELLA Elliott, 1953; LACAZELLA Munier-Chalmas, 1880; PAJAUDINA Logan, 1988

Subfamily THECIDEINAE Gray, 1840

Genera EUDESELLA Munier-Chalmas, 1880; MIMIKONSTANTIA Baker and Elston, 1984; KONSTANTIA Pajaud, 1970; THECIDIOPSIS Oehlert, 1887; BACKHAUSINA Pajaud, 1966; PARATHECIDEA Backhaus, 1959; THECIDEA Defrance, 1822; GLAZEWSKIA Pajaud, 1964

Elliottina Pajaud, 1963 is not included in the revised classification. The genus was never strongly placed and was soon relegated to sub-generic rank by Pajaud himself (Pajaud 1966b). The whole concept of the erection of a genus on the basis of the width of the ventral interarea is highly suspect in attached forms, where the morphology of the pedicle valve is so strongly influenced by the size and shape of the surface to which attachment is effected. It is rather surprising, therefore, that a new subfamily Elliottininae was proposed (Pajaud and Smirnova 1971) to include the resurrected *Elliottina* and also *Rioltina* and *Bifolium*. The Elliottininae was subsequently abandoned (Smirnova 1984), with *Rioltina*, *Bifolium*, and *Elliottina* being restored to the Thecidellininae.

The superfamily suffix -ACEA enjoys such a wide usage in current terminology that it would have caused considerable confusion to have changed it in the body of the paper. However, in compliance with the ICZN recommendation 29a (Ride *et al.* 1985, p. 55) -OIDEA is added to the superfamily stem as the preferred suffix in the revised taxonomy.

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