

THE DIMINUTIVE THECIDEIDINE BRACHIOPOD
ENALLOTHECIDEA PYGMAEA (MOORE)
FROM THE MIDDLE JURASSIC
OF ENGLAND

by P. G. BAKER

ABSTRACT. The discovery of new sources of material has enabled restudy of the minute *Thecideum pygmaeum* Moore, 1861. Although their general organization is close to that of the monoseptal representatives of the Moorellininae the new specimens differ from typical thecideidines in the absence of both dorsal median septum and hemispondylium and in the presence of an incomplete subperipheral rim. The form may prove to be important in tracing the phylogeny of the Thecideidina. It is assigned to a new genus *Enallothecidea* whose characters are considered to be sufficiently distinctive to warrant its inclusion in a new subfamily, the Enallothecideinae.

THE species investigated was, prior to the availability of the new material, known essentially from four figures in an account of micromorphic Brachiopoda from the Coral Rag, Lyneham, Wiltshire (Moore 1861, pl. 2, figs. 4-7). It is impossible to ascertain whether type specimens were ever designated. Davidson (1876) disagreed with Moore's (1861) interpretation of specific characters and refigured the species, although whether the new drawings were prepared from Moore's specimens or some of Davidson's own material is not known. Dr. C. H. C. Brunton (pers. comm. 1982) considers that the annotation on Davidson's original drawings, currently housed in the British Museum (Natural History) suggests that Davidson may have redrawn Moore's specimens, although Davidson in his monograph (1876, p. 105) simply refers to specimens 'that passed through my hands'. A tube containing nine specimens was listed as M2852 *Thecideum pygmaeum*, Corallian, when the major part of the Moore collection held in the Bath Literary and Scientific Institution was catalogued by Dr. F. S. Wallis in 1927. Examination of this material shows that the tube in fact contains specimens of *Rioulina ornata* (Moore). No specimens were found in that part of the Moore collection which had been passed on to the Revd. H. H. Winwood (Baker and Copp 1975) and is currently housed in the Somerset County Museum, Taunton Castle. In the absence of the original material, the new specimens must necessarily be compared only with figures; even so their morphology is so distinctive that there can be no doubt that they belong to the same species as that figured by Moore. However, as the species has remained so imperfectly known since its discovery it is here considered necessary to emend the original diagnosis.

Registration of material. The neotype and hypotypes are housed in the British Museum (Natural History) under numbers BB 81112-BB 81114.

Preparation of material. Bulk samples from unconsolidated or only partially consolidated horizons were washed through a nest of sieves. The thecideidines were then hand-picked from dried 350 μm and 175 μm residues under a binocular microscope. Specimens were transferred to glass tubes for further cleaning by weak sonication for periods of up to 10 seconds. Specimens selected for stereoscanning were gold-coated before photography.

SYSTEMATIC PALAEOLOGY

Order UNCERTAIN

Suborder THECIDEIDINA Elliott, 1958

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

Family THECIDEIDAE Gray, 1840

Subfamily ENALLOTHECIDEINAE subfam. nov.

Diagnosis. Minute forms with undivided brachial interior, dorsal median septum lacking, lophophore probably trocholophous; hemispondylium not developed. *Age*, Middle Jurassic.

Genus ENALLOTHECIDEA gen. nov.

Etymology. From the Greek *enallōs* (contrary) after the significant departure from typical thecideidine internal morphology.

Diagnosis. Characters of the subfamily.

Type species. *Thecideum pygmaeum* Moore, 1861.

Enallothecidea pygmaea (Moore, 1861)

Plate 69, figs. 1-9; text-fig. 1

1861 *Thecideum pygmaeum* Moore, p. 96, pl. ii, figs. 4-7.

1876 *Thecedium? pygmaeum* Moore; Davidson, p. 105, pl. XIII, fig. 16, 16a, b, c.

Type specimens. No holotype designated, syntypes lost. Neotype (here proposed) complete shell BB 81112. Hypotypes, brachial valve BB 81113 and pedicle valve BB 81114.

Dimensions of neotype. Length 0.6 mm, width 0.4 mm, thickness 0.4 mm.

EXPLANATION OF PLATE 69

Stereoscan photomicrographs of *Enallothecidea pygmaea* (figs. 1-9) and other specimens (figs. 10-12) for comparison. All figures are of specimens coated with evaporated gold before photography.

Figs. 1-3. Lateral, brachial, and anterior views of the neotype, BB 81112, $\times 100$.

Fig. 4. Interior of pedicle valve BB 81114 showing the apical attachment scar, the hinge teeth, and the strongly endopunctate shell; the pseudodeltidium is missing in this specimen, $\times 95$.

Fig. 5. Three-quarters profile view of brachial valve BB 81113, rotation and tilt angle 45° , to show the form of the subperipheral rim, the cardinal process (arrowed), and the dental sockets, $\times 90$.

Fig. 6. Interior of brachial valve BB 81113, $\times 105$.

Fig. 7. Near three-quarters profile view of pedicle valve BB 81114, rotation and tilt angle 60° , to show the relationship between the attachment scar and the growth lines, $\times 65$.

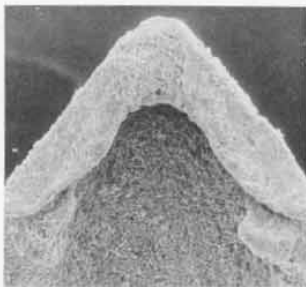
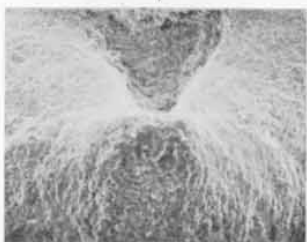
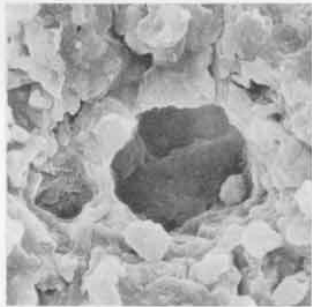
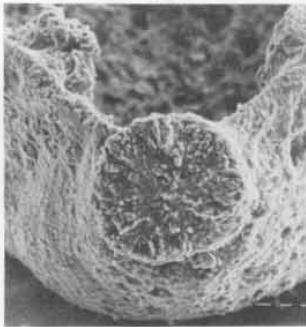
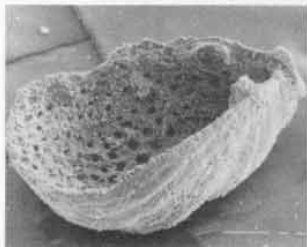
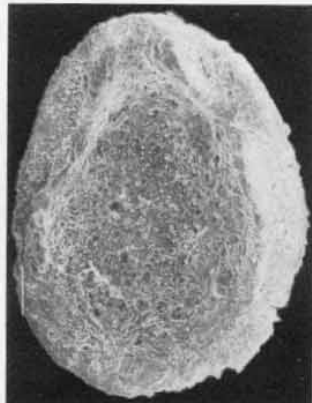
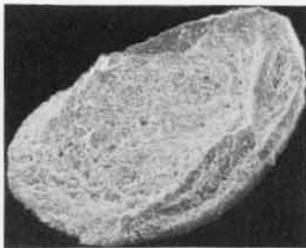
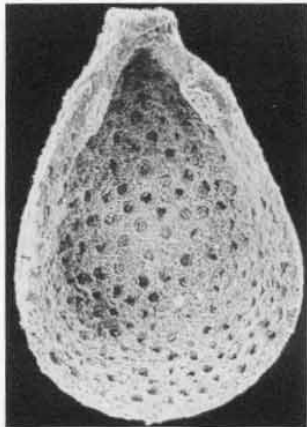
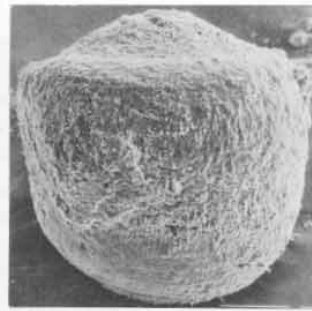
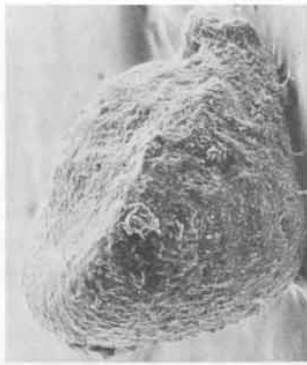
Fig. 8. Posterior view of specimen BB 81114, tilt angle 60° , showing detail of the apical attachment scar, $\times 225$.

Fig. 9. Disturbed secondary shell fabric adjacent to an endopuncta, $\times 2350$.

Fig. 10. Angled view (orientation as fig. 8) of the posterior portion of the pedicle valve of an early juvenile spiriferide, *Howellella* (author's collection, PB 1523), from the Much Wenlock Limestone Formation, Wren's Nest, Dudley, to show the form of the ventral umbonal region prior to the clear differentiation of an interarea, $\times 50$.

Fig. 11. Brachial view of the posterior portion of a pedicle valve of an early juvenile terebratulid, *aff. Plectothyris* (author's collection, PB 1524) from the Oolite Marl, Westington Hill, showing the pedicle collar filling the apex of the delthyrium and the incipient deltidial plates, $\times 80$.

Fig. 12. Brachial view of the posterior portion of a pedicle valve of an early juvenile terebratellid, *Zeilleria* (author's collection, PB 1525), from the Oolite Marl, Westington Hill, showing the beginning of shell resorption at the apex of the delthyrium, $\times 85$.



BAKER, *Enallothecidea*, *Zeillera*, aff. *Plectothyris*, *Howellella*

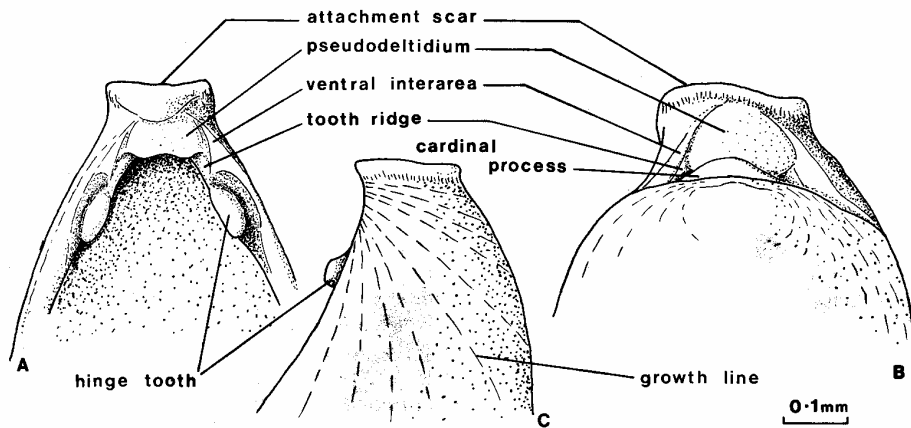
Original diagnosis (Moore 1861). Shell microscopic, longitudinally oval; both valves convex; attached to other bodies at the upper part of the ventral valve; beak slightly produced; area short; deltidium ill-defined. A thin raised ridge passes round the front and sides of the dorsal valve, until it reaches the dental sockets. It is without a central septum, nearly always present in other species, the only ornamentation within the ridge being numerous punctations.

Emended diagnosis. Minute *Enallothecidea*, markedly ventribiconvex, pyriform in outline with a small tuberosc apical attachment scar resulting in a poorly defined ventral inter-area. Pseudodeltidium small, indistinct, and not completely closing the delthyrium anteriorly. Subperipheral rim confined to the lateral and posterolateral regions of the brachial valve, dorsal median septum lacking. Hemispondylium lacking. Shell endopunctate.

Distribution. The locality from which Moore collected his material is given as the Coral Rag, Lyneham, Wiltshire, although the precise horizon from which the specimens were obtained remains unknown. *E. pygmaea* is now known to occur at various horizons at several other localities, e.g. from the Pea Grit (Upper Aalenian, *murchisonae* Zone) at Crickley Hill, grid ref. SO 930 162 near Cheltenham, and from the Oolite Marl (Upper Aalenian, *murchisonae* Zone) at Cleeve Cloud, grid ref. SO 948 261 near Cheltenham, and Westington Hill Quarry, grid ref. SP 142 368 near Chipping Campden, Gloucestershire; also from the Coral Rag (Middle Oxfordian, *tenuiserratum* Zone) at Shellingford Cross Roads Quarry, grid ref. SU 325 940 near Faringdon, and Cumnor Hill Road Cutting (temporary exposure), grid ref. SU 336 954 near Oxford.

Description. *External characters*. A very small species even by thecideid standards, reaching a maximum length of only about 0.7 mm, width about 0.5 mm, and thickness about 0.45 mm. The growth pattern of the pedicle valve gives it a distinctive ladle-shaped lateral profile (Pl. 69, fig. 1). The incomplete delthyrial cover means that part of the dorsal surface of the cardinal process remains visible (Pl. 69, fig. 2; text. fig. 1B) when the valves are closed. The pedicle valve began to grow away from the substrate at a very early age so that the area of attachment is always small and apical in position (Pl. 69, figs. 2, 4, 7, 8).

Internal characters. *Pedicle valve* (Pl. 69, fig. 4). Apart from the cyrtomatodont hinge teeth and strongly developed endopunctation the interior of the pedicle valve is otherwise featureless. *Brachial valve* (Pl. 69, figs. 5, 6). As previously noted there is no median septum. The valve is characterized only by the typical thecideid cardinal process, dental sockets, and incompletely developed subperipheral rim. There are no brachial lobes and no suggestion of a bridge but, as in the pedicle valve, strongly developed endopunctation is present.



TEXT-FIG. 1. Detail of the morphology of the posterior portion of the shell of *Enallothecidea pygmaea*. A, pedicle valve, brachial view. B, complete shell, brachial view. C, pedicle valve, lateral view.

Microstructure. The shell is differentiated into a thin granular primary layer and a fibrous secondary layer (Pl. 69, fig. 9) which most closely resembles the disturbed secondary shell mosaic of moorellinids (Baker 1970, pl. 20, fig. 1).

DISCUSSION

The tuberoso apical attachment scar and growth habit which results in a typical pyriform shape make the exterior of *E. pygmaea* distinctive in its morphology. The species is comparatively rare and apparently local in occurrence. It is probably more common than it appears but, owing to its extremely small size and somewhat unusual appearance, is either usually overlooked or not recognized as a brachiopod. In all cases *E. pygmaea* was found to be associated with coralliferous deposits. The specimens in my collection were all obtained from organo-detrital debris, but Morris (1980) has recovered specimens from unconsolidated residues obtained from small cavities in small reef mounds adjacent to the Crickley Coral Bed at Crickley Hill, suggesting that *E. pygmaea* may have occupied a cryptic niche. Owing to their minute size the possibility that the specimens are juveniles must be considered. Moore (1861) noted the association of *E. pygmaea* with *Rioulina ornata* (Moore) and *R. triangularis* (D'Orbigny) but was unable to relate it to the ontogeny of either species. The same maximum size is attained at all the localities in which *E. pygmaea* has been encountered. Equivalent-sized juveniles of associated small thecideidine species such as *Moorellina granulosa* (Moore) are clearly distinct. There is a remote possibility that the specimens represent juveniles of a hitherto undiscovered adult, but from their apparently localized occurrence and the absence of broken fragments of larger shells this seems unlikely and, in any case, has no bearing on their systematic position.

Because of its minute size Davidson (1876, p. 105) had difficulty in defining the characters of the species and was not completely convinced that it was thecideidine. Pajaud (1970, p. 345) without further discussion dismissed the species as 'non Thécidée'. Fortunately, the ability to study specimens by scanning electron microscopy has enabled the problem to be solved and confirms that the species may be properly assigned to the Thecideidina. The attachment scar, the cardinal process, the cyrtomatodont hinge teeth placed well forwards (Jaanusson 1971), and the secondary shell fabric are characteristically thecideidine. However, the incomplete subperipheral rim, the lack of a hemispondylium, and, more significantly, the lack of a median septum does pose a problem with regard to the systematic position of *E. pygmaea*. Although in many respects it appears to be related to the simple monoseptal forms *E. pygmaea* is the only thecideidine species so far recorded in which a median septum is not developed. As the form of the median septum is currently critical to the thecideidine classification (Pajaud 1970) its absence in *Enallothecidea* precludes the possibility of assigning the new genus to an existing subfamily. Throughout the history of the Suborder, representatives of the Thecideidina show the often profound effects of neotenus suppression of characters (Williams 1973). Non-development of a median septum through neotenus suppression may be of phylogenetic significance and the organization of *E. pygmaea* may reflect a condition recognizable in the ancestral stock. Rudwick (1968) and Baker (1970) have suggested a strophomenide ancestry for the Thecideidina. Williams (1973) has argued strongly in favour of a spiriferide ancestor and has shown that a number of characters previously regarded as strophomenide are by no means exclusive to the group. He considers that, as far as the thecideidines are concerned, the cyrtomatodont teeth, the cardinalia, and the shell structure preclude a strophomenide ancestry. Williams does, however, concede the probable importance of cementation, supplemented by the presence of a supra-apical foramen and an entire pseudodeltidium in determining strophomenide affinity. The beak ridges of *E. pygmaea* appear to come together posterior to the attachment scar; also the structure appears to lie ventral to the early growth lines (Pl. 69, figs. 2, 7) so that attachment initially may have been effected by a supra-apical structure. Unfortunately, the minute size of the specimens makes interpretation difficult even with the aid of stereoscan facilities. Care must be exercised as Brunton and MacKinnon (1972) have demonstrated that the supposed supra-apical foramina (Cowen and Rudwick 1966) of *Cadomella*, *Koninckella*, and *Amphiclina* are in fact apical. There is, however, some evidence (Baker

1970, p. 90) that the early juvenile *Moorellina* possessed a pedicle sheath in a supra-apical position. Because of the distorting effect of the attachment scar on the beak area generally, the possibility of a very early apical foramen in *E. pygmaea* should not be discounted.

I previously concluded (Baker 1970) that middle Jurassic thecideidines such as *Moorellina* were probably closely related to *Thecospira*. Work on *Thecospira* (Dagis 1973; MacKinnon 1974, p. 242) subsequently confirmed a remarkable similarity in the shell ultrastructure of the two genera. Dagis argued for a thecospirid ancestor for the thecideidines. It is here considered that this may be a little premature but, in view of what is now known about their shell microstructure, it does seem almost certain that thecospirids are not far diverged from the ancestral thecideidine stock. Both Williams (1973) and MacKinnon (1974) regarding *Thecospira* as a spiriferide anyway, argue for a punctate spiriferide ancestor for the thecideidines. As already noted the pseudodeltidium of *E. pygmaea* is not entire in the strophomenide sense and if one considers the position of the hinge axis (text-fig. 1A), the opening bounded by the tooth ridges should, technically, be regarded as a comparatively large delthyrium closed only in the apical region. Delthyrial covers are already well known among spiriferide brachiopods (Cowen 1968, 1969) and the imbricated delthyrial cover in the small, recently described, *Metriolepis naber* Cooper and Grant (1976) makes the spiriferides an even more inviting proposition as far as the recognition of an ancestral group is concerned. In *E. pygmaea*, if one disregards the distorting effect of the attachment scar, the growth lines of the pedicle umbonal region (Pl. 69, figs. 7, 8; text-fig. 1C) indicate a growth pattern very reminiscent of the ventral umbo of juvenile spiriferides before the inter-area can be clearly defined (Pl. 69, fig. 10). The morphology of the umbonal region of pedicle valve is also superficially similar to that of juvenile terebratulides. However, in view of the profound effects of neotenuous suppression of characters it is only to be expected that the ventral cardinalia of juvenile thecideidines will bear some resemblance to the early juveniles of other cyrtomatodont forms. The resemblance is probably most striking when *E. pygmaea* is compared with terebratulidine forms *aff. Plectothyris* (Pl. 69, fig. 11) where a rudimentary pedicle collar is developed very early. It will be noted in the latter, however, that the incipient deltidial plates and the much flatter dorsal surface of the ventral area underline differences in organization probably no less significant than the absence of an attachment scar. Terebratellidine juveniles, e.g. *Zeilleria* (Pl. 69, fig. 12), may be quickly discounted as the apex of the delthyrium is beginning to show signs of resorption even at this early stage of growth. Therefore, the new information regarding the form of the cardinalia in *E. pygmaea* greatly strengthens the argument advanced by Williams (1973) and with which I now concur, notwithstanding the possibility of this species having a supra-apical foramen, that the thecideidines were probably derived from punctate spiriferides. In view of its atypical morphology and potential phylogenetic importance it is here considered that *Enallothecidea* warrants new subfamilial assignment.

Acknowledgement. I thank Mr. P. G. Cooper, Derby Lonsdale College, for help with the preparation of the plate.

REFERENCES

- BAKER, P. G. 1970. The growth and shell microstructure of the thecideacean brachiopod *Moorellina granulosa* (Moore) from the Middle Jurassic of England. *Palaeontology*, **13**, 76-99.
- and COPP, C. J. T. 1975. Terebratulide affinity of the brachiopod *Spirifera minima* Moore. *Ibid.* **18**, 879-882.
- BRUNTON, C. H. C. and MACKINNON, D. I. 1972. The systematic position of the Jurassic brachiopod *Cadomella*. *Ibid.* **15**, 405-411.
- COOPER, G. A. and GRANT, R. E. 1976. Permian brachiopods of West Texas, V. *Smithson. Contr. Paleobiol.* **24**, 2609-3159.
- COWEN, R. 1968. A new type of delthyrial cover in the Devonian brachiopod *Mucrospirifer*. *Palaeontology*, **11**, 317-327.
- 1969. Stegidial structures in spiriferide brachiopods. *J. Paleont.* **43**, 538-539.
- and RUDWICK, M. J. S. 1966. A spiral brachidium in the Jurassic chonetoid brachiopod *Cadomella*. *Geol. Mag.* **103**, 403-406.

- DAGIAS, A. S. 1973. Ultrastructure of thecospirid shells and their position in brachiopod systematics. *Paleont. Zh.* **6** (3), 359-369.
- DAVIDSON, T. 1876. A monograph of the British fossil Brachiopoda. Vol. 4. Tertiary, Cretaceous, Jurassic, Permian, and Carboniferous Supplements. *Palaeontogr. Soc. [Monogr.]*, 105, Suppl. Pl. XIII.
- JAANUSSON, V. 1971. Evolution of the brachiopod hinge. *Smithson. Contr. Paleobiol.* **3**, 33-46.
- MACKINNON, D. I. 1974. The shell structure of spiriferide Brachiopoda. *Bull. Br. Mus. nat. Hist. (Geol.)* **24** (3), 189-261.
- MOORE, C. 1861. On new Brachiopoda and on the development of the loop in *Terebratella*. *Geologist*, **4**, 96-99, 190-194, pl. 2.
- MORRIS, P. H. 1980. A microfaunal and sedimentological analysis of some Lower Inferior Oolite sections of the Cotswolds. Ph.D. thesis (unpubl.), University of Wales, 316 pp.
- PAJAUD, D. 1970. Monographie des Thécidées (Brachiopodes). *Mém. Soc. géol. Fr.* **112**, 1-349.
- RUDWICK, M. J. S. 1968. The feeding mechanisms and affinities of the Triassic brachiopods *Thecospira* Zugmayer and *Bactrynum* Emmrich. *Palaeontology*, **11**, 329-360.
- WILLIAMS, A. 1973. The secretion and structural evolution of the shell of thecideidine brachiopods. *Phil. Trans. R. Soc. Lond. B*, **264**, 439-478.

P. G. BAKER

Department of Geology
Derby Lonsdale College of Higher Education
Kedleston Road
Derby DE3 1GB

Typescript received 8 April 1982

Revised typescript received 15 June 1982