

MANTLE-BODY ARRANGEMENT ALONG THE HINGE OF EARLY PROTREMATOUS BRACHIOPODS: EVIDENCE FROM *CROZONORTHIS*

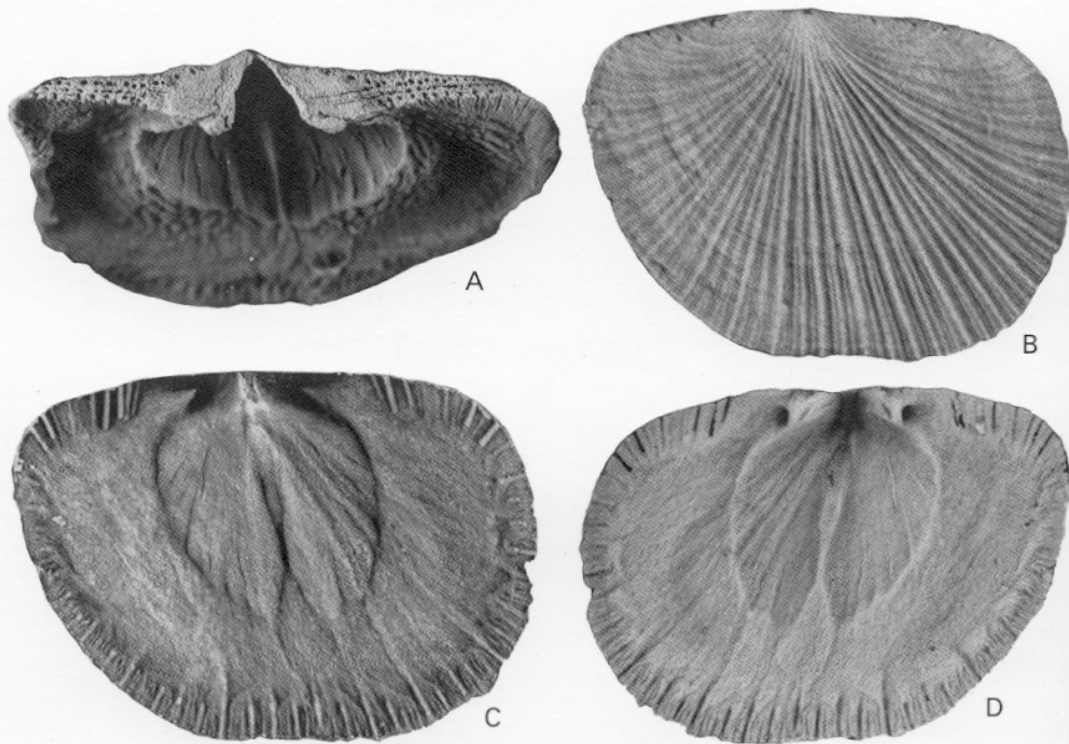
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ABSTRACT. The earlier discovery of mantle canals lining the interareas of protrematous brachiopods and the implication that these areas were lined with mantle and not simply outer epithelium is supported by evidence from *Crozonorthis*. In this genus the ventral interareas show a clear external differentiation, reflecting a lining of mantle laterally and of outer epithelium medianly. Moreover, this morphology provides clear evidence, contrary to popular opinion, that setae could develop along the growing margin of a protrematous interarea. A well-defined junction, between parts adjacent to the delthyrium which are smooth and lateral parts with perforations that housed successive generations of setae during life, marks the position where, on the interior, the inner epithelium separated from the outer epithelium to form the body wall.

THE discovery of mantle canals preserved on the interareas of some protrematous brachiopods (Wright 1994) implies that in life these areas were lined with mantle, and not simply outer epithelium as was previously thought (Williams and Rowell 1965, fig. 8). The mantle edge of brachiopods typically houses sensory setae, although this is not invariable. They are absent, for example, from the adults of modern *Neocrania* and *Lacazella*; and would appear to be absent from fossil *Acanthambonia*, where the sensory function was seemingly taken over by the spines (Wright and Nölvak 1997). The fossil evidence for differing setal densities, non-retractile setae relating to strongly differentiated and deep follicular embayments, setal incorporation into the shell via aditicules and a setal function for the perforations along the posterior margin of *Eochonetes* was considered recently (Wright 1996). The canals in *Eochonetes* as noted by Reed (1917), and in *Chonetoides* and *Sentolunia* as noted by Havlíček (1967) as opening to the exterior along the posterior edge of the interareas were interpreted as being incorporated into this position sequentially as each contained seta was developed at the cardinal angle (Wright 1996, p. 301).

Dr R. B. Neuman subsequently commented (pers. comm. to ADW) that perforations were present also in *Heterorthina macfarlani* Neuman, 1967, along the intersection of the interarea and the shell surface on the dorsal valves, a feature which had been drawn to his attention after seeing the illustrations of *Heterorthina* by Melou (1975). The perforations, termed cardinal canals by Melou (1975, p. 195), are like those of *Eochonetes* in that they pass through to the valve interior, but are much more densely distributed and have an orientation which grades from being perpendicular to the margin around the cardinal angles, through being perpendicular to the hinge and then, as their size reduces medianly, convergent towards the umbo. Melou (1975, p. 176) noted that these canals were present on several genera of Heterorthidae and that Williams (1974, p. 108) had observed that members of this family have reflexed costellae which open along the posterior edges of the shells with corresponding follicular embayments, indicating the presence of backwardly projecting setae, although Williams expressed doubt as to whether functional setae persisted much within the cardinal angles.

Wright (1996, p. 301) commented that there 'seems to be no case of setae developing along the growing margin of the interareas of protrematous brachiopods'. This was taken as indicating that although the interareas were lined with mantle, this mantle was modified so that it did not possess setal follicles, an arrangement which would not be exceptional in view of the lack of setae in some



TEXT-FIG. 1. *Crozonorthis musculosa* Melou, 1976. A, LPB 3784a; Schistes Botella, La Almeda, Jaen, Spain; posterior view of latex cast of ventral valve. B-D, LPB3780a; Schistes de Postolonnec, Postolonnec beach, Crozon, France; Ordovician (Llandeilo); latex cast of external mould, internal mould, and latex cast of internal mould of ventral valve. Repository: Laboratoire de Paléontologie, Brest (LPB). All $\times 6$.

extant stocks. This may be the general situation, but, nevertheless, successive rows of perforation are in fact well displayed on the ventral interareas of the heterorthid species described: *Crozonorthis musculosa* by Melou (1976). (Although this species has been ascribed to *Eorhipidomel* Hints, there are morphological differences and both genera will be recognized (D. A. T. Harpers pers. comm.) in the forthcoming revision of the brachiopod *Treatise*). The function of the perforations could only have been to accommodate setae, but it is their distribution (Melou 1976, p. 702 and pl. 8, partly re-figured here as Text-fig. 1) which provides significant additional evidence regarding mantle-body distribution in the hinge region.

As indicated by Melou (1976, p. 702), the interarea of the ventral valve of *C. musculosa* (Text-fig. 1A) is unusual in being divisible into two parts. The parts adjacent to the delthyrium are slightly raised and show striations parallel to the hinge; whilst laterally the lower area additionally shows at least three rows of perforations parallel to the hinge. The sporadic earliest canals together with the three rows of non-functional canals are followed by a row of functional canals seen as indentations or grooves on either side of the posterior margin of the hinge (Melou 1976, p. 704).

With the knowledge that the lateral parts of the interareas in protrematous brachiopods are underlain by mantle, the interpretation of the unusual area of *Crozonorthis musculosa* becomes clear. The outer parts would have been lined by normal mantle with functional setae, with successive rows becoming incorporated in the area with growth, whilst the median parts were lined simply by the shell-secreting outer epithelium within the body cavity of the animal. The position of the separation of the inner from the outer epithelium to form the body wall is clearly indicated by the

change in texture of the surface of the interarea lateral to the position of the teeth. Whilst the canals along the posterior edge of the area are related to the openings of the recurved costellae along this edge (Text-fig. 1B), the subsequent rows of canals are not so constrained, and simply reflect the distribution of setal follicles more-or-less perpendicular to the posterior growing edge (Text-fig. 1C-D). As commented by Melou (1976, p. 704), canals occur also on the dorsal valve; but it is on the ventral valve, with its relatively long interarea, where the distribution of the setal apertures is so well displayed.

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