VARIATION IN THE CARDINALIA OF THE BRACHIOPOD *PTYCHOPLEURELLA BOUCHARDI* (DAVIDSON) FROM THE WENLOCK LIMESTONE OF WENLOCK EDGE, SHROPSHIRE

by M. G. BASSETT

ABSTRACT. In specimens of the orthacean brachiopod *Ptychopleurella bouchardi* (Davidson) from the Wenlock Limestone of Wenlock Edge, Shropshire, the cardinalia display a wide range of variation, particularly in the development of the cardinal process. The variation can be explained partly by ontogeny but in some extreme cases it is suggested that it reflects environmental control due to turbulent water conditions in an area of active reef growth. These conditions led mainly to the progressive inflation of the cardinal process to produce an optimum attachment surface for the diductor muscle bases, but in two specimens no cardinal process is developed. In these the muscle bases appear to have covered the notothyrial platform from the earliest growth stage, thus preventing the secretion of a cardinal process from a central strip of epithelium. The effect of this was to employ a maximum attachment area throughout ontogeny as an alternative to the production of a bulbous cardinal process.

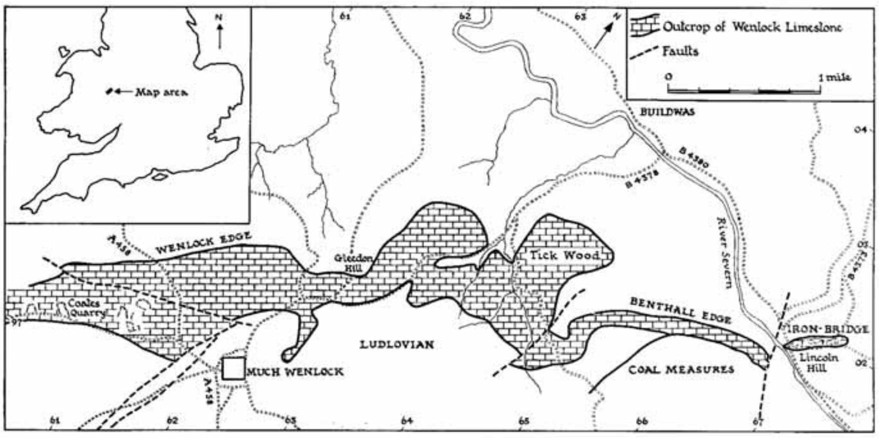
THE orthacean brachiopod species *Ptychopleurella bouchardi* (Davidson 1847) occurs fairly commonly throughout the Wenlock Limestone (Silurian) of the type area in the vicinity of Much Wenlock, Shropshire. Examination of the interiors of a number of brachial valves of *P. bouchardi* from this area reveals that the cardinalia display a wide range of morphological variation hitherto unrecorded in orthoid genera. This variation is seen mainly in the development of the cardinal process and to a lesser extent in the modification of the brachiophores and sockets. Since the valves studied are from collections made from single bedding planes, are associated with a single type of pedicle valve, and have a similar musculature and external morphology, the variation is regarded as being intraspecific in nature. Undoubtedly it is due partly to the ontogenetic development of the shell, but is here interpreted partially as a response to environmental control.

The observations and interpretation of the variation are based largely on a collection of 12 brachial valves from an area of about 5 sq. m. of a bedding plane in the Wenlock Limestone of Coates Quarry, Wenlock Edge, on the north side of the road approximately 1 mile south-west of Much Wenlock (Grid Ref. SO/6045.9935; text-fig. 1). Comparative evidence is provided by a collection of about 20 shells from a single bedding plane in the Wenlock Limestone of the old quarry on the west side of Lincoln Hill, Ironbridge (Grid Ref. SJ/6695.0381). Text-fig. 2 illustrates 7 representative specimens from Coates Quarry. Specimens A–E are members of a progressive growth series, indicated on the graph by a progressive increase in valve length coupled with an increase in the number of growth lamellae on the exterior of the valve. The approach to maturity of the larger specimens is further suggested by the close spacing of the growth lamellae at the anterior margin of the valve. Specimens F and G are also mature shells but the plot of the growth lamellae suggests that they are not a continuation of the growth series A–E.

[Palaeontology, Vol. 13, Part 2, 1970, pp. 297–302, pl. 53.]

The nature of the variation

1. *The cardinal process.* Figs. A–E in text-fig. 2 illustrate the progressive growth of the cardinal process in 5 of the specimens studied from Coates Quarry. At the young growth stage represented by A the floor of the notothyrial chamber is almost flat or slightly ridged and no definite cardinal process is developed. This probably indicates that at this stage the diductor muscle bases were implanted discretely on to the floor

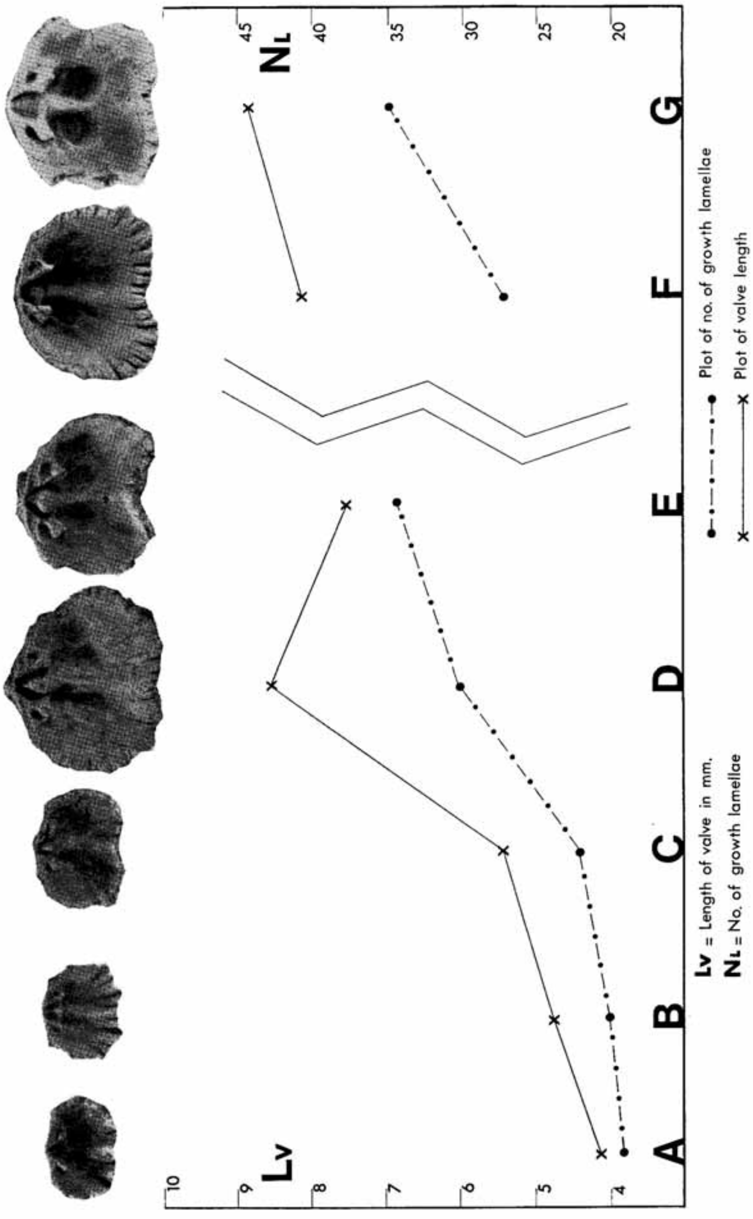


TEXT-FIG. 1. Map of the outcrop of the Wenlock Limestone along the north-east of Wenlock Edge and its continuation to Benthall Edge, showing the position of Coates Quarry and Lincoln Hill.

of the notothyrial platform. With increased shell growth, seen in B, a low, longitudinal, median ridge, representing an embryonic cardinal process is developed, presumably by the secretion of secondary calcite from the strip of outer epithelium between the muscle bases, following the pattern common to most orthoid brachiopods (Williams and Rowell, *in* Moore 1965, p. H118). In specimen C further anterior and ventral growth of the median ridge has led to the development of a clearly defined, slightly lobed cardinal process. This growth was probably accompanied by a medial migration of the diductor muscle bases from the floor of the notothyrial platform on to the lateral surfaces of the cardinal process. The further pronounced anterior and ventral inflation of the cardinal process seen in D and E must clearly reflect a response to the need for the muscle bases to be attached over a wider surface area.

In specimens collected from Lincoln Hill the stages A–C can be traced in valves at closely comparable growth stages to those described above. However, the maximum growth in the cardinal process in shells from Lincoln Hill is only slightly beyond that of stage C and even in larger specimens there is no extreme inflation comparable to that in specimens D and E from Coates Quarry. The extreme growth of the cardinal process in D and E from Coates Quarry would therefore appear to be controlled by factors other than ontogeny.

Specimens F and G in text-fig. 2 are two aberrant shells from Coates Quarry, in which



TEXT-FIG. 2. Diagram to illustrate the growth and variation of the cardinalia in 7 specimens of *P. bouchardi* from a single bedding plane in the Wenlock Limestone of Coates Quarry. Specimens A–E are part of a progressive growth series. Specimens F and G are two aberrant shells in which no cardinal process is developed.

the cardinal process is not developed. There is no evidence in these shells that the cardinal process has merely been broken off and although the two specimens are fairly large the plot of the number of growth lines does not suggest that they are gerontic members of the growth series A–E in which a condition has been reached where resorption has led to the disappearance of the cardinal process. Further evidence against this latter suggestion is presented by a study of the pattern of growth lines within the cardinalia. In the young shells A and B, for example, the fine growth lines on the floor of the notothyrial chamber are straight or very gently curved and are sub-parallel to the hinge line (see Pl. 53, fig. 9). After this stage the further pronounced ventral and anterior growth of the cardinal process is reflected in the development of a distinctive chevron-shaped pattern of growth lines across the notothyrial area, especially well seen in specimen D (see Pl. 53, fig. 10). In contrast, the growth lines seen in F and G (see Pl. 53, fig. 11) are again sub-parallel to the hinge line, similar to the pattern seen in young shells. This suggests that in these two aberrant specimens the cardinal process was never developed and implies that in their early growth stages the diductor muscle bases were attached over the whole of the central area of the notothyrial chamber so that no medial strip of epithelium was exposed to secrete secondary calcite in the form of a cardinal process. No shells from Lincoln Hill have been found in this aberrant condition.

2. *The brachiophores and sockets.* All the specimens of *P. bouchardi* studied from numerous localities in the Wenlock Limestone of Wenlock Edge exhibit modifications of the brachiophores and sockets with growth by the addition of secondary shell material.

EXPLANATION OF PLATE 53

Ptychopleurella bouchardi (Davidson). All specimens are from a single bedding plane in the Wenlock Limestone of Coates Quarry, north side of road, 1 mile south-west of Much Wenlock, Shropshire (Grid. Ref. SO/6045.9935). Figs. 8, 9, 10, 11 are ×8; all other figs are ×3.

Fig. 1. NMW.69.96.G1. Interior of brachial valve. Specimen A of text-fig. 2. Note the almost flat notothyrial platform.

Fig. 2. NMW.69.96.G9. Interior of brachial valve. Specimen B of text-fig. 2. Note the low ridge forming the embryonic cardinal process.

Fig. 3. NMW.69.96.G2. Interior of brachial valve. Specimen C of text-fig. 2. Note the slightly lobed cardinal process.

Figs. 4*a–c*. NMW.69.96.G3. Interior, exterior, and lateral views of brachial valve. Specimen D of text-fig. 2. Note the deep sockets, expanded cardinal process, and secondary calcite covering the floor of the valve.

Figs. 5*a*, *b*. NMW.69.96.G4. Interior and exterior of brachial valve. Specimen E of text-fig. 2. Note the bulbous cardinal process, deep sockets, and expanded brachiophores.

Figs. 6*a*, *b*. NMW.69.96.G5. Interior and exterior of brachial valve. Specimen F of text-fig. 2. Note the absence of the cardinal process.

Figs. 7*a*, *b*. NMW.69.96.G6. Interior and exterior of brachial valve. Specimen G of text-fig. 2. Note the absence of the cardinal process.

Fig. 8. Enlargement of the cardinalia of fig. 1.

Fig. 9. Enlargement of the cardinalia of fig. 2. Note the embryonic cardinal process and the fine growth lines across the notothyrial platform.

Fig. 10. Enlargement of the cardinalia of fig. 4*a*. Note the expanded cardinal process and the chevron-shaped growth lines across the notothyrial platform.

Fig. 11. Enlargement of the cardinalia of fig. 7*a*. Note the absence of the cardinal process and the fine growth lines across the notothyrial platform. Compare the growth lines with those in figs. 9 and 10.

Figs. 12*a–c*. NMW.69.96.G7. Interior, exterior, and lateral views of pedicle valve.

Figs. 13*a*, *b*. NMW.69.96.G8. Interior and exterior of pedicle valve.

This results in the building of 'walls' around the rims of the sockets leading to their rounding and apparent deepening, the development of socket pads, and the thickening of the bases of the brachiophores. In the specimens from Coates Quarry, including the aberrant shells F and G, these modifications of the cardinalia by the addition of secondary calcite are generally much more pronounced than in specimens from other localities.

Interpretation

The absence of a cardinal process in two shells, and the extreme modification of the brachiophores and sockets in other specimens from Coates Quarry cannot be regarded solely as a growth feature since these conditions are not seen consistently in shells of comparable size from other localities. Instead it is suggested that the variation observed in these 'abnormal' shells is related partially to the environment in which they lived.

The Wenlock Limestone of Wenlock Edge, and its continuation to Benthall Edge and Lincoln Hill, forms part of a reef complex aligned in a north-east to south-west direction. Scoffin (1965) suggested that a large bioherm which occupies the bulk of the thickness of the Wenlock Limestone around Hilltop (Grid. Ref. SO/5700.9630), about 3½ miles south-west of Much Wenlock, probably acted as a 'barrier' reef. No specimens of *P. bouchardi* have been found by the writer to the south-west of Hilltop in the off-reef area. Coates Quarry lies in the back-reef area about 2½ miles to the north-east of the 'barrier' reef and the specimens described from there were obtained from a thin shale parting on a bedding plane lying immediately adjacent to a large symmetrical bioherm. This and other bioherms in the vicinity probably formed part of an extensive patch reef development in the lee of the 'barrier' reef (Scoffin 1965, p. 190). The bioherms are composed of large colonial corals, stromatoporoids, algae, and crinoids, with interdigitations of skeletal debris and lime mud, while the surrounding bedded sediments consist of biomicrites and biosparites with thin grey shale partings. These deposits together suggest that conditions within and around the bioherms varied from periods of quiet water deposition to periods of moderate agitation, probably by wave action. (The interpretation of the depositional conditions outlined here is based on the classification of Plumley *et al.* 1962; the conditions within the reef area of Wenlock Edge were probably closely analogous with those described by Plumley *et al.* (op. cit., pp. 93–5) in their hypothetical example.) Relatively few other fossils are found immediately adjacent to the bioherms, a factor which supports this interpretation.

Any brachiopods which were to survive the periodical agitation of water in this environment would need relatively thick shells, powerful muscles with large attachment areas, and a strong articulatory mechanism. The specimens of *P. bouchardi* described from Coates Quarry possess all of these features. In some specimens the shell is further thickened by the addition of secondary calcite over the floor of the valve. The large dorsal adductor scars may be clearly seen in the specimens illustrated in text-fig. 2 and Plate 53; it appears that the progressive inflation of the cardinal process in specimens A–E reflects the rapid development of an optimum surface area for the attachment of the diductor bases, while in the aberrant shells F and G the muscle bases covered the whole of the central area of the notothyrial chamber to gain maximum attachment from the earliest growth stage. Thus in 2 specimens a broad, firm attachment area was employed throughout ontogeny as an alternative to the production of a bulbous cardinal process. The deepening of the sockets would produce a strong articulatory structure while the addition of secondary calcite to the whole of the cardinalia possibly acted as a stabilizer to maintain the shell in its posterior-downward life position. Bowen (1966, p. 1021) suggested a similar function for deposits of secondary calcite in the notothyrial area of specimens of *Atrypa reticularis* (Linnaeus). The few other species of brachiopods associated with *P. bouchardi* in Coates Quarry also exhibit thickening of the shell by the addition of secondary calcite. A few specimens collected by the writer from similar reef-bearing beds along Benthall Edge also possess many of the features described above, including a large cardinal process, but no further specimens have been observed in which the cardinal process is absent.

Lincoln Hill lies some 7 miles to the north-east of the Wenlock Edge 'barrier' reef in the back-reef lagoonal area. Here the abundance of many species of articulated brachiopods and solitary corals in fine biosparite limestones, and the rarity of colonial reef builders, suggests relatively quiet water conditions compared to areas further to the south-west. Under these conditions it appears that the cardinalia of *P. bouchardi* display only the normal features of growth. (Bioherms were probably once present in stratigraphically higher beds at Lincoln Hill, e.g. see Murchison 1839, p. 211, but they have long since been removed by quarrying and there is no evidence that active reef growth took place within the beds exposed today.)

Although the above discussion is based on the study of only a small number of specimens, it nevertheless serves to illustrate that the cardinalia of orthoid brachiopods may vary widely within a single species in different environments. The use of such features as stable characters for purposes of classification should therefore be treated with caution.

Acknowledgements. This work was carried out in the Department of Geology, University College, Swansea, as part of a larger study of British Wenlockian brachiopod faunas. I wish to thank Dr. V. G. Walmsley for his help and guidance, Professor F. H. T. Rhodes for providing research facilities, and Dr. T. P. Scoffin for discussing environmental conditions in the Wenlock Limestone. Financial support from the Sir Richard Stapley Educational Trust and the Natural Environment Research Council is gratefully acknowledged. All the specimens are housed in the Department of Geology, National Museum of Wales, Cardiff.

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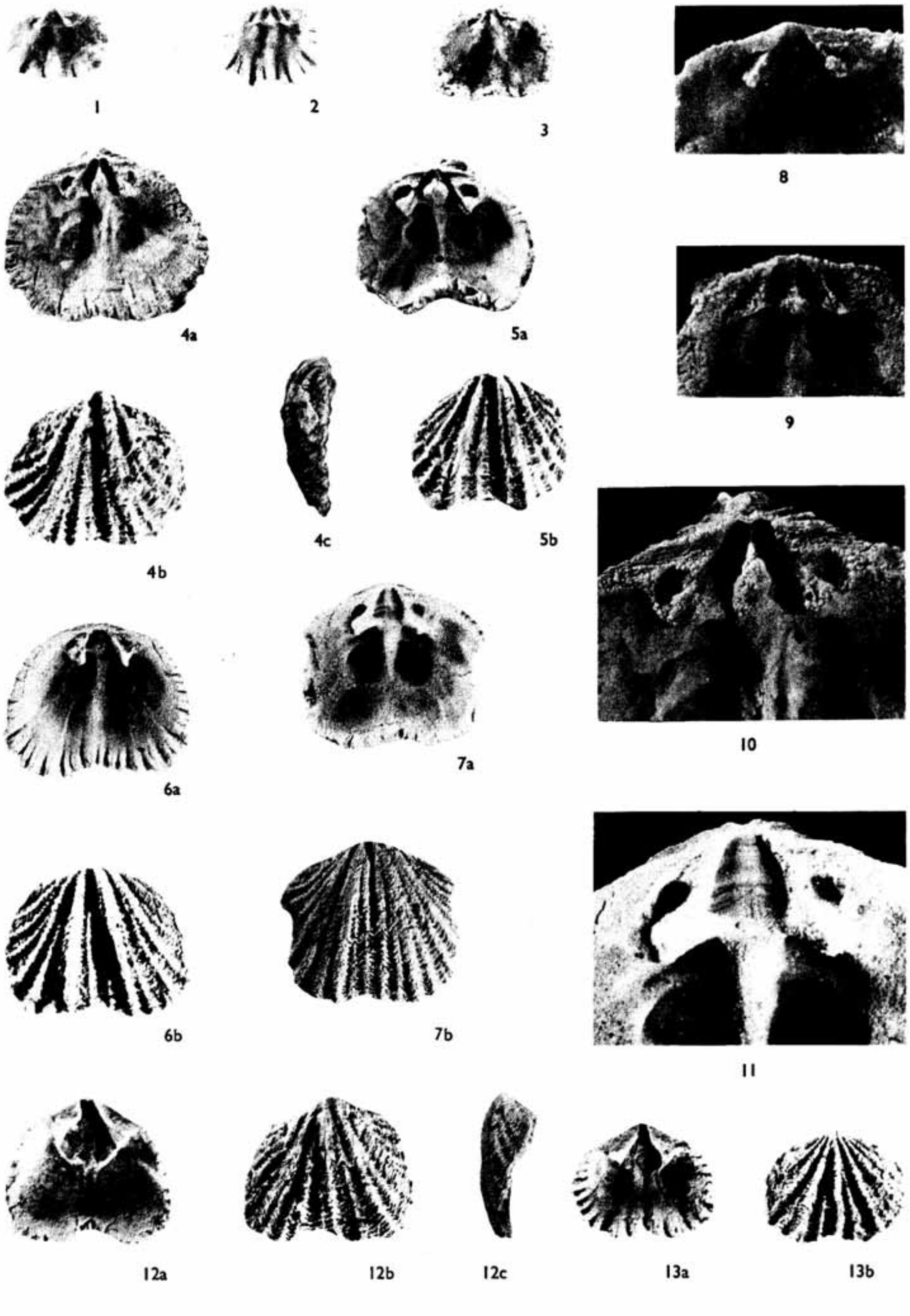
Typescript received 3 June 1969



BASSETT, Cardinalia of *Ptychopleurella bouchardi*