COMMENTS ON 'THE LOOP-DEVELOPMENT AND THE CLASSIFICATION OF TEREBRATELLACEAN BRACHIOPODS'

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DR. Joyce Richardson's (1975) study of patterns of loop-development in terebratellacean brachiopods is most welcome. Her review deals essentially with Caenozoic and Recent forms, chiefly from Australasia, but it has considerable implications for the Mesozoic faunas of Europe. In particular her new nomenclature for the phases of loop-development refers essentially to morphology and structure, and not to comparisons with adult loops as previously. Also very different significance and importance is assigned to certain elements of the loops than hitherto, and she evaluates this in detail. She indicates the occurrence of lacunae in some immature terebratellid loops, though they are still, in my experience, much more characteristic of laqueinid development.

Richardson rightly points out the close similarity in loop-development of the three families reviewed (Dallinidae, Laqueidae, and Terebratellidae) as compared with the very different loop-development seen in other families of the Terebratellacea, e.g. Kraussinidae, whatever the relationship of these other families to each other. Her text-fig. 3 indicates that some genera of the Laqueidae may even pass through the same series of phases as Terebratellidae (though the duration and importance of particular phases differs in the two). Even without adequately large studies on variation in loop-development within a single species, it does seem that the different forms of loop-development outlined are closer than previously regarded, and perhaps of less value for detailed taxonomy than previously supposed.

Of Mesozoic forms affected by this classification, Zeilleriidae as now constituted are in loop-development a composite group. Those studied whose loops are known to develop in connection with a septal pillar, e.g. the Jurassic *Zeilleria leckenbyi* (Davidson) (Baker 1972) appear to be probably early Laqueidae as now defined. Those where development, with ring and descending branches not dissimilar, takes place *without* a pillar, free of the dorsal valve floor, e.g. the Triassic *Z. bukowski* (Bittner) and a similar Liassic species (Dagis 1968) have similarity to this 'non-septal pillar' type of development, found in certain Palaeozoic genera (cf. the Carboniferous *Cryptacanthia*: Cooper 1957). Which of these two groups in the Mesozoic retains the name Zeilleriidae depends on the evaluation of the loop-development of the Liassic type species *Z. cornuta* (J. de C. Sowerby), if this character continues to be decisive in classification. The peculiar loop-development of the Jurassic *Hamptonina* is relevant to this. The study of Moore (1860), which antedated the pioneer studies on Recent genera (Friele 1875, 1877), showed a developmental series in *Hamptonina* involving different growth stages both free of the valve floor, and attached to a septal

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pillar. My restudy (Elliott 1950) was carried out both on Moore's original specimens and on fresh material from his original locality. It showed that *Hamptonina* had a laqueinid development ('dallinid' as then termed), with normal early axial and annular phases, but with a minority of abnormal individuals. From their shell-characters these were members of the same species, *H. buckmani* (Moore), but with delayed loop-development relative to shell size, and without a septal pillar, i.e. they showed the 'Palaeozoic' type of loop-development. I ascribed this to possible retarded development of the lophophore relative to size increase, and to appearance of the calcareous descending branches first, instead of the early septal pillar. Whatever the reason, the presence in one species of two such different modes of development, even with one as an abnormality, is significant and reinforces Richardson's assimilation of the far closer patterns within the 'septal pillar' type of development. It is probable that the rapid achievement of a plectolophe, so providing the maximum length of ciliated cirrated lophophore margin which can be accommodated, has been essential in development, both individual and phyletic. This may be due, as suggested (Elliott 1948, 1953) to intraspecific competition, since the replacement through geological time of brachiopods by bivalve mollusca is a fact, irrespective of brachiopod intra-regressive evolution. The elaborate and conspicuous loops and loop-developments are a consequence of the different calcification in the genera concerned superimposed on lophophore development, and the different patterns are not in themselves directly significant. The case of *Terebratulina* (Jurassic–Recent), as mentioned by Baker (1972, p. 468) is a pointer to this. In this the short posterior annular loop with heavy anterior spiculation of the lophophore seems as functional as any long loop, and it is a most successful brachiopod, so far as this term can be applied within this declining group after the Palaeozoic.

The tendency in biological classification has been for ever-increasing exploration of detail to be reflected in progressively more elaborate taxonomy, followed by a secondary simplification reflecting detailed understanding of underlying principles and their relative importance. Dr. Richardson's paper indicates perhaps a turning-point for our knowledge of long-looped brachiopods.

REFERENCES

BAKER, P. G. 1972. The development of the loop in the Jurassic brachiopod *Zeilleria leckenbyi*. *Palaeontology*, **15**, 450–472.

COOPER, G. A. 1957. Loop-development of the Pennsylvanian terebratulid *Cryptacanthia*. *Smithson. misc. Collns*, **134** (3).

DAGIS, A. S. 1968. (Jurassic and early Cretaceous brachiopods of northern Siberia.) *Trudy Inst. Geol. Geofiz. sib. Otd.* **41.**

ELLIOTT, G. F. 1948. The evolutionary significance of brachial development in terebratelloid brachiopods. *Ann. Mag. nat. Hist.* **(12) 1**, 297–317.

—— 1950. The genus *Hamptonina* (Brachiopoda); and the relation of post-Palaeozoic brachiopods to coral-reefs. Ibid. **(12) 3**, 429–446.

—— 1953. Brachial developments and evolution in terebratelloid brachiopods. *Biol. Rev.* **28**, 261–279.

FRIELE, H. 1875. Bidrag til Vestlandets Molluskfauna. *Forh. VidenskSelsk. Krist. f. 1875*, 57–64.

—— 1877. The development of the skeleton in the genus *Waldheimia*. *Arch. Math. Naturv.* **2**, 380–386.

MOORE, C. 1860. On new Brachiopoda, and on the development of the loop in *Terebratella*. *Geologist*, vol. for 1860, 438–445.

RICHARDSON, J. R. 1975. Loop development and the classification of Terebratellacean brachiopods. *Palaeontology*, **18**, 285–314, pl. 44.

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