

SHELL STRUCTURE OF THE BILLINGSSELLACEAN BRACHIOPODS

by ALWYN WILLIAMS

ABSTRACT. Sections of Cambrian articulate brachiopods from the U.S.S.R. show that the calcareous shell of the billingsellacean Nisusiidae probably consisted of normally developed primary and secondary layers with orthodoxly stacked fibres. Disposition of the recrystallized fibres further suggests that whereas *Nisusia* was impunctate, the related *Kotujella* was permeated by simple canals which must have been indistinguishable from the caeca accommodated within endopunctae of younger, unrelated articulate brachiopods.

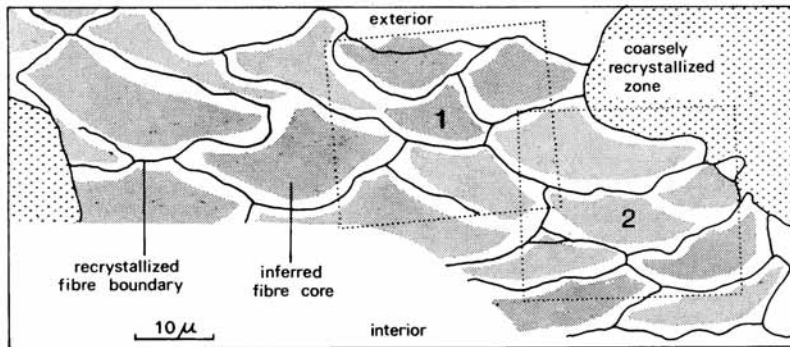
THIS note is intended as an addendum to the Special Paper on 'Evolution of the shell structure of articulate brachiopods' (Williams 1968) in that it supplements the information contained in that paper on the ultrastructure of the primitive articulate shell. When comparative studies of shell fabric of living and extinct articulate brachiopods were started, it was hoped to conduct a preliminary survey of the subphylum by examining representative genera drawn from all currently recognized superfamilies. This aim was largely achieved although, as stated in the Special Paper (p. 37), the taxa sampled did not include any billingsellaceans or, for that matter, any Lower Cambrian articulates. Such omission was particularly tantalizing because it involved *Nisusia* and related forms which, as the most primitive articulates yet discovered, are morphologically and stratigraphically nearest to the ancestral prototype. Suitable material was not lacking for want of help from many colleagues. Dr. J. Bergström of the Palaeontological Institute, Lund University, Dr. H. Brunton of the British Museum (Natural History), Dr. G. A. Cooper of the U.S. National Museum, and Dr. H. Mutvei of the Riksmuseum, Stockholm had all loaned or given specimens of *Billingsella* (?) *lindströmi* Linnarsson and *Oligomys exporrecta* Linnarsson from the Middle Cambrian of Sweden, and *Eorthis remnicha* Winchell and *Billingsella perfecta* Cooper from the Upper Cambrian of the United States. But when sectioned, the shell fabric of all these specimens was found to have been destroyed by gross recrystallization or by silicification or dolomitization.

It is therefore a matter of great satisfaction to have recently received from Dr. O. N. Andreeva, to whom I am indeed greatly indebted, over 80 specimens of articulate brachiopods from various Cambrian limestone formations of the Siberian Platform, and to find that four of the five genera represented in the collection are well enough preserved to indicate the original style of the shell fabric. Variation in preservation is not obviously related to differences in rock matrix. Specimens of Upper Cambrian *Bajanorthis tukolandica* Andreeva and Lower Cambrian *Nisusia ferganensis* Andreeva contained in grey, coarse, partially dolomitized calcarenites with conspicuous bioclastic constituents up to 1 mm. in size, usually display a discernible fabric, whereas those of *Bobinella kulumbensis* Andreeva which occur with the former species are less well preserved. Moreover, although the shell fabric of the Lower Cambrian *Matutella grata* Andreeva and *Nisusia* cf. *kotujensis* Andreeva, which have been collected from a pale-green marly limestone with more finely divided bioclasts, has been destroyed by recrystallization,

[Palaeontology, Vol. 11, Part 3, 1968, pp. 486-90, pls. 91, 92.]

contemporaneous *Kotujella calva* Andreeva, found in the same matrix, is not greatly affected. It thus seems likely that processes of recrystallization or replacement of these shells were as much controlled by local geological conditions as by their texture and the nature of the rock containing them.

Nearly all the shell of *B. tukolandica* and *B. kulumbensis* is made up of recrystallized fibres (Pl. 91, figs. 4-6; Pl. 92, fig. 1) which originally must have been identical in morphology and stacking with those composing the secondary layer of the majority of articulate brachiopods, including the Orthacea and Porambonitacea to which superfamilies the two species respectively belong. Also, where the shell exterior is covered by



TEXT-FIG. 1. Tracing of montage showing the relationship between recrystallized secondary fibres in a transverse section of a pedicle valve of *Nisusia ferganensis* Andreeva, with the inferred outlines of the original fibres; the areas occupied by figs. 1 and 2 of Plate 91 are indicated.

rock, a consistently thin layer of finely crystalline calcite, which is quite distinct from the enclosing granular cement, is seen to form an external skin to the fibres. If this skin represents the primary layer, as seems likely, secretion of *Bajanorthis* and *Bobinella* shells proceeded in the same way as in living rhynchonellides.

Judging from the ultrastructure of the shell, the mantle of *N. ferganensis* is also likely to have functioned in the same way as that of living rhynchonellides. A consistently thin coat of equidimensional grains, sharply distinguishable from the granular cement of the rock, forms an external skin to better-preserved valves and has been taken to represent a recrystallized primary layer. The fibres of the secondary layer, although recrystallized and tending to form aggregates in places, still retain much of the characteristic shape of orthodoxly stacked units (text-fig. 1; Pl. 91, figs. 1-3).

The most unexpected fabric was that found in *K. calva*. Again recrystallization could not disguise the fact that the shell almost certainly consisted of normally secreted primary and secondary layers. Yet the fibres are disposed in arches about $10\ \mu$ wide and $30\ \mu$ apart which are convex outwards (Pl. 92, figs. 2-6). Such deflections could only have been brought about by secretion of fibres around evaginations of the mantle (Williams 1968, p. 30). Their frequency and attitude are strongly reminiscent of the effects of caecal outgrowths from the mantle of endopunctate shells; since they indicate unbranched canals which appear to penetrate both internal and external shell surfaces, they probably accommodated caeca or related structures (text-fig. 2).

In assessing the significance of these Cambrian fabrics to the phylogeny of the articulate shell, some consideration must be given to the affinities of the stocks concerned. The relationships of both *Bajanorthis* and *Bobinella* are incontestable and simply confirm that orthodox primary and secondary shell was as characteristic of the late Cambrian orthaceans and porambonitaceans as of Ordovician representatives of the superfamilies (Williams 1968, pp. 34, 37). It is equally certain that the early Cambrian *Nisusia* with its rudimentary teeth and cardinalia, supra-apical foramen and strong pseudodeltidium is one of the most primitive articulate brachiopods known. These features are also characteristic of three contemporaneous genera, *Eoconcha* Cooper, *Kotujella* Andreeva, and *Matutella* Cooper. On the reasonable assumption that all four stocks are closely related, they have been classified as members of the Nisusiidae which, in turn, has been regarded as the root stock of the Billingsellacea and, more remotely, of all articulate brachiopods (Williams in Williams *et al.* 1965, p. H306). Andreeva (1962, p. 90), however, has drawn attention to the external resemblance between *Matutella* and *Kotujella* and porambonitaceans, and concluded that these two genera should be classified as pentamerides. No one can dispute the superficial likeness between the genera just referred to and certain early Ordovician stocks like *Alimbella* Andreeva. But apart from *Alimbella* having too many orthide characteristics to be generally accepted as a pentameride, there are much more fundamental links between *Matutella*, *Kotujella*, and *Nisusia*, like their possession of supra-apical foramina, poorly developed teeth, and other primitive internal features. In particular, one cannot attach as much importance as did Andreeva (1962, p. 94) to the 'open' delthyrium of *Kotujella* because it was permanently separated from the supra-apical pedicle passage and foramen by a 'concave plate'. It may well be that *Matutella* and *Kotujella* stocks were ultimately ancestral to the porambonitaceans, but that does not diminish the intimacy of their affinities with *Nisusia* and the Lower Cambrian Virginian genus *Eoconcha* (Cooper 1951, p. 5).

In view of the ultrastructure of the shell of *Kotujella* and *Nisusia* it now seems

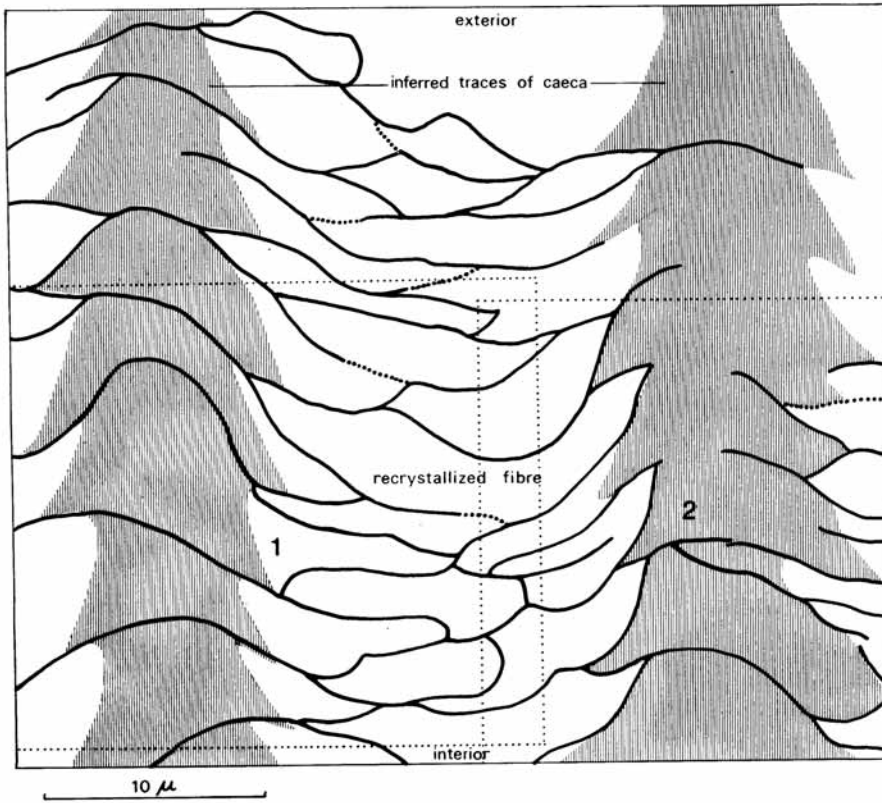
EXPLANATION OF PLATE 91

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left-hand corner of each figure, equivalent to 2 μ . Figs. 1–3. Transverse and oblique sections of recrystallized fibres of the secondary layer of *Nisusia ferganensis* Andreeva; Lower Cambrian Lensky Beds, Madygen region, Ferganskaya Dolina. Figs. 1 and 2 are part of montage illustrated in text-fig. 1. Figs. 4, 5. Oblique sections of recrystallized fibres of the secondary layer of *Bajanorthis tukolandica* Andreeva; Upper Cambrian limestones, R. Kulyumbe, Vostochnaya, Siberia. Fig. 6. Oblique sections of recrystallized fibres of the secondary layer of *Bobinella kulumbensis* Andreeva; Upper Cambrian limestones, R. Kulyumbe, Vostochnaya, Siberia.

EXPLANATION OF PLATE 92

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale at the bottom left-hand corner of each figure, equivalent to 2 μ . Fig. 1. Oblique section of recrystallized fibres of the secondary layer of *Bobinella kulumbensis* Andreeva; Upper Cambrian limestones, R. Kulyumbe, Vostochnaya, Siberia. Figs. 2–6. Oblique to transverse sections of recrystallized fibres of the secondary layer of *Kotujella calva* Andreeva; Lower Cambrian Lensky Beds, R. Dakhoi, Vostochnaya, Siberia. Figs. 2 and 4 are part of montage showing vertical range of punctum; figs. 5 and 6 are part of montage illustrated in text-fig. 2.

certain that the nisusiid exoskeleton was secreted as a triple-layered shell composed of an outermost periostracum, a finely crystalline primary layer, and a secondary layer made up of orthodoxy stacked fibres. This being so, the programme of secretion



TEXT-FIG. 2. Tracing of montage showing the disposition of recrystallized secondary fibres in a transverse section of a pedicle valve of *Kotujella calva* Andreeva in relation to two adjacent canals inferred to have accommodated caeca; the areas occupied by figs. 5 and 6 of Plate 92 are indicated as 1 and 2 respectively.

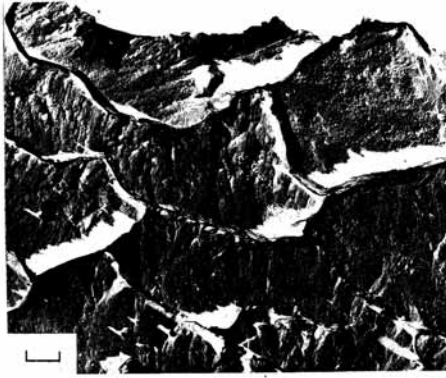
followed by the outer epithelial cells of the mantle of archetypal articulate was the same, even in detail, as that determining the growth of the shell in living rhychnonellides and terebratulides. It is also intriguing to discover that whereas *Nisusia* was impunctate, *Kotujella* bears all the evidence of having been endopunctate, thereby providing yet another example of the independent development of this condition during brachiopod evolution.

REFERENCES

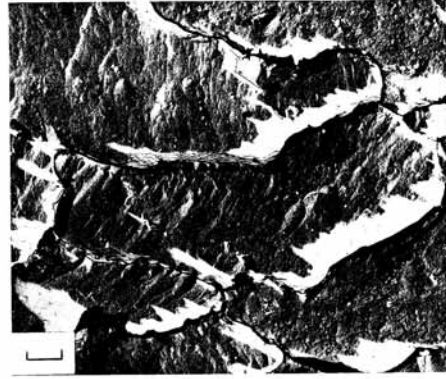
- ANDREEVA, O. N. 1962. Some Cambrian brachiopods of Siberia and Northern Asia. *Paleont. Zhurn.* **2**, 87-96.
- COOPER, G. A. 1951. New brachiopods from the Lower Cambrian of Virginia. *J. Wash. Acad. Sci.* **41**, 4-8.
- WILLIAMS, A. *et al.* 1965. *Treatise on Invertebrate Paleontology* (ed. MOORE, R. C.), Part H, *Brachiopoda*, **1**, H1-H521; **2**, H523-H927. Lawrence (Univ. of Kansas).
- 1968. Evolution of the shell structure of articulate brachiopods. *Spec. Pap. Palaeont.* No. 2, 1-55, pls. 1-24.

Typescript received 6 November 1967

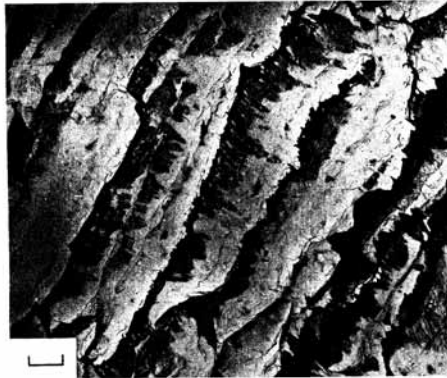
ALWYN WILLIAMS
Department of Geology
The Queen's University
Belfast, N. Ireland



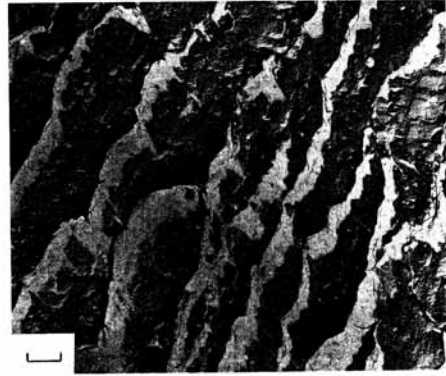
1



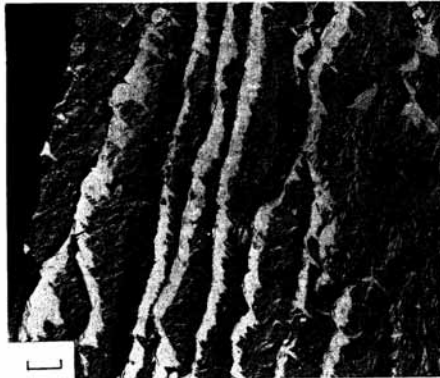
2



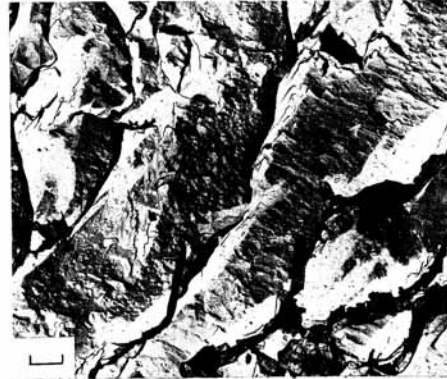
3



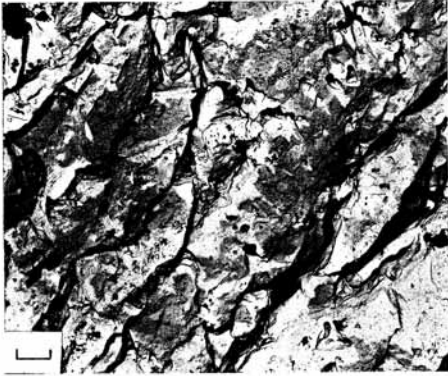
4



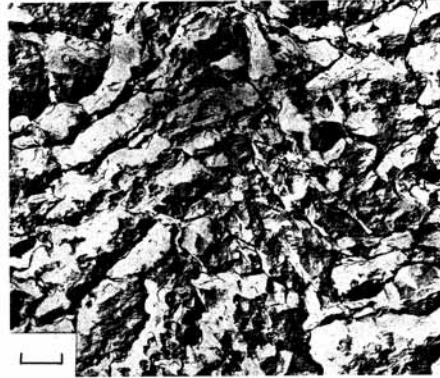
5



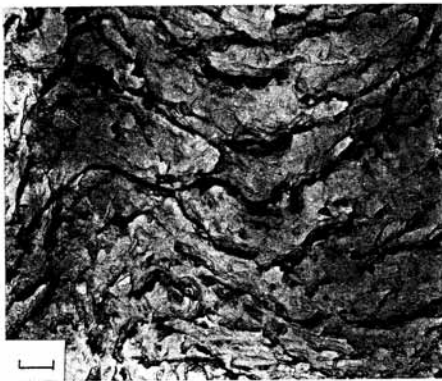
6



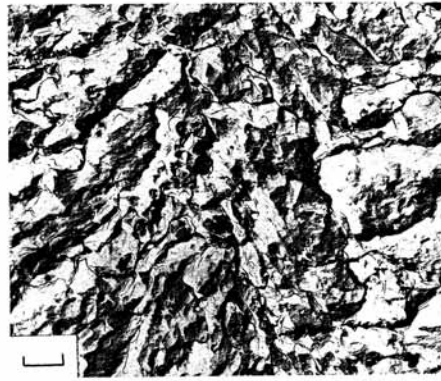
1



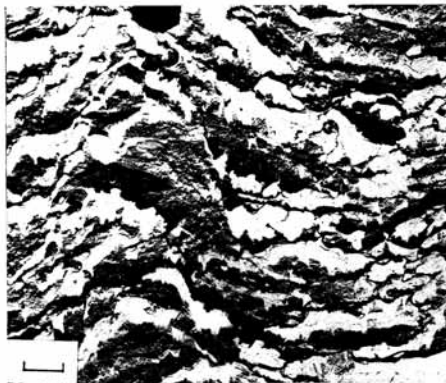
2



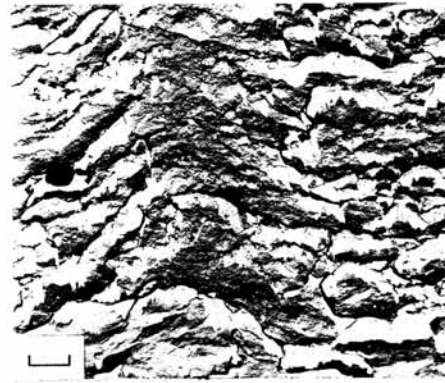
3



4



5



6

WILLIAMS, Shell structure of billingsellacean brachiopods
