A NEW MICROMORPHIC RHYNCHONELLIDE BRACHIOPOD FROM THE MIDDLE JURASSIC OF ENGLAND

by P. G. BAKER

ABSTRACT. Recent work on micromorphic brachiopod faunas from the Inferior Oolite reveals the presence of a new rhynchonellide species attributable to Nannirhynchia Buckman but with diagnostic beak characters. The new species N. longirostra is proposed. Although the presence of a pedicle collar has not previously been recorded in the Norellinae, the form of the shell, the definitely arcuifer crura and the way in which they curve ventrally into the pedicle valve are thought to justify its inclusion in the sub-family. Juveniles are easily recognizable but no characteristic transition to adult form is noted. Investigation of the shell microstructure leads to the conclusion that deltidial plates are not invariably developed. The possibility of synonymy with Spiriferina? minima Moore, is discussed.

THE species investigated was recovered from the Oolite Marl, a weakly coherent interbedded marl and biomicrite (Folk 1959) of Lower Bajocian age occurring in the Inferior Oolite of the mid-Cotswolds. Organo-detrital residue obtained from treated marl yields numerous other brachiopod micromorphs, notably *Moorellina granulosa* (Moore), juveniles of terebratulides such as *Zeilleria leckenbyi* (Walker) and 'Terebratula' whitakeri Walker, MS., also rare specimens of *Zellania davidsoni* Moore. A detailed account of the techniques adopted for preparation of the material for study may be found in Baker (1969, 1970).

Although the detail of separated valves is well preserved, the interior of uncrushed complete shells is invariably coated with minute crystals which makes determination of the form of the crura difficult. Fortunately, the strong beak resists diagenesis very well and its internal characters may be easily ascertained by serial sectioning.

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Registration of Material. The holotype and topotypes, together with sectioned material in the form of original and duplicate cellulose acetate peels are to be housed in the British Museum (Natural History) under the register numbers BB 45820–45829. Reference numbers quoted in the plate figures refer to stereoscan negatives of figured specimens which are to be retained in the negative library of the Department of Geology, University of Leicester.

Order RHYNCHONELLIDA Kuhn 1949 Family DIMERELLIDAE Buckman 1918 Genus NANNIRHYNCHIA Buckman 1918

Nannirhynchia longirostra sp. nov.

Plates 135-137; text-figs. 1, 2

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Diagnosis. Very small, biconvex Nannirhynchia, up to about 2·5 mm in length, 2·0 mm in width, and 1·0 mm in thickness. Pyriform in outline with well-developed intraplicate anterior commissure. Rostrate. Radial striae clearly seen on specimens in which the primary shell layer is weathered.

Type specimens. Holotype and nine topotypes to be housed in the British Museum (Natural History), register number BB 45820.

Distribution. Geographic distribution unknown. All the material studied was collected from Westington Hill Quarry, grid ref. SP142368, near Chipping Campden in Gloucestershire.

Stratigraphically the species is so far known only from a single horizon in the Lower Inferior Oolite (Lower Bajocian, Murchisonae Zone), notably at the base (Baker 1970) of the Oolite Marl, where it is associated with other micromorphic brachiopods such as *Moorellina granulosa* (Moore) and *Zellania davidsoni* Moore.

Dimensions of Holotype. Length 2·3 mm, width 1·8 mm, thickness 1·0 mm.

Description. External Characters. Study of 39 specimens and numerous shell fragments shows that the recorded dimensions of the holotype are very close to the maximum for the species and that the beak characteristics are stable throughout the material studied. The arguments advanced previously (Baker 1969), in favour of regarding the associated micromorphic brachiopods as adults, are equally applicable to this study. Ontogenetic stages are available which show that adults are characterized by a well-developed, rounded, central plication with complementary sulci on either side and occasionally a single, low, lateral costa on each side.

The shell is typically non-strophic sensu Rudwick and is biconvex throughout growth. In young forms, both the brachial and pedicle valves have a median sulcus and thus a ligate form. The central plication is produced by bifurcation of the brachial sulcus and subsequent deepening of the thus formed complementary sulci. Therefore as Ager (1967) has shown for N. pygmaea the plication in N. longirostra also is a consequence of the development of the sulci and thus intraplicate sensu Buckman, rather than uniplicate with lateral sulci. Striae when visible are a diagenetic development.

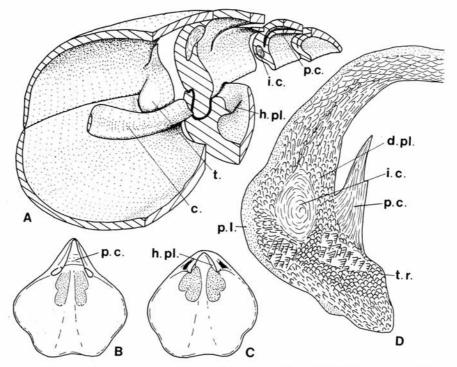
The beak is strong, sharp, projecting, and slightly incurved with narrow palintropes. The delthyrium is open, hypothyridid, and bounded by strongly developed tooth ridges, with or without narrow deltidial plates.

Internal Characters: Pedicle valve. The most characteristic feature of the pedicle valve is the well-developed, almost sessile pedicle collar with its clearly defined growth lines (Pl. 136, fig. 1). The hinge teeth of this species are relatively large.

Dental plates are present. These are inclined and show a strong lateral deflection so that the lateral umbonal cavities remain very small (Pl. 137, figs. 3, 4, text-fig. 2). The dental plates are easily overlooked in adult shells as the lateral umbonal cavities quickly become filled with subsequently deposited secondary shell so that the dental plates appear to form part of the umbonal wall (Pl. 136, fig. 1).

In young forms the dental plates are sometimes visible and the partially infilled lateral umbonal cavities appear as small perforations (Pl. 136, fig. 2).

The delthyrium is bounded by narrow widely disjunct structures usually interpreted as deltidial plates. Reference to these structures will be made later.



TEXT-FIG. 1. A. Block reconstruction of the posterior region of the right half of the shell of *N. longi-rostra*, based on superimposed cellulose acetate peels. The anterior faces of the block segments correlate with peels 37549/43, 26, 12, and 8 respectively, ×60 approx. B, C. Impressions of the ventral (B) and dorsal (C) muscle fields (stippled) of *N. longirostra* reconstructed from visible boundaries and the distribution of terminally pitted secondary fibres, ×17. D. Trace of a stereoscan montage ×225, of part of peel 37549/15 showing the orientation of the secondary shell fibres in the various structures depicted. c. ventrally deflected arcuifer crus, d.pl. dental plate, h.pl. hinge plate, i.c. infilled lateral umbonal cavity, p.c. pedicle collar, p.l. primary layer, t. hinge tooth, t.r. tooth ridge. Patches of recrystallized shell cross-hatched.

EXPLANATION OF PLATE 135

Stereoscan photomicrographs of specimens of Nannirhynchia longirostra sp. nov. Material of all figures coated with evaporated aluminium before photography.

Figs. 1-3. Brachial, anterior, and lateral views of the holotype 37550, × 30.

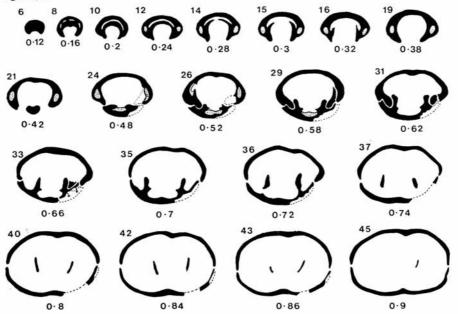
Figs. 4-7. Brachial, anterior, posterior, and lateral views of a juvenile 37551. The posterior view (fig. 6) shows the tooth ridges surmounted by small deltidial plates, ×40.

Fig. 8. Pedicle view of a juvenile 37552, showing the laterally deflected beak and radial striae, ×30.
Fig. 9. Interior of a brachial valve 37558, showing the hinge plates and the absence of a cardinal process and median septum. Crura broken, ×32.

Fig. 10. Interior of a pedicle valve 37546, showing the pedicle collar, hinge teeth, and denticula, \times 32.

Small denticula are present, clearly visible on separated valves (Pl. 135, fig. 10; Pl. 136, fig. 2) but not well defined in transverse sections.

Owing to the effects of diagenesis on the internal surface of shells it has not been possible to determine the true configuration of the muscle scars. The interior of separated valves, however, often shows impressions of the muscle fields and diagenesis has not completely obliterated the stellate pitting on the terminal faces of the secondary fibres lying within these areas (Pl. 136, fig. 7). The form of the muscle fields is shown in text-fig. 1B, C.



TEXT-FIG. 2. Nannirhynchia longirostra sp. nov., series of 21 serial transverse sections through specimen 37549, drawn from cellulose acetate peels, showing all the features of the species. Numbers refer to specific peels illustrated (top left) and the distance from the beak. Subsequent shell deposition stippled.

All ×20.

Brachial Valve. There is no cardinal process but the posterior end of the valve protrudes into the delthyrial cavity. Hinge plates are present (Pl. 135, fig. 9; Pl. 136, fig. 4) but not well developed and in the material examined they are horizontal and not fused posteriorly so that there is nothing approaching a septalium and no median septum (text-figs. 1A, 2). Crural bases arise dorsally from the hinge plates (Pl. 137, fig. 7) and give rise to ventrally deflected, arcuifer crura (Pl. 137, figs. 5, 6, 8). Outer socket ridges are present but as in the case of the denticula they are only clear in separated valves (Pl. 136, fig. 4).

Microstructure. The microstructure of shells is characteristically rhynchonellide (Williams 1968). The primary layer and the terminal faces of secondary fibres often

show some effects of diagenesis but the fabric of the secondary layer itself is generally remarkably well preserved (Pl. 136, figs. 6, 8; Pl. 137, figs. 1, 2). Individual fibres are very long, often extending from the junction with the primary layer, right through the secondary layer to its internal boundary. This produces a rather weak shell and half valves, fractured longitudinally are most common. Secondary fibres often show well-defined growth lines representing stages in the repeated advance of the terminal face during fibre growth (Pl. 137, fig. 2). The overall impression is that the secondary fibres are relatively flatter and much larger than in many other brachiopods. They do not show any marked decrease in size in the muscle fields but exhibit the curious stellate pitting of myotest fibres (Pl. 136, fig. 7). Williams (personal communication) suggests that these pits may represent differential diagenetic solution but in the author's opinion their regularity indicates a fundamental property of the underlying fibre. In section the fibres show the characteristic blurring of outline (Pl. 136, fig. 8) and at high magnification, the minute trails associated with myotest.

Ontogeny. Complete juveniles (Pl. 135, figs. 4–8) are apparently much more common than complete adults but there is no difficulty in assigning these to the same species owing to the fact that their typical morphology can easily be seen in the early growth lines of adult shells (Pl. 135, fig. 1). The pedicle collar as may be anticipated from its growth lines, is present in even the smallest pedicle valves studied. Brachial valves of a complementary size show broken crura so that the development of crura also is a very early feature. No characteristic ontogenetic stages are therefore present and the only

EXPLANATION OF PLATE 136

Stereoscan photomicrographs (except fig. 8) of specimens of *N. longirostra*. Material of all figures coated with evaporated aluminium before photography.

- Fig. 1. Interior of a pedicle valve 37546, tilted to show the relatively large hinge teeth and the pedicle collar with its characteristic growth lines. The dental plates are apparently merged with the shell wall owing to infilling of the lateral umbonal cavities. Deltidial plates not developed. Tilt angle 68°, ×75
- Fig. 2. Interior of a juvenile pedicle valve 37559, tilted to show the denticulum and the hinge tooth supported by a dental plate with the relic of the left lateral umbonal cavity (arrowed). Tilt angle 65°, × 165.
- Fig. 3. Enlarged view of the umbonal region of specimen 37551, showing the concave terminal face of each deltidial plate, ×100.
- Fig. 4. Enlarged view of the umbonal region of the interior of a brachial valve 37547, showing the inner and outer socket ridges, the crura, broken, the small hinge plates, and the absence of a cardinal process and median septum, ×95.
- Fig. 5. Enlarged view of the striae on the external surface of the shell of specimen 37552 to show that they are an expression of the diagenesis of the primary shell layer, ×1000.
- Fig. 6. Junction of the primary and secondary layers in an exfoliated shell 37564, showing the well-preserved secondary mosaic, left, and the primary shell with independently aligned striae, ×1000.
- Fig. 7. Enlarged view of a portion of specimen 37562 showing the stellate pitting of the fibres lying in the depressed areas interpreted as muscle fields. Location of section, floor of the brachial valve approaching the mid-line, ×4500.
- Fig. 8. Electron micrograph of a two-stage replica of an oblique section through the shell underlying a muscle field, showing the characteristic blurring of the outline of fibres associated with myotest. Location of section, approximately as in Fig. 7, ×2200.

significant change during growth is the rapid transition from opposite to alternate folding. Buckman (1918, p. 81) used the term pliciligate for the change from opposite to alternate folding by the formation of a fold within the dorsal sulcus. However, pliciligate as defined by Williams and Rowell (1965, H150) implies only a low folding in the brachial valve. The amplitude of the folding in *N. longirostra* is symmetrical through the plane of the commissure. As the distinction between intraplicate and pliciligate *sensu* Buckman is not clear and in order to avoid confusion, the term intraplicate adopted by Ager (1967, p. 139) is adhered to.

Remarks. Attention has been paid to the radial striae of Nannirhynchia (Buckman 1918, p. 67; Ager 1967, p. 139). Stereoscan photomicrographs of N. longirostra (Pl. 136, figs. 5, 6) show that the appearance of striae is an expression of diagenesis of the primary shell, which may but does not normally, reflect the orientation of the secondary fibres.

Work in progress on the origin and growth of deltidial plates shows that they arise from the dorsal surface of the tooth ridges. In numerous instances in *N. longirostra* and probably many of the other micromorphic forms with so-called very narrow deltidial plates, the epithelium responsible for initiating the development of the deltidial plates never received the necessary stimulus and the deltidial plates failed to develop. In which case the narrow ridges bounding the delthyrium and having the appearance of deltidial plates are in fact the exposed dorsal surfaces of the tooth ridges. Where deltidial plates are present (size of the animal seems to be no criterion) their development parallels the anterior extension of the teeth (Pl. 135, fig. 6) and they show a characteristic concave terminal face (Pl. 136, fig. 3).

The separation of the pedicle collar from the shell wall closely resembles that described by Copper (1965, p. 363, text-fig. 3A) in the atrypoid *Mimatrypa insquamosa* (Schnur.). Unfortunately, although the absence of lateral umbonal cavities is noted, the text-figure does not include a key to the shell-material type so it is not possible to determine whether they are secondarily infilled.

In Ager (1967) five nominal species have been previously recognized as belonging to the genus Nannirhynchia. These are N. milvina Buckman, N.? minima (Moore), N.? moorei (Davidson), N. pygmaea (Morris), and N. subpygmaea Buckman. N. milvina may be distinguished from N. longirostra by its shorter beak, episulcate folding, and later occurrence (Upper Bajocian). The original of Spiriferina? moorei is apparently lost and Davidson was probably correct in assuming that it was a juvenile Spiriferina. Ager (1967) discussed the possibility that the specimen might have been a stunted adult and stated that there is no particular reason for attributing it to Nannirhynchia as suggested by Buckman (1918). Distinction between N. pygmaea and N. subpygmaea is not indisputably established but Ager prefers to keep them taxonomically separate in view of the present lack of knowledge of N. subpygmaea and its later occurrence (N. pygmaea, Upper Lias; N. subpygmaea, Upper Bajocian). Both species may be easily distinguished from N. longirostra by their beak characters.

It is probable that the species is very closely related to the form described by Moore (1861, p. 190, pl. 2, figs. 19, 20) as *Spiriferina? minima* and the specimen illustrated in fig. 19 undoubtedly shows great similarity with the holotype of *N. longirostra*. However, significant differences exist between *N. longirostra* and the illustration of *S.? minima* in Davidson (1874, Suppl. pl. 11, fig. 17a) which in the context of the sentence (Davidson

1874, p. 103) purports to be a careful drawing of one of Moore's specimens. Davidson illustrates a correctly defined (Williams and Rowell 1965, H145) hinge line. His figure implies the presence of an interarea and therefore a strophic shell (Rudwick 1959, p. 19) differing from the non-strophic shell of N. longirostra. Moore himself states that the area is broad and flattened and refers to a broad hinge line but figures what is essentially a cardinal margin similar to that of N. longirostra. An interesting feature is the way Moore (1861, pl. 2, fig. 20) illustrates a lateral deflection of the beak. This character is commonly observed in young forms of N. longirostra in the material collected from Westington Hill quarry (Pl. 135, fig. 8). Buckman (1918, p. 68) noted the similarity between S.? minima and N. subpygmaea (Walker) but also commented on the large beak and apparently straight hinge line depicted by Davidson. Later (p. 74) Buckman assigns these characters to the genus Rectirhynchia and suggests both Moore and Davidson may have unwittingly combined details from more than one specimen, i.e. combined the characters of two species.

Both Moore and Davidson refer to the presence of a triangular deltidium yet none of the figures clearly shows the structure. Davidson's figure shows a constriction at the anterior of the delthyrial region, very similar to the disjunct deltidial plates of certain young terebratulides, whilst Moore (1861) figures either an open delthyrium bounded by very narrow deltidial plates or has shading to indicate a concave plate. Reference to their accounts of other micromorphic forms precludes the possibility that both authors could be mistaken with regard to the presence of a plate situated in the delthyrium. The conclusion must therefore be that S.? minima possessed a concave plate within the delthyrium, identifiable with the pedicle collar of N. longirostra.

Unfortunately a careful search through the micromorphic brachiopods in the Moore collection has failed to reveal the types of S.? minima. They were not listed by Dr. Wallis when he catalogued the collection in 1927 so it appears that the originals are lost. The degree of affinity between N. longirostra and S.? minima must therefore remain a matter of speculation. Demonstration of the close similarity between the two forms introduces the possibility that we are here, simply recording the discovery of S.? minima

EXPLANATION OF PLATE 137

Stereoscan photomicrographs (except figs. 5, 6) of N. longirostra. Material of all figures coated with evaporated aluminium before photography.

- Fig. 1. Portion of an exfoliated shell showing the extension of individual secondary fibres from the outer to the inner (upper left) boundary of the secondary layer, ×200.
- Fig. 2. Surface of an exfoliated secondary fibre showing growth lines, ×2200. Fig. 3. Enlarged portion of peel 37549/15 showing the dental plate and subsequently infilled lateral umbonal cavity, T.S. ×150.
- Fig. 4. Enlarged portion of peel 37576/19 showing the pedicle collar developed from the inner surface of the dental plate and the very small infilled lateral umbonal cavity, close to its posterior termination.
- Fig. 5. Photomicrograph, reflected light. Transverse section through specimen 37549 showing the crystallite coated interior of the shell and the crystallite encrusted, arcuifer crura, ×40.
- Fig. 6. Retouched copy fig. 5.
- Fig. 7. Enlarged portion of peel 37576/26, showing the crural base (c.b.) adjacent to the inner socket ridge and arising from the dorsal surface of the hinge plate (h.p.). T.S. $\times 150$.
- Fig. 8. Horizontal section through specimen 37587 showing the form of the left crus, ×175.

in a new locality, and raises the question of the validity of the new species. In view of the very limited knowledge of S.? minima and in view of the absence of the original types, it is felt that there is justification in the erection of a new species to include the Westington Hill material.

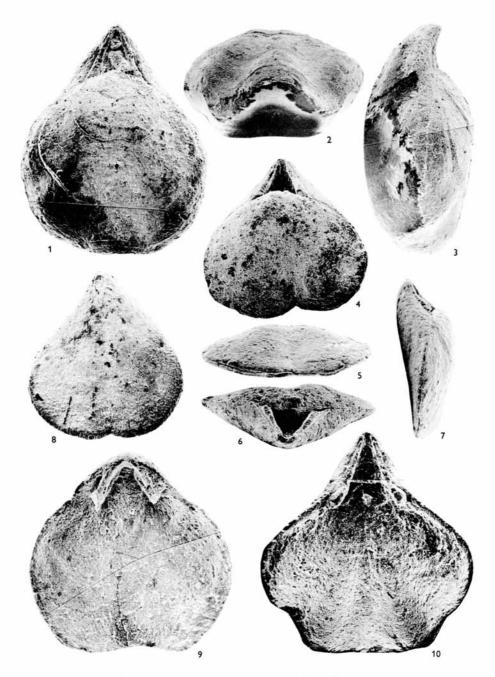
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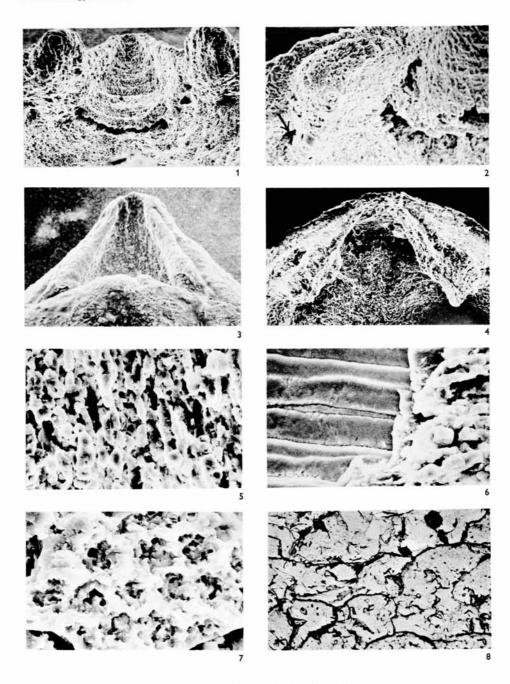
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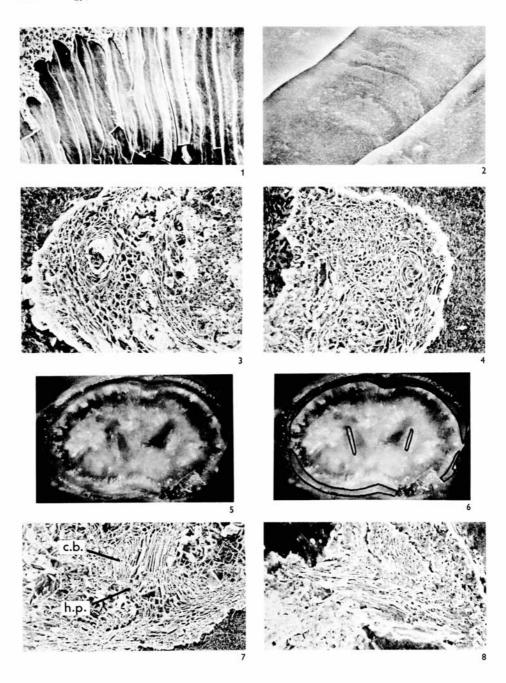
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Palaeontology, Vol. 14 PLATE 136



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Palaeontology, Vol. 14 PLATE 137



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