A REAPPRAISAL OF THE LOWER SILURIAN BRACHIOPODS *BOREALIS* AND *PENTAMERUS*

by ATLE MØRK

ABSTRACT. The pentamerids *Borealis borealis* and *Pentamerus oblongus* are redescribed and a new subspecies *B. borealis osloensis* subsp. nov. is erected. Specimens from the virtually continuous Llandovery succession of the Oslo Region show a gradational evolution from *B. borealis* to *P. oblongus*, with a transition within the Idwian. The occurrence of different evolutionary forms suggests a diachronous base for the limestone unit containing these fossils in the Oslo Region. The recognition of this phyletic lineage may further improve the correlation of lower Silurian shelly faunas of the Oslo Region, Estonia, and Great Britain.

PENTAMERIDS are common elements of Silurian faunas, and they therefore have a great potential in the correlation of lower Silurian shelly facies. A better understanding of their phylogenetic relationships, as demonstrated by Williams (1951) for the *Stricklandia* lineage, is fundamental in the stratigraphical use of these facies-dependent brachiopods. *Pentamerus oblongus* has a widespread distribution both in its type area (Wales and the Welsh Borderland), in Estonia, U.S.S.R., U.S.A., and Norway, while the *Borealis* fauna seems to be more restricted to the Baltoscandian area. The evolutionary relationships between these taxa must therefore be studied in the latter area, and the results may increase the value of these brachiopods in more universal correlations. Faunas from the virtually continuous Llandovery sections of the Oslo Region now seem to indicate a direct phyletic relationship between *B. borealis* and *P. oblongus*; this transition may be used as a chronostratigraphical horizon within the Idwian stage.

PREVIOUS WORK

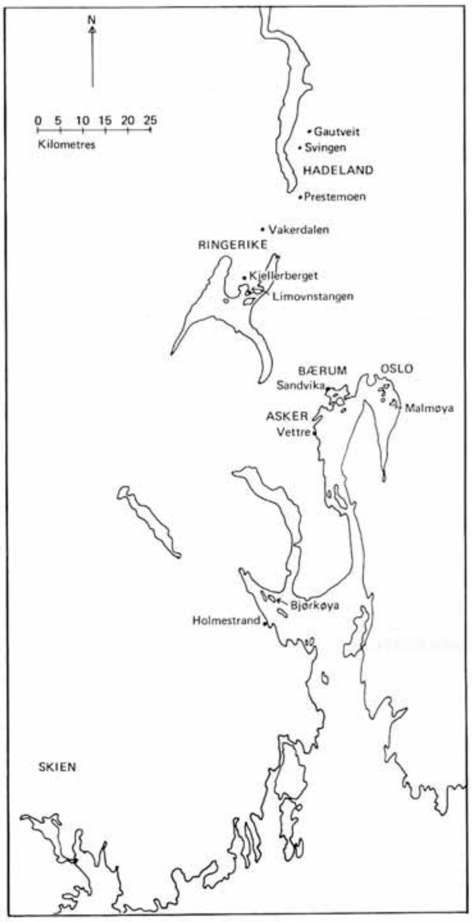
The history of the taxonomy of the genus *Pentamerus* was described in detail by Alexander (1948), and the names of the genus *Pentamerus* and its type species *P. oblongus* (in preference to its senior synonym *P. laevis*) were approved by ICZN opinion no. 297, 1954. *B. borealis* was long regarded as belonging to the genus *Pentamerus* (e.g. Eichwald 1860; Kiær 1908; St. Joseph 1938; Rubel 1970), but after the introduction of the subfamily Virgianinae (Boucot and Amsden 1963), the taxonomic position of '*P*'. *borealis* was questioned, and Gauri and Boucot (1968) argued that, although the pedicle valves of *P. oblongus* and '*P*'. *borealis* were very similar, the brachial valves, and especially the cardinalia, showed great differences. Subsequent investigation of Estonian material prompted Boucot, Johnson and Rubel (1971) to establish the genus *Borealis*. Although a close evolutionary relationship between '*P*'. *borealis* and *P. oblongus* has been indicated by various authors (Kiær 1908; St. Joseph 1938; Rubel 1970; Boucot, Kaljo and Nestor 1969), the different and selfcontradictory evolutionary lineages proposed by Boucot and Chiang (1974) and Boucot (1975) assume that *Borealis* and *Pentamerus* belong to different lineages. The taxonomic and stratigraphical implications of both proposals are important, and the present study was therefore undertaken in order to evaluate the important evidence given by representatives of these genera from the Oslo Region.

In his monumental work on the Silurian of the Oslo Region, Kiær (1908) described the distribution of *P. borealis*, his zone fossil for 'Etage' 7a, and *P. oblongus*, his zone fossil for 'Etage' 7b. His identifications were based on field observations and intensive sampling. Kiær's planned description of the pentamerids of the Oslo Region was never completed, although several plates were prepared, and Kiær's collection was described by St. Joseph (1938). St. Joseph did little fieldwork himself and his conclusions were influenced by Kiær's stratigraphy and plates. Reinvestigation of the Oslo

[Palaeontology, Vol. 24, Part 3, 1981, pp. 537–553, pls. 83–85.]

Region material described by St. Joseph (1938) shows that some of the specimens assigned to *P. borealis* in fact belong to *P. oblongus*. This has important consequences both for the dating of the Pentamerus Limestone of the Oslo Region and for our understanding of the relationship between the genera *Borealis* and *Pentamerus*. Both *B. borealis* and *P. oblongus* occur in continuously exposed sections in the Oslo Region. A revision of the stratigraphy of the marine Silurian succession of the Oslo Region (of Llandovery and Wenlock age) shows the chronostratigraphical relationships of the beds containing these fossils (Worsley, Aarhus, Bassett, Howe, Mørk and Olaussen, in press.), and in the present paper the 'Etage' system used by Kiær (1908) is replaced by lithostratigraphical units (text-fig. 4). However, for ease of comparison with existing literature, the 'Etage' system will be used here within *each* locality, but individual subunits (e.g. 7a) have no regional correlative significance.

Catalogue numbers. Material labelled PMO is stored in the Paleontologisk Museum, University of Oslo; SMC in the Sedgwick Museum, Cambridge; and USNM in the United States National Museum, Washington D.C.



TEXT-FIG. 1. Locality map.

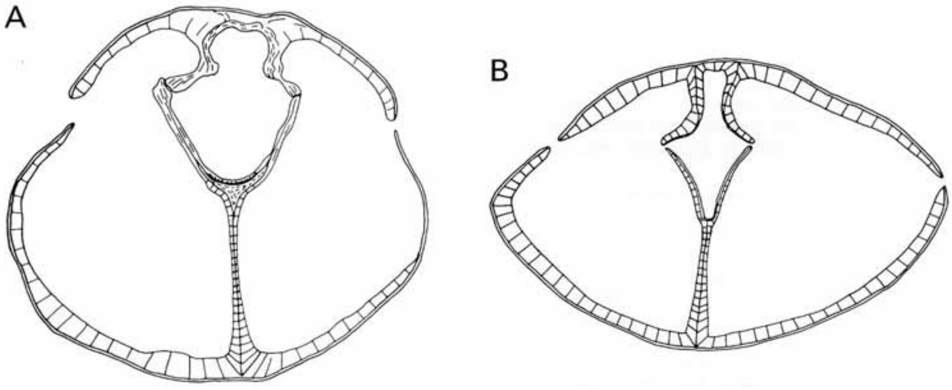
MORPHOLOGICAL CHARACTERS OF TAXONOMIC SIGNIFICANCE

The main problems encountered when comparing existing descriptions of pentamerids arise from the differing taxonomic criteria which have been used by various authors. Old descriptions usually refer only to external form, whilst more modern descriptions attempt to use as many properties as possible, including outer shape, inner structures, and shell structure. When comparing different populations it is of great importance to compare the same features; therefore topotype material of *B. borealis* from Estonia is here redescribed to include necessary information on shell structure to augment the description given by Rubel (1970).

External form. Although it is relatively easy to distinguish between 'typical' specimens of *B. borealis* or *P. oblongus* on the basis of external form, variation in this feature is striking and gives a wide overlap of form types. The pedicle valve is always the most strongly convex, while the convexity of the brachial valve seems to have increased through the Llandovery. The taxonomically reliable characters appear to include firstly, the site of maximum width (anteriorly in early forms), secondly, the existence of parallel or suboval lateral margins, and thirdly, the over-all convexity of the shell. The umbones differ a great deal, but the brachial umbo is usually weakly developed, especially in early forms.

Inner structure of the pedicle valve. The most prominent structure is the spondylium, which varies from being short, wide, and almost rhomboidal to long and narrow; all gradations between these end members are seen. The spondylium is always longer than the septum. The septum is of the duplex type (St. Joseph 1938) and wedges into the outer shell (text-fig. 2) and the central lamellar layer is always continuous with the outer lamellar layer in the shell. The septum continues along the outer shell to give a concave termination against both the shell and spondylium in all forms. Secondary thickening of the prismatic layer is common, and this is usually developed most strongly in the posterior part of the shell. This thickening seems to be environmentally controlled and therefore has no taxonomic value. A pseudodeltidium is observed only in *P. oblongus.*

Inner structure of the brachial valve. Great variation is found in the development of the cardinalia between different genera, these being short and broad in the Virgianinae and long in the Pentamerinae. The relative length of the brachial plates also seems to be an important feature, but



TEXT-FIG. 2. A, *Borealis borealis s.s.* Schematic cross-section. Note the lamellar layer from inner sides of plates, continuous also between plates. Based on topotype PMO A36772 thin section 5, 9·5 mm from posterior. Juuru stage (G1–2T) Kiltsi, Estonia (× 3). B, *Pentamerus oblongus*, the smooth morphotype. Schematic cross-section. Note the wedging plate fusion to the outer shell. Drawing based on PMO 97337 thin section 3, 3·8 mm from posterior; also fig. 4 on Plate 83. Bjørkøya 'Etage 7a' (× 3).

this is difficult to observe without extremely detailed sectioning of the shell. Thin-sections through the brachial plates show that the Virgianinae have a lamellar layer extending between the plates along the shell floor, while this position is occupied by a secondary prismatic layer in *Pentamerus*. The shape of the plates shows a striking development from strongly divergent outer plates, through subparallel plates, to forms with a marked inwardly directed geniculation at the junction of the inner and outer plates.

SYSTEMATIC PALAEONTOLOGY

Family PENTAMERIDAE M'Coy, 1844
Subfamily VIRGIANINAE Boucot and Amsden, 1963

Diagnosis. (Emended herein from Boucot and Amsden 1963.) Smooth to costate Pentameracea with palintrope either absent or poorly developed. Ventral supporting septum short or absent. Brachial apparatus abbreviated, consisting of very short coplanar plates supporting the brachial apparatus. The lamellar layer on the inner sides of the plates continues along the shell without any secondary prismatic layer between the plates.

Age. Late Ordovician (Ashgill) and early Silurian (Llandovery) (Boucot and Amsden 1963).

Genus BOREALIS Boucot, Johnson and Rubel, 1971

Type species. *Gypidia borealis* Eichwald (1842, p. 74, pl. 1, fig. 14).

Diagnosis. Biconvex smooth Virgianinae, but with a deeper pedicle than brachial valve. Spondylium short and broad. Brachial plates short, outer plates divergent. A lamellar layer extends continuously from the inner sides of each plate over the intervening shell floor.

Age. Lower to Middle Llandovery (Boucot and Johnson 1964; Boucot *et al.* 1969, and Boucot *et al.* 1971).

Description. (Emended herein from Boucot *et al.* 1971.) Shells elongately subpyriform in outline, varying to more rhomboidal in some specimens which narrow from about mid-length toward the anterior. In lateral profile the valves are unequally biconvex, with the pedicle valve two to three times as deep as the brachial valve, and with a relatively prominent umbo, but stubby, incurved ventral beak. The hinge line is narrow, and the postero-lateral margins widen evenly to mid-length or beyond. Specimens with a maximum width near mid-length are less common; typical valves have their maximum width in the anterior one-third and curve around the anterior margin without lobation. The anterior commissure is rectimarginate. Radial costae are lacking but on the anterior of some specimens there may be closely spaced growth lines and inconspicuous radial furrows laterally to one, more distinct, narrow, medial furrow in both valves.

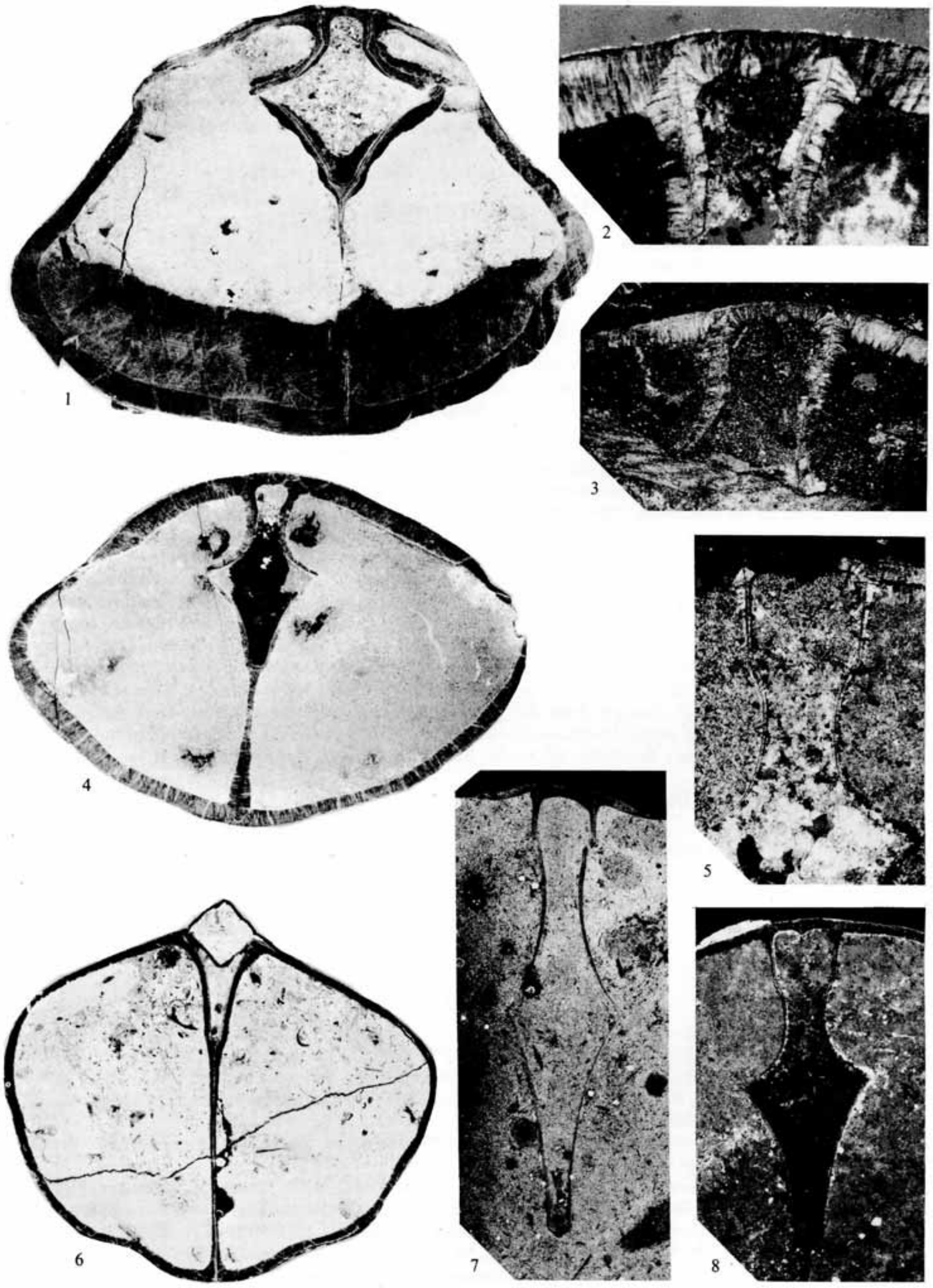
The interior of the pedicle valve bears a relatively broad, rhomboidal spondylium not supported along its whole length by the septum. The latter continues anteriorly on the valve floor past mid-length in some specimens.

EXPLANATION OF PLATE 83

Fig. 1. *Borealis borealis osloensis* subsp. nov. PMO 58550, thin section 2. 'Etage 7a', Ringerike (×4), negative print. Note the shape of the diverging plates and the broad spondylium. The lamellar layer from the plates continues along the shell floor between the plates.

Figs. 2–8. *Pentamerus oblongus* J. de C. Sowerby. 2. Detail of fig. 4 (×10). Note the plates wedging into the outer shell. 3. Smooth morphotype. PMO 97338 'Etage 7a', Skien (×10). From random section through coquina. 4. Smooth morphotype. PMO 97337, thin section 3. 3·8 mm from posterior. 'Etage 7a', Bjørkøya (×4). 5. Smooth morphotype. PMO 97339, thin section 2. 'Etage 7a', Bjørkøya (×4). (Same population as figured on Plate 85, figs. 4, 5, 6, 10, 12, 13.) 6. PMO 59127, thin section 2, also figured on Plate 85, figs. 8, 9. 'Etage 7b', Bjørkøya (×3). Note the pseudodeltidium on the top of the spondylium. 7. Same as fig. 6. Thin section 8 (×4). Note the long outdrawn plates and spondylium. 8. Same as fig. 5 (×6). Shape of spondylium and brachial plates.

PLATE 83



MØRK, *Borealis* and *Pentamerus*

The shell is strongly thickened posteriorly so that the umbonal cavities are almost obsolescent. In the brachial valve the outer plates are short and subparallel from the apex to their distal ends. Sections through the brachial valve show that inner and outer plates are of approximately the same length. The brachial plate lamellar structure also continues between the plates, and the plates do not wedge into the outer shell as in *Pentamerus*. The rodlike brachial processes continue anteriorly for a short way beyond the brachial plates.

Borealis borealis (Eichwald, 1842) *sensu strictu*

Plate 84, figs. 1–8; text-fig. 2A

1842 *Gypidia borealis* Eichwald, p. 74, pl. 1, fig. 14.
1860 *Pentamerus borealis* (Eichwald); Eichwald, p. 789.
1970 *Pentamerus borealis* (Eichwald); Rubel, p. 17, fig. 6, pl. 5; figs. 8–14, pl. 6; figs. 1–10, pl. 7; figs. 1–21.
1971 *Borealis borealis* (Eichwald); Boucot, Johnson and Rubel, p. 274, pl. 3, figs. 1–11.

Material. Topotype, PMO A36771, plastic cast, 4 thin sections and 4 acetate peels from Estonia, Kiltsi, Juuru Stage (G1–2T). Topotype, PMO A36772, plastic cast, 8 thin sections and 4 acetate peels. Estonia, Kiltsi, Juuru Stage (GT–2T) (text-fig. 2A, Pl. 84, figs. 1–3). Also from Estonia, PMO A36773 (Pl. 84, figs. 4–6) and PMO A36774–7.

Description. (partly based on Rubel 1970). Biconvex shells of medium size, but pedicle valve 2–3 times more convex than brachial valve. The lateral margin is long and more or less tapered posteriorly. Greatest width is in the anterior third of the specimens. The surface of the shell is smooth, often with closely spaced growth lines, especially in the anterior part. The pedicle valve is strongly convex with a short, strongly curved umbo impressed against the brachial valve. Some specimens show a small median sulcus or small sulcae in the anterior part of the shell. The delthyrium is triangular and open. Small hinge teeth occur on the immediate continuation of the delthyrial margin. The spondylium is long, curving weakly dorsolaterally and with a flat, rhomboidal bottom. The spondylium rests on a septum, wedged into the outer shell, and is shorter than half the shell length. The extreme posterior of the shell is often thickened secondarily by prismatic calcite. The brachial valve is weakly convex and more acute posteriorly than the pedicle valve. A weak sulcus extends along the middle part of the shell and widens anteriorly. The outer brachial plates are subparallel and relatively short, while the inner plates are a little longer and diverge strongly. Rod-like brachial processes continue anteriorly from the plates. The lamellar layer of the brachial plates continues along the shell floor between the plates (without any secondary thickening by a prismatic layer). Secondary thickening by a prismatic layer is common in the posterior part of the valve.

Dimensions of specimens from Estonia (mm):

No.	*length*	*width*	*thickness*
PMO A36771	37	31	20
PMO A36772	36	29	17
PMO A36773	38	33	31

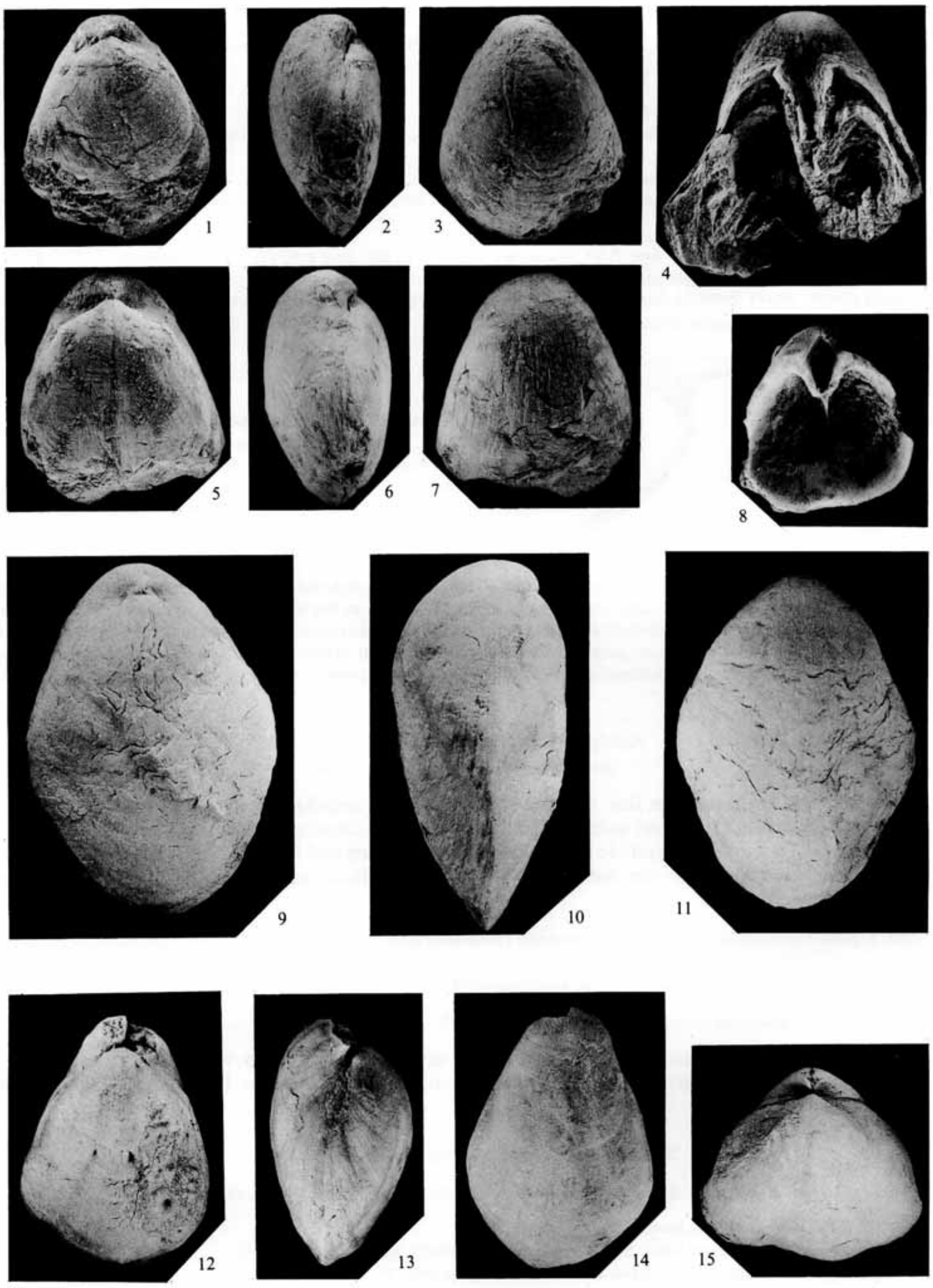
EXPLANATION OF PLATE 84

All figures natural size.

Figs. 1–8. *Borealis borealis* (Eichwald) sensu stricto. 1–3. PMO A36772. Topotype, Kiltsi, Estonia, Juuru Stage (G1–2T); this specimen is sectioned, see text-fig. 2A, and preserved as plastic cast. 4. PMO A36777. Kirimyae, Estonia, Juuru Stage (G1–2T). Inner structures of pedicle valve and spondylium. 5–7. PMO A36773. Topotype, Kiltsi, Estonia, Juuru Stage (G1–2T). 8. PMO A36776. Kirimyae, Estonia, Juuru Stage (G1–2T). Posterior part of pedicle valve.

Figs. 9–11. *Borealis borealis osloensis* subsp. nov. PMO 58553. Holotype, 'Etage 7a', Ringerike. (Also drawn by St. Joseph (1938), pl. 1, figs. 4–6.)

Figs. 12–15. *Pentamerus oblongus*, smooth morphotype. 12–14. PMO 54726, 'Etage 7a', Bjørkøya. Figured as *P. borealis*' by St. Joseph (1938), pl. 1, figs. 1–2. The convex brachial valve and plates seen through the brachial valve clearly show that this specimen belongs to the genus *Pentamerus*. 15. PMO 54834, 'Etage 7a', Bjørkøya. Figured as '*P. borealis*', by St. Joseph (1938), pl. 1, fig. 3. The plates here are also seen through the brachial valve and show that this should be assigned to *Pentamerus*.



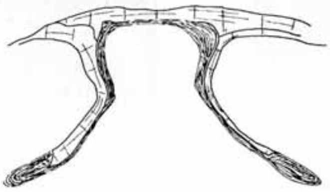
MØRK, *Borealis* and *Pentamerus*

Borealis borealis osloensis subsp. nov.

Plate 83, fig. 1; Plate 84, figs. 9–11; text-fig. 3

1908 *Pentamerus borealis* (Eichwald); Kiær, fig. 15.
1938 *Pentamerus borealis* (Eichwald); St. Joseph, p. 267, text-figs. 2, 1–4, text-fig. 3, pl. 1, figs. 4–6; pl. 5, figs. 1–4; *non* pl. 1, figs. 1–3, 7–9.
1964 Virgianidae gen. indet. Boucot and Johnson, p. 4, pl. 4, figs. 5–7.
1968 '*Pentamerus*' *borealis* (Eichwald); Gauri and Boucot, p. 105, fig. 16, pl. 10; figs. 4, 5, pl. 11; figs. 1, 2.

Holotype. PMO 58553 (Pl. 84, figs. 7–9). *Paratypes*. SMC A13502, peel series 0·15 mm intervals, 3–127. PMO 58550, 4 thin sections, 1 acetate peel. PMO 58419, 1 thin section, from Limovnstangen, also figured by Gauri and Boucot (1968). PMO 58479, 1 thin section from Svensrud, Ringerike, also figured by Gauri and Boucot (1968). PMO 58554, 2 acetate peels, from Limovnstangen.



TEXT-FIG. 3. *Borealis borealis osloensis* subsp. nov. Drawing of thin section. Note the continuous lamellar layer from the inner sides of plates which continue also along the shell floor between the plates. Figure 16*b* in Gauri and Boucot (1968). Specimens USNM No. 158526, thin section 2. 'Limåstangen', Ringerike, Oslo region.

Description. *B. borealis osloensis* is very similar to *B. borealis s.s.*, with the same plate system, diverging inner plates and *no* secondary calcite layer between the plates. It differs in the following features (in addition to its usually larger size), the shell is suboval with the greatest width at about mid-length, tapering both anteriorly and posteriorly. Folds and weak sulcae give the shell a weak trilobation, which is most pronounced in the anterior part of the pedicle valve. The umbonal cavities and sometimes the posterior part of the shell may be filled with prismatic calcite.

Subfamily PENTAMERINAE M'Coy, 1844 (ex. PENTAMERIDAE M'Coy, 1844)

Diagnosis. Moderate to large size, with smooth, costate or costellate shells generally lacking well-developed interareas; folds and sulcus absent or moderately developed. Outer plates are commonly discrete, but in a few genera unite to form a cruralium (Amsden and Biernat 1965). The lamellar layer extends continuously from the outer shell to the plates. Both septa and plates wedge into the prismatic shell layer.

Age. Upper Ordovician to Lower Devonian (Amsden and Biernat 1965).

Genus PENTAMERUS J. Sowerby, 1813

Type species. *Pentamerus oblongus* J. de C. Sowerby, 1839.

Diagnosis. Large, elongate, biconvex, relatively smooth. Spondylium and supporting septum commonly extending anteriorly less than half the length of pedicle valve. Brachial plates long and subparallel.

Pentamerus oblongus J. de C. Sowerby, 1839

Plate 83, figs. 2–8; Plate 84, figs. 12–15; Plate 85, figs. 1–16; text-fig. 2B

1813 *Pentamerus laevis* J. Sowerby, pl. 28
1839 *Pentamerus laevis* Sowerby, J. de C. Sowerby, p. 641, pl. 19, fig. 9.
1839 *Pentamerus oblongus* J. de C. Sowerby, p. 641, pl. 19, fig. 10.

1908 *Pentamerus oblongus* J. de C. Sowerby; Kiær, not figured.
1938 *Pentamerus laevis* J. Sowerby; St. Joseph, p. 274, text-figs. 4–6, pl. 1, figs. 1–3, 7–9; pl. 2, figs. 1–18; pl. 3, figs. 4–6, 10, 11; pl. 5, figs. 5, 6, 10.
1948 *Pentamerus oblongus* J. de C. Sowerby; Alexander, p. 146, figs. 1, 2.
1954 *Pentamerus oblongus* J. de C. Sowerby; ICZN, Opinion 297 (ed. Hemming).
1964 *Pentamerus oblongus* J. de C. Sowerby; Amsden, p. 225, text-fig. 1A, pl. 40, fig. 4.
1968 *Pentamerus oblongus* J. de C. Sowerby; Gauri and Boucot, p. 109, fig. 18, pl. 12; figs. 3–4.
1970 *Pentamerus oblongus* J. de C. Sowerby; Rubel, p. 19, pl. 8, figs. 1–6; pl. 9, figs. 1–6.

Material. SMC A13503, A13504.

PMO 40520, 40523, 42639, 53455a, b, c, 54697–8, 54726, 54834, 54862–3–4–5, 54945–6, 58479, 58555–6–7–8–9, 58563, 59127, 88208–9, 97810, 97812.

Smooth morphotypes 13506, 53454, 53455 (6 specimens), 97337, 97811, 97813–14.

Also many sections through specimens which show the wedging nature of plate/shell fusion.

Description. Shell often large (< 8–9 cm), oval, subpentagonal, or even sub-rounded in outline. Maximum breadth and depth often observed about half-way towards the anterior margin. Moderate folds sometimes produce trilobate forms. Hinge line short, curved. Outer surface smooth but sometimes with concentric growth lines. The outer form may vary a great deal, but small shells are commonly smooth and moderate trilobation is seen in large shells and later forms. The pedicle valve is strongly convex, with the highest part at the posterior end, and with the valve in-curved to conceal the dorsal umbo. Delthyrium small, triangular, and covered by a small pseudodeltidum at its apex. The spondylium is wide at the delthyrium but it extends anteriorly as a long narrow structure. The duplex septum supporting the spondylium is high and long and wedged into the outer shell. The valve may be thickened secondarily by an inner prismatic layer.

The brachial valve is convex with the highest point about midway to the anterior margin. The hinge line is curved and runs smoothly into the more straight sides. The outer plates are long (up to one-third of the length of the valve), sub-parallel, and with a small break at the junction with the inner plates. The plates, especially in gerontic and (stratigraphically) younger specimens form deep, narrow cardinalia, usually with the inner plates the deepest. Towards the umbo the outer plates bend to each side and grow together with the outer shell forming the umbonal cavities. The outer plates are somewhat longer than the inner plates in early forms, but longer in late forms. The lamellar layer is continuous from the plates to the outer shell. The brachial valve is usually thickened by a secondary prismatic layer along both sides of the plates and along the inner side of the shell, and the plates therefore wedge into the shell.

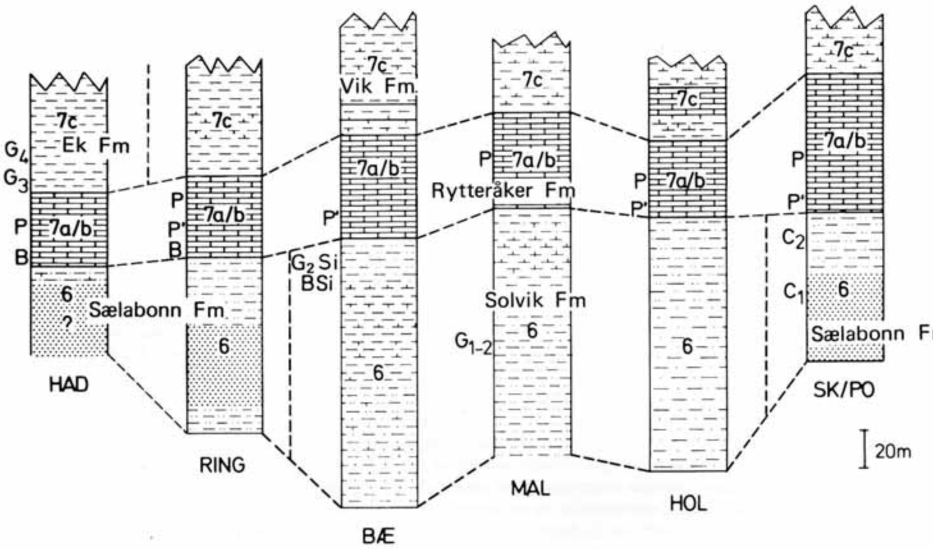
Variation. Great variation, especially in outer form, is seen both in specimens from different localities and to some degree also within each locality.

One common morphotype, here called the smooth *P. oblongus* morphotype, occurs in the lower part of the beds containing *P. oblongus* in the Oslo Region. It is usually small, with weakly developed folds. The brachial valve is only moderately convex and the shell may have almost the same width as length. The spondylium is short and is less narrow than is usual in later forms. Both brachial plates have about the same length and the outer plates do not have the characteristic strong incurving break found in later forms. The shell structure is of typical *Pentamerus* type, with wedging brachial plates, while the outer shape resembles *B. borealis*. This smooth morphotype is common on Bjørkøya, in Asker and Sandvika. Variation in trilobation and convexity is also striking. Although some variation is found within individual populations, both trilobation and especially convexity seem to increase with time.

OCCURRENCES IN THE OSLO REGION

Both *B. borealis* and *P. oblongus* are essentially confined to the Rytteråker Formation of Worsley *et al.* (1981). The relationship of this and adjacent formations to the 'Etage' nomenclature of Kiær (1908) is demonstrated in text-fig. 4.

Hadeland. Pentamerids are common in the lower part of the Rytteråker Formation (Etage 7a). In two sections, at Prestemoen (NM798817) and Svingen (NM794892), *B. borealis osloensis* occurs in a 3 to 4 m thick, massive biosparitic bank. The top of this bank shows weak erosion surfaces, and at Prestemoen *P. oblongus* is found immediately above the erosive top of the *Borealis* bank. In other sections (e.g. Gautveit NM806903) the transition from massive *Borealis* beds in the lower part of the formation to *Pentamerus*-containing limestones seems to be gradational.



TEXT-FIG. 4. Comparison of the lithostratigraphical units proposed by Worsley *et al.* (1981) with the 'Etage' nomenclature of Kiær (1908). Stratigraphically important faunal elements are noted. Broken line marks formational boundaries. HAD = Hadeland, RING = Ringerike, BÆ = Bærum and Asker, MAL = Malmøya, HOL = Holmestrand, and SK/PO = Skien and Porsgrunn districts. Fauna: B = *Borealis borealis osloensis*; P′ = *Pentamerus oblongus*, the smooth morphotype; P = *Pentamerus oblongus s.s.*; Si = *S. lens intermedia* (G. Baarli pers. comm.); G1 = *Orthograptus obuti*, G2 = *Rhaphidograptus toernquisti*; G3 = *Monograptus turriculatus*; G4 = *M. crispus*; C1 = *Icriodella* cf. *deflecta*; C2 = *Amorphognathus tenuis*.

Ringerike. Good exposures at Limovnstangen (NM692591, previously called Limåstangen), Kjellerberget (NM598618), and Vakerdalen (NM729677) all show gradational changes from beds composed of *B. borealis osloensis* (mostly pedicle valves, brachial valves are extremely rare) to beds with *P. oblongus s.s.* This agrees with Kiær's (1908) description. This transition is completed over a section of a few metres, and at Kjellerberget the smooth *P. oblongus* morphotype is found within these transitional beds. At Kjellerberget the size of the shells shows striking variation and beds rich in small specimens alternate with units with large shells. This suggests unstable life environments with appreciable post-mortem sorting and winnowing of the shells.

Bjørkøya (*Holmestrand*). Kiær (1908, p. 199 and fig. 41) gave a detailed description of the pentamerids from this locality (NL768653). He referred to specimens of *P. borealis*, transitional forms between *P. borealis* and *P. oblongus* and typical specimens of *P. oblongus*. He also points out that *P. borealis* is prolific in some beds, and these are marked on his fig. 41. St. Joseph (1938) also refers these brachiopods to *P. borealis*, and he says: '... Occasional individuals are of the characteristic, thick shelled form, but the greater number collected by the writer have a much thinner shell, and while agreeing with the typical *borealis* in shape and type of spondylium, are a little closer to *P. laevis*'. This statement is taken directly from Kiær, who also regarded these *Pentamerus* forms as transitional between *P. borealis* and what he calls the 'real' *P. oblongus* (Kiær 1908, pp. 197–201). In the present study many specimens, especially from what Kiær calls the 'Borealisschichten' have been sectioned. No fossil showing a virgianinid shell-plate structure has been found. In all the specimens from Bjørkøya the plates wedge into the outer shell and they also have the more parallel plates typical of *Pentamerus*. The outer shape of the specimens varies to some degree. Beds mostly containing the smooth morphotype may also contain specimens of more trilobate forms within the same population. Although most complete specimens are small (e.g. Pl. 85, figs. 4, 5, 6, 10, 12, 13), disintegrated valves of large specimens are common.

Specimens PMO 54726 and 54834 were figured by St. Joseph (1938, pl. 1, figs. 1–3). These specimens show traces of the plates on the outer wall of the brachial valve and therefore must be assigned to the genus *Pentamerus* and not *Borealis*. St. Joseph also figured (pl. 1, figs. 7–9) specimens with relatively convex valves and these should also be assigned to *Pentamerus* (cf. pl. 1, fig. 5 of St. Joseph and Pl. 84, figs. 9–11 herein).

Skien. Kiær (1908, p. 268) states that a few thick-shelled *P. borealis* and many thin-shelled pentamerids with the septal structure of *P. borealis* are found in the lower part of Etage 7a. New reconnaissance studies in the area have not produced any specimens which can be assigned to *Borealis*, and the forms mentioned by Kiær seem to be similar to the smooth *P. oblongus* morphotype found on Bjørkøya. In the lower part of the Sælabonn Formation (Etage 6) the conodont *Icriodella* cf. *deflecta* is found, while *Amorphognathus tenuis* occurs in the upper part of the formation. This should indicate a C_2 or older age of the strata immediately below beds with the smooth *P. oblongus* morphotype (R. J. Aldridge pers. comm).

Asker–Bærum. The first occurrence of *Borealis* was reported by Kiær (1908, p. 342) from Etage 6cβ in Asker: '... In keinem anderen Gebiete scheint die *Pentamerus oblongus*-Reihe so früh aufzutreten wie hier, und diese erste Mutation zeight denn auch in ihrem Septalbau sehr eigentümliche Verhältnisse, die zu *Stricklandinia lens* Sow. hinüberzuführen scheinen.' Kiær's allusion to the similarity of these forms to *Stricklandia lens* indicates that they had short, divergent cardinalia and there can be little doubt that these are virginianinid brachiopods.

Recent work by G. Baarli (pers. comm. 1979) shows great differences in stratigraphical thickness and also in facies in different parts of the area. At Vettre (NM663833, Asker) about 5 m above the base of Etage 6cα, she found specimens of *Stricklandia lens intermedia*, together with individuals with a well-defined spondylium. These finds seem to be overlain by 60–70 m of shales and siltstones before the boundary with 7a is seen. G. Baarli has also found graptolites in 6cβ; these include *Rhaphidograptus toernquisti*, which is known to range from the uppermost *atavus* to the lowermost *sedgwickii* Zone (M. P. A. Howe pers. comm. 1979). The well-defined spondylia in associated brachiopod specimens from Vettre show that these clearly belong to the Pentameridae. Similar Pentameridae occur in Sandvika (NM664849) from 8 to 16 m. below the base of Etage 7a. Limestones high in Etage 7a contain the typical smooth *P. oblongus* morphotype in a very similar development to the specimens from Bjørkøya. There seems to be little doubt that these finds of Pentameridae at Vettre and below the base of 7a at Sandvika refer to the same species reported by Kiær, and they are here regarded as marking the first occurrence of *Borealis* in the Oslo Region.

Malmøya. Kiær reports a ... 'sehr eigentümliche kleinen Form mit kurtzem Septen ...'. from Etage 7a. Neither Kiær nor later workers have reported any *Borealis*, although *P. oblongus* is present but not common. Kiær also reported a transition from short and wide forms with short inner structures in the lower parts of Etage 7b to longer more trilobate forms with longer inner structures higher in the succession.

PHYLOGENETIC RELATIONSHIP BETWEEN *BOREALIS* AND *PENTAMERUS*

In his monograph on the Silurian of the Oslo Region, Kiær (1908) regarded *P. borealis* as the ancestor of *P. oblongus*, and St. Joseph (1938) noted the existence of *borealis–laevis* transients. Following the introduction of the genus *Borealis*, this phylogenetic relationship is less obvious, especially as a result of the various proposals mentioned earlier.

In the Oslo Region, *B. borealis osloensis* is always found below the first occurrence of *P. oblongus*; at some localities (Limovnstangen and Hadeland) *B. borealis osloensis* and *P. oblongus* are found in continuous pentamerid-bearing sequences, but never together. The relative lack of brachial valves makes reliable identification difficult, but there is neither sedimentological nor faunal evidence for any break in deposition. (These pentamerids often occur in rocks which are difficult to disintegrate. Because of the differences in the fusion of the brachial plates to the shell, determination of either virgianids or *Pentamerus* can easily be made by sawing large blocks of rock, and then examining polished surfaces, where the nature of the plate/shell contact can be ascertained even in random sections through brachial valves.)

The existing 'Etage' nomenclature in which 7a is regarded as always being older than 7b throughout the Oslo Region implies that *P. borealis* is the zonal fossil for 7a. Both Kiær and St. Joseph reported *P. borealis* from the southern point of Bjørkøya. As already mentioned these beds do not contain any *Borealis*, but the smooth morphotype of *P. oblongus* with an outer shape similar to *B. borealis* is extremely common. The same morphotype is also found at Sandvika and in beds at the 7a to 7b transition at Kjellerberget, Ringerike. Reinvestigation of St. Joseph's (1938) material also shows that PMO 54726 and 54834, figured by him on plate 1, figs. 1-3, should in fact be assigned to *P. oblongus* and not *B. borealis*. In PMO 54834 the plates are clearly visible through the outer surface of the brachial valve and this proves the wedging nature of the plates.

Text-fig. 5 compares the different morphological features of the pentamerids discussed here. This clearly indicates that most features show gradational changes, the only significant exception being the nature of the junction between the brachial plates and the brachial valve. In the intermediate form (the smooth *P. oblongus* morphotype, '*P. borealis*' of Kiær and St. Joseph) the shell is still superficially similar to *B. borealis* but the wedging plate structure typical of *P. oblongus* has already evolved. This indicates that the transition from *Borealis* to *Pentamerus* is marked by the sudden development of forms which secreted a secondary prismatic calcite layer both inside the brachial plates and along the shell floor between the plates.

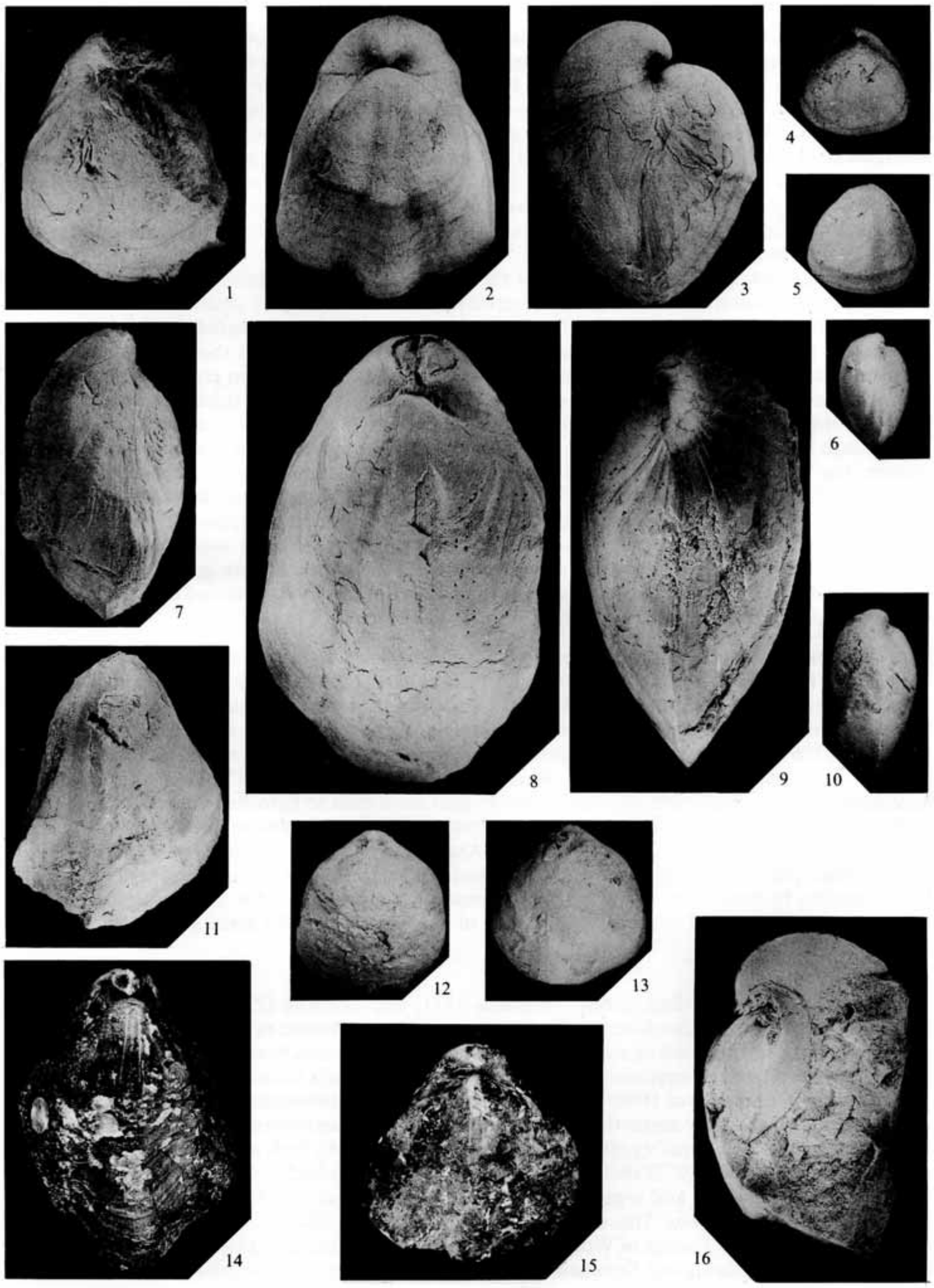
		SHAPE		SPONDYLIUM				CARDINALIA						
								relative length of plates		plates in section			plate-shell junction	
SPECIES	SPECIMENS	max. anterior width	max. median width	wide	intermediate	narrow	long, extended plates and spondylium	inner > outer	outer > inner	inner plate divergent	wide subparallell	long-narrow subparallell	continuous lamina	wedging plates
P. oblongus s.s.	Many descriptions		*			*	*		*			*		*
P. oblongus smooth morphotype	Asker, Oslo Region PMO 53455-6		*		*				?		*			*
P. oblongus smooth morphotype	Bjørkøya Oslo region PMO 97337		*		*				*		*			*
B. borealis osloensis	Ringerike, Oslo region SMCA 13502	*			*			*		*			*	
B. borealis osloensis	Ringerike, Oslo Region PMO 58550	?	?	*				*		*			*	
"P." Borealis schmidti	Siberian Platform Nikiforova & Andreeva 1961	*		*				*		*			?	?
B. borealis s.s.	Estonia PMO A36771-2	*		*				*		*			*	

TEXT-FIG. 5. Comparison of the taxonomically important criteria of the different species discussed.

EXPLANATION OF PLATE 85

All figures natural size.

Figs. 1-16. *Pentamerus oblongus* J. de C. Sowerby. 1, 7, 11. PMO 97812. 'Etage 7a', Bjørkøya. From the 'Borealisschichten' of Kiær (1908). Figured as a plastic cast. Thin sections show wedging plates. 2, 3. PMO 88208. 'Etage 7bβ', Bjørkøya. This stratigraphically late specimen shows strong convexity. 4, 5, 6. Smooth morphotype. PMO 97340. 'Etage 7a', Bjørkøya. From the 'Borealisschichten' of Kiær (1908). 8, 9. PMO 59127. 'Etage 7a', Bjørkøya. Figured as a plastic cast, thin sections, see Plate 83, figs. 5 and 7. 10, 12, 13. Smooth morphotype. PMO 97341. The same population as specimen on figs. 4, 5, 6, and Plate 83, fig. 6. 14. PMO 58558, 'Etage 7a', Bjørkøya. (Sketch by St. Joseph (1938), text-figs. 4, 2). Note the wedging plates seen on the outer side of the brachial valve. 15. PMO 53455, 'Etage 7', Sandvika. Note the traces of the wedging plates on the brachial valve. 16. PMO 58557, 'Etage 7', Bjørkøya. Section along the medial plane of the shell; both plates, the spondylium and the septum are clearly visible.



MØRK, *Pentamerus*

The wedging or lamellar fusion of the plates to the outer shell can only be investigated in thin sections or acetate peels. Few descriptions are published apart from the work of Gauri and Boucot (1968), but is is often possible to decide from published pictures or drawings which of these possibilities exist. The lamellar structure seen in *Borealis* seems to be a typical virgianinid feature and it is also found in *Virgiana* sp., *Holorhynchus giganteus* (Gauri and Boucot 1968, figs. 15*a* and 17), and *Brevilamnulella thebesensis* (Amsden 1974, pl. 1, figs. 8*b*, *c*). The wedging brachial plates typical of *P. oblongus* are also found in *P. oblongiformis* and *P. longiseptatus* (Sapelnikov and Rukavishnikova 1975, figs. 41, 42). No reports exist *either* of wedging plates in the virgianinids or of a lamellar layer in *Pentamerus*, although the inner secondary calcite layer might often be poorly developed in thin-shelled specimens of *P. oblongus*.

Although gradation in the outer shape of the shells is somewhat difficult to use as a taxonomic criterion, the gradation in form of the inner structures seems to be highly significant. The transition from short, broad cardinalia (typical of the Virgianinae) through almost parallel plates (in the smooth *P. oblongus* morphotype) to long, subparallel plates (in *P. oblongus s.s.*) shows clear gradational changes, but with distinct end members. In the pedicle valve the spondylium grows longer anteriorly with time, and the variation in shape from broad rhomboidal and relatively thick through a Y-shaped medium form to a long-drawn-out narrow spondylium in late *P. oblongus* is completely gradational.

Although Boucot and Chiang (1974) and Boucot (1975) regarded trilobation as a very important feature, the variation in degree of trilobation in the material that I have examined including a collection of *P. oblongus* from Iowa, U.S.A. (presented to me by M. Johnson), shows that this feature varies a great deal both stratigraphically and also locally within populations. In the Oslo Region small forms seem to be less trilobate, an observation also made on other material by Boucot and Johnson (1979). Trilobation is therefore not regarded as a diagnostic feature in the interpretation of the relationships of these pentamerids, and the implicit use of this by Boucot and co-workers in their erection of pentamerid lineages is in error.

Other material. Rubel (1977, fig. 6) reports *P.* cf. *oblongus* at a higher stratigraphical level than *B. borealis* and below beds containing *P. oblongus*. This may be a parallel to the situation observed in the Oslo Region. *P. borealis schmidti* Lebedev, 1892 appear to show all the features of the genus *Borealis* but the nature of the junction between the plates and the shell is not known. Nikiforova and Andreeva (1961) consider this latter species to be a subspecies of *B. borealis*, and Rubel (1970) suggests that it might be similar to *B. borealis* from the Oslo Region. The over-all size of these specimens suggests clearer affinities to the Norwegian form than to Estonian material.

P. oblongus forma *nana* Nikiforova and Andreeva, 1961 is regarded as belonging to the genus *Borealis* by Boucot *et al.* (1971). Nikiforova and Andreeva (1961) describe small oval specimens with parallel inner plates, which are always found in beds below those containing *P. oblongus*. This form may therefore be equivalent to the Norwegian smooth early morphotype of *P. oblongus*. Definite conclusions are hampered at present by the lack of suitable material for serial sectioning.

Age and correlation

Evolutionary lineages of *Stricklandia* (Williams 1951) and *Eocoelia* (Ziegler 1966) have been an important help in dating Llandovery sedimentary sequences. However, as previous publications have given only vague information on the age relationships of *Borealis* and *Pentamerus*, a review of them is presented here. Although virgianinids are regarded as being of early Llandovery age, precise data are rare. In Estonia, Boucot *et al.* (1969) report '*P*'. *borealis* in beds interbedded with *Stricklandia lens lens* or *S. lens prima*, and they argue that the *borealis* beds can be correlated within the '*Orthograptus*' *vesiculosus* or '*Pristiograptus*' *cyphus* Zone (equivalent to A_2 to A_4 beds of Wales). A revision of the stricklandiids by Rubel (1977) shows that *B. borealis* (which is found in the G_{1-2} Zone) is found at Kabala both interbedded and together with *S. lens intermedia*, and at Khelterma it occurs directly above beds with *S. lens lens*. This should indicate a correlation with A_3 to latest B_3 beds in Wales (using the evolutionary lineage of Williams 1951) or late Rhuddanian to Idwian stages (Cocks 1971, Cocks, Holland, Rickards and Strachan 1971). On the western side of the Siberian platform and to the north of the Taimyr peninsula *Virgiana* sp. occurs above graptolitic beds of the '*Pristiograptus*' *cyphus* to *Monograptus sedgwickii* Zones, and below beds containing brachiopods diagnostic of C_{1-2} or younger beds. *B. borealis schmidti* occurs in this region but its stratigraphical position is only vaguely known (Boucot *et al.* 1969).

In the Welsh Borderland, *P. oblongus* occurs throughout the Pentamerus Beds, which seem to be equivalent to the *convolutus* and *sedgwickii* Zones of the graptolite succession (Cocks and Rickards 1969). *S. lens progressa* also occurs in these Pentamerus Beds (Williams 1951).

In the Oslo region the graptolite information from the pentamerid sequences is sparse; although the find of *Rhapidograptus toernquisti* together with the first occurrence of Pentameridae (i.e. *Borealis* sp.) in Asker, and also the occurrence of *S. lens intermedia* in the same beds, is an indication of the Idwian Stage, although *R. toernquisti* has a somewhat greater range. At Hadeland ('Storskjæringa' NM841852), in the Ek Formation, *Monograptus turriculatus* occurs about 5 m above the top of the Rytteråker Formation, which contains *P. oblongus* in its upper parts. *M. crispus* (not *M. griestoniensis* as reported by Hagemann 1966) is also found higher in the Ek Formation (M. P. A. Howe pers. comm. 1978). On Malmøya, beds from the middle part of the Solvik Formation (Etage 6bβ) contain *R. toernquisti* (M. P. A. Howe pers. comm.) and *Orthograptus obuti* (Rickards and Koren, 1974). This association is also known in the Urals where additional material indicates a *cyphus* Zone age, or a little younger (Rickards and Koren 1974).

Thus information from Estonia, correlations with associated *Stricklandia*, and the few graptolite finds, indicate that the transition from *Borealis* to *Pentamerus* must have occurred not earlier than the early Idwian (*gregarius* Zone) and must have been completed by the late Idwian (*convolutus* Zone).

CONCLUSIONS

With the exception of the nature of the plate-shell junction, all features of taxonomic value show a gradational change from *Borealis* to *Pentamerus*, and they clearly indicate a direct phyletic lineage between these forms. However, this gradualistic process is punctuated (Gould and Eldredge 1977) by the appearance of forms with wedging plates. The functional significance of this development was most probably a strengthening of the shell and an even better adaption of these pentamerids to the high energy environments in which they lived. In contrast the *Pentamerus* found in marly deposits, deposited in lower-energy environments, have only a thin, weak prismatic calcite thickening. If one accepts this phyletic lineage it is clear that the *Borealis–Pentamerus* transition has important chronostratigraphical implications which are not restricted to the Oslo Region. The lineage can be used to supplement the evolutionary lineages of *Stricklandia* and *Eocoelia* in biostratigraphical studies of Llandovery shelly faunas.

STRATIGRAPHICAL IMPLICATIONS FOR THE OSLO REGION

A comparison of different localities within the Oslo Region (text-fig. 4) suggests a possible better correlation of the region's *Borealis* and *Pentamerus*-bearing beds with both the Estonian and the British type sections. The earliest occurrence of *Borealis* is seen in beds assigned to 6cβ in Asker. These beds directly overlie a coral-stromatoporoid marl facies, interpreted as a local shallow ?bank area by Mørk and Worsley (1980) because of the high algal content of the marls. The renewed deposition of sandstones and siltstones in 6cβ is accompanied by the disappearance of pentamerids from the area and the next occurrence is within the Rytteråker Formation where the *Borealis*-like morphotype of *P. oblongus* occurs. At Hadeland and Ringerike *B. borealis osloensis* occurs in banks which are directly overlain by beds with *P. oblongus*, while in Holmestrand and Skien the *Borealis*-like smooth morphotype of *P. oblongus* is the first form seen, passing upwards into populations with more usual individuals of *P. oblongus*. The only pentamerids seen on Malmøya belong to *P. oblongus s.s.*, although some smooth *Pentamerus* were reported by Kiær from his 'Etage' 7a.

Thus the pentamerid lineage proposed here demonstrates that sedimentation of the limestones of the Rytteråker Formation began first in the western area of the Oslo Region, the base of the formation younging progressively eastwards. Pentamerid communities established themselves in each district when environmental conditions permitted, and pentamerids *per se* have little time relevance; however, the particular stage reached in the evolutionary lineage can be used to show this diachronous relationship.

Studies of the continuation of the *Borealis–Pentamerus* lineage leading to *Pentamerus–Pentameroides*, as suggested by Kiær (1908) and St. Joseph (1938), are now in progress in the Oslo Region; they seem to support the continuation of the *Borealis–Pentamerus* lineage to *Pentameroides* as suggested by Johnson (1979).

Acknowledgements. Special thanks to my supervisor, D. Worsley for all his help, and to B. G. Baarli, M. G. Bassett, A. J. Boucot, and L. R. M. Cocks for information and discussion. M. P. Rubel presented topotypes of *Borealis borealis*; M. P. A. Howe identified most of the graptolites; N. Heintz translated some Russian descriptions; K. L. Kravik made most of the serial sections and P. Aas the photographic prints: all are cordially acknowledged for their help. The work was carried out at the Paleontologisk Museum, Oslo.

REFERENCES

ALEXANDER, F. E. S. 1948. A revision of the genus *Pentamerus* Sowerby 1813 and a description of the new species *Gypidula bravonium* from the Amestry Limestone of the main outcrop. *Q. Jl geol. Soc. Lond.* **103,** 143–161, pl. 7.

AMSDEN, T. W. 1964. Brachial plate structure in the brachiopod family Pentameridae. *Palaeontology*, **7,** 220–239.

—— 1974. Late Ordovician and early Silurian articulate brachiopods from Oklahoma, southwestern Illinois, and eastern Missouri. *Bull. Okla. geol. Surv.* **19,** 1–119.

—— and BIERNAT, G. 1965. Pentamerida. *In* MOORE, R. C. (ed.) *Treatise on Invertebrate Paleontology, part H.* Geol. Soc. of Amer. and Univ. of Kansas Press.

BOUCOT, A. J. 1975. *Evolution and extinction rate controls.* Developments in Palaeontology and Stratigraphy 1. Elsevier, Amsterdam, 1–428.

—— and AMSDEN, T. W. 1963. Virgianidae, a new subfamily of pentameracean brachiopods. *J. Paleont.* **37,** 296.

—— and CHIANG, KAM K. 1974. Two new lower Silurian virgianinid (family Pentameridae) brachiopods from the Nonda Formation, northern British Columbia. Ibid. **48,** 63–73.

—— and JOHNSON, J. G. 1964. Brachiopods of the Ede Quartzite (lower Llandovery) of Norderön, Jämtland. *Bull. geol. Instn Univ. Uppsala*, **42,** 1–11, pls. 1–7.

—— —— 1979. Pentamerinae (Silurian brachiopods). *Palaeontographica*, Abt. A, **163,** 87–129 pls. 1–15.

—— —— and RUBEL, M. 1971. Descriptions of brachiopod genera of subfamily Virgianinae Boucot et Amsden, 1963. *Eesti NSV Tead. Akad. Toime. Khim. Geol.* **20.** 271–280.

—— KALJO, D. and NESTOR, H. 1969. Stratigraphic range of the early Silurian Virgianinae (Brachiopoda). Ibid. **18,** 76–79.

COCKS, L. R. M. 1971. Facies relationships in the European lower Silurian. *In* Colloque Ordovicien-Silurien, Paris. *Mem. Bur. Rech. géol. Minièr.* **73,** 223–227.

—— HOLLAND, C. H., RICKARDS, R. B. and STRACHAN, I. 1971. A correlation of Silurian rocks in the British Isles. *Q. Jl geol. Soc. Lond.* **127,** 103–136.

—— and RICKARDS, R. B. 1969. Five boreholes in Shropshire and the relationships of shelly and graptolitic facies in the lower Silurian. Ibid. **124,** 213–238.

EICHWALD, C. E. 1842. *Die Urwelt Russlands durch Abbildungen erlaeutert*, **2,** 1–184, pls. 1–4, St. Petersburg.

—— 1860. *Lethaea Rossica.* **1,** 1–787, Stuttgart.

GAURI, K. L. and BOUCOT, A. J. 1968. Shell structure and classification of Pentameracea M'Coy, 1944. *Palaeontographica*, Abt. A, **131,** 79–135.

GOULD, J. G. and ELDREDGE, N. 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology*, **3,** 115–151.

HAGEMANN, F. 1966. Silurian bentonites in the Oslo region. *Norg. geol. Unders.* **242,** 44–61.

HEMMING, F. (ed.) 1954. *Opinions and declarations rendered by the international commission of zoological nomenclature*, **8,** Part 14, 179–198.

JOHNSON, M. E. 1979. Evolutionary brachiopod lineages from the Llandovery series of eastern Iowa. *Palaeontology*, **22,** 549–567, pl. 67.

KIÆR, J. 1908. Das Obersilur im Kristianiagebiete. *Skr. Vidensk Selsk. Christiania*, [for 1906], 1–596.

LEBEDEV, N. 1892. Obersilurische fauna des Timan. *Trudȳ geol. Kom.* **12,** (2), 1–49, pls. 1–3.

M'COY. 1844. *A synopsis of the characters of the Carboniferous Limestone fossils of Ireland*, 1-207, 29 pls. Dublin.
MØRK, A. and WORSLEY, D. 1980. The environmental significance of algae in the middle Llandovery succession of the central Oslo Region. *Lethaia* **13**, 339-346.
NIKIFOROVA, O. I. and ANDREEVA, O. N. 1961. Ordovician and Silurian stratigraphy of the Siberian Platform and its palaeontological basis (Brachiopods). Transactions of the AK-Union, *Geological Scientific Research Institute (VSEGEI)*, N.S., vol. 56., 1-200. [In Russian.]
RICKARDS, R. B. and KOREN, T. N. 1974. Virgellar meshworks and sicular spinosity in Llandovery graptoloids. *Geol. Mag.* **3**, 193-203.
RUBEL, M. P. 1970. *Brahkiopody Pentamerida i Spiriferida silura Estonii.* (Brachiopods Pentamerida and Spirifirida from the Silurian of Estonia.) Eesti NSV Teaduste Akadeemia Geologia Instituut, 1-75, pl. 40. [In Russian.]
—— 1977. Evolution of the genus *Stricklandia* (Pentamerida, Brach.) in the Llandovery of Estonia. *In Facies and Fauna of the Baltic Silurian*, ed. D. Kaljo, 193-212, pls 1-6. [In Russian, English summary].
SAPELNIKOV, V. P. and RUKAVISHNIKOVA, T. B. 1975. *Upper Ordovician, Silurian and Lower Devonian Pentamerida of Kazakhstan*, 1-222, pls. 1-43. Nauka, Moscow. [In Russian.]
SOWERBY, J. 1813. *The Mineral Conchology of Great Britain*. London, **1**, 73, pl. 28.
SOWERBY, J. DE C. 1839. Part 2, Organic remains, *In* MURCHISON, R. *The Silurian System*. John Murray, London, 579-765, pls. 1-37.
ST. JOSEPH, J. K. S. 1938. The Pentameracea of the Oslo region. *Norsk. geol. Tidsskr.* **17**, 225-336.
WILLIAMS, A. 1951. Llandovery brachiopods from Wales with special reference to the Llandovery district. *Q. Jl geol. Soc. Lond.* **107**, 85-136, pls. 3-8.
WORSLEY, D., AARHUS, N., BASSETT, M. G., HOWE, M. P. A., MØRK, A. and OLAUSSEN, S. 1981. The Silurian succession of the Oslo region. *Norsk geol. Unders.* (in press.).
ZIEGLER, A. M. 1966. The Silurian Brachiopod *Eocoelia hemisphaerica* (J. de C. Sowerby) and related species. *Palaeontology*, **9**, 523-543, pls. 83-84.
—— COCKS, L. R. M. and MCKERROW, W. S. 1968. The Llandovery transgression of the Welsh Borderland. Ibid. **11**, 736-782.

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Original manuscript submitted 17 March 1980

Revised manuscript submitted 31 May 1980