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DESCRIPTIONS OF BRACHIOPOD GENERA OF SUBFAMILY VIRGIANINAE BOUCOT ET AMSDEN, 1963

Introduction

The large number of papers appearing in the past twenty years dealing with the morphology, taxonomy, and evolution of the pentamerid brachiopods can be very confusing to the uninitiated reader as all of them disagree to a greater or lesser degree. This situation is basically a reflection of renewed interest in the group's morphology, and study of materials from a number of unstudied regions. The Virgianinae, as the first appearing members of the pentamerids (none is older than the Ashgillian age, however), elicit great interest as the potential stem group from which many, if not all, of the Silurian and younger groups have sprung. The present paper is another step up the ladder in our better understanding of pentamerid morphology, taxonomy, and evolution, but already Amsden, Boucot, and Johnson (in preparation) have begun study of still additional material from the New World as well as from the Old World that will permit further refinement and elaboration of the concepts expressed in the present paper.

The chief thrust of this paper is to try and unify the ribbed and smooth Ashgillian through Middle Llandoverian age shells lacking a clorindiform or stricklandiform external shape. We view the external ornament of these non-clorindiform, non-stricklandiform shells as of generic significance, but their assignment to the subfamily Virgianinae depends on internal features. However, not all of their internal features are identical, although we conclude that the overall similarity of internal structures justifies the decision to unite them within a single subfamily.

It may be of some interest to the reader to learn that the present paper is largely an outgrowth of the puzzlement over the generic identity of a few specimens of Borealis from Jämtland, collected by A. J. Boucot in 1966 and later published by A. J. Boucot and J. G. Johnson (1964) as generically unidentified smooth virgianids. After M. Rubel sent A. J. Boucot a few good specimens of Borealis from Estonia it became obvious just what the Jämtland shells were. The subsequent realization that Borealis in Estonia is restricted to Early Llandoverian age beds (Boucot, Kaljo, Nestor, 1969) made it possible to conceive of Borealis as the ancestor for the Pentamerinae of the later Silurian, giving the genus, which is restricted to northern Europe, a far greater evolutionary significance than had been previously recognized. J. Klaer (1908) realized that the Borealis types of the Oslo region graded up into Pentamerus oblongus types, but no subsequent advantage was taken of this observation until the present time.

We are indebted to H. Rozman, Geological Institute of the USSR Academy of Sciences, Moscow, for loaning and furnishing specimens of E. indigricum. Their collection numbers are indicated with the initial letters GIN No. 3573. The large collection of the genus Borealis from Estonia with the collection numbers of the Institute of Geology of the Estonian Academy (Tallinn), TAGI Br were essential to this study. The topotypes of B. nana, collected by H. Nestor in 1967, are preserved in this latter collection. We are indebted to H. Nestor for kindly furnishing these specimens. We are also indebted to Prof. G. Hemingsmoen, Oslo, for having helped A. J. Boucot collect excellent specimens of Holorhynchus from the Oslo region in 1956.
Subfamily VIRGIANINAE Boucet et Amsden, 1963

Diagnosis. Pentameridae with ventral septum of variable length; brachial valve with short inner plates, medial flanges lacking; outer plates subparallel apically.


Comparison. The short ventral septum (Pl. III, Figs 8, 11) or the absence of a septum is not a feature unique to virgianinids, as some subrianinid genera, i.e. Cymbidium, lack a ventral septum and some pentamerinids, i.e. "Lissocoelina", have a ventral spondylium and median septum thickened by a deposit of secondary shell material. Most important features of the virgianinids are seen in the brachial valve. The structure of the dorsal pseudo-interarea (Pl. VI, Fig. 2), or outer socket plates (Pl. II, Figs 6, 7) is essentially identical with the development of that structure in pentamerinids; however, the inner plates (Pl. III, Fig. 10) of virgianinids are relatively short and do not extend beyond their triangular, flattened, posterior portions (Pl. II, Figs 6, 7), whereas in Pentamerus and its relatives the inner plates curve smoothly and extend a great distance anteriorly as a pair of smoothly curving plates that merge with the outer plates which reach their greatest length in that subfamily (Pl. VI, Fig. 14). Except in E. muensteri and Virgiana sp. from Nevada the outer plates (Pl. II, Fig. 7) of virgianinids also are short, in some specimens extending a shorter distance anteriorly than the inner plates, or in some specimens extending slightly beyond them, but in no instance reaching the proportions of those plates as they are developed in the Pentamerinae. Moreover, the inner and outer plates do not join to form a smoothly curving pair of plates as is developed so characteristically in all the genera of the Pentamerinae.

Virgianinids somewhat resemble members of the Subrianinae in having short, triangular inner plates, but the inner plates of Conchidium and other subrianinids generally lack the trough dividing them posteriorly (Pl. II, Figs 5—7), and tend to be coalesced as in members of the Pentamerinae. Subrianinids and virgianinids are alike in that the inner and outer plates are commonly inclined at different angles from one another and do not join smoothly; however, virgianinids lack inner flanges. The outer plates of virgianinids tend to converge medially, somewhat in the manner of gypidulinae, whereas subrianinids typically have plates more widely divergent, and joining the dorsal floor of the valve along well defined tracks. K. L. Gauri and A. J. Boucet (1968, p. 104—108) have discussed the shell structure of the virgianinid genera. Comparison with Pentamerinae was illustrated in their Figs 7 and 8.

Genus Virgiana Twenhofel, 1914

Plate I, Figs 1—11; Plate II, Figs 1—9; Plate III, Figs 12—14; Plate VI, Fig. 15

Type species. Pentamerus barrandi Billings, 1857, p. 296; 1863; p. 316, Fig. 327.

Description. The shells are among the largest in the subfamily and are generally elongately pyriform in outline. The valves are unequally biconvex in lateral profile with a shallow but evenly curved brachial valve, and a pedicle valve two or three

Plate I

Figs 1—4. Virgiana barrandi (Billings), USNM loc. 11681. 1—3 — ventral, lateral, and dorsal views, X1.5; 4 — ventral view of pedicle valve, X1. Figs 5—11. Virgiana mayeillensis Savage, USNM loc. 11635. 5, 6 — ventral and dorsal views of internal mould of pedicle valve, X1; 7, 8 — ventral and dorsal views of internal mould of pedicle valve, X1; 9, 10 — posterior and lateral views of internal mould of shell, X1; 11 — dorsal view of internal mould of brachial valve, X2.
times as deep as the brachial valve, due mainly to the presence of a relatively prominent ventral umbo. The ventral beak is strongly incurved, but may protrude prominently to the posterior.

The external ornament consists of low, rounded costae that tend to be slightly more prominent on the mid-regions of the valves. The costae, increasing in number anteriorly, tend to form bundles.

The interior of the pedicle valve bears a short median septum and spondylium. Generally, shell material thickens the posterior part of the valve and the plates, composing the spondylium so that the spondylium and supporting septum become a single wedge-like structure, leaving a wide V-shaped groove in internal molds. In some of the largest specimens the spondylium may become relatively deep and U-shaped, extending a considerable distance to the anterior, but unsupported by an equally long median septum.

In the brachial valve, the inner plates are relatively large and triangular and do not meet at the apex. They are inclined toward the midline of the valve and supported by outer plates that are commonly of about the same length. The outer plates are nearly subparallel to the midline and to one another.

Comparison. *Virgiana* differs from *Holarhynchus* in the presence of a ventral septum and external radial costae. It differs from *Borealis* essentially in the presence of radial costae, *Borealis* being smooth, and it differs from *Platymerella* in its deeply unequally biconvex lateral profile. *Virgiana* has a much shorter median septum than *Eoconchidium.*

Species assigned to *Virgiana*

*Virgiana barrandei* var. *anticostiensis* Twenhofel, 1928, p. 206, Pl. 19, Figs 1—3.

*Pentamerus barrandi* Billings, 1857, p. 296.

*Virgiana mayvillensis* Savage, 1916.

*Virgiana major* Savage, 1916.


Genus *Platymerella* Foerste, 1909

Plate VI, Figs 6—12

Type species. *P. manniensis* Foerste, 1909, p. 70, Pl. 1, Figs 1a—d.

Description. The shells are suboval in outline, commonly elongate rather than transverse. In lateral profile the valves are slightly unequally biconvex, with the pedicle valve deeper than the brachial valve. Commonly, however, the pedicle valve is only about half as deep as the brachial, so that the resultant profile is nearly lenticular. The
xental umbo is relatively small and the ventral beak is very short and strongly incurved, protruding only very slightly further posteriorly than does the beak of the brachial valve. Both beaks are closely opposed at the hinge-line without the development of a well defined palintrope. The curvature around the margins from posterior to anterior is relatively even, so that maximum width is attained near midlength, but may occur more commonly slightly posterior to the midlength. The anterior commissure is rectimarginate.

The external ornament consists of indistinct, low, rounded costae separated by shallow, narrow interspaces. The costae increase in number anteriorly by bifurcation, and are less prominent on posterolateral flanks.

On the interior the spondylium is small and confined to the posterior part of the shell, supported by a very short median septum. In the brachial valve the brachial plates are short and subparallel.

Comparison. Platymerella differs from Holorhynchus and from Borealis in being costate. It differs from Virgiana and Eoconchidium in being relatively lenticular and in not possessing a posteriorly prominent pedicle valve.

Species assigned to Platymerella

*Platymerella manniensis* Foerste, 1909, p. 70, Pl. 1, Figs. 1a—d.

**Genus Borealis n. gen.**

Plate II, Figs 10–14; Plate III, Figs 1–11

**Type species.** *Gypidia borealis* Eichwald, 1842, p. 74, Pl. 1, Fig. 14.

**Diagnosis.** Unequally biconvex smooth Virgianinae with deep pedicle valve.

**Description.** The shells are elongately subpyriform in outline, varying to rhomboidal in some specimens which narrow from about midlength 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 posterolateral margins widen evenly to midlength or beyond. Specimens with a maximum width near midlength are less common; valves typically 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 large specimens there are a few concentric 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 in the same length by septum. The latter continues anteriorly on the valve.

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Plate III

**Figs 1–11. Borealis borealis** (Eichwald).

1—3 — ventral, dorsal, and lateral views, ×1.3, MR loc. 6, TAGI Br 3420; 4–6 — ventral, dorsal, and lateral views, ×1.3, MR loc. 19, TAGI Br 3287; 7 — dorsal view of internal mould of shell, ×1.4, MR loc. 6, TAGI Br 3421; 8 — interior of fragment of pedicle valve, ×1.5, USNM loc. 12683; 9 — dorsal view of internal mould of brachial valve, ×2, USNM loc. 12682; 10 — anterior view of fragments of umbonal portion interior of both valves, ×1.5, MR loc. 8, TAGI Br 3422; 11 — ventral view of internal mould of pedicle valve, ×1.5, MR loc. 15, TAGI Br 3423.

**Figs 12, 13. Virgiana barrandi** (Billings), USNM loc. 12153.

12 — dorsal view of internal mould of brachial valve, ×1.25; 13 — interior of fragment of pedicle valve, ×1.5.

**Fig. 14. Virgiana cf. decussatus** (Whiteaves), USNM loc. 11166. Dorsal view of internal mould of brachial valve, ×1.25.

s — ventral septum; ip — inner plates.
base past midlength in some specimens. The shells are strongly thickened posteriorly so that the umbo is nearly obsolete. In the brachial valve the outer plates are short and subparallel from the apex to their distal ends. The sections of the brachial valve show that inner and outer plates are of the same length. The rod-like brachial processes continue anteriorly, to some extent, from the brachial plates.

Comparison. Borealis differs from Platymerella, Virginiana, and Eoconchidium in lacking radial costae, although in shape it closely resembles Virginiana. It differs from Holorhynchus in the presence of a well-developed and relatively long median septum. Holorhynchus lacks a median septum. Borealis has a longer ventral septum than any of the other virginianinds except Eoconchidium muensteri and in this feature it is closer to members of the Pentamerinae. However, the brachial apparatus of Borealis is typical of the virginianinds.

Age. The known occurrences of Borealis suggest restriction to the Lower Llandoveryan (Kiaer, 1908, p. 52–57; Boucot and Johnson, 1964, Pl. 4, Figs 5–7; Boucot, Kaljo, Nestor, 1969).

Species assigned to Borealis

Gypidia borealis Eichwald, 1842, p. 74, Pl. 1, Fig. 14.

Pentamerus oblongus forma nana Nikiforova, 1961, p. 139, Pl. 24, Figs 4–6.


Genus Eoconchidium Rozman, 1967

Plate IV, Figs 1–16

Type species. E. indigiricum Rozman, 1967, p. 63, Text-figs 1, 2; Pl. 6, Figs 1–6.

Description. The shells are elongately oval in outline and unequally biconvex in lateral profile. Brachial valves are only gently curved, commonly a quarter as deep as the strongly convex pedicle valves. Brachial valves are moderately incurved at the umbo; pedicle valves have relatively prominent palpintrope and a stubby, incurved ventral beak that protrudes a short distance posterior to the hinge-line. The hinge-line is narrow and rounded, maximum width tends to be anterior to midlength, especially in pedicle valves. Neither fold nor sulcus is present on either valve. The anterior commissure is rectimarginate.

The ornament consists of relatively numerous, low, rounded or angular costae. The costae increase in number anteriorly by bifurcation and are crossed by a few inconspicuous concentric growth lines.

Internally the pedicle valve bears an elongate, rhomboidal spondylium that narrows basally to a narrow, trough-like configuration. It is supported by a long, thin median septum that apparently reaches to the anterior margin of the valve. The shells may be thickened posteriorly in various lengths and degrees.

Plate IV

Figs 1–14. Eoconchidium muensteri (St. Joseph), USNM loc. 12532.
1–3 — ventral, lateral, and posterior views of internal mould of pedicle valve, X1.5: 4 — impression of fragment of radial ornamentation, X1.5; 5 — ventral view of internal mould of pedicle valve, X1.5; 6 — dorsal view of internal mould of brachial valve, X1.5; 7 — dorsal view of internal mould of brachial valve, X1.5; 8, 9 — ventral and lateral views of internal mould of pedicle valve, X1.5; 10 — dorsal view of internal mould of brachial valve umbonal portion, X3; 11 — dorsal view of internal mould of brachial valve, X2; 12, 13 — dorsal view of internal mould and its latex replica of brachial valve, X3; 14 — latex replica of brachial valve interior, X4.
Figs 15, 16. Eoconchidium indigiricum Rozman, RIKM loc. 2.
15 — ventral view, X2, GIN No. 3573/49; 16 — ventral view of pedicle valve, GIN No. 3573/188.
In the brachial valve the brachial apparatus consists of short to moderate length inner and outer plates that extend anteriorly in a subparallel fashion, closely set along the floor of the valve. The outer plates in various lengths and degrees of development may be longer or shorter than the inner plates. The inner plates are small and triangular; their place of juncture with the outer plates at the bases of the brachial processes is not well marked. The outer plates are discrete posteriorly as in other virgianinids.

T. W. Amsden's (1964, Text-fig. 4, p. 230) serial sections of the brachial apparatus of *Eoconchidium muensteri* show that the bases of the brachial processes are circular in cross-section, emanating from near the base of the valve posteriorly. They extend anteriorly at a short distance above the base of the valve, much as in *Holorhynchus giganteus* (St. Joseph, 1938, Text-fig. 9).

**Discussion.** T. W. Amsden (1964, p. 229) thought that the internal structure of *E. muensteri* allied it with the subfamily Pentamerinace. The general configuration of the inner and outer plates does resemble the configuration of brachial plates in the subfamily Pentamerinace in general aspect, although the plates of *Eoconchidium* are relatively shorter. However, the fact that the outer plates are discrete posteriorly, forming a median trough as in other virgianinids, seems now to be conclusive evidence that *Eoconchidium muensteri* belongs to the Virgianinace and not to the Pentamerinace.

A. Nikolayev and V. Sapelnikov (1969) proposed the new genera, *Tcherskidiium* and *Proconchidium*, for *Conchidium unicum* and *C. muensteri*, respectively. To his mind the main differences between three *Conchidium*-like Ordovician virgianinids lie in their internal structures.

In many respects (Williams, 1956; Amsden, 1964; Gauri and Boucot, 1968) the lamellar layer of the brachiopod valves seems to be responsible for the valve shape as well as the internal structures. The prismatic layer corresponds to the secondary deposits of the valves, and, therefore, it stimulates the configurations dictated by the lamellar layer. If it is so, then the differences of *E. indigiricum* and *C. muensteri* in their structure of the pedicle septum (Rozman, 1967) depend on the degree of development of the secondary deposits. To use the differences in thickness of such deposits for characterizing the genera (Nikolayev and Sapelnikov, 1969) is very disputable.

As for the different development of the outer brachial plates of genera *Tcherskidiium*, *Proconchidium*, and *Eoconchidium* then that structure has been used as a character of taxonomic importance in the phylogeny of the Stricklandiidae, but on the intraspecific and intrasubspecific level (Williams, 1951; Amsden, 1966). Moreover, to T. W. Amsden (1966) it is generally difficult to distinguish the outer plates from the base of the brachial processes.

**Comparison.** *Eoconchidium* differs from all the other members of the Virgianinaceae except *Borealis* in the possession of a long ventral median septum. It differs from *Borealis* and from *Holorhynchus* in being radially costate.

**Species assigned to Eoconchidium**

*Conchidium muensteri* St. Joseph, 1938, p. 301, Pl. 5, Figs 9, 11; Pl. 6, Figs 10, 11; Text-figs 7, 10.

*Eoconchidium indigiricum* Rozman, 1967, p. 63, Text-figs 1, 2; Pl. 6, Figs 1—6.


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**Plate V**

Figs 1—9. *Holorhynchus giganteus* Kier, X1, USNM loc. 10103.

1—4—ventral, dorsal, lateral, and posterior views; 5, 7, 6—dorsal and posterior views of internal mould of brachial valve and anterior view of its latex replica; 8, 9—latex replica of interior and posterior view of internal mould of brachial valve.
Genus *Holorhynchus* Kiaer, 1902

Plate V, Figs 1—9; Plate VI, Figs 1—5

**Type species.** *H. giganteus* Kiaer, 1902, p. 68, Text-figs 1—7.

**Description.** The shells of the type species attain very large size. Pedicle valves have a rhomboidal outline; brachial valves are rounded subtringular to transversely subovale. The valves are unequally convex in lateral profile with the pedicle valve about twice as deep as the brachial valve, and with a broad, stubby umbo and short incurved beak. The shells tend to be of about the same width and length, or may be slightly transverse.

The exterior is smooth except for concentric growth lines and irregularly developed radial corrugations on some specimens. In the type species there is a shallow medial furrow on the brachial valve and an additional pair of shallow radial furrows about 30 degrees away from the midline. The anterior commissure is rectimarginate.

Internally the pedicle valve has a short, rhomboidal, posteriorly situated spondylum, unsupported by a median septum. The dorsal pseudo-interarea is flat and orthocline, consisting of a pair of triangular flat surfaces between the valve margin and the sockets. The latter are long, shallow, diverging narrow grooves. The inner plates are relatively large and triangular, diverging anterolaterally and converging toward the base of the valve. Their dorsal edges lie close to the base of the valve where they are attached to rod-like brachial processes that either lie on the floor of the valve or may be elevated on very short, low outer plates. The outer plates are not present on small shells in which there is some thickening in the umbonal cavities; but in most large specimens they attain a length of about 3 to 10 mm. Commonly they diverge slightly anteriorly and converge slightly toward the base of the valve. In one specimen the shell material at the base of the valve is continuous between the outer plates, forming a sort of sessile cruralium, reminiscent of the structure developed in some gypidulinds.

**Comparison.** *Holorhynchus* differs from other virgianinid genera in lacking a median septum in the pedicle valve. The only other smooth virgianinid, *Borealis*, has a relatively well developed ventral septum. *Platymerella*, *Virgiana*, and *Eoconchidium* differ, in addition, in being radially costate.

**Species assigned to Holorhynchus**


*Holorhynchus giganteus* Kiaer, 1902, p. 68, Text-figs 1—7.

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Plate VI

Figs 1—9. *Holorhynchus giganteus* Kiaer, USNM loc. 10103.

1, 2 — dorsal view of internal mould of brachial valve and its latex replica, ×1.5; 3, 4 — dorsal view of internal mould of brachial valve and its latex replica, ×1.5; 5 — ventral view of internal mould of pedicle valve, ×1.5.


6—9 — ventral, lateral, anterior, and posterior views, ×1.5, USNM loc. 11660; 10 — ventral view of internal mould of pedicle valve, ×3, USNM loc. 12847; 11 — posterior view of internal mould of shell, ×2, USNM loc. 12681; 12 — posterior view of internal mould of shell, ×3, USNM loc. 12847.

Fig. 13. *Virgiana mayviellensis* Savage, USNM loc. 11635. Dorsal view of internal mould of brachial valve, ×2.

Fig. 14. *Pentamerus* sp., ×1, USNM 156219. Interior of brachial valve for comparison (see Amsden, Boucot, Johnson, 1967, Pl. 107, Fig. 1).

pii — pseudo-interarea.
Appendix of localities

MNVI loc. 65 (see Myahkova et al., 1963, Text-fig. 1)
Left bank of the River Moiero, 2.5 km downstream from the first rapid Moierokan, Siberia. Llandoveryian. Coll. by H. Nestor, 1967.

MR loc. 6 (see Rubel, 1970, Text-fig. 1)

MR loc. 8 (see ibid.)

MR loc. 15 (see ibid.)

MR loc. 19 (see ibid.)

RIKM loc. 2 (see Rozman et al., 1970, Text-fig. 5, 6II)
Left bank of the River Sakinndga, near junction of brook Us, Selenniakh Range.

USNM loc. 10103

USNM loc. 11166

USNM loc. 11635

USNM loc. 11660
Upper half of Brassfield Fm. at Ohio Brush Creek Bridge on state rte. 41, Adams Co., Ohio. Coll. by Summerson (loc. 5), 1963.

USNM loc. 11681

USNM loc. 12153

USNM loc. 12532
About 4 km NW of Skien, 100 m due W. of road bridge across the railroad and 760 m. SE of the station Hoppestad, Norway. Stage 5b. Coll. by A. M. Ziegler, 1965.

USNM loc. 12681

USNM loc. 12682

USNM loc. 12683

USNM loc. 12684
Loose block from Lime Island Fm. in field on Kalbsfleisch Farm, NE1/4 of NE1/4 of sec. 6, T. 41N., R. 17W Schoolcraft Co., Michigan. Coll. by A. J. Boucot, 1962.

USNM loc. 12847
USNM loc. 12886


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ALAMSSUGUKONNA VIRGIANINAE BOUCOT ET AMSDEN, 1963 PEREKONDADE KIRJELDUSED


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ОПИСАНИЯ РОДОВ БРАХИОПОД ИЗ ПОДСЕМЕЙСТВА VIRGIANINAE BOUCOT ET AMSDEN, 1963
