

LOUIS LILJEDAHL

SILURIAN
SILICIFIED BIVALVES
FROM GOTLAND



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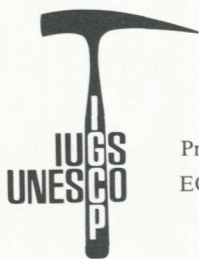
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ABSTRACT

Liljedahl, Louis, 1983: Silurian silicified bivalves from Gotland. Sveriges Geologiska Undersökning, Ser. C. No. 804, pp. 1-82. Uppsala 1984.

Eleven Homerian (Wenlockian, Silurian) species of Bivalvia are treated. Five of these are described as new and three are treated under open nomenclature. Four new genera are described. The unusually well-preserved material made it possible to reconstruct the anatomy of the soft-parts with bearing on the life position and life habit of most taxa. In most species the morphological variation is documented by a fair statistical material. The protoconch shape and size of *Nuculoidea lens* Liljedahl and *Nuculodonta gotlandica* Liljedahl are discussed. The diagnosis of the Strabinae Prantl & Růžicka, formerly referred to the Ctenodontidae Wöhrmann but now assigned to the Mallettiidae Adams & Adams, is emended and includes the new genus *Palaeostraba*. *Caesariella* n.gen. shows some resemblance to all three nuculoid superfamilies and its systematic position is therefore uncertain. The oldest known solemyoid, *Janeia silurica* n.sp., extends the stratigraphic range of the order Solemyoidea into the Silurian. *Freja fecunda* n.gen. and n.sp., an intermediate between Cyrtodontacea and Arcacea, is possibly related to Cardiolacea as well. A few fragments of *Mytilarca?* sp. are described. *Molinicola gotlandica* n.gen. and n.sp. shows striking external similarities to *Pteronitella retroflexa* (Wahlenberg), the generic identity of which is considered in connection with pterineid origin. The generic affinity of *Goniophora* Phillips is discussed and *Goniophora onyx* n.sp. is distinguished. *Maminka* sp. is the oldest representative of the genus and the first one in which the interior is known.

INTRODUCTION

When Hede (1927a:35) described the limestone at Möllbos 1, he found no bivalves and as a whole considered the fossil content fairly poor. Today extraction of silicified fossils in large quantities through etching is made from a number of localities in Gotland abounding in well-preserved, silicified organism remains, the limestone of Möllbos 1 being the most prolific. Due to the efficiency of the method the fossils are recovered in great numbers to be studied externally as well as internally, and in many cases the shells are extremely well-preserved, minute, rarely preserved details may be observed (Liljedahl 1981). Almost the whole fauna is thus obtained, viz. organisms with carbonatic hard parts and organisms with phosphatic and chitinous hard parts. The limestone at Möllbos 1 (for geographical location see Appendix), contains a highly diversified fauna (see Liljedahl 1983) including eleven bivalve species. Two of these were described in a recent paper (Liljedahl 1983) while the rest will be treated below.

More than 60 bivalve species have been reported from Gotland (among others by Hisinger 1837, Lindström 1880, 1888, Munthe 1921, Hede 1921, 1925, 1927a, 1927b, 1928, 1933, 1936, 1940, 1960, and Soot-Ryen 1964). The present paper contains 11 recorded taxa, of which 8 species and 5 genera are new, which might seem disputable. However, with only two exceptions, the bivalves of Gotland

have not been critically investigated: Walmsley (1962) redescribed and discussed the identity of *Pteronitella retroflexa* (Wahlenberg). The second study is that of Soot-Ryen (1964). Prior to her work only two nuculoid species were recorded from Gotland, *Nuculoidea pinguis* (Lindström, 1880) and *Praectenodonta sulcata* (Lindström, 1880). Soot-Ryen accounted for 16 nuculoid species assigned to 8 genera; 9 species and 3 genera were new. Four new species were based upon a single specimen each and further 2 species on three and four specimens, respectively. The interior of three of these species is unknown. In the present paper the descriptions of the bivalve taxa from Möllbos are based on both external and internal features and most of them on well-preserved and statistically well-documented material.

When examining the prodigiously well-preserved fauna at Möllbos, one is encountered by the delicate problem that it is often futile to compare the specimens with already named taxa whose interior is unknown. Diagnostic features of most Palaeozoic bivalves are poorly known, non-silicified material from Gotland being no exception, and the generally accepted systematics are defective and in many cases not applicable to well-preserved material.

The immense number of bivalves from this locality, now exceeding 3400 determinable valves, provides a framework for statistical treatment unusual with Palaeozoic macrofossils. In a forthcoming paper this bivalve fauna will be subjected to palaeoecological analyses.

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MATERIAL

The silicified specimens of this study are deposited in the collections of the Museum department of the Geological Survey of Sweden, Box 670, S-252 36 Uppsala, Sweden. Data on measured specimens are kept together with the material. For further information and geographical location of Möllbos 1 see the Appendix.

SYSTEMATIC ATTRIBUTION

Class BIVALVIA LINNEAUS, 1758
 Subclass PALAEOTAXODONTA KOROBKOV, 1954
 Order NUCULOIDA DALL, 1889
 Superfamily NUCULACEA GRAY, 1824
 Family NUCULIDAE GRAY, 1824

Genus *Nuculoidea* Williams & Breger, 1916

Nuculoidea lens Liljedahl, 1983

Figs. 1, 2, 3, 4, 5, 34:1

(see Liljedahl 1983 for detailed description)

Superfamily ?

Family ?

Genus *Nuculodonta* Liljedahl, 1983

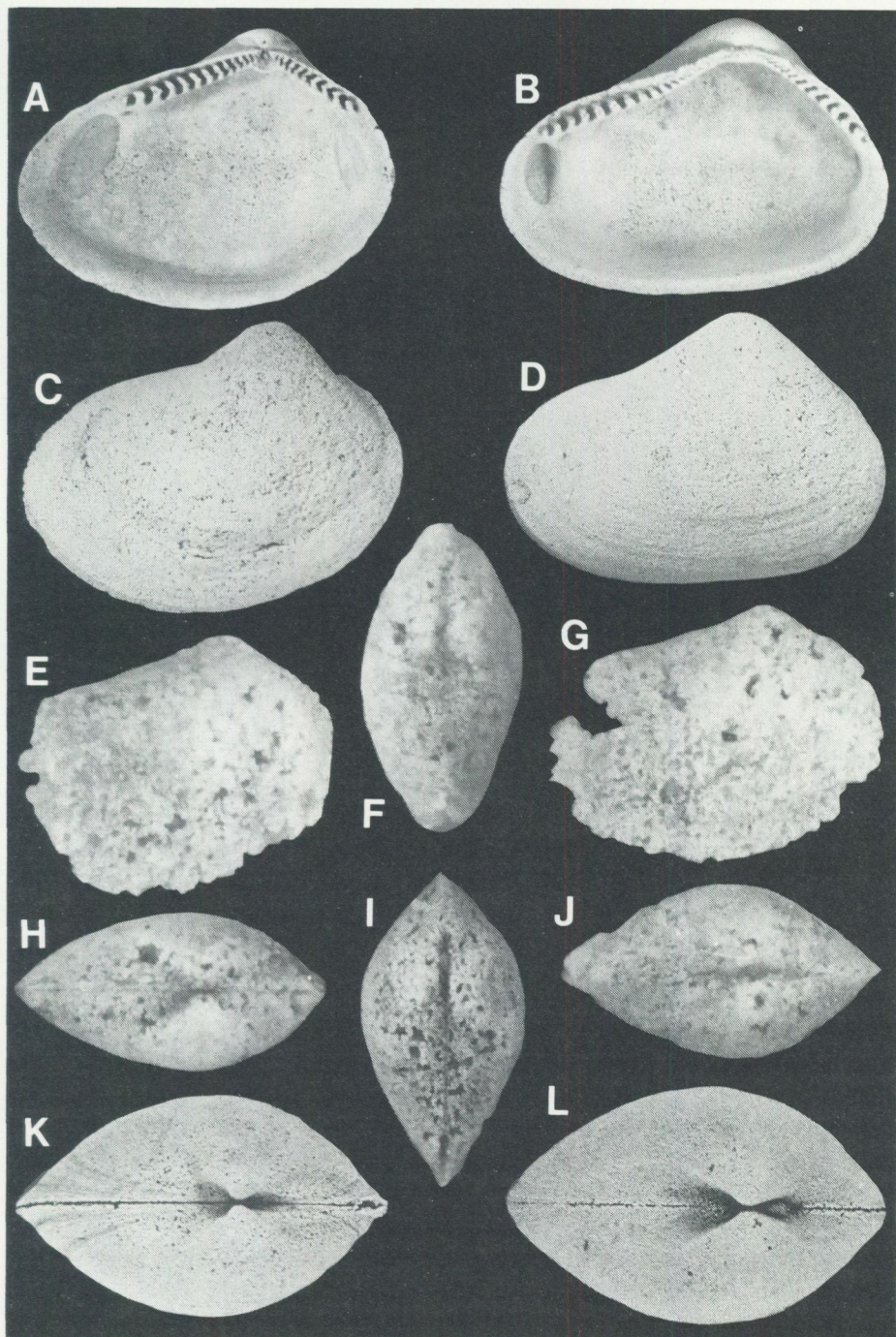
Nuculodonta gotlandica Liljedahl, 1983

Figs. 1, 2, 3, 4, 5, 34:2

(see Liljedahl 1983 for detailed description)

The systematic position of *Nuculodonta gotlandica* is difficult to evaluate since the species has characters in common with each of several nuculoid superfamilies established in the *Treatise on Invertebrate Paleontology* (Newell 1969) i.e. elongated anterior end (as in Nuculacea), external and internal ligament (as in Nuculacea and Nuculanacea). *Nuculodonta gotlandica* resembles *Nuculoidea lens* in the general shape of the shell (Fig. 1) and in muscular impressions, but differs from it in dentition and ligament construction (Liljedahl 1983; see also Fig. 1).

Fig. 1. A. *Nuculoidea lens* Liljedahl, internal lateral view of holotype (right valve); SGU Type 842, $\times 3.3$, sample G77-28LJ. B. *Nuculodonta gotlandica* Liljedahl, internal lateral view of holotype (left valve, reversed here); SGU Type 1056, $\times 4.1$, sample G77-28LJ. C. *N. lens*, external lateral view of left valve; SGU Type 890, $\times 3.6$, sample G78-2LL. D. *N. gotlandica*, external lateral view of left valve; SGU Type 1036, $\times 4.4$, sample G78-2LL. E. *N. lens* or *N. gotlandica*, external lateral view of articulated specimen, anterior to the left; SGU Type 1722/1723, $\times 25$, sample G77-28LJ. F. *N. lens* or *N. gotlandica*, dorsal view of articulated specimen, anterior downwards, same specimen as in E, $\times 23$. G. *N. gotlandica*, external lateral view of articulated specimen, anterior to the left; SGU Type 1861/1862, $\times 22$, sample G78-1LL. H. *N. lens*, dorsal view of articulated specimen, anterior to the left; SGU Type 2043/2044, $\times 17$, sample G79-78LJ. I. *N. gotlandica*, dorsal view of articulated specimen, anterior downwards; SGU Type 1859/1860, $\times 18$, sample G78-1LL. J. *N. gotlandica*, dorsal view of articulated specimen, anterior to the left; same as G, $\times 22$. K. *N. lens*, dorsal view of articulated specimen, anterior to the left; SGU Type 2049/2050, $\times 4.3$, sample G79-78LJ. L. *N. gotlandica*, dorsal view of articulated specimen, anterior to the left; SGU Type 2167/2168, $\times 4$, sample G79-79LJ.



In the first paper on silicified bivalves from Möllbos (Liljedahl 1983) some 371 valves of *Nuculoidea lens* and *Nuculodonta gotlandica* were included. The total number of valves of these two species is now more than 2400. A considerable number of small specimens, shorter than 3 mm, are available and will therefore be accounted for and the discussion on the shell first formed, the prodissoconch, of *N. lens* and *N. gotlandica* will be resumed (see Liljedahl 1983).

The prodissoconch of living bivalves (generally 0.2–0.6 mm long) is equivalve and equilateral and the external characters are usually insufficient for comparison between different taxa (LePennec 1978:31, 211). However, Drew (1901:340) observed a clear difference in the shape of the prodissoconch between the extant *Nucula* and *Yoldia*. When the primitive hinge structure exhibits the first real hinge teeth it has developed sufficient characters to make it possible to determine with certainty which family it belongs to (LePennec 1978:212). Not until the shell has reached 2–3 mm in length does it start to assume the shape of the adult. At this stage the number, form and disposition of the hinge teeth may reveal which species it belongs to (LePennec 1978:213).

It is difficult to distinguish the smallest shells of *N. lens* from those of *N. gotlandica*. Single valves of adults, with their interior visible and well-preserved, show a hinge structure which differs markedly in the two species (Fig. 1). With decreasing size it becomes more difficult to discern the hinge teeth, because of the relatively coarse-grained silicification in shells less than about 3 mm in length. However, the conspicuous external ligament in *N. gotlandica* (Fig. 1:I,J) generally enables articulated specimens 2.0 mm long to be identified. Smaller shells (Fig. 1:E,F) lack diagnostic characters as far as the silicified material is concerned.

Fig. 2 shows the height/length ratio of shells of both *N. lens* and *N. gotlandica* shorter than 3 mm. 32 valves of *N. lens* exhibit a mean H/L ratio of 0.87 while the mean H/L ratio of 34 shells of *N. gotlandica* is 0.82. There is an obvious change in shape with increasing size, which is clearly seen when these values are compared with the H/L ratios of shells of *N. lens* that are more than 3 mm in length (0.79) and *N. gotlandica* (0.72). The shells change in outline from almost circular to ovate that is more pronounced in the latter species (see Liljedahl 1983, Figs. 6 and 11).

The highest H/L ratio for *N. lens* is 1.0 in a specimen 2.2 mm long, and almost circular in outline. The smallest identifiable shell of this species is 1.8 mm long. The maximum H/L value for *N. gotlandica* is 0.95, this too, of course, resulting in an almost circular shape. The smallest identifiable specimen of this species is 1.5 mm long.

88 articulated valves less than 3 mm in length lack specific features, although they show close resemblance to the two species in question when compared with other taxa. The mean H/L value of these shells is 0.82, with a maximum of 0.91 and a minimum of 0.72.

As previously suggested (Liljedahl 1983) the first shell of both *N. lens* and *N.*

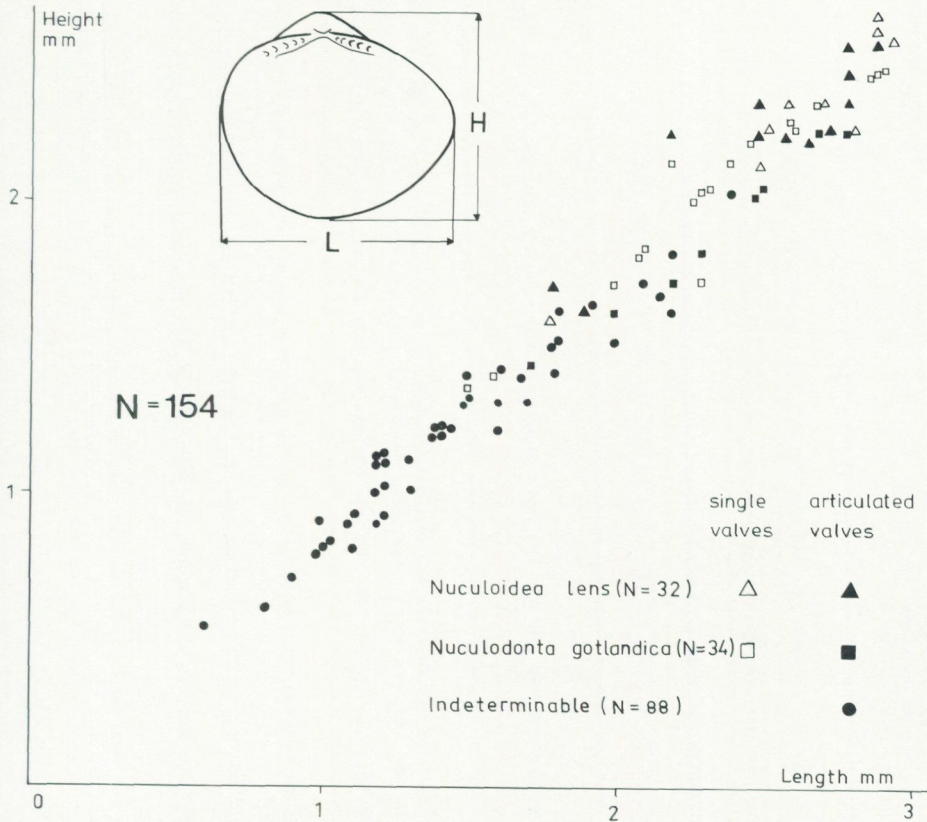


Fig. 2. *Nuculoidea lens* Liljedahl and *Nuculodonta gotlandica* Liljedahl showing height/length relation of shells less than 3 mm in length (for discussion see p. 8; see also Liljedahl 1983 treating larger shells).

gotlandica was probably almost circular in outline. Since the smallest specimen recorded measures 0.55 mm in length I believe that the protoconch of these two nuculoids was at most 0.5 mm long.

FUNCTIONAL MORPHOLOGY AND LIFE HABIT – In extant bivalves an anteriorly expanded shell generally indicates an enlarged foot and a rapid burrowing habit (Stanley 1970:66). The orientation of *N. lens* is discussed by Liljedahl 1983, the two main criteria for orientation being the point of maximum opening of the valves indicating the site of pedal emergence and the arrangement of pedal muscle traces. A reconstruction of the foot was thus possible (Fig. 3:A).

The relative values of length, height and breadth, constituting the bivalve shell form, were compared by Stanley (1970, Fig. 25) to show the relation of burrowing rate to gross shell shape. Most values of *N. lens* (Fig. 4) are within the region of slow burrowing, the exception being one juvenile specimen.

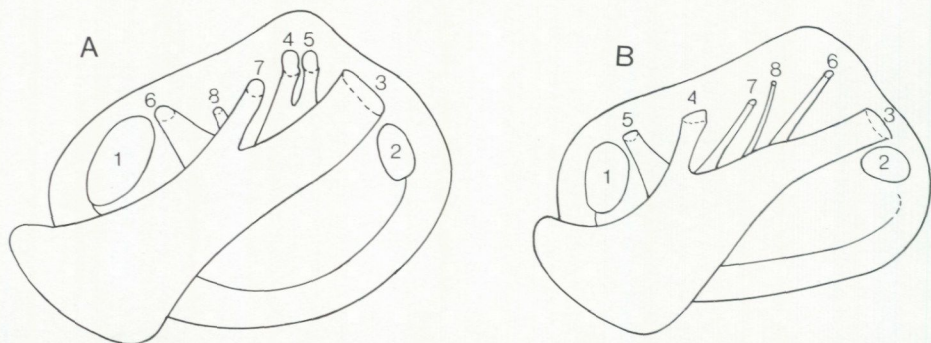


Fig. 3. Reconstruction of the foot and its muscles. A. *Nuculoidea lens* Liljedahl. B. *Nuculodonta gotlandica* Liljedahl (for discussion see p. 9, 10).

Compared with other species from the same locality *N. lens* has a relatively thick shell. This generally indicates a slow rate of locomotion (Stanley 1970:61). The outer shell surface, characterized by vague concentric growth lines, is not necessarily an indication of rapid burrowing (which is usually the case with smooth shells) since there are slow burrowers that have little or no ornamentation (Stanley 1970:62). However, the inferred extremely large foot of *N. lens* suggests, in analogy with living nuculoids, a moderately rapid burrowing habit (Stanley 1970:67).

The similarity in gross shell morphology and size, form and arrangement of the muscular impressions between *N. lens* and extant *Nucula* s.s. speaks in favour of a similarity in soft-part anatomy, i.e. *N. lens* was probably a protobranch deposit-feeder. Furthermore there are no indications of any siphons, *N. lens* being thus considered a non-siphonate species (Fig. 34:1).

The recent *Nucula delphinodonta* (Mighels) "... normally feeds beneath the surface of the mud ..." (Drew 1901:314), like other species of the genus (Yonge 1941:83). The feeding depth of extant *Nucula proxima* is 2–22 mm (mean c. 8 mm) below the sediment surface (Levinton 1977:204). There is no reason to assume that *N. lens* differed notably in life habit from that of extant *Nucula* s.s.

Nuculodonta gotlandica is anteriorly extended which, together with a distribution pattern of muscular imprints of the foot similar to that in *N. lens* although the incisions in the former are more delicate (Liljedahl 1983), suggests a large foot (Fig. 3:B) and a moderately rapid burrowing (Stanley 1970:66).

In Fig. 4 (cf. Fig. 25 in Stanley 1970) *N. gotlandica* lies within the region of slow burrowing (except for one juvenile specimen). The shell of *N. gotlandica* is thick compared with that of the other species at Möllbos, even thicker than that of *N. lens*. The heavily impressed adductor muscle scars of *N. gotlandica*, especially the anterior one, indicate powerful closure of the valves, probably more so than in *N. lens*. This is also indicated by the difference in shell margin contact between the

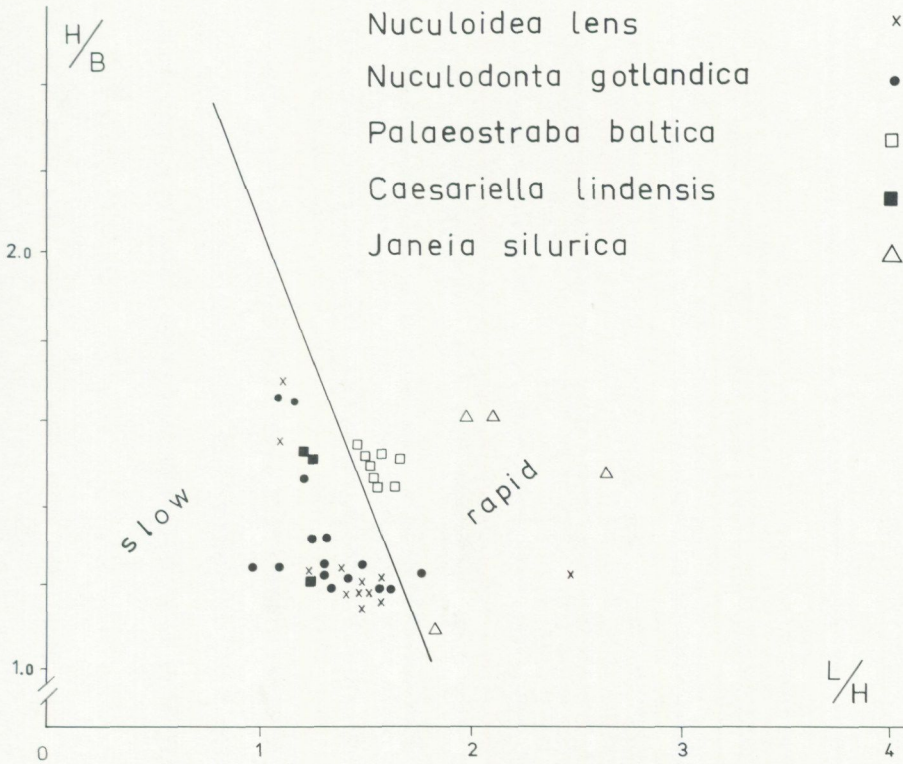


Fig. 4. Shell shape related to burrowing rate (after Stanley 1970, Fig. 25).

two species, the outermost edge of the shells of *N. gotlandica* meeting with a larger shell margin contact compared with *N. lens* (Fig. 5). The hinge teeth of *N. gotlandica* extend over almost 90% of the total length of the shell while the corresponding value for *N. lens* is only about 70% (see Liljedahl 1983). This condition reflects more secure closure in *N. gotlandica*, where environmental lateral shearing forces were more efficiently counteracted by a greater number of hinge teeth.

The shell sculpture of *N. gotlandica* consists of faint commarginal growth lines. As argued for *N. lens*, the smooth external surface does not necessarily indicate rapid burrowing. Rather, all features taken together imply that the life position of *N. gotlandica* was just beneath the sediment while *N. lens* moved somewhat deeper and more rapidly (Fig. 34:1,2).

Whether *N. gotlandica* was a siphonate form or not is difficult to say because of the diffuse posterior continuation of the pallial line (see Liljedahl 1983), but since this species dominates the bivalve fauna at this locality it was presumably non-siphonate (Liljedahl in prep.). Morphological similarities with extant nuculoids suggest that it was a protobranch deposit-feeder.

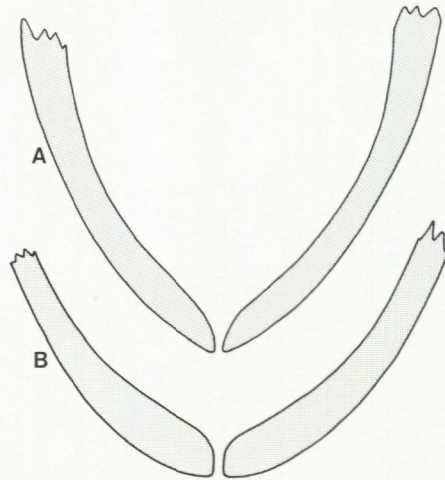


Fig. 5. Vertical sections of shell margin contact. A. *Nuculoidea lens* Liljedahl. B. *Nuculodonta gotlandica* Liljedahl (for discussion see p. 11).

Superfamily NUCULANACEA ADAMS & ADAMS, 1858

Family MALLETIIDAE ADAMS & ADAMS, 1858

Subfamily STRABINAE PRANTL & RŮŽIČKA, 1954

DISCUSSION OF SYSTEMATIC POSITION – In 1954 Prantl & Růžička identified a new subfamily, Strabinae, of the family Ctenodontidae Wöhrmann, 1893. This subfamily, containing the genera *Straba* and *Palaeostraba*, was based on the new genus *Straba* Prantl & Růžička, 1954 from the Devonian of Bohemia. *Straba* is closely related to *Palaeostraba* n.gen. However, since *Palaeostraba baltica* n.sp. is considered to be a siphonate form with an outer ligament only the subfamily Strabinae is placed in the family Malletiidae Adams & Adams, 1858.

EMENDED DIAGNOSIS OF STRABINAE – Shell small, characterized by unequal dentition of right and left valves; in the left valve anterior teeth continue into posterior teeth, most proximal tooth of posterior hinge plate either conspicuously enlarged, usually subcircular, or equalling adjoining minute teeth of both hinge plates: in the left valve anterior teeth separated from posterior teeth by a socket corresponding to tooth of opposite valve; remaining teeth usually simply, more rarely compoundly broken or straight; hinge plate under umbo interrupted so that anterior and posterior hinge plates form an obtuse angle; anterior and posterior internal septa present or wanting; lunule and escutcheon lacking; external, opisthodetic ligament, possibly initial stage of an additional internal part.

TYPE GENUS – *Straba* Prantl & Růžička, 1954.

GENERA – *Straba* Prantl & Růžička, 1954.

Palaeostraba n.gen.

OCCURRENCE – Silurian of Gotland and Devonian of Bohemia.

Genus *Palaeostraba* n.gen.

DERIVATION OF THE NAME – Latinized Greek *palae-*, ancient, compounded with the earlier established generic name *Straba*.

TYPE SPECIES – *Palaeostraba baltica* n.sp.

SPECIES – Monotypic at the time of description.

DIAGNOSIS – Strabinae with slightly elongated posterior end, distinct anterior internal septum and less conspicuous posterior septum; central tooth and socket extremely small like adjoining anterior and posterior teeth; oblique external sulcus extending from postero-umbonal slope to postero-ventral margin.

Palaeostraba baltica n.sp.

Figs. 4, 6, 7, 8, 9, 34:3

DERIVATION OF THE NAME – Latin *Balticus*, referring to the Baltic Sea where Gotland is situated and where the species was first recorded.

HOLOTYPE – One complete left valve, SGU Type 3498 from sample G78-2LL, Figs. 8:B,D,E. Length 12.9 mm, height 8.6 mm, breadth 2.9 mm. Several growth inhibition furrows on the exterior; hinge teeth not perfectly preserved, somewhat diffuse just below the beak.

TYPE STRATUM – Halla Beds, Homerian, Late Wenlockian, Silurian.

TYPE LOCALITY – Möllbos 1, Gotland, Sweden.

MATERIAL – 25 valves, 2 of which are articulated (measurements and terminology on Fig. 6).

DIAGNOSIS – As for the genus.

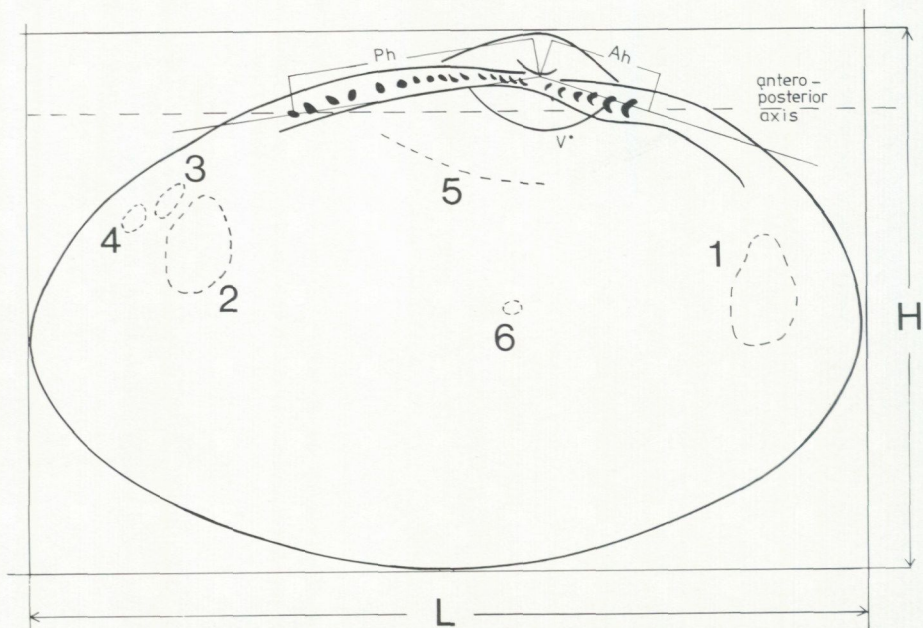


Fig. 6. *Palaeostraba baltica* n.gen. and n.sp. Left shell with antero-posterior axis (ap) running through most distal tooth in each hinge plate. L = total length of shell. H = total height of shell. Ah = length of anterior hinge plate, Ph = length of posterior hinge plate. V° = hinge angle. Muscular impressions: 1 = anterior adductor muscle scar. 2 = posterior adductor muscle scar, 5 = attachment for visceral floor?, 3, 4 and 6 = doubtfully traces of muscles (for discussion see p. 16).

EXTERNAL FEATURES – Shell small, ovate, equivalve (Fig. 8:C), subequilateral, moderately inflated, margins even, no gap present. In Fig. 7 the height and breadth are related to the total length of the shell. Because of the scarcity of the material, 25 valves only, 8 of which are measurable, variation is difficult to estimate, but seems to be slight; external opisthodetic ligament; faint commarginal growth lines sometimes with growth increment furrows; beaks minute, close together, slightly prosogyrate, extending a little beyond sagittal plane, in anterior half of shell; maximum convexity somewhat anterior to mid-length and slightly above mid-height of shell; no lunule, no escutcheon; dorsal margin convex; anterior margin strongly rounded; posterior margin narrow; ventral margin long with about same convexity as dorsal margin with its deepest point at mid-length of shell; sulcus from posterior side of umbo obliquely postero-ventral to ventral part of posterior margin (Fig. 8:D), possibly indicating the presence of siphons (cf. corresponding shell features in extant siphonate forms).

INTERNAL FEATURES – Hinge line convex, anterior hinge plate (Ah) short, broad and lobate, about 1/10 of total length of shell; posterior hinge plate (Ph) long, about 4/10 of total length of shell and narrow; the relation Ah/Ph equalling the

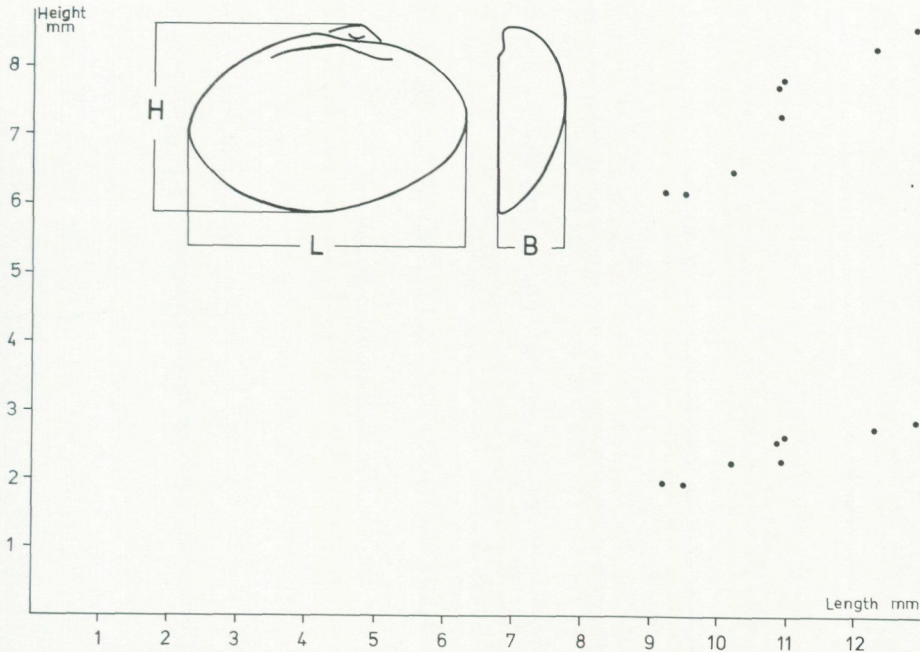


Fig. 7. *Palaeostraba baltica* n.gen. and n.sp. Scatter diagram showing height/length relation (for discussion see p. 14).

ratio Ph/L ; hinge angle almost constant ranging from 146° – 154° (mean of 7 valves 150°).

The central part of the hinge is preserved in only 4 valves while there are 3 additional fragmentary valves with the anterior hinge plate only preserved. The state of preservation is not good in the region immediately below the beak where the anterior tooth row meets the posterior one. However, one can observe that the most proximal tooth of both rows is minute, equal in size and shape, and that there is a distinct break between anteriors and posteriors consisting of an aberrant triangular tooth in the left valve (Figs. 8:A, 9) and a matching socket in the right. Another structure worth recording is the central edentulous ventral part of the hinge plate (Fig. 9), possibly an early evolutionary stage in the formation of an internal part of the ligament.

In a valve 12.9 mm long there are 6 strong, coarse teeth in the anterior hinge plate, the proximalmost ones small and lamellar, the median ones large and chevron-shaped with a shorter dorsal limb, their apices pointing towards the beak, distally larger and broader, the most distal one subconical to lamellar. The most proximal and the most distal tooth occupy about half the breadth and the medians almost the entire breadth of the hinge plate (Fig. 9).

There are about 20 small, narrow teeth in the posterior hinge plate in a valve 12.9 mm long. They increase progressively in size in distal direction; they are

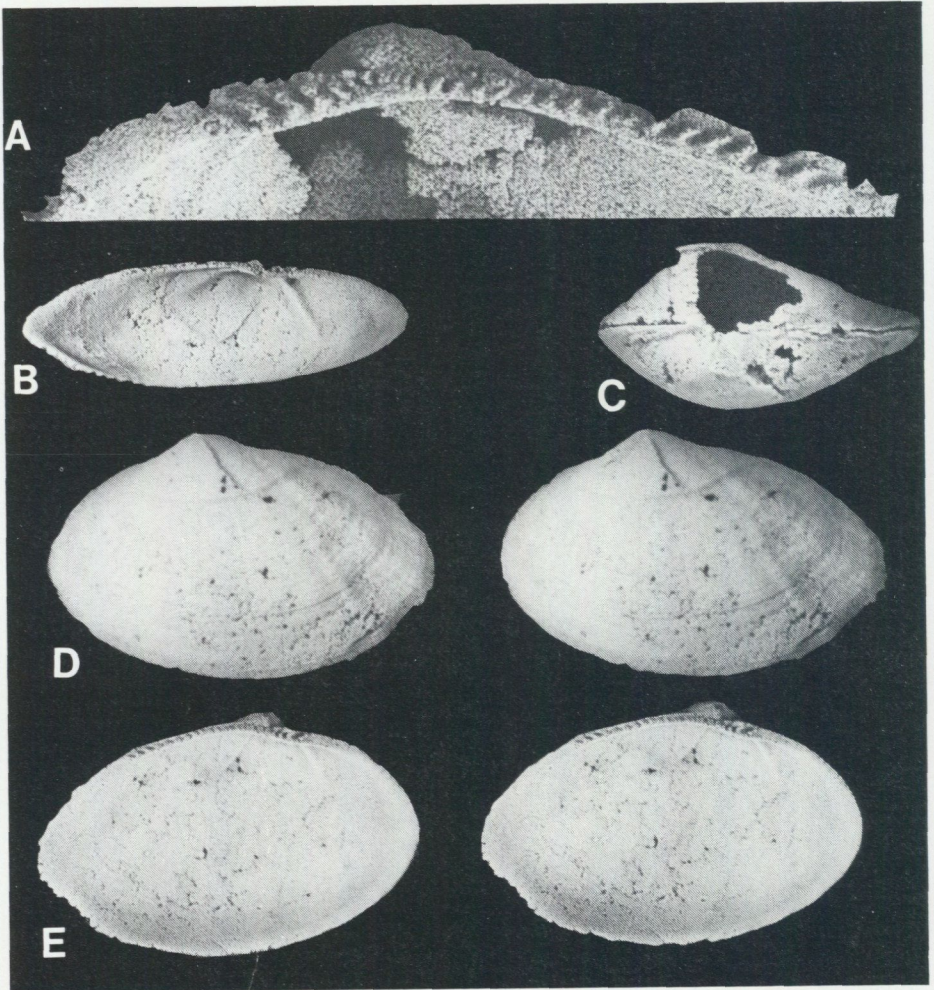


Fig. 8. *Palaeostraba baltica* n.gen. and n.sp. A. Hinge of right valve; SGU Type 3607, $\times 16$, sample G79-78LJ. B. Internal ventro-lateral view of holotype (left valve); SGU Type 3498, $\times 4$, sample G78-2LL. C. External dorsal view, anterior to the left; SGU Type 3638/3639, $\times 4.3$, sample G79-79LJ. D. Stereo pair, external lateral view of holotype, anterior to the left, $\times 4.3$ (note oblique posterior sulcus). E. Stereo pair, internal lateral view of holotype, $\times 4.3$.

lamellar and dorsally divergent, the proximalmost ones slightly chevron-shaped with their apices towards the beak.

The muscular impressions are few and extremely faint. The most distinct one is the anterior adductor muscle scar (No. 1 in Fig. 6), but like the posterior adductor muscle scar (No. 2 in Fig. 6) only the marginal limitation is discernible. The scars numbered 3 and 4 in Fig. 6 are dubiously muscle insertions since they occupy positions difficult to explain functionally (pedal retractors?). A conspicuous

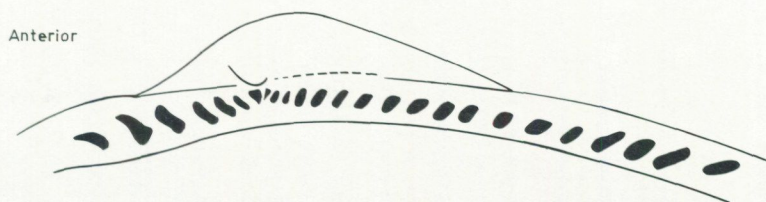


Fig. 9. *Palaeostraba baltica* n.gen. and n.sp., diagrammatic drawing of the hinge of the right valve, SGU Type 3607 (same as in Fig. 8:A).

depression (No. 5 in Fig. 6) is limited posteriorly by a smooth, indistinct ridge and ventrally by a faint feature fading out anteriorly, possibly indicating the limitation of the visceral mass (cf. discussion on p. 24). Scar No. 6 in Fig. 6 is small and its function is difficult to explain. Pallial line not observed.

Fig. 8:B shows posterior and anterior ridges, the anterior ridge actually being a low internal septum similar to that present in *Nuculites* s.s. It should be emphasized, however, that the "internal septum" described by Prantl & Růžička (1954:22, Fig. 8, Pl. 4:1) in *Straba* (*Strabina*) *formosa* differs completely from the internal ridge in *Palaeostraba baltica* and *Nuculites* s.s. (see following discussion).

DISCUSSION OF CLOSELY RELATED TAXA – The Devonian *Straba* Prantl & Růžička, 1954 seems to be most closely related to *Palaeostraba baltica* n.sp. Within the genus *Straba*, Prantl & Růžička differentiated three natural groups separated as subgenera: *Straba* (*Straba*), *Straba* (*Strabiella*) and *Straba* (*Strabina*). *Straba* (*Straba*) is separated from *S.* (*Strabiella*) by its simple, more or less straight (lamellar) teeth, *S.* (*Strabiella*) having strong, compound and broken teeth. *S.* (*Strabina*) is distinguished from *S.* (*Straba*) on the narrow ridge running from the posterior side of the beak crossing the anterior hinge plate and forming a ridge-like septum in the inner anterior part of the valve. However, McAlester (1968:54) believed the "internal septum" of *S.* (*Strabina*) to be "...an artifact of the preservation rather than an original feature of the shell morphology." On a visit to the National Museum in Prague Prantl & Růžička's type material had been lost. There is little hope that the types will turn up. So I tend to agree with McAlester's assumption and consequently consider *S.* (*Strabina*) a synonym of *S.* (*Straba*).

Palaeostraba baltica appears to be more closely related to *S.* (*Strabiella*) than to *S.* (*Straba*) since *P. baltica* and *S.* (*Strabiella*) have a similar type of anterior hinge teeth (chevron-shaped). *P. baltica* also has a beak more similar to that in *S.* (*Strabiella*), for the beak is relatively high above the hinge line, while *S.* (*Straba*) has a low beak. Further, *P. baltica* differs from *S.* (*Straba*) in having a smoothly arcuate posterior hinge plate (the posterior hinge plate in *S.* (*Straba*) being straight), and in that the posterior teeth of *P. baltica* occupy the major part of the breadth of the hinge plate while those of *S.* (*Straba*) take up only about half the

breadth of the hinge plate. However, the anterior hinge plate of *P. baltica* resembles that of *S. (Straba)* with an evenly arcuated ventral part (Fig. 8 in Prantl & Růžicka 1954:12) while that of *S. (Strabiella)* is tongue-like with an abruptly angular limitation (Prantl & Růžicka 1954:25). *P. baltica* differs from both subgenera of *Straba* in its most proximal posterior teeth covering only a minute part of the breadth of the hinge plate, while in *Straba* the proximal posterior teeth are fairly broad, covering the entire breadth of the hinge plate.

One of the most important features that distinguishes *P. baltica* from the Bohemian taxa is the absence of an enlarged tooth in the junction of the two rows of teeth in *P. baltica*, in which both anterior and posterior teeth decrease progressively in size proximally. The Bohemian *Straba* has fairly large proximal teeth, both anteriors and posteriors, and has a conspicuous robust tooth and corresponding socket in the opposite valve just below the beak. This makes it easy to distinguish anterior and posterior teeth from each other contrary to the diminutive central tooth and socket in *P. baltica* (Figs. 8:A, 9). The teeth of *P. baltica* are generally smaller and slenderer than those of the Bohemian species.

The second important difference between *P. baltica* and *Straba* is the presence of true internal septa in the former (Fig. 8:B). The hinge angle of *S. (Straba)* s.s. ranges from 120°–140° and is about 140° in *S. (Strabiella)*, while in *P. baltica* it varies from 140°–151° (mean value 150° in 7 valves). The H/L ratio of *P. baltica*, *S. (Straba) barrandei*, and *S. (Strabiella)* is 0.68, 0.78, and 0.83 respectively. Thus in general outline *P. baltica* is more elongate and ovate, resulting in a wider hinge angle, and has slenderer teeth, while the Bohemian taxa are more compact and have a narrower hinge angle and coarser hinge teeth.

Prantl & Růžicka 1954:27 suggested that the Bohemian (Middle Devonian) subgenera of *Straba* were the result of convergent evolution, and had adopted similar shell characters. Possibly *P. baltica* was a primitive forerunner of the Devonian strabinids, its minute central tooth and socket evolving into the corresponding prominent features of *Straba*.

Palaeostraba baltica may also be in the ancestral lineage of the Carboniferous genus *Anthraconeilo* Girty, 1911 since there are similarities in general shell habitus and the posterior hinge plate is longer than the anterior (Girty 1911:131). Furthermore, *Anthraconeilo* has a distinct pallial sinus. The posterior oblique external sulcus of *P. baltica* suggests that this species, too, accommodated siphons, which is also indicated by its more pronounced posterior end (cf. sulcus in siphonate nuculanaceans). In the fairly strong anterior septum *P. baltica* resembles the septum-bearing taxa of the family Mallettiidae (e.g. *Nuculites* and *Arisaiga*).

OCCURRENCE—At the time of description the species is known exclusively from the Silurian (Late Wenlockian) Halla Beds at Möllbos 1, Gotland.

FUNCTIONAL MORPHOLOGY AND LIFE HABIT – As just mentioned the slightly elongated posterior end of *P. baltica* with an oblique sulcus suggests that siphons were present although no positive evidence of this has been observed. This suggestion may find a certain support in the assumption of Levinton & Bambach (1975) that the increase in the water-content of sediments that is produced by the activity of burrowing populations of extant deposit-feeding *Nucula proxima* probably disturbs the respiratory function of the siphonate *Yoldia limatula* that occurs together with it. Levinton & Bambach (1975:108) stated that “Nuculacean bivalves that depend on a siphon for respiration will be competitively excluded by the presence of numerous non-siphonate nuculoid bivalves, due to this interference mechanism.” Since the bivalve fauna at Möllbos is dominated by two, presumably deposit-feeding non-siphonate nuculoids (*Nuculoidea lens* and *Nuculodonta gotlandica* = 70%), and since *Palaeostraba baltica* comprises only 0.7% of all bivalves, the assumption that the latter is a siphonate species seems to be reasonable.

Extant siphon-bearing nuculaceans live preferably in muddy bottoms (Yonge 1941:89). Some are very rapid burrowers (e.g. *Yoldia limatula*) and feed in an oblique position 1–2 cm below the sediment surface with the ends of the siphons protruding 2–3 cm above the sediment surface (Stanley 1970:118, Pl. 2).

Palaeostraba baltica is a smooth, thin-shelled form with delicate dentition and in Fig. 4 falls within the rapid-burrowing region (cf. Stanley 1970, Fig. 25). *P. baltica* was presumably a siphonate deposit-feeder. Accordingly, by analogy with siphonate nuculaceans whose life habit is known (e.g. *Yoldia limatula* and *Yoldia perprocta* in Stanley 1970) the suggested life position of *P. baltica*, as shown in Fig. 34:3, is oblique, some centimetres below the sediment surface.

Superfamily ?
Family ?

Genus *Caesariella* n.gen.

DERIVATION OF THE NAME – Feminine diminutive of Latin *Caesarius*, alluding to Caesar, my constant field companion.

TYPE SPECIES – *Caesariella lindensis* (Soot-Ryen, 1964). Original combination: *Ctenodonta lindensis* Soot-Ryen, 1964.

SPECIES – Monotypic at the time of description.

DIAGNOSIS – Nuculoid with prosogyrate, anteriorly extended and posteriorly truncated shell, external ligament posterior to beaks; margins even; teeth forming

an uninterrupted series below beak, anterior and posterior part of hinge almost equal, most distal teeth chevron-shaped, apices pointing towards beak, proximal teeth lamellar; pallial line slightly sinuate.

DISCUSSION OF SYSTEMATIC POSITION – *Caesariella* shows similarities with representatives of all three nuculoid superfamilies, diagnostic characters of which are:

Ctenodontacea Wöhrmann, 1883	Nuculacea Gray, 1824	Nuculanacea Adams & Adams, 1858
shell equilateral	shell posteriorly truncated	shell posteriorly elongated
pallial sinus lacking	pallial sinus lacking	pallial sinus usually present
resilifer absent, external ligament present	resilifer present or absent	resilifer present or absent

Caesariella lindensis has a somewhat truncated posterior end, an external ligament and a slightly sinuate pallial line (Figs. 11:C,G and 12). If the sinuation of the pallial line of this species is interpreted as indication of the presence of siphons, *Caesariella lindensis* then holds an intermediate systematic position between Nuculacea and Nuculanacea. Furthermore, if we accept the suggestion of Allen & Sanders (1969:392) that ctenodontaceans were possibly the ancestors of extant Malletiidae (in Nuculanacea), *Caesariella lindensis* whose shell morphology resembles that of *Malletia pacifica* Dall, for example, may also be considered as belonging to Ctenodontacea.

Caesariella lindensis (Soot-Ryen, 1964)

Figs. 4, 10, 11, 12, 34:4

SYNONYMY – *Ctenodonta lindensis* n.sp. – Soot-Ryen, 1964:495, Pl. 1:1,2,3,5.

The orientation of the shell suggested by Soot-Ryen (posteriorly elongated) cannot be correct. There is an outer ligament, which is generally accepted as being posterior to the beaks, as far as nuculoids are concerned (Cox, Nuttall & Trueman 1969). The beaks thus point anteriorly, i.e. the shell is prosogyrate and anteriorly elongated. Further, if the feature in the anterior part of the umbonal cavity is accepted as being the trace of the visceral floor (see following discussion) it may along with the sinuate pallial line serve as a means of orientation. This interpretation agrees with the implication of the position of the ligament.

TYPE STRATUM – Hemse Beds, Early Ludlovian, Silurian.

TYPE LOCALITY – Linde, Gotland, Sweden.

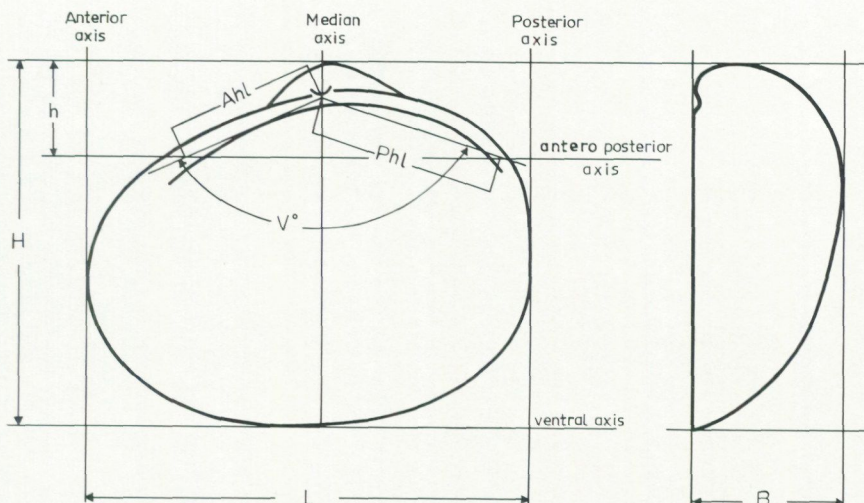


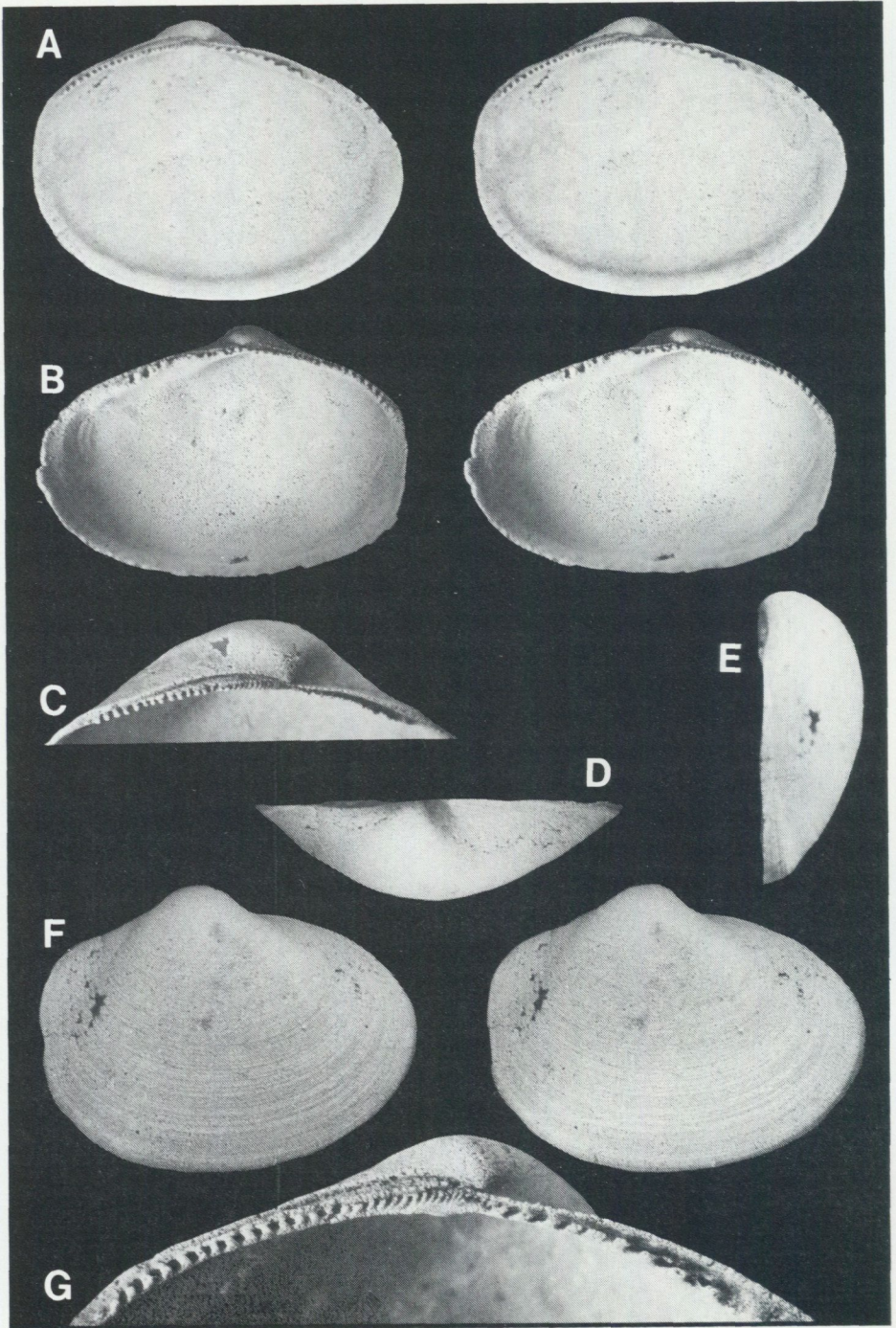
Fig. 10. *Caesariella lindensis* (Soot-Ryen). Diagram of right valve showing lateral dimensions. L = total length of shell, H = total height of shell, B = total breadth of shell, h = hinge height, Ahl = length of anterior hinge plate, Phl = length of posterior hinge plate, V° = hinge angle (for definitions and further explanations see Liljedahl 1983).

MATERIAL – 12 valves, 3 of which are complete. Measurements and terminology on Fig. 10.

EXTERNAL FEATURES – Shell of medium size, rounded, subovate, equivalve, almost equilateral, moderately inflated (Fig. 11:D,E), margins even, no gap present; external opisthodethic ligament; faint commarginal growth lines; umbones low and rather broad, beaks small, close together, prosogyrate, situated almost centrally in posterior half of shell; maximum convexity about mid-length and at 2/3 of height; escutcheon well-defined housing ligament running from immediately below beaks along dorsal margin to posterior part of hinge, covering nearly entire part of tooth row posterior to beaks (Fig. 11:C), most probably mainly external but edentulous area below beak possibly indicating the incitement to an internal part of the ligament (see Internal features); dorsal margin convex, antero-dorsal part sloping, postero-dorsal part rounded at the posterior end; posterior margin truncate, nearly straight; anterior margin narrow and rounded; ventral margin long and convex, with its deepest point about mid-length of shell;

Morphological variation is small. The H/L ratio of 5 measurable valves is 0.80, 0.80, 0.80, 0.79, and 0.73 (mean 0.78) and B/L ratio 0.21, 0.25, 0.27, 0.27, 0.33, and 0.41 (mean 0.29). The lateral outline of 3 complete valves is almost identical.

INTERNAL FEATURES – Hinge line convex, anterior hinge plate about 1/3 of total length of shell, posterior hinge plate about 2/5 of total length of shell, the Ah/L



ratio in 6 measurable specimens being 0.32, 0.32, 0.33, 0.47, 0.51, and 0.53 (mean 0.41), Ph/L 0.41, 0.41, 0.43, 0.43, and 0.57 (mean 0.43), see Fig. 10; one right valve, 15 mm long, containing 12 anterior teeth, most proximal one blunt, fairly large, the 5 following short, oblique, lamellar, decreasing in size, 7th–10th increasing in size, the 10th being the largest anterior tooth, 11th and 12th teeth low and undeveloped; one left valve 15 mm long, containing 10 anterior teeth similar to those in the right valve except for most proximal tooth being small and having a large socket proximally to it fitting enlarged most proximal tooth of right valve; 4th–5th most proximal teeth covering almost entire breadth of hinge plate, gradually teeth covering less breadth, most distal teeth occupying about 1/4 of breadth of hinge plate; dorsal to teeth a conspicuous groove running along dorsal margin; a right valve, 15 mm long, having 28 posterior teeth, 9 most proximal vertical, narrow and lamellar, fairly long covering entire breadth of hinge plate, 10th–28th short, covering 1/2 breadth of hinge plate; edentulous region below most proximal posterior teeth, region broader in left than in right valve.

Fig. 12 shows a diagrammatic representation of the internal features. Impressions Nos. 1 and 2 are the scars of the anterior and posterior adductor muscles, respectively. The pattern of commarginal striae inside the adductor muscle scars was probably conditioned by decrease in growth and probably does not reflect the “quick-and-catch” portions of the adductors. This assumption is based on the fact that the deep incisions or rugae in the marginal part of the outer shell surface are typical of periods of low growth rate.

The discussion of the interpretation of the impressions of accessory muscles is based on the fundamental work of Heath (1937) and on the observations of Driscoll (1964) and Liljedahl (1983). Scar No. 3 in Fig. 12 is extremely faint and is probably the impression of the posterior pedal retractor muscle. Driscoll (1964) stated that the large attachment area of this huge muscle compensates for the often insignificant or wanting incisement in the shell. Moreover, impressions of accessory muscles in extant bivalves are generally rare and when present often reflect an aberrant or even pathological state. No. 4 in Fig. 12 may be the impression of an anterior pedal protractor muscle since it occupies a position appropriate to this purpose. No. 5 in Fig. 12 is presumably the trace of an anterior pedal retractor muscle because of its position and extreme depth. Nos. 6 and 7 in Fig. 12 are small shallow traces of, as I believe, muscles that served as the lateral attachment of the visceral floor referred to by Schenck (1934:21) as “central

Fig. 11. *Caesariella lindensis* (Soot-Ryen) A. Stereo pair, internal lateral view of holotype (left valve); SGU Type 3607, $\times 3.4$, sample G79–78LJ. B. Stereo pair, internal ventro-lateral view, note boundary of pericardial region in upper part of umbonal cavity (cf. Fig. 12, for discussion see p. 24); SGU Type 3642, $\times 3$, sample G79–79LJ. C. External dorso-lateral view of holotype (left valve); SGU Type 3607, showing extension of outer ligament, $\times 6.5$. D. External dorsal view of holotype (right valve); SGU Type 3606, $\times 3.4$. E. External posterior view of holotype (right valve); SGU Type 3606, $\times 3.4$. F. Stereo pair, external lateral view of holotype (right valve); SGU Type 3606, $\times 3.4$. G. Internal view of holotype (left valve), detail of hinge; SGU Type 3607, $\times 12$.

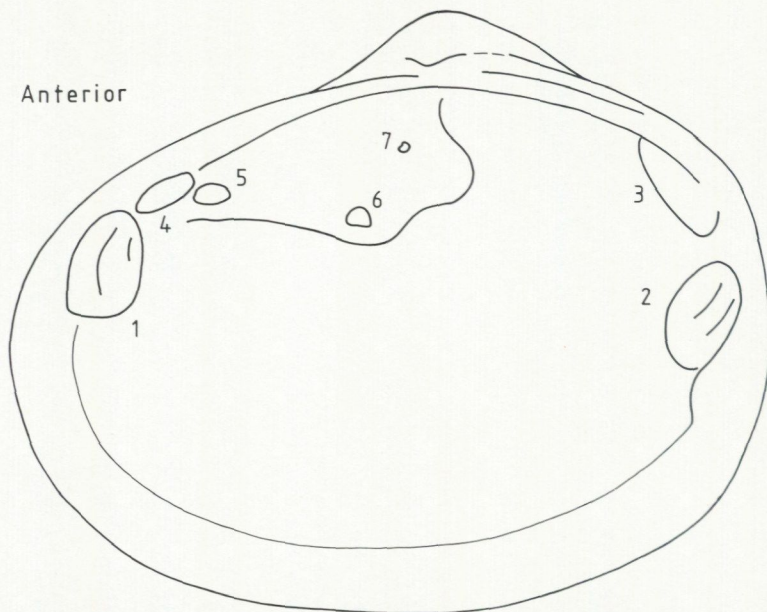


Fig. 12. *Caesariella lindensis* (Soot-Ryen) Diagrammatic representation of right valve showing muscle scars. 1 = anterior adductor muscle scar, 2 = posterior adductor muscle scar, 3 = posterior pedal retractor muscle scar, 4 = anterior pedal protractor muscle scar, 5 = anterior pedal retractor muscle scar, 6 and 7 = attachment muscle scars for visceral floor? Note extension of visceral floor in anterior region of shell.

muscle scar" or "median muscle scar" of *Nucula nuculeus* and *Ennucula obliqua* (cf. Heath 1937:12 and Soot-Ryen 1964, Pl. 1:3).

The conspicuous ridge enclosing the upper part of the umbonal cavity (Figs. 11:B, 12) may well represent the extension of the visceral floor. If so, this limit also marks the position of the ventral border of the gonads. The restricted area thus enclosed the pericardial region with heart, intestine, etc. Bradshaw (1978) gave an elaborate account of the position and morphology of the soft parts of extant palaeotaxodonts and suggested how to reconstruct soft-part features in fossil ancestors of the group. The location of the feature in question in the umbonal cavity of *Caesariella lindensis* closely resembles the position of the gonads of *Acila* (Bradshaw 1978, Fig. 10). The orientation of the shell, indicated by the outer opisthodontic ligament in combination with the posterior pallial sinus, supports the suggestion that the region shown in Fig. 12 of *Caesariella lindensis*, (see also Fig. 11:B), is the site of the gonads which in extant nuculoids are situated in the anterior part of the shell.

DISCUSSION OF CLOSELY RELATED TAXA – Soot-Ryen (1964) described *Ctenodonta lindensis* from the Hemse Beds (Early Ludlovian) of Gotland. Her topotype material consists of non-silicified single and articulated valves. Three valves have

a fairly well-preserved hinge, making it possible to establish conspecificity with the Möllbos material. The non-silicified, Ludlovian material represents a somewhat larger and slenderer type than the Wenlockian material from Möllbos, the B/L ratio of which is about 0.3 while the corresponding value for the non-silicified material is about 0.2.

The species that is most closely related to *Caesariella lindensis* seems to be the Ordovician *Ctenodonta hartvillensis* Safford. Pojeta (1971, Pl. 5:7–10, 13, 17, 19, 20) illustrated it and assigned it to *Deceptrix* Fuchs, 1919. The following features are of interest in comparisons between *Deceptrix hartvillensis* and *Caesariella lindensis*.

	<i>Deceptrix hartvillensis</i>	<i>Caesariella lindensis</i>
Total height/total length (H/L)	0.82	0.73–0.80 (0.77)
Length of anterior hinge plate/total height (Ah/H)	0.32	0.39–0.53 (0.47)
Length of anterior hinge plate/total length (Ah/L)	0.26	0.32–0.53 (0.41)
Length of posterior hinge plate/total height (Ph/H)	0.43	0.47–0.67 (0.53)
Anterior hinge plate (Ah)	concave, short, broad tapering at both ends	convex, long, narrow slightly broader distally
Posterior hinge plate (Ph)	slightly arcuate, almost straight	evenly rounded, extending posteriorly to almost mid-height of shell
Anterior teeth	broad, chevron-shaped, proximals straight	narrow, most proximals lamellar, oblique postero-ventrally
Posterior teeth	lamellar, vertical, most distal teeth conical	chevron-shaped, most proximal teeth lamellar
Junction of hinge plates	posterior to and at some distance from beak, where teeth are rather coarse and bifurcate and trifurcate	immediately below beak, teeth fragile and simple
Beaks	strongly prosogyrate	slightly prosogyrate
Shell shape	dorsal margin meeting posterior margin at almost right angles	dorsal margin meeting posterior margin in a smoothly rounded transitional zone
Posterior margin	straight to concave	weakly convex, truncate
Ventral margin	strongly convex	slightly convex

When the Early Devonian *Deceptrix carinata* Fuchs 1919, type species of the genus, and *Caesariella lindensis* are compared the following differences are noted: The ratio H/L, Ah/L and Ph/L is 0.92 and 0.73–0.80; 0.20 and 0.39–0.53; 0.38 and 0.47–0.67 in *Deceptrix carinata* and *Caesariella lindensis*, respectively. The anterior hinge of *Deceptrix carinata* is extremely short while in *Caesariella lindensis* it is nearly half the height of the shell. The Ah/Ph ratio is 0.47 for *D. carinata* and for *C. lindensis* 0.78.

In *D. carinata* the anterior teeth are conical, s-shaped and lamellar (in a distal-proximal direction), while in *C. lindensis* they are chevron-shaped and lamellar. The posterior teeth of the former are short and straight becoming long and narrower proximally. Some of the proximal posterior teeth are dorsally bifurcate in much the same way as in *D. hartvillensis* (see Pojeta 1971, Pl. 5:20). The posterior teeth of *C. lindensis* are chevron-shaped thus differing notably from the posterior teeth of both *D. carinata* and *D. hartvillensis*. As a whole the teeth of the two *Deceptrix* species are much coarser and stronger than in *Caesariella lindensis*.

OCCURRENCE – Wenlockian Halla Beds, Möllbos 1 and Ludlovian Hemse Beds, Linde, Mannagårda and Tänglingshällar.

FUNCTIONAL MORPHOLOGY AND LIFE HABIT – *Caesariella lindensis* is the largest taxodont species from Möllbos. Similarities in gross shell morphology with some extant Malletiidae, e.g. *Malletia pacifica* Dall, may indicate analogous life habits.

Malletia obtusata, for instance, is a siphonate active burrower in soft extremely fine-grained mud, and has a life position just beneath the sediment surface, the siphons protruding somewhat above the sediment (Yonge 1941:88, 89, Fig. 6).

In Stanley's diagram showing burrowing rate in relation to shell shape (Stanley 1970, Fig. 25) *Caesariella lindensis* falls within the region of slow burrowing (Fig. 4). The shell of *C. lindensis* is smooth and only slightly elongated anteriorly which indicates a fairly large foot. Compared with the other nuculoid species from this locality the shell is rather thick and the dentition rather strong, suggesting a life position below and close to the sediment surface (Fig. 34:4). The truncate posterior end lay presumably close to and parallel with the sediment surface if the species was not siphonate, otherwise the life position may have been like that of extant *Malletia* s.s., viz. with the dorsal margin parallel to the sediment surface at some distance from or immediately below it (Yonge 1941:89).

Following the same line of ecological reasoning as for *Palaeostraba baltica* (cf. p. 19), it is reasonable to assume that *Caesariella lindensis*, comprising only 0.3% of all bivalves at Möllbos, was siphonate.

Subclass ?
Order SOLEMYOIDA DALL, 1889
Superfamily SOLEMYACEA ADAMS & ADAMS, 1857
Family SOLEMYIDAE ADAMS & ADAMS, 1857

Genus *Janeia* King, 1850

DISCUSSION OF GENERIC IDENTITY – The living representatives of the genus *Solemya* Lamarck, 1818 differ considerably in morphology from other extant bivalves and are therefore placed in an order of their own. A number of soft-part characters of the genus, e.g., foot, blood system, digestive system, gills, etc., suggest a close relationship with the protobranchs (Palaeotaxodonta, Quenstedt 1930; Yonge 1941; Allen & Sanders 1969 and others).

The controversy over the generic affiliations of the Palaeozoic solemyoids was initiated by the erection of the new genus *Janeia* by King 1850. As type species King chose the Devonian *Solemya primaeva* Phillips, 1837 but the diagnosis of *Janeia* contained no generic characters. However, Beushausen (1895:290) emended the diagnosis of *Janeia* stating the following differences between the extant and Palaeozoic forms: The most important character of the fossil solemyoids is the inequivalve nature of the shells. In *Janeia silurica* n.sp. the beak of the left valve overlaps the beak of the right valve. This feature is also clearly seen on the Carboniferous "*Solemya*" *puzosiana* de Koninck, 1885, Pl. 23:24 for example. Hind (1896–1900:436) on the other hand felt that the overlapping of the valves was accidental, the edentulous nature of the hinge having prevented it from keeping the valves in line after burial. He stressed the fact that the valves were equal, although he added to his description of the Carboniferous "*Solemya*" *costellata*, in which all specimens have their left valve overlapping the right one, that "... doubtless there is some structural reason why the left always overrides the right valve" (Hind 1896–1900:444). Furthermore, he was of the opinion that no character of generic importance separates the Palaeozoic forms from the extant *Solemya*.

In the Recent species of *Solemya* either the anterior or posterior end, or both, gape (Newell 1969:N 241–43). Beushausen (1895) felt that the fact that the shell gapes should not allow generic distinction. According to him (Beushausen 1895:292), the anterior end of the type species *Janeia primaeva* gapes and "*Solemya*" *biarmica* de Verneuil (1845:294) gapes at both ends. Further Beushausen (1895:292) reported of a complete articulated specimen from the Middle Devonian of Eifel with closely fitting valve margins, i.e. the valves do not gape, but no illustration nor even a specific name was given. In *Janeia silurica* n.sp. the valve margins fit closely together, except for in the dorsal part where they overlap.

Further difference between *Solemya* and *Janeia* established by Quenstedt

(1930) is displayed by *Solemya parkinsoni* Gray and *Janeia truncata* (Goldfuss) as seen on Plate 1:3,4 which shows vertical sections through the umbonal part of these species. The chondrophore is thicker and more massive in *Solemya parkinsoni* than in *Janeia truncata*.

As minor differences Beushausen (1895:292) described the thicker shell and the more pronounced ornamentation of the Palaeozoic forms as compared with the living ones. *Janeia silurica*, however, is almost devoid of sculpture. Quenstedt (1930) described further differences between the Palaeozoic and living forms. The length/height ratio of the Recent *Solemya* is c. 3:1, while in *Janeia* it is c. 2:1 or less. The breadth in extant species of *Solemya* is by comparison somewhat less than in the Palaeozoic species. As a whole the living solemyoids are much slenderer and adapted to fast and effective burrowing and even to a free-swimming life. Representatives of the order Solemyoidea show an evolutionary trend of change in preferred habitat from the Palaeozoic carbonate sediments to the hard, sandy mud bottoms of today (Quenstedt 1930).

Janeia silurica n.sp.

Figs. 4, 13, 14, 15, 34:5

DERIVATION OF THE NAME – Latin *Siluricus*, referring to the age of the species. This is the first Silurian species of *Janeia* to be described and the oldest solemyoid hitherto known.

HOLOTYPE – An individual consisting of two disarticulated valves, SGU Types 3608 (right valve), 3609 (left) from sample G79–79LJ, Fig. 14:A. Length 17.4 mm, height 6.8 mm, breadth 2.0 mm. Right valve slightly damaged in its posterior extremity, otherwise well-preserved. Left valve damaged in the posterior part of the ventral margin, otherwise perfectly preserved.

TYPE STRATUM – Halla Beds, Late Wenlockian, Silurian.

TYPE LOCALITY – Möllbos 1, Gotland, Sweden.

MATERIAL – 597 valves (190 of which are articulated)

DIAGNOSIS – *Janeia* with overlapping valves (left overriding right); no gap, both inner and outer part of posterior ligament in connection with internal/external ligament supported by a chondrophore in right valve; shell surface with concentric growth lines and faint radial striae; extraordinarily deep traces of pallial muscles.

EXTERNAL FEATURES – Shell thin, elongate, sub-equivalve, sub-lanceolate, inequilateral, anterior end much longer than posterior end, moderately inflated;

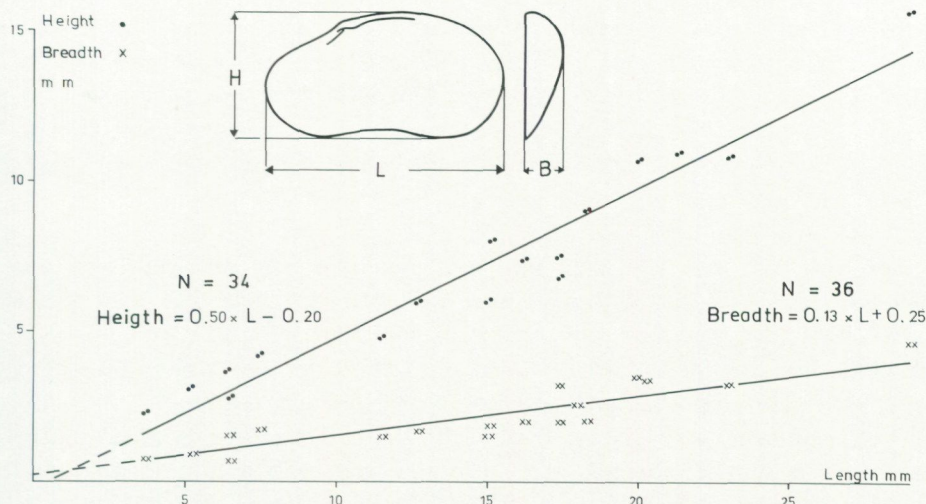


Fig. 13. *Janeia silurica* n.sp. Scatter diagram showing height/length and breadth/length relations. Unbroken lines are based on regression analysis.

valve margins fitting closely together; both external and internal portion of ligament present; faint concentric growth lines and radial striae; beaks small, extending over sagittal plane, low, opisthogyrate, in posterior third of shell, posterior part of beak with a fairly deep groove, beak of left valve overlapping beak of right valve, incision just anterior to beak along dorsal margin in left valve; maximum convexity about mid-length and mid-height of shell; no lunule; no escutcheon; conspicuous laceolate fulcrum accommodating the opisthodontic, parivincular outer ligament occupying most of the posterior part of dorsal margin; dorsal margin slightly convex, anterior part of dorsal margin long, approximately $2/3$ of total length of shell, slightly curved, posterior part short, approximately $1/3$ of total length of shell, concave, formed as a postero-umbonal "stop"; anterior margin rounded; ventral margin long, slightly concave; posterior margin short, rounded and narrow; smooth, broad, almost vertical, somewhat arcuate sulcus or constriction extending from beak, widening and reaching ventral margin slightly posterior to mid-length of shell.

DISCUSSION OF EXTERNAL FEATURES – The height-length (H/L) and breadth-length (B/L) ratio of about 30 shells are recorded (Fig. 13). Variation in shape within this species is slight at Möllbos (H/L min. = 0.39, max. = 0.71, mean = 0.49; B/L min. = 0.10, max. = 0.23, mean = 0.15). The smallest specimen measured (Fig. 14:B) shows the highest H/L ratio (0.71), another juvenile (Fig. 14:D,E) a high B/L ratio (0.21) owing to their immature characters, i.e. by comparison they are less elongate and more gibbous than adult shells (Fig. 14:C,F).

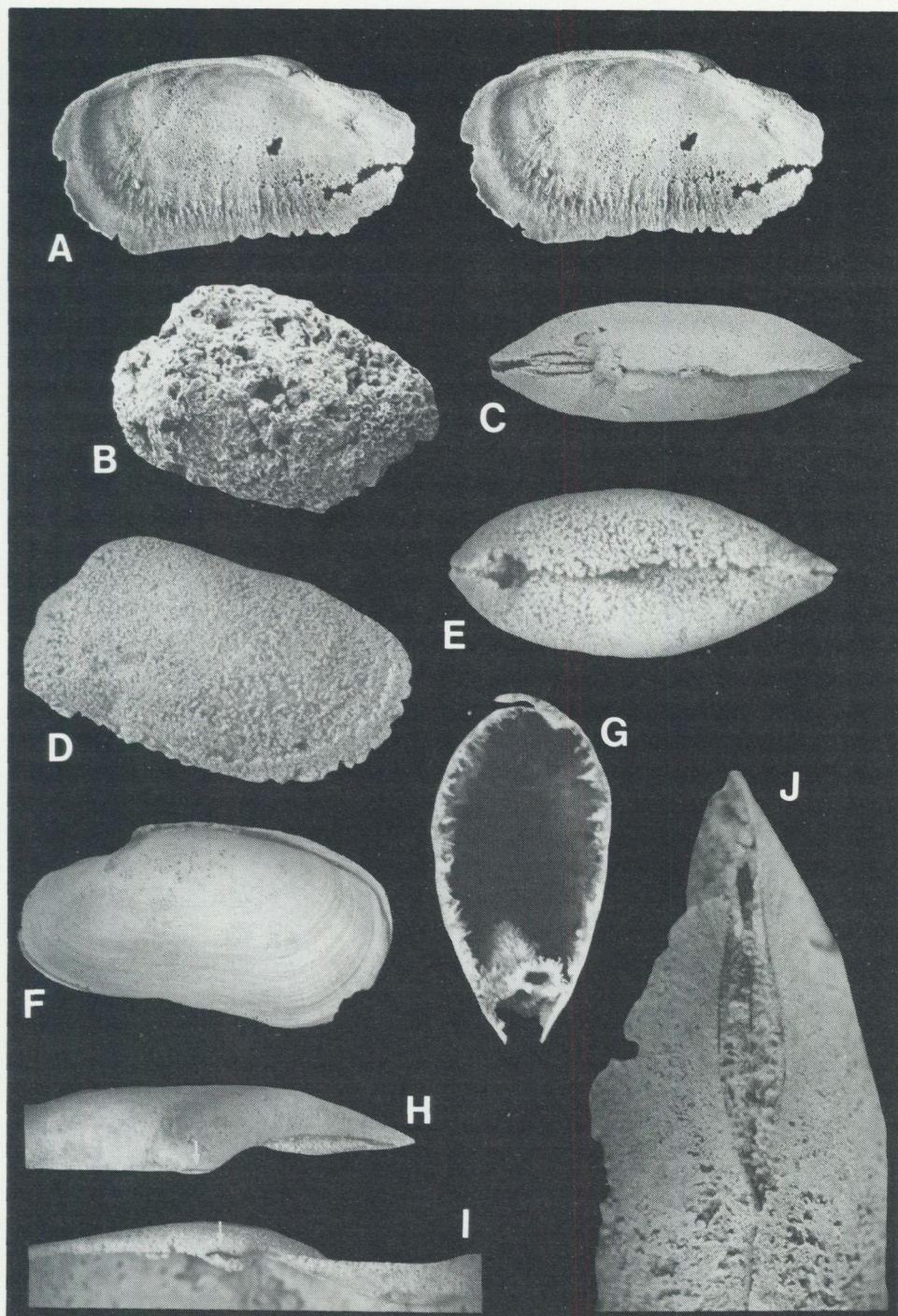
Most shells that can be identified as *Janeia silurica* consist of the beak and the strong ligament support (Fig. 14:H,I) only, these being the thickest parts of the shell. In both valves there is a strong thickened plate constituting the posterior part of the dorsal margin which house the posterior part of the ligament (Fig. 14:C,H,I,J). The shell is also thickened at the beak, the right valve being thicker than the left one.

INTERNAL FEATURES – Hinge edentulous, containing two conspicuous arcuate ridges extending posteriorly from a point just posterior to beak, below and along posterior part of dorsal margin to about half the length of ligament extension. Arcuate chondrophore attached to beak in right valve, (Fig. 14:H,I), projecting above and beyond beak, containing inner part of anterior ligament.

The postero-umbonal groove (Fig. 14:C,J) together with incisions on the thickened ligamental support (Fig. 14:I), indicates the extension of the inner portion of the ligament which evidently must have been strong (cf. similar features of extant *Solemya* and *Solemyarina* in Cox 1969:N242, Fig. B1:3 and 2b). The chondrophore of *Janeia silurica* suggests that in this species an inner part of an anterior ligament was connected with a posterior ligament. In fact, in one specimen remnants of ligament tissue are preserved as pyrite, situated between the chondrophore and the beak as well as on the posterior fulcrum (Fig. 14:H,I). In living solemyids the outer part of the ligament covers almost the entire anterior dorsal margin (see Owen 1959:217, Fig. 3). It is possible that the overlapping of the valves and a ligament-bearing chondrophore in *Janeia silurica* furnished this species with a ligament function of similar strength as in living solemyids. *Janeia silurica* presumably accommodated an unusually large ligament-area of corresponding strength.

With the presence of a chondrophore extending above and beyond the beak of the right valve, *Janeia silurica* thus displays a morphological character that explains the overlapping of the valves (cf. discussion on p. 27). In undistorted specimens the left valve always overlaps the right one (Fig. 14:G).

Fig. 14. *Janeia silurica* n.sp. A. Stereo pair, internal lateral view of holotype (right valve); SGU Type 3608, $\times 2.4$, sample G79-79LJ. B. Scanning micrograph of smallest specimen of the species, external dorso-lateral view of articulated specimen, anterior to the right; SGU Type 3654/3655, $\times 25$, sample G79-83LJ. C. External dorsal view of articulated specimen, anterior to the right, note overlapping left valve and conspicuous posterior ligament; SCU Type 3426/3427, $\times 1.8$, sample G77-29LJ. D. External lateral view of right valve of articulated specimen, anterior to the right; SGU Type 3428/3429, $\times 8.9$, sample G77-29LJ. E. External dorsal view of articulated specimen, same as in D, anterior to the right, $\times 8.9$. F. External lateral view of articulated specimen, anterior to the right, note overriding left valve, same specimen as C, $\times 1.8$. G. Vertical section of an articulated specimen, note possible silicified folded in ventral margin of mantle (for discussion see p. 32); SGU Type 3592/3593, $\times 4.4$, sample G79-78LJ. H. External dorsal view of posterior end of right valve, note anterior part of internal ligament below beak (at arrow, see also I); SGU Type 3318, $\times 4.8$, sample G77-28LJ. I. Internal lateral view of umbonal part of right valve (same as H), note pyritized anterior ligament just below beak (at arrow), $\times 6.7$. J. External dorsal view of posterior end, detail of ligament; SGU Type 3316/3317, $\times 8.3$, sample G77-28LJ.



The pattern of muscular impressions in *Janeia silurica* (Fig. 15) shows a striking resemblance to the distribution of muscles in extant *Solemya* (Pelseneer 1891:178, Pl. 15). Accordingly, the foot of *Janeia silurica* presumably resembled and functioned in the same way as the foot of *Solemya*. Fig. 15 shows a reconstruction of the foot of *Janeia silurica* based on observable muscular imprints and on comparisons with extant solemyids (Pelseneer 1891; Stempell 1900). The assumed large foot of *Janeia silurica* primarily, of course, served as a burrowing organ but probably also had an important role in cleaning the mantle cavity. When the foot was withdrawn rapidly this, together with the folding in of the mantle edge (cf. Fig. 14:G), created a strong exhalant current discharging posteriorly. Cf. cleaning action of *Solemya* in Yonge (1941), Drew (1900) and others.

The anterior adductor muscle scar (No. 1 in Fig. 15) is the largest impression. Since scar No. 2 in Fig. 15 is in contact with the anterior adductor muscle scar it probably indicates the position of an anterior pedal protractor. Scar No. 3 in Fig. 15 is presumably the trace of the anterior pedal retractor, while Nos. 4 and 5 show the positions of assumed pedal elevators (cf. the well-developed pedal elevator of *Solemya* in Pelseneer 1891:178, Pl. 15:25). Scar No. 6 in Fig. 15 indicates, I believe, the position of the posterior pedal retractor muscle. The posterior adductor muscle scar (No. 7 in Fig. 15), second in size, is the most strongly imprinted incisement, possibly owing to the great thickness of the valve in this region.

The pallial line consists of rather sharp ridges in an irregularly radiating pattern running from the anterior adductor muscle scar to the posterior end of shell, the anterior part weakly impressed, heavier accentuated and broader in mid-region and almost entirely lacking at the posterior end of the shell. The deeply incised scars of the attachment of mantle to the shell (Fig. 14:A) show that the radial muscles must have been extraordinarily strong, being able to withdraw the mantle edges with great force (cf. mantle anatomy of extant *Solemya* in Yonge 1941 and Drew 1900). It is possible that the mantle edge of *Janeia silurica* was partly fused since the pallial scars are somewhat fainter anteriorly indicating an opening for the foot (cf. Drew 1900:263, Fig. 8). There are hardly any pallial impressions in *Janeia silurica* posteriorly which suggests a second opening for the exhalant current as in extant solemyids.

In a number of articulated specimens of *Janeia silurica* the ventral margins are not completely closed, the opening exhibiting silicified infilling within the shells (Fig. 14:G). In extant representatives of Solemyidae a large portion of the ventral margin of the mantle is fused, covered with periostracum and furnished with exceptionally strong radial muscles (see Drew 1900:263, 264, Fig. 8, 10; cf. conspicuous traces of pallial muscles in *Janeia silurica*). The mantle margin is folded in when the valves are drawn together (Drew 1900:265). It is possible that the mantle margin is preserved as a sheet of silicified matter in *Janeia silurica* (Liljedahl in prep.).

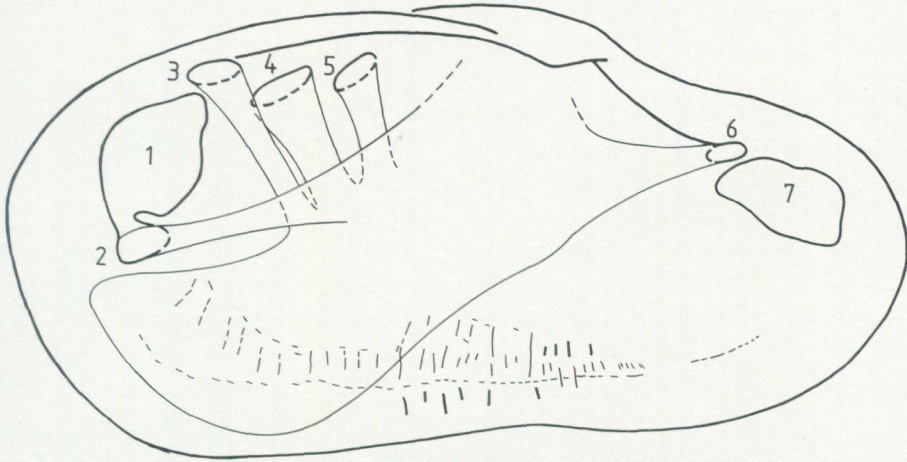


Fig. 15. *Janeia silurica* n.sp. Diagrammatic reconstruction of the foot and its musculature. 1 = anterior adductor muscle scar, 2 = anterior pedal protractor muscle scar, 3 = anterior pedal retractor muscle scar, 4 and 5 = pedal elevator scars, 6 = posterior pedal retractor muscle scar, 7 = posterior adductor muscle scar. Note pallial muscle scars.

CLOSELY RELATED SPECIES – The solemyid most closely related to *Janeia silurica* seems to be the Belgian Carboniferous “*Solemya*” *excisa* de Koninck, 1885 (de Koninck 1885:122, Pl. 9:13, 14; Pl. 23:30, 39, 40, 42, 43, de Koninck’s orientation of the animal is the opposite of that assumed by me). The specimens illustrated by de Koninck, however, generally show a somewhat more compact shortened form than *Janeia silurica* (H/L ratio about 0.6; cf. *Janeia silurica* H/L = 0.39–0.62). The conspicuous broad anterior end, the convex, sometimes evenly rounded ventral margin and comparatively prominent umbo together with the heavily incised, almost angular posterior ridge of “*Solemya*” *excisa* distinguish this species from *Janeia silurica*. According to de Koninck 1885, Pl. 9:14 “*Solemya*” *excisa* seems to be equivalve and not overlapping in contrast to *Janeia silurica*.

The British form assigned to “*Solemya*” *excisa* by Hind (1896–1900:441, Pl. 50:11–16) differs markedly from de Koninck’s Belgian material in being much more elongated (H/L = 0.4). This species shows a closer resemblance to *Janeia silurica* than do the Belgian specimens, but differs from it in having a less pronounced umbo, the anterior adductor muscle scar situated somewhat more dorsally and in lacking the conspicuous postero-umbonal stop typical of *Janeia silurica*.

The British Permian “*Janeia*” *biarmica* (de Verneuil) as described and illustrated by Logan (1967:61, Pl. 10:11,12) is equivalve with straight almost parallel dorsal and ventral margins. “*Solemya*” *homwoodensis* Dickins, 1963 (Dickins 1963, Pl. 7) from the Permian of Western Australia resembles *Janeia silurica* in being posteriorly constricted. However, the dorsal and ventral margins

are straight and roughly parallel. "*Solemya*" *holmwoodensis* seems to be inequivalve and presumably belongs to the genus *Janeia*.

OCCURRENCE – Wenlockian Slite Beds, Lauks; Halla Beds, Möllbos 1; Ludlovian Hemse Beds, Hammarudden and Kaupungsklint; Hamra Beds, Norrgårde. All these localities are situated on Gotland.

FUNCTIONAL MORPHOLOGY AND LIFE HABIT – The hard-part morphology of *Janeia silurica* agrees in a number of characters with extant representatives of the genus *Solemya*. The gross shell form is similar although minor differences occur. *Janeia silurica* is almost as elongated as *Solemya velum* but more compressed, both having the same extreme anterior extension of the shell. It should be noted that the breadth of *Solemya velum* was probably measured on shells with intact outermost shell margins, built entirely of periostracum and thus making the breadth much greater. *Solemya parkinsoni* (in Quenstedt 1930, Pl. 1:3) has a H/B ratio of 2.6, being slightly more compressed than *Janeia silurica* (H/B = 2.5). When placing the values obtained for *Janeia silurica* and *Solemya velum* in the diagram on Fig. 25 in Stanley 1970, both forms fall into the section of rapid burrowing (Fig. 4).

Extant species of *Solemya* have large anterior and posterior gaps (Stanley 1970:119) making it possible for water to be inhaled and expelled with closed valves. In *Janeia silurica* there are no gaps. This indicates that this species possibly had a somewhat different life habit from that of *Solemya*.

Janeia silurica has low, opisthogyrate beaks and an edentulous hinge just as in *Solemya*, with a large opisthodontic external/internal ligament and partly an anterior portion of the ligament and thus presumably had a ligament as strong as that in *Solemya* (cf. Owen 1959:217, Fig. 3). Furthermore, *Janeia silurica* displays conspicuously deep and broad traces of pallial muscles (Fig. 14:A), evidently reflecting strong radial muscles of the mantle and possibly, due to their uneven impression, suggesting partially fused mantle edges (see p. 32). These muscles could probably withdraw the mantle edges with great power, perhaps in a similar manner as in extant *Solemya* (cf. Drew 1900:265, Fig. 12).

The extremely elongated anterior part of the shell of *Janeia silurica* further suggests, in comparison to extant *Solemya*, that the foot was correspondingly enlarged. The insertion pattern of pedal muscles observable indicates that the foot protruded much in the same way as in its living relatives, i.e. anteriorly (cf. Drew 1900:259 "The movement of burrowing, and the muscular systems, are quite similar in all three genera" that is *Nucula*, *Yoldia* and *Solemya*). The way the foot of *Janeia silurica* protruded is also supported by the supposed partial fusion of the mantle edge, if this interpretation is accepted (Fig. 15).

The edentulous hinge of *Solemya* enables it to perform sudden vigorous repeated closures of the valves in order to clean the mantle cavity from non-ingestible matter (Yonge 1941:136). The fused periostracum-covered ventral

mantle edge is folded in with great force by the unusually strong radial muscles of the mantle. This effective closure of the valves also allows the animal, while above the surface of the sediment, to execute a rapid series of "leaps" so that the animal actually accomplishes a free-swimming motion (Drew 1900:261).

Extant solemyids, having protobranch ctenidia (Yonge 1959:213), are considered to be deposit-feeders by some investigators and suspension-feeders by others. They are moderately rapid burrowers and live in hard, often sandy mud (Quenstedt 1930:15; Stanley 1970:119) 6–50 cm below the surface of the sediment (Stanley 1970:119, de Saulcy 1838:103). They penetrate the substratum with the foot and form a Y-shaped burrow in which they lie and draw in water through the anterior arm of the burrow and expel it through the other (Stanley 1970:120). The labial palps, which are small, collect food from the exceptionally large protobranch ctenidia (occupying almost half the mantle cavity) instead of from the outside of the shell like nuculoids (deposit-feeding protobranchs). While still a deposit-feeder it can also be regarded as a "suspension-feeder" within the mantle cavity (Yonge 1941:91, 135).

The mutual qualities in *Janeia silurica* and the extant *Solemya* imply that the former was a fast-burrowing deposit-feeder. Since it had a thin shell devoid of sculpture it was possibly a moderately deep-burrowing form (Stanley 1970:69). *Solemya velum* thrives in sulfide rich sediments which might be explained by its procaryotic symbionts (Cavanaugh *et al.* 1981). Maybe *Janeia silurica*, too, lived in symbiosis with chemoautotrophic bacteria. If so, it was possible for this species to occupy a deep life position in which other bivalves could not survive because of the hydrogen sulfide-rich environment. Consequently *Janeia silurica* probably did not compete for food with other deposit-feeders (Liljedahl in prep.). The posterior umbonal slope, or stop, of this species makes an entirely posterior exhalant current (like that in *Solemya*) out of the question, since the posterior adductor muscle scar is in an extreme dorso-posterior position (Fig. 15). Free-swimming must thus be ruled out in *Janeia silurica*. The possibility of a postero-ventral exhalant opening remains, however, and is in fact highly probable because of the absence of deeply impressed pallial muscle scars in this region.

The size of the gills and the foot can, of course, only be conjectured, but the shell shape and the positions of the traces of the pedal muscles may indicate a closer similarity to the nuculoids which have smaller gills and a larger foot than the solemyoids. I suggest that if the gills of *Janeia silurica* were smaller than those of the extant *Solemya* and the foot comparatively larger, *Janeia silurica* must then have been a more constant burrower than the extant *Solemya* (cf. Yonge 1941:136).

It seems plausible that the solemyid branch later adopted a more immobile life position and evolved larger gills. Accordingly it compensated for the more active burrowing of its Palaeozoic ancestors by the larger gills. The stationary life habit, in combination with enlarged gills, became more effective and simultaneously

opened the way to the suspension-feeding habit. *Janeia silurica*, as the oldest solemyoid known, possibly represents a transitional form between nuculoid protobranchs and solemyoids, i.e. between the deposit- and suspension-feeding modes of life (Fig. 34:5).

Subclass PTERIOMORPHIA BEURLÉN, 1944

Order ARCOIDA STOLICZKA, 1871

Superfamily ?

Family ?

Genus *Freja* n.gen.

DERIVATION OF THE NAME – After the Norse goddess *Freja*.

TYPE SPECIES – *Freja fecunda* n.sp.

SPECIES – Only one (the type species) out of several species from Gotland so far described.

DIAGNOSIS – Equivalved, subcircular to somewhat ovoid, opisthocline shell, umbones slightly anterior to median axis, acline beaks; concentric growth lines; triangular cardinal area with ligamental grooves forming a chevron pattern between hinge margin and beak in each valve; straight hinge line, subequal anterior and posterior lateral teeth ventrally divergent at each end, numerous vertical narrow cardinal teeth along hinge margin between lateral teeth; two subequal adductor muscle scars, posterior byssal/pedal? retractor muscle scar and several additional accessory muscle scars; non-sinuate pallial line.

DISCUSSION OF SYSTEMATIC POSITION – Taxonomists often endeavour to indicate a “link” between different groups of higher taxa. Where such “links” exists they are often difficult to place in the existing classification because they have characters in common with more than one of the groups concerned. *Freja* is difficult to incorporate into any known family or even superfamily within the order Arcoida because of its unique hinge construction and gross shell morphology.

Freja resembles the cyrtodontaceans in its dimyarian, somewhat prosocline shell and straight hinge line. However, the ligament construction and the morphology, composition and arrangement of the hinge teeth deviate considerably from the corresponding cyrtodontacean characters. *Freja* resembles the arcaceans in its straight hinge line, interumbonal growth, chevron-shaped duplivinacular ligament and continuous hinge with teeth along the entire hinge line.

Freja fecunda was probably a semi-infaunal, byssate form. Considering its life habit and general morphology, it possibly descended from an ancestor of the cardiolaceans (see following discussion, cf. Kříž 1979:36–37).

I suggest that *Freja*, arcaceans, cardiolaceans and possibly also pterioids had a common ancestor originating from the “actinodonts”, from which the cyrtodontacean lineage also branched off in the Early Ordovician (Fig. 16).

DISCUSSION OF EVOLUTION WITHIN PTERIOMORPHIA – The mosaic of Palaeozoic cyrtodontacean forms has led to the assumption that these represented the radical to arcaceans, ambonychiaceans, pteriaceans, and pectinaceans and probably originated from *Actinodonta*-like ancestors (e.g., Douvillé 1912; Beurlen 1944; Newell 1954; Cox 1960; Vogel 1962; Babin 1966, 1977; Stanley 1970, and Pojeta 1971, 1975, 1978).

The primitive “actinodont” hinge is primarily ventrally divergent (Pojeta 1971:9). In the Ordovician *Actinodonta naranjoana* (de Verneuil & Barrande 1855, see Babin 1966:230, Fig. 59) there are hinge teeth along the entire dorsal margin, which can be divided into antero-lateral, cardinal and postero-lateral teeth (A in Fig. 16).

Juveniles of the Silurian *Freja fecunda* n.gen., n.sp. (G in Fig. 16) are equilateral and have a straight dorsal margin with a symmetrical hinge, i.e. ventrally divergent anterior and posterior lateral teeth of equal size and with numerous uniform, vertical cardinal teeth in between. The smooth, equivalved circular shells suggest that *Freja fecunda* was infaunal in the early ontogenetic stages of its life. The reduction in size of the anterior adductor muscle scar, a strongly developed byssal retractor muscle scar, change in shell form to obliquely prosocline and development of long, strong postero-lateral teeth indicate an endobyssate, semi-infaunal mode of life in adults. This species exhibits certain arcacean features which are thought to be primitive such as straight hinge line with teeth along its entire length, a duplivincular ligament and extensive interumbonal growth (G in Fig. 16), and its ancestors probably deviated from a lineage leading to the parallelodontids in Early Ordovician times.

In Vogel's (1962:41, Fig. 17) chart of the phylogeny of Lower Palaeozoic bivalves, “*Cyrtodonta*” *gibbosa* Salter (Early Llandovery, Silurian. In Hind 1910:512) holds a central position, since it according to him may be a descendant of the “actinodonts” and a predecessor to the cyrtodontids. It shows a ventrally divergent hinge-teeth pattern (F in Fig. 16) somewhat more asymmetrical than *Actinodonta naranjoana* with anterior elements reduced in length. In contrast to the arcuated dorsal margin with relatively few teeth in *Actinodonta naranjoana*, the dorsal margin in “*Cyrtodonta*” *gibbosa* is straight, carries more teeth and accommodates a duplivincular ligament with interumbonal growth (arcacean characters). But “*Cyrtodonta*” *gibbosa* does not belong to the Cyrtodontacea in which the anterior and posterior teeth are separated by a conspicuous edentulous

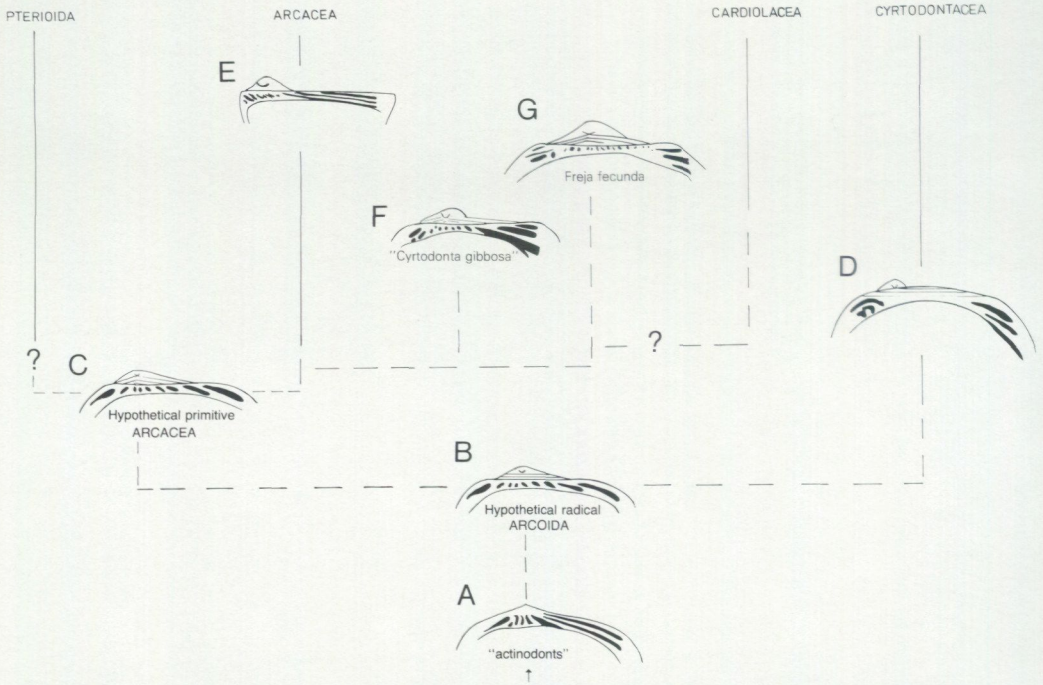


Fig. 16. Suggested arcoid phylogeny. Unbroken lines are based on fossil evidence, broken lines are hypothetical. A. *Actinodonta naranjoana* (de Verneuil & Barrande), left valve (reversed here), Arenig (L. Ord.), from Babin 1966:230, Fig. 59:6. B. Hypothetical radical arcoid assumed to have had straight hinge line, continuous dentition and "preduplivincular" ligament. C. Hypothetical primitive arcacean with straight hinge line, continuous dentition and true duplivincular ligament. D. *Cyrtodonta grandis* Ulrich, left valve (reversed here), L. Silurian, from Ulrich 1897:547, Fig. 43:g. E. *Parallelodon rugosum* (Buckman), right valve, M. Jurassic, from Arkell 1930:299, Fig. 1. F. "*Cyrtodonta*" *gibbosa* Salter BM(NH) L49858, left valve (shell, teeth and sockets reversed here), L. Silurian, also illustrated by Hind 1910, Pl. 4:17 and Vogel 1962, Pl. 5:3. G. *Freja fecunda* n.gen. and n.sp. SGU Type 3367, right valve, Wenlockian (Late Silurian).

space and which lack a duplivincular ligament (Pojeta 1978:235, 236). The entire dorsal margin of "*Cyrtodonta*" *gibbosa* has ventrally divergent teeth while the hinge of cyrtodontaceans contains anterior teeth pointing antero-dorsally/postero-ventrally (e.g. Fig. 16:D *Cyrtodonta grandis* Ulrich, in Ulrich 1897, Fig. 43:9), separated from the posterior lateral teeth by a non-denticulated region. In my opinion the hinge and gross shell morphology of the Silurian "*Cyrtodonta*" *gibbosa* shows typically arcacean features and in fact more closely resembles *Freja fecunda* than the Ordovician cyrtodontaceans suggesting a primitive arcacean ancestor in common (C in Fig. 16).

The oldest known Pteriacea (in the Order Pterioida) is of early Middle Ordovician age while the oldest duplivincular ligament seems to be found in *Palaeopteria* sp. from the early Late Ordovician (Pojeta 1978:237, 238). Representatives of the superfamily Pteriacea are characterized by a straight hinge

line above which is situated a duplivincular ligament, hinge teeth either continuous, i.e. along the entire hinge margin in a ventrally divergent pattern (e.g., *Pteronitella*, Fig. 26:1; cf. hypothetical primitive Arcacea Fig. 16:C) or with anterior teeth separated from posterior ones by an edentulous region (e.g., *Pterinea* and *Molinicola*, Fig. 25:3).

Thomas (1978b:336) suggested that the Arcoida evolved from an ancestral form closely related to the pteriods. The oldest arcaceans, the parallelodontids (late Early Ordovician; E in Fig. 16), are elongate and strongly inequilateral. They have a continuous hinge with a few postero-lateral teeth almost parallel to the dorsal margin and numerous oblique, horizontal or falcate anterior and median cardinal teeth (Newell 1969:N256; Arkell 1930; cf. similar hinge of *Parallelodon rugosum* (Buckman) in Arkell 1930, Pl. 14:1,2 and *Pteronitella retroflexa* in Walmsley 1962:353, Pl. 1:4,5). Their shape, dentition and radial ornamentation indicate an endobysate or epibysate life habit (Stanley 1970, Fig. 6).

Thomas (1978a:187, Fig. 5) felt that the ancestral form of the Arcoida was closely related to the pteriods and suggested that the hinge pattern of cyrtodontids and "actinodonts" shows functional and morphological similarities. According to him (Thomas 1978b:336) the earliest true Arcacea are of Devonian age. However, the oldest specimen assigned to Parallelodontidae, *Parallelodon antiquus* Barrois 1891, is reported from the Arenig (late Early Ordovician) of Brittany, France. The only known specimen, studied by Babin 1966, is damaged and does not reveal the hinge construction as illustrated by Barrois (Barrois 1891, Pl. 3:3b). Pojeta (1971:18) suggested that it might belong to *Pseudarca* Tromelin & Lebesconte, 1875, but that genus has a taxodont-like dentition (see McAlester 1962:131, Pl. 32). The drawing by Barrois shows anterior and posterior teeth almost meeting under the beak on a straight hinge margin.

Morphological and microstructural features suggest a possible close phylogenetic relationship between the Arcoida and the primitive Pterioda, i.e. Pterineidae (Carter & Tevez 1978:371, 372, Fig. 6; Pojeta 1978:237). The duplivincular ligament, interumbonal growth and continuous hinge teeth of Pterioda and Arcacea implies a common ancestor of these (C in Fig. 16) possibly originating from a hypothetical primitive arcoid (B in Fig. 16) evidently descending from the "actinodonts". The same stock of hypothetical primitive arcoids probably gave rise to the cyrtodontaceans (D in Fig. 16) characterized by a ligament made up of fine, horizontal sheets (Pojeta 1978:236, 237; Thomas 1978a:185, Fig. 3:b) and a hinge dentition composed of antero-lateral teeth separated from postero-lateral teeth by a conspicuous edentulous space (Pojeta 1978:237).

As mentioned above, it is generally assumed that the cyrtodontaceans were ancestors of the Arcacea. However, the oldest Arcacea like the oldest Cyrtodontacea are Arenig in age (Pojeta 1978:236) suggesting an older common origin.

Furthermore the Cyrtodontacea differ from both the arcacean and from the pteriacean lineage in the following respects: The cyrtodontacea have no interumbonal growth, no duplivincular ligament but a "preduplivincular" ligament (Pojeta 1978:238), no continuous hinge teeth and no ventrally divergent hinge-teeth pattern (e.g. *Cyrtodonta grandis*, Fig. 16:D).

The ancestors of the cardiolids are probably to be found in Lower Silurian or even Upper Ordovician rocks (Kříž 1979:34). The first cardiolids (Wenlock, Early Silurian) are considered semi-infaunal or epifaunal and it is suggested that they had endobysate cyrtodontid ancestors (Kříž 1979:37). These early cardiolids differ from *Freja*, among other things in their complicated ontogeny, edentulous hinge and radial ribs (Kříž 1979:37). In *Cardiolopsis alpina* Stache, however, grooves interpreted as possible remnants of posterior lateral teeth occur (Kříž 1979:26). The suggested life habit of *Freja*, endobysate and semi-infaunal, makes its forrunner a presumed ancestor of the early semi-infaunal and epifaunal cardiolids.

Freja fecunda n.sp.

Figs. 16, 17, 18, 19, 20, 21, 22, 34:6

DERIVATION OF THE NAME – From Latin *fecundus*, fertile, prolific.

HOLOTYPE – A complete, extremely well-preserved right valve. SGU Type 3367, from sample G77-28LJ. Figs. 18:A, B, D, E, F, G, I, 20:A, 21. Length 9.0 mm, height 8.3 mm, breadth 3.0 mm.

TYPE STRATUM – Halla Beds, Late Wenlockian, Silurian.

TYPE LOCALITY – Möllbos 1, Gotland, Sweden.

MATERIAL – 164 valves (18 articulated valves)

DIAGNOSIS – *Freja* with 2–3 anterior and 3 posterior lateral teeth in the right valve and 3 anterior lateral and 3 posterior lateral teeth in the left. Numerous cardinal teeth in contact with the lateral teeth at both ends. One pseudocardinal tooth in the left valve and a corresponding socket in the opposite valve. The lateral teeth being strong, lamellar and parallel to one another and almost parallel to the hinge margin; the cardinals are small, narrow and vertical. All teeth are ventrally divergent (cf. also the generic discussion, p. 37).

EXTERNAL FEATURES – Shell small, subcircular to moderately transversely subovate, opisthocline, moderately to strongly inflated, margins even, no gap present; external duplivincular ligament; faint commarginal growth lines; beaks

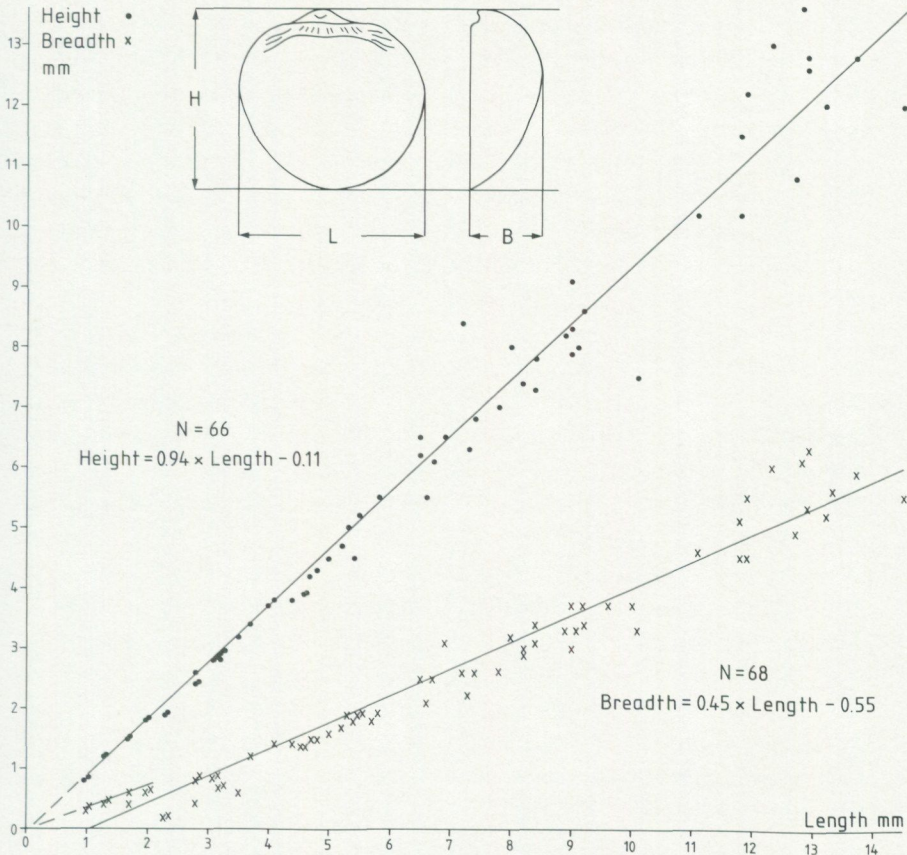


Fig. 17. *Freja fecunda* n.gen. and n.sp. Scatter diagram showing height/length and breadth/length relations. Unbroken lines are based on regression analysis.

fairly small, erect, apart, orthogyrate, sometimes raised above hinge line in anterior half of shell; maximum convexity about mid-height and just anterior to mid-length of shell; cardinal area with ligament grooves forming a chevron pattern; dorsal margin straight; anterior margin evenly rounded sometimes with ventral part long and straight; ventral margin rounded with deepest point in posterior half of shell; posterior margin slightly arcuate sometimes with a distinct angle in most posterior part.

DISCUSSION OF EXTERNAL FEATURES – The lateral outline of the shell may vary considerably. Fig. 17 shows the total height/total length ratio of 66 specimens ranging from 0.74–1.17, mean value 0.94. The H/L ratio of shells shorter than 9 mm is generally less than 0.94. These shells are almost circular in shape while the largest specimens have a more variable H/L ratio.

The largest individuals are distinctly transversely elongate (opisthocline) and they are often rather thin-shelled (Fig. 18:J). Fig. 17 also shows the breadth/length relation ranging from 0.09–0.49 with a mean value of 0.45. Three valves, about 2–4 mm long have extremely low B/L values which may be due to lateral deformation of the shells. The smallest specimens seem to have a B/L ratio which appears to satisfy a regression line pointing towards origo. These smallest shells are generally articulated valves. As with the H/L ratio, the B/L ratio of the largest specimens is highly variable having a proportionally greater breadth than the smaller ones, i.e. the shells become more gibbous with increasing age.

Only 9 articulated specimens were found, 5 of which being equivalve. In 3 of 4 inequivalved specimens the left valve was more convex while in the remaining one the right valve was more convex. The mean B/L ratio of 31 complete left valves is 0.35 and for 25 complete right valves 0.33. The B/L ratio of 30 complete left valves of the equivalved *Nuculoidea lens* is 0.28 and for 28 right valves 0.29. Thus, the two species exhibit similar statistical deviation suggesting that *Freja fecunda*, too, is equivalved.

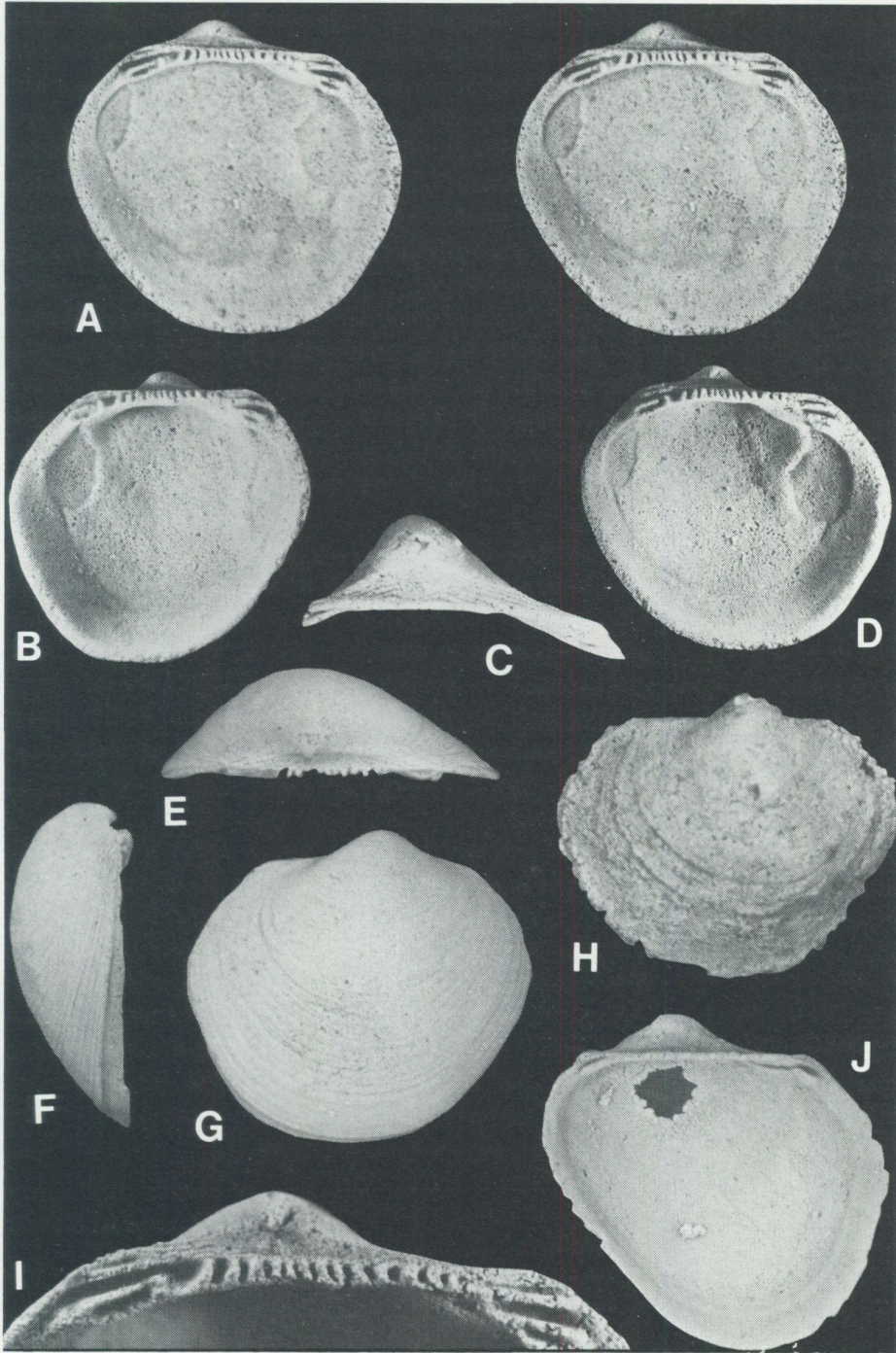
The position of umbo relative to total length is diagrammatically shown in Fig. 19. There is a clear trend for the smallest shells to have an a/L relation of 0.40–0.46, i.e. the umbones are almost on the median axis of the shell (Fig. 18:A, H). The ratio of the largest valves, however, is 0.30–0.40 and as a consequence their umbones are in a somewhat pronounced anterior position (Fig. 18:J).

The ligament area is divided into two lateral halves exhibiting a striated chevron-shaped pattern of grooves. The chevrons occur centrally and increase in length centrifugally (Fig. 18:C, 21).

INTERNAL FEATURES – The hinge line is straight, constituting the entire dorsal margin with ventrally divergent anterior lateral, cardinal and posterior lateral teeth (Figs. 18:I, 20:A). In adults there are 2–3 anterior lateral and 3 posterior lateral teeth, long, lamellar, rather deep and almost parallel to the antero-dorsal and postero-dorsal margin, respectively. The holotype has 13 cardinal teeth and sockets equal in size and shape, short, lamellar rather deep, radiating from the beak and one rather deep conical pseudocardinal tooth and corresponding socket between the anterior lateral teeth and cardinal teeth.

Fig. 20:A is a diagrammatic representation of the hinge of the holotype. The teeth are arranged in a ventrally divergent pattern, the cardinals radiate from a

Fig. 18. *Freja fecunda* n.gen. and n.sp. A. Stereo pair, internal lateral view of holotype (right valve); SGU Type 3367, $\times 5$, sample G77–28LJ. B. Internal postero-lateral view of holotype showing muscular impressions, $\times 4.8$. C. External view of ligament area; SGU Type 3409, $\times 5$, sample G78–2LL. D. Internal antero-lateral view of holotype showing muscular impressions, $\times 4.5$. E. External dorsal view of holotype, $\times 5.1$. F. External anterior view of holotype, $\times 5.3$. G. External lateral view of holotype, $\times 5.2$. H. External lateral view of right valve; SGU Type 3461, $\times 10$, sample G79–86LJ. I. Detail of hinge, holotype, $\times 12$. J. Internal lateral view of right valve; SGU Type 3379, $\times 3.7$, sample G77–28LJ.



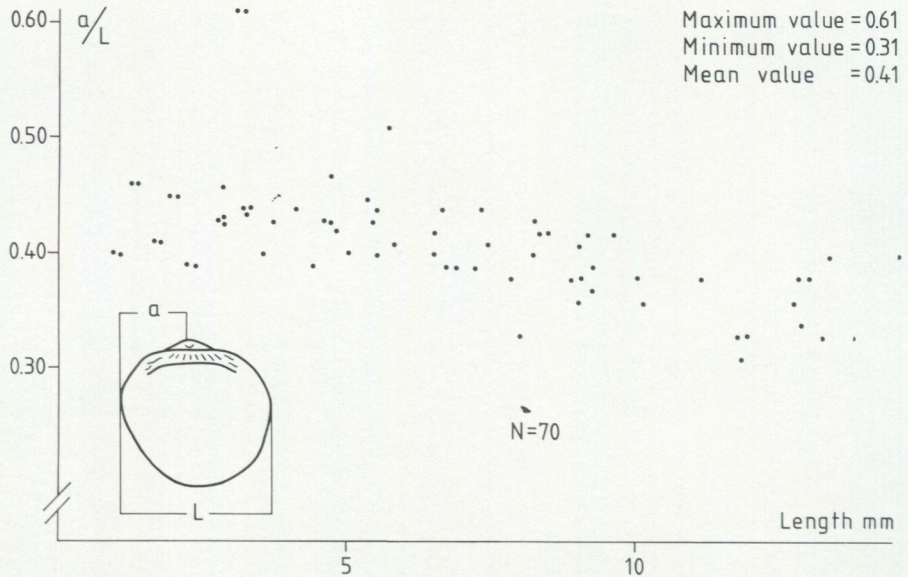


Fig. 19. *Freja fecunda* n. gen. and n. sp. Scatter diagram showing lateral position of umbo in relation to total length (for discussion see p. 42).

point well above the hinge line, the laterals from a point just above the hinge line. The position and length of the ventralmost posterior lateral teeth may vary considerably from being rather short, and then arranged in much the same manner as the anterior lateral teeth, to being extremely long and then extending below and along the inside of the umbonal area (cf. *Cyrtodonta huronensis* Billings, in Pojeta 1971, Pl. 7:2) sometimes (in large shells) extending from the junction of the dorsal margin and the posterior margin halfway to the umbo.

In large shells all hinge teeth are proportionately minute while the interumbonal ligamental area is considerably enlarged compared with smaller specimens. In the largest specimens no cardinal teeth have been observed. It is possible that the central part of the hinge was overgrown by the ventrally expanding ligament which is the case in many extant arcoids (Thomas 1978a:188).

The anterior adductor muscle scar (No. 1 in Fig. 21) is always the deepest impression, while the posterior adductor muscle scar (No. 2 in Fig. 21) is the largest. The scar below the posterior lateral teeth (No. 3 in Fig. 21) probably indicates the position of a posterior byssal/pedal retractor muscle. Scars 4-7 in Fig. 21 may be the traces of the muscles of the foot. The small incisions in the vicinity of the anterior adductor muscle scar (No. 8 in Fig. 21) probably served as attachment of the gills, while the impressions at No. 9 in Fig. 21, similar in size and form to No. 8 but placed close to the posterior adductor muscle scar, are presumably traces of visceral muscles. Compared with the most abundant

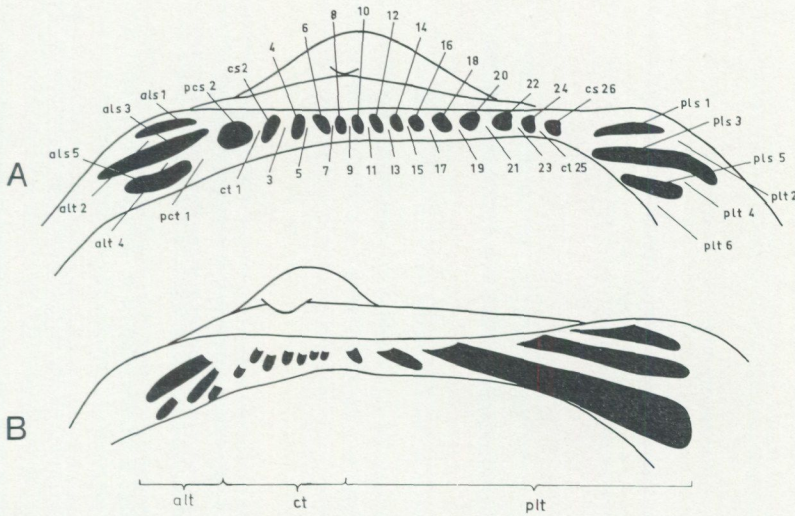


Fig. 20. Diagram of the hinge. A. *Freja fecunda* n.gen. and n.sp., SGU Type 3367 (holotype) sample G77-28LJ, alt = anterior lateral teeth, als = anterior lateral sockets, Pct = pseudocardinal tooth, Pcs = pseudocardinal socket, ct = cardinal teeth, cs = cardinal sockets, plt = posterior lateral teeth, pls = posterior lateral sockets. B. "*Cyrtodonta*" *gibbosa* Salter, BM(NH) L49858, left valve (shell, teeth and sockets reversed here), alt = anterior lateral teeth, ct = cardinal teeth, plt = posterior teeth.

nuculoids found at Möllbos (Liljedahl 1983) the largest specimens of *Freja fecunda* show unusually faint muscular imprints.

DISCUSSION OF CLOSELY RELATED TAXA – The Silurian rocks of Gotland contain a few other specimens belonging to the genus *Freja*. Among previously described species the closest relative seems to be "*Cyrtodonta*" *gibbosa* Salter from the Silurian of Scotland, represented by one specimen only, a left valve (Fig. 20:B; see also Hind 1910, Pl. 4:17; Vogel, 1962, Pl. 5:3).

Freja fecunda has a prominent umbo, a relatively shorter dorsal margin than in "*Cyrtodonta*" *gibbosa* and is smaller, the greatest difference, however, being the hinge. In *Freja fecunda* there are 2–3 anterior laterals forming an acute angle with the dorsal margin (Fig. 20:A) while there are at least 4 anterior laterals in "*Cyrtodonta*" *gibbosa* deviating from the dorsal margin at an obtuse angle (Fig. 20:B). The 13 cardinals in the holotype of *Freja fecunda* are uniform, in "*Cyrtodonta*" *gibbosa* there are about 7 of different size and shape. The posterior laterals of *Freja fecunda* have almost the same length as the anteriors, i.e. about 1/3 of the length of the dorsal margin, while the posterior laterals in "*Cyrtodonta*" *gibbosa* are long, extending over half the length of the hinge line. The hinge of *Freja fecunda* is almost symmetrical but in "*Cyrtodonta*" *gibbosa* it is asymmetrical, the posterior part being longest and with the largest teeth. As a whole the dentition of *Freja fecunda* is delicate, that in "*Cyrtodonta*" *gibbosa* being strong.

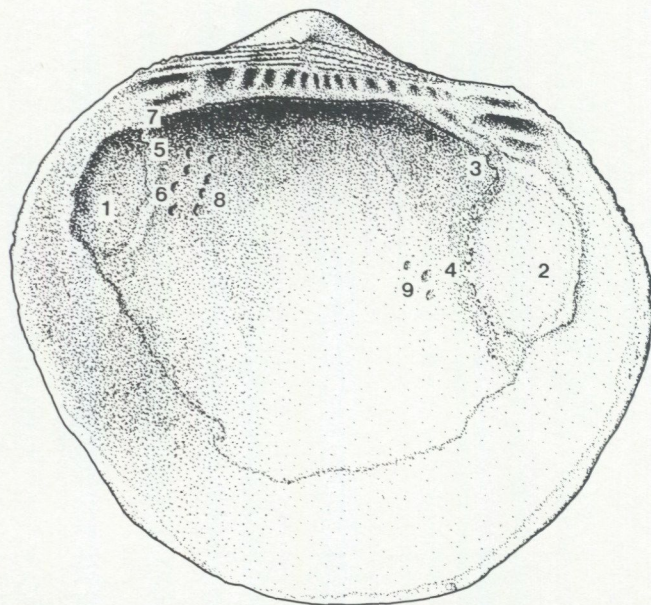


Fig. 21. *Freja fecunda* n.gen. and n.sp. Internal view of holotype showing hinge and muscular impressions (SGU Type 3367, sample G77-28LJ). 1 = anterior adductor muscle scar. 2 = posterior adductor muscle scar. 3 = posterior byssal/pedal retractor muscle scar. 4-7 = accessory muscle scars of the foot. 8-9 = muscle traces of the gills?

OCCURRENCE—Halla Beds, Wenlockian, Silurian, at Möllbos 1, Gotland, Sweden.

FUNCTIONAL MORPHOLOGY AND LIFE HABIT. — *Freja fecunda*, belonging to the order Arcoidea, exhibits features characteristic of both byssally attached and free-burrowing forms. The straight antero-ventral margin and the low maximum life position breadth make for good physical stability for the shell (Fig. 22:A). The anterior adductor muscle scar is somewhat smaller than the posterior one, close to which is situated an assumed, comparatively large posterior byssal or/and pedal retractor muscle scar, suggesting byssal attachment of the valves.

In bivalves reduction in size of the anterior adductor muscle is generally accompanied by reduction of the whole anterior shell region, the posterior shell region thus being elevated so that the inhalent currents of closely crowded individuals are not obstructed (as often among e.g. mytilids; Yonge 1953:452). The anterior reduction (in mytilids) also causes the byssal retractor muscles to lie in a position just above the byssus, enabling the ventral margin to be close to the substratum with great strength (Stanley 1970:25).

The anterior region of *F. fecunda* is somewhat smaller than the posterior region, the anterior adductor muscle scar is slightly reduced in size and the shell as a whole is slightly prosocline with the umbones lying anteriorly.

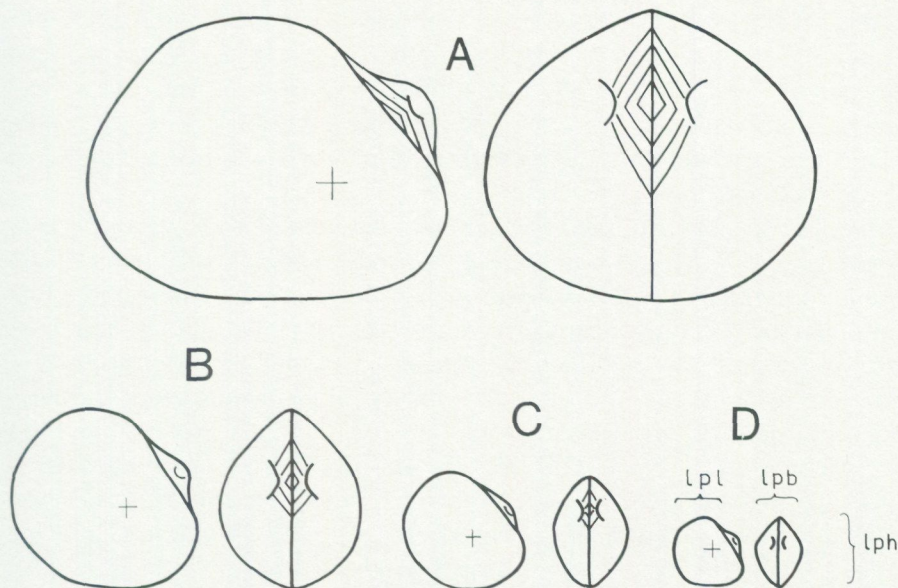


Fig. 22. *Freja fecunda* n.gen. and n.sp. Shell form modification during ontogeny. A. SGU Type 3379, sample G77-28LJ. B. SGU Type 3414, sample G79-2LL. C. SGU Type 3434, sample G79-79LJ. D. SGU Type 3480, sample G79-95LJ, all left valves, articulated specimens based on mirror image of left valves. Note increasing gibbosity with growth. lph = life position height, lpb = life position breadth, lpl = life position length. Point of maximum breadth at +.

The morphology of juvenile *F. fecunda* deviates from that of the largest specimens. The smallest shells show typical burrowing characters (cf. Lucinacea), i.e. circular shape, beaks almost on the median axis, point of maximum gibbosity being above half life position height, life position length being about half life position height (No. D in Fig. 22 = 0.7 and 0.5, respectively) and ventral margins of the two valves forming an acute angle. The dentition is strong and the ligamental area small. The largest specimens of *F. fecunda* exhibit characters of byssally attached forms, i.e. opisthocline shells, beaks in an anterior position, point of max. gibbosity at somewhat less than half the life position height, life position length slightly greater than life position height, A in Fig. 22 = 0.4 and 1.1, respectively. The dentition is delicate compared with immature individuals and the ligament is conspicuously enlarged.

Thus, with increasing size the region of maximum width gradually approaches the substrate (Fig. 22). Furthermore, the antero-ventral margin becomes straight and shell breadth increases in relation to height. These ontogenetic changes in shell morphology, together with the reduced anterior adductor muscle scar, suggest that *Freja fecunda* holds an intermediate position between typical infaunal and epifaunal species, i.e. it was presumably a semi-infaunal, endobysate suspension feeder (Fig. 34:6).

Extant arcoids with chevron-shaped teeth are active burrowers, while those with vertical teeth are either epifaunal, or they have well-developed marginal crenulations (Thomas 1978a:188). The primitive mixture of vertical cardinal and oblique lateral teeth in *Freja fecunda* probably indicates a mode of life intermediate between one of active burrowing and epifaunal attachment, i.e. it was endobyssate.

Phylogenetic aspects of the intermediate characters of *Freja fecunda* are of paramount interest (Fig. 16). According to Yonge (1962) adult byssate forms arose in the course of evolution by neoteny. Stanley (1975:369) suggested that transitional species between epifaunal (epibyssate) and infaunal (non-byssate as adult) species would be found in the fossil record, i.e. endobyssate forms. Most of these early endobyssate ancestors of epifaunal forms were cyrtodontids and modiomorphids (Stanley 1975:381).

As pointed out by Pojeta (1971:35) the ecological status of cyrtodontids is difficult to evaluate since no similar extant bivalves are known. Ordovician cyrtodontids show a variety of forms probably reflecting diverse modes of life (Pojeta 1971:35). On the basis of features typical of byssally attached bivalves in *Vanuxemia* type cyrtodontids and the presence of epibionts on the posterior part of some of the shells, Pojeta (1971:32, Fig. 8) made a reconstruction of semi-infaunal endobyssate life habit for them, with the posterior end protruding above the sediment. Other cyrtodontids (of the *Cyrtodonta* type), resembling *Freja fecunda* more than the *Vanuxemia* type were also suggested to have been byssally attached, because of reduction of the anterior part of the shell and anterior displacement of the beaks. Other species, *Glycymeris*-like and *Noetia*-like shells, were suggested to have been shallow burrowing, non-byssate infaunal forms (Pojeta 1971:37).

Stanley (1972:204) suggested that semi-infaunal suspension-feeding Ordovician cyrtodontids might have had a weak byssus "... for added stability in shallow life positions", as endobyssate habits, according to him evolved in cyrtodontids leading to the early paralleodontids (Stanley 1972:183, 204, Fig. 15). I believe, however, that endobyssate forms evolved from primitive infaunal arcoids (like *Freja fecunda* and "*Cyrtodonta*" *gibbosa*) which later separately produced endobyssate cyrtodontids and endobyssate or epibyssate paralleodontids and possibly the epibyssate pteroids (cf. discussion on p. 55, Fig. 16).

The cardiolids, being epibyssate, probably descended from infaunal or semi-infaunal "cyrtodontids" (Kříž 1979:36, 37, Fig. 37). Characters in common to cardiolids and *Freja fecunda* are straight hinge line with interumbonal growth, triangular ligament area, reduced anterior adduct muscle and prosogyrate umbones (cf. Kříž 1979:36). Thus, *Freja fecunda* probably originated from a primitive, semi-infaunal, endobyssate arcoid, also being radical to the alleged semiinfaunal, endobyssate early cardiolids (Fig. 16).

Order PTERIOIDA NEWELL, 1965
Suborder PTERIINA NEWELL, 1965
Superfamily AMBONYCHIACEA MILLER, 1877
Family AMBONYCHIIDAE MILLER, 1877

Genus *Mytilarca* Hall & Whitfield, 1869

For extensive synonymy list, diagnosis, description as well as discussion of the synonymy, see Pojeta 1966:185–187.

DISCUSSION OF GENERIC AFFILIATION – The concentric growth-striae prosopon (external surface sculpture or ornamentation, Gill 1949; Pojeta 1962) of *Mytilarca?* sp. agrees with the prosopon of the ambonychiid genera *Mytilarca* Hall & Whitfield, 1869, *Cleionychia* Ulrich, 1892, and *Anoptera* Ulrich, 1893. However, the hinge of *Mytilarca?* sp. differs from that in *Cleionychia*, which has one cardinal tooth only and no lateral elements. *Cleionychia* also exhibits a more quadrangular shell shape compared to *Mytilarca?* sp. In shell form *Mytilarca?* sp. resembles *Anoptera* in being erect and subovate. The hinge and ligament of *Anoptera* is not known, although Ulrich (1893:649) considered it to be edentulous. *Mytilarca?* sp. shows similarities in shell shape with species of *Mytilarca* having a subovate form, the height exceeding the length. *Mytilarca* is the only one of three genera in question in which the hinge and ligament is well known. It has 1–3 strong, oblique anterior teeth and 2–4 posterior parallel teeth. In detail this dentition differs from that of *Mytilarca?* sp. though, since the posterior teeth in species of *Mytilarca* are divergent, the ventral ones being shorter than the marginal one. However, it seems more plausible that *Mytilarca?* sp. belongs to the genus *Mytilarca* rather than to either of the two other ambonychiid genera.

Mytilarca? sp.
Figs. 23, 24, 34:10

MATERIAL – One almost complete right valve and three fragments of silicified specimens as well as three non-silicified valves from the Swedish Museum of Natural History, Stockholm.

DESCRIPTION – Shell small, suboval, inequilateral with prominent anterior truncation, strongly convex; height slightly greater than length, breadth about 1/3 of length; obliquely prosocline, beaks terminal, prosogyrate; byssal sinus shallow; anterior byssal gap; ligament area with longitudinal grooves; dentition in right valve consisting of two small, elongate, cardinal teeth immediately posterior to and below beak, pointing postero-ventrally, two elongated, contiguous posterior teeth in posterior extremity of dorsal margin almost parallel to shell

margin, situated on a broad plate just below and posterior to most distal part of ligament area; external shell surface with faint to more pronounced commarginal, smooth lines and furrows; posterior muscular impression below and posterior to posterior teeth, laterally; angle between anterior margin and dorsal margin about 80°.

DISCUSSION OF DESCRIPTION – One of the specimens is an almost complete right valve (Fig. 23:A, C). It is fractured in its posterior and ventral ends, fairly eroded, so that the hinge and ligament are hardly discernible and the tip of the beak is broken. However, the dorsal margin is preserved in its full length and the posterior teeth thus observable, although poorly preserved. The exterior of the shell has an almost smooth surface with faint commarginal growth lines (Fig. 23:A). There is probably a byssal opening but the valve is too incompletely preserved for certainty. Another specimen consists of half a right valve with the anterior part extremely well-preserved showing cardinal teeth and ligament in detail (Fig. 23:B). In the most anterior end of the ligament area the ligament grooves are not discernible. Instead thin coatings of pyrite can be seen, probably representing remnants of the ligament.

The reconstruction of *Mytilarca?* sp. as seen in Fig. 24 is based on the silicified specimens SGU Type 3839 and SGU Type 3840 from Möllbos in combination with three non-silicified specimens from Gotland (see under Occurrence). In one of these specimens (MO. 22900) the entire lateral outline can be seen, in another (MO. 22895) a preserved hinge line with anterior as well as posterior elements of the hinge are present. The teeth resemble those in the silicified material, posterior teeth being better preserved, consisting of two narrow lamellar contiguous teeth lying parallel to each other and to the valve margin. Two of the non-silicified specimens are eroded to some extent so that most of the shell material has been lost and thus they are, with the exception of the beak and the hinge margin, internal moulds. The external surface of the first specimen (MO. 22900) is well-preserved, showing a pattern of close, fine concentric growth lines. One of the non-silicified specimens (MO. 22865) possibly has an anterior byssal opening.

DISCUSSION OF CLOSELY RELATED TAXA – Some previously described species of *Mytilarca* show external similarities to *Mytilarca?* sp., e.g. the Middle Devonian *Mytilarca suberectus* (Pohl, 1929) the dentition of which is unknown (Pojeta 1966:190, Pl. 39:5), and the two late Devonian *Mytilarca lata* Hall, 1883 and *Mytilarca simplex* Hall, 1883. Since these and most other species of *Mytilarca* are often recognized on their exterior only, specific comparisons are of little value and a meaningful taxonomic discussion impossible.

OCCURRENCE – Wenlockian Slite Beds at Lanså, Fårö, and Halla Beds at Möllbos 1; Ludlovian Hemse Beds at Mannagårda and Burgsvik Beds at Grötlingbo. All localities on Gotland, Sweden.

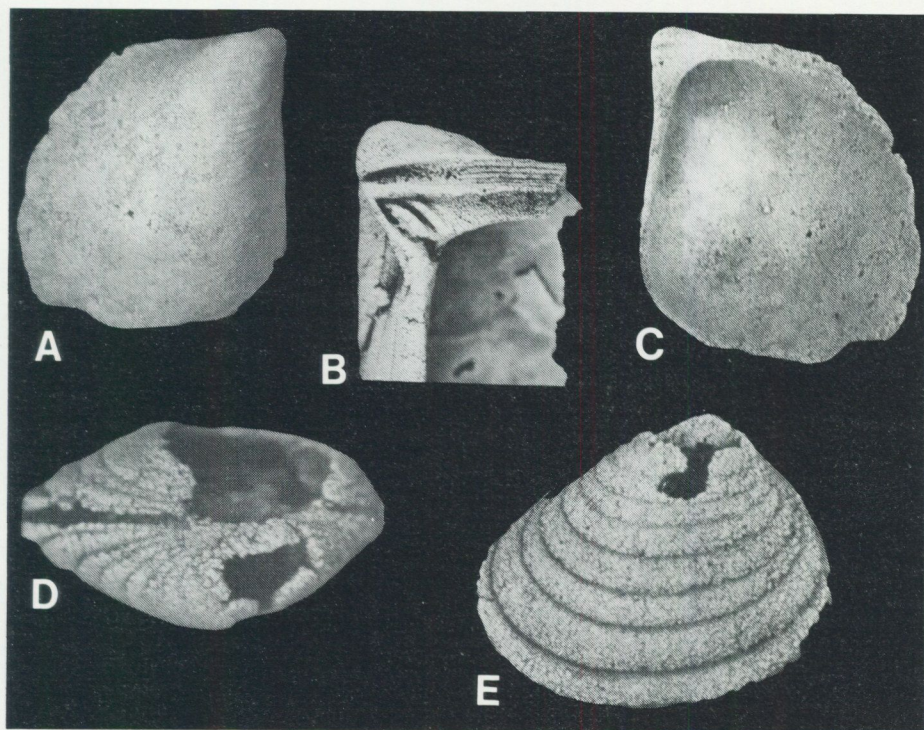


Fig. 23. A. *Mytilarca?* sp. External lateral view of right valve; SGU Type 3839, $\times 2.9$, sample G79-95LJ. B. *Mytilarca?* sp. Internal view of right valve, detail of anterior part of the hinge; SGU Type 3840, $\times 5.2$, no sample number. C. *Mytilarca?* sp. Internal lateral view of right valve (same as A), $\times 2.9$. D. Gen. and sp. indeterminate. External dorsal view, anterior to the left; SGU Type 3836/3837, $\times 11.7$, sample G77-28LJ. E. Gen. and sp. indeterminate, external lateral view of left valve, same specimen as D, $\times 11.5$.

FUNCTIONAL MORPHOLOGY AND LIFE HABIT – The Siluro-Devonian genus *Mytilarca* belongs to the extinct family Ambonychiidae, representatives of which are probably related to the modern pteriinids (Newell 1969:285). This genus existed for almost 100 million years and vanished without leaving any known descendants (Pojeta 1966:200, Fig. 3).

The hard-part morphology of *Mytilarca?* sp. shows adaptation for epifaunal mode of life, i.e. probably it was an epibyssally attached suspension-feeder. This assumption is based on the following reasons: It has (1) a principally triangular shape (in dorsal view of articulated specimen; Fig. 24:C) with straight anterior margin presumably in contact with the substratum, (2) pronounced anterior reduction (lacking anterior lobe), (3) maximum breadth close to the straight anterior margin touching the substratum (Fig. 24), (4) a fairly thin unornamented shell (Fig. 23:A).

The slightly sinuate, almost straight anterior margin accommodating a byssal

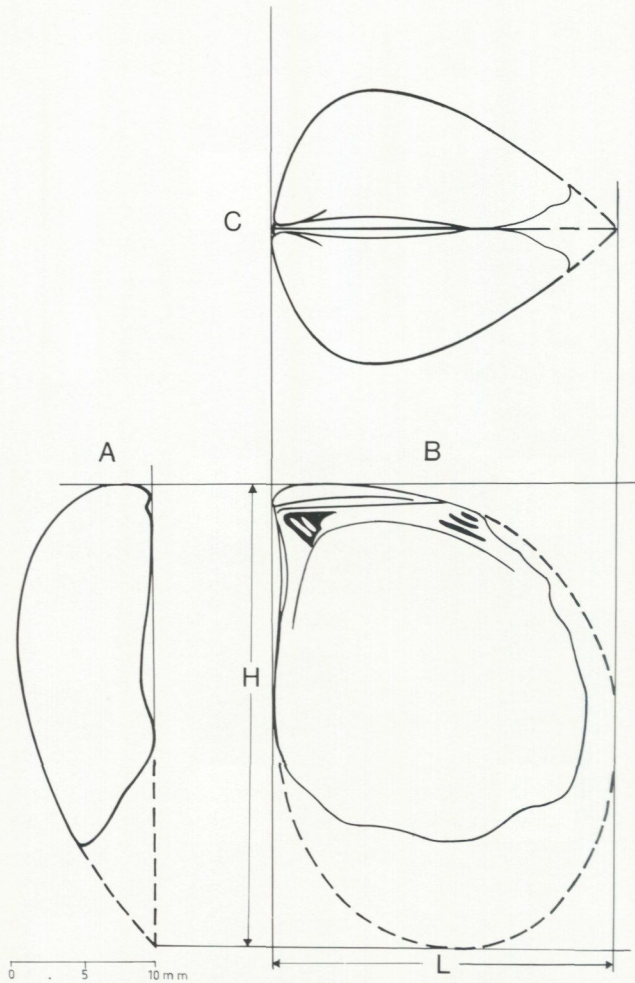


Fig. 24. *Mytilarca?* sp. Diagrammatic drawing of reconstructed right valve. A. Anterior view, note byssal opening. B. Internal lateral view. C. Dorsal view, left valve mirror image of right valve. L = total length of shell. H = total height of shell (for discussion see p. 50).

opening, suggests byssal attachment (Figs. 24, 34:10). In *Mytilarca?* sp. the point of gravity is closer to the substratum than in other ambonychiids although the breadth is not as great as that of extant *Mytilus*. Furthermore, *Mytilarca?* sp. is higher and has a comparatively narrower base, i.e. it has a less physical stability than *Mytilus* which lives in an extremely high energy environment, implying a less high-energy habitat for the former.

The fact that the silicified material investigated contains three fragmentary valves and one extremely worn shell of *Mytilarca?* sp. only, in combination with the assumed epibyssate life habit in a relatively high-energy environment (hard

substrate), suggests that this species was exotic and the individuals were transported into the fossil assemblage mentioned which inhabited a soft, muddy sediment (Fig. 34:10).

Superfamily PTERIACEA GRAY, 1847

Family PTERINEIDAE MILLER, 1877

Genus *Molinicola* n.gen.

DERIVATION OF THE NAME – Latin *molin-* (from *molina*, mill) and *-cola*, inhabitant, alluding to the place name of Möllbos.

TYPE SPECIES – *Molinicola gotlandica* n.sp.

SPECIES – *Molinicola gotlandica* n.sp., *Molinicola venusta* (Billings), *Molinicola curta* (Billings), *Molinicola oblonga* (Billings), and possibly *Molinicola? compressiformis* (McLearn).

DIAGNOSIS – Pterineid with left valve somewhat more convex than right valve; erect, subrectangular in lateral outline; concentric and in dorso-posterior part retroflex sculpture of growth lines, in anterior extremity consisting of growth rugae; delicate hinge, in adults about 5 ventrally divergent anterior teeth just anterior to beak and 1–2 narrow, elongate relatively short posterior teeth closely below and almost parallel to dorsal margin, about mid-length of dorsal margin; anterior and posterior adductor muscle scar and a number of additional accessory muscle scars.

DISCUSSION OF GENERIC ATTRIBUTION – Billings (1874:141) distinguished the genus *Pteronitella* including shells with separated anterior and posterior teeth, stressing that this arrangement was entirely different from the hinge type of both *Avicula* Klein and *Pterinea* Goldfuss, and added that as a whole, in fact, it closely resembled the hinge structure of *Cyrtodonta* Billings, 1858. He erroneously considered his material of *Molinicola venusta*, *Molinicola oblonga*, and *Molinicola curta* to be congeneric with *Pteronitella retroflexa* (Wahlenberg) since he based his concept of that species on the description of *Pterinea retroflexa* made by McCoy 1855:263.

Frech (1891:97, 80) described the genus *Micropteria* for pterineid shells with a continuous hinge, principally resembling the hinge of *Pteronitella retroflexa*. *Micropteria* is possibly a younger synonym of *Pteronitella*.

In 1899 Philippi described and illustrated the interior of a left valve (from the type locality) of what he considered to be *Pteronitella retroflexa*. He noted 5

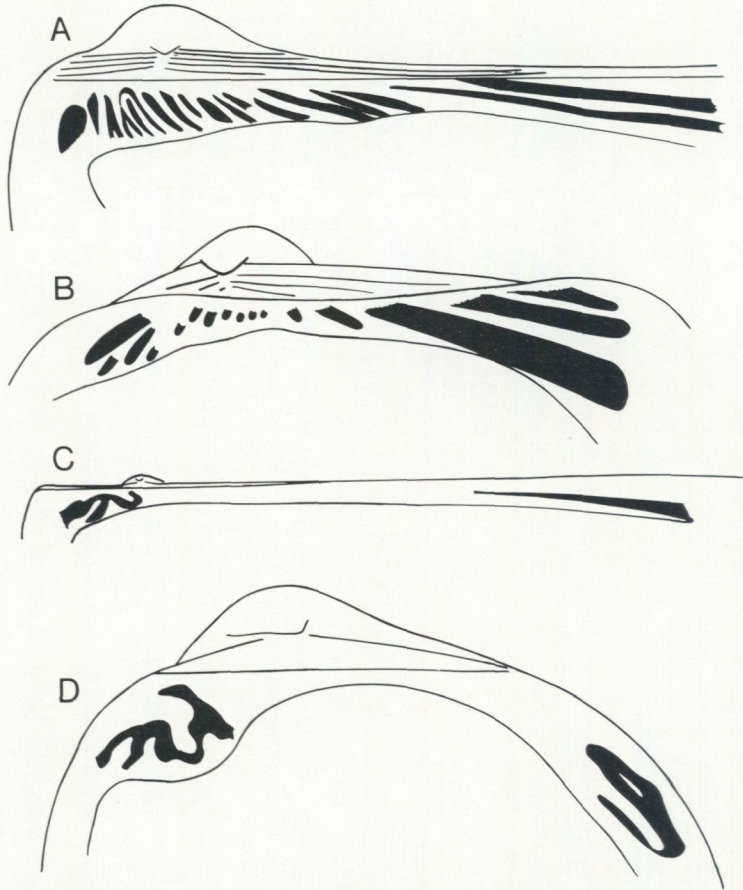


Fig. 25. A. *Pteronitella retroflexa* (Wahlenberg), MO 154001, left valve reversed here, U. Silurian. Also illustrated by Walmsley 1962:353, Pl. 1:4. B. "*Cyrtodonta*" *gibbosa* Salter, BM(NH) L49858, left valve, reversed here, L. Silurian. Also illustrated by Hind 1910, Pl. 4:17 and Vogel 1962, Pl. 5:3. C. *Molinicola gotlandica* n. gen. and n. sp.; SGU Type 3392 (holotype), sample G77-28LJ, right valve, U. Silurian. D. *Cyrtodonta saffordi* (Hall), USNM 46191, right valve, U. Ordovician, from Pojeta 1971, Pl. 7:1. (The specimens are not to scale relative to each other but made equal for easy comparison.)

anterior teeth which are clearly limited posteriorly by an edentulous area. Possibly the specimen is heavily eroded so that the remaining teeth have disappeared.

Billings did not select a type species for the genus *Pteronitella* but Williams & Breger (1916:193) stated that *Pteronitella retroflexa* was the type species. McLearn (1924:119), however, chose *Molinicola venusta* (Billings) as the genotype. According to the *International Code of Zoological Nomenclature* 1961:69, Art. 69. a iii (cf. discussion in Walmsley 1962:355) the choice of *Pteronitella retroflexa* (Wahlenberg) has priority over *Molinicola venusta* (Bil-

lings). Hence, Billings generic description of *Pteronitella* is erroneous, since it is not in accordance with the actual morphology of the type species.

Walmsley (1962) was the first to describe and illustrate the complete hinge of *Pteronitella retroflexa*. The three specimens of this species illustrated by Walmsley from the type locality (Hoburgen, Gotland) have a hinge that completely differs from that of *Molinicola*. The hinge of *Pteronitella retroflexa* as seen in these three specimens as well as in those of additional specimens from the type locality consists of a thick, broad and strong hinge plate carrying numerous ventrally divergent, lamellar teeth extending over the entire hinge line. The teeth are continuous and therefore not differentiated into anterior and posterior teeth. They are narrow, becoming progressively longer and broader towards the posterior end, those nearest that end being parallel to the dorsal margin, those nearest the anterior end perpendicular. The right valve of *Pteronitella retroflexa* on Pl. 1:3 in Walmsley 1962 is rather heavily eroded so that the photograph does not reveal the continuous nature of the teeth.

DISCUSSION OF PTERINEID ORIGIN – The straight dorsal margin and the hinge teeth pattern of *Pteronitella retroflexa* (Fig. 25:A), i.e. continuous hinge teeth along the entire hinge line reminiscent of the “actinodont” hinge type (Fig. 16:A), and the duplivincular ligament show a striking resemblance to similar features in “*Cyrtodonta*” *gibbosa* Salter (Fig. 25:B), suggesting a common origin (Fig. 16:C). These two species probably had different life habits (shallow semi-infaunal, see discussion on p. 62, and deep semi-infaunal, respectively), thus their similar “primitive arcoid” hinge and ligament construction indicating conservative features of morphology.

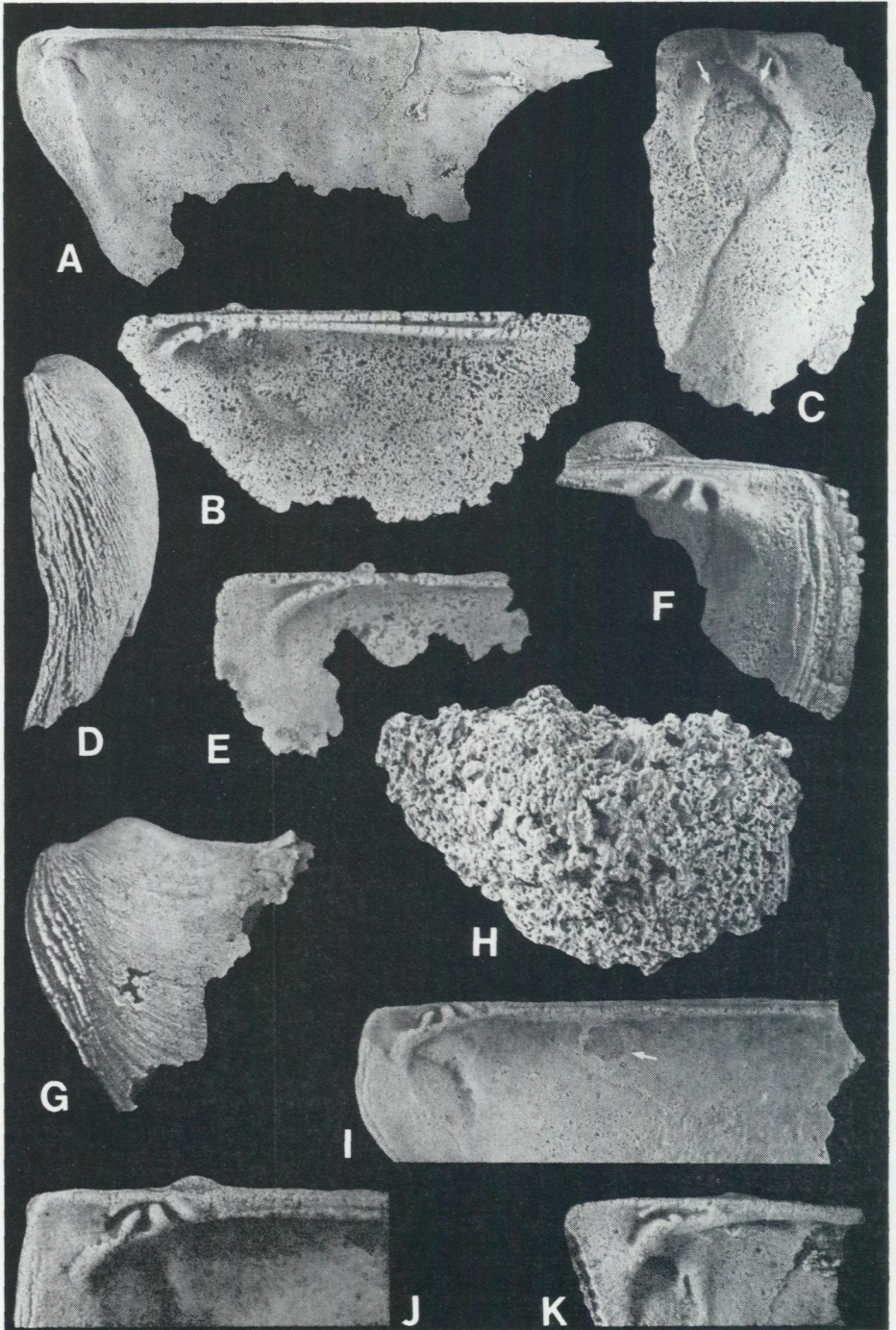
The hinge of *Molinicola gotlandica*, with separate anterior and posterior elements, (Fig. 25:C), resembles that in *Cyrtodonta* s.s. (Fig. 25:D), probably reflecting a reduction of cardinal teeth, in the cyrtodont and pterineid lines presumably owing to change of life habit from endo- to epibyssate (cf. shell morphology versus assumed life habit of *Freja*, p. 46).

Molinicola gotlandica n.sp.

Figs. 25, 26, 27, 28, 34:7

DERIVATION OF THE NAME – Latin for *Gotland*, referring to where it was first recorded.

HOLOTYPE – A right valve, SGU Type 3392 from sample G77–28LJ, (Figs. 26:I, J, 27:D) reconstructed height about 25 mm. Postero-ventral and postero-dorsal parts missing, existing part well-preserved, anterior region of hinge with one dorsal tooth and four ventral teeth, only most proximal part of two posterior teeth



preserved. Ligamental area preserved. External shell surface evidently eroded, lacking sculpture and partly covered by epibionts such as tabulates and possibly stromatoporoids.

TYPE STRATUM – Halla Beds, Late Wenlockian, Silurian.

TYPE LOCALITY – Möllbos 1, Gotland, Sweden.

MATERIAL – 138 valves with preserved beak and anterior hinge, some with posterior hinge preserved, one complete articulated juvenile specimen and an uncounted number of fragments.

DIAGNOSIS – *Molinicola* with relatively thin shell, erect and subquadrangular in lateral outline; anterior ear truncate, umbo almost terminal, angle formed by dorsal margin and ventral part of anterior margin in adults about 60°; about 4 small anterior teeth, in left valve 1 and in right valve 2 posterior teeth.

EXTERNAL FEATURES – Adult shell large, pteriiform, erect, inequivalve, inequilateral, compressed; left valve moderately convex with umbo clearly above dorsal margin, right valve less convex with umbo slightly above dorsal margin; byssal opening in anterior end just below hinge line in left valve (Fig. 26:D); external, duplivincular ligament; concentric growth lines and in anterior extremity growth lamellae (Fig. 26:D, G), in postero-dorsal part retroflex sculpture of growth lines; beaks apart, small, slightly prosogyrate at some distance from the sagittal plane; dorsal margin long, straight, forming maximum length of shell (Fig. 26:B); anterior margin meeting dorsal margin at an obtuse angle, straight in its dorsal part which forms an angle of about 60° with the dorsal margin and straight to slightly S-shaped ventrally; ligamental area between hinge line and beak extending from anterior extremity not reaching beyond distal end of posterior hinge teeth posteriorly, with ligamental grooves forming a chevron pattern.

Fig. 26. *Molinicola gotlandica* n.gen. and n.sp. A. Internal lateral view of right valve; SGU Type 3393, ×1.2, sample G77–28LJ. B. Internal lateral view of right valve; SGU Type 3394, ×7.9, sample G77–28LJ. C. Internal lateral view of left valve, detail of anterior region, note pedal protractor muscle scar (at arrows), cf. 28:4 and 8 (see p. 60 for discussion); SGU Type 3703, ×4.2, sample G79–84LJ. D. External anterior view of left valve (note byssal opening); SGU Type 3827, ×2.2, sample G79–115LJ. E. Internal lateral view of right valve (cf. Fig. 27:A); SGU Type 3487, ×5.9, sample G78–2LL. F. Internal lateral view of left valve, detail of anterior hinge region; SGU Type 3395, ×4.8, sample G77–28LJ. G. External lateral view of antero-dorsal part of left valve; SGU Type 3828, ×1.8, sample G79–115LJ. H. External lateral view of left valve of smallest and only articulated specimen of the species; SGU Type 3683/3684, ×33, sample G79–83LJ. I. Internal ventro-lateral view of holotype (right valve), note byssal/pedal retractor muscle scar (at arrow, cf. Fig. 28:3); SGU Type 3392, ×3.6, sample G77–28LJ. J. Internal lateral view of holotype, right valve, detail of anterior part of hinge (cf. Fig. 27:D), ×4.9. K. Internal lateral view of right valve, detail of anterior part of hinge (cf. Fig. 27:C,D); specimen lost.

DISCUSSION OF EXTERNAL FEATURES – The usually preserved part of the shell is the anterior end including the umbo and the anterior part of the hinge. No complete adult specimen is known. The incomplete valves show no sign of pre-lithification breakage but seems to be unsufficiently silicified. Only one articulated specimen was found, this juvenile ($L = 1.8$ mm) being the smallest record for this species (Fig. 26:H). The umbo of this specimen is fairly prominent and situated high above the hinge line with the beak somewhat anterior to mid-length of the shell. The umbo of adults is almost terminal and becomes less pronounced with increasing age. The left valve of this articulated specimen is only slightly more convex than the right one, with maximum convexity just anterior to mid-length and slightly above mid-height of the shell. The angle formed by the dorsal margin and the oblique ventral part of anterior margin is about 40° in this specimen. In another juvenile valve this angle is also about 40° and in a third small valve about 50° . The angle increases with growth and is in adults about 60° .

INTERNAL FEATURES – Hinge line straight, anterior part of hinge on a small, delicate plate below and just anterior to beak, posterior part of hinge along dorsal margin. Hinge somewhat variable in adult right valves, anterior part of hinge containing either one marginally elongated tooth, three short, somewhat elongated, ventrally divergent teeth, and one blunt, anterior ventral tooth and three sockets similar in shape and size to the three ventrally divergent teeth, sockets united and limited dorsally by the marginal tooth, a fourth posterior socket just below beak pointing postero-ventrally, alternatively one marginal, antero-ventrally directed tooth and one ventral, antero-ventrally directed tooth limited dorsally and posteriorly by an arcuated socket. In adult right valves posterior part of hinge at a considerable distance from both anterior and posterior extremities of shell, respectively, containing two low, lamellar teeth and a socket between them almost parallel to dorsal margin (Fig. 26:A). In adult left valves anterior and posterior teeth and sockets fit into corresponding features on right valve (Fig. 26:F).

In juveniles the hinge construction is simple, in the right valve consisting of a short, narrow oblique anterior tooth (*at* in Fig. 27:A), and in later ontogenetic stages of two long, slightly radiating anterior, see Fig. 26:B, E (*adt* and *avt* in Fig. 27:B), and posterior lamellar teeth (Fig. 26:B). They originate from just below the beak and extend over almost the entire hinge line (Fig. 26:B). The posterior teeth become relatively shorter with increasing age, being in adults situated at about mid-length of shell. Thus the dorsal margin has a long edentulous part between the anterior and posterior elements of the hinge as well as posterior to the posterior teeth (Fig. 26:A).

In the right valve the most proximal part of the anterior dorsal tooth in juveniles (*adt* in Fig. 27:B, C) becomes an antero-ventrally directed tooth in its anterior part (*at5* in Fig. 27:D) and a postero-ventrally directed tooth in its posterior part (*at4* in Fig. 27:D) being the most proximal of the anterior teeth. The anterior ventral

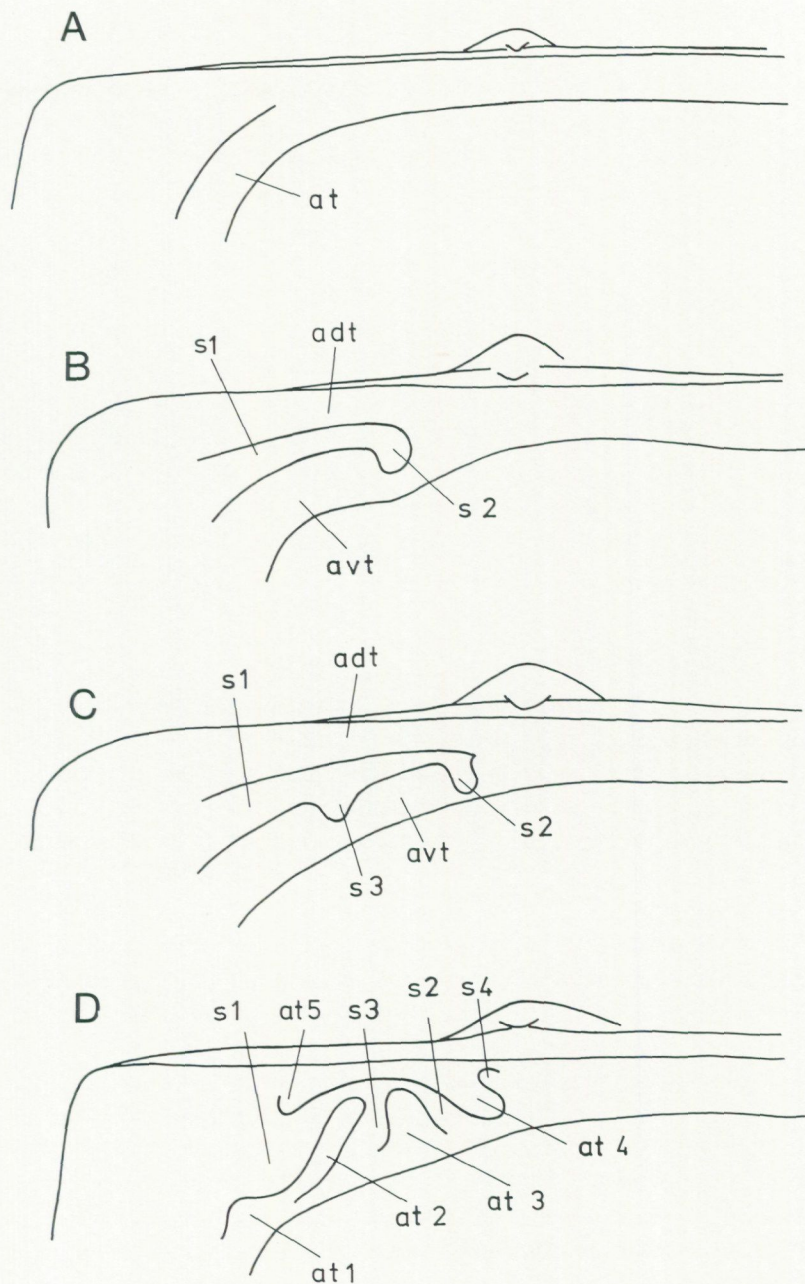


Fig. 27. *Molinicola gotlandica* n.gen. and n.sp. Hinge ontogeny. A, B, C = juveniles, D = adult (not to scale to each other), at = anterior tooth, adt = anterior dorsal tooth, avt = anterior ventral tooth, s = socket.

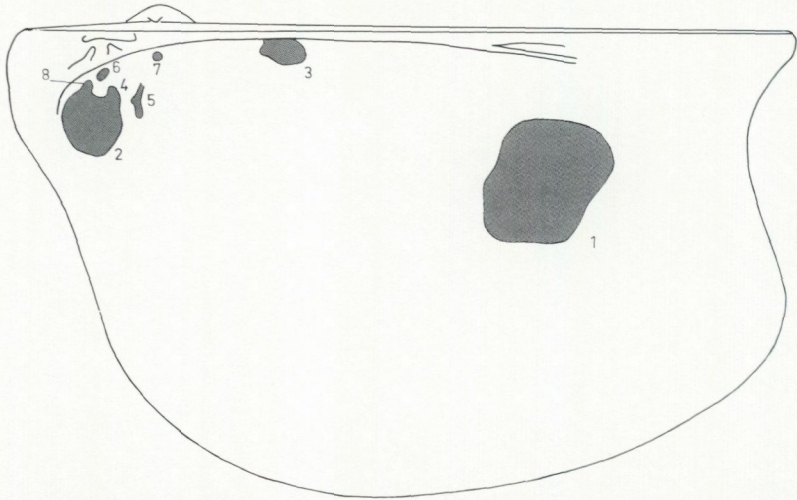


Fig. 28. *Molinicola gotlandica* n.gen. and n.sp. Muscular imprints. 1 = posterior adductor muscle scar. 2 = anterior adductor muscle scar. 3 = byssal and pedal retractor muscle scar. 4 = pedal protractor muscle scar. 5 = byssal retractor muscle scar. 6 = pedal elevator muscle scar. 7 = byssal retractor muscle scar. 8 = pedal protractor muscle scar.

tooth (*avt* in Fig. 27:B, C) is cut off in the middle and proximal parts so that the two ventrally divergent sockets open ventrally (*s2* and *s3* in Fig. 27:D) the rest of the tooth forming the two remaining ventrally divergent anterior teeth (*at2* and *at3* in Fig. 27:D). The most distal part of the ventral tooth (*avt* in Fig. 27:B, C) is the most anterior tooth (*at1* in Fig. 27:D) on the hinge (see also Fig. 26:K, *at1* and *at2* not yet developed).

MUSCULAR IMPRESSIONS – The representatives of the family Pterineidae, to which *Molinicola gotlandica* belongs, became extinct in Late Palaeozoic times (Newell & LaRoche 1969). So that the functional morphology of *Molinicola gotlandica* can be understood comparisons are made with living Pteriidae.

The medium-sized, heavily impressed anterior adductor muscle scar (No. 2 in Fig. 28) is somewhat smaller than the posterior adductor muscle scar (No. 1 in Fig. 28). Scar No. 3 in Fig. 28 (see also Fig. 26:I) probably shows the position of a byssal and pedal retractor muscle (cf. pedal retractor anterior to and connected with the hypertrophied, central posterior adductor muscle of *Pinctada maxima* in Takemura *et al.* 1957, Pl. 2). Scars Nos. 5 and 7 in Fig. 28 are possibly the attachment of a bifid anterior byssal retractor (cf. Newell 1942:30, Fig. 6). Scars Nos. 4 and 8 in Fig. 28 are probably the impressions of pedal protractors (see also Fig. 26:C). Scar No. 6 in Fig. 28 has a position similar to the levator of the foot in *Pinctada maxima*, i.e. just below the hinge line in the anterior part of the shell (Takemura *et al.* 1957, Pl. 2).

The pallial muscles of *Pinctada maxima* are most heavily impressed in the anterior part of the shell as in *Molinicola gotlandica* (Fig. 26:C).

DISCUSSION OF CLOSELY RELATED FORMS – Only forms with a documented hinge are of interest since external features are considered taxonomically inferior. Unfortunately, only a few descriptions treat the interior, since pterineids are seldom well-preserved owing to their epifaunal habit. Most fossils of pterineid are heavily eroded and this is so even with the exceptionally well-preserved silicified material from Möllbos. However, a few specimens of this species from this locality are almost intact, at least in the hinge region.

Molinicola venusta as illustrated by Billings (1874, Pl. 9:5b) displays only a general view of the teeth arrangement. It agrees principally with *M. gotlandica* although no details are given. In lateral outline the anterior ear of *M. venusta* is acute while *M. gotlandica* has a truncate anterior ear. The dorsal half of the anterior margin in *M. venusta* is evenly rounded while in *M. gotlandica* it is straight, making a sharp bend where it meets the ventral margin. The right valve of *M. venusta* is almost flat while in *M. gotlandica* it is convex. In his description of *M. oblonga* Billings only accounts briefly for several anterior teeth and it is thus impossible to compare it with *M. gotlandica* in further detail. There are 2–3 posterior teeth in *M. oblonga*, i.e. at least one more than in *M. gotlandica*. The angle between the dorsal margin and the anterior margin is 85–90° in *M. oblonga* which thus deviates in shape from the more acute shape of the anterior extremity of *M. gotlandica*, the corresponding angle of which is about 60°. In *M. curta* (Billings) there are 3 posterior teeth, that is one more than in *M. gotlandica*. The height is greater than the length by contrast to *M. gotlandica*. The angle between the dorsal and ventral margins in *M. curta* is more than 90°, and the anterior margin is nearly straight or slightly concave in the upper third, while in *M. gotlandica* the anterior margin is rounded in its dorsal part with a distinct postero-ventral bend giving the shell a somewhat oblique appearance.

Molinicola? compressiformis (McLearn, 1924) is difficult to evaluate since the dentition of the type material is only poorly preserved. The relative height of *Molinicola? compressiformis* is much greater than in *M. gotlandica* and it thus deviates greatly from this form superficially. *M. quadrata* (Williams & Breger), assigned to *Pteronitella* by these authors, has no anterior hinge preserved so that its affinities are questionable.

In external features *Molinicola gotlandica* closely resembles *Pteronitella retroflexa*, for instance in being erect and subquadrangular. However, the hinge construction of these two species differ considerably making it necessary to separate them.

OCCURRENCE – So far known exclusively from the Wenlockian Halla Beds, Möllbos, Gotland.

FUNCTIONAL MORPHOLOGY AND LIFE HABIT – The prodissoconch of extant Pteriomorphia exhibits two subequal adductor muscle scars, the anterior of which atrophies in early ontogenetic stages in all inequivalve forms of this subclass (Newell & Boyd 1970:235) resulting in byssal fixation in most adults of Pteriinae (Anthony 1905, Yonge 1953). In extant bivalves anterior reduction and posterior enlargement of the shell, as well as anterior reduction of the anterior adductor muscle generally are related to functional byssal apparatus (Yonge 1962:119, 121).

The slightly sinuated antero-ventral margin, with a small byssal opening in the left valve of *Molinicola gotlandica* (Figs. 26:D, G and 34:7), and a strong attachment of a byssal retractor, suggest a byssate life habit for this species. However, *Molinicola gotlandica* exhibits characters indicating epibyssate as well as endobyssate modes of life.

The left valve is slightly more convex than the right. An inequivalve condition is a prerequisite for increased stability of epifaunal bivalves that rest on one side with a horizontal sagittal plane (Stanley 1970:30; 1972:184, Fig. 16). However, such epifaunal species are restricted to hard substrates (Stanley 1970:184) and a possible epibyssate life habit for *Molinicola gotlandica* is rejected for the following reasons.

The specimens of *M. gotlandica* were extracted from highly argillaceous limestone and probably lived in this sediment, the well-preserved details of the shells not supporting transportation of the material. The broadly rounded anterior end, the shallow byssal sinus, valves of almost similar convexity and the presence of the anterior adductor muscle scar (heavily impressed in *M. gotlandica*) indicate upright or oblique attachment in soft sediments (Stanley 1972:184). The left valve of *M. gotlandica* exhibits growth lamellae in its anterior end and evident commarginal growth lines on the remaining part of the valve, while the right valve is almost devoid of sculpture. This inequivalve ornamentation pattern suggests an oblique life position (cf. *Actinopteria boydi* (Conrad) in Stanley 1972:184, 185, Fig. 17) in a low angle fixation (Fig. 34:7) which Stanley (1972:185) suggested provided more stability in less deeply buried life positions. It is not, however, completely excluded that *M. gotlandica* was epifaunally attached to algae or such in a modern pterineid way (cf. *Pteria* and *Pinctada* in Stanley 1970, Pl. 11; see discussion in Liljedahl, in prep.).

Molinicola gotlandica is thus considered a primitive, shallow semi-infaunal, endobyssate suspension-feeding form (Fig. 34:7) part of an evolutionary lineage from infaunal to epifaunal life habit within the Arcoida. In being slightly inequivalve, it is a more advanced form than the equivalve Devonian *Actinopteria boydi* (see Stanley 1972:185, Fig. 17:A) although the gross shell morphology with its hinge and conspicuous anterior adductor muscle scar emphasizes its relationship with other primitive semi-infaunal arcoids, e.g. arcaceans and cyrtodontaceans (Figs. 16 and 25).

Subclass PALAEOHETERODONTA NEWELL, 1965

Order MODIOMORPHOIDA NEWELL, 1969

Superfamily MODIOMORPHACEA MILLER, 1877

Family MODIOMORPHIDAE MILLER, 1877

Genus *Goniophora* Phillips, 1848

DISCUSSION OF SYSTEMATIC ATTRIBUTION – The systematic position of *Goniophora* is difficult to evaluate without knowledge of its ontogeny: it is necessary to know whether the posterior reinforcement flanges are the incitement to a lateral element of the hinge or whether during ontogeny there has been a reduction of lateral teeth.

For the time being, I prefer to place *Goniophora* in the family Modiomorphidae of the order Modiomorphoidea. These taxa accommodate species both with and without lateral teeth.

TYPE SPECIES – *Goniophora cymbaeformis* Sowerby, 1839

EMENDED DIAGNOSIS – Shell equivalve, strongly inequilateral, longitudinally elongated, rather inflated with strong, angular umbonal ridge extending from beak diagonally to inferior angle; beaks small, closely incurved, prosogyrate; umbo prominent; margins even; external opisthodetic ligament, possibly with additional internal portion; commarginal growth lines; hinge plate small, fairly strong, supported by anterior and posterior ridge forming a septum anteriorly and a slender plate or flange posteriorly; hinge either with a single tooth in left valve and a corresponding socket in right valve, or in each valve with one conspicuous cardinal tooth in ventral part of hinge plate and one marginal tooth, sometimes two, in dorsal part of hinge plate with corresponding sockets, teeth and sockets diagonally arranged; no lateral elements of hinge; anterior and posterior adductor muscle scars; pallial line simple.

DISCUSSION OF GENERIC AFFINITY – The identity of the genus *Goniophora* Phillips, 1848 has been disputed for more than a century. When Phillips introduced the name *Goniophora* for *Cypricardia cymbaeformis* Sowerby, 1839 from the British Silurian he presented no diagnostic characters for the genus. Nor did he define a type specimen for the species. Since most descriptions of species assigned to *Goniophora* treat the exterior only, the hinge characters of these taxa are unknown. Only descriptions including the hinge are considered of value in this discussion and they alone can form a basis for establishing the true identity of the genus.

McCoy (1855:275) was the first to give a description of *Cypricardia cymbaeformis* Sowerby including internal characters. The hinge was interpreted as having a

“... moderately slender tooth . . .” (see Sowerby’s original drawing in Murchison 1839, Pl. 3:10; see also below for further comments). However, McCoy placed it within the genus *Orthonotus* Conrad, 1841. But since McCoy used *Orthonotus* for species now considered to belong to three different genera it is regarded as a synonym to *Goniophora* Phillips, 1848 (see Williams & Breger 1916:224).

Hall (1885:XXIII–XIV) presented a description of *Goniophora* based on American material. It included the hinge, viz. “. . . no lateral teeth . . . a strong oblique fold or tooth in the left valve . . .” and “. . . a corresponding depression in the right valve . . .” (my italics).

In the description of his Devonian *Goniophora applanata*, *G. bipartita* and *G. schwerdi* Beushausen (1895:196) recorded a faintly indicated tooth in the right valve in addition to the cardinal tooth present in the left valve. Beushausen (1895:198) was of the opinion that a reduction of lateral teeth as well as of one of the central elements of the hinge had taken place in *Goniophora* when comparing it to the Devonian *Mecynodon* Keferstein, 1857, and accordingly placed it in the family Cyprinidae Neumayr, 1883. He also commented on Sowerby’s drawing of the type species of the genus, stating that the features interpreted by McCoy as a lateral tooth were in fact elements of the ligament (Leiste), and continued: “. . . dagegen kein Zahn, da die Furchen in den beiden abgebildeten Gegenklappen gleichliegend sind.” (Beushausen 1895:197).

The original drawing of *Cypricardia cymbaeformis* Sowerby is of two right valves and not two opposite valves as Beushausen stated. By courtesy of the Institute of Geological Science, London, I have examined photographs of the material pictured by Sowerby 1837 on Pl. 3:10. The actual slab of stone contains one right valve only. This was drawn by Sowerby in two views and arranged on the plate as two specimens on the slab.

Without giving any explanation Ulrich (1897:485) in his turn was of the opinion that *Goniophora* should be placed in the family Modiolopsidae Ulrich, 1897.

Hind (1899:339) stated that the name *Goniophora* was invalid since a genus of crinoids were termed *Goniophorus* and instead proposed the name *Mytilomorpha*. In the description of his Carboniferous material of *Mytilomorpha* Hind stressed the lack of lateral teeth.

Drevertmann (1902) described *Goniophora cognata* and *G. praecedens* as having an additional, smaller triangular tooth in the right valve below the cardinal socket and a corresponding socket in the left valve. He also described an additional posterior hinge tooth in *Goniophora stürzti* Beushausen, 1895 and pointed out that its presence distinguishes this type of hinge from that of typical *Goniophora* s.s. Drevertmann (1902) also stressed the fact that since there were no lateral teeth in *Goniophora stürzti* it accordingly did not belong to *Mecynodon* Keferstein, 1857:158 but to *Goniophora* Phillips, 1848. *Mecynodon* exhibits an “equivalved hinge type” (with regard to cardinal elements). Moreover, in addition to one strong tooth in the middle of the hinge and a small narrow tooth at

the hinge margin and two sockets between them in the right valve and the corresponding features in the left one, it has two conspicuous lateral teeth in the right valve and one lateral tooth in the left valve (Keferstein 1857:158; Haffer 1959:176, Pl. 13:9).

Williams & Breger (1916:226), however, discussed the possibility that the type of *Goniophora* was more closely related to *Mecynodon* since they interpreted lateral teeth in *Cypricardia cymbaeformis* as well as in *Goniophora perangulata* Hall, 1885, Pl. 34:1 and in *Goniophora applanata* Beushausen 1895, Pl. 17:18, 20 and thus supported the interpretation by McCoy 1852 of the type species of the genus, i.e. that it had lateral teeth.

Isberg's (1934:205, 207) Ordovician *Goniophorina* and *Cosmogoniophora* are edentulous and were placed by him in the family Modiolopsidae Fischer, 1887 since they were considered to be primitive forms from which the younger genus *Goniophora* had evolved. He thus suggested an evolutionary course contrary to that proposed by Beushausen.

Růžicka & Prantl (1959) described to well-preserved specimens of *Goniophora secans* Barrande, 1881 as having a "goniophorous hinge": "... consisting of an equal number of cardinal teeth in both valves ..." ("equivalved type") "... and a different number of marginal teeth in both valves." They stated that their observation agreed with the original diagnosis given by Phillips 1848 (who by the way gave no diagnostic characters for the genus), but stressed that the hinge construction is much more complex than that of the type species. Růžicka & Prantl (1959:56-57) pointed out that *Goniophora secans* has neither posterior nor anterior lateral teeth, nor was there "... obscure indication on the hinge plates of such teeth being either obsolete or reduced." Therefore I find it strange that in his diagram of the hinge of *Goniophora*, based on the description of Růžicka & Prantl, Babin (1966:296, Fig. 74:2) interprets a minute crest on the posterior hinge plate as comprising possible traces of a lateral tooth. Accordingly Babin placed *Goniophora* in the family Mecynodontidae Haffer, 1959.

Unfortunately the specimen illustrated by Sowerby is not intact today, the umbonal part having been destroyed. However, the disputed feature that McCoy and others interpreted as a lateral tooth remains and has proved to be two narrow ridges or flanges probably originating from the umbonal cavity or from the hinge plate, extending along the shell margin, the one close to it and the other some distance removed, to about half the length of the shell were they fade out. The same structure can be clearly seen in Fig. 29:C of *Goniophora onyx* n.sp. Since the internal mould of the specimen upon which Sowerby based his description of *Goniophora* does not reveal the hinge, one must await additional material of the type species in order to establish the true character of the hinge of *Goniophora cymbaeformis* Sowerby.

Variation in hinge structure is considerable in the species referred to the genus *Goniophora*. The hinge of *G. sturtzi* Beushausen, 1895, *G. applanata*

Beushausen, 1895, *G. schwerdi* Beushausen, 1895, and *G. cognata* Drevermann, 1902 resembles the "goniophorous hinge" (Růžička & Prantl 1959) of *G. secans* Barrande, 1881, and *G. onyx* n.sp. in being principally "equivalve" even though it is simpler, i.e. containing only one tooth and one socket in each valve and no additional marginal tooth or teeth. In contrast to these species *G. glaucus* Hall, 1885 and *G. hamiltonensis* Hall, 1885 contain an "inequivalve" type of hinge, i.e. containing one tooth only in the left valve and a corresponding socket in the opposite valve.

The fact that there is a multitude of *Goniophora*-like shells with similar shell habitus (above all the typical diagonal keel) having several types of hinges may be the result of convergent evolution. Species now assigned to the genus *Goniophora* may belong to two or more genera which may be instituted when further specimens of the different *Goniophora* species with preserved hinge are available.

Goniophora onyx n.sp.

Figs. 29, 30, 31, 34:8

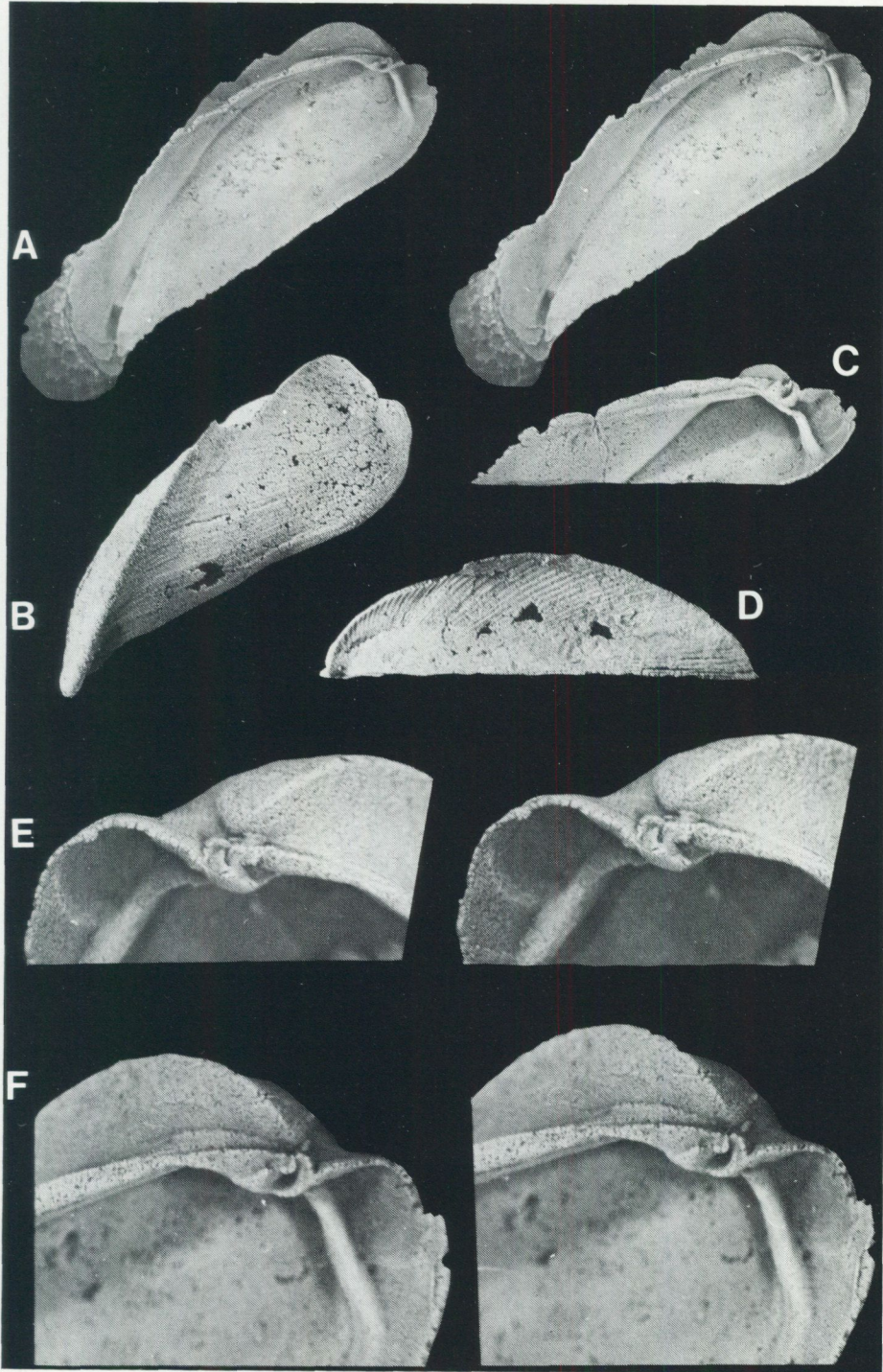
DERIVATION OF THE NAME – Greek *onyx*, claw, referring to the shape of the shell in lateral outline.

HOLOTYPE – One right and one left valve, SGU Type 3735 and SGU Type 3736 from sample G79–90LJ, Fig. 29:A,C,E,F. Length 28 mm, height 28 mm, breadth 8 mm, diagonal length 33 mm; right valve almost complete, posterior marginal extremity damaged as well as most proximal part of umbonal keel, healed fracture running through shell perpendicular to shell margin, an additional fracture in the umbonal cavity; hinge excellently preserved; ventral half of shell inadequately preserved seen as holes in the shell; left valve almost complete, posterior marginal extremity damaged, also part of the anterior margin in addition to most proximal part of diagonal keel; healed fracture identical in appearance and location to that in the opposite valve; ventral half of the shell inadequately silicified; tabulate epibiont attached to posterior external end of shell.

TYPE STRATUM – Halla Beds, Late Wenlockian, Silurian.

TYPE LOCALITY – Möllbos 1, Gotland, Sweden.

Fig. 29. *Goniophora onyx* n.sp. A. Stereo pair, internal lateral view of holotype (left valve); SGU Type 3736, $\times 1.9$, sample G79–90LJ. B. External lateral view of right valve; specimen lost. C. Internal ventro-lateral view of holotype (left valve); SGU Type 3736, $\times 2.5$. D. External dorsal view of right valve, same as in B. E. Stereo pair, internal view of holotype (right valve), detail of hinge; SGU Type 3735, $\times 5.9$. F. Stereo pair, internal lateral view of holotype (left valve), detail of hinge; SGU Type 3736, $\times 5.8$.



MATERIAL – 42 single valves and identifiable fragments, 8 of which have fairly well-preserved hinge (measurements and terminology on Fig. 31).

DIAGNOSIS – *Goniophora* with posterior margin evenly rounded, ventral margin straight except for at its proximal end where it has a claw-like appearance laterally; hinge plate with one large cardinal tooth and one smaller marginal tooth with corresponding sockets separating them, obliquely placed in relation to hinge line, two ridges, or septa, supporting and originating from underneath the hinge plate, the one anteriorly the other posteriorly.

EXTERNAL FEATURES – Shell medium-sized, lanceolate, longitudinally elongated, equivalve, strongly inequilateral, conspicuously inflated, anterior part rounded, posterior part extremely narrow, margins even, fitting together tightly; external opisthodontic ligament; commarginal growth lines (Fig. 29:B,D); beaks small, close together, strongly incurved at some distance from the hinge line, prosogyrate, at anterior end of shell; umbo conspicuous with strong, sharp, high sinuous diagonal crest or ridge extending to posterior extremity, crest parallel to sagittal plane at posterior end, angle gradually decreasing towards beak almost parallel to sagittal plane; maximum convexity about mid-length and about 1/3 of height; dorsal margin short, somewhat S-shaped forming a rather abrupt almost right-angled junction with anterior margin, its posterior part gently sloping to posterior margin; anterior margin short, almost truncate; ventral margin long, somewhat concave; posterior margin long, slightly convex; junction between ventral margin and posterior margin forming a narrow, claw-like hooked extremity (Figs. 29:A,B and 30, 31).

On the whole the material of this species is fragmentary. Less than a quarter of the countable material (i.e. including umbonal parts) comprises complete valves. The umbonal part of the shell is usually well-preserved while the proximal part of the umbonal, diagonal crest is never intact.

The extension of the ligament in anterior direction is somewhat more difficult to establish, since the striated area of the fulcrum ends at some distance to the beak. However, in the right valve of the holotype immediately posterior to the beak fragmentary remains of what might be silicified ligament tissue can be seen (Fig. 29:E).

INTERNAL FEATURES – Sublanceolate hinge plate just below beak. Dentition of left valve (Fig. 29:F): one large, almost conical, pointed, somewhat incurved cardinal tooth below and posterior to beak at some distance from dorsal margin in posterior part of hinge plate; one bifurcate “marginal” tooth, its posterior part slender and lamellar, perpendicular to dorsal margin, its anterior part wedge-shaped sloping abruptly ventrally immediately below beak in anterior part of hinge plate; one conspicuous, deep almost conical “cardinal socket” immediately

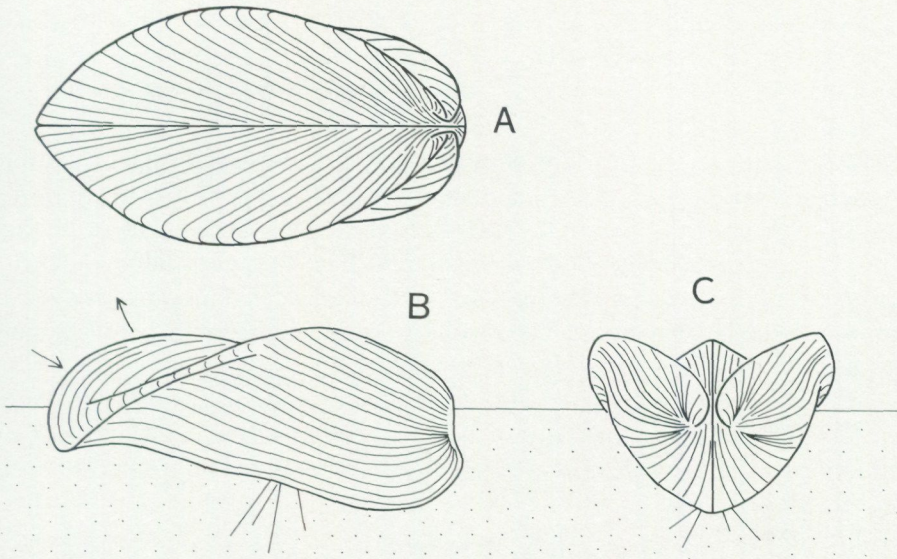


Fig. 30. *Goniophora onyx* n.sp. Suggested life position. A. Dorsal view of articulated specimen. B. Lateral view or right valve. C. Anterior view of articulated specimen. Arrows indicating hypothetical inhalant and exhalant currents. All drawings based on holotype; SGU Type 3735/3736, sample G79-90LJ.

anterior to cardinal tooth; one broad, shallow "marginal socket" immediately dorsal to cardinal tooth; teeth and sockets diagonally placed. Dentition of right valve (Fig. 29:E): one large, almost conical, pointed somewhat incurved cardinal tooth with a conspicuous slit and sharpe-edged ridge at its base matching "cardinal socket" of opposite valve, immediately below beak at some distance from dorsal margin; one erect, wedge-shaped "marginal tooth" matching "marginal socket" of opposite valve below and posterior to beak; one conspicuous, deep, almost conical "cardinal socket" matching cardinal tooth of opposite valve central to "marginal tooth"; one shallow bifurcate "marginal socket" matching "marginal tooth" of opposite valve; septum from umbonal cavity antero-ventrally, posterior to and supporting hinge plate continuing as a distinct, low ridge below and along dorsal margin gradually disappearing where dorsal margin meets posterior margin (Fig. 29:C).

The antero-ventrally oriented ridge, originating from below the hinge plate and forming a strong internal septum (Fig. 29:A,C,E,F), continues posteriorly as a simple septum being high only in its proximal part, low and fainter distally. This low, posterior flange has, contrary to the assumption of some students (see discussion above) no contact with the corresponding feature of the opposite valve since it is situated at some distance from the shell margin. For this reason, and since it occurs in identical positions in both valves, it cannot be regarded as a lateral element of the hinge but is an reinforcement of the valve (Fig. 29:C). At least two

similar additional reinforcement ridges are present. The same structure is present in the syntype (Pl. 3:10 in Sowerby 1839) of the type species, which has variously been interpreted as lateral teeth (McCoy 1852) and as ligament furrows (Beushausen 1895).

There is a low second inconspicuous ridge with an appurtenant sulcus below it extending from the top of the umbonal cavity below the first ridge posterodorsally to the posterior end of the shell and a third ridge, fairly small, extending from about 1/3 of the length of the anterior margin in the ventral half of the shell, antero-posteriorly reaching the umbonal crest at about mid-length of the shell. Internally the diagonal crest is filled with shell material except for the marginal part where a deep groove can be seen (Fig. 29:A).

The only muscle trace visible is the anterior adductor muscle scar (Figs. 29:E and 31) limited by the anterior part of the dorsal margin and internal septum. The pallial line is observed only in its middle part and is commarginal, at some distance from the shell margin.

DISCUSSION OF CLOSELY RELATED FORMS – The Devonian *Goniophora secans* Barrande, 1881, seems to be the form most closely related to *Goniophora onyx*. However, they differ from each other in the following respects: *G. secans* has a more complicated hinge than *G. onyx*. In the right valve of *G. secans* there is an anterior marginal tooth in addition to the posterior marginal tooth (Růžicka & Prantl 1959:54–55, Figs. 3 and 4) while *G. onyx* contains one marginal tooth only being situated posteriorly in the right valve (Fig. 29:E). The cardinal tooth of *G. secans* is elongated in transverse section perpendicular to the dorsal margin while in *G. onyx* it is diagonally elongated. The posterior part of the hinge plate of *G. secans* (left valve) has a crest while on the anterior part of the hinge plate there are three conspicuous tubercles. In *G. onyx* there are possibly low blunt projections on the inside of the anterior part of the dorsal margin. Otherwise the hinge of *G. onyx* shows no morphologically differentiated features.

Variation of the hinge in 8 fairly well-preserved valves of *G. onyx* is slight and total variation probably cannot include the complicated type of hinge present in *G. secans*. Although the number of specimens available is statistically insignificant, the simple hinge of *G. onyx* is considered to be a reliable specific character.

Fine striae on the wall of the ligamental groove of *G. secans* were interpreted by Růžicka & Prantl 1959 as traces of an inner portion of the ligament. In *G. onyx* there are no traces of any internal part of the ligament.

The general habitus of the two species also differs in some respects (cf. Barrande 1881, Pl. 255:11–16). The posterior margin of *G. onyx* displays an evenly arcuate, convex outline (Fig. 31) while in *G. secans* it is straight in its anterior part, the posterior part being abruptly strongly convex. The umbonal keel of *G. onyx* is strongly tilted over dorsally, covering the anterior half of the posterior margin seen externally in lateral view (Fig. 29:B), while in *G. secans* it is straight and

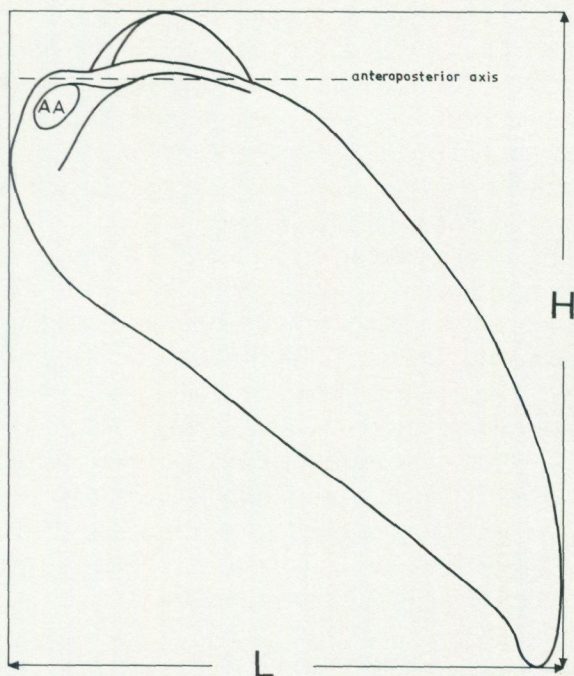


Fig. 31. *Goniophora onyx* n.sp. Measurements and terminology. Antero-posterior axis running through hinge axis, parallel to length axis and perpendicular to height axis. L = length, H = height, AA = anterior adductor muscle scar.

crosses the shell almost diagonally leaving the entire posterior margin visible in lateral view. In *G. secans* the ventral margin is not as smoothly rounded as in its anterior part like *G. onyx*. The concave posterior extremity of the ventral margin of this species gives it its unusual, hook- or claw-like appearance in lateral view.

OCCURRENCE – Wenlockian Halla Beds, Möllbos 1, Gotland.

FUNCTIONAL MORPHOLOGY AND LIFE HABIT – *Goniophora*, the most salient character of which is the oblique conspicuous, angular keel, lacks any known living successors. Though the posterior adductor muscle scar present in several specimens of other *Goniophora* species (e.g. *G. perangulata* Hall, *G. rugosa* Conrad, and *G. truncata* Hall, in Hall 1885, Pl. 42:2, 8, 9, 10 and in undescribed material from Gotland) was not observed in *G. onyx*, it probably did have such a muscle, larger than the anterior one. Furthermore, this species shows an elongation of the shell, anterior reduction and a long slightly sinuate antero-ventral margin in conformity with the arcoids *Freja fecunda* and *Molinicola gotlandica*, suggesting a primitive byssate mode of life, i.e. endobysate suspension-feeding life habit (Stanley 1975:369).

Stanley (1972:194, Fig. 28:F) suggested a semi-infaunal, endobysate life position for *Goniophora chemungensis* (Vanuxem) in an oblique position, its straight posterior margin being parallel to the sediment surface and the only part of the shell protruding above it. However, Drevermann (1902, Pl. 11:4) illustrated an articulated specimen of *Goniophora stürtzi* Beushausen in its life position on a bedding plane with the diagonal keels and the beaks lying just at the sediment/water interface (see also Stanley 1972:194, Fig. 28:G).

The angular keel of each valve of *G. onyx* is well-developed and distinct and may have served as a surface-enlarger, keeping the valves from sinking in the presumably extremely watery sediment (Liljedahl in prep.). I suggest that the life position of *G. onyx* was as in Figs. 30 and 34:8, the animal lying with the angular keels parallel to and on a level with the sediment surface and with the anteroventral part of the shell below the surface. Although no positive evidence of byssal attachment was observed, the features, accounted for above, suggest that *G. onyx* was byssally attached. Because of the considerable breadth in relation to life position height giving the animal good physical stability (Fig. 30), the byssal anchorage of *G. onyx* did not necessarily need to be strong. The inhalent and exhalent currents shown in Fig. 30 are hypothetical.

Subclass ?

Order ?

Superfamily ?

Family possibly ANTIPLEURIDAE NEUMAYR, 1891

Subfamily possibly ANTIPLEURINAE NEUMAYR, 1891

Genus *Maminka* Barrande, 1881

DISCUSSION OF SYSTEMATIC POSITION – In the *Treatise on Invertebrate Paleontology* (Newell & LaRoche 1969) *Maminka* is placed in the family Lunulacardiidae Fischer, 1887, characterized for instance by being equivalve and edentulous.

Maminka is inequivalve (Barrande 1881), accommodates fairly strong hinge teeth and does not, for these reasons, belong to this family. *Maminka* possibly belongs to the family Antipleuridae Neumayr, 1891 since *Maminka* bears superficial resemblance to the type genus *Antipleura* Barrande, 1881. However, more research must be done before the systematic position of *Maminka* can be established.

REMARKS – Since *Maminka* sp. is the first species of the genus with known internal features, the most important diagnostic character being the hinge construction, an emendation of the original diagnosis is suggested as given below.

EMENDED DIAGNOSIS – Shell subtrigonal, inequivalve, subequilateral, margins even, no gap present; external ligament; ornamented with radial costae; beaks median, opisthogyrate, junction discordant; lunule formed by angular posterior umbonal ridge; posterior part of dorsal margin almost straight meeting posterior part of dorsal margin at a decided angle, posterior part of dorsal margin composed of a straight proximal part and an arcuate distal part; ventral, posterior and anterior margins variable; one of the valves, sometimes the right and sometimes the left, much more gibbous than the other; less gibbous valve divided by a furrow, or sulcus, dividing valve into two unequal parts, sulcus never median; hinge plate of left valve central with one robust, elongated anterior marginal tooth, one smaller, elongated vertical tooth, one deep posterior socket, one narrow socket between the two teeth; hinge plate continues anteriorly as an internal septum; fairly large anterior adductor muscle scar antero-ventrally at some distance from shell margin.

DISCUSSION OF GENERIC AFFILIATION – The main feature of the genus *Maminka* Barrande, 1881 is the external sulcus which in the Bohemian type material is either anterior or posterior. This sulcus is present in either the right or the left valve as in the British species *Maminka anglica* Reed, 1931.

Although the sulcus in *Maminka* sp. is rather indistinct, the rest of the gross shell morphology clearly shows that the material belongs to *Maminka* Barrande.

TYPE SPECIES – No type species was established by Barrande 1881, but three Bohemian species form the basis for his generic description, i.e. *Maminka comata*, *Maminka tenax* and *Maminka rarissima*.

SPECIES – *Maminka comata*, *Maminka tenax*, *Maminka rarissima*, *Maminka anglica*, and *Maminka* sp.

Maminka sp.

Figs. 32, 33, 34:9

REMARKS – In principle a single specimen is no adequate basis for the description of a new species, but since the state of preservation is extremely good and this specimen differs from the previously mentioned forms in diagnostic characters, there is good reason to place it in a different species.

HOLOTYPE – A partly pyritized left valve, SGU Type 3838 from sample G77-29LJ. Figs. 32:A,B,C,D,E,F and Fig. 33. Length 20.7 mm, height 16.7 mm, breadth 6.4 mm.

TYPE STRATUM – Halla Beds, Late Wenlockian, Silurian.

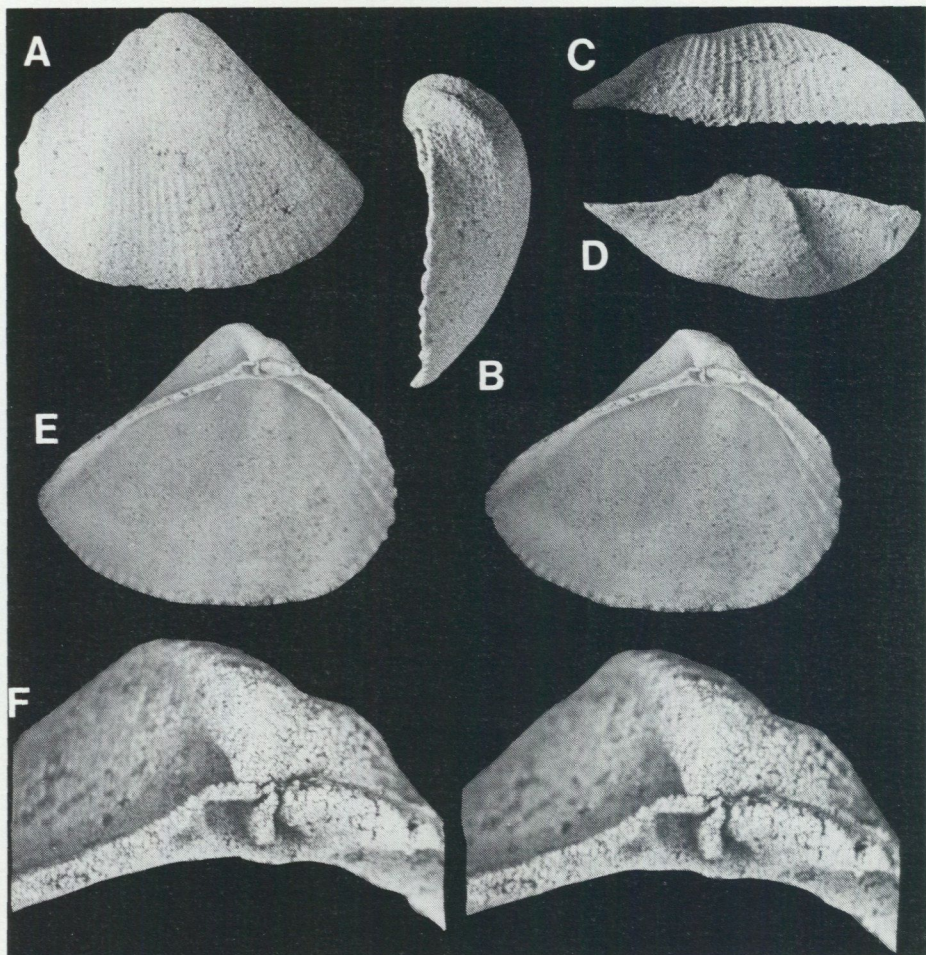


Fig. 32. *Maminka* sp. All figures of the holotype (left valve); SGU Type 3838, sample G77-29LJ. A. External lateral view, $\times 2.3$. B. Anterior view, $\times 2.5$. C. Ventral view, $\times 2.3$. D. Dorsal view, $\times 2.1$. E. Stereo pair, internal lateral view, $\times 2.3$. F. Stereo pair, external lateral view, detail of hinge, $\times 6.4$.

MATERIAL – One complete left valve (measurements and terminology on Fig. 33).

DIAGNOSIS – *Maminka*, left valve with broad indistinct vertical sulcus; umbo prominent, beak opisthogyrate; hinge with one robust and one slender tooth and two sockets, one of which is deep; anterior end of hinge plate continuing as internal septum halfway to anterior extremity.

EXTERNAL FEATURES – Shell of medium size, subtrigonal, inequilateral, inflated; external ligament, ornamented with radial costae; beak prominent, slightly opisthogyrate, extending somewhat beyond sagittal plane; umbo high above

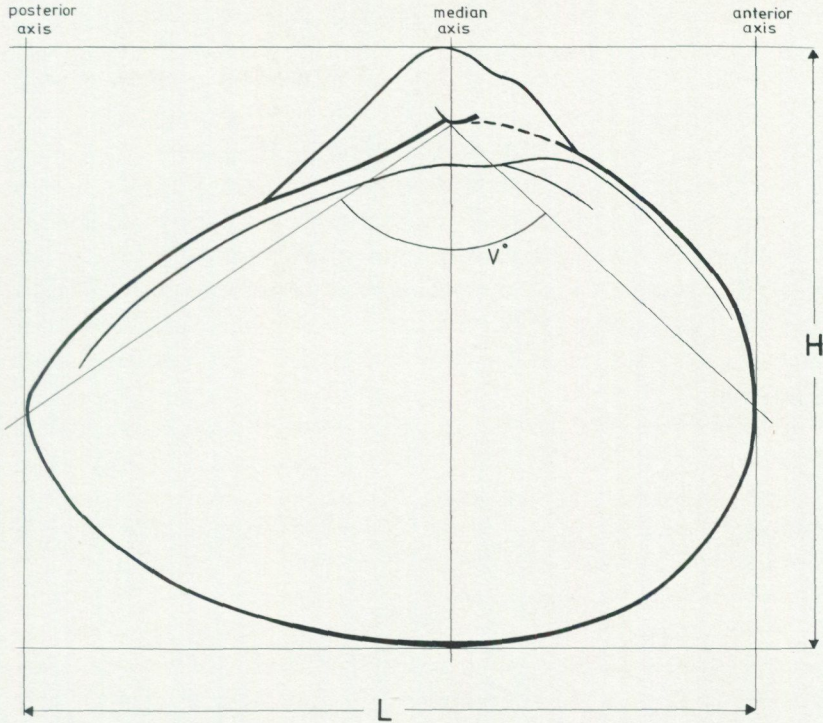


Fig. 33. *Maminka* sp. Diagrammatic representation of left valve (Holotype, SGU Type 3838, sample G77-29LJ). L = maximum length of shell, H = maximum height, B = maximum breadth, V° = hinge angle.

hinge line in anterior half of shell; maximum convexity somewhat above mid-height and slightly posterior to mid-length of shell; sharp posterior umbonal ridge; dorsal margin V-shaped, posterior part slightly convex, long, about $3/5$ of total length of shell, anterior part strongly convex, about $2/5$ of total length of shell; anterior margin short, convex with its extreme point at $2/5$ of total height; ventral margin long, convex with a slight undulation where sulcus affects margin, deepest point immediately anterior to median axis; posterior margin short, pointed, forming a narrow angle with extreme point at $2/5$ of total height of shell.

According to Barrande (1881:105) the representatives of the genus *Maminka* are inequivalve, but since the Möllbos material comprises one valve only this character cannot be established. However, since the shell margin is not in the sagittal plane this suggests that the opposite valve of *Maminka* sp. is of a different shape, i.e. it is inequivalve.

In *Maminka* sp. the sulcus characteristic of the genus is parallel to the median axis and indistinct (Fig. 32:A), in contrast to other species of the genus.

The radial costae are not pronounced. It is suggested that this is the condition of

the original surface sculpture, since the excellent preservation of the hinge teeth indicates that no transportation with accompanying abrasion has taken place.

INTERNAL FEATURES – Hinge plate central (Fig. 32:E,F); one robust, broad, elongated anterior marginal tooth; one small, vertically elongated tooth posterior to the large one; one narrow, shallow socket between teeth and one conspicuous, deep square socket just below beak at posterior end of hinge plate; hinge plate continuing anteriorly as a strong, evident internal septum fading out at extreme anterior end of shell; external sulcus being a low, smooth-edged vertical ridge dividing shell into two parts; faintly impressed, subrectangular anterior adductor muscle scar fairly close to ventral margin; a number of small, circular, rather deep pits in posterior part of anterior adductor muscle scar.

The hinge angle is c. 100°. The hinge is fairly strong, the dominant feature being the anterior strong tooth. The central, vertical tooth is slender and both teeth extend well beyond the sagittal plane.

The small pits are doubtfully traces of muscles and may instead be indications of shell-destroying organisms (see Liljedahl in prep.).

DISCUSSION OF CLOSELY RELATED FORMS – The three Bohemian (Devonian) species of *Maminka* show similarities as well as dissimilarities to *Maminka* sp. *Maminka tenax*, *Maminka comata* and *Maminka rarissima* are inequivalve, they have one valve with an external sulcus and one valve without. The following characters separate *Maminka* sp. and the sulcus-bearing valve of *Maminka tenax* (cf. Barrande 1881, Pl. 187).

Maminka sp. (left valve)

indistinct sulcus

sharp, slightly concave posterior part of dorsal margin is visible in lateral view (Fig. 32:A)

posterior part of dorsal margin meeting posterior margin in a smooth transition, together forming an evenly arched outline

beak slightly opisthogyrate (Fig. 32:F), umbo high, straight and erect

Maminka tenax (in some specimen left in some right valve)

clear, fairly deep sulcus

sharp, concave posterior umbonal ridge covering most proximal part of dorsal margin when seen in lateral view

posterior part of dorsal margin meeting posterior margin at an angle

beak opisthogyrate, umbo comparatively low

The size of *Maminka* sp. (L = 20.7 mm) falls within the size range of the illustrated specimens of *Maminka tenax* (L = 7–45 mm) and the H/L ratio of *Maminka* sp. (0.81) also falls within the H/L ratio range of *Maminka tenax* (0.61–0.87). The convexity (B/L ratio) of the sulcus-bearing valve of *Maminka tenax* varies from 0.22 to 0.31 while the corresponding ratio of *Maminka* sp. is 0.31.

Maminka sp. differs from the sulcus-bearing valve of *Maminka comata* (cf. Barrande 1881, Pl. 186:I) as follows.

<i>Maminka</i> sp. (left valve)	<i>Maminka comata</i> (left valve)
beak strongly incurved, in contact with dorsal margin	beak slightly incurved, at some distance from and above dorsal margin
sulcus faint, parallel to median axis	sulcus prominent, oblique either in postero-ventral or antero-ventral direction
posterior umbonal ridge slightly concave, covering proximal part of posterior part of dorsal margin when seen in external lateral view	posterior umbonal ridge slightly to strongly convex, in most cases covering posterior part of dorsal margin to posterior extremity when seen in external lateral view
anterior end evenly rounded	anterior extremity angular to rounded

Size range of *Maminka comata*, L = 17–34 mm (*Maminka* sp. L = 20.7 mm), H/L ratio 0.64–0.89 (*Maminka* sp. H/L = 0.81) and B/L ratio 0.18–0.27 (*Maminka* sp. B/L = 0.31) indicate gross shell similarities between these two species.

Maminka sp. differs from the sulcus-bearing valve of *Maminka rarissima* (cf. Barrande 1881, Pl. 186:II) as follows.

<i>Maminka</i> sp. (left valve)	<i>Maminka rarissima</i> (right valve)
beak strongly incurved, in contact with dorsal margin	beak moderately incurved, close to dorsal margin
umbo high	umbo low
sulcus faint, parallel to median axis	sulcus prominent, slightly oblique antero-ventrally

H/L ratio of *Maminka rarissima* ranges from 0.79 to 0.84 (*Maminka* sp. 0.81) and the B/L relation is 0.26 for one specimen (*Maminka* sp. 0.31). Thus these two species are similar in general shape.

Reed described a left, prosogyrate valve of the Ludlovian (Late Silurian) *Maminka anglica* (Reed 1931, Pl. 2). However, the posterior part of the dorsal margin of this valve resembles the anterior part of the dorsal margin of all other *Maminka* species and the anterior part of the dorsal margin resembles the posterior part of the dorsal margin of all other *Maminka* species. *Maminka anglica* is the only prosogyrate species within the genus. Further it differs from *Maminka* sp. in the more concave posterior part of the dorsal margin, almost truncate anterior margin and much more deeply impressed sulcus. *Maminka anglica* as pictured on plate 7:2 in Reed 1931 closely resembles *Maminka tenax* (cf. Barrande 1881, Pl. 187:15).

- 1 *Nuculoidea lens*
- 2 *Nuculodonta gotlandica*
- 3 *Palaeostraba baltica*
- 4 *Caesariella lindensis*
- 5 *Janeia silurica*

- 6 *Freja fecunda*
- 7 *Molinicola gotlandica*
- 8 *Goniophora onyx*
- 9 *Maminka* sp.
- 10 *Mytilarca?* sp.

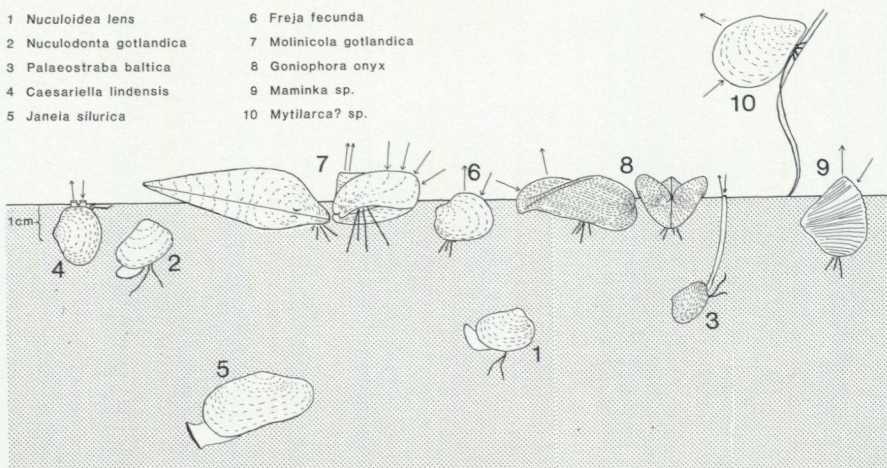


Fig. 34. Suggested life positions of the bivalves of Möllbos. Sizes relative to one another.

OCCURRENCE – For the time being known exclusively from the Silurian (Late Wenlockian) Halla Beds, Möllbos 1, Gotland, Sweden.

Functional morphology and life habit speculations of *Maminka* sp. must await more knowledge of the species. The life position shown in Fig. 34:9 is conjectured.

Genus and species indeterminate

One single, articulated specimen of an undetermined bivalve is present in the Möllbos material (Fig. 23:D,E). It is small ($L = 4.1$ mm), damaged in the umbonal region of both valves but otherwise well-preserved. The shell margins are intact, and the valves are in close contact so that it is not possible to examine the hinge. It has typically nuculoid shape.

Juveniles of *Nuculodonta gotlandica* and *Nuculoidea lens* have smooth shells, although faint growth lines are visible. In contrast the shell surface of this specimen has a deep, conspicuous concentric sculpture.

The systematic position of this specimen cannot possibly be established until additional material is available. Anyway, the specimen probably belongs to the order Nuculoida.

REFERENCES

- ALLEN, J. A. & SANDERS, H. L., 1969: *Nucinella serrei* Lamy (Bivalvia: Protobranchia), a monomyarian Solemyid and possible living actinodont. – *Malacologia* 7:381–396.
- ANTHONY, R., 1905: Influence de la fixation pleurothétique sur la morphologie des mollusques Acéphales Dimyaires. – *Ann. Sci. Nat., Zool.* 1:165–397.
- ARKELL, W. J., 1930: The generic position and phylogeny of some Jurassic Arcidae. – *Geol. Mag.* 67, 7:297–310.
- BABIN, C., 1966: Mollusques bivalves et céphalopods du Palaeozoïque armoricain. – Brest, 470 pp.
- 1977: Étude comparée des genres *Babinka* Barrande et *Coxiconcha* Babin (Mollusques bivalves de l'Ordovicien) intérêt phylogénique. – *Geobios* 10, 69 pp.
- BARRANDE, J., 1881: Système Silurien du centre de la Bohême, Vol. 6. – Prague, 342 pp.
- BARROIS, C., 1891: La faune du Grès armoricain. – *Soc. Géol. Nord. Annales* 19:134–237.
- BEURLEN, K., 1944: Beiträge zur Stammgeschichte der Muscheln. – *München Ak. Sb.* 11:133–143.
- BEUSHAUSEN, H. E. L., 1895: Lamellibranchiaten des rheinischen Devon mit Ausschluss der Aviculiden. – *Abh. K. Preuss. Geol. Landesanst. New Ser.* 17, 514 pp.
- BILLINGS, E., 1874: Palaeozoic fossils, 2:1. – *Geol. Surv. Can.*, 144 pp.
- BRADSHAW, M. A., 1978: Position of soft parts in fossil palaeotaxodont bivalves as suggested by features of the shell interior. – *Alcheringa* 2:203–215.
- CARTER, J. G. & TEVESZ, M. J. S., 1978: The shell structure of *Ptychodesma* (Cyrtodontidae; Bivalvia) and its bearing on the evolution of the Pteriomorpha. – *Phil. Trans. R. Soc. London. B.* 284:367–374.
- CAVANAUGH, C. M., GARDINER, S. L., JONES, M. L., JANNASCH, H. W. & WATERBURY, J. B., 1981: Prokaryotic cells in the hydrothermal vent tube worm *Riftia pachyptila* Jones: Possible chemoautotrophic symbionts. – *Science*, 213:340–342.
- COX, L. R., 1960: Thoughts on the classification of the Bivalvia. – *Proc. Mal. Soc. London* 34, 2:60–88.
- 1969: Systematic descriptions. In R. C. Moore, ed: *Treatise on Invertebrate Paleontology, Part N, Mollusca 6, Bivalvia 1.* – *Geol. Soc. Am. and University of Kansas Press*, 489 pp.
- COX, L. R., NUTTALL, C. P. & TRUEMAN, E. R., 1969: General features of the Bivalvia. In R. C. Moore, ed: *Treatise on Invertebrate Paleontology, Part N, Mollusca 6, Bivalvia 1.* – *Geol. Soc. Am. and University of Kansas press*, 489 pp.
- DICKINS, J. M., 1963: Permian pelecypods and gastropods from Western Australia. – *Dep. Nat. Dev. Bureau Min. Res. Geol. and Geogr. Bull.* 63, 150 pp.
- DOUVILLÉ, H., 1912: Classification des Lamellibranches. – *Soc. Geol. France, Bull.* 4, 12:419–467.
- DREVERMANN, F., 1902: Die Fauna der Untercoblenschichten von Oberstadtfeld bei Daun in der Eifel. – *Palaeontogr.* 49.
- DREW, G. A., 1900: Locomotion in *Solenomya* and its relatives. – *Anat. Anz.* 17, 15:257–266.
- 1901: The life history of *Nucula delphinodonta* (Mighels). – *Quart. J. Micr. Sci.* 44:313–391.
- DRISCOLL, E. G., 1964: Accessory muscle scars, an aid to protobranch orientation. – *J. Paleontol.* 38:61–66.
- FRECH, F., 1891: Die devonischen Aviculiden Deutschlands. – *K. Preuss. Geol. Landesanst. Berlin*, 253 pp.
- GILL, E. D., 1949: Prosopon, a term proposed to replace the biologically erroneous term ornament. – *J. Paleontol.* 23:572.
- GIRTY, G. H., 1911: On some new genera and species of Pennsylvanian fossils from the Wewoka formation of Oklahoma. – *Ann. N. Y. Acad. Sci.* 21:119–156.
- HAFFER, J., 1959: Der Schlossbau früh-heterodonter Lamellibranchiaten aus der rheinischen Devon. – *Palaeontogr.* 112:133–192.
- HALL, J., 1885: Lamellibranchiata 2. Descriptions and figures of the Dimyaria of the Upper Helderberg, Hamilton, Portage and Chemung groups. – *N. Y. Geol. Surv. Paleontol.* 5:269–562.
- HEATH, H., 1937: The anatomy of some protobranch mollusks. – *Musée R. D'hist. Nat. Belg. Mem.* 2, 10:1–26.
- HEDE, J. E., 1921: Gottlands silurstratigrafi. – *Sver. geol. unders. C* 305, 100 pp.
- 1925: Berggrunden (Silursystemet). In H. Munthe, J. E. Hede & L. von Post, 1925: *Beskrivning till kartbladet Ronehamn.* – *Sver. geol. unders. Aa* 156, 34 pp.
- 1927a: Berggrunden (Silursystemet). In H. Munthe, J. E. Hede & L. von Post, 1927: *Beskrivning till kartbladet Klintehamn.* – *Sver. geol. unders. Aa* 160, 37 pp.
- 1927b: Berggrunden (Silursystemet). In H. Munthe, J. E. Hede & L. von Post, 1927: *Beskrivning till kartbladet Hemse.* – *Sver. geol. unders. Aa* 164, 36 pp.
- 1928: Berggrunden (Silursystemet). In H. Munthe, J. E. Hede & L. von Post, 1928: *Beskrivning till kartbladet Slite.* – *Sver. geol. unders. Aa* 169, 49 pp.

- 1933: Berggrunden (Silursystemet). *In* H. Munthe, J. E. Hede & L. von Post, 1933: Beskrivning till kartbladet Kappelshamn. - Sver. geol. unders. Aa 171, 45 pp.
- 1936: Berggrunden. *In* H. Munthe, J. E. Hede & L. von Post, 1936: Beskrivning till kartbladet Fårö. - Sver. geol. unders. Aa 180, 29 pp.
- 1940: Berggrunden. *In* H. Munthe, J. E. Hede & L. von Post, 1940: Beskrivning till kartbladet Visby och Lummelunda. - Sver. geol. unders. Aa 183, 58 pp.
- 1960: *In* G. Regnéll & J. E. Hede, 1960: The lower Palaeozoic of Scania, The Silurian of Gotland. Guide to excursions Nos. A 22 and C 17, 44-89. - Int. Geol. Congr. Sess. Norden 1960.
- HIND, W., 1896-1900: British Carboniferous Lamellibranchiata. 1. - Palaeontogr. Soc. London, 486 pp.
- 1910: The lamellibranchs of the Silurian rocks of Girvan. - R. Soc. Edinburgh, Trans. 47:479-548.
- HISINGER, W., 1837: Lethaea Svecica seu Petrificata Sveciae, iconibus et characteribus illustrata. - Stockholm, 124 pp.
- International code of zoological nomenclature, 1961. - Int. Trust for Zool. Nomencl. London, 176 pp.
- ISBERG, O., 1934: Studien über Lamellibranchiaten des Leptaenakalkes in Dalarna. - Lund, 492 pp.
- KEFERSTEIN, W., 1857: Ueber einige deutsche devonische Conchiferen aus der Verwandtschaft der Trigoniaceen und Carditaceen. - Zeitschrift Deutsch. Geol. Gesells. 9:149-162.
- KING, W., 1950: A monograph of the Permian fossils of England. - Palaeontol. Soc. London, 258 pp.
- KONINCK, L. G. DE, 1885: Faune du calcaire Carbonifère de la Belgique, 5, Lamellibranches. - Mém. Mus. Roy. Hist. Nat. Belg., 283 pp.
- KŘÍŽ, J., 1979: Silurian Cardiolidae (Bivalvia). - J. Geol. Sci. 22, 157 pp.
- LAUFELD, S., 1974: Reference localities for palaeontology and geology in the Silurian of Gotland. - Sver. geol. unders. C 705, 172 pp.
- LE PENNEC, M., 1978: Génèse de la coquille larvaire et postlarvaire chez divers bivalves marins. - Univ. de Bretagne, Brest, diss. text and atlas, 229 pp.
- LEVINTON, J. S., 1977: Ecology of shallow water deposit-feeding communities Quisset Harbor, Massachusetts. - Ecology of Marine benthos 2:191-228.
- LEVINTON, J. S. & BAMBACH, R. K., 1975: A comparative study of Silurian and recent deposit-feeding bivalve communities. - Paleobiol. 1:97-124.
- LILJEDAHL, L., 1981: Silicified bivalves from the Silurian of Gotland. *In* S. Laufeld, ed.: Proceedings of Project Ecostratigraphy plenary meeting, Gotland, 1981. - Sver. geol. unders. Rapp. & Medd. 25:22.
- 1983: Two silicified Silurian bivalves from Gotland. - Sver. geol. unders. C 799, 51 pp.
- in prep.: Ecological aspects of a silicified bivalve fauna from the Silurian of Gotland.
- LINDSTRÖM, G., 1880: *In* N. P. Angelin & G. Lindström, 1880: Fragmenta Silurica e dono Caroli Henrici Wegelin. - Holmiae 1880, 60 pp.
- 1888: List of the fossil faunas of Sweden. - Stockholm 1888, 73 pp.
- LOGAN, A., 1967: The Permian Bivalvia of northern England. - Palaeontogr. Soc. (Monogr.) 121:1-72.
- MCALISTER, A. L., 1962: Upper Devonian pelecypods of the New York Chemung stage. - Yale Univ. Peabody Mus. Nat. Hist. Bull. 16, 88 pp.
- 1968: Type species of Paleozoic nuculoid bivalve genera. - Geol. Soc. Am. Mem. 105, 143 pp.
- MCCOY, F., 1855: Description of the British Palaeozoic fossils. *In* A. Sedgwick, 1855: A synopsis of the classification of the British Palaeozoic rocks. - London and Cambridge. 661 pp.
- MCLEARN, F. H., 1924: Palaeontology of the Silurian rocks of Arisaig, Nova Scotia. - Geol. Surv. Can., Mem. 137, 180 pp.
- MUNTHE, H., 1921: Beskrivning till kartbladet Burgsvik jämte Hoburgen och Ytterholmen. - Sver. geol. unders. Aa 152, 79 pp.
- NEWELL, N. D., 1942: Late Paleozoic Mytilacea. - Kansas State Geol. Surv. 10, 2, 115 pp.
- 1954: Status of Invertebrate Paleontology, 1953, 5, Mollusca: Pelecypoda. - Bull. Mus. Comp. Zool. 112, 3:161-172.
- 1969: Systematic descriptions. *In* R. C. Moore, ed.: Treatise on Invertebrate Paleontology, Part N, Mollusca 6, Bivalvia 1. - Geol. Soc. Am. and Univ. of Kansas Press, 489 pp.
- NEWELL, N. D. & BOYD, D. W., 1970: Oyster-like Permian bivalvia. - Bull. Am. Mus. Nat. Hist. 143, 4:224-281.
- NEWELL, N. D. & LAROCHE, A., 1969: Systematic descriptions. *In* R. C. Moore, ed.; Treatise on Invertebrate Paleontology, Part N, Mollusca 6, Bivalvia 1. - Geol. Soc. Am. and Univ. of Kansas Press, 489 pp.
- OWEN, G., 1959: The ligament and digestive system in the taxodont bivalves. - Malacol. Soc. London. Proc. 33:215-223.
- PELSENEER, P., 1891: Contribution à l'étude des Lamellibranches. - Archives de Biologie 11:147-312.
- PHILIPPI, E., 1899: Ueber das Schloss von *Pterinaea retroflexa* Wahlenb. sp. - Zeitschr. Deutsch. geol. Gesellsch. 51:181-183.

- PHILLIPS, J., 1848: The Malvern Hills, compared with the Palaeozoic districts of Abberley, Woolhope, May Hill, Tortworth, and Usk. – Geol. Surv. G. Br. Mem. 2:1, 330 pp.
- POJETA, J. JR., 1962: The pelecypod genus *Byssonychia* as it occurs in the Cincinnati at Cincinnati, Ohio. – Paleontogr. Am. 4, 30:169–216.
- 1966: North American Ambonychiidae (Pelecypoda). – Paleontogr. Am. 5, 36:129–241.
- 1971: Review of Ordovician pelecypods. – Geol. Surv. Prof. Paper 695, 46 pp.
- 1975: *Fordilla troyensis* Barrande and early Pelecypod phylogeny. Studies in Paleontology and Stratigraphy. – Bull. Am. Pal. 67, 287:363–379.
- 1978: The origin and early taxonomic diversification of pelecypods. – Phil. Trans. R. Soc. London, B. 284:225–246.
- PRANTL, F. & RŮŽIČKA, B., 1954: *Straba* nov. gen., a new Devonian pelecypod from Bohemia. – Acta Mus. Nat. Prague 10:3, 29 pp.
- QUENSTEDT, W., 1930: Die Anpassung an die grabende Lebensweise in der Geschichte der Solenomyiden und Nuculaceen. – Geol. Palaeontol. Abh. New Ser. 18, 1, Jena, 119 pp.
- REED, F. R. C., 1931: New lamellibranchs from the Silurian of the Ludlow district. – Ann. and Mag. of Nat. Hist. 8:290–303.
- RŮŽIČKA, B. & PRANTL, F., 1959: The hinge apparatus of the genus *Goniophora* Phillips (Pelecypoda). – Acta Mus. Nat. Prague, B:49–60.
- SAULCY, E. DE, 1838: Note sur l'animal de la Solémye. – Revue Zoologique par Société Cuvierienne. 6. Paris.
- SCHENCK, H. G., 1934: Classification of nuculoid pelecypods. – Musée Royal Hist. Belg. Bull. 10:20, 78 pp.
- SOOT – RYEN, H., 1964: Nuculoid pelecypods from the Silurian of Gotland. – Ark. Min. Geol. K. Sven. Vetensk. Acad. 3, 28:489–519, also Pal. Contr. Univ. Oslo, 54, 31 pp.
- SOWERBY, J. DE C., 1839: *In* R. I. Murchison, 1839: The Silurian System, Part 2, 768 pp.
- STANLEY, S. M., 1970: Relation of shell form to life habits of the Bivalvia (Mollusca). – Geol. Soc. Am. Mem. 125, 296 pp.
- 1972: Functional morphology and evolution of byssally attached bivalve mollusks. – J. Pal. 46, 2:165–212.
- 1975: Adaptive themes in the evolution of the Bivalvia (Mollusca). – Ann. Rev. Earth and Plan. Sci. 3:361–385.
- STEMPELL, W., 1900: Zur Anatomie von *Solemya togata* Poli. – Zool. Jahrb. Abt. Anat. Ont. 13:89–170.
- TAKEMURA, Y. & KAFUKU, T., 1957: Anatomy of the Silver-lip pearl oyster *Pinctada maxima* (Jameison). – Bull. Tokai reg. fish. res. lab. 16:39–40. Pls. 1–8.
- THOMAS, R. D. K., 1978a: Shell form and the ecological range of living and extinct Arcoida. – Paleobiol. 4, 2:181–194.
- 1978b: Limits to opportunism in the evolution of the Arcoida (Bivalvia). – Phil. Trans. R. Soc. London., B 284:335–344.
- ULRICH, E. O., 1893: New and little known Lamellibranchiata from the Lower Silurian rocks of Ohio and adjacent states. – Ohio Div. Surv. Rept. Inv. 7, 2:627–693.
- 1897: The Lower Silurian Lamellibranchiata of Minnesota. – Minn. Geol. and Nat. Hist. Surv. final report 3, 2, Paleontology, 475–628.
- VOGEL, K., 1962: Musceln mit Schlosszähnen aus dem spanischen Kambrium und ihre Bedeutung für die Evolution der Lamellibranchiaten. – Akad. Wiss. & Lit., Mainz, Abhandl., Math.-Naturwiss. Kl. 4, 52 pp.
- WALMSLEY, V. G., 1962: The identity and a new description of *Pteronitella retroflexa* (Wahlenberg) from the Upper Silurian of Gotland and the Welsh Borders. – Geol. Fören. Förh. 84, 4:351–362.
- WILLIAMS, H. S. & BREGER, C. L., 1916: The fauna of the Chapman Sandstone of Main including descriptions of some related species from the Moose River Sandstone. – U.S. Geol. Surv. Prof. Paper 89, 347 pp.
- YONGE, C. M., 1941: The protobranchiate Mollusca: A functional interpretation of their structure and evolution. – Phil. Trans. R. Soc. London. B 230:79–147.
- 1953: The monomyarian condition in the Lamellibranchia. – Trans. R. Soc. Edinburgh 62:443–478.
- 1959: The status of the Protobranchia in the bivalve Mollusca. – Proc. Mal. Soc. London 33:210–214.
- 1962: On the primitive significance of the byssus in the Bivalvia and its effect in evolution. – J. Marine Biol. Assoc. U. K. 42:113–125.

APPENDIX

GEOGRAPHICAL LOCATION OF MÖLLBOS I – CJ 4826 7445, c. 3150 m W of Sjonhem church. Topographical map sheet 6 J Roma NV & NO. Geological map sheet SGU Aa 160 Klintehamn (see Laufeld 1974).

For description of lithology see Laufeld 1974 and Liljedahl 1983.

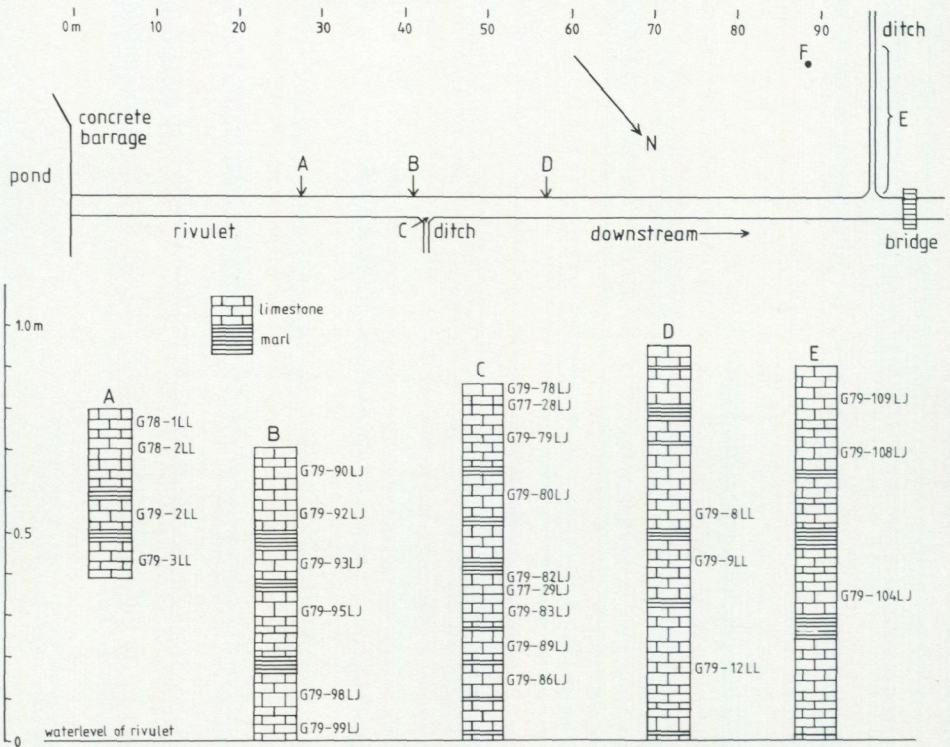


Fig. 35. Sections and surface exposure at Möllbos 1 from which the samples have been collected. C is located on the north-east side of the rivulet and A, B, D, E, and F on the south-west side. Distance downstream from the concrete barrage across the rivulet: A = 27 m, B = 41 m, C = 43 m, D = 57 m, E = 96 m, and F = 89 m. The surface exposure F is situated 16 m from the rivulet perpendicular to it.

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