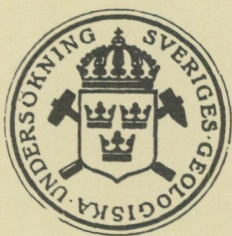


SVERIGES GEOLOGISKA UNDERSÖKNING

SERIE C NR 799 AVHANDLINGAR OCH UPPSATSER ÅRSBOK 77 NR 1

LOUIS LILJEDAHL

TWO SILICIFIED
SILURIAN BIVALVES
FROM GOTLAND



UPPSALA 1983

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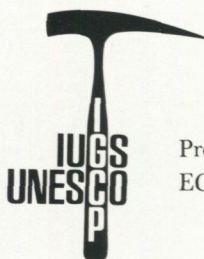
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TO MY PARENTS

CONTENTS

Abstract	6
Introduction	7
Material	8
Orientation of the nuculoid shell	9
Measurements and terminology	11
Systematic attribution	13
<i>Nuculoidea</i> Williams & Breger, 1916	13
Relevance of family diagnosis	13
Type species	13
Emended generic diagnosis	14
Discussion	14
<i>Nuculoidea lens</i> n. sp.	15
Synonymy	15
Derivation of the name	15
Holotype	15
Type stratum	15
Type locality	15
Material	15
Diagnosis	15
External features	16
Discussion of external features	18
Internal features	18
Muscular impressions	20
Discussion of internal features	20
Interpretation of muscular impressions	22
Discussion of closely related forms	26
Occurrence	31
<i>Nuculodonta</i> n.g.	31
Derivation of the name	31
Type species	31
Species	31
Diagnosis	31
Discussion	31

<i>Nuculodonta gotlandica</i> n. sp.	33
Synonymy	33
Derivation of the name	33
Holotype	33
Type stratum	33
Type locality	33
Material	33
Diagnosis	33
External features	33
Discussion of external features	34
Internal features	36
Muscular impressions	37
Discussion of internal features	39
Interpretation of muscular impressions	44
Discussion of closely related forms	45
Occurrence	47
References	48
Appendix	50

ABSTRACT

Liljedahl, Louis, 1982: Two silicified Silurian bivalves from Gotland. Sveriges geologiska undersökning, Ser. C. No. 799, pp. 1-51. Uppsala 1983.

Two silicified nuculoid bivalves from the Silurian (Wenlockian) Halla Beds of Gotland, Sweden, are described, viz. *Nuculoidea lens* n.sp. and *Nuculodonta gotlandica* n.g., n.sp. The excellent state of preservation made it possible to examine fragile and rarely fossilized parts of the shell. A reconstruction of the foot of *Nuculoidea lens* and its muscles is presented. The resulting orientation of the shell with the anterior end extended, confirms earlier assumptions. Some of the parts of *Nuculodonta gotlandica* the functional aspects of which are not clear but that may be of taxonomic value, are recorded and discussed. The two species are represented by 371 measured shells. The material was treated statistically and a clear picture of the morphologic variation within each species obtained. The size and shape of the prodissoconch are discussed on the basis of the extensive data.

INTRODUCTION

Laufeld & Jeppsson (1976) recently found silicified fossils in samples from the island of Gotland in the Baltic. Jeppsson later organized the large-scale extraction of silicified fossils from several localities; Project Silicified Fossils from Gotland (PSFG). The material presented here comes from Möllbos in the Wenlockian Halla Beds, one of the richest localities on Gotland which since the 1950s has been known to abound in silicified organisms.

Silicification offers many advantages. As a rule large numbers of specimens can be easily obtained, and the excellent state of preservation often allows even the smallest details to be examined.

The late Wenlockian fauna at Möllbos includes the following groups of silicified organisms: stromatoporoids, tabulates, rugose corals, bryozoans, trilobites, ostracodes, polyplacophorans, gastropods, bivalves, cephalopods, rostroconchs, scaphopods?, serpulids, tentaculitids, brachiopods, crinoids and other echinoderms, and machaeridians; also non-silicified graptolites, polychaete jaws, chitinozoans, conodonts, inarticulate brachiopods, additional ostracodes and trilobites, fish, hyolithelminths, ceratiocarids, conularids, and foraminifers (see Hede 1960:67, with extensive faunal list; Martinsson 1962:63, Laufeld 1974:101 for position of locality; Larsson 1979:178).

The organisms have been subjected to varying degrees of silicification, some groups being remarkably well preserved (cf. Laufeld & Jeppsson 1976:33-36). Within the groups as well the state of preservation varies.

There are 11 bivalve species, two of which, *Nuculoidea lens* n.sp. and *Nuculodonta gotlandica* n.g., n.sp. are described here. These two species make up more than 60% of all determinable bivalves, which motivates extensive morphologic analysis and taxonomic treatment. In a forthcoming paper the remaining species will be described and will be followed by a paper treating the palaeoecology of the entire bivalve fauna.

The comparatively primitive morphology and ecological requirements of extant nuculoids have always attracted the interest of students of bivalves. Some knowledge of the extant nuculoid species is essential for an understanding of their extinct ancestors. On the other hand, in some respects fossil nuculoids provide information about the evolution of the group which have possibly given rise to many extant bivalve groups and concurrently to a few unspecialized nuculoid genera.

The taxonomy of the Silurian members of the order Nuculoida needs to be thoroughly revised, largely because the descriptions of most taxa are based on locally restricted material and because it is unusual to find bivalve specimens that can be studied both externally and internally.

I am most grateful to the following for valuable help and guidance. Sven Laufeld and Lennart Jeppsson have encouraged me throughout, their never ceasing enthusiasm having helped me through many difficulties. They critically

read and improved the manuscript as did Anita Löfgren, Gerhard Regnéll, John Pojeta Jr., and Anders Martinsson. Valdar Jaanusson, Naturhistoriska Riksmuseet, Stockholm, and Hermann Jaeger, Paläontologisches Museum, Berlin, kindly lent me material for comparison. Lennart Månsby ran the computer, Inga Palmaer, Christine Ebner, and Claes Bergman helped with the drawings. Agneta Ek typed part of and Ingrid Lineke and Erna Hansson most of the manuscript. Margaret Greenwood-Petersson gave linguistic help. Kristina Lindholm and Gunnar Thuning made most of the extraction. Last but not least Sven Stridsberg did a formidable job of photography. Project Ecostratigraphy and the Geological Survey of Sweden financed my field work. To all I wish to express my sincere thanks.

MATERIAL

The Silurian bivalves previously collected on Gotland have generally been preserved as carbonate shells of varying quality and as external and internal moulds. Except for the silicified specimens the best-preserved nuculoids are found in the marls. The hard crystalline limestones yield the poorest specimens, while the oolitic limestones are intermediate in this respect (cf. Angelin & Lindström 1880; Hede 1921; Soot-Ryen 1964).

The Halla beds at Möllbos 1 (Laufeld & Jeppsson 1976) consist of a few metres of light brownish-grey to yellowish-grey, compact, fine-grained, extremely argillaceous limestone intercalated by thin marly beds. The limestone is fairly hard as a result of silicification (Laufeld & Jeppsson 1976), and the individual beds vary in thickness from about 5 to 10 cm, while the marly intercalations are soft and generally 1–5 cm thick. The silicified specimens were extracted from material collected within two restricted areas of about 15 m² each and approximately 50 m apart. The stratigraphic difference between the uppermost and lowermost samples is 0.7 m. For geographical location and sample numbers, see Appendix.

So far about 400 kg of limestone from Möllbos 1 has been dissolved in acetic acid. Among a multitude of other fossils about 1 200 determinable bivalve shells and an undetermined number of fragments have been isolated. The state of preservation of most of the bivalves is good or fairly good. However, silicification of the shell has occasionally been poor or incomplete so that the non-silicified parts were lost during the diagenesis or during the processing of the samples (Fig. 14:C).

Some articulated valves are filled with secondary calcite crystals which survived the acid bath owing to the efficiency of the tightly fitting valve margins. In these valves almost no silicification has affected the original inner side of the shells. Finally, some shells have fractures, thin sheets of silica traversing the shells (Fig. 5:C).

The specimens of the two nuculoid species described here are, to my knowledge,

by far the best-preserved Silurian, and possibly Palaeozoic, nuculoids ever recorded. Since the material is outstanding, both in quality and quantity, it warrants as detailed a description as possible. The 371 specimens and the numerical data are now stored in the Type Collection of the Geological Survey of Sweden, Museum Dept., Box 670, S-751 28 Uppsala, Sweden.

ORIENTATION OF THE NUCULOID SHELL

The generally accepted and often-used criteria of orientation of bivalve shells, viz. that if ligamental nymphs are present they are invariably on the posterior side of the beaks, and if a pallial sinus is seen this is invariably near the posterior end (Cox, Nuttall & Trueman 1969), cannot be applied to *Nuculoidea lens*, since it lacks these features. Instead, the orientation is deduced from the position, size and shape of the muscular impressions of the foot (accessory muscle scars) and the point of maximum opening of the valves. These features can be directly compared with those of extant taxa in which the orientation is known from the soft tissues (Heath 1937). For a detailed discussion see below under Internal features, p. 18. Since the shell of *Nuculoidea lens* is inequilateral and the beaks are posterior to mid-length of the shell, it is thus anteriorly elongated. *Nuculoidea* has of tradition been regarded as being anteriorly elongated but the evidence on which this rests has not previously been thoroughly discussed and explained.

The same two criteria which apply to *Nuculoidea lens* are used for *Nuculodonta gotlandica*. Furthermore, there is an additional feature, viz. the presence of an outer ligament. Its position agrees with the orientation suggested. Both species thus have a "reversed" orientation (see Bradshaw 1970:629).

The orientation thus deduced coincides with observations made by several other authors. Williams & Breger (1916) asserted that the umbonal scars are always antero-umbonal, and are among the first to use this character as a means of orienting the shell. Quenstedt (1930:55) initiated a general discussion on the orientation of the nuculoid shell, referring to the many earlier contradictory ideas, and stressed the importance of the direction in which the umbo and the resilifer point. He stated that the opisthogyrate shape had not yet evolved in Devonian times. Later authors have placed this as far back as the Ordovician (Pojeta 1971, Pl. 4:6, 8, 13, 14, 18, Pl. 6:9). Further, Quenstedt (1930:58) suggested that the prolonged end of the shell should be treated as the anterior end until the contrary could be proved. Bradshaw (1970:624; Bradshaw & Bradshaw 1971) put forward two criteria for the orientation of palaeotaxodonts: the nature of the hinge teeth and the position of the accessory muscle scars. If the first criterion is applied, the relative movement of the valves can be determined, and the point of maximum opening (presumably being in the anterior part where the large foot protruded) can be deduced, a method that has proved to be useful in this material (Figs. 4:C, 5:B, 10:A, B).

Other species resembling *Nuculodonta gotlandica*, for which the opposite orientation has been suggested, deserve closer examination. In Bradshaw's (1970:629 and Fig. 6) discussion of "normal" orientation (i.e. with the shorter end regarded as anterior) of *Tancrediopsis ezquerrae* (Sharpe, 1853) she compares the two scars "... situated along the dorsal side of the umbonal cavity close to the hinge plate ..." with scars in *Tancrediopsis contracta* (Salter, 1859) in a corresponding position. According to McAlester (1963:6) the shells of this taxon exhibit "... faint impressions just below the posterior hinge plate ...". In his description of these impressions he refers to his Figs. 75 and 77. However, the orientation of this species is mainly based on the position of the outer ligament, generally accepted as being posterior to the umbones (Cox, Nuttall & Trueman 1969). As the species described by Bradshaw (1970:629) is preserved as internal moulds, there can be no evidence of a possible outer ligament, and she therefore suggested the positions of the scars referred to above as a clue to a "normal" orientation. Since the arrangement of the incisions in Figs. 75 and 77 in McAlester (1963) differs wholly from those in Bradshaw 1970, Fig. 6, I consider the comparison between *Tancrediopsis ezquerrae* and *Tancrediopsis contracta* irrelevant.

Bradshaw's argument that the two scars are on the posterior side of the shell is even less convincing in the light of evidence from a number of different extant species drawn by Heath (1937, Pl. 10:83, Pl. 7:56, Pl. 6:51) showing that the accessory muscles are found mainly in the anterior part of the animal. *Tancrediopsis ezquerrae* as illustrated by Bradshaw (1970) exhibits a similar pattern of accessory muscle scars. Rather a "reversed" orientation of *T. ezquerrae* is supported by the similarity in position of accessory muscle scars in this species and in *Nuculodonta gotlandica*.

Bradshaw's (1970:632, Figs. 9, 12) other species, referred to as *Praeleda costae* (Sharpe, 1853) and *Praeleda ciae* (Sharpe, 1853) and which she herself proves to have a "reversed" orientation, also closely resemble *Tancrediopsis ezquerrae* in these respects. All four species are also roughly uniform in general outline with the prolonged, more evenly rounded end presumably being the point of maximum opening of the valves.

The two species referred to by Bradshaw (1970) as *Praeleda costae* and *Praeleda ciae* are worth examining. Her two basic arguments for a "reversed" orientation of these forms are, first, the largest teeth are situated on the long side of the shell, secondly, the point of maximum opening of the valves indicates the anterior end. This statement agrees with the generally accepted idea of the orientation of Palaeozoic nuculoids (Quenstedt 1930:58) and coincides with my interpretation of the orientation of both *Nuculoidea lens* and *Nuculodonta gotlandica*. Thus I agree that in the species assigned to *Praeleda* by Bradshaw the orientation is "reversed" with a prolonged anterior end. After having been referred to the genus *Ctenodonta* Salter, 1852 by several authors among others by Babin (1966), *Nucula costae* and *N. ciae*

where placed under the genus *Praeleda* Pfab, 1934 by Bradshaw (1970). Bradshaw claimed that they closely resembled *Praeleda* Pfab, 1934 in "... general shape, dentition and accessory muscle scars ...". Nevertheless, when referring to Plate 3 in Pfab (1934) she does not note the two major criteria for recognizing the genus *Praeleda*, viz. the more prolonged posterior end and the posteriorly placed omnipresent pallial sinus. If these features are not present in Bradshaw's material I find her assignment of *Nucula costae* Sharpe, 1853 and *Nucula ciae* Sharpe, 1853 within the genus *Praeleda* Pfab, 1934 invalid.

MEASUREMENTS AND TERMINOLOGY

The original definition of the antero-posterior axis (Fischer 1886), implying that it touches the lower margin of the two adductors, could not be applied to this material, since the impression of these muscles are not always discernible. Instead I prefer to place this axis on the apex of the most distal tooth in each hinge plate (Fig. 1). Perpendicular to this are the anterior axis which is tangential to the anterior edge of the valve and the posterior axis, which is tangential to the posterior edge of the valve. The ventral axis is parallel to the antero-posterior axis and tangential to the valve at the extreme point of the ventral margin. The median

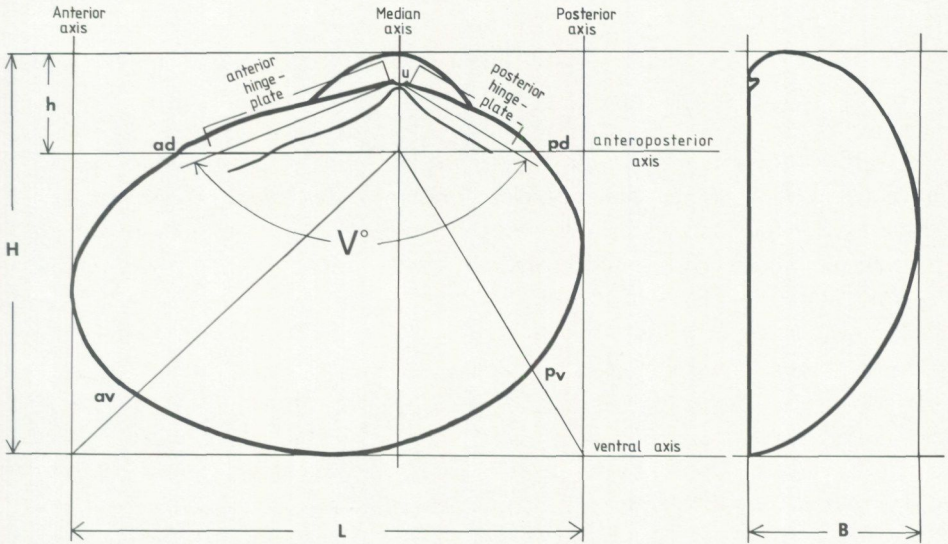


Fig. 1. Terminology of shell. Margin: The part between *ad* and *pd* is denoted the dorsal margin, *u* to *ad* anterior part of dorsal margin, *ad* to *av* anterior margin, *av* to *pv* ventral margin, *pv* to *pd* posterior margin, and *pd* to *u* posterior part of dorsal margin; V° = hinge angle, *H* = total height, *h* = hinge height, *L* = total length and *B* = breadth (for definitions and further details see text, pp. 11–13).

axis runs through the tip of the beak perpendicular to the antero-posterior axis. The definitions of the last four axes are generally accepted and have been explained by several authors (cf. Heinberg 1976). The length of the anterior (Ah) and posterior (Ph) hinge plate is measured from the most proximal tooth to the tip of the most distal one. The distance between the highest point of umbo and the antero-posterior axis I name the hinge height (h). The total length of the shell (L) is measured from the anterior axis to the posterior axis and the total height (H) from the highest point of umbo to the ventral axis. The breadth (B) of each valve is measured from the sagittal plane to the point of maximum convexity, laterally.

The point u is located where the median axis crosses the dorsal margin, ad and pd where the antero-posterior axis cuts the shell margin antero-dorsally and postero-dorsally, respectively, av and pv where the lines originating from the junction between the antero-posterior axis and the median axis meet the shell margin antero-ventrally and postero-ventrally, respectively. The distance $u-ad$ is the anterior part of the dorsal margin, $ad-av$ the anterior margin, $av-pv$ the ventral margin, $pv-pd$ the posterior margin, $pd-u$ the posterior part of the dorsal margin, and $pd-ad$ the dorsal margin. The distance $ad-av$ comprises a dorso-anterior and a ventro-anterior part united at the point where the anterior axis touches the shell. Likewise $pd-pv$ may be divided into a dorso-posterior and a ventro-posterior part. The hinge angle (V^0) is measured from the tip of the beak to the most distal tooth in both hinge plates.

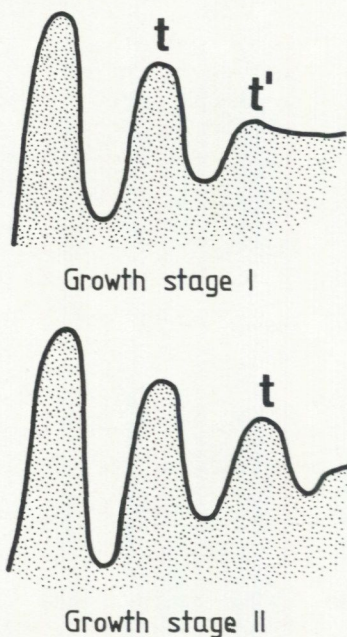


Fig. 2. Counting of hinge teeth. Terminal tooth counted only when socket (distally) next to it is present (t' = not counted).

The hinge teeth were counted in the following way. As each tooth develops, a corresponding socket in the opposite valve is formed simultaneously. Since the tooth grows gradually, and as I have encountered all stages of growth, I counted the terminal tooth only in specimens where the distal socket next to it has begun to form (Fig. 2).

Seven shell variables have been measured: total length (L), total height (H), hinge height (h), breadth (B), length of anterior (Ah) and posterior (Ph) hinge plates and the hinge angle (V^0). The number of hinge teeth on the anterior (NAh) and posterior (NPh) hinge plates have been counted. The Appendix contains minimum, maximum and mean values, and the number of specimens measured. It also shows the ratios between the total length and each of the other variables. In all 1 720 measurements were made. A Zeiss stereomicroscope was used (magnification X 10, accuracy ± 0.1 mm).

Regression analyses were carried out by computer (Norman *et al.* 1971, program SPSS) at *Lunds Datacentral*. All variables were run against each other, and out of 56 scatter diagrams for the two species described here, 7 have been chosen for each species (Figs. 6, 7, 11, 12).

SYSTEMATIC ATTRIBUTION

The two genera treated in this paper belong to Class Bivalvia Linnaeus, 1758, Subclass Palaeotaxodonta Korobkov, 1954, Order Nuculoida Dall, 1889. The genus *Nuculoidea* is assigned to the Superfamily Nuculacea Gray, 1824, Family Nuculidae Gray, 1824, whilst the genus *Nuculodonta* cannot be assigned to a family-group taxon as nuculoid systematics now stand (cf. p. 31).

Nuculoidea Williams & Breger, 1916

RELEVANCE OF FAMILY DIAGNOSIS — In the systematics proposed in *Treatise on Invertebrate Paleontology, Part N, vol. 1* (McAlester 1969), the family diagnoses as given virtually exclude some of the traditionally accepted genera of Nuculidae. The genus *Nuculoidea*, which in the *Treatise* is referred to the family Nuculidae, is characterized by orthogyrate or actually faintly prosogyrate beaks, contrary to the definition of the family Nuculidae, viz. opisthogyrate beaks. However, since *Nuculoidea* has an internal ligament and the superfamily Nuculacea comprises two families, one of which is characterized by an external ligament and the other by an internal ligament, the genus *Nuculoidea* is temporarily placed within the family Nuculidae, without any attempt to formal redefinition herein.

TYPE SPECIES — *Cucullea opima* Hall, 1843 (= *Nucula randalli* Hall, 1869).

EMENDED GENERIC DIAGNOSIS — Outline of shell highly variable; external shell surface smooth to commarginally striate; inner side of ventral margin smooth to microscopically pectinate; resilifer distinct; hinge plates variable in size and shape and containing a varying number of teeth.

DISCUSSION — In all artificial classification many problems are encountered, and several authors have commented upon the unsatisfactory systematics of the Palaeozoic nuculoids (e.g. Soot-Ryen 1964 and McAlester 1968). Numerous attempts have been made to understand the phylogenetic relationships of the taxa concerned (Beushausen 1895, Pfab 1934, Schenck 1936, 1939, etc.). The difficulties of placing a genus in the correct family are many, especially when new intermediate forms are to be added and classified. At generic and specific levels the commonest problem is the difficulty and sometimes even the impossibility of determining the range of natural variation within a population of a fossil species owing to the limited amount of material available. The greatest problem, however, is to decide whether the population in question is a deme or a species in its own right.

These difficulties are exemplified in McAlester's (1963:10–13) description of the Ordovician *Tancrediopsis cuneata* (Hall). The material formerly assigned to *Ctenodonta contracta* Salter, 1859, the correct name of which according to McAlester is *Tancrediopsis cuneata* (Hall), comprises two species. One of these, *T. cuneata* itself, may be considered to belong to the family Ctenodontidae Wöhrmann, 1893, as it satisfies the family criteria (McAlester 1969:228): shell equilateral, pallial sinus lacking, resilifer absent, cylindrical external ligament posterior to umbones. The other species, *Tancrediopsis "abrupta"* (Billings) resembles *T. cuneata* in several respects but has a truncate posterior extremity, i.e. it is inequilateral, a characteristic of members of the family Praenuculidae McAlester, 1969 which belongs to a different superfamily. The external difference between these two *Tancrediopsis* species is greater than that between *Nuculoidea lens* and *Nuculodonta gotlandica*. For comparison, consider the insignificant variations in the shell of the different species of the modern genus *Nucula* Lamarck, 1799.

Williams & Breger (1916) established *Nuculoidea* as a subgenus of *Nucula* Lamarck, 1799, and their diagnosis stresses the presence of a distinct resilifer and a non-pectinate ventral margin. According to their description, the subgenus *Nuculoidea* is sufficiently comprehensive to include three heterogeneous groups: *Nucula opima* Hall, *Nucula aquisgranensis* (Beushausen) and *Nucula? notica* Hall. Several authors have criticized this rather vague and practically all-embracing subgeneric description. Soot-Ryen (1964:509) disagreed with the assignment of the two latter groups to the subgenus, which she accepts as a genus, pointing out that they are "... quite different from the type species ...". McAlester (1962a:21–22) stated that the second main feature in the diagnosis by Williams & Breger (1916) "... lacks value as a generic character ...". McAlester himself described clear, fine radial ridges on the ventral margin on specimens of *Nuculoidea opima*, the type species of

the genus. Further, McAlester was of the opinion that "... no clear generic-level distinction has yet been made between the recent genus *Nucula* Lamarck, 1799 and the many similar chondrophore-bearing Palaeozoic shells formerly assigned to this genus...", i.e. species now generally referred to *Nuculoidea*. However, Vokes (1949:363) emphasized the "... unique nature of the marginal pectination observed in *Nuculoidea opima* ...", and together with the nature of the hinge, and even more of the condrophore, "... the generic entity of *Nuculoidea*..." is emphasized. Further Vokes felt that *Nuculoidea* should be kept apart from the group that has a different kind of denticulate margin present in, for instance, *Nucula* s.s. (see Schenk's classification 1934:18).

***Nuculoidea lens* n.sp.**

Figs. 3, 4, 5, and 9

SYNONYMY — ?1880 *Ctenodonta pinguis* G. Lindström—Lindström, p. 19; ?1921 *Nucula anglica* d'Orbigny—Hede, p. 32. The question-mark indicates that the species name presumably included at that time several forms now treated as separate species (Richter 1948:54).

DERIVATION OF THE NAME — Latin *lens* refers to the shape of an articulated specimen as seen in dorsal or ventral view.

HOLOTYPE — A right valve, SGU Type 842 from sample G77-28LJ, Figs. 4:E, 9:A, B, C. Length 14.8 mm, height 11.5 mm, breadth 4.0 mm. Several growth increment furrows on the exterior, the last one modifying the slightly arched outline seen in anterior view; apex of beak damaged; all hinge teeth present, though some of tips broken; anterior hinge plate with 16 teeth, the 5 most proximal ones within the area of the resilifer; posterior hinge plate with 12 teeth, 4 within the resilifer area; muscular impressions comprising anterior and posterior adductor muscle scars, posterior pedal retractor muscle scar, anterior pedal protractor muscle scar, median muscle scars and anterior pedal retractor muscle scar (see the interpretation of muscle scars, p. 22).

TYPE STRATUM — Halla Beds, Upper Wenlockian, Silurian.

TYPE LOCALITY — Möllbos 1, Gotland, Sweden.

MATERIAL — 153 measured specimens, as well as an undetermined number of fragments.

DIAGNOSIS — *Nuculoidea*, lens-shaped in dorsal or ventral view and sub-circular to

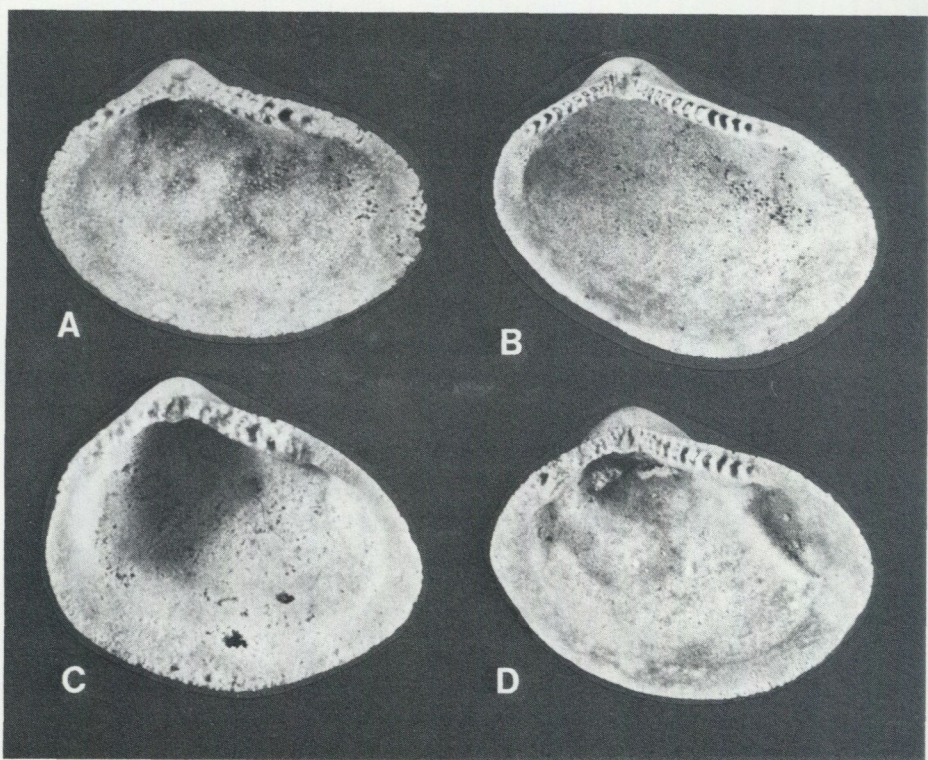


Fig. 3. *Nuculoidea lens* n.sp. Variation in lateral outline. — A. SGU Type 1131, $\times 5.3$, sample G79-90LJ. — B. SGU Type 1137, $\times 3.5$, sample G79-84ALJ. — C. SGU Type 876, $\times 8.3$, sample G77-28LJ. — D. SGU Type 886, $\times 4.3$, sample G77-29LJ. All specimens are left valves.

suboval in lateral outline. Umbo low, beaks contiguous and orthogyrate, lunule and escutcheon circumscribed. Dorsal margins only slightly raised on both sides of umbo. Ventral margin strongly convex. Teeth both anterior and posterior to resilifer, chevron-shaped, apices pointing towards umbo. In adult specimens anterior teeth more numerous than posterior ones.

EXTERNAL FEATURES — Shell small, subcircular, equivalve, inequilateral, rather inflated, anterior part protruding, margins even, no gap present; no trace of external ligament; faint commarginal growth lines, sometimes with conspicuous irregularities; beaks small, close together, orthogyrate in posterior half of shell; maximum convexity about midway along the shell and at $2/3$ of height; lunule present but only faintly visible; escutcheon scarcely visible; dorsal margin convex, antero-dorsal part sloping, meeting anterior margin in a smooth transition, sometimes at a distinct angle at most distal end of hinge plate, postero-dorsal margin

sloping, meeting posterior margin in a more or less discernible projection at posterior end of hinge plate; anterior margin well rounded, narrow and protruding, dorso-anterior part generally longer than ventro-anterior part; posterior margin evenly rounded to truncated and sometimes tapering, dorso-posterior part much shorter than ventro-posterior part; ventral margin long and rather convex with deepest point in anterior part and at about midway along the shell.

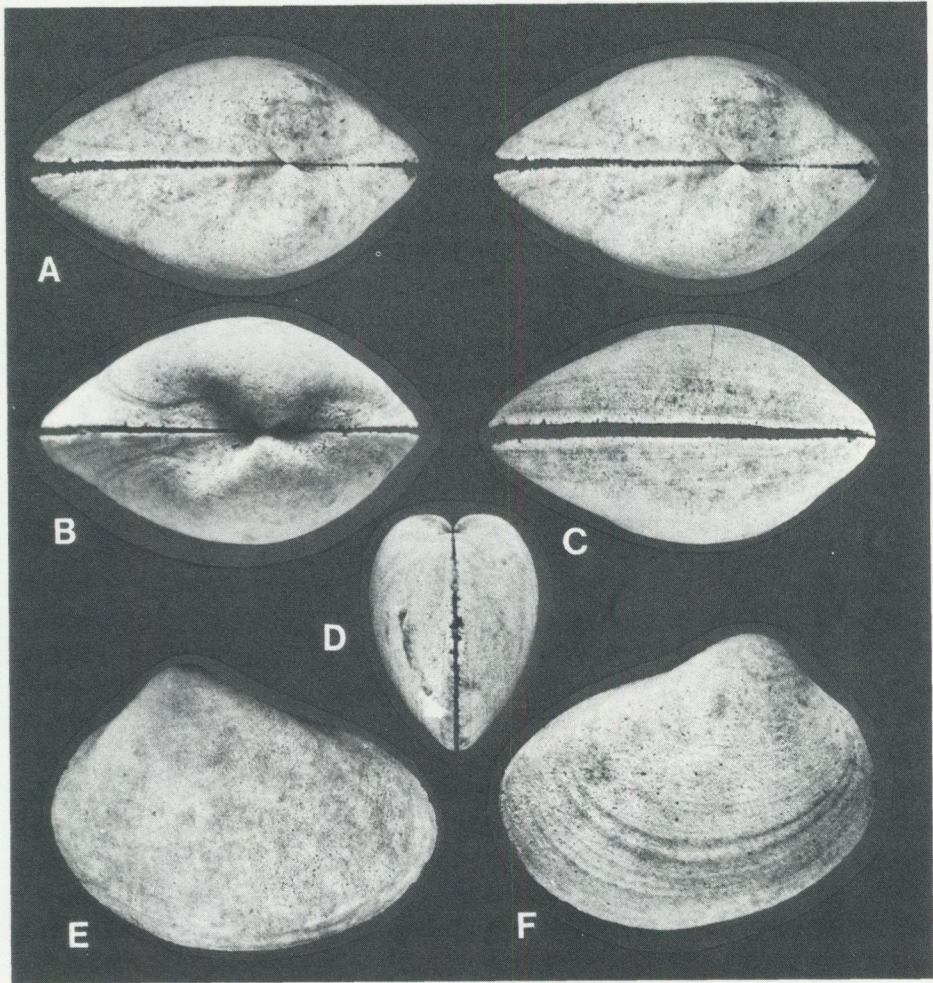


Fig. 4. *Nuculoidea lens* n.sp. External features. — A. Stereo pair, dorsal view, anterior end to the left. Note orthogyrate beaks and lens-shaped outline of the shell; SGU Types 894, 895, $\times 3.4$. — B. Dorsal view, anterior to the left. Note lens-shaped lunula and escutcheon; SGU Types 900, 901, $\times 3.9$. — C. Ventral view, anterior to the left. Note maximum opening of the valves antero-ventrally; SGU Types 894, 895 (same specimens as in A), $\times 3.4$. — D. Anterior view showing closely fitting valve margins; SGU Types 914, 915, $\times 4$. — E. Lateral view of holotype (right valve) showing smooth external valve surface; SGU Type 842, $\times 3.4$. — F. Lateral view of a left valve. Note commarginal growth stop markings; SGU Type 901 (same specimen as in B), $\times 3.9$. All specimens from sample G77-28LJ.

DISCUSSION OF EXTERNAL FEATURES — It has been possible to consider many aspects of variation within the species, thanks to the large number of specimens available. The dorsal, ventral, anterior and posterior margins, which constitute the lateral outline of the shell, may vary greatly in shape depending on individual differences unrelated to ontogeny. Some of these variations in outline are shown in Fig. 3. Variation in other, more easily measured features, viz. length, height and breadth, is recorded and discussed below.

The outer surface of the shell has no sculpture in the proper sense of the word though faint commarginal growth lines occur (Fig. 4:C, D). Occasionally the normal lens-shaped outline, as seen in dorsal or ventral view, is noticeably modified by one or several commarginal rugae, presumably caused by a temporary reduction in growth rate (Fig. 4:B, F), perhaps indicating seasonal variation or spawning periods. The beaks are dorsal, almost touching and are mainly orthogyrate, sometimes slightly prosogyrate. Though the true direction of the beaks can sometimes be difficult to determine in small shells the larger ones are distinctly orthogyrate (Figs. 4:A, 5:B).

Anterior to the beaks on the external valve surface is a lens-shaped area that corresponds to the extension of the underlying hinge teeth (Fig. 5:E; cf. Carter 1967:245–247). This is the lunule (Fig. 4:B), defined by a subtle change in the shell texture. The flattened area has a minor central crest formed by the opposite edges of the dorsal margin (Fig. 4:A, B, D). This is also true of the escutcheonal area posterior to the beaks. Here the limits are less clearly defined and, like the borders of the lunule, they circumscribe the position of the underlying hinge teeth, here the posterior ones. Just below the beaks a small opening leads into the ligamental pit (see the discussion of ligament, p. 20).

The shell margins are smooth and fit closely together (Fig. 4:A, B, C, D). No microscopical crenulation of the inner ventral margin is present. The shell margins are rather thin, which may have enabled the valves to close more effectively.

In Fig. 6:A two external features of *Nuculoidea lens*, viz. height and breadth, are related to the total length of the shell. The H/L-ratio ranges from 0.91 to 0.72. Since none of the shells in this material are less than 2.8 mm long the inclination of the regression line close to origo is uncertain and the size and shape of the prodissoconch can only be inferred (see the discussion of hinge teeth, p. 22). Moreover the B/L-ratio line does not pass through origo but below it. As with the H/L-ratio, shells that are less than 5 mm seem to lie along a line passing through or near origo. A gerontic character, clearly seen in the B/L-diagram, is that shells more than 10 mm long have a more gibbous appearance than the smaller, or younger, shells.

INTERNAL FEATURES — Hinge line convex, anterior part roughly concave in outline and posterior part straight, interrupted by a symmetrical, almost vertical resilifer just below beaks; anterior hinge plate long, about 1/3 of total length of shell, with

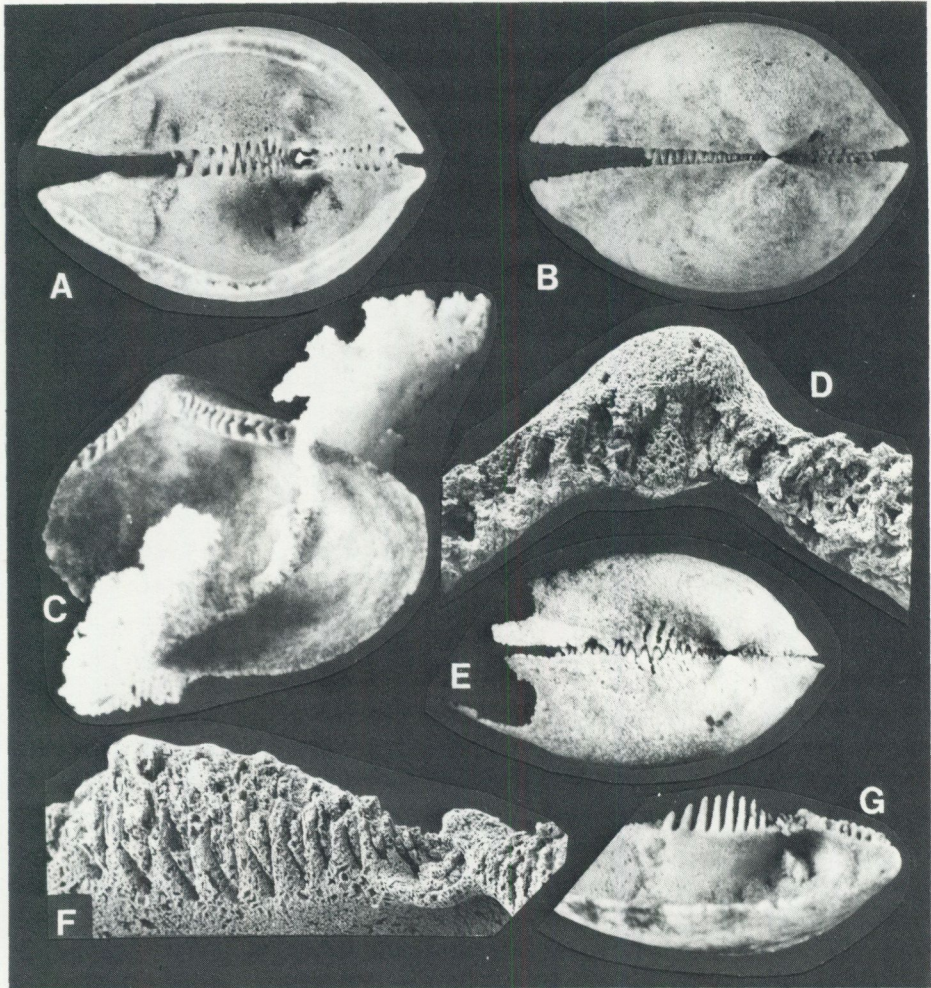


Fig. 5. *Nuculoidea lens* n.sp. — A. Ventral internal view, anterior to the left. Note resiliifer opening; SGU Types 1188, 1189, $\times 4$, sample G78-1LL. — B. Exterior of same specimens, dorsal view, anterior to the left. Note maximum opening anteriorly. — C. Internal lateral view of a left valve through which runs a silica-filled joint; SGU Type 1190, $\times 3.8$, sample G79-84ALJ. — D. SEM photograph of a left valve showing silicified replica of resilium; SGU Type 876, $\times 29$, sample G77-28LJ (same specimen as in Fig. 3:C). — E. External dorsal view showing worn lunular area and parts of the underlying anterior hinge teeth. Note arcuate form of teeth, anterior to the left; SGU Type 1191, 1192, $\times 3.8$, sample G79-84ALJ. — F. SEM photograph of a right valve showing ligamental pit and arcuate anterior hinge teeth in ventral view; SGU Type 1208, $\times 110$, no sample number. — G. Internal ventral view of a right valve with intact anterior hinge teeth; SGU Type 1193, $\times 4$, sample G79-78LJ.

about 14 teeth in a specimen 14.8 mm long, most distal tooth almost conical, medians long, chevron-shaped with longer dorsal limb, apices directed towards beak, progressively narrower and smaller proximally, becoming more or less

transverse in shape, most proximal tooth extremely small, occupying whole breadth of hinge plate, most distal tooth about 2/3 of the plate; posterior hinge plate short, nearly a quarter of total length of shell, with approximately 11 teeth in a specimen 14.8 mm long, teeth similar in shape and arrangement to anterior ones; teeth slightly arcuate in dorsal view; hinge angle ranging from 119° to 134° (average of 38 specimens = 127°).

MUSCULAR IMPRESSIONS — Two large, subequal, suboval adductor muscle scars below distal ends of hinge plates, often with faint concentric growth lines parallel to distal margins; anterior scar largest and often heavily impressed; one scar impressed to varying degrees slightly triangular and elongated extending from top of posterior adductor muscle scar antero-dorsally along and below posterior hinge plate; two elongated, rather deep impressions occasionally with strong concentric growth lines laterally in umbonal cavity; one moderately deep, triangular to subcircular impression postero-dorsal to top of anterior adductor muscle scar immediately below the most distal tooth in anterior hinge plate; two minute scars of different size latero-dorsally just below anterior hinge plate, the larger one sometimes slightly elongated; a low ridge from umbonal cavity antero-ventrally half-way to ventral margin in one shell; pallial line often a series of scars extending in an arc from one adductor muscle scar to the other; no sinus.

DISCUSSION OF INTERNAL FEATURES — Hinge composed of two plates, one anterior to and one posterior to beak, about 2/5 and 1/3 respectively of total length of shell, posterior plate about 4/5 of length of anterior plate. In Fig. 6:B three internal characters are illustrated: length of anterior hinge plate (Ah) and posterior hinge plate (Ph) and hinge height (h) are plotted against total length of shell.

The two plates are separated by a triangular resilifer, or ligamental pit, which is symmetrically placed dorso-ventrally. The recent genera *Nucula* Lamarck, 1799 and *Nuculana* Link, 1807 have internal as well as external ligaments that function as a unit, i.e. as an alivincular ligament (Trueman 1952:202; Owen 1959:216–217). Since there is an opening in the dorsal part of the resilifer construction in *Nuculoidea lens* (Fig. 5:A), leading to the outside, it is possible that the ligament in this species also had anterior and posterior external components in addition to the internal part. In some specimens the ligamental pit is not cup-shaped (Fig. 5:F), but suggests rather the presence of a pit filled with material, possibly remnants of the inner calcified part of the ligament preserved as a silicified replica (Fig. 5:D). No remnants of an outer ligament were observed. On the other hand nor have I seen any trace of the outer parts of the ligament on empty shells of *Nucula* and *Nuculana*.

In the shell with the best-preserved anterior hinge teeth these are all nearly intact (Fig. 5:G). They are arcuate in dorsal view as can be clearly seen on a specimen with a worn-down lunular surface (Fig. 5:E; see also Fig 5:F showing

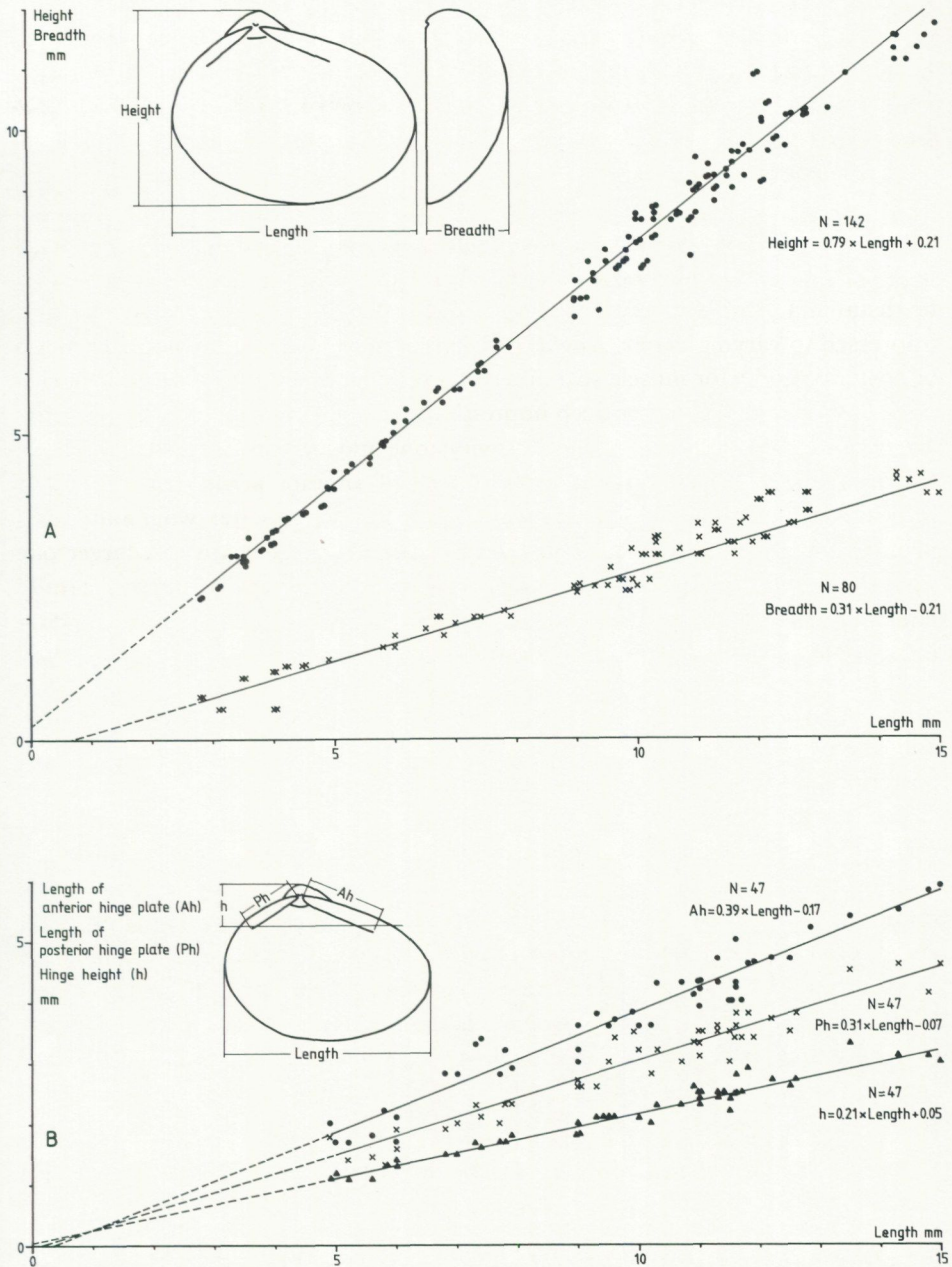


Fig. 6. *Nuculoidea lens* n.sp. Ontogeny and variation in outline. Scatter diagrams with computer-calculated regression lines. — A. Height and breadth of shell in relation to total length. — B. Length of anterior and posterior hinge plate and hinge height in relation to total length of shell (for discussion see text, pp. 18, 20).

arcuate teeth in ventral view). Two scatter diagrams are combined in Fig. 7. They show the number of anterior hinge teeth (A) and posterior hinge teeth (B) in relation to the total length of the shell. In all diagrams the correlation lines are whole in the interval representing measured specimens and dotted outside this interval. Some of the variation arises from the fact that the smallest of the most proximal teeth are sometimes extremely difficult to discern, which makes the estimated error of counting of least one. Furthermore, only whole numbers have been counted, even though in some specimens there are also small teeth but lack an adjoining socket distally (see the discussion of counting, p. 13). Thus, within an error of ± 2 almost all values agree with the computer-calculated regression lines in Fig. 7. Unfortunately in shells less than 3 mm long, the hinge teeth are poorly preserved, if at all, and have consequently not been included.

The regression lines for numbers of anterior and posterior teeth converge to intercept the y-axis at about 5. Thus in a 15 mm long shell the lines indicate a constellation of anterior/posteriors of 15/12 and in a hypothetical shell 0.1 mm long the relation would be 5/5. Yet the smallest shell with countable teeth, about 3 mm long, has the same number of teeth on each of the hinge plates. The graphs indicate that there are about 5 teeth on each hinge plate in the prodissoconch. However, the prodissoconch of the living *Nucula* (Bernard 1896:56) has no real hinge teeth, only small "crenulations". As the shell begins to grow the teeth appear, one at a time simultaneously on each side of the beak. If the prodissoconch of *Nuculoidea lens* resembled that of the living *Nucula*, then the number of teeth must have increased rapidly if 5 were to develop in each hinge plate in shells about 3 mm long.

I have estimated that the prodissoconch of *Nuculoidea lens* was less than 1.0 mm long, the first shell in most living bivalves usually being 0.2 to 0.6 mm in length (Trueman 1969). As the 3 mm long shells of *N. lens* have the same number of teeth anterior to and posterior to the beak with the same spacing in the two hinge plates, the plates in the prodissoconch should have been of equal length, symmetrically placed to the umbo. Accordingly, the shell would have been almost circular and agrees well with Bernard's (1896:56) general description of the prodissoconch. If the first shell of *N. lens* was almost circular growth could not have been strictly isometric (Stanley 1972:60) in the earliest stages, which is not uncommon in the early stages of many living bivalves (Jackson 1890:327-329).

The only character not presented diagrammatically is the hinge angle which proved to be extremely variable and independent of shell size.

INTERPRETATION OF MUSCULAR IMPRESSIONS — Evidence of how the soft parts were attached to the shell in fossil bivalves is generally recorded from internal moulds, most fossil shells and external moulds being directed towards the sediment with the interior and thus usually difficult to uncover from the matrix (Driscoll 1964; Bradshaw 1970, etc.). In most shells of *Nuculoidea lens* only three to four muscular

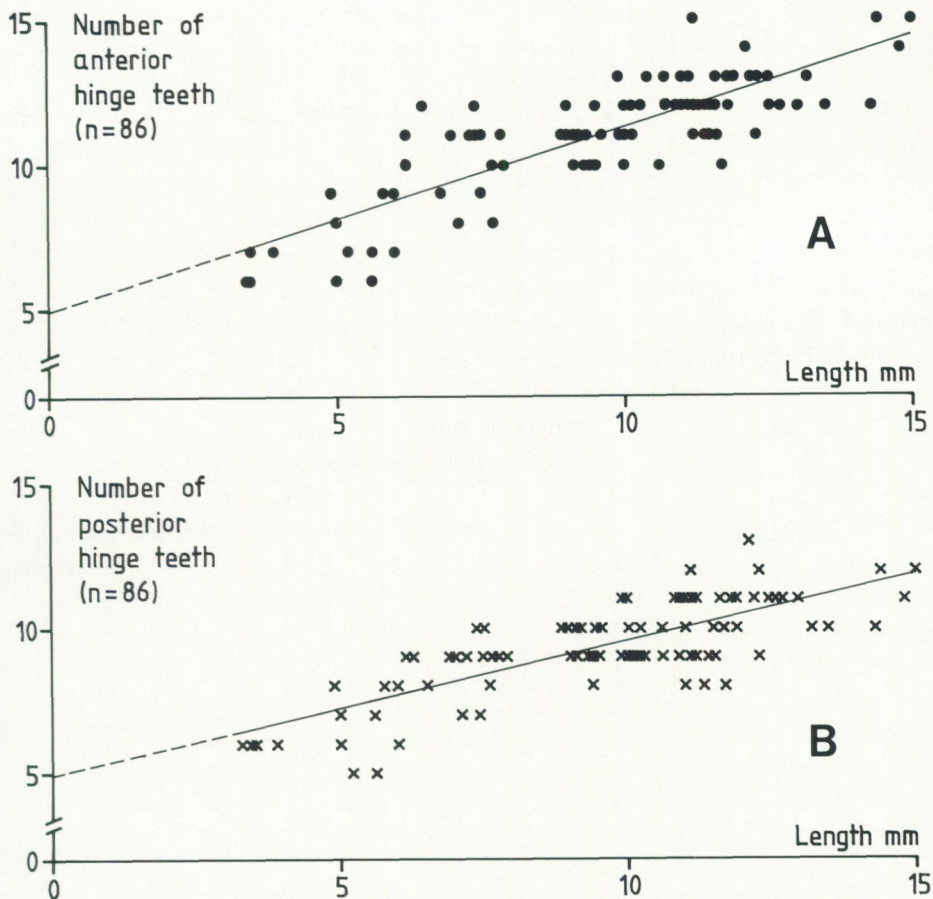


Fig. 7. *Nuculoidea lens* n.sp. Number of hinge teeth in relation to total length of shell. — A. Anterior. — B. Posterior. Regression lines calculated by computer (for discussion see text, p. 22).

impressions are discernible in each valve. Fig. 8 is a hypothetical shell displaying the maximum number of muscular imprints observed in the entire material examined in this study. It also shows a reconstruction of the foot and its muscles based on available observations together with comparisons with the morphology of living nuculoids. The impressions of the accessory muscles have their counterparts in the opposite valve, the muscles functioning as pairs of bundles.

The anterior adductor muscle scar (No. 1 in Fig. 8) is the most deeply incised scar and is in accordance with the general rule for representatives of closely related taxa in later geological periods (Quenstedt 1930:59). It is limited proximally by a conspicuous, rounded wall. At some distance from the anterior margin the most anterior part of the scar displays a more gradual change towards the anterior

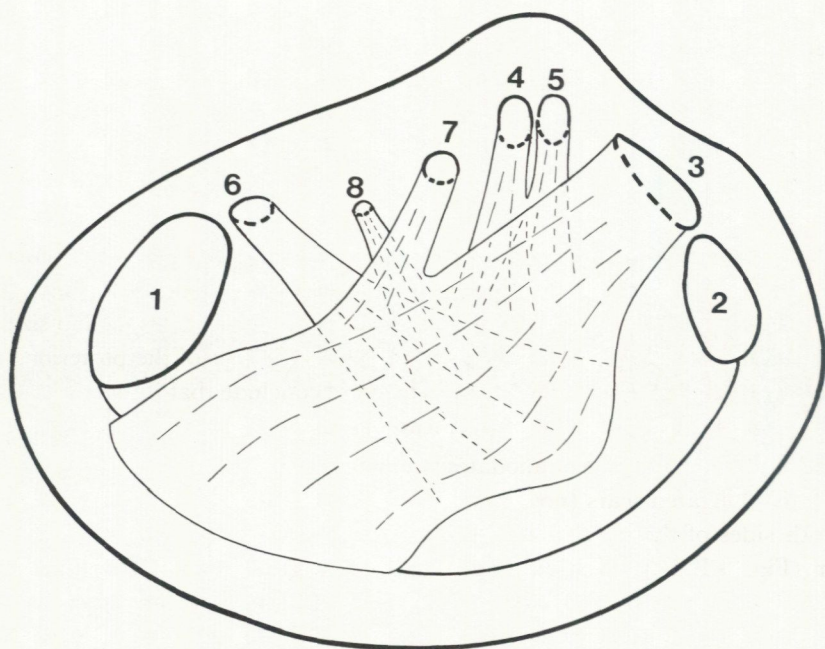


Fig. 8. *Nuculoidea lens* n.sp. Maximum number of muscular impressions and reconstruction of foot with appurtenant muscles. Anterior to the left. Scars numbered in order of size. 1 = anterior adductor muscle scar, 2 = posterior adductor muscle scar, 3 = posterior pedal retractor muscle scar, 4 = median muscle scar, 5 = median muscle scar, 6 = anterior pedal protractor muscle scar, 7 = anterior pedal retractor muscle scar, 8 = anterior pedal protractor muscle scar. Note the non-sinuate pallial line (for discussion see text, pp. 22-26).

margin (Fig. 9:B). The posterior adductor muscle scar (No. 2 in Fig. 8) is clearly delimited distally. This edge, limiting a plateau which constitutes the posterior margin, runs roughly parallel to the sagittal plane. Ventrally the scar merges into the pallial line. In the holotype this scar has clear commarginal growth lines and a pronounced ridge at an oblique angle to the growth lines. This ridge could be the limitation of the "quick" and the "catch" part of the muscle (Fig. 9:C). Pfab (1934:209 and Pl. 1:11a) described and illustrated the same phenomenon in an adductor muscle scar in some of his Bohemian material that showed two interfering systems of lines.

The third largest scar (No. 3 in Fig. 8) is sometimes hard to distinguish because of being indistinctly limited in some shells, especially against the posterior hinge plate. Anteriorly it forms a rather low broad ridge, but is occasionally well defined (Fig. 9:C). In some shells it extends beyond the entire length of the posterior hinge plate (Fig. 9:D). According to Heath (1937, Pl. 8:63) the posterior pedal retractor muscle consists of a long series of fibres. The attachment area of these extends from the posterior adductor muscle dorsally almost covering the entire length of

the posterior dorsal margin, leaving only the umbonal cavity free from attached fibres. According to Driscoll (1964:65) "... the absence of any evidence of a posterior (pedal) retractor scar on the valves may be due to the larger diameter of this muscle. Possessing large area of shell muscle contact may well have reduced the need to form a deeply indented scar in the shell." This may explain the sometimes weak impression of this muscle in the shells of *Nuculoidea lens*. Heath reports (1937:12) "... the posterior pedal retractor (Pl. 10:83 rp) is usually larger than all of the protractors combined." He considered that it functioned as a definite retractor. The scar in *N. lens* is the only impression on the posterior side except for the posterior adductor muscle scar, and in position, shape and size and in being weakly incised it also agrees with the attachment of the posterior pedal retractor muscle described by Heath. I therefore conclude that it is an impression of the posterior pedal retractor muscle scar.

The umbonal cavity accommodates two, often equal in size, rounded, somewhat vertically elongated scars (nos. 4 and 5 in Fig. 8). They are symmetrically placed on both sides of the median axis, one being occasionally more distinct than the other (Fig. 9:B, E). Well-developed concentric growth lines sometimes occur inside these imprints. Bradshaw (1970:632, Fig. 9) illustrated two umbonal scars in the same position but did not suggest their probable function. Bradshaw (1978), however, interpreted scars as being traces of a primitive muscular visceral floor of Devonian species. In Ordovician forms with scars in the umbonal region she found no evidence for the existence of a muscular visceral floor. In the description of the type species of *Nuculoidea* Williams & Breger (1916:174) stated that "... a fourth minute and strong muscular scar is situated at the tip of umbo...". In *Ennucula obliqua* (Lamarck) Schenck (1934:21 and Pl. 3:4) differentiated two unequal impressions as the "median" and the "central" muscle scar, respectively. The first is described as "narrow and elongate" the second as "small, oval or round". They are, however, not situated in the umbonal cavity. In a discussion of living nuculoids (1937:14 and Pl. 5:39) Heath accounted for "... two pairs of conspicuous muscles which appear to be a constant feature of the protobranches in general...", and designated them "dorsomedian" and "ventromedian" muscles. According to Heath the "dorsomedian" muscle serves as a visceral support and most of it is connected to the pedal tissue. He also states that even the "ventromedian" muscle distributes its fibres both to the wall of the visceral mass and to the upper part of the foot. Driscoll (1970:63) referring to Heath (1937:14) suggests that the function of the median and central muscles in *Acila divaricata* are principally attachments for the visceral mass serving as a firm anchorage during, as Heath assumed, "... the vigorous movement of the foot."

The muscles attached in the impressions observed in *Nuculoidea lens* (nos. 4 and 5 in Fig. 8) were probably considerably larger than the muscles referred to above. Thus they probably had a more important role as elevators of the foot rather than

as supporters of the wall of the visceral mass (see above, discussion of Bradshaw 1978). Since they are of equal size these muscles presumably had the same function, or almost so, and probably acted in combination. I propose to designate them the median pedal elevator scars.

There are three minor impressions below the hinge plate in the dorsal region of the anterior half of the shell (nos. 6, 7, 8 in Fig. 8). The most distal one (No. 6 in Fig. 8), situated just posterior to the top of the anterior adductor muscle scar, is the sixth or sometimes the seventh in size and the second deepest (Fig. 9:B). This and the smallest scar observed (No. 8 in Fig. 8; Fig. 9:B) are probably the impressions of anterior pedal protractors. I designate them the major and minor pedal protractor muscle scar respectively, since they occupy roughly the same position as the anterior pedal protractors in recent nuculoids both in relation to each other and to the anterior adductor muscle scar.

The remaining scar (No. 7 in Fig. 8; Fig. 9:B), the seventh in size, and the most proximal of the three scars below the anterior hinge plate, may correspond to what Heath (1937:13) calls "... the most posterior one (Pl. 10:83r)" which "... appears to function as a definite retractor." Hence I call it the anterior pedal retractor muscle scar. Bundles of fibres from the muscles of the foot probably also served other purposes, as in living protobranchs (Heath 1937:13).

The pallial line is often clearly visible. It lacks a sinus and runs in an arc from the ventralmost part of the posterior adductor muscle scar to the ventralmost part of the anterior one (Fig. 8).

DISCUSSION OF CLOSELY RELATED FORMS — *Nuculoidea lens* shows features characteristic of the group with *Nuculoidea opima* (Hall) established by Williams & Breger, 1916, viz. orthogyrate or actually faintly prosogyrate shell with the anterior end longer. *Nuculoidea lens* differs from the type species in the following characters.

<i>Nuculoidea opima</i>	<i>Nuculoidea lens</i>
Umbo prominent to low	Umbo low
Anterior area semi-lunate	Anterior as well as posterior areas circumscribed (Fig. 4:B)
Dorsal margin forming a ridge	Dorsal margin imperceptibly raised in lunule and escutcheon areas (Fig. 4:A, B, D)
Posterior end extremely short and truncated, i.e. umbo situated very near this end	Posterior end somewhat more protruding and usually evenly rounded causing a lens-shaped configuration of an articulated shell when seen in dorsal or ventral view (Fig. 4:A, B, C)
Dorsal and ventral margins almost straight, giving the shell an oblong lateral shape	Dorsal margin convex and ventral margin strongly convex, producing an evenly rounded, subcircular lateral outline (Fig. 4:E, F; 9:A)

The internal features of the shell of *Nuculoidea lens* on the whole agree with the corresponding characteristics of the type species, i.e. both have a well-developed resilifer under the beaks. The amount and configuration of the impressions of the accessory muscle scars are also similar. Williams & Breger (1916:174) stated that Hall illustrated five "umbonal scars", while "... usually three are visible..." *Nuculoidea lens* has four scars in the umbonal region, i.e. one less than reported in the type species. The microscopically pectinate ventral margin, mentioned above and observed by Vokes (1949), is lacking in *Nuculoidea lens*.

The hinge features of *Nuculoidea opima* were not known to Williams & Breger, but Vokes (1949, Fig. 1) described and illustrated the interior of a single specimen of this species. There are c. 12 hinge teeth on this specimen (23 mm long) on the anterior hinge plate and about 11 on the posterior hinge plate. In *Nuculoidea lens* shells with a corresponding number of teeth are generally only half that size. Furthermore the posterior teeth in *N. opima* are narrow and transverse, whereas in *N. lens* they are distinctly chevron-shaped. The anterior teeth in *N. lens* are also chevron-shaped, while in *N. opima* they are transverse, although the most proximal ones tend to be somewhat chevron-shaped.

Lindström (1880) recognized three species of the bivalve material from the Mulde Marl of Gotland as belonging to the genus *Ctenodonta* Salter, 1856, one of which is *Ctenodonta pinguis*. This species is not a true ctenodont, i.e. it does not belong to the superfamily Ctenodontacea Wöhrmann, 1893 because it lacks the external ligament characteristic of this taxon. Since *Ctenodonta pinguis* has an internal ligament I place it in the genus *Nuculoidea* Williams & Breger, 1916, as is also suggested by Soot-Ryen (1964:509). She states its resemblance to the *Nuculoidea opima* group erected by Williams & Breger 1916, and continues: "The variation in form and the absence of distinct morphological characters make comparisons of the species within the genus difficult. Nearly all illustrations and also very often the descriptions, treat the exterior of the shell only" (Soot-Ryen 1964:511). She recognized two subspecies of *Nuculoidea pinguis* (Lindström, 1880) viz. *Nuculoidea pinguis pinguis* (Lindström, 1880) from the Mulde Marl and *Nuculoidea pinguis burgsvikensis* Soot-Ryen, 1964 from the Burgsvik Oolite.

According to Soot-Ryen (1964:511), *Nuculoidea pinguis pinguis* resembles *Nucula levata* Hall but seems to be comparatively lower than the species mentioned. Further, Soot-Ryen finds a resemblance between *Nuculoidea pinguis pinguis* and six other species, viz. *Nuculoidea opima* (Hall, 1843), *Nucula fornicata* Goldfuss, 1822, *Nucula sandbergi* Beushausen, 1895, *Nucula pelmensis* Beushausen, 1895, *Nuculoidea lodanensis altaica* Khalifin, 1948, and *Nucula arisaigensis* McLearn, 1924. According to Soot-Ryen 1964 the Burgsvik subspecies, *Nuculoidea pinguis burgsvikensis*, resembles *Nucula pelmensis* Beushausen, 1895.

Nuculoidea lens superficially resembles two Bohemian specimens assigned to *Nucula fornicata* Goldfuss, 1822 by Beushausen (1895:53, Pl. 4:9, 15a—b). As the

figures do not clearly show details of organization I was anxious to examine the actual fossil material. The exterior of the specimen in Fig. 15a and 15b (in Beushausen 1895, Pl. 4) resembles *Nuculoidea lens* in general appearance except for the conspicuous commarginal sculpture of striae. However, in the short end (referred to by Beushausen as "anterior") there is a conspicuous fulcrum close to the beaks, which probably enclosed an outer ligament. Firstly, this indicates an orientation directly opposed to that suggested by Beushausen, i.e. the specimen is anteriorly elongated (Cox, Nuttall & Trueman 1969). Secondly, since *Nucula s.s.* has an internal ligament the specimen must be assigned to another genus.

The other Beushausen specimen (Beushausen 1895, Pl. 4:9), a composite mould, superficially resembles *Nuculoidea lens* in a number of features. However, the Beushausen specimen is larger (L = 16.1 mm) than the largest specimen of *N. lens* (max. L = 15.0 mm). Its beaks are rather high, straight and not incurved as in *N. lens*. They also point slightly towards the longer end of the shell while in *N. lens* the beaks are orthogyrate. The ventral margin of Beushausen's specimen is less strongly convex than in *N. lens*. The longer of its dorsal margins is decidedly concave while the anterior part of the dorsal margin in *N. lens* is convex. There are fewer hinge teeth than in *N. lens*. The Beushausen specimen has fewer teeth (11 and 8) than a specimen of *N. lens* of corresponding size (see Fig. 7). The ligamental pit in *N. lens* is deeper than that in Beushausen's specimen.

There are four accessory muscle scars in the umbonal region of the composite mould, situated in a row at the preumbonal ridge with the topmost scar just at the tip of the beak. The pedal muscle scars in the umbonal cavity of *N. lens* are located laterally and are of a different shape (Fig. 9:E). Finally, traces of regular, commarginal striae are seen on both sides of the composite mould (cf. McAlester 1962b). *Nuculoidea lens* lacks this sculpture.

Beushausen (1895:53, Pl. 4:9, 15a, b) was in doubt as to whether his figured specimens were conspecific with *Nucula fornicata* Goldfuss 1822:151, shown in Pl. 124:5c. The Beushausen specimens differ too much from the illustration in Goldfuss so I share Beushausen's hesitation.

Beushausen's (1895) specimen in Pl. 4:15a-b not only belongs to a completely different genus from *Nucula* Lamarck, 1799, but it must also be excluded from the superfamily Nuculacea Gray, 1824, the specimen having an external ligament. The diagnosis of the Nuculacea excludes an external ligament.

I consider that the other specimen (Beushausen 1895, Pl. 4:9) belongs to the genus *Nuculoidea* Williams & Bregner, 1916, since it closely resembles the type species, *Nuculoidea opima* (Hall), in general outline and appearance and in having a symmetrically placed and distinct resilifer.

Since the two subspecies of *Nuculoidea pinguis* (Lindström, 1880) from Gotland differ from each other in some important respects I shall compare each of them separately with *Nuculoidea lens*. I hold *Nuculoidea lens* from Möllbos to be distinct

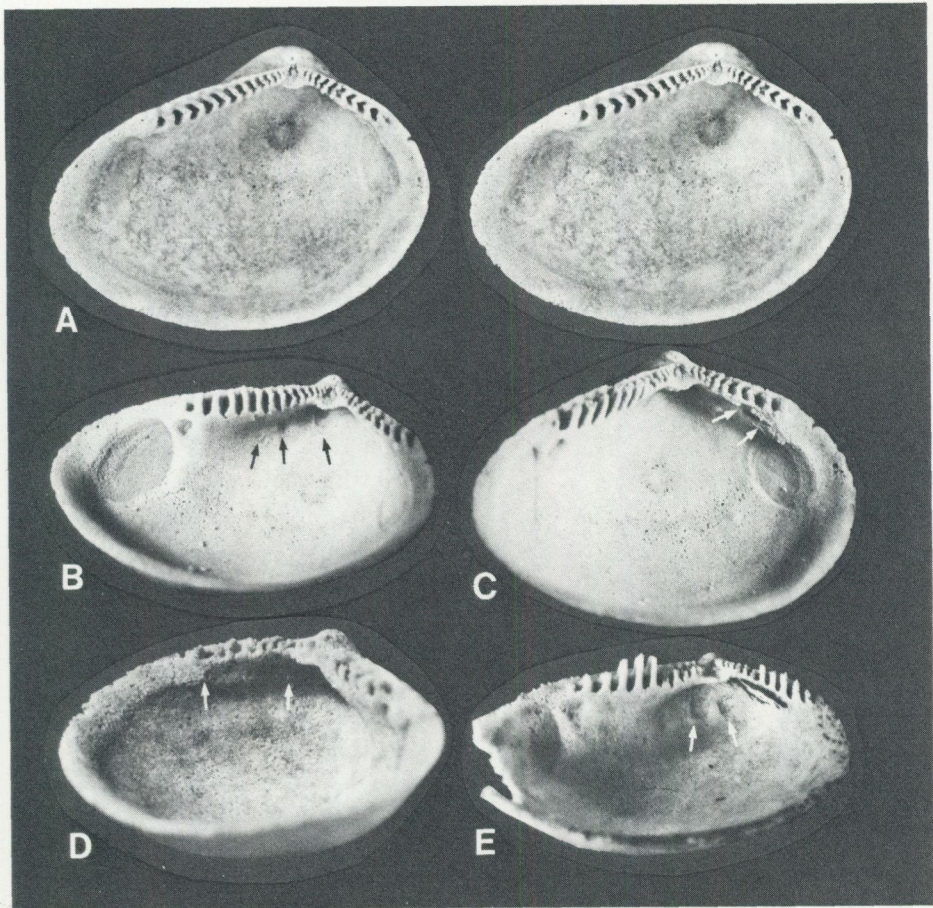


Fig. 9. *Nuculoidea lens* n.sp. Internal views. — A. Stereo pair of holotype (right valve); SGU Type 842, $\times 3.4$. — B. Holotype, postero-ventral lateral view showing from the left anterior adductor muscle scar, anterior pedal protractor muscle scar, anterior pedal protractor muscle scar (first arrow from the left), anterior pedal retractor muscle scar (second arrow) and median muscle scar (third arrow), $\times 3.5$. — C. Holotype, antero-ventral lateral view showing posterior pedal retractor muscle scar (arrows) and posterior adductor muscle scar, $\times 3.5$. — D. Antero-lateral view of a left valve with an extremely long posterior pedal retractor muscle scar (length indicated by arrows); SGU Type 865, $\times 5$. — E. Ventro-lateral view of a right valve with two heavily impressed median muscle scars (arrows); SGU Type 844, $\times 4$. All specimens from sample G77-28LJ.

from *Nuculoidea pinguis pinguis* (Lindström, 1880) and *Nuculoidea pinguis burgsvikensis* Soot-Ryen, 1964, for the following reasons.

While *Nuculoidea pinguis pinguis* has a clearly prosogyrate shell (Soot-Ryen 1964:509), *Nuculoidea lens* is on the whole orthogyrate. The umbo of *Nuculoidea pinguis pinguis* is limited anteriorly by a well-defined umbonal ridge and is less

gibbous than in *Nuculoidea lens*. The dorsal margins of *Nuculoidea pinguis pinguis* are raised, forming a "keel" or a moderately high crest both anterior to and posterior to the umbo, while in *Nuculoidea lens* these margins are only slightly raised within low, flat areas. The lunule of *Nuculoidea pinguis pinguis* is not circumscribed, but is marked by a change in the direction of the growth lines so that the lunule is seen only as a slight variation in the texture of the surface, whereas both the lunule and escutcheon of *Nuculoidea lens* are circumscribed by a more distinct morphological feature. The ventral margin in *Nuculoidea pinguis pinguis* is usually long and straight, while in *Nuculoidea lens* it is strongly convex to a varying degree, giving it an almost subcircular lateral outline.

According to Soot-Ryen (1964:510) the posterior hinge plate of *Nuculoidea pinguis pinguis* is longer than the anterior one. An examination of one of Soot-Ryen's specimens corroborates this statement. The 14 mm long specimen has 15 teeth on the posterior hinge plate and 11 on the anterior hinge plate. In *Nuculoidea pinguis pinguis* the relation of the hinge to its teeth is the opposite of that in *Nuculoidea lens*. In *Nuculoidea lens* only very small shells have the same number of teeth in both hinge plates. In the larger ones there are more anteriors than posteriors, which results in the anterior hinge plate being longer. The hinge angle of *Nuculoidea lens* varies from 119° – 134° (mean value 127°), while in *Nuculoidea pinguis pinguis* it is c. 145° .

In *Nuculoidea pinguis burgsvikensis* the shell is prosogyrate, although not as clearly so as in *Nuculoidea pinguis pinguis*, while in *Nuculoidea lens* it is orthogyrate. The umbo of *Nuculoidea pinguis burgsvikensis* is somewhat higher than that in *Nuculoidea lens*. The dorsal margins of *Nuculoidea pinguis burgsvikensis* are typically raised, but in its posterior part not distinctly so. *Nuculoidea lens* has no "keel" formed by the raised margins of the opposing valves as in *Nuculoidea pinguis burgsvikensis*, but has a very low crest. In *Nuculoidea pinguis burgsvikensis* the posterior end is more truncated than in *Nuculoidea lens* and in this respect resembles the type species *Nuculoidea opima*. The posterior umbonal slope is steeper than in *Nuculoidea lens*. The ventral margin in *Nuculoidea pinguis burgsvikensis* is usually long, and is straighter than in *Nuculoidea lens* which in lateral view is more nearly circular.

In the holotype of *Nuculoidea pinguis burgsvikensis*, which is 19 mm long, the anterior and posterior hinge plates are of equal length and have 10 and 9 teeth respectively. Two additional specimens, 19 mm and 20 mm long, also examined by me, have 10 anteriors and 11 posteriors and 12 anteriors and 14 posteriors, respectively. Thus *Nuculoidea pinguis burgsvikensis* is intermediate between *Nuculoidea pinguis pinguis* and *Nuculoidea lens* as regards the relation of numbers of anteriors/posteriors. There are more anterior teeth than posterior teeth in all specimens of *Nuculoidea lens* examined, except for a few juvenile shells which have the same number on both hinge plates. The hinge angle in *Nuculoidea pinguis burgsvikensis* is c. 115° , i.e. decidedly narrower than that of *Nuculoidea lens* (mean 127°).

When the height and breadth are plotted against the length in scatter diagrams this not only gives an interesting picture of the variation within each species or subspecies but also reflects close similarities between the taxa. The height/length ratios of *Nuculoidea pinguis pinguis*, *Nuculoidea pinguis burgsvikensis* and *Nuculoidea lens* are approximately the same. This is also true of some other species of the genus, e.g. the type species *Nuculoidea opima* and the Beushausen specimen discussed above (Beushausen 1895, Pl. 4:9) described by him as *Nucula fornicata* Goldfuss, 1822. The breadth/length relation of *Nuculoidea pinguis pinguis* is less than that of *Nuculoidea lens*, owing to the slenderer shape of the former. *Nuculoidea pinguis burgsvikensis* varies more in breadth and may also attain a considerable length, commonly about 20 mm. The longest specimen of *Nuculoidea lens* from Möllbos is about 15 mm, and *Nuculoidea pinguis pinguis* from the Mulde Marl attains a length of about 18 mm. The height/length ratio of the specimen of the type species illustrated by Hall (1885, Pl. 45) and McAlester (1968, Pl. 13) is about the same as for *Nuculoidea lens*, i.e. 0.8. The length of the three lecto- and paratypes of *Nuculoidea opima* is 19 mm, 19 mm and 21 mm, which exceeds the maximum value for *Nuculoidea lens*. The mean breadth/length ratio of these three specimens, 0.33, gives *Nuculoidea opima* a more gibbous outline than the three taxa from Gotland.

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

Nuculodonta n.g.

DERIVATION OF THE NAME — From the Latin morphemes *nuc-ul-*(small nut) and the Greek morpheme *odont-*(tooth); deliberately a hybrid name to harmonize with nearby genera.

TYPE SPECIES — *Nuculodonta gotlandica* n.sp.

SPECIES — Monotypic at the time of description.

DIAGNOSIS — Nuculoid with umbones situated in the posterior half of the shell, with slightly prosogyrate beaks. Lunule and escutcheon well defined. Conspicuous external ligament posterior to umbo. Two series of hinge teeth interrupted by a non-denticulate resilifer-like structure.

DISCUSSION — Several morphological traits make it difficult to incorporate *Nuculodonta gotlandica* in any existing nuculoid family. Owing to the chaotic state of nuculoid higher classification *Nuculodonta gotlandica* has not been assigned to a superfamily and family.

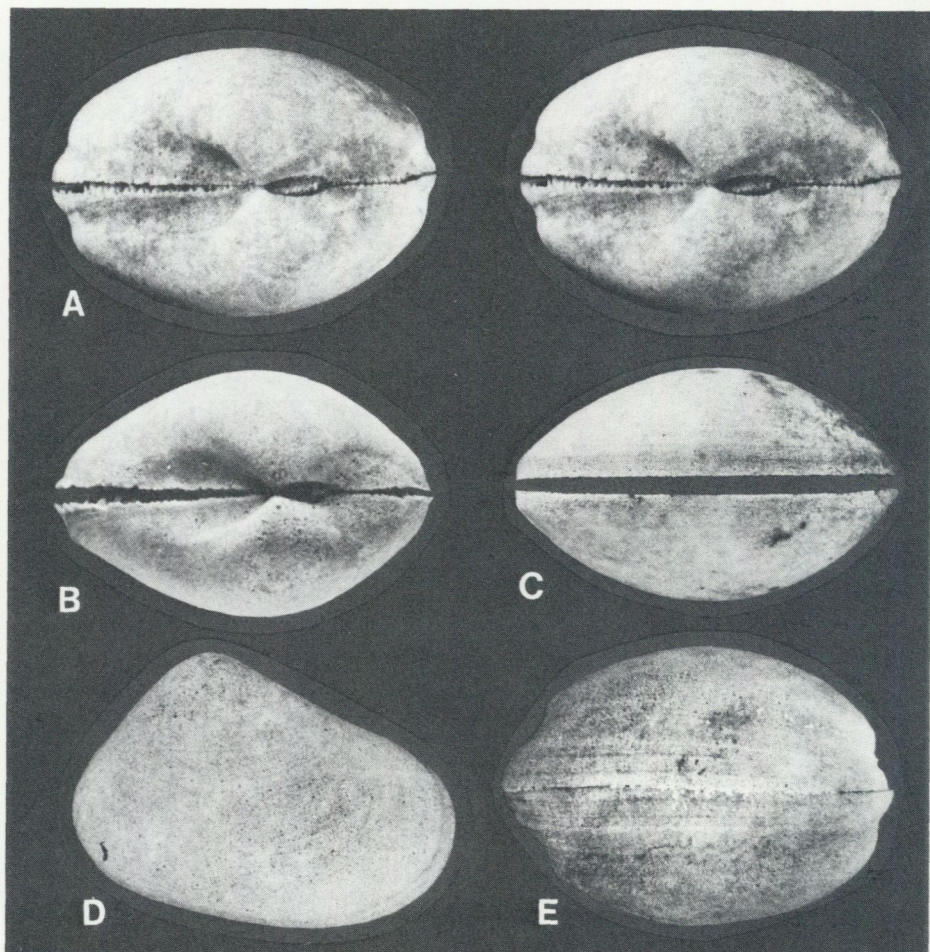


Fig. 10. *Nuculodonta gotlandica* n.g., n.sp. External views. — A. Stereo pair, dorsal view, anterior end to left. Note prosogyrate beaks and conspicuous external ligament posterior to umbones; SGU Types 1202, 1203, $\times 3.9$, sample G79-82LJ. — B. Dorsal view showing lunula and escutcheon, anterior to left, note maximum opening anteriorly; SGU Types 1070, 1071, $\times 4.6$, sample G77-28LJ. — C. Ventral view, anterior end to left. Note gaping valve margins; SGU Types 1060, 1061, $\times 4.1$, sample G77-28LJ. — D. Lateral view of a right valve showing smooth external valve surface; SGU Type 940, $\times 3.8$, sample G77-28LJ. — E. Ventral view showing valve margins fitting closely together, anterior end to left; SGU Types 1194, 1195, $\times 4.5$, sample G78-1LL.

Nuculodonta gotlandica n.sp.

Figs 10, 13, 14, 17, 18

SYNONYMY — v?1964 *Ctenodonta* sp. A n.sp. — Soot-Ryen, p. 47. v? implies that the condition of the original specimens is such that no clear decision is possible (Richter 1948:55).

DERIVATION OF THE NAME — Latin *gotlandicus*, from the island of Gotland where the species was first recorded.

HOLOTYPE — A left valve, SGU Type 1056 from sample G77-29LJ, Fig. 14:A. Length 12.8 mm, height 9.3 mm, breadth 4.5 mm. One major growth increment furrow is seen on the exterior near the valve margin, the furrow modifying the strongly convex outline as seen in dorsal or ventral view; all hinge teeth present, the most proximal ones broken; anterior hinge plate with 24, posterior with 14 teeth; non-denticulate area seen as an arched structure. Muscular impressions: anterior and posterior adductor muscle scars, anterior pedal protractor muscle scar, posterior pedal retractor muscle scar, anterior pedal retractor muscle scar, posterior pedal elevator muscle scar and median muscle scars.

TYPE STRATUM — Halla Beds, high Wenlockian, Silurian.

TYPE LOCALITY — Möllbos 1, Gotland, Sweden.

MATERIAL — 218 measured specimens plus an undetermined number of fragments.

DIAGNOSIS — As for the genus.

EXTERNAL FEATURES — Shell small, obliquely ovate, equivalved, inequilateral, strongly inflated, anterior end longer than posterior end; margins even, no gap present; external ligament; faint concentric growth lines, often with rugae, sometimes conspicuously modifying the outer sculpture and profile of the valves; beaks small, very close together, slightly but clearly prosogyrate, in the posterior half of the shell; maximum convexity at about mid-length and mid-height and anterior to the umbo which anteriorly forms a concave umbonal ridge bounding the lunule; escutcheon discernible, with the outer ligament area limited by a sharp-edged truncation serving as a fulcrum close to and posterior to the umbo; conspicuous, opisthodontic, parivincular outer ligament within escutcheon area occupying 1/3 of the length of posterior part of dorsal margin; dorsal margin convex; anterior part longest, concave and sometimes slightly s-shaped, its proximal part sloping gently to become more evenly rounded distally; posterior part of dorsal margin somewhat sloping, evenly arched in the junction of posterior margin; anterior margin strong-

ly to moderately rounded with dorso-anterior part somewhat shorter than ventro-anterior part; posterior margin strongly rounded to truncate, almost vertical; dorso-posterior part much shorter than ventro-posterior part; ventral margin long, somewhat convex to straight, slightly rounded where it merges into anterior and posterior margin, respectively, its ventralmost part in anterior half of shell.

DISCUSSION OF EXTERNAL FEATURES — Owing to the abundance of well-preserved material a high degree of morphologic variation within the species can be recorded (see Fig. 14:B, C, D). Since the shell is strongly gibbous the breadth/length ratio of the valves is high.

The outer surface of the shell lacks sculpture in the proper sense (Fig. 10:D). However, a moderate number of specimens have deep, irregular commarginal furrows (Figs. 10:A, E, 14:G, 18:A, B) indicating periods of low growth rate, and sometimes also leaving traces on the inside of the shell. Muscular incisements which are left in deserted non-functional positions are not completely overgrown by the inner calcareous layer and correspond in location to the external traces of growth-rate disturbances (Fig. 18).

The beaks are minute, incurved and almost touching. They are slightly prosogyrate (Fig. 10:A). A concave, smooth-edged anterior-umbonal ridge runs from the beak on the anterior umbonal slope and antero-dorsally together with the corresponding feature in the opposite valve forms the lunule (Fig. 10:B). This is a flat lens-shaped area corresponding to the extension of the underlying anterior hinge teeth (cf. Carter 1967:245). The escutcheonal area appears as a slight modification in the texture of the valve surface (Fig. 10:B). Its configuration reveals the position of the underlying hinge teeth. This area accommodates the ligamental nymph with the ligament, which is often fossilized as a conspicuous node (Figs. 10:A, 14:G, H), sometimes with pyritized remnants of the periostracum (cf. Clark & Lutz 1980). Margins even (Figs. 10:A, B, C, 14:H), closely fitting (Figs. 10:E, 14:G).

Variation in the height/length ratio (Fig. 11:A) varies from 0.56 to 0.85. This is the shell with the highest H/L value, i.e. with the least elongated form seen in Fig. 14:D. It is 11.5 mm long and 9.2 mm high, with a subcircular outline and the ratio 0.8. The specimen with the lowest H/L value is seen in Fig. 14:B. The length is 13.6 mm and the height only 7.8 mm, giving a ratio of 0.56, an extremely low value and is the result of an unusually elongated form. In consequence this shell deviates markedly from the normal H/L-ratio (0.75; cf. Fig. 11:A).

The more elongated shape of *Nuculodonta gotlandica* as compared with *Nuculoidea lens* is evident from the H/L-ratio diagrams (Figs. 6:A, 11:A). The B/L-relation in *Nuculodonta gotlandica* (Fig. 11:A) is almost the same as that in *Nuculoidea lens*, but as the height in *Nuculodonta gotlandica* is about 10 % less than in *Nuculoidea lens*, *Nuculodonta gotlandica* is more gibbous.

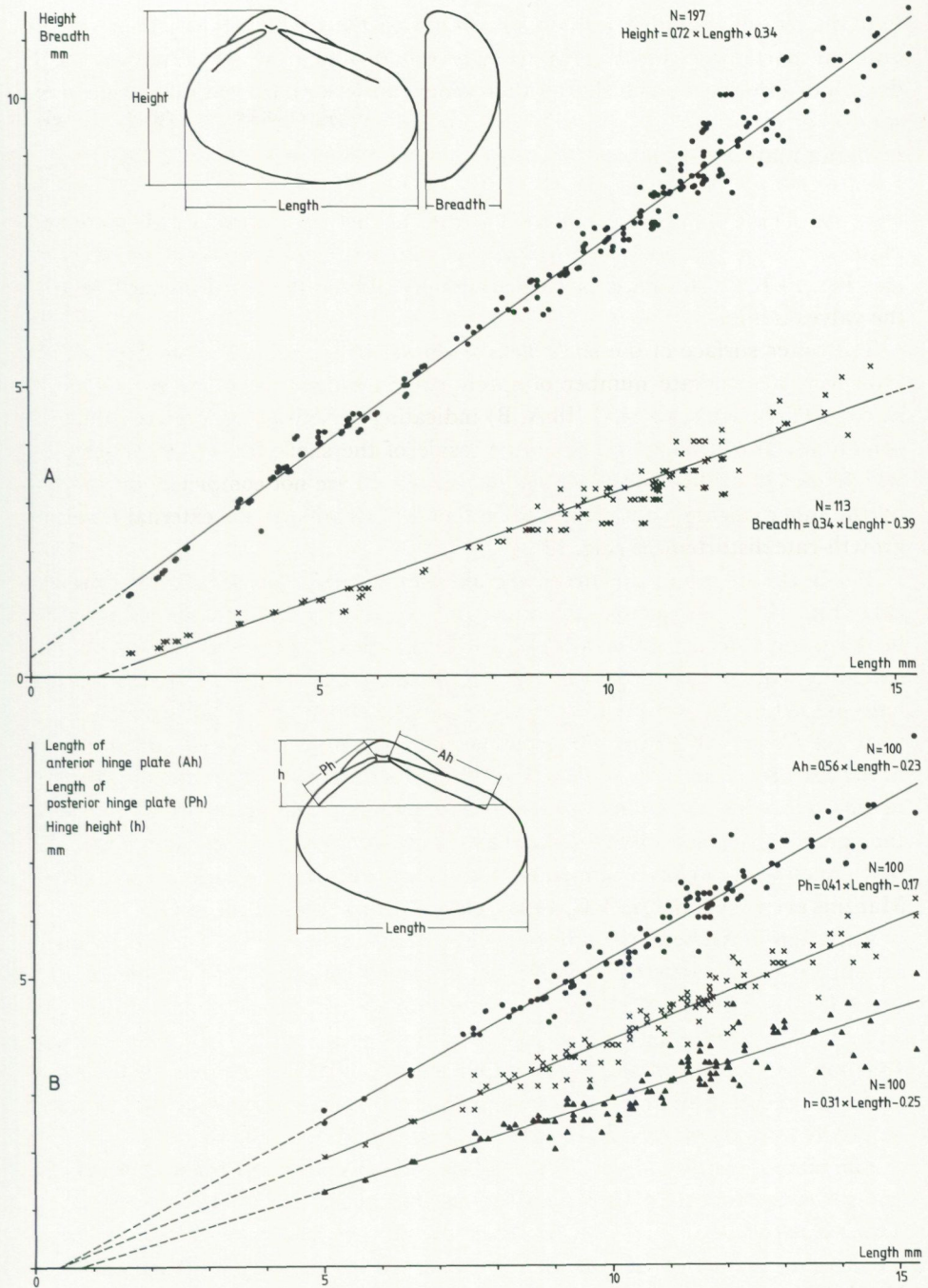


Fig. 11. *Nuculodonta gotlandica* n.g., n.sp. Ontogeny and variation in outline. Scatter diagrams with computer-calculated regression lines. — A. Height and breadth of shell in relation to total length. — B. Length of anterior and posterior hinge plate and hinge height in relation to total length of shell (for discussion see text, pp. 34, 39).

INTERNAL FEATURES — Hinge line convex; anterior tooth row separated from posterior tooth row by a minute triangular edentulous plate; anterior hinge plate long, somewhat more than half total length of shell, slightly concave to s-shaped, in one of the largest specimens ($L = 15.3$ mm) with about 20 teeth which in proximal and median part occupy about $1/2$ the breadth of hinge plate, in distal part $2/3$; a fairly shallow rounded furrow between dorsal margin and teeth limits tooth row dorsally, from just anterior to beak to distal end of hinge plate; anterior teeth straight, most distal ones conical, medians roughly z-shaped, proximals lamellar, narrow, close together and very small near beak, occupying position parallel to antero-posterior axis, teeth increasing in size distally from proximal 11th or 12th tooth to 16th–19th teeth in one of the largest specimens ($L = c. 15$ mm), teeth ventrally flattened; posterior hinge plate short, slightly more than $1/3$ of total length of shell and a little more than half the length of anterior one, nearly straight in outline to somewhat convex, one of the largest specimens containing 13 teeth occupying about $3/5$ of breadth of hinge plate in distal part and almost entire breadth in proximal part; teeth separated from posterior dorsal margin by a

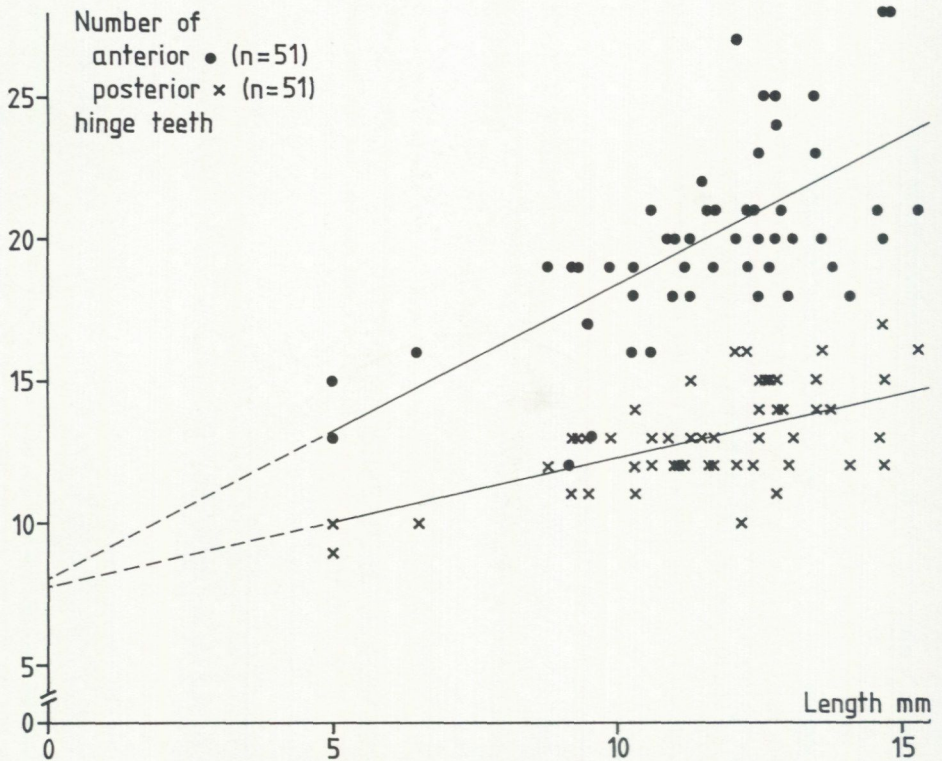


Fig. 12. *Nuculodonta gotlandica* n.g., n.sp. Number of hinge teeth in relation to total length of shell. Regression lines calculated by computer (for discussion see text, p. 39).

furrow similar to that in anterior plate, extending from distal end of plate to about 1/3 of the way to beak, dorsal margin here cut off by ligamental nymph which is depressed correspondingly into hinge plate; teeth conical in section and towards beaks becoming successively more chevron-shaped with apices pointing to umbo, 5th to 6th tooth from beak z-shaped, most proximal ones extremely small, narrow and lamellar and almost parallel to antero-posterior axis, size increasing distally, to 3rd or 4th most distal tooth; hinge teeth not quite perpendicular to hinge margin but slightly oblique; hinge angle c. 124° .

MUSCULAR IMPRESSIONS — Two large subequal adductor muscle scars beneath hinge line at anterior and posterior end; the anterior, elongated dorso-ventrally, posterior and dorsal outline conspicuous, other sides fainter but clearly visible; subcircular posterior adductor muscle scar evenly incised, unlike anterior one; at top of posterior adductor muscle scar a subrounded to elongated muscular impression at distal end of posterior hinge plate; one muscular impression circular to elongated, beneath and at about mid-length of anterior hinge line dorso-laterally; a subcircular impression anterior to last-mentioned scar, posterior to top of anterior adductor muscle scar and just below most distal end of anterior hinge plate; beneath proximal end of posterior hinge plate and about midway between posterior adductor muscle scar and umbo is a small circular scar; laterally at about mid-length of hinge plate is a distinct circular scar, fairly deeply imprinted into anterior umbonal slope; smallest scar situated immediately dorsal to the former and similar in shape and depth to the two last-mentioned scars; pallial line extending from ventralmost end of anterior adductor muscle scar and along ventral margin to posterior adductor muscle scar, junction between the latter and

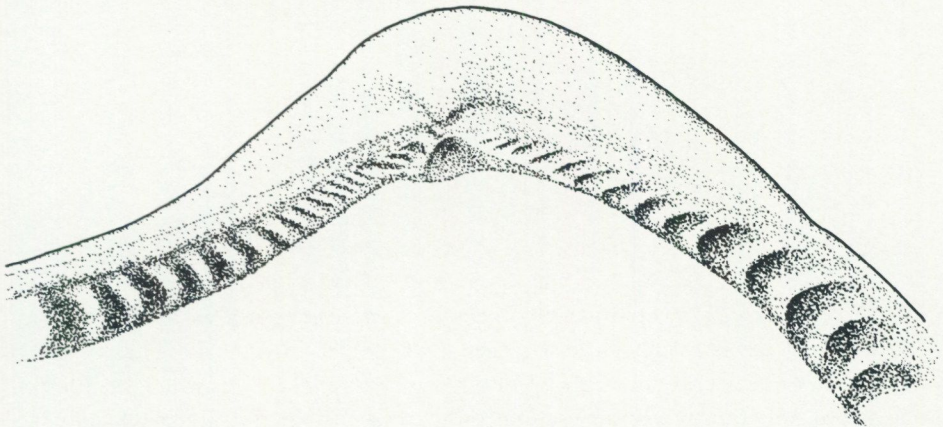
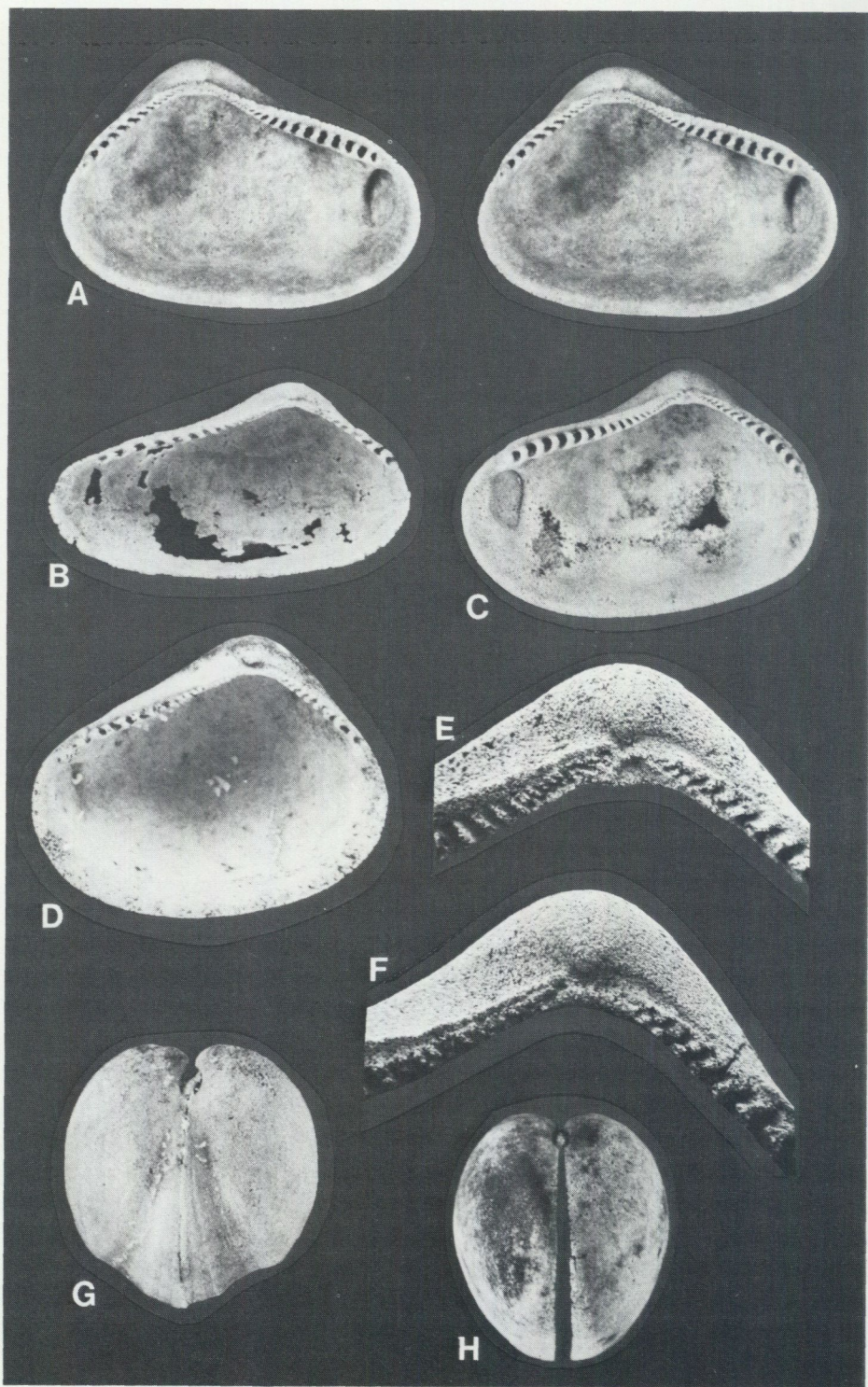


Fig. 13. *Nuculodonta gotlandica* n.g., n.sp. Internal view of a right valve showing non-denticulate area dividing the two tooth rows just below the beak (for discussion see text, p. 40; see also Fig. 14:E); SGU Type 1026, $\times 28$, sample G78-2LL.



pallial line diffuse; a conspicuous smooth-edged ridge, breadth almost equal to size of posterior adductor muscle scar, reaching point of maximum convexity of the valve.

DISCUSSION OF INTERNAL FEATURES — In Fig. 11:B three internal characters, viz. length of anterior hinge plate (Ah) and posterior hinge plate (Ph) and the hinge height (h) are related to the total length of the shell. The length of the anterior hinge plate in *Nuculodonta gotlandica* is more than 50 % of the total length of the shell, that of the posterior hinge plate about 40 %, while in *Nuculoidea lens* the corresponding numbers are only 40 and 30 %. In dorsal view the hinge in *Nuculodonta gotlandica* is 90 % of the entire length of the shell (Fig. 10:A) while in *Nuculoidea lens* the hinge is at most only 70 % of the total length of the shell (Figs. 4:A, 5:B). In *Nuculodonta gotlandica* the hinge plates are proportionately longer than those of *Nuculoidea lens*. This lends greater stability to the hinge in *Nuculodonta gotlandica*, as the plates house more hinge teeth which is essential for ensuring firm closure of the valves.

Fig. 12 shows the relation of numbers of hinge teeth in each hinge plate to total length of shell. Within the estimated error of ± 2 more than 85 % of all values satisfy the regression lines in the diagram. Most shells in which the number of teeth could be counted are between 9 and 15 mm long, while only 3 shells are 5–9 mm long. The fact that the regression lines for anterior and posterior teeth converge to about the same value may indicate that the prodissoconch had almost the same number of teeth on both hinge plates. Therefore, the hinge plates, which constitute about 90 % of the total length of the shell, must have been of equal length in the first shell, as the anterior and posterior teeth are almost equal in thickness. Furthermore, these hinge plates must have been symmetrically placed relative to the umbo giving the prodissoconch an almost circular appearance.

There is no reason to assume that the first shell of *Nuculodonta gotlandica* exceeded the normal prodissoconch size, 0.2–0.6 mm in length in living bivalves (Trueman

Fig. 14. *Nuculodonta gotlandica* n.g., n.sp. — A. Stereo pair of holotype (left valve), internal lateral view. Note the extremely deeply incised anterior adductor muscle scar; SGU Type 1056, $\times 3.9$, sample G77–29LJ. — B. Internal lateral view of a right valve with the most elongated shape of all specimens; SGU Type 1000, $\times 3.6$, sample G78–1LL. — C. Internal lateral view of a right valve showing incomplete silicification of shell; SGU Type 1026, $\times 3.8$, sample G78–2LL. — D. Internal lateral view of the least elongated shell of all, a right valve (for discussion see text, p. 34); SGU Type 1001, $\times 4.3$, sample G78–1LL. — E. SEM photograph of a right valve showing non-denticulate "resilifer"-like construction between tooth rows below beak (for discussion see text, pp. 40–42, and Fig. 13), $\times 13$ (same valve as in C). — F. SEM photograph of a right valve showing the non-denticulate area corresponding to the construction on E (for discussion see text, pp. 40–42); SGU Type 1049, $\times 17$, sample G79–80LJ. — G. External posterior view showing deep commarginal furrows modifying outline of shell; SGU Types 1194, 1195, $\times 4.2$, sample G78–1LL, same specimens as in Fig. 10:E. — H. External posterior view showing the gently arched outline of a specimen with undisturbed growth (cf. G); SGU Types 1060, 1061, $\times 4$, sample G77–28LJ.

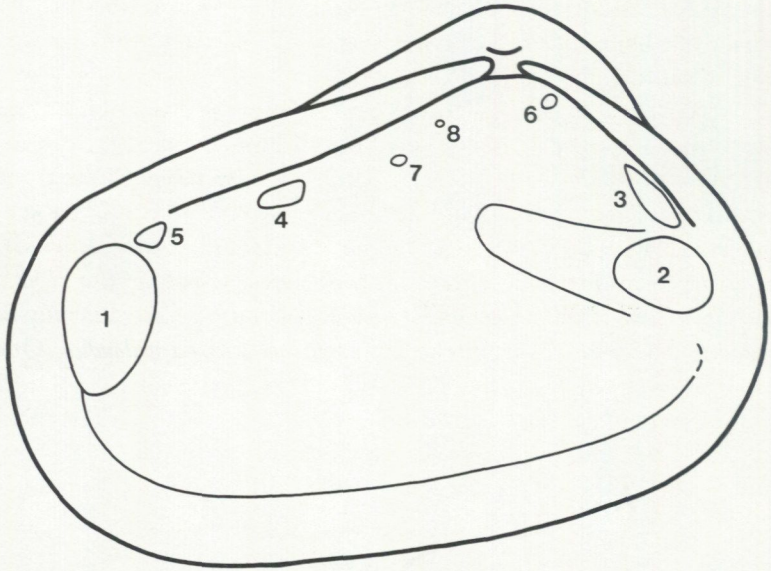


Fig. 15. *Nuculodonta gotlandica* n.g., n.sp. Maximum number of muscular impressions. Anterior end to left. Scars numbered in order of size. 1 = anterior adductor muscle scar, 2 = posterior adductor muscle scar, 3 = posterior pedal retractor muscle scar, 4 = anterior pedal retractor muscle scar, 5 = anterior pedal protractor muscle scar, 6 = posterior median muscle scar, 7 = anterior median muscle scar, 8 = anterior median muscle scar. Note conspicuous ridge.

1969), or that it had true hinge teeth (Bernard 1896:56). Then, as with *Nuculoidea lens*, (see p. 22), the increase in number of hinge teeth increased rapidly, more so than in *Nuculoidea lens*.

discriminant factor of major taxonomical value. The state of preservation does not usually allow these minute features to be seen, and in a number of species descriptions the teeth only "appear" to be continuous below the beak. Sometimes the evidence is contradictory and it is often difficult to establish whether the teeth are continuous below the beak or not. For instance in the discussion of the genus *Nuculopsis* Girty, 1911, Girty (1911:133-134) argued that "... the dentition consists of a continuous series of taxodont denticles not apparently interrupted by a chondrophore. This cannot, however, be positively asserted as a fact."

In most of the shells of *Nuculodonta gotlandica* the region below the beak is fragile and incompletely preserved if at all. However, in a few specimens the proximal ends of the tooth rows can be seen, the most proximal anterior teeth being situated below and just anterior to the beak, and the most proximal posterior teeth below and somewhat posterior to the beak. The tooth rows are separated by a triangular, edentulous area just below the beak. In one of the valves, usually the right one,

this area consists of a fairly shallow socket (Figs. 13, 14:E). In the corresponding valve there is a blunt curved structure (Fig. 14:F) partially covering the socket when seen in ventral view.

The interpretation of the function of this structure can only be a conjecture, similar structures not previously having been illustrated and described in detail. However, some species of *Nucula* s.s. have a specially robust "tooth", denoted "cardinal tooth" by Lamarck (1805:125), with a corresponding socket in the opposite valve. Quenstedt (1930, Pl. 2:10, 12 Bz) gives an elaborate description of the *Bandgrubezahn* and concludes that this is not a hinge tooth in the proper sense. Here too the "tooth" and socket may change places the socket generally being in the right valve and the tooth in the left as in *Nuculodonta gotlandica*. Quenstedt

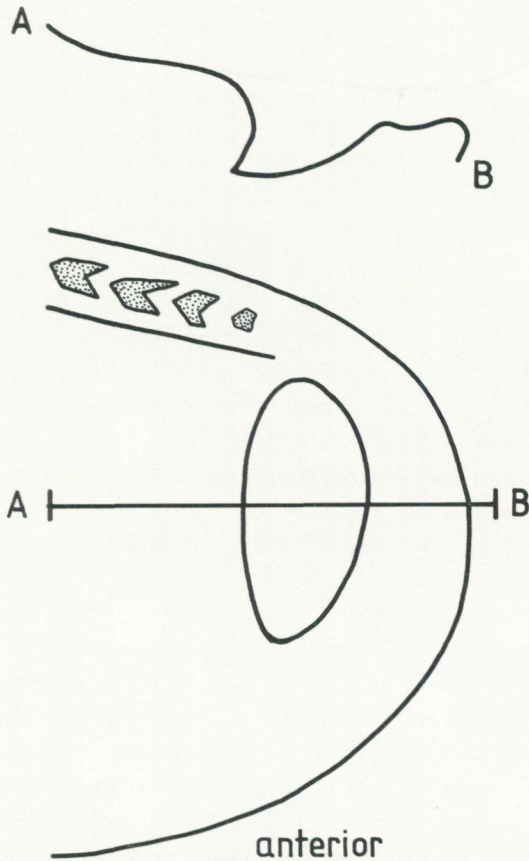


Fig. 16. *Nuculodonta gotlandica* n.g., n.sp. Diagrammatic representation of the anterior adductor muscle scar. A-B is a cross-section in antero-posterior direction showing the depth of the imprint.

(1930:43) claims that this feature is an exclusively post-Jurassic characteristic. The socket in *Nuculodonta gotlandica* is too shallow to have any stabilizing effect, so a comparison with the *Bandgrubezahn* may be doubtful.

Ulrich (1897:581) described some nuculoids from the Ordovician as having a socket below the beak. Quenstedt (1930:66) interpreted this as the possible beginning of the migration of the outer ligament. Sharpe (1853), in his description of *Nucula ciae* och *Nucula ezquerrae* from the Middle Ordovician, noted a "vacant space" which divides the tooth row into two parts. In her description of Middle Ordovician nuculoids Bradshaw (1970:625) made the following statement: "... the featureless area of *Cardiolaria beirensis* (Sharpe, 1853) does not resemble the clearly defined resilifer of modern palaeotaxodonts, but may indicate a very early stage in the migration of the external ligament onto the hinge plate."

Pfab's description of the genus *Praenucula* Pfab, 1934 includes one important characteristic which according to him may be interpreted as the beginning of the migration of the ligament (beginnende Bandeinwanderung: Pfab 1934:234). A groove situated just beneath the beak is open from above and below. This is interrupted by an oblique triangular structure which according to Pfab prevents the outer ligament from connecting with the alleged inner one, a strange statement indeed, since the inner ligament must be connected with the outer as the two constituents in fact must be considered as a single unit in nuculoids (Owen 1959; Trueman 1952). However, in Pfab's discussion of transitional forms (1934:213) he correctly postulated the probable characteristics of a functional connection between the outer and inner ligament as being one of the main characteristics of the genus *Praenucula*. His description is accompanied by some non-informative photographs (Pfab 1934, Pl. 3:15a, b) which lend no support to his statements. McAlester (1968), however, re-photographed the lectotype and, ignoring Pfab's discussion, stated in his redescription of the type species of *Praenucula* (McAlester 1968:47) that "... the lectotype and the paratype preserve impressions of large taxodont teeth of uniform size which are *continuous* below umbo. *Resilifer absent*. Ligament otherwise unknown" (My italics). I have examined the actual fossil material and fully agree with McAlester.

The edentulous area in *Nuculodonta gotlandica* may be a ligamental structure, since the separation of the tooth rows is a prerequisite for connection between the existing external part of the ligament and a presumed internal part. The similarity to a true resilifer in both shape and construction is easily recognized, although this edentulous plate is minute, which may be due to a primitive stage of development. On the other hand, since the bivalve larval shell exhibits a primary functional ligament (Cox *et al.* 1969:N96-N98) and only later develops an outer one (in relevant forms), it is more probable that evolution proceeded in the opposite direction. If so, the edentulous plate may be a remnant of a former, non-functional internal ligament.

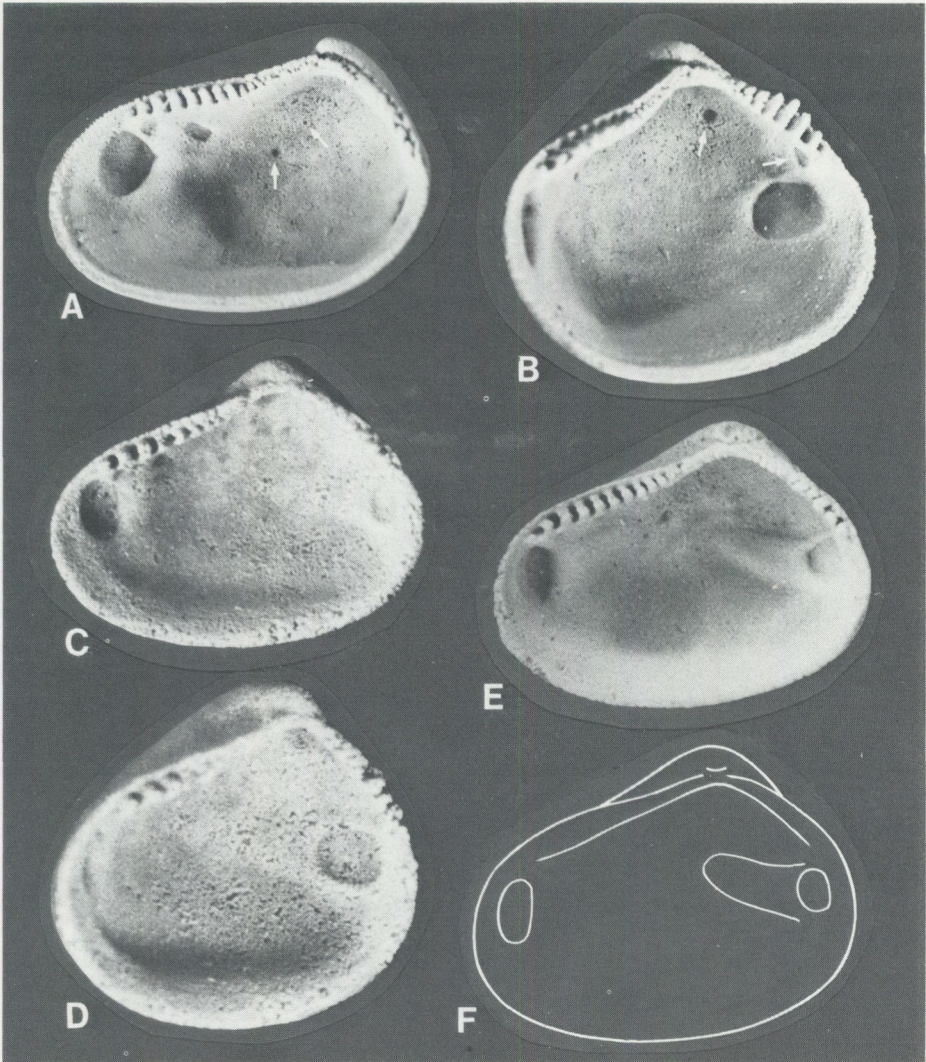


Fig. 17. *Nuculodonta gotlandica* n.g., n.sp. Muscular impressions. — A. Postero-ventral view of a right valve showing (from left to right) anterior adductor muscle scar, anterior pedal protractor muscle scar, anterior pedal retractor muscle scar and anterior median muscle scars (arrows); SGU Type 1200, $\times 4$, sample G79-82LJ. — B. Same specimen in antero-ventral view showing posterior median muscle scar (first arrow from left), posterior pedal retractor muscle scar (second arrow) and posterior adductor muscle scar, $\times 4$. — C. Lateral view of a right valve showing pallial line running from ventralmost point of anterior adductor muscle scar to posterior end of the shell where it seems to make an inward bend just below the posterior adductor muscle scar; SGU Type 1198, $\times 5$, sample G77-29LJ. — D. Same specimen rotated to antero-lateral view showing smooth-edged ridge at posterior end of shell (for discussion see text, p. 44). — E. Lateral view of a right valve showing same kind of ridge as in D; SGU Type 942, $\times 4.3$, sample G77-28LJ. — F. Diagrammatic representation of E, showing above-mentioned ridge.

The hinge angle in *Nuculodonta gotlandica* is independent of shell size and varies considerably. For this reason it has not been presented here in diagrammatic form.

INTERPRETATION OF MUSCULAR IMPRESSIONS — The size of the muscular impressions, i.e. area size, may vary from one shell to another. Fig. 15 shows the average size order of the total number of observed incisions in the entire material. A well-preserved shell does not usually contain more than 3–4 scars, some more distinct than others, the highest number of imprints in a single shell being eight (Fig. 17:A, B). The general pattern of distribution of scars in *Nuculodonta gotlandica* is similar to that of *Nuculoidea lens*. Thus the musculature of the foot in *Nuculodonta gotlandica* apparently resembled that in *Nuculoidea lens*.

If we follow the same line of reasoning as for *Nuculoidea lens*, the muscular incisions of *Nuculodonta gotlandica* can be inferred as follows: No. 1 in Fig. 15 is the anterior adductor muscle scar and the largest and by far the deepest of all imprints, while the posterior adductor muscle scar (No. 2 in Fig. 15) is always shallower. Fig. 16 is a diagrammatic cross-section of the anterior adductor muscle scar, showing that its depth is well suited for anchoring this presumably huge muscle. No. 3 in Fig. 15 I consider to be the mark of the posterior pedal retractor muscle. No. 4 in Fig. 15 (see also Fig. 17:A) probably indicates the position of an anterior pedal retractor muscle. No. 5 in Fig. 15 (see also Fig. 17:A), is, I propose, the anterior pedal protractor muscle scar although it is not as deeply impressed as the corresponding scar in *Nuculoidea lens*. The muscles corresponding to nos. 6, 7 and 8 in Fig. 15 (see also Fig. 17:B, A) probably functioned as pedal elevators as they are so deeply incised in spite of being small. Bradshaw (1978:214) suggested that the evolution of the visceral floor might have taken place much earlier in nuculanids than in nuculoids. Since the systematic position of *Nuculodonta gotlandica* remains highly uncertain, i.e. since the species may have possessed a pallial sinus and in addition probably a resilifer together with the conspicuous outer ligament (primitive nuculanid?), at least two of the three scars last mentioned (nos. 6 and 8 in Fig. 15) could have supported an early, primitive visceral floor.

One fairly inflated valve is remarkable in that the inner surface of the shell is almost smooth. Although the shell is of moderate size and therefore presumably adult there is only an extremely faint indication of the anterior adductor muscle. In a few shells a smooth-edged ridge, the function of which is uncertain (muscle scar?), extends antero-dorsally about half-way to the anterior margin (Fig. 17:C, E, F).

To a varying degree the pallial line can be seen in a number of valves of *Nuculodonta gotlandica*. In a non-silicified state of preservation the entire outline of the pallial line is seldom preserved. Occasionally part of it remains, usually in the anterior of the shell where the deepest adductor muscle scar is situated (Quenstedt 1930:61). In *Nuculodonta gotlandica* as well the part of the pallial line most heavily

impressed is situated close to the deepest adductor muscle scar i.e. at the anterior end of the shell. Here the pallial line forms a clear junction with the ventralmost end of the anterior adductor muscle scar (Fig. 17:C). At the posterior end, however, a number of shells show no evidence of a pallial line in contact with the posterior adductor muscle scar. The interpretation of the diffuse posterior continuation of the pallial line of *Nuculodonta gotlandica* must wait until better-preserved shells revealing the true shape of their pallial line have been discovered.

Periods of decrease in growth rate are not rarely indicated inside the shell by more or less distinct modifications on the surface of the muscular imprints. One particular valve is a good example of this phenomenon. The posterior adductor muscle scar has a conspicuous ridge inside the impression. On the outside of the valve several irregularities are represented by shallow commarginal furrows two of which are conspicuous and completely modify the dorsal outline of the shell. Another shell displays growth increment markings in all muscular impressions present.

A most spectacular evidence of disturbances in growth rate occurs in one valve (Fig. 18). It is externally deformed by a major irregularity (Fig. 18:A, B). On the inside is a large, subcircular, faintly delimited depression at some distance from and postero-lateral to the anterior adductor muscle scar. This and another faint subequal impression, situated in the posterior part of the valve antero-dorsal to the posterior pedal retractor muscle scar, together constitute the remnants of the former anterior (aa in Fig. 18:F) and posterior (pa in Fig. 18:D) adductor muscle scars. Furthermore, two minor scars, one situated close to and antero-dorsal to, the other postero-dorsal to the old posterior and anterior adductor muscle scars, mark the positions of the former posterior retractor muscle and anterior protractor muscle. All older scars correspond in commarginal position to the outer disconformity of the shell.

Environmental disturbances apparently caused the animal to stop growing and gave rise to the unusually deep muscle insertions pa, aa and pl (posterior adductor muscle scar, anterior adductor muscle scar and pallial line) in Fig. 18:D, F. When conditions again became favourable the animal started growing rapidly anew, and consequently the inner shell layer did not completely cover these prints while the muscles moved to their functional positions pa', aa' and pl' in Fig. 18:D, F.

DISCUSSION OF CLOSELY RELATED FORMS — Soot-Ryen (1964:497, Pl. 2:1) described and illustrated a nuculoid *Ctenodonta* sp. A, suggesting that it was the oldest ctenodont from Gotland. Although the state of preservation of this species does not reveal important structures, *Ctenodonta* sp. A seems to belong to *Nuculodonta gotlandica*. (My suggested orientation of the species is, by the way, opposite to Soot-Ryen's.)

The oldest known form more obviously related to *Nuculodonta gotlandica* appears

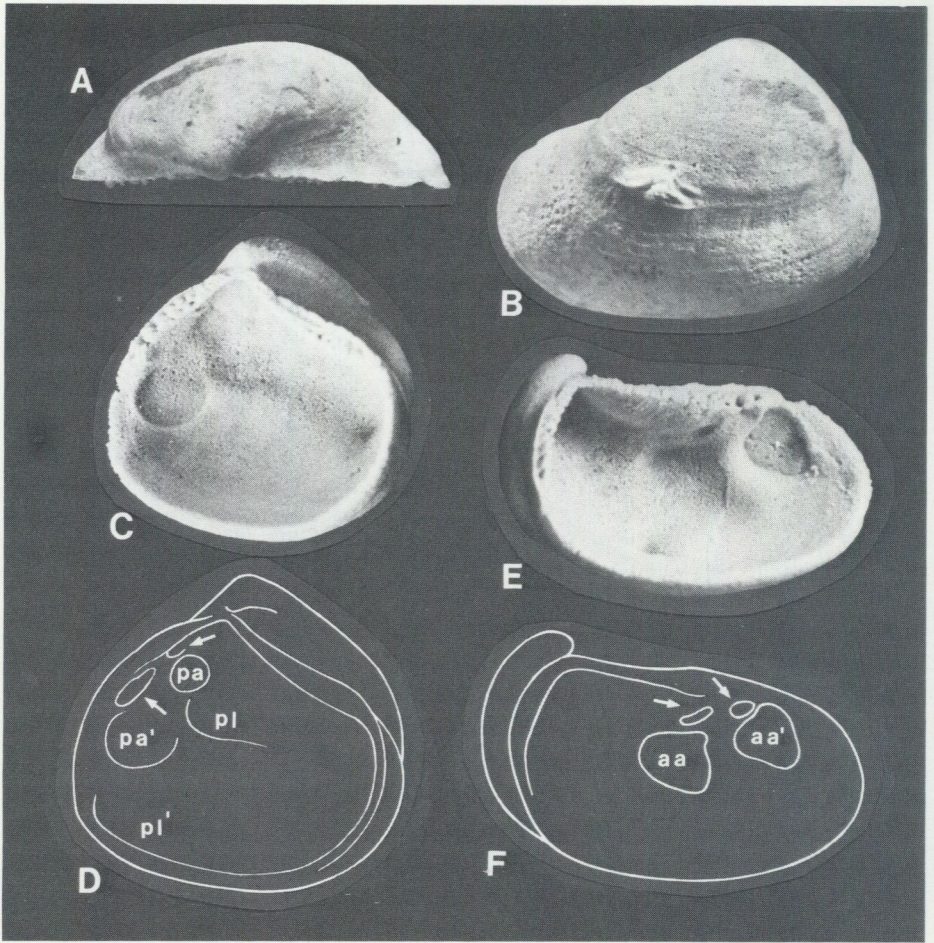


Fig. 18. *Nuculodonta gotlandica* n.g., n.sp. External and internal evidence of growth inhibition in a single shell. — A. Dorsal view of a left valve, outline conspicuously modified by irregular growth: SGU Type 976, $\times 3.5$, sample G77-28LJ. — B. Exterior of same shell in lateral view. — C. Interior of same shell, ventro-anterior lateral view showing two generations of muscular impressions (see D for explanation), $\times 4$. — D. Diagrammatic representation of C showing old, non-functional muscle scars: posterior adductor muscle scar (pa), posterior pedal retractor muscle scar (second arrow from left), pallial line with diffuse posterior end (pl). Close to the valve margins the final, functional positions of the following scars: posterior adductor muscle scar (pa'), posterior pedal retractor muscle scar (first arrow from left), and posterior part of pallial line (pl'). — E. Same shell in postero-lateral view showing the two generations of muscular imprints at the anterior end of the shell (see F for explanation). — F. Diagrammatic representation of E showing anterior adductor muscle scar (aa); anterior pedal protractor muscle scar (first arrow from left); corresponding scars i.e. anterior adductor muscle scar (aa') and anterior pedal protractor muscle scar (second arrow from left).

to be the Ordovician *Tancrediopsis* "abrupta" (Billings) in McAlester 1963. The general outline of *Tancrediopsis* "abrupta" is superficially reminiscent of *Nuculodonta gotlandica*. However, there are a number of differences which I consider warrent placing the two species in separate genera. I am inclined to interpret the striking resemblance in external habit, to some extent, as being ecophenotypic parallelism. Internal features, such as the arrangement of the hinge teeth and resilifer or similar structures in connection with ligament function, as well as possible traces of siphons and musculature, are less prone to be affected by ecological factors. Even if these internal characters, too, may be modified by ecological conditions, they are likely to retain more of truly genetically based elements of morphology.

The major differences between *Tancrediopsis* "abrupta" (Billings) and *Nuculodonta gotlandica* n.g., n.sp. are summarized below.

<i>Tancrediopsis</i> "abrupta"	<i>Nuculodonta gotlandica</i>
Chevron-shaped teeth pointing away from umbo	Chevron-shaped teeth pointing <i>towards</i> umbo (Fig. 14:A, C)
Teeth continuous below umbo	Two series of teeth interrupted by a resilifer (Figs. 13, 14:E, F)
Beaks opisthogyrate	Beaks prosogyrate (Fig. 10:A, B)

In McAlester's description (1963) of *Tancrediopsis* "abrupta" nothing is said about the lunule, escutcheon, number of hinge teeth, size and form and position of ligament, the arrangement of the pedal muscle scars or the dimensions of the shell.

OCCURRENCE — At the time of the description known exclusively from the Silurian (high Wenlockian) Halla Beds, Möllbos, Gotland.

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APPENDIX

Nuculoidea lens n. sp.

Number of cases	Variable	Min. values	Max. values	Mean values	Ratios
143	L	2.8	15.0	9.0	
144	H	2.3	13.0	7.4	H/L 0.82
84	B	0.5	4.3	2.6	B/L 0.29
49	h	1.1	3.3	2.2	h/L 0.24
49	Ah	1.7	5.9	3.8	Ah/L 0.42
49	Ph	1.4	4.6	3.0	Ph/L 0.33
92	NAh	6	15	10.8	NAh/L 1.2
89	NPh	5	13	9.2	NPh/L 1.0
38	V	120	142	127	V/L 14.1
					NPh/NAh 0.85

Nuculodonta gotlandica n. g., n. sp.

Number of cases	Variable	Min. values	Max. values	Mean values	Ratios
197	L	1.7	15.3	9.3	
198	H	1.4	11.5	7.0	H/L 0.75
113	B	0.4	5.3	2.7	B/L 0.29
102	h	1.3	5.0	3.1	h/L 0.33
103	Ah	2.5	9.1	5.7	Ah/L 0.62
103	Ph	1.9	6.3	4.2	Ph/L 0.46
57	NAh	12	28	20.1	NAh/L 2.2
52	NPh	9	17	12.9	NPh/L 1.4
50	V	118	130	124	V/L 13.4
					NPh/NAh 0.64

Minimum, maximum and mean values of the variables.

The ratios of all other variables in relation to total length of shell are based on the mean values (for discussion see the text, p. 13 and Figs. 6, 7, 11, 12).

All measured specimens have a type number and are listed below.

Nuculoidea lens: SGU Types 842–935, 1108–1159, 1188–1193, 1208 (153 specimens).

Nuculodonta gotlandica: SGU Types 936–1107, 1160–1187, 1194–1207, 1209–1212 (218 specimens). The SGU Type numbers correspond to the following samples (all samples are from Möllbos 1):

G77–28LJ: 842–880, 894–997, 1058–1107

G77–29LJ: 884–886, 1049–1057, 1198

G78–1LL: 881–883, 998–1021, 1188–1189, 1194–1197

G78–2LL: 887–893, 1022–1048

G79–2LL: 1122

G79–3LL: 1108–1121, 1165–1168, 1211–1212

G79–78LJ: 1132–1135, 1169–1173, 1193

G79–80LJ: 1147–1159, 1174–1187

G79–82LJ: 1138–1146, 1199–1205

G79–84ALJ: 1136–1137, 1163–1164, 1190–1192

G79–86LJ: 1123–1125

G79–90LJ: 1126–1131, 1160–1162, 1206–1207

No sample No. 1208–1210

All types and numerical data are deposited in the Type Collection of the Geological Survey of Sweden, Museum Dept., box 670, S-751 28 Uppsala.

Geographical location of Möllbos 1.

CJ 4826 7445, c. 3150 m west of Sjonhem church. Topographical map sheet 6 J Roma NV & NO. Geological map sheet SGU Aa 160 Klintehamn (see Laufeld 1974).

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