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i Syd- og Sønderjylland og deres miljø

I kommission hos
C. A. REITZELS FORLAG (JØRGEN SANDAL)
KØBENHAVN 1958

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GENERAL CONCLUSIONS AND REMARKS ON SHELL MORPHOLOGY

Although the number of species in which variation of shape has been investigated is relatively small, due to the broken state of the material, it is possible to outline some new fundamental features of shell morphology.

The investigations of *Yoldia glaberrima*, *Leda Westendorpii*, *Leda pygmaea*, and *Spisula subtruncata* indicate that the length/height ratio of pelecypod valves is very seldom constant throughout the life of the animal. This is important, but some workers are apparently not aware of this principle, to judge by the significance which is often attached to the calculation of means of length/height ratios, or other quantitative expressions of shape. Mean values of this sort have no taxonomic significance unless they are accompanied by information on the size groups of the shells measured.

The determination of Nuculid shells is generally rather difficult, as has also been demonstrated in this treatise. Examination of the hinge dentition in the Nuculid shells from the Arnum formation disclosed that the number of teeth is obviously not constant, and probably not even confined within strict limits, since the number increases with growth. The number of hinge teeth is accordingly not a valid specific character. It should be noted that the numbers of radial elements in the outer shell layer in species of the genus *Nucula* are apparently normaly distributed around a mean, but future more extensive investigations must decide whether these means are constant specific characters or not.

Particular new observations in pelecypod genera are: the ductus between the inner and outer layers on the posterior end of the right valve in *Corbulid* species, and the discovery of a previously unknown initial dissoconch stage in the *Pectinidae*. The biological significance of these features is as yet unknown.

A parallel to the length/height ratio in pelecypods is the height/diameter ratio in gastropods. The variation of this ratio in *Nassa Schlotheimi*, *N. subobesa*, *N. cimbrica*, *Ringicula buccinea* etc. is clearly correlated with growth. With the exception of *Ringicula buccinea*, the ratio increases with the size of the shell. Such increase is also evidenced by the height/diameter values hitherto obtained in *Bittium spina*, *B. tenuispina*, *Nassa Woodwardi*, *N. cavata*, *Odostomia mutinensis*, and *O. pallidaeformis*. It has therefore to be anticipated that a change of the ratio with growth is the normal in most gastropods.

The observations in gastropods also indicate that means of dimension ratios are insignificant without information on size grouping.

The statistics on collabral sculptural features in *Bittium tenuispina*, *Nassa Schlotheimi*, *N. subobesa* and *Terebra Hörnesi* and other species illustrate that the number of collabral elements per whorl are often not constant. The number of ribs per whorl generally increases with growth, although a smaller or almost unchanged number of ribs may be found. It seems to be common in ribbed *Nassae* that the first ribbed whorl has a greater number of ribs than the second, but thereafter the number of ribs increases (see e. g. *N. Schlotheimi* and *N. subobesa*).

The delicate protoconch features of the family *Turridae* have provided an interesting basis for a morphological subdivision of this very variable family. It is belived that research on this part of the shell, and the corresponding animal stage, in recent representatives of the family should throw light on the problems of taxonomy in both recent and fossil species.

MARINE PELECYPODA AND GASTROPODA IN RELATION TO THEIR ENVIRONMENT

Since the earliest paleontological research, students of fossils have endeavoured to apply the principles of the environmental relationships of recent faunas. Numerous far-reaching generalizations have been made in spite of the fact that comparatively little is known about the control which environmental factors exert upon biology even in the living representatives of the most important groups of fossil animals. In this connection the Mollusca are no exception.

Although pertinent data on the environment relations of recent mollusca are still rather scanty, it must be admitted that considerable progress has been made during the last two decades. Some of the results and principles arrived at will be briefly outlined as an introduction to a discussion of the middle Miocene fauna already described. Since this fauna is European, the references to recent marine biology and ecology are mainly concerned with the faunas of European and adjacent waters. The faunas of the North Sea, the Baltic, the North Atlantic and the Arctic seas have particularly been considered. Even in this limited field some essential features may have escaped notice. It is hoped, however, that the following record may encourage further studies of the environmental evidence of recent marine molluscan faunas, since it must never be forgotten that thorough knowledge of recent marine zoology is a fundamental prerequisite for the interpretation af fossil marine faunas, however remote they may be in time.

1. CONTROLLING FACTORS

Animal life in the sea is dependant on a number of well known factors of which the following may be mentioned: 1. food, 2. salinity, 3. temperature, 4. depth, 5. enemies and competitors, and, in the case of the bottom fauna, 6. bottom configuration and deposits. There may be other factors, both known and unknown, but those listed may be regarded as essential. Variation of any of these factors will result in more or less pronounced change in the marine animal communities and the distribution of the individual species.

The importance of knowledge of factors such as salinity, temperature, and depth of water, during the sedimentation of ancient formations is obvious from a geological point of view. It is easy to understand, therefore, why geologists have tried to draw inferences concerning paleo-environments from extinct faunas.

A careful study of fossils, their manner of preservation, their wear, their embedding in the sediment, and also a meticulous study of the sediment itself will often reveal whether the animal was buried where it lived, or not. If one can be sure that the animals found as fossils lived where they were buried, it should in many cases be possible to reconstruct the bottom configuration and physical properties of the former sea bottom, on or in which the fossil fauna lived.

The salinity of the water in which a fossil fauna lived may be approximately estimated in most instances. The distribution of recent pelecypods and gastropods shows that it is possible to discriminate between marine genera, and genera which live exclusively in freshwater. Fossil mollusca are often referrable to modern genera, or, if extinct, they may have near allies in the recent fauna. By means of an analysis of the genera, supplemented by thorough lithologic studies, it should be relatively easy to decide whether a fossil fauna lived under marine or non-marine conditions. The degree of certainty regarding the salinity of the water in which a fossil fauna lived may depend only upon the proportion of non-extinct species and genera in the fauna.

Concerning the temperature conditions of paleo-environments, the evidence of fossil marine molluscan faunas may at first be considered less reliable than the evidence they provide for salinity. However, this is due to defects in our information about recent ecology, and not to failure of the paleoecologic method itself. In principle, the degree of certainty arrived at in inferring temperatures from fossil faunas may—as in the case of salinity—be proportional to the modernity of the fauna.

Depth, acting as a controlling factor, was considered more significant in the older literature of marine zoogeography than it is now. Studies of the sea bottom infaunas have clearly shown that depth may be relatively unimportant as a limiting agent, as demonstrated by C. G. JOH. PETERSEN (1914, p. 34 and 1915, p. 13–14 and see also this paper p. 390).

The regulative effect of enemies and competitors on individual species needs no comments. Being important factors, enemies and competitors should not be neglected when attempting to explain differences in the occurence of particular species in related animal communities, either living or fossil. However, biotic factors are often used to explain away difficulties.

Besides the above named factors, hydrographic phenomena like ocean currents, tide, waves, etc. may exert a great influence on the distribution of species, either directly or indirectly.

Therefore it is obvious that deductions regarding the significance of individual factors on marine animals depend primarily upon a thorough knowledge of the hydrography of the area in which the animals live. A study of zoological literature reveals, however, that this prerequisite is rarely satisfactorily fulfilled. A second point is that environmental conditions vary widely from year to year, and unless data are carefully reported with due attention to the dates of observation, etc., as ORTON (1920) points out, it may be extremely difficult to disentangle the separate effects of the many factors in the environmental complex.

It has been unavoidable that the somewhat fortuitous location of laboratories has had an important effect on the investigational coverage of the different parts of the oceans. Due to the scarcity, and unsystematic distribution of exact data, we are thus confronted with an unknown number of sources of error in trying to determine the principles of ecology of the mollusca. It should be particularly stressed that the study of faunas in hydrographically complex and atypical areas may have been over-emphasized. It is of interest in this connection to point out for instance that the Baltic, in its widest sense, is an extremely complicated brackish-marine region that exhibits pronounced variation and even discontinuity of several factors like temperature, salinity, currents, etc. Attention should also be drawn to deep fiords, as found in Scandinavia, Greenland and elsewhere, and to estuaries all over the world. Such areas rank among the best known regarding marine mollusca, but at the same time they display the most extreme hydrographic conditions.

From this it becomes evident how desirable it would be if ecologic research could be concentrated on seas in which only a single environmental factor varies on a major scale. For example the effect of temperature on reproduction and distribution could obviously best be studied in areas where salinity is relatively uniform throughout the year, and where the water is mixed sufficiently to reduce to a minimum the temperature gradient from the surface layer to the bottom. Such an ideal area for the study of the effects of temperature is more nearly approximated by the North Sea than by the hydrographically complex Baltic. In the relatively uniform shelf area of the North Sea, where wave action and tides ensure rapid mixing of water masses, the dominant environmental variable is certainly temperature.

In summary, the following observations seem to be fundamental in any investigation of marine ecology: 1. date, 2. salinity, 3. temperature, 4. depth, 5. bottom deposit, 6. bottom temperature, 7. currents, and 8. tide. The lack of data on several of these subjects renders many otherwise valuable treatises useless for the present analysis of environment relations, and accounts in part for the small number of observations utilized in the following.

2. FEATURES OF THE LIFE HISTORIES OF SOME MARINE PELECYPODA AND GASTROPODA

Any species has definite ranges for the possible variation of the environmental factors which control its survival. In the case of marine mollusca we may talk about upper and lower limits in dealing with temperature and salinity. A similar distinction may also be applied in connection with the nature of bottom deposit, exposure to the atmosphere in littoral species, and other factors, although it may be more difficult to define these limits in quantitative terms. A natural consequence of this viewpoint is, that each factor has an optimum value within the range of survival, and that values above and below this optimum are less favourable for the animal, provided all others are equal.

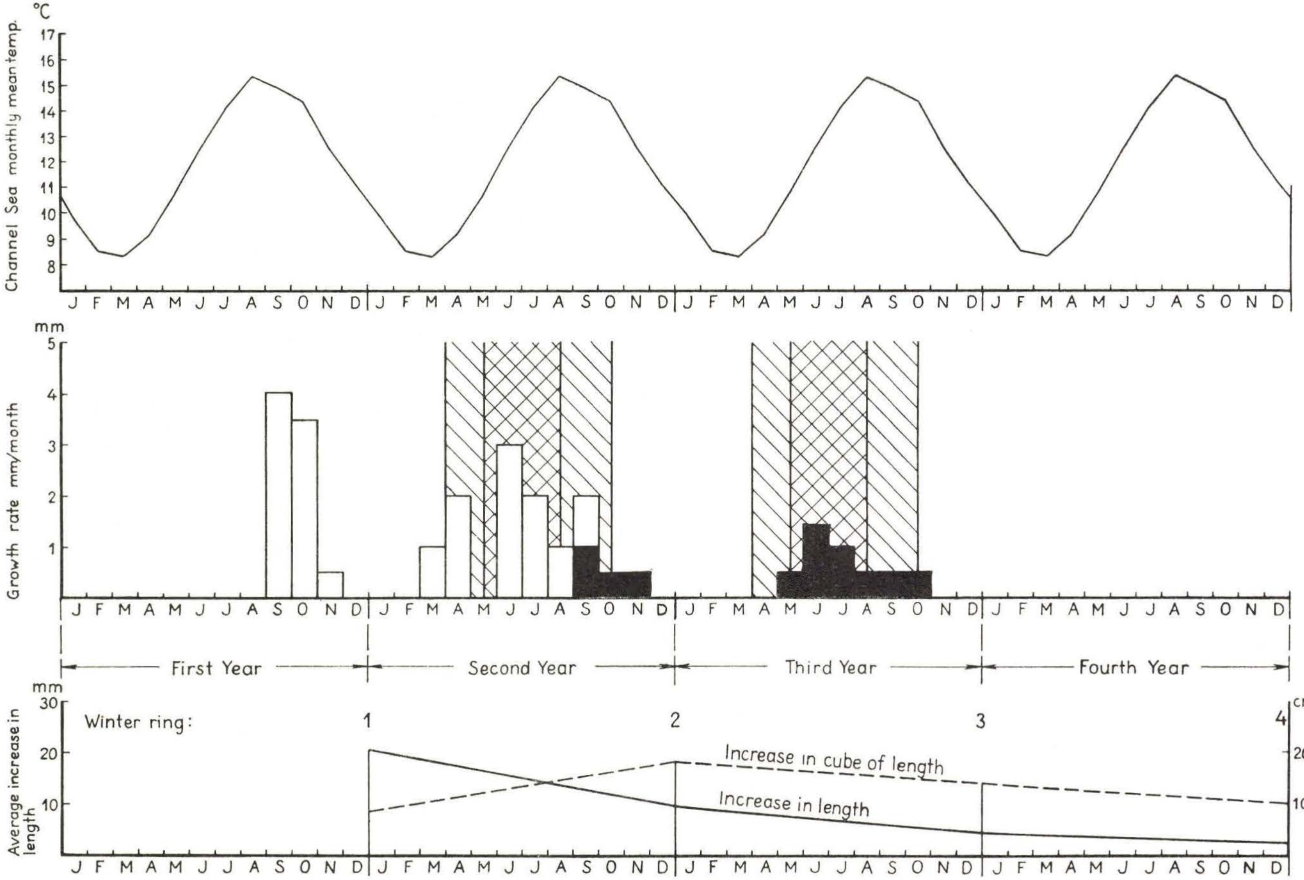
The influence of some factors on the main life periods of marine Pelecypoda and Gastropoda will be illustrated by examples taken from living species.

A. Animal Growth and the Variation of some Shell Properties

Very interesting investigations on the growth of shell and tissue in molluscan species have at intervals been carried out at the Plymouth Laboratory by ORTON (1926, *Cardium edule*), STEPHEN (1936, *Tellina tenuis, T. fabula, Abra alba*, and *Cardium edule*), and MOORE (1936–38, *Purpura lapillus*, and *Littorina littorea*). Similar studies have been made by RICHARDS (1946, *Mytilus edulis, M. californianus*), THAMDRUP (1935, *Cardium edule, Macoma baltica*), and by SMIDT (1951, *Cardium edule*).

Cardium edule has been studied most intensively, perhaps partly because it offers good possibilities for obtaining material and partly because of

Fig. 24.



Cardium edule (Yealm) Growth rates (acc. to ORTON 1926) and sea water temperatures off Plymouth (ORTON 1922)

☐ Group A, spatted in 1919 ■ Group B, spatted in 1918 ▧ Spawning period (ORTON 1926) ⊠ Main spawning period (LEBOUR 1938) the clarity of the annual cessations in growth of the shell known as winter rings (ORTON 1926). From study of the winter rings, the authors mentioned above have claimed to be able to follow the growth of various groups of *Cardium edule* rather closely, although it should be noted that PURCHON (1939) found it impossible to use growth as an indication of age in his investigations.

Summarizing the results arrived at by the authors mentioned it may be stated that the growth rate of *Cardium edule* varies from region to region, and that it also varies from year to year in the same area. The authors quoted have all used shell lenght as an indication of growth. The most detailed results regarding number of specimens, measured groups, and number of measurements per annuum have been presented by ORTON (1926).

ORTON kept a number of individuals of *Cardium edule* in an experimental box at the River Yealm estuary from August 1919 to October 1920, during which period the length of the individuals was measured monthly, except for January 1920. A final measurement was made Sept. 6, 1921. It was possible to discriminate between two groups, the *A* group that was the spat of 1919, and the *B* group which was mainly the spat of 1918. When the cockles were first placed in the experimental box they were marked with file marks cutting the growing edge of the shell. ORTON has illustrated the monthly growth by means of graphs showing length, as derived from monthly measurements of marked individuals throughout the experiment, plotted against number of shells in one millimeter size-classes. It is interesting to note from the graphs that the younger group (*A*) gradually catches up and merges with the older group (*B*). In 1921 the two-year-old and three-year-old animals were indistinguishable by size. ORTON also gives a table showing the monthly shift of the peaks of the two groups. The growth of the modal individual is not necessarily the same as that of the average individual, but we are forced to assume that it is if we wish to infer growth rates from the data available. The graph, fig. 24, that has been prepared by the present writer on the basis of ORTON's figures show accordingly the monthly shift as an approximate growth rate for the *A* and *B* groups. The average increase in lenght is shown for four years on the basis of the *A* and *B* groups and for *Cardium* grown in the box 1921–23. The annual increase in the cube of length (being a measure of volume increment) is calculated on the same material. The Channel monthly mean temperature off Plymouth, and the spawning period of *Cardium edule* off Plymouth are added to show the possible effect of spawning and temperature on growth.

The graph suggests:

1. Some correlation between variation of temperature and variation of growth.
2. A decrease in the annual increment of shell length with age, as illustrated by the curve showing monthly increase, and by the declining winter ring curve.
3. Maximum growth during the second and third years and thereafter decreasing growth rate as indicated by the curve of the annual increase in the cube of length.

It is impossible to decide with certainty whether any of the minima of the monthly growth rate during the spawning period may be related to spawning activity. This may, however, well be the case, since the species, according to ORTON, matures at an early age. The lows on the growth histogram for the two-year-old animals may thus indicate retardation of growth due to spawning.

Before leaving ORTON's investigations it should be mentioned that the animals were apparently severely shocked by the process of file marking, since cessation in growth occured immediately afterwards, causing the occurrence of disturbance rings on the shell surface, similar to—though weaker— than the winter rings. Such disturbance rings were also formed by merely taking the shells out of the box for measurement. Rings on the shell surface of *Cardium* do, therefore, not necessarily mean winter rings.

The influence of salinity on the shell growth of *Cardium edule* is illustrated by BATESON (1889), BRANDT (1897) and PURCHON (1939).

BATESON visited the Aral Sea area in 1886. He studied shells of *C. edule* along the shore of the Aral Sea itself, and in some local depressions formerly connected with the Aral Sea, but dry when he visited the area. One of the depressions, the Shumish Kul, was especially interesting because seven very well defined terraces were found on its shore clearly indicating stages in the drying up of the former lake. The highest terrace might have corresponded to water of a salinity comparable with that of the present Aral Sea whereas the lower terraces clearly indicated lake stages of increasing salinity as also evidenced by the salt pan, which covered the lowest part of the lake. On each of the terraces great quantities of *Cardium* were found. A great number of the shells were paired, and the ligament was preserved in many cases. Further, it turned out that each terrace had its special variety of *Cardium* which differed from the terraces above and below both in colour and texture of the shell. The general changes which occured in relation to successive stages of evaporation of the lake are, according to BATESON:

1. Diminution in the thickness of the shells (starting on the third terrace from the top) proceeds to such an extent that the shells of the lowest terrace (corresponding to the lake stage with highest salt concentration) are almost horny and semi-transparent.
2. Size of the umbo is greatly reduced. In shells of the lower terraces the umbo hardly forms a projection on the outside of the shell.
3. The shells become highly coloured.
4. The grooves between the ribs appear on the inside of the shell as ridges with rectangular faces. On the lowest terrace all ribs are affected.
5. On the lowest terrace (corresponding to water of high salt concentration) the shells are greatly diminished in size.
6. The length of the shells increases in proportion to their breadth (lenght/ greatest antero-posterior dimension: breadth/dorso-ventral measurement at right angles to the length).

BATESON measured length (L) and breadth (B) of 30 shells and calculated the ratio: $\frac{B}{L}$ for shells from the Aral Sea and the terraces of the Shumish Kul, and got in this way expressions for the relative elongation of the shells (fig. 25). The average ratios and length intervals are given below, for further details reference is made to BATESON.

The water of the Aral Sea has a salt content of about $10\,^0/_{00}$ at the surface.

Due to the special nature of this investigation it is impossible to give any quantitative expression for the change in salinity, or the time which elapsed during evaporation of the lake in the Shumish Kul depression while the

Cardium edule L. Aral Sea area. Shape and Weight of Shell related to Salinity

Collecting areas	Length interval	$\frac{B}{L}$	Length of 20 specimens	Total weight in grammes of 20 specimens
Aral Sea:	22–18.5 mm.	0.761	21–17 mm.	13.3 g.
Shumish Kul:				
Terrace I (highest)	21–16 -	0.799 -	21–17 -	14.1 -
Terrace II	21–16 -	0.782	21–17 -	14.5 -
– II	26–20 -	0.770		
– III	22–16 -	0.751		
– IV	21–16 -	0.735	21–17 -	6.5 -
– IV	26–18 -	0.730		
– V	21–16 -	0.743	21–17 -	6.1 -
– V	27.5–21 -	0.731		
– VII	21–16 -	0.725	21–17 -	4.6 -

development of the different types of *Cardium* took place. There is, however, sufficient evidence for the correlation of shell properties with increase in salinity to render this study important in the present connection. BATESON has also studied *C. edule* in two other depressions at the Aral Sea; Jaksi Klich and Jannan Klich, and in the Egyptian lagoon Abu Kir. However, the lack of any record on salinity change renders the application of his conclusions impossible in this discussion.

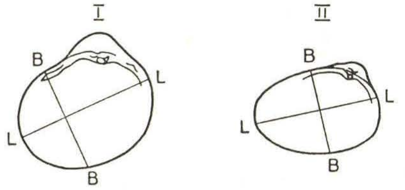


Fig. 25.

Cardium edule L. Aral Sea area.

Diagrams showing the directions in which the length and breadth of the shells were measured. I shell from the shore of the Aral Sea. II shell from the Jaksi Klich. LL = length, BB = breadth. (Acc. to BATESON 1889, p. 304).

In 1934 LARSEN investigated the fauna of the Dybsø Fjord, a very shallow lagoon-like bay of the Baltic in southern Sjælland, Denmark. The average depth is about 1–2 meters, and the salinity is about $13^0/_{00}$. The bottom deposits consist of sand, gravel and silty deposits, and organic detritus.

The fauna of the bay includes *Cardium edule*, which is very abundant. LARSEN observed that the growth rate of this species was in general inferior to the growth rate of the cockles studies by ORTON off Plymouth, and he stated, moreover, that the animals living on sand attained a larger size than those living on organic detritus. LARSEN (1936, p. 13–14), concluded, therefore: 1. that the small size of *C. edule* in Dybsø Fjord was due to the low salinity of the water, and 2. that the variation in size of Cardium in the bay area could be correlated with variation of the substatum. No serious objections can be raised against this conclusion.

PURCHON (1939) collected samples of *Cardium edule* from the following localities and substrata:

A. Fairlie Sands, Millport. Marine, clean intertidal sand.
B. Pier Cellars Plymouth. Marine, clean sand, rarely above low water mark.
C. St. John's Lake, River Tamar. Estuarine, soft, intertidal mud.
D. Portishead Dock. Estuarine, soft mud, below low water mark.
E. Bawdsey. Brackish (?) mud in shallow lagoon.

Samples of fifty shells from each locality were investigated regarding the number of ribs, weight and sculpture of the shells, and measure of asymmetry. Investigation of the rib number resulted in the following figures:

Cardium edule L. British waters. Number of Ribs related to Environment. (Loc. A–E see above).

Locality	Amount of shells with: 15	16	17	18	19	20	21	22	23	24	25	26	27 ribs	Mean number of ribs	Standard deviation
A									1	11	19	13	6	25.24	1.13
B							1	4	9	19	13	4		24.01	1.12
C				3	2	9	12	10	11	2	1			21.40	1.74
D	2	9	12	17	9	1								17.50	1.03
E		3	4	5	9	14	11	3	1					19.54	1.56

Purchon does not give any figures for the weight of the shells, but states that shells taken from estuarine mud were lighter than these taken from marine sand. Quoting Loppens, Purchon states further, that the mean numbers of ribs and asymmetry of the shell apparently are related to the same environmental factor, which he thinks is either salinity or texture of the substrate. The asymmetry is illustrated by fig. 26. Purchon made plasticene casts of the shells and weighed the casts, the weights being taken as representative of volume. Also the measure of asymmetry, i.e. *ac* as a percentage of *ab* (see, fig. 26) was calculated, *ab* being the greatest length of the shell, and *c* the projection of the umbone on *ab*. The measure of asymmetry was plotted against weight classes (0–1.5 g.; 1.5–3.0 g. etc.) and graphs were drawn as shown in fig. 26.

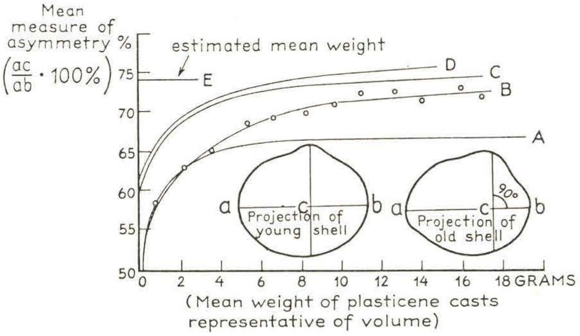


Fig. 26.

Asymmetry of Shells of *Cardium edule* related to volume.

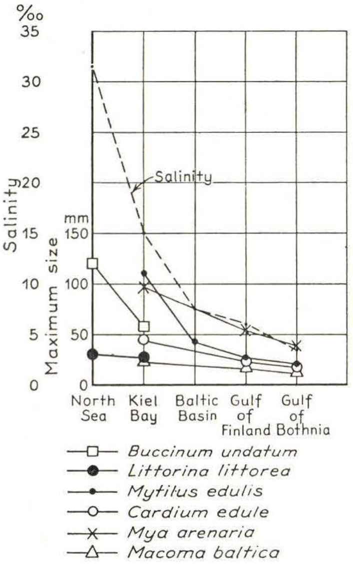
A. Shells from Fairlie Sands, Millport (marine, clean intertidal sand).
B. Shells from Pier Cellars, Plymouth (marine, clean sand rarely above LWM).
C. Shells from St. Johns Lake, River Tamar (estuarine, soft, intertidal mud).
D. Shells from Portished Dock (estuarine, soft mud below LWM).
E. Shells from Bawdsey (brackish (?) mud, never exposed; fragile shells, no plasticene casts made).

Graph B has been taken as typical, and observations are plotted to indicate the degree of acuracy.

First half of C and D graphs confluent. (Acc. to Purchon 1939).

From his material Purchon concludes: 1. Shells from sheltered estuarine mud are more lightly built and are more asymmetrical than those from marine wave beaten sand. 2. The measure of asymmetry increases logarithmically with age*), and the greatest rate of increase and highest measure of asymmetry are found in estuarine samples. He finally suggests that the increase of the initial measure of asymmetry from 50% for "normal" shells, to 60% for estuarine shells, and above 70% for shells living in extreme brackish environments may be due to delayed metamorphosis. Subsequent increase in asymmetry may according to PURCHON be caused by variation of the environment, or by variation in genetic constitution.

PURCHON's investigations suggest that the development of the shell is mainly dependent on salinity and bottom deposit. It may, however, be objected that the number of old shells measured from the localities B, C, D, and E is too low to make the conclusions safe. Quantitative data on salinity for the areas investigated would have been desirable. The assumption that delayed metamorphosis should be responsible for an initial asymmetry appears to be rather speculative. The present writer believes that the measurements of the asymmetry of the smallest sizes are too inexact to provide a basis for discriminating different cathegories of asymmetry. Although PURCHON's investigations did not decide whether salinity, bottom deposit or both may be responsible for the observed growth variation, they suggest very strongly the influence of these environmental factors.



Maximum size of various Mollusca at different locations in the North Sea and the Baltic (Acc. to K. BRANDT 1897)

Fig. 27.

In a brief paper on the fauna of the Baltic BRANDT (1897) mentions the maximum size of six molluscs, including *Cardium edule*, from the North Sea and the following areas of the Baltic region: Bay of Kiel, Baltic Basin, Gulf of Finland and Gulf of Bothnia. His data are shown graphically in fig. 27 together with the salinities of the areas concerned. Unfortunately BRANDT does not give the number of shells investigated, it is accordingly impossible to be sure how much weight should be attached to his statements. Since his data certainly illustrate a significant trend in the response of marine animals to variation of salinity, they have been included here.

The growth of **Mytilus californianus** was studied by COE & FOX during the years 1940–43 at La Jolla, California. On the basis of their data RICHARDS (1946) calculated a growth rate curve which summarizes the seasonal trends for the four year period. This is shown on fig. 28, which has been copied from the WOODS HOLE report of 1952, p. 85. Curves showing the sea water temperature at La Jolla and spawning intensity at the pier colony La Jolla (YOUNG 1946) have been plotted on the same graph.

RICHARDS measured the growth of **Mytilus edulis** on the Atlantic coast at Woods Hole Massachusetts during the years 1931–34. The calculated

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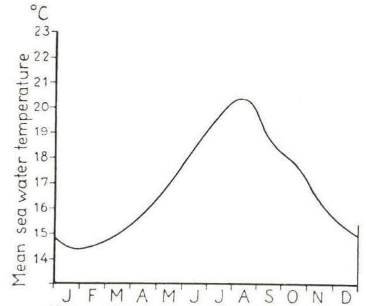
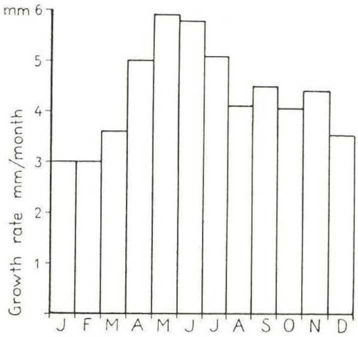
*) "with volume" would be more correct.

growth rate is shown on fig. 29 together with the surface temperature of the ocean and the breeding season according to FIELD (1911) and FISH (1925) ("WOODS HOLE" 1952).

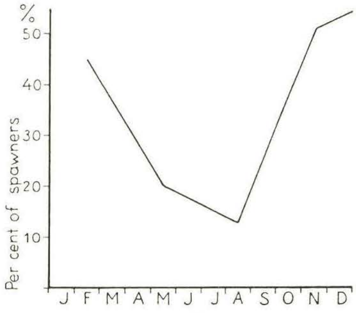
It should be emphasized that the studies on *M. californianus* and *M. edulis* were carried out on two different species in very different environments. A detailed record of the discussion of the evidence of the two growth rate curves



Sea water temperature, La Jolla California («Woods Hole 1952»)

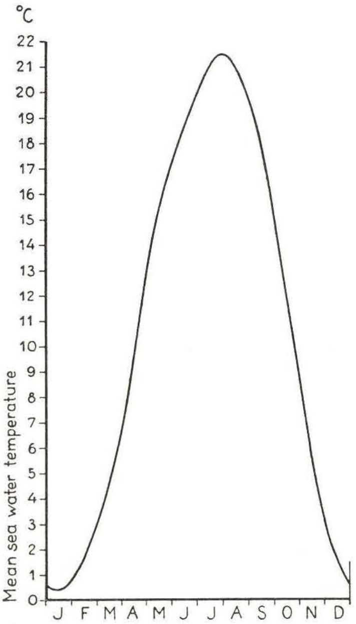


Mytilus californianus
La Jolla, California
Growth rates (RICHARDS 1946)

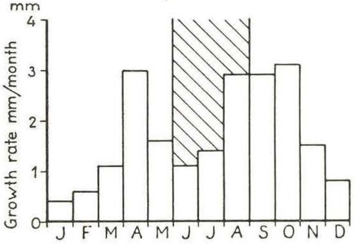


Mytilus californianus
La Jolla, California, Pier colony
Averaged percentages of spawners for three month periods (YOUNG 1946)

Fig. 28.



Sea water temperature,Woods Hole



Mytilus edulis L
Woods Hole, Massachusetts
Growth rates (RICHARDS 1946)
▨ Spawning period (FIELD 1911, FISH 1925) & Sea watertemperatures (SUMNER, OSBURN & COLE 1911) From »Woods Hole« 1952.

Fig. 29.

by RICHARDS (1946) and members of the staff at WOODS HOLE is published in Woods Hole Contribution No. 580, and will not be given here. Except for COE & FOX those concerned obviously agreed that there is some correlation between variation of temperature and growth. In the case of *M. californianus* COE & FOX believe that there is an inverse relationship between growth and temperatures above 20° C. Attempts have further been made by these workers to correlate the growth variations with other factors such as diatom concentration, solar radiation etc. In the case of *M. californianus* COE & FOX found the only positive correlation to be with the nutrient supply. RICHARDS (1946, p. 370) just touches on the possibility that the reduced growth rate which periodically occurs in both species may result from less energy being available for growth due to sexual activity. From "WOODS HOLE" (1952) the following is quoted: "The growth curves do not follow the temperature cycle very exactly. This may indicate that some factor other than temperature, such as the nutrient supply, is influencing the growth rate".

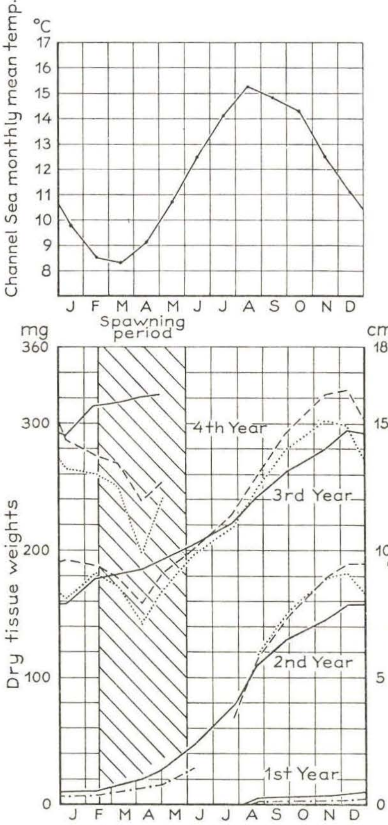
The present writer agrees with RICHARDS in his statement that no direct correspondance should be expected for instance between the dinoflagellate abundance and the growth of *Mytilus*. There is, moreover, very little evidence on lack of nutrient supply being responsible for the depression of growth rates in the two species mentioned, since the depressions occur at a time of the year when sufficient nourishment should be available. It is suggested, therefore, that the apparent coincidence of decline in growth rate and sexual activity is significant and should be correlated. The most simple, and likely explanation is that the energy required for reproduction reduces the growth rate during the breeding period. Sexual activity may thus mainly be responsible for the lowered growth rate in *M. californianus* during the summer. This is in agreement with the statement set forth by COE & FOX (1942, p. 24) that some of the growth rings on the shell of this mussel, and the corresponding cessation in growth, may indicate spawning periods. It must be admitted that the data on spawning in *Mytilus californianus* may have been too much generalized. In this connection the curve shown on fig. 28 has only been used to indicate the period in which the main spawning has probably taken place. Since the curve for the "Pier Colony" of *Mytilus* is very similar to that of the "Rock Colony", but different from the one from 'Alligator Head" (YOUNG 1946), the "Pier Colony" spawning has been considered relatively close to the mean spawning period.

The reaction of *Mytilus edulis* to variation in salinity, as far as growth is concerned, is indicated on the graph fig. 27. Growth rate in relation to duration of life and environmental factors such as salinity and nutrient supply has been treated by FISCHER-PIETTE (1941) in *Patella* and *Mytilus*.

The growth of **Littorina littorea** has been thoroughly studied by H. B. MOORE (1937) near Plymouth at the following locations:

A. Trevol. Mud flat in the middle of St. John's Lake, opposite Trevol Pier at mid-tide level. On most of the ground there is no macroscopic algal growth.
B. Drake's Island. Stony beach on the north side of the island, medium amount of Fucoid growth, mid-tide level to mean low water of neap tides and spring tides.
C. Yealm Misery Point. About mean low water of spring tides. Very little Fucoid growth. The *Littorina* cluster in very large numbers on *Fucus*. A tidal stream of about 2 ½ knots maximum flows past the point.

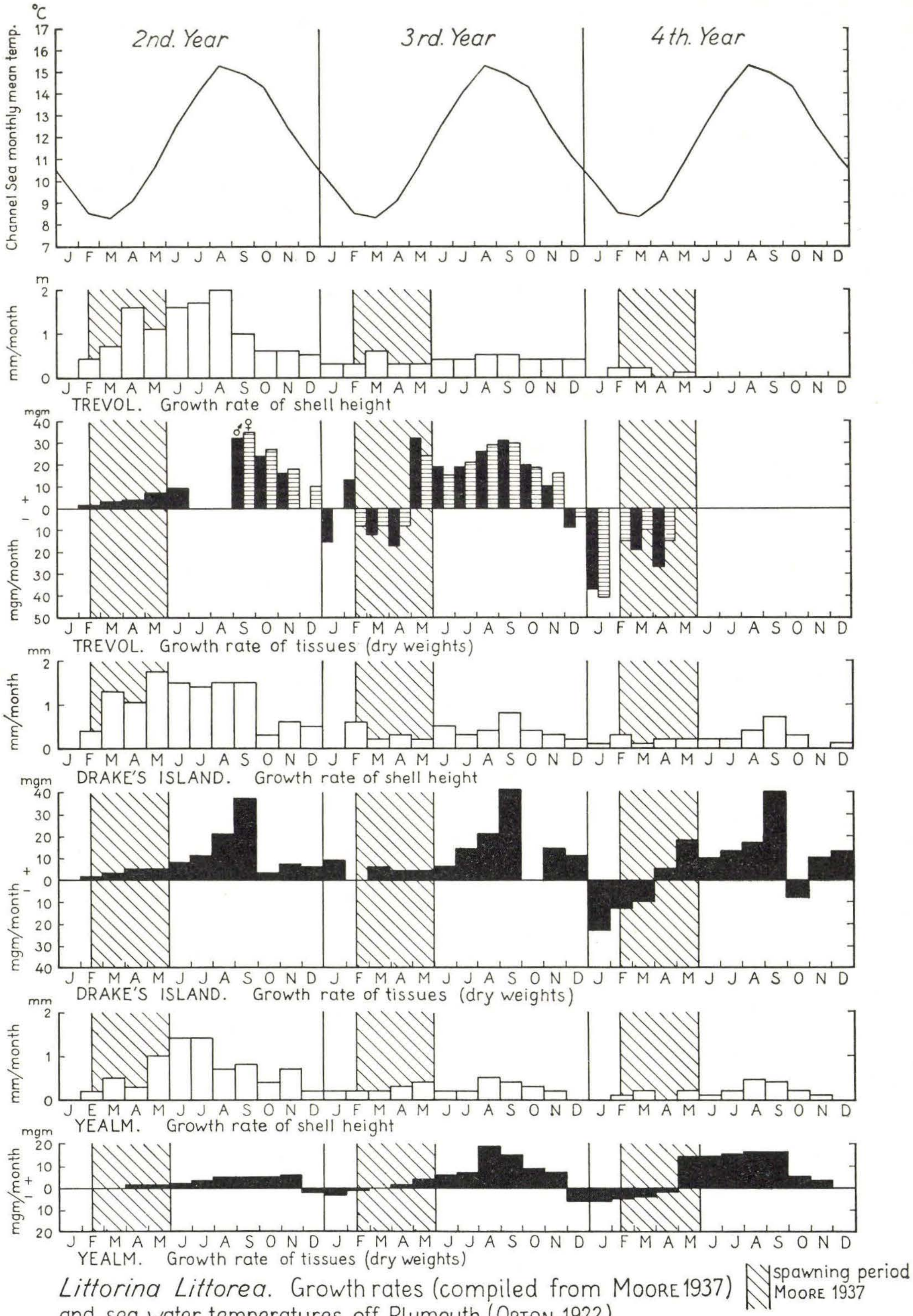
MOORE illustrates the growth of *Littorina* by means of the cube of the height and by the tissue growth, as for instance shown in fig. 30 (copied from MOORE), which displays the conditions in successive year groups at Trevol. The values are calculated from monthly measurements of representative samples of *Littorina* that were collected from Aug. 1934 to June 1936. There is good correlation between tissue growth and the cube of shell height. The decrease in tissue weight from February to May in the 3rd and 4th year groups is due to spawning activity as clearly shown by MOORE. The dependence of growth on temperature is not so striking in this mode of illustration, and MOORE's graphs have therefore been used for the calculation of approximate growth rates. For this purpose height cubed and tissue weight for the middle of each month were read off from the curves, and the height was calculated. On the basis of the figures thus obtained, representing approximate monthly means, growth rates were calculated for shell height and tissue weight, and expressed in mm/month and mgm/month respectively. This illustration of growth (fig. 31) is thus comparable with the growth curves shown above for *Cardium* and *Mytilus*. It should be noticed, however, that in the present case the measurements are made on different year classes of *Littorina* during periods of 15, 16 and 23 months respectively at Drake's Island, Yealm and Trevol, and not on single year classes that are followed for four years.



Littorina littorea. Trevol, Plymouth. Growth of the shell (height^3) and the tissues in successive year groups.
——— Shell height^3
–·–·– Tissue weights, males & females
.... " " males
– – – – " " females
(Acc. to MOORE 1937)

Fig. 30.

The graphs fig. 30 and 31 suggest that the rate both of shell and tissue growth are related to the annual temperature cycle. The main growth apparently takes place during the months of August and September when the sea temperature is at its highest, and growth is at a minimum during the period of minimum temperatures and the breeding season. Growth seems in general to be greatest in the second and third year groups, except that the population at the Yealm exhibits maximum growth in the third and fourth year groups. It might be assumed, therefore, that maximum growth occurs during the second or third year in *Littorina*, and the conditions at the Yealm may reflect overcrowding and a harder struggle for either room or food than in the two other locations. This would explain why the oldest and most vigorous group grows mostly at the Yealm. Another interpretation is, that the salinity differs in the three



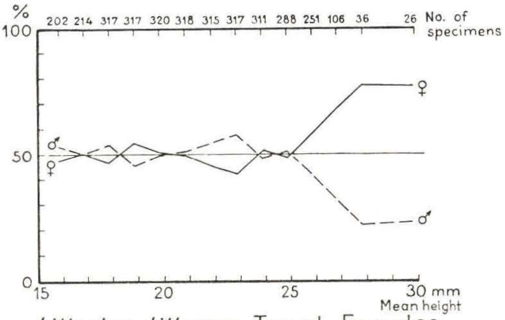
Littorina Littorea. Growth rates (compiled from Moore 1937) and sea water temperatures off Plymouth (Orton 1922)

Fig. 31.

places, and that estuarine conditions prevail in the Yealm area, whereas salinity is more normal at Trevol and Drake's Island.

MOORE's measurements also reveal that the females of *Littorina littorea* attain a greater final size than the males; this is illustrated by graph fig. 32.

The investigations by MOORE are very important. Similar investigations should also be carried out in other areas in order to determine whether the principles suggested by MOORE are generally applicable. Research of this kind should be followed by hydrographic studies to secure an adequate interpretation of the results.



Littorina littorea. Trevol. Females and males in relation to mean height (MOORE 1937 p. 731)

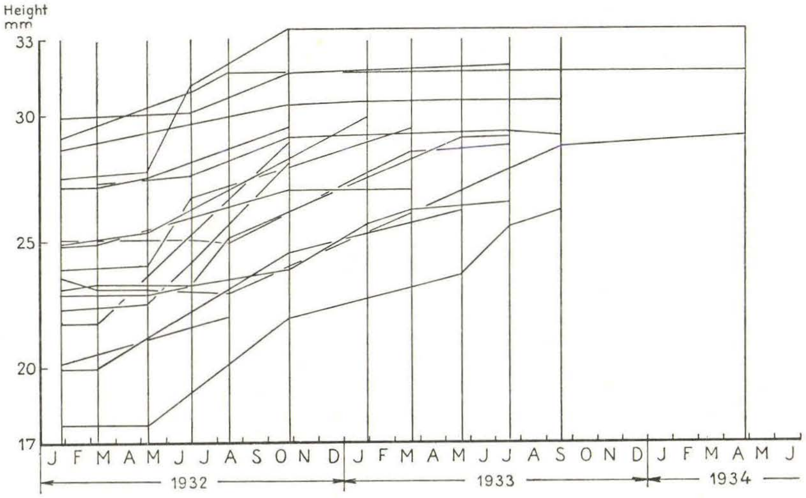
Fig. 32.

An indication of the reaction of *Littorina littorea* to different salinities regarding growth is shown by fig. 27, p. 366 Maximum size obviously decreases with decreasing salinity.

Purpura lapillus has been the object of very incisive studies by MOORE (1936, 1938). This gastropod differs from *Littorina* in that as growth ceases at sexual maturity. The growth rate is rather difficult to determine in this species partly due to the fact that it appears impossible to separate individual year groups as in *Littorina*. MOORE therefore marked individual animals in various ways and measured their increase in shell growth at intervals. The small sizes had to be kept in laboratory tanks whereas the larger ones were living in nature. Observations were made on Drake's Island near Plymouth and on the shores of the Isle of Man. The figure showing the growth of individual *Purpura* on the shore of the Isle of Man, fig. 3 in MOORE's paper from 1938 (a), is reproduced here as fig. 33. The graphs relate height to the time of observation, and illustrate how growth ceases in various individuals at different shell heights corresponding to the onset of maturity in the individual concerned. The numbers of individuals and measurements is too small to warrant the calculation of growth rates for comparison with temperature variations. In this connection it is noteworthy, however, that the steepest parts of the curves indicating the most rapid growth occurs in spring and summer while the flatter parts of the curves are mainly found opposite cold periods of the year. This might suggest direct or indirect correlation of growth with temperature variations, as in *Littorina*, *Mytilus* etc.

Fig. 34 shows the annual variation in tissue weight of mature *Purpura* and also the spawning period. The weight minimum is doubtless mainly caused by spawning activity. The low temperature and maybe a lack of nutrient supply during winter may, however, be responsible for part of the tissue weight decrease.

MOORE's investigation of the influence of the diet of *Purpura* on the shell colour is now a classical study (1936 a). In a convincing manner MOORE succeeded in proving that increase of *Mytilus* in the diet of *Purpura* increased the proportion of the two shell colour types: brown-black and mauve-pink, and that specimens of these types, which were put to feeding on *Balanus* or *Chthamalus* gradually lost their pigmentation and grew white. The factor responsible



Purpura lapillus. Growth of individual animals on the shore at Point Erin, Isle of Man. (Acc. to MOORE 1938)

Fig. 33.

for yellow shells appeared, however, to be very doubtful, although there seemed to be some correlation with exposure to wave action.

The effect of salinity on growth has been treated above in the cases of *Cardium edule*, *Mytilus edulis*, and *Littorina littorea*. The graph fig. 27 on p. 366 shows, moreover, maximum sizes of *Buccinum undatum*, *Mya arenaria*, and *Tellina baltica* at different salinities. All curves agree in showing decrease in size if the salinity falls below the normal values for the marine areas of distribution.

From this review of growth in Pelecypoda and Gastropoda we may conclude the following:

1. Growth is marked by seasonal rythms.
2. Maximum growth rate may be related to the temperature optimum of the individual species.
3. The annual size increment reaches a maximum at a certain intermediate age, after which it declines.
4. The age at which the annual growth increment is at a maximum may be definite, but considerable variation occurs in some species, as shown for instance by *Littorina littorea*.
5. Spawning periods are generally characterized by decreased tissue and shell growth, in those cases where growth does not cease altogether at sexual maturity.
6. Salinity may affect growth considerably. Salinities above or below the normal range of a species generally result in decreased size and shell thicknesses.
7. Different salinities may result in different shell shapes and colours.
8. Different habitats may give rise to different morphological types of a species.
9. Diet may in some species act upon shape and colour of the shell.

It is not known whether the variations mentioned under 6–9 are hereditary. Probably most are not, but knowledge of such variation is nevertheless extremely important for the geologist and paleontologist.

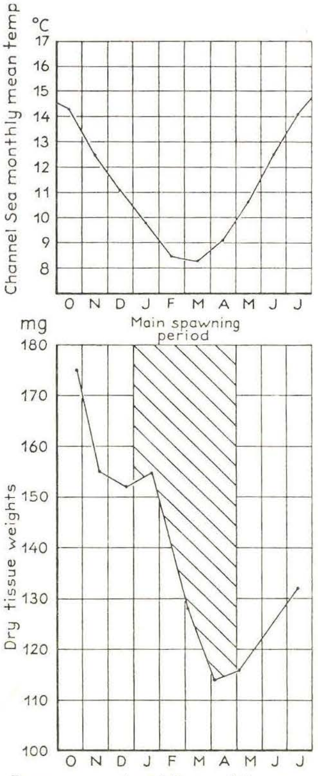
B. Reproduction

The reproduction of Pelecypoda and Gastropoda has been the subject of studies by N. Odhner (1914), M. V. Lebour (1932 a–c, 1933 b–e, 1937 a–b, 1938 a–b), B. Werner (1939), G. Thorson (1933, 1934, 1935, 1936, 1946), C. Barker Jørgensen (1946), and others. The different phases in reproduction have especially been discussed by Lebour, and Thorson, and particularly Thorson's paper of 1946 gives a comprehensive record on this topic. (l.c. p. 417, etc.).

Reproduction may be subdivided into the following phases: a. ripening of sexual products, b. fertilisation, c. spawning, d. hatching, e. larval stage, and f. metamorphosis. It is well known, that several prosobranchs for instance hatch in the crawling stage, and that the larval stage is passed in the egg or the egg capsule (see Lebour 1937 b, p. 110, and Thorson 1936, p. 38, and 1946, p. 240). The pelagic larval stage has thus been abandoned in some species, and the subdivision above gives accordingly the aspect of a complete succession of phases that may be modified in various regards in some species.

The influence of environment upon the individual phases of reproduction is still little known, but it is generally realized that salinity and temperature have important effects. The effect of some environmental factors will be illustrated in the following.

Food is an important prerequisite for growth, and consequently for development of the sexual products of the animals. In the case of *Littorina littorea* off Plymouth it is significant that the first spawning apparently occurs when the animal has attained a certain size regardless of age (viz. when the tissue weight is about 130–180 mg) (see p. 369). In *Purpura lapillus* we find an example of growth ceasing at maturity, with the age of maturity being dependent on diet (see Moore 1936, 1938). No such examples are known in Pelecypoda.



Purpura lapillus. Misery Point, Yealm, Plymouth.
Seasonal variation in tissue weight of mature (non-growing) individuals, 25.5mm high.
(Acc. to Moore 1938)

Fig. 34.

Salinity must undoubtedly be within certain limits to enable the eggs to develop. The salinity range for the development of the eggs is in most cases probably narrower than the range for survival of the adults.

Hayes' (1926) experiments with eggs of *Littorina littorea* are illustrative of the effect of salinity on development. The eggs were kept in bottles with sea water diluted to salinities of 0, 5, 10, 15, 20, 25 and $30^{0}/_{00}$, and the bottles were hung off the breakwater at the Atlantic Biological Station St. Andrews, New Brunswick, during the summer of 1925. It appeared that no development took place in the bottles with salinities of 0 and 5, and no development past early segmentation stages could be found with salinity conditions of 10. In water with a salinity of 20 and 25 development progressed normally although the lowered salinity retarded the development somewhat. In normal water the veliger hatched on the sixth day.

The lower limit of the salinity range for the larvae of *Aporrhais pes pelicani*, *Montacuta bidentata*, *Eulimella nitidissima*, *Anomia squamula*, and *Cultellus pellucidus* from the Öresund has been stated to be $20^{0}/_{00}$ by Thorson (1946, p. 382). Spärck (1925) kept larvae of *Ostrea edulis* alive for 8 days in water of salinities $23^{0}/_{00}$ and $19^{0}/_{00}$, whereas larvae only lived for 3–4 days in $16^{0}/_{00}$ saltwater, the lower limit of survival is thus apparently about $25\ ^{0}/_{00}$.

Temperature. The significance of temperature as a controlling factor in breeding has been treated by many authors. Apellöf (1912) drew attention to the fact that the eggs of *Cucumaria frondosa*, an arctic relict Holothurian living on the boreal coasts of Norway, would not develop in water of a higher temperature that 13° C and that the main breeding period of this animal on the Norwegian coast is in February and March when the temperature of the sea is at a minimum. He concluded that the vegetative processes of the adult animal are adapted to temperatures higher than those prevailing in the main area of distribution of the animal in the Arctic, while reproduction is restricted to the coldest part of the year at the Norwegian coast and thus indicates less adaptability of reproduction in relation to temperature. Apellöf discussed also the breeding period of *Ostrea edulis* and *Tapes decussatus* in southern Norway and mentioned that these southern forms apparently need a temperature of about 20° C for reproduction.

Orton (1920) attempted to relate breeding to temperature and geographic distribution. Among other facts, he mentioned that *Ostrea edulis* breeds earlier in southern areas than in northern waters. He stated, moreover, that this species begins to breed at a temperature of about 15°–16° C, and that it continues its activity as long as the temperature is above that figure. Data on the reproduction of *Cardium edule*, *Patella vulgata* etc. are given, and Orton finally concludes that a temperature stimulus may be the normal impulse for inducing sexual activity in marine animals assuming normal biological conditions. Orton clearly regarded particular temperature limits as critical and the significance of temperature is accordingly that of intensity.

Spärck (1925) is apparently of a somewhat different opinion. In the case of *Ostrea edulis*, he thinks that strictly speaking, reproduction is independent of a particular temperature. According to Spärck the critical factor of temperature is one of capacity, not intensity, i.e. the total accumulation of heat.

Runnström's investigations (1928) of the spawning seasons of various marine animals living on the Norwegian coast are of outstanding importance. He arrived at the conclusion that the arctic-boreal species breed during winter, the boreal species during spring, and the Mediterranean species during summer. Twelve species were examined among which *Mytilus edulis* was the only mollusc.

In addition to the observations on breeding Runnström also made experiments in the laboratory on the development of eggs under various temperature conditions, and thus determined the temperature range for this stage of reproduction. In the case of *Mytilus edulis* it appeared that at 1°–3° C the development was pathologic, the lower limit for normal development being about 4° C. The upper limit proved to be about 16° C, above which temperature the eggs also developed pathologically.

On the basis of his experiments RUNNSTRÖM stated the following temperature ranges for the normal development of eggs:

Three arctic species: −1°–+11° C.
Four boreal species (including *Mytilus edulis*): 3°–16° C.
Five mediterranean-boreal species: 7°–23° C.

RUNNSTRÖM thus confirms APELLÖF's suggestion concerning correlation of spawning season with geographic distribution, and he concludes that in all probability restricted spawning seasons mean that particular ranges of temperature are the main controlling factors. However, RUNNSTRÖM also states how important it is to study the reaction of each individual stage of reproduction to temperature. The experiments by PELSENEER (1901) with larvae of marine animals from the English Channel are mentioned. PELSENEER concluded that the younger the larvae are, the more sensitive they are to temperature. PELSENEER made experiments with 13 species of molluscs: 2 cephalopods, 8 gastropods, 1 pelecypod, and 9 nudibranchs. He subjected 3 nudibranchs and the following 2 gastropods to low temperatures: *Littorina obtusata* (embryo near hatching) and *Patella vulgata* (three days old larvae). Both gastropod larvae resisted a temperature of −2.5° C. The temperature could not be lowered more due to freezing, and an admixture of salt would have killed several of the larvae. Upper death limits were found by experiment in the following 6 gastropods and 1 pelecypod (l.c. p. 282):

Species	Larval stage	Upper death limit	Zoogeographic range acc. to BRÖGGER (1901)
Patella vulgata	two days old larvae	34° C	boreal
Patella vulgata	four days old larvae	36°	
Nassa reticulata	embryo before rotating	30°	lusitanian
Nassa reticulata	hatched veliger	35°	
Littorina littorea	veliger near hatching	37°	boreal
Littorina obtusata	embryo beginning to rotate	30°	
Littorina obtusata	embryo near hatching	35°	
Lacuna pallidula	veliger near hatching	32°	boreal
Lamellaria perspicua	veliger near hatching	35°	(lusitanian)*)
Pholas candida	trochosphere	32°	lusitanian

PELSENEER mentions the occurrence of heat stupor and cold stupor long before the lethal temperatures were attained (p. 287). He gives, however, no exact figures for these temperature levels.

It should be mentioned that EKMAN (1935, p. 173, and 1953, p. 113) also drew attention to the difference in reaction to temperature in the adult and reproductive stages of marine animals. He distinguished consequently between vegetative and reproductive eurythermy and stenothermy.

THORSON (1946, p. 421) also discussed the effect of temperature upon reproduction. Of particular interest is his statement that breeding in *Mya truncata* and *Saxicava arctica* in arctic East Greenland may not be dependant on temperature as a spawning inducer, although spawning is clearly limited to the summer season. This opinion is supported by various arguments based

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*) *L. perspicua* not mentioned by BRÖGGER.

on the hydrography of the surveyed fiords. The fact that spawning began in May at temperatures as low as those observed earlier in January, when THORSON started his investigations, is considered to disprove temperature as a (direct) regulator of breeding. Phytoplankton maxima that occurred simultaneously with spawning in *Mya* and *Saxicava* led THORSON to the assumption that phytoplankton increase may induce spawning in marine invertebrates.

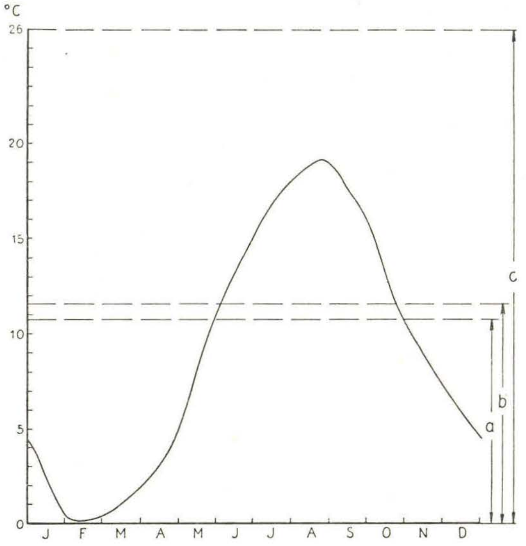

Fig. 35. **Thermal intervals of cold water species *A*.** Seasonal sea water temperature curve of temperate area, and thermal interval of: period of spawning (*a*) larval stage (*b*) adult stage (*c*).

The mechanism of temperature control may not be a very simple one. Heat capacity, heat intensity, and temperature changes have been suggested as significant. None of the views hitherto set forth in this connection appear, however, to explain adequately all observations. It may be reasonable to assume heat capacity and intensity as well as temperature changes to be important, and it must furthermore be anticipated that temperature control may work in different ways in different species.

The reaction of arctic species to temperature at their southern limit of distribution indicates that the temperature requirements in such species may not be dominated by heat capacity demands (see for instance JENSEN 1905b, *Yoldia arctica*). A general suggestion that heat capacity is the critical factor may thus be wrong. It is also a question whether temperature changes are generally critical, provided that the changes do not exceed certain critical temperatures or rates of change, and it is certainly inadvisable to regard specific temperatures as inducers of the different physiological processes which contribute to reproduction.

From a general viewpoint it seems to be safest at present to accept the fact that the physiological processes of different animals are adjusted to specific temperature ranges by some means or other, and that each individual process may continue as long as the temperature is within its specific range. In the case of reproductive processes it is obvious that temperature limits may be particularly critical, since annual temperature cycles may result in restricted activity, reproduction being confined to short periods of the year. The result of this effect on the geographic distribution of marine life has been treated by APELLÖF (1912), ORTON (1920), HUTCHINS (1947) and others, and it is also briefly treated on p. 387 in this paper.

The diagrams fig. 35 and 36 illustrate some of the fundamental relationships connecting the annual temperature cycle, the temperature requirements of the main reproductive stages, the season of reproduction, and the geographic distribution of marine mollusca. Both diagrams refer to the same temperate marine area, the seasonal temperature curves of the water are accordingly identical in the two figures. Fig. 35 illustrates the temperature characteristics of a species that lives near its climatic warm limit, and fig. 36 shows the same features in a species that lives near its climatic cold limit.

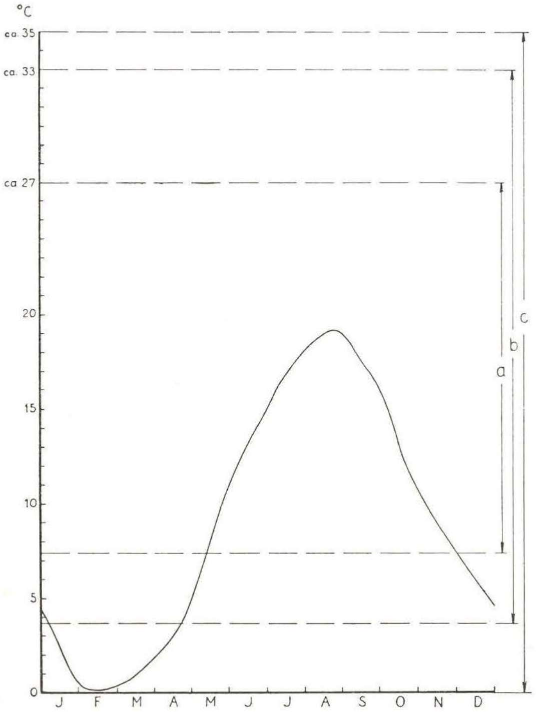

Fig. 36. **Thermal intervals of warm water species *B*.** Same sea water temperature curve as in fig. 35 and thermal interval of: period of spawning (*a*) larval stage (*b*) adult stage (*c*).

In accordance with the statements above regarding the salinity requirements of a species, we may accept that each reproductive stage as well as the adult stage is also adapted to a particular temperature range that briefly may be called the thermal interval of the stage. The thermal interval of a stage is signified by various thermal values viz. upper and lower limits of survival, an optimum value lying between, and possibly some other significant temperatures. Our present knowledge regarding thermal intervals is very fragmentary. It must, however, be anticipated that a considerable number of combinations of values and limits will occur, and it is therefore inadequate to characterize a species simply as eurythermal. The definitions of eurythermy and stenothermy are in any case arbitrary, and their application to particular cases may be biased by accidental geographic phenomena. At the limits of its distribution we may be inclined to designate a species as stenothermal, whereas it may be regarded as eurythermal in the center of its geographical range. It would accordingly be more correct to express temperature dependency by means of thermal intervals and corresponding thermal values for each stage of life in the animal concerned. To characterize a species by a complete set of thermal ranges is one goal of ecology, but one that is very far from being realized.

Ekman's (1935, 1953) discrimination between the thermal characteristics of reproductive and vegetative stages is an advance in the right direction. It should, however, be remembered that Ekman's distinctions are based on subjective judgement of where the boundary between stenothermy and eurythermy should be placed, and even Parr's subdivision of stenothermy and eurythermy suffers from being more or less subjective (Parr 1933, p. 80).

A species may be related to the following fundamental thermal intervals:

1. Period of spawning —interval *a*.
2. Larval stage —interval *b*.
3. Adult stage —interval *c*.
4. Period of ripening of sexual products —interval *d*.

The length of time required for development from one stage to the next should perhaps be added to the above list. The duration of each stage may vary with temperature, provided all other conditions are equal, as is illustrated by the well known case of warm water forms developing more slowly at lower temperatures (see e.g. SPÄRCK 1925, p. 44 etc., and THORSON 1946, p. 452). The rate of development may be more or less proportional to the excess of temperature above a certain minimum in possibly most species (see e.g. ALLEE etc. 1949, p. 111 etc.), which is in agreement with the concept that a certain amount of heat is necessary for the completion of a stage (theory of the thermal constant: time × temperature = constant). For a general outline of the problems involved the reader is referred to textbooks on ecology, e.g. HESSE et al. 1951, ALLEE et al. 1949. While it is not intended to enter into a general discussion here, the significance of the duration of the larval stage will be briefly discussed in the following. The length of time required in the larval stage has for practical reasons been indicated as constant, 2 months, regardless of the temperatures at which development takes place.

The conditions shown in fig. 35 reveal that the cold water species *A* may spawn at any time from about November to about May, and the emerging larvae may survive between about October and June. Only larvae that have emerged before April will complete their development before the temperature of the water rises above the upper death limit of the larval stage due to the two months required in the larval stage.

The first eggs shed, i.e. the ones shed shortly after the temperature has fallen below the upper thermal limit of the spawning stage in November, have the best chance of survival. The resulting individuals consequently form the main stock of the next first year group. Presupposing that this group becomes sexually mature it may spawn and contribute to the brood in the second autumn. As time goes on the population of species *A* may thus be adjusted to the local thermal conditions, and the main spawning will presumably take place during the time of declining temperature in the autumn and winter. A favourable nourishment supply during the summer months may also encourage tendencies toward spawning in the autumn by providing the physiological basis for such acitivity.

Fig. 36 illustrates the reproductive characteristics of the warm water species *B* which, as is mentioned, is living near the lower thermal limits of its reproductive stages. The diagram shows that spawning may take place from about May to December. Development of the larvae may proceed until about January, but only the larvae that have emerged before November survive, due to the time required by the larval stage. As in species *A*, it is obvious that species *B* may gradually become adjusted to summer spawning, since the eggs shed early in summer will have the best chance for further development.

It is of particular interest to note that larvae of species *A* and *B* may be present contemporaneously in the plankton, viz. during November and December, in spite of the fact that species *A* is a cold water form, and species *B* a warm water form.

The spawning of *Mya truncata* in Danish waters (BOYSEN JENSEN, 1920, p. 35 etc., BARKER JØRGENSEN, 1946, p. 306) could be explained in accordance with species *A* above, and that of *Pecten opercularis* in accordance with species *B* (BARKER JØRGENSEN ibid. p. 306). Larvae of these two species may occur contemporaneously in the Öresund (this was the case in October 1941). Many similar examples may be found in temperate waters where cold and warm species overlap.

It should be realized that the thermal limits discussed above must be statistical mean values. The temperature requirements of single individuals differ more or less and therefore may deviate from the mean values for the species, and also the thermal intervals may not be identical in different parts of the geographical range of a species due to the development of local races.

From the above we can conclude that seasonal spawning may be common in areas where there is considerable seasonal variation of temperature. However, seasonal spawning need not be directly governed by thermal regulation. If a species lives all the year round with temperature conditions between the thermal limits of all its stages of development, other potential cyclic factors, like food supply etc., which affect reproduction may cause seasonal spawning. *Mya truncata* in East Greenland may be mentioned in this connection (Thorson 1946, p. 424). It is possible that the seasonal variation of food supply in Greenland waters is responsible for the seasonal spawning of *Mya*, as the animal lives above the lower and below the upper thermal limit for spawning activity throughout the year. This problem has, however, not yet been settled satisfactorily.

In accordance with the statements above, it should be stressed that the writer does not consider specific temperatures to be spawning "inducers", but they are regarded as spawning "requirements". The complete series of thermal intervals covering the developmental stages of a species control reproduction. The thermal intervals act as a set of screens of different meshes which determine the survival, but, contrary to e. g. mechanical sorting, nature initiates sorting with the smallest mesh, i.e. the narrowest thermal interval, when reproduction starts.

C. The Pelagic Larval Stage

The pelagic larval stage in some British pelecypods and gastropods has been studied by M. V. Lebour (1932–38), and Thorson (1946) has treated species living in Danish waters in great detail. The effect of environment on this stage has been discussed by Thorson (1946, p. 431–47) and reference is therefore made to his treatise.

The pelagic stage is of considerable interest as it represents that period of development in Mollusca during which the widest dispersal of the species may take place, and its significance with respect to geographic distribution is accordingly obvious.

As mentioned on p. 378 the duration of any developmental stage may depend upon temperature. The relationship between temperature and the duration of the larval stage have not yet been determined. However, Thorson (1946, p. 453) has compiled the data shown in the following table:

Table 4. Duration of Larval Stage (from Thorson 1946)

Gastropoda:	Locality	In (E)xperiment or (N)ature	(n)ormal fertilization	Temperature	Duration of larval stage	Author
Rissoa membranacea	Plymouth	E	n	?	3 weeks or less	Lebour 1934
Nassa reticulata	Isefjord	N	n	?	2–3 weeks	Thorson 1940
	Plymouth	E	n	?	abt. 2 months	Lebour 1931
Nassa incrassata	Plymouth	E	n	?	at least 2 months	Lebour 1931
Littorina littorea	Öresund	N	n	?	4–5 weeks	Thorson 1940
	Isefjord	N	n	?	abt. 4 –	Thorson 1940
Bittium reticulatum	Isefjord	N	n	?	abt. 3 –	Thorson 1940

Pelecypoda:	Locality	In (E)xperiment or (N)ature	(n)ormal fertilization	Temperature	Duration of larval stage	Author
Mytilus edulis	Massachusetts	N ?	n	less than 20° C	abt. 3 weeks	Nelson 1928
	Isefjord	N	n	?	abt. 4 weeks	Thorson 1940
Mya arenaria	Massachusetts	N ?	n	less than 20° C	abt. 3 weeks	Nelson 1928
	Isefjord	N	n	?	abt. 2 weeks	Thorson 1940

Thorson (1946, p. 415) has made an estimate of the average duration of the pelagic larval stage of invertebrates living in Danish waters. He states that the duration may be about 3 weeks in summer, and 2 to 3 months in winter. This must, however, be regarded as very approximate, and much research must be carried out before more exact data can be furnished.

During the pelagic stage the larvae may be widely dispersed by currents, and the larvae may also themselves contribute to transportation on a minor scale by swimming with their velum. Consequently the greatest potential dispersal will be obtained in species with a lengthy pelagic stage. Very little is apparently known about the distances travelled by pelagic larvae. The only observation in this connection of which the writer is aware, being that by Craven (1877, p. 124) who observed several "sinusigera"-larvae, the pelagic larvae of prosobranchs probably living in shelf areas of the Indian Ocean, drifting in the sea in a position 11° S 80° E, more than 1300 kilometres from the nearest land, the coral islands of Pona Molulique. It may be significant that the shells of the pelagic larvae observed by Craven all have relatively many whorls as shown by his illustrations:

Species		Plate	fig.	Approximate number of whorls
Sinusigera reticulata	Craven	III	3	5
Sinusigera perversa	–	III	4	6–7
Sinusigera minima	–	III	5	4
Sinusigera cancellata	–	III	2	4
Sinusigera Broeckiana	–	IV	6	4
Sinusigera striata	–	IV	4	5
Sinusigera dubia	–	IV	3	6
Sinusigera d'Orbigny	–	II	3	3

Lemche (1948, p. 11) has made an observation which is of particular interest, he states that the protoconch of the tectibranch gastropod *Diaphana minuta* from depths of more than 1000 m in the North Atlantic near Iceland may have more, or larger whorls than the shells of individuals living in shallow water. Lemche believes this to be due to retardation of metamorphosis on account of the larvae remaining in deep water at the normal time of metamorphosis, when it should settle on the bottom. Lemche's viewpoint is supported by Thorson (1946, p. 466).

Through his studies of Danish pelagic larvae Thorson (1946, p. 199) arrived at the conclusion that Pyramidellid larvae with a pelagic stage have a large, sinistral, scalariform shell exposed, whereas the *Pyramidellidae* with non-pelagic larvae have no such larval shell visible at the apex.

The fact that the larval part of molluscan shells is in many cases easily recognizable in the fossil state renders knowledge of the larval stage highly important in the interpretation of this feature. Fossil species which had a long pelagic stage and correspondingly great power of geographic dispersion must be among the most useful paleontologic and stratigraphic index forms.

D. Substratum Requirements of the Adult Stage

Marine pelecypods and gastropods may be subdivided into two large groups with regard to the substratum: animals belonging to the infauna that includes species living in the bottom deposits, and the animals of the epifauna living on the bottom, on stones, rocks, seaweeds etc. (C. G. Joh. Petersen 1918). *Ostrea edulis*, and species of the genera *Solen*, *Patella* and *Acmaea*, as well as several others, are rather fastidious in selecting their substratum, but most molluscs will apparently settle in rather different environments, and at a wide range of depths. For example *Cardium edule* is able to live in mud or detrital mud and sand, and the same is true of *Corbula gibba*, *Cyprina islandica*, and numerous other species. *Mytilus edulis*, a species that prefers attachment to stones, seeweeds etc. may under certain conditions be forced to settle on the level sea bottom. A modern change of biotope has been mentioned by Dexter (1947, p. 273) from the coast at Cape Ann, Massachusetts, where the disappearance of the eel grass *Zostera marina* in 1932 due to an epidemic, forced *Lacuna vincta*, which formerly lived on it, to change to the brown alga *Laminaria digitata*.

These examples are chosen at random to illustrate the general adaptability of the animals concerned. It should be emphasized, however, that each species will probably thrive best with particular combinations of bottom configuration, depth, currents, etc. Also the adaptability of a species concerning substratum in most cases is confined to either the infauna or epifauna environment, although some animals, such as predatory snails, may succeed well in both environments.

E. Adaptation

The topics treated above are all more or less illustrative of the power of adaptation. One of the main statements of animal ecology is that the ability to adapt is particularly well demonstrated near distributional boundaries where limiting factors attain extreme values. Local races may develop under such conditions, and it is also probable that new species emerge. When dealing with adaptability we are therefore concerned with the inconstancy of species, and adaptation may have an important bearing on the evidence of fossil faunas, particularly when paleobiology is applied as a stratigraphic or paleogeographic tool.

Knowledge regarding the adaptability of marine invertebrates is apparently very scanty, and in the past efforts have been concentrated particularly on the study of acclimatization to temperature and salinity conditions. A general outline of adaptation could be obtained by study of the geographic distribution of a number of species and genera followed by a detailed investigation of the various environments, but the results obtained would have to be verified by experiment. The inductive part of the research on adaptation is, however, very laborious, and this may partly account for the scarcity of exact experimental data.

Adaptation in pelecypods and gastropods will not be treated in detail in the present section, which will be devoted to a brief discussion of relevant physiological processes, while the geographic aspects of adaptation form the subject of the next section.

Osmotic adaptation. The modifications of osmotic behavior in species that are capable of living under a wide range of salinities has not apparently been studied in detail. Marine molluscs are generally in osmotic equilibrium with the surrounding sea water (KROGH 1939), and species that are able to migrate into brackish or abnormally concentrated salt water must accordingly develop adaptive features in those physiological processes which are related to osmotic regulation. There is apparently very little information available on this subject. According to REMANE (1940, p. 14) dilution of sea water, and corresponding lowering of osmotic pressure, may result in increased oxygen consumption in various animals, among which *Hydrobia jenkinsi* is mentioned. Whether this is a permanent or temporary change has not been stated.

Metabolic adaptation. It is well known that metabolism in marine animals is related to temperature. (A. KROGH 1914, A. GOLDSBOROUGH MAYER 1914, H. M. THAMDRUP 1935, G. THORSON 1936, R. SPÄRCK 1936). SPÄRCK's investigations on oxygen consumption in marine pelecypoda revealed characteristic metabolic reactions in individuals belonging to the same species, but living under different climatic conditions. He states that the oxygen consumption of *Mytilus edulis* from Danish waters is higher (related to temperature) than that of *M. edulis* from the warmer Mediterranean. Similarly *Astarte borealis, A. elliptica, A. Montagui* and *Saxicava arctica* from Greenland waters have a higher oxygen consumption (related to temperature) than individuals of the same species living in the warmer Danish waters. SPÄRCK relates these differences in metabolism to the development of physiological races. SPÄRCK's study suggests that the metabolism of the pelecypods mentioned may be adaptable to different temperature conditions. Reversing SPÄRCK's statement, and relating similar values of oxygen consumption to temperature it may be stated that oxygen consumption may attain nearly identical values within different local temperature ranges of the individual species. SPÄRCK's diagrams illustrate these relations. It is of interest to note that the difference between the highest and lowest temperatures to which a species may be able to adjust its oxygen consumption may be regarded as a measure of its thermal adaptability.

Although sufficient research has not yet been carried out in the field of metabolic adaptability in general, studies suggest that physiological processes other than oxygen consumption should, within limits, be adaptible to extreme environmental conditions. This renders deductions concerning paleo-environments based exclusively on fossil species a difficult task.

Discussions of thermal adaptation may be found in papers by VERNON (1899), A. GOLDSBOROUGH MAYER (1914), RUNNSTRÖM (1927, 1936), and EKMAN (1935, 1953); for further information reference is made to textbooks on animal ecology and geography. The inheritability of adaptive qualities is considered beyond the scope of this work.

3. GEOGRAPHIC DISTRIBUTION

The total geographic distribution of a species may be regarded as representing the sum of its dispersive and adaptive powers. The local variation in distribution within the geographic range of a marine bottom dweller may be mainly related to variation of a few environment factors such as substratum, depth, oxygen content of the water, dispersal power, enemies, etc. The location of the regional geographic boundary of a species is determined by the geologic history of the area of dispersal and the species, and by one or more environment factors varying beyond the limits controlling the survival of the species.

Temperature and salinity are undoubtedly the most significant factors controlling geographic distribution in marine biology on a regional scale. Salinity might be considered as a factor of lesser importance because brackish waters should not be included in the marine areas. However, since brackish transition areas attract considerable interest from a geologic point of view, the limiting effect of salinity upon the distribution of marine mollusca should also be treated in this connection.

A. Temperature Conditions of the Oceans

Uniformity and relatively slight oscillations of temperature are characteristic features of the water masses of the oceans (SCHOTT, 1935, 1942). From a physical point of view one may discriminate between the cold Arctic and Antarctic water masses located around the poles, with annual mean temperatures lying between −2 and +3° C, and the warm water masses located on both sides of the equator with maximum mean temperatures of about 25–28° C. These cold and warm water masses are more or less separate due to difference in density, although the salinity deficit of polar waters, ocean currents, wave action, etc. counteract the separation. The annual temperature oscillations of the surface water within the warm and cold water areas are very slight, and amounting to about 1° to 5° C.

The most complex temperature conditions in the oceans are found in the transition areas between warm and cold waters, these areas being characterized by greater annual temperature oscillations and by a more or less pronounced stratification. The annual mean temperature of the surface water in the transition zones is between 3° and 25° C, and the seasonal temperature oscillations 5° to 20° C. The areas of maximum oscillation (from 10°–20° C) are found in the northern hemisphere, in the western parts of the oceans and in the marginal seas around Europe. In a generalized way the transition zone in this hemisphere may be defined as the area between the Tropic of Cancer and the Polar Circle. This rough demarcation must be modified considerably in detail, especially in the North Atlantic on account of the effect of the Gulf Stream and the Polar Current.

Knowledge of the thermal gradient of the ocean, and the bottom temperature, is of paramount importance in dealing with the effect of temperature on the distribution of marine faunas. Data on bottom temperatures are very scarce, whereas it is possible to get an outline of water temperatures at depth, on the basis of observations made by deep-sea expeditions. Vertical thermal sections may thus be established for different parts of the oceans, see EKMAN (1953, p. 358). The writer has compiled similar sections for the North Atlantic on fig. 37 with special emphasis on the boundary between the cold and warm water areas around Iceland. It appears from these graphs that the temperature of the transition zone in the North Atlantic generally decreases rather rapidly from surface to a depth of 100 to 200 metres, dependent upon latitude and season. The thermal drop in these sections reaches a maximum (off Cape Finisterre) of about 6° and 7½° C down to 100 and 200 m respectively. Below 200 m the temperature of the warm water is between 4° and 17° C whereas the polar water has a temperature less than 2° C.

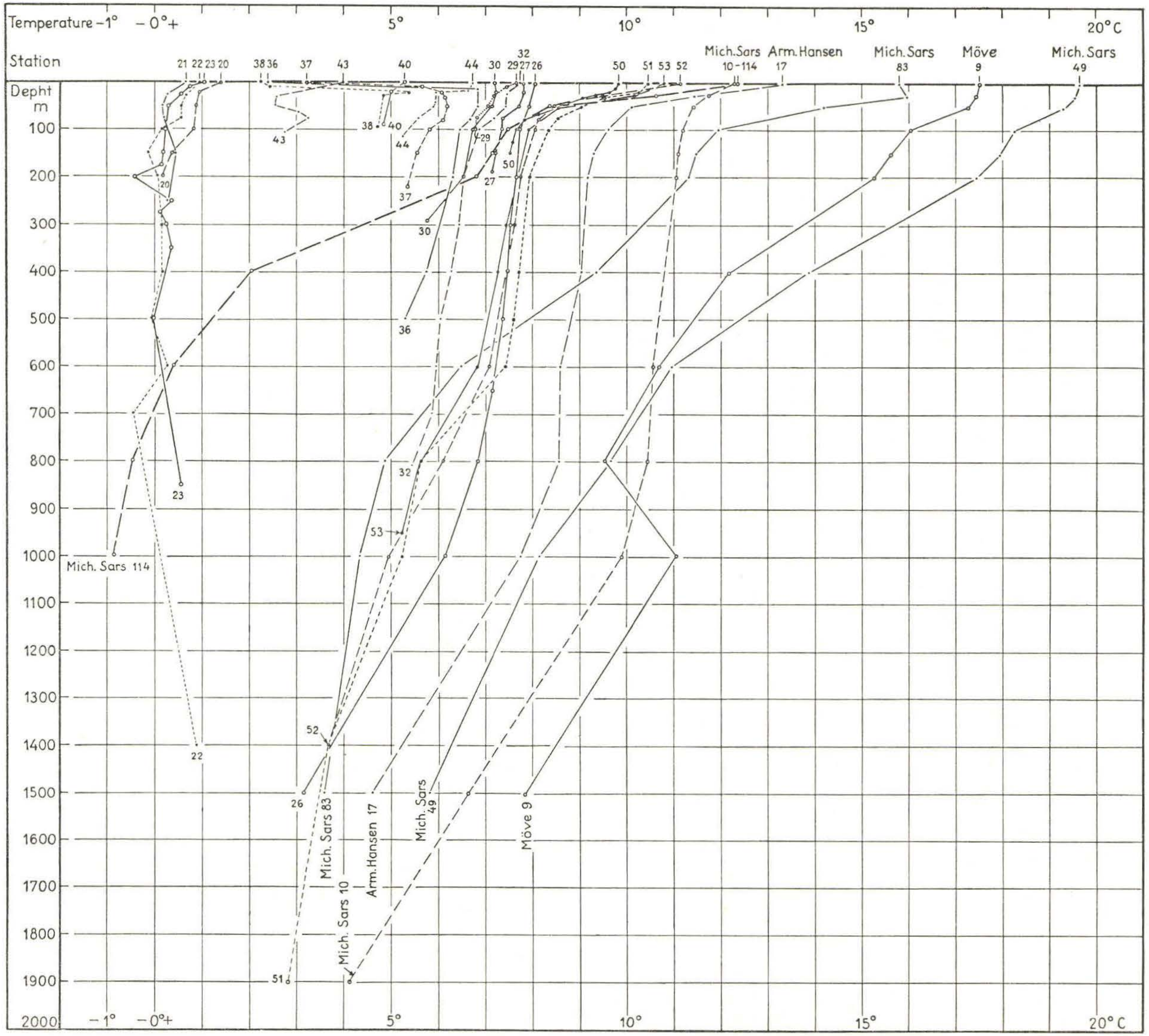
Temperature −1° −0°+ 5° 10° 15° 20° C
Station
21 22 23 20 38 36 37 43 40 44 30 32 29 27 26 50 51 53 52
Mich. Sars 10–114
Arm. Hansen 17
Mich. Sars 83
Möve 9
Mich. Sars 49
Depht m
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
1400
1500
1600
1700
1800
1900
2000
38 40 43 44 29 50 27 37 30 36 20 23 32 53 52 22 26 51
Mich. Sars 114
Mich. Sars 83
Arm. Hansen 17
Mich. Sars 49
Möve 9
Mich. Sars 10
−1° −0°+ 5° 10° 15° 20° C

Fig. 37.

In considering the molluscan fauna we are mainly concerned with the shelf area down to a depth of about 200 m. By means of available surface water temperatures, and using the nearest vertical thermal section as a reference, it should be possible to estimate the mean temperature of the sea bottom within a few degrees. Wave action, currents and tide may cause much intermixture of the water in near-shore areas along open coasts, up to depths of about 100 m. The surface temperatures may consequently represent fair approximations of the bottom temperatures in such areas.

Temperature conditions in the deep sea are relatively homogenous over vast areas. From the graphs fig. 37 it appears that the sections in that part of the eastern North Atlantic which is influenced by the Gulf Stream, viz. the sections off S. Iceland (63°15′N, 14°20′W), S of Wyville Thomson Ridge (58°0′N, 11°0′W), and in the Bay of Biscay (45°26′N, 9°20′W) are practically conformable to a depth of about 1500 m., the difference in temperature being about 1.5° C between the first and second section and about 2° C between the second and third. This indicates a thermal gradient of about 3.5° C from Iceland to the Bay of Biscay, a distance of about 2000 kilometres. The transitional area in the western Atlantic is much narrower than off the European coast due to the North Polar Current. This area displays accordingly sharper thermal brakes at the surface, and the temperature may be somewhat lower at depth

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Fig. 37. Temperature curves from the northern part of the Atlantic Ocean (°C).

St.	N.Lat.	W.Long.	Iceland	Date	Decline 100m.	Decline 200m.	Decline 100—200 m.	August Surface mean	August 100m. (Estimates)	August 200m. (Estimates)
20	65°43′	12°30′	NE	24/5 1903	0.6°	1.2°	0.6°	6.5°	2.5°	1°
21	65°57′	11°31′	NE	24/5 1903	0.4°			6.5°	2.5°	1°
22	65°15′	10°44′	NE	24/5 1903	0.8°	1.0°	0.2°			
23	66°08′	11°13′	NE	24/5 1903	0.8°	1.4°	0.6°	6.5°	2.5°	1°
26	63°15′	14°20′	SE	31/5 1903	0.4°	0.5°	0.1°			
27	63°41′	14°30′	SE	31/5 1903	0.45°	0.65°	0.2°	10.5°	8.5°	8°
29	64°10′	23°22′	W(S)	10/6 1903	0.85°			10.5°	8.5°	8°
30	64°10′	24°22′	W(S)	11/6 1903	0.45°	0.7°	0.25°	10.5°	8.5°	8°
32	64°13′5	27°30′	W(S)	11/6 1903	0.80°	1.2°	0.4°	10.5°	8.5°	8°
36	65°45′	27°03′	W(N)	13/6 1903	−4.0°	−3.9°	0.1°	9.5°	7.5°	7°
37	65°38′	25°38′	W(N)	13/6 1903	−2.6°	−2.1°	0.5°	9.5°	7°	6.5°
38	66°08′	24°37′	W(N)	13/6 1903	−2.4°			9°	6.5°	6°
40	66°33′	22°27′5	N(W)	16/6 1903	0.5°			8°	6°	5.5°
43	66°36′5	18°06′	N	30/6 1903	1.2°			8°	4–5°	4°
44	66°19′	23°22′	W(N)	2/7 1903	1.3°			9°	6°	5.5°
50	63°24′	20°02′	S	12/7 1903	2.2°			11°	8.5°	8°
51	62°11′	19°36′	S	13/7 1903	2.15°	2.5°	0.35°	11°	8.5°	8°
52	62°35′	19°48′	S	14/7 1903	3.1°	3.4°	0.3°	11°	8.5°	8°
53	62°57′	19°58′	S	14/7 1903	2.9°	3.2°	0.3°	11°	8.5°	8°

(From J. N. NIELSEN 1904).

	St.	N.Lat.	W.Long.		Date	Decline 100m.	Decline 200m.
Mich. Sars	114	61°8′	3°14′	North of Wyville Thompson Ridge	12–13/8 1910	4.8°	5.5°
Arm. Hansen	17	58°0′	11°0′	South of Wyville Thompson Ridge	29/7 1913	3.7°	4.1°
Mich. Sars	83	48°30′	33°55′	Central Atlantic Ocean	14/7 1910	3.9°	4.5°
Mich. Sars	10	45°26′	9°20′	Biscay	19–20/4 1910	1.1°	1.25°
Möwe	9	31°29′	11°37′	West of Mogador	1/6 1911	1.5°	2.3°
Mich. Sars	49	29°2′	25°30′	West of the Canaries	2/6 1910	1.5°	2.2°

(From EKMAN 1953).

than off Europe. The annual mean temperature of 5° C for surface water extends from about 70° N. lat. off Europe to about 46° N. lat. off the east coast of North America. This illustrates the scale of the southerly shift of the isotherms in the western North Atlantic. Farther to the south, in the central part of the Atlantic, the situation is reversed due to upwelling cold bottom water off western Africa. The 25° C isotherm runs from about 15° N. lat. on the African coast to about 28° N. lat. off Florida, and the isotherms are thus spread fanlike from north to south along the eastern Atlantic coasts. The hydrography of the eastern Atlantic consequently exhibits a very uniform picture, with only slight temperature changes, no temperature break of importance, and it is relatively difficult to define faunistic boundaries (EKMAN 1953 and others).

Table 5. Mean Surface Temperatures and Annual Oscillation of Temperature in the North Atlantic and Adjacent Seas in °C.

			Febr.	May	Aug.	Nov.	Annual mean temp.	Annual oscill. of temp.
Pacific	Northern Japan		1–7	8–12	15–20	10–15	10–17	15–20
	Bering Sea		−1–2	2–5	5–9	2–4	2–4	7–10
North Atlantic	N. American E. coast		0–5	2–15	15–22	5–15	3–10	>15
	West Greenland		−1–0	0–2	3–5	−1–4	−1–3	5–6
	Spitzbergen (Svalbard)		−1–0	−1–2	0–5	<2	0	2–4
	East Finmark		0–2	0–3	8–10	4	3–4	7–8
	West Finmark		2	3–5	10–11	4–5	4–5	7–8
	Lofoten		3–5	5	11–12	5–6	5–6	7–8
	West Norway		5	5–8	11–12	6–8	6–8	9–10
	South Norway		4–5	8–9	15–16	8–9	8–9	10–14
	South Iceland		5–6	5–7	10–11	5–7	5–8	6–7
	North Sea, Horns Rev (at 0, 15, and 20 m. depth)	0 m.	4	9	17	10	10	14
		15 -	4	8	16	10	9.5	13
		20 -	4	8	16	11	9	13
	Öresund, Lappe Grund (at 0, 10 and 20 m. depth)	0 -	2	10	18	8	9	17
		10 -	3	8	17	9	9.5	15
		20 -	5	6	12	11	9	9
	England		6–9	8–11	13–16	9–13	10–12	6–12
	Bay of Biscay		10–12	12–14	17–20	13–15	13–14 ½	7–9
	Lisbon		14	16	19	16	16	5–6
	Madeira		16	18	23	20	19	6
	Azores		15–16	17	23	18	18–20	8
	Canaries		18–20	18–20	20–23	20–21	20	5
	Senegal		20	22–24	27	25–27	25	3–7
Mediterranean	Balearics		14	17	25	17–18	18	>10
	Spain		12–14	17	25	17–18	18	>10
	South France		12	15–16	22–24	16	17	10–13
	Corsica, Sardinia		12–14	16–17	23–25	17–18	18–19	13
	North and Central Italy		12–13	16–17	23–25	16–17	17–18	10–13
	South Italy		13–14	17	25	17–18	19	10–12
	Sicily, Malta		14	17–18	25	20	19–20	10
	Adriatic		10–14	17	24–25	15–17	14–19	14
	Morea, Ægean Sea		10–15	17–18	25	15–20	18–20	10–11
	Syria, Ægypt		16–17	20–22	26–28	21–23	20–21	<10
	Tunisia, Algeria		13–14	17–18	25–26	17–18	19–20	10
	Black Sea		0–7	13–16	23	11–14	10–15	17–20

The temperature of the surface water in parts of the North Atlantic and adjacent seas is shown in table 5, in which the mean temperatures for the months of February, May, August, and November, the annual mean temperature, and the annual temperature oscillation of the surface water is shown. Most of the surface water temperatures are taken from SCHOTT's maps (1935 and 1942), but the temperatures for the North Sea and the Öresund have been calculated from the data published by the Danish Meteorological Institute in the Nautical-Meteorological Annual for the years 1932–1956.

B. Marine Faunal Regions

Several authors have established zoogeographic subdivisions of the marine areas. In 1856 WOODWARD published a subdivision that was based on the distribution of the mollusca, and in 1896 ORTMANN gave a comprehensive outline of previous attempts, rejecting most of the earlier zoogeographic systems including that by WOODWARD. In the same paper ORTMANN proposed a new classification of the marine areas on the basis of the distribution of Decapoda, emphasizing the importance of the physical properties of the individual parts of the oceans.

Considerable progress has been made in the field of zoogeography since the days of ORTMANN. The works of MURRAY and HJORTH (1912), HESSE, ALLEE and SCHMIDT (1924, 1951) and EKMAN (1935, 1953) represent some of the significant steps forward during the twentieth century. Of particular interest is the paper published by HUTCHINS (1947) on temperature zonation based on the geographic distribution of species. In this paper HUTCHINS drew attention to the significance of limiting temperatures in the geographic distribution of marine species. It is worth-while to quote the following statements (HUTCHINS 1947, p. 325): "In the case of a species spreading toward the poles an extreme temperature .... is encountered first as a winter temperature. The boundary comes into being where the species is subject to winter killing. For a species spreading toward the equator the comparable boundary arises where summer temperatures first become too high, and dispersal is checked by inability of the individuals to survive the excessive heat.

The second sort of relationship to temperature stressed in distributional studies involves the critical temperatures necessary for reproduction of life cycles. In such cases species spread toward the poles as far as summer temperature conditions are adequate, and towards the equator as far as requisite low temperatures can be obtained in winter. A number of critical phenomena may lead to boundaries of this type, among them trigger temperatures necessary to induce spawning, and growing seasons of adequate duration as well as intensity". With these words HUTCHINS undoubtedly touches on some fundamentals of marine zoogeography.

The classifications that were established by WOODWARD, ORTMANN and others have not been revised in detail, and WOODWARD's subdivision of the North Atlantic has generally been accepted in spite of ORTMANN's rejection. In the Atlantic Ocean WOODWARD's Celtic province has been rejected as an independent province, and its area is included in the Boreal province (see e.g. EKMAN 1953). The North Atlantic is, according to WOODWARD, subdivided into the following provinces: 1. The Arctic, 2. The Boreal, 3. The Lusitanian-Trans Atlantic, and 4. The West African-Carribean provinces. EKMAN (1935,

1953) has subdivided these provinces further on the basis of extensive studies of the entire known marine fauna. His classification appears to be well founded and is generally accepted, it is listed below together with WOODWARD's system.

Table 6. Marine Faunal Regions in the North Atlantic.

WOODWARD (1856)	EKMAN (1953)	
	American coasts	European-African coast
Arctic	High arctic Low arctic	
Boreal	Temperate fauna of North American Atlantic	Boreal fauna of Europa
Lusitanian		Mediterranean-Atlantic fauna
Carribean-West African	Tropical and Subtropical faunas of the American Atlantic	Tropical and Subtropical faunas of West Africa

It will be seen from the table that WOODWARD's and EKMAN's subdivisions do not cover each other exactly, but the differences are of minor importance in the present connection.

The main reason why WOODWARD's molluscan provinces turned out to be valid may be that WOODWARD succeeded in defining natural faunal units which parallel significant climate zones, although the latter were not yet clearly recognized when the classification was set up. We are not yet aware of the full influence of environmental factors upon the physiological processes which affect the dispersive power of marine animals, but it is obvious that the distribution of individual species and whole faunas in the two great ocean areas are limited by temperature. From a study of the history of zoogeography it appears that useless discussions have been held concerning the importance of different animal groups in defining animal provinces. The uselessness results from the fact that life will not fit into any rigid system, and that any zoogeographic subdivision must be artificial from some point of view. In order to avoid further misconceptions it might be useful to consider the possibility of defining marine faunal regions by means of the thermal properties of the individual water masses to which the faunas obviously are related. In accordance with such a standpoint EKMAN (1953, p. 176) has subdivided the Arctic seas into high arctic and low arctic zones separated by the 0° C isotherm. Similarly, the boundaries of the boreal zone on the European coasts are defined by coldest and warmest temperatures and annual mean temperatures (loc. cit. p. 102) etc.

The writer has finally attempted a consistent classification of the faunal regions of the North Atlantic shelf areas off Europe and Africa, based on thermal boundaries, as shown on table 7. The boundaries are defined by the mean temperatures of the surface water during the coldest and warmest months, and by the annual means, since these temperatures are regarded as most significant in marine faunal distribution.

It should be noted that the Tropic and Subtropic regions practically cover the warm water areas, that the Lusitanian and Boreal regions correspond to the transition zone, and that the Arctic region is identical with the cold water area

Table 7. Temperatures at the Boundaries of Faunal Regions in the Eastern North Atlantic.

		Mean temperatures (°C)		
Faunal region	Boundary	February	August	Annual
Arctic region				
	New Foundland— N. Iceland—E. Finmark	0°	8°	4°
Boreal region				
	SW entrance English Channel	10°	16–17°	12°
Lusitanian region				
	Cape Blanco	18°	23–25°	20°
Subtropic region				
	Cape Verde	20°	27–28°	25°
Tropic region				

(see p. 383). Regardless of how ill-defined the individual boundaries may be from a faunal viewpoint, they approximate distributional borders of some value.

The distribution of very few species corresponds strictly to the faunal regions defined above. In particular the fauna of the Boreal region includes very few endemic species. Among the molluscs, the following are mainly restricted to the Boreal region although some overlap to the Arctic or the Lusitianian region:

Anomia squamula
Pecten tigrinus
Modiola modiolus
Cyprina islandica
Panopea norvegica
Mya arenaria
Zirphaea crispata
Evalea (Auriculina) insculpta
Philine quadrata
Littorina littorea
Purpura (Nucella) lapillus
Sipho propinquus
Neptunea antiqua
Taranis Mörchi

Table 8 shows the temperature conditions at the distributional limits of 6 of these species. The data on distribution are compiled from the following sources: Áskelsson (1935), Harmer (1918, p. 646) Ad. S. Jensen (1900, 1902), Ad. S. Jensen & Spärck (1934), Johnson (1934), Locard (1892), Moore (1936a), Nicol (1951), Nordmann (1912), Posselt (1898), and Schott (1942). For each species the mean temperature at the northern and southern boundaries on both the American and European coasts are shown. None of the areas of distribution coincides exactly with the Boreal area as defined above, nor do the temperatures at the distributional limits quite agree with the temperatures found at the limits of the Boreal region.

The physical properties of deep sea water are very different from those of shelf waters, especially regarding temperature and oxygen content. The thermal variations are obviously much less extreme than near the surface, and the molluscs that inhabit the deeper parts of the oceans are generally considered to be more stenothermal than shallow water molluscs. Most shallow water molluscs can be referred to more than one shallow water faunal division. In case of the deep water fauna, however, it is difficult to classify the affinities of a number of species which occur at great depths at latitudes ranging from Arctic to Subtropic or Tropic regions. It is therefore reasonable to refer to such species as deep water species, and to regard the deep ocean bottom, that is relatively cool and subject to less variable temperature conditions than the shelf waters, as an independant faunal region.

Table 8.

Mean Temperature at the Distributional Northern (N) and Southern (S) Limits of some Boreal Molluscan Species in the North Atlantic.

		Mean Temperatures °C					
Species		February		August		Annual	
		N. America	Europe	N. America	Europe	N. America	Europe
Anomia squamula	N	0°	0−−1°	13°	10°	4°	4°
	S	19°	12°	25°	20°	20°	15°
Cyprina islandica	N	−1°	0−−1°	13°	10°	4°	4°
	S	19°	11°	25°	20°	20°	14°
Mya arenaria	N	(−1°)	0−−1°	(13°)	10°	(4°)	4°
	S	22°	12°	27°	22°	23°	15°
Zirphaea crispata	N	−1°	0−−1°	13°	10°	4°	4°
	S	22°	12°	27°	20°	23°	15°
Littorina littorea	N	−1°	0−−1°	10°	10°	4°	4°
	S	5°	15°	21°	21°	14°	17°
Purpura (Nucella) lapillus	N	−1°	0−−1°	5°	5°	0°	1°
	S	3–4°	15°	20°	20°	10°	17°

Some shallow cold water species do occur at deeper levels toward the equator. This equatorial submergence (HAECKER 1908, EKMAN 1935, 1953, REMANE 1940), is apparently related to the temperature requirements of the species.

Table 9 shows the depth range of some molluscs in the Skagerak area on the basis of investigations by C. G. JOH. PETERSEN (1915). PETERSEN's bottom samples were taken during the months of July and August in 1911 and 1914. The bottom deposits were not very different in the various sampling areas, most of the samples being taken on clay bottom. Thermal stratification was apparently most pronounced in the Oslo Fjord. A bottom temperature of 10° C was encountered at the following depths: about 12 metres N of Dröbak, about 13–25 m. S of Dröbak, and about 90 m. in the Skagerak. The temperatures were generally higher above and lower below these levels.

It will be seen from the table that *Nucula tenuis* and *Macoma calcarea* apparently display submergent tendencies in the Skagerak. The two other cold water forms *Thyasira flexuosa* and *Syndosmya nitida* are definitely soft bottom species in which it is difficult to decide whether their occurrence at depth is the result of temperature conditions, bottom character or the combined effect of both these factors.

The temperate and boreal forms are most abundant where the temperature is above about 10° C during July-August i.e. the warmest period of the year.

Table 11, p. 394 is a survey of the molluscan fauna of the transition area between the North Sea and the brackish Baltic. It has been attempted to classify the species in accordance with their geographic occurrence, into "arctic", "boreo-arctic", "boreal", "boreo-lusitanian", and "deep-water" species.

This table is the result of an objective study of the literature. However, future research should rectify such erroneous inferences as have undoubtedly been made. Nevertheless the table may even in its present form, illustrate the elements of the recent boreal molluscan fauna of Europe. Faunas of other regions, and also fossil faunas, may be analyzed in a similar way.

Table 9.

The Depth Range of some Molluscs in the Skagerak and Oslo Fjord, and Corresponding Bottom Temperatures.

(From C. G. JOH. PETERSEN, 1915, profiles I, II and III).

Thermal affinity *)	Species	Depth metres	Bottom temperatures		Remarks
			Total range	Maximum of occurrence at:	
t	*Nucula tenuis*	12–410	10.2–5.5°C	5.5–7°C	Littoral in the Arctic
c	*Nucula nitida*	14–68	abt. 10–abt. 7°	?	
c	*Thyasira flexuosa*	14–410	9.6–6.4°	6–7°	Soft bottom species
t	*Cardium fasciatum*	4–24	abt. 17–5.5°	10–15°	
b	*Cyprina islandica*	7–24	abt. 18–5.5°	18°	
t	*Macoma baltica*	0.3–13	abt. 18–abt. 9°	abt. 18°	
a	*Macoma calcaria*	7–73	18.2–5.5°	abt. 7°	Littoral in the Arctic
c	*Syndosmya nitida*	10–410	15.2–5.5°	6–7°	Soft bottom species
t	*Syndosmya alba*	6–41	abt. 18–5.5°	10–18°	
t	*Corbula gibba*	6–320	abt. 18–5.5°	10–15°	
t	*Aporrhais pes pelecani*	8–29	abt. 18–6.5°	8.5°	
t	*Nassa reticulata*	4–14	abt. 18–abt. 7°	15–17°	
t	*Akera bullata*	9–14	16.6–abt. 8.5°	15°	

C. The Effect of Salinity on Distribution

The transition area between the North Sea and the Baltic is the best known major brackish water region as far as both hydrographic conditions and the distribution of the fauna are concerned. The temperature and salinity of the water at various depths is regularly measured from a number of lightships, particularly in Danish waters, as reported in the Nautical-Meteorological Annual of the Danish Meteorological Institute. Monthly mean values for temperature and salinity have been calculated by JACOBSEN (1908) and A. J. C. JENSEN (1937). The fauna of the sea bottom has been studied by many workers. The investigations of the animal communities by C. G. JOH. PETERSEN have especially contributed to our knowledge of the distribution of molluscan species in the Skagerak, the Kattegat, The Belt Sea and the Baltic (C. G. JOH. PETERSEN 1888, 1918). The Pelecypoda have been treated by JENSEN & SPÄRCK (1934).

The deposits of the sea floor have been outlined by C. G. JOH. PETERSEN (1888, 1913) and BRATTSTRÖM (1941). Nearly every kind of bottom deposit may be encountered, since the variable glacial sediments of the Quaternary form both the source and the substratum of the recent sediments over a great part of the area. The bottom deposits should therefore be suitable for the distribution of most marine species of bottom dweller, provided all other factors are equal.

The hydrography of the area has been summarized by EKMAN (1953, p. 105). The outstanding hydrographic feature is the flow of brackish water out from the Baltic as surface currents through the Belts around the Danish islands, and the inflowing bottom current that carries salt water from the North Atlantic into the Baltic. The two water masses are relatively well separated, although wave action and the currents themselves cause a gradual mixing. The deepest hollows

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*) a = arctic species, b = boreal species, c = boreo-arctic species, t = boreo-lusitanian species.

in the sea floor contain the most saline water, and the most brackish water is found in the northern parts of the Baltic. The surface current is least saline near the west coast of Sweden. For further reference see JACOBSEN (1908), A. J. C. JENSEN (1937), and BRATTSTRÖM (1941).

The thermal conditions of the surface water vary slightly from the marine region around North Jutland to the brackish regions around the island of Bornholm. The thermal conditions are, however, apparently more stable in the deep parts of the Baltic than in the deep parts of the Kattegat and the Belt Sea.

Reviewing the physical properties of the transition area, it becomes appearent that the only consistently variable environmental factor is salinity. Considering the multitude of different substrata, and the relatively unimportant temperature differences between the marine and brackish areas, it seems reasonable to conclude that salinity is the main limiting factor in the geographic distribution of species in the transition area. The limiting effect of salinity on the distribution of some molluscs in the Baltic and in Randers Fjord (Denmark) was dealt with by JOHANSEN (1916, 1918). Table 11, p. 394 has been compiled to illustrate the mode of salinity control in a number of the molluscs of marine origin in the entire transition area between the North Sea and the Baltic. In this table the distribution of the Pelecypoda and Gastropoda as reported by PETERSEN (1888), and JENSEN & SPÄRCK (1934) are related to the salinity at the limits of distribution of the species. The average salinities listed are based on the data published by the Danish Meteorological Institute, and on JACOBSEN's (1908) and JENSEN's (1937) mean values. Although the salinities represent the best estimates, the writer is aware of their approximate character.

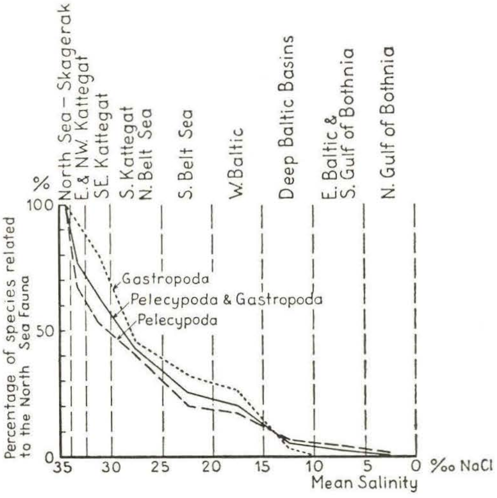
It should be emphasized that the variation in thickness of the surface currents accounts for the rather violent changes in salinity shown by the figures in the table. It has been preferred to list the individual species instead of giving only the numbers of species in various salinity classes, since potentially significant features of the reaction of species and genera to salinity variation would otherwise not be apparent. The thermal affinity of the species is indicated in relation to the geographic distribution of the same species in true marine regions outside the transition area, as is mentioned on page 390. The table also records the majority of mollusca known at present from the transition area, but excludes some species living off the coast of Bohuslän (e.g. rock dwellers etc.), whose geographic distribution is obviously limited by factors other than salinity. The table has been elaborated on the basis of the following references: ALLEN (1931), ÁSKELSSON (1935), BRØGGER (1901), BUCQUOY, DAUTZENBERG & DOLLFUS (1886–1898), DONS (1931), FORBES & HANLEY (1853), GIGNOUX (1913), GOULD (1870), HARMER (1914–1925), JEFFREYS (1862–1869), JENSEN (1900), (1902), (1905), JENSEN & SPÄRCK (1934), JOHNSON (1934), LOCARD (1892), NICOL (1951), NORDMANN (1912), PETERSEN (1888), POSSELT (1898), SARS (1878), STOSSICH (1880), THORSON (1941), (1944), VLES (1907), and WEINKAUFF (1867–1868).

The salinity columns in table 11 refer to the following parts of the transition area:

Table 10. Salinities in the Transition Area between the North Sea and the Baltic.

		Salinity in $^0/_{00}$		Mean-Minimum Range
		Minimum	Mean	
I	North Sea at Esbjerg	31.5	33	1–2
II	Deep parts of the Skagerak	25–30	34	4–9
III	Western part of the Limfjord	26–27	31	4–5
IV	Deep parts of the eastern Kattegat	20–25	33.5	9–14
V	Kattegat off Frederikshavn and E of the Limfjord	22–25	28–32.5	3–11
VI	Kattegat Anholt-Djursland	15–20	32	12–17
VII	– Hesselö-Hjælm	15–16	31	15–16
VIII	– Hjælm-Sjællands Odde-Hellebæk	15	30	15
IX	– Samsö	13–15	25–30	12–15
X	Northern Öresund to Hven	10–15	25	10–15
XI	Öresund at Hollænderdyb Lillebælt, Brandsö Bredning	10–13	20	5–10
XII	Storebælt, Svendborg-Langeland	9–10	20	10–11
XIII	Öresund, southern part Baltic, western part	8–10	18–20	10–12
XIV	Baltic, Kiel-Warnemünde	8–9	15–20	6–12
XV	Baltic, deep Arkona and Bornholm basins	7–10	10–20	10–13
XVI	Baltic, S of the Åland island	5–6	6–10	1–5
XVII	Gulf of Bothnia	4–5	6	1–2
XVIII		3.4–4	4	1–2

From the distribution of mollusca in the North Sea—Baltic transition area we may infer that the adaptive power in relation to decreasing salinity is equally well developed in various genera of both pelecypoda and gastropoda.



Decrease in number of molluscan species in the North Sea-Baltic transition area related to mean salinities

Fig. 38.

Table 12, p. 399, and figure 38 summarize the data in table 11. Concerning the Pelecypoda it may be seen from the curve in fig. 38 that the number of species has already been considerably reduced in water of 32½–34$^0/_{00}$ salinity, and thereafter it declines steadily, although at a somewhat decreasing rate, to a salinity of about 15$^0/_{00}$. This is apparently a particularly critical limit. A few pelecypod species are able to live in water of salinity as low as 3–4$^0/_{00}$. In contrast to the Pelecypoda, the Gastropoda are obviously less sensitive to minor salinity variations. The major drop in the number of gastropod species occurs at a salinity of about 30$^0/_{00}$, but the 15$^0/_{00}$ limit is probably as critical for Gastropoda as for Pelecypoda in the Baltic area. Considering both Pelecypoda and Gastropoda, it is remarkable that the number of marine species is halved in water of about 28 to 29$^0/_{00}$ mean salinity. The decrease in the number of species with progressive dilu-

Table 11.

Distributional Limits of Recent Mollusca in the Transition Area between the North Sea and the Baltic, and Corresponding Mean Salinities.

Distribution according to AD. S. JENSEN & SPÄRCK (1934) and C. G. JOH. PETERSEN (1888).
Regions I–XVIII see table 10, p. 393.
Thermal affinities: *a*: arctic species; *c* (= cold): boreo-arctic species; *b*: boreal species; *t* (= temperate): boreo-lusitanian species; *d*: deep-water species.

Thermal affinity	**Pelecypoda**	Region of lowest mean salinity inhabited																	
		I, 33 ‰	II, 34 ‰	III, 31 ‰	IV, 33,5 ‰	V, 28–32,5 ‰	VI, 32 ‰	VII, 31 ‰	VIII, 30 ‰	IX, 25–30 ‰	X, 25 ‰	XI, 20 ‰	XII, 20 ‰	XIII, 18–20 ‰	XIV, 15–20 ‰	XV, 10–20 ‰	XVI, 6–10 ‰	XVII, 6 ‰	XVIII, 4–6 ‰
c	1. *Nucula tenuis* (MONTAGU)	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..
t	2. – *nitida* SOWERBY	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..
d	3. – *tumidula* MALM	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
t	4. – *nucleus* L.	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..
d	5. – *sulcata* BRONN	..	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..
d	6. *Malletia obtusata* (M. SARS)	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
c	7. *Leda pernula* (MÜLLER)	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..
c	8. – *minuta* (MÜLLER)	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..
d	9. *Portlandia lucida* (LOVÉN)	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
c	10. – *frigida* (TORELL)	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
d	11. – *tenuis* (PHILIPPI)	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
d	12. – *intermedia* (SARS)	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
d	13. *Arca pectunculoides* (SCACCHI)	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
t	14. – *nodulosa* MÜLLER	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
t	15. – *tetragona* POLI	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
t	16. *Glycimeris glycimeris* (L.)	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
t	17. *Limopsis aurita* (BROCCHI)	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
t	18. *Ostrea edulis* L.	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
t	19. *Anomia patelliformis* L.	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..
b	20. – *squamula* L.	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..
t	21. *Pecten maximus* (L.)	..	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..
d	22. – *vitreus* CHEMNITZ	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
c	23. – *imbrifer* LOVÉN	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
t	24. – *septemradiatus* MÜLLER	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..
t	25. – *opercularis* (L.)	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..
t	26. – *varius* L.	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
d	27. – *aratus* GMELIN	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
b	28. – *tigrinus* MÜLLER	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..
t	29. – *striatus* MÜLLER	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..
t	30. – *similis* LASKEY	..	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..
t	31. – *testae* BIVONA	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..
t	32. *Lima hians* GMELIN	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
t	33. – *Loscombi* SOWERBY	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..
t	34. – *Gwyni* SYKES	..	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..
d	35. *Lima subauriculata* MONTAGU	..	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..
d	36. – *Sarsi* LOVÉN	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
c	37. *Crenella decussata* (MONTAGU)	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..
t	38. *Mytilus edulis* L.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	+	..	..
t	39. *Modiola adriatica* LAMARCK	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..	..
t	40. – *phaseolina* PHILIPPI	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..	..
b	41. – *modiolus* (L.)	..	..	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..

Table 11 (*continued*).

Thermal affinity	Pelecypoda	Region of lowest mean salinity inhabited																	
		I, 33 $^{0}/_{00}$	II, 34 $^{0}/_{00}$	III, 31 $^{0}/_{00}$	IV, 33,5 $^{0}/_{00}$	V, 28–32,5 $^{0}/_{00}$	VI, 32 $^{0}/_{00}$	VII, 31 $^{0}/_{00}$	VIII, 30 $^{0}/_{00}$	IX, 25–30 $^{0}/_{00}$	X, 25 $^{0}/_{00}$	XI, 20 $^{0}/_{00}$	XII, 20 $^{0}/_{00}$	XIII, 18–20 $^{0}/_{00}$	XIV, 15–20 $^{0}/_{00}$	XV, 10–20 $^{0}/_{00}$	XVI, 6–10 $^{0}/_{00}$	XVII, 5 $^{0}/_{00}$	XVIII, 4–6 $^{0}/_{00}$
t	42. *Modiolaria marmorata* (FORBES)													+					
t	43. – *discors* (L.)													+					
a	44. – *nigra* GRAY													+					
a	45. *Astarte borealis* (CHEMNITZ)															+			
a	46. – *montagui* (DILLWYN)													+					
c	47. – *sulcata* (DA COSTA)						+												
a	48. – *elliptica* (BROWN)															+			
t	49. *Goodallia triangularis* (MONTAGU)	+																	
t	50. *Diplodonta rotundata* (MONTAGU)	+																	
d	51. *Thyasira ferruginosa* (FORBES)	+																	
c	52. – *Sarsi* PHILIPPI				+														
d	53. – *eumyaria* (M. SARS)		+																
d	54. – *croulinensis* (JEFFREYS)	+																	
c	55. – *flexuosa* (MONTAGU)										+								
t	56. *Lucina borealis* (L.)								+										
d	57. – *spinifera* (MONTAGU)	+																	
t	58. *Lepton nitidum* TURTON	+																	
t	59. – *squamosum* (MONTAGU)	+																	
t	60. *Montacuta ferruginosa* (MONTAGU)								+										
c	61. – *Dawsoni* (JEFFREYS)				+														
t	62. – *substriata* (MONTAGU)								+										
t	63. – *bidentata* (MONTAGU)													+					
t	64. *Kelliella miliaris* (PHILIPPI)		+																
t	65. *Cardium echinatum* L.										+								
t	66. – *minimum* (PHILIPPI)										+								
t	67. – *exiguum* GMELIN																+		
t	68. – *fasciatum* MONTAGU													+					
t	69. – *edule* L.																	+	
t	70. – *nodosum* TURTON						+												
t	71. *Laevicardium norvegicum* SPENGLER						+												
b	72. *Cyprina islandica* L.														+				
t	73. *Isocardia cor* (L.)						+												
t	74. *Dosinia exoleta* (L.)					+													
t	75. – *lincta* (PULTENEY)							+											
t	76. *Lucinopsis undata* (PENNANT)								+										
t	77. *Tapes aureus* (GMELIN)	+																	
t	78. – *decussatus* (L.)	+																	
t	79. – *pullastra* (MONTAGU)					+													
t	80. – *edulis* (CHEMNITZ)		+																
t	81. *Venus gallina* L.								+										
t	82. – *ovata* PENNANT									+									
t	83. – *fasciata* (DA COSTA)						+												
t	84. *Petricola pholadiformis* LAMARCK													+					
t	85. *Gouldia minima* (MONTAGU)	+																	
t	86. *Macoma baltica* (L.)																		+
a	87. – *calcaria* (CHEMNITZ)															+			
t	88. *Tellina crassa* (GMELIN)	+																	
t	89. – *pusilla* PHILIPPI								+										
t	90. – *tenuis* DA COSTA										+								

Table 11 (*continued*).

Thermal affinity	Pelecypoda	Region of lowest mean salinity inhabited																	
		I, 33 $^0/_{00}$	II, 34 $^0/_{00}$	III, 31 $^0/_{00}$	IV, 33,5 $^0/_{00}$	V, 28–32,5 $^0/_{00}$	VI, 32 $^0/_{00}$	VII, 31 $^0/_{00}$	VIII, 30 $^0/_{00}$	IX, 25–30 $^0/_{00}$	X, 25 $^0/_{00}$	XI, 20 $^0/_{00}$	XII, 20 $^0/_{00}$	XIII, 18–20 $^0/_{00}$	XIV, 15–20 $^0/_{00}$	XV, 10–20 $^0/_{00}$	XVI, 6–10 $^0/_{00}$	XVII, 6 $^0/_{00}$	XVIII, 4–6 $^0/_{00}$
t	91. *Tellina fabula* GRONOVIUS									+									
t	92. – *squalida* PULTENEY	+																	
t	93. *Scrobicularia plana* DA COSTA														+				
t	94. *Syndosmya prismatica* (MONTAGU)							+											
d	95. – *longicallus* (SCACCHI)		+																
c	96. – *nitida* (MÜLLER)											+							
t	97. – *alba* (WOOD)												+						
t	98. – *tenuis* (MONTAGU)	+																	
t	99. *Psammobia ferroensis* (CHEMNITZ)								+										
t	100. – *vespertina* (CHEMNITZ)	+																	
t	101. – *tellinella* LAMARCK	+																	
t	102. *Donax vittatus* DA COSTA	+																	
t	103. *Solecurtus antiquatus* (PULTENEY)				+														
t	104. *Cultellus pellucidus* (PENNANT)													+					
t	105. *Ensis ensis* (L.)									+									
t	106. – *siliqua* (L.)									+									
t	107. *Solen vagina* (L.)	+																	
t	108. *Mactra stultorum* MONTAGU				+														
t	109. *Spisula subtruncata* (DA COSTA)											+							
t	110. – *solida* (L.)									+									
t	111. *Lutraria eliptica* LAMARCK	+																	
b	112. *Panopœa norvegica* (SPENGLER)										+								
t	113. *Arcinella plicata* (MONTAGU)										+								
t	114. *Saxicava arctica* (L.)											+							
b	115. *Mya arenaria* L.																	+	
c	116. – *truncata* (L.)														+				
t	117. *Corbula gibba* (OLIVI)														+				
b	118. *Zirphaea crispata* (L.)													+					
t	119. *Pholas candida* L.													+					
t	120. – *dactylus* L.					+													
t	121. *Xylophaga dorsalis*										+								
t	122. *Pandora inœquivalvis* (L.)	+																	
t	123. *Lyonsia norvegica* (CHEMNITZ)				+														
t	124. *Thracia papyracea* POLI										+								
t	125. – *convexa*, WOOD						+												
t	126. – *distorta* MONTAGU	+																	
t	127. *Cochlodesma prœtenue* PULTENEY				+														
t	128. *Cuspidaria rostrata* (SPENGLER)	+																	
t	129. – *abbreviata* (FORBES)	+																	
d	130. – *obesa* (LOVEN)				+														
t	131. – *cuspidata* (OLIVI)				+														
t	132. – *costellata* (DESHAYES)		+																
t	133. *Poromya granulata* NYST & WESTENDORPH	+																	
	Totals Pelecypoda	28	16	2	13	3	7	2	9	7	19	3	2	10	4	3	2	2	1

Table 11 (*continued*).

Thermal affinity	Gastropoda	Region of lowest mean salinity inhabited																	
		I, 33 $^0/_{00}$	II, 34 $^0/_{00}$	III, 31 $^0/_{00}$	IV, 33,5 $^0/_{00}$	V, 28–32,5 $^0/_{00}$	VI, 32 $^0/_{00}$	VII, 31 $^0/_{00}$	VIII, 30 $^0/_{00}$	IX, 25–30 $^0/_{00}$	X, 25 $^0/_{00}$	XI, 20 $^0/_{00}$	XII, 20 $^0/_{00}$	XIII, 18–20 $^0/_{00}$	XIV, 15–20 $^0/_{00}$	XV, 10–20 $^0/_{00}$	XVI, 6–10 $^0/_{00}$	XVII, 6 $^0/_{00}$	XVIII, 4–6 $^0/_{00}$
c	134. *Acmaea testudinalis* (Müller)													+					
t	135. – *virginea* (Müller)										+								
c	136. *Lepeta coeca* (Müller)										+								
t	137. *Calliostoma miliare* (Brocchi)						+												
t	138. *Gibbula tumida* (Montagu)								+										
c	139. – *cineraria* (L.)													+					
c	140. *Lacuna divaricata* (Fabricius)														+				
c	141. – *pallidula* (Da Costa)														+				
t	142. *Littorina obtusata* L.													+					
t	143. – *rudis* Mat.															+			
b	144. – *littorea* L.													+					
c	145. *Onoba striata* (Montagu)													+					
t	146. – *vitrea* (Montagu)								+										
t	147. *Alvania punctura* (Montagu)								+										
t	148. – *abyssicola* Forbes								+										
t	149. – *cimicoides* (Forbes)	+																	
t	150. – *zetlandica* (Montagu)	+																	
t	151. *Rissoa inconspicua* Alder														+				
t	152. – *membranacea* Adams													+					
t	153. – *parva* Da Costa						+												
t	154. – *violacea* Desm.						+												
t	155. – *soluta Phil.*							+											
t	156. *Hydrobia ulvae* Pennant															+			
t	157. *Turritella communis* Lamarck										+								
t	158. *Bittium reticulatum* Da Costa										+								
t	159. *Triphoris perversa* (L.)													+					
t	160. *Scala clathrus* L.								+										
t	161. *Clathrus clathratulus* (Adams)								+										
t	162. – *trevelyana* Leach						+												
t	163. *Aclis minor* (Brown)								+										
t	164. *Eulima distorta* (Deshayes)											+							
t	165. – *intermedia* Cantraine							+											
t	166. *Odostomia decussata* Montagu					+													
t	167. – *unidentata* Montagu									+									
t	168. – *eulimoides* Hanley								+										
t	169. – *albella* Lovén								+										
t	170. – *turrita* (Hanley)								+										
t	171. – *umbilicaris* Malm.	+																	
t	172. *Liostomia clavula* (Lovén)								+										
t	173. *Brachystoma rissoides* (Hanley)														+				
b	174. *Evalea* (*Auriculina*) *insculpta* (Montagu)								+										
t	175. *Parthenia indistincta* (Montagu)								+										
t	176. – *interstincta* (Montagu)								+										
t	177. – *spiralis* (Montagu)								+										
t	178. *Pyrgiscus* (*Chemnitzia*) *rufus* (Philippi)								+										
t	179. – *lactea* (L.)				+														
t	180. – *scalaris* (Philippi)				+														
t	181. *Eulimella acicula* (Philippi)						+												
t	182. – *scillae* Scacchi				+														

Table 11 (*continued*).

Thermal affinity	Gastropoda	Region of lowest mean salinity inhabited																	
		I, 33 $^0/_{00}$	II, 34 $^0/_{00}$	III, 31 $^0/_{00}$	IV, 33,5 $^0/_{00}$	V, 28–32,5 $^0/_{00}$	VI, 32 $^0/_{00}$	VII, 31 $^0/_{00}$	VIII, 30 $^0/_{00}$	IX, 25–30 $^0/_{00}$	X, 25 $^0/_{00}$	XI, 20 $^0/_{00}$	XII, 20 $^0/_{00}$	XIII, 18–20 $^0/_{00}$	XIV, 15–20 $^0/_{00}$	XV, 10–20 $^0/_{00}$	XVI, 6–10 $^0/_{00}$	XVII, 6 $^0/_{00}$	XVIII, 4–6 $^0/_{00}$
t	183. *Eulimella nitidissima* (MONTAGU)	..	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..
t	184. *Capulus hungaricus* L.	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..
t	185. *Aporrhais pes pelecani* L.	..	..	..	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..
c	186. *Amauropsis islandica* (GMELIN)	..	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..
c	187. *Lunatia pallida* (BRODERIP & SOWERBY)	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..
c	188. – *nitida* (DONOVAN)	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..	..
c	189. – *Montagui* FORBES	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..	..
t	190. *Natica catena* (DA COSTA)	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..
c	191. *Velutina velutina* (MÜLLER)	..	..	..	..	..	..	..	..	..	..	..	..	..	+	..	..	..	..
c	192. *Trophon truncatus* (STRØM)	..	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..
b	193. *Purpura (Nucella) lapillus* (L.)	..	..	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..
b	194. *Sipho propinquus* (ALDER)	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..	..
b	195. *Neptunea antiqua* (L.)	..	..	..	..	..	..	..	..	..	..	..	..	..	+	..	..	..	..
c	196. *Buccinum undatum* L.	..	..	..	..	..	..	..	..	..	..	..	..	..	+	..	..	..	..
t	197. *Nassa reticulata* (L.)	..	..	..	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..
t	198. – *pygmaea* LAMARCK	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..
c	199. *Bela trevelyana* TURTON	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..
c	200. – *turricula* (MONTAGU)	..	..	..	..	..	..	..	..	..	..	..	..	..	+	..	..	..	..
t	201. *Philbertia linearis* (MONTAGU)	..	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..
t	202. – *teres* (FORBES)	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
b	203. *Taranis Mörchi* MALM	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
t	204. *Mangelia brachystoma* (PHILIPPI)	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..	..
t	205. – *attenuata* (MONTAGU)	..	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..
t	206. – *coarctata* (FORBES)	..	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..
t	207. – *nebula* MONTAGU	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..
t	208. *Actaeon tornatilis* L.	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..	..
t	209. *Diaphana minuta* (BRONN)	..	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..
t	210. *Cylichna cylindracea* (PENNANT)	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..	..	..
t	211. *Rhizorus acuminatus* (BRUGUIÈRE)	..	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..
t	212. *Retusa umbilicata* (MONTAGU)	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..
t	213. – *truncatula* (BRUGIÈRE)	..	..	..	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..
t	214. – *obtusa* (MONTAGU)	..	..	..	..	..	..	..	..	..	..	..	..	..	..	+	..	..	..
t	215. *Scaphander lignarius* (L.)	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
t	216. *Roxania utriculus* (BROCCHI)	..	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..
t	217. *Philine aperta* (L.)	..	..	..	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..
t	218. – *scabra* (MÜLLER)	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..
b	219. – *quadrata* (S. WOOD)	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..	..
t	220. – *punctata* (ADAMS)	..	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..	..	..
t	221. – *pruinosa* (CLARK)	..	..	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..
c	222. – *Loveni* (MALM)	..	..	..	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..
t	223. *Akera bullata* MÜLLER	..	..	..	..	..	..	..	..	..	..	..	..	+	..	..	..	..	..
	Totals Gastropoda	5	1	..	9	3	7	2	22	1	11	6	..	12	8	3	..	..	..
	Sum totals Pelecypoda & Gastropoda	33	17	2	22	6	14	4	31	8	30	9	2	22	12	6	2	2	1

Table 12. Decrease in number of molluscan species in the North Sea-Baltic Transition area and salinities of passage belts between the different waters of the transition area.

	Salinities $^0/_{00}$		Number of molluscan species								
	Minimum	Mean	Pelecypoda		Retained*) %	Gastropoda		Retained*) %	Pelecypoda and Gastropoda		Retained*) %
			no.	%		no.	%		Sum total no.	%	
North Sea–Skagerak	...	...	133	100	...	90	100	...	223	100	...
Passage belt 1	25	34	...	...	33	...	...	7	...	...	23
E & NW Kattegat	...	...	89	67	...	84	93	...	173	77	...
Passage belt 2	20	32.5	...	...	14	...	...	7	...	...	13
SE. Kattegat	...	...	71	53	...	72	80	...	143	64	...
Passage belt 3	15	30	...	...	13	...	...	34.5	...	...	22
S. Kattegat N. Belt Sea	...	...	53	40	...	41	45.5	...	94	42	...
Passage belt 4	12.5	25	...	...	20	...	...	13.5	...	...	17
S. Belt Sea	...	...	27	20	...	29	32	...	56	25	...
Passage belt 5	10	20	...	...	4.5	...	...	6	...	...	5
W. Baltic	...	...	22	16.5	...	23	26	...	45	20	...
Passage belt 6	9	15	...	...	10.5	...	...	23	...	...	15
Deep Baltic Basins	...	...	8	6	...	3	3	...	11	5	...
Passage belt 7	7	10	...	...	2	...	...	3	...	...	2.8
E. Baltic & S. Gulf of Bothnia	...	...	5	4	...	...	...	...	5	2.2	...
Passage belt 8	4	5	...	...	3	...	...	...	...	...	1.7
N. Gulf of Bothnia	...	...	1	1	...	...	...	...	1	0.5	...

tion of the sea water may thus be much more pronounced in the mollusca than in the total fauna of the Baltic, which, it was suggested by REMANE (1940, p. 6), is reduced to half at 17–18 $^0/_{00}$ salinity.

The behaviour of mollusca in relation to changes of salinity is further illuminated by the vertical distribution of the following species:

Mytilus edulis L. belongs to the epifauna; it is commonly found above 10 m. in marine areas around Denmark, where it lives on stones, rocks etc. In the Baltic the mussel also settles on the level bottom at depths down to about 40 metres.

Astarte borealis (CHEMNITZ) is considered to be a relict in the Baltic area by some authors. It occurs in great numbers particularly in the deep Bornholm and Arkona basins, while it is found at shallower depths in the Kattegat, which has a higher surface salinity than the Baltic.

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*) Percentage of molluscs which do not occur in subsequently listed regions of lower salinities.

Astarte elliptica (Brown) has a similar distribution in the Baltic and the Kattegat as *A. borealis*.

Cardium edule generally prefers the shallow waters in marine areas, and here it lives mainly at about 2–3 m. depth. In the most brackish parts of the Baltic it is, however, found down to 20–30 m.

Macoma baltica has a vertical range both in marine areas and in the Baltic corresponding to that of *C. edule*. It may be found to depths of 50 m. or more in the Baltic.

Mya arenaria is found mainly above 6–7 m. in marine areas, whereas it has invaded much deeper levels (down to about 40 m.) in the Baltic.

Retusa obtusa lives on *Zostera* and other seaweeds at relatively shallow levels (above about 20 m.) in marine areas. In the Baltic Petersen (1888) has found it at about 60 m.

Hydrobia ulvae is a shallow water species that is mainly found above 6–8 m. in marine water. It has been reported from about 20 m. in the Baltic.

Johansen (1916) was the first to draw attention to the peculiar vertical distribution of these molluscs, with the exception of *Retusa obtusa*. He assumed salinity to be the limiting factor, while lack of competitors and enemies, and the relatively low temperature of the water were the causes favoured by Jensen & Spärck (1934, p. 129). In their description of *Macoma baltica*, Jensen & Spärck also mention the possibility that the higher salinity of the deep water masses may possibly account for the distribution of *M. edulis* and *M. baltica* in the Baltic.

The present writer adheres to the hypothesis that salinity is the main controlling factor. The peculiar hydrographic conditions of the Baltic are undoubtedly mainly responsible for the "abnormal" distribution of the species mentioned. The accumulation of the most saline water masses near the bottom where it fills the deep basins and hollows, and the "ceiling" of brackish water above, may favour the settling of the larvae at depth. It should, however, be added that the lack of enemies, echinoderms for instance, may well play an important part in the success of the mollusca in the Baltic, while it may be questioned whether competition from other mollusca is of significance. Remane (1940, p. 16) has termed the submergence of species due to salinity (here called salinity submergence) "Brackwasser Submergenz".

The change of biotope, and the occurrence of the species under discussion at depth must undoubtedly be due mainly to salinity submergence of the larvae. This leads to the inference that even though mollusca are able to withstand considerable variation in salinity, as for instance in the case of *Hydrobia ulvae*, they tend to approach the optimum as closely as possible, if they have a choice.

In table 13 the salinities in the deep Bornholm basin are shown as an example of the great vertical variation of this environmental factor. It is only to be expected that the fauna will reflect these variations. The occurrence of *Astarte borealis* and *A. elliptica* in this basin is accordingly explained as salinity submergence.

Table 13. Salinity of the Bornholm Basin 1949–52*).

	1949–50			1951–52		
Depth	Minimum	Maximum	Mean	Minimum	Maximum	Mean
0 m.	7.41 $^0/_{00}$	8.06 $^0/_{00}$	7.77 $^0/_{00}$	7.12 $^0/_{00}$	8.21 $^0/_{00}$	7.79 $^0/_{00}$
50 -	7.96	12.77	10.26	8.60	13.77	10.69
60 -	7.96	15.17	13.21	12.61	17.70	15.10
100 -	15.43	17.68	16.78	19.85	21.09	20.55

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*) Calculated on the basis of the data in the Nautical-Meteorological Annuals.

4. MARINE ANIMAL COMMUNITIES

Aggregations of animals of similar aspect, and living under similar environmental conditions on the sea bottom, were termed animal communities by C. G. JOH. PETERSEN (1913) who was probably the first to introduce this concept. From quantitative studies using his bottom sampler, PETERSEN obtained an extensive knowledge of the various faunal regions in Danish waters. The concept of the community was established by analogy with plant associations, thus emphasizing the mutual inter-relationships between the different members of the faunal communities, and considering the animals from the viewpoint of producers and consumers in relation to their physical environment. PETERSEN was aware of difficulties regarding the definition of the communities, as appears from the following quotation (1913, p. 27): "It should not be thought that a very accurate eye, great experience or a very intimate knowledge is required for discovering and separating the above mentioned animal communities in the Danish waters; we can see at once, even on using the dredge that there is a great difference between them, but their characterization has been found difficult and further we have known too little about the quantity of common animals on each m^2".

The communities were named after species that were considered characteristic owing to their abundance, their weight or some other quality. These species were related to the guide fossils of the geologist and were particularly chosen from among the molluscs and echinoderms.

Regarding the recognition of the characteristic species PETERSEN says (1913, p. 4): "It is— —impossible by means of a single valuation list, giving the number and quantity of the species of animals from a certain community, to directly indicate the animals characteristic of that community. Only by experience gained from different places are we able to determine this.— — —The animals, which are not seasonal and which compose an important part of the whole mass of the community owing to number or weight, will presumably be best suited for characterizing the community and must also be considered as giving a good idea of the outer conditions on which the community is dependent."

MAC GINITIE's (1939) discussion of littoral-marine communities reveals that a purely objective means of defining communities had not been found, since he said: "The first problem is to determine what constitutes a community, that is, to delimit or set boundaries.— — —I know of no way of making any hard or fast rule for determining the limits of a community other than the good judgement of the investigator".

The problem of defining the community was also discussed by REMANE (1940, p. 32) who correctly pointed out that any classification such as that of communities, suffers from being schematic, and therefore has limitations. If we want to obtain a true picture of the ecologic distribution of the animals we have to realize this fact. The advice given by MAC GINITIE to ecological investigators: to present the material in a concise, understandable way, using a minimum of technical language, could also be used advantageously by other scientists. In the case of communities we should also realize that the concepts of different authors may be different.

It would carry us too far to enter further into the problems of the marine animal communities. Reference may however be made to the papers by C. G. JOH. PETERSEN (1911, 1913, 1914, 1915 and 1918), FORD (1923), DAVIS (1923), HAGMEIER (1925, 1929), BLEGVAD (1922, 1930), MOLANDER (1928), GISLEN

(1929, 1930), SPÄRCK (1931, 1933, 1937), THORSON (1933, 1934), MAC GINITIE (1939), REMANE (1940) and HESSE (1952) in which there are further references. Particularly the papers by GISLEN and REMANE include comprehensive bibliographies, and the discussions on methods and concepts by SPÄRCK (1937), MAC GINITIE and REMANE give a good account of the recent state of ideas concerning the marine animal community.

What particularly concerns us is the significant relationships between the animal community and its environment, a matter to which several of the authors named above have drawn attention. PETERSEN (1914) emphasized the importance of the animate environment, and MOLANDER (1928) stated that it was possible to establish connections between the distribution of the communities in the Gulmar Fjord, the hydrographic conditions, and the nature of the bottom deposits.

Reviewing the literature on marine animal communities, there can hardly be any doubt that the existence of different communities is dependent on the combination of specific environmental factors and the adaptive powers of the animals concerned. However, the present state of knowledge regarding the life histories of the animals, and the characterization and distribution of the communities, does not admit of far-reaching generalizations concerning the relationship of the individual community to its physical environment.

This brief treatment of communities has been included in the discussion in spite of the extremely poor inferences which may be drawn at present, partly for the sake of completeness, and partly on account of the great importance which may be ascribed to the recognition of animal communities both in recent and fossil faunas. This topic is discussed further in the following.

THE AGE OF THE MOLLUSCAN ASSEMBLAGES OF THE ARNUM FORMATION

Remarks on Correlation Procedure

Biostratigraphic correlation is actually a statistical science. It deals with the occurrence or non-occurrence and the frequency of occurrence of fossils and fossil biologic features, and inferences on probabilities are made on such data. Several faunal groups are generally compared with regard to the species they have in common, and similarities and differences are outlined. The inclusion of stratigraphic successions both of strata and fossils in the procedure of correlation may sometimes obscure the picture, but the statistical nature of biostratigraphy remains basically unchanged.

The use of megafossils in stratigraphy has generally been limited to the demonstration of unique species to serve as index or guide fossils, or to the comparison and correlation of faunal lists. The latter method will be briefly discussed on account of its frequent use.

A faunal list may be arranged in tabular form as shown for instance in table 14, p. 422, where it includes a primary column (A) in which the species of the fauna to be correlated are listed taxonomically, alphabetically, or otherwise. Secondary columns (B, C, ...) indicate the presence or absence of the species of the primary column in other fossil localities, generalized faunas, stages, etc., which are classified stratigraphically. The percentages of the species of fauna A which are also present in the faunas B, C, etc., are generally calculated and compared. Inferences regarding stratigraphical relations are finally made on this basis.

This or similar "percentage" methods have been applied by several workers on faunas from different formations. The following authors may be mentioned from the literature on Tertiary faunas: GOTTSCHE (1878), GRIPP (1915), KAUTSKY (1925), STAESCHE (1930), PEYROT (1933), SORGENFREI (1940), VIGNEAUX & MAGNE (1951).

In 1940 the writer pointed out that percentages calculated in this way are not significant, since the total numbers of species in the faunas dealt with have an important statistical effect on the percentages.

The comparison of two faunules with respect to species is closely considered a test of whether they may be random samples of one fauna. This means that in comparing two faunules we try to estimate a statistical probability.

Species in a sample are statistical events. If n designates the total number of species in a fauna, and r and s the number of species in two random faunules to be compared with n, the probabilities P_r and P_s of the events r and s are approximated by their relative frequencies in relation to n:

$$P_r = \frac{r}{n} \quad \text{and} \quad P_s = \frac{s}{n}$$

From these equations we may derive expression for the probability P_α of the occurrence of α species in both r and s:

$$P_\alpha = P_r\,P_s = \frac{rs}{n^2} \tag{1}$$

It is a fact that the total number of species in fossil faunas is unknown in most cases. We are generally forced to consider sections of faunas as practical approximations to the whole faunas. In the present example we may consider fauna n as the unknown total number of species in a certain fauna, and r and s as the two faunules to be compared with each others. If we presuppose that r and s are samples of one fauna, and α the species in common, it is possible to arrive at two further equations for the probability P_α:

The relative frequencies of α related to r and s respectively are:

$$P'_\alpha = \frac{\alpha}{r} \quad \text{and} \quad P''_\alpha = \frac{\alpha}{s}$$

Hence the probability P_α of α species occurring both in r and s is:

$$P_\alpha = P'_\alpha P''_\alpha = \frac{\alpha^2}{rs} \tag{2}$$

by applying the classical rule of the probability of simultaneous occurrence of two independent events being the product of their respective probabilities.

Since by definition:

$$P_\alpha = \frac{\alpha}{n}$$

we can substitute α with nP_α which in accordance with formula (1) is:

$$n\,P_\alpha = n\,\frac{rs}{n^2} = \frac{rs}{n}$$

in formula (2) which then may be written:

$$P_\alpha = \frac{\left(\frac{rs}{n}\right)^2}{rs} = \frac{rs}{n^2}$$

and it is thus shown that formula (2) is identical with formula (1).

P_α may finally also be expressed as the relative frequency of a related to $n' = r+s-\alpha$, n' being considered as an approximation to fauna n.

$$P_{\alpha'} = \frac{\alpha}{n'} = \frac{\alpha}{r+s-\alpha} \tag{3}$$

The relations between equations (1), (2), and (3) can be illustrated by assuming:

$$r \to n;\ \text{then}\ \alpha \to s,$$

and P_α will in all three cases show the following convergence:

$$P_\alpha \to \frac{s}{n}$$

It is evident that (3) yields higher values for P_α than (1) and (2).

P_α may serve as a preliminary estimate of the faunal affinity between groups to be compared, even in cases where age differences are obvious. If P_α is multiplied by 100, the affinity is expressed in percent.

Various objections may be raised against the use of P_α as the only criterion of correlation. One is that the number of specimens has not at all been considered. However, P_α is certainly of much greater significance than the "percentage" method explained above.

In stratigraphic correlation it is believed to be advantageous to calculate P_α by means of equation (2) which implies the smallest errors in P_α.

Formula (3) may possibly be more suitable for comparisons intended for use in facies relationship studies.

Only faunal lists from well defined formations which singly consist of beds of practically the same age, or display a high degree of uniformity are fitted for correlation according to the suggested correlation test. However, as it was pointed out in the introduction (p. 11–19), it is unfortunalety very difficult to define Miocene molluscan faunas on the basis of data in the literature. This regretable situation has been mainly brought about by the lumping together of species from different localities in the lists of fossils, and by failure to discriminate between rock-stratigraphic and time-stratigraphic units. In the European Miocene fauna it is thus extremely difficult to obtain a clear concept of the individual faunas of the Aquitanian Basin, the Basin of Vienna and the Mediterranean area.

The writer has accordingly restricted calculation of correlation ratios to the faunas of the North Sea Basin. The faunas of the columns in table 14, p. 422 are:

Germany:

Vierlande stage	Fauna at Itzehoe	(Gripp 1914)
Hemmoor stage	- - Hemmoor	(Kautsky 1926)
Reinbek-Dingden stage	- - Reinbek	(Gottsche 1878)
Glimmerton stage	Total fauna	(Banke Rasmussen 1956)

Belgium:

Boldérien	- -	(Glibert 1945–1954)
Horizon of Houthaelen		
Anversien		

Denmark:

Klintinghoved clay	- -	(Sorgenfrei 1940)
Gram formation	- -	(Banke Rasmussen 1956)

The publication of the fauna of the "Middle Miocene" in Holland has not yet been completed, and the "Middle Miocene" of Denmark is not a well defined entity. The species of these stratigraphic units are accordingly of rather restricted value in stratigraphic correlation.

The Biostratigraphic Record of the Miocene of the North Sea Basin

Maximum thickness of the Miocene of Northwest Germany is about 520 m. according to Schad (1947). Knowledge of the molluscan faunas of this sequence is extremely limited as indicated by the literature. The fauna of the Vierlande stage is known chiefly from displaced floes of the Vierlande formation in the glacial drift, and the Hemmoor fauna has been found in fossiliferous boulders which were also embedded in the glacial drift. Only the Reinbek and the Glimmerton faunas have been collected in situ.

It is particularly due to the efforts of GRIPP (1914, 1915, 1933, 1956) that the difficult correlation problem of these Miocene faunas was preliminarily solved as already stated p. 13–14. However, a completely satisfactory biostratigraphic subdivision of the Miocene in the North Sea Basin will first be approached when a sufficient number of well sections having fossiliferous beds in all important formation units have been drilled and adequately examined. The stratigraphic position of both the Vierlande and the Hemmoor faunas, as known from the glacial drift occurrences cannot be determined very exactly in drilled sections. The correlation of subsurface intervals with corresponding stages may, therefore, in many cases prove to be erroneous.

GRIPP (1915, 1933), KAUTSKY (1925) and HINSCH (1952, 1955) have selected a number of index fossils for the different stages and substages of the Miocene. Some of these may be genuine index fossils, while others certainly will be found to have a more extensive vertical range than known at present. In this connection reference should be made to BANKE RASMUSSEN's discussion on the subdivision of the German Glimmerton (1956, p. 126 etc.).

Very few authors, if any, have tried to make an estimate of the total number of molluscan species in the faunas of the Tertiary seas. This is no doubt due to the fact that the need for such an estimate was not previously felt. However, the above discussion on correlation procedure and the problem of the validity of index fossils, show that it is very important to have some idea concerning the total number of species in a fauna.

An estimate of the total size of an inadequately known fossil fauna should be based on knowledge of the faunas of recent seas. It is admittedly true that we cannot be certain that the number of species was the same in fossil faunas as it is in living faunas. There is, however, a reasonable probability that the number of species was of a similar order of magnitude in fossil faunas as in related recent faunas. The following table showing the number of species in the seas around Europe are accordingly given for comparison. The numbers of species are undoubtedly too small because knowledge of the marine faunas has increased considerably since the papers from which the data have been taken were published. Exact figures are, however, not particularly important, since at best only a rough estimate of the fossil faunas can be obtained.

	Number of species
Northern boreal and arctic fauna off Norway northeastwards from Lofoten (SARS 1878)	549
British Waters (JEFFREYS 1863–1869)	552
Portugal (NOBRE 1932)	784
Mediterranean off southern France (BUCQUOY, DAUTZENBERG & DOLLFUS 1887–1898)	745
Mediterranean (MONTEROSATO 1878 acc. to BUCQUOY, DAUTZENBERG & DOLLFUS 1887–1898)	1000

The faunas of the northwest European Miocene formations were undoubtedly boreal or boreo-lusitanian as stated below, p. 415. It is reasonable therefore to conclude that each marine stage at least included 500 to 600 species, and that the richest faunas comprised 700 to 800 species.

In making this inference it is of interest to notice the possibility offered by formulas (1) and (2) p. 404 of calculating the total number of species in a fauna. From these two formulas we get the equation.

$$\frac{rs}{n^2} = \frac{\alpha^2}{rs}$$

whence

$$n^2 = \left(\frac{rs}{\alpha}\right)^2;$$

and taking the square root

$$n = \frac{rs}{\alpha}, \tag{4}$$

n being the total number of species in the fauna from which the faunules r and s were taken.

The faunule of the Arnum formation comprises 266 species of which 141 are in common with the Hemmoor faunule which consists of 311 species. Provided these two faunules belong to the same fauna, which well might be possible, then by using formula (4) and substituting r, α, and s with 216, 141, and 311 respectively we get the total number of species in the fauna

$$n = \frac{266 \times 311}{141} = 586.7 = 587 \text{ species}.$$

Provided the faunules of the Arnum formation and the Reinbek-Dingden stages belong to the same fauna then correspondingly:

$$n = \frac{266 \times 107}{52} = 547.3 = 547 \text{ species}.$$

The agreement between the figures thus calculated and the estimated number of species given above is remarkable. The two approaches are quite independent, and the estimate on the basis of recent faunas was made long time before the formula was developed. The suggested number of species in the Miocene formations of northwestern Europe is therefore apparently a rather close approximation.

Comparison of the estimates and the calculation of the number of Hemmoor species with the number of species now known from the different stages shows how far we are from knowing the entire Miocene fauna. A consequence of our inadequate knowledge is that considerable reserve should be exerted in the definition and use of index fossils in the present premature phase of Miocene faunal research.

Correlation of the Assemblages of the Arnum Formation with known Molluscan faunas of the North Sea Basin

The Vierlande and Hemmoor faunas are probably composite assemblages of fossils from different horizons. In correlating the faunal zones of the Arnum formation in Southern Jutland with the German faunas, it is therefore reasonable to regard all the fossiliferous beds as belonging to one fauna. This is justifiable because these fossiliferous beds are probably all parts of the same marine stage, and furthermore the dominant species occur in practically all the horizons.

It appears from table 14, p. 434, that the correlation ratio P_α of the faunas of the Arnum formation and the Hemmoor fauna is the maximum figure, if P_α calculated by using formula (2) p. 404 is considered. If we assume about 500 species in the Miocene faunas, it is possible by means of formula (1) p. 404 to calculate the probability, P_{α_1} of the species which should be common to the fauna of the Arnum formation and the other faunas provided they were random samples of one fauna, as also shown in the table. Finally α_1 has been calculated and listed beneath the respective figures for α.

It is obvious that the closest agreement between α and α_1 is displayed by the faunas from Reinbek-Dingden, Houthaelen, Hemmoor, and Klintinghoved. The figures for α are too low in the other faunas to suggest any marked cronological affinity.

The conclusion based on this purely statistical test and on the stratigraphy of the well sections is that the fauna from South Jutland has probably the closest affinity with the Hemmoor fauna. The affinities with the Klintinghoved and Reinbek-Dingden faunas are conspicuous enough to suggest continuity in the North Sea Basin from the Klintinghoved fauna to the Hemmoor fauna, and from the latter to the Reinbek-Dingden fauna.

The reference of the Arnum fauna to the Middle Miocene as defined in Northern Germany agrees with its stratigraphic position below the upper Miocene Gram formation as stated p. 27. It is considered useless to attempt a more detailed correlation with the German sequence at present. This is substantiated by the discontinuous faunal records of Northwestern Germany compared with the Arnum formation, the composite nature of the Hemmoor fauna, etc. It is suggested, therefore, to use the Arnum formation as a reference in future biostratigraphic correlation since without any doubt it displays the best known faunal development.

It would have been very interesting to compare the Arnum fauna with the rich molluscan assemblages of the Aquitanian Basin. However, the obscurity of the formations and their correlation in the Aquitanian Basin itself renders any comparison very unsatisfactory at present. VIGNEAUX & MAGNE (1948 & 1952) and GRIPP & MAGNE (1956) have recently reported the preliminary results of study of the Miocene faunas encountered in drilled wells in various parts of the Aquitanian Basin. It is claimed by these authors that both the Aquitanien and the Burdigalien are facies of one faunal stage, the Girundien. The Aquitanien is referred to as Girundien inférieure, and the Burdigalien is identified as Girundien supérieure. A number of index fossils are designated for the substages of the Girundien and the Helvétien.

It is hoped that these preliminary papers will be followed by thorough descriptions of species and faunas. Lists of index fossils such as those published, are of rather little use without documentation, and statistics on the entire faunas are necessary in order to estimate the value of the index fossils as well as the paleoecological development of the faunas. A series of fossiliferous well samples from a thick and important Miocene sequence such as the one encountered in the Aquitanian Basin, ought to be a challenge in this connection.

There is not yet any sound paleobiologic basis for a reliable and detailed correlation of the beds in the Aquitanian Basin with those in the North Sea Basin, and it will be necessary strictly to redefine the formations of the Aquitanian Basin by means of explicitly described sedimentary sections, and also to give a comprehensive record of the faunal development in each formation unit, before an exact time-stratigraphic subdivision can be established.

ANALYSIS OF THE FAUNA AND ITS DEVELOPMENT

Remarks on the Sedimentation of Molluscan Shells

The assemblages of molluscs in a formation or in a fossiliferous bed is generally called the molluscan "fauna" of the lithologic unit concerned. It is of importance to remember that the term "fauna" may often be inappropriate, insofar as the assemblages of shells are in many cases accumulated after the death of the animals.

JOHANSEN (1901) studied the transport of shells by wave actions and currents in Danish Waters and in the Atlantic off the Färöes and Iceland. He found that wave action forms a belt of movement parallel to the coast down to a depth of about 15 m. along open coasts. Shells are moved up or down in this belt. An upward movement prevails on gently dipping shores, while on steep, rocky shores the shells mostly move into deeper water.

Shell accumulations in the belt of movement accordingly do not represent true molluscan animal communities.

Although the shells of molluscs living beyond the 15 m. contour are hardly ever moved up to the shore line, it cannot be inferred that they remain where the animals lived. Very little is known about the transport of shells at depth, but it must be assumed that currents and even wave action contribute considerably to the spreading of shells on the sea bottom even below a depth of 15 m.

The dispersal of shells on the sea bottom is of some use from a biostratigraphic point of view, but we have to realize that the paleoecological background of biostratigraphy thereby becomes rather intricate. One useful conclusion to be drawn from JOHANSEN's observation, is, however, that molluscan specimens which show traces of wave action and posthumous transport must have had their upper limit of distribution at depths less than 15 m., provided they have not been redeposited. Another rule is that fossil molluscan assemblages are generally only approximations to the original molluscan association. This does naturally not mean that they always are poor approximations.

The Significance of the Fossil Molluscan Assemblages of the Arnum Formation

The molluscan assemblages from the well samples of the Arnum formation are not only approximations of molluscan associations on account of sedimentation, but also on account of sampling. Although the drilling method used should secure relatively well located samples from the borehole, it has to be realized that the samples include fossils from a vertical interval of the sedimentary section.

The term "fauna" has been used abundantly in the present paper for fossil assemblages of mollusca. Although it is almost a truism to say that nobody would think about more than the molluscan fauna in this connection, the particular application of the term should be emphasized. The statistics on the different samples have been provided in order to create a basis for a paleoecological evaluation. It should, however, be understood that our ignorance of a very large part of the fauna, including the non-molluscan benthonic and pelagic animals, constitutes a considerable limitation of our endeavours. If, therefore, terms like community, fauna, associations, etc., which have a very strict meaning in recent marine biology, are used in the following it should be remembered that this is done with all the reservation required by the nature of the material and the incomplete faunal record.

Finally an answer should be given to the question whether there is any basis at all for discussing the present molluscan assemblages as representing approximations of animal communities.

Study of the list of fossils in the samples shows that the commonest species occur in almost all the samples. A comparison of the fossil content of some of the closely spaced samples furthermore reveals that the percentages of the individual species are much the same. It seems reasonable to conclude that this is due to a rather slow change of the aspect of the fossil communities concerned. This means, however, that it is permissible to discuss the approximations to molluscan faunules (constituted by the fossil assemblages of the samples) as if they were identical with faunules.

The Faunal Development. A study of table 15, p. 436, which lists all the species found in the samples, will show that some species attain relatively high percentages in most samples. Those species which make up or exceed 1 % of the fossils in a sample are shown on table 16, p. 460, and these 30 species are termed "abundant" in the following discussion, whereas the rest are termed "rare". Particularly conspicuous percentages and maximum figures for individual species are printed in heavy type. The samples from the two wells at Arnum are arranged in a single group according to depth, this has been done because the two wells are located only a few metres apart and therefore the samples can be considered representatives of one section.

The Evidence of the Abundant Species. The fossils and percentages in table 16, p. 460, should be discussed first.

The sum of percentages of this small number of species show that they constitute the most important group of the fossils by number, actually between 80 and 98 percent of the total numbers of fossils in the samples. A remarkable feature of the sum totals of the percentages is that they increase almost uniformly from the lowest to the uppermost sample in the Glejbjerg, Arnum and Toftlund wells. In case of the Gramby well the sum of the percentages is very high in all samples, practically agreeing with the figures for the uppermost samples in the other wells. The assemblage of the sample from 28–40 m. in Arnum well 150.13 which is referred to the Gram formation is clearly different from the assemblages immediately below by its lower percentage of "abundant" species. This suggests a pronounced change in environments in passing from the Arnum to the Gram stage. The assemblage from Bramminge is of the high percentage type.

The increase in the number of specimens of abundant species during the sedimentation of the Glejbjerg, Arnum and Toftlund sections is doubtless due to some selective factor. The assemblages at Gramby were apparently subjected to less consistently changing factors in the environment.

A study of the sedimentary records of the the wells (p. 21-27) reveals that there is apparently no permanently increasing or decreasing quality or quantity in the sediments which could be responsible for the increase of the number of specimens. The selective factor does not therefore appear to be related to the substratum.

Since depth of water might be the unknown factor, it should be mentioned that the sample from Bramminge displays the typical features of a shore assemblage. The shells are generally very robust and are the most heavily rolled of all shells examined. This fact, and the experience that thick tests are the rule in recent litoral shells proves that the Bramminge molluscs represent a shore assemblage from the belt of movement (see p. 407). The animals concerned lived accordingly in the litoral region with their upper limit of distribution somewhere between the shore line and depths of about 15 to 20 m.

There is good evidence for shallow conditions also in case of the 53.75 m. horizon in the Glejbjerg well. However, the general impression is that the shells are less rolled than at Bramminge. It is reasonable, therefore, to suggest that at Bramminge the selective factor was grinding resulting from wave action and surf, which only the strongest shells could resist.

The other assemblages with high specimen percentages for the abundant species are not littoral—or at least not shore—assemblages. Accordingly the selective factor was probably not wave action. Since thus neither substratal features nor bathymetric conditions may come into account, the only solution is that the unknown factor is related to the physical properties of the water body, or that it is some biotic factor. The last possibility seems to be rather improbable since there is no evidence for such a factor.

Of the physical properties of the water, temperature and salinity are of greatest interest, but it is difficult to decide which of these is likely to have been most important. However, the relatively thin tests of the shells in the uppermost samples is weak evidence in favour of salinity being the responsible factor. It has not been possible to find any evidence in support of a temperature change which would be more significant than the suggested salinity difference.

The inference to be made from the faunal changes and properties of the sediments and shells is that there was a steady decrease in salinity during the deposition of the Arnum formation at Glejbjerg, Arnum, and Toftlund.

The Gramby assemblages apparently reflect a fundamentally different development from the other three sections. The general aspect at Gramby is similar in some respects to the topmost assemblages at Glejbjerg, Arnum, and Toftlund, while the shells are not as worn as the Bramminge shells. It seems reasonable to explain the high specimen percentages of the abundant species at Gramby by assuming that brackish conditions such as suggested during the last sedimentation at Glejbjerg, etc., prevailed all the time. Gramby is the most marginal location of all wells treated, and it should be recalled that siderite beds and concretions are a particular feature of this section. The abundance of siderite may indicate the flow of iron rich fresh water from a land area and subsequent precipitation in the more or less brackish environment. Both the character of the sediments and the rather extreme aspect of the faunal assemblages thus support the assumption of a brackish environment.

The conclusions is that Gramby was a marginal area close to a shore where river water diluted the sea water creating extreme environments in which a fauna of a brackish water type lived.

Relations between Species. The frequency of occurrence of the individual species in table 16, p. 460, reveals some striking relations between allied species. The most impressive distribution is displayed by the 4 species of the genus *Nassa*, specially arranged at the base of table 16.

The occurrence in the Glejbjerg well is the most illustrative. *Nassa cimbrica* and *N. Schlotheimi* obviously dominate in the samples from 42 m. and upwards while *N. Fuchsi* and *N. Facki* are mainly found below this depth. Comparison with the other assemblages disloses similar features in the Toftlund and Arnum wells, while the Gramby well maintains its special position.

It is very tempting to explain the occurrence of the *Nassae* similarly to the increase of the specimen percentage of the abundant species, by assuming a decrease in salinity to have been favourable for *N. cimbrica* and *N. Schlotheimi*, and unfavourable for *N. Facki* and *N. Fuchsi*. This hypothesis is supported by the Gramby assemblages where *N. Facki* and *N. Fuchsi* are very rare while *N. cimbrica* and *N. Schlotheimi* are found in practically all samples.

A close examination of the frequencies in the Gramby, Toftlund, and Arnum samples shows, however, that the change of salinity is not a sufficient explanation. *N. cimbrica* tends to increase in number during sedimentation both in the Gramby assemblages, which probably represent relatively continuous brackish environments, and in the more marine assemblages at Toftlund and Arnum. It is furthermore remarkable that the couple *N. cimbrica—N. Schlotheimi* is nearly always dominant to *N. Fuchsi—N. Facki* in the samples from Toftlund and Arnum in which they occur together.

It is impossible to arrive at a safe conclusion regarding the reasons for the particular vertical distribution of the 4 *Nassae*. The frequencies suggest *N. Fuchsi* and *N. Facki* to have been the dominant species during the lower, most marine stage of the sequence, and apparently *N. Fuchsi* was biologically the stronger of the two. The rare occurrence of these species at Gramby indicates that they may have been sensitive to a decrease in salinity.

N. cimbrica and *N. Schlotheimi* seem therefore to have been competitive to *N. Fuchsi* and *N. Facki*, the latter two species being at last almost completely conquered. It is interesting to note that *N. cimbrica* and *N. Schlotheimi* were apparently also competitors themselves. It appears that high frequencies of *N. cimbrica* were associated with low frequencies of *N. Schlotheimi*, since *N. Schlotheimi* increases considerably in the samples where *N. cimbrica* is absent or rare. With one exception (Arnum 107.5 m.) *N. cimbrica* is always more numerous than *N. Schlotheimi* in assemblages where they occur together.

N. cimbrica and *N. Schlotheimi* were undoubtedly less sensitive to a decrease in salinity than *N. Fuchsi* and *N. Facki*. However, their high frequencies compared with *N. Fuchsi* and *N. Facki* even in the lower assemblages of the Toftlund and Arnum sections—which have a genuine marine aspect—indicate, as is mentioned, that the superiority of *N. cimbrica* and *N. Schlotheimi* was not alone due to decrease of salinity. Their success was probably in part secured by some biological preference other than adaptability to salinity change. It is, however, not possible to verify this assumption at present.

PETERSEN (1915, p. 17) was possibly the first to recognize a competitive attitude between allied molluscan species, displayed by their distribution in different animal communities on the recent sea bottom of Danish and adjacent waters. In discussing the distribution of *Macoma calcarea* in the Oslo (Christiania) Fjord he writes: "HJORT has (l.c.) called attention to the slight degree of circulation, and paucity of oxygen, etc., in the water of the closed fjords; even this, however, does not explain, why Macoma calcarea should exhibit particularly rich development here rather than elsewhere; if it can live here, then one might well suppose that it could live anywhere. I may in this connection refer to my remarks in Report XXI, p. 29 ff. but would here briefly mention that we have doubtless in this case to reckon with the question of competition between different species, where chemico-physical explanations alone will not suffice. In my opinion it is highly likely that the struggle of species against species may be a far more important factor in the formation of communities than is generally supposed; the destruction or exclusion of certain forms on a given ground, instead of being occasioned by the slight differences in external conditions, might well be rather due to competition on the part of other species better adapted to such conditions as there prevail.—In this connection also I recall a circumstance noted years ago on the cruises of the "Hauch"; that closely related species, especially those of the same genus, are scarcely ever found living in one and the same area of a given water; they may meet, and fight out their war on a frontier line, but are never found to cover the same area of distribution altogether. Each has its own region, its own community. The competition must be greatest between those species which are most closely related".

It is of course very difficult to decide the part played by environment and the "competitive force" in the distribution of pelecypoda, in which the "active" phase is largely identical with the larval stage, which is probably much influenced by the environment. In predatory snails such as species of *Nassa*, however, it is easy to immagine that some may have biological preferences by which they are able to "fight their war" more succesfully than their competitors.

The evidence of balanced frequencies in the four *Nassae* appears to be relatively good, and it should be mentioned that there may be another instance of antagonism in the assemblages under discussion. In question are the species *Leda Westendorpii* and *Yoldia glaberrima* which seem to alternate in frequency in the Arnum and Toftlund assemblages. It must be admitted, however, that the evidence is weaker than in the *Nassae*.

Before ending the discussion of the abundant species shown on table 16, it might be useful to group them in accordance with their behaviour during the sedimentation of the sequences at Glejbjerg, Toftlund, and Arnum. The species of the progressive group generally increase their frequency from the lower to the upper assemblages, the stationary group maintains its relative frequency, and the recessive group decreases in number of specimens. Some species were considered inadequate or too poorly represented to provide a basis for an estimate.

This subdivision of the species must be considered a preliminary attempt at characterisation. Much more material is needed before it can be decided whether the subdivision is valid, and the answer to the question of the significance of recession, progression, and status quo in the individual species must also be postponed.

Table 17. Behaviour of abundant species during sedimentation of the Glejbjerg, Toftlund and Arnum sequences.

Recessive	Progressive
Nucoloma hanseata	*Leda pygmaea*
Nassa Fuchsi	*Varicorbula gibba*
Nassa Facki	*Nassa cimbrica*
Gemmula boreoturricula	*Ringicula buccinea*
Fusiturris Duchastelii	

Stationary	
Leda Westendorpii	*Turritella tricarinata*
Leda emarginata	*Bittium tenuispina*
Yoldia glaberrima	*Aporrhais alata*
Kellyella rotunda	*Nassa Schlotheimi*
Thyasira cf. flexuosa	*Terebra Hörnesi*
Ervilia pusilla	*Retusa umbilicata*
Spisula subtruncata	*Spiratella atlanta*
Abra prismatica	*Vaginella depressa*
Saxicava arctica	

Inanimate Environment Relations. All sedimentary evidence suggests that the assemblages here dealt with mainly lived on a silty bottom and on seaweeds growing on the bottom. The question of salinity has been discussed above in the treatment of the abundant species, on the basis of which it was inferred that salinity decreased during sedimentation. The evidence on bathymetry and temperature requirements should finally be examined.

The Bramminge assemblage is, as already mentioned, a typical shore assemblage. We may, therefore, take it as almost certain that the species contained in this assemblage lived in water shallower than 15–20 m. Important shallow water species in this assemblage are:

Leda pygmaea
Yoldia glaberrima
Varicorbula gibba
Aporrhais alata
Nassa Schlotheimi
Nassa cimbrica
Terebra Hörnesi
Ringicula buccinea

It is essential to notice, however, that these species were not restricted to the shallow belt of movement. Their areas of distribution undoubtedly extended deeper than this part of the sea bottom.

In trying to make an estimate of the bathymetric conditions in the areas represented by the assemblages, the high frequencies of the "shallow water" species should be particularly considered. The abundance of these species and the evidence provided by the sediments are sufficient for assuming relatively shallow water not deeper than 20 to 50 m. during the main part of the period, and it was probably shallower during short time intervals in some parts of the area.

The temperature conditions can be estimated on the basis of still living species. The assemblages include 39 species of which representatives, or closely related species, still live in Lusitanian regions, and with few exceptions also in the Boreal region. Three species are also found in Arctic seas.

In using these species as indicators of climatic conditions we have to realize that the temperature requirements of the species may have changed since the deposition of the Arnum formation. Since it is unlikely, however, that all species should have altered their temperature requirements to the same extent, there is obviously no risk in suggesting the assemblages to be either of a Boreal or Lusitanian type.

Two species are of particular interest on account of their significant recent distribution viz. *Pecten tigerinus* and *Cancellaria cancellata.*

Pecten tigerinus is now almost the prototype of a Boreal species in the northern Atlantic. It extends from western Finmark to northern Spain on the west coast of Europe. *Cancellaria cancellata* is an almost as typical Lusitanian and subtropical species which lives in the Mediterranean and in the Atlantic from the coasts of Portugal to Senegal.

Although the evidence of these two species must not be overemphasized, it suggests that the fossil assemblages lived under Boreo-Lusitanian conditions comparable with the situation off the coasts of the northwestern part of the Iberian peninsula. Mean temperatures of the surface water in the North Sea area and off northern Spain and Portugal are shown in table 18 according to the maps of G. SCHOTT 1942.

Table 18.

Mean Temperature of Surface Water (°C).

	North Sea	Northern Spain-Portugal	Difference
Annual mean	9–10°	14–15°	5°
February	3– 5°	12–13°	8–9°
May	9–10°	13–15°	4°5°
August	15–17°	19–17°	3–4°
November	9–10°	14–15°	5°

The thermal situation of the Miocene Sea Basin was undoubtedly not identical to that of the Atlantic off Portugal and Spain. It is believed that there was a connection from the North Sea to the Atlantic south of England in the Channel area (GRIPP 1915, KAUTSKY 1925), and the middle Miocene deposits of Holland and Belgium support this hypothesis. It has to be remembered, however, that the Miocene Channel—if it existed—was certainly narrower than the recent strait between Dover and Calais. The North Sea Basin was accordingly probably a partly closed shelf basin, as it is to day, in which temperature variation was greater than in the open Atlantic. If we therefore assume that the temperature of the North Sea Basin was in general about 5°C higher than it is to day, and that the annual variation was similar to that now obtaining, we may have a rather accurate picture of the Miocene conditions.

Classification of the Molluscan Assemblages of the Arnum Formation

Since the assemblages of the Arnum formation obviously approximate the animal communities of the present seas, however indefinable in precise terms the latter may be, it is suggested that the fossil assemblages be classified in a similar way. It is proposed to follow PETERSEN's (1913) concept of the animals on the sea bottom being either producers or consumers, and to apply assemblage names consisting of the species names of the most characteristic producer and consumer followed by the term "assemblage".

By comparison with living mollusca it should be possible to subdivide fossil mollusca in a very generalized way into organic detritus or plant eaters, predatory animals, and animals of unknown feeding habits. The third group will certainly prove to be the largest both among living and fossil animals since relatively little is known about the nourishment of the majority of recent molluscan species. Reference is otherwise made to BLEGVAD (1914), SPÄRCK (1927), MOORE (1936), YONGE (1946), ANKEL (1948), and THORSON (1951).

In the case of the South Jutland fossil assemblages of the Arnum formation a detailed analysis is not intended. Interest has been concentrated on the abundant species, and it should be pointed out that the pelecypoda are classed among the producers together with species like *Aporrhais alata*, *Turritella subangulata*, and *T. tricarinata*. The species of the genera *Nassa* and *Natica* are without exception ranged among the consumers.

The following is the proposed classification of the assemblages of the different sections:

Glejbjerg

23 m.	*Varicorbula gibba—Nassa cimbrica*	assemblage
25 -	*Varicorbula gibba—Nassa cimbrica*	–
32 -	*Aporrhais alata—Nassa cimbrica*	–
38 -	(Atypical assemblage)	
42 -	*Spisula subtruncata—Nassa Schlotheimi*	–
53 -	*Aporrhais alata—Natica*	–
53.5 -	*Aporrhais alata—Nassa Fuchsi*	–
53.75 -	*Aporrhais alata—Nassa Fuchsi*	–
54 -	*Aporrhais alata—Nassa Fuchsi*	–
55 -	*Aporrhais alata—Nassa Fuchsi*	–

Bramminge

70–80 m.	*Aporrhais alata—Nassa cimbrica*	–

Ribe

113–114 m.	*Aporrhais alata* (*Venus multilamella*)—*Nassa Fuchsi*	–

Gramby

82.7–83.8 m.	*Aporrhais alata—Nassa cimbrica*	–
84.7–87.2 -	*Varicorbula gibba—Nassa cimbrica*	–
90.4–92.7 -	*Spisula subtruncata—Nassa cimbrica*	–
92.7–109.3 -	*Leda pygmaea—Nassa cimbrica*	–
109.3–110.9 -	*Spisula subtruncata—Nassa cimbrica*	–
110.9–121.5 -	*Varicorbula gibba* (*Leda pygmaea*)—*Nassa cimbrica*	–

Toftlund

75–100 m.	*Varicorbula gibba* (*Aporrhais alata*)—*Nassa cimbrica*	–
100–105 -	*Aporrhais alata—Nassa cimbrica*	–
105–110 -	*Aporrhais alata* (*Spisula subtruncata*)—*Nassa cimbrica*	–

Toftlund		
110–115 m.	*Aporrhais alata* (*Yoldia glaberrima*)— *Nassa cimbrica*	assemblage
Arnum		
28–40 m.	*Leda pygmaea*—*Nassa Schlotheimi*	–
62.7–62.9 -	*Spisula subtruncata*—*Nassa Schlotheimi*	–
53–83 -	*Leda pygmaea*—*Nassa cimbrica*	–
83–94 -	*Aporrhais alata*—*Nassa cimbrica*	–
95.0–95.3 -	*Aporrhais alata*—*Nassa cimbrica*	–
104.3–107.5 -	*Abra prismatica* (*Spisula subtruncata*)— *Nassa Fuchsi*	–
107.5 -	*Spisula subtruncata* (*Leda pygmaea*)— *Nassa Schlotheimi*	–

It appears as if all these assemblages are variations of the same theme: the *Aporrhais alata—Nassa ssp.* assemblage. This assemblage may be very closely related to the type of animal communities identified by PETERSEN (1913) in recent seas. The *Aporrhais alata—Nassa ssp.* "community" of the Arnum formation was apparently the community on the silty bottom of shallow waters, as evidenced by the Bramminge assemblage and the often small size and great numbers of individuals in the samples (see PETERSEN 1911).

CORRELATION OF THE WELL SECTIONS

The well sections may be subdivided biostratigraphically by means of the species zones of *Nassa Fuchsi* and *N. cimbrica**).

The *Nassa Fuchsi* zone is the lowermost biostratigraphic division of the known part of the Arnum formation. It must be noted that the lower boundary of the formation has only been encountered in the Ribe well, and that the fossil record of the drilled section in this well is rather poor. We do thus not know for certain whether *N. Fuchsi* is characteristic of the whole Miocene section of the Ribe well or not.

The upper boundary of the *Nassa Fuchsi* biostratigraphic zone is defined as the base of the *Nassa cimbrica* species zone. This boundary is relatively well defined in the Glejbjerg section at about 50 m. (–25 m.).

In the Bramminge sequence we only know that the assemblage at 70–80 m. belongs to the *Nassa cimbrica* species zone, which by definition is identical with the *Nassa cimbrica* biostratigraphic zone. The possibility exists that the base of the *N. cimbrica* zone is found below the 70–80 m. (–56– –66 m.) level.

The Gramby sequence as a whole must be referred to the *N. cimbrica* zone.

The Arnum section may represent the *N. cimbrica* zone from its top, which apparently is identical with the base of the Gram formation, to its base.

The Toftlund boring encountered only the *N. cimbrica* zone and stopped before the base of this zone was reached.

The base or the probable base of the *N. cimbrica* zone is shown on the cross section, fig. 2, p. 28.

It is impossible to decide with certainty on the basis of our present knowledge whether the appearance of *N. cimbrica* was a synchronous event in all sections. It has already been pointed out above that the possibility exists that *N. cimbrica* is a brackish water species. However, there is some evidence for *N. cimbrica* being an immigrant from outside the North Sea Basin. If this is so we are entitled to regard the base of the *N. cimbrica* species zone as a synchronous level.

It is not practicable to make a more detailed subdivision and correlation of the well sections on the basis of the present fossil evidence. One parallelism between the Toftlund and Arnum sections should, however, be mentioned. In comparing the frequencies of the abundant species in table 16, p. 460, it will be noticed that the following species attain a maximum in the Toftlund 115 m. and the Arnum 104.3–107.5 m. assemblages:

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*) The term species zone is here and in the following used for the entire vertical and horizontal distribution of the species concerned. If "zone" is applied in connection with a species name it is used in this sense.

Yoldia glaberrima
Abra prismatica
Natica ssp.
Nassa Fuchsi
Nassa Facki
Gemmula boreoturricula
Fusiturris Duchastelii

This coincidence of 7 maximum frequencies out of 30 species probably means that the assemblages are closely related. We have, however, not yet any proof that this amounts to contemporaneity.

The Ribe formation which underlies the Arnum formation in the Ribe well has not been penetrated at Ribe. Its non-fossiliferous sands and gravels are undoubtedly non-marine, and a fluviatile origin is suggested.

Since the well sections treated do not provide evidence on the time stratigraphic position of the Ribe formation, except to indicate its pre-Arnum age, the log of the Tertiary section of the deep test Arnum no. 1 will be given:

Arnum No. 1 (Deep test) D.G.U. file no. 150.24

DANISH AMERICAN PROSPECTING CO. Well drilled 1952.
Rotary drilling; no casing while drilling.
Samples: Ditch samples.

Formation	Elevation	Depth	(Preliminary Log compiled by LEIF BANKE RASMUSSEN):
(Pleistocene)	+ 40.8 m.	0– 42.4 m.	Quaternary deposits
Gram formation and upper part of Arnum formation (Upper Miocene and part of Middle Mioc.)	— 1.6 -	42.4– 80.5 -	Mica clay, dark gray, silty, occasional fossil fragments
Arnum formation (Middle Miocene)	— 39.7 -	80.5– 86.6 -	Quartz sand, fossiliferous, small shells
	— 45.8 -	86.6–103.3 -	Mica clay, silty, dark gray, fossiliferous
	— 62.5 -	103.3–106.4 -	Fossiliferous bed, *Ditrupa* zone
	— 65.6 -	106.4–144.5 -	Mica clay, silty, probably with beds of mica sand and quartz sand, fossiliferous
Ribe formation (Middle Miocene)	—103.7 -	144.5–191.7 -	Quartz sand and grave probably limnic-fluviatile
Klintinghoved clay(?) (Lower Miocene)	—150.9 -	191.7–220.7 -	Mica clay, silty, brownish gray, non calcareous
Transition zone (Transition Oligocene-Miocene)	—179.9 -	220.7–223.7 -	Lignite
	—182.9 -	223.7–255.7 -	Mica clay, silty non calcareous brownish gray with lumps of lignite
Cilleborg clay(?) (Upper Oligocene)	—214.9 -	255.7–263.4 -	Mica clay, brownish gray, glauconitic and pyritic. A few microfossils
Sövind marl (Probably Upper Eocene)	—222.6 -	263.4–275.5 -	Clay, sticky, light gray, calcareous
Lillebelt clay (Eocenc)	—234.7 -	275.5–349.6 -	Clay, sticky, greenish gray

Formation	Elevation	Depth	Log:
Rösnæs clay (Eocene)	−308.8 m.	349.6–359.4 m.	Clay, reddish brown, calcareous
Clays with tuff, and Kerteminde clay (Lowermost Eocene and Paleocene)	−318.6 -	359.4–395.9 -	Clay, gray, non-calcareous upper part probably with Tuff, lower part with beds of shale
Kerteminde marl (Paleocene)	−355.9 -	395.4–400.5 -	Clay, light gray, calcareous, glauconitic
Danian limestone (Upper Cretaceous)	−359.7 -	400.5–408.1 -	Bryozoan limestone

The quartz sands and gravels from 144.5 to 191.7 m. are, as is shown, correlated with the Ribe formation, and the underlying mica clays are tentatively referred to the Klintinghoved and Cilleborg formations. Their ages are lower Miocene and upper Oligocene respectively.

The log gives an indication of the approximate thickness of the Arnum formation. The biostratigraphic analysis of the interval in this well is rather difficult on account of the mixing of fossils from different horizons due to the ack of casing, and it has therefore not yet been attempted.

REMARKS ON THE STRUCTURE OF THE AREA

The suggested correlations indicate that some crustal movements must have taken place during or after sedimentation of the Arnum formation. It is clear that the Glejbjerg sequence is lying at a much higher level than the other sequences, and there is evidence for believing the Arnum section to be uplifted in relation to the Gramby and the Toftlund sections.

The structural evidence thus provided by the fossiliferous beds of the Miocene in South Jutland was placed at the disposal of the DANISH AMERICAN PROSPECTING CO. at an early stage of the investigations in 1947. There was a remarkable agreement between the structural evidence of the Miocene sequence and the residual gravity map of the area elaborated by the GULF RESEARCH & DEVELOPMENT CO. The high situation of the Arnum and the Glejbjerg sections correspond to gravity highs, and the low lying Gramby, Toftlund, and Ribe sequences were located in gravity lows.

The area was subsequently investigated seismically by the DANISH AMERICAN PROSPECTING CO. The seismic mapping, and a number of shallow core holes and deep tests finally proved the structural significance of the fossil evidence.

Table 14. Stratigraphic and Geographic Distributi

The molluscan species of the Arnum formation	Mediterranean Basin								Vienna Bas	
	Olig.	Miocene				Pliocene			Miocene	
	Tongriano	Aquitaniano	Langhiano	Elveziano	Tortoniano	Piacenziano	Astiano	Monte Mario	Eggenburg beds	Grund beds
Pelecypoda										
1. *Nucula nucleus* (Linne)	....	....	....	+	....	+	+	+	....	+
2. – *Jeffreysi* Bellardi	....	....	....	....	....	+	+	+	....	....
3. – *cromata nov. sp.*	....	....	....	....	....	....	....	....	....	....
4. – *cf. nitida* Sowerby	....	....	....	....	....	+	+	+	....	....
5. – *sp.*	....	....	....	....	....	....	....	....	....	....
6. *Nuculoma hanseata* (Kautsky)	....	....	....	....	....	....	....	....	....	....
7. – *cf. Haesendonckii* (Nyst & Westendorp)	....	....	....	....	....	....	....	....	....	....
8. *Leda (Jupiteria) pygmaea* (Münster)	....	....	....	....	....	....	....	....	....	....
9. – *(Ledina) Westendorpii* (Nyst & Westendorp)	....	....	....	....	....	....	....	....	....	....
10. – *(Lembulus) emarginata* (Lamarck)	....	....	....	+	....	....	....	....	....	+
11. *Yoldia glaberrima* (Münster)	....	....	....	....	....	....	....	....	....	....
12. *Arca diluvii* Lamarck	....	....	....	+	+	+	+	+	....	+
13. *Bathyarca pectunculoides* (Scacchi)	....	....	....	+	....	....	....	+	....	....
14. *Glycymeris sp.*	....	....	....	....	....	....	....	....	....	....
15. *Limopsis aurita* (Brocchi)	....	....	....	+	+	+	....	+	....	....
16. – *anomala* (Eichwald)	....	....	....	+	....	+	+	+	....	....
17. *Modiolus sp. a*	....	....	....	....	....	....	....	....	....	....
18. – *sp. b*	....	....	....	....	....	....	....	....	....	....
19. *Musculus saucatsensis* (Cossmann)	....	....	....	....	....	....	....	....	....	....
20. *Arcoperna sp.*	....	....	....	....	....	....	....	....	....	....
21. *Pecten ex aff. Brummelii* Nyst & *liberata* Cossmann & Peyrot	....	....	....	....	....	....	....	....	....	....
22. *Pecten radians* Nyst	....	....	....	....	....	....	....	....	....	....
23. – *tigerinus* Müller	....	....	....	....	....	+	....	....	....	....
24. – *Gerardii* Nyst	....	....	....	....	....	....	....	....	....	....
25. – *ssp. indet.*	....	....	....	....	....	....	....	....	....	....
26. *Lima (Limea) strigilata* (Brocchi)	....	....	....	+	+	+	+	+	....	....
27. *Anomia squamula* (Linne)	....	....	....	+	....	+	+	+	....	....
28. *Ostrea sp.*	....	....	....	....	....	....	....	....	....	....
29. *Astarte cf. concentrica* Goldfuss	....	....	....	....	....	....	....	....	....	....
30. – *(Goodallia) triangularis* Montagu	....	....	....	....	....	....	....	....	....	....
31. *Cardita (Cyclocardia) orbicularis* (Sowerby)	....	....	....	....	....	....	....	....	....	....
32. *Kellyella (Lutetia) rotunda nov. sp.*	....	....	....	....	....	....	....	....	....	....
33. – – *patera nov. sp.*	....	....	....	....	....	....	....	....	....	....
34. *Isocardia sp.*	....	....	....	....	....	....	....	....	....	....
35. *Sportella cimbrica* Kautsky	....	....	....	....	....	....	....	....	....	....
36. *Thyasira cf. flexuosa* (Montagu)	....	....	....	....	....	....	....	+	....	....
37. *Phacoides cf. Schloenbachi* (von Koenen)	....	....	....	....	....	....	....	....	....	....
38. *Loripes cf. niveus* (Eichwald)	....	....	....	....	....	....	....	....	....	....
39. *Lucina (Loripinus) Nørregaardi nov. sp.*	....	....	....	....	....	....	....	....	....	....
40. *Codokia jutensis nov. sp.*	....	....	....	....	....	....	....	....	....	....
41. – *sp.*	....	....	....	....	....	....	....	....	....	....
42. *Erycina (Scacchia) Degrangei* Cossmann & Peyrot	....	....	....	....	....	....	....	....	....	+

f the Molluscan Species of the Arnum formation

Aquitanian Basin				North Sea Basin															Recent Seas			
Miocene				Middle Oligocene	Upper Oligocene	Miocene Germany				Miocene Belgium			Middle Miocene. Holland	Miocene Denmark			Pliocene England		Mediterranean	North Atlantic Provinces		
Aquitanien	Burdigalien	Helvétien	Tortonien			Vierlande stage	Hemmoor stage	Reinbek-Dingden stage	Glimmerton stage	Boldérien	Horiz. of Houthaelen	Anversien		Klintinghoved clay	Middle Miocene	Gram formation	Lenham Beds & Coralline Crag	Red Crag		Lusitanian	Boreal	Arctic
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Table 14 (*continued*).

The molluscan species of the Arnum formation	Mediterranean Basin								Vienna Basi		
	Olig.	Miocene				Pliocene			Miocene		
	Tongriano	Aquitaniano	Langhiano	Elveziano	Tortoniano	Piacenziano	Astiano	Monte Mario	Eggenburg beds	Grund beds	Steinabrunn beds,
43. *Erycina (Hemilepton) coarctata* (WOOD)	....	....	....	....	....	....	....	....	....	....	....
44. – – *striatissima* (CERULLI-IRELLI)	....	....	....	....	....	....	....	+	....	....	....
45. *Lepton nitidum* TURTON	....	....	....	....	....	....	....	+	....	....	....
46. *Montacuta substriata* MONTAGU	....	....	....	....	....	....	....	+	....	+	....
47. *Laevicardium cyprium* (BROCCHI)	....	....	....	+	+	+	....	....	....	....	+
48. – *dingdense* (LEHMANN)	....	....	....	....	....	....	....	....	....	....	....
49. – *straeleni* GLIBERT	....	....	....	....	....	....	....	....	....	....	....
50. *Cardium sp. cf. hanseatum* KAUTSKY	....	....	....	....	....	....	....	....	....	....	....
51. *Gouldia minima* (MONTAGU)	....	....	....	+	+	+	+	+	....	+	+
52. *Pitar chione* (LINNE)	....	....	....	+	....	+	+	+	....	....	....
53. *Meretrix cf. incrassata* (SOWERBY)	+	....	....	....	....	....	....	....	....	....	....
54. *Dosinia cf. Basteroti* (AGASSIZ)	+	....	....	+	....	....	....	....	+	....	....
55. *Venus (Ventricola) multilamella* (LAMARCK)	....	....	....	....	+	+	+	+	+	+	+
56. *Ervilia pusilla* (PHILIPPI)	....	....	....	+	....	....	....	+	....	....	....
57. *Spisula subtruncata* (DA COSTA) *var.*	....	....	....	+	+	+	+	+	....	+	....
58. – *solida* (LINNE)	....	....	....	....	....	+	....	....	....	....	....
59. *Donax sp.*	....	....	....	....	....	....	....	....	....	....	....
60. *Abra prismatica* (MONTAGU) *var.*	....	....	....	....	....	+	....	+	....	....	....
61. *Angulus donacinus* (LINNE)	....	....	....	+	+	+	+	+	....	+	+
62. *Tellina cf. fallax* BEYRICH	....	....	....	....	....	....	....	....	....	....	....
63. *Pharus saucatsensis* DES MOULINS	....	....	....	....	....	....	....	....	....	....	....
64. *Cultellus sp.*	....	....	....	....	....	....	....	....	....	....	....
65. *Ensis Degrangei* COSSMANN & PEYROT	....	....	....	....	....	....	....	....	....	....	....
66. *Saxicava arctica* (LINNE)	....	....	....	+	+	+	+	+	....	....	....
67. *Saxicavella pusilla nov. sp.*	....	....	....	....	....	....	....	....	....	....	....
68. *Panopea sp.*	....	....	....	....	....	....	....	....	....	....	....
69. *Varicorbula gibba* (OLIVI)	....	....	....	+	+	+	+	+	+	+	+
70. *Lentidium donaciformis* (NYST)	....	....	....	....	....	....	....	....	....	....	....
71. *Sphenia sp.*	....	....	....	....	....	....	....	....	....	....	....
72. *Pholas sp.*	....	....	....	....	....	....	....	....	....	....	....
73. *Pholadidea sp.*	....	....	....	....	....	....	....	....	....	....	....
74. *Martesia sp. cf. rugosa* (BROCCHI)	....	....	....	....	....	+	+	....	....	....	....
75. *Teredo sp. cf. saucatsensis* BENOIST	....	....	....	....	....	....	....	....	....	....	....
76. *Pandora copiosa nov. sp.*	....	....	....	....	....	....	....	....	....	....	....
77. *Thracia sp.*	....	....	....	....	....	....	....	....	....	....	....
78. *Cuspidaria cf. cuspidata* (OLIVI)	....	....	....	+	....	+	+	+	....	+	+
79. – *cf. rostrata*	....	....	....	....	....	+	+	+	....	....	....
80. – – *costellata* (DESHAYES)	....	....	....	....	....	....	+	+	....	....	....
Scaphopoda											
81. *Cadulus gadus* (MONTAGU)	....	....	....	?+	+	+	....	....	....	....	+
82. *Dentalium cf. Michelotti* HÖRNES *var.*	....	....	....	+	+	+	+	+	....	....	+
83. – *novemcostatum* LAMARCK	....	....	....	....	+	+	+	+	....	....	+
84. – *sp. cf. badensis* PARTSCH	....	+	+	+	....	....	+	....	....	....	+

Aquitanian Basin				North Sea Basin															Recent Seas			
Miocene				Middle Oligocene	Upper Oligocene	Miocene Germany				Miocene Belgium			Middle Miocene. Holland	Miocene Denmark			Pliocene England		Mediterranean	North Atlantic Provinces		
Aquitanien	Burdigalien	Helvétien	Tortonien			Vierlande stage	Hemmoor stage	Reinbek-Dingden stage	Glimmerton stage	Boldérien	Horiz. of Houthaelen	Anversien		Klintinghoved clay	Middle Miocene	Gram formation	Lenham Beds & Coralline Crag	Red Crag		Lusitanian	Boreal	Arctic
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Table 14 (*continued*).

The molluscan species of the Arnum formation	Mediterranean Basin								Vienna Basin		
	Olig.	Miocene				Pliocene			Miocene		
	Tongriano	Aquitaniano	Langhiano	Elveziano	Tortoniano	Piacenziano	Astiano	Monte Mario	Eggenburg beds	Grund beds	Steinabrunn beds,
Gastropoda											
85. *Acmea compressiuscula* (KARSTEN)	....	....	....	....	....	....	....	....	....	....	...
86. *Calliostoma sp.*	....	....	....	....	....	....	....	....	....	....	...
87. *Starkeyna hanseata* (KAUTSKY)	....	....	....	....	....	....	....	....	....	....	...
88. – *jutensis nov. sp.*	....	....	....	....	....	....	....	....	....	....	...
89. – *nov. sp.*	....	....	....	....	....	....	....	....	....	....	...
90. *Liotia miosuturalis* KAUTSKY	....	....	....	....	....	....	....	....	....	....	...
91. *Alvania Partschi* (HÖRNES)	....	....	....	....	....	....	....	....	....	....	+
92. *Rissoa Ravni nov. sp.*	....	....	....	....	....	....	....	....	....	....	...
93. – *cf. succincta* NYST	....	....	....	....	....	....	....	....	....	....	...
94. *Rissoina Ödumi nov. sp.*	....	....	....	....	....	....	....	....	....	....	...
95. *Adeorbis subcirculus* COSSMANN & PEYROT	....	....	....	....	....	....	....	....	....	....	...
96. – *cf. carinata* (PHILIPPI)	....	....	....	....	....	....	....	....	....	....	...
97. – *planorbillus* (DUJARDIN)	....	....	....	+	....	....	....	....	....	....	...
98. *Turritella tricarinata* (BROCCHI)	+	....	....	+	+	+	+	....	....	....	...
99. – *subangulata* (BROCCHI)	....	....	....	+	+	+	+	....	....	....	+
100. *Solarium carocollatum* LAMARCK	+	....	....	+	....	....	....	....	....	+	+
101. – *trochleare nov. sp.*	....	....	....	....	....	....	....	....	....	....	...
102. – *angustiforatum* COSSMANN & PEYROT	....	....	....	....	....	....	....	....	....	....	...
103. *Bittium spina* (PARTSCH)	....	....	....	+	+	+	+	....	....	....	...
104. – *tenuispina nov. sp.*	....	....	....	....	....	....	....	....	....	....	...
105. *Cerithiopsis Vignali* COSSMANN & PEYROT	....	....	....	....	....	....	....	....	....	....	...
106. *Triphora perversa* (LINNE)	....	....	....	+	+	+	+	....	....	....	+
107. *Cirsotrema Thais* DE BOURY	....	....	....	....	....	....	....	....	....	....	...
108. *Scala frondicula* (WOOD)	....	....	....	....	....	+	+	....	....	....	...
109. – (*Acrilla*) *cf. amoena* PHILIPPI	....	....	....	+	....	....	....	....	....	....	+
110. *Janthina cimbrica nov.sp.*	....	....	....	....	....	....	....	....	....	....	...
111. *Niso acarinatoconica* COSSMANN & PEYROT	....	....	....	....	+	+	+	....	....	....	+
112. *Melanella similis* (D'ORBIGNY)	....	....	....	....	....	....	....	....	....	....	...
113. – *taurostricta* (COSSMANN & PEYROT)	....	....	....	+	....	....	....	....	....	....	...
114. *Calyptraea chinensis* (LINNE)	....	....	....	+	+	+	+	....	....	+	+
115. *Xenophora Deshayesi* (MICHELOTTI)	+	....	....	+	....	+	+	....	....	+	+
116. *Aporrhais alata* (EICHWALD)	....	....	....	?+	?+	....	....	....	....	+	+
117. *Natica* (*Lunatia*) *catena* (DA COSTA)	+	....	....	+	+	+	?+	....	....	....	...
118. – (*Naticina*) *hanseata* KAUTSKY	....	....	....	....	....	....	....	....	....	....	...
119. – – *Beyrichi* VON KOENEN	....	....	....	....	....	+	....	....	....	....	...
120. – – *protostriata nov. sp.*	....	....	....	....	....	....	....	....	....	....	...
121. – – *praeclausa* KAUTSKY	....	....	....	....	....	....	....	....	....	....	...
122. – – *tectula* BONELLI	....	....	....	?+	+	+	+	....	....	....	...
123. – – *miopusilla* KAUTSKY	....	....	....	....	....	....	....	....	....	....	...
124. – – *submamillaris* D'ORBIGNY	....	....	....	+	+	....	....	....	....	....	...
125. – (*Polynices*) *affinis* (GMELIN)	....	....	....	....	....	....	....	....	....	....	...
126. – (*Neverita*) *Josephinia* (RISSO)	+	....	....	+	+	+	+	....	....	+	+
127. – *sp.*	....	....	....	....	....	....	....	....	....	....	...

Aquitanian Basin				North Sea Basin															Recent Seas			
Miocene						Miocene Germany				Miocene Belgium				Miocene Denmark			Pliocene England			North Atlantic Provinces		
Aquitanien	Burdigalien	Helvétien	Tortonien	Middle Oligocene	Upper Oligocene	Vierlande stage	Hemmoor stage	Reinbek-Dingden stage	Glimmerton stage	Boldérien	Horiz. of Houthaelen	Anversien	Middle Miocene. Holland	Klintinghoved clay	Middle Miocene	Gram formation	Lenham Beds & Coralline Crag	Red Crag	Mediterranean	Lusitanian	Boreal	Arctic
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Table 14 (*continued*).

The molluscan species of the Arnum formation	Mediterranean Basin								Vienna Basin		
	Olig.	Miocene				Pliocene			Miocene		
	Tongriano	Aquitaniano	Langhiano	Elveziano	Tortoniano	Piacenziano	Astiano	Monte Mario	Eggenburg beds	Grund beds	Steinabrunn beds, Baden clay etc.
128. *Globularia sp*.	....	....	....	....	....	....	....	....	....	....	....
129. *Sigaretus sulcatus* (GRATELOUP)	....	....	....	....	....	....	....	....	....	....	....
130. – *cf. aquensis* RECLUZ	+	....	....	+	....	....	....	....	....	....	....
131. *Semicassis sp*.	....	....	....	....	....	....	....	....	....	....	....
132. *Tritonium sp*.	....	....	....	....	....	....	....	....	....	....	....
133. *Pyrula simplex* BEYRICH	....	....	....	....	....	....	....	....	....	....	....
134. – *condita* BRONGNIART	+	....	....	+	+	....	....	....	....	+	....
135. *Murex cf. aturensis* COSSMANN & PEYROT	....	....	....	....	....	....	....	....	....	....	....
136. – *inornatus* BEYRICH	....	....	....	....	....	....	....	....	....	....	....
137. *Typhis cf. horridus* (BROCCHI)	+	....	....	....	+	+	....	....	....	....	+
138. – *fistulosus* (BROCCHI)	....	....	....	....	....	+	....	....	....	....	+
139. *Tritonalia coelata* DUJARDIN	....	....	....	....	....	....	....	....	....	....	....
140. *Pyrene* (*Atilia*) *nassoides* (GRATELOUP)	....	....	....	....	....	+	....	....	....	+	+
141. – (*Anachis*) *sp*.	....	....	....	....	....	....	....	....	....	....	....
142. *Phos decussatus* VON KOENEN	....	....	....	....	....	....	....	....	....	....	....
143. *Nassa tenuistriata* (BEYRICH)	....	....	....	....	....	....	....	....	....	....	....
144. – *serraticosta* (BRONN)	....	....	....	+	+	+	....	+	....	....	+
145. – *bocholtense* (BEYRICH)	....	....	....	....	....	....	....	....	....	....	....
146. – *turbinella* (BROCCHI)	....	....	....	....	+	+	....	....	....	....	+
147. – *Fuchsi* VON KOENEN	....	....	....	....	....	....	....	....	....	....	?+
148. – *Schlotheimi* (BEYRICH)	....	....	....	....	....	....	....	....	....	....	....
149. – *holsatica* (BEYRICH)	....	....	....	?+	....	....	....	....	....	....	....
150. – *Facki* VON KOENEN	....	....	....	....	....	....	....	....	....	....	....
151. – *laevissima* BRUSINA	....	....	....	....	....	....	....	....	....	....	+
152. – *cavata* BELLARDI	....	....	....	....	+	+	....	....	....	....	....
153. – *Woodwardi* HARMER	....	....	....	....	....	....	....	....	....	....	....
154. – *subobesa* DEGRANGE-TOUZIN	....	....	....	....	....	....	....	....	....	....	....
155. – *cimbrica* RAVN	....	....	....	....	....	....	....	....	....	....	....
156. – *pölsense* (AUINGER)	....	....	....	....	....	....	....	....	....	....	....
157. *Lathyrus* (*Dolicholathyrus*) *Rothi* (BEYRICH)	....	....	....	....	+	....	....	....	....	+	+
158. *Fusus cf. sexcostatus* BEYRICH	....	....	....	....	....	....	....	....	....	....	....
159. – (*Aquilofusus*) *Grippi* (KAUTSKY)	....	....	....	....	....	....	....	....	....	....	....
160. *Ancilla obsoleta* (BROCCHI)	....	....	....	....	+	....	....	....	....	....	+
161. *Oliva minutissima* (KAUTSKY)	....	....	....	....	....	....	....	....	....	....	....
162. *Mitra cf. Bellardii* HOERNES & AUINGER	....	....	....	....	....	....	....	....	....	....	+
163. – *cf. planicosta* BELLARDI	....	....	....	....	....	+	....	....	....	....	+
164. *Cancellaria* (*Cancellaria*) *cancellata* LINNE	....	....	....	+	+	+	+	....	....	+	+
165. – – *contorta* BASTEROT	....	....	....	+	....	....	....	....	....	+	+
166. – (*Trigonostoma*) *acutangula* FAUJAS DE SAINT FOND	....	....	....	+	....	....	....	....	....	....	....
167. – – *boreobsoleta* KAUTSKY	....	....	....	....	....	....	....	....	....	....	....
168. – (*Narona*) *calcarata* (BROCCHI)	....	....	....	+	+	+	+	....	....	....	....
169. – – *varicosa* (BROCCHI)	....	....	....	+	+	+	+	....	....	+	+
170. *Admete cf. fusiformis* (CANTRAINE)	....	....	....	....	+	+	+	....	....	....	....
171. *Conus Dujardini* DESHAYES	....	....	....	+	+	....	+	....	....	+	+

Aquitanian Basin				North Sea Basin															Recent Seas			
Miocene				Middle Oligocene	Upper Oligocene	Miocene Germany				Miocene Belgium			Middle Miocene. Holland	Miocene Denmark			Pliocene England		Mediterranean	North Atlantic Provinces		
Aquitanien	Burdigalien	Helvétien	Tortonien			Vierlande stage	Hemmoor stage	Reinbek-Dingden stage	Glimmerton stage	Boldérien	Horiz. of Houthaelen	Anversien		Klintinghoved clay	Middle Miocene	Gram formation	Lenham Beds & Coralline Crag	Red Crag		Lusitanian	Boreal	Arctic
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Table 14 (*continued*).

The molluscan species of the Arnum formation	Mediterranean Basin								Vienna Basin		
	Olig.	Miocene				Pliocene			Miocene		
	Tongriano	Aquitaniano	Langhiano	Elveziano	Tortoniano	Piacenziano	Astiano	Monte Mario	Eggenburg beds	Grund beds	Steinabrunn beds, Baden clay etc
172. *Gemmula cf. rotata* (BROCCHI)	....	....	....	....	....	....	....	....	....	....	...
173. – *badensis* (HÖRNES)	....	....	....	....	....	....	....	....	....	....	+
174. – *boreoturricula* (KAUTSKY)	....	....	....	....	....	....	....	....	....	....	...
175. – *Stoffelsi* (NYST)	....	....	....	....	....	....	....	....	....	....	...
176. – *Zimmermanni* (PHILIPPI)	....	....	....	....	....	....	....	....	....	....	...
177. *Fusiturris Duchastelii* (NYST)	....	....	....	....	....	....	....	....	....	....	...
178. – *inermis* (HÖRNES)	....	....	....	+	....	....	....	....	....	....	+
179. *Bathytoma cataphracta* (BROCCHI)	....	(+)[1]	....	+	+	+	+	....	....	+	+
180. *Turricula Steinvorthi* (VON KOENEN)	....	....	....	....	....	....	....	....	....	....	...
181. *Clinura sp.*	....	....	....	....	....	....	....	....	....	....	...
182. *Tahusyrinx cf. Corneti* (VON KOENEN)	....	....	....	....	....	....	....	....	....	....	...
183. *Clavatula boreointerrupta* KAUTSKY	....	....	....	....	....	....	....	....	....	....	...
184. – *sp.*	....	....	....	....	....	....	....	....	....	....	...
185. – *obliplicatula* KAUTSKY	....	....	....	....	....	....	....	....	....	....	...
186. *Genota ramosa* (BASTEROT)	....	....	....	+	....	....	....	....	....	+	+
187. *Acamptogenotia cf. Escheri* (MAYER)	....	....	....	....	....	....	....	....	....	....	...
188. – *cf. Straeleni* GLIBERT	....	....	....	....	....	....	....	....	....	....	...
189. *Inquisitor obeliscus* (DES MOULINS)	....	....	....	....	....	....	....	....	....	....	+
190. *Spendrillia Selenkae* (VON KOENEN)	....	....	....	....	....	....	....	....	....	....	...
191. *Boreodrillia toftlundensis nov. gen. & nov. sp.*	....	....	....	....	....	....	....	....	....	....	...
192. *Asthenotoma cf. pannus* (BASTEROT)	....	....	....	+	+	....	....	....	....	+	+
193. *Brachytoma electa nov. sp.*	....	....	....	....	....	....	....	....	....	....	...
194. – *Grateloupi* (PEYROT)	....	....	....	....	....	....	....	....	....	....	...
195. – *obtusangula* (BROCCHI)	....	....	....	+	+	+	....	....	....	....	+
196. – *sp.*	....	....	....	....	....	....	....	....	....	....	...
197. *Aphanitoma glejbjergensis nov. sp.*	....	....	....	....	....	....	....	....	....	....	...
198. *Neoguraleus calais* (KAUTSKY)	....	....	....	....	....	....	....	....	....	....	...
199. – *tenella* (MAYER)	....	....	....	....	....	....	....	....	....	....	...
200. – *Gürichi* (KAUTSKY)	....	....	....	....	....	....	....	....	....	....	...
201. *Pleurotomoides Johannae* (PEYROT)	....	....	....	....	....	....	....	....	....	....	...
202. – *elatior* (VON KOENEN)	....	....	....	....	....	....	....	....	....	....	...
203. – *simplex nov. sp.*	....	....	....	....	....	....	....	....	....	....	...
204. – *cf. Luisae* (VON KOENEN)	....	....	....	+	....	+	....	....	....	....	...
205. – *campanulata nov. sp.*	....	....	....	....	....	....	....	....	....	....	...
206. *Teretia anceps* (EICHWALD)	....	....	....	....	....	....	+	+	....	....	+
207. – *sp.*	....	....	....	....	....	....	....	....	....	....	...
208. *Philbertia scabra* (PHILIPPI)	....	....	....	....	....	....	....	....	....	....	...
209. – *sinuosula nov. sp.*	....	....	....	....	....	....	....	....	....	....	...
210. *Eubela trochlearis* (HÖRNES)	....	....	....	+	....	....	....	....	....	....	+
211. – *sp.*	....	....	....	....	....	....	....	....	....	....	...
212. *Metuonella Grippi* (KAUTSKY)	....	....	....	....	....	....	....	....	....	....	...
213. *Oenopota sp.*	....	....	....	....	....	....	....	....	....	....	...
214. *Terebra Hörnesi* BEYRICH	....	....	....	....	....	....	....	....	....	....	...
215. – *acuminata* BORSON	....	....	....	+	+	+	+	....	....	....	...

(+)[1] "Miocene inferiore"

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Table 14 (*continued*).

The molluscan species of the Arnum formation	Mediterranean Basin								Vienna Bas		
	Olig.	Miocene				Pliocene			Miocene		
	Tongriano	Aquitaniano	Langhiano	Elveziano	Tortoniano	Piacenziano	Astiano	Monte Mario	Eggenburg beds	Grund beds	Steinabrunn beds
216. *Acteon semistriatus* (BASTEROT)	....	....	....	+	+	+	+	....	....	....	
217. – *laevigatus* (GRATELOUP)	....	....	....	....	....	....	....	....	....	....	.
218. – *cf. pinguis* D'ORBIGNY	....	....	....	....	....	....	....	....	....	....	.
219. – *arnumensis nov. sp.*	....	....	....	....	....	....	....	....	....	....	.
220. – *tornatilis* (LINNE)	....	....	....	....	....	+	+	+	....	+	
221. – *sp.*	....	....	....	....	....	....	....	....	....	....	.
222. *Actæonidea sp.*	....	....	....	....	....	....	....	....	....	....	.
223. *Chrysallida cf. cimbrica* (KAUTSKY)	....	....	....	....	....	....	....	....	....	....	.
224. – *nodifera nov. sp.*	....	....	....	....	....	....	....	....	....	....	.
225. – *toftlundensis nov. sp.*	....	....	....	....	....	....	....	....	....	....	.
226. – *acuticostata nov. sp.*	....	....	....	....	....	....	....	....	....	....	.
227. – *semireticulata nov. sp.*	....	....	....	....	....	....	....	....	....	....	.
228. – *modesta nov. sp.*	....	....	....	....	....	....	....	....	....	....	.
229. – *pygmaea* (GRATELOUP)	....	....	....	....	+	+	+	....	....	....	
230. *Kleinella* (*Leucotina*) *Nordmanni nov. sp.*	....	....	....	....	....	....	....	....	....	....	.
231. *Odostomia conoidea* (BROCCHI)	....	....	....	....	+	+	+	....	....	....	?
232. – *subintermedia* (COSSMANN & PEYROT)	....	....	....	....	....	....	....	....	....	....	.
233. – *sallespissensis* (COSSMANN & PEYROT)	....	....	....	....	....	....	....	....	....	....	.
234. – *pallidaeformis* (SACCO)	....	....	....	+	....	....	....	....	....	....	.
235. – *mutinensis* (SACCO)	....	....	....	....	+	....	....	....	....	....	.
236. – (*Syrnola*) *subumbilicata* (GRATELOUP)	....	....	....	....	....	....	....	....	....	....	.
237. – – *dubia* (GRATELOUP)	....	....	....	....	....	....	....	....	....	....	.
238. *Eulimella concinna nov. sp.*	....	....	....	....	....	....	....	....	....	....	.
239. – *Scillae* (SCACCHI)	....	....	....	....	+	+	+	+	....	....	.
240. – *acicula* (PHILIPPI)	....	....	....	....	....	....	....	....	....	....	.
241. – *crassitesta nov. sp.*	....	....	....	....	....	....	....	....	....	....	.
242. *Turbonilla costellata* (GRATELOUP)	....	....	....	....	....	....	....	....	....	....	.
243. – *lactea* (LINNE)	....	....	....	....	....	+	+	+	....	....	.
244. – *rufa* (PHILIPPI)	....	....	....	....	....	....	....	+	....	....	.
245. – *pseudoterebralis* (SACCO)	....	....	....	....	+	....	....	....	....	....	
246. – *sp.*	....	....	....	....	....	....	....	....	....	....	.
247. *Pyramidella plicosa* BRONN	....	....	....	+	+	+	+	....	....	....	
248. *Ringicula ventricosa* (SOWERBY)	....	....	....	?+	?+	?+	?+	....	....	....	.
249. – *buccinea* (BROCCHI)	....	....	....	?+	+	+	+	....	....	+	
250. – *Ravni nov. sp.*	....	....	....	....	....	....	....	....	....	....	.
251. *Cylichna cf. cylindracea* (PENNANT)	....	....	....	+	+	+	+	+	....	....	
252. – *Bellardi* (VON KOENEN)	....	....	....	....	....	....	....	....	....	....	.
253. *Rhizorus acuminatus* (BRUGUIÈRE)	....	....	....	....	....	+	+	+	....	....	.
254. *Retusa elongata* (EICHWALD)	....	....	....	+	+	+	+	....	....	....	
255. – *umbilicata* (MONTAGU)	....	....	....	....	....	+	....	+	....	....	.
256. – *obtusa* (MONTAGU)	....	....	....	....	....	....	+	+	....	....	.
257. *Acteocina sp.*	....	....	....	....	....	....	....	....	....	....	.
258. – *Lajonkaireana* (BASTEROT)	....	....	....	+	....	....	....	....	....	....	.
259. *Scaphander lignarius* (LINNE)	....	....	....	+	+	+	+	+	....	+	.

Aquitanian Basin				North Sea Basin															Recent Seas			
Miocene						Miocene Germany				Miocene Belgium				Miocene Denmark			Pliocene England			North Atlantic Provinces		
Aquitanien	Burdigalien	Helvétien	Tortonien	Middle Oligocene	Upper Oligocene	Vierlande stage	Hemmoor stage	Reinbek-Dingden stage	Glimmerton stage	Boldérien	Horiz. of Houthaelen	Anversien	Middle Miocene. Holland	Klintinghoved clay	Middle Miocene	Gram formation	Lenham Beds & Coralline Crag	Red Crag	Mediterranean	Lusitanian	Boreal	Arctic
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+	+	+	....	....	....	+	+	+	+	....	....	+	....	+	....	....	+	+	+	+	+	....

(+)[1] Gulf of Biscay

Table 14 (*continued*).

The molluscan species of the Arnum formation	Mediterranean Basin								Vienna Basi		
	Olig.	Miocene				Pliocene			Miocene		
	Tongriano	Aquitaniano	Langhiano	Elveziano	Tortoniano	Piacenziano	Astiano	Monte Mario	Eggenburg beds	Grund beds	Steinabrunn beds,
260. *Roxania utriculus* (BROCCHI)	....	....	....	+	+	+	+	+	....	....	+
261. *Philine sp. a*	....	....	....	....	....	....	....	....	....	....	..
262. – *sp. b*	....	....	....	....	....	....	....	....	....	....	..
263. *Spiratella atlanta* (MØRCH)	....	....	....	....	....	....	....	....	....	....	..
264. – *cf. valvatina* (REUSS)	....	....	....	....	....	....	....	....	....	....	..
265. *Clio sp.*	....	....	....	....	....	....	....	....	....	....	..
266. *Vaginella depressa* DAUDIN	....	....	....	+	....	....	....	....	....	....	+
Number of dubious cases of species in common	....	1	....	6	2	1	2	....	....	....	
Recorded number of species in common (α)	10	1	1	59	51	66	53	39	3	29	5
[1] Calculated number of species in common (in accordance with formula (1)) (α_1)	....	....	....	....	....	....	....	....	....	....	..
Total number of species in the individual faunas (s):	....	....	....	....	....	....	....	....	....	....	..
Correlation ratio $P_\alpha = \frac{\alpha^2}{rs} 100\%$ (2)	....	....	....	....	....	....	....	....	....	....	..
Correlation ratio $P_{\alpha_1} = \frac{rs}{n^2} 100\%$ (1)	....	....	....	....	....	....	....	....	....	....	..

$n = 500$ (assumed total number of species in the individual faunas).

$r = 266$ (number of species in the Arnum formation).

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[1] For discussion of the formulas see p. 401–408.

Aquitanian Basin				North Sea Basin															Recent Seas			
Miocene						Miocene Germany				Miocene Belgium				Miocene Denmark			Pliocene England			North Atlantic Provinces		
Aquitanien	Burdigalien	Helvétien	Tortonien	Middle Oligocene	Upper Oligocene	Vierlande stage	Hemmoor stage	Reinbek-Dingden stage	Glimmerton stage	Boldérien	Horiz. of Houthaelen	Anversien	Middle Miocene. Holland	Klintinghoved clay	Middle Miocene	Gram formation	Lenham Beds & Coralline Crag	Red Crag	Mediterranean	Lusitanian	Boreal	Arctic
....	+	+	....	....	+	+	+	+	+	....	+	+	....	+	+	....	....	....	+	+	+	....
....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
....	....	....	....	....	....	....	?+	....	+	....	....	?+	....	....	+	+	....	....	....	....	....	....
....	....	....	....	....	....	+	+	....	+	....	....	+	....	....	....	....	....	....	....	....	....	....
....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
....	+	+	....	....	+	....	+	+	....	....	....	+	....	+	+	....	....	....	....	....	....	....
9	13	7	1	....	....	....	5	4	1	2	....	3	....	....	4	....	....	....	1	....	2	1
28	77	59	2	12	29	24	141	52	66	35	36	87	(43)	33	43	28	33	20	39	42	39	5
....	....	....	....	....	....	40	165	57	88	45	34	126	....	34	....	35	....	....	....	....	....	....
....	....	....	....	....	....	79	311	107	165	84	64	236	....	63	....	65	....	....	....	....	....	....
....	....	....	....	....	....	2.7	24.0	9.5	9.9	6.1	7.6	12.1	....	6.5	....	4.5	....	....	....	....	....	....
....	....	....	....	....	....	8.4	33.1	11.4	17.6	8.9	6.8	25.1	....	6.7	....	6.9	....	....	....	....	....	....

Table 15, (part 1). The Frequencies of th

Roman types: per cent

		Glej- Arnum						
	Depth (m.):	23	25	32	38	42	48	52
	Pelecypoda							
1.	*Nucula nucleus* (Linné)	...	...	...	...	...	...	...
2.	– *Jeffreysi* Bellardi	...	...	...	...	...	*1*	*1*
3.	– *cromata nov. sp.*	0.5	0.7	7.9	...	...	...	...
4.	– *cf. nitida* Sowerby	...	...	...	...	...	...	...
5.	– *sp.*	0.6	...	...	...	...	...	*1*
6.	*Nuculoma hanseata* (Kautsky)	...	0.4	1.0	1.3	0.9	...	...
7.	– *cf. Haesendonckii* (Nyst & Westendorp)	...	...	...	...	...	...	...
8.	*Leda* (*Jupiteria*) *pygmaea* (Münster)	21.1	17.5	...	...	16.1	...	...
9.	– (*Ledina*) *Westendorpii* (Nyst & Westendorp)	0.2	0.2	0.8	1.3	...	...	...
10.	– (*Lembulus*) *emarginata* (Lamarck)	...	...	1.3	...	...	...	...
11.	*Yoldia glaberrima* (Münster)	2.5	3.9	1.5	2.6	1.7	*1*	*1*
12.	*Arca diluvii* Lamarck	0.2	...	0.3	...	0.9	...	...
13.	*Bathyarca pectunculoides* Scacchi	...	...	...	...	...	...	...
14.	*Glycymeris sp.*	...	...	...	...	...	...	...
15.	*Limopsis aurita* (Brocchi)	...	...	...	...	...	...	*1*
16.	– *anomala* (Eichwald)	...	...	...	...	...	...	...
17.	*Modiolus sp. a.*	...	...	...	...	...	...	...
18.	– *sp. b.*	...	...	...	...	...	...	...
19.	*Musculus saucatsensis* (Cossmann)	...	...	...	...	...	...	...
20.	*Arcoperna sp.*	...	...	...	...	...	...	...
21.	*Pecten ex aff. Brummelii* Nyst & *liberata* Cossmann & Peyrot	...	...	...	...	...	...	...
22.	– *radians* Nyst	...	...	...	...	...	...	...
23.	– *tigerinus* Müller	0.2	0.2	...	...	...	...	...
24.	– *Gerardii* Nyst	0.2	...	...	...	...	...	...
25.	– *ssp. indet.*	0.2	0.2	...	...	...	...	...
26.	*Lima* (*Limea*) *strigilata* (Brocchi)	...	...	...	...	...	...	...
27.	*Anomia squamula* (Linné)	0.2	...	0.3	...	...	...	...
28.	*Ostrea sp.*	...	...	...	...	...	...	...
29.	*Astarte cf. concentrica* Goldfuss	...	...	...	...	...	...	...
30.	– (*Goodallia*) *triangularis* Montagu	...	...	...	...	...	...	...
31.	*Cardita* (*Cyclocardia*) *orbicularis* (Sowerby)	...	...	...	...	...	...	...
32.	*Kellyella* (*Lutetia*) *rotunda nov. sp.*	0.5	1.1	5.4	...	1.7	...	*1*
33.	– – *patera nov. sp.*	...	...	...	...	...	...	...
34.	*Isocardia sp.*	0.2	0.2	...	...	0.9	...	...
35.	*Sportella cimbrica* Kautsky	...	...	...	...	...	...	...
36.	*Thyasira cf. flexuosa* (Montagu)	...	...	0.3	...	...	...	...
37.	*Phacoides cf. Schloenbachi* (von Koenen)	...	...	...	...	...	...	...
38.	*Loripes cf. niveus* (Eichwald)	...	...	...	...	...	...	...
39.	*Lucina* (*Loripinus*) *Nørregaardi nov. sp.*	...	...	...	...	...	...	...
40.	*Codokia jutensis nov. sp.*	...	...	...	...	...	...	...
41.	– *sp.*	...	...	...	...	...	...	...
42.	*Erycina* (*Scacchia*) *Degrangei* Cossmann & Peyrot	...	...	...	...	...	...	...
43.	*Erycina* (*Hemilepton*) *coarctata* (Wood)	...	...	...	...	...	...	...
44.	– – *striatissima* (Cerulli-Irelli)	...	...	...	...	...	...	...
45.	*Lepton nitidum* Turton	...	...	...	...	...	...	...

Molluscan Species in the Well Sections

Italics: number of specimen

bjerg formation					**Bramminge** Arnum formation	**Ribe** Arnum formation											
53	53.5	53.75	54	55	70–80	113–114	114–115	115–116	116–117	117–118	118–119	119–120	120–121	121–122	122–123	123–124	124–125
…	0.1	…	…	…	0.003	*4*	*1*	…	…	…	…	…	…	…	…	…	…
…	0.6	0.6	*1*	0.3	0.006	…	…	…	…	…	…	…	…	…	…	…	*1*
…	…	…	…	0.3	0.009	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	*1*
7.9	0.9	1.2	*1*	0.3	0.106	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	*1*	…	…	…	…	…	…	…	…	…	…	…
…	0.2	…	…	1.0	7.92	*2*	*1*	…	…	…	…	…	…	…	…	…	*5*
…	0.1	0.3	*1*	0.3	0.509	*1*	…	*1*	…	*1*	…	*1*	…	…	…	*1*	*1*
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
2.9	5.6	5.4	*1*	8.3	3.19	*1*	*1*	…	*1*	…	…	*1*	…	*1*	*1*	…	*1*
0.7	0.1	0.3	…	0.3	0.012	…	…	…	…	…	…	…	…	…	…	*1*	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	0.1	0.3	…	0.3	…	*4*	…	…	…	…	…	…	…	…	*1*	…	…
…	…	0.3	…	…	0.012	*3*	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	0.3	…	*1*	…	*1*	…	*1*	…	…	…	…	…	…	…
…	…	…	…	…	0.006	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.003	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	0.3	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
0.7	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	0.3	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.019	*1*	…	*1*	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.009	*1*	…	…	…	…	…	…	…	…	…	…	…
…	0.1	…	…	…	0.027	*1*	…	…	…	…	…	…	…	…	…	…	*2*
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
0.7	0.1	…	…	0.3	0.006	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	0.1	…	…	…	…	…	…	…	…	*1*	…	…	…	…	…	…	*1*
…	0.1	0.3	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	*1*
…	0.1	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…

Table 15, part 1 (*continued*).

							Glej- Arnum
	Depth (m.):	23	25	32	38	42	48	52
46.	*Montacuta substriata* Montagu	...	...	...	...	...	...	...
47.	*Laevicardium cyprium* (Brocchi)	...	...	...	...	...	...	...
48.	– *dingdense* (Lehmann)	0.2	0.2	0.3	...	0.9	*1*	*1*
49.	– *Straeleni* Glibert	...	0.2	...	...	0.9	...	...
50.	*Cardium sp. cf. hanseatum* Kautsky	...	...	...	...	...	...	...
51.	*Gouldia minima* (Montagu)	...	...	...	...	...	...	...
52.	*Pitar chione* (Linné)	...	...	...	...	...	...	...
53.	*Meretrix cf. incrassata* (Sowerby)	...	...	0.8	1.3	0.9	...	...
54.	*Dosinia cf. Basteroti* (Agassiz)	...	...	...	...	...	...	...
55.	*Venus (Ventricola) multilamella* (Lamarck)	0.2	...	...	...	...	...	...
56.	*Ervilia pusilla* (Philippi)	...	...	...	...	...	...	...
57.	*Spisula subtruncata* (Da Costa) *var.*	1.6	1.1	2.3	1.3	12.7	...	*2*
58.	– *solida* (Linné)	...	...	...	...	...	...	...
59.	*Donax sp.*	...	...	...	...	...	...	...
60.	*Abra prismatica* (Montagu) *var.*	0.5	0.7	0.8	...	11.9	...	*3*
61.	*Angulus donacinus* (Linné)	...	...	...	...	...	...	...
62.	*Tellina cf. fallax* Beyrich	...	...	0.3	...	0.9	...	...
63.	*Pharus saucatsensis* Des Moulins	...	...	...	...	...	...	...
64.	*Cultellus sp.*	...	...	...	...	...	...	...
65.	*Ensis Degrangei* Cossmann & Peyrot	...	...	...	...	0.9	...	...
66.	*Saxicava arctica* (Linné)	0.8	0.2	0.3	...	4.2	...	...
67.	*Saxicavella pusilla nov. sp.*	...	...	...	...	...	...	...
68.	*Panopea sp.*	...	...	...	...	...	...	...
69.	*Varicorbula gibba* (Olivi)	15.9	11.3	...	...	0.9	...	*1*
70.	*Lentidium donaciformis* (Nyst)	...	0.2	...	...	...	...	...
71.	*Sphenia sp.*	...	...	...	...	...	...	...
72.	*Pholas sp.*	...	...	...	...	...	...	...
73.	*Pholadidea sp.*	...	...	...	...	...	...	...
74.	*Martesia sp. cf. rugosa* (Brocchi)	...	...	...	...	...	...	...
75.	*Teredo sp. cf. saucatsensis* Benoist	...	...	0.3	...	...	...	...
76.	*Pandora copiosa nov. sp.*	0.8	...	...	...	...	...	...
77.	*Thracia sp.*	...	...	...	...	...	...	...
78.	*Cuspidaria cf. cuspidata* (Olivi)	0.2	0.2	0.3	...	0.9	...	*1*
79.	– *cf. rostrata*	...	...	...	...	...	...	...
80.	– – *costellata* (Deshayes)	...	...	...	...	...	...	...
	Scaphopoda							
81.	*Cadulus gadus* (Montagu)	0.2	0.4	...	...	...	...	...
82.	*Dentalium cf. Michelotti* Hörnes *var.*	...	...	...	...	...	...	...
83.	– *novemcostatum* Lamarck	...	...	...	...	...	...	...
84.	– *sp. cf. badensis* Partsch	...	...	...	...	...	...	...
	Gastropoda							
85.	*Acmaea compressiuscula* (Karsten)	...	...	...	...	...	...	...
86.	*Calliostoma sp.*	...	...	...	...	...	...	...
87.	*Starkeyna hanseata* (Kautsky)	...	...	...	...	...	...	...
88.	– *jutensis nov. sp.*	...	...	...	...	...	...	...
89.	– *nov. sp.*	...	...	...	...	...	...	...
90.	*Liotia miosuturalis* Kautsky	...	...	...	...	...	...	...

bjerg formation					**Bramminge** Arnum formation	**Ribe** Arnum formation											
53	53.5	53.75	54	55	70–80	113–114	114–115	115–116	116–117	117–118	118–119	119–120	120–121	121–122	122–123	123–124	124–125
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	*1*	…	…	…	…	…	…	…	…	…	…	…
1.4	0.1	…	*1*	…	0.045	…	…	…	…	…	…	…	…	…	…	…	…
…	0.1	…	…	…	…	*1*	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.027	…	…	…	…	…	…	…	…	…	…	…	…
…	0.1	0.3	…	0.3	…	…	…	…	…	…	…	…	…	…	…	…	…
…	0.1	0.3	*1*	0.3	0.003	*1*	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	0.1	…	…	0.3	0.003	*3*	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
4.3	3.8	2.7	*1*	3.2	0.299	…	*1*	*1*	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
3.6	2.9	1.8	*1*	1.3	0.051	…	…	*1*	…	…	…	…	…	…	…	…	*1*
…	…	…	…	0.3	…	…	…	…	…	…	…	…	…	…	*1*	…	…
0.7	0.1	0.3	…	…	0.042	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	0.1	0.3	…	…	0.039	*1*	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	*1*	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
2.2	1.9	1.8	…	2.5	7.88	*4*	…	*1*	…	…	…	…	…	…	…	*1*	*2*
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	0.1	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	0.1	…	…	…	0.006	*1*	…	…	…	…	…	…	…	…	…	…	…
…	0.1	0.3	…	0.1	0.015	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.198	…	…	…	…	…	…	…	…	…	…	…	*1*
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	1.0	1.2	*2*	0.6	0.048	*1*	*1*	…	…	…	…	…	…	…	…	…	…
…	…	0.3	…	…	0.003	*1*	…	…	…	…	…	…	…	…	…	…	…
…	0.1	…	…	0.3	…	*1*	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	*1*	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	0.3	…	0.3	…	…	…	…	…	…	…	…	…	…	…	…	…

Table 15, part 1 (*continued*).

	Glej- Arnum						
Depth (m.):	23	25	32	38	42	48	52
91. *Alvania Partschi* (Hörnes)	...	...	...	...	...	...	...
92. *Rissoa Ravni nov. sp.*	0.3	0.9	...	...	...	...	...
93. – *cf. succincta* Nyst	...	...	...	...	...	...	...
94. *Rissoina Ödumi nov. sp.*	...	...	...	...	...	...	...
95. *Adeorbis subcirculus* Cossmann & Peyrot	...	...	...	...	...	...	...
96. – *cf. carinata* (Philippi)	...	...	...	...	...	...	...
97. – *planorbillus* (Dujardin)	...	...	...	...	...	...	...
98. *Turritella tricarinata* (Brocchi)	0.2	0.2	...	...	...	...	...
99. – *subangulata* (Brocchi)	...	...	...	...	...	...	...
100. *Solarium carocollatum* Lamarck	...	...	...	...	...	...	...
101. – *trochleare nov. sp.*	...	...	...	...	...	...	...
102. – *angustiforatum* Cossmann & Peyrot	...	...	...	...	...	...	...
103. *Bittium spina* (Partsch)	...	...	...	...	...	...	...
104. – *tenuispina nov. sp.*	1.1	0.4	...	...	...	...	...
105. *Cerithiopsis Vignali* Cossmann & Peyrot	...	...	...	...	...	...	...
106. *Triphora perversa* (Linné)	...	...	...	...	...	...	...
107. *Cirsotrema Thais* de Boury	...	...	...	...	...	...	...
108. *Scala cf. frondicula* (Wood)	...	...	...	...	...	...	...
109. – (*Acrilla*) *cf. amoena* Philippi	...	...	0.3	...	...	...	...
110. *Janthina cimbrica nov. sp.*	...	...	...	...	...	...	...
111. *Niso acarinatoconica* Cossmann & Peyrot	...	...	...	...	...	...	...
112. *Melanella similis* (d'Orbigny)	...	...	...	...	...	...	...
113. – *taurostricta* (Cossmann & Peyrot)	...	...	...	...	...	...	...
114. *Calyptraea chinensis* (Linné)	...	...	...	...	...	...	...
115. *Xenophora Deshayesi* (Michelotti)	...	...	...	...	0.9	...	...
116. *Aporrhais alata* (Eichwald)	2.3	1.1	31.5	1.3	...	...	*9*
117. *Natica* (*Lunatia*) *catena* (da Costa)	...	...	3.1	...	...	...	...
118. – (*Naticina*) *hanseata* (Kautsky)	...	...	0.5	...	...	...	...
119. – – *Beyrichi* von Koenen	...	...	...	...	...	...	...
120. – – *protostriata nov. sp.*	0.2	...	...	...	...	...	...
121. – – *praeclausa* Kautsky	...	...	...	...	...	...	...
122. – – *tectula* Bonelli	...	...	...	...	...	...	...
123. – – *miopusilla* Kautsky	0.6	0.4	0.8	...	...	...	...
124. – – *submamillaris* d'Orbigny	...	...	...	...	...	...	...
125. – (*Polynices*) *affinis* (Gmelin)	...	...	...	...	...	...	...
126. – (*Nerita*) *Josephinia* (Risso)	...	...	...	...	...	*1*	...
127. – *sp.*	1.7	0.7	0.3	9.1	...	...	...
128. *Globularia sp.*	...	...	...	...	...	...	...
129. *Sigaretus sulcatus* (Grateloup)	...	...	...	...	...	...	...
130. – *cf. aquensis* Recluz	...	...	0.3	...	...	...	...
131. *Semicassis sp.*	...	...	...	...	...	...	...
132. *Tritonium sp.*	...	...	...	...	...	...	...
133. *Pyrula simplex* Beyrich	...	...	...	...	...	...	...
134. – *condita* Brongniart	...	0.2	0.3	...	0.9	...	...
135. *Murex cf. aturensis* Cossmann & Peyrot	...	...	...	...	...	...	...
136. – *inornatus* Beyrich	...	...	...	...	...	...	...
137. *Typhis cf. horridus* (Brocchi)	...	...	...	...	...	...	...
138. – *fistulosus* (Brocchi)	...	0.2	...	...	...	...	...
139. *Tritonalia coelata* Dujardin	...	...	...	...	...	...	...

jerg ormation					**Bramminge** Arnum formation	**Ribe** Arnum formation											
53	53.5	53.75	54	55	70–80	113–114	114–115	115–116	116–117	117–118	118–119	119–120	120–121	121–122	122–123	123–124	124–125
…	…	…	…	…	0.036	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.003	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.003	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	0.3	0.41	*1*	…	…	…	…	…	…	…	…	…	…	…
…	0.1	…	…	…	0.012	…	…	…	…	…	…	…	…	…	…	…	…
…	0.1	…	…	0.3	0.045	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	0.1	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	0.2	0.3	…	…	0.012	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	0.3	0.518	*1*	*1*	…	…	…	…	…	…	…	…	*1*	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.051	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	0.1	…	…	…	0.093	…	*1*	…	…	…	…	…	…	…	…	…	…
…	…	…	…	0.3	0.003	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.027	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	0.1	…	…	…	0.006	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
0.7	0.1	…	…	0.3	0.012	*1*	…	…	…	…	…	…	…	…	…	…	…
51.7	31.0	24.7	*4*	36.5	42.4	*3*	*1*	…	…	…	*1*	*1*	*1*	*1*	…	*1*	*1*
2.2	5.0	0.3	…	2.9	0.051	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.027	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.015	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.033	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.039	…	…	…	…	…	…	…	…	…	…	…	…
…	0.5	0.3	…	…	0.09	…	…	…	…	…	…	…	…	…	…	…	…
…	…	0.6	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
0.7	…	…	…	…	0.039	…	…	…	…	…	…	…	…	…	…	…	…
2.2	0.2	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	3.3	…	3.5	1.92	…	…	…	…	…	…	…	…	…	…	…	…
…	…	0.3	…	0.3	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	0.1	…	…	0.3	0.006	…	…	…	…	…	…	…	…	…	…	…	…
0.7	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	0.1	…	…	…	…	*1*	…	…	…	…	…	…	…	…	…	…	…
…	0.1	…	…	…	0.009	*1*	…	…	…	*1*	…	…	…	…	…	…	…
…	…	…	…	…	0.012	…	…	…	…	…	…	…	…	…	…	…	…
0.7	0.6	0.3	…	0.3	0.189	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	0.2	…	…	0.3	0.371	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.006	…	…	…	…	…	…	…	…	…	…	…	…

Table 15, part 1 (*continued*).

	Glej Arnu					
Depth (m.):	23	25	32	38	42	48
140. *Pyrene (Atilia) nassoides* (Grateloup)	...	...	...	...	...	...
141. – *(Anachis) sp.*	...	...	...	...	...	...
142. *Phos decussatus* von Koenen	...	...	...	...	...	...
143. *Nassa tenuistriata* (Beyrich)	0.2	0.2	0.8	1.3	0.9	...
144. – *serraticosta* (Bronn)	...	...	...	...	...	...
145. – *bocholtense* (Beyrich)	...	...	...	...	...	...
146. – *turbinella* (Brocchi)	...	...	...	...	...	...
147. – *Fuchsi* von Koenen	...	...	...	2.6	...	*1*
148. – *Schlotheimi* (Beyrich)	3.7	3.6	4.9	3.9	22.9	...
149. – *holsatica* (Beyrich)	...	...	...	...	...	...
150. – *Facki* von Koenen	...	...	1.0	...	0.9	...
151. – *laevissima* Brusina	...	...	...	...	...	...
152. – *cavata* Bellardi	...	...	...	...	...	...
153. – *Woodwardi* Harmer	...	...	...	...	...	...
154. – *subobesa* Degrange-Touzin	...	...	...	...	...	...
155. – *cimbrica* Ravn	35.6	43.1	28.4	66	...	...
156. – *pölsense* (Auinger)	...	...	...	...	...	...
157. *Lathyrus (Dolicholathyrus) Rothi* (Beyrich)	...	...	...	...	...	...
158. *Fusus cf. sexcostatus* Beyrich	...	...	...	...	...	...
159. – *(Aquilofusus) Grippi* (Kautsky)	...	...	...	...	...	...
160. *Ancilla obsoleta* (Brocchi)	...	...	...	...	...	...
161. *Oliva minutissima* (Kautsky)	...	...	...	...	...	...
162. *Mitra cf. Bellardii* Hoernes & Auinger	...	...	...	...	...	...
163. – *cf. planicosta* Bellardi	...	...	...	...	...	...
164. *Cancellaria (Cancellaria) cancellata* Linné	...	...	...	...	...	...
165. – – *contorta* Basterot	...	...	...	...	...	...
166. – *(Trigonostoma) acutangula* Faujas de Saint Fond	...	...	...	...	...	...
167. – – *boreobsoleta* Kautsky	...	...	...	...	...	...
168. – *(Narona) calcarata* (Brocchi)	...	...	...	...	...	...
169. – – *varicosa* (Brocchi)	...	...	...	...	...	...
170. *Admete cf. fusiformis* (Cantraine)	...	...	...	...	...	...
171. *Conus Dujardini* Deshayes	...	...	...	...	...	...
172. *Gemmula cf. rotata* (Brocchi)	...	...	...	...	...	...
173. – *badensis* (Hörnes)	0.2	0.2	...	1.3	0.9	*1*
174. – *boreoturricula* (Kautsky)	...	0.2	...	...	...	...
175. – *Stoffelsi* (Nyst)	...	...	...	...	...	...
176. – *Zimmermanni* (Philippi)	...	...	...	...	...	...
177. *Fusiturris Duchastelii* (Nyst)	...	0.2	...	...	2.5	...
178. – *inermis* (Hörnes)	...	...	...	...	...	...
179. *Bathytoma cataphracta* (Brocchi)	...	...	...	1.3	...	...
180. *Turricula Steinvorthi* (von Koenen)	...	...	...	...	0.9	...
181. *Clinura sp.*	...	...	...	...	...	...
182. *Tahusyrinx cf. Corneti* (von Koenen)	...	...	...	...	...	...
183. *Clavatula boreointerrupta* Kautsky	...	...	...	...	...	...
184. – *sp.*	...	...	...	...	...	...
185. – *obliplicatula* Kautsky	...	...	...	...	...	...
186. *Genota ramosa* (Basterot)	...	...	...	...	...	...
187. *Acamptogenotia cf. Escheri* (Mayer)	...	...	...	...	...	...

jerg ormation					**Bramminge** Arnum formation	**Ribe** Arnum formation											
53	53.5	53.75	54	55	70–80	113–114	114–115	115–116	116–117	117–118	118–119	119–120	120–121	121–122	122–123	123–124	124–125
...	0.2	0.3	...	...	0.018	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.003	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.003	...	...	...	...	...	...	...	...	...	...	...	...
...	1.0	1.2	*1*	1.3	0.132	...	...	...	...	...	...	...	*1*	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.003	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
0.7	22.2	28.0	*10*	11.8	0.549	*5*	*1*	...	...	...	...	...	...	*1*	*1*	*1*	...
...	0.4	...	...	...	2.47	*1*	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.036	...	...	...	...	...	...	...	...	...	...	*1*	...
0.7	0.9	0,9	...	1.3	0.255	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.036	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.006	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.031	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	16.7	...	...	...	...	...	...	...	...	...	...	...	...
...	0.1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	0.6	...	...	...	0.069	...	...	...	...	...	...	...	...	...	...	...	...
...	0.1	...	...	...	0.102	...	...	...	...	...	...	...	...	...	...	...	...
0.7	0.1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	0.1	...	...	...	0.102	...	...	...	...	...	...	...	...	...	...	...	...
...	0.1	...	...	...	0.006	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.012	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	0.1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	0.3	...	...	0.003	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.006	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.063	...	...	...	...	...	...	...	...	...	...	...	...
...	0.2	0.6	...	0.3	0.036	...	...	...	...	...	...	...	...	...	...	...	...
0.7	0.1	...	...	0.6	0.141	...	...	...	...	...	...	...	...	...	...	...	...
...	0.2	0.3	...	0.6	0.105	...	...	...	...	...	...	...	...	...	...	...	...
1.4	1.2	0.6	...	1.6	0.204	...	...	...	...	...	...	...	...	...	...	...	...
...	0.6	0.6	*1*	1.0	0.099	*1*	...	...	...	...	...	...	...	...	...	...	*1*
...	0.1	0.3	...	0.3	0.105	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.003	...	...	...	...	...	...	...	...	...	...	...	...
...	0.7	...	...	1.3	0.246	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.084	...	...	...	...	...	...	...	...	...	...	...	...
...	0.1	0.3	*1*	0.3	0.042	*1*	...	...	...	...	...	...	...	...	...	...	...
0.7	0.1	...	...	...	0.006	...	...	...	...	...	...	...	...	...	...	...	...
...	0.1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	*1*	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.003	...	...	...	...	...	...	...	...	...	...	...	...
1.4	...	0.3	...	0.3	0.012	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	0.3	0.036	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...

Table 15, part 1 (*continued*).

	Glej Arnu						
Depth (m.):	23	25	32	38	42	48	52
188. *Acamptogenotia cf. Straeleni* Glibert	...	...	...	...	...	...	...
189. *Inquisitor obeliscus* (Des Moulins)	...	...	0.3	...	...	...	...
190. *Splendrillia Selenkae* (von Koenen)	...	...	...	...	...	...	...
191. *Boreodrillia toftlundensis nov. gen. & nov. sp.*	...	...	...	...	...	...	...
192. *Asthenotoma cf. pannus* (Basterot)	...	...	...	...	1.7	...	...
193. *Brachytoma electa nov. sp.*	...	...	...	...	...	...	...
194. – *Grateloupi* (Peyrot)	...	...	...	...	...	...	...
195. – *obtusangula* (Brocchi)	...	...	...	...	...	...	...
196. – *sp.*	...	...	...	...	...	...	...
197. *Aphanitoma glejbjergensis nov. sp.*	...	...	...	...	...	...	...
198. *Neoguraleus calais* (Kautsky)	0.2	0.2	...	1.3	...	...	...
199. – *tenella* (Mayer)	0.2	0.2	...	1.3	...	...	...
200. – *Gürichi* (Kautsky)	...	...	...	...	...	...	...
201. *Pleurotomoides Johannae* (Peyrot)	...	...	...	...	...	...	...
202. – *elatior* (von Koenen)	...	...	...	...	...	...	...
203. – *simplex nov. sp.*	...	...	...	...	...	...	...
204. – *cf. Luisae* (von Koenen)	...	...	...	...	...	...	...
205. – *campanulata nov. sp.*	...	...	...	...	...	...	...
206. *Teretia anceps* (Eichwald)	...	...	...	...	...	...	...
207. – *sp.*	...	...	...	...	...	...	...
208. *Philbertia scabra* (Philippi)	...	...	...	...	...	...	...
209. – *sinuosula nov. sp.*	...	...	...	...	...	...	...
210. *Eubela trochlearis* (Hörnes)	...	...	...	...	...	...	...
211. – *sp.*	...	...	...	...	...	...	...
212. *Metuonella Grippi* (Kautsky)	...	...	...	...	...	...	...
213. *Oenopota sp.*	...	...	...	...	...	...	...
214. *Terebra Hörnesi* Beyrich	0.3	0.4	0.3	...	0.9	...	...
215. – *acuminata* Borson	...	...	...	...	...	...	...
216. *Acteon semistriatus* (Basterot)	0.2	...	...	...	0.9	...	...
217. – *laevigatus* (Grateloup)	...	0.2	...	...	...	...	...
218. – *cf. pinguis* d'Orbigny	...	...	...	...	...	...	...
219. – *arnumensis nov. sp.*	...	...	...	...	...	...	...
220. – *tornatilis* (Linné)	...	...	...	...	...	...	...
221. – *sp.*	...	...	...	...	...	...	...
222. *Actæonidea sp.*	...	...	...	...	...	...	...
223. *Chrysallida cf. cimbrica* (Kautsky)	...	...	...	1.3	...	...	...
224. – *nodifera nov. sp.*	0.5	0.7	...	...	...	...	...
225. – *toftlundensis nov. sp.*	...	...	...	...	...	...	...
226. – *acuticostata nov. sp.*	...	...	...	...	...	...	...
227. – *semireticulata nov. sp.*	...	...	...	...	...	...	...
228. – *modesta nov. sp.*	...	...	...	...	...	...	...
229. – *pygmaea* (Grateloup)	...	...	...	...	...	...	...
230. *Kleinella (Leucotina) Nordmanni nov. sp.*	0.1	0.2	0.5	...	...	...	...
231. *Odostomia conoidea* (Brocchi)	...	...	...	...	...	...	...
232. – *subintermedia* (Cossmann & Peyrot)	0.1	...	...	...	...	...	...
233. – *sallespissensis* (Cossmann & Peyrot)	...	...	...	...	...	...	...
234. – *pallidaeformis* (Sacco)	...	...	...	...	...	...	...
235. – *mutinensis* (Sacco)	...	...	...	...	2.5	...	...
236. – *(Syrnola) subumbilicata* (Grateloup)	...	0.2	...	...	...	...	...

jerg ormation					**Bramminge** Arnum formation	**Ribe** Arnum formation											
53	53.5	53.75	54	55	70–80	113–114	114–115	115–116	116–117	117–118	118–119	119–120	120–121	121–122	122–123	123–124	124–125
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	0.2	0.3	*1*	…	0.228	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.012	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	0.3	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0,048	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	0.3	…	…	0.195	…	…	…	…	…	…	…	…	…	…	…	…
…	0.6	…	…	0.3	0.090	*1*	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	0.3	…	…	…	…	…	…	…	…	…	…	…	…	…
0.7	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	0.3	0.096	…	…	…	…	…	…	…	…	…	…	…	…
…	0.2	0.3	…	…	0.664	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.003	…	…	…	…	…	…	…	…	…	…	…	…
…	0.4	0.3	…	…	0.018	*1*	…	…	…	…	…	…	…	…	…	…	…
…	…	0.3	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.078	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	0.3	0.009	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.009	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.009	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	1.0	0.006	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.003	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
2.9	0.9	2.4	…	1.0	1.2	…	…	…	…	…	…	…	…	…	…	…	…
0.7	…	0.3	…	…	0.015	…	…	…	…	…	…	…	…	…	…	…	…
1.4	0.4	0.6	…	…	0.156	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.012	…	…	…	…	…	…	…	…	…	…	…	…
…	0.1	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.003	…	…	…	…	…	…	…	…	…	…	…	…
1.4	…	…	…	…	0.018	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	0.3	…	…	0.009	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.048	…	…	…	…	…	…	…	…	…	…	…	…
…	0.1	…	…	0.6	0.051	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	0.009	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	*1*	…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	0.1	…	…	1.0	…	…	…	…	…	…	…	…	…	…	…	…	…

Table 15, part 1 (*continued*)

							Glej Arnu
Depth (m.):	23	25	32	38	42	48	5
237. *Odostomia* (*Syrnola*) *dubia* (GRATELOUP)	...	...	...	...	...	...	..
238. *Eulimella concinna nov. sp.*	...	...	...	...	...	...	..
239. – *Scillae* (SCACCHI)	...	...	...	...	...	...	..
240. – *acicula* (PHILIPPI)	...	...	...	...	...	...	..
241. – *crassitesta nov. sp.*	...	...	...	...	...	...	..
242. *Turbonilla costellata* (GRATELOUP)	...	...	...	...	...	...	..
243. – *lactea* (LINNÉ)	...	...	...	...	...	...	..
244. – *rufa* (PHILIPPI)	...	...	...	...	...	...	..
245. – *pseudoterebralis* (SACCO)	...	...	...	...	...	...	..
246. – *sp.*	...	...	...	...	...	...	..
247. *Pyramidella plicosa* BRONN	...	...	...	...	...	...	..
248. *Ringicula ventricosa* (SOWERBY)	...	...	...	...	...	...	..
249. – *buccinea* (BROCCHI)	4.0	6.8	0.3	...	0.9	...	
250. – *Ravni nov. sp.*	...	...	...	...	...	...	..
251. *Cylichna cf. cylindracea* (PENNANT)	...	...	...	...	...	...	..
252. – *Bellardi* (VON KOENEN)	...	...	...	...	...	...	..
253. *Rhizorus acuminatus* (BRUGUIÈRE)	0.6	0.2	0.8	1.3	...	...	..
254. *Retusa elongata* (EICHWALD)	...	0.4	0.5	...	...	...	..
255. – *umbilicata* (MONTAGU)	0.2	0.2	1.0	...	...	...	..
256. – *obtusa* (MONTAGU)	...	...	...	...	...	...	..
257. *Acteocina sp.*	...	...	...	...	...	...	..
258. – *Lajonkaireana* (BASTEROT)	...	...	...	...	...	...	..
259. *Scaphander lignarius* (LINNÉ)	...	...	...	...	...	...	..
260. *Roxania utriculus* (BROCCHI)	0.2	...	0.8	...	...	...	..
261. *Philine sp. a*	...	...	...	...	...	...	..
262. – *sp. b*	...	...	...	...	...	...	..
263. *Spiratella atlanta* (MØRCH)	0.2	...	...	...	...	...	..
264. – *cf. valvatina* (REUSS)	...	...	...	...	...	...	..
265. *Clio sp.*	...	...	...	...	...	...	..
266. *Vaginella depressa* DAUDIN	0.5	0.5	...	...	5.9	...	
Sum total per cent	100.4	100.7	100.9	99.8	100.9	...	..
Percentage share of 1 specimen	0.2	0.2	0.3	1.3	0.9	...	..
Sum total of specimens (= 100 %)	*643*	*559*	*391*	*77*	*118*	*6*	*3*

jerg ormation					**Bramminge** Arnum formation	**Ribe** Arnum formation											
53	53.5	53.75	54	55	70–80	113–114	114–115	115–116	116–117	117–118	118–119	119–120	120–121	121–122	122–123	123–124	124–125
...	...	...	...	...	0.003	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	*1*	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.003	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.006	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.003	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.003	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.027	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.003	...	...	...	...	...	...	...	...	...	...	...	...
...	0.2	0.9	...	0.6	0.102	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
0.7	6.9	7.4	*1*	4.8	7.53	*2*	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.006	*1*	...	...	...	...	...	...	...	...	...	...	...
1.4	0.9	0.3	...	0.3	0.162	...	...	...	...	...	...	...	...	...	...	...	...
...	0.2	0.3	...	0.3	0.072	...	...	...	...	...	...	...	...	...	...	...	...
...	0.1	0.3	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	0.1	0.3	...	0.3	...	...	...	...	...	...	...	*1*	...	...	...	...	...
...	0.4	0.3	...	...	0.045	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	0.1	0.3	*1*	...	0.162	...	...	*1*	...	...	...	...	...	...	...	...	...
99.5	98.7	97.6	...	99.5	99.777	...	...	...	...	...	...	...	...	...	...	...	...
0.7	0.1	0.3	...	0.3	0.003	...	...	...	...	...	...	...	...	...	...	...	...
139	*821*	*336*	*31*	*315*	*33165*	*59*	*9*	*7*	*1*	*4*	*1*	*4*	*2*	*3*	*4*	*8*	*19*

Table 15, (part 2). The Frequencies of th

Roman types: per cent

		Gramby Arnum formation							
	Depth (m.):	81.9- 82.2	82.2- 82.7	82.7- 83.8	84.7- 87.2	90.4- 92.7	92.7- 109.3	109.3- 110.9	110. 121
	Pelecypoda								
1.	*Nucula nucleus* (Linné)	...	...	...	...	...	...	...	...
2.	– *Jeffreysi* Bellardi	...	...	...	...	...	...	...	...
3.	– *cromata nov. sp.*	...	...	1.5	1.12	2.16	2.22	1.58	3.
4.	– *cf. nitida* Sowerby	...	...	...	...	...	...	...	...
5.	– *sp.*	...	...	...	0.11	...	...	...	...
6.	*Nuculoma hanseata* (Kautsky)	...	...	0.2	0.27	0.15	...	...	...
7.	– *cf. Haesendonckii* (Nyst & Westendorp)	...	...	...	...	...	...	...	...
8.	*Leda* (*Jupiteria*) *pygmaea* (Münster)	*2*	*1*	6.3	6.06	12.5	31.6	3.15	28.
9.	– (*Ledina*) *Westendorpii* (Nyst & Westendorp)	*1*	...	0.2	...	...	0.44	0.79	...
10.	– (*Lembulus*) *emarginata* (Lamarck)	...	...	...	0.17	0.15	...	0.39	0.
11.	*Yoldia glaberrima* (Münster)	...	...	3.7	0.61	2.46	1.33	0.79	4.
12.	*Arca diluvii* Lamarck	...	...	0.1	0.24	0.15	...	...	...
13.	*Bathyarca pectunculoides* Scacchi	...	...	...	...	...	...	...	...
14.	*Glycymeris sp.*	...	...	...	...	...	...	...	...
15.	*Limopsis aurita* (Brocchi)	...	...	...	...	...	...	...	...
16.	– *anomala* (Eichwald)	...	...	...	...	...	...	...	...
17.	*Modiolus sp. a.*	...	...	...	...	...	...	...	...
18.	– *sp. b.*	...	...	...	...	...	...	...	...
19.	*Musculus saucatsensis* (Cossmann)	...	...	...	0.03	...	...	0.39	...
20.	*Arcoperna sp.*	...	...	...	...	...	...	...	...
21.	*Pecten ex aff. Brummelii* Nyst & *liberata* Cossmann & Peyrot	...	...	...	...	...	...	...	...
22.	– *radians* Nyst	...	...	...	...	...	...	...	...
23.	– *tigerinus* Müller	...	...	...	...	...	...	...	...
24.	– *Gerardii* Nyst	...	...	...	...	...	...	...	...
25.	– *ssp. indet.*	...	...	...	0.03	...	...	...	...
26.	*Lima* (*Limea*) *strigilata* (Brocchi)	...	...	...	...	...	...	...	...
27.	*Anomia squamula* (Linné)	...	...	...	...	...	...	...	...
28.	*Ostrea sp.*	...	...	0.1	...	...	...	...	...
29.	*Astarte cf. concentrica* Goldfuss	...	...	...	...	...	...	...	...
30.	– (*Goodallia*) *triangularis* Montagu	...	...	...	...	...	...	...	...
31.	*Cardita* (*Cyclocardia*) *orbicularis* (Sowerby)	...	...	...	...	...	...	...	...
32.	*Kellyella* (*Lutetia*) *rotunda nov. sp.*	*2*	...	0.6	3.28	2.31	5.77	7.48	4.
33.	– – *patera nov. sp.*	...	...	...	...	...	...	...	...
34.	*Isocardia sp.*	...	...	...	0.3	...	0.44	0.39	...
35.	*Sportella cimbrica* Kautsky	...	...	...	0.07	...		...	...
36.	*Thyasira cf. flexuosa* (Montagu)	...	...	...	0.03	...		...	...
37.	*Phacoides cf. Schloenbachi* (von Koenen)	...	...	...	...	...		...	
38.	*Loripes cf. niveus* (Eichwald)	...	...	...	...	...		...	
39.	*Lucina* (*Loripinus*) *Nørregaardi nov. sp.*	...	...	...	0.03	...		...	
40.	*Codokia jutensis nov. sp.*	...	...	...	...	...		...	
41.	– *sp.*	...	...	...	...	...		...	
42.	*Erycina* (*Scacchia*) *Degrangei* Cossmann & Peyrot	...	...	...	0.24	0.15		0.39	
43.	*Erycina* (*Hemilepton*) *coarctata* (Wood)	...	...	...	...	...		...	
44.	– – *striatissima* (Cerulli-Irelli)	...	...	...	...	...		...	
45.	*Lepton nitidum* Turton	...	...	...	...	...		...	

Molluscan Species in the Well Sections

Italics: number of specimen

Toftlund Arnum formation					Arnum							
					Well no. 150.13			Well no. 150.25 b				
					Gram formation	Arnum formation		Arnum formation				
75–100	100–105	105–110	110–115	115	28–40	53–83	83–94	62.7–62.9	95.0–95.3	101.0–104.3	104.3–107.5	107.5
.0223	...	0.008	...	0.14	...		...	...	3.36	...	0.19	...
...	0.49	0.361	0.28	...	...	...	0.6	...	0.23	...	...	...
.585	0.014	...	...	...	...	0.96	...	3.48	...	...	...	...
.0004	0.014	0.008	...	...	...	...	...	0.046	...	...	...	...
.382	0.27	...	...	...	4.3	...	...	0.828	...	*1*	...	...
.286	0.20	2.13	2.2	1.76	...	0.073	1.2	0.006	2.36	*1*	0.76	1.4
...	...	...	...	...	...	...	...	...	...	...	...	...
5.27	25.7	1.02	5.32	0.47	14.3	21.82	4.9	12.2	1.3	*11*	7.9	18.7
.492	1.41	5.54	3.97	1.42	...	0.129	0.6	0.029	11.6	*2*	1.32	1.4
.0318	...	0.084	0.07	0.14	...	0.073	...	0.017	...	...	...	...
1.022	3.57	1.31	1.23	5.43	2.5	0.184	1.2	2.9	2.52	*2*	6.24	0.7
.0272	0.014	0.092	0.26	0.20	0.6	0.055	...	0.145	0.08	*1*	...	0.7
...	...	...	...	...	...	...	...	...	...	...	0.19	...
...	...	...	...	0.07	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...
.0008	...	0.023	0.09	...	...	...	...	...	0.08	...	...	...
...	...	...	...	...	...	...	...	0.006	...	...	...	...
...	...	...	0.024	...	...	...	...	...	...	...	...	...
...	0.014	0.023	0.05	0.07	...	...	...	...	0.15	...	...	0.7
...	...	...	...	...	...	...	...	...	...	...	...	...
.0087	0.014	0.008	0.024	0.07	...	0.037	...	...	...	...	...	...
.0004	0.014	0.008	0.024	0.07	...	...	...	...	0.08	...	...	...
...	...	...	0.024	0.07	...	...	...	...	...	...	...	...
...	...	0.008	...	...	...	...	...	...	...	...	...	0.7
...	0.014	...	...	...	...	...	...	0.006	...	...	...	...
...	0.014	...	...	...	...	...	...	...	...	...	...	...
.014	0.158	0.338	0.21	0.07	...	0.018	...	...	0.23	...	0.19	...
.0011	0.043	0.008	0.024	...	...	...	...	...	...	...	...	...
...	...	...	0.024	...	...	...	...	...	0.15	...	...	...
...	...	...	0.024	...	...	...	...	...	...	...	...	...
...	...	...	...	...	0.6	...	...	0.006	...	...	...	...
.706	2.09	1.12	3.73	0.54	1.9	0.496	...	4.8	3.89	*6*	3.02	11.5
...	...	...	...	...	...	0.018	...	...	...	...	...	...
.0113	0.014	0.123	0.84	0.68	...	0.037	...	0.017	0.53	*3*	0.57	4.3
.0042	0.043	0.015	0.05	...	...	...	...	0.029	...	...	0.38	...
.0125	0.058	0.454	0.47	0.14	...	...	...	0.012	1.14	*2*	1.89	1.4
...	...	...	0.024	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	0.018	...	...	...	...	...	...
.0057	...	0.031	0.05	...	...	0.018	...	...	...	...	...	...
...	...	0.008	0.07	...	...	...	...	0.006	...	...	0.19	...
...	...	...	...	...	...	...	...	...	...	...	...	...
.0189	0.014	0.092	0.12	...	...	0.018	...	0.017	0.08	...	0.19	0.7
...	0.014	0.031	...	...	...	0.018	...	...	...	...	...	...
...	...	0.008	...	...	...	...	...	...	...	...	...	...
.0004	...	0.008	...	...	...	...	...	...	...	...	...	...

Table 15, part 2 (*continued*).

	Gramby Arnum formation							
Depth (m.):	81.9- 82.2	82.2- 82.7	82.7- 83.8	84.7- 87.2	90.4- 92.7	92.7- 109.3	109.3- 110.9	110. 121.
46. *Montacuta substriata* MONTAGU	...	...	...	0.03	...	...	...	...
47. *Laevicardium cyprium* (BROCCHI)	...	...	...	...	...	...	...	...
48. – *dingdense* (LEHMANN)	...	...	...	0.07	...	0.44	...	...
49. – *Straeleni* GLIBERT	...	...	...	...	...	...	...	...
50. *Cardium sp. cf. hanseatum* KAUTSKY	...	...	...	...	0.15	...	...	...
51. *Gouldia minima* (MONTAGU)	...	...	...	...	...	...	...	...
52. *Pitar chione* (LINNÉ)	...	...	...	...	...	...	...	...
53. *Meretrix cf. incrassata* (SOWERBY)	...	...	...	...	0.15	...	...	...
54. *Dosinia cf. Basteroti* (AGASSIZ)	...	...	...	...	0.31	...	...	0.5
55. *Venus* (*Ventricola*) *multilamella* (LAMARCK)	...	...	0.1	...	...	0.44	...	...
56. *Ervilia pusilla* (PHILIPPI)	...	...	...	...	...	...	...	...
57. *Spisula subtruncata* (DA COSTA) *var.*	*2*	...	8.5	10.83	13.9	7.10	23.6	20.0
58. – *solida* (LINNÉ)	...	...	...	...	...	...	...	...
59. *Donax sp.*	...	...	...	...	...	...	...	...
60. *Abra prismatica* (MONTAGU) *var.*	...	...	...	1.42	...	0.44	0.39	0.5
61. *Angulus donacinus* (LINNÉ)	...	...	...	0.03	...	0.44	...	...
62. *Tellina cf. fallax* BEYRICH	...	...	...	0.03	0.15	0.44	...	0.5
63. *Pharus saucatsensis* DES MOULINS	...	...	...	...	...	...	...	...
64. *Cultellus sp.*	...	...	...	0.03	...	...	...	...
65. *Ensis Degrangei* COSSMANN & PEYROT	...	...	...	0.03	0.15	...	...	...
66. *Saxicava arctica* (LINNÉ)	...	...	0.2	0.44	0.15	...	0.79	0.5
67. *Saxicavella pusilla nov. sp.*	...	...	...	0.03	0.15	...	...	...
68. *Panopea sp.*	...	...	...	0.03	...	...	...	...
69. *Varicorbula gibba* (OLIVI)	...	*2*	1.0	27.7	5.54	5.33	0.39	10.5
70. *Lentidium donaciformis* (NYST)	...	...	0.1	0.03	...	...	...	0.5
71. *Sphenia sp.*	...	...	...	...	...	...	...	...
72. *Pholas sp.*	...	...	...	...	...	...	...	...
73. *Pholadidea sp.*	...	...	...	...	...	...	...	...
74. *Martesia sp. cf. rugosa* (BROCCHI)	...	...	...	...	...	...	...	...
75. *Teredo sp. cf. saucatsensis* BENOIST	...	...	...	...	...	...	...	...
76. *Pandora copiosa nov. sp.*	...	...	...	0.07	...	...	...	...
77. *Thracia sp.*	...	...	...	0.03	...	...	...	...
78. *Cuspidaria cf. cuspidata* (OLIVI)	...	...	...	0.03	...	...	0.39	0.5
79. – *cf. rostrata*	...	...	...	...	...	...	...	...
80. – – *costellata* (DESHAYES)	...	...	...	...	...	...	...	...
Scaphopoda								
81. *Cadulus gadus* (MONTAGU)	...	...	0.1	0.03	0.62	...	...	0.5
82. *Dentalium cf. Michelotti* HÖRNES *var.*	...	...	0.2	0.03	0.31	...	...	0.5
83. – *novemcostatum* LAMARCK	...	...	...	0.1	...	0.44	...	...
84. – *sp. cf. badensis* PARTSCH	...	...	...	...	...	...	...	...
Gastropoda								
85. *Acmaea compressiuscula* (KARSTEN)	...	...	...	...	...	...	...	...
86. *Calliostoma sp.*	...	...	...	...	...	...	...	...
87. *Starkeyna hanseata* (KAUTSKY)	...	...	...	0.03	0.31	...	...	...
88. – *jutensis nov. sp.*	...	...	...	...	...	...	...	...
89. – *nov. sp.*	...	...	...	...	...	...	...	...
90. *Liotia miosuturalis* KAUTSKY	...	...	...	...	...	...	...	...

Toftlund Arnum formation					**Arnum**							
					Well no. 150.13			Well no. 150.25 b				
					Gram formation	Arnum formation		Arnum formation				
75–100	100–105	105–110	110–115	115	28–40	53–83	83–94	62.7–62.9	95.0–95.3	101.0–104.3	104.3–107.5	107.5
...	...	...	...	...	...	...	...	...	...	...	...	...
0.0011	0.029	0.054	...	0.14	...	...	...	...	0.08	...	0.19	0.7
0.0165	0.043	0.038	0.12	0.41	...	0.018	0.6	0.012	...	...	0.38	0.7
0.0064	0.014	0.061	0.14	0.2	0.6	0.018	...	0.017	0.08	*1*	0.19	0.7
0.0004	...	...	0.024	...	...	...	...	...	...	...	...	...
0.0072	0.058	0.038	0.024	0.07	...	0.037	...	0.029	0.08	...	0.19	...
0.0004	...	...	...	...	...	...	...	...	...	...	...	...
0.0004	...	0.745	0.09	0.14	...	...	...	0.012	0.84	...	...	...
0.0079	...	...	...	...	...	...	...	0.006	...	...	...	...
0.0261	0.014	0.023	0.07	...	...	...	...	0.012	0.08	...	...	...
0.0477	...	0.038	0.43	0.14	1.2	0.165	...	2.43	0.15	*1*	0.19	0.7
2.85	7.61	6.71	14.7	5.36	8.7	1.32	1.2	12.70	3.84	*5*	10.59	10.8
0.133	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	0.19	...
0.149	0.244	0.208	1.47	2.85	1.9	0.055	...	0.585	0.31	*5*	12.65	2.9
...	...	0.008	...	...	...	0.018	...	0.029	...	...	...	...
0.003	0.029	0.023	0.05	0.34	...	...	0.6	...	...	...	0.38	0.7
...	...	...	...	...	...	...	...	0.012	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	0.19	...
...	...	0.008	0.05	...	...	...	...	...	...	...	...	...
0.173	0.259	0.584	0.76	0.34	0.6	0.312	...	0.555	0.61	*1*	0.94	4.3
0.0004	...	0.008	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...
0.58	0.877	0.323	0.83	0.20	1.9	2.53	1.9	0.84	1.37	*1*	0.19	...
0.0019	...	...	...	...	...	...	...	...	...	...	0.19	...
...	...	0.015	0.024	0.07	...	...	...	...	0.08	...	...	...
...	...	...	...	...	...	...	...	0.006	...	...	...	...
...	...	...	0.024	...	...	...	...	...	...	...	...	...
...	...	0.008	...	...	...	...	...	...	...	...	...	...
...	...	0.008	...	...	...	...	...	...	0.08	...	0.19	...
0.0113	0.115	0.131	0.17	...	...	0.018	...	0.006	0.23	...	0.38	...
0.0008	0.014	0.015	...	...	...	...	...	...	...	...	...	...
0.0079	0.043	0.154	0.12	0.14	...	0.018	...	0.162	0.38	*1*	0.19	1.4
...	...	0.008	...	...	...	...	...	...	...	...	...	...
0.0004	0.014	...	...	...	...	...	...	...	...	...	...	...
0.171	0.014	0.015	0.17	...	1.2	0.551	1.2	0.122	...	...	...	...
0.0068	...	0.192	0.19	...	...	0.018	0.6	0.035	0.53	...	...	...
0.0242	...	0.008	0.024	...	...	0.018	...	0.006	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	0.07	...	...	...	...	...	...	...	...	...
...	...	0.008	...	...	...	...	0.6	...	0.08	...	...	...
0.0061	...	...	0.024	...	...	0.018	...	0.243	...	...	...	...
...	...	0.023	...	...	...	...	...	...	0.08	...	...	...
...	...	0.008	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...

Table 15, part 2 (*continued*).

		Gramby Arnum formation							
	Depth (m.):	81.9-82.2	82.2-82.7	82.7-83.8	84.7-87.2	90.4-92.7	92.7-109.3	109.3-110.9	110 121
91.	*Alvania Partschi* (Hörnes)	...	...	...	...	0.15	...	...	.
92.	*Rissoa Ravni nov. sp.*	*1*	...	...	0.03	...	...	...	.
93.	*cf. succincta* Nyst	...	...	...	0.03	...	...	...	.
94.	*Rissoina Ödumi nov. sp.*	...	...	...	...	...	...	...	.
95.	*Adeorbis subcirculus* Cossmann & Peyrot	...	...	...	0.07	...	...	...	.
96.	– *cf. carinata* (Philippi)	...	...	...	...	...	...	...	.
97.	– *planorbillus* (Dujardin)	...	...	...	...	...	...	...	.
98.	*Turritella tricarinata* (Brocchi)	...	...	...	...	0.92	0.89	0.39	0.
99.	– *subangulata* (Brocchi)	...	...	...	...	...	...	...	.
100.	*Solarium carocollatum* Lamarck	...	...	...	...	...	...	...	.
101.	– *trochleare nov. sp.*	...	...	...	...	...	...	...	.
102.	– *angustiforatum* Cossmann & Peyrot	...	...	...	...	...	...	...	.
103.	*Bittium spina* (Partsch)	...	...	0.1	...	...	...	...	.
104.	– *tenuispina nov. sp.*	...	...	0.6	0.88	0.62	4.89	0.79	0.
105.	*Cerithiopsis Vignali* Cossmann & Peyrot	...	...	...	...	...	...	...	.
106.	*Triphora perversa* (Linné)	...	...	...	...	...	...	...	.
107.	*Cirsotrema Thais* De Boury	...	...	...	...	...	...	...	.
108.	*Scala cf. frondicula* (Wood)	...	...	...	...	...	...	...	.
109.	– (*Acrilla*) *cf. amoena* Philippi	...	...	...	...	...	...	...	.
110.	*Janthina cimbrica nov. sp.*	...	...	...	0.03	...	...	...	.
111.	*Niso acarinatoconica* Cossmann & Peyrot	...	...	...	...	...	...	...	.
112.	*Melanella similis* (d'Orbigny)	...	...	...	...	...	...	...	.
113.	– *taurostricta* (Cossmann & Peyrot)	...	...	...	0.10	0.15	...	0.39	.
114.	*Calyptraea chinensis* (Linné)	...	...	...	...	...	...	...	.
115.	*Xenophora Deshayesi* (Michelotti)	...	...	...	...	...	...	...	.
116.	*Aporrhais alata* (Eichwald)	*1*	*1*	11.0	3.48	2.16	0.89	0.39	1.
117.	*Natica* (*Lunatia*) *catena* (Da Costa)	...	...	0.9	0.1	...	...	...	.
118.	– (*Naticina*) *hanseata* Kautsky	...	...	...	0.14	...	...	...	.
119.	– – *Beyrichi* von Koenen	...	...	...	...	...	...	...	.
120.	– – *protostriata nov. sp.*	...	...	0.1	0.03	0.15	...	...	.
121.	– – *praeclausa* Kautsky	...	...	0.1	0.07	...	...	...	.
122.	– – *tectula* Bonelli	...	...	...	...	...	...	...	.
123.	– – *miopusilla* Kautsky	...	...	...	0.03	...	...	...	.
124.	– – *submamillaris* d'Orbigny	...	...	...	...	...	...	...	.
125.	– (*Polynices*) *affinis* (Gmelin)	...	...	...	0.07	...	...	...	.
126.	– (*Nerita*) *Josephinia* (Risso)	...	...	...	...	...	...	...	.
127.	– *sp.*	...	...	0.2	0.51	...	...	...	.
128.	*Globularia sp.*	...	...	...	...	...	...	...	.
129.	*Sigaretus sulcatus* (Grateloup)	...	...	...	...	...	...	...	.
130.	– *cf. aquensis* Recluz	...	...	...	...	...	...	...	.
131.	*Semicassis sp.*	...	...	...	0.03	...	...	...	.
132.	*Tritonium sp.*	...	...	...	...	...	...	...	.
133.	*Pyrula simplex* Beyrich	...	...	...	...	...	...	...	.
134.	– *condita* Brongniart	...	...	...	0.03	...	...	...	.
135.	*Murex cf. aturensis* Cossmann & Peyrot	...	...	...	...	...	...	...	.
136.	– *inornatus* Beyrich	...	...	...	...	...	...	...	.
137.	*Typhis cf. horridus* (Brocchi)	...	...	...	...	...	...	...	.
138.	– *fistulosus* (Brocchi)	...	...	0.6	0.07	0.15	...	...	.
139.	*Tritonalia coelata* Dujardin	...	...	...	...	...	...	...	.

Toftlund					Arnum							
Arnum formation					Well no. 150.13			Well no. 150.25 b				
					Gram formation	Arnum formation		Arnum formation				
75–100	100–105	105–110	110–115	115	28–40	53–83	83–94	62.7–62.9	95.0–95.3	101.0–104.3	104.3–107.5	107.5
0.0344	0.043	…	…	…	…	0.092	…	0.017	…	…	…	…
0.0803	0.014	…	0.024	0.14	…	0.165	…	0.266	0.08	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	0.006	…	…	…	…
0.0129	…	0.038	0.05	…	…	0.037	…	…	0.08	…	…	…
0.0034	…	…	…	…	…	…	…	…	…	…	…	…
0.0129	…	…	…	…	…	0.018	…	…	…	…	…	…
0.0829	0.115	0.108	0.36	1.36	1.9	0.477	0.6	4.35	0.61	*1*	0.19	…
0.0038	…	0.031	…	…	…	0.202	…	…	0.08	…	…	…
0.028	0.014	0.008	…	…	…	0.055	…	…	…	…	…	…
…	0.014	…	…	…	…	…	…	…	…	…	…	…
…	…	0.008	…	…	…	…	…	…	…	…	…	…
0.067	0.086	0.015	0.12	0.14	…	0.294	…	0.006	0.91	…	…	…
1.135	1.7	0.254	0.95	…	15.5	8.39	1.2	26.98	0.31	*1*	1.14	…
…	…	0.008	0.05	…	…	…	…	…	…	…	…	…
…	…	0.008	…	…	…	…	…	…	…	…	…	…
0.0072	…	0.008	…	…	…	…	…	…	…	…	…	…
…	0.014	0.023	…	…	…	…	…	…	…	…	…	…
0.0004	…	0.023	0.024	0.07	…	0.037	…	…	0.08	…	…	0.7
…	…	…	…	…	…	…	…	0.006	…	*1*	…	…
0.0189	0.029	…	0.024	0.07	…	…	…	0.058	…	…	…	…
0.0023	…	…	…	…	…	…	…	…	…	…	…	…
0.0322	…	0.008	…	…	…	0.018	0.6	0.029	…	…	…	…
0.0004	0.014	0.015	…	0.07	…	…	…	…	…	…	…	…
0.0113	…	0.031	0.024	0.07	…	…	…	0.017	0.08	…	…	0.7
4.66	11.49	8.22	3.81	9.22	0.6	0.807	34.6	…	20.8	…	0.57	0.7
0.236	0.187	0.038	2.67	0.75	…	0.514	1.2	…	…	…	1.51	5.0
0.112	0.029	0.031	0.05	0.14	…	0.239	…	…	…	…	…	…
0.0295	…	…	…	0.35	…	…	…	…	…	…	…	…
0.0768	0.072	…	…	…	…	0.220	…	…	…	…	…	…
0.0768	0.101	…	…	…	0.6	0.055	…	…	0.08	…	…	…
0.106	0.115	0.015	…	0.54	…	0.112	…	…	…	…	…	…
0.431	0.072	0.092	0.21	1.9	…	0.073	…	…	…	…	1.51	…
0.0117	0.014	…	…	…	…	…	…	…	…	…	…	…
0.171	…	0.008	…	…	…	0.037	1.2	…	…	…	…	0.7
0.0356	…	…	…	…	0.6	0.018	…	…	…	…	…	…
…	0.316	1.69	0.12	7.32	…	0.477	0.6	1.06	2.44	*2*	3.21	4.3
…	…	…	…	…	…	…	…	…	…	…	…	…
0.0011	…	…	…	…	…	…	…	…	…	…	…	…
0.0011	…	0.015	…	…	…	…	…	…	…	…	…	…
0.0011	…	0.008	…	0.20	…	…	…	…	0.08	*1*	0.19	…
…	…	…	…	0.07	…	…	…	…	…	…	…	…
…	…	0.008	…	…	…	…	…	…	…	…	0.19	…
0.0011	…	0.023	0.024	0.07	…	0.018	0.6	0.006	…	*1*	0.19	…
0.0015	…	…	…	…	…	0.018	…	…	…	…	…	…
0.0079	0.144	0.246	0.21	0.07	…	0.165	0.6	…	0.08	…	…	0.7
…	…	…	0.024	…	…	…	…	…	…	…	…	…
0.0855	0.029	0.577	0.17	0.20	…	0.073	…	0.127	0.31	…	…	…
0.0008	…	…	…	…	…	…	…	…	…	…	…	…

Table 15, part 2 (*continued*).

	Gramby Arnum formation							
Depth (m.):	81.9-82.2	82.2-82.7	82.7-83.8	84.7-87.2	90.4-92.7	92.7-109.3	109.3-110.9	110 121
140. *Pyrene (Atilia) nassoides* (GRATELOUP)	...	...	...	...	...	...	...	.
141. – *(Anachis) sp.*	...	...	...	...	...	...	...	.
142. *Phos decussatus* VON KOENEN	...	...	...	...	...	...	...	.
143. *Nassa tenuistriata* (BEYRICH)	...	...	0.4	0.03	0.15	...	0.39	.
144. – *serraticosta* (BRONN)	...	...	...	...	...	...	...	.
145. – *bocholtense* (BEYRICH)	...	...	...	...	...	...	...	.
146. – *turbinella* (BROCCHI)	...	...	...	...	...	...	...	.
147. – *Fuchsi* VON KOENEN	...	...	...	0.03	...	...	...	.
148. – *Schlotheimi* (BEYRICH)	*2*	...	3.7	4.87	1.54	2.66	5.51	0.
149. – *holsatica* (BEYRICH)	...	...	...	...	...	...	...	.
150. – *Facki* VON KOENEN	...	...	0.1	0.1	0.15	0.44	...	.
151. – *laevissima* BRUSINA	...	...	...	...	...	...	...	.
152. – *cavata* BELLARDI	...	...	...	...	...	...	...	.
153. – *Woodwardi* HARMER	...	...	...	...	...	...	...	.
154. – *subobesa* DEGRANGE-TOUZIN	...	...	...	...	...	...	...	.
155. – *cimbrica* RAVN	*5*	*1*	43.7	23.1	43.7	16.43	22.4	20.
156. – *pölsense* (AUINGER)	...	...	...	...	...	...	...	.
157. *Lathyrus (Dolicholathyrus) Rothi* (BEYRICH)	...	...	...	...	...	...	...	.
158. *Fusus cf. sexcostatus* BEYRICH	...	...	...	...	...	...	...	.
159. – *(Aquilofusus) Grippi* (KAUTSKY)	...	...	...	...	...	...	...	.
160. *Ancilla obsoleta* (BROCCHI)	...	...	...	...	...	...	...	.
161. *Oliva minutissima* (KAUTSKY)	...	...	...	0.03	...	...	...	.
162. *Mitra cf. Bellardii* HOERNES & AUINGER	...	...	...	...	...	...	...	.
163. – *cf. planicosta* BELLARDI	...	...	...	...	...	...	...	.
164. *Cancellaria (Cancellaria) cancellata* LINNÉ	...	...	...	...	...	...	...	.
165. – – *contorta* BASTEROT	...	...	...	...	...	...	...	.
166. – *(Trigonostoma) acutangula* FAUJAS DE SAINT FOND	...	...	...	...	...	...	...	.
167. – – *boreobsoleta* KAUTSKY	...	...	...	...	...	...	...	.
168. – *(Narona) calcarata* (BROCCHI)	...	...	...	...	...	...	...	.
169. – – *varicosa* (BROCCHI)	...	...	...	...	...	...	...	.
170. *Admete cf. fusiformis* (CANTRAINE)	...	...	...	...	...	...	...	.
171. *Conus Dujardini* DESHAYES	...	...	...	0.03	...	...	...	.
172. *Gemmula cf. rotata* (BROCCHI)	...	...	0.2	0.03	...	...	...	.
173. – *badensis* (HÖRNES)	...	...	...	0.03	...	...	...	.
174. – *boreoturricula* (KAUTSKY)	...	...	...	...	...	...	...	.
175. – *Stoffelsi* (NYST)	...	...	...	...	...	...	...	.
176. – *Zimmermanni* (PHILIPPI)	...	...	...	...	...	...	...	.
177. *Fusiturris Duchastelii* (NYST)	...	...	...	...	...	...	...	.
178. – *inermis* (HÖRNES)	...	...	...	...	...	...	...	.
179. *Bathytoma cataphracta* (BROCCHI)	...	...	...	...	...	...	...	.
180. *Turricula Steinvorthi* (VON KOENEN)	...	...	...	...	...	...	...	.
181. *Clinura sp.*	...	...	...	...	...	...	...	.
182. *Tahusyrinx cf. Corneti* (VON KOENEN)	...	...	...	...	...	...	...	.
183. *Clavatula boreointerrupta* KAUTSKY	...	...	...	...	...	...	...	.
184. – *sp.*	...	...	...	...	...	...	...	.
185. – *obliplicatula* KAUTSKY	...	...	...	...	...	...	...	.
186. *Genota ramosa* (BASTEROT)	...	...	...	...	...	...	...	.
187. *Acamptogenotia cf. Escheri* (MAYER)	...	...	...	...	...	...	...	.

Toftlund Arnum formation					**Arnum**							
					Well no. 150.13			Well no. 150.25 b				
					Gram formation	Arnum formation		Arnum formation				
75–100	100–105	105–110	110–115	115	28–40	53–83	83–94	62.7 62.9	95.0–95.3	101.0–104.3	104.3–107.5	107.5
.0011	...	0.008	0.05	...	...	...	...	0.006	...	...	...	...
...	...	0.008	...	...	...	...	...	0.006	...	...	...	...
.0064	...	0.054	0.07	0.47	...	...	0.6	...	...	...	...	...
.201	0.101	0.292	0.33	0.54	...	0.092	0.6	0.041	0.76	*1*	0.19	...
.003	...	...	0.024	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...
.0034	...	...	...	...	...	...	...	...	...	...	...	...
.18	0.259	1.375	1.85	5.15	...	0.165	1.9	...	1.98	*2*	12.3	0.7
.44	3.14	10.82	9.06	9.5	23.6	4.15	6.2	6.89	5.11	*1*	2.83	5.0
.0008	...	...	...	...	...	0.018	...	...	...	...	...	...
.17	0.058	0.169	0.38	2.78	...	0.239	...	0.006	0.46	*1*	3.21	0.7
.0038	...	...	...	...	...	0.073	...	...	...	...	...	...
.0004	...	0.054	0.59	0.81	...	...	...	0.023	...	...	1.32	...
...	...	...	0.07	2.64	...	...	...	...	...	...	...	...
.152	...	...	...	...	...	...	...	...	0.15	...	...	...
.1	29.8	44.6	27.0	13.57	...	41.8	21.6	...	18.4	...	...	2.2
...	...	...	...	...	...	...	...	...	0.08	...	...	...
.0008	...	0.023	0.024	...	...	...	...	...	...	...	...	...
.0034	0.058	0.077	0.14	0.27	...	0.037	...	...	0.23	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...
.0023	0.014	0.038	...	0.14	...	0.018	...	...	...	...	...	...
.0079	...	...	...	...	...	0.055	...	...	...	...	...	...
.0004	...	0.008	...	...	...	...	1.2	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	0.07	...	...	...	...	...	...	0.38	...
...	...	...	...	...	...	...	0.6	...	...	...	...	...
...	...	0.008	...	0.07	...	...	...	...	...	...	...	...
...	...	...	...	0.07	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...
.0102	0.014	0.015	0.024	0.27	...	...	0.6	...	0.08	...	...	...
.0136	...	0.1	0.07	0.07	...	0.018	...	0.017	0.08	...	0.57	0.7
.0466	0.043	0.038	0.024	0.07	...	0.129	0.6	0.006	...	...	...	...
.0934	0.201	0.261	0.12	0.20	0.6	0.018	...	0.157	...	*1*	...	...
.065	0.173	0.123	0.19	0.68	...	0.184	0.6	...	0.15	...	...	...
.014	0.014	0.115	0.33	2.64	...	...	0.6	...	...	...	3.78	0.7
.0125	...	0.038	0.09	0.75	...	0.055	0.6	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...
.0219	0.014	0.169	0.36	1.83	...	...	0.6	0.006	0.61	...	1.51	0.7
.0182	...	0.038	0.024	0.07	...	0.037	...	0.006	0.08	...	...	0.7
.0015	0.014	0.054	0.17	0.14	0.6	...	...	0.006		...	0.19	...
.0061	...	0.008	...	0.41	...	...	...	...		...	0.38	...
...	...	...	...	...	...	...	...	...		...	...	...
...	...	...	...	...	...	...	...	...		...	...	...
...	...	0.015	0.024	...	...	0.018	0.6	0.041		...	...	...
...	0.014	0.031	...	...	...	...	...	0.017		...	...	...
...	...	...	...	...	...	...	...	...		...	...	...
.0008	...	0.015	...	...	...	...	...	...		...	...	...
...	...	...	...	0.27	...	...	...	...		...	...	...

Table 15, part 2 (*continued*).

		Gramby Arnum formation							
	Depth (m.):	81.9-82.2	82.2-82.7	82.7-83.8	84.7-87.2	90.4-92.7	92.7-109.3	109.3-110.9	110 121
188.	*Acamptogenotia cf. Straeleni* GLIBERT	...	...	...	...	...	...	...	.
189.	*Inquisitor obeliscus* (DES MOULINS)	...	...	...	...	...	...	...	.
190.	*Splendrillia Selenkae* (VON KOENEN)	...	...	...	...	...	...	...	.
191.	*Boreodrillia toftlundensis nov. gen. & nov. sp.*	...	...	...	...	...	...	...	.
192.	*Asthenotoma cf. pannus* (BASTEROT)	...	...	...	...	0.15	...	...	.
193.	*Brachytoma electa nov. sp.*	...	...	...	...	...	...	...	.
194.	– *Grateloupi* (PEYROT)	...	...	...	...	...	...	...	.
195.	– *obtusangula* (BROCCHI)	...	...	...	...	...	...	...	.
196.	– *sp.*	...	...	...	...	...	...	...	.
197.	*Aphanitoma glejbjergensis nov. sp.*	...	...	...	...	...	...	...	.
198.	*Neoguraleus calais* (KAUTSKY)	...	...	...	0.17	0.31	...	...	.
199.	– *tenella* (MAYER)	...	...	0.1	0.14	...	...	...	.
200.	– *Gürichi* (KAUTSKY)	...	...	...	...	...	...	...	.
201.	*Pleurotomoides Johannae* (PEYROT)	...	...	...	...	...	...	...	.
202.	– *elatior* (VON KOENEN)	...	...	...	...	...	...	...	.
203.	– *simplex nov. sp.*	...	...	...	0.03	...	...	...	0.
204.	– *cf. Luisae* (VON KOENEN)	...	...	...	...	...	...	...	.
205.	– *campanulata nov. sp.*	...	...	...	...	...	...	...	.
206.	*Teretia anceps* (EICHWALD)	...	...	...	0.03	...	...	...	.
207.	– *sp.*	...	...	...	...	...	...	...	.
208.	*Philbertia scabra* (PHILIPPI)	...	...	...	...	...	...	...	.
209.	– *sinuosula nov. sp.*	...	...	...	...	...	...	...	.
210.	*Eubela trochlearis* (HÖRNES)	...	...	...	...	...	...	...	.
211.	– *sp.*	...	...	...	...	...	...	...	.
212.	*Metuonella Grippi* (KAUTSKY)	...	...	...	...	...	...	...	.
213.	*Oenopota sp.*	...	...	...	...	...	...	...	.
214.	*Terebra Hörnesi* BEYRICH	...	...	0.2	0.17	0.46	...	...	.
215.	– *acuminata* BORSON	...	...	...	...	...	...	...	.
216.	*Acteon semistriatus* (BASTEROT)	...	...	0.7	0.27	0.15	0.44	...	0.
217.	– *laevigatus* (GRATELOUP)	...	...	...	0.03	0.46	...	...	.
218.	– *cf. pinguis* D'ORBIGNY	...	...	...	...	...	...	0.39	.
219.	– *arnumensis nov. sp.*	...	...	...	...	...	...	...	.
220.	– *tornatilis* (LINNÉ)	...	...	...	...	...	...	...	.
221.	– *sp.*	...	...	...	...	...	...	...	.
222.	*Actœonidea sp.*	...	...	...	...	...	...	...	.
223.	*Chrysallida cf. cimbrica* (KAUTSKY)	...	...	...	0.07	...	...	...	.
224.	– *nodifera nov. sp.*	...	...	0.5	0.17	0.15	...	0.39	.
225.	– *toftlundensis nov. sp.*	...	...	...	...	...	...	...	.
226.	– *acuticostata nov. sp.*	...	...	...	...	...	...	...	.
227.	– *semireticulata nov. sp.*	...	...	...	...	...	...	...	.
228.	– *modesta nov. sp.*	...	...	...	...	...	...	...	.
229.	– *pygmaea* (GRATELOUP)	...	...	...	...	...	...	...	.
230.	*Kleinella (Leucotina) Nordmanni nov. sp.*	...	...	0.1	...	...	...	...	.
231.	*Odostomia conoidea* (BROCCHI)	...	...	0.1	...	0.15	...	...	.
232.	– *subintermedia* (COSSMANN & PEYROT)	...	...	...	0.03	...	...	...	.
233.	– *sallespissensis* (COSSMANN & PEYROT)	...	...	...	0.03	...	...	...	.
234.	– *pallidaeformis* (SACCO)	*1*	...	...	0.03	...	...	...	.
235.	– *mutinensis* (SACCO)	...	...	0.1	...	0.15	...	...	.
236.	– *(Syrnola) subumbilicata* (GRATELOUP)	...	...	0.1	...	...	0.44	...	.

Toftlund Arnum formation					**Arnum**							
					Well no. 150.13			Well no. 150.25 b				
					Gram formation	Arnum formation		Arnum formation				
75–100	100–105	105–110	110–115	115	28–40	53–83	83–94	62.7–62.9	95.0–95.3	101.0–104.3	104.3–107.5	107.5
…	…	…	…	0.07	…	…	…	…	…	…	…	…
0.0405	0.043	0.046	0.09	0.88	…	0.112	…	…	0.31	…	0.19	…
0.0004	…	0.008	…	…	…	0.018	…	…	…	…	…	…
…	…	…	0.024	…	…	…	…	…	…	…	…	…
0.0061	0.014	0.015	0.024	0.20	…	0.018	…	…	…	…	0.19	…
0.0004	…	…	…	…	…	…	…	…	…	…	…	…
0.0514	0.072	0.038	…	…	…	0.092	…	0.023	…	…	…	…
0.0711	0.043	0.284	0.26	0.68	…	0.073	…	0.035	0.31	*1*	1.89	1.4
…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…
0.165	0.101	0.054	0.28	0.20	…	0.312	…	…	0.15	…	…	…
0.239	0.058	1.33	0.59	0.54	…	0.331	…	0.052	0.23	…	…	0.7
…	…	…	…	…	…	…	…	…	…	…	…	…
0.0113	0.043	0.084	0.05	0.14	…	0.055	…	…	0.08	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…
0.0367	…	…	…	…	…	0.055	…	0.023	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	0.07	0.07	…	…	…	…	…	…	…	0.7
0.0068	…	…	…	…	…	0.073	…	0.035	…	…	…	…
	…	…	…	…	…	0.018	…	0.023	…	…	…	…
0.0076	…	0.046	0.07	0.27	…	0.055	…	…	…	…	0.38	…
0.0057	0.043	0.161	0.07	0.14	…	0.018	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…
…	0.014	…	…	…	…	…	…	…	…	…	…	…
…	…	0.008	…	0.07	…	…	…	…	0.08	…	…	…
…	…	…	0.024	…	…	…	…	…	…	…	…	…
0.375	0.55	1.07	0.97	1.15	1.9	0.9	0.6	1.18	0.31	…	0.38	…
…	…	…	0.024	…	…	…	…	…	…	…	…	…
0.201	0.417	0.323	0.76	0.34	0.6	0.55	…	0.064	0.31	…	0.75	…
0.037	0.014	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	0.14	…	…	…	…	…	…	…	…
…	0.014	…	…	…	…	0.055	…	0.261	…	…	…	…
0.0019	…	…	…	…	…	…	…	…	…	…	…	…
0.0019	…	…	…	…	…	…	…	…	…	…	…	…
0.0011	…	…	…	0.07	…	…	…	…	…	…	…	…
0.0291	0.014	0.061	0.024	…	0.6	0.073	…	0.318	…	…	…	…
0.128	0.115	0.008	0.12	…	…	0.98	…	0.65	0.08	…	…	0.7
0.0004	…	…	…	…	…	…	…	…	…	…	…	…
0.0008	…	0.008	…	…	…	…	…	0.09	…	…	…	…
…	…	…	…	…	…	…	…	0.012	…	…	…	…
0.0231	…	0.008	…	…	…	0.037	…	0.058	…	…	…	…
…	…	0.008	…	0.14	…	0.037	…	…	…	…	…	…
0.0522	0.029	0.015	…	…	…	0.037	…	…	0.08	…	0.19	…
0.0847	0.316	0.346	0.73	0.41	…	0.055	…	0.017	0.46	*1*	0.38	0.7
…	…	…	…	…	…	0.055	…	0.255	…	…	…	…
0.0284	0.043	0.008	0.05	…	…	0.220	…	0.029	…	…	…	…
0.0284	0.029	0.064	0.048	…	…	0.239	…	0.313	…	…	…	…
0.0473	0.058	0.267	0.352	0.07	…	0.055	…	0.029	0.15	…	…	0.7
0.0231	0.043	0.008	0.05	…	…	0.112	…	0.017	…	…	…	…

Table 15, part 2 (*continued*).

	Gramby Arnum formation							
Depth.(m.):	81.9-82.2	82.2-82.7	82.7-83.8	84.7-87.2	90.4-92.7	92.7-109.3	109.3-110.9	110.9 121.
237. *Odostomia* (*Syrnola*) *dubia* (GRATELOUP)	...	...	...	...	...	...	...	...
238. *Eulimella concinna nov. sp.*	...	...	...	0.03	...	...	...	...
239. – *Scillae* (SCACCHI)	...	...	...	...	...	...	...	...
240. – *acicula* (PHILIPPI)	...	...	...	...	...	...	...	...
241. – *crassitesta nov sp.*	...	...	...	...	...	...	...	...
242. *Turbonilla costellata* (GRATELOUP)	...	...	...	...	0.15	...	...	...
243. – *lactea* (LINNÉ)	...	...	...	...	0.15	...	...	...
244. – *rufa* (PHILIPPI)	...	...	...	0.03	...	0.44	...	...
245. – *pseudoterebralis* (SACCO)	...	...	...	...	...	...	...	...
246. – *sp.*	...	...	...	...	...	...	...	...
247. *Pyramidella plicosa* BRONN	...	...	...	0.07	0.15	0.44	...	...
248. *Ringicula ventricosa* (SOWERBY)	...	...	...	...	...	...	...	...
249. – *buccinea* (BROCCHI)	...	*1*	6.9	3.69	2.31	5.77	0.79	1.0
250. – *Ravni nov. sp.*	...	...	...	...	...	...	0.39	...
251. *Cylichna cf. cylindracea* (PENNANT)	...	...	...	...	...	...	...	...
252. – *Bellardi* (VON KOENEN)	...	...	...	...	...	...	...	...
253. *Rhizorus acuminatus* (BRUGUIÈRE)	*1*	...	0.2	0.17	...	...	...	...
254. *Retusa elongata* (EICHWALD)	...	...	...	0.17	0.31	...	0.39	...
255. – *umbilicata* (MONTAGU)	...	...	...	0.41	0.15	2.22	...	...
256. – *obtusa* (MONTAGU)	...	...	...	...	...	...	...	...
257. *Acteocina sp.*	...	...	...	...	...	...	...	...
258. – *Lajonkaireana* (BASTEROT)	...	...	...	0.03	...	...	...	...
259. *Scaphander lignarius* (LINNÉ)	...	...	...	...	...	...	...	...
260. *Roxania utriculus* (BROCCHI)	...	...	0.4	0.1	...	...	...	...
261. *Philine sp. a*	...	...	...	0.03	...	...	...	...
262. – *sp. b*	...	...	...	...	...	...	...	...
263. *Spiratella atlanta* (MØRCH)	*5*	...	2.7	3.05	0.62	0.89	24.4	0.5
264. – *cf. valvatina* (REUSS)	...	...	...	0.68	...	...	...	...
265. *Clio sp.*	...	...	...	...	...	...	...	...
266. *Vaginella depressa* DAUDIN	*2*	...	2.6	2.71	2.46	6.22	1.97	1.0
Sum total per cent	...	...	99.3	99.9	100.04	99.93	99.89	102.2
Percentage share of 1 specimen	...	...	0.1	0.03	0.15	0.44	0.39	0.5
Sum total of specimens (= 100 %)	*25*	*6*	*810*	*2954*	*650*	*225*	*254*	*185*

Toftlund Arnum formation					**Arnum**							
					Well no. 150.13			Well no. 150.25 b				
					Gram formation	Arnum formation		Arnum formation				
75–100	100–105	105–110	110–115	115	28–40	53–83	83–94	62.7–62.9	95.0–95.3	101.0–104.3	104.3–107.5	107.5
...	...	...	...	...	...	...	...	...	...	...	...	...
0.0023	0.043	0.208	0.26	0.07	...	0.018	0.6	0.017	0.15	...	0.38	...
...	...	0.015	...	...	...	...	...	...	0.08	...	...	...
...	...	...	...	...	...	0.018	...	0.006	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...
0.0026	...	...	...	...	...	0.018	...	0.017	...	...	...	...
0.0038	0.029	0.131	0.05	0.07	0.6	0.037	...	0.116	0.23	...	0.19	...
0.0117	0.014	...	0.024	...	...	0.055	...	0.012	...	...	...	...
0.0057	...	0.015	...	0.07	...	...	...	...	0.84	...	...	...
...	...	...	0.024	...	...	...	...	...	...	...	...	...
0.0424	0.086	0.131	0.12	0.81	...	0.257	...	0.023	...	...	0.38	...
...	...	...	...	0.07	...	...	...	...	0.15	...	...	...
4.3	3.35	0.369	0.54	1.36	5.6	2.52	...	4.31	0.91	*1*	1.70	...
...	...	1.09	1.37	0.88	...	...	0.6	...	...	*2*	0.94	...
0.084	...	...	0.05	...	...	0.018	...	0.098	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...
0.245	0.345	0.806	0.66	0.75	1.9	0.496	1.2	0.046	0.76	*1*	0.19	0.7
0.099	0.101	0.115	0.38	0.95	...	0.459	...	0.041	0.61	...	0.19	...
0.127	0.517	0.231	0.73	0.27	2.5	0.974	...	1.57	0.91	...	0.38	2.2
0.0004	...	...	...	...	...	...	...	...	...	...	...	...
...	0.014	0.008	...	...	...	0.037	...	0.017	0.23	...	0.19	...
0.0333	...	0.008	0.17	...	...	0.037	...	0.006	0.08	...	...	...
0.0004	0.014	0.054	0.05	0.27	...	...	...	...	0.08	...	0.19	...
0.175	0.187	0.254	0.14	0.33	...	0.275	0.6	0.052	0.15	*1*	0.57	0.7
...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	0.008	...	...	...	...	...	...	...	...	...	...
0.0178	0.058	0.054	0.12	...	0.6	1.87	...	6.92	0.69	*5*	0.94	0.7
...	...	...	...	...	...	...	...	...	0.61	...	...	...
...	...	...	...	...	...	...	...	0.023	...	...	...	...
1.78	1.63	0.215	0.99	0.61	1.2	0.735	2.5	0.794	0.31	*5*	3.78	0.7
.9317	100.553	100.412	99.062	100.06	99.8	101.262	99.4	100.077	100.21	...	99.98	99.2
.0004	0.014	0.008	0.024	0.07	0.6	0.018	0.6	0.006	0.08	...	0.19	0.7
64167	*6951*	*13022*	*4226*	*1474*	*161*	*5449*	*162*	*17266*	*1311*	*74*	*529*	*139*

Table 16. The Frequencies of Abundan

Roman types: per cent

	Glejbjerg Arnum formation												Bramminge Arnum
Depth (m.):	23	25	32	38	42	48	52	53	53.5	53.75	54	55	70–80
1. *Nucula nucleus* (LINNÉ)	...	...	...	...	...	...	...	...	0.1	...	...	...	0.00
3. – *cromata nov. sp.*	0.5	0.7	7.9	...	...	...	...	...	...	...	...	0.3	0.01
6. *Nuculoma hanseata* (KAUTSKY)	...	0.4	1.0	1.3	0.9	...	...	**7.9**	0.9	1.2	...	0.3	0.11
8. *Leda (Jupiteria) pygmaea* (MÜNSTER)	**21.1**	**17.5**	...	...	**16.1**	...	...	...	0.2	...	...	1.0	**7.92**
9. – *(Ledina) Westendorpii* (NYST & WESTENDORP)	0.2	0.2	0.8	1.3	...	...	...	...	0.1	0.3	*1*	0.3	0.51
10. – *(Lembulus) emarginata* (LAMARCK)	...	...	1.3	...	...	...	...	...	...	...	...	...	...
11. *Yoldia glaberrima* (MÜNSTER)	2.5	**3.9**	1.5	2.6	1.7	*1*	*1*	2.9	5.6	5.4	*1*	**8.3**	3.19
32. *Kellyella (Lutetia) rotunda nov. sp.*	0.5	1.1	**5.4**	...	1.7	...	*1*	...	0.1	...	...	...	0.03
34. *Isocardia sp.*	0.2	0.2	...	...	0.9	...	...	0.7	0.1	...	...	0.3	0.01
36. *Thyasira cf. flexuosa* (MONTAGU)	...	...	0.3	...	...	...	...	...	0.1	...	...	...	...
56. *Ervilia pusilla* (PHILIPPI)	...	...	...	...	...	...	...	...	...	...	...	...	...
57. *Spisula subtruncata* (DA COSTA) *var.*	1.6	1.1	2.3	1.3	**12.7**	...	*2*	4.3	3.8	2.7	*1*	3.2	0.30
60. *Abra prismatica*	0.5	0.7	0.8	...	**11.9**	...	*3*	3.6	2.9	1.8	*1*	1.3	0.05
66. *Saxicava arctica* (LINNÉ)	0.8	0.2	0.3	...	**4.2**	...	...	...	0.1	0.3	...	...	0.04
69. *Varicorbula gibba* (OLIVI)	**15.9**	**11.3**	...	...	0.9	...	*1*	2.2	1.9	1.8	...	2.5	**7.88**
98. *Turritella tricarinata* (BROCCHI)	0.2	0.2	...	...	...	...	...	...	...	...	...	0.3	0.41
104. *Bittium tenuispina nov. sp.*	1.1	0.4	...	...	...	...	...	...	...	...	...	0.3	0.52
116. *Aporrhais alata* (EICHWALD)	2.3	1.1	**31.5**	1.3	...	...	*9*	**51.7**	**31.0**	**24.7**	*4*	**36.5**	**42.4**
117–127. *Natica sp. sp.*	2.5	1.1	4.7	**9.1**	...	...	...	5.1	5.7	4.5	...	6.4	2.21
147. *Nassa Fuchsi* VON KOENEN	...	...	...	2.6	...	*1*	*1*	0.7	**22.2**	**28.0**	*10*	**11.8**	0.55
148. – *Schlotheimi* (BEYRICH)	3.7	3.6	4.9	3.9	**22.9**	...	*1*	...	0.4	...	...	...	2.47
150. – *Facki* VON KOENEN	...	...	**1.0**	...	0.9	...	...	0.7	0.9	0.9	...	**1.3**	0.26
155. – *cimbrica* RAVN	**35.6**	**43.1**	28.4	**66**	...	...	*2*	...	...	...	...	...	**16.7**
174. *Gemmula boreoturricula* (KAUTSKY)	...	0.2	...	...	...	...	...	...	0.6	0.6	*1*	**1.0**	0.1
177. *Fusiturris Duchastelii* (NYST)	...	0.2	...	...	**2.5**	...	...	...	0.7	...	...	**1.3**	0.25
214. *Terebra Hörnesi* BEYRICH	0.3	0.4	0.3	...	0.9	...	...	**2.9**	0.9	**2.4**	...	**1.0**	**1.2**
249. *Ringicula buccinea* (BROCCHI)	4.0	**6.8**	0.3	...	0.9	...	*1*	0.7	6.9	**7.4**	*1*	4.8	**7.53**
255. *Retusa umbilicata* (MONTAGU)	0.2	0.2	**1.0**	...	...	...	...	...	0.1	0.3	...	...	...
263. *Spiratella atlanta* (MØRCH)	0.2	...	...	...	...	...	...	...	...	...	...	...	...
266. *Vaginella depressa* DAUDIN	0.5	0.5	...	...	**5.9**	...	*1*	...	0.1	0.3	*1*	...	0.16
Sum total per cent	94.4	95.1	93.7	89.4	85.0	...	...	83.4	85.4	82.6	...	82.2	94.81
Percentage share of 1 specimen	0.2	0.2	0.3	1.3	0.9	...	...	0.7	0.1	0.3	...	0.3	0.003
Sum total of specimens (= 100 %)	*643*	*559*	*391*	*77*	*118*	*6*	*30*	*139*	*821*	*336*	*31*	*315*	*33165*

Frequencies of the abundant Nassidae:

155. *Nassa cimbrica* RAVN	35.6	43.1	28.4	66	...	...	*2*	...	...	...	...	...	16.7
148. – *Schlotheimi* (BEYRICH)	3.7	3.6	4.9	3.9	22.9	...	*1*	...	0.4	...	...	...	2.4
150. – *Facki* VON KOENEN	...	...	1.0	...	0.9	...	...	0.7	0.9	0.9	...	1.3	0.2
147. – *Fuchsi* VON KOENEN	...	...	...	2.6	...	*1*	*1*	0.7	22.2	28.0	*10*	11.8	0.5

Molluscan Species in the Well Sections

Italics: number of specimens

Gramby Arnum formation							Toftlund Arnum formation					Arnum							
												Gram formation	Arnum formation (Wells no. 150.13 & 25 b combined to one section)						
82.2–82.7	82.7–83.8	84.7–87.2	90.4–92.7	92.7–109.3	109.3–110.9	110.9–121.5	75–100	100–105	105–110	110–115	115	28–40	62.7–62.9	53–83	83–94	95.0–95.3	101–104.3	104.3–107.5	107.5
...	...	...	...	...	...	...	0.02	...	0.01	...	0.14	...	...	...	...	**3.36**	...	0.19	...
...	1.5	1.12	2.16	2.22	1.58	**3.24**	0.59	0.14	...	...	...	...	**3.48**	0.96	...	...	...	...	...
...	0.2	0.27	0.15	...	...	...	0.29	0.2	2.13	**2.2**	1.76	...	0.01	0.07	1.2	**2.36**	*1*	0.76	1.4
1	6.3	6.06	12.5	**31.6**	3.15	**28.1**	**15.27**	**25.7**	1.02	5.32	0.47	14.3	12.2	**21.82**	4.9	1.3	*11*	7.9	**18.7**
...	0.2	...	...	0.44	0.79	...	0.49	1.41	**5.54**	3.97	1.42	...	0.03	0.13	0.6	**11.6**	*2*	1.32	1.4
...	...	0.17	0.15	...	0.39	0.54	0.03	...	0.084	0.07	0.14	...	0.02	0.07	...	...	...	...	...
...	**3.7**	0.61	2.46	1.33	0.79	**4.32**	1.02	**3.57**	1.31	1.23	**5.43**	2.5	2.9	0.18	1.2	2.52	*2*	**6.24**	0.7
...	0.6	3.28	2.31	**5.77**	**7.48**	4.16	0.71	2.09	1.12	3.73	0.54	1.9	4.8	0.50	...	3.89	*6*	3.02	**11.5**
...	...	0.3	...	0.44	0.39	...	0.01	0.01	0.12	0.84	0.68	...	0.02	0.04	...	0.53	*3*	0.57	**4.3**
...	...	0.03	...	...	...	...	0.01	0.06	0.45	0.47	0.14	...	0.01	...	...	1.14	*2*	**1.89**	**1.4**
...	...	...	...	...	...	...	0.05	...	0.04	0.43	0.14	1.2	**2.43**	0.17	...	0.15	*1*	0.19	0.7
...	8.5	**10.8**	**13.9**	7.10	**23.6**	**20.0**	2.85	7.61	6.71	**14.7**	5.36	8.7	**12.7**	1.32	1.2	3.84	*5*	**10.59**	**10.8**
...	...	1.42	...	0.44	0.39	0.54	0.15	0.24	0.21	1.47	2.85	1.9	0.59	0.06	...	0.31	*5*	**12.65**	2.9
...	0.2	0.44	0.15	...	0.79	0.54	0.17	0.26	0.58	0.76	0.34	0.6	0.56	0.31	...	0.61	*1*	0.94	**4.3**
2	1.0	**27.7**	**5.54**	**5.33**	0.39	**10.50**	**10.58**	0.88	0.32	0.83	0.20	1.9	0.84	2.53	1.9	1.37	*1*	0.19	...
...	...	...	0.92	0.89	0.39	0.54	0.08	0.11	0.11	0.36	**1.36**	1.9	**4.35**	0.48	0.6	0.61	*1*	0.19	...
...	0.6	0.88	0.62	**4.89**	0.79	0.54	1.14	1.7	0.25	0.95	...	**15.5**	**26.98**	8.39	1.2	0.31	*1*	1.14	...
1	**11.0**	3.48	2.16	0.89	0.39	1.08	**4.66**	**11.49**	**8.22**	3.81	**9.22**	0.6	...	0.81	**34.6**	**20.8**	...	0.57	0.7
...	1.3	0.96	0.15	...	...	...	1.29	0.91	1.87	3.05	**11.00**	1.2	1.06	1.75	3.0	2.52	*2*	**6.23**	**10.0**
...	...	0.03	...	...	...	...	0.18	0.26	1.38	1.85	**5.15**	...	...	0.17	1.9	1.98	*2*	**12.3**	0.7
...	3.7	**4.87**	1.54	2.66	**5.51**	0.54	4.44	3.14	**10.82**	9.06	9.5	**23.6**	6.89	4.15	6.2	5.11	*1*	2.83	**5.0**
...	0.1	0.1	0.15	0.44	...	...	0.17	0.06	0.17	0.38	**2.78**	...	0.01	0.24	...	0.46	*1*	**3.21**	0.7
1	**43.7**	23.1	**43.7**	16.43	22.4	20.60	**45.1**	29.8	**44.6**	27.0	13.57	...	...	**41.8**	21.6	18.4	...	...	2.2
...	...	...	...	...	...	...	0.01	0.01	0.12	0.33	**2.64**	...	...	...	0.6	...	...	**3.78**	0.7
...	...	...	...	...	...	...	0.02	0.01	0.17	0.36	**1.83**	...	0.01	...	0.6	0.61	...	**1.51**	0.7
...	0.2	0.17	0.46	...	...	...	0.38	0.55	**1.07**	0.97	**1.15**	**1.9**	1.18	0.9	0.6	0.31	...	0.38	...
1	**6.9**	3.69	2.31	**5.77**	0.79	1.08	**4.3**	3.35	0.37	0.54	1.36	**5.6**	4.31	2.52	...	0.91	*1*	1.70	...
...	...	0.41	0.15	2.22	...	...	0.13	0.52	0.23	0.73	0.27	**2.5**	**1.57**	0.97	...	0.91	...	0.38	**2.2**
...	2.7	3.05	0.62	0.89	**24.4**	0.54	0.02	0.06	0.05	0.12	...	0.6	**6.92**	1.87	...	0.69	*5*	0.94	0.7
...	2.6	2.71	2.46	**6.22**	1.97	1.08	**1.78**	1.63	0.22	0.99	0.61	1.2	0.79	0.74	2.5	0.31	*5*	**3.78**	0.7
...	95.0	95.65	94.56	95.97	96.38	97.94	95.94	95.77	89.294	86.52	80.05	87.6	94.66	92.95	84.4	86.91	...	85.39	82.4
...	0.1	0.03	0.15	0.44	0.39	0.54	0.0004	0.014	0.008	0.024	0.07	0.6	0.006	0.018	0.6	0.08	...	0.19	0.7
6	*810*	*2954*	*650*	*225*	*254*	*185*	*264167*	*6951*	*13022*	*4226*	*1474*	*161*	*17266*	*5449*	*162*	*1311*	*74*	*529*	*139*

1	43.7	23.1	43.7	16.43	22.4	20.6	45.1	29.8	44.6	27.0	13.57	...	...	41.8	21.6	18.4	...	...	2.2
...	3.7	4.87	1.54	2.66	5.51	0.54	4.44	3.14	10.82	9.06	9.5	23.6	6.89	4.15	6.2	5.11	*1*	2.83	5.0
...	0.1	0.1	0.15	0.44	...	...	0.17	0.06	0.17	0.38	2.78	...	0.01	0.24	...	0.46	*1*	3.21	0.7
...	...	0.03	...	...	...	...	0.18	0.26	1.38	1.85	5.15	...	...	0.17	1.9	1.98	*2*	12.3	0.7

DANSK SAMMENDRAG

MOLLUSK SELSKABER FRA DET MARINE MELLEM-MIOCÆN I SYD- OG SØNDERJYLLAND OG DERES MILJØ

Indledning

Miocænstratigrafiens udvikling i Europa afspejler den biostratigrafiske metodes fortrin og mangler på iøjnefaldende måde. Dette skyldes ikke, at kendskabet til miocænseriens formationer og fossilindhold er særligt ringe, eller at metoderne til miocænets udforskning er principielt afvigende sammenlignet med andre formationsintervaller. Det er tværtimod således, at miocænets fossiler har været studeret ret indgående af et stort antal forskere, og at de miocæne formationers udbredelse er kortlagt ret detailleret. Man kan også i litteraturen møde den opfattelse, at man ved korrelationerne og inddelingerne har fulgt: »stratigrafiens metoder og de almindelige palæontologiske regler« (MAYER-EYMAR 1857).

Tertiærtidens sedimentationsområder i Europa grupperer sig i følgende aflejringsbassiner:

1. Nordsøbassinet og tilgrænsende områder i Sydengland, Nordfrankrig, Belgien, Holland, Danmark, Nordtyskland og Polen.
2. Marginale sedimentationsområder ved Atlanterhavskysten omfattende det Aquitanniske bassin, Loire bassinet og Guadalquivir bassinet.
3. De mediterrane aflejringsområder omfattende bl. a. Podalen i Norditalien samt Wienerbassinet.
4. Aflejringsområderne vest og nord for Alperne repræsenteret ved Rhone dalen og Molassebassinet i Schweiz, Sydtyskland og det nordlige Østrig.

I alle disse sedimentationsområder er aflejret lag, som er henført til miocænserien.

Fremgangsmåden ved studiet og paralleliseringen af de miocæne dannelser har været, at man i de enkelte bassiner på palæontologisk grundlag har grupperet de mange adskilte formationsdele i biostratigrafiske systemer. Man har dernæst jævnført de opstillede stratigrafiske enheder i de forskellige aflejringsområder med hverandre så godt det kunne gennemføres. Endelig har man på denne basis etableret en tidsstratigrafisk inddeling, hvis universelle gyldighed efterhånden stiltiende er akcepteret af stratigrafer og palæontologer verden over.

Den historiske gennemgang, som danner indledningen til den engelske tekst, viser, at man til forskellige tider har været klar over, at der var en ret stor usikkerhed ved korrelationerne mellem f. eks. aflejringsområderne i Sydvestfrankrig og i de mediterran-alpine områder (MAYER-EYMAR 1857, RUTSCH 1929, MAGNE & VIGNEAUX 1948, JANOSCHEK 1951). Det er dog ganske betegnende, at man i det store og hele derved ikke er kommet ind på en vurdering af den stratigrafiske metode, som er anvendt ved korrelationerne.

Idet usikkerheden og vanskelighederne ved dateringer og korrelationer uden tvivl står i forbindelse med de anvendte metoder, er det værd at fremhæve, at de kritiske punkter i en stratigrafisk forskningsgang først og fremmest er at søge i korrelationen af adskilte eller ikke direkte iagttagelige formationer. I almindelighed kan biostratigrafiske korrelationer karakteriseres ved følgende tre stadier.

1. Til trods for, at det ikke altid formuleres klart, forsøger de fleste forskere at finde frem til »ledefossiler«. Dette forudsætter, at begrebet »ledefossil« er en realitet, d.v.s. at der findes arter med universel horisontal og begrænset vertikal udbredelse. Et formodet ledefossil bliver ofte meget hurtigt betragtet som et gyldigt korrelationsredskab.
2. Ifald ledefossiler ikke forefindes, eller såfremt lagenes faunaer ikke fremviser særligt iøjnefaldende lighedstræk, består det næste skridt i en vurdering af lagenes relative alder på grundlag af deres fossilindhold.
3. Den endelige korrelation gennemføres dernæst hovedsagelig ved en sammenligning af lagenes indhold af arter. Et lag korreleres i almindelighed med den formation udenfor dets eget aflejringsområde, hvormed det har flest arter fælles. Procenten af fællesarter udregnes i forhold til artsantallet i laget, der skal korreleres, men stilles normalt ikke i relation til artsantallene i formationerne, hvormed man korrelerer.

Denne metode medfører uundgåeligt muligheder for fejlslutninger, idet fossilmaterialets bevis- og bærekraft overvurderes, således som det fremgår af følgende:

a. Ledefossilernes gyldighed er meget sjældent baseret på statistiske undersøgelser i et tilstrækkelig stort antal lagserier. De postulerede ledefossilers betydning bliver derved yderst begrænset.
b. Tilstedeværelsen eller ikke tilstedeværelsen af en art behøver ikke alene at være en funktion af tiden. Palæo-miljøforholdenes indflydelse kan ofte være mere afgørende for en arts udbredelse end tidsfaktoren.
c. Tendensen til at negligere miljøforholdene som kontrollerende faktorer synes at vokse proportionalt med afstanden mellem lagserierne, der sammenlignes.
d. Den ved korrelationer almindeligt anvendte »procentmetode«, som er omtalt ovenfor, kan medføre alvorlige dateringsfejltagelser. Til eksempel nævnes det i 1940 fremhævede forhold at 52% af molluskarterne ved Norges kyster er fælles med Middelhavsfaunaen, mens disse fællesarter kun udgør ca. 25% af Middelhavets meget større molluskfauna. Antallet af fællesarter afhænger altså af artsantallet i begge de to faunaer, som sammenlignes.
e. Antallet af arter i et faunaselskab kan betragtes som een af dyreverdenens reaktioner overfor de miljøforhold, som naturen har stillet til rådighed. Et andet udtryk for faunaens reaktion overfor miljøet er de enkelte arters individantal.

f. En løselig gennemgang af den biostratigrafiske litteratur viser, at oplysninger om arters hyppighed med få undtagelser er holdt i meget ubestemte vendinger som: »hyppig«, »sjælden«, »almindelig« o.s.v. Ofte findes ingen oplysninger om hyppighed.

g. Mangelen på statistiske oplysninger om arternes hyppighed og sedimenternes fysiske egenskaber har hindret erkendelsen af fossile arters og dyresamfunds afhængighed af miljøet. Det har derfor ikke været muligt klart at skelne mellem tidsfaktorens og miljøfaktorernes indflydelse på faunaen.

Der er ingen tvivl om, at vort kendskab til de miocæne aflejringer i Europa endnu er yderst begrænset, og at en del af de hidtil gennemførte korrelationer er udført på et for tidligt stadium af vor erkendelse af fossilernes stratigrafiske bærekraft. Ved fremtidige undersøgelser må man utvivlsomt stræbe efter først og fremmest at nå frem til en mere sikker opfattelse af sedimentationshistorien og den faunistiske udvikling i hvert enkelt bassin. Man bør stile efter klare beskrivelser af formationsenhederne og så enkle definitioner af disse som muligt.

Studiet af boreprofiler og prøver fra boringer, der almindeligvis omfatter større lagserier end daglokaliteter, vil kunne yde overordentlig værdifulde data, hvis arbejdet på dette felt gennemføres på rette måde.

Beskrivelsen af boreprofilerne fra Syd- og Sønderjylland og af molluskselskaberne fra boringernes miocæne lagserier, som fremlægges i dette arbejde, er tænkt som et bidrag til forståelsen af den geologiske historie for en lille del af det miocæne Nordsøbassin ud fra disse synspunkter.

Afsnittet om de miocæne aflejringer i Sønderjylland er en meget kortfattet oversigt over formationerne ved basis af kvartæret, og kapitlet vedrørende de behandlede boringer giver en detailleret beskrivelse af boreprofilerne og boreprøverne. Endelig defineres Arnum og Ribe formationerne, og der sluttes med følgende samlede oversigt over vort nuværende kendskab til sedimentationsudviklingen i Syd- og Sønderjylland fra linien Vejlefjord-Varde til grænsen:

Tidsstratigrafisk datering	Formation	Facies
Øvre Miocæn	Gram formation (Banke Rasmussen 1956)	ler og finsand, marint
Mellem Miocæn	Arnum formation, nov. form.	hovedsagelig finsand, marint
	Ribe formation, nov. form.	finsand, sand og grus, sandsynligvis limnisk fluviatilt
Mellem–nedre miocæn	Vejlefjord formation (Dinesen & Larsen 1956)	øverst: finsand og sand, sandsynligvis hovedsagelig marint nederst: ler og finsand, sandsynligvis hovedsagelig marint
Nedre Miocæn	Klintinghoved ler (Sorgenfrei 1940)	ler, marint

Den palæontologiske del

Indledningsvis diskuteres det palæontologiske artsbegreb, idet opfattelsen af den fossile art og artsdefinitionen anses for at være af fundamental betydning for biostratigrafiske konklusioner. Det vises, at man indenfor palæontologien må lade sig nøje med en så primitiv morfologisk definition på arten som f. eks. foreslået af ARKELL & MOY THOMAS (1940, p. 395). Ifølge disse to forfattere er den palæontologiske art: »a practical and convenient unit by which fossils are distinguished«. Heraf følger det elementære krav, at fossiler, som ikke kan skelnes fra hverandre ved væsentlige morfologiske forskelle bør henregnes til samme palæontologiske art.

Samtidig med denne kraftige metodiske begrænsning af forskningen med hensyn til den systematiske klassifikation af fossiler må opgaven indenfor denne del af biologien dog naturligvis være at tilstræbe en så stor overensstemmelse med systematiken indenfor den levende verden som muligt. Dette må nævnes, selvom det oftest opfattes som en selvfølge, idet man ikke gør sig klart, hvor principielt forskellige mulighederne for artserkendelse indenfor palæontologien og neontologien er. Det er vigtigt at understrege, at den palæontologiske art er et mindre objektivt begreb end den recente art, og at fuldkommen overensstemmelse mellem de to artsbegreber måske aldrig opnås.

Med hensyn til den »systematiske værdi« af molluskskallens morfologiske bygningstræk henledes opmærksomheden på, at den herskende systematik bygger på evolutionstanken, som forudsætter kontinuert morfologisk udvikling og en vis variation af de fleste morfologiske egenskaber. Til trods for denne kendsgerning postuleres ikke sjældent i diskussioner, at visse morfologiske egenskaber er af »større systematisk betydning« end andre, hvilket i praksis oftest har til følge, at de andre egenskaber negligeres.

Efter en diskussion af protoconch og teleoconch og deres betydning for den systematiske forskning sluttes med et citat af THORPE (1940, p. 342), hvori det understreges, at en art er nøje karakteriseret ved biologiske og fysiologiske egenskaber i ethvert af dens udviklingsstadier. Heraf drages den slutning, at man ikke bør udelukke nogen del af dyret eller noget stadium af dets udvikling ved bedømmelsen af molluskers systematiske stilling.

Den systematiske inddeling af molluskerne støtter sig til THIELE's Handbuch der systematischen Weichtierkunde (1931–35). Det må imidlertid fremhæves, at THIELE's systematiske inddeling er mere eller mindre subjektiv som enhver anden inddeling af denne art, og at materialemængden indenfor den systematiske malakologi efterhånden er blevet så omfattende, at en virkelig kritisk vurdering af de mange opstillede arter øjensynlig vanskeligt kan gennemføres. Såvel i THIELE's håndbog som i andre lignende værker savnes velfunderede begrundelser for opretholdelsen af de mange slægter og underslægter, ligesom også argumentationen for inddelingen i familier, ordener m.v. ofte synes at være ret tilfældig og svag. Grundene hertil er sandsynligvis at søge dels i det uoverkommelige i en gennemført verifikation, og dels i manglende typemateriale, utilstrækkelige definitioner o.s.v.

Af den almindelige usikkerhed følger, at de systematiske kategorier, som ligger over arten, lige fra underslægter, slægter og familier m.v. har mindre objektiv værdi end arten. På grund af den stadige risiko for fejlvurderinger i eksisterende systematiske inddelinger har jeg kun betragtet dem som foreløbige praktiske løsninger på et ordningsproblem. Jeg har tilstræbt en binær nomenklatur, idet jeg med få undtagelser har undgået at henføre til underslægter. Dette er i overensstemmelse med mit synspunkt, at der i de fleste tilfælde savnes en konsekvent linie og begrundelse for inddelingen i underslægter. Endvidere er den videnskabelige og praktiske nytte af underslægtsbegrebet efter min opfattelse ofte ret problematisk.

Undersøgelsen af materialet omfatter dels en bestemmelse af de enkelte arter i prøverne samt en statistisk behandling af skalmaterialet, idet antallet af individer i prøverne er bestemt ved tælling. Hvert umbonalparti af en pelecypodskal er talt som et halvt individ, og hvert fragment af en gastropodskal med protoconch er talt som et individ. Nærmere enkeltheder vedrørende talte eksemplarer og undtagelser fra nævnte fremgangsmåde (*Aporrhais alata* og *Turritellidae*) er omtalt side 33.

Ved beskrivelsen af arterne er der tilstræbt en så nøjagtig omtale af væsentlige træk i skallens morfologiske bygning som muligt, idet finere detailler er undersøgt under mikroskop og tegnet. Der er anvendt tegneprisme ved tegningen af skalomridsene.

Da det for erkendelsen af arten i almindelighed og for den palæontologiske art i særdeleshed er meget vigtigt at kende grænserne for de morfologiske egenskabers variation, er der lagt vægt på en statistisk behandling af skulpturelementer og skalform, hvor dette var muligt. Bestemmelsen af arterne har måttet ske ved hjælp af litteraturen. Da der i en del tilfælde har været tale om ret mangelfuld dokumentation i den tilgængelige litteratur, har det sikkert ikke kunnet undgås, at der er indtruffet fejlbestemmelser. Det er mit håb, at den store målestok, hvori illustrationerne er tegnet, samt den i de fleste tilfælde ret detaillerede beskrivelse af skalmaterialet vil gøre en identifikation og sammenligning med udenlandsk skalmateriale forholdsvis let til trods for eventuelle fejlbestemmelser.

Ved beregningen af middelværdierne for $\frac{L}{H}$ og $\frac{H}{D}$ forholdene*) er de almindelige statistiske beregningsmetoder fulgt (se f. eks. KEMP 1942). Grænserne for de beregnede middelværdier er i hvert tilfælde $\pm 3\,e$ hvor $e = \frac{s}{\sqrt{n}}$ (n = antallet af observationer, s = standard afvigelsen).

Artsbeskrivelserne omfatter en synonymliste med de vigtigste referencer til litteraturen. Hovedværker med gode afbildninger og enkelte andre betydningsfulde værker er citeret, idet hensigten har været at belyse den enkelte arts udbredelse i Middelhavsområdet, Atlanterhavsområdet og Nordsøbassinet i tertiærtiden. En fuldstændig synonymliste har ikke været tilsigtet.

Såvidt muligt er den originale diagnose, beskrivelse eller uddrag deraf citeret. Derefter følger en oversigt over det til arten henførte skalmateriale fra boringerne, og derpå beskrivelsen af skalmorfologien. I afsnittet »Remarks« findes eventuelle bemærkninger til beskrivelsen, diskussioner o.s.v.

Oversigten over udbredelsen er ordnet stratigrafisk og regionalgeologisk efter de enkelte marine aflejringsområder. Kilderne til denne oversigt findes almindeligvis i synonymlisten. Hvor dette ikke er tilfældet, er der henvist med forfatter og årstal til det arbejde, hvorfra oplysningen stammer. Det vil kunne findes i litteraturlisten.

Generelle slutninger vedrørende skalmorfologien.

Til trods for, at kun et ringe antal arter har kunnet undersøges med hensyn til variationen af skalformen, er det muligt at udlede en række lovmæssigheder af målingerne, ligesom det også er lykkedes at påvise morfologiske ejendommeligheder hos visse grupper af arter.

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*) L = længde, H = højde, D = diameter.

Resultaterne fra undersøgelsen af f. eks *Yoldia glaberrima*, *Leda Westendorpii*, *Leda pygmaea*, *Spisula subtruncata* og *Varicorbula gibba* tyder på, at forholdet længde/højde hos pelecypodskaller meget sjældent er konstant, men er underkastet en bestemt lovmæssig ændring under væksten. Dette er en vigtig regel, som en række forfattere øjensynlig ikke er klar over, at dømme efter de ikke få tilfælde, hvor man har udregnet middelværdier for dette eller lignende forhold uden at angive de pågældende skallers størrelsesinterval. Sådanne middelværdier er naturligvis af ret problematisk værdi.

Bestemmelsen af skaller tilhørende arter af slægten *Nucula* er ofte temmelig vanskelig på grund af den ringe morfologiske variation af en række arter. Undersøgelsen af recente skaller af *N. nitida* og af Nuculiderne, som er behandlet i dette arbejde, har vist, at antallet af hængseltænder ikke er konstant, men tiltager med væksten af skallen. Man kan udtrykke tandantallets afhængighed af skalvæksten grafisk som vist på fig. 5, s. 42.

Antallet af radialelementer i det ydre skallag hos arter af slægten *Nucula* synes at være ret uforandret under væksten af skallen, idet disse elementer yderst sjældent forgrener sig. Det kan endnu ikke afgøres, om radialelementernes antal er så artskonstant, at deres middeltal kan bruges som artskarakterer.

Ved undersøgelsen af Pectiniderne viste det sig, at der kan skelnes mellem tre skalstadier: 1. prodissoconchen, 2. dissoconchens initialstadium og 3. den egentlige dissoconch. Hvert stadium er karakteriseret ved sin særlige skulptur (eller mangel på skulptur). På side 74 er givet en oversigt over de tre skalstadiers udseende hos de recente: *Pecten septemradiatus*, *P. opercularis*, *P. varius*, *P. tigerinus* og *P. islandicus*. Den biologiske betydning af dissoconchens initialstadium har jeg endnu ikke kunnet klarlægge.

Under tegningen af *Varicorbula gibba* opdagedes en ejendommelig pore på bagenden af højreskallen på overgangen mellem skallens prismelag og det indre skallag. På lukkede skaller findes poren udenfor venstreskallens rand. Denne marginalpore, som hos levende dyr er fyldt med en geléagtig dannelse, er ikke fundet omtalt i litteraturen. Tegneren, som har fremstillet illustrationerne til VOKES' (1945) monografi over Corbuliderne, har gengivet poren på en række arter, som findes opført side 131, men den er ikke omtalt af VOKES. Marginalporen synes således at være karakteristisk for en del af familien. Dens funktion er endnu ukendt.

En parallel til længde/højde forholdet hos pelecypoder er højde/diameter forholdet hos gastropoder. Variationen af dette forhold, som er belyst ved *Nassa Schlotheimi*, *N. subobesa*, *N. cimbrica* og *Ringicula buccinea* er korreleret med skallens vækst, hvilket navnlig er iøjnefaldende hos de tre Nassider. Der er grund til at tro, at denne regel vil gælde for de fleste gastropodarter. På baggrund heraf må det endnu engang understreges, at alle middelværdiberegninger over relationer mellem skaldimensioner bør være ledsaget af oplysninger om skalmaterialets størrelsesforhold.

Statistiken over collabrale skulpturelementer hos *Bittium tenuispina*, *Nassa Schlotheimi*, *N. subobesa*, *Terebra Hörnesi* o. a. illustrerer den velkendte erfaring, at collabrale elementers antal ikke er konstant hos adskillige arter. Almindeligvis tiltager antallet af ribber under væksten, den modsatte tendens kan dog også gøre sig gældende, ligesom et omtrent konstant antal ribber kan findes hos enkelte arter og eksemplarer. Hos de undersøgte Nassider synes det at være en regel, at den første teleoconchvinding har et større antal ribber end vinding nr. 2, hvorefter ribbeantallet pr. vinding atter tiltager med væksten.

Hos arterne af familien *Turridae* er protoconchen meget karakteristisk. Med protoconchen hos arter af slægten *Daphnella* som udgangspunkt har jeg inddelt protoconchens helicoconus i tre afsnit: 1. det initiale, let heterostrofe afsnit, 2. medial afsnittet, som hos Daphnelliderne har en fin, diagonal netskulptur, og 3. terminal afsnittet, der er udviklet med køl hos en del Daphnellider. Ved den systematiske inddeling af arterne har jeg i princippet fulgt POWELL's (1944) systematik, som er baseret på protoconchens morfologi.

Den biologiske værdi og betydning af protoconchens tre stadier hos Turriderne er endnu ukendt. Det er ikke usandsynligt, at initialstadiet kunne svare til dyrets larvestadium før torsionen. Udforskningen af larvestadierne af nulevende arter af familien ville være af stor betydning for den fremtidige forståelse af Turridernes meget artsrige familie.

Marine pelecypoder og gastropoder i forhold til deres miljø

Da fossilers anvendelse som stratigrafisk hjælpemiddel i så høj grad beror på kendskabet til lovene for de fossile dyrs reaktioner overfor miljøet og dets forandringer, er dette kapitel om recente molluskers afhængighed af deres fysiske og biologiske omgivelser gjort ret omfattende. Målet har været ved eksempler fra litteraturen at belyse sider af molluskbiologien og -økologien, der på en eller anden måde har indflydelse på skallens bygning og arternes spredning, og som derved er af særlig interesse for palæobiologien og biostratigrafien.

Jeg har måttet se bort fra, at jeg som ikke-specialist på dette felt kan savne visse forudsætninger for den økologiske vurdering, og at jeg kan være ukendt med vigtige arbejder og betydningsfulde fremskridt, som burde have været medtaget i oversigten. I et grænseområde mellem to forskningsgrene som palæo- og neobiologien må risikoen for ufuldstændig behandling altid være til stede, hvad enten man vover sig ind i området med den ene eller anden disciplin som udgangspunkt.

1. Kontrollerende miljøfaktorer

I dette afsnit diskuteres velkendte faktorer, som har afgørende indflydelse på marine molluskers udbredelse. 1. føde, 2. saltholdighed, 3. temperaturforhold, 4. vanddybde, 5. fjender og konkurrenter samt 6. bundens beskaffenhed, anses for at være de vigtigste. Disse faktorers betydning for molluskernes forskellige udviklingsstadier belyses som det fremgår af det følgende ved eksempler fra den recente marinbiologi.

2. Træk af marine molluskers biologi

A. Dyrets vækst og variationen af skalegenskaber.

ORTON (1926) har undersøgt væksten af *Cardium edule* i tidevandsområdet ved Yealm flodens munding ved Plymouth. BATESON (1889) og PURCHON (1939) har undersøgt saltholdighedens indflydelse på skalformer hos *C. edule* henholdsvis i saltsøområder ved Aralsøen og ved den engelske kanalkyst ved Plymouth. På grundlag af disse undersøgelser og vækstundersøgelser af: *Mytilus californianus* og *M. edulis* (RICHARDS 1946), *Littorina littorea* (MOORE 1937), *Purpura lapillus* (MOORE 1936, 1938), *Mya arenaria*, *Tellina baltica* og *Buccinum undatum* (BRANDT 1897) kan man drage følgende konklusioner:

1. Dyrets vækst er karakteriseret ved årlige rytmer.
2. Den største væksthastighed falder øjensynlig ofte sammen med og er betinget af den enkelte arts temperaturoptimum.
3. Den totale årlige størrelsestilvækst når et maksimum på et intermediært alderstrin, hvorefter den årlige tilvækst aftager.
4. Alderen ved den maksimale årlige tilvækst synes hos nogle arter at være ret veldefineret, mens der er betydelig variation hos andre arter (f. eks. hos *Littorina littorea*).
5. Gydningsperioden markeres i almindelighed ved aftagende vækst både af det levende væv og af skallen, bortset fra de arter, hvor væksten standses helt ved kønsmodenhed.
6. Saltholdigheden har en betydelig indflydelse på væksten. Saltholdigheder over og under den enkelte arts optimum synes at resultere i aftagende størrelse og skaltykkelse.
7. Forskellige saltholdigheder kan forårsage, at der udvikles forskellige skalformer og -farver hos en og samme art.
8. Forskellige kombinationer af faktorer, som udgør biotopen, kan give anledning til udviklingen af forskellige morfologiske typer af samme art.
9. Fødens beskaffenhed har i nogle tilfælde indflydelse på skallens form og farve.

Der foreligger ingen oplysninger om hvorvidt de under 6–9 nævnte forandringer er arvelige.

B. Forplantning.

De sidste 20 års marinbiologisk forskning har resulteret i overordentlig store fremskridt med hensyn til kendskabet til molluskernes forplantning. Der kan især henvises til THORSON's banebrydende arbejde fra 1946, hvori der iøvrigt findes en meget fyldig litteraturliste over tidligere arbejder.

Indenfor molluskernes forplantningscyklus kan man skelne mellem følgende faser, som ikke alle behøver at være repræsenteret hos den enkelte art, og som også kan være modificeret på forskellig vis: a. forplantningsorganernes modning, b. befrugtning, c. gydning, d. klækning, e. larvestadiet, f. metamorfosen.

Endnu er kendskabet til miljøfaktorernes indflydelse på de enkelte faser ret mangelfuldt. Saltholdighed og temperatur har en betydelig indflydelse. I afsnittet behandles ernæringsforholdenes, saltholdighedens og temperaturens virkninger på de enkelte faser, forsåvidt oplysninger herom foreligger.

Hovedsynspunktet ved analysen af saltholdighedens og temperaturens indflydelse har været, at hvert udviklingsstadium har sin øvre og nedre grænse for saltholdighed og temperatur med mellemliggende optimum. Kendskabet til disse salinitets- og termalintervaller er endnu ret begrænset. Deres betydning for en række stadier hos enkelte arter diskuteres, idet der især lægges vægt på termalintervallernes spredningsbiologiske konsekvenser.

Der konkluderes, at årstidsbetonet gydning er almindelig i områder, hvor der er en tydelig variation af temperaturen med årstiderne. Gydningen efter årstid behøver ikke altid at være tegn på en temperaturregulering af de pågældende forplantningsfaser. Hvis en art hele året lever indenfor forplantningsfasernes termalintervaller, vil andre cyklisk varierende faktorer, der har indflydelse på forplantningsaktiviteten, som f. eks. ernæringen, kunne forårsage, at gydningen knyttes til bestemte årstider.

C. Det pelagiske larvestadium.

Dette stadium har meget stor spredningsbiologisk betydning, og den omstændighed, at larvestadiets skal ofte kan studeres på fossile mollusker, gør det ikke mindre interessant for paleobiologisk forskning. Larvestadiets varighed og transporten af larverne i havet belyses ved få eksempler. Også på dette felt er konkret viden øjensynlig ret begrænset.

D. Det voksne stadiums krav med hensyn til bundforhold.

Molluskerne synes at have ret stor tilpasningsevne overfor bundforholdene, selv om også de seneste undersøgelser (THORSON 1946) viser, at larverne indenfor visse grænser er i stand til at vælge og vrage mellem de muligheder, der byder sig. De fleste arter er knyttet til infauna eller epifauna miljøet. En række arter, deriblandt visse rovsnegle, trives i begge miljøerne.

E. Tilpasning.

Alle i de tidligere afsnit diskuterede livsstadier og -processer afspejler molluskernes tilpasningsevne. I foreliggende afsnit behandles kun den osmotiske tilpasning og stofskiftetilpasningen hos et par arter. Af særlig interesse er stofskiftetilpasningen til forskellige temperaturforhold, således som SPÄRCK's (1936) undersøgelser over *Mytilus edulis*, *Astarte borealis*, *A. eliptica*, *A. Montagui* og *Saxicava arctica* viser.

3. Den geografiske udbredelse

En arts naturlige geografiske udbredelse kan betragtes som et udtryk for summen af dens sprednings- og tilpasningsevne. Temperaturforhold og saltholdigheden er uden tvivl af den største betydning som regionalt begrænsende faktorer.

Som indledning gives en oversigt over Atlanterhavets temperaturforhold, idet den nordlige kolde og den sydlige varme vandmasse samt overgangsbæltet mellem dem karakteriseres.

I afsnittet om faunabelterne diskuteres WOODWARD's (1856) zoneinddeling, som sammenstilles med EKMAN's (1953) seneste afgrænsning af Atlanterhavets faunaprovinser i tabel 6, side 388. I oversigtsskemaet side 389 er fremsat et forslag til en definition af grænserne mellem WOODWARD's provinser baseret på geografiske lokaliteter og konkrete middeltemperaturer. Dernæst diskuteres enkelte boreale arters udbredelse.

De særlige hydrografiske forhold i dybhavet omtales, og ved en række molluskarters udbredelse i Skagerakområdet (efter C. G. JOH. PETERSEN 1915) vises, at der er en antydning af korrelation mellem arternes temperaturaffinitet, som den kendes fra deres geografiske udbredelse, og deres optræden i forhold til temperaturzonerne i Skagerak (temperatur submergens).

Som eksempel på saltholdighedens indflydelse på den marine fauna analyseres molluskfaunaens udbredelse fra Nordsøen til Østersøens mest ferske områder. I oversigtstabel 11, side 394 vises de enkelte arters omtrentlige inderste udbredelsesgrænse i Kattegat, Belthavet og Østersøen, og de tilsvarende omtrentlige middelsaltholdigheder er opført i tabel 10, side 393.

Antallet af marine arter er omtrent halveret ved en middelsaltholdighed mellem 28 og 29 $^0/_{00}$; og 15 $^0/_{00}$ grænsen er øjensynlig særlig kritisk både for pelecypoder og gastropoder. Meget få marine mollusker kan leve i vand med en middelsaltholdighed på 3–4 $^0/_{00}$.

Ligesom A. C. JOHANSEN (1916) sætter jeg den vertikale udbredelse af *Mytilus edulis, Astarte borealis, A. eliptica, Cardium edule, Macoma baltica, Mya arenaria*, og *Hydrobia ulvae* i Østersøen i relation til saltholdigheden, og til denne række føjes yderligere *Retusa obtusa*. Arternes tendens til at gå ned på større dybde på grund af saltholdigheden er af REMANE (1940) kaldt »Brackwasser Submergens«. Betegnelsen salinitets submergens, der anses for mere adækvat, foreslås i stedet for.

4. Marine dyresamfund

I en meget kort oversigt gøres rede for begrebet det marine dyresamfund med udgangspunkt i C. G. JOH. PETERSENS arbejder og med henvisninger til vigtige diskussioner om emnet i litteraturen. Dyresamfundenes afhængighed af miljøet er endnu et ret uoplyst felt. I enkelte tilfælde har man kunnet påvise, at samfundene er betinget bl. a. af hydrografiske forhold og bundens beskaffenhed (MOLANDER 1928).

Alderen af Arnum formationens molluskselskaber

Bemærkninger om fremgangsmåden ved korrelation

Biostratigrafisk korrelation er nærmere betragtet en statistisk videnskab, idet man ved denne metode beskæftiger sig med fossilers tilstedeværelse eller ikke tilstedeværelse. Et antal faunagrupper sammenlignes med hensyn til deres artsindhold og antallet af fællesarter, og ligheder og uligheder i faunasammensætningen belyses. At man også benytter stratigrafiske data som præmisser ved konklusionerne ændrer ikke biostratigrafiens statistiske præg.

Anvendelsen af makrofossiler ved stratigrafisk forskning har som nævnt tidligere i mange tilfælde indskrænket sig til påvisningen af såkaldte ledefossiler eller til sammenligningen af faunalister. Den sidstnævnte fremgangsmåde skal diskuteres på grund af dens almindelige anvendelse.

En faunaliste kan være opstillet i form af en tabel, således som f. eks. vist på tabel 14, side 422. Tabellen består af en primær søjle (*A*) i hvilken arterne i faunaen, som skal korreleres, er opført i systematisk, alfabetisk eller anden rækkefølge. Sekundære søjler (*B, C, ... K*) angiver de enkelte arters tilstedeværelse eller ikke tilstedeværelse på andre lokaliteter eller i andre faunaer, etager el. lign., som har fået en stratigrafisk placering. Man udregner derefter, hvor stor procentdel af sit artsantal fauna *A* har tilfælles med henholdsvis fauna *B, C, D* o. s. v. og procenterne sammenlignes. De endelige slutninger om fauna *A*'s stratigrafiske relationer drages ofte på grundlag af en sådan sammenligning.

Fra tertiærlitteraturen kan følgende eksempler nævnes: GOTTSCHE (1878), GRIPP (1915), KAUTSKY (1925), STAESCHE (1930), PEYROT (1933), SORGENFREI (1940), VIGNEAUX & MAGNE (1951).

Jeg har som nævnt i 1940 fremhævet, at procenter udregnet på den ovenfor skitserede måde ikke er karakteriserende, fordi de er afhængige af summen af arter i de enkelte faunaer, som sammenlignes. I det følgende gøres rede for andre simple statistiske fremgangsmåder, som tager hensyn til faunaernes samlede artsantal ved beregningen af sandsynlighederne for faunaernes identitet.

Sammenlignes to faunaer med hensyn til graden af deres lighed på grundlag af de indeholdte arter, vil det sige, at man undersøger sandsynligheden for, at de to faunaer er tilfældigt udtagne prøver af een og samme tredie fauna.

Arter i en prøve er statistiske begivenheder. Lad n betegne det samlede antal arter i en fauna og r og s antallet af arter i de to tilfældige prøver, som er udtaget af n. Sandsynlighederne P_r og P_s for begivenhederne r og s kan herefter udtrykkes ved de relative hyppigheder for r og s i forhold til n:

$$P_r = \frac{r}{n} \quad \text{og} \quad P_s = \frac{s}{n}$$

Ved hjælp af disse ligninger kan man bestemme sandsynligheden P_α for, at der samtidig i r og s forekommer α arter:

$$P_\alpha = P_r \cdot P_s = \frac{r \cdot s}{n^2} \tag{1}$$

Da det samlede antal arter i fossile faunaer praktisk taget aldrig kendes, er n en ubekendt størrelse. Man har derfor kun den udvej i formel (1) at indsætte en tilnærmet værdi for n eller at udlede et andet udtryk for sandsynligheden P_α.

I det forelagte eksempel, hvor vi går ud fra, at r og s er tilfældige prøver af een og samme fauna, og at α er antallet af fællesarter, kan man udlede yderligere to ligninger for P_α forskellige fra ligning (1).

De relative hyppigheder af α i forhold til henholdsvis r og s er:

$$P'_\alpha = \frac{\alpha}{r} \quad \text{og} \quad P''_\alpha = \frac{\alpha}{s}$$

Sandsynligheden P_α for at der optræder α arter samtidig i både r og s er efter den klassiske regel om, at sandsynligheden for, at to hændelser, der er uafhængige af hinanden, begge indtræffer, er lig med produktet af sandsynligheden for hver af dem:

$$P_\alpha = P'_\alpha \cdot P''_\alpha = \frac{\alpha^2}{r \cdot s} \tag{2}$$

Ifølge definitionen for sandsynlighed er

$$P_\alpha = \frac{\alpha}{n}$$

heraf og af formel (1) følger:

$$\alpha = n\ P_\alpha = \frac{rs}{n}$$

Ved at indsætte dette udtryk i formel (2) fås:

$$P_\alpha = \frac{\left(\frac{rs}{n}\right)^2}{n} = \frac{rs}{n^2}$$

hvorved umiddelbart fremgår, at ligning (2) er identisk med (1).

Endelig kan sandsynligheden for fællesarternes tilstedeværelse også udtrykkes som den relative hyppighed af α i forhold til $n' = r+s-\alpha$

$$P_{\alpha'} = \frac{\alpha}{n'} = \frac{\alpha}{r+s-\alpha} \tag{3}$$

Relationerne mellem ligningerne (1), (2) og (3) kan illustreres ved at antage at:

$$r \rightarrow n\,,$$

heraf følger:

$$\alpha \rightarrow s\,,$$

hvilket viser, at både P_α og $P_{\alpha'}$ konvergerer mod $\frac{s}{n}$

P_α eller de tilnærmede udtryk $P_{\alpha'}$, som i det følgende vil blive kaldt korrelationsforhold, kan anvendes som sammenligningsgrundlag og som udtryk for affinitet også i tilfælde, hvor aldersforskellen mellem de sammenlignede faunaudsnit er udenfor diskussion. Korrelationsforholdene udtrykkes i procent ved at multipliceres med 100.

Selv om der kan rejses indvendinger mod at anvende korrelationsforhold beregnet efter ovenstående formler som eneste korrelationsprøve er sammenligninger på grundlag af korrelationsforhold uden tvivl en bedre metode end »procentmetoden«.

Ved stratigrafisk korrelation er det sandsynligvis mest fordelagtigt at udregne P_α ved hjælp af ligning (2), som giver de mindste fejl for P_α.

Formel (3) er muligvis velegnet ved sammenligninger, som har studiet af faciesindflydelser til formål.

Kun faunalister fra velafgrænsede formationer, hvis enkelte lagserier er tilstrækkeligt ensartede, kan bruges ved stratigrafiske korrelationer efter den her foreslåede metode. Som allerede nævnt i indledningen er det desværre meget vanskeligt at få et overblik over de forskellige europæiske molluskfaunaer på basis af oplysningerne i litteraturen. Dette skyldes navnlig, at man i fossillisterne ofte finder arter fra flere lokaliteter blandet sammen, og at man ikke altid klart har skelnet mellem bjærgartsstratigrafiske og tidsstratigrafiske enheder. Det er således endnu yderst vanskeligt at nå til en klar opfattelse af de forskellige faunaer i det aquitaniske bassin, i Wienerbassinet og i de mediterrane områder. På grund af denne usikkerhed er beregningen af korrelationsforhold kun foretaget for aflejringerne i Nordsøbassinet.

De forskellige faunaer, som er opført i korrelationslisten tabel 14, side 422, refererer til følgende etager, faunaer og forfattere:

Tyskland:		
Vierlande etage	Itzehoe faunaen	(Gripp 1914)
Hemmoor etage	Hemmoor faunaen	(Kautsky 1925)
Reinbek-Dingden etage	Reinbek faunaen	(Gottsche 1878)
Glimmerton etage	Hele faunaen	(Banke Rasmussen 1956)
Belgien:		
Boldérien	Hele faunaen	(Glibert 1945–54)
Houthaelen etage	Hele faunaen	
Anversien	Hele faunaen	
Danmark:		
Klintinghoved ler	Hele faunaen	(Sorgenfrei 1940)
Gram formation	Hele faunaen	(Banke Rasmussen (1956)

Den samlede fauna fra Hollands mellemmiocæn er endnu ikke offentliggjort, og de tidligere til det danske mellemmiocæn henførte molluskselskaber udgør øjensynlig ikke nogen veldefineret enhed. Arterne fra disse to formationsintervaller har derfor ingen større værdi ved den stratigrafiske korrelation.

Den biostratigrafiske dokumentation indenfor Nordsøbækkenets miocæn

I dette afsnit gives en kort oversigt over, hvor mangelfuldt kendskabet til molluskfaunaerne i de forskellige afdelinger af de maksimalt 520 m mægtige miocænaflejringer i Nordsøbækkenet er. Ved at sammenligne med recente faunaer langs Vesteuropas kyster antages molluskfaunaen i hvert stadium at have omfattet 500–800 arter.

Ved at gå ud fra formlerne (1) og (2) side 472 kan det samlede artsantal n i en fauna, hvorfra der foreligger to tilfældige prøver med artsantallet r og s og med fællesantallet α beregnes, idet:

$$\frac{rs}{n^2} = \frac{\alpha^2}{rs}$$

Ved at løse denne ligning for n fås:

$$n = \frac{rs}{\alpha} \qquad (4)$$

Faunaen fra Arnum formationen omfatter 266 arter, af hvilke 143 er fælles med Hemmoor faunaen, der består af 311 arter. Forudsat at disse to molluskselskaber stammer fra samme fauna fås artsantallet n i denne efter (4):

$$n = \frac{266 \cdot 311}{141} = 586{,}7 = 587 \text{ arter.}$$

Hvis Arnum formationens og Reinbek-Dingden etagens mollusker hører til een og samme fauna fås tilsvarende:

$$n = \frac{266 \cdot 107}{52} = 547{,}3 = 547 \text{ arter.}$$

De beregnede artsantal svarer påfaldende godt til artsantallet, som blev anslået på grundlag af de recente molluskfaunaers størrelse. Da der er tale om helt uafhængige metoder, er der grund til at antage, at der herved er nået til en forholdsvis god tilnærmelse for antallet af molluskarter i den mellemmiocæne Nordsø's enkelte udviklingsstadier.

Den biostratigrafiske korrelation af Arnum formationens molluskselskaber

Da der ikke kan herske tvivl om, at Vierlande og Hemmoor faunaerne samt de belgiske faunaer i nogen grad hidrører fra forskellige fossilzoner, er arterne fra Arnum formationens fossilhorisonter betragtet under eet ved korrelationen med de hidtil fra Nordsøområdet kendte faunaer. Dette kan også forsvares ud fra synspunktet, at Arnum formationen temmelig sikkert repræsenterer kun eet marint stadium, og at de dominerende arter praktisk taget optræder i alle niveauer.

De udregnede værdier for P_α og P_{α_1} ved foden af tabel 14, side 434 viser, at Arnum formationens fauna har størst affinitet til Hemmoorfaunaen, og Reinbek-Dingden faunaen, som den også korreleres med stratigrafisk og aldersmæssigt. Samtidig er der imidlertid også ret stor affinitet til Klintinghoved faunaen. Dette kunne tyde på faunistisk kontinuitet i de dybere dele af Nordsøbækkenet fra Klintinghoved etagen over Hemmoor etagen og videre til Reinbek etagen.

Det anses for unyttigt at forsøge en mere præcis korrelation med det nordvesttyske mellemmiocæn i øjeblikket. Det tyske fossilmateriale tillader ikke dette. Faunaudviklingen i Arnum formationen er nu den bedst kendte, derfor egner denne formation sig bedre til at være standard profil end det nordvesttyske mellemmiocæn.

Analyse af faunaudviklingen i Arnum formationen

Bemærkninger om sedimentationen af molluskskaller

Da molluskskallerne efter dyrets død er underkastet de samme love for transport som sedimenterne på havbunden, behøver fossile molluskselskaber ikke at være identiske med dyresamfundene, hvorfra de stammer.

På grundlag af A. C. JOHANSENS (1901) studier over transporten af molluskskaller i forskydningszonen langs det åbne havs kyster kan man slutte, at fossile molluskselskaber med tydeligt littoralt præg i form af tykskallede individer og rullede skaller stammer fra mollusksamfund, hvis arter havde deres øvre bathymetriske grænse ovenfor ca. 15 m dybdekurven.

Betydningen af de behandlede molluskselskaber fra Arnum formationen

De undersøgte molluskselskaber er kun tilnærmede udsnit af mollusksamfund ikke alene på grund af eventuel transport af skalmaterialet efter dyrenes død, men også i kraft af, at de som boreprøver repræsenterer et vist sedimentationsinterval.

Faunaudvikling og betydningen af hyppige arter

Diskussionen af den faunistiske udvikling baseret på den statistiske oversigt over de enkelte prøvers fossilindhold i tabellerne 15 (p. 436) og 16 (p. 460). Tabel 15 viser alle bestemte og talte individer, mens tabel 16 indeholder alle »hyppige« arter, d.v.s. arterne som i en eller flere af prøverne repræsenterer 1 % eller mere af de samlede antal fossiler i prøven. Prøverne fra de to Arnumboringer, som kun ligger med et par meters afstand, er ordnet i eet faunaprofil i tabel 16.

De hyppige arter udgør mellem 80 og 98 % af fossilerne i prøverne. Det er bemærkelsesværdigt, at deres andel i faunaen stiger op gennem lagserien i boringerne Glejbjerg, Arnum og Toftlund. I Gramby boringen ligger procenterne højt i alle prøver og svarer til procenterne i de øverste prøver i Glejbjerg, Arnum og Toftlund profilerne. En undtagelse fra reglen om høje procenter i de øverste prøver er prøven fra 28–40 m i Arnum boringen (150.13). Bramminge faunaen hører til typen med høje procenter for de hyppige arter.

Forøgelsen af de hyppige arters individantal i Glejbjerg, Arnum og Toftlund profilerne skyldes uden tvivl en selektiv faktor, som antages at være aftagende saltholdighed under sedimentationen af Arnum formationen.

Gramby profilets høje procenter for de hyppige arter forklares ved at antage, at sedimentationsområdet lå i nærheden af kysten under hele sedimentationsforløbet, og at vandet var mere eller mindre brakt på grund af udstrømmende ferskvand fra landområdet øst herfor. Denne forklaring støttes ved betragtninger over sedimenterne i profilet.

Bramminge molluskselskabet er en typisk strandakkumulation fra forskydningsbæltet. Det synes rimeligt at antage, at den høje procent af hyppige arter ved Bramminge er et udtryk for sekundær selektion som følge af bølgebevægelse og brænding, hvorved kun de kraftigste skaller har undgået at blive ødelagt.

Forholdet mellem arterne

De enkelte arters hyppighed i tabel 16 afslører visse påfaldende relationer mellem beslægtede arter. Særligt iøjnefaldende er forholdet mellem *Nassa cimbrica*, *N. Schlotheimi*, *N. Fuchsi* og *N. Facki*, hvis procenter er uddraget og sammenstillet særskilt forneden på tabel 16.

Det er fristende at forklare Nassaernes optræden på lignende måde som ændringen i de hyppige arters procenter ved at antage, at en ændring af saltholdigheden har favoriseret *N. cimbrica* og *N. Schlotheimi* på de to andre arters bekostning. En sådan forklaring støttes af procenterne i prøverne fra Gramby, som netop alle formodes at repræsentere brakvandsfaunaer.

En nøjere undersøgelse af hyppighederne i Gramby, Toftlund og Arnum prøverne tyder dog på, at salinitetsændringen ikke er hele forklaringen. *N. cimbrica* tiltager opefter både i Gramby, Toftlund og Arnum profilerne, og det er endvidere bemærkelsesværdigt, at *N. cimbrica* og *N. Schlotheimi* altid dominerer over *N. Fuchsi*–*N. Facki* i prøver, hvor de optræder samtidig.

Det er vanskeligt på nuværende tidspunkt at nå til nogen helt sikker opfattelse af årsagssammenhængen i dette forhold. Alt tyder på, at *N. Fuchsi* og *N. Facki* har domineret i Arnum formationens nedre del, og at *N. Fuchsi* har været den biologisk stærkeste af de to arter. Deres sjældne optræden ved Gramby tyder på, at de har været følsomme overfor aftagende saltholdigheder.

N. cimbrica og *N. Schlotheimi* synes at have dannet en konkurrerende gruppe overfor *N. Fuchsi* og *N. Facki*, som de tilsidst har fortrængt. *N. cimbrica* og *N. Schlotheimi* konkurrerede øjensynlig også indbyrdes, idet høje procenter for *N. cimbrica* svarer til lave værdier for *N. Schlotheimi*. Det er ligeledes påfaldende, at *N. Schlotheimi* tiltager betydeligt i de prøver, hvor *N. cimbrica* ikke findes, eller hvor den er sjældnere. Med en enkelt undtagelse (Arnum (25b) 107.5 m) ligger procenterne for *N. cimbrica* altid over *N. Schlotheimi* i molluskselskaberne, hvori de begge forekommer.

De to arter var uden tvivl mindre følsomme overfor aftagende saltholdighed end *N. Fuchsi* og *N. Facki*. Deres høje procenter i de nederste prøver fra Arnum og Toftlund — hvor alle fire arter optræder samtidig — tyder imidlertid på, at *N. cimbrica* og *N. Schlotheimi* også havde andre biologiske fortrin end tilpasningsevnen overfor forandringer i saltholdighed, hvorved de var i stand til at udkonkurrere *N. Fuchsi* og *N. Facki*.

Sandsynligheden for, at der foreligger en biologisk balance mellem de nævnte 4 Nassa-arter er således ret stor.

Hyppighederne for *Leda Westendorpii* og *Yoldia glaberrima* i prøverne fra Toftlund og Arnum tyder på, at der også mellem disse arter er en eller anden form for antagonisme.

De almindelige arter reagerer forskelligt med hensyn til deres hyppighed i løbet af sedimentationen af lagserierne ved Glejbjerg, Toftlund og Arnum. Nedenfor er arterne grupperet i tre grupper, idet et par ukarakteristiske arter dog er udeladt. Den recessive gruppes arter aftager, den progressive gruppes arter tiltager, og den stationære gruppes procenter er nærmest uforandret i løbet af Arnum formationens dannelse.

»Hyppige« arters reaktion i løbet af sedimentationen af lagserierne ved Glejbjerg, Toftlund og Arnum.

Recessive	Progressive
Nuculoma hanseata	*Leda pygmaea*
Nassa Fuchsi	*Varicorbula gibba*
Nassa Facki	*Nassa cimbrica*
Gemmula boreoturricula	*Ringicula buccinea*
Fusiturris Duchastelii	

Stationære

Leda Westendorpii
Leda emarginata
Yoldia glaberrima
Kellyella rotunda
Thyasira cfr. flexuosa
Ervilia pusilla
Spisula subtruncata
Abra prismatica
Saxicava arctica
Turritella tricarinata
Bittium tenuispina
Aporrhais alata
Nassa Schlotheimi
Terebra Hörnesi
Retusa umbilicata
Spiratella atlanta
Vaginella depressa

Denne karakteristik af arterne er naturligvis kun foreløbig. Det er nødvendigt at undersøge mere materiale før inddelingens værdi kan siges at være endelig belyst. Svaret på spørgsmålet om årsagerne til arternes reaktioner må også udskydes indtil videre. En vis indkredsning af problemstillingen kan dog opnås ved et studium af Bramminge faunaen, der som nævnt er en lavvandsfauna. Vigtige lavvandsarter i molluskselskabet fra Bramminge er:

Leda pygmaea
Yoldia glaberrima
Varicorbula gibba
Aporrhais alata
Nassa Schlotheimi
Nassa cimbrica
Terebra Hörnesi
Ringicula buccinea

Det bør dog understreges, at disse arters udbredelse sikkert ikke alene var knyttet til dybder ovenfor 15–20 m, men at de også fandtes nedenfor dette niveau.

De fysiske miljøforhold er delvis blevet omtalt i diskussionen over de hyppige arter, hvor et spørgsmål som aflejringsområdets saltholdighed blev drøftet. De bathymetriske forhold strejfedes ovenfor ved omtalen af lavvandsarterne ved Bramminge.

Ser man på lavvandsarternes hyppighed i prøverne og på sedimenternes beskaffenhed, er det rimeligt at slutte, at vanddybden i det undersøgte område var ret ringe, formodentlig mellem 20 og 50 m.

Temperaturforholdene kan man med nogen tilnærmelse slutte sig til ved at gå ud fra udbredelsen af de endnu eksisterende arter i nutidens have. Molluskselskaberne omfatter 39 arter, som endnu findes i lusitanske og boreale områder, mens 3 arter også findes i arktiske have. Selv med de nødvendige forbehold overfor eventuelle ændringer af arternes miljøkrav i løbet af den tid, der er gået siden Arnum formationens dannelse, synes der således at være stor sandsynlighed for, at dens fauna var en boreal eller lusitansk fauna.

Blandt de nulevende arter har *Pecten tigerinus* og *Cancellaria cancellata* særlig interesse. *P. tigerinus* er næsten paradigmatisk boreal i sin nutidige udbredelse, og *C. cancellata* er omtrent lige så typisk lusitansk. Uden at overdrive disse to arters betydning kan man derfor slutte, at man i Arnum formationens aflejringsperiode har haft temperaturforhold i Nordsøområdet, der omtrent svarede til temperaturen i nutiden i havet ved det nordlige Spanien og Portugal, hvor de to arter mødes. En oversigt over havets middeltemperatur ved Nordspanien og Portugal og en diskussion af temperaturligheden mellem dette område og den miocæne Nordsø findes side 415.

Inddelingen af Arnum formationens molluskselskaber. På side 455 findes en redegørelse for inddelingen af molluskselskaberne. I oversigtstabellerne karakteriseres de enkelte fossilselskaber ved dominerende producenter og konsumenter.

Alle molluskselskaber synes at være derivater af *Aporrhais alata* — *Nassa ssp.* samfundet, som således kan betragtes som det typiske grundthavssamfund i den miocæne Nordsø.

Korrelation af boreprofilerne

Boreprofilerne kan inddeles biostratigrafisk ved hjælp af *Nassa Fuchsi* og *N. cimbrica* species zonerne*).

Nassa Fuchsi zonen er den nederste biostratigrafiske afdeling af den kendte del af Arnum formationen. Det må dog understreges, at formationens nedre grænse kun er nået i Ribe boringen og at fossilmaterialet fra denne boring er ret utilstrækkeligt som stratigrafisk dokumentationsmateriale. Vi ved således ikke, om *Nassa Fuchsi* er karakteristisk for hele det marine interval ved Ribe eller ej.

Den øvre grænse for den biostratigrafiske *Nassa Fuchsi* zone defineres som basis af *N. cimbrica* zonen. Denne grænse ligger ved ca. 50 m (—25 m) i Glejbjerg profilet.

Med hensyn til Bramminge profilet ved vi kun, at laget ved 70–80 m hører til *Nassa cimbrica* zonen. Det er muligt at zonens nedre grænse ligger dybere end 80 m dybde (−66 m).

Hele Gramby serien må henføres til *N. cimbrica* zonen.

Arnum profilet repræsenterer *N. cimbrica* zonen fra dens top ved basis af

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*) Betegnelsen species zone er her brugt som synonym for biozone (se f. eks. TROELSEN & SORGENFREI 1956), som af forskellige grunde er en mindre konsekvent betegnelse. Ved species zone forstås en arts totale vertikale og horisontale udbredelse. I de tilfælde, hvor der i det følgende anvendes et artsnavn efterfulgt af betegnelsen 'zone', menes hermed species zone.

Gram formationen til den nedre grænse, som øjensynlig lige er nået. Toftlund boringen nåede tilsyneladende ikke gennem *N. cimbrica* zonen.

Det er umuligt på nuværende tidspunkt at afgøre, om *N. cimbrica*'s opdukken er samtidig i alle profilerne. Det er allerede nævnt tidligere, at *N. cimbrica* måske er en brakvandsart. På den anden side tyder meget på, at arten er indvandret udefra. I så fald er det berettiget at betragte *Nassa cimbrica* zonens basis som et synkront niveau.

Det er vanskeligt at nå til en mere detailleret korrelation af de enkelte boreprofiler på grundlag af de fossilførende lag. En enkelt parallelitet mellem Toftlund og Arnum profilet er dog omtalt. Ved en sammenligning af hyppighederne af arterne i tabel 16 for prøverne Toftlund 115 m og Arnum 104.3–107.5 m ses, at følgende arter fremviser maksimale frekvenser i begge prøver:

Yoldia glaberrima
Abra prismatica
Natica sp. sp.
Nassa Fuchsi

Nassa Facki
Gemmula boreoturricula
Fusiturris Duchastelii

Denne sammenfalden af 7 maksima ud af 30 muligheder viser, at de to molluskselskaber ligner hinanden meget. Vi har dog endnu ikke beviset for, at dette betyder, at de er synkrone.

For at give en oversigt over de omtrentlige formationstykkelser og den tertiære lagserie i Sønderjylland, anføres boreprofilet for dybdeboringen Arnum no. 1 fra terræn og til basis af daniets bryozokalk. Arnum formationens fossilserie i denne boring er kun repræsenteret ved skylleprøver, der endnu ikke er analyseret nærmere på grund af deres ringe kvalitet, idet der er boret uden forerør.

Bemærkninger om områdets struktur

Korrelationen af boreprofilerne (fig. 2) viser, at der må have fundet tektoniske bevægelser sted under og efter Arnum formationens aflejringer. Glejbjerg serien ligger i et højere niveau end de andre lagserier, og der er tilstrækkelig begrundelse for at antage, at lagserien ved Arnum er hævet i forhold til Gramby og Toftlund områderne.

Allerede på et tidligt tidspunkt af mine undersøgelser (1947) blev de foreløbige biostratigrafiske resultater stillet til rådighed for DANISH AMERICAN PROSPECTING CO. ved fortolkningen af selskabets geofysiske og geologiske undersøgelser i Sønderjylland. Det viste sig, at der var en bemærkelsesværdig overensstemmelse mellem strukturerne, som antydedes af den miocæne lagserie, og residualtyngdekortet udarbejdet af GULF RESEARCH & DEVELOPMENT CO. Lagseriens høje beliggenhed ved Arnum og Glejbjerg svarede til maxima på tyngdekortet, og de lavere liggende Gramby, Toftlund og Ribe profiler svarede til lokale tyngdeminima.

Området er senere undersøgt seismisk af DANISH AMERICAN PROSPECTING CO. De seismiske undersøgelser og en række strukturboringer har bekræftet rigtigheden af den strukturelle fortolkning, som den miocæne lagserie gav anledning til.

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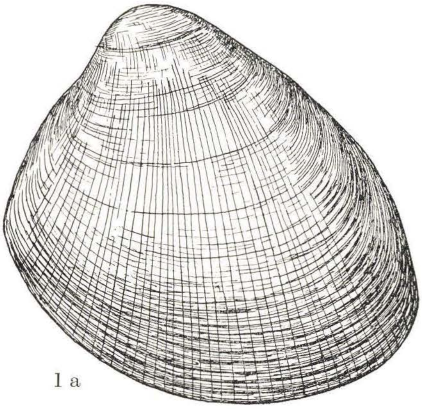
PLATES

Plate 1.

	Location	Depth	Length	Height	Width	Page
1a–b. *Nucula nucleus* (LINNÉ) Right valve. (×10).	Toftlund	75–100 m.	5.7	5.1		39
2a–c. *Nucula Jeffreysi* BELLARDI	Glejbjerg	53.5 -				43
a–b. Right valve, c paired valves,		a–b:	3.39	2.93		
dorsal view. (×18).		c:	2.54		1.35	
4a–b. *Nucula cf. nitida* SOWERBY Left valve. (×12).	Toftlund	75–100 m.	3.85	3.05		46

Shell dimensions in millimeters



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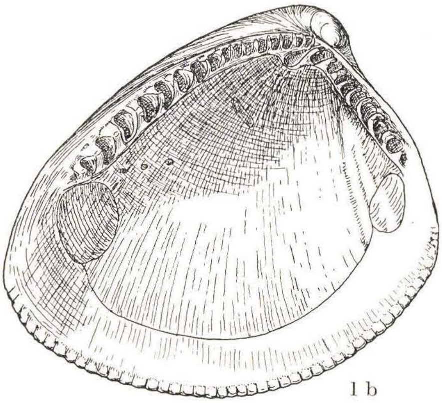

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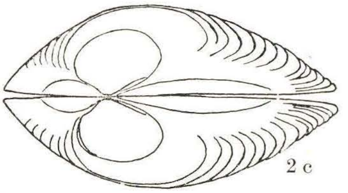

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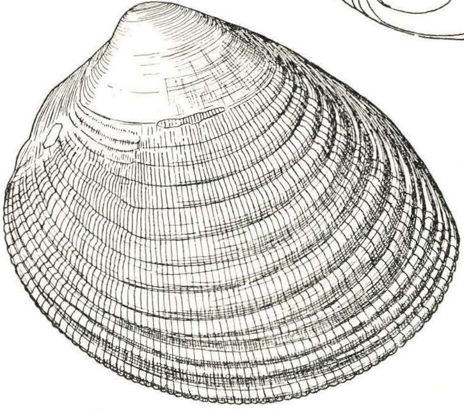

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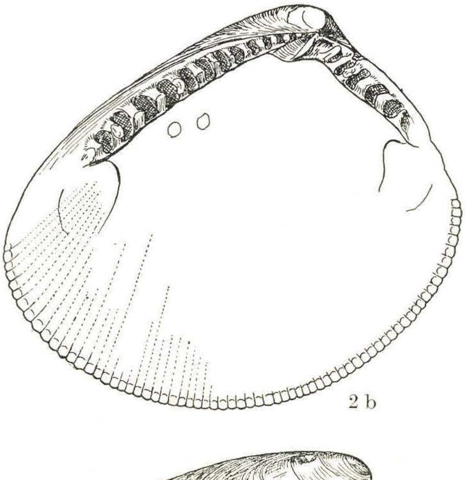

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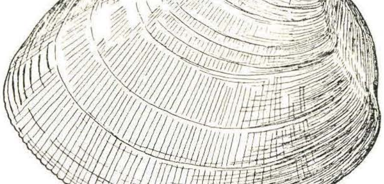


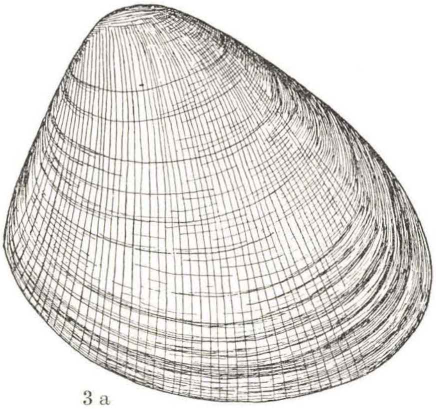
4 b

Th. S. del.

Plate 2.

	Location	Depth	Length	Height	Width	Page
3a–b. *Nucula cromata nov. sp.* Right valve. (×11). Holotype	Toftlund	75–100 m.	5.20	4.65		44
8a–b. *Leda (Jupiteria) pygmaea* (MÜNSTER). Left valve. (×12.5).	Toftlund	75–100 -	3.95	2.78		51
10a–e. *Leda (Lembulus) emarginata* (LAMARCK).	Toftlund	75–100 -				57
a. Left valve with widely spaced concentric ribs and oblique lines. (×12).			4.55	2.61		
b–d. Right valve, concentric ribs obliterated, few oblique lines. (×12).			5.02	2.75		
c. Paired valves, dorsal view. (×12).			3.40		1.33	
e. Right valve narrowly spaced concentric ribs and oblique lines. (×12).			4.55	2.82		

Shell dimensions in millimeters.



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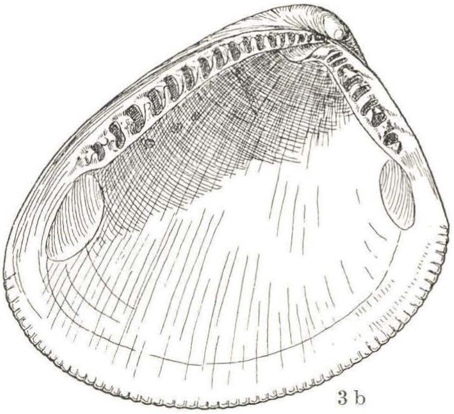

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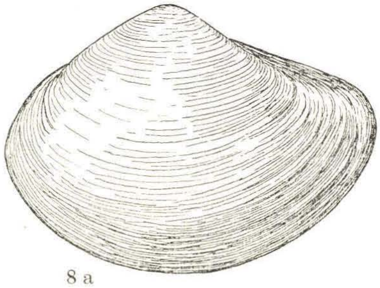

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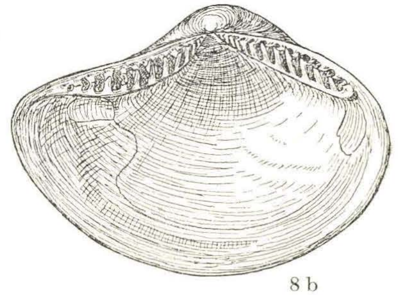

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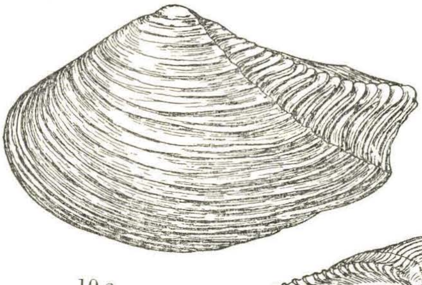

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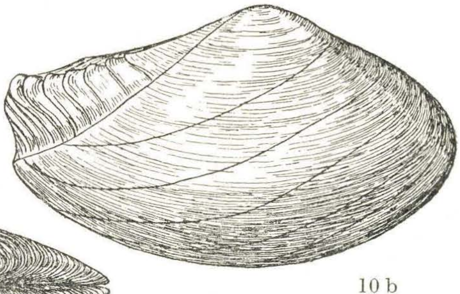

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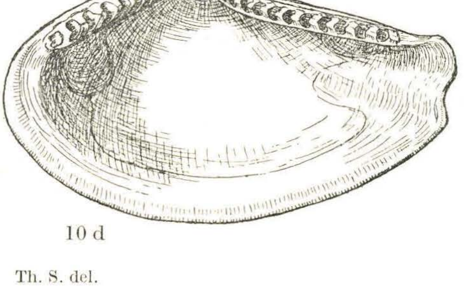

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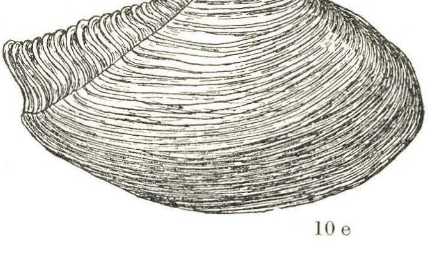

10 e

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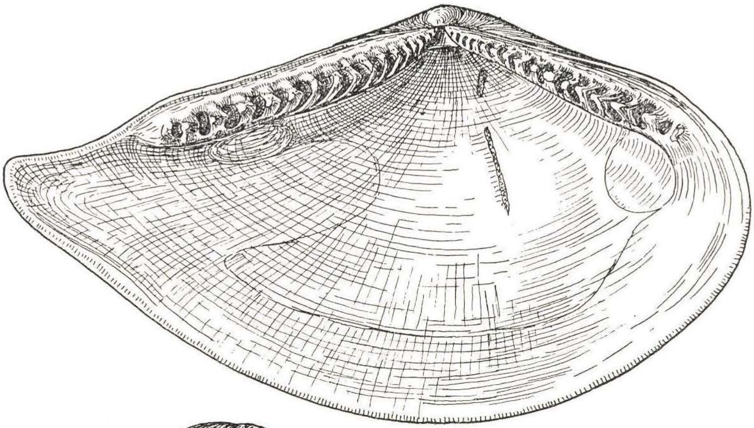
Plate 3.

	Location	Depth	Length	Height	Width	Page
9a–c. *Leda (Ledina) Westendorpii* (NYST & WESTENDORF)	Toftlund	75–100 m.				54
a. Left valve. (×15).			6.63	3.70		
b. Paired valves, dorsal view (×15).			2.90		1.16	
c. Right valve. (×12.5).			8.80	4.53		
12a–c. *Arca diluvii* LAMARCK.	Toftlund	75–100 -				63
a–b. Right valve. (×13.5).			4.85	3.70		
c. Left valve. (×13.5).			3.75	2.78		

Shell dimensions in millimeters.



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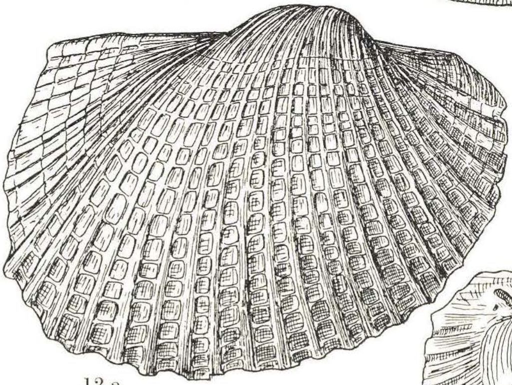

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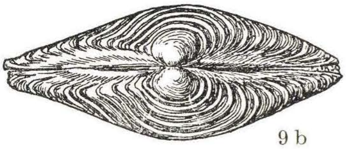

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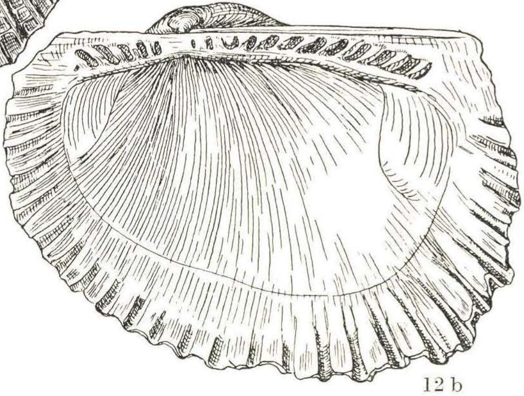

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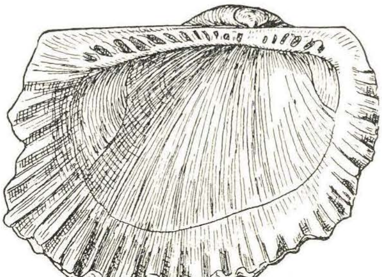

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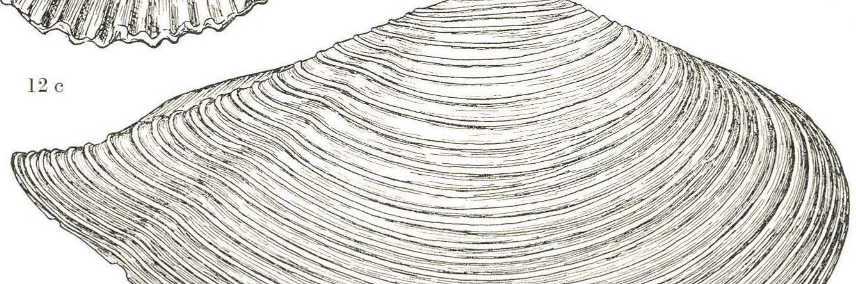

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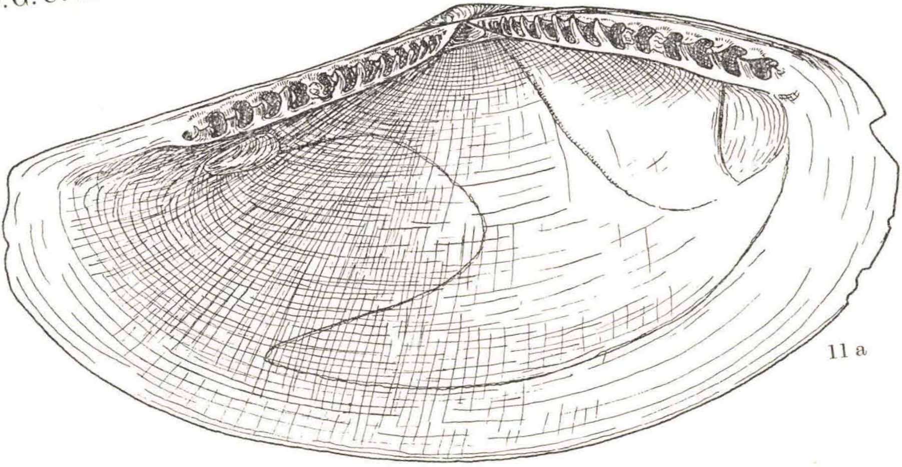
Plate 4.

	Location	Depth	Length	Height	Page
11a–b. *Yoldia glaberrima* (MÜNSTER) Left valve. (×15).	Toftlund	75–100 m.	7.82	3.95	59
16a–b. *Limopsis anomala* (EICHWALD) Left valve. (×13.5).	Toftlund	75–100 -	4.28	4.10	69

Shell dimensions in millimeters.

Plate 4



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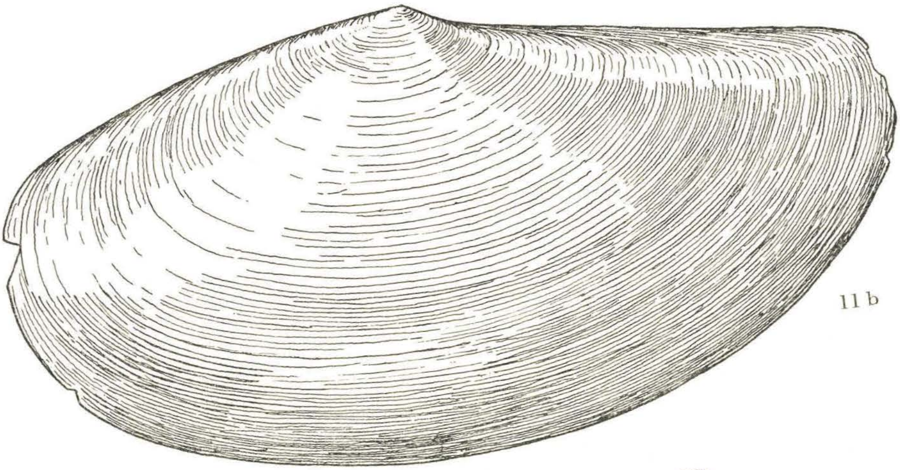

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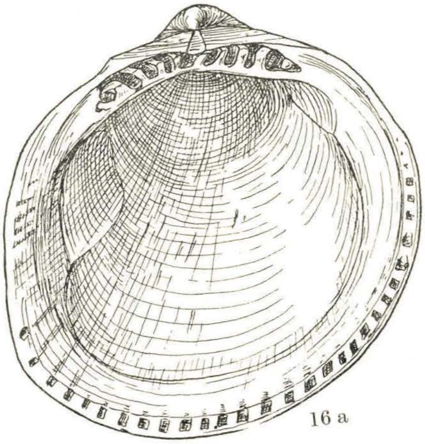

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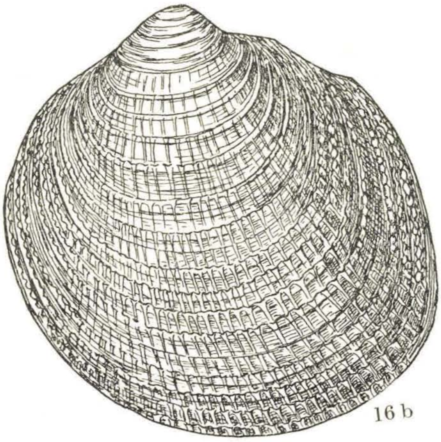

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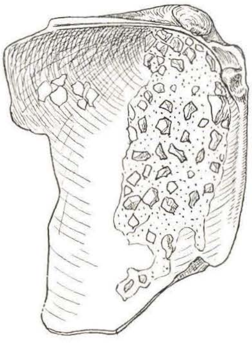
Th. S. del.

Plate 5.

		Location	Depth	Length	Height	Page
17a–b.	*Modiolus sp. a.* Left valve. (×33).	Arnum(25b)	62.7–62.9 m.		1.37	71
18a–b.	*Modiolus sp. b.* Right valve. (×33).	Toftlund	110–115 -		0.85	71
19a–d.	*Musculus saucatsensis* (COSSMANN)					71
a.	Left valve. (×15.5).	Toftlund	75–100 -	1.98	1.0	
b.	Left valve. (×15.5).	Toftlund	105–110 -	1.29	1.24	
c–d.	Left valve. (×15.5).	Toftlund	105–110 -	4.33	2.77	
24.	*Pecten Gerardi* NYST					
	Left valve (×20).	Arnum(25b)	107.5 -		2.74	78

Shell dimensions in millimeters.



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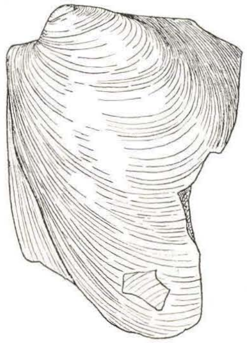

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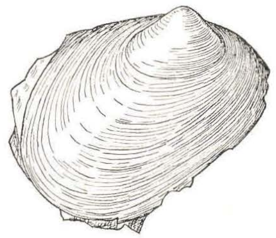
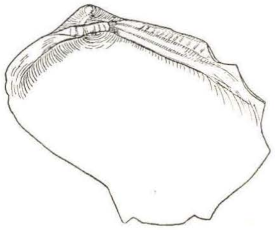
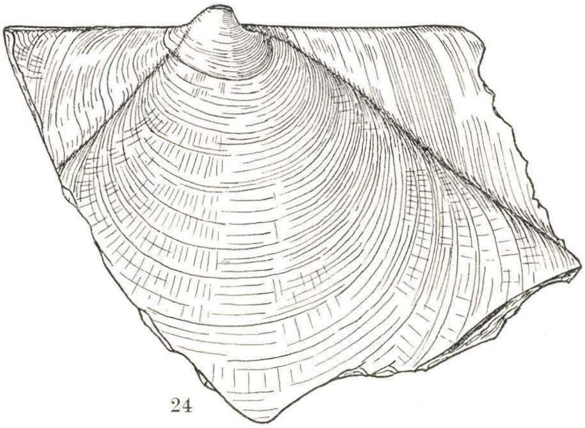


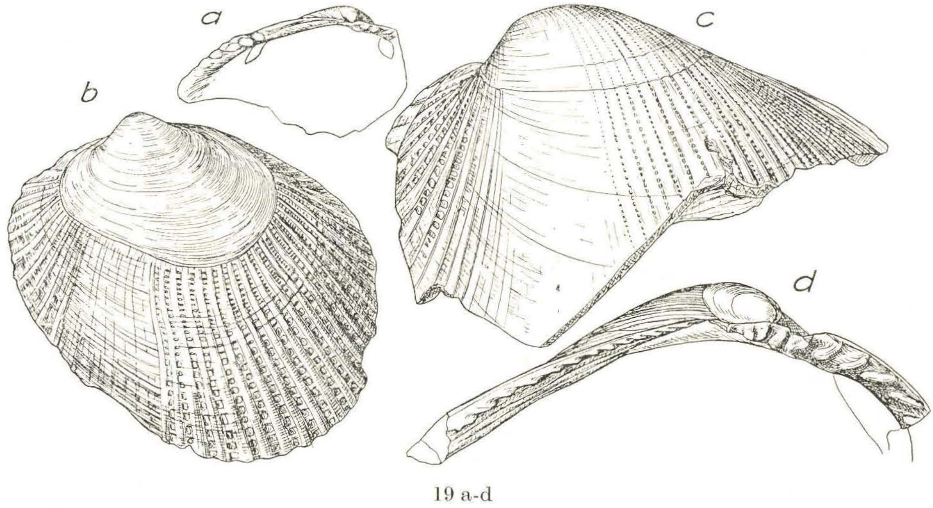
18 a



18 b



24



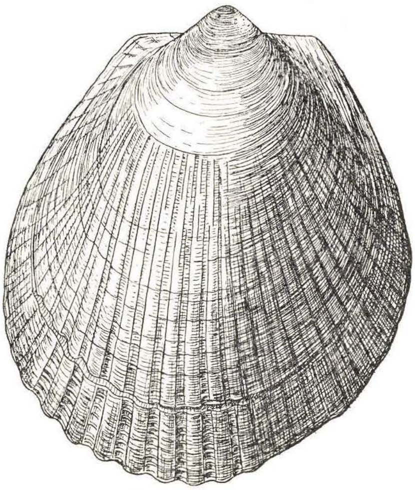
19 a-d

Th. S. del.

Plate 6.

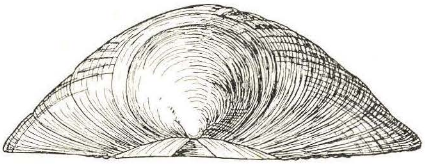
	Location	Depth	Length	Height	Width	Page
26a–c. *Lima* (*Limea*) *strigilata* (Brocchi) Right valve. (×35).	Toftlund	100–105 m.	1.55	1.82	0.57	79
27a–c. *Anomia squamula* Linné Left valve. (×18).	Toftlund	105–110 -	2.31	2.31	0.77	80

Shell dimensions in millimeters.

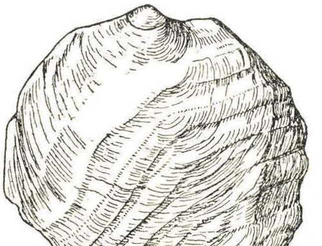


26 a

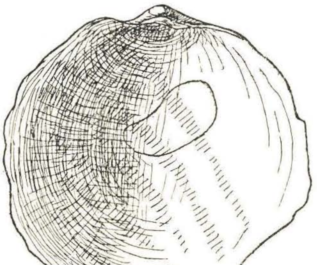
26 b



26 c



27 a



27 b

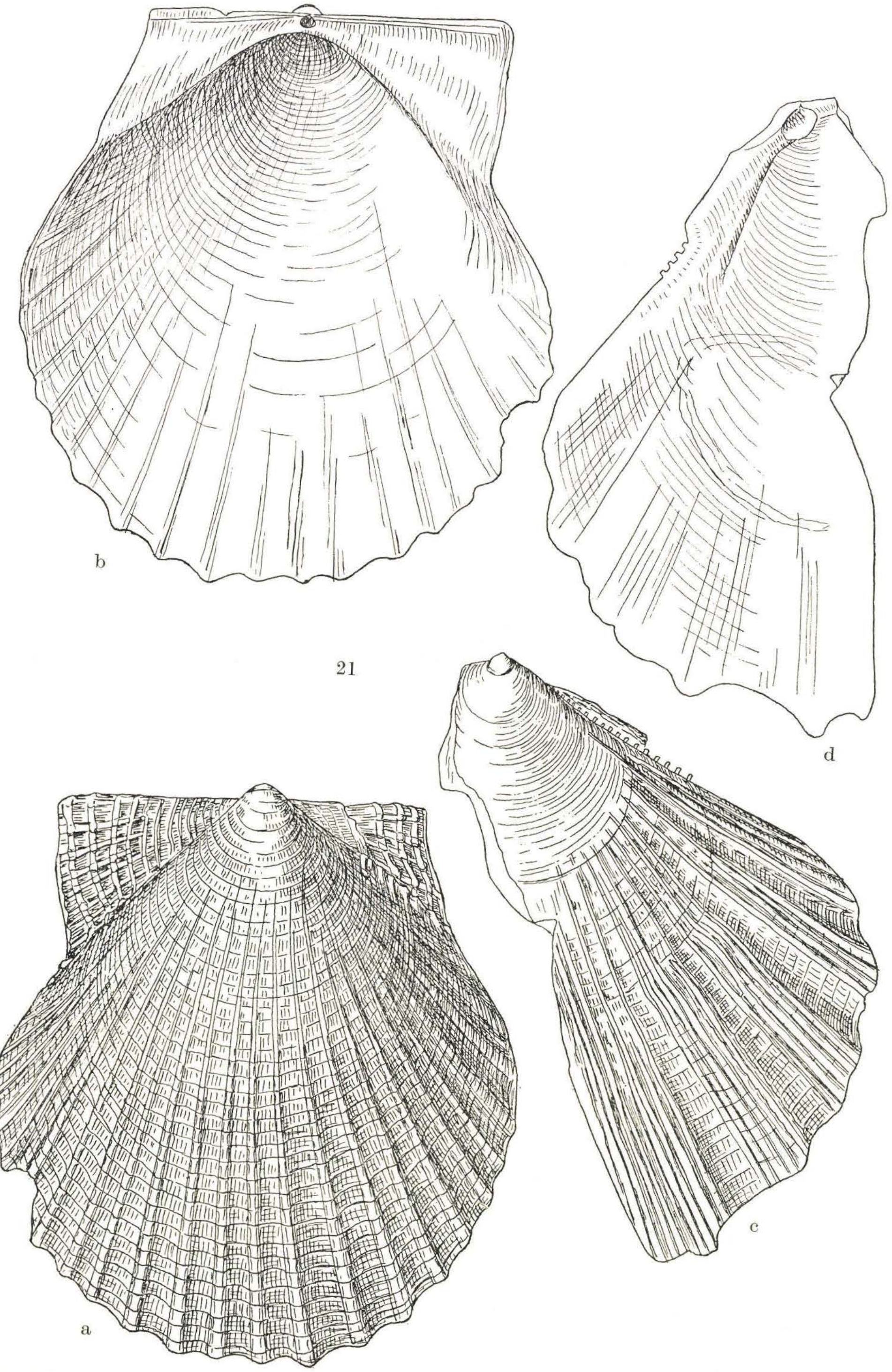
27 c

Th. S. del

Plate 7.

	Location	Depth	Length	Height	Page
21a–d. *Pecten ex. aff. liberata* Cossmann & Peyrot	Toftlund	75–100 m.			74
a–b. Left valve. (×15).			4.95	5.4	
c–d. Right valve. (×15).		Greatest dimension: 6.05 mm.			

Shell dimensions in millimeters.



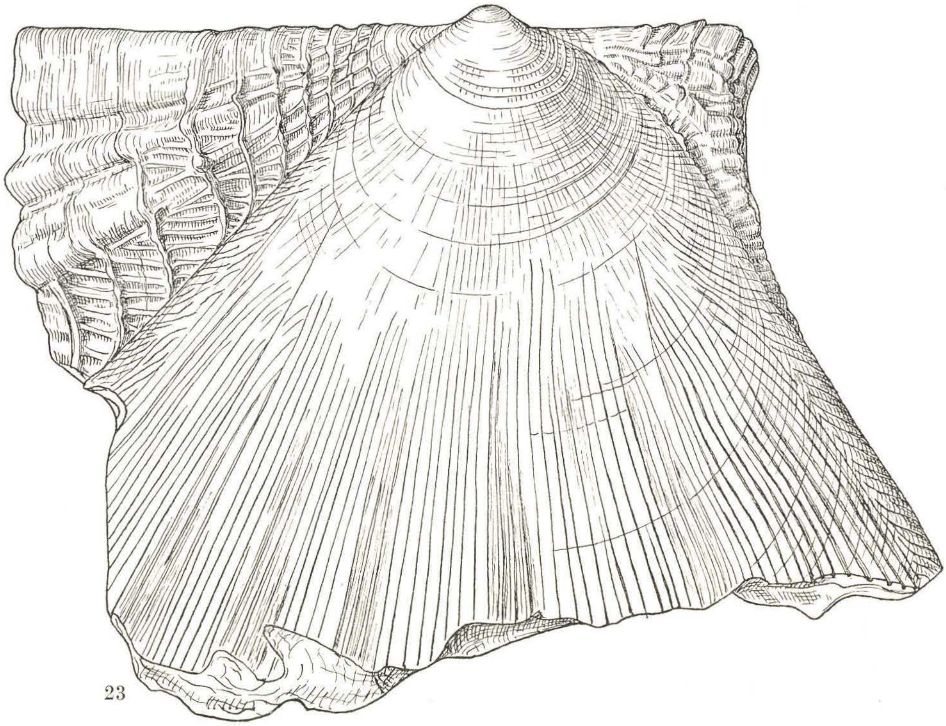
21

Th. S. del.

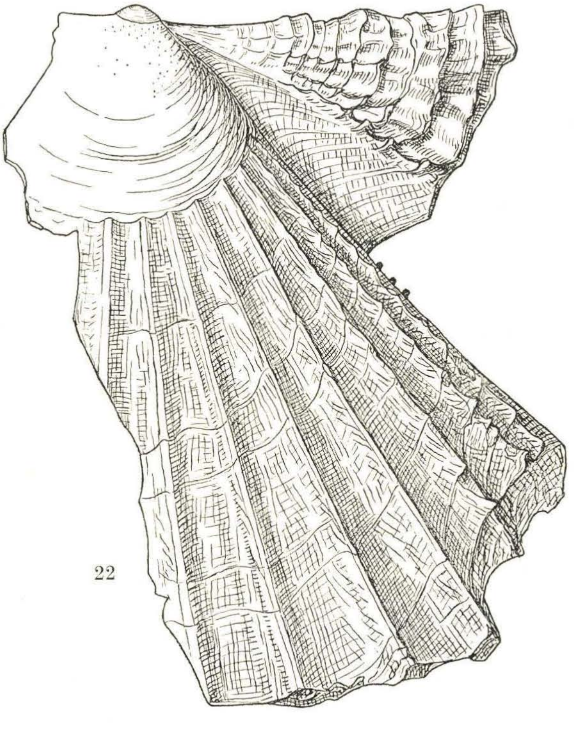
Plate 8.

		Location	Depth	Height	Page
22.	*Pecten radians* NYST				
	Right valve. (×18).	Toftlund	115 m.	4.67	76
23.	*Pecten tigerinus* MÜLLER				
	Left valve. (×21).	Toftlund	115 -	4.57	77

Shell dimensions in millimeters.



23



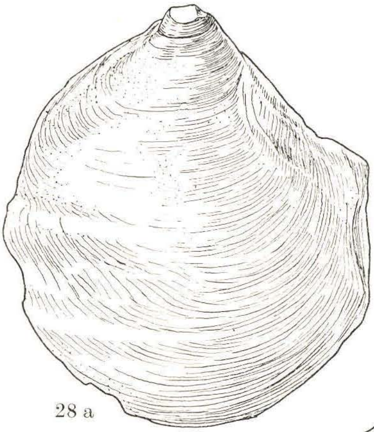
22

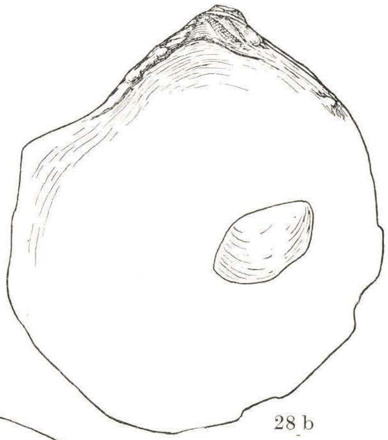
Th. S. del.

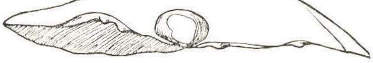
Plate 9.

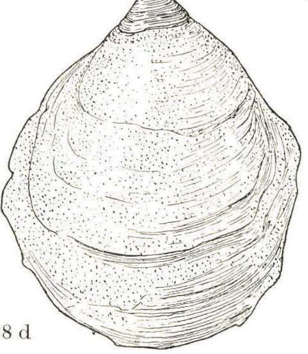
	Location	Depth	Length	Height	Width	Page
28a–i. *Ostrea sp.*						82
a–c. Right valve. (×18).	Toftlund	100–105 m.	2.81	3.2	0.62	
d–f. Right valve. (×18).	Toftlund	100–105 -	2.17	2.68	0.69	
g–i. Right valve. (×25).	Toftlund	75–100 -				

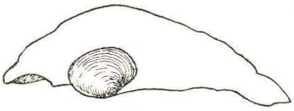
Shell dimensions in millimeters.

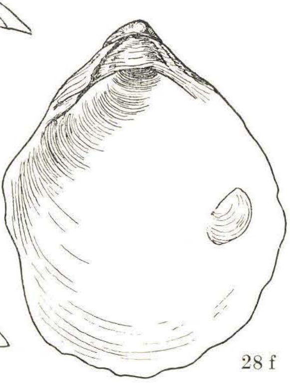

28 a

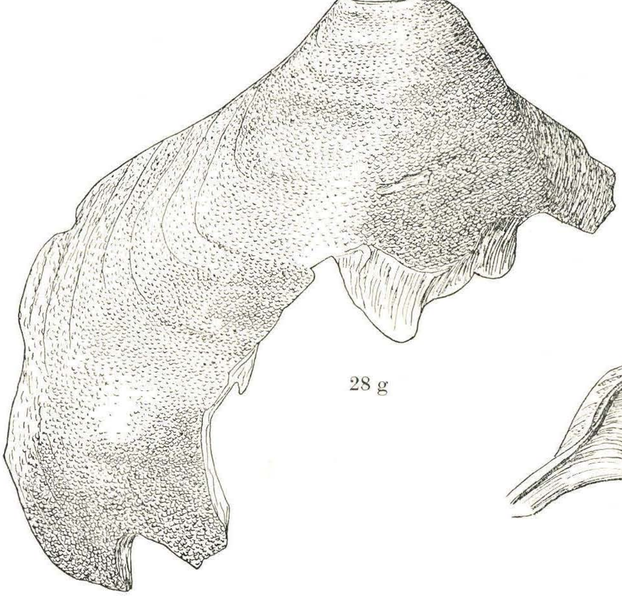

28 b

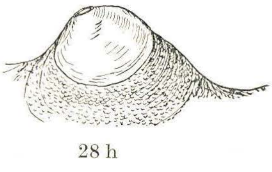

28 c

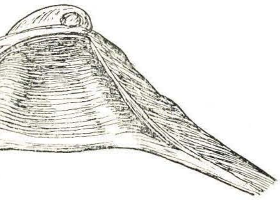

28 d


28 e


28 f


28 g


28 h

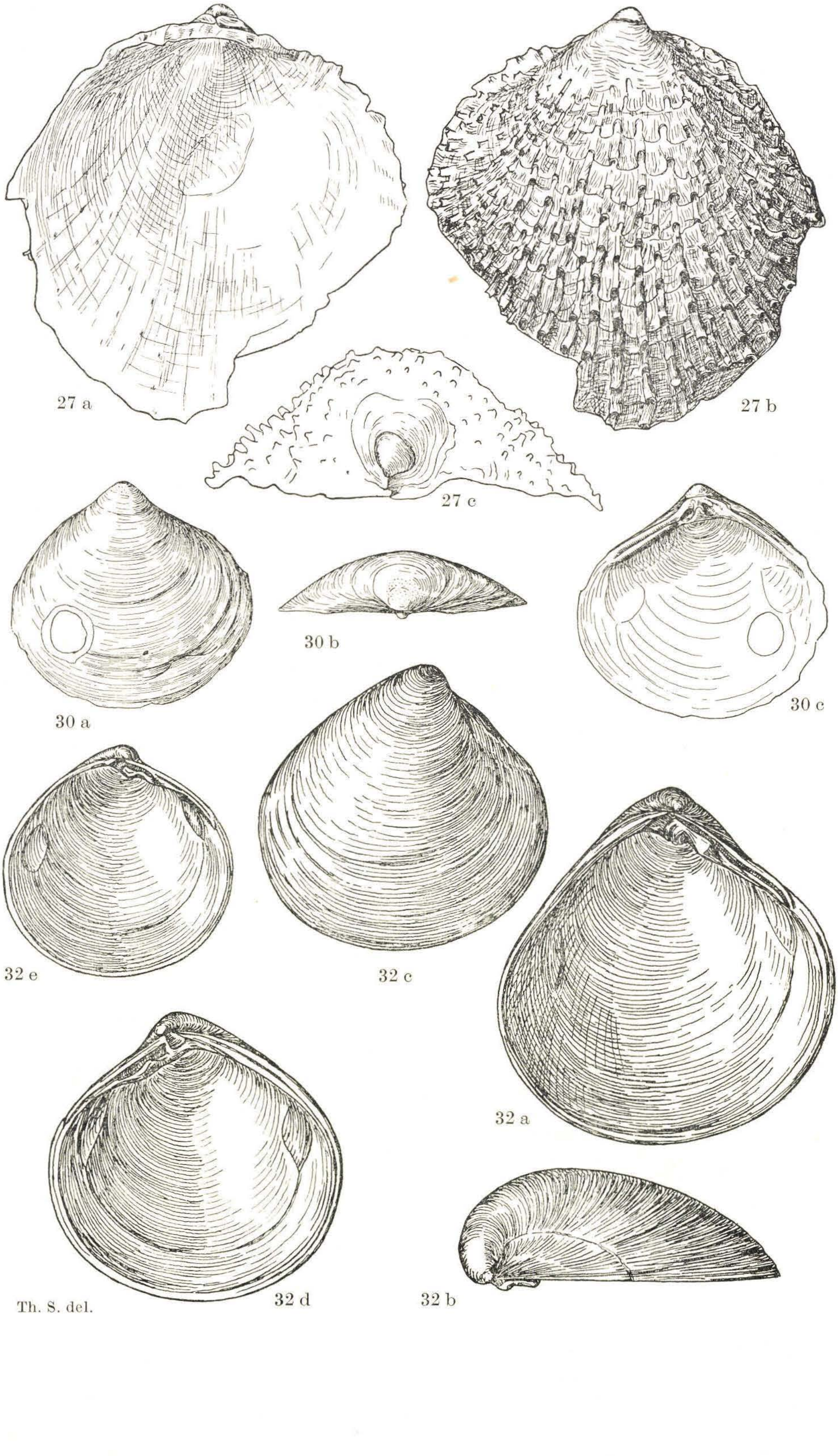

28 i

Th. S. del.

Plate 10.

	Location	Depth	Length	Height	Width	Page
27a–c. *Anomia squamula* LINNÉ Left valve. (×17.5).	Toftlund	100–105 m.	3.45	3.56	1.33	80
30a–c. *Astarte (Goodallia) triangularis* (MONTAGU) (×20).	Toftlund	110–115 -	2.3	1.76	0.47	84
32a–e. *Kellyella (Lutetia) rotunda nov. sp.*	Arnum (13)	53–83 -				86
a–b. Left valve. (×30).			1.71	1.75	0.6	
c–d. Right valve. (×30). Holotype.			1.50	1.46		
e. Left valve. (×30).			1.16	1.16		

Shell dimensions in millimeters.

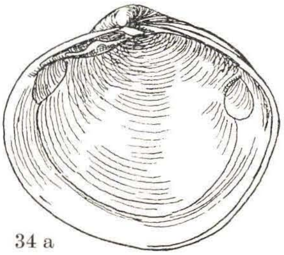


Th. S. del.

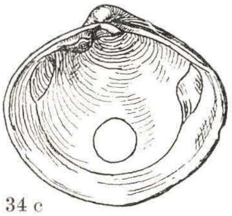
Plate 11.

		Location	Depth	Length	Height	Page
33a–b.	*Kellyella patera nov. sp.*	Arnum (13)	53–83 m.			87
	Right valve. (×28.5).			0.98	1.00	
	Holotype.					
34a–f.	*Isocardia sp.*	Arnum (13)	53–83 -			88
a–b.	Right valve. (×32).			1.14	1.00	
c–d.	Right valve. (×30).			1.00	0.91	
e–f.	Left valve. (×30).			1.12	1.02	
35a–b.	*Sportella cimbrica* KAUTSKY	Toftlund	75–100 -	5.2	3.8	89
	Left valve. (×12).					
36a–b.	*Thyasira cf. flexuosa* (MONTAGU)	Glejbjerg	53.5 -	3.78	3.65	89
	Left valve. (×15).					

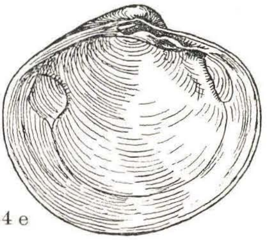
Shell dimensions in millimeters.



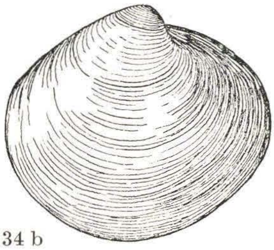
34 a



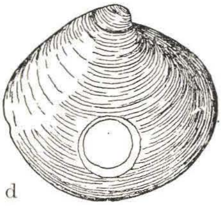
34 c



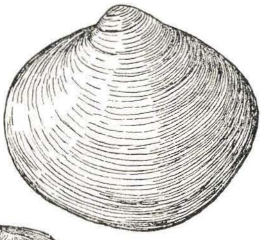
34 e



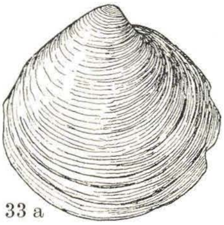
34 b



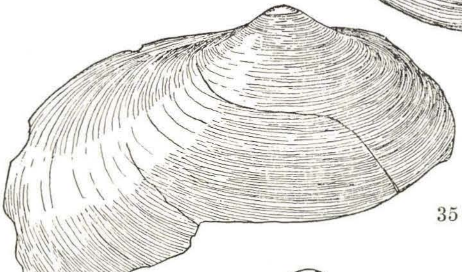
34 d



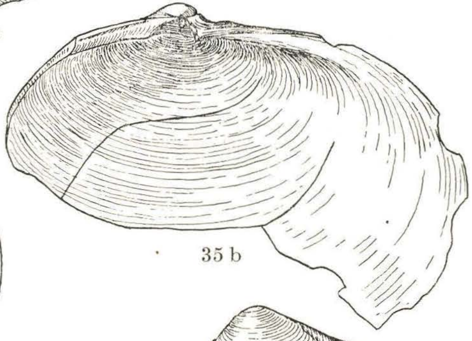
34 f



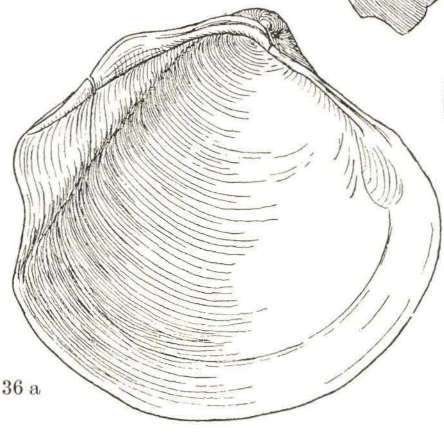
33 a



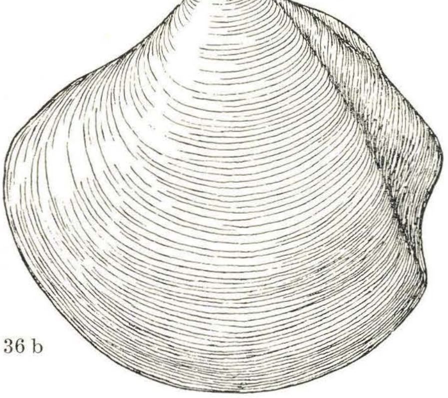
35 a



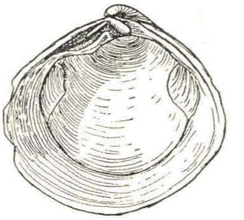
35 b



36 a



36 b



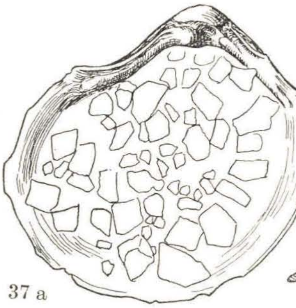
Th. S. del.

33 b

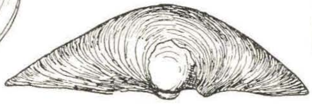
Plate 12.

		Location	Depth	Length	Height	Width	Page
37a–c.	*Phacoides cf. Schloenbachi.* (von Koenen). Right valve. (×40).	Toftlund	110–115 m.	1.05	0.9	0.30	91
38a–c.	*Loripes cf. niveus* (Eichwald) Right valve. (×30).	Arnum (13)	53–83 -	1.1	1.08	0.33	91
39a–b.	*Lucina (Loripinus) Nörregaardi nov. sp.* Right valve. (×15). (cf.)	Toftlund	75–100 -	abt. 4			92
c–e.	Right valve. (×40). Holotype.	Toftlund	110–115 -	1.35	1.24	0.37	

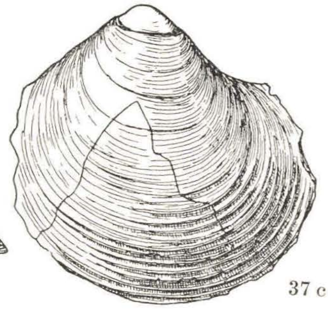
Shell dimensions in millimeters.



37 a

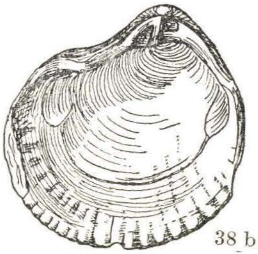


37 b

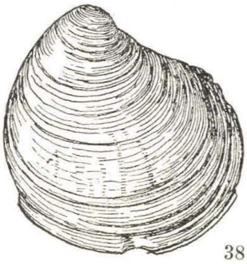


37 c

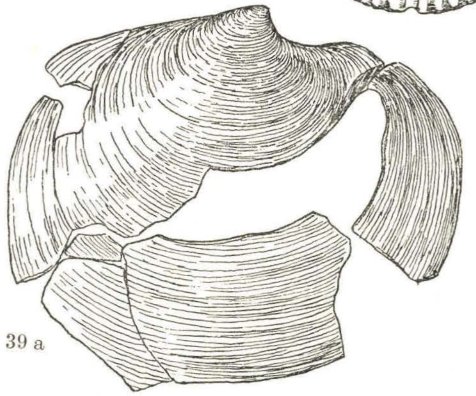
38 a



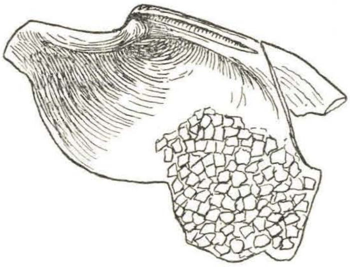
38 b

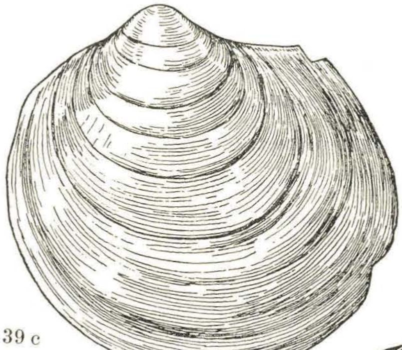


38 c



39 a





39 c

39 d

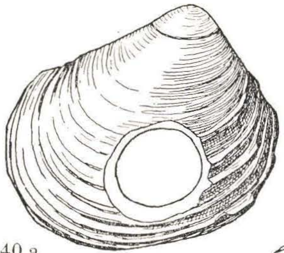
39 e

Th. S. del.

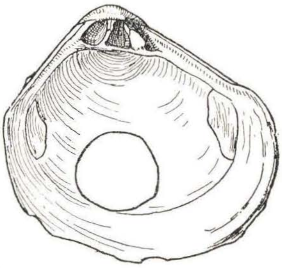
Plate 13.

		Location	Depth	Length	Height	Width	Page
40a–h.	*Codokia jutensis nov. sp.*	Toftlund	110–115 m.				93
a–d.	Paired valves. (×39).			0.94	0.84		
a–b.	Left valves. (×39).						
c–e.	Right valve. (×39).					0.25	
f–h.	Left valve, holotype. (×19).			2.70	2.41	0.59	
42a–b.	*Erycina (Scacchia) Degrangei* Cossmann & Peyrot.						
	Right valve. (×30).	Arnum (13)	53–83 -	1.76	1.41	0.44	94
43a–b.	*Erycina (Hemilepton) coarctata* (Wood).						
	Right valve. (×30).			1.56	0.98	0.27	96

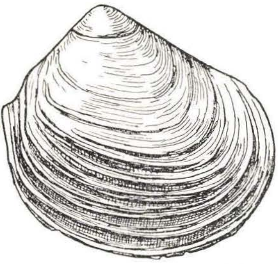
Shell dimensions in millimeters.



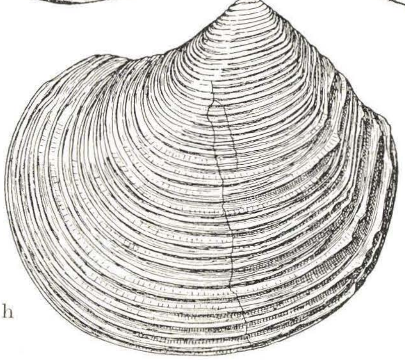
40 a



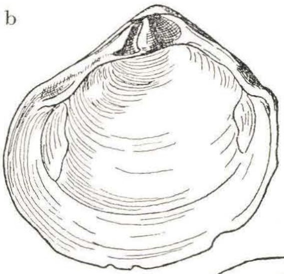
40 b



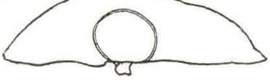
40 c



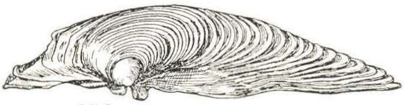
40 h



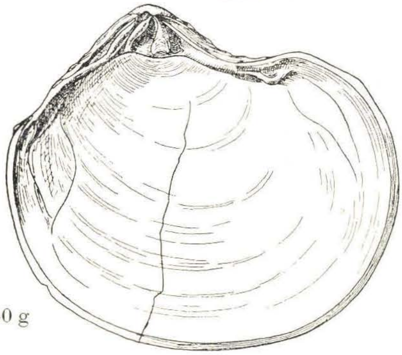
40 d



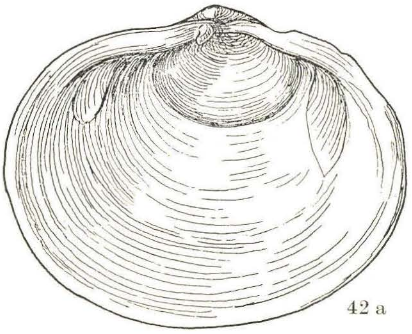
40 e



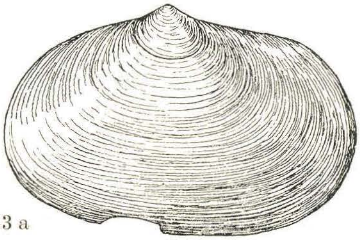
40 f



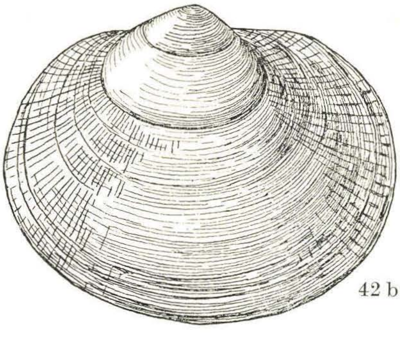
40 g



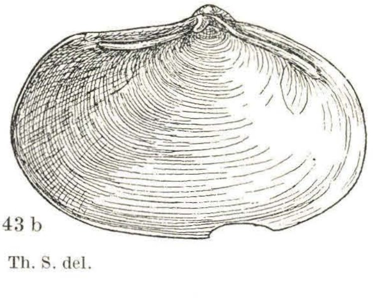
42 a



43 a



42 b



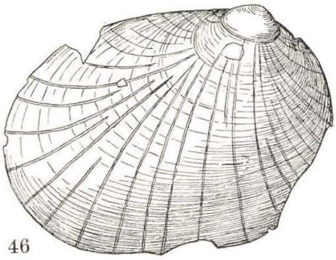
43 b

Th. S. del.

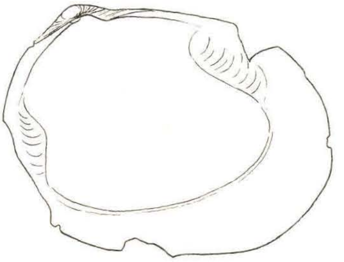
Plate 14.

	Location	Depth	Length	Height	Width	Page
46a–b. *Montacuta substriata* (MONTAGU) (× 33)	Gramby	84.66–87.16 m.	1.24	1.14	0.255	99
50a–b. *Cardium cf. hanseatum* KAUTSKY Right valve. (×21).	Toftlund	75–100 -	2.8	2.8	0.94	104
51a–c. *Gouldia minima* (MONTAGU)						
a–b. Left valve. (×16).	Toftlund	75–100 -	3.17	2.95	0.69	105
c. Right valve. (×16).	Arnum (13)	53–83 -	2.33	2.25	0.59	

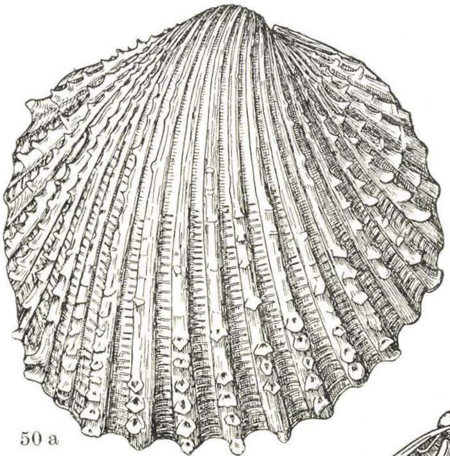
Shell dimensions in millimeters.



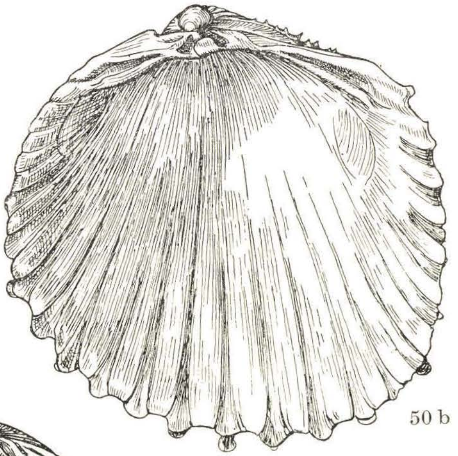
46



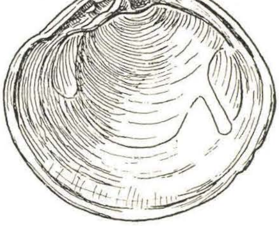
46 b



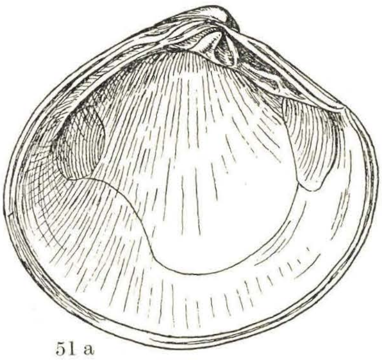
50 a



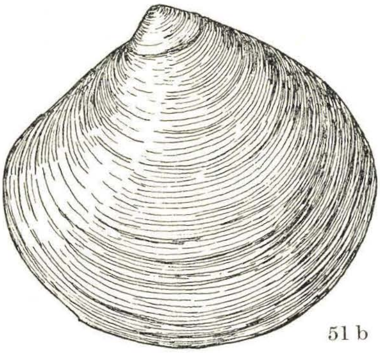
50 b



51 c



51 a



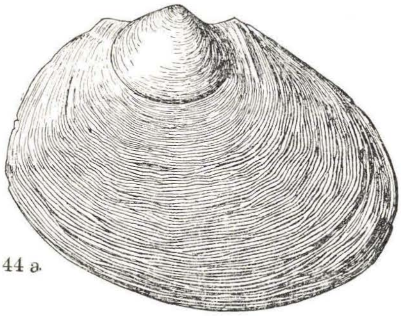
51 b

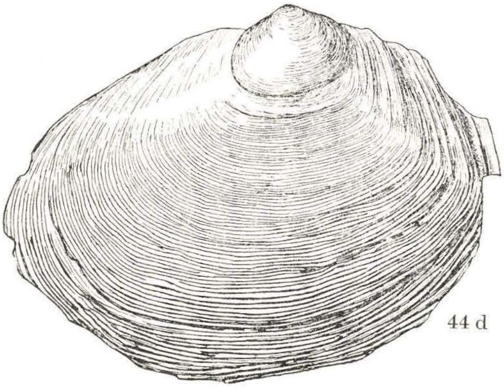
Th. S. del.

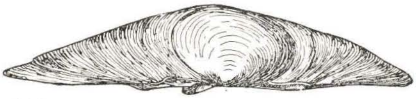
Plate 15.

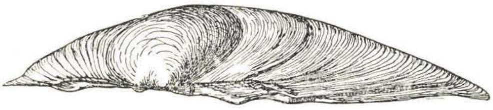
		Location	Depth	Length	Height	Width	Page
44a–f.	*Erycina (Hemilepton) striatissima* (Cerulli-Irelli)	Toftlund	105–110 m.				97
a–c.	Left valve. (×30).			1.8	1.41	0.33	
d–f.	Right valve. (×30).			2.2	1.6	0.40	
45a–b.	*Lepton nitidum* Turton (×16).	Toftlund	75–100 -	abt. 3.2	2.5		98

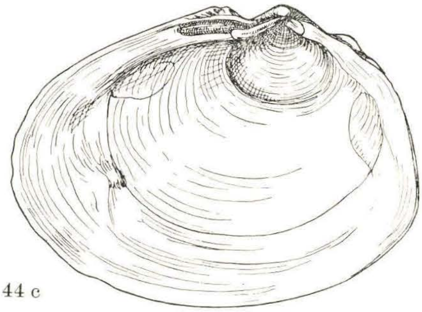
Shell dimensions in millimeters.

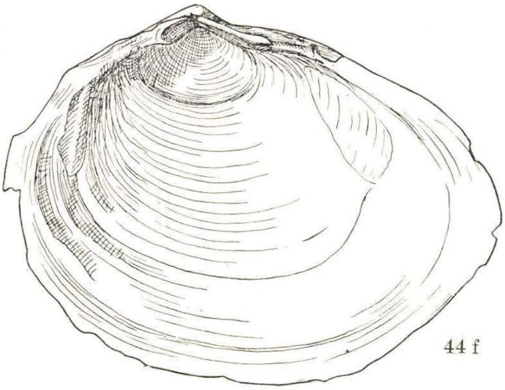

44 a

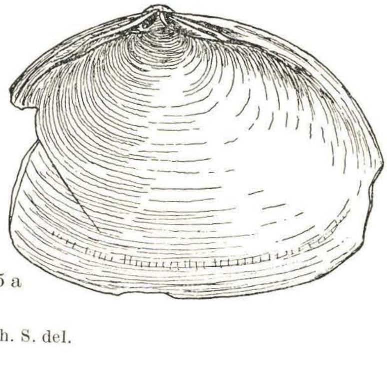

44 d

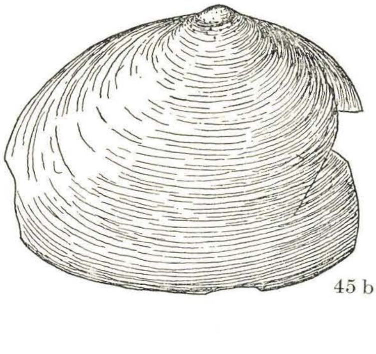

44 b


44 e


44 c


44 f


45 a

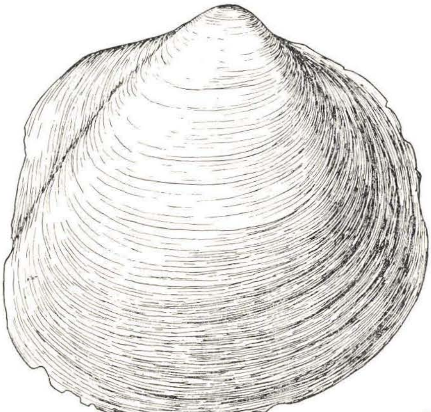

45 b

Th. S. del.

Plate 16.

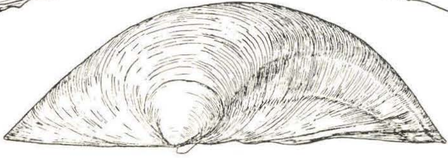
		Location	Depth	Length	Height	Width	Page
48a–e.	*Laevicardium dingdense* (LEHMANN)						101
a–c.	Juvenile shell, right valve. (×30).	Toftlund	105–110 m.	1.93	1.89	0.65	
d–e.	Adult shell, right valve. (×10.5).	Toftlund	75–100 -		ca. 6.25		
49a–b.	*Cardium Straeleni* GLIBERT						102
	Right valve. (×30).	Toftlund	75–100 -	1.49	1.45	0.51	

Shell dimensions in millimeters.



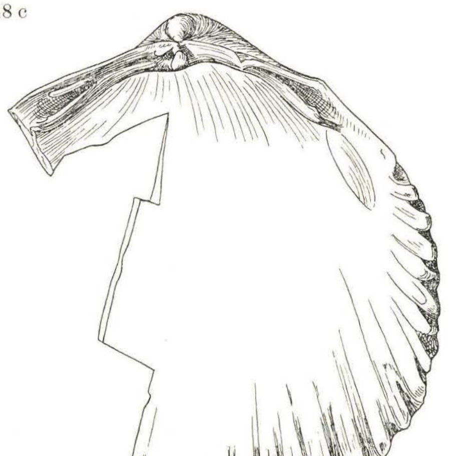
48 a

48 b

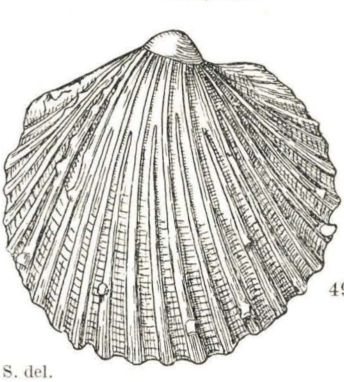


48 c

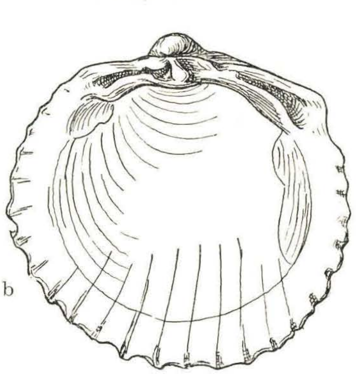
48 d



48 e



49 a



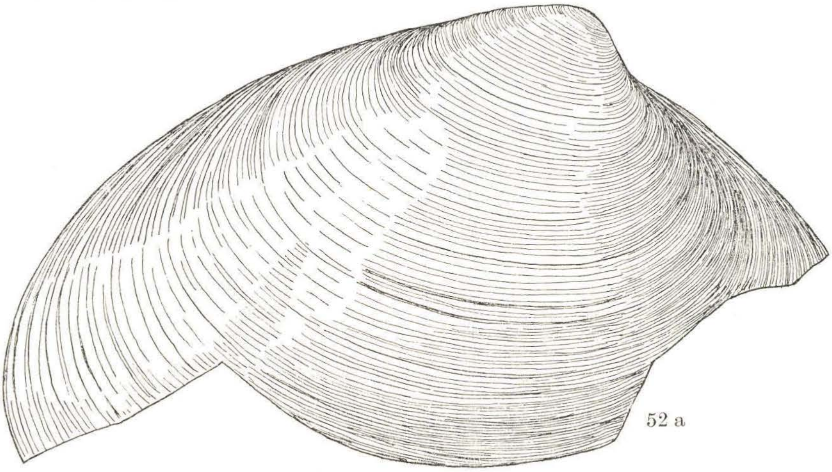
49 b

Th. S. del.

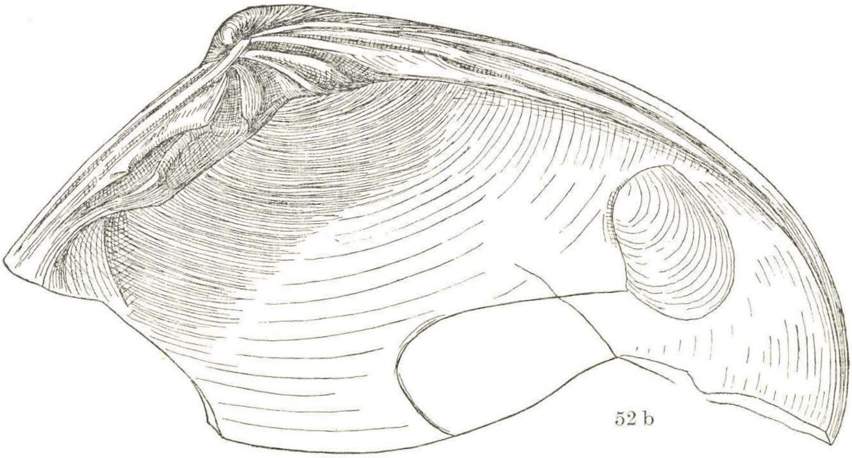
Plate 17.

	Location	Depth	Length	Height	Page
52a–b. *Pitar chione* (LINNÉ) Fragment of right valve. (×12.5).	Toftlund	75–100 m.	8.55		107
53a–b. *Meretrix cf. incrassata* (SOWERBY) Left valve. (×15).	Toftlund	75–100 -	3.73	3.40	108

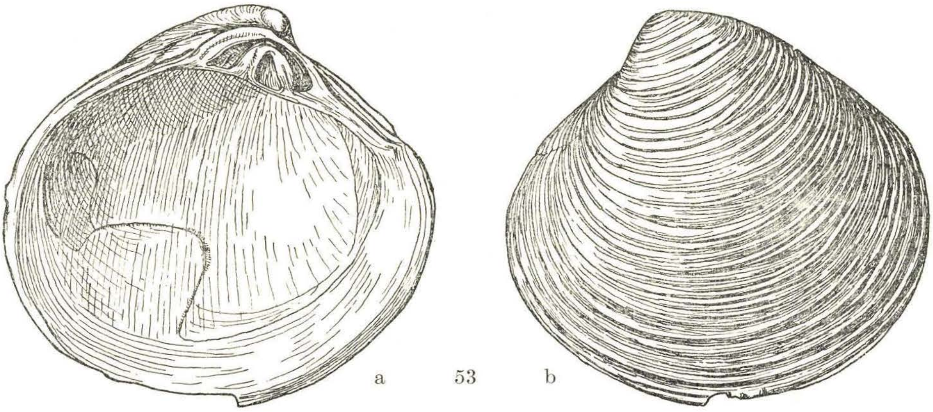
Shell dimensions in millimeters.



52 a



52 b



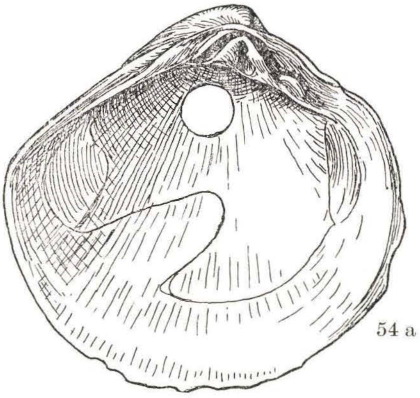
a 53 b

Th. S. del.

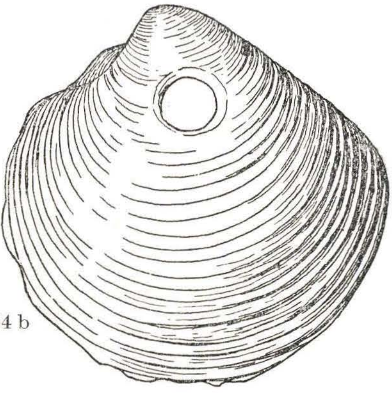
Plate 18.

	Location	Depth	Length	Height	Width	Page
54a–b. *Dosinia cf. Basteroti* (Agassiz). Left valve. (×15.5).	Toftlund	75–100 m.	3.40	3.29	0.90	110
55a–d. *Venus (Ventricola) multilamella* (Lamarck)	Toftlund	75–100 -				111
a–c. Right valve. (×15).			3.27	3.1	0.9	
d. Left valve. (×15).			2.19	2.12	0.6	
56a–d. *Ervilia pusilla* (Philippi)	Arnum (13)	53–83 -				113
a–c. Right valve. (×15.5).			2.25	1.81	0.6	
d. Left valve. (×15.5).			2.0	1.5		

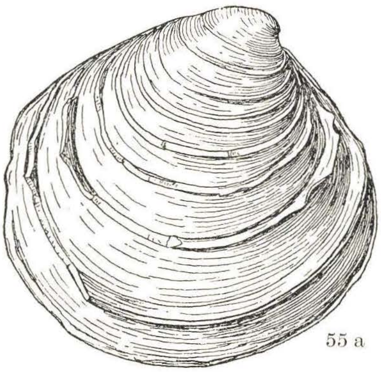
Shell dimension in millimeters.



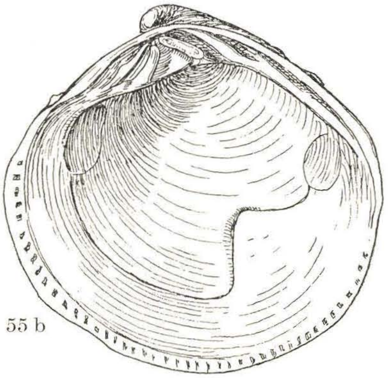
54 a



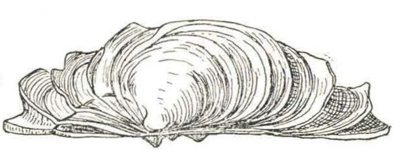
54 b



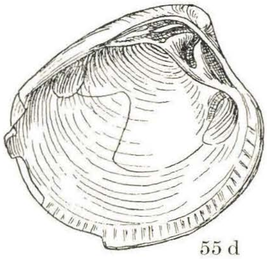
55 a



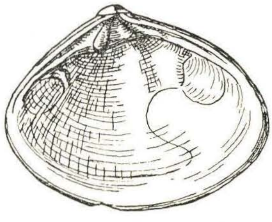
55 b



55 c



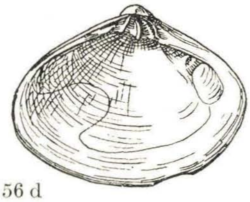
55 d



56 b

56 a

56 c



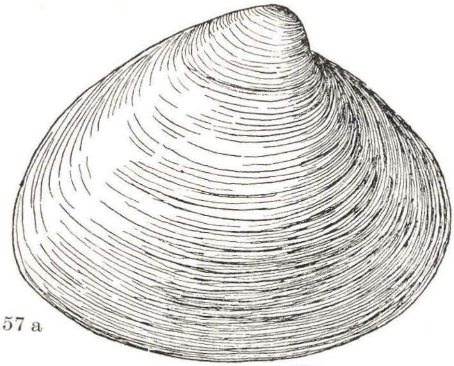
56 d

Th. S. del.

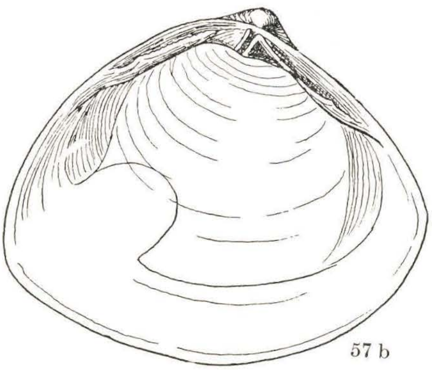
Plate 19.

		Location	Depth	Length	Height	Page
57a–c.	*Spisula subtruncata* (Da Costa) *var.*	Toftlund	75–100 m.			114
a–b.	Right valve. (×15)			3.90	3.15	
c.	Left valve. (×15).			3.70	3.15	
58.	*Spisula solida* (Linné)	Toftlund	75–100 -			117
	Left valve. (×10.5).			7.24	5.08	
60.	*Abra prismatica* (Montagu) *var.*	Toftlund	115 -			119
	Right valve. (×10.5).			10.6	6.7	

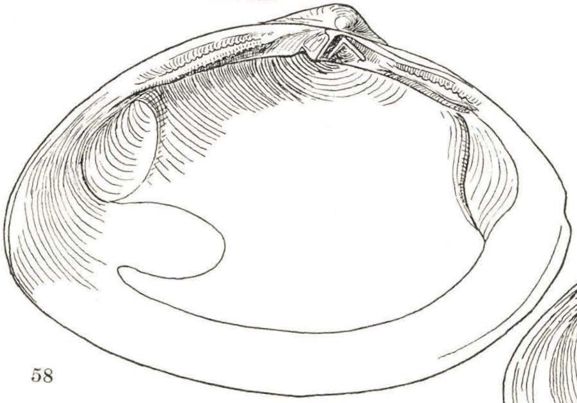
Shell dimensions in millimeters.



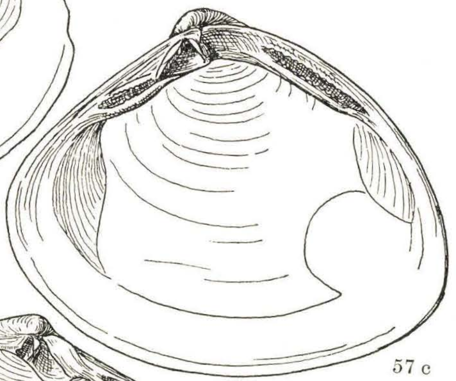
57 a



57 b



58



57 c

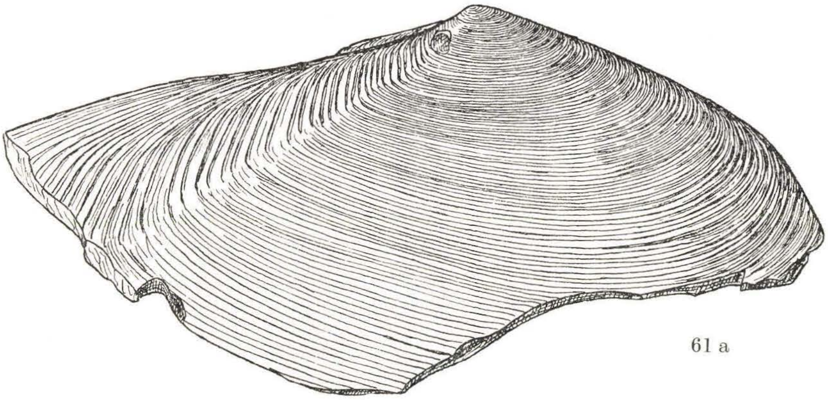
60

Th. S. del.

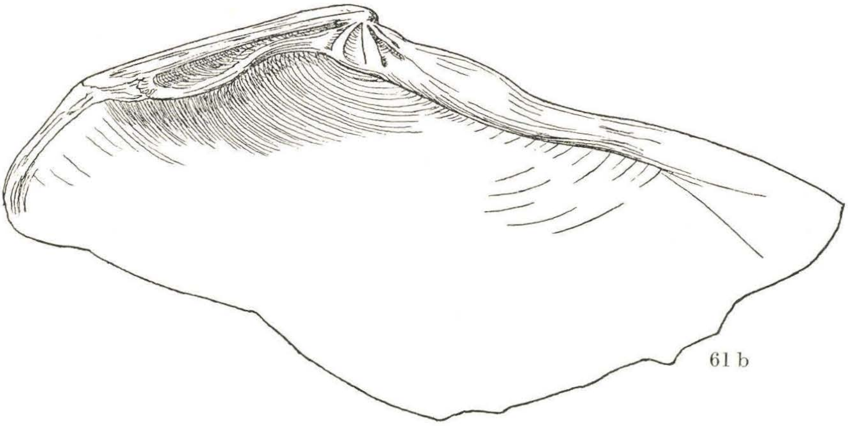
Plate 20.

		Location	Depth	Length	Height	Width	Page
61a–b.	*Angulus donacinus* (LINNÉ) Fragment of left valve. (×15).	Glejbjerg	55 m.	7.55			120
66a–e.	*Saxicava arctica* (LINNÉ)	Toftlund	75–100 -				125
a–b.	Right valve. (×13).			3.25	1.83		
c–d.	Left valve. (×13).			3.40	1.83	1.8	

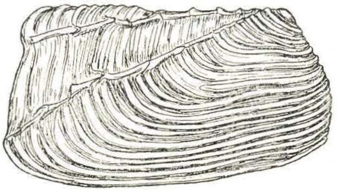
Shell dimensions in millimeters.



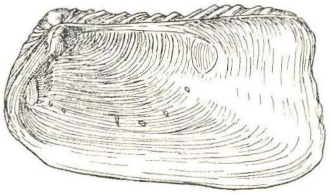
61 a



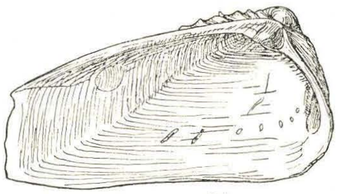
61 b



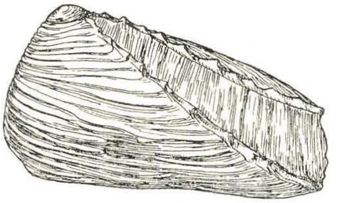
66 a



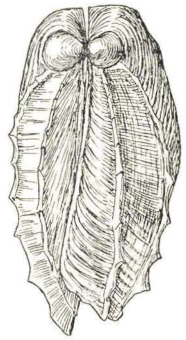
67 b



66 c



66 d



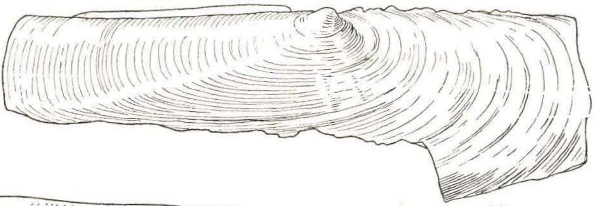
66 e

Th. S. del.

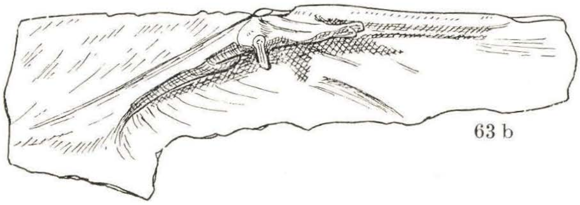
Plate 21.

		Location	Depth	Length	Page
63a–c.	*Pharus saucatsensis* (DES MOULINS)	Gramby	82.66–83.76 m.		123
	Right valve. (×10.5).			7.23	
65a–b.	*Ensis Degrangei* COSSMANN & PEYROT	Gramby	90.42–92.72 -		124
	Left valve. (×20).			3.62	

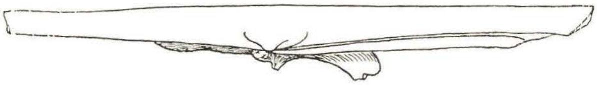
Shell dimensions in millimeters.



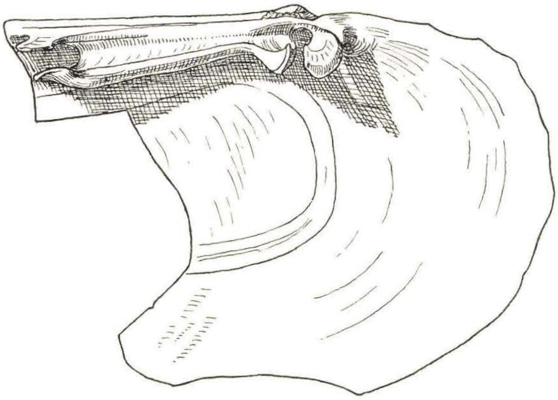
63 a



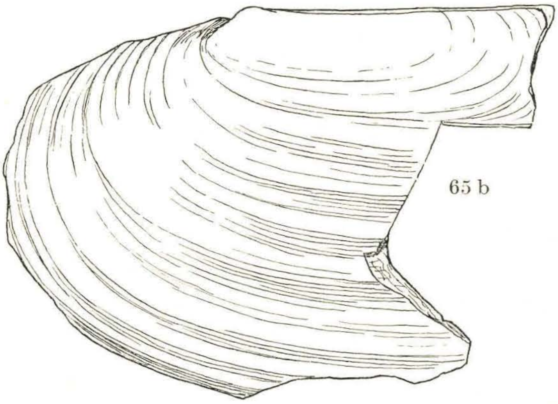
63 b



63 c



65 a



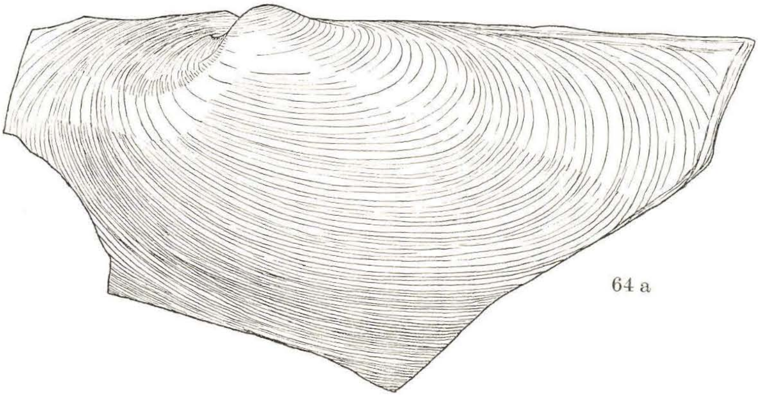
65 b

Th. S. del.

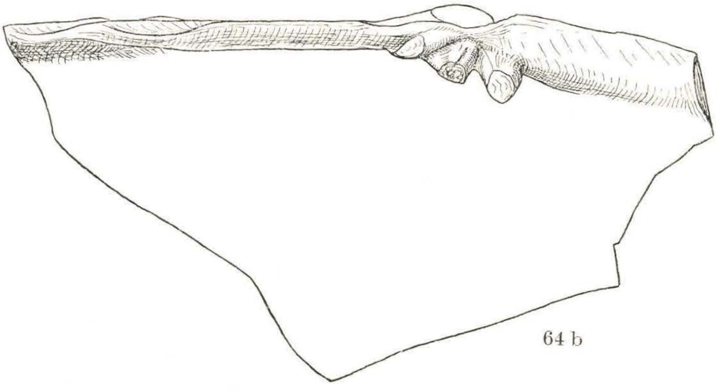
Plate 22.

	Location	Depth	Length	Page
64a–b. *Cultellus sp.* (×37).	Arnum (25b)	62.7–62.9 m.	2.52	124

Shell dimensions in millimeters.



64 a



64 b

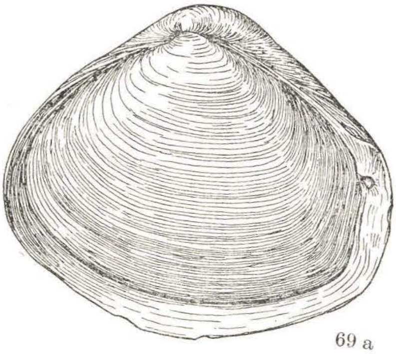
Th. S. del.

Plate 23.

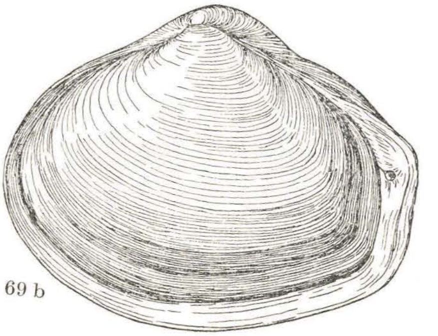
		Location	Depth	Length	Height	Page
69a–h.	*Varicorbula gibba* (OLIVI)	Toftlund	75–100 m.			129
a. b.	Paired valves with marginal pore in right valve. (×12.8).			4.06	3.49	
c–d.	Right valve with marginal pore. (×12.8).			4.27	3.45	
e.	Fragment of right valve with marginal pore. (×15.5).			4.54	3.99	
f.	Same fragment with detached internal shell layer showing the trend of the marginal pore in the outer shell layer. (×15.5).			3.65		
g–h.	Left valve. (×15.5).			3.15	2.62	

Shell dimensions in millimeters.

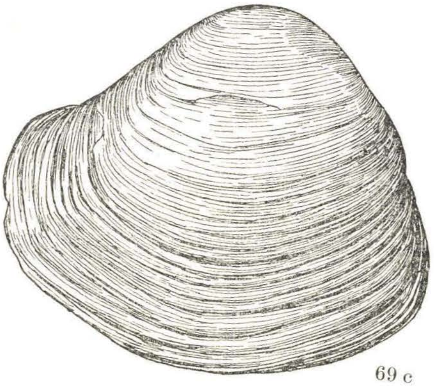
Plate 23



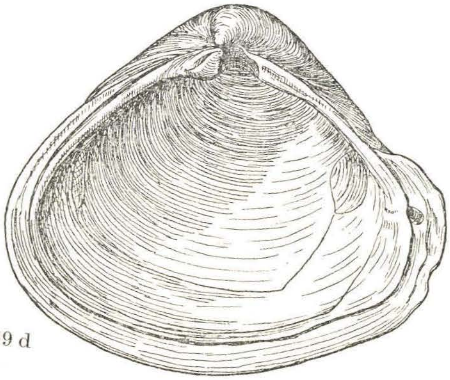
69 a



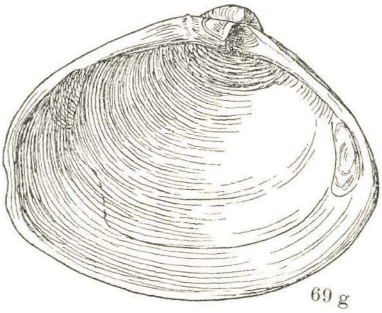
69 b



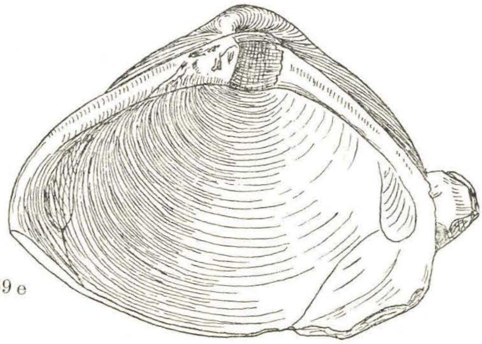
69 c



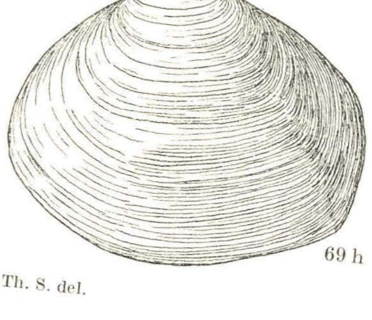
69 d



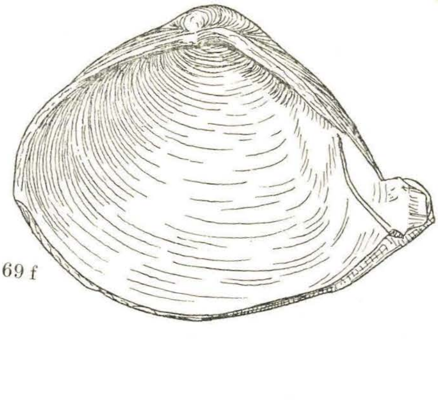
69 g



69 e



69 h



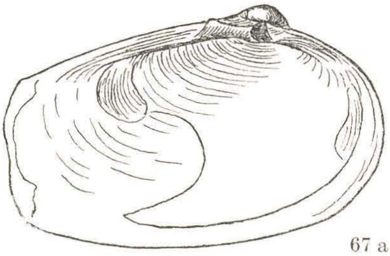
69 f

Th. S. del.

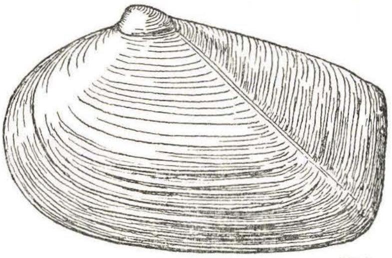
Plate 24.

		Location	Depth	Length	Height	Width	Page
67a–c.	*Saxicavella pusilla nov. sp.* Left valve. Holotype. (×30).	Toftlund	75–100 m.	1.6	1.05	0.31	128
70a–c.	*Lentidium donaciformis* (Nyst)						133
	Left valve. (×30).	Glejbjerg	25 -	1.84	1.16	0.42	
	Right valve. (×21).	Gramby	84.66–87.16 -	2.23	1.51		
76a–e.	*Pandora copiosa nov. sp.*						138
a–c.	Left valve. Holotype. (×9).	Toftlund	105–110 -	6.10	3.28	1.21	
d–e.	Right valve. (×17.5)	Toftlund	100–105 -	1.73	0.92		

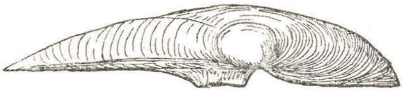
Shell dimensions in millimeters.



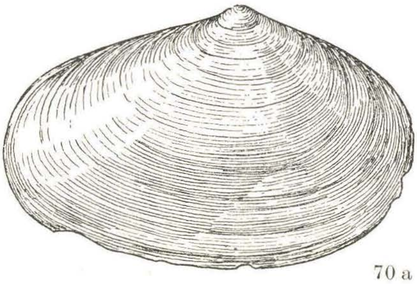
67 a



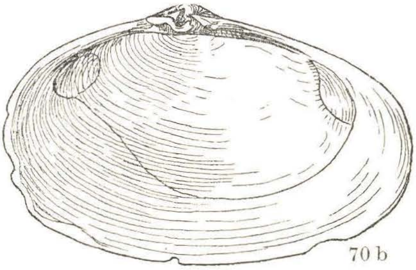
67 b



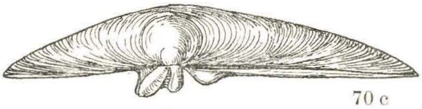
67 c



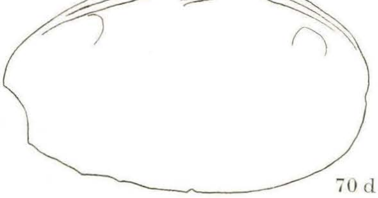
70 a



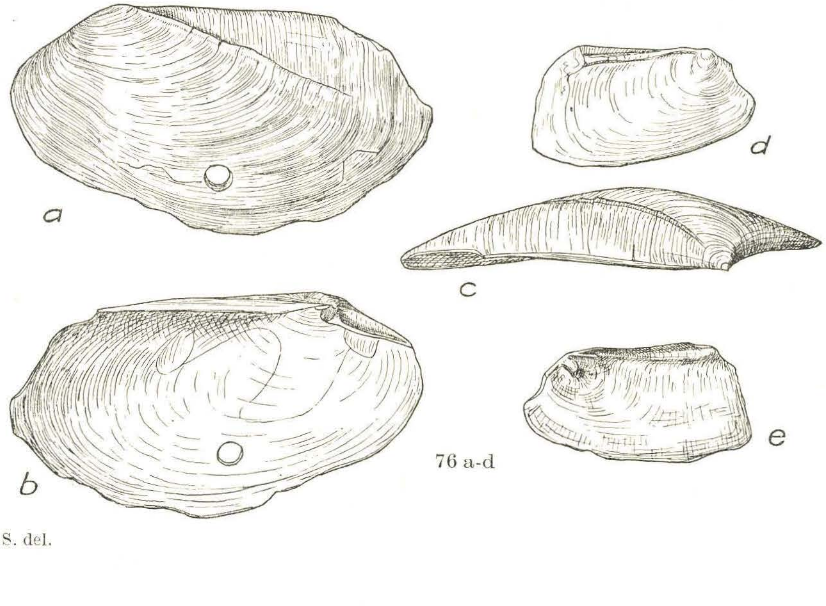
70 b



70 c



70 d



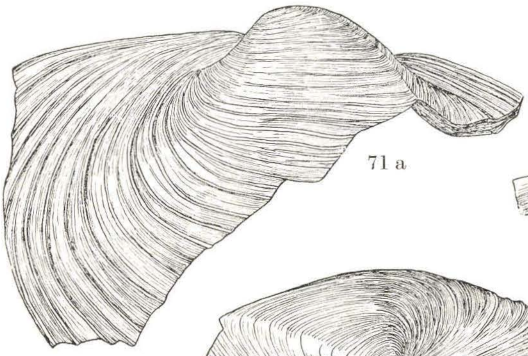
76 a-d

Th. S. del.

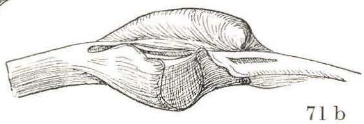
Plate 25.

	Location	Depth	Length	Height	Page
71a–c. *Sphenia sp.*	Toftlund	105–110 m.			134
Left valve (×21).			3.0		
72a–b. *Pholas sp.*	Arnum(25b)	62.7–62.9 -			135
Left valve. (×21).			1.85		
73a–b. *Pholadidea sp.*	Toftlund	110–115 -			135
Left valve. (×21).			1.49		
74a–b. *Martesia cf. rugosa* (BROCCHI). (×21).	Toftlund	105–110 -	1.41	1.45	136

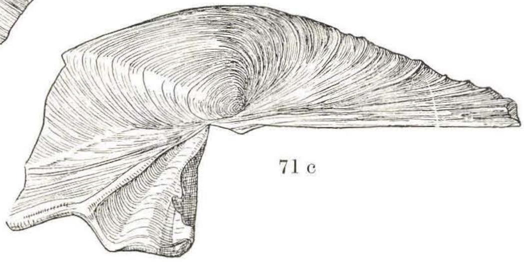
Shell dimensions in millimeters.



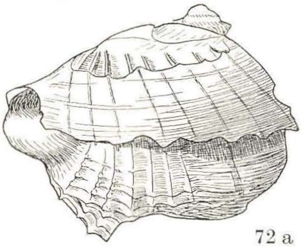
71 a



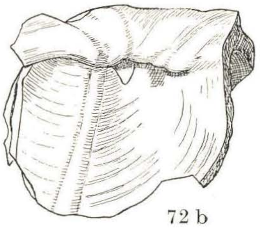
71 b



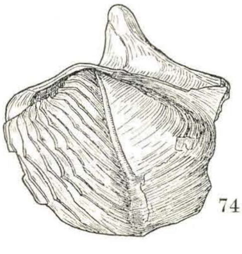
71 c



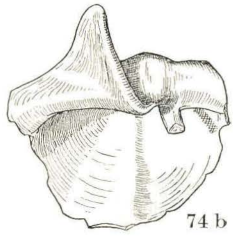
72 a



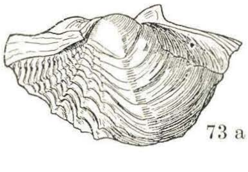
72 b



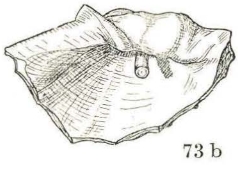
74 a



74 b



73 a



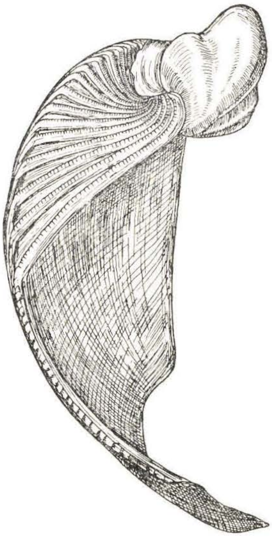
73 b

Th. S. del.

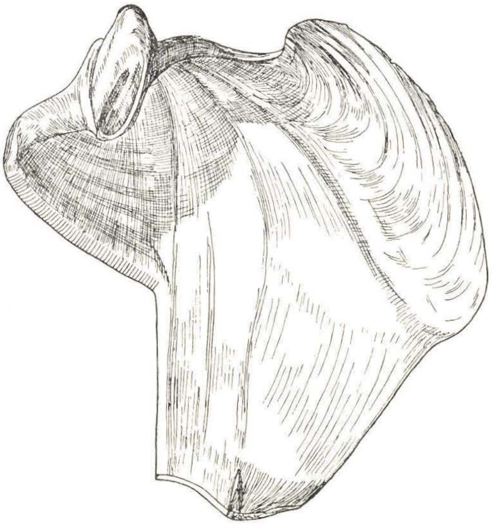
Plate 26.

	Location	Depth	Length	Height	Width	Page
75a–c. *Teredo cf. saucatsensis* BENOIST. (×32).	Toftlund	105–110 m.	1.97	2.08	0.77	137

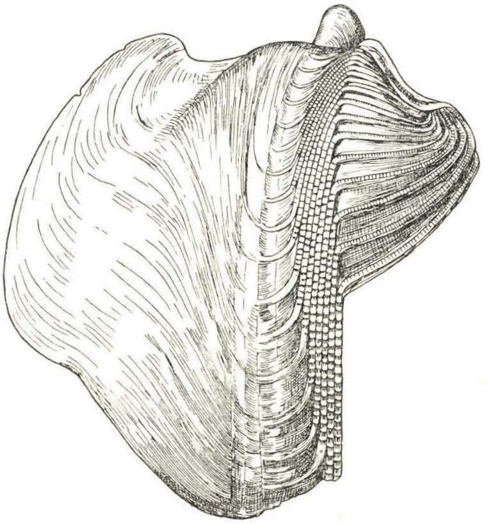
Shell dimensions in millimeters.



75 a



75 b



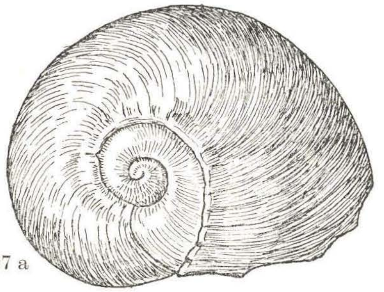
75 c

Th. S. del.

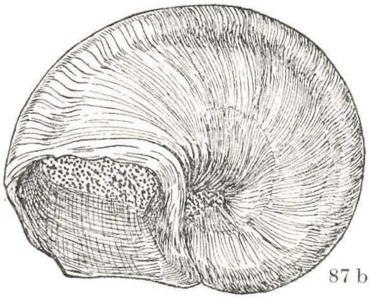
Plate 27.

		Location	Depth	Diameter	Height	Page
87a–c.	*Starkeyna hanseata* (KAUTSKY). (×31).	Toftlund	75–100 m.	1.56	0.68	149
88a–c.	*Starkeyna jutensis nov. sp.* (×25). Holotype.	Toftlund	105–110 -	1.64	0.61	150
90a–c.	*Liotia miosuturalis* KAUTSKY. (×15).	Glejbjerg	55 -	2.3	1.65	152
91a–c.	*Alvania Partschi* HÖRNES. (×30).	Arnum (13)	53–83 -	0.77	1.16	153
d–e.	*Alvania Partschi* HÖRNES. (×26).	Toftlund	75–100 -	1.06	1.96	153

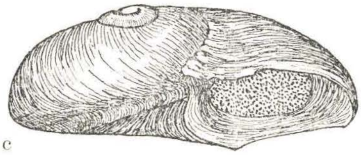
Shell dimensions in millimeters.



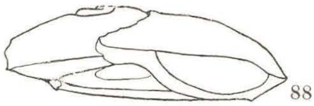
87 a



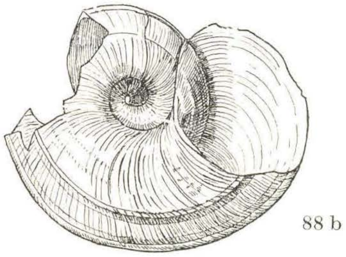
87 b



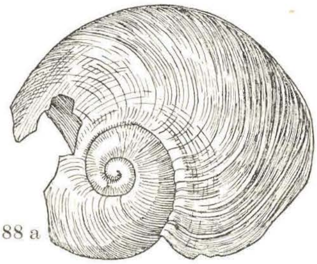
87 c



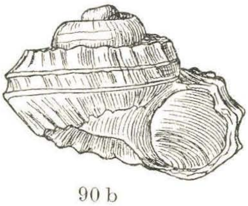
88 c



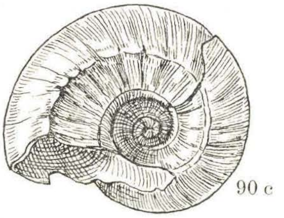
88 b



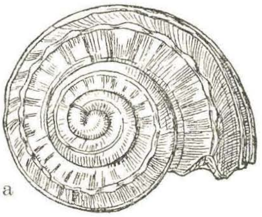
88 a



90 b



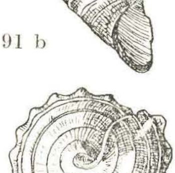
90 c



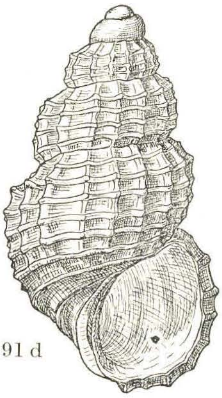
90 a

91 b

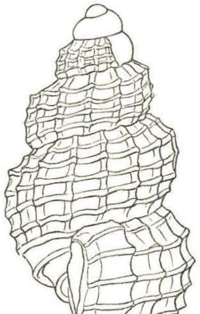
91 a



91 c



91 d



91 e

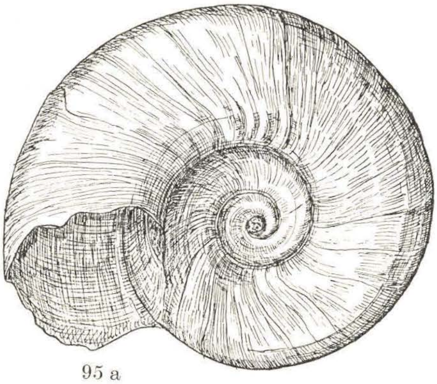
Th. S. del.

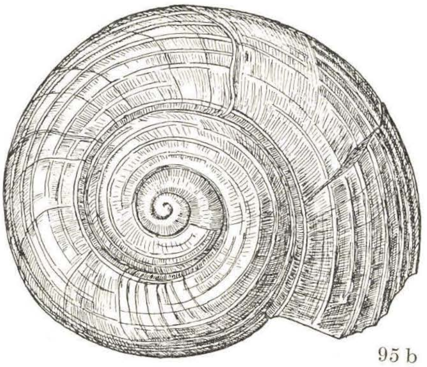
Plate 28.

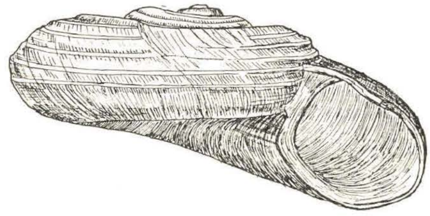
	Location	Depth	Diameter	Height	Page
95a–c. *Adeorbis subcirculus* (Cossmann & Peyrot). (×22.5).	Toftlund	75–100 m.	2.54	1.12	157
96a–c. *Adeorbis cf. carinata* (Philippi) (×25).	Toftlund	75–100 -	2.14	0.97	158
97a–c. *Adeorbis planorbillus* (Dujardin). (×27).	Arnum (13)	53–83 -	1.47	0.74	159

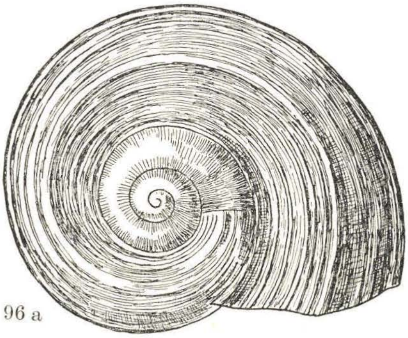
Shell dimensions in millimeters.

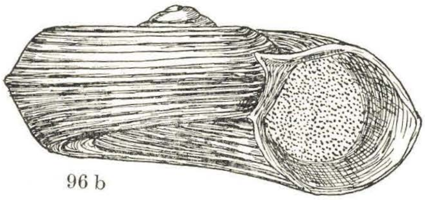
Plate 28

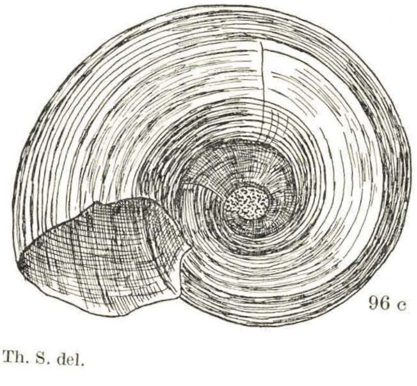

95 a

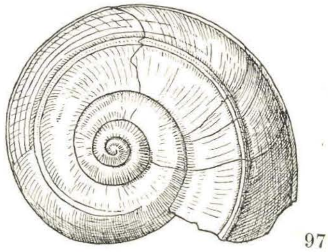

95 b

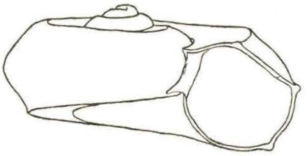

95 c

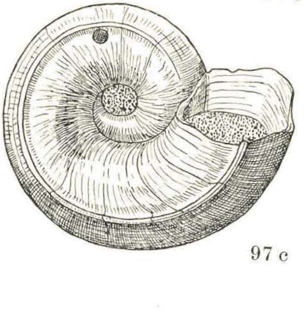

96 a


96 b


96 c


97 a


97 b


97 c

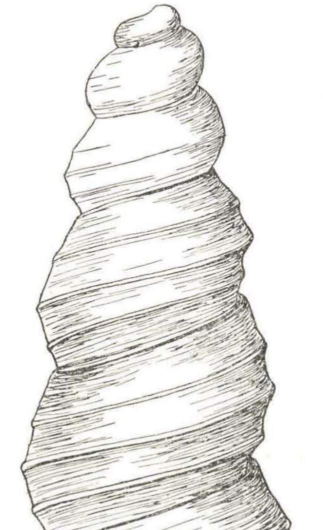
Th. S. del.

Plate 29.

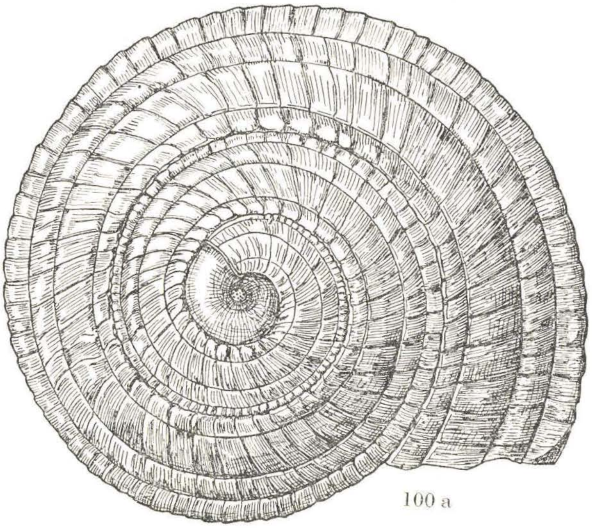
	Location	Depth	Diameter	Height	Page
98a–b. *Turritella tricarinata* (Brocchi). (×56).	Arnum (13)	53–83 m.	0.83	2.58	160
100a–c. *Solarium carocollatum* Lamarck. (×15).	Toftlund	75–100 -	5.23	1.95	162

Shell dimensions in millimeters.

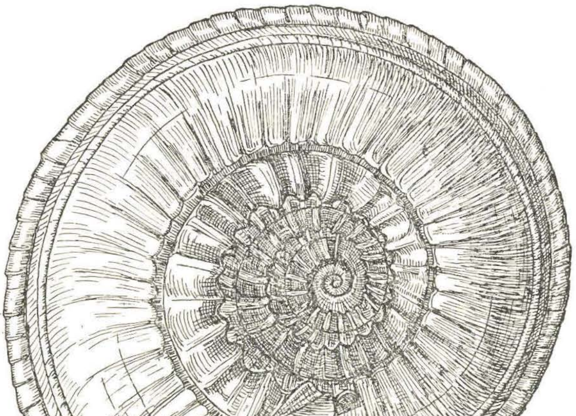
98 b



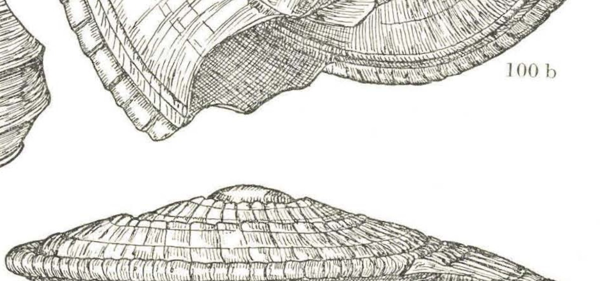
98 a



100 a



100 b



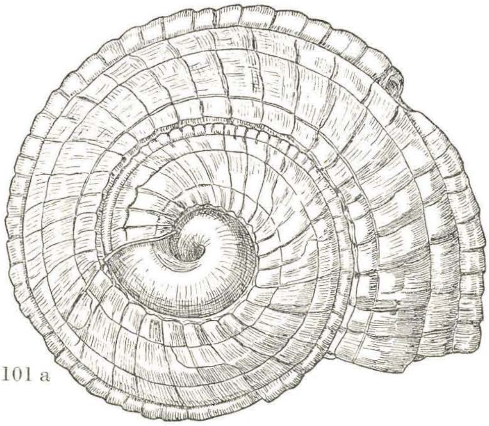
100 c

Th. S. del.

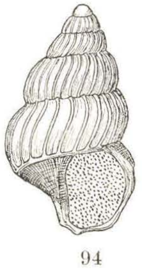
Plate 30.

		Location	Depth	Diameter	Height	Page
92.	*Rissoa Ravni nov. sp.* Holotype. (×60).	Arnum (13)	53–83 m.	0.81	1.02	154
94.	*Rissoina Ödumi nov. sp.* Holotype. (×27).	Arnum (25b)	62.7–62.9 -	0.65	1.14	156
99a–b.	*Turritella subangulata* (Brocchi). (×60).	Arnum (13)	53–83 -	0.50	0.83	161
101a–c.	*Solarium trochleare nov. sp.* Holotype. (×20.5).	Toftlund	100–105 -	3.14	1.40	163

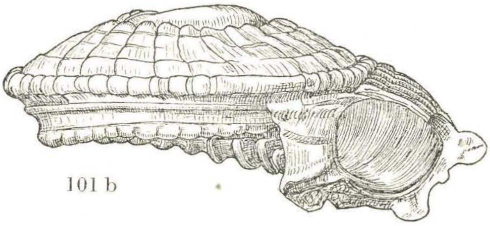
Shell dimensions in millimeters.



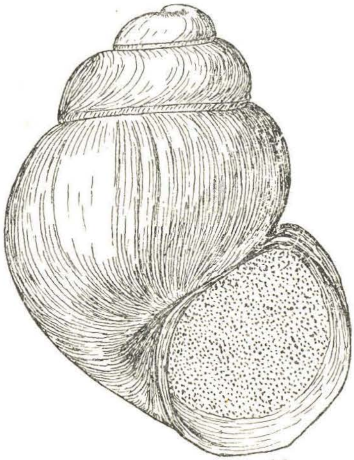
101 a



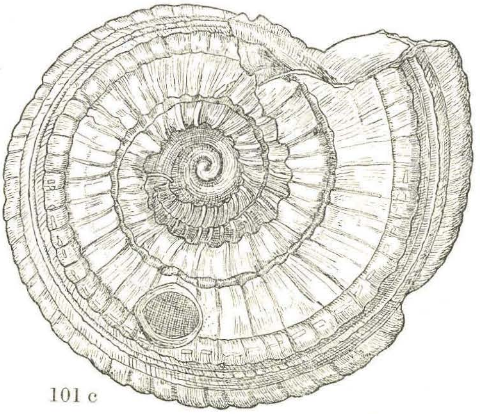
94



101 b

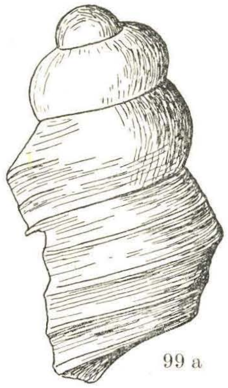


92



101 c

99 b



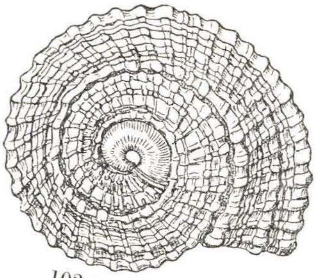
99 a

Th. S. del.

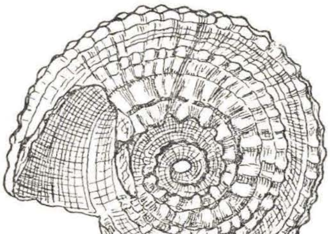
Plate 31.

		Location	Depth	Diameter	Height	Page
102a–d.	*Solarium angustiforatum* COSSMANN & PEYROT. (a–c × 15; d × 60).	Glejbjerg	53.5 m.	2.8	1.14	164
103.	*Bittium spina* (PARTSCH). (× 30).	Toftlund	75–100 -	1.66	4.52	165
104.	*Bittium tenuispina nov. sp.* Holotype. (× 29).	Toftlund	75–100 -	1.49	4.48	167
105a–b.	*Cerithiopsis Vignali* COSSMANN & PEYROT.					170
	a. (× 40).	Toftlund	110–115 -	0.74	1.96	
	b. (× 18).	Toftlund	105–110 -	0.83	2.35	

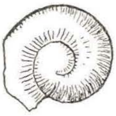
Shell dimensions in millimeters.



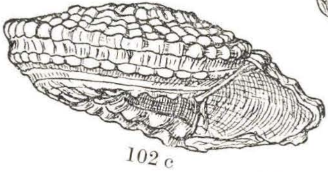
102 a



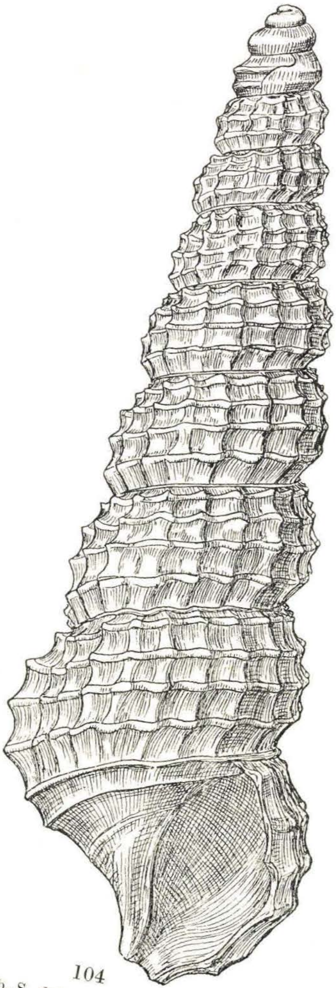
102 b



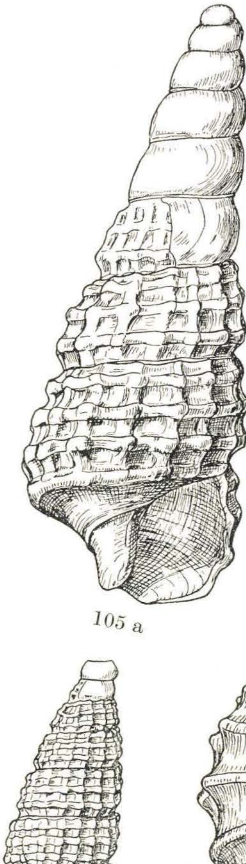
102 d



102 c

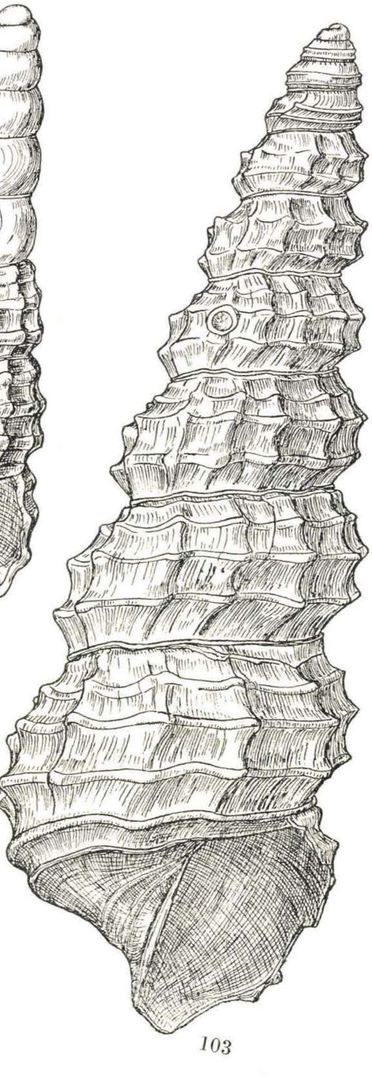


104



105 a

105 b



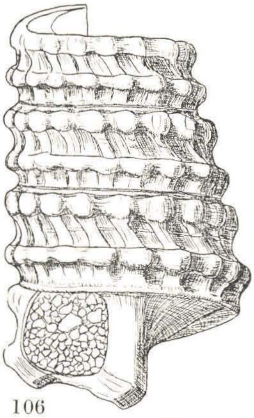
103

Th. S. del.

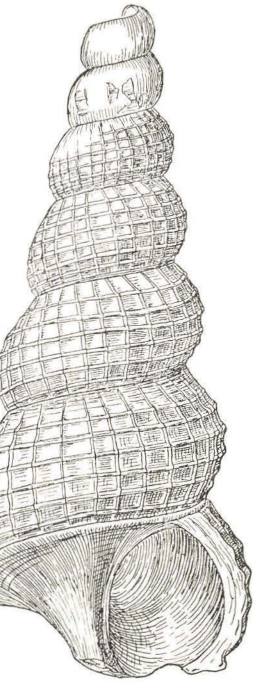
Plate 32.

		Location	Depth	Diameter	Height	Page
106.	*Triphora perversa* (Linné). (×30).	Toftlund	105–110 m.	1.16	1.77	171
107.	*Cirsotrema Thais* de Boury. (×25).	Toftlund	75–100 -	2.83	4.60	173
109.	*Scala* (*Acrilla*) *cf. amoena* Philippi. (×12.5).	Toftlund	75–100 -	3.07	7.08	174
110.	*Janthina cimbrica nov. sp.* Holotype. (×30).	Glejbjerg	55 -	1.37	1.68	176
111.	*Niso acarinatoconica* Cossmann & Peyrot. (×25).	Toftlund	75–100 -	2.16	4.78	176

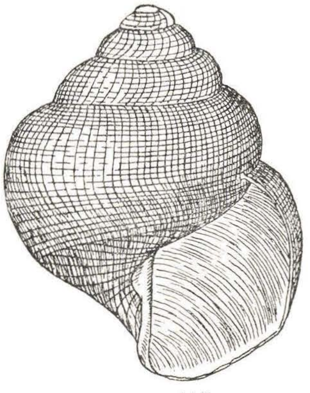
Shell dimensions in millimeters.



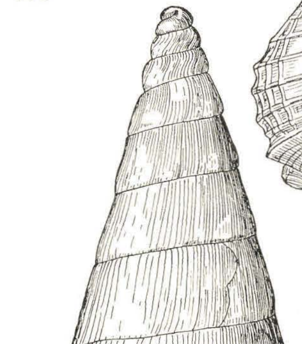
106



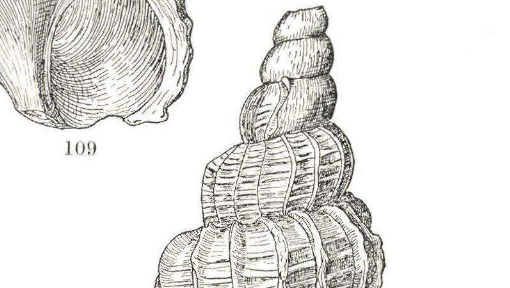
109



110



111



107

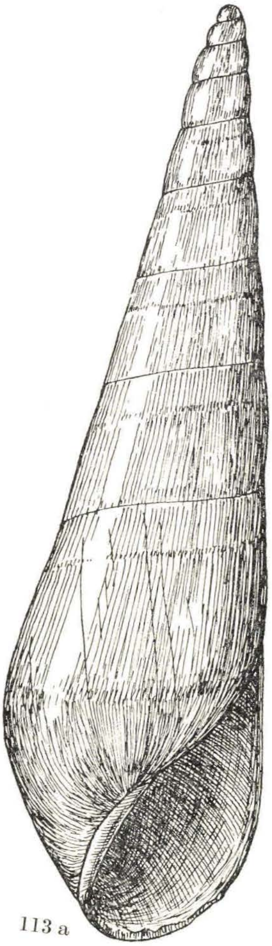
Th. S. del.

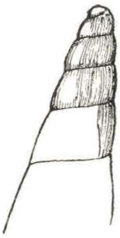
Plate 33.

		Location	Depth	Diameter	Height	Page
112.	*Melanella similis* D'ORBIGNY. (×27).	Toftlund	115 m.	0.90	2.36	178
113a–b.	*Melanella taurostricta* (COSSMANN & PEYROT). (×30).	Toftlund	75–100 -	1.16	4.14	179
114a–b.	*Calyptraea chinensis* (LINNÉ). (×19).	Toftlund	75–100 -	4.7		180
116.	*Aporrhais alata* (EICHWALD). Protoconch. (×30).	Arnum	53–83 -	1.08	1.10	182

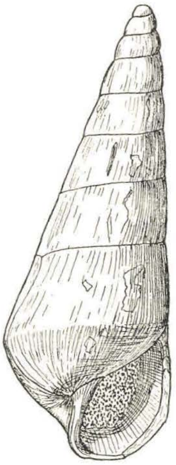
Shell dimensions in millimeters.

Plate 33


113 a


113 b


114 a


112


114 b

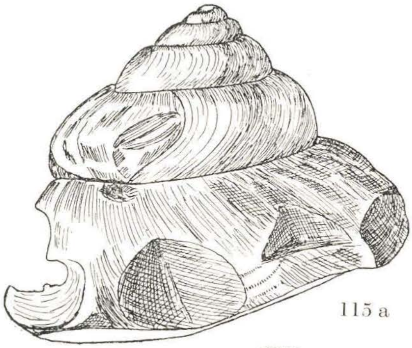

116

Th. S. del.

Plate 34.

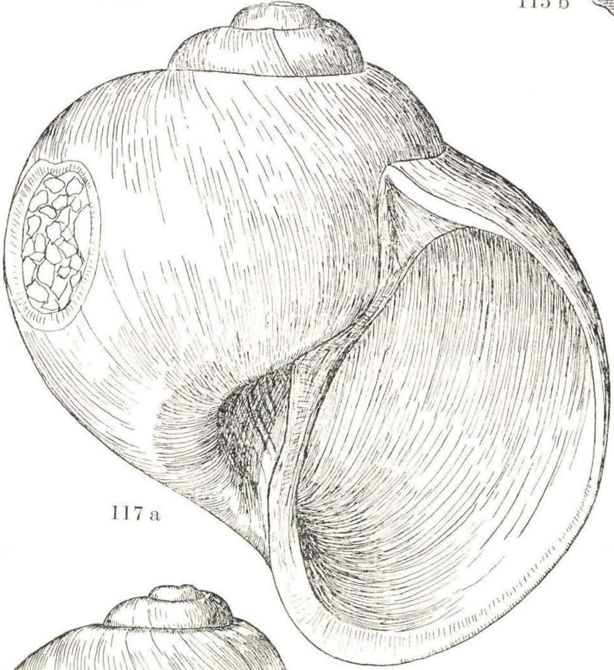
	Location	Depth	Diameter	Height	Page
115a–c. *Xenophora Deshayesi* (MICHELOTTI) c. Protoconch. (×25).	Toftlund	75–100 m.	2.41	1.83	181
117a–b. *Natica (Lunatia) catena* (DA COSTA) b. Protoconch. (×25).	Toftlund	75–100 -	3.35	3.60	185
118a–b. *Natica (Naticina) hanseata* KAUTSKY. (×23).	Toftlund	75–100 -	2.50	2.53	186

Shell dimensions in millimeters.

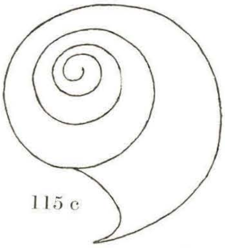


115 a

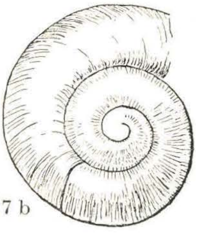
115 b



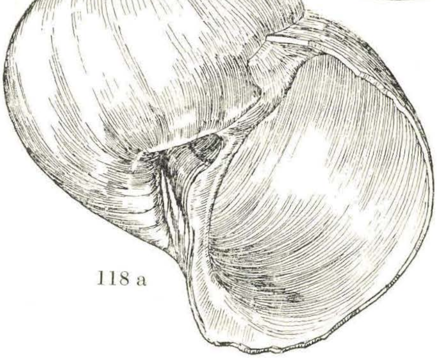
117 a



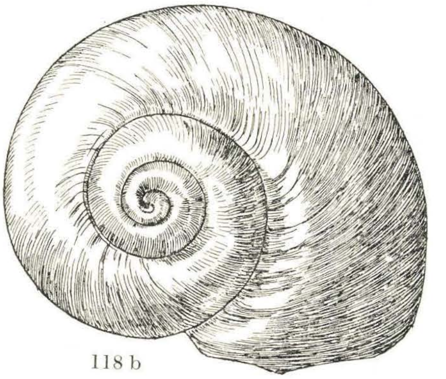
115 c



117 b



118 a



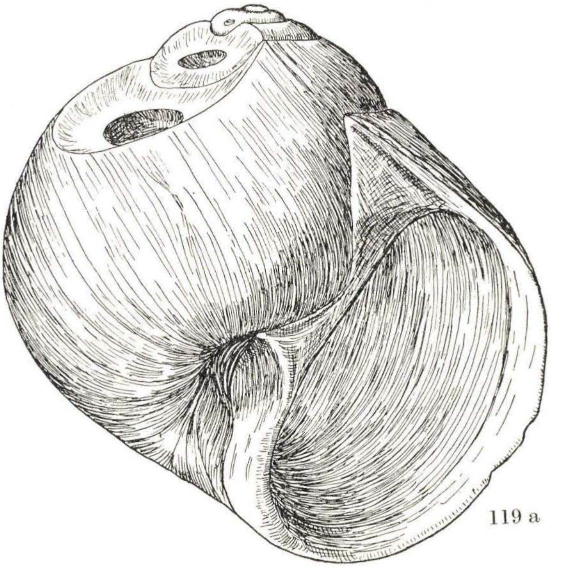
118 b

Th. S. del.

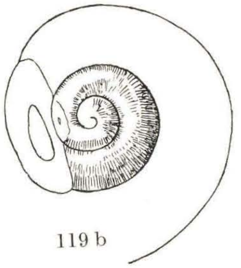
Plate 35.

	Location	Depth	Diameter	Height	Page
119a–c. *Natica (Naticina) Beyrichi* von Koenen. b. Protoconch. (a–b ×20; c ×10).	Toftlund	75–100 m.	3.56	3.56	187
121a–c. *Natica (Naticina) praeclausa* Kautsky. (×25).	Toftlund	75–100 -	2.12	2.14	189

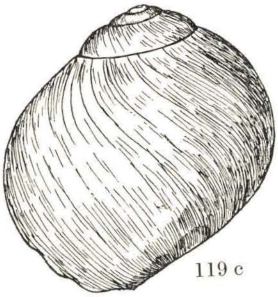
Shell dimensions in millimeters.



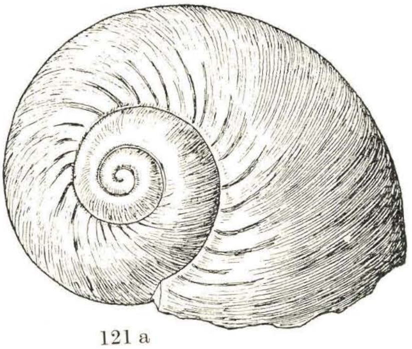
119 a



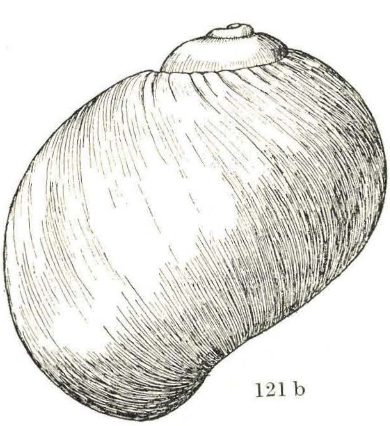
119 b



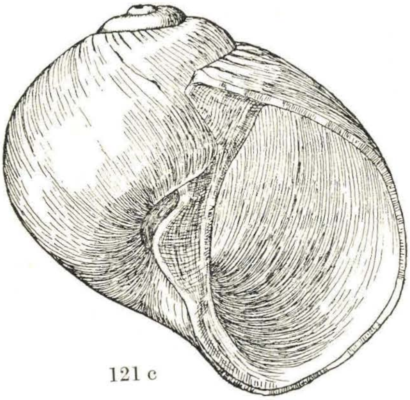
119 c



121 a



121 b



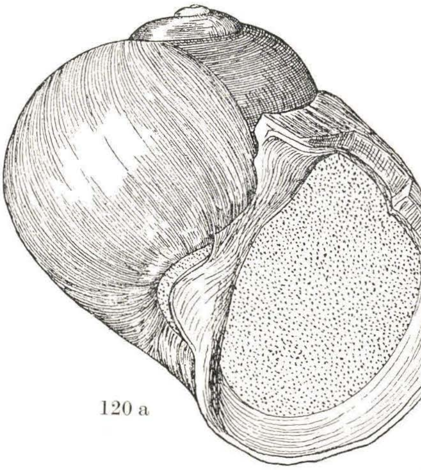
121 c

Th. S. del.

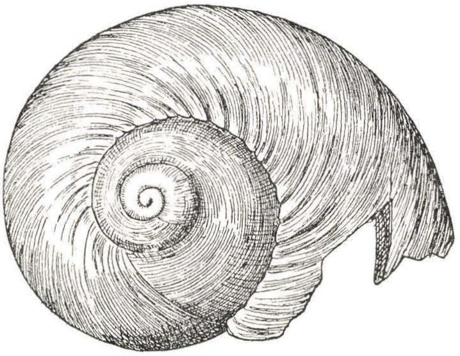
Plate 36.

	Location	Depth	Diameter	Height	Page
120a–b. *Natica* (*Naticina*) *protostriata nov. sp.* Holotype. (×30).	Toftlund	75–100 m.	1.96	2.13	188
124a–c. *Natica* (*Naticina*) *submamillaris* D'ORBIGNY. (a–b ×25; c ×12.5).	Toftlund	75–100 -	3.32	3.41	192

Shell dimensions in millimeters.

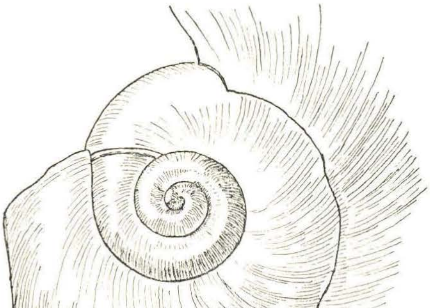


120 a



120 b

124 a



124 b

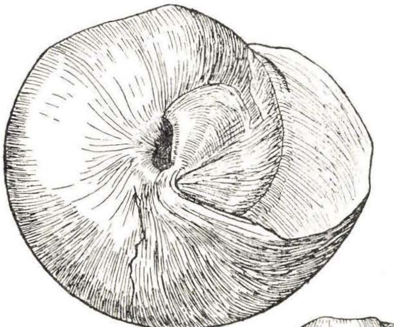
124 c

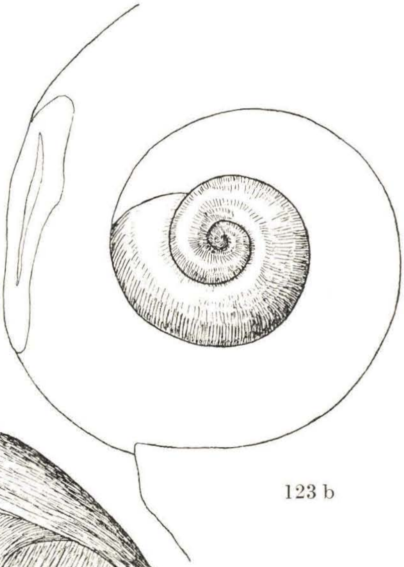
Th. S. del.

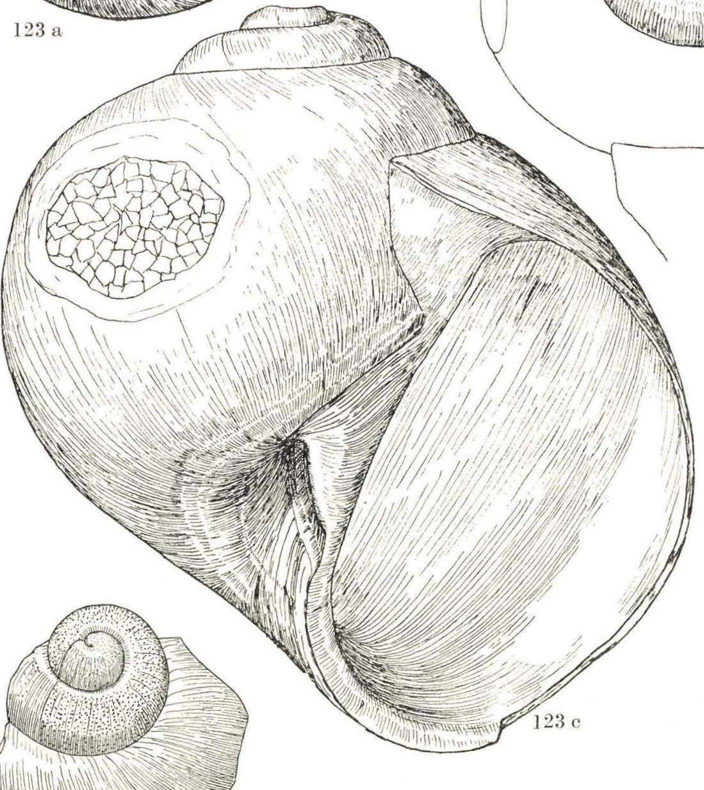
Plate 37.

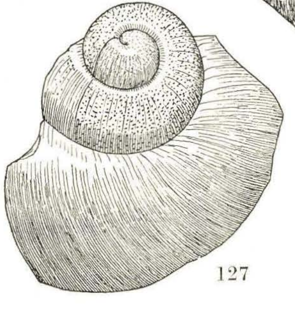
		Location	Depth	Diameter	Height	Page
123a–c.	*Natica (Naticina) miopusilla* KAUTSKY. (a ×12.5; b–c ×25).	Toftlund	75–100 m.	3.66	3.99	191
127.	*Natica sp.* (×40).	Toftlund	115 -		1.0	195
128a–c.	*Globularia sp.* (×20).	Glejbjerg	55 -	1.72	1.95	196

Shell dimensions in millimeters.


123 a


123 b


123 c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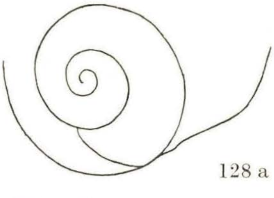
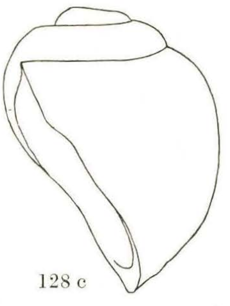

128 a


128 b

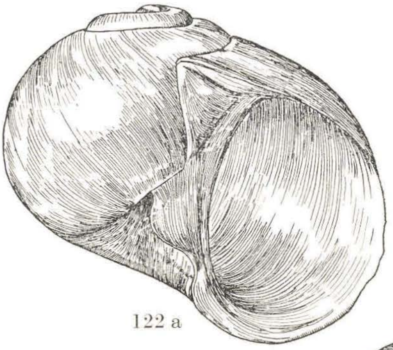

128 c

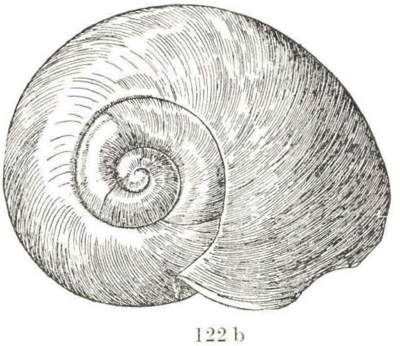
Th. S. del.

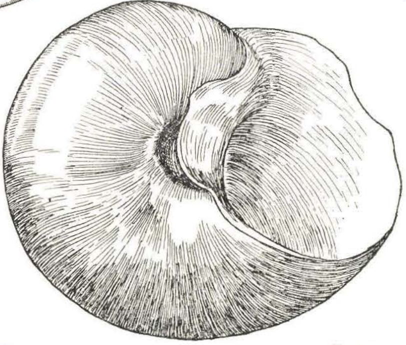
Plate 38.

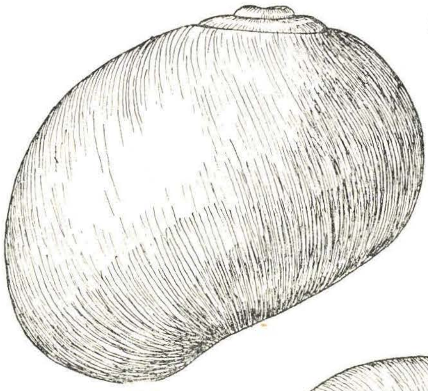
	Location	Depth	Diameter	Height	Page
122a–c. *Natica (Naticina) tectula* BONELLI. (×20).	Toftlund	75–100 m.	2.50	2.25	190
125a–c. *Natica (Polynices) affinis* (GMELIN). (×25).	Toftlund	75–100 -	2.33	2.12	193

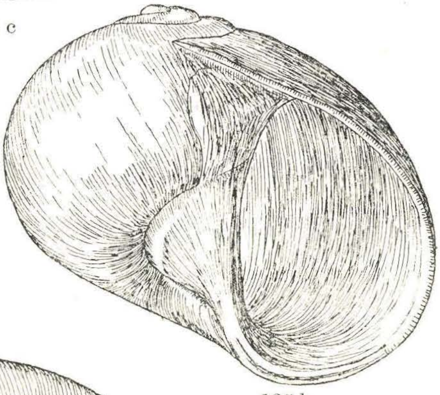
Shell dimensions in millimeters.

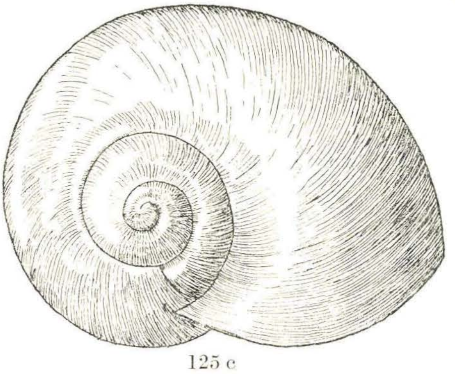

122 a


122 b


122 c


125 a


125 b

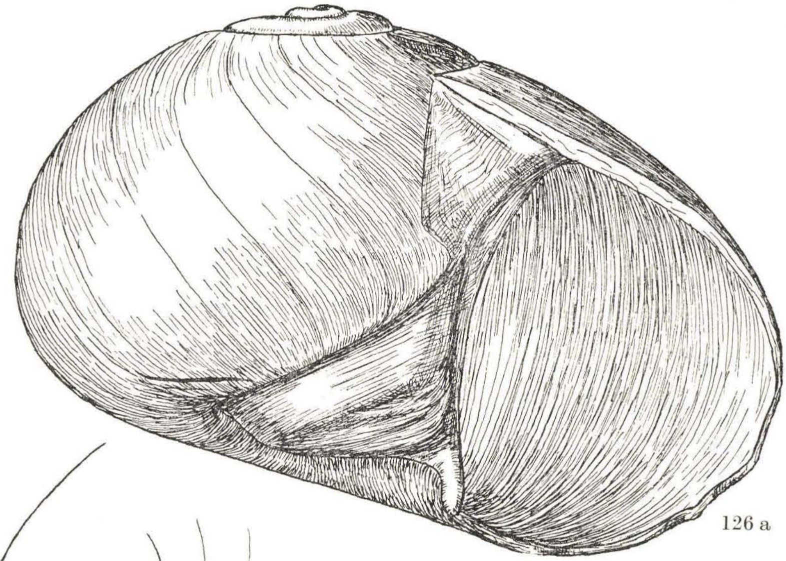

125 c

Th. S. del.

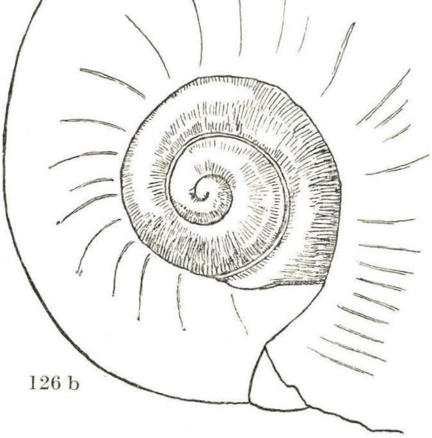
Plate 39.

	Location	Depth	Diameter	Height	Page
126a–c. *Natica* (*Neverita*) *Josephinia* (RISSO). (a–b ×30; c ×15).	Toftlund	75–100 m.	3.41	2.50	194
129a–b. *Sigaretus sulcatus* (GRATELOUP) (×22).	Toftlund	75–100 -	2.54	2.33	196

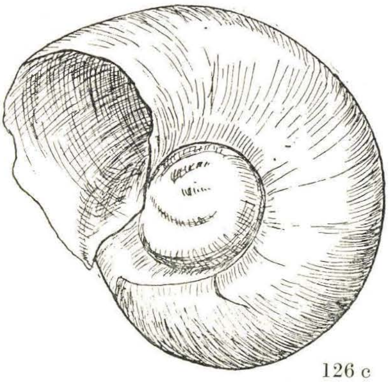
Shell dimensions in millimeters.



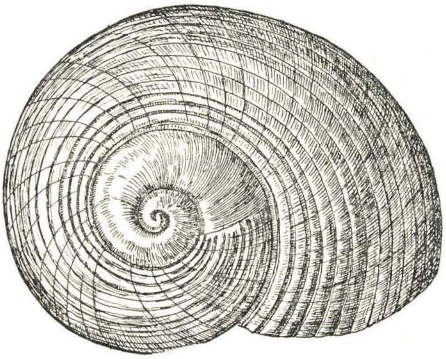
126 a



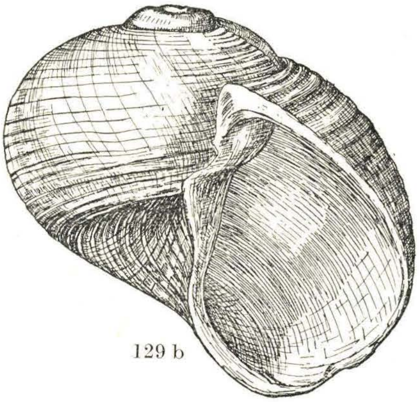
126 b



126 c



129 a



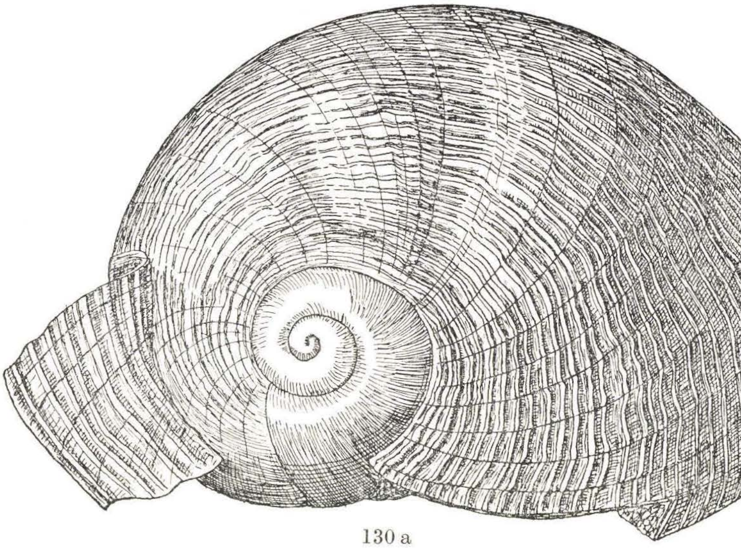
129 b

Th. S. del.

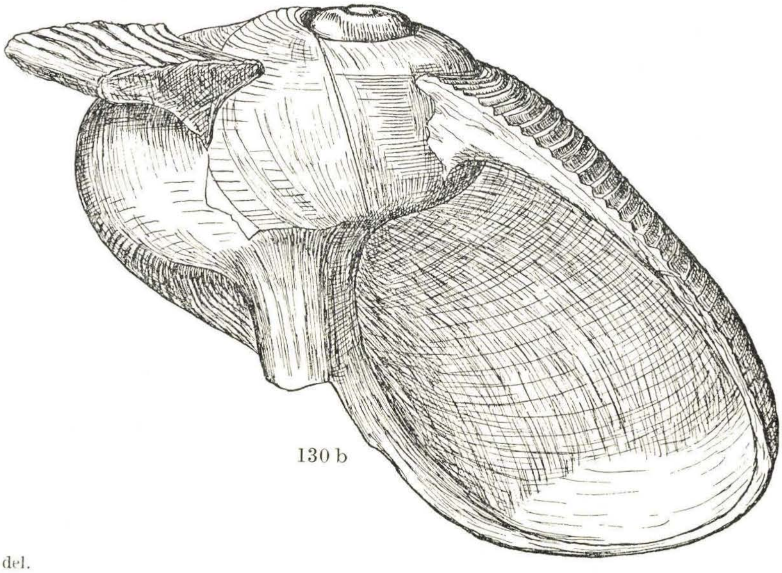
Plate 40.

	Location	Depth	Diameter	Height	Page
130a–b. *Sigaretus cf. aquensis* RECLUZ. (×30).	Toftlund	75–100 m.	3.65	2.41	197

Shell dimensions in millimeters.



130 a



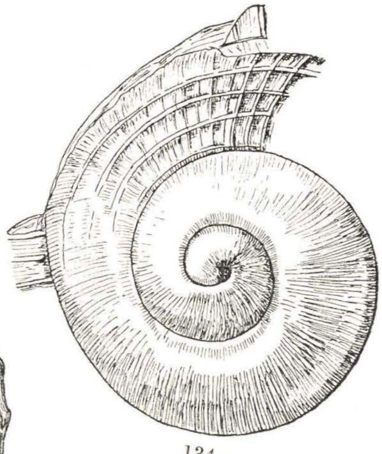
130 b

Th. S. del.

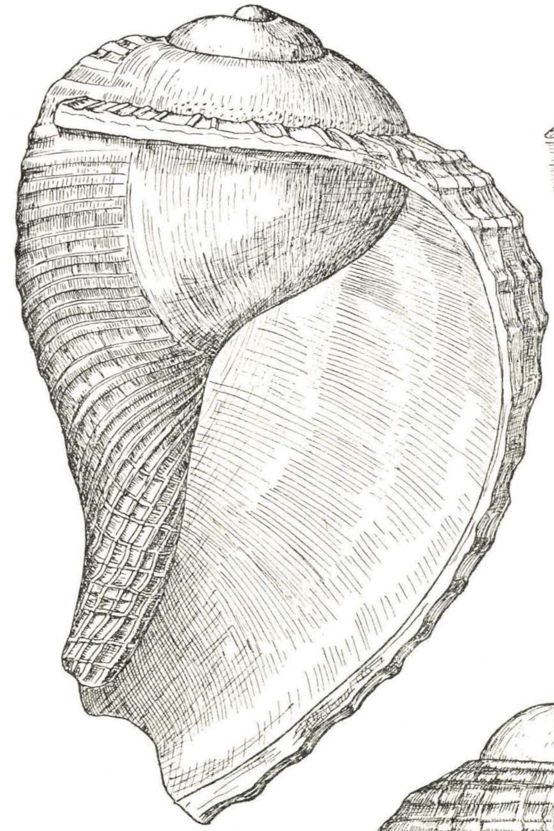
Plate 41.

		Location	Depth	Diameter	Height	Page
131.	*Semicassis sp.* (×30).	Toftlund	75–100 m.	2.07	2.74	198
134a–b.	*Pyrula condita* BRONGNIART. (×25).	Toftlund	75–100 -	3.07	4.32	200

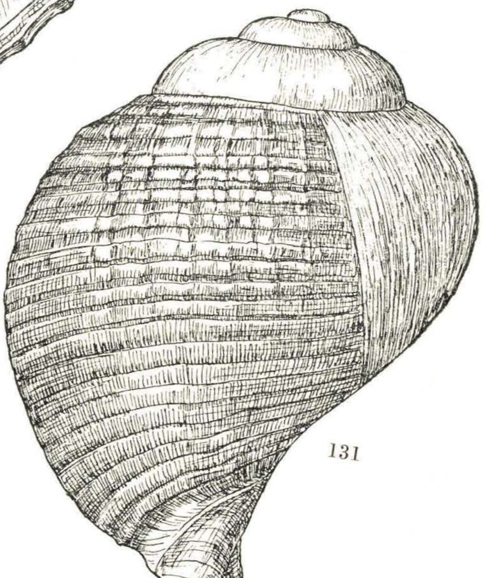
Shell dimensions in millimeters.



134 a



134 b



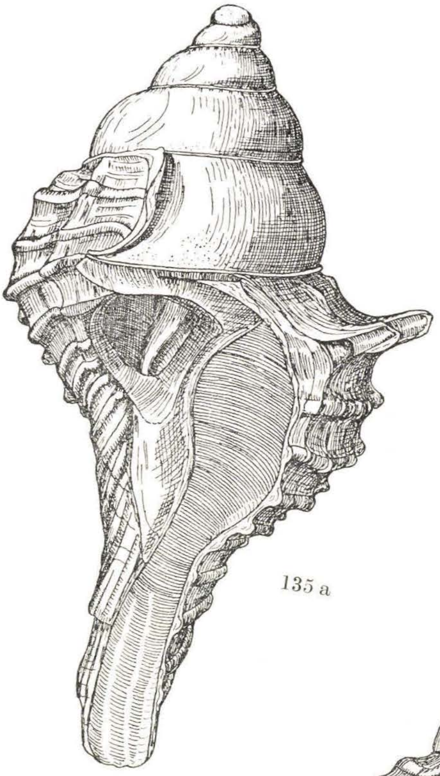
131

Th. S. del.

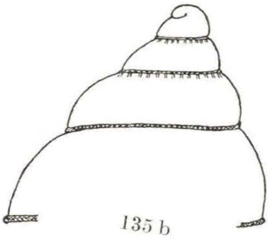
Plate 42.

		Location	Depth	Diameter	Height	Page
135a–b.	*Murex cf. aturensis* Cossmann & Peyrot. (×30).	Toftlund	75–100 m.	1.83	3.41	201
136a–b.	*Murex inornatus* Beyrich. (×30).	Toftlund	75–100 -	1.79	3.79	202
139.	*Tritonalia coelata* Dujardin. (×5).	Bramminge	70–80 -	6.0	15.3	206

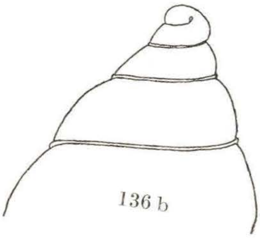
Shell dimensions in millimeters.



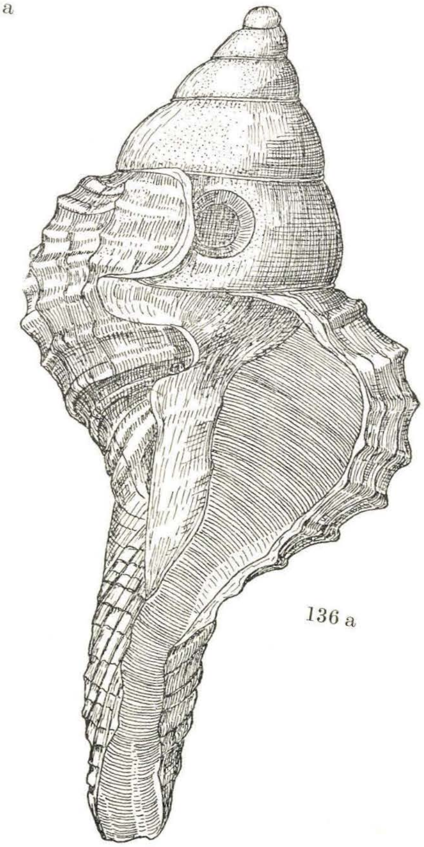
135 a



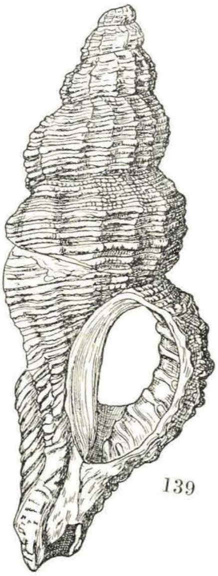
135 b



136 b



136 a



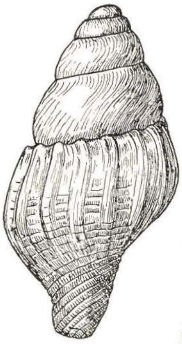
139

Th. S. del.

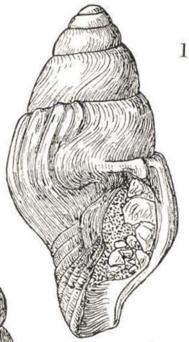
Plate 43.

		Location	Depth	Diameter	Height	Page
138.	*Typhis fistulosus* (BROCCHI). (×25).	Toftlund	75–100 m.	2.90	5.48	204
140.	*Pyrene* (*Atilia*) *nassoides* (GRATELOUP). (×25).	Toftlund	75–100 -	2.3	5.6	206
141a-d.	*Pyrene* (*Anachis sp.*)					208
a–b.	(×25).	Arnum (25b)	62.7–62.9 -	0.91	1.73	
c.	(×20).	Toftlund	105–110 -	1.7	2.7	
d.	(×20).	Bramminge	70–80 -	1.8	3.9	

Shell dimensions in millimeters.

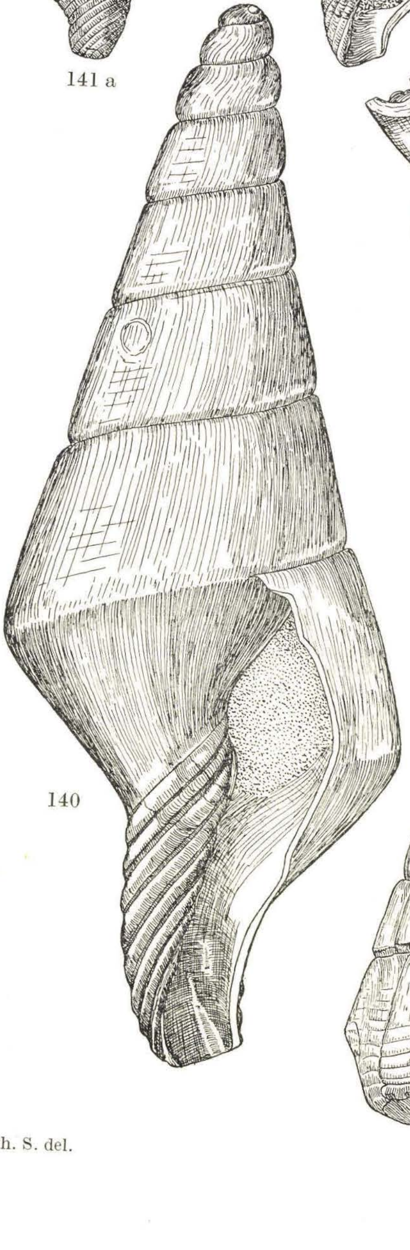


141 a

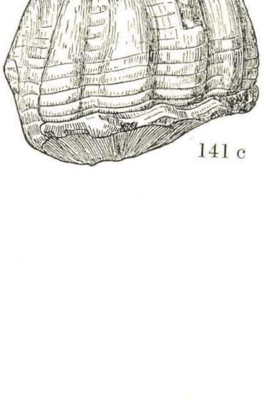


141 b

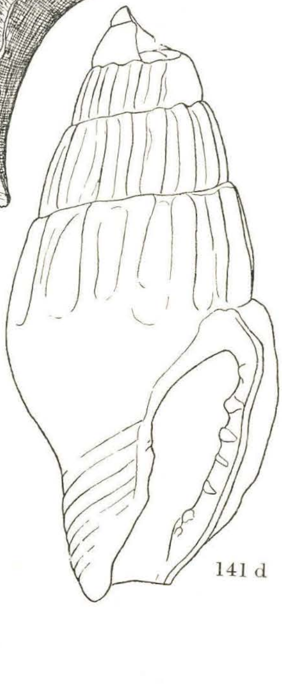
138



140



141 c



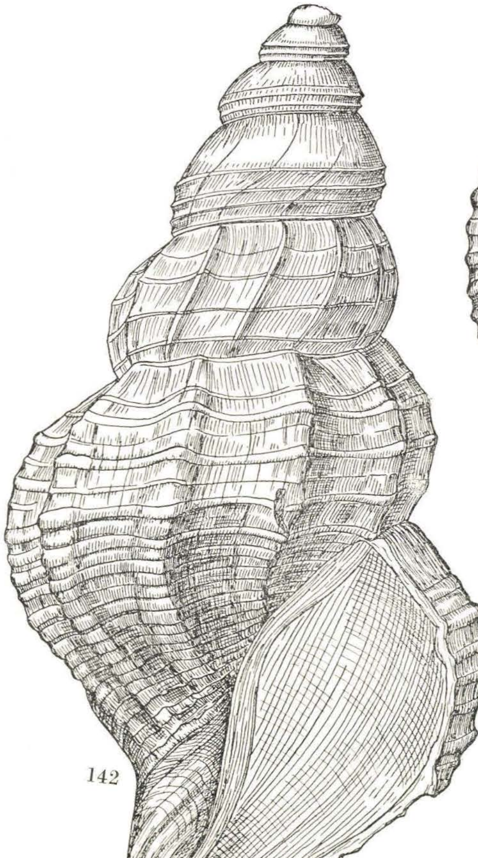
141 d

Th. S. del.

Plate 44.

		Location	Depth	Diameter	Height	Page
142.	*Phos decussatus* von Koenen. (×25).	Toftlund	110–115 m.	2.65	4.90	208
143.	*Nassa tenuistriata* (Beyrich). (×25).	Toftlund	75–100 -	2.52	3.99	210
147.	*Nassa Fuchsi* von Koenen. (×27).	Toftlund	75–100 -	2.02	3.33	215

Shell dimensions in millimeters.



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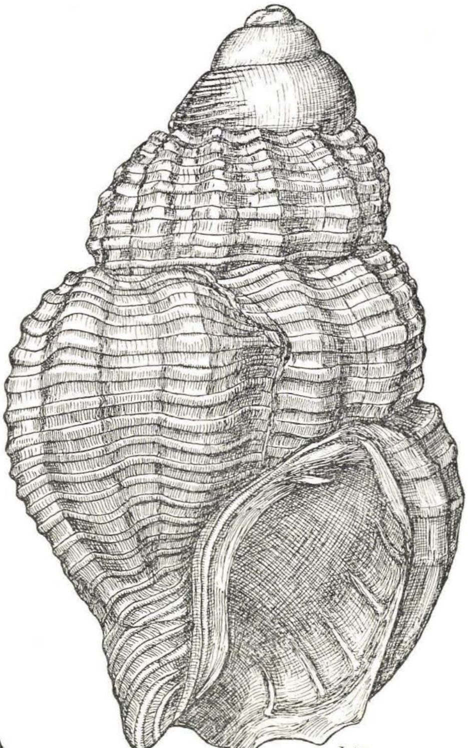
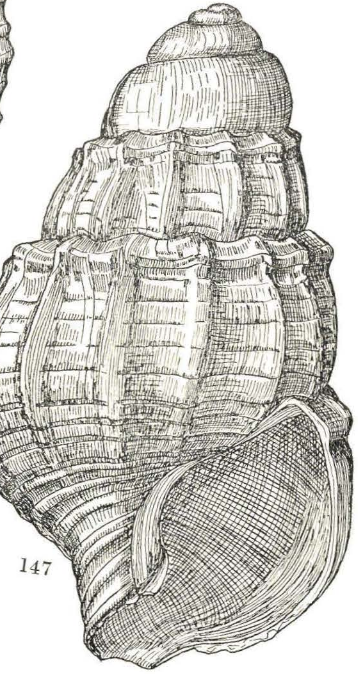


143



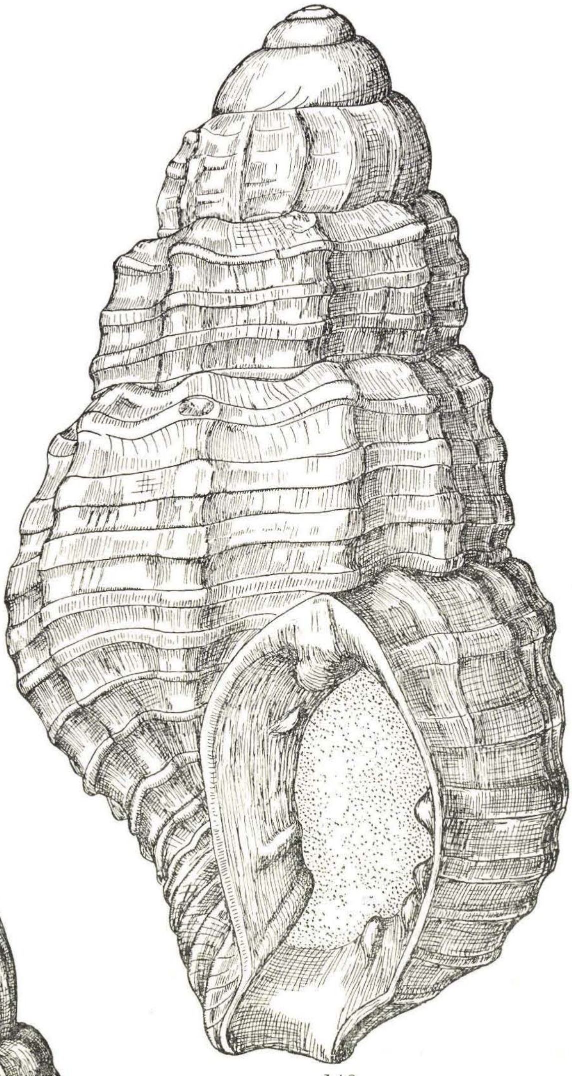
147

Th. S. del.

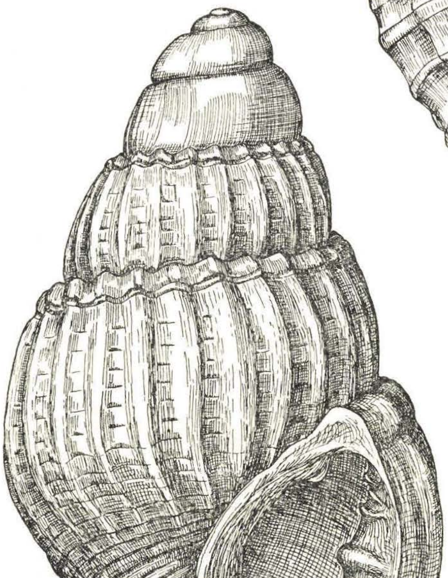
Plate 45.

		Location	Depth	Diameter	Height	Page
146.	*Nassa turbinella* (BROCCHI). (×26).	Toftlund	75–100 m.	2.90	5.35	214
148.	*Nassa Schlotheimi* (BEYRICH). (×25).	Toftlund	75–100 -	2.38	3.91	216

Shell dimensions in millimeters.



146



148

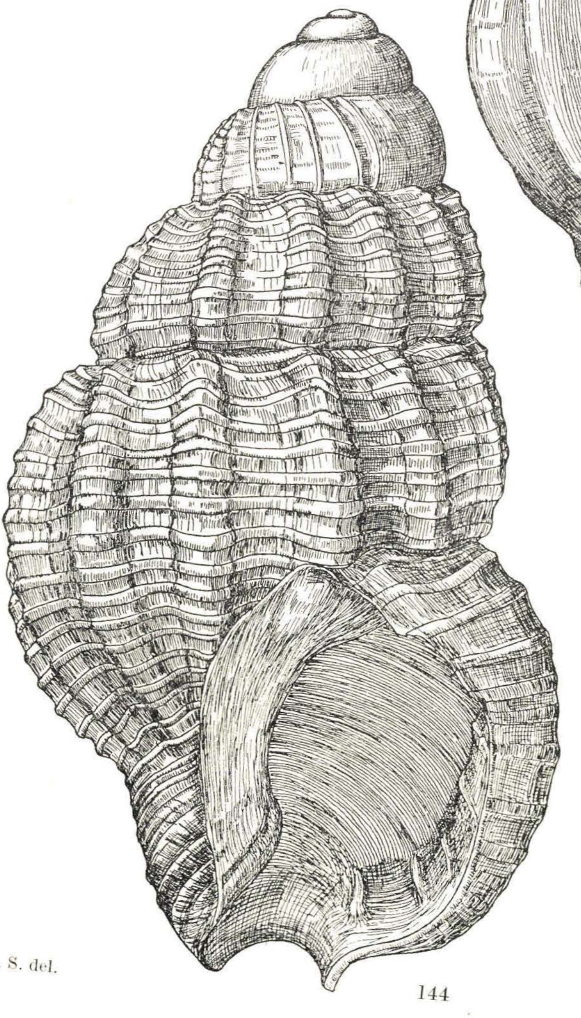
Th. S. del.

Plate 46.

		Location	Depth	Diameter	Height	Page
144.	*Nassa serraticosta* (BRONN). (×25).	Toftlund	75–100 m.	3.00	5.22	212
154.	*Nassa subobesa* DEGRANGE-TOUZIN. (×26).	Toftlund	75–100 -	2.45	4.07	226

Shell dimensions in millimeters.

154



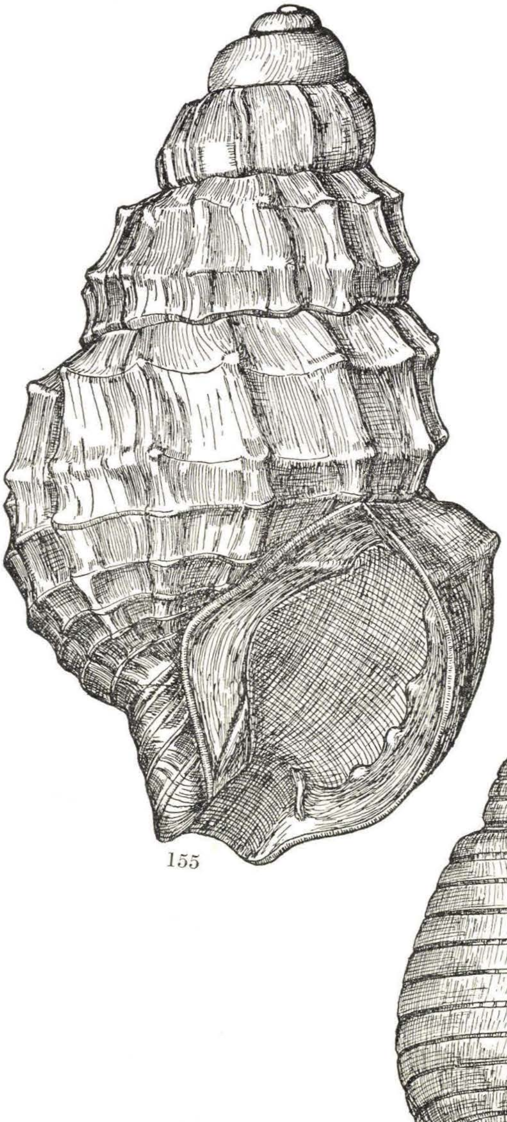
Th. S. del.

144

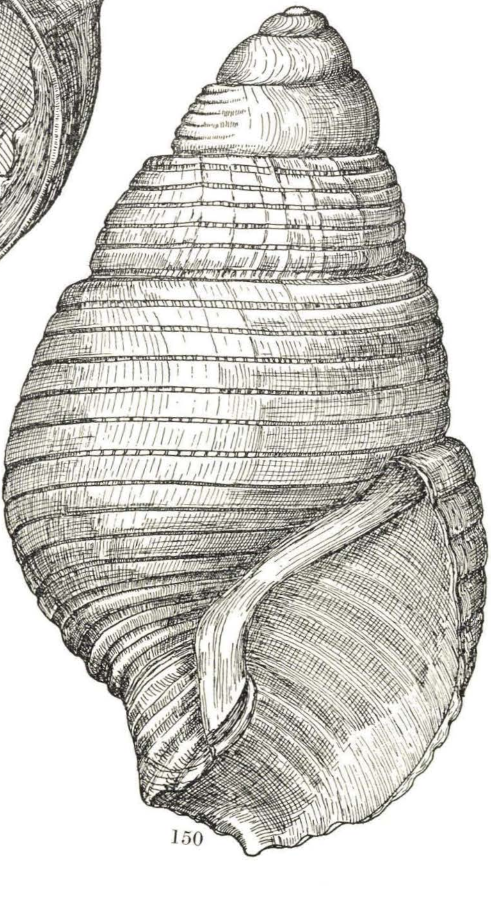
Plate 47.

		Location	Depth	Diameter	Height	Page
150.	*Nassa Facki* von Koenen. (×26).	Toftlund	75–100 m.	2.57	4.40	220
155.	*Nassa cimbrica* Ravn. (×26).	Toftlund	75–100 -	2.57	4.40	228

Shell dimensions in millimeters.



155



Th. S. del.

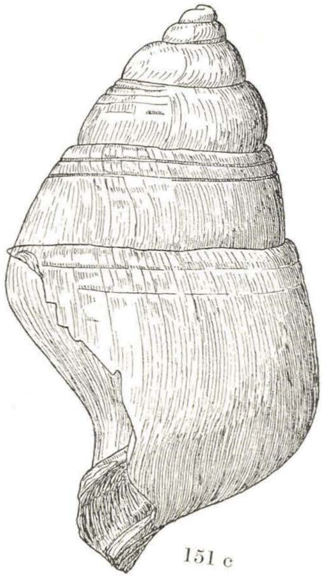
150

Plate 48.

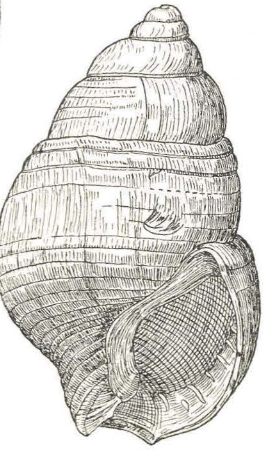
		Location	Depth	Diameter	Height	Page
149.	*Nassa holsatica* (BEYRICH). (×22.5).	Bramminge	70–80 m.	2.62	4.46	219
151a–c.	*Nassa laevissima* BRUSINA	Toftlund	75–100 -			222
a.	(×20.5).			1.89	3.37	
b.	(×20.5).			1.77	2.81	
c.	(×20.5).			2.12	3.70	
156.	*Nassa pölsense* (AUINGER). (×26).	Glejbjerg	53.5 -	2.08	3.04	231

Shell dimensions in millimeters.

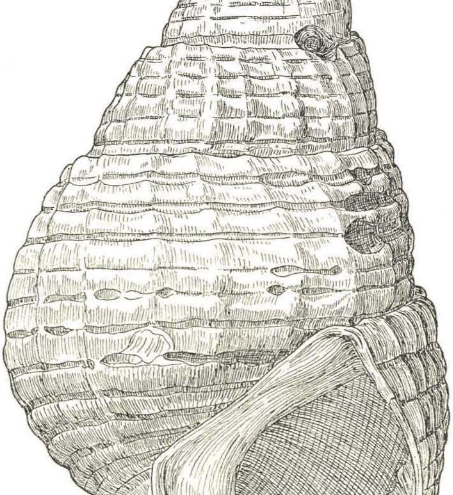
151 a



151 c



151 b



149

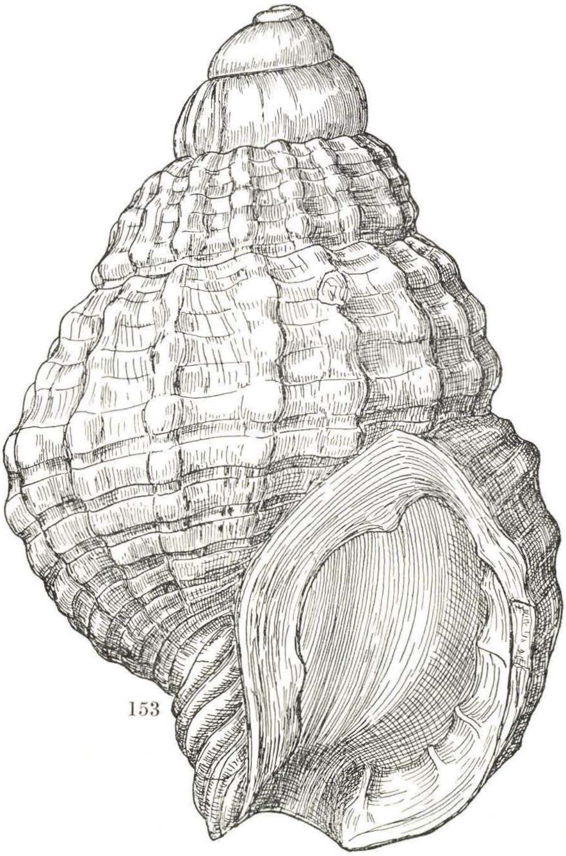
156

Th. S. del.

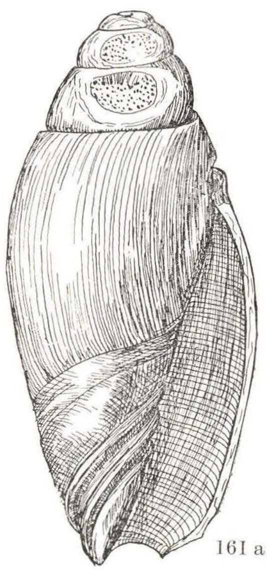
Plate 49.

		Location	Depth	Diameter	Height	Page
153.	*Nassa Woodwardi* Harmer. (×25).	Toftlund	110–115 m.	2.99	4.57	225
160a–c.	*Ancilla obsoleta* (Brocchi). (×15).	Toftlund	75–100 -	2.00	4.15	236
161a–c.	*Oliva minutissima* (Kautsky). (×15).	Toftlund	75–100 -	2.17	4.85	237

Shell dimensions in millimeters.

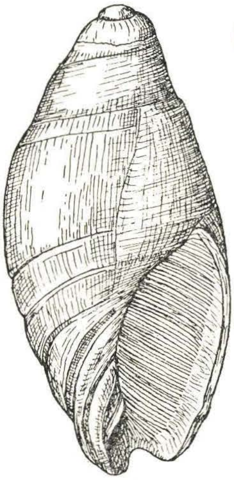


153



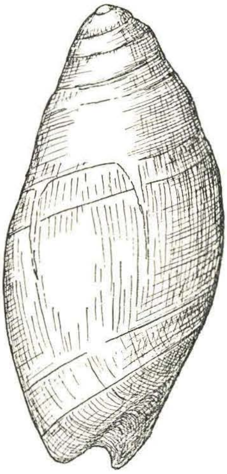
161 a

161 b

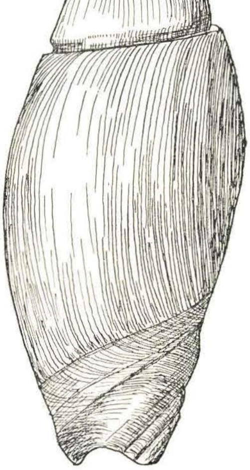


160 a

160 c



160 b



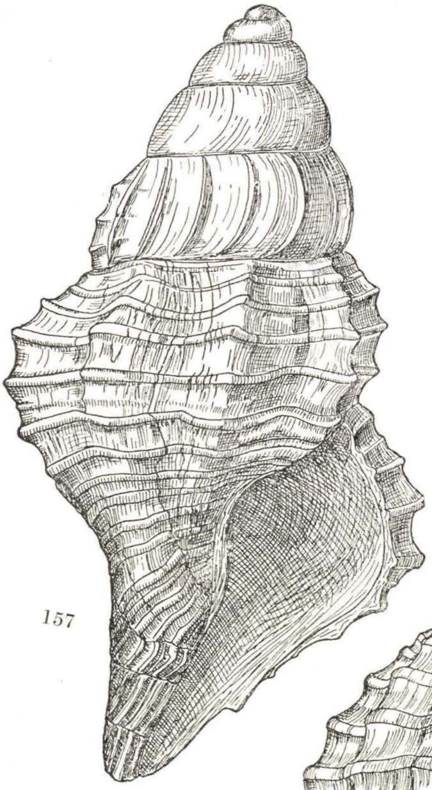
161 c

Th. S. del.

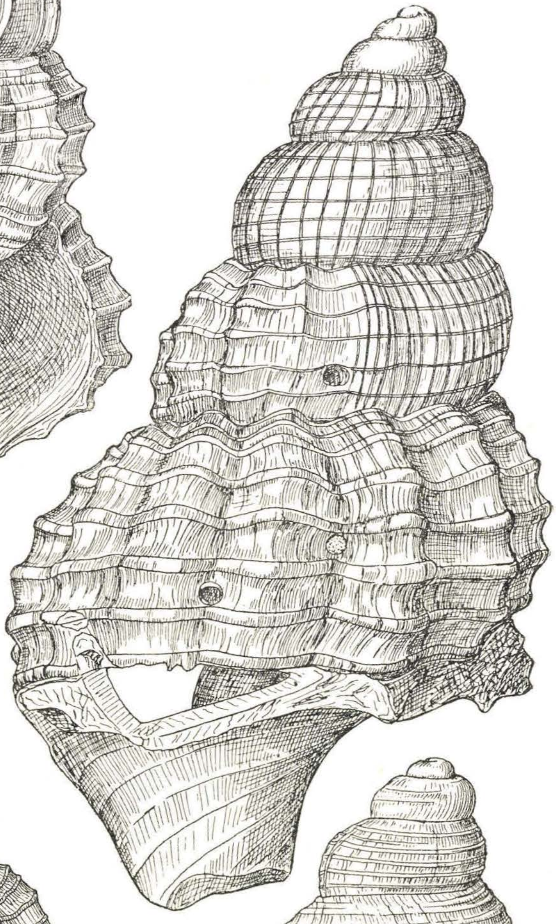
Plate 50.

		Location	Depth	Diameter	Height	Page
157.	*Lathyrus (Dolicholatyrus) Rothi* (BEYRICH). (×26).	Toftlund	75–100 m.	2.20	4.15	232
158.	*Fusus cf. sexcostatus* BEYRICH. (×29).	Toftlund	75–100 -		4.25	233
159.	*Fusus (Aquilofusus) Grippi* (KAUTSKY). (×13).	Glejbjerg	53.5 -	3.35	5.75	235
164.	*Cancellaria (Cancellaria) cancellata* (LINNÉ). (×11).	Toftlund	115 -	5.15	7.58	239

Shell dimensions in millimeters.

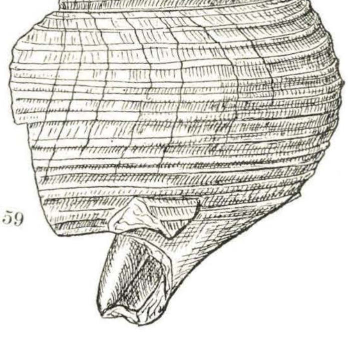


157



158

164



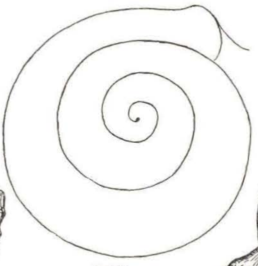
159

Th. S. del.

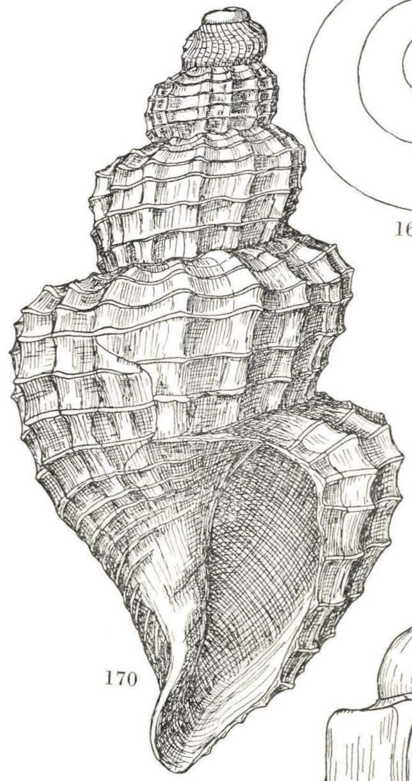
Plate 51.

		Location	Depth	Diameter	Height	Page
166.	*Cancellaria (Trigonostoma) acutangula* Faujas de Saint Fond. (×15).	Toftlund	110–115 m.	3.62	5.03	241
168a–b.	*Cancellaria (Narona) calcarata* (Brocchi)	Bramminge	70–80 -			243
a.	(×17).			2.77	4.07	
b.	(×17).			2.28	3.29	
169a–b.	*Cancellaria (Narona) varicosa* (Brocchi). (×25).	Toftlund	75–100 -	2.57	4.15	244
170.	*Admete cf. fusiformis* (Cantraine). (×15).	Toftlund	75–100 -	3.65	6.75	246

Shell dimensions in millimeters.

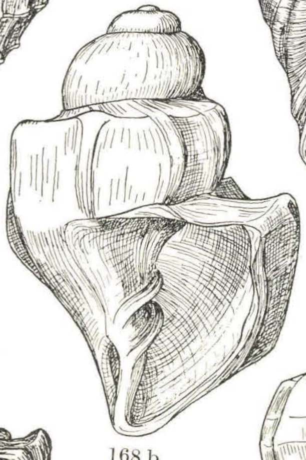


169 a

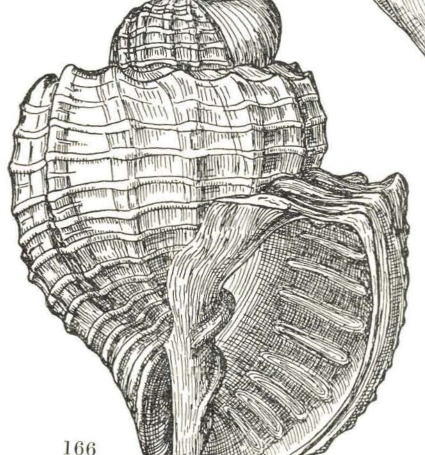


170

169 b



168 b



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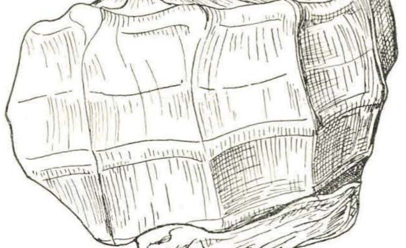


168 a

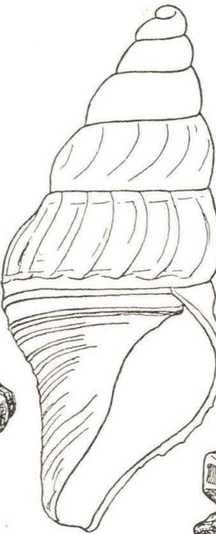
Th. S. del.

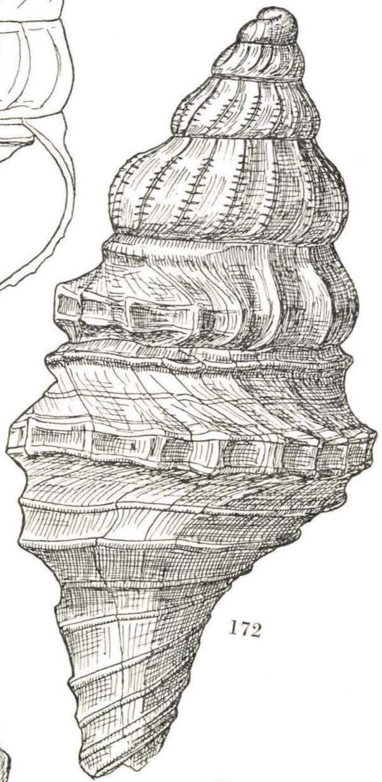
Plate 52.

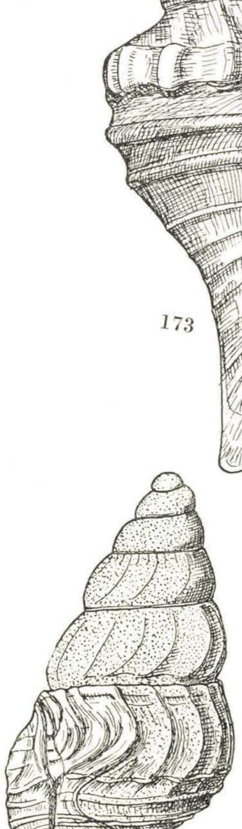
		Location	Depth	Diameter	Height	Page
171.	*Conus Dujardini* DESHAYES. (×25).	Bramminge	70–80 m.	1.82	4.25	248
172.	*Gemmula cf. rotata* (BROCCHI). (×30).	Toftlund	75–100 -	1.66	3.41	251
173.	*Gemmula badensis* (HÖRNES). (×30).	Toftlund	75–100 -	1.83	3.92	252
174a–c.	*Gemmula boreoturricula* (KAUTSKY). (×21).	Toftlund	105–110 -	1.43	3.31	254

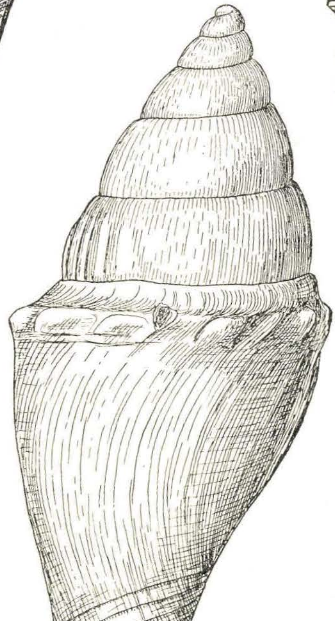
Shell dimensions in millimeters.


173


174 b


172


174 a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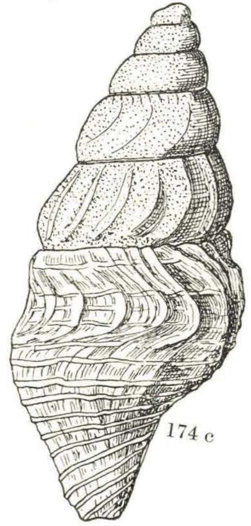
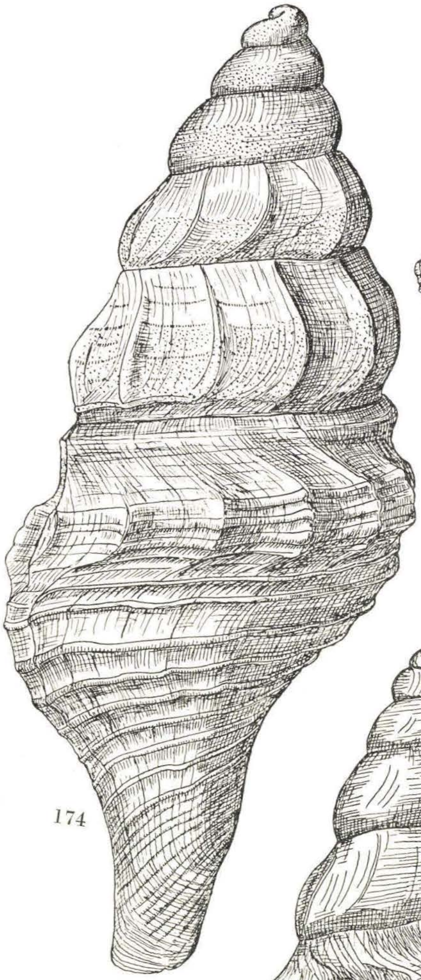

174 c

Th. S. del.

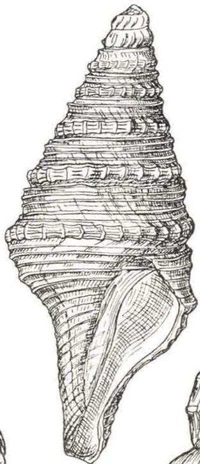
Plate 53.

		Location	Depth	Diameter	Height	Page
174.	*Gemmula boreoturricula* (Kautsky). (×31).	Toftlund	75–100 m.	1.79	4.15	254
175.	*Gemmula Stoffelsi* (Nyst). (×30).	Toftlund	75–100 -	1.91	3.99	256
176.	*Gemmula Zimmermanni* (Philippi). (×5).	Bramminge	70–80 -	5.2	12.2	257
178.	*Fusiturris inermis* (Hörnes). (×30).	Toftlund	75–100 -	1.54	3.50	259
180a–b.	*Turricula Steinvorthi* (von Koenen). (×12).	Toftlund	110–115 -		7.2	262

Shell dimensions in millimeters.



174



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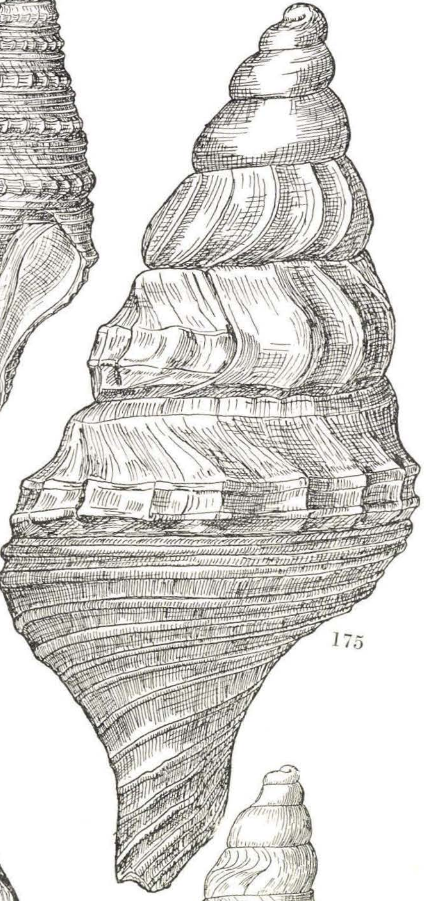
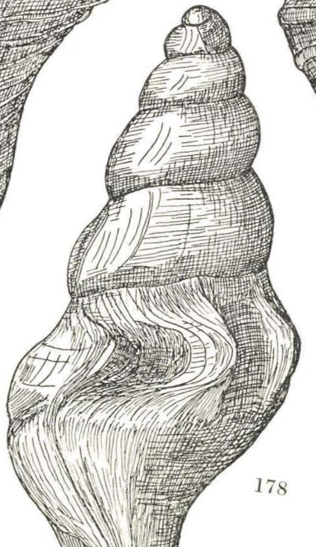
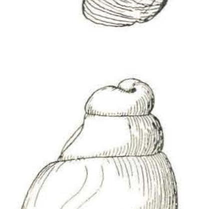


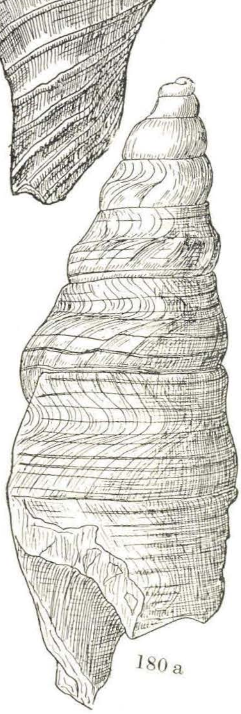
175



178



180 b



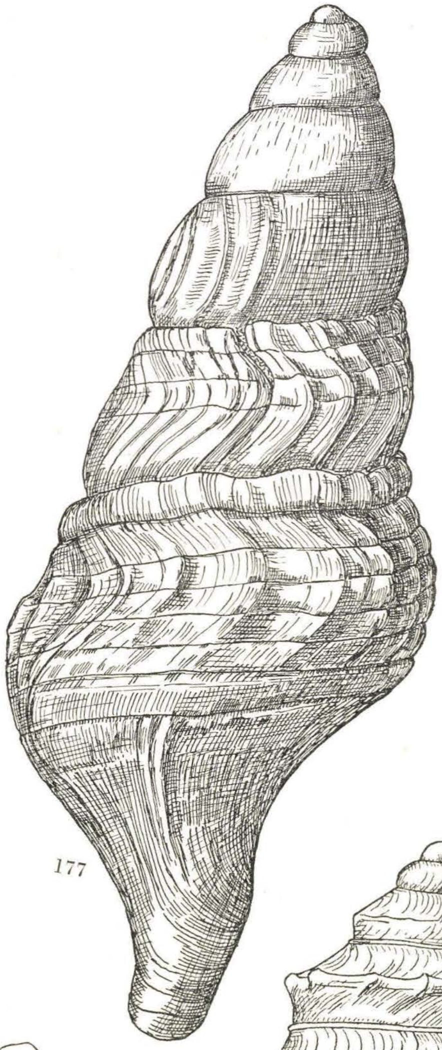
180 a

Th. S. del.

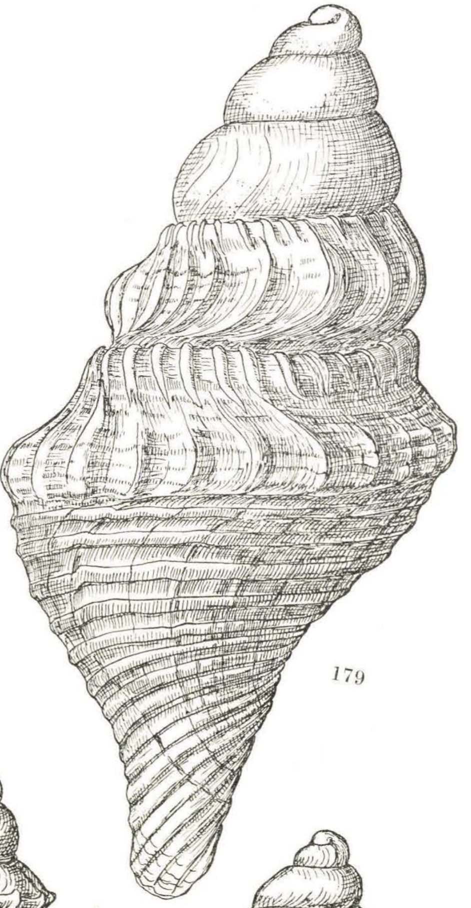
Plate 54.

		Location	Depth	Diameter	Height	Page
177.	*Fusiturris Duchastelii* (NYST). (×31).	Toftlund	75–100 m.	1.87	4.45	258
179.	*Bathytoma cataphracta* (BROCCHI). (×30).	Toftlund	75–100 -	1.94	3.99	260
181a–b.	*Clinura sp.* (×30).			1.62	2.63	263
183a–b.	*Clavatula boreointerrupta* KAUTSKY. Juvenile shell. (×18).	Toftlund	105–110 -	1.55	2.35	264

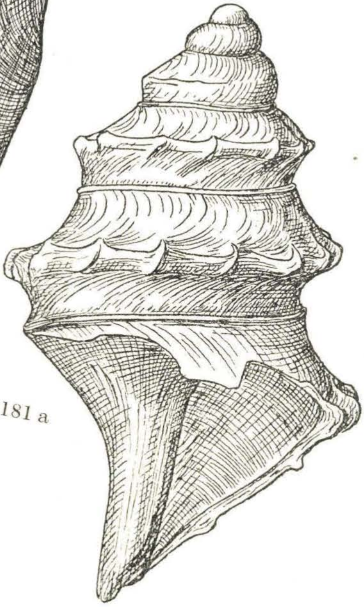
Shell dimensions in millimeters.



177

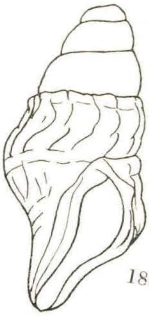


179

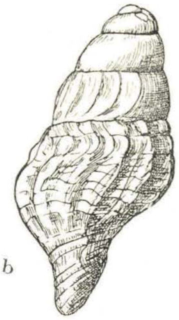


181 a

181 b



183 a



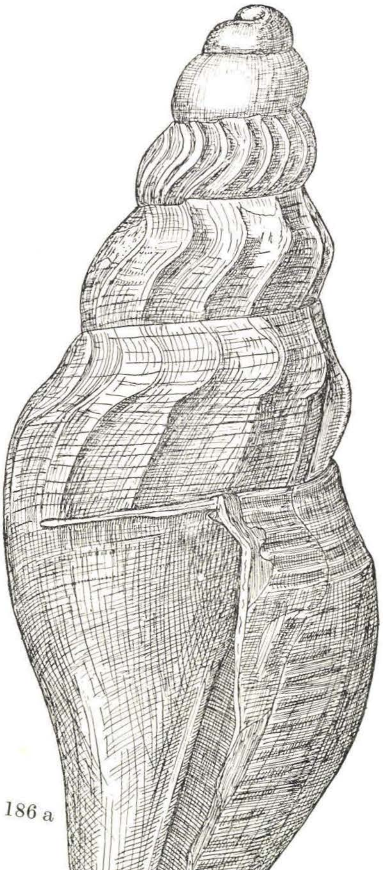
183 b

Th. S. del.

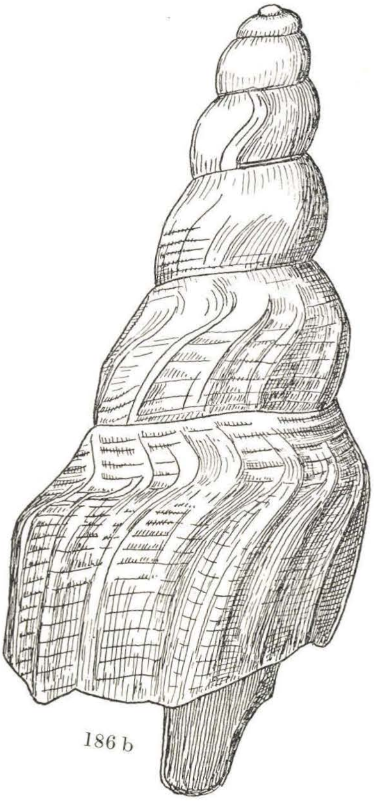
Plate 55.

		Location	Depth	Diameter	Height	Page
184.	*Clavatula sp.* (×37).	Toftlund	100–105 m.	1.15	2.04	265
186.	*Genota ramosa* (BASTEROT)					266
	a. (×25).	Toftlund	75–100 -	2.08	6.07	
	b. (×15).	Bramminge	70–80 -	3.15	7.15	

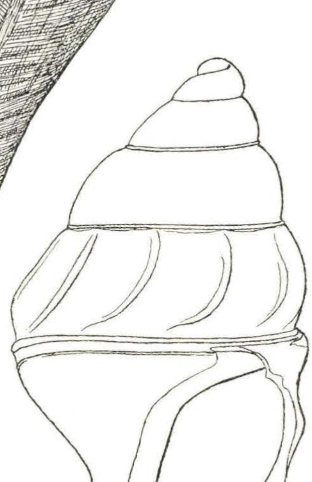
Shell dimensions in millimeters.



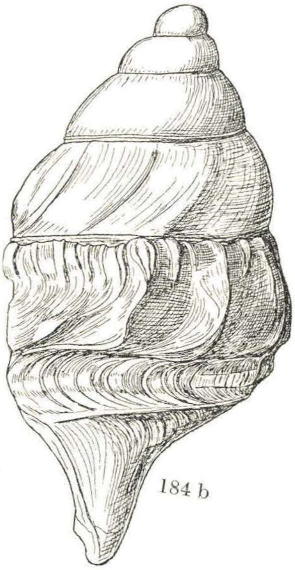
186 a



186 b



184 a



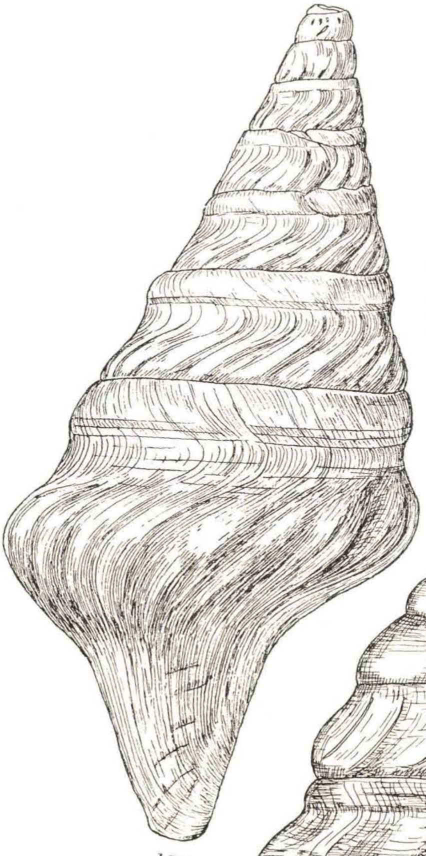
184 b

Th. S. del.

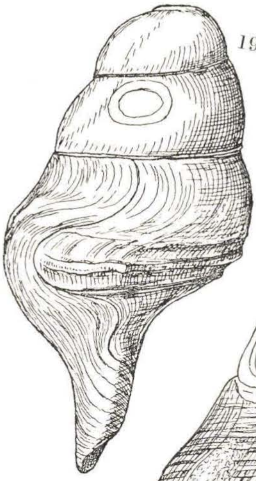
Plate 56.

		Location	Depth	Diameter	Height	Page
185.	*Clavatula obliplicatula* KAUTSKY. (×13).	Glejbjerg	55 m.	4.11	8.6	266
187.	*Acamptogenotia cf. Escheri* (MAYER). (×12).	Toftlund	110–115 m.	4.07	8.55	267
189.	*Inquisitor obeliscus* (DES MOULINS). (×25).	Toftlund	75–100 -	1.89	4.40	268
190a–c.	*Splendrillia Selenkae* (VON KOENEN). Protoconch (×40).	Toftlund	105–110 -	0.86	1.58	270

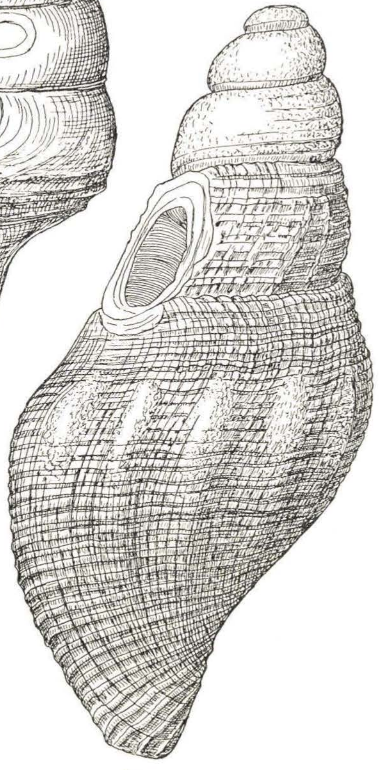
Shell dimensions in millimeters.



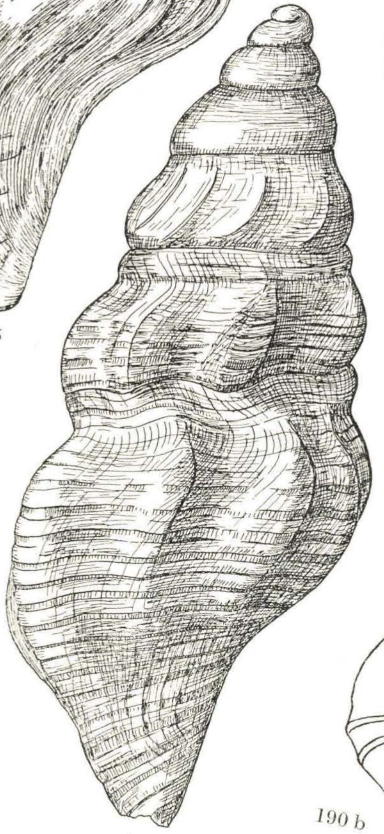
185



190 c



187



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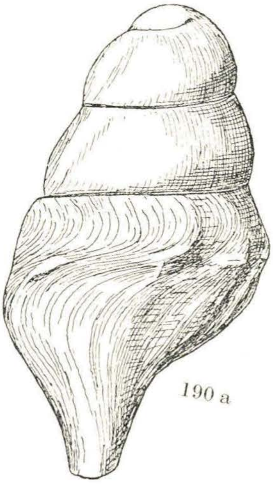
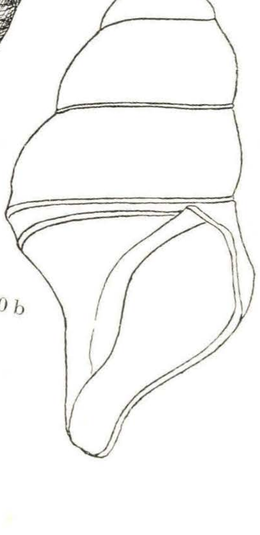


190 a



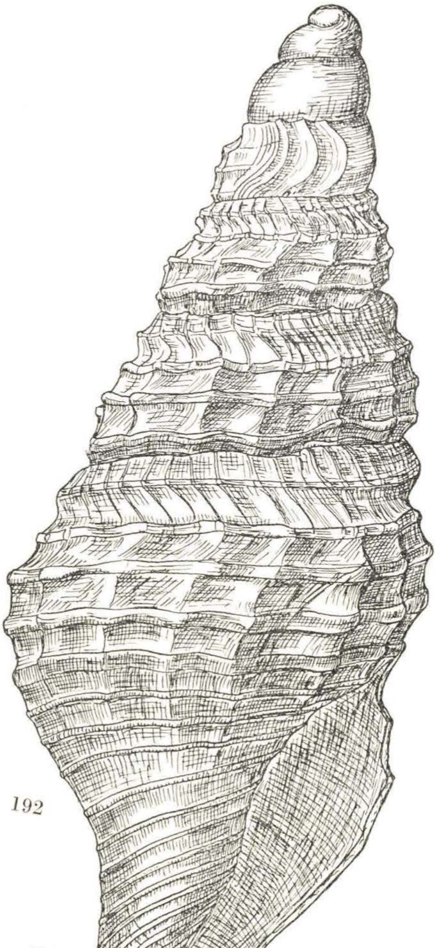
190 b

Th. S. del.

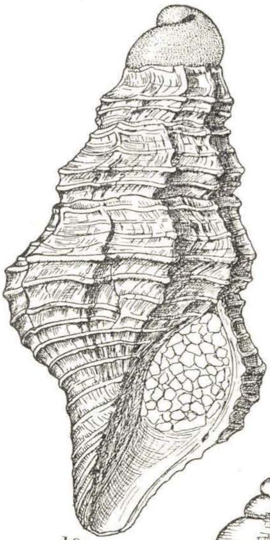
Plate 57.

		Location	Depth	Diameter	Height	Page
191a–b.	*Boreodrillia toftlundensis nov. gen. & nov. sp.* (×20). Holotype.	Toftlund	110–115 m.	1.85	3.65	271
192.	*Asthenotoma cf. pannus* (Basterot). (×30).	Toftlund	75–100 -	2.00	4.82	272
193.	*Brachytoma electa nov. sp.* (×30). Holotype.	Toftlund	75–100 -	1.74	4.32	273
196a–b.	*Brachytoma sp.* (×10).	Glejbjerg	55 -	2.45	5.85	277

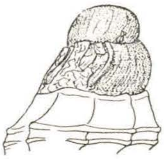
Shell dimensions in millimeters.



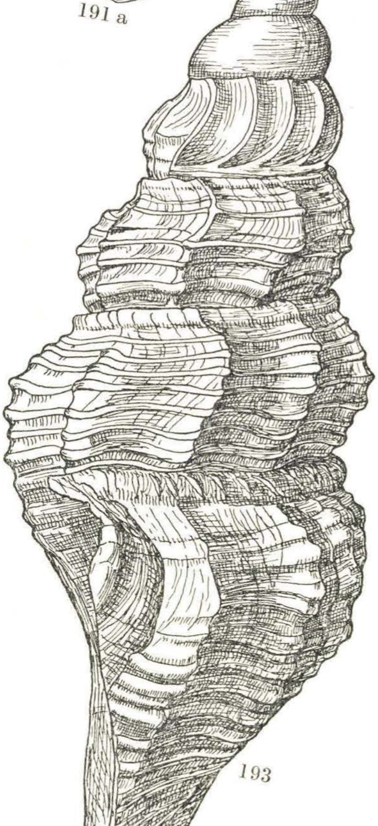
192



191 a



191 b



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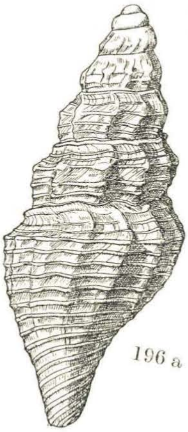
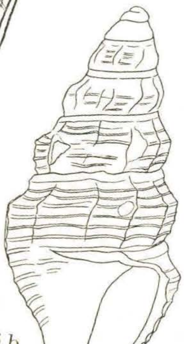


196 a



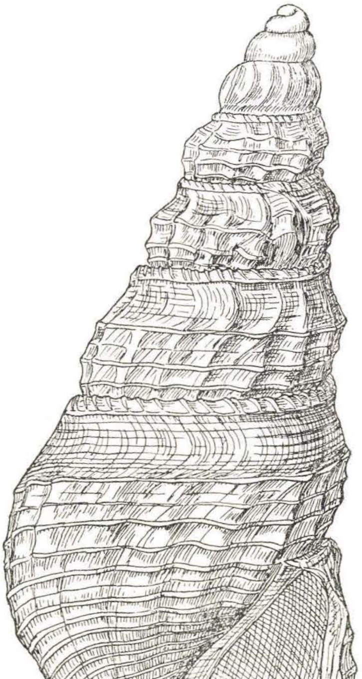
196 b

Th. S. del.

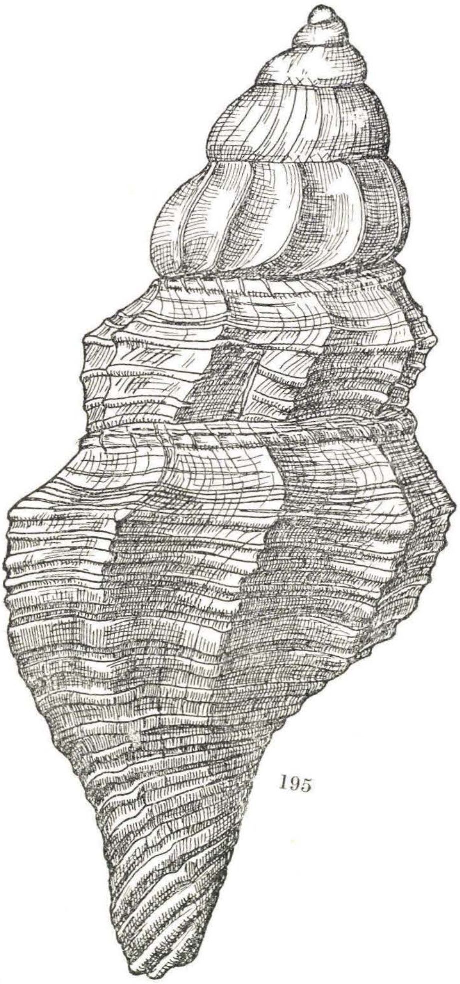
Plate 58.

		Location	Depth	Diameter	Height	Page
194a–c.	*Brachytoma Grateloupi* (PEYROT) (a ×15; b–c ×30).	Bramminge	70–80 m.	3.33	8.80	274
195.	*Brachytoma obtusangula* (BROCCHI) (×30).	Toftlund	75–100 -	2.00	4.35	275
196.	*Brachytoma sp.* (×10).	Bramminge	70–80 -	2.20	6.70	277

Shell dimensions in millimeters.



194 a



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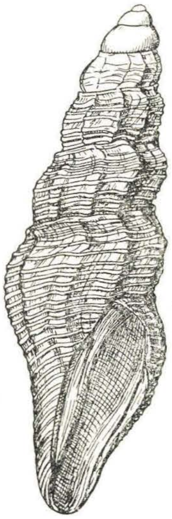
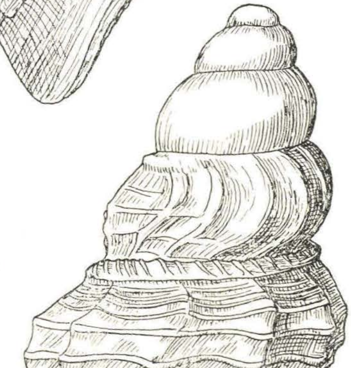
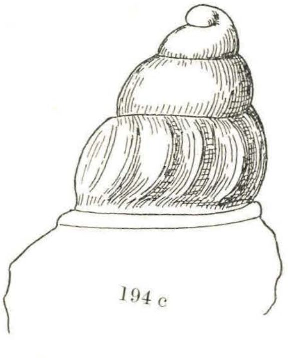


196



194 b



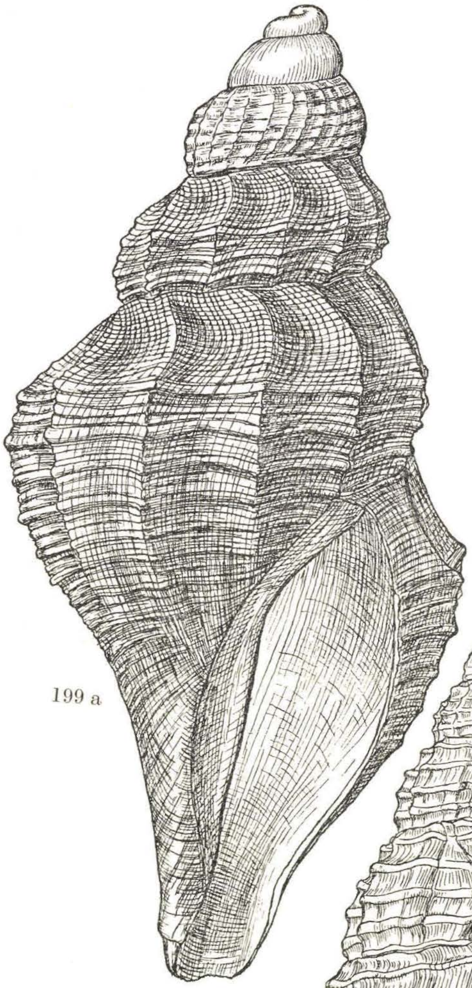
194 c

Th. S. del.

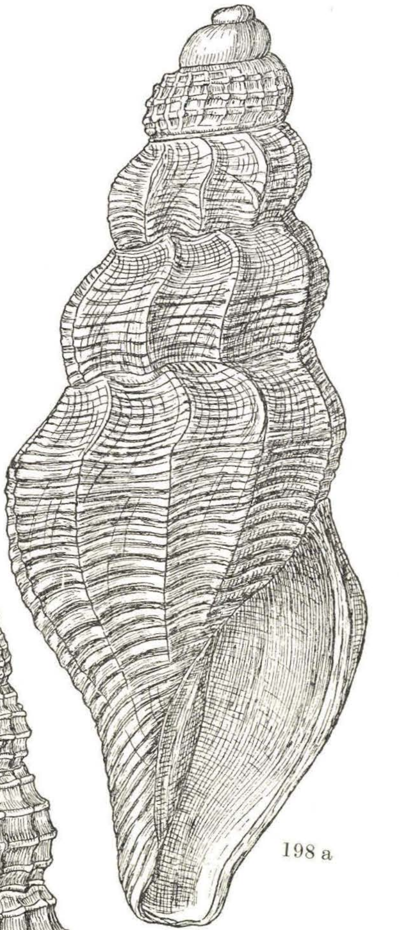
Plate 59.

		Location	Depth	Diameter	Height	Page
197.	*Aphanitoma glejbjergensis nov. sp.* (× 13). Holotype.	Glejbjerg	53 m.	3.4	8.4	277
198a–c.	*Neoguraleus calais* (KAUTSKY.) (× 30).	Toftlund	75–100 -	1.70	4.15	278
199a–b.	*Neoguraleus tenella* (MAYER). (× 30). Shell with granulated spirals and wide apical angle.	Toftlund	75–100 -	2.10	4.32	279

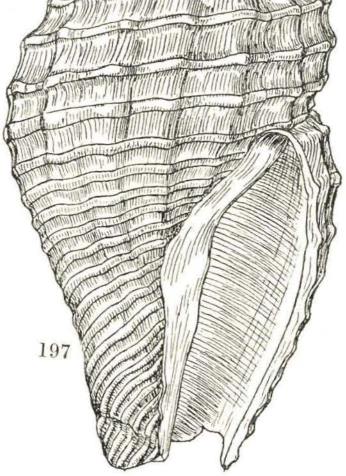
Shell dimensions in millimeters.



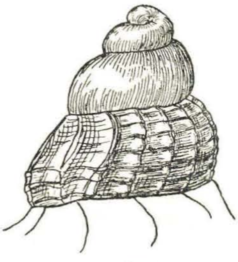
199 a



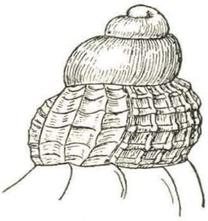
198 a



197



199 b



198 b

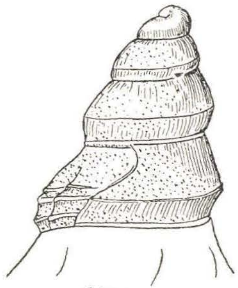
198 c

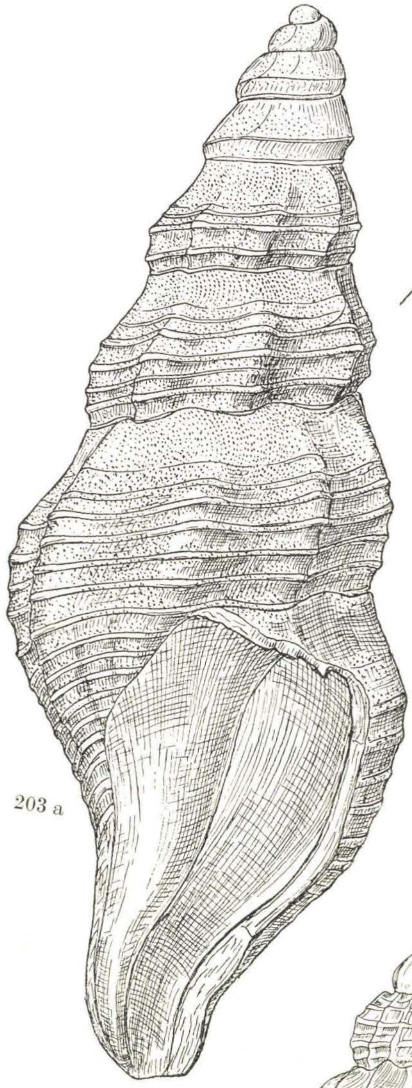
Th. S. del.

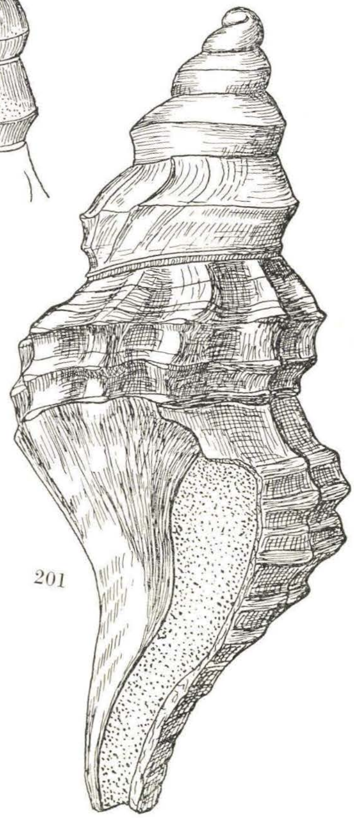
Plate 60.

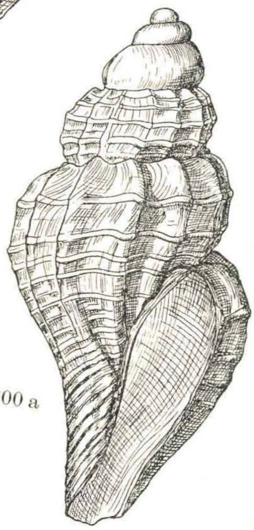
	Location	Depth	Diameter	Height	Page
200a–b. *Neoguraleus Gürichi* (KAUTSKY). (×25).	Bramminge	70–80 m.	1.28	2.7	281
201. *Pleurotomoides Johannae* (PEYROT). (×30).	Toftlund	75–100 -	1.58	3.65	282
203a–b. *Pleurotomoides simplex nov. sp.* (×30).	Toftlund	75–100 -	1.83	4.81	284

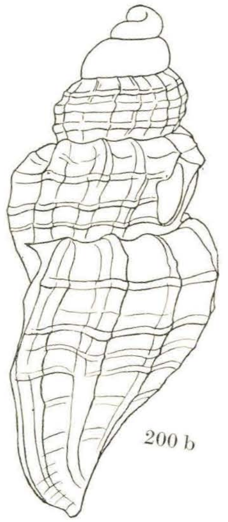
Shell dimensions in millimeters.


203 b


203 a


201


200 a

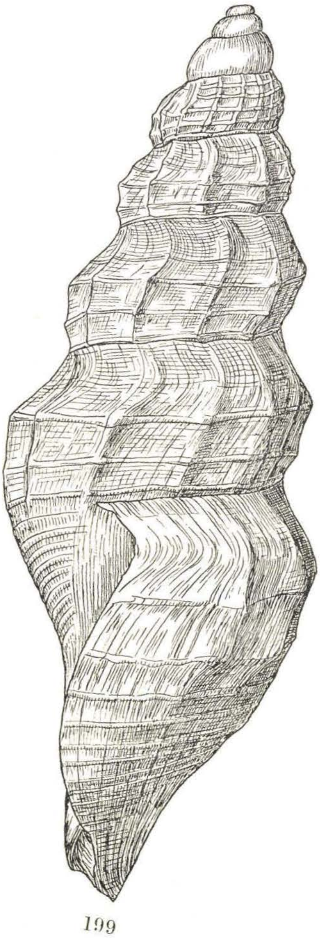

200 b

Th. S. del.

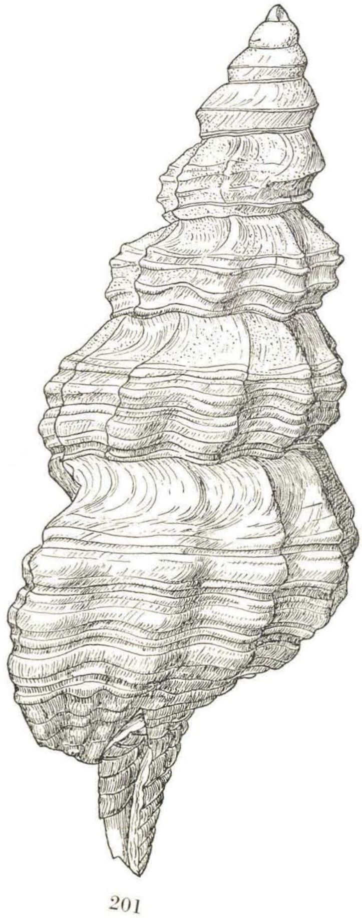
Plate 61.

		Location	Depth	Diameter	Height	Page
199.	*Neoguraleus tenella* (Mayer). (× 24). Normal type.	Toftlund	75–100 m.	1.77	4.96	279
201.	*Pleurotomoides Johannæ* (Peyrot). (× 21).	Toftlund	75–100 -	2.20	5.7	282

Shell dimensions in millimeters.



199



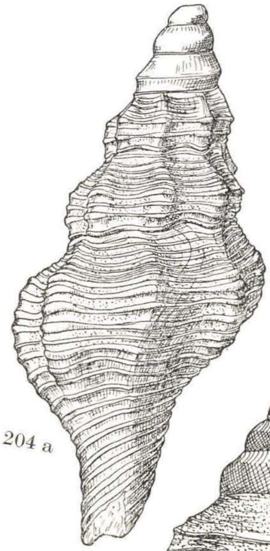
201

Th. S. del.

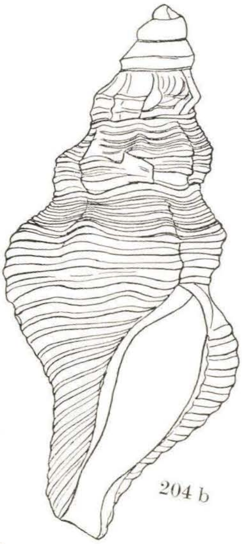
Plate 62.

		Location	Depth	Diameter	Height	Page
204a–b.	*Pleurotomoides cf. Luisae* (von Koenen). (×15).	Bramminge	70–80 m.	2.16	4.80	285
206.	*Teretia anceps* (Eichwald). (×30).	Toftlund	75–100 -	1.33	3.50	287
208.	*Philbertia scabra* (Philippi). (×30).	Toftlund	75–100 -	2.50	4.72	289

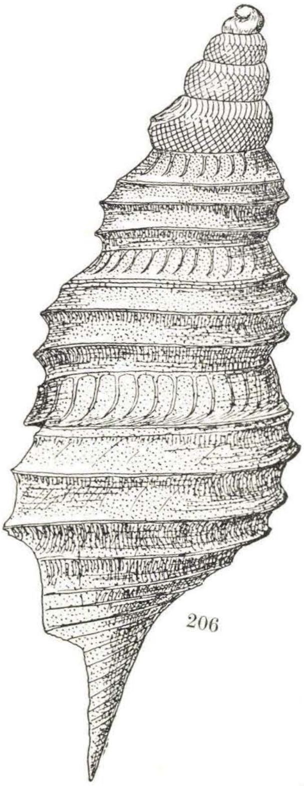
Shell dimensions in millimeters.



204 a



204 b



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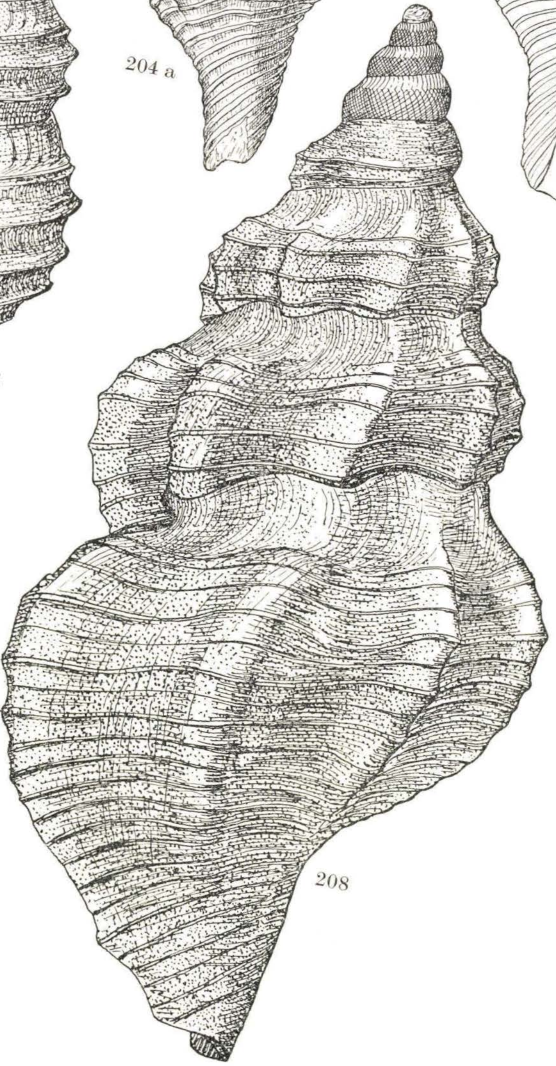


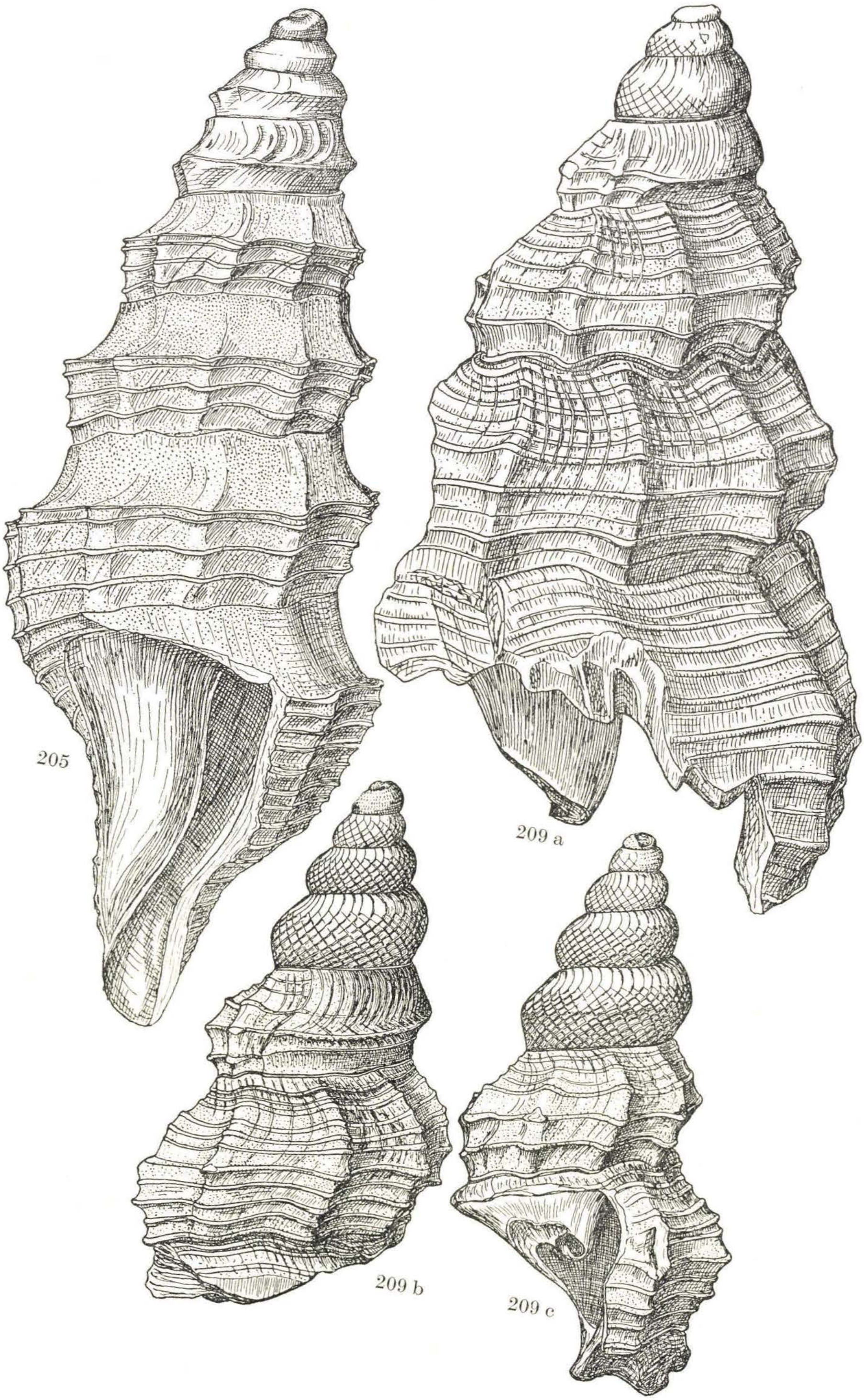
208

Th. S. del.

Plate 63.

		Location	Depth	Diameter	Height	Page
205.	*Pleurotomoides campanulata nov. sp.* (×30). Holotype.	Toftlund	75–100 m.	1.87	4.74	286
209a–c.	*Philbertia sinuosula nov. sp.*					290
a.	(×30).	Bramminge	70–80 -		4.08	
b–c.	(×39).	Toftlund	110–115 -	1.00	1.98	

Shell dimensions in millimeters.



205

209 a

209 b

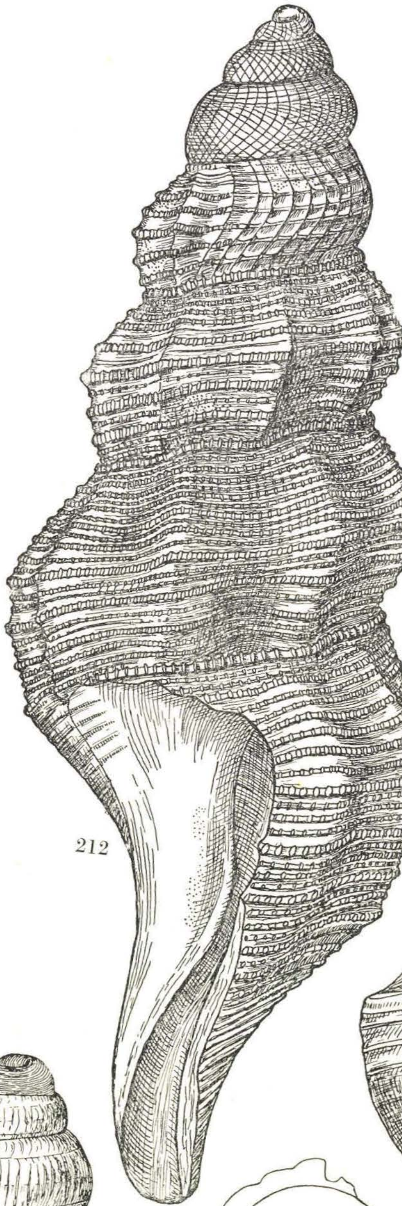
209 c

Th. S. del.

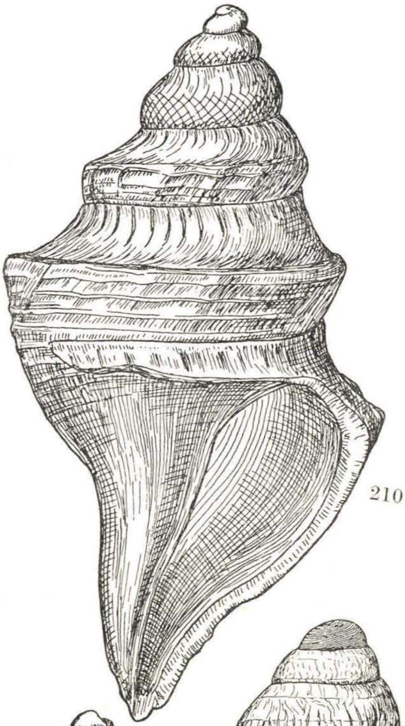
Plate 64.

		Location	Depth	Diameter	Height	Page
210a.	*Eubela trochlearis* (HÖRNES). (×29).	Bramminge	70–80 m.	1.75	3.30	291
210b.	*Eubela trochlearis* (HÖRNES). Shell from the Lower Miocene at Klintinghoved. (×29).					
212.	*Metuonella Grippi* (KAUTSKY). (×31).	Toftlund	115 -	2.05	5.1	293
213a–c.	*Oenopota sp.* (×40).	Toftlund	110–115 -	0.68	1.05	295

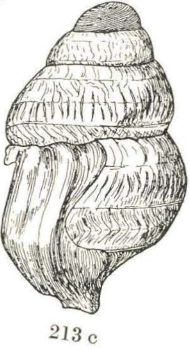
Shell dimensions in millimeters.



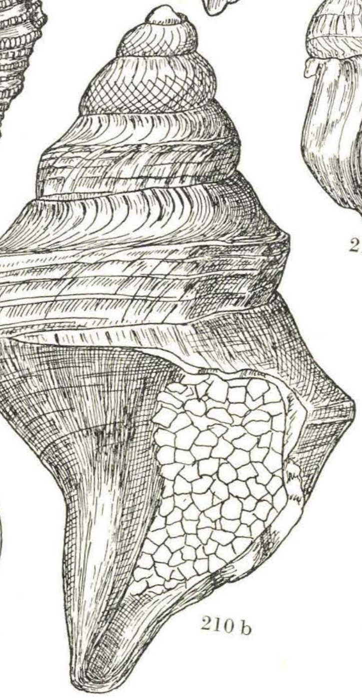
212



210 a

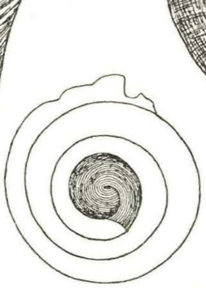


213 c



210 b

213 a



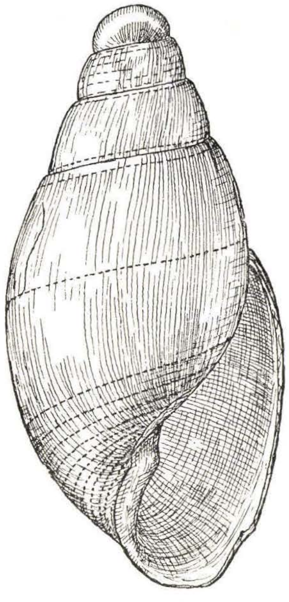
213 b

Th. S. del.

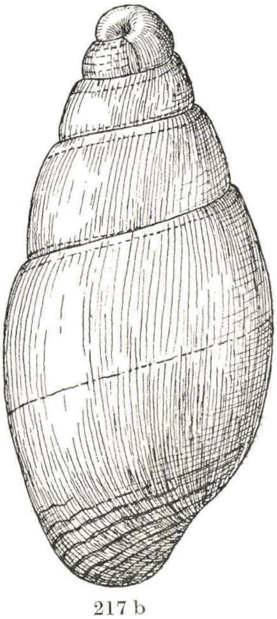
Plate 65.

		Location	Depth	Diameter	Height	Page
214.	*Terebra Hörnesi* BEYRICH. (×31).	Toftlund	75–100 m.	1.72	4.97	295
216.	*Acteon semistriatus* (BASTEROT). (×30).	Toftlund	75–100 -	1.58	2.91	298
217a–b.	*Acteon laevigatus* GRATELOUP. (×30).	Toftlund	75–100 -	1.20	2.60	300

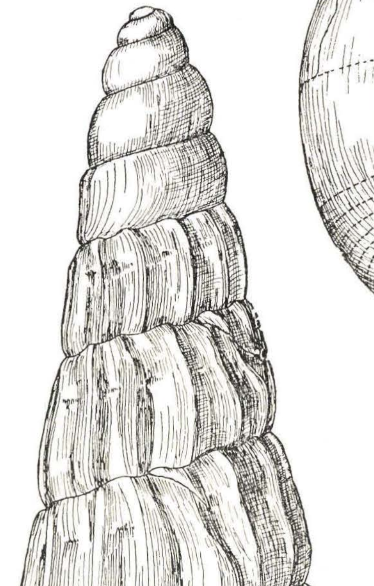
Shell dimensions in millimeters.



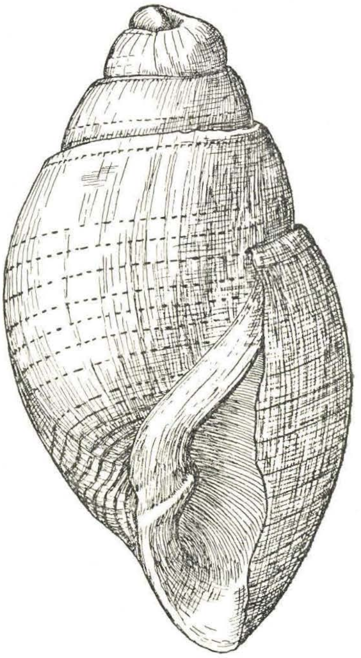
217 a



217 b



214



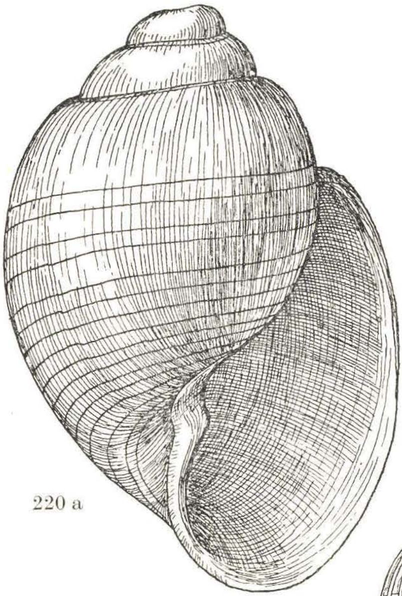
216

Th. S. del.

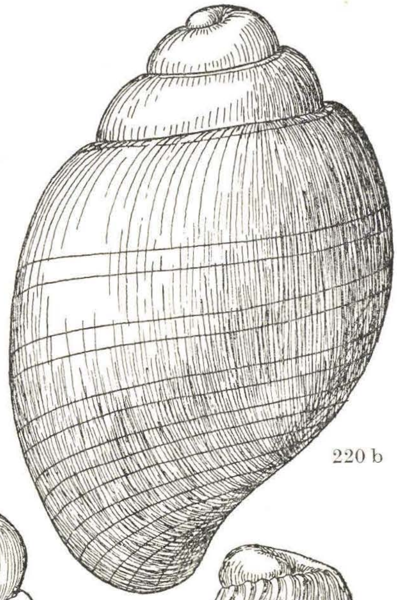
Plate 66.

		Location	Depth	Diameter	Height	Page
220a–c.	*Acteon tornatilis* (LINNÉ). (×30).	Toftlund	75–100 m.	1.75	2.63	303
221a–b.	*Acteon sp.* (×15).	Toftlund	75–100 -	2.58	3.41	304
223a–b.	*Chrysallida cf. cimbrica* (KAUTSKY). (×58).	Arnum (13)	53–84 -	0.58	1.25	305
224.	*Chrysallida nodifera nov. sp.* (×55).	Toftlund	75–100 -	0.66	1.42	306

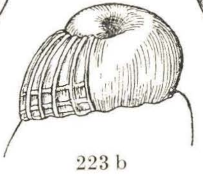
Shell dimensions in millimeters.



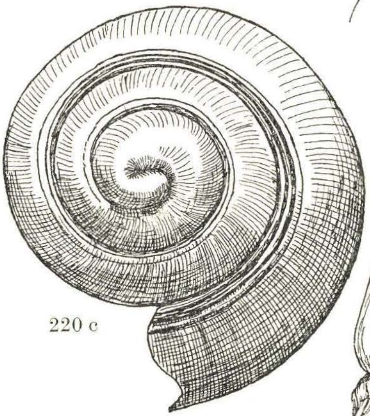
220 a



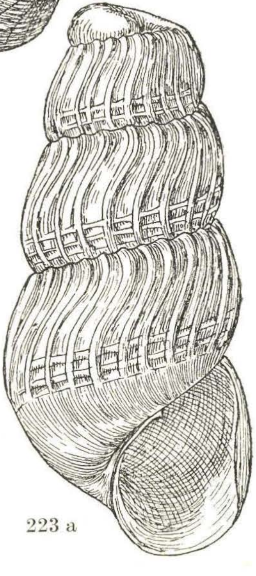
220 b



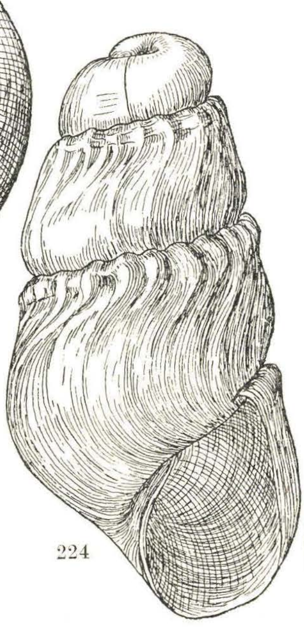
223 b



220 c



223 a



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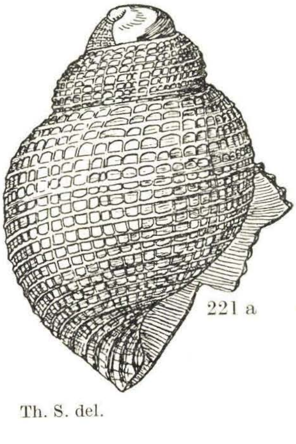
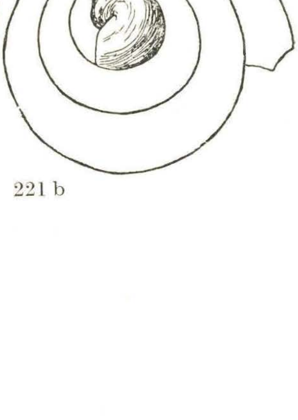


221 a



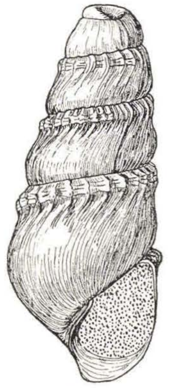
221 b

Th. S. del.

Plate 67.

		Location	Depth	Diameter	Height	Page
224.	*Chrysallida nodifera nov. sp.* (× 26). Holotype.	Toftlund	75–100 m.	0.81	1.92	306
225.	*Chrysallida toftlundensis nov. sp.* (× 42.5). Holotype.	Toftlund	75–100 -	0.55	1.24	307
226a–b.	*Chrysallida acuticostata nov. sp.* (× 42). Holotype.	Arnum (25b)	62.7–62.9 -	0.81	1.68	307
227a–b.	*Chrysallida semireticulata nov. sp.* (× 42). Holotype.	Arnum (25b)	62.7–62.9 -	0.69	1.50	308
228a–b.	*Chrysallida modesta nov. sp.* (× 42). Holotype.	Arnum (25b)	62.7–62.9 -	0.56	1.47	309

Shell dimensions in millimeters.



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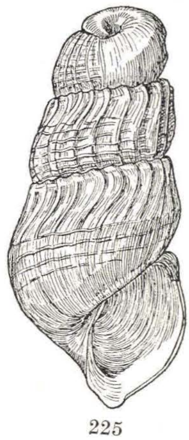

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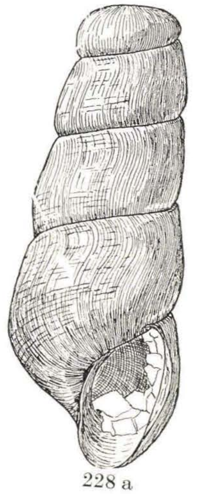
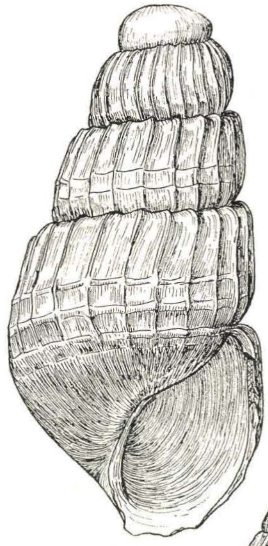
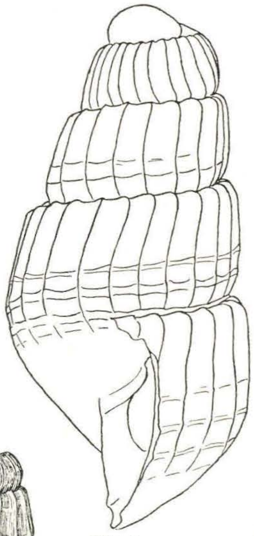


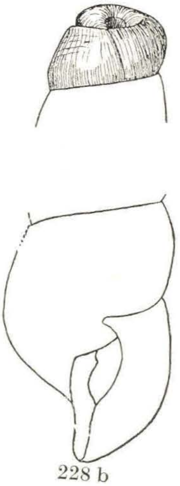
228 a



226 a

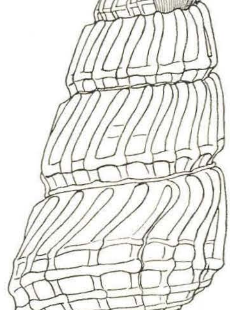


226 b



228 b

227 a



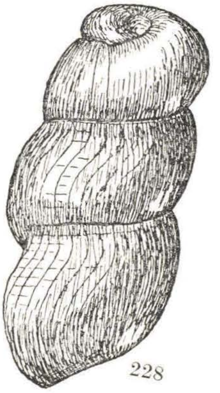
227 b

Th. S. del.

Plate 68.

		Location	Depth	Diameter	Height	Page
228.	*Chrysallida modesta nov. sp.* (×60).	Arnum (13)	53–83 m.	0.42	0.87	309
229.	*Chrysallida pygmaea* (Grateloup) (×60).	Arnum (13)	53–83 -	0.66	1.08	309
230a–c.	*Kleinella (Leucotina) Nordmanni nov. sp.*					310
a.	Holotype. (×30).	Toftlund	75–100 -	1.16	2.54	
b–c.	juvenile shell. (b ×17; c ×45).	Toftlund	105–110 -	0.92	1.45	
233a–b.	*Odostomia sallespissensis* (Cossmann & Peyrot) (×30).	Toftlund	75–100 -	1.08	2.50	315
234a–e.	*Odostomia pallidaeformis* (Sacco)					316
a–b.	(×30).	Toftlund	75–100 -	1.04	2.33	
c–e.	(×30).	Arnum (13)	53–84 -	0.66	1.45	

Shell dimensions in millimeters.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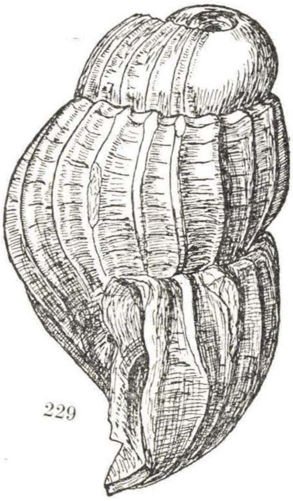
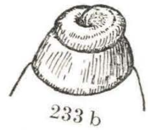
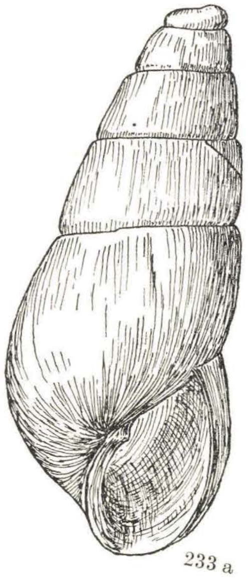
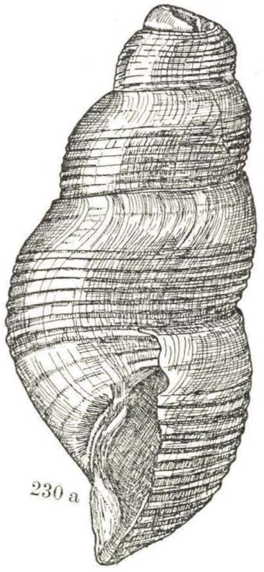
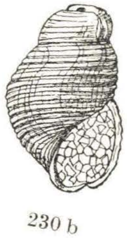
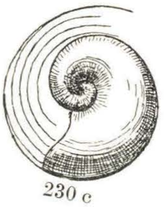

229


233 b

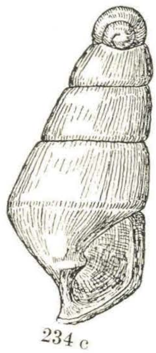

233 a

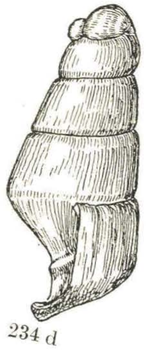

230 a

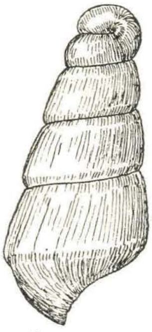

230 b

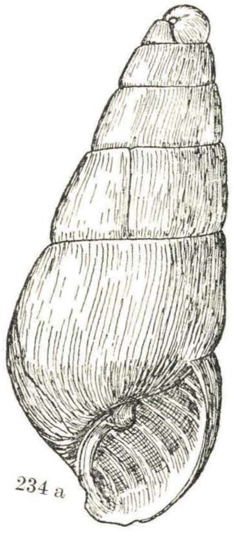

230 c


234 b


234 c


234 d


234 e

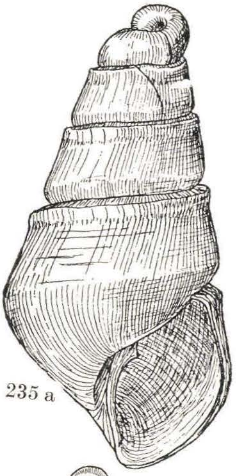

234 a

Th. S. del.

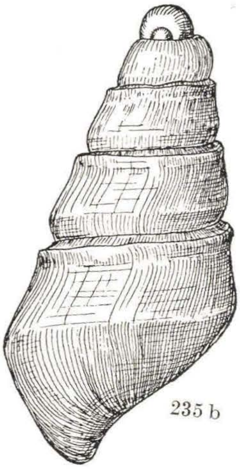
Plate 69.

		Location	Depth	Diameter	Height	Page
235a–b.	*Odostomia mutinensis* (Sacco). (×30). Normal type with shoulder.	Toftlund	75–100 m.	1.08	2.08	317
237.	*Odostomia (Syrnola) dubia* (Grateloup). (×10).	Bramminge	70–80 -	1.91	4.78	321
238a–b.	*Eulimella concinna nov. sp.* (×60).	Arnum (13)	53–83 -	0.58	1.69	321
239a–c.	*Eulimella Scillae* (Scacchi) (×18).	Toftlund	105–110 -	0.97	3.2	322
241a–b.	*Eulimella crassitesta nov. sp.* (×18).	Bramminge	70–80 -	1.21	3.63	325
243a–b.	*Turbonilla lactea* (Linné). (×60).	Arnum (13)	53–83 -	0.44	0.88	326

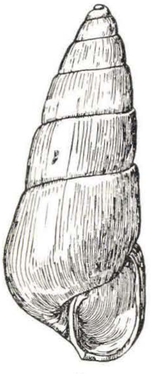
Shell dimensions in millimeters.



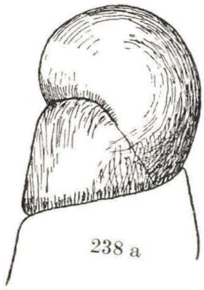
235 a



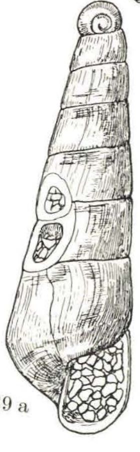
235 b



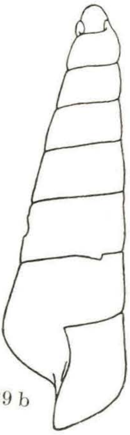
237



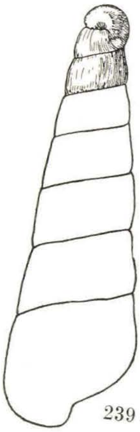
238 a



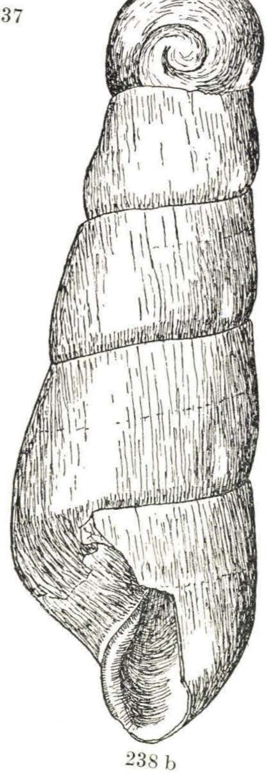
239 a



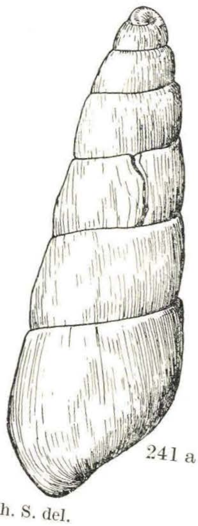
239 b



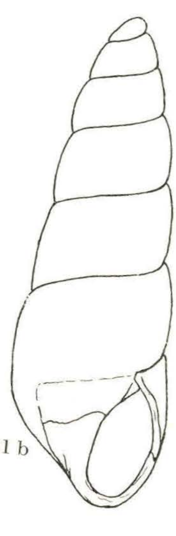
239 c



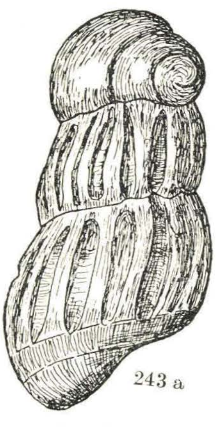
238 b



241 a



241 b



243 a

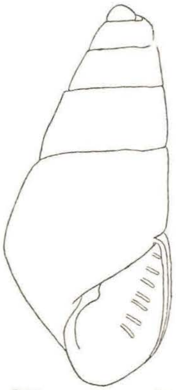
243 b

Th. S. del.

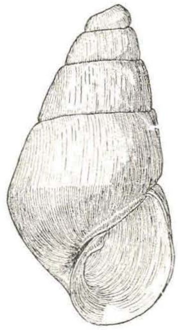
Plate 70.

		Location	Depth	Diameter	Height	Page
231a–c.	*Odostomia conoidea* (Brocchi).	Toftlund	105–110 m.			312
	a. (×21).			1.14	2.44	
	b. (×21).			1.12	2.02	
	c. (×21).			1.08	1.93	
232.	*Odostomia subintermedia* (Cossmann & Peyrot). (×21).	Arnum (25b)	62.7–62.9 -	0.77	1.70	314
234.	*Odostomia pallidaeformis* (Sacco). (×21).	Toftlund	105–110 -	0.82	1.84	316
235.	*Odostomia mutinensis* (Sacco). Smooth type without shoulder. (×21).	Toftlund	105–110 -	1.21	2.54	317
236.	*Odostomia (Syrnola) subumbilicata* (Grateloup). (×21).	Glejbjerg	53.5 -	1.34	4.16	320
238.	*Eulimella concinna nov.sp.* (×21,5). Holotype.	Toftlund	105–110 -	1.09	4.45	321
241.	*Eulimella crassitesta nov.sp.* (×26). Holotype.	Gramby	82.66–83.76 -	0.96	2.46	325
242.	*Turbonilla costellata* (Grateloup). (×26).	Arnum (25b)	62.7–62.9 -	0.79	2.35	325

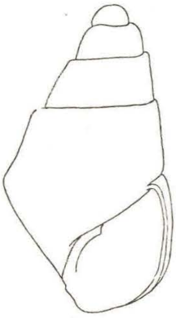
Shell dimensions in millimeters.



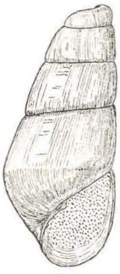
231 a



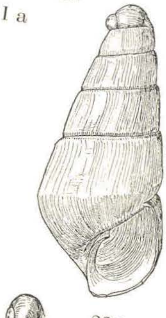
231 b



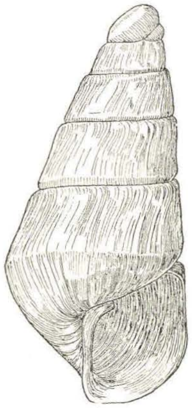
231 c



232



234



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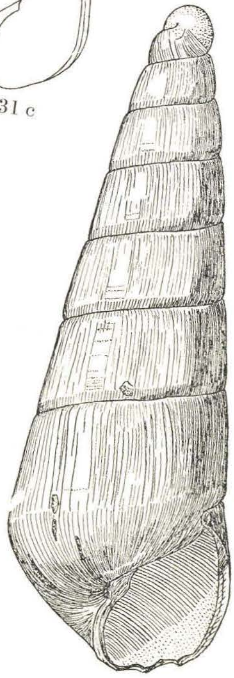

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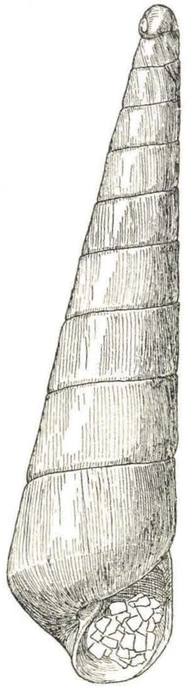
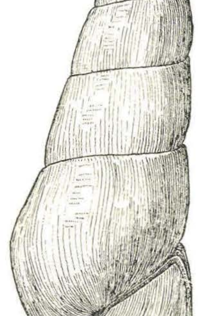


238



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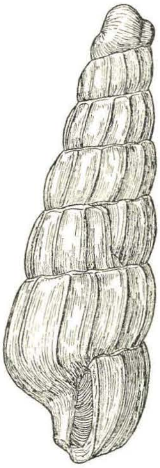


242

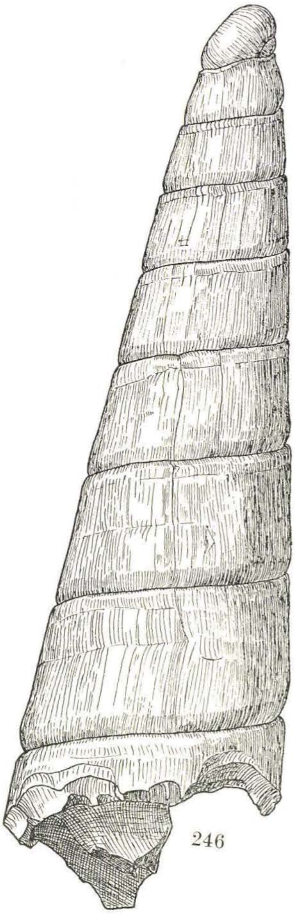
Th. S. del.

Plate 71.

		Location	Depth	Diameter	Height	Page
243.	*Turbonilla lactea* (L.). (×26).	Arnum (25b)	62.7–62.9 m.	0.89	3.27	326
246.	*Turbonilla sp.* (×26).	Gramby	82.66–83.76 -	1.41	4.65	331

Shell dimensions in millimeters.

243



246

Th. S. del.

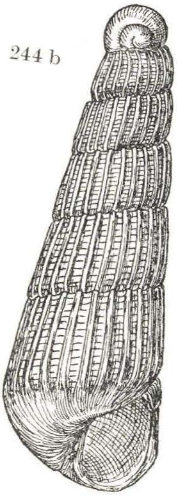
Plate 72.

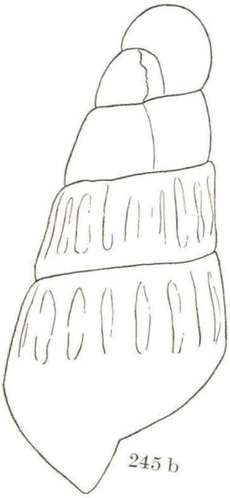
		Location	Depth	Diameter	Height	Page
244a–c.	*Turbonilla rufa* (PHILIPPI). (×30).	Arnum (13)	53–83 m.	0.75	2.19	328
245a–c.	*Turbonilla pseudoterebralis* (SACCO). (×36)	Toftlund	105–110 m.	0.85	1.81	329
247.	*Pyramidella plicosa* BRONN. (×24).	Toftlund	75–100 -	1.83	5.25	332
248a–b.	*Ringicula ventricosa* (SOWERBY). (×10).	Toftlund	115 -	4.99	6.65	333

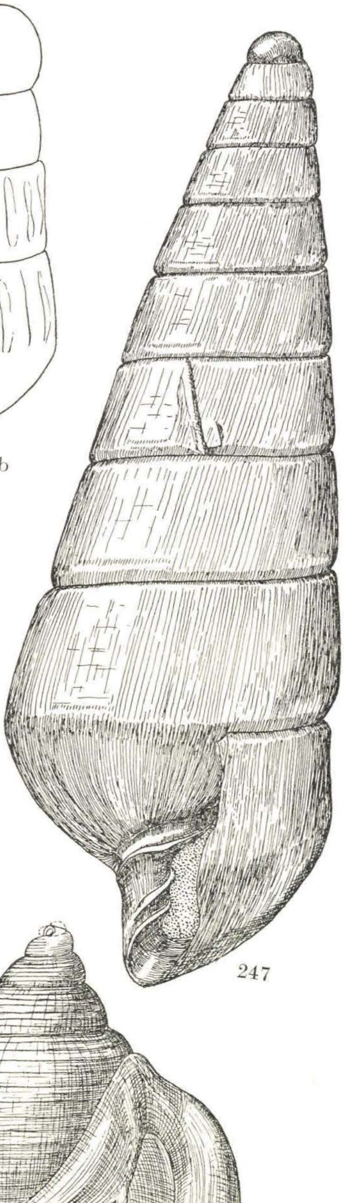
Shell dimensions in millimeters.


244 b


244 c


244 a


245 b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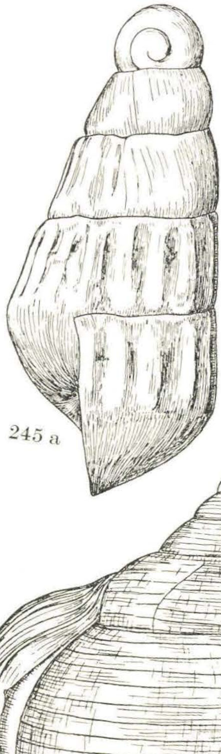
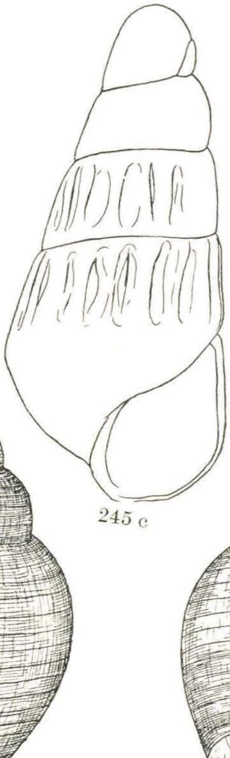
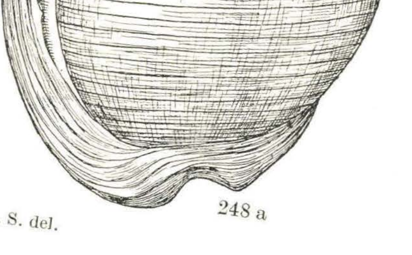
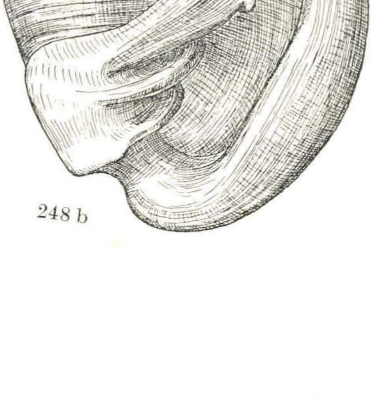

245 a


245 c


248 a

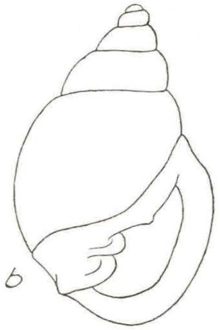

248 b

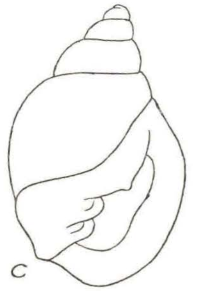
Th. S. del.

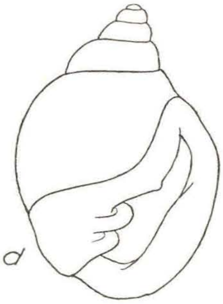
Plate 73.

	Location	Depth	Diameter	Height	Page
249a-m. *Ringicula buccinea* (BROCCHI)	Toftlund	75–100 m.			334
a–h. (× 10).					
j. (× 10).			2.52	3.93	
k–m. (× 15).			2.74	4.07	
250a–c. *Rinjicula Ravni nov. sp.* (× 20). Holotype.	Toftlund	110–115 -	1.64	2.76	340

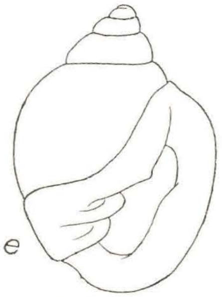
Shell dimensions in millimeters.

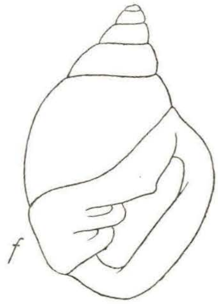


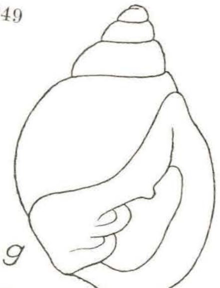




249

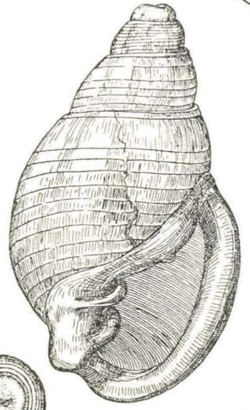




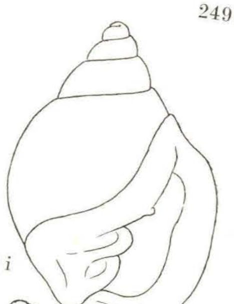


249 a–h

250 c



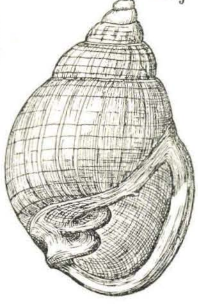
250 b



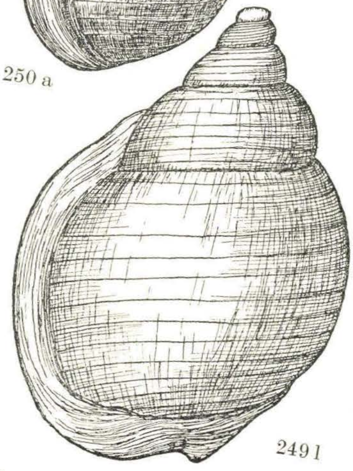
249 i

250 a

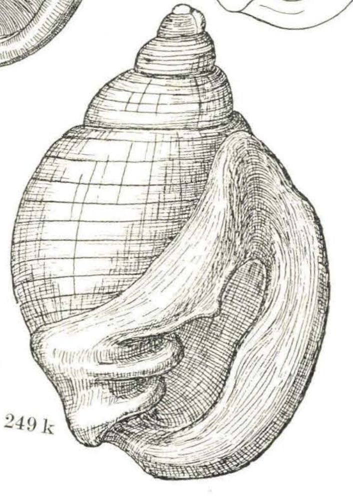
249 m



249 j



249 l



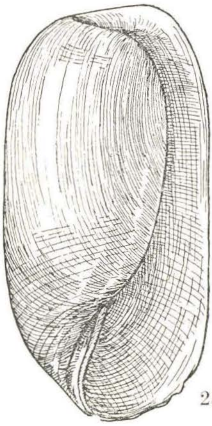
249 k

Th. S. del.

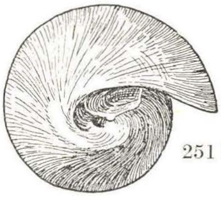
Plate 74.

	Location	Depth	Diameter	Height	Page
251a–c. *Cylichna cf. cylindracea* (PENNANT). (×40).	Toftlund	110–115 m.	0.69	1.37	342
253a–c. *Rhizorus acuminatus* (BRUGUIÈRE). (×60).	Arnum (13)	53–83 -	0.83	2.02	344
254a–c. *Retusa elongata* (EICHWALD). (×60).	Arnum (13)	53–83 -	0.92	1.59	345

Shell dimensions in millimeters.

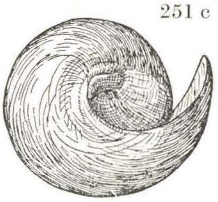


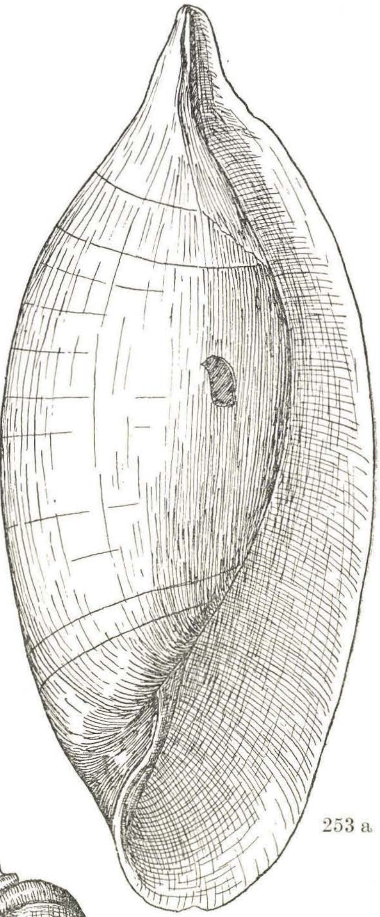
251 a



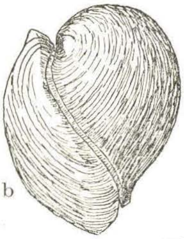
251 b

251 c

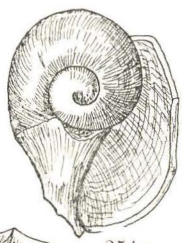




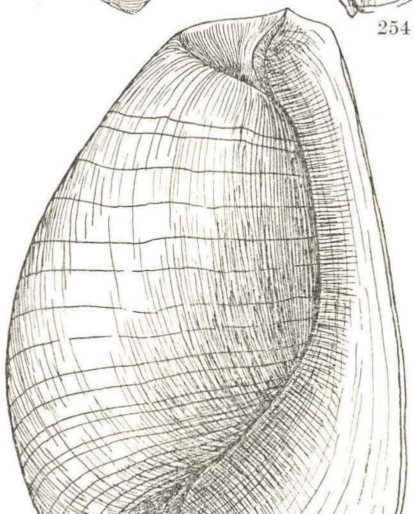
253 a



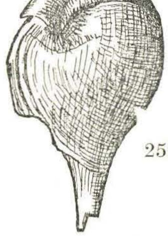
254 b



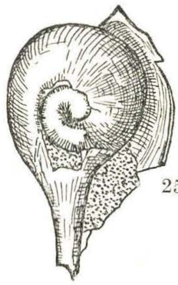
254 c



254 a



253 b



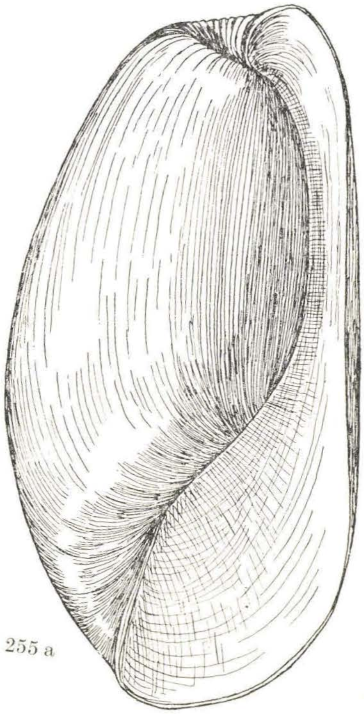
253 c

Th. S. del.

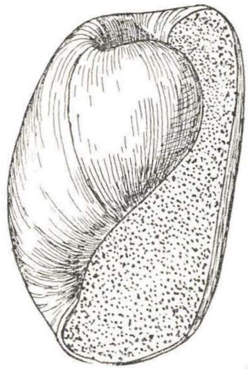
Plate 75

	Location	Depth	Diameter	Height	Page
255a–c. *Retusa umbilicata* (MONTAGU)	Arnum (13)	53–83 m.			346
a. (×50).			0.97	1.87	
b. (×60).			0.50	0.83	
c. Protoconch. (×60).			0.25		
255d–e. cf. *Retusa umbilicata* (MONTAGU). (×30).	Toftlund	105–110 -	0.98	1.96	
258a–c. *Acteocina Lajonkaireana* (BASTEROT). (×60).	Arnum (13)	53–83 -	0.71	1.50	348

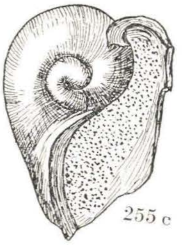
Shell dimensions in millimeters.



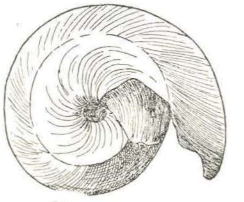
255 a



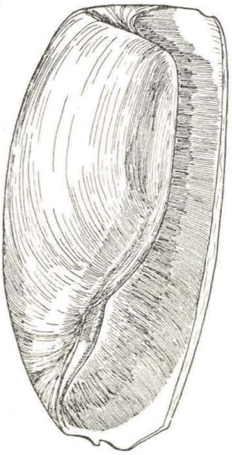
255 b



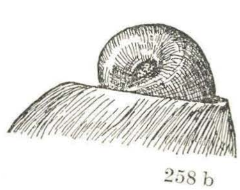
255 c



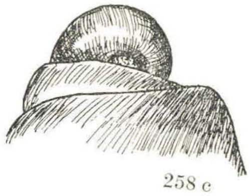
255 d



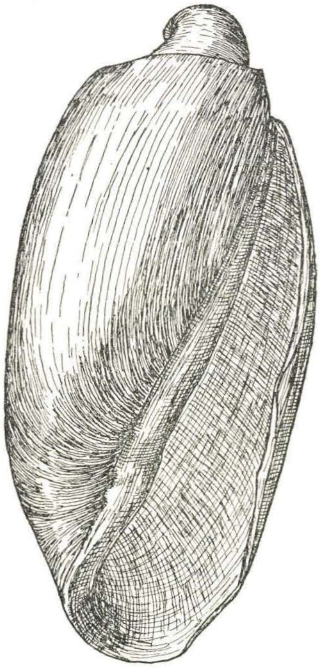
255 e



258 b



258 c



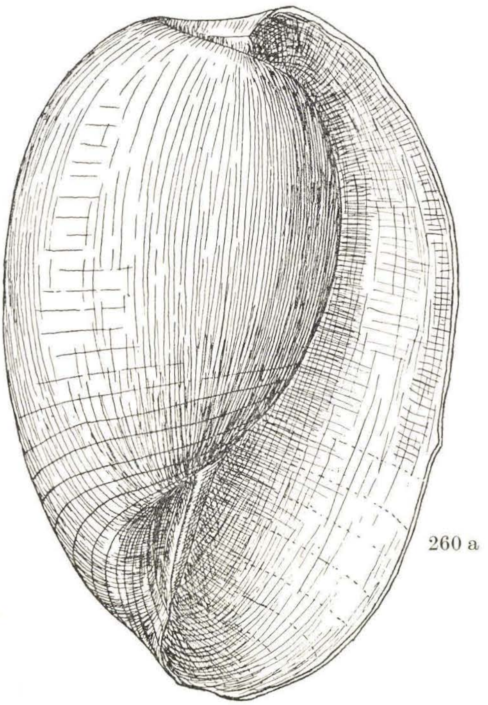
258 a

Th. S. del.

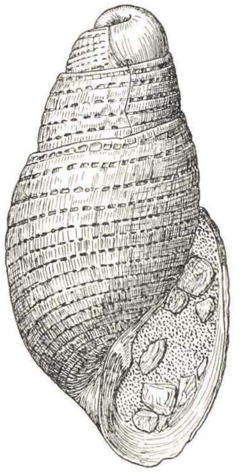
Plate 76.

		Location	Depth	Diameter	Height	Page
209.	*Philbertia sinuosula* *nov. sp.* (×23) Holotype	Toftlund	105–110 m.	1.74	3.49	290
219.	*Acteon arnumensis* *nov. sp.* (×37) Holotype	Arnum (25 b)	62.5–62.7 m.	0.81	1.65	302
260a–b.	*Roxania utriculus* (BROCCHI). (×60).	Arnum (13)	53–83 m.	1.04	1.62	350

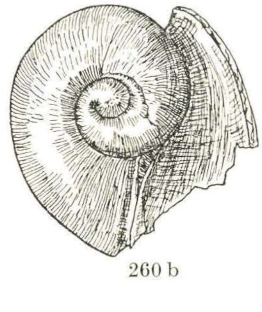
Shell dimensions in millimeters.



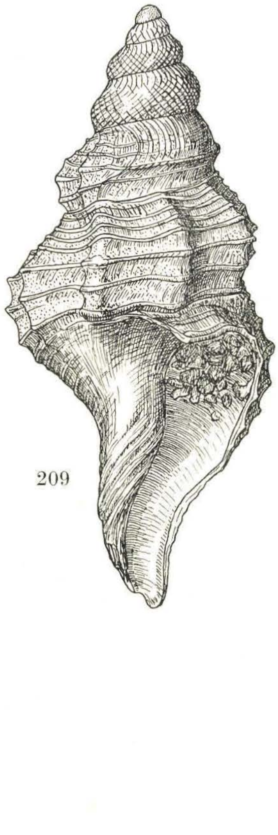
260 a



219



260 b



209

Th. S. del.

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