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ON THE DISTRIBUTION OF BRACHIOPODS IN THE LOWERMOST LLANDOVERY OF ESTONIA

Introduction

Five benthic communities have been defined in the Llandovery shelly facies (Ziegler, 1965; Ziegler, Cocks and Bambach, 1968). They occupied large parts of the British Isles, Norway and North America in Late Llandovery time, and are probably depth and temperature controlled (Cocks, 1967; Berry and Boucot, 1968). W. B. N. Berry and A. J. Boucot (1967) have suggested that the same communities existed around the margins of the Russian Platform during the Late Llandovery. The evidence from Sweden to Moldavia is very good; that from the western slope of the Urals, Pai-Hoi, Vaigatch, southern Novaya Zemlya and northern Timan more scattered. Brachiopods have been used for this purpose.

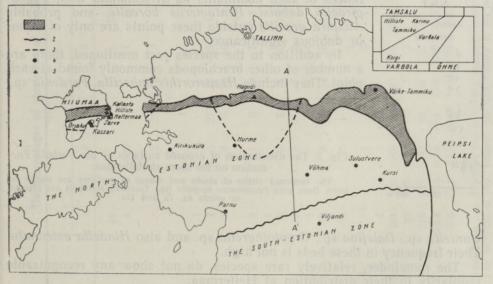


Fig. 1. The distribution of the Juuru Stage in Estonia with a key to the stratigraphic units on the line AA' (after Nestor, Kala, 1968).

1- outcrop area, 2- boundary between zones, 3- southern boundary of the district with bioherms, 4- borings, 5- localities. Relationships between the stratigraphic units are given in the quadrangles on the upper-right: member names are given within it and formation names outside, in capital letters.

The recent stratigraphic revision of the lowermost Llandovery in the northern East Baltic area (Nestor, Kala, 1968) is a very useful basis for discussing synecological problems within the Juuru Stage of Estonia. In the area studied H. Nestor and E. Kala distinguished two facial zones: the North- and South-Estonian (Fig. 1). The fauna occurring in these two zones is almost entirely different (see Nestor, in press).

The aim of this article is to interpret the distribution of the brachiopods of the Juuru Stage in terms of communities.

I gratefully acknowledge the help of H. Nestor, who collected a great number of the samples and prepared them for study, of K. Kajak, who provided me with samples from the borings of the South-Estonian zone, and of A. J. Boucot, who critically read and corrected the manuscript.

Outcrop area

The best locality for demonstrating the brachiopod sequence in the Juuru Stage is the eastern shore of Hiiumaa Island at Heltermaa. Separate beds, mainly of the Varbola Formation, are exposed on both sides of Heltermaa Haven, along the shore stretching for 2.0 or 2.5 km (Fig. 2).

They commonly follow the order shown in the mapped section. It is necessary to note that the fossils are largely collected from loose material on the shore. However, my experience at points 15a and 7a (these are the beds with *Pentamerus borealis*) has shown the absence of significant movement of this loose material.

Actually, the Varbola Formation sequence is twice repeated at Heltermaa. In both "sections", the first four species from Table 1 were always collected in certain beds (=points). In spite of active search, the occurrences of such dominants as Stricklandia lens, Zygospiraella duboisi, Pentamerus borealis, and probably Alispira gracilis outside these points are only of minor or dubious significance.

In addition to the species just mentioned, there are a number of other brachiopods commonly found at each point. They include *Hesperorthis imbecilla*, *Fardenia* sp.,

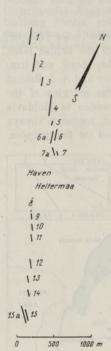


Fig. 2. The distribution of exposed surfaces of the Varbola Formation on the shore at Heltermaa:

The supposed strike of strata and extent of surfaces are shown by lines. Beds with *Pentamerus borealis* (the Tammiku Member) are exposed at points 6a, 7a and 15a.

Onniella sp., Dalejina sp., Cryptothyrella sp. and also Hindella extenuata. Their frequency in these beds is not high.

The remainder, relatively rare species, do not show any recognizable regularity in their distribution at Heltermaa.

The experience at Heltermaa and other localities has shown that we cannot establish a noticeable variation in brachiopod distribution within the Varbola Formation. The dominant species *Stricklandia lens* and *Zygospiraella duboisi* may be exceptional because they have been found to be limited vertically. Nevertheless, these species are also repeated twice or three times over in sections of the Juuru Stage.

The third dominant, *Pentamerus borealis*, occurs in profusion only once, viz., in the Tamsalu Formation, where it forms a true brachiopod bank (the Borealis Bank, = the Tammiku Member). In a typical case, this bank is formed only by disarticulated valves and isolated tabulates and stromato-

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* The percentages have been calculated in the following manner: complete shells, and brachial and pedicle valves have each been taken as one specimen. For location of the "points" see text Figure 2. All points except for 15a (= the Tamsalu Formation) belong to the Varbola Formation. For calculation of the ecological indices, see pp. 77—78. All fractional percentages were rounded off.

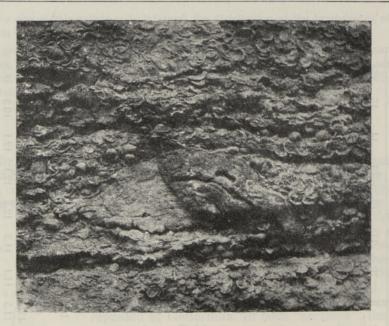


Fig. 3. A photograph of the brachiopod bank of the Tammiku Member at Hagudi.

poroids (Fig. 3). However, rare specimens of Hesperorthis imbecilla, Far-

denia sp., and solitary corals have been found within such banks.

In the marginal area of the bank, its dominant *Pentamerus borealis* occurs together with other species of the Varbola Formation, except for *Zygospiraella duboisi* and *Alispira gracilis*. *Stricklandia lens* is also common in this area of the Tammiku Member. Nevertheless, the influence of the Borealis Bank was so great that we may speak of the recurrence of the Varbola brachiopod fauna in the top of the Juuru Stage. The discontinuous occurrences of *Zygospiraella duboisi* and *Stricklandia lens* best demonstrate this phenomenon. The revival of the Varbola brachiopods in the Karinu Member is not absolute, e. g. *Alispira gracilis* is absent.

Within the North-Estonian zone, there are great deviations from the brachiopod sequences described above in the bioherm localities. This type of deviant deposit is associated with the Hilliste Member bioherms (see Fig. 1). So far, only a few bioherms have been studied. Whether there were some temporal or ecological differences between the separate bioherms is not known. But there are many brachiopods occurring only or predominantly in this type of deposit (see Table 2). *Pentamerus borealis* is totally absent in these bioherms, and the biohermal species tend to not occur

with it.

In conclusion, we may say that all the variations in the Juuru Stage brachiopod fauna distribution in the outcrop area suggest in a general way some type of ecological control.

Subsurface area

If the Juuru Stage in the outcrop area contains brachiopods which fall naturally into three assemblages, then the same situation should be observed in borings as well. As we have to deal with a relatively fast regression of the Llandoverian sea in the East Baltic, this situation may be observed in a single boring.

Table 2

Distribution of the brachiopods from the Hilliste Member bioherms

not the same in the whote exten-		Locali	ties	
Species boltogram	Sarve	Hilliste	Hilliste loose material	Kallasto
pearance has the same obvious	1 3			
Anastrophia sp. Atrypopsis reclinis	+	_	+	+
Clorinda sp.	T +			
Dictyonella capewelli			+	
Dalmanella cyclica	+	+ "	+	+
Fardenia sp.			+	
Furcitella sp.		10.0	+	
Hesperorthis hillistensis	+	+	+	+
Leptaena sp. Linoporella punctata	The state of the s	+	+	- 84
Parastrophinella indistincta	4	+	+ 1	+
Platystrophia affabilis	Maria St.	+	+	3 1 1 2
Ptychopleurella erecta	+		+	+
Spirigerina hillistensis	+		+	+
Stegerhynchus sp.		+	+	8 24
Triplesia maennili		+	+	+

It is obvious that in our case the examination of borings for ecological purposes should be more promising than the outcrop study. But the statistical method for studying Silurian communities suggested by A. M. Ziegler

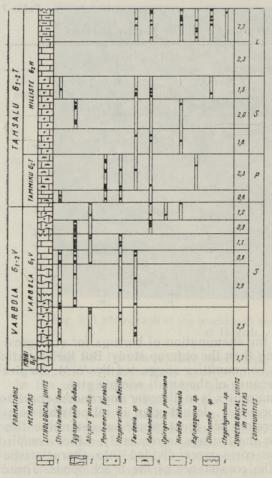
is not suitable for the borings because of the small sample size.

The main idea in defining communities is to discover nonrandom coexistence of certain animals, "..all species... do not occur in all possible combinations" (Johnson, 1964). Therefore we must somehow determine this coexistence. Brachiopods occur in the borings infrequently, which complicates sampling. Accordingly, the cores were divided into characteristic intervals adequate for defining the coexistence of the brachiopods. These intervals, in which a similar group of brachiopods and/or other benthic animals occurs, are named here synecological units (in a manner similar to the way a lithologist describes a core in terms of lithological units). They are only aids for determining the coexistence of the taxa for an ecological description of the core. It is clear that we must beware of long intervals rather than short ones. The determining of the intervals is very concrete, but note that in general they depend reciprocally on the abundance of fossils and the number of borings studied (i. e. frequency in regard to kind of community).

Two types of evidence are utilized here for this purpose: (1) the single supposed continuous occurrence of *Pentamerus borealis, Stricklandia lens, Zygospiraella duboisi* and *Alispira gracilis* as the most ubiquitous and abundant species in the North-Estonian zone; (2) the same for *Meifodia ovalis, Clorinda undata, Sowerbyella* sp., *Skenidioides lewisi* in the South-Estonian and transitional zones; (3) the boundaries of lithological units. If such boundaries did not coincide, then the former ones were preferred.

One example of such stratification is represented by the data from the Orjaku boring (Fig. 4). Nine borings have been studied (see Fig. 1).

Like brachiopod distribution in the outcrop area, the discontinuous occurrences of the dominant species appear clearly in the borings. Of course, the recognition of a true gap between successive occurrences of one species recorded intermittently in borings is a problem. But, following



the occurrence of dominant species, we may assume that (1) the frequency of their finds is not the same in the whole extent of one core, (2) their occurrence is repeated, boring by boring, in the same parts of the Juuru Stage core, or (3) their disappearance has the same obvious geographical trend. It seems that other species (not dominant) do not occur in the whole of the Juuru Stage core. Therefore we may speak of the discontinuous occurrences of the studied brachiopods.

It is obvious that all these phenomena are predominantly controlled by ecological reasons, viz. by the presence of certain communities occurring inter-

mittently.

Fig. 4. A synecological stratification of the core in the Orjaku boring. The supposed continuous occurrences of the species (taxa) are framed by parallel lines. See also text.

1 — limestone, 2 — nodular limestone, 3 — detrital matter, 4 — coquina, 5 — argil-

laceous admixture, 6 - discontinuity surface.

In the borings, all the brachiopod assemblages known in the outcrop area are present. As an example, the last interval (2.2*) of the Orjaku boring contains the bioherm brachiopods, the large interval (4.4) of the Väike-Tammiku boring is the pure Borealis Bank, the lower part (6.0, 1.5, 3.3) of the Kirikuküla boring contains the brachiopod fauna of the normal nearer-shore facies, and almost the whole Viljandi boring contains the typical off-shore community.

If only certain communities range throughout the whole area studied here, then we may define the assemblages of brachiopods by means of their coexistence recorded by the accepted synecological units, independent of the geographical location of the borings containing these units. This situation permits us to estimate the coexistence on the basis of the frequency of such events. But this is a special problem which will not be treated in this paper in detail. I confine myself to a representation of the coexistence of the studied brachiopods in the form of absolute observed numbers.

Let us regard the Orjaku boring again (Fig. 4). The Koigi Member (G_1K) forming one synecological unit does not contain brachiopods. The Varbola Member (G_1V) has been divided into six synecological units by supposed continuous occurrences of three dominant species recorded there. In the first unit (with thickness of 2.5 m) Stricklandia

^{*} The thicknesses of the corresponding synecological units are given in brackets.

lens (S) occurs together with Alispira gracilis (A), Hesperorthis imbecilla (He), and Fardenia sp. (Fa). That may be denoted as

also in the same unit

In all cases the coexistence recorded is denoted by "1". Adding up all data from the first synecological unit, we obtain

	A	He	Fa			S	A	He	Fa
S	1	1	1		S		1	1.	1
A		1	1	or	A	1		1	1
He			1		He	1	1		1
	OF SER				Fa	1	1	1	

In the more complete table (matrix), we do not show the logical coexistence of S with S. A and A etc., except when the taxon occurs alone within such units (then also 1).

Adding to the last matrix the data from the second synecological unit of a thickness of 2.9 m, we have

	S	A	He	Fa	Z			S	A	He	Fa	Z
S		1	1, 1	1, 1	1		S		1	2	2	1
A	1		1	1			A	1		1	1	
He	1, 1	1		1, 1	1	or	He	2	1		2	1
			1, 1				Fa	2	1	2		1
Z	1		1	1			Z	1		- 1	1	

The final data produced from all borings are conveniently represented in the form of a triangular half matrix, the other half of which is the mirror

image of that shown in Table 3.

The conspicuous clustering of the numbers in Table 3 is produced by an arrangement of the given taxa in a fixed order (removing some species to another place in this order, we get a less distinct, unclustered picture). This arrangement might also be obtained by special (formalized) techniques. In this article it has been made, however, on the following basis: (1) the occurrence of the given brachiopod in certain zones, the order of which was previously known, (2) its appearance within one zone (by which we assume that the trend of facial changes within one zone is the same as in the whole sequence), e. g. Stricklandia lens occurs nearer to the South-Estonian zone than Zygospiraella duboisi, (3) an occurrence in one or several zones, in other words on the basis of the number of taxa coexisting together with the given taxon.

The last four taxa in Table 3 seem to make up a specific group. They occur together with all the taxa of the North-Estonian zone. Their location at the right side of the table shows their indifference to coexisting with other taxa (except for the taxa of the South-Estonian zone) or to inadequacy in their identification. The latter case is probably in effect with the *Clorinda* located in the right part of the table. *Clorinda undata* is a typical representative of the South-Estonian zone. I am not able, at this time, to distinguish the true *Clorinda undata* from three specimens found in the Sarve bioherm. However, the conceivable taxonomical difference of these specimens has been denoted here not as a coexistence of true *Clorinda undata*, but by the symbol "sp". In a similar way, the rare occurrences of *Platystrophia* sp. outside the biohermal deposits are probably not identical

Table 3

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Species

6. Leptellininae, gen. indet.

Dicoelosia sp.

5. Sowerbyella sp.

Clorinda undata, sp.

Skenidioides lewisi

Triplesia insularis

1. Meifodia ovalis

Spirigerina porkuniana

Zygospiraella duboisi

Alispira gracilis Rafinesquina sp.

Stricklandia lens

10. 12.

Dolerorthis sp.

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1000	29.	Cr F	2 4 - 3 - 8 4 1 1 3 - 3 - 4 1 1 3 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	
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	4.	CIO :	in other words on the basis of the munber of lax a	
	2. 3.	Tri Sk	replaced location of the borings containing these u	
1	24	H	c taratta d'ag la commitaga la que adampatrament le la la la material co	

Platystrophia affabilis, sp.

16. 15.

Ptychopleurella sp. Clintonella aprinis

Leptaena sp.

8. 19.

Pentamerus borealis Hindella extenuata

Parastrophinella indistinct

Stegerhynchus sp.

Furcitella sp.

Dictyonella capewelli

Atrypopsis reclinis

23. 23. 24.

Dalmanellids: Onniella, Dalmanella, Dalejina

Hesperorthis imbecilla, hillistensis

Fardenia sp.

Linoporella cf. punctata

Triplesia maennili

Anastrophia sp.

Spirigerina hillistensis

Cryptothyrella sp.

22 6

^{*} The coexistence of the taxa at Heltermaa are given by asterisks.

with the *Platystrophia affabilis* occurring in profusion in certain bioherms. The correctness of the taxonomy is critical. But in our case, a favourable feedback is in action; it makes us at least more attentive to the taxonomical problem.

The order of the taxa, taken singly below (Table 4) and produced by the above-mentioned basis, however, is not sufficient for the numerical determination of the ecological position of each taxon. Ideally, these ordinal numbers should characterize numerically the dwellingplaces of taxa with regard to the shoreline. For instance, if the numeration commences with offshore species, then we may easily get the order: 1. Clorinda undata, 2. Stricklandia lens, 3. Pentamerus borealis. But it is meaningless to order the taxa within one cluster, e. g. the biohermal species, especially if they are known in al! regions of such type deposits only, and anyway we cannot order the separate bioherms with regard to the shoreline. Therefore, if we want to utilize this order for the numerical estimation of the ecological position of each taxon, it must be done in another way than the simple ordinal numbers of taxa. I have used here the "tied ranks *" of G. U. Yule and M. G. Kendall (1950), i. e. the average of the ordinal numbers of these taxa, the position of which in a given order is not clearly related to one another. In Table 4 they are framed. The ranks of the four last taxa are shown as their conceivable ecological po-

If the rank of each taxon shows its ecological position, then the same for each synecological unit consisting only of certain taxa may be calculated as an average from the ranks of these animals. This estimate is here designated as the ecological index. For example, the ecological index of the first synecological unit of the Varbola Formation from the Orjaku boring is

Index = $\frac{S}{9+12+12+12}$ = 11.25 \approx 11.3

Table 4

The ecological positions of the taxa studied

Taxa	Ordinal	Ranks
lana	numbers	Maiins
Me	tos en l	1.
Tri	2	2
Sk	3 3	3
Clo	(9) 4	4
So	5	5
Lep	4 5 6 7	4 5 6 7
Di		
Spp	8	9
Do S	9	9
S	10	9
Z	11	11
A	12	12
Hi	13	13
Ra	14	14
P	15	15
Pl Pl	16	18
Cli	17	18
Le Pt	18	18
Pt	19 20	18
Fu		18
St	21	21
Pa	22	25
At	23	25
Dic	24	25
An -	25	25
Trm	26	25
Li	27 28	25
Sph		25
- Cr	29	13
He	30	12 12
Fa	31 32	11
da	02	11

In spite of its roughness, this index at least formalizes in a reasonable manner the ecological classification of the core or fossiliferous deposits. Note that the ecological index may be calculated simply or weighted. The weighted ecological index takes into consideration relative frequencies of observed taxa. It suffices the data from Table 1 only to check the influence of these frequencies. This influence has a most dramatic form in the case of dominant species. For instance, the data for the beds with *Pentamerus boralis* (column 15a from Table 1):

Simple index =
$$\frac{\Pr{\begin{array}{c} \text{Cr} \ da \ \text{Fa He da Ra Spp} \\ \frac{15+13+11+12+12+11+14+9}{8} = 12.125 \cong 12.1}}{8}$$

^{*} Abbreviated as ranks hereafter.

Weighted index =
$$\frac{P \quad \text{Cr} \quad \text{da} \quad \text{Fa} \quad \text{He} \quad \text{da} \quad \text{Ra} \quad \text{Spp}}{87 + 21 \cdot 1 + 12 \cdot 2 + 12 \cdot 3 + 11 \cdot 3 + 14 \cdot 2 + 9 \cdot 2} = 14.52 \cong 14.5$$

Since the simple index is exempt from burial and sampling effects, it is preferred to the weighted index.

Discussion

There are some problems concerning the ecological classification of the Juuru Stage in terms of previously defined communities: (1) the Lower Llandovery of Wales is synecologically undifferentiated (see Ziegler, 1965, text Fig. 1); (2) the fossils of the Juuru Stage are quite different from those of Wales. There are many more corals, stromatoporoids, and ostracodes besides brachiopods predominating in the Juuru Stage of Estonia. We also have a number of brachiopods unknown in Wales or vice versa in the Lower Llandovery (compare Nestor, in press, and Williams, 1951).

I think that, like biological taxa, the ecological ones are also "...indefinable each on its own, the categories are definable in relation to each other as ascending or descending steps in the process and system of classification" (Öpik, 1967). On the whole, we have too scanty information for assigning proper names to the communities of the Juuru Stage. In any case, we can determine the ecological position of a number of the brachiopods unknown in the classic area, but widespread in other regions, e. g. Zygospiraella duboisi, Alispira gracilis.

Because of this, I utilize the following community names for the studied brachiopod assemblages as a rough approximation. Each of them is fixed by means of the taxa (they have been shown by their ordinal numbers) from Table 3.

Names of the community	Abbreviations	Brachiopods occurring there
Clorinda .	La C yam axai	1—7, 32
Stricklandia	S S S S S S S S S S S S S S S S S S S	8-14, 29-32
Pentamerus	P	15, 29—32
Linoporella	le, line ecold eleal	16—32

The Linoporella Community is a new name. In spite of the geographically limited distribution of the bioherms, their fossils are always different (compare also Nestor, in press). Probably the closest or possibly even identical community to the *Linoporella* Community is the "rocky bottom community" of A. M. Ziegler, L. R. M. Cocks, and R. K. Bambach (1968, pp. 22-24), characterized by Linoporella punctata and Ferganella transversaria.

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BRAHHIOPOODIDE LEVIKUST EESTI KÕIGE ALUMISEMAS LÄNDOUVERIS

Vaadeldakse lähemalt Juuru lademe brahhiopoodide levikut bentoonsete faunakoosluste

Eraldatakse neli brahhiopoodikooslust. Nende nimetused on esialgsed, kuid nad võimaldavad orienteeruda uuritud brahhiopoodide sünökoloogias.

М. РУБЕЛЬ

О РАСПРОСТРАНЕНИИ БРАХИОПОД В НИЗАХ ЛЛАНДОВЕРИ ЭСТОНИИ

Рассматривается распространение брахнопод юуруского горизонта по бентонным

фаунистическим сообществам.

Послойное изучение выходов названного горизонта, в частности обнажения Хельтермаа, показало явные перерывы в вертикальном распространении по крайней мере четыpex видов: Stricklandia lens, Zygospiraella duboisi, Pentamerus borealis и, возможно, Alispira gracilis. Обращено внимание на повторное появление брахиоподовой фауны низов юуруского горизонта после так называемой бореалисовой банки и на существенное различие в составе брахиопод из биогермов и из остальных одновозрастных прибрежных фаций.

Исходя из этого, замена брахиоподовых фаун в каком-то известном разрезе юуру-

ского горизонта объясняется прежде всего как экологическое явление.

В связи с этим главное внимание обращено на материал из буровых скважин, охватывающий нескольке различных фаций юуруского горизонта как по географическому расположению скважин, так и по вертикальной последовательности фаций в каждой из них. Девять буровых скважин изучены синэкологически. Для этого каждая из них расчленена на так называемые синэкологические единицы на основе характера вертикального распространения доминирующих видов, а также по литологии керна. Сосуществование рассмотренных брахиопод в пределах каждой такой единицы сведено в полуматрицу так, чтобы порядок рассмотренных таксонов соответствовал наилучшим образом их расположению относительно береговой линии и чтобы при этом сохранилась наглядность таблицы. Для числовой характеристики названной экологической позиции использованы объединенные ранги, которые служат в свою очередь основой для вычисления экологического индекса синэкологических единиц. В данном случае экологический индекс имеет значение только как формализующая оценка для экологической классификации керна.

С помощью порядковых номеров таксонов из табл. 3 в пределах юуруского горизонта выделены четыре сообщества. Названия их, в том числе одно новое, даны в первом приближении с целью помочь ориентироваться в синэкологии брахиопод этого времени.