TAXONOMY OF DICOELOSIID BRACHIOPODS FROM THE ORDOVICIAN AND SILURIAN OF THE EAST BALTIC

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ABSTRACT. The sequence of taxonomic procedure is considered to be: (1) a definition of the morphological basis, (2) a determination of the variability, (3) an examination of the evolutionary rates against the stratigraphic background, (4) a grouping directed towards the formation of rational taxa, and (5) the comparison of these taxa with existing taxa and the modification of these taxa. Any kind of numerical methods in palaeontology must also consider this procedure. These problems are discussed in relationship to the East Baltic dicoelosiids: *Dicoelosia anticipata, D.* aff. *osloensis, D. osloensis, D. biloba, D. oklahomensis, Epitomyonia glypha* of Ashgillian to Ludlovian ages. Descriptions and occurrences of these species are given.

THE study of *Dicoelosia biloba* (L.) and related species (Wright 1968a) is an intriguing basis for a systematic study of material from the East Baltic. The phylogeny of *Dicoelosia* has been used as a basis for intercontinental correlation (Amsden 1968, text-fig. 21) and this aspect has also prompted the present study.

The collection includes 92 well-preserved specimens of the family Dicoelosiidae Cloud 1948, from borehole cores in Latvia and Estonia and outcrops in Estonia.
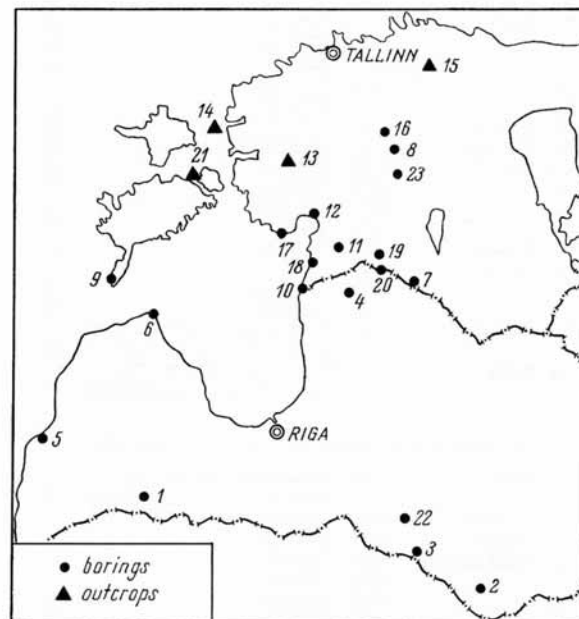
The identification or comparison of new specimens with described material is very much concerned with variability. The variability of brachiopod species may be demonstrated in several ways. Calculation of the morphological variability of each sample has been used here for a numerical appraisal.

Theoretically, each sample must be taken from one local fossil population (Imbrie 1956). The samples used here have been taken from core intervals or from particular beds at outcrop. Observation suggests that each sample of *Dicoelosia* or *Epitomyonia* is from a homogeneous population. The samples may be arranged into groups by special techniques. The rank and name of each such group are obtained by comparison with type material of known taxa on the same morphological basis.

In general the dicoelosiids are more closely associated with the graptolitic than the shelly facies and in most cases the samples can be correlated with a graptolite zone. The graptolite zonation used is that of R. Ulst (*in* Gailite *et al*. 1967) and D. Kaljo (personal communications).

TEXT-FIG. 1. Location of borings and outcrops.

MATERIAL

The samples have been numbered consecutively S_1, S_2, etc. followed by the location and depth in the borehole or location of the outcrop, and the number of shells measured.

The numbered geographical location and stratigraphic position of each sample are shown in text-figs. 1 and 2. These numbers are shown between brackets in the list below.

A. *Samples with measured specimens*

S_1	Ezere	(1)	1056·0 m	18
S_2		(1)	1059·0 m	2
S_3		(1)	1077·3 m	5
S_4		(1)	1077·6–1077·7 m	8
S_5		(1)	1078·95 m	5
S_6	Mezciems	(2)	331·2 m	1
S_7	Akniste	(3)	542·5–542·7 m	1
S_8	Staicele-4	(4)	280·6 m	1
S_9		(4)	280·3 m	1
S_{10}		(4)	279·7 m	1
S_{11}		(4)	276·6 m	4
S_{12}		(4)	276·0 m	2
S_{13}		(4)	275·0 m	1
S_{14}	Pavilosta	(5)	736·5 m	8
S_{15}	Kolka-54	(6)	400·9 m	3
S_{16}		(6)	445·8–446·0 m	1
S_{17}		(6)	574·3 m	1

S_{18}	Kolka-54	(6)	605·7 m	1
S_{19}	Holdre	(7)	348·8 m	2
S_{20}		(7)	304·9 m	1
S_{21}		(7)	304·1 m	1
S_{22}		(7)	301·5 m	1
S_{23}		(7)	295·5 m	1
S_{24}	Kabala	(8)	111·8–112·0 m	4
S_{25}	Ohesaare	(9)	372·95–373·0 m	1
S_{26}	Ikla	(10)	276·3 m	2
S_{27}		(10)	277·0 m	1
S_{28}		(10)	281·0 m	1
S_{29}		(10)	286·0 m	1
S_{30}	Ristiküla	(11)	160·9 m	1
S_{31}	Pärnu	(12)	89·5 m	2
S_{32}		(12)	90·40–90·44 m	1
S_{33}		(12)	91·68–91·72 m	4
S_{34}	Lätiküla	(13)	Material excavated from strata on the bottom of the river	2
S_{35}	Saxby	(14)	Material derived from the upper 0·5 m of a small quarry	3

B. *Samples with fragmentary preserved specimens*

|				
S_{36}	Moe	(15)	Material derived from the upper 0·5 m of a small quarry	2
S_{37}	Äiamaa	(16)	133·53–133·56 m	2
S_{38}	Seliste	(17)	334·1 m	1
S_{39}	Häädemeeste	(18)	394·6 m	1
S_{40}		(18)	390·9 m	1
S_{41}		(18)	343·0 m	1
S_{42}		(18)	213·7 m	2
S_{43}		(18)	206·8 m	1
S_{44}	Ikla	(10)	482·0 m	2
S_{45}		(10)	287·0 m	4
S_{46}	Abja	(19)	271·8 m	1
S_{47}	Staicele-4	(4)	400·3 m	1
S_{48}		(4)	345·0 m	1
S_{49}		(4)	341·0 m	1
S_{50}		(4)	281·5 m	1
S_{51}		(4)	279·0 m	1
S_{52}		(4)	275·5 m	4
S_{53}	Kolka-54	(6)	605·4 m	2
S_{54}		(6)	604·3 m	1
S_{55}		(6)	603·0 m	2
S_{56}		(6)	461·0 m	2
S_{57}	Druvas	(20)	274·2 m (Gailite *et al.* 1967, p. 175)	0
S_{58}		(20)	258·4 m (ibid.)	0
S_{59}	Kõinastu	(21)	Material from a small cliff	1
S_{60}	Viesite	(22)	626·3 m (Gailite *et al.* 1967, p. 175)	0
S_{61}	Ristiküla	(11)	161·6 m	1
S_{62}		(11)	160·8 m	1
S_{63}		(11)	154·2 m	1
S_{64}	Pavilosta	(5)	731·5 m	1
S_{65}		(5)	723·5 m	1
S_{66}	Ezere	(1)	1052·0 m	3
S_{67}	Mezciems	(2)	347·85 m (Gailite *et al.* 1967, p. 175)	0
S_{68}	Võhma	(23)	192·0 m (Wright 1968*a*, p. 302)	0
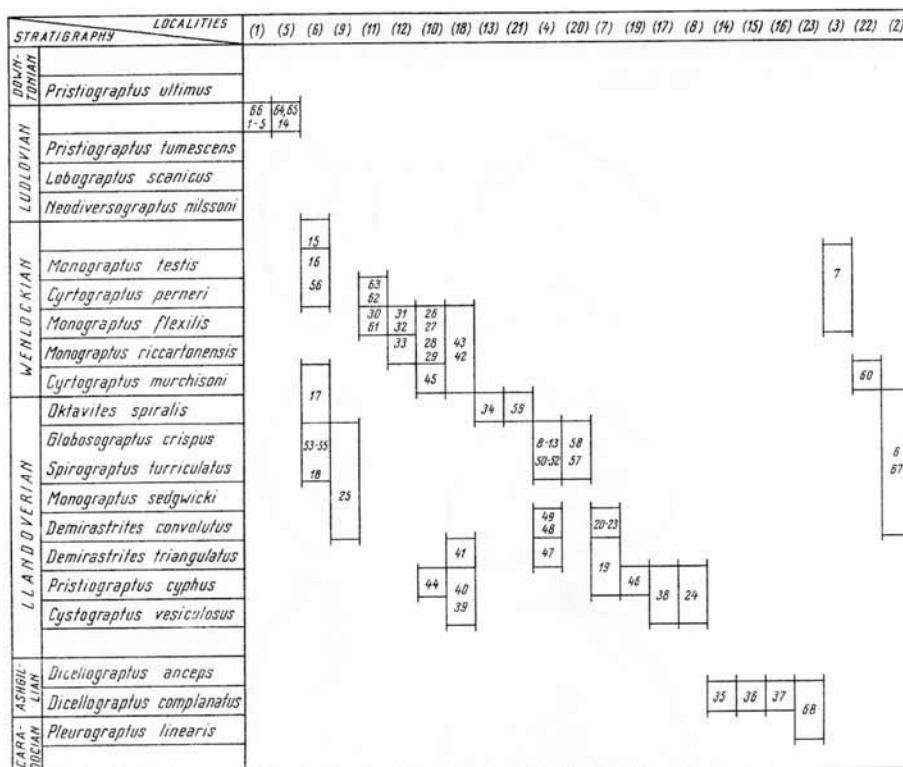
TEXT-FIG. 2. Distribution of samples according to locality numbers. The graptolitic zones follow R. Ulst (*in* Gailite *et al.* 1967, text-fig. 6) and modified by D. Kaljo (pers. comm.). The samples with numbers 1–5, 14, 64–66 are assigned to *Dicoelosia oklahomensis*; 6–13, 15, 16, 26–28, 30–33, 50–52, 56, 61–63 to *D. biloba*; 29, 42, 43, 45 to *D.* sp. indet.; 17, 18, 20–23, 25, 34, 53–55, 59 to *D. osloensis*; 19, 38–41, 44, 46–49 to *D.* aff. *osloensis*; 24 to *Epitomyonia glypha*; 35–37 to *D. anticipata*; 68 to *D. transversa*; and 57, 58, 60, 67 to *D.* spp.

The specimens used in this study are preserved at the Geological Museum of the Estonian Academy of Sciences (Tallinn) and the All-Union Scientific Research-Institute of Marine Geology (Riga). Catalogue numbers are indicated with the initial letters 'Br' and 'Br 30/' respectively. The numerical data are stored at Tallinn.

MORPHOLOGICAL BASIS

Every morphological feature may be represented by a certain number of measurements. These make it possible to estimate the morphological variability numerically. Eighteen measurements on the shell (see text-fig. 3) are used in this study. The measurements are, in part, those used by Wright (1968*a, b*). The level of identification and other conclusions are governed by these measurements, and I consider that they are superior to any visual estimation.

The measurements taken are concerned with the shell shape. The ribbing, capillae, sulci, and cardinal extremities normally considered in descriptions of dicoelosiids are excluded from this inspection.
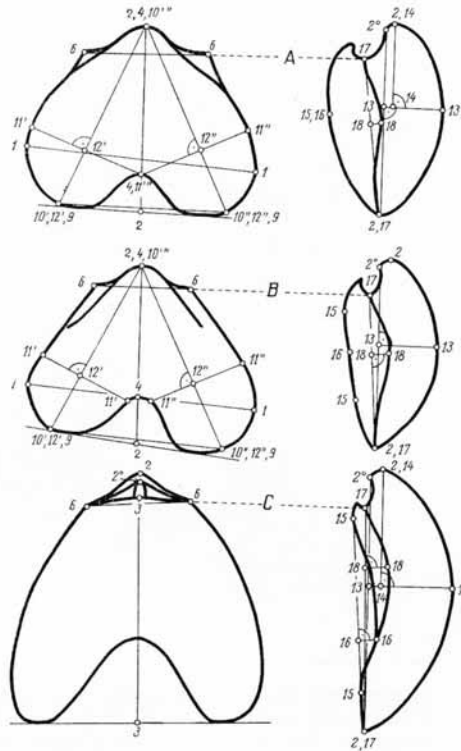
TEXT-FIG. 3. Positions of measurements made on the material.

At the same time most individual measurements express a growth stage of a shell. Comparisons of values obtained from very young specimens of one species with those from gerontic specimens of another taxon show differences in rate of growth rather than taxonomic position. Taxonomically of course they do differ. The simplest way to exclude the growth factor is to express the measurements as ratios, i.e.:

1. Maximum length (x_2): maximum width (x_1) of pedicle valve.
2. Maximum length (x_3): maximum width (x_1) of brachial valve.
3. Maximum length of pedicle valve (x_2): maximum length of brachial valve (x_3).
4. Mid-line length (x_4): maximum length (x_2) of pedicle valve.
5. Mid-line length (x_4): length along rectilinear rib as ($x_{10'}+x_{10''}$)/2 of pedicle valve.
6. Width of interarea (x_6): maximum width (x_1).
7. Lobes width as ($x_{11'}+x_{11''}$)/2: lobes length as ($x_{12'}+x_{12''}$)/2 of pedicle valve.

8. 'Lobes divergence' (x_9): length along rectilinear rib as $(x_{10'}+x_{10''})/2$ of pedicle valve.
9. Maximum thickness (x_{13}): maximum length (x_2) of pedicle valve.
10. Distance 14–14 (x_{14}): maximum length (x_2) of pedicle valve.
11. Distance 17–17 (x_{17}): maximum distance 18–18 (x_{18}).
12. Distance 16–16 (x_{16}): distance 15–15 (x_{15}). Note: if the brachial valve is convex or flat then $x_{16} = 0$, and if the brachial valve is convex then $x_{15} = 0$.

It is well known that young specimens of different taxa are more similar than are the adults, and this feature is particularly clear with the present material. For this reason specimens with the pedicle valve less than 2·0 mm have been discarded, reducing the number of specimens studied numerically to 75.

In order to simplify further calculation the ranges of all ratios are divided into ten classes, each of which is coded by the ordinal number 1 to 10. The class-intervals of each such ratio are summarized in Table 1.

TABLE 1. Class-intervals of ratios in the East Baltic collection of dicoelosiids

Ratios	x_2/x_1	x_3/x_1	x_2/x_3	x_4/x_2	x_4/x_{10}	x_6/x_1
Maximum	1·028	0·932	1·243	0·938	0·891	0·776
Minimum	0·643	0·559	0·949	0·637	0·575	0·406
Class-interval	0·039	0·039	0·031	0·031	0·033	0·038

Ratios	x_{11}/x_{12}	x_9/x_{10}	x_{13}/x_2	x_{14}/x_2	x_{18}/x_{17}	x_{16}/x_{15}
Maximum	2·909	1·040	0·509	0·613	0·150	0·147
Minimum	0·891	0·536	0·194	0·336	0·025	0·000
Class-interval	0·202	0·052	0·032	0·029	0·014	0·015

The ratios studied throughout the collection have a certain degree of correlation between them. These coefficients are just the basis on which the weighting of their diagnostic values lies, and, more important, from which the operational features may be defined. Thus, the ratios with a high degree of correlation may be regarded as uni-directional factors or, simply, diagnostic features. The features so defined have an equal weighting in subsequent taxonomic procedures.
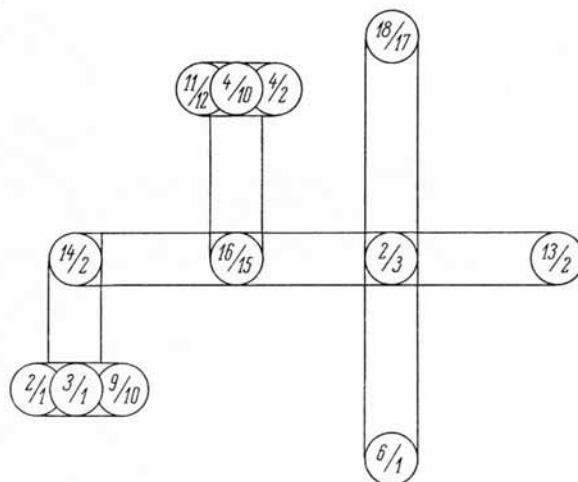
The correlation between all pairs of coded ratios, X and Y, is computed by the estimator, $r = \text{cov } X, Y/(\text{var } X \text{ var } Y)^{1/2}$.

The statistically significant correlation between most ratios (Table 2) allows them to be regarded as a co-operative system in the whole collection. The maximum informa-tion of the multivariate system is obtained by arrangement of its variates into such a scheme where n variates are linked with $n-1$ lines so that a sum of the coefficients of correlation along these lines is maximal (Võhandu 1964). The corresponding scheme for the ratios is given in text-fig. 4.

It is used here for the selection of the most diagnostic ratios. They include the ratios x_3/x_1, x_{14}/x_2, x_{16}/x_{15}, x_4/x_{10}, x_2/x_3, x_6/x_1, x_{13}/x_2, and x_{18}/x_{17}. Although these ratios are significantly correlated after their maximal correlation lines (with the exception of x_{18}/x_{17}) they do it relatively in like manner, especially in relation to the ratios of high degree of correlation, e.g., the ratios x_2/x_1, x_3/x_1, and x_9/x_{10}. Each ratio chosen may be regarded as representative of one feature. Only they are used as a morphological basis for further calculation.

TABLE 2. Linear correlation coefficients, r, between the coded ratios in the East Baltic collection. The coefficients where $|r| > 0.192$ differ significantly ($P > 95$ %) from zero.

	x_9/x_{10}	x_3/x_1	x_2/x_1	x_{14}/x_2	x_{16}/x_{15}	x_{13}/x_2	x_2/x_3	x_6/x_1	x_4/x_{10}	x_{11}/x_{12}	x_4/x_2	x_{18}/x_{17}
x_9/x_{10}	1·000											
x_3/x_1	−0·822	1·000										
x_2/x_1	−0·787	0·847	1·000									
x_{14}/x_2	0·458	−0·502	−0·449	1·000								
x_{16}/x_{15}	0·299	−0·265	−0·093	0·381	1·000							
x_{13}/x_2	−0·189	0·112	0·251	0·040	0·021	1·000						
x_2/x_3	0·099	−0·290	−0·200	0·152	0·338	0·355	1·000					
x_6/x_1	0·078	−0·037	−0·043	0·129	0·094	0·021	0·227	1·000				
x_4/x_{10}	−0·195	0·076	0·150	−0·118	−0·349	0·140	0·205	0·184	1·000			
x_{11}/x_{12}	−0·015	0·112	0·081	−0·016	−0·250	0·055	0·099	0·151	0·868	1·000		
x_4/x_2	−0·017	−0·063	0·016	0·036	0·124	0·106	0·221	0·214	0·854	0·831	1·000	
x_{18}/x_{17}	0·069	−0·082	−0·026	0·058	0·118	0·143	0·149	−0·072	−0·027	−0·040	−0·004	1·000

TEXT-FIG. 4. Relationships of ratios after the 'maximum correlation lines' (for full explanation see text).

STANDARD VARIABILITY

Some differences in morphology are found between any specimens, i.e. taxonomic distances can never be zero in any biological collection, and the concept of variability follows from this. It is well known of course that some specimens (e.g. dogs) are more similar between themselves than in relation to other specimens (e.g. cats). The concept of taxa follows from this.

The variability necessary in taxonomy may be expressed by means of estimators of similarity. Such estimators are offered by numerical taxonomy (see further Sokal and Sneath 1963). This can be realized by comparing all features (processed previously) of compared units in the following manner:

$$\Delta_{ik}^2 = (x_1-y_1)^2 + \ldots + (x_i-y_i)^2 + \ldots + (x_k-y_k)^2$$

where x_i and y_i are the corresponding values of k features of two specimens or taxa, X and Y respectively. Δ_{ik}^2 is the measure of the so-called taxonomic distance, i.e. a reciprocal value of the similarity. It is easy to show that the average value of the distances between the n specimens, $\Delta_{ik}^2 = 2\Sigma\Delta_{ik}^2/n(n-1)$, is also an estimator of the variability for these specimens (Frey and Võhandu 1967).

The distances, Δ_{ik}^2, between all specimens of the largest sample, S_1 (see text-fig. 5), are presented in Table 3. It should be noted that, if there are only eight features, then Δ_{ik}^2 ranges within the limits $0 \leqslant \Delta_{ik}^2 \leqslant 648$ in our case. However, the maximum distance observed was only 303 (between the specimens in S_5 and S_{35}). From Table 3 the maximum value of Δ_{ik}^2 is 85, i.e. far less than the observed and, of course, theoretically possible values. These specimens may probably be regarded as representatives of one local population.
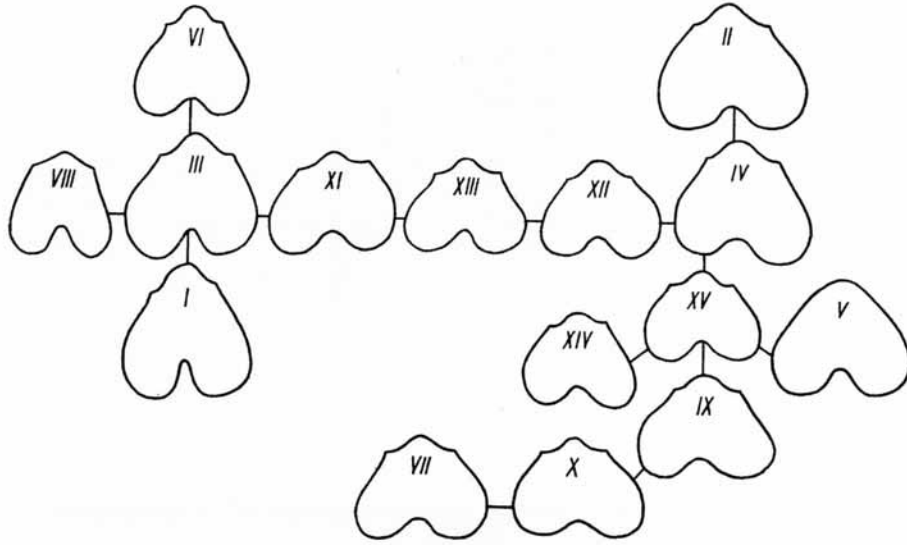
TEXT-FIG. 5. Shell outlines of sample S_1 and their relationships after the 'minimum distance lines'.

TABLE 3. The distances between the specimens of S_1

	I	III	VIII	VI	XI	XIII	XII	IV	II	XIV	V	XV	IX	X	VII
I	—	21	23	30	37	41	32	29	43	40	31	32	32	43	31
III		—	14	15	16	42	43	44	64	43	72	49	39	26	22
VIII			—	27	32	40	39	48	62	69	70	57	59	56	26
VI				—	47	63	56	59	67	66	73	64	54	39	23
XI					—	16	23	28	48	45	58	31	21	20	24
XIII						—	5	16	26	69	30	23	19	36	24
XII							—	7	9	68	23	22	24	47	29
IV								—	8	47	28	19	29	56	40
II									—	85	34	39	47	78	56
XIV										—	63	24	40	51	47
V											—	15	19	52	36
XV												—	12	37	23
IX													—	11	19
X														—	18
VII															—

However, this judgement acquires practical significance for further taxonomic procedures if, (1) this sample is indeed statistically homogeneous, and (2) it is indeed representative of one population (paradigm).

1. Checking the homogeneity of the sample, S_1, by means of an arrangement of all specimens into the scheme used previously, but now by means of the minimal distance sum, shows that the smaller specimens, XI–XV, placed 'centrally' divide the S_1 specimens at least into two distinct groups of specimens, I, III, VI, VIII and II, IV, V, IX, X, VII (text-fig. 5). Such branching could be due to differences in the manner of attachment, or, more likely to sexual dimorphism.

Taxonomic problems emerge from this phenomenon. Our largest sample, S_1, is the best test for checking the identifications of other dicoelosiids. For instance, if the similarity of two compared samples or specimens is less than the similarity indicated by the variability of S_1 then they may be considered mutually conspecific. Because of the obvious morphological heterogeneity of S_1 such conclusions are less definite. Nevertheless, S_1 is taken to be homogeneous for taxonomic purposes in spite of its 'biological' heterogeneity. Any sample, i.e. a natural group of specimens, may be regarded as statistically homogeneous; that is, a single objective homogeneity (Öpik 1967) in our case.

2. If we are using the standard above for classification, then we must know on which level we are working. It must be asked whether the significant differences between samples are equivalent to the differences between populations or species. The problem lies in a rational agreement between traditions and the fixing of the proper rank to the operational taxonomic units. Each sample here is considered as representative of one population.

There is also the possibility that S_1 consists of more than one population. In our case, however, the presence of a mixed population in samples is rejected because possible heteromorphy has been attributed to sexual dimorphism.

The variability of S_1, i.e. numerically 37·85, is only an estimation of the variability of the Silurian dicoelosiids in a particular place and for a given length of time. Applying the same variability to the whole collection is equivalent to the hypothesis of similar variabilities of all samples throughout the time and locations under consideration.

EVOLUTIONARY SEQUENCES

The sample distance, i.e. the average distance between all specimens of two samples, is a function of time in one unidirectionally evolving sequence. In other words, the taxonomic distances of a reference sample in relation to other samples must in some way increase according to their stratigraphic ordering in the section. Because of possibly uneven evolution, unequal sedimentation rates, or of variation in the size of the samples, only the increase as such testifies to evolution. From the preceding discussion the evolution must be at the population level.

TABLE 4. Sample distances between and within (framed) samples of the Ezere boring

	S_1	S_2	S_3	S_4	S_5	N	Depth in the core (m)
S_1	37·85	30·13	32·95	39·42	40·95	15	1056·0
S_2		32·00	36·60	47·00	44·25	2	1059·0
S_3			23·20	22·13	28·25	5	1077·3
S_4				23·33	25·42	3	1077·6–1077·7
S_5					19·50	4	1078·95

This can be demonstrated from the Ludlovian of the Ezere boring, although the specimen numbers are rather low. It was evident that the average distance between all specimens of samples (= the sample distances) expressed their stratigraphic order in the fittest manner (Table 4). From these data the Spearman correlation coefficient, +0·770, is obtained.

Let us arrange the sample distances, Δ_{ik}^2, of Table 4 by their increase. The stratigraphic arrangement of all sample pairs is obtained by the differences of their core intervals, DCI. The correlation coefficient is calculated after corresponding ranks as follows:

Sample pair No.	3/4	4/5	3/5	1/2	1/3	2/3	1/4	1/5	2/5	2/4
Ranks of Δ_{ik}^2	1	2	3	4	5	6	7	8	9	10
Ranks of DCI	1	2	3	4	8	5	9	10	7	6

Thus, the samples form a sequence not only stratigraphically but also numerically, clearly indicating a degree of evolution at the population level during the Ludlovian. It is noteworthy that the sample distances of S_4 and S_5 with S_1 and S_2 respectively are greater than the sample standard, 37·85. On the other hand, the distance between S_1 and S_2, also between S_3 and S_4, are less than the variabilities of each.

There are five borings with a continuous series of samples. In spite of the small size of the samples in each the correlations of their morphological and stratigraphic relationships are remarkably good: S_{28}—S_{26}—S_{27} ($\rho = +0.625$, $n = 3$) in the Ikla boring, S_{31}—S_{32}—S_{33} ($\rho = +1.000$, $n = 3$) in the Pärnu boring, S_{20}—S_{21}—S_{23}—S_{22} ($\rho = -0.129$, $n = 6$) in the Holdre boring, and less regular series in the Staicele boring, S_{10}—S_{12}—S_{11}—S_9 and S_8—S_{13} ($\rho = -0.067$, $n = 15$). The degree of correlation is higher in series with larger samples. Some stratigraphically close samples are linked in order to give greater prominence to the evolution (Table 5). The linked samples are indicated, as for instance, $S_8 + S_9 + S_{10} = S_{8-10}$. In the latter case the correlation between morphological and stratigraphic relationships is maximum.

TABLE 5. Sample distances between and within (framed) sample groups in the Staicele boring

	S_{8-10}	S_{11}	$S_{12, 13}$	N	Depth in the core (m)
S_{8-10}	58·66	45·58	45·89	3	280·6–279·7
S_{11}		35·17	37·08	4	276·7
$S_{12, 13}$			35·33	3	276·0–275·0

Taxonomic problems arise because of the heterogeneity of linked samples. The linkage may increase the variability of linked samples and, therefore, decrease the possibilities of showing the degree of evolution prominently. On the other hand, if small samples are not linked no positive conclusions can be made. Therefore, in spite of the presumed evolution at the population level it is better to link some samples.

The main evolutionary trend of the dicoelosiids (see Amsden 1968, text-fig. 21) can be seen in the continuously evolving sequences described above. Such unidirectional brachiopod lineages have been used at various levels of stratigraphic correlation as, for instance, in the Llandoverian with the genera *Stricklandia*, *Eocoelia*, and *Leptostrophia* (see Ziegler *et al.* 1968). It is possible to classify the East Baltic collection through its main evolutionary trends. Table 6 demonstrates the evolution of features separately. There are on average at least two features changing regularly with time: the invagination of shells (x_4/x_{10}) decreases, whilst the brachial valves change from concave to convex (x_{16}/x_{15}), in stratigraphically younger specimens. These features are, of course, quite clear visually.

The corresponding distances between the sample groups (Table 7) increase according to their stratigraphic position, demonstrating the main trend. The amount of evolution is not surprising considering the length of time involved. There is one critical sample group, S_{8-13}, which has one of its distances equal to its variability, namely, between the S_{8-13} and $S_{26-28, 30-33}$. That indicates the intermediate nature of the Upper Llandoverian dicoelosiids with those from the Wenlock in the collection (text-fig. 6).

TABLE 6. Averages and variances, s^2 (in brackets), of the coded ratios after the sample groups in the collection

Ratios	x_3/x_1	x_2/x_3	x_4/x_{10}	x_6/x_1	x_{13}/x_2	x_{14}/x_2	x_{18}/x_{17}	x_{16}/x_{15}	N
Samples									
$S_{1-5, 14}$	7·30 (2·52)	3·88 (2·32)	5·03 (2·03)	3·42 (1·25)	3·91 (3·00)	3·09 (1·85)	5·45 (4·32)	1·00 (0·00)	33
$S_{26-28, 30-33}$	5·83 (3·46)	4·75 (1·27)	4·00 (1·45)	4·83 (3·46)	4·33 (1·35)	4·17 (2·73)	4·92 (1·35)	1·83 (2·36)	12
S_{8-13}	6·30 (1·79)	4·50 (2·95)	3·60 (2·71)	3·20 (1·51)	3·20 (1·51)	4·80 (4·18)	5·20 (3·74)	3·40 (2·71)	10
S_{20-23}	8·25 (1·00)	6·50 (0·33)	2·75 (2·92)	4·50 (1·67)	7·00 (2·00)	4·25 (0·92)	4·75 (0·92)	6·75 (1·58)	4

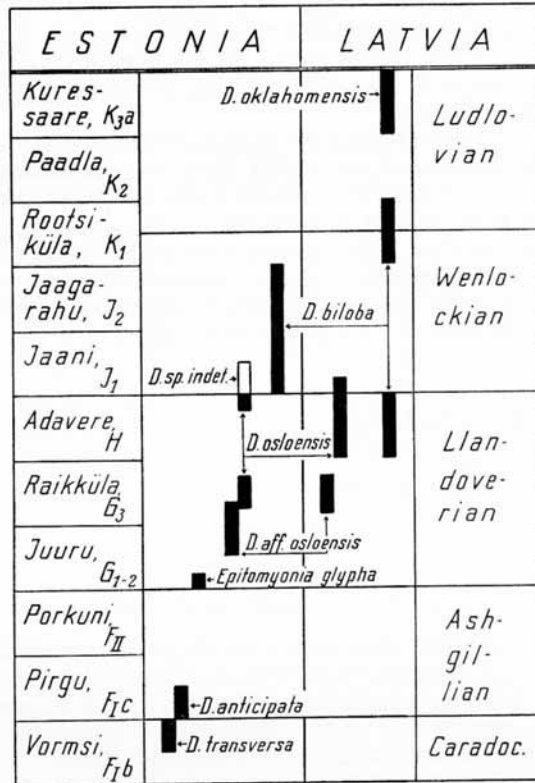TABLE 7. Sample distances between and within (framed) the sample groups in the collection

	$S_{1-5, 14}$	$S_{26-28, 30-33}$	S_{8-13}	S_{20-23}	N	Stratigraphy
$S_{1-5, 14}$	33·98	40·62	48·47	83·48	33	Ludlovian
$S_{26-28, 30-33}$		34·61	42·18	66·19	12	Wenlockian
S_{8-13}			42·18	63·05	10	Upper Llandoverian
S_{20-23}				22·50	4	Middle Llandoverian

TAXONOMIC GROUPING

The ineffectiveness of existing clustering methods when applied to continuously evolving sequences of fossils by means of their pure morphology (Kaesler 1967) has become evident during the present study. It seems certain that the stratigraphic and ecological arrangements of the morphological variability add significant information (Westbroek 1967).

The Groups $S_{1-5, 14}$, $S_{26-28, 30-33}$, S_{8-13}, and S_{20-23}, may be regarded as representatives of one main evolving sequence. The known occurrences of each group are separated from each other by varying stratigraphic intervals. Therefore, they represent useful standards for taxonomy. In other words, the basic idea of classification of all samples appeared in a form according to Table 8 including the assignment of the 'free' samples to the standard groups.

It may be done by the minimum distances of the 'free' samples but corrected finally by the estimation of the variability of new groups. In other words, the assignment of any 'free' sample to standard groups could be to decrease the variability of the new group or, at least, the increase of its variability must be minimal in relation to other possible linkage. The linkage must be ended on the critical level chosen.

TABLE 8. Sample distances between and within (framed) the sample groups and samples in the collection

	$S_{1-5,\,14}$	S_{15}	S_{16}	S_7	$S_{26-28,\,30-33}$	S_{29}	S_{8-13}	S_6	S_{17}	S_{34}	S_{18}	S_{30-33}	S_{25}	S_{19}	S_{24}	S_{35}
$S_{1-5,\,14}$	[33·98]															
S_{15}	42·24	[18·00]														
S_{16}	45·64	24·33	[0·00]													
S_7	46·42	45·67	18·00	[0·00]												
$S_{26-28,\,30-33}$	40·62	30·94	38·17	37·00	[34·61]											
S_{29}	56·06	57·00	76·00	50·00	41·00	[0·00]										
S_{8-13}	48·47	46·93	45·00	32·20	42·18	52·40	[42·18]									
S_6	53·03	56·00	99·00	101·00	56·83	55·00	80·20	[0·00]								
S_{17}	80·15	88·67	115·00	81·00	70·67	61·00	60·40	68·00	[0·00]							
S_{34}	62·00	50·67	73·00	56·00	45·25	55·00	48·20	53·00	28·00	[30·00]						
S_{18}	77·21	75·00	66·00	50·00	74·50	110·00	53·40	99·00	45·00	48·00	[0·00]					
S_{30-33}	83·48	60·42	73·25	64·75	66·19	94·75	63·05	71·25	49·25	30·75	27·75	[22·50]				
S_{25}	81·39	70·33	62·00	40·00	68·83	96·00	52·20	97·00	51·00	42·00	6·00	20·75	[0·00]			
S_{19}	144·09	115·33	102·00	70·00	107·83	125·00	85·20	212·00	92·00	79·50	83·00	93·25	73·00	[30·00]		
S_{24}	165·82	106·33	160·00	182·00	136·00	186·00	164·40	163·00	219·00	136·00	220·00	165·25	200·00	194·00	[0·00]	
S_{35}	220·21	160·00	207·00	187·00	168·17	169·00	155·60	236·00	128·00	112·00	171·00	141·75	159·00	73·00	155·00	[0·00]

TEXT-FIG. 6. Distribution of taxa in terms of the Estonian stratigraphic scale.

TABLE 9. The assignments of the 'free' samples to the standard groups. 1, Standards. 2, Samples assigned by their minimal distances, within limits of each standard variability. 3, As 2, but within limits of the most numerous standard variability, 33·98. 4, Check of previous assignments by minimal increase of the standard variability after linkage of the indicated sample(s). 5, Final assignments by the minimal increase. 6, The closest samples by the minimal increase. In round and square brackets are indicated the minimal distances and the variabilities respectively

	1	2	3	4	5	6
$S_{1-5, 14}$	[33·98]					S_6 [35·10]
						S_{29} [35·28]
$S_{26-28, 30-33}$	[34·61]	S_{15} (30·94)		S_{15} [32·85]	$S_{15, 7}$ [33·58]	S_{29} [35·08]
				S_7 [35·16]	$S_{15, 7, 16}$ [33·67]	S_6 [36·79]
S_{8-13}	[42·18]	S_7 (32·20)		S_7 [40·37]		S_{29} [44·04]
S_{20-23}	[22·50]	S_{25} (20·75)	S_{18} (27·75)	S_{25} [21·80]	$S_{25, 18, 34, 17}$	S_6 [39·89]
			S_{34} (30·75)	$S_{25, 18}$ [22·33]	[31·67]	S_{29} [42·13]
				$S_{25, 18, 34}$ [28·35]		S_{19} [49·64]

Thus, the variability of the most numerous sample, S_1, was 37·85. After assignments of the S_2, S_3, S_4, S_5, and S_{14} to it the variability of the new group, $S_{1-5,\ 14}$, decreased to 33·98. Both variability levels may be used in classification of the collection. The level 33·98 obtained by linkage of morphologically and stratigraphically close samples is critical in species determination.

Such results obtained for this series are presented in Table 9 and appear to be very satisfactory. The three samples S_{19}, S_{24}, and S_{35} have too great distances between themselves and from others, and must be considered as taxonomically independent. It is also noteworthy that the variabilities of the groups $S_{1-5,\ 14}$, $S_{26-28,\ 30-33}$, S_{8-13} are nearly equal to the distances between them. This is a sequence of relatively close standards.

In conclusion, five or six groups satisfy taxonomically the requirements of 'species'. Together with visual assignment of fragmentary preserved specimens (samples S_{36} to S_{68}) the final classification of the collection is as follows:

Group I: $S_{1-5,\ 14}$, S_{64-66}
   Intermediate: S_6
Group II: $S_{26-28,\ 30-33}$, S_{15}, S_7, S_{16}, S_{56}, S_{61-63}
   Intermediate: S_{8-13}, S_{50-52}
   Intermediate: S_{29}, S_{42}, S_{43}, S_{45}
Group III: S_{20-23}, S_{25}, S_{18}, S_{34}, S_{17}, S_{53-55}, S_{59}?
   Intermediate: S_{19}, S_{38-41}, S_{46-49}, S_{44}?
Group IV: S_{24}
Group V: S_{35}, S_{36}, S_{37}

SYSTEMATIC PALAEONTOLOGY

The preceding discussion of 'shape taxonomy' suggests its appropriateness in identification. However, there is a greater variability in the morphology of all known species than in the material from the East Baltic. In calculation of the corresponding distances between the five groups (above) and the seven related species the rank scales are increased in both directions by means of the same class-intervals.

The taxonomic relationships of the seven related species are shown in Table 10. Most species are represented by their type material. Unfortunately, no exact horizon or locality was ascribed to the type material of *Dicoelosia biloba* and *D. verneuiliana* (Wright 1968a).

The same features are used in the construction of Table 11 as for the East Baltic collection so that direct comparisons of the sample distances can be taken for the following nomenclatorial conclusions.

Family DICOELOSIIDAE Cloud 1948
Genus DICOELOSIA King 1850

Dicoelosia anticipata Wright 1968

Plate 8, figs. 1–7

1968a   *Dicoelosia anticipata* Wright, pp. 308–9, pl. 5, figs. 15–19.

Description of topotypes. Pedicle valve from five-sixths to two-thirds as long as wide, mid-line length just five-sixths of maximum valve length. Valve thickness averages

TABLE 10. Distances between the specimens of seven species of *Dicoelosia* with abbreviations of specimen numbers, repositories, and publications

	a	b	c	d	e	f	g	h	i	j	k	l	m	n	p	
a	—	36	68	68	54	40	216	143	227	133	131	153	105	164	329	D. oklahomensis, OU 6286 (Amsden 1968, pl. 8, figs. 4d, e)
b		—	38	28	56	30	170	181	275	79	115	87	47	116	279	D. oklahomensis, USNM 115251 (Amsden 1968, pl. 15, figs. 1–7)
c			—	24	40	28	260	271	373	117	109	135	55	124	347	D. biloba, Linnaean Coll., BM (Wright 1968a, pl. 1, figs. 1–4, 7)
d				—	44	28	192	207	333	75	95	69	33	116	327	D. biloba, OU 6282 (Amsden 1968, pl. 8, figs. 3a, b, d)
e					—	22	192	175	225	69	69	113	55	154	392	D. bilobella, USNM 158103 (Amsden 1968, pl. 3, figs. 6a–e)
f						—	152	135	239	59	53	83	43	76	257	D. bilobella, USNM 158104 (Amsden 1968, pl. 3, figs. 6f–g)
g							—	87	193	53	137	143	181	134	233	D. verneuiliana, PIU No. G746 (Wright 1968a, pl. 7, figs. 1, 4, 5)
h								—	80	136	106	200	242	207	325	D. verneuiliana, PIU No. G747 (Wright 1968a, pl. 7, figs. 2, 3, 6)
i									—	238	152	372	380	423	628	D. verneuiliana, PIU No. G748 (Wright 1968a, pl. 7, figs. 10, 12, 14)
j										—	88	46	44	85	244	D. 'verneuiliana', OU 6276 (Amsden 1968, pl. 8, figs. 1b–f)
k											—	160	136	149	382	D. alticavata, GSM No. 82551 (Wright 1968a, pl. 2, figs. 11–15)
l												—	26	97	228	D. osloensis, PMO No. 74564 (Wright 1968a, pl. 6, figs. 8–10)
m													—	87	258	D. osloensis, PMO No. 74565 (Wright 1968a, pl. 5, figs. 6–8, 11)
n														—	73	D. indenta, PIU No. D1177 (Wright 1968a, pl. 4, figs. 4–6)
															—	D. indenta, PIU No. D1176 (Wright 1968a, pl. 4, figs. 7–11)

TABLE 11. Minimum, maximum, and sample distances between the East Baltic dicoelosiids and type material of the related species of the genus *Dicoelosia*

		D. oklahomensis a, b	*D. biloba* c, d	*D. bilobella* e, f	*D. verneuiliana* g, h, i	*D. 'verneuiliana'* j	*D. alticavata* k	*D. osloensis* l, m	*D. indenta* n, p
	Minimum	13	14	18	67	54	29	42	84
$S_{1-5,\,14}$		51·33	63·94	49·52	170·63	86·09	76·39	103·79	214·05
	Maximum	94	112	108	305	119	128	170	440
	Minimum	17	24	16	82	42	52	45	51
$S_{26-29,\,30-33}$		48·83	61·33	42·50	186·89	83·17	82·00	76·42	184·67
	Maximum	97	161	81	332	128	124	138	334
	Minimum	11	20	10	82	61	55	45	32
S_{8-13}		55·90	74·90	48·40	169·87	86·00	86·80	98·10	158·10
	Maximum	116	142	120	341	127	117	157	306
	Minimum	46	75	28	61	16	61	40	35
S_{20-23}		83·00	98·25	59·75	146·08	27·75	95·60	52·25	121·00
	Maximum	121	131	107	280	46	128	75	234
	Minimum	100	104	64	194	109	189	71	36
S_{19}		134·00	152·50	118·50	287·00	148·00	210·00	126·50	89·00
	Maximum	190	204	174	431	187	231	187	133
	Minimum	126	92	144	257			69	224
S_{24}		135·00	136·00	156·00	335·33	167·00	273·00	84·00	296·50
	Maximum	144	180	168	463			99	369
	Minimum	139	167	125	304			120	173
S_{35}		153·00	170·00	134·00	378·33	194·00	304·00	136·00	223·50
	Maximum	167	173	143	490			152	274

a little more than one-third of maximum length, moderately convex in lateral profile. Lobes broad, divergence of about 49–63°, gently convex in transverse profile and separated by well-developed sulcus originating at umbo. Hinge-line slightly more than half shell width; cardinal extremities obtuse, ears weakly developed. Sulcus defined by first costae fairly well developed, 0·6–1·4 mm wide at 2 mm growth stage.

Ribbing well developed over whole shell surface, with 8–9 costae; costellae commonly arising by bifurcation; capillae also developed. Ribs fairly angular, with 4–6 ribs per mm, recorded at 2 mm distance antero-laterally from brachial umbo in 1, 3, 1 valves respectively. Commissure crenulated along whole length.

Brachial valves concave, with slightly convex umbonal region forming part of overall concavity of adult. Sulcus of umbonal region rapidly broadening and shallowing, becoming poorly defined anteriorly, 1·5–2·2 mm wide at 2 mm growth stage.

Brachial valve interior with feebly developed notothyrial platform; cardinal process with apparently bilobed myophore and shaft. Brachiophores s.s. plate-like, as swellings to ventral edge of brachiophores s.l. Cardinalia about half as long as wide and a quarter as long as valve. Adductor field situated anteriorly from shaft, distinctly impressed into valve floor; follicular eminences and embayments well developed. No clearly defined dorsal ridge in brachial valve interior.

Measurements of type material (in mm)

	Length	Width
Br 4145	4·0	6·1
Br 4146	3·4	5·4

Material. The following samples are assigned to this species: S_{35}, S_{36}, and, doubtfully, S_{37}.

Discussion. The taxonomic distance of *D. anticipata* to other species (Table 11) is in every case sufficient for it to be regarded as an independent species. Sample S_{37} is represented by too few specimens for firm assignment, though it is possible that it may belong to *D. transversa* Wright 1968 which was recorded from Estonia (Wright 1968a, p. 302). This is also likely since $S_{68} = D.$ *transversa* occurs in almost contemporaneous strata.

Facies association. The Baltoscandian Ashgillian is characterized by local reef developments (Männil 1966). Reef bodies are absent in the outcrops and borings where the species has been found, but many Ordovician dicoelosiids from Baltoscandia are closely associated with reef or reef flank facies.

<center>

Dicoelosia aff. *osloensis* Wright 1968

Plate 8, figs. 18–25

</center>

Description. Pedicle valve about three-quarters as long as wide, with mid-line length about two-thirds of maximum valve length. Valve thickness ranges from one-fifth to three-tenths maximum length, moderately convex in lateral profile. Lobes narrow, diverging between 57° and 75°, gently convex in lateral profile, separated by well-developed rounded sulcus, 1·6 mm wide at 2 mm growth stage. Hinge-line averages about half shell width; cardinal extremities obtuse, slightly flattened.

Ribbing on lobes well developed, with six angular costae (in one well-preserved specimen). Costellae appear to arise by bifurcation. Commissure crenulation developed only at lobe margins. One submedian rib appears to be on the sulcus floor.

Brachial valve concave with small convex umbonal region. Sulcus not deep, with flattened floor.

Brachial valve interior poorly preserved (Pl. 8, fig. 25). Valve surface generally smooth, follicular eminences and embayments well developed.

Measurements of figured material (in mm)

	Length	Width
Br 3402	4·3	5·0
Br 30/301	2·3	3·4
Br 30/302	2·2	3·4

Material. The samples forming this group are: S_{19}, S_{38-41}, S_{46-49}. Sample S_{44} is assigned to it doubtfully.

Discussion. Only the two relatively young specimens of sample S_{19} can be used for numerical comparison. Table 8 demonstrates that there is a greater similarity between sample S_{19} and the stratigraphically and geographically closer samples of groups 20–23, 25, 18, 34, 17 than with other samples. Table 11 shows that *D. indenta* is the most closely related species, particularly in the similar degree of divergence of the lobes and the brachial concavity. The distance with *D. osloensis* is greater than expected. However, it is appropriate to associate S_{19} with *D. osloensis*, especially since it and the unmeasured specimens of the group lack Ordovician-type ribbing on the sulci. The differences with *D. osloensis* are too great, both visually and numerically in shell shape, for the samples to be considered as conspecific with *D. osloensis*. It is possible that *D.* aff. *osloensis* includes dicoelosiids intermediate between the Ordovician species, *D. indenta* or *D. transversa*, and *D. osloensis*.

Facies association. *D.* aff. *osloensis* is widely distributed in the *Clorinda* Community (see Ziegler 1965) characterized by the brachiopods *Clorinda undata* (Sow.), *Meifodia ovalis* (Williams), *Skenidioides lewisi* (Dav.), etc. The sediments are mainly calcareous siltstones.

EXPLANATION OF PLATE 8

All specimens ×6.

Figs. 1–7. *Dicoelosia anticipata* Wright. 1–5, Ventral, dorsal, posterior, anterior, lateral views of complete shell, Br 4145, from S_{35}. 6, 7, Interior and exterior of brachial valve, Br 4146, from S_{35}.

Figs. 8–17. *Epitomyonia glypha* Wright. 8–12, Ventral, dorsal, anterior, posterior, lateral views of complete shell, Br 3400, from S_{24}. 13, Dorsal view of complete shell, Br 3401, from S_{24}. 14, 15, Exterior and interior of brachial valve, Br 3418, from S_{24}. 16, 17, Exterior and interior of brachial valve, Br 3419, from S_{24}.

Figs. 18–25. *Dicoelosia* aff. *osloensis* Wright. 18, Ventral view of complete shell, Br 3402, from S_{41}. 19–21, Ventral, dorsal, lateral views of complete shell, Br 30/301, from S_{19}. 22–24, Ventral, dorsal, lateral views of complete shell, Br 30/302, from S_{19}. 25, Interior of brachial valve, Br 3403, from S_{38}.

Figs. 26–31. *Dicoelosia osloensis* Wright. 26–28, Ventral, anterior, lateral views of complete shell, Br 3406, from S_{25}. 29–31, Ventral, dorsal, lateral views of complete shell, Br 3404, from S_{34}.

Dicoelosia osloensis Wright 1968

Plate 8, figs. 26–31; Plate 9, figs. 1–14

1967 *Dicoelosia biloba* (L.), Rybnikova, p. 174, pl. 15, figs. 1.
1968a *Dicoelosia osloensis* Wright, pp. 309–11, pl. 5, figs. 6–11, pl. 6, figs. 1, 7–10.
1968 *Dicoelosia verneuiliana* (Beecher); Amsden, pl. 8, figs. 1.

Description of material from the East Baltic. Pedicle valve about nine-tenths as long as wide, with mid-line length averaging seven-tenths (three-quarters to five-eighths) of maximum valve length. Lobes broad, with slightly narrowing anterior part, strongly arched in lateral profile, diverging between 40° and 48° (average 45°). Lateral profile convex with valve thickness about one-third of valve length. Sulcus broad, with flattened floor, averaging about 1·1 mm wide at 2 mm growth stage. Interarea curved, apsacline, between one-sixth to one-seventh as long as valve. Hinge-line three-fifths to three-sevenths as wide as maximum width, cardinal extremities obtuse, slightly rounded.

Ribbing well developed on lobes, rib density 5–7 ribs per mm recorded at 2 mm distance antero-laterally from dorsal umbo in 2, 2, 1 valves respectively. Capillae rare. Ribbing weakly developed, not branching on the floor of sulci.

Brachial valve always gently concave in lateral profile, sulcus well defined, deep, originating at apically convex umbonal region. Transverse profile of lobes strongly arched to flattened.

Brachial valve interior (in one gerontic specimen) possesses extremely long lobes for the species with bilobed myophore of cardinal process and long shaft; ridges well-developed along lobes (Pl. 2, fig. 14); follicular eminences and embayments strongly developed.

Measurements of figured specimens (in mm)

	Length	Width
Br 30/303	7·2	7·4
Br 30/39	4·1	4·6
Br 3407	3·5	3·8
Br 3406	3·8	3·9
Br 3405	3·2	3·6
Br 3404	3·1	3·8

Material. The species includes samples S_{20-23}, S_{17}, S_{18}, S_{25}, S_{34}, S_{53-55} and, doubtfully, one deformed pedicle valve S_{59}.

Discussion. The topotypes of *D. osloensis* are poorly preserved. Nevertheless, the distance between samples S_{20-23} and the topotypes is less than between all other samples (Table 11). Of course, the variability of $S_{20-23, 25, 18, 34, 17}$ (i.e. 31·67) does not formally identify the sample with *D. osloensis*. However, firstly, the variability is reduced by the low number of specimens in the topotype sample, and, secondly, no other association is at present possible, excepting *D. 'verneuiliana'*.

In this respect the use of the name *D. verneuiliana* arises. Amsden (1968) figured the dicoelosiids (see synonymy) from the Upper Visby Marls, distinguishing them clearly from those selected for the types of *D. verneuiliana* by Wright (1968a, pl. 7). The latter

were collected in the last century and 'little more can be said categorically about the type material except that it came from the Visby Marls of N.W. Gotland' (op. cit., p. 313). My specimens, more like *D. osloensis* than other species, seem to be very close to Amsden's specimens (see Table 11), which are therefore considered synonymous with *D. osloensis*. The dicoelosiids identified by me as *D. verneuiliana* from the lectotypes seem to be distributed in stratigraphically younger beds than the specimens I consider synonymous with *D. osloensis*. A sample in our collection of *D. verneuiliana* sensu Wright from the Högklint Group (Pl. 9, figs. 15–19), unfortunately labelled only as 'probably' from these beds, and the other specimens figured by Amsden (1968, pl. 13, fig. 10*a*) certainly obtained from the Högklint Group, must be assigned to *D. verneuiliana*. Nevertheless, it appears certain that *D. osloensis* and *D. verneuiliana* both occur in the Upper Visby Marls, though geographically isolated.

D. osloensis, as at present understood, is undoubtedly very variable, though stratigraphically limited. Some specimens may be considered as extreme variants and close to *D. verneuiliana*, as for instance, the brachial valve (Pl. 9, fig. 14).

Facies association. It is likely that the variation in *D. osloensis* is connected with the relatively large range of sediment types in which it is found. The facies map of Gailite *et al.* (1967, text-fig. 11) shows that *D. osloensis* occurs in at least two facies. In terms of the brachiopod communities (Ziegler 1965) it occurs in the graptolitic facies (Kolka boring), the *Clorinda* Community (the Holdre and Ohesaare? borings), and, probably the *Costistricklandia* Community (Lätiküla and Kõinastu outcrops).

Dicoelosia sp. indet.

Plate 9, figs. 20–25

Four samples, S_{29}, S_{45}, S_{42}, S_{43}, from the boundary beds between the Llandoverian and Wenlockian cannot be readily associated with any other samples. The lowest distance of S_{29} from other samples is 41·00 (see Table 8) showing its resemblance with the standard series, $S_{26-28, 30-33}$. The latter and related samples show features typical of *D. biloba*, i.e. the concave lateral margins which are absent in all four samples. However, these samples are characterized by a convex brachial valve in lateral profile, a feature quite absent in *D. osloensis* and related samples. The assignment of *D.* sp. indet.

EXPLANATION OF PLATE 9

All specimens ×6.

Figs. 1–14. *Dicoelosia osloensis* Wright. 1–5, Ventral, dorsal, lateral, anterior, posterior views of complete shell, Br 30/39, from S_{22}. 6–10, Ventral, dorsal, lateral, anterior, posterior views of complete shell, Br 3405, from S_{34}. 11–13, Ventral, dorsal, lateral views of complete shell, Br 3407, from S_{17}. 14, Interior of brachial valve, Br 30/303, from S_{23}.

Figs. 15–19. *Dicoelosia vernuiliana* (Beecher). Ventral, dorsal, anterior, posterior, lateral views of complete shell, Br 3408, from Högklint Group?, Gotland.

Figs. 20–25. *Dicoelosia* sp. indet. 20–24, Ventral, dorsal, anterior, posterior, lateral views of complete shell, Br 3410, from S_{29}. 25, Interior of brachial valve, Br 3409, from S_{43}.

Figs. 26–31. *Dicoelosia biloba* (L.). 26–30, Ventral, dorsal, lateral, anterior, posterior views of complete shell, Br 30/304, from S_{11}. 31, Interior of brachial valve, Br 3414, from S_{15}.

Fig. 32. *Dicoelosia oklahomensis* Amsden. Interior of brachial valve, Br 30/311, from S_1.

to *D. osloensis* is subjectively likely, but the distances of S_{29} with topotypes of *D. oslo-ensis* and *D. 'verneuiliana'* are too great, 139, 99, and 123 respectively.

Dicoelosia biloba (Linnaeus 1758)

Plate 9, figs. 26–31; Plate 10, figs. 1–22

1968a *Dicoelosia biloba* (Linnaeus); Wright, pp. 291–6, pl. 1, figs. 1–17; pl. 2, figs. 1–10.
1968   *Dicoelosia biloba* (Linnaeus); Amsden, pl. 8, figs. 3; pl. 13, fig. 12a.

Three stratigraphically separate groups of samples are included in *D. biloba*. The Llandoverian samples constitute the earliest representatives of the species.

Description of the Upper Llandoverian samples (Pl. 9, figs. 26–30; Pl. 10, figs. 1–5). Pedicle valve about four-fifths as long as wide, with mid-line length about three-quarters of maximum valve length (from four-fifths to two-thirds); fairly convex in lateral profile, with valve thickness about two-sevenths of maximum length. Lobes fairly broad, sometimes narrow, divergence ranges between 40° and 59° (average 48°). Hinge-line a little less than half shell width, cardinal extremities obtuse with small flattened ears. Interarea curved, apsacline. Sulcus deep, originating at umbo, 1·0 mm wide at 2 mm growth stage, without clear radial ornament.

Brachial valve about three-quarters as long as wide, flatly to moderate convex in lateral profiles; sulcus originating at umbo rounded, shallower than ventral one. Ornamentation on lobes of costae and branching costellae. Rib density of about 4 ribs per mm recorded at 2 mm distance antero-laterally from dorsal umbo in one specimen.

Measurements of figured material (in mm)

	Length	Width
Br 30/304	3·4	4·5
Br 30/305	3·8	4·6
Br 30/306	2·3	2·7
Br 30/307	3·4	3·8

Material. Samples S_{8-13}, S_{50-52} are included in this group.

Discussion. The main features which distinguish the species from other Llandoverian dicoelosiids are the flattened to convex brachial valve in lateral profile, and, so far as the present collection is concerned, the concave lateral margins in the posterior region of the shell.

Formal comparison suggests affinities with *D. bilobella* and *D. oklahomensis* (see Table 11). However, samples S_{8-13} are quite distinct from other Llandoverian samples (Table 8). Previously mentioned samples have been assigned to *D. osloensis* and samples S_{8-13} may be considered intermediate between *D. osloensis* and *D. oklahomensis*. *D. biloba* occupies this position in Europe and the samples are assigned to it although the numerical comparison is not completely adequate.

Facies association. The described material occurs in the *Clorinda* Community, characterized by *Clorinda* sp., *Skenidioides lewisi* (Dav.), *Meifodia ovalis* (Williams), *Cyrtia exporrecta* (L.), *Leangella scissa* (Salter), etc.

Description of the Wenlockian samples (Pl. 9, fig. 31; Pl. 10, figs. 6–17). Pedicle valve about four-fifths as long as wide, with mid-line length about three-quarters of maximum valve length. Lateral profile strongly convex, valve thickness about one-third of maximum length. Lobes broad, divergence ranging between 38° and 58° (average 50°). Hinge-line averaging a little more than half shell width, cardinal extremities obtuse with small flattened ears. Interarea curved, apsacline. Sulcus deep and narrow, originating at umbo, 0·8 mm wide at 2 mm growth stage, without clearly defined ornament.

Brachial valve about three-quarters as long as wide, flatly to moderately convex in lateral profile; cardinal extremities flattened, lobes posteriorly arched. Sulcus originating umbonally, slightly wider than ventral sulcus, without radial ornament. Ornamentation on lobes of angular costae and costellae.

Measurements of figured material (in mm)

	Length	Width
Br 3411	3·6	3·9
Br 3412	3·5	4·8
Br 30/308	3·0	4·0
Br 3415	3·3	3·6
Br 3416	2·9	3·7
Br 3417	2·7	3·3

Material. Samples $S_{26-28, 30-33}$, S_{15}, S_7, S_{16}, S_{56}, S_{61-63}.

Discussion. The Wenlockian *D. biloba* described differs only slightly from the Llandoverian material. The described material has the least distances with *D. bilobella* and *D. oklahomensis* (Table 11).

It must be noted that the distances between the post-Llandoverian dicoelosiids such as *D. biloba*, *D. bilobella*, and even *D. oklahomensis*, is too low (Table 10). But the type material of these species, two specimens of each measured from their printed photographs, does not allow a certain decision.

Nevertheless, the lowest distances of *D. bilobella* with the East Baltic material just described suggest that *D. bilobella* is a younger synonym of *D. biloba*. Maybe these Wenlockian representatives of two dicoelosiid stocks, North American and European, differ only in shell size, the former being smaller (see also Amsden 1968, p. 34). If so, then the name *biloba* should be preferred for the East Baltic specimens under discussion.

EXPLANATION OF PLATE 10

All specimens ×6.

Figs. 1–22. *Dicoelosia biloba* (L.). 1–5, Ventral, dorsal, anterior, lateral, posterior views of complete shell, Br 30/305, from S_{11}. 6–8, Ventral, dorsal, lateral views of complete shell, Br 3411, from S_{33}. 9–11, Ventral, dorsal, lateral views of complete shell, Br 30/308, from S_{16}. 12–14, Ventral, dorsal, lateral views of complete shell, Br 3412, from S_{31}. 15–17, Ventral, dorsal, lateral views of complete shell, Br 3413, from S_{15}. 18–22, Ventral, dorsal, anterior, lateral, posterior views of complete shell, Br 30/306, from S_6.

Figs. 23–40. *Dicoelosia oklahomensis* Amsden. 23–25, Ventral, dorsal, lateral views of complete shell, Br 30/312, from S_{14}. 26–30, Ventral, dorsal, anterior, posterior, lateral views of complete shell, Br 30/313, from S_5. 31–35, Ventral, dorsal, lateral, posterior, anterior, views of complete shell, Br 30/41, from S_1. 36–39, Ventral, dorsal, posterior, lateral views of complete shell, Br 30/40, from S_1. 40, Interior of pedicle valve, Br 30/42, from S_1.

Facies association. D. biloba is found in calcareous siltstones. It is associated with the brachiopods *Skenidioides lewisi* (Dav.), *Cyrtia exporrecta* (L.), *Resserella* sp., *Atrypa* sp. This would indicate that *D. biloba* belongs to the off-shore association.

Material of doubtful assignation (Pl. 10, figs. 18–22). Sample S_6, a single shell, Br 30/309, from the Llandoverian beds of the Mezciems boring is quite distinct morphologically (Table 8) and geographically (text-fig. 1). Further material is required before a proper assignation can be made.

Dicoelosia oklahomensis Amsden 1951

Plate 9, fig. 32; Plate 10, figs. 23–40

1951 *Dicoelosia oklahomensis* Amsden, p. 77, pl. 15, figs. 1–7.
1967 *Dicoelosia oklahomensis* Amsden; Rybnikova, p. 175, pl. 14, figs. 7, 8.
1968 *Dicoelosia oklahomensis* Amsden; Amsden, pl. 8, fig. 4.

Description of material from East Baltic. Pedicle valve about five-sixths as long as wide, with mid-line length about three-quarters of maximum length; lateral profile strongly convex, valve thickness about two-sevenths of maximum length. Lobes fairly broad, divergence varying between 32° and 53° with an average of 46°. Hinge-line about half shell width, cardinal extremities obtuse with very small ears. Interarea curved, apsacline, relatively long. Sulcus deep and narrow, originating at umbo, only slightly widening, without radial ornament. Ribbing on lobes of low costae and costellae, capillae common.

Brachial valve four-fifths as long as wide, fairly convex in lateral profile, sulcus originating at umbo, slightly wider than ventral one, without ribs. Interarea flat, anacline, shorter than ventral one. Lobes strongly arched in transverse profile.

Pedicle valve interior with smooth surface, muscle field only slightly raised with low median ridge extending to anterior margin. Follicular eminences and embayments strongly developed.

Brachial valve interior with small cardinalia, cardinal process with bilobed myophore and low shaft; brachiophore processes extend for one-third of valve length. Adductor field not clearly defined, follicular eminences and embayments strongly developed.

Measurements of figured material (in mm)

	Length	Width
Br 30/40	2·6	3·3
Br 30/41	3·1	3·1
Br 30/42	2·7	c. 3·5
Br 30/311	c. 2·2	2·7
Br 30/312	2·5	3·5
Br 30/313	3·1	3·4

Material. The standard group, $S_{1-5, 14}$, and the poorly preserved samples S_{61-66}.

Discussion. The well preserved and abundant material may be readily identified by the degree of the brachial valve convexity with *D. oklahomensis* from the same level of the Upper Silurian of North America.

But the numerical comparison (Table 11) indicates that the closest species for $S_{1-5, 14}$ is *D. bilobella*, although *D. oklahomensis* has nearly the same average similarity. The maximum and minimum distances of the $S_{1-5, 14}$ specimens in relation to the type material of *D. oklahomensis* and *D. bilobella* are both lower in the case of *D. okla-homensis*.

The comparison of the described material by separate samples (Table 12) shows the greater similarity of the stratigraphically younger samples, S_1, S_2, S_{14}, with *D. okla-homensis* than with *D. bilobella*. Thus, only the stratigraphically younger part of the sequence, i.e. S_1—S_2—S_{14}, may be identified by 'shape' taxonomy with *D. okla-homensis*. The relatively greater similarity of the older part, i.e. S_3—S_4—S_5, with *D. bilobella* than *D. oklahomensis* is due to the main evolutionary trend of dicoelosiids. In spite of that the whole sequence is named as *oklahomensis*.

TABLE 12. Sample distances between the type specimens of *D. oklahomensis* (DO), *D. bilo-bella* (DB) and the Ludlovian samples of the collection. The samples are arranged in order by their minimal similar lines

	S_1	S_2	S_{14}	S_3	S_4	S_5
DO	46·73	28·50	39·25	55·20	66·00	76·25
DB	50·07	48·50	47·75	40·00	46·00	69·25

Facies association. D. oklahomensis occurs in silty limestones characterized by *Eospirifer radiatus* (Sow.), *Cyrtia* sp., *Dalejina hybrida* (Sow.), *Gypidula* sp., *Brachyprion* sp., *Atrypa* sp.

Genus EPITOMYONIA Wright 1968

Epitomyonia glypha Wright 1968

Plate 8, figs. 8–17

1968b *Epitomyonia glypha* Wright, pp. 128–38, pl. 1, figs. 1–16.

Material. Two complete shells and two brachial valves in sample S_{24}.

Description. Pedicle valve four-fifths as long as wide, mid-line length four-fifths of maximum valve length. Lateral profile evenly convex, valve thickness about half maximum length. Lobes broad, diverging 60° in one specimen and 62° in the other; moderately convex with flattened crests in transverse profile. Hinge-line about four-fifths shell width in one specimen, and about three-fourths in the other. Cardinal extremities obtuse with small flattened ears. Sulcus shallow, well defined by prominent fascicle of branching ribs, 0·9 mm wide at 2 mm growth stage.

Ornamentation on lobes and sulci of angular costae, intercalated and branching costellae, and rare capillae in intercostal spaces; on cardinal extremities ribs less distinct. Rib density measured at 2 mm antero-lateral to umbo along crest of brachial lobe, 5 and 4 costae or costellae per mm respectively. Ribbing at the edges of sulcus somewhat more elevated. Commissure crenulated though less so towards ears.

Brachial valve gently concave in lateral profile, typically slightly convex umbonally. Prominent edge of brachial sulcus corresponds to flattened crest of ventral lobe, 1·9 and 2·3 mm wide at 2 mm growth stage respectively. Sulcus of umbonal region rapidly broadening and shallowing, sometimes divided longitudinally by one prominent rib into two parts.

Brachial valve interior typical of species; notothyrial platform not greatly thickened, cardinal process with bilobed myophore and shaft anteriorly; sockets narrow, bounded medially by low ridges of brachiophores s.l. from which hook-like brachiophores s.s. arise. Median septum rises anterior to shaft and extends almost to shell margin. Adductor field not clearly impressed, anteriorly elevated above valve floor. Follicular eminences and embayments strongly developed, orthid-like.

Measurements of figured material (in mm)

	Length	Width
Br 3400	4·2	5·1
Br 3401	2·4	3·5

Discussion. The species differs from other dicoelosiids in its peculiar internal structure. The closest species is *D. anticipata.* This lacks such structures, and also differs in having a more transverse outline and greater invagination of the shell.

Facies association. Sample S_{24} comes from close to the local boundary between the Silurian and the Ordovician in approximately 0·5 mm of calcareous siltstones, similar lithologically to the immediately overlying beds. The latter contain abundant brachiopods of the *Stricklandia* Community; the underlying Ordovician beds were formed under regressive conditions, when bioherms were common (Männil 1966).

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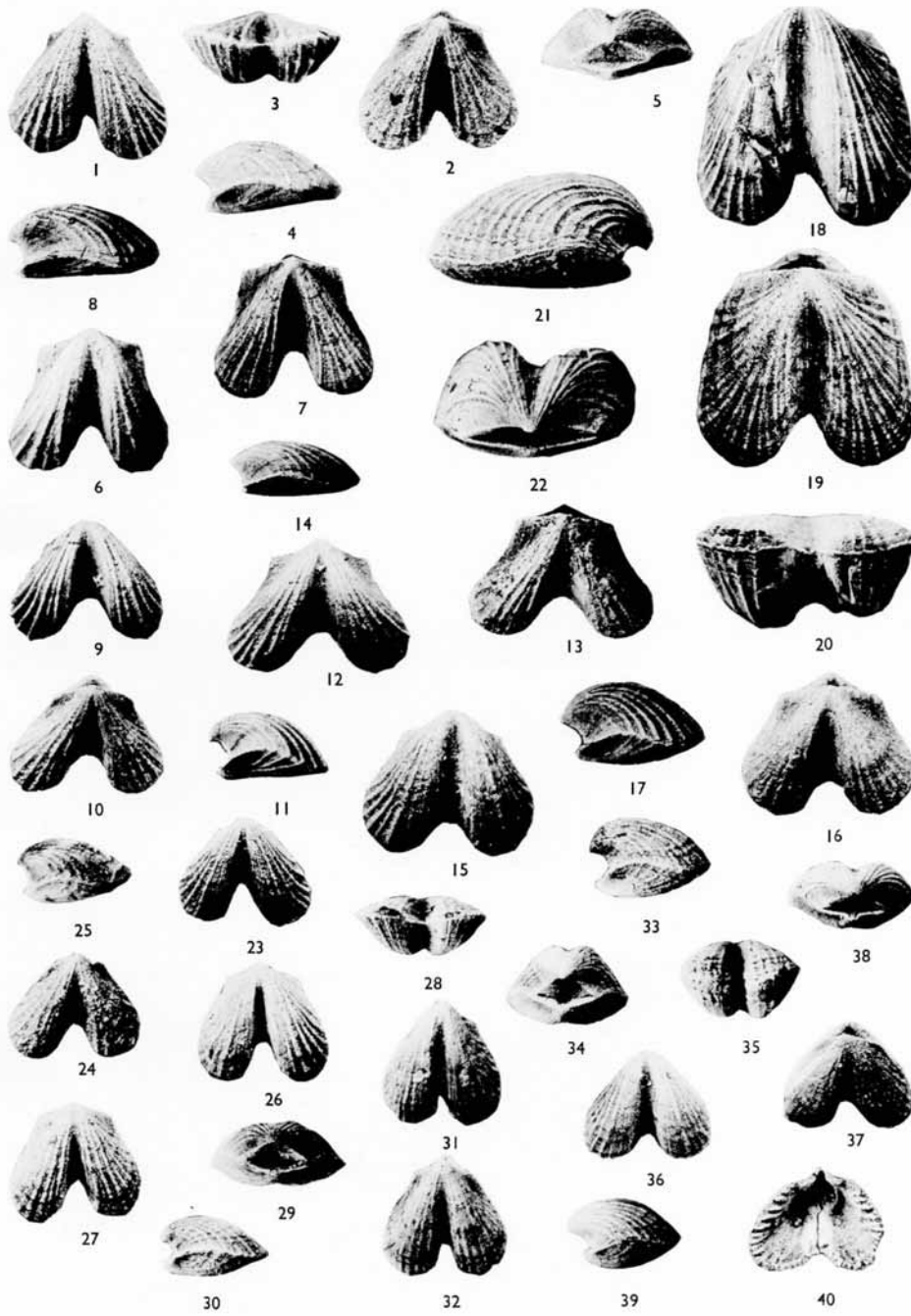Academy of Sciences of the Estonian S.S.R.
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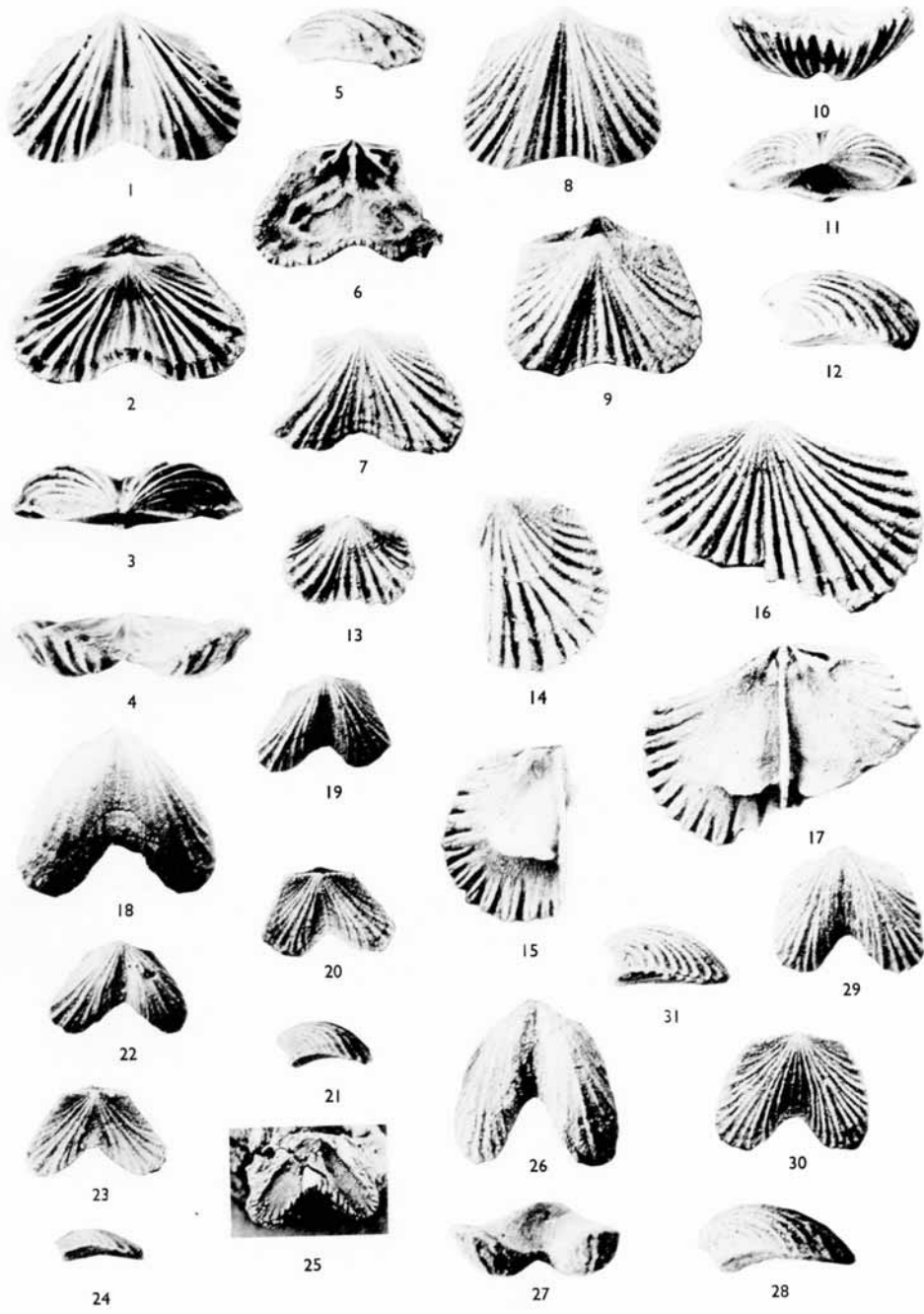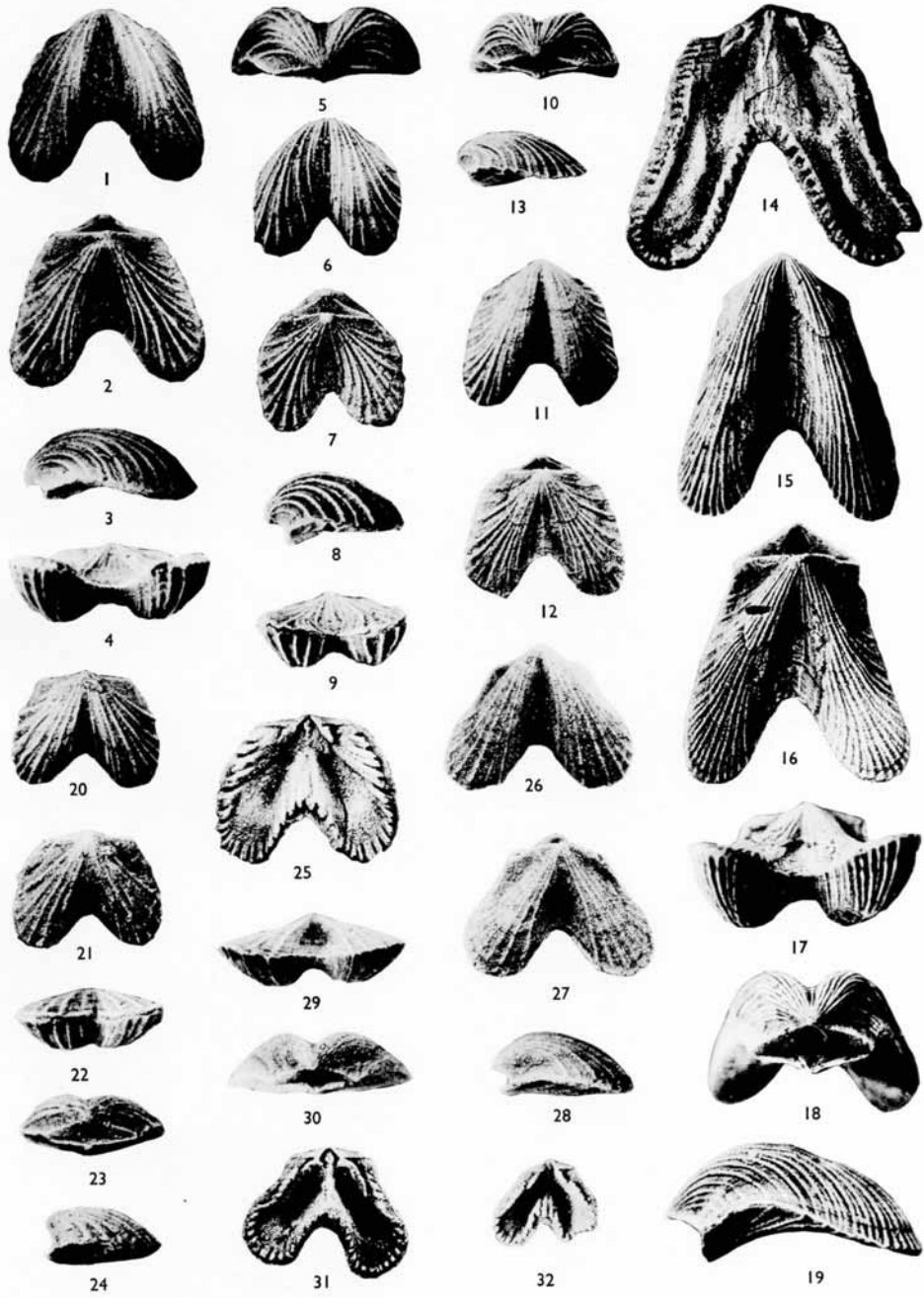
RUBEL, Dicoelosiid brachiopods

RUBEL, Dicoelosiid brachiopods

PLATE 10

RUBEL, Dicoelosiid brachiopods