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SOME TEREBRATULID POPULATIONS FROM THE LOWER KIMMERIDGIAN OF POLAND AND THEIR RELATIONS TO THE BIOTIC ENVIRONMENT

Populations of *Epithyris 'subsella'* in different Lower Kimmeridgian fossil assem-
blages show different size-frequency distributions although they exhibit a simi-
lar shape of survivorship curves. A population with large-sized adult speci-
mens of *E. 'subsella'* was characteristic for a community in which most abun-
dant were bivalves: *Isognomon subplana, Lopha gregarea* and *Trichites saussu-
rei*. A population with small adult specimens was characteristic for a commu-
nity with abundant dasyclad alga *Goniolina geometrica*. Here, among shelled
suspension-feeders the most important producers were brachiopods *E. 'subsella'*,
Zeilleria humeralis, and *Septaliphoria pinguis*. Thalli of *G. geometrica* were the
substrate for most of the sedentary organisms in this community. The estimation
of biomass and productivity of particular species in fossil communities is dis-
cussed.

INTRODUCTION

Terebratulid brachiopods constitute an important component of the
fossil assemblages in the Upper Jurassic of Poland but their biological
and geological importance have yet found only a small expression in
the literature. The main reason is the increasingly complex taxonomy of
this group of fossils. Their determination is difficult and seems to be
mostly subjective due to the present limited knowledge of intrapopula-
tion variability and to taxonomic splitting. It has been documented that
representantives of the order Terebratulida show very wide population
variability (Kozłowski 1929; Müller 1952; Singeisen-Schneider 1976;
Brügge 1973, 1974, 1977; Thayer 1976; Auxenfant *et al.* 1976; Feldman
1977; Pajaud 1977). Therefore studies on whole populations seem to be
the essential first step in the research of this group.

The purpose of this paper is to discuss the following aspects of populational biology of Jurassic terebratulids, which are important for their systematics:

1. the complexity of some Jurassic brachiopod communities and relations between particular coexisting brachiopod species;
2. the variability within particular terebratulid populations and differences between populations of single biological species;
3. the influence of environmental factors (expressed by structures of fossil assemblages, especially their non-brachiopod components) on the variability of some Jurassic terebratulids.

Fossil assemblages from the Lower Kimmeridgian of Wierzbica (Holy Cross Mts., Central Poland) and Czarnogłowy (West Pomerania, Northern Poland), both containinig rich and well preserved fauna, have been selected as a basis of this study. Their terebratulids are compared with several other Lower Kimmeridgian populations from the Holy Cross Mts. The material is housed in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

FOSSIL ASSEMBLAGE WITH TEREBRATULIDS FROM WIERZBICA

The cement plant quarry in Wierzbica is one of the best outcrops of marls with oyster coquinas widely developed in Lower Kimmeridgian of the Holy Cross Mts., Poland. The rich fauna of this locality has been partially described by Pugaczewska (1971) and Barczyk (1969). A layer of *Lopha gregarea* (Sowerby) coquina about 3 m thick occurs in the upper part of the sequence. Laminated unfossiliferous marls are overlain, with a distinct boundary, by more calcareous marls containing rare, irregularly silicified oysters and terebratulids. Marly coquina limestone with abundant *Lopha* and subordinate diverse fauna of molluscs and brachiopods overlie with sedimentary continuity about one meter above (fig. 1). Nearer the top of the coquina, *Isognomon subplana* (Etallon) becomes more common. The top part of this layer consists of numerous *Isognomon* shells and other rarer bivalves. Above the oyster coquina occur pure, non-laminated marls with rare intercalations of detritus of *Exogyra nana* (Sowerby) shells.

Terebratulids are most frequent in the assemblage intermediate between those dominated by *Lopha* and *Isognomon*. The structure of this assemblage is similar to the Oyster/*Isognomon promytiloides* assemblage of Fürsich (1977) but strongly differs in the frequency of particular groups of fossils. Terebratulids are not important components of assemblages in the English Corallian (Fürsich 1977; Brookfield 1978). Such a difference between the Polish and English Jurassic assemblages is a rule.
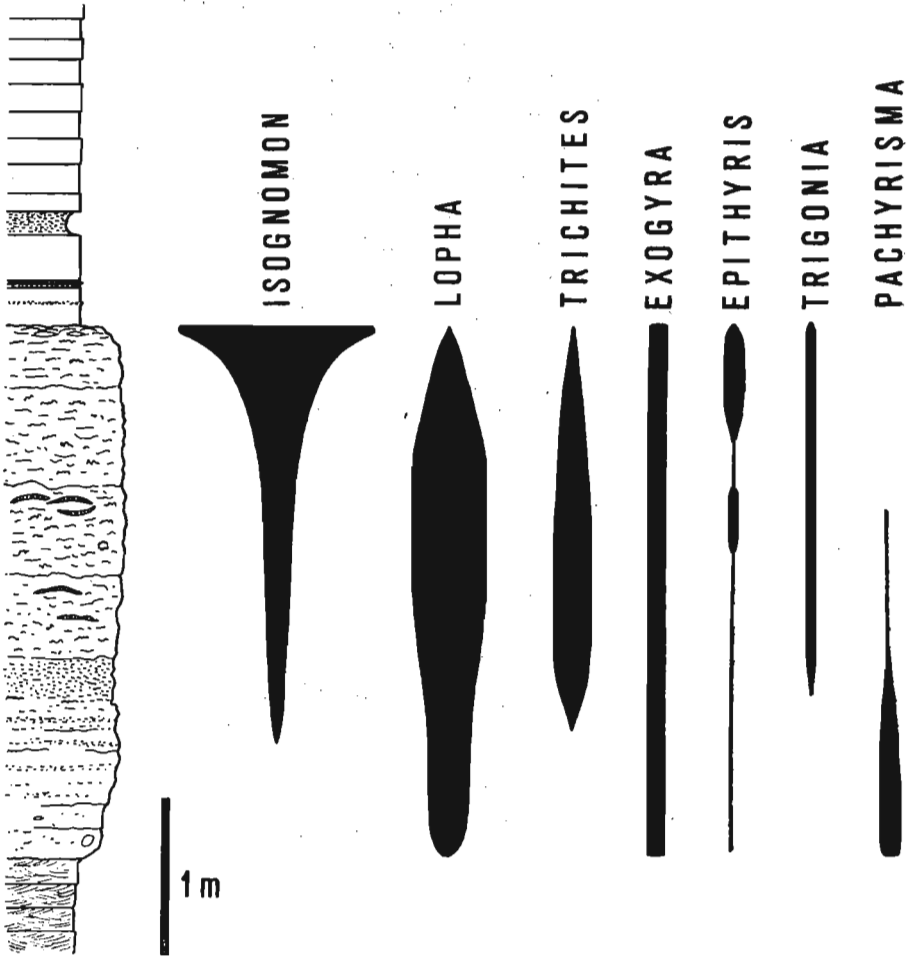
Fig. 1. Oyster coquina from Wierzbica quarry, Lower Kimmeridgian of the Holy Cross Mts., Poland. Changes in the frequency of the most important species within coquina layer schematically presented (strongly simplified).

None of the many types of assemblages from Wierzbica quarry are identical with those from Corallian of England, although most of them have a close analogue among the English (i.a. *Myophorella clavellata* ass., *Nucleolites scutatus* ass., *Lopha gregarea* ass., etc.). Some questions arise here concerning the sense of classification of fossil communities. It seems that continuous connections exist, at least between most described communities (Cisne and Rabe 1978). If this is so, discrete groups of samples separated by multivariate analysis mainly express how and where samples were taken from a continuous spectrum of communities within the ecosystem. Description of a single large sample from a fossil assemblage seems to be more important as the primary data for subsequent interpretations than typological classification.

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The assemblage with frequent terebratulids from Wierzbica is dominated in number as well as in volume (weight) of fossils by *Isognomon subplana* (fig. 2). *Trichites saussurei* Voltz and *Lopha gregarea* represent an important percentage in volume in spite of the low number of specimens. On the contrary small-sized but numerous oysters *Exogyra nana* and *Liostrea* sp. do not constitute by weight an important part of this assemblage. There are a few data regarding the rate growth of Jurassic bivalves and brachiopods. By analogy with Recent molluscs it seems that large-sized *Trichites* and *Isognomon* lived much longer than small *Liostrea* and *Exogyra*. Then the most important components of biomass in this community were *Isognomon subplana* and *Trichites saussurei* and participation of other species of suspension-feeders in the living community was much smaller than in the fossil assemblage.

The number of fossils is not a direct function of the biomass of living species as many authors have assumed (Walker 1972; Stanton 1976; Peterson 1976) but depends on the biological productivity (understood as an increase of number or weight plus elimination). The biovolume of fossil species can be compared with the biomass of living species only in such a case where the rate of growth is similar (see data of Peterson 1976). The structure of a fossil assemblage expresses the productivity of a particular species in terms of the total biological productivity of a living community. The structure of a sample taken from a living community express the biomass of a particular species in terms of the total biomass. For this reason numerical data on fossil assemblage and living communities are not comparable. In ecological investigations realtions between productivities of populations of different species within a community can be calculated from the biomass, age structure, growth curve, and production of gonads of each species. In palaeoecology distribution of particular species productivities within a community is a primary data. An estimation of a biomass distribution requires here the inverse operation. However, Kranz (1977) has presented an attempt to directly estimate biomass (standing crop) in fossil communities. He has assumed that anastrophic (accidental) burial is the main reason of death and preservation of benthic animals. Kranz's model is based on two factors: probability of failure to escape after burial and time that the remains of an individual will persist after death estimated for all size classes in a population. Both must be applied by analogy with Recent processes of fossilization. The main trouble lies here in recognizing which type of Recent fossilization process is represented by a particular fossil assemblage. Interpretations of conditions during sedimentation, based on lithology and sedimentary structures are still very inadequate in most cases. This is almost impossible to state with any great degree of certitude, therefore making the usefulness of Kranz's method problematical. The application of data on relative productivities and lifespans of
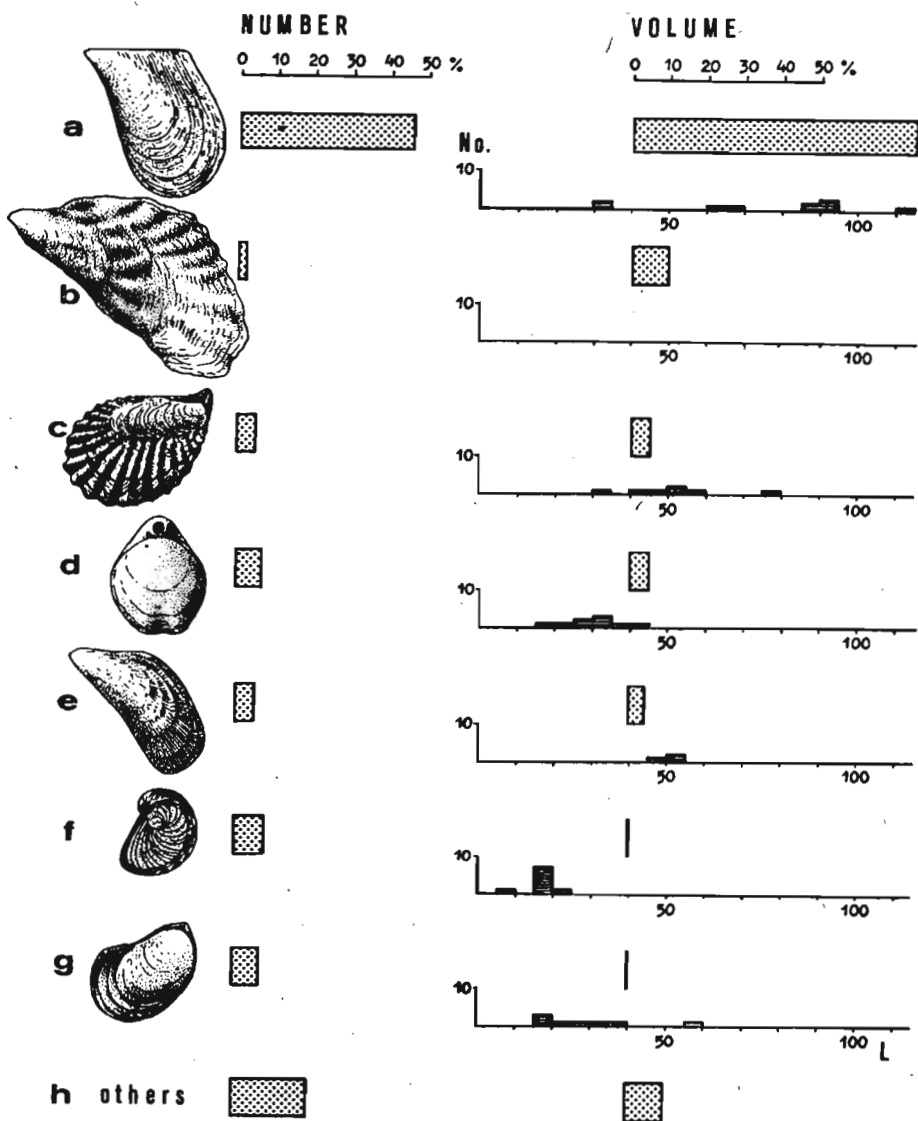
Fig. 2. Distribution of productivity within trophic group of shelled suspension feeders in community of Wierzbica coquina. Participation of most important species per cent of number of specimens (*left*) and volume (estimated by weighing of fossils; *right*). Size frequency distribution of better preserved specimens added. Collecting area 2.88 sq m; number of specimens 128. a. *Isognomon subplana* (Etallon); b. *Trichites saussurei* Voltz; c. *Lopha gregarea* (Sowerby); d. *Epithyris "subsella* (Leymerie)" e. *Arcomytilus pectinatus* (Sowerby); f. *Exogyra nana* (Sowerby); g. *Liostrea* sp.; h. *Camptonectes lens* (Sowerby), *Trigonia papillata* Agassiz, *Pleuromya uniformis* (Sowerby), etc. Other trophic groups are represented in this assemblage by gastropode *Ampullina* sp. and echinoid *"Rhabdocidaris"* sp. Their contribution is less than one per cent of volume of fossils.

particular species for estimation of relative biomasses within a fossil community seems to be more perspective. Robertson (1979) has found on , equation describing the relationship between annual production, biomass, and lifespan. It should be helpful in palaeoecological investigations.

Terebratulid specimens in the Wierzbica quarry are dispersed in rock and clusters of their shells are very rare. I have found only one single scar of pedicle attachment on a Wierzbica terebratulid shell. This single scar indicates the possibility of Wierzbica brachiopods being able to dissolve calcareous substrate. No evident pedicle boring has been found on any oyster but rarity of such scars may be caused by relatively small participation of terebratulids in the community. It undoubtedly seems that shells of sedentary bivalves were the substrate for attachment of brachiopod larvae in the Wierzbica community. Rhynchonellids do not occur in the Wierzbica coquina. Zeilleriids are extremely rare — I have found only three adult but very small-sized specimens (fig. 9 c).

The population of terebratulids from Wierzbica

Traditionally, the shape of the brachidium is treated as taxonomically the most important feature in terebratulid brachiopods. Singeisen-Schneider (1976) has shown however, that the brachidium proportions are clearly correlated with the shape of the shell, and are little differentiated within many groups of terebratulids. Well preserved silicified specimens from Wierzbica support this view. Specimens of very different morphology show brachidia of similar structure although relation between the length of the loop to the length of brachial shell is variable and lateral proportions of brachidium depend on the shape of shell. Asymmetrical specimens also have an asymmetrical loop. Reconstructions of brachidia of specimens from the same layer presented by Barczyk (1969) are incorrect (see fig. 3). None of my specimens show the dorsoventral undulation of crura typical of Barczyk's reconstructions.
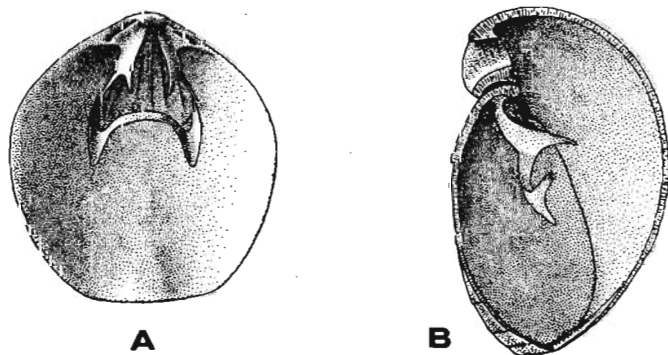

A   **B**

Fig. 3. *Epithyris "subsella* (Leymerie, 1840)", Lower Kimmeridgian of Wierzbica, Holy Cross Mts., Poland. Reconstruction of internal structures based on many silicified specimens. A. Brachial valve. B. Sagittal section of adult specimen. Both nat. size.

External features of shells are much more differentiated than the shape of the brachidium. The following features were measured: length (L), width (W), thickness (G), distance between anterior comissure and widest part of a shell (R), height of brachidial valve sinus (K), height of pedicle valve sinus (N), and width of pedicle valve sinus (F) (figs 4—5). The changes of each character during ontogeny were examined. They are important from the taxonomical point of view because indices based on features which are changeable during ontogeny can be used only in comparing specimens (or populations) at an identical stage of growth. An increase in the participation of a particular ontogenetic stage in a fossil population involves changes in the distribution of features.

The W/L index (width to length of the shell) is relatively stable during ontogeny. It shows a similar distribution during the whole course of ontogeny (fig. 4 A). The index of the position of the widest part of the shell to the width (W/R) or length (L/R) is not so stable but it seems to be very characteristic for a population and of high taxonomical importance. Index W/R shows a more linear distribution than L/R (fig. 5). Scattering of the former feature decreases during growth. Both the time of the appearance of sinuses and their shape are very variable. The pedicular (ventral) sinus is always larger than the brachial (dorsal) one but both sinuses develop together (fig. 4 B). They are of little importance in distinguishing population or species. The thickness of the specimens is very variable and is not distinct between populations.

The most useful indices for systematic studies are thus: length to width (L/W) and position of widest part of the shell to width (W/R). Histograms of frequency of these indices in the Wierzbica terebratulid population show a distribution close to normal. Some asymmetry of histograms is caused by slightly non-linear development of some characters during ontogeny (fig. 5). It can be inferred that terebratulids from Wierzbica represent homogenous population of a single species. Seven species of five genera (*Sellithyris subsella* (Leymerie), *S. pseudosella* Barczyk, *Epithyris oxonica* Arkell, *Goniothyris amoena* Seiffert, *Loboidothyris valfinensis* (Loriol), *L. zieteni* (Loriol), and *Lobothyris baltzeri* (Haas)) recognized by Barczyk (1969) in this locality are all considered to be morphotypes within this population.

Relationship between terebratulids from Wierzbica and other Lower Kimmeridgian terebratulid populations from Poland

Many other Lower Kimmeridgian localities with lithologically different beds contain terebratulid morphotypes identical with those in Wierzbica but in different numerical contributions. A distribution of features similar to that of Wierzbica population is presented by terebratulids from
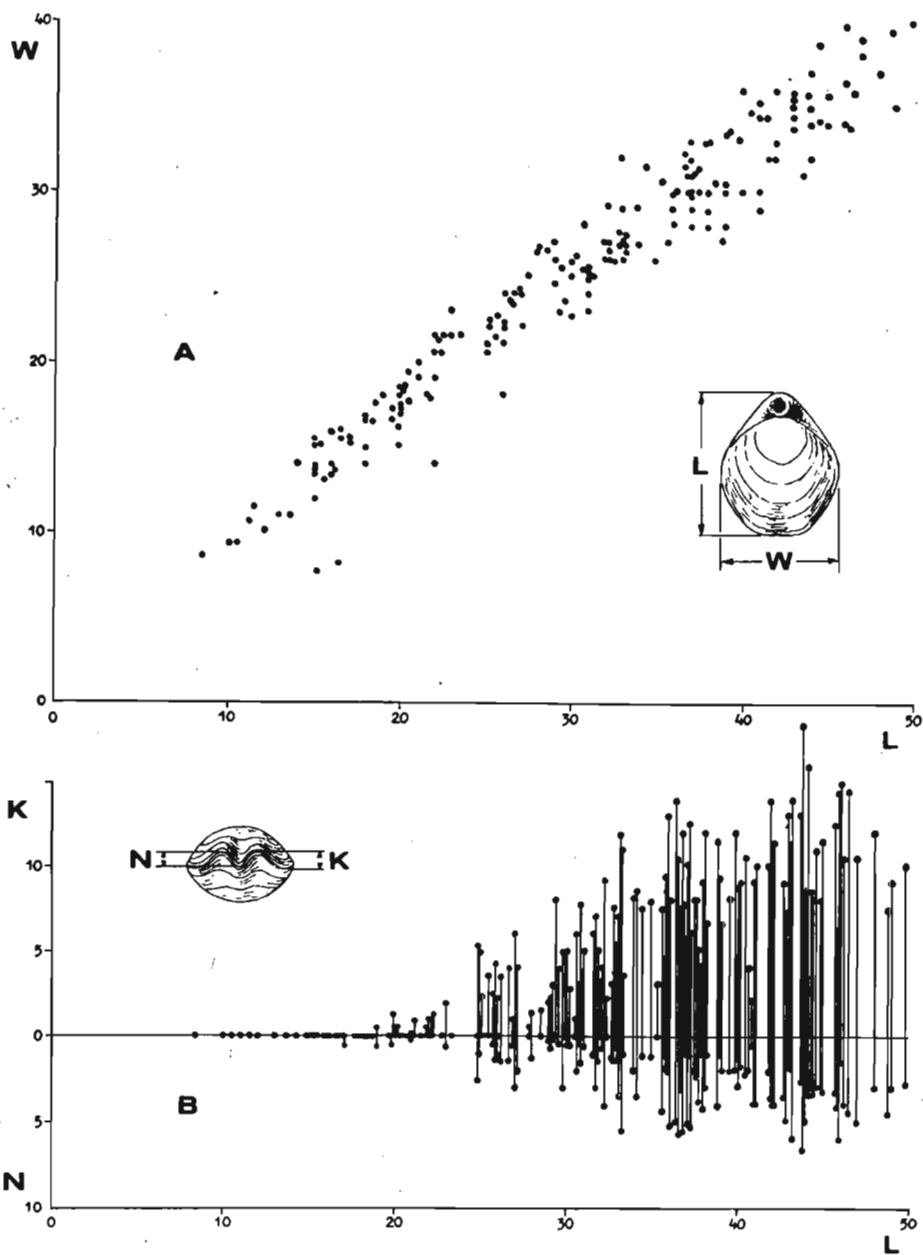
Fig. 4. Intrapopulation variability of *Epithyris "subsella* (Leymerie, 1840)" from Lower Kimmeridgian of Wierzbica, Poland. A. Scattergram showing relation of width of the shell (W) to length (L). B. Development of pedicular (K) and brachial (N) sinuses plotted against the length (L). Values of each specimen connected by vertical line.
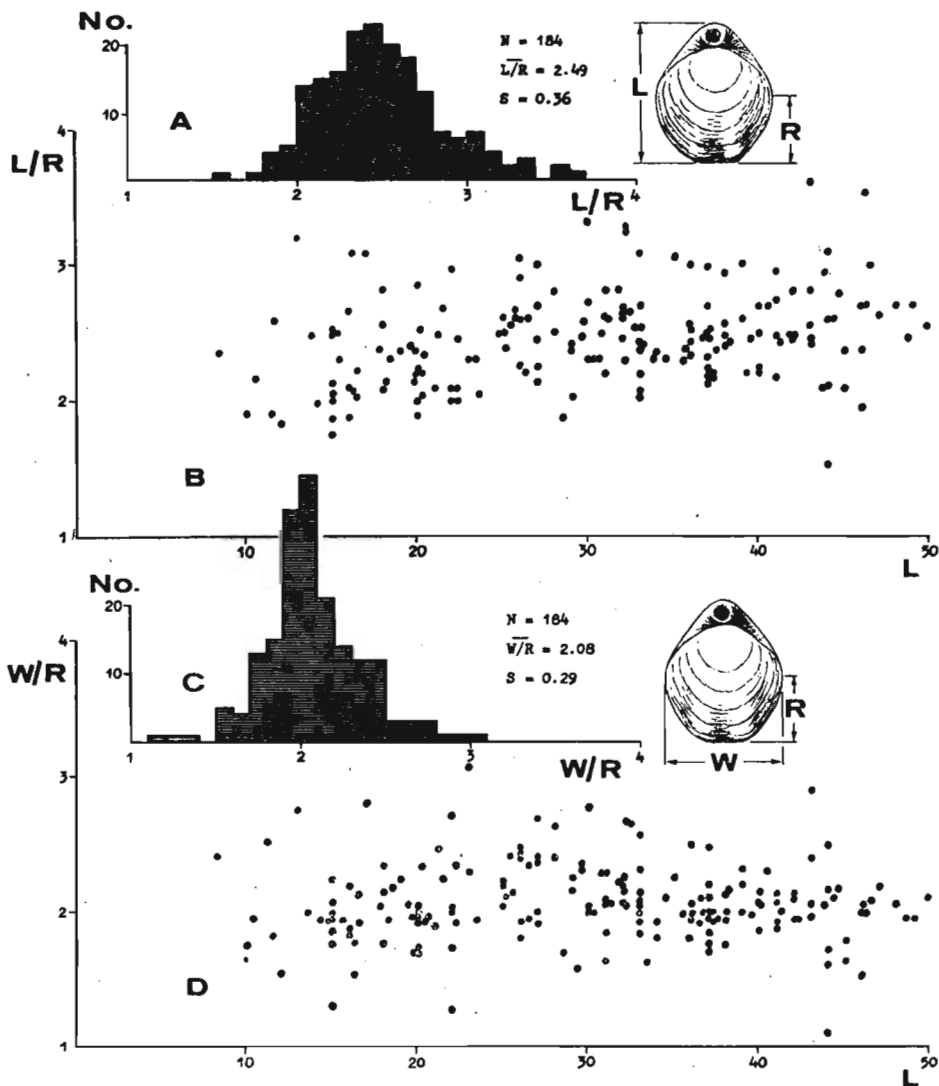
Fig. 5. Intrapopulation variability of *Epithyris* "*subsella* (Leymerie, 1840)" from Lower Kimmeridgian of Wierzbica, Poland. A. Distribution of the index indicating the relation of length of the shell (L) to distance between anterior comissure and widest part of the shell (R). Scattergram of index L/R plotted against length (L). C. Distribution of the index indicating the relation between width (W) and R. D. Scattergram of index W/R plotted against width (W). Number of specimens measured, mean value of index, and standard deviation indicated.

oolitic marly limestone of Korytnica in the southern part of the Holy Cross Mts. (figs. 6 C, 9 G; Barczyk 1969). There, adult specimens are about one third smaller in size than in Wierzbica. The fossil assemblage from Korytnica is dominated by the small oyster, *Exogyra nana*; poorly preserved mobile bivalves and gastropods are frequent. The rhynchonellid *Septaliphoria pinguis* (Roemer), unknown in Wierzbica, occurs here (1.5

per cent of the brachiopod specimens within the assemblage). Terebratulid shells are covered with encrusting cyclostomatous Bryozoa.

Much greater morphological differences in relation to Wierzbica are shown by a population of terebratulids from Czarnogłowy in West Pomerania, Poland. Adult specimens are even smaller than in Korytnica and wide specimens are more frequent (figs 6 B, 9 B). Together with terebratulids *Septaliphoria pinguis* occurs here (9.0 per cent of total brachiopod number within the assemblage). The most common brachiopod in this assemblage is *Zeilleria humeralis* (Roemer), very rare in Wierzbica. Adult specimens of this species are twice as large as those in Wierzbica (fig. 9 A). The sediment in which enumerated brachiopods occur is poorly consolidated, marly oolitic limestone.

The terebratulids which differ the most from those of Wierzbica occur in white oolitic limestone exposed below the castle in Iłża (see Barczyk 1962). My materials from this locality are rather poor, so a comparison can be only superficial, but even in such a small sample, an unusually
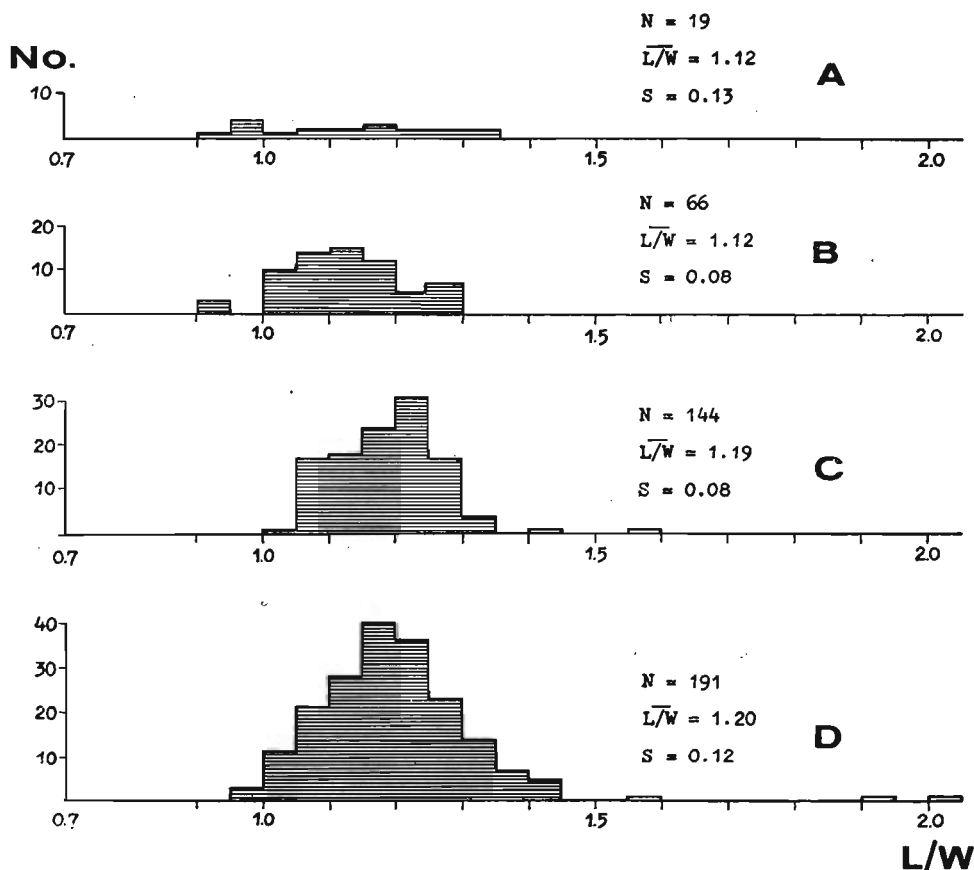

Fig. 6. Differences in distribution of index length (L) to width (W) of the shell between some populations of *Epithyris* "*subsella* (Leymerie, 1840)" from Lower Kimmeridgian of Poland. A. Iłża. B. Czarnogłowy. C. Korytnica. D. Wierzbica.

high frequency of very wide specimens can be recognized (fig. 6 A). Besides terebratulids small specimens of *Zeilleria humeralis* occur here, whereas rhynchonellids are rare. The fossil assemblage is dominated by small trigoniids and other mobile bivalves.

Data presented above strongly indicate different ecological requirements of Lower Kimmeridgian terebratulids (*Epithyris*), zeilleriids (*Zeilleria*), and rhynchonellids (*Septaliphoria*). This has also been postulated for Liassic brachiopods by Tchoumatchenko (1972; also Fürsich and Hurst 1974). It is significant that together with the largest specimens of *Epithyris* in Wierzbica very small and rare adult specimens of *Zeilleria* occur, and with the largest specimens of *Zeilleria* in Czarnogłowy relatively small specimens of *Epithyris* occur. A reason for such difference supposedly lies in environmental conditions; most probably in the energy of the environment and contribution of suspended clayey substances. Differences in environmental conditions should also be expressed in the composition of particular fossil assemblages.

FOSSIL ASSEMBLAGE WITH TEREBRATULIDS FROM CZARNOGŁOWY

The large cement plant quarry in Czarnogłowy, Western Pomerania, Poland (Zarnglaff of German authors) (see Richter 1934; Dmoch 1970) has not been exploited since 1962 and there is no good outcrop of layers with terebratulids. Data presented here are based on material collected from a single disintegrated loose block of limestone in the northern part of the quarry. The area from which specimens were collected was about 4 sq. metres but material may be enriched by natural washing of the sediment. On a weight basis, *Epithyris* is the dominant species but *Zeilleria* is more numerous (fig. 7). Other groups of fossils occur sporadically. Mobile oolites cannot be the substrate for the attachement of brachiopods. It might be expected that shells of brachiopods were used as substrates by terebratulid larvae, because oysters and other molluscs were relatively rare in this community. A similar terebratulid dominated assemblage from Middle Triassic of Opole Silesia shows a high frequency of pedicle borings (Małkowski 1975). It is surprising that in Czarnogłowy no pedicle attachment scars have been found. Lack of efficiency in dissolving calcareous matrix by Kimmeridgian terebratulids is improbable because closely related forms from the Valanginian of Wąwał near Tomaszów Mazowiecki, Poland produced distinct borings on oyster shells.

This matter can be resolved after determination of the substrate to which oysters from the Czarnogłowy assemblage were attached. The mode of early growth of an oyster shell involves preservation of substrate ornamentation on both valves (see Pugaczewska 1971). The mantle margin 'crawls' on the surface of the substrate and the secreted shell reflects surface morphology — the negative on the lower valve and positi-
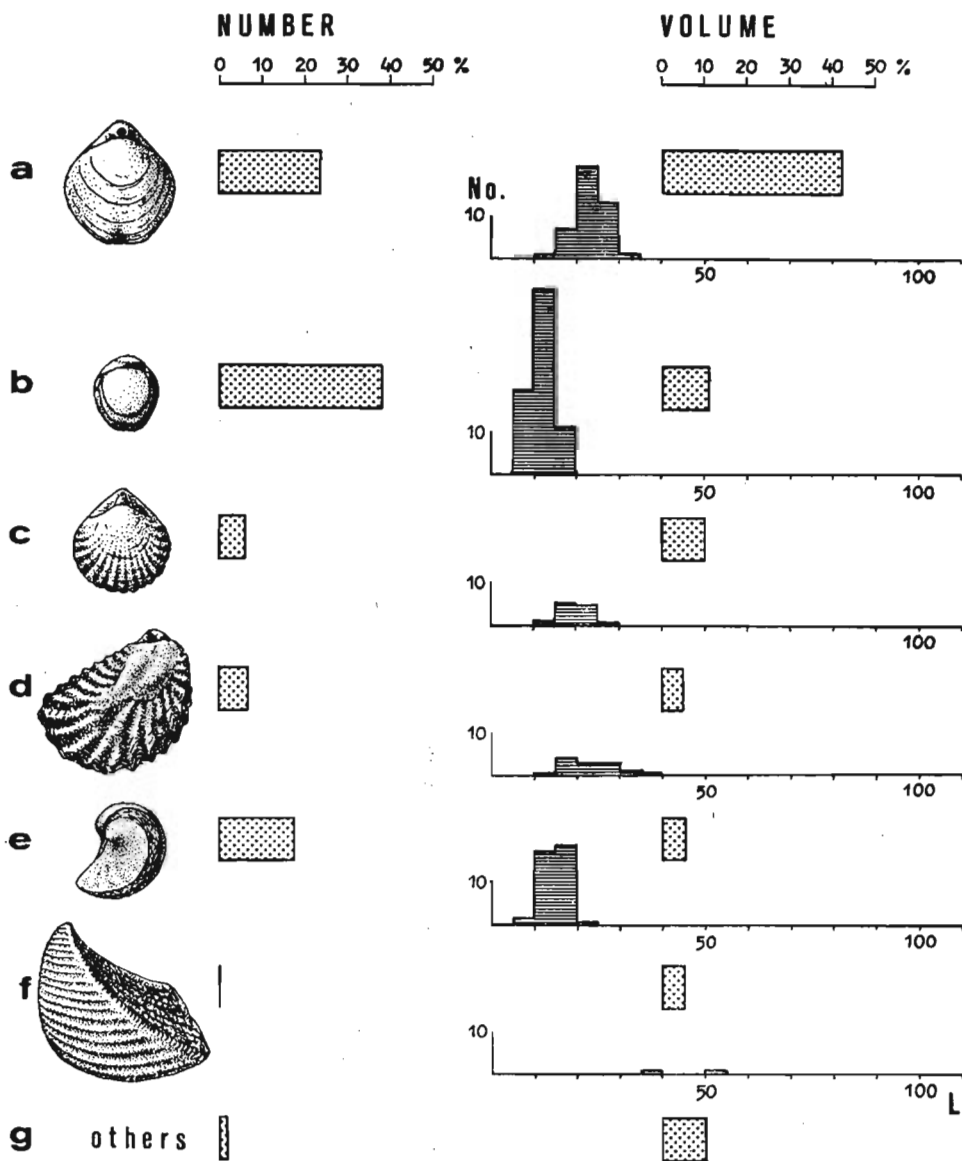
Fig. 7. Distribution of productivity within trophic group of shelled suspension feeders in community of Czarnogłowy oolite. Collecting area about 4 sq. m, number of specimens 404. a. *Epithyris "subsella* (Leymerie)"; b. *Zeilleria humeralis* (Roemer); c *Septaliphoria pinguis* (Roemer); d. *Lopha gregarea* (Sowerby); e. *Exogyra reniformis* (Goldfuss); f. *Trigonia papillata* Agassiz; g. *Pholadomya protei* (Brongniart), *Trichites* sp., *Cucullaea texta* Roemer, *Inoperna perplicata* (Etallon), *Mactromya* sp., etc. Other trophic groups are represented in this assemblage by gastropods *Nerinella ornata* (Orbigny), *Nerinea* sp., *Pseudomelania* sp., etc. Their contribution is less than one per cent of volume of fossils in the assemblage.
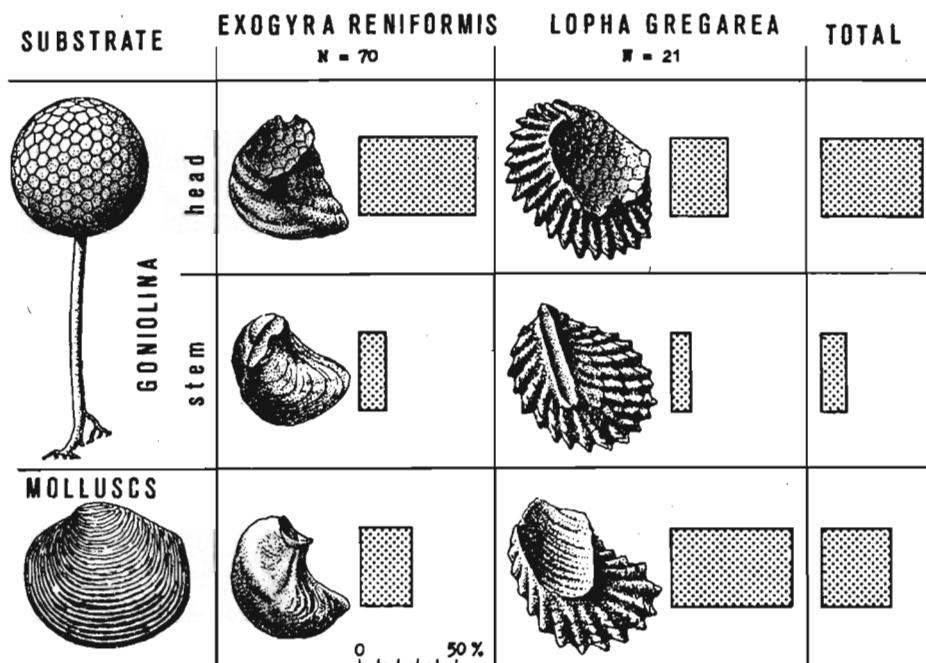
Fig. 8. Distribution of the types of substrate for settlement of oysters in Czarnogło-
wy assemblage.

ve on the upper one. The most common substrates for attachment of Czar-
nogłowy oysters were very characteristic thalli of a dasyclad alga
Goniolina geometrica Goldfuss (weakly calcified *Goniolina* thalli are not
preserved; see Pugaczewska 1971; Silva-Pineda 1977; Bassoullet *et al.*
1978 for review). More than 50 per cent of oysters were attached to a
'head' of *Goniolina*, about 13 per cent to a stalk. Only 35 per cent of
oysters lived on other oysters, shells of dead mobile bivalves or gastropods
(fig. 8). The presence of *Goniolina* thalli allows these sessile animals,
which need a hard substrate for attachment, to colonize oolitic sands.
It seems very probable that *Goniolina* was also the substrate for attach-
ment of *Epithyris*.

No sings of any changes in the diameter of *Goniolina* heads during
growth of an oyster have been noted. Most probably the growth cycle
of *Goniolina* was many times longer than that of small oysters from
Czarnogłowy, but settlement on dead thalli cannot be excluded.

TAXONOMICAL DETERMINATION OF TEREBRATULIDS FROM THE LOWER
KIMMERIDGIAN OF POLAND

The homogeneity of populations described here (with the possible
exception of Iłża materials) seems to be well-founded. A much more
difficult question is the relationship among these populations, and

consequently determination of their specific assignement. In all populations almost identical specimens occur. Therefore, even if they represent different species, the determination is possible only by studying the whole population structure. The determination of one single specimen is usually impossible. The question if different fossil populations represent one or many species is practically unanswerable because genetic isolation cannot be established from fossils. There are, however, some possibilities to demonstrate specific distinctness of fossil populations by either finding two types of populations together (in this case bimodal variability within one sample should be documented) or to demonstrate specific identity of different populations by finding intermediate types of population structures (they must be synchronous from the evolutionary point of view). In the case of Polish Lower Kimmeridgian terebratulids it seems that they form a continuous morphological sequence from populations of the Iłża type to populations of the Wierzbica type. The structure of fossil assemblages and composition of sediments exhibit parallel sequentional changes.

The probable reason for the different structure of populations may be the difference in the substrate for settlement of larvae. Specimens attached to the stable substrate of large bivalve shells (Wierzbica) achieved the largest size. Mobile oolite sand caused difficulties in settlement — in such conditions brachiopods were attached to erect algal thalli (Czarnogłowy). The shape of survivorship curves (fig. 9 F) plotted as a function of valve length (in the same manner as Thayer 1977) seems to be in concordance with such an interpretation because the population from Czarnogłowy shows very low mortality of juvenile postlarval stages. This means that the strongest elimination occurs at the time of recruitment. Lack of these stages is not a preservational feature because associated Z. humeralis shells of the same size are very common (see fig. 9). The curve clearly presents a logistic shape — distribution of mortality is symmetrical to class size 24 mm. The biological meaning of its shape is difficult to define. Maybe a true survivorship curve based on age (instead of size) would be more understandable but because of high variability of size within age classes and usually irregular development of growth lines it has been impossible to use such a coordinate.

The population from Wierzbica strongly differs from the Czarnogłowy one in the shape of the survivorship curve (fig. 9 H). Mortality of juvenile postlarval stages was relatively higher. If number of produced larvae was similar in the Wierzbica and Czarnogłowy terebratulids, the mortality in the time of recruitment was much larger in the latter one. Distribution of growth lines on terebratulid shells from Wierzbica suggest that the age of adult specimens was approximately 4—5 years. Unfortunately, because of large size-variability within each age group, much more material than is to my disposal is needed to establish the
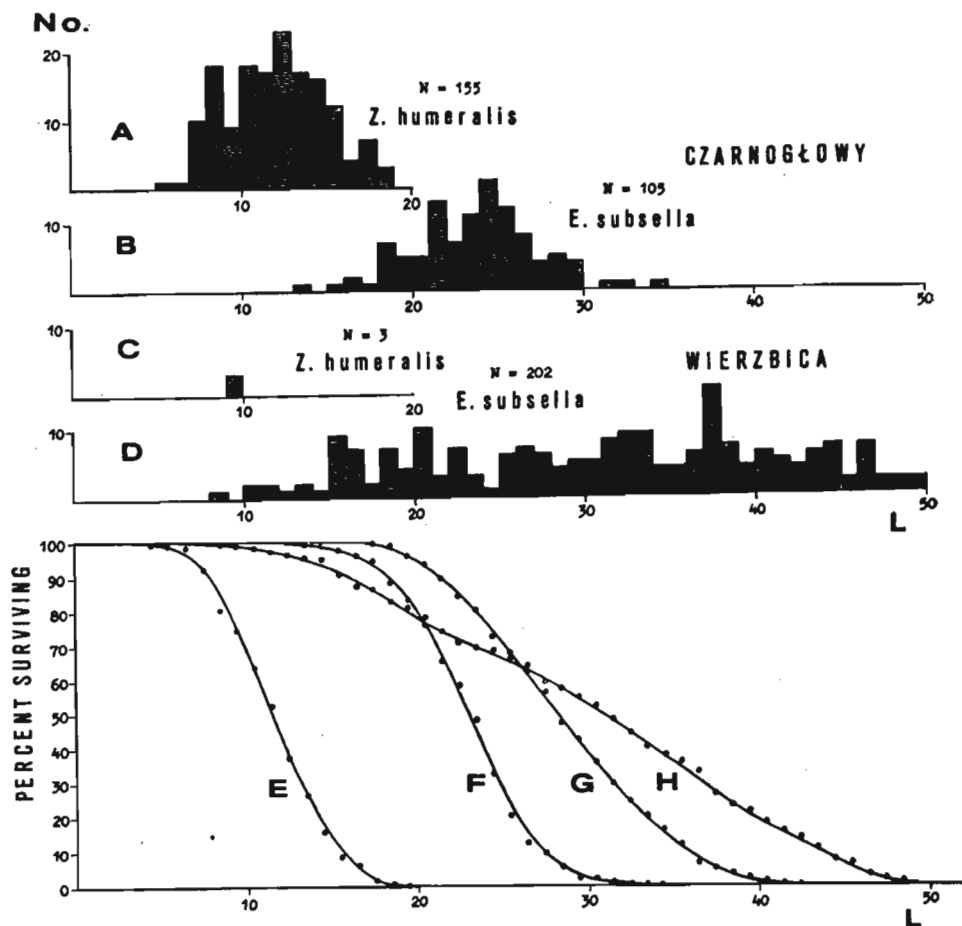
Fig. 9. A-D. Differences in size-frequency distribution of *Zeilleria humeralis* (Roemer, 1839) and *Epithyris "subsella* (Leymerie, 1840)" between Czarnogłowy and Wierzbica Lower Kimmeridgian assemblages. A. *Z. humeralis* from Czarnogłowy. B. *E. "subsella" from* Czarnogłowy. C. *Z. humeralis* from Wierzbica. D. *E. "subsella"* from Wierzbica. E-H. Survivorship curves of terebratulid populations from Lower Kimmeridgian of Poland plotted as a function of shell length. E. *Z. humeralis* from Czarnogłowy. F. *E. "subsella"* from Czarnogłowy. G. *E. 'subsella'* from Korytnica. H. *E. "subsella"* from Wierzbica.

growth equation. It may be that undulations of survivorship curves express seasonal mortality. Recent terebratulids living in littoral environments present similarly irregular shapes of survivorship curves (Thayer 1975, 1977).

The population from Korytnica shows a mortality pattern intermediate between that of Czarnogłowy and Wierzbica (fig. 9 G). Low mortality of juvenile postlarval stages (expressing a low rate of stabilizing selection) characteristic of these terebratulid populations may be the reason for wide intrapopulation variability.

The attribution of name to the described terebratulids requires comparison with topotype populations of previously designated species. The

variability of none of the Kimmeridgian terebratulid species has been described as yet. The morphotype dominating in Wierzbica has usually been named *Epithyris subsella* (Leymerie, 1840); the morphotype dominating in Czarnogłowy is close to *Epithyris cincta* (Cotteau, 1886) (see Barczyk 1965, 1969; Dubar 1967). I propose to provisionally use the first name concerning the Lower Kimmeridgian terebratulids from Poland described here.

Acknowledgements

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JERZY DZIK

POPULACJE TEREBRATUL Z DOLNEGO KIMERYDU POLSKI
I ICH ŚRODOWISKO BIOTYCZNE

Streszczenie

Terebratule należą do najpospolitszych skamieniałości naszej jury a mimo to nader rzadko wykorzystuje się je w opracowaniach geologicznych. Wynika to nie tyle z niewielkiej ich wartości jako wskaźników wiekowych czy środowiskowych, co z trudności w oznaczaniu gatunków przez niespecjalistę. Nadzwyczajna prostota budowy nie uchroniła jurajskich terebratul od podzielenia na dziesiątki rodzajów i gatunków o trudnych do określenia, nawet dla autorów nazw, różnicach. Warto więc przyjrzeć się bliżej zasadom, na których podstawie można byłoby bardziej obiektywnie określić zakres gatunku wśród terebratul. Podstawą przedstawionych w tej pracy analiz była populacja terebratul występująca w zlepach ostrygowych dolnego kimerydu z Wierzbicy koło Radomia. Terebratule te są często skrzemionkowane i przez trawienie w kwasach można wydobyć ze skały skorupki z zachowanym szkieletem lofoforu (pl. 12: 1—4). Standardowe wskaźniki biometryczne, wykorzystywane przy określaniu populacji ramienionogów, w przypadku populacji z Wierzbicy zgodnie wykazują rozkład zbliżony do normalnego (fig. 4—6). Nie ma zatem podstaw do wydzielania więcej niż jednego gatunku biologicznego terebratul w obrębie ławicy ostrygowej z Wierzbicy. Siedem gatunków z pięciu rodzajów wyodrębnionych przez Barczyka (1969) wśród wierzbickich terebratul to morfotypy obrazujące zmienność wewnątrzpopulacyjną jednego gatunku.

Duża zmienność wewnątrzpopulacyjna terebratul uniemożliwia określenie gatunku na podstawie pojedynczych okazów. W obrębie każdej z populacji terebratul z dolnego kimerydu Polski można znaleźć liczne wspólne morfotypy, mimo iż okazy typowe dla populacji różnią się niekiedy znacznie. To zachodzenie na siebie zmienności wewnątrzpopulacyjnych, przy znacznych różnicach między populacjami, utrudnia określenie zakresu gatunku (rozumianego jako zespół równowiekowych nieizolowanych genetycznie populacji). W praktyce paleontologicznej nie jesteśmy w stanie sprawdzić czy kopalne populacje krzyżowały się między sobą — nie oznacza to jednak, że jesteśmy całkowicie bezradni przy rozstrzyganiu tego podstawowego problemu systematyki biologicznej. Można bowiem wykazać odrębność gatunkową dwu różnych populacji przez znalezienie próby, w której one współwystępują wykazując nieciągły rozkład diagnostycznych cech. Można wykazać gatunkową identyczność dwu populacji przez znalezienie ciągu prób wiążących je morfologicznie. Podstawowy warunek to synchroniczność, z ewolucyjnego punktu widzenia, wszystkich rozpatrywanych populacji, tzn., że różnice wiekowe między nimi nie mogą być na tyle duże, ażeby procesy ewolucyjne mogły być przyczyną różnic między populacjami. W przypadku populacji wolno ewoluujących terebratul z dolnego

kimerydu, datowanych przy pomocy bardzo szybko ewoluujących amonitów, wpływ ewolucji może być pominięty.

Struktury populacji terebratul z dolnego kimerydu Polski tworzą ciąg, na którego jednym skraju znajdują się populacje o przewadze szerokich muszli i o małych dojrzałych okazach (Iłża, Czarnogłowy) a na drugim populacje o ilościowej przewadze wydłużonych morfotypów i dojrzałych okazach dużych rozmiarów (Wierzbica) (fig. 6, 9). Przypuszczenie, że populacje te reprezentują jeden gatunek biologiczny znajduje dodatkowe uzasadnienie w porównaniu struktur biocenoz z poszczególnych lokalizacji. Wykazują one zróżnicowanie równoległe do zróżnicowania morfologii i dynamiki populacji terebratul. Populacje małych (na dojrzałych stadiach) terebratul bytowały w środowisku o ruchliwym dnie (oolity) i prawdopodobnie przytwierdzały się do plech glonów *Goniolina geometrica* (fig. 7—9). Populacje dużych terebratul żyły w środowisku ławic małżowych i skorupy małżów stanowiły podłoże, do którego przytwierdzały się terebratule (fig. 2, 9). Populacje o cechach pośrednich pochodzą ze środowisk o pośrednich strukturach biocenoz.

Wykorzystywanie rekonstrukcji biocenoz do rozważań ekologii kopalnych terebratul wymaga wyjaśnienia paru podstawowych problemów metodologicznych. Przedstawione tutaj dane (fig. 1, 6, 9) potwierdzają pogląd, że klasyfikacja biocenoz (communities) niewiele ma wspólnego z rzeczywistością i że pomiędzy różnymi typami biocenoz występują ciągłe przejścia (por. Cisne and Rabe 1978). Wyjątek stanowią jedynie biocenozy, które same dla siebie tworzą odpowiednie warunki środowiskowe, np. rafy czy ławice ostrygowe. Inne zagadnienie to stosunek struktury kopalnego zespołu skamieniałości (fossil assemblage) do struktury żywej biocenozy (living community), z której ten zespół powstał. Zazwyczaj porównuje się ilościowy skład gatunków skamieniałości w kopalnym zespole z udziałem poszczególnych gatunków w biomasie biocenozy. Udział skamieniałości w kopalnym zespole nie jest jednak prostą funkcją biomasy poszczególnych gatunków w żywym zespole lecz ich produktywności biologicznej. Tak więc udział procentowy gatunków o krótkim cyklu życiowym (a więc zazwyczaj dużej produktywności w liczbie osobników) w kopalnym zespole jest znacznie zawyżony w stosunku do ich udziału w biomasie biocenozy. Jeśli się więc chce odtworzyć kopalne biocenozy na podstawie zespołów skamieniałości należy przeliczyć struktury kopalnych zespołów na strukturę biomasy biocenozy (jest to bardzo trudne) lub opisywać kopalne zespoły w kategoriach względnej produktywności poszczególnych gatunków (fig. 2, 7). Odrębne zagadnienie, wykraczające poza zakres tej pracy, to wpływ deformacji w trakcie fosylizacji skamieniałości na strukturę kopalnego zespołu.

Stwierdzenie, że wszystkie przebadane terebratule z dolnego kimerydu Polski reprezentują jeden gatunek biologiczny wcale nie ułatwia podania jego nazwy. Holotypy opisanych dotąd gatunków, mimo identyczności z poszczególnymi morfotypami występującymi w omawianych populacjach, wcale nie muszą być z nimi identyczne gatunkowo. Mogą bowiem reprezentować skraje zmienności zupełnie odmiennych populacji. Przy braku biometrycznych opracowań topotypowych dla poszczególnych gatunków populacji można jedynie podać prowizoryczną nazwę dla naszych terebratul: *Epithyris „subsella* (Leymerie, 1840)".

EXPLANATION OF THE PLATES 11 AND 12

Plate   11

1, 2. *Epithyris* "*subsella* (Leymerie, 1840)", Lower Kimmeridgian, Wierzbica near
Radom, Poland; two extremely large, adult specimens, $\times$ 2.

Plate   12

1—4. *Epithyris* "*subsella* (Leymerie, 1940)", Lower Kimmeridgian, Wierzbica near
Radom, Poland; brachial valves of silicified specimens, $\times$ 2.