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Ecology of the Upper Jurassic brachiopod bed from Julianka, Polish Jura Chain

ABSTRACT: Brachiopod bed in the uppermost Oxfordian chalky limestones from Julianka, Polish Jura Chain, is dominated by terebratulids that are to be considered as conspecific variants attributable to *Sellithyris engeli* (Rollier). The associated microfacies, distributional pattern of the fauna, and taphonomic analysis point to the autochthonous nature of the fossil assemblage. Most brachiopod species were displaying rapid early growth at the rate decreasing in ontogeny, and low early post-larval mortality at the rate increasing in ontogeny. The assemblage is to be interpreted as a pioneer, opportunistic one preceding the growth of coral patch-reefs. It includes species with habitat preferences for both inter-reef (*Sellithyris engeli, Zeilleria delmontana,* possibly also *Septaliphoria moravica*) and reefoid environments (*Lacunosella cracoviensis, Septaliphoria astieriana, Terebratulina substriata*).

INTRODUCTION

Brachiopod faunas of the Polish Jura Chain are rich and diverse but nonetheless, rather poorly known. The rhynchonellaceans have been monographed by Wiśniewska (1932) and discussed in biostratigraphic context also by Różycki (1948) and Wierzbowski (1970). The only other significant contribution to the knowledge of those faunas is that by Wiśniewska-Żelichowska (1971) on the sponge bioherms from Rudniki and their brachiopod-rich fossil assemblage.

The present paper is aimed to evaluate the ecology of another brachiopod fauna from that area with use of modern paleoecological and taxonomical methods. The authors hope that the results will serve as a reference point for further research.

The investigated collection is stored at the Institute of Geology and Mineral Resources of the Upper Silesia of the Silesian University, Sosnowiec.

GEOLOGIC SETTING

The investigated brachiopod bed occurs in the chalky limestones exposed in the quarries at Julianka, Polish Jura Chain (Text-fig. 1). As evidenced by an ammonite specimen identified as *Idoceras* sp., these strata are representative of the uppermost Oxfordian *Idoceras planula* Zone (Marcinowski 1969). This is also consistent with the occurrence of the brachiopods *Lacunosella cracoviensis* and *Septaliphoria astieriana* indicative of the Oxfordian and Kimmeridgian boundary in the Polish Jura Chain (Wierzbowski 1970).

The chalky limestones from Julianka (see Różycki 1960) are biomicrites and biopelmicrites with bioclasts including mostly sponge spicules and skeletal fragments, problematic calcispheres, and brachiopod, echinoderm, mollusk, and bryozoan detritus. Here and there, they contain abundant calcisponges and corals (cf. Roniewicz & Roniewicz 1971). Apart from some silicified zones (Heliasz 1980), non-carbonate matter amounts to less than 1% of the rock.

A thin bed of a little darker, often secondarily ferrugineous, macrofossiliferous limestone (Text-fig. 2) is easily discernible in the easternmost part of the southern quarry (cf. Text-fig. 1). It can be traced over some forty meters in distance. It differs in microfacies from the associated chalky limestones exclusively in containing a little larger amounts of micrite and non-carbonate matter (mostly quartz, iron minerals, and clay). The chalky limestones are much finer-grained and poorer in corals than those from the northern quarry.

MATERIAL

Spatial distribution and orientation of fossils found in the bed have been mapped over some 15 m in distance (Text-figs 3—4). The investigated collection exceeds 600 specimens in number, out of which 281 specimens have been derived from the brachiopod bed and almost 140 specimens from the underlying and overlying strata.
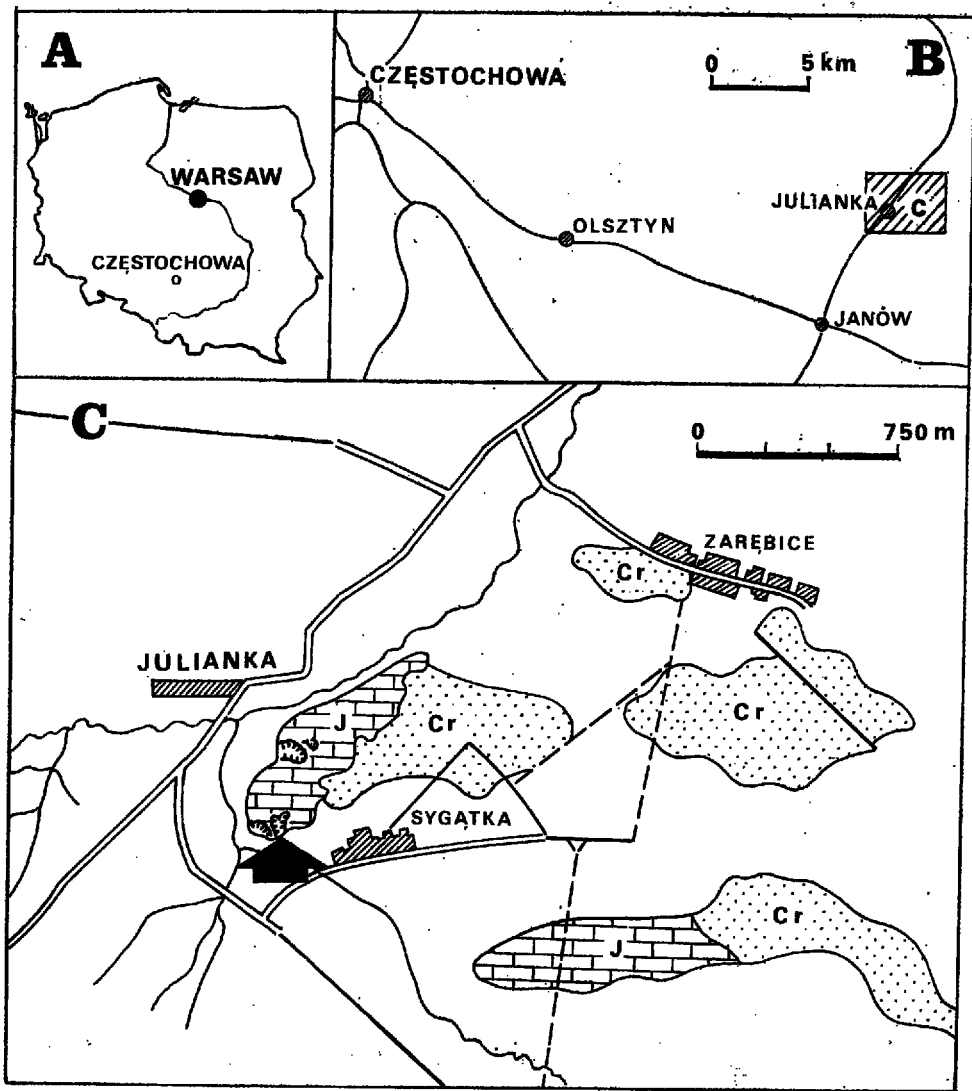
Fig. 1. Localization of the investigated area in Poland (**A**) and in Częstochowa region in the Polish Jura Chain (**B**), and geological sketch (**C**) of the investigated area (simplified *from* Marcinowski 1969). Marked are Jurassic (*J*), Cretaceous (*Cr*), and Quaternary deposits (*blank areas*); arrowed is the quarry displaying the brachiopod bed

Fig. 2. General view of the northern wall of Julianka quarry (**A**) to show the position of the brachiopod bed (*arrowed*), and a fragment of the wall (**B**) displaying the brachiopod bed (*arrowed*)

Spatial distribution of fauna in the brachiopod bed exposed at Julianka

Legend:

- S Sellithyris engelt
- Z Zeillerta delmontana
- L Lacunosella cracoviensis
- Sa Septaliphoria asteriana
- B bivalves
-    crinoids
-    corals
- E echinoids
- T Terebratulina substriata
- G sponges
- A ammonites
-    cherts
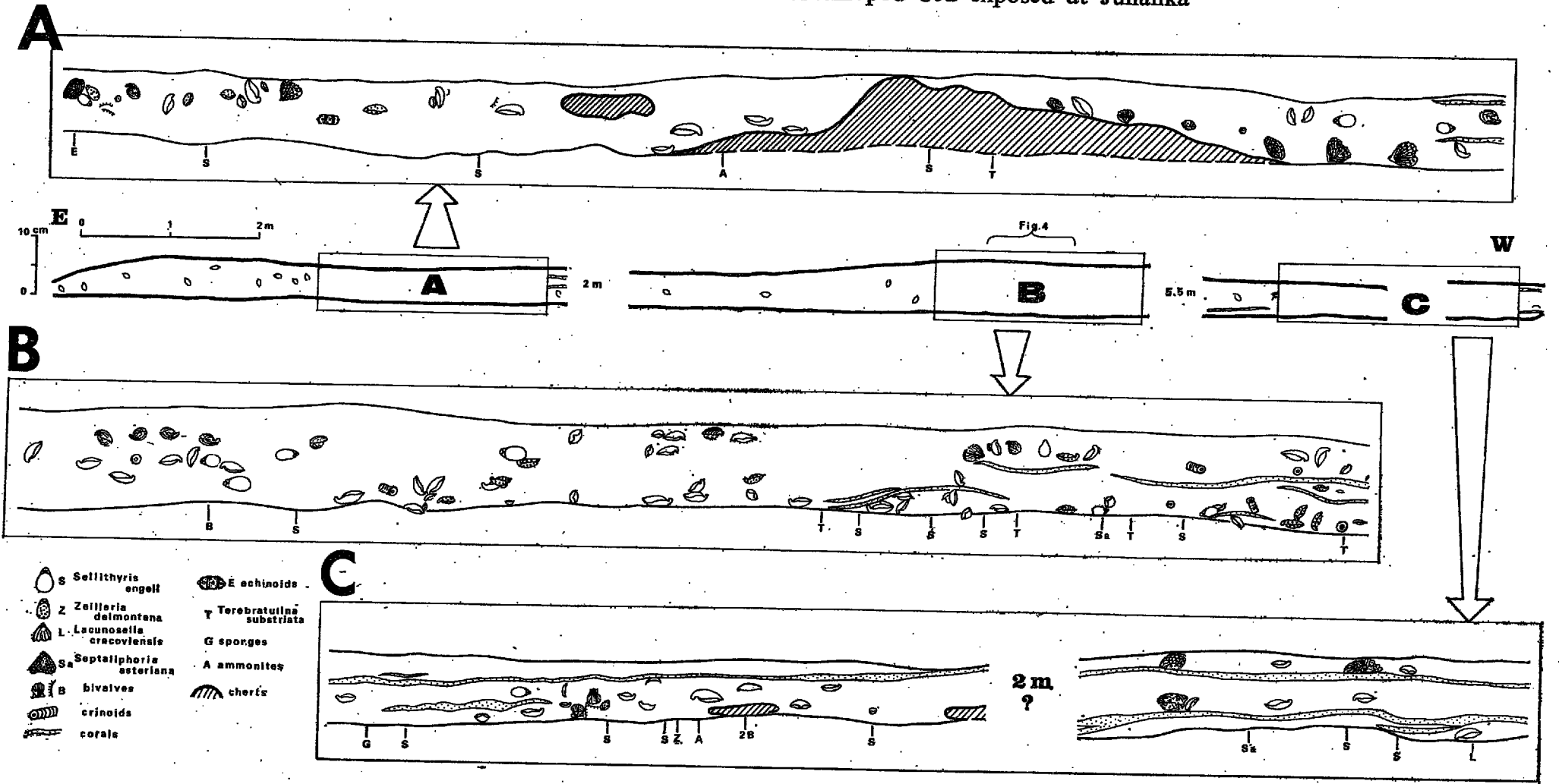
Specimens collected from the waste are indicated by leaders; the most important faunal patches (A—C) are also shown in a greater scale (cf. also Text-fig. 4)

Most brachiopod specimens are more or less silicified shells (less than 10%
are disarticulated valves), often with compaction deformations. The deformations
range from a flattening to a complete crushing or even fragmentation, depending
mostly upon the position of a specimen in the rock (cf. Ferguson 1962). They
have mainly affected large-sized terebratulids, while smaller-sized brachiopods
(e.g. *Terebratulina substriata*) are commonly intact.

The associated fauna is similarly preserved except for the bivalves being
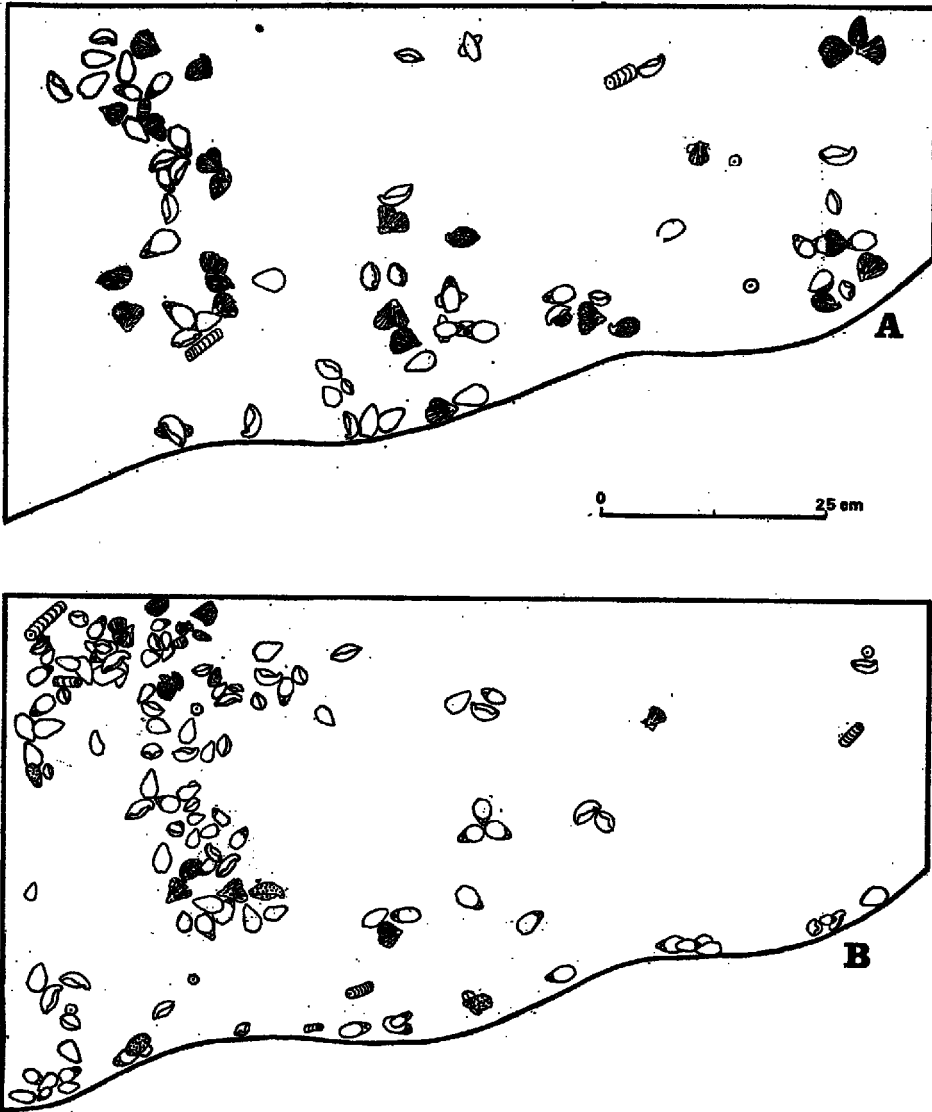more frequently represented by singular valves or their imprints.

Fig. 4. Spatial distribution of fauna in a fragment (upper part — A, lower
part — B) of the investigated brachiopod bed (see Text-fig. 3, also for explana-
tions); corals and sponges are omitted

TAXONOMIC REMARKS

The only problems involved in taxonomic identification of the investigated rhynchonellacean brachiopods were with *Septaliphoria astieriana* (d'Orbigny) and *S. moravica* (Uhlig), the former being assigned by Childs (1969) to the genus *Torquirhynchia*, and the latter regarded by that author as a possible junior synonym of *Somalirhynchia moeschi* (Haas). To resolve ultimately these problems was beyond the scope c' the present study and hence, the names traditionally associated wit' the fossils under discussion have been retained.
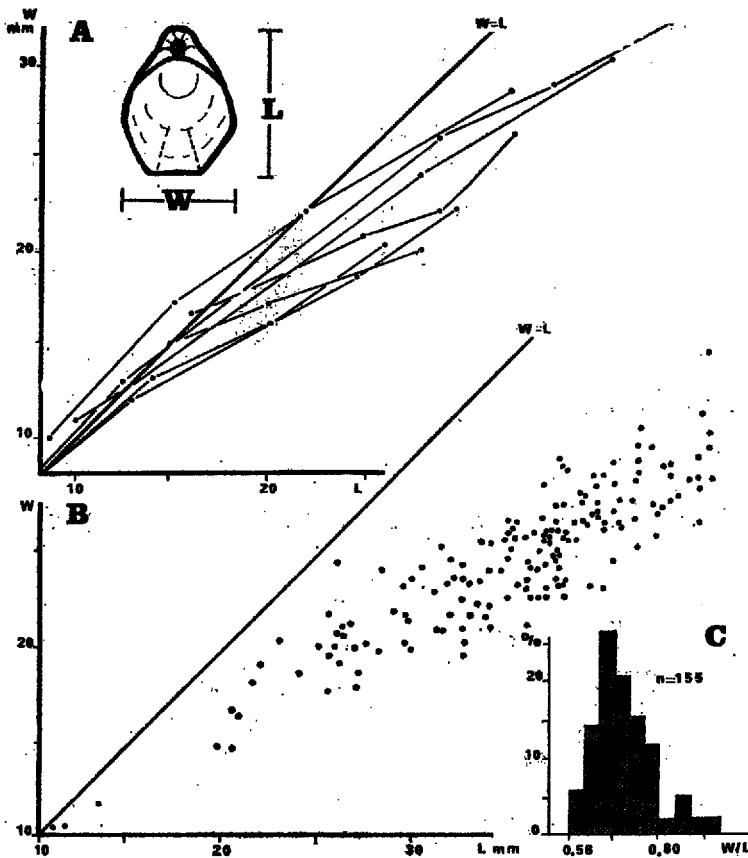

Fig. 5. Ontogenetic variation in shell width to length ratio in *Sellithyris engel* (Rollier), after growth line analysis of 7 specimens (A) and after shell size analysi of the whole collection (B); moreover, frequency distribution of this character ir the collection (C)

Taxonomic identification of the investigated terebratulids has been a much more complex problem because the ranges of intraspecific variability among the Terebratulidae remain thus far very poorly known, while there is little doubt that they are very wide as a rule (cf. McKerrow 1954, Makridin 1964, Enay
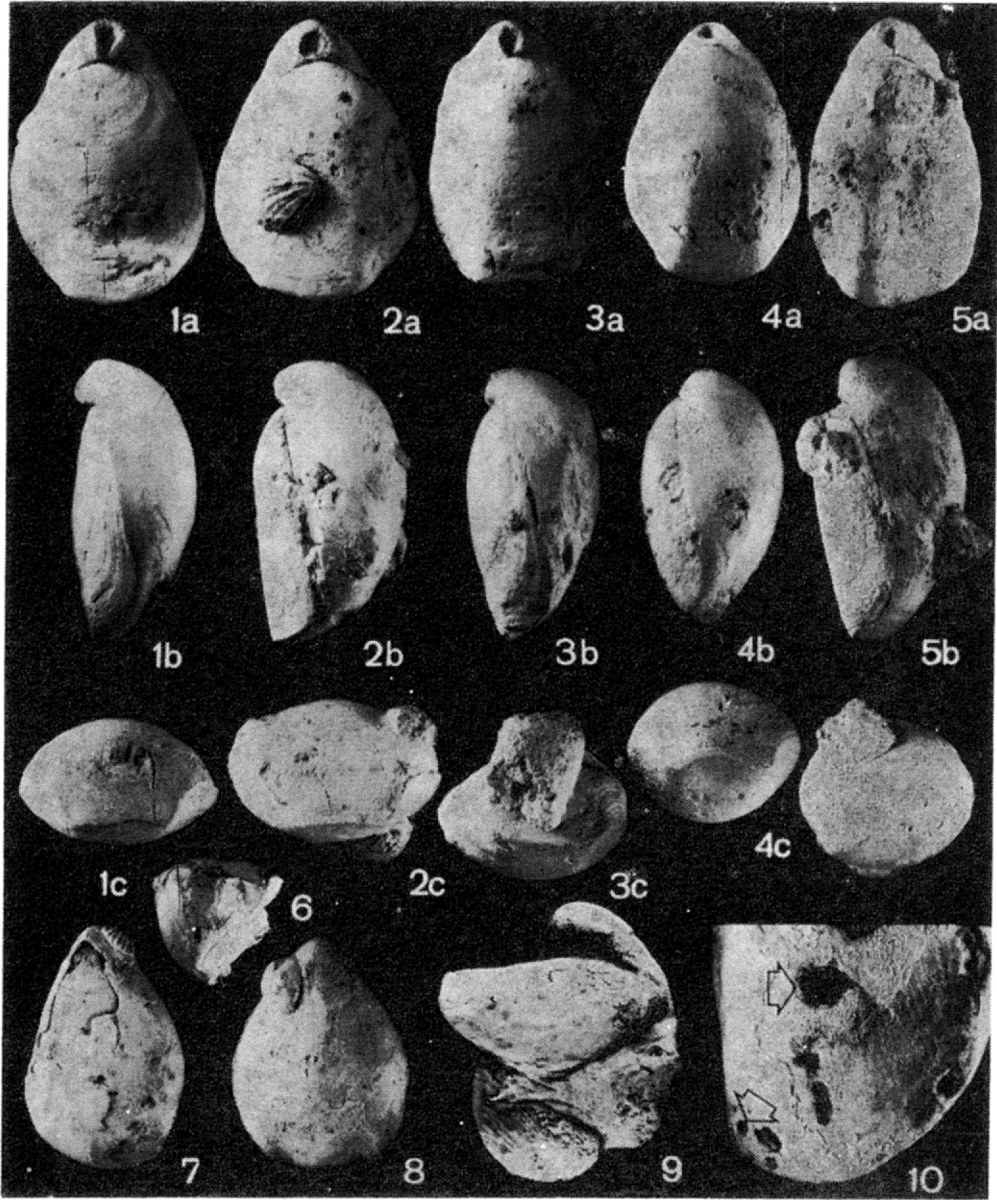
Sellithyris engeli (Rollier); slightly reduced

1—5 Very large-sized specimens in dorsal (*a*), lateral (*b*), and anterior (*c*) view
  6 Strongly flattened specimen in anterior view
  7 Slightly flattened specimen in lateral view, with attached small specimen of *Acantho-thyris*
  8 Specimen with attached small-sized terebratulid
  9 Three moderately-sized specimens attached to each other due to compaction
10 Borings variable in diameter (*arrowed*) in a shell; ×1.8
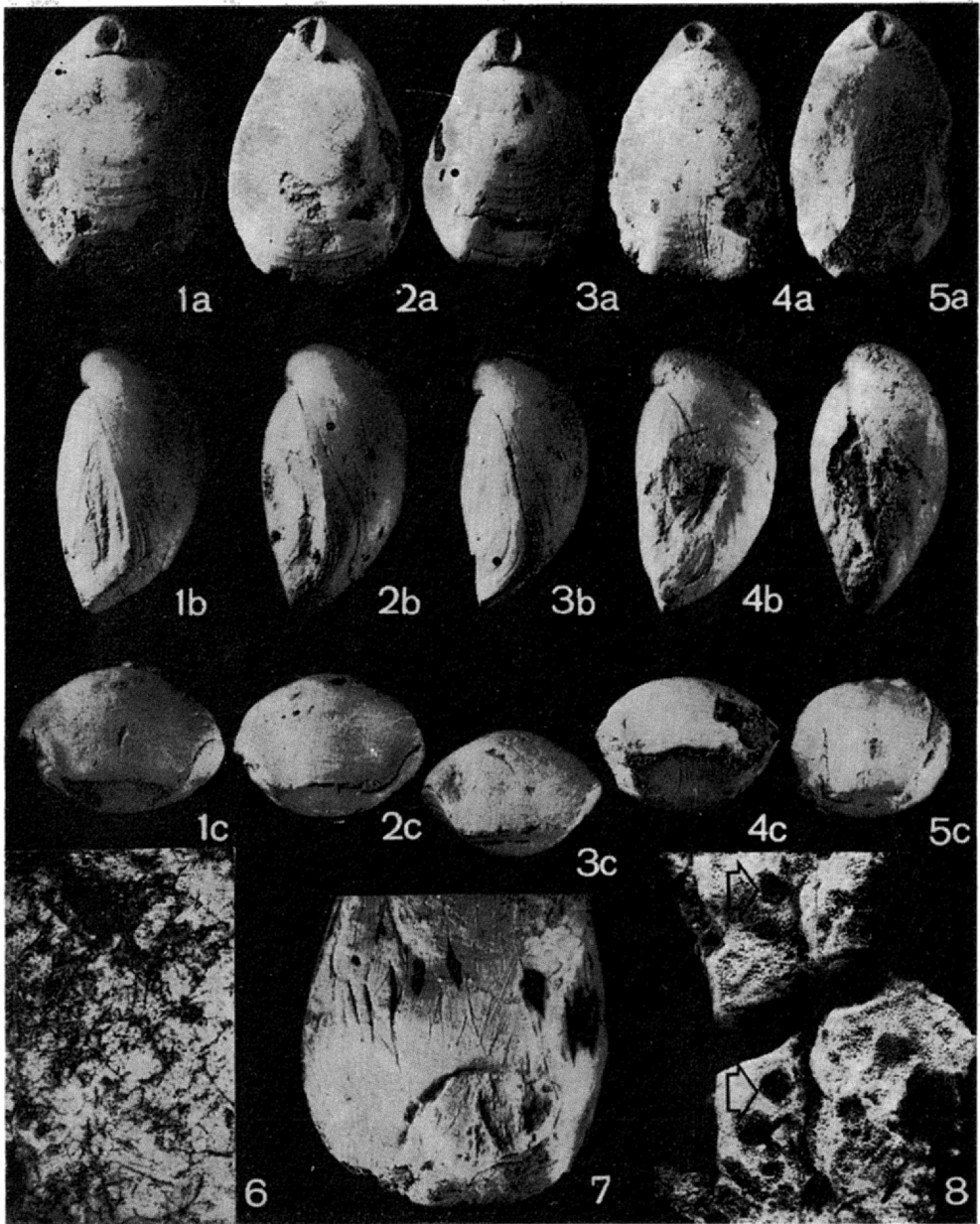
1—5 *Sellithyris engeli* (Rollier): large-sized specimens in dorsal (*a*), lateral (*b*), and anterior (*c*) views; slightly reduced
6 Borings of fungal or algal origin in a brachiopod shell; ×6
7 Incisions in a brachiopod shell, probably a trace of predation; ×2
8 Sponge with fragmented small-sized terebratulids (*arrowed*) in cavities; slightly reduced
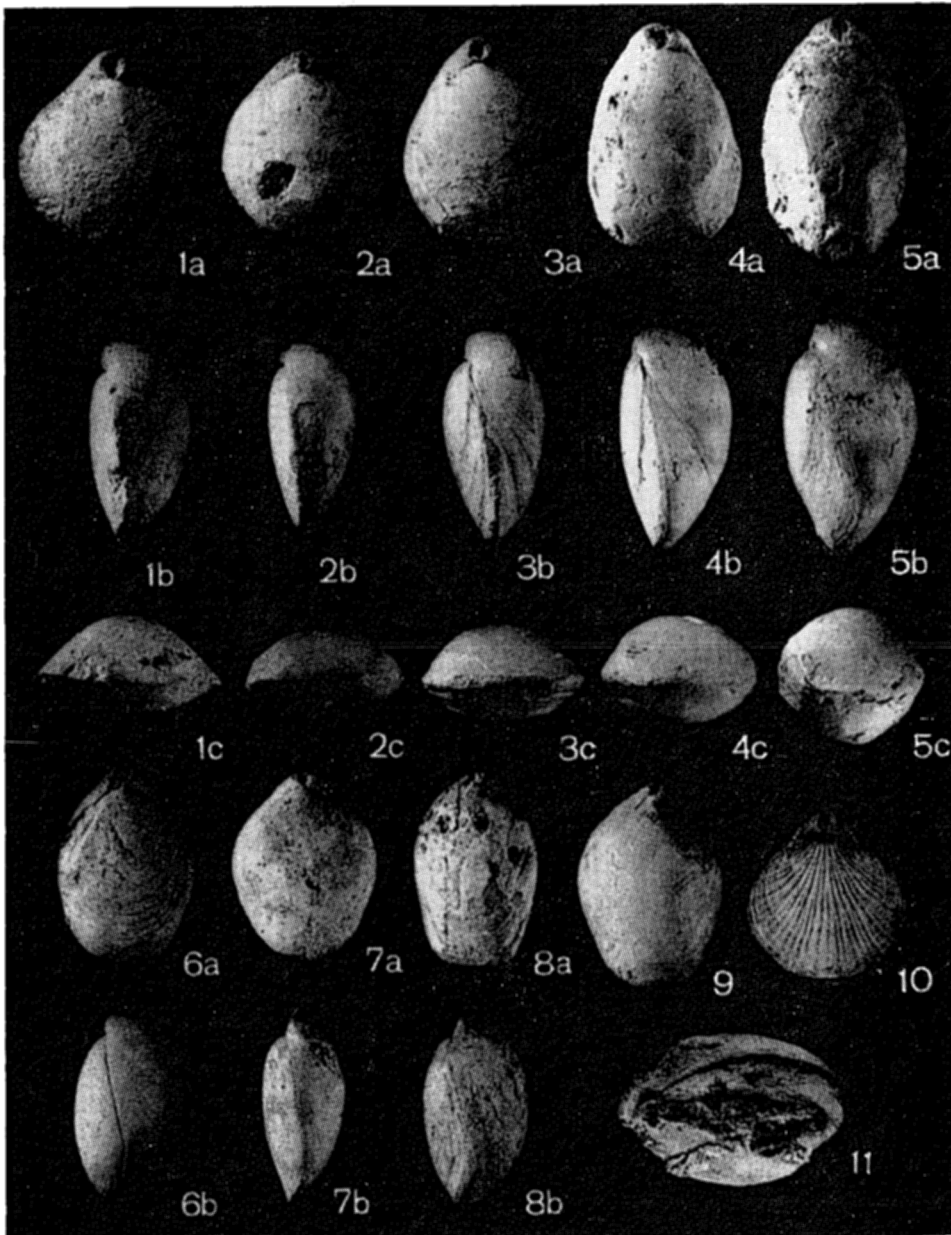
1—5 *Sellithyris engeli* (Rollier): small- to moderately-sized specimens in dorsal
(a), lateral (b), and anterior (c) views; natural size
6—9 and 11 *Zeilleria delmontana* (Oppel): 6—8 large-sized specimens in dorsal
(a) and lateral (b) views, 9 large-sized and strongly asymmetrical specimen,
11 specimen with attached bivalve; natural size
10 *Terebratulina substriata* (Schlotheim): large-sized specimen in dorsal view;
×2
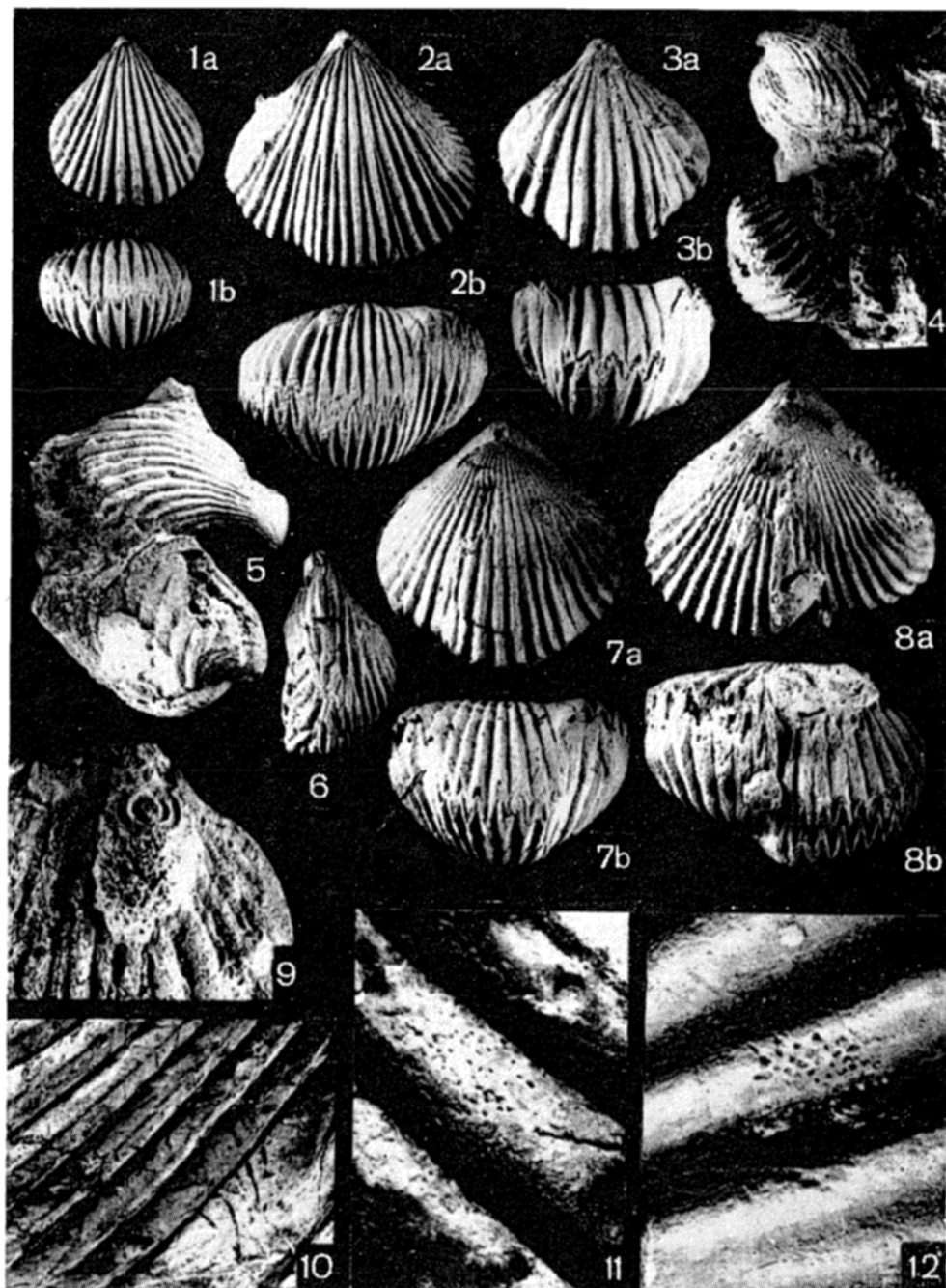
1—4, 6, and 9 *Lacunosella cracoviensis* (Quenstedt): 1—2 asymmetrical specimens in dorsal (*a*) and anterior (*b*) views, 3 symmetrical and strongly ribbed specimen in dorsal (*a*) and anterior (*b*) views, 4 two specimens clustered with a bivalve, 6 strongly flattened specimen in lateral view; natural size, 9 specimen encrusted with a sponge and *Spirorbis* (?), ×2
5 Two specimens of *Septaliphoria* attached to each other; natural size
7 *Septaliphoria moravica* (Uhlig): large-sized specimen in dorsal (*a*) and anterior (*b*) views; natural size
8 and 10 *Septaliphoria astieriana* (d'Orbigny): 8 large-sized specimen with epifauna in dorsal (*a*) and anterior (*b*) views, natural size; 10 incised shell fragment, ×3
11 Phoronid(?) microborings and an incomplete larger boring in shell of *Lacunosella*; ×7
12 Etching produced by a brachiopod pedicle in shell of *Lacunosella*; ×7

& Rollet 1966, Rousselle 1967, Rollet 1968, McCammon 1970, Schumann 1976, Thayer 1977, Feldman 1977, Dzik 1979). There is also no reason to claim that a brachiopod internal structure is less variable than its external form (McKerrow 1954, Rudwick 1970) and furthermore, the reliability of internal-structural reconstruction after serial sections has been recently greatly undermined (Singeisen--Schneider 1976, Dzik 1979). Therefore, the shell morphology of the terebratulids from Julianka has been analysed in quantitative terms. There is indeed a considerable variation in most morphological characteristics (Text-figs 5—7 and Pls 1—3) and three morphotypes can be distinguished:

Morphotype A — shell elongate, strongly biconvex, sometimes asymmetrical, with uniplicate to sulciplicate anterior margin and elongate foramen provided with a peculiar lip;
Morphotype B — shell pentagonal in outline, strongly biconvex, with anterior margin and foramen as in morphotype A;
Morphotype C — shell ovate in outline, with almost flat dorsal valve, straight to uniplicate anterior margin, and circular foramen.
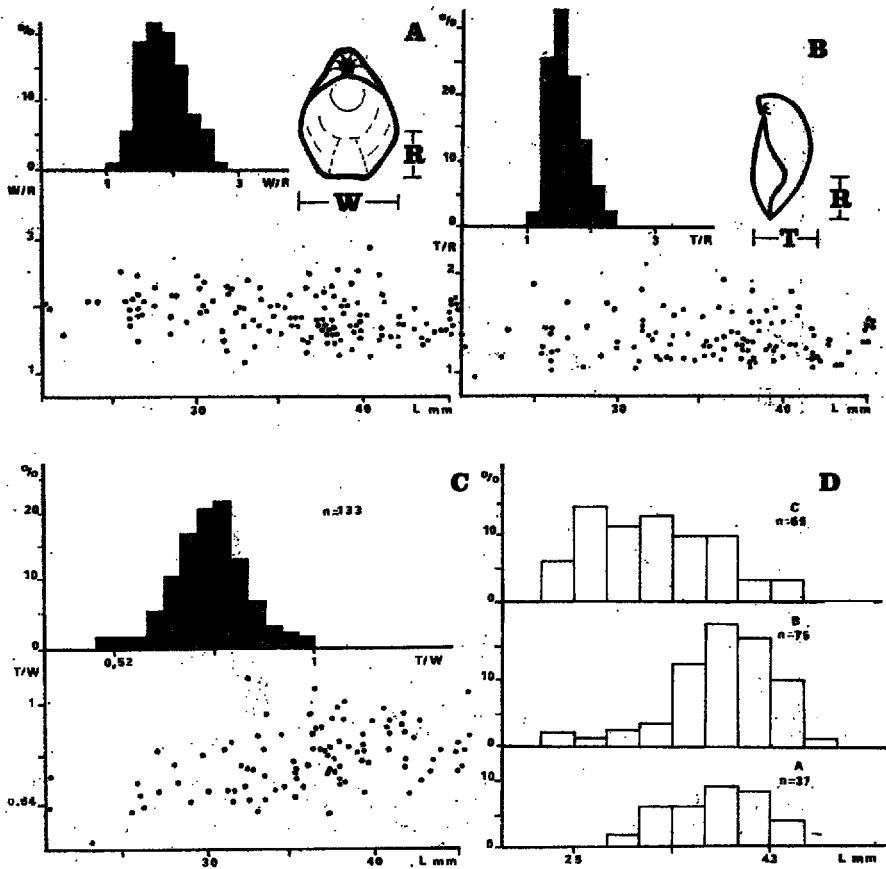

Fig. 6. Ontogenetic variation and frequency distribution (A—C) of morphological characteristics in the whole collection of *Sellithyris engeli* (Rollier); size--frequency-distribution of particular morphotypes (D) in the collection (*see* text for identification of the morphotypes)

The three morphotypes can be easily assigned each to a distinct species, as did indeed Wiśniewska-Żelichowska (1971). The morphotype *A* resembles *Loboidethyris rozyckii* Wiśniewska-Żelichowska, the morphotype *B* resembles *Sellithyris engeli* (Rollier), and the morphotype *C* resembles *Loboidethyris zieteni* (Loriol). The point is however that the morphotypes do continuously intergrade with each other (Pls 1—3); there are also some asymmetrical forms (*e.g.* Pl. 2, Fig. 3) showing each the characteristics of two morphotypes. Furthermore, the morphotypes *B* and *C* intergrade also with *L. valfinensis* (Loriol), *L. baltzeri* (Haas), *S. engeli krzyzanowiczi* Barczyk, *S. subsella* (Leymierie), *Epithyris cincta* (Cotteau), and others. One can thus hardly regard the three terebratulid morphotypes from Julianka as attributable to distinct species, and so more genera and subfamilies.

The original diagnostic indices of *Loboidethyris zieteni*, *L. rozyckii*, and *S. engeli* are ontogeny-dependent (Text-figs 5, 6c and 7); hence, they are of little taxonomic value. The relative position of maximum shell width and convexity is less dependent upon terebratulid ontogeny and therefore, these characters are recognized for the best taxonomic indices of the investigated terebratulids (*cf.* Dzik 1979). As indicated by the unimodal, often close to normal distributions of these indices (Text-figs 5—6), one deals at Julianka with a monospecific terebratulid population. This conclusion is also supported by a close affinity of the three morphotypes in their shell internal structure (*cf.* Makridin 1964, Wiśniewska-Żelichowska 1971), as well as by a disorderly pattern of their spatial distribution at Julianka (see below).
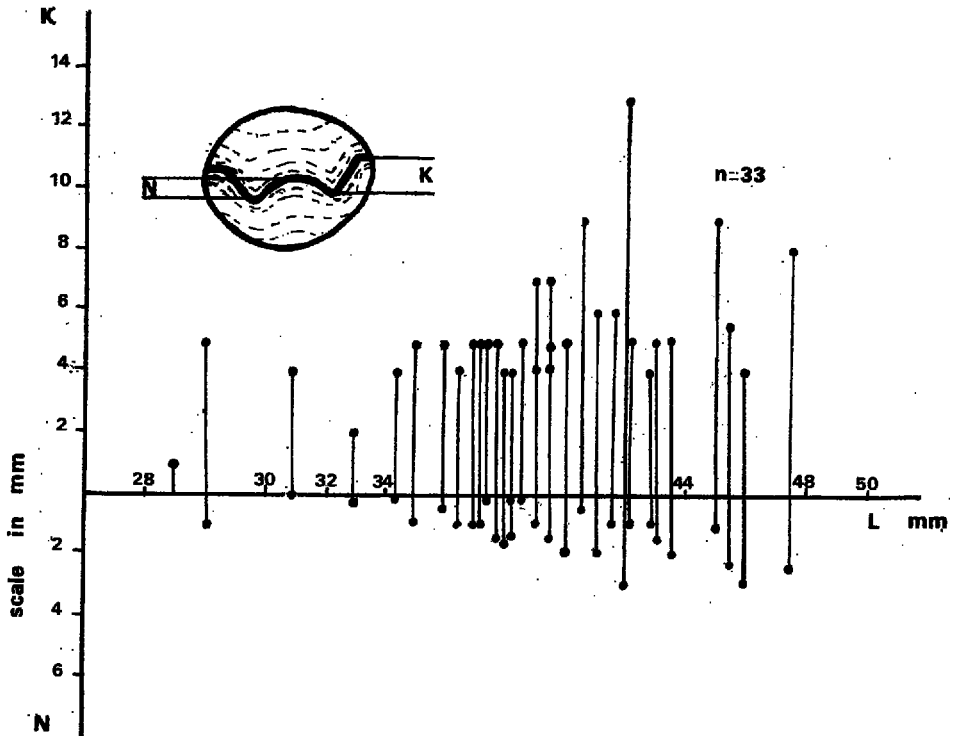

Fig. 7. Ontogenetic variation of the anterior fold in *Sellithyris engeli* (Rollier), taken since that size at which the fold appears

The name *Loboidethyris zieteni* (Loriol) has certainly a priority relative to *Sellithyris engeli* (Rollier) and *Loboidethyris rozyckii* Wiśniewska-Żelichowska, but it has been based upon a juvenile type specimen (Professor W. Barczyk, *oral communication*) and hence, all the investigated terebratulids are here tentatively assigned to *Sellithyris engeli* although their actual generic position remains unknown.

A similar problem arises with taxonomic identification of the zeilleriids from Julianka, among which three morphotypes can be easily distinguished (Pl. 3, Figs 6—8).

Morphotype *A* — shell ovate in outline, strongly biconvex;
Morphotype *B* — shell ovate in outline, weakly biconvex;
Morphotype *C* — shell elongate pentagonal in outline, most commonly strongly biconvex.
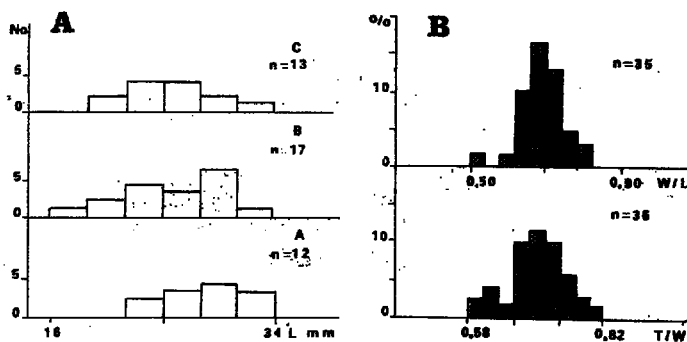
Fig. 8. Size-frequency-distribution of particular morphotypes (A) of *Zeilleria delmontana* (Oppel) (see text for identification of the morphotypes); frequency distribution of the most important morphological characteristics (B) in the whole collection

These morphotypes can be assigned each to a distinct species, namely the morphotype *A* to *Zeilleria delmontana* (Oppel), morphotype *B* to *Z. lagenoides* (Rollier), and morphotype *C* to *Z. quenstedti* (Rollier). However, as judged from the occurrence of continuous morphological intergradations and the distribution of the diagnostic characters (Text-fig. 8), they are to be considered as conspecific variants. They are hereinafter described under the name *Zeilleria delmontana*.

BRACHIOPOD BED FROM JULIANKA

The investigated fossil assemblage is by far predominated by brachiopods (80% in number; see Text-fig. 9), first of all representatives of the Terebratulida. The most abundant species (Text-fig. 10) are: *Sellithyris engeli* (over 50% of the assemblage in number), a terebratulid, and *Zeilleria delmontana* (12%). The rhynchonellaceans amount to some 20% of the brachiopod assemblage and are represented mostly by asymmetrical forms, *Lacunosella cracoviensis* (Quenst.) and *Septaliphoria astieriana* (d'Orb.). The species *Terebratulina substriata* (Schloth.) and

Septaliphoria moravica (Uhlig) occur in minor amounts, and the genera *Acanthothyris* and *Dictyothyropsis* are represented each by a single specimen.

The associated fauna includes mostly calcisponges (small-sized singular forms representative mainly of *Peronidella*), lamellar coral colonies (*Microsolena* and, subordinately, *Thamnasteria*; identified by Docent E. Roniewicz), and rather diverse bivalves. The bivalve assemblage (identified by Dr. L. Karczewski) is dominated by various pterioids (*Lima*, *Ctenostreon* cf. *proboscideum* (Sow.), *Chlamys*, *Gryphaea*, and oysters) but there are also some veneroids (*Anisocardia globosa* (Roemer), *Opis*, *Astarte*), arcoids (*Parallelodon* cf. *productum* Rollier, *Isoarca lexata* Quenst.), and mytiloids (*Mytilus*). Some crinoids (fragmented stems of *Millericrinus*), echinoids (cidarid spines), bryozoans (both branched and encrusting forms), serpulids, and ammonites (perisphinctids, mostly *Neorasenia*;
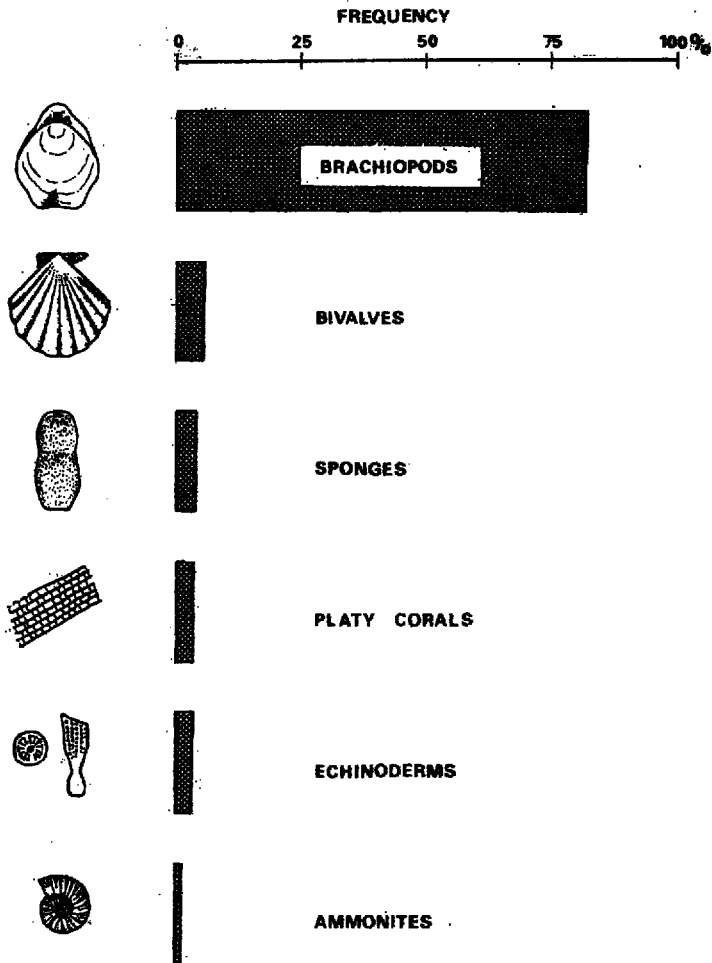
9. Taxonomic composition of the fauna of the brachiopod bed from Julianka

identified by Professor J. Kutek), and ostracodes have been recorded in the brachiopod bed. Thus, the fossil assemblage is rather diverse even though highly dominated by a single terebratulid species.
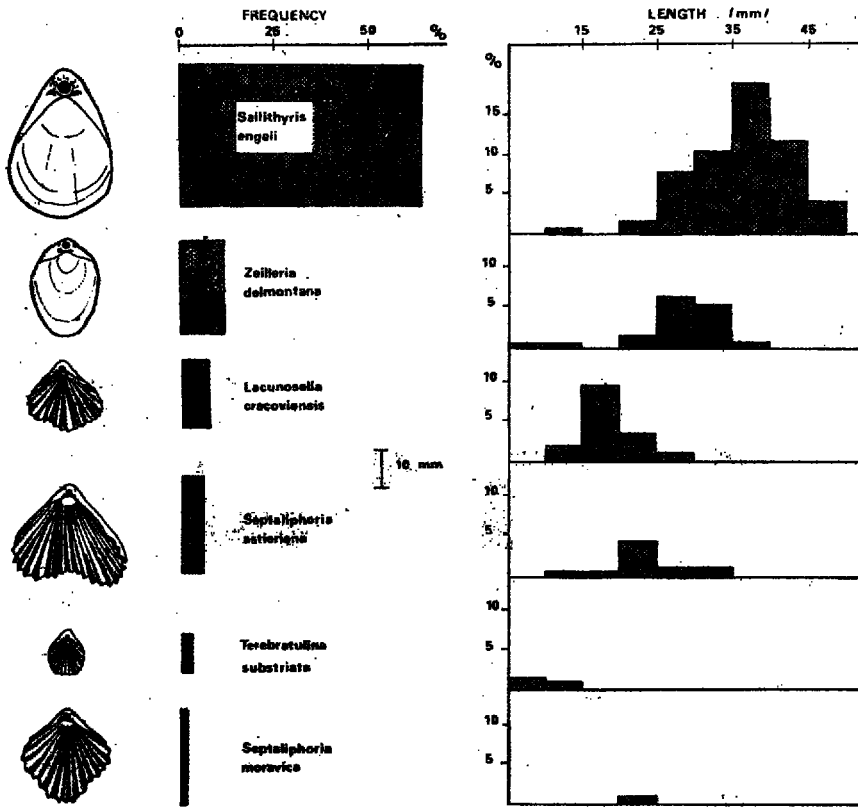
Fig. 10. Taxonomic composition of the brachiopod assemblage of the investigated brachiopod bed from Julianka, and size-frequency-distribution of particular species

Outside the brachiopod bed, the assemblage contains much larger proportions (up to 30% in number) of *Terebratulina* and other small-sized representatives of the Terebratulida. Some patches resembling the bed very closely in both taxonomic composition and spatial distribution of fossils occur however here and there in the chalky limestones.

The fossil density is largely variable in the brachiopod bed (Text-figs 3—4). The greatest and best exposed patch occurs in the central part of the mapped portion of the bed. It shows unusually high proportions of the morphotype A of *Sellithyris engeli* and *Lacunosella cracoviensis*, and strongly developed coral layers (up to 3—4 in number within the bed). In turn, the easternmost of the mapped patches shows an increase in abundance of *Septaliphoria* and *Zeilleria*; the brachiopods are confined mostly to the upper part of the bed, and the corals occur infrequently. Even these patches display each a wide range of variation

in fossil density (Text-fig. 4), while there is no significant vertical change in taxonomic composition of the brachiopod assemblage.

Prior to any ecological interpretation of a fossil assemblage, the role of post-mortem hydrodynamic biases is to be estimated (see Kauffman & Scott 1976, Fürsich 1978). The following characteristics of the brachiopod bed from Julianka indicate that the hydrodynamic biases may be considered as insignificant for paleoecological analysis: The fossils occur in patches or more or less monospecific clusters in places (Text-figs 3—4). Most brachiopod specimens are preserved as articulated shells with well preserved epifauna; most commonly in presumed life positions (Text-fig. 11), with only a subordinate fraction of the

Fig. 11. Shell orientation of the brachiopods in the investigated brachiopod bed

assemblage being preserved in presumed mechanical positions (sensu Ager 1963). There are also many coral colonies preserved in life positions and the crinoids occur in form of long fragments of stems instead of singular trochites. The fossil assemblage includes fossils widely variable in size but coherent in ecology. The rock matrix is by far dominated by micrite, and there is no evidence of intraformational reworking or redeposition. Most deformations of the specimens are attributable to the action of compaction rather than of any hydrodynamic agents. One may thus conclude that the investigated fossil accumulation originated with only a minor contribution of post-mortem transportation; the latter process may have only caused a decrease in proportion of small-sized specimens in the assemblage, and disarticulation of some shells (mostly bivalves). The brachiopod bed is then to be considered as an ecologically controlled fossil accumulation (biostrome of Aigner & al. 1978).

As judged from the microfacies characteristics of the associated sediment, the brachiopod bed cannot be regarded as a residual accumulation originated due to winnowing of fine-grained sediment. Its origination was first of all related

to a disturbance of the equilibrium between organic production and carbonate deposition (*cf.* Fürsich 1978). The microfacies characteristics of the sediment and the occurrence of abundant epifauna and borings (up to 2—3 generations; Pl. 4, Fig. 9) indicate that this disturbance resulted from a temporary (and local ?) decrease in bioclastic influx to the basin (*cf.* Brookfield 1973b, Fürsich 1977).

AUTECOLOGY

The biostromal nature (*sensu* Aigner & *al.* 1978) of the brachiopod bed from Julianka permits analysis of morphological variation and life positions of the dominant brachiopod species, as well as of their growth and mortality patterns.

MORPHOLOGICAL VARIATION

The dominant terebratulid species, *Sellithyris engeli*, occurs at Julianka in three morphotypes different from each other in shell shape and plication of the anterior margin (Pls 1—3). There is no orderly pattern in spatial distribution of the morphotypes and in fact, morphologically extreme individuals often occur in a close neighborhood of one another in a lithologically homogeneous sediment. This indicates that contrary to the common explanation for such morphological variation in extant and extinct terebratulids (*cf.* Makridin 1964, Barczyk 1969, McCammon 1970, Schumann 1976, Feldman 1977), the observed variability of *S. engeli* cannot be attributed to any direct effect of environmental parameters (*e.g.* hydrodynamics) on phenotype (*cf.* Alexander 1975, Auxenfants & *al.* 1978). The only exception may be the westernmost part of the bed where the proportion of the elongate morphotype *A* is the highest as was also the environmental energy level. The variation may rather be interpreted as an effect of population density, in a close analogy to McCammon's (1970) supposition with respect to shell asymmetry. The observed variability in *S. engeli* is also much too wide to be attributed to a sexual dimorphism (*cf.* Rudwick 1970, Alexander 1975). The most plausible explanation is by reference to a genetic polymorphism, in analogy to Thayer's (1977) suggestion in the case of an extant population of *Terebratalia transversa*, which may result in development of distinct ecotypes effected by the process of habitat selection (*cf. also* McCammon 1970, Alexander 1975, Rousselle 1978). This might be accentuated by a low selection pressure at the post-larval ontogenetic stages (McKerrow 1954, Dzik 1979), and a considerable variation in growth rate (*see* below).

A continuous intergradation of conspecific asymmetrical and symmetrical rhynchonellacean forms (Pl. 4, Figs 1—4) is commonly regarded

as a purely phenotypic effect of high population density (Brookfield 1973a; Lee 1978a, b); whereas a constantly asymmetrical shell shape, as in *Septaliphoria astieriana*, is regarded as an adaptation to environments with water currents highly variable in direction, *e.g.* the tidal zone (Brookfield 1973a; *cf. also* Makridin 1964, Asgaard 1968). This is counterevidenced by the present observations that point to the genetical background of shell asymmetry maintained by a species irrespective of the particular environmental conditions. Furthermore, asymmetrical rhynchonellaceans do not seem to be confined to tidal environments (*cf.* Fürsich 1977).

LIFE POSITIONS

The ontogenetic changes in morphology of the investigated representatives of the Terebratulida consist mostly in an increase in shell elongation and convexity, beak curvature, and commissural fold depth (Text-figs 5 and 7, Pls 1.—3; *cf.* Makridin 1964, Barczyk 1969). This must have been related to a decrease in pedicle significance for shell orientation. As judged from the relationship of foramen to shell size, *Terebratulina substriata* probably maintained an active pedicle even at the late ontogenetic stages. This small-sized, erect-beaked form sup-
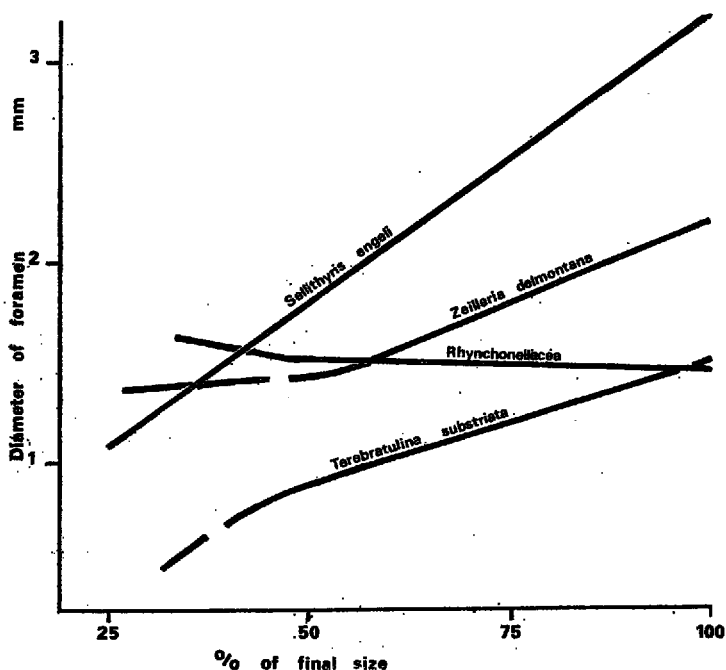

Fig. 12. Ontogenetic change in diameter of the foramen in the investigated brachiopods

posedly could attach not only to skeletal fragments but also directly to
fine-grained sediment, as it was also the case with its close relative from
the Upper Cretaceous, *T. chrysalis* (see Surlyk 1972). This was possible
owing to the root-like pedicle variable in both length and form, typical
of the cancellothyridids (Muir-Wood 1965, Bromley & Surlyk 1973,
Zezina 1976).

In all the other representatives of the Terebratulida, the pedicle was
becoming with age reduced to a tethering function under conditions of
temporarily increased water turbulence (supported mode of attachment
of Makridin 1964; *cf.* Rudwick 1970). This is not counterevidenced by
the large-sized mesothyrid foramen of *Sellithyris engeli* because
a foramen size may not reflect the strength of pedal muscles (Thayer
1975b). No doubt however that a difference in growth pattern of the
foramen between the Terebratulida and Rhynchonellacea, the foramen
increasing in size in ontogeny in the Terebratulida and being gradually
covered with deltidial plates in the Rhynchonellacea (Text-fig. 12), is
indicative of the role of the pedicle having been much more important
in the former than in the latter group.

Taken for granted that *Sellithyris engeli* and *Zeilleria delmontana*
displayed a pedicle even at the late ontogenetic stages, one may suppose
that their evenly biconvex morphotypes could lie at the bottom with
either of the valves downwards, or stand erect in oblique position (*cf.*
Makridin 1964, Surlyk 1972). The latter inference is indeed supported by
the relatively high frequency of suberect-beaked shells attributable to
the morphotype A of *S. engeli*. If a brachiopod with an active pedicle
lies horizontally with its ventral valve downwards (consider the morpho-
type C of *S. engeli*; *cf.* Surlyk 1972), the pedicle should be very long, as
it is *e.g.* in the genera *Laques, Macandrevia,* or *Cryptopora* (cf. Makridin
1964, Stehli 1965, Bromley & Surlyk 1973), and provide the organism
with ability to change its position in response to environmental changes.
That this could indeed be the case with *S. engeli* and *Z. delmontana*
may be suggested by the lack of any unrefutable evidence for beak
abrasion in their shells, but the nature of a brachiopod pedicle can
rarely be ultimately recognized in the fossil record. The observed
prevalence of the horizontal position of specimens of these pedunculate
species in the brachiopod bed from Julianka (Text-fig. 10) may therefore
or may not reflect the life position. This indicates that contrary to the
opinion of Delance & Menot (1968), the orientation of brachiopod shells
cannot be recognized for an important criterion of autochthonism or
allochthonism of a fossil assemblage.

As to the rhynchonellaceans, their life position is related to shell asymmetry.
The specimens of *Septaliphoria* most commonly occur at Julianka with a side
downwards, which is consistent with the presumed life position (*cf.* Brookfield

1973a). It is notable that specimens of *Lacunosella cracoviensis* usually lie horizontally with their dorsal valve downwards.

ONTOGENIC GROWTH AND MORTALITY PATTERNS

As indicated by the size-frequency distributions (see Text-fig. 10), the dominant brachiopod populations from Julianka contain each a high proportion of large-sized, often gerontic individuals. This is a common phenomenon among brachiopods (Brookfield 1973a; Worsley & Broadhurst 1975; Thayer 1975a, 1977; Dzik 1979) which may either reflect the original population structure, or result from various secondary factors. The investigated fossil assemblage is close to autochthonous, originated under very weak current action, and with post-mortem biases being negligible with respect to specimen size. Hence, the observed size-frequency distributions are to be considered as indicative of low mortality rate at the juvenile post-larval stages (cf. Neall 1970, Brookfield 1973a, Dzik 1979) and/or local failure of the recruitment due to a patchy distribution of larvae (Thayer 1975a, 1977). A failure in recruitment might also be partly due to the exclusion of larvae by adults (Neall 1970, Brookfield 1973a, Lee 1978b) but this is largely counterevidenced by the occurrence of juvenile specimens and their traces at the adult shells (Pl. 1, Figs 7—8 and Pl. 4, Fig. 12; *see also* Thayer 1975a, Lee 1978a). The low early post-larval mortality rate increasing later on in ontogeny was indeed recognized by Richards & Bambach (1975) for typical of brachiopods confined to firm bottom under conditions of slow sedimentation, which seems to be compatible with the biotope of the investigated brachiopods from Julianka.

The ontogenetic growth patterns of the dominant brachiopods have been estimated after their growth lines. The results must be treated with some caution because the observed growth line patterns (Text-fig. 13) allowing to distinguish true annual growth rings from disturbance ones (cf. Craig & Hallam 1963) are much more ambiguous than those presented e.g. by Surlyk (1972) or Alexander (1977). This may reflect a higher variability in environmental parameters as well as in growth pattern in the brachiopods from Julianka. All the investigated brachiopod species show a rapid early growth but the rhynchonellaceans grow more rapidly as a rule. The growth rate decreases also more rapidly with age in the rhynchonellaceans probably due to their earlier shift towards a free-living habit indicated by the ontogenetic decrease in foramen size (Text-fig. 12; *cf. also* Surlyk 1972).

The investigated representatives of the Terebratulida show a more slowly decreasing growth rate as a rule. It is however to be noted that the lowest early growth rate and the most rapid decrease in growth rate

are displayed by *Terebratulina substriata*, which may be related to its
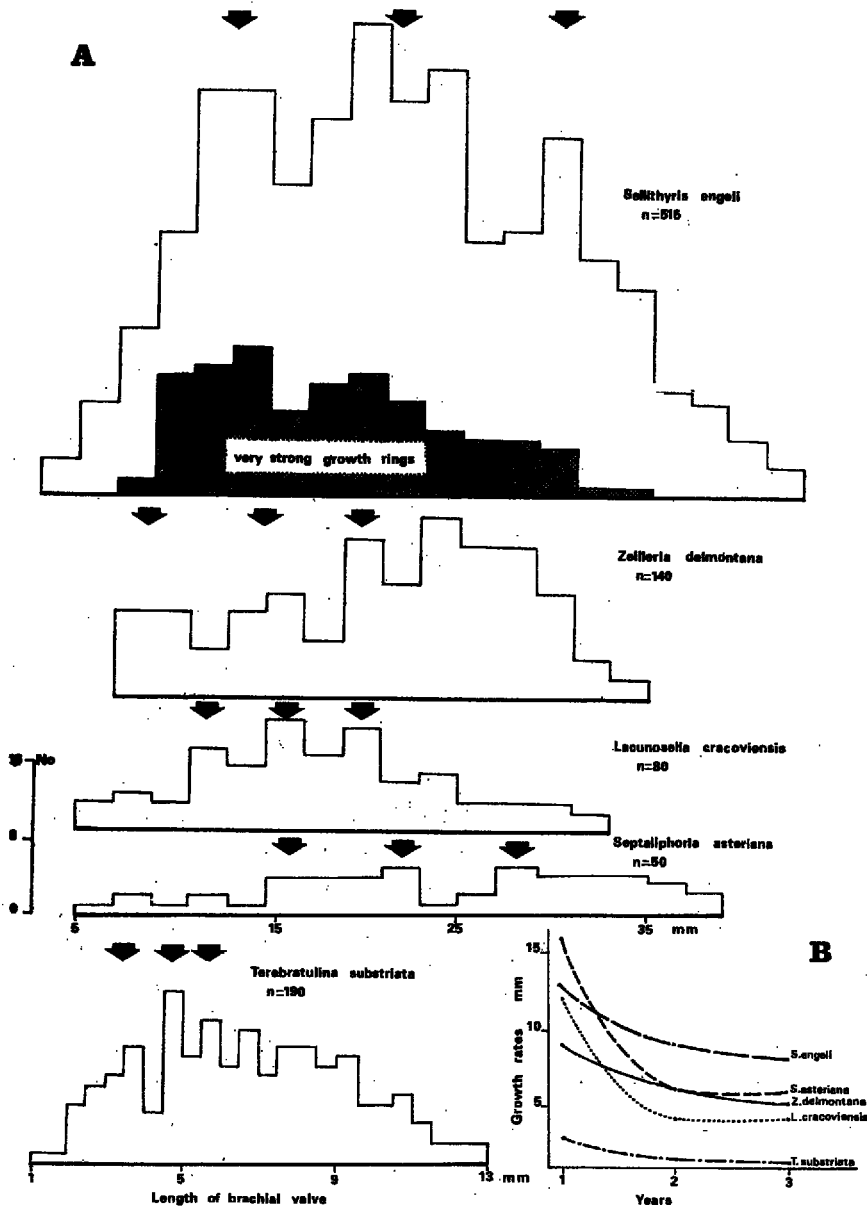maintenance of an active pedicle throughout the life span (*see* Surlyk
1972).

Fig. 13. Growth line analysis for 5 brachiopod species: shell length-frequency-
-distribution at particular growth rings (A), with values taken for the analysis
of growth rate indicated by arrows; growth rate during the first three years
of life (B)

As judged from the maximum number of growth lines, *Sellithyris engeli* (10—12 growth lines) and *Zeilleria delmontana* (16—18 growth lines) lived longer than *Terebratulina substriata* (7—9 growth lines) and especially the rhynchonellaceans (5—8 growth lines). These figures give obviously overestimates of the total life span of the considered species. Note however that extant terebratellids live up to 13 years (Paine 1969; *see also* Rudwick 1970, Surlyk 1972, Richards & Bambach 1975, Thayer 1975a for longevity data on fossil brachiopods) which suggests that the bias may not be very large.

SYNECOLOGY AND BIOTOPE

Brachiopod larvae settled commonly at Julianka at various epibenthic organisms, adult brachiopods including. This is evidenced by traces (Pl. 4, Fig. 12) resembling very closely *Podichnus centrifugalis* Bromley & Surlyk, 1973 (*see also* Małkowski 1975, Michalik 1977). They occur most commonly at the strongly ribbed shells of *Lacunosella cracoviensis* and associated bivalves (Pl. 3, Fig. 11; *cf. also* Logan & *al.* 1975, Zezina 1976, Lee 1978a), which may point to larval rugophyly induced by a search for protection from currents and predators (Zezina 1976). Juvenile brachiopods also are often attached to adults (Pl. 1, Figs 7—8). This pattern of colonization, possibly caused by very weak dispersal potential of the larvae (Rudwick 1970, Webb & *al.* 1976), has resulted in development of mono- or polyspecific clusters of brachiopods in the investigated bed (Text-figs 3—4, Pl. 1, Fig. 9 and Pl. 4, Figs 4—5; *see also* Hallam 1961, Middlemis 1962, Ager 1967, McCammon 1973, Blake 1977, Lee 1978a).

Brachiopod larvae settled obviously not only at adult brachiopods but also at bivalves, crinoids, corals, and sponges. Some small-sized terebratulids have been recorded in cavities in a sponge (Pl. 3, Fig. 8) which resulted probably from their overgrowing by the sponge (*cf.* Middlemis 1962, Zezina 1976). In turn, the brachiopods from Julianka make commonly a substrate for various epibionts. Epibionts and their traces (identified by Professor A. Radwański) occur at some 70% of the brachiopod shells. They are dominated in number by diverse bryozoans and serpulids, but include also sponges, oysters, and indeterminate spat. They may cover a considerable proportion of a brachiopod shell and be represented by 2—3 distinct generations (Pl. 4, Fig. 6). The rhynchonellaceans were more commonly settled than the representatives of the Terebratulida, possibly also because of larval rugophyly. Some epibionts settled doubtless after the death of a brachiopod, as they occur at the commissure. Nevertheless, the apparent lack of intercorrelation between shell orientation and epibiont distribution, and the preference of epibionts for ventral valves suggest that at least some brachiopods were settled alive. Most borings preserved at the brachiopod shells are of thallophyte type (Pl. 2, Fig. 6), and they possibly reflect algal mats (*cf.* Neall 1970, Surlyk 1972, Lee

1978a). Larger-sized borings variable in diameter (Pl. 1, Fig. 10) may be referred to some sponges and/or gastropods, whereas infrequent clusters of microborings (Pl. 4, Fig. 11) can be attributed to the Phoronidea. In turn, some longitudinal incisions (Pl. 2, Fig. 7) may have been executed by predatory crabs or fish.

The investigated macrobenthic fossil assemblage is extremely homogeneous in trophic terms. More than 97% of the total biovolume of the preserved fauna are represented by sessile suspension-feeding epibenthic organisms. These are mostly low-level feeding brachiopods. Their broad trophic niche could however be sub-divided owing to a dietary specialization (cf. Faber & al. 1977), as the brachiopods are able to exploit a wide variety of food resources, viz. phytoplankton, bacteria, particulate, colloidal, and dissolved organic matter (see Steele-Petrović 1976, Zezina 1976 for review). Some brachiopods (as well as the associated epibyssate bivalves) could attach to sponges, crinoids, bryozoans, or non-preserved algae and feed at a higher level above the sediment-water interface. The trophic pyramid also included some scavengers (echinoids, ostracodes) and predators (ammonites and supposedly crabs and/or fish). The absence of herbivores and infaunal deposit feeders might be interpreted as reflecting diagenetic destruction of small arago-nitic shells, but their occurrence (various gastropods and a nuculoid bivalve, *Nuculana*) in the same and neighboring exposures points rather to some ecological limiting factors, first of all to food shortage and unfavorable substrate.

Bottom areas stabilized to a certain degree by the brachiopod shell accumulations were colonized by lamellar corals twice during the forma-tion of the investigated brachiopod bed (cf. Text-fig. 3), which relation-ship resembles the Oxfordian reef complex from Yonne valley, France (Delance & Menot 1968). This pattern may reflect an ecological succes-sion typical of reef biocoenoses (Walker & Alberstadt 1975) or an effect of slight changes in environmental parameters, e.g. sedimentation rate, and hence an interplay of intrinsic and extrinsic controls (cf. Boucot 1975, Hoffman & Narkiewicz 1977). The brachiopods, especially the domi-nant species *Sellithyris engeli*, are then to be regarded as a pioneer, opportunistic assemblage preceding the growth of coral patch-reefs. In a sense, they are ecological equivalents of e.g. some Ordovician stropho-menids (Walker & Alberstadt 1975) or Devonian atrypids (Racki & Ba-liński 1981).

The terebratulids from Julianka were able to accomplish this bottom--stabilizing function under the conditions of generally low environmental energy level, slow sedimentation, abundance and diversity of suspended and/or dissolved organic matter, normal salinity, and good water circula-tion in a shallow subtidal zone of vast carbonate shelf (cf. Kutek 1969). Because of their patchy distribution, one may suppose that they settled only at those bottom areas that had undergone an early lithification or cover by organic film, and/or those with an increased proportion of skeletal grains (due e.g. to the winnowing action of some weak local currents). The biotope of the brachiopod bed from Julianka resembles in

fact very closely the depositional environment of the lower part of the Oxfordian reef complex of Yonne valley, France (Delance & Menot 1968), as well as those of various other brachiopod-rich Jurassic deposits of Poland (Merta 1972) and England (Brookfield 1973b, Palmer 1979).

In non-reef facies, mixed terebratulid-rhynchonellacean assemblages are commonly regarded as transported associations (Ager 1965, Blake 1977). The point is however that the fauna of the brachiopod bed from Julianka is largely autochthonous and differs from that one associated at Julianka with coral build-ups (northern quarry; see Text-fig. 1). In fact, large-sized and smooth-shelled as well as small-sized and strongly ornamented representatives of the Terebratulida, large-sized and asym-metrical rhynchonellaceans, and small-sized cemented thecideids and craniids are very often related to Mesozoic organic build-ups (Różycki 1948; Makridin 1964; Pajaud & Patrulius 1964; Ager 1965; Philip 1965; Aldinger 1968; Asgaard 1968; Childs 1969; Barczyk 1969, 1970; Pajaud 1974; Hallam 1975; Palmer 1979). This diverse ecological group is represented at Julianka by *Lacunosella cracoviensis, Septaliphoria astieriana,* and *Terebratulina substriata,* and in addition by the genera *Juralina, Cheirothyris,* and dallinids (northern quarry). In turn, ordinary-looking moderately--sized, often nested terebratulids, zeilleriids, and rhynchonellaceans are typical of inter-reef Jurassic communities (Różycki 1948, Hallam 1961, Ager 1965, Rollet 1968, Soutoul 1971, Brookfield 1973b, Blake 1977, Dzik 1979). This ecological group is represented in the investigated brachiopod assemblage by *Sellithyris engeli, Zeilleria delmontana,* and supposedly also *Septaliphoria moravica.*

The investigated brachiopod assemblage from Julianka is then to be regarded as representative of a mosaic of adjacent intra-reef and reef habitats. In terms of Ager (1965, 1976), this was a transitional zone from perireefal environments to the sandy subtidal zone.

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EKOLOGIA GÓRNOJURAJSKIEJ ŁAWICY RAMIENIONOGOWEJ Z JULIANKI KOŁO CZĘSTOCHOWY

(Streszczenie)

W wapieniach kredowatych najwyższego oksfordu w Juliance koło Częstochowy stwierdzono cienką ławicę z bardzo licznym i dość urozmaiconym zespołem ramienionogów (*patrz* fig. 1—13 oraz pl. 1—4). Dominujące terebratulidy zinterpretowano jako morfotypy silnie zróżnicowanego gatunku *Sellithyris engeli* (Rollier). Dane mikrofacjalne, nierównomierny, a czasem nawet gniazdowy rozkład fauny w ławicy oraz wyniki analizy tafonomicznej wskazują na autochtoniczny charakter zespołu. Większość gatunków ramienionogów odznaczała się szybkim wzrostem, którego tempo malało podczas ontogenezy, oraz niską wczesną polarwalną śmiertelnością rosnącą z wiekiem. Muszle ramienionogów zasiedlane były przez liczną epifaunę, częściowo pośmiertnie, ale częściowo jeszcze za życia. Badany zespół ramienionogów reprezentuje pionierską, oportunistyczną asocjację stabilizującą dno morskie i poprzedzającą rozwój struktur koralowcowych. Mieszany, terebratulidowo-rhynchonellidowy charakter tego zespołu odzwierciedla zapewne współwystępowanie w nim form typowych dla jurajskich struktur biogenicznych (*Lacunosella cracoviensis, Septaliphoria astieriana, Terebratulina substriata*) oraz dla stref śródbiohermowych (*Sellithyris engeli, Zeilleria delmontana*, przypuszczalnie także *Septaliphoria moravica*).