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CYCLIC ECOLOGICAL REPLACEMENT OF BRACHIOPOD ASSEMBLAGES IN THE TOP-EIFELIAN DOBRUCHNA BRACHIOPOD SHALE MEMBER (SKAŁY FORMATION) OF THE HOLY CROSS MOUNTAINS (POLAND)

Paweł WOŹNIAK[1], **Adam T. HALAMSKI**[2] & **Grzegorz RACKI**[3*]

[1] *Polish Geological Institute – National Research Institute, Upper Silesian Branch in Sosnowiec,1,*
Królowej Jadwigi Str., 41-200 Sosnowiec, Poland; e-mail: pawel.wozniak@pgi.gov.pl
[2] *Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, 00-818 Warszawa, Poland;*
e-mail: ath@twarda.pan.pl
[3] *Institute of Earth Sciences, Faculty of Natural Sciences, University of Silesia in Katowice,*
Będzińska Str. 60, 41-200 Sosnowiec, Poland; e-mail: racki@us.edu.pl
**Corresponding author: racki@us.edu.pl*

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Abstract: The palaeoecology of fossiliferous shales, belonging to the upper part of the Dobruchna Brachiopod Shale Member (= set XIV) of the Skały Formation (northern Holy Cross Mountains), was studied quantitatively in a succession in the transient (1989) trench A, 5.6 m thick, near the village of Skały. The top-Eifelian strata, recording the carbonate crisis during the global Kačák Bioevent, are well known for having a particularly diverse brachiopod fauna. The four brachiopod assemblages, recognised herein, were mainly controlled by the evolving bottom-sediment properties of the outer carbonate ramp basin. Soft, unstable substrates were inhabited by the poorly-diversified *Poloniproductu*s assemblage, associated with a distinctive, ‘incumbent’ set of largely semi-infaunal, generalist species. The pioneer community, as a result of progressive consolidation of bioclast-enriched sediment, evolved toward a more diverse biota. This consequent stabilisation of the substrate resulted in the progressive growth of crinoid thickets or bryozoan-dominated biostromes and patches, associated with rich, subordinate, sessile and vagile benthos. In this stage, diverse brachiopod assemblages were dominated by the pedunculate, eurytopic, ribbed spiriferide *Eleutherokomma* or specialized orthides (*Aulacella*, *Costisorthis*) in the Dobruchna Mbr, and by the expansive, large, free-lying orthotetide *Xystostrophia* in the overlying set XV of the Skały Fm The cyclic ecological replacement, with the characters of ecological succession in the final phase, was evidently stimulated by an irregular transition from soupy muds to a mosaic of bioclast-rich and firmer, biogenic sediments, within the cyclic pattern of distal tempestite sedimentation. The three episodes of variously reduced deposition rate, recorded in the more diverse benthos, culminated in the pioneer bryozoan/coral reef growth and abundance of epibionts, alternating with times of destructive storm activity and deposition from suspension clouds in the muddy habitats.

Key words: Brachiopods, palaeoecology, Eifelian, Kačák Event, Skały Formation, Devonian, Holy Cross Mts.

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INTRODUCTION

In the Palaeozoic Era, and particularly in the Devonian Period, brachiopods were a major element of the marine biosphere. It is thus self-evident that any reconstruction of benthic communities should take brachiopod-related data into account. The palaeoecology of Middle Devonian brachiopods living on the northern shelf of the Rheic Ocean is relatively well understood on a regional scale, among others, thanks to Struve’s (1992) synthesis of data from the Eifel region and applications of the scheme of Benthic Assemblages, introduced by Boucot (1975). In-depth studies on the scale of single localities are, quite paradoxically, less numerous.

The purpose of the present paper is a detailed palaeoecological study of an exceptionally brachiopod-rich, lithostratigraphic unit, the Dobruchna Brachiopod Shale Member of the Skały Formation, in the Łysogóry Region of the Holy Cross Mountins, Central Poland (see Racki *et al.*, 2022; Fig. 1A, B). A faunistic analysis was presented by Halamski and Zapalski (2006), who listed 144 animal and protist taxa from this single unit and reached conclusions about its character as a Konzentrat-Lagerstätte. This paper is a counterpart to this faunistic list and is devoted to the palaeoecology of animal communities that lived in the area, corresponding at present to the environs of Skały Village, in the latest Eifelian time, at ca. 386 my (Becker *et al.*, 2020). The results presented here, based on fieldwork done over thirty years ago, are of special significance, insofar as the exposures in the right bank of the Dobruchna valley, described by generations of researchers (among others, by Pajchlowa, 1957 and Malec and Turnau, 1997) and later exploited by fossil collectors ('pits'; see Halamski *et al.*, 2022, fig. 1C), have recently been destroyed during the extension of the 'Skała' Quarry (Fig. 2; see Racki *et al.*, 2022).

The present paper is based on the MSc. thesis of the first author (PW) at the University of Silesia (Woźniak, 1992), completed under the supervision of the third author (GR). The succession under study was temporarily exposed in a trench, dug in 1989 (Figs 1C, 2A, B, 3B), and was also the object of other unpublished studies at the University of Silesia; three of these MSc. theses are quoted here (Czaplikowska, 1990; Nowak, 1992; Klejszta, 1998).

GEOLOGICAL SETTING

Regional geology and lithostratigraphy

The Skały Shaly-Calcareous Formation, formerly the Skały Beds or Skały Series, is a lithostratigraphic unit of the Bodzentyn Syncline in the Northern (or Łysogóry) Region of the Holy Cross Mountains, Central Poland (Pajchlowa, 1957; Halamski, 2005; Halamski and Racki, 2005; Narkiewicz *et al.*, 2006; for a formal definition see Racki *et al.*, 2022). Its depositional environment was the northern shelf of the Rheic Ocean, or the southern shores of Laurussia.

The Skały Fm is characterised by significant, lithological diversity as well as by abundance and variety of the fossil fauna. The lithologically variable suite, ca. 250–280 m thick, consists dominantly of marly and clay shales, interbedded many times with various types of limestone, including platy and nodular/concretionary lithologies, and crinoid-rich, coquinoid and organic-buildup varieties (Racki *et al.*, 2022). Fossil animals were first described by Zeuschner (1869). Brachiopods were dealt with by, among others, Gürich (1896), Sobolew (1904, 1909), Biernat (1959, 1964, 1966), Biernat and Lazarev (1988), Baliński *et al.* (2003) and Halamski (2004a, b, 2009). The taxonomic studies of various fossil groups have been numerous (see partial reference lists in Pajchlowa, 1957; Halamski and Zapalski, 2006, and Racki *et al.*, 2022). On the other hand, palaeoecological studies on the Skały Formation have been few (e.g., Piotrowski, 1977; Głuchowski, 1993, 2005; Stolarski, 1993;

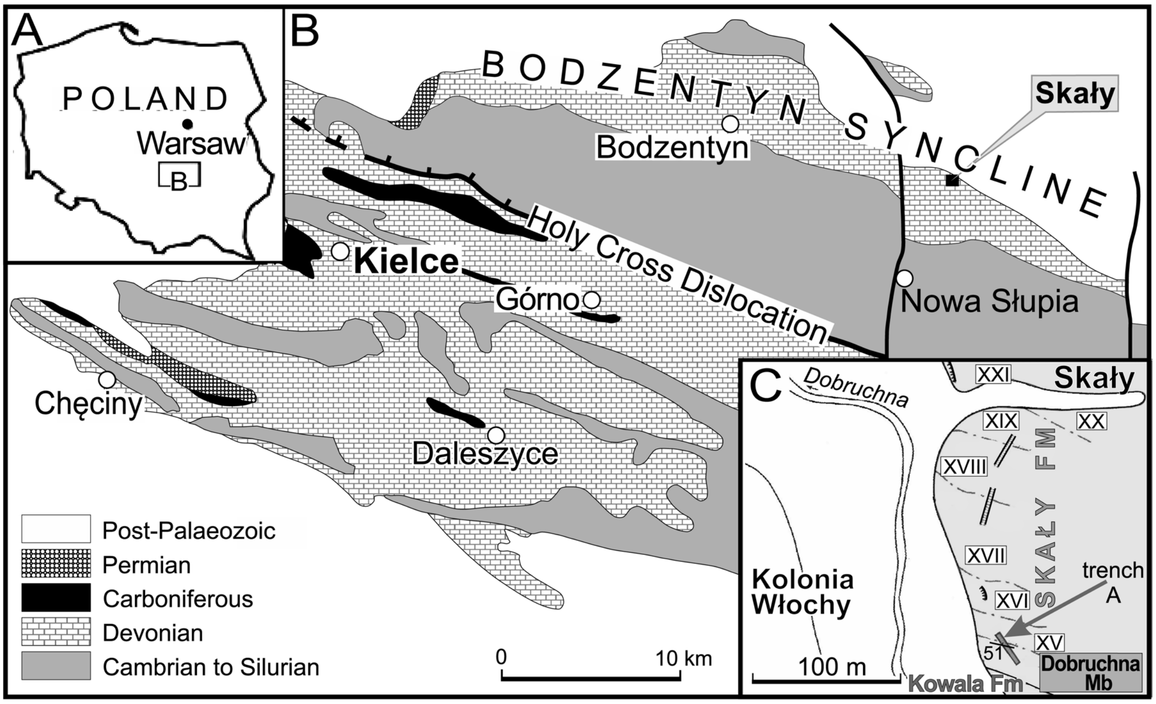

Fig. 1. Location of the studied outcrop of the Skały Formation. **A.** Location of the study area (rectangle) in Poland. **B**. Geological sketch map of the Holy Cross Mountains (after Racki *et al.*, 2022, fig. 1B), with the Skały Formation studied at Skały indicated. **C**. Sketch of outcrops (trench A arrowed; Fig. 2A, B) exposed in 1989 along the Dobruchna Stream, near Skały Village (based on fig. 3 in Nowak, 1992; for currently existing outcrops, see fig. 1 in Halamski, 2022 and fig. 2 in Racki *et al.*, 2022); XV–XXI – lithological sets of Pajchlowa (1957; see Fig. 3).

Fig. 2. Field photos, showing artificial exposures, that no longer exist, of the Dobruchna Brachiopod Shale Mbr (= set XIV of Pajchlowa, 1957). **A**, **B**. Views of the southern end of the hill, near the village of Skały in the Dobruchna valley, in 1989 (A; see the Skały Fm succession in Fig. 3A), as the setting of trench A, which temporarily uncovered the brachiopod shale (B, after Czaplikowska, 1990, pl. 1A, B, and Nowak, 1992, pl. 1A, B; for section see Fig. 3B). **C**. Another temporary outcrop in the late 1990s and early 2000s that exposed the Eifelian strata below the Quaternary loess in a 1-m-high excavation (informally called 'fundamental pit' or 'brachiopod pit', photo by ATH in May 1998; see also http://inkluzja.eu/artykuly/skaly-kultowe-odsloniecie-dewonu).

Zapalski, 2005; Gorzelak *et al*., 2011; Dubicka *et al*., 2021), especially those related to community ecology (Zapalski *et al*., 2017). In the case of brachiopods, brief remarks on palaeoecology (e.g., on the species-lithofacies relations) are given in Biernat (1959, 1964, 1966). It is noteworthy that the original colour pattern has been preserved in rhynchonellide brachiopod shells of the Dobruchna Mbr (Biernat, 1984; see also Halamski and Zapalski, 2006, fig. 6f).

The Silurian to Upper Devonian Grzegorzowice-Skały section in the southern limb of the Bodzentyn Syncline is located in the Dobruchna Stream valley (Halamski *et al*., 2022, fig. 1), about 6 km NE of the town of Nowa Słupia (Figs 1B, 3A). In the type area, the Skały Fm is present under a thin to moderately thick (a few metres) loess cover and in places also under moraine and alluvial sediments. The formation crops out sparsely in a series of small, natural exposures and obscured excavations, scattered along the eastern slope in a stretch of ca. 700 m (Fig. 1C). This fossiliferous succession, described for the first time by Zeuschner (1869), was systematically studied, including a subdivision into sets ('complexes'), numbered from XIV to XXV by Pajchlowa (1957) on the basis of research trenches (Fig. 3A). Additional field data were provided by Malec and Turnau (1997).

The strata studied herein correspond to the upper part of the Dobruchna Brachiopod Shale Member (= set XIV *sensu* Pajchlowa, 1957) and to the basal portion of the overlying set XV (Fig. 3B).

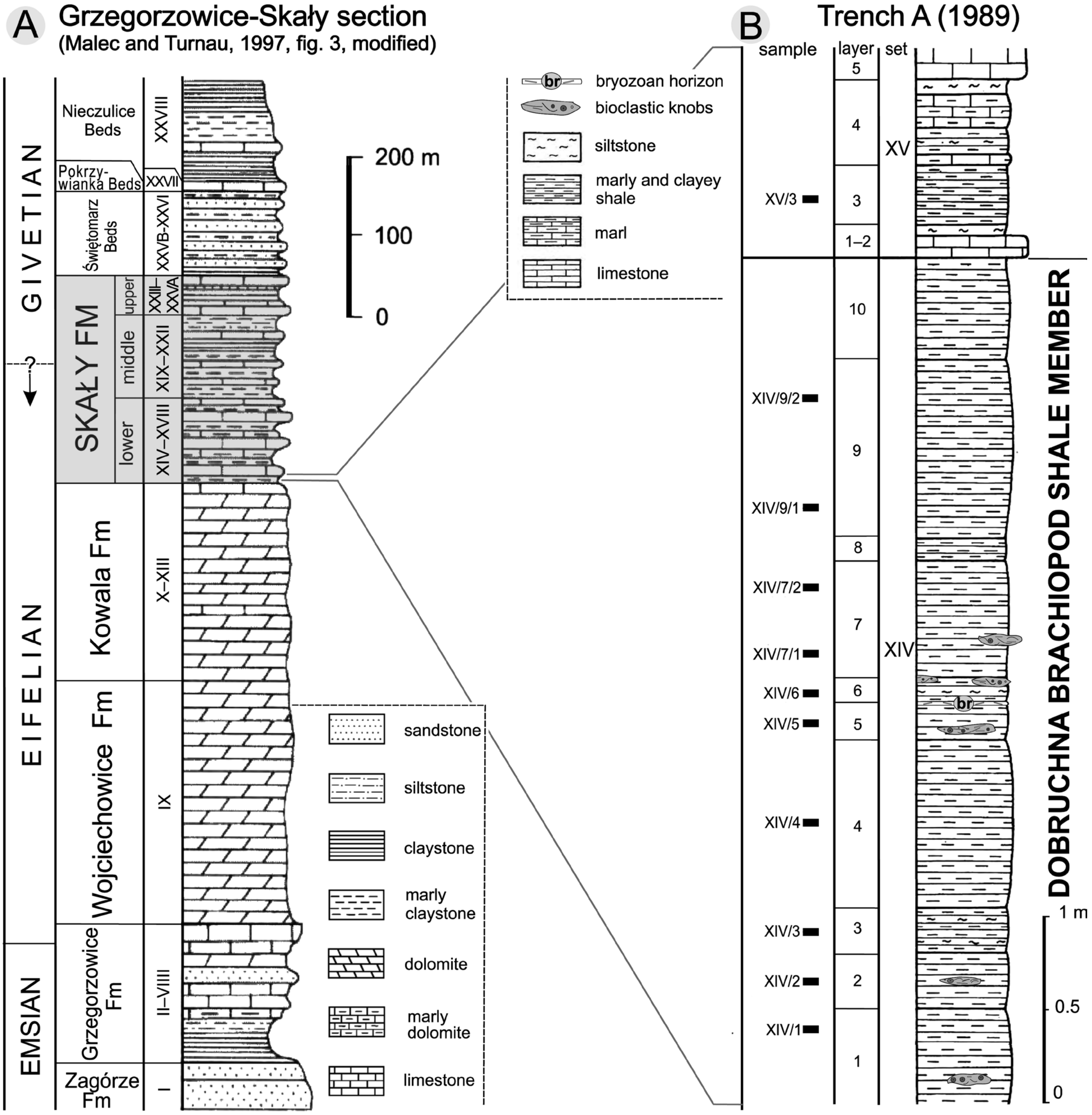

Fig. 3. Stratigraphic setting of the Eifelian brachiopod shales studied. **A**. Emsian-to-Givetian lithostratigraphic column of the Grzegorzowice-Skały section after Pajchlowa (1957, fig. 1; I–XXVIII – lithological sets), updated by Malec and Turnau (1997, fig. 3) and Racki *et al.* (2022, fig. 5). The grey arrow marks the possibly lower position of the Eifelian–Givetian stage boundary (after Narkiewicz in Halamski *et al*., 2022). **B**. The studied section of trench A (see Figs 1C, 2A, B), exposing the basal slice of the Skały Fm (compare fig. 6 in Racki *et al*., 2022; supplemented in the basal part after Czaplikowska, 1990, fig. 3).

Biostratigraphy

The Middle Devonian age of the strata near Skały Village has been clear since the work of Zeuschner (1869), but there were significant discrepancies in the location of the Eifelian–Givetian stage boundary (see the reviews in Pajchlowa, 1957; Dzik, 1981, and Racki *et al*., 2022). Recent conodont and palynostratigraphic studies indicate that the formation ranges from the Upper Eifelian, comprising roughly the conodont *ensensis* Zone, to the Middle Givetian (see Fig. 3A), reaching at least the *rhenanus/varcus* Zone (summary in Halamski *et al*., 2022).

In addition to sparse conodont data (K. Narkiewicz in Halamski *et al.*, 2022), the top-Eifelian assignment of the Dobruchna Mbr is supported by the occurrence of the pelagic, dacryoconarid *Nowakia otomari* (see Dzik, 1981), an index fossil of an important global event, the Kačák Crisis (see Walliser, 1996; Narkiewicz *et al.*, 2021), as well as by the presence of the specific, button-like, rugosan *Microcyclus* in the overlying strata (see Racki *et al.*, 2022). The radical facies changeover corresponds to the carbonate decline during the Ie eustatic highstand (*sensu* Brett *et al.*, 2011; formerly If of Johnson *et al.*, 1985; see fig. 7D in Halamski et al., 2022). Another indication of Late Eifelian age of the Dobruchna Mbr is given by the brachiopod fauna, coeval with that of the Upper Eifelian Freilingen Fm of the Eifel Mountains, as evidenced especially by the presence of *Isospinatrypa aspera* and *Primipilaria primipilaris* (Halamski, 2005, 2009).

LITHOLOGICAL SUCCESSION

The research was carried out in trench A, dug by employees of the University of Silesia in 1989 in a small ravine (Fig. 2A, B), near a pit, which was probably an abandoned excavation, outcrop 73 *sensu* Pajchlowa (1957; see e.g., Piotrowski, 1977). This corresponds approximately to outcrop SK-3 *sensu* Halamski (2004b, 2009), but in the 2000s, the outcrop was much larger, owing to frequent fossil collecting by professional palaeontologists, geology students, visiting the area during field courses, and amateurs (Fig. 2C). The length of trench A was 16 m, and exposed layers were oriented 112/51 N. Currently, owing to extension of the active Skała Quarry, neither the once famous outcrops in the right bank of the Dobruchna valley (e.g., Pajchlowa, 1957) nor a transient outcrop in a road escarpment, studied by Gajewska (2022), exist anymore, but the Dobruchna Mbr. and adjacent strata crop out at a distance of a few dozen metres in the quarry (see Halamski *et al.*, 2022, fig. 1 and Racki *et al.*, 2022, figs 6, 7).

The succession exposed in trench A, ca. 5.6 m thick, includes the uppermost 4 m of the Dobruchna Mbr, subdivided somewhat arbitrarily into ten lithological intervals (‘layers’), and the lowest part of the overlying set XV (including five layers; Fig. 3B). The total thickness of the Dobruchna Mbr is now estimated to be 15.1 m on the basis of new outcrops in the Skała Quarry (12 m after Pajchlowa, 1957), and the interval studied corresponds approximately to its upper quarter. The brachiopod-rich, argillaceous succession in places contains a coquinoid-like, knobby variety (locally with a significant proportion of crinoid debris; ‘bioclastic marls’ in Racki *et al.*, 2022). The fossiliferous strata are represented by mostly dark grey (battleship-grey or slate-grey), marly to clayey shales, variable in colour (mainly grey-olive to -greenish in the weathered rocks), lamination, fissility, and firmness. In petrological terms, the brachiopod shales have a $CaCO_3$ content of between 6.7 and 42.3% and can be classified as marly claystones and clayey marls (see Pettijohn, 1957, fig. 99) or argillaceous mudstones (Lazar *et al.*, 2015).

In some parts, the shales are stained by iron oxides, becoming of rust- or brick-coloured. Orange and brown siltstones form very thin intercalations and interlayers, scattered throughout the succession, that likely in part part correspond to tuffites, recognised in the adjacent quarry (Racki *et al.*, 2022). Besides the omnipresent brachiopods, other ubiquitous representatives of the macrofauna include crinoids (columnals and stem fragments; Nowak, 1992; Głuchowski, 1993), bryozoans (Kiepura, 1965, 1973), and corals (Różkowska, 1956; Stasińska, 1958; see a complete list of the fauna in Halamski and Zapalski, 2006).

Towards the top of the Dobruchna Mbr, a transitional zone, consisting of thin partings of marls and limestone, can be observed. Brown-red marls contain a rich coral fauna (mainly solitary forms), as well as massive and ramose bryozoans and brachiopods. The first layer of a dark bryozoan limestone, 12 cm thick, corresponds to the base of set XV (Fig. 3B). This unit mainly comprises marls and limestones with numerous tabulate and rugose corals and brachiopod faunas (compare fig. 6 in Racki *et al.*, 2022; see also Pajchlowa, 1957; Halamski and Zapalski, 2006, fig. 2; Zapalski *et al.*, 2017).

METHODS

After the detailed logging of the succession in trench A (Fig. 2B), 11 bulk samples from 3 to 22 kg were taken from the ‘layers’ distinguished at intervals of between 0.15 and 1.05 m (Fig. 4A); the total weight was about 125 kg. The laboratory work consisted mainly of water maceration and sieving of these easily disintegrated rocks in order to obtain the fossil material (‘skeletal biomass’), which was the subject of later research. Brachiopods (in the grain fraction above 5 mm) were separated from the samples (articulated shells and single valves), as well as their shelly detritus (from coquinoid partings), juvenile specimens (less than 5 mm in size of the species attaining >15 mm as adults), and fragments of bryozoans, corals, crinoids and other fossils (e.g., gastropods, trilobites, some ostracods).

The work ultimately resulted in a rich fossil collection (Fig. 3B), in particular 3,390 articulated brachiopod shells, 527 isolated valves, and 375 juvenile specimens. The relative abundances of the identified brachiopod taxa in individual samples, based on the number of articulated shells, pairs of valves and juveniles (considered as ‘individuals’; Fig. 5), are presented in 11 tables, included in the digital Supplementary Material (SM 1). Data on relative abundance of a fossil group (Fig. 4C), quoted from an earlier, comprehensive, palaeontological study by Czaplikowska (1990), are derived from a different series of smaller samples (1.2 to 3 kg), disintegrated using a 30% water solution of hydrogen peroxide on the heated shaly rocks (see also Boczarowski, 2001).

SUCCESSION OF THE FAUNAL ASSEMBLAGES

General characteristics of the macrofauna

In all of the marly rock samples studied, in addition to the brachiopod remains, only fragments of crinoid stems are present, but in terms of ‘skeletal biomass’ they mostly form less than 1% of the total skeletal material (Fig. 4B). The content of the fossil material in the rock samples varies from 1.8% in sample XIV/6 to 16% in sample XIV/7/2, corresponding mostly to brachiopod shell abundance (up to 100 per kg; see Fig. 4A). In fact, the mass occurrence of massive, lamellate and ramose bryozoans in a continuous horizon, in the top part of the layer XIV/5, is the most outstanding difference, encountered in the brachiopod-rich succession. Unfortunately, the very numerous species of bryozoans from the Skały Fm (Czaplikowska, 1990, fig. 3B), mostly of the order Trepostomata (mainly Stenoporidae) and Fenestellidae (new species of *Exfenestella* and *Rectifenestella* described from set XIV by Morozova *et al.*,

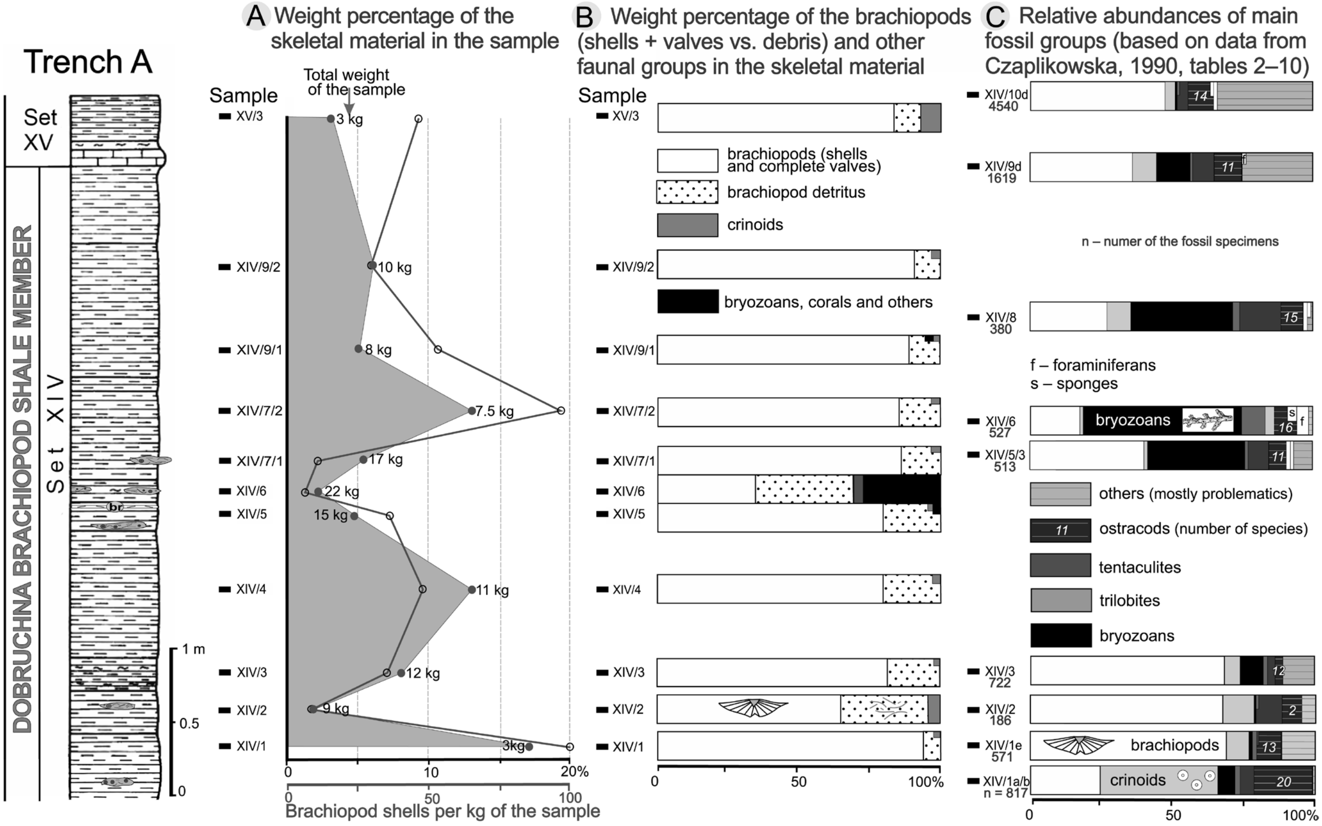

Fig. 4. Characteristics of fossil content for the samples from the trench A section at Skały (see Fig. 3B for explanation). **A.** Weight percentage of the 'skeletal biomass' and brachiopod articulated shell frequency. **B.** Taxonomic composition of the skeletal material in terms of weight percentage. **C.** Frequency percentage of main fossil groups for two series of the samples, analyzed by Woźniak (1992) and Czaplikowska (1990), respectively. Taxonomic diversity is shown only for the ostracod microfaunas, for which detailed identifications by Czaplikowska (1999, tab. 11 – see SM 4) are available.

2006), are still waiting for systematic research (see Kiepura, 1965, 1973). In addition, an increased proportion of other non-brachiopod, macrofaunal elements (including corals, trilobites, gastropods, and bivalves) characterize sample XIV/6, as well as samples XIV/2 and XV/3 (Fig. 4B).

In supplementary samples, Czaplikowska (1990) provided evidence of the crinoid-rich horizon in the basalmost part of the trench section, as well as bryozoan-rich levels in its middle slice (layers 7 and 9; Fig. 4C). Furthermore, in the light of her detailed study, noteworthy is the variable, but continuous co-occurrence of microfossils and micro-remains of several macrofossil groups, such as tentaculites (*Nowakia*, styliolinids: Dzik, 1981), diverse ostracods (Adamczak, 1976; SM 4), non-pelmatozoan echinoderms (especially holothuroids, ophiuroids, echinoids, and ophiocystoids, maximally 1.5% in sample XIV/5/3; see also Boczarowski, 2001), and – in the upper part only – octactinellid calcisponges and foraminiferans (Gajewska, 2022).

Taxonomic characteristics of the brachiopod fauna

A preliminary remark on the brachiopod taxonomy used in the present paper is needed, insofar as there is no single up-to-date overview of the fauna. Identifications by Biernat (1959, 1964, 1966) and Baliński *et al.* (2003) were partly updated by Halamski (2004b, 2009; see also Halamski and Zapalski, 2006). A more detailed comment is needed in three cases. The atrypide, described by Biernat (1964) as *Atrypa squamifera*, corresponds to an undescribed species of *Kyrtatrypa*, here called *Kyrtatrypa* sp. A. The smooth spiriferides, belonging to the family Reticulariidae, described by Biernat (1966) under the names *Eoreticularia eifeliensis* and *Eoreticularia aviceps*, belong probably to the genera *Rhenothyris* and *Thomasaria* (see Halamski, 2004b; Halamski and Baliński, 2013; Baliński and Halamski, in press). However, owing to their revision being still in progress on the one hand and difficulties in distinguishing these two species on the other hand, both are here collectively referred to as reticulariids. *Uncinulus primipilaris sensu* Biernat (1966) corresponds to two species of the genus *Primipilaria*, namely *P. primipilaris* and *P. praeprimipilaris*, as proposed by Struve (1992; see also Halamski, 2004b); here they are collectively referred to as *Primipilaria* spp.

As far as the succession investigated in trench A is concerned, the productides were distinctly predominant in the fauna studied (above 52%), as a consequence of the high frequency of *Poloniproductus varians* (42.2%), supplemented by *Devonaria zeuschneri* and *Dagnachonetes supragibbosus* (Fig. 4A). The spriferides are another abundant order (4 species, 17.1%), followed by the atrypides (5 species, 9%), orthides and protorthides (6 species, 8.6%), and strophomenides (4 species, 7.1%). Conversely, among 27 identified taxa, a minimal contribution of rhynchonellides (1 taxon, 0.5%) and athyridides (3 species, 1.1%), and the absence of pentamerides and terebratulides are noteworthy.

It should be stressed that the accurate frequency data, based on the fossil material obtained from stratigraphically ordered samples (Fig. 4A), concern the upper quarter of the brachiopod shale. Of course, comparable abundance data for the entire Dobruchna Member are not available, but the systematic list of brachiopod species from there (Halamski and Zapalski, 2006, pp. 146–147) consists of 44 species, over 60% more than those noted in trench A (27). As far as the entire brachiopod shale is concerned, *Aulacella prisca* is a particularly frequent species; no data for this particular level exist, but about half of the total material from the Middle Devonian of the Łysogóry Region studied by Halamski (2004b) corresponds to *A. prisca* (about 8,000 out of 17,000 specimens). *Primipilaria* spp. and *Xystrostrophia umbraculum*, infrequent in trench A, were also quite often found over the years of collecting at outcrop SK-3. Of course, such hand collection of loose specimens, released from weathered, shaly horizons to the loess cover, is certainly susceptible to a variety of biases (see Wallace, 1978). Nevertheless, it is clear that the frequencies of brachiopod species and resulting interpretations presented here should not be uncritically extended to the totality of the Dobruchna Mbr at Skały.

Brachiopod succession

Successional changes within the brachiopod fauna in the trench A section are presented in Figure 5. In the lowest sample XIV/1, high frequency (above 45%) of *Eleutherokomma diluvianoides* (Mucrospiriferidae), the ribbed alate spiriferide, characteristic of the Dobruchna Mbr, is observed. Productides and atrypides are also numerous, like *Poloniproductus varians* (Productidina, Monticuliferidae), *Devonaria zeuschneri* (Chonetidina, Anopliidae) and *Atrypa* (*Planatrypa*) *depressa* (Atrypidae), associated with numerous juveniles of smooth spiriferides (reticulariids).

There is a major turnover in assemblage composition in the succeeding sample, XIV/2. It is shown in the increased importance of *P. varians* that accounts for almost 50% of the identified brachiopod taxa, in association with atrypides, *D. zeuschneri*, and the small strophomenide *Parastrophonella anaglypha*. In the next two samples, XIV/3 and XIV/4, the dominating role of *Poloniproductus* is even more important. This species reaches its maximum abundance in sample XIV/3 (almost 75%; Fig. 5). In these three samples, the next frequent taxa are *Eleutherokomma*, *Devonaria*, and *Parastrophonella* that reach abundances just over 5%.

The most diverse brachiopod faunas are those in samples XIV/5 (24 taxa) and XIV/6 (20 taxa). Small orthides (*Aulacella prisca*, *Costisorthis canalicula)*, absent in the lower samples, appear here and are predominant over the other species. Also, *Parastrophonella* is reaching its relative maximum in this level, whereas chonetidines and atrypides are moderately numerous. They are associated with rare rhynchonellide and athyridide species, limited to these two samples, like *Primipilaria* spp., *Nucleospira lens*, and *Bifida lepida*. In terms of skeletal biomass, sample XIV/6 is characterised by the lowest percentage of articulated brachiopod

Fig. 5. Characteristics of the brachiopod succession in the trench A section at Skały (see Fig. 3B for explanation). **A**. Successional dynamics within the fauna. Total relative abundance, largely above 50%, of the 'Big Five' incumbent species [*P. polonicus, E. diluvianoides, Devonaria zeuschneri, Pa. anaglypha, A.* (*P.*) *depressa*] is shown as a dropped field (see also Figs 7, 8). *Pa. – Parastrophonella*, *A.* (*P.*) *– Atrypa* (*Planatrypa*). *C. – Costisorthis*, *D. – Dagnachonetes*. **B.** The stratigraphic variation of mortality and disarticulation indices. **C.** The stratigraphic variation of the Simpson's Diversity Index (see SM 1; Hammer, 2009).

specimens in the entire section (35.5%), coupled with the highest content of shelly, especially orthide detritus (34%), crinoids, bryozoans and corals, as well as fragmented trilobites, bivalves and gastropods (Fig. 4A, B).

Sample XIV/7/1 is distinguished by the next compositional changeover, as well as by better preservation of the strongly brachiopod-dominated fauna. A distinctive increase in the frequency of *Eleutherokomma* is paired with a slight decrease in abundance of *Poloniproductus* and the total disappearance of the orthides. The flat-shelled orthotetide *Xystostrophia umbraculum* appears in greater numbers for the first time in the investigated succession, making up 9% of all specimens.

The top part of the layer 7 (sample XIV/7/2) is characterised by strong, numerical predominance of *Poloniproductu*s, whereas solely *Parastrophonella*, *Devonaria*, and *Atrypa* constitute more than 5% of all brachiopods. The faunal composition is almost the same in the lower part of layer 9 (sample XIV/9/1), whilst the highest sample, XIV/9/2, from the Dobruchna Mbr exhibits a further increase in the predominance of *Poloniproductus*, occasionally forming shell clusters. Chonetidines and atrypides together do not exceed 13%.

Sample XV/3 belongs already to the lower part of the overlying set XV of the Skały Formation, above the bryozoan-rich limestone layer. It is highly specific, owing to the relatively high proportion (38.6%) of *Xystostrophia umbraculum*. The brachiopod assemblage is far less diversified (7 taxa), when compared with the samples from the brachiopod shales. *Eleutherokomma* and *Poloniproductus* are still numerous, forming a few coquinoid concentrations, with the presence of atrypides and chonetidines. The occurrence of crinoid stem fragments, up to 2 cm long, is another distinctive feature.

Brachiopod mortality and taphonomy

When considering the effectiveness of individual survival, only at the most 10 larger-sized (>15 mm) taxa clearly show a juvenile mortality index (MI) above 5% (Tab. 1). Even if some taphonomic bias cannot be excluded, several species evidently display extremely high, relative abundance of juveniles, paired with their low presence in the faunas studied. This subdued development on the boundary of life tolerance seems to characterise some rare atrypides (*Isospinatrypa*) and athyridides (*Athyris*), but three infrequent, small to micromorphic athyridide and spiriferide species (*Bifida*, *Crurispina* and *Nucleospira*) are likewise distinguished by a lot of immature specimens (see SM 1). This hypothetical hindrance may also have been in place in the case of far more common, smooth spiriferides (reticulariids), represented in the samples studied by only 16% mature individuals. An increased killing rate in the early ontogenetic phase (MI between 12 and 22%) also affected the orthide *Costisorthis,* atrypides, and the widespread productide *Devonaria.* In this context, the most stressful conditions for colonising larvae were recorded in the lowest and middle intervals (samples XIV/1, XIV/5 and XIV/6), where more than 20% of the juveniles were killed (Fig. 5B).

Good preservation of intact shells, including fine ornamentation details (Biernat, 1959, 1964, 1966; Halamski, 2009), and their patchy distribution in an assumed life position within the clayey laminated matrix strongly indicate parautochthonous and autochthonous (*in situ*) fossil occurrences. Nevertheless, episodes of increased hydrodynamic activity and bottom sediment reworking are clearly shown by bioclastic, coquinoid-type concentrations (see below), especially in layers 2 and 6. Also, the degree of valve separation reflects these hydrodynamic stimuli, because relatively high disarticulation is found in samples XIV/5 and XIV/6 (Fig. 4B), compared with the other samples. In particular, in the layer 5, apart from single, articulated orthide shells, clumpy accumulations of their valves and isolated valves, were particularly common. The orthides rank first, according to the disarticulation index (DI, Tab. 2), thanks to the top position of *Aulacella prisca* (minimum 56.5% disarticulated shells) and *Costisorthis canalicula* (46%), followed by *Schizophoria schnuri* (18.9%). Such a situation, noted also by Biernat (1966, p. 10; Tab. 2), is rather common in the Palaeozoic (e.g., Alexander and Gibson, 1993). This taphonomic character can be readily explained by the weakness of deltidiodont teeth of the orthides, compared to more evolutionarily advanced cyrtomatodont teeth (Harper *et al.*, 2004, p. 174) of the 'neoarticulates' (all rhynchonellates, except protorthides and orthides; Carlson, 2016, p. 414).

In total, only at the most 10 taxa among 27 display DI higher that 10%, with noteworthy positions of *Primipilaria* spp., *Eleutherokomma diluvianoides* and *Atrypa* spp. (DI between 16.4 and 18.2%). The most abundant species, *Poloniproductus varians*, exhibits only 3.9% disjointed shells.

Table 1

Brachiopod taxa marked by the highest mortality among juvenile individuals.

No.	Taxon	Number of individuals (NI)	Number of juveniles	Mortality Index (%; MI)
1.	*Isospinatrypa* sp.	17	16	94.1
2.	*Athyris concentrica* s.l.	12	11	91.7
3.	Reticulariidae	194	163	84.0
4.	*Costisorthis canalicula*	92	20	21.7
5.	*Atrypa* & *Kyrtatrypa*	250	37	14.8
6.	*Devonaria zeuschneri*	328	39	11.9
7.	*Desquamatia subzonata*	65	5	7.7
8.	*Eleutherokomma diluvianoides*	377	25	6.6
9.	*Xystostrophia umbraculum*	153	8	5.2

Table 2

Brachiopod taxa characterised by the highest shell disarticulation, shown for the Eifelian fauna studied, in comparison with the Eifelian–Givetian faunas from the entire Skały Fm, monographed by Biernat (1959, 1964, 1966).

No.	Taxon	Maximal number of individuals	Number of disarticulated individuals	Disarticulation Index (%; DI)	Approximated DI (%;) after data from Biernat (1959, 1964, 1966)
1.	*Aulacella prisca*	255	144	56.5	10
2.	*Costisorthis canalicula*	87	40	46.0	44.9
3.	*Schizophoria schnuri*	37	7	18.9	9.8
4.	*Primipilaria spp.*	22	4	18.2	4
5.	*Eleutherokomma diluvianoides*	426	77	18.1	5
6.	*Atrypa* & *Kyrtatrypa*	238	39	16.4	7.2
7.	*Desquamatia subzonata*	66	9	13.6	8.4
8.	*Dagnachonetes supragibbosus*	242	30	12.4	9.1
9,	Reticulariidae	65	8	12.3	27.3
10.	*Poloniproductus varians*	1703	67	3.9	3
	Xystostrophia umbraculum	152	6	3.9	6

Brachiopods as epizoans and hosts

Primary data. The brachiopod collection, made by the first author (PW) and used for the MSc. thesis (Woźniak, 1992) and the present study, was also slightly enlarged and studied by Klejszta (1998) in terms of epibiont associations. In total, 220 out of 3,980 specimens were found as hosts (5.5 %), which were encrusted by 406 epizoans. These results are briefly summarised here and compared with newer observations, as already was done in part by Zatoń *et al.* (2022a).

Brachiopods as hosts. According to Klejszta (1998), a selective preference for finely ribbed species of different sizes is observed (Fig. 6), especially the frequently colonised orthides (*Schizophoria schnuri* – 52.6% of the collected specimens have epizoans; *Aulacella prisca* – 24.3%; *Costisorthis canalicula* – 15.9%) and the atrypide *Atrypa* (*P.*) *depressa* (14.9%).

Still, according to Klejszta (1998), among the rarer but large-sized species, this positive selection occurred notably in *Leptagonia analogaeformis* (57.4%), *Kyrtatrypa* sp. A 33.3%), and *Gibbodouvillina interstrialis* (28.6%). Conversely, smooth brachiopods, like *Eoreticularia*, were apparently unfavourable for epizoan attachment (0.5% encrusted specimens). The same may be said about spinose and/or semi-infaunal species (0.1% shells of *Poloniproducus* were overgrown and 3% of those of *Devonaria*). The coarsely ribbed spiriferide *Eleutherokomma* was also overgrown only quite seldom (2.2%).

In summary, the analysed data seem to confirm the occurrence of the phenomenon of larval rugophily (settlement of larvae in substrate pits and narrow crevices; see Railkin, 2004, p. 95), related to a search for protection from currents and predators among extant brachiopods (Zezina, 1976; for a Jurassic example, see Heliasz and Racki, 1980). This conclusion is partly disputable in the light of the study by Zapalski (2005), dealing with a numerically smaller amount of material, but coming from several Middle Devonian levels of the Skały Fm: substrate specificity is indeed the case, but solely over a minimum host brachiopod size (compare Fig. 6 and reviews in Mistiaen *et al.*, 2012 and Zatoń *et al.*, 2022a).

According to Klejszta (1998), crinoids and microconchid tentaculitoids (see Halamski and Zapalski, 2006, figs 5, 7; Zatoń and Krawczyński, 2011) dominate the suspension-feeding epizoic fauna (35 and 31% of the collection, respectively). It is worth noting that among the crinoid columnals and stem fragments, specific elements of *Ammonicrinus* are relatively numerous (almost 11% of the collection of Nowak, 1992; see also Piotrowski, 1977).

Brachiopods as epizoans. In the Dobruchna Mbr, brachiopods are not particularly frequent as epizoans, but the large size of the collections and good preservation of the material allowed the description of a few species of epibiontic brachiopods. The most frequent one is the inarticulate brachiopod (craniide) *Deliella deliae* (Halamski, 2004a; see also Halamski and Zapalski, 2006, figs 3, 4; formerly misidentified as *Philhedra*), often occurring in several individuals per single brachiopod host shell. Other brachiopod epizoans include the craniide *Acanthocrania* (Halamski, 2009, pl. 1, figs 4–7) and the productide *Auchmerella* (Halamski, 2009, pl. 7, fig. 24). On the other hand, Klejszta (1998) recognized *Devonaria* as the most frequent epizoan among rhynchonellates (‘articulates’) and also noted the intraspecific colonization by successive spatfalls in the *Xystostrophia* population.

General character of the epizoan associations. According to Klejszta (1998), the most common interactions between host and encrusters were commensalism and mutualism (but see Zapalski, 2011), evidenced by the coloniser orientation, controlled by the feeding streams of the host. The association of *in vivo* epizoans on brachiopods differs thus from the crinoid-hosted epibionts from set XVII of the Skały Fm,

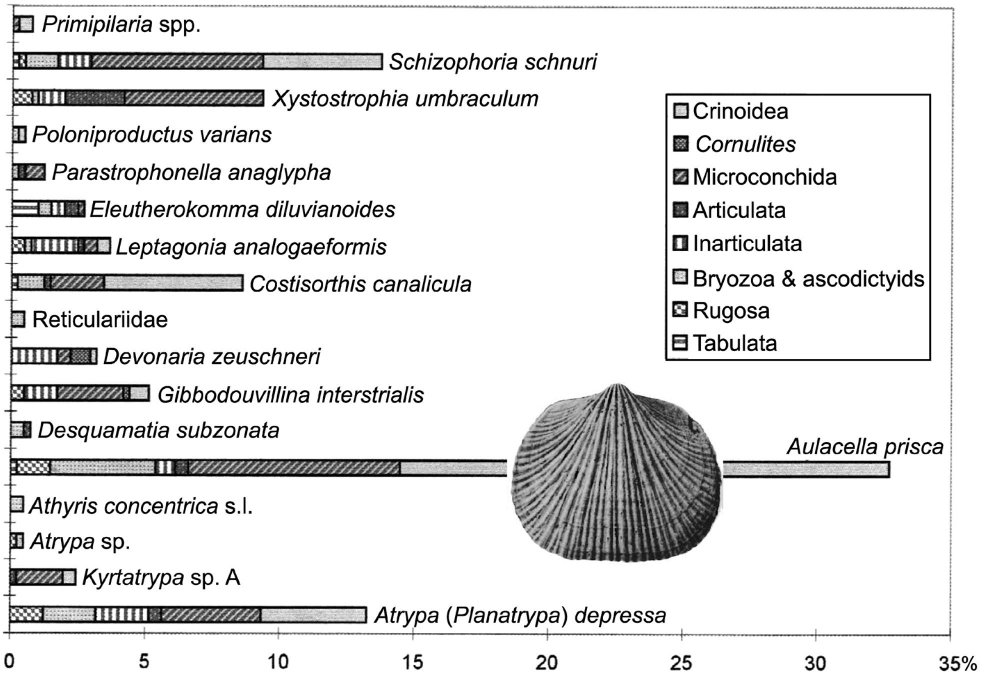

Fig. 6. Percentages of the epizoan association, shown for the particular host-brachiopod taxa (fig. 6 from Klejszta, 1998). Note the leading position of finely ribbed species, regardless of their size (see Fig. 7).

dominated by diverse ascodictyids ("ctenostome" bryozoans of Głuchowski, 2005) and bryozoans that utilized dead, isolated crinoid remains as a hard substrate for attachment (Głuchowski, 2005). Generally speaking, epizoan assemblages may be very different, even between spatially close sites (Zatoń *et al.*, 2022b, this volume).

ENVIRONMENTAL SETTING

The argillaceous-calcareous facies of the Dobruchna Mbr is typical of the outer facies belt of the gently sloping carbonate ramp (Halamski *et al.*, 2022; Pisarzowska *et al.*, 2022; for the model summary see Flügel, 2010, pp. 664–666, 716–719). The Middle Devonian brachiopod muddy habitat corresponded to moderately deep (45–60 m; see Jansen *et al.*, in press), fairly well oxygenated, open shelf environments of the tropical zone, optimal for blooming of the shelly benthos (Brachiopodetum of Struve, 1963; see also Copper, 1965; Faber *et al.*, 1977; Vogel, 1980; Vogel *et al.*, 1989; Racki *et al.*, 1993). For example, abundant and diverse (34 taxa; SM 4) ostracods in this part of Skały Fm (Czaplikowska, 1990) also represent an association, corresponding to the brachiopod zone of the Eifelian Ecotype (biotope 6 – Becker, 2000).

The initial, depositional phase of the Skały Fm was promoted by rapid drowning of the carbonate platform during the end-Eifelian sea-level rise, paired with the collapse of the carbonate factory during the global Kačák Crisis (see Narkiewicz *et al.*, 2021; Racki *et al.*, 2022). This overall, high-stress time during a warming/hypoxic episode was unexpectedly accompanied in the Łysogóry Region by the immigration wave and significant benthos diversification, so conspicuously recorded in the Konzentrat-Lagerstätte of the Dobruchna Mbr (Halamski and Zapalski, 2006).

This paradox may be explained by offshore thriving of the brachiopod-dominated community in low-nutrient regimes, as recognized in Carboniferous and Triassic seas (Pérez-Huerta and Sheldon, 2006; Tomašových, 2006). The partly actualism-based interpretation is favoured herein for three reasons: (1) preservation of original, depositional lamination and absence of bioturbation, which contrasts with eutrophic Givetian brachiopod habitats, recorded in the nearby Miłoszów succession (Pisarzowska *et al.*, 2022); (2) a strong predominance of productides over spire-bearing brachiopods, the latter being the group adapted especially to oligotrophic settings, owing to their higher lophophore efficiency (the ability of generating multi-directional inhalant currents – Pérez-Huerta and Sheldon, 2006); and (3) absence of terebratulide brachiopods, preferring nutrient-rich water masses on a modern, upwelling-influenced, tropical shelf (Kowalewski *et al.*, 2002).

SYNECOLOGICAL INTERPRETATION

Succession of brachiopod assemblages

Brachiopod assemblages can be easily distinguished in the studied samples from the Skały Fm on account of the different proportions of the most numerous species (Figs 5A, 7; SM 1, 2). In autecological terms, the brachiopods included are representatives of a sessile, filtering epifauna (pedunculate guild) and semi-infauna (free-lying guild; for a review of brachiopod habits see Fürsich and Hurst, 1974; Thayer, 1975, 1983; Alexander, 1977, 2001; Faber *et al.*, 1977; Vogel, 1980; Tomašových, 2006). The lowest part of the section (sample XIV/1) is characterised by the acme of *Eleutherokomma*, a spiriferide brachiopod with an alate shell attaching to skeletal grains with a short, functional pedicle

(Schumann, 1967; Thayer, 1974) within partly consolidated muds. However, this distinctive species is widespread at various levels of the trench A succession (Figs 5, 7). As demonstrated by Richardson (1981), some living brachiopods may show different habits on soft muds and hard bedrock, free-lying and attached, respectively. The lifestyle of the American mucrospiriferid *Tylothyris* is interpreted in a similar way, which used its pedicle to anchor only in high-energy conditions, and in calm settings stabilized the shell by means of its alate hinge line (Bush and Brame, 2010; see a similar ambocoeliid case, described by Zambito and Schemm-Gregory, 2013).

The succeeding *Poloniproductus* assemblage is evidenced during a relatively long interval (samples XIV/2 to XIV/4). Mass occurrences of *Poloniproductus* point to the softer nature of the quickly deposited muds, which facilitates colonization of it by brachiopods stabilized in the mobile ‘soupy’ substrate with aid of a dense brush of spines (Rudwick, 1970). Juvenile productides fixed themselves by means of spines (Sun and Baliński, 2008, fig. 16A) to protruding, epibenthic objects, such as crinoids (see evidence in Głuchowski, 2005), sponges, or algae (Grant, 1966; Bowen *et al*., 1974), and a similar hypothesis was presented for different groups from the Skały Fm (the coral *Calceola* – Stolarski, 1993; microconchids – Zatoń and Krawczyński, 2011). Mature individuals fell down and continued living, partially buried in the sediment. On the other hand, the productide spinosity also is sometimes viewed as protection from durophagous predation (Leighton, 2000; Johnsen *et al*., 2013).

Like *Eleutherokomma*, *Poloniproductus* tolerated a variety of substrate conditions by utilising different life orientations in different benthic niches. This eurytopy is indirectly recorded in high intraspecific variability, including deformation of the ventral umbo, as emphasized by Biernat (1966, pp. 24–26). A similar, semi-infaunal (‘snowshoe’) habit probably also characterised concavo-convex chonetidines and strophomenides, such as *Devonaria*, *Parastrophonella* and *Dagnachonetes* (see statistical data below), consistently associated with *Poloniproductus*. Thanks to their flat, thin shells, they could maintain an unchanged position on a slightly consolidated bottom (‘mud-floater’ adaptation; Thayer, 1983, tab. 8), even coping with some current activity. In the top part of the *Poloniproductus*-dominated slice, bryozoans occur more abundantly, gradually leading to stabilization of patches of mud and increasing consolidation of the bioclast-enriched bottom sediments.

In the upper part of the XIV/5 layer, there is a bryozoan biostrome, a few centimetres thick, leading to a maximal diversification of brachiopod niches (see below).

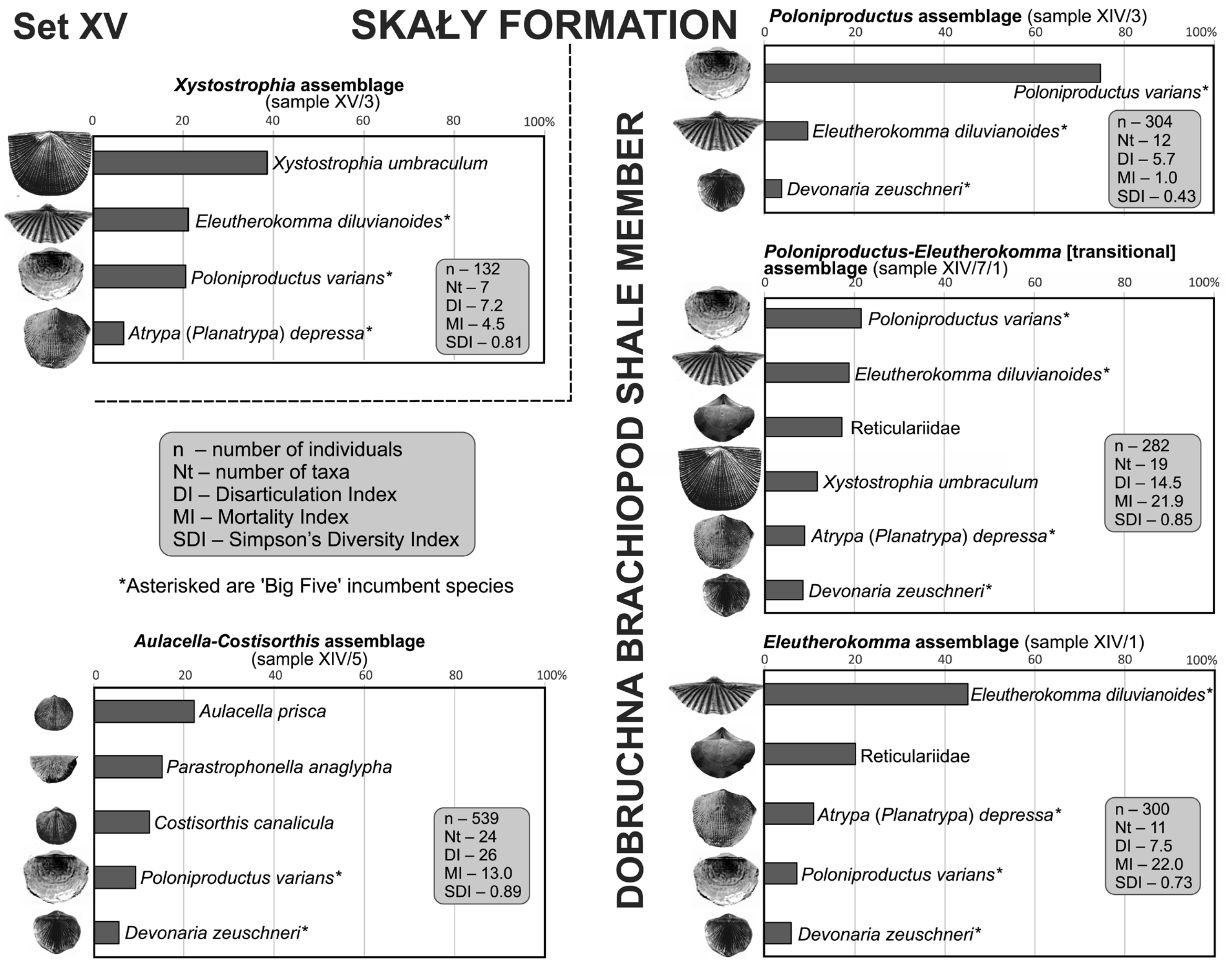

Fig. 7. Species composition of characteristic brachiopod assemblages of the lowest Skały Fm (Dobruchna Mbr and set XV, see Fig. 3B) in the trench A succession at Skały (compare Fig. 5A and SM 1).

The assemblage, associated with the most consolidated sediments (samples XIV/5 and XIV/6), includes relatively small-sized, pedunculate individuals of the orthides *Aulacella* and *Costisorthis*, presumably attached to skeletal grains or concretionary parts of the muds during the relative starvation in sedimentation. This depositional pause was noted by Klejszta (1998), because the middle part of the succession is distinguished by a clearly increased frequency of encrusted shells, with the maximum in samples XIV/5 (21.3%) and XIV/6 (18.3%). On the other hand, a negligible number of epibionts characterises intervals with productides predominant, in particular layers 2 to 4 (between 0.4 and 2%), as well as the set XV (0.7%).

Higher in the trench A succession, the properties of the bottom muds were gradually modified by a significant admixture of brachiopod detritus and a skeletal contribution of bryozoans, corals, and crinoids (Fig. 3B, C). The 'transitional' *Poloniproductus–Eleutherokomma* assemblage is constrained to sample XIV/7/1. Therefore, the intermediate habitat most likely records a subtle, lateral variation of bottom muds (see below), locally enriched in skeletal grains (shown by the relatively high content of bryozoan zoaria; see Fig. 3C). Both of these incumbent species of *Poloniproductus* and *Eleutherokomma* are essentially shale-limited in the Skały Fm (Biernat, 1966; Halamski, 2009) and their overlapping, ecological generality was limited to the Brachiopodetum oligotrophic biotope. On the other hand, they showed little tolerance to eutrophic regimes and intensively bioturbated, calcareous-clayey muds (common in the Givetian part of the Skały Fm – Pisarzowska *et al*., 2022), opposed to *Devonaria zeuschneri*, *Aulacella prisca*, *Schizophoria schnuri*, *Gibbodouvillina interstrialis* and *Leptagonia analogaeformis* (see Baliński and Halamski, in press, tab. 1).

In the uppermost Dobruchna Mbr, the *Poloniproductus* assemblage persistently thrived again in the semi-fluid mud conditions. The *Xystostrophia* assemblage was tentatively identified on the basis of a single sample, taken in the lower part of complex XV. It still contains the 'Big Five' incumbent species, but is dominated by *Xystostrophia umbraculum*, occurring in ten samples. The faunal composition implies some consolidation of the bottom sediments, because localized, skeletal-rich 'islands' are evidenced by fragmentary crinoid stems. It is noteworthy that Pajchlowa (1957, p. 186, fig. 1) and Biernat (1966, p. 17, fig. 3) noticed the mass occurrences of large-sized *Xystostrophia* not only in set XV, but also in the Givetian levels of the Skały Fm (sets XX–XXII), e.g., in association with rare, juvenile *Leptagonia* in shales of locality 112. So, it can be seen as a transitional grouping between the *Poloniproductus* assemblage (see correlation relationships in SM 2) and almost monospecific occurrences of the genus. For this type of flat, slightly concavo-convex shells, mobility via pectenoid-like propulsion was suggested by Rudwick (1970, p. 91; Alexander, 1977, 2001). This adaptation was likely to be successful only with immature orthotetides, characterised by a generally reclining lifestyle (e.g., Walker and Parker, 1976; Thayer, 1983). Summarising the relative abundance pattern of the brachiopod assemblages in the trench A section (Fig. 4A; see SM 1–3), the presence of two distinct, substrate-related sets of species is evident:

1. The five most frequent species are also the most widely distributed in the samples studied, i.e., absent at the most in one sampled level (Figs 5, 7), and thought therefore to be the most eurytopic, 'incumbent' generalists. However, a correlation analysis (SM 3) indicates that they constitute two synecological subgroups with somewhat different, temporal distributions (see also Biernat, 1966): (1) mud floaters (*Poloniproductus varians*, associated with *Devonaria zeuschneri* and *Parastrophonella anaglypha*, accompanied by rarer *Dagnachonetes supragibbosus* and *Desquamatia subzonata*, the latter possessing short fringes and most likely inactive pedicle in maturity; see Biernat, 1964), and (2) pedicle-attached inhabitants of more stable, bioclast-bearing and skeletal patches. The second set includes *Eleutherokomma diluvianoides*, moderately paired with non-fringed *A*. (*P.*) *depressa*, showing an obsolete foramen in mature specimens (Biernat, 1964, p. 297). The relatively rare orthide *Phragmophora schnuri* and reticulariid spiriferides, living on the edge of tolerance (see Tab. 1), occur here as well. As shown statistically by Bush and Brame (2010), a gradient in brachiopod community composition was controlled primarily by substrate (grain size) and disturbance intensity/frequency within the benthic regimes. Therefore, most of the time, the negligible differentiation of the bottom sediment properties controlled the proportion of the both groups, i.e. the low-diversity *Poloniproductus* assemblage (Simpson Diversity Index, SDI, typically below 0.5) and more diverse biota with *Eleutherokomma* (SDI = 0.7–0.74). Notably also, the two leading, competing species exhibit only a very weak negative relation (r_s = -0.23). The synecological overlap can be seen in sampled level XIV/7/1 (Figs 4A, 6, 7). In a statistical context (see SM 3), the Spearman correlation coefficients r_s are low, however, mostly between 0.4 and 0.6 (p<0.2), and only slightly higher for the Pearson correlation coefficient (r_s between 0.45 and 0.79, p<0.09). The data indicate evolving heterogeneity of the brachiopod habitats. In fact, in the light of the correlation indices (see SM 2), only two samples provided a clearly distinct brachiopod fauna in this community continuum: XIV/1 (= *Eleutherokomma* assemblage) and XIV/5 (= *Aulacella-Costisorthis* assemblage).
2. As highlighted above, the main innovation, disrupting the *Poloniproductus-Eleutherokomma* supremacy, was the brachiopod colonization of bryozoan bioconstructions, recorded in layers XIV/5–7. The 'invasive' newcomers occupied a variety of overall higher-energy, episodically current-swept and firmed, skeletal/bioclastic substrates, as shown by increased disarticulation and mortality indices (Fig. 4B). The assemblage, characterised by mostly pedunculate species with orthides in the main role, was formed by a relatively coherent pair of small-sized species *Aulacella prisca* and *Costisorthis canalicula* (r_s = 0.84), also with large-sized *Schizophoria* (r_s = 0.87 and 0.9, respectively) and uncinuloid rhynchonellides (r_s = 0.87 and 0.84, respectively). Some distributional affinity (r_s = 0.65) with *A. prisca* is shown also by the most generalist members of the first group, *Desquamatia subzonata* and *Devonaria zeuschneri*, possibly successful also in protected, more muddy 'inter-reefal' places.

The final dominator, *Xystostrophia*, is distinguished by lacking meaningful co-occurrences with other species (the highest $r_s = 0.5$ with *Devonaria zeuschneri*). Similar individuality also characterises *Eleutherokomma*, the subordinate strophomenide *Gibbodouvillina interstrialis,* as well the weakly paired spiriferide *Crurispina* and spiriferinide *Cyrtina*, displaying some links only with *Desquamatia subzonata* ($r_s = 0.51$–0.55). *Cyrtina* is named by Biernat (1966, p. 23) as being distinguished by frequent asymmetry of the shells and distortion of the ventral area, due to dense, gregarious growth in variable bottom currents.

Temporal changes of diversity

The most characteristic feature of the temporal changes in diversity (Fig. 5C) is its peak during patchy development of bryozoan bioconstructions in the middle interval of the section, manifested in the highest Simpson indices in sample levels between XIV/5 and XIV/7/1 (SDI = 0.74 to 0.81). In particular, layer XIV/5 provided 24 taxa of 27, collected from the trench A section. As stressed above, a variety of infrequent and sporadic, mostly small-sized, attached species is limited to this interval, as is perfectly shown by three species of athyridides, but also by the atrypides *Peratos* and *Isospinatrypa*, and the orthide *Biernatium*. Some of them display high, juvenile mortality (see above; Tab. 1), and *Bifida* is more frequent in the eutrophic habitats, recorded in the Givetian part of the Skały Fm at Miłoszów (Halamski *et al*., 2022). In addition, Biernat (1966, p. 125) noted a dwarfed character of the distinctive athyridide and *Crurispina–Cyrtina* pair from the shaly facies.

The biostrome-related habitats, alluring for a large number of species, are evidenced also in the distribution and diversity of other sessile and vagile, benthic groups, such as non-pelmatozoan echinoderms, but only partly by ostracodes (Czaplikowska, 1990; SM 4). The common crustaceans were more diverse in crinoid-rich sample XIV/1a/b (SID = 0.78) than in bryozoan-bearing levels (maximum in XIV/6 – SID = 0.69). In fact, the highest diversity indices of the three benthos groups are similar: 0.82 for brachiopods, 0.78 for ostracods and 0.82 for crinoids (in terms of generic, columnal parataxonomy, Nowak, 1992, tab. 8). However, the data might have increased taphonomically, following the storm-related winnowing by waves and currents (see below), when the resulting bioclastic concentrations were populated by newcoming species (Finnegan and Droser, 2008).

The brachiopod fauna of the Dobruchna Mbr is particularly diversified on a regional scale. Three younger brachiopod faunas (upper part of the Skały Fm, Lower to lower Middle Givetian) at Miłoszów are composed of 21, 22, and 28 species, respectively (Baliński and Halamski, in press). The *Bifida*-dominated fauna from Błonia Sierżawskie near Świętomarz (probably Nieczulice Beds, upper Middle Givetian) is composed of 33 species (Halamski, 2004b; see also Halamski and Segit, 2006). Similar, diverse benthos re-appeared in the Skały-Grzegorzowice succession in the almost unstudied, coeval fauna from the lower Nieczulice Beds at the locality Włochy-studnia (Halamski and Baliński, 2018), also characterised by an abundance of *Bifida*. The Dobruchna Member, with 44 brachiopod species (Halamski and Zapalski, 2006), contains undoubtedly the richest Devonian brachiopod fauna in the Holy Cross Mountains.

Brachiopodetum at Skały at regional and local scale

The ecological distribution of Middle Devonian brachiopods was studied on a regional scale in the Eifel by Struve (1992). These results most likely are largely applicable to the Holy Cross Mountains, given the same age of the strata and general similarity of brachiopod faunas (Halamski, 2008). The 'brachiopod meadows' or *brachiopodeta*, brachiopod-dominated, moderately deep ecosystems (lower BA3 to BA4 *sensu* Boucot, 1975) are the richest communities in terms of brachiopod diversity (44 species at Skały, Halamski and Zapalski, 2006; over 60 species at Gees, Eifel region, Struve, 1982).

The strength of the present study is the bed-by-bed analysis, showing that a brachiopodetum, considered on a regional scale, can be decomposed into several smaller-scale associations on a local scale. This is an especially important conclusion, as brachiopodeta were ecosystems with no equivalent in the present biosphere, owing to the post-Palaeozoic decline of brachiopods and their large-scale replacement by bivalves (Gould and Calloway, 1980, and references therein).

Another point to be noted is that at Skały, the brachiopods that lived in a brachiopodetum are preserved probably without any admixture of representatives of the same phylum from different palaeoecological settings. This is in strong contrast to the situation in outcrop M1-IIa, at Miłoszów, belonging to a higher (Givetian) part of the Skały Formation, where the brachiopod assemblage consists of species from several adjacent fossil biocoenoses near a coral thicket (at least cespitetum and brachiopodetum in the Struve's 1963 model, see Halamski *et al*., 2022, especially fig. 27). The brachiopod species in common at the Skały and Miłoszów brachiopodeta include above all common and long-ranging taxa, like *Leptagonia analogaeformis*, *Aulacella prisca*, and *Schizophoria schnuri*; otherwise, the taxonomic compositions at Skały-XIV and at M1-IIa are rather different (the Jaccard similarity coefficient between the Dobruchna Mbr fauna and the total Miłoszów fauna is 0.13–0.23, a relatively low value; Baliński and Halamski, in press).

Storm-controlled ecological replacement vs. ecological succession

As shown in Figure 5B, C, the brachiopod diversity (and assemblage succession) is strikingly correlated with the juvenile mortality and disarticulation indices in the brachiopod shale succession, documented in the trench A section. Therefore, the depositional evolution is interpreted in general terms as a record of episodic sedimentation, driven by recurring, heavy storm activity, at least partly controlled by sedimentation of fluid muds from suspension clouds below the storm-wave base (distal tempestites; see e.g., Walker and Parker, 1976; Brett *et al*., 1986; Walker and Diehl, 1986; Miller *et al*., 1988; McFarland *et al*., 1999; Finnegan and Droser, 2008; Pérez-López and Pérez-Valera, 2012). The higher-energy events resulted in fostering obrution deposition of mud blankets (see review in Horodyski *et al*., 2019). These event episodes were superimposed on the background regime, driven mainly by constant siliciclastic and carbonate mud shedding by waves and tides within the low-energy, mud-dominated ramp slope (Flügel, 2010, p. 718). The interaction of the processes has been taphonomically recorded in the preserved, original distribution of brachiopod shells, owing to the overall negligible reworking of bottom sediments.

The distal ramp belt was characterised by a soft-bottom, unstable, benthic environment, inhabited primarily by pioneer productides (cycle stages A in Fig. 8). The cyclical, storm-controlled, episodic sedimentation and the related changes in substrate consistency, due to the varying depositional rate, stimulated the selective colonization by benthos (see summary in Walker and Diehl, 1986). During the course of reduced mudflows, the concentrated brachiopod shells and valve pavements on the muddy substrate created favourable ‘benthic islands’ for progressive benthos colonization. Gradually, there was an increasing diversification of the brachiopod fauna and associated array of benthic groups, such as trilobites, molluscs, echinoderms, calcareous sponges and foraminiferans (Czaplikowska, 1990). The successive change is finalised in the bryozoan-rich, middle interval of the upper Dobruchna Mbr (XIV/5 to at least XIV/7/1) and the bryozoan limestone layer in the basal set XV. The diverse, massive, lamellate and erect, branched zoaria contributed not only to mud stabilization, but also had sediment-baffling and sediment-filling functions, resulting in great microhabitat complexity (see the coeval Eifel case in Ernst *et al*., 2011, and also the Givetian Moroccan example in Ernst and Königshof, 2008). A similar role of corals, mostly solitary rugosans (see Różkowska, 1956;

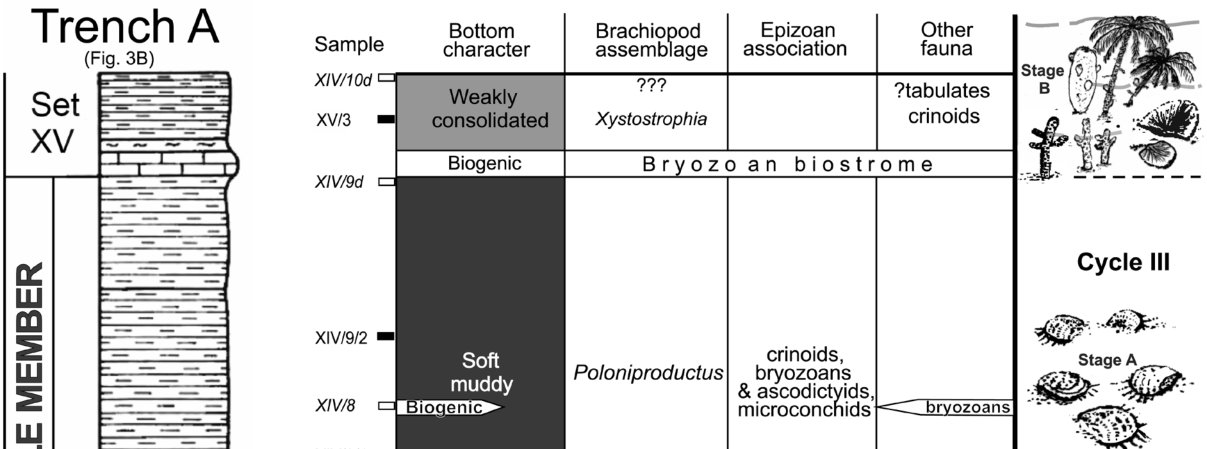

Fig. 8. Evolution of the environment and the resulting benthic responses, recorded in the trench A succession (partly based on fig. 9 in Czaplikowska, 1990), focused on the schematically figured pioneer colonization of the muddy bottom by brachiopods (stage A), followed by current-affected, diverse bryozoan/crinoid biota (stage B in cyclic ecological replacements I–III; see Figures 5 and 7 for brachiopod successional dynamics and diversity indices; epizoan associations after Klejszta, 1998). Fossil reconstructions (drawings by W. Bardziński) based on Schumann (1967, fig. 3), Thayer (1974, fig. 18) and Racki (1993, fig. 29).

Pajchlowa, 1957, p. 212), was rather subordinate. From set XV, the tabulate-rich horizons of frondescent and encrusting coenitids and platy and mushroom-shaped alveolitids were described as a mesophotic variety of coral reef by Zapalski *et al.* (2017). Coenitids were also noted in the brachiopod shales by Stasińska (1958), possibly associated with the bryozoan bioconstructions. In facies terms, the upward change from brachiopod shales to coral-rich marls and limestones indicates a shallowing tendency, in line with Struve's classic (1963) model.

This orderly succession indicates the periodic growth of bryozoan-dominated bioconstructions and accompanying crinoid clusters (cycle stages B in Fig. 8), which were destroyed by heavy storms and rapidly buried finally in storm-generated, muddy, downslope sediment. Some coarse-grained debris horizons may record even sporadic tsunami events (Massari *et al.*, 2009; see Pisarzowska *et al.*, 2022). Thus, an additional bottom hardening may be related to the destructive activity of storm-related currents that enlarged the mosaic pattern of co-existing benthic niches. The abrupt, temporal and spatial changes record passages from less or more consolidated muds to variable, bioclastic, mostly crinoid/shelly, sandy pavements, to hard, skeletal covers and knolls. These passages are accompanied by transitions from marly claystones to marl varieties.

The recurring benthic settlement of the seabed was interrupted twice in the trench A succession, which indicated the presence of three sedimentary/ecological cycles (the oldest one in its final stage B only; Fig. 8). This cyclicity was first recognized in a mostly differing sample set by Czaplikowska (1990; see Fig. 4C), but the pattern still needs verification by more high-resolution sampling, especially crucial for the level-bottom phase of cycle III in the light of Czaplikowska's (1990) data on high bryozoan frequency.

Orderly change through time from an impoverished level-bottom assemblage to a diverse biota, related to the mass growth of crinoids, bryozoans and corals, is usually attributed to the pioneer phase of reef development (arrested succession of Copper, 1988; see also McCall and Tevesz, 1983 and Walker and Diehl, 1986). As discussed by Copper (1988), Brenchley and Harper (1998, pp. 253–256) and McFarland *et al.* (1999), among others, the ecological (autogenic) succession is the pioneer-to-climax process within an essentially unchanging habitat, as opposed to ecological replacement (allogenic succession), driven by abiotic factors in response to changing abiotic factors. It is generally difficult to conclude whether the sequential community changes reflect a real ecological succession or merely living-dead interactions ('taphonomic feedback'; Kidwell and Jablonski, 1983), i.e. a subsequent colonization of dead pioneer populations that had merely formed a suitable, skeletal substrate for benthic expansion. In the case of the Dobruchna Mbr succession, a key role of storm-related depositional effects is undoubted and paired with common, taphonomic feedbacks. On the other hand, initial colonization and the stabilization of the soupy muds is thought by Copper (1988) as initiation of the pioneer reef stage that was partly driven by growing competition among so numerous, benthic groups for space, due to the limited availability of substrates (as indicated by the high mortality of juvenile brachiopods; Fig. 5B). However, this crowded-nests effect was also noticeable among some pioneering brachiopods, because Biernat (1966, p. 22) observed shell asymmetry and other growth disturbances in many incumbent species, including *Poloniproductus*.

CONCLUSIONS AND FINAL REMARKS

1. The top-Eifelian brachiopod shales of the upper portion of the Dobruchna Member of the Skały Formation, deposited during the carbonate decline in the Kačák Crisis, contain a diverse brachiopod fauna (27 taxa), dominated by productides (*Poloniproductus* and *Devonaria*), atrypides and spiriferides (*Eleutherokomma*). Orthides, and particularly rhynchonellides played a subordinate role; terebratulides are absent. Only one species, *Poloniproductus varians*, occurs in the entire section, with frequencies above 5% in all samples. This generalist species was the best adapted to the mostly unstable, episodically and quickly deposited, muddy sediments.
2. The brachiopod-dominated biota lived in moderately deep (45–60 m), fairly well oxygenated and oligotrophic outer-ramp habitats, clearly optimal for the Devonian shelly benthos. Muddy substrates, inhabited initially by a low-diversity *Poloniproductus* assemblage, evolved as a result of consolidation of progressively bioclast-enriched sediments and bryozoan bioconstruction growth into diverse sessile and vagile benthic biota. The ecological replacement is recorded in the domination of more specialised species, like *Eleutherokomma diluvianoides* and, finally, by an extremely diverse community, dominated by orthides (*Aulacella*, *Costisorthis*) in the uppermost part of the Dobruchna Mbr, succeeded eventually by the *Xystostrophia* assemblage in the overlying coral-rich set XV of the Skały Fm. Thus, a brachiopodetum (brachiopod meadow, moderately deep, brachiopod-dominated biota; Struve, 1963), considered on a regional scale, can be decomposed into several smaller-scale associations on a local scale.
3. A similar differentiation between level-bottom and pioneer reef brachiopod assemblages is not known from the younger Devonian strata of the Kielce Region, even if similar productide-dominated, mud-dwelling faunas are reported, e.g., the Late Givetian *Praewaagenoconcha*(?) *sobolevi* association of Racki (1993; see also Early Frasnian faunas in Racki *et al.*, 1993 and Baliński *et al.*, 2016). This dissimilarity seems to be related to a negligible role of bryozoans in the carbonate platform habitats, replaced by stromatoporoid-coral communities (Racki, 1993; Morozova *et al.*, 2002). The high-diversity productide biofacies was replaced in the new setting by the low-diversity, hypoxia-tolerant rhynchonellide biofacies (Racki *et al.*, 1993). Thus, this type of brachiopod succession is a notable character of the bryozoan-populated gentle slope of the Middle Devonian carbonate ramp only in the Łysogóry Region. A similar association was frequent, especially in Ordovician epeiric seas (e.g., Walker and Parker, 1976; Walker and Diehl, 1986), but continued into Cenozoic carbonate ramps (see the cool-water Pleistocene case in the Central Mediterranean, in Pedley and Grasso, 2002, fig. 3).

4. The ecological replacement, with characters of ecological succession in the final step, is recognised for the first time for the Skały Fm. The depositional/ecological cyclicity in the Central Mediterranean was evidently forced by the progressive consolidation of the bottom sediments, from largely unstable muds to a mosaic of less or more consolidated muds to firm bioclast-rich and finally, to hard, skeletal substrates (Fig. 8). Three episodes of variously reduced rates of deposition, recorded in the more diverse associated benthos, pioneer bryozoan/coral reef growth and abundance of epibionts, alternate with times of destructive storm activity and rapid deposition of fluid muds from suspension clouds in the distal ramp habitats. The storm-influenced development of benthic biota confirms the conclusions of Miller *et al*. (1988) and McFarland *et al.* (1999) that allogenic, taphonomic feedback was the main mode of small-scale, substrate-controlled community replacement in Palaeozoic muddy, epeiric seas.

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