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An explanation for low endemism of Triassic crinoids from the epicontinental Germanic Basin, Poland

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A summary of known crinoid taxa in the Polish part of the Triassic Germanic Basin, including their presence elsewhere, is documented. At present, 13 taxa and 3 ecophenotypes of crinoids have been recorded from that area, only one of them being endemic. In the Lower Muschelkalk and lower part of the Middle Muschelkalk, taxa widespread both in the Tethys and Germanic Basin, or Tethyan taxa, dominate. In the Upper Muschelkalk crinoids are very rare in Poland, being represented by *Encrinus liliiformis* and *Holocrinus* sp. Many of the species occurring in the central part of the Germanic Basin in the Upper Muschelkalk have not been recorded in the eastern part of the basin. The degree of endemism of the crinoid fauna in the Muschelkalk is markedly lower than the degree of endemism of the rest of the benthonic macrofauna. This probably resulted from huge number of crinoids forming "crinoid gardens" that produced large number of larvae, increasing the chances of successful geographical expansion of crinoids.

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INTRODUCTION

Almost 160 years of research on the occurrence of Triassic crinoids in the Polish eastern part of the Germanic Basin has revealed 13 taxa and 3 ecophenotypes (Table 1, Fig. 1). Almost all the species are known from Upper Silesia (except for *Holocrinus* sp.), where the crinoid research has long been undertaken and from where the richest material comes from, including almost all of the complete specimens collected so far.

9 taxa, represented by isolated skeletal elements, occur in the Holy Cross Mountains (Salamon, 2003), and 5 taxa in the North-Sudetic Basin (Głuchowski and Salamon, 2005; Table 1). However, in the latter area the upper part of the Lower Muschelkalk, as well as the Middle and Upper Muschelkalk is not exposed. Some undetermined crinoidal fragments were recorded in boreholes in the Fore-Sudetic Monocline and Podlasie area (Senkowiczowa and Kotański, 1979). Crinoids in the Tatra Mountains are rare. 120 calyces and crowns assigned to *Dadocrinus grundeyi* have been found in a single thin layer in the Middle Triassic deposits of the Zawrat Kasprowy (Lefeld, 1958). Apart of this, in many sites of the Tatra Mountains, there are crinoid limestones or dolomites which, however, contain only isolated, mostly undeterminable skeletal fragments. This article analyses the degree of endemism of crinoidal assemblages from Southern Poland in comparison with the endemism of other benthonic macrofauna.

THE DEGREE OF ENDEMISM OF THE MUSCHELKALK CRINOID FAUNA

Published work suggests a considerable proportion of endemic taxa (as endemic fauna we state species known only from Upper Silesia, the Holy Cross Mountains and the North-Sudetic Basin) among the crinoid fauna of the Polish Muschelkalk (Table 1; see also Fig. 1). According to Assmann (1937), 5 out of 10 taxa mentioned by him from Upper Silesia area were endemic. Later investigations, however, showed that 3 of them (*Holocrinus dubius, Silesiacrinus silesiacus* and *Encrinus spinosus*) occur in the Tethys, one species (*Encrinus robustus*) is known from the entire Germanic Basin and the last one (*Dadocrinus kunischi*) probably is an ecophenotype (*cf.* Głuchowski, 1986; Hagdorn and Głuchowski, 1993; Hagdorn *et al.*, 1997). Therefore, at present, none of the 5 endemic spe-

Table 1

The endemism of crinoids from Polish part of the Germanic Basin; modern data according to Hagdorn and Głuchowski (1993), Hagdorn (1995), Niedźwiedzki (2002*b*), Salamon (2003), Salamon *et al.* (2003) and Głuchowski and Salamon (2005)

Crinoid species	Palaeogeographic distribution of Silesian crinoids (Assmann, 1937)	Palaeogeographic distribution of Silesian crinoids (modern data)	Other locations of described crinoids in Poland
Dadocrinus gracilis	Tethyan	both in the Tethys and the Germanic Basin	Holy Cross Mts?; Lower Silesia?
Dadocrinus kunischi	endemic	Ecophenotypes (for distribution see *D. gracilis*)	–
Dadocrinus grundeyi	unknown from Silesia	Ecophenotypes (for distribution see *D. gracilis*)	–
Dadocrinus sp. nov.	unknown from Silesia	Ecophenotypes ?(for distribution see *D. gracilis*)	–
Holocrinus acutangulus	unknown from Silesia	both in the Tethys and the Germanic Basin	Holy Cross Mts.; Lower Silesia
Holocrinus dubius	endemic	both in the Tethys and the Germanic Basin	Holy Cross Mts.; Lower Silesia
Holocrinus meyeri	unknown from Silesia	endemic	Holy Cross Mts.
Holocrinus sp.	no data	?	Holy Cross Mts.
Encrinus radiatus	unknown from Silesia	Tethyan	Holy Cross Mts.; Lower Silesia
Silesiacrinus silesiacus	endemic	Tethyan	Holy Cross Mts.
Encrinus aculeatus	Tethyan	Tethyan	–
Encrinus spinosus	endemic	Tethyan	–
Encrinus robustus	endemic ?	Germanic	–
Carnallicrinus carnalli	Germanic	both in the Tethys and the Germanic Basin	Holy Cross Mts.
Encrinus liliiformis	unknown from Silesia	both in the Tethys and the Germanic Basin	Holy Cross Mts.
E. brahli	Tethyan	both in the Tethys and the Germanic Basin	–
„*Encrinus*” cf. *granulosus*	Tethyan	no data	–

cies *sensu* Assmann (1937) can be considered as endemic. Moreover, *Carnallicrinus carnalli* (formerly *Chelocrinus carnalli*; see discussion in Hagdorn, 2004), the species considered by Assmann (1937) as a Germanic species (i.e. occurring in the whole Germanic Basin), also occurs in the Tethys. Additionally, Hagdorn (1985), Hagdorn and Głuchowski (1993), Hagdorn *et al.* (1996), Salamon (2003), Salamon *et al.* (2003) and Salamon (2005) proved the occurrence in the Polish part of the Germanic Basin of 5 additional crinoid taxa, one of which is endemic (*Holocrinus meyeri*; Table 1). According to Hagdorn and Głuchowski (1993) and Hagdorn (1996), *Holocrinus meyeri* occurs only in Upper Silesia. This species is now known also from the Holy Cross Mountains (Salamon, 2003). However, the geographical range of *H. meyeri* is quite uncertain because this species has been established recently on the basis of isolated columnals only (Hagdorn and Głuchowski, 1993). Therefore, the lack of any data about this taxon from the Tethys may result from insufficient recognition of Tethyan material. Recently, Salamon (2005) has described a crinoid of uncertain palaeogeographic status (*Holocrinus* sp., known only from the Holy Cross Mountains; Table 1, Fig. 1), probably an immigrant from the Tethys. Additionally, the species *Dadocrinus grundeyi* and *Dadocrinus* sp. nov. described by Głuchowski (1986) and Hagdorn and Głuchowski (1993) from Upper Silesia, are now considered as ecophenotypes (e.g. Hagdorn, 1996). This was also shown by morphological analysis of calyces of *D. gracilis, D. kunischi* and *D. grundeyi* (Salamon and Niedźwiedzki, 2004). It is worth noting that all crinoid taxa known from the North-Sudetic Basin and the Holy Cross Mountains are Tethyan or occur both in the Tethys and the Germanic Basin (with the exception of *H. meyeri*).

13 species from the Polish part of the Germanic Basin are known, one of them considered to be endemic (see also Figs. 2–5). To compare the degree of endemism of crinoids with the general macroinvertebrate endemism of the Muschelkalk of Upper Silesia, we have analysed published data from Upper Silesia (Assmann, 1937, 1944; Hagdorn and Głuchowski, 1993). The benthic macrofauna of the North-Sudetic Basin and especially of the Holy Cross Mountains remains relatively poorly known, making an analysis of endemism for these areas difficult. The results are shown in Table 2.

DISCUSSION

The degree of endemism in benthic and nektobenthic macroinvertebrate faunas from Upper Silesia (Table 2) is very high, especially as regards fossils from organodetrital and crinoidal limestones (almost all endemic taxa are known from such deposits; see e.g. Assmann, 1937; Bodzioch, 1994; Niedźwiedzki, 1998) assigned to the Lower Gogolin Beds, the Górażdże and Karchowice formations and the *Diplopora* Beds.

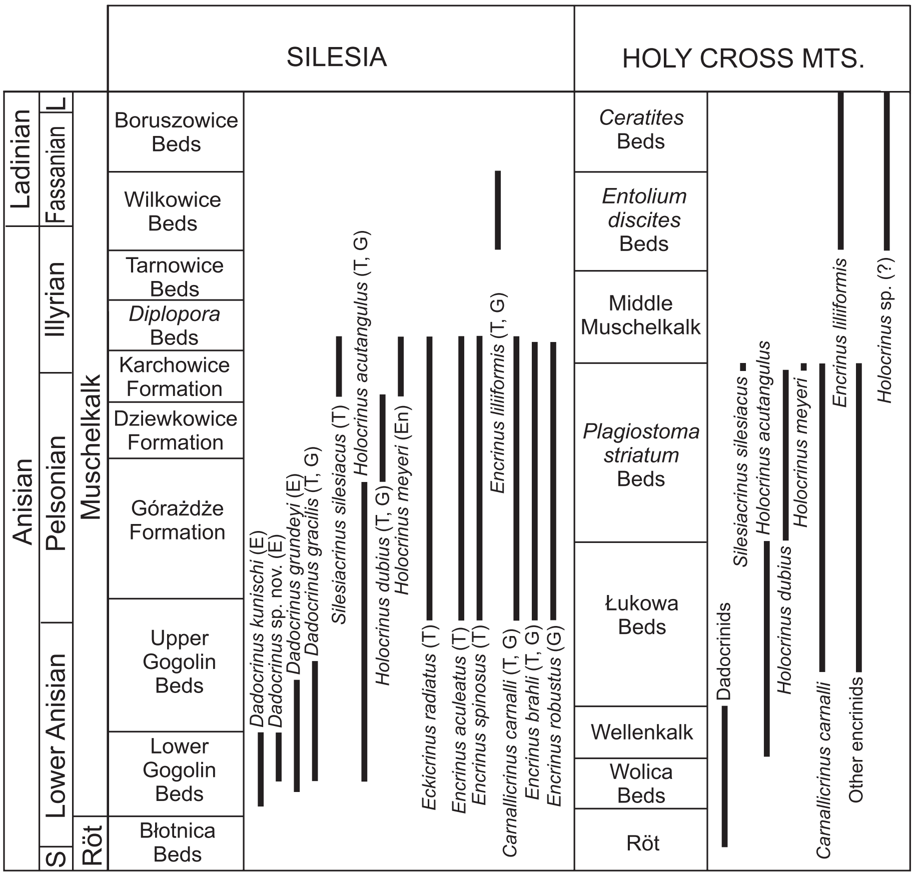

Fig. 1. Stratigraphic ranges of cosmopolitan and endemic crinoids in Holy Cross Mts. and Silesia regions

S — Scythian, L — Longobardian; E — ecophenotypes, En — endemic, T — known from Tethys, G — known from Germanic Basin (chronostratigraphy according to Trammer, 1975; Trammer and Zawidzka, 1976; lithostratigraphy according to Assmann, 1944; Senkowiczowa, 1957 and formalized by Bodzioch, 1997; Niedźwiedzki, 2000); stratigraphic distribution of crinoids partly taken from Hagdorn and Głuchowski (1993) and Salamon (2003, 2005)

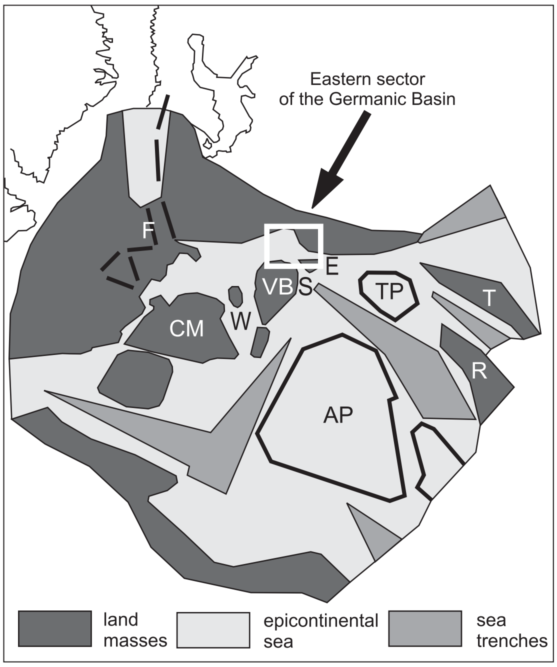

Fig. 2. Palaeogeographic position of the eastern part of the Germanic Basin (according to Szulc, 2000; simplified)

F — Fennoscandia, VB — Vindelician-Bohemian Massif, CM — Central Massif, TP — Tisia Plate, AP — Adria Plate, R — Rodopes, T — Transcaucasus, E — East-Carpathian Gate, S — Silesian-Moravian Gate, W — Western Gate

A typical feature of these strata is that they originated within barrier belts of shoals in which sedimentation of calcarenites prevailed (Górażdże and Karchowice formations, and in part the *Diplopora* Beds; for sedimentological and palaeoenvironmental data see Bodzioch, 1989; Myszkowska, 1992; Niedźwiedzki, 1998, 2002*a*), or that they represent similar sediments deposited in the coastal zone (Lower Gogolin Beds). Individual belts of shoals were separated by wide areas of deeper-water settings characterized by soft, muddy bottoms, with common anoxia and poor benthic faunas. This kind of substrate is generally unsuited for the majority of benthic faunas. Similarly differentiated bottom morphologing and depositional regimes have been observed in Germany, although a lime mud facies with poor faunas is more widely distributed in this area (see e.g. Lukas, 1993). Therefore, the migration of benthic or nektobenthic faunas which inhabited such barrier belts was strongly impeded, which in turn favoured the origination of endemic species.

A significant decrease in endemism during deposition of the Dziewkowice Formation is related to deterioration of ecological conditions at that time, caused by maximum deepening of the basin in Silesia and frequent oxygen deficiencies (see e.g. Dżułyński and Kubicz, 1975; Kaim, 1997; Niedźwiedzki, 1998). This caused the retreat of many taxa and the disappearance of the majority of endemic forms. A small degree of endemism during the deposition of the Upper Gogolin Beds and Wilkowice Beds, on the other hand, may have resulted from a minor transgressive peak during their deposition. The absence of endemic taxa in the Tarnowice and Boruszowice

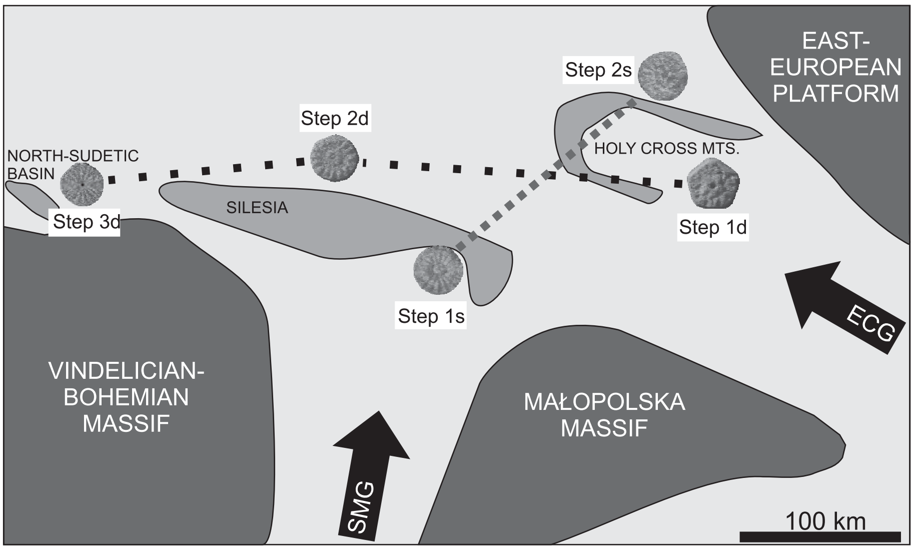

Fig. 3. Migration/immigration routes of dadocrinids and silesiacrinids from the Tethys into and within the Germanic Basin

SMG — Silesian-Moravian Gate, ECG — East-Carpathian Gate (the map according to Hagdorn and Głuchowski, 1993; modified); Step 1d — dadocrinid immigration from Tethys into the Germanic Basin through the East-Carpathian Gate (early Anisian); Step 2d — intra-basinal dadocrinid migration from the Holy Cross Mountains (early Anisian); Step 3d — intra-basinal dadocrinid migration from Upper Silesia (early Anisian); Step 1s — *S. silesiacus* immigration from Tethys through the SMG (latest Pelsonian); Step 2s — *S. silesiacus* migration from Silesia (only northern part of the area; latest Pelsonian)

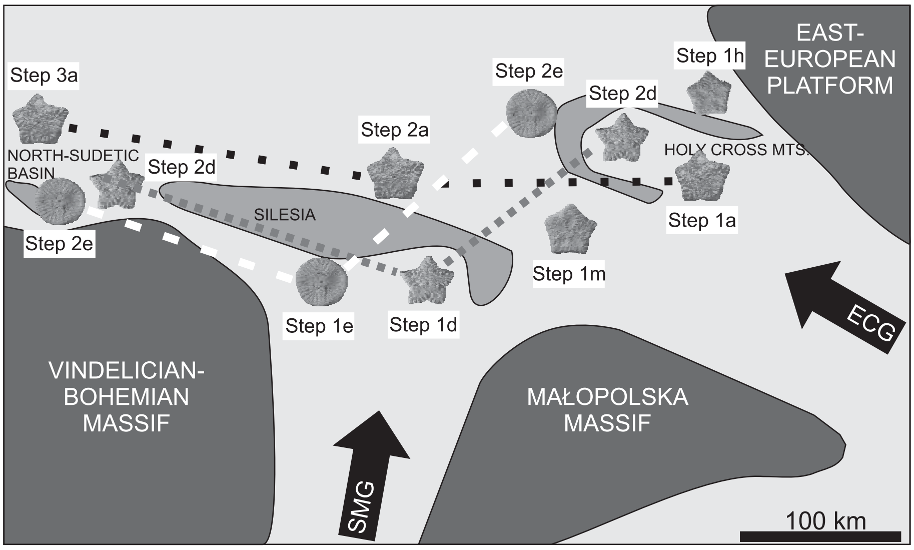

Fig. 4. Migration/immigration routes of holocrinids from the Tethys into and within the Germanic Basin

Step 1a — *H. acutangulus* immigration from Tethys into the Germanic Basin through the ECG (lower Anisian); Step 2a — intra-basinal migration of *H. acutangulus* from the Holy Cross Mts. (early Anisian); Step 3a: intra-basinal migration of *H. acutangulus* from Silesia (early Anisian); Step 1d — *H. dubius* immigration from Tethys through the SMG (Pelsonian); Step 2d — intra-basinal migration of *H. dubius* from Upper Silesia (Pelsonian); Step 1m — population of *H. meyeri*, first occurrence in Upper Silesia and slightly later in the Holy Cross Mts. (latest Pelsonian); Step 1e — *E. radiatus* immigration from Tethys through the SMG (Pelsonian); Step 2e — intra-basinal migration of *E. radiatus* from Upper Silesia (Pelsonian); Step 1h — population of *Holocrinus* sp. only in the Holy Cross Mts. (latest Illyrian-earliest Longobardian); other explanations as on Figure 3

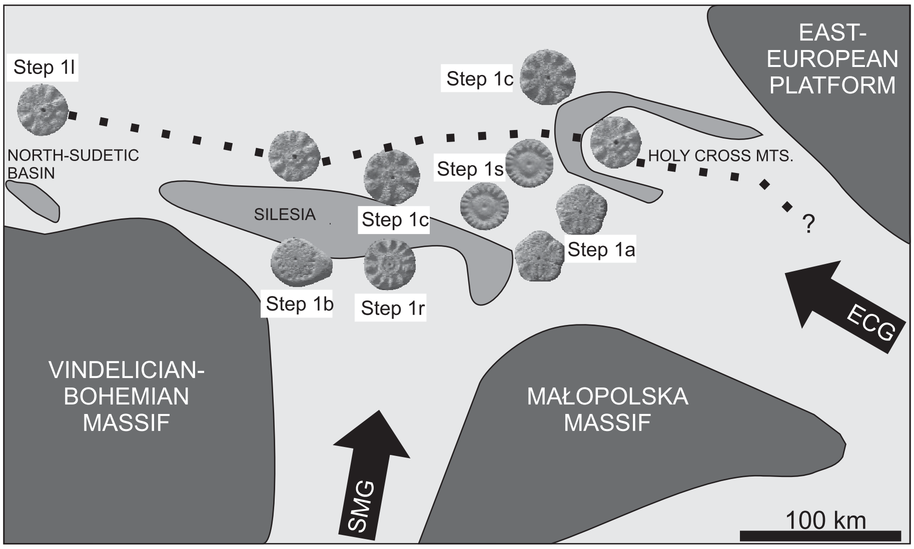

Fig. 5. Migration/immigration routes of encrinids from the Tethys into and within the Germanic Basin

Step 1a — occurrence of *E. aculeatus* in Upper Silesia, immigration route unknown (Pelsonian); Step 1c — occurrence of *C. carnalli* in the Holy Cross Mts. and slightly later in Upper Silesia, migration route unknown (early Anisian in the Holy Cross Mts. and Pelsonian in Upper Silesia); Step 1s — occurrence of *E. spinosus* in Upper Silesia, immigration route unknown (Pelsonian); Step 1r — occurrence of *E. robustus* in Upper Silesia; Step 1b — occurrence of *E. brahli* in Upper Silesia, immigration route unknown (Pelsonian); Step 1l — occurrence of *E. liliiformis* in the Sudetic Monocline, Silesia and the Holy Cross Mts., migration/immigration probably from west, but ECG cannot be excluded (latest Illyrian); other explanations as on Figure 3

Table 2

Comparision of the degree of endemism of the Silesian crinoids and other macrofauna (with exception of vertebrates); data about endemism of the macrofauna after Hagdorn and Głuchowski (1993)

Lithostratigraphy	Crinoid species occurring in the Tethys and Silesia	Crinoid species occurring both in the Tethys and the Germanic Basin	Crinoid species occurring in all areas of the Germanic Basin	Silesian endemic crinoid species	Degree of endemicity of the Silesian macrofauna
Boruszowice Beds	0	0	0	0	0%
Wilkowice Beds	0	1	0	0	5%
Tarnowice Beds	0	0	0	0	0%
Diplopora Beds	3	2	1	1	96%
Karchowice Fm.	3	3	1	1	55%
Dziewkowice Fm.	2	4	1	0	20%
Górażdże Fm.	2	4	1	0	64%
Upper Gogolin Beds	3	3	1	0	24%
Lower Gogolin Beds	0	2	0	0	74%

beds may be linked with rapid deterioration of habitat conditions (anoxia and/or salinity increase), which triggered a notable decrease in biodiversity. Thus, most faunal groups were unable to develop endemic forms. The scarcity of endemic crinoid species in Poland (only one species) illustrates the wide distribution of Lower Muschelkalk and lower Middle Muschelkalk crinoid assemblages, without any tendency towards endemism. A comparison of crinoids with other macroinvertebrates shows (Table 2) that crinoids were much less endemic than other benthic groups which were characterized by considerable provinciality and endemism. Low crinoid endemism has so far been observed in the Tethys and Panthalassa (e.g. Kristan-Tollmann, 1988*a*, *b*). Our analysis shows that this phenomenon also occurred in the eastern part of the Germanic Basin. Nevertheless, in the Tethys Basin, in contrast to Upper Silesia, the predominance of cosmopolitan taxa is seen not only among crinoids, but also in numerous other sessile and vagile benthic groups, which suggests a lack of real barriers that would have impeded migration.

What was the real reason for low endemism in Triassic crinoids from Southern Poland in comparison to other, co-occurring macrofaunal groups? Among the causes of endemism are ecological barriers isolating some populations of a given species and hindering its broad expansion. A short-lived mobile larval ontogenetic stage is such a factor. Many publications (e.g. Steele-Petrović, 1979; Smith, 1984) discussing influences on the expansion rate of bivalves, brachiopods and crinoids. Crinoids are stenotypic i.e. there are numerous factors limiting their distribution. Their low larval mobility is important, as the larvae of living Articulate crinoids are nonplanktotrophic and thus cannot migrate extensively (Jablonski and Lutz, 1983). The free-swimming larvae of modern crinoids are able to survive between 5 hours and 5 days (Breimer, 1978). On the other hand, the free-swimming larval stage of modern echinoids lasts approximately for one or two months (Smith, 1984) and larvae of bivalves are able to survive about five weeks (Muus, 1973, *fide* Steele-Petrović, 1979). Crinoid larvae are less mobile than larvae of other benthic groups. Therefore, it is probable that the main factor for the rapid migration of Triassic crinoids in the Germanic Basin was their mass occurrence as widespread "crinoid gardens", well documented in thick beds of crinoidal limestones. Recent "crinoid gardens" are characterized by high densities (according to Klikushin, 1992 about 400 individuals per square metre). Such a large number of individuals produces a huge amount of larvae.

Migratory success was dependent on crinoid numbers, which explains why in the Polish sector of the Germanic Basin during the latest Illyrian-earliest Longobardian (Upper Muschelkalk) only the most numerous taxa from the westerly portions of the basin were present. In the western and central part of the Germanic Basin, *Encrinus lilliformis* was very common and thus formed thick layers of so-called "Trochitenkalk". On the other hand, other taxa (i.e. *Chelocrinus schlotheimi, Encrinus greppini, Holocrinus doreckae*) were less common, which explains why only a few individuals migrated into the Polish area from the west, and why the commonest species (*Encrinus lilliformis*) found in the centre of the basin, is here represented by sporadic isolated fragments only. The same phenomenon occurs with ceratitid ammonoids (nektobenthos or vagile benthos), where the number of species occurring in Poland is much lower than in coeval deposits in western Germany and where any endemic or Tethyan species occur in Poland (Niedźwiedzki *et al*., 2001). Conodonts (nekton) from the Upper Muschelkalk (see Trammer, 1975; Zawidzka, 1975; Narkiewicz, 1999; Narkiewicz and Szulc, 2004), on the other hand, are very similar to counterparts from the western part of the Germanic Basin and comprise numerous cosmopolitan as well as Tethyan species. It is noteworthy that in the entire Upper Muschelkalk in Upper Silesia, the benthic fauna is taxonomically very poor. Even those species (e.g. *Coenothyris* *vulgaris, Entolium discites*) that form mass occurrences in the nearby (about 200 km) Holy Cross Mountains are extremely rare. In the uppermost part of the Silesian Upper Muschelkalk (Boruszowice Beds), benthic faunas are not only poor, but also very rare. However, the presence of numerous stenohaline conodonts and ceratitids suggests normal salinity conditions in this area. It is likely that the primary causes of taxonomic paucity were very short-lasting marine conditions in the Polish part of the Germanic Basin (latest Illyrian and Fassanian). Additionally, during deposition of the Boruszowice Beds (late Fassanian), most benthic animals were adversely affected by suspended clay matter and small water depths. Consequently, the relatively slowly-migrating benthic (including crinoids) and nektobenthic faunas were only slowly able to colonise the easterly regions of the Germanic Basin, in particular Upper Silesia, while the more mobile nekton is much more similar to faunas from the centre of the Germanic Basin.

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