Pokornyopsis (Ostracoda) from submarine fissure fillings and cavities in the Late Jurassic of Czorsztyn Unit and the possible origin of the Recent anchialine faunas

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With 8 figures in the text

Abstract: Mesozoic Tethyan ostracod faunas of horizontal submarine fissures and caves are dominated by troglobite faunal elements. They are missing or extremely rare in sea-bottom sediments of the same age and water depth, e. g. *Pokornyopsis feifeli* from Callovian to Oxfordian neptunian dykes and crevices in the Czorsztyn Unit (Western Carpathians). They are direct forerunners of Recent anchialine and submarine cave ostracod faunas, e. g. *Danielopolina*, doubtlessly a successor (and perhaps a junior synonym) of *Pokornyopsis*, 6 out of 7 Recent *Danielopolina* species live in anchialine caves; one species occurs in deep-water environment.

Zusammenfassung: Mesozoische tethyale Ostracodenfaunen aus horizontalen submarinen Spalten und Höhlen werden von Troglodyten dominiert. In gleichaltrigen, in gleicher Wassertiefe abgelagerten Meeresboden-Sedimenten fehlen solche Ostracoden oder sind extrem selten, z. B. *Pokornyopsis feifeli*, die in horizontalen Spaltenfüllungen von Callovian-Oxfordian-Alter der Czorsztyn-Einheit (Westkarpaten) massenhaft vorkommt. Diese Faunen sind die direkten Vorläufer der rezenten anchialinen Ostracoden-Faunen mit *Danielopolina*, die sicher der Nachfolger und vielleicht ein jüngeres Synonym von *Pokornyopsis* ist. 6 der 7 bekannten Arten von *Danielopolina* sind auf anchialine Ostracodenfaunen und eine auf das Tiefwasser beschränkt.

1. Introduction

Recent anchialine and marine caves contain an enigmatic ostracod fauna with Mesozoic relicts, which is definitely different from contemporaneous ostracod faunas of the shallow-water sea-bottom. The original definition of anchialine habitats by HOLTHUIS (1973) ("pools with no surface connection with the sea, containing salt or brackish water, which fluctuates with the tides") was re-defined by STOCK et al. (1986) as follows: "Anchialine habitats consist

of bodies of haline waters, usually with a restricted exposure to open air, always with more or less extensive subterranean connections to the sea, and showing noticeable marine as well as terrestrial influence". Anchialine waters are usually brachyhaline or euhaline, but sometines mesohaline or hyperhaline. The transition between the anchialine caves below oceanic islands and submarine caves is gradual and anchialine habitats, especially the brachyhaline to euhaline ones, have very similar faunas as the marine caves.

Some similarities to modern deep-water ostracod faunas are present. The latter faunistic similarities have led to the opinion that the ostracod faunas of marine and anchialine caves were derived from deep-water faunas (ILIFFE et al. 1983, HART et al. 1985, MANNING et al. 1986, WILKENS et al. 1986, ILIFFE 1990, 1992). Other authors (NEWMAN 1985, STOCK 1986, DANIELOPOL 1990) have rejected this possibility. According to these latter authors the faunas of cre-vicular habitats are not relics, but young elements which evolved not earlier than in the Oligocene to Miocene time from shallow-water ancestors. For parts of the ostracod fauna, this is surely not the case.

It is generally assumed that the faunas of submarine and anchialine caves have evolved from ancestors, pre-adapted to cave life. According to STOCK (1986) these ancestors were living in cracks, crevices, and macroporous inter-stitia of the infra- and circalittoral zones. In that type of sciophilous habitat, they will have lost eyes and body pigmentation. Moreover, they will have acquired tolerance towards low oxygen concentrations. According to this model, the fauna of the anchialine and submarine caves should be very different from Mesozoic faunas and have the nearest relations to Cenozoic shallow-water or interstitial faunas. The well known relations of anchialine or marine cave inhabitants to deep-water faunas is explained by common and geographically wide-spread shallow-water ancestors of both the deep-water and caverniculous species.

According to POULSON (1971), POULSON, & WHITE (1969) and ILIFFE (1992) both caves and the deep-sea are old, climatically stable and non-rigorous environments. There are some further similarities between cave habitats and the deep-sea, such as darkness and the absence of wind- or wave-generated turbulent water movements. For this reason, also deep-water forms may be pre-adapted to submarine or anchialine cave habitats. According to HART et al. (1985), ILIFFE (1990, 1992) a continuum of crevicular habitats (submarine fissures, crevices and caves) at any depth within the ocean could provide a link between shallow-water caves and deep-water environments. This could be the migration route for deep-water faunas into shallow-water submarine caves and would explain the striking similarities of many troglobitic faunal elements to deep-water faunal elements. Deep-water faunas from a non-rigorous, cli-matically stable, dark environment without turbulent water movement would be pre-adapted in many respects to the submarine shallow-water or anchialine cave environments.

In this case, the submarine and anchialine caves should have a high percentage of Mesozoic relict forms or other ancient elements and a low percentage of forms which evolved in the Late Tertiary from shallow-water ancestors. This is the case. However, the same picture can be explained by the assumption that submarine caves, fissures, crevices are old stable environments, even if most of the Recent submarine and anchihaline caves are very young features. These younger submarine or anchialine caves are in this case colonized through crevicular environments from older crevicular habitats.

For the question of the origin of the anchialine and submarine cave faunas the study of such crevicular habitats in the geologic past is most important. The present paper yields the first results of the study of fossil marine troglobitic faunas (restricted to marine caves or, more generally, to marine crevicular habitats).

2. Geologic setting and data on the studied locality

The Czorsztyn Ridge of the Pieniny Klippen Belt is a rather permanent Jurassic-Cretaceous submarine ridge with continuous limestone deposition between two deep-water troughs of oceanic to suboceanic character, the Pieniny Trough in the south and the Magura Trough in the north (BIRKENMAJER 1977). The present day outcrops of the Czorsztyn Ridge are a narrow strip along the whole Pieniny Klippen Belt, to a large part exposed in northern Slovakia territory (Fig. 1). The investigated localities (Fig. 1) are situated mainly in the western part of the former Czorsztyn Ridge. Bajocian-Bathonian white and red crinoidal limestones and reddish nodular limestones contain vertical and horizontal neptunian dykes of Callovian to Oxfordian age often with polyphase fillings. The youngest fillings contain mass occurrences of *Pokornyopsis feifeli* (TRIEBEL), especially in the horizontal neptunian dykes, which had originally the character of submarine caves. The Oxfordian and Kimmeridgean limestones contain neptunian dykes of Tithonian age. The position of the Czorsztyn Ridge between two suboceanic to oceanic troughs leads to tectonic unrest and often to a tensional regime to which the neptunian dykes are connected (MIŠÍK 1979). Contemporaneous with the Callovian-Oxfordian neptunian dykes also tectonic limestone breccias have been developed (MIŠÍK & SÝKORA 1993). The neptunian dykes originated due to the combined tectonic movements and eustatic sea-level changes in the Czorsztyn sedimentary area during the Callovian-Oxfordian as indicated by the microfacial content of the dykes. The neptunian dykes originated as tension fractures (MIŠÍK 1979). A contemporaneous global sea-level rise caused a facies change in this area. Instead of crinoidal limestones with brachiopods, the Czorsztyn Limestone (nodular limestone) was sedimented. On the more elevated parts, where the submarine dissolution was not so strong, its nodular character was less pronounced. The neptunian dykes occur mainly in these originally shallower parts. Mass occurrences of *Pokornyopsis* occur both in horizontal neptunian dykes and in
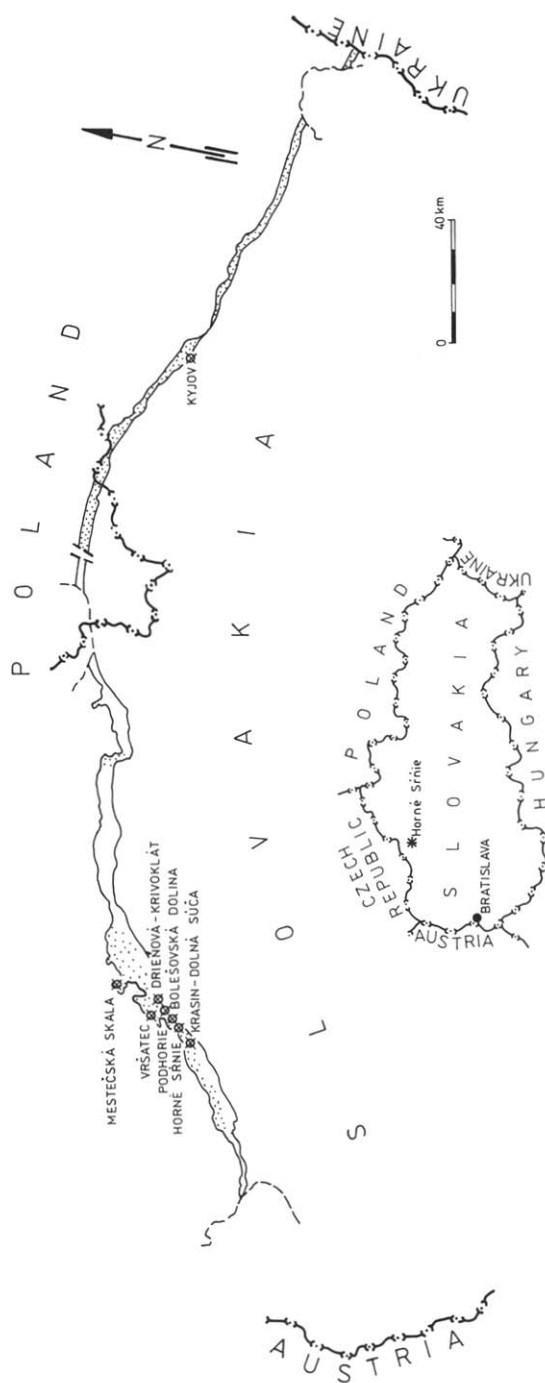
Fig. 1. Czorsztyn Unit (stippled) with the investigated occurrences of crevices and neptunian dykes containing the *Pokornyopsis* ostracod fauna. The position of the Horné Srnie locality is indicated.
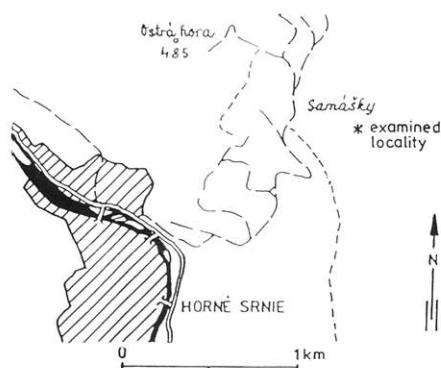
Fig. 2. Location map of the Horné Srnie - Samášky locality where the well preserved *Pocornyopsis* fauna has been found.

interspaces between limestone breccia. In general, *Pokornyopsis* could be only found in thin sections and it was then mostly indeterminable at least at species level. Recently, an occurrence with well-preserved negative prints of numerous *Pokornyopsis* has been found at the Samášky locality near Horné Srnie village (Fig. 2). They occur in the last phases of the interspace fillings between the clasts of the limestone breccia. These interspaces are by far bigger than interstitial spaces. The limestone breccias originated probably along a fault. The brecciation is probably connected to the same tectonic process by which the contemporaneous Callovian-Oxfordian neptunian dykes have been formed in this area. The clasts in the breccia, represented mainly by crinoidal limestone, are initially coated by cyanoliths; later an isopachous radiaxial cement was formed. The remaining open interspaces were filled by blocky spar-calcite or, if they had more connection to the sea bottom, also with sediment. The initial sediment filling is represented by crinoidal detritus. After the communication with the sea-water was restricted, a micrite full of *Pokornyopsis* has sedimented (Fig. 6). The shells, filled mainly by the sparite, form the main part of the sediment (Fig. 6a), sometimes without matrix. This fact played a very important role in the diagenesis and in the preservation of the ostracods. We succeeded to make several positive latex prints (Fig. 5) from the weathered parts of the breccia interspace fillings, in which ostracod prints were preserved.

3. Known occurrences of *Pokornyopsis* and closely related forms and their biofacial interpretation

Two species of *Pokornyopsis* have been described as *Thaumatocypris feifeli* TRIEBEL, 1941 and *Thaumatocypris bettenstaedti* BARTENSTEIN, 1949 by TRIEBEL (1941) and BARTENSTEIN (1949) from the Jurassic of Germany. Both species occur there very rarely im marine claystones. Only a little more than 100

specimens of both species together are known. From the Tethys, this genus was for a long time unknown or the ostracod nature of remnants in thin sections was not recognized. For the first time Mišík (1979, pl. VI, fig. 4) figured thin sections of pokornyopsid ostracods from neptunian dykes of the Czorsztyn Unit in the Vršatec klippen, but he could not determine the taxa. Later also Jurkovičová (1980, see fig. 7a) described thin sections of *Pokornyopsis* from the Drieňová klipper near Krivoklát, but also she did not recognize the systematic position of these ostracods. Aubrecht (1992) found *Pokornyopsis* dominated ostracod associations in polyphase fissure fillings in the Mestečská Skala klippe. The ostracod occurrence (Fig. 8) in the latest filling phase of the originally horizontal neptunian dykes is noteworthy. These horizontal neptunian dykes had originally the character of submarine caves. Mišík & Sýkora (1933, Pl. VI, Fig. 1) reported about "*Pokornyella*" (incorrect spelling of *Pokornyopsis* determined by us) from the crevices in crinoidal limestone and from Tithonian neptunian dykes of the Kyjov - Pusté Pole klippe in Eastern Slovakia (Fig. 4). There, the ^{18}O and ^{13}C proportions in calcite from all the phases of filling
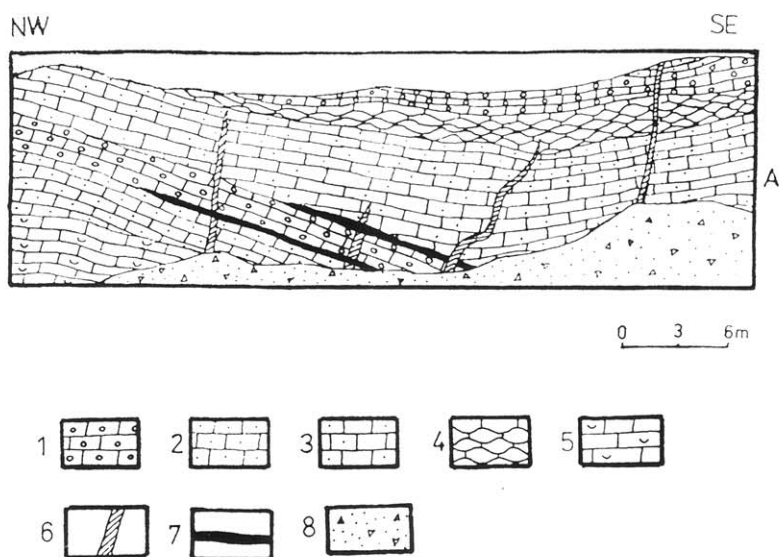

Fig. 3. Schematic frontal view of the Mestečská skala quarry. The sequence is tectonically overturned. − 1. White crinoidal limestone (Bathonian Smolegowa Lst.). − 2. Red crinoidal limestone (Bathonian Krupianka Lst.). − 3. Red limestone with few crinoids (Bathonian Krupianka Lst.). − 4. Red nodular limestone (Bathonian). − 5. Pink micritic limestone with juvenile ammonoids. Filamentous to "*Protoglobigerina*" microfacies (Callovian-Oxfordian). − 6. Older generation of perpendicular neptunian dykes (Oxfordian). − 7. Younger generation of originally horizontal neptunian dykes containing *Pokornyopsis* (Oxfordian). − 8. Debris cover.
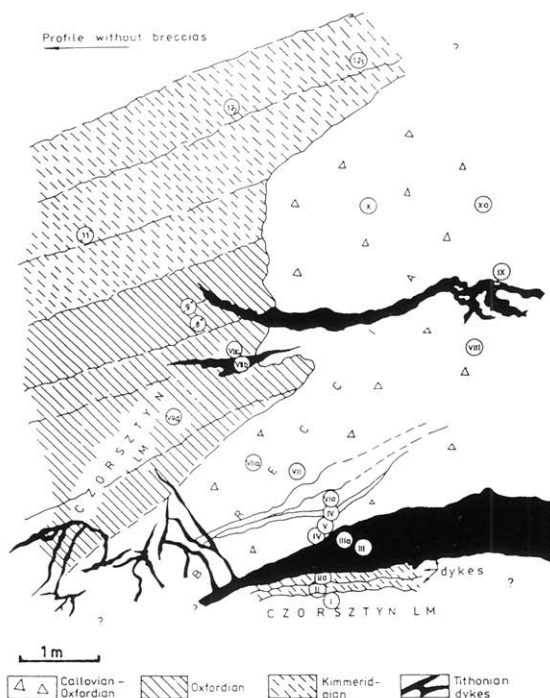
Fig. 4. Detail scheme of Callovian-Oxfordian breccias and Oxfordian Czorsztyn Lime-stone with Tithonian, mostly horizontal neptunian dykes (originally partly in the size of submarine caves) in the Kyjov-Pusté Pole locality (after Mišík & Sýkora 1993). The scheme is turned to the normal position (in the field overturned).

indicate precipitation from euhaline marine water. *Pokornyopsis* has been also found in several other, so far unpublished occurrences in the Czorsztyn Unit. In all cases they occur in the last phase of fissure or crevice fillings. There is no other fauna present in this phase. This indicates, that *Pokornyopsis* lived in these crevices and horizontal fissures or submarine caves and was not transported to these crevicular habitats together with sea bottom sediments. All Tethyan Late Jurassic occurrences of *Pokornyopsis feifeli* (Triebel) in horizontal fissure fillings (submarine caves) are mass occurrences, nearly without any other ostracods. The presence of several 1000 to several 10000 specimens in one kg sediments of the fossil submarine caves can be estimated from the number of specimens per thin section. In contemporaneous Tethyan sea-bottom sediments of the same area *Pokornyopsis* is totally absent. Therefore these ostracods were in the Tethys true marine troglobites, but lived in the Germanic Jurassic, from where no submarine caves are known, in marine sea bottom sediments deposited in about 100-200 m water depth. Especially interesting are the mass occurrences of *Pokornyopsis feifeli* in the interspaces of contemporaneous lime-

stone breccias. This indicate that the marine cave inhabitants lived also in crevices, cracks and macroporous interstitia. They were therefore pre-adapted to cave life. This mode of colonization of marine caves corresponds to the mode of colonization proposed by MANNING et al. (1986), who regard the marine cave fauna as a part of a crevicular fauna, which lived not only in marine caves, but also in fissures, cracks and crevices of rocks in different water depths. The Recent genus *Danielopolina* KORNICKER & SOHN, 1976 with 6 species from anchihaline and marine caves and one species from deep water (sampled in more than 3000 m water depth, (KORNICKER & SOHN, 1976, ILIFFE, 1992) is surely the successor of the Mesozoic *Pokornyopsis* KOZUR, 1974 and probably even a junior synonym of the latter genus. The only difference between *Pokornyopsis* and *Danieloplina* is the stronger sculpture (which has otherwise a similar pattern) in *Pokornyopsis*. However, the differences in sculpture within the Recent genus *Danielopolina* are about of the same degree as the differences in sculpture between the strongest sculptured *Danielopolina* and *Pokornyopsis feifeli*, the type species of *Pokornyopsis*. Moreover, *Pokornyopsis* was established for two very similar species with the same sculpture pattern and only some differences in the convexity of the shell. There are Triassic *Pokornyopsis* with the same weak sculpture as in *Danielopolina*. Independent from the question of the synonymy of the two genera (which will be discussed after finishing the studies of Triassic *Pokornyopsis*), *Pokornyopsis* is clearly the ancestor of *Daniëlopolina* and there are extremely small changes within this stock since the Triassic. This confirms the assumption of ILIFFE (1992) that a part of the marine troglodites are old Mesozoic relics which survived in the stable, old crevicular habitat from the Mesozoic Tethys. The view of STOCK (1986) that the Recent biota of anchialine and marine caves have developed not earlier than in the Oligocene-Miocene time cannot be supported. We can also not confirm the view of STOCK (1986) that the ancestors of the marine and anchialine cave biotas lived in the infra- and circalittoral zones. The investigated Late Jurassic crevicular habitats (submarine caves, vertical and horizontal fissures, crevices) had connections with the sea water at water depths of about 30-100 m. This is concluded from the depositional depth of sea bottom sediments which were partly filled into the crevicular habitats. *Pokornyopsis* was not found in these sea-bottom sediments. Also in other Tethyan regions, the Jurassic ostracod fauna of shallow-water sediments deposited in water depth between 0 and 100 is well investigated. *Pokornyopsis* was not reported from these sediments. On the other hand, *Pokornyopsis* is a very rare component in sediments of the German Jurassic deposited in a maximum water depth of

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Fig. 5. Positive latex prints of *Pokornyopsis feifeli* (TRIEBEL) from the Samášky locality. — **a**. Right valve. — **b**. Left valve. — **c**. Right valve. — **d**. Left valve. — **e**. Negative outprints in rock - right valve of the upper specimen.
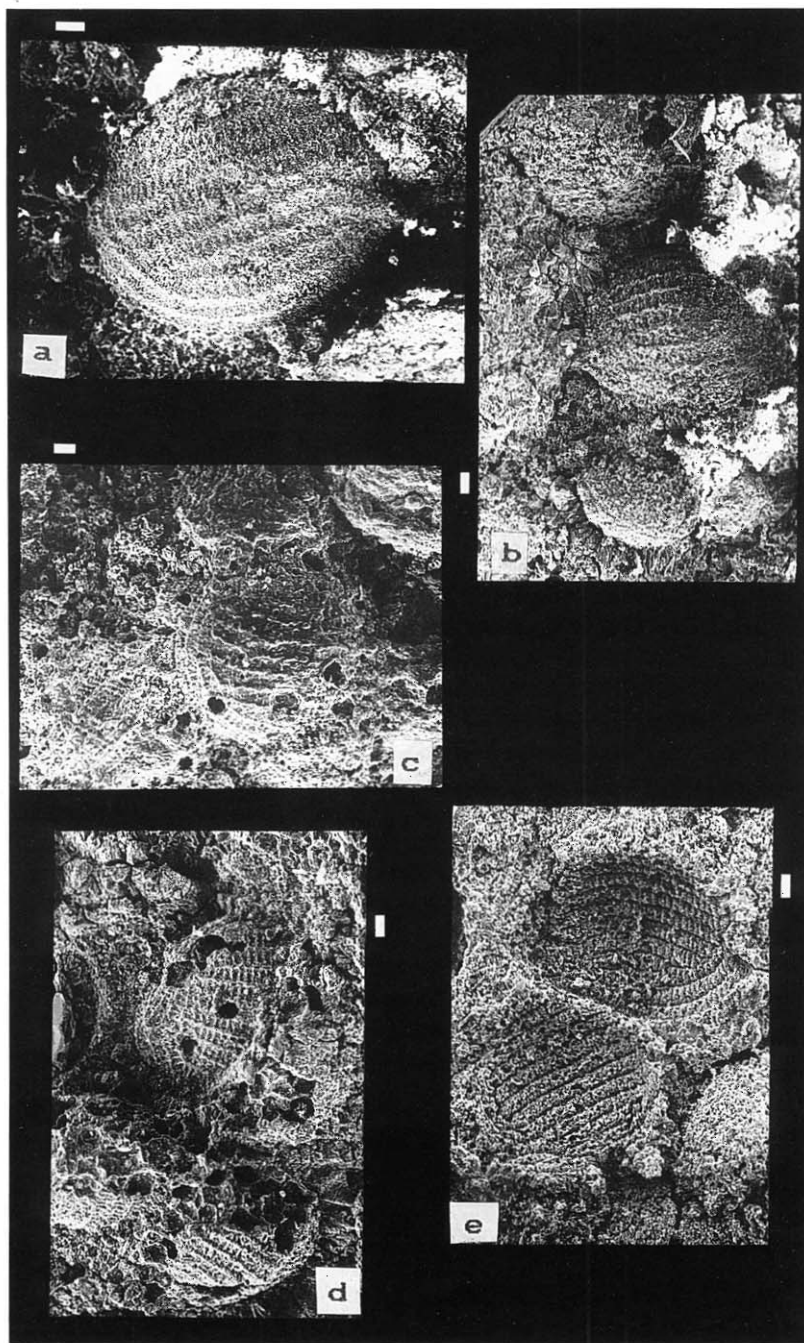Scale bars = 100 μm.

Fig. 5 (Legend see p. 8)

200 m assumed for the type locality of *P. bettenstaedti* and in a water depth between 100 and 200 m assumed for the occurrence of *P. feifeli* (TRIEBEL 1941, KORNICKER & SOHN 1976). This is seemingly the upper limit of the water depth range of *Pokornyopsis*. The colonization of the Late Jurassic submarine caves and other crevicular habitats in the shallow-water environments above 100 m water depth was seemingly through a continuum of crevicular habitats from greater water depth (below 100 m water depth) in agreement with the view of HART et al. (1985), MANNING et al. (1986), ILIFFE (1990, 1992). As shown by KOZUR (1991), the Toarcian and younger Mesozoic ocean was thermospheric. Therefore no thermocline barrier for the crevicular migration of deep-water ostracods into shallow marine caves was present. Whether or not this migration route was also possible under psychrospheric conditions, is not yet clear. In this case the thermocline was doubtlessly an important barrier for deep-water ostracods to reach warm-water shallow marine caves or other crevicular habitats. However, for troglobites without very mobile larval stage, the deep-water migration route is the only possibility for colonization of crevicular habitats in oceanic islands. Our investigation have shown that the common ancient components of crevicular habitats are, at least with respect to the thaumatocyprid ostracod *Danielopolina* (a very striking component of the Recent anchihaline and marine cave faunas), taxa which have already lived in the Jurassic in the same habitats. This shows that the crevicular habitats are stable and old habitats, in which relics from the Mesozoic troglobite faunas could well survive. The marine crevicular habitat is indeed wide-spread in the Mesozoic Tethys. Especially on submarine ridges within oceanic or sub-oceanic realms, like the Czorsztyn Ridge or at oceanic slopes in areas with low input of terrigenous material (e. g. Triassic Hallstatt Limestones, see KOZUR, 1991 a, b) often tensional regimes can be observed. By this, a lot of vertical and horizontal fissures have been originated. They are well known from Triassic and Jurassic Tethyan areas. Along the mid-oceanic ridges a wide-spread basic volcanism was present. In these areas a lot of interpillow spaces and hollow lava tubes were present. These crevicular habitats are not so well known from the geologic past, because most of the ocean floor has been later subducted. Moreover, mostly interpillow spaces from the deep-sea floor below the CCD are preserved. They are filled with chert without fossils with calcareous shells. Nevertheless, on the mid-oceanic ridges crevicular habitats in shallow-water were surely present during the Tethyan evolution.

Fig. 6. **a.** Thin section of the void among the clasts of the breccia (Horné Srnie - Samášky locality). The first phase of filling is represented by the cyanolith, the second one by the radial fibrous calcite. Both are disturbed by the initial compaction. Later the void was filled with the ostracod shells with little lime mud preserved among them. − **b.** Detail of the tangentially cut shell of *Pokornyopsis* sp. (marked also on the upper picture). Scale bar = 1 mm for Figure 2 a and 100 μm for Figure 2 b.
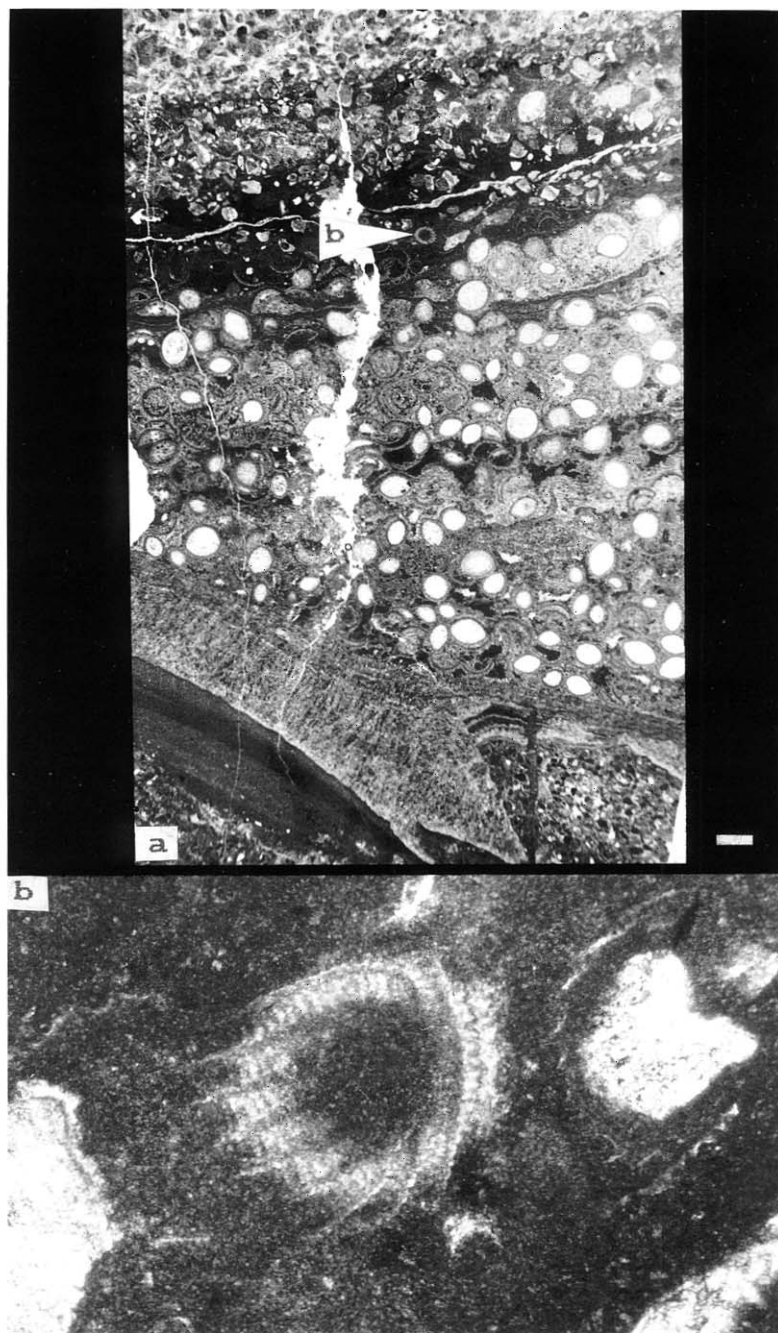
Fig. 6 (Legend see p. 10)

Most of the preserved Tethyan Mesozoic crevicular habitats are situated immediately adjacent to deep-water environments (KOZUR 1991 a, b). The colonization of the shallow marine crevicular habitats by deep-water species through a continuum of crevicular habitats is therefore probable. The crevicular habitats investigated in the present paper have their connections with the sea water in shallow water depth. However, some of the tensional fissures within the Tethyan Triassic Hallstatt Limestones were originally in the psychrospheric domain as shown by the presence of paleopsychrospheric ostracods in these Hallstatt Limestones (KOZUR & MOCK, in preparation). In continuation of our research program we will investigate the fauna of these deep-marine crevicular habitats.

The Late Jurassic troglobitic ostracod fauna, nearly totally dominated by *Pokornyopsis*, was surely not the oldest one. According to a personal communication of Prof. MOSTLER, Innsbruck, such faunas occurred also in the Lower Jurassic. The only published record of Lower Jurassic (Toarcian) *Pokornyopsis* in thin sections can be found in FÜLÖP (1976, Pl. XXIII, Fig. 7) under the name *Microcalamoides* (FÜLÖP has not recognized that these fossils were ostracods) from Toarcian limestones at Csurgókút in the Gerecse Mts., Hungary. We presume, that the sample came also from a neptunian dyke. In contrast to the Late Jurassic crevicular habitats, *Pokornyopsis* is not yet dominating in this Toarcian crevicular habitat. This could indicate that the colonization of the crevicular habitats by *Pokornyopsis* (= *Danieloplina* ?) began during the Toarcian, where for the first time thermospheric conditions prevailed in the ocean after a long interval with psychrospheric conditions (KOZUR 1991 c).

However, it cannot be excluded that the colonization of the crevicular habitats with *Pokornyopsis* began already in the Triassic. So far, only two occurrences of *Pokornyopsis* (with *Danielopolina* sculpture !) are known from the Triassic which both cannot be investigated for the moment. One occurrence was in material of H. KOZUR from Ladinian pelagic limestones at Strimtura (Northern Apuseni Mountains, Romania). It derived from beds that have been deposited under water depth of 100-300 m. *Pokornyopsis* is a subordinate, but not very rare element of the ostracod fauna. The fauna was from sea bottom sediments.

This material was in 1985 by order of the former communist leadership (Dr. GÓCZÁN, Dr. HÁMOR) of the Hungarian Geological Institute (MÁFI) confiscated and intentionally destroyed. Also the rock samples from this locality were not among the material that was given back to H. KOZUR by the new leadership of the MÁFI and therefore seemingly thrown away like a lot of Recent ostracod material, because according to an order of the new leader of the MÁFI, Prof. GAÁL, all present material was given back to H. KOZUR.

Fig. 7. **a**. Laminated fissure filling of Callovian-Oxfordian age in the Kyjov-Pusté Pole locality (after MIŠÍK & SÝKORA 1993). The cm scale right. − **b**. Pokornyopsid ostracods in a neptunian dyke from the Drieňová Klippe (after JURKOVIČOVÁ 1980). The initial stromatolitic coat is visible in the lower right corner.
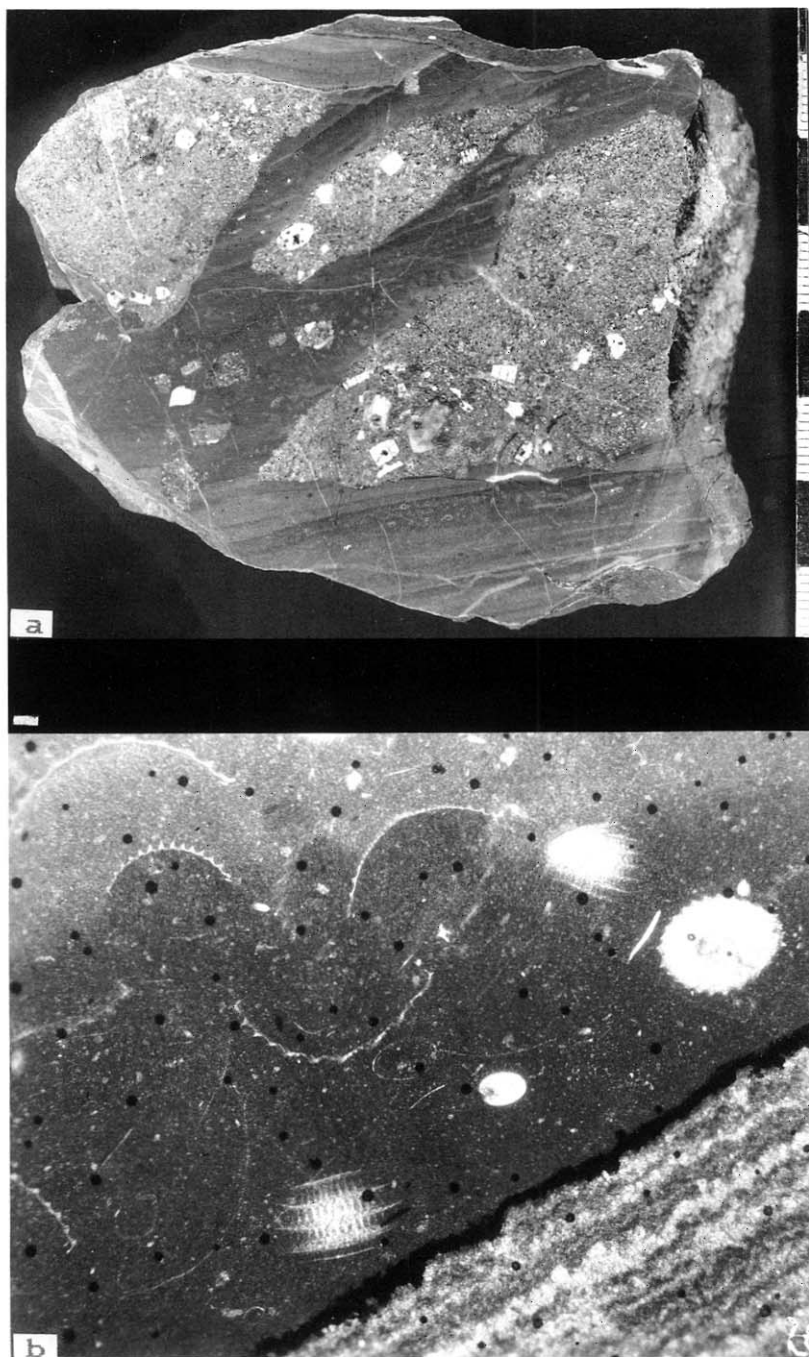The scale bar above represents 100 μm.

Fig. 7 (Legend see p. 12)

The second occurrence is from an unknown locality in the Western Carpathians. This material from the late Prof. Bystrický was from a Middle Carnian black limestone with red spots. According to the microfauna, it was not a paleopsychrospheric fauna (water depth below 200-500 m), but also not a shallow-water fauna above 100 m water depth. The water depth during the sedimentation was probably between 100 and 200 m. Among the ostracods *Pokornyopsis* with *Danielopolina* sculpture was common in a conodont-dominated sample with *Gladigondolella tethydis* (Huckriede) and *Paragondolella polygnathiformis noah* (Hayashi). Unfortunately, in the moment neither the material nor the locality data are present in the collection of the Slovak Academy of Science or in the Dionýz Štúr Institute.

So far, we have studied only 10 thin sections of Triassic fissure fillings. None of them had yielded *Pokornyopsis*. *Pokornyopsis* absents in the Triassic shallow-water environments, but also the rather well known paleopsychrospheric Triassic ostracod faunas have not yielded any *Pokornyopsis*. According to the present data, *Pokornyospsis* was a rare element of the Triassic ostracod faunas in water depth between 100 and 300 m. In the moment is not clear, whether *Pokornyopsis* preferred also in this time already crevicular environments, like in the Toarcian. *Pokornyopsis*-dominated crevicular faunas, like in the Late Jurassic, were seemingly not yet present during the Triassic.

Acknowledgements

Fig. 8. **a**. Laminated neptunian dyke originally horizontal, now in tectonically overturned position (Mestečko Klippe - see Aubrecht 1992). The dyke contains two phases of fillings (marked by the triangles b and c). — **b**. First phase is represented by biomicrite with juvenile ammonoids, bivalve shells and mass occurrence of *Globuligerina* sp. indicating most probably Callovian-Oxfordian age. — **c**. Final filling represented by micrite with mass occurrences of *Pokornyopsis*. The scale bar below represents 100 μm (for both b and c).
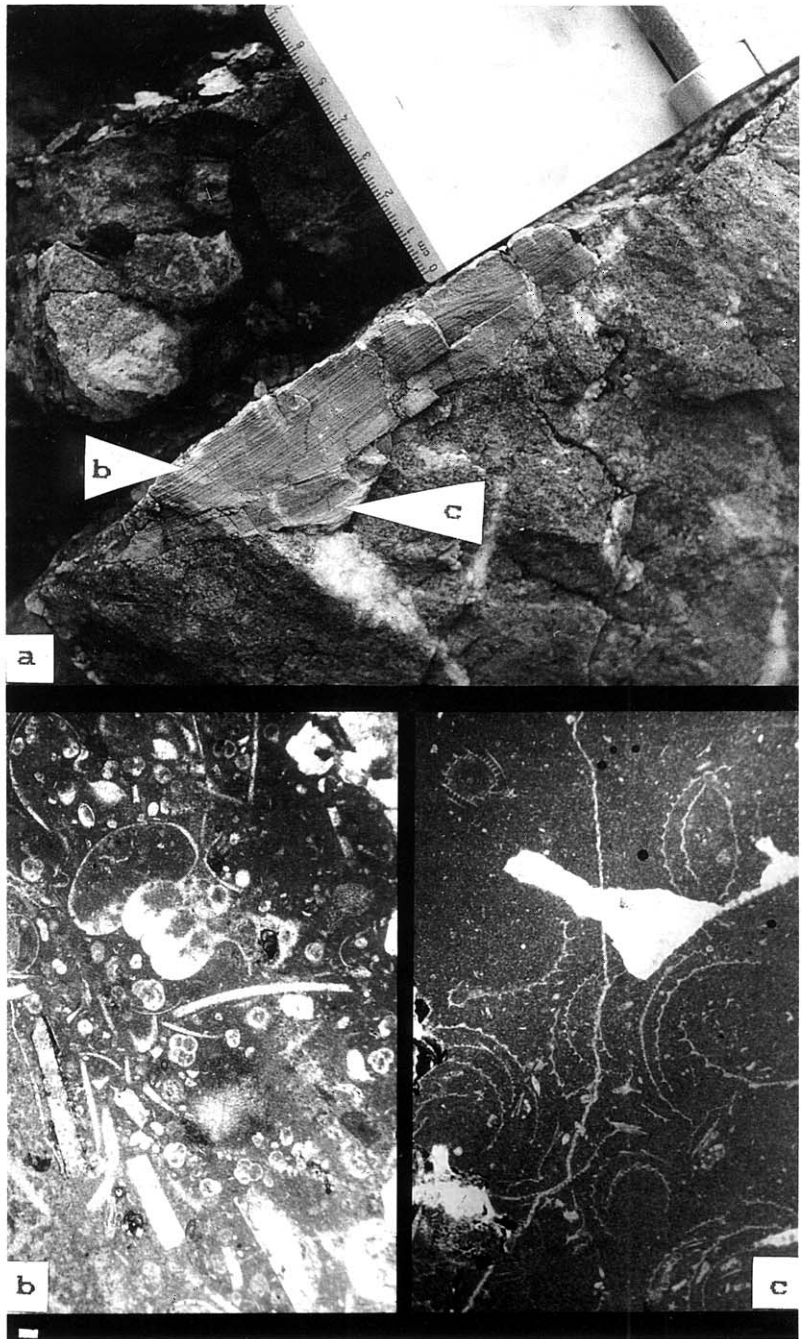
Fig. 8 (Legend see p. 14)

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