

The epiplanktic anthozoan, *Kolihaia eremita* Prantl, 1946 (Cnidaria), from the Silurian of the Prague Basin (Bohemia)

Epiplanktonní korál, *Kolihaia eremita* Prantl, 1946 (Cnidaria), ze siluru pražské pánve (Čechy)

(3 figs, 2 plates)

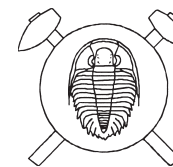
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New material makes it possible to classify the epiplanktic species *Kolihaia eremita* Prantl, 1946, supposed to be a worm or cornulitid, from the Silurian of the Prague Basin as a member of the phylum Cnidaria and a possible member of Rugosa or Tabulata.

Key words: Silurian, Prague Basin, Bohemia, Cnidaria, Rugosa?, Tabulata?



Introduction

For more than two hundreds years zoologists have used an artificial system for a classification of the animal kingdom. Amongst the many categories used for classification of species the phylum represents the most satisfactory taxa. There is a good general consensus about the rank of phylum which should include all those animals sharing a particular body plan. Modern zoology has recognised around 32–36 phyla in which all extant animals may be placed. However, our interpretation of the phylum-level position of extinct animals is much more difficult because it is considerably limited by the loss of many characters during the fossilisation processes. Commonly only hard body parts like skeleton or shell have been preserved. For this reason our interpretation of the higher taxonomic position of any extinct animal is based on a comparison of the preserved hard body parts with those of extant animals or on their functional analysis. These limitations make the placement of fossils into the categories used by zoologists much more difficult (sometimes even impossible) than that of the living animals. In addition, many animal groups of the order or class level are extinct and it is very probable that even some groups of the phylum rank are extinct. The placement of some fossils in one of the extant phyla is not always the only possible solution of their taxonomic position. Thus, a determination of the higher taxonomic position in many extinct animals has to be considered as “the best solution” based on the present level of our knowledge.

Change of mode of life is typically connected with a loss or reduction of some body structures and with the development of new body structures. In such cases a correct interpretation of the ancestral body plan and subsequent placement of the animal into any phylum is sometimes difficult even in living animals. Determination of correct taxonomic position in fossil animals which were adapted to a quite different mode of life than their ancestors is often a serious problem. The present paper is focused on one of such fossils, *Kolihaia eremita*, from the

Silurian strata of the Prague Basin, Bohemia. Prantl (1946) placed this ecologically interesting new genus and species in the phylum Annelida Lamarck, 1809 (Serpulidae Burmeister, 1837). Fischer (1962, 1966) included the genus *Kolihaia* Prantl, 1946 within the family Cornulitidae Fischer, 1962 with uncertain phylum, class and order relationship together with the genera *Cornulites* Schlotheim, 1820, *Conchicolites* Nicholson, 1872 and *Cornulitella* Howell, 1952. In 1990 Turek considered *Kolihaia* to be of uncertain affinity and supported the idea of its epiplanktic mode of life in agreement with Prantl’s original interpretation on the base of new observations in the field.

In 1975 one of us (J. K.) collected more than 1000 specimens of *Kolihaia eremita* in the upper Wenlock (*Monograptus belophorus* Zone) at a new locality in Koněprusy near Beroun (private property 200 m SW of the village cemetery) and later also at other localities. The very good preservation of the material makes it possible to contribute to the systematic classification of the genus *Kolihaia*.

Systematic paleontology

Genus *Kolihaia* Prantl, 1946

1946 *Kolihaia* gen. nov.; Prantl, p. 1–3.

1962 *Kolihaia* Prantl, 1944; Fischer, p. W138.

1966 *Kolihaia* Prantl, 1944; Fischer, p. W138.

1992 *Kolihaia* Prantl, 1946; Gnoli, p. 383.

Type species: *Kolihaia eremita* Prantl, 1946.

Diagnosis: Solitary, loosely dendroid or gregarious, relatively small animal with almost regularly annulated very thin conical calcareous corallites, usually curved at its proximal part. In the proximal and also distal parts characteristic, relatively long, thin, hollow and mostly branched radiceform processes are developed. Internal features most probably reduced to minimum due to the epiplanktic mode of life. Individual corallites increase laterally by production of offsets.



Fig. 1 Colony of *Kolihaia eremita* Prantl, 1946, from the upper Wenlock rocks (*Monograpthus belophorus* Zone) at Koněprusy near Beroun. Specimen JK 8383, x5.

Remarks: Prantl (1946) related *Kolihaia* to the phylum Annelida Lamarck, 1809 (Serpulidae Burmeister, 1837) and Fischer (1962, 1966) included the genus *Kolihaia* Prantl, 1946 within the family Cornulitidae Fischer, 1962 with uncertain phylum, class and order relationship together with the genera *Cornulites* Schlotheim, 1820, *Conchicolites* Nicholson, 1872 and *Cornulitella* Howell, 1952. According to Richards (1974) Cornulitidae represent a family of extinct worm-like organisms of unknown biologic affinities showing a commonly epizoic mode of life on other fossils as solitary commensals, gregarious commensals, unattached cornulitids and parasitic cornulitids. When living as commensals they are cemented to the substrate by the proximal part of the tubes directly and absorb calcium carbonate partly from the host (Fischer 1962, 1966). Their vesicular wall (Bather 1923) is similar to calcareous hydroids, stromatopora and some fusulines (Fischer 1962, 1966)

Kolihaia developed characteristic, relatively long, thin, hollow and mostly branched radiceform processes (Fig. 1, Pl. I/1, 4, 5, 6, Pl. II). On the other hand, no annelid can produce similar radiceform processes in the proximal part of the tube. The shape of the tube and similar processes may be expected in some cnidarians. Hydrozoa are excluded since polyps do not bud from an existing polyp and new buds/offsets develop from the supporting stolons or stems of the polyps only (Schäfer 1972). Rugosa and Tabulata (Cnidaria, Anthozoa) represent the only groups of cnidarians characterized by increase of origi-

nal protocorallites by offsets produced laterally (Hill 1956, 1981; Sokolov 1962). The corallites of Rugosa are generally characterized by complex internal features of skeleton, mainly radial plates and tabulae (tabularium) or dissepiments (dissepimentarium) (Hill 1956). Rugosa are both solitary and colonial. On the other hand, Tabulata often lack both vertical and horizontal inner structures but are usually colonial.

Corallites of *Kolihaia* are extremely thin-walled and preserved fully compressed. We were unable to observe any internal features between the compressed walls of the corallites. The only massive structures are the radiceform processes in the proximal parts of the corallites. The radiceform processes formed by carbonate are hollow and grow directly from the wall (Fig. 1, Pl. I/1, 4, 5, 6, Pl. II). They are branching, circular in cross-section and their diameter distally decreases continually.

The existence of radiceform processes in the proximal parts of *Kolihaia* is rather puzzling. Short blunt rootlets are known in Rugosa but rugosans never lack inner structures as often as Tabulata. Tabulates, on the other hand, are unknown to develop radiceform processes. In our opinion, such processes could have developed as an adaptation to their epiplanktic mode of life, either in the same way as the rootlets of Rugosa, or possibly from the connecting structures. In any case, we suggest that the increase of the corallites by offsets produced laterally relates the genus *Kolihaia* to the phylum Cnidaria, and an absence of internal structures such as tabulae or sep-



Fig. 2 Colonies and single corallites of *Kolihaia eremita* covering bedding plane of the Silurian shale (*Monograptus belophorus* Zone at Koněprusy near Beroun; x5).

ta and probably also mural pores demonstrates most probably a relationship to Tabulata, probably Auloporida. The absence of the internal features of the corallite in *Kolihaia* may be the result of the adaptation to an epiplanktic mode of life, where the maximal reduction of the weight/mass is one of the important features. We consider the presence of the conspicuous radiciform processes, unknown in other Tabulata or Rugosa, as a further adaptation to an epiplanktic life as the processes may have served to attach the colony to floating or buoyant objects, probably algae.

Species: *Kolihaia eremita* Prantl, 1946 (Silurian of the Prague Basin, Bohemia) and *Kolihaia sardiniensis* Gnoli, 1992 (Lower Silurian of the SW. Sardinia).

***Kolihaia eremita* Prantl, 1946**

Figs 1–3, Plates I–II

- 1946 *Kolihaia eremita* sp. nov.; Prantl, p. 3–7, 9–13, Pl. 1.
 1962 *Kolihaia eremita* Prantl, 1944; Fischer, p. W138, Fig. 78/4.
 1966 *Kolihaia* Prantl, 1944; Fischer, p. W138, Fig. 78/4.
 1990 *Kolihaia eremita*; Turek, p. 345–346, Pl. 8, Figs 1, 2.

Holotype: Specimen figured by Prantl, 1946 on Pl. 1, Fig. 1, refigured by Fischer, 1962 and 1966 on Fig. 78/4 and deposited in the National Museum, Prague under No. 22 129/9.

Paratypes: Other specimens figured by Prantl, 1946 on Pl. 1.

Type horizon: Motol Formation.

Type locality: Koněprusy near Beroun.

Occurrence: Prague Basin, Bohemia, Praha-Malá Chuchle (Vyskočilka) – upper Motol Formation, *M. riccartonensis* Zone; Loděnice (Černidla), Koněprusy, 200 m SW from the cemetery,

Všeradice – *Monograptus belophorus* Zone, Motol Formation; Bykoš near Zdice, *Testograptus testis* Subzone; Kosov Quarry near Králův Dvůr – *C. lundgreni* Subzone; Praha-Stodůlky – *S. chimaera* Zone.

Description: The description of the species is given by Prantl (1946). Only the morphological features considered important for interpretation of its taxonomic position as well as newly observed features are mentioned below. Characteristic radiciform processes are developed in the proximal part of the conical calcareous corallites and are more common on their convex side. The first processes occur typically about 3–5 mm from the apex of the corallite. Radiciform processes are hollow with an inner diameter slightly more than one half of the process width (Pl. II/3). The processes are branched irregularly and dichotomously and their length reaches up to half of the corallite length. Individual corallites increase laterally by production of offsets.

Dimensions: Length of the corallites up to 25 mm, maximum width of the compressed corallite at distal end is up to 5 mm, width of rootlets about 0.2 mm.

Note: Pronounced annulations of the corallite walls are the most conspicuous feature of *Kolihaia eremita*. They resemble rejuvenations known in Rugosa but they differ in their regularity. Thick annulations are usually arranged in pairs: after the wall withdrawal toward the corallite axis the diameter abruptly increases into two annulations close to each other. It seems to contradict the cnidarian affinities of *Kolihaia*.

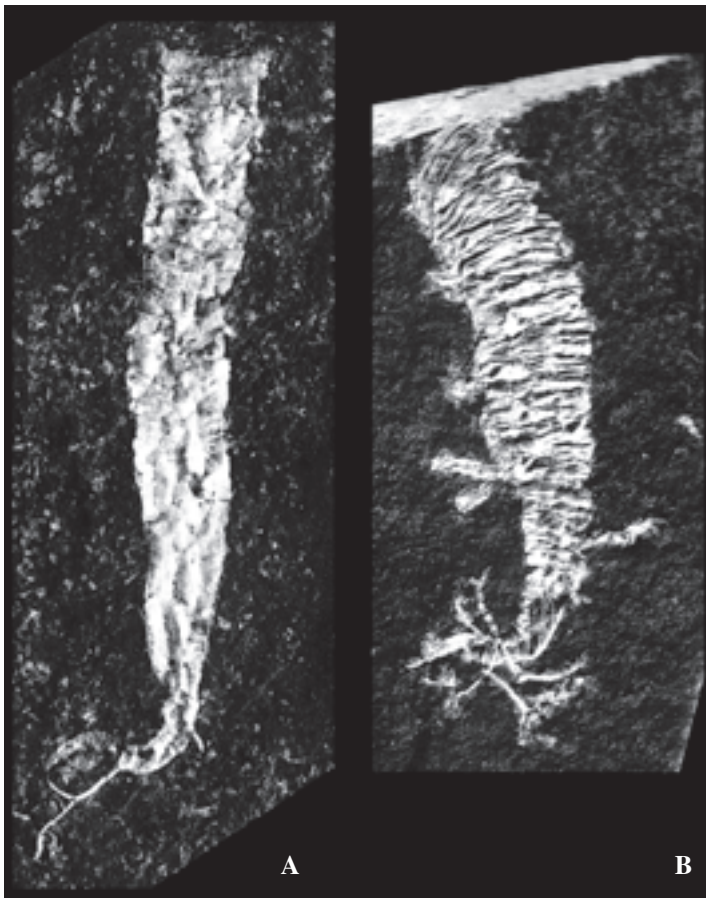


Fig. 3 Single corallite of *Kolihaia eremita* from the *Monographus belophorus* Zone at Koněprusy near Beroun; A – specimen JK 8393a, x6, B – specimen JK 8383, x11.

Relationships: Gnoli (1992) described the new species *Kolihaia sardiniana* from the lowermost Ludlow of SW Sardinia. Its comparatively very small corallite has a similar general shape to *Kolihaia eremita* but distinctly differs in the type of the processes which are regularly distributed along the corallite, probably due to adaptation of the animal to a benthic mode of life.

Paleoecology: *Kolihaia eremita* single corallites and colonies are preserved in a black shale facies of the Silurian scattered or covering one or several bedding planes in the sequence (Fig. 2), occurring mainly together with graptolites and rare single valves of brachiopods (*Niorhynx*, *Valdaria*). They were obviously fossilised in an abiotic environment. Prantl (1946) and Turek (1990) supported the idea of an epiplanktic life based on the presence of unbroken branching radiceform and fragile processes at the proximal part of the individuals and whole colonies and because of their occurrence in the abiotic environment of the black graptolitic shales. The branching processes most probably assisted in anchoring the individuals and colonies in the algal clumps floating in the ventilated upper parts of the water column. The rock surface in the vicinity of the radiceform processes is usually whitened by reduction processes when frag-

ments of organic matrix (algae and body soft parts) on them decayed during fossilisation (Fig. 1, Pls I–II). The same whitening is well demonstrated also on the distal ends (body soft parts) of the corallites around the aperture (Fig. 1; Pl. I, Fig. 2). Another feature supporting an epiplanktic mode of life is the minimal weight of the tubes (corallites) without internal features.

Conclusion

Interpretation of the Silurian *Kolihaia eremita* as a member of the class Anthozoa with an epiplanktic mode of life completes our view on the life strategy of the fossil members of the phylum Cnidaria. The latter phylum forms a clearly defined animal group (by formation of their unique cnidoblast) with a very long fossil record. There is evidence for hydrozoans, pennatulid-like anthozoans, and primitive scyphozoans even in the Precambrian strata (Glaessner 1984). Cnidarians have had a quite unique position in the zoological system and resolution of some basic, but still unsolved questions regarding their phylogeny would have an influence on the interpretation of the phylogenetic relationships of many animal phyla. One of such questions is the symmetry of the first Metazoa. Radiata uniting “lower” animals with radial symmetry have been considered to represent more primitive animals than Bilateria uniting Metazoa with a bilaterally symmetrical body. For this reason, radial symmetry is tradi-

tionally considered to be the body symmetry of the first metazoans. On the other hand, some analyses of symmetry in animals has suggested that radiality is a secondary feature and so is not a symmetry of ancestral Metazoa (Willmer 1996 and reference therein). Cnidarians are a metazoan group uniting animals with both body symmetries, bilateral Anthozoa (disposition of mesenteries, muscles and siphonoglyphs) and radial Hydrozoa (Willmer 1996). Resolution of the question whether evolution has been from hydrozoan ancestors to later anthozoans or vice versa is of crucial significance for our understanding of the evolution of the early Metazoa. For a solution to the latter question we have to analyze all the available data on the phylogeny of the Cnidaria. The present paper describing an unknown life strategy of the Silurian Anthozoa represents a small contribution to this subject.

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References

- Bather, F. A.* (1923): The shell of *Cornulites*. – Geol. Mag., London, 60: 542–545.
- Fischer, D. W.* (1962): Small conoidal shells of uncertain affinities, W98 – W143. – In: Moore, R. C. (Ed.) Treatise on invertebrate paleontology, Part W, Miscellanea. – The University of Kansas and The Geological Society of America, Inc., New York and Lawrence, Kansas, W1–W259.
- (1966): Small conoidal shells of uncertain affinities, W98 – W143. – In: Moore, R. C. (Ed.) Treatise on invertebrate paleontology, Part W, Miscellanea. – The University of Kansas and The Geological Society of America, Inc., New York and Lawrence, Kansas, W1–W259.
- Glaesner, M. F.* (1984): The Dawn of Animal Life. A biohistorical study. – Cambridge University Press.
- Gnoli, M.* (1992): The problematic organism *Kolihaia sardiniensis* sp. nov. of the latest Wenlock – earliest Ludlow of SW Sardinia. – Boll. Soc. Paleont. Ital., Modena, 31(3): 383–385.
- Hill, D.* (1956): Rugosa, F233 – 245. – In: Moore, R. C. (Ed.) Treatise on invertebrate paleontology, Part F, Coelenterata. – The University of Kansas and The Geological Society of America, Inc., New York and Lawrence, Kansas, F1–F498.
- (1981): Rugosa and Tabulata. – In: Teichert, C. (Ed.) Treatise on invertebrate paleontology, Part F, Supplement 1. – The Geological Society of America, Inc. and The University of Kansas, Boulder, Colorado and Lawrence, Kansas, F1–F762.
- Prantl, F.* (1946): *Kolihaia eremita* gen. et sp. nov. (Annel. Tubicola) ze středěčeského siluru (*Kolihaia eremita* nov. gen., nov. spec. a new Tubicolar Annelide from the Silurian of Bohemia). – Věst. Král. Čes. Společn. Nauk, Tř. mat.-přírodověd., Praha, (24): 1–12.
- Richards, R. P.* (1974): Ecology of the Cornulitidae. – J. Paleont., Tulsa, 48(3): 514– 523.
- Schäfer, W.* (1972): Ecology and palaeoecology of marine environments. – The Univ. of Chicago Press, Chicago, 1–568.
- Sokolov, B. S.* (1962): Gubki, archeociaty, kishchnopolostnye, chervi. – In: Orlov, Yu. A. (1962) Osnovy paleontologii, Moskva, 1–430.
- Turek, V.* (1990): Comments to upper Wenlock zonal subdivisions in the Silurian of Central Bohemia. – Čas. Min. Geol., Praha, 35(4): 337–353.
- Willmer P.* (1996): Invertebrates relationships – patterns in animal evolution. – Cambridge University Press, 400 pp.

Epiplanktonní anthozon, *Kolihaia eremita* Prantl, 1946 (Cnidaria), ze siluru pražské pánve (Čechy)

Nový materiál umožňuje přiřadit epiplanktický druh *Kolihaia eremita* Prantl, 1946, považovaný za červa nebo kornulitida, ke kmeni Cnidaria a pravděpodobně k Rugosa nebo Tabulata.

Explanations of plates

Plate I

Kolihaia eremita Prantl, 1946, Koněprusy near Beroun, Bohemia, Motol Formation, Wenlock, Sheinwoodian, *Monograptus belophorus* Biozone:

- 1 – detail view of specimen JK 8369 showing branched radiform processes, x20.
- 2 – detail view of specimen JK 8383 showing whitening around the aperture, x10.
- 3 – specimen JK 8376a, x25.
- 4 – detail view of corallite, specimen JK 8372, x20.
- 5 – detail view of specimen JK 8383a showing branched radiform processes, x30.
- 6 – specimen JK 8390a, showing an apex of the corallite, x20.

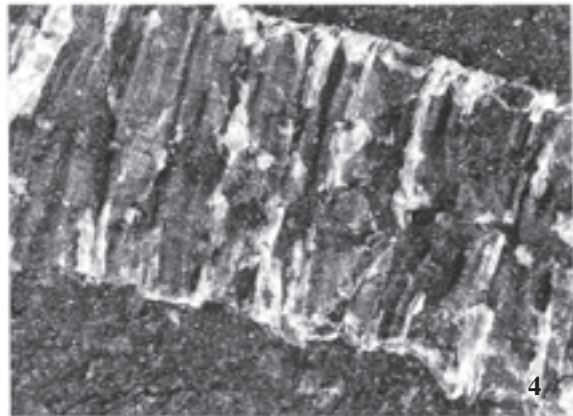
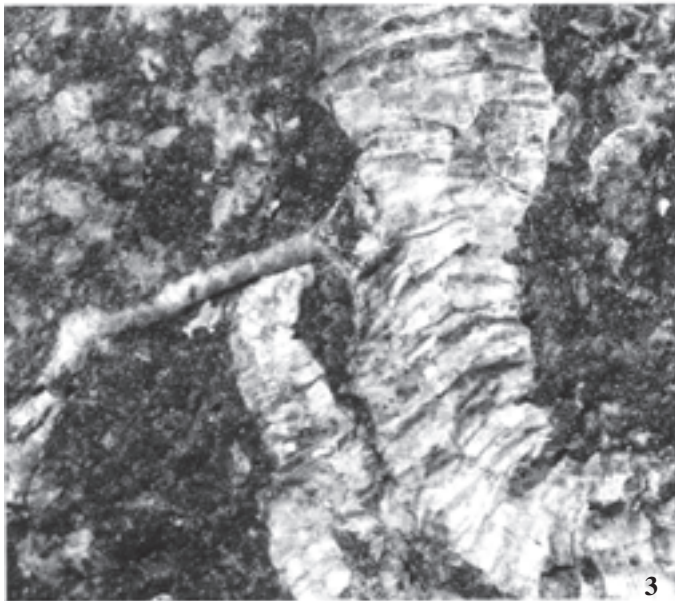
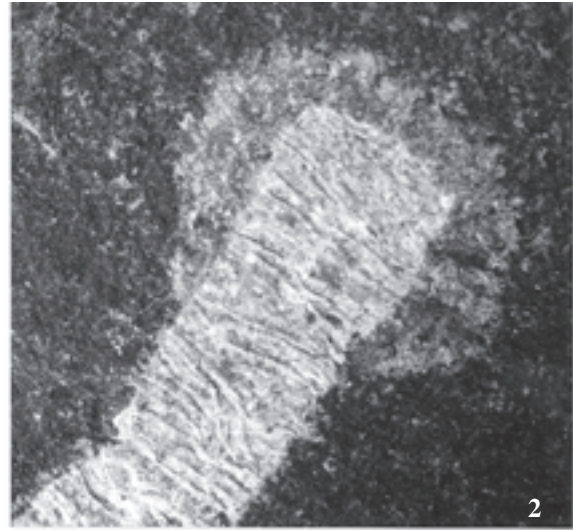
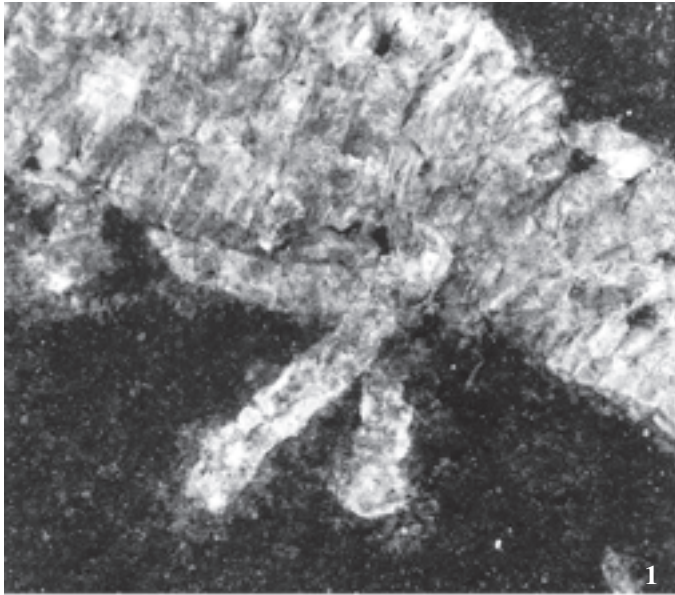
Plate II

Kolihaia eremita Prantl, 1946, Koněprusy near Beroun, Bohemia, Motol Formation, Wenlock, Sheinwoodian, *Monograptus belophorus* Biozone:

- 1 – specimen JK 8388, x40.
- 2 – detail view of specimen JK 8369 showing whitening around radiform processes, x10.
- 3 – detail view of branched radiform process, specimen JK 8379a, x45.
- 4 – specimen JK 8393a, x25.
- 5 – specimen JK 8370, x30.



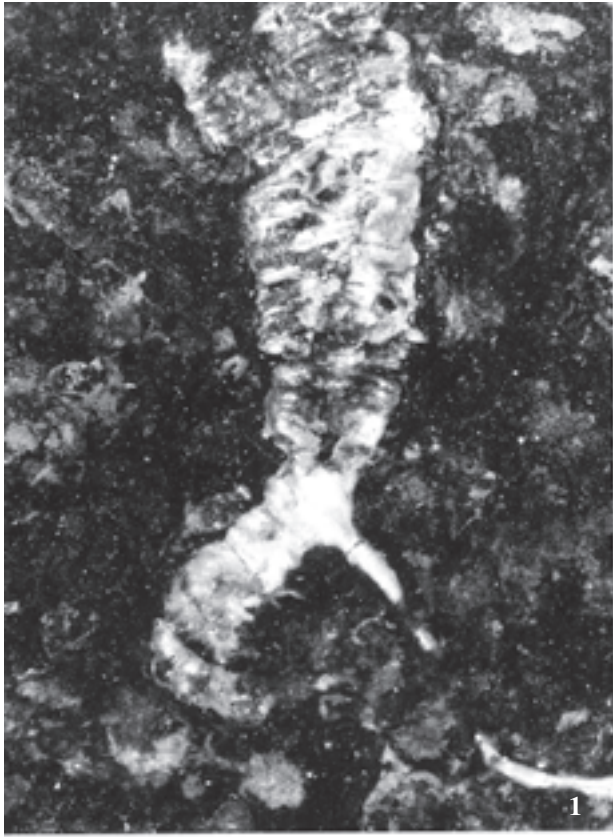
J. Kříž – J. Frýda – A. Galle: The epiplanktic anthozoan, *Kolihaia eremita* Prantl, 1946 (Cnidaria), from the Silurian of the Prague Basin (Bohemia) (Pl. I)



For explanation see p. 243



J. Kříž – J. Frýda – A. Galle: The epiplanktic anthozoan, *Kolihaia eremita* Prantl, 1946 (Cnidaria), from the Silurian of the Prague Basin (Bohemia) (Pl. II)



For explanation see p. 243

