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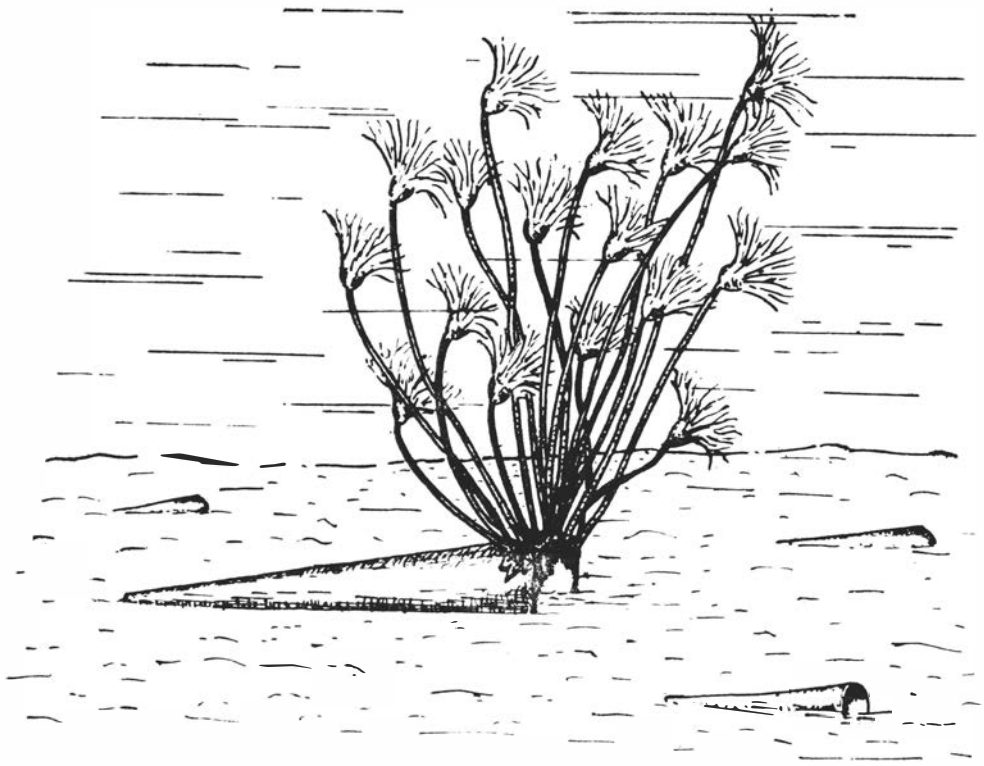
paleozoologie

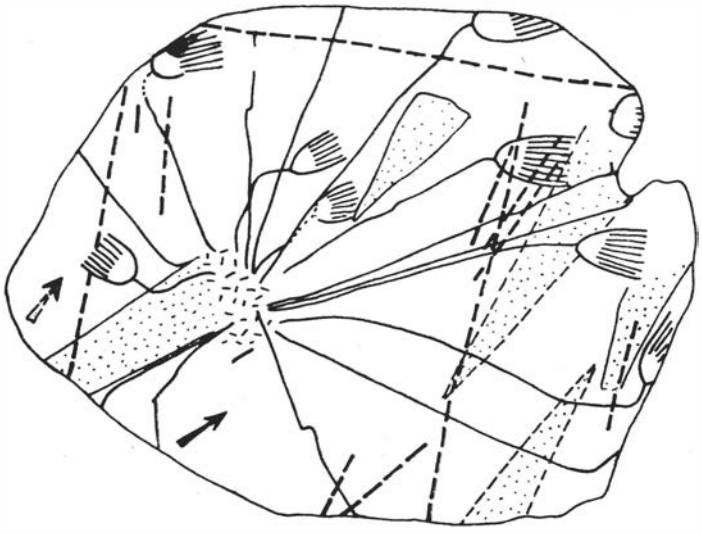
UNIKÁTNÍ NÁLEZ SILURSKÝCH FLEXIBILNÍCH KRINOIDŮ, PŘISEDLÝCH NA SCHRÁNKU ORTHOKONNÍHO NAUTILOIDA

Při revizi starých fondů uložených ve sbírkách paleontologického oddělení Národního muzea v Praze byl nalezen úlomek černé vápnité, slabě kontaktně metamorfované břidlice, která podle původní etikety pochází z vrstev Ee1 z lokality „Dvorce". Na její vrstevní ploše je mj. zachováno 17 krinoidů (z toho 9 se zachovanými korunami), upevněných bázemi stonků k apertuře schránky orthokonního nautiloida. Zjistit přesné stáří břidlice je dosti obtížné. Podle litologické povahy horniny a nevalně zachovaných graptolitů z okruhu druhů *Monoclimacis flumendosae* nebo *M. hemipristis* (podle určení A. Přibyla), náleží břidlice stratigraficky k liteňskému souvrství svrchního wenlocku. Nález je pozoruhodný nejen proto, že se jedná o první zjištění flexibilních krinoidů v graptolitové facii středočeského siluru, ale zejména z hlediska paleoekologického.

1. — Rekonstrukce dna s žijící „kolonií" flexibilních krinoidů přisedlých na schránku ortokonního nautiloida, x 0,7

1. — Reconstruction of the sea bottom with living „colony" of flexible crinoids attached to the shell of an orthocone nautiloid, x 0,7





2. — Schéma úlomku břidlice s vyznačenou orientací fosilií na vrstevních plochách. Plnou čarou jsou značeni krinoidi, hlavonožci a graptoliti na svrchní ploše, předpokládaný směr proudu ukazuje plná šipka. Úlomky rhabdosomů graptolitů a schránky hlavonožců ze spodní plochy břidlice jsou značeny čárkovaně, směr proudění označen prázdnou šipkou, x 0,6

2. — Schematic orientation of fossils on shale bedding planes. The crinoids, cephalopods and graptolites on the upper plane marked by solid line, proposed current-direction by solid arrow. The remains of graptolites and the cephalopod shells from the lower plane marked by dashed line and the current-direction by empty arrow, x 0,6

Z charakteru zachování a pozice nalezených fosilií lze učinit následující závěry (podrobněji viz anglický text): Flexibilní krinoidi, blízcí rodu *Protaxocrinus* SPRINGER, se usadili v poměrně krátké linii u okraje apertury schránky ležící na dně a částečně již zabořené do substrátu. Nelze akceptovat předpoklad, že se larvy krinoidů usadily na schránku živého hlavonožce, ani na prázdnou, dosud plovoucí, tj. nekroplanktonní schránku. K zakotvení larev krinoidů mohlo dojít postupně, ale je pravděpodobnější, že k němu došlo víceméně současně. Co se týče způsobu života nalezených krinoidů, lze konstatovat, že patřili k bentózním rheofilním formám s pohyblivými korunami, širokou plochou ramenního vějíře a dlouhými, jemnými, pružnými stonky, které sloužily ne jako podpůrné, ale jen upevňovací zařízení. Koruny se vznášely nad dnem, neseny vztlakem mírného, ale persistujícího proudu. Různou velikost krinoidů a různou délku jejich stonků (přestože jde o dospělé exempláře), lze interpretovat jako důsledek adaptace jedinců v „kolonii", tj. snahou o vyplnění prostoru v různých hladinách nad dnem, což bylo z hlediska zachycování potravy nejvýhodnější.

Postmortální uložení krinoidů na vrstevní ploše je víceméně radiální vzhledem k ústí schránky hlavonožce. Krinoidi leží v jedné horizontální rovině a lze proto předpokládat, že uhynuli zároveň. Příčinou zániku celé kolonie mohl být výron bahenních plynů ze dna, který způsobil přímou otravu kolonie, nebo pokles hladiny kyslíku pod životní minimum. Jinou příčinou mohl být třeba jen lokální a krátkodobý pokles perzistujícího proudu, takže se koruny lilijic neudržely ve vznosu a bezmocně klesly na dno. První varianta je však vzhledem k zřetelnému usměrnění všech fosilií pravděpodobnější. Zachovaná thanatocenóza na obou stranách břidlice, vzdálených od sebe cca 5 mm (krinoidi, 5 schránek hlavonožců a 12 rhabdosomů graptolitů) dokazuje, že během sedi-

mentace této vrstvičky nedošlo k výraznější změně hydrodynamických poměrů (srovnej text obr. 2). Dále umožňuje determinovat vektorovou veličinu proudění a navzájem konfrontovat usměrnění schránek a koster tří skupin organismů. Z celkového počtu 5 schránek orthokonních nautiloidů 4 směřují vrcholem v podstatě proti proudu, jedna je orientována obráceně. Přestože toto pozorování o orientaci schránek orthokonních nautiloidů nelze generalizovat, domníváme se, že jde o cenný poznatek, který by bylo třeba v břidličné facii českého siluru dále ověřovat. Zejména na lokalitách s hojnějším výskytem hlavonožců spolu s další faunou, která může proudění přesněji determinovat.

K tisku doporučil dr. Josef Beneš

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A UNIQUE DISCOVERY OF SILURIAN FLEXIBLE CRINOIDS ATTACHED TO AN ORTHOCONE NAUTILOID SHELL

While revising early materials housed in the collection of the Palaeontological Dept., National Museum, Prague, the present authors discovered a fragmentary, black, weakly contact-metamorphosed calcareous shale with an poorly preserved orthocone nautiloid. The nautiloid shell bears 17 crinoids attached by their stem bases to its orifice and post mortem distributed more or less radially along its bedding plane. Nine crinoid specimens are nearly complete; the remaining specimens are stems not uncommonly reaching the fragmentary shale border. Furthermore, two small fragmentary shells of orthocone, crinoid-free nautiloids have been found together with minute graptolite remains to lie in the close proximity of the nautiloid mentioned earlier. The lower part of the ca. 5 mm-thick shale is covered by two additional, strongly compressed shells of orthocone nautiloids and some 10 incomplete remains of graptolite rhabdosomes, the latter attaining as much as 105 mm in size in one specimen. The high compression of otherwise clearly visible graptolite rhabdosomes makes their precise identification difficult. Dr. Přibyl places them in the species *Monoclimacis* ex. gr. *flumendosae* or *Monoclimacis hemipristis* ranged to the Upper Wenlockian, an equivalent of the upper part of the Liteň Formation. This stratigraphical assignment is supported both by the mode of graptolite preservation and by the weak contact metamorphism of the shale. The other fossils also show a poor state of preservation. The original, mostly aragonite cephalopod shells are leached. Crinoid skeletal elements built up of more stable calcite are more prominent, particularly their stems. Fine structures of the calyces and arms are partly covered by the rock or preserved only as impressions. Additional studies were also hampered by the fact that the shale is broken, glued and damaged especially at the crinoid attachment to the cephalopod shell margin.

The shale is labelled Ee1 (former designation), loc. Dvorce. This name was previously used to denote both the quarry of the former cement factory „V Dvorcích" in Prague-Podolí and small exposures in the sequence of shale, limestone, tuff and diabase on the slope south of that quarry, just above the former community Dvorce.

Data on the locality and discoverer (donator?) were provided by A. Frič (Mr. Bukovský), with O. Jaekel's attached label *„Nach der Gesammtform der Kronen wohl am ehesten zu den Articulosa in der Nähe von Taxocrinus zu stellen,* Jaekel".

We are assentially in agreement with O. Jaekel's opinion regarding the systematic position of the crinoids. As may be judged from the long, thin and flexible stems attached by their muscles (i. e. movably) to the calyceal base, and with regard to the principal shape and pattern of the fine calyces, it is assumed that the crinoids under consideration are those of flexible nature, showing close affinities to the genus *Protaxocrinus* SPRINGER, 1906. Although the crinoids are impossible to identify in greater detail because of their poor state of preservation, it is evident that they are the first representatives of the order *Flexibilia* ever recorded from the Silurian shale facies of Bohemia.

The find is remarkable especially in paleoecological context. The calcareous graphitic shale facies, with its disseminated pyrite in the Liteň Formation of the Bohemian Silurian, consists of sediments of a deeper, ill-aerated sea bottom with weak currents. The shallow muddy bottom did not create favourable conditions for benthonic animal attachment, including crinoids. Various shells of invertebrates, particularly those of mollusks, may have served as a reliable substratum for larvae or adult crinoids to attach to the sea floor. Crinoid attachment to cephalopod shells is fairly frequent but so far has not been explained in a satisfactory manner (comp. e. g., J. Bouška 1946, O. Ganss 1937, R. J. Prokop 1976, pl. I, fig. 3). But the attachment of 17 crinoids to one cephalopod shell is quite a unique event not recorded so far. This leads us to the following conclusions:

a) Crinoid attachment

1. The crinoids did not attach to the cephalopod until after the death of the orthocone nautiloid, with its shell laid down and partly sunken into the surrounding sediment. The assumption that the shell to some extent sank into the sediment is supported by the fact that all the 17 crinoids lie in one line extending over a relatively short distance along the shell margin. The line coincides with an apical part of the curve forming the free shell margin above the bottom. There was a tendency for the stems to attach to the apertural margin rather than to the rounded shell surface. This may to some extent be analogous to the crinoid attachment to the margin of transverse fractures of a floating wood (comp. J. W. Wells 1939, 1941).

2. It can generally be stated that a living and hence defensible cephalopod prevented crinoids from being attached to, and subsequently developing on, its shell (cf. point 4). Furthermore, the inner shell margin of the cephalopod in life was in immediate contact with its mantle and the inner apertural margin was thus impossible to serve for attachment.

3. Nor can it be assumed that crinoid larvae had settled on an empty still floating, i. e. necroplanktonic nautiloid shell. If so, the larvae or adult crinoids would have inhabited the entire apertural periphery. In our case, however, the crinoids have been found grouped over a short distance and post mortem decomposed radially, but none of them have been observed under the dissolved cephalopod shell.

4. Evidence supporting this assumption also stems from the fact that the necroplanktonic stage of minute shells of Paleozoic cephalopods was relatively short, lasting probably a few days to weeks. On the contrary, the crinoids dealt with in this paper are adults requiring for their ontogenetic stage at least several months, as may be judged by analogy with recent types.

5. This type of crinoids may have been settled either in larval or adult stage. We believe that in this particular case it was the larvae that found their fixed and permanent position, as may be inferred from the extinction of all specimens in response to changing ecological conditions. As a result, they were incapable of detaching in danger from the cephalopod shell to occupy a new site. It must be pointed out, however, that this statement is left open to further discussion on p. 185.

b) Crinoids under study: Their mode of life

6. The flexible crinoids discussed in this paper belong to benthonic rheophile forms having movable cups, a broad arm fan and a long, fine, elastic stem serving not as a supporter but merely for their attachment. The cups float above the bottom under the action of buoyant current (see text-fig. 1). Weak but persistent currents are needed by the cups to float. Evidence supporting our assumption regarding the current intensity in the sedimentation basin of the graphitic shales of the Liteň Formation is provided by the predominant arrangement of the faunal remanins on the bedding plane of the described sample (see also discussion on p. 185).

7. Various sizes of the specimens and different lengths of their stems, however adult they may be, indicate that the persistent current flow occurred at a certain level above of the sea bottom. It is assumed that the crinoid larvae settled at once and that the size differences in the specimens are due to a various environmental adaptation or an ontogenetic differentiation within a „colony". The possibility cannot be ruled out, however, that the crinoid larvae may have attached to the solid basement of the cephalopod shell at several stages. The specimens attached earlier have a longer stem and may have inhabited higher-lying levels above the muddy bottom under more favourable feeding conditions. On the contrary, crinoids attached to the cephalopod shell at a later stage or stages posses finer skeletons, attain smaller sizes, and lived at lower-lying levels.

c) Supposed causes of crinoid extinction

The crinoid remains were post mortem distributed radially related to the nautiloid shell aperture, with one stem resting on the shell margin and the two extending along its length. As all the stems lie in one horizontal plane, it may be inferred that the crinoids died all at once. The ill-aerated sedimentation environment of black pyrite-rich shales in large part created extreme conditions for life of the benthonic crinoids with any change leading to considerable consequences. It is thus possible that a whole „colony" was destroyed by such mud gases as CO_2, CH_4 or H_2S escaping from the bottom. This is not to say that the „colony" was directly poisened by the gases, but that the extinction was caused by the lowering of oxygen level below its critical point.

In our opinion, the sudden death of the crinoids can also be explained by the local change in the intensity of a persistent current originally supplying food to them and keeping their cups upwards. If an obstacle made the current change its original direction and prevented it from reaching the living crinoid „cluster", food supply ceased and even thin stems were unable to keep fairly large crinoid cups upwards. Consequently the crinoids helplessly fell down to die on the sea bottom (see the principal radial arrangement of their remains on the bedding plane). Most of the cups did not change their position until after death by a weak residual current on the bottom. The residual current also allowed extinct remains to be covered by a mud sediment and prevented the finely structured skeletons of flexible crinoids from being decomposed. That the nautiloid shell was weakly distorted after the crinoids had died and sunk to the bottom is also indicated by the slight asymmetry in the distribution of crinoid basal parts.

Remarks

The find discussed in this paper is also note worthy in that it shows a thanatocoenosis of three groups of organisms, their shells and skeletons being arranged in a distinct manner. Fragmentary graptolite rhabdosomes and orthocone nautiloid shells are not usually suitable for interpreting the current direction in an unequivocal manner, whereas fine, freely moving cups of flexible crinoids are. It is thus possible to deduce reversibly local hydrodynamic conditions and to compare the „behaviour" of extinct shells and skeletons on the floor. The text — fig. 2 scheme shows both bedding planes of the studied samples some 5 mm apart. All the preserved crinoid crowns are more or less perfectly orientated or at least indicate the current effect on their position on the bottom. No marked variation has been noted in the current direction during the sedimentation of the layer. With the exception of a single fragment, all straight graptolite rhabdosomes are arranged in a similar manner, as are also the cephalopod shells. Of the five nautiloid shells resting on both bedding planes, four have their apical parts orientated countercurrentwise and only one is inverted. The position of the empty cephalopod shells related to the current direction is controlled by several factors (cf. R. A. Reyment 1958, V. Turek 1974). Experimental modelling of these conditions is by no means an easy task, and the results available still suffer from obvious imperfections. In the „Orthoceras" limestones of the Central Bohemian Silurian cephalopod shells mostly follow one direction, with their aperture orientated more or less in a uniform manner. Their relationship to the current direction is not yet based on reliable evidence. As may be inferred from the specimen under study, this problem might ultimately be resolved, at least in the Barrandian area, by investigations in the shaly facies of the Central Bohemian Silurian rather than in „Orthoceras" limestones. Studies should be concentrated on the localities yielding cephalopods accompanied by other fauna, particularly graptolites. The latter are useful especially in that their rhabdosomes may unequivocally indicate the current direction, especially if attached to, and deviated from their original direction by, an obstacle on the sea bottom.

VYSVĚTLIVKY K TABULKÁM

Tab. I.

Úlomek břidlice se 17 krinoidy přisedlými k apertuře schránky ortokonního nautiloida. Praha-Dvorce, silur, liteňské souvrství, x 1. Sbírky Národního muzea v Praze, kat. č. NM — L 20041.

Tab. II.

1. Detail apertury schránky hlavonožce s proximálními částmi stonků přisedlých krinoidů. Báze stonků odlomeny; cca 2,3 x.
2. Detail korun flexibilních krinoidů s distálními částmi dlouhých stonků; cca 2,3 x.

Tab. III.

1. Detail koruny krinoida s krátkým stonkem, spolu s masívními dlouhými stonky krinoidů žijících ve vyšších potravních hladinách; cca 2,3 x.
2. Původní etiketa s Jaekelovými poznámkami k nálezu; cca 1,5 x.

Běleno chloridem amonným, foto Vojtěch Turek.

EXPLANATION OF THE PLATES

Pl. I.

Shale fragment with 17 crinoids attached to the aperture of an orthocone nautiloid's shell. Praha-Dvorce, Silurian, Liteň Formation, x 1. Collections of the National Museum, Prague, cat. no. NM — L 20041.

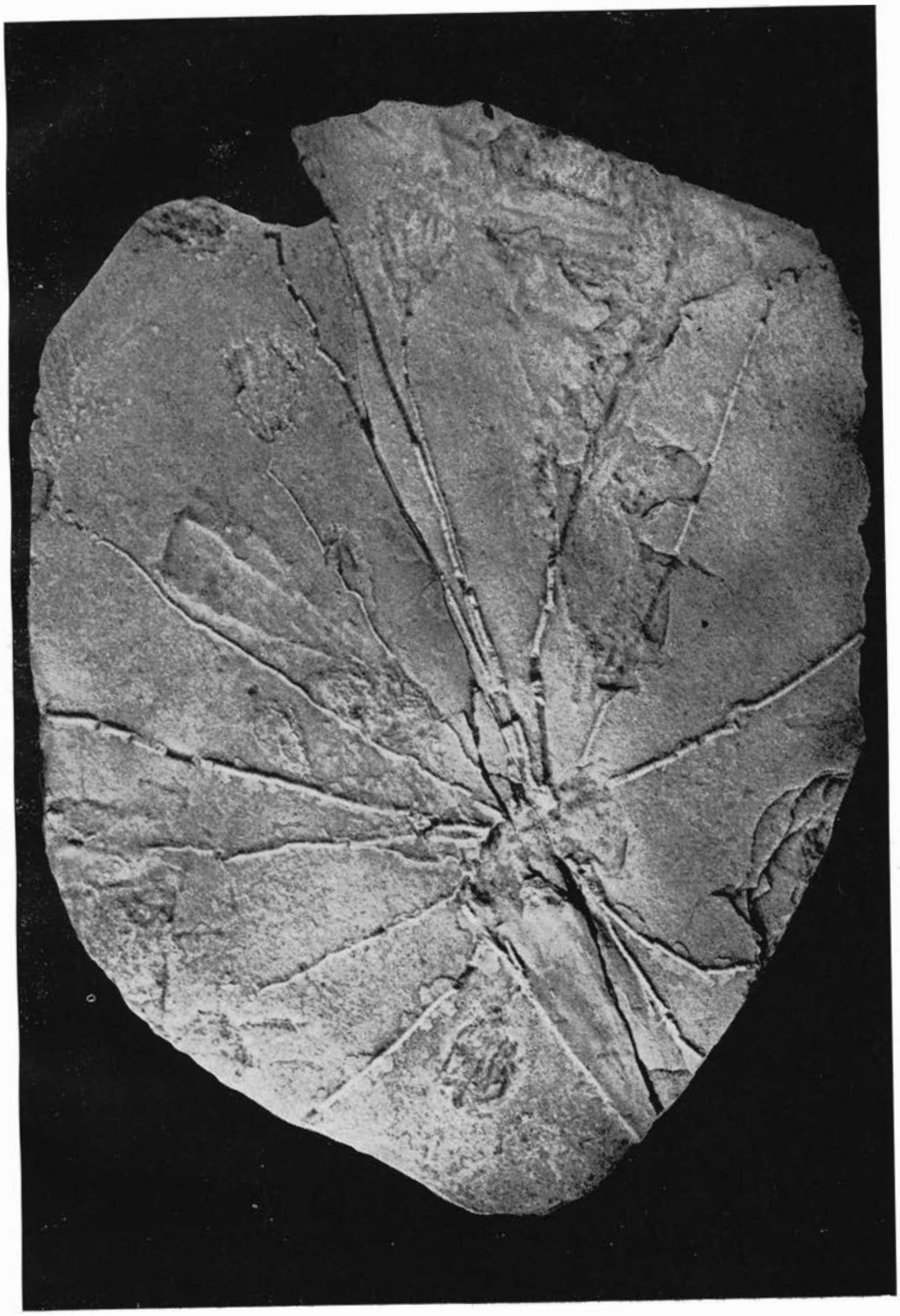
Pl. II.

1. Detail of the aperture of nautiloid shell with the proximal parts of attached crinoids. Stems' bases are broken off; cca 2,3 x.
2. Detail of the crowns of flexible crinoids with distal parts of a long stems; cca 2,3 x.

Pl. III.

1. Detail of the crinoid's crown with the short stem, together with the massive long stems of crinoids lived in the higher feeding-levels; cca 2,3 x.
2. Original label with Jaekel's comments, cca 1,5 x.

Whitened by amonium chloride, photographs by Vojtěch Turek.

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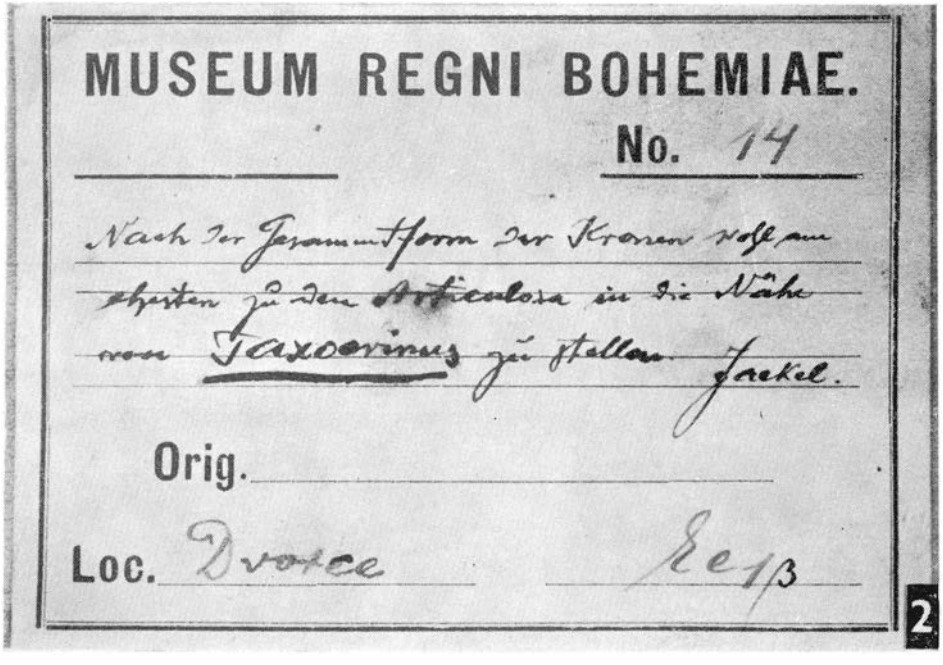
MUSEUM REGNI BOHEMIAE.
No. 14
Nach der Gesammtform der Kronen wohl am
ehesten zu den Articulosa in die Nähe
von Taxocrinus zu stellen. Jaekel.
Orig.
Loc. Dvorce Er 1/3

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