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REVISION OF MORPHOLOGY AND ECOLOGY OF BOHEMURA JAHNI JAEKEL, 1903 (OPHIUROIDEA, PROTASTERIDAE) FROM BOHEMIAN MIDDLE ORDOVICIAN

INTRODUCTION

The material of the discussed rare ophiuroid *Bohemura jahni* Jaekel, 1903 was originally collected by J. Barrande at the well-known Middle Ordovician locality Zahořany near Beroun, Barrandian area (Berounian stage, Zahořany Formation, corresponding approx. to Upper Caradocian). In Barrande' s collections these brittle-stars were designated as *„Asterias Bohemica"*, but this manuscript name was only mentioned in BIGSBY (1868, p.197). J. Barrande published no paper on the Bohemian asterozoans. The first description and illustration was given by O. JAEKEL (1903, short notes p. 109, 110, 112, text-fig. 6, p. 111). His description was only brief, but the text-figure showing oral side of one arm, MAPs, and outline of the disk of the ophiuroid was good, only slightly incorrect in shape of the „boot-shaped" ambulacral ridges, in number of ambulacrals in the disk, in length of groove spines, and in shape of the disk margin. In this Jaekel's work the brittle-star was named *Bohemura jahni.* The above mentioned figure was reproduced by SCHUCHERT, (1915, p. 224, fig. 21) but Schuchert did not study the original material. This was lent to W. K. Spencer who made from the specimens gutta-percha impressions (at least from the specimen NM L 10066 which is the lectotype now) and presented some remarks, short diagnosis, and an illustration (SPENCER, 1934, p. 479, p. 473, fig. 305), however, no photographs. Unfortunately, the Spencer's drawing is incredibly incorrect and invented, and is reproduced in SPENCER and WRIGHT (1966, in Treatise..., p. U86, fig. 75 2a). The original material (10 slabs) was sent back from London after the Second World War, and was deposited in collections of the Paleontological Dept. of the National

Museum (abbrev. NM), Praha. Only one incomplete specimen is added now to the original material from new findings (collected at the original locality by a lucky chance by dr. R. J. Prokop from National Museum, Praha). Although the original material reflects many details not only of oral sides, but also of aboral aspects of the specimens, nothing was written about the aboral side of *Bohemura jahni.* No correct illustrations were made, and no photographs were given by the previous authors. *Bohemura jahni* not defined in great detail by any of the previous authors. Therefore, photographs of latex casts, new figures, and a detailed description are presented in this paper. A new diagnosis for the genus *Bohemura* Jaekel, 1903, and a modified diagnosis for the family *Protasteridae* S. A. Miller, 1889 are given. New conclusions are made about the ecology and feeding behaviour of *Bohemura jahni.*

The author is much indebted to dr. R. J. Prokop from the National Museum, Praha for lending the material, and for all his kind help.

DESCRIPTIVE PART

Class *Stelleroidea* LAMARCK, 1816

Subclass *Ophiuroidea* GRAY, 1840

Order *Oegophiurida* MATSUMOTO, 1915

Suborder *Lysophiurina* GREGORY, 1896

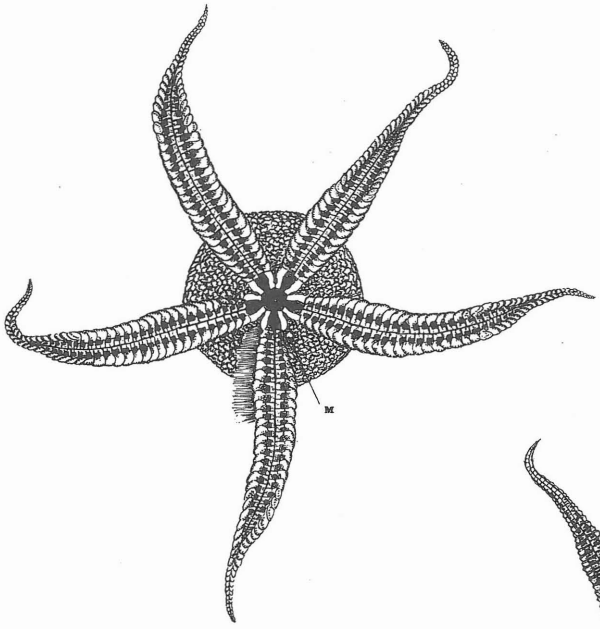
Family *Protasteridae* S. A. MILLER, 1889

Diagnosis (after SPENCER and WRIGHT, 1966, in Treatise..., p. U87, and after KESLING, 1970, p. 74, modified):

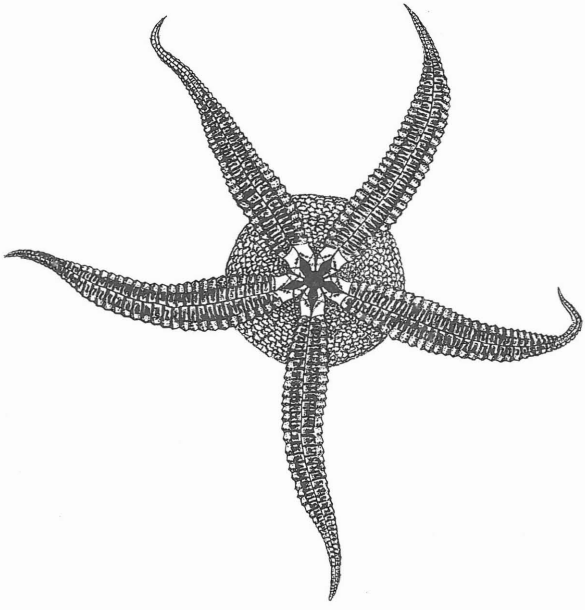
Laterals wrapped around sides of arms, forming side shields; no thickening or marginal frame on the edges of disk; oral sides of ambulacrals provided with „boot-shaped" ridges; laterals with vertical (distal) spines; groove (oral) spines commonly present.

Remarks: There are two modifications of the original diagnosis of SPENCER and WRIGHT (1966, in Treatise..., p. U87) in the diagnosis stated above. After Spencer and Wright the „edges of disk may be thickened but have no well-developed marginal frame". It must be rectified here because no thickening of edges of disk (in life), and no good or poorly developed marginal frame are present in any of the species of the family *Protasteridae.* The thickening of the edges of disk may be present in protasterids preserved as fossils but it was not present in life. This thickening of the disk margins in some species (e. g., *Taeniaster spinosus* (Billings, 1857), *Bohemura jahni* Jaekel, 1903, and *Strataster ohionensis* Kesling et Le Vasseur, 1971) is evidently caused by folding of the disk which is in the fossils much flatter than it was in life. This fact was previously reported e.g., by HOTCHKISS (1970, p. 67) for *Taeniaster spinosus.* Protasterids possibly may have possessed a rather rotund disk which indubitably has collapsed after death. SPENCER (1934, p. 473 — fig. 305, p. 475 — fig. 307, p. 477— fig. 308) figured *Bohemura jahni* Jaekel, 1903 and *„Bohemura" groomi* Spencer, 1934 as brittle-stars with distinct marginal plates on the edges of their disks. Owing to these text-figures „marginalia in protasterids" entered into the paleontological literature. In fact, these

„marginalia" exist only in the incorrect Spencer's drawings. Even, SPENCER (1934, p. 479) wrote: „*Bohemura jahni*... Specific characters. — Disc without marginalia..." The latter note is only 6 pages later than his figure of *Bohemura jahni* with marginalia. This figure was reproduced by SPENCER and WRIGHT (1966, in Treatise..., p. U86, fig. 75 2a) and, therefore, the poorly developed marginalia were by these authors added to the diagnosis of the whole family. The present author did not study the original material of „*Bohemura*" *groomi* Spencer, 1934, but from the photographs given by SPENCER (1934, Pl. 30, figs. 1—4) it seems to be evident that the latter are very different from the text-figures 307, 308 which are probably also very incorrect and invented. There is no marginal frame visible on the photographs.



Text-fig. 1a): Schematic sketch of the oral face of the brittle-star *Bohemura jahni* Jaekel, 1903. Groove spines almost omitted. M ... madreporite. × 2/3.



Text-fig. 1b): Schematic sketch of the aboral face of the brittle-star *Bohemura jahni* Jaekel, 1903. Vertical spines, and the integument covering mouth frame and arms are omitted. × 2/3.

In the diagnosis of SPENCER and WRIGHT (1966, in Treatise..., p. U87) there is also a second note which needs modification: „oral edges of ambulacrals narrow". This note possibly expresses the small width of the ambulacral „boot-shaped" adaxial ridge (see KESLING, 1970, p. 74). However, the shape and width of these ridges are very variable. In the proximal part of ambulacrals, i.e., where the „boot" covers the „foot", there is the ridge typically almost as wide as the ambulacral ossicle itself. So, the note „narrow oral edges" can be replaced by „boot-shaped ridges". However, the term „boot-shaped" must be used only conventionally because the shape of the raised ridges on the oral surface of ambulacrals commonly leaves in resemblance to „boot" much to imagination (KESLING and LE VASSEUR, 1971, p. 325). In the classical sense the „boot" is oriented with „sole" in proximal end, outlining the proximal excavation for the insertion of ventral longitudinal muscles, with top of the „leg" outlining the distal excavation for the insertion of ventral longitudinal muscles, and with the „toe" pointing outwards. Directly in the „toe" there is a socket for attachment of the adambulacral „nose".

It is also necessary to notice that almost all of the protasterid genera are in need of redefinition. The diagnoses given by SPENCER and WRIGHT (1966, in Treatise..., p. U87) are very short, incomplete, and sometimes incorrect (see also HOTCHKISS, 1970; KESLING, 1970; and KESLING and LE VASSEUR, 1971). Many type-specimens are in need of reexamination. Many species are inadequately or poorly described. No details are visible on the photographs given by Spencer, and his figures are probably all much invented. The protasterid genera, therefore, are also of exceptional geologic duration (commonly from Middle Ordovician to Lower Carboniferous). It is unlikely that such active and ecologically responsive animals were so conservative (KESLING, 1969, p. 38).

Stratigraphic and geographic distribution: Middle Ordovician — Lower Carboniferous; North America (U.S.A. and Canada), Europe (England, Wales, Germany, Belgium, France, and Bohemia), and U.S.S.R. (South Kazakhstan).

Bohemura Jaekel, 1903

Type species: *Bohemura jahni* Jaekel, 1903; Middle Ordovician of Bohemia.

Diagnosis (new): A protasterid with extremely long adambulacral „nose"; madreporite near first two right laterals; mouth-angle plates strong and long.

Remarks: The new diagnosis of the genus is necessary because diagnoses given by previous authors were not utilizable. The diagnosis wrote by SPENCER (1934, p. 427) is incorrect. After Spencer: „Adambulacralia in proximal and median arm-regions set at a distinct angle to the groove so as to expose their inner wall". However, in some parts of some arms in several specimens of the type species the inner walls of laterals are perpendicular to the plane of the ambulacral groove. In the fossils, naturally, the inner walls of laterals, adambulacral „noses", groove spines, and ambulacrals lie commonly in the same plane, but it is due of compression. In life, the laterals were movable in these arm-regions, and were able to rotate owing to the joint of adambulacral „nose" in the socket of the „toe" of the ambulacral „boot". Therefore, the position of laterals has no taxonomic value. The

second note in Spencer's generic characteristic is: „Oral edge of adambulacralia in these same arm-regions with straight border." This is not very clear sentence, but it is evident that the laterals of the type species are provided with straight borders only at places of junction with ambulacrals, straight is the vertical ridge on the aboral side, and straight is adambulacral „nose" on the oral side. The adoral and lateral margins of adambulacrals from oral view are commonly curved in the type species. The last Spencer's note in his generic diagnosis is: „Groove spines prominent, vertical spines weak". This is also incorrect because in the type species the most abaxially situated vertical spines are of the same length as and slightly thicker than the groove spines.

The diagnosis of the genus *Bohemura* presented by SPENCER and WRIGHT (1966, in Treatise..., p. U87) is very brief, and not clear. In classification of protasterids there are no guidelines for distinguishing strong depressions for attachment of dorsal longitudinal muscles from those which are weak. The depth of the aboral depressions between ambulacrals cannot be determined in well-preserved specimens because their aboral surfaces are covered with integument (see also KESLING, 1970. p. 74). By far, some descriptions given by Spencer for the depth of above mentioned depressions are at variance. For example, in SPENCER (1934, p. 476) there is a note for the genus *Bohemura:* „Apically the ambulacralia are very weakly convex, with but slight excavations for the dorsal longitudinal muscles." However, one page later is presented a text-figure of apical view of *„Bohemura" groomi,* showing very broad and deep excavations for these muscles. It is same as with the genus *Taeniaster* Billings, 1858 (see SPENCER and WRIGHT, 1966, in Treatise..., p. U87, and compare with HOTCHKISS, 1970, p. 61, 63). After the Spencer and Wright's diagnosis of the genus *Bohemura* its depressions for attachment of dorsal arm muscles are weak. This definition is incorrect. From the original material of the type species *Bohemura jahni* at the disposal of the present author, it is evident that those depressions are broad and deep, which is seen at places affected only slightly by compression, and not covered by integument. The last sentence given by SPENCER and WRIGHT (1966, in Treatise..., p. U87) for the generic characteristic of the genus *Bohemura* is: „... articulating nose of laterals plain, distant from oral edge". The term „oral edge" is not very clear, here possibly meaning the adoral margin of laterals. If it is so, this note is also unavailable because in the type species the adambulacral „noses" are variable in position, and much more commonly are situated directly near the adoral margin of laterals.

Eventually, because no correct characteristics were given by the previous authors for genus, many strange species were placed within *Bohemura* Jaekel, 1903. The list of the species placed within the discussed genus, with a brief revision, is presented below. Except the type species *Bohemura jahni* Jaekel, 1903 which is described in great detail in this paper, the species are following:

„Bohemura" groomi Spencer, 1934, coming from Middle Ordovician (Caradocian) of Shropshire, England, is a species known from two small specimens (see SPENCER, 1934). The photographs of the paratype were presented by SPENCER (1934, Pl. 30, figs. 1—4). As mentioned here above, the photographs are very different from the Spencer's text-figures of the same specimen. Photographs show no detail, therefore, the assignment of this species to the genus *Bohemura* Jaekel, 1903 is questionable and the type-specimens need reexamination.

„Bohemura" granifer (Whidborne, 1898), coming from Lower Carboniferous of

North Devon, England (WHIDBORNE, 1898, p. 207) — one specimen, and (after SPENCER, 1934. p. 482—483) from Haut Banc near Boulogne, France — a small portion of one large arm. This species seems to be very strange. It is necessary to make latex casts from the type specimen because the gutta percha ones were not good (see SPENCER, 1934, p. 482). Possibly, this species belongs to a new genus.

„Bohemura" constellata (Thorent, 1838), coming from Lower Devonian (Lower Gedinian) of Belgium and North France, was described in great detail by UBAGHS (1942). It is a very small species, good known, with adambulacrals not similar to *Bohemura* Jaekel, 1903. The adambulacral „noses" are short and, therefore, it does not belong to the genus *Bohemura,* but to a new one.

Bohemura primaeva Fedotov, 1936, coming from Middle Ordovician of South Kazakhstan (U.S.S.R.) seems to be a good representant of the genus *Bohemura* Jaekel, 1903. Unfortunately, the present author did not see the original paper of FEDOTOV (1936), only the photographs in GEKKER (ed., 1964, Pl. 19, fig. 1—3).

Stratigraphic and geographic distribution: After the above given brief revision of species, the genus *Bohemura* Jaekel, 1903 does not exhibit such exceptional geologic duration as stated by SPENCER and WRIGHT (1966, in Treatise..., p. U87). Its occurrence is restricted to Middle Ordovician of Bohemia, and possibly of South Kazakhstan.

Bohemura jahni, JAEKEL, 1903

(All plates and figures)

1903 *Bohemura jahni* Jaekel; JAEKEL, p. 109—112, and slightly incorrect text-fig. 6.
1915 *Bohemura jahni* Jaekel; SCHUCHERT, p. 223, and text-fig. 21 on p. 224 (reproduction of text-fig. 6 of JAEKEL, 1903).
1934 *Bohemura jahni* Jaekel; SPENCER, p. 479, non text-figs. 305—306.
non 1966 *Bohemura jahni* Jaekel; SPENCER et WRIGHT, text-fig. 75 2a. (reproduction of text-fig. 305 of SPENCER, 1934).

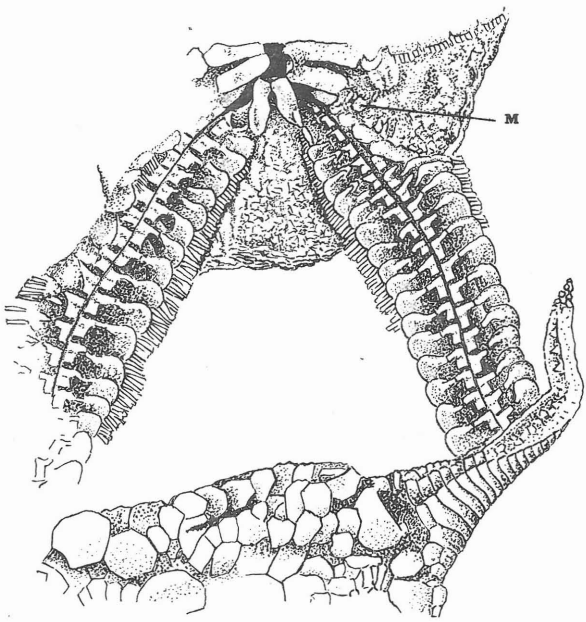
Lectotype (here stated): Specimen NM L 10066 preserved as external mould of incomplete oral face in greywacke. The brittle-star is associated with fragment of solutan „carpoid" *Dendrocystites sedgwicki* Barrande, 1887. The chosen specimen of *Bohemura jahni* served very probably as the main model for the slightly incorrect JAEKEL's (1903) text-figure 6 (reproduced by SCHUCHERT, 1915, text-fig. 21). This served certainly as the main model for SPENCER's (1934) text-figure 305, because it carries old (inventory?) number E. H. 146 and this number was mentioned by Spencer in the text to the text-fig. 305. In the present paper, the first photograph (see Pl. I) and the first drawing from photograph (see text-fig. 2) are given.

Locus typicus: Zahořany near Beroun, Barrandian area, Bohemia.

Stratum typicum: Zahořany Formation, Berounian stage of Middle Ordovician (approx. Upper Caradocian).

Material: Except the lectotype, the original material consists of 9 slabs with remains of brittle-stars: NM L 10170—10171, L 10175—10181. Except the original material, only one incomplete specimen collected at present.

Description: General shape. The disk is subpentagonal (see e. g., Pl. I,



Text-fig. 2: Lectotype of *Bohemura jahni* Jaekel, 1903 (NM L 10066) (see also PL. I.). Drawing made from a photograph. The theca with arm below belongs to solutan carpoid *Dendrocystites sedgwicki* Barrande, 1887. The specimen of brittle-star served probably as the main model for Jaekel's drawing (1903, p. 111, fig. 6) and certainly as the main model for drawing given by Spencer (1934, p. 473, fig. 305). × 1,2.

VI), its margins are slightly convex, never concave as drawn by JAEKEL (1903, p. 111, text-fig. 6). Arms are of medium length, very slightly broadening from the mouth frame to about the margin of the disk, then tapering to very thin, flexible tips. The radial arm radius (measured from the centre of the disk) is almost 4 times as long as the interradial disk radius. All specimens at the disposal have their disks of about identical radius, 20 mm. Arms extend about 75 mm. from the centre of the disk, and their diameter at the margin of the disk is one-fourth that of the disk, i. e., uniformly 10 mm. (when the inner wall of laterals is exposed and compressed into the plane of the ambulacral groove).

Disk. All disks are flattened on the bedding planes, with their oral or aboral sides above, In fossils, the margins of the disk are thickened by folding caused by collapse of the slightly rotund disk after death. No more or less developed marginal frame. The integument covering both oral and aboral surfaces of the disk, and extending onto the aboral surface of arms, is studded with dense, numerous small papillae. The latter sometimes not preserved on the oral surface of the disk. The integument is formed of an outer layer bearing the above mentioned granules or papillae, and of a lower layer hardened by a dense mosaic of very irregular scales, about 1—2 mm. in diameter. These scales are of the same type as in *Strataster ohionensis* Kesling et Le Vasseur, 1971 (p. 318), not joined by sutures (compare with the text-fig. 305 of SPENCER, 1934, p. 473, showing large, non-existent hexagonal disk plates joined by sutures). In some specimens, there are broken tips of groove and vertical spines scarcely scattered on the surface of the disk, but no disk spines or pustules for attachment of disk spines observed.

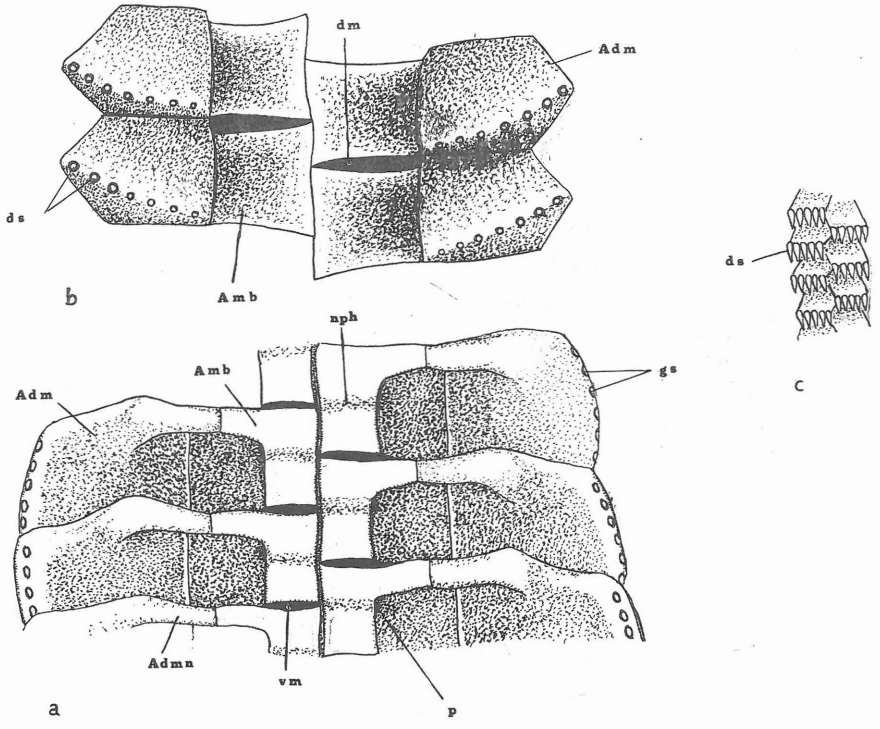
Madreporite. This plate is preserved in three specimens, but in two ones (lectotype, text-fig. 2, Pl. I, and in the specimen NM L 10181, Pl. IV, fig. 1 in the

interradius above right) not clearly discernible, represented only by a suboval to subround convex plate with smooth, weathered surface. Madreporite is very good preserved in the specimen NM L 10178 (text-fig. 6, and Pl. VII), provided with relatively dense, deep and very narrow furrows meandering on its surface. As in many protasterids, the madreporite is situated near first two laterals, particularly at about the boundary-line between the first two laterals or it can be shifted toward the first lateral. In every case, the neighbouring laterals have their inner walls overturned, touching the ambulacrals and completely disclosing the madreporite. The latter would be closed by them if they were not overturned. In life, these neighbouring laterals were possibly moving to create good water circulation through the madreporite when the brittle-star was burrowed (see also the chapter on ecology below).

Arms — general character. The arms before becoming free are very slightly broadening to about the margin of the disk. At this place and commonly yet to some distance from the disk, the arms are of greatest width. Then they taper distally to a small diameter at a distance from their very flexible tips which are very thin, tapering evenly. The laterals in the distal part of each arm converge from the two sides to close off the ambulacral groove (see e. g., text-fig. 4). The ambulacral groove of the flexible arm tips is never seen in any of the specimens. The groove is completely closed by overturning laterals and only the latter, with their vertical (not groove!) spines, are visible from the oral view. This feature, commonly present among protasterids, was possibly caused by mortal closure before death, and was preserved in rigor mortis of the ophiuroid (see KESLING et LE VASSEUR, 1971, p. 318). Therefore, it is of no taxonomic value. The whole aboral surface of arms is covered with relatively thick integument, provided with numerous small papillae which are sometimes slightly larger than those covering the disk. The integument is, however, absent from the whole oral face of arms (i. e., from oral surface of ambulacrals and laterals, if we accept that the oral surface of the latter is represented by so-called adambulacral „noses" and by „inner walls"). Both groove (ventral) and vertical (distal) spines present, well-developed.

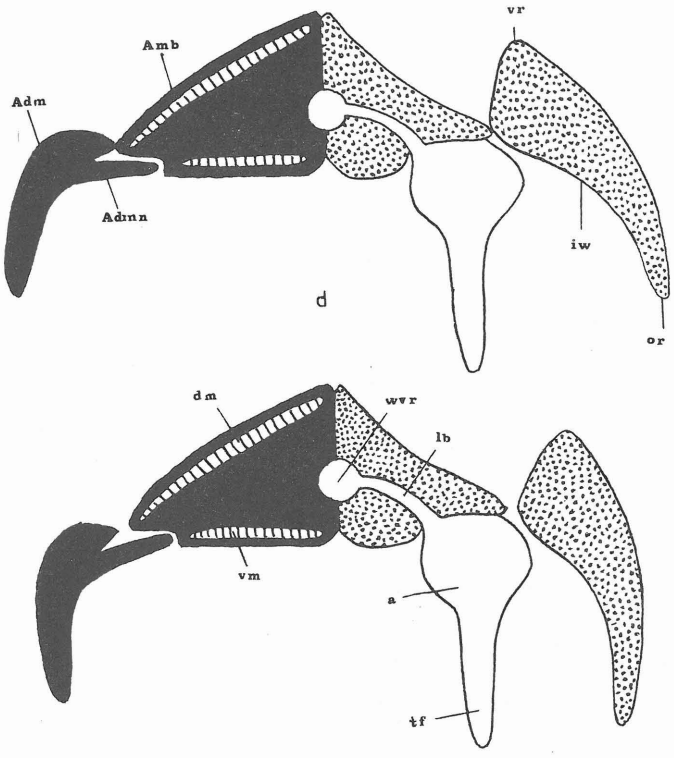
Arm plates. As seen from the specimen NM L 10175 in which one arm is preserved in its full length (Pl. IV., fig. 2), each half of an arm of *Bohemura jahni* consists of about 50 ambulacrals (below abbrev. as Amb; pl., Ambb) and 50 laterals or adambulacrals (below abbrev. as Adm; pl., Admm). Ambb are known from their oral and aboral sides (in the latter only where the integument is absent). Nothing is known about their inner sides. In cross-section, the Ambb have the shape of right-angled triangles (inner sides are at rights with oral sides) (text-fig. 3d). Ambb of the left and right sides of the arm alternate, and fit closely together. The ventral groove (or the median groove of the ambulacrum) is slightly sinuous (text-fig. 3a) and, therefore, inner face of each Amb is slightly concave to accommodate proximal and distal ends of the two opposite Ambb. No type of junction of the opposite Ambb is visible, however, it could possibly present dorsally from the radial canal of the water-vessel system. Unfortunately, as mentioned above, the inner faces of Ambb are not exposed in any of the specimens. The dorsal groove betweeen the opposite Ambb seems to be slightly narrower than the ventral groove. The insertions for the ventral longitudinal muscles are poorly visible from above because of strong compression of the adaxial „boot-shaped" Amb ridges, and because of position of these insertions more proximally and distally than orally.

They are never exposed orally to the extent as drawn by SPENCER (1934, p. 473, fig. 305, and p. 474, fig. 306a) (compare with the text-fig. 3a herein). The insertions for the dorsal longitudinal muscles are better visible from above (text-fig. 3b), and are broad and deep. However, they are also situated more proximally and distally than aborally.



Text-fig. 3a): Sketch of oral face of a portion of arm of *Bohemura jahni* drawn after several specimens, showing a typical proximal part of an arm with inner walls of adambulacrals (or laterals) compressed into the plane of the ambulacral groove. Enlarged.
Text-fig. 3b): An idealized sketch of aboral (or apical) face of a portion of arm of *Bohemura jahni* drawn after three specimens. It represents a proximal part of arm. The integument is omitted. Enlarged.
Text-fig. 3c): Sketch of oral side of an arm tip of *Bohemura jahni.* The ambulacral groove not seen, closed over by laterals. The groove spines not visible, the distal (vertical) spines good developed. Enlarged.
Fos explanations see p. 10

Oral face of each Amb is provided by the so-called „boot-shaped" adaxial ridge which occupies about one half of the whole oral surface of the Amb ossicle. The ridge is in every case compressed. In this paper, the „boot-shaped" ridge or „boot"-orientation is approached as normally used in many classical works on Paleozoic ophiuroids. The „sole" and the top of the „leg" are in direct contact with the insertions for ventral longitudinal muscles; „sole" proximal, top of „leg" distal.



Text-fig. 3d): Schematic reconstruction of cross-section through arm of *Bohemura jahni* showing two positions of rotating adambulacrals (or laterals). Aboral side above. At the left side of each figure (black arm plates) the proximal face is presented, showing longitudinal muscles (stripped) of the ambulacral ossicle. In this view, the vertical ridge of the adambulacral ossicle is not visible. At the right side of each figure (dotted arm plates) a cross-section is presented, showing the water-vessel system (in outline). Inner face of ambulacral, and external ampulla with its tube-foot are invented. Enlarged.

Amb — ambulacral ossicle.
Adm — adambulacral ossicle (or lateral).
Admn — adambulacral „nose" (connected by lateral muscles with a socket in the „toe" of the ambulacral „boot-shaped" adaxial ridge).
gs — insertions for the groove (or oral, ventral) spines
ds — insertions for the distal (or vertical) spines (in text-fig. 3c the distal spines themselves).
or — oral ridge (serving for attachment of groove spines).
vr — vertical ridge (serving for attachment of vertical spines).
nph — groove supporting possibly the nerve and pseudohemal canal.
iw — inner wall of the adambulacral ossicle
vm — excavations for the insertions of the ventral longitudinal muscles.
dm — excavations for the insertions of the dorsal longitudinal muscles.
wvr — water-vessel radial
lb — lateral branch from the radial canal of the water-vessel system.
a — external ampulla.
tf — tube foot.

In proximal part of Amb, the portion of „boot" covering the „foot" forms a lateral (abaxial) extension of the ridge. Directly in the „toe", there is a socket for insertion of lateral muscles connecting the Adm „nose" with Amb. The „heel" is in adaxial part, „toe" points abaxially (outwards). At the level of the upper end of the „instep", there is a shallow groove crossing the adaxial „boot-shaped" ridge in transverse direction. In Paleozoic ophiuroids, this groove is commonly interpreted as support for the branch of nerve and pseudohemal canal. At the adaxial end of this groove, there is the place of connection of the two opposite Ambb (distal and proximal impressions of the ventral longitudinal muscles). At its abaxial end (i. e., at the upper part of the „instep"), there is the pore serving for passage of the lateral branch of radial canal of the water-vessel system to the external ampulla of the tube-foot. The „boot-shaped" ridge is simple, without lateral extensions except the „foot". The „leg" is about as wide as the „foot", and the length of the „foot" is generally the same as the height of the „leg". The „toe" points bluntly. The „instep" and the front of the „leg" outline a large podial basin which occupies the remaining half of the whole oral surface of the Amb ossicle, and slightly extends onto the inner wall of the neighbouring Adm ossicle. The aboral sides of Ambb are covered in almost all cases by a relatively thick layer of integument bearing numerous, distinct papillae. In the very rare places, where the integument is absent, the aboral faces of Ambb show deep insertions for the dorsal longitudinal muscles. These insertions are conspicuously broader abaxially, and are bordered by raised ridges. Each Amb bears two these ridges curved around the aboral surface and converging slightly toward the narrow lateral edge of the Amb. The two ridges are separated by very broad and deep (much deeper abaxially) channel throughout their extent. The lateral (outer) face of Amb, except the socket for attachment of Adm „nose", is probably restricted to narrow edge serving possibly as a simple support for the straight contact face of the neighbouring Adm. The movement of Admm was very probably facilitated only by the lateral muscles connecting the Adm „nose" with the socket in the „toe" of the Amb „boot" (see text-fig. 3d).

As mentioned above, in cross-section each Amb have the shape of a right-angled triangle, and, therefore, the aboral extent of each Amb is greater than its oral extent. The ratio width:length in an Amb is variable, but generally, the width is slightly greater than the length.

The Admm (or laterals) are commonly distinctly flattened (at least in proximal and median parts of arm), exposing their inner walls and the Adm „noses" compressed into the plane of ambulacral groove. The Adm „nose" is nearly as long and as wide as the Amb „foot" of the Amb adaxial „boot-shaped" ridge. The conspicuous length of the Adm „nose" is unique among protasterids and, in this paper, it is assumed as the main diagnostic feature of the genus *Bohemura*. The adaxial part of the Adm inner wall could possibly serve as part of the podial basin. The Adm oral face proper is restricted to a very narrow, groove-spines-bearing oral ridge. Commonly, where the Admm are flattened, the oral ridges and their groove spines are directed laterally, outwards. The aboral face of each Adm ossicle is provided by distinct, distal-spines-bearing vertical ridge crossing the Adm from about proximal to median part of its lateral end to the distal part of its adaxial end. Each Adm bears about 6 groove (or ventral) spines and about 7 distal (or vertical) spines. The groove spines are not observed in the flexible arm tips (text-fig. 3c). In almost all specimens, it seems that both types of spines are generally broken at about one half of their length (e. g., text-fig. 2, 4), and in few cases are preserved

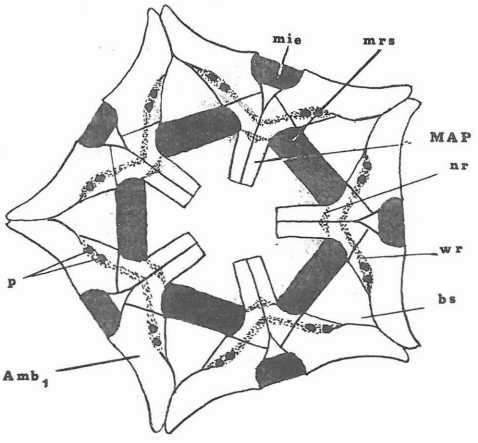
in their full length. The groove spines are generally flattened, and are possibly slightly thinner than the vertical ones. The vertical spines are conspicuously shortened adaxially (see Pl. III., fig. 3). The largest abaxial vertical spines are of about the same length as the groove spines. The latter represent in their length about one half of the cross-section through the flattened arm (se text-fig. 1a). Both types of spines are distinctly striated longitudinally.

Text-fig. 4: Drawing of oral face of arm of *Bohemura jahni* (NM L 10180) (see also Pl. III., fig. 1) showing the ambulacral groove gradually closed over by laterals in the distal portion. × 1,5.

Mouth frame. The $Ambb_1$ (first ambulacral ossicles) and the MAPs (mouth-angle plates) are the only preserved components of the mouth frame in *Bohemura jahni*. The mouth frame is not covered by an integument in any of the specimens which facilitates the study of $Ambb_1$ and MAPs. In each half-ray, the Amb_1 and MAP are very firmly joined at an angle of about 110°. Each MAP, viewing from its oral side, is strong, with slightly flattened surface, about as wide as is long the „foot" of the Amb „boot", and about three times as long as the Amb itself (if we calculate with Ambb from the proximal half of arm). From the oral view, the impressions for attachment of muscles connecting MAPs with tori (or musculus interradialis internus inferior) are very good visible, deep and broad. Aborally, the MAPs are never flattened, having curved surface (Pl. II., fig 2), and being crossed by concentric grooves for the nerve and water ring (text-fig. 5). The groove for the circumoral nerve ring crosses each MAP transversely at about one half of its length. The water ring groove (outer from the two concentric grooves) crosses each MAP from about one quarter of its length at the interradial side, continuing across the suture between MAP and Amb_1 onto the Amb_1. The distal (adoral) three-quarters of the interradial side of MAP are straight, fitting closely against the adjacent MAP. At the proximal end of the radial side of MAP, particularly between the proximal end and the nerve ring groove, there is a broad, distinct impression serving for attachment of strong musculus radialis superior (text-fig. 5).

The oral face of Amb_1 is not clearly visible in any of the specimens, but it seems, that it is not very different from those of other Ambb, provided with a similar

boot-shaped ridge. The aboral side of Amb_1 is good known. The aboral extent is much greater, and in radial direction the Amb_1 is elongated. The water ring groove continues from MAP onto Amb_1 curving to the end of the buccal slit. On each Amb_1, the water ring groove is provided with a pair of pores serving as entries to canals from the water ring to the first two podia (or tube-feet) of the half-ray. At the interradial side of each Amb_1, there is a broad, distinct impression for attachment of strong musculus interradialis externus (text-fig. 5).



Text-fig. 5: Schematic sketch of the mouth frame of *Bohemura jahni* from aboral view, showing closed (or contracted) position with restoration of inferred musculature (black). Tori and denticles unfortunately not preserved in any of the specimens. Enlarged.

mie — musculus interradialis externus
mrs — musculus radialis superior
MAP — mouth-angle plate
Amb_1 — first ambulacral
wr — water ring groove
nr — nerve ring groove
bs — buccal slit
p — pores (entries to canals from water ring to tube feet of the first two podial basins of the half-ray)

Dimensions (in mm):

Specimen	Interradial disk radius	Radial arm radius	Width of arm at the place where becomes free
L 10170	22	80	10
L 10171			9
L 10175	20	70	9
L 10176	20		10
L 10177			10
L 10178	20		10
L 10179	20		10
L 10180	20		10
L 10181	18		7,5

The table of dimensions shows only approximate measurements, and the width of arm at place where it becomes free shows (except the last measurement) only the case with inner walls of laterals flattened into the plane of the ambulacral groove. The inventory number L 10176 belongs to the slab containing three brittle-stars, two with oral faces exposed, and one with aboral face exposed. The measurements in the table are given for the latter specimen.

Discussion: The relations are discussed above in the chapter on the genus. Many strange species were previously placed within the genus *Bohemura*. In this paper, only the type species, and *B. primaeva* Fedotov, 1936 from Middle Ordovician of South Kazakhstan, U.S.S.R. are supposed to be representatives of this genus.

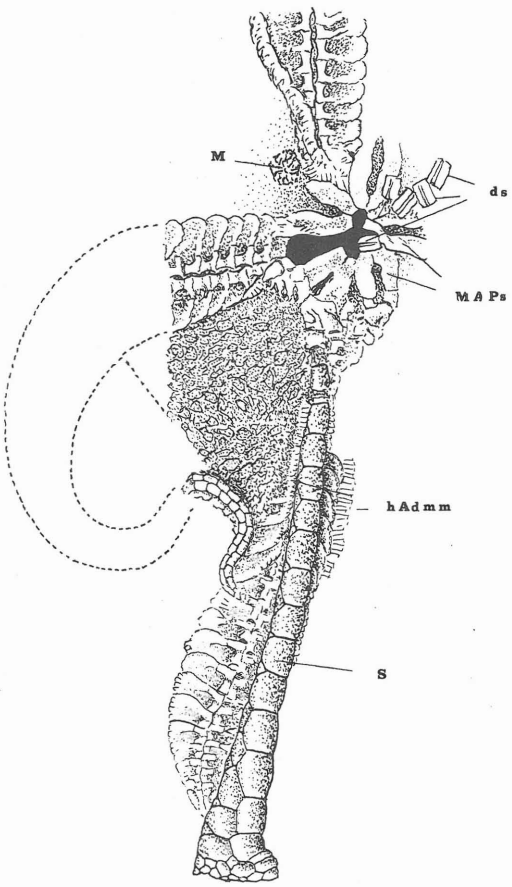
Occurrence: Probably all specimens come from the type locality — Zahořany near Beroun (i. e., from the small reserve behind the school in Beroun 7 — Králův Dvůr, left from the road leading to Zahořany), a classical Barrande's locality, serving as the stratotype of the Zahořany Formation. For stratigraphic position of the Zahořany Formation in the Bohemian Middle Ordovician see the work of HAVLÍČEK and MAREK (1973, p. 228).

Remarks on ecology and feeding behaviour of Bohemura jahni

All specimens of *Bohemura jahni* come from greywacke of the above mentioned locality Zahořany near Beroun (Zahořany Formation, Berounian stage, approx. Upper Caradocian). At this place, the very rich fauna is entirely shown by external moulds into which ground water has precipitated iron oxide. The ophiuroids were derived from a layer (at present not recovered) in which they were associated with rhombiferan cystoids *Echinosphaerites infaustus* Barrande, 1887, homoiostelean „carpoids" *Dendrocystites sedgwicki* Barrande, 1887, and with conulariids. The ecological relationships between these animals are discussed below.

With regard to the sedimentary environment and to the temperature and salinity of the sea, several works were published by previous authors, however, it is necessary to notice some important results. During the Ordovician, the Barrandian area was situated in the Mediterranean province corresponding to the miogeosynclinal and eugeosynclinal regions of the proto-Tethys, bordering the northern margin of Gondwana and the adjacent shelves. With regard to zoogeography, it corresponded to the *Selenopeltis* province. The proto-Tethys was a cold-water region influenced by the position of South pole approximately in the centre of Sahara (HAVLÍČEK, 1974). Its cold temperate fauna was characterized by relatively small number of animal species, particularly by very small number of cephalopods, bryozoans, and almost total absence of corals (HAVLÍČEK and VANĚK, 1966). In the Ordovician sediments of the Barrandian area (from the earliest to the latest) the ferruginous constituent decreases and the calcareous increases. This development is due to the gradual increase of pH medium which was influenced by the increased salinity of water (KUKAL, 1963a). The increase of salinity was evoked by increasing temperature of the sea (PŘIBYL and VANĚK, 1976). The salinity increased to some degree at approximately the boundary between Letná and Vinice Formations. In the Vinice and Zahořany Formations, there is an increase in number of bryozoans, articulate brachiopods, pelecypods, gastropods, echinoderms, and ostracods, however, there is a decrease in number of inarticulate brachiopods, and particularly graptolites and dendroids (PŘIBYL and VANĚK, 1976). According, to the grain-size (i. e., according to the ratio of the three fractions, sand : silt : clay), the Middle Ordovician sediments of the Barrandian area are at the transition between geosynclinal and platform tectofacies. The character of the sedimentary environment was reconstructed from petrographical and lithological kind of clastic material, and from the type of fossil content (KUKAL, 1963b). There is a very small facies differentiation of the sediments of the Zahořany Formation and, therefore, the reconstruction was very difficult. It was probably a shallow basin environment supplied by denudation detritus transported by water courses from land. The denudation material came mostly from eruptive rocks and a smaller amount from earlier sediments and metamorphic rocks (KUKAL, 1963b).

With regard to the mode of life of *Bohemura jahni,* it seems a partial similarity between the latter and some of the Recent amphiurids. In this paper, the life habit of *Bohemura jahni* is compared with the classical observations on *Amphiura chiajei* in aquaria of the biological station of the Museum of Bergen, performed by Louis des Arts in the years 1908—1910 (see DES ARTS, 1910). The conclusions about ecology and feeding behaviour of *Bohemura jahni* were made from the study of its mode of preservation and from some of its morphological features.



Text-fig. 6: Drawing of *Bohemura jahni* (specimen NM L 10178, see also Pl. VII, and Pl. VIII) preserved in feeding position. × 1,3.

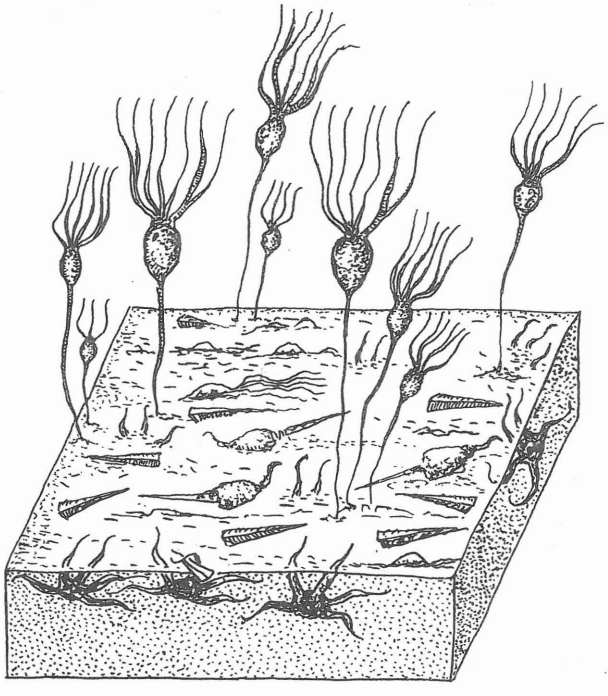
MAPs — mouth-angle plates
M — madreporite
S — stele of solutan carpoid *Dendrocystites sedgwicki* Barrande, 1887
hAdmm — proximal adambulacrals (or laterals) of the brittle-star holding the distal portion of the stele of the carpoid
ds — disarticulated elements of the stele scattered around and within the mouth frame of the brittle-star

As can be seen from the slabs containing *Bohemura jahni,* at the time of sudden extinction of the above mentioned subcommunity formed of ophiuroids, cystoids, carpoids, and conulariids, the ophiuroid population was represented only by old adults. There seems to be a possibility that the population of brittle-stars arose from one heavy settlement of larvae when the bottom-current velocity was very low. Probably, in the breeding seasons the velocity of currents was higher, and the new larvae could not be able to establish themselves in the currents and were swept away. The population of adults prospered until the whole subcommunity met with

a catastrophic death. Some ophiuroids are preserved in feeding positions and, therefore, it seems that smothering by rapid sedimentation was the cause of their death.

The specimens at the author's disposal are very good preserved, showing only a slight compression. In fossilization the disk has been pressed down onto the mouth frame, the ambulacral „boot-shaped" ridges have been compressed, and the adambulacral „noses" and the groove spines have been pressed into the same plane as the disk. Except the mouth frame, the integument covering the aboral surface of the disk and that of the arms is good preserved. The brittle-stars are kept in their entirety except for some arm tips of some of the individuals. It suggests that the ophiuroids were not exposed to the bottom currents at the time of their death; and that they led a burrowing mode of life. As seen from the slab NM L 10176, some were buried with their oral side above, some with their aboral side above. This slab shows two specimens from their oral side and one specimen from its aboral side (see Pl. II). The latter specimen exposes one of its arm tips pressed along the arm, turning back to the compressed disk, as if the arm tip had been withdrawn into the burrow before death. It seems that *Bohemura jahni* was buried with only one or two of its arm tips exposed above the sea bottom as in a Recent amphiurid species of Japan, not as in *Amphiura chiajei,* in which all the ends of arms are protruding (DES ARTS, 1910, p. 4). Living ophiuroids always exhibit a negative response to light (HYMAN, 1955, p. 657), and the Paleozoic brittle-stars possibly developed a similar aversion for strong illumination. The shallow-water species *Bohemura jahni* was cryptozoic at least during the day and could embed itself to avoid the light of day. The deeper-water protasterids coming from the overlying Bohdalec Formation (uppermost Berounian) led evidently different, epifaunal mode of life, moving freely on the sea floor (the species are new, not described, manuscript in preparation). *Bohemura jahni* burrowed possibly downward into the substrate by means of its podia, rotating laterals, spines, and contingently by thrusts of mouth-angle plates, covering itself by sandy particles. The tube feet, possibly large (large podial basins), were of great functional importance in respiration, food perception, food catching, and probably served also as scoops in burrow-excavating. By far, some of the vertical (or distal) spines were convenient to digging. The most abaxially situated vertical spines are much longer than those situated most adaxially (see Pl. III, fig. 3). These long spines are regarded here as specialized to digging, used as scratching shovels or simply propelling by the movement of laterals. In *Bohemura jahni,* the laterals were able to rotate on the ambulacral ossicles, enabling to the animal to close or open (to some extent) the ambulacral groove (see text-fig. 3d) and to disclose the madreporite (see text-fig. 2 and 6). The movement of laterals could be used also in burrow-excavating. The rotation was facilitated by muscles connecting the adambulacral „nose" with the socket on the „toe" of the ambulacral „boot" or „boot-shaped" ridge (see the description above). This movement of laterals was mentioned previously by SPENCER (1925, p. 256—257) for genera: *Eospondylus* Gregory, 1897, *Lapworthura* Gregory, 1897, *Hallaster* Stürtz, 1886, and *Furcaster* Stürtz, 1886. Both disk and arms of *Bohemura jahni* probably laid in cavities in the substrate, maintained by mucus as can be seen also in the Recent species *Amphiura chiajei* (DES ARTS, 1910, p. 5), and the water circulation through the burrow could be created by disk pumping facilitated by a muscle layer (not visible in the fossils) in the disk wall, providing the animal for respiration.

SPENCER (1934, p. 475) was of the opinion that *Bohemura* was always a „discriminating suspension-feeder", however, from the material it is evident that the discussed brittle-star was a scavenger feeding on large-sized dead animals brought by bottom currents over the burrow. Contingently, this animal could be a combined scavenger and predator. The ophiuroid clearly grasped the large carrion (conulariids, cystoids, carpoids) by its very flexible arm tips, holding it by podia, drawn its prey into the burrow, passed it to the mouth, destroyed it by jaws, digested the soft parts, and ejected the hard remains. The feeding behaviour outlined above is conspicuously observable from the mode of preservation of three of the specimens at the author's disposal. The specimen NM L 10179 (Pl. V) is holding by its arm tip (below) the apical tip of a conulariid theca. The oral end of the latter is pressed under the ophiuroid disk indicating that the conulariid soft parts were in contact with the brittle-star's mouth frame. The specimen NM L 10170 (Pl. VI) is holding by its arm (above) a slender theca of ?*Sphenothallus* sp. The most instructive example is that with the specimen NM L 10178 (text-fig. 6, Pl. VII, VIII)



Text-fig. 7: Schematic reconstruction of the echinoderm-conulariid subcommunity in the Middle Ordovician Zahořany Formation of Bohemia. The large stalked crinozoans are rhombiferan cystoids of the species *Echinosphaerites infaustus* Barrande, 1887 representing high-level-filterers, while the one-armed carpoids, homoiosteleans of the species *Dendrocystites sedgwicki* Barrande, 1887, collect the food in suspension from lower levels above the substrate (contingently they could be potential detritus-feeders). The only infaunal components of the subcommunity are the brittle-stars *Bohemura jahni,* Jaekel, 1903 meeting their food requirements by scavenging on large-sized dead animals. Only empty conulariid test scattered on the sea floor are figured. Nothing is known about conulariid life and systematic affinities.

showing *Bohemura jahni* and a specimen of the solutan carpoid *Dendrocystites sedgwicki* Barrande, 1887. The rotating laterals of the brittle-star are holding the carpoid stele. The distal end of the stele is oriented to the centre of the ophiuroid mouth. The disarticulated pieces of the distal extremity of the stele are scattered around and within the mouth frame of *Bohemura jahni.* It is questionable if the carpoid, moving across the substrate above the burrow was able to escape from the „loop" of the arm and from the holding force of podia and laterals, however, it seems likely that these ophiuroids were only exclusive scavengers. The Recent species *Amphiura chiajei* feeds only upon surface detritus or dead organisms falling on the bottom, but completely avoids the live animals. Even small live copepods, falling into the funnel-shaped burrow of the arms are not eaten by this brittle-star (DES ARTS, 1910, p. 9). However, it has been assumed (see PÉRÈS, 1982, p. 140), that some brittle-stars, particularly on deep-sea bottoms meet their food requirements either by scavenging or by predation on very small animals (their blind stomach, as in protasterids, prevents them from swallowing substrate particles).

The whole subcommunity was formed (see text-fig. 7) by rhombiferan cystoids *Echinosphaerites infaustus* (high-level-filterers), solutan carpoids *Dendrocystites sedgwicki* (low-level-filterers or ?detritus-feeders), protasterid ophiuroids *Bohemura jahni* (infaunal scavengers), and conulariids (uncertain feeding behaviour). It is very conspicuous that no trilobites invaded the subcommunity although they almost prevail in all other layers of the Zahořany Formation. This fact suggests a strong competitive relationship between trilobites and brittle-stars because both were inhabitants of the same type of substrate. It is possible that the brittle-star could secret a mucous repellent with its podia, and thus protect its territory against other scavengers.

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VÁCLAV PETR

REVIZE MORFOLOGIE A EKOLOGIE HADICE *BOHEMURA JAHNI* JAEKEL, 1903 (OPHIUROIDEA, PROTASTERIDAE) ZE STŘEDNÍHO ORDOVIKU ČECH

Práce se zabývá revizí střednoordovického druhu hadice *Bohemura jahni* z proslulé Barrandovy lokality Zahořany u Berouna (v současné době chráněné naleziště a stratotyp zahořanského souvrství). Dnes je známo celkem 11 drobových destiček se zbytky těchto hadic (všechny jsou uloženy ve sbírkách Národního muzea v Praze), z toho pouze jediná byla nalezena v nedávné době. Původní materiál shromáždil J. Barrande a označil tyto ostnokožce manuscriptním jménem *Asterias bohemica* (viz BIGSBY, 1868, str. 197), ale nakonec ani o nich a ani o jiných českých hvězdýších nepublikoval žádnou práci. Materiál byl pak zapůjčen O. Jaekelovi do Greifswaldu. JAEKEL (1903, str. 109—112, text-obr. 6) druh poprvé vyobrazil (i když poněkud nepřesně) a velmi stručně popsal. Kresba byla převzata do Schuchertovy monografie (SCHUCHERT, 1915, str. 224, text-obr. 21). Materiál byl podruhé a naposledy studován W. K. Spencerem v Londýně. Bohužel, Spencerův textový obrázek (1934, str. 473, obr. 305), později přejatý do Treatise (SPENCER et WRIGHT, 1966, str. U86, obr. 75 2a), se nesmírně liší od skutečné podoby diskutované hadice a spolu s jinými dvěma obrázky (SPENCER 1934, str. 475, obr. 307; str. 477, obr. 308) navíc nesprávně ovlivnil i diagnózu celé čeledi *Protasteridae* S. A. Miller, 1889. Zde je třeba poznamenat, že všechny diagnózy rodů v uvedené čeledi (viz SPENCER et WRIGHT, 1966, in Treatise..., str. U87) jsou nepřiměřeně stručné a často i chybné, a proto jednotlivé rody protasteridů zaujímají neúměrně dlouhá časová rozpětí (běžně střední ordovik

až spodní karbon). Tím mohlo dojít i k tomu, že ze řady druhů doposud kladených do rodu *Bohemura* Jaekel, 1903 (jejich výčet je zde uveden) pouze *B. primaeva* Fedotov, 1936 ze středního ordoviku Kazachstánu vykazuje diagnostické znaky tohoto rodu (nepočítáme-li typický druh *B. jahni* Jaekel, 1903).

V této práci je podána pozměněná diagnóza čeledi *Protasteridae* S. A. Miller, 1889 a zcela nová diagnóza rodu *Bohemura* Jaekel, 1903. Druh je zde poprvé podrobně popsán, poprvé je popsána aborální strana živočicha, poprvé jsou zde publikovány fotografie (pořízené z latexových odlitků) a neidealizované kresby podle těchto fotografií.

V kapitole o ekologii je opraveno i dosavadní chápání způsobů výživy těchto hadic, považovaných za požírače suspenze. Ze zachování některých exemplářů je zcela nepochybné, že *Bohemura jahni* byla buď (a to pravděpodobněji) výlučným nekrofágem (mrchožroutem) nebo kombinovaným predátorem a nekrofágem. Pomocí ramen vtahovala do svého „doupěte" těsně pod povrchem písčitého dna mrtvá těla velkých cystoidů, karpoidů a konulárií a živila se jejich měkkými částmi. Zajímavým zjištěním bylo i to, že žádní trilobiti nezasahovali do areálu těchto hadic, i když byli obyvateli stejného typu substrátu. To by svědčilo o výrazných kompetičních vztazích vedoucích až k vytěsnění trilobitů mimo areál dané populace hadic.

EXPLANATIONS TO THE PLATES

Pl. I. *Bohemura jahni* Jaekel, 1903. Lectotype (see also text-fig. 2). × 2, 9. NM L 10066.

Pl. II. *Bohemura jahni* Jaekel, 1903.
1. Aboral face of a specimen from the slab in which three specimens are preserved. Natural size. NM L 10176.
2. The same specimen. Detail of the mouth frame. × 3,5.

Pl. III. *Bohemura jahni* Jaekel, 1903.
1. Oral face of a portion of disk and arm (see also text-fig. 4). × 2. NM L 10180.
2. Aboral face of a portion of disk and arm covered by a thick layer of integument. × 2. NM L 10171.
3. Aboral face of margin of the disk and proximal part of free arm, showing the vertical spines on laterals, and the deep insertions for dorsal longitudinal muscles on ambulacrals in places where the integument is absent. × 8. NM L 10177.

Pl. IV. *Bohemura jahni* Jaekel, 1903.
1. Oral face of good preserved specimen. × 2. NM L 10181.
2. Oral face of an incomplete specimen. The left arm is preserved in its full length. Associated with carrion of *Dendrocystites sedgwicki* Barrande, 1887. × 2. NM L 10175.

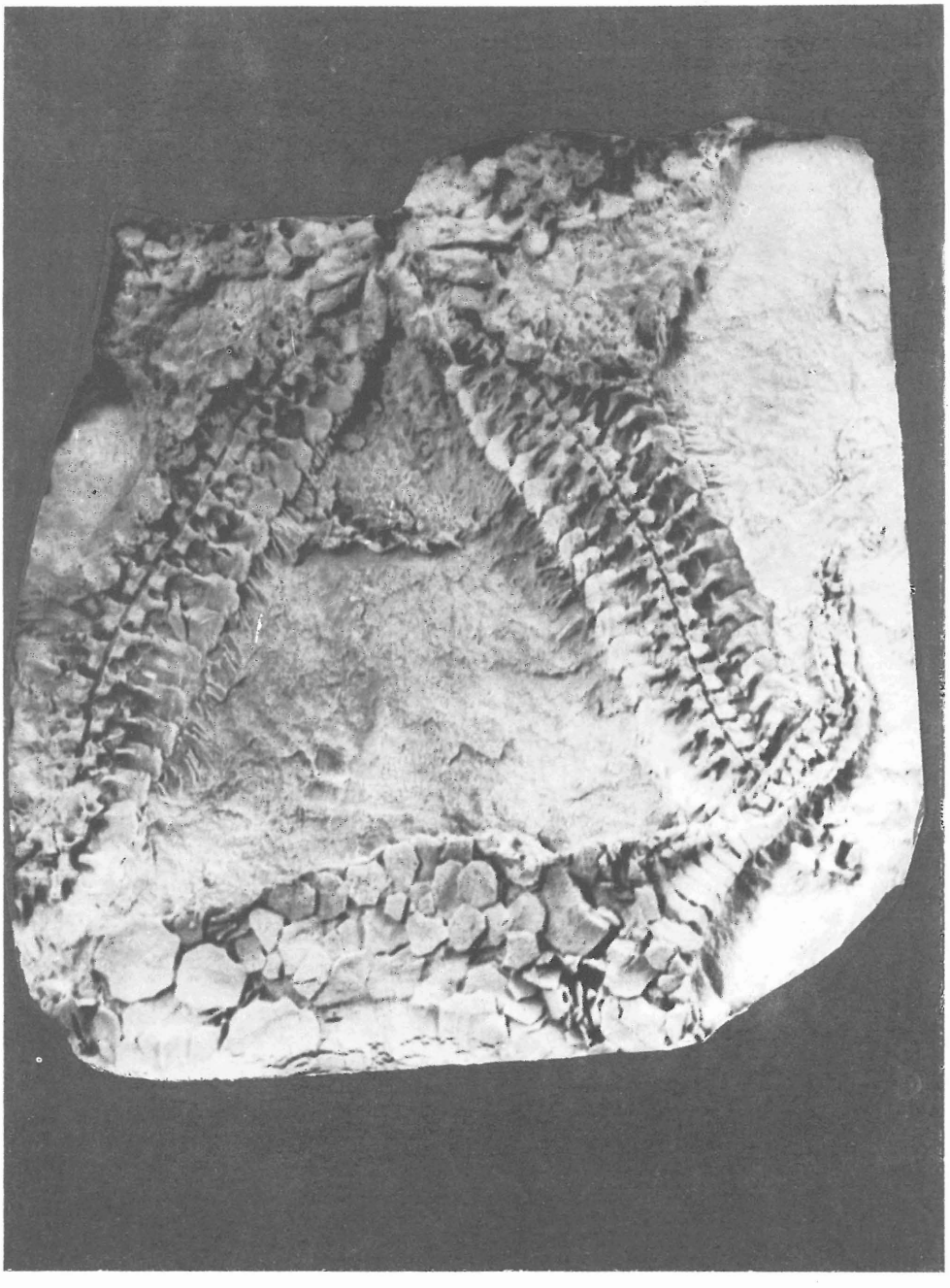
Pl. V. *Bohemura jahni* Jaekel, 1903. Aboral face of a specimen holding by one arm a conulariid test in position indicating that soft parts of the carrion were in contact with mouth frame of the brittle-star. × 2,1. NM L 10179.

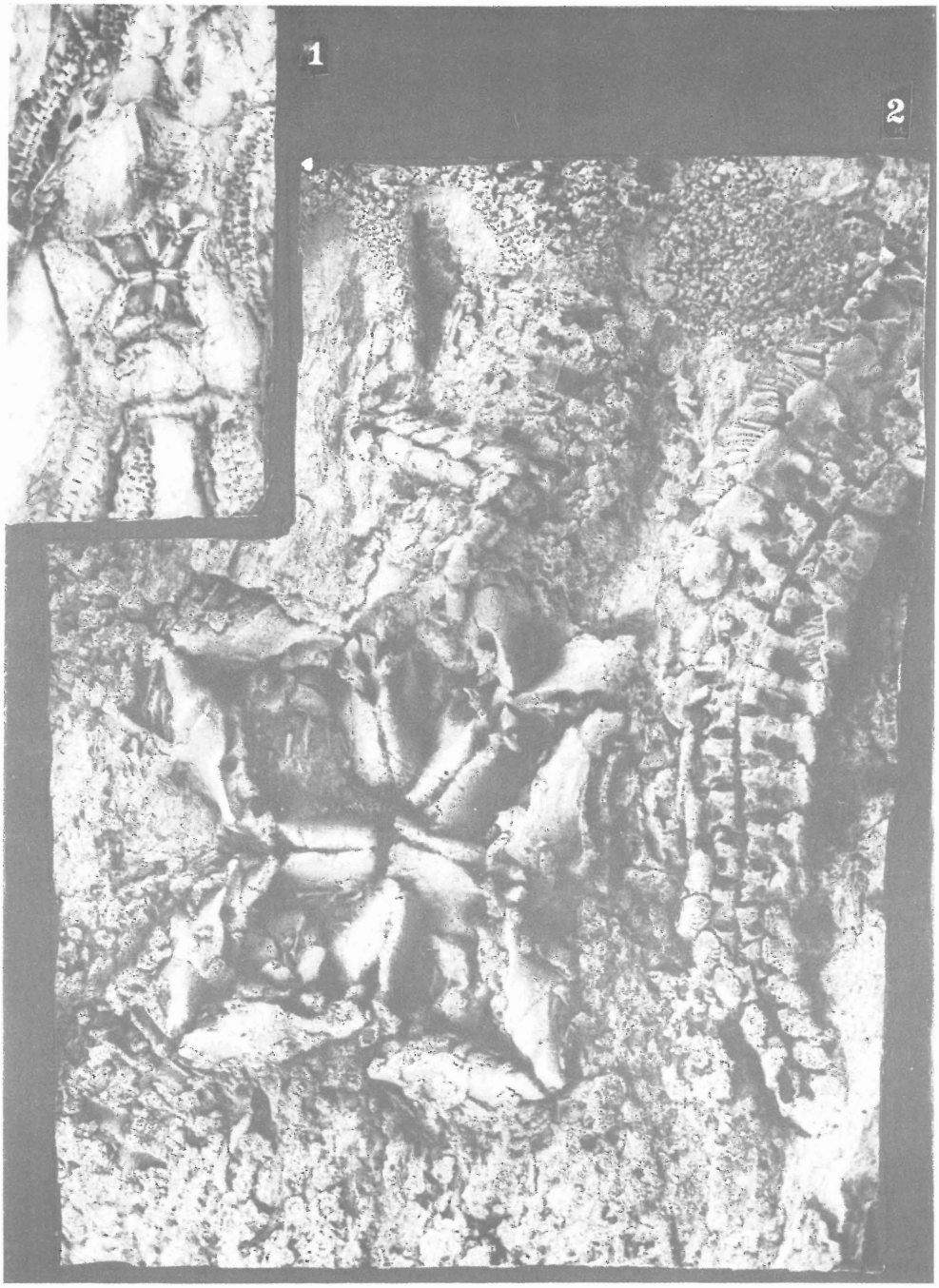
Pl. VI. *Bohemura jahni* Jaelel, 1903. Oral face of a specimen holding by one arm a slender test of *?Sphenothallus* sp. × 2. NM L 10170.

Pl. VII. *Bohemura jahni* Jaekel, 1903. Oral face of a specimen eating on the distal extremity of stele of *Dendrocystites sedgwicki* (see also text-fig. 6). × 2,3. NM L 10178.

Pl. VIII. *Bohemura jahni* Jaekel, 1903. Detail from the same specimen as on Pl. VII. × 10.

Photographs by the author, made from latex casts, slightly coated by NH_4Cl prior to photographing.

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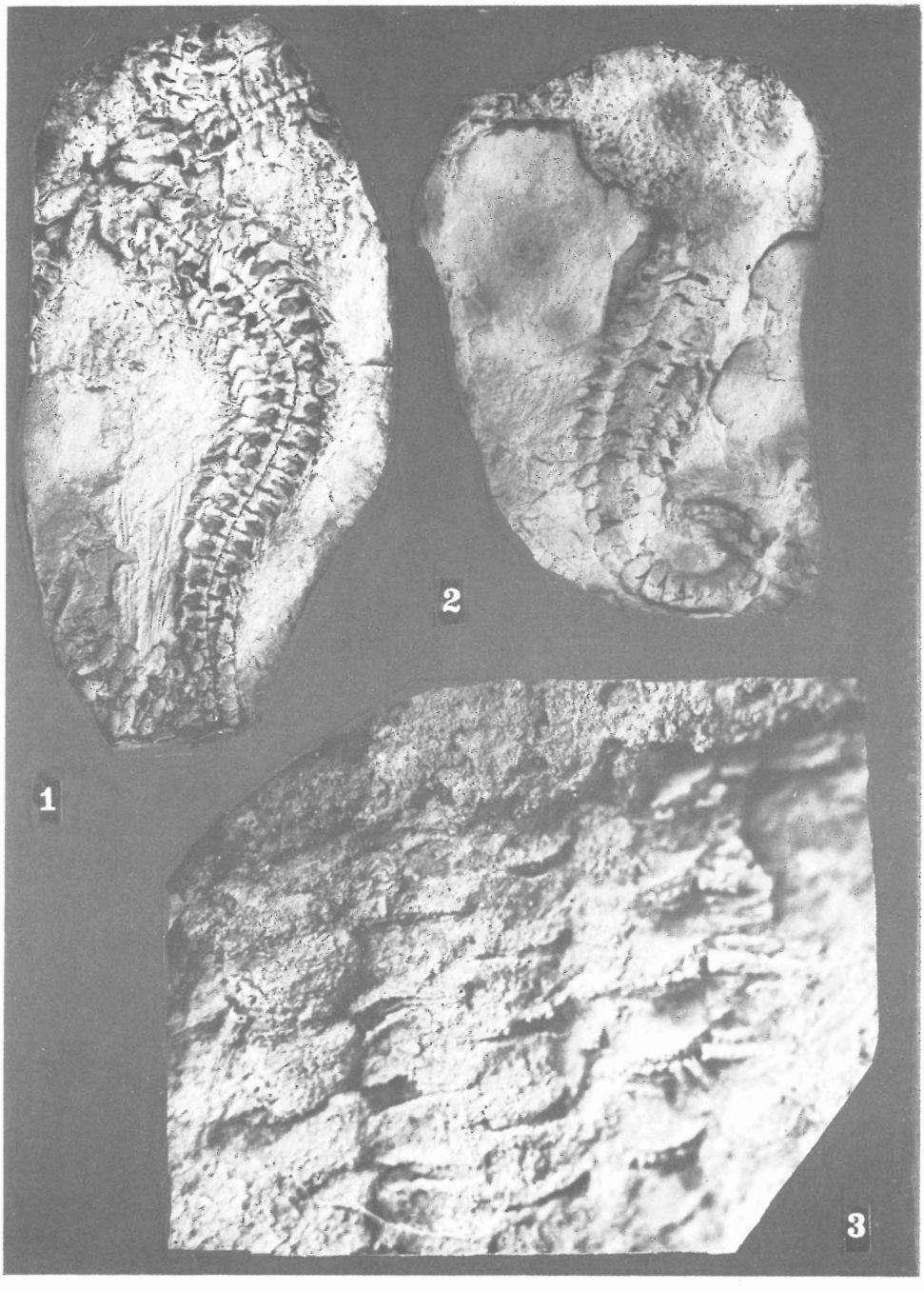
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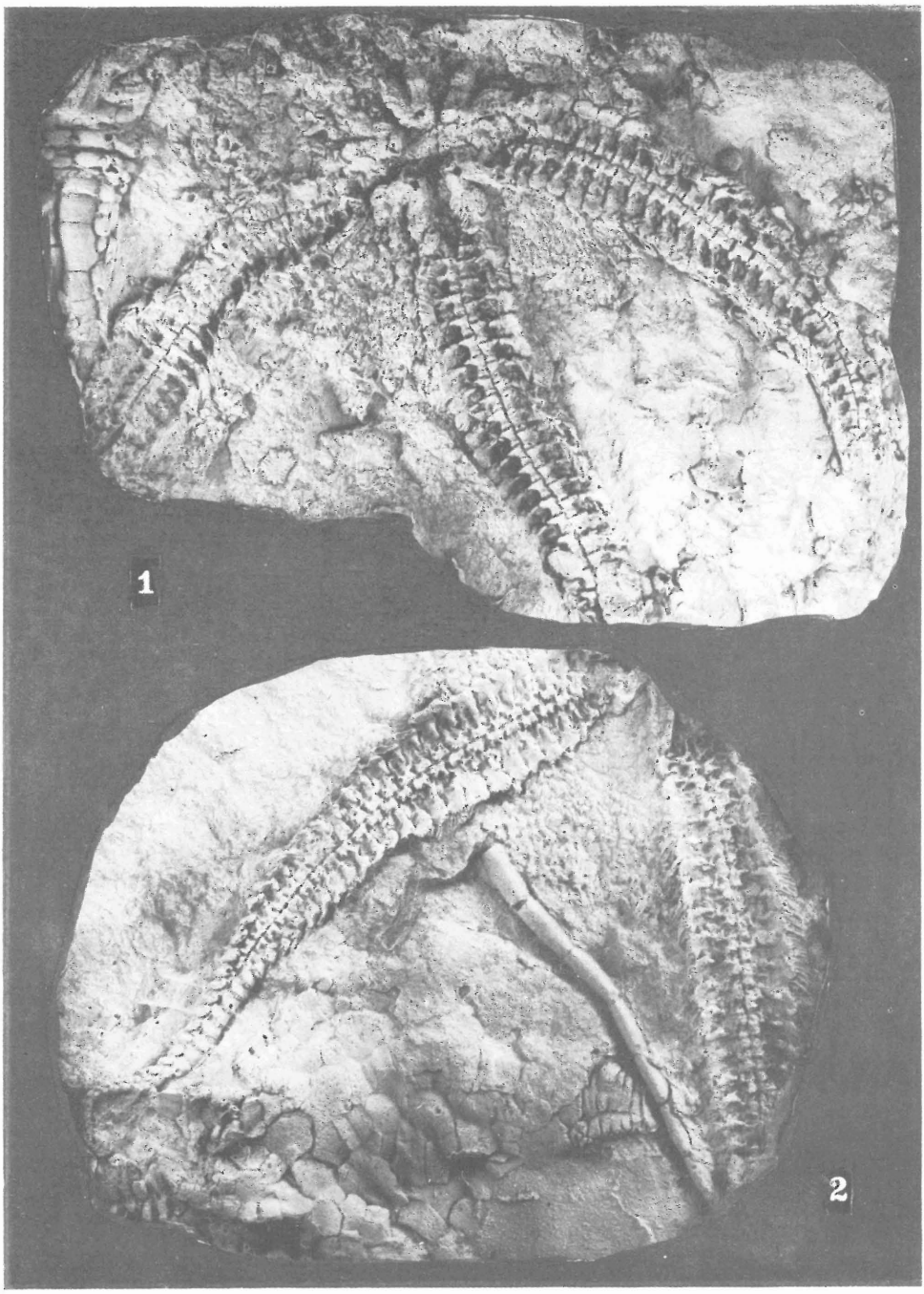
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