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Tithonian crinoids from Rogoźnik (Pieniny Klippen Belt, Poland) and their evolutionary relationships

By ANDRZEJ PISERA¹⁾ and JERZY DZIK²⁾

ABSTRACT

A rich crinoid fauna from the Tithonian of Rogoźnik (Pieniny Klippen Belt, Poland) contains representatives of Isocrinida (*Balanocrinus*), Cyrtocrinida (*Hemicrinus*, *Sclerocrinus*, *Phyllocrinus*, *Apsidocrinus*, *Lonchocrinus*, *Psalidocrinus*, *Eudesicrinus*, *Tetanocrinus*) and Roveocrinida (*Saccocoma*). Two new species, *Hemicrinus tithonicus* and *Lonchocrinus staszici*, are proposed.

Reconstructions of life habits are presented based on isolated ossicles. The great intrapopulation variability of cyrtocrinids is shown. The ecological structure of the fossil assemblage is described on the basis of analysis of associated organisms. Ecological competition among some cyrtocrinids, as indicated by size frequency distributions, is also shown.

The Rogoźnik crinoid fauna is stratigraphically and morphologically intermediate between well-known Oxfordian and Valanginian crinoid faunas. Evolutionary relationships within the order of Cyrtocrinida and among orders of Mesozoic crinoids are discussed.

ZUSAMMENFASSUNG

Eine reiche Krinoiden-Fauna aus der Tithonischen Stufe von Rogoźnik (Pieniny-Klippen-Zone, Polen) enthält Vertreter von Isocrinida (*Balanocrinus*), Cyrtocrinida (*Hemicrinus*, *Sclerocrinus*, *Phyllocrinus*, *Apsidocrinus*, *Lonchocrinus*, *Psalidocrinus*, *Eudesicrinus*, *Tetanocrinus*) und Roveocrinida (*Saccocoma*). Es werden zwei neue Arten vorgeschlagen: *Hemicrinus tithonicus* und *Lonchocrinus staszici*. In der Cyrtocrinida-Population wird eine grosse Variabilität nachgewiesen. Aufgrund der isolierten Elementen werden Krinoiden-Rekonstruktionen vorgestellt. Die ökologische Struktur der fossilen Lebensgemeinschaft wird aufgrund der Begleitfauna-Analyse gegeben. Zwischen manchen Cyrtocriniden kam, wie Verteilungsdiagramme zeigen, eine ökologische Konkurrenz vor. Die Krinoiden-Fauna von Rogoźnik besitzt stratigraphisch und morphologisch einen Übergangscharakter zwischen den bekannten Krinoiden-Faunen aus Oxfordium und Valangis. Schliesslich werden die Evolutionszusammenhänge zwischen Cyrtocriniden und mesozoischen Krinoiden-Ordnungen diskutiert.

Introduction

The rich fauna of Rogoźnik, Polish Carpathians, has been under investigation for a long time (ZEJSZNER 1833, PUSCH 1836). It includes many species of ammonoids, brachiopods, echinoids, pelecypods, gastropods, etc. (ZITTEL 1870, ZARĘCZNY 1876, BIRKENMAJER 1963 and others). Some crinoid cups have previously been described by ZITTEL (1870) and ZARĘCZNY (1876).

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The Rogoźnik crinoid fauna is especially interesting because of its stratigraphical position. Most data on Mesozoic crinoid morphology and ecology are based on materials of Oxfordian (HESS 1975, LORIOL 1882) and Valanginian (REMEŠ 1905, 1912, ŽITT 1974a, 1974b, 1975) age.

The majority of our crinoid material has been collected from the reddish brown shelly limestone (Rogoźna Coquina Member in BIRKENMAJER 1977) with rich ammonoid fauna. According to BIRKENMAJER (1958, 1963, 1977), the ammonoids indicate Early to Middle Tithonian age of this layer (*Lithographicum* to *Semiforme* zones). Only a few cups along with an abundant fauna of ammonoids have been obtained from the white shelly limestone (Rogoźnik Coquina Member in BIRKENMAJER 1977). This white limestone represents Middle to Upper Tithonian and/or Lower Beriasian (BIRKENMAJER 1977).

The crinoids cups and isolated ossicles have been gathered by means of maceration of weathered rock fragments. The material is well-preserved but the interradial processes are often somewhat damaged.

Material described in this paper is housed in the Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, for which the abbreviation ZPAL is used.

Descriptions

Order *Isocrinida* SIEVERT-DORECK 1953

Family *Isocrinidae* GISLEN 1924

Genus *Balanocrinus* LORIOL 1879

Type species: Balanocrinus subteres (MÜNSTER 1833)

Emended diagnosis. – Low, pentagonal basal plates touching one another. Columnals round to pentagonal, with petaloids.

Remarks. – *Balanocrinus* LORIOL differs from *Chariocrinus* HESS in the round shape of stem ossicles. It differs also from *Isselicrinus* ROVERETO in the larger size and pentagonal shape of basal plates.

Balanocrinus cf. *subteres* (MÜNSTER 1833)

Pl. 1, Fig. 1-5; Fig. 1-2

Description. – Stem. Diverse columnal types which occur in our material and which have usually been assigned to different species of the genera *Balanocrinus* (*B. subteres*, *B. subteroides*, *B. pentagonalis*) and *Pentacrinus* do in reality grade into one another (Pl. 1, Fig. 1-5, Fig. 2).

The smallest investigated columnals are high and pentagonal in cross-section (Fig. 2g-i). The larger ones are low, round in cross-section, and concave in side view (Pl. 1, Fig. 3-4). This variability probably reflects ontogenetic modifications. Moreover, there is also variability in both the side view and articulation surface among equal stem ossicles. The most common columnals are round, smooth and straight-sided (Fig. 2m), rarely concave-sided. The pentagonal forms with nodes on

their lateral surfaces (Pl. 1, Fig. 1, 5, Fig. 2a-b) are less common. This variability probably reflects differentiation within one specimen. The ornamentation suggest that the investigated columnals come from near calyx base (proximal ossicles). This may also reflect an intrapopulation variability. However, it can not be excluded that our material represents two or more species. According to Roux (personal communication) observed variability exceeds that of *B. subteres*.

The nodals (Fig. 21, n) show a variability pattern similar to that displayed by the internodals. The larger and lower ones are distinctly pentagonal in shape because of the large cirral facets (Fig. 21). Their distal surfaces are concave and smooth as are the respective top surfaces of nodals. Top surfaces of nodals show petaloids (Fig. 21).

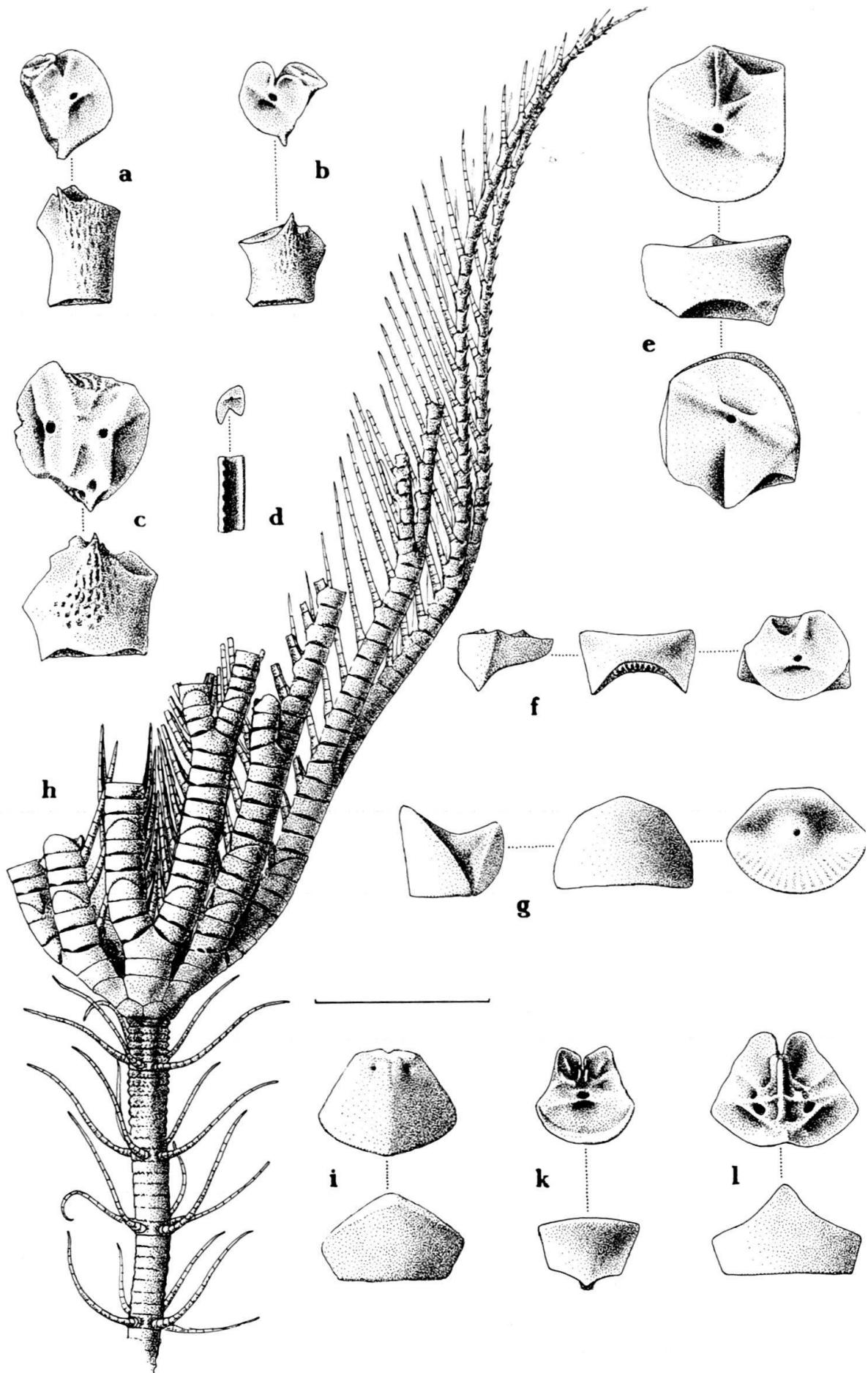
Cirrals. The basal (or older) ossicles are short and dorso-ventrally flattened (Fig. 2d-e). The distal (or younger) ones are longer and laterally flattened, they are drop-shaped in cross-section and exhibit a dorsal rib (Fig. 2f). The cirrals are articulated by synarthry.

Crown. The basals are very thick, low and pentagonal in shape (Fig. 1i). They touch one another laterally in the cup. Their basal surfaces exhibit petaloids, whereas the top surfaces are smooth with two nerve canals at the inner side. The radials (Fig. 1k) are relatively high with a saddle-shaped outer surface. The small angle between the lateral surfaces of the radials suggest that the cup was high. The first primibrachials (IBr1) have not been found, but the morphology of adjacent elements indicates that their lower articulation surface was of the muscular type, whereas the upper one was of the synostosis type (smooth) and articulated with a smooth surface of primaxillary (IAx), which is low (Fig. 1l). The upper medial ridge separates large and remarkable articulation surfaces (of muscular types) of secundibrachials. Some arm ossicles (Fig. 1f-g) display a smooth, saddle-shaped articulation surface with only a weak crenulation at the margins (symmorphy in the sense of HESS 1972 and MACURDA & MEYER 1975). Judging from an analogy with *Chariocrinus* HESS (cf. HESS 1972a), we consider those ossicles the third and fourth secundibrachial, respectively. Two kinds of symmorphic articulation (shallow and very deep) have been observed. This suggests that the third and fourth IIIBrBr have also been articulated in the same way. An effect of variability cannot be excluded however. The proximal brachials (Fig. 1e) are flat with large muscular articulation surfaces of pinnules. The distal and juvenile ones (Fig. 1a-b) are long and bear a single lateral spine. The articulation surfaces of pinnules are almost as large as those between brachials.

Remarks. – In our collection there are some elements of pinnules morphologically similar to isocrinid pinnulars (Fig. 1d). They are laterally flattened and exhibit sharp lower edges. The upper edges are parallel and oblique teeth bearing. We assign these elements to *Balanocrinus* cf. *subteres* (MÜNSTER). However, they differ remarkably from the pinnule ossicles attributed by HESS (1975) to *Balanocrinus*. Thus our ossicles may also be ascribed to a cyrtocrinid.

We have found a single plate that seems to be a centrodorsal plate of a young individual of *Balanocrinus* (Fig. 2c).

Material. – Single radial and basal plates, centrodorsale, more than 250 columnals, more than 100 brachials, more than 20 cirrals and a few pinnulars.



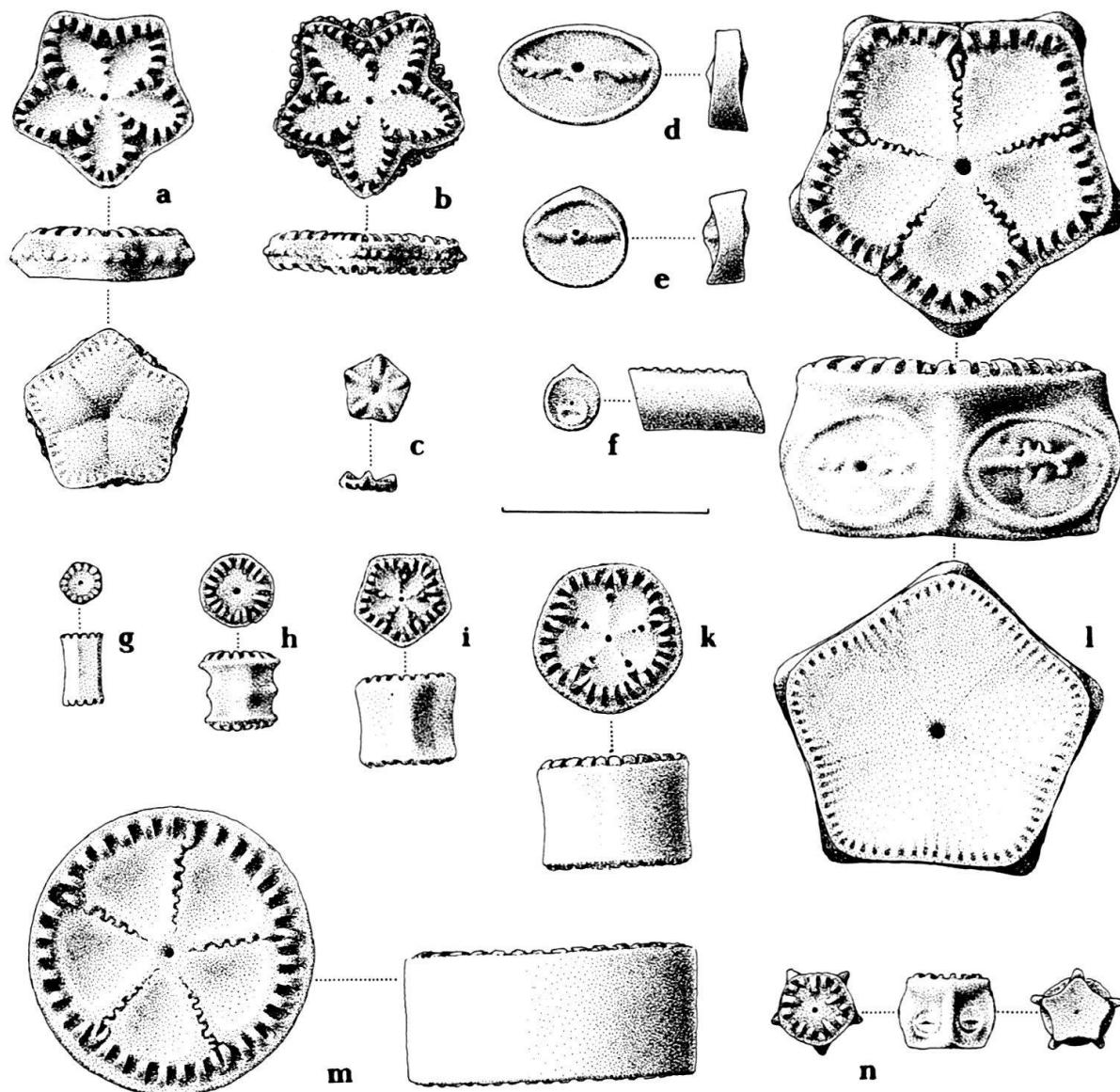


Fig. 2. *Balanocrinus* cf. *subteres* (MÜNSTER 1833). a-b = proximal columnals, lateral view and articular surfaces, c = ?centrodorsal plate of young specimen, lateral and proximal view, d-e = proximal cirrals, lateral view and articular surfaces, f = distal cirral, lateral view and articulation surface, g-h = columnals of immature specimens, lateral and proximal end view, i = proximal columnal of young specimen, lateral and articulation surface view, k = medial columnal, lateral and articulation surface view, l = nodal of mature specimen, lateral and articulation surfaces view, m = distal columnal of mature specimen, lateral and articulation surface view, n = nodal, probably distal of immature specimen, lateral and articulation surfaces view. Scale bar 5 mm.

Fig. 1. *Balanocrinus* cf. *subteres* (MÜNSTER 1833). a-b = distal brachials, dorsal and distal end view, note large affixes of pinnules, c = axillary of higher order, dorsal and distal end view, d = pinnular element, ventral and distal end view, e = proximal brachial, distal end, dorsal and proximal end view, f = proximal brachial, lateral, dorsal and proximal end view, g = proximal brachial, lateral, dorsal and distal end view; these brachials were connected in arms by symmorph, h = reconstruction of animal in life position, i = basal, dorsal and upperside view, k = radial, dorsal and upperside view, l = second primibrachial = primaxillary (IAx), dorsal and upperside view. Scale bar 5 mm.

Occurrence. – Red Rogoźnik coquina, Early or Middle Tithonian, Rogoźnik, Poland.

Order ***Roveacrinida*** SIEVERT-DORECK 1953

Family ***Saccocomidae*** D'ORBIGNY 1852

Genus ***Saccocoma*** AGASSIZ 1853

Type species: *Saccocoma tenella* GOLDFUSS 1962

Saccocoma tenella GOLDFUSS 1862

Pl. 1, Fig. 8–9, Pl. 2, Fig. 1–7, Pl. 3, Fig. 1–3; Fig. 3

1892 *Saccocoma tenella* GOLDFUSS, JAEKEL, p. 659–694, Pl. XXX.

1960 *Saccocoma tenella* GOLDFUSS, VERNIORY, p. 250–257, Fig. 1–2.

Description. – The radials (Pl. 1, Fig. 8–9, Pl. 2, Fig. 1) are thin-walled, each with a distinct medial ridge culminating in a bulbous articular facet. A similar but thinner ridge runs over the inner surface. The outer surface is covered with variable reticulate sculpture. The edges are denticulated. The articulation surface of first primibrachial (IBr1) is of muscular type.

The most common radial plates in red Rogoźnik coquina are assigned to *Saccocoma tenella* GOLDFUSS. The most common types of brachials, therefore, may also belong to this species. Some brachials, however, may belong either to *Saccocoma tenella* GOLDFUSS or *Saccocoma* cf. *quenstedti* VERNIORY. First primibrachial (IBr1) (Pl. 2, Fig. 6–7, Fig. 3h) has no lateral wings; there are only weakly developed ventral processes which border ambulacral grooves. The articulation between radial plate and the first primibrachial (IBr1) is of muscular type, while the first primibrachial and the primaxillary (IAx) are articulated by cryptosynarthry or synostosis (see discussion by HESS 1972b). The primaxillary (Pl. 2, Fig. 3; Fig. 3e) bears symmetric, large lateral wings (“Schwimmplatten” of JAEKEL 1892) strongly convex in their proximal parts. The ventral processes are weakly marked but a distinct medial process does occur. The short and massive trunk is ornamented like the radials. The wing edges are curved downward. The distal articulation surface of primaxillary is of the muscular type. The first secundibrachial (Fig. 3b) probably morphologically resembles first primibrachial. The first secundibrachial is articulated with the second secundibrachial (IIBr2) by cryptosynarthry or synostosis. Distally, the brachials (Pl. 2, Fig. 2, Pl. 3, Fig. 3; Fig. 3c–d) have their lateral wings gradually shorter and their ventral processes are gradually higher. The most distal brachials (Pl. 3, Fig. 1–2; Fig. 3f–g) have no lateral wings at all, whereas they display high and flat ventral processes. Some brachials probably represent ramules (pinnular segments).

Remarks. – *Saccocoma tenella* GOLDFUSS differs from *S. quenstedti* VERNIORY in its radials lacking any spines. Unclear are differences between it and *Saccocoma pectinata* GOLDFUSS.

The radials display a similar pattern of variability in surface sculpture as shown by VERNIORY (1960).

Material. – More than 500 radials and more than 2,000 brachials.

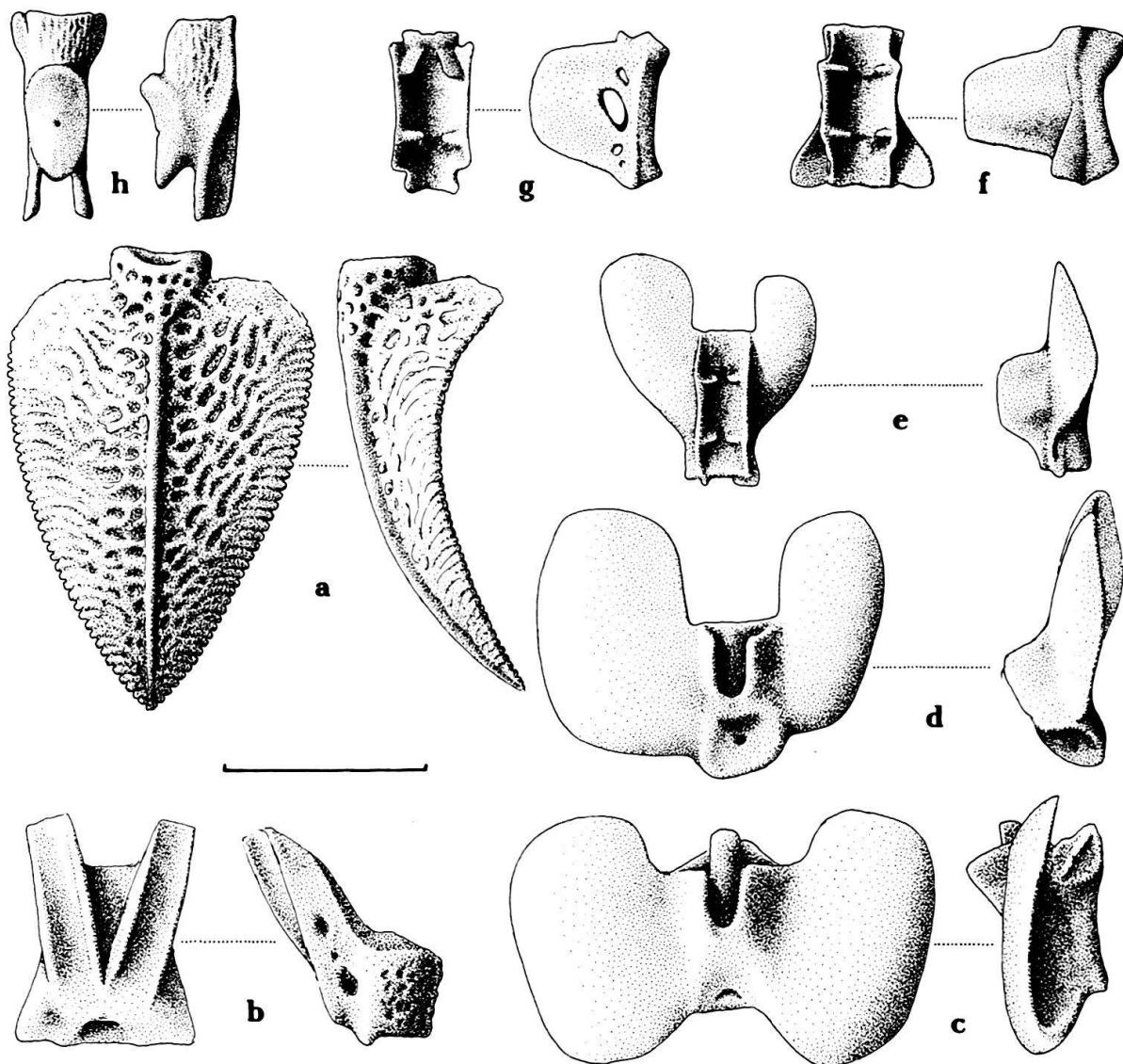


Fig. 3. *Saccocoma tenella* GOLDFUSS 1862. a = radial, dorsal and lateral view, b = brachial, ventral and lateral view, this kind of brachials were probably intercalated with proximal brachials with wings, c-d = brachials of higher order, ventral and lateral views, e = second primibrachial = primaxillary (IAx), ventral and lateral view, f-g = brachials from distal part of arm, ventral and lateral view, h = primibrachial, dorsal and lateral view. Scale bar 5 mm.

Occurrence. – Red Rogoźnik coquina, Early or Middle Tithonian, Rogoźnik, Poland.

Saccocoma cf. quenstedti VERNIORY 1961

Pl. 1, Fig. 6-7; Fig. 4a, c-e

Cf. 1961 *Saccocoma quenstedti* SIEVERT-DORECK, VERNIORY, p. 315-320, Fig. 1-11.

Cf. 1972b *Saccocoma cf. quenstedti* SIEVERT-DORECK, HESS, p. 631-634, Pl. 2, Fig. 29-30, 34-36, 40-41, Pl. 4, Fig. 54.

Description. – The radials (Pl. 1, Fig. 6-7; Fig. 4a) resemble those of *Saccocoma tenella* GOLDFUSS but they exhibit two branched spines near the base of the articula-

tion surface. A single broken radial (Fig. 4b) displays very massive and separated spines which may reflect an intrapopulation variability or may belong to a separate species.

In the investigated material there are no ossicles resembling the one illustrated by VERNIORY (1961) as the first primibrachial. There are a few unusual brachials (Fig. 4c-d) that might belong to the same species as the radial plates do; they slightly resemble the specimen illustrated by HESS (1972b, Pl. 2, Fig. 26). They bear strongly convex wings each with a high transversal crest on the ventral side. They are either extremal variants of *Saccocoma* cf. *quenstedti* VERNIORY, or the ranges of variability of *S. tenella* GOLDFUSS and *S. quenstedti* VERNIORY overlap considerably. However, the investigated brachials may also represent another species.

Remarks. – The name *Saccocoma quenstedti* was introduced by SIEVERT-DORECK in an unpublished manuscript and used subsequently by VERNIORY (1961) and HESS (1972b). VERNIORY (1961) was the first who diagnosed and illustrated the species

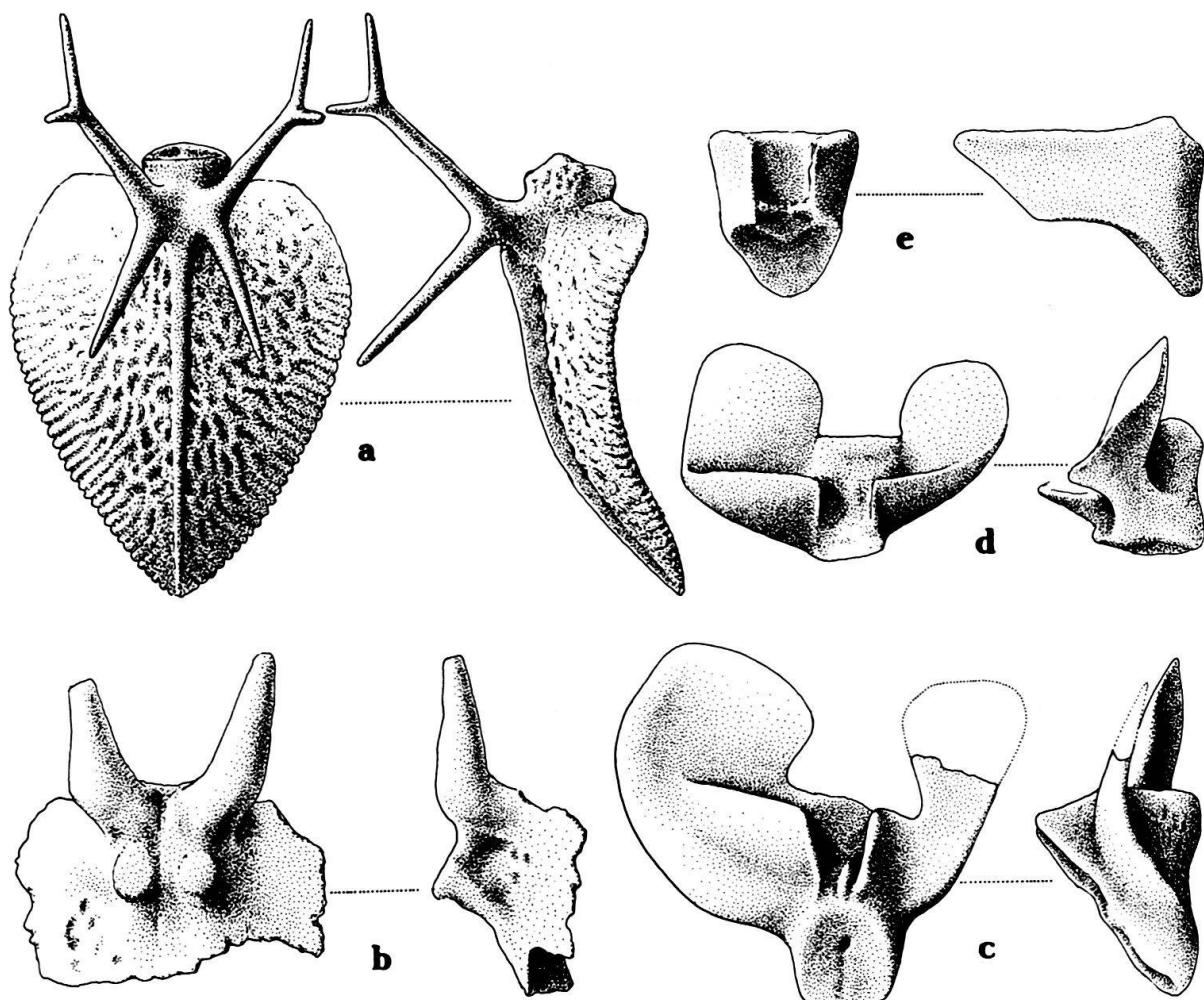


Fig. 4a, c-e. *Saccocoma* cf. *quenstedti* VERNIORY 1961. a = radial, dorsal and lateral view, c-d = proximal brachials, ventral and lateral view, e = brachial which was intercalated with proximal brachial with wings. Scale bar 5 mm.

Fig. 4b. *Saccocoma* sp. Dorsal view of broken radial. Scale bar 5 mm.

and hence (according to rules of ICZN), he is to be regarded as the author of the species *Saccocoma quenstedti*.

Material. – More than 30 radials and a few brachials.

Occurrence. – Red Rogoźnik coquina, Early or Middle Tithonian, Rogoźnik, Poland.

Order *Cyrtocrinida* SIEVERT-DORECK 1953

Family *Sclerocrinidae* JAEKEL 1918

Genus *Sclerocrinus* JAEKEL 1879

Type species: *Sclerocrinus strambergensis* JAEKEL 1891

Sclerocrinus sp.

Pl. 3, Fig. 5; Fig. 5

Description. – Stem. The columnal articulation surfaces display thick and sparse crenulae. The lateral surfaces are covered with large nodes (Fig. 5f). The height of ossicles is variable which may reflect ontogenetic variability as well as variability within one stem.

Crown. The cup is small and low (Pl. 3, Fig. 5; Fig. 5g), markedly widening downward. Its outer surfaces are covered with nodes. It is always distinctly pentagonal with strong interradial lobes in its dorsal part. The dorsal cavity is rounded and wide, with deep furrows at its radial sutures. The arm facets are prominent and bend steeply outwards. The lower articulation surface of the first primibrachial (IBr1) is of the muscular type, the upper one is smooth (synostosis). The first primibrachial (Fig. 5e) is rectangular in outline and displays large, strongly expanded processes which border the ambulacral groove. The primaxillary (IAx) (Fig. 5d) is large and asymmetrical. The secundibrachial facets are separated by a deep furrow. Their ambulacral grooves are bordered by wing-shaped processes. Other brachials are strongly asymmetrical because of their large pinnular facets. All brachial elements (Fig. 5b-e) are covered with nodes.

Remarks. – There is variability in cup height, development of nodes, and width of dorsal cavity.

The investigated cups are very similar to *Sclerocrinus pentagonus* JAEKEL 1891, especially to the juveniles (see ŽITT 1974b, Pl. 4, Fig. 7-12). The difference is in the smaller width of the upper part of our cups. Our specimens also have arm facets more steeply bent outwards and a wider basal cavity. The latter feature makes them close to *Sclerocrinus compressus* GOLDFUSS. Numerous unusual brachials have been found in red Rogoźnik coquina. Because of their primitive marks and dense granulation identical with the granulation on cups of *Sclerocrinus* sp., we attribute them to the latter species. This is contrary to the illustration and descriptions of *Sclerocrinus pentagonus* JAEKEL by ŽITT (1974b) and the reconstruction of JAEKEL (1907). ŽITT (1974b) has found a cup of this species with articulated first primibrachial (IBr1) which is at the same time the primaxillary (IAx) and is different from our brachials. We consider the investigated brachial as belonging to *Sclerocrinus* sp. This is

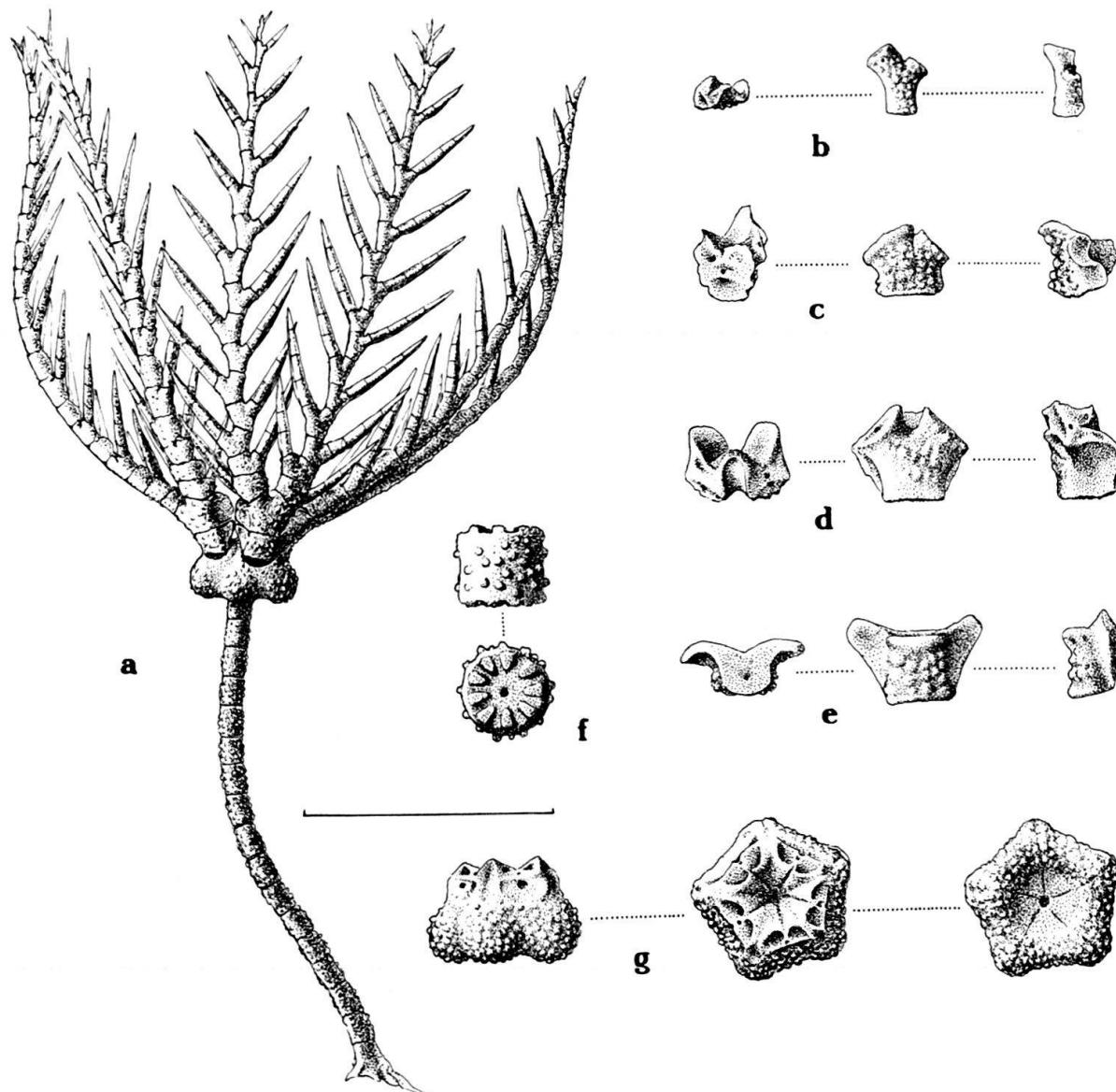


Fig. 5. *Sclerocrinus* sp. a = reconstruction of animal in life position, b-c = brachials of higher order, distal, dorsal and lateral view, d = second primibrachial = primaxillary (IAx), distal, dorsal and lateral view, e = ? first primibrachial, distal, dorsal and lateral view, f = columnal, lateral and articulation facet view, g = cup, lateral oral and basal view. Scale bar 5 mm.

because these brachials cannot be correlated with any other known cup from Rogoźnik, and any other known arm ossicles cannot be correlated with the cup of *Sclerocrinus* sp.

Material. – 8 cups, about 20 columnals and about 80 brachials.

Occurrence. – Red Rogoźnik coquina, Early or Middle Tithonian, Rogoźnik, Poland.

Family ***Hemicrinidae*** RASMUSSEN 1961

Genus ***Hemicrinus*** D'ORBIGNY 1850

Type species: *Hemicrinus astierianus* D'ORBIGNY 1850

Hemicrinus tithonicus n. sp.

Pl. 3, Fig. 6-7; Fig. 6

Holotype. – Specimen CaI/1356, Plate 3, Figure 6.

Type locality. – Rogoźnik, Pieniny Klippen Belt, Poland.

Type horizon. – Red Rogoźnik coquina, Early or Middle Tithonian.

Derivation of the name. – After the age of the type horizon.

Diagnosis. – Cup and the stem axes make an angle of 100–110°. Arm facets are equal in size and occur at almost the same level.

Description. – Stem. No well-preserved stem has been found and hence, we do not know whether free columnals did exist or not, and their number in the stem. On the immature specimens the suture between the proximal columnal and the cup can be observed, as well as suture between the first two columnals.

Crown. The cup (Pl. 3, Fig. 6-7; Fig. 6) and the stem axes usually make an angle of 100–110°, rarely 90°. The sutures between radial plates are weakly marked. The interior is widely conical and relatively deep. The arm facets are equal in size, strongly developed, wide and low. The cup displays a pentagonal symmetry at the ventral side. Sometimes, the arm facet nearest to the stem is placed slightly higher than the others. Two unspecialized brachial types have been found in red Rogoźnik coquina which may belong to *Hemicrinus tithonicus* n. sp. One of them displays the synostosis type of articulation between the first primibrachial and the second primibrachial (IBr1–IBr2); while in the other it is of the muscular type. One of these brachial types must belong to *Hemicrinus tithonicus* n. sp. We attribute those brachials with muscular articulation (Fig. 6d–e) to *Hemicrinus tithonicus* n. sp. because they are concordant with the cups of this species in size, functional morphology as well as frequency. We claim that the other considered brachials belong to *Psalidocrinus armatus* (ZITTEL). There is but a single specimen of the first primibrachial (IBr1) (Fig. 6f) with both articulation surfaces of the muscular type. It is rectangular in outline and low. We assigned it to the investigated species. In juveniles, primaxillary (IAx) is rather low; in mature individuals, it is massive, pentagonal in shape, usually asymmetrical, and with ribbed lateral surfaces (Fig. 6e). Both that ribbing and the muscular articulations suggest that when the arms were coiled the primaxillaries were attached closely together. Other brachials (Fig. 6b–c) are trapezoidal in section with a single long lateral extension (probably bordering the ambulacral groove). The pinnular articulation surfaces are indistinct and difficult to identify. Morphology of the brachials suggests that folded arms gave a massive armour.

Remarks. – *Hemicrinus tithonicus* n. sp. differs from the most similar species *H. thersites* JAEKEL in its more bent cup axis. From other congeners, it differs in its pentagonal shape and larger cup; moreover, one of its arm facets occurs usually just opposite to the stem. There are also some differences in brachial morphology (see JAEKEL 1891). The latter feature indicates that the investigated species belongs to a different evolutionary line.

H. tithonicus n. sp. exhibit a slight variability in degree of separation of the radial plates, outline regularity, and stem thickness.

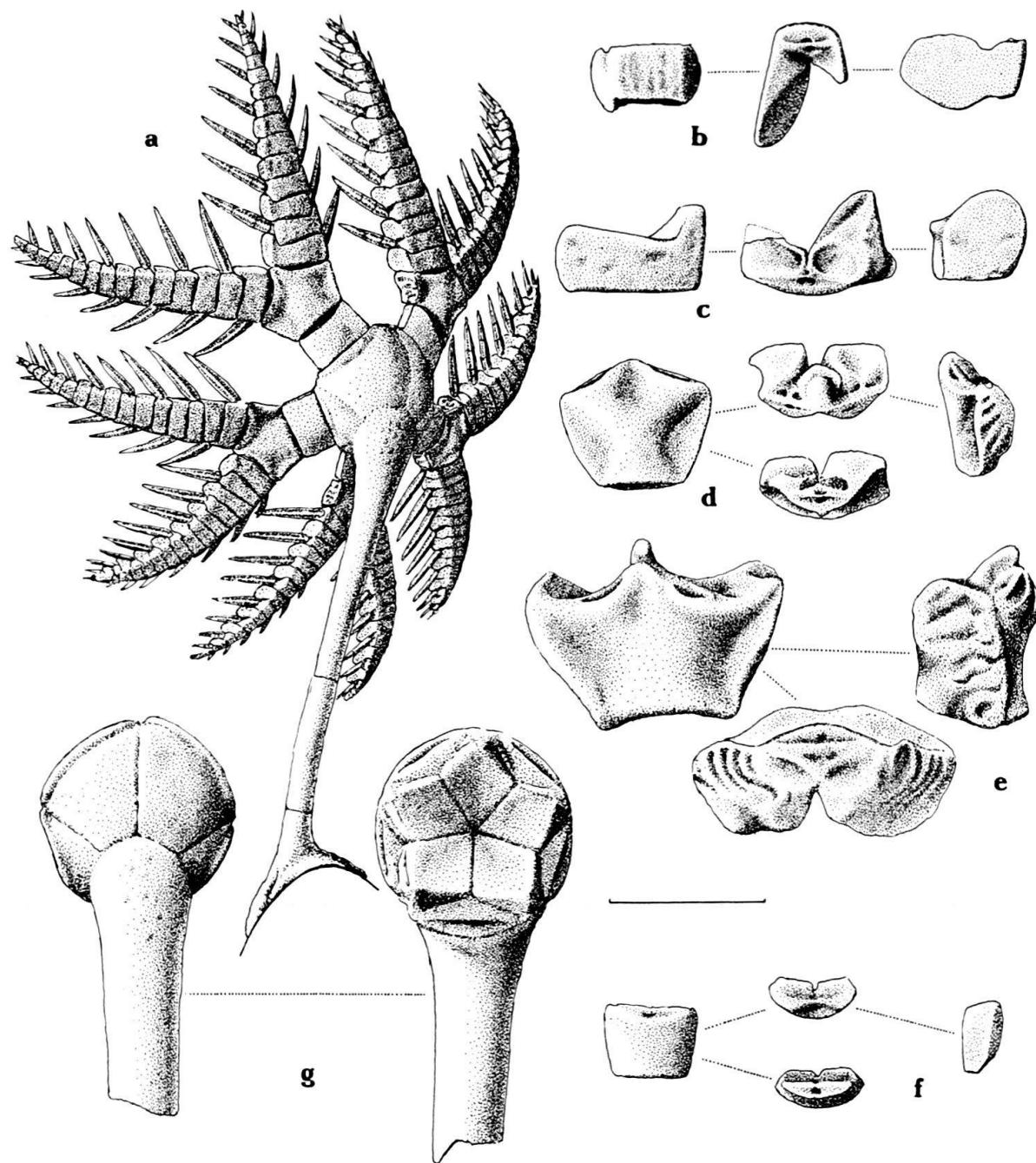


Fig. 6. *Hemicrinus tithonicus* n.sp. a = reconstruction of animal in life position, b = secundibrachial, dorsal, proximal and lateral view, c = first secundibrachial, dorsal, distal and lateral view, d = axillary of immature specimen, dorsal, distal, lateral and proximal view, e = axillary of mature specimen, dorsal, proximal and lateral view, note crenulation on sides, f = first primibrachial, dorsal, distal, lateral and proximal view, g = cup, dorsal and ventral view. Scale bar 5 mm.

Material. – 19 cups, 10 brachials and few broken columnals.

Occurrence. – Red Rogoźnik coquina, Early or Middle Tithonian, Rogoźnik, Poland.

Genus *Tetanocrinus* JAEKEL 1891

Type species: Tetanocrinus aberrans (LORIOL 1882)

Tetanocrinus cf. aberrans (LORIOL 1882)

Pl. 2, Fig. 8; Fig. 7a-b

Cf. 1882 *Eugeniacrinus aberrans* LORIOL, p. 148-151, Pl. 15, Fig. 4-6.Cf. 1891 *Tetanocrinus aberrans* (LORIOL), JAEKEL, p. 628-630, Fig. 15.

Description. – Crown. Only a single cup (Pl. 2, Fig. 8; Fig. 7a) is represented in our collection. It is very high, cylindrical in the lower part. The sutures between radials are invisible. The cup interior is very small and deep. The arm facets are very large with very large ligament pits and bent steeply outwards. A single brachial (Fig. 7b) which is strongly convex, has been also found in Rogoźnik white coquina. The latter element may belong to *Tetanocrinus cf. aberrans*. However, *Cyrtocrinus nutans* (GOLDFUSS) does exhibit very similar brachials.

Remarks. – Our specimen differs from those earlier illustrated in its straight and short cup axis.

Material. – One cup, one brachial.

Occurrence. – White Rogoźnik coquina, Middle or Upper Tithonian, Rogoźnik, Poland.

Family *Eugeniacrinidae* ZITTEL 1879Genus *Lonchocrinus* JAEKEL 1907

Type species: *Eugeniacrinites remesi* BIESE 1937

Emended diagnosis. – The primaxillary (IAx) with a long spine-like process between articulation surfaces of the secundibrachials.

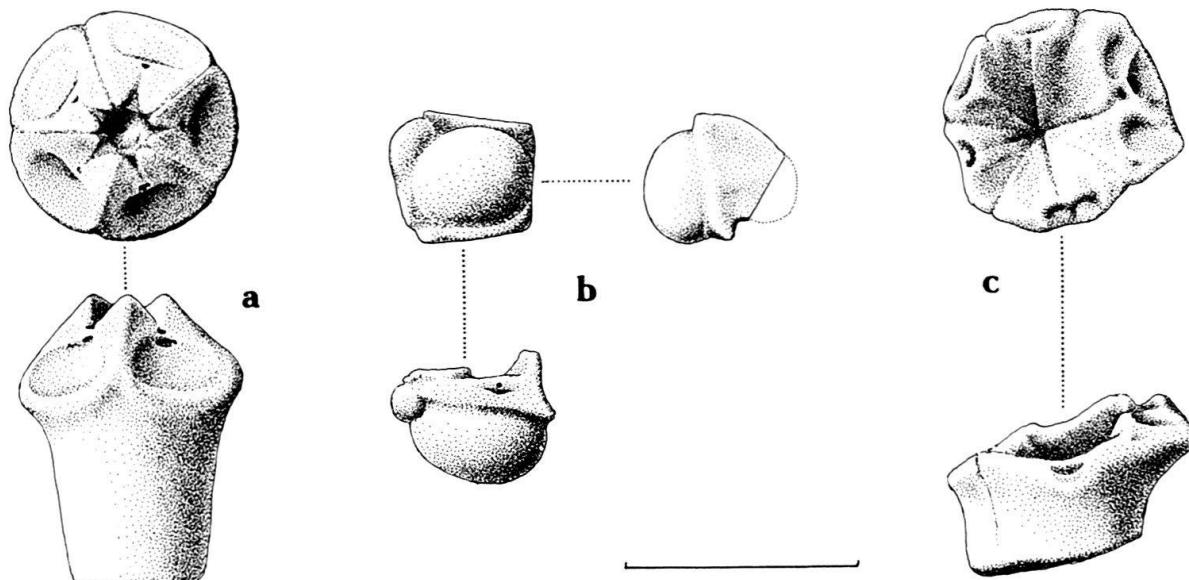


Fig. 7a-b. *Tetanocrinus cf. aberrans* (LORIOL 1882). a = cup, lateral and oral view, b = ? first primibrachial which could belong to this species, distal, dorsal and lateral view. Scale bar 5 mm.

Fig. 7c. ? *Eudesicrinus* sp. Cup, oral and lateral view. Scale bar 5 mm.

Remarks. – The genus *Lonchocrinus* has been erected by JAEKEL (1907) who did, however, not designate any type species. BIESE (1937) recognized *Eugeniacrinites granulatus* D'ORBIGNY described also from Štramberk by REMEŠ (1902) as a new species *E. remesi* BIESE. However, JAEKEL (1907) demonstrated that the former species to represent his genus *Lonchocrinus* and hence, ARENDT (1974) proposed the latter species as type species. Unfortunately, *E. remesi* BIESE has been based only on the cup, while there are at the same locality axillaries of both *Eugeniacrinites* and *Lonchocrinus* type which makes any determination of the actual generic position of *E. remesi* BIESE cups impossible. Probably, the Štramberk species of *Lonchocrinus* and *Eugeniacrinites* do not differ in the morphology of their cups. This is the reason for the present emendation of diagnosis stressing the shape of the axillary.

Lonchocrinus staszici n.sp.

Pl. 4, Fig. 5-6; Fig. 8, 13g-h

Holotype. – Specimen CaI/809, Plate 4, Figure 5.

Type locality. – Rogoźnik, Pieniny Klippen Belt, Poland.

Type horizon. – Red Rogoźnik coquina, Early or Middle Tithonian.

Derivation of the name. – In honour of Stanisław Staszic (1755–1825), Polish geologist and investigator of the Carpathians.

Diagnosis. – Cup low. Basal diameter only slightly smaller than at the level of the arm facets. Convex radial plates. Stem facet placed in concavity.

Description. – Crown. The cup is rounded-pentagonal and low (Pl. 4, Fig. 5-6; Fig. 8g-h). The cup base is wide with a large concave stem facet. The sutures between radial plates are distinct and sunken. The interradial processes are short, rounded and convex. Their inner sides are flat. The arm facets are large and wide. The first primibrachial (IBr1) is slightly convex and probably rectangular in outline (Fig. 8f). Its upper articulation surface is smooth (synostosis), the lower one is of the muscular type. It can hardly be distinguished from the first primibrachial of *Psalidocrinus*. The axillary (Fig. 8b-e) is typical for the genus and bears a long spine-shaped process. The axillaries show great variability. Their lower articulation surface is smooth (synostosis); the upper ones are of the muscular type, which are situated at the inner side of the axillary and separated by a rhomboidal process. There is a continuous transition from wide to narrow axillaries which reflects an intrapopulation variability. With the arms closed, the axillar spines may have performed a similar defensive function as did the interradial processes in the genus *Phyllocrinus*.

Remarks. – *Lonchocrinus staszici* n.sp. differs from other species of the genera *Lonchocrinus* and *Eugeniacrinites* in shape of the cup and interradial processes as well as in size of the arm facets.

Material. – 20 cups, more than 60 axillaries and one first primibrachial.

Occurrence. – Red Rogoźnik coquina, Early or Middle Tithonian, Rogoźnik, Poland.

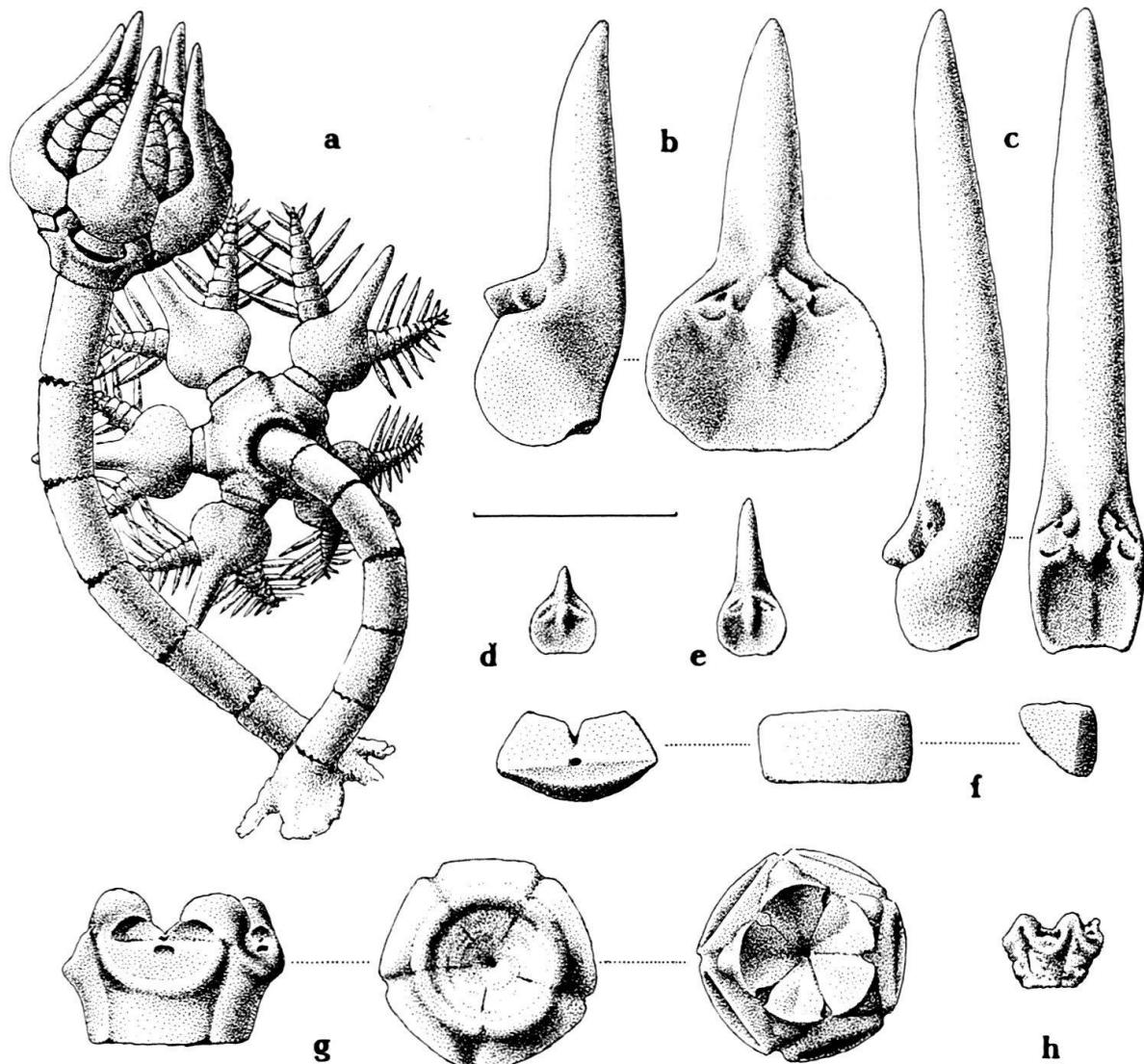


Fig. 8. *Lonchocrinus staszici* n.sp. a = reconstruction of animal in life position, b-e = differently sized second primibrachials = primaxillaries, ventral and lateral view, note their great variability, f = first primibrachial, proximal, dorsal and lateral view, g = cup of mature specimen, lateral, basal and oral view, h = cup of immature specimen, lateral view. Scale bar 5 mm.

Family *Phyllocrinidae* JAEKEL 1907

Genus *Psalidocrinus* REMEŠ & BATHER 1913

Type species: *Psalidocrinus remesi* BATHER 1913

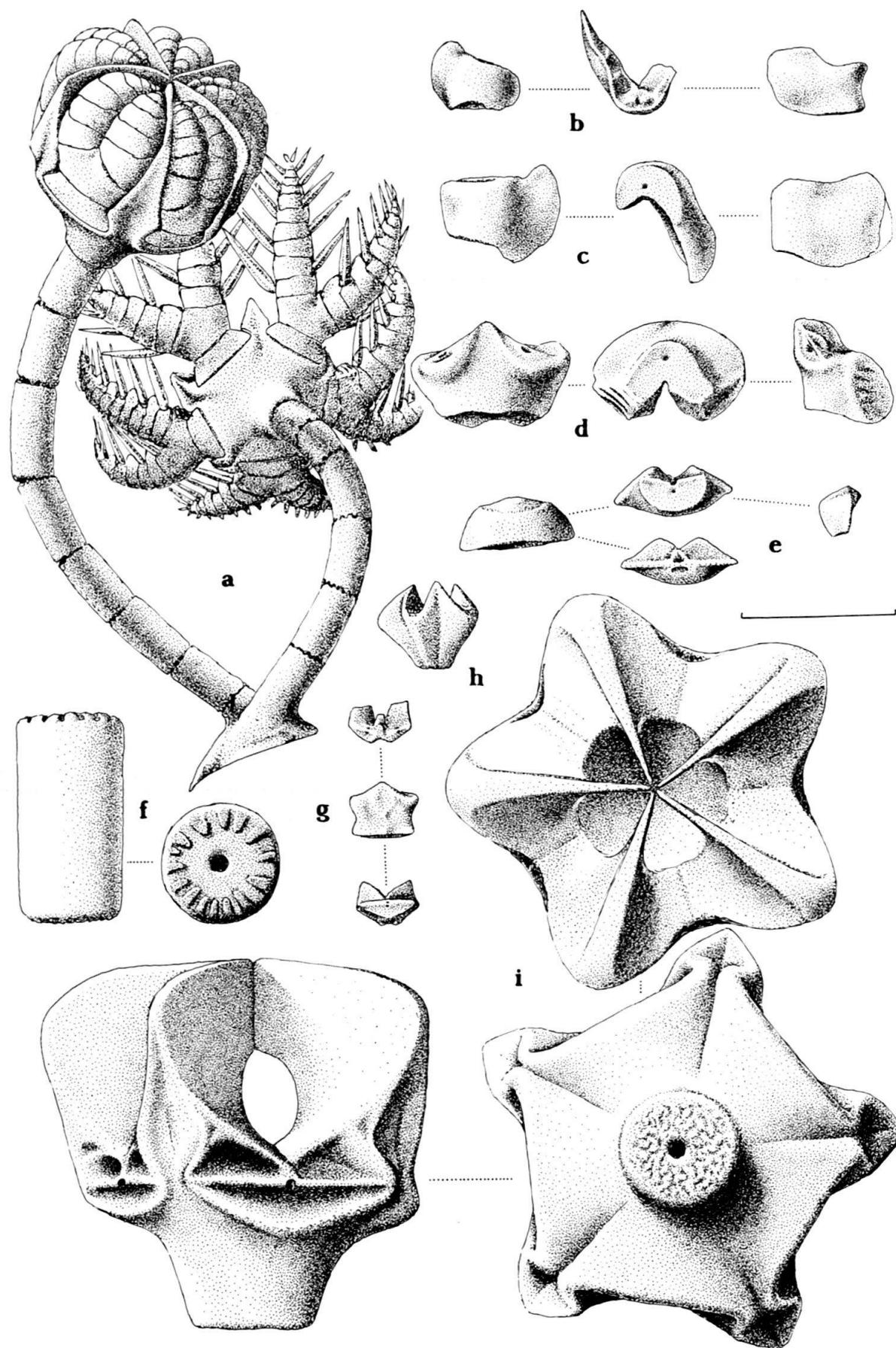
Psalidocrinus armatus (ZITTEL 1870)

Pl. 5, Fig. 1-6; Fig. 9, 13a-c

1870 *Eugeniacrinus armatus* sp.nov., ZITTEL, p. 158-159, Pl. 15, Fig. 15-16.

1876 *Eugeniacrinus armatus* ZITTEL, ZARĘCZNY, p. 212.

Emended diagnosis. - Cup with high blade-like interradial processes almost attached to one other at the top.



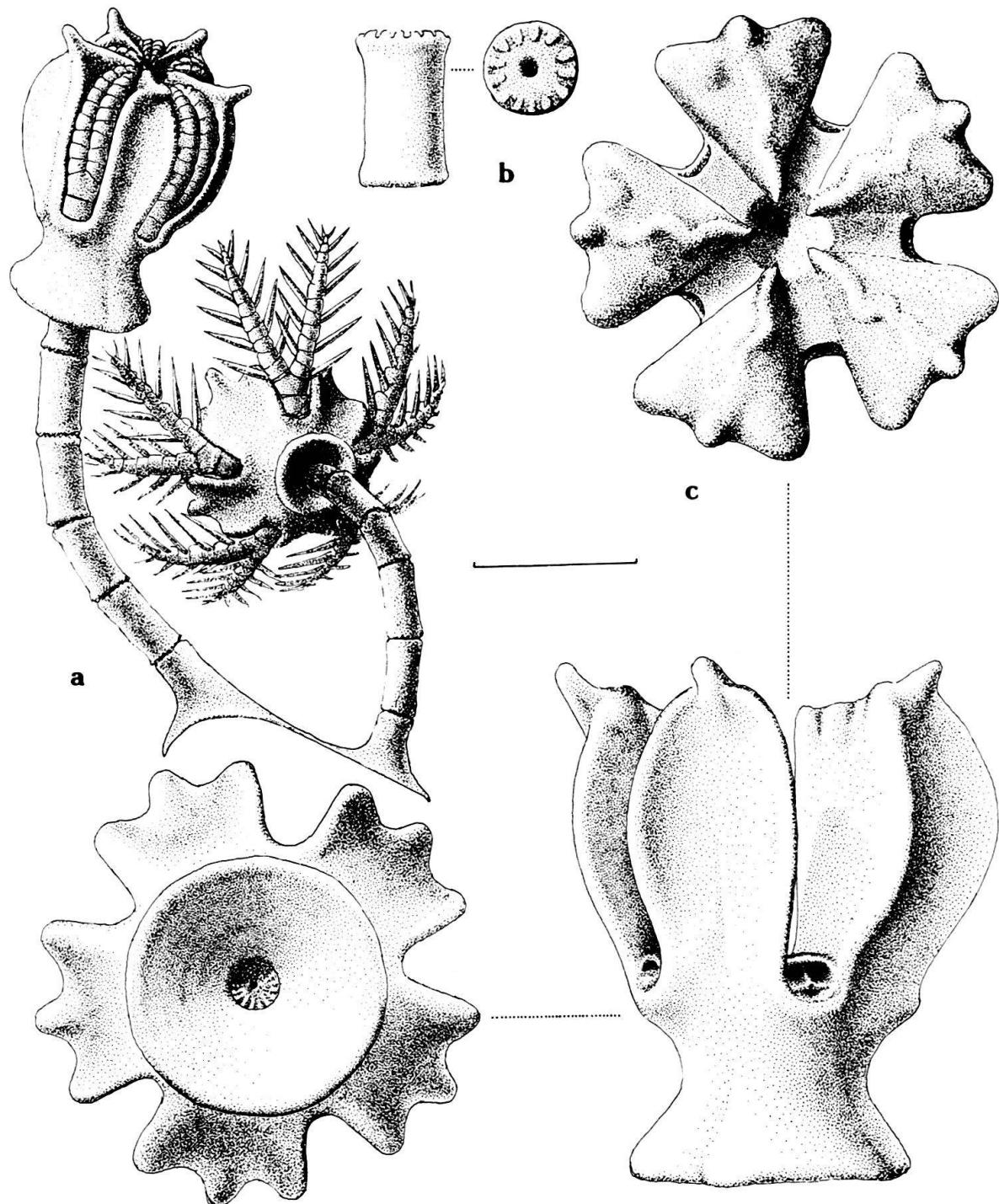


Fig. 10. *Apsidocrinus moeschi* (ZITTEL 1877). a = reconstruction of animal in life position, b = columnal, c = cup, basal, lateral and oral view. Scale bar 5 mm.

Fig. 9. *Psalidocrinus armatus* (ZITTEL 1870). a = reconstruction of animal in life position, b-c = distal brachials, dorsal, articular facet and lateral view, this kind of brachials were placed one by one in arms, d = second primibrachial = primaxillary, dorsal, proximal and lateral view, e = first primibrachial, dorsal, distal, lateral and proximal view, f = columnal, g = ? fused first and second primibrachials which could belong to this species, distal, dorsal and proximal view, i = cup of adult specimen, lateral, basal and oral view, h = cup of immature specimen, lateral view. Scale bar 5 mm.

Description. – Stem. The columnals are smooth, cylindrical and rather high (Fig. 9f). The articulation surface is thickly crenulated near the edge.

Crown. In the mature specimens the cup extends concavely from the base to the level of the arm facets (Pl. 5, Fig. 1; Fig. 9i). The sutures between radial plates occur in furrows on an elevation. There is a large variability in the morphology of the surfaces; they are either concave, convex, or flat. The interradial processes are high, flat, and wedge-shaped in cross-section. They expand toward the center of the cup. They attain their maximum width at $\frac{1}{4}$ – $\frac{1}{3}$ of the height. The cup interior is wide and deep. The arm facets are very large and wide, almost touching one another. They have distinctly developed ligament pits and muscular fossae. The stem facet is as wide as the base of the cup and covered with an irregular crenulation. The first primibrachial (IBr1) is trapezoidal and slightly convex (Fig. 9e). The lower articulation surface is of the muscular type. The upper one is smooth (synostosis). The primaxillary (IAx) is pentagonal in outline, slightly convex and symmetric (Fig. 9d). It displays large articulation surfaces. The lower surface is smooth (synostosis) and the upper one is of the muscular type. The distal articulation surfaces are separated by a weakly marked process. The lateral surfaces of the axillary are covered with indistinct ribs. More distal brachials are asymmetric, each with a large wing-shaped process bordering an ambulacratal groove (Fig. 9b–c). The pinnules are probably attached to one side of a brachial only. Some brachials have one articulation surface smooth (synostosis), while in others both the surfaces are of the muscular type.

Remarks. – The investigated species shows great ontogenetic and intrapopulation variability (see Pl. 5, Fig. 2–6). The variability is mostly in the character of the radial surfaces, lower part of the cup and arm facets. In young specimens, the stem facet occurs in a concavity of the cup. In mature ones, it covers the base entirely. Most investigated specimens as well as all those of ZITTEL derived from Rogoźnik have their interradial processes broken. In effect ZITTEL (1870) placed this species in genus *Eugeniacrinites*, from which it differs in strongly deeper interior of the cup and axillary morphology as well.

The investigated species differs from the most similar species *Psalidocrinus remesi* BATHER and *P. strambergensis* (REMEŠ) (compare REMEŠ & BATHER 1913, ŽITT 1978) in its unfused interradial processes.

Material. – More than 120 cups, 160 brachials (part of brachials could belong to *Hemicrinus tithonicus* n. sp., however).

Occurrence. – Red Rogoźnik coquina, Early or Middle Tithonian, Rogoźnik, Poland.

Genus *Apsidocrinus* JAEKEL 1907

Type species: *Apsidocrinus remesi* JAEKEL 1907

Apsidocrinus moeschi (ZITTEL 1877)

Pl. 4, Fig. 7–8; Fig. 10

1879 *Phyllocrinus moeschi* ZITTEL, LORIOL, p. 235–236, Pl. XIX, Fig. 18–22.

Emended diagnosis. – Tongue-shaped interradial processes with short, outward directed thorns at their ends. Funnel-shaped cup base.

Description. – Stem. We have found only a single, relatively small columnal (Fig. 10b), the cup base probably formed an elevation around it. However, the next, unknown stem ossicles may have been much larger.

Crown. The interradial processes are robust, wide and tongue-shaped with roundly concave external surface. At the top, they bear distinct, blunt thorns directed outwards and upwards (Pl. 4, Fig. 7-8, Fig. 10c). The cup attains its maximum width somewhat below the arm facets. Beneath that level, the cup becomes quickly very wide and forms a characteristic collar around the stem facet. The latter is rather small and deeply placed, covered with a weak crenulation. The sutures between radial plates are weakly marked. The arm facets are very small and hidden between interradial processes. The ventral cavity is narrow and deep (Fig. 10c).

Remarks. – The investigated species differs from its congeners in shape of the cup base and the interradial processes.

We have not recognized any elements of arms. Thus, the reconstruction is based on the analogy to other phyllocrinid species and the functional analysis.

Material. – 4 cups, one columnal.

Occurrence. – Red Rogoźnik coquina, Early or Middle Tithonian, Rogoźnik, Poland.

Genus *Phyllocrinus* D'ORBIGNY 1850

Type species: *Phyllocrinus malbosianus* D'ORBIGNY 1850

Phyllocrinus stellaris ZARĘCZNY 1876

Pl. 4, Fig. 2-4; Fig. 11a-b, 13e-f

1876 *Phyllocrinus stellaris* sp. nov., ZARĘCZNY, p. 213, Pl. 1, Fig. 9.

Emended diagnosis. – Cup low and hemispherical. Radial plates strongly convex with a rib in the middle. Interradial processes sharp and triangular.

Description. – The cup is low, pentagonal in outline and strongly incise (Pl. 4, Fig. 2-4, Fig. 11a-b). The sutures of radial plates are placed in depressions and weakly marked. The cup is very wide cone, the greatest median is at the level of the arm facets, above it again becomes narrow. The interradial processes are large, triangular in outline, and convex in the middle. Every radial plate bears a rib and a few weakly marked nodes. The arm facets are small and separated from the ventral cavity by a strong ridge. The cup interior is deep, round and narrow. The stem facet is round, shallow and bordered by a distinct elevation.

Remarks. – There is but a slight variability in the investigated species. The species differs from the most similar species *Phyllocrinus belbekensis* ARENDT in shape of the cup. The stem facet and interradial processes are also different.

We have not identified any arm ossicles attributable to the investigated cup. The columnals are very similar among diverse species of the genus *Phyllocrinus*.

This species was erected by ZARĘCZNY (1876) in material from Rogoźnik. In the same paper he also described other new species i.e. *Ph. elegans*, *Ph. minutus* which

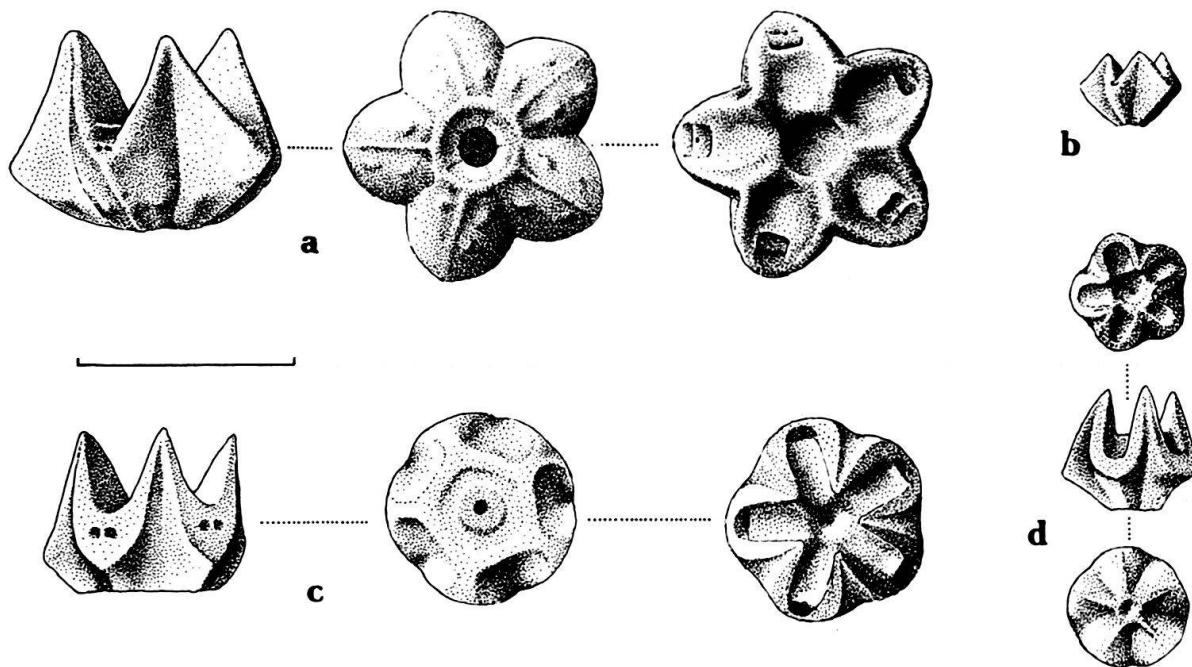


Fig. 11a-b. *Phyllocrinus stellaris* ZARECZNY 1876. a = cup of mature specimen, lateral, basal and oral view, b = cup of immature specimen, lateral view. Scale bar 5 mm.

Fig. 11c-d. *Phyllocrinus belbekensis* ARENDT 1974. c = cup of mature specimen, lateral, basal and oral view, d = cup of immature specimen, basal, lateral and oral view. Scale bar 5 mm.

have not been found by us. Unfortunately the whereabouts of the material is unknown, therefore making redescription impossible. In our opinion, they are probably juvenile forms, partly destroyed, of the known species of *Phyllocrinus*.

Material: 60 cups.

Occurrence: Red Rogoźnik coquina, Early or Middle Tithonian, Rogoźnik, Poland.

Phyllocrinus belbekensis ARENDT 1974

Pl. 4, Fig. 1; Fig. 11c-d, 13d

1974 *Phyllocrinus belbekensis* sp. nov., ARENDT, p. 118-119, Pl. XIV, Fig. 1-21; Fig. 14d-k)

Emended diagnosis. - Low cup with flat belts around the arm facets. These flat surfaces are distinctly separated from other, concave surfaces of the cup. They run upwards, toward the interradial processes.

Description. - The cup is small and low, pentagonal in outline (Pl. 4, Fig. 1; Fig. 11c-d). It expands gradually up to the arm facets; above that level, it narrows more or less distinctly. The interradial processes are long and narrow, acute triangular. The sutures between radial plates are weakly marked and placed in furrows. The upper edges of radials form ledges distinctly separated from the cup surface. The base is small but very variable in adult individuals. The stem facets covers the base surface entirely. It bears a distinct ledge around. There is a small elevation in the central part of the facet.

Remarks. – Only one adult specimen has been found (Pl. 4, Fig. 1); it quite differs from the forms described by ARENDT (1974). The other investigated specimens closely resemble the holotype (Fig. 11d).

We found a great intrapopulation variability, which is in agreement with ARENDT's findings (1974). The investigated species differs from the most similar species *Ph. stellaris* ZARĘCZNY in the outline of the cup, shape of interradial processes and stem facet.

Material. – More than 60 cups.

Occurrence. – Red Rogoźnik coquina, Early or Middle Tithonian, Rogoźnik, Poland.

Family *Eudesicrinidae* BATHER 1899

Genus *Eudesicrinus* LORIOL 1822

Type species: *Eudesicrinus mayalis* (DESLONGCHAMPS & DESLONGCHAMPS 1858)

? *Eudesicrinus* sp.

Pl. 3, Fig. 4; Fig. 7c

Remarks. – A single cup has been found in white Rogoźnik coquina, which probably belongs to the genus *Eudesicrinus*. The cup is low and wide, markedly asymmetrical (Pl. 3, Fig. 4; Fig. 7c). It is cylindrical at the base, quickly expanding outwards. The sutures between radial plates are invisible. Only one arm facet is normally developed. It occurs a little higher than the other which appears only weakly marked and small. The cup interior is deep and wide, with small furrows. Our specimen shows some affinities with the family Hemibrachiocrinidae as regards the character of the arm facets, the cup interior and asymmetrical shape. One can hardly determine whether the investigated cup had a stem or not. If it did, it might be assigned to genus *Cyrtocrinus*.

Material. – A single cup.

Occurrence. – White Rogoźnik coquina, Middle or Upper Tithonian, Rogoźnik, Poland.

Palaeoecological characteristics of Rogoźnik crinoid association

In the limestone quarry at Rogoźnik, many blocks of strongly tectonized rocks of different age (Aalenian to Campanian) are exposed. The cyrtocrinid crinoids have been recorded only in white and red micritic shelly limestones of Tithonian age.

Only singular cups of *Tetanocrinus* cf. *aberrans* (LORIOL) and *Eudesicrinus* sp. have been gathered from the white limestone. This limestone contains a very rich and diverse ammonoid and brachiopod fauna but the fossils are almost impossible to extract.

The red limestone exposed at the northern side of the Rogoźnik Rock (old Rogoźnik quarry) contains rich fauna within which pelagic and benthic assemblages may be recognized.

Pelagic assemblage

The most common species of macrofauna is *Protetragonites quadrisulcatum* (D'ORBIGNY). "Phylloceras" *ptychoicum* QUENSTEDT, *Neolissoceras carachteis* ZEJSZNER, *Bochianites* sp. are also common. *Holcophylloceras* sp., *Protancyloceras* sp., *Aspidoceras rogoznicense* (ZEJSZNER) and perisphinctids occur rarely, as do fish remains.

The species of *Saccocoma* are the main microscopic-sized macrofossils in the red limestone. There are at least two well-separated species; viz. *Saccocoma tenella* GOLDFUSS and *S. cf. quenstedti* VERNIORY. The first dominant species exhibits relatively massive radial plates; the second, *S. quenstedti* VERNIORY, has relatively delicate radials with long spines.

Occurrence of pelagic echinoderms – organisms characterized by low physiological activity, because of presumably low efficiency in food utilization (cf. BINYON 1972) and high alimentary requirement – is worth considering. These organisms required a stable energy flow which allowed them to carry their calcareous skeletons in water. This may indicate a large concentration of phyto- and zooplanktonic organisms that is, high biological productivity in the Tithonian sea of Rogoźnik.

JANICKE (1970) suggested that coprolites *Lumbricaria*, containing as a rule large amounts of *Saccocoma* remains, are to be assigned to cephalopods. Mass occurrence of *Saccocoma* remains together with ammonoids (which were supposedly the next level in the trophic pyramid) support the view that those animals were an important part of ammonoids' food.

Benthic assemblage

Small clusters of *Pygope janitor* (PICTET) occur commonly. There are also some other brachiopods [“*Rhynchonella*” *capillata* ZITTEL, *Nucleata rupicola* (ZITTEL), *Aulacothyris* sp.]. An important part of the volume of fossils is represented by irregular echinoids (*Cardiolampas altissimus* ZEJSZNER). Thick spines of *Hemicidaris zignoi* COTTEAU are fairly common. Asteroid and ophiuroid ossicles are rare.

The cyrtocrinid and isocrinid crinoids appear as an important component of the assemblage. They are represented by seven species. The most common are *Psalidocrinus armatus* (ZITTEL), *Balanocrinus* cf. *subteres* (MÜNSTER), *Phyllocrinus stellaris* ZARĘCZNY and *Phyllocrinus belbekensis* ARENDT. *Lonchocrinus staszici* n.sp., *Apsidocrinus moeschi* (ZITTEL), *Sclerocrinus* sp. are rare.

There is but a single solitary coral species *Trochocyathus truncatus* ZITTEL in the assemblage. Some small-sized species of gastropods (*Spinigera tatica* ZEJSZNER, *Emarginula* sp., *Chilodonta* sp. and others) are present in the residue. Along with very rare byssally-attached pelecypods those gastropods may have represented epiplanctic organisms.

As judged from the size frequency distribution of the most common cyrtocrinid species (Fig. 12), they displayed reverse mortality patterns. Thus, *Phyllocrinus stellaris* ZARĘCZNY, *Ph. belbekensis* ARENDT and *Lonchocrinus staszici* n.sp. show a high juvenile mortality (Fig. 12a, c-d). In the case of *Psalidocrinus armatus* (ZITTEL) (Fig. 12b), low juvenile mortality resulted in most individuals attaining a large size

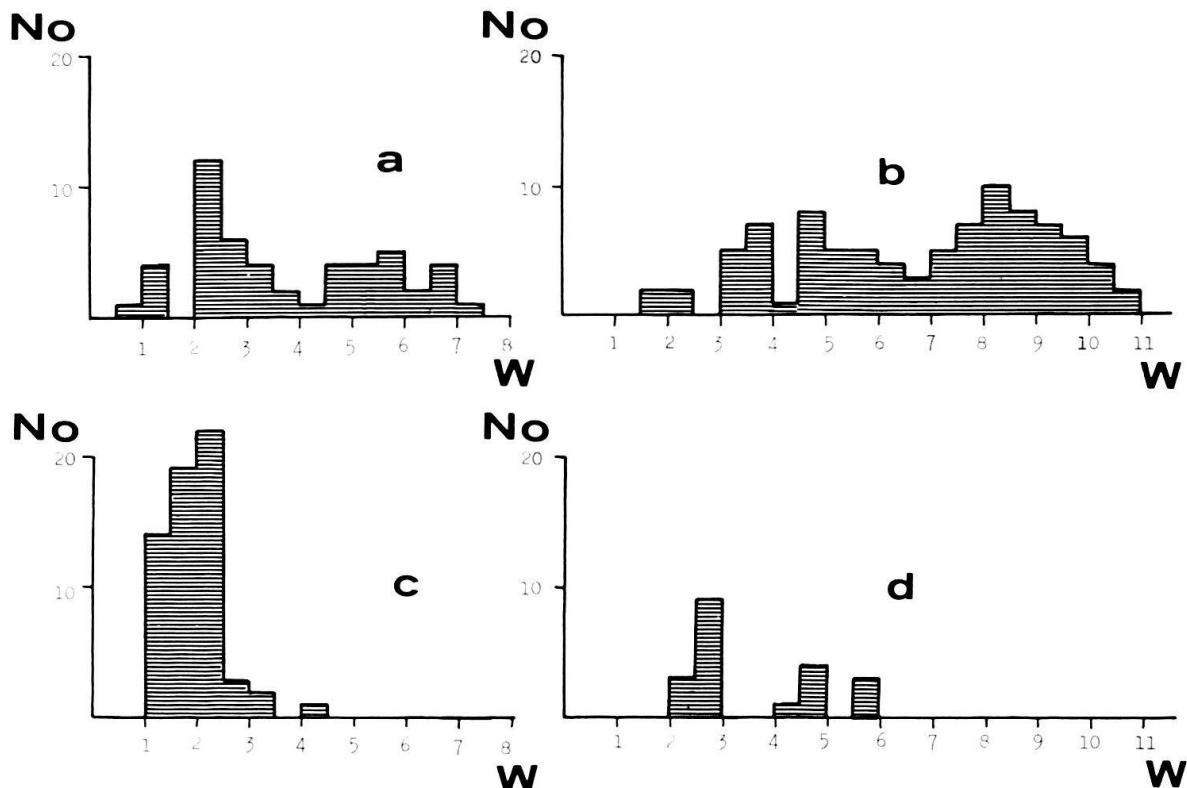


Fig. 12. Size frequency distribution of some cyrtocrinid species (for diameter of cup: W) from Lower Tithonian of Rogoźnik, Poland. a = *Phyllocrinus stellaris* ZARECZNY 1876, b = *Psalidocrinus armatus* (ZITTEL 1870), c = *Phyllocrinus belbekensis* ARENDT 1974, d = *Lonchocrinus staszici* n.sp.

implying the adult age. We claim that this differentiation in mortality patterns reflects a variability in adaptability to sedimentary environment. Supposedly, the bottom was settled by similar number of larvae of each species but the former three species were subject to a stronger selection.

With such a taxonomic composition of the assemblage taken into account, one may attempt to reconstruct the structure of the red Rogoźnik coquina community. The sessile brachiopods *Pygope*, small cyrtocrinids and the larger crinoid species *Balanocrinus* cf. *subteres* (MÜNSTER), and rare solitary corals were high level filter feeders. The irregular echinoids were infaunal swallowers feeding on detritus. A higher trophic level is represented by regular echinoids that can be regarded as omnivores and/or carnivores. Some ammonoids may have profited from the benthic organisms as a food source.

Most of the red Rogoźnik coquina fossils are broken and show traces of erosion. This seemingly appears to contradict the ecological characterization of the assemblage which lacks any littoral species. Supposedly, this is an effect of sediment reworking below wave base (probably at the top of a sea mount), due to storm waves or strong episodical currents.

Remarks on cyrtocrinid phylogeny

When studying cyrtocrinid evolution, one has first to investigate their intrapopulation variability and determine the boundaries among the contemporaneous

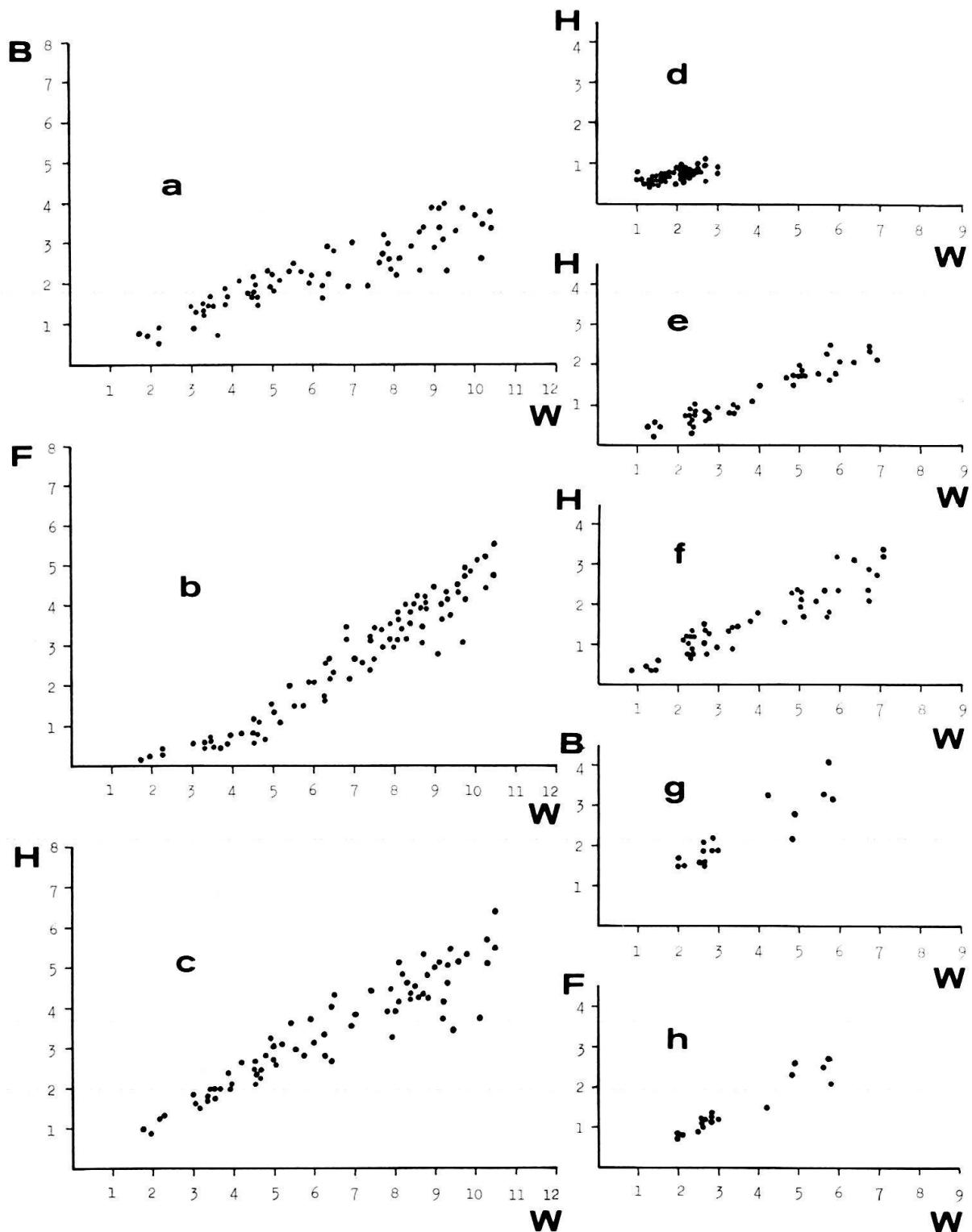


Fig. 13. Scatter diagrams showing relation between width of arms facet (F), height of cup from base to the facets level (H), diameter of the base of cup (B) and diameter of cup (W) at the facets level, for most common cyrtocrinid species from Lower Tithonian from Rogoźnik, Poland. a-c = *Psalidocrinus armatus* (ZITTEL 1870), d = *Phyllocrinus belbekensis* ARENDT 1974, e-f = *Phyllocrinus stellaris* ZARECZNY 1876, g-h = *Lonchocrinus staszici* n.sp.

species. Otherwise, artificial "evolutionary lineages" could be created, which run within a single homogenic population sequence. The first biometrical study of the Mesozoic crinoids was undertaken by ŽITT (1974a, 1974b, 1975). The present study confirms a great variability in the cup shape in the Late Jurassic cyrtocrinids. This has also been demonstrated by classical papers of JAEKEL (1891, 1892) and LORIOL (1882-4). It seems then that the number of described species of Cyrtocrinida is far too great. Unfortunately, one can determine an objective boundary between species only within contemporaneous and ecologically homogeneous population from a single locality. The taxonomic significance of differences between populations differing in occurrence in either space or time can be assessed only subjectively.

Deviations from pentaradial symmetry are very common among the cyrtocrinids (see BATHER 1889, 1900, JAEKEL 1892, ARENDT 1974). Fixation of a quart- or hexaradial symmetry together with fusion of the basal plates gives rise to the genus *Plicatocrinus* MÜNSTER (= *Tetracrinus* MÜNSTER). Morphologically, the latter genus very closely resembles some primitive species of *Sclerocrinus* JAEKEL. *Plicatocrinus* MÜNSTER is usually claimed to have possessed fused basal plates (JAEKEL 1892, SIEVERT-DORECK 1964b, ARENDT 1974). Because in many crinoids (and among cyrtocrinids in genus *Cyrtocrinus* JAEKEL) swollen proximal elements of the stem are morphologically identical with fused basal plates, additional data should be taken into account for discerning some species of the genus *Plicatocrinus* MÜNSTER. Furthermore, no ancestral forms with partly fused basal plates are known. Because of the symmetry instability within Cyrtocrinida, it seems that the number of symmetry planes cannot be regarded as diagnostic for a genus. Therefore, population studies of the genera *Plicatocrinus* and *Tetracrinus* are badly needed.

Sclerocrinus deslongchampsi (LORIOL) is among the oldest well-known cyrtocrinids. At the same time, it is very generalized in morphology (Fig. 14). Its second primibrachial (axillary) is nonspecialized and does not differ from homological elements of other articulate crinoids. The evolution of *Sclerocrinus* JAEKEL is expressed mainly in swelling and shortening of the cup. At least two evolutionary lineages originated within this genus in the Late Jurassic, viz. *Sclerocrinus strambergensis* group with pentagonal smooth and casky cup, and *Sclerocrinus pentagonus* group with pentagonal cup covered with thick nodes (Fig. 14). In the Tithonian limestones of Rogoźnik, a sclerocrinid species has been found with the cup morphology closely resembling *Sclerocrinus pentagonus* JAEKEL. Its first primibrachial (IBr1), however, was probably free and second primibrachial (IAx) facets were separated by a deep furrow. The Valanginian specimens of *Sclerocrinus pentagonus* JAEKEL from Štramberk have an accreted first and the second primibrachial (ŽITT 1974b). The evolutionary lineages of *Sclerocrinus strambergensis* JAEKEL continued up to the end of the Barremian (see ARENDT 1974). The genus *Pilocrinus* JAEKEL (known only from the Oxfordian) is derived from *Sclerocrinus* stock. *Pilocrinus* appears, however, so close to the advanced sclerocrinids that its separation from *Sclerocrinus* does not seem useful.

Folding of the cup axis already appeared in the oldest known cyrtocrinids. This is the only feature which separates the species "*Eugeniacrinites*" *mayalis* DESLONGCHAMPS (see LORIOL 1882) from its contemporaneous species *Eugeniacrinites*

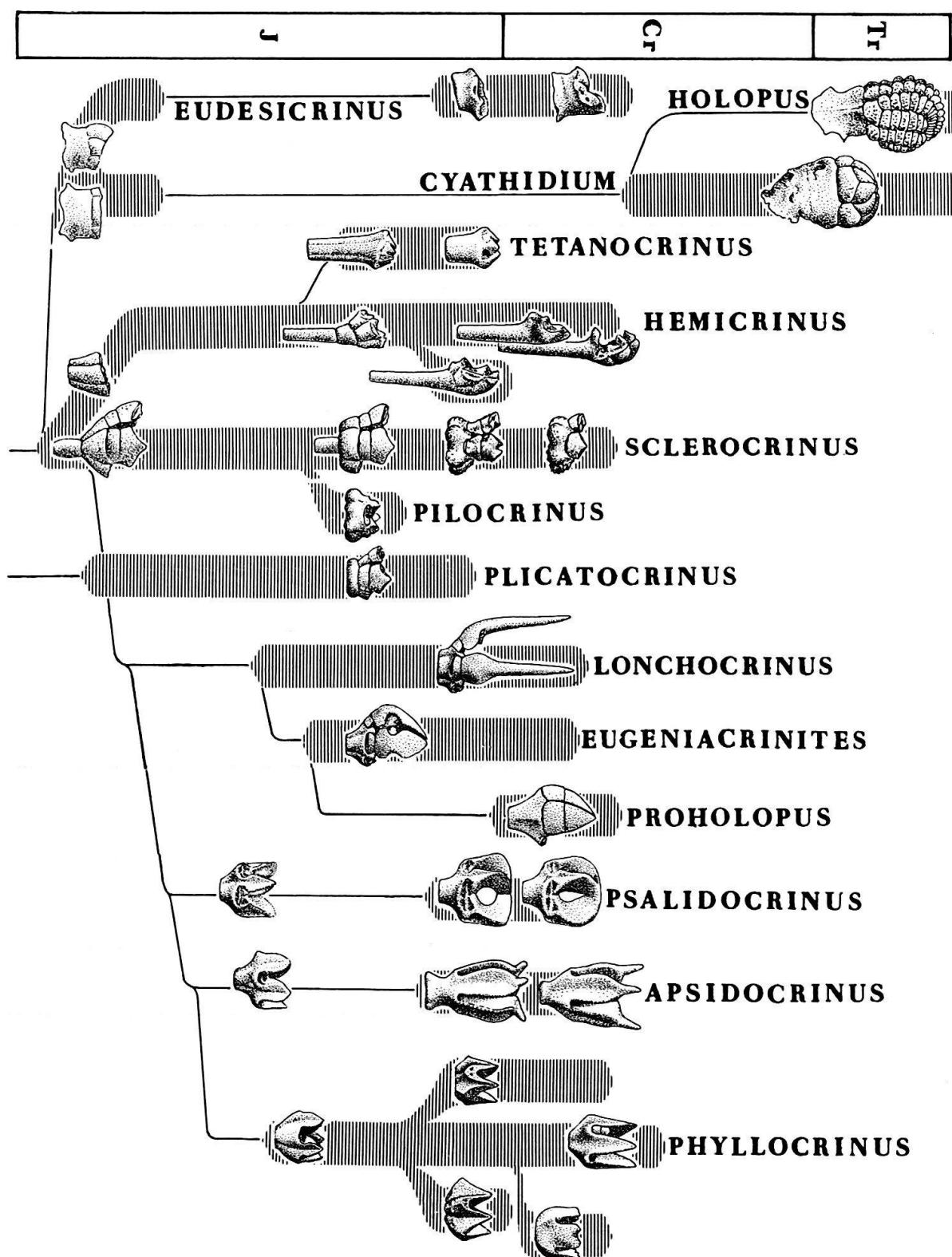


Fig. 14. Supposed phylogeny of Cyrtocrinida.

deslongchampsi LORIOL. If this is not merely a manifestation of intrapopulation variability (which cannot be excluded), the first species might be regarded as the first representative of the genus *Cyrtocrinus* JAEKEL. The type species *Cyrtocrinus nutans* GOLDFUSS (see illustrations in JAEKEL 1891 and HESS 1975) is very close morphologically to the advanced sclerocrinids. Parallel evolution is not out of the question; but an independent origin of the bend of the axis appears equally possible. Such a bend occurs very commonly in sessile organisms. Furthermore, isolation of the genus *Cyrtocrinus* JAEKEL linking directly the genera *Sclerocrinus* JAEKEL and *Hemicrinus* d'ORBIGNY does not seem appropriate.

The oldest typical *Hemicrinus* d'ORBIGNY is known from the Tithonian of Rogoźnik. It is somewhat specialized as shown by the angularity of brachials. The morphology of the arm ossicles, relatively strongly bent cup axis, and in most cases the position of the lower arm (opposite to the stem) tends to suggest that this form is a lateral branch of the main evolutionary line of the genus *Hemicrinus*. The main line itself is known beginning with the Valanginian species *Hemicrinus thersites* JAEKEL (Fig. 14). In the latter species, the cup axis is less oblique and the lower arms are placed by the stem sides (see JAEKEL 1891, ARENDT 1974). The position of arms relative to the symmetry plane, the ornamentation type, and the distinctness of sutures between radial plates appear highly variable in the genus *Hemicrinus*. Since the Barremian, more advanced species begin to appear, viz. *Hemicrinus astierianus* d'ORBIGNY and *Hemicrinus saligerensis* ARENDT. Their cup is very strongly bent and the lower arms occur by the stem sides (compare RASMUSSEN 1961, ARENDT 1974). *Hemicrinus kabonovi* ARENDT of which only a single cup is known, probably belongs to an independent, more conservative, evolutionary lineage.

The genus *Tetanocrinus* (= *Dolichocrinus*) known only from the Oxfordian (JAEKEL 1891, LORIOL 1882) and Tithonian, may be derived from either primitive sclerocrinids or from the "Eugeniocrinites" *mayalis* group. Sometimes, it is excluded from the cyrtocrinids (see BATHER 1900, ARENDT 1974) because of its similarity in the arm-facet morphology to the genus *Bourgueticrinus* d'ORBIGNY. In our opinion, however, the cup morphology demonstrates that it is more closely related to primitive cyrtocrinids than any other group of the Jurassic crinoids. Additional evidence for the relation of *Tetanocrinus* with cyrtocrinids can be the occurrence of a similar form in the Lower Cretaceous of Štramberk; it is *Hemicrinus*-like with visible sutures between very long radial plates (Žitt, personal communication). Actually, we do not claim that our Tithonian specimen is a cyrtocrinid. More data on the stem, cup and arm morphology are needed to solve this problem.

The cyrtocrinids with an extremely short stem fused with the cup form the family Holopidae. Representatives of this family occur along with the oldest stemmed cyrtocrinids (see LORIOL 1882). They may be related phylogenetically to the genus *Sclerocrinus* (Fig. 14) even though they are very different in morphology. Among those Early Jurassic stemless cyrtocrinids, there are forms with a normally developed cup ("Cotyloiderma") as well as ones with an oblique cup axis (*Eudesicrinus*). The presence of sutures between radial plates appears as the only difference from the younger holopids. Undoubtedly, this is an archaic feature that disappeared gradually during evolution. To base a generic diagnosis upon such a primitive feature appears very impractical. Chronologically, the next typical Holopidae have

been recorded in the Middle Cretaceous (RASMUSSEN 1961). They display short and massive arms, and in addition they lack visible sutures between radial plates; they are hardly distinguishable from the Early Jurassic forms. Hence, we suggest not to separate the genera *Cotyloderma* QUENSTEDT and *Cyathidium* STEENSRUP (Fig. 14). The evolutionary line of Holopidae with an oblique cup axis appeared in the Early Jurassic [assuming that *Eudesicrinus mayalis* DESLONGCHAMPS & DESLONGCHAMPS) does not actually represent an extreme form of "*Cotyloderma*" *docens* (DESLONGCHAMPS & DESLONGCHAMPS) population].

In the Tithonian of Rogoźnik, a single cup has been found that may belong to this line. However, because of its poor preservation we can not reject a possibility of its relation to "*Cyrtocrinus*". ARENDT (1974) described from the Lower Valanginian of Crimea the species *Hemibrachiocrinus manesterensis* ARENDT, *Brachiomonocrinus simplex* ARENDT, *B. subcylindricum* ARENDT, *Dibrachiocrinus elongatus* ARENDT and *D. rarus* ARENDT. These species are characterized by strongly differing arm size. They differ also in the height of the cup and the size of the arm facets. Sessile short-stemmed holopids display a great variability (see LORIOL 1882-4) and hence, we consider all the above mentioned species as conspecific. This is supported by the fact that ARENDT (1974) described a similar set of species from the Barremian, viz. *Hemibrachiocrinus pumilus* ARENDT, *Brachiomonocrinus exiguus* ARENDT, *Dibrachiocrinus biassalensis* ARENDT, and *D. solovievi* ARENDT. An identical range of morphological variability is also displayed by the Valanginian stemless cyrtocrinids from Štramberk (Žitt, personal communication).

In the course of cyrtocrinid evolution, there is a trend to form a strong armoured structure from the arms and the cup. In Holopidae, this is accomplished by shortening and thickening of the arms; the same with genera *Sclerocrinus* and *Hemicrinus*. The evolution of the families Phyllocrinidae and Eugeniacrinidae ZITTEL appears interesting. Both those groups are very closely related and descend from primitive sclerocrinids (Fig. 14). The early stage of their evolution is characterized by the conical shape of the cup with distinct processes among the arm facets. In the line leading to the genus *Eugeniacrinites* MILLER, the second primibrachial (axillary) underwent a transformation consisting in either a considerable elongation of the process between facets of the first secundibrachial (*Lonchocrinus* JAEKEL) or both elongation and thickening of the process (*Eugeniacrinites* MILLER). These processes defend the rest of the arms which are hidden and rolled in between. Axillaries assigned to *Lonchocrinus* have been recorded since the Callovian (ARENDT 1974) while typical *Eugeniacrinites* axillaries make their appearance in the Oxfordian. As judged from the morphology, cups attributable to both genera occurred already in the older stages (BIESE 1937). Probably they belong to the level of axillary evolution of some species of *Sclerocrinus*. Both *Lonchocrinus* and *Eugeniacrinites* persisted up to the Early Valanginian (see REMEŠ 1902, 1905, 1912, ŽITT 1974a, RASMUSSEN 1961). The ontogenetic development of eugeniacrinid axillaries and their stratigraphic sequence suggest that they developed from axillaries of *Sclerocrinus* type by elongation of the median process (*Lonchocrinus*) and subsequent widening of the distal part (*Eugeniacrinites*). Consequently, the arm branches are hidden within an armour formed by the axillary processes; only small openings remain. They are completely closed in *Proholopus strambergensis* ŽITT from the Valanginian of

Moravia (Žitt, personal communication). Thus, the evolution of this line ended in a closed box formed by the cup and two first arm segments (Fig. 14). A different way of evolution is represented by the genus *Psalidocrinus* REMEŠ & BATHER. It formed high plate-shaped interradial processes which are expanded to the center of the cup. Massive arms form together with these processes a strong armour. In mature individuals of the Tithonian species *Psalidocrinus armatus* (ZITTEL) interradial processes touch one another in the upper part of the cup. In the Valanginian species *Psalidocrinus remesi* BATHER (see ŽITT, 1978) these processes are fused in the center and form a stellar callus. The oldest species characterized by such high interradial processes and wide arm facets is *Eugeniacrinites caucasicus* ARENDT recorded in the Aalenian and Bajocian (ARENDT 1974). This species appears ancestral to the genera *Apsidocrinus* JAEKEL and *Phyllocrinus* D'ORBIGNY. These genera formed by reducing the size of arm facets and simultaneously changing the shape of interradial processes. Processes leaf-shaped in a side view and triangular in cross-section are typical of the genus *Apsidocrinus* JAEKEL. *Phyllocrinus clapsensis* (LORIOL) of Bathonian age (LORIOL 1882-4), may be its ancestral species. The Tithonian species *Apsidocrinus moeschi* (ZITTEL) has massive interradial processes leaving the central (axial) part of the cup interior free. In *Apsidocrinus cyclamen* (REMEŠ) (see REMEŠ 1912) of Valanginian age, these processes touch one another in the axial part of the cup. The funnel-like cup base is probably reduced. The interradial processes of *Phyllocrinus* D'ORBIGNY are sharp, triangular in side view, and less massive than in *Apsidocrinus* JAEKEL. *Phyllocrinus alpinus* (D'ORBIGNY) of the Callovian is the first typical representative of this genus. There are at least three evolutionary lines in the Tithonian (Fig. 14); viz. the typical phyllocrinid line persisting up to the Cenomanian (see ARENDT 1974); the line of *Phyllocrinus belbekensis* ARENDT with angular edges of the interradial processes and the cup; and the line of *Phyllocrinus stellaris* ZARĘCZNY with strongly convex radial plates. A species with bifurcated interradial processes (*Phyllocrinus chalupai* ŽITT, ŽITT in press) occurs in the Valanginian of Štramberk (Fig. 14). It probably derived from the main phyllocrinid line (*Phyllocrinus malbosianus* group). An assessment of other evolutionary lines requires detailed population studies.

Remarks on the evolution of Mesozoic crinoids

Recently, the evolution of and relationship among the suprafamilial crinoid taxa have been discussed by SIEVERT-DORECK (1953); older papers in this field are by BATHER (1900), JAEKEL (1918) and GISLEN (1924). A lot of new data on Mesozoic crinoid morphology and taxonomy have been published since that time. Especially important have been studies by HESS (1955, 1972a, 1972b, 1975), KRISTAN-TOLLMANN (1970, 1977) KRISTAN-TOLLMANN & TOLLMANN (1967), PECK (1948, 1955, 1973), PECK & WATKINS (1972), SCOTT, ROOT, TENERY & NESTEL (1977), SIEVERT-DORECK (1958, 1964a, 1964b), SZÖRENYI (1959), VERNIORY (1954, 1955a, 1955b, 1956, 1960, 1961, 1962a, 1962b). All of these have considerably improved our knowledge of Articulata evolution.

Only three crinoid families are known to occur in the Early and Middle Triassic. The Encrinidae ROEMER with their concave base of the cup and biserial arms appear

to be closely related to the Paleozoic Erisocrinidae MILLER; it is difficult, however, to find their direct ancestors among the Permian crinoids, though it may be *Stemmatocrinus* TRAUTSCHOLD as suggested by GISLEN 1924. The encrinids are not related to other Mesozoic crinoids. The families Dadocrinidae LOWENSTAM and Holocrinidae JAEKEL are closely related. Both have well-developed infrabasal plates and uniserial arms (see LEFELD 1958, WAGNER 1891). The stem of *Dadocrinus* is round with a crenulation around the margin. Near the base of the cup, the stem segments are pentagonal in cross-section and the crown of crenulae becomes transformed into petaloids (see KRISTAN-TOLLMANN 1967, also our unpublished data). The holocrinids display a pentagonal stem with cirri. One can hardly find a form ancestral to both these families. *Erisocrinus araxensis* JAKOVLEV based entirely upon its stem fragments (see TEICHERT, KUMMEL & SWEET 1973) shows the segment morphology and crenulation pattern consistent with *Dadocrinus*, and displays also some cirri bases. Pentagonal columnals have been described by CLARK & TWITCHELL (1915) from the Lower Triassic of America, by BIESE (1927, 1934) and others from the Triassic of Europe, and by BATHER (1917) from the Triassic of New Zealand. All these data suggest to us that *Dadocrinus* represents a form ancestral to Articulata (Fig. 15). One can easily derive the isocrinids of the *Chariocrinus* type (i.e. with reduced infrabasal plates, HESS 1972a) from those *Dadocrinus* species which clearly tend to reduce basal plates and develop pentagonal columnals with petaloidal arrangement of crenulation. Morphologically primitive basal plates have persisted in the genus *Balanocrinus* LORIOL but its columnals secondarily developed a round cross-section with only remnants of petaloid crenulation. Since the Early Jurassic there have been isocrinid genera with reduced, separated basal plates, e.g. *Seirocrinus* GISLEN and *Pentacrinus* BLUMENBACH (GISLEN 1924, HESS 1955, SIEVERT-DORECK 1953). Several long cirri are typical of these genera. It has been shown (GISLEN 1924, HESS 1950) that Comatulida descended from such isocrinids (Fig. 15). The late Bajocian species *Paracomatula helvetica* HESS (HESS 1950) appears as a transitional form. It shows well-developed rudiments of the basal plates along with the reduced stem covered by cirri bases. Neither the Bathonian (BIGOT 1938), nor later comatulids show remnants of basal plates. Since the Middle Cretaceous, free-living comatulids are the most common crinoid group.

Typical dadocrinids with a rounded stem probably gave way to Jurassic apiocrinids and millericrinids (Fig. 15). The extremely specialized family Apocrinidae d'ORBIGNY displays a very thick stem with a radially arranged delicate crenulation, which participates in the formation of the large and thick-walled cup. Sometimes even the basal parts of the arms are incorporated into the cup. This also took place in the Late Cretaceous Uintocrinida ZITTEL. Nevertheless, there is a large morphological and stratigraphical gap between Apocrinida and Uintocrinida. The family Millericrinidae JAEKEL evolves approximately parallel to the isocrinid evolution. The millericrinids exhibit a round (with radial arrangement of crenulation) to pentagonal stem (with petaloids) and a small cup with well-developed basal plates. The Triassic genus *Holocrinus* WACHSMUTH & SPRINGER may be their ancestor. Unspecialized apocrinids probably were ancestral to the Cretaceous to Recent Bourgueticrinidae LORIOL and Bathycrinidae BATHER (Fig. 15) characterized by the columnals articulated by synarthry and a very small elongated cup. However, a

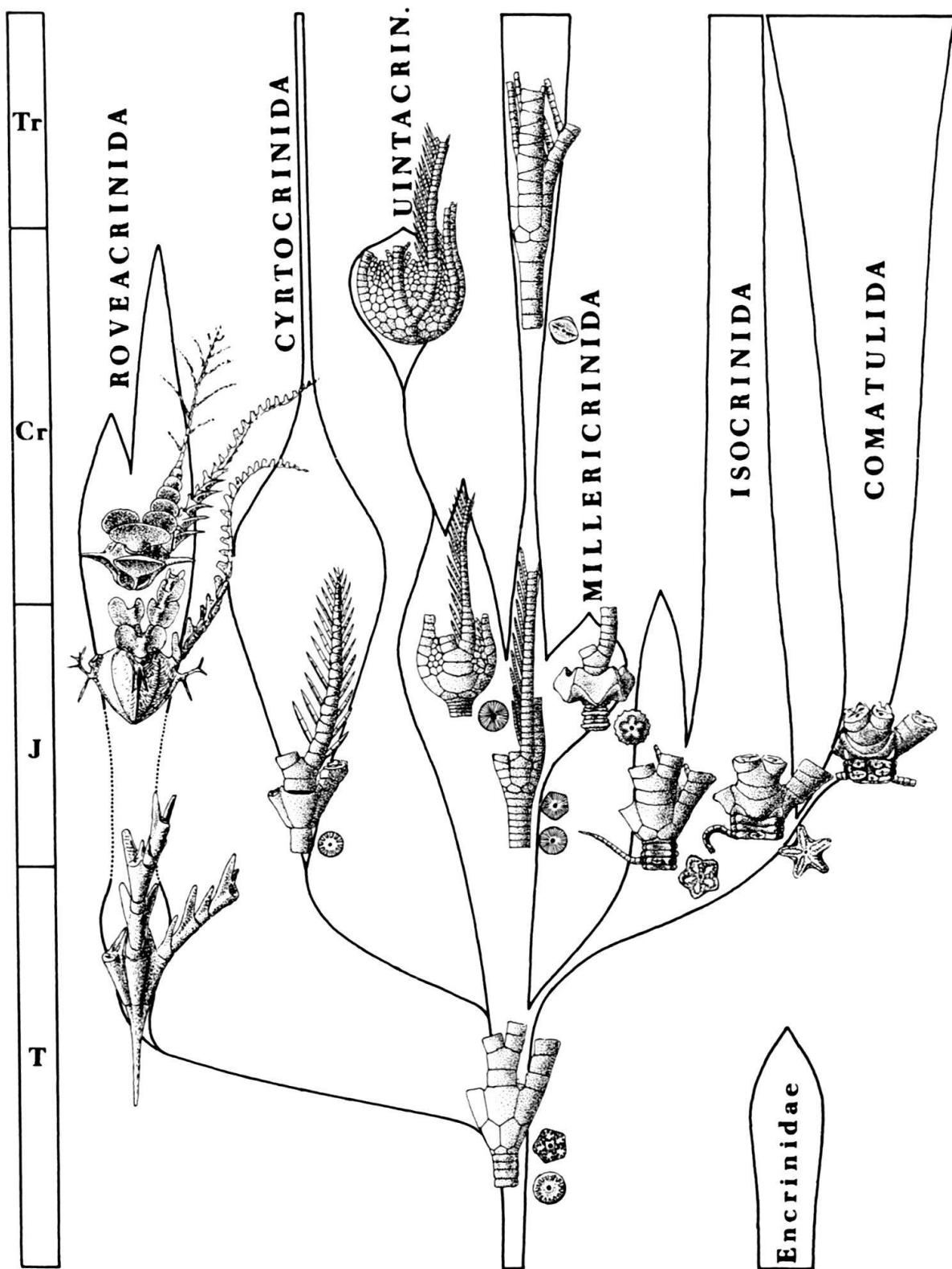


Fig. 15. Supposed phylogeny of Articulata.

transformation of Jurassic apiocrinids into bourgeticrinids has not so far been shown.

The Early Jurassic cyrtocrinids were already diversified; their Triassic history is not known. They are characterized by entirely reduced infrabasal and basal plates (except Plicatocrinidae which retained basal plates). Their columnal morphology (thick radially arranged crenulae) and uniserial arms suggest their origin from *Dadocrinus* stock. *Calathocrinus digitatus* MEYER from the Middle Triassic of Upper Silesia (MEYER 1851) might be an ancestor to the order; this species is poorly known and unfortunately it cannot be revised because the whereabouts of the type material is unknown.

There is also little information on the early evolutionary history of Roveocrinida SIEVERT-DORECK. The oldest roveocrinids have been reported from the Upper Triassic rocks of Mexico (PECK 1948). At that time, they were already widely diversified. The Carnian species *Somphocrinus mexicanus* PECK appears as the most specialized form. It shows long, massive centrodorsal and radial plates of morphology similar to *Saccocoma*. PECK (1948) suggested that the radial plates are separated from one another. We feel, however, that the radial plates of *Somphocrinus* are morphologically very close to those of *Osteocrinus spinosus* KRISTAN-TOLLMANN (see KRISTAN-TOLLMANN 1970, 1977) and clearly shown lateral contact surfaces. In our opinion, the considered species does not differ from other Roveocrinida in the arrangement of radial plates. The brachials of *Somphocrinus* are slightly elongated, with ventral (? ambulacral) processes in the form of small wings. In the specialized Carnian *Osteocrinus* species (KRISTAN-TOLLMANN 1970, 1977), the radial plates are usually more elongated but the ventral wings remain small. The faunas which are next in geological sequence have been recorded in the Callovian (LEFELD 1974) and Kimmeridgian (VERNORY 1955a, 1955b, 1962a). In fact, the thin-walled cup of *Saccocoma* AGASSIZ may have been derived from a cup of the *Somphocrinus* type (Fig. 15) due to a reduction of the centrodorsal plate and development of the ridges and spines. The brachials are short with wing-shaped ventral processes and additional lateral ones. The proximal brachials have small ambulacral processes and very large lateral wings. In contrast, the distal brachials have large ambulacral wings and rudimentary lateral ones. There are some species of *Saccocoma* whose wings and spines on the radial plates have a different morphology which represents an obvious adaptation to a pelagic mode of life. An extreme development of the brachial lateral wings is shown by the Albian *Poecilocrinus* PECK (Fig. 15); in this genus, spines on the radial plates are also replaced by large wings (SCOTT, ROOT, TENERY & NESTEL 1977). Nevertheless, the authors consider it as a benthic animal. The genus *Roveocrinus* DOUGLAS known from the Middle and Upper Cretaceous shows different modifications. All its skeletal elements are more massive than in *Saccocoma* AGASSIZ; the cup along with the basals and radials forms a cone-shaped structure (RASMUSSEN 1961, 1972). Sometimes, longitudinal ridges on the radials are strongly developed. The Cenomanian *Stylocrinus* PECK, with its elongated brachials resembling the Triassic *Osteocrinus* KRISTAN-TOLLMANN, may also be derived from the evolutionary line under discussion. There are also other genera of strange morphological characters, e.g. *Applinocrinus* PECK (PECK 1973). The genus *Pseudosaccocoma* REMEŠ is also placed in the Roveocrinida; a very thick wall and

arrangement of plates in the cup (see BACHMAYER 1958, RASMUSSEN 1961) as well as the sculpture of the interior of the cup show, in our opinion, that it is the basal portion of an apiocrinid cup (compare Pl. 25, Fig. 1a-b, in LORIOL 1882-4). This opinion appears also to be confirmed by an occurrence of *Apocrinus* at Štramberk where the holotype of the considered species was described for the first time (REMEŠ 1905, BLASCHKE 1911). The isolation in time of particular roveocrinid faunas does not permit any more detailed evolutionary studies. New findings of this interesting crinoid group are needed, particularly in the Lower and Middle Jurassic.

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Plate 1

Fig. 1-5 *Balanocrinus cf. subteres* (MÜNSTER 1833).

1: Proximal columnal, CaI/279. 2: More distal columnal, CaI/277. 3: Distal columnal, CaI/276. 4: Distal columnal, CaI/275. 5: Proximal columnal, CaI/281. All figures $\times 5$.

Fig. 6-7 *Saccocoma cf. quenstedti* VERNIORY 1961.

Radials, upperside view, visible muscular articulation surface and long spines (here partly broken). 6: Specimen CaI/1016. 7: Specimen CaI/1007. All figures $\times 50$.

Fig. 8-9 *Saccocoma tenella* GOLDFUSS 1862.

Radials. 8: Specimen CaI/1018, dorsal view, $\times 40$.
9: Specimen CaI/1009, inner view, $\times 50$.

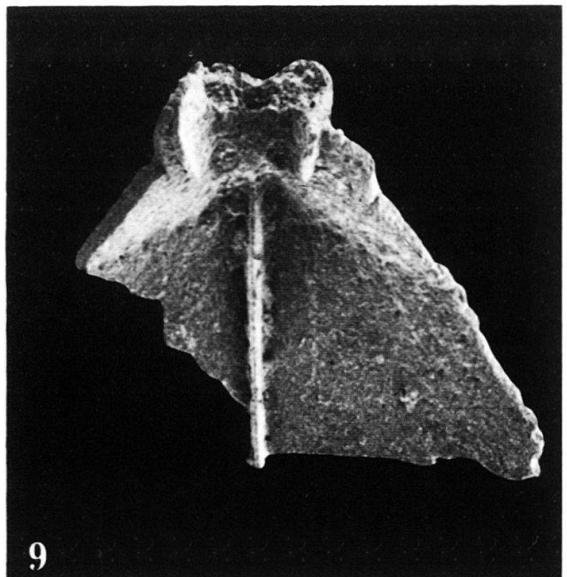
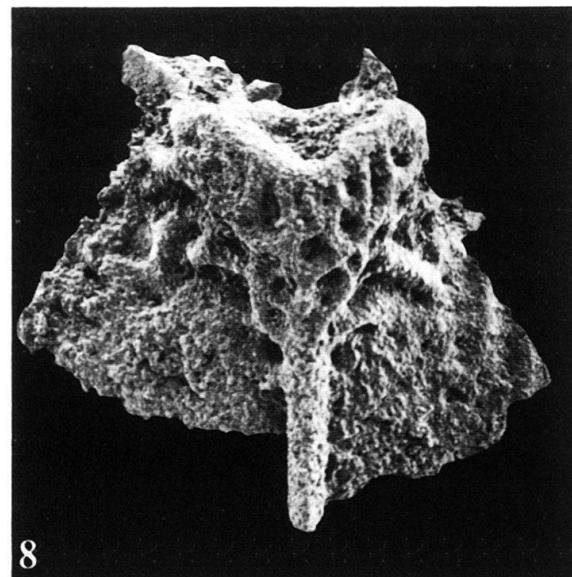
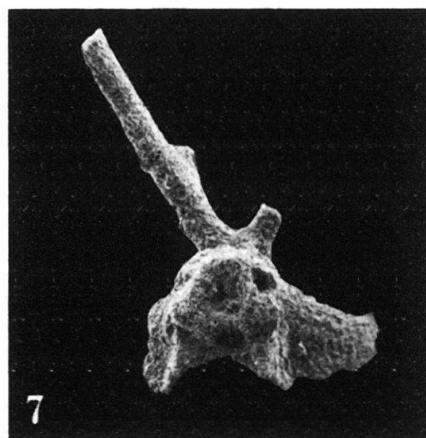
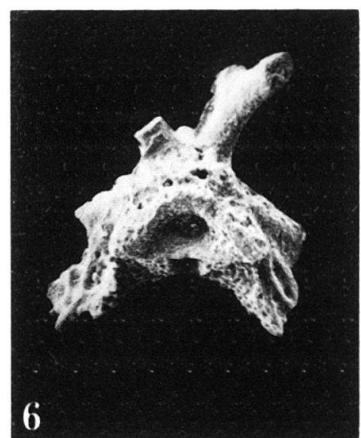
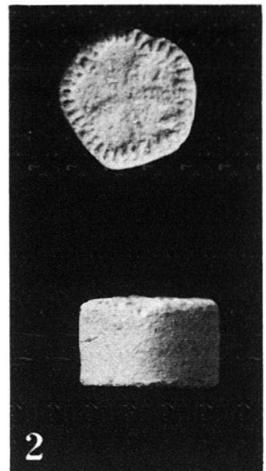


Plate 2

Fig. 1-7

Saccocoma tenella GOLDFUSS 1862.

1: Radial, CaI/1411, dorsal and inner view, $\times 25$. 2: Proximal brachial, CaI/1015, note sculpture of trunk, $\times 40$. 3: Primaxillary (IAx1), CaI/1019, ventral view, note large proximal articulation surface, $\times 40$. 4: Axillary of higher order, CaI/1006, dorsal view, $\times 30$. 5: Proximal axillary with very massive trunk, CaI/1010, wings probably broken, ventral view, $\times 40$. 6: First primibrachial (IBr1), CaI/1012, dorsal view, large distal articulation surface visible, $\times 40$. 7: First primibrachial (IBr1), CaI/1011, ventral view, $\times 40$.

Fig. 8

Tetanocrinus cf. aberrans (LORIOL 1882).Cup, CaI/998, oral and lateral view, $\times 5$.

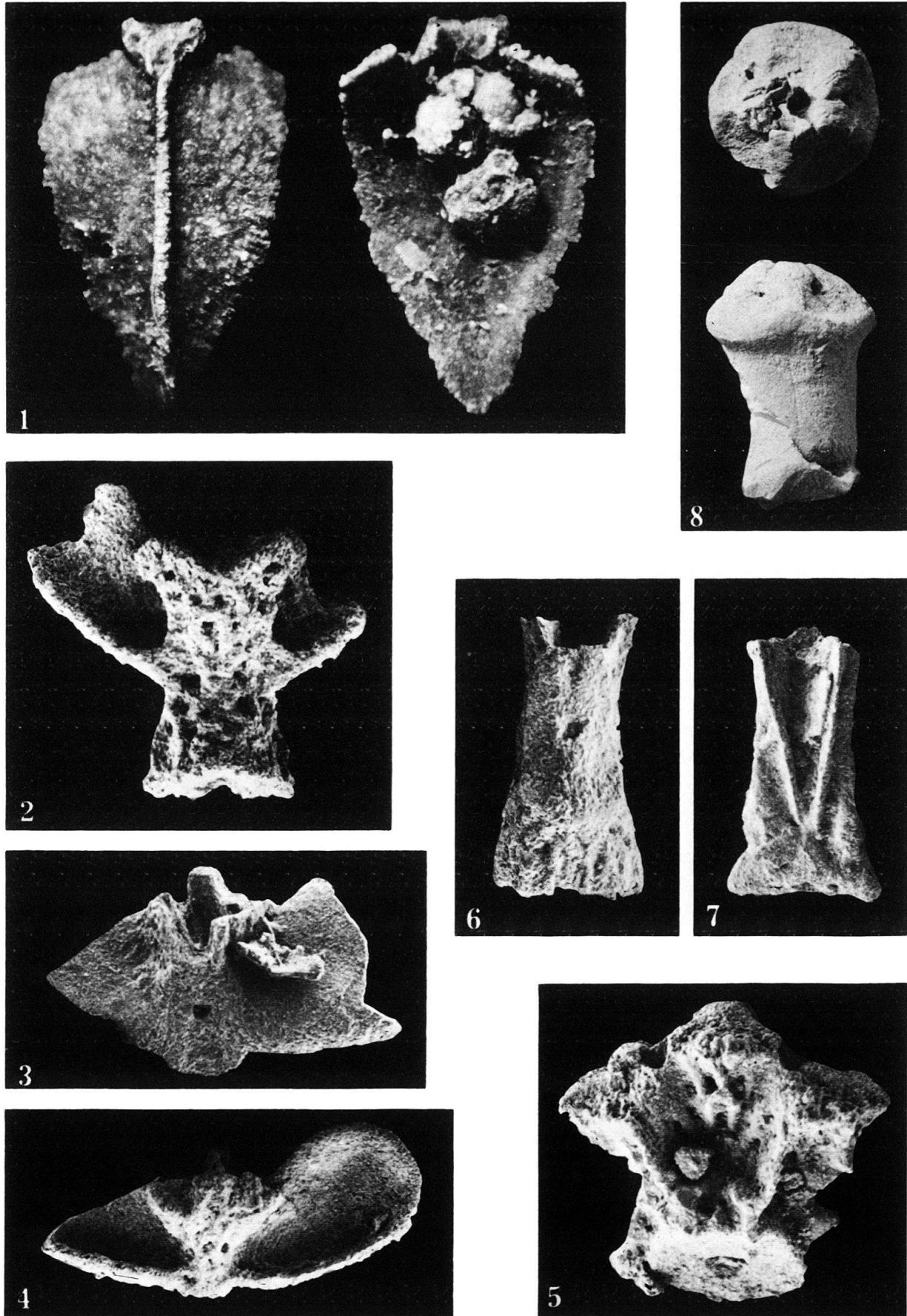


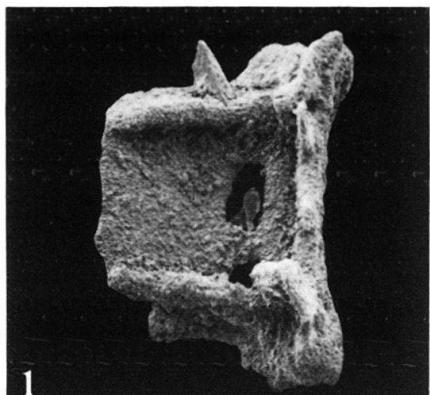
Plate 3

Fig. 1-3 *Saccocoma tenella* GOLDFUSS 1862.
1: Distal brachial, CaI/1013, lateral view, $\times 50$. 2: Distal brachial, CaI/1014, lateral view, $\times 45$. 3: Mid-placed brachial, CaI/1008, dorsal view, $\times 45$.

Fig. 4 ? *Eudesicrinus* sp.
Cup, CaI/1000, oral and lateral view, $\times 5$.

Fig. 5 *Sclerocrinus* sp.
Cup, CaI/1797, oral, lateral and basal view, $\times 5$.

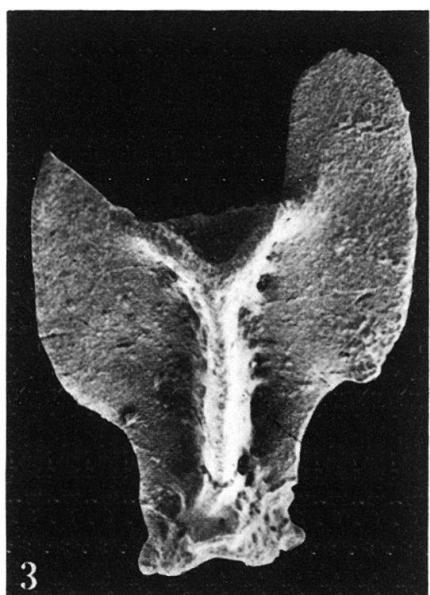
Fig. 6-7 *Hemicrinus tithonicus* n. sp.
6: Holotype, cup, CaI/1356, oral, lateral and basal view, $\times 3$. 7: Cup, CaI/1355, oral, lateral and basal view, $\times 3$.



1



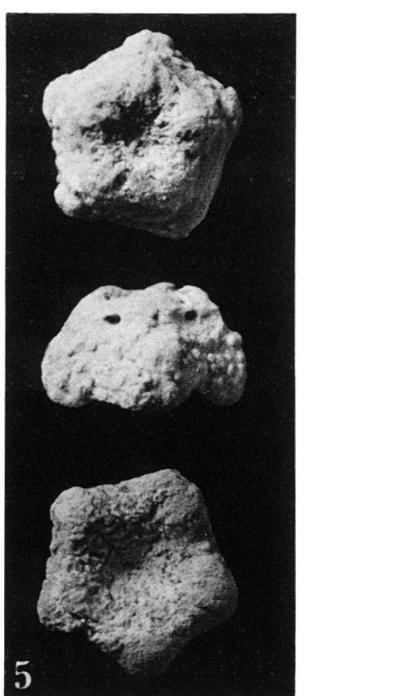
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Plate 4

Fig. 1 *Phyllocrinus belbekensis* ARENDT 1974.
Adult cup, CaI/1003, lateral and basal view, $\times 5$.

Fig. 2-4 *Phyllocrinus stellaris* ZARĘCZNY 1876.
2: Cup of young specimen, CaI/1004, lateral and basal view. 3: Cup, CaI/999, lateral and basal view. 4: Cup, CaI/1005, basal view. All figures $\times 5$.

Fig. 5-6 *Lonchocrinus staszici* n.sp.
5: Cup, CaI/809, holotype, lateral and basal view, 6: Cup, CaI/810, lateral and basal view. All figures $\times 5$.

Fig. 7-8 *Apsidocrinus moeschi* (ZITTEL 1877).
7: Cup, CaI/1354, lateral view. 8: Cup, CaI/1353, basal view, note strong collar around stem base. All figures $\times 3$.

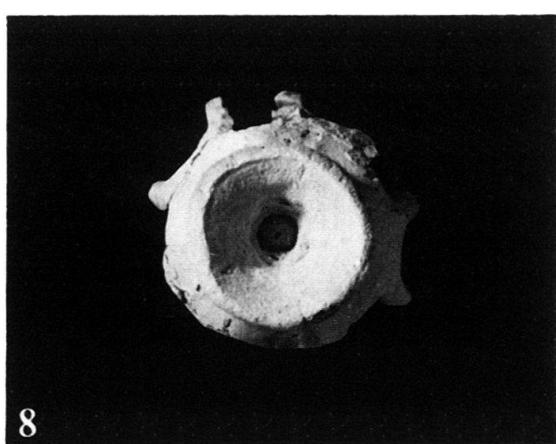
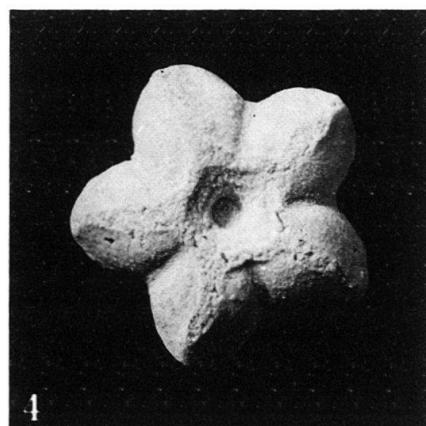
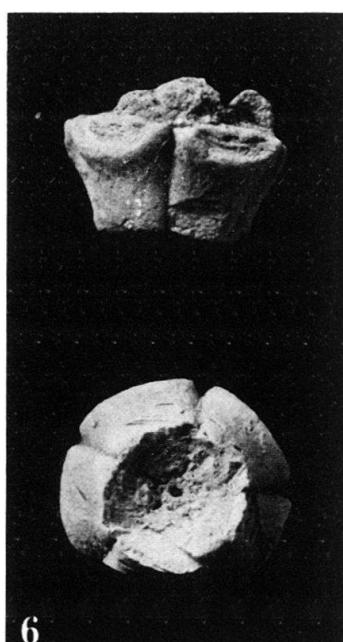
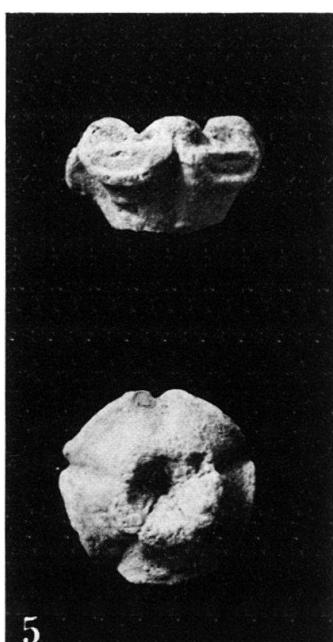
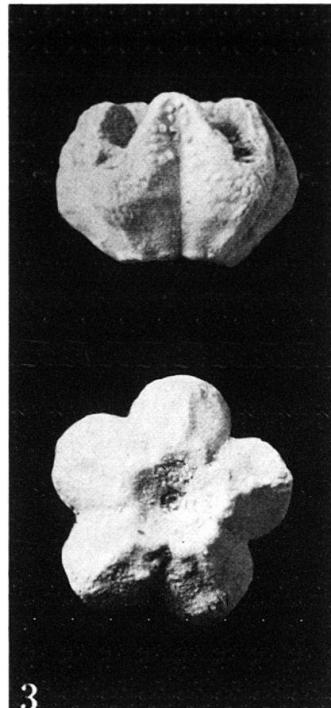
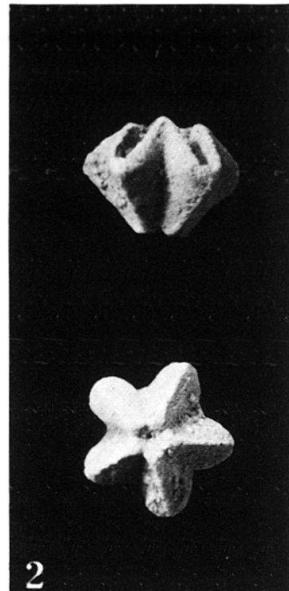
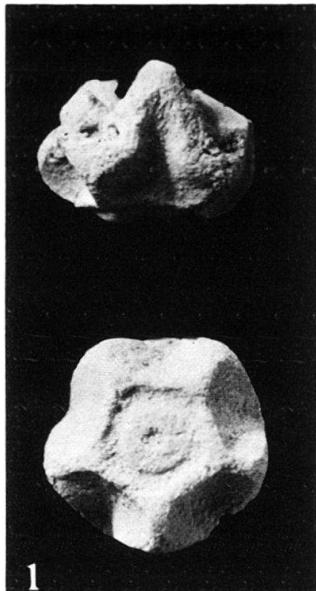


Plate 5

Fig. 1-6

Psalidocrinus armatus (ZITTEL 1870).

1: Cup of mature specimen, CaI/1020, interradial processes well visible, lateral view.
2-6: Cups, CaI/1021-1025, lateral and basal view, note great variability, interradial processes strongly damaged. All figures $\times 3$.

