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SPOON-LIKE CRINOIDS FROM ŠTRAMBERK (LOWER CRETACEOUS, ČSSR)

Results of the study of curious cyrtocrinids which are distinguished by the development of a spoon-like element bearing the arms are presented.

After a detailed study of morphology and arrangement of skeletal units of Štramberk and foreign specimens [England, U.S.S.R., Switzerland], a probable evolution of spoonlike element was established. On the basis of homeomorphy, the genus *Torynocrinus* SEELEY, 1866 was restituted within the family *Hemicrinidae* RASMUSSEN. Whereas the stem part of *Hemicrinus* spoon is of columnal origin, the whole spoon of *Torynocrinus* including the stem part consists of radials only.

The paper deals with the species *Hemicrinus astierianus* d'ORBIGNY, 1850, *H. thersites* (JAEKEL, 1891), *H. digitatus* (REMEŠ, 1905), *H. robustus* sp. n., *H. angulatus* sp. n., *"H."* cf. *kabanovi* ARENDT, 1974, *Torynocrinus canon* SEELEY, 1866, *T. variabilis* (ARENDT, 1974) and *T. cristatus* sp. n.

The fusion of skeletal elements in relation to their crystaloptic orientation (c-axes) is discussed. Paleoecological and functional morphological parts of the paper primarily focus on the orientation of the animal in water currents. The author presumes the hemicrinids to have been moderate-energy rheophiles with weak filtration apparatuses (binipular SBrBr) oriented ventrally downcurrent.

INTRODUCTION

The most comprehensive recent study of hemicrinids has been realised by Arendt (1974). Besides a description of 2 known and 4 new species, and of the stratigraphically oldest (Lower Valanginian) *Torynocrinus* (i. e. *Cyrtocrinus variabilis* ARENDT), his paper has brought many new opinions and views, particularly as regards the functional morphology and paleoecology of the group. At present, 6 species of *Hemicrinus* and one species of *Torynocrinus* are known from Crimean localities.

Szörényi (1959) described 9 species of *Hemicrinus* from the Hungarian localities situated along the Zirc-Borzavar railway (Neocomian). However, nearly all specimens are hardly preserved well enough to guarantee

the species objectivity. Štramberk, therefore, seems to be the richest locality of the world (6 species of *Hemicrinus* and 2 species of *Torynocrinus*).

Apart from JAEKEL (1891, 1907) and REMEŠ (1902, 1905) it was KAREL PALIVEC who studied the Štramberk hemicrinid material for a short time. Results of his study were summarized in his graduate thesis at Charles University, Prague (1967). Unfortunately, owing to his tragic death, his work has remained fragmentary and unpublished. Since that time a large amount of material and a lot of new important data concerning the geology, stratigraphy and paleontology of Štramberk have been assembled, and much information of importance on the ecology of recent and fossil crinoids has been obtained. From these facts the necessity of a new, more extensive and detailed study has emerged. The results of such a study are here presented. All the original Palivec's ideas are of course respected and duly cited.

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COMMENTS TO THE ORGANISATION OF SPOON

In describing the morphology of hemicrinids it is rather difficult to find a suitable term for the skeletal part including and bearing the morphologically differentiated calyx. According to RASMUSSEN (1961), the terms "proximale" for the narrowed stem part and "calyx" for the morphologically distinct calyx part have been used. The term proximale is derived from the proximal part of the stem. In *Hemicrinus*, the usage of "proximale" seems to be right but *Torynpcrinus* has the "stem part" of another origin (see below). To make all descriptions simple and uniform I think it suitable to use the non-genetic but morphologically appropriate term "spoon-like element" or simply "spoon". This term was used even by RASMUSSEN (1961, p. 235), even though only figuratively. (Note SEELEY'S (1866) comparison of *Torynocrinus* to the "bowl of a ladle" or a popular Stramberk name "little paw" — in Czech — "pacička".)

Cyrtocrinus. The whole skeleton unknown. Spoon developed in a few percent of specimens. The stem part of evident columnal origin, with partly outlasting and probably moderately mobile articulation to calyx. If the spoon is present, the existence of further distal columnals is probable. Holdfast known inadequately.

Hemicrinus. Complete skeleton unknown. Some authors (most recently ARENDT 1974) assume the subbrachial skeleton to consist of two parts joined by symplexy. On the basis of the composition of Štramberk crinoidal associations I also share this opinion. The upper of the two mentioned elements is the spoon which includes the calyx, and the lower one is the holdfast. The spoon itself consists of six separate plates, five of which are radials constituting the calyx well differentiated in shape. The sixth element beings to the narrowed stem part invariably of columnal origin (see the next chapter). All six elements are firmly united, being separated by sutures or at least by crystallographic discontinuities. This part rarely and only in some species participates in the composition of calyx.

Torynocrinus. Subbrachial skeleton completely known. It consists of the spoon and hold-fast joined by symplexy. The spoon, in contrast to *Hemicrinus*, is built up of radials only, including a narrowed "stem part". In such a way every radial forms a segment

of unusual length. All the five segments are separated from each other by sutures or at least by crystallographic features (discontinuities in cleavage, extinction, etc.). Torynocrinid spoon, in fact, represents a highly modified calyx differentiated into the calyx s. s. (i. e. upper) and lower stem-like parts. Neither columnal (in contradiction to RASMUSSEN 1961), nor any further calyx elements (basals and the like, SEELEY 1866) are present.

 $\operatorname{Holdfast}$ is a solid, firm element of monocrystalline nature without any systematically important characters.

"Hemicrinus" cf. kabanovi ARENDT, 1974. At Štramberk its position appears to be rather unique. All uncertainties as to its taxonomic assessment arise from a completely monocrystalline nature of the spoon, a character quite unusual not only among hemicrinids, but also within a subclass. This character, unfortunately, raises the problem of which primary elements the spoon had originated. Is it a *Hemicrinus* with fused radials and columnals, or does it represent a *Torynocrinus* with fused radials only? Or is it some completely different species? Judged strictly morphologically, this species is clearly of *Hemicrinus* type.

SKELETAL ELEMENTS IN PHYLOGENY

Cyrtocrinus and *Hemicrinus*. Untill the year of 1973 only the *Hemicrinus* d'ORBIGNY, 1850 has been classed within the family *Hemicrinidae*. ARENDT (1974) placed a *Cyrtocrinus* JAEKEL, 1891 in the family. The fundamental cause of this step was the occurrence of circular constriction of the stem part of the spoon, which he observed in the Crimean *Cyrtocrinus variabilis* ARENDT. Arendt believed to have found a species possessing the columnals in process of fusion, i. e. a form ancestral to *Hemicrinus*. Besides, he thought to discern a suture separating calyx from the stem. Arendt interpreted the *Cyrtocrinus variabilis* as an evolutionary transitional form from a crinoid of *Cyrtocrinus nutans* type to the true *Hemicrinus* having the stem part of monocrystalline nature.

Thanks to the kindness of Arendt, I had an opportunity to study some specimens of *C. variabilis* from the Crimea and to see for myself the real nature of their skeletons. I have found out that the inner structure of the stem part has no traces of columnals and that Arendt's constrictions merely represent some surface structures or growth irregularities. On the contrary, the constitution of the spoon is of *Torynocrinus* type (see below). However, Arendt's decision on the systematic position of *Cyrtocrinus nutans* within the family *Hemicrinidae* is in my opinion, quite right.

1 — Pattern showing probable evolution of *Hemicrinus* spoon (e) from *Cyrtocrinus nutans*-like ancestor (a). b, c, d — intermediate forms. Figs. b—e with suggested growth relations expressed by hypothetical growth lines. Black nuclei — the youngest stages, 1, 2 — ontogenetically 1st and 2nd columnals, c — calyx, s — stem, h — holdfast. Orig.



According to the present knowledge, the columnal origin of the stem part of *Hemicrinus* spoon is unquestionable. The best evidence for this phenomenon, which was formerly only presumed, is offered by *Hemicrinus astierianus* (type species) found at Štramberk localities. Two specimens [the better preserved specimen see pl. 1, figs. 1—3] with broken-off calyx and stem parts show well preserved symplexy, typical columnal articulation with circular areola, crenularium and axial canal. The question arises which articulation from the sequence of articulations of the original stem does it represent. It is possible to exclude the calyx — stem articulation, as a substantial part of columnal substance exists above (proximally) the disclosed symplexy. For this reason

it must be one of the more distal articulations. No traces of them, however, were observed within the distal parts of stems (in sections). All these facts, therefore, support a conclusion that the preserved symplexy may represent the most distal articulation of juvenile spoon, i. e. the direct spoon-holdfast articulation of a young. The whole stem part of a young must therefore be hidden within the little piece of stem substance above (proximally) the preserved symplexy of the mature animal. From this it follows that the whole part of the adult stem underlying (distally) the preserved symplexy is of a secondary nature, and that it originated by growing of the young stem distally in the crystallographically identical orientation. This process seems to explain most readily the complete crystallographic homogeneity and the absence of distal articulations within the stem part of the spoon.



2 — Crystaloptic orientation of skeletal elements of *Hemicrinus astierianus* spoon in longitudinal section, ventrally directed to the observer. Arrows indicate direction and angle of plunge of the c-axes. C — columnal part, R — radials, x c. 2.

Extraordinarily interesting are the interrelations of the crystaloptic orientation and morphology of the stem part of the spoon. The only orientation of the c-axis in crinoid columnals observed up to date, is parallel to the stem or perpendicular to columnal facets. *Hemicrinus*, however, displays a deviation of more than $20-30^{\circ}$ from this generally preferred orientation (see text-fig. 3). This important departure is so far impossible to explain reasonably. The columnal c-axis could change its position quite



3 — Crystaloptic orientation of skeletal elements of *Hemicrinus digitatus* spoon in longitudinal section. Symbols as in fig. 2. x c. 2.

independently of morphology, or it could rotate together with the whole juvenile element. This question yet deserves further deep study, if it can be resolved by traditional methods at all.

4 — Crystaleptic orientation of juvenile spoon of "*Hemicrinus*" cf. *kabanovi* in longitudinal section. Symbols as in fig. 2. x c. 3.

As mentioned above, the stem part of *Hemicrinus* spoon represents a well defined single element both in structure and crystallography. On the contrary, the same characters of *Cyrtocrinus* are very variable. Some specimens have clearly defined columnals of variable length even immediately below the calyx. The most proximal columnal articulates with it by a special facet, identical morphologically with that of *Sclerocrinus*. Other calices articulate with a very long columnal, provided proximally with the same special facet (see above). This development gives a specimen the appearance of a spoon. The long columnal has no inner sutures (observed externally) and coalesces with calyx even though a certain degree of mobility often remains. Whether further columnals were joined distally or not is unknown but very possible, at least in a part of specimens. It seems to be right that the stem part represents a very pronounced columnal enlarged lengthways. This implies that fusion of columnals in *Cyrtocrinus nutans*, which is often supposed by the authors, most probably does not exist. Specimens from the same locality may posess both types of stems [LORIOL 1879, 1882—1884, HESS 1975].

The more we deliberate about the mechanism of the hemicrinid spoon evolution, the greater appears the need for revision and extensive deep study of classic materials of *Cyrtocrinus nutans*. For the time being, no symptoms of columnal fusion have been ascertained by surface study. Does they exist in *Hemicrinus* ? Any traces of such a process could be present only within the juvenile part of the stem, i.e. above preserved symplectial articulation, but no fusion could be proved so far.

One of the possible ways of *Hemicrinus* spoon evolution is a retardation in producting new columnals. Their formation during growth of the animal ceases in progressively younger growth stages and gradually a stage with only a few elements is achieved [*Cyrtocrinus nutans* stage]. The animal can lengthen his stem merely by lengthening of the remaining columnals. In the last stage of reductive process, when the only element is retained, this possibility is yet more limited. When a fusion with calyx takes place, further growth of the stem part is only realized undirectionally i. e. dorsally to the articulation of spoon-holdfast. The spoon-like element thus arises from a one-columnal stage (see text-fig. 1). The eventual complete reduction of stem could even represent an ancestral form to *Torynocrinus* (see below).

The true *Hemicrinus* spoon, however, is not simply identical to the one-columnal stem coalesced with calyx, as mentioned above. With respect to the completely compact structure of the very young spoons of *Hemicrinus*, the process of coalescence of calyx and stem had to be accelerated to the younger stages. The above course of *Hemicrinus* spoon evolution is to be assumed not only for *H. astierianus*, but also for the other species with proximal part of the stem wedged between the upper radials (e. g. *H. salgirensis* ARENDT). Other species whose radials form a non-interrupted circle (e. g. *H. thersites*) do not present any trace of articulation within their spoons, but their stem parts, being the sixth element of a spoon (in addition to 5 radials) must also be attributed a columnal origin. The deviation of the c-axes (see above) attains the maximum values. Therefore, the above described process of fusion accomplished during the spoon evolution may be here yet more intensive.

The question of the probable participation of columnals in the construction of holdfast remains open, as any evidence of such a fusion is lacking. ARENDT (1974) supposed one half of the original number of columnals to be included into the spoon, one half into the holdfast. The principal (and the only) evidence is, according to Arendt (op. cit.), the nearly identical length of the two parts. Enormous heights of some holdfasts may also be achieved by prevailing undirectional growth, as usually appears in the spoons. Generally, however, some possibility of columnal presence in holdfasts does exist.

A complete fusion of echinoderm skeletal elements is by no means possible unless the orientation of crystal lattices is identical. Some elements, e. g. columnals, could at least theoretically, achieve this special position relatively easily, as their c-axes are primarily parallel. On the contrary, radials being oriented differently (see text-figs. 2, 3) cannot fuse so easily. The majority of fused radials are in Stramberk only apparent, as the well developed sutures and their surface manifestations (e.g. furrows) are missing. Externally, the sutures proper are not often observable, being very thin. Nevertheless, the crystallographic properties of radials always remain unaffected by any type of changes. The only case when the sutures are not developed not only externally but also internally is represented by the species "Hemicrinus" cf. kabanovi ARENDT. Its inner construction is completely unique among the crinoids, as independent radials are lacking and not only calvx but also the whole spoon on the top of it are of monocrystalline nature. A gradual change of crystallographic orientation during the ontogeny of elements in connection with the change in the position of the elements proper, produced by growth irregularities (see MÄRKEL 1976, plates of echinoids) is, in my opinion, impossible. An alternative achievement of identical crystallographic orientation is the rotation of a plate. In crinoids, such a process is well known in Antedon rosaceus (see KIRCHNER 1929, fig. 7). Here, the infrabasals change their position on the body surface by shifting relatively to the top of the stem, with which then fuse forming a centrodorsal. The relative crystallographic orientation of an element changes, naturally, with the change of position in space. The final crystallographic orientation of centrodorsal is that of the top of larval stem.

In "Hemicrinus" cf. kabanovi, however, the orientation of the single-crystal matter of the spoon corresponds not only to the orientation of a radial, but also to that of the stem part of the spoon of evidently columnal origin (see above). This situation offers various explications as to the number and type of incorporated elements, but the stem could hardly adopt the role of completely disappeared radials. It apears most probable that at least the calyx part is of radial origin. To admit the hypohesis that all radials are present, some type of drift of four of them during early ontogeny should be presumed, or if the stem is present, all radials would have to approach the orientation of it. A variety of other possibilities does exist too. Undoubtful is only the existence of the monocrystalline spoon alone. Its uncertain composition remains the chief cause of the doubtful systematic position of the species (see the preceding chapter).

Torynocrinus. The above mentioned distinction between the stem parts of *Hemicriuns* and *Torynocrinus* spoon is of fundamental importance. ARENDT'S (1974) interpretation of lengthwise oriented segments of some of his *Cyrtocrinus variabilis* specimens as a secondary phenomenon is untenable. Two important antagonistic evolutionary processes would have to affect the crinoid. The first one — achievement of one single-element stage (whether by fusion or by reduction of columnals), and the second — a lengthwise division of this stem element into 5 segments. Moreover, the segments of the stem should have to fuse precisely with the segments of calyx, i. e. with radials. Therefore, it seems to me much simpler and more probable that the segments of torynocrinid spoon represent radials only. Crystaloptic investigation has verified a homogeneous nature of every segment from the radial facet up to the dorsal articulation.

Ontogeny of *Torynocrinus* remains, unfortunately, little known. The young specimens are very variable as concerns the development of their stem parts. The Stramberk specimens of *T. variabilis* (ARENDT), judged by their growth lines in sections, show a relatively rapid lengthening of radials dorsally, while the diameter of calyx grows slowly (see text-fig. 5). The Crimean specimens of the species and the Stramberk species *T. cristatus* sp. n. also present this allometry to a lesser degree.

Evolution of the torynocrinid spoon is very problematical. I suppose, the main reason of dorsal lengthening of radials was necessity of rising above the substrate. Contemporaneously, the oblique position of the calyx part was firmly fixed. Such a development was probably of the greatest importance for low forms, with very short or any stem at all.

l symmetry of mberk. Growth dial sectioned

5 — Longitudinal section near the plane of bilateral symmetry of *Torynocrinus variabilis* (ARENDT) spoon from Štramberk. Growth lines perceptible within the 3 radials. The 4th radial sectioned ventrally only. R — radials. x c. 2.

Two of the possible modes of evolution of torynocrinid spoon are figured in text-fig. 6. In the first case it is necessary to suppose a so far undiscovered form with completely reduced stem, so that direct articulation of calyx to holdfast occured (ontogeny seems to indicate this possibility — see chapter on ontogeny). The animal attained a secondary elevation by extensive growth on both sides of articulation. The other mode of spoon evolution might be a gradual substituting of the hemicrinid stem part by dorsally growing radials, similarly as in *Hemicrinus angulatus* sp. n. (see text-fig. 7b). The purpose of such a substitution, however, is not yet clear. The relationship of *Hemicrinus* and *Torynocrinus* lines would then be still more evident, as instead of homeomorphy (the first possible way), the relation of ancestor-descendant would occur.

6 — Two possible ways of *Torynocrinus* spoon evolution (d, c') from a *Cyrtocrinus nutans*like ancestor (a). a-d — evolution through the *Hemicrinus* (b, c). a'-c' — evolution through the hypothetical form with completely reduced stem (b')). Orig.



The relations between the two genera are supplemented by their stratigraphical ranges. *Hemicrinus* is known from the uppermost Jurassic [the Lower Tithonian — PISERA, DZIK 1979], up to the Lower Barremian (ARENDT 1974) and possibly Albian (RASMUSSEN 1961), while *Torynocrinus* from the Lower Valanginian (ARENDT 1974) till the Albian (SEELEY 1866). The species at the ends of both lines are conspicuous by very high spoons [e. g. *H. salgirensis X T. canon*].



7 — Various types of spoon structure, viewed laterally. Not to scale. a - H. thersites, b - H. angulatus sp. n., c - H. robustus sp. n., d - H. astierianus. Solid lines — sutures between the elements, dashed lines — internal boundary of calyx and stem parts. Orig.

The above mentioned "H." cf. kabanovi from the Upper Valanginian [Hauterivian?] of Štramberk, possibly identical with H. kabanovi from the Aptian of the Crimea (ARENDT 1974), showes features of a hemicrinid side-branch surviving until the early Barremian, thus having a very short history.

THE FUNCTIONAL SPOON-HOLDFAST SYSTEM AND PALEOECOLOGY

The curious morphology of hemicrinids has been most recently evaluated functionally and paleoecologically by ARENDT (1974), although he only adapted the original Jaekel's model of a living animal. Arendt (op. cit.) has also presented two reconstructions of hemicrinids in a feeding position. From the published figures his paleoecological conception of the animals as rheophiles living in moderate unidirectional water currents is evident. According to him, the animal was oriented ventrally upcurrent. This conception, being in my opinion only partially right, needs to be complemented and a little changed as a result of some important newly discovered details.

A calyx with its fixation to immobile stem maintains a stable position that cannot be influenced by any other way than by leaning of the whole spoon. The nature of articulation of spoon-holdfast, however, admits such a motion in a very limited measure. Even though the ligament is relatively strong, with attachement surfaces (areolae) mostly concave, their power is limited by their small areal extent. Why has this only articulation been retained, while all the others had completely disappeared? Wouldn't it be more advantageous to suppress all subbrachial joints, as developed e. g. in holopodids and hemibrachiocrinids? Although such an "imperfection" became apparently a limiting factor in the utilization of stronger currents it is evidently well founded. Having the spoon-holdfast articulation preserved, crinoids could grow more rapidly in this region and thus elevate the calyx with the arm-apparatus above the substrate more efficiently.

The asymmetrical development of the spoon caused a small change in the position of the center of gravity of the animal, which was no longer in the axis of the stem, but shifted a little forward. Taking into account the strong and heavy arm-apparatus, this small change was increased and the centre of gravity was shifted yet more forward. The articulation spoon-holdfast would thus be irregularly loaded and a permanent danger of overturning of the spoon would exist, but it is nearly certain that some unknown mechanism of preventing the overturning of the animal had developed [if it was necessary in the water environment at all].

The arm-apparatus of hemicrinids (excluding *H. digitatus*) was strong and most probably very mobile, with massive brachials and facets well developed. Of particular importance, however, is the occurence of bipinnulate secundibrachs. Althoug they have not yet been found in situ, they occur in the majority of fossil hemicrinid associations known and their taxonomic identification is, in my opinion right. Some of these elements have been determined by the authors specifically, e.g. *H. thersites* (see JAEKEL 1891, 1907), *H. asterianus, H. latus, H. salgirensis* (see ARENDT 1974) and most recently *Cyrtocrinus nutans* (see HESS 1975); here also some elements of *Sclerocrinus compressus* are figured). Unfortunately, in Štramberk such precise determinations are not possible for the present.

As for the pinnulation of the arms, in hemicrinids it seems to be well and richly developed, at least proximally. The arms possessed large bipinnulate secundibrachials. Pinnules were probably relatively long and thin, as facets on brachials are mostly minute but with well developed articular structures; thus the arms were probably much more mobile than it follows from Arendt's reconstruction (ARENDT 1974, text-fig. 5, p. 45). (Note: In this connection the occurence of a certain number of unusually large bipinnular brachials is interesting. Under the "normal" development, these ossicles could not be part of the arm-apparatus of even the largest known spoon. Therefore, some possibility of unusual, very specific development of arms emerges).

Massive arms of some species when coiled, could be supported by the opposite calyx sides they contact. These calyx parts are often deformed, forming irregular rounded depressions, which are situated near or directly on the hypertrophied lower interradial process and are markedly pronounced in *Hemicrinus robustus* sp. n. (analogy of depressions — imprints in *Hemibrachiocrinidae* and *Strambergocrinus*, see ARENDT 1974, ŽITT 1979a, b).

Unfortunately, recent cyrtocrinid forms can not be of assistance in the functional reconstruction of hemicrinid arm-apparatus. The very massive arm-apparatus of *Holopus rangii*, as recently observed by MACURDA and MEYER [1974]in Discovery Bay (Jamai-ca), serves probably as a collection bowl in a relatively calm environment at a depth of 270 to 300 meters. The ten short arms with monopinnular brachials were observed extended in a funnel-like arrangement. This is an only information available on *Holopus* life habit. It seems probable that obliquity of the ventral part in some degree eliminates the orientation of animals, observed to be cemented to vertical rock-outcrops. Thus the crinoid can feed on a planktonic rain coming from above, his relatively low nutritive demands being easily satisfied. The great massivness of arms seems to be mainly a protection from the predator activity. Other investigation of the species is indispensable.

The *Cyrtocrinus nutans* living in the sedimentary environment of the Birmenstorfer Schichten (Oxfordian, Switzerland) was reconstructed [HESS 1975, p. 52, fig. 27] as cemented to a sponge. Two individuals are attached obliquely to the surface of a sponge, one of them having 2 columnals and a slightly oblique ventral part of calyx. The arms of other crinoid are in quiet position (coiled). Nevertheless, the author evidently regards them as rheophobes, probably using a collection bowl. The reconstructed Birmenstorf community, however, also includes the genera *Isocrinus* and *Balanocrinus*, the posture of which is typically rheophile. The rheophile habit is, therefore, to be supposed for at least some period of *Cyrtocrinus* life even in the lower water strata, nearer to the bottom. In some bottom sections (e.g. among stones, greater benthic animals etc.) moderate currents of only certain directions could be emphasized. These very mild currents without producing traces of sedimentological character may considerably improve living conditions, mainly the quantity of food. It is probable that the evolution of hemicrinid stock of cyrtocrinids was directed to a full utilization of these special habitats. Hence, such a prominent accentuation of rheophility without real living in strong currents.

The orientation of the animal with respect to the current direction raises another problem. Some recent forms using the horizontal fans, orientate them ventrally downcurrent. Ambulacral parts of the arms are turned off the current and the transportation of food within the ambulacral furrows is not disturbed. In another type of arm--apparatus oriented ventrally upwards, a torsion of downcurrently located arms takes place, so that all arms face ambulacrally downcurrent (some comatulids, see Meyer 1973).

It seems probable that the orientation of arms ventrally downcurrent is by far most advantageous in those filtrators who live in unidirectional currents without a possibility of torsion (see above). In hemicrinids this position is yet more logic supposing that the *Cyrtocrinus*-*Hemicrinus* line evolved from a plicatocrinid ancestor. The main hypothetical evolutionary stages are figured in text-fig. 8. The ancestral plicatocrinid stem was mobile, having a relatively high number of low columnals and mobile articulation to calyx. In currents the stem was able to tilt and the arms formed a horizontal filtration fan. The obliquity of calyx (see below) is not developed, as the flexibility of the polycolumnal stem warrants its necessary oblique position (similar recent crinoids see e. g. MACURDA, MEYER 1974, 1976a, 1976b, MEYER, LANE 1976, fossil crinoids most recently e. g. HAUGH 1979, ROUX 1978). If the current slacks the strong



8 — Evolutionary pattern of hemicrinid spoon with regard to the orientation of the animal in water current. a, b, c — successive stages, d — improbable development, α angle between the plane of facets and horizontal plane, β — angle between the plane of facets and the contact surface between calyx and stem. r arms. Orig.

ligaments bring the stem back to the vertical position. Under the conditions of prevailing unidirectional current it would be advantageous for the arm-apparatus to be fixed in oblique position. A mere fusion of stem elements into an arch-like support of arms was practically impossible (see text-fig. 8, d). The only way for making the stem immobile, therefore, was a gradual removal of intercolumnal articulations (see the preceding chapter) and the development of arm-apparatus obliquity by a gradual and contemporaneous tilting of the calyx itself, i. e. by its asymmetrical development. This process led to the creation of the morphology that is functionally homological to the corresponding body part of an ancestor (plicatocrinid) in feeding position.

From all above said it follows that the preservation of ancestral feeding posture is most probable. Thus, hemicrinids do position themselves ambulacrally (ventrally) down-current and not in the way suggested by ARENDT (1974), i. e. ambulacrally upcurrent.

It is to conclude that hemicrinids were rheophile animals thriving in moderate, unidirectional horizontal currents. They were attached subvertically to the substrate, facing ambulacrally downcurrent, and used most probably a weakly developed horizontal filtration fan. They were moderate-energy rheophiles.

Specific habitat requirements of the hemicrinid species are not possible to demonstrate reliably. The quality of filtration fans was doubtless considerably differentiated. It was best developed in the Štramberk species *Hemicrinus astierianus*, "H" cf. *kabanovi*, *H. angulatus* sp. n. and *H. thersites* and non - Štramberk *H. salgirensis*, *H. elongatus*, *H. latus*, *H. phialaeformis* etc., all belonging to the most usual types. Two extremes exist, however, the very robust and massive *H. robustus* sp. n. and a form with very subtile arms *H. digitatus* (Remeš).

The explication of all adaptations solely by a different power (or velocity) of water currents and accompanying factors (amount of food, respiration etc.) is not possible. The rheophile posture certainly showed some variations but only within the limits of the weak calyx-holdfast articulation. Therefore, I do not think the great massiveness of H. robustus to be a symptom of the high-energy environment.

The overturning of calicinal part of the spoon toward the substrate and/or frequent shift of the lowest facets (and arms) backward represents another problem. This character occuring in many species (e.g. *H. astierianus, H. salgirensis*) is supposed to be an adaptation to the microturbulence which originates under the conditions of horizontal currents close to the irregular relief of the bottom (see text-fig. 9 in comparison with *H. thersites*). This feeding posture could be similar to the radial posture of some comatulids (MEYER 1973) with pinnules arranged in 4 rows for catching food from all directions. This suggests a certain specialization in exploitation of different water strata (some protection of the ventral parts against sedimenting particles is, however, also possible).

The length of the stem part of a spoon is individually variable and only rarely it acquires some taxonomic value (i.e. *H. salgirensis, T. canon*). The height of holdfast varies individually, probably in a yet higher degree.



9 — Orientation of hemicrinids in water current (schematically), On the left — species with calyx tilted to substrate (e. g. *H. astierianus*), on the right — a species with "normally" oriented calyx (e. g. *H. thersites, Torynocrinus*). Orig.

Some species [at Štramberk above all "H." cf. kabanovi] have a laterally flattened and anteriorly wedge-like tapering stem part. ARENDT [1974] was inclined to explain this feature in terms of hydrodynamic adaptation of the body. In his interpretation of hemicrinids oriented ventrally upcurrent, the wedge-like stem would be an appropriate adaptation, indeed. In my interpretation (see above) the flattening of the stem was effected by drawing the lowest arms close to its flanks when the animal was not feeding [this function as accessory, is also cited by Arendt op. cit.]. The wedge-like structure would be more efficient if developed on the opposite side of the stem, i. e. posteriorly, directed against the current. Such a development was found in Štramberk species H. angulatus sp. n., but only in about 30 percent of specimens [i. e. in 2 specimens]. This character is, therefore, most likely of another origin (e. g. growth irregularities, strengthening of the stem]. Moreover, in this species with a relatively very short stem part seems such adaptation to be senseless.

Hemicrinids, judging from their holdfasts, were attached to the firm substrates, either the rock bottom or firm objects of various kinds on a soft bottom. Infrastructure of the substrate had to be very prominent, as a large number of holdfasts was attached laterally, i. e. on an oblique or subvertical surface. The bases of holdfasts sometimes partly extend irregularly in finger-like manner, demonstrating the overgrowing to the surrounding soft sediment. The attachment surfaces of some holdfasts were probably of ambracing type (for analogy see hemibrachiocrinids, ŽÍTT 1979b).

In the sedimentary area of the Olivetská hora and Kopřivnice Formations (Upper Tithonian — Upper Valanginian, see HOUŠA 1976) the most frequent substrate of hemicrinids was the surface of rather solid older beds and accumulations of softer detritus, sedimenting in calmer areas. In the area of Valanginian (? Hauterivian) sedimentation of source material for the following Plaňava Formation (HOUŠA 1976), where hemicrinids along with phyllocrinids predominated in cyrtocrinid fauna, larger quartz grains and small pebbles, which were found cemented within the bases of some specimens (icluding hemibrachiocrinids) formed a suitable substrate. The relief of the bottom was in some places strongly diversified (very high curved holdfasts give evidence of growth in very narrow spaces, e. g. in surface crevices of coarse sediment acumulations, deeply corroded rock surface, etc.).

NOTES ON ONTOGENY OF HEMICRINIDS

The smallest specimen of *Hemicrinus* known so far belongs to *H. astierianus* and was figured by ARENDT (1974. pl. 24, fig. 2, No. PIN 2278/30). The height of this specimen [i.e. the spoon] equals about 2.1 mm. Then follows *H. latus* (in ARENDT op. cit., pl. cit., pl. 23, fig. 2, No. PIN 2278/190) with a height equal to 3.5 mm. Relatively large is the smallest specimen of *H. salgirensis* (see Arendt op. cit., pl. 26, fig. 1, No. PIN 2278/291) with height of 4.25 mm. All the mentioned specimens were included by ARENDT as the youngest members in the growth series of corresponding species.

At Štramberk the juveniles of *Hemicrinus* are much scarcer and therefore, no growth series can be constructed. The smallest specimen found has a height of 4.4 mm. Between

small and large individuals there exist relatively great size hiatuses, which makes the specific determination of morphologically uniform specimens difficult.

Most typical for the morphology of juveniles [in addition to H. digitatus - see below] is the prevailing development of three (occasionally two) upper radials (especially of the uppermost one), whereas two (or three) lower radials use to be very minute and sometimes only indicated by vertical grooves and very shallow depressions, showing the position of facets (see also ARENDT 1974, p. 136, 139, 143). All juveniles are dorsally lobated, i. e. with very convex surfaces of radials, separated by deep groove--like depressions. Such a development does not depend on the presence of sutures and crystallographically individualized radials (see "H." cf. kabanovi). Suture between the radial and stem parts, if developed, is nearly straight or slightly convex upwards, the same as in the adult H. thersites. On the other hand, a deep dorsal lobation of calices, emphasizing sutures between radials seems to be a very progressive character in some species (e. g. *H. astierianus*) persisting into the adult stages, even if considerably modified. Older juveniles of this species are easily determined not only by their lobation disappearing in some other species (e.g. H. thersites), but also by separation of their lowest facets (and the whole radials) and their shift dorsally. These characters are very useful for determining the juvenile H. astierianus at some localities. At the BPOL locality (in Obecní quarry), however, the morphologically very similar "H." cf. kabanovi along with H. astierianus are found. Relatively frequent juveniles could not normally be determined unamiguously, but in this case a lucky chance of monocrystalline nature of "H." cf. kabanovi spoons is of great assistance.

Of special interest is the species *H. digitatus* (the smallest specimen found has D_{Scal} (diameter of calyx) = 2.0 mm; the stem part fragmentary), the juveniles of which are relatively easy to determine, with regard to relatively little morphological changes during ontogeny and, particularly, very specific and easily recognizable morphological features without analogies among other hemicrinids. This relates to special lobation and finger-like processes of ventral part with small radial facets.

Juvenile specimens of *Torynocrinus* have not yet been found at Štramberk, and thus it only remains to analyze the very rarely preserved growth lines of the adults (see the part "Skeletal elements in phylogeny"). This is the case of *T. variabilis* from Štramberk. Growth lines indicate a relatively rapid increase in length of the spoon during the late ontogeny. This phenomenon is confirmed by a Crimean juvenile, whose height equals about 1.7 mm and has no stem narrowing dorsally (ARENDT 1974, p. 132, fig. 27a - v). Also the smallest Štramberk exemplar of *T. cristatus* (height of spoon equal to 6.0 mm) has a very short stem part. Although the ontogeny of *T. canon* remains unknown, a completely different pattern within the two genera, *Hemicrinus* and *Torynocrinus*, is evident. The development of *Hemicrinus* spoon is, in the main, completed as early as in the youngest stages, whereas in *Torynocrinus* this element arises gradually much later during the late ontogeny (for growth of spoon height in ontogeny see text-fig. 5).

SYSTEMATIC PART

Cyrtocrinida SIEVERTS-DORECK, 1953 Hemicrinidae RASMUSSEN, 1961

Type genus: *Hemicrinus* d'ORBIGNY, 1850

Diagnosis: Calyx and proximal part of the stem with a tendency to fusion, or fused together firmly into a spoon-like element. Axes of both parts make angles of $0-145^{\circ}$, according to ARENDT (1974) as much as 170° . The stem constituted of a few columnals or an only long element of columnal origin, or is missing and substituted by radials. Calyx always composed of five radials. Radial facets great, with very pronounced muscle fossae. Transverse ridge very prominent, axial canal small, ligament fossa expressive and mostly deep. PBr₁ often massive with hinge-

-like lateral processes, SBrBr at least partly bipinnulate. Genera: *Cyrtocrinus* JAEKEL, 1891; *Hemicrinus* d'ORBIGNY, 1850; *Torynocrinus* SEELEY, 1866.

Notes: For the illustration of mutual relations of *Hemicrinus* and *Cyrtocrinus*, the latter genus, even if not present at Štramberk, was included in this paper. With regard to the recently discovered radial construction of *Torynocrinus* spoon, the redescription of type species T. canon on the basis of material borrowed from the British Museum (Nat. Hist.) has been added.

Stratigraphic range: Hettangian — Albian

Cyrtocrinus JAEKEL, 1891

Type species: Eugeniacrinites nutans GOLDFUSS, 1826

Diagnosis: Stem composed of a small number of columnals of highly variable length. A long columnal element often present below the calyx. Calyx composed of five radials tends to incomplete fusion with the stem part, often preserved separately; in this case the calyx-stem articulation well developed. Angle between calyx axis and stem axis does not attain the value of 90 °, often equals zero.

Species: *Cyrtocrinus nutans* (GOLDFUSS, 1826), Hettangian, Sinemurian, Aalenian, Bathonian, Oxfordian, Kimmeridgian — France; Oxfordian, Kimmeridgian — F. R. G.; Oxfordian — Switzerland, Hungary; Upper Jurassic — ? Poland *C. ? nutans* (GOLD-FUSS), Callovian — France. *C. nutans apertus* (QUENSTEDT, 1874—1876), Oxfordian, Kimmeridgian — F. R. G. *C. nutans cidaris* (QUENSTEDT, 1874—1876), Oxfordian — F. R. G. *C. nutans tenuis* JAEKEL, 1891, occurrence unknown.

Notes: The old conception of these species is too extensive, the variation of them not being natural at first sight. For example, the taxa *C. n. cidaris* and *C. n. apertus* are, in my opinion, very well differentiated species. A taxonomic high-level heterogeneity is documented on pl. 5, figs. 7–12, where two specimens from LORIOL's material (1879, Birmenstorfer Schichten, early Middle Oxfordian, Argovian facies) are figured. The former species (pl. 5, figs. 7–9; in LORIOL 1879, pl. 18, fig. 41) resembles the *Sclerocrinus* in having calyx of similar type, the latter one (pl. 5, figs 10–12; in LORIOL 1879, pl. 18, fig. 39) has very prominent hemicrinid features. In HESS (1975, pl. 23, figs. 11, 13) the two types are not differentiated and are classified as *C. nutans*.

Some differences are also distinct when comparing the original GOLDFUSS' material (GOLDFUSS 1826—1833) and the material of QUENSTEDT (1874—1876) from the Malm of Bavaria and Württemberg with that of LORIOL (1879, 1882—1884) from Switzerland and France. This difference has already been known to JAEKEL (1891). As for the other forms, JAEKEL's *C. nutans* from an unknown locality is also problematical. A new study of this and all the other European material of *C. nutans* would be very useful, especially from the point of view of phylogeny of the entire group. At the same time, relationships between *Cyrtocrinus* and *Sclerocrinus* could be definitely elucidated. Stratigraphic range: Hettangian — Kimmeridgian

Hemicrinus d'ORBIGNY, 1850

Type species: *Hemicrinus astierianus* d'ORBIGNY, 1850

Diagnosis: Calyx composed of five radials, separated from each other and from the stem part by mostly well distinct sutures. Both parts (i. e. calyx and stem parts) are firmly fused, non separable. The stem part of apparently mono-elemental nature is always of columnal origin. Angle of calicinal and stem parts varies around 90°, but often attains very high values (in Štramberk 145°, after ARENDT (1974), as much as 170°).

Species: H. astierianus d'ORBIGNY, 1850, Upper Valanginian, ? Hauterivian — ČSSR (Štramberk); Lower Barremian — U.S.S.R.; Neocomian, ? Upper Albian — France. H. thersites (JAEKEL, 1891), Lower Valanginian, Barremian — U.S.S.R.; Upper Valanginian — ČSSR (Štramberk). H. digitatus (REMEŠ, 1905), Upper Valanginian — ČSSR (Štramberk). H. digitatus (REMEŠ, 1905), Upper Valanginian — ČSSR (Štramberk). H. latus ARENDT, 1974, Lower Valanginian — U.S.S.R. H. elegans ARENDT, 1974, H. salgirensis ARENDT, 1974, Lower Barremian — U.S.S.R. H. kabanovi ARENDT, 1974, Lower Aptian — U.S.S.R. H. hungaricus (SZÖRÉNYI, 1959), H. floriformis (SZÖRÉNYI, 1959), H. sulcatus (SZÖRÉNYI, 1959), H. bellus (SZÖRÉNYI, 1959), H. pulcher (SZÖRÉNYI, 1959), H. labiatus (SZÖRÉNYI, 1959), H. minor (SZÖRÉNYI, 1959), Neocomian — Hungary. H. tithonicus PISERA et DZIK, 1979, Lower or Middle Tithonian — Poland.

Stratigraphic range: Lower or Middle Tithonian — Lower Aptian, ? Upper Albian

Hemicrinus astierianus d'ORBIGNY, 1850

Pl. 1, figs. 1-12, pl. 2, figs. 1-9

- 1850 Hemicrinus astierianus; d'ORBIGNY, p. 90
- 1891 Cyrtocrinus Thersites n. sp., in part; JAEKEL, p. 611, fig. 12, probably pl. 35, fig. 3
- 1891 Cyrtocrinus granulatus; JAEKEL, p. 611, pl. 36, figs. 1-4
- 1902 Cyrtocrinus marginatus n. sp.; REMEŠ, p. 199—200, pl. 18, figs. 18, 20, probably also figs. 13, 16, 17 [figs. 14, 15 indeterminable deformations]
- 1907 Torynocrinus granulatus; JAEKEL, p. 282-288, figs. 6-8
- 1959 Torynocrinus (Torynocrinus) granulatus (JAEKEL, 1891); Szörényi, p. 241–243, pl. 1, figs. 25–28
- 1961 Hemicrinus astierianus d'ORBIGNY, 1850; RASMUSSEN, p. 235-237, pl. 33, fig. 9
- 1967 Hemicrinus (Collarocrinus) astierianus d'ORBIGNY, 1850; PALIVEC, p. 50-55, pl. 12, fig. 6, pl. 13, figs. 1-3, pl. 14, figs. 1, 2
- 1974 Hemicrinus astierianus d'ORBIGNY, 1850; ARENDT, pl. 24, figs. 1—18, pl. 25, figs. 10—13, p. 139, text-figs. 29a—v, p. 140, 141, text-figs. 30a—t

?1974 Hemicrinus astierianus d'ORBIGNY, 1850; ARENDT, pl. 25, figs. 1-9, 14-24.

Lectotype: Specimen designated and figured in Rasmussen (1961), pl. 33, fig. 9, deposited in d'Orbigny's collection in Paris under the No. 5251.

Type horizon and locality: Neocomian, Les Lattes (Var), France.

Material: 36 relatively well preserved spoons or their larger parts, 20 shorter fragments

Description: Spoon-like element massive to subtile. Radials in calyx arranged symmetrically around the central radial, bearing a facet in the highest position. This radial rapidly narrows dorsally to the stem part. Sutures between radials mostly well distinct, pronounced by deepenings (depressions). Oblique position of calyx on the stem part (angle α) very expressed, always highly exceeding 90°. Calyx part then turned obliquely down t₀ the substrate. The lower facets together with corresponding radials shifted posteriorly even in specimens having α of low values. Between these radials penetrates the proximal part of the stem, thus forming part of an anteriorly directed interradial process. A tongue-like outgrowth also often penetrates dorsally (posteriorly) (pl. 1, fig. 1).

Radial facets very well developed, muscle fossae large and deep, transverse ridge prominent and sharp, reaching nearly over the whole facet. Ligament fossa also large and deep with prominent and deep ventral grooves. Radials dorsally (posteriorly) smooth, coarsely granulated or covered with irregular wrinkle-like ridges.



10 — Relation of H_{Scal} to H_{Scol} in *Hemicrinus*. Circles — *H. robustus*, points — *H. digitatus*, crosses — *H. astierianus* (Štramberk), crosses in squares — *H. astierianus* ((Crimea, ARENDT 1974, p. 139), x — *H. thersites* (Štramberk), x in squares — *H. thersites* (Crimea, Arendt 1974, p. 135), K — "H". cf. kabanovi.

Stem part separated from calyx by a distinct, slightly to highly proximally convex suture. Transverse section of the stem circular to slightly wedge-like, narrowing anteriorly. Dorsal articular facet symplectial with a variable number of mostly poorly visible culmina arranged into a narrow peripheral crenularium. Areola large and concave, lumen indistinct.

Variation: Relation of H_{Scal} (= height of calicinal part) to H_{Scol} (= height of stem part) is figured in text-fig. 10. It is evident that a majority of Stramberk specimens have greater H_{Scol} than the Crimean ones (for data on 4 specimens see Arendt 1974, p. 139). The numbers of specimens are, however, little representative. Relatively stable is the position of radial facets with respect to the plane of bilateral symmetry. Twenty specimens of thirty three (i. e. 60.6 %) are completely symmetrical, having one facet in the uppermost position and the other arranged symmetrically down towards the stem. Six specimens are entirely asymmetrical. Location of their upper facets is turned about by 36° , so that a suture occurs in the uppermost position. This pattern (virtually another type of bilateral symmetry) is always accompanied by a highly disturbed development near the stem, as its proximal part cannot pass between the lower radials along the suture. A great asymmetry thus arises, lower radials being irregularly arranged, which in some degree negatively influence even the symmetry of the uppermost calyx parts. Joint of stem with calyx is often moved laterally; virtually it remains in the same position (interradial) located against a facet at the opposite side of calvx. Seven calices are of transitional, moderately asymmetrical development.

The depth of sutures between radials is dorsally very variable; in specimens from the Lower Blücher quarry they are almost imperceptible. The above mentioned tongue-like extension of proximal part of the stem, as well as the narrowing of radials downward is most pronounced in large specimens (see e. g. pl. 1, fig. 1). Such exemplars have only been collected at the localities of Lower Blücher quarry and BPOL in Obecní quarry. The lower interradial process is best developed in the symmetrical specimens and its massiveness is positively correlated to the angle α , which mostly equals 100—145°. The relation of D_{Scol-2} to α is shown in text-fig. 11.

Remarks and relations: At Stramberk the species is morphologically relatively stable, only some most likely gerontic specimens, are somewhat different (see above). On the other hand, the specimens from French localities Les Lattes (Var, Neocomian) and St. Pierre de Cherenne (Isère, Hauterivian) are conspicuously different (RASMUSSEN 1961, p. 325, 326]. These differences mainly concern a specimen described by JAEKEL (1891) as Cyrtocrinus granulatus and later (1907) included together with other figured specimens in the genus Torynocrinus by the same author (see synonymy). RASMUSSEN (op. cit.) mentions that both the type locality Les Lattes and St. Pierre de Cherenne are marked by gradual transition of granulated to non granulated specimens. Therefore, the presence of granulation cannot be of taxonomic importance. However, all figured specimens (JAEKEL 1891, 1907) including lectotype (RASMUSSEN 1961) are distinctly granulated or, at least, bear some traces of non-preserved granulation. Their granulation is either limited to calyx (JAEKEL 1891, RASMUSSEN 1961), or it covers the whole spoon (JAEKEL 1907). The Hungarian specimen figured by SZÖRÉNYI (1959), pl. 2, figs. 24-26) shows granulation of a similar type, but its surface extent is not known, as only a calyx part is preserved. The Stramberk specimens are smooth and only rarely in the largest (gerontic?) ones wrinkle-like structures occur dorsally on the calyx parts. These wrinkles are sometimes very high and, what is of particular importance, this granulation is of completely different type relative to the specimens known from France. Many Crimean specimens are probably also wrinkled, similarly as the Stramberk ones.

Except for the less taxonomically important differences in sculpture, the specimens of France are conspicuous by a somewhat diverse constitution of the calyx skeleton, that is, their radials are dorsally only a little narrowed towards the stem (figured specimens). In this development they approximate other species, above all *Hemicrinus robustus* sp. n. from Štramberk (see below). Of interest are also small body dimensions in France "populations", their individuals reaching a maximum height of 27 mm, but on the average less then 20 mm (RASMUSSEN 1961).

As a whole, the material of H. astierianus from the type locality is rather different from Štramberk, Crimean and Hungarian specimens, which at the utmost represent a distinct, even if closely related species. The relations of the mentioned "populations" may be established, without any doubt, only by a revision of the type material supplemented by extensive new collections.

Geographic distribution: Les Lattes (Var), France, Neocomian; after RASMUSSEN (1961, p. 235) — N. D. d. Ongles, B. Alps, France, ? Upper Albian; St. Pierre de Cherenne, Malleval (Isère), France, Hauterivian; Le Muret, France, Lower Hauterivian. Verkhnyaya Stroganovka, Crimea, U. S. S. R., Lower Barremian. Štramberk, ČSSR, Upper Valanginian, ? Hauterivian.

Distribution at Štramberk: Kopřivnice Formation — Kotouč, Š-2, 4, 11a2, 11a3, 11c1, 20, 25, 29, 34, 53; Lower Blücher quarry; Š-3, east of Obecní quarry. Plaňava Formation — BPOL in Obecní quarry.

Hemicrinus thersites (JAEKEL, 1891)

Pl. 3, figs. 4-12, pl. 4, figs. 1-3, 7-9

- 1891 Cyrtocrinus Thersites n. sp.; JAEKEL, p. 610-611, pl. 35, figs 1, 2. Figs. 4, 5 hardly determinable isolated brachials, fig. 6 specimen with deformed calyx part, difficult to determine
- ?1901 Cyrtocrinus Thersites JAEKEL; REMEŠ, p. 5-6, pl. 1, figs. 3-8, (specifically indetermiable fragments of deformed specimens)
- ?1902 Cyrtocrinus Thersites JAEKEL; REMEŠ, p. 198—199, pl. 18, figs. 6, 8—12 (indeterminable fragments of deformed specimens)

- Torynocrinus Thersites JKL. sp.; JAEKEL, p. 286-287, figs. 9, 10, probably fig. 13 1907 (indeterminable isolated holdfast) and fig. 14 (isolated brachial)
- Torynocrinus Thersites var. difformis JAEKEL; JAEKEL, p. 286—287, fig. 11 Torynocrinus thersites (JAEKEL, 1891); SZÖRÉNYI, p. 236—237 Torynocrinus (Labiocrinus) difformis (JAEKEL); SZÖRÉNYI, p. 238 1907
- 1959
- 1959
- figs. 3-6, pl. 11, figs. 1-4, probably fig. 5 (specimen deformed by pressure); pl. 12, figs. 1, 2,
- 1967 Hemicrinus [Torynocrinus] thersites (JAEKEL, 1891); PALIVEC, p. 44-47, pl. 10,
- 1974 Hemicrinus thersites (JAEKEL, 1891); ARENDT, pl. 134—135, pl. 20, figs. 10—12, pl. 21, figs. 1—5, probably figs. 6, 7 (isolated brachials); pl. 22, figs. 1, 2, text-
- figs. 11m—o, 16d—z non 1901 *Cyrtocrinus Thersites* JAEKEL; REMEŠ, p. 6, pl. 1, fig. 9 (probably deformed Strambergocrinus remesi)
- non 1902 Cyrtocrinus Thersites [AEKEL; REMEŠ, p. 198, pl. 18, figs. 5, 7 [= Hemicrinus robustus sp. n.].

Holotype: Specimen figured in [AEKEL [1891], pl. 35, fig. 1, deposited in the Naturhistorisches Museum d. Humboldt Universität, Berlin (G. D. R.).

Type horizon and locality: Upper Valanginian, Kopřivnice Formation, Štramberk.

Material: 68 relatively well preserved spoons or their greater parts, 80 ill-preserved fragments.

Description: Spoon-like element with morphologically well differentiated calyx. Calyx subpentagonal to rounded in shape, sutures between all elements (i. e. radials and stem) mostly indistinct and only sometimes made more pronounced by shallow depressions. A contact of calyx and stem parts dorsally convex upwards. Arrangement of radial facets mostly asymmetrical, lower interradial process developed a little more than the others. Radial facets large, often nearly in contact. Muscle fossae large but shallow, transverse ridge less pronounced than in H. astierianus. ligament fossa large, shallow. Angle α only rarely exceeds 90°, being mostly of lower values. The surface of calyx always smooth or only shallowly granulated or wrinkled dorsally near the contact with stem. The stem part mostly slender, in some specimens widest under the calyx and distally narrowing. Cross section circular. Surface of the stem mostly smooth, in some specimens with shallow wrinkle-like sculpture or a rough irregular granulation. Dorsal articulation furnished with a narrow indistinct crenularium and often very deeply concave areola.

Variation: Relation of H_{Scal} to H_{Scol} is figured in text-fig. 10. It is evident that H_{Scal} (= height of calyx part) is relatively smaller than in *H. astieri*anus. The Crimean specimens (ARENDT 1974, p. 125) are in this respect not distinct enough from the Stramberk ones. Variation of angle α is evaluated in text-fig. 11. Forty-four of fifty specimens (= 88 %) possess $\alpha \leq 90^{\circ}$ and only six (= 12 %) have this angle larger than 90°. In one of the specimens the angle amounts to maximum value of 110°.

Surface granulation also varies within a wide range. It occurs mainly on the stem part and disappears near the suture to RR. Granulation of calyx part is far scarcer, especially on the higher situated radials. If developed, it is represented rather by wrinkles than by rounded granules, which on the contrary prevail on the stem part. Of interest is the limitation of wrinkle-like sculptures to the club-shaped spoons, i. e. those gradually narrowing from calyx dorsally. Club-shaped specimens do not form, however, a separate morphological unit, as various intermediates do exist.



11 — Relation of D_{Scol-2} to α in Hemicrinus. Triangles — H. angulatus sp. n. Other symbols as in fig. 10. $^{\circ}$

Slender types prevailing at Štramberk, do not occur in the Crimea (ARENDT 1974, pl. 20, figs. 10-12, pl. 21, figs. 1-5, pl. 22, figs. 1, 2).

Ontogeny: Juveniles are very rare. The youngest ones are dorsally strongly lobated and have 3 central radials which are the highest and most robust. Interradial sutures distinctly developed, situated within deep depressions. The size of radial facets depends on the size of radials. The lowest two occurring on either side of the proximal stem part are always very minute, sometimes hardly recognizable.

Dorsal lobation of calyx diminishes ontogenetically and disappears, and the calyx part assumes a circular to subpentagonal outline. The angle between calyx and stem parts of the spoon equals 70 to 90 $^{\circ}$ and during ontogeny does not change essentially.

Remarks and relations: The importance of *H. thersites* consists in having all radials and their facets circularly arranged, not interrupted by stem penetration between them. The stem does not penetrate there even when the calyx overturnes forward ($\alpha = 110^{\circ}$ as a maximum). The lower interradial process is not strengthened. These characters appear within a familly also in *H. digitatus* and *H. angulatus* sp. n, and probably in some species from the Hungarian Neocomian (Zirc-Borzavar, Szörényi 1959), e. g. *H. floriformis*, *H. hungaricus*, *H. compactus*, *H. sulcatus* and *H. compactus* to *H. thersites* from Stramberk emerges. An exact appreciation of the relations of these species, however, will be possible only after examining the true nature of the spoon construction of

Hungarian specimens. The above mentioned *H. digitatus* differs substantially from *H. thersites* by its finger-like calyx processes; *H. angulatus* shows a fundamentally different trend in radial growth. Only superficially is H. thersites approximated by some individuals of Torunocrinus variabilis (see below).

Geographic distribution: Štramberk, ČSSR, Upper Valanginian. Manester, Crimea, U.S.S.R., Lower Valanginian. Verkhnyaya Stroganovka, Crimea, Lower Barremian.

Distribution at Štramberk: Kopřivnice Formation — Kotouč, Š-2, 2a, 4, 5, 6, 6a, 7, 8, 11a1, 11a2, 11a3, 11c, 12, 20, 21, 25, 29, 34, 35, 43, 44, 53, 57, 61, 62, 64; Lower Blücher quarry; Š-6, east of Obecní quarry.

Hemicrinus digitatus (REMEŠ, 1905)

Pl. 4, figs. 4-6, 10-15, pl. 5, figs. 1-6

1905 Cyrtocrinus digitatus n. sp.; REMEŠ, p. 60, pl. 7, fig. 1

Torynocrinus digitatus REMEŠ; JAEKEL, p. 286 1907

1959

Torynocrinus (Torynocrinus) digitatus (REMEŠ); SZÖRÉNYI, p. 234 Hemicrinus (Torynocrinus) digitatus (REMEŠ, 1905); PALIVEC, p. 41-43, pl. 9, 1967 figs. 1-3, pl. 10, figs. 1, 2

Holotype: Specimen figured in REMES (1905), pl. 7, fig. 1 and once more in this paper on pl. 5, figs. 1-3; deposited in the Department of Paleontology, Charles University, Prague, under the number O-240.

Type horizon and locality: According to REMES (1905) it was collected in Stramberk limestone (Tithonian), Kotouč or Obecní quarry, Štramberk. According to yellowish siltstone adhering to its surface, the specimen comes doubtless from the Kopřivnice Formation (Upper Valanginian), which occurs at both sites.

Material: In addition to holotype other 12 well and 5 poorly preserved spoons and their fragments, all from the Upper Valanginian of the Kopřivnice Formation.

Description: Spoon-like element mostly slender, in gerontic specimens massive (pl. 4, figs. 10-15). Calyx part with indistinctly marked sutures between radials. Neither the suture to the stem part is well visible. Radials regularly developed, with straight or only slightly curved mutual sutures. Suture to the stem part slightly ventrally convex. Radial facets situated on the finger-like radial lobes of calyx, which are ventrally open, with very deep and narrow ventral grooves. The lobes of the adults are directed laterally, those of gerontic specimens (e.g. holotype) being curved slightly forwards and occasionally rather short and massive. Radial facets occupy the whole surfaces of the lobe ends. They are very small but with articular structures well pronounced. Muscle fossae are large, even if not very deep, transverse ridge strong, ligament fossa wide and shallow. Ventral cavity extensive with not too deep ventral grooves. Calyx part on the stem part in oblique position at about 90, but usually less degrees. Surface of calyx smooth or granulated (pl. 5, fig. 5). Stem part slender, of maximum thickness immediately under the calyx, circular in cross--section. Dorsal articular facet small, with a narrow crenularium and concave areola. The surface of stem part mostly smooth.

Variation: Species variation cannot be appreciated for a small number of specimens. In a majority of specimens from the Kotouč localities a slender and non-massive development predominates. The relation of H_{Scal} to H_{Scol} is illustrated in text-fig. 10. Deep calyx lobation is through intermediates connected with a very shallow development. In worse preserved specimens with not very pronounced lobation there is some danger of

confusion with *H. tersites*. The most massive and large specimens derive from Lower Blücher quarry. Their stem parts are, unfortunately, always fragmentary. These specimens seem to represent gerontic stages, similarly as the holotype, even though none of them reaches such a depth of lobation. Angle α (obliquity) of calyx and stem parts ranges from 73 to 100°, but the most usual values are less than 90° (text-fig. 11). Tilting of the calvx part forward is sometimes achieved by mere pipe-like bending of a specimen proximally, on the boundary with the stem part. Ontogeny: Juveniles of this species are very easily recognizable. Up to date, two specimens were found, the smaller one having the D_{Sral} (= diameter of calyx part) equal t_0 2.0 mm. The two juveniles are deeply lobated, with very minute to indiscernible radial facets and oblique position of calvx on the stem; the latter is very thin (complete stem part is preserved in only one specimen) and relatively long. Even if intermediate stages to the adults were not found, the morphology of both juveniles and adults is very similar, which suggests that very little changes occured during ontogeny.

Remarks: By the nature of mutual radials-stem contact is the species nearest to *H. thersites.* The finger-like lobation and minute radial facets, however, separate *H. digitatus* from the other species.

Geographic distribution: Štramberk, ČSSR.

Distribution at Štramberk: Kopřivnice Formation - Kotouč, Š-2, 11a2, 11a3, 12, 21, 25, 40, 53; Lower Blücher quarry; ? Obecní quarry (holotype, according to Remeš, see above).

Hemicrinus angulatus sp. n.

Pl. 2, figs. 10-12, pl. 3, figs. 1-3

Holotype: Specimen figured in this paper, pl. 2, figs. 13–15, deposited in the Silesian Museum, Opava, under the number Z-2516.

Paratypes: Specimens figured in this paper, pl. 2, figs. 10-12, pl. 3, figs. 1-3, numbers Z-2518 and Z-2520, and unfigured specimens numbers Z-2517, Z-2519 and Z-2521-2522, all deposited along with holotype.

Derivation of name: angulatus = angular (in Latin)

Type horizon and locality: Upper Valanginian, Kopřivnice Formation, Kotouč quarry, $\tilde{S}\text{-}2$ locality, Štramberk.

Material: In addition to the types, 2 fragments

Description: Spoon very short with massive calyx part and relatively very subtile and short stem part. Calyx part of trapezoid outline. Sutures between radials distinct, emphasized by deep and narrow depressions. The suture between calyx and stem mostly indiscernible. Radials of uneven development, mostly arranged bilaterally symmetrically. The uppermost (central) radial is of greatest dimensions, and, on the contrary, the lowest ones are the smallest. The upper radials narrow rapidly towards the stem, similarly as in *H. astierianus*. Radial facets very strongly developed, nearly contacting one another, their size being dependent on the size of radials. Muscle fossae large and deep, transverse ridge very prominent, ligament fossa small and deep, ventral grooves deep. The lowermost interradial process weakly developed, although stronger than

the others. Angle α approximates 90°, never exceeding this value. All radial facets arranged circularly, the lowermost never shifted posteriorly. Calyx part dorsally coarsely wrinkled or granulated. Sculpture extends as far as the margins of ligament fossae.

Stem part of the spoon proximally distinctly separated from calyx by prominent narrowing. This most proximal part is covered with a thin stereom layer extending from the lower parts of radials. At the suture between radials and the stem, the latter begins narrowing cone-like into the calyx. The stem is always circular in cross section. Surface without granulation or any other sculptures. Dorsal articular facet minute with narrow crenularium and concave areola.

Variation: The number of specimens is too small for variation to be assessed. The relation of D_{Scol-2} to α illustrated in text-fig. 11 shows the stem of *H. angulatus* being the most slender within a genus. A majority of specimens is not perfectly symmetrical, radials at one side being usually larger. Two specimens have the stem posteriorly provided with an inexpressive ridge, aligned vertically in the plane of bilateral symmetry. Similar ridges located anteriorly are developed in "*H.*" cf. *kabamovi* (see below).

Ontogeny: The only juvenile ever found at Štramberk demonstrates a very coarsely developed sculpture of ligament margins of the uppermost radial facets. The sutures between all skeletal elements are very distinct. Proximal part of the stem is overgrown by radials inclined at a very acute angle. Other characters for species determination do not exist.

Remarks and relations: *H. angulatus* seems to be at Štramberk very rare. Up to the present it was only found in the western parts of the Kotouč quarry. In having 3 upper radials narrowed dorsally and depressed sutures between radials it most resembles *H. astierianus*. All other characters are, however, very different. The overgrowing of the radials superficially down the proximal part of the stem, as well as a cone-like development of the stem inside the calyx are unique features among hemicrinids. There must have existed rather different growth conditions for the spoon. General features of *H. angulatus* are very similar to those of the younger juveniles of other species [mainly uneven development of radials and deeply depressed sutures between them].

Distribution at Štramberk: Kopřivnice Formation - Kotouč quarry, Š-2, 25, 29 localities.

Hemicrinus robustus sp. n.

Pl. 6, figs. 1-9, pl. 7, figs. 1-9

- 1901 Cyrtocrinus Thersites JAEKEL; REMEŠ, p. 5, pl. 1, figs. 1, 2
- 1902 Cyrtocrinus Thersites JAEKEL; REMEŠ, p. 198, pl. 18, figs. 5, 7 (the same specimens as in REMEŠ 1901)
- 1967 *Hemicrinus (Collarocrinus) robustus* sp. n.; PALIVEC, p. 55-58, pl. 14, figs. 2, 3, pl. 15, figs. 1-3.

Holotype: Specimen figured on pl. 7, figs. 1-3, deposited in the Silesian Museum, Opava, under the number Z-2540/1. Holotype, originally designated by PALIVEC [MS, 1967] and selected from REMEŠ's material insufficiently localized, is here included among the paratypes.

Paratypes: Specimens figured here on pl. 7, figs. 4-9, Nos. Z-2540/2 and 2540/3, deposited along with the holotype. Paratypes are also two other specimens figured in PALIVEC (MS, op. cit.), pl. 14, fig. 3 and pl. 15, fig. 2 and here on pl. 6, figs. 4-9, deposited in the Department of Paleontology, Charles University, Prague, numbers 0-242 and 0-243.

Derivation of name: rubustus — robust (in Latin)

Type horizon and locality: Upper Valanginian, Kopřivnice Formation, Š-3 locality east of Obecní quarry, Štramberk (holotype and paratypes Z-2540/ 2, 2540/3); Obecní quarry without more precise location (paratypes O-242, O-243):

Material: In addition to the types further 18 better preserved spoons and about $40\ poorly\ preserved\ ones$

Description: Spoon-like element very massive. Calyx part mostly irregularly developed. Sutures between incorporated elements visible only in sections. Mutual contact of radials irregular, undulated or toothed. Radial facets very unevenly developed, the uppermost being the largest. Lower interradial process extremely strong, long and often irregular with small side processes and elliptical to irregular fossae (imprints). Two lowermost facets usually located on either side of this process, which is built up of radials and proximal part of stem. Muscle fossae large, not too deep, transverse ridge weak, ligament fossa shallow. Ventral cavity shallow with not very marked ventral grooves.

Stem part of circular outline, strong and often gently narrowing distally from the calyx part. Articular facet to the holdfast small, culmina unrecognizable, probably very slightly developed.

Variation: A majority of material is unmeasureable owing to a very irregular development and postmortal deformations. The relation of H_{Scal} to H_{Scol} is figured in text-fig. 10. The value of H_{Scal} is relatively highest within the whole genus. This fact is partly due to that the measurable boundary between calyx and stem parts had to be shifted down the stem, because the sutures between radials and stem, the lowest point of which serves as a boundary for measurements in other species, are indistinct. Therefore, a new line had to be introduced at the level of the lower interradial process base.

The species varies extraordinarily in many characters, the most conspicuously, however, in the morphology of internadial process (e. g. its symmetry, massiveness, shape, size). On the contrary, angle α varies relatively little, within 73–90° (see text-fig. 11).

By sectionning some specimens a great irregularity in the relative internal range of radials was ascertained. Very variable is also the structure of the lower internadial process. It may consist of two or only one lower radial, or mainly of the stem part.

Remarks and relations: The specimens of *H. robustus sp.n.* were well known to REMEŠ, who thought (1901, p. 5) the interradial process to have originated by adjoining of the axillary to calyx (REMEŠ 1901, pl. 1, fig. 1). He also mentioned that in one specimen two opposite axillaries had fused, thus forming an arched little bridge above ventral cavity (see REMEŠ op. cit., pl. 1, fig. 2). Remeš ascribed both these developments to deformations of *Cyrtocrinus thersites* (= *Hemicrinus*). In my opinion, only the second specimen represents a true deformation; in this some brachial elements could have really fused with the lower interradial process. This specimen, however, is to be included in the species *H. robustus* sp. n. and not in *H. thersites*.

A great massiveness of *H. robustus* spoon is unique within the genus. As concerns the relative range of incorporated elements, the species does not differ markedly from some other forms [*H. thersites, H. digitatus, d'Orbigny's original specimen of H. astieri*-

anus from Les Lattes, etc.), but all these species have not such a large lower interradial process. In this connection it should be noted that the massiveness of the interradial process has no influence on the position of the lower radials and radial facets. The species studied closely resembles *Hemicrinus labiatus* (SZÖRÉNYI, 1959) from the Neocomian of Zirc-Borzavar (Hungary), which has also a lower interradial process, even if not so large. This process is, however, directed sharply to the ventral cavity and has a lip-like (i. e. labium in Latin) shape. Moreover, the stem part of H. labiatus is longer and not so massive.

Distribution at Štramberk: Obecní quarry (old collections of REMEŠ, not localized precisely, deposited at the Department of Paleontology, Charles University, Prague); Lower Blücher quarry; Š-3 east of Obecní quarry.

"Hemicrinus" cf. kabanovi ARENDT, 1974

Pl. 8, figs. 1-9, pl. 9, figs. 5-10, pl. 10, figs 10-12

Type horizon and locality: Upper Valanginian (? Hauterivian), Plaňava Formation. Obecní quarry, BPOL locality, Štramberk.

Material: 18 well preserved spoons and 30 worse preserved

Description: Spoon-like element relatively massive, with calyx and stem parts well differentiated. All elements fused to a monocrystal, from which follows the absence of any sutures. Calyx part of pentagonal to subpentagonal outline, radial facets large, muscle fossae large and deep, transverse ridge prominent, ligament fossa narrow and deep. Radial facets arranged bilaterally symmetrically, with a facet in uppermost position. Calyx part mostly overturned forwards ($\alpha > 90^{\circ}$). Lower interradial process prominent, very wide and often relatively thin in lengthwise direction. Its flanks often bear irregular rounded depressions. Lower facets on either side of the process strongly shifted posteriorly. Ventral cavity large and deep, ventral grooves expressive. The surface of calyx part dorsally (posteriorly) smooth to coarsely granulated or covered with wrinkle-like sculptures.

A stem part thick to slender, laterally flattened often as far as the dorsal articulation. Cross section elliptic to wedge-shaped, narrowed anteriorly. Lateral flattening of stem adjoins small planes which extend from the periphery of lower radial facets, and are oriented subparalell to the plane of symmetry of the spoon. Dorsal articular facet with very narrow peripheral crenularium and deeply concave areola.

Variation: Relation of H_{Scol} to H_{Scal} is figured in text-fig. 10. It is interesting that the measurements show the same pattern as in *H. astierianus*. Also angle α (text-fig. 11) is of similar values (111—137°). Bilateral symmetry mostly well expressed. The flattening of the stem varies in a high degree, but is invariably well discernible. Wrinkles developed posteriorly on the calvx part may be even nearly imperceptible.

Ontogeny: All juveniles found so far at the BPOL locality belong to this species, even though adults of similar *H. astierianus* are present there. It is of importance that the smallest specimens known ($H_s = 4.8 \text{ mm}$) have monocrystalline spoons. Strictly morphologically, all juveniles of "*H.*" cf. *kabanovi* resemble closely juveniles of other species (e. g. *H. astierianus*, *H. salgirensis*, *H. latus*, see ARENDT 1974).

Remarks and relations: The Crimean *Hemicrinus kabanovi* was described on the basis of the only specimen, the spoon of which has all elements fused (ARENDT, op. cit.). Since the true constitution may be established only after a detailed study of thin sections, the conspecificity of this species with the Stramberk specimens is uncertain. The generic determination of Stramberk specimens is not clear either, as we know nothing about the type of all skeletal elements incorporated in the spoon; not only radial, but also columnal (even if less probably) elements, i. e. elements of both *Torynocrinus* and *Hemicrinus* may have been present originally.

The species studied externally closely resembles *H. astierianus*, but the more prominent lower internatial process of "*H*." cf. *kabanovi* differentiates them unambiguously. Also the absence of depressed sutures on the dorsal part of calyx distinguishes "*H*." cf. *kabanovi* from *H. astierianus* and other similar species (*H. elegans*, *H. latus* a. o.). The only species externally similar without depressed sutures is *H. phialaeformis* (SZÖ-RÉNYI) from the Neocomian of Zirc-Borzavar (Hungary) and has a different type of granulation on the whole spoon.

Distribution at Stramberk: Obecní quarry, BPOL locality.

Torynocrinus SEELEY, 1866

1864 Koninckocrinus SEELEY; SEELEY, p. 277

1866 Torynocrinus SEELEY; SEELEY, p. 174

1907 Torynocrinus SEELEY; in part, JAEKEL, p. 281

1961 Hemicrinus d'ORBIGNY; in part, RASMUSSEN, p. 233

1967 Hemicrinus (Torynocrinus); in part, PALIVEC (MS, p. 34)

1974 Hemicrinus d'ORBIGNY; in part, ARENDT, p. 133

Type species: Torynocrinus canon SEELEY, 1866

Diagnosis: Calyx and stem parts of the spoon form a unit consisting of five longitudinal radial segments (i. e. radials). Calyx part morphologically well differentiated. Sutures between radials at least partly distinct, disappearing dorsally on the stem part, if not made pronounced by longitudinal ridges. Radial facets more or less evenly developed, articular structures prominent. Muscle fossae large, transverse ridge strong, ligament fossa shallow. Angle α never exceeding 90°. Spoon articulates directly with holdfast, which, if isolated, is indistinguishable from holdfast of Hemicrinus. PBr₁ stout, probably with variably fused lateral hinges.

Species: *Torynocrinus canon* SEELEY, 1866, Albian — England, *T. variabilis* (ARENDT, 1974), Lower Valanginian — U.S.S.R.; Upper Valanginian (? Hauterivian) — ČSSR (Štramberk). *T. cristatus* sp. n., Upper Valanginian — ČSSR (Štramberk).

Remarks: The observation of SEELEY (1866, p. 173) that calyx unseparably joined to stem consists of two circles of plates (with five plates in each), proved to be erroneus. Five-segment structure of the *Hemicrinus canon* spoon (type species) was recognized only after new examination of the British material (British Museum (Nat Hist.)). These specimens were lent to the late Karel Palivec but he probably did not study them, or did not notice the above mentioned feature. He recorded it, however, in his *Hemicrinus (Torynocrinus) cristatus* sp. n. (MS, 1967), even though he did not appreciate it adequately. A subgenus name *Torynocrinus* he used in the same sense as SZÖRÉNYI [1959], i. e. for a taxon based on the morphology only, not taking into account the characters of the inner structure of the skeleton. How erroneous was this approach follows from his classification of completely different species such as *Hemicrinus thersites* and *H. digitatus* together with *Torynocrinus canon* and *T. cristatus* sp. n. Stratigraphic range: Lower Valanginian — Albian

Torynocrinus canon SEELEY, 1866

Pl. 12, figs. 1-9

1864 *Koninckocrinus agassizi*; SEELEY, p. 277 (nomen nudum)

1866 Torynocrinus canon; SEELEY, p. 173

1885 Torynocrinus canon; PHILLIPS, p. 487

1907 Torynocrinus canon; JAEKEL, p. 281, fig. 15

1961 Hemicrinus canon (SEELEY); RASMUSSEN, p. 237-238, pl. 33, figs. 7, 8

Holotype: According to RASMUSSEN [1961] a specimen figured for the first time in PHILLIPS [1885] and once more in JAEKEL (1907), deposited in the Collections of Cambridge [U. K.] under the number B-18178.

Type horizon and locality: Albian, Red Chalk of Hunstanton, England.

Material: Specimens lent from the British Museum (Nat. Hist.), numbers E-6 641, 6857 - 6863, 6868, 6870, 6871, 6885 - 6891, 6893, 6894, 6899 - 6902, 14621, 21534, 21535, 26328, 50592 - 50594, 51519, 51520, 51723 - 51726, 51733, 51735, 67312 - 67342.

Description: Spoon mostly very high, articulated directly to holdfast. Calyx part morphologically well differentiated. The sutures between radials partly visible, mainly on the calyx part. Angle α not exceeding 90°. Calyx part mostly rounded, radial facets with less prominent articular structures than in *T. cristatus* sp. n. (see below). Muscle fossae large, transverse ridge prominent, ligament fossa wide and of variable depth. The lower interradial process non-developed. Radial facets usually aranged bilaterally symmetrically with respect to the anterior-posterior plane of symmetry, with a facet and not a suture in the uppermost position. Ventral cavity subpentagonal, shallow, with expressive ventral grooves. The entire spoon smooth.

The stem part circular in cross section, length variable. Cleavage surfaces of spoon fragment resemble a pencil stump sharpened by knife. Dorsal facet corresponding to the holdfast articulation circular, crenularium peripheral, narrow, areola deeply concave, lumen large.

The arms at least partly with massive axillaries (PBr_1), furnished with fused hinge-like processes elongated forwards (ventrally), with an orifice in the center for the food-groove (see pl. 12, figs. 4, 5). The element suggests a *Gymnocrinus*.

Variation: Only specimens representing complete or nearly complete spoon were evaluated, i. e. Nos. E 51519, 51520, 51723, 67316. This number, however, is rather small for the variability to be appreciated. The specimens measured displayed the greatest variation in relative length of the stem part within the range of family (text-figs. 12, 13). The absolute height of spoons might reach as much as 10 cm (considering all specimens lent by the British Museum). The height of a complete individual without arm-apparatus may then be 15—20 cm and possibly greater.

Some difficulties arose in measuring angle α , as the plane of facets (i. e. plane projected through the ligament pits of all five radial facets) is curved. As a result, a determination of calyx axis, being perpendicular to this plane. is very difficult. Therefore, the obtained values are not quite accurate.

The length (i. e. height) of holdfasts also varies widely.



12 — Relation of H_{Scal} to H_{Scal} in *Torynocrinus*. T. — *T. canon*, C. — *T. cristatus* sp. n., V. — *T. variabilis* (Štramberk), V in circles — *T. variabilis* (Crimea, material obtained from ARENDT), V in squares — *T. variabilis* (Crimea, ARENDT 1974, p. 133).

Remarks and relations: Some specimens of T. canon have irregularly swollen holdfasts (e. g. Nos. E 67 215, 6888). Two specimens (Nos. E 6893 and 67 317) manifest a fusion of spoon and holdfast, a phenomenon observed for the first time in the history of their investigation. The spoon of these specimens appears as if it were set into the deep distal depression of the holdfast. The skeletal substance adjacent to the holdfast facet obviously hypertrophied and grew over the sides of the distal part of the spoon, which it firmly encircled. The overall development is well visible owing to the different cle avage of the two parts.

Geographic and stratigraphic range: England, Red Chalk of Hunstanton, Albian.

Torynocrinus cristatus sp. n.

Pl. 11, figs. 1-9

1967 Hemicrinus (Torynocrinus) cristatus sp. n.; PALIVEC, p. 38-41, pl. 7, figs. 1, 2, pl. 8, figs. 1, 2, pl. 12, figs. 3, 4

Holotype: Specimen designated and figured in PALIVEC (MS, 1967), pl. 7, fig. 1 and in this paper figured once more on pl. 11, figs. 1—3, deposited in the Department of Paleontology, Charles University, Prague, under the number O-246.

Paratypes: Two specimens figured in PALIVEC (op. cit.), pl. 7, fig. 2, pl. 8, fig. 2, once more in this paper on pl. 11, figs. 4-9, deposited under the numbers O-244, O-245 along with the holotype.

Derivation of name: cristatus — crested (in Latin)

Type horizon and locality: Upper Valanginian, Kopřivnice Formation; after Palivec's data a wall situated closely north of the road descending from the 2nd to the 3rd quarry level, Kotouč, Štramberk

Material: In addition to the types, 20 well preserved spoons, 15 fragments

Description: Spoon with the stem part only slightly narrowing distally; the calyx part thus seems to be relatively small. Its outline is usually strictly pentagonal with internadial sutures emphasized by depressions. Radial facets wide, muscle fossae large and deep, transverse ridge strong,

ligament fossa narrow and deep. Arrangement of facets is not influenced by bilateral symmetry. Ventral cavity large and deep, ventral grooves narrow, deeply depressed. Angle α never exceeds 90 °. The surface smooth.

The stem part often very strong, with sutures pronounced by interradial ridges running lengthwise as far as the dorsal articulation. A cross section at all levels circular to subpentagonal, with five minute elevated ridges trending interradially. The surface completely smooth, without granulation. Dorsal symplexy with narrow peripheral crenularium and concave areola. Lumen, as a rule, indiscernible (badly preserved).

Variation: Relation of H_{Scal} to H_{Scol} is figured in text-fig. 12. The values of H_{Scal} are relatively higher than in the Crimean specimens of *T. variabilis* but they approximate those of the Štramberk individuals. The stem part of the Štramberk specimens of *T. cristatus* and *T. variabilis* is, therefore, relatively shorter. Relation of D_{Scol-2} (i. e. diameter of the stem part below calyx) to α is figured in text-fig. 13. Internadial ridges of the stem part are relatively stable and may be only slightly curved when radials are developed irregularly. Angle α equals 50—90°.

Remarks and relations: The species is easy to differentiate from other species of the genus according to the characteristic ridges mentioned above. This feature makes it unnecessary to study the internal structures of the spoon. By the morphology of radial facets *T. cristatus* is more similar to *H. canon* than to *H. variabilis*.

Distribution at Štramberk: Kotouč, Š-2, 6, 6a, 11a1, 11a2, 25, 34 localities.

Torynocrinus variabilis (ARENDT, 1974)

Pl. 8, figs. 10-12, pl. 9, figs. 1-4, pl. 10 figs. 1-9, pl. 11, figs. 10-15

1974 Cyrtocrinus variabilis sp. nov.; ARENDT, p. 131-133, text-figs. 11a-l, 16a-g, 27, pl. 18, figs. 8-17, pl. 19, figs. 1-10, pl. 20, fig. 1

?1974 Cyrtocrinus variabilis sp. nov.; ARENDT, pl. 20, figs. 2—6 (isolated holdfasts). Holotype: Specimen designated and figured by ARENDT (1974), pl. 18, fig. 8, p. 62, text-fig. 11b—d, deposited in the Paleontological Institute of the AN U.S.S.R. in Moscow under the number PIN 2278/474.

Paratypes: All the other specimens figured by Arendt (op. cit.) (see synonymy).

Type horizon and locality: Lower Valanginian, Manester, Crimea, U.S.S.R.

Material: 13 well preserved spoons, 20 fragments, all from the BPOL locality (Plaňava Formation, Upper Valanginian, ? Hauterivian).

Description: The spoon varies morphologically within a wide range. Calyx part often morphologically poorly differentiated. Sutures between radials mostly indiscernible, in calyx part sometimes accentuated by their deepening. Calyx part pentagonal to rounded in outline. Radial facets large, muscle fossae large but shallow, transverse ridge slightly developed, ligament fossa shallow. Ventral cavity small, shallow, with less pronounced ventral grooves. Angle α never exceeds 90°. Surface granulation coarse to very fine, or missing.

The stem part very variable, always without interradial sutures, either completely smooth or granulated in the same manner as the calyx (see above). Transverse constrictions often occur at irregular intervals, super-

ficially simulating intercolumnal sutures. Cross section always circular. Dorsal symplexy with very concave areola.

Variation: The species was named after its unusually high variability even within one locality. Relation of H_{Scal} to H_{Scol} is figured in text-fig. 12. In comparison with the Crimean material the Štramberk specimens, as a whole, appear to have higher spoons but shorter stem parts. Angle α equals 30—90° (see text-fig. 13).



13 — Relation of D_{Scol-2} to α in *Torynocrinus*. Symbols as in fig. 12. Arrows — direction of the original angle dimensions (precise measurements were not obtained).

Very conspicuous is the highly varying shape differentiation of calyx and stem parts. Either the widest calyx part narrows gently dorsally (down) (club-shaped spoons), or the stem narrows immediately under the rounded calyx. It is of interest that the club-shaped spoons have often a very low α .

Transverse constrictions of the stem part are often accompanied by very coarse irregular granulation or wrinkles. Such a development is far more usual in the Crimean specimens. Another type of granulation, which is of very fine appearance (pl. 10, figs. 4—9), always covers the whole spoon surface excluding radial facets. This feature being accompanied by very slender stem parts is so distinctive for these specimens that some possibility of a different taxonomic unit is suggested. However, any taxonomic conclusions have to be postponed until sufficient material will be available.

Remarks and relations: The species, especially the smooth slender specimens superficially resemble most closely *Hemicrinus thersites*, which it could be easily confused for.

In comparison with the Crimean specimens, those of Štramberk attain a larger individual size. *T. variabilis* is noted for a weaker development of radial facets in relation to other species, which phenomenon gives evidence of a somewhat reduced arm mobility. Štramberk is the second locality in the world where the species occurs. Distribution at Štramberk: Obecní quarry, BPOL locality.

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JIŘÍ ŽÍTT

LŽICOVITÉ LILIJICE ZE ŠTRAMBERKA (SPODNÍ KŘÍDA, ČESKOSLOVENSKO)

Detailní výzkum morfologie a krystaloptiky štramberských zástupců cyrtokrinidní čeledi Hemicrinidae RASMUSSEN ukázal opodstatněnost samostatného postavení rodu Hemicrinus RASMUSSEN a Torynocrinus SEELEY, které jsou zastoupeny těmito druhy: Hemicrinus astierianus d'ORBIGNY, H. thersites (JAEKEL), H. digitatus (REMEŠ), H. robustus sp. n., H. angulatus sp. n., "H." cf. kabanovi ARENDT, Torynocrinus cristatus sp. n. a T. variabilis (ARENDT). Současně je provedena i revize a redeskripce druhu Torynocrinus canon SEELEY (Anglie) a zčásti prostudován druh Cyrtocrinus nutans (Švýcarsko). Rody Hemicrinus a Torynocrinus se podstatně liší stavbou lžicovitého elementu (= funkční ekvivalent kalicha a stonku ancestrálních forem), který u rodu Hemicrinus sestává z 6 elementů (5 RR + komunální partie), u rodu Torynocrinus z 5 elementů (pouze RR). Chybějící kolumnální část je u tohoto rodu nahrazena extrémním dorzálním prodloužením vlastních radiálií. Kolumnální původ stonkové části rodu Hemi*crinus* byl poprvé jasně dokumentován na druhu *H. astierianus.* Vzhledem k mono-krystalické stavbě celé stonkové části, a to nejen u dospělců, nýbrž i u nejmladších zjištěných stadií, a vzhledem k nepřítomnosti stop po splývání kolumnálních elementů, autor neuvažuje o možnosti homologie stonkové části lžicovitého elementu s podstatnější částí stonku ancestora, nýbrž o homologii pouze s jeho nejproximálnější částí. Vlivem retardace vývoje stonku se počet jeho elementů ve fylogenezi podstatně snížil. Jeho konečné splynutí s kalichem jako následný proces bylo silně akcelerováno do mladých ontogenetických stadií. Tím byl znemožněn růst na styku kalicha a stonku a veškeré další prodlužování stonkové části se dělo pouze dorzálně, směrem k artikulaci vůči holdfastu (bazální upevňovací části lilijice). Extrém první vývojové tendence (tj. retardace stonku), reprezentovaný hypotetickým stadiem s přímou artikulací kalich holdfast, mohl představovat ancestrální formu rodu Torynocrinus.

Ontogeneze lžicovitého elementu se u obou rodů výrazně liší. Zatímco u rodu *Hemicrinus* je tento element vytvořen již v nejranějších známých stadiích v hotové podobě, u rodu *Torynocrinus* se teprve postupně vytváří během pozdní ontogeneze.

U obou rodů se diskutuje splývání kosterních elementů různého typu (RR, kolumnalia) v závislosti na krystaloptické orientaci. Fuze kolumnálií, jakožto nejsnadněji uskutečnitelná (paralelní c-osy) nebyla u čeledi *Hemicrinidae* prokázána. Popsaný výskyt u druhu *Torynocrinus variabilis* (ARENDT), jemuž byl přisuzován velký fylogenetický význam, vyplynul, jak se ukázalo, z povrchního studia a pozorování autora druhu (Arendt). Pro splývání RR, jež by bylo dosti složitým procesem a jehož výsledkem by byl monokrystal s pravděpodobnou krystaloptickou orientací jednoho z RR, neexistují u čeledi rovněž žádné důkazy. Tento proces je uvažován pouze jako jedna z možností vzniku poprvé evidentně zjištěného monokrystalického stavu celého lžicovitého elementu druhu *"Hemicrinus"* cf. *kabanovi.* Rovněž významná odchylka krystaloptické orientace stonkové části lžicovitého elementu (úhel c-osy až 90° k morfologické ose) rodu Hemicrinus je více méně nejasná.

Dosavadní koncepce hemikrinidní lilijice s přímou artikulací lžicovitého elementu k holdfastu, tedy dvoudílná stavba (mimo ramenní aparát), se ukázala být naprosto správná a nález celých jedinců (kromě ramen) v materiálu druhu *Torynocrinus canon* jí alespoň u rodu *Torynocrinus* skýtá jasný důkaz, Podobné nálezy pro rod *Hemicrinus* jsou podle autorova názoru jen otázkou času.

Paleoekologicky jsou hemikrinidi interpretováni jako mírně reofilní formy, orientované slabě vyvinutými filtračními aparáty po proudu (opak dosavadní Arendtovy koncepce (1974)]. Nemožnost přežití v silných proudech se vysvětluje poměrnou slabostí artikulace lžicovitý element—holdfast. Přítomnost filtračního aparátu, byť ne nejtypičtěji vyvinutého, dokládají podle autorova názoru nálezy bipinulátních brachiálií. Existence těchto unikátních elementů u rodu *Hemicrinus a Cyrtocrinus* je jedním z důkazů jejich těsných vývojových vztahů. U některých druhů (*H. astierianus, "H"*. cf. *kabanovi*) byl ramenní aparát skloněn k substrátu, zvláště dorzálně (nazad) driftující spodní ramena. Tyto formy mohly využívat ke své výživě i tzv. "radial posture" (viz MEYER 1973).

EXPLANATION OF PLATES VYSVĚTLIVKY K TABULÍM All photographs made by Mrs. M. Páralová from the Institute of Geology and Geo-

technics of ČSAV, Prague. Specimens whitened with ammonium chloride. All specimens, if not noted otherwise, deposited in the Silesian Museum, Opava (SMO). Pl. I 1.— 3. Hemicrinus astierianus d'Orbigny; dorsal, lateral and ventral views. Štramberk, Obecní quarry, BPOL. No. Z-2576/1 SMO. x 3. 2. Ditto; the same orientation and locality. No. Z-2576/2 SMO. x 3. 2. 4.- 6. Ditto; the same orientation. Štramberk, Lower Blücher quarry. No. Z-2576/3 7.- 9. SMO. x 3. 2. 10.-12. Ditto; the same orientation and locality. No. Z-2576/4 SMO. x 3. 2. Pl. II 1.- 3. Hemicrinus astierianus; dorsal, lateral, ventral views. Štramberk, Kotouč, old Remeš's collections Figured in PALIVEC (1967), pl. 12, fig. 6. No. O-247, Department of Paleontology, Charles University, Prague x 2. 5. Ditto; the same orientation. Štramberk, Lower Blücher quarry. No. Z-2576/5 4.- 6. SMO. x 3. 0. Ditto; the same orientation. Štramberk, Obecní quarry, BPOL. No. Z-2576/6 7.- 9. SMO. x 3. 0. Hemicrinus angulatus sp. n.; ventral, lateral, dorsal views. Štramberk, Kotouč, 10.-12. Š-25 locality. No. Z-2518 SMO. x 4. 2. Ditto, holotype; dorsal, ventral, lateral views. Štramberk, Kotouč, Š-2 locality. 13. - 15.No. Z-2516 SMO. x 4. 2. Pl. III 1.- 3. Hemicrinus angulatus sp. n.; ventral, lateral, dorsal views. Štramberk, Kotouč, Š29 locality. No. Z-2520 SMO. x 3. 5. 4.- 6. Hemicrinus thersites (JAEKEL); the same orientation and locality. No. Z--2577/1 SMO. x 3. 0. Ditto; the same orientation. Štramberk, Kotouč, Š-25 locality. No. Z-2577/2 7.- 9. SMO. x 2. 2. Ditto; the same orientation. Štramberk, Kotouč, Š-11a2 locality. No. Z-2577/3 10. - 12.SMO. x 3. 0. Pl. IV. 1.— 3. Hemicrinus thersites; ventral, lateral, dorsal views. Štramberk, Kotouč, Š-12 locality. No. Z-2577/4 SMO. x 3_0. Hemicrinus digitatus; ventral, dorsal, lateral views. The same locality. No 4.-6.Z-2578/1 SMO. x 2. 4. Hemicrinus thersites; ventral, lateral, dorsal views. Štramberk, Kotouč, Š-29 locality. No. Z-2577/5 SMO. x 3.5. 7.- 9. Hemicrinus digitatus; the same orientation. Štramberk, Lower Blücher quarry. 10. - 12.No. Z-2578/2. x 2.5. 13. - 15.Ditto; the same orientation and locality. No. Z-2578/3 SMO. x 2.5. Pl. V 1.- 3. Hemicrinus digitatus, holotype; ventral, lateral, dorsal views. Štramberk, Kotouč or Obecní quarry (REMEŠ 1905). No. O-240, Department of Paleontology, Charles University, Prague. x 2.5. Ditto; ventral, dorsal, lateral views. Štramberk, Kotouč, Š-11a2 locality. No. 4.- 6. Z-2578/4 SMO. x 3.2. 7.— 9. Cyrtocrinus nutans (GOLDFUSS); ventral, lateral, dorsal views. Middle Oxfordian, Birmensdorf, Switzerland. Figured also in LORIOL (1879), pl. 18, fig. 41. Collections of ETH Zürich. x 3.5. 10.-12. Ditto; the same orientation and locality. Figured also in LORIOL (1879), pl. 18, fig. 39. Collections of ETH Zürich. x 3.5. Pl. VI

 Hemicrinus robustus sp. n.; ventral, lateral, dorsal views. ? Lower Blücher quarry, Štramberk. Figured also in Remeš (1901), pl. 1, fig. 1 and (1902), pl. 18, fig. 5. No. O-241, Department of Paleontology, Charles University, Prague. x 2. 2.

- 4.-- 6. Ditto: the same orientation. Obecní guarry Štramberk (old Remeš's collection). Figured also in PALIVEC (1967), pl. 14, fig. 3, No. 0-242, Department of Paleontology, Charles University, Prague, x 2.2.
- Ditto; the same orientation and locality. Figured also in PALIVEC (1967), 7 - 9pl. 15, fig. 2. No. O-243, Department of Palentology, Charles University, Prague x 2 2
- Pl. VII
- 1 3Hemicrinus robustus, holotype; ventral, lateral, dorsal views. Štramberk, Š-3 locality (east of Obecní quarry). No. Z-2540/1 SMO. x 2.2.
- Ditto; the same orientation and locality. No. Z-2540/2 SMO, x 2.2. 4 - 6
- Ditto; the same orientation and locality. No. Z-2540/3 SMO x 2.2. 7.- 9.
- Pl. VIII
- "Hemicrinus" cf. kabanovi ARENDT; ventral, lateral, dorsal views, Štramberk, 1.- 3. Obecní quarry, BPOL locality. No. Z-2579/1. x 3.0.
- 4 6Ditto; the same orientation and locality. No. Z-2579/2 SMO. x 3.0.
- 7. 9. Ditto: the same orientation and locality. No. Z-2579/3 SMO, x 3.0.
- 10. 12.Torynocrinus variabilis (ARENDT); the same orientation and locality. No. Z-2580/1 SMO. x 3.0.
- PL IX
- Torynocrinus variabilis; ventral, lateral, dorsal views, Štramberk, Obecní quarry, 1.-- 4.
- BPOL locality. No. Z-2580/2 SMO. x 2. 5. *"Hemicrinus"* cf. *kabanovi*, juvenile specimen; ventral, lateral, dorsal views. The same locality. No. Z-2579/4 SMO. x 5. 4. 5 - 7
- Ditto: the same orientation and locality. No. Z-2579/5 SMO x 5.7. 8. - 10.
- 11.-13. Hemicrinus thersites; the same orientation. Stramberk, Lower Blücher quarry. No. Z-2577/6 SMO. x 3, 2.
- 14.-16. Hemicrinus digitatus; the same orientation and locality. No. Z-2578/5 SMO. x 3. 2.
- Pl. X
- 1.— 3. Torynocrinus variabilis; ventral, lateral, dorsal views. Štramberk, Obecní quarry, BPOL locality. No. Z-2580/3. x 2.5.
- Ditto: the same orientation and locality. No. Z-2580/4 SMO. x 2.5. 4. - 6.
- 7.— 9. Ditto; the same orientation and locality. No. Z-2580/5 SMO. x 2.5.
- 10 12"Hemicrinus" cf. kabanovi, juvenile specimen; the same orientation and locality. No. Z-2579/6 SMO. x 5.8.
- Pl. XI
- 1.- 3. Torynocrinus cristatus sp. n., holotype; ventral, lateral, dorsal views. Stramberk. Kotouč, from the wall situated closely north of the road descending from the 2nd to the 3rd quarry level. Figured also in PALIVEC (1967), pl. 7, fig. 1. No. O-246, Department of Paleontology, Charles University, Prague. x 3.0.
- Ditto; the same orientation and locality. Figured also in PALIVEC (1967), pl. 4. - 6. 7, fig. 2. No. O-244, deposited along with the holotype. x 2. 8.
- 7.— 9. Ditto; the same orientation and locality. Figured also in PALIVEC (1967) pl. 8, fig. 2. No. O-245, deposited along with the holotype x 3. 0.
- 10. 12.Torynocrinus variabilis; ventral, dorsal, lateral views. Štramberk, Obecní quarry, BPOL locality. No. Z-2580/6 SMO. x 3.0. Ditto; ventral, dorsal, lateral views. The same locality. No. Z-2580/7 SMO.
- 13. 15.x 3.0.
- Pl. XII
- Torynocrinus canon SEELEY; ventral, lateral, dorsal views. Albian, Red Chalk of Hunstanton. No. E-51 520, British Museum (Nat. Hist.), London. x 2.5.
 5. Ditto; ventral, lateral views. The same locality. No. E-51 723, deposited at the
 - same place. x 1.1.
 - 6 Ditto; cleavage surfaces of the spoon stem part; axially. The same locality. The lower fragment of No. E-51 520 (see figs. 1-3 of this plate), deposited at the same place. x 3.5.
- 7.- 8. Ditto; lateral, dorsal views. The same locality. No. E-50 592, deposited at the same place. x 2.5.
 - 9. Ditto; lateral view. The same locality. No. E-51 519, deposited at the same place. x 1.1.













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