ofessor L. A. Jägerskiöld tillgivnast fr. förf

€45

ZOOLOGISKA BIDRAG FRÅN UPPSALA. Band 9
ZOOLOGISCHE BEITRÄGE AUS UPPSALA

ECHINODERM STUDIES

ACADEMICAL DISSERTATION

BY

TORSTEN GISLÉN

UPPSALA 1924
ALMQVIST & WIKSELLS BOKTRYCKERI-A.-B.

Lakat 2/

ECHINODERM STUDIES

ACADEMICAL DISSERTATION

BY

TORSTEN GISLÉN

◆

UPPSALA 1924
ALMQVIST & WIKSELLS BOKTRYCKERI-A.-B.

To

my parents

Echinoderm Studies.

By

TORSTEN GISLÉN.

Preface.

This work treats for the most part questions regarding the morphology and phylogeny of the Crinoids. It is only in Chap. 5, in connexion with a discussion of the biology, ciliary currents, and feeding of the Crinoids, that I have found a suitable opportunity for treating these conditions among the Echinoderms in general.

My investigations have partly, and for the most part, been carried out at the Zoological Institution at Uppsala, where the Superintendent, Professor A. Wirén, has endeavoured in every way to facilitate my work by placing the collections of the Institution at my disposal. It was Professor Wirén, too, who 7 years ago introduced me to this field of labour and who ever since then has always followed my investigations with interest. If this work shows any knowledge of the way in which scientific problems should be treated, it must in great part be ascribed to him, who by his stimulating lectures guided my first steps when I was learning to do scientific work.

I have carried out part of my investigations at the Kristineberg Zoological Station, Fiskebäckskil, where I spent parts of the summers of 1913, 1918, 1919, 1922, and 1923. The expenses of my visits there have been partly defrayed by a grant of money from Kungl. Vetenskapsakademien and by gifts from the Bjurzon Fund. The President of the Zoological Station, Professor Hj. Théel and its Managers, Dr. Hj. Östergren and Fil. lic. Magnus Aurivillius, have always placed boats and material at my disposal in the most courteous manner. Parts of the summers of 1920 and 1921 I spent at Hægdalen, the Biological Station at Trondhjelm, Norway, where the Director, Dr. O. Nordgård, with his never-failing knowledge of the fauna of the different localities gave me an opportunity of studying many rare forms from this very interesting fjord. His kindly and attractive personality made my stay there a very pleasant experience.

My material, with the exception of what I have collected during my own journeys, has been obtained in different quarters. A smaller collection of Crinoids existed in the Zoological Museum at Uppsala before 1914. This was increased to many times its origial size by the abundant collection of Crinoids brought home by Docent S. Bock from his journeys to Japan in 1914 and to the South Sea Islands in 1917. In 1919 I received from Dr. E. Mjöberg from the Riksmuseum at Stockholm a small collection of Australian Crinoids to investigate. Besides this I have had the opportunity, through the kindness of Professor Th. Odhner, of studying a large number of types from tropical, Arctic, and Antarctic seas, preserved at the Riksmuseum. I also owe a great debt of gratitude to Dr. Nils Odhner for sorting and sending various kinds of material to me.

In regard to the study of fossil Crinoids I have also met with the greatest kindness, and have had placed at my disposal a generous supply of rare and extraordinarily beautiful forms. Professor C. Wiman of Uppsala has been kind enough to support me in this part of my work and Professors Holm and Stensiö have lent me from the collections in the Riksmuseum all the fossils I needed for my studies. The latter has very kindly sent me a number of very interesting photos of a polished slab containing Pentacrinids in the possession of the Riksmuseum. For his trouble in picking out material on my account from the stores of the Riksmuseum I offer Fil. lic. A. Hägg my most grateful thanks. Dr. Astrid Cleve-Euler has with her usual skill determined a number of diatoms taken from the stomachs of various Crinoids.

Among foreigners, there are four to whom I am chiefly indebted and owe my thanks.

Mr. F. A. Bather, D. Sc., Keeper of the Dept. of Geology, British Museum, London, has been kind enough to place at my disposal a variety of literature, difficult of access, from his ample library. And not content with this, he has kindly verified the information taken from a number of other works which I have not been able to verify myself. Besides this he has with great liberality placed at my disposal a collection of unnamed Comatulids in the British Museum and also some descriptions which he had himself made previously. Through his intervention I have also had the chance of examining two small but interesting collections, those of Mr. R. M. Brydone, F. G. S. and Dr. A. Rowe of Margate. Unfortunately there has not been time for me to treat more than the most important of the new forms.

Mr. A. H. Clark, Curator at the Smithsonian Inst., Washington, has carried on a continual correspondence with me, and has always discussed the problems which have arisen with the greatest friendliness.

Through his intervention I have been able to obtain, by means of exchange, a small but choice collection of recent Crinoids. If I have differed from him on certain points, my criticism in no way touches his merits as a pioneer in systematization nor, as I hope, our friendship which I value very highly. My work has to a great extent been made possible through the mass of new facts he has brought to light respecting recent Comatulids.

Geheimerat Professor O. JÆKEL of Greifswald has placed his valuable advice and a couple of drawings at my disposal. He has also lent me a very beautiful collection of Comatulids from the upper Cretaceous of Rügen belonging to the well-stocked collections in the Greifswald Museum, and with his usual kindness has allowed me to describe and figure some pieces of rock containing the rare and interesting form *Palermocrinus.*

Finally to Dr. TH. MORTENSEN of Copenhagen, for whose personal interest, generosity, and willingness to take any amount of trouble in his eagerness to obtain for me valuable information and material of various kinds when I required them, I cannot be sufficiently grateful. When my work was hindered by illness I was able to retain, by his kind indulgence, a beautiful collection of Japanese Crinoids, from which I have gathered, as I hope, some valuable observations.

Besides these four gentlemen there are also some other foreign scientists to whom I owe my hearty thanks. Conservator H. ENGEL, at the Zool. Mus., Amsterdam, gave me some valuable information respecting the specimen of *Atopocrinus sibogae* preserved there. Stadtrat HAHNE of Stettin spared no trouble in order to search out on my account the old type-specimen of *Hertha mystica,* once described by Hagenow. Through the intervention of Prof. W. JANENSCH I was able to borrow from the Berlin Museum some very interesting Comatulids from upper Cretaceous, Maastricht figured by Prof. Jækel in 1901 under the name of *Atelecrinus belgicus.* Finally Mr. F. SPRINGER of Las Vegas, New Mexico, U. S. A., has been kind enough to send me some information on the young of Encrinids.

I have also to thank Dr. G. v. LÀSZLÓ, Chefgeologe, Budapest, Prof. A. REICHENSPERGER, Freiburg, Switzerland, and Mag. Sc. R. SPÄRCK of Copenhagen, for their help in procuring or veryfying literature which it was impossible for me to obtain in this country.

Miss A. STARUP has drawn my figures in Indian ink and has devoted great care and patience to this tedious work. Miss A. WÄSTFELDT has carried out with her usual skill all the sectional work in recent forms.

Here I wish also to thank all the officials of the University Library who with never-ceasing kindness have done all they could to meet my, I fear, often troublesome and numerous requisitions of literature.

The translation has been carried out by Mrs. E. GÖTHLIN, née Harris, (Chap. 2, 4, 5), Mr. L. J. POTTS, B. A., English Lector at the University, (Chap. 1) and by myself (Chap. 3). The English of the whole has been supervised by Mr. Potts. It is my pleasant duty to thank them here for their help with this work.

For the terminology and abbreviations employed I may refer to the system employed in my work of 1922. The small deviations appearing in this treatise will be easily understood without further explanation e. g. I Ax instead of I Brax, etc.

Uppsala, May 1924.

Torsten Gislén.

CHAPTER I.

Arm-ramification in recent Crinoids.

I. Introduction.

As early as 1884 P. H. Carpenter, in his first great Challenger work on Crinoidea, saw that "the pinnula of a Neocrinoid is practically a reduced copy of an arm" (p. 61). He considers that the chief reason for the increasingly marked difference between arms and pinnules during phylogenetic development is to be sought in the fact that the pinnules become a receptacle for the gonads. It is open to doubt whether this explanation is satisfactory; for many stalked Crinoids, and even some Comatulids such as *Notocrinus* and *Comatula* have to this day fertile gonad in their arms. Recently A. H. Clark, in his monograph of 1915 and in a number of papers, has championed a fantastic theory of the development of Crinoids from forms closely resembling Cirripedia. In this connexion he interprets the phylogenetic origin of pinnules and cirri in an extraordinary way, considering them to be "the original type of Crinoid appendage" and "these appendages were arranged in five pairs, the two components of each pair being, so to speak, back to back" (p. 274). Mortensen, in his two works of 1920, has rightly opposed this idea. Guided by his researches and observations in pathological and embryological material he considers himself bound to vindicate the theory of Carpenter that pinnules correspond morphologically to dwarfed arms.

II. The phylogenetic development of the pinnule.

To throw light on phylogenetic development I will give below some diagrams showing arm-ramification in certain fossil Crinoids. They are based on some of the type specimens for Angelin's Iconographia Crinoideorum, which are in the Riksmuseum at Stockholm.

Some of the oldest fossil *Pentacrinoidea*[1] e. g. *Perittocrinus* (lowest Ordovician), have simple, unramified arms without pinnules. A somewhat more complicated stage is shown in the fistulate *Cyathocrinus,* which has a few arm-ramifications of an isotomic or heterotomic type, but still lacks pinnules.

Example of arm-ramification of *Cyathocrinus ramosus* Ang. Follingbo, Gotland, Silurian f.[2] (cf. Lindström, 1888 and Bather, 1893) = The Slite group Hede, 1921. According to this author the English equivalent is Wenlock limestone.

- R I 1—3
  - II 1—2
    - III 1—4
      - IV 1—6
        - V 1—12
          - 1—17 . . .
          - 1—13 . . .
        - 1—30 . . .
      - IV 1—6
        - 1—26 . . .
        - V 1—14
          - 1—12 . . .
          - 1—7 . . .
    - III 1—5
      - IV 1—9
        - 1—2 . . .
        - 1—4 . . .
      - IV 1—7
        - 1—10 . . .
        - V 1—10
          - 1 . . .
          - 1 . . .
  - II 1—3
    - 1 . . .
    - III 1—4
      - IV 1—12
        - V 1—17
          - 1 . . .
          - 1 . . .
        - 1—25 . . .
      - 1 . . .

A similar arm-ramification is seen in *Enallocrinus* sp. (Gottland, Silurian).

- R I 1
  - II 1—4
    - 1 . . .
    - III 1—7
      - 1 . . .
      - 1 . . .
  - II 1—3
    - III 1—7
      - IV 1—6
        - V 1—7
          - VI 1—(?)81
            - 1— . .
            - 1 . . .
          - 1 . . .
        - V 1—25
          - 1 . . .
          - VI 1—27
            - 1 . . .
            - 1 . . .
      - 1 . . .
    - III 1—4
      - IV 1—13
        - V 1—16
          - VI 1—33
            - 1 . . .
            - 1 . . .
          - 1 . . .
        - V 1—24
          - VI 1—44
            - 1 . . .
            - 1 . . .
          - 1 . . .
      - IV 1—8
        - 1 . . .
        - 1 . . .

---

[1] In this particular instance I follow the notation of Jaekel (1918).

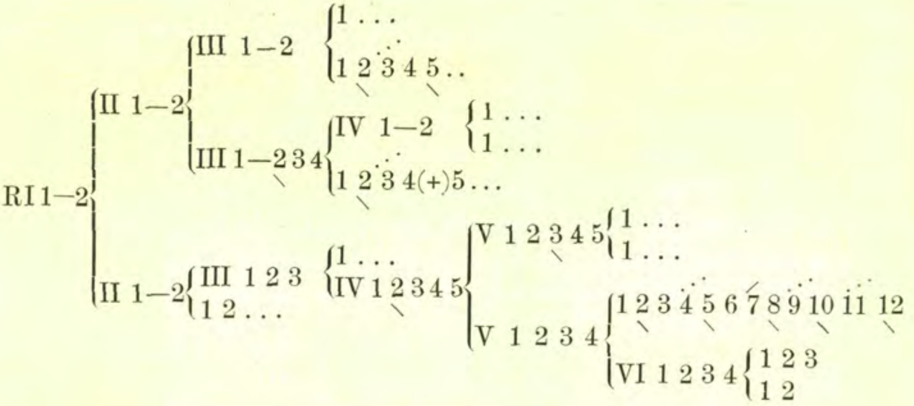
[2] The dots in these diagrams represent hidden or broken parts of arms.

We find more frequent arm-ramification in *Gissocrinus umbilicatus* ANG. (Follingbo, Gotl., Silurian, cf. also ANGELIN's Iconographia, Tab. XXI.)

- R I 1—2
  - II 1—2
    - III 1—2
      - IV 1—4
        - 1 . . .
        - 1 . . .
      - 1 . . .
    - III 1—4
      - IV 1—9
        - 1 . . .
        - 1 . . .
      - IV 1—4
        - 1—13 . . .
        - V 1—9
          - 1 . . .
          - 1 . . .
  - II 1—2
    - III 1—3
      - IV 1—4
        - V 1—8
          - 1—12 . . .
          - 1—16 . . .
        - 1 . . .
      - IV 1—7
        - 1—20 . . .
        - V 1—9
          - 1 . . .
          - 1 . . .
    - III 1—3
      - IV 1—7
        - V 1—10
          - 1 . . .
          - 1—15 . . .
        - 1—13 . . .
      - IV 1—4
        - 1 . . .
        - V 1—9
          - 1—15 . . .
          - 1—16 . . .

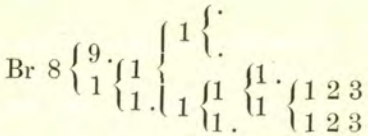
In the proximal parts of the arms the ramification thus recalls that of the recent Comatulids very closely — an analogy. Types with even closer arm-ramification are, however, to be found within this genus (e. g. *Gissocrinus arthriticus* PHILL.). As a result of this extraordinarily close ramification the arms are very densely situated, and in the most aberrant families, the *Crotalocrinidae* and *Petalocrinidae,* they grow together laterally, forming folded leaves. Now the Crinoids are detritus-collectors. Possibly the massing of the arms into solid leaves was somewhat unsuited to this way of living, since it implied impeded cleaning and no circulation of water round the individual arms, with impeded breathing as a result. Anyhow, these types disappear during the following periods, and forms appear which, instead of the exaggerated arm-ramification, have pinnules, replacing the many arms.

An intermediary stage between arms and pinnules is seen in the so-called "armlets" (BATHER, P. H. CARPENTER, WACHSMUTH and SPRINGER, — "ramiculi", JAEKEL), which appear in the metatomically ramifying *Barycrinites*. The ramification in *Botryocrinus ramosissimus* ANG. (Follingbo, Gottl. Silurian, cf. also Iconographia, Tab. XX, 8) is shown in the following diagram.



The oblique strokes represent "armlets".

The ramification of one of these armlets (from Br 8 after V Ax 4 from the above diagram) is: —



The small arms are clearly in process of development into pinnules. Muscular articulations and also typical syzygies are still lacking. The latter were not distinctly differentiated till after the appearance of pinnules, and constitute in their recent form preformed breaking-places for autotomy, during which the hypozygal makes a suitable base surface for regeneration. As for the arrangement of the small arms along the sides of the arms of the forms discussed above, these small arms are seen to lie alternately to the right and to the left, but some Br-joints may lack armlets, thus anticipating the formation of future hypozygals. Some of the articulations between these pre-hypozygals and following arm-joints seem also to be somewhat denser than the other articulations, and may be interpreted as the beginnings of syzygial formations.

Botryocrinus (*Dictenocrinus* Jaekel) *decadactylus* and *pinnulatus* (Upper Wenlock limestone, Bather 1891, 1892) have gone a step further still.

In *B. decadactylus* the arm formula may be written:

$$\begin{cases} \mathrm{Br}\ 1\,\bar{2}\,3\,\underline{4}\,\bar{5}\,\underline{6}\,\bar{7}\ldots \\ \mathrm{Br}\ 1\,\underline{2}\,3\,\bar{4}\,\underline{5}\,\bar{6}\,\underline{7}\ldots \end{cases}$$

P_1 is not infrequently forked, and can therefore best be regarded as an armlet.

B. pinnulatus has an arm formula of the following kind:

$$\mathrm{I}\ 1\,2\,3\,4\begin{cases}\mathrm{II}\ 1\,2\{\\ \mathrm{II}\ 1\,2\{\end{cases}$$

The ramifications on the outer sides are armlets, whose size is only $^3/_5$ of that of the main arm. The more distal parts of the arm have ordinary pinnules. It is to be remarked that BATHER thinks these two species may be directly derived from the older *P. ramosus* (*Bathericrinus* JKL.), which is supplied with armlets and is very closely related to the Gotland species *B. ramosissimus* (BATHER 1891, p. 409).

From lower Devonian, forms where only pinnules (ramuli, JAEKEL) have been developed, are known (*Rhenocrinidae*, JAEKEL). These are succeeded in Carboniferous and Permian by the *Poteriocrinites,* from which it may be considered that the recent forms in their turn developed. It is, however, doubtful whether the *Poteriocrinites* are to be derived directly from the series sketched above. As is shown in BATHER's work of 1893 even certain *Cyathocrinus* and *Gissocrinus* species in Silurian were canaliculate. Most *Poteriocrinites* are still non-canaliculate. The series described above had in the main developed its pinnules by the end of the Silurian period. But we still find in Carboniferous *Poteriocrinites* in which P_1 is very long and ramose, circumstances which strongly recall *Botryocrinus decadactylus* (see above).

In *Scaphiocrinus multiplex* (TRAUTSCHOLD) I have found that the most proximal pinnules are prodigiously long (P_1 40 mm.) and slightly forked: cf. diagram, which represents the ramification of the right posterior radius:

$$\mathrm{I}\ 1\,2\begin{cases}\mathrm{II}\ 1\begin{cases}\mathrm{P}\ 1\,2\,3\,4\,5\,6\,7\,8\,9\begin{cases}1\,2\,3\,4\,5\,6\ldots\\ 1\,2\begin{cases}1\,2\,3\,4\,5\,6\ldots\\ 1\,2\,3\,4\,5\ldots10\ldots\end{cases}\end{cases}\\ 2\begin{cases}\mathrm{Br}\ 1\,2\,3\ldots\\ \mathrm{Br}\ 1\,2\,3\ldots\end{cases}\end{cases}\\ \mathrm{II}\ 1\,2\,3\begin{cases}\mathrm{Br}\ 1\,2\,3\ldots\\ \mathrm{Br}\ 1\,2\,3\ldots\end{cases}\end{cases}$$

The thickness of the pinnule is only 1·5 mm., while the breadth of the arm is 4·5 mm. (fig. 306).

Presumably therefore it is more correct to assume that the *Poteriocrinites* developed from some more primitive Cyathocrinid form, and did not reach the canaliculatae and pinnulate stage till after the series described above.

Bather (1890, p. 375) stated that the only difference between pinnules and arms is that pinnules contain fertile gonad. This distribution of the gonads does not, however, always exist (cf. above, p. 5). Distal pinnules and pinnules in the anterior radii of Comasterids may also lack fertile gonad.

What difference is there then between arms and pinnules? The only difference that should be made use of in a definition of the different types is that the pinnule is a small, unramified arm, as a rule considerably shorter than the main arm. Moreover as far as I have observed the mutual articulations of the pinnulars in recent Crinoids in proximal arm-parts are always unlike those between Brr, if one excepts the articulations between pinnulars 1 and 2 — syzygoid articulations between pinnulars are to be found in *Hyocrinus* (cf. data and figg. in Döderlein, The Valdivia Expedition, 1912); cf. also e. g. the P_2 in *Stephanometridæ,* Chap. 2.

The genus *Hyocrinus* has, however, very long pinnules, approaching the main arm in size. The pinnule-bearing Br-joints may therefore have the appearance of axillaries. When pinnules are of nearly the same size as the arms on which they rest, it is a matter of taste whether they are to be called pinnules or arms. The genus *Cyathocrinus* lacks pinnules; but between the two small unramified, most distal arms and pinnules no definable difference exists.

The phylogenetic development has doubtless been that an isotomic type of ramification was succeeded by a heterotomic, which in its turn was replaced by a metatomic; the lateral ramifications began to appear at regular intervals, diminished in relative size and became unramified. So we reach the holotomic or pinnulate type. We should thus regard the arm of the recent Crinoids as a sympodium which has arisen in the following way: right and left ramifications alternately have remained at their full development, while corresponding left and right have been suppressed into pinnules. This then is the evolution of the pinnule, looked at from the phylogenetic point of view.

III. Appearance of pinnules at the ends of the arms, and intermediate forms between arms and pinnules.

Mortensen showed in his embryological work of 1920 that W. B. Carpenter's report of a sympodial growth of the arm during ontogenetic development is false. The pinnule segments are weaker from the very first, but on the other hand their longitudinal growth is at first more rapid. P. H. Carpenter (1879, p. 40) and also A. H. Clark (1915 c, pp. 79, 81) have said of the *Comasteridae* that their arms with limited growth, i. e. the posterior ones, which have no ambulacral furrow, end in an axillary supporting two pinnules of equal size. From the examples of *Comatula pectinata* and *Comanthus parvicirra* that I have examed — the same species as are drawn by Carpenter and Clark — I have, however, been able to ascertain that this statement too is inaccurate. In the anterior radii the arms end in the same way as is described by Mortensen (1920 a, p. 79) for *Antedon petasus* (cf. also fig. 1). The main arm always keeps its character of chief branch, and the pinnules break out like small buds alternately to right and left. On the posterior arms (cf. figg. 2 & 3) the only difference is that the growth of the main arm is retarded, so that the pinnules reach their full size, while the main arm grows not at all or only slowly. Therefore the arm does not end in an axillary supporting two pinnules, but on the last joint that gives rise to a ramification there is an (almost) full-grown pinnule and a main arm composed of a few joints. As soon as more than one or two joints have been formed on to the main arm a new pinnule breaks out; the main arm, therefore, keeps its ramified character and never develops as a pinnule.

The obstructive factor which causes the formation of pinnules instead of arms may in certain abnormal cases develop two pinnules on a Br instead of one pinnule and one main arm or two main arms. A case of that kind is quoted by P. H. Carpenter (1884) for *Actinometra strota* (= *Comatula solaris*). Reichensperger (1914) has similar observations to report for *Comatella stelligera* and *Amphimetra discoidea*. Sometimes one may conclude from this abnormal pinnulation that the suppressive factor has produced a reversed effect, i. e. that what ought to have been main arm has become a pinnule, and vice versa (cf. exx. of *Metacrinus rotundus* and *Pectinometra flavopurpurea* below pp. 18, 54, fig. 40). The examples, quoted below in another connexion, of hypertrophied pinnules should be interpreted as the result of removed obstruction.

In this connexion I ought perhaps to mention a few examples of ramified pinnules, which thus form a recent counterpart to the armlets described above. Mortensen (1910) reproduces a pinnule of *Polimetra prolixa* which was forked after the second joint. I have myself observed a combed pinnule in *Comanthus pinguis,* in which the pinnule was forked at the beginning of the comb (cf. fig. 4). A similar case occurs in a genital pinnule of *Heliometra eschrichti* (fig. 5). I have another example in which P_1 cannot be said to be either a pinnule or an arm from *Antedon petasus*. The arm-formula may be expressed in the following way:

$$\mathrm{I}\ 1\text{—}2\begin{cases}\mathrm{Br}\ 1\text{—}2\begin{cases}\mathrm{P}\ 1\,2\,3\,4\,5\,6\,7\,\underline{8}\,\bar{9}\,\underline{10}\,\overline{11}\,12\,13\,14\ldots 26\\ 3+4\,5\,6\ldots\end{cases}\\ \mathrm{Br}\ 1\text{—}\underline{2}\,3+\end{cases}$$

Br 3 on the right side supports a slight regenerate. The pinnule-bearing pinnulars 8—11 are thickened and furnished with oblique articulations. The pinnule on Br 2 on the right side is normal.

On another example of *Antedon petasus,* which gave the impression of being XI-armed because one P_1 in the left anterior radius was developed like an arm, one P_1 in the anterior radius was also forked. The length of this pinnule was about 10 mm. It always kept the character of a pinnule, however; the forking joints were not thickened or furnished with oblique articulations. Its formula may be written: —

$$\mathrm{I}\ 1\text{—}2\left\{\begin{array}{l}\mathrm{Br}\ 1\text{—}\bar{2}\ 3+\underline{4}\ \bar{5}\ \underline{6}\ \bar{7}\ ..\ 10+\underline{11}\ \ldots\\ \mathrm{Br}\ 1\text{—}2\left\{\begin{array}{l}3+\bar{4}\ \ldots\ 9+\underline{10}\ \ldots\\ \mathrm{P}\ 1\,2\,3\,4\,5\,6\,7\,8\left\{\begin{array}{l}1\,2\,3\,4\ \ldots\ 18\\ 1\,2\left\{\begin{array}{l}1\,2\,3\,4\ \ldots\ 13\\ 1\,2\,3\,4\ \ldots\ 17\end{array}\right.\end{array}\right.\end{array}\right.\end{array}\right.$$

Cf. above, p. 9, *Scaphiocrinus multiplex.*

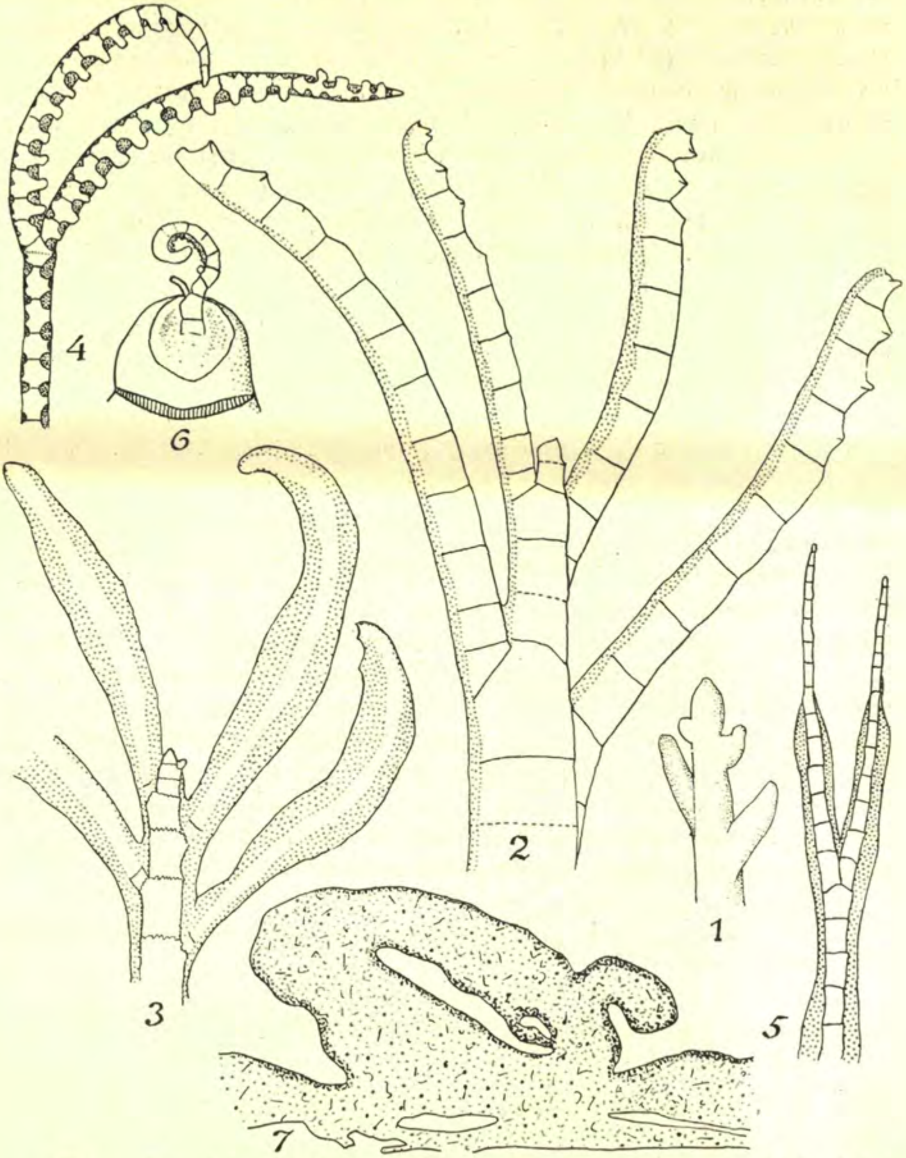
A similar forked pinnule was observed by me in another, XII-armed (6-rayed), example of *Antedon petasus.* This example had 6 radials and 6 pairs of arms, and the right posterior ambulacral furrow, though at its beginning unramified, was soon divided into two main trunks. One of the supernumerary arms of the most adanal pair had a forked P_3. The length of the pinnule was ± 7 mm. This pinnule is the first in the species that has a genital gland. While in ordinary cases this gonad reaches from segments 3 to 8 or 9, here it reached only from segments 3 to 5. The segments were here never thickened, and the pinnule kept its character of pinnule. The formula may be written: —

$$\mathrm{I}\ 1\text{—}2\left\{\begin{array}{l}\mathrm{Br}\ 1\text{—}\bar{2}\ 3+\underline{4}\ \ldots\ 9+\overline{10}\ \ldots\\ \mathrm{Br}\ 1\text{—}\underline{2}\ 3+\bar{4}\ \underline{5}\ \bar{6}\ 7\left\{\begin{array}{l}\bar{8}\ 9+\underline{10}\ \ldots\\ \mathrm{P}\ 1\,2\,3\,4\,5\,6\,7\,\underline{8}\,\bar{9}\,\underline{10}\,\overline{11}\,\underline{12}\,13\,14\ \ldots\ 19\end{array}\right.\end{array}\right.$$

IV. **Arm-ramification after a I Ax.**

A. **Ontogeny.**

The young Pentacrinula, in the Comatulids, has always, as far as is known, X arms. Many of the now living unstalked Crinoids have more than X arms. How does this multibrachiate stage arise? It might perhaps be thought that this might happen in the same way as when the



Figg. 1—7. 1—2 *Comatula pectinata* 1) Arm-tip from one of the anterior radii, decalcified, $^{30}/_{1}$. 2) Arm-tip from a posterior ungrooved ray; distalmost pinnules strongly developed, the two last segments of the main arm small, $^{30}/_{1}$. 3) *Comanthus parvicirra* γ *vaniipinna*, arm-tip from one of the posterior, ungrooved arms, distal pinnulars not indicated, $^{16}/_{1}$. 4) *Comanthus pinguis*. A combed, forking pinnule, $^{8}/_{1}$. 5) *Heliometra eschrichti* A genital pinnule forking from the 15th. segment, $^{5}/_{1}$. 6—7) *Antedon petasus.* 6) A simple arm, regenerated from I Br 1, one small pinnule to the left, $^{16}/_{1}$. 7) The same in cross-section, at about the level of the left proximal pinnule, in the arm the small hole after the hydrocel and a larger one of the coelom is visible, $^{40}/_{1}$.

first arm-ramification is formed. Here two ramifications of equal size grow out directly from a I Ax., and each of them give rise to an arm. MINCKERT (1905) was the first to show that multibrachiate forms produce their many arms by autotomy and subsequent "augmentative arm-regeneration". This means, in other words, that the young X-armed Comatulid grows for some time without increasing the number of its arms, but then at a certain size arms break off at a proximal non-muscular articulation, and from it an axillary and a pair of new arms are regenerated. He speaks of duplicative arm-regeneration when only one new axillary and two new arms are formed (I have quoted an example of this (1922) under *Stenometra dentata* Sp. 5). Multiplicative arm-regeneration is a rarer kind of arm-augmentation. This term is used when several series of arm-divisions following on one another are regenerated direct from the fracture. Of this kind of arm-augmentation I have given (1922) an example under *Asterometra anthus* Sp. 18, and also in my description of Sp. 3 of *Comaster delicata grandis*. (Note the possibility that these examples may be of a pseudo-multiplicative nature; cf. below.)

In order to facilitate a grasp of the different terms used by me below, I here give the following synopsis.

Regeneration in recent Crinoids may be: —

1) Restorative: re-forming of a single arm broken off; occurs in all Crinoids.

2) Reproductive or pseudo-augmentative: from a fracture one or more axillaries with two or more arms are re-formed; thus the number of arms is the same as before the breakage. Occurs presumably in all more or less full-grown Crinoids. It is called pseudo-duplicative when one axillary and two arms are re-formed; pseudo-multiplicative when several axillaries following on one another, and therefore more than two arms, are re-formed from the same fracture.

3) Augmentative: from a fracture a greater number of arms are formed than the broken limb possessed: occurs in Comatulids, and presumably also in *Diplocrinus* and *Teliocrinus*. It may be duplicative, when one axillary and two arms are formed from the fracture; or multiplicative, when several axillaries following on one another, and therefore more than two arms, are newly formed from the fracture.

4) Reducing: from a fracture a smaller number of arms are regenerated than the broken limb possessed. This case is theoretically conceivable, but has scarcely been observed with certainty before (cf. however p. 29 below).

Increase in the number of arms occurs in all the Comatulids, as far as is known, in this discontinuous way. It might possibly be presumed that a more direct development took place when the arms of certain multibrachiate *Capillasterinae* increase in number. Indeed A. H. CLARK

(1909 b, p. 121) states that even very tender young of *Capillaster* and *Nemaster* are multibrachiate. In the Siboga work (1918), however, he withdraws this statement.

Young of stalked Crinoids are only known in a very small number of examples, and in ordinary cases they are in such an advanced stage that not much can be determined about their method of arm-augmentation.

Augmentative arm-regeneration in Pentacrinids occurs probably in *Teliocrinus* and also in *Diplocrinus* acc. to DÖDERLEIN (1912). The drawing left by P. H. CARPENTER of a young *Isocrinus (Pentacrinus) decorus* seems to show that the formation of arms from II Ax. takes place in the same simple way as the formation of the two arms on I Ax. in the Comatulid Pentacrinula; the end of the arm ramifies into two processes, which are equally favoured in further growth, and so develop into two new arms.

DÖDERLEIN states of young of the genus *Metacrinus* (from the Valdivia exp.), which he has examined (p. 29): "Ich konnte bei den jungen Exemplaren nachweisen, dass sich an einem oder dem anderen Armstrahl noch unmittelbar vor seinem Ende eine Axillare ausgebildet hatte, d. h. eine Gabelung angelegt wurde". In his somewhat earlier work on the *Metacrini* of the Siboga Expedition (1907) he published a figure of an arm-ramification in *M. acutus,* in which "die Arme auffallend ungleich sind".

The young of *Metacrinus* described in my systematic work of 1922 are very instructive on this question. My observations show distinctly that the formation of II, III and IV Br-series takes place in the following way. On the simple arm certain pinnules begin to gain strength and grow. On the sides of the strengthened pinnules new small pinnules arise, and the new arm gradually reaches the same length as the main arm. The place for this strengthening of the pinnules is to be found in the region of transition between the large and rudimentary pinnules of the main arm. As that part of the arm which is supplied with the latter is shorter the younger the specimen is, it is clear that the arm-ramification for the formation of II Ax. will occur fairly near the top of the arm. Therefore the main arm and the new arm are not very unequal in length there, whereas the new arms on III, and to a still greater extent on IV Ax. are very different in length at earlier stages. Thus the lengths of a main and a side arm on a II Ax. (*M. interruptus* Sp. 16) are 2 and 3 mm. respectively; of two young arms from III Ax. (*M. interruptus* Sp. 17) 5 and 1 mm.; of arms from IV Ax. (*M. interruptus* Sp. 13) 12 and 2 mm., and (*M. nobilis tenuis* Sp. 9) 5·0 and 1·2, or 3·0 and 0·8 (cf. Tab. 2, Figg. 13–15, GISLÉN, 1922).

Here the factor of obstruction only succeeds in acting temporarily on the pinnule which is destined to become an arm. Thus arm-ramification in the genus *Metacrinus* is more direct and primary than in the Comatulids; a pinnule is strengthened, it ramifies, and then it grows till it is equivalent to the main arm.

B. Arm-ramification in adults.

There is also, however, a regeneration of broken arms in the Pentacrinids, just as in the Comatulids; and as in them the fracture is most often at the syzygies. When an arm-ray has been broken before a last axillary, regenerates appear which are like the augmentative regenerates of the Comatulids. A pseudo-duplicative arm-regeneration of this kind in *M. nobilis tenuis* (Loose crown 1, St. 9, Gislén 1922) may be written: —

$$\left\{\begin{array}{l} \\ \mathrm{IV}\ \underline{1}\,\overline{2}\,3+\underline{4}_1\dots\underline{10}_1\,11_1\left\{\begin{array}{l}\mathrm{Br}_1\ 3+4\dots43\\ \mathrm{Br}_1\ 3+4\dots45\end{array}\right.\end{array}\right.$$

The inner arm is 17·5, the outer arm 19·5 mm.

And in *M. rotundus* Sp. 2: —

$$\left\{\begin{array}{l}\mathrm{II}\ 3+\overline{4}\dots7\left\{\begin{array}{l}\mathrm{III}\\ \mathrm{III}\end{array}\right.\\ \mathrm{II}\ 3+\underline{4}\dots8\left\{\begin{array}{l}\mathrm{III}\ 3+\overline{4}_1\dots\overline{12}_1\,13_1\left\{\begin{array}{l}\mathrm{IV}_1\ 3+\overline{4}-16\text{ mm.}-\overline{22}\,23\left\{\begin{array}{l}\mathrm{Br}_1\ 12{\cdot}5\text{ mm.}\\ \mathrm{Br}_1\ 9{\cdot}5\text{ mm.}\end{array}\right.\\ \mathrm{Br}_1\ 31\text{ mm.}\end{array}\right.\\ \mathrm{III}\ 1+\underline{2}_1\dots\underline{12}_1\,13_1\left\{\begin{array}{l}\mathrm{Br}_1\ 27\text{ mm.}\\ \mathrm{IV}_1\ 3+\underline{4}-10\text{ mm.}-\underline{14}\,15\left\{\begin{array}{l}\mathrm{Br}_1\ 11{\cdot}5\text{ mm.}\\ \mathrm{Br}_1\ 13\text{ mm.}\end{array}\right.\end{array}\right.\end{array}\right.\end{array}\right.$$

It is only by following series of different stages of development that the difference in principle between Comatulids and *Metacrinus* in the way their arms increase can be ascertained. Thus the pseudo-augmentative arm-regeneration of which examples have been given above is only of a reproductive nature. In this connection I may point out with regard to the Comatulids that reproductive arm-regeneration appears in them too. It is therefore necessary to beware of interpreting an axillary regenerate off-hand as an augmentative arm-formation. But the Comatulids undoubtedly have augmentative arm-regeneration as a means for increasing the number of their arms, whereas *Metacrinus* uses a more direct and primitive way. A forerunner to augmentative arm-regeneration is reproductive arm-regeneration, which occurs in *Metacrinus* as well as the primitive method of augmentation described above. In the more specialized Comatulids the strengthening of a pinnule into an equivalent of the main arm never occurs normally (with the possible exception of *Comatula etheridgi*). There arm-regeneration also becomes augmentative, as the surfaces of syzygies in proximal parts of the arms get the power to form axillaries with a greater number of arm-ramifications than the broken arm-ray had. The apparently simpler arm-ray of the Comatulids *must be considered as potentially forked, but the ramification does not* come to light because the factor of obstruction permanently restrains the efforts of the pinnules to develop directly into side arms. This ramification does not appear until after an arm-breakage (in the Comatulids, autotomy), when the dormant tendency is released at regeneration.

On an examination of the genus *Metacrinus* one is struck by the extent to which the odd numbers are commoner than the even in the division series — that is, if the hypozygals are counted as independent segments. In *M. nobilis tenuis,* among the specimens examined by me (1922) of II to V Br series, there are 233 odd to 26 even; in *M. rotundus* 217 odd to 70 even; in *M. interruptus* 372 odd to 59 even. Moreover, if one examines more closely the number of syzygies in the different arm-division series, one soon discovers the rule that the series with an odd number almost always have an odd number of syzygies, while those with an even number either lack syzygies or have an even number of them. That means, in other words, that if one treats segments joined by syzygies as units, as Carpenter did, the division series have an even number of segments. Counting in this way, *M. nobilis tenuis* has 258 series with an even number of segments, and only one with an odd number; *M. rotundus* has 275 even to 12 odd; and *M. interruptus* has 422 even to 9 odd — i. e. a total of 955 even series to 22 odd. Sperry (1904) has made a curve for the variability of II Br and a similar one for III Br in *M. rotundus*, and he also gives a strong preponderance to the even series. He looks for the reason for this in the fact that pinnules on the inside of the arm are closer than on the outside. If the number of segments is even, there will be a smaller number of pinnules on the inside in the division series than on the outside. Example (modern notation): —

$$\left\{\begin{matrix}\text{III} & \\ \text{III} & 1\ \overline{2}\ 3+\underline{4}\ \overline{5}\ \underline{6}\ \overline{7}\ \underline{8}\ \overline{9}\ \underline{10}\ 11\end{matrix}\right.\left\{\begin{matrix}\text{IV}\\ \text{IV}\end{matrix}\right.$$

This is of course a correct observation, though it does not give an explanation of the phenomenon. The real explanation is presumably that if there is an even number of segments (syzygial pairs counted as units) then the new arm will be formed as a branch on the inside of the arm, where it is more protected during its first period than on the outside (cf. Gislén 1922, Pl. 2, photos 13—15). How far-reaching this rule is may best be seen from the figures quoted above. It can also be strengthened with other facts. I quoted above (p. 16) some examples of reproductive arm-regeneration. A measurement of the regenerated arms shows that the inner arms, even in the case of reproduction, are to begin with weaker than the outer (= main) arms. This phenomenon is explained by the rule demonstrated above; for the regenerate suggests the form that the actual ontogenetic development took. When, as sometimes happens, a new arm develops on the outer side of the main arm, the ramification often takes an abnormal form. The base of the new arm bends out in a wide curve, and the two arms diverge not (as is usual) at equal angles from the main axillary. Sometimes. in spite of an uneven number of components in the series, the new arm still appears on the inner side owing to abnormal pinnulation: e. g. *M. interruptus* Sp. 5:—

$$\begin{cases}\text{III } 1\,\bar{2}\,\underline{3}\,\bar{4}\,\underline{5}\,6+\bar{7}\,\underline{8}\,\bar{9}\,10\,\Big\{\\ \text{III}\end{cases}$$

The explanation of an abnormal number in the division series is generally that the main arm has aborted and become a pinnule, while a pinnule has hypertrophied and taken over the function of the main arm; or in other words that a shifting of the suppressive factor has taken place. A regenerate from IV Br 3 in *M. rotundus* Sp. 2 gives a pretty example of this: —

$$\text{III Br}\;..\,3+\underline{4}\dots 13\begin{cases}\text{Br}\\ \text{IV } 1\,\bar{2}\,3+4_1\dots\end{cases}$$

$$\dots\underline{12}\,13\,\underline{14}\,15\begin{cases}\text{V}_1\;\bar{1}\,\underline{2}\,\bar{3}\,\underline{4}\,5\,6\,7+\bar{8}\,\underline{9}\,10\begin{cases}\text{Br}_1\ 5{\cdot}5\text{ mm}\\ \text{Br}_1\ 9\text{ mm}\end{cases}\\ \text{P } 4{,}5\text{ mm}\end{cases}$$

On a IV Br 15, which has developed as an axillary, there is here a pinnule instead of the main arm to the right. IV Br 14 and 15 therefore both have pinnules on their right sides. The original pinnule on IV Br 15, on the other hand, is strengthened into a V Br arm with two new arms, the left-hand one 5·5 mm., and the right-hand one 9 mm. The left-hand arm is in the position of an inner arm, because the main ramification from IV Ax has aborted into a pinnule. The abnormality of number in the V Br series is due to the pinnulation of IV Br 14 and 15 and the consequent demand for an uneven number in the following division series in order that the two arms resulting from that may develop in a normal way. A similar example from *Florometra tanneri* has been described and drawn by A. H. CLARK (1908 a).

As far as can be judged from AGASSIZ' work on *Calamocrinus* (1892). in this genus too it is most frequently an inner pinnule that is strengthened into an arm.

CARPENTER's figure of the young *(Pentacrinus) Isocrinus decorus* in the Challenger work (1884) shows that in this genus the new arm is formed by the splitting of the growing point. Thus in this case it cannot be said that a new arm developing on the inner side of the main arm would be more protected than one developing on the outer side. Therefore in this case the number of even segments (syzygial pairs counted as units) in II Br and following series is not strikingly higher than that of odd segments, which occur pretty often to judge by the figures. I may here point out that in the Cyathocrinids odd and even series occur mixed (cf. p. 6). In the Pentacrinids, two separate series develop: one with an arm in the place of an inner pinnule and another with an arm in the place of an outer pinnule. In *Teliocrinus,* with its few-jointed division series the new arm is usually, though by no means always, in the place of an inner pinnule. In *Diplocrinus* on the other hand the number of segments in the division series is odd (counting syzygial pairs as units) = 1, and the new arm is therefore in the place of an outer pinnule. The genus *Cenocrinus* to some extent forms a link between *Isocrinus* and *Metacrinus,* since the outer series of divisions seem usually to have an even number of segments, while the inner have an odd number.

Among the Comatulids it is only in fam. *Comasteridae,* subfam. *Capillasterinae* that the form of pinnulation appearing in the genera *Metacrinus, Teliocrinus* and *Isocrinus* and represented by the formula $\{1\ 2+3\{$ reappears. This type is, as far as pinnulation is concerned, to be compared with $\{1\pm 2\ 3+4\{$, though there the first syzygial pair has coalesced into a single ossicle. All the other Comatulids have either 2 or 4 components in their division series. With regard to pinnulation these are to be considered as 1 and 2 ossicles respectively, since segments 1 and 3 in the division series never have pinnules. Thus in the former case the new arm must be considered to have developed on the outside of the main arm, in the latter case on the inside.

The indifference to whether it is an outer or an inner pinnule that is strengthened into an arm which meets us in certain Pentacrinids, and which is to be explained by the shortening of the division series, recurs in certain primitive families of Comatulids. Thus the *Charitometridae* have about as many forms with 2 as with 4 components in the division series. The mixed type is also found in the *Capillasterinae, Comasterinae* and *Zygometridae* (the last two with a tendency for 4 components to predominate), the *Calometridae* and *Thalassometridae* (though most of the genera in these last two families are bidistichal). The family *Himerometridae* has almost exclusively forms with 4 components in the division series, while the *Comactiniinae, Stephanometridae, Mariametridae, Colobometridae* and *Antedonidae* have taken the other path and have practically always two segments in the division series.

As the division series here have few segments, the young arms will be situated near the base of the arms. As in the case of *Isocrinus decorus,* an inner pinnule is not more protected during development than an outer pinnule. Moreover in the Comatulids direct increase in the number of arms has been replaced by augmentative regeneration, and the small arm-regenerates, hidden between the bases of the arms, are not very much exposed to breakage. This, in my opinion, must be taken to be the explanation of the indifference to the number of segments in the division series. In the tendency of the axillaries to shift towards the proximal parts of the arms, a tendency which can be traced in the form-series of all the Crinoids, there is this advantage: if the arms are exposed to a bending that will result in fracture, these fractures will occur distally to the axillaries, and will therefore only affect single arms. On the other hand, in *Metacrinus* and forms of a similar type whole clusters of arms are easily broken off, and so there is a greater per cent loss of ambulacral furrow.

Occasionally in the Comatulids also there occurs a direct strengthening of pinnules to equality with arms. A very interesting case of this kind in *Antedon petasus* is described by Dr. Mortensen (1920 b, pp. 73 ff.). In 5 arm-rays out of 10 both P_1 and P_a have developed into more or less complete pinnule-bearing arms (n. b. P_a is often stronger than P_1). Another specimen of *Antedon petasus* which I have myself had an opportunity of examining (cf. above p. 12) had a P_1 in the left anterior radius developed into an arm which was as strong as the other arms (L = 75 mm.). From segment 6, where the pinnules begin on the hypertrophied P_1, appeared stout segments and oblique articulations, as on the other arms. It is to be noted that syzygies of normal appearance and distribution also occur, (in distal arm parts with an interval of 3 oblique articulations.) The arm-formula may be written: —

$$\mathrm{I}\ 1-2\left\{\begin{array}{l}\mathrm{Br}\ 1-\overline{2}\ 3+\underline{4}\ \overline{5}\ \underline{6}\ \overline{7}\,..\,9+\overline{10}\,..\\ \mathrm{Br}\ 1-2\left\{\begin{array}{l}3+\\ \mathrm{P}\ 1\ 2\ 3\ 4\ 5\ \overline{6}\ \underline{7}\ 8\ \underline{9}\ 10+11\,..\,15+\overline{16}\,..\end{array}\right.\end{array}\right.$$

$$..\,20+\overline{21}\,..\,24+\underline{25}\,..\,29+\underline{30}\,..\,32+\underline{33}\,..\,36+\overline{37}\,..$$

or possibly $\mathrm{P}\ 1\ 2\ 3\ 4\ 5+6\ 7\ \underline{8}\ \overline{9}\ \underline{10}\ 11+\overline{12}$ etc.

A similar case, possibly normal, is found in *Comatula etheridgi.* Here every P_1 is developed into a small pinnule-bearing arm shorter than the main arm (A. H. Clark, 1918, p. 26). If, as has been supposed, *C. etheridgi* is a young *C. rotalaria,* we are here faced with a direct arm-development like that of *Metacrinus.*

In a specimen of *Cyllometra pulchella* from Dr. Mortensen's collection (St. 10) the right posterior radius took the following form: —

$$\mathrm{I}\ 1-2\left\{\begin{array}{l}\mathrm{II}\ 1-2\ 3\left\{\begin{array}{l}\mathrm{Br}\ 1-\overline{2}\ 3+4\ \overline{5}\ 6\ \overline{7}\ ...\ 15+16\ ...\\ \mathrm{Br}\ 1+2\ 3\ \underline{4}\ \overline{5}\ \underline{6}\ \overline{7}\ ...\ 16+\underline{17}\ ...\end{array}\right.\\ \mathrm{Br}\ 1-\underline{2}\ 3+\overline{4}\ \underline{5}\ 6\ \underline{7}\ 8\ 9+\underline{10}\ ...\ 14+\underline{15}\ ...\end{array}\right.$$

Frank Springer describes (1901) a case of *Uintacrinus socialis* in which this usually X-armed Crinoid has become XI-armed by the development of a P_a into an arm. Possibly this case should be ranked with those that have been enumerated in this connexion.

Occasionally, for one reason or an other, pinnules develop directly into arms in more distal parts of the arm also.

I can quote an example of this from *Asterometra anthus* (Gislén, 1922, Sp. 33), whose arm-ramification may be written: —

$$\mathrm{I}\ 1\text{—}2\left\{\begin{array}{l}\mathrm{Br}\ 1\text{—}2\ 3+4\ 5\ \underline{6}\ 7\ldots 11+12\ldots 17+18\ldots\\ \mathrm{Br}\ 1-2\ 3+\bar{4}\ 5\ 6\ 7\left\{\begin{array}{l}8\ 9\ 10+11\ 12\ \overline{13}\ 14\ 15+\overline{16}\ldots 21+22\ldots\\ \mathrm{P}\ 1\ 2\ 3\ 4+5\ 6\ 7\ 8\ 9\ 10\ \overline{11}\ 12+13\ldots\\ \qquad\qquad\ldots 19+20\ldots 27+\overline{28}\ldots\end{array}\right.\end{array}\right.$$

At the abnormal place for arm-ramification an entoparasitic gasteropod is encysted, and it is possibly the irritation caused by it that has released the dormant tendency (note, however, that many other specimens of the same species have encysted gasteropods in their arms without arm-ramification taking place). For some reason or other there are no soft parts on Br 8—12 (the distal part of the original arm still has an ambulacral furrow). This is the most probable cause of the hypertrophy of P_3 on the original arm. The flow of sap to the distal parts of the main arm has been cut off, and P_3 has received the surplus and so developed into a complete arm. It is to be noted, however, that no such abnormal flow of sap can be adduced in the three cases, observed by me, which are described below. Mortensen (1920 b) has described a hypertrophic pinnule in *Antedon pelasus*. Here too it is P_3 that has developed into an arm.

In Dr. Mortensen's collection of Japanese Crinoids I have found the following three examples of the development of distal pinnules into arms.

1). *Comanthus pinguis* Sp. 6 (St. 10), right posterior radius. Arm formula: —

$$\mathrm{I}\ 1\text{—}2\left\{\begin{array}{l}\mathrm{II}\ 1-2\ 3+4_1\left\{\begin{array}{l}\mathrm{III}_1\ 1\text{—}2\ 3+4\ 5+6\ 7+8\left\{\begin{array}{l}\mathrm{Br}_1\ 1\text{—}2\ 3+\\ \mathrm{Br}_1\ 1-2\ 3+\end{array}\right.\\ \mathrm{III}_1\ 1-2\ 3+.\end{array}\right.\\ \mathrm{II}\ 1\text{—}2\ 3+4\left\{\begin{array}{l}\mathrm{III}\ 1\text{—}2\ 3+\\ \mathrm{III}\ 1-2\ 3+4\left\{\begin{array}{l}\mathrm{Br}\ 1\text{—}2\ 3+\\ \mathrm{Br}\ 1-2\ 3+\end{array}\right.\end{array}\right.\end{array}\right.$$

2). *Cyllometra pulchella* Sp. 5 (St. 10), disk thrown off. Arm formula: —

$$\mathrm{I}\ 1{-}2\left\{\begin{array}{l}\mathrm{II}\ 1{-}2\ 3+4\ 5\ \underline{6}\ \overline{7}\ 8\left\{\begin{array}{l}\mathrm{Br}\ \overline{1}\ \underline{2}\ 3\ \underline{4}\ 5\ 6+7\\ \mathrm{Br}\ 1+\overline{2}\ \underline{3}\ 4\ \underline{5}\ 6+7\ldots 11+12\ldots\end{array}\right.\\ \mathrm{Br}\ 1{-}\underline{2}\ 3+4\ 5\ 6\ldots 9+\underline{10}\ldots\end{array}\right.$$

3). *Neometra multicor* Sp. 11 (St. 24), left posterior radius. Scheme of the arm: —

$$\mathrm{I}\,1{-}2\left\{\begin{array}{l}\mathrm{II}\,1{-}2\left\{\begin{array}{l}\mathrm{Br}\,1{-}2\,3+4\ldots\\ \mathrm{Br}\,1{-}\underline{2}\,3+\overline{4}\ldots\end{array}\right.\\ \mathrm{II}\,1{-}2\left\{\begin{array}{l}\mathrm{III}\,1{-}\overline{2}\,3+4\,\overline{5}\,\underline{6}\,7\,\underline{8}\,9\,\underline{10}\,11\left\{\begin{array}{l}\mathrm{Br}\,1\,\underline{2}\,3\,4+5\,\underline{6}\ldots 9+10\ldots 13+\overline{14}\ldots 17+18\ldots\\ \mathrm{Br}\,1\,2+\overline{3}\,4\,\overline{5}\,\underline{6}\,7+8\ldots 11+\underline{12}\ldots\end{array}\right.\\ \mathrm{Br}\,1{-}\underline{2}\,3+4\ldots \underline{9}\,\overline{10}\,11\,12\,\overline{13}\,\underline{\overline{14}}\,15\,16\,\overline{17}\,18+\underline{19}\ldots\end{array}\right.\end{array}\right.$$

In cases 1 and 2 it is an inner pinnule that has developed into an arm. The first example is perhaps the most remarkable; there we get a picture of the repetition, as far as possible normal, in more distal parts of the arm of the proximal arm-ramification and its distribution of non-muscular articulations.

A. H. Clark has described and illustrated an arm of *(Decametrocrinus) Thaumatocrinus* sp. (1912, pp. 249—50) twice forked in its distal part. The proximal branch seems to be due to a sheer splitting of the point of growth — I have observed a similar case in *Cyllometra pulchella* — the distal branch, on the other hand, seems to be caused by a hypertrophied pinnule.

V. Arm-ramification at and before a I Ax, and pinnulation of simple arms.

So far I have discussed the relation between arms and pinnules in distal parts of the arms, as well as the connexion between pinnules and 2nd and following arm-ramifications, and allied phenomena. It remains for me to treat of the connexion between arms and pinnules at the 1st arm-ramification.

A. Metacrinus.

We have already seen how the new arms in the genus *Metacrinus* develop in normal cases on the inner side of a main arm. What, then, is the condition at the first ramification — I Ax? Here there can be no question of the new arm developing on the inner side of an arm-fork. A comparison of the material that has been dealt with shows that in a great majority of the cases it is the right hand pinnule that has been strengthened and become equivalent to the main arm; i. e. corresponding to a pinnulation in e. g. *M. interruptus* of:

$$\mathrm{R\ I}\ 1+2\ 3\ 4+5\ 6\ 7\left|\begin{matrix}\mathrm{II}\\ \mathrm{II}\end{matrix}\right.$$

In *M. nobilis tenuis* (9 spp.) the right hand pinnule is strengthened into an arm in 24 cases, the left hand pinnule in 11. In *M. rotundus* (7 spp.) 25 right pinnules and 11 left pinnules are strengthened into arms; and in *M. interruptus* (19 spp.) 73 right pinnules and 15 left pinnules. In all 122 right pinnules strengthened as against 37 left pinnules. The reason for this can moreover be traced. In far the greater number of cases the first pinnule is on the right of I Br 2; in other words, it is the right arm-fork that is suppressed at the first ramification. When the first real arm-ramification at last takes place, it is on the right side that the suppressed impulse to arm-formation is stronger, and therefore it is more often a right than a left pinnule that develops into an arm. In *M. nobilis tenuis* (9 spp.) P_1 is on the right of I Br 2 in 24 cases out of 35, in *M. rotundus* (7. spp.) in 26 cases out of 30, and in *M. interruptus* (21 spp.) in 85 cases out of 100; in all, in 135 cases out of 165.

Thus it is the right hand arm that is suppressed in the genus *Metacrinus*. What is the case in other types where arm-ramification takes place after the first pinnule, and in the forms that have simple arms?

B. **Hyocrinidae.**

We will first examine the family *Hyocrinidae*. Of the genera belonging to this family, *Calamocrinus* has its first arm-ramification after the first pinnule, while the other genera have simple arms.

A scheme of the segments in the arm-bases and of the pinnulation in *Calamocrinus* may be written: —

$$\mathrm{R\ I}\ 1+2\ 3\ 4\ 5+6\ 7+8\ 9\ 10\left\{\begin{matrix}\mathrm{II}\\ \mathrm{II}\end{matrix}\right. \text{ or } \mathrm{R\ I}\ 1+2\ 3\ 4\ 5+6\ 7\ 8+9\ 10\left\{\begin{matrix}\mathrm{II}\\ \mathrm{II}\end{matrix}\right.$$

The first pair of pinnules is thus completely suppressed, and the first pinnule develops in the great majority of cases to the left of I Br 4 — the suppressed first pinnule would, as we remember, also have appeared on the left if it had developed. The first arm-ramification is also usually caused by the strengthening of a left pinnule. Thus here too there is a connexion between the development of the 1st pinnule and of the 1st arm-ramification similar to that which could be established in the genus *Metacrinus*. The difference is that P_1 and the first arm-ramification developed to the right in *Metacrinus,* while they are to be found on the left in *Calamocrinus.*

The other genera of the family of *Hyocrinidae* are, like *Calamocrinus,* defective in their pinnulation. Information as to the position of the pinnules is only sporadical and incomplete. A reconstruction of the defective rows of pinnules shows, however, that in the great majority of cases the suppressed P_1 must have been on the left of Br 2.

The arm-bases of the *Ptilocrinus* species may be written: —

$$\mathrm{R\ Br}\ 1+2\ 3\ 4\ 5+\underline{6}\ 7\ 8+9\ \overline{10}\ 11\ldots$$

A specimen of *Pt. pinnatus* in our museum had this distribution in all 5 cases (cf. also A. H. Clark, 1907 b, p. 552; Bather, 1908).

Of *Gephyrocrinus* there are only three specimens known (Koehler & Bather, 1902; Koehler 1909). The pinnulation and distribution of syzygies of the arm-bases up to and including Br 6 are for the most part like that in *Ptilocrinus.* The 1st pinnule is on Br 4. According to the description and figures the first, suppressed, pinnule was on the left of Br 2 in 10 cases out of 11.

In *Thalassocrinus* the first developed pinnule is on Br 5. According to A. H. Clark's figure (1915 c) it was on the left. The formula is: —

$$\mathrm{R\ Br}\ 1+2\ 3\ 4+5\ 6+7\ldots$$

Hyocrinus bethellianus has its first pinnule to the left on Br 6, or: —

$$\mathrm{R\ Br}\ 1+2\ 3+4\ 5+6\ 7+8+\underline{9}\ 10+11+12\ldots$$

according to Carpenter's statement (1884, p. 219) and Döderlein's photo (1912) — N. B. Carpenter's figure is inaccurate, as the whole picture has got reversed.

C. **Phrynocrinidae.**

In fam. *Phrynocrinidae,* the genus *Naumachocrinus* is only known from very defective specimens, while there is a pretty well preserved specimen of *Phrynocrinus* (A. H. Clark, 1907 a). This has its first arm-ramification at about I Br 20 – 25. The first developed pinnule is on I Br 7 or 8, to the right in 2 cases and to the left in 3; and the formula may be written: —

$$\mathrm{R\ I}\ 1+\underline{2}\ 3\ 4+5\ 6\ 7+8\ \overline{9}\ \underline{10}\ \overline{11}\ldots$$

A reconstruction of the pinnulation on the 5 rays of the only known specimen of *Phrynocrinus nudus* shows that the (suppressed) P_1 stood to the right of the first epizygal in 3 cases, and to the left in 2.

D. Bathycrinidæ.

The family *Bathycrinidae* is represented in recent seas by 6 genera, of which 3 have X arms after a I Br 2 as axillary, and 3 have V arms — *Rhizocrinus*, *Bythocrinus* and *Democrinus*. In the chapter on the phylogeny of the Comatulids I have explained how the *Bathycrinidae* contain two different series: one with short and coalescent BB — to it belong, among other genera, *Rhizocrinus;* and one with very long BB, joined together by sutures — to it belong, among other genera, *Bythocrinus* and *Democrinus*. It has its interest here to see that the position of the first pinnule is different in the different series.

In *Rhizocrinus lofotensis* the first developed pinnule appears almost always on Br 8 and usually to the right — according to my examinations of specimens from the Trondhjem Fjord, for instance, in 22 cases out of 30. The arm-formula can thus be written:

$$\mathrm{R\ I}\ 1+\overline{2}\,3+\underline{4}\,5+\overline{6}\,7+\underline{8}\,9+\overline{10}\ldots$$

P_1 should therefore, if developed, usually appear on the left of Br 2.

The genus *Bythocrinus,* on the other hand, has a different arrangement. The arm-formula in *B. cf. braueri* may be written: —

$$\mathrm{R\ Br}\ 1+\underline{2}\,3+\overline{4}\,5+\underline{6}\,7+\overline{8}\,9+\underline{10}\ldots$$

Thus the first pinnule appears most frequently (to the left on Br 4 or) to the right on Br 6, — in the 4 specimens observed, in 9 cases out of 11. P_1 would therefore, if developed, usually appear to the right of Br 2.

E. Comatulida.

Among the Comatulids 4 genera have simple arms. It is of some interest to see that the only one of these genera that is of an Oligophreate type *(Eudiocrinus)* has P_1 (P_C) to the left, whereas of the 3 remaining genera, which are of a Macrophreate type, at least 2 in the great majority of cases have P_1 to the right.

The scheme for the type of arm in *Eudiocrinus* may be written: —

$$\mathrm{R\ Br}\ 1+\overline{2}\ 3-\underline{4}\,5+\overline{6}\,\underline{7}\,\overline{8}\,\underline{9}\ldots$$

or

$$\mathrm{R\ I}\ 1+\overline{2}\ \mathrm{Br}\ 1—\underline{2}\,3+\overline{4}\,\underline{5}\,\overline{6}\,\underline{7}\ldots$$

I have found no deviation from this type among the specimens I have seen.

The 3 Macrophreate genera that have simple arms are: *Thaumatocrinus* (with X arms), *Pentametrocrinus* and *Atopocrinus* (with V arms).

In *Thaumatocrinus* the 1st pinnule appears as often to the right as to the left in the species I have had the opportunity of seeing. In the specimen of *Thaumatocrinus jungerseni* which is in the Uppsala museum P_1 appears to the right on Br 2 in 5 cases out of 9. Dr. MORTENSEN has been kind enough to examine for me ten more specimens of the same species in the Copenhagen museum. The result was as follows: Sp. 1, r. twice, l. 8 times; Sp. 2 (9 arms), r. 4, l. 5 times; Sp. 3, 4 and 5, r. 4, l. 6 times; Sp. 6 (9 arms), r. 5, l. 4 times; Sp. 7 and 8, r. 6, l. 4 times; Sp. 9, r. 7, l. 3 times; Sp. 10, r. 8 times, l. twice. Totals, r. 50, l. 48. It might be thought that this peculiarity is accounted for by the genus being X-rayed. But, unfortunately for that theory, the same distribution may be traced in the five-rayed young of the genus too. In *Thaumatocrinus renovatus* (P. H. CARPENTER, 1888, p. 67) P_1 appears to the right on Br 2 in 3 cases and to the left in 2. The position of P_1 also varies in a young of *Th. jungerseni*, with V arms (A. H. CLARK, 1923, figg. 3, 4).

In *Pentametrocrinus* and *Atopocrinus* the type of arm-ramification seems generally to correspond to the formula: —

$$\mathrm{R\ Br}\ 1-\underset{\cdots}{2}\,\overset{\cdots}{3}\,4+\underline{5}\,\overline{6}\,\underline{7}\ldots \quad \text{or} \quad \mathrm{R\ Br}\ 1-\underline{2}\,\overline{3}\,4+\underline{5}\,\overline{6}\,\underline{7}\ldots$$

P. H. CARPENTER states (1884, p. 85) that in *Pentametrocrinus japonicus* the first pinnule (on Br 5) appeared to the right in 11 cases out of 12. P_1 also appears to the right on Br 2 in *P. varians* (op. cit. p. 81). It is also stated to be more common on the right than on the left in *P. semperi* (p. 83). Of *P. diomedeae* I have myself seen two specimens; here the first pinnule is on the right in 9 cases out of 10. Judging by KOEHLER's figures (1909) there seems also to be a similar state of affairs in *P. atlanticus*.

Mr. H. ENGEL, curator at the zoological museum at Amsterdam, has kindly given me the following information about the pinnulation of the only known specimen of *Atopocrinus sibogae*. (Arms broken at the 2nd or 3rd syzygies.)

Left posterior arm: $\mathrm{R\ Br}\ 1-\underline{2}\,\overline{3}\,4+\underline{5}\,\overline{6}\,7+\underline{8}\,\overline{9}\,10+$

» anterior » : $\mathrm{R\ Br}\ 1-\overline{2}\,\underline{3}\,4+\overline{5}\,\underline{6}\,7+\overline{8}\,\underline{9}\,10+$

Anterior » : $\mathrm{R\ Br}\ 1-\underline{2}\,\overline{3}\,4+\underline{5}\,\overline{6}\,7+$

Right anterior arm: R Br 1—2 3 4+5 6 7+8 9 10+

» posterior » .: R Br 1—2 3+4 5 6+7 8 9+

Thus P_1 is in 4 cases out of 5 to the right on Br 2.

I will now give certain examples of the suppression of a right or a left arm in other Comatulids also. The examples I can quote still show a tendency for the suppression to be located differently in certain Oligophreate families on the one hand and certain Macrophreate types on the other.

Docent CARL AURIVILLIUS brought home from Java some Crinoids, which are preserved in the collections of the Uppsala museum. Among them is a IX-armed specimen of *Comatula pectinata.* It is here, as in *Eudiocrinus,* the left arm that is rudimentary. It is composed of a small calcareous lump of 2 ossicles joined together by a syzygial articulation. The right arm has three consecutive syzygial pairs, and its formula can accordingly be written: —

$\boxed{1+2}$

R I 1+2 Br 1+2 3+4 5 6 . . . or R Br 1+2 3+4 5+6 7 8 . . .

FRANK SPRINGER, in his work, referred to above (p. 21), on the pelagian Cretaceous form *Uintacrinus,* maintains that this Crinoid is closely related to the *Comasteridae.* It is significant that in an abnormal IX-armed specimen it is the left arm that is suppressed to a pinnule.

W. B. CARPENTER, in 1866, made a drawing of a IX-armed specimen of *Antedon bifida.* The simple ray may be written:

R I 1 Br 1—2 3+4 5 6 7 . . . or R Br 1 2—3 4+5 6 7 8 . . .

I found a similar example in a IX-armed specimen of *Antedon petasus.* Here, however, the formula for the simple ray (left anterior) is: —

R I 1 Br 1—2 3+4 5 6 7 8 9+10 . . . or R Br 1 2—3 4+5 6 7 8 9 10+11 . . .

The unforked arm is as strong as the others. On both sides of the arm the first genital gland is supported by P_3. It is to be noticed that the unusual distribution of non-muscular articulations is the same in both cases. These cases may be explained in two ways. Either the reduction has gone so far that both the suppressed arm and the ossicle to which it was attached have disappeared; or the arm alone has been suppressed, while I Br 2 has coalesced with I Br 1 into one ossicle. Since there is a muscular articulation between I 1 and Br 1, the second possibility seems the more probable. In one of these cases it is clearly a right arm, and in the other a left arm, that has been suppressed. It is to be desired that more data about the pinnulation of similar forms with simple rays should become available, to enable us to decide whether the tendency to suppression is commoner in the one arm or in the other, or, as in *Thaumatocrinus,* equally common in both.

I have mentioned above (p. 14) that during ontogenetic development the first arm-ramification is formed by the development of 2 equally strong arms. Sometimes, however, it seems that a difference in length between the two arms, which is very insignificant and in larger young soon disappears, arises, at least in certain cases. Thus we have here a difference in length between the two arms of a pair; not a difference between pairs of arms, such as is illustrated and described by PERRIER (1886, pp. 219 ff., Pl. 2). This latter, in fact, seems not to occur (cf. MORTENSEN, 1920 a, p. 72). The slight difference between the arms in pairs of arms has so far been scarcely discussed (MORTENSEN, 1920 a, denies it), occasionally illustrated, and possibly sometimes overlooked on account of its transitory nature.[1] Where it is marked, it seems to be strongest in arms with 10 to 15 Brr.

The observations I have made on very small young of the Thalassometrids *Asterometra anthus* and *Stenometra dentata* (cf. GISLÉN, 1922, pp. 109, 110, 118) point to the conclusion that one arm, and then usually the right arm, is less favoured in earlier stages of development.

It seemed to me to be possible that in reproductive arm-regeneration the growth of one or the other arm might be more or less favoured, and that that might open up a possibility of drawing certain conclusions as to the tendency to suppression.

In order to discover whether this could be established for regenerates from I Br 1, I carried out at the Kristineberg zoological station experiments in regeneration with *Antedon petasus.* Owing to a number of unfortunate accidents, out of all the hundreds of specimens operated on I only obtained 10 with regenerated arms.

---

[1] We may compare the stalked immature forms with post-axillary elements of which figures have been published. They are as follows: — *Comactinia meridionalis* (A. AGASSIZ 1888, Vol. 2, p. 117, SPRINGER 1920, pll. 1 and 2); *Crotalometra porrecta(?)* (P. H. CARPENTER, 1888, Pl. 14, figg. 5—7, cf. also A. H. CLARK, 1922, p. 521); *Glyptometra tuberosa* (P. H. CARPENTER, 1888, Pl. 14, fig. 9, A. H. CLARK, 1922, p. 523); *Ptilometra mülleri* (=*Himerometra paedophora*, H. L. CLARK, 1909, p. 525, Pl. 47); *Antedon mediterranea* (A. H. CLARK, 1922, Pl. 51); *Antedon bifida* (WYV. THOMSON , 1865, Pl. 27; W. B. CARPENTER, 1866, Pll. 39—41; PERRIER, 1886, Pl. 2; CHADWICK, 1907, Pl. 7); *Antedon petasus* (MORTENSEN, 1910, Pl. 10, fig. 3); *Compsometra serrata* (MORTENSEN, 1920 a, Pll. 12, 13); *Isometra vivipara* (K. A. ANDERSSON, 1904, fig. 11, MORTENSEN. 1920 a, Pl. 21 – 23); *Heliometra eschrichti* (LEVINSEN, 1887, Pl. 35, fig. 8, P. H. CARPENTER, 1888, Pl. 14, fig. 3 fide A. H. CLARK, 1922; MORTENSEN, 1910, Pl. 10, fig. 1); *Promachocrinus kerguelenensis* (A. H. CLARK, 1922, figg. 917 ff.); *Poliometra prolixa* (P. H. CARPENTER, 1888, Pl. 14, fig. 2 fide A. H. CLARK, 1922, MORTENSEN, 1910, Pl. 9, figg. 4, 5, Pl. 10, fig. 2); *Hathrometra tenella* var. *sarsii* (M. SARS, 1868, Pl. 5); *Thaumatometra nutrix* (MORTENSEN, 1918, Pl. 5 and 1920 a, Pl. 28).

In 1918 I amputated arm-rays between I Br 1 and 2 on 15 specimens. The animals so treated were placed in a fairly large box with a lid which was perforated for the sake of water circulation with holes 1 cm. in diameter. The box was sunk off Blåbergsholmen, Kristineberg, at a depth of about 15 M., and was anchored by a line to a crevice in a rock just above high-water-mark. When it was taken up a month later all the specimens except one had escaped through the perforations (1 cm. in diameter!). Fine-meshed netting was now nailed over the perforations, and in 1919 the box was again exposed, this time with 50 amputated specimens. The strong September storms, however, tore away the cable, and the box was lost. In 1922 the same procedure was repeated with a new box, but then the water circulation was too weak and the animals died. Finally, in 1923, of the exposed animals, I obtained 9 specimens with regenerated arms.

The regenerates so obtained do not, however, give a final solution of the problem discussed above, even if they give certain indications. The specimen obtained in 1918 had its anterior ray amputated. The regenerate may be written: —

$$\mathrm{R\ I\ 1{-}2_{1}}\begin{cases}\mathrm{Br_{1}}\ \ 1\,2\,3+4\,5\,6\,7\,8\,(9)\\ \mathrm{Br_{1}}\ \ 1\,2\,3\,4\,5\,6\,7\end{cases}$$

As will be seen the development of the right arm is the weaker (L. 1·2 mm.); that of the left arm is somewhat stronger (L. 1·5 mm.).

An opposite result is, however, shown by one of the 9 regenerates obtained in 1923. Here too it is the anterior radius that is re-formed. The left arm is distinctly shorter (L. 1·4 mm.) and has 10 segments, while the right arm is longer (L. 1·6 mm.), with 11 segments. No pinnules are here developed yet. Four other specimens showed no, or an almost imperceptible, difference in the length of the arms. The first of these had both to the right and to the left after a re-formed I Ax (in the right posterior radius) 3 Br-segments. The other three (two with the regenerate in the anterior, and one with the regenerate in the left anterior radius) had almost exactly equal arms with 15 to 20 Brr supplied with 2 to 4 pairs of minute pinnules distally. About 12 proximal Br-segments lack pinnules (though sometimes there are rudiments of P_1 and P_a) as in the young. Of the 4 remaining regenerates 3 had only 3 to 4 regenerated segments developed — 2 specimens with the regenerate in the left anterior, and one with the regenerate in the anterior radius. A minute ramification (1 segment) appeared in one case to the right, and in one case to the left. Finally, the last specimen, with about 11 Brr (in the left anterior radius; L. = 2·5 mm.) had a simple arm with the point bent to the left (cf. also figg. 6, 7). The arm formula may be written: —

$$\mathrm{R\ I\ 1{-}2_{1}\,3_{1}\,4_{1}\,5_{1}\,6_{1}\,7_{1}\,8_{1}\ldots}$$

To judge by our slight knowledge of simple arms in *Antedon,* the signs seem to indicate that we have here the same variable tendency as in *Thaumatocrinus.*

F. **Resumé.**

We may sum up what has been said above concerning the relations between arms and pinnules at the first arm-ramification as follows. If the first ramification is suppressed this process occurs differently in different families, but with a certain regularity for more closely related forms. Usually it can then be demonstrated how the tendency to suppression affects predominantly the right or the left ray, which becomes a pinnule or disappears altogether. If the arm is defective in its pinnulation, the first pinnule, and, more distally, the first arm-ramification, appear as a rule on the same side of the arm as that on which the suppressed first pinnule would have been according to what the reconstruction shows.

The family *Hyocrinidae* has usually both the suppressed and the first developed pinnule, and in *Calamocrinus* the first arm-ramification, to the left.

Among the Pentacrinids, *Metacrinus* had both the first pinnule and the first arm-ramification to the right.

The *Phrynocrinidae* provided too little material to judge the position of the first pinnule.

The family *Bathycrinidae* could be divided into two natural groups. To the one group belonged *Rhizocrinus,* which had its first developed pinnule to the right on Br 8, whereas the suppressed first pinnule was to the left on Br 2. This type was the only exception to the rule, formulated above, that the first pinnule appears on the same side of the arm as the suppressed first pinnule. On the other hand, the genus *Bythocrinus,* which belonged to the second group of the family of *Bathycrinidae,* had its suppressed first pinnule usually to the right.

Among the Comatulids, *Eudiocrinus (Zygometridae)* had P_1 (P_C) to the left. A similar tendency when arms were suppressed seemed also to show itself in a few examples of *Comasteridae* and *Uintacrinidae. Pentametrocrinus* and *Atopocrinus* showed an opposite tendency, P_1 usually appearing to the right. In some young of certain *Thalassometridae* the right arms were often for a time more weakly developed. In the genus *Thaumatocrinus* the position of P_1 was variable; and this was also the case in a few specimens with simple arm-rays of the genus *Antedon.* The regenerates pointed in the same direction.

A connexion, in the sense that the families that have their first pinnule developed in the same way are more closely related, cannot be assumed so long as there are no further facts forthcoming to support such a supposition. The *Thalassometridae* and certain *Macrophreata* do, however, coincide in a number of characteristics (cf. the chapter on The Phylogeny of the Comatulids, below). It is probable that they are rather closely related. Possibly also *Thaumatocrinus* is more closely related to the *Antedoninae* than to *Pentametrocrinus* (cf. below, Chap. 4).

At least the majority of the Comatulids have presumably not developed from forms with simple rays. It may be supposed that forms with simple arms arose in different Comatulid families at different times, and are thus only parallel types. The fact that in certain *Zygometridae (Comasteridae* and *Uintacrinidae)* it is the left, and in certain *Macrophreata* (and *Thalassometridae*) the right arm-ramification that is developed more weakly or suppressed seems to me, however, to support the conjectural supposition of Kirk (1912) that the Comatulids are of polyphyletic origin. In the light of the facts which I have brought forward in the chapter on The Phylogeny of the Comatulids in support of a similar supposition, this idea also seems to me to gain in probability.

VI. **On the reversibility of development.**

Let us look back at what has been said and draw the resulting conclusions.

Pinnulate forms have developed phylogenetically out of non-pinnulate types with rich arm-ramification. The holotomic recent type is descended from the metatomic. Pinnules are thus simplified armlets or ramiculi. That the tendency to arm-ramification is in all cases present latently is shown by the fact that pinnules in certain cases abandon their character of small unramified arms and grow into complete arms with pinnules (pp. 20 ff.). We can most easily explain the appearance of pinnules by assuming the occurence of obstructive factors, at whose removal the pinnule again develops into a ramified arm.[1] Moreover from this point of view the appearance of axillaries with 2 pinnules (p. 11) and of case of abnormal pinnulation otherwise difficult to explain (p. 18) are easily accounted for as examples of two-sided and reversed obstruction respectively. In *Metacrinus* also obstruction (of a temporary nature) may be said to occur, retarding the development of the inner arms so that they remain in the form of pinnules for a fairly long time.

In 1893, on the basis of his experiences, Dollo laid down the law of the irreversibility of development, which was afterwards formulated by Abel as follows: an aborted organ never recovers its former strength, and an organ that has disappeared never reappears (at least not devel-

---

[1] In order to avoid misunderstanding I wish to add my opinion that in that case the phylogenetic development has presumably passed through a great number of obstructive mutations.

oped in the same way). Broadly speaking this rule is certainly correct; but it is also clear that the facts that I have recorded and the conclusions to which they led suggest that we can find exceptions to DOLLO's law. From the point of view of heredity it may be maintained that DOLLO's law is valid if the tendency to an organ has really disappeared; in that case a return to the original type would be out of the question. When a return really appears this may be interpreted as the removal of a factor of obstruction. This idea might perhaps be considered from the palaeontological standpoint as rather perilous, but in reality it is not. As a matter of fact such reversibility occurs presumably very seldom in nature. The reason for this would seem to be that the type of organization reached is the one which is most suitable from the point of view of selection and structure and most economical; and it has often been reached in a round-about way by an infinity of adaptations.

That in certain cases the conditions necessary for "Rückschläge" really occur is shown, however, by the specimen with hypertrophied pinnules. The state of affairs might be pictured thus hypothetically. In any collection of some thousands of Comatulids there are always a number with one or other of their pinnules replaced by a more or less ramified arm — e. g. in 270 specimens of *Antedon petasus* which I got at a single haul off the Kristineberg zoological station at Flatholmen, 3 specimens had abnormal ramification. Assuming that these variations were of any advantage from the point of view of selection, and provided that they were inheritable, the old character would reappear normally in all specimens after some few generations.

We seem actually to have a good example of a reversion of this kind in the phylogeny of the Comatulids. In the chapter on The Phylogeny of the Comatulids I have discussed among other things the reason for the appearance in the Comatulids of a gap in the pinnulation. The results at which I arrive there may be briefly summarized as follows. At one time, towards the end of the palaeozoic period, the proximal pinnules were suppressed by the disk which swelled up between the arms. They reappeared when the disk collapsed again. But we still have a relic of this development in the gap that appears in the pinnulation of young Comatulids, though in most full-grown forms it is filled in by the subsequent development of the proximal pinnules.

CHAPTER II.

The articulations of the arm-joints in the Crinoids.

I. History.

JOHANNES MÜLLER 1843 introduced the term syzygy as a designation for expressing the sutural connection between the arm joints in a Crinoid in order to differentiate this connection from the mobile muscular articulation. The term syzygy was adopted by the scientists following after him, such as both the CARPENTERS, WYV. THOMSON, PERRIER, etc., but was often used not only in its original meaning but also to denote the joints connected by syzygy or even the intervals between two syzygies (POURTALES 1867, p. 111). BATHER (1896) pointed out this very clearly and logically and the term was again restricted to its original significance. According to his opinion (p. 60) syzygial development is a specialization of the usual articulation, taking place gradually during paleontology, more common among younger than older forms. BATHER took a long step forward, when he asserted that the pair of ossicles connected by syzygy should be considered as two separate ossicles and not be reckoned as a unity, where the hypozygal had lost its individuality (cf. P. H. CARPENTER 1884). This idea was followed up and explained still further in MINCKERT's work (1905).

In 1908(d) A. H. CLARK drew up a clear and perspicuous grouping of the articulations of the arms in recent Crinoids. These were divided as muscular and non-muscular; in the former group straight and oblique articulations were distinguished, and in the latter synarthries and syzygies. To show the mutual correspondence of the terms used by P. H. CARPENTER, MINCKERT and A. H. CLARK I give the tabular grouping found below:

CARPENTER	MINCKERT[2] Do. REICHENSPERGER 1912, p. 19	A. H. CLARK
Muscular articulation[1]	Synartrie	Straight muscular articulation
		Oblique » »
Bifascial and trifascial articulation		Synarthry
Syzygy	Syzygie	Syzygy

In the discussion following it is of importance that we should know CLARK's view; I give therefore a short account of certain morphological facts and the ideas which CLARK connects with them.

The muscular articulations are, as the name shows, always provided with muscles, and nearly always bear a pinnule plus an arm or a double arm; the non-muscular lack muscles and never bear a pinnule or double arm. The former therefore exercise some influence on the pinnulation, the latter do not do so.

In the straight muscular articulations the transverse ridge and the dorso-ventral axis of the joint-face (= the grove or ridge that runs from the nerve-lumen between the interarticular ligaments and the muscular fossæ towards the ventral side) meet at a right angle, in the oblique they cross at an oblique angle. The straight muscular articulations (according to CLARK 1908 d) never appear after a last axillary and are restricted to the articulations between R and I Br 1 and to the articulations between the axillaries and the primi-postaxillar ossicles. (Also often between the second and third ossicles where there are 4 components in the division-series.) The oblique articulations appear from the second articulation after the last straight muscular connection, and immediately after the last synarthry, and distally of this in all the muscular arm-connections (they may in exceptional cases appear in the muscular axillary articulations).

Synarthries are distinguished by two ligament pits, separated by a ridge in the dorso-ventral axis of the joint, syzygies usually have the joint-face of radiating calcareous ridges divided into several portions which radiate from the central canal towards the periphery of the joint. Synarthries appear, according to CLARK, only on the distal joint-ends of ossicles, where the proximal part bears a straight muscular articulation. They may be replaced by more or less well-developed syzygies, which are then called by CLARK pseudo-syzygies. The most distal synarthry is always followed by an oblique articulation.

CLARK draws from the above the following conclusion: Two ossicles: "the joints on either side of the last synarthry", are sharply distin-

---

[1] CARPENTER (1884, p. 11) remarks that the muscular articulation between R and I Br 1 is symmetrical.

[2] MINCKERT (p. 168) remarks that synarthries sometimes appear with muscles, sometimes without them.

guished from all the others. These ossicles are called Z_1 and Z_2. Z_1 has a proximal joint-face furnished with a straight muscular articulation, the distal joint-face is united to Z_2's proximal one by synarthry. Z_2's distal end has an oblique articulation. Z_1 and Z_2 are considered by CLARK as "homologous" among all (recent) Crinoids. He discusses and draws representatives for *Pentametrocrinidae*[1], *Zygometridae (Eudiocrinus, Zygometra, Catoptometra), Atelecrinidae, Antedonidae, Tropiometridae, Thalassometridae, Himerometridae, Comasteridae (Comaster, Comatula, Capillaster), Uintacrinus, Pentacrinidae (Diplocrinus, Isocrinus, Cenocrinus, Hypalocrinus, Metacrinus).*

Two different types are demonstratrated. (1) One, where a number of ossicles are found between R and Z_1 and no arm-division is present beyond Z_2: this is the interpolated type; (2) another, where Z_1 comes immediately after I Ax and the further division takes place outside Z_2: this is the extraneous type *(Capillaster, Nemaster).* When both these types appear at the same time in the same specimen (cf. CLARK 1908 e) we get the compound arm-type *(Comatella).*

It is evident that this reasoning can only be correct according to the measure in which we can really draw a sharp dividing line between straight and oblique muscular articulation. If this is not possible and the boundaries between them are diffuse, it becomes uncertain which ossicles may be assumed as corresponding to Z_1 and Z_2.

Some examples. The arms of *Eudiocrinus* may be denoted:

$$\mathrm{R\ I}\ 1+2\ \mathrm{Br}\ 1-2\ 3+4\ 5\ 6\ 7\ldots$$

CLARK considers here that Br 1–2 corresponds to Z_1 and Z_2, for the proximal end of Br 1 would have straight muscular articulation and the distal end of Br 2 oblique (cf. below p. 46). Now, if the boundary between these two types of muscular articulation were indistinct in the present case, it would be quite as easy to consider I Br 1 + 2 or Br 3 + 4 as corresponding to Z_1 and Z_2 (observe that synarthries could be replaced by syzygies).

Another example. *Comanthus* and *Himerometra* may generally be denoted:

$$\mathrm{I}\ 1-2\begin{cases}\mathrm{II}\ 1-2\ 3+4\begin{cases}\mathrm{III}\ 1-2\ 3+4\begin{cases}\mathrm{Br}\ 1-2\ 3+4\ldots\\ \mathrm{Br}\ 1-2\ 3+4\ldots\end{cases}\\ \mathrm{III}\ 1-2\ 3+4\begin{cases}\\ \end{cases}\end{cases}\\ \mathrm{II}\ 1-2\ 3+4\end{cases}$$

Here CLARK considers that Z_1 and Z_2 are corresponded to by Br 1—2. We cannot accept this unless we presume that the articulations

---

[1] The names when necessary are altered to the modern nomenclature.

between II Br 2 and 3, between III Br 2 and 3 and between the axillaries and primi-postaxillar ossicles are straight. If they are not. Z_1 and Z_2 should be assigned to I 1—2 and the type becomes extraneous and not as CLARK asserts interpolated.

Capillaster and *Nemaster* may be denoted:

$$\mathrm{I}\ 1-2\begin{cases}\mathrm{II}\ 1-2\ 3+4\begin{cases}\mathrm{III}\ 1\ 2+3\begin{cases}\mathrm{Br}\ 1\ 2+3\ldots\\ \mathrm{Br}\end{cases}\\ \mathrm{III}\end{cases}\\ \mathrm{II}\end{cases}$$

According to CLARK the type is extraneous here, for he considers that Br 1 "can not (p. 123) be Z_1 for it bears a (oblique) muscular articulation instead of a non-muscular articulation distally"[1]. He considers that Z_1 and Z_2 correspond to II Br 1—2 for these, in contradiction to those of the previous example, should be followed by an oblique articulation between II Br 2 and 3. The same type recurs (p. 126) in some *Isocrini* (*Cenocrinus* WYV. THOMS. and *Isocrinus* L. AG.). *Metacrinus* shows a still more exclusive extraneous type, in which Z_1 and Z_2 follow directly after R.

CLARK's reasoning (p. 125) on *Uintacrinus*, whose formula is as follows:

$$\mathrm{I}\ 1+2\begin{cases}\mathrm{Br}\ 1+2\ 3+4\ 5\ 6\ 7\ldots\\ \mathrm{Br}\ 1+2\ 3+4\ 5\ 6\ 7\ldots\end{cases}$$

seems to me rather questionable. "In the Comatulids the pinnule on Z_1 is almost universally different from that on all succeeding brachials, but resembles those on all interpolated repetitions of Z_2". Br 3 + 4 should here correspond to Z_1 and Z_2 because "the second pinnule resembles the first"; "hence, the conclusion is reached that the joint which bears the second pinnule is homologous with that which bears the first". On the same grounds we might consider that Br 3 + 4 should correspond to Z_1 and Z_2 in e. g. *Tropiometra*, *Heliometra*, *Iridometra*, and certain Comasterids.

In 1909 a CLARK unfolds his views on the nature of the non-muscular articulations. His proposition (p. 581): "that proximal to the first oblique muscular articulation only straight muscular articulations and synarthries are found, while distal to the first oblique muscular

---

[1] Here the author takes the view that Z_1 and Z_2 must be found in all Crinoids and must appear according to the definition he has given. One might, in the present case, imagine that the *Capillaster*-type proceeded from the *Comanthus*-type demonstrated above, by the anchylosis of the first two post-axillar ossicles. Another explanation given by CLARK is discussed later on (cf. below).

articulation occur only oblique muscular articulations and syzygies", will be elucidated later on and does not hold good regarding the Comasterid, the Zygometrid and the Himerometrid types. His view of synarthry as a coalescent production of 2 straight muscular articulations, syzygy as a pair of coalesced oblique muscular articulations, where in both cases the joints have revolved through an angle of 90°, can scarcely be considered correct (p. 584 "the muscles and interarticular ligaments, being recessive when compared with the dominant dorsal ligament, disappear"). No trace of such a fusion can be found either in the phylogeny or the ontogeny of the Comatulids. CLARK's reasoning stated above rests partly upon the assumption of a fundamental difference between the straight and oblique muscular articulation, an assumption which, as will be shown later, is incorrect, and partly on the fact that two oblique muscular articulations following each other have the transverse ridges placed at an angle of about 90° to each other. Regarding the last-mentioned he says (p. 580): "In reality of course the alternation of the pinnules is the fundamental cause of the alternation in the direction of the transverse ridge, but from the absence of pinnules on oblique muscular articulations in certain recent types it is more convenient to speak of it as if the reverse were the case". Nor can I accept his proof that the monoserial arms of the recent Crinoids have been derived from biserial ones (cf. p. 585) — it must be observed that the young of Comatulids have no triangular or obliquely wedge-shaped brachials in the proximal third of the arms; their brachials are, on the contrary, nearly rectangular. Even in fully grown Comatulids usually the most proximal brachials are less pronouncedly triangular than the more distal ones; this, however, is a secondary phenomenon (cf. below).

In the first part of his monograph on the Comatulids (1915 c) CLARK defines (p. 78) the new term cryptosynarthy as being a synarthy with almost smooth joint-faces, where a slight remnant of the synarthrial median-ridge is visible (cf. also 1922, p. 177). This occurs in certain species of the genus *Comatula*.

In his big work of 1922, the continuation of the preceding, CLARK expresses somewhat modified views on the articulations. A tabular statement of his conception of the different types of connection is given on page 116 and is reproduced below.

(1) Simple arm-structure where Z_1 and Z_2[1] follow immediately after R and the arm is a simple one *(Atopocrinus, Pentametrocrinidae).*

(2) Interpolated arm-division with one or several (simple or multiple arm-division) interpolated joint-pairs between R and Z_1 and Z_2.

---

[1] The ossicles are called here the first brachial pair (cf. figg. 140—174, »homologies of ossicles»).

When the division series consists of 2 ossicles the type is called primary, when there are 4, secondary (most of the Comatulids).

Defective interpolated division series are found in *Capillaster, Nemaster,* where III and the following division-series have only 3 components.

Compound interpolated type is found in *Comatella, Neocomatella, Palaeocomatella* (the outer arms with multiple arm-division, the inner "lack the first brachial pair").

(3) Simple extraneous division is found in *Metacrinus,* where a number of division series appear distally to Z_1 and Z_2 which come directly after R.

(4) In *Isocrinus* and *Pentacrinus,* which have an interpolated series, followed by extraneous series, the division-series are reckoned as heterotypic.

Contrary to his views in 1908, Br 1 in *Capillaster* and *Nemaster* is thus reckoned as corresponding to Z_2 (the original Br 1 is considered as being suppressed), and the type therefore becomes interpolated. His conception of the division-series of 4 ossicles has also been changed a little, as he now considers (p. 108) that they are "reduplications of the first four brachials"; division-series of 2 should correspond to the first two brachials. He does not consider any longer (p. 179) that the articulations between the axillaries and the primi-postaxillaries are really straight articulations, but says they are "commonly intermediate" between the straight and the oblique. "The only straight articulation is that between the R and the I Br I. The other muscular articulations are all of the oblique type and always double."[1] He also expresses himself rather more vaguely on the difference between synarthries and syzygies (p. 174), "there is no fundamental difference between synarthries and syzygies . . . All the postradial non-muscular articulations are really homologous". Rather higher up on the same page he considers all syzygial pairs as: "strictly homologous with the first brachial pairs of the arms" (as with the pairs of ossicles in the division series, "which have remained unmodified during the course of the development"). In spite of this he still considers (p. 103), of "The first 2 ossicles of the free individual arms of the Comatulids . . . that this pair of ossicles is strictly homologous throughout the whole group and furthermore . . . very readily identifiable".

In order to explain this interpolation phenomenon, which has arisen out of his method of argument, he elucidates the matter as follows: Br 1 and Br 2 (Z_1 and Z_2) are stated (p. 103) to have "an invariable fixed position on the border of the disk" and (p. 84) "the periphery of the disk always reaches the level of the second brachials of the free

---

[1] That is, bear an arm and pinnule, or a double arm on them.

undivided arms".[1] Therefore (p. 125) "the presence of additional division series is correlated with extreme atrophy of the calyx plates" (i. e. IBB, BB, and RR) "and the consequent relative increase in size of the visceral mass". . . . "With the appearance (p. 126) of a gap between the radial and the arm base as a result of the shrinking of the calyx the appearance of V" (Br) "is necessitated and subsequently also of IV, III, II and I". . . . (Cf. also p. 196.)

Chiefly there are two, as I consider, incorrect points of view upon which the reasoning sketched above is founded, and which often lead, as a result of the incorrect premises, to strange conclusions.

The first is CLARK's conception of what is meant by homology, the other his ideas on the biogenetical law.

At present one calls those parts of different organisms homologous, where it is possible to trace the same tendency, and which therefore may be considered as having the same descent. CLARK uses the expression partly in this sense — generally, however, one might replace his term either by homodynamic or analogous (cf. the quotations above; cf. also p. 176: "With the brachial synarthries the articulations in the column of the larval Comatulids, . . . are in all ways homologous"). Instead of saying that certain pairs of ossicles are homologous, it would have been more correct to say that they are differentiated in the same manner, and, from that point of view, interpret the proofs of "homology" which appear on p. 103 (1922).

He makes no difference either between palingenetic and coenogenetic factors during ontogeny. He therefore interprets all the characteristics from earlier stages of development as being phylogenetically older. The arm bases, for example, being ontogenetically older are considered to represent stages of greater phylogenetic age, and therefore present a number of primitive characteristics (p. 110). "In none of the Comatulids are the I Br series, the oldest and presumably the most primitive of the division series, of more than two ossicles normally." This idea appears again in his reasoning on the more distal division series (pp. 108—109): "Divisions series of 4 (3 + 4) . . . . appear themselves to represent a high state of brachial specialization, and to be a considerable phylogenetic advance over the division series composed of two

---

[1] This is, however, contradicted by the information given on p. 107 where the following statement appears: »in *Thaumatocrinus, Pentametrocrinus* and to a lesser degree *Atopocrinus*, the ventral disk runs for a considerable distance up the arms». In reality the disk reaches among the Comatulids, as I have observed, e. g. in *Clarkometra elegans*, to Br 3+4, in *Tropiometra afra macrodiscus* and *Antedon petasus* to Br 4 or 5, in *Leptonemaster venustus* to Br 5, in *Promachocrinus* to Br 6, in *Notocrinus* to Br 7, in *Pentametrocrinus diomedeæ* to Br (5—)8, in *Amphimetra crenulata* (II Br 4) and *Heterometra jaquinoti* to Br 6, in *Heliometra* and *Anthometra* to Br 7—8 (in *Atopocrinus* to Br 9, Siboga Exp. 42 B, p. 264), in *Comanthus pinguis* only to III Br 2 or 4 and in *Comaster novae-guineae* only to II Br 3 or 4.

ossicles only." Syzygies are considered as being more specialized than synarthries, which "have remained unmodified during the course of the development of the immensely elongated and highly specialized arm" (p. 174). This leads him to the conclusion that, because the outermost arm of an axillary bears more specialized P_1 than the inner arms, the outer divisions themselves are more specialized, i. e. of later phylogenetic origin (pp. 90, 124, 194; cf. also 1909 a, p. 585).

I shall now pass on to give an account of my own views respecting these questions as they have developed during my examination of the material at my disposition. The muscular articulations will be treated first, and afterwards the non-muscular.

II. Muscular articulations of the arms.

In order to estimate the worth of CLARK's reasoning, it is of great importance, as was emphasized above, to make sure of the extent to which the straight and oblique muscular articulations differ from each other. In his last big work (1922) CLARK no longer entertains the extreme opinions regarding straight and oblique muscular articulations which first led him to urge his theory of Z_1 and Z_2. None the less, he, as the above quotation shows, still uses when reasoning the same conclusions at which he arrived in 1908 by the use of the sharply defined distinctions he employed then.

When examining the obliqueness of a joint one has to distinguish two different kinds of obliquity. If one observes an arm from the dorsal side one notices at once that the lines that mark the connections between each joint do not run at right angles to the arm's longitudinal direction, but more or less in an oblique direction transversely over the arm. This I call exterior obliqueness. If one separates the arm-joints from each other and observes them from the short end, one finds that the dorso-ventral crista and the transverse ridge do not usually meet at a right angle, and that the corresponding muscles and inter-articular ligaments on each side of the dorso-ventral axis are not of the same size: this is interior obliqueness.

A. Obliquity of the articular connections, or exterior obliqueness.

A straight articulation seen from the outside is, as A. H. CLARK (1908 d) remarks very rightly, characterized by two points of contact situated at the same distance from the dorsal median line; an oblique articulation, on the contrary, has a (distinct) dorso-lateral point of contact and a (less distinct) ventro-lateral one. This difference is, however, obvious only in the types where the course of the articular lines is fairly oblique, while in those Comatulids where the articular lines run nearly at right angles over the dorsal side of the arms it is indistinct or not visible at all. As this characteristic thus stands in a certain relation to the exterior obliqueness of the arm-joint I have considered there would be a certain amount of interest in discovering the degree of obliqueness in the course of the articular lines on the dorsal side of the arms of the Comatulids (see table).

Species	Length of arms mm.	Number of segments per cm.				Longest side of the Br: the br.	Angle of the distal articulations with the longitudinal axis of the arm.
		Proximal part of the arm.	br of the segments mm.	Distal part of the arm.	br of the segments mm.		
Comissia parvula	45	(15)17[1]	1·1	(12)15	0·6	$\frac{1}{1}$–$\frac{3}{2}$	66—72°
» peregrina magnifica .	160	(9)12	2·5	(12)16	1·2	$\frac{1}{2}$—$\frac{2}{3}$	69—77
Comatula solaris	100+	(9)10	3·5	(13)15	2·0	$\frac{1}{2}$	72–76
» pectinata	70	—	—	—	—	$\frac{2}{3}$	67–79
Capillaster sentosa	80	(11)11	2·4	(13)15	1·7	$\frac{1}{2}$	80—89
Comaster delicata grandis . . .	105	(7)8	3·0	(11)14	1·3	$\frac{1}{2}$—$\frac{2}{3}$	73—82
Comanthus japonica	120	(9)10	2·4	(18)22	1·6	$\frac{1}{5}$—$\frac{1}{4}$	87—90
Zygometra elegans	105	(16)16	1·7	(22)24	1·3	$\frac{1}{4}$	82—90
Eudiocrinus loveni	45	—	1·4	(11)14-15	0·8	$\frac{1}{1}$—$\frac{6}{5}$	75—78
Heterometra jaquinoti	120	(11)13	2·4	(25)28	1·5	$\frac{1}{5}$	86—90
Himerometra magnipinna . . .	105	(13)13	1·7	(22)23	0·8	$\frac{1}{4}$—$\frac{1}{3}$	81—89
Stephanometra spicata	130	(11)12	1·5	(15)16-17	1·1	$\frac{1}{2}$	78—87
Liparometra grandis	120	(13)14	2·0	(16)18	1·2	$\frac{1}{4}$—$\frac{1}{3}$	82—89
Cenometra bella	90	—	—	(17)20	0·8	$\frac{2}{3}$—$\frac{3}{4}$	78—82
Cyllometra disciformis	90	(14)17	1·2	(15)20	0·7	$\frac{1}{1}$—$\frac{4}{3}$	72—82
Tropiometra encrinus	105	(9)11	2·2	(14)16	1·0	$\frac{3}{4}$	80—85
Pectinometra flavopurpurea . .	65	(12)13	1·0	(15)17	0·7	$\frac{5}{6}$—$\frac{1}{1}$	64—72
Asterometra anthus	85	(12)14	1·6	(15)18	1·1	$\frac{1}{2}$—$\frac{2}{3}$	69—77
Diodontometra bocki	60	(11)12	1·3	(14)15	0·7	($\frac{3}{4}$—)$\frac{1}{1}$	69—75
Antedon petasus	75	(12)15	1·2	(14)17	1·0	$\frac{1}{1}$	64–75
Heliometra eschrichti	200	(7)9	3·2	(12)15	1·5	$\frac{1}{2}$—$\frac{2}{3}$	68—78
Poliometra prolixa	±100	(9)12	1·6	(11)14	1·0	$\frac{1}{1}$	66—74
Pentamentrocrinus diomedeae .	90	(10)13	0·6	(11)14	0·5	$\frac{3}{2}$—$\frac{2}{1}$	59—66

---

[1] The figures put in brackets show the number of segments when the syzygial pairs are counted as units.

This investigation has shown that distinctly oblique articulations, i. e. articulations where the articular line makes an angle with the longitudinal axis of the arm of 59° to 79° (average 71°) are found in *Comasteridae* (*Comasterinae* and *Capillaster* excluded), *Thalassometridae, Charitometridae*, *Calometridae* and *Macrophreata,* but that, on the contrary, indistinctly acute, to right angles, of 72° to 90° (average about 83°) are found in *Comasterinae*, *Capillaster*, *Zygometridae, Himerometridae, Mariametridae, Stephanometridae, Tropiometridae*, and *Colobometridae.*

From the table it can also be seen that the number of joints per cm., and the relative length of them has a certain connection with the thickness of the arms, i. e. generally with the size of the animal. In the majority of cases, however, the greatest number of joints per cm. and the shortest segments without comparison are found among the latter group (i. e. those with nearly right angles).

The numbers referring to the angles given in the table above are taken from the middle or distal parts of the arms. Below I give some figures of the size of the angles in the arms' proximal parts. The figures here, as above, are taken from the distal border of the ossicle and refer to the angles of the pinnular side. Figures omitted denote hypozygals.

Comanthus japonica: II 2: 80°, III 2: 78, (Br 1: 110), 2: 87, 4: 84, 5: 90, 6: 84, 7: 80, 8: 78, 9: 76, 10: 78, 11: 78, after Br 23 straighter angles up to 85 or 90°.

Eudiocrinus loveni: I 2: 89°, Br 2: 88, 4: 85, 5: 83, 6: 74, 7: 69, 8: 60, 10: 69, 11: 64, 13: 66°.

Heterometra jaquinoti: Br 2: 86°, 4: 92, 5: 96, 6: 100, 7: 101, 8: 95, 10: 90, 11: 87, 12: 84, 13: 83, 14: 88, then (81—)86—90°.

Pontiometra andersoni: Br 2: 88°, 4; 91, 5: 92, 6: 94, 7: 93, 8: 93, 9: 90, 10: 89, 11: 85, 12: 78, 13: 74, 14: 80. Distal segments 80—90°.

Pectinometra flavopurpurea: Br 2: 80°, 4: 80, 5: 80, 6: 78, 7: 78, 8: 76, 9: 76, 10: 71, 11: 72, 12: 73, 14: 72°.

Asterometra anthus: (Br 1: ± 100°), 2: 84, 4: 87, 5: 92, 6: 95, 7: 87, 8: 84, 9: 77, 10: 69, 12: 71, 13: 70°.

Diodontometra bocki: Br 2: 83°, 4: 86, 5: 87, 6: 93, 7: 96, 8: 97, 9: 93, 10: 91, 11: 90, 12: 81, 13: 78, 14: 73, 15: 75, 16: 73°.

Clarkometra elegans: Br 2: 72°, 4: 92, 5: 94, 6: 90, 7: 83°.

Antedon petasus: (Br 1: 103°), 2: 68, 4: 87, 5: 105, 6: 106, 7: 83, 8: 60, 10: 69, 11: 65, 12: 64, 13: 62, 15: 65, then about 64°.

Heliometra eschrichti: Br 2: 67°, 4: 87, 5: 95, 6: 105, 7: 106, 8: 108, 10: 108, 11: 96, 12: 87, 13: 75, 15: 82, 16: 70, 17: 74, then about 70°.

Hypalometra defecta: Br 2: 78°, 4: 96, 5: 100, 6: 97, 7: 86, 8: 80, 10: 62°.

Thaumatocrinus jungerseni: Br 2: 98°, 3: 101, 5: 93, 6: 90, 7: 86, 8: 82, 9: 77, 11: 62, 12: 63, 13: 58, 14: 63, 15: 61, 17: 60°.

Pentametrocrinus diomedeae: Br 2: 98°, 3: 98, 5: 88, 6: 84, 7: 80, 8: 78, 10: 60, 11: 66, 12: 53°. In a larger specimen Br 2: 98°, 3: 96, 5: 92, 6: 88°.

Atelecrinus helgae: Br 2: 64°, 4: 67, 5: 72, 6: 67°.

Metacrinus nobilis tenuis: I 2: 82°, 3: 90, II 1: 90, 2: 82, 4: 80, 5: 88, 6: 84, III 1: 98, 2: 91, 4: 85, 5–12 about 90, IV 1: 102, 2: 99, 4—10: ±90, Br 1: 93, 2: 98, 4 and the following ones ± 90°.

From the result of the above figures — they might have been completed with those from about 40 other specimens examined but not noted in figures, which point in the same direction — we learn the following: The first Br-pair after an axillary always has a relatively broad outer side and a narrower inner side. The distal articular line of the Br-joint therefore makes a relatively large angle with the proximal. The arms which after the arm division would spread greatly apart are by this means brought nearer each other, which on account of room is of considerable importance. In reality the breadth of these ossicles' outer side is so much larger than that of the inner side, that the distal articular line of Br 2 slopes inwards. In *Metacrinus* the proximal and distal margins of the arm-joints, after the first or second post-axillar ossicle, are fairly parallel, but in the rest of the types examined a more or less pronounced obliqueness usually sets in sooner or later. In the Br-pair 3+4 this obliqueness is generally only slight — the greater breadth of the inner side in this Br-pair has nullified almost precisely the inward slope which was apparent on Br 2's distal margin. Br 4's distal margin is therefore very often nearly at a right angle to the longitudinal axis of the arm. Afterwards a greater or lesser number of joints usually follow, where the articular lines show a tendency to be more or less parallel, then the obliqueness increases again after Br 7—13 and reaches its maximum at Br 15 to 20. In the middle portion of the arms the obliqueness decreases, but it increases a little again in the distal parts.

B. The reversion phenomenon.

This exterior obliqueness manifests itself by the acute angle, formed by the articular line with the arm's longitudinal axis, facing now outwards and now inwards. The Br-joints are therefore broader, now on the inside and now on the outside. In usual cases the pinnule is fixed to the broader side of the Br-joint; this is always the case in the middle and distal parts of the arms. In the proximal parts of the arm, however, the peculiarity often arises that the opposite is found, i. e. the antipinnular side of the arm-joint is the broader — which I will call the reversion of the articulations (cf. above pp. 42—43, angles > 90°).

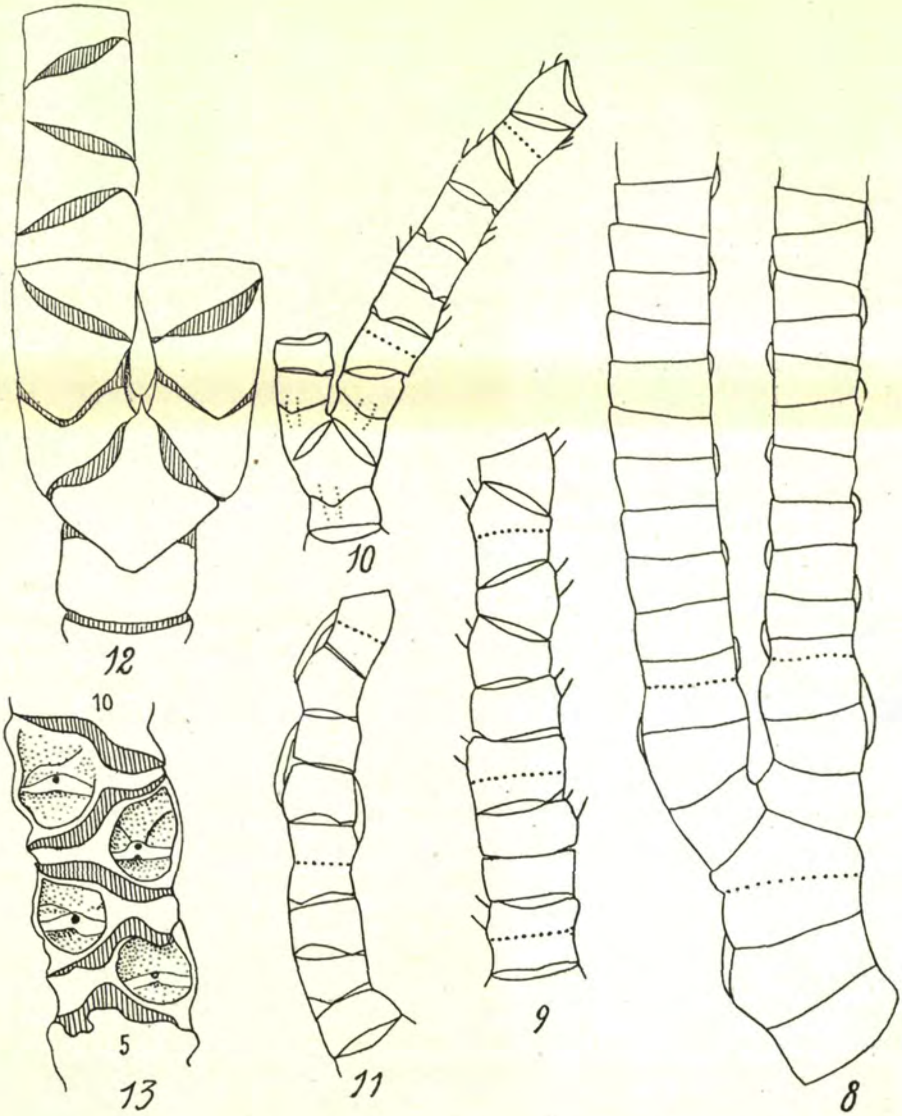
This is lacking or is very little developed in certain *Comastridae, Eudiocrinus,* (fig. 9), *Calometridae,* and *Atelecrinus* (fig. 12), where the pinnular Br-side is the longer along the whole arm. Reversion, on the contrary, is most clearly developed in *Antedonidae* and *Charitometridae.* The joints Br 2 and, usually, Br 4, on which P_1 and P_a are situated are more strongly developed on the pinnular side, but from Br 5 reversion appears in a variable number of segments, to be gradually effaced and followed in the middle part of the arm by the normal type.

The reversion is only slight in *Capillaster sentosa, Comanthus japonica, Tropiometra afra macrodiscus,* and *Pterometra trichopoda,* where Br 5 is only a trifle, sometimes not perceptibly, narrower on the pinnular side, and where Br 6 is already furnished with parallel articulations or has an obviously broader pinnular side. The same is the case in *Notocrinus virilis*, where Br 6 or 7 has a broader pinnular side, and in *Clarkometra elegans* (fig. 10) and *Stephanometra spicata,* where Br 7 or 8 is broader on the pinnular side. The reversion appears more distinctly in *Comaster delicata grandis,* where Br 7, in *Stenometra diadema, Cyllometra disciformis,* and *Himerometra magnipinna* (fig. 8), where Br 7 or 8, in *Zygometra elegans, Amphimetra crenulata,* and *Asterometra anthus,* where Br 7—9, and in *Liparometra grandis,* where Br 11 first shows a longer pinnular side. This phenomenon, however, appears most markedly in *Pentametrocrinus diomedae*[1] (fig. 11), where Br 4 + 5, in *Isometra vivipara* and *Hypalometra defecta,* where Br 8, in *Crossometra septentrionalis* and *Antedon petasus,* where Br 7—9, in *Diodontometra bocki*, where Br 10—12, in *Heliometra eschrichti* (fig. 44), where Br 12, and in *Promachocrinus kerguelensis* and *Monachometra* cf. *fragilis* (fig. 14), where Br 13 first has the pinnular side longer.

One might imagine that the slenderness of the pinnule-bases had something to do with this phenomenon, and this theory seems to be favoured by the Calometrids *Pectinometra flavopurpurea* and *Neometra multicolor,* furnished with very thick pinnule bases, having the pinnular side longer right from the most proximal parts of the arm (fig. 40). This is possibly the case with the family mentioned. The lack of reversion in *Comatula solaris, Comanthus parvicirra,* and *Atelecrinus* cannot, however, be explained in this way. The two former have, in fact, slender pinnules, the last-mentioned genus lacks pinnules entirely in the proximal parts of the arm. The explanation of this phenomenon cannot be given until after I have first treated interior obliqueness.

---

[1] The non-pinnulate pinnular side of Br 2 and 3 is shorter here than the antipinnular side.



Figg. 8—13. 8) *Himerometra magnipinna,* III Br and 2 arms, regenerated from Br 3, $^{8}/_{1}$. 9) *Eudiocrinus loveni,* An arm (I 1+2 etc.), $^{10}/_{1}$. 10) *Clarkometra elegans,* $^{16}/_{1}$. 11) *Pentametrocrinus diomedeae,* An arm (Br 1—2 etc.), $^{10}/_{1}$. 12) *Atelecrinus helgae,* $^{10}/_{1}$. 13) *Pectinometra flavopurpurea,* Brr 6—9 viewed from the ventral side, with the muscles removed, $^{16}/_{1}$.

C. Obliquity of the joint-faces, or interior obliqueness.

As we have seen above, Clark has distinguished between straight and oblique muscular articulations also when treating the joint faces. In his work of 1922 he considers that really straight muscular joint-faces are only found in the facets between R and I Br 1. These facets he has discussed in a very excellent and detailed manner in the work quoted, and I shall therefore in the following pages devote myself to the subsequent muscular articulations chiefly.

To verify the degree of obliqueness in the angle between the transverse ridge and the radial intermuscular fossa (= the dorso-ventral axis of the ossicle), I have measured the angles between them in ossicle-series, from the arm-bases to more distal parts of the arm. The figures I obtained are given below. The angle measured was always that of the antipinnular side. Unless otherwise stated the figures always concern the facet on the distal end of the ossicle. The ossicle-numbers omitted correspond to hypozygals or hypoarthrals (i. e. the ossicle situated immediately proximally to a syzygy or synarthry).

Comanthus japonica II Br 2: 75—76°, III Br 2: 68–72, Br 2: 60, 4: 52, 5: 47, 6: 57, 7: 58, 8: 83, 9: 87, 11: 85, 12: 85, 13: 86, 14: 89, 16: 87, 17: 87, 18: 82, 19: 86, 20: 86, 22: 81, 23: 82, 24: 81, 25: 83, 27: 78, 28: 82, 29: 76, 30: 80, 31: 81°. Distal Br-segments 60—75°.

Eudiocrinus indivisus I Br 2: 75°, Br 2: 64, 4: 54, 5: 56, 6: 47, 7: 60, 9: 69, 10: 78, 11: 80, 12: 82, 13: 86, 14: 87°. The arm regenerated from Br 10.

Pontiometra andersoni Br 2 (after a V Ax): 66–67°, (after a IV Ax 76–78), 4: 62–67, 5: 61, 6: 66, 7: 62, 8: 68, 9: 67, 10: 68, 11: 72, 12: 77, 13: 78, 14: 80, 15: 81, 16: 84. From another series, probably beginning with Br 9, the figures are: Br 9: 69, 10: 72, 11: 74, 12: 84, 13: 86, 14: 83, 15: 84, 16: 87, 17: 87, 18: 90, 19: 85, 20: 87°.

Pectinometra flavopurpurea Br 2: 86, 4: 72, 5: 80, 6: 63, 7: 72, 8: 78, 9: 75, 10: 88, 11: 85, 12: 90, 14: 90, 15: 97, 16: 91, 17: 90, 18: 93, 19: 90, 21: 92, 22: 91, 23: 86, 24: 86, 25: 87°.

Asterometra anthus Br 2: 81—85°, 4: 61, 5: 64, 6: 65, 7: 63, 8: 74, 10: 86, 11: 88, 12: 80, 13: 82°.

Clarkometra elegans Br 2: 79, 80, 80, 83, 84°, Br 4: 67, 69, 70, Br 5: 65, 6: 57—61, 7: 76, 8: 80, 10: 82°.

Antedon petasus Br 2: 71°, 4: 68, 5: 62, 6: 65, 7: —, 8: 71, 10: 79, 11: 81, 12: 82, 13: 85, 15: 86, 16: 87, 17: 86. Distally ± 80°.

Heliometra eschrichti Br 2: 71°, 4: 67, 5: 64, 6: 64, 7: 60, 8: 67, 10: 65, 11: 70, 12: 75, 13: 83, 15: 78, 16: 87, 17: 79, 19: 92, 20: 84, 21: 86, 23: 85, 24: 88, 25: 85, 27: 90, 28: 84, 29: 89, 31: 86, 32: 83, 33: 84, 34: 86, 36: 87. Distally 70–80°.

Thaumatocrinus jungerseni Br 2: 76°, 3: 72, 5: 66, 6: 64, 7: —, 8: 69, 10: 75, 11: —, 12: 74, 13: 85, 14: 80, 15: 83, 17: 86°.

Pentametrocrinus diomedeae Br 2: 62°, 3: 60, 5: 65, 6: 62, 7: 65, 8: 70, 10: 72, 11: 75, 12: 75, 13: 82°.

Atelecrinus helgae Br 2: 80, 83°, 4: 87, 5: 85, 6: 89°.

Ilycrinus carpenteri Br 2: 82°, 3: 86, 5: 89, 6: 90, 8: 90, 9: 89, 11: 92, 13: 99, 15: 90, 17: 92°. Pinnules from Br 11.

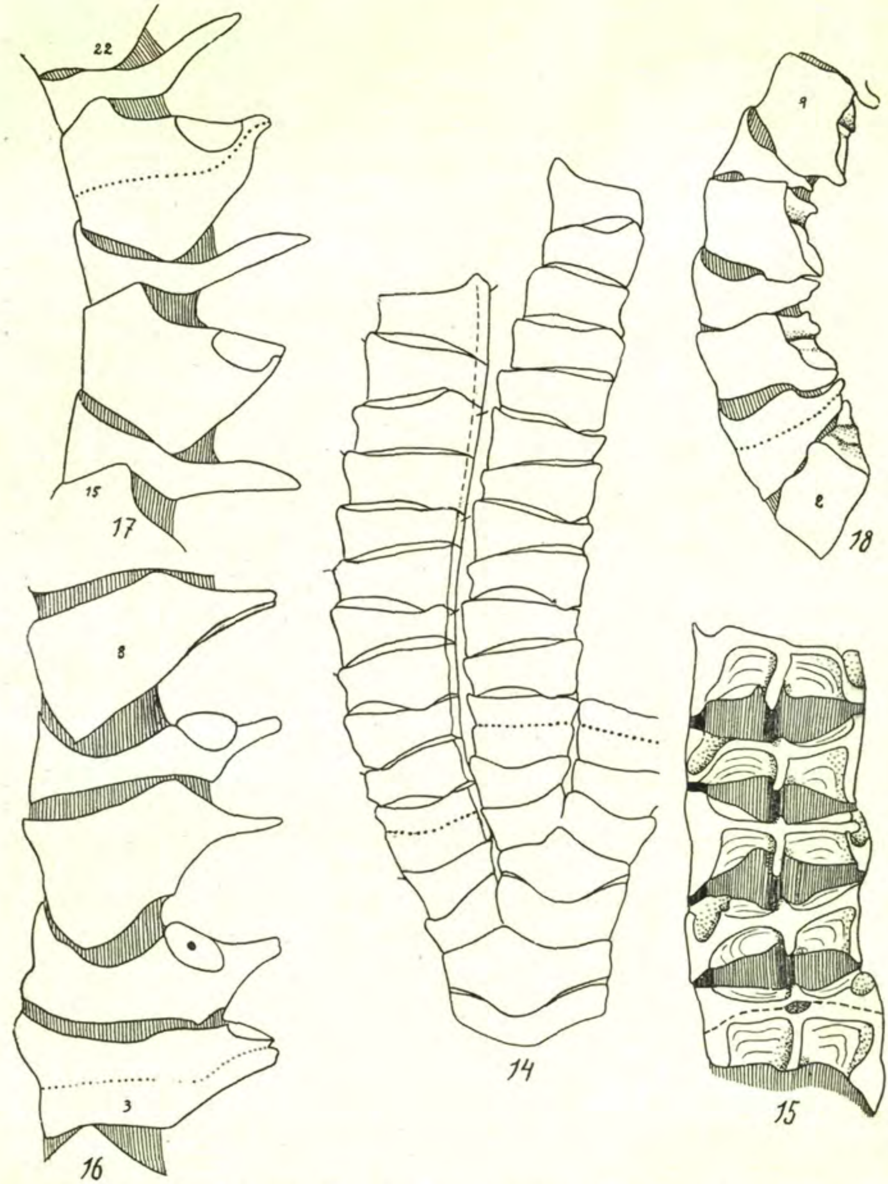
Rhizocrinus lofotensis Br 2: 90°, 4: 90, 6: 90, 8: 84, ± 12: 85°. Pinnules from Br 8.

Metacrinus nobilis tenuis I Br 2: 84°, 3: 75; II 1: 75, 2: 72, 4: 73, 5: 74, 6: 74; III 1: 69, 2: 77, 4: 74, 5: 74, 6: 70, 7: 71, 8: 72, 9: 72, 10: 79; IV 1: 71, 2: 75, 4: 72, 5: 69, 6: 70, 7: 64, 8: 69, 9: 69, 10: 76; Br 1: 75, 2: 73, 4: 80, 5: 72, 6: 73, 7: 69. Distally of this 72—75°.

We see from this that as a rule oblique muscular articulation is most strongly pronounced immediately after the axillaries, and that the more distal articulations afterwards become straighter, and then again, in the outer parts of the arm, somewhat more oblique. *Ilycrinus carpenteri* forms an exception to this, where the distal angle of the axillary (seen from the dorsal side) is very large (cf. below). Here the proximal joints, which also lack pinnules, are only slightly oblique, whether one observes them from the dorsal side or from the joint-face.

The oblique muscular articulation thus advances in usual cases — in the Comatulids practically without exception, judging from 20 specimens examined in addition to those given above without noting the figures, and pointing in the same direction — after the first Br-articulations in the proximal parts of the arm towards the straight type. It is evident from the figures of Br 27 of *Heliometra eschrichti* and Br 13 of *Amphimetra crenulata* how close this "oblique" muscular articulation in certain proximal Br-joints can come to the radial (figg. 23, 24, 33). This straight type reaches the Br-articulations more or less completely after a varying number of joints. It must be noticed, however, that discoidal joints, i. e. those with exterior straight articulation appear before Br 10, while the interior straightness of the articulations does not generally appear until after Br 10 or 15. These two types therefore are kept separate usually and seldom appear in the same ossicle.

Clarkometra elegans shows, for an Antedonid, rather high figures for the angle on Br 2. One might imagine that these were caused by the lack of pinnules, but Br 4 which is also non-pinnulated shows normal figures (figg. 30—32). That inner obliqueness can be extraordinarily strong in spite of the absence of pinnules is shown by *Pentametrocrinus,* where the first pinnule appears on Br 5. The *Atelecrinus* species lack pinnules as far out as about Br 15. In spite of this outer obliqueness is well developed (fig. 12). Inner obliqueness, on the contrary, is



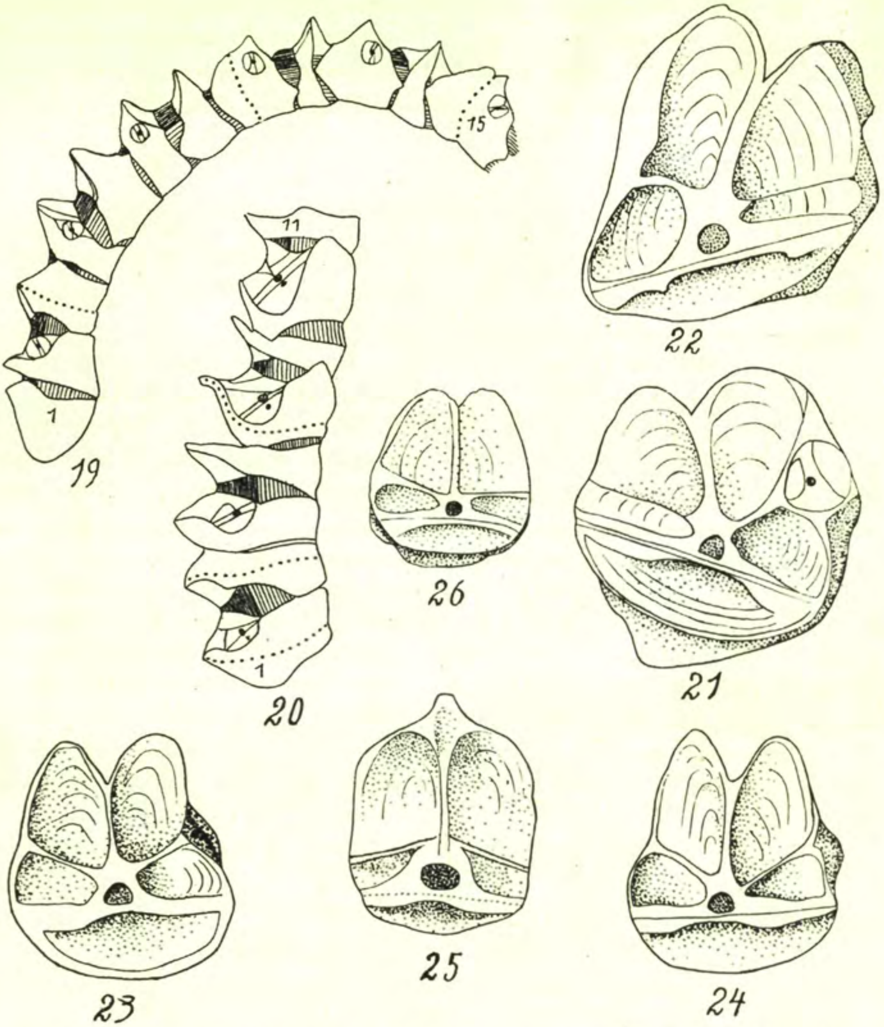
Figg. 14—18. 14) *Monachometra* cf. *fragilis*, $^{6}/_{1}$. 15—17) *Heliometra eschrichti.* 15) Brr 3—8 viewed from the ventral side with the muscles removed, $^{6}/_{1}$. 16) Brr 3—8viewed from. the right side (the outer side of the arm-division), $\times 7\,^{1}/_{2}$. 17) Brr 16—21 viewed from the right side, $\times 7\,^{1}/_{2}$. 18) *Pectinometra flavopurpurea*, Brr 2—9 viewed from the right side, $^{12}/_{1}$.

very little accentuated and straight articulations are attained already at about Br 6 (cf. above and figg. 25, 26). One can understand from this that in the Comatulids the presence or absence of pinnules plays rather a small part in regard to outer obliqueness in the proximal parts of the arm. It is of more importance to inner obliqueness, however, although it is obvious that in the more proximal parts of the arm other factors appear which influence the obliqueness of the muscular articulations. The low figures of the angles in *Eudiocrinus* may be caused by the fairly thick pinnule bases (cf. also below, the explanation of the reversion problem).

If one examines the morphological conditions for the oblique angle between the intermuscular fossa and the transverse ridge one finds the following: The difference in size between the two muscle-fossæ is usually of lesser importance (cf. figg. 21, 27, 28). The difference in size between the interarticular ligament of the pinnular side and that of the antipinnular side is, however, often much greater. This difference reaches its maximum in the Antedonids. Through the co-operation of muscle, pinnule-socket and interarticular ligament the pinnular side of the distal facet of the segment is enlarged ventrally of the transverse ridge, and owing to this the dorso-ventral intermuscular furrow or crest looks as though shot over towards the antipinnular side. In reality, however, it is not entirely so. If one observes the ventral side of an arm from which all the soft parts excepting the ligaments have been removed (cf. fig. W. B. CARPENTER 1866, *Antedon bifida;* my figg. 13, 15), one will find that the above-mentioned intermuscular furrow or crest is always orientated strictly dorso-ventrally. It is therefore more correct to express the inner obliqueness of the articulation by saying that muscle, pinnule-socket and interarticular ligament displace the transverse ridge towards the joint's dorsal side, on the pinnular side of the distal end of the ossicle — on the antipinnular side, if the ossicle is observed from the proximal end (figg. 21, 22).

*

I pass on now to give a short account of the distal joint-faces of the axillaries As was emphasized above, A. H. CLARK (1908 d) says that certain axillaries have straight. and others, on the contrary, oblique articulations; in 1922 the distal articulations of the axillaries are considered to be an intermediate between the straight and oblique articulations (p. 179). The really straight articulations would then only be found in the articulation between R and I Br 1. As it is of importance for the so-called homologizing of the proximal ossicles to see how the matter really stands, I give some figures below, gained by measuring the distal axillary angles (the lesser angle between the transverse ridge and the dorso-ventral crest):



Figg. 19—26. 19) *Antedon petasus* Brr 1—15, viewed from the left side, ${}^{10}/_{1}$. 20) *Comatula pectinata* Brr 1—11, viewed from the left side, ${}^{8}/_{1}$. 21—24) *Heliometra eschrichti*. 21) Br 6, distal face, ${}^{10}/_{1}$. 22) Br 7, proximal face, ${}^{10}/_{1}$. 23) Br 27, distal face, ${}^{10}/_{1}$. 24) Br 28, proximal face, ${}^{10}/_{1}$. 25—26) *Atelecrinus helgæ*. 25) I Br 1, proximal face, ${}^{16}/_{1}$. 26) Br 6, distal face, ${}^{16}/_{1}$.

Comanthus japonica: (I Br 1 prox. 87°, II Br 1 prox. 78), II Ax 67–70, III Ax 60. *Himerometra magnipinna* II Ax 50, III Ax 63, *Pontiometra andersoni* I Ax 87, II Ax 87, III Ax 82–85, IV Ax 78–82, V Ax 80, *Tropiometra afra macrodiscus* I Ax 80, *Cenometra bella* III Ax 76, *Oligometrides adeonae* I Ax 77, *Pectinometra flavopurpurea* I and II Ax 90, *Asterometra anthus* I Ax 87, *Notocrinus virilis* I Ax 87, *Clarkometra elegans* I Ax 84, 84, 85, 89, *Heliometra eschrichti* I Ax 86°.

Ilycrinus carpenteri I Ax 74°.

Metacrinus nobilis tenuis R 89, I Ax (4): 70°, II Ax (7): 63, III Ax (11): 67, IV Ax (11): 68°.

It is seen from this that *Comanthus, Himerometra, (Pontiometra), Tropiometra, Cenometra, Oligometrides, Ilycrinus*, and *Metacrinus* have oblique articulations, while the rest of the types examined have, on the contrary, nearly straight muscular articulations.

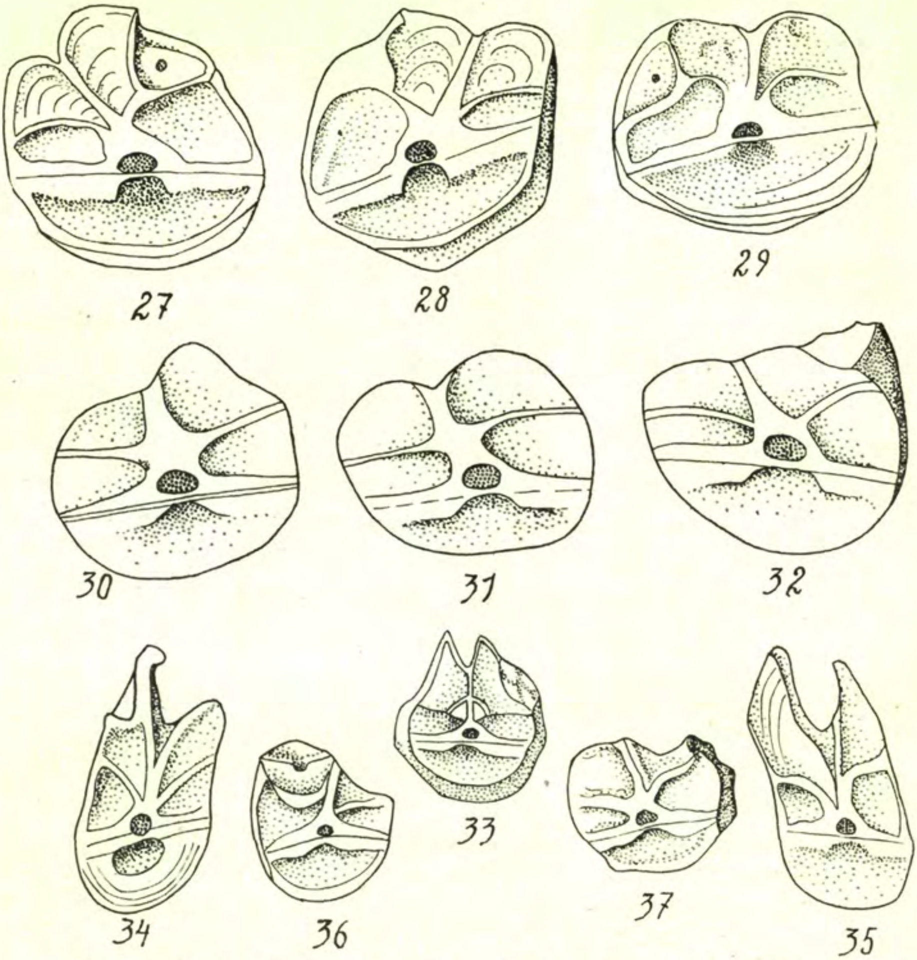
It is evident from the above that no sharply defined boundary can be found between straight and oblique muscular articulations. If one accepts the later of the standpoints taken by CLARK, one should be able to maintain that the straight muscular articulation on the distal face of the R was always single, while all the other ossicles, with muscular articulation, had double joint-facets, i. e. formed axillaries or bore an arm and a pinnule at their distal ends. (In this connection, however, one must remember there are types with defective pinnulation.) In such a case, however, CLARK's Z_1 and Z_2 would always correspond to I Br 1–2, which might also, with a certain justice, be called homologous in the recent Crinoids.

We can therefore state that the homologizations of certain proximal Br-segments that are founded on the basis of a supposed distinct difference between straight and oblique muscular articulations are erroneous.

D. Causes which influence the obliqueness.

1. The obliqueness of the most proximal ossicles.

I have pointed out above that the arm divisions were brought nearer to each other through Br 1 and 2 being broader on the outside. This is of a certain importance, for after the first arm division, the arms in 5-rayed forms cannot, if they are to expand in the same plane, diverge at a greater angle than about 72° ($\frac{360}{5}$). As a consequence of this the distal angle of the axillary ought not to be less than 108° (cf. fig. 38). It has, however, turned out that among the forms examined by me *Ilycrinus carpenteri* and *Monachometra* cf. *fragilis* only have an angle



Figg. 27—37. 27—29) *Comatula pectinata.* 27) Br 4, distal face, $^{16}/_{1}$. 28) Br 5, proximal face, $^{16}/_{1}$. 29) Br 8, distal face, $^{16}/_{1}$. 30—32) *Clarkometra elegans.* 30) Br 2, distal face, $^{38}/_{1}$. 31) Br 4 distal face, $^{38}/_{1}$. 32) Br 6 distal face, $^{38}/_{1}$. 33) *Amphimetra crenulata*, Br 13, distal face, $^{8}/_{1}$. 34—35) *Pontiometra andersoni.* 34) Br 5, distal face, $^{10}/_{1}$. 35) Br 6, proximal face, $^{10}/_{1}$. 36—37) *Pectiometra flavopurpurea.* 36) Br 6, distal face, $^{16}/_{1}$. 37) Br 7, proximal face, $^{16}/_{1}$.

rising to any great extent above this figure. In these two cases it reaches 162° and 145° respectively. All the other types excepting 2 have a I Ax angle of less than 108°: *Comanthus japonica* 88°, *Capillaster sentosa* 105°, *Heterometra jaquinoti* 106°, *Pontiometra andersoni* 105°, *Tropiometra afra macrodiscus* 105°, *Pectinometra flavopurpurea* 104°, *Diodontometra bocki* and *Asterometra anthus* 110°, *Notocrinus virilis* 83°, *Clarkometra elegans* 103°, *Hypalometra defecta* 96°, *Antedon petasus* 78°, *Heliometra eschrichti* 68 – 72°, *Atelecrinus helgæ* 81°, *Metacrinus nobilis tenuis* 98°.

In the 10-rayed *Promachoerinus kerguelenensis* the I Ax angle ought not to fall below 144°. In reality it is 107° here.

Axillaries of higher rank should, assuming the highest possible number of arms within the respective order of the division series, have angles as below: II Ax: 144°+, III Ax: 162°+, IV Ax: 171°+. The types examined had, however: *Comanthus japonica* II Ax: 104°, III Ax: 104; *Capillaster sentosa* II Ax: 126, III Ax: 120, IV Ax: 131, V Ax: 120; *Pontiometra andersoni* II Ax: 130, III Ax: 130, IV Ax: 115, V Ax: 105; *Pectinometra flavopurpurea* II Ax: 126, *Metacrinus nobilis tenuis* II Ax: 104, III Ax: 102, IV Ax: 108°.

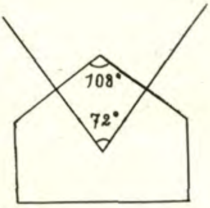


Fig. 38.

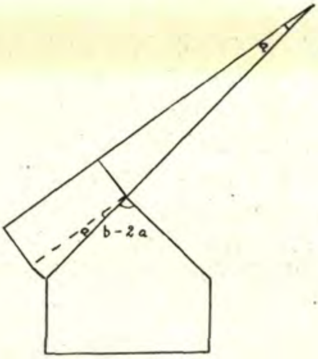


Fig. 39.

All the examples given above — short of the exceptions mentioned — have therefore their arms diverging far too rapidly. But owing to the first postaxillar ossicle being broader on the outer side of the arms this drawback is remedied. (If the arms were narrow proximally and not in lateral contact, the basal parts of the free arms could certainly diverge at angles greater than those theoretically possible. In such a case, however, the divergency must soon be lessened to prevent the arms colliding in the more distal parts.)

If for example the distal angle of an axillary is 2 $a°$ smaller than the theoretically possible angle b, then evidently the proximal and distal sides of the primi-postaxillar ossicles must, in order to restore the arms to the proper angle, get broader on the outside of the arms, and the angle which the proximal and distal sides form with each other must reach at least $a°$ (cf. fig. 39). It seems, however, to be a general rule that the divergence of the arms is diminished still farther, so that they become nearly parallel to each other. The postaxillar ossicles are therefore so much broader generally on the outside, that the distal suture of Br 1 forms nearly a right angle with the longitudinal axis of the preceding axillary, and the distal margin of Br 2 slopes somewhat inwards. The too strong convergence of the arms is usually compensated for by Br 3+4 being broader on the inside, so that the distal margin of Br 4 is almost parallel with the longitudinal axis of the arm. The influence of the arm-forking upon the obliqueness of the joints is thus nullified. The conditions found in *Clarkometra* and *Hypalometra* show that the presence or absence of P_1 and P_a has no influence worth mentioning upon the obliqueness of Br 1—4. As I have emphasized above, joints afterwards appear in special cases in the Comatulids, where the greater breadth of the pinnular side of the arms is already pronounced from the beginning; more often, however, a number of discoidal segments are found after Br 4, or the above-mentioned reversion phenomenon sets in, of which I shall give an explanation later on.

2. The influence of the pinnulation on the obliqueness of the Br-segments.

In the outer parts of the arm the position of the pinnules evidently has a decisive effect upon both the outer and the inner obliqueness of the Br-segments. The pinnular side of the ossicle becomes more strongly developed: from this comes its outer obliqueness. The pinnule's point of insertion enlarges the pinnular side of the articulation-face: this causes its inner obliqueness. Two beautiful examples of the decisive rôle which the position of the pinnules plays, as regards obliqueness, are found in *Pectiometra flavopurpurea* and *Heliometra eschrichti* (cf. figg. 40, 41). In the former 2 successive pinnules appear, both standing to the right, on Br 9 and 10. The proximal and distal margins of Br 10 are therefore parallel. In *Heliometra eschrichti* 2 pinnules appear on Br 92. The formula for the arm may be denoted thus:

$$\mathrm{I}\ 1{-}2 \begin{cases} \mathrm{Br}\ 1{-}\overline{2}\ 3{+}\underline{4}\ \ldots\ \overline{90}\ 91 + \underline{\overline{92}}\ \underline{93}\ 94 + \overline{95}\ \underline{96}\ \overline{97}\ 98 + \underline{99}\ \overline{100}\ \ldots \\ \mathrm{Br} \end{cases}$$

All the pinnules are normally developed, and are of normal size (19–20 mm. The pinnule on Br 93 is, however, a little more slender). The articulation between Br 92 and 93 is perfectly perpendicular to the longitudinal axis of the arm. The distal articular face of Br 92 is perfectly symmetrical (cf. fig. 42). One may compare the normal appearance of the articular face of the distal Br-segments, reproduced from Br 93 (cf. fig. 43).

In certain cases it seems as though one cannot altogether dismiss the thought that historical causes may have played a certain part in bringing about obliqueness. In *Atelecrinus,* which lacks pinnules as far out as Br 12 or 15, one really ought to expect, if the arm division and pinnulation were the only influential factors, to find straight articulations between at least Br 4 and 12. This seems to be the case regarding interior, but not as regards exterior obliqueness. The side of the ossicle that should have borne the pinnule is in fact always broader. It is presumable that actual historical facts must be resorted to here in order to explain the exterior obliqueness of the segments. The power of flexibility in a lateral direction here seems, apart from the synarthrial articulation, to be extremely slight, so that we get no trace of reversion in this case (cf. below on the reversion problem).

In the basal arm-joints the pinnule-socket always invades more or less the Br joint-face, and then either shoots down between the muscle and the interarticular ligament or lies ventrally of the muscular fossa (figg. 16—23, 27—29, 33—36). In more distal Br-joints 2 cases arise: either the pinnule-socket wanders out on to the lateral side of the Br-segments and is found lying completely isolated from the brachial articular-face (cf. W. B. CARPENTER 1866, Pl. 38, fig. 2, *Antedon bifida* and my own figg. 17, 19, 20); or else the pinnular face is found lying on the ventral side of the Br-segment, and therefore, as in the proximal parts of the arm, ventrally of the muscular-fossa (cf. figg. 13, 18, 34). In the former case we have more or less long segments and markedly oblique articulations, in the latter case the phenomenon is usually combined with short, discoidal segments. Here, however, the size of the pinnule bases plays a certain rôle. *Calometridae* ought on account of the insertion of the pinnule-bases to be placed in the latter group. The extraordinarily stout proximal pinnulars do not allow, however, such a pronounced shortening of the Br-joints as that which appears in *Mariametridae, Stephanometridae,* and *Himerometridae.* In the Calometrids the pinnule-attachment spreads itself out at the cost of the muscle-attachment of the pinnular side, which is diminished and gains a more horizontal position on the distal side of the Br-face (figg. 13, 18, 36, 37).

In other cases where the pinnule has a ventral starting point, the shortening of the Br-joints (ontogenetically as well as phylogenetically) may lead to discoidal joints, so that the proximal and distal articulations are parallel.

If, on the contrary, the pinnule has a more lateral position, then with the shortening of the joint and with a pinnule base of normal size, a tendency towards greater shortening of the antipinnular side may make itself felt, and a certain inclination to dichostichality or biseriality appears in the arms. This is, among recent forms, strongly pronounced in certain *Comasteridae,* where one may observe a thickening of the arm-bases, and at the same time a relative shortening of the Br-joints. This tendency to biseriality is very evident in e. g. *Comatula pectinata* (cf. 1919 GISLÉN, Pl. 1 fig. 2, 1924 fig. 46), but is developed best of all in *Comatulella brachiolata* (cf. A. H. CLARK 1911 a, 1913). It might be imagined that the thickening of the arms has been influenced by two causes. First the sexual organs in these types are developed in the arms, as shown in my sections (cf. Chap. 5); this circumstance, however, can scarcely play any very large part, considering that the gonads placed in the same position in various other recent Crinoids do not cause any thickening of the arms (cf. SPERRY 1904, on *Metacrinus,* MORTENSEN 1918, 1920 a, on *Notocrinus, Isometra*). Secondly one may refer to the rôle which the creeping motions typical of the Comasterids undoubtedly play (cf. H. L. Clark 1915, 1921).

3. **The influence of the lateral degree of flexibility on the appearance of the Br-joints.**

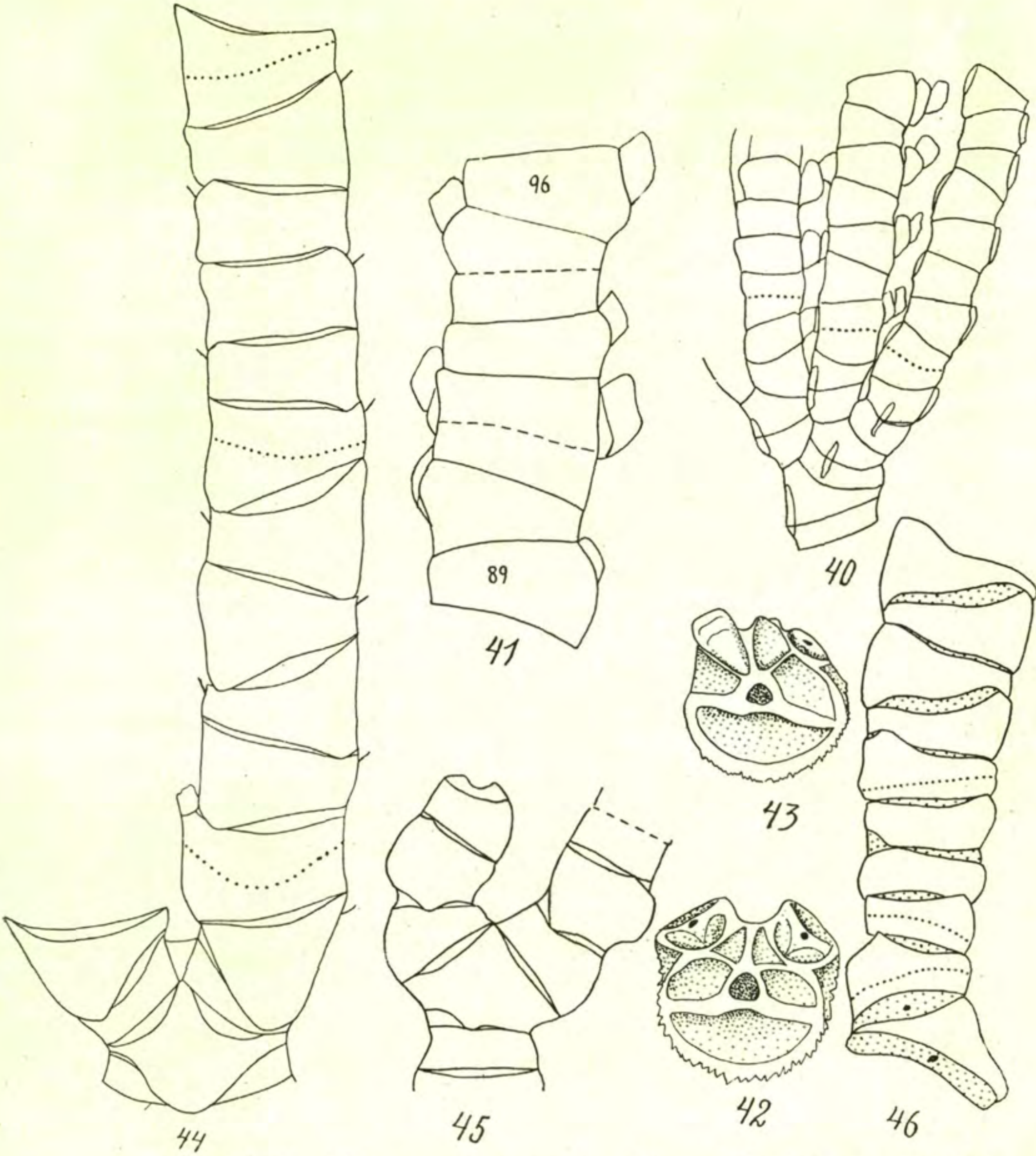
a) The active flexible power of the ligamentary elements.

Like every other author from JOH. MÜLLER downwards, BOSSHARD (1900), who studied the histological difference between muscles and ligaments, has stated the great dissimilarity in histological structure and capacity for colouring existing between them. He comes to the conclusion that the muscles must be active flexors, which flex the arm ventrally, while the ligaments only serve as elastic antagonists, which automatically flex the arms dorsally with the relaxation of the muscles. He admits himself, though, that this theory cannot explain the slight but distinct movements which the cirri of a Comatulid, whose cirrals are united by ligaments only, are capable of making (cf. also the observations of JICKELI 1884, HAMANN 1889, 1907 CUÉNOT 1891, REICHENSPERGER 1912, H. L. CLARK 1917, A. H. CLARK 1922, and myself). BOSSHARD, however, points out himself that this movement of the cirri takes place very slowly, and in quite another way than the movements of the arms. This movement of the cirri, which has been clearly verified, makes BOSSHARD's interpretation of the passivity of the ligaments with flexion of the arms, rather a weak one. This author evidently has not noticed either the information we have respecting the movements of the cirri in the *Pentacrinidae*. A. AGASSIZ (l. c. 1888, vol. 2, p. 120) says, of specimens of West Indian Pentacrinids, as to "their use of the cirri placed along the stem. These they move more rapidly than the arms[1] and use them as hooks to catch hold of neighbouring objects". The leader of the Bahama Expedition of 1893, Professor C. C. NUTTING, also writes (1895 Bull. Univers. Iowa, Nat. Hist. Vol. 3, p. 75, quoted by H. L. CLARK 1918, p. 15) of living specimens of *Isocrinus decorus:* "The cirri were also moved about as if seeking support, and there was some motion of the stem". It is thus indisputable that the ligaments of the cirri, which histologically cannot be distinguished from the ligament of the arm-joints, really have the power of active contraction.

But there are also other facts which point towards BOSSHARD's interpretation being less acceptable. The arm-joints move with the transverse ridge as a hinge. We know that there are ligaments on both sides of this ridge which are about equally powerful — the interarticular ligaments and the dorsal ligament. Now if the dorsal ligament were antagonistic to the muscles alone, it would be difficult to understand of what service the interarticular ligaments could be. Possibly one might imagine that with the relaxation of the muscles they serve to counteract a too hasty flexion of the arms in a dorsal direction, which might be thought to involve breaking of the arms. One might also imagine that with the ventral flexion of the arms the interarticular ligaments become somewhat pressed together, so that, when the muscles relaxed, they would co-operate with the dorsally flexing ligament. Both these suppositions are confuted, however, by the fact that when the muscles are cut through no very strong involution of the arm takes place dorsally. Certainly a little dorsal curvation often appears, which, however, is soon effaced (cf. also MARSHALL 1884. Experiments 12 and 16). Another circumstance speaking in favour of the ligament's capacity for motion is the fact that the two ligament-bundles of the synarthrial articulations may sometimes be rather unequally contracted, in this way giving the arm or arm-pair an oblique position (fig. 45). I consider therefore that the ligaments play a certain active part in the flexions of the arm.

---

[1] The arms of stalked Crinoids seem to move quite slowly in comparison with recent Comatulids, according to Dr. BOCK's observations of the living *Metacrinus* and my own observations of *Rhizocrinus*. It should be noticed too that the ligaments between the proximal cirrals in the Pentacrinids are very strongly developed, so that even a slight contraction gives a powerful result in the distal part of the very long cirrus.



Figg. 40—46. 40) *Pectinometra flavopurpurea.* Abnormal pinnulation on a Br 10, $^{8}/_{1}$. 41—44) *Heliometra eschrichti.* 41) Brr 89—96, abnormal pinnulation on Br 92 and 93, $^{16}/_{1}$. 42) Br 92, distal face, $^{16}/_{1}$. 43) Br 93, distal face, $^{16}/_{1}$. 44) A pair of arms, the left muscles and interarticular ligaments contracted, $^{8}/_{1}$. 45) *Antedon petasus,* unequal contraction of the paired synarthrial ligament-bundles from a living specimen, $^{16}/_{1}$. 46) *Comatula pectinata,* arm-base, the most proximal segments somewhat stretched apart by boiling in KOH, $^{8}/_{1}$.

b) The development of the ligamentary elements among creeping types.

Oligophreata in general and Comasterids in particular have only inconsiderable muscular attachments in comparison with their ligamentary connections. *Macrophreata* (and even certain *Oligophreata*), on the contrary, have extraordinarily powerful muscular attachments. We can, as was hinted above, show that the proximal parts of the arms in certain Comasterids are powerfully thickened and this enlargement, as far as regards the calcareous joint itself, is caused by the specially powerful development of the ligamentary connections (figg. 27–29, 46).

For a swimming type, like *Antedon,* a very important condition is that the formation of the arms should be light and slender; for creeping types, on the contrary, a clumsy construction is of less consequence if only the levers are powerfully built. We can, as I have hinted above, after we have dismissed the theory that the development of the sexual organs in the arms could have influenced their thickening to any extent worth mentioning, hardly avoid thinking that the thickness of the arm-bases bears a certain relation to the creeping habits[1] of the Comasterids. As the ligamentary fibres are much more closely connected with the calcareous mass of the ossicle than the muscle-bundles (cf. the histological works quoted above), as the muscles in these types are rather weakly developed, and as one must presume that the ligamentary elements possess an active capacity for motion, I see no obstacle to accepting the notion that an arm of the type mentioned above must answer better to the demand for an efficacious pull and push lever than do the more graceful and delicate arms found among the other Comatulids which are better suited for swimming.

I must here point out the peculiarity that a large number of the oldest — Jurassic — Comatulids also had very coarse arm-bases, which were often specially thickened proximally, where strangely enough the same tendency to biseriality as in *Comatulella* and *Comatula* appeared, although often it went much farther in the Jurassic Comatulids (cf. DE LORIOL 1888, *Antedon changarnieri* and *A. thiollieri*, Pll. 219, 224;

---

[1] Certain Comasterids in solitary cases seem to be capable of swimming, but are said to swim »spasmodically and not in the beautifully co-ordinated manner of a *Stephanometra*» (H. L. CLARK 1915, p. 110). On the other hand the *Tropiometra* species have not been observed swimming (H. L. CLARK 1917). There can be no doubt, however, that the Comasterids are creeping forms normally, and often with this form of motion very active animals, while the rest of the Comatulids are normally swimmers. As an exception *Tropiometra* may be mentioned, a very sluggish and inactive form (cf. H. L. CLARK 1917, 1921) The reversion of the proximal Br-joints in this genus can scarcely be observed either.

WALTHER 1886, *Solanocrinus costatus*, pl. 25; LEUTHARDT 1911, Pll. 6—8 and others). Here too the muscular attachments, as in all the older *Articulata,* are weakly developed in comparison with the ligamentary connections. One cannot help thinking that these phylogenetically old Comatulids, which had fairly recently given up their sedentary habits, had not yet gained any great capacity for swimming, but were chiefly creeping types. The Antedonids, on the contrary, who are good swimmers, would then be a later type, more suited for a free and active mode of life (cf. also the conclusions I have arrived at in the chapter on The Phylogeny of the Comatulids).

c) Solution of the reversion-problem.

I will now return to the discussion of the problem described above as the reversion phenomenon, i. e. the appearance in certain Comatulids of proximal Br-joints where the pinnular side is more or less greatly shortened, and endeavour to solve it. The causes of this shortening are, as we shall find, the following:

The degree of effect caused by an articulation's capacity for flexing the arm as a whole both ventrally and laterally increases as the position of the articulation becomes more proximal. The strongest capacity for flexion must therefore be considered to appear in the most proximal articulations of the arms. In the proximal articulations the interarticular ligament on the distal joint-face is developed much more strongly on the pinnular side than on the antipinnular side. Through the encroachment of the pinnule-socket, which is fairly strong in the proximal parts of the arm, the interarticular ligament of the pinnular side, and by it also the transverse ridge, is displaced dorsally on the pinnular side of the Br-joint's distal face. On the proximal face of the successive Br-ossicle it is the end of the transverse ridge running on the antipinnular side of the ossicle which, on the contrary, is displaced dorsally. In other words, we find in the dorsal part of the articulation a certain likeness to a synarthry, although a very oblique one. The dorsal end of the transverse ridge, which runs between the great interarticular ligament and the dorsal ligament, is now prolonged so that a process from the proximal margin of the more distal Br-joint fits into a notch in the distal margin of the more proximal ossicle. We get thus something very similar to an oblique synarthrial projection, where, as in the latter, the synarthrial process is directed backwards. At the same time as this prolongation of the proximal margin of the distal ossicle takes place backwards, the point of attachment for the great interarticular ligament spreads out on the lateral, inner side of the increased attachment surface. As the projection from the more distal ossicle fits into the more proximal ossicle on its pinnular side, it encroaches upon the breadth of the pinnular side of this joint, which thus becomes narrower than the antipinnular side. On the other hand, the more distal joint, which bears the process, is strengthened on the antipinnular, proximal side by the backwardly directed process and thus becomes broader there.

It is evident that such a construction as the one sketched above gives the arm increased flexible capacity in a lateral direction. An articulation where both the end-points for the transverse ridge are strictly lateral evidently does not allow any flexion at all in a lateral direction, whether the joint in other respects is oblique or not (cf. *Atelecrinus*).

If, for example, we observe the drawing of an arm of *Heliometra eschrichti* (fig. 44), we can see clearly that a contraction of the muscles and interarticular ligaments on the inner side must, as was the case, carry the arm in towards the main axis, while, on the contrary, a contraction of the muscles and interarticular ligaments of the outer side must lead to the arm being carried from the main axis. In the case shown in the drawing the contraction of the ventral muscles and ligaments of the left side causes an opening of the dorsal ligament fossa between the joints where the great interarticular ligament stands to the left, while the dorsal fossæ between the joints where the little interarticular ligament stands to the left are not expanded but are pressed together by the inflexion of the arm towards the main axis described above. A contraction of the ventral muscules and ligaments on the left side affects chiefly every other joint, but with a cumulative effect so that it can produce very considerable consequences in the distal parts of the arm.

The greater this reversion of the conditions of breadth in the proximal Br-joints, the greater becomes the lateral capacity for flexion in the arms. A certain amount of lateral flexion is possible in all the arms where synarthries are developed. In fossil types — where synarthry is found — and in recent stalked Crinoids this restricted lateral possibility of motion seems to be satisfactory. The same seems to be the case in the primitively organized genus *Atelecrinus*, where no decrease at all of the breadth of the pinnular Br-side appears in any part of the arms. Here one is able, from the primitiveness of the type in other respects, to assume an inconsiderable lateral mobility. An increased lateral mobility here would most likely give rise to discoidal segments.

Under certain conditions an apparently similar case to that of *Atelecrinus* may arise on account of an enormously enlarged pinnule-base *(Calometridae)*; in other cases the habit of creeping (a number of Comasterids), possibly combined with original primitiveness, may bring about a similar phenomenon.

In all the other Comatulids reversion may be observed. In the cases where it is little developed the influence of the pinnule is about equal in importance to the counteracting, reversional, lateral flexibility; here we get in the proximal parts of the arm a number of discoidal joints. In the cases where it is more strongly developed *(Antedonidae)* the lateral capacity for flexion is the strongest, and a number of joints appear, which are considerably narrower on the antipinnular side.

E. Contribution to the history of the muscles.

In the creeping Comasterids, as was pointed out above, the muscular attachments in comparison with the ligamentary connections are not very conspicuous. The same is also the case, in a more or less high degree, among various other families belonging to the *Oligophreata,* and in certain fossil — especially Jurassic — Comatulids; among the *Macrophreata*, well equipped as they are for swimming and living a free, active life, the muscular attachments, on the contrary, in comparison with the ligamentary connections, are powerfully developed.

It is very obvious how weak and scanty the development of the muscle-fossæ are in the Articulate, Jurassic *Apiocrinidae, Millericrinidae,* and *Pentacrinidae* (cf. e. g. DE LORIOL 1884—89). It is likewise of great interest to see that in the Silurian Inadunate species (cf. BATHER 1893) where one can occasionally verify the occurrence of a transverse ridge, not the least trace of the ventro-lateral crest that should mark the boundary between an interarticular ligament and a muscle-fossa is found. It is only with the appearance of free-living forms, such as Comatulids and certain Pentacrinids (cf. also the figg. of P. H. CARPENTER 1884) and not always in them even, that the muscles become considerably enlarged.

One may ask oneself, what are the histological and historical relations between the ligamentary connections and the muscles? Are the tissues fundamentally different, as BOSSHARD assumes, or are they from the beginning only the product by differentiation of one and the same tissue?

If we look at the question from the histological side, my own observations of sections through regenerated and young arms seem to give the same result as that to which MINCKERT (1905) and REICHENSPERGER (1912) came — that both kinds of tissue were at an early stage differentiated from similar tissue.

In regenerates the muscles appear somewhat later than the ligaments, and are at the beginning very difficult to distinguish from these latter. After that, they are differentiated in various ways, the fibres of the true muscles become spirally striated etc. (cf. REICHENSPERGER 1912 pp. 13 and 25).

I have stated the reasons above which speak in favour of an active capacity for locomotion, even if a rather slow and restricted one, of the ligamentary connections. I agree also with REICHENSPERGER that the ligamentary fibres are actively contractile and "eine primitive Form von Musculatur" (p. 17). One might compare them with the plain muscles, as their reactional velocity seems to be less than that of the striated ventral muscle-bundles.

Although I thus consider the ligamentary and muscular tissues rather nearly related physiologically, still I retain (on account of their clearly differentiated type histologically, and in order to have short and familiar terms, easy to keep apart) the names used above.

During the phylogenetic development one may imagine that two courses lay open. Either the two tissues were distinguished from each other histologically very early; in that case the true muscles from the beginning lay ventrally of the interbrachial joint-faces and only later were incorporated between them; or else the differentiation of the true muscles took place at a relatively late time. In the latter case they would have been formed from the ligamentary elements within the ventral part of the articulations.

The latter possibility is less probable for several reasons. One might, if this latter development had taken place, ask oneself, why no muscular fibres had ever been formed in the dorsal ligament which acts antagonistically to the ventral muscles, and why muscles are lacking in synarthries and in inter-cirral articulations which both have a fairly powerful motion of their own. A. H. CLARK in 1910 (a) in a noteworthy paper, has also pointed out certain other points of view which seem to me to speak in favour of the former course of development. He considers that from the beginning the ossicles in Crinoids were only bound together by "connective tissue", like the sutures between the ossicles of the Echinoids to this day. In Echinothurids and Holothurians we have radial, longitudinal muscle-bands inside the skin containing the calcareous plates or spicules. Above the periproct, in the dorsal posterior interradius of the Spatangids, transverse, striated muscles are met with. Both these are the remains of a muscular sac which existed once upon a time (cf. LUDWIG 1877, SARASIN 1888). A pair of longitudinal muscle-bands, like those in the Holothurians, presumably existed on the ventral side of the arms of the oldest Crinoids. With the demand for increased and more rapid motion in the arm-joints these muscle-bands began to play a more active part in flexing the arms, and therefore gained stronger attachments to the Br-joints. Crests and calcareous processes were developed in this way for the muscle-attachments, and these pushed into the longitudinal muscle-band and divided it into portions which now correspond to the interbrachial true muscles.

My view may thus be stated as follows: that for the only slightly movable arms of most of the palaeozoic Crinoids the ligamentary articulation in the proximal parts of the arm which still lacked flexional, real muscles was sufficient for the flexional power required; we therefore find in them only syzygial or more commonly more or less synostotical[1] articulations in the middle and distal parts of the arm. Later on, with the necessity for increased speed and effectiveness in movement, the proper muscles, which before had only been found in the soft parts situated ventrally of the arm, also became associated with the calcareous skeleton. We find that this incorporation took place earliest in the radial articulation, standing alone in its type, in *Flexibilia*, according to SPRINGER (1920) extinct in Upper Carboniferous, without leaving any descendants after it. *Articulata*, which it appears may be traced back to *Poteriocrinites*, which in its turn descends from some group of *Dendrocrinites* (BATHER 1900, JÆKEL 1918), have independently taken a similar course and developed the type usual in recent Crinoids (cf. figg. 47—52). Among the Jurassic Comatulids the muscle attachments are still relatively insignificant. In the radial muscular articulations they may even be lacking sometimes, as in a couple of recent forms (*Pontiometra* and *Stephanometra*, figg. 53, 54); but this phenomenon appears to be of a secondary nature (cf. the chapter on The Phylogeny of Comatulids).

The ligamentary articulations would thus be the oldest arm-flexors which, by their activity, have developed the transverse ridge. Therefore the interarticular ligaments are the original antagonists of the dorsal ligaments. The ligamentary articulations can be derived from the close sutural connections between the joint-pieces of the Cambrian, Ordovician, and Silurian Crinoids. The rôle of the true muscles as arm-flexors would be of later date, and caused by the necessity of increased and more rapid motion. The muscular articulations first reach their full development in certain recent eleutherozoic Comatulids, while other Comatulids less suited for the habit of swimming, many stalked recent Crinoids, and the Permian to Jurassic forms, have muscular attachments which are very modestly developed (cf. BEYRICH 1858, Pl. 1 figg. 4, 6, 7; P. H. CARPENTER 1884, Pll. 3, 12, 18, 20, 21, 26, 32, 34, 50; A. H. CLARK 1922, figg. 1—115; GOLDFUSS 1831, Pll. 51, 52, 54, 57; v. KOENEN 1887, Pl. 1 figg. 12—14; DE LORIOL 1884—89 Pl. 34 fig. 6; 59 fig. 1; 71, fig. 7; 94, fig. 7, 120, fig. 1; 134, fig. 1; 200, fig. 5; 213—229; QUENSTEDT 1876, Pll. 97, 100, 103; 105, 106; WANNER 1916, Pl. 101, fig. 12, 104, figg. 1, 5; 106, figg. 3, 4; 109, figg. 8, 10).

---

[1] Cf. below pages 65 ff.

III. Ligamentary articulations in the arms.

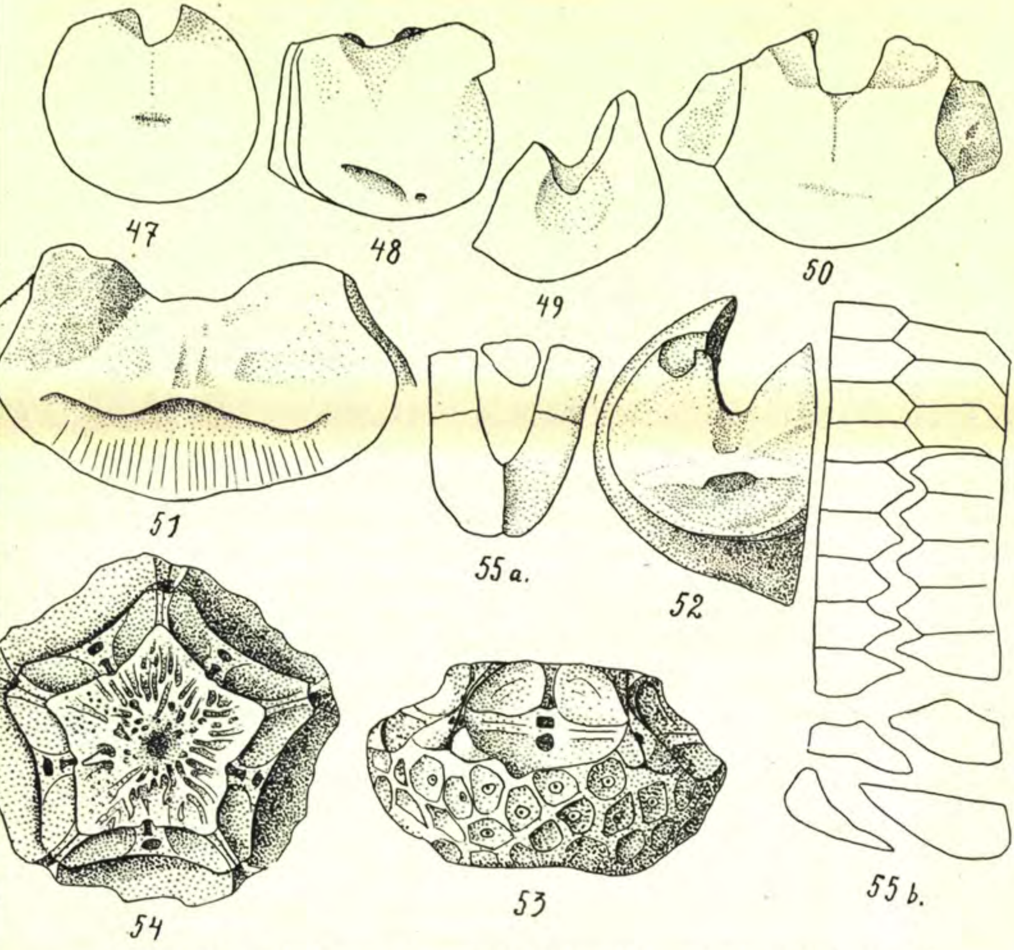
A. Nomenclature.

We have already in the introduction made acquaintance with the terms for the ligamentary articulations which were distinguished by A. H. Clark: syzygies, pseudosyzygies, synarthries, and cryptosynarthries. To these I will add the synostosis mentioned above, a connection between two ossicles where the facets are smooth. The mutual relations between these terms and their connection with the rest of the terminology employed, especially by paleontologists, I have endeavoured to explain and arrange in an easily surveyable scheme below:

I. Ligamentary articulations, lack striated muscle fibres (= non-muscular articulations A. H. Clark).
  A. Immovable articulations (= close suture auctorum).
    1. Flat smooth joint-face = close synostosis. Occurs between Cd and BB and RR, between most of the Br-joints in many palaezoic Crinoids up to Permian, in a number of cases instead of syzygies in recent, stalked forms. Between the nodal and infranodal joints in Pentacrinids. Between Cd and the 1st cirral in most of the recent Comatulids.
    2. Radially (in regard to the nerve-lumen) striated joint-face = syzygy s. str. In most of the immovable arm-articulations in the Comatulids, and also in many fossil forms. Between the stem-joints in most of the fossil Crinoids.
    3. Concentrically, round the nerve-lumen, or irregularly arranged points of contact between the joints = pseudosyzygy. In certain Comasterids between I 1 + 2. We find similar connections between the Calyx-plates of the *Flexibilia*. The sculpture in the last-mentioned case, is irregular and some mobility seems to have been found; is a transition type to the movable ligamentary articulations.
    4. Fusion of a couple of ossicles through calcareous deposits in the ligamentary articulation: anchylosis. In many fossil forms. Among recent forms between e. g. the calyx-plates of *Rhizocrinus;* in abnormal cases between the Br-joints in recent forms.
  B. Movable ligamentary articulations.
    1. Flexible in all directions, slightly movable (part. loose suture auctorum).

        (a). Stem-joints in Pentacrinids and similar types. Sculpture petaloidally developed.
        (b). No sculpture. The joints somewhat bi-concave: loose synostosis. Between all the Br-joints in the distal parts of the arms in many fossil forms; instead of syzygies in distal arm-parts in a number of recent forms.
        (c). See under A. 3.
    2. Strongly flexible in two directions with an articular ridge on which the joint moves.
        (a). One joint pit on each side of a ridge that divides the joint-face into two halves: synarthry. Occurs in the proximal parts of the arms (convergently developed in the *Cystidea,* as well as in *Camerata, Inadunata,* and *Articulata.* Between cirrals. Between stem-joints in certain full-grown Crinoids *(Platycrinidae, Thiolliericrinidae, Bourgueticrinidae, Bathycrinidae, Phrynocrinidae).* Also developed between the long stem-joints in the young of Pentacrinids and Comatulids. — Cryptosynarthry is a synarthry having weak and indistinctly developed articular-fossæ; it is slightly movable and forms a transition to synostosis (has the nature of a loose synostosis).
        (b). At least 3 joint pits, mobility normally in dorso-ventral direction. Probably only between the arm-joints (the same perhaps also in Burdigalocrinid stems; trifascial articulation P. H. CARPENTER): ligamentary articulation. Between RR and arms from Ordovician up to Carboniferous. Between certain arm-joints in *Flexibilia.* In solitary cases also between RR and I Br 1 in recent time *(Pontiometra, Stephanometra).* Instead of syzygies in *Bathycrinidae.*

II. Muscular articulations (with striated muscle-fibres).
    A. Mobility in dorso-ventral direction. One dorsal, two interarticular ligaments, 2 fairly strong muscular-fossæ: muscular articulation (s. str.). In the articulations between RR and the arms in *Flexibilia.* Between the arm-joints from Permian or Trias up to the present. Between the arms and the 1st pinnular, as well as between the 1st and 2nd pinnulars at least among recent Crinoids. In a modified form in the pinnular articulations of the distal pinnules.



Figg. 47—55. 47) *Scytalocrinus bijugus* Br 27 dist., small ventral articular fossæ, $^{4}/_{1}$. 48) *Zeacrinus wortheni* 2 dist. Brr, the pinnular attachment to the right, $^{16}/_{1}$. 49) *Aesiocrinus (Graphiocrinus) magnificus* Br 1 dist., ligamentary connection, $^{6}/_{1}$. 50) *Cromyocrinus ornatus* Br 6 dist., small, ventral articular fossæ, $^{6}/_{1}$. 51) *Scaphiocrinus multiplex* distal face of a radial, left posterior radius, $^{3}/_{1}$. 52) *Erisocrinus typus* Br 2 dist., non-canaliculate, a pinnule-socket to the left, primitive muscular articulation(?), $^{16}/_{1}$. 53—54) *Stephanometra spicata* Cd and the radial ring viewed laterally and from the ventral side, $^{8}/_{1}$. 55) *Callicrinus costatus* a) Distal part of an arm viewed from the short end, the first pinnular on each side is indicated, one covering plate, b) dorsal view of an arm, the brachial pieces are somewhat disjointed, $^{8}/_{1}$.

B. No dorsal ligamentary fossæ, the muscle-fossæ usually small. Mobility in the lateral direction only. **Pinnular articulation**. Between the pinnulars from the articulations between the 2nd and 3rd pinnular in the proximal part of the arm.

B. Ligamentary arm-articulations in fossil Crinoids.

1. Arm-joints in the oldest Crinoids.

Most of the Silurian, together with the older Crinoids (cf. e. g. *Perittocrinus,* JAEKEL 1918), had not yet canaliculate joints, i. e. the dorsal longitudinal nerve did not lie enclosed in the Br-joints, but was only sunk in a ventral groove. The non-canaliculate stage continued, at least among many Poteriocrinids, up to Carboniferous. Small Pentacrinulas of the recent *Antedon bifida* too, are stated to be non-canaliculate in the proximal arm-joints (cf. W. B. CARPENTER 1866 p. 729, Pl. 41, fig. 2). As far as I could find, the Br-joints in *Hathrometra tenella sarsii* are already canaliculated at about the time when the first cirri appear. Gradually, however, in different series at different times, convergently a calcareous bridge, ventrally of the dorsal nerve, is developed, through which the nerve becomes separated from the ventral soft parts. This is demonstrated beautifully in BATHER's work of 1893 on the *Inadunata* of Gotland (cf. e. g. Pl. 9, fig. 327). From the old, non-canaliculate type of Br-joints, the step backwards does not seem to have been long to the biserial arms of the the Cambrian Eocrinoids. BARRANDE's plate 33, figg. 17, 18, 1887 (of *Ascocystites drabowiensis*), which shows a section through such a biserial arm was not comprehensible to me; it is also according to what Geheimerat JAEKEL has stated in a letter to me completely wrong. Professor JAEKEL has also had the great kindness to place at my disposal a number of figures drawn from specimens of *Ascocystites drabowiensis* in the Greifswald Collection. These figures make it quite clear that the Eocrinoids had arm-joints tolerably corresponding in type to and surviving in the biserial arms of *Camerata* (cf. fig. 55).

One might ask the question how the monoserial arms appearing in Ordovician could be formed. Is it possible that this happened through the original joints being pushed in between each other? JAEKEL asserts in 1918 that this was the case with more advanced types among *Cladocrinoidea (= Camerata).* One might also imagine a displacement of the ossicles taking place in such a manner that, instead of lying alternately, they came to lie on the same level and afterwards coalesced in pairs in the median line. Geheimerat JAEKEL tells me, however, that such a development has not been traced among fossil forms. He considers, too, such a fusion "für mechanisch nicht durchführbar" (One should bear in mind, though, the extremely weak mobility of the arms in the older fossil Crinoids. JAEKEL has himself in 1901 given an example of just such a monoseriality, arising through the joints growing together, pp. 1067—1069). JAEKEL considers instead that the monoserial arms which appeared in the lowest Ordovician "aus der Kelchwand neu gebildet werden". He continues in a letter to me: "Das sehen wir innerhalb der Hybocriniden tatsächlich vorliegen. *Hybocystis* zeigt einfache Zapfen zur Verlängerung der radialen Kiemen, die dann bei *Hybocrinus* gegliedert werden. Für die Reihe der Porocriniden aber stehen uns Kelche mit radialen Plattenreihen zur Verfügung, die einfache oder geteilte Reihen bildeten und nun direct in die vorher reduzierte Armbildung übernommen werden konnten". This question scarcely seems to me to be completely solved in favour of the latter supposition.

The old components of the arm-joints arranged biserially seem to me to have been originally only superficial, alternating plates which protected the dorsal nerve. This I imagine as only forming from the beginning the distal part of the nervous, ciliated groove carrying nourishment. By the formation of the arms the distal part of this groove gained a dorsal position making it less suitable to function in carrying food, and thus it only retained its nervous function. It was sunk deeper into the arm and the alternating dorsal ossicles, standing at the margins of the nerve, began to cover the groove protectingly, and were connected by soft parts in the same way as happened to the proximal parts of the ventral nerve in *Camerata* and many *Inadunata*, and, among recent forms with the ambulacral nerve, in Holothurians, Echinoids, and Ophiurans.

In case this assumption were correct, one might interpret the biserially arranged arm-joints of the Eocrinoids as corresponding to the ad-ambulacral ossicles of the ventral side. Another postulate would be that in the development of the oldest arms in Cambrian, the hydrocoel either did not stretch as far as the distal parts of the ciliated groove or else, if it was present, that all trace of it is now completely obliterated in the ontogenetic development.

2. **Arm-joint articulations in other fossil Crinoids.**

Palaeontological facts speak in favour of at least most of the Br-joints in palaeozoic crinoids, and in certain cases in younger forms the segments of the distal parts of the arms too, having been united through the ligamentary articulation only, as is also the case to-day with, e. g. the ossicle plates of the Echinoids. Among the palaeozoic Crinoids we find, in fact, uniform, very close and usually smooth, sometimes striated joint-faces between the Br-segments. Such synostotic or syzygial arm-joint connections we find alike in *Camerata* and in *Flexibilia* and *Inadunata*. (Cf. BARRANDE 1899, Pl. 50 fig. 14; 53 fig. 1; 54, 65, 66, 68. BATHER 1893, e. g. Pl. 2, figg. 81, 82; 3, figg. 86, 87, 102; 5, fig. 151; 7, figg. 210, 213; 8, figg. 250, 256, 289; 9, figg. 299, 300, 306, 327–332; 10, figg. 366, 368. SPRINGER 1920, Pl. 39, figg. 17, 18; 57, figg. 6, 7; 61, figg. 4–9. WACHSMUTH & SPRINGER 1897, e. g. Pl. 22, fig. 7 a; 27; 37; 55, fig. 2; 58–61; 66, figg. 2, 3; 68, fig. 13; 74, fig. 6; 77, fig. 4 c).

These articulations were completely, or almost completely, immovable. Because of this the arms of *Crotalocrinus* and *Petalocrinus* have been able to grow together laterally into laminæ which got their motion almost exclusively from a proximal articulation (BATHER 1898, WACHSMUTH & SPRINGER 1889). If, however, the arms of the palaeozoic Crinoids were thus extremely rigid, they did not entirely lack mobility. (On the degree of flexibility in the distal parts of the arm, cf. WACHSMUTH & SPRINGER 1897, p. 87.) Any stronger capacity for flexing the arm seems, on the contrary, to have been restricted to the most proximal parts of the arm. Here we get movable articulations at an early stage in *Inadunata, Camerata* and *Flexibilia,* sometimes also between the fingers and theca in *Cystidea*. In the *Inadunata* we have a transverse ridge; dorsally of this the mark for a dorsal ligament, ventrally of that the attachments for the interarticular ligaments (cf. BATHER 1893, Pl. 1, figg. 10, 18; Pl. 3, fig. 88; Pl. 7, fig. 200). We find similar articulation in Cystideans (JAEKEL 1899, p. 90, fig. 14 c, Pl. 6, fig. 8, Pl. 7, fig. 4). In the *Camerata* the slight movements of the arm in the proximal parts seem generally to have been released in a lateral direction. When the joint-fossæ are pronounced in these forms, they are usually of the synarthrial type. As the arms here are often biserial, the two joint-fossæ in such cases are found upon different, adjacent ossicles. (WACHSMUTH & SPRINGER 1897, e. g. Pl. 36, fig. 7 b, Pl. 39, 2, 3; Pl. 41: 1–4; Pll. 54, 57, 74. Cf., however, WANNER too, 1916, Pl. 98, fig. 7; 99, figg. 1, 9.) We often find similar synarthrial articulations between the fingers and theca in Cystideans (JAEKEL 1899, p. 90, figg. 14 a and b, Pl. 14: 5–7; 16: 2; 17: 3.) In *Flexibilia* it seems, as is pointed out above, as if a peculiar articulation with true muscles developed early between the radials and the arms (SPRINGER 1920, Pl. 23, figg. 1, 10, 12; Pl. 24). The distal parts of the arm were movable too, but here no muscles seem to have taken part in the mobility, which was brought about by the somewhat more developed ligament-fibres only.

The ligamentary articulations in the recent Crinoids are therefore the articulations that answer most nearly to the interbrachial articulations found among the older fossil forms. During the course of ages they have scarcely altered from the original type. Either they have been allotted the specific power of lateral mobility (synarthries) or they have become preformed places for autotomy (brachial syzygies, synotoses, and, in certain cases also, synarthries). In the cirri it is only the articulation between the stem and centrodorsal respectively and the 1st cirral which presents such a locus minoris resistentiae — autotomic fractures between the joints of the cirri are not known and, if they really can take place, extremely rare. In recent forms we find further this differentiation in the brachial joints united by ligaments, that the brachial, appearing proximally of the ligamentary articulation, is always non-pinnulate: hypozygal (before a syzygy), hypoarthral (before a synarthry). This ossicle has no influence either on the pinnules which otherwise appear on every joint, now to the right, now to the left.

C. Ligamentary articulations in recent forms.

Among the ligamentary articulations synotosis, both ontogenically and also phylogenically, is the oldest (figg. 56—58. Cf. also W. B. Carpenter 1866, Pl. 41, fig. 2). Synarthry can thus scarcely be derived from syzygy, and neither can syzygy be derived from synarthry, but both are differentiated varieties of synotosis, specialized for particular purposes. The one or the other form has developed according to the different demands which have been made upon the articulation in question. Sometimes, however, the syzygial articulation seems to develop into the synarthrial articulation. In *Crossometra septentrionalis*, where in usual cases Br 1 and 2 are united by a syzygial articulation (cf. below). I have observed in one case 2 lateral concavities round the nerve-lumen. The centre of the joint-face therefore represents a synarthrial articulation; in the peripheral parts, on the contrary, it is of the normal syzygial type (fig. 80). *Catoptometra (magnifica minor)* shows possibly a somewhat different direction in its development. In full-grown individuals the articulation between I Br 1 and 2 is syzygial (cf. fig. 67); in the young the same articulation is furnished in its periphery with weak syzygial septa of which a median, dorso-ventral thickening becomes slightly stronger and thereby gives the joint-face a somewhat synarthrial touch (fig. 59).

In what follows I have endeavoured to give a full account of the ligamentary articulations in recent Crinoids. In regard to the Comatulids especially, I have tried to make my statement as complete as possible, as the information regarding this point in these forms has up till now been extremely deficient.

1. Immovable articulations.

a) Stalked Crinoids.

Perfectly typical syzygies are scarcely to be found in recent stalked Crinoids. *Calamocrinus* (AGASSIZ 1892) and *Ptilocrinus* (fig. 60) have typical synostoses, like a large number of Pentacrinids also. In the last-mentioned family one finds, however, an evident tendency against the development of syzygies. Here, as in the fossil forms, we find the first impulses towards syzygial formation hinted at by a weak rifling of the dorso-lateral margin of the joint-facet. The marginal ridges developed through this increase still more towards the centre, and when they reach it, we get the typical syzygy.

The species belonging to *Metacrinus* have almost typical synostoses, which, however, sometimes show a very indistinct marginal striation (cf. P. H. CARPENTER 1884, *M. angulatus,* Pl. 12, figg. 7, 10, *M. nodosus,* Pl. 50, figg. 7, 12, 13; DÖDERLEIN 1907, *M. acutus,* Pl. 10, fig. 13; and in this work *M. nobilis tenuis* fig. 61. The joint-faces have the same appearance in *M. rotundus*). The syzygies are indicated about as weakly in the *Diplocrinus* species (P. H. CARPENTER 1884, *D. wyville-thomsoni,* Pl. 18, figg. 8, 11, Pl. 21, figg. 2 d, 5 a). On the contrary, a syzygial type is rather distinct in *Hypalocrinus naresianus* (P. H. CARPENTER 1884, Pl. 30, figg. 20, 21), and in *Cenocrinus asteria* (op. cit. Pl. 12, figg. 18, 21).

b) Comatulida.

When describing the syzygial faces of the Comatulids I employ the following terms. Round the nerve-hole (the lumen cf. BATHER 1909), which pierces the centre of the joint, the margin may often be thickened; this ring-shaped elevation I call the areola. From the margin of the joint-facet calcareous ridges run centripetally; these are the septa. They may be complete, when they reach as far as the lumen or areola; they may be incomplete, when they only continue a bit in from the margin of the joint; they are called finished, when they first begin a bit in from the margin of the joint-facet and afterwards go forward to the centre. The septa are forked, when a couple of them fuse a bit in from the margin. When the septa are both incomplete and finished we get small, low, more or less rounded protuberances, the tubercles. In many of the larger forms the ventral septa specially show a disposition towards dividing into rows of tubercles. Sometimes concentric ribs run at certain distances from the nerve lumen: synapticulae. The areola is often connected with the ventral, usually groveless, part of the joint-face, by a more or less broad, smooth part, a ventral beam. Usually, however, the median part of this ventral beam is furnished with a pit or furrow, thus giving rise to 2 ventral beams. These ventral beams may be developed as coarse, bow-shaped septa which run out to the margin of the joint-facet.

All these elevations, found in different forms, are marked by different degrees of strength. I have denoted the degree of strength by figures from 1 to 4. The figure 1 has been assigned to forms having septa only weakly indicated (e. g. certain *Charitometridae*); syzygial articulations, where the septa appear very strongly, are denoted by the figure 4, e. g. in *Heliometra eschrichti*.

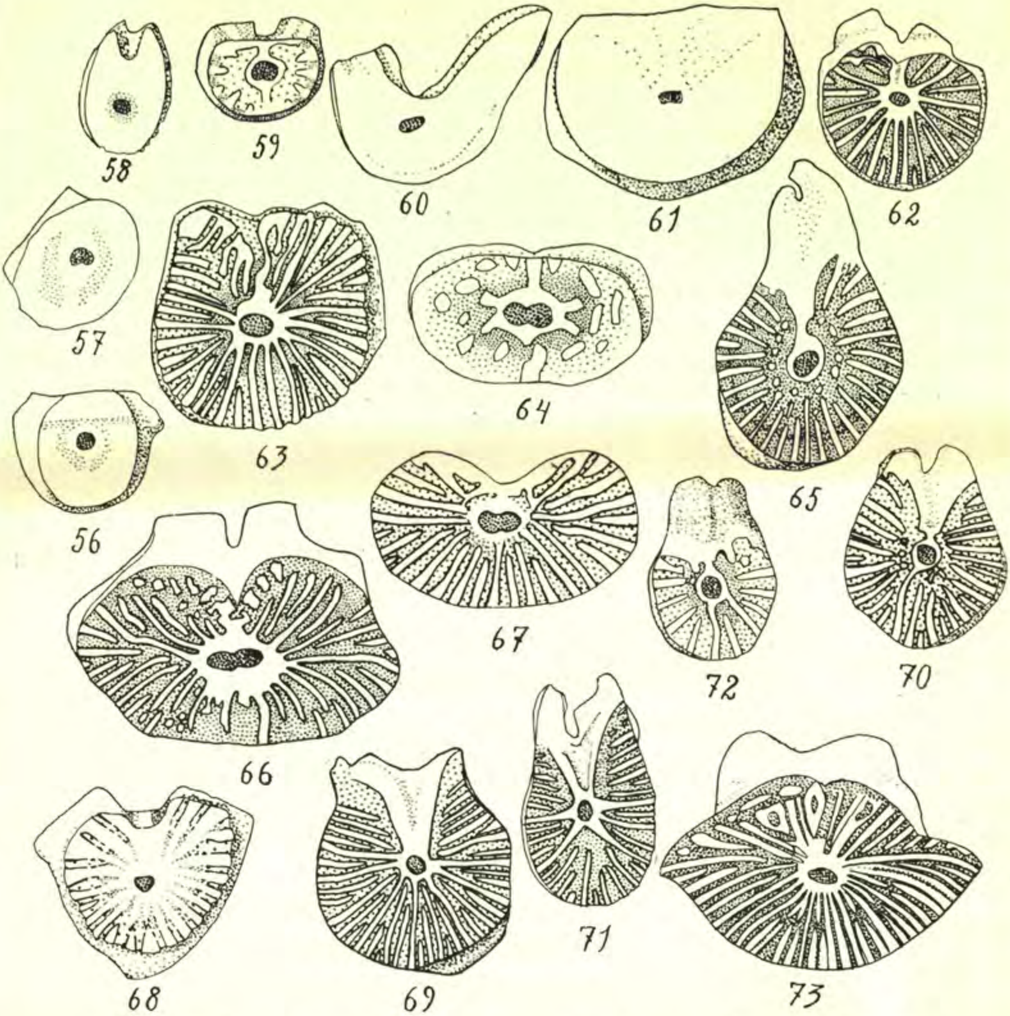
The prominences on the distal face of the hypozygal are matched by corresponding elevations on the proximal face of the epizygal. When the syzygial suture is observed from the dorsal side of the arms, this makes a characteristic dotted line appear, where the dots mark the canals drawn through by the ligaments which alternate with the septal contacts.

The same development in the change from synostosis to syzygy which we have established in the phylogenetic development of the Crinoids is found again also in the ontogenetic development of the Comatulids. Very young specimens of Comatulids have the ligamentary connections developed as synostosis (*Antedon petasus,* figg. 56—58). The distal facet of the hypozygal is somewhat concave, the proximal end of the epizygal, on the contrary, somewhat convex. The first change from synostosis to another form of ligamentary connection seems to appear in the young in this way: the synostotic articulation becomes less close, in other words, the ligamentary fibres between the ossicles in certain places become longer. The contact is retained round the lumen sometimes, and in such a case we get an areola here; the contact seems to be closer, too, at the margin of the ossicles. If the articulation is to develop into a synarthry, a strong areola always appears from which a ventral and dorsal beam grow out, and thus we obtain the ridge over which the ossicle, by lateral flexion, articulates (cf. figg. 56, 57, 93). If the connection, on the contrary, is developed into a syzygy, an areola may appear and be retained, or it may be lacking altogether. At this point the stage arrives when a number of septa, very weak at the commencement, begin to form. They appear first in the dorsal and lateral parts of the connections, and are prolonged outwards, because with the appositional increase of growth in the joint, they continue in contact with the margin of the joint. During the development of the animal the septa increase in number, and the new ones which are formed later arise in the same way from the border of the joints, intercalated between the septa first formed which reach forward into the neighbourhood of the central lumen. That the septa also must to some extent increase in growth towards the centre is seen by the increasing number of complete septa in older specimens. It is certainly true that the lumen is enlarged somewhat during the growth. But this is not enough to explain the increase of complete septa. In a young of *Antedon petasus* described below the diameter of the lumen is 0·06 mm., the diameter of the segment being 0·31 mm. Here 2 complete septa are found. In a full-grown specimen the lumen is 0·19 mm. and 12 complete septa are found.

The variation in the number of septa in certain species at a given age is rather small and unessential. In a *Mariametra subcarinata* for example, the number of septa on the distal end of 4 Br 3 varied between 15 and 16; on the same ossicle in a *Heliometra eschrichti,* between 36 and 39. I found about the same variation in *Promachocrinus kerguelenensis,* where the septa on Br 3 varied between 27 and 30; the type was otherwise, however, here as everywhere else, uniform within the same species. In strongly multibrachiate forms, the size of the segment and the number of septa may vary a little more, according to whether one examines an inner or an outer arm and to which number of the axillaries the arm in question is standing on (cf. e. g. *Capillaster*, *Comantheria*, *Stylometra*). Distally of the first syzygy the number of septa in a lesser number of ligamentary articulations may increase a little, but the septa decrease in number fairly soon, which is a natural consequence of the distal parts of the arms being younger and more slender than the proximal ones. Br 91 (about the 30th hypozygal ossicle) in a full-grown *Heliometra eschrichti* (length of arms about 200 mm.) had only 22 septa, consisting of 7 ventral rows of tubercles and 15 more or less incomplete septa. The next hypozygal (Br 94) had the same number of septa. In the small species *Isometra vivipara* (length of arms ± 60 mm.) Br 3 (1st hypozygal) had 14 septa. Here already the 4th or 5th syzygial articulation was developed as a synostosis, although not a close one, and lacked septa.

Larger and coarser forms have usually, for the systematic unity to which they belong, an unusually large number of septa, while lesser and more delicate forms have an unusually low number.

For the reason given above young, not yet mature, individuals have fewer septa than full-grown ones of the same species. A young *Heliometra eschrichti* from Taimyr (C. ± 18 mm.) had in two cases on the distal end of a Br 3: 18 septa; 2nd hypozygal (Br 9) had 18, and 3rd (Br 14) 15 septa. Another young of the same species from E. Greenland (C. 18 mm., arms 65 mm.) had on the distal end of Br 3 20 septa (one may compare the figures for full-grown specimens given above). A young of *Catoptometra magnifica minor* (length of arms 35 mm.) had 11 septa, 2 of them complete forming an indistinct dorso-ventral ridge. on the distal end of I Br 1. Br 3 had 16 septa (2 of them ventral beams and 6 complete septa). Degree of strength 1. No areola. Br 9: 14 septa, Br 14: 12 septa. A full-grown *Catoptometra rubroflava*



Figg. 56—73. 56—58) *Antedon petasus* a young specimen, arms 20 mm. 56) I Br 1 dist., 57) Br 1 dist., 58) Br 3 dist., $^{38}/_{1}$. 59) *Catoptometra magnifica minor*, young specimen, arms 35 mm., I Br 1 dist., $^{20}/_{1}$. 60) *Ptilocrinus pinnatus* Br 5 dist., $^{16}/_{1}$. 61) *Metacrinus nobilis tenuis* I Br 1 dist., $^{8}/_{1}$. 62) *Comissia peregrina magnifica* Br 3 dist., $^{10}/_{1}$. 63) *Comatula pectinata* Br 1 dist., $^{16}/_{1}$. 64) *Comaster serrata* I Br 1 dist., $^{20}/_{1}$. 65) *Comantheria grandicalyx* Br 3 dist., from the outer side of a IV Ax, $^{10}/_{1}$. 66) *Comanthus japonica* II Br 3 dist., $^{10}/_{1}$. 67) *Catoptometra rubroflava* I Br 1 dist., $^{16}/_{1}$. 68) *Eudiocrinus indivisus* Br 3 dist., $^{16}/_{1}$. 69) *Amphimetra crenulata* Br 3 dist., $^{16}/_{1}$. 70) *Stephanometra spicata* Br 3 dist., $^{16}/_{1}$. 71) *Pontiometra andersoni* Br 3 dist., $^{10}/_{1}$. 72) *Mariametra subcarinata* Br 3 dist., $^{20}/_{1}$. 73) *Tropiometra afra macrodiscus* Br 3 dist., $^{8}/_{1}$.

(length of arms ± 100 mm.) had on I Br 1 28 septa, Br 3: 25 septa, Br 9: 24 septa. A young of *Antedon petasus* (length of arms ± 16 mm.) had 2 (complete) very weak septa, visible only with the strongest magnification.

Comasteridae.

Comatella brachycirra. Arm-length ± 50 mm. The distal end of Br 3[1]: Septa 15 (2 of them ventral beams, 5 complete, broad septa). Areola narrow but stout. Degree of strength of the septa: 3. In another case the septa were 17. Br 16: 13 septa.

Comissia peregrina magnifica. Length of arms ± 150 mm. Br 3: septa 30, degree of strength 4 (2 ventral beams, 11 complete septa, one of them forked, 16 incomplete septa). Areola of medium breadth, stout and well marked (fig. 62). Br 13 (2nd hypozygal): 27 septa (13 incomplete septa, 3 ventral rows of tubercles). The septa run out into the dorsal margin of the ossicle.

Capillaster sentosa. Arm-length ± 90 mm. II Br 2: 45 septa (2 ventral beams, 6 complete septa), III Br 2: 44 septa (2 ventral beams, 8 complete septa) strength 4, a distinct areola, some septa forked. In 3 other cases the number of septa is 44, 43, and 42. IV Br 2: 37, 38, 39, and 43 septa, V Br 2: 33 and 38 septa, Br 2 (after V Ax): 28 and 25 septa (2 complete). In a 5th case the number of septa on a IV Br 2 is 44 (2 of them ventral beams). On the following Br 2 (case 1) the septa were 40 (2 complete septa), a narrow but distinct areola; degree of strength 3, in the 2nd case the Br 2 and 3 would not separate in spite of violent boiling in KOH (anchylosis). Br 29 (2nd hypozygal) 34 septa (2 ventral beams, 6—7 very small tubercle-shaped marginal and 3 complete septa), degree of strength 4. In another case 2nd hypozygal (± Br 31) had 29 septa.

Comatula pectinata. Arm-length ± 70 mm. I Ax (proximal face, the 1st epizygal ossicle): 58 septa, degree of strength 3 - 4. 45 septa are dorsally or laterally directed, the 13 septa directed ventrally are incomplete. Of the 45 dorsal ones 19 are complete, some septa are forked. The areola is indistinct. The surface of the ossicle is not as usual even or evenly curved, but divided into 3 or 4 faces which stand somewhat obliquely to one another and on different levels in the horizontal plane, when the ossicle is viewed from the proximal end (it recalls e. g. the proximal end of the metacarpal III of a horse). Over these faces the 58 septa run. Br 1: 42 septa, 8 of them ventrally directed and 34 dorsally (15 complete septa) (fig. 63). In another case 43 septa, of which 4 are rows of tubercles. Br 3 (2 cases investigated), 39 and 40 septa respectively. Br 8: 42 septa, Br 15: 43 septa, Br 20: 44 septa (10 of them complete).

---

[1] When not otherwise stated, the distal face of the ossicle is always meant.

— The areola is narrower than in the preceding species. Septa distinct, but broad and rather low.

Comaster delicata grandis. Arm-length ± 110 mm. Br 3: 34 septa, strength 3 (6 ventral rows of tubercles). Areola broad, but low and rather indistinct. In another case 37 septa.

Comaster serrata. Arm-length ± 60 mm. I Br 1 is a pseudosyzygy. Areola rather broad with 5 finished tubercle-shaped septa. Outside these, two rings of tubercles concentrically arranged. Degree of strength 3 (fig. 64). Br 3: 19 septa (of which 10 are complete) broad, low. Areola narrow.

Comantheria grandicalyx. Arm-length ± 120 mm. IV Br 3: about 31 septa, strength 4. All septa are incomplete and do not reach the stout areola. Between the areola and the inner end-points of the septa there is a ring of 8 or 9 tubercles. A stout ventral beam. There is also a similar short, finished, dorsal one. Br 3 (on the outer side of a division-series): 31 incomplete septa. As before there is an inner ring of (11) tubercles. One distinct synapticle-ring dorsally. The ventral beam rather indistinct. Areola stout (fig. 65). Br 3 (on the outer side of a division-series): 29 septa (3 of them complete ones). The ring of tubercles developed on one side only (6 tubercles). The ventral beam stout, lobated. A hypozygal ossicle from the distal parts of the arms with 15—17 septa. Degree of strength 3. All septa are incomplete. The areola narrow and insignificant.

Comanthus japonica. Arm-length ± 110 mm. II Br 3: ± 44 septa, strength 4 (21 complete septa, most of them finished, 5 ventral rows of tubercles, and 18 incomplete septa). Areola stout, well marked and rather broad (fig. 66). Br 26 (4th brachial hypozygal): 35 septa (of which 11 are complete). Areola rather narrow.

Zygometridae.

Catoptometra rubroflava. Arms ± 100 mm. I Br 1: 28 septa (of which 8 are complete) broad, rather low, strength 3(—4). Areola of medium breadth (fig. 67). Br 3: 25 septa, in another case 23. Br 9: 24 septa.

Zygometra microdiscus elegans. Arm-length 105 mm. IV Br 3: 30 septa (± 13 complete), degree of strength 3. Areola absent.

Eudiocrinus indivisus. Arms ± 70 mm. I Br 2 proximally: 16—17 septa. Br 3 (dist.): 21 septa, strength 2, especially towards the centre very low. Areola indistinct (fig. 68).

Himerometridae.

Himerometra magnipinna. Arms 105 mm. III Br 3: 35 septa, strength 2. Septa rather indistinctly marked towards the areola, which is also indistinct and situated in a central concavity.

Amphimetra crenulata. Arms ± 95 mm. Br 3: 41 septa, degree of strength (2—)3. Two stout, ventral beams, about 7 complete septa. The intervals between the septa are rather narrow. Areola narrow and rather indistinct (fig. 69). Br 16 (2nd hypozygal): 48 septa (2 ventral beams, ± 13 complete septa). Br 31 (3rd hypozygal): 50 septa.

Stephanometridae.

Stephanometra spicata. Arm-length 135 mm. Br 3: 31 septa, strength 3. (2 ventral beams, 1 complete septum) (fig. 70). Br 3 in another case with 29 septa (2 complete). Areola narrow, but rather distinct.

Mariametridae.

Pontiometra andersoni. Arm-length ± 160 mm. Br 3 (after a V Ax): 36 septa. (2 ventral beams, about 5 complete septa) strength 4 (fig. 71). Br 3 in other cases (after IV and V Ax) with 37, 39, and 39 septa. Areola stout, well marked, of medium breadth.

Liparometra grandis. Arms ± 120 mm. Br 3 with 37 septa (2 of them indistinct ventral beams and 10 complete septa), strength 3. Areola distinct. Br 9: 31 septa.

Lamprometra protectus. Arm-length 90 mm. Br 3 (after a IV Ax): 24 septa (2 ventral beams, 6 complete septa), degree of strength 4. Areola distinct, of medium breadth. In another case 23 septa. Br 22 (2nd hypozygal) 22 septa, Br 33 (3rd hypozygal) 24 septa (2 incomplete ventral beams, 5 complete septa). Distal Br segments (about Br 100—110, ± 10th hypozygal): 16 (incomplete) septa. The following hypozygal with 14 incomplete septa. Degree of strength (1—)2.

Mariametra subcarinata. Arms 60 mm. Br 3: 15 septa (including one ventral beam and 2 complete septa), strength 4—3 (fig. 72). In other cases the septa are 15, 16, 16 (with 3, 5, and 6 complete septa). Areola rather narrow, but usually stout.

Tropiometridae.

Tropiometra afra macrodiscus. Arm-length 190 mm. Br 3: ± 52 septa (the complete ones are about 25, some of them are finished) degree of strength 4. The ventral part of the joint face with rather irregular pits and a ring of tubercles which is synapticularly arranged. Areola large and stout, protruding as a small cone which rises from a surrounding concavity (fig. 73). In another case I counted 51 septa (± 27 of them complete).

Colobometridae.

Cenometra bella. Arm-length 90 mm. Br 3: 21 septa (2 of them indistinct ventral beams and 10 complete septa), degree of strength 3 (fig. 74). Br 30 (2nd hypozygal): 19 septa (about 6 complete). Reminds one of the *Liparometra*-type.

Cyllometra disciformis. Arm-length 90 mm. Br 3: 16 septa (2 ventral beams, 9 complete septa), degree of strength 3. Areola narrow, rather indistinct. Br 13 (2nd hypozygal): 17 septa, Br 18: 14 septa, Br 23: 15 septa, Br 29: 13 septa, Br 35 (6th hypozygal): 13 septa. Strength 1–2. Areola lacking.

Oligometrides adeonae. Arms 60 mm. Br 30: 30 septa (13 of them complete, one ventral beam), degree of strength 3. Areola indistinct (fig. 75). Br 19 (2nd hypozygal): 24 septa (ventral beam indistinctly bifurcated, about 11 complete septa). Traces of synapticulæ.

Austrometra thetidis. Arm-length ± 40 mm. Br 3: 15 septa (of which 5–6 are complete), strength 2. Areola rather narrow, but distinct, with a broad, smooth area united with the ventral part of the joint face.

Calometridae.

Pectinometra flavopurpurea. Arms 70 mm. Br 3: 14 septa (2 of them complete), strength 2. The ventral beam very broad. Areola broad and stout (fig. 76). Br 13: 15 septa, Br 20 (3rd hypozygal) ± 15 septa (similar to those of *Mariametra*).

Neometra multicolor. Arm-length ± 60 mm. Br 3: 19 septa (2 ventral beams, 5 complete septa), degree of strength 3. Areola broad and stout, though rather low (fig. 77), Br 13 (2nd hypozygal): 15 septa (5–6 of them complete).

Thalassometridae.

Asterometra anthus. Arms 80 mm. Br 3: 29 septa (14 complete), strength 3. Septa forked in some cases. Areola narrow. A concentric furrow appears about midway between the border of the face and the lumen (fig. 78). In another case the septa were 27. Br 9 (2nd hypozygal): 28 septa.

Ptilometra mülleri. Arm-length 50 mm. Br 5 (1st hypozygal) 21 septa (2 indistinct ventral beams), degree of strength 3. Areola indistinct. A concentric furrow as in *Asterometra* (here closer to the periphery of the ossicle). Br 15: 19 septa (about 9 complete). Br 23 (3rd hypozygal): 18 septa (7 complete).

Stylometra spinifera. Arms ± 90 mm. Br 3 (after a II Ax): 23 septa (2 ventral beams, indistinctly separated, 9 complete septa), degree of strength 3—4. Areola broad and stout. A couple of septa forked, some ventral ones partly subdivided into rows of tubercles. Br 3 (after a III Ax): 19 and 20 septa (ventral beam not subdivided). Areola as before. Septa somewhat lower.

Oceanometra annandalei. Arms 80 mm. II Br 3: ± 18 septa, Br 3: 19 septa (one ventral beam, 6 complete septa), degree of strength 2—3. Areola broad though rather low. Septa stout, running out as ribs into the margin of the ossicle. A marginal growth-ledge (fig. 79).

Stenometra dentata. Arm-length ± 50 mm. Br 3: 18 septa (2 low ventral beams, 8 complete septa), strength 2—3. Areola rather narrow and indistinct.

Charitometridae.

Perissometra cf. *aranea.* Arms ± 80 mm. Br 3: 22 septa (2 ventral beams, 4 complete septa), degree of strength 2. Areola indistinct. Br 13: 20 septa (2 ventral beams, 10 complete septa), Br 18: 19 septa, areola narrow. Br 23: 17 septa, Br 29: 17 septa (2 of them complete), Br 34 (6th hypozygal): 14 septa (all incomplete), no areola.

Crossometra, septentrionalis. Arms 70 mm. II Br 3: 17 very low septa (about 7 of them incomplete), degree of strength 1. Br 1: 14, 14, and 16 septa. Br 3: 16 septa (2 ventral beams, 4 complete septa). Areola of medium breadth, but low. Br 11: 15 septa (2 ventral beams, 3 complete septa), strength 2. Br 1 in one case a compromise between a synarthrial and syzygial articulation (fig. 80).

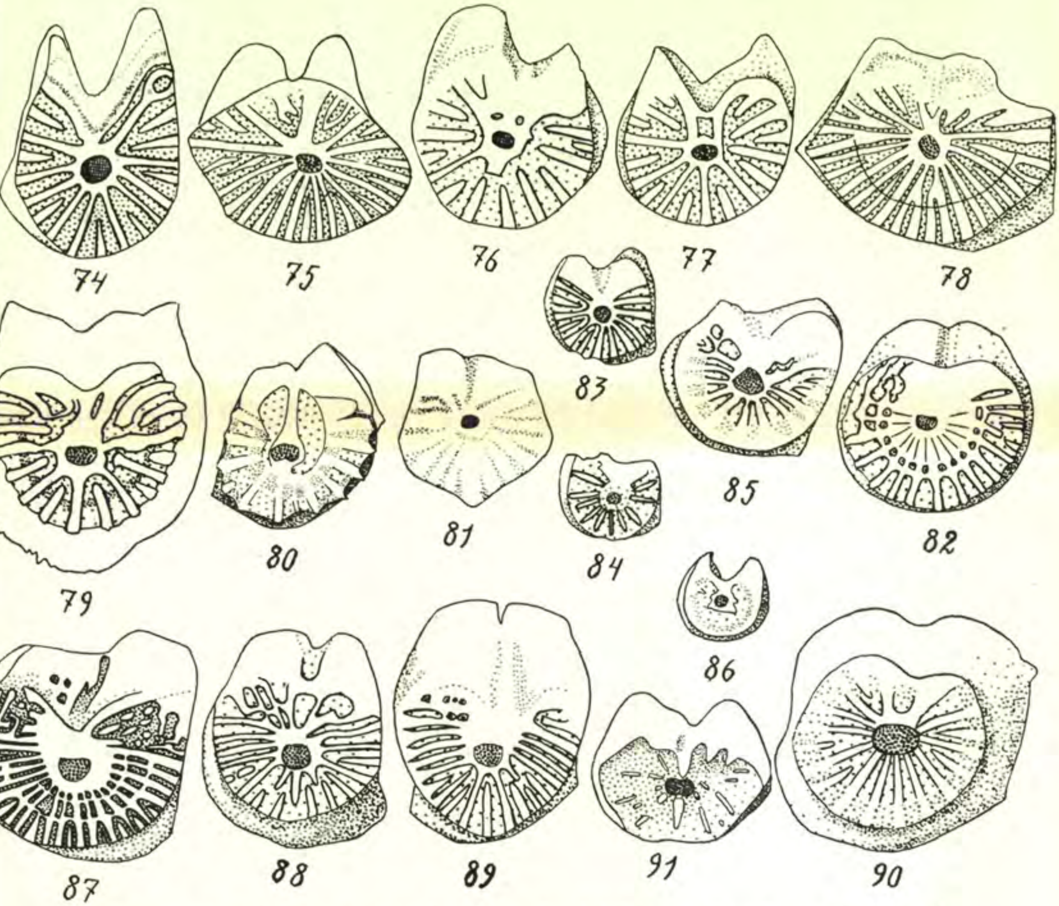
Diodontometra bocki. Arm-length 60 mm. Br 3: 16 septa (one partly divided and weakly developed ventral beam, 6—7 complete septa), degree of strength 1. Areola distinct (fig. 81).

Notocrinidae.

Notocrinus virilis. Arms 75 mm + (probably about 125 mm). Br 3: 18 septa (3 or 4 of them finished, only 2 incomplete), degree of strength 2. The areola itself is narrow, but there appears outside this a very broad, almost smooth area taking up about half the space between the lumen and the margin of the ossicle. Marginally to this area appears a stout concentric synapticula and beyond this a similar weaker one (fig. 82). In another case there were 19 septa (about 4 of them incomplete). Br 8 (2nd hypozygal): 19 and 20 septa respectively. Degree of strength 1. 2—3 weak synapticulæ.

Antedonidae.

Antedon petasus. Arms ± 80 mm. Br 3: 21 septa (12 of them complete), degree of strength 2—3. Areola indistinct. In another case



Figg. 74—91. 74) *Cenometra bella* Br 3 dist., $^{20}/_{1}$. 75) *Oligometrides adeonae* Br 3 dist., $^{16}/_{1}$. 76) *Pectinometra flavopurpurea* Br 3 dist., $^{20}/_{1}$. 77) *Neometra multicolor* Br 3 dist., $^{20}/_{1}$. 78) *Asterometra anthus* Br 3 dist., $^{16}/_{1}$. 79) *Oceanometra annandalei* Br 3 dist., $^{20}/_{1}$. 80) *Crossometra septentrionalis* Br 1 dist., $^{16}/_{1}$. 81) *Diodontometra bocki* Br 3 dist., $^{16}/_{1}$. 82) *Notocrinus virilis* Br 3 dist., $^{10}/_{1}$. 83) *Compsometra serrata* Br 3 dist., $^{20}/_{1}$. 84) *Clarkometra elegans* Br 3 dist., $^{20}/_{1}$. 85—86) *Isometra vivipara*, 85) Br 3 dist., 86) Br 26 (5th hypozygal) dist., $^{20}/_{1}$. 87) *Heliometra eschrichti* Br 3 dist., $^{8}/_{1}$. 88) *Leptometra celtica* Br 3 dist., $^{20}/_{1}$. 89) *Poliometra prolixa* Br 3 dist., $^{16}/_{1}$. 90) *Pentametrocrinus diomedeae* Br 4 dist., $^{20}/_{1}$, 91) *Atelecrinus helgae* Br 3 dist., $^{16}/_{1}$.

19 septa. Br 9: 19 septa. With an abnormal, large and stout areola. Br 15: 19 septa, Br 19: 19 septa (12 are complete). A narrow, distinct areola. In the two last hypozygals, moreover, a distinct ventral beam.

Compsometra serrata. Arm-length 30 mm. Br 3: 14 septa (9 of them complete), degree of strength 2. Areola narrow (fig. 83). In another case 12 septa (about 10 of them complete). Br. 9: 13 septa, including 2 indistinct ventral beams. Br 14 (3rd hypozygal): 14 septa.

Clarkometra elegans. Arms 25 mm. Br 3: 11 septa (scarcely any complete), strength 2—3. Areola narrow, indistinct (fig. 84).

Isometra vivipara. Arms 60 mm. Br 3: 14 septa (10 of them complete), strength 2. Areola narrow. Most septa finished half-way to the border of the ossicle (fig. 85). From the 4th or 5th syzygy the septa are lacking and the connection becomes a loose synostosis, i. e. round the lumen a rather marked areola, situated in the centre of a somewhat concave face (fig. 86).

Heliometra eschrichti. Arm-length about 200 mm. Br 3: ± 36 septa (A pair of rather distinct ventral beams, 22 complete septa, ± 6 ventral rows of tubercles), degree of strength 4. Areola dorsally rather moderate, ventrally very broad. 2—3 concentric synapticulæ; the most central one is the stoutest (fig. 87). In two other cases 39 septa (2 ventral beams, 22 complete septa, 6 tubercle-rows). Br 26 (6th hypozygal): 29 septa (two ventral rows of tubercles). Areola narrow. Septa somewhat lower than before.

Promachocrinus kerguelenensis. Arms ± 150 mm. Br 3: 27 septa (11 of them incomplete, and on each side of the median line 3—5 ventral tubercle-rows), degree of strength 4. In another case 30 septa (8 rows of tubercles). Areola narrow or of medium breadth, indistinct, sometimes lacking. Br 9: 32 septa, Br 14 (3rd hypozygal): 34 septa (7 ventral rows of tubercles; moreover many septa partly subdivided into rows of tubercles).

Leptometra celtica. Arms ± 70 mm. Br 3: 24 septa (2 of them ventral beams, ± 12 complete septa, 3 of them finished), strength 2. Areola narrow, indistinct (fig. 88). In another case 19 septa, Br 9: 19 septa, Br 15 (3rd hypozygal): 17 septa.

Psathyrometra wireni. Arms ± 60 mm. Br 3: 16 septa (11—12 of them complete), degree of strength 1. Areola narrow and indistinct. One indistinct, concentric synapticula. Br 9 (2nd hypozygal): ± 16 very low septa.

Poliometra prolixa. Arms ± 100 mm. Br 3: 21—22 septa (13 of them complete), strength 2. Areola ventrally in broad contact with the smooth ventral part of the ossicle, dorsally narrow and indistinct. The joint face is somewhat undulating (fig. 89). In another case ± 22 septa. Br 9: 21, Br 19 (3rd hypozygal): 18 septa.

Hathrometra tenella var. *sarsii.* Arm-length ± 50 mm. Br 3: 22

septa (2 ventral beams, 9 complete septa), degree of strength 3. No areola. In another case also 22 septa. Br 9 in 2 cases ± 18 septa. Br 14 (3rd hypozygal) in 2 cases 18 and 19 septa respectively. Degree of strength 2–3.

Pentametrocrinidae.

Pentametrocrinus diomedeae. Arm-length ± 100 mm. Br 4 (1st hypozygal): 18 septa (2 ventral beams, 11 complete septa), degree of strength 2—1. Areola scarcely indicated (fig. 90). Br 9: 16 septa.

Thaumatocrinus jungerseni. Arms ± 70 mm. Br 4: 11 septa (one ventral beam, 5—6 complete septa), degree of strength 2—3. No areola. Br 9: 11 septa (2 ventral beams), Br 16 (3rd hypozygal): 11 septa (2 ventral beams, 5 complete septa).

Atelecrinidae.

Atelecrinus helgae. Arm-length ?, perhaps 90 mm. Br 3: 10—11 septa (one broad ventral beam with a small ventral pit, ± 10 complete and finished or interrupted very narrow septa, 4 of them tubercles only, besides 3 ventral tubercles continuous with the ventral smooth part of the ossicle. Degree of strength 2–3. No areola (fig. 91). Br 7 (2nd hypozygal): 12 septa (one ventral beam, 11 very narrow and rather complete septa). Degree of strength 2.

Atopocrinus sibogae. Length of arms ?. According to A. H. CLARK Br 7 (2nd hypozygal) has only 5 (complete) septa (cf. 1915 c, fig. 227, 1922, pp. 165–166). Further CLARK says that there occur two small, ventral muscle bundles. If this statement can be verified this species presents syzygial connections of a very interesting and ancient type reminding one of the oldest articulate type. I have, however, never been able to find any trace of rudimentary muscles in ligamentary articulations either in sections through arms of young Comatulids, or in regenerating arms, or in ligamentary connections of *Ptilocrinus pinnatus, Rhizocrinus lofotensis,* or *Ilycrinus carpenteri.* Until it has been verified further I prefer, therefore, to regard the statement with some reservation.

c. Summary of the description of the immovable connections in the Comatulids.

The statement of A. H. CLARK that the number of syzygial septa is: "to a certain extent proportionate to the size of the articular face, and is greater in the *Oligophreata* than in the *Macrophreata*" (1922, p. 165), taken on the whole thus holds good. Some important exceptions, however, are found, especially to the latter assertion. Thus the Oligophreate families *Calometridae* and *Charitometridae* have unusually few septa. The same is true about most of the *Thalassometridae* and certain of the *Colobometridae.*

Comasteridae. Septa in proximal syzygies usually numerous (30—58), only in small forms under 20. Septa's degree of strength 3—4. Areola strongly developed, but rather narrow. Plenty of tubercles occur, often ventral tubercle-rows also. Pseudosyzygies sometimes appear among species of the genus *Comaster* between I 1 + 2 (cf. also 1915 c A. H. CLARK, fig. 37). These, like typical syzygies, often replace synarthries. Distal syzygies at an interval of 3—4 oblique articulations normally (exception e. g. *Capillaster*).

Zygometridae. Septa in proximal syzygies 16—30, degree of strength 2—3. Areola indistinct. A syzygy replacing the most proximal synarthry. The young stages of these syzygies often remind one of the pseudosyzygies in *Comaster.* Number of incomplete septa large. Distal syzygies at fairly short intervals: in *Eudiocrinus* with 3 and in *Catoptometra* with 4—8 muscular articulations. In *Zygometra* long intervals (10—30 muscular articulations).

Himerometridae. Septa of proximal syzygies 35—50, degree of strength 2—3. Areola indistinct. Sometimes 2 clearly marked ventral beams. Number of incomplete septa rather large. Distal syzygies at long intervals [(6)10—26 muscular articulations].

Stephanometridae. Septa of proximal syzygies 30, degree of strength 2—3. Areola narrow but distinct. Ventral beams 2. Very few complete septa. Distal syzygies at an interval of 5—10 muscular articulations.

Mariametridae. Proximal syzygies with 25—40 septa, excepting in the delicately built genus *Mariametra,* where we only have 15 septa[1], degree of strength 3—4. Areola well-developed, 2 distinct ventral beams. Few complete septa. Occasionally incidental irregularities in the distribution of the proximal ligamentary connections so that syzygies might replace synarthries. Distal syzygies at fairly long intervals (7—18 muscular articulations).

Tropiometridae. The most proximal syzygy's septa ± 50, degree of strength 4. Areola stout, on a little cone. A good many complete septa. Distal syzygies with 5—10 muscular articulations between them.

Colobometridae. Proximal syzygies with 15—30 septa, degree of strength 2—3. Areola narrow and distinct or indistinct. Rather a large number of complete septa. Great multiformity within this family: *Cenometra* reminding one of *Liparometra, Oligometrides* of *Tropiometra, Cyllometra* of the Antedonid type, *Austrometra* most nearly of certain *Thalassometridae.* Distal syzygial intervals 3 — > 10 muscular articulations.

---

[1] The heavily granulated disk also shows this genus to be a primitive type.

Calometridae. Proximal syzygies with 13—19 septa, degree of strength 2—3. Areola broad and stout. Few complete septa. Distal syzygies with 3—15 muscular articulations between them.

Thalassometridae. Proximal syzygies with 19—29 septa, degree of strength 2—3. In *Ptilometrinae* the areola is indistinct, in *Thalassometrinae* it is generally broad and stout. A concentric furrow appears very often parallel to the margin of the ossicle. Septa sometimes forked; 1—2 indistinct ventral beams. Proximal syzygies in *Ptilometra* and even *Asterometra* often irregular, sometimes also replacing synarthries (cf. also 1922 Gislén, p. 104). Distal syzygies usually with 5—10 muscular articulations between them (in exceptional cases 4—18).

Charitometridae. Proximal syzygies with 15—22 septa, degree of strength 1—2. Areola usually indistinct. Ventral beams 2, more or less indistinct. Rather few complete septa. Irregularities in the distribution of the proximal syzygies usual, often replacing synarthries.[1] Distal syzygies at an interval of 5—10 muscular articulations.

Notocrinidae. About 20 septa in proximal syzygies, degree of strength 2. Outside the narrow areola a broad, almost smooth area. Synapticulae occur. Most of the septa reach to the large, nearly smooth area and to the areola. Syzygial interval in the distal parts of the arm is 4—10 muscular articulations.

Antedonidae. Septa of proximal syzygies 11—24, only in the very large *Heliometrinae* from 27—39, degree of strength 1—3(—4 in *Heliometrinae*). Areola lacking or indistinct (exception *Heliometra,* where in full-grown specimens it reminds one somewhat of the conditions described in *Notocrinus*). Rows of tubercles in *Heliometrinae* alone. Many complete septa, usually more than half the total number. Distal syzygies at an interval of 2—4 muscular articulations.

Pentametrocrinidae. Proximal syzygies with 11—18 septa, degree of strength 1—3. No areola. Half or even the majority of the septa complete. Syzygies at an interval of 2—6 muscular articulations, distribution rather irregular.

Atelecrinidae. Few septa in the proximal syzygies, not more than 12, degree of strength 2—3. No areola. Generally complete septa, sometimes finished, and more or less like tubercles. Distal syzygies at an interval of 2—7 muscular articulations.

---

[1] N. B. 1922, Gislén, p. 124 $\begin{cases} \text{Br } 1\text{—}2\ 3\text{—}4 \\ \text{Br } 1\text{—}2\ 3\text{—}4 \end{cases}$ is a misprint for $\begin{cases} \text{Br } 1\text{—}2\ 3+4 \\ \text{Br } 1\text{—}2\ 3+4 \end{cases}$.

2. **Movable ligamentary connections.**

a. Stalked Crinoids.

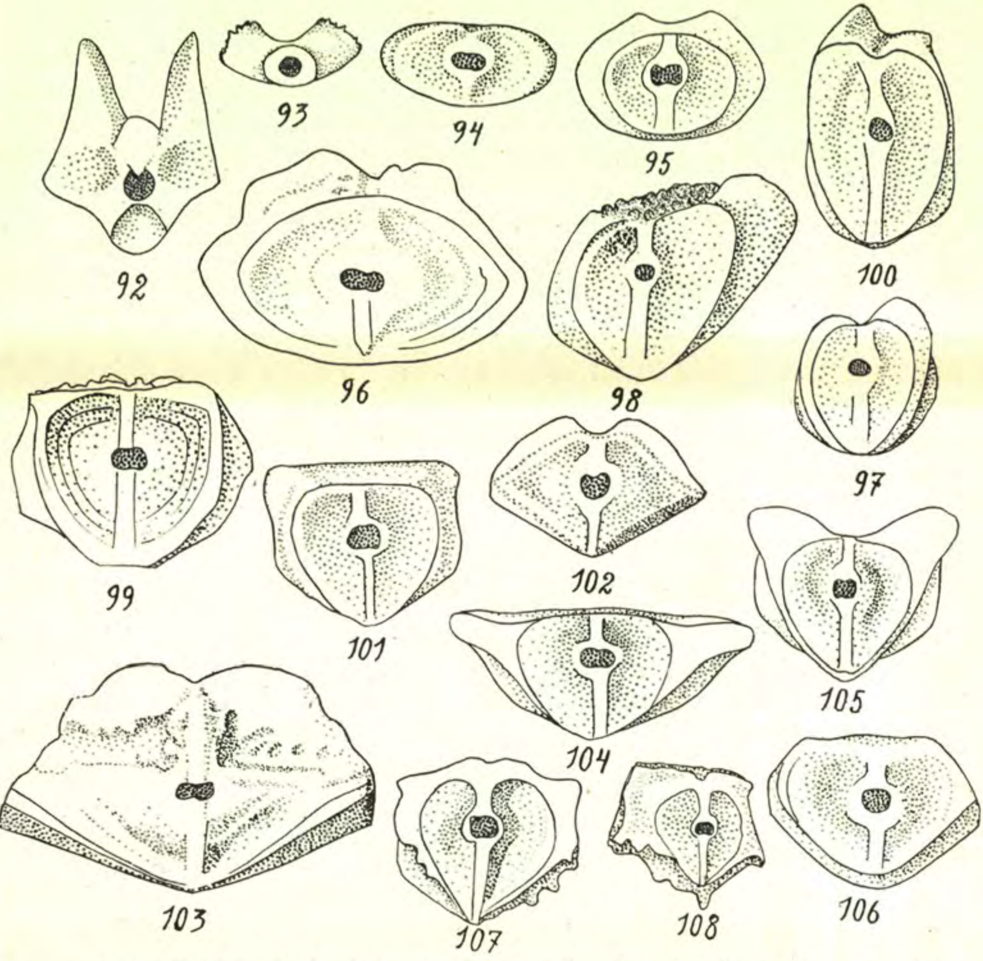
In the Pentacrinids the ligamentary articulations, as mentioned above, are generally immovable and more or less pronouncedly synostotic. In the division series and the first Br ligamentary articulation, however, evident indications of synarthries are sometimes developed. This is the case in *Hypalocrinus naresianus* and the *Isocrinus* species (1884, P. H. CARPENTER, Pl. 30, figg. 11, 12, 16, 17, Pl. 32, figg. 16, 17, Pl. 34, figg. 3, 6; 1912, DÖDERLEIN, p. 22). In *Isocrinus decorus* (1884, P. H. CARP., Pl. 37, fig. 4) the distal synostoses seem to indicate a development from this towards the trifascial type of articulation.

The latter we find developed typically in certain Bathycrinids, such as *Ilycrinus carpenteri* (fig. 92) as well as in *Bathycrinus aldrichianus* and *B. campbellianus* (1884, P. H. CARP., Pl. 7 a, figg. 19, 20, 22). *Rhizocrinus lofotensis* has, as M. SARS showed (1868, Tab. 5, figg. 52, 58, 69, 70) and as I have had an opportunity of corroborating, a loose synostotical type in the ligamentary articulations. *Democrinus rawsoni* (1884, P. H. CARP., Pl. 10, figg. 17, 18) seems to have an intermediate type between synarthy and synostosis. *Phrynocrinidae* and *Hyocrinidae* lack movable ligamentary articulations.

b. Comatulida.

Although the degree of flexibility is developed very differently in different forms, still the synarthrial type taken as a whole is generally the same. Cryptosynarthries may appear among *Comasteridae* (cf. e. g. 1915 c, A. H. CLARK, fig. 36). Here as in pseudosyzygies, and in the usual syzygy, the power of flexibility is practically nil.

Seen from the dorsal side, however, the synarthrial articulation shows a fair amount of variation. The articular line may be straight and not attended by any process; it may be straight and have a more or less strong process, directed straight outwards, attending it, the synarthrial tubercle; and it may be curved and the process (from the more distal joint only) directed proximally and encroaching on the more proximal segment, synarthrial backward projection. It is of importance to keep these two last-mentioned types apart. In the former only a dorsal prolongation of the synarthry takes place, thus causing an enlargement of the synarthrial face of the facet, but generally no increased flexibility worth mentioning, as the synarthrial fibres are not prolonged. To the latter type, on the contrary, great possibilities as regards flexibility are always attached, with long ligamentary fibres in large lateral notches between the ossicles.



Figg. 92—108. 92) *Ilycrinus carpenteri,* Br 7 dist., $^{38}/_{1}$. 93) *Hathrometra tenella* var. *sarsii*, Pentacrinula, no cirri have yet appeared. Proximal end of I Ax, $^{60}/_{1}$. 94) *Comissia cf. spinosissima,* I Br 1 dist., $^{20}/_{1}$. 95) *Comatella brachycirra,* I Br 1 dist., $^{20}/_{1}$. 96) *Comanthus japonica,* I Br 1 dist., $^{8}/_{1}$. 97) *Catoptometra rubroflava,* Br 1 dist., $^{10}/_{1}$. 98) *Himerometra magnipinna,* II Br 1 dist., $^{8}/_{1}$. 99) *Stephanometra spicata,* I Br 1 dist., $^{10}/_{1}$. 100) *Pontiometra andersoni,* V Br 1 dist., $^{10}/_{1}$. 101) *Lamprometra protectus,* I Br 1 dist., $^{16}/_{1}$. 102) *Oligometrides adeonae,* I Br 1 dist., $^{10}/_{1}$. 103) *Tropiometra afra macrodiscus,* I Br 1 dist., $^{6}/_{1}$. 104) *Neometra multicolor,* I Br 1 dist., $^{16}/_{1}$. 105) *Pectinometra flavopurpurea,* I Br 1 dist., $^{16}/_{1}$. 106) *Asterometra anthus,* I Br. 1 dist., $^{10}/_{1}$. 107—108) *Stenometra dentata,* 107) I Br 1 dist., $^{16}/_{1}$. 108) Br 1 dist., $^{16}/_{1}$.

We find, as a rule, very little flexibility among the *Oligophreata* from *Comasteridae* to *Calometridae*. The backward synarthrial projection among them also is very slight or lacking. Among *Macrophreata* together with most of the *Thalassometridae* and *Charitometridae* the synarthries allow, on the contrary, an especially strong lateral flexibility and the backward synarthrial projections are often developed enormously. They reach their maximum in *Zenometrinae* and *Bathymetrinae*. We find extraordinarily strongly developed synarthrial tubercles arising in solitary cases in different families, e. g. in the *Amphimetra* species, in *Neometra diana,* and in *Perometra diomedeae* (cf. A. H. CLARK, 1915 c, figg. 86, 112; 1922: figg. 192, 193, 200).

The synarthries in the youngest stages, as I have mentioned above, tend towards synostoses, but very early we get a stout areola (fig. 93).

Another type of mobile articulations, trifascial ligamentary connections or ligamentary articulation, flexible in a dorso-ventral direction only, are found in some cases among the recent Comatulids. They appear then, however, in the articulation between R and I Br 1 only. They have been observed in *Pontiometra andersoni* (1922, A. H. CLARK, p. 31, and fig. 51) and in *Stephanometra spicata* (fig. 53). Standing extraordinarily near to this type is the radial articulation in *Himerometra martensi* (1922, A. H. CLARK, p. 25 and fig. 41), where the muscles are indicated only rudimentarily as low bands. *Comasteridae* and *Calometridae* have also an articulation between R and I Br 1 which approaches this type. This type of trifascial articulation possesses its greatest interest, however, because several of the Jurassic Comatulids seem to have had a similar articulation between R and I Br 1.

Synarthries in Comatulids.

Comasteridae.

In regard to this family P. H. CARPENTER (1879) has given a number of good figures (Pl. 7, figg. 2, 3, 5, 6) of synarthries in the variable *Comanthus parvicirra*. From a pronounced synarthrial type the articulation seems sometimes to approach the cryptosynarthrial one, observed by A. H. CLARK among the slender-armed varieties of the *Comatula* species (1915 c, fig. 36, 1922, p. 177). The species I have observed generally have fairly typical synarthries. Divergences from this have been met with in the synarthry between I Br 1 and 2. In large species, such as *Comanthus japonica* (fig. 96), the areola round the lumen is very extensive, and the two ligament pits are not equally curved, but are excavated irregularly, here and there. The possibilities of flexion are slight here. The same is the case in those *Comaster* species in which the synarthries are replaced by pseudosyzygies. The small *Comissia* species (fig. 94) as well as *Capillaster sentosa* have an articulation between I Br 1 and 2 which approaches a cryptosynarthry. *Capillaster* may sometimes have but one single synarthry in each ray (between I Br 1 and 2). *Comatula* and *Comatulella(?)* alone lack synarthries. Synarthrial tubercles and synarthrial backward projections are lacking (N. B. *Comatonia* does not belong here).

Zygometridae.

As was pointed out above, the articulation between I Br 1 and 2 is developed as a syzygy. Normal synarthries always appear distally of this between the 2 first postaxillar ossicles (cf. fig. 97). Scarcely any synarthrial tubercles.

Himerometridae.

I have not seen any articulation between I Br 1 and 2, but more distal synarthries are typical (fig. 98). Synarthrial tubercles often knob-shaped, protruding; no synarthrial backward projections.

Stephanometridae.

The synarthrial articulation between I Br 1 and 2 shows a pair of deep and stout pits on both sides of a fairly narrow dorso-ventral beam. A broad contactual margin towards the succeeding ossicle is found in the periphery. The capacity of the articulation is certainly insignificant (cf. fig. 99). The more distal synarthries are typical. No synarthrial tubercles.

Mariametridae.

I have observed the articular-face between I Br 1 and 2 in *Pontiometra andersoni* and in *Lamprometra protectus* (fig. 101). It corresponds in a high degree to that in *Stephanometra.* The more distal synarthries are high and laterally compressed, as in all the forms with numerous arms (cf. fig. 100). Perhaps, however, it is still more pronounced here than in other multibrachiate types. Indistinct synarthrial tubercles.

Colobometridae.

Oligometrides represents a unique type, having rhomboidal joint-facets (fig. 102). Otherwise, among the forms I have observed, the synarthries in this family offer very little of interest. Synarthries have been observed between Br 1 and 2 in *Austrometra, Cenometra, Cyllometra*). No, or weak, synarthrial backward projections.

Tropiometridae.

The synarthrial facet between I Br 1 and 2 in *Tropiometra afra macrodiscus* reminds one very much of the same thing in the large Comasterids. The joint-pits are scarcely marked plainly, are bounded indistinctly, and are rather shallow as well. The flexibility here is certainly slight (fig. 103). Between Br 1 and 2 they are not developed in a semilunar shape, but only the dorsal half of every half-moon is found marked. Both the fossæ, however, are well circumscribed here. No, or only indistinct, synarthrial tubercles.

Calometridae.

RR often shoot up into points here between I Brr 1, and possibly because of this the 1st synarthrial face shows large, wing-shaped appendages on both sides of the joint-facet. The connection, when seen from the dorsal side, is often very close and the mobility, presumably, very poor. The fossæ are, however, well pronounced (figg. 104, 105). The more distal synarthries are of the usual type. The synarthrial tubercles are indistinct in general cases, but extraordinarily large in *Neometra diana. Calometra discoidea* has synarthrial backward projection.

Thalassometridae.

The contour of the synarthrial facet is often somewhat angular owing to the wall-sidedness which occurs in this family. This is specially marked in the more distal synarthries (figg. 106 – 108). The synarthrial facet is somewhat drawn out dorsally into an acute angle, where synarthrial tubercles are found. This is often developed in connection with longitudinal crests on the proximal Br-ossicles. There is never any synarthrial backward projection in *Ptilometrinae,* where the capacity for motion in a lateral direction is slighter than in *Thalassometrinae.* One often finds a synarthrial backward projection in the sub-family last mentioned and at the same time big notches between the joints, thus giving a possibility of greater flexional power laterally. The appearance of the synarthrial facet is approximate to that of the family described next. (Cf. also 1888 P. H. Carp. Pl. 15, fig. 6; 1915 c A. H. Clark fig. 97.)

Charitometridae.

Corresponds in many ways to the preceding family (figg. 109, 110). Has often a longitudinal crest on the proximal ossicles and sometimes synarthrial backward projection. Often big lateral notches. The synarthrial facet often shows a likeness to certain Antedonids, because it is confined to a rather small area of the joint.

Notocrinidae.

The synarthry reminds one of that in *Thalassometridae.* The median dorso-vental ridge is, however, extraordinarily powerful. The areola surrounding the lumen very broad (fig. 111). Synarthrial joint-pits deep. No synarthrial tubercles. A weak synarthrial backward projection.

Antedonidae.

Great variation exists here. It looks, however, as though one might trace the appearance of the synarthrial facets back to two types. The first of these is like that in e. g. *Asterometra* and *Notocrinus.* The joint-facet takes up practically the whole of the joint-face and the synarthrial backward projection is developed moderately (fig. 112). Rarely any synarthrial tubercles (in *Perometrinae). Antedoninae* belongs here, and *Perometrinae,* if this latter group should be reckoned to *Macrophreata, Isometrinae,* (and probably *Thysanometrinae*). The second type has the synarthrial facet restricted to the centre of the joint-face, and outside this a broad area without ligamentary fibres, the synarthrial facet is often prolonged in a dorso-ventral direction, the backward synarthrial projection is generally huge. *Heliometrinae, Zenometrinae,* and *Bathymetrinae* belong here (figg. 113 – 115).

Pentametrocrinidae.

The synarthrial facet takes up practically the whole of the joint-face, but relatively somewhat less in *Pentamentrocrinus* (fig. 116); the joint is narrower in *Thaumatocrinus,* evidently on account of this genus being a X-rayed one. The fossæ are moderately deep. The synarthrial backward projection is distinctly pronounced in *Pentametrocrinus,* imperceptible in *Thaumatocrinus.*

Atelecrinidae.

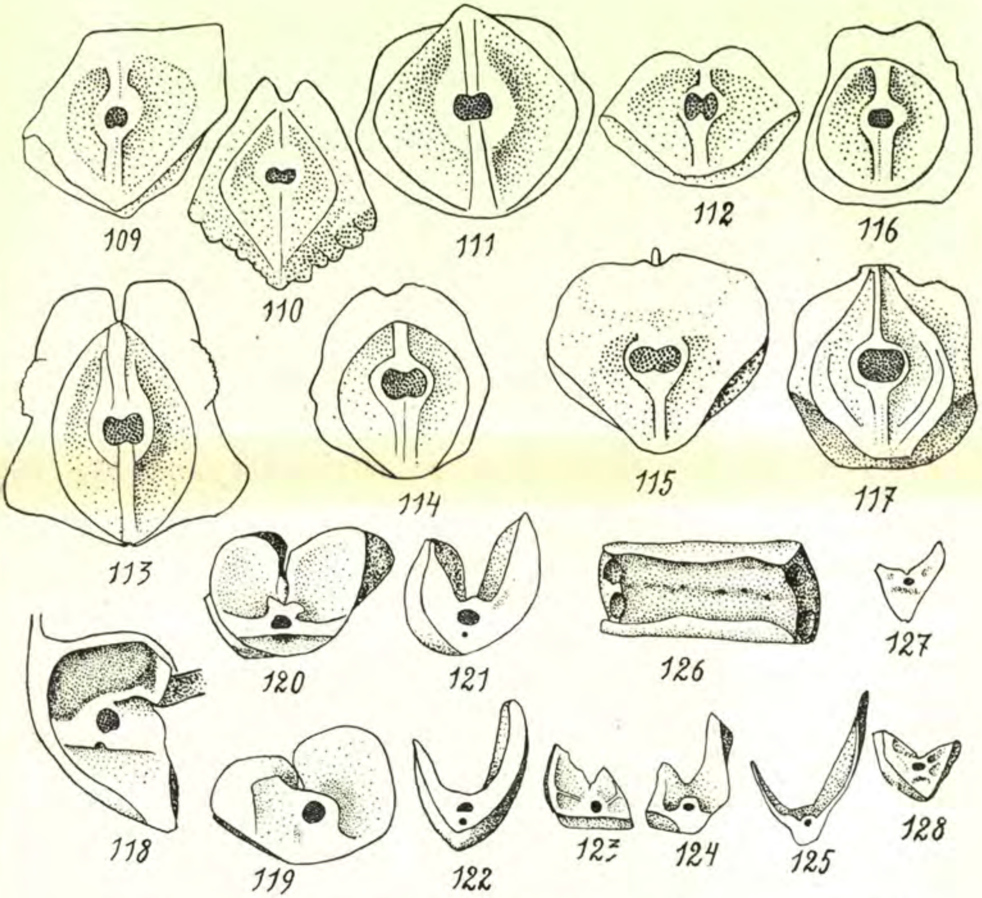
The synarthrial facet is very much like that in *Zenometrinae* (fig. 117). The synarthrial backward projection is distinct.

IV. Articulations of the pinnulars in recent Crinoids.

The information on this question found in the literature on the subject is but scanty. W. B. Carpenter (1866) has reproduced the pinnule-socket on a number of Brr in *Antedon bifida* (Pll. 36, 38). In P. H. Carpenter's first Challenger Report (1884) we find sometimes rather good drawings of the articulation between a Br and a pinnule; in one case even the joint-facet of a distal pinnular joint is reproduced (cf. Pll. 3, fig. 16, 13: 12, 17: 9, 23: 13, 30 a: 12 a, 33: 3, 47: 12). In two solitary cases A. H. Clark has also reproduced the joint-facet on distal pinnulars. (1915 c, fig. 54, 1922, fig. 659). Besides this W. B. Carpenter (1866, p. 724) has given a meagre description of the pinnular facets in *Antedon bifida* and A. H. Clark a very detailed one of the pinnular articulations in *Himerometra martensi* (1922, pp. 185 - 188).

The pinnular articulations seem to be on the whole very monotonously constructed in all the recent Crinoids. This, however, does not prevent us from finding large variations in several details. The typical form may be described as follows:

The articulation between a Br and the 1st pinnular is, as A. H. Clark very rightly emphasizes, an articulation of rather ordinary muscular type. While the angle that is formed between the transverse ridges of the two joint faces on the distal end of an axillary is about 90° (e. g. *Heliometra*, *Himerometra;* the axillary being looked at from the distal end), the transverse ridges of the pinnular facet and that of the brachial joint face at the distal end of a Br form a considerably greater angle usually (*Heliometra* 115°, *Metacrinus* 150°, *Himerometra* ± 165°, *Calometridae,* and others 180°). The pinnular facet on the Br is by this means twisted nearly half way round so that the side that should be the outer lateral one becomes the inner median one and vice versa. It gains such a position that its muscular fossæ still continue adjacent to the muscle pit of the brachial distal facet's pinnular side. The dorsal ligament of the pinnular facet, on the contrary, seems to be removed almost to the maximum distance from the dorsal ligament of the Br-facet, if the Br joint be viewed in plane projection. The pinnular facet-face forms an angle of about 110° with the brachial one, in e. g. *Heliometra, Himerometra;* at the distal end of I Br 2 in *Metacrinus nobilis tenuis* the corresponding angle was 140°. The dorsal ligament of the pinnular facet is sometimes better developed on the side adjacent to the median part of the Br-joint, and narrower on the side facing the lateral part of the Br joint. On the ventral side of the transverse ridge the lateral part, on the contrary, is always more strongly developed. The inter-muscular crest or furrow bends, therefore, considerably towards the median part of the Br joint. The proximal part of the 1st pinnular answers to the



Figg. 109—128. 109) *Crossometra septentrionalis* II Br 1 dist., $^{16}/_{1}$. 110) *Diodontometra bocki* I Br 1 dist., $^{10}/_{1}$. 111) *Notocrinus virilis* I Br 1 dist., $^{10}/_{1}$. 112) *Isometra vivipara* I Br 1 dist., $^{16}/_{1}$. 113) *Heliometra eschrichti* I Br 1 dist., $^{8}/_{1}$. 114—115) *Hathrometra tenella* var. *sarsii* 114) I Br 1 dist., $^{20}/_{1}$. 115) I Br 2 prox., $^{20}/_{1}$. 116) *Pentametrocrinus diomedeae* Br 1 dist., $^{16}/_{1}$. 117) *Atelecrinus helgae* I Br 1 dist., $^{16}/_{1}$. 118—122) *Ptilocrinus pinnatus* 118) Pinnule-socket on Br 6, $^{20}/_{1}$. 119—122) Pinnule on Br 6, 119) 1st pinnular, prox., 120) 1st pinnular, dist., 121) 2nd pinnular, dist., 122) 3rd pinnular, dist., $^{20}/_{1}$. 123—125) *Ilycrinus carpenteri.* 123) 1st pinnular from Br 13, dist., $^{38}/_{1}$. 124) 2nd pinnular from Br 13, dist., $^{38}/_{1}$, 125) distal pinnular from about Br 17, prox., $^{38}/_{1}$. 126—127) *Diplocrinus wyville-thomsoni.* 126) Distal segment of a distal pinnule, viewed from the ventral side, $^{20}/_{1}$. 127) Another distal pinnular of a distal pinnule from the short end, $^{20}/_{1}$. 128) *Metacrinus rotundus* distal segment of distal pinnule, $^{20}/_{1}$.

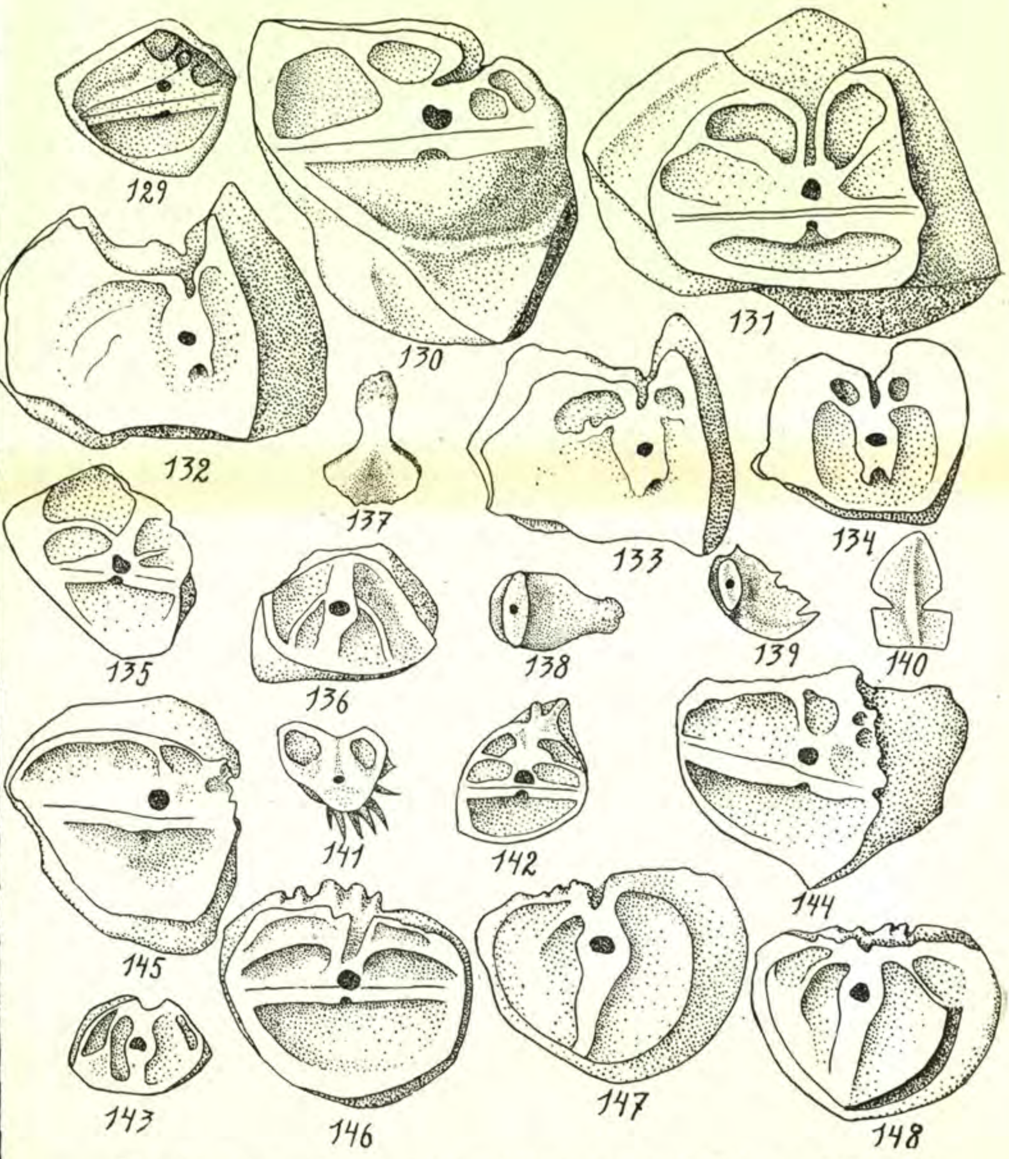
pinnular joint facet described on the brachial ossicle. Here, however, the joint fossæ are often marked indistinctly and the joint facet only bulges irregularly (especially in small forms). When the muscles are contracted in this articulation the pinnule is flexed aborally and in towards the side of the arm.

The proximal and distal facet-faces on the 1st pinnular are very nearly parallel. Also the distal joint face of the 1st pinnular shows here, usually, an almost straight muscular articulation. This, however, is oriented at about a right angle to the proximal facet of the ossicle, so that the transverse ridges of the two joint faces form an angle of about 90°. The proximal facet of the 2nd pinnular corresponds to the distal one of the 1st pinnular. In some Comatulids this articulation is most strongly developed on the adoral side. On contraction of the muscles in this articulation the pinnule is flexed ventrally.

The distal end of the 2nd pinnular also has a transverse ridge and this again makes an angle of 90° to the proximal face of the ossicle; here therefore it is a dorso-ventral crest. The articulation between the 2nd and 3rd pinnulars is distinguished, however, from the two preceding ones by the appearance of (small) ventral muscle-bundles on both sides of the ridge, and usually through the absence of the ligament pit which, supposing it occurs, sets a boundary for the dorsal development of the dorso-ventral crest. In these two characteristics this pinnular articulation diverges from synarthry, which in its general features it reminds one of rather strongly. It may be considered, as is shown by examples from the distal pinnulars of the distal pinnules, to be derived from an ordinary muscular articulation through the disappearance of the dorsal ligament.

When asymmetry is to be found in this and the following articulations, it is the aboral side of the joint facet which becomes more strongly developed than the adoral side. This is contrary to the conditions found in the articulation between the 1st and 2nd pinnulars (exception e. g. in *Metacrinus*). This stronger aboral development, of the articulations of the distal pinnules, expresses itself very strikingly in the development of the combs in the Comasterids, and of the pinnular calcareous flanges protecting the gonads in *Austrometra, Isometra,* and certain *Charitometridae.*

Both the ventral pits, mentioned above, for the muscle bundles on each side of the dorso-ventral crest are usually least distinct in the articulation between the 2nd and 3rd pinnulars where they may even be lacking entirely, but in the following articulations they are usually well circumscribed. In the not uncommon autotomy of the pinnules we, therefore, always find the fracture between the 2nd and 3rd pinnulars — the articulation that comes nearest to the ligamentary arti-



Figg. 129—148. 129) *Metacrinus nobilis tenuis* Pinnule-socket on I Br 2, $^{16}/_{1}$. 130—134) *Metacrinus rotundus* left P_1. 130) 1st pinnular, proximal face. 131) 1st pinnular, dist. 132) 2nd pinnular dist. 133) 3rd pinnular dist. 134) 5th pinnular, dist., $^{16}/_{1}$. 135—138) *Comanthus pinguis* P_2. 135) 1st pinnular dist. 136) 2nd pinnular, dist., $^{16}/_{1}$. 137) distal pinnular, lateral view. 138) distal pinnular, articular face, $^{26}/_{1}$. 139—140) *Comaster delicata grandis*, P_2. 139) distal combed pinnular; articular face. 140) Do., adoral view, $^{38}/_{1}$. 141) *Capillaster sentosa* 7th segment of distal pinnule, $^{38}/_{1}$. 142—143) *Zygometra microdiscus* P_2. 142) 1st pinnular, dist. 143) 2nd pinnular, dist., $^{20}/_{1}$. 144—148. *Himerometra magnipinna.* 144) II Br 2 pinnule-socket, $^{16}/_{1}$. 145—148) P_2, observe, not from the pinnule-socket, drawn as fig. 144. 145) 1st pinnular, prox. 146) 1st pinnular dist. 147) 2nd pinnular dist. 148) 4th pinnular dist., $^{16}/_{1}$.

culations of the arms which, as has been emphasized before, are preformed places for autotomy.

The articulation between the 3rd and 4th pinnulars, like all the following ones, is similar to that between the 2nd and 3rd pinnulars, as A. H. Clark has emphasized, but the pits for the muscular fossæ are better marked. The development of the muscle bundles shows, moreover, great variability (cf. below). In the distal parts of the proximal pinnules the movement thus takes place in the lateral direction.

In the distal articulations of the distal pinnules we usually find a pit in the dorsal part of the dorso-ventral crest. This pit harbours a little dorsal ligament. Here then, we have a possibility realized for a slight flexibility also in a dorso-ventral direction. Most strongly developed in certain *Comasteridae* (e. g. *Comatulella brachiolata*).

I shall now pass on to give a description of the appearance of the pinnular facets in various special cases.

Hyocrinidae (figg. 118—122).

The transverse crest of the pinnular face forms an angle with the brachial face of 150° in *Ptilocrinus pinnatus* (Br 6). The calcareous lamella over the muscle-insertion shoots forward as a large spout-shaped formation. The proximal joint face of the 1st pinnular is twisted peculiarly in relation to the distal face on the same ossicle (cf. fig. 119). This last face is a straight muscular articulation without interarticular ligaments. The 2nd and following articulations are very close, have a dorsal ligament pit, but lack otherwise nearly all sculpture (as is evidenced by sections, these connections are in reality synostoses and therefore lack muscles).

Pentacrinidae (figg. 126—134).

The two muscle attachments on the pinnular face of I Br 2 *(Metacrinus)* are very small and close together. They shoot rather a long way into the Br joint and are over-shadowed by a projecting calcareous lamella. The proximal face of the 1st pinnular makes an angle between the transverse ridge and the intermuscular furrow of about 50° (this angle facing towards the median part of the Br). The distal end of the 1st pinnular shows a typical straight muscular articulation, having the adoral part most strongly developed. The distal end of the 2nd pinnular shows only indistinct traces of muscular attachments. Here also, as in the nearest following ossicles, the adoral side is the one most strongly developed. The synarthroid type of articulation is very little accentuated here but approaches the synostotic. A dorsal ligament pit is still found. The joint-faces, which follow rectangular in transverse section, have small, ventral muscle pits, retain the dorsal ligament pit; the ligament pits are shallow, becoming very insignificant distally. The dorso-ventral crest is bounded dorsally by the dorsal pit.

The joints of the distal pinnules show the same type. The dorsal pit is retained, the dorsal ligament fossa, on the contrary, is accentuated more distinctly. The distal joints of the distal pinnules, in transverse section rectangular *(Metacrinus)* or triangular *(Diplocrinus)*, have only a very thin calcareous bridge separating the furrow for the ventral soft-parts from the dorsal nerve. This thin bridge is often sieve-like (for the ciliated pits?) and the joint therefore gets — seen from the ventral side — a certain likeness to the Silurian transition forms between the canaliculate and non-canaliculate types which BATHER has figured (1893, e. g. fig. 327).

The pinnulars of *Pentacrinidae,* when seen in transverse section, remind one rather much through their rectangular or triangular form of those found in *Thalassometridae.*

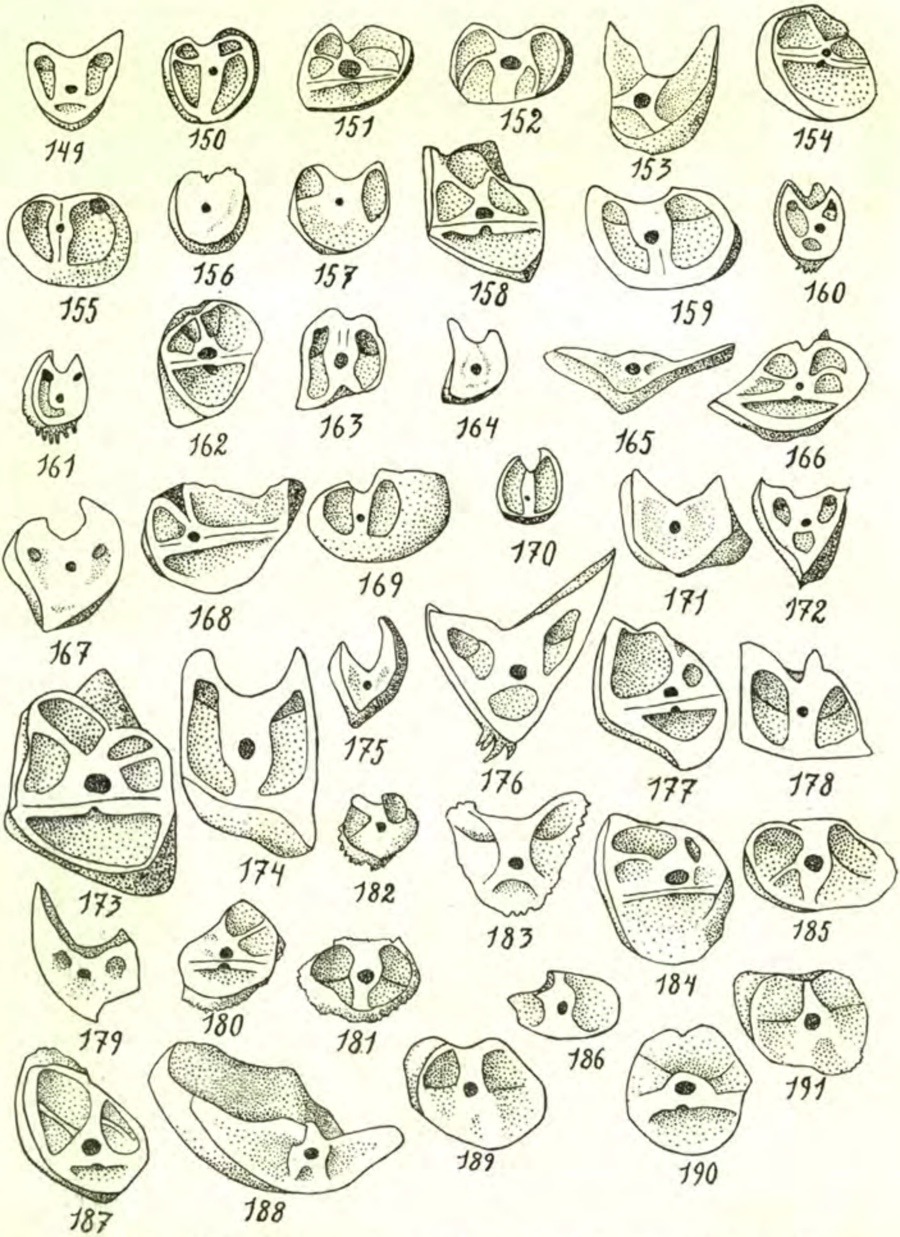
Bathycrinidae (figg. 123–125).

As is well-known, pinnules are lacking here on a number of the proximal Br segments. The pinnular joint-face on more distal Br segments reminds one rather much of that in *Ptilocrinus.* The articulation between the 1st and 2nd pinnulars is a muscular articulation of the usual brachial type. The dorsal ligament is, however, narrow and inconsiderable. The distal pinnular joints are distinguished chiefly by the large, extraordinarily thin, lateral processes, springing from the body of the pinnular joint itself and embracing the ventral soft parts.

Comasteridae (figg. 135–141).

In annother connection I have discussed (Chap. 5) the development of the combs on the tips of the pinnules in this family. The most characteristic thing about these pinnules is the enormously strong development of the muscle bundles, especially noticeable because the muscular attachments between the Brr are only modestly developed.

The angle which the transverse ridge of the brachial face and that of the pinnular face on a Br make with each other varies between about 130° *(Comaster)* and 180° *(Comissia, Capillaster).* The cavity into which the muscles of the 1st pinnular insert themselves on the brachial joint is not very deep usually. Distally of the articulation between the 2nd and 3rd pinnulars in the proximal comb-provided pinnules, very strong muscular attachments appear which take up the greater part of the surface of the facets. Here we have still another reason speaking in favour of these pinnules being specially adapted for making rapid



Figg. 149—191. 149) *Himerometra magnipinna* distal pinnular of distal, right pinnule, $^{38}/_{1}$. 150) *Lamprometra protectus,* right P_2, 9th pinnular, $^{20}/_{1}$. 151—153) *Pontiometra andersoni*. 151) P_1, right outer side, 1st pinnular dist. 152) P_1 2nd pinnular dist., $^{20}/_{1}$. 153) distal pinnule, 7th pinnular, dist., $^{38}/_{1}$. 154—156) *Stephanometra spicata* right P_2, 154) 1st pinnular dist. 155) 2nd pinnular dist. 156) 4th pinnular dist., $^{20}/_{1}$. 157) *Stephanometra spicata* P_7, 3rd pinnular dist., $^{38}/_{1}$. 158—159) *Tropiometra afra macrodiscus* left P_1. 158) 1st pinnular dist. 159) 2nd pinnular dist., $^{16}/_{1}$. 160—161) *Cenometra bella* P_2. 160) 6th pinnular dist. 161) 8th pinnular dist., $^{20}/_{1}$. 162—164) *Oligometrides adeonae* P_1. 162) 1st pinnular dist. 163) 2nd pinnular dist. 164) 6th pinnular dist., $^{20}/_{1}$. 165) *Austrometra thetidis* genital

and powerful movements (cf. Chap. 5). Muscles are developed in the distal parts of the pinnule, where the combs appear, enormously more powerfully on that side of the dorsal crest where the teeth are developed (the aboral side).

In the distal comb-less pinnules the muscles are more moderately developed. In their articulation between the 3rd and 4th pinnulars and distally of this, there appears as usual a little dorsal ligament fossa.

Zygometridae, Himerometridae, Mariametridae, Stephanometridae, Tropiometridae, and *Colobometridae* (figg. 142—165).

The pinnular articulations here, taken as a whole, agree with A. H. CLARK's description (1922, p. 185 ff.) as my figures show.

Unless in exceptional cases the muscular attachments are small everywhere here. The pits into which the muscles from the 1st pinnular insert themselves in the Br are generally fairly deep (exception e. g. *Himerometra*). Between the 2nd and 3rd pinnular scarcely any muscular fossæ are found in the large proximal pinnule in *Himerometra*.

In the very long and flexible P_1 in *Pontiometra andersoni* the articulations, distally of the one between the 2nd and 3rd pinnulars, are provided with large lateral muscle fossæ. In the more distal parts of the pinnule, as in the distal pinnules, the dorsal part of the dorsoventral crest disappears, and we therefore get a more or less distinctly marked dorsal ligament fossa. It must be observed that the lumen in this pinnule is unusually large. We may compare the conditions here with the size of the lumen in the immovable proximal pinnules in *Stephanometra* (cf. figg. 151—156). In this connection it may be pointed out that the *Macrophreata,* supplied with large brachial muscle-attachments have, in the same way, large nerve-lumina in the Brr — and a large central organ for these nerves in the Cd. We can thus trace the correlation: stout dorsal nerves - large muscle bundles - strong capacity for movement or swimming.

---

pinnule, 4th pinnular dist., $^{38}/_{1}$. 166—167) *Pectiometra flavopurpurea* proximal pinnule. 166) 1st pinnular dist., $^{20}/_{1}$. 167) 5th pinnular, $^{38}/_{1}$. 168—172) *Neometra multicolor.* 168—170) P_1, 168) 1st pinnular dist., 169) 2nd pinnular dist., 170) 3rd pinnular dist., $^{20}/_{1}$, 171—172) Distal pinnule. 171) 2nd pinnular dist., 172) 3rd pinnular dist., $^{38}/_{1}$. 173—174) *Asterometra anthus* P_2. 173) 1st pinnular dist. 174) 2nd pinnular dist., $^{38}/_{1}$. 175) *Ptilometra mülleri* P_4. 4th pinnular dist., $^{20}/_{1}$. 176) *Cosmiometra aster* distal pinnule, 4th pinnular dist., $^{38}/_{1}$. 177—179) *Diodontometra bocki.* 177—178) P_2. 177) 1st pinnular dist., 178) 2nd pinnular dist., $^{38}/_{1}$. 179) P_7, 3rd pinnular dist., $^{38}/_{1}$. 180—183) *Notocrinus virilis.* 180—182) P_1. 180) 1st pinnular dist., 181) 2nd pinnular dist., 182) 6th pinnular dist., $^{20}/_{1}$., 183) Distal pinnule, 7th pinnular dist., $^{38}/_{1}$. 184—186) *Heliometra eschrichti* P_1. 184) 1st pinnular dist., $^{20}/_{1}$. 185) 2nd pinnular dist., $^{20}/_{1}$. 186) distal pinnular, dist., $^{38}/_{1}$. 187) *Poliometra prolixa* P_1, 1st pinnular dist., $^{38}/_{1}$. 188) *Isometra vivipara*, genital pinnule, 3rd pinnular, dist., $^{38}/_{1}$. 189—191) *Pentametrocrinus diomedeae.* 189) proximal pinnule, 2nd pinnular dist., $^{38}/_{1}$. 190—191) distal pinnule, 190) 1st pinnular dist., 191) 2nd pinnular dist., $^{38}/_{1}$.

In *Stephanometra* the nail-shaped proximal pinnules deviate considerably regarding their articulations from the rest of the pinnules. The articulation between the 1st and 2nd pinnulars is, as usual, a muscular articulation, and that between the 2nd and 3rd pinnulars is a pinnular articulation, where, however, only the muscle of the aboral side is noticeably developed. Between the 3rd and 4th pinnulars we have, on the contrary, a great reduction of the sculpture of the face, and from the articulation between the 4th and 5th pinnulars we get typical synostoses. From this comes the nail-shaped appearance and stiffness of the pinnule. We find in certain *Colobometridæ* similar, although generally not so extreme, stiffening of some of the proximal pinnules.

In *Austrometra* the genital pinnules are provided with wing-like processes, as we found above was the case in *Bathycrinidae*. Here, however, the processes are extended almost horizontally, so that the joint gets a more disk-shaped appearance.

Calometridae, Thalassometridae, Charitometridae (figg. 166—179).

The pinnule-joints in all these families after the 3rd or 4th pinnular are decidedly triangular, more proximal segments (the 2nd—4th joints) in the proximal pinnules are sometimes rectangular (cf. also A. H. Clark 1915 c fig. 54 and 1922 fig. 659). The triangular form of the joints may sometimes be indistinct in the proximal pinnules (e. g. *Neometra, Stylometra,* where the segments are more or less rounded). In these families often the genital pinnules have flattened joints with small lateral processes which protect genital glands (cf. above *Austrometra* and below *Isometra*).

The proximal pinnules in the family *Calometridae* have, as is well known, enormously enlarged 1st and 2nd pinnulars, especially in the proximal pinnules. The pinnular face on the Br takes up a great part of the ventral surface of the latter. The muscle-attachment pushes its way, as is, moreover, usually the case also in the two other families, rather deeply into the brachial segment. The transverse crest of the pinnular face is here, in relation to that of the brachial face, twisted to an angle of at least 180°. The articular fossæ between the proximal pinnulars are extraordinarily strong in all the proximal pinnules. The interarticular ligaments are narrow or rudimentary. The connection between the 2nd and 3rd pinnules soon, however, becomes much closer than those between the other segments, and after about P_7 gains a synostotic character (this is specially evident in *Neometra*). Processes are also found on the proximal pinnulars of the proximal pinnules, though less localized or marked, in some of the *Charitometriaae;* outside this group in *Catoptometra* and certain Comasterids (e. g. *Comaster belli*).

Notocrinidae and *Macrophreata* (figg. 180—191).

Regarding these forms there is not much to be said. Within this group, the muscle-attachments are very well developed; otherwise the pinnule-articulations are fully typical, with the exception of a couple of cases mentioned below. The distal joints of the distal pinnules are more or less rounded and their joint fossæ are provided with the customary little dorsal fossa.

The more important exceptions to the typical construction are the following. *Heliometrinae* has long proximal pinnules with very short pinnulars. Here the pinnular muscle-fossæ are very powerful and the hypertrophy culminates between the distal pinnulars, where, as in *Comasteridae*, we get the most powerful muscle on that side of the joint where the rudimentary comb is situated (the aboral side). Another exception to the normal appearance is found in *Isometra*. From about P_6 in this genus the 3rd and 4th pinnulars are powerfully expanded, evidently as a protection for the genital gland. The hypertrophy is most strongly pronounced on the aboral side.

I have not had an opportunity of studying the pinnules of *Thysanometrinae* and *Atelecrinidae*.

CHAPTER III.

The fossil Comatulids.

I. **Introduction.**

Nothing is of greater value in making a correct estimate of the phylogeny of an animal group than a close knowledge of its fossil predecessors. Usually, however, the preserved remains are few and incomplete and therefore it is not an easy task, and sometimes an impossible one, to decipher the changes that the animal group has been subjected to during its development.

There are probably few groups of Invertebrates that give more abundant material in the direction alluded to above than the Echinoderms, and among these the Crinoids are especially rich in fossil forms. Among the Crinoids in recent times one branch only flourishes, the free-living unstalked Comatulids. From the paleontological point of view this branch is a very young one, for the oldest known forms are not older than from the lowest Jurassic; nevertheless, the Comatulids from almost their very first appearance have shown very great aptitude for abundant variation. While about 600 species of Comatulids are known from recent times (their number is daily increasing) the number of fossil species approaches a hundred and seventy. This figure is not in itself so very imposing, but it becomes more so when one considers that as yet only small parts of the earth are paleontologically examined and that those parts of the Comatulids that have been preserved — usually Cd, BB, and RR — do not allow a systematization to be carried out as thoroughly as in the recent forms.

Since the seventies the fossil Comatulids almost without exception have been ranged under the genera *Actinometra* and *Antedon.* This procedure might have had a certain reason as long as the now living species were grouped chiefly in the two genera above mentioned. Since 1907, however, A. H. Clark, as is well known, has carried out a very deep and necessary revision of the system of the recent Comatulids. The family *Comasteridae* arose from the old genus *Actinometra*, while *Antedon* is only used now to signify a small group of very closely related Atlantic forms. The system for the recent forms is built chiefly on the formation of the cirri and proximal pinnules, to a certain degree also on the number of the division series etc. The characteristics mentioned rarely or never present themselves in extinct Comatulids. When one takes all these circumstances into consideration it becomes perfectly evident that one cannot use any of the old genus-names mentioned above that are applied to recent forms.

Before one passes on to a revision of the system of the fossil Comatulids two things, however, are necessary. First one must make a survey of the forms described; secondly one must make clear the systematic characteristics that might be used for fossil Comatulids and the extent to which these characteristics reappear in recent forms.

I shall begin with a short historical survey of the literature on the fossil Comatulids.

II. **Historical review.**

The 18th century has very little information to give as regards our knowledge of fossil Comatulids. Excepting that SCHEUCHZER in 1716 and 1718 figured and described an object that is evidently the Cd and radial ring of a Comatulid, it is only the slabs from Solenhofen, where one often finds the remains of *Pterocoma pennata*, that have inspired the authors of the 18th century to describe and figure.

It was first by the excellent work of GOLDFUSS, Petrefacta Germaniae (1826—1840), that our knowledge of the fossil Comatulids advanced considerably. In his treatise 5 real Comatulids under the names of *Solanocrinites* (one species of this genus called by HARTMANN 1830 *Milleria* n. n.), *Comatula*, and *Glenotremites* are described and figured with a correctness unknown before. Nevertheless, many false ideas still prevailed. Thus under the name *Glenotremites* the Cdd of a couple of Comatulids were described. These Cdd, however, were regarded as Echinoids forming a transition stage to the Comatulids. They were said to have no anal opening, the impressions for the BB on the ventral side of the Cd were interpreted as ambulacral furrows, and the opening for the centrodorsal cavity was regarded as the mouth.

From the thirties to the first half of the sixties the knowledge of the fossil Comatulids increased only slowly.

A number of new species (18) were, however, described or mentioned by v. MÜNSTER (1839), HAGENOW (1840), PHILIPPI (1844), D'ORBIGNY (1850), THURMANN (1851), FORBES (1852), EMMONS (1858), QUENSTEDT (1858), ETALLON (1857 and 1862), MICHELOTTI (1861), and A. MÜLLER (1863).

During this time also a number of comprehensive works appeared.

They introduced few new views but tried to bring together into a whole the knowledge of that time. We therefore get such works as those of L. AGASSIZ (1835), BRONN (1835—1838 and 1848), GEINITZ (1846), D'ORBIGNY (1850—1852 and 1852), QUENSTEDT (1852, 1858, and 1875—76), PICTET (1857), OPPEL (1856—1858), and DUJARDIN & HUPÉ (1862).

Nevertheles, there were also some occasional efforts made at bringing forward a more thoroughly worked out systematical grouping of the Comatulids. As one only surmised obscurely what was systematically important these attempts, however, were fumbling or more or less unsuccessful. L. AGASSIZ (1835) correctly distinguished some of the Comatulæ of GOLDFUSS and called them *Saccocoma*. He ranged one species of the Goldfussian *Comatula*, the above mentioned *pennata* (mentioned by SCHLOTHEIM 1823 as *Comatulithes*), under a new genus *Pterocoma*. v. MÜNSTER called a probably very closely related or identical form (1839) *Comaturella wagneri*. HAGENOW (1840) created the new genus *Hertha* for a Comatulid from Cretaceous of Rügen and D'ORBIGNY (1852) rechristened a part of the Goldfussian species *Solanocrinites costatus* as *Comatulina*. EMMONS (1858) called the Cd of an eocene Comatulid from North Carolina *Microcrinus*, MICHELOTTI (1861) a miocene form from North Italy *Allionia*, and FRAAS (1878) a Cretaceous species from Lebanon *Geocoma*. Here, I do not include all the generic names that have been attributed to and diagnosed for recent forms and then transferred to fossil forms. Such names are *Alecto* (PHILIPPI 1844 after LEACH), *Decacnemos* and *Decameros* (BRONN 1835—1838 and D'ORBIGNY 1850—1852 after LINCK), *Comaster* (DUJARDIN & HUPÉ 1862 and LUNDGREN 1874 after L. AGASSIZ). I can enumerate in passing only some of the "variations of spelling" of the names of the genera mentioned above as *Solacrinus* (L. AGASSIZ 1835 and GEINITZ 1846), *Salocrinus* (MICHELOTTI 1861), *Solonærium* (ETALLON 1862), and *Glenocrinus* (D'ORBIGNY 1852).

With the exception of the genera *Pterocoma, Hertha, Comatulina,* and *Allionia* there is no description included of the generic names enumerated above, or else they referred to recent forms and ought therefore to be left out of account in what follows. The genus *Comatulina* which is described in a confused manner is said to lack "les pièces brachiales et basales" and to have arms directly articulating with the Cd. In reality such a form is not known. As the type D'ORBIGNY signifies *C. costata* (= GOLDFUSS Tab. 50 fig. 7 c), a species lacking visible basals, but with radials (the species described as *d'Orbignyi* in 1881 by P. H. CARPENTER). This genus of D'ORBIGNY is included as a sub-genus of the genus *Solanocrinus* (cf. below). Later on I shall return to the three remaining genera.

A new epoch arrives with the works of DE LORIOL and P. H. CARPENTER; the days of its glory may be identified with the eighties. The activity of the former scientist is spread over 40 years; during this time he described and figured in an excellent manner nearly 40 new species. The activity of P. H. CARPENTER, it is true, is much more restricted in time — his productivity on the whole falls within the eighties and during this time he describes more than 20 species as new — nevertheless, his contribution is of extraordinarily great importance on account of his deep knowledge of the morphology of the recent forms. The "Paléontologie Française, Crinoïdes Jurassiques" of DE LORIOL and "On the genus *Solanocrinus*" besides the two Challenger works of P. H. CARPENTER will always be regarded as classical.

Besides these two there might also be mentioned a number of scientists who have furthered the knowledge of the fossil Comatulids. Those who described and figured (23) new species were: OOSTER (1871), LUNDGREN (1874), FONTANNES (1877 and 1879), FRAAS (1878), SCHLÜTER (1878), WALTHER (1886), POMEL (1887, remarkable, because of its being the first real description of species outside Europe, cf. also FRAAS). Of these LUNDGREN, SCHLÜTER, and WALTHER deserve to be specially mentioned.

LUNDGREN points out a number of misinterpretations made by preceding authors and shows conclusively the special errors regarding the views taken of "the mouth" and the "ambulacral furrows" in the genus *Glenotremites*. SCHLÜTER, in his excellent paper containing a collocation of the fossil forms known up to then, attempts to make new boundaries for the genus *Solanocrinus*. This should, according to him, include forms having a round opening of the centrodorsal cavity, without any radial pits. Another group, on the contrary, should be distinguished by a lobed opening of the Cd-cavity and the occurrence of radial cavities. MENEGHINI (1878) wished to call the group mentioned first *Allionia*, a name which had previously been given by MICHELOTTI to the Cd of a North Italian form. WALTHER adopts SCHLÜTER's idea and reckons the Comatulids having a round opening of the Cd-cavity, without radial pits, with narrow BB, with 2—3 "Radialia", and 10—20 arms without syzygial connections, as belonging to the genus *Solanocrinus*, which he considers is the more primitive type. The genus *Antedon*, which then constitutes the rest of the fossil Comatulids, should be characterized by abundant syzygies. Although this author has excellently prepared material and makes many remarks of value, the presentation of it still suffers considerably from his imperfect knowledge of the morphology of the recent forms (cf. e. g. his comments on the "mediane Pinnula"). CARPENTER, in his important treatise quoted above (1881), "On the genus *Solanocrinus*", brings under discussion the question of the possibility of distinguishing the genera *Solanocrinus* and *Antedon*. In his criticism he proceeds to correct the numerous errors which were inherent in the presentations of many of the preceding authors, and to disentangle the often very complicated questions regarding synonyms which frequently resulted from these. He comes to the conclusion that *Solanocrinus*, characterized by the occurrence of exterior basals, cannot be maintained (cf. 1857 PICTET, p. 288; 1874 LUNDGREN, p. 64) but is practically the same as *Antedon*, in which genus he ranges all the forms which cannot be referred to *Actinometra*. His criticism, however, hardly touches SCHLÜTER's proposal mentioned above.

Towards the end of this period, which occurred contemporaneously with the publication of the great Challenger work on recent Comatulids, it had also become an admitted conception that the fossil Comatulids taken as a whole should be referred to the genus *Antedon*. A lesser number of forms, with a simple whorl of cirri or without cirri and with radial faces sloping only slightly inwards, are placed in the genus *Actinometra*. One species with V simple arms, described by DE LORIOL is placed in the genus *Eudiocrinus*.

Ever since the nineties up to quite recent times, there is scarcely anything to note regarding any new views which might assist in clearing up the problem of the fossil Comatulids. Resting on the authority of CARPENTER and DE LORIOL all the new species described have practically without exception been ranged in the genus *Antedon*. There has been more scepticism as regards the possibility of distinguishing representatives of the genus *Actinometra* and it is only seldom that forms have been described under that name. A new genus, *Pachyantedon*, was created during this time by JÆKEL (1891) for a type corresponding to WALTHER's *Solanocrinus*. The same author drew (1901) a Comatulid from maastrichtian which shows certain similarities to the recent genus *Atelecrinus*.

A good many new species (35) were described during this time, by ZAHALKA (1892), NICOLAS (1897), NOËLLI (1900), REMEŠ (1902), FRITSCH (1910 *Pentacrinus pusillus*), WEGNER (1911), SCHAFFER (1912), BRÜNNICH-NIELSEN (1913), CHAPMAN (1913), VADÁSZ (1915), VALETTE (1917). DE LORIOL continued with his descriptions until 1908, but with his exception, most of those who have busied themselves with new descriptions have been, more or less, occasional students in this field of labour — which is often to be traced in the descriptions themselves. Thus VALETTE in his work of 1917, which, moreover, contains rather good figures, still remains on the same plane as GOLDFUSS in 1831 as regards his conception of the parts surrounding the Cd-cavity and the radial cavity, which he considers as "le peristome de la bouche", and the marks after the BB which are considered as corresponding to "le cinq gouttières ambulacraires". The descriptions and figures of 6 new species by NICOLAS are so imperfect and unsatisfactory that it is quite impossible to get hold of their systematical relations. Presumably, however, a couple of his species are synonymous with species from the same districts described somewhat earlier by DE LORIOL (1897). The exceptions mentioned above consist of NOËLLI, BRÜNNICH-NIELSEN, and VADÁSZ in whose works good drawings and figures are united with a close knowledge of their subject. During this time also two interesting extra-European discoveries from Patagonia and Australia were described by de Loriol (1902) and Chapman (1913).

While the preceding period of time had a number of comprehensive works to show, among which that of de Loriol on the Jurassic Crinoids (1884—1889), P. H. Carpenter's: "On the genus *Solanocrinus*" (1881), and Schlüter's collocation (1878) were the most prominent, there has been less to notice in this way during the latest years. Zahalka (1892) has written in Czech a concise and very imperfect survey of the literature and species chiefly of the German and Austrian fossil Comatulids. In 1908 (c) A. H. Clark gave practically a complete list of the names of the fossil Comatulids described before that year, unfortunately, however, without making any references to the literature. In a later work (1915 a) he discusses shortly the genera of the fossil Comatulids which may be considered as having counterparts among the recent forms. He considers that the fossil Comatulids correspond in part to the recent genus *Eudiocrinus* (a Cretaceous form, not as Clark states a Jurassic), and partly belong to *Catoptometra,* which Clark states was spread abundantly and generally during Jurassic and Tertiary. He places (1915 b) *Antedon iheringi,* described by de Loriol (1902), in this genus, without, as it seems to me, any reason whatever. In Jækel's great work (1918), a very comprehensive though somewhat sketchy survey of all the fossil Pelmatozoa taken together, the Comatulids have been treated rather grudingly which, however, is more easily explainable when we consider the extent of Jækel's undertaking. The author takes the standpoint already disproved by Carpenter and distinguishes Comatulids with visible BB as belonging to the genus *Solanocrinus.*

The most important attempt made during this time to deduce some conception of the phylogenetical development of the Comatulids is undoubtedly to be found in Kirk's work (1912). Here (p. 67) for the first time[1], a detailed argument is given in favour of the idea that the Comatulids may represent "a number of genetic lines" and be "polyphyletic in origin . . . doubtless . . . from not widely divergent types". Although he admits that the forms which he imagines to be the ancestors "may not represent actual links in an evolutionary chain" (p. 74) he considers, however, that "they have the character that such ancestral forms undoubtedly possessed". He takes *Mesocrinus* as the original type and imagines a development proceeding through *Thiolliericrinus* to the Comatulid type. The forms of these genera which he discusses are, in the case of the two latter, from upper Jurassic or lower Cretaceous (the oldest Comatulids appear in the lowest Jurassic), and, in the case of the former, from uppermost Cretaceous, a fact which

---

[1] Cf. also 1891 Jækel p. 633.

somewhat weakens the value of his reasoning. In the following chapter I shall return to a criticism of his views on the late phylogenetic appearance of the cirri, on which he bases his reasoning sketched above, and which ends therefore in his deduction that the Comatulids have descended from a theoretical ancestral type, corresponding to Bourgueticrinoid forms. Later on he admits the probability of certain lines of Comatulids having been derived from Apiocrinid or possibly from Pentacrinid forms (p. 77). Regarding different types of Comatulids, KIRK considers that the Jurassic species provided with biserial arms represent an extinct older branch, while the slender-armed forms may possibly correspond to a younger one now living.

III. Species incorrectly placed among the Comatulids.

Especially during the first half of the 19th century we find numerous forms which have been erroneously referred to the Comatulids. I shall enumerate such forms below, alphabetically arranged, with their synonyms. In this section the synonymy comprises only some of the more important works that have dealt with the species mentioned.

1) **Comatula antiqua** GOLDFUSS 1835.

Comatula antiqua 1835 GOLDFUSS, p. 54; 1848 BRONN, p. 321.

Gasterocoma antiqua 1839 GOLDFUSS, Nova Acta etc., p. 350, Tab. 32, fig. 5; 1848 BRONN, p. 525.

Epactocrinus antiquus 1876 QUENSTEDT, p. 530, Tab. 108, fig. 55.

Is a Fistulate from middle Devonian, Germany.

2) **Ophiura carinata** GOLDFUSS 1831.

Ophiura carinata 1831 GOLDFUSS, p. 206, Pl. 62, fig. 5; 1876 QUENSTEDT, p. 143, Tab. 95, fig. 39.

Geocoma carinata 1850 D'ORBIGNY, Vol. 1, p. 381.

Comatula carinata 1878 FRAAS, p. 89.

Is an Ophiuran from Upper Jurassic, Solenhofen, Germany.

3) **Comatula bertrandi** THURMANN 1851.

Comatula Bertrandi 1851 THURMANN, p. 137, Pl. 2, fig. 21; 1858 OPPEL, p. 626.

Professor A. REICHENSPERGER of Freiburg, Switzerland, has kindly furnished me with information as to the evidently very rare original description. THURMANN says there of the new species: "Je nomme provisoirement ainsi des fragments d'une stelléride ou crinoïde fort rare, qui me paraît avoisiner les comatules. Ils proveniennent de la Combe d'Eschert. — Je les dédie à Elie Bertrand d'Orbe." The figure shows a part of an arm only, which may belong to a Crinoid, though probably it does not represent the Brr of any Comatulid (fig. 192 is a copy of THURMANN's figure kindly presented to me by Prof. REICHENSPERGER).

Upper Jurassic (oxfordian), Switzerland.

4) **Comatula filiformis** GOLDFUSS 1831.

Comatula filiformis 1831 GOLDFUSS, p. 205, Tab. 62, fig. 3; 1848 BRONN, p. 321.

Saccocoma filiformis 1835 L. AGASSIZ, p. 193; 1848 BRONN, p. 1151; 1893 b JÆKEL, p. 661 ff.; 1918 JÆKEL, p. 92.

Saccosoma filiformis 1850 D'ORBIGNY, Vol. 1, p. 381.

Is one of the *Saccocomidæ* found at Solenhofen, Upper Jurassic (virgulian), Germany.

5) **Antedon fischeri** GEINITZ 1871.

Antedon fischeri 1871 GEINITZ, Vol. 20: 1, p. 92, Vol. 20: 2, p. 18, Pl. 6, figg. 9—12; 1878 SCHLÜTER, p. 39; (?) 1893 FRIČ, p. 109, fig. 143; 1895 JAHN, pp. 145, 168, 169, 180; 1899 POPOVICI-HATZEG, p. 4; 1901 BRUNHUBER, p. 124; 1911 FRIČ, p. 76.

Mesocrinus fischeri 1881 a P. H. CARPENTER, p. 129, Pl. 6, fig. 2.

Belongs to the fam. *Bourgueticrinidae* and is reported from Upper Cretaceous, Saxony, Bohemia, and Bavaria.

6) **Comatula Geinitzii** REUSS 1844.

Comatula sp. 1839 (N. Ausg. 1850) GEINITZ, p. 89, Tab. 22, fig. 2.

Comatula Geinitzii 1844 REUSS, p. 177; 1846 REUSS, p. 59, Tab. 20, fig. 27; 1848 BRONN, p. 321.

Is a stump of an arm of an Ophiuran (or perhaps a Saccocomid) from Cretaceous, Bohemia.

7) **Solanocrinites Jægeri** GOLDFUSS 1831.

Solanocrinites Jægeri 1831 GOLDFUSS, p. 168, Tab. 50, fig. 9; 1879 P. H. CARPENTER, pp. 6, 104—106.

Solacrinus Jægeri 1835 L. AGASSIZ, p. 196.

Solanocrinus Jægeri 1839 MÜNSTER, p. 89; 1848 BRONN, p. 1150; 1857 PICTET, p. 288, Pl. 99, fig. 2; 1878 SCHLÜTER, p. 36; 1881 b P. H. CARPENTER, pp. 190, 207, 210.

Comatula Jægeri 1850 D'ORBIGNY, Vol. 1, p. 381.

Comaster Jægeri 1862 DUJARDIN & HUPÉ, p. 213.
Pentacrinus Jægeri 1881 b P. H. CARPENTER, p. 211, Pl. 11, fig. 24.

According to P. H. CARPENTER this species is the basal + radial rings of a *Pentacrinus* only. As the stem is unknown this is, however, not yet completely certain. One might, possibly, imagine that a Cd constituted its dorsal complement; in that case it would be an Atelecrinoid form, a supposition that is, however, not very likely.

From Upper Jurassic (oxfordian), Germany.

8) **Solanocrinites Jægeri** QUENSTEDT 1852.

Solanocrinites Jægeri 1852 QUENSTEDT, p. 601, Pl. 51, fig. 33 (2. Aufl. 1867, p. 717; 3. Aufl. 1885, p. 915, Tab. 72, fig. 14); 1858 QUENSTEDT, p. 723, Pl. 88, fig. 12; 1876 QUENSTEDT, p. 177, Tab. 96, fig. 51.

Solanocrinus Jægeri 1881 b P. H. CARPENTER, pp. 208, 209, Pl. 11, fig. 22; 1888 DE LORIOL, p. 559; 1908 ENGEL, p. 455.

Antedon (Solanocrinus) Jægeri 1920 MUSPER, p. 15.

The articular faces in this species are, contrary to those in the preceding one, low, the basals are small and indistinctly protruding. Dorsally of the basals there is a stem-joint without cirri. These facts point to the same conclusion as that reached by P. H. CARPENTER who considers the species of QUENSTEDT to be the remnant of a stalked Crinoid. I agree with DE LORIOL that one cannot refer it to *Thiolliericrinus*. It may be supposed rather to approach *Millericrinus*.

Upper Jurassic (virgulian), Germany.

9) **Comatula longimana** QUENSTEDT 1876.

Comatula longimana 1876 QUENSTEDT, p. 169, Tab. 96, fig. 22; 1885 QUENSTEDT, Petrefaktenkunde 3. Aufl., p. 916, Tab. 72, fig. 15; 1886 WALTHER, pp. 159, 160.

Millericrinus cf. *mespiliformis* 1886 WALTHER, p. 159, Tab. 24, fig. 3.

Antedon (Comatula) longimana 1888 DE LORIOL, p. 529.

Only the arms are known. Compared by QUENSTEDT himself with *Apiocrinus mespiliformis*. These are surely not the arms of any Comatulid, since the Br-segments are discoidal, very short and of uniform stoutness. It reminds one more of the arms of an Apiocrinid than of a Millericrinid form (cf. e. g. 1884—89 DE LORIOL, Pll. 37 and 73).

Upper Jurassic (tithonian), Germany.

10) **Comatula neocomiensis** JACCARD 1870.

Comatula neocomiensis 1870 JACCARD, p. 68.

Is a typographical error for the gastropod *Columbellina neocomiensis* (cf. 1869, p. 165).

Lower Cretaceous (neocomian), Switzerland.

11) **Asteriacites pannulatus** SCHLOTHEIM 1820.

Asteriacites pannulatus 1820 SCHLOTHEIM, p. 325; 1848 BRONN, pp. 119, 1105.
(Saccocoma) pannulatus 1876 QUENSTEDT, p. 155.
Antedon pannulatus 1908 c A. H. CLARK, p. 486.

BRONN considers this species to be, possibly, identical with a *Saccocoma*. Owing to the references given by SCHLOTHEIM to the *Stella coriacea* etc. of LINCK (1733), these species being starfishes, one must consider with QUENSTEDT SCHLOTHEIM's species to be an asterid.

Upper Jurassic (virgulian), Pappenheim bei Solenhofen, Germany.

12) **Comatula pectinata** GOLDFUSS 1831.

Comatula pectinata 1831 GOLDFUSS, p. 205, Tab. 62, fig. 2; 1852 QUENSTEDT, p. 599; 1878 SCHLÜTER, p. 35.
Saccocoma pectinata 1835 L. AGASSIZ, p. 193; 1848 BRONN, p. 1151; 1893 b JÆKEL, p. 661 ff., 1918 JÆKEL, p. 92.
Saccosoma pectinata 1850 D'ORBIGNY, Vol. 1, p. 381.

Is one of the *Saccocomidae* from Solenhofen.

Upper Jurassic (virgulian), Germany.

13) **Asterites scutellatus** BLUMENBACH 1803.

Asterites scutellatus 1803 BLUMENBACH, p. 24, Pl. 2, fig. 10.
Pterocoma scutellata 1850 D'ORBIGNY, Vol. 1, p. 381.
Ophiura scutellata 1876 QUENSTEDT, p. 146, Tab. 95, figg. 48—51.

This species is erroneously stated by D'ORBIGNY to be synonymous with *Pterocoma pennata*. It seems very doubtful to me if the species as QUENSTEDT says, is the same as *Ophiura loricata* of GOLDFUSS. More probably it is synonymous with *Aspidura ludeni* HAGENOW. Is an *Aspidura* from the Muschelkalk at Göttingen.

Middle Trias, Germany.

14) **Comatula sigillata** QUENSTEDT 1876.

Solanocrinites costatus part. 1831 GOLDFUSS, Tab. 51, fig. 2.
Comatula sigillata 1876 QUENSTEDT, p. 176, Tab. 96, figg. 49, 50; 1878 SCHLÜTER, p. 37; 1879 DE LORIOL, p. 267.
Solanocrinus sigillatus 1878 SCHLÜTER, p. 37.
Antedon sigillata 1881 b P. H. CARPENTER, pp. 201, 202, 209.
Thiolliericrinus sigillatus 1889 DE LORIOL, p. 558.

GOLDFUSS considered this species to be a young of *Solanocrinus costatus*. DE LORIOL, because of the dorsal "Kippgelenk" of the Cd, ranged it in the genus *Thiolliericrinus*.

Upper Jurassic (virgulian), Württemberg.

15) **Comatula teissenbergensis** SCHAFHÄUTL 1863.

Comatula teissenbergensis 1863 SCHAFHÄUTL, p. 112, Tab. 15, fig. 8; 1865 GÜMBEL, p. 140; 1866 GÜMBEL, p. 567; 1866 SCHAFHÄUTL, p. 786; 1878 SCHLÜTER, p. 38.

Probably GÜMBEL is right in considering this "species" to be a fragment of a belemnite (cf. *Belemnites*). Surely it is not a Br-segment of any Comatulid as SCHAFHÄUTL supposes.

Jurassic, Germany.

16) **Comatula tenella** GOLDFUSS 1831.

Comatula tenella 1831 GOLDFUSS, p. 204, Tab. 62, fig. 1; 1848 BRONN, p. 322.

Saccocoma tenella 1835 L. AGASSIZ, p. 193; 1848 BRONN, p. 1151; 1893 b JÆKEL, p. 661 ff.

Saccosoma tenella 1850 D'ORBIGNY, Vol. 1, p. 381.

Saccoma tenella 1918 JÆKEL, p. 92.

A member of the *Saccocomidae* of Solenhofen.

Upper Jurassic (virgulian), Germany.

17) **Antedon valdensis** part. DE LORIOL 1879.

Antedon valdensis part. 1879 DE LORIOL, p. 267, Pl. 20, fig. 20.

Thiolliericrinus arzierensis 1889 DE LORIOL, p. 560.

At first this species was considered by DE LORIOL to be a young of the species of *Antedon* mentioned above, but it was later on referred to the genus *Thiolliericrinus*.

Lower Cretaceous (valanginian), Switzerland.

18) **Antedon** sp. POPOVICI-HATZEG 1899.

Antedon sp. 1899 POPOVICI-HATZEG, pp. 2, 4.

Represents the stem joints of a Bourgueticrinoid form.

Upper Cretaceous (cenomanian), Rumania.

IV. **Undescribed or imperfectly described Comatulids.**

Before I pass on to discuss the system of the fossil Comatulids I must separate a small number of species which either are not described at all or have figures and descriptions so defective that they do not allow the author to form any opinon as to their systematical position. They are (from this point the synonymy is intended to be as exhaustive as possible):

1) **Antedon admirabilis** NICOLAS 1898.

Antedon admirabilis 1898 NICOLAS, p. 406.
Antedon avenionensis var. *minor* 1898 NICOLAS, p. 406.

Like all the species described by NICOLAS, it is impossible to identify this one with the aid of descriptions or figures.

Occurrence: Tertiary (miocene), France.

2) **Comatula angulati** ENGEL 1908.

Comatula angulati 1908 ENGEL, pp. 207, 210.

There is no description nor any figure.

Occurrence: Lower Jurassic (lias α), Württemberg.

3) **Antedon avenionensis** NICOLAS 1897.

Antedon avenionensis 1897 NICOLAS, pp. 104, 108, 131, 135; 1898 NICOLAS, pp. 405, 409, fig. 5; 1899 LAMBERT, pp. 122—123.

Cd and RR are known. Here, as in the following species described by NICOLAS, the figures show hardly more than a silhouette and no details. Possibly synonymous with *A. deperéti* DE LORIOL.

Occurrence: Tertiary (miocene), France.

4) **Antedon breviceps** TATE & DENNANT 1893.

Antedon breviceps 1893 TATE & DENNANT, p. 266.

Is a nomen nudum.

Occurrence: Tertiary (eocene), Australia.

5) **Comatula claudiana** ETALLON 1857.

Comatula claudiana 1857 ETALLON, p. 282; 1866 OPPEL et WAAGEN, pp. 258, 300; 1867 OGÉRIEN, p. 675; 1888 DE LORIOL, p. 524.

Is a nomen nudum.

Occurrence: Upper Jurassic (oxfordian), France.

6) **Antedon glandiferus** NICOLAS 1897.

Antedon glandiferus 1897 NICOLAS, pp. 104, 131, 135; 1898 NICOLAS, pp. 406, 408, fig. 6; 1899 LAMBERT, pp. 122, 123.

Cd + RR are known. Possibly synonymous with *A. anglesensis* DE LORIOL.

Occurrence: Tertiary (miocene), France.

7) **Comatula matheyi** Greppin 1870.

Comatula Matheyi 1870 Greppin, p. 83.
Antedon Matheyi 1888 de Loriol, p. 527.

Is a nomen nudum.

Occurrence: Upper Jurassic, Switzerland.

8) **Antedon miocenicus** Nicolas 1897.

Antedon miocenicus(-a) 1897 Nicolas, pp. 104, 131, 132; 1898 Nicolas, p. 404, fig. 2; 1899 Lambert, p. 122; 1900 Noëlli, p. 34.
Antedon miocensis 1908 c A. H. Clark, p. 484.

Cd + RR are known. Probably, according to Noëlli, synonymous with *A. rhodanicus.*

Occurrence: Tertiary (miocene), France.

9) **Antedon pertusa** E. V. Clark 1900.

Antedon pertusa 1900 E. V. Clark, p. 5; 1911 Howchin, p. 53.

Is a nomen nudum.

Occurrence: Tertiary (eocene), Australia.

10) **Antedon pilularis** Nicolas 1897.

Antedon pilularis 1897 Nicolas, pp. 104, 131, 134; 1898 Nicolas, p. 405, fig. 4; 1899 Lambert, p. 122.

Cd + RR are known. Seems to be a separate species.

Occurrence: Tertiary (miocene), France.

11) **Comatula polydactylus** d'Orbigny 1850.

Comatula polydactylus(-a) 1850 d'Orbigny, Tome 1, p. 320; 1862 Dujardin & Hupé, p. 213; 1888 de Loriol, p. 524.
Antedon polydactylus 1878 Schlüter, p. 49.

Only the arms are known. They are distinguished by their "nombreux ramules"! No figure. Very doubtful if it is really a Comatulid at all.

Occurrence: Middle Jurassic (bathonian), France.

12) **Antedon sphæroidalis** Nicolas 1897.

Antedon sphæroidalis 1897 Nicolas, pp. 104, 131, 134; 1898 Nicolas, p. 404, fig. 3; 1899 Lambert, p. 122.
Antedon sphæroides 1908 c A. H. Clark, p. 494.

The Cd + RR are known.

Occurrence: Tertiary (miocene), France.

13) **Comatulella wagneri** Münster 1839.

Comatula paradoxa 1836 Münster, p. 583 n. n.

Comaturella Wagneri 1839 Münster, p. 85, Tab. 8, fig. 2 (1843 2. Aufl. p. 97, Tab. 8, fig. 2); 1848 Bronn, p. 322; 1857 Pictet, p. 289; 1862 Dujardin & Hupé, p. 214; 1876 Quenstedt, p. 185, Tab. 96, fig. 104; 1878 Schlüter, p. 37.

Saccosoma Wagneri 1850 d'Orbigny, Tome 1, p. 381.

The cirri adhering to a Cd(?) are known. Probably very closely related to, if not identical with, *Pterocoma pennata* or *formosa*.

Occurrence: Upper Jurassic (virgulian), Solenhofen, Germany.

Here must also be recorded a number of forms signified as *Comatula (Eudiocrinus)* or *Antedon* sp. only. Either they are not described particularly or they consist of separate arms- or cirrus-joints only.

Comatula sp. 1857 Etallon, p. 328. A nomen nudum. Lower Cretaceous (neocomian), France.

Comatula sp.? 1867 Moesch, p. 104. A nomen nudum. Middle Jurassic (callovian), Switzerland.

Antedon sp. 1880 Downes, p. 433 (Devon Assoc. Trans. 12) and 1882 Downes, p. 86 »? *Glenotremites,* plates of». Centrodorsals, mentioned only. Upper Cretaceous, England.

Antedon sp. 1891 Stolley, pp. 255, 308, Br-segments. Upper Cretaceous (senonian), Schleswig Holstein.

Antedon sp. 1895 Jahn, p. 168. A nomen nudum. Upper Cretaceous, Bohemia.

Antedon sp. 1899 Hennig, p. 150. A nomen nudum. Upper Cretaceous (danian), Sweden.

Antedon sp. 1910 Chapman, pp. 301, 305, 311, Pl. 52, fig. 8. Br-segments. Tertiary (miocene), Australia.

Antedon sp. 1910 Furlani, pp. 89, 90, 92. A nomen nudum. Upper Jurassic, Dalmatia.

Antedon sp. 1911 Lörenthey, p. 135 (Budapest, Ertesitö math. term. 29). Br-joints only. Tertiary (miocene), Hungary.

Eudiocrinus sp. 1913 Brünnich-Nielsen, p. 28, fig. 28. Is a I Br 2(?). Upper Cretaceous (danian), Denmark.

Antedon sp. 1913 Chapman, p. 180, Pl. 18, fig. 19. A cirral. Tertiary, Australia.

The following species are also very incompletely known; they have, however, been indicated with special names.

Only Br-segments are known in the following species:

1) **Antedon granulata** Brünnich-Nielsen 1913.

Antedon granulata 1913 Brünnich-Nielsen, pp. 99, 108, Taf. 19, figg. 57—59.

Only a I Ax is known.

Occurrence: Upper Cretaceous (danian), Denmark.

2) **Antedon stevensis** Brünnich-Nielsen 1913.

Antedon stevensis 1913 Brünnich-Nielsen, pp. 99, 100, Taf. 12, figg. 63—68

Only the Br 2 and a hypozygal ossicle are known.
Occurrence: Upper Cretaceous (senonian), Denmark.

Only the radial ring and the attached basals are known in:

1) **Antedon caraboeufi** de Loriol 1888.

Antedon caraboeufi 1888 de Loriol, pp. 446, 524, Pl. 213, fig. 2.

Is, perhaps, the radial ring belonging to the Cd that is described as *A. morieri*.
Occurrence: Lower Jurassic (domerian), France.

2) **Actinometra cheltonensis** P. H. Carpenter 1881.

Actinometra cheltonensis 1881 b P. H. Carpenter, pp. 205—207, 212, 216, Pl. 11, fig. 20; 1888 P. H. Carpenter, pp. 26, 39; 1888 de Loriol, p. 540; 1912 Kirk, p. 79.
Antedon cheltonensis 1881 c P. H. Carpenter, p. 10, Pl. 6, figg. 4—5.

Occurrence: Middle Jurassic (bajocian), England.

3) **Antedon complanata** P. H. Carpenter 1881.

Antedon complanata 1881 b P. H. Carpenter, pp. 195, 201, 205, 212, Pl. 9, fig. 9; 1888 de Loriol, p. 528; 1908 Engel, p. 455.

Occurrence: Upper Jurassic (virgulian), Württemberg.

4) **Antedon prisca** P. H. Carpenter 1880.

Antedon prisca 1880 a P. H. Carpenter, p. 54, Pl. 5, fig. 7; 1888 de Loriol, pp. 447, 450, 525.

Reminds one rather closely of *A. caraboeufi*.
Occurrence: Middle Jurassic (bathonian), England.

V. Characteristics systematically applicable in fossil Comatulids.

I have pointed out in the introduction the unfitness of ranging the fossil Comatulids in the genera *Actinometra* and *Antedon*. On the whole it seems to me to be very little advisable to range any fossil Comatulids in recent genera, as is done e. g. with *Antedon iheringi*, which A. H.

Clark (1915 b) refers to the genus *Catoptometra,* or *Microcrinus conoideus* (here only the Cd is known) which has been ranged by Clark & Twitchell (1915) under *Zenometra.*

As is stated above, the system of the recent Comatulids, especially as to generic and specific characteristics, is mostly founded on such characteristics as are inaccessible in fossil forms. It will therefore always be a very difficult task to identify fossil genera and species with recent ones. If we take e. g. the fossil *Actinometra loveni* it is, probably, rather closely related to certain recent Comasterids such as *Comatula, Capillaster, Comantheria, Comanthus,* or *Comaster.* But it is impossible to state that it belongs to anyone of these genera, not only because the species mentioned differs from most of the genera enumerated above by the X, very stout arms, but also because it is impossible to investigate the pinnule characteristics that partly characterize the genera of *Comasteridae.* Taking another example, *Eudiocrinus hyselii,* this species is, probably, closely related to the recent *Eudiocrini* from which it differs, however, by the transverse crest in the cirrus-socket (unknown in the recent genus) and, probably, by the absence of syzygies. These two examples are purposely selected to show how difficult it may be even in the most favourable instances to say anything with exactness about the identity of genera and species in recent Comatulids and extinct ones.

Is it possible then to deduce any relation between the fossil and the recent forms? A close knowledge of the subject enables one to answer this question in the affirmative. In fact there are a number of characteristics that one finds both in fossil and recent forms, characteristics that are sufficient in number and importance to make it possible to conclude along what phylogenetic lines the evolution has taken place. These characteristics we find in Cd, BB, and RR. I give below a survey of the characteristics employed in my system for distinguishing the fossil Comatulids.

Cd. Systematic characteristics are found in the development of a discoidal, conical, columnar, or hemispherical Cd. One has reason to attach great importance to the so-called dorsal star, i. e., the star-shaped scar of the not yet perfectly obliterated cavities marking either the prolongation of the dorsal coelom or (presumably less common) the chambered organ in the stem. This star-shaped opening is always connected with a relatively large Cd-cavity and probably with the occurrence of ventral radial pits also (A large petaloid figure sometimes occurring on the dorsal side of the Cd, presumably marking the articulation facet against a discarded angular stem, must be carefully distinguished from this (Cf. Chap. 4)). One sometimes finds a dorsal pore in the Jurassic Comatulids, and always in *Thiollierierinus.* These forms were, however, always strongly microphreate and the pore here is very small and round. The development of radial pits on the ventral side of the Cd is a systematic characteristic of great importance. These radial pits have nothing at all to do with the 5-chambered organ and its cavities, but harbour, as P. H. CARPENTER pointed out quite correctly in 1879, the proximal continuation of the dorsal coelom of the arms. They have, in certain Cretaceous forms, an extremely powerful development, but in the recent forms they are generally not developed at all (deep in *Notocrinidae* and *Asterometridae*) or appear as shallow, meandering, branched canals between the radial ring and Cd (e. g. *Himerometridae*).

A very important characteristic, as A. H. CLARK emphasized specially, is the size of the Cd-cavity. In the older fossil forms this cavity is extraordinarily small, in the younger forms we come nearer and nearer to the large cavity which we find best developed among the *Macrophreata* distinguished by CLARK. Certain *Oligophreata*, on the contrary, correspond in this characteristic more nearly with the Jurassic forms.

The occurrence and arrangement of the cirri is very significant (in rows in the older forms, in whorls among the younger) and so is also the appearance of the cirrus-faces. In older forms the cirrus-faces are provided with a transverse crest as in the Pentacrinids, in younger ones this is divided into two lateral tubercles, or remains as an areola round the lumen, or may be completely obliterated, in which case the cirrus-faces may be either striated peripherally or perfectly smooth. This change marks the ever increasing tendency of the articulations between the Cd and cirri to become a pre-formative place for the discarding and regeneration of the cirri, as the syzygy is in the arms.

BB. These, which in the older forms are strongly developed, become more and more reduced in the younger ones. The absence of a rosette in these older forms, to which CARPENTER attached a certain amount of importance, is of less significance. His assumption that the BB in recent forms might be "compound basals", where the basal star is not analogous to the peripheral part of the BB in the fossil forms, does not seem to me to be correct. In reality we have a continuous series from true BB, as in Pentacrinids, through "compound basals" in a number of Comatulids, to the rosette found in the most modernly organized forms, the Antedonids. Such a form as *Notocrinus* cannot be said even to-day to have a rosette, as the proximal ends of the BB are only united with each other by weak sutures (fig. 197). On the other hand I have found in the Cretaceous form *Semiometra impressa* (fig. 237), a distinct rosette developed.

The appearance of the rosette is brought about by the ever increasing size of the nerves proceeding from the 5-chambered organ and the simultaneous reduction of the BB. In its perfect form the rosette forms only the central part of the coalesced BB, remaining at the same stage of calcification as that of the embryonic BB. The parts situated peripherally of the place where the nerves emerge are reduced altogether or remain in the shape of a basal star, which in such a case, from natural reasons, must be calcified as strongly as the surrounding Cd and RR.

RR. Here we find a number of significant characteristics. The dorsal, free, exterior part may be more or less developed according as the R is less or more hidden by the Cd and I Br 1. As CARPENTER pointed out, the inclination of the radial-faces is also of importance. Another important matter caused by this is the larger or smaller diameter of the radial cavity in some forms sloping evenly inwards, in other cases deepened abruptly into a central depression. The radial cavity may be filled more or less by the spongy calcareous tissue that CARPENTER called the central plug. Among fossil forms this tissue is scarcely developed or completely lacking. The appearance of the radial articular face seems, however, to offer the most important characteristic. The enlargement of the muscular fossæ stands, as I have emphasized in another connection, in a certain relation to the gradually increasing adaptation for greater mobility and power of swimming which most of the Comatulids, from the very beginning of their eleutherozoic life, have been submitted to. We thus find rather insignificant muscular attachments or even none at all among the Jurassic forms, while certain younger forms have very powerful muscle-attachments. Side by side with these forms, even in our own days there still remain descendants of the forms possessing insignificant muscular attachments. Sometimes it may happen among the fossil forms that the difference between the muscular fossa and the interarticular ligament is more or less indistinct owing to wear; in such a case one can conclude, at least very often, the extent of the muscular attachment from the height of the articular-face. It is chiefly through the splendid works on morphology by P. H. CARPENTER and A. H. CLARK especially (1888 and 1922) that we have now a fairly good knowledge of the appearance of the radial faces among recent forms, a knowledge allowing the results obtained to be used when regarding the fossil types.

Finally a few words on the arms among the fossil forms, and the systematic characteristics which may be drawn from them. The arms may be coarse or slender, with longer or shorter joints, monoserial or biserial, V, X, or numerous. Synarthries may be developed or be lacking. The syzygies may be few in number, usually among the older forms having few septa; or they may be numerous, in the younger forms, where we meet with many septa. I consider, however, that for several reasons it is less suitable to make use of characteristics taken from the arms in a systematization of the fossil Comatulids. First, the arms, as in the now living Pentacrinids, seem to be little differentiated and offer few systematic fixed points; secondly, and most important, they are known in an infinitesimal number of cases only. Where the arms have been preserved also, I have therefore first made use of the characteristics found in the Cd, BB and RR, upon which I consider a systematization of the fossil Comatulids must chiefly be founded. I have, however, in such cases tried to complete the idea of the characteristics belonging to the group, by giving the distinctive features found in the arms too.

VI. Species in which the arms are known, but the calyx-ossicles only imperfectly described.

In such cases where the arms are known, but not the (Cd) BB, or RR I have given up trying to bring these forms into the scheme under which the better known fossil Comatulids are ranged. The Comatulids first mentioned, however, have arms of two different types to which I have assigned two old generic names *Pachyantedon* and *Pterocoma*. Of these genera the first mentioned is only provisional and includes forms belonging either to *Palaeocomasteridae* or *Solanocrinidae*. When the Cd, BB, and RR of these forms are found, they ought therefore to be transferred to one of the above mentioned families. The other genus is probably, as will be shown later on, the ancestral type of one or two of the later Comatulid series.

A) **Pachyantedon** JÆKEL 1891.

A group of fossil Comatulids where the Cd and the radial face are not yet known. The arms are coarse and stout, X—XX, usually with very oblique articulations, tending strongly towards and often reaching the biserial stage. Syzygies very rare or lacking. Cirri long and coarse with short segment, $l < br$.

As to the characteristics of the arms the definition to a certain extent covers the one that is given by WALTHER (1886) for *Solanocrinus*. As, however, GOLDFUSS in his day assigned this name to the Cd and radial ring of certain well-known Jurassic Comatulids, this name ought, therefore, to be kept for the sphere of the Goldfussian species.

The type for *Pachyantedon* is *P. beyrichi*.

Three species belong to this genus *P. beyrichi* JÆKEL 1891, *gracilis* WALTHER 1886, *imperialis* WALTHER 1886.

1) **Pachyantedon beyrichi** JÆKEL 1891.

Pachyantedon beyrichi 1891 JÆKEL, pp. 627, 628, Tab. 43, fig. 5; 1912 KIRK, p. 78.

X arms, with very oblique joints.

Occurrence: Upper Cretaceous, North Germany.

2) **Pachyantedon gracilis** (WALTHER) 1886.

Solanocrinus gracilis 1886 WALTHER, pp. 173—175, 182, 183, Pl. 25, figg. 2, 4, Pl. 26, figg. 1—4; 1887 P. H. CARPENTER, pp. 85—87; 1888 P. H. CARPENTER, pp. 90, 93, 94.

Antedon (Solanocrinus) gracilis 1888 DE LORIOL, p. 530.

There are XX arms, I Br 1 and 2 probably grown together. II Brr are 1.

Occurrence: Upper Jurassic (virgulian), Bavaria.

3) **Pachyantedon imperialis** (WALTHER) 1886.

Solanocrinus costatus 1879 ZITTEL, fig. 283 a, 1913 ZITTEL—EASTMAN, fig. 340 a.

Solanocrinus imperialis 1886 WALTHER, pp. 168, 170, 171, 173, 174, 184, 188, Pl. 25, fig. 3, Pl. 26, fig. 6; 1887 P. H. CARPENTER, pp. 86, 87; 1888 P. H. CARPENTER, pp. 90, 93, 94.

Antedon (Solanocrinus) imperialis 1888 DE LORIOL, pp. 475, 530; 1915 ZITTEL, fig. 320 a.

XX arms. I Br 1 and 2 grown together. II Brr are 1, sometimes apparently formed by the anchylosis of two ossicles.

Ocurrence: Upper Jurassic (tithonian), Bavaria.

B. **Pterocoma** L. AGASSIZ 1835 (em.).

One of this species is known fairly closely and the diagnosis is chiefly made according to it.

A genus of fossil Comatulids where the Cd is very small, flattened, supporting about X cirri, with a central, rounded perforation dorsally. The cirri are very long and slender, composed of very long cirrals without dorsal or opposing spine, the l. several times the br. BB and radial faces unknown, radial cavity large. Arms X, very long and slender, composed of long and not very oblique Brr. The syzygies are numerous. I Ax probably had a synarthrial face proximally. The pinnules prismatic, proximally triangular, distally composed of long pinnulars. Large covering plates. Type *Pt. pennata*.

Here belong 3 species: *Pt. formosa* WALTHER 1886, *pennata* SCHLOTHEIM 1820, and *pinnulata* FRAAS 1878.

1) **Pterocoma formosa** (WALTHER) 1886.

Antedon formosus(-a) 1886 WALTHER, pp. 177, 178, Pl. 26, figg. 2, 12; 1888 DE LORIOL, p. 531.

According to WALTHER I Br 1 and 2 are grown together. This statement, however, ought to be verified.

Occurrence: Upper Jurassic (tithonian), Bavaria.

2) **Pterocoma pennata** (SCHLOTHEIM) 1820.

... *ein zusammengezogener Seestern (Caput medusae)* 1755 KNORR, pp. 7, 181, Tab. 11, fig. 1, Tab. 34 a, fig. 1.

? *Stella decem caudis crinitis* 1757 BAIER, p. 13, Tab. 7, fig. 2.

? *Stella decem radiis fissis* 1757 BAIER, p. 13, Tab. 7, fig. 3.

Der d'Annonische Pentacrinit 1769 WALCH, p. 104, Tab. L. I.

Un fossile rare 1775 COLINI, p. 103, Pl. 4, fig. 6.

Asteria caput medusae pennatum 1778 SCHRÖTER, pp. 377, 378, No. 17 and 19.

Asteriatites pennatus 1813 SCHLOTHEIM, p. 68.

Ophiurites pennatus 1820 SCHLOTHEIM, p. 326, Tab. 28, figg. 1—4; 1823 SCHLOTHEIM, p. 45.

Comatulithes mediterraneaeformis 1823 SCHLOTHEIM, p. 47; 1827 GERMAR, p. 107; 1848 BRONN, p. 322.

Comatula pinnata 1831 GOLDFUSS, p. 203, Tab. 61, fig 3; 1841 J. MÜLLER, p. 139; 1848 BRONN, p. 322; 1852 QUENSTEDT, p. 600, Pl. 51, fig. 27 (2. Aufl. 1867, p. 716, Tab. 65, fig. 27; 3. Aufl. 1885, p. 914, Tab. 72, fig. 4); 1858 QUENSTEDT, p. 801; 1876 QUENSTEDT, p. 167, Tab. 96, figg. 20, 21; 1878 SCHLÜTER, p. 35; 1891 JÆKEL, p. 627; 1908 ENGEL p. 470.

Pterocoma pinnata 1835 L. AGASSIZ, p. 193; 1839 MÜNSTER, p. 86 (*Pt. Comaluta p.*); 1848 BRONN, p. 1054; 1857 PICTET, p. 290, Pl. 99, fig. 4; 1862 DUJARDIN & HUPÉ, p. 215.

Decacnemos pennatus 1836 BRONN, p. 273, Taf. 17, fig. 17 a—c; 1848 BRONN, p. 405.

Alecto pinnata 1846 GEINITZ, p. 545.

Asteriacites pennatus 1848 BRONN, p. 119.

Geocoma pinnata 1878 FRAAS, p. 89.

Antedon pinnatus(-a) 1878 SCHLÜTER, p. 49; 1886 WALTHER, pp. 176, 177, Pl. 26, figg. 5, 7, 8, 10.

Antedon (Comatula) pinnata 1888 DE LORIOL, p. 530.

It seems to me that this species, which is generally called *pinnata* (GOLDF.), must be called *pennata* (SCHLOTHEIM). The latter author is the first who has given the species a binominal name and added to it some figures. It is true that GOLDFUSS' figures give a much better idea of the species and we find here also a good description, but as the figures of the oldest author mentioned are perfectly sufficient to enable us to identify the species with certainty, I use the name that is given by him. The preceding species seems to be very closely related to *Pt. pennata.* It occurs also in the same locality. The distinguishing marks given by Walther are scarcely correct: RR and I Br 1 are said to be anchylosed — if his statement is correct, a unique case among the Comatulids. As far as I have seen the proximal border of I Ax indicates a synarthry. Walther's statement as to the median pinnule is surely erroneous.

Occurrence: Upper Jurassic (tithonian), Bavaria.

3) **Pterocoma pinnulata** (Fraas) 1878.

Geocoma pinnulata 1878 Fraas, p. 89.
Geocoma libanotica (error lithogr.) 1878 Fraas, Pl. 2, fig. 2.
Antedon pinnulatus 1886 Walther, p. 178.

Occurrence: Upper Cretaceous (turonian), Lebanon.

VII. Comatulid species of which the Centrodorsals only are known.

A thorough study of the forms of which only the Cdd are known certainly not only leads to the view that a systematic classification is possible, but at the same time produces the conviction that the knowledge of the Cd only is not quite sufficient always to clear up the relationship of these species to the other fossil and recent forms. If the ventral aspect of the Cd were known in a larger number of species of which the Cd and the radial ring are described now, it is very probable that we should be able to settle the phyletic connection with a higher degree of certainty. As the matter stands now this is not always the case. I have therefore referred all the Comatulids of which only the Cdd are known to the genus *Glenotremites,* used already by Goldfuss to signify a Cd (though he misunderstood its relations). To attain greater perspicuity I have, however, made a scheme dividing the known forms into a number of groups, which seem to me to correspond approximately to the remaining groups of fossil Comatulids, which I have described later on. The genus *Glenotremites* is only provisional and the forms which are ranged here ought as soon as possible to be transferred to their respective fossil Comatulid genera.

A. **Glenotremites** GOLDFUSS 1831.

Syn. *Microcrinus* EMMONS 1858.
Allionia MICHELOTTI 1861.

By *Allionia* MICHELOTTI intended to signify a species *(oblita)* of which we now also have the radial ring. Nevertheless, he was aquainted himself only with the Cd, and by the new genus he intended to denote a Cd only, which he, like GOLDFUSS, supposed to have a mouth in the centre of the ventral face. The basal furrows, however, he, contrary to GOLDFUSS, interpreted rightly. Moreover, there is no diagnosis of this genus, and the same is the case as regards *Microcrinus*.

This group contains fossil Comatulids which are known by the Cdd only. The species referable here are the following 51:

abnormis P. H. CARPENTER 1880, *allardi* DE LORIOL 1897, *angelini* nov. sp., *anglesensis* DE LORIOL 1897, *arnaudi* DE LORIOL 1894, *atacicus* DONCIEUX 1911, *batheri* nov. sp., *bronnii* QUENSTEDT 1852, *brownii* FORBES 1852 (+ *woodwardi* FORBES 1852), *concavus* SCHLÜTER 1878, *conoideus* EMMONS 1858, *depereti* DE LORIOL 1897, *desori* ETALLON 1862, *essenensis* SCHLÜTER 1878, *exilis* DE LORIOL 1869, *faxensis* BRÜNNICH-NIELSEN 1913, *fontannesi* DE LORIOL 1897, *guirandi* DE LORIOL 1888, *hungaricus* VADÁSZ 1915, *hungaricus* var. *rotundatus* VADÁSZ 1915, *janeti* VALETTE 1917, *ladoixensis* DE LORIOL 1888, *laticirrus* P. H. CARPENTER 1880, *lettensis* SCHLÜTER 1878, *lorioli* REMEŠ 1902, *lundgreni* P. H. CARPENTER 1880, *minutissimus* VALETTE 1917, *miocaenicus* VADÁSZ 1915, *morieri* DE LORIOL 1888, *mülleri* P. H. CARPENTER 1880, *nicolaisi* NOËLLI 1900, *paradoxus* GOLDFUSS 1831, *paronai* NOËLLI 1900, *parvicavus* nov. sp., *pellati* DE LORIOL 1897, *perforatus* P. H. CARPENTER 1880, *protomacronema* CHAPMAN 1913, *pusillus* FRITSCH 1910, *pyropa* ZAHALKA 1892, *ransomi* FORBES 1852, *ranvillensis* DE LORIOL 1888, *rosaceus* GEINITZ 1871, *rotundus* P. H. CARPENTER 1880, *rugosus* P. H. CARPENTER 1880, *schlueterianus* GEINITZ 1871, *semiglobularis* BRÜNNICH-NIELSEN 1913 (here some brachials are known also), *stellatus* NOËLLI 1900, *striatus* P. H. CARPENTER 1880, *sulcatus* SCHLÜTER 1878, *tourtiae* SCHLÜTER 1878, *valetti* nov. sp.

Survey of the groups:

I. Cirrus-sockets large and stout, in rows (columns), if in a single whorl with a distinct transverse crest. Cd columnar to conical, more rarely discoidal.
    A. Centrodorsal cavity very small (diameter $^1/_7$—$^1/_{14}$ of the br. of Cd), its opening round, no radial pits or pores, no dorsal star. Cd flattened dorsally with a large area devoid of cirri.

  1. Cirrus-socket with a stout transverse crest, the *exilis*-group (Middle Jurassic to Lower Cretaceous).
     a. Cirri in X rows *bronnii.*
     b. Cirri in XV—XX rows. Cd. h < $^1/_3$ br. *desori, exilis, guirandi, ranvillensis.*
  2. Cirrus-socket without distinct transverse crest.
     a. Cd discoidal, the *parvicavus*-group (Upper Cretaceous — Tertiary) *parvicavus, protomacronema.*
     b. Cd conical, Upper Jurassic *lorioli.*

B. The centrodorsal cavity of medium size to large (diam. at least $^1/_4$—$^1/_3$ of the diameter of Cd).
  1. No radial pits or pores. No dorsal star.
     a. Cd strongly flattened dorsally, with a large area which lacks cirri, the *pellati*-group, Cretaceous — miocene.
        α. Cirrus-socket without sculpture. The opening of the Cd-cavity perfectly round. Cirri in X rows. *atacicus, fontannesi, pellati, stellatus.*
        β. Cirrus-socket with a weak transverse crest and peripherally striated. 8 large cirri only. Opening of the Cd-cavity indistinctly lobated *laticirrus.*
     b. Cd a pointed or truncated cone. No, or indistinct, sculpture of the cirrus socket, the *anglesensis*-group, Upper Cretaceous — miocene.
        α. Cd distinctly conical. Cirri in X rows, continued almost to the top of Cd. Opening of the Cd-cavity perfectly round or indistinctly lobate, *anglesensis, concavus conoideus, faxensis, pyropa, nicolaisi, paronai, semiglobularis, sulcatus.*
        β. Cd a truncated cone. Cirri in XV—XX rows *allardi, depereti.*
  2. With radial pits or pores. No dorsal star, the *lettensis*-group, Upper Cretaceous.
     a. Small radial deep pores *lettensis, lundgreni.*
     b. Large and deep radial pits *arnaudi.*
  3. With a dorsal star, Upper Cretaceous.
     a. Only 5 cirrus-sockets. Dorsally a large pentagonal impression of a stem (probably a young). No radial pits. *janeti.*
     b. Cirri at least XX, large radial pits, the *essenensis*-group.
        α. Cirri in X rows *essenensis.*
        β. Cirri in XX rows *batheri, tourtiae.*

II. Cirrus-sockets usually smaller, in close alternating whorls; if in a single whorl without sculpture. Cd discoidal — hemispherical.

A. Cd-cavity very small and shallow (diameter about $^1/_9$ of the diameter of Cd), the opening round, no radial pits, no dorsal star (one must not confound with this the large petaloid figure sometimes occurring). No, or indistinct, sculpture of the cirrus-socket, the *morieri*-group, Lower to Middle Jurassic *ladoixensis*, *morieri*, *mülleri*.

B. Cd-cavity rather large (the opening usually $^1/_4$—$^1/_3$ of the diameter of Cd), usually radial pits or pores.
  1. Cd strongly flattened, Cd-cavity $^1/_5$—$^1/_3$ of the diameter of Cd, very shallow. Cirrus-sockets small, in a single or double whorl, the *angelini*-group (? Middle Jurassic —) Upper Cretaceous — miocene, ? *abnormis*, *angelini*, *hungaricus* with var. *rotundatus*, *miocaenicus*.
  2. Cd-cavity deep. Cirrus-sockets in at least a double whorl.
    a. With a dorsal star (and radial pits). Cd low. Cirrus-sockets rather large, often peripherally striated, the *paradoxus*-group, Upper Cretaceous, *paradoxus*, *perforatus*, *pusillus*, *rosaceus*, *rugosus*, *schlueterianus*, *striatus*, *valetti*.
    b. Without distinct dorsal star. Cirrus-sockets moderate or rather small.
      α. Cd hemispherical; small radial pits, the *rotundus*-group, Cretaceous.
        +. Cirrus-socket with two small tubercles *minutissimus*.
        ++. Cirrus-socket without sculpture *rotundus*.
      β. Cd very flattened, no radial pits, the *ransomi*-group. Tertiary *brownii*, *ransomi*.

Below the species of *Glentotremites* follow in alphabetic order.

1) **Glenotremites abnormis** (P. H. Carpenter) 1880.

Actinometra abnormis 1880 a P. H. Carpenter, pp. 40, 53, Pl. 5, fig. 8; 1888 de Loriol, p. 541.

In this species, as in *Gl. mülleri*, there occurs a shallow petaloid impression dorsally which is (?) radially oriented. It is not to be confounded with the dorsal star (cf. Chap. 4) of e. g. the *paradoxus* group. It is open to doubt if this species really belongs to the *angelini* group. Perhaps it would be more suitable to place it in the *morieri* group, but the Cd-cavity is rather large; possibly, however, this is due to erosion (opening $^1/_5$ of the diam. of Cd). In the dorsal centre perhaps a round opening.

Occurrence: Middle Jurassic (bathonian), England.

2) **Glenotremites allardi** (de Loriol) 1897.

Antedon allardi 1897 de Loriol, p. 126, Pl. 4, fig. 12; 1897 Pellat, p. 112; 1898 Nicolas, pp. 398, 409, 410, fig. 11; 1899 Lambert, p. 123; 1900 Noëlli, p. 43; 1915 Vadász, pp. 10, 11, 171, Pl. 1, figg. 14, 17.

Occurrence: Tertiary (miocene), S. France, Hungary.

3) **Glenotremites angelini** nov. sp. (figg. 200—202).

This species I have dedicated to the late N. P. Angelin of the Riksmuseum, Stockholm.

Dimensions: Cd diameter: 6·7 mm., h: 2·8 mm. Dorsal cirrus-free part: 4·9 mm. Diameter of the Cd-cavity: 1·3 mm.

Cd discoidal, dorsally flattened, somewhat deepened in the centre; the dorsal face with an indistinct central pit surrounded by an areola, radiating from this indistinct impressions. Cirrus-sockets in about 2 irregular alternating close whorls, without sculpture, XXXIV in all, some of them proceeding from the ventral face of Cd. Cd-cavity very shallow (depth ± 0·4 mm.), surrounded by still shallower radiating pits, probably the dorsal continuations of the dorsal coelom (cf. e. g. *Pontiometra*). Basal impressions narrow and indistinct. The specimen is somewhat worn.

Occurrence: Upper Cretaceous (danian), Annetorp, Limhamn near Malmö, S. Sweden. The type specimen in the Riksmuseum, Stockholm.

4) **Glenotremites anglesensis** (de Loriol) 1897.

Antedon anglesensis 1897 de Loriol, pp. 115, 121, Pl. 4, fig. 7; 1897 Pellat, p. 112; 1898 Nicolas, pp. 398, 408, 410, fig. 9; 1899 Lambert, p. 123; 1900 Noëlli, pp. 20, 41, 43, Tav. 1, fig. 67; 1905 Bellini, p. 641; 1915 Vadász, p. 9.

Nicola's figure seems to be rather(?) incorrect.

Occurrence: Tertiary (miocene), S. France, N. Italy.

5) **Glenotremites arnaudi** (de Loriol) 1894.

Antedon arnaudi 1894 de Loriol, p. 479, Pl. 24, figg. 1—2.

Occurrence: Upper Cretaceous (campanian), S. France.

6) **Glenotremites atacicus** (Doncieux) 1911.

Antedon atacicus 1911 Doncieux, p. 160, Pl. 15, fig. 28.

Occurrence: Tertiary (eocene), France.

7) **Glenotremites batheri** nov. sp. (figg. 203—205).

After a description kindly handed over to me by Dr. F. A. BATHER to whom I dedicate this new species.

Dimensions: Cd h: 6·5 mm., br: 14·4 mm.; the diameter of the dorsal, concave surface is ± 9·5 mm.

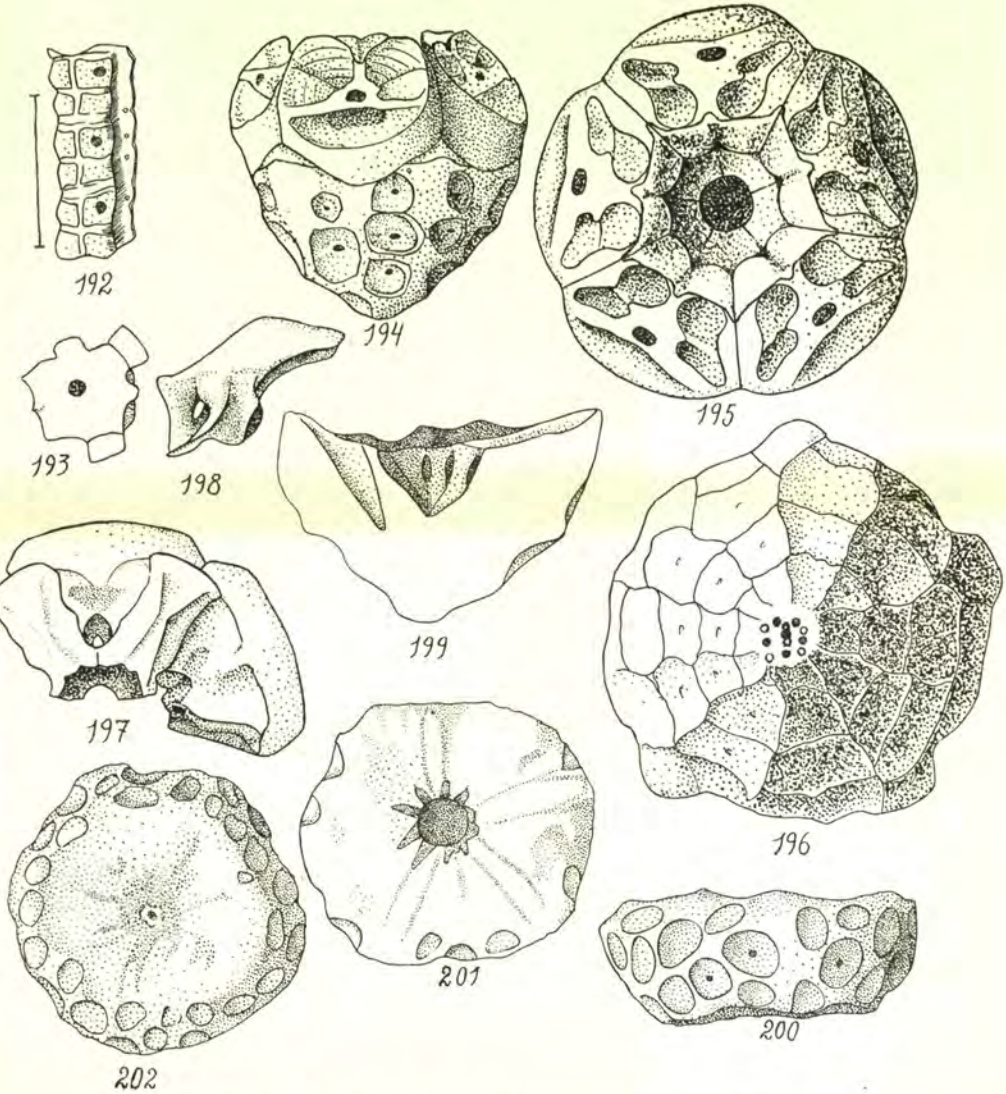
Dorsal surface deeply concave, greatest depth 2·5 mm. marked by a 5-rayed dorsal star, with radial rays reaching 1·9 mm. from centre and widening into deepened and rounded distal ends. On the sides of the concavity are 5 slight, interradial grooves. There are also occasional markings where a canal of a dorsal cirrus crops out after passing through the stereom.

Ventral surface slightly concave; central cavity quinquelobate, the radial pits reaching to 2·2 mm. from centre. Radial pits deeper than the Cd-cavity. The radial sectors of the ventral surface are raised in folds. Evidently there have been deep subradial clefts, when the radial ring was in situ. The basal grooves are rather narrow, wider and deeper distalwards, greatest br. about 1·0 mm.; bounded by a slight ridge. In the distal parts of the basal furrows possibly traces of plication.

The sides of the Cd may be divided into 5 radial areas by lines drawn from the basal furrows to the slight interradial furrows of the dorsal face. In 2 or perhaps 3 cases these interradial lines occupy flattened or slightly concave areas. In other cases they are encroached on by the cirrus-facets and become imaginary. In each of the radial areas the cirrus-sockets are arranged in 4 vertical rows and each row contains 3 or 4 facets, the dorsal or ventral ones being occasionally obscure. In two adjacent rows one cannot make out more than 2 facets per row and this is correlated with a radially situated depression on the ventral surface of Cd (cf. fig. 203). There are LXII cirrus-sockets in all. The facets in adjacent rows alternate with one another to some extent, and being pressed together, their outline tends in some cases to be (roundedly) hexagonal. The edges of the sockets are finely and indistinctly striated here and there. The nerve-lumen for the cirrus-socket approximates to keyhole shape. The lateral swellings end more abruptly on their ventral side and slope off more gradually dorsalwards. In one case there are 2 holes to a facet as though the elevations had met across the canal. The diameter of one of the largest cirrus-sockets is 2·0 mm.

This new species approaches closest to *Gl. tourtiae* from which, however, it differs by the radial pits being much larger and deeper, confluent with the Cd-cavity (a secondary phenomenon?), and by the outline of Cd being much more rounded. Further, there is no indication of any sculpture in the drawings of the cirrus-socket in *Gl. tourtiae.*

Occurrence: Upper Cretaceous (lower senonian, zone of *Micraster*



Figg. 192—202. 192) *Comatula bertrandi* Copy of the original figure of THURMANN kindly presented by Prof. A. **REICHENSPERGER**, inconsiderably magnified; 193) *Pterocoma pennata* A Cd with two appendant cirrals and a central hole, $^8/_1$; 194—199) *Notocrinus virilis.* 194) A Cd with the basal and radial rings in lateral view, $^6/_1$; 195) Basal and radial rings in ventral view, $^8/_1$; 196) The Cd described by **MORTENSEN** 1918, p. 2, in dorsal view. The five black dots are radially arranged, nearly perforate the Cd, and are the continuations of the chambered organ; the 5 interradial rings are small pits only, $^{18}/_1$; 197) Two BB and two RR in dorsal view, $^8/_1$; 198) A basal viewed from the side, $^{10}/_1$; 199) A vertical section prepared by grinding through a Cd, a radial pit to the left, $^8/_1$. 200—202) *Glenotremites angelini* 200) Cd in lateral view, 201) Cd in ventral view; 202) Cd in dorsal view, $^6/_1$.

cor-testudinarium), Seaford Head, Sussex, England. Found by C. D SHERBORN. Type specimen in the collections of Dr. A. W. ROWE, Margate.

8) **Glenotremites bronnii** (QUENSTEDT) 1852.

Solanocrinites Bronnii 1852 QUENSTEDT, p. 601, Taf. 51, fig. 32 (2. Aufl. 1867, p. 716, Taf. 65, fig. 32; 3. Aufl. 1885, p. 915, Taf. 72, figg. 11—12); 1876 QUENSTEDT, p. 181, Tab. 96, figg. 91—97.

This species differs very considerably from the *bronnii* of v. MÜNSTER (1839).

Occurrence: Upper Jurassic, Switzerland.

9) **Glenotremites brownii** (FORBES) 1852.

Comatula sp. (pars) 1843 MORRIS, p. 50.

Comatula Brownii 1852 FORBES, p. 19, Pl. 1, fig. 19; 1876 QUENSTEDT, p. 185; 1878 SCHLÜTER, p. 38; 1879 a FONTANNES, p. 498; 1879 b FONTANNES, p. 414; 1897 NICOLAS, p. 131.

Comatula Woodwardi 1852 FORBES, p. 19, Pl. 1, fig. 20; 1878 SCHLÜTER, p. 38; 1879 a FONTANNES, p. 498; 1879 b FONTANNES, p. 414; 1897 NICOLAS, p. 131.

Antedon Brownii 1878 SCHLÜTER, p. 50; 1879 a FONTANNES, p. 500; 1879 b FONTANNES, p. 416.

Antedon Woodwardi 1878 SCHLÜTER, p. 50; 1879 a FONTANNES, p. 500; 1879 b FONTANNES, p. 416.

Antedon (Comatula) Brownii 1896 A. BELL, p. 6; 1920 A. BELL, p. 12.

Antedon (Comatula) Woodwardi 1896 A. BELL, p. 6; 1920 A. BELL, p. 12.

I cannot see that the two species mentioned above in the synonymous list differ in any systematically important characteristic. The species *woodwardi* is a somewhat younger specimen and therefore has a somewhat larger Cd-cavity and fewer cirri. Both the species, besides, are from the same locality and therefore I do not hesitate to join them into one.

Occurrence: Tertiary (pliocene, plaisancian), England.

10) **Glenotremites concavus** (SCHLÜTER) 1878.

Antedon concavus 1878 SCHLÜTER, pp. 37, 48, 49, Pl. 3, figg. 4—7.

Occurrence: Upper Cretaceous (maastrichtian), Holland.

11) **Glenotremites conoideus** (EMMONS) 1858.

Microcrinus conoideus 1858 EMMONS, p. 311, figg. 246, 247; 1866 CONRAD, p. 31.

Zenometra(?) *conoideus* 1915 CLARK & TWITCHELL, p. 112.

To judge from the description and figures given by EMMONS, this species seems to fall into the same natural group as the *conoideus* of

Goldfuss (cf. *Amphorometra*). Evidently, therefore it is rather closely related to this species and will possibly be referred to the same genus as *Gl. conoideus* Goldfuss when it is more perfectly known. Perhaps there are shallow radial pits (cf. fig. 247 of Emmons).

Occurrence: Tertiary (eocene), North Carolina, U. S. A.

12) **Glenotremites depereti** (de Loriol) 1897.

Antedon depereti 1897 de Loriol pp. 115, 125, Pl. 4, fig. 14; 1897 Pellat p. 112; 1898 Nicolas pp. 398, 409, 410, fig. 10; 1899 Lambert p. 123; 1900 Noëlli pp. 20, 37, Tav. 1, figg. 53—57; 1905 Bellini p. 641.

Occurrence: Tertiary (miocene), S. France, N. Italy.

13) **Glenotremites desori** (Etallon) 1862.

Comatula desori 1862 a Etallon p. 341.

Antedon desori 1879 de Loriol pp. 263, 264, 290, Pl. 20, figg. 8—9; 1888 de Loriol pp. 468, 510, 512, 517, 524.

Occurrence: Upper Jurassic (pterocerian), France, Switzerland.

14) **Glenotremites essenensis** (Schlüter) 1878.

Antedon essenensis 1878 Schlüter pp. 40, 44, 49, Tab. 1, figg. 1—3; 1880 c P. H. Carpenter pp. 39, 53.

Occurrence: Upper Cretaceous (tourtia), W. Germany.

15) **Glenotremites exilis** (de Loriol) 1869.

Comatula exilis 1869 de Loriol p. 59, Pl. 4, fig. 2; 1870 Greppin p. 139.

Antedon exilis 1878 Schlüter pp. 40, 49; 1879 de Loriol pp. 273, 275, 290, Pl. 20, fig. 18.

Occurrence: Lower Cretaceous (neocomian, urogonian), Switzerland.

16) **Glenotremites faxensis** (Brünnich-Nielsen) 1913.

Atelecrinus faxensis 1913 Brünnich-Nielsen pp. 24, 99, fig. 26, Tab. 12, figg. 60—62.

Brünnich-Nielsen says that in this species the BB meet, forming a continuous circlet as in *Atelecrinus*. Possibly this is really the case, but it is very difficult to settle. His fig. 26, however, seems to show that the five strongest intercirral ridges which are generally interradially situated do alternate with some faint elevations on the ventral side of Cd. Possibly, these swellings mark the contact lines between the BB. Figg. 39—41 of Tab. 12 which have been referred to *Antedon* *semiglobularis* seem to approach the Cd of *faxensis* very closely. Nevertheless, one has here a very distinct basal star. The matter would be easily explained if we presumed that *faxensis* was a young of *semiglobularis* figg. 39—41, a supposition that is made rather probable by the smaller size and greater Cd-cavity of *faxensis*.

Occurrence: Upper Cretaceous (danian), Denmark.

17) **Glenotremites fontannesi** (DE LORIOL) 1897.

Antedon fontannesi 1897 DE LORIOL pp. 115, 126, Pl. 4, fig. 13; 1897 PELLAT p. 112; 1898 NICOLAS pp. 398, 407, 409, fig. 8; 1899 LAMBERT p. 123; 1900 NOËLLI pp. 20, 35, Tav. 1, figg. 50—52; 1905 BELLINI p. 641; 1915 VADÁSZ pp. 12, 164, 171, Pl. 1, figg. 22—23.

Occurrence: Tertiary (miocene), S. France, N. Italy, Hungary.

18) **Glenotremites guirandi** (DE LORIOL) 1888.

Antedon guirandi 1888 DE LORIOL pp. 467, 524, Pl. 216, fig. 5.

Occurrence: Upper Jurassic (oxfordian), France.

19) **Glenotremites hungaricus** (VADÁSZ) 1915.

Actinometra hungarica 1915 VADÁSZ pp. 13, 171, Taf. 1, figg. 27—29.

Occurrence: Tertiary (miocene), Hungary.

20) **Glenotremites hungaricus var. rotundatus** (VADÁSZ) 1915.

Actinometra hungarica var. rotundata 1915 VADÁSZ p. 13, Taf. 1, figg. 30—32.

Occurrence: Tertiary (miocene), Hungary.

21) **Glenotremites janeti** (VALETTE) 1917.

Antedon janeti 1917 VALETTE pp. 170, 176, 177, fig. 30.

Judging from the small size and the dorsal impression this species is probably a young. The size of the cirri is, however, remarkable and so is the relatively moderate development of the BB, circumstances that speak against the theory of the youth of the specimen.

Occurrence: Upper Cretaceous (turonian), France.

22) **Glenotremites ladoixensis** (DE LOROIL) 1888.

Antedon ladoixensis 1888 DE LORIOL pp. 450, 524, Pl. 214, fig. 1.

Occurrence: Middle Jurassic (bathonian), France.

23) **Glenotremites laticirrus** (P. H. CARPENTER) 1880.

Antedon laticirra 1880 b P. H. CARPENTER pp. 551, 555, Pl. 23, fig. 6; 1912 KIRK Pl. 8, figg. 1—2.

Occurrence: Upper Cretaceous, England.

24) **Glenotremites lettensis** (SCHLÜTER) 1878.

Antedon lettensis 1878 SCHLÜTER pp. 43, 49, Tab. 2, figg. 1—2; 1880 a P. H. CARPENTER p. 38; 1913 WAGNER p. 188.

Occurrence: Upper Cretaceous (senonian), W. Germany.

25) **Glenotremites lorioli** (REMEŠ) 1902.

Antedon lorioli, 1902 REMEŠ pp. 208, 216, Tab. 20, fig. 18.

Very closely related to, if not identical with, *Archæometra kopřivnicensis* from the same locality.

Occurrence: Upper Jurassic (tithonian), Moravia, Czecko-Slovakia.

26) **Glenotremites lundgreni** (P. H. CARPENTER) 1880.

Antedon lundgreni 1880 b P. H CARPENTER pp. 550, 551, 555, Pl. 23, fig. 3; 1880 c P. H. CARPENTER p. 11; 1881 b P. H. CARPENTER Pl. 12, fig. 30.

Occurrence: Upper Cretaceous (senonian), England.

27) **Glenotremites miocaenicus** (VADÁSZ) 1915.

Actinometra miocænica 1915 VADÁSZ pp. 14, 171, Taf. 2, figg. 1—3.

Occurrence: Tertiary (miocene), Hungary.

28) **Glenotremites minutissimus** (VALETTE) 1917.

Antedon minutissimus 1917 VALETTE pp. 169, 176, 177, fig. 29.

Occurrence: Upper Cretaceous (santonian), France.

29) **Glenotremites morieri** (DE LORIOL) 1888.

Antedon morieri 1888 DE LORIOL pp. 444, 448, 451, Pl. 213, fig. 1.

Occurrence: Lower Jurassic (domerian), N. France.

30) **Glenotremites mülleri** (P. H. CARPENTER) 1880.

Actinometra mülleri 1880 a P. H. CARPENTER pp. 40, 54, Pl. 5, fig. 6; 1888 DE LORIOL pp. 535, 541.

Occurrence: Middle Jurassic (bathonian), England.

31) **Glenotremites nicolaisi** (NOËLLI) 1900.

Antedon Nicolaisi 1900 NOËLLI pp. 20, 40, Tav. 1, figg. 64—66; 1905 BELLINI p. 650; 1915 VADÁSZ p. 10.

Occurrence: Tertiary (miocene), N. Italy.

32) **Glenotremites paradoxus** GOLDFUSS 1831.

Glenotremites paradoxus 1831 GOLDFUSS pp. 159, 168, Tab. 49, fig. 9, Tab. 51, fig. 1; 1835 L. AGASSIZ p. 194; 1838 BRONN p. 606, Taf. 29, fig. 14; 1839 GOLDFUSS, Petrefacta germaniæ, p. 286; 1840 HAGENOW p. 661; 1846 GEINITZ p. 544; 1848 BRONN p. 523; 1852 QUENSTEDT p. 601 (2. Aufl. 1867 p. 717, 3. Aufl. 1885 p. 915); 1857 PICTET p. 290, Pl. 99, fig. 5; 1862 DUJARDIN & HUPÉ p. 214; 1868 DEVALQUE p. 380 (2ᵉ Ed 1880, p. 429); 1870 SCHLÜTER p. 957; 1871 GEINITZ p 91; 1871 OOSTER pp. 131, 132; 1874 LUNDGREN p. 69; 1876 QUENSTEDT p. 183, Pl. 96, fig. 99; 1878 SCHLÜTER pp. 34, 37, 39, 42, 47; 1888 DE LORIOL p. 37.

Comatula paradoxa 1850 D'ORBIGNY Tome 2 p. 180; 1878 SCHLÜTER p. 43.

Antedon paradoxus(*-a*) 1878 SCHLÜTER pp. 42, 49; 1880 a P. H. CARPENTER pp. 37—40, 46—49, Pl. 5, fig. 1; 1880 b P. H. CARPENTER pp. 549—551, 555; 1894 DE LORIOL p. 481; 1895 DEEKE p. 71.

It seems somewhat doubtful to me if the English form can really be precisely the same as the species of GOLDFUSS, or if it should not rather be regarded as a closely related species. It is said by CARPENTER to have the cirri in rows, while the specimen of GOLDFUSS had cirri which were arranged more alternately. The forms that are described by VALETTE (1917) as belonging to this species I consider a quite distinct species which I have called *Gl. valetti.*

Occurrence: Upper Cretaceous (senonian), N. and W. Germany, Belgium, England (Dover).

33) **Glenotremites paronai** (NOËLLI) 1900.

(?)*Antedon (conico-piramidata)* 1878 MENEGHINI p. XXXI.

Antedon paronai 1900 NOËLLI pp. 20, 42, Tav. 1, fig. 68; 1905 BELLINI p. 641.

Occurrence: Tertiary (miocene), N. Italy.

34) **Glenotremites parvicavus** nov. sp.

Antedon danica (pars) 1913 BRÜNNICH-NIELSEN p. 100, Pl. 10, figg. 39—43.

It seems to me beyond doubt that the Cd figured on Pl. 10 by BRÜNNICH-NIELSEN, belongs to a different species from the remaining specimens. The Cd-cavity here is only $^1/_{14}$ of the diameter of Cd (Diam. of Cd 2·8 mm) while the Cd-cavity of an only slightly smaller Cd (diameter 2·0 mm) of *Antedon danica* (Pl. 11, fig. 4) measures $^1/_3$ of the diameter of Cd. This difference cannot be due to reduction by growth only. Besides this the figures first mentioned are drawn from a form from the lower danian while the figures on Pl. 11 originate from another locality and upper danian.

Occurrence: Upper Cretaceous (danian), Denmark.

35) **Gleotremites pellati** (DE LORIOL) 1897.

Antedon pellati 1897 DE LORIOL pp. 115, 124, Pl. 4, fig. 11; 1897 PELLAT p. 112; 1898 NICOLAS pp. 398, 407, 409, 412, fig. 7; 1900 NOËLLI pp. 20, 44, 45, Tav. 1, figg. 72—76; 1905 BELLINI p. 641.

NOËLLI's specimens differ by the lesser height of their Cdd. Perhaps a different species, but according to NOËLLI the species is variable.

Occurrence: Tertiary (miocene), S. France, N. Italy.

36) **Glenotremites perforatus** (P. H. CARPENTER) 1880.

Antedon perforata 1880 b P. H. CARPENTER pp. 549—550, 555—556, Pl. 23, fig. 2; 1888 P. H. CARPENTER p. 8.

Occurrence: Upper Cretaceous (senonian), England.

37) **Glenotremites protomacronema** (CHAPMAN) 1913.

Antedon protomacronema 1913 CHAPMAN p. 179, Pl. 17, fig. 18.

Occurrence: Tertiary (miocene, janjukian = burdigalian?), Australia.

38) **Glenotremites pusillus** (FRITSCH) 1910.

Pentacrinus pusillus 1910 FRITSCH p. 18, Taf. 6, fig. 7; 1911 FRIČ p. 77, fig. 332.

This species is undoubtedly a Comatulid; closely related to *Gl. rosaceus*, but with more and smaller cirri. Possibly the species possessed a stalk even when nearly full-grown.

Occurrence: Upper Cretaceous (cenomanian), Bohemia.

39) **Glenotremites pyropa** (ZAHALKA) 1892.

Antedon pyropa 1892 ZAHALKA pp. 722—723, Tab. 1, figg. 1—5.

Occurrence: Upper Cretaceous (the pyrope beds, senonian or turonian), Bohemia.

40) **Glenotremites ransomi** (Forbes) 1852.

Comatula sp. (part.) 1843 Morris p. 50.

Comatula ransomi 1852 Forbes p. 20, and woodcut below; 1878 Schlüter p. 38; 1879 a Fontannes p. 498; 1879 b Fontannes p. 414; 1897 Nicolas p. 131.

Antedon ransomi 1878 Schlüter p. 50; 1879 a Fontannes p. 500; 1879 b Fontannes p. 416.

Antedon (Comatula) ransomii 1896 A. Bell p. 6; 1920 A. Bell p. 12.

Antedon ransomei 1908 c A. H. Clark p. 491.

Occurrence: Tertiary (pliocene, plaisancian), England.

41) **Glenotremites ranvillensis** (de Loriol) 1888.

Actinometra ranvillensis 1888 de Loriol pp. 534, 540, Pl. 227, fig. 1; 1898 Bigot p. 49.

Occurrence: Middle Jurassic (bathonian), N. France.

42) **Glenotremites rosaceus** Geinitz 1871.

Glenotremites rosaceus 1871 Geinitz p. 92, Tab. 23, fig. 10; 1874 Lundgren p. 69; 1876 Quenstedt p. 184, Tab. 96, fig. 100; 1878 Schlüter p. 39; 1910 Fritsch p. 18; ?? 1911 Frič p. 77, fig. 321 (1—4).

It seems very doubtful to me if the figures of Frič (1911) are really drawn from specimens belonging to this species. In his works Frič urges the view that a species described as *Pentacrinus lanceolatus* should be the stem of the species first mentioned. Such stem-joints are reproduced in the paper of 1911. To judge from this and the work of Geinitz (1871) they seem to be typical Pentacrinoid stems with cirrus-whorls at regular intervals.

Occurrence: Upper Cretaceous (cenomanian), Saxony?, Bohemia.

43) **Glenotremites rotundus** (P. H. Carpenter) 1880.

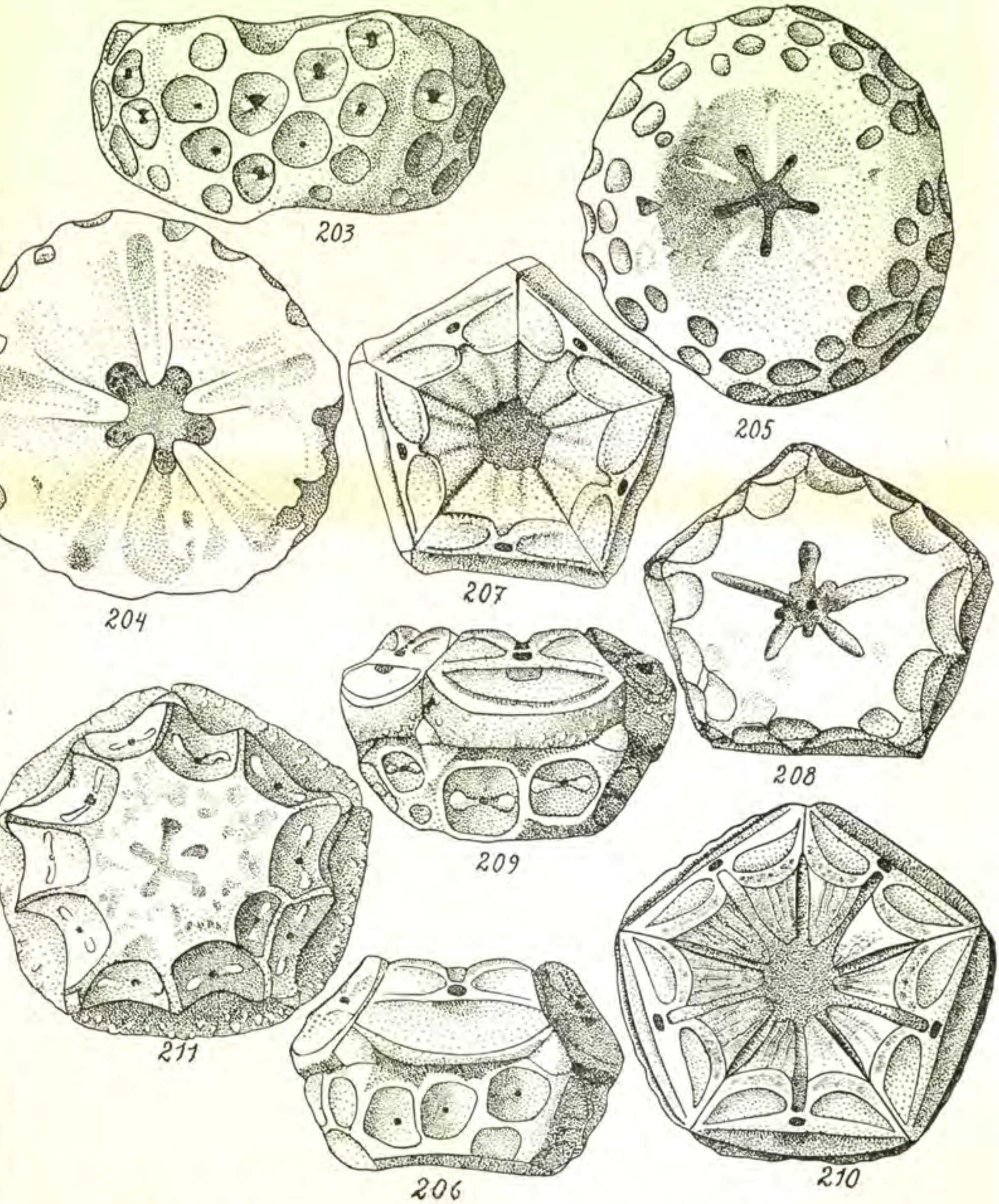
Antedon rotunda 1880 a P. H. Carpenter pp. 40, 52, Pl. 5, fig. 5; 1880 b P. H. Carpenter pp. 553—554.

Occurrence: Lower Cretaceous (neocomian), England.

44) **Glenotremites rugosus** (P. H. Carpenter) 1880.

Antedon rugosa 1880 a P. H. Carpenter pp. 46, 47, 49, Pl. 5, fig. 2; 1880 b P. H. Carpenter pp. 549—551, 555, Pl. 23, fig. 4; 1888 P. H. Carpenter p. 8.

Occurrence: Cretaceous, England (Sussex).



Figg. 203—211. 203—205) *Glenotremites batheri* 203) Cd, lateral view, 204) Cd, ventral view, 205) Cd, dorsal view, $^{4}/_{1}$; 206—208) *Palæocomaster stellatus* 206) Cd + basal and radial rings in lateral view, 207) Radial and basal rings, ventral view, 208), Cd, dorsal view, $^{8}/_{1}$; 209—211) *Solanocrinus ooliticus* 209) Cd + basal and radial rings in lateral view, 210) Radial ring, ventral view, 211) Cd + basal and radial rings, dorsal view, $^{6}/_{1}$.

45) **Glenotremites schlueterianus** Geinitz 1871.

Glenotremites schlueterianus 1871 Geinitz p. 92, Tab. 23, figg. 8, 9; 1874 Lundgren p. 69; 1878 Schlüter p. 39; (*schlütterianus*) 1910 Fritsch p. 18.
Antedon schlueterianus 1878 Schlüter p. 49.

Occurrence: Upper Cretaceous (cenomanian), Saxony.

46) **Glenotremites semiglobularis** Brünnich-Nielsen 1913.

Antedon semiglobularis 1913 Brünnich-Nielsen pp. 16, 24, 99, 100, 107, Tab. 12, figg. 36—53 (?? whether figg. 39—41 really belong to this species).

As I have already pointed out above, figg. 39—41 probably belong to *Gl. faxensis*. In addition, Brr and axillaries (both I and II Ax?) and syzygial joints are known of *Gl. semiglobularis*. The syzygial septa were numerous.

Occurrence: Upper Cretaceous (danian), Denmark.

47) **Glenotremites stellatus** (Noëlli) 1900.

Antedon stellatus 1900 Noëlli pp. 20, 44, Tav. 1, figg. 69—71; 1905 Bellini p. 641.

Occurrence: Tertiary (miocene), N. Italy.

48) **Glenotremites striatus** (P. H. Carpenter) 1880.

Antedon striata 1880 b P. H. Carpenter pp. 551—552, 555, Pl. 23, fig. 5; 1888 P. H. Carpenter p. 8.

Occurrence: Upper Cretaceous (senonian), England.

49) **Glenotremites sulcatus** (Schlüter) 1878.

Antedon sulcatus(-*a*) 1878 Schlüter pp. 37, 47, 49, Tab. 2, figg. 8, 9; 1880 a P. H. Carpenter p. 38.

Occurrence: Upper Cretaceous (senonian), S. Sweden.

50) **Glenotremites tourtiæ** (Schlüter) 1878.

Antedon tourtiæ 1878 Schlüter pp. 41—42, 49, Taf. 1, figg. 4—6; 1880 a P. H. Carpenter p. 39; 1881 a P. H. Carpenter p. 136; 1888 P. H. Carpenter p. 8.

Occurrence: Upper Cretaceous (cenomanian, tourtia), W. Germany.

51) **Glenotremites valetti** nov. sp.

Antedon paradoxus 1917 VALETTE, pp. 166, 169, 173, 174, 176, 177, fig. 28.

This species differs from *Gl. paradoxus* of GULDFUSS in the appearance of the cirrus-socket. It is, in addition to the peripheric striation, also provided with two tubercles situated laterally of the lumen. The impressions for the BB are also considerably narrower and of another shape. The specimens are from older stages of upper Cretaceous than the German forms.

Occurrence: Upper Cretaceous (cenomanian—turonian), France.

VIII. Comatulids of which at least the Cd and the basal and radial ring are preserved.

It now remains for me to treat the species (about 90) of which the Cd and the (basal and) radial ring are described. As has been mentioned before they seem to me to present so many characteristics of value that it is possible to subject them to a more thorough systematisation. I have divided them below into 14 groups which seem to me to be natural, and these groups I have given special generic names. Of old generic names it has been possible to revive two: *Solanocrinus* GOLDFUSS and *Hertha* HAGENOW. By the genus first mentioned GOLDFUSS indicated a couple of upper Jurassic forms. Though the diagnosis of the genus is unsatisfactory the figures are good and therefore I cannot see any reason for not using his genus though in a somewhat modified sense. HAGENOW's diagnosis of the genus *Hertha* is, as matters then were, rather good and so are also the figures which he gives of the type-specimen.

The 14 genera might be distributed among 5 different families: 1) *Comasteridae* including the fossil genus *Palaeocomaster* only; 2) *Solanocrinidae* including *Archaeometra, Solanocrinus,* and the diverging genus *Cypelometra;* 3) *Conometridae* including *Amphorometra, Placometra, Conometra,* and *Jaekelometra;* 4) *Notocrinidae* including *Loriolometra, Sphaerometra,* and 5) *Palaeantedonidae* including *Semiometra, Hertha, Discometra,* and *Palaeantedon.*

Survery of the genera:

I. BB large, contiguous laterally *Jaekelometra.*
II. BB smaller, not contiguous laterally.
    A. Cirri in rows (columns).
        1. Cd-cavity small. Cirrus-sockets never peripherally striated. No dorsal star. Muscular fossæ inconspicuous and superficial $\leqq$ than the interarticular ligament fossæ.

- a. Cd discoidal — low columnar. Cirrus-sockets with a stout transverse crest, the facets very deep and with a stout border, therefore (often) longitudinal crests between the rows. BB moderate or hidden. Radial face low, h < br. Muscular fossæ lacking or low and broad, either forming horizontal bands or sloping towards the nerve-lumen; if so often broader towards the median line of the ossicle. The dorsal, free part of the RR variable. Radial cavity large with a small and shallow central depression *Solanocrinus.*
- b. Cd discoidal — sub-hemispheric. Cirrus-sockets without sculpture or with an indistinct transverse crest. BB moderate. Radial face: h < br. Radial cavity large, with a large and deep central depression *Palaecomaster* part.
- c. Cd conical — a truncated cone, or high columnar. Cirrus-sockets shallow, with or without a weak transverse crest. Only an interradial longitudinal crest between the cirrus-rows. BB very conspicuous. Radial face h ≥ br. Muscular fossæ more or less vertical bands surrounding the intermuscular furrow. Free dorsal part of the RR broad. Radial cavity deep, of medium size to rather small *Archaeometra.*
- d. Cd hemispherical. Cirrus-sockets rather superficial without a transverse crest. Cirrus-rows arranged 2 and 2 with broad, radial interspaces. BB nearly hidden. No free dorsal part of the RR. Radial cavity rather small. *Cypelometra.*

2. Cd-cavity large. Cirri set closely, sometimes peripherally striated and with weak swellings laterally of the nerve-lumen. Muscular fossæ deep and large (≥ than the interarticular ligament fossæ). The free dorsal part of the RR usually broad. Radial cavity moderate, with a deep central depression.
    - a. Deep sub-radial clefts. BB projecting in the interradial corners. Cd conical or columnar. Cirrus-socket with a faint transverse swelling and sometimes striated peripherally.
        - α. No dorsal star; no radial pits. Muscular fossæ high and tolerably narrow. *Amphorometra.*
        - β. Usually a dorsal star, deep radial pits. Muscular fossæ large and broad. *Loriolometra.*
    - b. No subradial clefts. No BB visible. Cirrus-socket without distinct sculpture.
        - α. Cd conical. Radial ring not overlapping the border of Cd. *Conometra.*

β. Cd discoidal. Radial ring strongly overlapping the border of Cd. *Placometra.*

B. Cirri in more or less distinctly alternating whorls. Nearly always smooth cirrus-sockets. BB hidden or inconspicuously visible (in the latter case generally in some of the interradii only). Free dorsal part of the RR usually nil.

1. Cd-cavity very small. Cirrus-sockets small, in close whorls or lacking. Radial faces sloping inconspicuously inwards. The radial cavity therefore large, $\geq {}^1/_2$ of the br. of the radial ring. Central depression large and deep. Muscular fossæ low and inconspicuous. *Palaeocomaster* part.

2. Cd-cavity large and deep. Cirrus-sockets always present. Radial fossæ sloping inwards, the radial cavity therefore generally not more than ${}^1/_3 - {}^1/_4$ of the br. of the radial ring. Muscular fossæ large and deep.

a. A dorsal star and radial pits. Cirri not pronouncedly alternating, cirrus-sockets large and rather sparse, often striated peripherally. BB protruding in most interradii. A narrow, free, dorsal border of the RR. *Sphaerometra.*

b. Cirrus-sockets small, pronuncedly alternating, without sculpture. BB hidden. The free dorsal part of the RR missing or very indistinct.

α. Usually a dorsal star. Cd low — hemispheric. Radial face sunken in the median line leaving bare a broad part of the ventral face of Cd. *Semiometra.*

β. Without a dorsal star. Radial face not noticeably sunken in the median line.

+. Radial cavity very small, diameter ${}^1/_6 - {}^1/_{10}$ of the br. of the radial ring. *Hertha.*

++. Radial cavity larger, at least ${}^1/_5$ of the br. of the radial ring.

!. Cd very much flattened, dorsally often free from cirri and somewhat depressed. Muscular fossæ rather small, radial face low, $h < br$. *Discometra.*

!!. Cd more or less hemispheric, dorsally not depressed or with a large area devoid of cirri. Muscular fossæ rather high, radial face $h \underset{(=)}{>}$ br. (exception *P. danica*). *Palaeantedon.*

Comasteridae.

A. **Palaeocomaster** nov. gen.

Cd very much flattened, without cirri dorsally. Cd-cavity very small, the opening round. No radial pits. No dorsal star; sometimes, however, a petaloid interradial figure dorsally. Cirrus-sockets may be absent. If they are present, they are rather small and arranged in close, often alternating whorls, with or without an indistinct, transverse crest. BB inconspicuous or not protruding at all. Radial fossæ sloping inwards very little or vertical. Therefore the radial cavity is large, at least $^1/_2$ of the br. of the radial ring. The central depression also very large and deep owing to the steep inward slope of the RR. Muscular fossæ superficial, low, linear bands or broader towards the lumen.

Arms are in known cases V or X. Type *P. guirandi*.

Besides the species of *Palaeocomaster* mentioned below, the *morieri* group of the genus *Glenotremites* belongs here.

Geological appearance: Lower Jurassic — Tertiary (miocene).

The following 8 species belong here: *calloviensis* P. H. CARPENTER 1882, *formae* NOËLLI 1900, *guirandi* DE LORIOL 1888, *latiradius* P. H. CARPENTER 1882, *loveni* P. H. CARPENTER 1880, *schlumbergeri* DE LORIOL 1888, *stellatus* nov. sp., *wurtembergicus* P. H. CARPENTER 1881.

Survey of the species:

I. Cirri well developed.
    A. Cirri distinctly alternating. *guirandi.*
    B. Cirri in more or less distinct rows.
        1. BB visible in the corners.
            a. Cd discoidal.
                α. C. in X rows; no dorsal stellate impression *schlumbergeri.*
                β. C. in about XV rows; a large, interradial stellate impression dorsally *stellata.*
            b. Cd ± hemispheric. Cirri in X indistinct rows.
                α. Cirri about XXX. The free dorsal part of RR visible as a narrow band *calloviensis.*
                β. Cirri about XL. The free dorsal part of RR hidden in the median lines *latiradius.*
        2. BB hidden. Cirri i XX rows *wurtembergicus.*
II. Cirri rudimentary (in a single whorl) or lacking. No BB visible.
        1. C. rudimentary. The dorsal free part of the RR = 0. *formae.*
        2. C. lacking. The dorsal free part of the RR broad. *loveni.*

1) **Palaeocomaster calloviensis** (P. H. CARPENTER) 1882.

Comatula 1881 P. H. CARPENTER London Proc. Geol. Soc., p. 242 (= *Actinometra calloviensis* Abstracts No. 407, p. 98).

Antedon calloviensis 1882 P. H. CARPENTER, pp. 40—42, fig. 2; 1885 QUENSTEDT (3. Aufl. Petrefactenkunde), p. 915.

Actinometra calloviensis 1888 DE LORIOL, p. 541.

The arms are X. I Br 1 and 2 are united in a close synarthrial connection. P_1 on Br 2. Br 3 usually connected with Br 4 in a syzygial articulation.

This species is very closely related to *P. latiradius,* and is, like that species, still incompletely known.

Occurrence: Middle Jurassic (callovian), England.

2) **Palaeocomaster formae** (NOËLLI) 1900.

Actinometra formae 1900 NOËLLI, pp. 20, 46, Tav. 1, figg. 77—79; 1905 BELLINI, p. 641.

Occurrence: Tertiary (miocene), N. Italy.

3) **Palaeocomaster guirandi** (DE LORIOL) 1888.

Actinometra guirandi 1888 DE LORIOL, pp. 535, 540, Pl. 227, fig. 2.

Occurrence: Upper Jurassic (oxfordian), France.

4) **Palaeocomaster latiradius** (P. H. CARPENTER) 1882.

Antedon latiradia 1882 P. H. CARPENTER, p. 38, fig. 1.

The radial faces, if they were correctly drawn, should be high and provided with rather large muscular fossæ. CARPENTER states (p. 39) that "the greater part of the articular face is taken up by the . . . muscles and ligaments, but the boundaries of their respective fossæ are not very distinct."

The figure that is given by CARPENTER is, however, incorrect inasmuch as the radial faces are much lower than is indicated in the drawing. Certainly the boundaries between the interarticular ligament and the muscular fossæ in specimens that I have seen are indistinct, but the h. of the whole radial face (2·7 mm.) is considerably less than the br. of the transverse crest (4·0 mm.).

The cirrus-sockets are arranged in X not very distinct rows. Between I Br 1—2 and Br 1—2 there is a synarthry. Between Br 3 and 4 a syzygy with few septa (± 10). The arms are X.

Occurrence: Middle Jurassic (bathonian), England.

5) **Palaeocomaster loveni** (P. H. CARPENTER) 1880.

Actinometra loveni 1880 a P. H. CARPENTER, p. 51, with figure on the same page; 1881 b P. H. CARPENTER, p. 213; 1884 P. H. CARPENTER, p. 132; 1888 P. H. CARPENTER, pp. 16, 26, 38; 1891 WOODS, p. 37.

The arms are X, very coarse and broad. The articulation between Br 1 and 2 is a synarthry. I Br 1 and 2 are connected in a close articulation.

Occurrence: Lower Cretaceous (gault), England.

6) **Palaeocomaster schlumbergeri** (DE LORIOL) 1888.

Antedon schlumbergeri 1888 DE LORIOL, pp. 498, 524, Pl. 213, fig. 3; 1898 BIGOT, pp. 41—43, 49.

Thanks to BIGOT we now know that the arms of this species were V. Perhaps among the 100 or so specimens that this author has investigated there were also other species, as BIGOT speaks of variation of the form of the Cd towards the conical type. The author, however, has made the important observation that the spread of the muscular and ligamentar fossæ does not vary. In young specimens he has seen IBB.!

Occurrence: Middle Jurassic (bathonian), N. France.

7) **Palaeocomaster stellatus** nov. sp. (figg. 206—208).

Dimensions: Cd + radial ring h: 3·7 mm., Cd h: 1·7 mm., br: 5·1 mm. Radial ring br: 5.6 mm.; radial cavity 3·5 mm. in diameter, central depression 1·2 mm. in diameter.

Cd a thick disk; dorsal face flat with a large stellate impression, interradially arranged, the rays surround a deep central pit. Diameter of the flat, dorsal part of Cd: 3·0 mm. Cirri rather irregular, in about XIV, sometimes indistinct, rows; 1—2 cirrus-sockets in each row; ± XX in total. Cirrus-sockets rather large, without sculpture.

BB projecting at the corners, their surface is smooth.

The free dorsal part of the RR narrow, horizontal, in lateral view almost invisible. Dorsal ligament fossæ: h = $^1/_3$ br., with a rather broad and well marked, though rather low, pit, br. = twice the nerve-lumen. Interarticular fossæ distinct, larger than the muscular ones, from which they are usually indistinctly separated. A shallow intermuscular furrow. On the inward slope of the radial cavity there are deep furrows interradially; between each of these deepenings about 2 faint furrows. The central depression deep, sharply marked off from the sloping inner faces of the RR.

This species is most closely related to *P. schlumbergeri* from which however, it differs by the cirrus-rows being XIV instead of X, and by the large dorsal stellate impression.

Occurrence: Middle Jurassic (bathonian), Hampton Down, near Bath, England. Type specimen in the British Museum (Möckler Collection).

8) **Palaeocomaster wurtembergicus** (P. H. CARPENTER) 1881.

Actinometra wurtembergica 1881 b P. H. CARPENTER, p. 198, Pl. 9, fig. 7; 1882 P. H. CARPENTER, p. 42; 1888 P. H. CARPENTER, pp. 26, 39; 1888 DE LORIOL, p. 541.

Actinometra wurtembergiae 1891 WOODS, p. 37.

Occurrence: Upper Jurassic (virgulian), Württemberg.

Solanocrinidae nov. fam.

Cd discoidal—columnar. Dorsal surface without cirri and dorsal star, smooth or granulated, sometimes with an interradial stellate impression. Cd-cavity strongly microphreate (diameter $^1/_7 - ^1/_{14}$ of the br. of Cd). No radial pits or pores; sometimes, however, on the ventral face of Cd shallow, meandring, forked furrows (as in e. g. recent *Mariametridae*). Cirri large and stout, in rows, rarely in a single whorl, generally with a transverse crest. BB often protruding at the corners; sometimes, however, hidden. Radial face only slightly sloping inwards. Muscular fossæ of the radial face small and superficial, evidently sometimes lacking. When they are present they are either low linear bands or broader towards the lumen (the crest between the interarticular ligament and the muscular fossa in such cases slopes more or less towards the nerve-lumen). Usually a large radial cavity.

Large and stout species, often with biserial arms. I Br 1 and 2 united in close connection or grown together. Syzygies (with few septa) rare or perhaps sometimes lacking, at least in distal parts of the arms. Typical in upper Jurassic—lower Cretaceous (modified in upper Cretaceous—Tertiary).

Here, besides the genera mentioned below *(Solanocrinus, Archaeometra*, and *Cypelometra)*, belong probably also some species of the genus *Pachyantedon* (seems to be closest to *Solanocrinus*), and the *exilis* group of the genus *Glenotremites*. The *angelini* and *parvicavus* groups most probably are descendants of this family, as is also the above mentioned, rather diverging genus *Cypelometra*.

A) **Solanocrinus** GOLDFUSS 1831

em. P. H. CARPENTER, WALTHER, GISLÉN.

Cd discoidal to low columnar. Cirrus-sockets with a strong transverse crest and with a thickened border by which are also formed longitudinal crests between the rows. BB relatively inconspicuous (sometimes hidden = subgen. *Comatulina* D'ORBIGNY). Radial face, especially ventrally of the transverse ridge, low. Muscular fossæ seem either to be lacking, or to be linear horizontal bands, or triangular, the hypotenuse sloping towards the nerve-lumen. The free dorsal part of RR variable. Radial cavity large, sloping gradually towards the relatively small and shallow central depression.

The arms were V (e. g. *hiselyi*), X (e. g. *changarnieri, thiollieri*), XI—XX (e. g. *beltremieuxi*, II Br 1; *depressus*, II Br 2; *jutieri*, II Br 3 or 4; *burgundiaca*, II Br probably 7—8).

Type *S. costatus*.

Geological appearance: Middle Jurassic—lower Cretaceous. The following 35 species belong to this genus:

almerai DE LORIOL 1900, *beaugrandi* DE LORIOL & PELLAT 1875, *beltremieuxi* DE LORIOL 1888, *bituricensis* DE LORIOL 1888, *burgundiacus* DE LORIOL 1888, *campichei* DE LORIOL 1879, *canaliculatus* P. H. CARPENTER 1881, *changarnieri* DE LORIOL 1888, *choffati* DE LORIOL 1880, *costatus* GOLDFUSS 1831, *decameros* P. H. CARPENTER 1881, *delgadoi* DE LORIOL 1890, *depressus* D'ORBIGNY 1850, *gaioensis* DE LORIOL 1890, *gevreyi* DE LORIOL 1902, *gillieroni* DE LORIOL 1879, *greppini* DE LORIOL 1879, *gresslyi* ETALLON 1862, *herberti* DE LORIOL 1888, *hiselyi* DE LORIOL 1869, ? *humilis* nov. nom., *infracretaceus* OOSTER 1871, *jutieri* DE LORIOL 1879, *lamberti* DE LORIOL 1888, *leenhardti* DE LORIOL 1908, *obliticus* nov. sp., *d'orbignyi* P. H. CARPENTER 1881, *peroni* DE LORIOL 1888, *picteti* DE LORIOL 1879, ? *ricordeanus* D'ORBIGNY 1850, *tessoni* P. H. CARPENTER 1881, *thiollieri* DE LORIOL 1888, *truncatus* P. H. CARPENTER 1881, *vagnacensis* DE LORIOL 1888, *valdensis* DE LORIOL 1868.

Survey of the groups:

I. BB distinctly visible in all interradii *(Solanocrinus* s. str., type *costatus)*. Muscular fossæ usually triangular, with the hypotenuse sloping towards the lumen.
    A. Cirri in a single whorl. The free dorsal part of RR broad (upper Jurassic) *delgadoi*.
    B. Cirri in a double whorl at least.
        1. Cirri in X (rarely XI or XII) rows.
            a. The free dorsal part of RR broad (upper Jurassic) *beaugrandi, bituricensis, burgundiacus, costatus* (part.), *depressus, gresslyi, jutieri, ooliticus, tessoni, ? thiollieri*.

  - b. The free dorsal part of RR narrow or = 0 (upper Jurassic) *costatus* (part.), *truncata*.
- 2. Cirri in XV rows (young spp. of *gaioensis* with only X rows, *lamberti* with XVIII rows). The free dorsal part of RR usually rather broad, upper Jurassic—lower Cretaceous (the latter *valdensis* only) *beltremieuxi*, *gaioensis*, *greppini*, *lamberti*, *valdensis*.

II. BB not visible at all or in solitary interradii only. Muscular fossæ lacking or horizontal, linear bands (sub-genus *Comatulina* D'ORBIGNY. Type *C. d'orbignyi*).

- A. Cirri in a single whorl chiefly (lower Cretaceous).
  - 1. The free dorsal part of RR broad. Cd truncated-conical *campichei*.
  - 2. Free dorsal part of RR narrow. Cd ± discoidal *hiselyi*, *picteli*, ? *ricordeanus*, *vagnacensis*.
- B. Cirri in a double whorl at least.
  - 1. Cirri in X rows (upper Jurassic).
    - a. Free dorsal part of RR broad *herberti*.
    - b. Free dorsal part of RR narrow *canaliculata*, *changarnieri*, *decameros*.
  - 2. Cirri in XV rows (young *choffati* with X rows only), upper Jurassic (3 spp.)—lower Cretaceous (5 spp.).
    - a. Free dorsal part of RR broad *choffati*, *grevreyi*.
    - b. Free dorsal part of RR narrow or = 0 *almerai*, *gillieroni*, ? *humilis*, *leenhardti*, *d'orbignyi*, *peroni*.
  - 3. Cirri in XX rows. Free dorsal part of RR = 0 (lower Cretaceous) *infracretaceus*.

When not otherwise stated, in the following species only Cdd (and basal) and radial rings are known.

1) **Solanocrinus almerai** (DE LORIOL) 1900.

Antedon almerai 1900 DE LORIOL, p. 74, Pl. 8, fig. 5; 1908 DE LORIOL, p. 156.

Occurrence: Lower Cretaceous (neocomian, aptian), Spain.

2) **Solanocrinus beaugrandi** DE LORIOL & PELLAT 1875.

Solanocrinus beaugrandi 1875 DE LORIOL & PELLAT, p. 294, Pl. 26, figg. 15—20; 1879 DE LORIOL, pp. 261, 266; 1891 RIGAUX, p. 69.

Antedon beaugrandi 1888 DE LORIOL, pp. 500, 508, 520, 524, Pl. 222, figg. 3—5; 1890 DE LORIOL, p. 163.

I Br 1 and 2 grown together. Possibly more than X arms. II Brr are 1. Arms approaching biseriality.

Occurrence: Upper Jurassic (pterocerian), N. France.

3) **Solanocrinus beltremieuxi** (DE LORIOL) 1888.

Antedon beltremieuxi 1888 DE LORIOL, pp. 504—505, 518, 521, 524, Pl. 223.

I Br 1 and 2 anchylosed. II Brr are 2. Arms XX.
Occurrence: Upper Jurassic (pterocerian), France.

4) **Solanocrinus bituricensis** (DE LORIOL) 1888.

Antedon bituricensis 1888 DE LORIOL, pp. 481, 524, Pl. 218, fig. 6.

Occurrence: Upper Jurassic (sequanian), France.

5) **Solanocrinus burgundiacus** (DE LORIOL) 1888.

Antedon burgundiaca 1888 DE LORIOL, pp. 471, 483, 486, 498, 524, Pll. 217, 218, figg. 1—5; 1900 LISSAJOUS, p. 25.

Pl. 218, fig. 1, of DE LORIOL 1888 seems to differ rather essentially from the type. — I Br 1 and 2 are united in a close connection. According to DE LORIOL a complete crown with Cd and radial ring (Pl. 218, fig. 3) also belongs to this species. II Brr are here 7 in 2 cases, 8 in 1 case. II Br 2 bears the first pinnule on its outer side. II Br 3 with P_a. At least XX arms.
Occurrence: Upper Jurassic (sequanian), France.

6) **Solanocrinus campichei** (DE LORIOL) 1879.

Antedon campichei 1879 DE LORIOL, pp. 269, 290, Pl. 20, figg. 21—27; 1884 P. H. CARPENTER, p. 144; 1912 KIRK, p. 77.

Pl. 20, fig. 23, differs by the rather sharply flattened Cd.
Occurrence: Lower Cretaceous (neocomian, valanginian), Switzerland.

7) **Solanocrinus canaliculatus** (P. H. CARPENTER) 1881.

Antedon canaliculata 1881 b P. H. CARPENTER, pp. 195, 199, 212, 214, Pl. 9, fig. 6; 1888 DE LORIOL, p. 528; 1908 ENGEL, p. 455.

Occurrence: Upper Jurassic (virgulian), Württemberg.

8) **Solanocrinus changarnieri** (DE LORIOL) 1888.

Antedon changarnieri 1888 DE LORIOL, pp. 484, 524, Pll. 219, 220.

In this species we are acquainted with impressions only. Arms are X, sharply tending towards biseriality. I Br 1 and 2 united in close connection.
Occurrence: Upper Jurassic (rauracian), France.

9) Solanocrinus choffati (de Loriol) 1880.

Antedon choffati 1880 a de Loriol, p. 11, Pl. 1, figg. 12—16; 1890 de Loriol, pp. 161, 163, 172, Pl. 29, figg. 7—11.

Pl. 29, fig. 8, represents a young specimen still having X cirrus-rows only. The prominences of the dorsal free part of RR are also still but little developed.

Occurrence: Upper Jurassic (lusitanian = sequanian), Portugal.

10) Solanocrinus costatus Goldfuss 1831.

Milleria costata 1830 Goldfuss in Hartmann's Catalogue, p. 45. No description of the genus nor of the species.

Solanocrinites costatus 1831 Goldfuss, pp. 166, 168, Tab. 50, fig. 7 a, b, e—f (reviewed in Neues Jahrb. f. Mineralogie 1833, p. 104); 1833 v. Münster, »Verzeichniss», p. 31 (2. Aufl. by F. Braun 1840, p. 16); 1835 v. Mandelsloh, p. 15; 1836 Bronn, p. 272, Taf. 17, fig. 14 a—b, e—f; 1851 Quenstedt, p. 469; 1852 Quenstedt, p. 601, Tab. 51, figg. 35, 36 (2. Aufl. 1867, p. 717, Tab. 65, figg. 35, 36; 3. Aufl., p. 915, Tab. 72, figg. 5—9); ? 1858 Quenstedt, p. 722, Tab. 88, figg. 9—11; 1879 P. H. Carpenter, pp. 6, 104—105.

Solacrinus costatus 1835 L. Agassiz, p. 196.

Solanocrinus costatus 1848 Bronn, p. 1150; 1857 Pictet, pp. 288—289, Pl. 99, fig. 1; ? 1863 b A. Müller, p. 62 (2. Aufl. 1884, p. 88); 1871 Ooster, p. 132; 1875 de Loriol et Pellat, p. 286; 1876 Quenstedt, p. 172, Tab. 96, figg. 26—48; 1878 Schlüter, p. 36; 1880 a P. H. Carpenter, p. 48, 54; 1881 b P. H. Carpenter, pp. 191, 196—197; 1884 P. H. Carpenter, p. 402; 1886 Walther, pp. 171—173, 183, 188, Pl. 25, figg. 1, 5, and 6, Pl. 26, fig. 11; 1887 P. H. Carpenter, pp. 83—87; 1888 P. H. Carpenter, pp. 90, 93, 101, 211, 372; 1892 Engel, p. 49.

Comatula costata 1850 d'Orbigny, Tome 1, p. 381; 1852 d'Orbigny, figg. 286, 463; 1867 Moesch, p. 205; (?) 1867 Ogérien, p. 675.

Comaster (Solanocrinus) costatus 1862 Dujardin & Hupé, p. 213; 1874 Lundgren, pp. 68, 69.

Solonaerium costatus part. 1862 a Etallon, p. 341.

Antedon costatus(-a) 1878 Schlüter, p. 49; 1879 de Loriol, pp. 261, 263, 266; 1881 b P. H. Carpenter, pp. 192—196, 199—205, 207—209, 212, 213, 215, Pl. 9, figg. 1—2, ? 4—5; 1888 P. H. Carpenter, pp. 93, 135, 214, 372; 1888 de Loriol, pp. 463, 470, 475—478, 486, 490, 515, 525; 1891 Woods, p. 37; 1895 de Loriol, p. 4; 1902 Schmierer, p. 572, 587; 1908 Engel, p. 455; 1911 Leuthardt, p. 109 ff., textfigg. 1—3, Pll. 6—8; 1920 Musper, p. 14.

This species, so often mentioned and with its present limits so very multiform, is surely in great need of a more thorough review, giving an analysis of the types. As was stated by Carpenter (1881 b) the figures that are found in Quenstedt's work (1858) differ very evidently from Goldfuss's species (1831, Pl. 50, figg. 7 a and b. Fig. c - d is *Sol. d'orbignyi* and. Pl. 51, fig. 2 is *Thiollierierinus sigillatus*). With the exception of Quenstedt 1858, Pl. 88, fig. 11, the BB project at the interradial corners and the cirri are arranged in X rows on a low columnar Cd.

The chief variations concern the free dorsal part of Cd which may be broad (= the type) or absent (QUENSTEDT 1858, Pl. 88, fig. 9), and the ventral border of the radial face which may be topped (= the type) or truncated (QUENSTEDT 1858, Pl. 88, fig. 10, P. H. CARPENTER 1881 b, Pl. 9, fig. 2).

The arms are usually X(—XI ENGEL 1892; XII, a six-rayed specimen. LEUTHARDT 1911). I Br 1 and 2 are united in a close connection or anchylosed. As to the form of the Brr we have different types, which also corroborates the belief that several different species have been confounded under *S. costatus*. Thus WALTHER (1886) reproduces both arms of the common type that QUENSTEDT had already figured, where the Brr in the middle arm-parts are oblique, tending towards, but scarcely reaching the biserial stage (Pl. 25, fig. 6, cf. also 1911 LEUTHARDT, Pll. 6—8), and arms of an exclusively biserial type, reminding one of the arms of *Encrinus liliiformis* (Pl. 25, fig. 5). The syzygies seem to have been provided with few septa. The dorsal nervous system (ring-canal etc.) and radial coelomic processes (type as in *Lamprometra*) are shown beautifully in a drawing by LEUTHARDT (1911).

Occurrence: Upper Jurassic (sequanian?—virgulian), S. Germany, Switzerland, ?France (the French localities given by D'ORBIGNY and OGÉRIEN, callovian and oxfordian, are very doubtful).

11) **Solanocrinus decameros** (P. H. CARPENTER) 1881.

Antedon decameros 1881 b P. H. CARPENTER, pp. 198, 201, Pl. 10, fig. 11; 1882 P. H. CARPENTER, p. 42; 1888 P. H. CARPENTER, p. 38; 1888 DE LORIOL, p. 528; *(decamerus)* 1908 ENGEL, p. 455.

Occurrence: Upper Jurassic (virgulian), Württemberg.

12) **Solanocrinus delgadoi** DE LORIOL 1890.

Antedon delgadoi 1890 DE LORIOL, pp. 164, 172, Pl. 29, fig. 15.

Occurrence: Upper Jurassic (lusitanian = sequanian), Portugal.

13) **Solanocrinus depressus** (D'ORBIGNY) 1850.

Comatula depressa 1850 D'ORBIGNY, Tome 2, p. 28; 1862 DUJARDIN & HUPÉ, p. 213.

Antedon depressus(-a) 1878 SCHLÜTER, p. 49; 1888 DE LORIOL, pp. 493, 524, Pl. 221, figg. 1—6; 1912 KIRK, pp. 79—80, Pl. 8, figg. 7—8.

I Br 1 and 2 united in a close connection. Arms probably XI. II Br is 1. Syzygies with few septa. Distal Brr with strong processes on the dorsal and pinnular sides.

This species is completely different from *Decameros depressus* D'ORBIGNY to which I have given the name *S. humilis*.

Occurrence: Upper Jurassic (sequanian), France.

14) **Solanocrinus gaioensis** (DE LORIOL) 1890.

Antedon gaioensis 1890 DE LORIOL, pp. 162, 172, Pl. 29, figg. 12—14.

A younger specimen has only X rows of cirri.

Occurrence: Upper Jurassic (lusitanian = sequanian), Portugal.

15) **Solanocrinus gevreyi** (DE LORIOL) 1902.

Antedon Gevreyi 1902 DE LORIOL, p. 38, Pl. 2, fig. 5; 1908 DE LORIOL, p. 156.

Occurrence: Lower Cretaceous (valanginian), France.

16) **Solanocrinus gillieroni** (DE LORIOL) 1879.

Antedon Gillieroni 1879 DE LORIOL, pp. 271, 290, Pl. 21, figg. 6—8.
Antedon gillerioni 1881 b P. H. CARPENTER, pp. 199, 206.

Occurrence: Lower Cretaceous (valanginian), Switzerland.

17) **Solanocrinus greppini** (DE LORIOL) 1879.

Antedon Greppini 1879 DE LORIOL, pp. 262, 290, Pl. 20, fig. 10; 1882 P. H. CARPENTER, p. 42; 1888 P. H. CARPENTER, p. 38; 1888 DE LORIOL, pp. 510, 529.

Occurrence: Upper Jurassic (sequanian), Switzerland.

18) **Solanocrinus gresslyi** (ETALLON) 1862.

Comatula gresslyi 1862 a ETALLON, p. 340, Pl. 49, fig. 1; 1864 WAAGEN, p. 223; 1867 MOESCH, p. 157; 1869 JACCARD, p. 200; 1870 GREPPIN, p. 105; 1873 DE TRIBOLÉT, p. 28.

Solanocrinus sequanus MÉRIAN, M. S., 1863 a A. MÜLLER, p. 146; 1863 b A. MÜLLER, p. 62 (2. Aufl. 1884, p. 88); 1873 DE TRIBOLÉT, p. 28; 1879 DE LORIOL, p. 261.

Antedon gresslyi 1879 DE LORIOL, pp. 258, 263, 266, 290, Pl. 20, figg. 1—7; 1881 b P. H. CARPENTER, pp. 196, 198; 1888 P. H. CARPENTER, p. 214; 1888 DE LORIOL, pp. 478, 479, 488, 498, 514, 524, Pl. 222, fig. 1; 1895 DE LORIOL, p. 4; 1902 SCHMIERER, p. 587; 1911 LEUTHARDT, p. 110; 1920 MUSPER, p. 14.

Br-segments are also known.

Occurrence: Upper Jurassic (sequanian), W. France, S. W. Germany, Switzerland.

19) **Solanocrinus herberti** (DE LORIOL) 1888.

Antedon depressa 1881 b P. H. CARPENTER, p. 201, Pl. 10, figg. 12, 13; 1888 DE LORIOL, p. 499; 1891 WOODS, p. 37.
Antedon herberti 1888 DE LORIOL, pp. 499, 529; 1908 ENGEL, p. 455.

Occurrence: Upper Jurassic (virgulian), Württemberg.

20) **Solanocrinus hiselyi** (DE LORIOL) 1869.

Comatula (Ophiocrinus) hiselyi 1869 DE LORIOL, p. 57, Pl. 3, fig. 13.
Comatula hiselyi 1870 GREPPIN, p. 139; 1878 SCHLÜTER, p. 40.
Comatula hyselyi 1870 JACCARD, p. 28.
Antedon hiselyi 1878 SCHLÜTER, p. 49.
Ophiocrinus hyselii 1879 DE LORIOL, pp. 277, 290, Pl. 21, figg. 9—14; 1881 b P. H. CARPENTER, p. 199.
Eudiocrinus hyselyi 1888 P. H. CARPENTER, pp. 37, 75.

The arms are V, the syzygies seem to be lacking. Br 1 with a large pinnule, possibly most often to the left.

Occurrence: Lower Cretaceous (neocomian, urogonian), Switzerland.

21) **Solanocrinus humilis** nov. nom.

Decameros depressus 1850 D'ORBIGNY, Tome 2, p. 121; 1857 PICTET, p. 289; 1862 DUJARDIN & HUPÉ, p. 197; 1876 QUENSTEDT, p. 184; 1900 DE LORIOL, p. 77.
Antedon depressus 1878 SCHLÜTER, p. 49.

According to the complementary information of DE LORIOL this species may have a low Cd with a low radial ring; the cirri are XXXIII in total, in a double whorl, here and there a triple one, i. e. 3 cirrus-rows per radius. Will perhaps turn out to be a *Palaeocomaster*.

Occurrence: Lower Cretaceous (neocomian, aptian), France.

22) **Solanocrinus infracretaceus** OOSTER 1871.

Glenotremites infracretaceus 1871 OOSTER, pp. 131, 142, Pl. 19, figg. 2—5, 24.
Solanocrinus infracretaceus 1871 OOSTER, p. 132, Pl. 19, figg. 6—7.
Antedon infracretaceus(-a) 1879 DE LORIOL, pp. 274, 290, Pl. 20, figg. 34—36; 1881 b P. H. CARPENTER, pp. 199, 201; 1882 P. H. CARPENTER, p. 42; 1888 P. H. CARPENTER, pp. 26, 39.

Occurrence: Lower Cretaceons (valanginian), Switzerland.

23) **Solanocrinus jutieri** (DE LORIOL) 1879.

Antedon jutieri 1879 DE LORIOL, pp. 265, 290, Pl. 21, figg. 1—5; 1888 DE LORIOL, pp. 510, 519, 524, Pl. 226, figg. 1—5.

I Br 1 and 2 anchylosed. Arms usually X, in 2 cases out of 7, XI; II Brr 3 or 4. Cirri long, with short and stout segments, $l = {}^1/_2 - {}^2/_3$ br. Br segments rather slightly oblique with lateral prominences on the pinnular side. Syzygies not distinguishable.

Occurrence: Upper Jurassic (virgulian), France.

24) **Solanocrinus lamberti** (DE LORIOL) 1888.

Antedon lamberti 1888 DE LORIOL, pp. 504, 515, 524, Pl. 225, figg. 2—4; 1893 LAMBERT, p. 209; 1899 LAMBERT, p. 122; 1902 LEMOINE & ROUYER, p. 105.

Occurrence: Upper Jurassic (virgulian), France.

25) **Solanocrinus leenhardti** (DE LORIOL) 1908.

Antedon leenhardti 1908 DE LORIOL, p. 154, Pl. 5, figg. 13—19.

Occurrence: Lower Cretaceous (aptian), France.

26) **Solanocrinus ooliticus** nov. sp. (figg. 209—211).

Dimensions: Cd + radial ring, h: 5·2 mm. Cd, br: 7·2 mm., h: 2·0 mm. Radial ring, br: 8·0 mm., radial cavity 4·7 mm. in diameter; central depression 2·0 mm. in diameter.

Cd truncated-conical, with a flattened surface dorsally, its dorsal diameter being 4·2 mm. The dorsal surface is provided with irregular shallow pits and has an indistinct, stellate deepening in the centre. The diameter of this star is 1·5 mm., its rays being interradially situated. Cirri in X rows, in each row 1—2 large cirrus-sockets provided with stout transverse crests; these crests are claviformly thickened at both the lateral ends; stout longitudinal ridges between the cirrus-rows.

BB protruding at the interradial corners, their surface indistinctly granulated.

The free dorsal part of RR rather broad, nearly horizontal, sloping sharply inwards, the surface granular. The radial ring somewhat overlapping the ventral border of the Cd. Dorsal ligament fossa low, $h = {}^1/_4 - {}^1/_5$ br. Ligament pit well marked, br: 0·7 mm., twice as broad as the nerve-lumen. The fossæ of the interarticular ligaments truncated-triangular, larger than the muscular fossæ, which become somewhat broader towards the median radial lines. Between the muscular fossæ there are 5 stout intermuscular grooves which, like the interradial furrows, continue on the centripetal slopes of the radials towards the central shallow depression. Between each of these 10 rows there appear about 3 shallow furrows on the inner slopes of the RR.

A Cd (diameter 8·3 mm), possibly belonging to the same species, has an opening of the Cd-cavity measuring 0·5 mm. The h. of this Cd is 4·0 mm; 2—3 cirri appear in each row. A small central pit dorsally.

This species reminds one of *S. jutieri* by the granular free dorsal part of the RR. It differs, however, from this species by the appearance of the dorsal face of the Cd, by the higher Cd, and by the stout and pronounced ribs between the cirrus-rows.

Occurrence: Middle Jurassic (Oolite; according to a complementary letter from Dr. F. A. BATHER this means bajocian or bathonian), England. The type specimen in the British Museum.

27) **Solanocrinus d'orbignyi** (P. H. CARPENTER) 1881.

Solanocrinites costatus (part.) 1831 GOLDFUSS, Tab. 50, fig. 7 c—d; 1836 BRONN, Taf. 17, fig. 14 c—d.

Comatulina costata 1852, D'ORBIGNY, p. 139.

Antedon (d')Orbignyi 1881 b CARPENTER, p. 197, Pl. 9, fig. 8; 1888 P. H. CARPENTER, p. 38; 1888 DE LORIOL, pp. 492, 527; 1908 ENGEL, p. 455.

Solanocrinus costatus 1908 ENGEL, p. 449.

It is open to some doubt whether the figure that CARPENTER gives of this species is really the same as was once figured by GOLDFUSS.

Occurrence: Upper Jurassic (virgulian), Württemberg.

28) **Solanocrinus peroni** (DE LORIOL) 1888.

Antedon peroni 1888 DE LORIOL, pp. 490, 524, Pl. 222, fig. 2.

Occurrence: Upper Jurassic (sequanian), Algiers.

29) **Solanocrinus picteti** (DE LORIOL) 1879.

Antedon picteti 1879 DE LORIOL, pp. 268, 272, 276, 290, Pl. 20, figg. 28—31; 1881 b P. H. CARPENTER, pp. 196, 199, 201; 1882 P. H. CARPENTER, p. 42; 1888 P. H. CARPENTER, pp. 26, 39.

?*Antedon valdensis* 1879 DE LORIOL, Pl. 20, fig. 33.

Occurrence: Lower Cretaceous (valanginian), Switzerland.

30) **Solanocrinus ricordeanus** (D'ORBIGNY) 1850.

Decameros ricordeanus 1850 D'ORBIGNY, Tome 2, p. 121; 1857 PICTET, p. 289; 1862 DUJARDIN & HUPÉ, p. 197; 1876 QUENSTEDT, p. 184; 1878 SCHLÜTER, p. 38; 1900 DE LORIOL, p. 76.

Antedon ricordeanus 1878 SCHLÜTER, p. 49.

According to DE LORIOL (1900) this species is, perhaps, the same as *Act. (Sol.) vagnacensis,* which seems rather likely when one also takes into consideration the fact that the two species are of the same geological age.

Occurrence: Lower Cretaceous (aptian), France.

31) **Solanocrinus tessoni** (P. H. Carpenter) 1881.

Antedon Tessoni 1881 b P. H. Carpenter, pp. 198, 200—201, Pl. 10, fig. 10; 1882 P. H. Carpenter, p. 42; 1888 P. H. Carpenter, p. 38; 1888 de Loriol, pp. 469, 524, Pl. 216, fig. 6.

Occurrence: Upper Jurassic (oxfordian), N. France.

32) **Solanocrinus thiollieri** (de Loriol) 1888.

Antedon Thiollieri 1888 de Loriol, pp. 513, 524, Pll. 224; 225, fig. 1; 1895 de Loriol, p. 3, Pl. 1, fig. 2; 1912 Kirk, p. 78.

The arms are X, very stout and coarse, partly strongly biserial, especially in the middle, excessively thickened parts. Cirri long and stout, with rather short segments ($l = {}^2/_3$ br.), without discernable dorsal spines.

Occurrence: Upper Jurassic (virgulian), E. France.

33) **Solanocrinus truncatus** (P. H. Carpenter) 1881.

Antedon truncata 1881 b P. H. Carpenter, pp. 194, 200, Pl. 9, fig. 3; 1888 de Loriol, p. 527.

Quenstedt's figure (1852, Pl. 51, fig. 36) of *Solanocrinites costatus* possibly belongs to the same species as Carpenter's specimen.

Occurrence: Upper Jurassic (virgulian), Württemberg.

34) **Solanocrinus vagnacensis** (de Loriol) 1888.

Actinometra vagnacensis 1888 de Loriol, pp. 538, 540, Pl. 227, fig. 3; 1900 de Loriol, p. 76.

It must be observed that the first statement given by de Loriol as to the geological age of the species is incorrect.

Occurrence: Lower Cretaceous (aptian), France.

35) **Solanocrinus valdensis** de Loriol 1868.

Solanocrinus valdensis 1868 de Loriol, p. 83, Pl. 7, fig. 19 a—c; 1871 Ooster, p. 132.

Antedon valdensis 1879 de Loriol, pp. 266, 290, Pl. 20, figg. 19, 32; 1902 de Loriol, p. 39.

Pl. 20, fig. 33, 1879 DE LORIOL seems me should be referred to *S. picteti*. Fig. 20 of the same plate DE LORIOL himself (1889) called *Thiollierierinus arzierensis*.

Occurrence: Lower Cretaceous (neocomian, valanginian), Switzerland.

B. **Archaeometra** nov. gen.

Cd a truncated cone, conical, or a high column. Cirrus-socket (not bordered by a thickened rim) with a weak or indiscernable transverse crest. Never any radial, longitudinal crests between the rows on Cd. In the interradial corners of Cd, on the other hand, there are stout longitudinal crests, which separate the radial cirrus-areas from each other. BB powerfully protruding. The free dorsal part of the RR broad and overlapping the border of Cd. Radial face rather high. Muscular fossæ more or less vertical bands surrounding the intermuscular furrow. Radial cavity of medium size to rather small, the central depression deep. Type: *A. aspera.*

Geological appearance: Upper Jurassic. The following 5 species belong to this genus: *aspera* QUENSTEDT, *bronnii* MÜNSTER, *carpenteri* nov. sp., *kopřivnicensis* REMEŠ, *scrobiculata* GOLDFUSS.

Survery of the species.

A. Cirri in a single whorl. Cd strongly flattened.
    1. Visible parts of BB granulated. Radial face broader than high. Muscular fossæ of uniform breadth. Without fulcral ligament. *aspera.*
    2. BB smooth. Radial face higher, h = br. Muscular fossæ narrowing dorsally. With accessory interarticular ligaments (fulcral ligaments). *carpenteri.*

B. Cirri in a double whorl. Cd conical—columnar.
    1. The visible part of BB and free dorsal part of RR granular. Radial cavity $^1/_4$ of the diameter of the radial ring. *kopřivnicensis.*
    2. BB and dorsal free part of the RR smooth. Radial cavity $^1/_3$—$^1/_2$ of the diameter of the radial ring.
        a. Interradial costæ of Cd conspicuously prominent *bronnii.*
        b. Interradial costæ of Cd not conspicuously prominent *scrobiculata.*

1) **Archaeometra aspera** (QUENSTEDT) 1858.

Solanocrinites asper 1858 QUENSTEDT, p. 659, Tab. 81, figg. 23—33; 1863 CARTIER, p. 52; 1891 JÆKEL, p. 627.

Solanocrinus asper 1866 Oppel, p. 300; 1874 Moesch, p. 50; 1876 Quenstedt, p. 182, Tab. 96, figg. 77—90; 1881 b P. H. Carpenter, p. 202.

Comatula aspera 1867 Moesch, p. 136.

Antedon asper(-a) 1878 Schlüter, p. 49; 1879 de Loriol, pp. 257, 290, Pl. 20, figg. 13—17; ? 1881 b P. H. Carpenter, p. 202, Pl. 11, fig. 19; 1888 de Loriol, pp. 458, 465, 524, Pl. 215, figg. 2—4, Pl. 216, figg. 1—4; 1891 Woods, p. 37; 1902 Remeš, pp. 207, 208; 1908 Engel, pp. 376, 429.

Carpenter (cf. above) has figured a form with this name which probably does not belong here; the specimen is, however, so fretted that it is impossible to say anything as to its relationship.

Of this species numerous Brr are known which are granulated like the free dorsal part of RR. The connection between I Br 1 and 2 (axillary) was close, something intermediate between synostosis and synarthry. Syzygial faces with 4 or 5 septa.

According to Jækel (1891) Quenstedt's figures of Brr (1876, Pl. 96, figg. 77 – 87) represent Brr of *Sclerocrinus compressus*. It must, however, be observed that similar Brr also are figured by de Loriol (1888), and this shows that the Brr of *A. aspera* really were granulated.

A four-rayed specimen is figured by Quenstedt (1876).

Occurrence: Upper Jurassic (oxfordian), S. Germany, France, Switzerland.

2) **Archaeometra bronnii** (Münster) 1839.

Solanocrinus Bronnii 1839, Münster, p. 89, Tab. 11, fig. 7 (1843 2. Aufl., p. 101, Tab. 11, fig. 7); 1848 Bronn, p. 1150; 1857 Pictet, p. 289; 1878 Schlüter, p. 36; 1879 de Loriol, p. 261; 1881 b P. H. Carperter, Pl. 10, fig. 16.

Comatula Bronnii 1850 d'Orbigny, Tome 1, p. 382.

Solanocrinites Bronnii 1858 Quenstedt, p. 657.

Comaster Bronnii 1862 Dujardin & Hupé, p. 213.

Solanocrinus scrobiculatus (part.) 1876 Quenstedt, p. 181, Tab. 96, figg. 52—53.

Antedon Bronni(i) 1878 Schlüter, p. 49; 1888 de Loriol, pp. 456, 526.

Occurrence: Upper Jurassic (oxfordian), Bavaria.

3) **Archaeometra carpenteri** nov. sp.

Antedon scrobiculatus 1881 b P. H. Carpenter, Pl. 10, fig. 17; 1891 (part.) Woods, p. 37.

Cd flattened with cirri in an, at least partly, double whorl. BB very conspicuously protruding at the corners, overlapping the Cd border. Their visible surface is smooth. The free dorsal part of RR broad, granulated. Radial faces very high, h $\geq$ br. The transverse ridge with fulcral ligament. The br. of the muscular fossæ decreasing towards the nerve-lumen. Radial cavity rather large, diameter nearly $^1/_2$ of the radial ring.

Is well distinguished from *A. aspera* to which it is most closely related.

Occurrence: Upper Jurassic (oxfordian), Bavaria.

4) **Archaeometra kopřivnicensis** (Remeš) 1902.

Antedon kopřivnicensis 1902 Remeš, pp. 207, 216, Pl. 20, fig. 17.

Occurrence: Upper Jurassic (tithonian), Moravia, Czecho-Slovakia.

5) **Archaeometra scrobiculata** (Goldfuss) 1831.

? *Modioli rarissima species* 1716 Scheuchzer, p. 99, No. 120; 1718 Scheuchzer, p. 330, fig. 167.

Solanocrinites scrobiculatus 1831 Goldfuss, p. 167, Tab. 50, fig. 8; 1840 Hagenow, p. 665; 1840 F. Braun, Verzeichniss p. 16; 1852 Quenstedt, p. 601, Tab. 51, fig. 34 (2. Aufl. 1867, Tab. 65, fig. 34; 3. Aufl. 1885, p. 915, Tab. 72, fig. 13); 1858 Quenstedt, p. 657, Tab. 81, figg. 12—22; 1863 Cartier, p. 52; 1879 P. H. Carpenter, pp. 6, 104—105.

Solacrinus scrobiculatus 1835 L. Agassiz, p. 196.

Solanocrinus scrobiculatus 1839 a Münster, p. 89 (2. Aufl. 1843, p. 101); 1848 Bronn, p. 1150; 1857 Pictet, p. 289; 1860 Bronn, Pl. 29, fig. 5; 1866 Oppel, p. 300; 1874 Moesch, p. 50; 1876 Quenstedt, p. 177, Tab. 96, figg. 54—74; 1878 Schlüter, pp. 36—37; 1879 Zittel, fig. 283 b—d; 1880 a P. H. Carpenter, p. 38; 1884 P. H. Carpenter, p. 402; 1887 P. H. Carpenter, p. 83; 1891 Jækel, p. 631, Tab. 43, fig. 3; 1913 Zittel-Eastman, fig. 340 b—d; 1915 Zittel, fig. 320 b—e; 1918 Jækel, fig. 68.

Comatula scrobiculata 1850 d'Orbigny, Tome 1, p. 381; 1858 Oppel, p. 689; 1867 Moesch, pp. 136, 138, 277; 1869 Jaccard, p. 210; 1873 de Tribolét, p. 7.

Comaster scrobiculatus 1862 Dujardin & Hupé, p. 213; 1874 Lundgren, p. 69.

Antedon scrobiculatus(-a) 1878 Schlüter p. 49; 1879 de Loriol, pp. 255, 290, Pl. 20, figg. 11—12; 1880 c P. H. Carpenter, p. 10, Pl. 6, fig. 9; 1881 b P. H. Carpenter, pp. 198, 202—205, 207—208, 212, 215, Pl. 10, figg. 14, 15, (?) 18; 1882 P. H. Carpenter, p. 42; 1884 P. H. Carpenter, p. 336; 1888 de Loriol, pp. 452, 455, 464, 465, 468, 524, Pl. 214, figg. 2—4, Pl. 215, fig. 1; 1891 (part.) Woods, p. 37; 1900 Lissajous, p. 24; 1908 Engel, p. 429; 1912 Kirk, pp. 69, 79, 80, Pl. 8, figg. 3—4.

It seems to me to be rather desirable to get a revision of this species. Cd varies from a rather low cone to a high and narrow column. BB also, and to a certain degree the muscular fossæ, are somewhat variable. The types that are figured by P. H. Carpenter (1881 b, Pl. 10, fig. 18) and de Loriol (1888, Pl. 214, fig. 4) differ most.

Occurrence: Upper Jurassic (oxfordian), W. France, S. Germany (Bavaria, Württemberg), Switzerland.

C) **Cypelometra** nov. gen.

From κύπηλλον = bowl, with reference to the form of Cd.

Cd hemispheric. Cd-cavity small. Cirrus-sockets large, rather shallow, without transverse crest. Cirri in X rows, coupled two and two, with wide radial interspaces. BB almost completely hidden. The free dorsal part of RR indistinct. Radial face sloping rather sharply inwards. The radial cavity therefore only $^1/_4 - ^1/_3$ of the br. of the radial ring. Muscular fossæ horizontal bands, rather broad, h = br. Type: *C. iheringi.*

Geological appearance: Tertiary (miocene). One species only belongs here.

1) **Cypelometra iheringi** (DE LORIOL) 1902.

Antedon iheringi 1902 DE LORIOL p. 22, Pl. 2, figg. 3—4; 1906 AMEGHINO p. 172.

Catoptometra iheringi 1915 b A. H. CLARK p. 112.

I cannot see any cause why this species should be referred to the recent genus *Catoptometra,* to which it shows scarcely any close similarity.

Occurrence: Tertiary (patagonian = miocene), S. America.

Conometridae nov. fam.

Cd conical or discoidal. Cd-cavity at least $^1/_4$ of the diameter of Cd. No radial pits or pores on the ventral side of Cd. No dorsal star. Cirri in more or less distinct rows. Cirrus-sockets rather large with or without indistinct sculpture. BB from large and contiguous to hidden. The free, dorsal part of RR visible as broad bands or hidden. Muscular fossæ large when compared with the interarticular ligament fossæ. Radial cavity large to medium-sized.

Geological appearance: Upper Cretaceous—Tertiary (miocene).

Probably, besides the genera *Amphorometra, Placometra, Conometra,* and *Jaekelometra,* the *pellati* and *anglesensis* groups of the genus *Glenotremites* belong here.

A) **Amphorometra** nov. gen.

From 'αμφορεύς = vase.

Cd conical. No dorsal star, no radial pits. Cd-cavity rather large. Cirrus-sockets in X rows, with very faint indications of a transverse ridge. BB visible at the interradial corners. Free dorsal part of RR broad; deep subradial clefts. A distinct dorsal ligament pit. Muscular fossæ larger than the interarticular ligament fossæ. Radial cavity rather large, about $^1/_3$ of the diameter of the radial ring. Type *A. conoidea.*

Probably the majority of the *anglesensis* group of the genus *Glenotremites* must also be reckoned here.

Geological appearance: Upper Cretaceous. Two species belong here: *brydonei* nov. sp. and *conoidea* GOLDFUSS 1839 (with var. *lævior* and var. *granulata*).

Survey of the species:

A. 3—4 cirrus-sockets in each row, size of the Cd-cavity moderate (diameter $^1/_4$ of the br. of Cd). Muscular fossæ moderate. *conoidea.*
   1. The free dorsal part of RR almost smooth. Cd slightly truncated. var. *lævior*
   2. The free dorsal part of RR granulated. Cd a pointed cone. var. *granulata.*

B. 5 cirri in each row. Cd-cavity very large and deep (probably considerably more than $^1/_3$ of the br. of Cd). Muscular fossæ about twice the size of the interarticular ligament fossæ. *brydonei.*

1) **Amphorometra brydonei** nov. sp. (figg. 212, 213).

Dimensions: Cd + radial ring, h : 7.1 mm. Cd, h : 4.0 mm., br. : 4.4 mm. Diameter of the radial ring : 4.8 mm., of the radial cavity: 1.5 mm.

Cd a high, somewhat bulgy cone. Cirri in X rows, with (4-)5(-6) cirrus-sockets in each row. About L in total. Interradial interspaces free from cirri in the ventral half of Cd. Cirrus-sockets with two large, indistinctly bordered swellings laterally of the lumen.

BB small, visible in the interradial corners.

Deep subradial clefts. The free dorsal part of the RR rather broad, smooth, almost horizontal. Dorsal ligament pit 1 $^1/_2$ times as broad as the rather large nerve-lumen of the radial face. Muscular fossæ high, rather narrow, about twice as large as the interarticular ligment fossæ. Radial cavity wide and very deep, directly continued dorsally in the large Cd-cavity (depth of radial and Cd-cavity 5.0 mm.).

The species reminds one of certain recent species of *Atelecrinus.*

This magnificent species I have dedicated to Mr. R. M. BRYDONE F. G. S.

Occurrence: Upper Cretaceous (lower senonian, zone of *Actinocamax quadratus*) Seaford, England. The type specimen in the collections of Mr. R. M. BRYDONE.

2) **Amphorometra conoidea** (GOLDFUSS) 1839.

Glenotremites conoideus 1839 GOLDFUSS Petref. German., 2. Theil p. 286, Pl. 160, fig. 18; 1840 HAGENOW p. 661; 1848 BRONN p. 532; 1857 PICTET p. 290; 1862 DUJARDIN & HUPÉ p. 214; 1870 SCHLÜTER p. 957; 1871 OOSTER p. 131; 1874 LUNDGREN pp. 65, 69; 1878 SCHLÜTER pp. 37, 38; 1879 P. H. CARPENTER p. 73.

Comatula conoidea 1850 D'ORBIGNY Tome 2. p. 275; 1868 DEVALQUE p. 380 (2e Ed. 1880 p. 429); 1878 SCHLÜTER p. 39.

Antedon conoideus 1878 SCHLÜTER pp. 41, 44, 47—49; 1895 DEEKE p. 71.

Occurrence: Upper Cretaceous (senonian), N. Germany, Holland.

Var. laevior nov. var. (figg. 214—216).

Dimensions: Cd + radial ring, h : 6·4 mm. Cd h : 3·5 mm., br : 3·8 mm. Radial ring h : 2·9 mm., br : 4·4 mm. Radial cavity, diameter: 1·2 mm.

Cd conical, somewhat truncated dorsally. Cirri in X rows, 3—4 in each row, the sockets with 2 weak swellings laterally of the lumen. No radial pits. Cd-cavity about $^1/_4$ of the diameter of Cd. Cd strongly sloping in under the RR, therefore deep sub-radial clefts.

BB rather stout and large, projecting at the interradial corners.

The free dorsal parts of RR broad, indistinctly pitted to smooth, sloping strongly inwards towards the sub-radial clefts, therefore partly horizontal. Radial facet narrower ventrally of the transverse ridge than dorsally of it. Muscular fossæ about 1 $^1/_2$ times the size of the interarticular ligament fossæ.

The type specimen for this description is in the Greifswald museum (the radial ring separated from the Cd by insignificant pressure; thus the figures from the ventral face of the Cd, from the dorsal face of the radial ring, and from the lateral view of Cd + radial ring originate from the same specimen).

Var. granulata nov. var. (figg. 217—218).

This variety differs from preceding one by the Cd being somewhat more pointedly conical and by the free dorsal surface of the RR being strongly granulated.

The type specimen for this variety is found in the British Museum.

Of this species I have seen numerous Cdd, some of the more truncated type, others of the more pointedly conical type. It is not always possible to keep the two types apart with certainty. Possibly GOLDFUSS when giving his figure of *Glenotremites conoideus* had a representative of the latter variety.

Occurrence of the varieties described: Upper Cretaceous (upper senonian, zone of *Belemnitella mucronata*), Rügen, N. Germany.

B. **Placometra** nov. gen.

From πλάξ = disk, because of the shape of Cd.

Cd discoidal, without stellate impression dorsally. Cirri large, in X rows, their sockets without distinct sculpture. BB hidden. Radial ring overlapping the ventral border of the Cd. Free dorsal part of the RR nearly horizontal. Nerve-lumen of the radial facet very large. Muscular fossæ conspicuous. Radial cavity large, about $^{1}/_{2}$ of the diameter of the radial ring. Type and only species *P. mortenseni* nov. sp.

Probably the *pellati* group of the genus *Glenotremites* may also be reckoned here.

Geological appearance: Upper Cretaceous (—Tertiary, miocene).

1) **Placometra mortenseni** nov. sp. (figg. 230—232).

This species I have dedicated to Dr. TH. MORTENSEN of the Zoological Museum, Copenhagen.

Dimensions: Cd + radial ring, h : 2·6 mm. Cd h : 0·9 mm., br : 1·6 mm. Radial ring br : 2·3 mm., radial cavity 1·0 mm. in diameter.

Cd discoidal, irregularly pentagonal, smooth and flattened dorsally. With large cirrus-sockets in X rows laterally, 1 or 2 in each row, in all about XII. Cirrus-sockets with very indistinct eminences on both sides of the nerve-lumen, ortherwiese without sculpture.

BB hidden. The radial ring strongly overlapping the ventral border of Cd. The free dorsal part of RR smooth, rather broad, horizontal. Dorsal ligament fossa rather low and angular without a distinctly marked off ligament pit. Nerve-lumen very large. Interarticular ligament fossæ truncated-triangular, smaller than the muscular fossæ, which are indistinctly separated from one another by an intermuscular ridge, visible in some of the interradii only. Between the muscular fossæ a notch radially. Radial cavity large, its diameter nearly $^{1}/_{2}$ of the br. of the radial ring.

Occurrence: Upper Cretaceous (turonian, zone of *Terebratulina lata*) Compton Bay, Isle of Wight, England. Type specimen in the collections of Mr. R. M. BRYDONE, F. G. S.

C. **Jaekelometra** nov. gen.

Called after Geheimerat O. JÆKEL, Greifswald who kindly permitted me to borrow the type specimens for a new description.

Cd (bluntly) conical. Cirrus-sockets more or less distincly arranged in X rows with a weak transverse crest. Cd-cavity of medium size. No radial pits. BB large, contiguous, forming centrally a primitive rosette. Radial face low and triangular. Interarticular fossæ low and indistinct. Muscular fossæ broad and low. Radial cavity large and deep. Type *J. belgica*.

Geological appearance: Upper Cretaceous. Two species: *J. belgica* JÆKEL 1901 and *J. columnaris* nov. sp. belong here.

Survey of the species:

1. BB high, h ≥ br. Cirri ± XV *belgica*.
2. BB low, h = $^1/_3$ br. Cirri ± XXXV *columnaris*.

1) **Jaekelometra belgica** (JÆKEL) 1901 (figg. 219—227).

? einen neuen Comatuliden-typus 1878 SCHLÜTER p. 66.
Atelecrinus belgicus 1901 JÆKEL p. 1084, Fig. 15 B; 1918 JÆKEL fig. 69.

Cd + BB + RR: h = 7 mm. Cd, h : 2·7 mm., br : 2·6 mm. BB, h : 1·8 mm.; br of the BB ring ± 3·5 mm. RR, br of the radial ring 5·6 mm., h of the dorsal free part 2·3 mm., br of the radial face 2·8 mm., h : 1·2 mm., radial cavity br: 3·7 mm.

Cd bluntly conical. Cirri about XV, ± 3 per radius, tending to arrange themselves in X sparse columns, cirrus-sockets large with a weak transverse crest.

BB large and high, pentagonal, h > br, smooth, bent slightly outwards.

The free dorsal part of RR large and high with a median longitudinal crest except in the proximal quarter. The RR are strongly bent outwards. Radial face low and broad, nearly triangular. Muscular fossæ deepened towards the intermuscular crest. Interarticular fossæ indistinct but indicated here and there as weak depressions. Evidently they were rather low. Radial cavity very large and deep. The bottom of it is formed by centripetal processes from the BB.

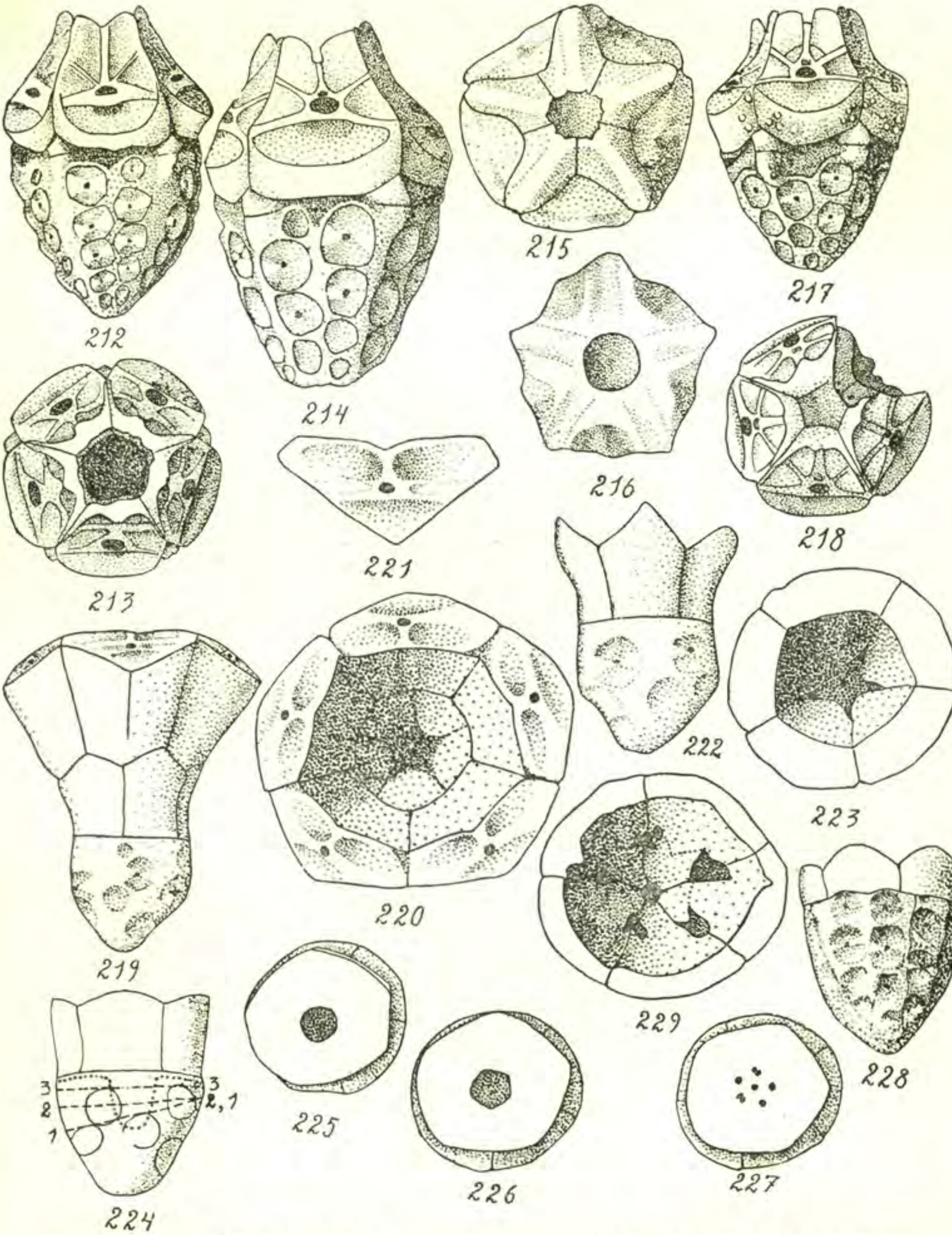
A Cd with adhering basal ring belongs also here. It differs only by an inconspicuously lower Cd and a basal ring that is less bent outwards. This Cd has a small pit dorsally. The dimensions of the BB here are: h : 1·5 mm., br of the basal ring 3 mm., basal cavity br : 1·5 mm. Thickness of the BB $^3/_4$ mm.

Occurrence: Upper Cretaceous (senonian, maastrichtian), Holland. Two spp. in the Berlin Museum, Coll. Binkhorst.

2) **Jaekelolometra columnaris** nov. sp. (figg. 228—229).

Only Cd and the BB ring are preserved.

Dimensions: Cd + BB-ring h : 4·2 mm. Cd h : 3·2 mm., br : 3 mm.



Figg. 212—229. 212—213) *Amphorometra brydonei* 212) Cd + basal and radial rings in lateral view, 213) Basal and radial rings, ventral view, $^{6}/_{1}$; 214—218) *Amphorometra conoidea* 214—216) var. *lævior*, 214) Cd + basal and radial rings, lateral view, 215) Basal and radial rings, dorsal view, 216) Cd, ventral view, $^{8}/_{1}$; 217—218) var. *granulata*, 217) Cd + basal and radial rings, lateral view, 218) Do. ventral view, one radial has dropped out, $^{8}/_{1}$; 219—227) *Jaekelometra belgica* 219) Cd + basal and radial rings, Sp. 1, lateral view, $^{6}/_{1}$; 220) Basal and radial rings, ventral view, $^{8}/_{1}$; 221) A radial facet, $^{10}/_{1}$; 222) Cd + basal ring, lateral view,

H. of the basal ring: 0·6 mm. interradially, 1·0 mm. radially, br of the basal ring: 3·3 mm. Size of the basal cavity br : 2·5 mm. Thickness of the BB : 0·4 mm.

Cd conical, no pit dorsally. Cirrus-sockets with a distinct, but rather weak, transverse crest. Cirri in X rows, 3 or 4 in each row, total ± XXXV. The rows are closely set and nearly reach the dorsal top of Cd. At the ventral border of Cd they leave narrow radial spaces free from cirri.

BB pentagonal, low, $h = \pm {}^{1}/_{3}$ br, scarcely bent outwards.

This species cannot be an older specimen of the preceding species. As is well-known, new cirri form on the ventral border of the growing Cd, and as the Cd of *columnaris* is only inconspicuously larger than that of *belgica* one cannot explain the many cirri of the former species by the increase in the growth of Cd. The cirrus-sockets here are also smaller and arranged in X distinct close rows, Cd is pronouncedly conical, and the BB essentially different, much lower and thinner.

Occurrence: Upper Cretaceous (senonian, maastrichtian), Holland. One sp. in the Berlin Museum, Coll. Binkhorst.

At the bottom of the basal cavity in both species there appears a central and 5 surrounding pits radially situated. The last mentioned should possibly have been interpreted as openings to radial pits and therefore I had sections prepared by grinding through the Cd of Sp. 2 of *Jaekelometra belgica* (cf. figg. 225—227). It has, however, turned out that no radial pits occur in Cd. Nevertheless, when approaching the ventral side of Cd there appear marks of a central and 5 surrounding pores. The latter do not reach beyond the diameter of the opening of the Cd-cavity and are interradially arranged. They must therefore represent the entrances of the nerves from the chambered organ into the BB. These nerves are continued on the ventral side of the thin centripetal processes from the BB which form the bottom of the basal cavity, in radially emerging paired nerves. The perforations for these nerves, however, are not here, as in recent Comatulids, separated by a calcareous bridge. Nevertheless, we have a trace of this condition in *J. columnaris*, where in some radii there are two openings close together. Perhaps in other cases the narrow calcareous bridge was destroyed at the fossilisation or during the preparation of the specimens. The BB are therefore interesting since the are only thick and massive peripherally. In the centre, on the other hand, they form only a thin plate, which

---

${}^{8}/_{1}$; 223) Basal ring, Sp. 2, ventral view, ${}^{10}/_{1}$; 224) Cd + basal ring, Sp. 2, lateral view; the figures laterally of the Cd mark the different sections prepared by grinding and reproduced in figg. 225—227; the size of the Cd-cavity is indicated by a dotted line, ${}^{8}/_{1}$; 225) Grinding-section 1—1; 226) Do. 2—2, 227) Do. 3—3, ${}^{8}/_{1}$; 228—229) *Jaekelometra columnaris* 228) Cd + basal ring, lateral view, ${}^{8}/_{1}$; 229) Basal ring, ventral view, ${}^{10}/_{1}$.

separates the centrodorsal cavity from the ventral weak parts and thus represents a primitive rosette.

It seems to me incorrect to range these forms in *Atelecrinidae*. In *Jaekelometra* the Cd-cavity is very much smaller. The appearance of the cirrus-sockets is quite different (among recent forms *At. anomalus* is the closest, cf. A. H. CLARK 1915 c, fig. 414). According to P. H. CARPENTER *Atelecrinus* lacks the rosette completely. Finally and most important, the radial faces are quite different. *Jaekelometra*, in virtue of its median carina on the free dorsal part of RR, of its low radial face and certain other characteristics, is closer to the recent *Thalassometridae*.

D. **Conometra** nov. gen.

Cd conical. Cirrus-sockets in X—XX rows. BB hidden. No subradial clefts. The free dorsal part of RR broad to hidden. The radial faces high, muscular fossæ large. The radial cavity about $^1/_4$ of the br. of the radial ring. Type *C. alticeps*.

Geological appearance: Upper Cretaceous—Tertiary (miocene).

Three species: *alticeps* PHILIPPI 1844, *hungaricus* VADÁSZ 1915, and *rugiana* nov. sp. belong here.

Survey of the species:

A. Cirri in X rows. No free dorsal part of the RR visible *rugiana*.
B. Cirri in XV rows. The free dorsal part of the RR broad. Muscular fossæ considerably larger than the interarticular ligament fossæ *alticeps*.
C. Cirri in ± XX rows. Muscular fossæ of about the same size as the interarticular ligament fossæ *hungarica*.

1) **Conometra alticeps** (PHILIPPI) 1844.

Alecto alticeps 1844 PHILIPPI pp. 540—542, Taf. 6 B, figg. a—d; 1876 QUENSTEDT p. 185, Tab. 96, fig. 103; 1878 SCHLÜTER p. 38; 1879 P. H. CARPENTER p. 13; 1879 a FONTANNES p. 498; 1879 b FONTANNES p. 414; 1900 NOËLLI pp. 42—43.

Alecto anticeps 1846 GEINITZ p. 545.

Antedon alticeps 1878 SCHLÜTER p. 50; 1878 MENEGHINI p. XXXI; 1879 a FONTANNES p. 500; 1879 b FONTANNES p. 416; 1881 b P. H. CARPENTER p. 213; 1888 P. H. CARPENTER p. 38; 1897 DE LORIOL p. 121; 1897 NICOLAS p. 131; 1898 NICOLAS pp. 408, 410; 1915 VADÁSZ pp. 9, 10.

Occurrence: Tertiary (eocene), S. Italy.

2) **Conometra hungarica** VADÁSZ 1915.

Antedon hungarica 1915 VADÁSZ pp. 9, 171, Tab. 1, figg. 7—9.

Occurrence: Tertiary (miocene, helvetian), Hungary.

3) **Conometra rugiana** nov. sp. (figg. 233—234).

Dimensions: Cd + radial ring h: 2·5 mm., diameter: 2·0 mm. Cd h: 1·3 mm., radial ring h: 1·2 mm. The specimen very flattened owing to pressure.

Cd conical, without any impression dorsally. Cirrus-sockets rather deep, in X rows, about 3 cirri in each row, XXVII in total. No sculpture of the cirrus-sockets. Between the rows a narrow area devoid of cirri interradially.

BB hidden. The free dorsal part of RR hidden in the median line, indistinctly visible at the interradial corners. Dorsal ligament fossa broad and nearly rectangular; a large but indistinct dorsal pit occurs. Interarticular ligament fossæ small and triangular, muscular fossæ high and rather narrow. Radial cavity small, evidently compressed.

Occurrence: Upper Cretaceous (upper senonian, zone of *Belemnitella mucronata*), Rügen, N. Germany. Type specimen in the British Museum.

Notocrinidae Mortensen 1917.

Cd conical to hemispherical. Cd-cavity mesophreate (diameter of the opening $^1/_3$ — > the diameter of Cd). Radial pits or pores occur, or a strongly lobated opening of the Cd-cavity. Often a dorsal star. Cirri in rows or alternating indistinctly. Cirrus-sockets large, sometimes with a weak transverse crest, often peripherally striated. BB protruding more or less at the corners. The free dorsal part of RR visible as more or less broad bands, rarely hidden in the median line. Radial faces with muscular fossæ that are ≥ than the interarticular ligament fossæ. Radial cavity large — medium-sized.

To this family belong, besides the genera *Loriolometra* and *Sphaerometra* and the recent genus *Notocrinus*, the *essenensis* and the *paradoxus* groups, probably also the *lettensis* and *rotundus* groups of the genus *Glenotremites*.

Geological appearance: Lower — upper Cretaceous — recent.

A. **Loriolometra** nov. gen.

Named in honour of M. P. de Loriol.

Cd a truncated cone — bluntly columnar. Often a stellate depression dorsally, or a real dorsal star. Large and very deep radial pits. Cirri in X rows, cirrus-sockets with indistinct sculpture, peripherally striated, with 2 small and indistinct tubercles laterally of the lumen. BB protruding at the corners. Deep sub-radial clefts. The free dorsal part of the RR broad. Radial faces large and broad, h about $^{4}/_{5}$ of br. Radial cavity rather large, diameter ± $^{1}/_{2}$ of the radial ring.

The arms seem to have been X, as only axillaries of one size are known from the same locality. The Br-segments were of normal obliqueness. Syzygies well developed with numerous septa.

The *essenensis*, and perhaps the *lettensis* groups also, belong to this genus. Type *L. retzii.*

Geological appearance: Upper Cretaceous. The only species with a radial ring known is *L. retzii.*

1) **Loriolometra retzii** (Lundgren) 1874 (figg. 235, 236).

Comatula sp. 1870 Schlüter, p. 957.

Comaster Retzii 1874 Lundgren, pp. 66—70, Taf. 3, figg. 1—13; 1876 Quenstedt, p. 183, Taf. 96, fig. 98; 1878 Schlüter, pp. 37, 39.

Antedon Retzii 1878 Schlüter, pp. 42, 44, 48—49, Taf. 2, figg. 3—7; 1880 a P. H. Carpenter, pp. 38, 45—47; 1880 b P. H. Carpenter, p. 555; 1888 P. H. Carpenter pp. 8—9; 1894 de Loriol, p. 482.

I have investigated more than 50 Cdd and one specimen with the radial ring preserved of this species, all of which I received on loan from the Riksmuseum, Stockholm. Lundgren speaks of the great variability in the development of the radial pits and of the Cd-cavity. He figures not less than 3 different types: 1) With a central cavity and 5 surrounding isolated pits, 2) All these pits confluent to a stellate figure, 3) 6 indistinct and shallow deepenings. In reality, however, only the first mentioned type is the correct expression of the normal condition. The 2nd type appears when, as is often the case, the thin and very fragile calcareous walls which separate the Cd-cavity and the radial pits are damaged. Finally, the 3rd case occurs by a partial filling out of the Cd-cavity and pits with the surrounding limestone. Lundgren states furthermore that the perforations for the cirrus-nerves start from the walls of the radial pits, a completely inexplicable fact, if these pits really contained the proximal ends of the dorsal coelom. This information, however, is incorrect; the nervous perforations are always situated in the interradial interspaces between the radial pits where they emerge from the Cd-cavity in paired rows (as is also indicated on Schlüter's figure 1878, Tab. 2, fig. 3 c).

The radial pits are very deep and somewhat converging towards the dorsal tip of Cd (cf. fig. 236). It is therefore very probable that the dorsal star is a remnant of the continuation of these pits in the stem rather than of the cavities of the chambered organ (as e. g. in *Notocrinus* fig. 196).

Among the 56 specimens investigated 54 have a diameter of 4·5—9 mm. Two specimens (only the Cdd preserved), on the other hand, are enormously large, measuring 12·5 and 13·5 mm. in diameter. They differ besides from the other specimens by having, usually, 4 instead of 3 cirrus-sockets in each row; on the ventral margin of Cd there is radially an area devoid of cirri, often more or less deepened. I shall only mention them here as a separate variety, *gigantea,* which approaches *Genotremites arnaudi.*

B. **Sphaerometra** nov. gen.

Cd hemispherical. A stellate impression dorsally or a dorsal star. Opening of the radial cavity surrounded by radial pits or pores or else stellate (secondary?). Cirrus-sockets indistinctly alternating, tending to arrange themselves in rows, large, sometimes with peripheral striation. BB inconspicuously protruding at the interradial corners. The free dorsal part of RR visible as bands which are sometimes interrupted in the radial median lines, broader towards the interradii. Radial face rather high. Muscular fossæ conspicuous. Radial cavity about $^{1}/_{4}$—$^{1}/_{6}$ of the br. of the radial ring.

The *paradoxus* group of *Glenotremites* also belongs to this genus. Type. *S. semiglobosa.*

Geological appearance: Lower — upper Cretaceous. The following 5 species belong here: *aequimarginata* P. H. Carpenter 1880, *carentonensis* de Loriol 1894, *incurva* P. H. Carpenter 1880, *semiglobosa* Schlüter 1878, *tetensi* Wegner 1911.

Survey of the species:

A. Radial facets high, $h \geqq br$. *incurva.*
B. Radial facets broader than high.
  1. Radial cavity about $^{1}/_{6}$ of the br. of the radial ring. Large species. *semiglobosa.*
  2. Radial cavity about $^{1}/_{4}$ of the br. of the radial ring.
    a. Cirri about LX. *carentonensis.*
    b. Cirri about XL.
      α. Diameter of Cd 9·5 mm. Cd in the median radial lines protecting the RR and a part of I Brr 1. *aequimarginata.*
      β. Diameter of Cd 5·3 mm. The free dorsal part of the RR visible as narrow bands. *tetensi.*

1) **Sphaerometra aequimarginata** (P. H. Carpenter) 1880.

Antedon aequimarginata 1880 a P. H. Carpenter, pp. 44, 45, 49, 54, Pl. 5, fig. 4; 1880 b P. H. Charpenter, pp. 553—555; 1881 b P. H. Carpenter, p. 199; 1888 P. H. Carpenter, pp. 26, 28.

Occurrence: Lower Cretaceous (gault), England.

2) **Sphaerometra carentonensis** (DE LORIOL) 1894.

Antedon carentonensis 1894 DE LORIOL p. 483, Pl. 24, fig. 3.

Occurrence: Upper Cretaceous (coniacian), France.

3) **Sphaerometra incurva** (P. H. CARPENTER) 1880.

Antedon incurva 1880 b P. H. CARPENTER, p. 552, Pl. 23, fig. 1; 1882 DOWNES, p. 86; 1888 P. H. CARPENTER, p. 38; 1894 DE LORIOL, p. 484.

Occurrence: Upper Cretaceous (cenomanian), England.

4) **Sphaerometra semiglobosa** (SCHLÜTER) 1878.

Antedon semiglobosus(-a) 1878 SCHLÜTER, pp. 41, 49, Taf. 1, figg. 7—12; 1880 a P. H. CARPENTER, pp. 38, 45, 49—50; 1880 b P. H. CARPENTER, pp. 553—555; 1888 P. H. CARPENTER, p. 8; 1894 DE LORIOL, p. 482.

Occurrence: Upper Cretaceous, Germany.

5) **Sphaerometra tetensi** (WEGNER) 1911.

Comatula tetensi 1911 WEGNER, pp. 21, 32; 1913 WEGNER, p. 187, fig. 2.

Occurrence: Upper Cretaceous (senonian), Germany (Silesia).

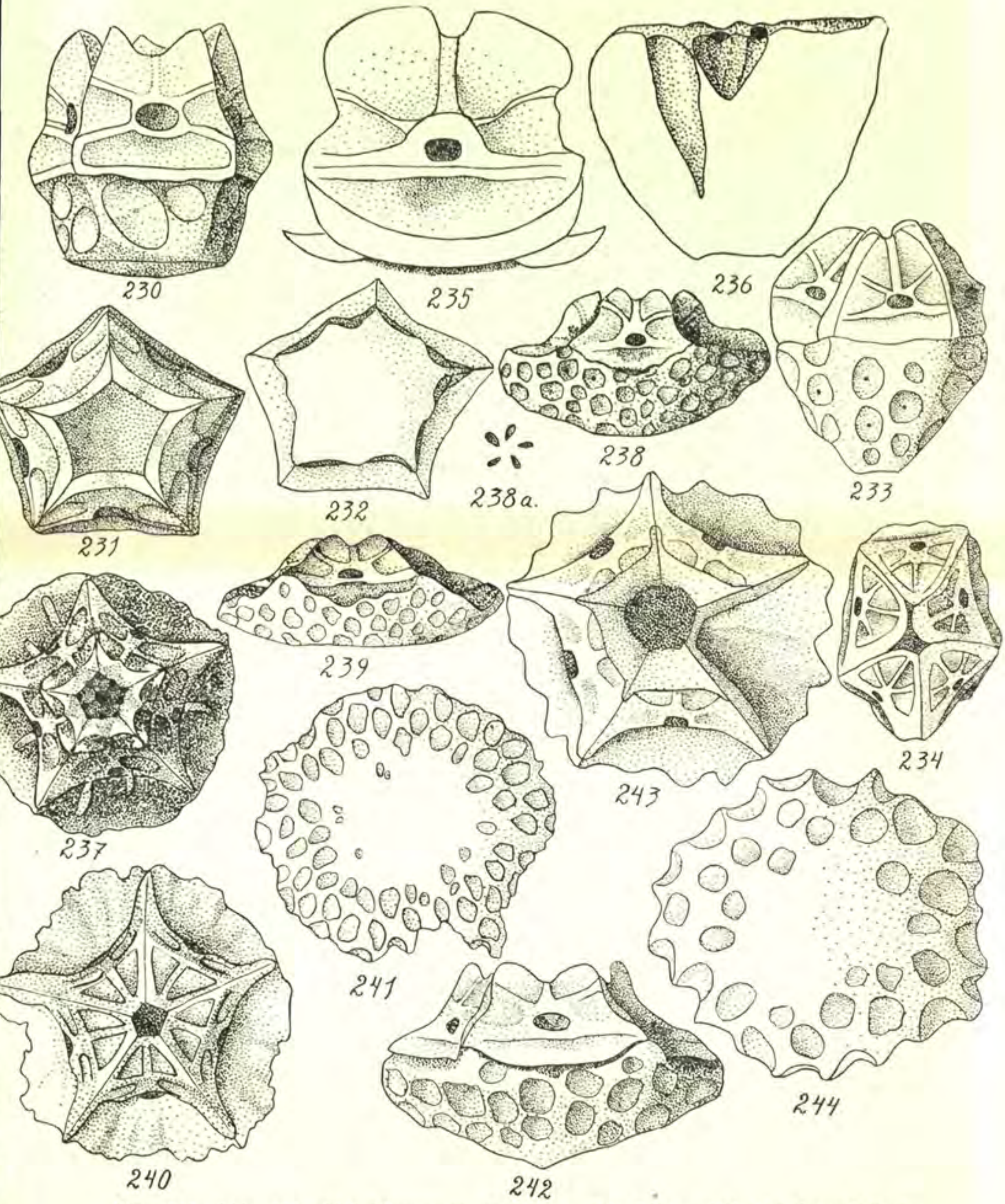
Palaeantedonidae nov. fam.

Cd sharply flattened, to hemispherical. Cd-cavity meso—macrophreate. Very rarely a dorsal star and radial pits (shallow: in *Semiometra*). Cirrus-sockets small, in close and alternating whorls, without transverse crest or peripheral striation. BB hidden. The free dorsal part of RR scarcely visible. Radial faces sloping inwards, muscular fossæ from rather high to very high and large. Radial cavity rather small to very small.

Slender forms with moderately oblique Br-joints. No biserial arms. Synarthries and syzygies well developed. Arms in the known cases X. Cirrus segments long.

Besides the genera *Semiometra, Hertha, Discometra*, and *Palaeantedon* included below, the *ransomi* group of the genus *Glenotremites* also seems to belong here.

Geological appearance: Upper Cretaceous—Quarternary.



Figg. 230—244. 230—232) *Placometra mortenseni*, 230) Cd + radial ring, lateral view, 231) Radial ring, ventral view, 232) Cd and radial ring, dorsal view, $^{16}/_{1}$. 233—234) *Conometra rugiana*, 233) Cd + radial ring, lateral view, 234) Radial ring rather compressed, ventral view, $^{16}/_{1}$. 235—236) *Loriolometra retzii*, 235) A radial facet and two BB, 236) A transverse section through a Cd, a large and deep radial pit to the left, $^{8}/_{1}$. 237—238) *Semiometra impressa* Cd and radial ring in lateral and ventral view, 238 a) The dorsal star from the dorsal centre of Cd, $^{8}/_{1}$. 239—241) *Semiometra plana*, 239) Cd + radial ring, lateral view, 240) Do, ventral view, 241) Cd, dorsal view, $^{16}/_{1}$. 242—243) *Semiometra pommerania*, 242) Cd + radial ring, lateral view, 243) Do., ventral view, one radial has dropped out, two basal rods are visible, 244) Cd, dorsal view, $^{16}/_{1}$.

A. **Semiometra** nov. gen.

From σημεῖον = seal.

Cd a low hemisphere to very flattened, usually with a more or less distinct dorsal star. The radial pits are very shallow or lacking. The Cd-cavity large. BB hidden, sometimes visible at single corners. Cd in the median radial lines projecting very much beyond the radial faces, which are deeply sunken in. Generally the radial face is rather low. Radial cavity usually $^1/_3$—$^1/_5$ of the br. of the radial ring. Type: *S. impressa.*

Geological appearance: Upper Cretaceous – eocene.

The following 8 species belong here: *courvillensis* VALETTE 1917, *impressa* P. H. CARPENTER 1881, *italica* SCHLÜTER 1878, *lenticularis* SCHLÜTER 1878, *plana* BRÜNNICH-NIELSEN 1913, *pommerania* nov. sp., *rowei* nov. sp., *scanica* nov. sp.

Survey of the species:

A. Cirri in a double or triple whorl, XXX—XL.
  1. Cd very much lower than the radial ring. Radial cavity about $^1/_4$ of the br. of the radial ring. *courvillensis.*
  2. H. of the Cd and radial ring nearly equal.
    a. Radial cavity about $^1/_3$ of the br. of the radial ring. *pommerania.*
    b. Radial cavity about $^1/_8$ of the br. of the radial ring. *rowei.*

B. Cirri in 3 or 4 whorls, at least about L.
  1. Radial face 1 $^1/_2$ times as high as Cd. Radial cavity large, sloping slightly inwards. Muscular fossæ large and broad. *scanica.*
  2. Radial face about = the h. of Cd. Radial cavity smaller, $^1/_3$—$^1/_7$ of the br. of the radial ring.
    a. Radial cavity ± $^1/_7$ of the br. of the radial ring. Muscular fossæ almost horizontal. *plana.*
    b. Radial cavity $^1/_3$ – $^1/_5$ of the br. of the radial ring. Muscular fossæ directed dorso-ventrally.
      α. With a distinct stellate impression dorsally.
        +. Large species (Cd br: 8·5 mm.). The dorsal impression situated in a concavity. *lenticularis.*
        ++. Smaller species (Cd br: 4 mm.). The dorsal impression level with the Cd surface. *impressa.*
      β. With a dorsal pit only. *italica.*

1) **Semiometra courvillensis** (Valette) 1917.

Antedon courvillensis 1917 Vallette, pp. 172, 176—177, fig. 31.

Occurence: Upper Cretaceous (santonian), France.

2) **Semiometra impressa** (P. H. Carpenter) 1881 (figg. 237, 238).

Antedon impressa 1881 a P. H. Carpenter, p. 135, Pl. 6, figg. 8—9; 1910 Hennig, p. 56.

I have a specimen of this species with the radial ring preserved from the Riksmuseum, Stockholm.

Dimensions. Cd, diameter: 4·7 mm. Cd + RR, h: 3 mm. Cd, h: 1·5 mm. RR, h: 1·5 mm. Radial ring, diameter: 4 0 mm.

Cd flattened with cirri in about 4 close alternating whorls; cirri about LXV. Cd with a real dorsal star.

BB hidden. Radial ring deeply sunken in the radial median lines, the interradial angles just reaching the border of Cd. In the radial median lines about 0·7 mm. of the ventral surface of Cd is visible. The distal parts of the thickenings described by Carpenter are also visible surrounding the shallow radial pits. The dorsal ligament fossa is narrow, the dorsal pit about twice as broad as the nerve-lumen. The interarticular ligament and muscular fossæ of about equal size. Between the paired muscular fossæ a weak notch. Radial cavity 1·1 mm., sloping sharply inwards. The central depression measures 0·6 mm. At the bottom of this the rosette is visible.

Occurrence: Upper Cretaceous (senonian), S. Sweden. The specimen described above is from Köpinge, Scania.

3) **Semiometra italica** (Schlüter) 1878.

Antedon italicus(-a) 1878 Schlüter, pp. 37, 46, 48—49, Tab. 3, figg. 8—10; 1878 Meneghini, p. XXXI; 1879 a Fontannes, pp. 498, 500; 1879 b, Fontannes, pp. 412, 415; 1880 a P. H. Carpenter, pp. 38—40, 44—45, 50; 1880 b P. H. Carpenter, pp. 553—554; 1881 b P. H. Carpenter, pp. 199, 213; 1888 P. H. Carpenter, p. 38; 1897 de Loriol, pp. 123, 127; 1897 Nicolas, p. 131; 1910 Doncieux, p. 161.

Occurrence: Tertiary (eocene), Italy.

4) **Semiometra lenticularis** (Schlüter) 1878.

Antedon lenticularis 1878 Schlüter, pp. 44, 46, 48—49, 66, Tab. 3, figg. 1—3; 1879 b Fontannes, p. 412; 1880 a P. H. Carpenter, pp. 38—40, 44—45, 50; 1880 b P. H. Carpenter, pp. 553—554; 1881 b P. H. Carpenter, p. 199; 1897 de Loriol, p. 124; 1897 Nicolas, p. 131.

Occurrence: Upper Cretaceous (senonian, maastrichtian), Holland.

5) **Semiometra plana** (Brünnich-Nielsen) 1913 (figg. 239—241).

Antedon plana 1913 Brünnich-Nielsen, pp. 24, 99, 100, 106, Tab. 12, figg. 54—56.

Dimensions: Cd + radial ring h: 1·3 mm. Cd br: 2·8 mm., h: 0·6 mm. Radial ring h: 0·7 mm,, br: 2·0 mm. Diameter of the radial cavity 0·3 mm. Dimensions of separate Cdd: diameter: 1·8—4·5 mm, h: 0·5—1·0 mm. Diameter of the Cd-cavity: 0·4—1·0 mm.

Cd strongly flattened, with an irregular notched border. Cirri LX—LXX in 3—4 close alternating whorls. Cirrus-sockets small, rhomboid, with ridges between them, forming a characteristic net-work on the dorsal side of the Cd. The dorsal centre of Cd without any star, often rather smooth, sometimes with cirri covering the whole dorsal surface. Large parts of the ventral face of Cd bare because of the RR being very deeply sunken in the median radial lines. Cd-cavity large and deep. Basal furrows narrow, distinct in small specimens only. Sometimes very shallow radial pits. The ventral face of Cd often inconspicuously wavy with shallow radiating impressions.

BB hidden. No dorsal free part of the RR, which are deeply sunken in the radial median lines. Radial faces very low and concave, only the interradial tips reaching the border of Cd. Dorsal ligament fossa low, with a stout ligament pit. Nerve-lumen transversely oval, large. Interarticular ligament fossæ rhombic, smaller than the rather long and deep muscular fossæ. These are almost horizontal, surrounding the small radial cavity, the diameter of which is about $^1/_7$ of the br. of the radial ring.

As far as I can ascertain the appearance of the Cd is exactly the same as in the species described by Brünnich-Nielsen as *Antedon plana*.

Occurrence: Upper Cretaceous (upper Senonian, zone of *Belemnitella mucronata*), Rügen, N. Germany, and (danian), Denmark. The type specimen of the description given above is in the British Museum. Besides this I have seen numerous specimens (Cdd + radial rings and Cdd only) both from the Greifswald and British Museums.

6) **Semiometra pommerania** nov. sp. (figg. 242—244).

Dimensions: Cd + radial ring h: 2·0 mm. Cd br: 3·0 mm., h: 0·9 mm. Radial ring h: 1·1 mm., br: 1·5 mm. Diameter of the radial cavity 0·7 mm.

Cd a flattened hemisphere, somewhat pointed dorsally. The central dorsal parts lack cirri usually. There is no stellate impression. Cirrus-sockets in 2—3 whorls, ± XXXV in all, rather sparse and large. The border of Cd somewhat notched by the encroaching lateral cirrus-sockets.

No BB visible to external view. Between the Cd and the RR they form 5 rods almost reaching the border of Cd. The RR sunken in the median radial lines, leaving about 0·5 mm. of the ventral face of Cd bare in each radius. Narrow subradial clefts. Radial faces with a rather narrow dorsal ligament fossa without distinct pit. Interarticular ligament and muscular fossæ of about the same size. Radial cavity large, diameter $^1/_3-^1/_2$, central depression about $^1/_4$ of the diameter of the radial ring.

Moreover, I have seen 14 other specimens of this species with the radial rings preserved, some of them rather worn, from the collections of the Greifswald and British Museums. In some of them the ventral free border of Cd is rather more insignificant than in the type-specimen. The numerous loose Cdd occurring may be distinguished from the Cdd of *S. plana* which are found in the same localities by the cirrus-sockets being larger and fewer; moreover the Cd is not so flattened.

Occurrence: Upper Cretaceous (upper senonian, zone of *Belemnitella mucronata*), Rügen, N. Germany. Type specimen in the Greifswald Museum.

7) **Semiometra rowei** nov. sp. (figg. 245—247).

Dimensions: Cd + radial ring h: 2·7 mm. Cd h: 1·0 mm. radially, 1·5 mm interradially, br: 5·0 mm. Radial ring diameter: 4·0 mm. Diameter of radial cavity: 0·5 mm.

Cd a flattened hemisphere, concave ventrally, irregularly pentagonal in dorsal view, with about XL cirri in 2–3 whorls. A small stellate impression in the dorsal centre; diameter of this 1·2 mm. Very large areas of the ventral face of Cd bare, as the RR are sunken in the radial median lines very considerably. About 2 swellings in each radius running towards the peripheral margin of Cd.

BB hidden. Radial facets, as usual, very concave, reaching the border of Cd at the interradial corners only. Nerve-lumen large, though somewhat smaller than the indistinctly bounded ligament pit. Muscular fossæ narrow, somewhat larger than the interarticular ligament fossæ. The radial face is rather narrow ventrally of the transverse ridge. Radial cavity very small, its diameter about $^1/_8$ of the br. of the radial ring.

The new species seems to be rather closely related to *S. courvillensis,* but differs from this species by the Cd and radial ring being of about equal h., by the radial cavity being considerably smaller, and by the ventral part of the radial faces being more narrow.

I have dedicated this species to Dr. A. Rowe of Margate.

Occurrence: Upper Cretaceous (lower turonian, zone of *Rhynchonella cuvieri*), Branscombe, S. Devon, England. Type specimen in the collections of Dr. A. Rowe.

8) **Semiometra scanica** nov. sp. (figg. 248—250).

Dimensions: Cd + radial ring h: 4 mm. Cd h: 1·5 mm, br: 5·5 mm. RR h: 2·5 mm. Radial ring br: 4·5 mm.

Cd sharply flattened, when viewed from the dorsal side pentagonal, with the angles interradially. In the dorsal centre 5 radial, shallow pits. Cirri about LX, small, in ± 4 close, alternating whorls.

BB hidden. No free dorsal parts of RR. Radial faces sloping inconspicuously inwards, somewhat sunken in the median radial lines. The Cd thus in the radial median lines shows about 0·6 mm of its ventral face. The dorsal ligament fossa rather narrow with a large and broad dorsal pit. Interarticular ligament fossæ triangular, somewhat smaller than the muscular fossæ. Muscular fossæ partly separated by a deep radial notch. Radial cavity rather large, pronouncedly pentagonal, diameter 3 mm., slowly sloping inwards towards the central depression, the diameter of which is 0·5 mm.

Occurrence: Upper Cretaceous (senonian), S. Sweden. The type specimen in the Riksmuseum, Stockholm, from Köpinge, Scania.

B. **Hertha** HAGENOW.

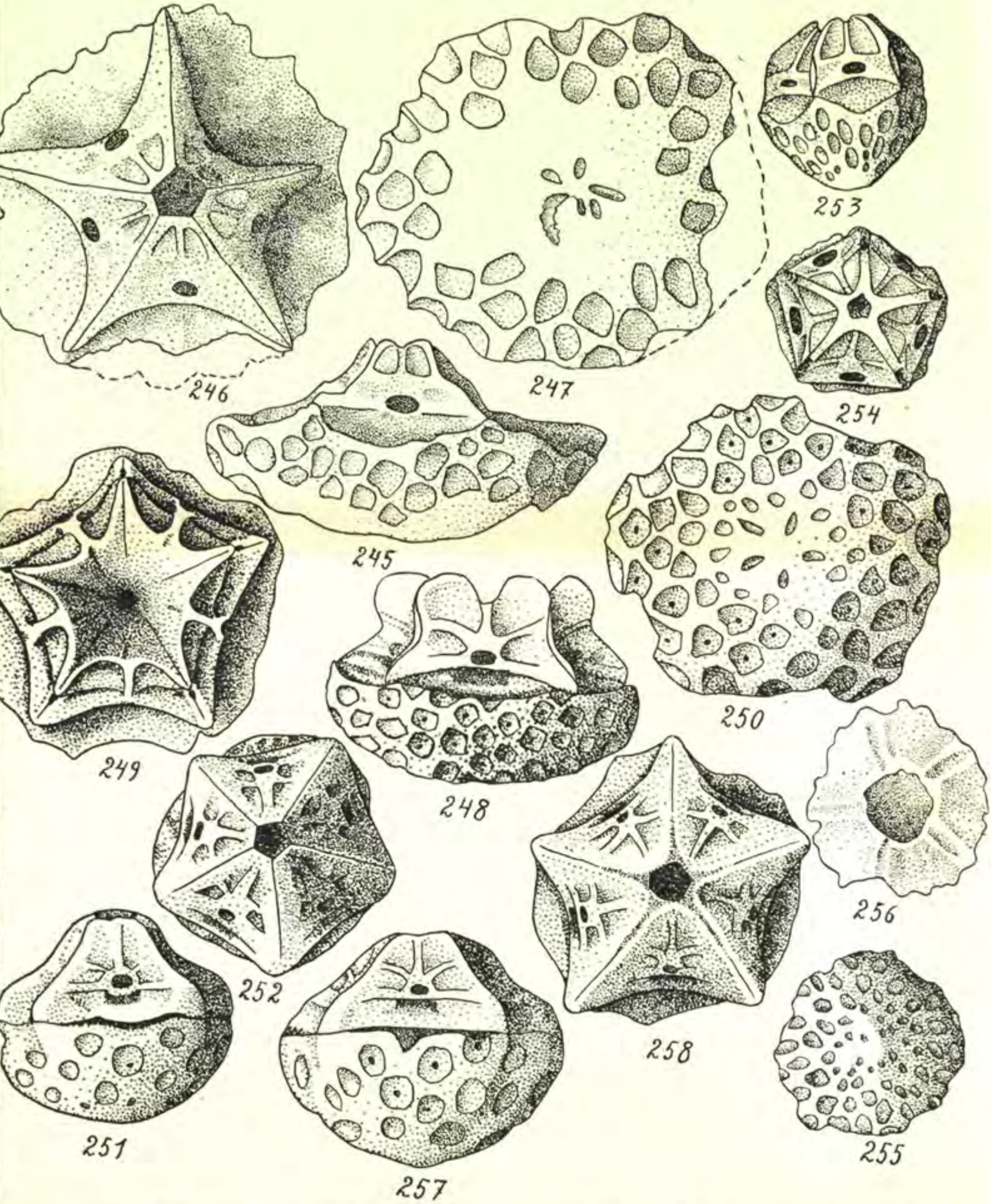
Cd hemispherical, without a dorsal star. Cirrus-sockets tolerably large, in alternating whorls. No radial pits. BB hidden. No free dorsal part of the RR. Radial faces sometimes inconsiderably sunken in the radial median lines, high, sloping sharply inwards. Muscular fossæ rather high. Radial cavity very small. Diameter of it $^1/_6$—$^1/_{10}$ of the br. of the radial ring. Type *H. mystica.*

Geological appearance: Upper Cretaceous—Tertiary (miocene). The following 5 species belong here: *cava* BRÜNNICH-NIELSEN 1913, *mystica* HAGENOW 1840, *pygmea* nov. sp., *suecica* nov. sp., *taurinensis* NOËLLI 1900.

Survey of the species:

A. Cd about as high as, or higher than, the radial ring.
  1. Very small species, the br. of Cd not exceeding 2 mm. Cirri numerous *pygmea.*
  2. A large species, br. of Cd 4—5 mm. Cirri ± XL *suecica.*

B. Cd lower than the radial ring.
  1. Radial facets sloping evenly inwards. Muscular fossæ rather broad. Cirri ± L *cava.*
  2. Radial facets somewhat bent at an angle between the interarticular ligament and the muscular fossæ. Muscular fossæ rather narrow. Cirri ± XXXV.



Figg. 245—258. 245—247) *Semiometra rowei.* 245) Cd + radial ring, lateral view, 246) Do., ventral view, 247) Cd, one margin somewhat broken, dorsal view, $^{10}/_{1}$; 248—250) *Semiometra scanica.* 248) Cd + radial ring, lateral view, 249) Do., ventral view, 250) Cd, dorsal view, $^{8}/_{1}$; 251—252) *Hertha mystica* Cd + radial ring in lateral and ventral view, $^{8}/_{1}$; 253—256) *Hertha pygmea.* 253—254) Cd + radial ring in lateral and ventral view, $^{20}/_{1}$; 255—256) A Cd in dorsal and ventral view, $^{16}/_{1}$; 257—258) *Hertha suecica* Cd + radial ring in lateral and ventral view, $^{8}/_{1}$.

a. Diameter of Cd 4·1 mm. Cd dorsally rounded *mystica*.
b. Diameter of Cd 2·4 mm. Cd with a shallow pit in the dorsal centre *taurinensis*.

1) **Hertha cava** (Brünnich-Nielsen) 1913.

Antedon cava 1913 Brünnich-Nielsen, pp. 16, 24—25, 99, 100, 104, Tab. 11, figg. 45—49, Tab. 12, figg. 1—35.

Axillar segments of this species are also known, having a synarthry proximally and distal syzygial joints with a rather high number of septa. The cirrals are long and slender.

Occurrence: Upper Cretaceous (danian), Denmark.

2) **Hertha mystica** Hagenow 1840 (figg. 251—252).

Hertha mystica 1840 Hagenow, p. 665, Taf. 9, fig. 8; 1841 J. Müller, p. 139; 1852 Quenstedt, p. 601 (2. Aufl. 1867, p. 717, 3. Aufl. 1885, p. 915); 1857 Pictet, p. 289, Pl. 99, fig. 3; 1868 Devalque, p. 380 (2e Ed. 1880, p. 429); 1870 Schlüter, p. 957; 1874 Lundgren, p. 63; 1876 Quenstedt, p. 184, Tab. 96, fig. 101; 1878 Schlüter, pp. 38—39, 46; 1879 P. H. Carpenter, pp. 8, 9; 1880 b P. H. Carpenter, p. 553; 1881 b P. H. Carpenter, pp. 199, 213.

Alecto mystica 1846 Geinitz, p. 545.

Comatula mystica 1848 Bronn, p. 321.

Antedon mysticus(-a) 1878 Schlüter, p. 42; 1880 b P. H. Carpenter, p. 554; 1881 b P. H. Carpenter, p. 213; 1894 de Loriol, p. 484; 1895 Deeke, p. 71.

With the kind assistance of Stadtrat Hahne of Stettin, I have had an opportunity of studying the type-specimen of Hagenow.

Dimensions: Cd + RR ring, h: 3·8 mm. Diameter of Cd: 4·2 mm., h: 1·7 mm. Radial ring, h: 2·1 mm., br: 4·1 mm. Radial cavity, diameter: 0·5 mm.

Cd a low hemisphere, somewhat worn dorsally; thus the small dorsal cirri are nearly effaced. The ventral cirrus-sockets are large and deep with a very indistinct transverse crest. No dorsal star. Cirri XXX +, in 2—3 alternating whorls.

No BB visible. The free dorsal part of RR = 0, radial face somewhat sunken in the median radial lines, protruding at the interradial corners. Dorsally of the dorsal ligament a distinct sub-radial furrow. The dorsal ligament pit broad and flattened, only slightly broader than the rather large nerve-lumen. Radial face sloping rather sharply inwards, somewhat concave. Muscular fossæ twice as high and somewhat narrower than the interarticular fossæ. Radial cavity very small, $^1/_8$—$^1/_9$ of the diameter of the radial ring.

Occurrence: Upper Cretaceous (senonian), N. Germany, Belgium.

3) **Hertha pygmea** nov. sp. (figg. 253—256).

Dimensions: In the largest Cd the diameter is 1·8 mm., h: 1·0 mm., diameter of the Cd-cavity: 0·6 mm. In the smallest Cdd the diameter is 0·7 and 0·8 mm., h: 0·5 mm., diameter of the Cd-cavity: 0·4 mm. The type specimen described below has h. of Cd + radial ring: 1·3 mm., diameter: 1·2 mm., h. of Cd: 0·65 mm. Diameter of the radial cavity 0·2 mm.

Cd sub-conical, the ventral border indistinctly pentagonal and serrated by the encroaching cirrus-sockets. Cirrus-sockets small, in 3—4 alternating close whorls, XLV—LV, without any sculpture. Cd-cavity large and deep, the opening bordered by a lip. Basal furrows rather distinct, but narrow; no radial pits.

BB not protruding between Cd and the radial ring. No free dorsal part of RR. Radial faces insignificantly sunken in the radial median lines; rather strongly concave, so that the interradial ridges project distinctly. Dorsal ligament fossa large, as is also the nerve-lumen. Muscular fossæ larger than the interarticular fossæ. Radial cavity $^1/_6$—$^1/_7$ of the diameter of the radial ring.

This species is easily distinguished from the other species of the genus by its small size, by its numerous cirri, and by its sub-conical Cd.

Occurrence: Upper Cretaceous (upper senonian, zone of *Belemnitella mucronata*), Rügen, N. Germany. The type specimen in the British Museum. I have seen numerous (± 55) Cdd, both in the collections of the Greifswald and British Museum, and 4 specimens with the radial ring preserved.

4) **Hertha suecica** nov. sp. (figg. 257, 258).

Dimensions: Cd + radial ring, h: 4·3 mm. Diameter of Cd: 5·1 mm., h: 2·2 mm. Radial ring h: 2·1 mm., diameter: 4·7 mm. Radial cavity, diameter: 0·7 mm.

Cd hemispherical, pentagonal when viewed dorsally. No dorsal star. Cirrus-sockets rather large, in 2—3 alternating whorls, ± XL. There is no sculpture of the cirrus-facets.

No BB visible. No free dorsal part of RR. Deep sub-radial furrows. Dorsal ligament pit considerably larger than the nerve-lumen. Muscular fossæ sloping evenly inwards, not as high and narrow as in *H. mystica*, though larger than the interarticular fossæ. Radial cavity about $^1/_7$ of the br. of the radial ring.

In another specimen the dimensions are as follows: Cd + radial ring h: 3·7 mm.; diameter of Cd: 4·8 mm., h: 2·1 mm. H. of the radial ring: 1·6 mm.

A separate Cd measures 4·7 mm. in diameter. The opening of the Cd-cavity decagonal, measuring 1·2 mm. There are no radial pits. Basal fossæ narrow.

The specimens are somewhat worn.

Occurrence: Upper Cretaceous (danian), S. Sweden. The specimens described above originate from Annetorp, near Malmö, Scania. The type specimen is in the Riksmuseum, Stockholm.

5) **Hertha taurinensis** (Noëlli) 1900.

Antedon taurinensis 1900 Noëlli, pp. 20, 38, Tav. 1, figg. 58—60; 1905 Bellini, p. 641.

Occurrence: Tertiary (miocene), N. Italy.

C. **Discometra** nov. gen.

Cd thickly discoidal, usually somewhat deepened and without cirri dorsally. No dorsal star. Cd-cavity large with a rounded opening. Cirrus-sockets small, closely set in alternating whorls, without sculpture. BB not at all or indistinctly protruding. The free dorsal part of RR = or approximates to 0. Radial face rather low, h ≤ br. Muscular fossæ relatively small. Radial cavity $^3/_4$—$^1/_5$ of the diameter of the radial ring.

I am not quite sure that this genus is of exactly uniform character. The species I have referred to it are known in a couple of cases by rather worn specimens only. The survey of the species therefore is only provisional. The Cd-cavity is only known in a couple of cases, and therefore it is possible that some solitary species on a closer examination may turn out to be of Oligophreate origin. Nevertheless, the species included here show so many characteristics in common that I think it reasonable to unite them at least temporarily. Type *D. rhodanica.*

Geological appearance: Tertiary (miocene). The following 6 species seem to belong here: *eggenburgensis* Schaffer 1912 (syn. *excavata* Schaffer 1912), *meneghiniana* Fontannes 1879, *michelotti* Noëlli 1900, *oblita* Michelotti 1861, *rhodanica* Fontannes 1877, *speciosa* Pomel 1887.

Grouping of the species:

A. Radial cavity ≥ $^1/_2$ of the diameter of the radial ring.
   1. Radial face = the h. of Cd *oblita.*
   2. Radial face nearly twice as high as Cd *speciosa.*

B. Radial cavity about $^1/_3$ of the diameter of the radial ring.
   1. The central depression at the bottom of the radial cavity as large as the opening *meneghiniana.*

2. The bottom of the radial cavity scarcely half the diameter of the opening *eggenburgensis, rhodanica.*

C. Radial cavity only $^1/_5$ of the br. of the radial ring *michelotti.*

1) **Discometra eggenburgensis** (Schaffer) 1912.

Antedon rhodanicus part. 1904 Schütze, p. 159 ff.
Antedon eggenburgensis 1912 Schaffer, p. 185, Taf. 58, figg. 14—16.
Antedon excavatus 1912 Schaffer, p. 186, Taf. 58, figg. 9—13, 17—19.

I cannot detect any difference between the two species described by Schaffer except the different size. A somewhat more flattened Cd in this group always seems to go with increasing age. This species is surely very closely related to if not identical with *rhodanicus*.

Occurrence: Tertiary (miocene), Austria.

2) **Discometra meneghiniana** (Fontannes) 1879.

Antedon meneghinianus 1879 a Fontannes, p. 479; 1879 b Fontannes, pp. 412, 415—416, Pl. 2, fig. 11; 1897 de Loriol, p. 127; 1897 Nicolas, pp. 130—131.

This species seems to be rather closely related to *D. oblita,* as described by Noëlli. The radial cavity in *D. oblita* has, however, a larger, and gradual, inward slope of the radial cavity.

Occurrence: Tertiary (miocene), France.

3) **Discometra michelotti** (Noëlli) 1900.

Antedon michelotti 1900 Noëlli, pp. 20, 34, Tav. 1, figg. 47—49; 1905 Bellini, p. 641.

Occurrence: Tertiary (miocene), N. Italy.

4) **Discometra oblita** (Michelotti) 1861.

Allionia oblita 1861 Michelotti, p. 353, Pl. 10, fig. 1; 1878 Meneghini, p. XXXI; 1879 a Fontannes, pp. 498—499; 1879 b Fontannes, pp. 415—416; 1897 de Loriol, p. 125; 1897 Nicolas, p. 131; 1898 Nicolas, p. 410; 1900 Noëlli, p. 33.

Antedon oblitus(-a) 1879 a Fontannes, p. 500; 1879 b Fontannes, p. 416; 1897 de Loriol, p. 123; 1900 Noëlli, pp. 20, 31, Tav. 1, figg. 39—46; 1904 Airaghi, p. 46; 1905 Bellini, p. 641.

Occurrence: Tertiary (miocene), N. Italy.

5) **Discometra rhodanica** (FONTANNES) 1877.

Eugeniacrinus (?) *rhodanicus* 1877 FONTANNES, p. 669; 1897 NICOLAS, p. 130. *Antedon rhodanicus(-a)* 1879 a FONTANNES, pp. 499—500; 1879 b FONTANNES, pp. 410, 415—416, figg. 1—3, Pl. 2, fig. 10; 1884 P. H. CARPENTER, p. 144; 1888 P. H. CARPENTER, p. 40; 1897 DE LORIOL, pp. 115, 121, 123, Pl. 4, figg. 8—10; 1897 NICOLAS, pp. 104, 131—132; 1897 PELLAT, pp. 112, 114; 1898 NICOLAS, pp. 398, 403, 408, fig. 1; 1899 LAMBERT, p. 123; 1900 NOËLLI, pp. 32—34; 1904 AIRAGHI, pp. 44—45, figg. 14—15; 1904 SCHÜTZE, p. 156, Taf. 2, figg. 4—5; 1908 ENGEL, p. 520; 1912 SCHAFFER, p. 185; 1915 VADÁSZ, pp. 11, 12, 164, 171, Taf. 1, figg. 24—26.

Occurrence: Tertiary (miocene), S. Germany, W. France, N. Italy, Hungary.

6) **Discometra speciosa** (POMEL) 1887.

Antedon speciosus 1887 POMEL, p. 337, D. Pl. 3, figg. 1—4(—? 10); 1897 DE LORIOL, p. 123; 1915 VADÁSZ, p. 12; ? 1920 FOURTAU, p. 94.

POMEL figured an axillary with a synarthry proximally, which possibly belongs to this species. It seems to be very doubtful if FOURTAU's specimen really belongs here. He only saw "un pièce basale" (= Cd?).

This species seems to me to be well distinguished from *rhodanica* by the large opening of the radial cavity and by the proportional height of the radial face.

Occurrence: Tertiary (miocene, sahelian, vindobonian), Algiers, ? Sinai.

D. **Palaeantedon** nov. gen.

Cd hemispherical, no impression dorsally and no large area devoid of cirri, sometimes with a small dorsal cone. Never any dorsal star or radial pits. Cd-cavity large, the opening sometimes slightly lobate. Cirrus-sockets closely set, in alternating whorls, small, without sculpture or with an areola only. BB strongly reduced, not protruding at the interradial corners (exception *danica?*). The free dorsal part of RR inconspicuously visible (broader at the corners). Radial face usually high (exceptions *depressa, lineata, pannonica*); the muscular fossæ rather large to very broad and high. The diameter of the radial cavity $^1/_3$—$^1/_4$ of the diameter of the radial ring. Type *P. soluta*.

Geological appearance: Upper Cretaceous—Quaternary. I have included the following 10 species here: *ambigua* POMEL 1887, *cartenniensis* POMEL 1887, ? *danica* BRÜNNICH-NIELSEN 1913, *depressa* nov. sp., *globosa* POMEL 1887, *lineata* POMEL 1887, *minima* NOËLLI 1900, *pannonica* VADÁSZ 1915, *rosacea* POMEL 1887, *soluta* POMEL 1887.

Survey of the species:

I. Cirrus-sockets rather large, but ± 3 in each radius, i. e. in total XV—XX	*danica.*
II. Cirrus-sockets smaller, at least XXX.	
A. Cd with a small point dorsally	*minima.*
B. Cd dorsally rounded.	
1. Radial ring $^1/_2$ as high as Cd.	
a. Radial face h = $^1/_2$ br.	*depressa.*
b. Radial face h = br.	
α. Cirri about XXX	*soluta.*
β. Cirri about XL	*cartenniensis.*
2. Radial ring and Cd of equal height.	
a. Radial face h = $^1/_2$ br.	
α. Cirri ± XXX	*lineata.*
β. Cirri ± L	*pannonica.*
b. Radial face h = br.	*rosacea.*
3. Cd $^1/_2$ as high as the radial ring	*globosa.*

1) **Palaeantedon ambigua** (POMEL) 1887.

Antedon ambiguus 1887 POMEL, pp. 337, 344, D. Pl. 2, fig. 15.

Occurrence: Tertiary (miocene, cartennian = burdigalian), Algiers.

2) **Palaeantedon cartenniensis** (POMEL) 1887.

Antedon cartenniensis 1887 POMEL, pp. 333, 335, 337, D. Pl. 2, figg. 10—12.

Antedon carten(n)ensis 1897 DE LORIOL, p. 125; 1898 NICOLAS, p. 410.

Occurrence: Tertiary (miocene, cartennian), Algiers.

3) **Palaeantedon danica** (BRÜNNICH-NIELSEN) 1913.

Antedon danica 1913 BRÜNNICH-NIELSEN, pp. 24—25, 99—100, 106, Tab. 11, figg. 1—44.

As has already been pointed out, the differing Cd on Pl. 10 is thought by me to represent another species, *Glenotremites parvicavus.*

The arms seem to have been X. I Br 1 and 2 were united by synarthry. The syzygial faces had numerous well-marked septa, especially peripherally. A segment is figured with 2 pinnule-sockets. BB were perhaps inconspicuously visible at the interradial corners.

This species may perhaps be derived from *Sphaerometra,* but can scarcely be referred to this genus because of the lack of any dorsal star and radial pits.

Occurrence: Upper Cretaceous (danian), Denmark.

4) **Palaeantedon depressa** nov. sp.

Antedon taurinensis 1915 VADÁSZ, pp. 11, 164, 171, Taf. 1, figg. 1—6.

The *taurinensis* of VADÁSZ is something quite different from NOËLLI's species. Distinguishing marks for this new species are: great size of the Cd-cavity; pentagonal, low and depressed Cd, lacking cirrus-sockets in the dorsal centre; XL cirri; broad radial face with low muscular fossæ, their size about = the interarticular fossæ; radial cavity = $^1/_3$ of the br. of the radial ring.

This species resembles the *Discometra*-species rather closely because of its low and broad radial faces, as do also *P. lineata* and *pannonica*.

Occurrence: Tertiary (miocene), Hungary.

5) **Palaeantedon globosa** (POMEL) 1887.

Antedon globosus 1887 POMEL, pp. 334, 337, D. Pl. 2, figg. 13—14; 1897 DE LORIOL, p. 126; 1915 VADÁSZ, p. 9.

Occurrence: Tertiary (miocene, cartennian), Algiers.

6) **Palaeantedon lineata** (POMEL) 1887.

Antedon lineatus 1887 POMEL, pp. 335, 337, 338, D. Pl. 2, figg. 16—18; 1897 DE LORIOL, p. 125; 1898 NICOLAS, p. 410.

Occurrence: Tertiary (upper miocene, sahelian), Algiers.

7) **Palaeantedon minima** (NOËLLI) 1900.

Antedon minimus 1900 NOËLLI, pp. 20, 39, Tav. 1, figg. 61—63.

Occurrence: Tertiary (miocene), N. Italy.

8) **Palaeantedon pannonica** (VADÁSZ) 1915.

Antedon pannonicus 1915 VADÁSZ, pp. 10, 11, 171, Pl. 1, figg. 10—13.
? *Antedon allardi* 1915 VADÁSZ, pp. 10, 11, 171, Pl. 1, figg. 14—17.

It is quite possible that the *allardi* of VADÁSZ represents a distinct species which in that case is closely related to *P. pannonica*. Under any circumstances it is quite different from the *allardi* of DE LORIOL, which has a rather small opening of the Cd-cavity and larger cirrus-sockets in (indistinct) rows.

Occurrence: Tertiary (miocene), Hungary.

9) **Palaeantedon rosacea** (Pomel) 1887.

Antedon rosaceus? 1887 Pomel, pp. 336, 337, D. Pl. 2, figg. 19—21.

Possibly this species is identical with *Antedon mediterranea;* this, however, cannot be settled before seeing the original specimen. The drawing differs rather considerably as to the appearance of the radial faces.

This species resembles *P. lineata* very closely, but is distinguished by the somewhat higher radial faces.

Occurrence: Quaternary, Algiers.

10) **Palaeantedon soluta** (Pomel) 1887.

Antedon solutus 1887 Pomel, p. 336, D. Pl. 2, figg. 22—27; 1897 de Loriol, p. 127; 1898 Nicolas, p. 410.

Pomel, though with hesitation, has referred some axillaries of rather different shape to this species.

Occurrence: Tertiary (upper miocene, sahelian), Algiers.

IX. **Appendix.**

For the sake of completeness I include here the known *Thiolliericrinidae.* They seem to me to require revision, and are also rather closely treated in the chapter on The Phylogeny of the Comatulids.

Thiolliericrinidae Jækel 1918.

Stalked *Articulata* with a Cd which articulates with the stem by a synarthry. The lumen of the dorsal side of Cd is round and small. Cd-cavity small. Stem-joints coarse and clumsy, l. = $^1/_3$ — 2 × br, short, obliquely conical or hour-glass-shaped, united by synarthry or, rarely, trifascial articulation. The synarthrial transverse crest of the proximal face of a stem-joint forms an angle with that of the distal face. Cd with shallow cirrus-sockets, which are sometimes rudimentary or (?) lacking. BB small or hidden. Radial faces low and broad. Radial cavity large and shallow.

Besides the species of the genera *Thiolliericrinus* and *Burdigalocrinus* mentioned below, probably the two following species, known by stem-joints only, also belong here:

1) **Apiocrinites flexuosus** Goldfuss 1831.

Apiocrinites flexuosus 1831 Goldfuss, p. 186, Pl. 57, fig. 4; 1836 Bronn, p. 262; 1851 Quenstedt, p. 468; 1852 Quenstedt, p. 612, Tab. 53, fig. 17 (2. Aufl. 1867, p. 729, Tab. 67, fig. 17; 3. Aufl. 1885, p. 931, Tab. 73, figg. 26); 1858 Quenstedt, p. 721, Tab. 87, fig. 11.

Bourgueticrinus flexuosus 1848 Bronn, p. 173; 1858 d'Orbigny, p. 96, Pl. 17, figg. 13—15.

Thiollierierinus flexuosus 1859 Etallon, p. 445; 1862 Etallon, p. 222; 1908 Engel, p. 455; 1920 Musper, p. 15.

Apiocrinus flexuosus 1876 Quenstedt, p. 367, Pl. 104, figg. 57—58; 1879 de Loriol, p. 195.

This species, known as stem-joints from Württemberg only, is usually identified with French specimens from Valfin which are considerably better known. For various reasons this procedure seems to me somewhat unsuitable. The first and least important reason is that it is not fitting to group together stem-joints from one locality and similar stem-joints and a calyx from another. The second reason is that the German stem-joints originate from the white Jurassic ε or virgulian while the French ones are from sequanian. The third and last reason is that there is already known at Nattheim, Württemberg, the calyx of a species of *Thiolliericrinus (sigillatus)*. If the stem-joints mentioned above are to be referred to any species with a known calyx they should therefore most suitably be referred to *Th. sigillatus*.

Occurrence: Upper Jurassic (virgulian), S. Germany.

2) **Bourgueticrinus ooliticus** Mc Coy 1848.

Bourgueticrinus ooliticus 1848 Mc Coy, p. 405; 1879 de Loriol, p. 195; 1880 de Loriol, p. 11; 1889 de Loriol, p. 559.

Occurrence: Middle Jurassic (bathonian), England.

Geological appearance of the family: (Middle?—) upper Jurassic—lower Cretaceous.

A. **Thiolliericrinus** Etallon 1859.

Thiolliericrinids whose cirrus-sockets are large and stout with a more or less distinct transverse crest. Cirri arranged in rows or in a (close) single whorl. Type *Th. favieri*.

Geological appearance: Upper Jurassic—lower Cretaceous.

The following 4 species belong here: *arzierensis* de Loriol 1889; *favieri* de Loriol 1879; *ribeiroi* de Loriol 1880; *sigillatus* Quenstedt 1876.

Survey of the species:

A. Cirri in a single whorl.
  1. Cirrus-sockets reach from the dorsal to the ventral border of the flattened Cd. Transverse crests weak.
    a. Cirri about X, close together *favieri.*
    b. Cirri fewer, cirrus-sockets not contiguous laterally *arzierensis.*
  2. Cirrus-sockets do not reach from the dorsal to the ventral border of the high and cup-shaped Cd. Stout transverse crests *ribeiroi.*
B. Cirri in a double whorl and X rows *sigillatus.*

1) **Thiolliericrinus arzierensis** de Loriol 1889.

Antedon valdensis (part.) 1879 de Loriol, p. 267, Pl. 20, fig. 20.
Thiolliericrinus arzierensis 1889 de Loriol, p. 560.

Occurrence: Lower Cretaceous (valanginian), Switzerland.

2) **Thiolliericrinus favieri** (de Loriol) 1879.

Thiolliericrinus flexuosus 1859 Etallon, p. 445; 1860 Etallon, p. 188; 1862 b Etallon, p. 222; 1867 Ogérien, p. 621; 1879 de Loriol, p. 194, Pl. 18, figg. 8—10; 1880 a de Loriol, pp. 12—13; 1889 de Loriol, p. 553, Pl. 229, figg. 2—8; 1890 de Loriol, pp. 166, 168; ?1897 Roman, pp. 88, 331, 334; ?1900 Bather, p. 195, fig. 117: 1; ?1912 Kirk, p. 75, Pl. 7, figg. 4—5.

Humberticrinus Favieri Etallon M. S.; 1879 de Loriol, p. 195; 1889 de Loriol, p. 556.

Under the name of *Thiolliericrinus flexuosus* at least 3 species seem to have been brought together. First the stem-joints described by Goldfuss (cf. above). Secondly the species here treated, which Etallon, at least to begin with, thought to be identical with the first-mentioned one. Thirdly a species which Remeš described under the name mentioned above, but which must be ranged under *Burdigalocrinus.*

Roman's species, which is of younger geological age than the typical *favieri,* possibly does not belong here. The form that is figured by Bather (the figure reproduced by Kirk) is perhaps another species.

Occurrence: Upper Jurassic (sequanian—?tithonian), France.

3) **Thiolliericrinus ribeiroi** de Loriol 1880.

Thiolliericrinus Ribeiroi 1880 a de Loriol, pp. 11, 14, Pl. 1, figg. 3—11; 1881 (P. H. Carpenter) Nature, Vol. 23, p. 377; 1889 de Loriol, p. 558, Pl. 229, fig. 9; 1890 de Loriol, pp. 165, 168, Pl. 29, figg. 16, 18—22; 1900 Bather, p. 195, fig. 117: 2.

Thiolliericrinus choffati 1889 de Loriol, p. 556 (err. typ.).

Occurrence: Upper Jurassic (lusitanian = sequanian), Portugal.

4) **Thiolliericrinus sigillatus** (Quenstedt) 1876.

Solanocrinites costatus (part.) 1831 Goldfuss, p. 166 part., Tab. 51, figg. 2 a and b; 1862 b Etallon, p. 222.

Solonœrium costatus part. 1862 a Etallon, p. 341.

Comatula sigillata 1876 Quenstedt, p. 176, Tab. 96, figg. 49—50; 1878 Schlüter, p. 37; 1879 de Loriol, p. 267.

Solanocrinus sigillatus 1878 Schlüter, p. 37.

Antedon sigillata 1881 b P. H. Carpenter, pp. 201—202, 209.

Thiolliericrinus sigillatus 1889 de Loriol, p. 558; 1908 Engel, p. 455.

Occurrence: Upper Jurassic (virgulian), Württemberg.

B. **Burdigalocrinus** Jækel 1918.

Thiolliericrinids whose cirrus-sockets are small and insignificant when compared with the size of Cd (sometimes lacking when the species is mature?). Cirri appear in a single whorl towards the ventral margin of Cd or in several, alternating whorls.

This genus, created by Jækel in 1918, seems to me to be well grounded. de Loriol, when he got specimens with small and indistinct cirrus-sockets, always thought that this was caused by the fossil being worn and rolled by the waves. It might then be questioned why the waves did not also wear off the borders of the Cd and the radial faces, which are often well preserved in the same specimens. In the genus *Solanocrinus* we sometimes have worn specimens (cf. e. g. the type specimen of *S. d'orbignyi*). As in such specimens we ought also in *Burdigalocrinus* to have a remnant of the transverse crest in worn specimens; or, where the crest is weakly developed, a rather large, diffuse facet ought to remain (cf. e. g. *Th. favieri*). In *Burdigalocrinus*, on the contrary, we find small, rather well bounded cirrus-sockets, sometimes more or less indistinctly visible. Though these forms were probably forms from shallow water, "Rifftypus", I do not think that one can ascribe the lack or small size of the cirrus-sockets to fretting alone. Possibly the age of the individual plays a certain rôle. We might hint at the upper-Jurassic genus *Loriolocrinus*, created by Jækel, which, at least often, seems to lack cirri completely, and which reminds one rather strongly of the Cretaceous *Bourgueticrinus*. We have here, probably, a series tending towards the loss of cirri. The small cirrus-sockets in *Burdigalocrinus* under such circumstances would then be analogous to those in certain recent Comasterids. Type *B. lorioli*.

Geological appearance: Upper Jurassic—lower Cretaceous. I have referred the following 5 species to this genus: *algarbiensis* de Loriol 1888, *crassus* nov. sp., *heberti* de Loriol 1868, *lorioli* Jækel 1918, *remeši* nov. sp.

Survey of the species:

A. Cirri in several alternating whorls *lorioli.*
B. Cirrus-sockets in a single whorl, often 3 per radius and indistinct.
  1. Cd ventrally contracted under the radial ring *algarbiensis.*
  2. Cd not contracted ventrally.
    a. Cd rather high, the dorsal facet situated on a high transverse ridge *remeši.*
    b. Cd low, dorsal facet not especially projecting.
      α. The free dorsal part of RR broad. The radial cavity ± $^3/_4$ of the diameter of the radial ring *crassus.*
      β. Free dorsal part of RR narrow or 0. The radial cavity about $^1/_2$ of the diameter of the radial ring *heberti.*

1) **Burdigalocrinus algarbiensis** (DE LORIOL) 1888.

Thiollierierinus algarbiensis 1888 b DE LORIOL, pp. 111, 117, Pl. 22, figg. 10—11; 1889 DE LORIOL, p. 560; 1900 CHOFFAT, p. 185.

Occurrence: Lower Cretaceous (neocomian, hauterivian), Portugal.

2) **Burdigalocrinus crassus** nov. sp.

Apiocrinites flexuosus etc. part. 1861 HOHENEGGER, p. 21.
Thiollierierinus Heberti 1905 REMEŠ, p. 60, Taf. 7, figg. 2(—3?).

Besides its occurrence in a stage of different geological age, the species figured by REMEŠ differs from *B. heberti* by the free dorsal part of RR, which is strongly developed, and by the larger radial cavity. Fig. 3 perhaps belongs to another species, but the species is too worn to allow the distinction of close details.

Occurrence: Upper Jurassic (tithonian), Moravia, Czecko-Slovakia.

3) **Burdigalocrinus heberti** (DE LORIOL) 1868.

Eugeniacrinus Heberti 1868 b DE LORIOL, p. 281, Pl. 42, figg. 7—8; 1871 PILLET, p. 140; 1875 PILLET & FROMENTEL, p. 162, Pl. 10, figg. 31—35.

Thiollierierinus heberti 1888 b DE LORIOL, p. 111; 1889 DE LORIOL, p. 545, Pl. 228, figg. 1—11, 229, fig. 1; ? 1897 ROMAN, pp. 88, 331, 334; 1912 KIRK, p. 75, Pl. 7, fig. 3; 1913 JOUKOWSKY & FAURE, p. 386, Pl. 15, figg. 1—6; 1920 FAURE-MARGUERIT, p. 27.

ROMAN's statements about finding-places for this species are rather dubious. DE LORIOL's figures Pl. 228, figg. 5 (6), probably do not belong to this species.

Occurrence: Upper Jurassic (? sequanian—tithonian), France.

4) **Burdigalocrinus lorioli** Jækel 1918.

Thiolliericrinus Ribeiroi (part.) 1890 de Loriol, pp. 165, 168, 172, Tab. 29, fig. 17.

Burdigalocrinus lorioli 1918 Jækel, p. 71, fig. 64.

Occurrence: Upper Jurassic (lusitanian = sequanian), Portugal.

5) **Burdigalocrinus remeši** nov. sp.

Apiocrinites flexuosus etc. part. 1861 Hohenegger, p. 21.

Thiolliericrinus flexuosus 1905 Remeš, p. 61, Taf. 7, figg. 4—6 (?7—14).

This species, referred by Remeš to *Thiolliericrinus flexuosus,* differs from that species by the shape of Cd — high, rounded with a stout transverse ridge dorsally, where the dorsal synarthry is situated — and by the small, solitary cirrus-sockets. Also the form of the RR and the inward slope of the radial face is quite different.

Occurrence: Upper Jurassic (tithonian), Moravia, Czecko-Slovakia.

---

de Loriol once described a *Thiolliericrinus* devoid of cirri. This species Jækel in 1918 made the type of a new genus, *Loriolocrinus,* which he ranged under *Bourgueticrinidae.* In the 4th Chapter I have tried to show that his interpretation of the proximal is incorrect, and that this species is a real Thiolliericrinid, though in many respects approaching *Bourgueticrinidae.* Whether it should be ranged in a separate genus is still somewhat doubtful, for if, as de Loriol states (1890, p. 169), some specimens belonging to this species really have ventral rudimentary cirrus-sockets, the species may be referred to *Burdigalocrinus.* The type and only species of the genus is:

Loriolocrinus insuetus (de Loriol) 1890.

Thiolliericrinus insuetus 1890 de Loriol, pp. 167, ?169, Pl. 29, figg. 23—29.

Loriolocrinus insuetus 1918 Jækel, p. 72, fig. 65.

The species described on p. 169 seems possibly to have possessed a number of ventral rudimentary cirri. The BB here are not visible in external view.

Occurrence: Upper Jurassic (lusitanian = sequanian), Portugal.

X. Summary of the geological appearance of the Comatulids.

I give below a summary of the geological appearance of the Comatulids. The Comatulids that are incompletely known or not described at all, and to which I have not given any special generic names, are put in brackets, and so are the Thiolliericrinids.

The following Comatulids are known from **lower Jurassic**: *(Antedon angulati, caraboeufi), Glenotremites morieri* or 1 (3) Comatulids.

In **middle Jurassic** appear: *(Comatula polydactylus, Com. sp.* MOESCH, *Actinometra cheltonensis, Antedon prisca), Glenotremites abnormis, ladoixensis, mülleri, ranvillensis, Palaeocomaster calloviensis, latiradius, schlumbergeri stellatus, Solanocrinus ooliticus, (Bourgueticrinus ooliticus)*, or in all 9 (13) Comatulids.

In **upper Jurassic** appear: *(Comatula claudiana, matheyi, Comaturella wagneri, Antedon spp.* DOWNES, FURLANI, *Antedon complanata), Pachyantedon gracilis, imperialis, Pterocoma formosa, pennata, Glenotremites bronnii, desori, guirandi, lorioli, Palaeocomaster guirandi, wurtembergicus, Solanocrinus beaugrandi, beltremieuxi, bituricensis, burgundiacus, canaliculatus, changarnieri, choffati, costatus, decameros, delgadoi, depressus, gaioensis, greppini, gresslyi, herberti, jutieri, lamberti, d'orbignyi, peroni, tessoni, thiollieri, truncatus, Archaeometra aspera, bronnii, carpenteri, kopřivnicensis, scrobiculata (Apiocrinites flexuosus, Thiolliericrinus favieri, ribeiroi, sigillatus, Burdigalocrinus crassus, heberti, lorioli, remeši)* or in all 37 (43) Comatulids.

In **lower Cretaceous** are found: (*Comatula sp.* ETALLON), *Glenotremites exilis, rotundus, Palaeocomaster loveni, Solanocrinus almerai, campichei, gevreyi, gillieroni, hiselyi, humilis, infracretaceus, leenhardti, picteti, ricordeanus, vagnacensis, valdensis, Sphaerometra aequimarginata (Thiolliericrinus arzierensis, Burdigalocrinus algarbiensis)* or in all 16 (17) Comatulids.

In **upper Cretaceous** appear: *(Antedon spp.* STOLLEY, JAHN, HENNIG, *Eudiocrinus sp.* BRÜNNICH-NIELSEN, *Antedon granulata, stevensis), Pachyantedon beyrichi, Pterocoma pinnulata, Glenotremites angelini, arnaudi, batheri, concavus, essenensis, faxensis, janeti, laticirrus, lettensis, lundgreni, minutissimus, paradoxus, parvicavus, perforatus, pusillus, pyropa, rosaceus, schlueterianus, semiglobularis, striatus, sulcatus, tourtiae, valetti, Amphorometra brydonei, conoidea* (var. *laevior* and var. *granulata*), *Placometra mortenseni, Jaekelometra belgica, columnaris, Conometra rugiana, Loriolometra retzii, Sphaerometra carentonensis, incurva, semiglobosa, tetensi, Semiometra courvillensis, impressa, lenticularis, plana, pommerania, rowei, scanica, Hertha cava, mystica, pygmea, suecica, Palaeantedon danica.* Or in all 49 (55) species.

One species recorded from Cretaceous only: *Glenotremites rugosus.*

In **Tertiary (eocene)** occur: *(Antedon breviceps, pertusa) Glenotremites atacicus, conoideus, Conometra alticeps, Semiometra italica* or 4 (6) species.

In **Tertiary (miocene)** appear: *(Antedon admirabilis, avenionensis, glandiferus, miocenicus, pilularis, sphaeroidalis, Antedon spp.* CHAPMAN 1911, 1913), *Glenotremites allardi, anglesensis, depereti, fontannesi, hungaricus, hungaricus* var. *rotundatus, miocaenicus, nicolaisi, paronai, pellati, protomacronema, stellatus, Palaeocomaster formae, Cypelometra iheringi, Conometra hungarica, Hertha taurinensis, Discometra eggenburgensis, meneghiniana,* *michelotti, oblita, rhodanica, speciosa, Palaeantedon ambigua, cartenniensis, depressa, globosa, lineata, minima, pannonica, soluta.* In all therefore 30 (38) species.

In **Tertiary (pliocene)** are found: *Glenotremites brownii, ransomi* — 2 species.

From **Quaternary** we have *Palaeantedon rosacea* — 1 species.

If we look at the lists given above, it seems evident that the Comatulids flourished at 3 different times, and that in each of these periods different types dominated.

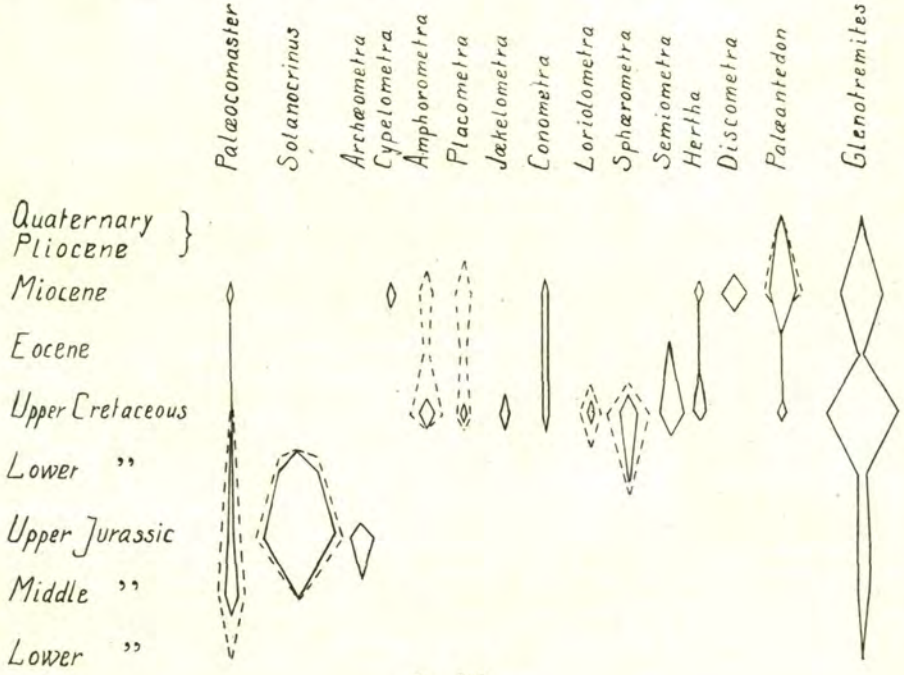


Fig. 259.

The first period falls in upper Jurassic, where we have an overwhelming predominance of Solanocrinids. Certainly, a rather considerable number of this family remain in lower Cretaceous (12 species of *Solanocrinus*) but of these 6 reach only to the oldest stage of neocomian and none occurs higher than aptian.

The next period in which the Comatulids flourished falls in upper Cretaceous. Here the *Conometridae, Notocrinidae, Semiometra*, and *Hertha* dominate. During the preceding period, with its massive and firmly built Solanocrinids, the connection between the Cd and the radial ring was very firm, just as in certain recent *Oligophreata*. The *Glenotremites* species from this period are therefore few in number. In upper Cretaceous, on the contrary, we get a very large number of species of which the

Cdd only are known. Most of these show affinities to the *Conometridae* or *Notocrinidae* which, like the recent *Thalassometridae* and *Notocrinus*, had an extremely loose connection between the Cd and the radial ring as well as between the RR mutually. The number of species where both Cd and the radial ring are known is therefore rather small here.

The third and last flourishing period for the Comatulids we get in miocene, the Palaeantedonidae being predominant. Here we get also an increase of the *Glenotremites* species, which however now, at least partly, represent other types than during upper Cretaceous.

Of course these three flourishing periods are partly only apparent. As the predominating number of discoveries refer to Europe and N. Africa they show the Crinoid fauna of these regions in the first place. The paucity of Crinoids in the upper part of lower Cretaceous is partly explained by the fact that smaller parts of Europe were submerged at that time. Nevertheless, in miocene also we find a similar condition, but at this time a rich Comatulid fauna prevails. It is, however, a noteworthy circumstance that certain types disappear so completely and that new forms appear in their place. The complete disappearance of the older types from such relatively large territories as those discussed makes a hypothesis of extinction or of strong transformation plausible. The appearance of new forms makes the question of their descent from preceding forms and immigration from other places important. In the Chapter on The Phylogeny of the Comatulids I have tried as far as is possible at present to clear up these questions.

I have made a diagrammatical sketch above (fig. 259) showing the frequency of different genera during different times. The groups of the genus *Glenotremites* which I suggest stand in a certain relation to the genera mentioned below are indicated by dotted lines. The *morieri* group is referred to *Palaeocomaster*, the *exilis* group to *Solanocrinus*, the *anglesensis* group to *Amphorometra*, the *pellati* group to *Placometra*, the *essenensis* group to *Loriolometra*, the *paradoxus* group to *Sphaerometra*, and the *ransomi* group to *Palaeantedon*.

CHAPTER IV.

Phylogeny of the Comatulids.

I. Introduction.

In the historical sketch leading up to the description of the fossil Comatulids, I gave a short account of KIRK's views on the question of the origin and development of the Comatulids. In the hypothetical line of evolution according to which this author imagined the development to have taken place (about corresponding to the series *Mesocrinus — Thiolliericrinus* — free Comatulid) the cirri first made their appearance after liberation (p. 74). Only through the acquisition of cirri did the first real Cd make its appearance. The author continues: "The extreme irregularity as regards the appearance of these cirri and their variable number point to the conclusion that they are not modified verticils of cirri originally borne by a nodal. In such forms, indeed, I think we have to look among stalked Crinoidea without verticils of cirri upon the column for the ancestors of the free types."

Let us see now how these assertions agree with the facts known. "The extreme irregularity as regards the appearance of the cirri" is a sentence, which, as far as the ontogeny of the Comatulids is concerned, is completely erroneous. In reality among all known cases[1] in young of recent Comatulids, the first 5 cirri appear in a single verticil. This verticil is always oriented radially, as e. g. in the Pentacrinids, or in other words, as in dicyclic forms. The Comatulid larvæ, where the first appearance of the cirri is known, are: *Comactinia meridionalis, Lamprometra sp., Tropiometra carinata, Crotalometra porrceta* (?), *Ptilometra mülleri* (which I have had the opportunity of controlling myself), *Antedon petasus, A. bifida, Compsometra serrata, Isometra vivipara, Heliometra eschrichti, Promachocrinus kerguelenensis* (1922 A. H. CLARK, Sp. 43), *Anthometra*

---

[1] W. B. CARPENTER informs us (1866) that the first 5 cirri in *A. bifida* appear interradially. MORTENSEN (1920 a, p. 77) has pointed out that this information is incorrect, besides which CARPENTER's fig. (Pl. 41, fig. 6) also shows a radial position of the cirri.

adriani, *Poliometra prolixa, Hathrometra tenella tenella* and *H. t.* var. *sarsii* (fig. 263), *Thaumatometra nutrix*. I can add to these from my own experience *Notocrinus virilis* (fig. 260, cf. also figg. 261, 277, 280). We are thus able to assert with certainty that the first ontogenetical appearance of the cirri is specially regular, and that a Cd with the first verticil of cirri reminds one very much of a nodal in a stalked Crinoid.

If we turn to the fossil species of the Comatulids, we meet, excepting *Comasteridae*, with the same amount of regularity in the oldest forms. The above-mentioned family forms, as I shall try to show later on, a special phylogenetical line, presumably much older than the *Solanocrinidae* and therefore compared with this family representing a phylogenetical advance in the structure of Cd. During the whole Jurassic and lower Cretaceous we meet, excluding the Comasterids, Cdd with cirri arranged in rows only. These rows are X originally, as is seen from the figures given below. If we examine the 5 species of *Glenotremites* belonging to the *exilis* group, the 35 species of *Solanocrinus* and the 5 species of *Archaeometra* we find the following: In middle and upper Jurassic we have 22 species with cirri in X rows (1 species in middle and 21 in upper Jurassic), and 10 species with cirri in XV to XX rows (1 in middle, 9 in upper Jurassic). In lower Cretaceous we have, on the contrary, only 3 species with cirri in X rows, but 10 species with cirri in XV to XX rows.

Not the least sign is found which would indicate that the cirri in the Jurassic Comatulids appeared first at a late ontogenetical stage.[1]

The connection between, on the one hand, a Cd having cirri, appearing with regularity both among the older fossil Comatulids and among the young of recent types and, on the other hand, the nodal cirrus-provided joint in stalked Crinoids will become evident later on.

The regularity of the appearance of cirri both during ontogeny and phylogeny seems to me to point towards the correctness of the theory that the cirri are not a new acquisition in the Comatulids, obtained in connection with their transition to an eleutherozoic manner of life. When in certain recent *Comasteridae* we have forms whose Cd forms a stellate plate devoid of cirri, we always find in the young well-developed cirri which are replaced, with increasing age of the animal, by rudimentary cirri finally disappearing altogether. The lack of cirri in *Comasteridae* is, therefore, nothing primary, but may be ascribed to a secondary condition. If, like KIRK, we were to imagine cirri appearing quite suddenly in irregular numbers among *Thiolliericrinus (= Burdigalocrinus) heberti,* this theory meets with several difficulties. First, it conflicts with the ontogenetic and phylogenetic facts emphasized above; secondly, it is contradicted by the fact that the development of the cirri in the

---

[1] Cf. 1912 KIRK, p. 74: »These cirri appearing first in the free-swimming stages perhaps are progressively found earlier and earlier in the ontogeny.»

Crinoids is, in all other cases, a gradually advancing process of specialization of the distal, rhizoidal appendages of the stem, which only in the final stages stretched as far as to the crown.

Before passing on to consider where among the stalked Crinoids one should look when seeking the ancestors of the Comatulids, I shall give a short description of the appearance of the cirri among the stalked Crinoids.

II. **The appearance of the cirri among the fossil Crinoids.**

I have mentioned above that the cirri developed from the distal rhizoidal appendages of the stem. A beautiful example of this is found in Bather's work of 1900 (p. 107, fig. 16: 1) where the stem and the primary cirri of a Silurian Crinoid are drawn. Here the cirri are still forked in the distal parts and not arranged on any specially marked nodals. In reality the rhizoidal type of stem-appendages is the ruling one during the greater part of the older palaeozoicum. The stem is, therefore, usually without appendages proximally and finished off distally by a bunch of rhizoids, more rarely attached by a lobate plate. This concerns *Camerata* (cf. e. g. 1897 Wachsmuth & Springer, Pl. 30 figg. 1—2, Pl. 64 fig. 1, Pl. 72 fig. 1, Pl. 82 fig. 1) as well as *Flexibilia* (cf. 1920 Springer, Pl. 4 figg. 22–23, Pl. 50 fig. 1, Pl. 56 fig. 3, Pl. 63 fig. 6) and the fistulate *Inadunata* (cf. e. g. 1831 Goldfuss *Cyathocrinites pinnatus*, Pl. 58 fig. 7; 1878 Angelin *Crotalocrinus*, Tab. 8 fig. 9; 1893 Bather *Gissocrinus*, Pl. 10 fig. 342; 1895 Jækel *Parisocrinus, Lophocrinus,* Tab. 4 fig. 2, Tab. 7 fig. 1).

In order to fix the stem in an upright position against foreign objects strong ribs or spinous processes, when necessary, perform the function of the cirri (1897 Wachsmuth & Springer, Pl. 22 fig. 3, Pl. 57 fig. 7, Pl. 59 figg. 1—2).

It is only with the increasing prefection of the cirri that they spread upwards towards the more proximal parts of the stem. (Among *Camerata*, cf. 1897 Wachsmuth & Springer, P. 1 fig. 2, Pl. 33 fig. 5, Pl. 45 fig. 4, among *Inadunata,* cf. e. g. 1854 Koninck et le Hon, *Woodocrinus,* Pl. 8 fig. 1, 1883 Meek & Worthen *(Poteriocrinus =) Woodocrinus, Scaphiocrinus*, Tab. 28 figg. 2—8, cf. also 1909 Bather, p. 249.)

The nerve canal to the cirrus always runs out through one segment, but the joint-face itself for the primitive cirrus may often be stretched out over several stem-joints (cf. further 1844 the Austins, Pl. 9 fig. 2 a, *(Poteriocrinus) Scytalocrinus;* 1876 Quenstedt, Tab. 108 figg. 40—41, *Poteriocrinus).*

It is only in extremely rare cases that the cirri spread up over the distal half of the stem, as among *Camerata* in *Camptocrinus* (1897

WACHSMUTH & SPRINGER, Pl. 75 figg. 1—2, Pl. 76 fig. 13) or *Cordylocrinus* (cf. 1861 HALL "*Platycrinus parvus*", Pl. 4 figg. 6—7), among the fistulate *Inadunata* in *Herpetocrinus* (1893 BATHER, Pl. 1 fig. 24 ff.). Among all these, however, there are none having a nodal with pentamerous verticils of cirri, but the cirri appear to a number of (1—)2, seldom 3—4, on every or every other joint and form longitudinal rows of supporting appendages on both sides of the stem.

In the lower Devonian Inadunate *Gastrocrinus* we find, on the contrary, completely typical nodals bearing pentamerous verticils of cirri (1895 JÆKEL, p. 81, fig. 25). Only in some solitary and special cases do we find verticils of 5 cirri among *Camerata,* cf. *Lenneocrinus* (1918 JÆKEL, fig. 25, lower Devonian), *Hapalocrinus retiarius* (BATHER 1900, p. 156, fig. 69, upper Silurian; referred by JÆKEL, under the name of *Clematocrinus* to his group *Costata* 1918, p. 91). *Flexibilia* have never developed nodals with pentamerous cirrus-whorls.

Among the Carboniferous Poteriocrinids, on the contrary, we find in numerous cases forms where the stem-joints are pentagonal and bear verticils of cirri up to the crown; either with 2—3 cirri in each verticil, as I found in *Scaphiocrinus unicus* (HALL), *Aesiocrinus magnificus* MILL. & GURL., and *Erisocrinus typus* MEEK & WORTHEN, or with regular pentamerous cirrus-whorls as in e. g. *Euphachycrinus* and *(Poteriocrinus =) Scaphiocrinus* (1875 MEEK & WORTHEN, Pl. 32 fig. 2, 1883 Pl. 29 fig. 15). Stems with joints bearing verticils with 5 cirri from the Australian Permo-Carboniferous have been drawn by ETHERIDGE 1892. We also find a similar case in the Permian genus *Palermocrinus* (JÆKEL 1918, p. 67).

Geheimerat JÆKEL has kindly entrusted to me, for description and figuring, 6 stem-fragments of the type-species, still undescribed, of the genus *Palermocrinus.* It is a mere tribute of gratitude when I dedicate the new species to him.

Palermocrinus jækeli nov. sp. (figg. 270—273).

Sp. 1. Dimensions: br. of nodal 18·5—19·0 mm., h: 4·2 mm.; br. of internodals 14·5—15·0 mm., h: 0·5—1·2 mm. Length of an internodium 8 mm., l. of 4 nodals and 3 internodia: 42 mm.

The nodals with some few indistinct tubercles, much larger and broader than the internodals, which are 15 to each internodium. The midmost of the internodals is largest, h. 1·2 mm.; on each side it is surrounded by 7 very low internodals. The midmost of these 7 ossicles is often likewise somewhat higher with 3 narrower segments on each side of it. The suture lines between the nodals are distinctly wavy. Nerve-lumen very large, diameter about 4 mm., surrounded by ± 100 radiating septa. The stem is somewhat abraded on one side; it is therefore impossible to say if it supported any cirrus-sockets; possibly, however, there was not more than one per nodal; on the other side there occur (2—)3 cirrus-sockets. The lumen of these sockets proceeds from the margin of the nodal. The facet stretches out over 3—4 internodals and a part of the nodal; diameter of it rather variable: 2·2—4·0 mm. The cirrus-sockets on a nodal are not situated at equal distances; between the 3 cirrus-sockets described above the distance is 5·5 and 8—10·5 mm. respectively. Nevertheless, the longitudinal rows seem to correspond. Three cirrals remain in a smaller cirrus-socket; the br. is 2·4 mm., the h. of each is 0·6 mm.

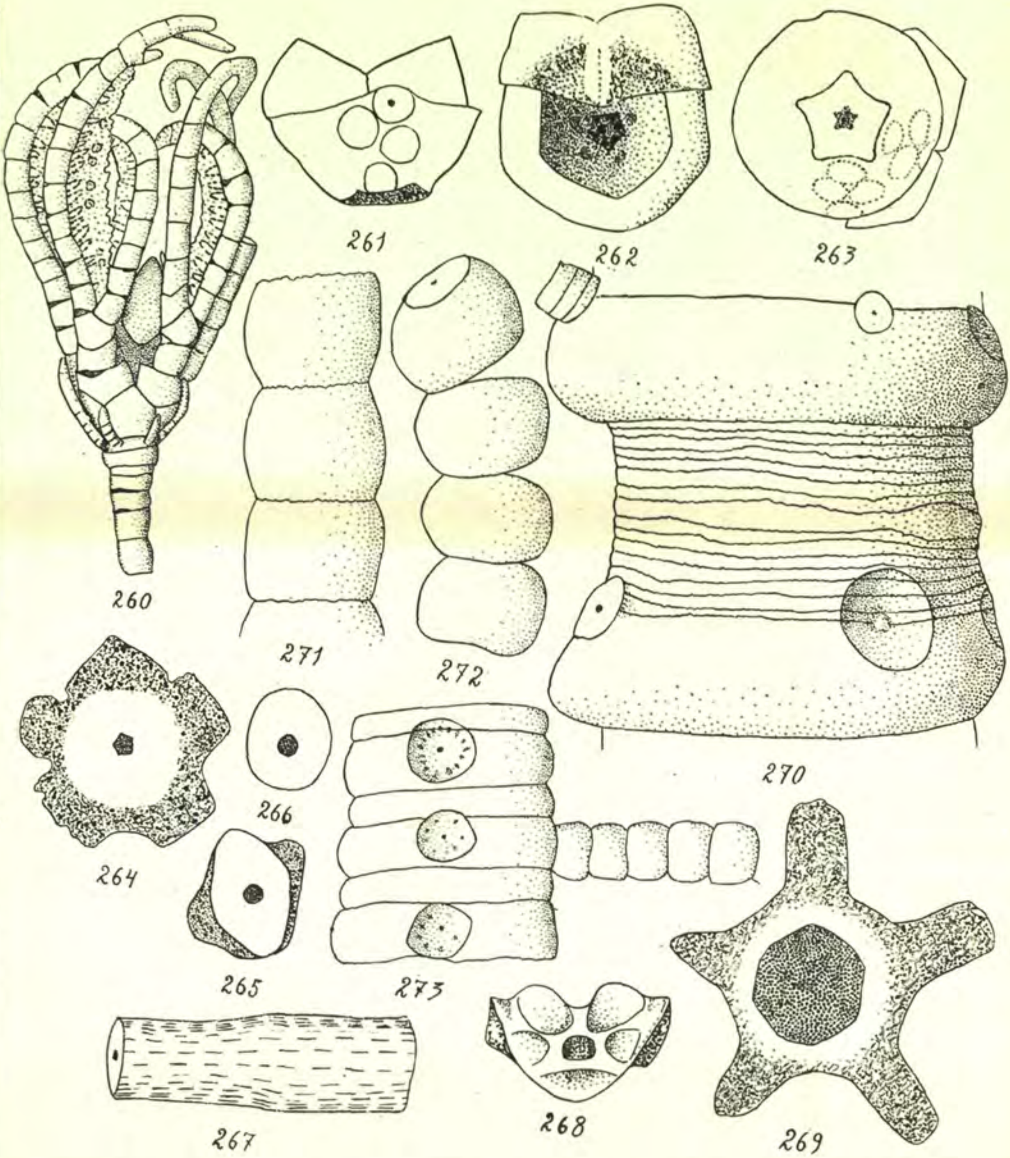
Sp. 2. There are 2 nodals and one internodium (l. 8 mm.) with 15 internodals. The surface of the nodals is ornamented with a low and fine calcareous reticulum and provided with 5 tubercles round the lateral border. The tubercles are situated at nearly equal distances. There are only 1—2 distinct cirrus-sockets per nodal. The nerve-lumen, as in Sp. 1, large.

Sp. 3. A loose nodal. There are 6—7 tubercles on the lateral border.

Sp. 4. Half embedded in matrix. Two(–three) nodals, br: 15 mm., h: 3·8 mm., and two internodia, l. of each of them 5 mm. only; br. of internodals: 10·5 mm. The number of internodals is also here 15. The nodals are tuberculated as in Sp. 2. No cirrus-sockets visible. In the same piece there occurs also a loose part of a cirrus: 14 segments, l: 46 mm., br. of each cirral 4·3 mm., h: 2·4—3·5 mm. Nerve-lumen of the stem large.

Sp. 5. Four nodals, weakly tuberculated, 4 internodia; br. of nodal 15·8 mm., of internodals 11 mm. L. of internodium only 4 mm.; there are about 7 internodals, the midmost of them is the largest. Cirrus-sockets restricted to the nodal, about 4 per nodal. Nerve-lumen small, diameter 1·3 mm. Septa of an internodal articular facet ± 60. In the same piece two cirrus fragments occur, one with 10 segments, total l. ± 34 mm. (l. of each cirral 3·2 mm., br: 4·3 mm.), another with 6 segments, total l. 27 mm. (l. of each cirral 4·0—4·6 mm., br. 5·6 mm.). The segments are globular.

Sp. 6. There are 37 segments in all, total length 58 mm. Every second segment thicker and stouter, a nodal, supporting 2—3 cirrus-sockets; br. of nodal 8·1 mm., h: 1·7 mm. Internodal, br: 7·7 mm., h: 1·0 mm. Cirrus-sockets, br: 1·5 mm. In proximal(?) parts the stem is somewhat thicker (diameter 9 mm.) and seems to lack cirri almost completely. In one case 9 cirrals are visible proceeding from a nodal (total l: 12·3 mm., br: 1·5 mm., l. of each cirral ± 1·2 mm.). The nerve-lumen is small, diameter 0·4 mm.



Figg. 260—273. 260) *Notocrinus virilis* Pentacrinula from the Swedish Antarctic Expedition 1901—1903, St. 5 (Graham Land, S. E. of the Seymour Island, 64° 20′ S., 56° 38′ W., 150 M., sand and gravel, $^{16}/_{1}$ 1902), viewed from the anal interradius, $^{10}/_{1}$; 261—268) *Hathrometra tenella* var. *sarsii*, 261) Cd + 2 BB in lateral view, 262) Do. ventral view, 263) Do. dorsal view, 264) The uppermost stem-joint, 265) The 4th stem-joint, articular facet, 266) The 5th stem-joint, do., 267) The 7th stem-joint, distal part to the left. 268) Distal articular facet of a radial. All these drawings from a Pentacrinula with about XX C. and an arm-length of about 8 mm., $^{60}/_{1}$. 269) *Metacrinus nobilis tenuis*, the 2nd very young stem-joint, $^{38}/_{1}$; 270—273) *Palermocrinus jækeli*, 270) Two nodals and an internodium of Sp. 1, the more distal part of the stem, as in fig. 273, is probably represented by the upper part of the drawing, 271) Some cirrus-joints from Sp. 4, 272) Do. from Sp. 5, 273) Some stem-joints from Sp. 6, $^{4}/_{1}$.

I considered at first that these 6 specimens represented 2 or 3 different species, but a closer examination has shown me that they in reality belong to the same species. Spp. 1–3 probably originate from the distal part of the stem of a full-grown specimen. The internodals are here of full size and definite in number. Sp. 1 is somewhat abraded. In Spp. 4 and 5 the length of the internodia is shorter, especially in the specimen last mentioned where also the internodals are fewer. Probably they belong to a more proximal part of the stem. Finally, Sp. 6 evidently represents a part of the stalk of a young, as the diameter of the stem and cirri is smaller and the internodals only one per internodium. It is open to doubt whether the large nerve-lumen in Spp. 1–4 is due to a secondary phenomenon.

It is evident from the description given above that each cirrus-whorl consists of not more than 4 cirrus-sockets which are rather irregularly situated.

The stems described and figured by ETHERIDGE (1892, pp. 116, 117, Pl. 17 fig. 5 and Pl. 18 fig. 4) seem to present certain, though rather weak, similarities (cf. also 1885 WAAGEN, Pl. 96 fig. 11).

Occurrence: Upper Permian, Palazzo Adriano, Sicily, Italy. The specimen kindly lent out from the Greifswald Museum by Geheimerat O. JÆKEL.

In the Triassic *Articulata* verticils of cirri become still more usual. The genera *Holocrinus, Isocrinus, Balanocrinus,* and *Pentacrinus* appear now, all of them furnished with cirri. (Cf. BATHER 1909, SCALIA 1910, SCHAFHÄUTL 1851.) It appears to be open to some doubt whether those species of *Encrinus* that are said to have verticils of cirri do not belong to some of the genera mentioned first. BRONN states in 1837 (pp. 32–33, Taf. 2, cf. also v. MEYER 1837) that *Encrinus (Chelocrinus) pentactinus* has verticils with 5 cirri. According to WAGNER (1892, p. 99) this is a case of a stem of *Holocrinus wagneri*. BRONN's figure cannot, however, represent any *Holocrinus*. BEYRICH states (1858, p. 5) that he has seen cirrus-bearing stems, "die vielleicht zum *Encrinus aculeatus* gehören". KOKEN's figure of *Entrochus rotiformis* (1900, Tab. 10 fig. 16) ought probably to be ranked with *Holocrinus* or *Balanocrinus*.

The genus *Holocrinus* is the oldest genus among those mentioned above in which cirri occur. The older of the two species belonging to this genus, *H. wagneri* (= *Encrinus gracilis* WAGNER 1887 a and b, cf. also BENECKE 1887) has only 2–3 cirri per nodal-joint, the younger, *H. beyrichi* (= *Encrinus B.,* PICARD 1883, Tab. 9 fig. 1, cf. also 1893 JÆKEL) has, on the contrary, pentamerous verticils of cirri.

The two Triassic types remaining, *Dadocrinus* and *Apiocrinus re-*

cubariensis[1], lack cirri (BATHER 1897, *Crema* 1896, GÜRICH 1887, v. KOENEN 1895, KUNISCH 1883, v. MEYER 1851).

Apiocrinidae and *Millericrinidae* are added with Jurassic, and from the first beginning they had non-cirriferous stems. The *Eudesicrinidae*, *Eugeniacrinidae*, and *Holopodidae*[2], appearing from the very oldest Jurassic are attached to the botton by a broad, undivided, basal surface and also lack cirri.

Among the Jurassic forms we have thus *Pentacrinidae* (Trias—recent) and *Thiollierierinidae* (upper Jurassic and lower Cretaceous) remaining, all of which possess cirri; in the latter group, however, they show a tendency towards disappearing in the younger forms (cf. Chap. 3 and below). But it is only the former family that has real nodals with pentamerous verticils of cirri; the latter has a Cd developed as in the Comatulids.

III. The appearance of cirri during the ontogeny of the Pentacrinids.

During the ontogeny of the Pentacrinids the verticils of cirri make their appearance on still longer joints and at still shorter intervals the younger the specimens are (1884 P. H. CARPENTER *Isocrinus decorus* Pl. 35, fig. 1, crown-length 15—18 mm.; 1909 c. A. H. CLARK *Isocrinus decorus* p. 88, fig. 3 (cf. footnote 1922 T. GISLÉN, p. 175), and 1918 H. L. CLARK, Pl. 3, figg. 2—3, crown-length 16 mm.; 1912 A. H. CLARK *Comastocrinus (Teliocrinus) liliaceus,* pp. 259, 263, fig. 55, crown-length 70 mm.; 1922 T. GISLÉN *Metacrinus interruptus,* sp. 15, p. 171 and sp. 16, p. 172, Pl. 2, figg. 13—14, crown-length 18 mm.).

Dr. MORTENSEN, who brought home from the Kei Islands (Taam) an extraordinary collection of extremely young *Metacrini* (the crowns are only 7 mm. long) has with his usual kindness placed at my disposal the following facts regarding the first appearance of the cirri. He writes that it seems to be perfectly certain that the most distal joints of the stem, in the specimens examined, bear no cirri at all. The stems in these specimens give the impression of lacking only a very few joints to the point of attachment. I give a table below showing the number of internodal joints and the number of cirri in the verticils, based on the

---

[1] JÆKEL (1918) has given this species the name of *Cremacrinus*, a name which, however, is anticipated (cf. e. g. 1913 ZITTEL-EASTMAN, p. 213). Instead of this name I propose that of **Recoarocrinus**.

[2] The Permian *Prophyllocrinidae* are denoted by WANNER (1916, p. 276) as »Vorläufer» to *Eugeniacrinidae*; *Palaeholopus* (p. 283) as a form leaving »Beweis für eine wirkliche Verwandschaft des regenten *Holopus* mit den *Flexibilia Impinnata*». SPRINGER (1923) in carefully chosen words agrees with him. Both these forms are Impinnate. JÆKEL suggests (1918) that we have here a case of convergent developement.

information given by Dr. MORTENSEN. In this table the 1st internodium is taken as being the internodium appearing between the most proximal cirrus-bearing nodal-joint and the 2nd nodal. In the column for cirri (C) the number of cirri in the verticils is given. I = the number of internodals; D.S = distal segments without cirri.

	C	I	C	I	C	I	C	I	C	I	C	D. S.
Sp 1	5	8	5	6	5	6	4	3	3	1	2	5
2			5	8	5	5	3	2	3	1	1	9
3			5	7	5	4	2	3	3	1	1	7
4			5	6	4	4	2	3	3	1	1	8 (?9)

It is seen from this not only that the number of internodal joints decreases in tiny young, but also, and this is of importance, firstly that a number of the most distal segments lack cirri, secondly that the pentamerous symmetry of the cirrus-whorl is not yet attained in the younger stages, which thus in this case stands at the same level as the case I described above in palaeozoic Crinoids (cf. also *Holocrinus wagneri*). The cirri are, in all the specimens described above, of the usual type, and therefore not rhizoidal. In *Metacrinus interruptus* Sp. 16 (GISLÉN 1922) I have found in the two most distal nodal joints the same defective verticils of cirri (only 3 cirri on every nodal-joint). One may compare also 1884 P. H. CARPENTER's figure of the young *Isocrinus decorus* (Pl. 35, fig. 1). In certain Pentacrinids this peculiarity is evidently retained even among full-grown specimens (*(Pentacrinus) Diplocrinus alternicirrus* 1884 P. H. CARPENTER, certain *Balanocrini* 1917 F. A. BATHER). Among the Comatulids we find an analogous case in the development of the 1st (radial) verticil of cirri on Cd, as the 5 cirri do not appear simultaneously but successively, so that the cirrus in the right posterior radius is often developed last (cf. MORTENSEN 1920 a, p. 77).

IV. The predecessors of the Comatulids.

If we look at the stalked forms from Trias - Jurassic which have verticils of cirri — and it is among these one ought to search for the forerunner of the Comatulids — they are not so very abundant. Cirri were found in Trias. among *Encrinidae* possibly in certain *Encrini,* among *Holocrinidae* in *Holocrinus,* among *Pentacrinidae* in *Balanocrinus, Hypalocrinus, Isocrinus,* and *Pentacrinus* (from Rhætic). In Jurassic none of these remain excepting *Pentacrinidae,* within which family also the genus *Pentacrinus* becomes more abundantly represented all the way from lias. During the previous Carboniferous and Permian ages there remained, according to the results of the investigations of WANNER and others, a large amount of the palæozoic fauna, although often in modified and aberrant forms (e. g. *Embryocrinidae*). From these ages we find forms with real verticils of cirri in e. g. *Scaphiocrinidae, Eupachycrinidae, Graphiocrinidae,* and *Palermocrinus.*

We will first study the appearance of the nodal-joints and cirrus-sockets in the Jurassic *Pentacrinidae,* where they are known particularly well. We find here two things which are deserving of careful attention. Firstly, the cirrus faces of the nodal-joints are always provided with a strong transverse crest, precisely the same condition as we have found before in *Solanocrinidae.* (This appearance of the cirrus-face we find likewise in *Isocrinus* — also in the Triassic *Isocrini,* cf. BATHER 1909 — and in *Balanocrinus* and *Pentacrinus.* The cirrus faces of the Triassic *Holocrinus wagneri* have a similar appearance; cf. 1887 a. WAGNER, p. 14 and Tab. 1, fig. 7). Secondly, the stem shows the same conditions regarding the articulations as we find among the recent *Pentacrinidae,* i. e. all the joint-faces, with one exception only, bear a sharply cut petaloid figure, and the joints are connected by loose suture (cf. 1884—89 DE LORIOL, e. g. Pl. 148, fig. 3 b; Pl. 178, fig. 2 b; Pl. 192, figg. 8 b, 12 b; Pl. 201, figg. 2 b and c). The exception mentioned above consists of the articulation between a nodal and an infranodal which is of synostotic character, sometimes approaching anchylosis. We find here, therefore, smooth or almost smooth joint-faces (Cf. DE LORIOL, op. cit. Pl. 148, fig. 5 a; Pl. 178, fig. 5 c; Pl. 180, fig. 5; Pl. 183, fig. 7 c; Pl. 192, figg. 4 a, 10 b). It seems to approach anchylosis in certain *Balanocrini* (Pl. 185, fig. 5 a; Pl. 193, fig. 24 a; Pl. 195, fig. 1 a; Pl. 196, fig. 2 b; Pl. 197, figg. 3 c, 4 b). Usually a number of internodal joints are intercalated between the nodal joints. In this case there is great power of flexibility in the stem. According to observations made on living specimens the stem may be flexed to such an extent that the head may become hanging (1895 NUTTING, p. 75, quoted by H. L. CLARK 1918). In the species belonging to *Pentacrinus* we get a reduced number of internodals in the proximal parts of the stem — they may in certain cases even be lacking. In the case last mentioned we thus have a stem in which the proximal part consists of nodals only. Here the connection between the stem-joints becomes considerably closer and the capacity for motion more inconsiderable. Regarding the question of the degree of closeness, the articulation is a compromise between the infranodal and the supranodal connection (cf. DE LORIOL op. cit., Pl. 206, e. g. figg. 2 b, 8 a, 12 b).

One may imagine that the fusion of the nodal-joints may have been prepared for in this way. If the nodal-joints are high, the cirrus-socket has sufficient room to retain its original place in the radial median line of the joint (DE LORIOL op. cit. Pl. 200, fig. 1 a). If, on the contrary, the nodal-joints are shortened, the cirrus-sockets in successive nodals come into contact with, and press against, each other. In such a case we get a displacement of the row of cirri, now to the right, now to the left of the radial median line, which in extreme cases may lead to the appearance of not V but X rows of cirri on the stem (cf. 1884—1889 DE LORIOL, Pl. 212, figg. 2 a and c; 1897 POMPECKJ, Tab. 30, fig. 12 and description; 1876 QUENSTEDT, Pl. 101, fig. 16). If one imagines a fusion of, let us say, 4 nodal joints of the type described above, where the nodal joints are only a little more shortened, one would get a perfectly typical Cd of a Solanocrinid.

It is obvious now that among the forms depicted above, the genus *Pentacrinus* especially supplies the illustrations showing the course of evolution sketched above, although it scarcely contains the real transition forms. This becomes clear to us if, for a moment, we compare the appearance of the *Pentacrinus*-form with the stalked young Comatulid. The most distal part of the stem in the latter consists of a fixation plate, similar to that in e. g. *Encrinidae,* then follow a number of non-cirrate joints, and immediately after these a cirrus-bearing Cd. The hypothetical ancestor of the Comatulids must thus, with the development of the 1st verticil of cirri, have ceased to form individualized nodal joints for the successive verticils of cirri, or expressed more correctly, all the nodal joints must have coalesced. The observations of Dr. MORTENSEN's young of the genus *Metacrinus* described above offer very great interest in this connection. These show, firstly that the most distal part of the stem lacks cirri — exactly as in the young Comatulid — secondly that the nodal joints which from the very beginning bear cirri of the usual type, at this stage are very much nearer each other than in full-grown specimens. These young, therefore, approach the type which I have depicted above as the hypothetical primitive form of the Comatulids. The difference, however, among other things, is that these young, like all the other Pentacrinids, develop a large number of individualized nodal joints, while the Jurassic Comatulids, on the contrary, only get a few verticils of cirri proceeding from a unit Cd. The genus *Pentacrinus* in this character goes still a step nearer towards the Comatulid type, as the distal internodia are very long, with as many as 80 or even more internodal joints; the proximal ones are extremely short consisting of 1—2 joints only, and may even be lacking altogether (cf. DE LORIOL, op. cit. and 1897 POMPECKJ, 1876 QUENSTEDT, 1918 SPRINGER).

V. Thiolliericrinidae and their descendants.

It has generally been considered that the transition form sought, between the stalked type with individual nodals and the free Comatulid having a Cd, ought to be found among the *Thiolliericrinidae.* I must confess that at the beginning I shared this conception. It cannot be denied either that forms like *Thiolliericrinus sigillatus* stand very near to *Solanocrinidae*. Nevertheless, it has become still clearer to me that one is more nearly right in looking upon the *Thiolliericrinidae* as a type derived together with *Solanocrinidae* from a common ancestor, but which quickly started on a special course of evolution. It has been emphasized before, that *Thiolliericrinidae* are distinguished by the strong synarthry between Cd and the stem. Such a connection is never found among the Comatulids in this articulation.

W. B. CARPENTER in his work (1866, Pl. 41 fig. 6) has drawn the dorsal side of a Cd in the Pentacrinula of *Antedon bifida*. The mark after the uppermost stem-joint here, as in the Pentacrinids, is pentagonal with the angles situated interradially. I have drawn the dorsal side of the Cd of a young stalked *Hathrometra tenella* var. *sarsii*. Here too we have a pentagonal mark after the stem, where the corners are situated interradially (fig. 263). The perforated impression for prolongations of the 5-chambered organ, descending in the stem, is likewise pentagonal and the corners are directed interradially. The uppermost stem-joints are also pentalobate, reminding one very strongly of the young stem-joints of the Pentacrinids (cf. figg. 264, 269). We do not get a more rounded transverse section until we reach the 5th stem-joint (figg. 265, 266). A distinct synarthrial articulation between the stem-joints, now very long (fig. 267), appears first at about the 10th joint — evidently for the purpose of giving this part of the stem, which in a given length has few joints only, increased power of flexibility.

If we look at the fossil forms among the Comatulids, we do not find in them either any indication that the articulation between the Cd and the uppermost stem-joint has been synarthrial. Distinct marks after an articulation with the stem are hardly to be found, but, on the other hand, a dorsal star is often present, which always seems to be oriented radially. It seems possible that the radial dorsal coelomic canals may have passed through it. This dorsal star occurs in most of the *Notocrinidae*. A large indistinct stellate impression seems to be found too, even if rather rarely, in a number of *Comasteridae (Glenotremites abnormis* and *mülleri, Palaeocomaster latiradius* and *stellatus)*, in some *Solanocrinidae* (as *ooliticus* and *beltremieuxi*), and in *Notocrinidae (Glenotremites batheri)*. As the cavity of the Cd is particularly tiny in most of these forms and any impressions for the radial coelom-canals are lacking on the ventral side of the Cd, the stellate impression being, on the other hand, very large and taking up the greater part of the Cd's cirrus-free dorsal side, there can hardly be any question here of scars after coelomic pores. One ought probably instead to interpret it as the remains of a petaloid articulation face towards the stem. As in the Pentacrinids these marks are almost without exception directed interradially (only in *Glenotremites abnormis* and *mülleri* they seem to be radially situated, as in *Balanocrinus*).

Among recent forms we do not find any indication of a dorsal star among nearly full-grown individuals, excepting in one single case — in the genus *Notocrinus,* as MORTENSEN (1918, p. 2) has mentioned. I have had the pleasure of borrowing Dr. MORTENSEN's specimen and give a figure of the Cd's dorsal side here (fig. 196). Elucidated by reflected light, 5 pores placed radially are lighter — they were the places for the passage of the prolongation of the 5-chambered organ. Besides this a number of smaller pits are found which collectively form an indistinct pentagon, with the corners oriented interradially (cf. above Cd of the young of Comatulids). I have found, moreover, a similar pentagonal, but not perforative, impression in a very young specimen of *Asterometra anthus* (fig. 277, length of arms 15 mm., C : XX, orals 0, P_2 small. All pinnules developed).

After stating all these facts it seems to me fairly probable that the Comatulids descended from forms having a pentagonal stem which had no synarthrial articulations in its proximal part.

I will now return to *Thiollierierinidae.* The strongly pronounced synarthrial articulation which we find here between the Cd and the uppermost stem-joint and between the stem-joints themselves, is not a usual type of stem-connection. It occurs further only among *Bourgueticrinidae, Bathycrinidae, Phrynocrinidae,* between the long stem-joints in the young of Comatulids and Pentacrinids, as well as in a somewhat similar form evidently developed convergently among *Platycrinidae.* This type of articulation is often connected with long joints, when a smaller number of articulations must be able to carry out movements sufficiently great to correspond to the total amount of flexibility of all the articulations between shorter joints which are more closely connected and where each connection can only accomplish insignificant flexions. Stem-connections where the synarthrial type of articulations seems to be presupposed by very long juvenile joints, are met with in the young of Comatulids and Pentacrinids — here therefore, most probably, it is of a coenogenetic nature. The stem-joints in *Thiollierierinidae* are, on the contrary, relatively short (l. often $\leq$ br.). The power of flexibility in the stem has therefore been very great here.

The cirrus-sockets in *Thiollierierinidae*, although owing to the size and transverse crest similar to those among *Solanocrinidae*, are much shallower and more weakly marked. Along the ventral edge of the Cd small pits appear which evidently derive from the attachments for rudimentary cirri, like those one meets with among the recent *Comasteridae.* It has been emphasized that the obliteration of the cirrus-sockets either in part or entirely might indicate that the Cd has been rolled by the waves. This may well have been the case sometimes. The dorsal synarthrial articulation towards the stem is never, however, obliterated, scarcely even worn, which shows both that the rolling must have been rather moderate, and also that this connection was much deeper and stronger than the cirrus-facets. The genus *Burdigalocrinus,* which taken as a whole is younger than *Thiollierierinus,* shows small or weak cirrus-sockets only, or even no sculpture at all on the sides of Cd. These forms are more strongly and stoutly built and of pronounced "Rifftypus" as JÆKEL calls it. They were certainly shallow-water forms, and this also explains, at least partly, the reason for the great power of flexibility found in the stem (cf. above).

It seems to me that we have here a series showing a strong tendency towards the loss of the cirri. The non-cirriferous type developed in this way approaches *Bourgueticrinus,* a genus from upper Cretaceous, characterized by the occurrence of a non-cirriferous proximal, provided dorsally with a synarthry.[1] We have thus on the one side the genus *Thiollierierinus* with representatives having distinct cirrus-sockets, geological occurrence (middle? —) upper Jurassic—lower Cretaceous, and on the other side the genus *Bourgueticrinus* (upper Cretaceous) with a non-cirriferous proximal; and both these types are connected through the intermediate genus *Burdigalocrinus* (*Loriolocrinus* included), which has a Cd with more or less indistinct cirrus-sockets[2]

---

[1] JÆKEL has distinguished one of these non-cirriferous forms (*Th. insuetus* DE LORIOL 1890, from lusitanian = sequanian) as a particular genus *Loriolocrinus* (1918). This genus, which I consider can scarcely be separated from *Burdigalocrinus,* he went so far as to include in the family *Bourgueticrinidae* with the information that the proximal consists of the coalesced BB. This interpretation, however, seems to me lacking in probality. The proximal in *Bourgueticrinidae* disappears as a specially marked ossicle first in the very uppermost Cretaceous and among eocene forms. Among younger forms we often find an ossicle similar to a proximal, but formed by the coalesced BB. We never, however, find that the coalesced BB have any synarthrial connection with the stem. One might, on the other hand, imagine that the proximal in *Loriolocrinus* was formed both by the original proximal and the coalesced basal ring. Nevertheless, it seems to me that DE LORIOL's point of view is presumably the most correct, as in one specimen he found small pits after rudimentary cirri close under the radial ring. The BB did not appear here at the corners. It seems possible to me, however, that the cirrus-bearing specimens ought properly to be referred to *Burdigalocrinus lorioli.* In such a case *Loriolocrinus* stands so near to this species that there can be no doubt on the question of the similarity of structure found in their Cdd.

[2] In 1896 CREMA described, under the name of *Apiocrinus recubariensis,* an interesting form from the middle Trias of Italy. BATHER (1897) referred this species to the genus *Millericrinus,* and JÆKEL (1918) created a special genus *Cremacrinus* for this form (as was pointed out above, p. 201, this generic name is anticipated). The author last mentioned considers, possibly rightly, that this form is a connecting link between *Dadocrinus* and *Millericrinidae.* A. H. CLARK considered in 1912 (p. 277) that this form might approach certain *Bathycrinus*-forms which he described in ZITTEL-EASTMAN's Textbook in 1913 under the name of *Monachocrinus.* Hence the statement that Bourgueticrinids appear in the Muschelkalk is derived from this.

or even none at all. The genus *Bourgueticrinus* mentioned above, which stands nearest to the Thiolliericrinids, has stoutly built, powerful reef-forms to show. Only in later forms do we get a more slender type, presumably in connection with the transference to deeper and calmer water. It seems to me that we may almost assume that the Thiolliericrinids stand near to the ancestral forms of the Bourgueticrinids. Such an explanation seems to me best to solve the problem as to how we get a large proximal in *Bourgueticrinus,* which would then be nothing else than a non-cirriferous Cd.

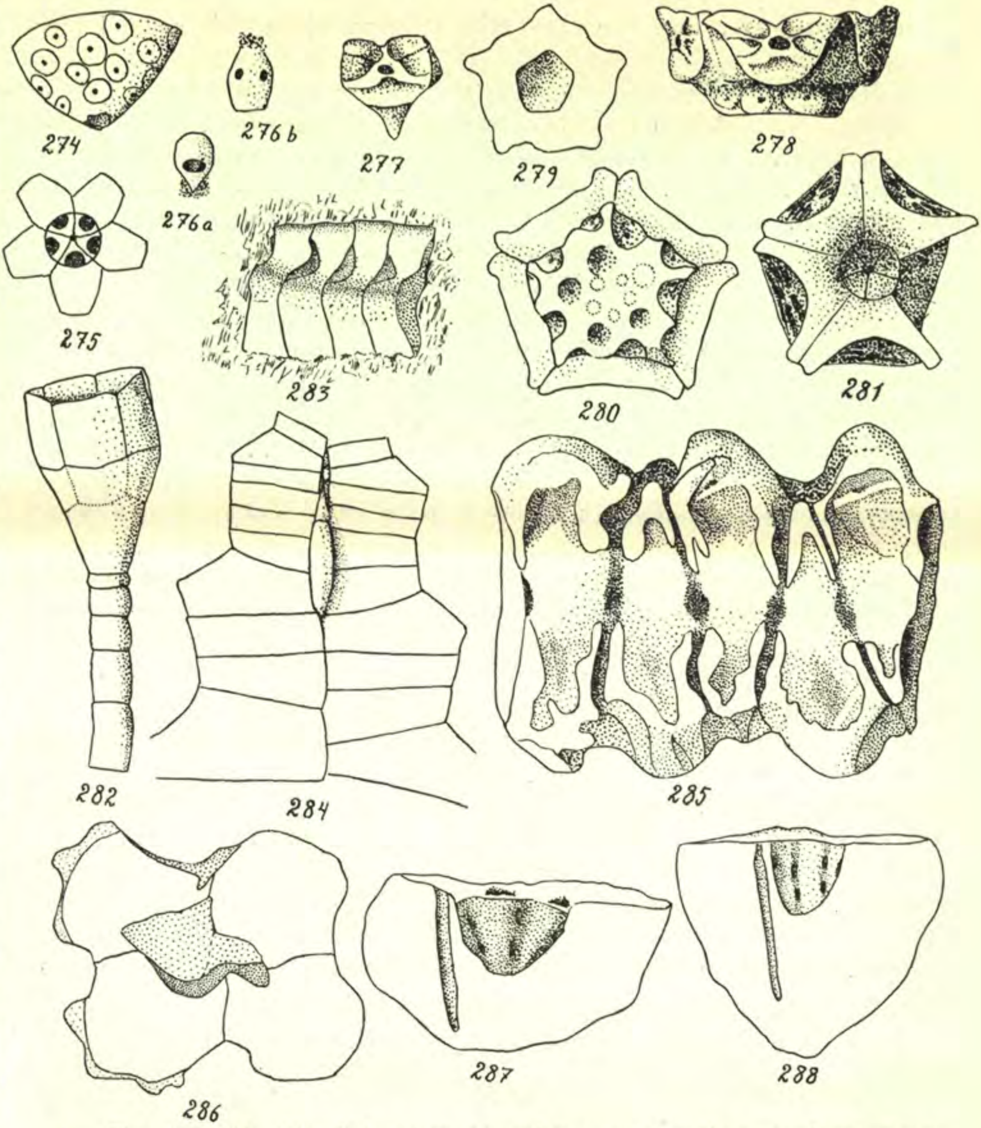
Perhaps someone will demur here that a couple of other form-series may be found which in the characteristics mentioned above offer an approach to the Bourgueticrinid-type, and which therefore might, with the same right, be looked upon as ancestral forms of the *Bourgueticrinidae.* Certain species of the families *Apiocrinidae* and *Millericrinidae,* in fact, show a development of an, if not always so well marked, still distinctly stronger uppermost stem-joint, which might foreshadow a proximal. I refer to e. g. *Apiocrinus elegans, meriani, roissyanus, magnificus* (1884 de Loriol Pll. 34, 35, 40, 41, 46–48) and also to *Millericrinus nodotianus, dilatatus, scalaris, goldfussi, charpyi, brevis, elatus* (de Loriol op. cit. Pll. 91–93, 100, 117, 119). We find a similiarty to the high BB of the fossil genus *Conocrinus* and the recent *Bythocrinus* and *Democrinus* in *Millericrinus fleuriausianus* (de Loriol Pl. 106). All these forms, however, lack every trace of prolonged stem-joints or synarthrial articulations between the joints mutually as well as between the proximal and the stem. These similarities I consider therefore ought most probably to be interpreted as convergent phenomena, which are found in greater number in form-groups the nearer these are related — a natural consequence of the fact that the greater the similarities offered by heredity — the more hereditary factors they possess in common — the more often similarly combined constellations will make their appearance[1].

In the genus *Bourgueticrinus* we have the synarthrial articulation between the proximal and the 1st stem-joint remaining in most cases (cf. 1900 Bather fig. 115, p. 193; 1913 Brünnich-Nielsen; 1876 Quenstedt Tab. 104, fig. 76). In *Mesocrinus* the proximal has been reduced in size and is connected with the uppermost stem-joint by a joint-face without any sculpture. The synarthrial articulations between the more

---

This statement slipped also into Zittel's Grundzüge (1915). The similarity between the Triassic form mentioned above and the Bourgueticrinids is certainly of a superficial nature only. A. H. Clark too (1915 b) has dropped the statement now, and states regarding *Monachocrinus:* »nur rezent bekannt».

[1] The relationship between *Bourgueticrinidae* and the two families mentioned above is most likely that during Trias, perhaps earlier, they issued from a common Articulate root.



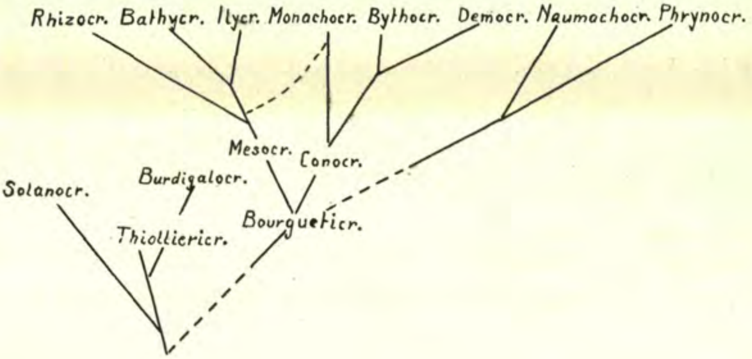
Figg. 274—288. 274—277) *Asterometra anthus*, a young specimen, arm-length 15 mm, C. ± XX, no orals, all the pinnules developed, P_2 small, 274) Cd lateral view, interradial spaces free from cirri, 275) The basals in dorsal view, 276) One basal a) from the dorsal side, the central end of the ossicle; b) from the ventral side, 277) Distal articular radial facet, $^{20}/_{1}$. 278—281) A Comasterid young. Arms about 20 mm, a pinnule-gap after P_1, 278) Cd + radial ring, lateral view, 279) Cd ventral view, N. B. no basal star, 280) Cd and radial ring, dorsal view, 281) Cd and radial ring, ventral view, one radial has dropped out, $^{20}/_{1}$. 282) *Rhizocrinus lofotensis* proximal portion of the stem, calyx with RR and Brr 1, $^{16}/_{1}$. 283—284) *Zeacrinus wortheni* 283) Some Brr from the proximal portion of the stem, ventral view, half embedded in matrix, $^{8}/_{1}$. 284) Right posterior interradius, $^{3}/_{1}$. 285) *Cromyocrinus ornatus* Brr 2—6, ventral view, $^{6}/_{1}$; 286) *Aesiocrinus (Graphiocrinus) magnificus* Grinding-section through the ventral sac, a pore-shaped slit is seen in the upper part of the drawing, $^{5}/_{1}$; 287) *Pterometra trichopoda* Section through a Cd, a radial pit to the left, $^{16}/_{1}$; 288) *Asterometra anthus* Section through a Cd, a radial pit to the left, $^{10}/_{1}$.

distal stem-joints, however, are still pronounced in this and all the younger forms.

Many species of the genus *Bourgueticrinus* acquire a greatly prolonged proximal which may take very different forms (cf. 1913 BRÜNNICH-NIELSEN). In the eocene *Conocrinus thorenti,* on the contrary (1846 D'ARCHIAC p. 200, Pl. 5 fig. 20 a, *Bourgueticrinus Th.;* 1850 Tome 2 D'ORBIGNY p. 332, *Conocrinus Th.*), we find a proximal like that in *Mesocrinus,* but the BB are extraordinarily prolonged and united by close sutures. That it is a question here of prolonged BB is evident from the description and from the figure which above the 5 prolonged ossicles shows 5 short RR alternating with the BB. On one of D'ARCHIAC's figures, the proximal has by mistake been drawn with 5 parts which cannot be right because these 5 ossicles would then represent IBB. One may, moreover, compare the description: "Tête . . . composée à la base d'une seule pièce arrondie sur la quelles s'articulent cinq pièces basales, longues, étroites, et surmontées de cinques pièces supérieures courtes, portant en dessus un nombre égal d'attachés brachiales . . ."

Among recent forms we get a usual stem-joint immediately dorsally of the basal ring, which is connected with this stem-joint by a more or less pronounced synostosis. The uppermost part of the stem consists in *Ilycrinus* and *Bathycrinus* of some 20 short discoidal joints; in *Monachocrinus* these are often fewer; and in *Bythocrinus, Democrinus,* and *Rhizocrinus* the joints already become longer than they are broad after the 1st or 2nd joint.

We never find, however, that the uppermost stem-joint is enlarged as among *Bourgueticrinidae (Bourgueticrinus, Mesocrinus, Conocrinus).* In *Ilycrinus, Bathycrinus, Rhizocrinus,* and some of the species belonging to *Monachocrinus* we really find a large ossicle between the radial ring and the uppermost stem-joint reminding one of the proximal in the *Bourgueticrinidae.* In this case three possibilities may be imagined: (1st) the BB are reduced as in the recent Comatulids, (2ndly) the ossicle is formed by the coalesced BB, the proximal has disappeared, (3rdly) the joint is formed by both the coalesced basal ring and the proximal. The first of these solutions was defended by many of the older scientists (cf. 1884 P. H. CARPENTER's history pp. 226 and 246 ff.). A calcareous plug in the centre between the RR was interpreted as "the rosette". CARPENTER showed, however, the similarity between this and the central plug in *Pentacrinidae.* The second interpretation is favoured by DANIELSSON's observation (1892, Pl. 1 fig. 2) that in the young of *Ilycrinus carpenteri* "the proximal" in its whole extension is divided into 5 not yet coalesced BB. The discovery of P. H. CARPENTER that *Bathycrinus aldrichianus* shows in section a division of the proximal into 5 different parts, corresponding to the 5 BB (1884, Pl. 76 fig. 2, p. 226) points in the same direction. One might imagine, in the third case, that the proximal had coalesced with the anchylosed basal ring. This, however, is contradicted by the fact, that in the cases where one finds sutures between the BB (*Bythocrinus, Democrinus, Monachocrinus,* and the two cases mentioned above) they run through the whole "proximal". Owing to this the uppermost stem-joint often also shows 5 slightly marked ridges on its proximal face which fitted in between the sutures of the BB (1884 P. H. Carpenter, Pl. X fig. 9). It is thus seen that in all cases where the BB are known in the family *Bathycrinidae*, it is these BB alone which form the "proximal". The only exception to this would, possibly, be formed by the genus *Rhizocrinus*. Here the anchylosed RR ring also forms a part of its large "proximal", where, however, the boundaries of the different radials are often distinct, even if they cannot be separated by boiling in KOH (cf. fig. 282). In this genus, moreover, we have no observations on the BB which however, probably form the dorsal half of the "proximal". In this genus one might imagine the possibility of a real old proximal having coalesced with the other two rings.



If the Bathycrinids are more or less direct descendants of *Bourgueticrinus* — and their appearance in other respects makes this very probable — they have then, presumably, lost a once well-marked proximal completely. The fam. *Phrynocrinidae* stands near the Bathycrinids and like this family lacks a specially set off proximal. *Phrynocrinus* is the least differentiated genus, having both its radial and basal rings of normal size. *Naumachocrinus,* on the contrary, has its dorsal cup prolonged as in certain Bathycrinids, but while in the Bathycrinids it was the BB which were prolonged, it is the RR here which have been lengthened. It is interesting to notice that *Phrynocrinus,* which of all the recent *Bathycrinidae* and *Phrynocrinidae* is the most primitive in type (the least modified basal and radial rings, high disk, cf. below) has also a short and coarse stem, similar to that of the *Bourgueticrinidae* and *Thiolliericrinidae*.

The family last mentioned had, as I mentioned above, forms approaching the Bourgueticrinids. The Thiolliericrinids, however, can scarcely be the direct ancestral forms of the Bourgueticrinids, for their BB are greatly reduced, while the genus *Bourgueticrinus* has 5 free, certainly rather low, but still laterally contiguous BB. The phyletic development of the forms discussed in this connection would therefore probably be drawn most correctly as above, p. 211.

VI. The pinnule-gap in the proximal parts of the arm among Articulata.

It has long been known that a pinnule-gap appears in the proximal parts of the arm in the young of Comatulids, i. e. the first pinnules, at the ends of the arms, are not developed until these latter have first developed a certain number of Brr. The arm-part devoid of pinnules is not filled up till later on by the successive appearance of P_1, then usually P_3, and finally P_2 and P_4 (Cf. MORTENSEN 1920 a, p. 28). This appearance of a pinnule-gap seems to be universal in the young Comatulids. In *Macrophreata* the first pinnules appear on Br 10—12, when about 15 arm-joints have developed. Among other Comatulids the pinnule-gap is possibly in certain cases somewhat smaller, and possibly the formation of the proximal pinnules does not always take place as regularly as MORTENSEN stated (Cf. 1922 GISLÉN, pp. 57—63, 110, 118). Among full-grown Comatulids we have the pinnule-gap retained in *Atelecrinus*, where up to 15 Br-joints lack pinnules, and in a reduced degree in *Comatilia*, *Hypalometra*, *Clarkometra*, *Balanometra*, *Pentametrocrinus*, as well as in certain *Colobometridae* and *Perometrinae* (in the two last-mentioned groups, however, only P_a and in rare special cases P_1 are lacking).

A. H. CLARK (1922) has tried to explain the cause of this by assuming (pp. 191—192) that the Comatulids, before the appearance of the first pinnules, might be "a fairly typical representative of the Flexibilia Impinnata". He mentions also several other similarities to this group, which might support the assumption of a nearer relationship. As regards the part of the arm found proximally of the 2nd syzygy in a full-grown Comatulid, these similarities are, according to him: 1) Short, oblong, wedge-shaped brachials. I have investigated the cause of this in the Chapter on the Obliqueness of the joints. 2) The absence of syzygies after the 1st syzygial pair, which is of course a correlative to the statement above. The syzygial interval between the 1st and 2nd syzygies is also said to be the greatest in the whole arm. This, however, only concerns those Comatulids which have very short syzygial intervals distally and the 2nd syzygy about Br 10. In certain *Mariametridae,* in *Ptilometra, Notocrinidae, Pentametrocrinidae,* and *Atelecrinidae* the interval is, on the contrary, often very short and the 2nd syzygy appears as early as about Br 7. 3) Before the 2nd syzygy the pinnules are said to "be absent until after the brachials are completely formed". This sentence only becomes explicable if we understand it as meaning: until after the brachials that form the 2nd syzygial pair are completely formed. The assertion, however, does not concern forms where the 2nd syzygy first appears far out on the arm (certain *Oligophreata*).

Among the young of Comatulids there also appear, according to CLARK these similarities to *Flexibila Impinnata:* 1) All the Br articulations are of the same nature. This, however, is not correct, for when the first pinnules begin to be developed one can distinguish histologically between muscular and non-muscular articulations. 2) The flexibility of the arm is caused by a continuous ventral muscle-band which is not subdivided into interbrachial muscles. It is easy to prove by means of dissection or section of young Comatulids that interbrachial muscles really occur. There are other similarities found there certainly, but they are of a too general nature to point directly towards *Flexibilia Impinnata* — they might just as well be mentioned as similarities with the *Inadunata* (excepting his paragraphs 4 and 9 about the pinnule-gap and the formation of a Cd).

Here, however, the point concerned is the closer discussion of the pinnule-gap. For a long time this was a puzzle to me, until at last through comparison with the condition in the recent genus *Phrynocrinus* (Cf. 1907 a, A. H. CLARK) I began to see the matter more clearly. The disk here extends at least as far as the 20th Br-joint, half burying a number of pinnules in the perisome. The first pinnules appear about I Br 8; proximally of this they are suppressed completely, evidently because, even if they had been present, they would have been far from reaching up to the surface of the disk, and therefore would have been of no use for obtaining nourishment here. If the pinnule-gap of the Comatulids was caused by historical factors, it seemed to me that one ought perhaps, in analogy with the case quoted above, to be able to find something similar in the fossil ancestors of the Comatulids. One should then most likely seek first among the Pentacrinids which, as was mentioned above, come nearest in other respects to the Comatulids.

My investigations of recent forms gave, however, only a negative result. The young of *Metacrinus interruptus* (Sp. 16), which I described in my work of 1922, have a complete series of pinnules. Dr. MORTENSEN has been kind enough to give me the information that among his small young of the same genus (total length of the crown 7 mm) there can also be no question of the oral pinnules being developed later on as among the Comatulids. The specimens had one pinnule to the right and one to the left before the first axillary and 2 pinnules on the arm-branches. The most proximal pinnules are the largest. — The disk is also unusually thin and insignificant. It extends, in Sp. 16 mentioned above, only as far as I Br 2 inclusive, the anal tube is likewise short, only reaching to I Br 3 inclusive. Among full-grown specimens the disk is somewhat larger and reaches, when the arms are spread out, to I Br 5—6, when the arms are folded up, to I Br 6. The corresponding figure in *Metacrinus rotundus* is (folded up arms) I Br 7, in *Metacrinus nobilis tenuis* (full-grown specimen, folded up arms) II Br 2 inclusive (I Br 4 Ax.). In the young specimen 9 of this species (Gislén 1922) it reached only to I Br 2 inclusive. Among young specimens of *Isocrinus decorus* (1884 P. H. CARPENTER Pl. 35) the disk likewise seems to extend only as far as I Br 2 inclusive. In a specimen of *Diplocrinus wyville-thomsoni* which I examined the disk extended (folded up arms) to II Br 2 inclusive (I Br 2 Ax).

VII. **Defective pinnulation in the Articulata.**

It was not until I turned to the fossil species of *Pentacrinus* — it should be noticed that just this genus, as we found above, comes nearest to the Comatulids — that I found the solution. Here, in fact, the ventral perisome rises between the arms to half their length or to the 5th or 6th arm-division; in other words, to at least the 40th Br-joint, if all the series are reckoned consecutively (Cf. 1837 BUCKLAND, Pl. 51 fig. 2, 1844 The AUSTINS, Pl. 12 fig. 18., 1891 a JÆKEL). JÆKEL has now pointed out (1891 a) that the high perisome in BUCKLAND's specimen was probably caused by the folding up of the arms, by which the disk was pressed up between the arms. This is partly true.

If we compare the disk in *Heliometra eschrichti,* where we find an unsually voluminous one, it reaches with folded up arms and seen in profile to Br 15—18, the anal tube in one case observed up to Br 21 inclusive; with outspread arms it reaches to Br 8 only or, in other words, as far as it is connected with the arms. In *Notocrinus virilis* the disk with folded up arms reaches to Br 8 or 9, the arms are grown fast as far as Br 5 or 6. In *Hathrometra tenella* var. *sarsii* (full-grown specimens) the disk extends to Br 5 to 7 with folded up arms; these are grown fast to Br 3 or 4. The anal tube is very long here and reaches to Br 12. It possesses its own interest to notice that already in the older Pentacrinulas of the same species the disk reaches about as high as in full-grown specimens or to Br 6 (the disk grown fast to Br 4 or 5), the anal tube reaching Br 10. And none the less the arm-joints are relatively longer in the young than in the full-grown specimens. In still younger Pentacrinulas, where the budding of the pinnules in the distal parts of the arm has recently begun, the disk reaches, however, only to Br 1 and the anal cone to Br 4, but then the reduction of the BB and RR has not yet set in to any degree worth mentioning either.

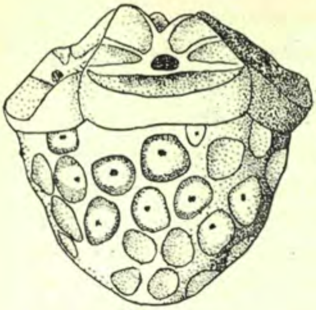
Among forms having thin disks the difference, on the contrary, is hardly noticeable. The disk is attached as far as to Br 6 or 7 (II Br 4 Ax.) in e. g. *Heterometra crenulata,* but does not reach noticeably higher with folded up arms. In *Asterometra anthus* we have a similar condition; the disk here reaches to Br 3 (Cf. the specimen of *Metacrinus interruptus* given above). The Triassic *Encrinidae* also possibly had such thin disks (cf. 1894 JÆKEL, p. 158). *Encrinus carnalli* which JÆKEL has drawn had therefore a disk which, with folded up arms, did not reach farther than to Br 3 (I Br 2, II Br 2). The anal tube was short here (op. cit. fig. 2).

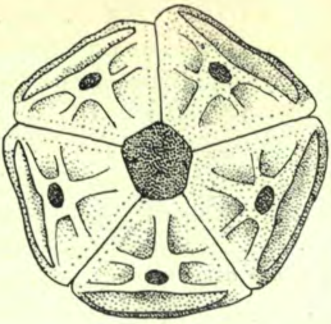
We may therefore assume that the arms in BUCKLAND's specimen were grown fast to the disk, at least to the 15th or 20th Br-joint or to the III Br series. (N.B. the arms are only folded up about half way in the specimen in his drawing). If the proximal pinnules are very long and slender they may, in spite of a fairly high disk, be of use in taking up nourishment or act as tactile organs round the mouth (oral pinnules) — this is seen e. g. in *Heliometra eschrichti.* With an enlarged disk, however, it may come to the point where the proximal pinnules cannot reach up to the ventral side of the disk; they are then excluded from playing any part in conveying nourishment or as tactile oral pinnules. It is evident that this has often been the case in a number of *Pentacrinus* species. If the perisome then bulged out round them and they became imbedded in it, evidently their reduction and disappearance was not far off. This seems hardly to have been the case in the *(briareus =) fossilis* group, while, on the contrary, the *subangularis* group shows evident reduction of the proximal pinnules. Among other matters this is evidenced by QUENSTEDT's figures of *P. subangularis* and *colligatus* (cf. 1876 QUENSTEDT, Pl. 101 figg. 34, 35, 39).

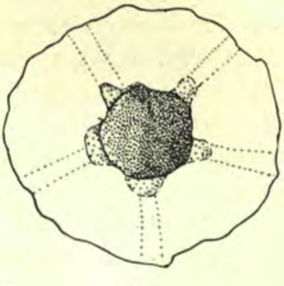
J. MILLER, however, as early as 1821 gave a figure of *P. subangularis* (p. 59, Pl. 1). He says, too (p. 61): "The plated integument... extended beyond the scapulæ" (I Br) "connecting the sides of the arm-joints and the hands as far as the first finger-joints" (IV Br 1) "together" (i. e. to about the 16th Br-joint, reckoned from R) and continues: "A question here suggests itself, whether the animal in age loses the tentacula" (pinnules) "of the arms", (II Br) "and those of the commencement of the hand" (III Br). I will not quote further from this interesting argument here, only proving that MILLER supposed that the greater extension of the integument, caused by the increase of the apparatus for obtaining food, gave rise to a reduction of the proximal pinnules. The two AUSTINS, who in their work (1844, Pl. 13 fig. 1 a) have figured a specimen of *Extracrinus lepidotus,* i. e. *Pentacrinus subangularis,* from the English lias, give a figure of the reduction of the proximal pinnules in this species. Their figure indicates a perisome to about IV Ax, i. e. to about the 40th Br-joint. In the description (p. 108) it is stated: "From the manner in which the plates . . . adhere laterally to the lower portion of the rays it is evident that the outer sides of the leading rays . . . are devoid of tentacula" (i. e. pinnules). QUENSTEDT, in the work quoted above, says (p. 304) on the extension of the perisome, that it is united with the arms till about the first IV Brr. He continues (p. 303) (es) "lässt sich nach oben hin nicht sicher entscheiden, wann die Zwischenplatten aufhören und die Pinnulæ beginnen". (p. 304) "An den Interbrachialplatten fig. 35 beginnen auf der linken Handseite" (III Br) "die Platten sich alsbald in Reihen zu stellen und scheinbar in Pinnulæ überzugehen". Further down on the same page: "die unteren Plättchen . . . sind offenbar noch Zwischenplatten, die erst oben sich zu Pinnulæ gestalten". QUENSTEDT's specimens from the *Posidonia* schist are possibly not to be considered as belonging to the species *subangularis,* even if they stand near it. In a specimen from this locality preserved in the Riksmuseum, Stockholm, I have observed the first pinnule on III Br 1 and III Br 4 (II Brr in the first case ± 13, in the latter 10 +). Besides this there is a large polished slab in the Riksmuseum in which occur more than 10 crowns of the species mentioned above. About 5 of them have been cut by chance in a longitudinal direction and we can verify a large and high disk in them all (cf. fig. 303). The length of the arms varies between 100 and 150 mm., and the height of the disk in the 3 cut almost medially between 30 and 40 mm. (the 2 specimens remaining, evidently cut somewhat laterally of the median longitudinal line, had disks 20—25 mm. in height). The horizontal section of the mouth surrounded by ambulacral furrows is, probably, to be seen in one specimen (cf. fig. 304).

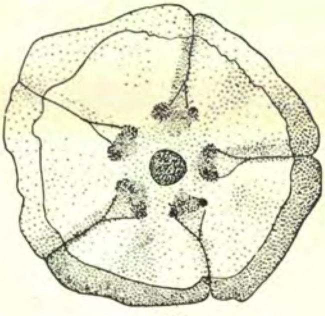
One may learn from this that at least 15 of the proximal arm-joints in the species of the *subangularis* group lacked pinnules, and that the bases of the first pinnules appearing later, as in *Phrynocrinus,* were hidden by the perisome, here plated.

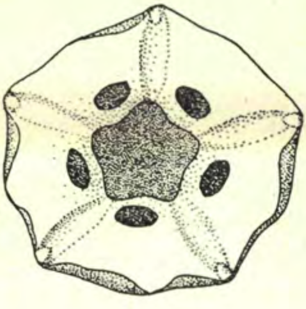
The genus *Pentacrinus,* according as we understand it now, includes, as is indicated above, two groups which might suitably be characterized as two separate genera. The first, the *fossilis* (*briareus*) group: Pentacrinus *s. str.,* is characterized by short stems which along their whole length have closely set nodals carrying long stout cirri. These cirri, at least in the proximal half, are pronouncedly rhombic when seen in transverse section. The perisome extends high up among the arms, but does not seem to have caused any defective pinnulation worth

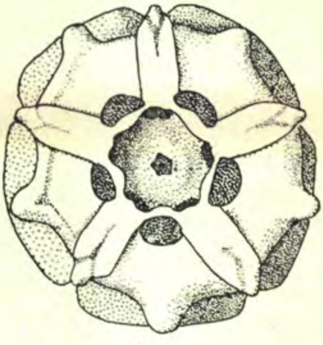

289

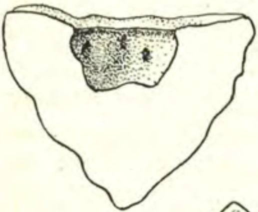

290

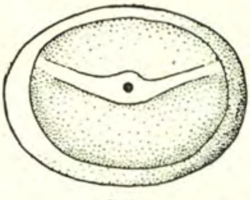

291

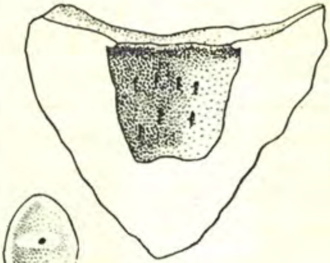

292

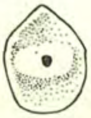

293


294


301


295


302


296


297


298


299


300

Figg. 289—302. 289—292) *Isometra vivipara.* 289) Cd + radial ring, lateral view; 290) radial ring, ventral view; 291) Cd ventral view; 292) Radial ring, dorsal view, 16/1. 293—294) *Pterometra trichopoda.* 293) Cd, ventral view; 294) Radial ring and basal star, dorsal view, 16/1. 295) *Metacrinus rotundus* 2nd cirral, dist. articular facet, 16/1. 296—298) *Pterometra trichopoda* Cirrals from different parts of a cirrus; fig. 298 from the distal part of the cirrus, 16/1. 299) *Asterometra anthus* A cirral, 16/1. 300) *Pectinometra flavopurpurea* A cirral, 16/1. 301) *Leptometra phalangium* Section through a Cd, 16/1. 302) *Poliometra prolixa* Section through a Cd, 10/1.

mentioning. Type, *P. fossilis* Blumenb. The other group, the *subangularis* group, is distinguished by very long stems, carrying nodals which are extremely closely placed in the proximal part of the stem, and having a slowly, constantly increasing, number of internodals distally, according to Quenstedt (1876) reaching to more than 80, according to Springer (1918) to at least 63, perhaps 120, joints per internodium. The cirri are short and rudimentary. The perisome, which here too stretches high up among the arms, has caused a more or less powerful reduction of the proximal pinnules. I call this genus on account of the long rope-like stems Seirocrinus (from σειρά = rope). Type *S. subangularis* (J. Miller) (? = *Chladocrinus* L. Agassiz 1835).

It is now evident that the hypothetical ancestral form of the Comatulids described above unites in itself characteristics belonging to both these genera. It approaches *Pentacrinus* by its short stem, consisting, after the development of the first nodal, of nodals only, as well as by the strong cirri. Among known forms *P. dargienesi* comes nearest here to the Comatulids (cf. 1888 de Loriol, pp. 417—420). The stem in this case did not reach more than 60—70 mm., while the cirri were 100 mm. de Loriol says too (p. 420): "Suivant tout probabilité, ce crinoïde . . . flottait librement". The Comatulids approach *Seirocrinus* through the defective pinnulation appearing during their ontogeny which, as seems probable, is caused by the perisome once upon a time having swelled out between the arms. Perhaps we may conclude from this that a *Pentacrinus*-type existed once which united these characteristics, and which was older than both the genera mentioned above.

The oldest form of *Pentacrinus* we know is *P. versistellatus* from the uppermost Trias, described by Schafhäutl (1851; cf. also 1909 Bather, p. 23). The recent type of Pentacrinid had then already flourished for a long time. Typical *Isocrini* are known already in middle Trias (1915 Clark & Twitchell. Those from lower Trias, on the contrary, are uncertain). The middle Triassic forms had, however, even then the following distinctive characteristics appearing also in recent forms and deviating from *Pentacrinus* and *Seirocrinus:* Rapid attainment of the maximum number of internodals (usually between 5 and 15), IBB hidden, normal RR with their proximal ends not directed backwards, rounded or dorso-ventrally flattened cirri, complete pinnulation, insignificant arm-branching, and, as far as we know, a small disk. It appears evident to me that *Isocrinus* and the Pentacrinids that correspond to this genus in the definition given above, already form during the Triassic age a well-defined and out-crystallized form-group distinct from the *Pentacrinus*-type. I propose therefore that they are discriminated as a family of their own, Isocrinidae. *Pentacrinidae* will then include *Pentacrinus* and *Seirocrinus* only, and may be characterized thus: Cirrus-provided nodals very closely set proximally, often without internodals; when retreating distally of the crown a slowly increasing number of internodals sets in, in long stems reaching a very high number. The cirri in transverse section rhombic, either powerful or rudimentary. IBB hidden. RR with long, often segmented, processes, pointing downward, inlaid in the stem. Often defective proximal pinnule-series, very extensive and characteristic arm-branching (cf. example below), high disk.

Example of the mode of arm-division in a *Seirocrinus subangularis* (Posidonia schist, Holzmaden):

$$\mathrm{I}\;11?\;\mathrm{Ax}\begin{cases}\mathrm{III}\;18\begin{cases}\mathrm{IV}\;10\\ \mathrm{Br}\end{cases}\begin{cases}\mathrm{V}\;13\\ \mathrm{Br}\end{cases}\begin{cases}\mathrm{VI}\;11\\ \mathrm{Br}\end{cases}\begin{cases}\mathrm{VII}\;13\\ \mathrm{Br}\end{cases}\begin{cases}\mathrm{VIII}\;11\\ \mathrm{Br}\end{cases}\begin{cases}\mathrm{IX}\;13\\ \mathrm{Br}\end{cases}\begin{cases}\mathrm{X}\;11\\ \mathrm{Br}\end{cases}\begin{cases}\mathrm{XI}\;9\\ \mathrm{Br}\end{cases}\begin{cases}\mathrm{XII}\;11\\ \mathrm{Br}\end{cases}\begin{cases}\mathrm{XIII}\\ \mathrm{Br}\end{cases}\\ \mathrm{III}\;64\begin{cases}\mathrm{Br}\\ \mathrm{IV}\;15\end{cases}\begin{cases}\mathrm{Br}\\ \mathrm{V}\end{cases}\end{cases}$$

$$\mathrm{I}\;5+\mathrm{Ax}\begin{cases}\mathrm{III}\;51\begin{cases}\mathrm{IV}\;21\\ \mathrm{Br}\end{cases}\begin{cases}\mathrm{V}\;15\\ \mathrm{Br}\end{cases}\begin{cases}\mathrm{VI}\;11\\ \mathrm{Br}\end{cases}\begin{cases}\mathrm{VII}\;13\\ \mathrm{Br}\end{cases}\begin{cases}\mathrm{VIII}\\ \mathrm{Br}\end{cases}\\ \mathrm{III}\;15\begin{cases}\mathrm{Br}\\ \mathrm{IV}\;15\end{cases}\begin{cases}\mathrm{Br}\\ \mathrm{V}\;15\end{cases}\begin{cases}\mathrm{Br}\\ \mathrm{VI}\;11\end{cases}\begin{cases}\mathrm{Br}\\ \mathrm{VII}\;13\end{cases}\begin{cases}\mathrm{Br}\\ \mathrm{VIII}\;11\end{cases}\begin{cases}\mathrm{Br}\\ \mathrm{IX}\end{cases}\end{cases}$$

N. B. The odd figures prevail, as in the recent forms (cf. Chap. 1).

It is not, however, only among the *Articulata* discussed above that we find a pinnule-gap proximally.

Among recent forms it appears also in some full-grown stalked types. It is met with throughout in *Bathycrinidae*. In *Bythocrinus* the first pinnule appears on Br 4—12 (*B.* cf. *braueri* 4—6, *braueri* 8, *chuni* 10—12), in *Democrinus (rawsoni* and *weberi)* on Br 6, in *Rhizocrinus (lofotensis)* on Br 8, in *Bathycrinus* on Br 8—10 (*B. pacificus* 8, *campbellianus* 9, *serratus* 10?), in *Ilycrinus* on Br 9—?12 (*australis* 9—11, *carpenteri* 11—12, *complanatus* 10—12), in *Monachocrinus (sexradiatus)* on Br 10—14. In *Phrynocrinidae* only the arms of *Ph. nudus* are known. The first pinnule appears here on I Br 8. Among *Hyocrinidae* too a proximal pinnule-gap is found, as one pinnule to the right and one to the left is lacking. The first pinnule therefore appears on (I) Br 4—6 (the variation is due to the different distribution of the syzygies).

In case the idea is correct which I have expressed above concerning the derivation of the Bathycrinids from *Bourgueticrinidae,* and the descent of these latter from a form nearly related to the Comatulids and Thiolliericrinids, the explanation of the pinnule-gap in the Bathycrinids will be the same as that given in the case of the Comatulids. The disk in the Bathycrinids of the present time does not reach far; in *Rhizocrinus* (V arms) to Br 2 and in *Ilycrinus* (X arms) to Br 2 (i. e. to the 4th Br reckoned from the R). It seems, however, in many cases as though this may be explained partly by the disk having sunken in between the greatly prolonged BB *(Bythocrinus, Democrinus,* and some species of *Monachocrinus).*

In *Phryocrinus* we have, as was mentioned above, a very large perisome which reaches up to about Br 20. The disk and arms of *Naumachocrinus* are not known; the RR here are very prolonged.

A high disk is also found in certain *Hyocrinidae.* In *Ptilocrinus,* where it stretches out to Br 6, the arms are grown fast up to Br 5. In *Calamocrinus,* where the disk is connected with the arms to I Br 9—10, the anal proboscis reaches to II Br 3 (I Br 10 Ax.; cf. A. Agassiz 1892). *Thalassocrinus* and *Hyocrinus* seem, on the contrary, to have thin disks. *Gephyrocrinus* takes a middle position.

Among fossil *Articulata* we notice that *Saccocomidae* lacked pinnules until about Br 15 (cf. e. g. 1893 b Jækel).

But among certain of the fossil *Articulata* which have complete pinnulation we also have evidence of a plated perisome which might extend rather a long way up between the arms. We find this in *Apiocrinus* and *Uintacrinus* (cf. 1887 de Loriol, 1901 Springer).

The genus *Holocrinus* from middle Trias shows us the appearance of a primitive Isocrinid. It answers completely, with the exception of the occurrence of visible IBB, to the definition for *Isocrinidae* given above, but its primitiveness is marked by the cirri appearing 2—3 in each whorl only (in one of the species), by the large BB, as well as by the powerful development of the IBB (cf. Picard 1883, Wagner 1887, Jækel 1893 a). There is therefore a certain interest in seeing how the conical disk, which in *H. wagneri* was covered by rather stout and large calcareous plates, had grown fast at least to Br 3 and reached up even to Br 8, i. e. higher than in any now living ten-armed Isocrinid (Wagner 1887 b and 1891, v. Koenen 1895).

Dadocrinus gracilis, which may be considered as the representative of the prototype for Millericrinid forms had, likewise, a relatively high disk[1] (Gürich 1887, v. Koenen 1887 a and b, 1895).

We find in the Encrinids, on the contrary, a thin disk formed of small calcareous granules which reaches only to Br 3 (I, II Br 2) (cf. Jækel 1894). Jækel is right when he points out (p. 162) that here we have already a differentiated type of disk which was first attained by the *Pentacrinidae* (= *Isocrinidae*) and Comatulids in post-liassic times. The Encrinids show, as he rightly points out, an extensive specialization in this characteristic as well as in others. It was once supposed by Wachsmuth and Springer that, possibly, young Encrini had a disk which

---

[1] Possibly the Millericrinid type has developed from a number of convergent types, partly descending from ancestors similar to *Dadocrinus,* partly, through the suppression of cirri, deriving from *Isocrinidae* (cf. *Proïsocrinus*).

stretched considerably higher up between the arms (cf. 1885 WACHSMUTH & SPRINGER, p. 263). This observation was, however, modified later on (1886, p. 183). Mr. SRINGER has had the great kindness to inform me that the whole statement is due to a misconception of the young, caused by the specimen being subjected to abrasion, from which one gets the impression that there was a small groove separating some few perisomatic plates and the Brr. But this is merely a superficial appearance. According to him it is, moreover, impossible to say if there was any gap in the proximal pinnule-series, but, so far as Mr. SPRINGER was able to see, the young specimen does not seem to differ from the larger ones except in size.

Finally we may conclude that a voluminous disk is of very common occurrence among the primitively organized *Articulata*. Sometimes this high disk is combined with the loss of the proximal pinnules. In the Comatulids we have evidence of defective pinnulation having once been present in the occurrence of a proximal pinnule-gap during the juvenile stages.

VIII. **The cause of the enlargement of the disk.**

Two views have been brought into opposition with each other in attempting to establish the ancestors of the *Articulata*. The first maintains that they were descended from the fistulate *Inadunata,* the other emphasizes their similarity to *Flexibilia*. In the first school we have above all to reckon BATHER, JÆKEL, NEUMAYR, WACHSMUTH & SPRINGER, in the latter one A. H. CLARK and WANNER. SPRINGER, during later years has taken up the former opinion, after having inclined during an earlier peroid towards the latter one (cf. BATHER 1900, 1909, JÆKEL 1918, NEUMAYR 1889, WACHSMUTH & SPRINGER 1885, A. H. CLARK 1922, WANNER 1916, SPRINGER 1920, 1923, cf. too ZITTEL-EASTMAN 1913, p. 227).

Whichever of these standpoints one has taken up, similarities can be pointed out and difficulties have arisen. In the last representatives of the fistulate *Inadunata, Poteriocrinites,* one may find numerous similarities with *Encrinidae,* to which the transition through *Erisocrinus – Stemmatocrinus* may be considered as fairly unbroken. In *Fistulata* we have, however, as is well-known, a subtegminal mouth and covered ambulacral furrows on the disk ever since the Silurian period (cf. e. g. 1897 WACHSMUTH & SPRINGER, Pl. 3; 1900 BATHER, figg. 39, 43, pp. 127, 128). In *Articulata* the ambulacral groove is open and the mouth uncovered. A disk is found in *Flexibilia* from the oldest times which very much resembles that of the *Articulata,* but in this group neither pentamerous cirrus-whorls nor pinnules have ever been developed. One thing worth pointing out is the fact that V simple arms is an arm-type which is unknown in *Flexibilia* but, on the contrary, is common both in *Poteriocrinites* and *Articulata*. Among *Flexibilia* the Carboniferous genus *Onychocrinus* comes nearest to the pinnulate stage, but the similarities between its armlets and real pinnules are rather distant. It is therefore quite natural that SPRINGER (1920) comes to the conclusion (pp. 92, 97, 106—107) that, "The Inadunate type . . . is in its essential features carried forward with the Articulate type", and was not "a pinnulate division of the *Flexibilia*", and that *Flexibilia* became extinct near, or shortly after, the end of palaezoicum. He did not know then of WANNER's investigations (1916), but these seem to have made him doubtful in certain respects. In his Supplement to the Crinoidea Flexibilia he says (1923) that: "*Prophyllocrinus* . . . seems to anticipate some characters of Mesozoic types". He is thinking here of *Eugeniacrinidae* and *Holopodidae*, which among the *Articulata* represent a type well-distinguished even in Jurassic, and sharply separated from the other members of the order. These have not been touched upon in the previous discussion, as their derivation seems to me still to be veiled in mystery.

It seems to me as if JÆKEL (1918) interpret the opinions of his partisans in a very happy manner, when he (p. 65) sketches the transition of *Fistulata* to *Articulata* as a "Sprengung der primären Kelchkapsel (des Cyathocrinidenstadiums) . . ." by which "der Analtubus die ganze Kelchdecke in sich aufnahm, hob und von den Radialien ablöste. Sie wurde nun zwischen den unteren Teilen der Arme ausgebreitet". We know that in Poteriocrinids the anal opening lay on the aboral side usually at or near the base of the ventral sac (cf. 1897 WACHSMUTH & SPRINGER, pp. 137—138, Pl. 7). We know further that there existed in the older Crinoids, between the anal opening and the mouth, a pore for the primitive gonad, to which the present axial gland corresponds (= labial plexus part. 1884 P. H. CARPENTER, p. 97, "der dem drüsigen Organ angelagerte Zellpolster" 1905 REICHENSPERGER, p. 183). According to what REICHENSPERGER's investigations brought to light, the genital glands of the pinnules are to be considered from the beginning as processes from the organ above-mentioned. It is only at a later stage that they lose their connection with it. As I have pointed out in another connection, the gonads, in some of the recent forms, do not appear in the pinnules but in the arms *(Metacrinus, Notocrinus, Comatula)*. Thus no decided correlation between the pinnule and the gonad, as one was inclined to assume earlier (P. H. CARPENTER 1884; WACHSMUTH & SPRINGER 1885, p. 289; 1897, p. 80), really exists. On the contrary, all the ontogenetic signs indicate a late migration of the gonads in the arms and in the pinnules.

We may therefore suppose that the ventral sac enclosed, besides a part of the intestine, at least a part of the gonad (cf. also 1897 WACHS-

MUTH & SPRINGER, pp. 114, 138, *Aulocrinus* Pl. 7 fig. 9).[1] When the ventral sac later on absorbed the whole of the disk, we may assume that the gonad stretched out under all the inter-radii. The perisome then rose between the arms and caused, at least in a number of forms, a reduction of the proximal pinnules. When finally the disk once more dwindles in size the migration of the gonad into the arms has begun. In a number of forms there still remains, as a reminder of the high disk and pinnular reduction, a proximal pinnule-gap in full-grown forms, marked best among *Bathycrinidae* and *Atelecrinidae* and appearing during ontogeny among all Comatulids. It is noticeable that *Flexibilia,* which never developed pinnules and had no ventral sac, always had a perisome extending high up between the arms.

There has seemed to me to be a certain amount of interest in trying to ascertain the total volume of the genital glands in some of the recent forms. One might suppose that if the perisome was increased by this volume, one would get about the measure of how far the disk would extend up between the arms in recent forms, in case the gonads had not migrated out into the arms or pinnules. I therefore picked loose all the genital glands from an arm in some specimens with greatly swollen genital pinnules — a rather troublesome undertaking — weighed the mass thus obtained, multiplied by the number of arms, divided by the specific weight, which for the soft parts should not be placed higher than 1·1 (cf. Chap. V), and in this way obtained the total volume of the gonad. From this I calculated the raising of the disk and obtained the following results: *Heliometra eschrichti:* (genital pinnules relatively inconspicuously distended) weight of genital glands 7·43 gr., volume 6·76 ccm., radius of the disk 10·5 mm. Raising of disk 19·5 mm. or corresponding to 14 Br-joints. As the disk before reached to Br 10, a disk with the gonad included would thus reach to about Br 24. *Antedon petasus:* total weight of the gonads 0·53 gr. Volume 0·48 ccm. Radius of the disk 3·3 mm. Raising 14·1 mm. or 18 Br-joints. As the disk with folded up arms before reached to Br 7 a disk with the gonads included would reach to about Br 25. *Compsometra serrata:* total weight of the gonads 0·36 gr. Volume 0·33 ccm. Radius of the disk 3·4 mm. Raising 9·1 mm. or 16—17 Br-joints. As the disk before reached to Br 6 it would reach, with the gonads included, up to about Br 22. It seems therefore as though the enlargement of the disk, under the conditions given above, was

---

[1] TRAUTSCHOLD supposed (1882) that certain depressions on the sides of the ventral sac were genital openings. This, however, at least in many instances, seems scarcely to have been the case (1890, 1893 BATHER). As these depressions are here found in the suture-lines between the plates which form the ventral sac it is easy to assume that the pits sheltered flexing ligament-bundles. Probably BATHER's view is right here, though it may be possible that there existed real pores in certain *Poteriocrinites* (fig. 286).

rather considerable and fully sufficient to give rise to the reduction of the proximal pinnules.

This assumption, of the extension of the gonads under the interradii being the chief cause for the enlargement of the perisome, makes it clear also why in young Comatulids we do not get a high disk in connexion with the pinnule-gap, for at this stage the gonads are perfectly rudimentary.

IX. The re-opening of the subtegminal mouth.

At about the same time as the disk rose between the arms, the subtegminal mouth and the covered proximal parts of the ambulacral grooves were presumably opened again. The Permian form *Timorechinus,* offering the interesting figure of an Inadunate[1], where the anal tube has absorbed the whole disk which reaches up over the ends of the short arms, still has subtegminal ambulacral furrows (cf. WANNER 1912, 1916). Whether *Encrinidae* and *Pentacrinidae* had open ambulacral furrows must still be considered as not quite settled, although it may be assumed that such was the case (cf. also fig. 304). The middle Triassic *Holocrinus* had certainly, however, open ambulacral furrows (1895 v. KOENEN, p. 292).

It seems to me that valid ontogenetic evidence of the descent of recent forms from forms having a subtegminal mouth is found in the formation of the marsupium over the mouth of the young Comatulid *Pentacrinula.* Directly after the larva has become attached and the first beginning of the development of the stem has set in, a mound appears round the mouth which grows over the latter. It develops a closed cavity beneath the roof so formed in which, besides the mouth, the developing primary tentacles are also contained. The marsupium is not opened until after the orals have reached their full size, and at about the same time as the first radials appear (cf. 1886 PERRIER, 1920 a MORTENSEN).

X. The pinnule-gap in the Poteriocrinids.

The above-mentioned large ventral sac which often attained quite gigantic proportions, was developed in the anal interradius (cf. 1911 SPRINGER). It may be questioned now whether under such circumstances the proximal pinnules in the anal interradius had room to develop. On many occasions this was certainly the case. In *Scytalo-*

---

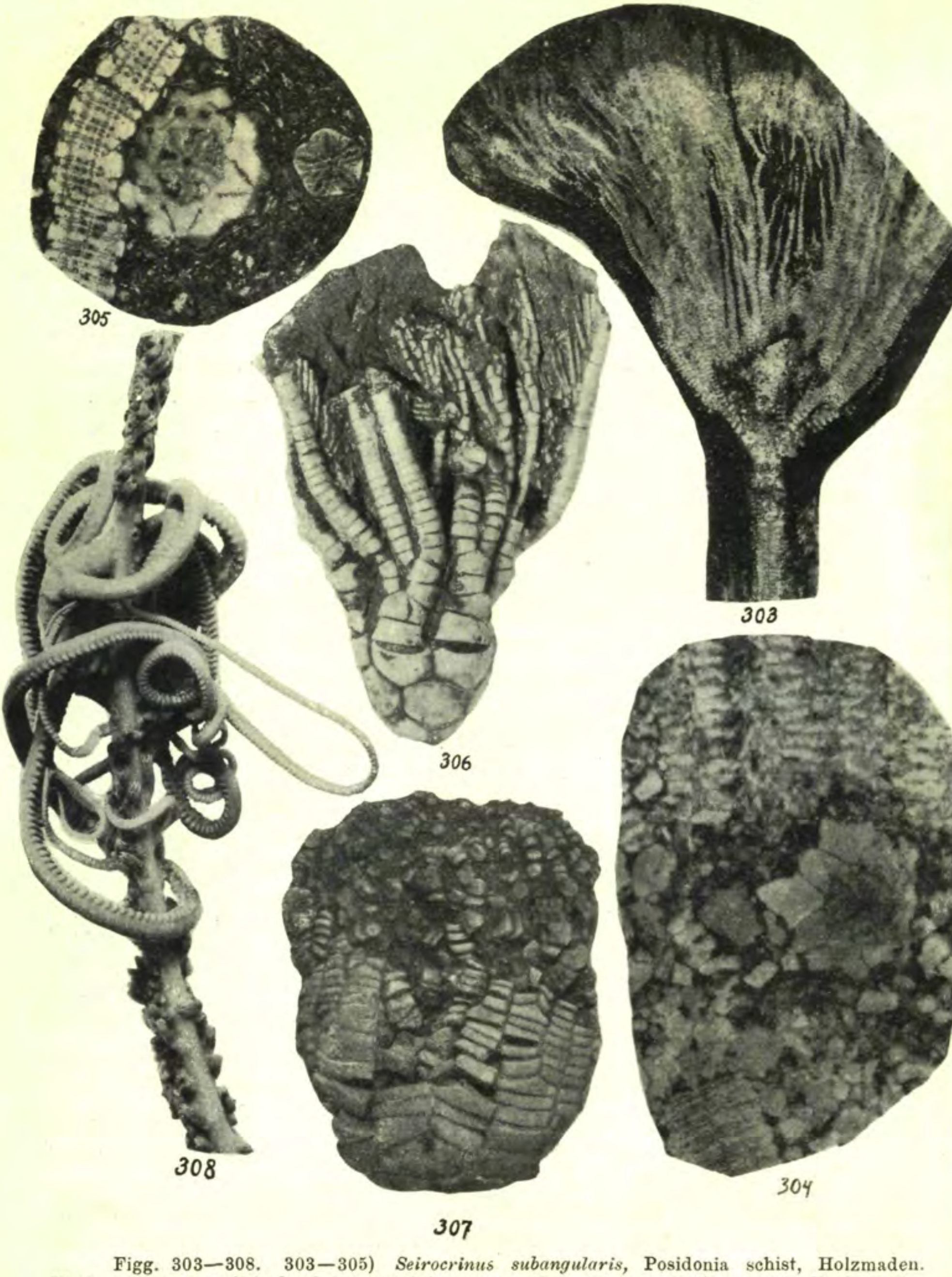
[1] I agree here with JÆKEL (1918) on the question of the systematical position of this form. The subtegminal ambulacral grooves show that it cannot be a member of the *Flexibilia.*

crinus bijugus (Trautschold) I have found in the anal area a large and powerful P_1 on Br 1 and afterwards on the following Brr pinnules, now to the right, now to the left. In *Scaphiocrinus unicus* (Hall) too, as well as in *Scaphiocrinus multiplex* (Trautschold), I have found a complete row of pinnules in the anal area. I have also seen completely pinnulated arms in *Graphiocrinus (Aesiocrinus) magnificus* (Miller & Gurrley) and in *Erisocrinus typus* (Meek & Worthen). In *Cromyocrinus ornatus,* on the contrary, I did not find the first pinnule-face until Br 4 (fig. 285). One also sometimes finds in the literature figures which seem to show the possibility of a number of pinnules being missing in the anal area, e. g. (*Poteriocrinus Coreyi* =) *Scytalocrinus decadactylus* (1875 Meek & Worthen, Pl. 29, fig. 3 b), *Coeliocrinus* (*Zeacrinus*) *lyra* (1873 Meek & Worthen, Pl. 1, fig. 11 b), *Zeacrinus elegans* (1858 Hall, Pl. 9, fig. 2), *Bursacrinus procerus* and *pyramidatus* (1916 Wanner, Pl. 106, figg. 7 c, 8 b). It has been stated several times that the proximal pinnules in forms with large ventral sacs must have been short, smaller than the distal ones; cf. 1911 Springer (p. 155) on *Poteriocrinus magniventrus* and 1912 Bather (p. 69) on *Hydreionocrinus woodianus. Hydreionocrinus* is a form in which the ventral sac takes up the whole of the disk. In the species last mentioned the pinnules were possibly missing on the proximal parts of the arms. Thus Bather says: "The pinnules in the American species are said to be very short. I can see no trace of them in the specimens from Invertiel and there cannot have been much room for them between the arms and the ventral sac".

In a specimen of *Zeacrinus wortheni* Hall, observed by me, the baso-anal plates fill up completely the space between the radii I—V up to III Br 3 (I Br 1, II Br 3). But in 3 of the other interradii too (between radii II—III, III—IV, IV—V) a narrow oval appears, formed of 3—4 calcareous plates (cf. fig. 284). When an arm was removed it turned out that these continue in between the arms and evidently form the covering of the disk bulging out interradially between the arms (fig. 307). On the basal arm-joints I could observe no trace of pinnule-facets (fig. 283). It seems to me that in this case we have an interesting first stage of the condition which we meet with in *Timorechinus* in an exaggerated form.

It seems therefore as though here also a suppression of the proximal pinnules may take place with the extension of the disk up between the arms — exactly as we found in the *Pentacrinidae.*

A form in which this enlargement of the disk has gone so far as to reach absurdity is, as was said before, *Timorechinus.* Here the disk pushes its way up and out between the arms and reaches as far as their ends. Whether the few arm-branches should be interpreted as pinnules or as arms it may be rather difficult to decide. It seems to me, however, more plausible to consider them, with Wanner, as weakly divided, non-pin-



Figg. 303—308. 303—305) *Seirocrinus subangularis,* Posidonia schist, Holzmaden. Photos from a polished plate containing more than 10 spp. 303) A longitudinal section through a crown. N. B. the powerful disk, ½ nat. size. 304) Plane section of the mouth and the 5 surrounding ambulacral furrows. The proximal part of the stem below, some arms in the upper part of the photo, ²/₁. 305) Section through the basal ring (narrow BB), the radial backward processes (broad) and one of the uppermost stem joints (star-shaped), ²/₁.

nulate arms (the side-branches are scarcely weaker than the chief branches, the pinnules are generally markedly weaker than the Br-joints). Wanner, however, has drawn from this the conclusion that the form should be referred to *Flexibilia Impinnata*. Jækel points out (1918) that the structure of the ventral capsule excludes such a supposition. The approach towards the *Flexibilia Impinnata* which the non-pinnulation implies is therefore only a convergent phenomenon caused by the excessive development of the disk.

Among the short-armed late-palaeozoic *Inadunata* it seems therefore as though sometimes a condition of secondary non-pinnulation may have taken place. In cases of pinnule-reduction in more long-armed forms, the enlargement of the disk caused only a proximal pinnule-gap. But if, as is often the case, only the bases of the arms are preserved, one may here, in some cases, get an impression of an impinnate Crinoid.

XI. Summary of the probable manner of evolution of the Articulata treated above.

If we summarize what has been said above, we obtain a picture of the evolution of the *Articulata* of about the following kind.

In the Carboniferous age a number of Crinoid forms of the Poteriocrinid type left the fistulate stage, the organs contained in the ventral sac spreading out under the whole disk. In this way the disk was raised up between the arms and the subtegminal mouth and the proximal ambulacral furrows were again opened. We seem to have an ontogenetic reminder of this in the marsupium of the young of the recent Comatulids. With the elevation and dilation of the disk between the arms the proximal pinnules often became suppressed. We find evidence of this at the present time in the pinnule-gap in a number of full-grown Crinoids and in the young of Comatulids. After this the gonad proceeded first to the arms, and then to the pinnules — as ontogenetic evidence shows. Then the disk contracted, so that the suppressed proximal pinnules could again develop. That it was the gonad which caused the enlargement of the disk explains why in young Comatulids we do not find any enlargement of the disk worth mentioning. Among the older *Articulata*, a large disk is found in *Apiocrinidae, Uintacrinus,* and *Pentacrinidae.* In the family last-mentioned the enlarged perisome gave rise to a reduction of the proximal pinnules.

Presumably the Encrinid type developed first. Through *Erisocrinus* and *Stemmatocrinus* we are carried as early as Carboniferous in an

---

306) ***Scaphiocrinus multiplex.*** **The distal parts of the long and branched P_1 are distinctly visible. The anal interradius to the right, ± nat. size. 307)** ***Zeacrinus wortheni.*** **A part of the heavily plated disk visible between ray II—III. The left arm-divisions of ray II are removed by preparation, $\times 1^{1}/_{2}$. 308)** ***Asteronyx loveni*** **on a** ***Funiculina quadrangularis.*** **The ophiuran has grazed away all the polyps on the part of the rachis where it is situated, $^{3}/_{4}$.**

even series to the Encrinids. For this reason we find that the Triassic Encrinids show very far-reaching specializations, not reached by *Pentacrinidae* and Comatulids until a much later time. The specialized characteristics of the Encrinids are: the fixation of the component number of the division-series as well as of the number of arms, the biseriality of the Br-joints (more usual in younger than older Triassic forms, cf. 1879 ECK), the small and thin disk, plated with small granules, ? the lack of cirri (probably at least certain of the *Encrinidae* have developed from forms with cirrus-provided stems similar to e. g. *Palermocrinus;* cf. the stems of *Encrinus liliiformis,* where the development of the stem-joints takes place according to the usual type of stem-growth in *Pentacrinidae* and *Isocrinidae* — interpolation of internodals between the, here, non-cirrate nodals; 1837 BUCKLAND, 1887 v. KOENEN).

Later on *Isocrinidae* developed from forms similar to *Holocrinus.* At the latest in middle Trias this type was definitely out-crystallized and was of about the same type as in our own time. We find in *Dadocrinus* and *Recoarocrinus,* about contemporary with *Holocrinus,* the prototypes of *Millericrinidae* and *Apiocrinidae.* Finally, the Pentacrinid type appeared, which still in lower Jurassic preserves several old characteristics, such as the irregular number of component parts in the division-series, the enormously far-advanced forking of the arms, the primitive development of the cirri (no dorsal spines, no opposing spine), the relatively powerful IBB, the high and large disk, the pinnule-series often with proximal pinnule-gaps, the primitive arrangement of the calcareous plates on the anal-cone (cf. 1891 a JÆKEL).

The type last-mentioned divided into 2 branches which rapidly became highly specialized and, presumably, soon died out. The Comatulids and ?*Uintacrinus* (cf. 1901 SPRINGER) seem to be derived from some nearly allied form. The Comatulids which presumably arose late from the Pentacrinid type appear therefore even to-day as fairly old-fashioned in comparison with *Isocrinidae,* owing to the occurrence of a couple of embryonic characteristics: the embryonic pinnule-gap, and a comparatively late disappearance of the orals and anal x; my sp. 16 of *Metacrinus interruptus* (GISLÉN 1922), with only about 27 Br joints in total from the R to the end of the arm (total length of crown 18 mm.), lacked both orals and anal x.

A branch nearly allied to the Comatulids gave rise to *Thiolliericrinidae,* which soon lost their cirri and whose typical representatives disappeared in lower Cretaceous with the more or less non-cirrate genus *Burdigalocrinus.* Presumably *Bourgueticrinidae, Bathycrinidae,* and *Phrynocrinidae,* which together form a distinctly related unit descend from a form nearly allied to the Thiollierierinids.

Hyocrinidae seem to represent the terminal point of a special line which reached the Articulate stage by its own way. Probably its forms are related to the Jurassic Plicatocrinids (N. B. these are X-armed, lack syzygies, and have no proximal pinnule-gap). It does not seem necessary to me, however, to link them together, as JÆKEL did, with certain palaeozoic forms whose last representatives are found in middle Devonian. It seems to me that they proceeded from some Poteriocrinid form in a similar manner to that of the other *Articulata,* but independently, through the suppression of the IBB and the anal plates, through the acquirement of flexible arms, through the absorption of the disk by the ventral sac, and through the sinking in of the disk after the gonads had made their way out into the arms (cf. e. g. 1918 JÆKEL, *Culmicrinus* fig. 53). I consider it to be incorrect to place *Calamocrinus* close to *Millericrinidae* and in a position in the system totally different from the rest of the Hyocrinids. *Calamocrinus* is distinguished from *Millericrinidae* by its proximal pinnule-gap, and by the arms being forked first at about Br 10, characteristics which are entirely foreign to all the Millericrinids known. On the other hand the relationship between *Calamocrinus* and *Ptilocrinus* is unmistakable, and if it were not for the different mode of arm-division one would scarcely be able to distinguish them from each other even generically. *Hyocrinus* shows by the strong fusion of its BB., by its numerous syzygies, and by the small size of its disk that it is the terminal point in this series.

Among the Articulate forms which I have not mentioned above there remain *Eugeniacrinidae, Phyllocrinidae,* and *Holopodidae; Marsupites, Eudesicrinidae,* and *Saccocomidae.* The 3 first-mentioned families seem to form a more closely related group (JÆKEL 1891 b, 1907). Regarding the two families last mentioned JÆKEL has made himself the interpreter of the idea that they may stand in genetic connection with *Plicatocrinus* and *Hyocrinus,* but apart from this the phyletic origin of these forms is still veiled in obscurity.

XII. **Mutual relationship of the Comatulids.**

A. **Natural groups among recent Comatulida.**

Before passing on to discuss the relationship of the fossil Comatulids to the recent forms, I must carry out a grouping of the latter. The recent Comatulids, it seems to me, may be brought together into not 2, but 4, natural groups or tribes which may be distinguished by the following characteristics:

(1) **Comasterida.** Cd discoidal.[1] Centrodorsal cavity (excepting in

---

[1] *Comatonia* is an exception to this, as it deviates from all Comasterids by having a rounded-conical Cd, with cirri in 3—4 whorls and powerful synarthrial backward projections, and by the occurrence of sacculi. This form, according to my opinion, is a Macrophreate form, possibly related to *Heliometrinae.*

small forms, e. g. *Comatilia*) small and shallow. Cirri often rudimentary or lacking, rarely more than in a double whorl, nearly always alternating whorls (exception *Palaeocomatella*). Cirrus-sockets without sculpture. Basal star sometimes developed. Radial joint-faces vertical. Radial cavity large, filled up by a large central calcareous plug. Muscular fossæ between RR and I Brr 1 very low, broad bands. Arms X or more. Number of the component parts of the division-series in the multibrachiate forms often very variable in systematically proximal groups as well as in different rays of the same individual. Synarthries weakly developed, often replaced by cryptosynarthries, pseudosyzygies, or syzygies. No synarthrial tubercle or synarthrial backward projection. Many syzygial septa (except in small forms). The syzygies are usually numerous. Covering plates in *Nemaster* and *Comatilia*. Pear-shaped organs instead of sacculi. The proximal and sometimes the distal pinnules also with a comb. (In the following groups only *Heliometrinae* with a rudimentary comb.) P_1 is the longest proximal pinnule, the following proximal pinnules decreasing evenly. Distal pinnules with strong hooks on the most distal segments. Disk often exocyclic, sometimes with calcareous granules. Genital glands especially well developed in the posterior arms. Creeping forms. The only family belonging to this group is *Comasteridae*.

(2) **Mariametrida**. Cd more or less distinctly discoidal, very rarely a low hemisphere. The Cd-cavity generally small and shallow. Radial coelomic processes usually protruding between Cd and the RR, and harboured in shallow depressions or meandering grooves. Cirri, as in all the following groups, always well-developed. The cirrus-sockets sometimes with an areola, otherwise without sculpture, rarely in more than two alternating whorls. Seldom any basal star. BB rarely protruding. The radial cavity large to moderate, usually filled up by a central plug. The muscular fossæ on the radial face of moderate size, sometimes very reduced or even lacking. Synarthries usually well-developed, only in *Zygometridae* partly replaced by syzygies. Arms generally more than X. The number of the segments which constitute the division-series most frequently fixed (exceptions, *Zygometridae* and *Himerometridae*). No synarthrial backward projections; synarthrial tubercles in some *Himerometridae*. Syzygial septa numerous (except in small forms). Syzygies occurring at rather long intervals on the arms. No side- or covering-plates. Sacculi present in this and all the following groups. No combs. Proximal pinnules in *Zygometridae*, certain *Himerometridae*, and *Mariametridae* of about the same length and unmodified; in the other families one or more pinnules are distinguished by their length, thickness or stiffness. The distal segments of the pinnules in this and the following groups without hooks or with rudimentary ones only. Disk here as in the following groups always endocyclic, rarely with calcareous granules *(Mariametra)*. Swimming forms = the following

groups. *Zygometridae, Himerometridae, Mariametridae, Stephanometridae, Tropiometridae,* and *Colobometridae* belong to this group.

(3) **Thalassometrida.** Cd conical to discoidal, very variable. The Cd-cavity rather deep. Cirri usually in rows. Cirrus-sockets often somewhat sculptured — contrary to the rest of the Comatulids excepting *Atelecrinidae.* A basal star generally. Basals often protruding at the corners. The muscular fossæ of the radial articular face rather large, often narrow and high and bent at an angle towards the rest of the facet. Radial cavity usually of medium size or small. Calcareous plug inconspicuous or lacking. Arms usually wall-sided and betwen X and XX. The number of the components in the division-series rather fixed (exception, e. g. *Crinometra*). Synarthries well-developed. Sometimes a synarthrial backward projection. The syzygial septa rather few. The interval between the syzygies variable. The side- and covering-plates well-developed. Arms usually laterally flattened distally, in cross section triangular. The ends of the arms terminate abruptly with 5—7 segments supporting rudimentary pinnules (a contrast to all the other Comatulids). The proximal pinnules insignificantly specialized. The pinnulars generally rectangular or pronouncedly triangular (contrary to the rest of the Comatulids). Disk often covered with calcareous plates or granules.

There are 2 sub-tribes here.

(a) *Thalassometrida* s. str. No radial pits. Articular facets of the synarthries narrow, only occupying a part of the synarthrial face. *Thalassometridae, Charitometridae, Calometridae.*

(b) *Notocrinida.* Deep radial pits. Articular facets occupying almost the whole of the synarthrial face.

  (1) Side- and covering-plates moderate. Brr and pinnulars rounded. Genital glands in the arms. *Notocrinidae.*

  (2) Side- and covering-plates well-developed. Brr and pinnulars prismatic—triangular. Genital glands in the pinnules. **Asterometridae** n. fam. (*Asterometra, Pterometra,* figg. 287, 288, 293, 294).

(4) **Macrophreata.** Cd conical, hemispherical, or, rarely, discoidal. The Cd-cavity large and deep. Basal star generally reduced (*Atelecrinidae* with large BB). The muscular fossæ of the radial facet very large, $\geq$ the rest of the face (relatively smallest in *Antedoninae*). No calcareous plug. Synarthrial backward projection present. Syzygies numerous with few septa (except in the largest forms). Arms X with very rare exceptions. Side- and covering-plates strongly reduced (largest in *Heliometrinae*). Proximal pinnules strongly polymorphous and differentiated. Two groups: (1) Cd more or less hemispherical (rarely discoidal — *Eumetra* and others). The Cd-cavity rather moderate. Cirri in alternating whorls.

Synarthrial backward projection moderate. Articular facets of the synarthries occupying almost the whole of the synarthrial face. *Antedoninae, Perometrinae*[1], *Thysanometrinae,* perhaps also *Thaumatocrinus.* (2) Cd conical – columnar. The Cd-cavity large — excessively large. Cirri in rows or tending towards rows. Synarthrial backward projection generally very large. Articular facets narrow, occupying a part of the synarthrial face only. *Zenometrinae, Bathymetrinae, Heliometrinae,* ? *Comatonia, Isometrinae* (figg. 289—292), *Atelecrinidae, Pentametrocrinidae* (perhaps excluding *Thaumatocrinus*).

B. The evolution of certain Comatulid characteristics.

When in connexion with a description of the appearance of the stem in *Pentacrinus* I gave an account of the transition-stages leading to a typical Cd, it was shown that the cirri were arranged originally in 5 longitudinal radial rows. It is not until the suppression of the internodals and the increased shortening of the nodals took place that we find two alternating, longitudinal rows, for the sake of space, in every radius. As after the development of the Cd the number of cirri increased still more, a third radial row appeared, but finally the arrangement was converted into close irregular alternating whorls. This course of development may also be noticed more or less distinctly in the ontogeny of the Comatulids. Cdd with close alternating whorls are therefore the last developed and most highly specialized in the evolution series.

Originally the cirrus-sockets had a distinct sculpture, but this has disappeared more or less completely among the younger forms.

The cavity of the Cd was originally, as all the fossil Comatulids show, fairly small to very inconspicuous, never larger than in the corresponding recent forms. It has been supposed that from the considerably larger size of the Cd-cavity in the young we might conclude that a smaller Cd-cavity represents a more specialized stage (A. H. CLARK 1915 c, p. 234). This character has, however, just as little phyletical significance as the longer joints in the young, and must be attributed to a yet unfinished calcareous deposit in the walls round the chambered organ. Small, weakly calcified species always have, in comparison with the usual type of their family, an unusually large Cd-cavity.

The stronger development of the BB is a more primitive feature, noticeable both during the phylogeny and during the ontogeny of the Comatulids.

The joint-facet of the RR seems originally to have been moderately developed and to have had an inwardly broader muscular fossa of about

---

[1] *Perometrinae* is, possibly, a type developed convergently towards the *Macrophreata* from the *Colobometridae.*

the same size as the interarticular ligament. This muscular fossa was reduced later on to a low, broad band which may even disappear entirely (cf. *Comasterida, Mariametrida*) or may also become enormously enlarged in comparison with the interarticular ligament *(Macrophreata)*. This expresses itself in the ontogeny by the young of the group first mentioned having relatively larger muscular attachments, while the young in the latter group have, on the contrary, relatively smaller ones (figg. 268, 277, 278). A small radial cavity is found only in later Comatulids (from upper Cretaceous and upwards), and a radial cavity filled with spongy calcareous tissue is never found in the earlier Comatulids but, in recent times, it is found in *Comasterida* and *Mariametrida*.

As far as we are acquainted with the fossil Comatulids, syzygies appear in the older forms, and synarthries not till the younger ones. In the great majority of the older forms the syzygies seem to have been few in number and their septa not very many. The arms were usually X in number, sometimes V, or, if greater, the number of the component parts in the division-series was very variable in older times.

C. The evolution of the Comasterid type.

The oldest Comatulids we know are found in lowest Jurassic and belong to the Comasterid type. This type had, even then, a highly developed Cd with small, closely set, and alternating cirrus-sockets, usually indistinctly or not at all sculptured, and rather strongly reduced BB. We may therefore assumme that the Comasterid type even at that period of time had a fairly long development behind it. Primary characteristics in the older forms are as follows: the Cd-cavity is still extremely small and the radial face has inwardly broader, fairly large muscular fossæ. The characteristics which even to-day distinguish the Comasterids were developed early. We meet with the first non-cirrate form in lower Cretaceous. The Cd is always more or less flattened. The radial fossæ are, ever since the very beginning, vertical and the radial cavity large, its central depression broad and deep, filled up, in recent forms, with spongy calcareous tissue. The muscular fossæ in the younger forms are low and broad. The arms in fossil forms are very little known, but, as far as we are acquainted with them, V—X, uniserial. Two unique characteristics which in recent times specially mark the separation of this group, are the exocyclic mouth and the pear-shaped organs instead of sacculi.

We may reckon the following as primitive features which are retained in forms now living: the clumsiness, the often undeveloped synarthries (e. g. *Comatula, Comaster*), the usually variable number of division-series and the number of component parts in them, the plating of the disk occurring sometimes, and the covering-plates in *Nemaster* and *Comatilia,* the gonads (best developed in the posterior radii) sometimes appearing in the arms, the creeping mode of locomotion. Specialized features are the reduction of the cirri, the numerous arms and syzygial septa, the powerful hooks on the distal pinnules, and the comb on the proximal pinnules and sometimes also on the distal ones.

D. **The evolution of the Solanocrinid type.**

The Solanocrinids appear first in the Middle Jurassic and become more common in the upper. None the less they have Cdd which are more primitively developed than in *Palaeocomaster,* and the appearance of the cirrus-sockets approaches more closely to the Pentacrinid type; moreover the BB in the oldest forms are strongly developed. We may suppose, therefore, that the Solanocrinids developed into Comatulids later than *Palaecomaster.*

It is also possible that they are derived from another branch of the Pentacrinids. In *Palaeocomaster,* and in its descendants the recent Comasterids, a strong tendency is found towards reduction of the cirri — as in *Seirocrinus.* A reduction of the cirri never takes place in *Solanocrinidae,* which always have large and powerful cirrus-sockets as in *Pentacrinus.* Possibly therefore the type first mentioned may have descended from a form more nearly related to the former Pentacrinid genus, the second type from a form more nearly related to the later one.

Among Solanocrinids, *Archaeometra* is the most primitive as regards the BB, which are very powerful. The cirrus-sockets are still rather few and large here. In *Solanocrinus* the number of cirrus-whorls and rows is increased and in lower Cretaceous XV cirrus-rows become usual. In typical Solanocrinids, however, a Cd with cirri in alternating whorls is never attained. The genus *Solanocrinus* seems, on the other hand, to show more primitive features in respect to the size and shallowness of the radial cavity and to the sculpture of the cirrus-socket.

It may now be asked whether the Solanocrinids died out or whether they survive in any of the recent forms. The former has probably been the case with a number of clumsy forms from upper Jurassic having biserial arms. Besides these we have, on the other hand, in upper Jurassic as well as in lower Cretaceous fully typical Solanocrinids with monoserial arms. Among the younger of these we find rows of large cirri on a flattened Cd, the sculpture of the cirrus-sockets has, however, nearly disappeared, the muscular fossæ are low and broad, and are possibly sometimes missing. The Cd-cavity still continues small and shallow; the radial facets lean only inconspicuously inwards and the radial cavity is therefore large (possibly it is beginning to be filled by spongy calcareous tissue, *S. leenhardti?*).

It seems to me very probable that in the recent tribe *Mariametrida,* we have the recent descendants of the Solanocrinids. The difference is that the sculpture of the cirrus-sockets in the younger forms has been still further reduced and therefore at its highest consists only of an areola and that the cirri, generally at least, alternate distinctly. We have further the following specialized features: the reduction of the muscular fossæ (distinctly pronounced already in *Solanocrinidae*) is often very advanced and sometimes complete *(Pontiometra, Stephanometra);* the radial cavity is generally filled up with spongy calcareous tissue; the syzygial septa have increased; the BB are generally strongly reduced (exceptions, certain *Himerometridae, Tropiometridae*).

Most of the primitive characteristics are shown by *Zygometridae,* certain *Himerometridae,* and *Mariametridae.* Such charateristics are: syzygy between I Br 1 and 2 in *Zygometridae,* undecided number of components in the division-series (*Zygometridae,* certain *Himerometridae*), few connecting fibres between the parietal and visceral layer of the coelom-sacs in the disk (thus the disk is easily thrown off; especially marked in *Zygometridae*), the disk covered by calcareous granules, few syzygial septa (*Mariametra, Zygometridae*), non-differentiated proximal pinnules (*Zygometridae,* certain *Himerometridae* and *Mariametridae*).

The whole of the group *Mariametridae* (with the exception of *Colobometridae*) has a rather coarse and clumsy structure, a small and shallow Cd-cavity and sparse syzygies. Among these characteristics the 2 first mentioned at least and probably also the last mentioned are primitive features. Besides this we have Solanocrinid characteristics in the discoidal Cd with rather coarse cirri, as well as in the shallow, often meandering, branched furrows which have lodged the dorsal coelom between the Cd and the radial ring.

As regards the structure of Cd, and in *Comasterida* and *Mariametrida* as regards the radial ring too, there seems, taken on the whole, to appear a struggle towards a similar ideal type. The farther the Comatulids had reached in their development, the nearer they advanced towards this goal usually, and it is therefore often more difficult to distinguish later forms of different groups than is the case with earlier ones. This explains also why the Cd and radial ring in certain recent forms of *Comasterida* and *Mariametrida,* although in many instances easy to distinguish from each other, in some cases cannot be diagnosed with certainty. The same is the case in a number of younger fossil forms. We find types among the forms from upper Cretaceous known only by the Cd which can only doubtfully be referred to *Comasteridae* or to the descendants of the Solanocrinids. To these latter it seems to me, however, that the *parvicavus* group of the genus

Glenotremites may be assumed to belong on account of the size of the cirrus-faces. Presumably the *angelini*-group may be referred here too (N. B. Shallow furrows after the dorsal coelom on the ventral face of Cd). It seems to me that we find in *Cypelometra* a specialized descendant of the Solanocrinids, which as regards the appearance of the cirrus-faces has reached the Mariametrid stage.

E. The evolution of the Notocrinid and Conometrid type.

These two form-series may be treated most suitably in connection with one another.

In the first-mentioned series the most primitive type is *Loriolometra*, represented among the species belonging to *Glenotremites* by *Gl. arnaudi* and the *essenensis* group. *Loriolometra* is continued by *Sphaerometra*, represented among the *Glenotremites* species by the *paradoxus* and, possibly, the *rotundus* groups. With the genus *Semiometra* the type has acquired so many new characteristics that I must place it in the family *Paleantedonidae*. The series has originally rather few large cirrus-sockets, arranged in rows, with a weak transverse crest, often peripherally striated, protruding BB, broad free margin of the dorsal side of the RR, relatively large radial cavity, a more or less distinct dorsal star, and, most important of all, the specially characteristic, deep radial pits in the Cd for the dorsal coelom (cf. fig. 236). The youngest representatives have numerous small cirrus-sockets without sculpture, in alternating rings, hidden BB, no free dorsal margin of the RR and a fairly small radial cavity; the radial pits are shallow or obliterated. I have observed a rosette in *Semiometra impressa*. The recent form *Notocrinus* may suitably be inserted in this series, as it is undoubtedly nearly related to *Loriolometra*, from which genus it deviates by its shallower and wider radial coelom-pits, by having a relatively larger Cd-cavity and, in full-grown individuals, by the absence of sculpture on its cirrus-sockets. The later forms of this series advance towards group 1 of *Macrophreata* (cf. above p. 231). The *lettensis* group with its fine radial pores is a corresponding form as regards this character to the *Asterometridae*, where we have deep but very narrow radial pits (cf. figg. 287, 288).

The second series, represented relatively insignificantly among species where the radial ring is also known by the genera *Amphorometra*, *Placometra*, *Conometra*, and *Jaekelometra*, is more numerously represented within the genus *Glenotremites* by the *anglesensis* and *pellati* groups. This series is distinguished from the previous one by the absence of radial coelomic pits. Among recent forms it has its analogy in *Thalassometrida* s. str.

It is very remarkable in both these series, contrary to the Solanocrinid series, what a large number of species are found of which only the Cd is known. In the genus *Glenotremites* of the Solanocrinid type only 5 species are found (the *exilis* group). But as species which can certainly be included in the two series now under discussion we have 30 species. This is due to the components in the radial ring in the case last mentioned being weakly connected both with one another and with Cd. In the recent *Thalassometrida* we find that with boiling in KOH the corresponding ossicles soon fall apart from each other and extraordinarily easily. A feature to be noticed is that the Cd and radial ring are very closely connected with each other in the recent *Mariametrida,* exactly as the case seems to have been in the fossil Solanocrinids.

It seems scarcely probable to me that the Notocrinids can have descended from any of the Comasterids or Solanocrinids. In the latter family, certainly, we sometimes find offshoots from the dorsal coelom between the Cd and radial ring, indicated by the meandering branched shallow furrows mentioned above. This, however, is something entirely different to the deep and stout, perpendicularly penetrating, pits which we find in *Loriolometra.* On account of their depth — they pierce through nearly the whole of the Cd even in full-grown individuals (cf. figg. 199, 236, 287, 288) — it is easy to assume their prolongation into the stem in stalked young.

Although we find a good many similarities as regards general features between *Archaeometra* and *Amphorometra* it is not very probable that the Conometrids either are derived from either of the 2 families first mentioned. This is made still less likely by the fact that in upper Jurassic we meet with a form which it seems might fairly well be considered a primitive ancestral form of *Thalassometrida* and *Conometridae* in general and of *Placometra* in particular.

We therefore reach the conclusion in these 2 cases also that these 2 families possibly represent one or, perhaps, two special offshoots from the Pentacrinid stock which in that case have attained the Comatulid type by independent paths.

In *Pterocoma pennata* from upper Jurassic we have a form exhibiting many characteristics in common with certain Comatulids from upper Cretaceous as well as with *Thalassometrida.* This early form does not show the least approach towards the contemporary Solanocrinids. Possibly in this species we have a type standing near to the ancestral form of one or, perhaps, both of the series mentioned above, *Thalassometrida* and *Notocrinida.* The slender shape, the long, non-differentiated, rather scanty cirri, the numerous syzygies, the prismatic pinnules with powerful side- and covering-plates (cf. GOLDFUSS 1831, WALTHER 1886) all of them indicate that *Pterocoma pennata* should be placed in the nearest connexion with the younger Comatulid types and that it has nothing in common with the Solanocrinids. Although masses of this species, otherwise almost perfectly preserved, are known, yet it is remarkable how extremely seldom the Cd has been noticed. This is presumably due to the fact that the Cd very easily becomes detached from the other parts of the animal, and possibly also that at the animal's death it was left remaining upon a still existent stem. In fact WALTHER (1886), in the only specimen among 81 examined where he found a Cd preserved, observed and figured a large round opening in the centre of the dorsal face of Cd. I observed a similar pore on the dorsal side of a Cd in a specimen I examined where the Cd had been preserved (fig. 193).

A circumstance possibly speaking in favour of *Thalassometrida* and *Notocrinida* having reached the eleutherozoic mode of life at different times is the very different point of time at which their Pentacrinulas detach themselves from the stem — in the former very early, in the latter type at a very late stage.

Thalassometrida and *Notocrinida* among the Comatulids are the groups which, in recent times, have retained most of the characteristics belonging to the stalked forms. We find these specially numerous among *Thalassometrida:* Cirri long, in transverse section somewhat rhombic (figg. 296–300, cf. fig. 295). Cd with cirri in rows, sometimes in an almost simple radial row. BB relatively well-developed. The free dorsal surface of RR generally broad. Arm-bases closely set, wallsided, ending abruptly with a piece of arm bearing rudimentary pinnules. The pinnules prismatic to triangular in transverse section. The side- and covering-plates strongly developed. The disk often closely studded with calcareous granules or plates.

F. The evolution of the Palæantedonids.

Semiometra, as was mentioned above, is a final type in the Notocrinid series and constitutes a transition form to the Palaeantedonids. The genus *Palaeantedon* is typical of this family. I do not consider it can possibly be doubted that this genus constitutes a corresponding type to the recent Antedonins or, in other words, group 1 among the *Macrophreata.* This is guaranteed by the Cd being closely set with numerous unsculptured cirrus-sockets in alternating whorls, by the large Cd-cavity, by the lack of any radial pores or pits on the ventral face of Cd, by the obliterated BB, by the large radial muscular fossæ, by the inward inclination of the radial faces, by the slender oblique Br-joints, etc. The genus *Hertha* may be considered as a predecessor of the Palaeantedonid type, specialized and characterized by the development of high narrow muscular fossæ and a small radial cavity. The recent genus *Coccometra* is a typologically corresponding form to the genus *Hertha.*

The genus *Discometra* too comes nearest to the Macrophreate type, although, as I have pointed out above, it is possible that with better knowledge the type may prove not to be genetically completely uniform. Among recent *Macrophreata* belonging to group 1, *Antedoninae* exhibit a number of more primitive characteristics, such as a relatively small Cd-cavity, rather inconspicuous muscular fossæ, weak synarthrial backward projection. It is interesting to notice that we sometimes get here radial prolongations of the dorsal coelom which reach down to the ventral side of Cd and there form small and shallow pits (cf. 1879 P. H. CARPENTER, Pl. 4 figg. 15, 16).

It seems also to me very plausible to assume that the 2nd group of *Macrophreata* mentioned above proceeded from a type nearly allied to *Thalassometridae* as well as to the fossil genera *Amphorometra* and *Conometra*. If we imagine a reduction of the side- and covering-plates in the Thalassometrid type, we get a form extremely similar to the more primitive types within group 2 — the sub-family *Zenometrinae*. The size of the Cd-cavity for which this group 2 among more advanced forms is remarkable, shows, as moreover the synarthrial backward projection also does, a more moderate development in certain *Zenometrinae* (cf. figg. 301 with 302). If it were a question of placing the genus *Conometra* in one of the recent groups, it would be difficult to decide whether it should be referred to *Thalassometridae* or *Zenometrinae*. In the same way it would be nearly impossible, in certain cases, to distinguish between recent *Thalassometrida* and *Zenometrinae* if the Cd and radial ring only were known. The genus *Amphorometra* like *Placometra* shows, on the contrary, distinct points of contact to Thalassometrid forms (to *Thalassometridae* and *Charitometridae*). It seems hardly possible that the genus *Jaekelometra* can have been the ancestral form of *Atelecrinidae*. We certainly find similarities here in the size of the BB-ring, but the relative smoothness of the cirrus-faces in *Jaekelometra*, the small size of the Cd-cavity and the steep inward inclination of the radial faces provided with relatively insignificant muscular fossæ, deviate radically from *Atelecrinidae*, where the cirrus-faces have a strong crest and where the Cd-cavity and the radial muscular fossæ are extraordinarily large. It looks too as if in *Jaekelometra* we are able to find an indication of the development of a rosette, through thin centripetal continuations on the BB. According to the scanty information we possess about *Atelecrinus* no such formation seems to be present there (cf. HARTLAUB 1912). *Jaekelometra* is thus a type standing nearer certain primitive *Thalassometrida*.

G. **Final survey of the evolution of the Comatulids.**

Our investigation of the mutual relations between the Comatulids has led us therefore to assume the possibility of 3, or perhaps 4, cases of stalked Crinoids of the Pentacrinid type having reached the eleutherozoic mode of life and become Comatulids.

The first and oldest branch of the Comatulids is represented by *Palaeocomaster,* to which the recent Comasterids correspond. They still show at the present time their unique nature by the strong tendency towards reduction of the cirri, by the frequent occurrence of exocyclic forms, by the absence of sacculi which are replaced by the pear-shaped organs, by the combs, and by the dorsal hooks. Contrary to all the other Comatulids they have never acquired the capacity for swimming, but still continue to employ a creeping mode of locomotion.

The second somewhat younger branch consists of the Solanocrinids. We find forms among these in upper Jurassic having strongly biserial arms, very clumsily built. These were, as I have pointed out in another connexion, very probably creeping forms. This type has, presumably, died out, while less specialized Solanocrinids with monoserial arms have given rise to the recent tribe *Mariametrida.* This is more specialized than the Solanocrinids through the appearance and arrangement of the cirrus-sockets, through the far advanced reduction of the BB, through the development of the calcareous plug, through the numerous arms, through the many syzygial septa. The relatively coarse arms, the small Cd-cavity, and, probably, the scanty syzygies also may be reckoned as primitive characteristics which have been retained. Besides this the *Zygometridae, Mariametridae,* and certain *Himerometridae* show a number of primitive features.

The third group which possibly has a double origin is found in *Notocrinidae* and *Conometridae.* It is divided into two distinct series of which the one, *Notocrinidae,* leads towards *Palæantedonidae* and group 1 of *Macrophreata,* the other to *Thalassometrida* and group 2 of *Macrophreata.* A form which possibly may be interpreted as a prototype to one or possibly both of these series is found in *Pterocoma pennata. Thalassometrida* has preserved a number of Pentacrinid characteristics in the long cirri, somewhat prismatic in transverse section, arranged in radial rows, in the prismatic or triangular Brr and pinnulars, in the relatively well-developed BB, in the broad free dorsal surface of the RR, in the strong development of the side- and covering-plates, and in the covering of the disk with calcareous granules.

The nearer one comes to the present time, the more difficult it may become in critical cases to distinguish the types of these different groups from each other. If I except the Comasterids, which, as is pointed out below (Chap. 5), have followed their own particular course of development, and certain *Mariametrida,* where a reduction of the radial muscular fossæ is strongly pronounced, the Comatulid groups tend toward an ideal type of Comatulid. For this reason it becomes extremely difficult to keep apart the converging forms which by different paths have approached this ideal type.

In my work of 1922 I pointed out that I considered the sub-family *Perometrinae,* which A. H. CLARK referred to *Antedonidae,* as one such series, leading from Colobometrid forms towards the Antedonid type. It might have been desirable to divide the *Macrophreata* into more groups which could afterwards have been placed at the apices of the different series of the older Comatulid types. I have not, however, chosen this way as in special cases it seemed to me to be systematically unpractical and unfeasible. I have contented myself with depicting instead as nearly as possible, guided by the facts known, the different paths of development through which the distinctly emphasized polyphyletic character of the Macrophreate group becomes explicable.

CHAPTER V.

Ciliary currents on the surface of the body of Echinoderms.

I. Introduction.

To begin with, I thought of studying only the feeding of the Crinoids and the ciliary currents connected with this, but I soon found that the task could be extended with advantage so as to include an examination of the ciliary currents found on the surface of the body in other groups among the Echinoderms too.

The feeding by means of ciliary currents in the Echinoderms is not in any way special for the Crinoids although it has long been known, and is most obvious, among the class of lily-stars. For the complete understanding of these ciliary currents, however, one must not regard them from the standpoint of supplying nourishment only. For often they also play a larger rôle in respiration and in cleansing the surface of the body. Sometimes the division of labour is more thoroughly realised, so that certain ciliary currents are more exclusively of service for one or the other of these purposes, but usually the boundary is less distinctly defined and the ciliary currents satisfy at the same time the need of nourishment, renewal of the water for respiration, and cleansing of the surface of the body.

By the guidance of the literature on this subject, together with my own investigations, I hope to be able to give in what follows an account of the occurrence and resulting effects of the ciliary currents found among the various groups of Echinoderms. As I have devoted my most profund studies to the Crinoids, the chief interest will be found to lie in the investigation of this class.

When treating of the forms in which the taking up of nourishment takes place by means of the ciliary currents, I shall use the term plankton-catcher only for the animals that live upon real plankton, and detritus-catcher for those where the food preponderatingly consists of detritus or benthonic organisms.

When observing the ciliary currents I have used carmine, finely powdered and mixed with sea-water. Very often some fresh crab-liver has been added.

It has proved of great importance that the animals were in good condition, otherwise it might happen that some of the weaker ciliary currents might not be seen, and the strong ones might appear weak. Unfortunately *Ophiactis balli*, *Amphilepis norvegica*, and *Pteraster pulvillus* were dying and could not therefore be included in this comparison. *Ophioscolex glacialis* and *Poraniomorpha hispida*, on the contrary, have been included although they might have been in better condition; they showed, however, a number of ciliary currents which made it possible to place them in their right connexion. This is done, however, with the reservation that more and stronger currents might be found in these forms.

I have obtained the material partly from the Kristineberg Zoological station, and partly from the Biological station of Hægdalen at Trondhjem (the Echinoderms marked by an asterisk originate from tha last-mentioned place).

II. Holothurioidea.

I can express myself rather shortly on the *Holothurioidea*. Even in quite young Holothurians all exterior ciliation is completely lacking. I have examined **Echinocucumis hispida* (Barrett), *Cucumaria lactea* (Forbes), **Psolus squamatus* (Koren), *Mesothuria intestinalis* (Ascan), *Leptosynapta bergensis* (Östergren), and *Labidoplax buski* (McIntosh) and could only find that the statements made by other authors respecting the absence of ciliation were correct.

The taking up of nourishment, as is well known, is performed by the tentacles round the mouth, abundantly provided with glands secreting mucus. Thus tiny particles of mud, crustaceans, molluscs, bryozoans, etc., are collected and stuck together, and by *Dendrochirota* and *Synaptidae* afterwards swept off by pushing the tentacles down into the gullet. Within the *Aspidochirota*, which shovel the mud into the mouth, this is glued together by the mucus. One obtains an interesting idea regarding the amount of bottom-material collected and ingested from Crozier's paper (1918).

A stream of water for respiratory purposes arises from contractions of the muscles of the respiratory trees, but exchange of gases is also performed through the thin skin. This breathing through the skin in Synaptids and Elasipods, which lack respiratory trees, is, as far as we know, the only manner of respiration in these animals. To facilitate the exchange of gases the walls of the coelom are strongly ciliated in all Holothurians and the coelomic fluid is thus kept in motion.

There is no question of cleansing the body-surface in the same sense as with other Echinoderms, and perhaps this is not so necessary either. Many Holothurians sit really buried, and these usually keep the surface of the body free from mud through the secretion of mucus in which the mud becomes imbedded. The tube of mud thus formed is kept away from the body by means of strong movements of the muscles in the body-wall (e. g. *Labidoplax*). Others cover the body with small stones and similar things which are fixed to the body by the sucker-feet, e. g. the *Cucumaria*-species. Such species as *Cucumaria lactea,* for example, have very feeble power of removing the particles that have rained down upon them, and grains of carmine would remain lying on the body-surface for days.

But still it is possible that within this class we shall find the only Echinoderm which is really a true plankton-catcher, and where the plankton is brought to the mouth by means of ciliary movement: *Pelagothuria.* Unfortunately no investigations concerning the ciliary currents have been carried out with living animals, and the material collected by the Valdivia expedition, which is said to contain fixated *Pelagothuria,* has not yet been examined. According to CHUN (1900, p. 511) typical plankton nourishment is found in the intestine. KEMNA (1905) has imagined the possibility of nourishment being collected by means of ciliary currents. In case of his assumption being right, it is easy to suppose that the whole of the ventral side of the disk or swimming-bell is ciliated. I may, however, point out the possibility of there being still another way for the catching of food which on the whole is more in accordance with the rest of the *Holothurians.* In *P. bouvieri* the tentacles are long, forked at the ends, and provided with small branches. Under these sit the finger-shaped appendages united by a swimming-web. One may imagine that the tentacles lick off the plankton which falls down on this disk and afterwards sweep the food into the gullet in the usual manner. The tentacles in the above-mentioned species are 35 mm. long, the finger-shaped appendages 70 mm. at most. In both the other species the tentacles are much shorter in comparison with the finger-shaped appendages. One may, however, express oneself like HEROUARD (1906) and say that the tentacles in these species are contracted to a very high degree.

GILCHRIST (1920) has described an interesting form from the Cape of Good Hope, *Planktothuria,* forming a link between *Pelagothuria* and the Elpidiid type by the occurrence of podia, a stone-canal in connexion with the surface of the body, and, although only weakly developed, a calcareous skeleton. The finger-shaped organs are not nearly so well-developed as in *Pelagothuria;* they consist of a number of oral podia, arranged in an incompletely closed hood-shaped circle round the ventral mouth and its tentacles. The transparent animal, deeply imbedded in gelatinous epidermis, is probably bentho-planktonic. The stomach contained: greenish flocculent material, radiolarians, foraminifera, many diatoms, sponge-spicules. One may assume that the typical form for the feeding is a combination of the usual Holothurian method of collecting mud (the appearance of sponge-spicules points in this direction) and the above sketched planktonic manner of food-catching in *Pelagothuria*.

III. **Echinoidea.**

In the sea-urchins the surface of the body has a ciliated epithelium which, however, does not extend over the spines.

The Echinoids I have examined are the following: *Psammechinus miliaris* (L.), *Strongylocentrotus dröbachiensis* (O. F. MÜLL.), *Echinocyamus pusillus* (O. F. MÜLL.), *Brissopsis lyrifera* (FORBES), **Brisaster fragilis* (DÜB. & KOR.), *Echinocardium cordatum* (PENN.), *E. flavescens* (O. F. MÜLL.), and *Spantangus purpureus* (O. F. MÜLL.).

The conditions exhibited by *Psammechinus* and *Strongylocentrotus* are fairly simple. The bases of the spines, like the epithelium appearing between them, are ciliated, and the ciliary movement drives a current towards the mouth. Centrifugal ciliation is found on the aboral side of the ten gills appearing in the region of the mouth. Other parts of the mouth-region, however, ciliate centrifugally. Usually the grains brought in by the ciliation are rejected at the bases of the teeth. The exterior of the tube-feet is scarcely ciliated, but a rapid current runs inside them which enters the feet through one of the ambulacral pores and goes out through the other. Even inside the gills the circulation of the coelomic fluid is very rapid, but here the exterior epithelium is also ciliated. In the periproct the current sets towards the anal opening. The carmine grains are often left lying on the calcareous plates of the periproct, but sometimes they are carried down by the currents into the anal opening. The madreporite in *Strongylocentrotus* ciliates, as in *Psammechinus*, from right to left along the proximal (= adperiproctal) margin; in other respects the current runs adorally or in a circle round the margin of the madreporite. The grains are glued together in large masses by the mucous secretion and may, like the excrement, be removed by the movements of the animal. The excrement in *Strongylocentrotus* was picked away from the animal by means of the pedicellariae and the small spines which acted like pincers and levers respectively.

Echinocyamus pusillus. The dorsal side shows centrifugal ciliation of the bases of the spines and the epithelium between them, as in the previous species. The currents on the ventral side are either centri- or axipetal (cf. fig. 309). Usually the grains of carmine pass over the mouth and afterwards continue at a quick speed to the anus, where there is a rapidly discharging current which whirls the particles out from the body.

Among these forms provided with teeth, the ciliary currents seem to serve in the first place to facilitate the circulation of the respiratory water; but to some degree they assist in the cleansing of the body. A great part of the cleasing is, however, performed by the pedicellariae and the spines which always come into activity when anything falls upon the animal. The latter are also used in some species, e. g. *Strongylocentrotus* and *Centrostephanes longispinosus,* for removing the excrement. VON UEXKÜLL (1900) has given an account of, and explained, the way in which the excrement is generally removed from the surface of the body (Klinken der Stacheln) e. g. in *Echinus* and *Spherechinus*. *Arbacia pustulosa* lacks ciliation and cannot "Klink" the spines, so that in the still water of the aquarium the excrement remains lying on the animal for days, and very soon poisons it (MANGOLD 1907 a, v. UEXKÜLL 1900, 1909). — The regular sea-urchins, like *Echinocyamus,* are predaceans, eaters of carrion, vegetables, or detritus, according to the statements of BLEGVAD (1914), EICHELBAUM (1910), MILLIGAN (1916), PETERSEN (1889), PROUHO (1887, p. 229), SÜSSBACH & BRECKNER (1911), and many others. The nourishment is caught either by the sucker-feet or by the strong teeth. Occasionally it is transported by the help of the spines to the mouth (*Echinus lividus,* according to EISIG 1883). Among most of the families belonging to *Regularia*, forms have been described which live in the surf or at the low-water mark in holes burrowed in the cliffs by themselves (JOHN 1887, SIMROTH 1888, and others). Presumably these forms have not developed any special manner of feeding. They are nearly related to, or even identical with, species living a free life, and as they live in the region of the surf, detritus and small animals are constantly being washed down into their holes. SIMROTH has stated that they often cover the entrance to their homes with a *Patella*-shell which is held fast by the tube-feet. Presumably this is a manifestation of the same instinct which causes certain of the free-living sea-urchins to disguise themselves. The stay-at-home sea-urchins may possibly in this way surprise a passing prey. The poisonous forms of *Diadematidae* and the Echinothurids which have been described by KÜKENTHAL (according to HAMANN), and SARASINS (1887) are presumably also endowed with predatory instincts.

Some forms are found among the *Gnathostomata* which are so flattened that the animal becomes a more or less thick disk only. Such forms are found partly within the sub-family *Arachnoidinae* of the *Clypeastridae*, and partly among the *Scutellidae.* The last-mentioned family contains genera with holes or incisions in the disk-shaped test, and the ambulacral groove is also very forcibly forked (cf. fig. 310). I have examined sections through the ambulacral groove of *Arachnoides placenta* (L.) and of *Astericlypeus manni* (VERILL) without being able to come to any certain conclusion concerning the presence or absence of ciliation. As regards the *Scutellidae* I suspect, however, that the extensive forking of the ambulacral groove has something to do with the manner of feeding. *Astericlypeus manni* is a littoral form from Japan which lives buried immediately below the surface of the sandy bottom. The intestine in comparison with the size of the body is very small, if one compares it for example with the intestine of the Spatangids. The contents of the intestine consisted of tiny grains of sand (0·05—0·15 mm., occasionally 0·30 mm.), bits of vegetable epidermis (to 0·5 mm.), detritus, diatoms, and foraminifera, tiny copepods (to 0·25 mm.), flagellata, algous fibres, siphonophores (the largest pieces 0·7×3·0 mm.), rotifers, single Acaridæ and Chætopode-bristles. I consider it probable that the subdivisions of the ambulacral groove, which all converge on the mouth, carry to the animal at least some part of these nutritive particles by means of ciliation, even if the ciliary currents, which undoubtedly appear on the surface of the animal, are also of considerable importance for the circulation of the respiratory water.

BLEGVAD, EICHELBAUM, GANDOLFI HORNYOLD, GRAVE, HOFFMANN, ROBERTSON, and v. UEXKÜLL have given their attention to the feeding, the ciliary currents, and the habits among the Spatangids, especially investigating these conditions in *Echinocardium cordatum, E. flavescens,* and *Spatangus purpureus;* GRAVE has devoted his studies to the examination of the biology of *Maera (= Moira).*

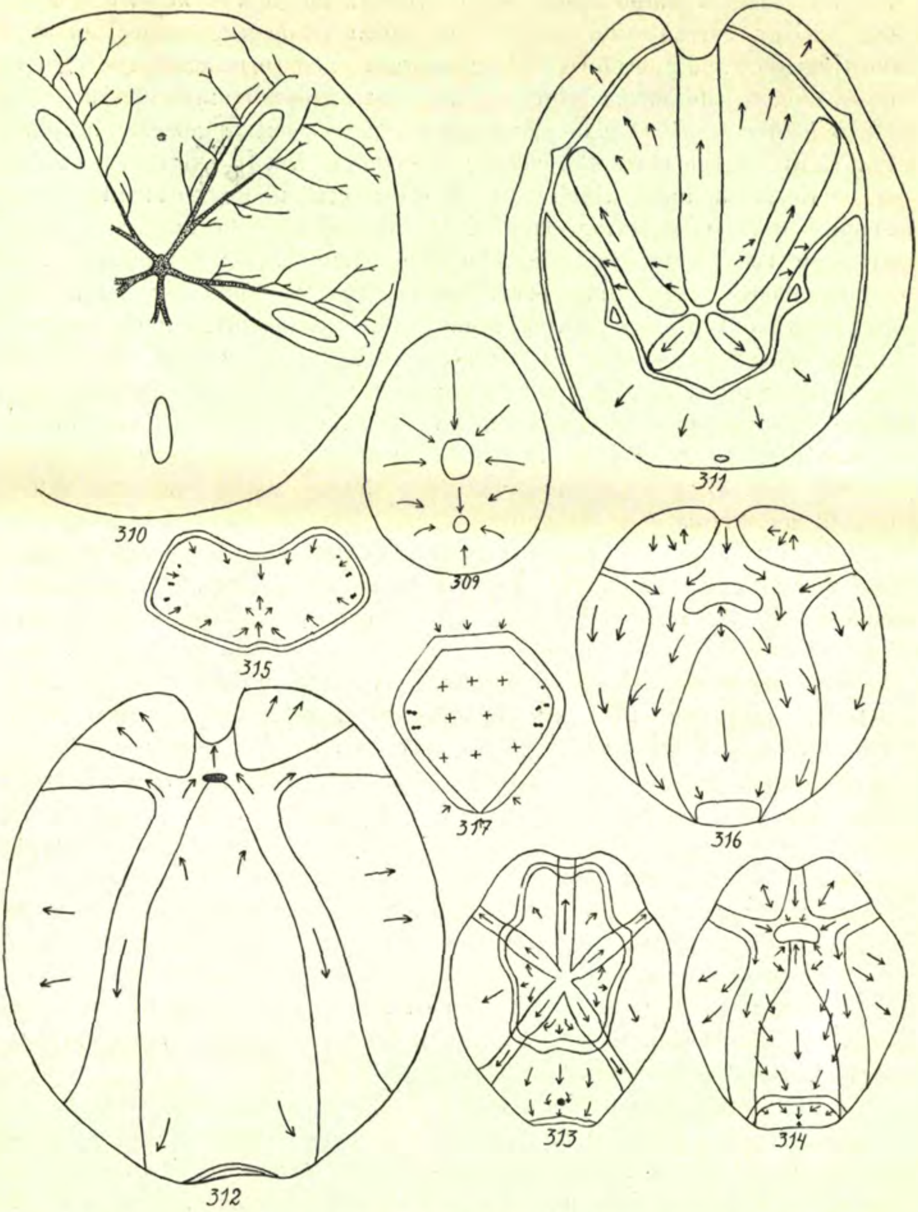
It is evident from the investigations of these authors that the Spatangids live buried in sand or mud in a burrow which is connected with the surface of the bottom by means of a canal, lined with mucus. Behind the anal opening a similar canal exists which is lengthened according as the animal slowly digs its way forward through the mud. By means of the canal leading to the surface, the aerating funnel, the animal is supplied with oxygenated water and the rosette feet draw down small grains of sand and nutritive particles which they have collected from the surface (CUÉNOT, ROBERTSON, v. UEXKÜLL). GANDOLFI HORNYOLD distinguishes between the rosette feet of the mouth, which pluck up grains of nourishment and carry them to the mouth, where the small circumoral spines push them down into the gullet, and the rosette feet of the median ambulacrum of the trivium, which are differently built and act chiefly as organs of sensation and sense, and at the same time according to v. UEXKÜLL probably assist in lining the aerating funnel with mucus. According to the observations of GANDOLFI

HORNYOLD and myself, there is no shovelling of the bottom material into the mouth, as some of the older authors and v. UEXKÜLL assume.

There is no necessity for the aerating funnel mentioned above to be always present, I even suspect that in normal cases it is often missing. I let down 20 specimens or so of *Echinocardium cordatum* on a loose mud-bottom (the same bottom from which the animals had been taken). After a quarter of an hour the majority had dug themselves down, after an hour they were all buried. Among them a number of young, 10—13 mm. high, could be seen through the glass-wall of the aquarium. They dug down deeply into the mud, the dorsal side was sometimes as much as 25 mm. under the surface of the bottom. Larger specimens did not dig down so deeply in proportion. No funnels could be observed leading from the burrows in which the animals were situated to the surface. The mud was, however, very loose and mellow so that presumably the circulation of the water was fairly active nevertheless. *Spatangus purpureus* lived for a fortnight in an aquarium, buried in shell-sand taken from the place of discovery (Bonden, a small Island, 6 miles outside the Kristineberg Zoological station). The height of the test was 19 mm., the dorsal spines shot up 7 mm. further. The dorsal surface was about 20 mm. below the surface of the bottom. I was not able to observe any funnel to the surface in this case either. The particles of clean-washed shell-sand lay very loosely, however, so it was certainly easy for the water to circulate between the particles. With this *Spatangus* I was also able to observe how the rosette feet of the mouth picked up tiny particles from the walls and floor of the burrow. Sometimes they let these go again, sometimes they carried them to the mouth. *Brissopsis* also buries itself in natural bottom, but not so deeply as both the preceding species do. One can therefore often observe the rosette feet from the median ambulacrum of the trivium moving over the surface of the bottom. The clay in which this sea-urchin lives is also much more tenacious and of a less penetrable consistency.

It may be remarked that diseased and dying animals, and those living in water insufficiently supplied with air, only bury themselves very slightly in the bottom or even not at all.

The epithelium of the surface of the body is ciliated. GANDOLFI HORNYOLD (1910 and 1914) expressed the view that the ciliary movements thus brought about, together with the mucous secretion, would assist in removing the small particles which have rained down on the surface of the body. (It is remarkable how clean the animal can keep itself in the aquarium, even in the most clayey water.) GANDOLFI HORNYOLD and v. UEXKÜLL consider that the spines cause the circulatory currents round the animal which are so important for the respiration. According to the former it is the oar-shaped sternal spines which cause the movements of the water. But doubtless the ciliary currents describ-



Figg. 309—317. 309) *Echinocyamus pusillus* Diagrammatical sketch of ciliary currents of ventral side, $^{5}/_{1}$; 310) *Astericlypeus manni* The ramifications of the ambulacral furrow, $^{2}/_{3}$; 311—312) *Brisaster fragilis* Diagrammatical sketch of the ciliary currents of the dorsal and ventral sides respectively, × 1 $^{1}/_{3}$; 313—315) *Brissopsis lyrifera* 313—314) Ciliary currents of the dorsal and ventral sides respectively, $^{2}/_{3}$, 315) Ciliary currents of the subanal fasciole, $^{2}/_{1}$. 316—317) *Echinocardium cordatum* 316) Ciliary currents of the ventral side, × 1 $^{1}/_{3}$, 317) Ciliary currents of the subanal fasciole; + means perpendicularly discharging currents, $^{3}/_{1}$.

ed below are of importance for the respiration too. The direction of these ciliary currents has not before been made the subject of any investigation, and therefore I shall now proceed to describe the course they take in the forms which I have had an opportunity of studying.

Brisaster fragilis. The dorsal side ciliates centrifugally. The part situated inside the peripetalous fasciole-band is freed by this means from the particles of mud which are thus collected upon the mucilaginous fasciole. In the posterior part of the dorsal side the mud is concentrated on the lateral fasciole. On the ventral side the lateral paired interambulacral areas ciliate centrifugally, and here the grains are therefore thrown out from the animal's sides. The sternal interambulacrum too ciliates centrifugally at its posterior margin; adorally the currents set towards the mouth. The ambulacra ciliate aborally with the exception of the adoral parts of the bivium, where the current runs in towards the mouth (cf. figg. 311, 312).

Brissopsis lyrifera. The dorsal side shows on the whole the same currents as *Brisaster*. The interambulacral parts inside the fasciole, however, all ciliate towards the ambulacra. Ventral side: Posterior part of sternum ciliates towards the subanal fasciole. The greater part of the ambulacral trivium ciliates towards the mouth. The margins of the subanal fasciole ciliate between the bases of the clavulæ towards the centre of the fasciole. Between the two tufts of spines runs a scattered band of clavulæ and the current proceeds along this a short way from both sides. Then the grains proceed out between the spines (cf. fig. 315). Rosette feet are found within the subanal fasciole as well as in the median ambulacrum of the ambulacral trivium. The rosette feet first-mentioned, and the tufts of spines, together with the grains of mud embedded in mucus, probably serve to keep open and model the posterior funnel as far as this goes. The grains of mud are therefore concentrated partly on the subanal, partly on the peripetalous fasciole; partly they are thrown off from the animal's sides, and lastly, an inconsiderable number of them are carried to the mouth. (Cf. figg. 313, 314.)

Echinocardium flavescens. Ventrally the ambulacral trivium ciliates adorally, .but the currents bend when passing the mouth and continue centrifugally in the ambulacral bivium. The particles of mud are concentrated on the subanal and the interior petalous fasciole, or are rejected from the body. According to the closely set spines round the interior petalous fasciole and the mucus secreted here, the grains of carmine, in normal cases, do not reach the body, but are embedded in a mucous layer, which is picked off by the movements of the spines.

Echinocardium cordatum. In this species the currents are practically identical with those in *E. flaveseens,* but the body-surface and so also the ciliary currents were easier to observe (fig. 316). In this species, as well as in the other Spatangids, it may be considered the rule that the young have proportionately more scattered spines, and it is easier therefore to observe the currents. From the interior part of the subanal fasciole run strong discharging currents (fig. 317). Two groups of rosette feet (in young specimens only 2) occur, which are exceedingly extensible and are certainly used in lining the subanal passage, to which the excrement is transported.

Spatangus purpureus lacks a dorsal fasciole. The dorsal side ciliates, as in the preceding species, centrifugally — on the posterior part of the test therefore, towards the subanal fasciole. The ciliation of the ventral side corresponds almost completely to that of the preceding species (cf. fig. 318).

We thus see that currents arise in all the Spatangids which serve partly to keep the animal clean — especially necessary and very effective, as one can ascertain from the specimens of *Brissopsis* creeping up from the mud in the "clay-tubs" at Kristineberg — partly to concentrate the grains of detritus on the fasciole bands. The grains are glued together here by the mucus secreted by the clavulæ. The detritus and sand respectively are removed and packed by the rosette feet and the dorsal long spines towards the walls of the funnel (cf. VON UEXKÜLL 1907, p. 316), which in this way is enabled to form a firm wall against the loose mud lying round it or against the surrounding sand. (Cf., however, also my biological observations recorded above.) In the same way the lateral and subanal fasciole respectively may assist in building a wall for the tunnel, proceeding from the posterior part of the animal, which is then held open and modelled by means of the two posterior tufts of spines and the posterior rosette feet. (Cf. VON UEXKÜLL 1907, fig. 7.) The ciliary currents have probably some significance as regards the circulation of water, although the work of the sternal spines must be considered of importance too, as these may give rise to considerable water-currents. Those currents chiefly used for cleansing, as has been shown above, are of insignificant importance as regards the feeding.

IV. **Ophiuroidea.**

A. **Different types of ciliary currents.**

In the brittle-stars the epithelium is usually rubbed off or is indistinct — a syncytium fused with the usually calcified corium (HAMANN). Only at the margin of and in the bursæ the epithelium is always developed in a normal way and is furnished here with ciliary bands too.

Corresponding to this I have often found ciliary currents in the neighbourhood of the bursæ only. But in many of the forms, as will be seen from the descriptions, currents also occur in other parts of the surface of the body.

The Ophiurans investigated were the following: *Ophiura texturata* LAMARCK, *O. albida* FORBES, *O. robusta* AYRES, *O. affinis* LÜTKEN, *Amphiura chiajei* FORBES, *A. filiformis* (O. F. MÜLL.), **Ophiacantha abyssicola* G. O. SARS, **O. anomala* G. O. SARS, *Ophiopholis aculeata* (O. F. MÜLL.), **Ophioscolex glacialis* MÜLL. & TROSCH., *Ophiothrix fragilis* ABILDG., *Ophiocomina nigra* (ABILDG.), *Asteronyx loveni* MÜLL. & TROSCH.[1], and **Gorgonocephalus caput-medusae* (L.).

For the sake of greater convenience, I have distinguished three different types of ciliary currents among the brittle-stars examined.

The first group includes the *Amphiura* species. The current in the bursæ takes a reverse direction here to that in the following groups, as the intruding current appears adorally and the extruding current, on the contrary, at the aboral angle. Along the lips of the bursal slits the ciliation runs orofugally. The animal has otherwise no currents, excepting in the radial corners of the mouth, and on the first proximal segment, where the current runs centripetally.

As typical of the second group I choose to describe *Ophiura texturata*. The currents round the bursal slits correspond on the whole to those which WINTZELL (1918) described in *O. ciliaris* (= *O. texturata*). On the dorsal side, at the bases of the arms where the bursal slits end, the water flows in; on the ventral side, especially adorally, the grains are thrown out from the bursæ. In the radial corners of the mouth runs an adoral current which may also be observed on 2 or 3 of the most proximal arm-joints. As is well known, this species has a row of pits on the ventral side in the articulations (organs of sense?). The three most proximal of these ciliate centripetally, one or two of the following ones only whirl up the grains, the 6th—8th of the pores have centrifugally directed currents. Otherwise the surface of the body lacks ciliation (fig. 320). *Ophiura albida* (like the following Ophiurids) lacks these pits and their ciliation, excepting on the first arm-joint, where the ciliation is centripetal. Otherwise its ciliation corresponds exactly to that of the preceding species (fig. 319). In *O. robusta* the bursal slits are short and therefore confined to the ventral side, where the aboral part, the bottom, and proximal margin ciliate adorally. Centripetal ciliation appears at the bases of the mouth-feet too, and in the radial

---

[1] I have not been able to observe this species alive, but the statements given below, regarding the ciliary currrents in this species, were made by Professor A. WIRÉN and Fil. lic. M. AURIVILLIUS. These gentlemen, during the summer of 1923, had the opportunity of studying living specimens at the Kristineberg Zoological Station, and were kind enough to observe this species on my account. The animals were dredged in the depths of the Skagerack (250 mtrs.) North of the Skagen. They were brought to the station alive in cooled and thoroughly aerated sea-water of the salinity obtainable out in the open sea.

corners of the mouth. Otherwise ciliation is lacking. The same ciliary currents appear in *Gorgoncephalus caput-meduse,* and in *Ophioscolex glacialis* also the currents are weak and confined to the bursal slits. In *Asteronyx loveni* Prof. WIRÉN and Lic. AURIVILLIUS could verify the absence of ciliary currents everywhere, excepting possibly in the small interradial cavities, into which the bursal fissures open. Here the grains were seen to flow from the bursal openings towards the centre of the cavity. It was impossible, however, fully to verify the presence of ciliary currents, as the animal made rapid contractions of the muscles of the ventral side, evidently in order to pump water in and out of the bursæ, and so started strong currents of water going.

Taken as a whole, *Ophiacantha abyssicola* and *O. anomala* correspond to *Ophiura albida.* I could not, however, verify any axifugal current towards the bursæ on the proximal arm-joints; and the ventral interradial parts of the disk ciliate centripetally. On 1 – 2 of the proximal arm-joints an adoral current is found (fig. 321).

Ophiura affinis forms a connecting link with the next group. The ventral interradial parts, excepting the mouth-shields ciliate centripetally, as in both the preceding species. Only the ventral part of the first arm-joint has adoral ciliary currents. The grains ciliate upward from the bursal slits towards the bases of the feet, i. e. radipetally. Radipetal currents are, however, distinctly visible still further out on the arm (even as far as the 9th arm-joint when the animal is viewed from the dorsal side). If the arm is observed in dorsal view the direction of the ciliation is axifugal. It only occurs between the rows of spines and stops at the bases of the ambulacral feet.

The third group. *Ophiocomina nigra.* Ventral side: In the distal portion of the interradial parts of the disk the water flows into the bursæ. The middle part of the distal margin of the interradii, however, ciliates centrifugally. The currents emerging from the bursæ upon the arms are weak. The 5 most proximal arm-joints have the currents directed adorally (fig. 323). Dorsally the disk shows centrifugal or confused currents; in the neighbourhood of the bases of the arms these currents are more decidedly centrifugal. In the proximal half of the arm, weak axifugal currents run between the rows of spines to the bases of the feet.

Ophiothrix fragilis has fairly strong currents. Ventral side: The bursal slits and the interradii ciliate as in *Ophicomina* (in the distal parts of the interradii the currents run towards the bursæ). Four proximal arm-joints have an adoral current. The currents between the transverse rows of spines to the bases of the ambulacral feet appear fairly well-developed in the whole of the proximal half of the arms (at least as far as the 10th arm-joint visible in dorsal view); distally the currents become slower, but are still evidently visible from the dorsal side as axifugal currents. The dorsal side of the disk ciliates between the bases of the spines with which the skin is studded chiefly centrifugally (fig. 322).

Ophiopholis aculeata. Ventral side: The interradial parts of the disk, as well as 3 of the proximal arm-joints, ciliate centripetally. The 4rd—8th ligaments between the 4rd—9th arm-joints have laterally a ciliation directed centrifugally; medially no current appears here (cf. fig. 324). Otherwise the same as in *Ophiocomina.* The arms between the rows of spines, as in *Ophiothrix,* show fairly strong currents, which in this case also reach as far as the bases of the feet. On the dorsal side of the disk confused circular currents or centrifugal ciliation is seen, the latter especially in the neighbourhood of the bursæ.

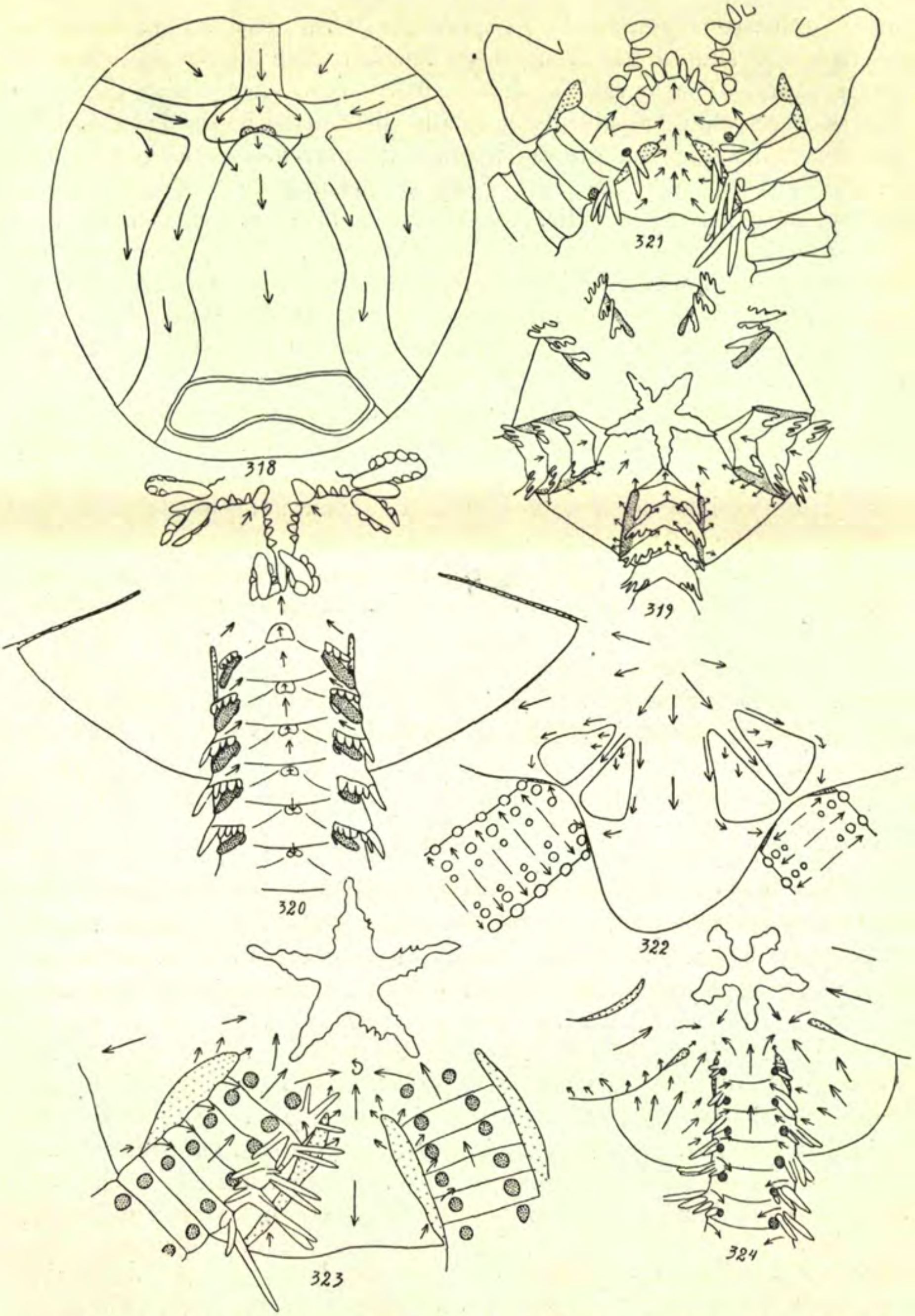
Thus among the Ophiurids examined by me the first group includes the *Amphiura* species. These have the bursal ciliary currents directed aborally.

In the second group come the genera *Ophiura, Ophioscolex, Ophiacantha, Asteronyx,* and *Gorgoncephalus,* all of them characterized by the lack of ciliation between the transverse rows of spines on the arms, and, like the following group, having centripetal (adoral) currents in the bursæ.

In the third group we find *(Ophiura affinis), Ophiocomina, Ophiothrix,* and *Ophiopholis,* distinguished by rather strong currents, between the rows of the arm-spines, reaching to the ambulacral feet.

B. **Biology.**

The *Amphiura* species live buried in the mud (cf. DES ARTS 1910), and feed on small particles of detritus which are conveyed to the mouth by the help of the feet. Possibly the deviating conditions of the ciliary currents found in this genus may have some connection with their subterranean manner of living. Another peculiarity which certainly can be placed in correlation with the sub-benthonic mode of life, is the respiratory movements, already observed by APOSTOLIDÈS (1882). WINTZELL (1918) denied that these movements were of a respiratory nature. The Ophiurids examined by him, however, were only "*Ophiura ciliaris* and *albida* and a few other Ophiurids" (p. 14). He has sometimes observed in these species a rythmical rise and fall of "skivans ryggvägg" (the dorsal wall of the disk). These movements were certainly of a different kind from those appearing in the *Amphiura* species, where the movements serve to dilate and contract alternately the bursal cavities. I have found this respiratory movement marked most plainly in *Amphiura filiformis* which is furnished with soft skin on the ventral side; it is also found, but is less pronounced, in *A. chiajei.* It is performed



Figg. 318—324. 318) *Spatangus purpureus* Ciliary currents of the ventral side, × $1\,{}^{1}/_{3}$. 319) *Ophiura albida* Ciliary currents of the ventral side, $^{7}/_{1}$. 320) *Ophiura texturata* Ciliary currents of the ventral side, $^{5}/_{1}$; 321) *Ophiacantha abyssicola* Ciliary currents of the ventral side, $^{7}/_{1}$. 322) *Ophiothrix fragilis* Ciliary currents of the dorsal side, $^{5}/_{1}$; 323) *Ophiocomina nigra* Ciliary currents of the ventral side, $^{5}/_{1}$; 324) *Ophiopholis aculeata* Ciliary currents of the ventral side, $^{5}/_{1}$.

once or twice a minute by *Amphiura filiformis* by strong dilatation of the soft skin of the ventral side, which after 35—50 seconds sinks down again. The bursal fissures usually stand open during the whole process. As the Amphiurids normally lie buried in the bottom-slime, one may imagine that these respiratory movements pump the water in and out through the narrow canals leading to the surface of the bottom in which the arms lie. One may often also see, round the openings of the canals through which the arms protude, a hasty whirling up of particles of mud which indicates that there is a strong discharge of water through the canals. (The same was observed by DES ARTS 1910.) The transport of food to the mouth takes place by the help of the feet (DES ARTS).

In the 2nd group the particles of nourishment reach their destination partly by the animal bringing its mouth near the prey, partly by the curving in towards the mouth of the rolled in arm-tips, partly, as verified by BLEGVAD, GRAVE, HAMMANN, VON UEXHÜLL, and others, by the food beeing carried along the arms with the aid of the tube-feet. I scarely consider it possible that the ciliary currents near the bursæ, as WINTZELL (1918, pp. 12 and 42) thinks probable, have the power of transporting any considerable amount of the bottom-slime into the stomach.

A group which in this connection deserves more detailed treatment is that of the Euryalids. The species belonging to the order *Euryalae* fasten themselves upon corals and similar objects, becoming interlaced with these. How then do they obtain nourishment and of what does their food consist?

They are able, probably, to capture a small amount of plankton from the water with their feet (Dr. ÖSTERGREN has mentioned to me that he found *Oikopleura* among the contents of their stomachs). As I shall show below, however, at least in certain cases the food consists of material scraped off from the sub-stratum and is carried to the mouth by the help of the tube feet or the distal arm-tips.

In 2 specimens of *Gorgoncephalus caput-medusae* which I examined the contents of the stomach seemed to consist mostly of remains of the crusts which covered the stem of *Tubularia imperialis* upon which the animal was fixed. I also examined the contents of the stomach in a number of specimens of *Asteronyx loveni.* I found here, too, masses of for the most part unrecognizable detritus, organic matter containing abundant fat globules. These animals are found clinging upon the Pennatulid *Funiculina quadrangularis,* which pushes down into the clay of the bottom, by its stalk. Owing to the complete absence in the stomach of *Asteronyx* of any bottom-material, one was enabled to form the conclusion that these animals do not leave their elevated position to collect food from the bottom. Regarding the origin of the masses of detritus, which filled the stomachs of the animals I was long doubtful. If it was of planktonic origin one might certainly have expected to meet with some identifiable remains, like those I shall describe from the stomachs of the Crinoids: crustacean casings, diatom-tests, etc. Softer objects also may usually be identified for a fairly long time in the stomachs of the Crinoids (cf. below). As the material was so transformed as to be quite unrecognizable, I thought it possible that in some way the animals, perhaps being commensals, might get up food out of the stomachs of the Funiculinas, and therefore I examined a number of these latter, but with a negative result. The inconsiderable remains I found there could not possibly be enough to supply an *Asteronyx* with food. I found an answer to the problem, however, in a couple of specimens which were fixated shortly after their capture — the rest of the animals were not preserved until some time after they were taken. I found in these specimens whole tentacle-crowns of Funiculinas, some in a completely, others in a partly, undigested condition. Even in the first specimens examined I had observed the tentacles, which disintegrate last, as small ovoid bodies, but could not explain their origin. The tentacle-crowns have no spicules, thus differing from the other parts of the *Funiculina*-colony, and may therefore be digested easily and quickly without leaving any traces after them. I assume therefore, contrary to MORTENSEN (1912), that *Asteronyx,* at least in certain cases, nourishes itself upon the pinched-off *Funiculina*-polyps. I have actually found that the rachis is sometimes scraped quite bare from polyps on the part where the *Asteronyx* sits (cf. fig. 308). In other cases it looks as though the parts scraped clean begin to regenerate small polyps anew.

The rôle evidently played by the transformed arm-spines must be noted here. Among various Ophiurans we often find that one or more of the arm-spines are transformed, usually into saw-shaped organs: tentacle-hooks. These appear sporadically, and then scantily developed among the *Ophiurae*, as in certain *Ophiothrichidae (Ophiothrix, Ophiopteron),* and in certain *Amphiuridae* (*Amphioplus ancistrotus, Ophiopholis).* In *Ophiomyxidae, Trichasteridae, Asteronychidae,* and *Gorgoncephalidae,* on the contrary, they are very numerous and well-developed. Besides this we find among the Gorgoncephalids a modified form of these tentacle-hooks in the so-called girdle-hooks. These usually appear in double rows on the dorsal side of every joint and are strongly curved, one- or two-pointed hooks of lesser dimensions than the tentacle-hooks which usually have several hook-processes only bluntly bent at an angle. We seem to have transition-forms between these two types in the *Asteronychidae* (cf. MORTENSEN 1912; cf. also BROCH 1922, DÖDERLEIN 1911, LUDWIG 1878, 1888, MATSUMOTO 1917, MORTENSEN 1920 b). I refer to the drawings of tentacle- and girdle-hooks from one and the same joint of *Gorgoncephalus* (figg. 325, 326).

It is probable that the first type of these hooks originally served only as anchors, the other type, resembling fish-hooks might, on the contrary, it seems to me, play a part in catching and holding fast detritus, and pinching off the Anthozoan polyps. DÖDERLEIN (1912 b) pointed out a peculiar circumstance connected with the *Gorgoncephalinae*. These may be arranged in an ascending series in which the lowest forms have mutually similar arm-divisions furnished with scanty tentacle-hooks and numerous girdle-hooks (*Gorgoncephalus* belongs to these). The highest forms in the series (*Astrodactylus, Astroboa,* etc.) have differentiated arm-divisions, so that the distal are long and slender and furnished only with girdle-hooks, while the proximal are short and thick and abundantly supplied with tentacle-hooks. The proximal parts of the arm in these cases also lack tube-feet. I imagine that a gradually progressive division of labour has taken place here, by which the most differentiated types obtained their slender greatly divided distal arm-divisions with their girdle-hooks, adapted exclusively for catching food, while the thick and short, insignificantly branched, proximal arm-divisions have gained the rôle of anchoring organs. In the Euryalids we thus find arms with countless small hooked spines, very suitable for capturing all the particles which come into their neighbourhood. In the *Trichasteridae* and *Asteronychidae* this apparatus for catching food is still rather primitive, but it reaches a high degree of perfection in the *Gorgoncephalinae.* This girdle-hook apparatus of the arms is found in its most original form among the *Asteronychidae* and reminds one very much, in its construction and, as it seems to me, also in its function, of the radula of certain predatory molluscs.

In the last group come those Ophiurans in which I have found ciliary currents running towards the ambulacral feet between the rows of spines. In this case, evidently, we may presume that some amount of detritus becomes concentrated at the bases of the tube-feet. By the aid of the feet the food may afterwards be transported to the mouth, as VON UEXKÜLL (1905) observed in *Ophiothrix fragilis.* It must be noted that two species included in this group, *Ophiothrix,* and in a still higher degree *Ophiopholis,* are especially sluggish animals, which for days or weeks may sit immovable, crept into a mussel-shell or into a bit of scoria. These species have very strongly papillate feet, a condition that is generally completely missing in the rest of the forms mentioned. The carmine grains as they rain down may fasten upon these *(Ophiopholis).* (Cf. also REICHENSPERGER's paper 1908 on the mucous glands in Ophiurids.) In *Ophiothrix* I have noticed that the feet are often bent towards the dorsal side in the furrows between the spines. It is evident that the ciliary currents of the arms play a part here in cleansing the body, but they may also assist in collecting particles of nourishment.

The currents I have described in the Ophiurans are thus chiefly of importance in respiration; in certain cases, however, they are of a certain importance for cleansing purposes, and in some solitary cases they may assist in supplying nourishment. In *Ophiacantha anomala,* which is viviparous, the currents of the bursal slits serve also to supply the young with fresh water for respiration.

Finally I must mention a genus of Ophiurans, *Ophiopsila,* where some very peculiar ciliary currents make their appearance on the middle and distal parts of the arms (Mangold 1907 b and Reichensperger 1908 a). Here it is partly the most ventral of the arm-spines, partly the ventral side of the arm which are furnished with ciliated epithelium, arranged in the form of ciliary bands. The ciliary bands on the spines are somewhat twisted, forming a spiral round them; on the ventral side of the arms the ciliary bands run transversely, one over every joint. When irritated the ciliated spines are flexed in towards the arm-joints; when not irritated they stand straight out from the ventral side at a right angle. Mangold considers the function of the ciliary currents described enigmatical. I agree with Reichensperger (1908 a) that they may have some importance for collecting nourishment. The ciliary bands of the ventral side, in spite of their course being transversely over the arm-joints, start a current running towards the mouth. Reichensperger (p. 179) has also observed how in this way small animals might be carried to the mouth. Naturally these ciliary currents, besides transporting nourishment, play a part in keeping the animal clean and facilitate the respiration.

V. Asteroidea.

A. Survey of the currents in different forms.

For the most part the body is ciliated in the sea-stars. Most of the Asterids employ these ciliary currents for respiratory and cleansing purposes, but occasionally, as Gemill (1915) showed in the case of *Porania,* and as I have observed also, they may be used as an apparatus for catching detritus. One is justified in saying that, taken as a whole, the Asterids are carrion-eaters or predaceans. J. M. Clarke (1912) gives an account of a *Palaeaster eucharis* from middle Devonian which was discovered together with the mussels *Pterinea* and *Grammysia* in situations making it probable that the Devonian sea-stars supported themselves in the same way as the recent predatory Asterids do. Schiemenz as a consequence of his investigations (1896) set up two biological types among the sea-stars: (1) the *Astropecten*-type, with pointed feet, living in sand and swallowing small mussels whole; and (2) the *Asterias*-type, with sucker-feet, climbing forms, living upon large mussels, which are opened by muscular power, during which process the sea-star takes up the characteristic mounted position. BLEGVAD (1914) has pointed out that these two types are not sharply distinguished from each other, and that the mussel attacked by the sea-star is presumably opened not only by muscular power but probably also by paralytical poisoning. Besides this most of the Asterids live on every kind of carrion or living animals (cf. p. 269). Among the latter they do not despise sea-anemones even. According to MILLIGAN (1916 a) *Solaster papposus* ate up *Sagartiae* without troubling about the thronging acontiæ it was covered with.

GEMILL has already in 1915 investigated the ciliary currents ot *Asterias rubens, Solaster papposus, Porania pulvillus,* and *Astropecten irregularis.* He mentioned in passing (p. 15) that he had also had an opportunity of examining the ciliary currents in *Asterias glacialis, A. mülleri, Henricia sanguinolenta, Asterina gibbosa,* and *Palmipes placenta.* For the sake of completeness I have included in the following also the species examined by GEMILL, when they have been the subject of my investigations; when my observations have differed from his, that has also been noted.

I have examined the following sea-stars regarding the ciliary currents found on the surface of the body:

**Pontaster tenuispinus* (DÜB. & KOR.), **Pseudarchaster parelii* (DÜB. & KOR.), *Astropecten irregularis* (PENN.), **Psilaster andromeda* (MÜLL. & TROSCH.), *Luidia sarsi* DÜB. & KOR., **Ctenodiscus crispatus* (BRUZ.), **Ceramaster granularis* (RETZ.), **Hippasteria phrygiana* (PARELIUS), *Porania pulvillus* (O. F. MÜLL.), **Poraniomorpha hispida* (M. SARS), (*)*Stichastrella rosea* (O. F. MÜLL.), **Pteraster militaris* (O. F. MÜLL.), *Solaster papposus* (L.), **S. endeca* (L.), **Lophaster furcifer* (DÜB. & KOR.), *Henricia sanguinolenta* (O. F. MÜLL.), **Pedicellaster typicus* M. SARS, *Asterias rubens* L., *A. mülleri* M. SARS, *A. glacialis* L.

The currents chiefly of value in regard to respiration and cleansing purposes are probably found in the species of *Asterias.* The current is slightly axifugal on both the ventral and dorsal sides of the arms, i. e. small particles are carried out to the sides of the arms and pushed off there. The interradial parts of the oral side ciliate centrifugally. I saw in *A. glacialis* the outside of the spines along the ambulacral groove ciliating from the tips towards the bases. On the dorsal side of the animal, it is partly the papulæ which ciliate (from the base to the apex, cf. JENNINGS 1907)[1] and partly the bases of the spines. The area nearest a spine is therefore usually clean. The grains which drop down are

---

[1] With strong and rapid contractions of the tube-feet, when the hydrocoelic fluid has not time to escape through the madreporic system, the points of the papulæ may be of service as an exit for superfluous fluid. This is illustrated beautifully by lifting up a very distended *Porania* out of the water in the aquarium. Fine jets, often a decimeter long, of the coelomic fluid then spring from the tips of the papulæ.

glued together by the mucus into larger lumps which are transported up on to the spines and afterwards, by the movements of the animal, pushed off from the surface of the body. No definite direction is taken by the currents on the animal's dorsal side, owing to the appearance of a multitude of spines and papulæ; only tiny local currents arise, but still these rapidly set the skin between the spines free from dirt. I have not been able to find any current in the ambulacral furrow. But my observations regarding the ciliary currents of the madreporite agree with those of GEMILL.

The dorsal side of *Hippasteria phrygiana* shows the same ciliation as is found in *Asterias,* i. e. weak circular currents, round the bases of the spines, directed centrifugally. The madreporite ciliates centrifugally. Currents on the ventral side: The mouth-membrane ciliates centrifugally. The ambulacral groove does not ciliate. In the furrows along the ventral sides of the arms the currents are weakly axifugal. At the angles of the arms the currents are eddying.

Solaster papposus, too, has rather weak ciliation on the dorsal side. The grains of carmine are whirled round the bases of the spines and, as the animal slopes on all sides, following the law of gravity, fall farther and farther out on the arms or towards their angles. In the ambulacral groove a slow current runs towards the mouth. The mouth-membrane is scarcely ciliated at all. The ciliation of the ventral side is shown in fig. 327 (centripetal in the ambulacral parts, centrifugal in the interradial ones). *S. endeca* shows some differences on the ventral side. The arms ciliate axifugally, the ambulacral groove weakly axifugally or centripetally, the mouth-membrane centrifugally. *Lophaster furcifer* shows currents very similar to those of *Sol. papposus.* (Weakly centrifugal at the angles of the arms, otherwise confused on the dorsal side. Centripetal in the ambulacral groove, with axifugal ciliation between the feet so that very few grains reach the membrane of the mouth, which scarcely ciliates at all.) *Stichastrella rosea* is very similar in type to the preceding species. The madreporite has centrifugal currents. The ciliation is axifugal on the dorsal side of the arms as well as between the adambulacral spines on the ventral side. The papulæ are small. On the outside of and between the tube-feet the grains are whirled up from and out of the ambulacral groove by the ciliation. The angles of the arms have centrifugal currents on the ventral side. The carmine-grains are also carried centrifugally upon the radial parts of the mouth-membrane, while the interradial parts have no currents or they take a contrary direction. The ambulacral groove has no currents (cf. fig. 328).

Psilaster andromeda has only weak axi- and centrifugal currents on the dorsal side; on the ventral side the ciliation is centripetal furthest in at the angles of the arms, otherwise it is centri- or axifugal. The ambulacral groove is not ciliated or has only weak axi- and centrifugal currents.

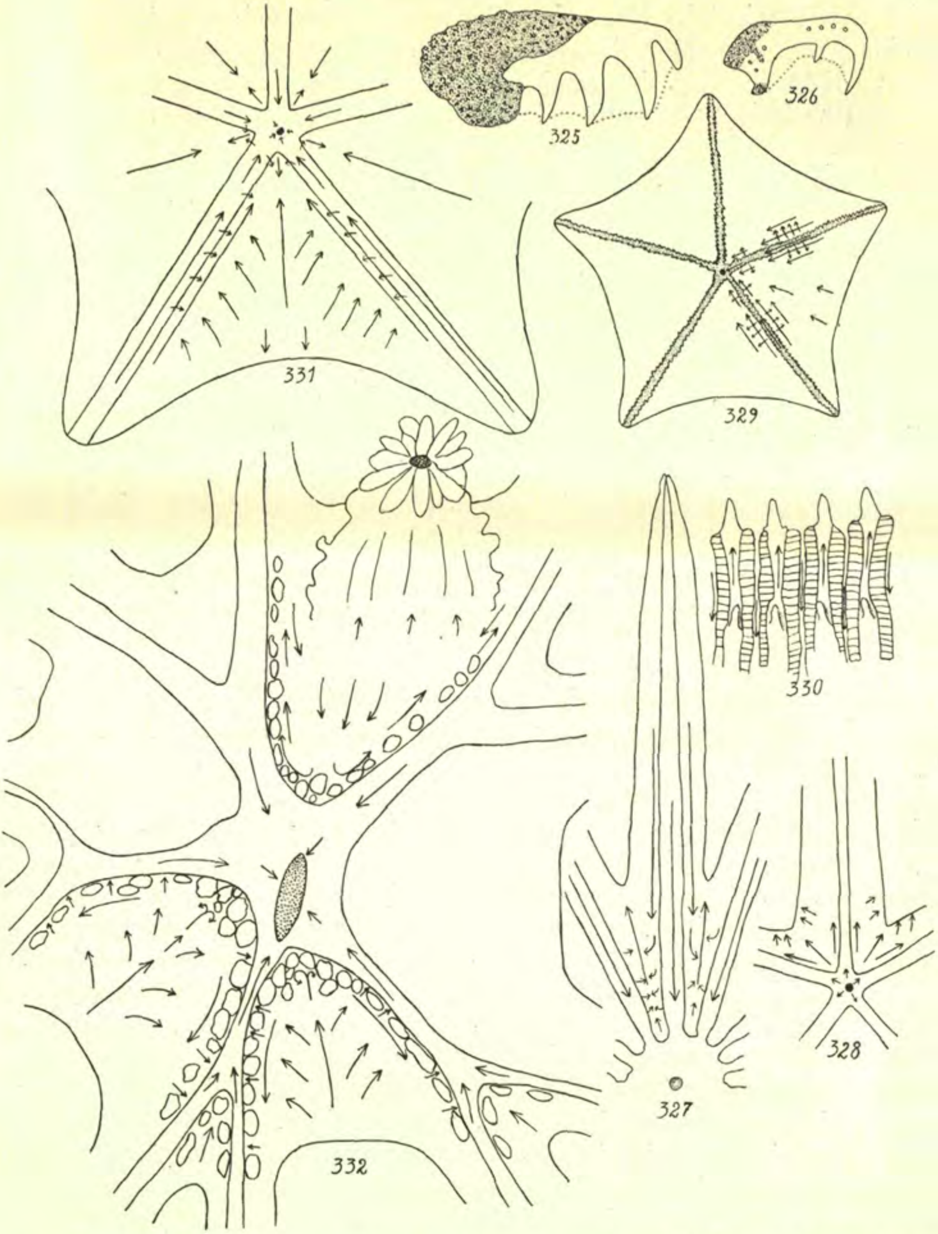
The dorsal side of *Henricia* has the same ciliation as *Asterias*. The ventral sides of the arms have axifugal currents. In the distal parts of the angles of the arms (the ventral side) centrifugal ciliation appears, but further in at the oral angles the carmine-grains flow towards the mouth. The ambulacral grooves ciliate strongly centripetally,

Similar currents are found in *Pedicellaster typicus* (ciliation of the arms on the ventral side indistinctly axifugal, an adoral current in the ambulacral groove).

Ceramaster granularis. The dorsal side ciliates centripetally towards the anal opening. Observe that the space between the flat spines – only this has any ciliation — may be enlarged or disappear, and thus many or only a few grains of detritus or carmine respectively, may fall down into these groove-like deepenings. In the neighbourhood of the anal opening the grains are often ciliated up between the spines. No currents appear on the marginal plates, but between them centripetal ciliation occurs. The interradial areas of the ventral side ciliate oropetally. In the ambulacral grooves and on the radial part of the buccal membrane, the grains are carried slowly centripetally. The interradial parts of the mouth-membrane ciliate, on the contrary, very inconspicuously. The margins of the ambulacral grooves ciliate axifugally, but between the two rows of spines a longitudinal current runs centripetally (cf. fig. 329 and *Porania*). The ciliary currents in this species are fairly strong.

Pseudarchaster parelii. Dorsal side: Little or no ciliation at the tops of the paxillæ. Centrifugal ciliation between the spines and their bases. The grains eddy up centrifugally or somewhat spirally from the sunken madreporite. The sides of the marginal plates ciliate towards the grooves, where the grains are carried dorso-ventrally. Ventral side: In the grooves between the calcareous plates, which do not ciliate themselves, the current flows centri- and axipetally respectively, in between the tube-feet. A number of grains, however, in the neigbourhood of the mouth are whirled out of the ambulacral groove. At the angles of the arms a centripetal current appears towards the mouth-disk. The ambulacral groove was very difficult to observe, as it was not easy to induce the animal to extend itself for a sufficient length of time; it appeared, however, as if the currents were centripetal here also.

The ciliary currents in *Astropecten irregularis* run axi- or centrifugally on the dorsal side, on the ventral side axi- and centripetally. In the ambulacral groove centripetally. *Luidia sarsi* has its currents directed similarly. The ciliation on the dorsal side is always confined to the bases of the star-shaped spines. The small white arm-tips ciliate centripetally. The furrows between the rows of spines on the ventral



Figg. 325—332. 325—326) *Gorgonocephalus caput-medusae.* 325) A tentacle-hook, 326) A girdle-hook, $^{140}/_{1}$; 327) *Solaster papposus* Diagrammatical sketch of the ciliary currents of the ventral side of an arm, the mouth and the buccal membrance below, $^{2}/_{3}$; 328) *Stichastrella rosea* Ciliary currents of the ventral side, $^{2}/_{3}$; 329) *Ceramaster granularis* Ciliary currents of the ventral side, × $1\,^{1}/_{3}$; 330) *Ctenodiscus crispatus* Ciliary currents on and between the cribriform organs on the sides of the arms, $^{3}/_{1}$; 331) *Porania pulvillus* Ciliary currents of the ventral side, $^{2}/_{3}$; 332) *Antedon petasus* Ciliary currents of the disk, in the adoral angle often perpendicular currents, mouth half opened, $^{10}/_{1}$.

side ciliate axipetally (the spines themselves do not ciliate). The interradial parts, like the ambulacral groove and the ventral side of the arm-tips, ciliate adorally. The ambulacral feet do not ciliate except at their bases (the inside) where the ciliation is directed towards the mouth. On the buccal membrane the grains are carried slowly, in the mouth-opening quickly, centripetally.

Similar, but still more powerful currents are found in *Pontaster tenuispinus*. The direction of the ciliary currents on the dorsal side is the same as in *Astropecten;* the direction is a little less marked on the disk, where small circular currents appear. The whole of the ventral side ciliates axi- or centripetally — the arms axipetally, the ambulacral groove and the interradial parts centripetally.

Ctenodiscus crispatus: Dorsal side: The angles of the arms and the disk as well as the middle parts of the arms ciliate centrifugally; the sides of the arms axifugally. Ventral side: The plates of the ventral side, both on the arms and in their angles, ciliate axi- or centrifugally. Between these plates deeper furrows are situated which ciliate centri- and axipetally, except in the more distal parts of the angles of the arms, where the current is weakly centrifugal. The combs on the sides of the arms ciliate ventro-dorsally, but in the parts lying deeper between the cribriform organs, the current flows dorso-ventrally, and continues on the ventral side as axipetal ciliation in the deeper furrows between the calcareous plates, as described above (cf. fig. 330). The ambulacral groove has no current itself, but a current is found in the groove on the outer side of the row of tube-feet. The ciliation of the buccal membrane is weakly centripetal. In this way the currents lying deeper are enabled to carry small particles of mud to the pointed tube-feet. (N. B. larger objects cannot pass between, or under, the combs.) On their way thither, the mucous secretion glues these mud-particles into soft lumps, and they are then carried, partly by the feet, and most likely also by the help of the centripetal currents running laterally of the tube-feet, towards the mouth. A simple experiment was made with one of these very sluggish animals. The dorsal side was syringed with grains of carmine. After some hours the animal, which had not moved noticeably from the original place, was examined. Grains of carmine were found imbedded in the mucous membrane of the stomach.

Porania pulvillus has the calcareous plates of the dorsal side covered by a smooth skin, on which the papulæ are strewn. Contrary to GEMILL I have not been able to find any centripetal currents on the dorsal side. If my observations are correct ciliation appears on the dorsal side only on the papulæ, and these, as usual, ciliate disto-petally; on the madreporite which ciliates strongly from its centre (somewhat curved in the directions of the hands of a clock); and on a number of white-coloured strips or narrow furrows, in which the current is strongly centrifugal, i. e.

directed towards the ventral side of the animal. The currents last mentioned are developed chiefly on the sides of the short arms, at right angles to their longitudinal direction and continue on the ventral side in axipetal furrows. The mud raining down on the dorsal side is imbedded in a layer of mucus, and this is drawn down and into the white-coloured furrows, and is then transported towards the mouth. — The currrents on the ventral side are demonstrated by the accompanying diagram (fig. 331) which agrees upon the whole with GEMILL's description. In the specimens examined by me, however, axifugal currents were found between the spines bounding the ambulacral groove. The spines themselves, which are arranged in two rows along the ambulacral groove, ciliate at their bases only, oropetally. Between the two rows of spines runs an oropetal current. Axifugal currents which, sooner or later, curve into the longitudinal oropetal currents, run between the spines at a right angle to the ambulacral groove. When the ambulacral groove is open the spines are flexed outwards. (When the furrow is half-closed the inner row is bent so as to cover the ambulacral groove.) The ambulacral groove itself ciliates centripetally, but the grains near the buccal membrane are often ciliated up from the ambulacral groove and carried interradially. I, like GEMILL, have verified the presence of short centrifugal currents in the interradial angles. Eddying currents are set up where this current and the centripetal interradial one meet, and the agglutinated grains of carmine are accumulated here.

In connection with this I must put in *Poraniomorpha hispida* of which I found a specimen S. of Tautra in the Trondhjem fjord. The specimen was sluggish and poorly when examined. The only currents observable were as follows: Dorsally: narrow furrows on the margin between the small spines ciliate centrifugally; the madreporite has centrifugal ciliation; the papulæ ciliate towards their points. Ventrally: centripetal currents appear in the interradial angles.

Finally, I will describe the currents in the only Asterid nursing young which I have observed, namely *Pteraster militaris*. The specimen had many young under the membrane of the back. Dorsal side: The web connecting the spines does not ciliate. The central opening has a constant, strongly discharging, current. M. SARS (1861) has pointed out the appearance of small pores in the dorsal membrane; the grains of carmine are also thrown out through these, though not so rapidly as through the central aboral funnel. Through rents in the membrane too a current flows outward. Ventral side: The ambulacral groove ciliates weakly adorally. Near the mouth, in the axial middle parts of the ambulacral groove, weak currents also appear leading outwards. (The radial parts of the buccal membrane and the lips ciliate slowly adorally; the interradial parts centrifugally.) At the tube-feet, i. e. in the lateral parts of the ambulacral groove, the currents swing to the oral side of the feet, pass out between them and continue axifugally right to the bottom of the depressions between the transverse combs, i. e. the rows of spines transversely arranged and connected by a membrane. The membrane itself does not ciliate.

Thus an in-current of water on the ventral side of the brood-pouch appears and an out-current on the dorsal side, principally through the central opening. The aerated water-supply for respiration of both mother and young in thus brought into circulation.

B. Summary of the action of the currents and interpretation of their result.

If we sum up the above and interpret the result we arrive at the following conclusion. One ought, when interpreting the function of the ciliary currents described above, to bear in mind the whole time that they are always of some importance both for respiration and cleansing purposes. (On the part played by the pedicellariæ for cleansing and protection cf. JENNINGS 1907.) In Asterids having ciliary currents running adorally these currents may not always be of very great importance for the feeding, owing to the appearance of axifugal currents which are able to eliminate the grains from the ambulacral groove, before they would reach the mouth (e. g. *Stichastrella*). Neverteless, one can easily follow in the Asterids described above how the ciliary currents are used to a greater or lesser extent in catching detritus, or are employed exclusively in the service of respiration and for cleansing the surface of the body. Ciliary currents of both the types mentioned last are found in *Asterias, Hippasteria, Stichastrella*, *Psilaster*, *Solaster*, *Lophaster*, and *Pteraster*. In *Solaster, Lophaster, Pteraster*, and *Pedicellaster* one can also verify weak centripetal ciliation in the ambulacral groove. In *Psilaster* certainly no such current can be found, but on the other hand an interradial ciliation, directed centripetally, occurs. In the other forms enumerated above the currents lead away from the mouth, i. e. the animal does not use the small particles accompanying the respiratory water, or transported by the cleansing currents, for nourishment. The centripetal current in the ambulacral groove is marked more strongly in *Henricia,* which has, besides, an interradial ciliation directed centripetally. *Ceramaster* has centripetal ciliation in the ambulacral groove. But here adambulacral and interradial currents also appear, running towards the mouth. A peculiarity remarkable for this species is the condition that the ciliary currents on the dorsal side are directed centripetally.

Nevertheless, the Asterids most suited as detritus-catchers which I have examined are: *Pseudarchaster, Astropecten, Luidia, Pontaster,* *Ctenodiscus, Porania,* and *Poraniomorpha(?)* which have well-developed adoral currents for the transportation of detritus-particles to the mouth. In *Pseudarchaster* and *Astropecten* these currents certainly all run towards the mouth, but in these genera they are rather weak and unimportant. *Astropecten* lives upon a sandy or gravel bottom, in which it buries itself, either entirely or partly. (As GEMILL 1915, p. 4 also mentions.) It finds there small mussels and such things and puts them into its stomach. I found in the stomach of an *Astropecten:* 3 *Astarte* sp., 1 *Helcion pellucida,* 4 *Syndosmya alba,* 1 small *Saxicava,* together with *Lacuna, Hydrobia,* a bit of *Lithothamnion* and some Polychæte-bristles; another specimen contained: 1 *Gibbula cineraria,* 1 *Cylichna,* 1 *Nucula,* 1 *Echinocyamus,* together with fragments of small mussel-shells. *Luidia* and *Pontaster* have ciliary currents corresponding to those of *Astropecten,* but they are more distinct here and more strongly developed. These two like, or even in a still higher degree than, *Astropecten*, ought to be able to exist on the particles transported by the ciliation. EICHELBAUM (1910) investigated the contents of the stomachs of a number of Asterids. While *Astropecten* and *Psilaster* nearly always had molluscs or small Echinoderms in the stomach, he found it empty in all the specimens of *Pontaster* he examined. I do not think his explanation of this fact can be fully correct. According to EICHELBAUM the specimens belonging to this species must have emptied their stomachs during the long journey up from a depth of 250 metres. But why then should not specimens of *Psilaster* brought up from a depth of 210 metres do the same thing? We may possibly assume that *Pontaster* does not often gather larger prey into its stomach as *Astropecten* and *Psilaster* do. *Porania,* as GEMILL has shown, can live for a long time on the detritus brought to the mouth by the ciliary currents, and in this species the stomach is generally empty. One ought to notice, however, that even typical predaceans like *Asterias* very often have empty stomachs.

Porania certainly has very evident and distinct currents; a small part of these currents, however, as is obvious from the description and diagram, counteract the carrying of particles to the mouth. Presumably the aboral current is of very slight importance. By means of the current mentioned some part of the particles are carried to a small interradial area, situated near the corners of the mouth. Many Asterids, as is well-known, are tolerably indifferent as to whether the prey to be digested is found inside or outside the stomach. In the latter case the stomach is simply turned out over the prey. One may imagine that if a small part of the food is also concentrated in the corners of the mouth, *Porania* can turn its stomach over these and thus digest the nourishment collected. If the accumulated material is not suitable for food it need not be absorbed by the mucous membrane of the stomach. (GEMILL's observations seem to make it probable that *Porania* is sensitive to certain kinds of food; he saw that a *Porania* soon died in water to which sperms had been added. It is possible, however, that the presence of the sperms spoilt the respiratory water.) GEMILL's investigations have made it evident that this sea-star can live for 9 months and retain its weight, without any other food than the microscopical nourishment brought into the acquariums at Plymouth by the circulation of the tank-water, while *Asterias* living under the same conditions dies after a shorter time (8 weeks).

Ctenodiscus lives practically speaking exclusively upon small particles of mud, and one nearly always finds its stomach powerfully distended by the mud in which the animal lives. These particles of mud, to a large extent, are brought to the animal by the ciliary currents described above. SLADEN in his Challenger work supposes that the cribriform organs serve to purify the respiration water. It is quite probable that the respiration is provided for by the ciliary currents described, but it is a fact that small particles are carried through the grooves between the cribriform organs to the ambulacral groove, to be transported thence to the mouth. When laid down on the natural mud-bottom the animal ploughs halfway down into the mud, leaving a deep track after it. When taken up again, the previously cleanly-washed grooves were found filled with mud, which was glued together by the secreted mucus into long strings. At the base of the feet, too, mud was found stuck together by mucus, and round the mouth was a veil of slime, covering a part of the mouth-membrane and connected with the contents of the stomach. According to my view the cribriform organs act principally as a sieve to get rid of coarser material.

The sluggishness of *Pontaster, Porania,* and *Ctenodiscus,* especially of the two latter, supports the view that they are detritus-catchers rather than predaceans. *Ctenodiscus,* in a vessel containing mud from the place of discovery, crept about 6 cm. in 2 hours. At the end of another 6 hours the specimen had travelled 11 cm.

In *Pteraster* the currents are made use of by the mother not only for respiratory purposes but also in nursing the young. The young, sitting under the dorsal membrane, obtain fresh water continually, and probably nourishment too, from the current flowing in through the mother-animal's ventral side and passing out through the dorsal openings. STIMPSON (1854, p. 15) and after him M. SARS (1861, p. 50) reported that the water flows "ind og ud av den i Ryggens Centrum beliggende Aabning ligesom en Holothuries Kloak" (in and out of the opening lying in the centre of the back, like the cloaca of a Holothurian). This, as we have seen above, is false, as is also the continued reasoning of M. SARS on p. 70 (op. cit). He says in the passage last-mentioned: "Det er sandsynligt, at det til Respirationen fornødne Søvand tilføres Aanderørerne (papulæ) gennem disse . . . . i den ydre Ryghud forekommende porer, og at det igjen udføres gjennem den . . . centrale Aabning". (It is probable that the sea-water necessary for respiration is brought to the respiratory tubes (papulæ) through these . . . pores, appearing in the exterior skin of the back, and that it is carried out again through the . . . central opening.) As we have seen, an extruding current appeared from the dorsal pores and the water was carried to the pouch containing the young exclusively from the ventral side. It is possible that the papulæ of the mother-animal can be stuck out through the small pores in the dorsal membrane.

Besides feeding by means of the ciliary currents those Asterids, ciliating adorally, under normal conditions support themselves in most cases on larger animals too (excepting e. g. *Ctenodiscus*). A large number of observations have been made on sea-stars, mostly on *Cryptozonia* showing the predatory nature of these forms. (Cf. BLEGVAD 1914, CHADWICK 1916, H. L. CLARK 1915 b, EICHELBAUM 1910, HESSE & DOFLEIN 1910–14, JENNINGS 1907, KJERSKOG-AGERSBORG 1918, MEAD 1900, MILLIGAN 1915, 1916 a, c.) It has been ascertained that the Asterids eat almost everything; carrion of all sorts and living prey, among which we find Porifera, Actiniæ, mussels, snails, worms, crabs, Balanids, Sea-urchins, Asterids, Ophiurids, fish, etc. Among vegetable remains are kelp and algæ. Even large stones up to $^1/_2$ pound in weight appear. In both the latter cases, however, the objects have been swallowed chiefly on account of the animals found upon them. I can add a couple of my own observations too, showing the kind of prey captured by the Asterids: I have seen *Solaster papposus* swallow a *Pennatula phosphorea;* I observed *Henricia* in the mounted position over a *Mytilus* (cf. the account given on p. 267 of the contents of the stomach in *Astropecten*).

The information in respect to predaceans or carrion eaters among the *Phanerozonia* is scantier. *Astropecten,* however, seems to be a genus with more decidedly predatory instincts. It is evident, from the description given above, that ciliary currents are rather commonly met with among the *Phanerozonia* which may be of importance in carrying nourishment. It is difficult to decide whether this is something primitive or not, but it is possible that this form of obtaining nourishment is very ancient for this group of *Echinodermata.* The feeding by means of ciliary currents existed almost certainly among the (*Thecoidea* or) *Edrioasteroidea* which may be considered as the primeval forefathers of the Asterids.

In support of the theory that the Asterids were originally detritus-catchers, I have observed that the young of *Asterias rubens,* while small, have certain currents directed adorally. The diameter of the young examined was 1·0 mm. These young had 2 to 3 pairs of tube-feet only, and the arm-processes were very short. The ciliary currents were relatively strong; centripetal on the dorsal side. On the ventral side the ambulacral groove ciliated centripetally, in the interradial parts the currents ran centrifugally and between the feet they were axifugally directed. In specimens with a diameter of 3 mm., the grains were carried centripetally in the distal half of the ambulacral grooves only; in the proximal parts they were eliminated from the furrow by axifugal currents. The buccal membrane ciliated weakly centrifugally.

VI. Crinoidea.

A. Previous investigations as to how the nourishment is obtained and what it consists of.

Earlier investigators who have handled living Crinoids have already observed that the ambulacral groove is ciliated, and since the sectional method now employed, came into use, the cilia of the epithelium of the ambulacral furrow were also observed. I refer here only to the works of W. B. CARPENTER 1866 and 1876, CHADWICK 1907, DUJARDIN 1835 (here, however, the origin of the adoral current is misunderstood, as it is considered to be caused by the tentacles), DUJARDIN and HUPÉ 1862 (corrected view), HAMANN 1889, LUDVIG 1877, PERRIER 1886 and 1890, VOGT and YUNG 1888.

Scattered accounts, respecting analyses of the contents of the stomach, are also found in the literature on the subject. W. B. CARPENTER (1866) mentions the appearance of *Peridinium (Ceratium) tripos* and (1876) Entomostracae, diatoms, spores of algæ, and *Peridinium tripos.* P. H. CARPENTER (1884) gives the most detailed information (cf. below). CHADWICK 1907 states that the food consists of diatoms, radiolarians, and foraminifera; A. H. CLARK (1908) that the food consists of small crustaceans and pelagic organisms; H. L. CLARK (1915 a) has found unicellular and thread-like green algæ, some diatoms, and foraminifera, together with a number of radiolarians, but no detritus; in a few other specimens, the species not noted in any case, but presumably Comasterids as these are usual at the place where he worked, he found in addition pieces of red algæ and small crustaceans (thus chiefly vegetable-eaters); in 1917 the same author studied the biology of *Tropiometra carinata,* whose food he found to consist of: living active plankton, a mixture of animal and vegetable food, the former predominating (plants: diatoms, unicellular green algæ with occasional fragments of other seaweeds), crustacea (amphipods, copepods, crab-zoëas), few foraminifera, all alive when ingested; DUJARDIN (1835): microscopical algæ, infusoria, diatoms, sponge-spicules (of *Tethya?*); HERDMAN (1906): diatoms and infusoria; KIRK (1912): no bottom material, only finely decomposed animal remains (in *Comanthus japonica*). KONINCK & LE HON 1854 mention that M. DUCHASSAING found in the stomach of *Pentacrinus caput-medusae* (= *Isocrinus decorus*) remains of small crustaceans; LOVÉN (1869) has also noted small crustaceans in the contents of the stomach of *Hyponome Sarsi* = *Zygometra* cf. *microdiscus*, and finally MÜLLER 1841 has drawn a number of microscopical particles of nourishment from the contents of the intestine of *Antedon rosacea* (*Ceratium*, diatoms, foraminifera, tintinnoids, radiolarians?).

The same kind of nourishment seems to occur in the stomachs of the young Pentacrinulas. (Cf. SEELIGER 1892, p. 397; BURY 1888, p. 281; MORTENSEN 1920 a, pp. 44, 45.) MORTENSEN (1918, 1920 a) relates a curious case of the young of *Isometra vivipara* being caught and eaten by its mother.

P. H. CARPENTER, as mentioned above, has made the most important statements in regard to food. He considers — quite correctly — that the food varies with the bottom — to be quite complete one must add, with the plankton nourishment in the surrounding water. According to P. H. CARPENTER one usually finds in the intestine the cuticularized casings of Entomostracae and the larvæ of larger crustaceans, as well as diatoms, spores of algæ, and among deep-sea types, such as *Bathycrinus, Rhizocrinus,* and *Pentacrinus,* radiolarians and foraminifera *(Globigerina, Biloculina).*

B. My material.

I have examined, at the Kristineberg Zoological Station, material consisting of *Antedon petasus* DÜB. & KOR. brought home from the outer parts of the Gullmar fjord, where the species is found on a shell- and gravel-bottom at a depth of 30—40 metres. At the Biological Station of Hægdalen, Trondhjem, I have studied *Hathrometra tenella* var. *sarsii* (DÜB. & KOR.) and *Rhizocrinus lofotensis* M. SARS taken between Leksviken and Tautra, on muddy bottom at a depth of 250 metres.

Antedon petasus, which I have had opportunities of studying in aquariums for a long time, I found at the beginning (1917, 1918) rather difficult to keep alive. It turned out that the temperature of the tank-water supplying the aquaria with water was too high (16—18° C.). It was not suitable either, when the dredged material was brought home, to use water fetched up from the bottom directly, for when this cold water became warmer, gas-bubbles was found adhering to the pinnules, and the animals floated up to the surface and soon died. This was prevented by setting the vessel containing the animals on ice. Afterwards, by setting the aquarium filled with water of very high salinity (taken from the outer parts of the Archipelago) in a tub filled with ice-water, I was able to keep *Antedon* alive and vigorous for weeks. The water did not need changing more than once every, or every other, week. The salinity of the sea-water varied between 26 to 28 ⁰/₀₀. The necessary supply of oxygen was obtained by means of an aerating apparatus of the usual type used at the station. The water was kept at a temperature of 10—12° C., occasionally it was a couple of degrees higher or lower. It was soon found that it was not advisable to let the temperature rise higher than 14° C. With a greater amount of salinity, however, the animals seemed able to stand a somewhat higher temperature. Another year (1919) I found they got on fairly well at a temperature of 15° C. when the sea-water had a salinity of 30 ⁰/₀₀. If the animals are to do well, it is absolutely necessary to supply the bottom of the aquarium with small pebbles or shells to which the cirri can cling, otherwise the Crinoids fall down and soon die.

C. Currents for cleansing purposes.

In the Crinoids, as in other Echinoderms, ciliary currents are found on the surface of the body for the purpose of keeping the animal clean. These are most pronounced in the interradial and interbrachial areas of the disk. On the median parts of the interradial areas centripetal (adoral) currents run. It is checked in the oral angle by the upright adambulacral fold on the margin of the ambulacral furrow (cf. fig. 332). Circular currents therefore, running vertically, often arise in the oral angles. Along the sides of this median centripetally directed current the grains of carmine are carried radipetally, and, in the area nearest the ambulacral groove, centrifugally. In this way all the grains in the interradial area are gradually carried away along the margin of the ambulacral furrow. Where the ossicles in this upright margin are rather low, or where there is a gap between them, the grains are sucked down into the centripetal current of the ambulacral groove, and in this way most of the particles, even those falling upon the interradial areas, reach the mouth at last. Some of them, however, are carried out to the sides of the body and fall off the animal. The interbrachial parts of the perisome have ciliary currents going in an oro- or radipetal direction. The oral pinnules ciliate slightly towards their points, and the grains of carmine carried thither thus sink down on to the surface of the disk, and usually reach the mouth sooner or later. The anal cone ciliates at the base only, where one may observe weak currents running upwards. The excrement consists of the undigested particles from the intestine, held together by a jelly-like substance, and formed into large yellow mucous balls. These lumps are too large to be transported by the ciliary currents. Instead of this they are removed from the surface of the disk, where they usually fall, by the movements of the animal when moving to another place, or by stronger movements of the water caused by the animal flexing its arms, etc. The cirri and the dorsal side of the animal do not ciliate. Nevertheless, they are kept clean by the movements of the animal.

The currents described above refer to *Antedon petasus*, but those of *Hathrometra tenella* var. *sarsii* are similar, with the exception that the marginal currents directed centrifugally may be followed farther out on the sides of the arms than in *Antedon*. In *Rhizocrinus* the interradial currents are centripetal only.

D. **Currents supplying nourishment and mode of feeding.**

After several unsuccessful attempts at colouring the ambulacral furrow in living specimens of *Antedon* with an intra-vitam staining substance, I succeeded at last, by putting the animal into a solution of neutral red mixed with sea-water, in getting the ambulacral groove distinctly tinted. The right colouring was obtained after a few hours in a saturated solution; after a longer time the part submerged was gradually coloured too diffusely dark red to be suitable for investigation. It answers capitally if one lays down a stump of an arm or pinnules only in the staining fluid, for as there is no centralized nervous system the ciliary currents in the ambulacral grooves continue towards the mouth, although the part of the body in question is cut off proximally. The movements of the tentacles are also vivacious and normal at least 24 hours after the arm or pinnule has been severed from the body — n. b., if the water in which they lie is kept fresh and cold (cf. also PREYER's observations 1887).

REICHENSPERGER (1908 c), by staining with thionin and mucin, has shown the occurrence of mucous glands in the epithelium of the ambulacral groove. These (unicellular) mucous glands are found in masses in the ambulacral groove — they are scanty outside it — and it is probably these that are coloured first, but presumably the nuclei of the nerve- and neuroglia-cells are stained too, and thus show clearly the spread of the ciliated epithelium.

A hungry *Antedon*, when not irritated, sits immovably fastened to the substratum with out-stretched arms, slightly curved upwards. The pinnules are spread out from the arms almost at right angles, and the tentacles, arranged in groups of 3 on the pinnules, are stiffly stretched out. If a plankton sample or a few grains of carmine with some crab-liver is put into the water of the aquarium, the arms and pinnules at once become very active. The tentacles all beat rapidly in towards the ambulacral furrow. This, the margins of which generally lie pressed tightly together, opens as soon as any grains fall upon it, with a wavy movement proceeding towards or away from the mouth. The mouth, only a narrow slit before, opens to its widest extent, and becomes rounded. (Cf. figg. 333, 336.) After some time the tentacles straighten themselves again, but now and then, when tiny grains fasten on the papillae, the tentacles are whipped with rapid, nervous movements towards the ambulacral groove, and then again straighten out as quick as lightning. Some of the groups opposite each other usually whip in at the same time towards the furrow, but one cannot observe any flexing in of the pinnules proceeding along the arms. As Reichensperger (1908 c) has shown, unicellular mucous glands open on the papillæ of the tentacles. Small particles are fastened to the tentacles by their secretion, and with rapid motions of the tentacles are cast into the ambulacral groove, where the ciliary current takes hold of them and carries them to the mouth.

Sensory hairs are found on the tentacles too, and it has been supposed therefore that these serve as sensory organs. The function of the tentacles is probably in reality manifold: 1st, they are certainly of considerable importance for the respiration; 2ndly, the mucous secretion, as is pointed out above, serves to fasten the falling grains of plankton or detritus upon the tentacles temporarily; 3rdly, the sensory cilia serve presumably as some kind of organ for taste and feeling. When I dropped picric acid upon them, the arms were flexed and relaxed violently; when I added a frew drops of sublimate the arms were also rapidly bent and twisted; the pinnules were stretched out and the animal made swimming motions, as if to escape. On a third occasion quinine sulphate + a few grains of carmine was added: the arms were waved actively to and fro, the pinnules were flexed in to the sides of the arms, or rubbed against each other, or laid over the place where the drops had fallen, the arms were turned upside down, with the evident intention of getting rid of the unpleasant matter (cf. Graber's statements 1889). When old putrefying crab-liver was added to the fluid containing the grains of carmine, the pinnules were flexed in towards the sides of the arms. This seems to indicate that a sense of taste is present which, presumably, may be considered as localized in the sensory hairs of the tentacles' papillæ.

I cannot decide with certainty whether Reichensperger's assumption is correct that the secretion of the papillæ of the tentacles is poisonous, and these papillæ, like the cnidoblasts in *Cnidaria,* are partly defensive organs. I allowed living pinnules to lie in contact with freshly caught plankton (Ephyrae, Peridineans, Diatoms, and Plutei). Nevertheless, I was not able to ascertain that any rapid unconsciousness or poisonous action took place. A small *Cladonema* seemed to make motions of escaping when touched by a tentacle, but usually the tentacle bent away from the irritating object. In the intestine of *Heliometra eschrichti* (see below) I have found quantities of copepods. The copepods have a tolerably strong power of motion of their own and it is very probable, that in this case the secretion of the papillæ of the tentacles in some way paralyses the prey. Otherwise it is difficult to imagine how the relatively weak ciliary currents can transport the captured prey to the mouth (N. B., however, the rudimentary combs on the proximal pinnules [cf. p. 287]).

I mentioned that the tentacles are arranged in groups of 3. The most proximal of these 3 tentacles is the shortest and is directed straight upwards, the middle one is longer and extended obliquely outwards; the most distal is the longest and is directed straight outwards. This concerns the pinnules; on the arms this differentiation is indistinct or not marked at all (cf. figg. 334, 335). In the proximal parts of the arm and on the disk the tentacles are unbranched. The tentacles are often more or less contracted, but with maximum extension the longest tentacle reaches 0·5–0·7 mm. As the pinnules are placed at a distance of 1·0–1·4 mm. from each other, of course with the maximum extension of the tentacles, the inter-pinnular region can be fished competely clean.

The ciliary epithelium, characteristic of the ambulacral groove, begins at the base of every group of tentacles. The ambulacral furrow itself is slightly concave and ciliates strongly towards the mouth. The mucus is secreted in the ambulacral groove by the mucous glands mentioned above, and the grains are glued together into larger lumps by it. These are transported to the mouth, the edges of which are often pressed together like a pair of lips, during movements similar to swallowing. The centripetal ciliary currents have also been verified in *Hathrometra* and *Rhizocrinus.*

In a healthy animal which does not receive any great amount of nourishment at the same time the mouth, as I mentioned before, is shaped like a slit. This slit in *Antedon petasus* is always (in all the cases observed by me) oriented from the anterior radius towards the posterior interradius, or in the anterior half twisted a little to the right of this line, in the posterior half twisted a little to the left of the same line. (See fig. 333.) A slit-shaped mouth with the same orientation I have observed in a specimen of *Thaumatometra comaster* preserved in spirit. In *Heliometra eschrichti* the slit has the same orientation as in *Antedon petasus* but is directed a little more obliquely (from the right anterior interradius towards the left posterior radius), and the same condition is found in specimens of *Poliometra prolixa, Asterometra anthus,* and *Oligometrides adeonae.* The mouth is twisted still more in the same direction in *Tropiometra afra macrodiscus,* where it looks as though it might become almost transversal in position, as in *Comasteridae.* (Most of the Crinoids preserved in spirit which have been examined have a rounded mouth-opening, like diseased or dying specimens of *Antedon petasus*).

E. Character of the nourishment.

All kinds of tiny particles, eddying up from the bottom owing to the movements of the animal or through currents in the water (mostly the latter) are carried to the mouth; in other words detritus and benthonic organisms, as well as some part of the plankton which rains down. My experience seems to show, however, that the benthonic nourishment is the most important.

Samples of excrement from living animals examined:

Antedon petasus. All the samples were brought home from "Smedjan", Kristineberg, Sweden, where the animals were dredged from a depth of 30—40 metres.

1. A rough sample. The recently dredged animals were put into a vessel of sea-water, where they were allowed to stay for some hours and the abundant excrement evacuated was collected. Contents: Detritus, small grains of sand, threads of algæ, diatoms, some peridineans, crustacean larvæ (0·30—0·50 mm. long), small copepods (0·09 × 0·18 mm.), macerated pieces of plants (one piece 0·40 × 0·60 mm.), a half-digested Myzostomid.

2. A lump of excrement, taken directly from the anal opening: Detritus, diatoms *(Coscinodiscus, Navicula, Nitschia,* etc.), copepods, an ostracod, a veliger larva, a *Ceratium,* a few living infusoria.

3. Some food, sucked from the mouth by means of a pipette: Detritus, diatoms, copepods (empty casings), some ostracods, 1 veliger larva, nauplius larvæ, empty podiæ of small crustaceans, a peridinean, some few sponge-spicules.

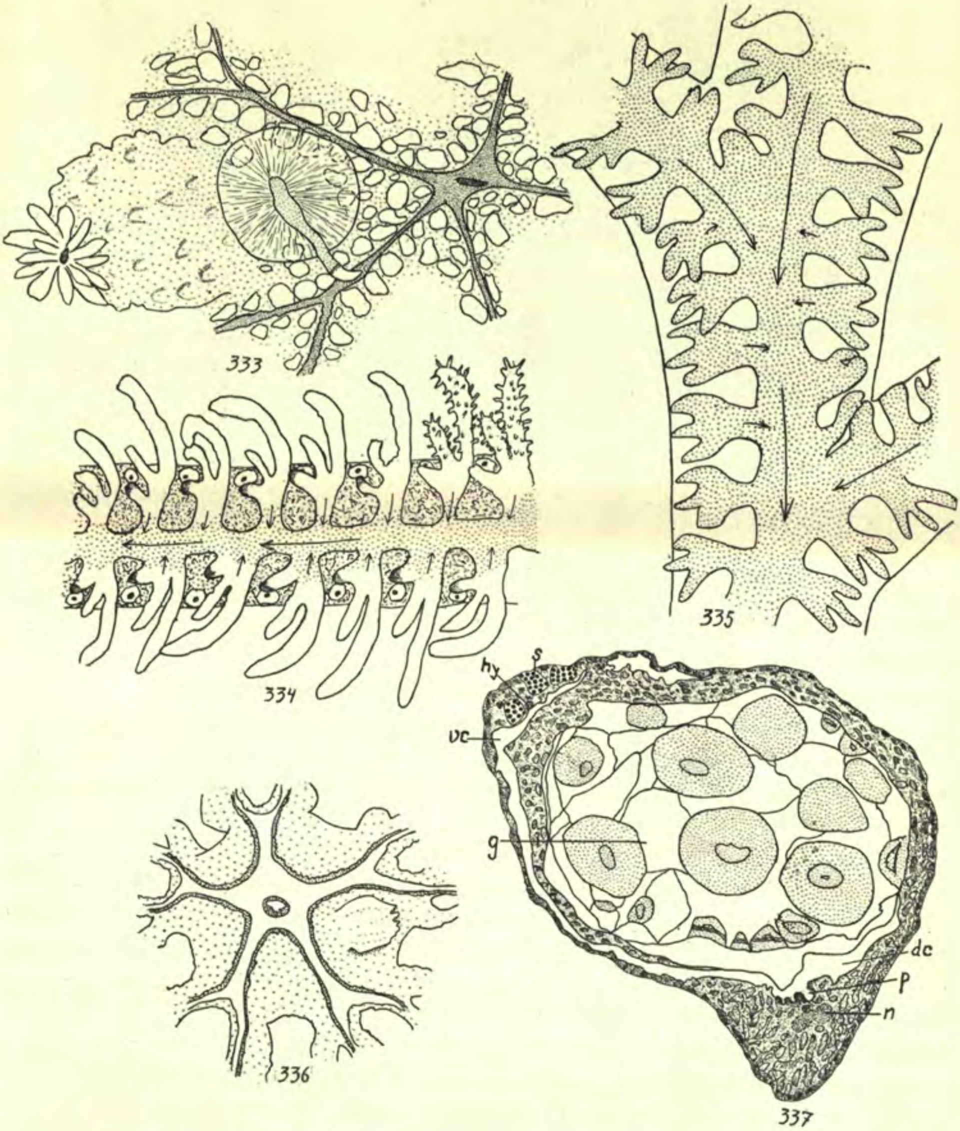
Samples of excrement from preserved specimens:

Metacrinus rotundus, Sagami, Japan, depth 180 metres. The excrement was collected from the bottom of the vessel in which the animal had been laid. Contents: Detritus, diatoms, tissues of more highly organized plants, solitary crustacean podiæ, and crustaceans, foraminifera.

Comantheria grandicalyx, Bonin Islands, 54—72 metres. The sample obtained in the same way as in *Metacrinus.* Contents: Detritus, threads of algæ, small grains of sand, diatoms, sponge-spicules, bits of leaves (the largest 4·5 × 1·25 mm.), bryozoans, solitary holothurian anchors, a syllid (2·1 × 2 mm.), and a syllid larva, a piece of a hydroid colony (length 5 mm., breadth of branches 0·15 mm.).

Comaster delicata grandis. Bonin Islands, 72 metres. The sample taken directly from the intestine. Contents: Algous threads and radiolarians (numerous), tintinnoids, crustacean podiæ, solitary diatoms, grains of sand, foraminifera, bits of bryozoans, sponge-spicules.

In another sample of the same species (Bonin Islands, 144 metres) the diatoms were more abundant (*Planktoniella, Thalassiothrix, Nitschia,* etc.), otherwise like the previous sample of the same species.



Figg. 333—337. 333—336) *Antedon petasus.* 333) Disk with almost completely closed ambulacral furrows and a slit-shaped mouth. In the anal interradius a *Myzostoma cirriferum,* its proboscis extended, robbing food from the ambulacral furrow. This drawing, like the two following ones, drawn from living animals, $^{10}/_{1}$; 334) The ciliary currents of a pinnule, sacculi alternating with the tentacle-groups, papillæ only indicated in a couple of cases, $^{56}/_{1}$; 335) Ciliary currents of the arm and the ramification of the tentacles, $^{53}/_{1}$; 336) Disk with a wide open ambulacral furrow and rounded mouth, $^{8}/_{1}$; 337) *Tropiometra afra macrodiscus* ♀, Genital pinnule, *dc* = dorsal coelom, *vc* = ventral coelom, *n* = dorsal nerve, *g* = genital gland, *hy* = hydrocoel, *p* = ciliary pit, *s* = sacculus, $^{68}/_{1}$.

Zygometra microdiscus. Broome, Australia, from the shore. The sample taken from the anal opening. Grains of sand, diatoms, small copepods, ostracods, foraminifera, veliger larvæ.

Tropiometra afra macrodiscus. Sagami (Misaki) Japan, 2—3 metres. 2 specimens dissected. The intestine nearly emptied. Inconsiderable remains of grains of sand, crustacean podiæ, and diatoms. In the gullet large parasitic Myzostomas.

Asterometra anthus, Bonin Islands, 180 metres. The sample taken from the intestine. Detritus, radiolarians, solitary bits of crustacean podiae, foraminifera, one *Ceratium.*

Heliometra eschrichti. W. of Spitzbergen (79° 30′ N, 10° 30′ E), 100 metres. Sample from the intestine. Numerous copepods, solitary ostracods, polynoid bristles, one tinntinnoid.

In order to discover the composition of the diatomaceous flora found among the contents of the intestine, I have treated a few samples in the usual manner for diatomaceous examination (boiling in $H_2SO_4 + NaNO_3$ together with washing) and sent them to Dr. Astrid Cleve-Euler who kindly carried out the investigation requested.

A sample of the excrement of *Antedon petasus* contained:

Actinocyclus crassus V.-H., *Actinoptychus undulatus* (Bail?) Ralfs., *Biddulphia aurita* (Lyngb.) Breb., *Campylodiscus Thuretii* Breb., *Cerataulus Smithii* Ralfs., *Coscinodiscus excentricus* Ehb., *Cosc. oculus iridis* Ehb., *Cosc.* sp. (with large meshes), *Cocconeis scutellum* Ehb., *Diploneis nitescens* Greg., *Grammatophora marina* (Lyngb.) Kg., *Hyalodiscus scoticus* (Kg.) Grun., *Hyal. stelliger* Bail., *Navicula cyprinus* (Ehb.) W. Sm., *Paralia sulcata* (Ehb.) Kg. +, *Nitschia longa* Grun., *N. seriata* Cl. ?, *Rhabdonema arcuatum* (Ag.) Kg., *Rh. minutum* Kütz., *Rhizosolenia setigera* Brig., *Trachyneis aspera* Cl., and, of Silicoflagellata: *Distephanes speculum* (E.) Hasch and *Ebria tripartita* (Schum.) Lemm.

The excrement of *Comantheria grandicalyx:*

Achnanthes longipes Ag., *Amphora* sp., *Actinoptychus undulatus* (Bail?) Ralfs, *Coscinodiscus* sp. (with large meshes), *Diploneis didyma* (Ehb.) Cl., *Dipl. litoralis* (Donk.) Cl., *Epithemia (Rhopalodia) gibba* (E.) Kg., *Grunoviella marina* (Greg.) V.-H., *Grammatophora marina* (Lyngb.) Kg., *Melosira nummuloides* (Borg.) Ag., *Orthosira splendida* (Greg.) Grun., *Paralia sulcata* (Ehb.) Kg., *Trachyneis aspera* Cl. Plentiful with sponge-spicules and star-shaped hairs.

Excrement of *Comaster delicata grandis:*

Few diatoms: *Asterolampa marylandica* var. *major* H. Per., *Nitschia marina* Grun., *Navicula lyra* E. all solitary. Silicoflagellata: *Dictyocha fibula.* Many radiolarians.

The excrement of *Metacrinus rotundus:*

Achnanthes mammalis Castr. rr, *Actinocyclus Ehrenbergi* Ralfs, *Actinoptychus undulatus* Ralfs, *Amphora costata* W. Sm. rr, *Amph. maci-*

lenta GREG. rr, *Climacospnenia elongata* BAIL. r, *Cocconeis reticulata* CL. r, *Cocc. dirupta* GREG. r, *Cocc. finmarchica* GRUN.? rr, *Cocc. pellucida* HANDGSCH. rr, *Coscinodiscus radiatus* E., *Cosc. excentricus* E., *Cosc. curvatulus* GRUN., *Cosc. oculus iridis* E., *Cyclotella striata* (KG.) GRUN., *Diploneis* sp. rr, *Grammatophora oceanica* var. *macilenta* SM. +, *Gr. angulosa* E. var. rr, *Isthmia nervosa* fragments rr, *Navicula libellus* GREG. rr, *Nitschia panduriformis* var. *minor* GRUN. rr, *Synedria affinis* KG. rr, *Trachyneis aspera* CL. r, *Thalassiosira gelatinosa* HENSEN, *Thalassiothrix nitschioides* GRUN. +.

Her opinion on the diatoms identified is as follows: The chief part of the species represented are of benthonic origin; the *Cocconeis* species are epiphytes on algæ and similar matters. Some of them, such as *Actinocyclus, Actinoptychus, Coscinodiscus, Cyclotella, Hyalodiscus stelliger,* and *Paralia* are tycho-pelagic (= semi-pelagic), mostly heavy types which keep to deeper water. *Thalassiothrix* is pelagic. Dr.CLEVE-EULER was not able to find any pronouncedly pelagic genus such as *Chaetoceras* in either of the first two samples. She says of the last two, "Possibly setæ of true pelagic plankton-types, such as *Chateoceras,* are present, but they could not be determined". And at the end: "It does not seem probable that they (true pelagic forms) are devoured to any extent worth mentioning by these animals".

Basing my opinion upon the evidence of the samples of excrement, and as a consequence of Mrs. CLEVE-EULER's statement, I consider it clearly manifest that the Crinoids live upon a mixed diet of detritus and benthonic micro-organisms and plankton, but that the detritus-nourishment plays a very important part, at least for some of them.

F. Formation of the ambulacral groove and feeding in the Comasterids.

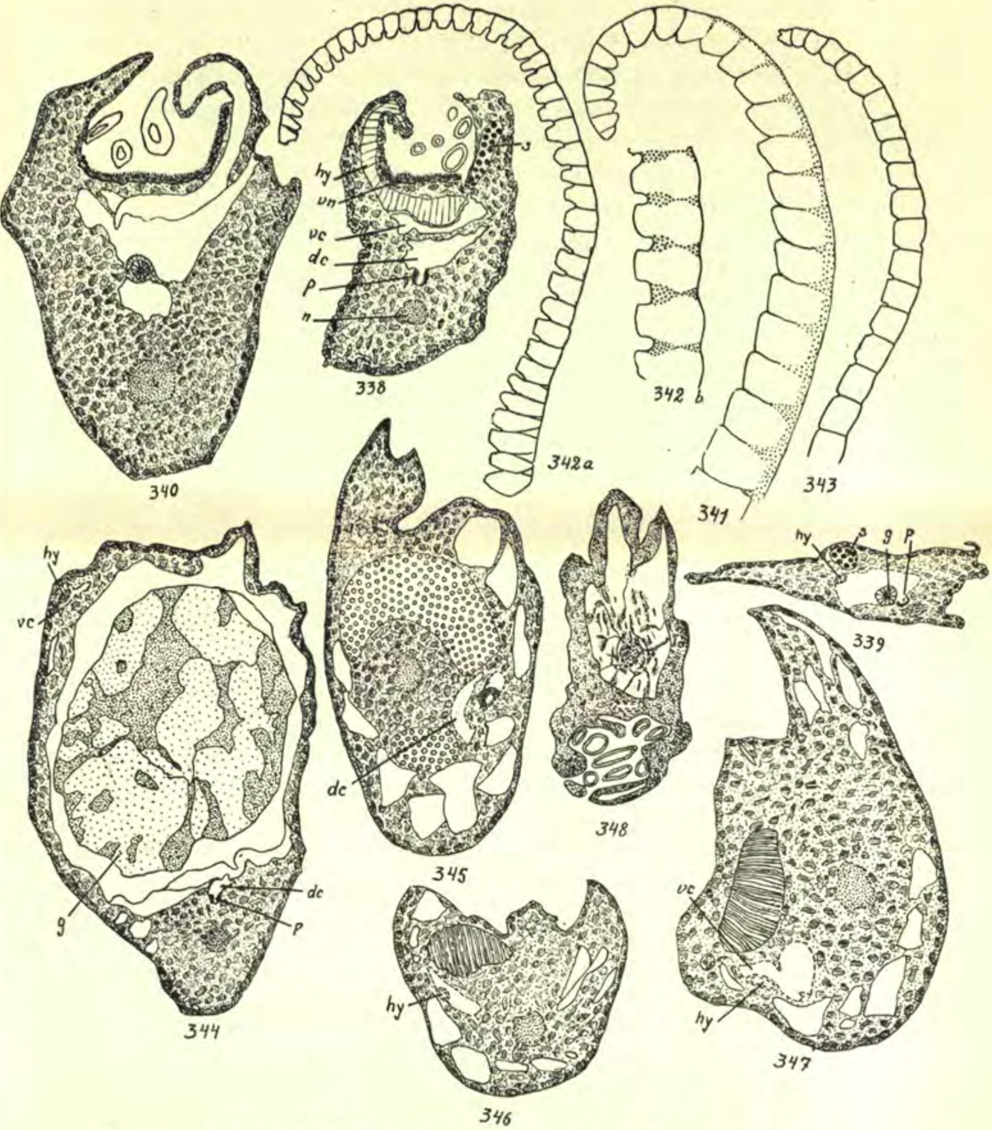
1. The extension of the ambulacral groove.

The apparatus for supplying food, the ambulacral groove, is very variable in its formation and offers a great deal that is interesting, if one follows its varying extension along the arms and pinnules.

The ambulacral groove originally extended to all the arms and appeared on all the pinnules. This primitive condition is still found in the stalked Crinoids, e. g. *Metacrinus* and *Rhizocrinus.* In the Comatulids, however, a varying number of proximal pinnules have developed into tactile organs, and have been transformed into the so-called oral pinnules which have no ambulacral groove or genital gland. Only one pair (per arm) of such organs are found, e. g. in most of the *Bathymetrinae, Antedon petasus* has 2 pairs, *Antedon mediterranea* 3. Simultaneously with the change of function, their appearance changes too, and they generally become long, whiplash-shaped and exceedingly flexible. They are very inconsiderably transformed in *Himerometridae, Stephanometridae, Charitometridae,* and *Thalassometridae,* while a number of the *Mariametridae, Calometridae, Colobometridae,* most of the *Macrophreata,* and *Comasteridae* show very advanced specialization.

Another reason why the extension of the ambulacral groove differs from the usual type on certain pinnules is found in the development of the gonads. In most of the Comatulids the 1st genital gland appears in the 1st post-oral pinnule, and afterwards they appear in all the following pinnules until far out on the arms; in the distal pinnules the genital glands are not so strongly developed, and gradually become partly, or completely, obliterated. In certain types, however, the gonads are restricted to certain pinnules, the genital pinnules, and, at the same time as these play exclusively the part of egg or sperm producers respectively, they have grown coarse and clumsy, and have their ambulacral groove and their hydrocoel more or less strongly reduced. The distal pinnules, on the other hand, begin to play the rôle of respiratory organs and to specialize for collecting nourishment. They often become very much longer and slenderer, and have their tentacles and ambulacral furrow very strongly developed. Thus at least certain species of the family *Tropiometridae* have no ambulacral groove on the first 8—12 pairs of pinnules which are developed as genital pinnules (cf. figg. 337, 338). P. H. CARPENTER, in his Challenger work (1884), reports how two representatives of the fam. *Charitometridae,* afterwards distinguished (*Poecilometra acoela, Pachylometra angusticalyx*), sometimes lack the ambulacral groove on as many as 20 pairs of the proximal pinnules; probably a similar phenomenon to that mentioned above. In accordance with this I have found in *Diodontometra* that the first 9 pairs of pinnules, which have transformed broad joints protecting the gonads, have no ambulacral groove at all (cf. fig. 339).

The reduction of the ambulacral groove in all these cases is the same upon all the arms. The Comasterids, which show far-going reduction of the apparatus for obtaining food, have gone in another direction. These animals are in a state of transition; from a radial type they are changing to a pronouncedly bilateral one. The mouth moves forward in the anterior radius, or towards the right anterior interradius, and often takes a marginal position on the disk. The anal funnel takes the central position of the mouth. (This is a consequence of a lengthening of the intestine. Cf. below.) The anterior arms lengthen and obtain long and slender pinnules, like the distal pinnules of *Tropiometra.* The posterior aboral arms are shortened and have limited longitudinal growth; they become thicker, coarser and more clumsy, perhaps, though not very likely (cf. Chap. 2), on account of the abundant formation of sex-products here; a co-operating factor with the enlargement of the joints is,



Figg. 338—348. 338) *Tropiometra afra macrodiscus* Distal pinnule of the same specimen as fig. 337; *vn*=ventral nerve; for the explanation of the other letters cf. under fig. 337, $^{89}/_{1}$; 339) *Diodontometra bocki.* Genital pinnule, $^{89}/_{1}$, 340) *Asterometra anthus.* Distal pinnule, ciliation continuing a little up the tentcular side, no ciliation of the side and covering plate, $^{140}/_{1}$; 341) *Heliometra eschrichti* Tip of P_1 with a rudimentary comb $^{14}/_{1}$, 342) *Anthometra adriani* P_a, the most distal segments are lacking, a) $^{7}/_{1}$, b) $^{18}/_{1}$; 343) *Promachocrinus kerguelenensis* Tip of P_1, $^{14}/_{1}$; 344) *Comanthus parvicirra α comasteripinna* ♂. Genital pinnule from a posterior ray, indication of letters as in fig. 337, $^{41}/_{1}$; 345—347) *Comaster delicata grandis* 345) Section through one of the most proximal tooth-provided segments of P_2, $^{89}/_{1}$. 346) The same pinnule cut through one of the most distal comb-provided joints, $^{89}/_{1}$. 347) Section through a comb-provided distal pinnule. Dorsal and ventral coelom not completely separated, $^{140}/_{1}$, 348) *Comatula pectinata* Section through the distal pinnulars of a distal pinnule to show the dorsal hooks, $^{140}/_{1}$.

certainly, to be found in the strengthened muscular and ligamentary connections between the Br-joints (H. L. CLARK 1915 a, cf. also p. 59). As a result of this division of labour between the anterior and posterior arms the ambulacral furrows lose their radial symmetrical arrangement, and are often present in the anterior radii only (cf. figg. 344, 354). It is to be observed that the ambulacral furrow really disappears, and is not found remaining "in a closed groove" (cf. A. H. CLARK, 1922, p. 93). Great variation prevails even in the same species. In a number of X-armed specimens of *Comatula pectinata*, and its variety *purpurea* from Cape Jaubert, Australia, the ambulacral furrow was missing in 0—IV of the posterior arms; in a *Comanthus parvicirra,* Sagami, Japan, out of XXXIII arms XIII in the posterior radii had no ambulacral groove, while IV neighbouring arms had it developed distally of the 15th or 20th pair of pinnules. According to P. H. CARPENTER (1879, § 22, 25 and 26), among the 48 species of Comasterids collected during the Challenger Expedition, no less than 23 had the ambulacral groove missing on one or several of the arms (one observes, however, that a great number of these species afterwards proved to be synonymous). The species in this work and in the Challenger Report of 1888 which show a partial reduction of the ambulacral groove are: *Actinometra polymorpha* (= *Comanthus parvicirra*) with $^{15}/_{31}$ of the arms without ambulacral furrow, *Act.* (*Comatula*) *solaris,* and *Act.* (*Comaster*) *belli; Act. regalis* and *nobilis* (= *Comanthina schlegeli*) the latter with a few arms in each ray without ambulacral groove, *Act.* (*Comantheria*) *magnifica,* and *Act.* (*Comatula*) *pectinata* (Synonyms according to A. H. CLARK 1915 c). A. H. CLARK mentions in 1912 that *Comatula micraster* may lack the ambulacral groove in as many as VI arms out of X.

The reduction of the ambulacral groove goes so far in this family that one is tempted to ask, if the apparatus for supplying food can really be sufficiently large to collect nourishment enough for these, in comparison with other Comatulids, coarse and clumsy animals. In order to form an opinion of the relations existing between the apparatus for collecting food and the size of the animal I have taken steps first to estimate the total length of the ambulacral groove, and secondly to measure the volume of the animal, and then by comparing the numbers obtained to find their relation to each other.

2. **The total length of the ambulacral groove and its relation to the volume.**

The total length of the ambulacral groove was obtained by measuring the length of the arms, multiplying by their number, and to the figure thus acquired adding the product of the number of pinnules per arm, the average length of the pinnules, and the number of arms. The final figure gives the approximate length of the ambulacral groove.

The investigations regarding the volume of the animal have been carried out at the Physical Institution, Uppsala, where balances suitable for the purpose were kindly placed at my disposal.

The total length of the ambulacral groove varies of course to a high degree, according to the size of the animal and the number of arms. Among the animals I measured *Rhizocrinus lofotensis,* which only has 4 to 5 pair of pinnules per arm, gave the lowest total figure. The length of the ambulacral groove (VI arms) was only 0·14—0·22 Metres. It is probably several times less in *Bathycrinus minimus,* the smallest Crinoid known. Among the Comatulids I measured, *Comissia ignota minuta* (X arms, 20 mm.) showed the shortest ambulacral groove, 1·30 M. It is about the same length in *Compsometra parviflora* (X arms, 25 mm.), where it measures 1·37 M. It is only inconsiderably longer in *Pentametrocrinus diomedeae* (V arms, 55 mm.) or 1·85 M., and in *Thaumatometra comaster* (X arms, 45 mm.): 2·98 M. *Oligometra chinensis* with X arms, 55 mm., has an ambulacral furrow of 7·15 M., while a large X-armed *Antedon petasus* (length of arms 110 mm.) shows a total of 16·28 M. *Stephanometra spicata* (XXVI arms, 130 mm.): 38·48 M. *Liparometra grandis* with XXVI arms, 120 mm. has an ambulacral groove 44·72 M. long, in the large *Heliometra eschrichti* (X arms, 200 mm.) it reaches a length of 54·5 M. and in the multibrachiate *Himerometra magnipinna* (XLIX arms, 90 mm.) it is 61·23 M. A large specimen of *Metacrinus rotundus* with LVI arms, which from the radial to the arm-tip measures 210 mm., has an ambulacral furrow of 71·68 M. The higest numbers are, however, found in the Comasterids, where the longest ambulacral furrow I have measured, reaches a length of 102·68 M. in *Comantheria grandicalyx* (LXVIII arms, 125 mm.). Further information respecting the length of the ambulacral groove in 13 more cases is given in the table found below.

Before I begin to examine this, it seems to me to be necessary to state in a few words several facts which may influence the relative length of the ambulacral furrow.

At great depths the nourishment is poorer (partly the bottom-life is not so abundant, partly the plankton does not rain down so plentifully, cf. A. H. Clark 1910 b), in the littoral zone the food is very abundant. The deep-sea forms ought therefore to have a relatively long ambulacral groove in comparison with their size, while shallow-water forms ought to be able to manage with a shorter one.[1]

---

[1] A. H. Clark in 1910 b has created a hypothesis to explain the function of the side and covering plates appearing in certain families which are found chiefly in deep water. According to his theory the side and covering plates are of service in increasing the surface taking up nourishment. Now it is noticeable, as

The degree of calcification probably plays some part too. A strongly calcified animal has relatively less organic substance than one which is inconsiderably calcified. The former has less substance to support, and ought to be able to obtain the necessary amount of nourishment with a proportionally shorter ambulacral furrow.

Two objects of similar shape, but different in size, stand in a proportion to each other answering to the square of the surface and the cube of the volume. If we take a given X-armed Comatulid of a certain size and compare it with a similar but much smaller one, the lesser ought therefore to have a comparatively greater surface in proportion to the volume. If again we compare the given type with a very large Comatulid, the larger one in proportion to the volume ought to have a lesser surface. The figure which the total length of the ambulacral groove represents is a function of the surface supplying nourishment and changes according to it. The ratio between the ambulacral groove and the volume gives, in very small Comatulids, an abnormally high figure, in very large Comatulids, an abnormally low one.

A glance at the table shows at once, in the column giving the ratio between the length of the ambulacral groove and the volume, that the average figure is much smaller in the *Comasterids* than among the rest of the Comatulids, or about *1·7* as against *5·0*.

---

sections of ***Asterometra anthus*** show (fig. 340), firstly that these plates are not covered with any ciliated epethelium which, however, stretches, as in *Antedon*, some way up the basal parts of the three-forked tentacle-groups, and secondly that these tentacle-groups which alternate with the side and covering plates are often, even in a contracted condition, at least as long as the plates mentioned above. When the ambulacral furrow is open and the tentacles extended, these cover the unfolded side and covering plates and, moreover, they fish clean, as in *Antedon*, a more or less broad strip outside the lateral margins of the pinnules. If CLARK's theory is correct, why do we not find side and covering plates in *Bathymetrinae*, the most exclusively deep sea group. The condition is not quite the same regarding the stalked families. In *Rhizocrinus* the side and covering plates are large, and it does not seem possible for the tentacles to stretch themselves to any extent worth mentioning outside their rayon. In this case one might imagine CLARK's theory to be correct. The tentacles here should be able to lick off the detritus falling upon the unfolded covering plates, and afterwards to throw the nourishment thus collected into the ambulacral groove (cf. mutatis mutandis *Pelagothuria*). The explanation of the reduction of the side and covering plates in the Comatulids may then be sought for in the enlargement and perfecting of the tentacles, by which means the region covered by the arms could be effectively fished clean, even without these capture-shields. The appearance of side and covering plates among certain of the Comatulids would then be a relic of primitive ancestors and denote a lower condition of organization. Among certain primitive families or genera (*Comatilia, Nemaster, Notocrinus, Calometridae, Thalassometridae,* and *Charitometridae*) these formations still remain well developed, but in other families they can only be traced as net-shaped open-work thin calcareous plates or as variously shaped calcareous spicules.

Species	Locality	A	B	C	D	E	F	G	
		Depth Metres	Number of arms	Length of arms mm.	Length ambulacral furrow. Metres	Weight Gram	Volume Ccm	Spec. Weight	$\frac{D}{F}$
Comissia parvula	Sagami, Japan	720	X	35	1·95	0·89	0·74	1·20	2·64
Comatula pectinata	Cape Jaubert, Australia	20	X (VI)	90	4·37	4·83	3·46	1·39	1·26
Comantheria grandicalyx	Bonin Islands, Japan	54—72	LXVIII	125	102·68	89·6	73·6	1·22	1·39
Comaster delicata grandis	Bonin Islands, Japan	72	XLVI	115	58·92	39·1	30·0	1·30	1·96
Comanthus parvicirra	Misaki, Japan	0—3	XXXIII (XX)	50	7·16	6·65	5·40	1·23	1·33
Catoptometra magnifica minor	Kiu Shiu, Japan	900	XXVII	95	34·50	6·70	5·42	1·24	6·37
Eudiocrinus loveni	Bonin Islands, Japan	144	V	43	2·47	0·65	0·47	1·38	5·26
Amphimetra crenulata	Cape Jaubert, Australia	21	XXX	75	43·05	11·55	8·28	1·39	5·20
Lamprometra protectus	Trincomalie, Ceylon	7	XLIII	50	23·44	7·15	5·75	1·24	4·08
Cyllometra pulchella	Kiu Shiu, Japan	± 200	XIV	40	6·02	0·72	0·60	1·20	10·02
Tropiometra afra macrodiscus	Misaki, Japan	0—3	X	255	47·69	39·8	34·4	1·16	1·39
Asterometra anthus	Bonin Islands, Japan	207	X	70	10·60	3·12	2·34	1·33	4·52
Pectinometra flavopurpurea	Sagami, Japan	720	XX	80	17·84	4·60	3·55	1·30	5·02
Perissometra aranea	Kiu Shiu, Japan	198	XI	100	7·04	1·93	1·46	1·32	4·83
Antedon petasus	Kristineberg, Sweden	30— 40	X	110	16·28	2·63	2·29	1·15	7·10
Heliometra eschrichti	East Greenland	80—100	X	200	54·5	50·0	45·0	1·11	1·21

The figures in brackets indicate the number of grooved arms.

Comissia parvula shows for a Comasterid an abnormally high figure, as it is partly a small species, partly endocyclic (see p. 294), and partly a deep-sea form. Owing to the last-mentioned reason the figure for *Catoptometra magnifica minor* is unusually high too. *Lamprometra protectus* is a littoral type and therefore shows a low figure. Species having a high specific weight, i. e. strongly calcified forms, usually show low figures too; in *Pectinometra flavopurpurea* the decrease is counter-balanced by the great depth at which the animal is found. On the contrary, the slightly calcified *Antedon petasus* and *Cyllometra pulchella,* which last is also very small, show very high figures. It is more difficult to explain the deviation in *Tropiometra afra macrodiscus* and *Heliometra eschrichti.* Both are, however, exceptionally large types and the former is at the same time a littoral species. Regarding *Heliometra eschrichti,* its body is not calcified very strongly, which should perhaps counter-balance its gigantic size, and so should also the fact that it is not a littoral form. An analysis of the intestinal contents showed a great abundance of almost exclusively copepods, i. e. very nourishing food. This Comatulid lives outside the great glaciers of Spitzbergen and Greenland, where an abundance of plakton is found. Possibly this may explain, to some degree, the low figure. The appearance of "rudimentary combs" on the proximal pinnules must, however, also be noticed (cf. p. 287 and fig. 341).

It should be noticed that I have chosen, for my investigations, the most divergent types from the most different localities I was able to obtain, and therefore one should not feel too much surprised, if a few divergences from the general rule appear. It is possible that, in the two cases of great divergency described above, some facts unknown to me may play a part. Taken as a whole, however, it seems to me that the difference between the low figure of the Comasterids and the high figure of the rest of the Comatulids is very remarkable. It is all the more noticeable that the figures given for the Comasterids in the table are low throughout, as 3 of the 5 species examined belong to Comasterids having ambulacral furrows on all the arms and most of the pinnules.

3) **Formation and contents of the intestine in the Comasterids.**

Although among the Comasterids the ambulacral groove is abnormally short in proportion to the animal's size, the intestine shows a peculiarity which suggests that the food is richer and at the same time more difficult to digest. In all the Comatulids, excepting the family mentioned above, the intestine on its way from the mouth to the anal opening makes a single turn. In most of the Comasterids the mouth is displaced towards the anterior radius, thanks to the circumstance that (as P. H. CARPENTER brought to light in his work of 1884, p. 92, and as I have observed myself in *Comanthus japonica*) the intestine, with the anal cone as centre is wound spirally 4 times. The intestine in the Comasterids is thus several times longer than in the other Comatulids. According to A. H. CLARK (1915 c, p. 343) exocyclic Comasterids, i. e. those with eccentric mouth and central anal cone, should be confined to shallow water and muddy bottom. He concludes from this that "the ingestion . . . of a large amount of inorganic material and the use of a very large percentage of plants with highly developed skeletons as food has caused . . . a sudden development of the intestine". This is only correct in part. Certainly the Comasterids in general are shallow-water types, particularly the exocyclic ones, but certain families with central mouths, e. g. *Himerometridae, Mariametridae, Stephanometridae, Tropiometridae* are so too. That the Comasterids are confined to muddy bottom is not correct, as may be seen from a critical glance at the localities explored by the Siboga Expedition (cf. A. H. CLARK 1918). From 65 localities (the description of bottom noted) Comasterids were brought home; 54 of these localities shelter exocyclic Comasterids. In 41 of these cases they were taken from a bottom consisting of stone, sand, "coral" and Lithothaminon; in 3 cases only has mud been found. My examination of the intestinal contents of the Comasterids shows that the vegetable food is certainly very plentiful and consists for the most part of Chlorophyceae, but that inorganic matter is specially inconsiderable or missing altogether (cf. also KIRK 1912 and H. L. CLARK 1915 a).

Analyses of the intestinal contents of both the Comasterids examined (p. 276) show that a considerably richer fauna and flora were found than in the contents of the intestines of other types. The occurrence of algous threads, bits of leaves, bryozoans, and small pieces of sponges was specially noticeable.

4) **The morphology of the combs and their biological function.**

The Comasterids differ from all the rest of the Comatulids, excepting a group discussed below, by the occurrence of the so-called combs, which usually appear on the proximal pinnules, but sometimes are found far out on the distal parts of the arm in *Comaster* and in solitary species of *Comanthus (Vania), Comanthina*, and *Capillaster*. As I have mentioned before, there is still a group of Comatulids where a comb, even if less perfectly developed, really makes its appearance. P. H. CARPENTER (1884) draws the proximal pinnules of *Antedon (Solanometra) antarctica, Antedon rhomboidea* (= *Florometra magellanica)*, and *Antedon (Heliometra) eschrichti*, where an insignificant comb is found on P_1 and P_2. A. H. CLARK (1915 c and 1918) states that rudimentary combs may also appear in *Anthometra* and the other species of *Florometra*. In this connection I only mention the genus *Comatonia*, which is supposed by me to be related to *Heliometrinae*. (The reasons for this genus not being a Comasterid are given in Chap. 4.) One may compare also my drawings of *Anthometra adriani*, *Promachocrinus kerguelenensis*, and *Heliometra eschrichti*, of which the first mentioned has a fairly well-developed comb on P_1 (figg. 341—343). LUDWIG, like P. H. CARPENTER (cf. A. H. CLARK 1922, p. 95), has observed that the terminal segments of the arms and pinnules have no ambulacral groove. All these forms belong to the *Macrophreata*, sub-family *Heliometrinae*. We thus find the remarkable coincidence that in a group not belonging to the Comasterids, where the ambulacral furrow, as we saw above, was unusually short, combs appear as in the Comasterids and that a change sets in hinting at a reduction of the ambulacral furrow. As was pointed out above, the intestinal contents in *Heliometra* show remarkable differences from those of the rest of the Comatulids catching plankton or detritus.

The combs are developed at the ends of the pinnules; only occasionally as in *Comantheria*, *Comanthus* (cf. the drawings in my work of 1922) the most distal segments of the comb-provided pinnules are smooth. In *Comatonia* teeth appear on P_1 and P_a (the only comb-provided pinnules) almost to the bases of the pinnules. The teeth are generally developed on one side only and are arranged in a single row on the side of that pinnule which is turned from the mouth. In *Nemaster* (A. H. CLARK 1922, fig. 609), *Comanthina* (fig. 645), and in *Comanthus* (figg. 651, 653, 655) two rows of teeth occur, an inner row of large ones, and an outer row of small ones. I have drawn a transverse section of one such comb of the *vania*-type from *Comanthus parvicirra* (see fig. 352). My transverse sections through the proximal comb-provided pinnule and the distal pinnule of *Comaster delicata grandis* (figg. 345—347, 350) show that in reality, at least in this form, a small interior tooth occurs inside the large exterior tooth, as in *Nemaster* etc., although it is not discernible to the naked eye. The sections make it evident too, that these teeth derive from the dorsal hooks, occurring in most of the Comatulids and especially well-developed in the Comasterids, which have grown stronger and have made their way up on one side of the pinnule (cf. fig. 349 and 1922 CLARK's fig. 645). Usually 3 dorsal hooks in breadth are situated on a pinnular that has not been transformed. When strengthened to form a comb the hook situated most adorally gains the preponderance and surpass the others, which become more or less supressed, in size. *Nemaster* is distinguished by the appearance of covering-plates, a primitive characteristic. In regard to the combs also it shows its primitive character, by the occurrence of two rows of combs. The inner comb is less evident in the more specialized genus *Comaster*, although quite distinct on sections. In *Comanthus (pinguis)* where the comb shows a, presumably secondary, tendency to reduction, the inner row of teeth is very indistinct (cf. fig. 353).

The ends of the comb-provided pinnules can, contrary to the distal ends of the other pinnules, be rolled into a tight spiral, as one of the interpinnular muscles — always the one found on the pinnule's aboral side — is very strongly developed. This muscle continues through a large part of the segment, penetrating deeper on the proximal side than on the distal one, and so locating the thin dividing wall between the muscles of every articulation somewhat distally of the centre of the joint. As a consequence of this exceedingly one-sided muscular development, the muscular side of the pinnule is very enlarged; the intruding hypertrophied muscle has pressed the dorsal coelom towards the adoral side (cf. figg. 345—347, 349—352). Presumably migration of the dorsal hooks towards the aboral side is explained by the stronger calcification and development of the side turned from the mouth.

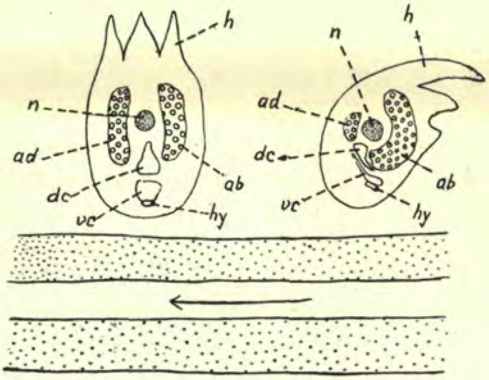


Fig. 349. Diagrammatical sketch to show the transformation of the dorsal hooks into combs, *ab* = aboral muscle, *ad* = adoral muscle, *dc* = dorsal coelom, *vc* = ventral coelom, *h* = hook and tooth respectively, *hy* = hydrocoel, *n* = dorsal nerve. The arrow denotes the direction of the ciliary current on the arm.

A. H. Clark (1909 b, p. 123) endeavoured to give an explanation of the biological function of the combs by assuming that they pick away foreign particles from the arms and pinnules, above all parasitic Myzostomids. The Comasterids are, however, almost more abundantly provided with these commensals than any other family of the Comatulids. (Cf. Clark's work 1922 pp. 619, 659—674, 680—681.) Of 109 Myzostomids no less than 31 species parasitize on the Comasterids. (I have moreover found an entoparasitic *Protomyzostomum (?)* on *Comaster delicata grandis* and ectoparasitic Myzostomids on *Comanthus pinguis* and *Comissia parvula.*) Owing to this I do not think the function of the combs can to any essential extent be the one given by Clark. The different species of *Myzostomidae* are in general each confined to its own particular Comatulid or to a few species of the latter only. Now if the principal task of the combs had been to free the animal from parasitic Myzostomids, either these parasites would soon have been rooted out on the Comasterids or else the Myzostomids must have been endoparasitic to escape the catching apparatus developed specially on their account. In either case the combs (as an organ for exterminating the Myzostomids) would have thus become superfluous at about the same time as they appeared. According to this theory it is also difficult to understand why certain genera should acquire combs far out on the distal pinnules, for the Myzostomids practically always occur on the disk or on the arms in its immediate neighbourhood — quite naturally as the particles of nourishment concentrate more and more the nearer they come to the mouth. Still, there is a possibility that in certain forms the combs have an all-round cleansing function (cf. below), like the ciliary currents and the pedicellariæ in the Asterids and Echinoids described above.

In my work of 1922 I championed the idea (p. 55) that the dorsal hooks in Comasterids with reduced cirri act as a compensation for the cirri, which are used by the rest of the Comatulids as anchoring organs.[1] I found this theory supported partly by the occurrence of the dorsal hooks, so generally and exceptionally strongly developed among the Comasterids, and partly by the reduction and disappearance of the cirri in species belonging to some of the Comasterids (*Comanthus pinguis* had strong cirri, weak dorsal hooks; in *Comanthus annulata* the conditions were reversed. We may compare in CLARK's work 1922, figg. 351—435, 525—526, and 593 with 436—524, 527—591). I have suggested above that the teeth of the combs are derived from the dorsal hooks. The biological development I imagine took place in the following manner.

At the beginning all the distal segments of the pinnules possessed small dorsal hooks. Dorsal hooks appear still in a more or less rudimentary form on the farthest segments of the more distal pinnules in most of the Comatulids. The oral pinnules, on the contrary, are smooth distally except in the sub-family *Heliometrinae*. The combs must be considered to have appeared first on the oral pinnules. In forms where the combs extend far out on the distal pinnules this characteristic appears only at an ontogenetically very late stage. (Cf. my investigations of 1922, pp. 36, 38—39, on the young of *Comaster serrata* and *C. delicata grandis*.) The oral pinnules in most of the Comatulids are developed into tactile organs and are very sensitive; in a number of forms,

---

[1] This seems to be the case too with the grooveless pinnules in *Comatulella brachiolata* (as A. H. CLARK 1922 asserts, pp. 136, 158, fig. 1332). It should be noticed that the coiling of the pinnule takes place more towards the latero-distal side than towards the dorsal side.

thanks to short pinnulars, they are also exceedingly flexible. On account of the formation of the facets of the pinnular this flexibility can only function in a lateral direction (cf. the investigation on this subject p. 97). Thanks to the dorsal hooks and the great flexibility of the oral pinnules, the latter were able to catch hold of objects falling upon the disk or outside the ambulacral grooves, and too great to be carried away by the ciliary currents. To do this the pinnule-tip has been greatly contracted aborally.

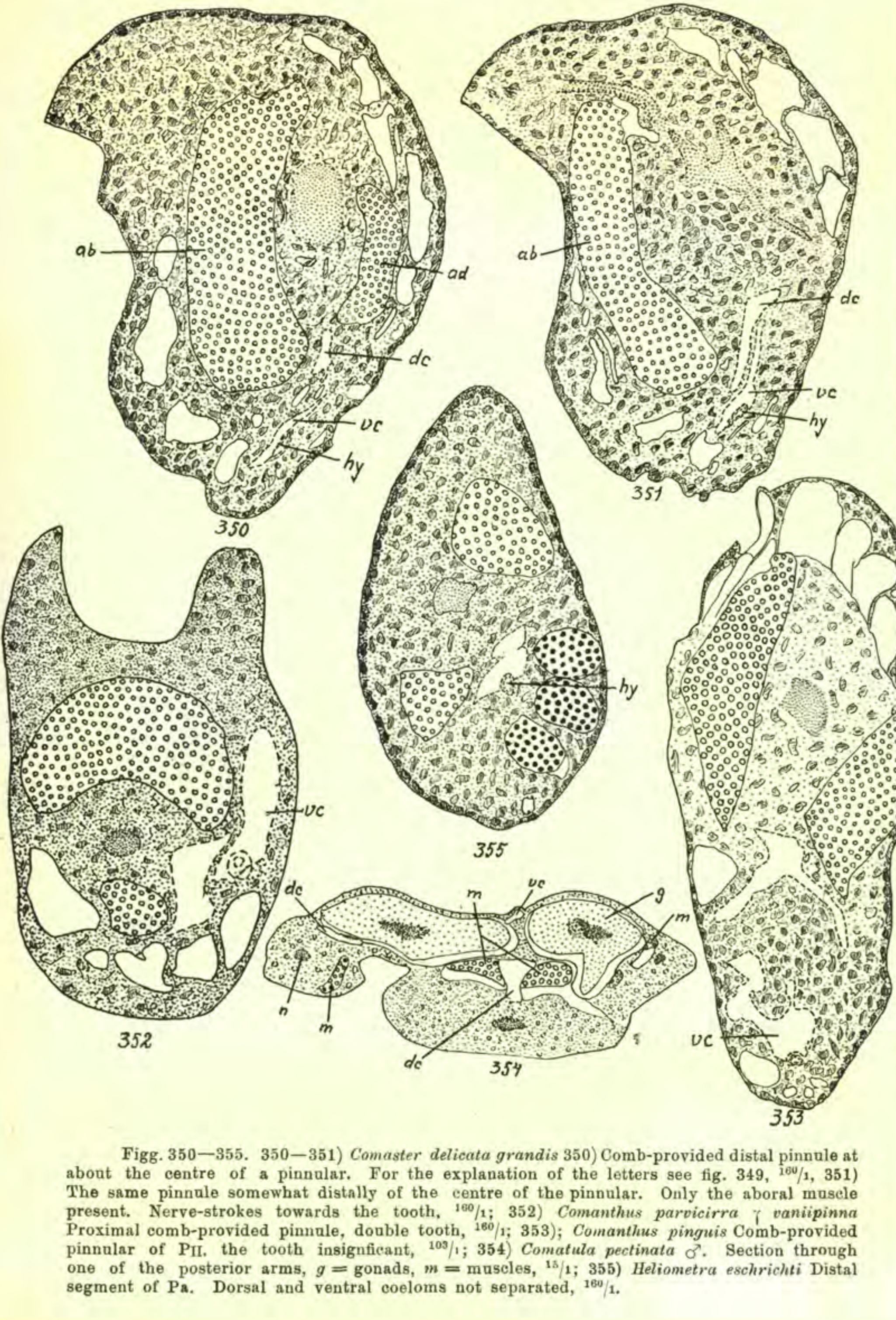
Between the usual distal pinnulars the transversely striated muscle-bundles are very small, nearly rudimentary, and the greater part of the facets of the segment is taken up by the ligamentary connections; this construction does not allow more than rather weak and slow contraction. Between the pinnules in the region of the combs, on the contrary, the transversely striated muscle-bundles, especially, as we have seen, those of the aboral part, are developed enormously which allows of strong and rapid contraction.

I imagine that the aboral muscle, by stronger growth, has gradually forced the weaker adoral muscle towards the side, and so obtained a more medio-ventral position for itself. Owing to this the pinnule-tip was no longer able to curve in laterally when contracted, but was rolled up ventrally and the comb must — not to lose its effect — proceed up the aboral side of the pinnule.

In this way we may explain the greatly one-sided strengthening of the muscles, the torsion of the pinnule-tip (twisted at 90° to the longitudinal direction) and the progress of the dorsal spines up the lateral side turned from the mouth.

As a consequence of the rich innervation the pinnule-tip should be able to distinguish if the object seized upon was inedible or edible. (In the Comasterids branches from the dorsal nerve run to the bases of the teeth, which possibly may be of some importance in connexion with the sense of touch or taste.) We have seen above how difficult it often proves to draw a sharp line between the ciliary currents for cleansing purposes and those carrying nourishment. Here too the possibility of an alternation of function may easily be presumed. When the combs have once begun to grasp small particles fallen upon the animal, it may easily be imagined that instead of letting the object seized drop down between the arms, they have put it into the ambulacral groove or into the mouth. It is not a very long step from this to beginning to pick up or pinch off small particles (algous threads, bits of bryozoans, pieces of leaves, etc.) which do not directly fall down upon the animal, but which are found in its immediate neighbourhood. The formation of the combs upon the oral pinnules may be explained in this way.

The dorsal hooks on the distal pinnules were used as anchoring organs. These would sometimes at the same time catch hold of some



Figg. 350—355. 350—351) *Comaster delicata grandis* 350) Comb-provided distal pinnule at about the centre of a pinnular. For the explanation of the letters see fig. 349, $^{160}/_{1}$, 351) The same pinnule somewhat distally of the centre of the pinnular. Only the aboral muscle present. Nerve-strokes towards the tooth, $^{160}/_{1}$; 352) *Comanthus parvicirra* γ *vaniipinna* Proximal comb-provided pinnule, double tooth, $^{160}/_{1}$; 353); *Comanthus pinguis* Comb-provided pinnular of P_{II}. the tooth insignficant, $^{103}/_{1}$; 354) *Comatula pectinata* ♂. Section through one of the posterior arms, *g* = gonads, *m* = muscles, $^{15}/_{1}$; 355) *Heliometra eschrichti* Distal segment of Pa. Dorsal and ventral coeloms not separated, $^{160}/_{1}$.

soft and loose object, from which small pieces could be severed. By curving in the tip of the pinnule over the ambulacral groove of the arm or of the pinnule itself, the combs were able to pass on the particles of food to the ciliary current to be transported thus to the mouth. In this way a torsion must also have been developed in the formation of the pinnule, owing to the one-sided development of the muscles. The combs upon the distal pinnules might have arisen in this way. The animal by means of these formations was supplied with an extra (and more heavily digested) contribution of food, the intestine therefore become lengthened and a part of the ambulacral groove was reduced as being unnecessary.

5) The Comasterids a family critical in systematization.

In my systematic work of 1922 I have discussed a number of reasons for the difficulty in systematization and the abundance of transition forms found in the Comasterids. The primary reason for this exceptional variability, development of small-species, and irregular combination of different characteristics through hybridization, is probably to be sought, at least to a large extent, in the change of habits sketched above.

6) Summary.

In the 5 points given below I may summarize the reasons for believing that the Comasterids obtain their food in a different manner from the rest of the Comatulids.

(1) Why is there an abnormally short ambulacral groove in the Comasterids, if not because they have other sources of help in obtaining nourishment than the other Comatulids?

(2) Why have the Comasterids an intestine proportionally several times longer than all the other Comatulids, if not because the nourishment is of another kind, more rich and heavier to digest?

(3) Why, in spite of the proportionally small ciliary apparatus, are the contents of the intestine more abundant, if not because organs exist among the Comasterids which (together with the ambulacral groove) can supply the intestine with additional nourishment?

(4) Why have the Comasterids these combs, appearing in some genera far out on the distal pinnules and on the grooveless arms? Why have the teeth of the combs, which are derived from the dorsal hooks, become flattened and tooth-like? Why are the transversely striated muscles so strongly developed in the combs, thus giving them the capacity of rolling themselves up rapidly? Why have the pinnulars of the teeth been so developed that the pinnule-tip is capable of curving in over the ambulacral groove, if not because the combs are organs

employed in picking up small particles of nourishment, thus supplying the animal with the necessary extra food?

(5) Why do we find such great variability in practically all of the systematic characteristics, elsewhere employed with success, if not because the external conditions are altered? As other Comatulids occur at all depths and in all latitudes where the Comasterids appear, it is most natural to think of the diet and different manner of feeding, when one is trying to find a reason for the instability of the systematic characteristics.

In certain Comasterids (the *Comissia* species, *Comatilia,* and some *Comactinia*) the combs are limited to one or two pairs of the proximal pinnules. These forms are endocyclic, i. e. like the rest of the Comasterids they have a central or sub-central mouth and a lateral anal cone, excepting possibly one species of *Comactinia.* I think that in these and other endocyclic Comasterids, thus even in the slender endocyclic *Comaster*-species mentioned below, the combs are of predominating importance in regard to cleansing and for anchoring purposes.

A specimen of the almost perfectly endocyclic *Comaster novae-guineae* had LXVII arms, + IX short regenerated. The average length of the arms was 63 mm. The weight was 11·6 gr., and the volume 8·25 ccm. If all the arms and pinnules had possessed a functioning ambulacral groove, its total length would have reached 38·1 M. The ratio between the ambulacral groove and the volume would have been in this case 4·6. Nevertheless, the two posterior radii (XXXIV arms) show a rudimentary ambulacral furrow on the arms, and a large number of pinnules — it is impossible to give the exact number in figures — which have no ambulacral furrow. The animal therefore has probably not more than at most a 25 to 30 M. long effective ambulacral groove, and the ratio would then be 3·0 to 3·6, i. e. unsually small for an ordinary Comatulid, and unusually large for a Comasterid.

Most of the Comasterids are exocyclic, with a marginal mouth, a central anal cone and an inflated disk. The most advanced types (*Comaster, Comanthina, Vania,* and *Capillaster*) have, as has been mentioned before, combs even upon certain of the distal pinnules and are in most cases exocyclic (excepting various *Comaster*-species of a very slender type, e. g. *C. minimus, novae-guineae,* and *sibogae*). Among these too the combs are most likely of importance also for collecting nourishment. The combs appear in the *Comaster*-type, as I have shown in my systematic work mentioned above, upon every other or every third pinnule. About half the number of genital pinnules are thus furnished with combs. As a result of the development of sex-products, these pinnules are greatly swollen, clumsy, and, presumably, not very flexible. It is easy to imagine that this somewhat impedes the combs when engaged in passing the collected food into the ambulacral groove, and that instead it is probably easier to pass the food from one comb to the other along the arm towards the mouth — in the same way an Ophiurid transports small particles of nourishment along the arms towards the mouth by means of the feet. As the combs occur also on the arms with no ambulacral groove, an explanation of this sort becomes a necessity, if the combs are to be assigned any importance in supplying food. (In e. g. a *Comanthus parvicirra* γ *vaniipinna* the most distal comb-provided pinnule on a grooveless arm was 7 mm. long, while the distance to the nearest ambulacral groove was 18 mm.)

We have an interesting parallel here to the similar method of obtaining nourishment found in the Ophiurids. The plan of evolution, however, is realized in two different ways in the two different cases, but the biological issue is the same. In the Ophiurids it is the tube-feet (= the tentacles in the Crinoids) which take over the transport of the food to the mouth. The ambulacral groove, which at the beginning was undoubtedly ciliated and used for transporting nourishment to the mouth, became unnecessary, was closed by the margins growing together, and ended by lying in the epineural canal. (N. B. Ontogenetic evidence of this is found in the ambulacral groove still being open in very yong specimens, cf. Cuénot 1891, p. 458 ff.) In the Comasterids it is the combs, i. e. the transformed dorsal hooks on the ends of the pinnules, which have begun to take over the transportation of nourishment. The process of evolution has not gone so far here, but there is an evident tendency to the elimination of the ambulacral furrow. The process, however, takes place in another way than among the Ophiurans; the epithelium of the ambulacral groove degenerates so that the difference between it and the surrounding epithelium disappears. In both cases we get a non-ciliated arm, but while in the former case the ciliary groove — as in the Echinoids and Holothurians — becomes enclosed in an epineural canal and is retained as a cord, now exclusively nervous, in the latter case within the Comasterids the ambulacral folds are smoothed out and the ambulacral groove obliterated, the complete disappearance in this case evidently being possible because there are already nervous systems developed in the arms.

List of papers and works referred to.

I have not myself seen the works marked with an asterisk, but the statments have been kindly verified by Messrs. F. A. Bather, A. Reichensperger, and R. Spärck.

Abel, O. Grundzüge der Palæobiologie, 708 pp., Stuttgart 1912.

Agassiz, A. Three Cruises with the »Blake«, 2 Vols., London 1888.

—— *Calamocrinus Diomedeæ*, a new stalked Crinoid. Mem. Mus. Comp. Zool. Harvard, Vol. 17, No. 2, 95 pp., Cambridge, Mass. 1892.

Agassiz, L. Prodrome d'une monographie des radiaires ou Échinodermes. Mém. de la Soc. des Sciences nat. de Neuchâtel, Tome 1, pp. 168—199, Neuchâtel 1835.

Airaghi, C. Echinodermi miocenici dei dintorni di S. Maria Tiberina (Umbria). Atti di Accad. Scienze di Torino, Vol. 40, pp. 43—54, Torino 1904.

Ameghino, T. Les formations sédimentaires du Crétacé supérieur et du Tertiaire de Patagonie. Ann. del Museo Nacional de Buenos Aires, Ser. 3, Tomo 8, 568 pp., Buenos Aires 1906.

Andersson, K. A. Brutpflege bei *Antedon hirsuta*. Wissensch. Ergebnisse der Schwed. Süd-Pol. Exp. 1901—03, Bd. 5, Lief. 1, pp. 1—7, Stockholm 1904.

Angelin, N. P. Iconographia Crinoideorum in stratis sueciæ siluricis fossilium. 62 pp., 29 Tabb., Stockholm 1878.

d'Archiac. Descriptions des fossiles recueillis par M. Thorent dans les couches a nummulines des environs de Bayonne. Mém. de la Soc. Géol., Tome 2, pp. 189—217, Tome 3, pp. 397—456, Paris 1846 et 1850.

des Arts, L. Über die Lebensweise von *Amphiura Chiajei* unter Berücksichtigung der anatomischen Verhältnisse. Bergens Mus. Aarbog 1910, No. 12, 10 pp., Bergen 1910.

Austin, Th. sen. & jun. A monograph on recent and fossil Crinoidea. London 1844—1847.

Baier, J. J. Monumenta rerum petrificatarum præcipua oryctographiæ noricæ supplementi. Norimbergæ 1757.

Barrande, J. Système Silurien du centre de la Bohème. 1ère Partie: Recherches Paléontologiques, Vol. 7 Echinodermes, I Ordre des Cystidées (Ouvrage posthume publié par W. Waagen), 233 pp., 39 Pll., Prague 1887.

—— Système Silurien etc., 2 Crinoidés (par Waagen et Jahn), 215 pp., 40 Pll., Prague 1899.

Bather, F. A. British fossil Crinoids. I Historical Introduction, II The Classification of the Inadunata Fistulata. Ann. & Mag. Nat. Hist., Ser. 6, Vol. 5, pp. 306—334, 373—388, 485—486, London 1890.

—— British fossil Crinoids, V *Botryocrinus*. Ann. & Mag. Nat. Hist., Ser. 6, Vol. 7, pp. 389—412, London 1891.

—— Suggested terms in Crinoid Morphology. Ann. & Mag. Nat. Hist., Ser. 6, Vol. 9, pp. 51—66, London 1892 (a).

Bather, F. A. British fossil Crinoids, VI *Botryocrinus quinquelobus* sp. nov. etc. Ann. & Mag. Nat. Hist., Ser. 6, Vol. 9, pp. 189—194, London 1892 (b).

—— The Crinoidea of Gottland, Part 1, The Crinoidea Inadunata. Kungl. Sv. Vet. Akad. Handl., Bd. 25, No. 2, 192 pp., Stockholm 1893.

—— The term syzygy in the description of Crinoids. Zool. Anzeiger, Vol. 19, pp. 57—61, 198, Leipzig 1896.

—— *Apiocrinus recubariensis* Crema from the Muschelkalk is a primitive *Millericrinus.* Geol. Magazine, Dec. 4, Vol. 4, pp. 116—123, London 1897.

—— *Petalocrinus.* Quaterly Journ. Geol. Society, Vol. 54, pp. 401—441, Pll. 25—26, London 1898.

—— *Ptilocrinus antarcticus* n. sp., a Crinoid dredged by the Belgian Antarctic Exp. Bull. de l'Acad. roy. de Belgique (Classe des sciences) 1908, pp. 296—299, Bruxelles 1908.

—— Triassic Echinoderms of Bakony. Resultate der wiss. Erforsch. des Balaton-Sees. 1. Bd., 1. Theil, Anhang Palæontologie. 1. Bd., 290 pp., Wien 1909.

—— Notes on *Hydreionocrinus.* Trans. of the Edinburgh Geol. Soc., Vol. X, part 1, pp. 61—76, Pl. 8, Edinburgh 1912.

—— British fossil Crinoids, XI *Balanocrinus.* Ann. & Mag. Nat. Hist., Ser. 8, Vol. 20, pp. 385—407, London 1917.

Bell, A. A synopsis of the Crustacea and Echinodermata of the upper tertiaries. Rep. Yorkshire Philos. Soc. 1896, pp. 1—12, York 1896.

—— Notes on the latter tertiary Invertebrata. Ann. Rep. Yorkshire Phil. Soc. 1920, pp. 1—21, 2 Pll., York 1920.

Bellini, R. Le varie facies del miocene medico nelle colline di Torino. Boll. della societá geologica italiana, Vol. 24, pp. 607—653, Roma 1905.

Benecke. Ref. von R. Wagner: Die Encriniten des u. Wellenkalks etc. Neues Jahrb. f. Mineralogie, Bd. 1887: 1, Referat, pp. 376—378, Stuttgart 1887.

Beyrich. Über die Crinoiden des Muschelkalks. Abhandl. der kgl. Akad. der Wiss. zu Berlin, Jahrg. 1857, pp. 1—49, 2 Taf., Berlin 1858.

Bigot, A. Echinodermes bathonien du Calvados. Bull. de la Soc. Linéenne de Normandie, 5^{e} Serie, 1er Vol., Année 1897, pp. 39—49, Caën 1898.

Blegvad, H. Undersøgelser over Næring og Ernæringsforhold hos Havbundens invertebrate Dyresamfund i danske Farvande. Med Tillæg. Beretning fra den danske biol. Station, Vol. 22, pp. 37—124 og Tillæg 45 pp., København 1914.

Blumenbach, J. F. Specimen archæologie telluris. Goettingæ 1803.

Bosshard, H. Zur Kenntnis der Verbindungsweise der Skelettstücke der Arme und Ranken von *Antedon rosacea* Linck (*Comatula mediterranea* Lam.). Jenaische Zeitschr. f. Naturwiss., Bd. 34, Heft 1, pp. 65—112, Pll. 3—8, Jena 1900.

Braun, F. Verzeichniss etc. 2. Aufl. 1840 (see Münster 1833).

Bronn, H. G. Lethæa geognostica. 2 Bdd., Stuttgart 1835—1838.

—— Ueber die Crinoideen-Reste im Muschelkalk. Neues Jahrb. f. Mineralogie 1837, pp. 30—33, 316, Taf. 2, Stuttgart 1837.

—— Index palæontologicus. Abth. 1. Nomenclator palæontologicus, 2 Voll., 1380 pp., Stuttgart 1848.

—— Die klassen u. Ordnungen des Thierreichs. Bd. 2. Aktinozoen. Leipzig 1860.

Brunhuber. Geologische Neuigkeiten II. Berichte des naturwiss. Vereines zu Regensburg, Vol. 7, pp. 123—128, Regensburg 1901.

Brünnich-Nielsen, K. Crinoiderne i Danmarks Kridtavlejringer. Danmarks Geol. Undersøgelse, 2. Række, No. 26, København 1913.

Buckland, W. Geology and mineralogy considered with reference to natural Theology, Vol. 2. The Bridgewater Treatises etc., London 1837.

BURY, H. The early stages in the Developement of *Antedon rosacea*. Philos. Transactions, Vol. 179 B, pp. 257—301, Pll. 43—47, London 1888.

CARPENTER, P. H. On the genus *Actinometra* MÜLL. with a morphological account of a new species *(A.) polymorpha* of the Philippine Islands. Trans. Linn. Soc., Ser. 2 Zoology 2, pp. 1—122, London 1879.

—— On some undescribed Comatulæ from the British Secondary Rocks. Quaterly Journ. Geol. Soc., Vol. 36, pp. 36—55, Pl. 5, London 1880 (a).

—— On some new Cretaceous Comatulæ. Quaterly Journ. Geol. Soc., Vol. 36, pp. 549—558, Pl. 23, London 1880 (b).

—— Featherstars, recent and fossil. Pop. Sci. Revue N. S., Vol. 4, 12 pp., London 1880 (c).

—— On two new Crinoids of the upper Chalk of Southern Sweden. Quaterly Journ. Geol. Soc., Vol. 37, pp. 128—136, Pl. 6, London 1881 (a).

—— On the genus *Solanocrinus* GOLDFUSS and its relations to recent Comatulæ. Journ. Linn. Soc. Zoology, Vol. 15, pp. 187—217, Pll. 9—12, London 1881 (b).

(——) Interesting new Crinoids. Nature, Vol. 23, p. 377, London 1881 (c).

—— On some new or little known Jurassic Comatulæ. Quaterly Journ. Geol. Soc., Vol. 38, pp. 29—43, Pl. 1, London 1882.

—— Report upon the Crinoidea collected during the Voyage of H. M. S. Challenger during the years 1873—76. Part 1. General Morphology with descriptions of the stalked Crinoids. Rep. Sci. Res. Explor. Voyage H. M. S. Challenger, Zoology, Vol. 11, London 1884.

—— The generic position of *Solanocrinus*. Ann. & Mag. Nat. Hist., Ser. 5, Vol. 19, pp. 81—88, London 1887.

—— Report upon the Crinoidea etc. Part 2. The Comatulæ. Rep. Sci. Res. Explor. Voyage H. M. S. Challenger, Zoology Vol. 26, London 1888.

CARPENTER, W. B. Researches on the Structure, Physiology, and Development of *Antedon rosaceus*. Part 1. Philosoph. Transact., Vol. 156, pp. 671—756, London 1866.

—— On the Structure, Physiology, and Development of *Antedon rosaceus*. Proceed. Roy. Soc., Vol. 24, pp. 211—231, London 1876.

CARTIER, R. Der obere Jura zu Oberbuchsitten. Verhandl. der naturforsch. Gesellsch. Basel, Tome 3, pp. 48—64, Basel 1863.

CHADWICH, H. C. *Antedon (bifida)*. Transactions of the Liverpool. Biol. Society, Vol. 21, pp. 371—416, Liverpool 1907.

—— Asteroids feeding upon living Sea Anemones. Nature, Vol. 96, p. 677, London 1916.

CHAPMAN, F. A study of the Batesford Limestone. Proceed. Roy. Soc. Victoria, Vol. 22 (N. S.) Part 2, pp. 263—312, Melbourne 1910.

—— Description of new and rare fossils obtained by deep-boring in the Mallee, Part 1. Proceed. Roy. Soc. Victoria, Vol. 26 (N. S.) Part 1, pp. 165—191, Melbourne 1913.

CHOFFAT, P. Recueil de monographies stratigraphiques sur le système crétacique du Portugal. 2^{me} Étude. Direction des services géologiques du Portugal, Lisbonne 1900.

CLARK, A. H. Two new Crinoids from the North Pacific Ocean. Proceed. U. S. Nat. Mus., Vol. 32, pp. 507—512, Washington 1907 (a).

—— A new species of Crinoid *(Ptilocrinus pinnatus)* from the Pacific coast, with a note on *Bathycrinus*. Proc. U. S. Nat. Mus., Vol. 32, pp. 551—554, Washington 1907 (b).

—— Some cases of abnormal arm-structure in recent Crinoids. Proc. U. S. Nat. Mus., Vol. 34, pp. 265—270, Washington 1908 (a).

CLARK, A. H. The Crinoid genus *Eudiocrinus* with description of a new species. Proc. U. S. Nat. Mus., Vol. 34, pp. 271—279, Washington 1908 (b).

—— The nomenclature of the recent Crinoids. Proc. U. S. Nat. Mus., Vol. 34, pp. 435—542, Washington 1908 (c).

—— The homologies of the arm-joints and the arm-divisions in the recent Crinoids of the families of the *Comatulida* and the *Pentacrinitidæ*. Proc. U. S. Nat. Mus., Vol. 35, pp. 113—131, Washington 1908 (d).

—— Preliminary notice of a collection of recent Crinoids from the Philippine Islands. Smithson. Miscell. Collections, Vol. 52, pp. 199—234, Washington 1908 (e).

—— The non-muscular articulations of Crinoids. American Naturalist, Vol. 43: 2, No. 514, pp. 577—587, Boston 1909 (a).

—— On a collection of Crinoids from the Copenhagen Museum. Videnskabl. Meddelelser fra den Naturhistoriske Forening, pp. 115—194, Kjøbenhavn 1909 (b).

—— The axial canals of the recent *Pentacrinitidæ*. Proc. U. S. Nat. Mus., Vol. 35, pp. 87—91, Washington 1909 (c).

—— The origin of the crinoidal muscular articulations. American Journal ot Science, Ser. 4, Vol. 29, pp. 40—44, New Haven Conn. 1910 (a).

—— An interesting structural analogy. Ann. & Mag. Nat. Hist., Ser. 8, Vol. 5, pp. 358—361, London 1910 (b).

—— (Die Fauna Süd-West Australiens.) Crinoidea. Ergebnisse der Hamburger S. W. Australischen Forschungsreise 1905 von Michaëlsen u. Hartmeyer, Bd. 3, Lief. 13, pp. 435—467, Jena 1911 (a).

—— The recent Crinoids of Australia. Australian Mus. Mem. IV. Scient. Results of the trawling Exp. H. M. S. »Thetis» etc., Part. 15, pp. 703—804, Sydney 1911 (b).

—— The Crinoids of the Indian Ocean, 325 pp., Calcutta 1912.

—— (Fauna Süd-West Australiens.) Crinoidea (Supplement). Ergebnisse der Hamburger Süd-West Austral. Forschungsreise 1905, Bd. 4, Lief. 6, pp. 307—315, Jena 1913.

—— A study of the recent Crinoids which are congeneric with fossil species. American Journ. of Science (Ser. 4), Vol. 40, pp. 60—66, Washington 1915 (a).

—— Die Crinoiden der Antarktis. Deutsche Südpolarexpedition 1901—03. XVI. Bd. Zool., VIII. Bd., Heft II, pp. 103—209, Berlin 1915 (b).

—— A monograph of the existing Crinoids. Vol. 1. The Comatulids. Part 1. Smithson. Inst. U. S. Nat. Museum, Bull. 82, 406 pp., 602 figg., Washington 1915 (c).

—— The unstalked Crinoids of the Siboga Expedition. Siboga Expeditie 42 B, 300 pp., Leyden 1918.

—— A monograph of the existing Crinoids. Vol. 1. The Comatulids. Part 2, Smithson. Inst. U. S. Nat. Mus., Bull. 82, 795 pp., 1364 figg., Washington 1922.

—— Crinoidea (of) The Danish Ingolf Expedition. Vol. 4, No. 5, 60 pp., Copenhagen 1923.

CLARK, E. V. Geological notes on the cliffs separating Aldringa and Myponga bays. Trans. Roy. Soc. South Australia, Vol. 24, part 1, pp. 1—5, Adelaide 1900.

CLARK, H. L. Echinodermata of the scientific results of the trawling Exp. of H. M. C. S. Thetis off the coasts of New South Wales. Austral. Mus. Mem. IV Part 11, Sydney 1909.

—— The Comatulids of Torres Strait. With special reference to their habits and reactions. Carnegie Institution, Pap. from the Dep. of Mar. Biol., Vol. 8, pp. 97—125, Washington 1915 (a).

CLARK, H. L. The Echinoderms of Ceylon other than Holothurians. Spolia Zeylanica, Vol. 10 part 37, pp. 83—102, Colombo 1915 (b).

—— The habits and reactions of a Comatulid, *Tropiometra carinata*. Carnegie Institution, Dep. Mar. Biol., Vol. 11, No. 6, pp. 111—119, Washington 1917.

—— Report on the Crinoidea and Echinoidea collected by the Bahama Exp. from the Univers. of Iowa in 1893. Bull. from the Laborat. of Nat. Hist. Iowa, Vol. 7, No. 5, Iowa 1918.

—— The Echinoderm Fauna of Torres Strait. Its composition and its origin. Carnegie Institution, Dep. Mar. Biol., Vol. 10, 223 pp., 38 Pll., Washington 1921.

CLARK, W. B., and TWITCHELL, M. W. The mesozoic and cenozoic Echinodermata of the U. S. Geolog. Survey. Monograph 54, 227 pp., Washington 1915.

CLARKE, J. M. Early adaptation in the feeding habits of the starfishes. Philadelphia Journ. of the Acad. of Nat. Science, 2nd Ser., Vol. 15, pp. 115—118, Pll. 14—16, Philadelphia 1912.

CHUN, C. Aus dem Tiefen des Weltmeeres, Jena 1900.

COLINI. Description de quelques Encrinites du Cabinet d'Histoire naturelle etc. Acta Academiæ Theodoro-Palatinæ, Tom. 3, Physicum, pp. 69—105, Mannheim 1775.

CONRAD, T. A. Check list of the invertebrate fossils of N. America. Eocene & Oligocene. Smithson. Misc. Coll., No. 200 (Vol. 7, No. 6), Washington 1866.

Mc COY, F. On some new mesozoic Radiata. Ann. & Mag. Nat. Hist., Ser. 2, Vol. 2, pp. 397—420, London 1848.

CREMA, C. Adizioni agli Echinodermi del Muschelkalk di Recoaro. Reale Instituto Veneto di Science etc., Atti (Ser. 7, Vol. 7), Vol. 54, pp. 854—860, Venezia 1896.

CROZIER, W. J. The amount of bottom material ingested by Holothurians *(Stichopus)*. Journ. of Exper. Zool., Vol. 26, pp. 379—389, Philadelphia Pa. 1918.

CUÉNOT, L. Etudes morphologiques sur les Échinodermes. Archives de Biologie, Tome 11, pp. 313—680, Gand 1891.

DEEKE, W. Die mesozoischen Formationen der Provinz Pommern. Greifswald. Mittheilungen aus dem naturwiss. Verein, Jahrg. 26, pp. 1—115, Berlin 1895.

DEVALQUE, G. Prodrome d'une description géol. de la Belgique, Bruxelles, 1re Ed. 1868, 2me Ed. 1880.

DÖDERLEIN, L. Die gestielten Crinoiden der Siboga Expedition. Siboga Expeditie, Vol. 42 A, Leiden 1907.

—— Über japanische und andere Euryalæ. Doflein. Beiträge zur Naturgeschichte Ostasiens. Abhandl. der II. Klasse der kgl. Akademie der Wiss., II. Suppl.-Bd., 5. Abhandl., 123 pp., 7 Taf., München 1911.

—— Die gestielten Crinoiden der deutschen Tiefsee-Expedition. Wissenschaftl. Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer Valdivia 1898—1899, Bd. 17, Heft 1, Jena 1912 (a).

—— Die Arme der Gorgonocephalinæ. Zoologische Jahrbücher, Supplement 15, 2. Bd., Jena 1912 (b).

DOLLO, L. Les lois de l'Évolution. Bull. Soc. Belge de Géol., de Paléont. & d'Hydrologie, Vol. 7, pp. 164—166, Bruxelles 1893.

DONCIEUX, L. Catalogue descriptif des fossiles nummulitiques de l'Aude et de l'Herault. Ann. de l'Université de Lyon. Nouv. Serie I, Fasc. 30, pp. 1—161, Lyon 1911.

DOWNES, W. The zones of the Blackdown Beds and their correlation with those at Haldon with a List of the Fossils. Quaterly Journ. Geol. Soc., Vol. 38, pp. 75—94, London 1882.

Dujardin, F. Sur la Comatule de la Mediterraunée. L'Institut, Vol. 3, p. 268, Paris 1835.

Dujardin & Hupé. Histoire Naturelle des Zoophytes Échinodermes I Crinoides, pp. 35—218, Paris 1862.

Eck, H. Ueber einige Triasversteinerungen, II Encrinen. Zeitschr. der deutsch. geol. Gesellschaft, Bd. 31, pp. 257—263, Berlin 1879.

Eichelbaum, E. Über Nahrung und Ernährungsorgane von Echinodermen. Wissenschaftl. Meeresuntersuch. N. F., Vol. 11, pp. 187—274, Kiel 1910.

Eisig, H. Biologische Studien angestellt in der Zool. Stat. in Neapel. Kosmos, Bd. 13, pp. 128—131, Stuttgart 1883.

Emmons, E. Agriculture Eastern Counties; together with descriptions of the fossils of the marl beds. Report of the North Carol. Geol. Survey, Raleigh 1858.

Engel, Th. Über einige neue Echinodermen des schwäbischen Jura. Jahreshefte des Vereins f. vaterl. Naturkunde im Württemberg, Vol. 48, pp. XLVII—LV, Stuttgart 1892.

—— Geognostischer Wegweiser durch Württemberg. 3. vermehrte und vollständig umgearbeitete Auflage. 645 pp., Stuttgart 1908.

Etallon, A. Esquisse d'une description geologique du Haut-Jura et en particulière des environs de St. Claude. Ann. des Sciences phys. et nat. d'Agriculture et d'Industrie de Lyon, Sér. 3, Tome 1, pp. 247—357, Lyon 1857.

*—— Etudes paléontologiques. Rayonnes du Haut-Jura de Montbéliard. Mém. de la Soc. d'Émulation du Doubs, 3^{me} Série, Tome 3, Besançon 1859.

*—— Paléontostatique du Jura. Faune de l'étage Corallien. Actes de la Soc. Jurass. d'Émulation, XI^{me} Session 1859, Porrentruy 1860.

—— Lethæa bruntrutana ou études paléontologiques ... sur les terrains jurassiques supérieurs du Jura Bernois (Suite). Neue Denkschr. der allg. schweizer. Gesellschaft f. Naturwiss., Vol. 19, Zürich 1862 (a).

*—— Études paléontologiques. Monographie du Corallien. Mém. de la Société d'Émulation du Doubs, 3^{me} Série, Tome 6, Besançon 1862 (b).

Etheridge, R., jun. A monograph of the Carboniferous and Permo-Carboniferous Invertebrata of N. S. W. Part 2 Echinodermata etc. Dep. of Mines, Mem of the geol. Soc. of New South Wales. Palæontology No. 5, Part 2, Sydney 1892.

Faure-Marguerit, G. Monographie paléontologique des assises coralligènes du promontoire de l'Échaillon (Isère). Trav. Laborat. de Géol. de l'Univers. de Grenoble, Tome 12, 2^{me} Fasc., pp. 9—108, Grenoble 1920.

Fontannes, F. Les terrains tertiaires superieures du Haut-Comtat Venaissin. Ann. de la Soc. d'Agricult. de Lyon, Ser. 4, Vol. 9, pp. 571—672, Paris 1877.

—— Note sur la découverte de deux espèces nouvelles du genre *Antedon* dans les terrains tertiaires sup. du bassin du Rhône. Bull. de la Soc. Géol. de France, 3^{e} Série, Tome 3, pp. 497—500, Paris 1879 (a).

—— Étude stratigraphique et paléontologique sur le tertiaire de bassin du Rhône, V Descriptions de quelques espèces noveau ou peu connues. Crinoides. Ann. de la Soc. d'Agricult. de Lyon, Ser. 5, Tome 1, pp. 410—416, Pl. 2, Lyon 1879 (b).

Forbes, E. Monograph of the Echinodermata of the British Tertiaries. Palæontographical Society, 38 pp., 4 Pll., London 1852.

Fourtau, R. Catalogue des invertébrés fossiles de l'Égypte. Terrains tertiaires, 2^{me} partie Échinodermes neogènes. Geolog. Survey of Egypt, Pal. Series, Vol. 4, Cairo 1920.

Fraas, O. Aus dem Orient. II. Theil. Geolog. Beobachtungen am Libanon, Stuttgart 1878.

FRENZEL, J. Beiträge zur vergleich. Phys. u. Histologie der Verdauung. I Mitteil. Der Darmkanal der Echinodermen. Arch. f. Anat. u. Physiol. Jahrg. 1892, pp. 81—114, Leipzig 1892.

FRIČ, A. Studien im Gebiete der Böhm. Kreideformation, V Priesener Schichten. Archiv f. naturwiss. Landesdurchforsch. von Böhmen, Bd. 9, No. 1, pp. 1—135, Prag 1893.

—— Miscellanea paleontologica, II Mesozoica, Prag 1910.

—— Studien im Gebiete der Böhm. Kreideformation. Illustr. Verzeichniss der Petrefakten der cenomanen Korycaner Schichten. Arch. f. die naturwiss. Landesdurchforsch. Böhmen, Bd. 15, No. 1, pp. 1—101, Prag. 1911.

FURLANI, M. Die Lemeš-Schichten. Jahrb. der k. k. geolog. Reichsanstalt, Vol. 60, pp. 67—98, Wien 1910.

GANDOLFI HORNYOLD, A. Über die Nahrungsaufnahme der Spatangiden. Biol. Zentralblatt, Bd. 29, pp. 759—762, Leipzig 1909.

—— Beiträge zur Anatomie u. Biologie der Spatangiden. Fribourg. Mém. Soc. Sci. Nat., Bd. 1, Heft 2, pp. 25—67, Freiburg (Schweiz) 1910.

—— Über die Nahrungsaufnahme der Spatangiden. Verhandl. Schweizer. naturforsch. Ges., Bd. 95, 2. Theil, p. 232, 1912.

—— Über den Aufenthalt im Sand, Eingraben, Kanalbau u. Schleimabsonderung der Spatangiden. IX Congrès Internat. de Zoologie à Monaco 1913, pp. 458—467, Rennes 1914.

GEINITZ, H. B. Characteristik der Schichten u. Petrefacten der sächsisch-böhmischen Kreidegebirges, Leipzig 1839 (N. Ausg. 1850).

—— Grundriss der Versteinerungskunde, Dresden u. Leipzig 1846.

—— Das Elbthalgebirge in Sachsen. Crinoidea. Palæontographica, Vol. 20: 1 and 2, pp. 91—94 and 17—19 respectively, Cassel 1871—1875.

GEMILL, J. F. On the ciliation of Asterids and of the question of ciliary nutrition in certain species. Proceed. Zool. Soc. of London 1915, pp. 1—21, London 1915.

GERMAR, E. F. Ueber die Versteinerungen von Solenhofen. Keferstein, Teutschland, geognostisch-geologisch dargestellt, Vol. IV: 2, pp. 89—110, Weimar 1827.

GILCHRIST, J. D. F. *Planktothuria diaphana* gen. et sp. n. Quaterly Journ. Microscop. Sci., New Series, Vol. 64, pp. 373—382, London 1920.

GISLÉN, T. Results of Dr. E. Mjöberg's Swedish Scientific Exp. to Australia 1910—13. Part 23 Crinoids. Kungl. Sv. Vetenskapsakademiens Handl., Bd. 59, No. 4, 37 pp., 1 Pl., Stockholm 1919.

—— The Crinoids from Dr. S. Bock's Exp. to Japan 1914. Nova Acta Reg. Soc. Sci. Upsaliensis, Ser. 4, Vol. 5, No. 6, 184 pp., 162 textfig., 2 Pll., Uppsala 1922.

GOLDFUSS, A. Petrefacta Germaniæ, Düsseldorf. Erster Theil 1826—1833, 2. Theil 1834—1840.

—— Verzeichniss der Crinoideen aus dem Übergangskalke. N. Jahrb. f. Mineralogie, Jahrg. 1835 p. 54, Stuttgart 1835.

—— Beiträge zur Petrefactenkunde. Nova Acta Leopold. Carol. Curiosum, Vol. 19, Part 1, pp. 326—364, Halle 1839.

GRABER, V. Über die Empfindlichkeit einiger Meerestiere gegen Riechstoffe. Biolog. Zentralblatt, Vol. 8, pp. 743—754, Erlangen 1889.

GRAVE, C. Feeding habits of a Spatangoid, *Mœra atropos*, a brittle-starfish, *Ophiophragma Wurdmanni*, and a Holothurian, *Thyone briareus*. Science, New Series, Vol. 15, p. 579, New York 1902.

GREPPIN, J. BTE. Matériaux pour la carte géol. de la Suisse. Livr. 8, Berne 1870.

GÜMBEL, C. W. Die Nummuliten-führenden Schichten des Kressenbergs. N. Jahrb. f. Mineralogie 1865, pp. 129—170, Stuttgart 1865.

—— *Comatula* oder *Belemnites* in den Nummuliten-Schichten des Kressenbergs. N. Jahrb. f. Mineralog. 1866, pp. 564—568, Stuttgart 1866.

GÜRICH, G. Ueber *Encrinus gracilis* von Gogolin in O.-S. Zeitschr. der deutsch. geol. Ges., Vol. 39, pp. 498—501, Berlin 1887.

v. HAGENOW, FR. Monographie der Rügen'schen Kreide Versteinerungen. N. Jahrb. f. Mineralogie, Jahrg. 1840, pp. 631—672, Stuttgart 1840.

HALL, J. Palæontology of New York. Nat. Hist. of N. Y., Part 6, Voll. 1—3. Albany 1847, 1852, 1859.

—— Report on the geol. Survey of the State Iowa, Vol. 1, part 2 Palæontology, 1858.

HAMANN, O. Histologie der Echinodermen, Jena 1884.

—— Anatomie der Ophiuren und Crinoiden. Jenaische Zeitschr. f. Naturwiss., Bd. 23 (N. F. 16), pp. 233—388, Jena 1889.

—— 1889—1907 see LUDWIG, H., u. HAMMANN, O.

*HARTMANN, FR. Systematische Übersicht der Versteinerungen Württembergs, 56 pp., Tübingen 1830.

HEDE, J. E. Gottlands Silurstratigrafi. Sveriges Geol. Undersökning. Årsbok 14 (1920), No. 7, 100 pp., Stockholm 1921.

HENNIG, A. Den baltiska yngre kritans bildningshistoria, Kap. 3. Geolog. Fören. Förhandl., Bd. 21, pp. 133—159, Stockholm 1899.

—— Guide pour la terrain Crétacé de la Suède. Geol. Fören. Förhandl., Bd. 32, Häfte 3, Stockholm 1910.

HERDMAN. 19th annual Report of the Mar. Biol. Stat. at Port Erin. Trans. of the Liverpool Biol. Soc., Vol. 20, p. 90, Liverpool 1906.

HÉROUARD, E. Sur *Pelagothuria Bouvieri* recuellie pendant la campagne du yacht »Princesse Alice» en 1905. Bull. du Musée Océanographique de Monaco, N° 60, 6 pp., 1906.

HESSE, R., u. DOFLEIN, F. Tierbau und Tierleben. 2 Bdd., Leipzig u. Berlin 1910—1914.

HOFFMANN, C. K. Zur Anatomie der Echiniden und Spatangen. Nederländisches Archiv f. Zoologie, Vol. 1, Heft 1, pp. 11—113, Haarlem 1871.

HOHENEGGER, L. Geognostische Karte der Nord-Karpathen etc. Gotha 1861.

HOWCHIN, W. Description of a disturbed area of Cainozoic Rocks in South Australia. Trans. & Proceed. of the Roy. Soc. of South Australia, Vol. 35, pp. 47—59, Adelaide 1911.

JACCARD, A. Description géol. du jura vaudois et neuchâtelois. Matériaux pour la carte géol. de la Suisse, 6^{me} Livr., 342 pp., Berne 1869.

—— Supplément à la descr. géol. du jura vaudois. Matériaux pour la carte géol. de la Suisse, 7^{me} Livr., Berne 1870.

JÆKEL, O. Kelchdecken von Crinoiden. Sitzungsberichte der Gesellschaft Naturforsch. Freunde 1891, pp. 7—12, Berlin 1891 (a).

—— Über Holopocriniden mit besonderer Berücksichtigung der Stramberger Formen. Zeitschr. der deutschen geol. Gesellschaft, Vol. 43, Heft. 3, pp. 555—671, Berlin 1891 (b).

—— Über *Holocrinus* W. & SPR. aus dem unteren Muschelkalk. Sitzungsberichte der Gesellsch. Naturforsch. Freunde 1893, pp. 201—206, Berlin 1893 (a).

—— Über Plicatocriniden, *Hyocrinus* und *Saccocoma*. Zeitschr. deutschen geolog. Gesellschaft, Bd. 44, Heft 4, pp. 619—696, Berlin 1893 (b).

—— Platte mit *Encrinus Carnalli* BEYR. Sitzungsberichte der Gesellsch. naturforsch. Freunde 1894, pp. 155—162, Berlin 1894.

JÆKEL, O. Beiträge zur Kenntniss der paläozoischen Crinoiden Deutschlands. Dames, W., und Kayser, E., Palæontologische Abhandlungen, Bd. 7 (116 pp., X Pll.), Jena 1895.

—— Stammesgeschichte der Pelmatozoen. I Thecoidea und Cystoidea. 442 pp., 18 Pll., Berlin 1899.

—— Verschiedene Wege phyletischer Entwickelung. Verhandlungen des V. internationalen Zool. Congresses zu Berlin 1901, pp. 1058—1117, Berlin 1901.

—— Über die Körperform der Holopocriniten. Neues Jahrb. f. Mineralogie 1907, pp. 272—309, 29 Textfigg., Stuttgart 1907.

—— Phylogenie und System der Pelmatozoen. Palæontologischer Zeitschrift, Bd. 3, pp. 1—128, Berlin 1918.

JAHN, J. Einige Beiträge zur Kenntniss der böhmischen Kreideformation. Jahrb. der k. k. geolog. Reichsanstalt, Vol. 45, pp. 125—218, Wien 1895.

JENNINGS, H. S. Behaviour of the starfish *Asterias Forreri* DE LORIOL. University of California Publ. in Zoology, Vol. 4, No. 2, pp. 53—185, Berkeley 1907.

JICKELI, C. F. Vorläufige Mittheilungen über den Bau der Echinodermen. Zoologischer Anzeiger, Vol. 7, pp. 346—349 und 366—370, Leipzig 1884.

JOHN, G. Über bohrende Seeigel. Archiv für Naturgeschichte Bd. 55: 1, pp. 268—302, Berlin 1889.

JOUKOVSKY, E. et FAVRE, J. Monographie géologique et paléontologique du Salève (Haute Savois). Mém. Soc. Phys. et Hist. Nat., Vol. 37, fasc. 4, Chap. 5 pp. 384—492 par J. FAVRE, Paris et Genève 1913.

KEMNA, A. L'Holothurie pelagique *Pelagothuria*. Soc. Zool. & Malacol. de Belgique. Annales, Tome 41, pp. 87—92, Bruxelles 1906.

KIRK, E. The structure and relationships of certain Eleutherozoic Pelmatozoa. Proceed. of the U. S. Nat. Mus., Vol. 41, pp. 1—137, Washington 1912.

KJERSKOG-AGERSBORG, H. P. Bilateral tendencies and habits in the 20-rayed starfish *Pycnopodia helianthoidea* (STIMPSON). Woods Hole, Mar. Biol. Laborat. Biol. Bull., Vol. 35, pp. 232—254, Woods Hole, Mass. 1918.

KNORR, G. W. Sammlung von Merckwürdigkeiten der Natur. Erster Theil. Nürnberg 1755.

KOEHLER, R. Échinodermes provenant des campagnes du yacht »Princesse Alice». Résultats des Campagnes Scient. accomplis sur son yacht par Albert I^{er}, Fasc. 34, Monaco 1909.

KOEHLER & BATHER. Gephyrocrinus Grimaldi. Crinoide nouveau provenant des campagnes de la Princesse Alice. Soc. Zool. de France, Mémoires, Tome 15, pp. 68—79, Paris 1902.

v. KOENEN, A. Beitrag zur Kenntniss der Crinoiden des Muschelkalks. Abhandl. der k. Gesellschaft der Wiss. zu Göttingen, Bd. 34, 44 pp., Göttingen 1887.

—— Über die Entwicklung von *Dadocrinus gracilis* v. BUSCH und *Holocrinus Wagneri* BEN. und ihre Verwandschaft mit anderen Crinoiden. Nachrichten der k. Gesellschaft der Wiss. zu Göttingen, Mat.-Phys. Klasse 1895, pp. 283—293, Göttingen 1895.

KOKEN, E. Ueber triassische Versteinerungen aus China. N. Jahrb. f. Mineralogie 1900: 1, pp. 186—215, Stuttgart 1900.

KONINCK, L., et LE HON, H. Recherches sur les Crinoides du Terrain Carbonifère de la Belgique. 217 pp., 7 Pll., Bruxelles 1854.

KUNISCH, H. Ueber den ausgewachsenen Zustand von *Encrinus gracilis* v. BUSCH. Zeitschr. der deutsch. geolog. Gesellschaft, Vol. 35, pp. 195—198, Berlin 1883.

LAMBERT, J. Étude stratigraphique sur le calcaire séquanien de Tonnère (Yonne). Mém. de la Soc. Paléontologique Suisse, Tome 20, N° 4, pp. 175—213, Genève 1893.

LAMBERT, J. Revue critique de NICOLAS, Étude des terrains tertiaires etc. COSSMANN, Revue critique de Palæozoologie, Tome 3, pp. 122—123, Paris 1899.

LANGE, W. Beitrag zur Anatomie u. Histologie der Asteriden u. Ophiuren. Morphol. Jahrb., Vol. 2, pp. 242—286, Leipzig 1876.

LEMOINE, P. et ROUYER, C. Note préliminaire sur l'étage Kimmeridgien. Bull. de la Soc. géol. de France, Ser. 4, Vol. 2, pp. 104—111, Paris 1902.

LEUTHARDT, F. Über das Vorkommen von *Antedon costatus* GOLDF. in den Hornsteinknollen der Hupperablagerungen von Lausen. Tätigkeitsbericht der naturforsch. Gesellschaft Baselland Liestal 1907—1911, pp. 109—118, Pll. 6—8, Liestal 1911.

LEVINSEN, G. M. R. Kara-Havets Echinodermata. Dijmphna Togtets Zoologisk Botaniske Udbytte, pp. 381—418, Tabb. 34—35, Kjøbenhavn 1887.

LINCK, J. H. De stellis marinis liber singularis, Lipsiæ 1733.

LINDSTRÖM, G. Über die Schichtenfolge des Silur auf der Insel Gotland. N. Jahrb. f. Mineralogie 1888: 1, pp. 147—164, Stuttgart 1888.

LISSAJOUS, M. Crinoïdes des environs de Mâcon. Bull. de la Soc. d'Hist. nat. de Mâcon, Nos. 16 and 17, pp. 1—27, Mâcon 1900.

*DE LORIOL, P. Monographie de couches de l'étage valangien des carrières d'Arzier (Vaud). F. J. PICTET, Matériaux pour la paléont. Suisse 4^me^ serie, Genève et Bale 1868 (a).

*—— in PICTET. Étude provisoire etc. 1868 (b) see PICTET.

—— Monographie des Crinoides fossiles de la Suisse. Abhandl. der Schweizer. paläontolog. Gesellsch., Vol. (4—)6, Genève (1878—)1879.

—— Description de quatre Echinodermes nouveaux. Abhandl. der Schweizer. paläontolog. Gesellsch., Vol. 7, No. 6, 15 pp., Genève 1880 (a).

—— Les crinoides fossiles de la Suisse. Association française pour l'avancement des Sciences. 8^{me} Session. Montpellier 1879, pp. 627—636, Paris 1880 (b).

*—— Note sur quelques Échinodermes fossiles des envirous de la Rochelle. Acad. de la Rochelle, Société des Sciences naturelles de la Charente inférieur, Annales de 1886, Tome 23, p. 313 ff., 1887.

—— Paléontologie française. Serie 1. Animaux Invertèbres. Terrain Jurassic, Tome XI, 1 et 2 Crinoïdes. 2 Voll., 627 and 580 pp., 229 Pll., Paris 1882—1889 (Comatulids and Thiolliericrinids 1888 and 1889).

—— Description des Échinodermes. Comission des Travaux géol. du Portugal. Recueil d'Études paléont. sur la faune crétacique du Portugal, Vol. 2. Description des Échinodermes, Fasc. 2, Lisbonne 1888 (b).

—— Desciption de la Faune Jurassic du Portugal. Embranchement des Échinodermes. Comission des Travaux Géologiques du Portugal. Mém., 179 pp., 29 Pll., Lisbonne 1890.

—— Note pour servir à l'étude des Échinodermes IV. Rev. Suisse de Zoologie, Tome 2, pp. 467—497, Pll. 22—24, Genève 1894.

—— Études sur quelques Échinodermes de Cirin. Arch. du Muséum d'Hist. Nat. de Lyon, Vol. 6, No. 4, pp. 1—7, Pl. 1, Lyon 1895.

—— Description de quelques Échinodermes. Bull. de la Soc. Géol. de France, Ser. 3, Vol. 25, pp. 115—129, Paris 1897.

—— Notes pour servir à l'étude des Échinodermes VIII. Revue Suisse de Zool. Tome 8, pp. 55—96, Pll. 6—9, Genève 1900.

—— Notes pour servir à l'étude des Échinodermes. II^{e} Serie, Fasc. 1. Avec 3 planches, 53 pp., Bale et Genève 1902.

—— Note sur deux Échinodermes fossiles. Revue Suisse de Zool., Annales de la Soc. Zool. Suisse, Tome 16, pp. 151—156, Pl. 5, Genève 1908.

DE LORIOL P. et GILLIERON, V. Monographie de l'étage urogonien inférieur de Landeron. Neue Denkschr. der allg. Schweizer. Gesellschaft f. Naturwiss., Vol. 23, No. 5, 114 pp., Zürich 1869.

DE LORIOL, P. et PELLAT, E. Monographie paléontologique et géologique des étages supérieurs de la formation jurassic des environs de Boulogne-Sur-Mer (Suite). Mém. de la Soc. de Physique et d'Hist. Nat., Tome 24, pp. 1—326, Genève 1875.

LOVÉN, S., Note on *Hyponome Sarsi;* a recent Cystidean, Ann. & Mag. Nat. Hist., Ser. 4, Vol. 4, pp. 159—160, London 1869.

LUDVIG, H. Beiträge zur Anatomie der Crinoideen. Siebold. Zeitschr. f. Zoologie, Bd. 28, pp. 255—353, Leipzig 1877 (a).

—— Ueber bewegliche Schalenplatten bei Echinoideen. Morphologische Studien an Echinodermen III. Zeitschr. f. wiss. Zool., Bd. 29, pp. 77—86 (Separat, pp. 131—139), Berlin 1877 (b).

—— Über die Function der Madreporenplatte und des Steincanals der Echinodermen. Zoologischer Anzeiger, Vol. 13, pp. 377—379, Leipzig 1890.

LUDWIG, H. und HAMMANN, O. Echinodermen I—V. Bronn, Klassen u. Ordnungen des Tierreichs, II. Bd., III Abt., I.—V. Buch, Leipzig 1889—1907.

LUNDGREN, B. Om en *Comaster* och en *Aptychus* från Köpinge. Övers. Kungl. Vetenskaps Akad. Handl. 1874, N:o 3, pp. 61—74, Stockholm 1874.

MANDELSLOH, F. DE. Mémoire sur la constitution géol. de l'Albe du Württemberg. Mém. de la Soc. d'Hist. Nat. du Strasbourg, Vol. 2, 42 pp., Paris 1835.

MANGOLD, E. Autointoxication der Seeigel. Mitteilungen des Naturwiss. Vereins. Bd. 39, Greifswald 1907 (a).

—— Leuchten der Schlangensterne und die Flimmerbewegung bei *Ophiopsila.* Pflügers Archiv der gesamt. Physiologie, Bd. 118, pp. 613—640, Bonn 1907 (b).

MARSHALL, A. M. On the nervous system of *Antedon rosaceus.* Quaterly Journ. of Microscopical Science N. S., Vol. 24, pp. 507—548, Pl. 35, London 1884.

MATSUMOTO, H. A monograph of Japanese Ophiuroidea arranged according to a new Classification. Journ. Coll. Sci. Imp. Univ. Tokyo, Vol. 37, Art. 2, 408 pp., 7 Pll., Tokyo 1917.

MEAD, A. D. On the correlation between growth and food-supply in starfish. American Naturalist, Vol. 34, pp. 17—23, Boston 1900.

MEEK, F. B., WORTHEN, A. H. etc. Geological Survey of Illinois, Palæontology. Voll. 2—3, 5—7, Springfield Ill. 1866, 1868, 1873, 1875, 1883.

MENEGHINI, G. Adunanza del di 7. luglio 1878. Atti Societá Toscana di Sci. Nat., Processi verbali 1878, p. XXXI, Pisa 1878.

v. MEYER, H. *Isocrinus* und *Chelocrinus,* zwei neue Typen aus der Abtheilung der Crinoideen. Museum Senckenbergianum. Abhandl. Bd. 2, pp. 249—263, Frankfurt am Main 1837.

—— Fische, Crustaceen, Echinodermen u. a. Versteinerungen aus dem Muschelkalk Oberschlesiens. Crinoideen. Palæontographica, Bd. 1, pp. 260—275, Cassel 1851.

MICHELOTTI, J. Description de quelque nouveaux fossiles du terrain miocène de la colline de Turin. Revue et Magasin du Zoologie, 2^me^ Série, Tome 13, pp. 353—355, Paris 1861.

MILLER, J. S. A natural history of the Crinoidea, Bristol 1821.

MILLER, S. A. and GURLEY, W. 9 papers in Bull. of the Illinois State Museum of Nat. Hist. Bull. Nos. 3—10, 12, Springfield Ill. 1893—1897.

MILLIGAN, H. N. The way in which a starfish eats a pipe fish. Zoologist, Vol. 19, pp. 147—150, London 1915.

MILLIGAN, H. N. Asteroids feeding upon living Sea Anemones. Nature, Vol. 96, pp. 619—620, London 1916 (a).

—— Observations of the feeding habits of the purple-tipped Sea-Urchin *(Ech. miliaris)*. Zoologist, Vol. 20, pp. 81—99, London 1916 (b).

—— Starfishes feeding on hermit-crabs. Zoologist, Vol. 20, p. 114, London 1916 (c).

MINCKERT, W. Über Regeneration bei Comatuliden nebst Ausführungen über die Auffassung und Bedeutung der Syzygien. Archiv für Naturgeschichte, Vol. 71: 1, pp. 163—244, Berlin 1905.

MOESCH, C. Der aargauer Jura. Beiträge zur geolog. Karte der Schweiz. 4. Lief., Bern 1867.

—— Der südliche aargauer Jura. Beiträge zur geolog. Karte der Schweiz. 10. Lief., Bern 1874.

MORRIS, J. A catalogue of British fossils comprising all the genera and species hitherto discribed, London 1843.

MORTENSEN, TH. Report on the Echinoderms collected by the Danmark Exp. at North East Greenland. Meddelelser om Grønland, Vol. 45 (No. 4), pp. 237 302, Pll. 8—17, Kjøbenhavn 1910.

—— Über *Asteronyx Loveni.* Zeitschr. f. wissenschafl. Zoologie, Bd. 101, pp. 264—289, Leipzig 1912.

—— *Notocrinus virilis* n. g., n. sp., a new viviparous Crinoid from the Antarctic Sea, Preliminary Notice. Videnskabl. Meddelelser. Dansk Naturhist. Foren., Bd. 68, pp. 205—208, Kjøbenhavn 1917.

—— The Crinoidea of the Swedish Antarctic Süd-Polar Expedition 1901—1903. Bd. 6, Lief. 8, 23 pp., 5 Pll., Stockholm 1918.

—— Studies in the development of Crinoids. Papers of the Dept. of Mar. Biol. Carnegie Institution, Vol. 16, 94 pp., 28 Pll., Washington 1920 (a).

—— Notes on some Scandinavian Echinoderms, with descriptions of two new Ophiurids. Videnskabl. Meddelelser, Bd. 72, pp. 45—79, Kjøbenhavn 1920 (b).

MÜLLER, ALB. Geognostische Karte des Cantons Basel etc. Verhandl. der naturforsch. Gesellschaft in Basel, Vol. 3, pp. 65—152, Basel 1863 (a).

—— Geol. Skizze des Cantons Basel. Beiträge zur. geolog. Karte der Schweiz. 1. Lief., Bern; 1. Aufl. 1863 (b), 2. Aufl. 1884.

MÜLLER, J. Über die Gattungen und Arten der Comatulen. Wiegmann Archiv für Naturgeschichte, Jahrg. 7, pp. 139—148, Berlin 1841.

—— Über den Bau des *Pentacrinus caput-medusæ.* Abhandl. der k. Akad. der Wissenschaften, Teil 1. 1841, pp. 177—248, Berlin 1843.

v. MÜNSTER, G. Verzeichniss der (Versteinerungen) in der Kreis Naturalien Sammlung zu Bayreuth. 1833.

—— Mittheilungen. Neues Jahrb. f. Mineralogie Jahrg. 1836, pp. 580—583, Stuttgart 1836.

—— Beiträge zur Petrefactenkunde Bayreuth; 1. Aufl. 1839, 2. Aufl. 1843.

MUSPER, F. Der Brenztaloolit, sein Fossilinhalt und seine Deutung. Jahreshefte des Vereins f. vaterl. Naturkunde in Württemberg, Bd. 76, pp. 1—61, Stuttgart 1920.

NEUMAYR, M. Die Stämme des Thierreiches. Wirbellose Thiere. Bd. 1., Wien und Prag 1889.

(NICOLAS, H.) Terrains Tertiaires des environs d'Avignon. Le miocène. Acad. de Vaucluse, Mémoires, Tome 16, pp. 60—152, Avignon 1897.

—— Études des Terrains tertiaires des environ d'Avignon. Miocène. Association française, 26e Session, St. Étienne 1897, pp. 393—413, Paris 1898.

Noëlli, A. Contribuzione allo studio dei Crinoidi terziari del Piemonte. Atti della Societá italiana di Scinze naturali, Vol. 39, pp. 19—49, Milano 1900.

Ogérien, Frère. Histoire naturelle du Jura et des départements voisins. Tome 1er, Géologie, 2e Fasc., Paris 1867.

Ooster, W. A. Die organischen Reste der Pteropodenschicht. Protozoae helvetica, Vol. 2, Abth. 3, pp. 89—151, Basel 1871.

Oppel, A. Die Jura-Formation Englands, Frankreichs u. des Südw. Deutschlands, Stuttgart 1856—1858.

Oppel, A. u. Waagen, W. Über die Zone des *Ammonites transversarius*. Benecke, Geognostisch-palæontologische Beiträge, Bd. 1, pp. 205—318, München 1866 (1868).

d'Orbigny, A. Prodrome de Paléontologie, Tome 1—3, Paris 1850(—1852).

—— Cours élémentaire de Paléontontologie, Tome 2, Paris 1852.

—— Histoire naturelle générale et particulière des Crinoides etc., Paris 1858.

Östergren, Hj. Über die Function der Füsschen bei den Schlangensternen. Biolog. Zentralblatt, Vol. 24, pp. 559—565, Erlangen 1904.

Pellat, E. Études stratigraphiques et paléontologiques sur les terrains tertiaires etc. Note No. 3. Bull. de la Soc. Géol. de France, Ser. 3, Tome 25, pp. 111—114, Paris 1897.

Perrier, E. Mémoire sur l'organisation et le développement de la Comatule de la Mediterranée. Nouv. Arch. du Mus. d'Hist. Nat. Sér. 2, Tome 9, pp. 53—348, Suite et fin dans Sér. 3, Tome 2, pp. 1—86, Paris 1886, 1890.

Philippi. *Alecto alticeps,* eine tertiäre Comatula von Palermo. Neues Jahrb. f. Mineralogie 1844, pp. 540—542, Tab. 6 B, Stuttgart 1844.

Picard, K. Über eine neue Crinoiden Art aus dem Muschelkalk der Hainleite bei Sondershausen. Zeitschr. der deutsch. geolog. Gesellschaft, Vol. 35, pp. 199—202, Berlin 1883.

Pictet, F. J. Traité de Paléontologie. Tome Quatrième. 2e Ed. Accompagnée d'un atlas, Paris 1857.

*—— Étude provisoire des fossiles de la Porte-de-France, d'Aizy et de Lémence. Mélanges paléontologiques. Tome 1, Livr. 4. Descriptions by de Loriol, Geneva 1868.

Pillét, L. L'étage tithonique a Lémenec (Savoie). Archives des Sciences phys. et nat., 2e Série, Tome 42, pp. 135—146, Genève 1871.

*Pillét, L. & Fromentel. Description géologique et paléontologique de Lémenec. Acad. des sciences ... de Savoi, Mémoires Sér. 3, Vol. 4, Chambéry 1875.

Pomel, A. Paléontologie ou description des animaux fossiles de l'Algérie, Zoophytes, 2e Fasc. Échinodermes. Figures in Livr. 1, text. in Livr. 2, Alger 1885—1887.

Pompeckj, J. F. Paläontologische und stratigraphische Notizen aus Anatolien. Zeitschr. der deutsch. geolog. Gesellsch., Vol. 49, pp. 713—828, Berlin 1897.

Popovici-Hatzeg, V. Contribution a l'étude de la faune de la crétacé de Roumanie. Mém. de la Soc. géol. de France, Paléontologie (No. 20), Tome 8, fasc. 3, 20 pp., Pll. 14, 16, Paris 1899.

Pourtales, L. F. de. Contributions to the Fauna of the Gulf Stream at great depths. Bull. Mus. Comp. Zool., Vol. 1, No. 6 (pp. 103—120), Cambridge Mass. 1867.

Preyer, W. Über die Bewegungen der Seesterne. II. Mittheil. aus der zool. Stat. zu Neapel, Bd. 7, pp. 191—233, Berlin 1887.

Prouho, H. Recherches sur le *Dorocidaris papillata* etc. Arch. de zool. expér. et génér. 2e Série, Tome 5, pp. 213—380, Paris 1887.

Quenstedt, F. A. Das Flötzgebirge Württembergs. 2. verbess. Aufl., Tübingen 1851.

—— Handbuch der Petrefactenkunde, Tübingen; 1. Aufl. 1852, 2 Aufl. 1867, 3. Aufl. 1885.

—— Der Jura, Tübingen 1858 (Neudruck 1907).

—— Petrefactenkunde Deutschlands, Abth. 1, Bd. 4, Echinodermen. Text und Atlas, Leipzig 1875—1876.

Rauschenplatt, E. Ueber die Nahrung von Tieren aus der Kieler Bucht. Wissensch. Meeresuntersuchungen N. F., Bd. 5, pp. 85—157, Kiel 1901.

Reichensperger, A. Zur Anatomie von *Pentacrinus decorus* Wyv. Th. (Rep. Res. Dredg. Gulf of Mexico etc. by the »Blake»). Bull. Mus. Comp. Zool. Cambridge Mass., Vol. 46 (No. 10), pp. 167—200, 3 Taf., Cambridge Mass., 1905.

—— Zur Kenntniss der Gattung *Ophiopsila*. Zeitschr. f. wiss. Zoologie, Bd. 89, pp. 173—192, Leipzig 1908 (a).

—— Die Drüsengebilde der Ophiuren. Zeitschr. f. wiss. Zoologie, Bd. 91, pp. 304—350, Leipzig 1908 (b).

—— Über das Vorkommen von Drüsen bei Crinoiden. Zoolog. Anzeiger, Vol. 33, pp. 363—367, Leipzig 1908 (c).

—— Beiträge zur Histologie und zum Verlauf der Regeneration bei Crinoiden. Zeitschr. f. wiss. Zoologie, Bd. 101, pp. 1—69, Leipzig 1912.

—— Ungestielte Crinoideen der Aru- und Kei-Inseln. Abhandl. der Senckenberg. naturforsch. Gesellschaft, Bd. 35, pp. 79—108, Frankfurt am Main 1914.

Remeš, M. Nachträge zur Fauna von Stramberg I. Die Fauna des rothen Kalksteins (Nesseldorfer Schichten). Beitr. zur Paläont. Österreich-Ungarns und des Orients, Vol. 14, pp. 195—217, Wien 1902.

—— Nachträge zur Fauna von Stramberg. Beitr. Paläont. Österreich-Ungarns, Vol. 18, pp. 59—63, Wien 1905.

Reuss, A. E. Die Kreidegebilde des westlichen Böhmens. Reuss, Geognostische Skizzen aus Böhmen, Vol. 2, Prag 1844.

—— Die Versteinerungen der böhmischen Kreideformation. Abth. 2, Stuttgart 1846.

Rigaux, E. Notice géologique sur le Bas Boulonnais. Mém. Soc. Acad. Boulogne-sur-Mer, Tome 16, pp. 1—108, Boulogne-sur-Mer 1891—1894.

Robertson, D. Notes on *Amphidetus cordatus* (Penn). Quaterly Journ. Microscop. Sci. N. Ser., Vol. 11, pp. 25—27, London 1871.

Roman, Fr., Recherches stratigraphiques et paléontologiques dans le Bas Languedoc. Ann. de l'université de Lyon, 345 pp., Paris 1897.

Sarasin, F. u. P. Die Augen und das Integument der Diadematiden. F. u. P. Sarasin: Ergebnisse naturwiss. Forsch. auf Ceylon, Bd. 1, pp. 1—19, Wiesbaden 1887 (a).

—— Über die Anatomie der Echinothuriden und die Phylogenie der Echinodermen. Ergebnisse naturwiss. Forsch. auf Ceylon, Bd. 1, pp. 129—154, Wiesbaden 1887 (b).

—— Die Längsmuskeln und die Stewartschen Organe den Echinothuriden. Zool. Anzeiger, Bd. 11, pp. 115—117, Berlin 1888.

Sars, M. Oversigt af Norges Echinodermer. 160 pp., Christiania 1861.

—— Mémoires pour servir à la conaissance des crinoïdes vivants. Programme du l'Université de Norvège, 65 pp., 6 Pll., Christiania 1868.

Scalia, S. La fauna del Trias superiore de gruppo di M^{te} Judica. Parte I. Atti Accad. Gioena di Sci. Nat., Ser. 5, Vol. 3, Mem. 9, Catania 1910.

Schaffer, F. X. Das Miocän von Eggenburg. Die Crinoiden. Abhandl. der k. k. geolog. Reichsanstalt, Bd. 22, pp. 185—186, Wien 1912.

Schafhäutl, K. E. Über einge neue Petrefakten des südbayerischen Vorgebirges. Neues Jahrb. f. Mineralogie 1851, pp. 407—421, Stuttgart 1851.

—— Süd-Bayerns Lethæa geognostica, Text u. Taf. Fol., Leipzig 1863.

—— Die Nummuliten-führenden Schichten des Kressenbergs. Neues Jahrb. f. Mineralogie 1865, pp. 769—788, Stuttgart 1865.

Scheuchzer, J. J. Museum diluvianum, Tiguri 1716.

—— Meterologia et Oryctographia helvetica oder Beschreibung der Lufft-Beschichten, Steinen, Metallen u. a. Mineralien des Schweizerlandes absonderlich auch der Überbleibseln der Sündfluth, Zürich 1718.

Schiemenz, P. Wie öffnen die Seesterne Austern? Mitteil. des deutsch. Seefischvereins, Bd. 12, pp. 102—118, Berlin 1896.

v. Schlotheim, E. F. Beiträge zur Naturgeschichte der Versteinerungen. Leonhard, Taschenbuch für die gesammte Mineralogie, Jahrg. 7, pp. 3—134, 1813.

—— Die Petrefactenkunde (mit XV Kupfertafeln), Gotha 1820.

—— Nachträge zur Petrefactenkunde. Zweyte Abth., Gotha 1823.

Schlüter, Cl. Bericht über eine geognostisch-paläontologische Reise in südl. Schweden. Neues Jahrb. f. Mineralogie 1870, pp. 929 - 969, Stuttgart 1870.

—— Über einige astyle Crinoiden. Zeitschr. der deutschen geol. Gesellschaft, Vol. 30, pp. 28—66, Berlin 1878.

Schmierer, Th. Das Altersverhältnis der Stufen ε und ζ der weissen Jura. Zeitschr. d. deutsch. geol. Gesellschaft, Bd. 54, pp. 525—607, Berlin 1902.

Schröter, J. S. Vollständige Einleitung in die Kenntniss u. Geschichte der Steine u. Versteinerungen. 4. Theile, Altenburg 1774—1784, 3. Theil 1778.

Schütze, E. Die Fauna des schwäbischen Meeresmolasse, I. Teil. Spongien u. Echinodermen. Jahresh. d. Vereins f. vaterl. Naturkunde in Württemberg, Vol. 60, pp. 147—188, Taf. 2—5, Stuttgart 1904.

Simroth, H. Zur Kenntniss der Azoren-Fauna. Arch. f. Naturgeschichte, Bd. 54: 1, pp. 179—234, Berlin 1888.

Sperry, W. L. Notes on *Metacrinus*. 4th Report of the Michigan Acad. of Sci. Ann. Arbor., pp. 195—199, Lansing Mich. 1904.

Springer, F. *Uintacrinus*, its structure and relations. Mem. Mus. Comp. Zool., Vol. 25, No. 1, 89 pp., 8 Pll., Cambridge Mass. 1901.

—— Some new American fossil Crinoids. Mem. Mus. Comp. Zool., Vol. 25, No. 3, pp. 117—161, Cambridge Mass. 1911.

—— A new species of fossil *Pentacrinus* from the East Indies. Jaarboek van het Mijnwezen in Ned. Oost-Indië, Jaarg. 45 (1916), Deel 1, pp. 57—65, s'Gravenhage 1918.

—— The Crinoidea Flexibilia. Smithson. Instit., 486 pp , with an Atlas of A—C and 76 plates, Washington 1920.

—— Notes regarding new Genera of the Crinoidea Flexibilia. Supplementaty sheet to the preceding, Washington 1923.

Stimpson, W. Marine Invertebrata of Grand Manan. Smiths. Contrib. to Knowledge, Vol. 6, Art. 5, 68 pp., 3 Pll., Washington 1854.

Stolley, E. Die Kreide Schleswig-Holsteins. Mittheil. aus den mineralog. Institut der Univers. Kiel, Vol. 1, pp. 191 - 309, Kiel 1891.

Süssbach, S. und Breckner, A. Die Seeigel, Seesterne und Schlangensterne der Nord- und Ostsee. Wissenschaftl. Meeresuntersuch. N. F., Vol. 12, pp. 167—300, Kiel 1911.

Tate, R. and Dennant, J. Correlation of the marine Tertiaries of Australia. Part 1. Victoria, Transactions. Roy. Soc. South Australia, Vol. 17, part 1, pp 203—226, Adelaide 1893.

Thomson, Wyville. On the embryogeny of *Antedon rosaceus* Linck. Philos. Transactions 1865, pp. 513—544, Pll. 23—27, London 1865.

*Thurmann, J. Abraham Gagnebin de la Ferrière. Fragments pour servir l'histoire scientifique du Jura bernois. Arch. Soc. Jurass. d'Émulation, Porrentruy 1851.

Trautschold, H. Über Crinoideen, Zusätze und Berichtigungen. Bull. de la Soc. Impér. des Naturalistes de Moscou, Année 1882, No. 1, pp. 140—145, Moscou 1882.

de Tribolét, M. Recherches geologiques et paléontologiques dans le jura supérieur neuchâtelois. Diss., Zürich 1873.

v. Uexküll, J. Die Physiologie des Seeigelstachels. Zeitschr. f. Biologie, Vol. 39 N. F. Vol. 21, pp. 73—112, München u. Leipzig 1900.

—— Studien über die Tonus II. Die Bewegungen der Schlangensterne. Zeitschr. f. Biologie, Vol. 46 (N. F. 28), pp. 1—38, München 1905.

—— Studien über die Tonus IV. Die Herzigel. Zeitschr. f. Biologie, Vol. 49 (N. F. 31), pp. 307—332, München u. Berlin 1907.

—— Umwelt und Innenwelt der Tiere, 259 pp., Berlin 1909.

Vadász, M. E. Die mediterranen Echinodermen Ungarns. Geologica Hungarica, Tome 1, Fasc. 2 (Ed. sep.), 175 pp., 6 Pll., Budapest 1915.

Valette, A. Note sur les crinoïdes de la craie blanche. Bull. de la Soc. des Sciences de l'Yonne, Année 1916, Vol. 70, pp. 79—178, Auxerres 1917.

Vogt, C. und Yung, E. Lehrbuch der Anatomie, Bd. 1, pp. 525—580, Braunschweig 1888.

Waagen, W. Der Jura in Franken, Schwaben und der Schweiz, München 1864.

—— Salt Range Fossils I. Productus Limestone Fossils, Echinodermata. Palæontologia Indica. Mem. Geol. Survey of India, Ser. 13, Vol. 1, No. 5, pp. 818—834, Calcutta 1885.

Wachsmuth, Ch. and Springer, F. Revision of the Palæocrinoidea, Part I. Proceed. Acad. Nat. Sci. 1879, pp. 226—378, 2 Pll., Philadelphia 1879.

—— Revision of the Palaeocrinoidea, Part III, Sect. 1, Proceed. Acad. Nat. Sci. 1885, pp. 225—364, Pll. 4—9, Philadelphia 1885.

—— Revision, Part III, Sect. 2, Proceed. Acad. Nat. Sci. 1886, pp. 64—226, Philadelphia 1886.

—— *Crotalocrinus,* its structure and zoological position. Proc. Acad. Nat. Sci. 1888, pp. 364—390, Pll. 19, 20, Philadelphia 1889.

—— The North-American Crinoidea Camerata. Mem. Mus. Comp. Zool., Voll. 20, 21, 837 pp. and one Atlas with 83 plates, Cambridge Mass. 1897.

Wagner, R. Die Encriniten des unteren Wellenkalkes von Jena. Jenaische Zeitschr., Bd. 20, pp. 1—32, Jena 1887 (a).

—— Ueber *Encrinus Wagneri* Ben. aus dem unteren Muschelkalk von Jena. Zeitschr. der deutsch. geol. Gesellsch, Bd. 39, pp. 822—828, Berlin 1887 (b).

—— Über einige Versteinerungen des unteren Muschelkalks von Jena. Zeitschr. der deutsch. geol. Gesellsch., Vol. 43, pp. 879—901, Pl. 49, Berlin 1891.

—— Beitrag zur genaueren Kenntniss des Muschelkalks bei Jena. Abhandl. der k. preuss. geolog. Landesanstalt, N. F. Heft. 27, 105 pp., Berlin 1897.

Walch, J. E. I. Die Naturgeschichten der Versteinerungen zur Erläuterung der Knorrisschen Sammlung von Merckwürdigkeiten der Natur. Zweyten Theils Zweyten Abschnitt. (Is included in Knorr, Sammlung von Merckwürdigkeiten der Natur), Nürnberg 1769.

Walther, J. Untersuchungen über den Bau der Crinoiden mit besonderer Berücksichtigung der Formen aus der Solenhofer Schiefer und dem Kehlheimer Diceras-Kalk. Palaeontographica, Vol. 32, pp. 155—200, Taf. 23—26, Stuttgart 1886.

WANNER, J. *Timorocrinus* n. g. aus dem Perm von Timor. Zentralblatt f. Mineralogie 1912, pp. 599—605, 5 Textfigg., Stuttgart 1912.

—— Die permischen Echinodermen von Timor, 1. Teil. Paläontologie von Timor, Lief. 6 (11), 329 pp., 19 Pll., Stuttgart 1916.

WEGNER, R. N. Umgelagerte Kreide u. Tertiär bei Oppeln, 42 pp., Diss., Breslau 1911.

—— Tertiär und umgelagerte Kreide bei Oppeln (Ober-Schlesien). Palaeontographica, Vol. 60, pp. 175—274, Stuttgart 1913.

WINTZELL, J. Bidrag till de skandinaviska Ophiuridernas biologi och fysiologi (mit einer deutschen Resumé), Diss., 148 pp., Uppsala 1918.

WOODS, H. Catalogue of the type fossils in the Woodwardian Museum, 180 pp., Cambridge 1891.

ZAHALKA, Č. *Antedon pyropa* n. sp. Rozpravy české akademie cisaře františka josefa, Ročnik 1, Třida 2, čislo 36, pp. 722—723, Prag 1892.

v. ZITTEL, K. Handbuch der Palæontologie, Bd. 1, München u. Leipzig 1876—1880 (1879).

—— Grundzüge der Paläontologie I. Invertebrata, 4. Aufl., 694 pp., München u. Berlin 1915.

v. ZITTEL, K. A. and EASTMAN, C. R. Textbook of Palæontology. 2nd Ed., Vol. 1., 839 pp., London 1913.

CONTENTS.

Chapter I.

Arm-ramification in recent Crinoids.

Chapter II.

The articulations of the arm-joints in the Crinoids.

Chapter III.

The fossil Comatulids.

Chapter IV.

Phylogeny of the Comatulids.

Chapter V.

Ciliary currents on the surface of the body of Echinoderms.

Printed 12/5 1924.

◆