

# A MONOGRAPH ON SPANISH PALAEOZOIC CRINOIDEA

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## ABSTRACT

It has been the aim of this study to give a comprehensive description of the important crinoid fauna's of the Palaeozoic core of North Western Spain (provinces Palencia, León and Asturias). This was opportune since fine collections of crinoids had been made during the years 1955—1960 by students of Leiden University (Holland). Moreover, existing collections of Spanish crinoids have not received hitherto due attention. Up to the present day only ten species of Palaeozoic crinoids have been known from Spain. Five new genera and sixteen new species of Spanish crinoids are now described. Fourteen previously described genera are reported for the first time to occur in Spain, either from new species or from species not yet sufficiently well known to allow specific arrangement. Six previously described species are recorded for the first time from Spain. So the total number of known Spanish crinoid species has now been raised to fifty six (thirty two genera): twenty five Emsian species, nine Couvinian species, six Givetian species, one Frasnian species, one Viséan species, four Namurian species and four Moscovian species. The other species, represented by museum specimens only, are of uncertain Devonian or Carboniferous age.

Camerates are far more numerous than inadunates, whereas flexibles are not known with any certainty. Camerates include thirty eight species (twenty two genera); inadunates eighteen species (ten genera).

Among camerates only seven species belong to the diplobathrids; stratigraphically they seem to be restricted to the Emsian. *Pterinocrinus decembrachiatus*, *Griphocrinus ovetensis*, *Orthocrinus robustus* and *Orthocrinus elongatus* are described as new species of diplobathrids. The genera *Diamenocrinus*, *Pterinocrinus*, *Macarocrinus* and *Griphocrinus* are recorded for the first time from Spain. *Orthocrinus* was already known. W. E. Schmidt's species *Orthocrinus planus* is regarded a *nomen dubium*, since only poor fragments are assignable to the species.

Camerates further include thirty one species of monobathrids, among which periechocrinids (fourteen species) and hapalocrinids/platycrinids (nine species) are of special importance. Stratigraphical distribution of the Spanish monobathrids is from the Lower Devonian to Upper Carboniferous.

Among periechocrinids (restricted to Devonian strata) *Pradocrinus* is held as an independent genus with the only species *P. Baylii* de Verneuil, 1850 as the type-species. The genus is only known to occur in Spain. The available generic names *Lenneocrinus* and *Pyxidocrinus* were used for assignment of Spanish species. *Lenneocrinus* is now definitely erected with *L. cirratus* Jaekel, 1918 as the type-species. A diagnosis has been given on p. 29. The genus is first reported to occur in Spain from the new Frasnian species *L. ventanillensis*. *Pyxidocrinus* was proposed as a conditional name but is now erected as genus with *Actinocrinus prumiensis* as type-species and J. Müller as the author. A diagnosis has been given on p. 35. *P. collensis* and *P. latus* are referred to it as new species. *P. San-Migueli* (Astre, 1925), formerly referred to *Periechocrinus* and *Pithocrinus*) and *P. bifrons* (W. E. Schmidt, 1932, formerly referred to *Megistocrinus* and *Pithocrinus*) have now been ranked under *Pyxidocrinus*. Although *Pyxidocrinus* has a German species as the type, it is essentially a Spanish genus. Strangely enough it is only now reported for the first time as occurring in Spain. The genus *Pithocrinus* Kirk, 1945, with *P. Cooperi* Kirk, 1945 as the type-species has been emended so as to include forms with globose dorsal cups, a variable number of free arms per ray and a stout subcentral anal tube. The arms are described for the first time. For emended diagnosis see p. 46. Although *Pithocrinus* has an American type it is essentially a Spanish genus. *P. ovatus* and *P. spinosus* are referred to this genus as new species, *P. Waliszewskii* (Oehlert, 1896, formerly referred to *Megistocrinus*) is kept within it, but *P. intrastigmatus* (Schmidt, 1932, formerly referred to *Saccocrinus*) is excluded and used as the type-species of the new genus *Stammocrinus* (diagnosis see p. 59) which is believed to include *Dorycrinus devonicus* Springer, 1911 and two more Spanish species, not yet sufficiently well known so as to allow definite description. *Stammocrinus* is restricted to Devonian strata. The new Emsian species *Corocrinus* ? *grandosensis* is provisionally referred to *Corocrinus* because it possesses characters unknown up to now from that genus. *Gennaecrinus* is first recorded from Spain from a species very similar to *G. nyssa*.

The study of the important Devonian periechocrinid fauna has revealed that no Devonian forms can be assigned to the type genus *Periechocrinus*, which genus must be of exclusively Silurian age. A group of Lower Carboniferous and Mississippian species, hitherto assigned to *Periechocrinus*, both for morphological as for stratigraphical reasons cannot belong to *Periechocrinus* nor to any of the Devonian periechocrinid genera.

The new genus *Aryballoocrinus* is erected for them with *Periechocrinus* ? *Whitei* Hall, 1861 as the type-species. A diagnosis for this genus is given on p. 72. The genus includes six species, four of which were formerly referred with doubt to *Periechocrinus*: *Aryballoocrinus Whitei* (Hall, 1861), *Aryballoocrinus tenuidiscus* (Hall, 1861), *Aryballoocrinus awthornsensis* (J. Wright, 1955) and *Aryballoocrinus* spec. 1 (Laudon & Severson, 1953). Further are included *Aryballoocrinus Sampsoni* (Miller & Gurley, 1896, formerly referred to *Corocrinus*) and *Aryballoocrinus parvus* (Wachsmuth & Springer, 1890, formerly referred to *Megistocrinus*).

Other monobathrids include specimens of *Iberocrinus multibrachiatus* Sieverts Doreck, 1951, which species proved to occur in the Moscovian of Spain. *Nunnacrinus* ? *stellaris* is first reported from the Namurian of Spain. The genus *Pimlicocrinus* is first recorded outside Great Britain. *Pimlicocrinus latus* occurs in the Namurian of Spain, whereas in England it is in the Dinantian. Another two species of *Pimlicocrinus* are not yet fully described. One of them is of Moscovian age and probably conspecific with a specimen from the Westfalian of Morocco. A single cup is assigned to *Aorocrinus*. This would mean the first occurrence of this genus outside the North American continent. *Platyhexacrinus Kegeli* W. E. Schmidt, 1932 is mentioned because two new specimens substitute for the lost types.

*Trybliocrinus Flatheanus* is redescribed in great detail. The species *Hadrocrinus hispaniae* Schmidt, 1932 is placed into synonymy with it. Much attention has been given to the ontogenetic growth. Ontogenetic phenomena are regarded as special characters of the family Polypetidae, in which family the genus *Himerocrinus* Springer, 1921 is placed on the ground that it is supposed to have an ontogenetic growth largely comparable to that here described for *Trybliocrinus*.

Platycrinicae form an important part of the Spanish fauna. Besides *Platycrinus* spec. ex gr. *bollandensis* of Namurian age and *Pleurocrinus* spec. ex gr. *coplowensis* of unknown provenance, they may all be found in Lower and Middle Devonian strata. The Spanish hapalocrinids and related platycrinids are characterized by aberrant positions of the smaller basal and by differentiation of the posterior interradius. The new hapalocrinid genus *Cantharocrinus* with *C. minor* spec. nov. as the type-species (diagnosis see p. 117) and the new species *C. simplex* as co-type, is still only known from Spain. The new platycrinid genus *Oenochoocrinus* with *Oe. princeps* spec. nov. as type-species (diagnosis see p. 124) and the new species *Oe. pileatus* and *Oe. scaber* as cotypes, is still known only from Spain. The genus is erected for platycrinids with a tegmen composed of five orals and five modified first axillar ambulacrals. The genus showed to possess affinity with the Permian genus *Neoplatycrinus*. The better understanding of modified first axillar ambulacrals, as a character consistent with the presence of but one first primibrach and two secundibrachs in trunked ambases led to a review of the morphological relations of genera in the Platycrinicae. A suggestion for their evolution is given, based on detailed morphological comparison (see textfig. 32).

Among the inadunates previously described from Spain *Storthingocrinus Haugi* Oehlert, 1896 and *Storthingocrinus labiatus* W. E. Schmidt, 1932 are regarded as *nomina dubia*. The incomplete nature of the specimens attributed to them, forces us to do this because their cups are undistinguishable from so many other inadunate cups.

The affinity of North American Devonian crinoids with the West European fauna is once more expressed by the first record from Spain of the species *Vasocrinus valens* Lyon, 1857; *Vasocrinus turbinatus* Kirk, 1929; *Vasocrinus stellaris* (Schultze, 1867) and *Vasocrinus* spec. cf. *V. sculptus* Lyon, 1857.

A highly interesting inadunate proved to be a form with pentalobate stem, composed of five different joint series, two anals in cup and enlarged thecal cavity by incorporation of a small number of interradians and the presence of a madreporite. It is described as the new genus *Situlacrinus* with *S. costatus* spec. nov. as the type-species (diagnosis see p. 153). The genus is placed provisionally among the Barycrinidae. It would be the first Devonian form of that family and the first record from Europe.

The Givetian cupressocrinid fauna has largely affinity with Middle Devonian fauna's in the Eifel region. *Cupressocrinites Townsendi*, *Cupressocrinites* spec. cf. *C. Schlotheimi*, *Cupressocrinites inflatus*, *Cupressocrinites Sampelayoi* and a species not sufficiently well presented to receive full description are described from Spain. *C. inflatus* and *C. aff. Schlotheimi* have their first mention outside Germany. The genus *Aviadocrinus* Almela & Revilla, 1950 is put into synonymy with *Cupressocrinites* Goldfuss, 1831 because all the

essential characters of its type-species *A. Sampelayoi* occur dispersedly among *Cupressocrinites* species.

The genera *Bactrocrinites*, *Lasiocrinus* (?), *Cromyocrinus* and *Paradelocrinus* are reported for the first time from Spain.

The Devonian crinoid faunas in the province of León occur in four different levels: at the top of the La Vid formation; at the base of the Santa Lucia formation; at the top of the Santa Lucia formation; and in the middle part of the Portilla formation. The first two faunas are of Emsian age. The Emsian fauna has affinities with the Lower Devonian fauna of Western Germany and with the Middle Devonian fauna of the region West-Central New York, Kentucky, Michigan, Indiana. The Spanish Emsian fauna is the richest of all known Spanish crinoid faunas.

## INTRODUCTION

Hitherto a remarkably small part of the Spanish Palaeozoic crinoid fauna has become known in scientific literature. No more than ten well-established Devonian species and a few rather badly established Carboniferous species have been described. Although collecting of fossil crinoids from this area dates from about 1850 and very fine collections have since been made, the number of described species is really very low. Casiano de Prado, De Verneuil and Paillette made a good collection of Devonian crinoids, but only *Pradocrinus Baylii* has been described from it; the rest of the material did not receive due attention. Barrois (1882) mentioned very summarily some Asturian crinoids, most of them of Carboniferous age. Some progress was made by Oehlert (1896) and W. E. Schmidt (1932) by the description of species from León (Santa Lucia) and Asturias (Arnao). An important study, revealing the affinities of some Spanish Periechocrinidae, was published by Kirk in 1945. In recent times Almela & Revilla (1950) and Sieverts Doreck (1951) did some further description of the rich faunas. Since the older existing crinoid collections from Spain have not received much attention and very fine collections have been made recently, it has been the aim of this study to give a comprehensive description of the important Palaeozoic crinoid faunas of North Western Spain (provinces of Palencia, León, Asturias).

The European standard practice in crinoid terminology, based on suggestions by Bather (1892) and recently improved by Ubaghs (1956, p. 516—519), has been followed. The classification of Crinoidea as given by Ubaghs (1953, in J. Piveteau's *Traité de Paléontologie*) has been used.

The Spanish crinoids here described are from two sources. (1) The existing crinoid collections in many Western European geological museums and geological institutes. The principal collections examined are from the Museo del Instituto geológico y minero de España, Madrid; Museo Nacional de Ciencias Naturales, Madrid; *École Nationale Supérieure des Mines*, Paris (coll. De Verneuil, coll. Paillette and coll. Oehlert) and Institut de Géologie, Lille (coll. Barrois). The collections of the British Museum (Natural History), London, and the Sedgwick Museum, Cambridge, have been studied. The staff of the United States National Museum, Washington; Senckenberg Museum, Frankfurt/Main; Museum of Humboldt University, Berlin; Swedish Museum of Natural History, Stockholm, helped with sending specimens, literature, photographs, casts and all the necessary information. (2) The large collections of crinoids, now stored in the Rijksmuseum van Geologie en Mineralogie at Leiden, Holland, made during the years 1955—1960 by students of Leiden University. These new crinoids have become known through field work in the Palaeozoic core of NW Spain (provinces Palencia and León) carried out by the Geological Institute of Leiden University.

My thanks for the loan of specimens are due to Prof. Dr. A. Almela, director of the Instituto Geológico y minero de España, Madrid; Prof. Dr. A. Duparque, Institut de Géologie, Université de Lille (France); Prof. Dr. W. Gross, Geologisch-Paläontologisches Institut und Museum, Humboldt Universität, Berlin; Dr. H. Malz, Geologische Abteilung des Forschungs-Instituts und Natur-Museums Senckenberg,

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## SYSTEMATIC DESCRIPTIONS

Class CRINOIDEA Miller 1821  
Subclass CAMERATA Wachsmuth & Springer 1885  
Order DIPLOBATHRIDA Moore & Laudon 1943  
Family RETEOCRINIDAE Wachsmuth & Springer 1885  
Genus DIAMENOCRINUS Oehlert 1891

*Diamenocrinus* spec.

Pl. I, fig. 7—9

*Material.* The collection of the Instituto geológico y minero de España at Madrid contains a rather poorly preserved theca of this genus under no. 126 D from the Lower Emsian deposits at Colle (near Sabero), province of León.

*Description.* The specimen is somewhat crushed at l.post. and r.post. sides, but a good idea of its configuration can be obtained. A small part of the stem and parts of the tegmen are preserved. The arms are missing. The dorsal cup — although somewhat flattened now — must have been cupuliform with a rather flat base. Its greatest width is at arm level. The ray ridges are conspicuous and in correspondence with this the interradial areas are slightly depressed. The very thick cup plates are highly convex to tumid, the proximal ones are each provided with a coarse spine. The plates have a radial ornamentation of ribs passing from the centre of a plate to adjoining plates. Some interradial plates show a fine granular ornament. The tegmen was flat. The anus cannot be traced. The height of the cup is about 22 mm, its width is estimated as about 20 mm.

The stem is distinctly stellate and which is made up by nodals, probably of two orders, and internodals. The right succession cannot be established. Cirri are not observed. The outline of the axial canal is undistinguishable. The lobes of the stem are in contact with the basals.

The base is flattened. The five small infrabasals all are rhomb-shaped. The outline of the infrabasal circlet is five-sided. The exterior surfaces are all separated by the interradially directed lobes of the most proximally situated columnals. The IBB are smooth plates, their height is 2.4 mm, their width 3 mm. The basals are very large plates. They are all seven-sided. The greatest width of the plates is in the lower part. All plates are provided with heavy spines; height 6.5 mm, width 7.5 mm.

*Radial series.* The radials are separated all around the cup. All are five-sided, pointed below, truncated above and intervening between the BB. The RR are of about the same size as the BB and are similarly spiny plates; height 6.8 mm, width 6.5 mm. Each radius has only two primibrachs, the first one six-sided, wider than high and but slightly smaller than the radials; height 5.2 mm, width 7.1 mm. The second primibach is axillary, five-sided and distinctly smaller than IBr1, height 4 mm, width 4.8 mm. At least three (sometimes four) secundibrachs are incorporated in the cup. The first secundibrachs are about as twice

as wide as high as the succeeding ones. An isolated part of the arm has very low disc-like brachials, about 4 times as wide as high. The specimen apparently has only two arms to the ray.

**Interbrachials.** On the shoulders of the IIBrr1 and between IIBrr2 and IIBrr3 rests an eight-sided iIBr1, 3 mm high and 2 mm wide. The plate is succeeded by two series of small elements merging with the tegmen.

**In normal interradii** the iR1 is a very large sevensided plate, height 6.5 mm, width 7.9 mm, resting on the truncated upper surfaces of the BB and intervening completely between the RR. This plate is followed in second and third ranges by two rather large plates, about 4.5 mm high and wide. The proximal three iRR are as tumid as BB and RR and equally provided with heavy spines. The largest width of the interradius is at the level of the iRR2. Distad the interradius only very little narrows and consists in that part of two or three series of smaller and less convex plates (1.5—3 mm).

The posterior interradius is wider than other interradii. A is six-sided, somewhat smaller than iRR1, its height 5.1 mm, its width 5.7 mm. It is, like other proximal iRR a very tumid and probably spinous plate, resting on the post. B and intervening between l.post. R and r.post. R. The plate is succeeded by three plates in next row, the central one being seven-sided and surmounted by two plates. From this fact one might expect that a median ray ridge would not occur. Unfortunately the distal part of the posterior interradius is crushed but it seems that the interradius narrowed more rapidly than other interradii.

The tegmen is flat and composed of very small, irregularly arranged plates. The anus cannot be traced due to the poor state of preservation of the tegmen.

*Remarks.* There can be but little doubt with regard to the generic position of the present specimen. The pronounced stellate nature of the stem is actually unknown within the genus *Diamenocrinus* but the peculiar low disc-like character of the first free brachials, the coarse ornament of the heavy cup plates support an arrangement under this genus, which is the only one known hitherto that includes such a form. The specimen resembles *Acanthocrinus* in possessing such prominent spines, but it cannot belong to this genus because the latter has distinctly a round stem.

Specific arrangement is more difficult. *Diamenocrinus Jouani* as described by Oehlert (1891, p. 837) shows differences, mainly in the characters of the distal cup part. At the first place the number of fixed brachials is fairly larger (up to six, perhaps seven); secondly the distal iRR are smaller and less numerous; consequently the whole cup narrows distad. The largest diameter in *D. Jouani* is at the level of the IIBrr1. Moreover *D. Jouani* is spineless and smaller. *Diamenocrinus Opitzi* as described by Schmidt (1934, p. 121) is a spiny form, but Schmidt suggested these plates would only occur on the IBB and BB and total at most ten. In the specimen described here more plates are of spiny nature, whereas the IBB are smooth. The specimen of *Diamenocrinus* (cf. *Opitzi*) described by Sieverts-Doreck (1957, p. 63, textfig. 1 a, 1 b) is a spiny form as well but its base is too fragmentary to permit a definite comparison with the Spanish species. The present form differs from the species originally described by Müller in Zeiller & Wirtgen, (1855, p. 12) as *Rhodocrinus gonatodus* in that the lobes of the stem are in contact with the BB. In *D. gonatodus* the IBB cirlet seems to be less depressed than in the Spanish species. This German species lacks spines. Ornamentation of the cup is best compared with the

neotype of *Diamenocrinus stellatus*, as described and figured by Schmidt (1941, p. 201, Pl. 11, fig. 3, 4).

The present species is a form rather apart from the other diamenocrini. Although comparable with *D. Opitzi* and *D. stellatus* one cannot place it in one of these species since the arrangement of plates in Schmidt's species is unknown and the Spanish specimen lacks the arms. The best will be to wait till more material becomes available for study, rather than establish a new species on a single incomplete cup.

Family DIMEROCRINITIDAE Zittel 1879  
Genus PTERINOCRINUS Goldring 1923

Goldring, 1923, p. 86; W. E. Schmidt, 1934, p. 127; Bassler & Moodey, 1943, p. 653; Moore & Laudon, 1943, p. 84; Ubaghs (in Piveteau III), 1953, p. 737.

*Genotype* by original designation: *Pterinocrinus quinquenodus* Goldring, 1923.

*Remarks.* Goldring established her genus for a form very similar to *Dimerocrinus*, but differing from it by arms of monoserial composition (p. 87). The supposed monoserial composition of the arms is contradictory to her statement (p. 88): 'The arms are strictly uniserial, made up of short quadrangular brachials, each bearing a pair of long slender pinnules one to each side.' It is perfectly clear from her statement that the genotype of *Pterinocrinus* has arms composed of compound brachials. As a consequence the genus *Pterinocrinus* is mainly characterized by the fact that the arms are composed of compound brachials. Only species with that type of arm composition can be included in the genus. Arms with compound brachials are quite exceptional among dimerocrinids. *Macarocrinus* and *Ptychocrinus* have real monoserial arms, whereas all other representatives of the family have biserial arms.

*P. quinquenodus* is not the only species which clearly has arms with compound brachials. Lehmann (1955, p. 136) stated for the arms of his species *P. Ehrlicheri*: 'An den Auserändern dieser Ventralrinne sitzen auf beiden Seiten die feinen gegliederten Pinnulae, die bei dieser neuen Art infolge der grossen Anzahl der niedrigen Armglieder dicht gedrängt stehen.' The only conclusion can be that the arms of *P. Ehrlicheri* are composed of compound brachials. The newly described Spanish Lower Devonian species *Pterinocrinus decembrachiatus* undoubtedly has the same arm composition as *P. Ehrlicheri* and *P. quinquenodus*. These three species at the moment constitute the real genus *Pterinocrinus*.

The species *Pterinocrinus Diensti* as described by W. E. Schmidt (1934, p. 128) in our opinion has to be excluded from *Pterinocrinus*. Schmidt (p. 129) stated for the arms of his species: 'Die Arme sind ungewöhnlich schlank, so dass die Pinnulae am Typus relativ weitläufig angeordnet sind. Im proximalen Teil sind die IIIBrr mindestens doppelt so hoch wie breit.' Judging further from his fig. 1, Pl. 22 it is suggested that *P. Diensti* has true monoserial arms, pinnulated in alternating order. The species should be referred to *Ptychocrinus*, rather than to *Macarocrinus*, because the latter genus has a very specialized tegmen structure.

The species to be included in the genus *Pterinocrinus* are:

*Pterinocrinus quinquenodus* Goldring, 1923  
*Pterinocrinus Ehrlicheri* Lehmann, 1955  
*Pterinocrinus decembrachiatus* spec. nov.

*Diagnosis.* A small-sized genus of the family Dimerocrinitidae, characterized by depressed interradiar areas and conspicuous radial series; arms simple or branching, composed of compound brachials; round stem, composed of nodals of one order with internodals. Tegmen unknown.

In the present interpretation of the genus *Pterinocrinus* it remains uncertain whether such a character as ribbed radial series passing their ribs on the basals constitutes a criterion for generic differentiation. In Schmidt's emendation of the genus (1934, p. 127) this character was included in its diagnosis, but since it is doubted whether *P. Diensti* in fact belongs to *Pterinocrinus* it is not certain whether this character is diagnostic for that genus.

*Distribution.* Representatives of the genus *Pterinocrinus* occur in Lower Devonian strata of Germany and Spain. In N. America the genus is known from the Upper Devonian (Lower Chemung) of New York.

*Pterinocrinus decembrachiatus* Breimer spec. nov.

Pl. I, fig. 3

*Holotype.* The specimen DH 1070 in the collection of the Museo Nacional de Ciencias Naturales at Madrid. It is the only known specimen of this species.

*Locus typicus.* Cape La Vela at Arnao, near Aviles, province of Oviedo.

*Stratum typicum.* The red calcareous shales in the Ferroñes limestone formation, corresponding to the Lower Emsian.

*Diagnosis.* A species of the genus *Pterinocrinus* Goldring 1923, characterized by a conical dorsal cup composed of slightly convex plates, probably without ornamentation; radial series up to IIBr1 incorporated in cup; relatively small interradiar areas, situated somewhat depressed between the radial series; stout arms, which remain unbranched in the free state; presence of long pinnules composed of elongated elements.

*Description.* The stem is preserved over a length of 2 cm, its diameter is 1.4 mm. The dorsal cup is widely conical with an basal angle of 60°. The radial series are conspicuous, mainly due to the larger degree of convexity of its plates. The interradiar areas are small. The cup plates probably lack any ornament. The height of the cup is about 8 mm, the largest width of about 11 mm is at arm levels. The arms are fairly stout 1.8 mm in diameter and at least 25 mm long. Their back sides are gently rounded. The pinnules are at least 4.5 mm long. The posterior side is not shown. Perhaps the specimen is a young one.

The stem is composed of nodals of only one order, each interlocking with one internodal. The stem is rather slender. The outline of the axial canal can not be observed.

The base. The five very small pentagonal IBB are visible in side view. Their height is 1 mm, width 1.8 mm. The basals are relatively large pentagonal plates, height 1.9 mm, width 2 mm. The posterior basal cannot be seen.

Radial series. The radials are in lateral contact as far as they can be observed. RR are fairly large plates, seven-sided and wider than high, height 2.3 mm, width 2.8 mm. It follows that the radials are the largest plates of the cup.

Two primibrachs occur per ray, both distinctly smaller than the RR. The first one is hexagonal, the second axillary and pentagonal. The total height of

the two IBrr is 3 mm, the width 1.8 mm. The plates are very convex and are the most conspicuous elements in the cup. The first secundibrachs are only slightly incorporated in the cup. Their proximal edges have sutures with the most distal range of interradiial plates. The IIBrr1 lack a pinnule.

The *i n t e r r a d i a l a r e a s* are but small. They are composed of relatively small iRR1, hexagonal and higher than wide (height 1.6 mm, width 1.3 mm) succeeded by five or six smaller plates arranged in two series. The interradius narrows distad. It is in contact with the tegmen.

The *a r m s* are free from the upper parts of the IIBrr1. The two IIBrr1 of the same ray are in lateral contact, so that there is no interbrachial. The arms are fairly stout and of usual length. The brachials are gently rounded at the back, showing a general horseshoe-shape. Their height is about a third of their width. The proximal brachials are slightly higher than the succeeding ones. Brachials apparently are smooth plates. The ventral sides of the arms are not observed in the type specimen. The most distal parts of the free arms are lacking. The arms are composed of compound brachials and they do not branch in the free state. Ten free arms are present.

*P i n n u l a t i o n*. The arms are pinnulated from IIBrr2. The first secundibrach is incorporated in the cup by its proximal edge only and lacks a pinnule. Pinnulation is regular, each brachial bearing a pinnule at each side. The pinnules are composed of small elements, about twice as wide as high with at least ten pinnulars making up a pinnule.

*Comparison of species*. The Spanish specimen markedly differs from the type species. First of all it has only ten free unbranching arms, very much stouter than in *P. quinquenodus*. The radii are not marked with ribs passing on the basals, but the radial series are entirely more convex, so becoming conspicuous. Basals furthermore lack nodes and are fairly well visible from aside. Last the interradiial areas are smaller, iRR1 succeeded by two plates in second and third ranges.

A comparison with *P. Ehrlicheri* is more difficult because the type of that species lies on a slab and does not show the composition of the dorsal cup very well. Two characters of *P. Ehrlicheri* may be highly diagnostic for that species. First the ornamentation of radial ribs passing from plate to plate in the dorsal cup and next its long slender arms, which branch shortly after becoming free. *P. decembrachiatatus* distinctly differs from the German species because its arms are short unbranching structures and any trace of ornamentation seems to be absent.

*Macarocrinus* (?) spec.

Pl. I, fig. 10—12

*Material*. Two specimens in the collection of the Museo del Instituto geológico y minero de España at Madrid are referred here with some doubt to the genus *Macarocrinus*. The specimen TB 62 comes from the Devonian of Orzonaga, near Matallana, province of León. The specimen TB 62a is of unknown provenance.

<i>Description</i> .	TB 62	TB 62a
Total height of the theca	22 mm	14.7 mm
Width of the cup	15.9	11.2
Height of the cup	10.0	6.0
Height of the tegmen	12.0	8.7

The cups are widely conical, distinctly lobed in their upper portions. The series of fixed brachials are conspicuous, due to the greater degree of convexity of these plates. Ray ridges passing from RR on the brachials do not occur. The proximal cup part is perfectly conical. Interradial areas are somewhat depressed and very reduced. Posterior interradius is differentiated, possessing a median ray ridge. The tegmen is highly arched to almost conical. The anus cannot be seen. The dimensions of the cup plates used in further description have been taken from the specimen TB 62.

The stem is not preserved but in both specimens the last columnal is still attached to the cup. Its outline is round and it is pierced by a very small and round axial canal.

Infrabasals five, all alike and pentagonal, fairly well visible from the side. IBB are relatively small plates. The infrabasal circler attains a height of only 1.2 mm.

Basals five, regularly pentagonal, except the posterior one, being regularly hexagonal and distinctly higher than other BB, ranging to about half the height of the radial circler. Basals are relatively large, height 2.8 mm, width 3.1 mm. Height of post. B is 3.2 mm, its width 3.2 mm.

Radial series. The radials are the largest plates of the cup, heptagonal and much wider than high, height 2.6 mm, width 4.1 mm. L.post. R and r.post. R are hexagonal plates, due to the position of the first anal plate which is not completely included in the radial circler but situated somewhat higher. All radials are in contact except at the posterior side.

In each ray only two primibrachs occur, the second one axillar. IBr1 is typically four-sided, very much wider than high and in lateral contact with iR1. Its height is 1.8 mm, its width 3.6 mm. In some radii IBr1 may be irregular five sided when it is in contact with an iR2 at only one side or even six-sided when it is in contact with two iRR2. The IAx is typically pentagonal and much wider than high, height 2.4 mm, width 3.9 mm. IAxx are in lateral contact with interradian plates of the second range. IIBrr2 and IIBrr3 are free. The second or third secundibrach is axillary; the second secundibrach may be very much higher as the first secundibrach when IIBr3 is axillary. Intersecundibrachs do not occur.

In normal interradian only three plates occur, situated somewhat depressed between the conspicuous series of fixed brachials. The plates have a tuberculate ornament. Interradian are distinctly narrow distad. The first interradian is a larger plate, generally six-sided, resting on the shoulders of the radials and in lateral contact with IBrr1 or sometimes even with IAxx. The first interradian plate is succeeded by two small plates only, situated between IAxx and IIBrr1. They are in contact with the tegmen.

The posterior interradius is differentiated. The first plate is a larger eight-sided plate, resting with a broad facet on post. B and with its proximal sides on l.post. R and r.post. R. It is in lateral contact with l.post. IBr1 and r.post. IBr1. The plate is succeeded by three plates in the next range, the middle one larger and hexagonal. The height and width of A are 2.8 and 3.1 mm respectively. The first anal plate is followed by a series of fairly large plates, all regularly hexagonal and distad decreasing in size. This series of plates forms a median ray ridge towards the tegmen. The median ray is laterally accompanied by single series of three peculiar small plates.

Tegmen. In both specimens the tegmen is very high and almost conical. It is composed of very small, irregular plates, most probably arranged in different

strata. A differentiation of plates in ambulacral and interambulacral areas can not be found due to the rather poor state of preservation of both tegmens. Larger dome plates certainly occurred in the tegmen. The r.ant. side of the tegmen of spec. TB 62 shows such a plate in an interambulacral position. Near the top of the tegmen of spec. TB 62a a very large dome plate occurs, perhaps surrounded by several minor dome plates. The larger dome plate of TB 62a is broken off and consequently one can observe that the plate was situated on a lower layer of very small irregularly arranged plates. It cannot be established whether the larger tegmen plates have to be interpreted as orals or not.

*Remarks.* The present specimens are referred with some doubt to *Macarocrinus*. One cannot be entirely sure of such an assignment as long as the arms are missing. The composition of the cup agrees in a large degree with the descriptions of Jaekel (1895, p. 37) and Schmidt (1934, p. 123, 124) of *Macarocrinus Springeri*, the type species. The only difference may be found in the larger degree of reduction of the interradial areas in the Spanish species. *M. Springeri* possessed at least five or six interradials whereas in the present form no more than three are present. An assignment of the Spanish specimens to *Macarocrinus* seems to be supported by Schmidt's statement on the occurrence of 'Kalkkörperchen' in the tegmen. Perhaps larger dome plates or true orals occurred in other species of *Macarocrinus* as well.

The dorsal cups of the form under consideration largely agrees with the description of *Pterinocrinus decembrachiatus* in this paper (cf. p. 12) but differs from the latter by the larger degree of reduction of the interradial areas and in the bifurcation of the free arms. Unfortunately it is impossible to state whether the arms are composed of monoserially arranged brachials or of compound brachials. Hence the species may belong to *Pterinocrinus* if the nature of arm composition is considered as the most important difference between *Macarocrinus* and *Pterinocrinus* as the writer is inclined to believe.

*Griphocrinus ovetensis* Breimer spec. nov.

Pl. I, fig. 1 and 2

*Holotype.* The specimen in the Instituto de geologia aplicada, Facultad de Ciencias, University of Oviedo (Asturias).

*Locus typicus.* Cueva de Múcaro at Grado (prov. of Asturias).

*Stratum typicum.* The exact horizon is unknown and has not been determined at the present, but the specimen undoubtedly comes from the Devonian.

*Diagnosis.* A species of the genus *Griphocrinus* Kirk, 1945 characterised by a rather high and narrow cup with subturbinate outlook; relatively few iRR; incorporation of only one IIBr and one iIIBr in the cup; presence of an anal tube; regularly dichotomous branching arms.

*Material.* Next to the holotype another *Griphocrinus* specimen has been found at Arnao, Cape El Mugaron, in the Lower Couvinian Arnao limestone. It is stored in the collection of the Rijksmuseum van Geologie en Mineralogie at Leiden under no. 97501 and is labelled *Griphocrinus* spec. cf. *G. ovetensis*. The specimen consists of a single somewhat crushed cup. It is not identical with the holotype.

*Distribution.* Although the age of the holotype cannot exactly be determined, it is certain however, that it comes from the Devonian, at least proving the presence

of *Griphocrinus* in Spanish Devonian strata. Moreover, the Arnao specimen perhaps indicates that this genus is restricted to Middle Devonian rocks, as it is in America and N. Africa.

*Description. Form and dimensions.*

Height of dorsal cup	15 mm
Width of dorsal cup	14 mm in lateral; 17 mm in antero-post. direction
Length of arms	50 mm at least
Diameter of arms	ca. 3 mm measured at base
Length of pinnules	5 mm at least

The dorsal cup is high, somewhat turbinate. At the upper portions of the cup its transverse sections must be somewhat oval. The radial series are not conspicuous, only slightly marked with a rib. Interradial areas are relatively small, non-depressed. The posterior interradius is marked by a median series of plates, but not ridged. Probably this series passes into an anal tube. Ornamentation is not very distinct. Basals were at lower edges provided with a downward directed spine or tubercle. From these spines two ribs diverge and pass on the radials, when they continue over the radial series, dividing again on the primaxil.

The base is dicyclic. The infrabasals are very low plates, ca. 1 mm high, visible in side view. Their joint outline is five-sided. Only four plates form this circle. The l.post. IB and r.post. IB are firmly anchylosed. A suture cannot be found between them. The lower part of this circle has a very shallow depression for the reception of the stem. The outline of this depression clearly proves that the stem was circular in outline. The basals are the largest plates of the cup. They are in lateral contact all around the cup. The post. B is regular six-sided, 5 mm high and wide; postero-right B is again six-sided but pointed above, 4.5 mm high; antero-right B is seven-sided, truncated above, 4.9 mm high; antero left B is seven-sided, truncated above, 5.1 mm high; postero left B is six-sided pointed above, 4.6 mm high. The seven-sided basals are at their upper margins in contact with the first interradiial plates.

The radials form the next circle of plates. The primanal is situated in this circle. The radials are not always in lateral contact. At antero left and antero right sides the first interradiial plates intervene so as to come in contact with the basals. The ant. R is five-sided 4.1 mm high and 5 mm wide; l.ant. R and r.ant. R are six-sided, much wider than high; l.post. R and r.post. R are seven-sided.

The radial series have two primibrachs and one or two secundibrachs incorporated in the cup. The first primibrach is typically six-sided, somewhat wider than high, 4.9 mm wide and 2.6 mm high. The primaxil is typically five-sided and somewhat smaller as the preceding brachial: 2.9 mm high and 3.1 mm wide. In r.post. and ant. radii primibrachs have aberrant forms. The primaxils are not in complete superposition to the first primibrachs; their form is six-sided because of a supplementary contact with an interradiial plate. The first primibrachs are five-sided because they lack one contact with interradiial plates.

One larger six-sided secundibrach per half radius is incorporated. These plates are 2 mm high. The second secundibrachs are small cuneate plates. They still may be regarded as incorporated in the cup, because they have sutures with



interradial plates. A very small intersecundibrach is situated between the cuneate IIBrr2 and rests on the upper sides of IIBrr1. Each radius bears two ranii.

Interradial series are not depressed. Only few elements compose these regions. In antero right and antero left interradius the first larger plates intervene between two radials so as to come in contact with the basals. In postero right and postero left interradii the first plates are six-sided, 3.4 mm high

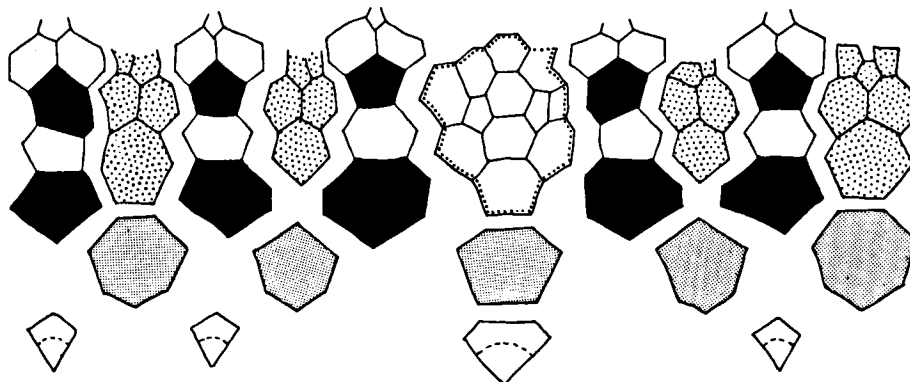


Fig. 1. Diagram showing the composition of the dorsal cup in the holotype of *Griphocrinus ovetensis* from Devonian deposits at Grado, Asturias (coll. Instituto de Geologia Aplicada, Oviedo).

and 3 mm wide. In all interradii the first plates are succeeded by two series of plates. A total of about seven plates make up these areas, the last two being very small.

The posterior interradius is very wide. The primanal is placed in the radial circlet. It is a regular six-sided plate 3.5 mm high and 4.5 mm wide. A is succeeded by three plates in the next range, the central one but slightly smaller than the primanal and six-sided. The two lateral plates of this range are six- and seven-sided. The central plate gives further rise of a median series of all six-sided plates, gradually becoming smaller, whereas the lateral plates of this range support two series of plates, more rapidly decreasing in size. Towards the upper part of the cup the central part of the posterior interradius becomes conspicuous, suggesting that it leads to an anal tube.

Free arms are composed of biserially arranged brachials directly after becoming free. Bifurcation is regularly dichotomous. Arms divide only two or three times in the free state. The brachials are rounded at back sides. The ventral side with the oral groove can never be seen. Some parts where brachials are broken off suggest that the ventral groove was a deep V-shape. The state of preservation is not sufficient as to show any trace of the articulation facets for insertion of the pinnules.

**Pinnulation.** The proximal parts of the arms are too much crushed or too deeply inserted in the matrix to show the pinnules in these regions. Hence it cannot be stated whether pinnulation started already at the first free brachials or not. Higher up at the arms pinnulation is regular, each brachial being provided with a pinnule. Pinnules were observed even at the most distal tips of the arms. At least four pinnulares were seen to constitute a pinnule, but the distal tips of the pinnules are embedded in the matrix. The pinnules are very fine and were

not in lateral contact with preceeding and succeeding pinnules. The pinnulars are very long, up to 1.5 mm, with a diameter of but 0.3 mm. At the dorsal side they are gently rounded. Thickening at the facets is absent. Only the facet with the brachial is somewhat swollen. Some pinnulars are weathered and show natural transverse sections. These sections prove that the pinnulars had a V-shaped ventral groove. No trace of cover plates has been found.

*Remarks.* The holotype agrees in all its essential characters to the diagnosis of *Griphocrinus* as given by Kirk (1945, p. 350). Some reasons forbid the assignment of this specimen in *Dimerocrinus*. In the first place this genus is mostly restricted to Silurian rocks of North America, England and Gotland. Only three species survived in Devonian times in North America. Representatives of this genus in the Devonian of Europe are unknown at the present moment. Next the typical *Dimerocrinus* species never have the radial circles interrupted by the contacts of basals and interradials. The genus *Griphocrinus* on the contrary is a typical Devonian genus known thus far from New York, Kentucky, France and Maroc (cf. Lemaitre, 1952, p. 96, Pl. XXII, fig. 10—12, textfig. 8; 1954, p. 2108; 1958, p. 345). One of the most peculiar characters of *Griphocrinus* is the contact of interradials and basals that intervenes between two radials. This character too, is known from *Lyriocrinus* and *Atactocrinus*. The present specimen certainly can not be assigned to the Silurian *Lyriocrinus* with its low globose cup and stout undividing arms. The genus *Atactocrinus* is still insufficiently known from a fragmentary cup only. It differs distinctly from our species in that only two plates succeed the primanal. Further it comes from Ordovician strata of North America. Much resemblance in composition of the dorsal cup and branching of the arms is shown to exist between the Spanish species and *Ambicocrinus aborescens*, but the latter form differs definitely by its substellate stem. Hence both for stratigraphical as for morphological reasons our species is best placed under *Griphocrinus*.

The present Asturian form differs from the genotype *G. nodulosus*, *G. insculptus* and *G. Wachsmuthi* by incorporation of less secundibrachs and intersecundibrachs. Perhaps *G. Halli* is the only known relative of the Spanish species that has similarly only one or two secundibrachs incorporated. It agrees to the genotype by the nodose basals and the slightly ribbed radial series. But the genotype has more nodose plates and has a wider dorsal cup. The only species to which the arm structure can be compared is the genotype. As far as can be judged from the figures (cf. Wachsmuth & Springer, 1897, pl. XIII, fig. 8; Goldring, 1923, pl. 2, fig. 1) *G. nodulosus* has arms that branch in a more or less regularly dichotomous manner, two or three times. This arm structure is directly comparable to that of *G. ovetensis*.

#### Family ORTHOCRINIDAE Jaekel 1918 Genus ORTHOCRINUS Jaekel 1895

O. Jaekel, 1895, p. 29; F. A. Bather, 1900, p. 198; F. Springer, 1913, p. 187; W. E. Schmidt, 1914, p. 305; W. E. Schmidt, 1941, p. 195; R. S. Bassler & M. W. Moody, 1943, p. 577; R. C. Moore & L. R. Laudon, 1943, p. 104, 117; G. Ubaghs (in Piveteau III), 1953, p. 737.

*Genotype* by monotypy: *Orthocrinus simplex* Jaekel, 1895.

*Diagnosis.* A genus of the family Orthocrinidae Jaekel, 1895 characterized by a more or less elongated cup, due to the very high IBB and BB circlets, ranging from about one third to two thirds the total height of the dorsal cup; fixed brachials two, the first one either four- or six-sided, the second one axillary and

typically five-sided; reduced interradial areas, if at all iR1 is followed by two plates only; A succeeded by three plates in next range; stout arms composed of compound brachials, branching but once on IAx or IIBr1, pinnules composed of long elements; very low tegmen composed of many minute elements; very delicate cylindrical stem with round axial canal.

*Distribution.* The genus *Orthocrinus* occurs in Lower and Middle Devonian rocks of Western Europe only. The German species *O. simplex* and *O. tuberculatus* are only known from the Middle Devonian of Sauerland. The Spanish species *O. robustus* occurs in the Middle Devonian of León and Asturias. The only certainly known occurrence of *O. elongatus* is in the Upper Emsian of León. *O. spec.* as described in this paper is from Lower Emsian deposits of León.

*Orthocrinus planus* W. E. Schmidt, 1932 (nomen dubium)

The collection of the Rijksmuseum van Geologie and Mineralogie at Leiden (Holland) has a fragment of a cup no. 97502 and some isolated free brachials and columnals from the type locality of *Orthocrinus planus* at Arnao (Cape El Mugaron) in Asturias. The present fragment is composed of those elements hitherto unknown from the type fragment. Unfortunately the two fragments from Arnao cannot be compared.

All cup plates of the newly found fragment are distinctly convex and apparently without ornamentation. All radials are broken off, their form and dimensions remain unknown. The width must have been 8 mm. The first primibrach is hexagonal, 5.4 mm high and 6.8 mm wide. The greatest width is slightly lower than the top of the plate. The second primibrach is axillary, very much wider than high. The first secundibrachs are but slightly incorporated in the cup. At the ventral sides they possess a V-shaped incision. The sutures between IAx and IIBr1, unlike other sutures, not depressed, so that the distal portion of the series of fixed brachials becomes conspicuous to the adjoining parts of the interradial areas. iR1 is a large hexagonal plate, higher than wide, 7 by 5.8 mm. It is in lateral contact with the IBrr1 only. The first interradial plate is succeeded by two very small elements, situated somewhat depressed between the IAxx, but possessing a small suture with the upper parts of IBrr1, the latter thus being hexagonal. iRR2 apparently are tuberculate plates. No further interradial elements can be traced. The anal side is not shown in the present specimen. In the matrix of this cup some isolated brachials and columnals are preserved. The brachials completely agree with Schmidt's description (1932, p. 30) for *O. planus*' brachials. The columnals prove that the stem was a very delicate one. The diameter of these columnals is about 2 mm. The axial canal was round and fairly large.

In establishing his species *Orthocrinus planus* (1932, p. 29) Schmidt used the following characters to distinguish it from the formerly known German species *O. simplex* and *O. tuberculatus*: (i) The flatter nature of the plates and consequently the non depressed sutures in his species. German species have a distinctly five-lobed outline at the level of the basals whereas *O. planus*' outline must have been circular in that region. (ii) The form of the basals. In German species these plates are higher and the lateral sides almost parallel to each other. The form of these cups is more cylindrical than nut- or cupshaped as Schmidt believed for *O. planus*.

When trying to compare the present cup fragment with Schmidt's description we find that it is hardly possible to do so. First the basals are lacking and the

nature of the calyx plates does not correspond to Schmidt's description. The plates are very convex and the transvers section is distinctly lobate. It can be concluded moreover from Schmidt's figures (1932, Pl. IV, fig. 1a) that the cup plates in *O. planus* were relatively thin, whereas in the present fragment the plates have a thickness of 3 mm (measured at RR). At last Schmidt's specimen was larger. Measured from his fig. 1b, Pl. IV, the radial has a width of at least 10.5 mm, whereas in our specimen width is no more than 8 mm for normal, probably hexagonal radials.

In our opinion it is impossible to trace the real characters for *O. planus*, since it is based on some fragments only. New fragments from the type locality are believed not to be conspecific with Schmidt's fragments. Unfortunately Schmidt's type fragment has been lost during the last World War. Among Spanish Orthocrini no such forms have become known that could possess characters as Schmidt established for *O. planus*. For all these reasons a status of *nomen dubium* is proposed for *Orthocrinus planus*. The Int. Comm. Zool. Nom. is requested to suppress the specific name *planus* W. E. Schmidt, 1932 under the Plenary Powers.

*Orthocrinus robustus* Breimer spec. nov.

1949 *Orthocrinus plannus* — Rodriguez Mellado, p. 657—662, Pl. 29, 30

*Holotype*. The specimen described by Mrs. Rodriguez Mellado, at present in the Museo Nacional de Ciencias Naturales at Madrid.

*Locus typicus*. At km 363 along the road leading from Pola de Gordon to Santa Lucia (province of León). See sheet 103 topographical map of Spain scale 1: 50.000. The locality is near the village Santa Lucia.

*Stratum typicum*. The highest beds of the Santa Lucia formation, corresponding to the lowermost Couvinian (M. Devonian).

*Diagnosis*. A very large *Orthocrinus* species, characterized by a dorsal cup composed of convex plates, probably without ornamentation, the largest width of the cup at the level of the IBrr1; very low infrabasal circling, low basal circling; basal circlings occupying about one third of the total height of the dorsal cup; very high radial series, in which the first primibach is very high and six-sided, the first secundibachs still incorporated in the cup; relatively large, vertically situated interradian areas with a high iR1; arms composed of very low brachials.

*Material*. The specimen TB 61 in the collection of the Museo del Instituto geologico y minero de España at Madrid is referred to *O. robustus*. It comes from Devonian strata near Orzonaga (province of León). The exact age can not be determined, but it is possible that it comes from about the same horizon as the holotype.

The Orzonaga specimen undoubtedly is conspecific with the Santa Lucia specimen. The cup is of the composition and proportions as the holotype. The width at the level of IBrr1 and iRR1 varies from 32—36 mm, just as in Rodriguez's specimen. The plates are convex, the sutures slightly depressed. Ornamentation can not be observed because the cup is somewhat weathered.

*Remarks*. Rodriguez Mellado referred her specimen to *Orthocrinus planus* probably because that species was the only known representative of the genus in Spain at that time. Moreover the specimens are of exactly the same age. There are however marked differences between the two species. The Santa Lucia specimen is very much larger than *O. planus* could have been. The basals are

17 mm high, but in Schmidt's specimen only 12. The specimen from Santa Lucia has a height of 55 mm, the width varies from 32—40 mm. Without doubt it is the largest *Orthocrinus* known at the present. The plates are convex and the sutures distinctly depressed, unlike Schmidt's description for *O. planus*. The form of the basals on the other hand is about the same, the lateral sides not parallel to each other. The form of the cup to a large degree will be determined by the form and size of the basals. It thus may be expected that the proximal parts of these two cups were about equally formed. Ornamentation in the Santa Lucia specimen is not distinctly shown.

*Orthocrinus elongatus* Breimer spec. nov.

Pl. III, fig. 10

*Holotype*. The specimen no. 97503 in the collection of the Rijksmuseum van Geologie en Mineralogie at Leiden (Holland).

*Locus typicus*. Grandoso, near Sabero, province of León.

*Stratum typicum*. The base of the Santa Lucia formation, corresponding to the Upper Emsian (Lower Devonian).

*Diagnosis*. An *Orthocrinus* species characterized by a very elongated dorsal cup, composed of flat and smooth plates; the largest width of the cup at the level of IIBrr1; very high infrabasal and basal circllets, occupying two thirds of the total height of the dorsal cup; lateral sides of the basals parallel to each other; radial series composed of small elements, IBr1 typically hexagonal, IAx pentagonal, IIBrr1 incorporated in the cup; relatively large interradial areas, composed of at least five plates.

*Material*. The specimen TB 71 in the collection of the Museo del Instituto geológico y minero de España at Madrid is referred with some doubt to the species *Orthocrinus elongatus*. It comes from Devonian strata near Orzonaga, province of León. The exact age is not determined.

*Description*. The dorsal cup is very elongated. The total height is no less than 37 mm. The largest width of 18 mm is at the base of the arm. The very base of the cup is cupuliform, the region of the basals more or less cylindrical and distad the cup widened gradually. The radial series are only slightly conspicuous, the interradial areas not markedly depressed. The cup plates are somewhat weathered in the holotype. The plates are flat and the sutures superficial. Ornamentation seems to be absent.

*Base*. Only three infrabasals are shown in the holotype. They gradually flare outward from the place of attachment of the stem. IBB are extremely high: 12 mm. The basals are six-sided and about twice as high as wide, height 13.3 mm, width 6.9 mm. The sides of the basals are parallel to each other. The total height of the basal circllets is 24 mm or two thirds the height of the dorsal cup.

The *radials* are relatively small, heptagonal plates, about as high as wide, height 6.7 mm, width 7.6 mm. The first primibrach is hexagonal, distinctly smaller than the radial, height 4.3 mm, width 5.1 mm, the largest width high up in the plate. The second primibrach is axillary. It is pentagonal in two of the rays shown, but hexagonal in the third ray due to the contact at its right side with two interradial plates. The height of the primaxil is 3.4 mm, the width 5.5 mm. It is a typically low plate. The first secundibrachs are still slightly

incorporated in the dorsal cup. They have sutures with the most distal range of interradial plates.

But two normal interradii are shown in the holotype. The interradial areas are composed of elements rather large for *Orthocrini*. The first interradial is a high, hexagonal plate, height 5 mm, width 4.2 mm. It is succeeded by two ranges of two very small plates, each about 1.5—2 mm high. The last range of plates is inclined toward the tegmen. The posterior interradius is not shown.

The tegmen is not exposed.

The arms are fairly stout, composed of low disc-like compound brachials. The diameter of a free brachial is about 3 mm, the height but 1 mm. Only the dorsal sides of the arms are exposed. Arms are preserved over a length of 70 mm. They remain unbranched throughout their length. At the distal parts of the arms the brachials are about 1 mm wide. The pinnules occur at both sides of the brachials. They attain a length of at least 15 mm. The pinnules are composed of elements all alike and about twice as high as wide.

The stem is a very delicate one. Its diameter is no more than 2.4 mm at the place of attachment to the cup. The columnals are round. The axial canal is not shown. The composition of the stem is: nodal of the first order (0.7 mm high) — 6 nodals of the second order (0.25 mm high) each alternating with a very low internodal — nodal of the first order.

The specimen TB 71 from Orzonaga, here referred to *Orthocrinus elongatus* and figured Pl. I fig. 4—6, differs in certain respects from the holotype. The differences perhaps may fall within the range of individual variation around the holotype. Infrabasals and arms are lacking. Thecal plates are smooth and flat. The proximal parts of the basals are slightly convex, the transverse section in this part of the cup is pentalobate. The plates are rather thick. The most striking resemblance with the holotype of *O. elongatus* is the very high circlet of the basals. BB are twice as high as wide. The most striking difference however, is the four-sided IBr1 and the very wide IAx and fixed IIBrr1, the latter almost in contact with each other. The sutures between IBr1 and IAx, IAx and IIBrr1 suggest a ligamentary articulation of symplectic type. This feature could not be observed in the holotype. The interradial areas are reduced, such in connection with the forementioned structure of the radial series. Interradii consist of only two or three plates. The most distal iR is but very small.

This cup, further, is very interesting with regard to our knowledge of the genus *Orthocrinus*. It is the first theca in which parts of the tegmen are preserved. Ambulacral parts of the tegmen have been broken off. In the depressed interambulacral areas traces of tegmen plates still occur. The total height of the tegmen is 6 mm. The posterior side of this specimen is very wide. The anal plate is rather small, but half the size of the RR. It is succeeded by three hexagonal plates, the central one somewhat smaller than the lateral ones. Five plates occur in the third range. Beyond this range the plates rapidly become smaller and grade into very small tegmen plates. A larger spiny plate occurs at the top of the tegmen. The very small anus is situated at about half the height if the tegmen. The tegmen most probably is entirely composed of minute elements. The ambulacral areas must have been rather highly arched over the food grooves. Remnants of plates which appear to be situated under the tegmen plates occur at the inside of the IIBrr1. The proper tegmen was spread as a mantle over these plates. It is deeply depressed in the very narrow interambulacral areas.

*Orthocrinus* spec. (nov.?)

Pl. III, fig. 1

The only known specimen of this type of *Orthocrinus* is in the collection of the Museo del Instituto geológico y minero de España at Madrid. It is the specimen no. 96 D from Lower Emsian deposits at Colle near Sabero, province of León. The specimen is described and figured here mainly for stratigraphical value. It is the oldest known *Orthocrinus* specimen.

*Description.* Infrabasal and basal circlets distinctly flare outward but the upper walls of the cup are situated vertical. The distal parts of the interradial areas are slightly depressed. The radial series are only very less conspicuous.

The cup is composed of flat plates. IBB and BB no thicker than half a millimeter; RR and distal cup plates 1 mm thick. The sutures are not depressed. Ornamentation of the cup plates can not be found due to the weathered surfaces. The r.post. side of the cup is crushed. The cup has its largest diameter at the level of RR, but does not widen distad. The height of the cup is 16 mm, the diameter at the level of RR is 12.5 mm.

*Base.* The infrabasal circlet is composed of five pentagonal plates, all alike. The height of an IBB is no more than 3 mm, the thickness 0.5 mm. The basal circlet is composed of hexagonal plates, higher than wide, 6.3 by 5.3 mm and 1 mm thick. The sides of the basals diverge a little. Posterior basal is heptagonal. The total height of the basal circlets is 8 mm or half the height of the dorsal cup.

*Radial series.* Radials are seven-sided plates much wider than high, 6.9 by 4.6 mm. L.post. R is hexagonal; r.post. R is absent. The first primibrachs are very low rectangular plates, in lateral contact with iR1 only. The height is 2.1 mm, the width 3.8 mm. The second primibrach is axillary, very low and wide, height 2 mm, width 4.8 mm. In most rays IAx is heptagonal (in one case probably pentagonal) in lateral contact with iR1 and iRR of the second range. The first secundibrach is incorporated in the cup, it has a suture with the second range interradials. The total height of the radials and fixed brachials is 9 mm, more or less equal to the height of the basal circlets.

In normal interradia iR1 is a fairly high plate, height 3.4 mm, width but 2.1 mm. The plate is situated vertically. It is in lateral contact with IBrr1 and the IAxx. It is succeeded by two iRR only. These plates are no higher than 1.2 mm. The distal interradials distinctly curve inward, but they remain in contact with the proximal sides of the IIBrr1.

*Arms* ten, simple, composed of a series of disc-like brachials. The arms are free from IIBrr1. The pinnules are not preserved. The brachials are 1 mm high and 2.5 mm wide. The dorsal side is gently rounded. The ligamentary articulation of the brachials is of symplectic type. Dentate sutures occur between IAxx and IIBrr1 and higher up between the free brachials. This type of suture could not be observed between IAx and IBr1. In some places on the dorsal sides of the arms occur nodes or tubercles. The nodose brachials are somewhat thicker than other brachials.

The tegmen is not exposed.

The stem is not preserved, but the place of its attachment is fairly wide, so that it might be expected that this species had an unusually stout stem.

*Remarks.* The Lower Emsian species of *Orthocrinus* resembles in certain respects *O. simplex*. Form and dimensions of the dorsal cup are about equal. It is particularly noteworthy that both species have nodose or spiny brachials. Some

difference is found in the ornamentation. The fine granulations on the cup plates of *O. simplex* almost certainly does not occur in the Spanish species. A rigorous comparison with *O. simplex* is rather difficult since the latter is badly figured. It is impossible to check whether Jaekel's figure of the holotype (1895, p. 31, fig. 6) is exactly drawn, since it is not known where it is at present stored (Schmidt, 1941, p. 195). The only known photograph is from the fragment figured by Schmidt (1941, pl. 21, fig. 7) and designated by him as the lectotype. The *Orthocrinus* specimen figured by Zeiller & Wirtgen (1855, pl. 7, fig. 1) as *Poteriocrinus rhenanus* is very fragmentary. For all these reasons it is hardly possible to get the correct conception of the composition of the cup and what might be the individual variation in shape and proportions. It remains uncertain whether the present specimen has to be referred to *Orthocrinus simplex* or not.

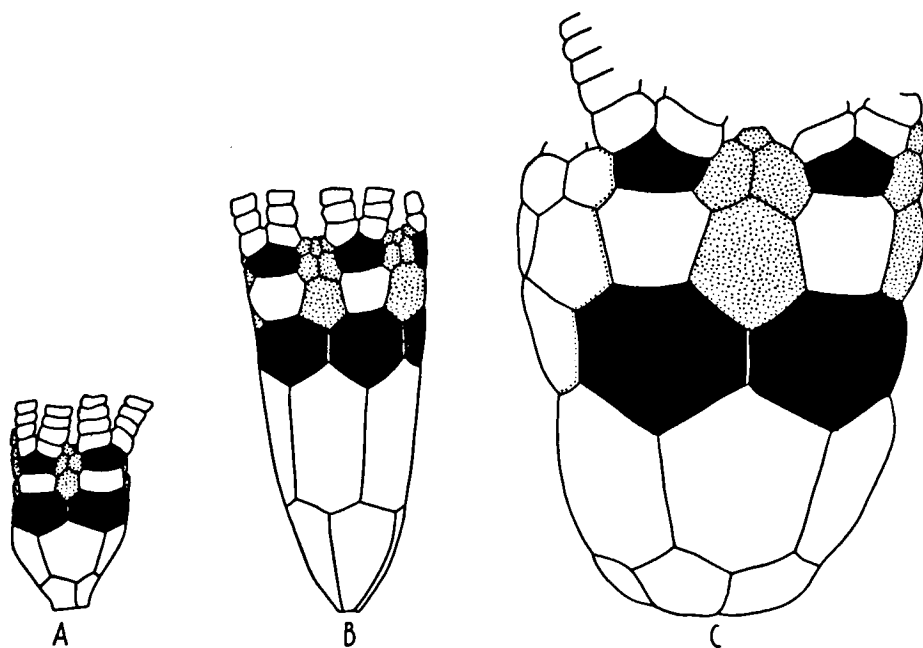


Fig. 2. Relative proportions and forms of dorsal cups in some *Orthocrinus* species. (A) *Orthocrinus* spec., from the La Vid formation, Colle, León (coll. Mus. Inst. Geol., Madrid, no. 96 D). (B) Holotype of *Orthocrinus elongatus*, from the Santa Lucia formation, Grandoso, León (coll. Mus. Geol. Min., Leiden, no. 97503). (C) Holotype of *Orthocrinus robustus* from the Santa Lucia formation, Santa Lucia, León (coll. Mus. Nacional Ciencias Nat., Madrid).

#### Comparison of species (see textfig. 2).

(1) Form and dimensions. *O. robustus* is far the largest species among Orthocrini known at the present day. The specimen described as *O. spec.* is the smallest one. In general Spanish Orthocrini are larger than the German representatives. Inflated dorsal cups occur in *O. robustus* as well as in *O. tuberculatus*. *O. spec.* and *O. simplex* have cylindrical cup walls, whereas *O. elongatus* stands a part in having the cup wall somewhat flaring outward.

(2) Ornamentation. No trace of ornamentation has been found among



Spanish Orthocrini. *O. elongatus* is smooth, but in *O. robustus* and *O. spec.* ornamentation may be lacking only due to weathering of the cup plates. The German species *O. simlex* and *O. tuberculatus* differ from the Spanish species by a granular resp. tubercular ornamentation.

(3) Height of the base in relation to the height of the cup. In *O. robustus* the basal circlets are very low, occupying only one third of the total height of the dorsal cup. In *O. elongatus* on the contrary, the basal circlets are extremely high, even attaining two thirds of the total height of the dorsal cup. In *O. spec.* the basal circlets are about half as high as the dorsal cup. It is notable that in this character *O. robustus* and *O. elongatus* stand apart from the German species.

(4) Interradial areas. Another obvious difference between the Spanish and German Orthocrini is the composition of the interradii. In the latter the interradii are more reduced and consequently the first interradii either as a whole or partly is curved inward to the tegmen. In Spanish Orthocrini on the contrary the larger parts of the well developed interradii areas (including the whole iR1) are situated vertically and only the most distal range of interradii plates is curved inward.

Order MONOBATHRIDA Moore & Laudon 1943  
Family PERIECHOCRINIDAE Bronn 1849 <sup>1)</sup>  
Genus PRADOCRINUS De Verneuil 1850

M. de Verneuil, 1850, p. 184; K. A. von Zittel, 1880, p. 369 (synonym of *Saccocrinus*); Ch. Wachsmuth & Fr. Springer, 1881, p. 409 (synonym of *Periechocrinus*); Ch. Barrois, 1882, p. 223; L. Mallada, 1885, p. 38; L. Mallada, 1891, p. 80; Ch. Wachsmuth & Fr. Springer, 1879, p. 521 (subgenus of *Periechocrinus* ?); L. Mallada, 1898, pp. 12, 16, 21, 37; F. A. Bather, 1900 (in Ray Lankaster), p. 168 (synonym of *Periechocrinus*); O. Jaekel, 1921, p. 35; G. Astre, 1925, p. 215 (synonym of *Periechocrinus*); R. S. Bassler & M. W. Moodey, 1943, p. 651 (synonym of *Periechocrinus*); R. C. Moore & L. R. Laudon, 1943, p. 92 (synonym of *Periechocrinus*); B. Melendez, 1947, p. 301; J. Wright, 1955, p. 193 (subgenus of *Periechocrinus* ?).

*Genotype* by monotypy: *Pradocrinus Baylii* De Verneuil, 1850

*Remarks.* *Pradocrinus* usually was considered a synonym of *Periechocrinus*. Only Barrois, Mallada, Jaekel and Melendez believed that *Pradocrinus* was an independent genus. Now some new facts in support to the last mentioned opinion have been found.

First the tegmen of *Pradocrinus* (cf. Pl. III, fig. 8), which was not figured before, is composed of rather large elements forming a competent structure. At the top is a central nodose plate. The anus passes directly through the tegmen. The tegmen of *Periechocrinus* on the contrary is composed of a great many of very small elements and the anus opens through a very stout anal tube.

The composition of the rays and the bifurcation of the rays in the dorsal cup, differs considerably in both genera. Some very fine preserved specimens of *Periechocrinus costatus* from Dudley could be studied in the Ecôle des Mines at Paris. It was shown that brachials up to at least IIIAxx are incorporated, even IVAx may be in contact with the cup. As a consequence about ten iIBrr and one iIIIBr are incorporated in the cup. The free arms are relatively slender. *Pradocrinus* never incorporates more than two IIBrr. The very stout arms are free from IIBrr3 and immediately become densely biserial.

For these reasons *Pradocrinus* is held as a separate genus in the family Periechocrinidae.

*Diagnosis.* A genus of the family Periechocrinidae characterized by a very high, urn-shaped calyx, composed of very thin, slightly convex plates with radial ornamentation; rays marked by a fine rib, passing on the free arms; two fixed primibrachs, first one hexagonal, second one axillary and heptagonal; incorporation of two secundibrachs per half-ray; non-depressed interradii, composed of seven to nine plates, merging with the tegmen; posterior interradius with median series

<sup>1)</sup> Ramsbottom (Ann. Mag. Nat. Hist., Ser. 12, vol. vii, p. 687, 1954) mentions that Bather (1899) is to be regarded as the author of the family name Periechocrinidae. Prof. Dr. G. Ubaghs drew my attention to the possibility that Bronn could have used this name earlier. In fact Bronn (Index Palaeontologicus, Enumerator p. 179, 1849) used the family name Periechocrinidae for grouping *Periechocrinus* Aust. and *Sagenocrinus* Aust. Bronn (1849) is previously held as the author of the family name Periechocrinidae.

of plates, forming a rib where it passes into the tegmen; very low tegmen, composed of rather large plates, with a central nodose plate; anus directly opening through the tegmen; ten stout densely biserial arms. Stem unknown.

*Distribution.* The genus only occurs in Lower Emsian strata of the provinces of León and Asturias.

*Pradocrinus Baylii* De Verneuil 1850

Pl. III, fig. 2—9

*Holotype.* The larger specimen figured by De Verneuil (1850, Pl. IV, fig. 11a, 11b) is to be regarded as the holotype of this species. The specimen is stored in the Verneuil collection of the *École Nationale supérieure des Mines* at Paris.

*Locus typicus.* The northern slope of the hill on which the church of the village Colle (near Sabero, prov. of León) is built.

*Stratum typicum.* Red detrital limestone band at the top of the La Vid formation, corresponding to the Lower Emsian.

*Diagnosis.* As unique species of *Pradocrinus* its diagnosis is provisionally the same as the genus diagnosis.

*Material.* (1) Museo del Instituto geológico y minero de España, Madrid: 12 specimens from the type locality at Colle (León), 1 specimen from unidentified Devonian of Fenolleda (Asturias), 1 specimen from unidentified Devonian of Moniello (Asturias), 1 specimen from Emsian strata of La Vid (León), 1 specimen of Lower Devonian strata of Orzonaga (León), 4 specimens of unknown provenance. (2) d'Orbigny collection of the *Museum d'Histoire Naturelle*, Paris: specimen 423 from Devonian of Spain, without further indication of age and locality. (3) Verneuil collection of the *École Nationale supérieure des Mines*, Paris: 2 specimens from the type locality at Colle. (4) Barrois collection of the *Institut de Géologie*, Lille, France: 2 specimens from the Lower Devonian of Santa Maria del Mar (Asturias). (5) British Museum (Natural History), London: specimens E 5514, E 5515, E 5518, E 5519 and E 50591 from Devonian of Las Navas. (6) *Naturhistoriska Riksmuseet*, Paleozool. Avd., Stockholm: specimen Ec. 19465 from the type locality at Colle. (7) *Rijksmuseum van Geologie en Mineralogie*, Leiden, Holland: 6 specimens no. 97510—97515 from the type locality at Colle, many fragments and isolated plates from the type locality under no. 97516, 2 specimens no. 97517 and 97518 from Lower Emsian deposits at Villayandre (León).

*Supplementary description.* Large specimens of *Pradocrinus Baylii* attain a height of 80 mm and a width of 40 mm. The greatest width frequently is at arm level, sometimes lower. Cups are high urn-shaped with a very low tegmen. The cup plates are very thin, thickness for mature specimen plates is no more than 1.5 mm. All plates are slightly curved both at inner and outer surfaces. The complex nature of ornamentation of the plates is best observed from Pl. III, fig. 9.

The high basal and radial circlets are very typical in this species. Basals are about 10 mm high and radials even 20 mm. RR always occupy thirty percent of the total height of the cup. No other cup plates are so large as the radials. Rays are not conspicuous. They are only marked by a fine rib, passing on each half ray. The rays typically have only two primibrachs. The only known exception is the r.post. ray with three primibrachs in the specimen 107 D from Colle. The

sutures between IBr1 and IAx always are very short. Only two secundibrachs per halfray are incorporated in the cup. The very stout arms are free and densely biserial immediately above the level of IIBrr2. The diameter of the base of the arms is 7.5—9.5 mm. Interradii are not depressed and composed of seven to nine plates, arranged in two series. Supplementary plates may occur. The posterior interradius is greatly differentiated. It is composed of 25—30 elements. The median series of plates is not conspicuous. It forms a rib where it passes on to the tegmen. The tegmen (Pl. 3, fig. 8) is composed of rather large elements, all about equal in size, 3—4 mm for mature specimens. The interambulacral parts are somewhat depressed. The top plate of the tegmen is provided with a node or spine. Further marks of ornamentation of tegmen plates seem to be absent. The anus is very small and situated high up in the tegmen.

Table I

	TB 55	TB 80	97512	TB 81	97511	97510	TB 82	104 D	423	107 D
Total height of theca	9.4	15.7	19.3	26.3	34.0	42.7	51.6	61.7	72.0	79.3
Width of theca	8.6	10.3	11.8	16.6	20.5	23.4	30.4	27.5	41.0	43.4
Height dorsal cup	6.2	11.6	14.3	20.5	25.3	29.7	40.7	51.0	51.0	65.1
Height tegmen	3.2	4.1	5.0	5.8	8.7	13.0	10.9	10.7	21.0	14.2
Height cup/height tegmen	1.90	2.83	2.86	3.53	2.91	2.28	3.73	4.79	2.43	4.60
Height cup/width cup	0.72	1.12	1.21	1.24	1.23	1.27	1.33	1.85	1.24	1.28

*Ontogeny.* Specimens of all different proportions are present among the examined material. A beautiful series from smaller to larger forms is presented by the specimens as arranged in table I. Some of these specimens have been figured on Pl. III fig. 2—7. It is assumed that the ten specimens of table I represent different growth stages. The total height of the theca is taken as an indicator for their age. The younger specimen TB 55 has a conical dorsal cup with a relatively high tegmen. The difference with the largest specimen 107 D is striking. Mature specimens have extremely high urn-shaped dorsal cups in which the largest width is below arm-level, whereas the tegmens are very low.

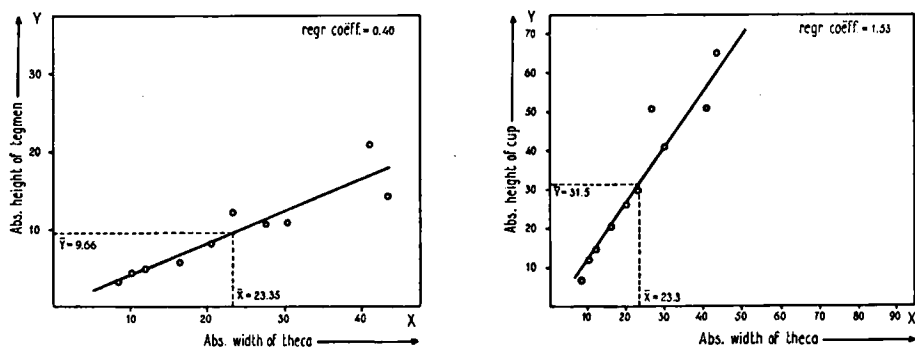


Fig. 3. Diagram showing the relation of height of the tegmen (A) and height of the cup (B) in relation to the absolute width of the theca, in 10 *Pradocrinus* specimens of different growth stages (expl. see text).

In diagram 1 the height of the dorsal cup is plotted against the width of the theca. A rank-correlation test<sup>1)</sup> showed the trend in the heights of the dorsal cup to be significantly positive ( $P = 0,0002$ ). The regression-coefficient of heights of the dorsal cup on the width of the theca is 1.53. This means that the increase of the height of the cup is 1.5 times as fast as the increase of the width of the theca and explains why the form and proportions of the dorsal cup during ontogeny change from conical to urn-shaped.

In diagram 2 the absolute height of the tegmen is plotted against the width of the theca. A rank-correlation test showed the trend in the heights of the tegmen to be significantly positive ( $P = 0,0005$ ). The regression-coefficient of the heights of the tegmen on the width of the theca is 0.40. This means that increase of the height of the tegmen is but 40 percent of the increase of the width. It explains why the tegmen in later growth-stages appears as a relatively low structure in relation to the dorsal cup.

Measurements of the ratio: height of the dorsal cup/width of the theca are given in table I. It may be expected from our first observations that this ratio is not constant. A rank-correlation test showed the trend in this ratio to be significantly positive ( $P = 0,004$ ). It is doubted, however, that the relationship between the height of the dorsal cup and the width of the theca is so simple that it can be expressed in the form of a straight line. Possibly this ratio changed during earlier ontogenetic stages and later remained constant. The relationship of this ratio to total height of the theca than should be expressed by a curved line.

The measurements of the ratio: height of the dorsal cup/height of the tegmen are indicated in table I. It is again expected that the ratio is not constant. A rank-correlation test showed the trend in this ratio to be significantly positive ( $P = 0,060$ ). The individual values of this ratio are somewhat scattered. It is assumed that the correlation between the two factors can in fact be expressed by a straight line.

#### GENUS *LENNEOCRINUS* Jaekel 1921

O. Jaekel, 1921, p. 35; Bassler & Moodey, 1943, p. 535.

*Genotype* by monotypy: *Lenneocrinus cirratus* Jaekel, 1921.

*Remarks.* The genus *Lenneocrinus* was proposed by Jaekel in 1921 without an exact description. All he stated was: "Lenneocrinus n.g., ein kleiner Saccocrinide mit Cirrenwirteln am Stiel, Unterdevon (Fig. 25)." He figured the new species *L. cirratus* from Elberfeld — apparently the only species to be included in the new genus. There can be no doubt that this very short definition validates the genus *Lenneocrinus* under the International Code of Zoological Nomenclature. The only species *Lenneocrinus cirratus* is to be taken as the genotype. Unfortunately a more detailed description of this species cannot be given at the moment since the holotype is not available for study. But the cotypes of the Museum of the Humboldt University at Berlin were kindly put at my disposal by Prof. dr. W. O. Dietrich. It is possible to get a rather good impression of the species from these cotypes. Together with the results of the new species *L. ventanillensis* as described in this paper one is able to define the generic characters for the genus.

*Diagnosis.* A small genus of the family Periechocrinidae, characterized by a conical dorsal cup, composed of thin plates with prominent radial ornamentation; radii

<sup>1)</sup> For the ranking methods applied in this paper the reader is referred to M. G. Kendall, 'Rank correlation methods', 1st ed., (1948, p. 37—42), London, Griffin Cy.

marked with a riblet; two primibrachs, the second seven-sided and axillary; one pair of secundibrachs incorporated, two free arms per radius; interradian areas composed of few elements somewhat depressed in upper portions; biserial arms with long slender pinnules, branching irregularly dichotomous; round stem with wide axial canal composed of nodals of two orders, nodals bear cirri.

*Distribution.* *Lenneocrinus cirratus* was found near Elberfeld (Germany) in Givetian strata, whereas *L. ventanillensis* occurs in the Frasnian of Ventanilla (Palencia, Spain).

#### Remarks on *Lenneocrinus cirratus* Jaekel 1921

1909 *Lenneocrinus Winterfeldi* Jkl, in litt. (nomen nudum) — H. Schmidt, p. 46.

1921 *Lenneocrinus cirratus* n.g., n.sp. — Jaekel, p. 35.

1943 *Lenneocrinus cirratus* Jaekel — Bassler & Moodey, p. 535.

The trivial name *Winterfeldi* has to be rejected. It was only listed in Schmidt's paper. A definite indication, definition or description is absent. So this name can have no status of availability under the rules of the I. C. Z. N. *Lenneocrinus cirratus* as proposed by Jaekel becomes the valid name for the species.

*Holotype.* As a holotype of this species must be regarded the specimen figured by Jaekel. The author was informed that the specimen is actually in Berlin. It is not available for study.

*Locus typicus.* Elberfeld (Germany).

*Stratum typicum.* Jaekel mentioned as such „Untere Coblenzstufe". Mrs. Sieverts Doreck kindly informed me, however, that the type was found in Middle Givetian Honsler Schichten. This was confirmed by the labels of the cotypes.

*Material.* The following cotypes or casts of cotypes could be studied. (1) a gutapercha cast of a specimen with arms in the collection Heinersdorf, coming from Elberfeld, (2) another gutapercha cast of a specimen from Elberfeld in the collection Heinersdorf, showing stem and parts of the calyx and the arms, (3) four gutapercha casts of specimens in the collection Winterfeld, showing parts of stem and calyx, (4) the "1898-specimen" of the collection Winterfeld coming from Elberfeld. The specimen is at present in Berlin.

A definite description or an adequate diagnosis for this species cannot be given. Only those characters in which it differs from its Spanish relative can be mentioned at the moment. First its stem is composed of nodals of two orders separated by numerous internodals, all alike. Both nodals of first and second order bear cirri. Probably six cirri were attached to the nodal. In *L. ventanillensis* nodals of only one order can be found to which four cirri were fixed. The number of internodals may be greater. Next the base of *L. cirratus* is higher as in *L. ventanillensis*, the basals are provided with a sharp outstanding tripartite rim, that is absent in *L. ventanillensis*. The ornamentation of the cupplates in *L. cirratus* is more simple. The arms bifurcate only three times, in a more regular, bilaterally heterotomous mode as in *L. ventanillensis*. The German species is even smaller than its Spanish relative.

#### *Lenneocrinus ventanillensis* Breimer spec. nov.

Pl. II, fig. 1, 2; Pl. III, fig. 11 and 13

*Holotype.* The specimens figured in Pl. II of this paper. It is stored under no's 97507 and 97508 (part and counterpart) in the Rijksmuseum van Geologie

en Mineralogie at Leiden (Holland). A small part of the specimen at the edge of the slab has been removed in order to study the posterior side. This part has no. 97509.

*Locus typicus.* The specimen was found about 1 km SW from the village Ventanilla, near Cervera de Pisuerga, prov. Palencia, Spain.

*Stratum typicum.* The khaki-coloured shales of the Frasnian.

*Diagnosis.* A *Lenneocrinus* species characterized by a stem composed of nodals of one order to which only four cirri were attached, internodals not all alike; basals provided with a concentric rib; very short sutures between primibrachs; complex ornamentation of upper part of interrarial areas: a gently curved rib between primaxils, radial ornamentation of plates may be replaced by series of papillae; four or five times bifurcating arms.

*Material.* The types are the only specimens of this species hitherto found in the Frasnian of the province of Palencia.

*Description.* Form and dimensions.

Height of dorsal cup	15 mm
Width " " "	ca. 12 mm
Diameter of the stem	3 mm
Diameter of the arms	2 mm (measured at the base)
Length " " "	ca. 50 mm
Length of pinnulae	10—15 mm

Although both cups are crushed it is evident that during life it must have had a conical shape. The radial series are marked with a rib that starts on the radials, divides on the primaxils to lead to the free arms. The upper parts of the interradians are slightly depressed. So the cup must have been somewhat lobate at its ventral edge.

The stem is cylindrical and pierced by a wide and round axial canal. The composition of the stem fragment figured in Pl. II, fig. 2 (lower right part) is: 13—14 thin internodals — a thick nodal, provided with facets for the attachment of the cirri — 22 thin internodals — a thick nodal — 17 thin internodals — a thick nodal. The thicker nodals are about 2 mm high, probably no more than four cirri were inserted on them. One nodal has been observed that is probably compound since a doubtful suture between two facets for the cirri has been found. The internodals are 0.2—0.5 mm high. Not all internodals are alike. In some parts of the stem one can distinguish internodals of two orders: thicker plates of 0.5 mm high and surrounded by a thicker rib as is the case in the smaller plates of but 0.2 mm high. The sequence of plates in these parts is: two lower — one higher — two lower internodals, etc. The thicker internodals do not bear cirri. But on the contrary some parts of the stem are composed of nodals separated by internodals which are all alike. The cirri are composed of identical plates, about 1.5 mm high cylindrical structures. The length of the cirri is at least 4 cm.

The base is composed of three equal basals with a perfect hexagonal total outline. The basals are 3.6 mm wide and 2 mm high. The lower parts of the basals are provided with a concentric rib, only broken at the spots of interbasal sutures. The upper parts of the basals are ornamented with short radial riblets.

The radials are large plates 4 mm high and wide, in lateral contact

except at posterior side where A is placed in the radial circlet. The radials are alternately seven- and six-sided. The rib marking the radial series starts at the centre of the radials.

**Radial series.** Only two primibrachs are incorporated in the cup (cf. Pl. III, fig. 11) the first six-sided and but slightly smaller than the preceding radial: 3.7 mm high and 3.5 mm wide, the greatest with relatively low in the plate.

The sutures of the first primibrach with R and IAx are remarkably short: less than two mm. The second primibrach is axillary-sevensided, about the same size as preceding first primibrach, 3.8 mm high and 3.2 mm wide, the greatest width being very low in the plate.

After each primaxil a series of two secundibrachs per half ray is incorporated. The IIBrr1 are very high: 3 mm. In the natural mold as shown in no. 97508 the impressions of the second IIBrr are observed. Beyond these plates arms are free so that only two radii occur to each ray. A small group of three miniscule intersecundibrachs is placed between the IIBrr2; the first plate rests on the upper facets of IIBrr1.

A complete interradial area could only be examined from the counterpart 97507. This area has only 9 plates. The first interradial plate is far the larger plate, six-sided, 3.3 mm high and 3 mm wide. It is succeeded by two series of plates. Between these two series a pair of small fivesided plates is intercalated.

The posterior interradius, as found in no. 97508 and figured Pl. III, fig. 13, is badly crushed. At the lower left side of the photograph the anal plate can be seen. It is placed in the radial circlet. Three plates certainly succeeded the anal, although these plates are now in abnormal position due to crushing. Many more elements once constituted the posterior region but its composition cannot be studied in detail.

**Ornamentation** of the dorsal cup is rather complicated and can best be seen from the photograph Pl. III, fig. 11. The radial series are marked by a rib. These plates generally have three to four riblets perpendicular to each suture. Interradial plates have essentially the same ornamentation as the radial series, but ribs may be replaced by series of papillae. A gently curved riblet passes between primaxils. It is somewhat more conspicuous as other ribs of the plates.

The **tegmen** is unknown.

**Free arms** are long and at the level were they become free stout structures. They are biserial directly after becoming free and throughout their lengths. Individual brachials are but 1.5 mm high. The dorsal sides of the arms are rounded. Ventral sides unfortunately are not preserved. The natural mold no. 97508 shows impressions of brachials throughout the length of some arms. The central part of these arms is formed by a rib that apparently represents the mold of the ventral groove of the arms. The biserial arrangement of brachials can easily be found from the impressions on the elongate mold. The transverse section of this mold indicates that the ventral groove was wider and V-shaped. Arms branch four to five times in the free state. The diagrams textfig. 4 give an impression of the mode of branching. The right ramus in fig. 4a shows a strong tendency towards exotomous heterotomy, whereas the left ramus of fig. 4d has perfect endotomous heterotomy in branching. The rami of fig. 4b have a bilateral heterotomous type of branching. Concluding one must state that a fixed mode of branching does not exist in this specimen. It is irregularly dichotomous with strong tendencies towards heterotomy. No ramus showing strictly dichotomous bifurcating has been found.



Pinnulation of the arms is complete and dense. The first pinnules occurred already at the first free brachials. It is unknown whether some pinnules were incorporated. The pinnules are fairly long, each one at least 13 mm long and composed of very elongate pinnulars of 2—3 mm length and a height of no more than 0.5 mm. At least four pinnulars formed a pinnule. Pinnules apparently became shorter towards the distal tips of the free arms. At least

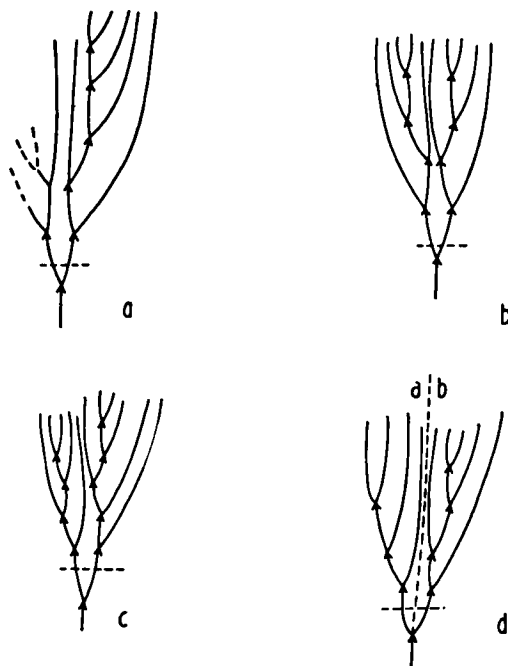


Fig. 4. Diagram showing the mode of bifurcation in different radii of the holotype of *Lenneocrinus ventanillensis*, Frasnian shales of Ventanilla, Palencia (coll. Mus. Geol. Min., Leiden, no. 97507/8).

four pinnulars formed a pinnule. Pinnules apparently became shorter towards the distal tips of the free arms. At these tips the arms were rolled in, as is indicated from the pinnular structure.

*Remarks.* The specimen described above shows striking similarity to the German species of *Lenneocrinus*. Without any doubt it belongs to this genus. The differences with *L. cirratus* were mentioned above, p. 30, when discussing the affinities of that species.

Among periechocrinids *Lenneocrinus* is certainly a peculiar form. Through its very small size and its stem with cirri it stands completely apart among the members of this family. The composition of the cup has many affinities to *Pradocrinus*, *Corocrinus*, *Thamnocrinus* and *Aryballocrinus* from which genera it differs however considerably in armstructure.

## GENUS PYXIDOCRINUS Müller 1855

Müller, 1855, p. 82 (conditional name); Müller, 1857, p. 254; Zittel, 1879, p. 369 (synonym of *Actinocrinus*); Wachsmuth & Springer, 1882, p. 302 (synonym of *Periechocrinus*); Wachsmuth & Springer, 1897, p. 519 (synonym of *Periechocrinus*); Bather, 1900, p. 168 (synonym of *Periechocrinus*); Goldring, 1923, p. 242 (nomen nudum); Bassler & Moodey, 1943, p. 597 (synonym of *Periechocrinites*); Moore & Laudon, 1943, p. 92 (synonym of *Periechocrinites*).

*Genotype* by monotypy: *Actinocrinus prumiensis* Wirtgen & Zeiller, 1855.

*Remarks.* The name *Pyxidocrinus* was introduced conditionally by Müller in Wirtgen & Zeiller's paper on the Devonian crinoids of the Eifel limestones (1855) for the reception of actinocrinids with larger interdistichals. Later, in 1857, he was inclined to believe that his genus was related to *Pradocrinus* as in fact it is. So it is difficult to understand why Zittel still puts the genus *Pyxidocrinus* in synonymy with *Actinocrinus*. Wachsmuth and Springer (1882) apparently were very much in doubt how to classify the genus. At page 302 they listed it as a synonym of *Periechocrinus*, whereas at page 354 they assigned the only species *A. prumiensis* to *Dorycrinus*. The first to doubt the validity of the genus *Pyxidocrinus* was Goldring (op. cit.). She did not see any reason to recognize *Pyxidocrinus* and to quote it as a synonym of *Periechocrinus* as Wachsmuth and Springer did (1897, p. 519). She was convinced that the name *Pyxidocrinus* had to be taken as a nomen nudum, because of the conditional nature of its proposal. All authors after Goldring, however, followed Wachsmuth & Springer's example in quoting *Pyxidocrinus* as a synonym of *Periechocrinus*. But at these times it was not yet fully realised that the type-species of *Periechocrinus* differed in so much a character from such species as *Periechocrinus prumiensis* and *P. Baylii* that they had to be separated from the larger genus as to bring them under different genera. Moreover the forms closely allied to *P. prumiensis* (the Spanish periechocrinids) were not yet described. Since the numerous specimens of Spanish periechocrinids have become available for study it has been evident that Müller's name *Pyxidocrinus* should be used for the reception of the majority of these Spanish crinoids. Since the International Committee for the Zoological Nomenclature accepted the proposal that the name of a taxon of any category, if published conditionally does not lose its status of availability (Decl. 24 ICZN — 24th May, 1956) the name *Pyxidocrinus* has the status of availability. The name was published in connection to a full description with figures of *Actinocrinus prumiensis*. There can be no doubt that the name *Pyxidocrinus* was meant to include *A. prumiensis* since Müller's proposal was given under the heading of *A. prumiensis* (p. 81) and definitely is stated (p. 82): "Diese Art kann auch zur Aufstellung einer Gattung noch benutzt werden, für welche der Name *Pyxidocrinus* Müll. schon in Bereitschaft ist." *Pyxidocrinus* also is a valid genus with *A. prumiensis* as the type species. Art. 21 of the rules of the Int. Com. Zool. Nom. indicates that Müller has to be regarded as the author of the genus because it is clear from Wirtgen and Zeiller's publication that they regarded Müller already as the author.

*Pyxidocrinus* is certainly not a synonym of *Periechocrinus* because it differs considerably from that genus by lack of ridged radial series, by lack of a median ray ridge in posterior interradius, by a fix number of four-rami rays, by a solid tegmen structure and lack of the anal tube. The only genus to which *Pyxidocrinus* has to be compared is *Stamnocrinus*. For this comparison see p. 71. The following species are to be included within the genus *Pyxidocrinus*:

- P. prumiensis* Wirtgen & Zeiller, 1855  
*P. collensis* sp. nov.  
*P. latus* sp. nov.  
*P. San-Migueli* (Astre, 1925)  
*P. ? bifrons* (W. E. Schmidt, 1932)

*Diagnosis.* A genus of the family Periechocrinidae, characterized by a conical dorsal cup, composed of thin, flat plates with gonioporoids at their angles; radii with small pentagonal IAxx, two IIBrr and two IIIBrr incorporated in cup; four arms per radius; relatively small interradian areas with iRR arranged in two series; few iBrr (up to 3); a relatively low tegmen, composed of irregularly arranged plates, with central nodose plate; four spiny plates, interambulacral in position may occur around central tegmen plate; anus directly in tegmen; stem unknown; arms not certainly known.

*Distribution.* The genus *Pyxidocrinus* occurs mostly in Spanish Lower Devonian strata: *P. collensis* from the Lower Emsian of León, where it occurs frequently in the uppermost limestone band of the La Vid formation; in some rare cases it is known from Asturias as well. *P. latus* is known from Lower Emsian deposits of Asturias and León. *P. San-Migueli* was found in undetermined Devonian strata near Burgos. *P. prumiensis* seems to be the only younger representative of the genus in Middle Devonian Strata of the Eifel (Germany). *P. ? bifrons* is certainly younger (M. Dev.), but its systematic position is not yet satisfactorily established.

*Pyxidocrinus prumiensis* Wirtgen & Zeiller 1855

- 1855 *Pyxidocrinus prumiensis* Wirtgen & Zeiller — Wirtgen & Zeiller, p. 81, 82, pl. 11, fig. 1—5  
 1867 *Actinocrinus prumiensis* Müller — Schultze, p. 172, pl. 6, fig. 6 (non 6 d—6 g)  
 1882 *Dorycrinus prumiensis* Müller — Wachsmuth & Springer, p. 354  
 1897 *Aorocrinus prumiensis* Müller — Wachsmuth & Springer, p. 470  
 1923 *Actinocrinus prumiensis* Wirtgen & Zeiler — Goldring, p. 242  
 1943 *Periechocrinus? prumiensis* (Zeiller & Wirtgen (nom. van.) — Bassler & Moodey, p. 600

*Holotype.* The specimen described and figured by Wirtgen & Zeiller. It is actually in Berlin.

*Locus typicus:* Near Prüm in the Eifel (Germany).

*Stratum typicum:* The exact level is not determined. But it is supposed that the species comes from Middle Devonian limestones.

*Diagnosis.* A small species of *Pyxidocrinus* characterised by a tegmen composed of few relatively large plates; central tegmen plate nodose and at anterior side surrounded by four larger plates.

*Distribution.* The species was first found by Mr. Kroeffges near Prüm in Eifel limestones. Later Schultze reported it to come from Ahütte and Kerpen as well. The specimens he mentioned to come from Gerolstein and figured in his plate VI, fig. 6d—6g are believed to be not conspecific with *P. prumiensis*. They have only two arms to the ray and have tegmens with high spines. *P. prumiensis* has never been found in Spain.

*Pyxidocrinus collensis* Breimer sp. nov.

Pl. VI, fig. 1—8

*Holotype.* The specimen 97539 in the collection of the Rijksmuseum van Geologie en Mineralogie at Leiden (Holland).

*Locus typicus.* The northern slope of the hill on which the church of the village Colle (near Sabero, prov. of León) is built.

*Stratum typicum.* The detrital limestone band at the top of the La Vid formation in the Devonian.

*Diagnosis.* A species of the genus *Pyxidocrinus*, characterized by a relatively high tegmen composed of many irregularly arranged plates, with four spines around central nodose plate, all interambulacral in position, anus high up in the tegmen: cup plates lack ornamentation; arms biserial.

*Material.* (1) Rijksmuseum van Geologie en Mineralogie, Leiden, Holland: specimens 97536—97579 from Lower Emsian La Vid shales at Colle (León) and specimens 97580—97586 from Lower Emsian La Vid shales at Villayandre (León). (2) Museo del Instituto geológico y minero de España, Madrid: 76 specimens from Colle (León), 11 specimens from La Vid (León), 5 specimens from Villayandre (León), 3 specimens from Orzonaga (León), 2 specimens from La Velilla (León), 1 specimen from Santa Lucia (León), 1 specimen from Nocado (León), 1 specimen from Fenolleda (Asturias). Although the specimens are labelled 'Devoniense', the writer is inclined to believe that the León specimens all come from the Lower Emsian La Vid formation. (3) Museo Nacional de Ciencias Naturales, Madrid: 1 specimen no. D-H-1074 probably from Colle (León). (4) Instituto de Geología aplicada, Oviedo, Asturias: 3 specimens from Torrestio (León), 4 specimens from San Fenolleda (Asturias). The specimens come from the 'Nivel de Arnao', that probably is to be placed in the Lower Devonian. (5) d'Archiac collection of the Museum d'Histoire Naturelle, Paris: 2 specimens no. 58 labelled as originating from Sabero (León). The specimens are thought to come from Lower Emsian deposits at Colle. (6) Verneuil collection of the École Nationale Supérieure des Mines, Paris: 10 specimens from Sabero. These specimens are believed to come from Lower Emsian deposits at Colle. (7) Sedgwick Museum, Cambridge: 1 specimen from Colle.

The species *Pyxidocrinus collensis* so proved to be abundant in the type level of the detrital limestone band at the top of the La Vid formation in the Devonian sequence of the province of León.

The few specimens from San Fenolleda in Asturias may originate from about the same stratigraphic level, since the crinoid fauna of that place has much in common with the large exposures at Colle: *Trybliocrinus Flatheanus* and *Stamno-crinus intrastigmatus* occur in both places but a detailed study of the brachiopod fauna of San Fenolleda has not been made at the moment, so an exact age determination cannot be given.

#### *Description.* Form and dimensions

	97584	97579	97567	97550	97581	97575	97539
height dorsal cup		11.0	10.1—12.7	14.8—17.6	21.3	19.1—23.2	25
width dorsal cup	11.4	15.4	16.2	26.1	27.3	30.8	32.9
height of tegmen	5.3	7.5	9.7	12.2	14.8	17.7	18.6

The heights of dorsal cups at posterior sides is sometimes lower than at anterior sides. Such specimens are somewhat asymmetrically built as seen in

lateral view. The posterior side is rather steep but anterior side is very much less inclined. Anterior sides even may be not flat but concave in outline. These forms have very wide cups as seen in posterior view. Other specimens — among which the holotype — have regularly conical cups, that are rather narrow elongated forms (see pl. VI). In the first group of species the tegmen is at posterior side somewhat concave and top plate directed somewhat to posterior side.

Among mature specimens of *P. collensis* a variation in the form of the theca can easily be seen. The forms most closely related to the holotype are characterised by high and narrow, strictly conical dorsal cups and regularly conical tegmens. Sides of the dorsal cups are only very slightly convex or concave. In many other specimens, however, it is seen that posterior side is more steep than anterior side, while posterior side is lower than anterior side. Anterior side in such a case can have a more pronounced degree of concavity. The tegmen than is at posterior side somewhat concave, with inclined spiny top plate, directed backwards. These forms generally have wider dorsal cups. But all kind of differences in sides of dorsal cup may occur. Seen from above all specimens have circular outlines. Young forms differ from large specimens in a more lobate upper portion of the cup where arms become free. In connection to it the lower part of the tegmen has more pronounced interambulacral depressions. (cf. Pl. VI, fig. 7). During growth the specimens more and more become inflated. A very peculiar thing is that young specimens (97579 and TB 54) have convex plates and sometimes a distinct radial ornamentation of the cup plates, whereas this has never been noticed in mature forms (cf. Pl. VI, fig. 8) III Brr of the r.post. ray in the holotype show a reticulate ornamentation, but this may be due to Polyzoa that were encrusted on it.

The base is hexagonal in outline and is composed of three equal basals. The lower edge of the basals directly forms the stem. The axial canal of the stem was rather wide and slightly trilobate. Each lobe cuts in the central part of the basal. Basals lack ornamentation. A rim such as known from other periechocrinids does not occur.

The five radials are in lateral contact except at posterior side where the anal plate is situated in the radial circlet. The plates are about equal in size: 8.6 mm high and 8.9 mm wide in the holotype; the greatest width high up in the plate. L.post. R, r.post. R and ant. R are hexagonal; r.ant. R and l.ant. r are seven-sided plates. The radial plates are distinctly the largest plates of the dorsal cup.

Radii. The radii are not conspicuous; the plates are flat and lie in one and the same surface as the adjoining interradials. A rib does not occur. Only two primibrachs per radius occur, the second is axillary. IBr1 typically is irregular six-sided, the greatest width high up in the plate. In the holotype they are 5.8 mm high and 8.2 mm wide. The plates thus are smaller than radials. The IAx is a remarkable small plate, only half the size of the IBr1, and even smaller than the succeeding IIBr1. In the holotype they are 3.5—5 mm high and 4.8—5.7 mm wide. Their form is variable. In the left anterior radius of the holotype (cf. Pl. VI, fig. 3) it has parallel lateral sides but in other radii of the same specimen it may be regular pentagonal or even a plate that is wider than high.

In the vast majority of the specimens the rays are straight and regularly built. But in the specimens 97580 and 97581 from Villayandre the radii show aberrant compositions. In specimen 97580 the l.post. radius is straight with six-sided IBr1 and small five-sided IAx. In all other rays the IBr1 is irregular five-sided, always with a long suture, at the upper left side, where it is in contact

with the primaxil. The latter plate, irregular six-sided in form, is not perfectly superposed on the first primibach but situated somewhat to the left. The form is then always six-sided. In the specimen 97581 a similar phenomenon is observed. The anterior radius is straight and regularly built, with five-sided IAx in superposition to the six-sided IBr1. L.ant. IAx and l.post. IAx are situated to the right of the IBrr1 of that rays. This is shown diagrammatically in textfig. 5.

These aberrant shapes of IBrr1 and aberrant positions of IAx have been observed in *Pithocrinus* species as well, but in the latter genus this is rather a rule as an exception.

In the half rays two secundibrachs occur, the second axillary. The first secundibrach is typically six-sided and larger than the primaxil. In the holotype 4 mm high and 5—5.5 mm wide. Secundaxils are typically five-sided wider than high, but may be six-sided if in lateral contact with two interradials. The second axils are smaller than IIBrr1: in the holotype 3.2—3.5 mm high and 4.4—5.6 mm wide. IIAxx are separated by the intervening iIIBr1.

In the specimens 97580 and 97581 with aberrant composition of primibrachs the series of secundibrachs and tertibrachs do not differ in form and composition from similar series in all other specimens.

After each IIAx two series of two tertibrachs occur; these plates are wider than high; in the holotype 2—2.5 mm high and 4—5 mm wide. An iIIIBr never occurs. The outer surfaces of the tertibrachs is rather convex. R radii so become somewhat lobed in this region (cf. Pl. VI, fig. 2 and 4), where the arms become free. The distal facets of IIIBrr2 or 3 are frequently exposed. They always show a deep U-shaped depression, leading to the foodgroove of the arms. In some few cases some brachials of higher order are still attached. They prove that the arms of this species must have been biserially arranged. Arms may have been biserial directly distal from the IIIBr2 or after a pronounced cuneate IIIIBr3.

The group of interbrachial plates is very small. Usually a larger intersecundibrach is only succeeded by one or two very small plates. The iIIBr1 is a very high seven- or eight-sided plate: 3.8—4.2 mm high and about 2.5 mm wide in the holotype. It rests on the upper internal surfaces of the IIBrr1, and is situated between the IIAxx and IIIBrr1. It does not come in contact with IIIIBr2. iIIBr1 is usually succeeded by an other high and narrow plate, that is mostly situated between the IIIBrr2 of different half-rays. It still is in contact with the upper left and right sides of IIIBrr1. In a few cases the iIIBr1 is succeeded by two very narrow plates next to the other; iIIBr1 is then eight-sided. As was mentioned above intertertibrachs do not occur.

The interradial areas are not depressed: the plates are smooth and flat and lie perfectly flat in the same plane as the adjoining radials and brachials. Lateral interradial areas are composed of 9 plates arranged in two series. They gradually narrow towards the tegmen. The smallest upper interradials are in contact with the tegmen plates. The first interradial plate is the larger one, six-sided and situated between the IBrr1 of different rays. In the holotype they are 7.4—8.3 mm high and 5.1—6.3 mm wide. The succeeding interradials are arranged in two series one of them has its plates somewhat higher in the cup as the adjoining one. A very peculiar feature is shown in the holotype. The left series in postero left and antero left interradial areas are situated higher up, whereas in postero right and antero right interradial areas the right series are situated higher up in the cup. Constantly the series with plates higher up in the cup starts with a seven-sided plate, while the lower series starts with a six-sided plate. This pattern is not constant among the specimens of this species. Several specimens

show interradia situated at the left side of the cup with the right series of interradial plates higher up in the cup as the left ones. Sometimes it is seen that the left series starts as the higher, but higher up in the cup the right series takes over. The specimen 97580 and 97581 may have irregularly built interradial areas. The first interradial plates even can be seven-sided if in contact with an abnormal six-sided IAx.

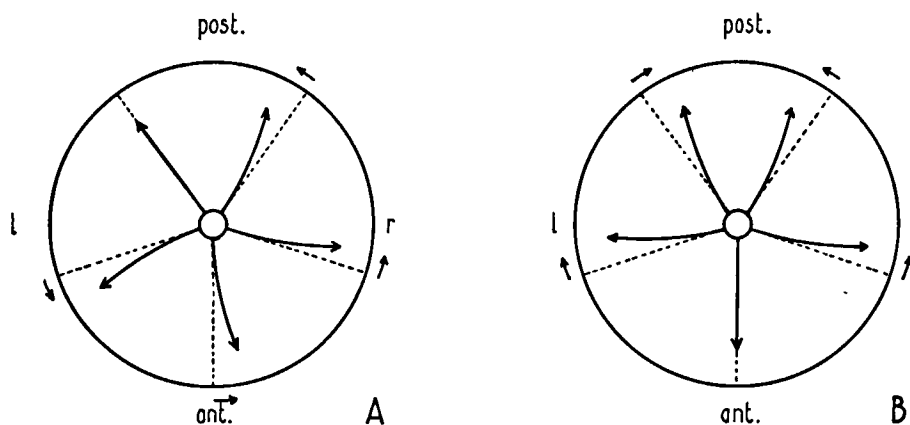


Fig. 5. Diagrams showing the direction of curvature of radii in *Pyxidocrinus collensis*. (A) specimen from the La Vid formation, Colle, León (coll. Mus. Geol. Min., Leiden, no. 97580). (B) *ibid.*, no. 97581.

The posterior interradius is much differentiated. The anal plate is situated in the radial circlet and is but slightly smaller than the radials. The plate is seven-sided; in the holotype 7.6 mm high and 7 mm wide; the greatest width high up in the plate. The anal is succeeded by a row of three larger plates. The middle one six-sided with greatest width high up in the plate and situated somewhat higher than the five-sided lateral ones. Another row of three plates succeeds the first. The middle one again six-sided but with greatest width low in the plate, flanked by wide eight-sided plates. These six plates that succeed the anal have heights and widths of 5—6 mm. The third row of plates consists of a central six-sided plate, lateral flanked by two smaller plates. So it is shown that a median series of four six-sided plates in perfect superposition to each other occurs, although this series does not form a rib. Ventrad to the last of these four anal plates the interradials are irregularly arranged small plates that come in contact with the tegmen plates (cf. Pl. VI, fig. 1 and 2).

The posterior interradius is not depressed. Its greatest width — 16 mm for the holotype — is at the level of the adjoining IAxx. Ventrad it narrows gradually. The zone that is in contact with the tegmen has a width of 6 mm in the holotype.

The aberrant specimen no. 97580 possesses a posterior interradius that agrees completely with the description of the posterior interradius in the holotype as described above. But spec. no. 97581 differs in that after two rows of three plates succeeding the anal again only three plates occur, the central one is large six-sided and at lateral sides in contact with the two outer IIBrr1 of l.post. and r.post. rays. The zone of contact with the tegmen plates is very small. This arrangement of anal plates also occurs in many young specimens as well.

Another aberration in the posterior interradius was found in the specimen TB 54 and figured in Pl. VI, fig. 7. A is followed by only two plates in next row. In relation to it the r.post. radius is quite abnormal constructed. R is a very small four-sided plate. Instead of two IBrr, as normally could be expected, three occur: the first very wide, seven-sided and at its lower left side in contact with the anal. It thus occupies the place where normally the third plate of the posterior interradius is situated. The IBr1 is succeeded by a six-sided IBr2 and IAxx.

**Articulation.** Many sutures, mostly between IIIBrr and IIBrr and even between IIBr1 and IAxx, are dentate; each riblet of a distal facet occupying the space between two riblets in the corresponding proximal facet. In some cases the facets are exposed. It is shown that these surfaces at the external borders are provided with an vermiculate ornamentation. To the centre of the facet this ornamentation becomes very much less pronounced.

**Tegmen.** The tegmen of this species is unusually high for a *Pyxidocrinus*. Its form is conical with a slight lobation in the lower part, where interambulacral regions are somewhat depressed. It is composed of many irregularly arranged smaller plates, with convex outer surfaces. The top plate of the tegmen is a somewhat larger plate, provided with a node. Directly around this plate is a circle of tegmen plates. Beyond this circle four larger plates interambulacral in position occur. That they bore spines is proved by the small specimen TB 54 (cf. Pl. VI, fig. 8). At the posterior side such a spiny plate is lacking, because an arm is situated exactly at the place where a spine would be expected. Weathered surfaces of miniscule plates, immediately surrounding the anus suggest that a very small protuberance may have been present here.

**Gonioporoïds.** Weathered specimens of this species always show pores at the angles of all cup and tegmen plates, but unweathered specimens show no trace of such pores. These pores in fact did not reach the outer surface of the skeleton. This is perfectly shown in the broken specimen 97555 from Colle. The specimen is not deeply weathered. Many fine facets of cup plates can be studied. All these surfaces show very fine vermiculate ornamentation. At all angles of the plates a deep pore filled with sediment can be observed. None of these pores reaches the outer surface of the skeleton. A part of the natural mold proves that pores must have intruded in the cupplates parallel to the outer surface of the skeleton as well. It is believed here that these structures are identical with those described by Schmidt (1932, p. 22 and 23) from *Stamnocrinus intrastigmatus* as gonioporoïds.

*Pyxidocrinus latus* Breimer sp. nov.

Pl. VI, fig. 9—14

**Holotype.** The specimen TB 58 in the collection of the Museo del Instituto geológico y minero de España at Madrid.

**Locus typicus.** The northern slope of the hill on which the church of the village Colle (near Sabéro, prov. of León) is built.

**Stratum typicum.** The exact level of provenance of the holotype cannot be determined. The specimen was labelled without such an indication. The writer is inclined to believe that it originates from the top of the La Vid formation (Lower Emsian) where almost all specimens from Colle were found.

**Diagnosis.** A species of the genus *Pyxidocrinus*, characterised by a dorsal cup



that is very wide in lateral direction, but narrow in antero-posterior direction; posterior side very steep to nearly horizontal, anterior side inclined; ventral part of cup lobate; very low tegmen with pronounced interambulacral depressions and four interambulacral spines surrounding central top plate.

*Material.* (1) Museo del Instituto geológico y minero de España, Madrid: 3 specimens from Colle (near Sabéro), among which the holotype; 1 specimen from Arnao (Asturias). (2) Museo Nacional de Ciencias Naturales, Madrid: 1 specimen from Arnao (Asturias), no. D-H-1071. (3) Instituto de geologica aplicada, Oviedo (Asturias): one specimen of *Pyxidocrinus* from San Fenolleda (Asturias) with very wide dorsal cup. The specimen lacks the tegmen, hence no species determination could be made. Probably it belongs to *P. latus*.

*Description.* Form and dimensions of the holotype.

Total height	29.5 mm
Height dorsal cup	21 mm at posterior side
	24 mm at anterior side
Width „ „	39 mm in lateral direction
	29 mm in antero-posterior direction
Height anal elevation	5 mm
Diameter of the stem	7 mm

The dorsal cup is very wide as seen in frontal view, (cf. Pl. VI, fig. 9) but in lateral view (cf. Pl. VI, fig. 12 and 14) much more flattened. A transverse section always would be elliptical (oval). Posterior side of the cup low and but very little inclined, in its upper part nearly horizontal. The anterior side on the contrary is very much inclined. The upper part of the tegmen is lobate. This is not only caused by the more flared position of the tertibrachs but by the interambulacral depressions of the tegmen as well. These depressions cut deeply between the arm trunks (cf. Pl. VI, fig. 13). The cup is composed of flat plates. Radii are not conspicuous and interradian areas are not depressed. No trace of ornamentation has been observed but ornaments may have been worn away judging by the state of the specimen. The tegmen is extraordinarily low with interambulacral depressions and central elevation with four spiny plates round a central nodose plate. The position of the anus is not certain.

The base is composed of three equal basals that form together a hexagonal outline. The height of the basals is 3.2 mm, the width 7.2 mm. The lower edge of the basals directly joins the stem. Evidently the stem must have been round. The axial canal is wide (2.5 mm).

The five radials are in lateral contact, all around except at posterior side where the anal plate is situated in this circle. The plates are about equal in size 5.8—6.1 mm high and 6.9—7.2 mm wide, the greatest width high up in the plate. L.post. R, r.post. R and ant. R are six-sided, l.ant. R and r.ant. R seven-sided. The radial plates are the largest plates of the dorsal cup.

Radii. The radii are not conspicuous. The plates seem to have been flat and lying in the same plane with the adjoining interradian plates. The composition of the fixed brachial plates always is regular. Aberrant positions of plates as described from *Pithocrinus* and *Pyxidocrinus collensis* do not occur in the few specimens that are available for study. Per radius only two primibrachs occur, the second axillary. IBr1 typically is six-sided, the greatest width high up in the plate; the height is 4.7—5.3 mm, the width 5.1—6 mm. These plates are wider than high and smaller than the radials. The primaxils are still smaller

than IBrr1, their form is five-sided, height 3.9—4.1 mm, width 4.8—5.1 mm. The r.post. IAx of the holotype is just six-sided because it is in lateral contact with two iRR of the postero right interradius. In another specimen from Colle it has been observed that IAx may become six- or seven-sided when one or both of the adjoining interradius has a small supplementary plate after the first five large interradial plates.

In the half-rays two secundibrachs occur, the second axillary. The first secundibrach is typically six-sided and slightly larger as the primaxil; height 3—4 mm, width 4.6—5.1 mm. Secundaxils are typically five-sided, wider than high, but may be six-sided if in contact with two adjoining interradials. The secundaxils are about as large as IIBrr1: 3.2—3.6 mm high and 4.2—5 mm wide. IIAxx are separated by the intervening iIBr1.

After each IIAx two series of two tertibrachs occur; these plates are very much wider than high: about 2 mm high and 4 mm wide. An iIIIbR never occurs. The region of the tertibrachs flares outwards more than the lower portion of the radius (cf. Pl. VI, fig. 12, upper right part of the photograph); IIBrr2 may have lost their contact with other cupplates. This phenomenon together with the depressions in the interambulacral parts of the tegmen gives the upper parts of the radii a trunk-like appearance.

No higher brachials as IIBr2 have been found, so it is not known whether the arms were biserial or not.

The group of interbrachial plates is very narrow. The iIBr1 is a high eight-sided plate (4 mm high, 2.2 mm wide) situated between the IIAxx of different half rays and resting on the upper internal sides of IIBrr1. At its upper side it has sutures with the IIBrr1 and the two succeeding iIBrr, that are situated next to the other between IIBr1. These last iIBrr come in contact with tegmen plates, but not with IIBrr2.

The interradial areas are not depressed. They attain their greatest width of 9 mm at the level of IAxx and gradually narrow distad, until it is in contact with tegmen plates. Lateral interradial plates are composed of 9 plates, arranged in two series. The first interradial plate is the larger one 6.1—6.8 mm high and 4.2—6.1 mm wide, six-sided and situated between the IBrr1 of different rays. The succeeding interradial plates are arranged in two series. In the r.post., r.ant. and l.ant. interradius of the holotype the right series is situated somewhat higher than the left series of plates, whereas in the l.post. interradius the left series is the higher one. In one of the other Colle specimens it has been observed that after 5 interradial plates a very small plate is intercalated between the two series. In connection to it the IAxx of adjoining radii are seven- or six-sided.

The posterior interradius is much differentiated. The anal plate is situated in the radial circlet and is as large as the radials. The plate is seven-sided, 6.8 mm high and 6.9 mm wide, the greatest width high up in the plate. The anal is succeeded by a row of three plates, the middle one irregular six-sided, the left one irregular seven-sided, the right one five-sided. The next row of plates again has a central six-sided plate but to the left two smaller plates and to the right one larger plate. The third row of plates has two smaller plates laterally from the six-sided central plates. After some more smaller, irregular plates the interradius merges with the tegmen. The greatest width (15 mm) of the interradial is at the level of the adjoining IAx, distad it narrows rapidly until it has a contact of only 5 mm with the tegmen. The median series of A + 3 six-sided plates is not straight (cf. Pl. VI, fig. 11).

**Tegmen.** The species has a very unusual tegmen for pyxidocrinids. It

is very low at the marginal parts and depressed in the interambulacral parts. The central part of the tegmen has a rounded elevation on which four spiny plates — interambulacral in position — are situated. The top of this elevation is directed backwards. The central plate is pierced by a small canal, either the anus or the canal of a hollow spine (cf. Pl. VI, fig. 13). The posterior part of the tegmen is concave. It cannot be undoubtedly stated that the anus was situated in this part of the tegmen.

The tegmen is composed of many small irregular plates, which are somewhat convex. At the anterior part of the tegmen the plates show a small and round central elevation as if they had nodes or tubercles. Further traces of ornamentation could not be seen due to the weathered state of the specimens.

**Goniopoids.** The frontal part of the holotype shows distinct pores at all angles of the cup plates (cf. Pl. VI, fig. 9). Even the tegmen had such goniopoids: five such pores could be observed round the central plate (cf. P. VI, fig. 13).

*Pyxidocrinus San-Migueli* (Astre 1925)

1925 *Periechocrinus San-Migueli* n. sp. — Astre, 1925a, p. 211, Pl. XIII, fig. 1—4

1925 *Periechocrinus San-Migueli* n. sp. — Astre, 1925b, p. 201, Pl. I, fig. 1—4

1943 *Periechocrinites sanmigueli* (Astre) — Bassler & Moody, p. 600

**Holotype.** The specimen found by Padre Saturio González and described and figured by G. Astre. The specimen is in the Cabinet of Natural History of the Abbey at Santo Domingo de Silos (prov. of Burgos).

**Locus typicus and Stratum typicum.** An exact locality and age cannot be given for this species. Astre mentions in his paper (p. 205, 206) that the specimen was found NW of the village Pinilla de los Baruecos (eastern part of the province of León). Only Cretaceous rocks have outcrop in this region.

**Diagnosis.** A species of the genus *Pyxidocrinus*, characterised by a very fine radial ornamentation of the calyx plates, radial series slightly marked with a rib; tegmen without spiny top plates; anus high up in the tegmen.

**Supplementary remarks at Astre's description.** In general this description has been carefully done. The l.post. radius clearly has two IIIBr instead of one as Astre mentioned. In fact in many regions of IIIBrr no sutures can be observed between what could have been IIIBrr1 and 2 due to the rather polished state in that particular part of the calyx. It is specially noteworthy that the l.ant. radius is the only one in which an iIBr occurs. Ventral from it the IIIBr1 of different half-rays meet again laterally. The left part of the half-ray indeed gives the impression as if only one high IIIBr1 occurs. It must be stated that the composition of interrays observed in this specimen is the same as described above for the holotype of *P. collensis*. Interradials are arranged in two series. In the antero left and postero left interradius the left series of plates is situated somewhat higher up as the right series, whereas in the antero right and postero right interradius the right series are placed higher than the left ones.

The tegmen is composed of many irregular plates. Spiny plates seem to be absent at the top. Perhaps some slightly larger plates at top of interambulacral regions may be interpreted as dome plates or weathered spines. In one ambulacral part of the tegmen a fragment of a spiny plate could be observed.

**Remarks on systematic position.** The present species was placed by Astre in the

genus *Periechocrinus*. At the same occasion he gave some differences, mainly concerning the interbrachial plates and — what is more important — the tegmen structure and composition. In fact a very striking difference exists between the tegmen of the type of *Periechocrinus* and this species. In *Periechocrinus* the tegmen is composed of many minute elements; central is a stout anal tube. Astre did not draw any attention to the difference in arm-structure between his form and the type species of *Periechocrinus*. The principal characters of this species as listed by Astre (1925b, p. 205) clearly show its affinity to other Devonian and Carboniferous periechocrinids, rather than to the Silurian genus *Periechocrinus* itself.

1) The IA<sub>x</sub> is five-sided, instead of seven-sided. Astre compared this character to *Periechocrinus Whitei*, a form from the Mississippian of Iowa, that is made in this paper the genotype of the new genus *Aryballocrinus*. But not only the Carboniferous periechocrinids have five-sided IA<sub>x</sub>. This is strictly typical for genera as *Pyxidocrinus* and *Pithocrinus*. Devonian periechocrinid genera as *Lenneocrinus*, *Pradocrinus* and *Stamnocrinus* on the contrary have seven-sided IA<sub>x</sub>.

2) The small group of iIB<sub>rr</sub> is very similar to those in the Devonian periechocrinid genera *Pithocrinus* and *Pyxidocrinus*. Astre mentions the affinity to *Pithocrinus Waliszewskii*.

3) The restricted number of three plates in the first and second rows succeeding the anal is very typical for Devonian periechocrinids and not for *Periechocrinus* itself.

4) The existence of the last characteristic — the presence of only one III<sub>Br</sub> — is doubted here. In one case two III<sub>Br</sub> were observed, just as is usual for Devonian periechocrinids.

There can be not the slightest doubt that *Periechocrinus San-Migueli* belongs with *Pyxidocrinus collensis* to one and the same genus. Its conical form, the presence of five-sided IA<sub>x</sub> in relation to interradial areas composed of plates arranged in two series; the four arms to the ray and the lack of an anal tube, definitely makes this species a *Pyxidocrinus*.

#### *Pyxidocrinus* ? *bifrons* (W. E. Schmidt 1932)

1932 *Megistocrinus* ? *bifrons* n. sp. — W. E. Schmidt, p. 23, Taf. IV, fig. 8 a—c

1943 *Megistocrinus* ? *bifrons* Schmidt — Bassler & Moodey, p. 550

1945 *Pithocrinus bifrons* (Schmidt) — Kirk, p. 346

*Holotype*. The specimen described and figured by Schmidt is still the only known representative of the species. At the type-locality no further material was found. Unfortunately the holotype has been lost during the second World War.

*Locus typicus*. This was the headland named "El Mugaron" to the north of the village Arnao (Asturias).

*Stratum typicum*. "Calcaire d'Arnao à *Spirifer cultrijugatus*". According to Comte this horizon corresponds to the lower Couvinian.

*Diagnosis*. The species seems to be mainly characterised by the vermiculate ornamentation of the cup plates. The very incomplete and crushed specimen does not allow to make an adequate diagnosis for the species which must wait until new material becomes available for study.

*Stratigraphic distribution.* If this species ever proves to belong in fact to *Pyxidocrinus* it will be the youngest representative of this genus in Spanish Devonian strata. *P. collensis* and *P. latus* are forms from the Lower Devonian.

*Remarks on systematic position.* Schmidt referred his species with doubt to *Megistocrinus*, to which genus it has but little in common. He mentioned the similarity of ornamentation of his species to *Megistocrinus Waliszewskii*, but Kirk proved the latter species to belong to *Pithocrinus*. But we cannot follow Kirk in referring *bifrons* to *Pithocrinus* as well.

In this paper *Pithocrinus intrastigmatus* and *P. bifrons* are excluded from this genus because *Pithocrinus* is here taken in a somewhat restricted sense. This is necessary since *P. intrastigmatus* and typical *Pithocrinus* species have become far better known than in the times of Schmidt and Kirk. *P. bifrons* has not become better known but it is perfectly clear that it is not so closely related to *P. intrastigmatus* as Kirk (1945, p. 346) was inclined to believe. Schmidt's figure 8a evidently shows two things: (1) the IAx is five-sided and (2) the interradius is composed of two series of interradiial plates. In *P. intrastigmatus* this is consequently resp. seven-sided and three series of interradiial plates.

So some doubt arises to what genus *bifrons* must be referred to if it does not belong with *intrastigmatus* in *Stannocrinus*. The characters as mentioned above may be that of *Pithocrinus* s.str. or of *Pyxidocrinus*. True pithocrini generally have convex or tumid cup plates, whereas *Pyxidocrinus* has forms with flat plates, eventually with less pronounced ornamentation. So it is preferred now to bring *P. bifrons* with some doubt under *Pyxidocrinus*, although one cannot be sure of that since so many important diagnostic characteristics are not known.

#### *Comparison of Pyxidocrinus species.*

The dorsal cups of all *Pyxidocrinus* species as described above show striking similarities. They are always conical and composed of flat plates with gonioporoids. Radii are not conspicuous and have typically a small five-sided IAx, two IIBrr and two IIIBrr. Throughout the genus four arms to the ray exist. Interradii are moderate in size, non-depressed. Posterior interradii are wide and with a median series of four six-sided plates that, however, is not conspicuous. Tegmens have the anus laterally. A central nodose plate occurs.

The differences between *Pyxidocrinus* species mainly concern the ornamentation of the cup plates and the form of the tegmen. The type of *P. prumiensis* does not show an ornamentation of the cup plates, but this may be entirely due to the weathered state of the specimen. The specimen from Ahütte as figured by Schultze (1867, pl. VI, fig. 6—6c) has a fine radial ornamentation of the cup plates. In this respect it resembles the Spanish *P. San-Migueli*, but the latter is readily distinguished by its different tegmen. In fact the organisation of the tegmen seems the most diagnostic feature of *P. prumiensis*. Among all *Pyxidocrinus* species it has the fewest amount of tegmen plates and the central nodose plate is flanked by four large orals along its anterior borders. Spines were not observed on the specimen. The spines mentioned by Schultze (p. 173, 1867) only occur on the smaller specimens figured in his Pl. VI, fig. 6g, that are believed not to be conspecific with *P. prumiensis*. The Spanish *Pyxidocrinus* species are readily distinguished. *P. latus* mainly by its wide cup and depressed interambulacral parts of the tegmen. *P. collensis* and *P. San-Migueli* although strikingly similar in general habitat, differ in the ornamentation and lack of spines in *P. San-Migueli*.

## Genus PITHOCRINUS Kirk 1945, emend. Breimer

E. Kirk, 1945, p. 341; G. Ubahgs, 1953, p. 739.

*Genotype* by original designation: *Pithocrinus Cooperi* Kirk, 1945.

*Remarks.* At the present many new specimens of crinoids referable to *Pithocrinus* have been found in Lower Devonian strata of the Spanish province of León. Moreover, paleontological collections in Madrid proved to possess very well preserved specimens of the species *Saccocrinus ? intrastigmatus*, W. E. Schmidt, 1932, a species referred to *Pithocrinus* by Kirk, but up to now insufficiently known. So it was possible to get a much better idea on the truly diagnostic characters of *Pithocrinus*. It appeared that *Pithocrinus intrastigmatus* is a form not so closely related to other typical *Pithocrini* as Kirk was inclined to believe. The differences between this species and the *Pithocrini* will be discussed below (p. 58). The species *Megistocrinus bifrons* W. E. Schmidt, 1932 from Middle Devonian limestones at Arnao is at present still insufficiently known. In fact the fragment is unclassifiable, but it shows more affinity to *Pyxidocrinus* than to *Pithocrinus*. So the genus *Pithocrinus* is taken here in a somewhat restricted sense to cover the species closely corresponding to the genotype in possessing a somewhat irregularly built globose dorsal cup, a variable number of arms and a high tegmen with stout subcentral anal tube.

The species listed below are to be included within this restricted genus *Pithocrinus*:

*P. Cooperi* Kirk, 1945

*P. Waliszewskii* (Oehlert, 1896)

*P. ovatus* sp. nov.

*P. spinosus* sp. nov.

*Pithocrinus intrastigmatus* and *Pithocrinus bifrons* are excluded from this genus and assigned resp. to *Stammocrinus* gen. nov. and *Pyxidocrinus* Müller, 1955.

*Emended diagnosis.* A genus of the family Periechocrinidae, characterised by a wide globose dorsal cup composed of rather thick, convex to tumid or spiny plates, with gonioporoids at their angles; a tripartite base forming a rim; two- to six-rami rays in older species, two- to four-rami rays in younger species; radii may be curved to anterior or posterior sides; relatively small interradiial areas with iRR arranged in two series; few iBrr; a convex to highly elevated tegmen composed of many relatively small plates, some of them bearing subspinous processes; a stout subcentral anal tube; a round stem; arms densely biserial, irregularly branching.

*Distribution.* The genus *Pithocrinus* occurs in Lower and Middle Devonian strata of Spain and in Middle Devonian strata of North America. The species *P. ovatus* and *P. spinosus* are certainly the older species. They come from Upper Emsian deposits of the provinces of León and Asturias. *P. Waliszewskii* was found in Middle Devonian limestones of the province of León. *P. Cooperi* comes from the Middle Devonian Traverse group (Alpena limestone) of Michigan.

*Pithocrinus Cooperi* Kirk 1945

1945 *Pithocrinus Cooperi* new species — Kirk, p. 343, pl. I, fig. 4—7

*Holotype.* The specimen described by Kirk, and figured Pl. I, fig. 4—6 is designated by him as the holotype. It is the specimen no. 111627 in the collection of the U. S. Nat. Museum at Washington.

*Locus typicus.* Michigan Alkali Quarry near Alpena, Michigan.

*Stratum typicum.* Alpena limestone (Traverse Group) — Middle Devonian.

*Remarks on diagnostic characters.* In his original description Kirk did not separate the specific characters of the genotype from those of the genus. Since another two species were discovered and described in detail in this paper the generic affinities of *Pithocrinus* are better understood. It seems logical therefore to separate the real specific characters of *P. Cooperi*. These are in our opinion: globose cups, with largest width at arm levels; 2—4 rami per radius; few interradial plates; wide posterior interradial area; high conical tegmen with large spines.

*Pithocrinus ovatus* Breimer spec. nov.

Pl. IV, fig. 1, 2; Pl. V, fig. 5—11

1882 *Pradocrinus Baylii* De Vern. (pars) — Barrois, p. 223, Pl. VIII, fig. 10.

*Holotype.* The specimen 97737 in the collection of the Rijksmuseum van Geologie en Mineralogie at Leiden, Holland, is designated the holotype.

*Locus typicus.* El Millar, near Pola de Gordon (León).

*Stratum typicum.* The Santa Lucia formation, corresponding to the Upper Emsian.

*Diagnosis.* A *Pithocrinus* species of normal size, characterized by a cup in which the greatest width is below arm level, composed of convex plates with gonioporoids at their angles; typically four-rami radii in which IAx is usually five-sided but may be six- or seven-sided when radii are curved to anterior or posterior sides; interradial areas composed of 9—11 plates; a relatively narrow posterior interradius, in which A is followed by three plates in second and third ranges; a highly arched tegmen without interambulacral depressions; a very stout anal tube; a round stem; stout arms, densely biserial, branching irregularly heterotomous.

*Material.* (1) Verneuil collection of the École Nationale Supérieure des Mines, Paris: 1 specimen from Emsian deposits of Grandoso (León), (2) Museo del Instituto geológico y minero de España, Madrid: 9 specimens no. 78 D, 80 D, TB 37 — TB 42a from Emsian deposits at Grandoso, 1 specimen from Devonian deposits at La Velilla (León), 1 specimen from Devonian deposits at Orzonaga (León), a slab with arms no. 198 D from Las Bodas. (3) Barrois collection of the Institut de Géologie, Lille, France: 3 specimens no. F 1—F 3 from Devonian deposits of San Fenollada (Asturias). (4) Rijksmuseum van Geologie en Mineralogie, Leiden, Holland: 7 specimens no. 97519—97525 from Upper Emsian Santa Lucia limestone at Grandoso (León), 2 slabs with arms no. 97533 and 97534 from Grandoso; the slab 97533 is labelled *P. spec.*, the specimen 97534 is believed to belong to *P. ovatus* and is labelled as such.

So it appears that this species with certainty comes from the Santa Lucia limestone formation in the Devonian of León, where it is not rare. Unfortunately the age of the San Fenollada deposits is not certainly known, but it is believed here, that they may originate from about the same level as at the type locality.

*Description.* Form and dimensions.

	TB 40	F 1	97519	80 D	Paris spec.	Holotype
height of dorsal cup	17	22—26	23—26	28—29	32—31	31—34
width of dorsal cup	23	31	31—35	36—37.5	35.6—38.5	39—41
height of tegmen	9	13	14	23	22	22
diameter anal tube	4.5	7.5	7	—	—	—
diameter stem	—	—	—	—	7.6	—

From the measurements already can be seen that the form of the dorsal cup is somewhat variable. The height of the cup is not always equal if measured at distinct cup sides. In F 1, 80 D and 97519 the posterior sides are lower than anterior sides but in the holotype the left side is higher than the right side. The greatest diameters of the cup in immature specimens are at arm levels and it is seen that they are in antero-posterior as well as in lateral direction the same. But in adult specimens the greatest diameters are at about the levels of IIBr1 and the antero-posterior diameter is somewhat larger. Seen from above the immature specimens show a circular outline, while adult specimens are very slightly oval.

In immature specimens the height of the tegmen is relatively low and more or less conical, but in adult ones its form is more and more arched and higher. The form of the theca during growth can be thought to become more and more inflated, developing at last an egg-shape.

None of the examined specimens shows any trace of ornamentation and the plates apparently were smooth. All specimens however have tumid cup plates.

The base is tripartite. Basals three, equal. In the central part of the base a depression for the reception of the stem occurs. The lower margin of the base is projected so as to form a rim. Basals do not become higher than 2 mm.

Radials five, laterally in contact with each other, except at posterior side, where the anal is situated in the radial circlet. Radials are wider than high ( $7 \times 9$  mm), alternately six- and seven-sided: l.post. R, r.post. R and ant. R six-sided; l.ant. R and r.ant. R seven-sided. The greatest width is about half the height of the plates.

The radial series are not conspicuous. Only two IBrr per ray occur, the second axillary. Regularly the IBr1 is a six-sided plate, somewhat smaller than the radials and wider than high, the greatest width high up in the plate 6.9—7.1 mm high; about 7 mm wide. The primaxil is five-sided in regular rays. The height of the plate 5.0—6.5 mm. The width varies from 7—8 mm. The plate is generally wider than high and is but slightly smaller than the preceding IBr1.

The form of the first primibrach and the primaxil is not always as described above. Frequently it is seen that the primaxil is not quite in superposition to the IBr1 (cf. Pl. V, fig. 8) but situated somewhat left or right from it. In extreme cases IBr1 than is five-sided and the primaxil six- or seven-sided. The oblique position of such primaxils gives the radial series a somewhat curved appearance.

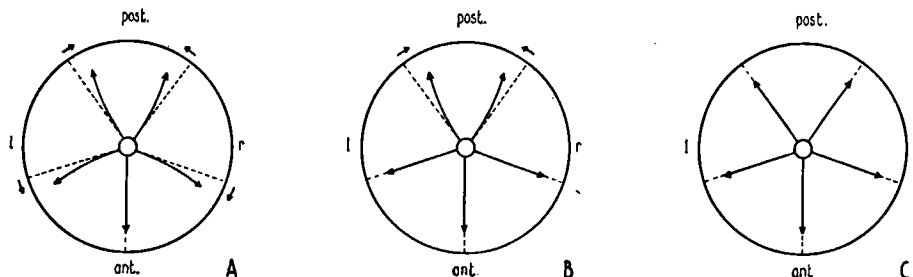


Fig. 6. Diagrams showing the direction of curvature of radii in *Pithocrinus ovatus*. (A) specimen from the Santa Lucia formation, Grandoso, León (École Nat. Sup. des Mines, Paris, Verneuil-coll.) (B) *ibid.* (coll. Mus. Inst. Geol., Madrid, no. 80 D). (C) *ibid.* (coll. Mus. Geol. Min., Leiden, no. 97519).



Textfig. 6 shows the direction of curvature of the rays in some specimens. The specimen 97519 appears to be a 'normal' species with all radii regularly built. Specimen 80 D however, shows the two posterior radii curved concave to the posterior interradius; the other radial series being "normal". The holotype too, has posterior radii curved concave to the posterior interradius, but the left and right anterior radii are curved convex to the anterior side. The anterior radius is the only "normal" radius. It is noteworthy that this species has never been observed to possess an anterior radius of an "abnormal" composition. Further more one gets the impression that the curved radii are placed symmetrically to an antero-posterior vertical plane.

Only two IIBrr per half ray occur, the first hexagonal wider than high, about 5 mm high and 6 mm wide. The second IIBr is axillary and usually hexagonal as well, because it is laterally in contact with two interradial plates. The secundaxil is somewhat smaller than IIBr1, the height is about 4 mm; the width 5 mm.

After each secundaxil two pairs of two IIIBrr are still incorporated in the cup. They are wide and low plates only two mm high. Between the IIIBrr2 is a small IIIIBr. Radii give rise to four free arms. A peculiar thing however is demonstrated in the l.ant. radius of 97519, where six free arms occur. The right half ray is aberrant: IBr1 is axillary. To the left, IIIIBr1 again is axillary, giving rise to two arms and to be right two IIIBrr occur, the second axillary, giving rise to another pair of arms. So the specimen has a total of 22 free arms. Another aberrant number of free arms has been observed in the specimen TB 40, where the anterior radius has only two free arms. The right half ray is developed as usually in this species, but the left half ray is not developed. Secundibrachs may be distinguished there but ventral follow irregular small plates.

The group of interbrachial plates is rather large. Generally five, but sometimes 7 intersecundibrachs occur. The first one is far the larger plate, situated between IIAXx and resting on the internal upper margins of the IIBrr1. The plate is generally six-sided and higher than wide, 4.5 mm high and 3.5 mm wide. It is succeeded by two pairs of very small plates, that merge with tegmen plates.

Interradial areas are not depressed. They occupy rather large parts of the cup. Their greatest widths (about 13 mm) are at the level of IBr1 or 2. Ventrally they narrow rapidly. The contact with the tegmen is but 2 or 3 mm wide. The first interradial plate is the larger one, about the size as radials and IBr1. It is six-sided, 7.5—8 mm high and 6.5—7 mm wide. It rests on two radial facets. The succeeding interradials are arranged in two series. In all 9—11 plates may occur.

The posterior interradial area is much wider than the lateral interradii. A is situated in the radial cirlet, seven-sided and of about the same size as the radials, 7.5 mm high and 8.5 mm wide, the greatest width high up in the plate. The anal is succeeded by a row of three plates, the central one large and six-sided, the greatest width high up in the plate, the lateral ones five- or six-sided, somewhat smaller than the central one. This first row of three plates is succeeded by another row of three plates, the central one may be six-sided (as in F I) but it may be seven- or even eight-sided as in 80 D, (cf. Pl. V, fig. 7). The left plate of this range is eight-sided but may be derived from two different plates firmly grown together. In most specimens only two ranges of three plates succeed the anal, the most ventral part of the interradius is occupied by very

small irregularly arranged plates. The interradius attains its greatest width at the level of the adjoining IAx<sub>x</sub> of different rays, but distad narrows rapidly. The zone of contact is extremely narrow; only 2—3 mm, as in the lateral interradiial areas. A median series of plates does not occur, but it may be seen that A has two six-sided plates in rather neat superposition to it.

**Tegmen.** In the two largest specimens TB 80 and the holotype the tegmen is highly arched and about as high as the dorsal cup. In all other specimens the tegmen is lower. Interambulacral depressions always are absent.

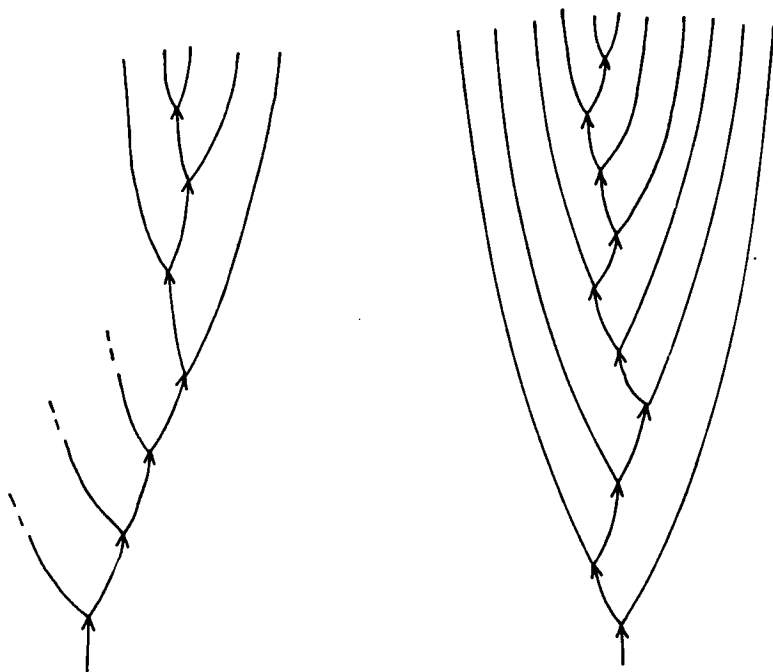


Fig. 7. Diagrams showing the mode of bifurcation of the arms in *Pithocrinus ovatus*. Based on specimens from the Santa Lucia formation, Grandoso, León (coll. Mus. Geol. Mus., Leiden, no's 97533 and 97534).

The tegmen is composed of irregularly arranged plates, 2—3 mm wide. Some of these plates are somewhat larger than others and have nodes or spines, about 25—30 of these spines occur, scattered over the tegmen. The anal tube is very stout and nearly central in position. The isolated tegmen TB 42 has a well preserved anal tube with a diameter of 6 mm. The tube itself lacks nodose or spiny plates (cf. Pl. V, fig. 5 and 6).

**Free arms** (cf. Pl. IV, fig. 1 and 2). At the type locality two slabs with crinoid arms were found together with the cups of *Pithocrinus spinosus* and *P. ovatus*. A third slab with arms was found near Las Bodas in the immediate neighbourhood probably from the same limestone as is exposed at the type-locality. This third slab is in the Museo del Instituto geológico y minero de España (no. 198 D). It is particularly fortunate that at the two first mentioned groups of arms parts of the cups are preserved. The structure of these cup parts justify

the conclusion that they should be attributed to *Pithocrinus*. There is some evidence in support to the opinion that the arms were from *P. ovatus*. The specimen 97534 has rather well preserved cup plates without a central spine, but with a gently convex surface. The last fixed brachials are strikingly similar if not identical to *P. ovatus* and their position proves that the arms came off vertically, as indeed is the fact in that species. No. 97534 therefore has been labelled as *P. ovatus*. Both the other specimens have too much weathered cup plates to allow a specific classification.

Due to the originally vertical position of the proximal parts of the free arms, many such parts are badly crushed. The contact between cup and free arms

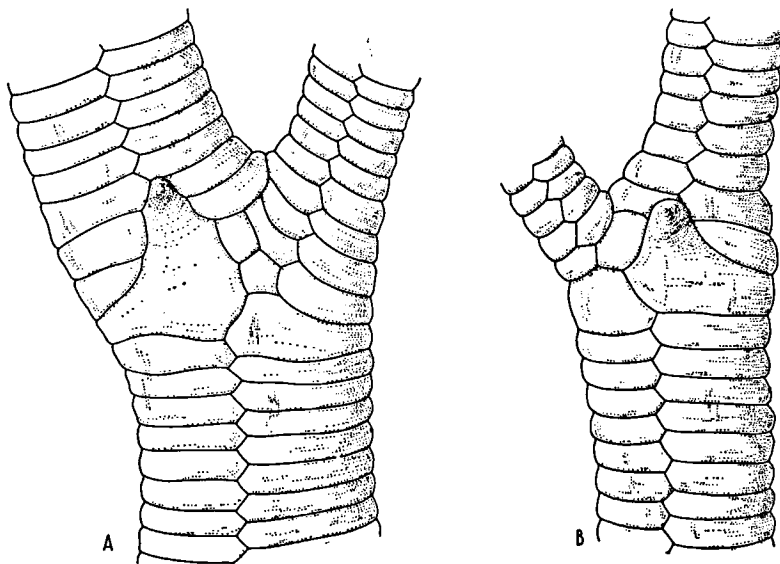


Fig. 8. Diagrams showing the arrangement of brachials at bifurcation of arms in *Pithocrinus ovatus*. (A) Third bifurcation of an arm, smaller arm is given off at the right, spiny plate situated left. Specimen from the Santa Lucia formation, Grandoso, León (coll. Mus. Geol. Min., Leiden, no. 97533). (B) sixth bifurcation of the same arm as (A), smaller arm is given off at the left, spiny plate situated right.

cannot be studied. Moreover in many cases it is impossible to find where the first bifurcation of the arms is.

Free arms have a diameter of at least 4 mm, at their proximal borders and of 1.5 mm at distal ends. The length of the arm is at least 75 mm, but may have been 80 or 90 mm. Arms bifurcate frequently — up to ten times. The way of bifurcation is heterotomous, but apparently a strict rule of branching does not exist. Some arms show a bilaterally heterotomous branching but others a strong tendency towards endotomous heterotomy. The specimen 97533 (Pl. IV, fig. 1) has an arm with seven armlets all coming off at the left side. The specimen 198 D from Las Bodas has an arm with six succeeding armlets coming off at the left side. The heterotomous nature of branching is particularly well indicated by the fact that one of the two branches is thicker than the other one. All thicker parts of the arms apparently form a kind of main arm trunk, as is illustrated by textfig. 7. This is a reconstruction of one of the arms of spec. 97534 showing bilaterally heterotomous branching.

Bifurcation of arms takes place without axillary plates. At the points of bifurcation a small upwards directed spine is situated at that side of the arm that is and will remain the thicker one. Textfig. 8 A shows an enlarged drawing of at least the third bifurcation of an arm of spec. 97533 (Pl. IV, fig. 1, right arm), where at the right side is given off a smaller armlet. The spine is placed at the left side. Textfig. 8 B shows the sixth bifurcation of the same arm. Here the smaller armlet is coming off at the left and the spine is placed at the right side.

Arms are strictly rounded at the back. They are composed of very low biserially arranged brachials. The height of the brachials in the proximal arm part is no higher than 0.4 mm. Isolated brachials show that the arm at its ventral side had a foodgroove with almost semicircular transverse section. The brachials

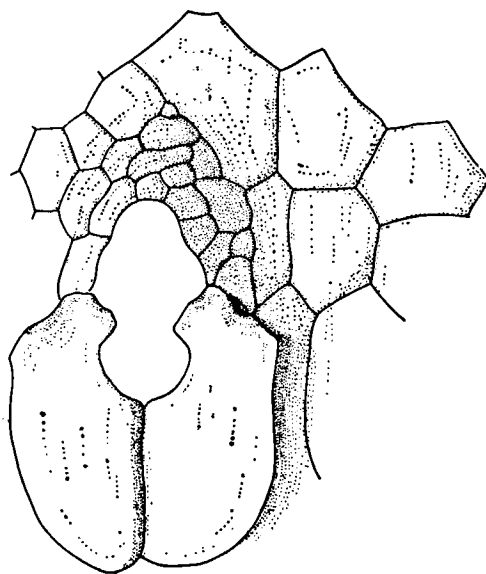


Fig. 9. Diagram showing the distal facets of a pair of brachials, with ventral groove and roofing structure in *Pithocrinus ovatus*. Based on a specimen from the Santa Lucia formation, Grandoso, León (coll. Mus. Geol. Min., Leiden, no. 97534).

are projected at the ventral side into a rim that lined the oral food groove. At external sides of this rim the articulation facets for the insertion of the pinnules were found.

A very peculiar structure was found in the most proximal part of one of the arms of spec. no. 97534, that is still fixed to the cup (cf. textfig. 9). The distal facets of a pair of brachials are exposed with the oral foodgroove and ventral projections. Immediately above these projections a group of very small plates form a highly arched structure, roofing the foodgroove of the arms. These plates are in contact with the larger tegmenplates behind them and apparently rested on the ventral projections of the brachials. This structure raises the question whether the foodgrooves were roofed throughout their length or not. Unfortunately the arms are much too crushed to show any further detail of their ventral sides. The spot figured in textfig. 9 is interesting in another sense as well. It shows distinctly a pore at the outer ventral edge of the right brachial, indicating that

a fixed pinnule occurred. Apparently the pinnule of the left brachial was free and opened directly in the food groove of the arms. The left brachial shows the articulation facet for the insertion of the pinnule. It consists of a rounded shallow depression, that may be interpreted as a ligament pit, and a small riblet that may have had a function in articulation.

**Pinnulation.** As pointed out above, the first pinnule may have been fixed to the dorsal cup, whereas the second one was free and must have communicated directly with the oral groove of the arm. The arms are densely pinnulated. As far as could be observed the arms are pinnulated throughout their lengths and both main arm trunk and smaller armlets are pinnulated. Pinnules were rather long. The specimen 97533 shows pinnules of at least 7 mm length. The pinnules are directed upwards and are lateral in contact with the pinnules of the preceding and succeeding brachials. At least six pinnulars constitute a pinnule. Pinnulars are about four times as long as high. They have somewhat rounded backs. Two parallel upstanding walls enclose a very deep groove, almost V-shaped in transverse section. Two series of alternating plates cover the groove at oral side. Laterally from these series of plates the upstanding

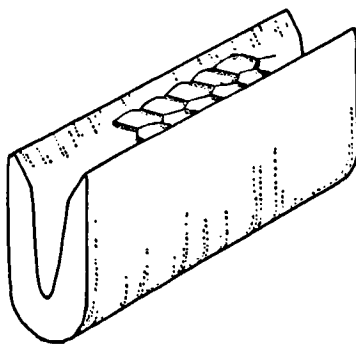


Fig. 10. Diagram showing an isolated pinnular of *Pithocrinus ovatus*, with deep V-shaped ventral groove and the two series of covering plates. Based on a specimen from the Santa Lucia formation, Grandoso, León (coll. Mus. Geol. Min., Leiden, no. 97533).

walls of the pinnular project any further (cf. textfig. 10). In one case a highly arched structure roofing over the oral side of the pinnular was observed.

**Stem.** The only specimen showing a part of the stem is the holotype. The last 4.8 mm of the stem are preserved. The stem was round in outline, the diameter 7.6 mm. The axial canal could not be observed. The succession of columnals in this fragment is nodal — two or three internodals — nodal.

**Distribution.** The exactly determined age of this species is at the type locality and at Grandoso in the base of the Santa Lucia limestone formation, corresponding to the Upper Emsian. The specimens in the Madrid and Paris collections are labelled "Colle", but the writer found no specimen of this species in the La Vid Shales at Colle. It is believed that these specimens must have come from Grandoso. Further details about the stratigraphical distribution of this species are unknown since the exact ages of the localities of specimens from Orzonaga, Le Velilla and San Fenolleda is not indicated on the labels. The

geographical distribution of the species is limited to the Spanish provinces of León and Asturias.

*Remarks.* Barrois probably was the first to publish on a Spanish *Pithocrinus* specimen. The diagram he gave (1882, pl. VIII, fig. 10) must have been inexactly drawn. It clearly represents a periechocrinid composition but no specimen has been seen showing characters as indicated in this diagram. Five-sided primaxils were never seen to occur together with an interradius composed of three series of plates. Reexamination of Barrois' specimens proved that the diagram must have been taken from the specimen F I, now referred to *Pithocrinus ovatus*. It must be stated that Barrois' diagram is inexactly drawn in the following points: basals and radials are drawn too large, only one IIIBr is drawn where in fact two occur, interradiial plates are never arranged in three series and the posterior interradius has a median series of only four plates in superposition to the preceding ones. Barrois' description (1882, p. 224) gives further support to the opinion that his material does not belong to *Pradocrinus*. He states: "La voûte est formée par un grand nombre de pièces assez irrégulières, à peu près lisses; elle se termine en une petite trompe submedianne, qui ne m'a pas présenté d'ouverture à son extrémité." This evidently indicates the presence of an anal tube. Indeed in the specimen F 1 the usual *Pithocrinus*' anal tube is present.

*Pithocrinus spinosus* Breimer sp. nov.

Pl. V, fig. 1—4

1945 New species of *Pithocrinus* — Kirk, p. 342, 343.

*Holotype.* The specimen 97526 of the Rijksmuseum van Geologie en Mineralogie at Leiden (Holland) is designated as the holotype.

*Locus typicus.* Grandoso, near Sabero, prov. of León (Spain).

*Stratum typicum.* The lower part of the Santa Lucia limestone formation, corresponding to the Upper Emsian.

*Diagnosis.* A large *Pithocrinus* species, characterized by a very wide dorsal cup, globose to somewhat bowl-shaped, composed of plates with long central spines; typically five-sided IAx; four arms to the ray; well developed intersecundibrachial and intertertibrachial areas; a highly arched tegmen composed of many very small plates; very stout central anal tube; arms unknown.

*Material.* (1) Rijksmuseum van Geologie en Mineralogie, Leiden, Holland: 7 specimens no. 97526—97532 from the type locality at Grandoso in Upper Emsian Santa Lucia limestone. Another specimen from the type locality, no. 97535, is labelled *P. spec. aff. P. spinosus*. (2) Springer collection of the United States National Museum, Washington: 1 specimen no. 54656 labelled as coming from Devonian of Colle (Spain). (3) Museo del Instituto geológico y minero de Espana, Madrid: 1 specimen no. 75 D from Devonian deposits at 'Colle' (León), 1 specimen no. 79 D from Devonian strata at Moniello (Asturias) now labelled as *Pithocrinus spec. aff. P. spinosus*.

*Description.* Form and dimensions.

	97526	97527	97528	97529	97530	97531
Height dorsal cup	35	30	ca. 30	18	15	11
Width dorsal cup	46	45	ca. 45	32	27—32	24
Height tegmen	27	24	18	18	16	12.5
Diameter anal tube	11	10	?	6	5.5	5

The dorsal cup is very wide, globose to somewhat bowl-shaped. The tegmen is highly arched, without depressions in interambulacral parts.

The height of the dorsal cup is equal at different cup-sides. The greatest width of the cup is at the arm level. In young specimens the width of the cup is twice the height, but in mature ones it does not reach this ratio.

It seems that the tegmen in younger specimens is relatively higher than in adult ones. In the latter the tegmen does not reach a height equal to that of the cup, but in earlier growth stages, it may have the same height, or even be somewhat higher.

The interradiar areas are well developed, but not depressed. Radial series are not conspicuous. All the cup plates are somewhat convex and have distinct central spines. This is particularly well demonstrated in the specimen 97532 (cf. Pl. V, fig. 4). Some specimens — as for example 97529 — show a fine radial ornamentation, perpendicular to the sutures and coming from the central spine.

The base is tripartite. The three equal and very low basals have a hexagonal outline. In the centre of the base a depression for the reception of the stem occurs. The base is pierced by an axial canal (cf. spec. 97529) with a diameter of 1.5 mm. The canal is slightly trilobate, the lobe situated in the central part of the basals.

Radials five, laterally in contact with each other except at posterior side, where the anal is situated in the radial circlet. Radials are wider than high; 6.5 mm high and 8 mm wide for adult specimens. They are alternately six- and seven-sided: l.post. R, r.post. R and ant. R six-sided, l.ant. R and r.ant. R seven-sided. The greatest width is high up in the plate.

The radial series are not conspicuous. Only two IBrr per ray occur, the second axillary. Regularly the IBr1 is a six-sided plate, about as high as the radials but narrower, the greatest width is high up in the plate. The height is 6.5 mm, the width 7—7.5 mm for adult specimens.

The primaxil is five-sided in regular rays. The height of the plate is 6.2—6.7 mm; the width may be 8 mm. The plate so generally is wider than high and is but slightly smaller than the preceding IBr1.

Just as described for *Pithocrinus ovatus* the first primibrach and the primaxil have not always the forms and sizes as described above. Again it is the position of the primaxil, somewhat left or right oblique from the first primibrach that is aberrant. These plates are not in perfect superposition to the preceding primibrach. Primaxils are observed to be five- or six-sided, the first primibrach may be five-sided when the succeeding primaxil is six-sided. In the r.post. radius of specimen 97529 both IBr1 and IAx are five-sided. It must be stated that usually the curved appearance of the radial series is due to the oblique position of the primaxil. However, it has been observed that, in a few cases the radial series are curved but that primibrach and primaxil kept their usual six- and five-sided forms respectively. Textfig. 11 gives an idea of the curving of radial series found among several *P. spinosus* species. It is very peculiar that in three specimens the left and right posterior radii are curved concave to the posterior interradius. Left and right anterior and the anterior radius are regularly built. But one cannot state that this arrangement of radial series occurs in all specimens. The left and right posterior radii of specimen no. 97527 are regular, with six-sided first primibrach and five-sided primaxil. But again — as was the case in the preceding species — one is inclined to believe that the curved radii are placed symmetrical to an antero-posterior vertical plane.

Only two IIBrr per half-ray occur, the first hexagonal, wider than high;

6—7 mm wide and about 4.5—5 mm high. The second IIBr is axillary and usually hexagonal as well, because it is laterally in contact with two interradial plates. In the holotype it is observed that the IIAx is seven-sided, caused by a small contact of that plate with an iIIBr2. The secundaxils are about as large as the IIBrr1.

Each secundaxil is succeeded by two pairs of IIIBrr1: six-sided plates,

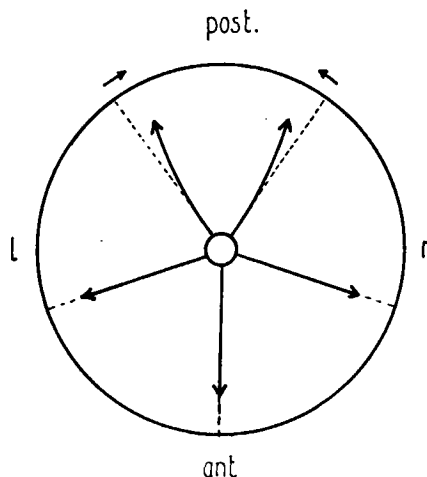


Fig. 11. Diagrams showing direction of curvature of postero-lateral radii in some specimens of *Pithocrinus ovatus*, from the Santa Lucia formation, Grandoso, León (coll. Mus. Geol. Min., Leiden, no's 97529, 97530 and 97531).

typically wider than high. The width generally is 5 mm, the height is no more than 3.5 mm. The IIIBr1 is followed by a cuneate IIIBr2. After that point brachials become biserially arranged, as can be judged from several brachials still attached to the cup. Between the cuneate IIIBr2 is a 2 mm high iIIIBr, resting on the upper internal facets of the IIIBrr1.

In all specimens examined only four arms to the ray occur. The positions of the uppermost fixed brachials show that free arms came off almost vertical.

The group of interbrachial plates is large. Generally seven, but sometimes eight or nine plates constitute this region. The first one is far the larger plate, situated between IIAxx and resting on the internal upper margins of the IIIBrr1. It is noteworthy that the iIIBr1 may lose contact with one or two adjoining IIIBrr2. The plate is six-, seven- or eight-sided. The plate may attain a height of 5 mm in mature specimens and a width of 4 mm. The plate is succeeded by two series three small plates that merge with tegmen plates. Sometimes another iIIBr is situated between these two series.

The interradial areas are not depressed. They occupy rather large parts of the cup. Their greatest width of max. 15 mm is at the level of the IIAxx. Distad they narrow gradually. The contact with the tegmen is but 3—4 mm wide. The first interradial plate is the larger one, slightly smaller than the radials and the first primibrachs. The plate is six-sided, higher than wide; 7.5 mm high and 6.5—7 mm wide. The succeeding interradials are arranged in



two series. In all 13—15 plates may occur. In young specimens the number of interradial plates seems to be somewhat less: 11—13.

The posterior interradial area is much wider than the lateral interradia. A is situated in the radial circlet, seven-sided and of about the same size of the radials, wider than high, the greatest width high up in the plate. The anal is succeeded by a row of three plates, the central one is typically six-sided, but smaller than the two lateral ones. In the specimen 97529 the plate directly succeeding the anal is very small and five-sided, flanked by two very large seven-sided plates. In the next range of three plates the central plate is not in good superposition to the preceding plate but placed somewhat left of it. It is flanked by one plate at each side. In the specimens 97530 and 97531 the second range of plates succeeding the anal have a central seven-sided plate in good superposition to the preceding interradial. In 97530 the central plate is flanked at both sides by only one plate but in 97531 to the left by two plates. Ventral from these two ranges of plates the interradials are irregularly arranged until they come in contact with the tegmen. The posterior interradius attains its greatest width at the level of adjoining I<sub>Axx</sub> and narrows rapidly towards the tegmen. The zone of contact with the tegmen is narrow: 3—4 mm only. A median series of plates does not occur.

**T e g m e n.** The proportions of the tegmen in relation to the dorsal cup were discussed above. The tegmen is composed of many very small plates. Interambulacral depressions do not occur. The holotype shows a very wide opening at the top where the anal tube has been attached. Many plates of the tegmen have small spinous processes.

#### *Pithocrinus Waliszewskii* (Oehlert 1896)

1896 *Megistocrinus Waliszewskii* n. sp. — Oehlert, p. 818, Pl. XXVI, fig. 1—4

1943 *Megistocrinus Waliszewskii* Oehlert — Bassler & Moody, p. 553

1945 *Pithocrinus Waliszewskii* (Oehlert) — Kirk, p. 344

*Holotype.* The specimen found by Mr. Waliszewski and described by Oehlert is still the only one known. It is to be regarded as the holotype. It is stored in the Oehlert collection of the *École Nationale Supérieure des Mines* at Paris.

*Locus typicus.* Santa Lucia, near Pola de Gordon, Prov. of León (Spain).

*Stratum typicum.* Top beds of the Santa Lucia limestone formation corresponding to the Lower Couvinian.

*Remarks on diagnostic characters.* It is rather difficult to trace the real diagnostic pattern for this species since only one specimen is known. Unfortunately it is a weathered one. For the moment only those characters in which the holotype distinctly differs from all other species can be mentioned. These are: its special ornamentation of fine ribs passing from plate to plate, accompanied by a fine vermiculate plate surface; its flattened posterior interradius; its very low tegmen without subspinous processes but with distinct interambulacral depressions; its rather slender anal tube.

*Remarks on original description.* The composition of the cup is best shown in Oehlert's diagram (1896, p. 819), that is exactly drawn, although it must be stated that Oehlert's figures are enlarged 1.5 times. The exact measurements are:

Total height:	22 mm
Height dorsal cup:	18 mm
Height of tegmen:	4 mm, measured at posterior side
Width of cup:	26.7 mm, in antero-posterior direction
	29.4 mm, in lateral direction

The greatest width is below the level of free arms. All upper cup parts are curved inward, but especially at anterior, left anterior and right anterior side. The posterior side is less curved than anterior side. Arms became free at an angle of 45 degrees.

*Affinities.* Without any doubt the present species belongs to *Pithocrinus* even in the restricted sense of the genus as it is taken here. It shows all the important characters of the genus. But among *Pithocrinus* species it may stand somewhat apart. The characters in which it differs from all other representatives of the genus are discussed above. Moreover it differs from the older *P. ovatus* and *P. spinosus* by a much wider posterior interrarial, a reduction of interrarial plates (only 7—8 iRR are present) and by the presence of 2—4 rami per radius. It agrees however in these characters with the younger *P. Cooperi*.

#### *Comparison of Pithocrinus species*

By exclusion of *Saccocrinus ? intrastigmatus* from *Pithocrinus* a well defined group of four species form the present genus *Pithocrinus*. The diagnosis for this group has been given on p. 46. Comparison of the *Pithocrinus* species that have become known up to now, shows some special differences between the younger Emsian forms from Spain on the one hand and the Middle Devonian forms from Spain and Michigan on the other. Firstly in the number of free arms. It seems that a reduction of the number of free arms took place during the development of the group. The Emsian *P. ovatus* proved to possess in some cases a radius with six arms, although a number of four arms has proved to be the rule in Pithocrini of that time. The younger *P. Waliszewskii* has radii with two, three or four free arms, but by the lack of more specimens it is not known what is typical for that species. Kirk described the holotype of *P. Cooperi* as having radii with two and with four arms. This reduction of free arms includes a reduction of brachials of higher order fixed to the cup.

Another trend of reduction is shown by the number of interrarial plates and the number of interbrachial plates. The older Emsian species *P. ovatus* and *P. spinosus* have interrarial areas composed of 11—15 plates and intersecundibrachials up to 7, moreover an intertertibrachial may occur.

*P. Waliszewskii* and *P. Cooperi* on the contrary have only 8—9 interrarial plates; about three intersecundibrachials and the intertertibrachial is absent.

A special trend however is seen in the posterior interradii. The older forms seem to have narrower posterior interradii, marked by the formula 1 - 3 - 3, than the younger species, where posterior interradius is governed by the formula 1 - 3 - 5. In the latter the zone of contact of the posterior interradius with the tegmen seems to be wider than in older species.

The features in which the different species are best characterized can be taken from ornamentation and the form of the tegmen in relation to the formation of the cup. *P. ovatus* is mainly characterized by its lack of ornamentation and gently rounded plate surfaces. *P. spinosus* is readily distinguished from all other species by its long spines on the cup plates and by its tegmen that is

composed of a great many rather miniscule plates. *P. Waliszewskii* may be recognized by the ornamentation of fine ribs passing from plate to plate, accompanied by a fine vermiculate plate surface and by its depressed tegmen with interambulacral depressions. *P. Cooperi* then would be mainly characterized by conical form of tegmen with large spines.

Genus STAMNOCRINUS Breimer gen. nov.

*Genotype.* *Saccocrinus* (?) *intrastigmatus* W. E. Schmidt, 1932

The genus *Stamnocrinus* is erected to include the Devonian periechocrinid species *Saccocrinus* (?) *intrastigmatus* W. E. Schmidt, 1932 and *Dorycrinus devonicus* Springer, 1911. Some specifically undeterminable forms are believed to belong to this genus as well. Recently many new specimens of *Stamnocrinus intrastigmatus* have been found, both at the type locality and at Colle (Léon). The structure and affinities of this species are by now far better understood than in the days of Schmidt. As a matter of fact *S. intrastigmatus* has many features in common with *Dorycrinus devonicus*. This last species has been the subject to uncertain treatment in palaeontologic classification. Springer (1911, p. 121) was inclined to believe that the German species "*Rhodocrinus*" *quinquelobus* was its most close relative, but Goldring (1923, p. 240) assigned it to her genus *Thamnocrinus*. Indeed the resemblances of cups and tegmens between *Thamnocrinus Springeri* and *Dorycrinus devonicus* are strong. But as will be demonstrated later, the arm structure of both species is completely distinct. This difference between both forms in our opinion separates them generically.

*Diagnosis.* A genus of the family Periechocrinidae characterized by a high turbinate dorsal cup; rays with seven-sided IAx bearing four free arms; interradial areas composed of many plates arranged in three series; fairly large intersecundibrachial parts; tegmen with anal tube and spines in ambulacral parts. Free arms and stem unknown.

*Distribution.* The genus occurs in Lower Emsian strata of the Spanish provinces León and Asturias. In America it is only known from the Middle Devonian of Indiana.

*Stamnocrinus intrastigmatus* (W. E. Schmidt 1932)

Pl. IV, fig. 5; Pl. VII, fig. 1—7

1932 *Saccocrinus* (?) *intrastigmatus* n. sp. — W. E. Schmidt, p. 21; Taf. IV, fig. 5a—c, 6, 7

1943 *Saccocrinus* (?) *intrastigmatus* Schmidt — Bassler & Moodey, p. 669

1945 *Pithocrinus intrastigmatus* (Schmidt) — Kirk, p. 345

*Holotype.* Schmidt designated the specimen figured in Pl. IV, fig. 5a, 5b as the holotype. The specimen was stored in the Geologische Landesmuseum at Berlin. The museum staff informed the author that the specimen has been lost during the second World War.

*Topotypes.* The Rijksmuseum van Geologie en Mineralogie at Leiden (Holland) has some topotypes, nrs. 97592—97597.

*Locus typicus.* The headland La Vela, NW from Arnao, Asturias (cf. Schmidt, 1932, p. 1; textfig. 1).

*Stratum typicum.* The red calcareous shales belonging to the "calcaire des Ferroñes" in the description of Ch. Barrois (1882, p. 470, Pl. XVIII). According

to Comte (p. 324; 331) these beds correlate with those of the La Vid shale formation in León and correspond to the Lower Emsian.

*Diagnosis.* A species of the genus *Stamnocrinus* characterized by high turbinate dorsal cup, at posterior side lower than at the curved anterior side, composed of flat smooth plates; a large seven-sided primaxil; four arms to the ray; low tegmen with central spine surrounded by four other spines interambulacral in position; a group of three spines at ambulacral parts of the tegmen; arms and stem unknown.

*Material.* (1) Rijksmuseum van Geologie en Mineralogie, Leiden, Holland: 4 specimens no. 97588—97591 from Lower Emsian La Vid formation at Colle (León), 6 specimens no. 97592—97597 from the type locality at Arnao (Asturias). (2) Museo del Instituto geológico y minero de España, Madrid: 1 specimen no. 77 D from undetermined strata at Grandoso (León), 6 specimens no. TB 46—TB 50 and TB 52 from Colle (León), 1 specimen no. TB 51 from La Vid (León), 1 specimen from La Velilla (León). (3) Verneuil collection of the Ecôle Nationale Supérieure des Mines, Paris: 3 specimens without indications of locality and age. (4) Barrois collection of the Institut de Géologie, Lille, France; 3 specimens no. MI—MIII from Santa Maria del Mar (Asturias). Barrois' labels have: '*Pradocrinus Baylii*, Vern., z. a. Orbignyana, Sta Maria del Mar'. (5) Museo Nacional de Ciencias Naturales, Madrid: 1 specimen no. D-H-1075 without indications of age and locality, but probably coming from Colle.

*Distribution.* This species occurs both in Asturias and in León. Exact age determinations are only available from the type locality, where deposits originate from the Lower Emsian. It is believed that Barrois' specimens from Santa Maria del Mar come from the same level as at the type locality. The specimens are of about the same preservation in red calcareous shales with much organic debris. Barrois' section in plate XVIII, 1882 gives 'Calcaire de Ferroñes' for both localities. The other certain age determination comes from Colle, where the present species was found in the top beds of the La Vid shale formation of Lower Emsian age. One of the specimens from the Museo del Instituto geológico y minero is said to come from Grandoso, but the author is strongly inclined to believe that *S. intrastigmatus* does not occur in the Santa Lucia limestone exposed there. In this limestone the *Pithocrinus* species, *Corocrinus* species and *Orthocrinus elongatus* were found, but no trace of *S. intrastigmatus*. Probably this specimen may be found in underlying La Vid shales, or even at Colle. It appears probable that *S. intrastigmatus* was restricted to Lower Emsian times.

*Description.* Form and dimensions.

	97591	DH 1075	TB 46	77 D	Vern. spec. 1
Total height	29	38.6	40.2	44.3	46
Height of cup (post. side)	22	24	25.8	29.4	32
Height of cup (ant. side)	24	26	30.2	37	38
Width of cup (lateral)	24	28	31	39	38
Height of tegmen (post. side)	7	12.6	14.4	13.9	14

The dorsal cup of this species is turbinate. The posterior side is lower than anterior side. In connection to it the plates forming the posterior side of the

cup generally are somewhat smaller than the plates at anterior side. The anterior side is more convex and at the level of free arms even somewhat curved inward (cf. Pl. VII, fig. 6). One of the specimens in the Verneuil collection however is at posterior side as high as at anterior side; but the anterior side still is somewhat convex. In relation to it the l.ant. IBr1 is six-sided. The widths of the cup in antero-posterior as well as in lateral direction are about the same. The species has a round diameter as viewed from above.

The cup is composed of very slightly convex plates, that apparently were smooth. No trace of ornamentation has been found in one of the specimens. The radial series are not conspicuous and in relation to it the interrarial areas are not depressed.

The tegmen is very low, steeper at posterior side than at anterior side. It has a very special ornamentation of groups of three spines placed along the marginal borders of ambulacral parts of the tegmen. At posterior side an anal tube is coming off. This tube at first is directed forward and later upward.

The base is composed of three equal basals and is hexagonal in outline. The specimen D-H-1075 has a few round columnals attached to the cup. The base is pierced by a rather wide axial canal. Basals are high plates, up to 5 mm. The greatest width is very high in the plate: 7.8 mm.

The five radials are in lateral contact to each other except at posterior side, where the anal is situated in the radial circlet. Radials are typically high plates, higher than wide; 7.5—8.5 mm high, but 6.5—7.1 mm wide; the greatest width very high in the plate. The plates are alternately six- and seven-sided; l.post R, r.post. R and ant. R six-sided; l.ant. R and r.ant. R seven-sided.

The two circles of basals and radials together are relatively high; they occupy more than one third the total height of the cup if measured along the cup surface.

The radial series are not conspicuous. Only two IBrr per ray occur, the second axillary. The IBr1 is a regular hexagonal plate, about 6 mm high and wide. So it is somewhat smaller than the radials. The primaxil is a large plate, even larger than the first primibrach. Its shape is always seven-sided. The height of the plate is 6.5 mm, its width about the same. IBr1 and IAx together occupy a third part of the total height of the cup.

Only two IIBrr per half ray occur, the first hexagonal, about as high as wide; width 5 mm; height 4 mm. The second IIBr is axillary and is usually six-sided but seven-sided if it has a small suture with one of the iIIBrr2. The plate is wider than high; 5 mm wide and 3.5 mm high.

Each secundaxil is succeeded by two pairs of IIIBr, six-sided plates, typically wider than high. The widths of IIIBrr1 is about 4 mm; the height 3 mm. IIIBrr2 are very low and about as wide as the preceding brachials. An iIIIBr does not occur in the specimens from León, but the topotype 97594 certainly has one in the r.post. radius. After IIIBr2 the arms became free. In the specimen D-H-1075 some higher brachials still are attached to the cup. They demonstrate clearly that arms must have been biserial, directly after becoming free. In all specimens examined four arms to the ray are present. The arms must have been almost vertical at anterior side; but more inclined at lateral side.

The group of interbrachial plates is rather large. Generally five plates constitute this region. The first interbrachial plate is the larger one, situated between IIAXx of different half rays and resting on the internal upper margins of the IIBrr1. At its upper margins the plate may have a very small suture with IIBr1. So the form of this plate is rather variable: six-, seven-

or eight-sided. The plate is 3 mm high and 2.5 mm wide. Each *iIBr1* is followed by two series of two small plates that merge with the tegmen. The zone of contact with the tegmen is 2 mm in the specimen TB 46. So it follows that the two arms of each half ray are grouped together and are separated by a small interbrachial gap from the group of two arms of the other half ray.

The *interradial areas* are not depressed. They occupy rather large parts of the cup. Not all *interradial areas* have the same widths. Antero left and antero right *interradii* are wider than postero left and postero right *interradii*, but the zones of contact are equal for all these four *interradial areas*. So *interradial contacts* with tegmen are wider than *interbrachial contacts*.

*Interradial areas* of the specimen TB 46 have the following compositions. In postero left and postero right *interradii* the hexagonal *iR1* is succeeded by two series of plates, but after five *iRR* a third series is intercalated between them, consisting of small plates. In all 14 plates form these *interradii*. The greatest width of 9 mm is at the level of *IAxx*. In antero left and antero right *interradii* the hexagonal *iR1* is succeeded by two six-sided plates. After these two plates the *interradii* are composed of three series of plates. In all 16 plates form the *interradius*. The greatest width of 12 mm is at the level of the suture between *IAx* and *IIBr1*. The specimen 77 D shows a very similar composition of *interradial areas*. The postero right *interradius* of specimen D-H-1075 is wide and composed of three series of plates, because the cup has somewhat convex sides at that point. These differences in composition may be entirely explained by the high and convex nature of the anterior part of the cup.

The *posterior interradius* is much wider than all the lateral *interradii*. *A* is situated in the radial circlet, is seven-sided and of about the same dimensions as the radials, higher than wide; the greatest width very high in the plate. The anal is succeeded by a range of three plates, the central one is typically six-sided, the lateral ones five-sided. *Posterior interradius* is not very constant as compared in different specimens. In most cases the first range of three plates is succeeded by four or five plates, irregularly arranged. The upper part of the *interradius* than is composed of many small irregular plates. But in the specimen 77 D the first range of three plates is succeeded by two other ranges of three plates with central hexagonal plates. After that a range of five plates occurs, the central one seven-sided. All the central plates of these ranges are in plain superposition to the preceding one, so as to form a kind of median series of plates. But this series is not conspicuous and dies out after five plates and before the contact with the tegmen. The zone of contact with the tegmen is very wide: 7.5 mm for the specimen TB 46. The greatest width of 17 mm is at the suture of *IAx* and *IBr1*. After that level the *interradius* narrows gradually.

*Gonioporioids* were found in several weathered specimens and especially in no. 97590, a deeply weathered specimen which shows these pores at all angles of the plates forming the posterior and right posterior part of the cup. A very special feature is shown in the topotype 97592. This is an immature specimen, beautifully preserved and certainly not weathered. The plates in the upper part of the cup have all depressed angles. A deep pit is observed at all plate angles. The question arises if these pits had connection to *gonioporioids* or not. Many pits are filled with matrix and it so seems that they may be interpreted as true pores, but some other pits show distinct connecting sutures at the bottom. These pits certainly were not pores and so this question remains very doubtful. But it must be stated that these pits have only been found in this specimen and

not in any other mature specimen. The importance of this feature is not known.

The tegmen is beautifully preserved in several specimens from León in which a distinct anal tube was found. This is clear from one of the topotypes (no. 97594) figured in Pl. IV, fig. 5. The anal tube is not at first vertical in position but is directed somewhat to the front; following the surface of the tegmen, however, higher up it must have become free. The diameter of the anal tube is 5—6 mm. It is composed of many small irregularly arranged plates.

The tegmen itself is very low; at posterior side more inclined than at anterior side. Interambulacral parts are not or but slightly depressed. No differentiation between ambulacral and interambulacral plates exists. All the plates are small, polygonal and irregularly arranged, but some other plates are differentiated. The central plate bore a spine (cf. Pl. VII, fig. 6). This is particular beautiful in the specimen 97596. The spine is broken, but the remnant has a height of 3 mm above the surface of the tegmen. The diameter of this spine was 3.5 mm at its base (measured at the specimen D-H-1075). A circle of plates occurs around the central spine, four more spines are placed in the next circle. They are all interambulacral in position. These four spines may have been somewhat more delicate than the central one. At the posterior side the spine is missing. The anal tube comes off at the position where it may be expected. Other spines are placed at the ambulacral parts of the tegmen (cf. Pl. VII, fig. 6). In each ambulacrum a group of spines occurs. A spine is placed directly behind each group of two arms coming from a half ray. The third spine of the group is placed between the other two and somewhat higher. Spines are directed vertical. It is believed that spines were rather long and stout. Remnants have reached a length of 4 mm above tegmen surface in the weathered specimen no. 97594. The greatest width at its base is 4 mm in the large specimen 77 D. Unfortunately the topotypes are too poorly preserved to show uncrushed tegmens. From some of these specimens one gets the impression that the tegmen must have been somewhat higher than is the case in the specimens from León. Although certainly larger spines occurred in the topotypes it cannot be determined whether the spines were located in groups at the ambulacral part of the tegmen or not. All we can say at the moment is that a central spine occurred and that in some places ambulacral spines were found.

*Remarks.* Thanks to Schmidt's careful observations and adequate description of what was once the holotype it is possible to classify the present specimens indisputably as *Stamnocrinus intrastigmatus*. The results from the new specimens of the type locality contributed greatly to this conclusion. Some features, already mentioned by Schmidt have now proved to be of real diagnostic value for this species. From the holotype he stated that anterior side was higher than posterior side and that the plates at the anal side were smaller than was the case in front. He interpreted this phenomenon as aberrant, but all the well preserved specimens that are available for study at this moment show this characteristic. Now it is even held as one of the most important structural peculiarities of the species. The new specimens appear to possess more characters in common with the figures and description of the holotype: the flat and smooth cup plates with gonioporoids at their angles, the large seven-sided primaxil, the large interradii with intercalating third series of plates, the presence of  $5 \times 4$  free arms. Although Schmidt did not draw attention to it, the tegmen of his third specimen (Pl. IV, fig. 7, 1932) shows distinctly two broken spines. All tegmens that are preserved show a fixed pattern of the spines on the tegmen. One important character was

not found by Schmidt. His specimen 3 had a part of the tegmen still attached to the cup, but it was not obvious whether this tegmen had a true anal tube or only a protuberance for the anus. The present specimens indisputably prove the presence of an anal tube.

There may be some difficulty in distinguishing single cups of the present species from those of *Pyxidocrinus collensis*. But the two species are readily recognized if studied in more detail. The first always shows a large seven-sided IAx in relation to a wide interradius composed of three series of plates. The series of IBrr and IIBrr are higher.

*Stamnocrinus devonicus* (Springer 1911)

1911 *Dorycrinus devonicus* sp. nov. — Springer, p. 120; Pl. III, fig. 12a—d, 13  
 1923 *Thamnocrinus devonicus* (Springer) — Goldring, p. 239  
 1943 *Thamnocrinus devonicus* (Springer) — Bassler & Moodey, p. 709

*Holotype*. The specimens figured by Springer and held in the Walker Museum, University of Chicago.

*Locus typicus*. Charleston, Indiana.

*Stratum typicum*. Not exactly described by Springer. The types come from the Hamilton group of the Middle Devonian.

*Remarks on systematic position*. This species is referred to *Dorycrinus* by Springer and to *Thamnocrinus* by Goldring, but in our opinion it does not belong to either of the two genera. It certainly cannot belong to *Dorycrinus* because its IBr1 is six-sided instead of four-sided as in typical Coelocrinidae to which family *Dorycrinus* is assigned by Ubahgs (1953, p. 740). This difference was already mentioned by Goldring (1923, p. 242).

The relations between *Stamnocrinus devonicus* and *Thamnocrinus Springeri* are only superficial. The tegmens are indeed similar and the composition of the cups are about the same but the organisation of the arms of *Thamnocrinus* with pronounced endotome branching and completely fixed main arm trunk must have differed considerably from *Stamnocrinus devonicus*. Moreover it seems to be evident that such organisation of arms as in *Thamnocrinus* is quite exceptional among periechocrinids of Devonian times. So the genus stands somewhat apart and is — in our opinion — mainly characterized by its special arm structure. Goldring (1923, p. 248) mentions the lack of the interradian integuments in *S. devonicus*. "In *devonicus* the remarkable interbrachial integument reaching up to the last bifurcation of the arms is absent. In this species the incorporation of the brachials scarcely extends above the secundaxil; the intersecundibrach alone firmly incorporates the adjacent brachials". She did not draw attention to the fact that in *S. devonicus* a fixed number of four arms to the ray exists. In our opinion these differences are of utmost importance because it proves that in *S. devonicus* arms must have been entirely free. This is indicated by the fact that interradian areas freely communicate with the tegmen and that the arms are grouped in the lobed upper portions of the cup, where four separate ambulacral openings are observed.

The characters as known from *S. devonicus* agree very much with those of *S. intrastigmatus* as described in this paper. They have the following characters in common: high turbinate dorsal cup, composed of flat, smooth plates; rays



with seven-sided IAx and four arms; interradial areas composed of three series of plates; tegmen with ambulacral groups of spines; the presence of an anal tube. On the other hand enough differences exist between both forms as to separate them specifically. The tegmen of *S. devonicus* is much higher and the spines more specialized. The upper part of the cup is more lobate and total height of basals and radials is higher. But nevertheless *S. devonicus* is to be referred to *Stamnocrinus* rather than to any other periechocrinid genus. Springer (1911, p. 122) mentioned already the resemblance between his species and some elongate forms from Colle (Spain) in his collection. The exact relation of "*Rhodocrinus*" *quinquelobus* to *Stamnocrinus* is not yet fully understood. Springer (1911, p. 121) mentioned that this species is the most nearly related form to *S. devonicus*, but it differs from that species by the presence of only two arms to the ray, a low tegmen without spines, and a laterally placed anus.

*Stamnocrinus* spec. 1

Pl. IV, fig. 4

At the type locality of *Stamnocrinus intrastigmatus* a crushed cup was found which is apparently referable to *Stamnocrinus* because it agrees in all the characters that can be examined with the diagnosis for that genus. It differs from *S. intrastigmatus* by a strong radial ornamentation of the cup plates. The lower plates also show a tubercular ornamentation.

One basal, 1 mm wide and 3 mm high, is preserved. The left posterior radius is complete. The radial is large, regular six-sided 6 mm high and wide. The IBr1 is six-sided as well but smaller, 4.2 mm high and 4 mm wide, the greatest width high up in the plate. IAx is seven-sided and of the same proportions as the IBr1. Two IIBrr per half ray occur, the first hexagonal, rather high; the second seven-sided and axillary. The IIAx is succeeded by two series of two IIIBrr; the last pair divided by an iIIIBr. A fairly large group of iIIIBrr occurred as well. The radius has four arms to the ray. The postero left interradius is crushed. It cannot be stated whether it is composed of two or three series. The posterior interradius is preserved. The anal is seven-sided, of the same dimensions as the radial. It is succeeded by three large plates in second row, the central one six-sided, the lateral ones five-sided. The next row has a central six-sided plates as well, flanked at each side by a seven-sided plate. The succeeding range has a small seven-sided plate and is flanked at each side by two small plates. Still another 15 small plates form the interradius. They are irregularly arranged. The gap between the radii at posterior side is 6 mm, at arms levels.

*Stamnocrinus* spec. 2

textfig. 12

The Verneuil collection of the Ecôle Nationale Supérieure des Mines at Paris has a specimen of unknown provenance. It is referable to *Stamnocrinus*, rather than to any other periechocrinoid genus. In part it is certainly an aberrant form. The base and the l.ant. side are lacking. The height of the complete theca must have been about 30 mm, the greatest width is at arm levels (33 mm). The height of the tegmen is 16 mm. The outline as seen from above is circular. The plates are flat and smooth. The specimen differs distinctly from *S. intrastigmatus* by its narrow interradial areas composed of only two series of plates,

by the incorporation sometimes of a third IIIBr in the cup; by larger numbers or intersecundibrachs and the presence of some iIIIBr; by the presence of a subcentral anal tube and the apparent lack of spines in the tegmen.

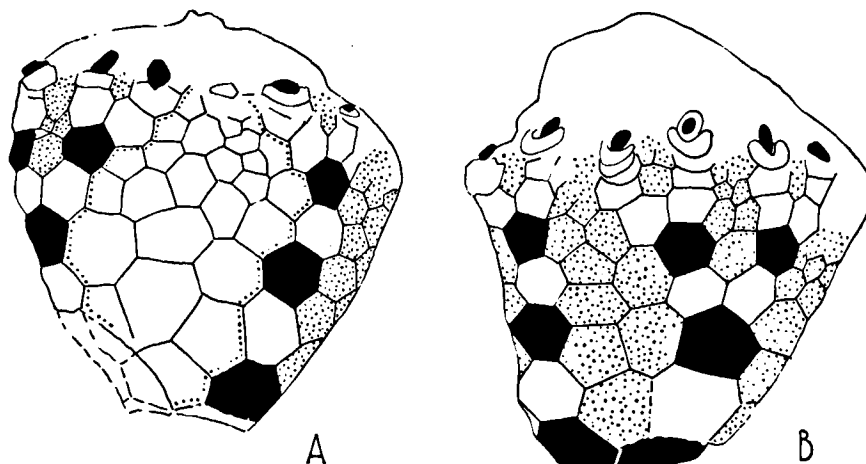


Fig. 12. Diagrams showing the composition of the dorsal cup in *Stamnocrinus* spec. 2. Specimen in the Verneuil-coll. Ecole Nat. Sup. des Mines, Paris (A) posterior view, (B) lateral view.

All the rays have differences with those in *S. intrastigmatus*, although their composition is similar. Two primibrachs, two secundibrachs and usually two tertibrachs are incorporated. The difference is mainly caused by the fact that IAx is irregular six-sided instead of heptagonal as might have been expected in a *Stamnocrinus* species. But this may be due to a curving of the radial series to the posterior side, similar to the same phenomenon as has been described from *Pithocrinus* and *Pyxidocrinus* species. The presence of four IBrr in the right anterior radius must be regarded as aberrant. The radius has only two arms, so that the total number of arms is 18. The posterior interradius is quite normal for *Stamnocrinus*. A is succeeded by three plates in first and second row, the central ones six-sided. The third range has five plates with a central six-sided one. So a low median series of plates is initiated but it is not conspicuous.

### Genus COROCRINUS Goldring 1923

In upper Emsian limestones near Grandoso (León) some well preserved crinoids were found which are probably referable to *Corocrinus*. Some difficulties were met when classifying these specimens. Our specimens do not agree in all their characters with typical *Corocrinus* species and the group of species brought together to form the genus *Corocrinus* are somewhat variable or inadequately known. In establishing this genus Goldring could not give an exact diagnosis due to the fact that in the genotype arms were lacking and the other species *Corocrinus ? calypso* to her opinion does not closely resemble the genotype. Later Schmidt (1941, p. 97) described his *Corocrinus imbecillus* from Lower Devonian rocks of Germany. This species strikingly resembles the genotype, but

differs from *C. calypso* by its monserial arms. In 1952 Kier (p. 67) described his species *C. nodosus* that differed from the holotype by wider cup and distinct ornamentation of nodes. Its arms were biserial as in *C. calypso*. The tegmen remained unknown. The species *Amphoracrinus Sampsoni* Miller & Gurley, 1896 from the Mississippian of Missouri, assigned to *Corocrinus* by Peck & Keyte (1938, p. 75; Pl. 29, fig. 10—13) does not in our opinion belong to this genus but, with other Carboniferous periechocrinids, to *Aryballocrinus* gen. nov. described in this paper. But nevertheless some distinct characters are readily found for all the *Corocrinus* species: Cup turbinate or bowlshaped with high radial circllet, rays marked with a rib; two smaller primibrachs, second axillary, seven-sided, few secundibrachs incorporated in the cup, two arms to the ray, each only once bifurcating in the free state, posterior interradius very wide with median series of plates. If *Corocrinus* really is characterized by these points our Spanish specimens are related to *Corocrinus*, but differ from it in certain respects. It cannot at the moment be determined whether these differences are of specific catagory or even of generic level. Hence our species is placed with some doubt under *Corocrinus*.

*Corocrinus* ? *grandosensis* Breimer spec. nov.

Pl. VII, fig. 8—12

*Holotype*. The specimen TB 45 in the collection of the Museo del Instituto geológico y minero de España at Madrid, is designated the holotype.

*Locus typicus*. Grandoso, near Sabéro, province of León.

*Stratum typicum*. Santa Lucia limestone, corresponding to the Upper Emsian.

*Diagnosis*. A species probably belonging to the genus *Corocrinus* characterized by a rather wide bowl-shaped dorsal cup, composed of plates provided with a node; radial circllet low, primibrachs of about the same size as the radials; two secundibrachs in two-rami rays; one pair of tertibrachs in three-rami rays; radii marked with a rib, interradian areas wide, composed of three series of plates; tegmen flat with five spiny or nodular plates, ambulacral in position. Arms and stem unknown.

*Material*. (1) Museo del Instituto geológico y minero de España, Madrid: the specimen TB 45 from the Santa Lucia limestone at Grandoso (León), the specimen TB 45a from near Villayandre. The precise horizon is not known, but it is believed that the specimen comes from the Upper La Vid shales or Lower Santa Lucia limestones, exposed near that village. (2) Rijksmuseum van Geologie en Mineralogie, Leiden, Holland: the specimen no. 97599 with crushed lower part of the cup, coming from the type locality of Grandoso.

*Distribution*. The only exact determined age for this specimen is at the type locality, where it is of Upper Emsian age.

*Description*. Form and dimensions of the holotype.

Height 20.2 mm, width 22.1 mm (in antero-posterior direction), width 18 mm, in lateral direction.

The form of the cup is wide bowl-shaped. The base is somewhat constricted. The radial circllet is flared outward; higher regions of the cup become more and more parallel-sided. The uppermost part of the cup is somewhat lobed, especially at l. and r.post. sides. The radii are marked with a rib that starts

at the central node of the radial. Otherwise the radii are not conspicuous and the wide interradiial areas are not depressed. The ornamentation of the cup plates — mainly on radials and interradials — consists of a central node. The tegmen is flat. Five nodes or spines are situated half way the ambulacral parts of the tegmen.

The base is very low, only 1.5 mm high. It is composed of three basals and is pierced by a rather wide axial canal, about 2 mm in diameter.

The radials are relatively low plates, slightly higher than wide; 4.8 mm high; 4.5 mm wide. Radial circling is not completely closed, at antero left side the very large iR1 intervenes between two RR and is in contact with the basals below. At anal side A is situated in the radial circling. Due to the abnormal position of antero left iR1 the l.ant. R is six-sided, ant. R. seven-sided and r.ant. R six-sided, l.post. R and r.post. R have usual periechocrinid six-sided forms.

The radial series are not conspicuous. They are marked by a small rib. Only two IBrr per ray occur, the second axillary. IBr1 is about regular six-sided, 4 mm high and wide; very slightly smaller than the radials. The primaxil is seven-sided and of the same proportions as the preceding brachial. The left anterior radius is abnormal: IBr1 is a large five-sided plate, the primaxil — although seven-sided — is abnormal in form and unusually large. All this is due to abnormal position of antero left iR1 (cf. Pl. VII, fig. 9).

In the two rami of anterior, left and right anterior rays two secundibrachs are incorporated, the second pair separated by a small intersecundibrach. The three rami of left and right posterior rays are especially well shown in the specimen 97599. In the l.post ray the left half-ray gives rise to one arm and in the r.post. ray the right half ray leads to one arm. In the half rays from which two arms are initiated two secundibrachs occur, the first hexagonal, the second axillary. The secundaxil is succeeded by two series of two tertibrachs, the upper two separated by an iIIIBr. The half rays that form only one arm have three rather high secundibrachs incorporated in the cup. Some lower free brachials still attached to one of the radii of specimen 97599 indicate that free arms were biserial directly after the fixed brachials.

Interbrachial areas are rather small. They have equal compositions in both two and three rami-rays. The iIIBr1 is a fairly large six-sided plate, 3 mm high and 2.5 mm wide. This plate is succeeded by only one pair of small interbrachials.

Interradiial areas are not depressed. The plates of this regions have a central node. iR1 is the larger plate, six-sided, slightly smaller than the radials. This plate is succeeded by two six-sided interradials and after these two plates three series of interradiial plates may occur. This third series may be commence even after five iRR. Antero left interradius in the holotype is quite abnormal, because the very large irregular eight-sided iR1 is in contact with the basals, so intervening between the adjacent radials. This plate is by far the largest plate of the cup: 6 mm high and 4.5 mm wide. It is succeeded by a smaller five-sided plate that makes contact laterally with the unusually large IAx. After this iR2 the interradius is composed of only two series of plates. In all but 10 plates take part in the formation of this interradiial area, whereas in other lateral interradii this may be up to 14. The zone of contact with the tegmen is 3—5 mm wide. The posterior interradius (cf. Pl. VII, fig. 12) is preserved throughout its length in the holotype. The anal side is much wider than lateral interradiial areas. A is situated in the radial circling, seven-sided and of about the same proportions as the radials. The anal is succeeded by a range of three plates the central one hexagonal with greatest width very high up in the plate, the two

lateral ones six-sided as well. The plates of this range are distinctly smaller than the anal plate. The next row is composed of already 5 plates and the range after it of 7 plates. The upper part of the posterior interradius is composed of smaller plates. A median series of plates can be more or less distinguished and the lateral parts of this interradius have similar composition, so that the whole posterior side has a more or less symmetrical appearance. The greatest width of 11.5 mm is at the levels of adjacent primaxils. Distad it narrows gradually till it has a zone of contact with the tegmen of about 7 mm wide.

The tegmen is preserved in both the holotype as the specimen 97599. It is very low to almost flat with slight interambulacral depressions. At the posterior side of the holotype a rather wide opening can be seen. A protuberance or perhaps a true anal tube may have been present. There is no differentiation of tegmen plates. Only five spiny or nodose plates may be distinguished. They are best shown by the specimen 97599. They are placed half way between the centre of the tegmen and the points where arms were inserted.

*Affinities.* The present species has certain affinities to *Corocrinus*: its high bowl-shaped cup; wide posterior interradius with median series of plates; the presence in some radii of only two arms. In ornamentation it differs from the holotype, *C. calypso* and *C. imbecillus*, but in this respect it resembles very much *C. nodosus*. Unfortunately the tegmen cannot be compared with other corocrini. Among the *Corocrinus* species the Spanish form is closest related to *C. nodosus* Kier, 1952. The form and composition of the dorsal cups are strikingly similar. But *C. nodosus* has higher radials and has only two arms in the posterior radii. The importance of the fact that *C. ? grandosensis* has three arms in both the posterior radii cannot be assessed at the moment, but it is now supposed that this may be only of specific category. The tegmen as shown by our species clearly indicates affinity to the tegmens of *Megistocrinus* (?) *abnormis*, *Megistocrinus depressus* and *Megistocrinus spinosulus* (cf. Wachsmuth & Springer, 1897, Pl. 48 and 49) on one hand but with the tegmen of *Thamnocrinus Springeri* on the other (cf. Goldring, 1945, p. 57; Pl. I, fig. 2). All these five species have spines half way up the ambulacral parts of the rather flat tegmens.

*Gennaeocrinus* spec. cf. *G. nyssa* (Hall 1862)

The spec. TB 79 in the collection of the Museo del Instituto geológico y minero de España is of unknown provenance, but is certainly from Devonian deposits. It is referable to *Gennaeocrinus* and is an incomplete dorsal cup, only the proximal part of which is preserved. Three equal basals with rosette-like rim; five radials alternately six- or seven-sided; A in radial cirlet, seven-sided, about equal in size as the radials; A succeeded by three plates in next range; IBr1 regularly six-sided; iR1 is also six-sided and about as large as IBr1, and is followed by two plates. The form of the cup is globose and it shows a very special ornamentation of central nodes, somewhat larger on the RR than succeeding plates. The nodes are accompanied by ribbing radiating from the centre and perpendicular to the sutures. The ornamentation is identical to that of *Gennaeocrinus nyssa* as figured by Goldring (1923, Pl. 31, fig. 2) from one of the types. The incompleteness of the cup forbids the definite determination of the specimens.

*Affinities of periechocrinid genera*

The present study reveals that periechocrinids occur most frequently in NW Spain. They are dominant over all other crinoids of the region, not only

in the number of individuals but also in the number of species. Among the 56 species of crinoids known at the present from the Palaeozoic of Spain 13 species belong to the periechocrinids. The species richest in individuals *Pyxidocrinus collensis*, belongs to them. One may even hold that the Devonian of NW Spain is the most favourable area for the study of periechocrinids. No less than seven of the total amount of 15 genera of Periechocrinidae are represented in Spain.

In order to get some idea of the bearing on Periechocrinid systematics of the newly discovered Spanish fauna it seems worthwhile to review briefly the stratigraphic and paleogeographic distribution of the genera of periechocrinids. The Middle Silurian of the U. S. A. has seven species assigned by Kirk to his genus *Stiptocrinus*. All other periechocrinid species of Silurian times at the present are placed under *Periechocrinus*. This group embraces species from the Isle of Gothland, from England and N. America. This group is rather variable and may be revised completely. It is unfortunate that the Silurian strata of NW Spain lack any trace of crinoids. No contributions to the solution of the problem of classification of Silurian periechocrinids may be expected from this region. But at present already can be found that the genus *Periechocrinus* did not occur any higher than the Silurian since the Devonian species formerly assigned to it have to be referred to different genera. The Devonian of Europe has some genera completely restricted to that part of the world. This group includes species of *Beyrichocrinus*, *Lenneocrinus*, *Pyxidocrinus* and *Pradocrinus*. In Lower and Middle Devonian times some connection between European and American faunae have existed as is indicated by the fact that the next genera have species in both regions: *Gennaeocrinus*, *Corocrinus* and *Megistocrinus* predominantly in N. America; *Pithocrinus* and *Stamnocrinus* predominantly in Europe. *Thamnoocrinus* seems to be a form fully restricted to N. America. In Mississippian times *Megistocrinus* still occurs. Both in Europe as in N. America. *Maligneocrinus* and *Athabascacrinus* are scarcely represented in N. America.

A well defined group of species related to *Periechocrinus*? *Whitei* has been subject to uncertain treatment during paleontological classification. They have usually been placed under *Periechocrinus* itself, but since the present study revealed that *Periechocrinus* has to be regarded as a genus restricted to Silurian times these species have to be reclassified.

The type genus has to be taken as the base of a morphological comparison of the genera described under Periechocrinidae. The author has studied some very fine specimens of *Periechocrinus moniliformis* Phillips from Dudley in the collections of the Ecôle des Mines at Paris and the Rijksmuseum van Geologie en Mineralogie at Leiden (Holland). The most important characters of this species and hence of the genus *Periechocrinus* itself seem to be: high unshaped dorsal cup, composed of thin and flat plates; radial series marked with a riblet passing on the arms; two primibrachs, second axillary seven-sided; many brachials of higher order up to IVAx incorporated; mode of arm branching bilateral heterotome; short slender arms; interradian areas not depressed and composed of many plates arranged in two series; posterior interradian with median series of plates marked with a rib; incompetent tegmen (Kirk, 1946, p. 34) made up of a great many of small plates; anal tube is a short and wide incompetent structure; stem composed of alternately one nodal — one internodal.

The Spanish Devonian periechocrinids all differ considerably from the type-genus by (1) a shorter theca (except for *Pradocrinus*). (2) by lack of incorporation of higher brachials as IIIBr2. (3) lack of median ray ridge in posterior interradian (low median series of plates may occur but they become never ridged) (4) by competent tegmen structures. (5) by different type of arm branching.

In separating the genera a new set of characters was used which has largely been ignored up to now. It was found that a remarkable constancy exists in the relation: form of the primaxil — number of interradian plates. Primaxils have been found to be five-sided when the interradius is composed of only two series of plates without supplementary plates intercalated between them. When primaxils are seven-sided it is found that interradian areas have supplementary plates between the two main series. Much stress has been laid on the type of branching of the arms.

Among periechocrinids a group of genera may be distinguished which have many characters in common, these are *Lenneocrinus*, *Pradocrinus* and *Corocrinus*. They agree in the following characters: conical or elongated dorsal cups with typically a radial ornamentation of the cup plates, radial series marked by a rib, interradian areas depressed in upper parts, posterior side with median series of plates, primaxils seven-sided, supplementary plates in interradians may be present. Unfortunately the tegmens of these genera cannot be compared since tegmens of *Corocrinus* and *Lenneocrinus* are unknown. But although the composition and ornamentation of the cups of these three genera are strikingly similar, enough data are available to separate the genera definitely. These characters mainly must be taken from the arm structures. Although arms are biserial in the representatives of these genera (except for *Corocrinus imbecillus*) the mode of branching differentiates them. *Corocrinus* arms bifurcate only once in the free state, whereas in *Lenneocrinus* an irregular dichotomous branching exists. Another difference is indicated by the size. *Lenneocrinus* is a peculiar small form and certainly the smallest periechocrinid known thus far. *Pradocrinus* on the contrary is amongst the largest periechocrinids. *Corocrinus* is medium-sized. Lastly *Lenneocrinus* stands apart through its cirri-bearing stem and the exert base of its genotype. The question arises how relations of this group of genera to *Stiptocrinus* are. This Silurian genus agrees with the above mentioned Devonian forms by the presence of only two-rami rays. But further the resemblance is merely superficial because *Stiptocrinus* lacks radial ridges, depressed interradians and median ray ridge in posterior interradius. Arms and tegmens cannot be compared.

It must be stated that this group of genera has the "primitive" characters such as median ray ridge and radial ridges in common to *Periechocrinus*.

It seems now that among Spanish Devonian periechocrinids *Pyxidocrinus* and *Stamnocrinus* stand a little apart. They have no strong affinities to other Devonian genera. *Thamnocrinus* has too specialized arms to be a close relative. *Lenneocrinus*, *Pradocrinus* and *Corocrinus* although they present elongated cups as well, differ in the characters described above. All other Devonian periechocrinids have globose or depressed dorsal cups and lack the special fixed number of only four arms to the ray. *Pyxidocrinus* and *Stamnocrinus* are strongly related by the lack of a ridge on radial series, by non-depressed interradian areas and the weakly developed median series of plates in posterior interradius that however, are not ridged, and by four-rami rays. In these ways they differ distinctly from the type genus. But on the contrary enough arguments can be brought forward to separate the genera. *Stamnocrinus* differs from *Pyxidocrinus* by its large heptagonal primaxil in relation to the supplementary plates of the interradius and mostly in tegmen structure with ambulacral spines and lateral anal tube. Perhaps the main arguments for classification of these two genera may exist in the arms. Unfortunately the arms of both genera are unknown.

*Pithocrinus* is mainly related to *Megistocrinus* as was already pointed out

by Kirk (1945, p. 342). But it is differentiated from that genus by its exsert base, the smaller number of secundibrachs, the lack of incorporation of the higher orders of brachials and the presence of a stout, subcentral anal tube. The same affinities and differences exist to *Gennaeocrinus* as well, except for the tripartite base that both genera have in common.

Carboniferous species assigned to Periechocrinidae proved to be very interesting. Laudon, Parks and Spreng (1952, p. 564, 567) set out already the affinities of *Maligneocrinus medicinensis* and *Athabassocrinus colemanensis*. Some true *Megistocrinus* species survived in Carboniferous times include *M. Evansi* from the Burlington of Iowa, *M. globosus* from the Lower Carboniferous of England and *M. nobilis* from the Mississippian of Iowa.

Perhaps it is not too far from the scope of this paper to deal with the systematic position of the group of Carboniferous and Mississippian crinoids related to *Periechocrinus*? *Whitei*. Their systematic position once more has become uncertain by the fact that Devonian species up to now referred to *Periechocrinus* had to be assigned to different genera. So both morphological as stratigraphical reasons indicate that these species cannot be assigned to *Periechocrinus* and we are forced to look in more detail for their true affinities. This group proved to embrace the species *Periechocrinus* ? *Whitei* (Hall, 1861), *Periechocrinus* ? *tenuidiscus* (Hall, 1861), *Megistocrinus parvus* Wachsmuth & Springer, 1890, *Corocrinus Sampsoni* (Miller & Gurley, 1896), *Periechocrinus* spec. 1 Laudon & Severson, 1953 and *Periechocrinus* ? *awthornsensis* Wright, 1955.

The species *Periechocrinites* ? *indicator* as described by Etheridge from the Carboniferous of Australia is a very doubtful form, probably not belonging to the Periechocrinidae at all.

All the authors describing these species were in doubt as to how to classify their forms. So they have been subject to uncertain treatment during paleontological classification. While describing his species *awthornsensis* Wright (1955, p. 192) discussed its affinity to *P.* ? *Whitei* and *P.* ? *tenuidiscus*. Laudon & Severson (1953, p. 527) more specially mentioned *P.* ? *Whitei* as the closest relative of their species. Wachsmuth & Springer (1897, p. 531) were the first to mention the close relationship of *P.* ? *Whitei* and *P.* ? *tenuidiscus*. With regard to classification of these species they stated: (p. 520). "These species we have marked with a query, as it is possible they may have to be separated subgenerically, perhaps under *Pradocrinus*." This proposal cannot be followed since *Pradocrinus* itself has to be separated generically from *Periechocrinus*. The six species mentioned above both for morphological as for stratigraphical reasons are placed in a proper genus for which I propose the name *Aryballocrinus* gen. nov. with *Periechocrinus* ? *Whitei* as the genotype. The diagnosis for this new genus must read: A genus of the family Periechocrinidae characterized by a globose dorsal cup, composed of thin plates; high radial cirlet; radial series that may be slightly marked with a rib; two primibrachs, second axillary, five-sided; very few secundibrachs incorporated; two-rami rays; non depressed interradian areas composed of few plates; very wide posterior interradius; regularly dichotomous branching, biserial arms, densely pinnulated; low tegmen with anus excentric, rising but little above the surface of the tegmen; stout stem, composed of all equal plates.

*Aryballocrinus Whitei* (Hall 1861)

*Synonymy*: Bassler & Moodey, 1943, p. 601

This species, originally described from the Burlington formation of Iowa,



seems to be characterized by the greatest width of the cup at the levels of primaxils and by its smooth plates. Meek & Worthen (1861, p. 133) described from their *Actinocrinus* (*Pradocrinus* ?) *amplus* that the primanal supports only two sub-hexagonal pieces in the next range, but Wachsmuth & Springer (1897, p. 530) gave the number of plates succeeding the primanal as three, as is usual for periechocrinids. Perhaps the specimen of Meek & Worthen is an aberrant one. It is remarkable that the young specimen of the Kinderhook group of Iowa as figured by Wachsmuth & Springer (1897, Pl. LI, fig. 10) shows radii marked with a rib. Moreover, the stem seems to be composed of nodals and internodals. The radial circlet is relatively low. Wachsmuth & Springer's statement that the specimen is conspecific with *A. Whitei* is somewhat doubted. Laudon & Beane (1937, p. 246) regarded the specimen as belonging to *Megistocrinus parvus*. It certainly has strong affinities to that species.

*Aryballocrinus tenuidiscus* (Hall 1861)

*Synonymy*: Bassler & Moodey, 1943, p. 601.

This species comes from the Lower Burlington limestone at Burlington, Iowa. It is the most peculiar form among *Aryballocrinus* species. Radial series may be marked with a slight radial ridge as the median series of plates in the posterior interradius may as well. The interradian areas are unusually large as additional plates occur in the upper margins of this regions. Hence the greatest width of the cup is at arm levels and the primaxils have additional sutures with some more interradian plates. The ornamentation of the cup plates consists of radial ridges perpendicular to the sutures.

*Aryballocrinus awthornsensis* (Wright 1955)

1955 *Periechocrinus* ? *awthornsensis* sp. nov. — J. Wright, p. 192, Pl. LXIII, fig. 7; textfig. 109

The only specimen founding this species was found near Awthorns in Gloucestershire (England) in the Tournaisian. It is a perfect *Aryballocrinus* agreeing in its essential characters to the genotype. Again it is mainly characterized by the ornamentation. The plates are rounded, much folded along their margins with raised portions meeting corresponding portions on adjoining plates. Sutures deeply impressed between the plications. The species much resembles *A. Whitei* in general appearance because its greatest width, too, is low in the cup; but the total height in relation to the width of the cup may be higher in this species.

*Aryballocrinus Sampsoni* (Miller & Gurley 1896)

1896 *Amphoracrinus sampsoni* nov. sp. — Miller & Gurley, p. 27, Pl. I, fig. 28, 29  
 1898 *Amphoracrinus sampsoni* Miller & Gurley — Weller, p. 83  
 1938 *Corocrinus sampsoni* (Miller & Gurley) — Peck & Keyte, p. 75, Pl. 29, fig. 10—13  
 1943 *Corocrinus sampsoni* (Miller & Gurley) — Bassler & Moodey, p. 372

This species from the Mississippian Chouteau limestone of Sedalia, Missouri, is referable to *Aryballocrinus* rather than to any other periechocrinid genus. It certainly does not belong to *Corocrinus* as it has almost nothing in common to the genotype of that genus. Its wide globose dorsal cup with lack of radial ridges and lack of ridged median series of plates in the posterior interradius separates

the species widely from *Corocrinus*. It is difficult to find specific characters for this species. The cotype as figured by Peck & Keyte (Pl. 29, fig. 12, 13) is wider than it is high. Moreover, the radials seem to be somewhat lower than usual in *Aryballocrinus*.

*Aryballocrinus parvus* (Wachsmuth & Springer 1890)

- 1890 *Megistocrinus parvus* n. sp. — Wachsmuth & Springer, p. 171, Pl. 15, fig. 7  
 1897 *Megistocrinus nobilis* Wachsmuth & Springer — Wachsmuth & Springer, p. 537, Pl. 51, fig. 8  
 1937 *Megistocrinus parvus* Wachsmuth & Springer — Laudon & Beane, p. 246, pl. 17, fig. 2  
 1943 *Megistocrinus parvus* Wachsmuth & Springer — Bassler & Moodey, p. 553

This species represents an *Aryballocrinus*. It is the smallest species in that genus. It stands apart through its low globose dorsal cup and rather low radial circlet. The plates of the cup show a considerable tendency to be nodose. A rib marking the radial series is absent. So it is doubted whether Laudon & Beane are right in regarding the specimen figured in Wachsmuth & Springer (1897, Pl. LI, fig. 10) as belonging to *A. parvus*. It is related to *A. Whitei* by the presence of ridged radial series.

*Aryballocrinus* spec. (Laudon & Severson 1953)

- 1953 *Periechocrinites* spec. 1 — Laudon & Severson, p. 527, Pl. 52, fig. 1—2

The two specimens figured by Laudon & Severson from the Mississippian Lodgepole formation of Montana represent a perfect *Aryballocrinus* species. Due to the rather fragmentary nature of the specimens an exact diagnosis cannot be given.

The newly established genus *Ayballocrinus* has relations to a certain group of periechocrinids with two arms to the rays: *Lenneocinus*, *Pradocrinus* and *Corocrinus*, but it differs from that group of genera by its globose dorsal cup, non-depressed interradial areas and strictly dichotomous branching arms. The most outstanding characteristics of the genus are the reduction of elements forming part of its dorsal cup and the quite unique strictly dichotome branching arms. Perhaps the genus has been derived from *Pithocrinus* by further reduction of interradial series and incorporation of less brachials in the cup, and increasing size of lower circles of the cup plates. Without doubt some relations to *Megistocrinus* have existed as well.

Family PARAGARICOCRINIDAE Moore & Laudon 1942  
Genus IBEROCRINUS Sieverts-Doreck 1951

*Iberocrinus multibrachiatus* Sieverts-Doreck, 1951

Pl. VIII, fig. 1—4

1952 *Iberocrinus multibrachiatus* n. sp. — Sieverts-Doreck, p. 109; Pl. 8, fig. 1a—d; textfig. 3

*Holotype*. The specimen described and figured by Sieverts-Doreck, 1951, pl. 8, fig. 1a—d; textfig. 3.

*Locus typicus*. 1.3 km east of Herrerueta, prov. of Palencia, Spain.

*Stratum typicum*. Sieverts-Doreck mentioned as such: Kalkmergel des Unteren Ober-Karbon (Westfal B). At the type locality the limestones that are exposed have now become known as Cotarazzo-limestone. Immediately below these limestones a coal group occurs. This coal seam is lowermost Westfalian D in age according to Wagner 1955, p. 159, so that the Cotarazzo-limestone member therefore is held to be Westfalian D. The foraminiferal fauna of this limestone corresponds to the *Fusulinella* ex gr. *brañoserae*-subzone of Van Ginkel (1960, p. 709, 715).

*Remarks*. The specimen no. TB 64 in the collection of the Museo del Instituto Geológico y minero de España at Madrid is referable to this species. It comes from the village Muda (Valdebreto) some kilometers south of the type locality. The specimen may have been found in exactly the same horizon as at the type-locality. The Muda specimen differs in certain respects from the holotype, but it is placed under *I. multibrachiatus* because it is only the second specimen so far found of this genus. Hence nothing is known of individual variation within the genus nor of its ontogeny.

*Description of the Muda-specimen. Form and dimensions.*

	Muda spec.	Holotype
Height dorsal cup	8 mm	7 mm
Total height of theca	13.6 mm	18 mm
Largest diameter of cup	17.1 (lateral)	21 mm
Smallest " " "	16.2 (antero-post)	18 mm

The base of the dorsal cup, including basal and radial circlets are flat. The circle of IBrr1 and iRR1 flares distinctly upwards. The higher plates are placed vertically. This all gives the dorsal cup a somewhat cylindrical shape. The lateral and antero-posterior diameters are almost equal. The specimen lacks the oval outlook of the holotype. The tegmen is low conical with a distinct depression at the posterior side. The anus is placed half way the height of the tegmen. The spiny top plate is only slightly developed. Due to the rather worn state of the specimen no ornamentation is observed.

The basals are not shown. They were apparently concealed by the stem. The diameter of the depression in which basals must have been situated and which was entirely occupied by the stem is 5.5 mm.

The five radials are in lateral contact, except at posterior side, where the primanal is situated in the radial circlet. The radials are all six-sided plates, wider than high, 4—4.5 mm wide and 2.4—2.7 mm high. The primanal differs from the radials in shape and proportions.

The radial series (cf. textfig. 13) have two primibrachs; the first one is typically low and almost rectangular. Only in the l.ant. rad. it is perfect rectangular but in all other radii these plates have a supplementary suture with one of the interradial plates. IBrr1 are about 2.5—3 mm high and as wide as high. The second primibrach is axillary; only in the l.post. rad. it is perfect five-sided but in all other rays its shape becomes six-sided through small supplementary sutures with interradial plates. These primaxils are not in perfect superposition to the first primibrachs, in r.post. rad., r.ant. rad. they are distinctly placed somewhat to the left. In l.ant. rad. the primaxil has a supplementary suture with postero left iR1 but nevertheless it is in good superposition to the preceding primibrach. In the l.post. rad. the primaxil is five-sided but is not in good superposition to IBrr1. Its position is somewhat to the right. This phenomenon is related to the number of arms as is described below.

Only one secundibrach occurs in each half ray. These secundaxils are

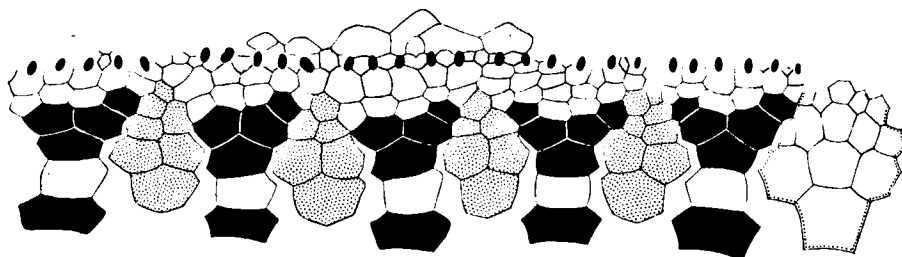


Fig. 13. Diagram showing the composition of the dorsal cup in *Iberocrinus multibrachiatus*. Specimen from the Westfalien of Mudá, Palencia (coll. Mus. Inst. Geol., Madrid, no. TB 64).

usually six-sided but they may become seven-sided if in lateral contact with more interradial plates or in upper contact with more brachials. The first tertibrachs may be axillary plates when three rami commence from that half ray. The tertaxils are then succeeded by one to three quartibrachs. If only two rami are born two or three tertibrachs occur. The distribution of arms over the half rays best can be studied from textfig. 13. It appears that that l.ant. radius has six arms, whereas in other radii only five arms occur (l.post. rad. probably has six arms as well, but due to weathering in this place one cannot be sure). It is peculiar that in r.post. rad., r.ant. rad. and ant. rad. the right half rays bear three arms and the left half rays only two. In connection with this the primaxils are placed somewhat to the left as if they make space for the greater number of arms in their right half rays. It is noteworthy also that the 6-rami l.ant. rad. is situated between radii that diverge at little from this almost straight radius. Sufficient room is thus made for the larger number of arms.

The uppermost incorporated tertibrachs or quartibrachs have very large facets for the reception of the free arms. The facets are placed almost vertical. The ambulacral openings are oval and roofed by the lower surfaces of the tegmen plates. Between these openings small iIII Brr or iIV Brr are placed.

The interradial areas are relatively small and generally composed of only six or seven plates. Interradial areas do not merge with the tegmen, since

the most distal brachials are in lateral contact ventral from the interradius. The first interradiial plate is the larger one, somewhat larger even than the first primibrachs. The succeeding interradiials gradually decrease in size upwards. Unfortunately the most distal part of the postero left interradius cannot be studied in detail due to weathering of the plates in that region. It cannot be stated whether the interradiial plates do come in contact with tegmen plates.

The posterior interradius is much differentiated and upwards it comes in contact with the tegmen over a width of about 3.5 mm. A is situated in the radial circllet. The plate is higher than wide, six-sided and the greatest width high up in the plate. A median series of three more six-sided plates is present. The primanal is succeeded by three plates in the next range. The lateral plates are slightly larger than the central one. Left and right of the median series the plates are arranged in two series. The posterior interradius is rather symmetrical.

The tegmen is low conical with a depression at the posterior side. The anus opens directly through the tegmen at about half its height. Differentiation of plates can hardly be distinguished. Some larger plates certainly occur along the margin of the tegmen. These plates roof two ambulacral openings of the arms and are in direct contact with iIVBrr or iIIIBrr, but a regular distribution of such plates as occurs in the holotype is absent. The top plates of the tegmen are larger; the central plate even may have been a spiny or nodose plate.

*Comparison with the holotype.* The specimen from Muda as described above certainly belongs to *Iberocrinus*, but it has some differences when compared to the holotype of *I. multibrachiatus*. These differences are now thought to be of minor importance possibly of the rank of individual variation or due to a different growth stage. But to be certain one must wait until much more material is available for study. In the meantime our specimen is placed under *I. multibrachiatus*.

The differences with the holotype are mainly in the shape and proportions. The holotype has a dorsal cup with distinctly flaring sides and is oval when looked at from above. The tegmen is about as high as the cup (in Sieverts-Doreck's description the total height of the top spine of the tegmen is given as 18 mm). The present specimen is somewhat smaller, with cylindrical dorsal cup and a tegmen that attains only half the height of the dorsal cup. All trace of ornamentation is lacking, but this may be entirely due to weathering of the specimen. So in this respect it cannot be compared with the holotype. The distribution of arms over the different rays is not identical with the holotype but this is not surprising in view of the irregular way of branching. The general rule that two primibrachs, one secundibrach and either two or three tertibrachs or a tertaxil with some quartibrachs are present is more diagnostic. The Muda-specimen shows iIIIBrr and iIVBrr at regular intervals between the most distal brachials whereas in the holotype these plates seem to be restricted to ordinary interradiial and interbrachial positions, where they come in contact with very small interambulacral plates of the tegmen. The alternation of small interambulacral plates and larger ambulacral plates roofing over the arm openings at the margin of the tegmen seems to be absent in our specimen, although some larger plates are seen to occur in a similar position.

## Family ACTINOCRINITIDAE Bassler 1938

## Genus NUNNACRINUS Bowsler 1955

*Nunnacrinus ? stellaris* (De Kon. & Le Hon 1854)

Pl. VIII, fig. 7

- 1854 *Actinocrinus stellaris* sp. nov. — De Kon. & Le Hon, p. 136, Pl. III  
 1943 *Actinocrinites stellaris* (De Kon. & Le Hon) — Bassler & Moodey, p. 274  
 1955 *Actinocrinites stellaris* (De Kon. & Le Hon) — J. Wright, p. 217, Pl. LIII, fig. 1—3;  
 Pl. LIV, fig. 17, Pl. LV, fig. 6, Pl. LVI, fig. 16  
 1955 *Nunnacrinus ? stellaris* (De Kon. & Le Hon) — Bowsler, p. 22

Only one incomplete specimen of the important Lower Carboniferous group of actinocrinids is known from Spain. It is stored in the collections of the Laboratorio de Paleontología, Universidad Central de Madrid (no. 101). The specimen comes from Lower Carboniferous limestones of the Sabero district (León). The right part of the tegmen with a piece of the dorsal cup are broken off.

The specimen represents a species referable to *Nunnacrinus* since it demonstrates all the diagnostic features of that genus. Its dorsal cup is low conical to somewhat rounded, the tegmen higher than dorsal cup, conical to somewhat arched, with centrally located anal tube. Only four arms to the ray. Each ray is composed of plates, much wider than high; IBr1 six-sided, IAx axillary five-sided, IIBr1 six-sided axillary, the IIIBr1 separated by a small elongate inter-brachial plate. Ligamentary fossae are seen to occur on the distal facet of the IIIIBr1. The arms are grouped in somewhat protuberant ray trunks. Interradial series are composed of only a few plates, openly connecting with the tegmen.

It is believed that the specimen has to be assigned to the species *N. ? stellaris*. It agrees with descriptions and plates of De Koninck en Le Hon (1954) and J. Wright (1955) in that the dorsal cup is somewhat rounded; the basal cup is low and first visible in side view; the tegmen is composed of large strongly tubercular plates. The ornamentation of the plates is finely granular, accompanied by weak radial ridges.

## Family COELOCRINIDAE Bather 1899

## Genus AOROCRINUS Wachsmuth &amp; Springer 1897

*Aorocrinus* spec.

Pl. VIII, fig. 5—6

From the Namurian Rabanal limestone a single dorsal cup is stored in the collection of the Rijksmuseum van Geologie en Mineralogie at Leiden (Holland) under no. 97600. It is a globose dorsal cup rather worn with some type of radial ornamentation on the calyx plates. The three basals are equal, rather low and but just visible in side view. The radials are very large, 4 mm high and about 5 mm wide, alternately six- and seven-sided. The primanal is situated in the radial circler. The first primibrach is low quadrangular, 2 mm high and 3.5 mm wide. The second primibrach is axillary, low five-sided. No higher brachials are preserved. The first interradianal plates are very large polygonal plates, in lateral contact with radial series of plates up to IAx. The primanal is succeeded by two plates in next range. The total height of the preserved fragment is 7 mm, the diameter 11.5 mm. The facet for the reception of the stem has a diameter of 4 mm and is circular in outline.

*Remarks.* The cup under consideration at first was thought to belong to *Amphoracrinus*, mainly because the two plates succeeding the primanal. But undoubtedly the low quadrangular first primibrach and low five-sided primaxil point rather to *Aorocrinus*. The cup especially resembles the dorsal cup of *Aorocrinus radiatus* as figured by Wachsmuth and Springer (1897, Pl. XLV, fig. 1) and Laudon and Beane (1937, Pl. XV, fig. 18), except that the primanal in that species has three plates in next range. Perhaps the presence of two plates in post. interradius of our specimen may be interpreted somewhat analogous to the differentiation in *Amphoracrinus* species of America with three anal plates and European forms with only two anal plates. It is noteworthy that *Aorocrinus banffensis* as described by Laudon, Parks and Spreng (1952, p. 568, Pl. 67, fig. 18—19; Pl. 69, fig. 19) has only two anal plates succeeding the primanal. Our specimen would then represent a European stock of *Aorocrinus* species. But it is realized that it is still the only form known in European Carboniferous strata.

#### Family AMPHORACRINIDAE Bather 1899

##### Genus PIMLICOCRINUS Wright 1943

J. Wright, 1942, p. 272 (generic name proposed in footnote); J. Wright, 1943, p. 89 (original description); G. Ubahgs, 1953, p. 739; J. Wright, 1955, p. 208.

*Genotype* by original designation: *Amphoracrinus clitheroensis* Wright, 1942.

*Diagnosis.* A genus probably belonging to the family Amphoracrinidae, characterized by a low dorsal cup, composed of plates with coarse granular or vermiculate ornamentation; very low basals that may be covered by the column; quadrangular first primibrach; axillary first secundibrach; usually two tertibrachs incorporated; tegmen much higher than cup, without conspicuous orals and with subcentral anal tube. Arms unknown.

*Distribution.* Up to the present day the genus *Pimlicocrinus* was only known from two species of the British Tournaisian: the genotype and *P. latus*. A representative of the latter species now has been found in strata of probably Namurian age in the Spanish province of Palencia. Two new species are recognized. One occurs in Westfalian strata of Asturias and Marocco, the other is a museum specimen of unknown provenance.

*Remarks.* The genus *Pimlicocrinus* as defined at the present days covers a close assemblage of forms from Carboniferous strata in Europe and the Mediterranean area. Some problems arise however when its systematic position is regarded. Wright (1943) pointed out that *Pimlicocrinus* is mainly characterized by its indistinct orals and subcentral anal tube. Today it seems probable that some more stress may be laid on the fact that the first primibrach is a low quadrangular plate. This is seen to be a rule, in all known specimens now assigned to *Pimlicocrinus*, without exception. Low quadrangular first primibrachs are an exception among Periechocriniticae. It is perhaps the only genus within this group to show this character. Some American *Amphoracrinus* species have low quadrangular first primibrachs as well, but this cannot be thought typical for *Amphoracrinus* as a whole. The neotype of *Amphoracrinus Gilbertsoni* has five- or six-sided first primibrachs, not very well defined in form. This is often seen among *Amphoracrinus* species. It is found that *Pimlicocrinus* has certain affinities to some coelocrinid forms in the general appearance and composition of the dorsal cup. But it differs definitely from Coelocrinidae by absence of

the three plates succeeding the primanal, by absence of a median series of plates in the posterior interradius, by absence of distinct orals and by the presence of an anal tube.

A particularly interesting problem is the exact affinity of *Pimlicocrinus* with the American *Amphoracrinus* species, that seem to be somewhat related, and to *Agaricocrinus*. In view of this problem it is particularly unfortunate that the arms of *Pimlicocrinus* are still unknown. It may well be that the arm-structure shows diagnostic features, but no suggestion or contribution to solve this problem can be given at the moment.

*Pimlicocrinus latus* Wright, 1943

Pl. VIII, fig. 8—10

1942 *Pimlicocrinus latus* (footnote) — J. Wright, p. 272

1943 *Pimlicocrinus latus* sp. nov. — J. Wright, p. 91, Pl. III, fig. 1—11, 14—17, 22, 21

1955 *Pimlicocrinus latus* Wright — J. Wright, p. 210, Pl. LI, fig. 6—10, 13, 14, 21—25, 33—37; Pl. LXI, fig. 8

*Holotype*. Wright (1955, p. 210, Pl. LI, fig. 6—10) designated his specimen A. C. 2391 as the holotype.

*Locus typicus*. Coplow Knoll, near Clitheroc, Lancashire, England.

*Stratum typicum*. Tournaisian.

*Diagnosis*. A *Pimlicocrinus* species of moderate size, characterized by a low cup which is usually visible from the side; wide area of basals and radials; incorporation of brachials up to IIIBrr2; brachial lobes projecting beyond the edge of the tegmen; interrarial areas deeply sunken between the brachial lobes; moderately high tegmen, consisting of relatively few, thick plates, provided with spines which are more frequent in the post. interradius; rather coarse granular ornamentation of cup plates. Column unknown; arms unknown.

*Material*. The specimen 97601 in the collection of the Rijksmuseum van Geologie en Mineralogie at Leiden (Holland) from Namurian limestones at Rabanal de los Caballeros (prov. of Palencia), Spain. It is the first specimen of this species found outside Great Britain.

*Description*.

	97601	Paratype 2389	Holotype
Height	16.0	19.6	23.7
Width of cup between IIIBrr	25.0	29.0	39.8
Width of cup between iRR	18.5	19.7	24.0
Width of tegmen at base anal tube	4.6	3.9	—

The dorsal cup is very low with a flat base. The radial series give rise to four free arms that are grouped together in trunks. As a consequence the interrarial areas are sunken between these trunks. The cup is strongly lobate in its upper portion. The tegmen is high conical, about twice as high as the cup. An anal tube must have been present in a subcentral position. The ornamentation of the cup is of a coarse nature. The tegmen plates are all nodose.

The three equal basals have a total joint hexagonal outline. The central



part is slightly depressed for the reception of the rounded stem. The axial canal is small. The basals are provided with a rib that continues all around the stem; it is tripartite by constrictions at the interbasal sutures.

The five radials are large hexagonal plates, very much wider than high, the greatest width occurs rather high up in the plate, greatest width 7.1 mm, height 3.2—3.5 mm. The radials are in lateral contact, except at the posterior side where the primanal is situated in the radial circlet. The radials have a sharp high rim running concentrically around the stem; it passes even on to the primanal. The region of the radiobasal sutures is smooth and depressed.

The radial series include two primibrachs, the first very low quadrangular, the second five-sided axillary. The first secundibrach is axillary, generally six-sided, laterally in contact with two interrational plates. Each secundibrach is succeeded by series of two tertibrachs. So four free arms are borne on each radius. They must have come off almost horizontal. The regions of secundibrachs and tertibrachs are grouped in lobes.

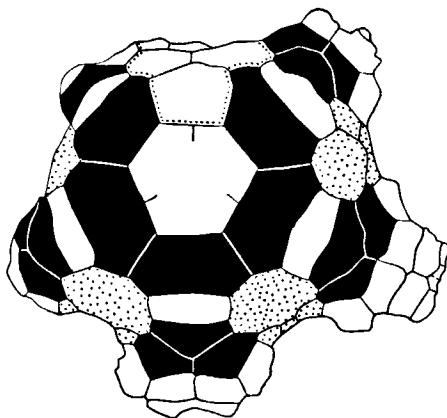


Fig. 14. Diagram showing arrangement of plates in the basal view of the dorsal cup in *Pimlicocrinus latus*. Specimen from Namurian limestone at Rabanal de los Caballeros (coll. Mus. Geol. Min., Leiden, no. 97601).

In lateral interrational areas a large polygonal iR1 occupies most of the space. The plate is succeeded by two, or occasionally three narrow and high plates. The interrational areas are deeply sunken between the arm trunks. The zone of contact with the tegmen is about 3 mm wide. The posterior interrational is differentiated. The primanal is a comparatively small five-sided plate situated in the radial circlet. It is 4 mm both wide and high. The primanal is succeeded by two fairly large polygonal plates laterally in contact with the radial series of plates up to IIAXx. Their height is about 4.5 mm. Four plates are seen to occur in the next range. Higher portions of posterior interrational and posterior side of the tegmen are broken off.

The tegmen is high conical in its upper regions, but strongly lobed in the lower parts that are in contact with the tegmen. It is composed of many small irregularly arranged plates, all nodose. Towards the subcentral anal tube, that apparently was broken off, the plates become somewhat larger but orals cannot be distinguished. No differentiation of tegmen plates exists.

*Remarks.* Up to now the species *Pimlicocrinus latus* was only known from the seven specimens of the Tournaisian in Lancashire and one incomplete specimen

from the Tournaisian of Pembrokeshire. All these specimens were described by Wright. The specimen 97601, although somewhat smaller than Wrights' specimens, fully agrees with the genus- and species diagnosis. It is especially comparable to the paratype no. 2389. The ratio of dimensions, too, is correct. The coarse, nodose ornamentation of the tegmen plates is even better shown than in Wright's specimens. Since the posterior side of the tegmen is lacking, it cannot be seen if the tegmen plates in this region are as small and numerous as in the British specimens. The arms of the Spanish specimen are free from the IIBrr2, so that, according to Wright, it should be an adult one. Wright did not mention the presence of interbrachial plates in his specimens and no such a plate can be seen in any of his figures. The r.ant. radius of 97601 probably has two very small elements between the two series of tertibrachs, which are either iIIBrr or projections of the IIBrr2, surrounding the ambulacral opening. The sutures between these elements and the second tertibrachs are not distinct enough as to conclude to independent iIIBrr.

The specimen at Leiden is still the only known representative of *P. latus* in Spanish Carboniferous strata. Its supposed Namurian age is surprising when it is realised that all the British specimens are found in strata of Tournaisian age. However, representatives of the genus *Pimlicocrinus* have been found in still younger strata of Westfalian age in Asturias and Marocco.

*Pimlicocrinus* spec. 1

textfig. 15 A, B

In the Verneuil-collection of the Ecôle Nationale Supérieure des Mines at Paris four thecae of crinoids from Westfalian strata near Pola de Lena (Asturias) are stored. They all have very low dorsal cups, high conical tegmens with subcentral anal tube and a very pronounced ornamentation of sharp and high rims. The arms are grouped. The composition of the dorsal cup is shown in textfig. 15 A. 3BB equal. Radials six-sided, in lateral contact, except at posterior side where smaller primanal is placed in radial circler. IBr1 low quadrangular, IBr2 axillar. First IIBr axillar, followed by one or two tertibrachs without iIIBr. First interrarial plates very large polygonal plates, succeeded by two smaller plates. In one of the specimens A is followed by three plates in next range, in another specimen only by two plates but here the primanal intervenes a little between two basals.

*Remarks.* De Verneuil (1846, p. 456) listed *Actinocrinites triacontadactylus* among a series of fossils collected in Westfalian strata at El Valle near Pola de Lena. This is his only record on Carboniferous crinoids from Spain. No other crinoids from Carboniferous strata of Spain are present in the Verneuil-collection. It is thought therefore that Verneuil's record of *A. triacontadactylus* relates to the specimens under consideration. However, it is obvious that the specimens from Pola de Lena cannot be assigned to *Actinocrinites*. The composition of cup plates, the low cup and high tegmen with subcentral tube, the grouped arms all support the assignment of these specimens to *Pimlicocrinus*, rather than to any other genus.

The only known specimens to which the Asturian species has to be compared is the "*Actinocrinites stellaris*" from the Westfalian of the vicinity of Colomb-Béchar (Marocco) as described by G. & H. Termier (1950, p. 84, Pl. CCXIV, fig. 1). It is exactly the same as the Spanish species (cf. textfig. 15 B). IBr1 is

quadrangular, IBr2 axillary; single IIBr, some IIIBrr incorporated; very large polygonal iR1, A followed by two large plates; low dorsal cup, very high tegmen, grouped arms. The ornamentation of the cup plates is precisely the same as in the Asturian specimens. Hardly any difference between the Moroccan and the Spanish specimens can be found. It is supposed that both forms belong to one and the same species. This new species of *Pimlicocrinus* only can be established if the Moroccan specimens are confronted with the Asturian ones. Such a close comparison is impossible at the moment, perhaps it will come later. But among *Pimlicocrinus* species this new species will be mainly characterized by its large size, its especially coarse ornamentation and its younger age.

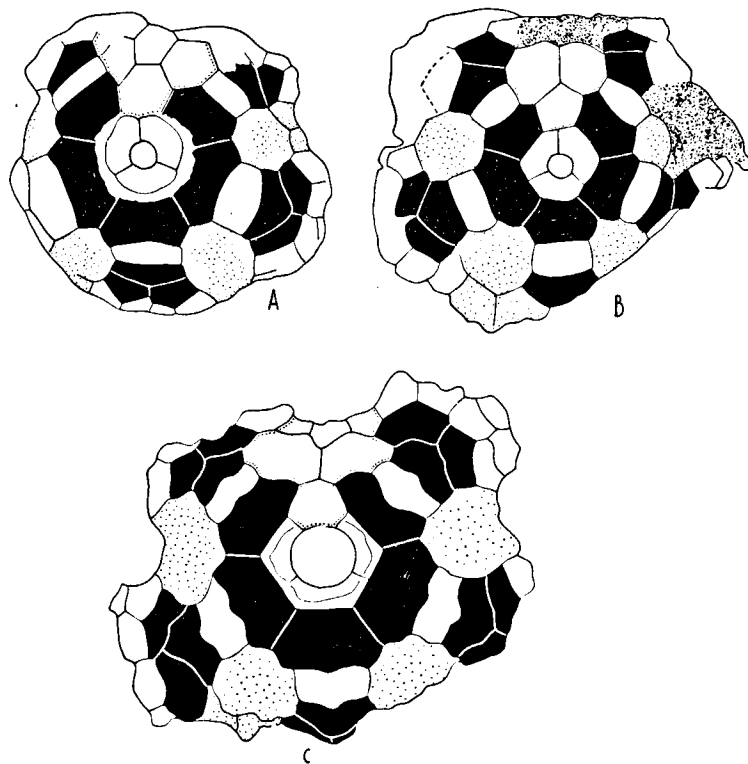


Fig. 15. Diagrams showing a comparison of arrangements of plates in the dorsal cups of the *Pimlicocrinus* species 1 and 2. (A) *Pimlicocrinus* spec. 1, the specimen in the Verneuil collection at Paris. (B) *Pimlicocrinus* spec. 1, the specimen from Morocco described by H. & G. Termier. (C) *Pimlicocrinus* spec. 2, specimen in the coll. Mus. Inst. Geol. Min., Madrid, no. TB 83.

*Pimlicocrinus* spec. 2

Pl. VIII, fig. 11

textfig. 15 C

This species is represented by a single dorsal cup, without tegmen, in the collection of the Museo del Instituto geológico y minero de España at Madrid (no. TB 83). Age and location are not indicated on the labels.

The dorsal cup is depressed (about 8 mm high), its diameter is 24 mm.

Some ambulacral parts of the tegmen still attached to the dorsal cup suggest that the tegmen was very high.

The impression of the stem on the base of the cup is circular in outline with a diameter of 3,6 mm. The axial canal of the stem was five-sided about 1 mm in width. The base of the cup is flat. The three basals are not in contact at the posterior side, the primanal intervenes between two basals so as to come in contact with the stem. The lower portions of the basals are provided with a rim that surrounds the stem. The rim does not continue over the primanal. The radials are large six-sided plates, laterally in contact except at posterior side where the upper part of the primanal separates l.post. R from r.post. R. The lower portions of the radials are smooth and form a circular depression around the stem. The first primibrach is a low quadrangular plate, the second primibrach is axillary, five-sided. The first secundibrachs are also axillary plates. Each secundaxil may be followed by two or three tertibrachs. Interbrachial plates are not incorporated. Each radius bears four rami. The arms are distinctly grouped in trunks. The position of the articulation facets for insertion of free arms suggests that the arms came off almost horizontally. The first interradianal plates are very large and certainly the largest elements forming part of the cup. In most interradiani it is the only plate present. But in postero right interradius iR1 is smaller and succeeded by two smaller plates. The posterior interradius has two large plates succeeding the small primanal. Three smaller plates are present in the second range.

The cup plates have a pronounced radial ornamentation of coarse rounded ribs. The centres of the plates are swollen. It is very noticeable that radial ornaments does not pass from the radials on to the basals.

*Remarks.* The composition of this cup, its shape and proportions in relation to the tegmen justify its assignment to *Pimlicocrinus*. The strange position of the primanal between radial and basal circlets may be regarded as aberrant. It is however observed from another *Pimlicocrinus* specimen as well. The present specimen cannot be compared to any other *Pimlicocrinus* species. The English Lower Carboniferous species lack such a typical ornamentation. The Upper Carboniferous Spanish and Moroccan species have a distinct ornamentation and differ in shape and proportions. The cup under consideration may be thought as to belong to a new species. However, it is deemed as far better not to establish a new species on only a single cup.

#### Family HEXACRINITIDAE Wachsmuth & Springer 1881

##### *Platyhexacrinus Kegli* W. E. Schmidt 1932

The types of this species have been lost, together with all the material of Schmidt's collection. Two new specimens consisting of fragmentary dorsal cups have been collected from the type locality at Arnao. They are lodged under no. 97735 in the collection of the Rijksmuseum van Geologie en Mineralogie at Leiden (Holland). The new specimens do not contribute any further to the species description.

## Suborder GLYPTOCRININA Moore 1952

### Family POLYPELTIDAE Angelin 1878

On the occasion of grouping *Polypeltes*, *Trybliocrinus* and *Hadrocrinus* in the family Polypeltidae, Ubaghs (1953, p. 742) gave a provisional diagnosis for that family. Later, in 1956, when describing in detail the morphology of *Polypeltes*, a definite diagnosis was published (p. 553). Some elements of that diagnosis will be discussed now in the light of new knowledge of the morphology of *Trybliocrinus*. The study on the ontogeny of *Trybliocrinus* proves Ubaghs to be correct when he states: "plaques capsulaires proximales progressivement résorbées, ne bénéficiant pas du même coefficient de croissance que les autres éléments thécaux, mais restant petites". Such zone of low growth rates in the proximal part of the cup in *Trybliocrinus* was proved to exist (cf. p. 103 of this work). This low growth may be thought to occur in all Polypeltidae. Ubaghs further statement that the plates even may be affected by a process of resorption leading to complete disappearance of the basals, has been proved not to hold for *Trybliocrinus*. Basals are still well developed, even in mature specimens. So it seems advisable to omit the statement on resorption of cup plates from the family-diagnosis. Ubaghs moreover included a statement on the arm structure. Since the arm structure of *Trybliocrinus* has proved to be very complicated and highly specialized, arms of Polypeltidae are very diverse, or even unknown. The only thing in common is the biserial arrangement of brachials. So the diagnostic characters of *Trybliocrinus*' arms have been included in its genus diagnosis and not in the family-diagnosis. The only statement in the family-diagnosis on characters of the arms must read that arms are biserial.

### Genus TRYBLIOCRINUS Geinitz 1867

Geinitz, 1867, p. 284; Zittel, 1879, p. 377; Wachsmuth & Springer, 1881, p. 233; Bather, 1900 (in E. Ray Lankaster), p. 163; Springer, 1913 (in Zittel-Eastman), p. 191 (as *Tribliocrinus*, by error); Jaekel, 1921, p. 32; W. E. Schmidt, 1932, p. 5 (as *Hadrocrinus*); Bassler, 1938, p. 189; Bassler & Moodey, 1943, p. 717; Moore & Laudon, 1943, p. 105, 117; Ubaghs, 1953 (in Piveteau III), p. 742; Ubaghs, 1956, p. 551.

*Genotype* by monotypy: *Glyptocrinus* (in error for *Trybliocrinus*) *Flatheanus* Geinitz, 1867.

*Remarks.* A perfect explanation of the synonymy and former classification of *Trybliocrinus* was already given by Ubaghs (1956, p. 551, 552). To his observations nothing can be added at the moment.

*Diagnosis.* A genus of the family Polypeltidae Angelin, 1878, characterized by wide bowlshaped dorsal cup; two primibrachs per ray, numerous secundibrachs monoserially arranged in proximal part of half ray but distad passing into biserial arrangement; largely developed interradiation and interbrachial areas; commonly a non-differentiated posterior interradius; low tegmen, composed of prismatic plates, many of them with bulbous expansions forming an underlying structure, anus opening directly through tegmen; vessel system within tegmen plates; biserial arms with ramules placed in alternating order along both sides

of the rami; first ramule may be fixed to dorsal cup; all ramules pinnulated; oral sides of ramules and rami roofed with stratified ambulacral plates; thick stem with large pentalobate axial canal, lobes interradial in position; proximal part of stem provided with branching cirri for attachment; coelomic vessel system, probably for respiratory function present: in the stem differentiated as the radial canals between the columnals, in the cup as gonioporoids and in the tegmen as a system of vessels and lacunes between lower parts of tegmen plates.

*Distribution.* Up to now the only known species *Trybliocrinus Flatheanus* has been found in Lower Devonian strata both in Asturias and León. A representative of this genus is probably present in Devonian strata of Germany (cf. W. E. Schmidt, 1941, p. 218, fig. 62, as *Crinoideorum* gen. et. spec. indet.).

*Trybliocrinus Flatheanus* Geinitz, 1867

Pl. VIII	fig. 12, 13
Pl. IX	fig. 1—4
Pl. X	fig. 1—7

- 1867 *Glyptocrinus Flatheanus* Gein. — Geinitz, p. 284; Pl. III, fig. 1, 2 (*Glyptocrinus* in error for *Trybliocrinus*)  
 1932 *Hadrocrinus Hispaniae* n. sp. — W. E. Schmidt p. 7; Pl. I—III, pl. IV, fig. 11a—c  
 1943 *Trybliocrinus flatheanus* (Geinitz) — Bassler & Moodey, p. 717  
 1950 *Trybliocrinus flatheanus* (Geinitz) — Ubaghs, p. 107, footnote  
 1953 *Trybliocrinus flatheanus* (Geinitz) — Ubaghs, p. 692, fig. 33h  
 1956 *Trybliocrinus flatheanus* (Geinitz) — Ubaghs, p. 558, fig. 3  
 1958 *Hadrocrinus Hispaniae* Schmidt — Almela & Sanch, Pl. IX, fig. 4, 4a  
 1960 *Trybliocrinus Flatheanus* (Geinitz) — Breimer, p. 258, 259, fig. 6, 7

*Holotype.* The specimen described and figured by Geinitz (1867, p. 284, Pl. III, fig. 1, 2) and Ubaghs (1956, p. 558, fig. 3 B) has to be regarded as the holotype. Geinitz did not state where his specimen was stored, but after investigation it appeared to be housed in the Staatliche Museum für Mineralogie und Geologie at Dresden (Germany). Dr Prescher, the Director of the Museum, Dresden, informed me that the holotype of *Trybliocrinus* was destroyed during the Second World War.

*Locus typicus.* The Western Cape of the Bay of Arnao near Aviles (Asturias). This headland is referred to as Cape La Vela by W. E. Schmidt (1932, p. 1, text fig. 1).

*Stratum typicum.* The red calcareous shales belonging to the "calcaire de Ferroñes" in the description of Ch. Barrois (1882, p. 470, Pl. XVIII). According to Comte (p. 324, 331) these beds are correlable to those of the La Vid shale formation in León and correspond to the Lower Emsian.

*Diagnosis.* As the unique species of *Trybliocrinus* its diagnosis provisionally will be the same as the genus diagnosis.

*Material.* (1) Naturmuseum of Senckenberg, Frankfurt am Main, Germany: the original specimens of W. E. Schmidt no. F XXIII 46b, F XXIII 47a and F XXIII 48b all from the type locality at Arnao. The specimens are labelled *Hadrocrinus hispaniae*. (2) Rijksmuseum van Geologie en Mineralogie, Leiden, Holland: 3 plaster casts of W. E. Schmidt's specimens in Frankfurt, 46 fragmentary dorsal cups no. 97602—97647 from the type locality at Arnao, 27 fragmentary dorsal cups no. 97648—97674 from Lower Emsian La Vid formation at Colle, many stem fragments no. 97675 from Lower Emsian La Vid formation at Colle

(León), 9 fragments of dorsal cups no. 97676—97684 from Lower Emsian La Vid shales at Villayandre (León), 10 fragments with polished surfaces no. 97689—97698 from the type locality at Arnao. (3) Museo Nacional de Ciencias Naturales, Madrid: 46 specimens no. DH 1001—DH 1044, DH 1068 and DH 1069 from the type locality at Arnao, some of which are complete and even have the tegmen attached to them; 23 fragments of stems no. DH 1045—DH 1067 from the type locality at Arnao, some of which have beautiful cirri attached to them. (4) Museo del Instituto geológico y minero de España, Madrid: spec. no. 2.393 from the type locality at Arnao, 39 more specimens from the type locality, 2 fragments of cups and 2 stem fragments from Lower Emsian deposits at Colle (León), 1 fragment of a dorsal cup from Orzonaga (León), 1 fragment of a dorsal cup from La Velilla (León), many isolated arm fragments from Colle. (5) Escuela de Minas, Madrid: 3 specimens no. 6417, 6418 and 6420 from the type locality at Arnao. The specimens 6417 and 6418 are very well preserved. They are amongst the most complete and most interesting specimens. There are even parts of the arms attached to them. (6) Instituto de Geología aplicada, Oviedo, Asturias: 1 dorsal cup from the type locality at Arnao, 1 dorsal cup and 5 fragments of cups from San Fenolleda (Asturias). (7) Verneuil collection of the *École Nationale Supérieure des Mines*, Paris: 2 fragments of cups, labelled as originating from Sabero. It is believed that they come from the La Vid shales at Colle.

*Description.* Form, dimensions and organisation of the theca.

The theca of *Trybliocrinus* is probably the largest known among crinoids. Both the height as the width of the theca may attain such unusual dimensions as 11—12 cm. The maximum height for the dorsal cup is 6.5 cm, and for the tegmen 4.5 cm.

The form of the dorsal cup is most variable, but as a rule the width of the cup exceeds the height. Its form generally appears to be more or less bowl-shaped. The basal part of the cup is commonly flat or even a little inverted near the stem. The walls of the cup in a few specimens (probably only the largest ones) are perfectly vertically disposed. In most of the small specimens however, both walls are flaring, approaching the ideal bowl-shape. But in the vast majority of specimens one of the walls flares out, whereas the opposite wall is vertical or even incurving. The cups of most specimens viewed from above appear to be oval. The direction of the longer axis in relation to the antero-posterior axis usually cannot be defined since the posterior interradius frequently is not differentiated. There does not seem to be a preferred direction of the longer axis to the diameter between incurving and outflaring walls.

In young specimens only the basals are found to be covered by the stem. In adult forms however the most proximal cycles of cup-plates are covered by the stem. Only parts of the first primibrachs and first interradians may project beyond the stem. The cup itself is composed of the radial series (two primibrachs and a large number of secundibrachs) and large interradian and interbrachial areas. There seems to be a relation between the measure in which the proximal cup-plates are free from the covering of the stem and the incurving or outflaring position of the wall. The distance from the stem to the ventral margin of the cup (if measured over the surface of the cup) may be larger in an incurving or outflaring part of the cup than elsewhere in the same cup. If such a distance in adult specimens is found to be larger than usual for that cup, it is seen that even the radial may be at least partly free from the stem. The specimen 6420

(coll. Escuela de Minas, Madrid) and TB 10 (coll. Mus. Inst. Geol., Madrid) have all the radials partly projecting beyond the stem boundary. This may be attributed to the aberrant low globose form of these cups.

The ornamentation of the dorsal cup is diverse. Some specimens have thecal plates with fine vermiculate to granular ornamentations, others show some plates with small central tubercles. Traces of ornamentation are only seldom found. Most times the cup plates appear to be smooth. It is not certain always whether this is due to weathering or not. So in this particular case one cannot use this characteristic for diagnostic purposes.

The tegmen is not very high. It is composed of a great many of small plates. An anal tube was missing. A somewhat excentric depression occurs, apparently for the anus. In a few specimens the tegmen is asymmetric: the posterior side somewhat steeper than the anterior side. No traces of ornamentation were ever seen on the tegmen.

The arms are unusually stout and very complex in composition. They came off in an almost horizontal position. The bases of the arms at the level where they become free, may have widths up to 2.5 cm for adult individuals. The width decreases gradually and most probably the position of the arms changes to horizontal. A few arm fragments showed a granular or finely tuberculate ornamentation.

**The base.** The changes during ontogeny of the basal part of the dorsal cup of *Trybliocrinus* is discussed below in a separate paragraph (see p. 103). For the moment only the organisation of the plates in connection to other plates will be reviewed. Only three basals occur, unequal, the smaller one l. anterior in position. The basals are in lateral contact all around their circle. The cycle of basals is pierced by a very wide axial canal (up to 12 mm in adult specimens). This opening is pentalobate, each of the five lobes interrarial in position. In young specimens the central elevation at the internal side of the cup is entirely formed by the basals. This elevation is not visible at external side of the cup due to its covering by the stem. So basals — even in the smallest specimens examined — never can be observed in external views. In more advanced growth-stages this central elevation gradually becomes formed by distally situated plates (i.c. radials and primibrachs), the basals so entering in a position quite on top of this elevation. This top of the elevation becomes more and more differentiated during ontogeny. In young specimens it is convex but in later stages it differentiates to a distinctly pentalobate structure of five ribs that separate five depressions. The depressions coincide with the lobes of the axial canal and are interrarial in position; the ribs radial in position.

The radials are five in number and all about equal in size and shape, distinctly wider than high. The radials are commonly in lateral contact even at the posterior side, where the first anal plate never has been found to be situated in the circle of the radials. In a few specimens the completely lateral contact of all the radials may be lost by an intervening contact of basals and first interradians. The smaller basal of spec. 97680 is in contact with the antero left iR1, all other radials in lateral contact. In spec. 97661 the circle of radials is interrupted at two spots by basal-interrarial contacts. In 97679 this happens perhaps three times and in 97646 four times. One cannot be very sure of course that these contacts between basals and first interradians really intervene between two adjacent radials, in this sense that they completely separate such radial plates. It seems possible that the contact of basals and first interradians is rather superficial, so that radials might be in lateral contact under a thin covering part of



the basal. Not enough evidence can be found in support to this supposition since the sutures between radials and basals in quite a many cases can only be observed with difficulty, probably due to some anchylozing between these plates.

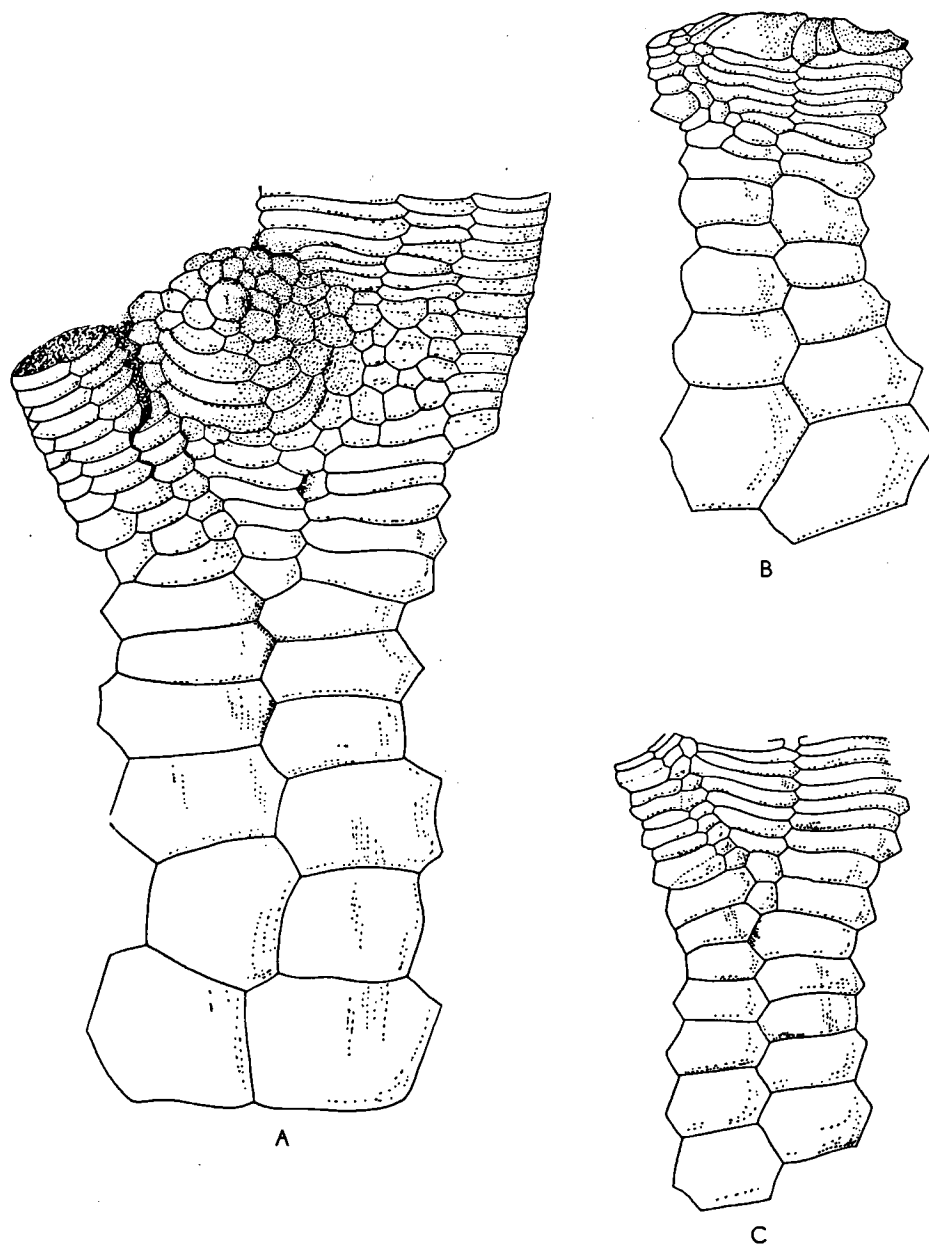


Fig. 16. *Trybliocrinus Flatheanus* Geinitz — Morphology of the radial series of fixed brachials. (A) Radius with basal part of fixed ramule and base of the main arm trunk; between both structures a blind ending ramule. Specimen from Emsian shales at Arnao, Asturias (coll. Escuela de Minas, Madrid, no. 6418). (B) Radius with irregular arrangement of plates at the level where brachials divide. Specimen from Emsian shales at Arnao, Asturias (coll. Mus. Geol. Min., Leiden, no. 97608). (C) Radius with regular arrangement of plates at the level where brachials divide. Specimen from Emsian shales at Arnao, Asturias (coll. Mus. Geol. Min., Leiden, no. 97636).

**Radial series.** The radial series of fixed brachials are incorporated in the dorsal cup to a large extent. A fixed number of two primibrachs per ray is found; the first one generally six-sided, the second one five-sided and axillary. The proximal portions of the series of primibrachs may be covered by the stem in adult specimens, including the complete covering of the first primibrach. Completely covered primaxils have never been observed, only the proximal edges of these plates are occasionally covered in apparently senile individuals, such as spec. 2393.

The brachials of higher order incorporated in the cup have all to be regarded as secundibrachs. Their arrangement at first is monoserial but quickly changes into biserial. The monoserially arranged parts of the half-rays include two to five plates (generally three). There seems to be a relation between the number of uniserially arranged secundibrachs of a radius and the position of such a radius in an incurving, outflaring or higher part of the cup wall. In such cases the number of secundibrachs may be higher than in other rays of the same specimen. The biserially arranged parts may be very high and even include fifteen to twenty pairs of brachials. The first five to ten pairs of these brachials commonly are fairly high plates although their heights never exceed their widths. The most distally situated pairs of secundibrachs rapidly become lower. The row of plates that finally leads to the main arm trunk is generally situated higher than the row leading to the fixed ramule. In most cases the two series of secundibrachs of one half ray become divided by intervening plates (cf. text fig. 16 B, C) that have a function in the formation of the arm as well. These intervening plates soon become arranged biserial as well, so that at the level where the arms become free four series of brachials occur. Two series give off the biserial fixed ramule; the plates belonging to the other series are very wide plates that form the biserial main arm trunk (ramus). In the young specimen TB 4c the intervening brachials occur at a level where the main arm trunk may be considered as free, whereas in the young form TB 4e no trace of these intervening brachials can be found. Fixed ramules do not occur in either specimen.

The **interradial areas** constitute very large parts of the dorsal cup. These areas separate the rays completely from the first primibrachs to the distal edge of the dorsal cups. Up to 60 plates may take part in the constitution of the interradian areas, most of them irregular in shape and gradually decreasing in size distad. The area itself does not narrow in distal direction; it is in contact with the tegmen over 2 cm in mature specimens.

The first interradian plate is situated in one circle with the first primibrachs. This circle still belongs to the allometric growth-zone of the cup and consequently the first interradians gradually become covered by the stem until it cannot longer be observed at external side in mature specimens. The first interradian is a regular six-sided plate, if not in contact with a basal. In lateral interradian areas this plate always is succeeded by two plates, six- or seven-sided in shape. In most specimens the most proximal interradian is followed by two or three ranges of two elements, after which a range of at least three plates follows. At this level the interradian areas attain their greatest width: i. e. approximately at the level where the secundibrachs become biserially arranged. The distal portion of the interradian areas consists of irregular plates, generally four to six plates wide. The posterior interradius is frequently not differentiated. If differentiated a seven-sided primaxil may be distinguished, situated in the circle of first primibrachs and first interradians. Its position in this circle implies that it gradually

becomes covered by the stem until it disappears completely from the external surface of mature specimens. The primanal is followed by three plates in the next range, all smaller than the proximal anal; the central one is five-sided, the lateral ones six-sided. The next range consists of four plates and at this level the posterior interradius attains its greatest width. The higher part of the posterior interradius is very similar in composition to the lateral interradian areas and hardly can be distinguished from them. No median series of plates ever occurs.

**Interbrachial areas.** The areas formed by the intersecundibrachs are remarkably large. These areas gradually widen towards the distal edge of the cup at which places they enter in contact with the tegmen. These joins are as wide as the contacts of the interradian areas with the tegmen. The total amount of plates forming these areas may rise to thirty in large specimens. Usually the arrangement of intersecundibrachs is rather irregular.

The first intersecundibrach generally rests upon distal facets of IIBrr1; in a few specimens (as for example the l.post. iIBr1 of specimen DH-1014) it was found to separate the IIBrr1 completely, and so is in contact with the primaxil; but this is an exception rather than a rule. iIBr1 is variable in form, depending entirely of the amount of plates that succeed it. iIBr1 generally is followed by one or two plates, but in one of the interbrachial series of spec. 2393 a range of three plates succeed it (cf. text fig. 17). In this last mentioned interbrachial area some plates in a perfectly median position give the whole area a suggestion of a symmetrical appearance suggesting a regular arrangement of the plates. The distal part of the intersecundibrachial areas comprises more and more plates that gradually become smaller.

**Ornamentation** of the dorsal cup. In the vast majority of *Trybliocrinus* specimens the cup plates appear perfectly flat and smooth with non-depressed sutures and only rare traces of ornamentation. This will be mainly due to the rather weathered state of most specimens examined. But some exceptions have been found: the spec. 2393 and 6417 have slightly depressed sutures and traces of a vermicular type of ornamentation are clearly visible on some interbrachial plates in the upper part of the cup. The ornamentation of the plates in the young specimens TB 4c and TB 4e is quite different. The plate-surfaces are strongly convex, the centres of the plates are produced into a coarse tubercle or spine. This ornamentation is much more prominent in the distal part of the cup and occurs both in radial and interradian areas. Proximally situated plates have more delicate tubercles. The fragment 97665 has only slightly convex plates and very fine tubercles or spines in the centre of the plates. A node in spec. TB 20 is most unusual, occupying the whole surface of an intersecundibrach. Small riblets pass from its centre onto the adjoining plates. Strangely it is the only ornament occurring in the specimen.

The few observations we could make do not permit us to conclude upon the diagnostic value of ornamentation in *Trybliocrinus*. The diverse nature of ornamentation suggests that different varieties or even species may exist. It remains impossible to subdivide the only known species, since no regular and separate patterns of ornamentation are found to exist amongst the examined material. Moreover it is not yet fully understood how ontogeny may change the nature of the surfaces of the plates and how it affects the ornamentation. Perhaps it is a usual development during growth that young individuals have convex plates and more prominent ornamentation, whereas later growth can reduce it all. Such an indication has been met with in *Pyxidocrinus collensis* as well.

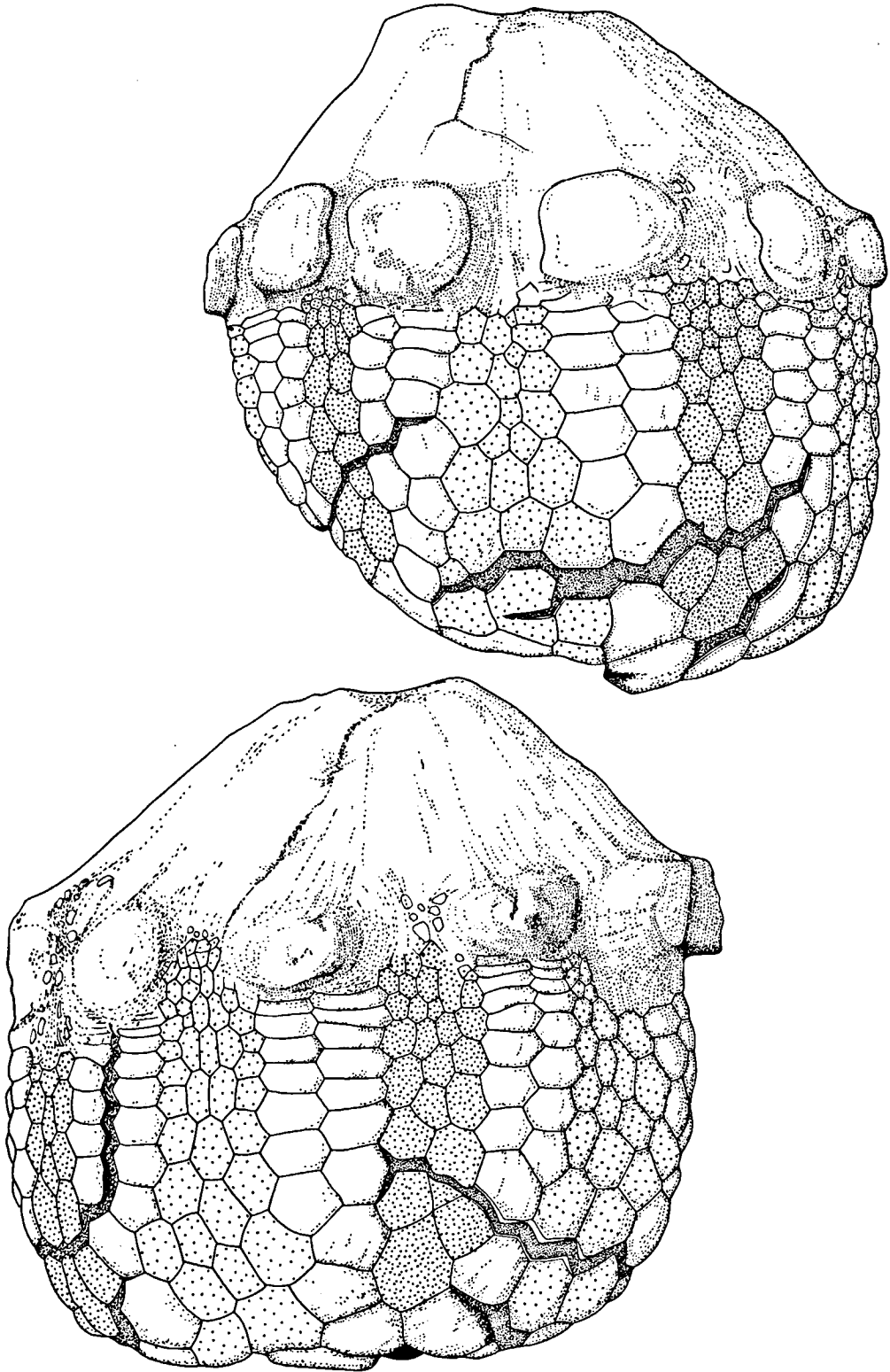


Fig. 17. Two lateral views of *Trybliocrinus Flatheanus*, from Emsian shales at Arnao, Asturias (coll. Mus. Inst. Geol., Madrid, no. 2393).

**Tegmen.** Complete tegmens are preserved in specimens 2393 and TB 20 (Museo Inst. Geol. Madrid), 6417 and 6418 (Esc. Minas, Madrid). Specimens no's 97643, 97693 and 97694 (Mus. Geol. Min., Leiden) are only fragments of tegmens. The tegmen is a rather low structure, its height does not exceed about half the height of the dorsal cup. In 2393 and 6417 the tegmen is somewhat asymmetrical, one side distinctly steeper than the other. The steeper side cannot be defined because the posterior part of the cups are not differentiated. At the top of the tegmen a shallow depression occurs, apparently for the anus. In 6418 a large gasteropod shell covers this region.

In the external view the tegmen appears to be composed of a great many of irregularly arranged polygonal plates generally of 2—3 mm in diameter. The specimen TB 20 has special interest for the study of the tegmen, because of its perfect conservation allowing a detailed study of distribution of tegmen plates. Firstly it is observed that a differentiation of ambulacral plates and adambulacral plates does not exist. But there is a regular distribution of smaller plates of only one millimeter in diameter in an area surrounding the anus and in the areas immediately surrounding the proximal arm parts. From these areas of small plates the tegmen-plates gradually increase in size to 3 mm for the whole remaining part of the tegmen. At the places where arms are broken off the deeper structure of the tegmen is exposed. These spots reveal that the tegmen in this area certainly has a stratified composition of some three to four layers of very small, more or less isometric plates. The same features has been observed on other specimens in the most distal parts of the cup walls, where these come into contact with the tegmen. The area surrounding the anus of spec. TB 20 is partly crushed so that fortunately the deeper structure of this part is visible. It is found that this anal part of the tegmen is composed of only one layer of prismatic elements, each of about 3 mm height and but  $\frac{1}{2}$ —1 mm in width. So these areas have a composition much different from that in the parts surrounding the arm base. In order to investigate the structure and composition in the main part of the tegmen, sections have been cut through the isolated tegmen-fragments no. 97643, 97644 and 97693. The sections are drawn in text fig. 18 B, C, D. The three sections reveal that the main part of the tegmen is composed of two sorts of plates. The most specialised plates are those plates that appear to be more or less bottle-shaped. The lower parts are more or less isometric — although often very irregular in shape — the upper part is prismatic. The lower isometric parts of these plates are in lateral contact at many spots. The spaces between the upper prismatic parts of these plates are filled with other simple prismatic plates, in between which other superficial plates may intervene. Spec. 97693 (fig. 18 B) is interesting in the sense that it shows the connection between the lateral edge of the tegmen (at left hand in the drawing) with its more central parts. The gradual transition of the stratified edge of the tegmen with what we would call the pallisade-structure of the main part is shown.

Two more highly interesting features can be learnt from these sections. The lower parts of the tegmen plates are in many places not in contact with the adjoining plates. Very irregular spaces between these plates easily are distinguishable. In the figures they are indicated as the dotted parts. In fact these spaces are filled in with the same sediment as the coelomic cavity is. So it is reasonable to suppose that they had open connections to the coelomic cavity. A naturally weathered fracture surface through the tegmen of 97693 fully confirms this. Here a distinct canal-system between the lower parts of the tegmen plates is exposed and there can

be no doubt that it is in open connection with the coelomic cavity, because, here too, the sediment has filled in the entire canal-system uninterrupted from the internal surface of the tegmen. The same vessel-system has been figured by Schmidt, 1932, pl. III, fig. 86. Therefore it seems logical to interpret this lacunar system as a coelomic vessel-system, penetrating from the coelomic cavity between the lower parts of the tegmen plates.

But another vessel-system is present. It is prominently displayed by spec. 97643 (textfig. 18 C, E). The section through this tegmen differs in so far that the sections show the larger plates project rather deeply into the interior of the coelomic cavity. The upper prismatic part seems to be less developed. Within the body of the plates a vessel-system is clearly present. The diameter of these vessels constantly is about 0.5 mm, but their direction within the plates seems to be highly variable. The vessels are even found to pass from plate to plate, parallel to the surface of the tegmen.

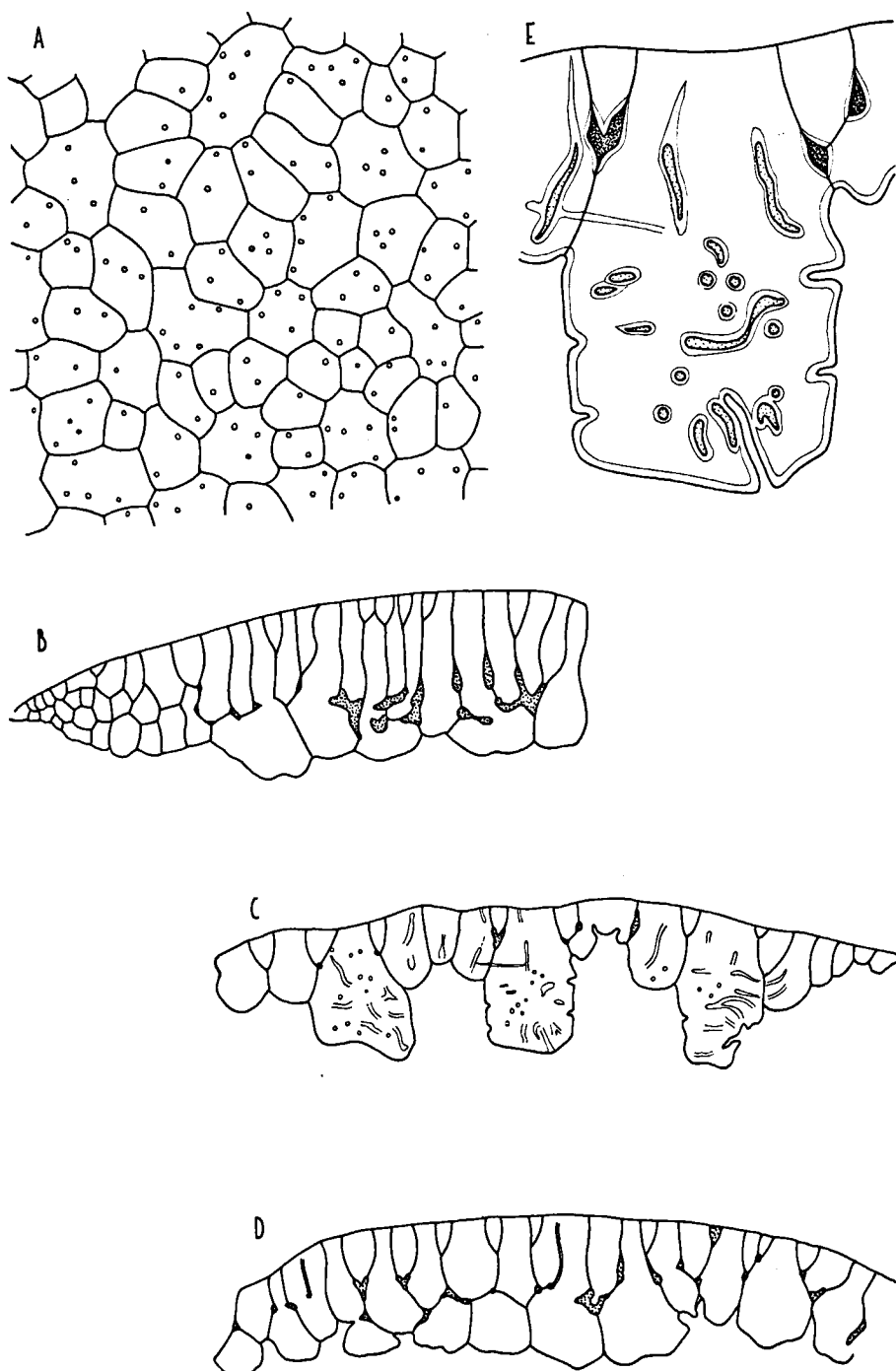
The connection of the vessel-system with the exterior was probably not open. Beyond any doubt many of the vessels are directed perpendicular to the outer surface of the tegmen but they did not reach the surface itself. This is proved by the slightly weathered surface of spec. 97643. The weathered part of this surface (as reproduced in textfig. 18 A) shows a pore system most clearly, the pores regularly distributed over the separate plates. Unweathered parts of the same tegmen definitely lack these pores. So one must conclude that the pore system ended blindly just below the external surface of the tegmen.

The vessel system certainly had a direct open connection with the coelomic cavity. The outlets of the vessels at the internal surfaces of the larger plates are clearly distinguishable (central plate in textfig. 18 C). In the specimen 97693 such vessels are found to communicate with the coelomic vessel system.

As has been drawn in textfig. 18 E the vessels are bordered by narrow strips of white material, whereas the tissues of the body of the plate have been altered in a grayey sort of calcite and the vessels themselves seem to be filled in with clayey mud. All along the contact of the tegmen plates with the coelomic cavity such a strip of white material occurs as well. It remains unknown whether this difference in composition originates from a primary difference in the living tissues constituting the vessels and the bodies of the plates, or has been the result of secondary alteration during fossilisation. The distribution of these white strips of calcite shows a close connection of this vessel system with the coelomic cavity.

The vessel system as described above has, in our opinion, a certain analogy with the water vascular system of recent crinoids as described from tegmen and

Fig. 18. *Trybliocrinus Flatheanus* Geinitz. — Morphology of the tegmen. (A) External view of slightly weathered surface, showing a pore-system. Pores regularly distributed over the separate plates. Specimen from Emsian shales at Arnao, Asturias (coll. Mus. Geol. Min., Leiden, no. 97643). (B) Section through the tegmen; the left side of the figure represents the lateral margin of the tegmen with stratified structure. Specimen from Emsian shales at Arnao, Asturias (coll. Mus. Geol. Min., Leiden, no. 97693). (C) Section through the tegmen; larger plates penetrating into the coelomic cavity with vessel-system. Note outlets of the vessels in the coelomic cavity (central larger plate). Specimen from Emsian shales at Arnao, Asturias (coll. Mus. Geol. Min., Leiden, no. 97643). (D) Section through the tegmen; lacunar coelomic vessel-system penetrating between lower parts of tegmen plates. Note the connection of the vessel-system with coelomic lacunes (dotted). Specimen from Emsian shales at Arnao, Asturias (coll. Mus. Geol. Min., Leiden, no. 97644). (E) Strongly enlarged tegmen plate. Note strips of white material, all along the internal surface of the plates and along the vessels. These strips do not occur along the sutures between tegmen plates. Specimen from Emsian shales at Arnao, Asturias (coll. Mus. Geol. Min., Leiden, no. 97643).



proximal arm parts in different *Antedon* species by Hamann (1889, p. 320—322, pl. 19, fig. 4, 5; pl. 23 fig. 10). His figs. 4 and 5 of pl. 19 (as reproduced by Hyman, 1955, p. 52, fig. 21 B) for the vessel system and his plate 22, fig. 12 for the different sort of tissues in the disk plates are of interest. The pore system of *Antedon* is regarded a part of the water vascular system. The pores and vessels are in open contact with the coelomic vessels and the coelomic cavity, through which it comes in connection with the stone canals. The pores freely communicate with the exterior. From *Antedon* it is known that the water canals are ciliated canals bordered by a special ciliated tissue.

The vessel system within the tegmen plates of *Trybliocrinus* differs markedly from that in *Antedon* by its blind ended vessels and the absence of external hydropores. Moreover, it is not certain that these vessels were entirely open. They could have been filled in with organic tissue, facilitating the circulation of fluids and nutritious substances in the skeletal tissues of the tegmen. The vessels could also be interpreted as a structure allowing fluids to communicate with the exterior through the superficial stereom for oxygenation. The system is perhaps best explained by describing it as an extension of the coelomic cavity in between and even in the tegmen plates, with a feeding and/or respiratory function.

**Gonioporoids.** Schmidt (1932, p. 16) dealt with these structures to a large extent. Our observations fully confirm those of Schmidt. Some remarks about nature and origin of the gonioporoids can still be made. The basal half of specimen TB 20 is destroyed, so permitting a view of the interior. A remarkable film of calcite is distinguishable, provided with tubercles closely corresponding to the gonioporoid pattern and indeed in places was found to penetrate into these pores, thus lining the internal surface of the cup wall. At other places it is detached from the wall and is now found as a sort of plicated mantle in the shale matrix filling in the body cavity. This structure reflects closely the pattern of gonioporoids. It is not understood what it may represent. The gonioporoid system itself is comparable to the coelomic vessel-system between the tegmen plates and the vessel-system between the columnar plates. All these pores, vessels and lacunes can be explained as penetrations of the coelomic cavity in between skeletal elements. They all may be thought to be of coelomic origin and could be analogous in function. It does not indeed seem impossible that these systems are to be regarded as respiratory organs.

**Arms.** The free arms still are attached to specimens TB 5 (Mus. Inst. Geol.-Madrid) and 6417 (Esc. Minas, Madrid). The first specimen is a young one, the latter surely mature. The arm structure could be studied more in detail from the many isolated arm fragments in the collection of the Geol. Mus. at Leiden from the type locality at Arnao. The arms of *Trybliocrinus* are very complicated structures and are made up of hundreds of plates. Without any doubt such arm structures as from this genus are only comparable to those described from *Rhipidocrinus* (Breimer, 1960, p. 252, fig. 1) and from an indeterminable genus of the Eifel region (Schmidt, 1941, p. 219, fig. 62).

The total arm structure is best described as a biserial main arm trunk (ramus) with biserial ramules placed in alternating order along the ramus; the first ramule is fixed to the dorsal cup. All ramules are pinnulated. The ambulacral groove of the ramus is roofed by a stratified structure.

The younger specimen TB 5 has a somewhat bowl-shaped cup with flaring walls. In this specimen the arms come off in a position at an angle of 45° with the vertical axis. This in contradiction to the larger individual where the



cup has almost vertical walls and arms come off almost horizontally. The main arm trunks may attain a width of 2 cm at the level where they become free, distad they narrow gradually and probably change their direction to almost vertical. This probably is the best explanation for the fact that many isolated

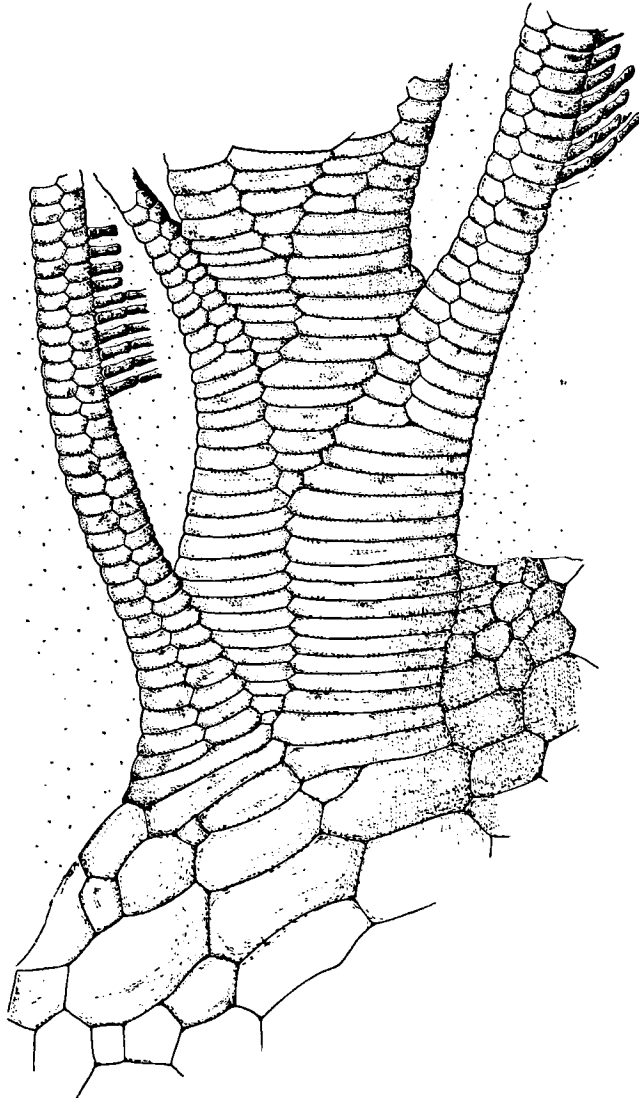


Fig. 19. Diagram showing the proximal portion of an arm in a young specimen of *Trybliocrinus Flatheanus*. Specimen from Emsian shales at Arnao, Asturias (coll. Mus. Inst. Geol., Madrid, no. TB 5).

arm fragments are somewhat curved. Nothing is known with certainty about the length of the rami, but it may be estimated as reaching at least 15 cm and probably 20 cm for large specimens.

**Fixed ramules.** As mentioned above in the discussion of the radial

series the two series of secundibrachs become divided by intervening plates near the place where arms become free (cf. fig. 18 B, C). These intervening plates distad become biserially arranged as well, so making the total mass of brachials in that region to be arranged in four series. Two such series start to give off the first ramule that still is fixed to the dorsal cup (cf. textfig. 19 and textfig. 20). The arms of specimen TB 20 are broken off, clearly showing the distal facets of the brachials belonging to a ramus and left of it the brachials of the first ramule. At the distal edge of the cup there are two ambulacral openings, the larger one for the reception of the food-groove of the ramus and the smaller one apparently for the ambulacral groove of the first ramule. This affords certain proof that the first ramule is to be regarded as fixed. Further indication in support of this opinion is the fact that the brachials that form the first ramule

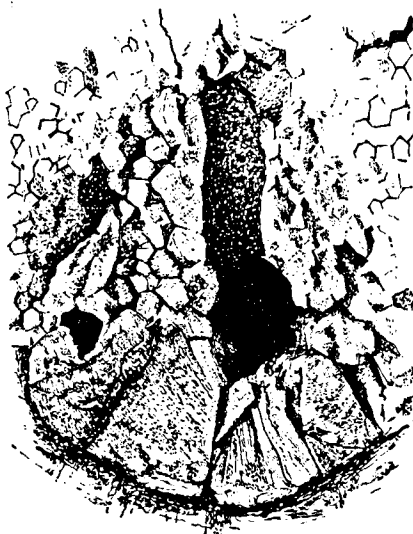
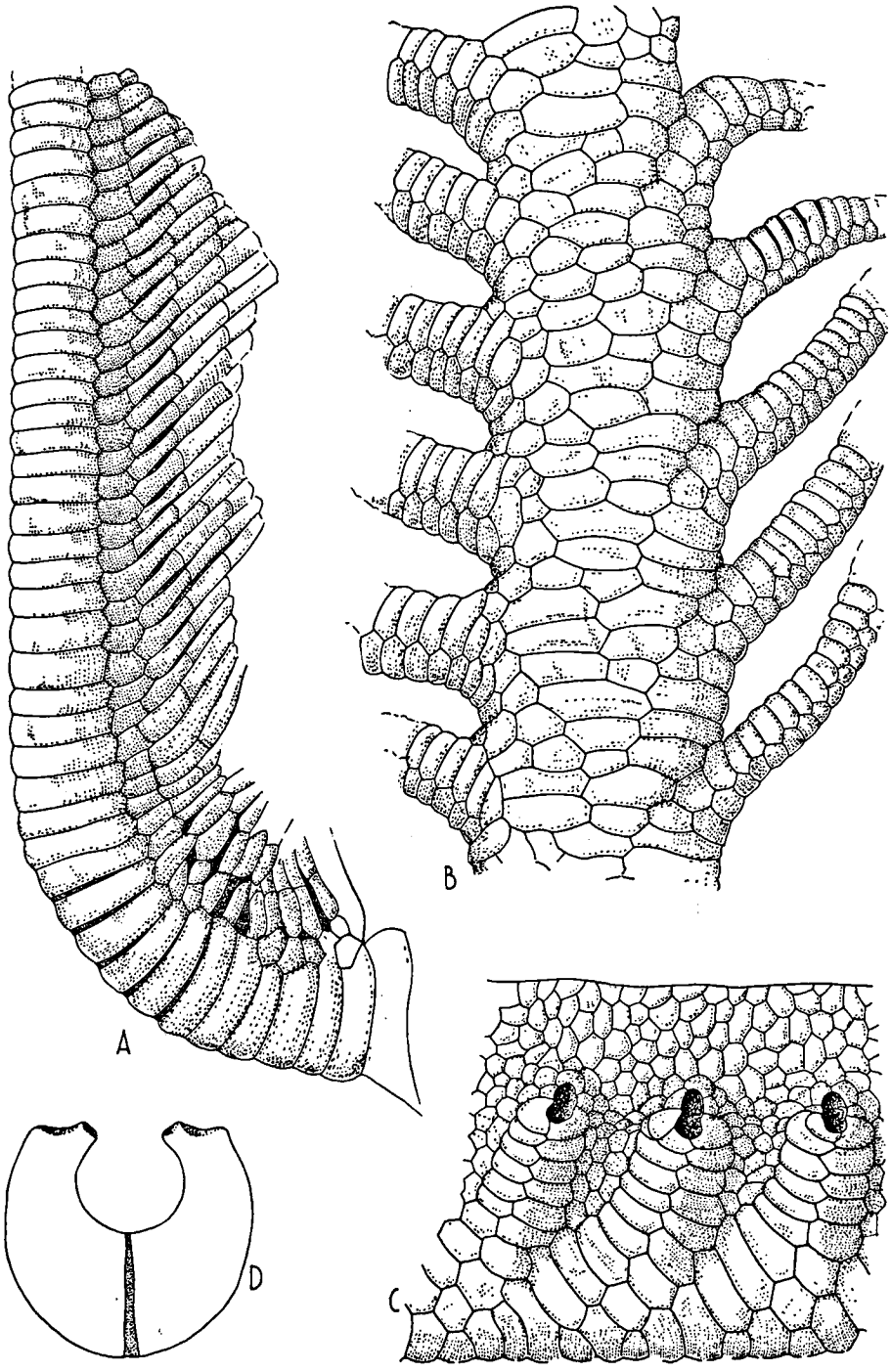


Fig. 20. Diagram showing a portion of the ventral edge in a dorsal cup of a mature specimen of *Trybliocrinus Flatheanus*. Note ambulacral openings of main arm trunk and fixed ramule. Specimen from Emsian shales at Arnao, Asturias (coll. Mus. Inst. Geol., Madrid, no. TB 20).

separate from the brachials that form the main arm trunk within the dorsal cup. It is not certain that the first ramule always was fixed to the dorsal cup. In the few cases that are available for study it was found that the first ramule comes off at the interradial side of the radius but there is not enough evidence as to conclude that the first ramule as a rule is fixed and always comes off in this way.

Fig. 21. *Trybliocrinus Flatheanus* Geinitz. — Morphology of the arms. (A) Lateral view of pinnulated ramule. Specimen from Emsian shales at Arnao (coll. Mus. Geol. Min., Leiden, no. 97689). (B) Dorsal view of main arm with ramules placed in alternating order. Specimen from Emsian shales at Arnao, Asturias (coll. Mus. Geol. Min., Leiden, no. 97690). (C) Lateral view of main arm showing oral plates along the ventral margin; ramules broken off. Specimen from Emsian shales at Arnao, Asturias (coll. Mus. Geol. Min., Leiden, no. 97691). (D) Distal facet of a brachial belonging to a ramule. Specimen from Emsian shales at Arnao, Asturias (coll. Mus. Geol. Min., Leiden, no. 97689).



**Main arm trunk.** The composition of the adoral side of the ramus appears at first glance to be very irregularly composed, but in fact some system in its organization can be found. Throughout the length of the arms the brachials are placed biserially. This is evident in the proximal part of one of the rami in spec. TB 5 as figured in textfig. 19. Each of the two series of brachials changes its composition into a biserial arrangement of plates in order to form an independent ramule so losing its function in the formation of the ramus. Somewhat below the level where a series of brachials passes into biserial arrangement, an intervening series of brachials starts to take its place in the formation of the main arm trunk. The intervening series of brachials generally starts with a small five-sided plate and widens rapidly. Each such a series that started by intervening between two lower brachial series for a certain distance after splitting of a ramule becomes entirely involved in the formation of the main arm trunk until it passes

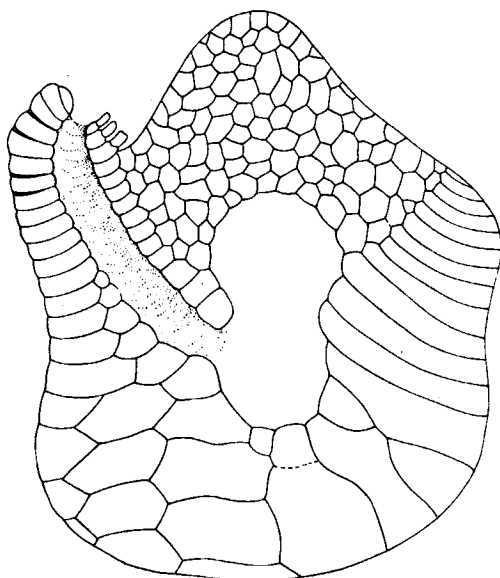


Fig. 22. Diagram showing transverse section through a proximal part of the arm in *Trybliocrinus Flatheanus*. Specimen from Emsian shales at Arnao, Asturias (coll. Mus. Geol. Min., Leiden, no. 97689).

into a biserial arrangement of plates itself in order to give rise to the next pinnule. The intervening series lead alternately left and right to ramules, so that ramules are placed in alternating order along the ramus. In the proximal part of the ramus the intervening series of brachials may comprise up to 20 plates before they pass into biserial arrangement. All these plates are much wider than high. Distad the intervening series include less plates (cf. textfig. 21 B) until no more than two or three plates constitute them. These brachials are but twice as wide as high.

Many isolated fragments showed beautifully preserved ventral sides of the main arm. The oral side of the ramus proved to be an entirely closed structure of many irregularly arranged plates. These plates partly project between the ramules at the lateral sides of the ramus (cf. textfig. 21 C). At some spots their arrangement suggest that these plates continued over the oral side of the

ramules as well, but since no ventral sides of ramules are sufficiently well exposed, one cannot be sure that this is true. In order to find the connection between ventral and dorsal sides of the ramus and to learn the internal structure of the arm transverse sections have been made. One of these sections is given in textfig. 22. This section has been made in a distal arm portion where ramules are placed at minimum distances to each other. The section reveals that the ventral plates are stratified and form a highly arched roof over the ambulacral canal in the arm. Moreover it shows that the ramules penetrate rather deeply into the interior of the arm, so more or less dividing the ambulacral canal into upper and lower compartments. The left side of the section just cuts the ambulacral groove of one of the ramules, so showing beautifully its contact with the main ambulacral canal. The regular series of plates just ventral from the ambulacral groove in the ramule are believed to represent the upper sides of the same brachials as are shown immediately left from the ambulacral groove. Hence the section must have been cut slightly oblique through the ramule i. e. not perfectly parallel to its longer axis. The right side of the section cuts through the lateral parts of a series of brachials that belongs to the succeeding ramule.

Most arm fragments are in rather a worn state, however some are beautifully preserved and clearly show traces of ornamentation (pl. IX, fig. 3). A fragment has thickened brachials at regular intervals that form kinds of nodes or tubercles, each of them provided with some very small pits. Ornamentation on the ramus has only been found on the dorsal sides. It is not evident whether ornamentation of the arms must eventually be used to separate different species of *Trybliocrinus* since the types, presence or absence of ornamentation is not definitely known for all specimens. The knowledge of arm structure in *Trybliocrinus* rests mostly on isolated fragments, so it is not known at the moment which special characters of the arms are consistent with specific characters of stem and theca.

**R a m u l e s.** The ramules are placed in alternating order along both sides of the ramus. From the level where they become free they are strictly biserial. In the proximal part of the ramus the ramules are placed rather wide, with intervals of 6—7 mm in some specimens. This is due to the fact that the series of brachials becoming involved in the formation of the ramules include a fairly large number of plates before they pass definitely into a biserial arrangement. The position of the proximal ramules is at 60° to the longer axis of the main arm, so being directed somewhat upward. The length of the proximal ramules is considerable; in the younger specimen TB 5 it is 15 mm. For mature specimens one perhaps may estimate their length as at least 25 mm. In more distal parts of the ramus however, the ramules are situated much closer to each other because the brachial series becoming involved in their formation include only a few plates. The position of the distal ramules is about perpendicular to the longer axis of the ramus. Nothing is known about the length of distal ramules with certainty, but some fragments have ramules of still 25 mm in length.

The individual form of a separate pair of brachials in the ramule is drawn in textfig. 21 D. The dorsal side of the pair of plates is gently rounded; the facets of the plates have a distinct vermiculate texture. At the ventral side a rather deep and perfectly rounded ambulacral groove runs along the ramule. Ambulacral plates on this groove were not observed due to the fact that no good ventral sides of the ramules can be seen in the naturally weathered specimens. But the fact that the groove at its upper margins is somewhat constricted perhaps indicates that such plates were present. Left and right from the ambulacral groove facets for the reception of the first pinnulars occur. The facets are placed

perfectly ventral on the brachials and occupy nearly the whole thickness of the brachial.

**Pinnulation.** Pinnules were observed in nearly all specimens or fragments examined. It is probable that all ramules throughout their length were pinnulated. Pinnules are placed at both sides along the ventral groove of the ramules. In many arm fragments pinnules on left and right side of the ramule were observed to be in close contact to each other and to be situated perpendicular to the longer axis of the ramule. Pinnules have about the same thickness as the brachials on which they are placed (cf. textfig. 21 A). Specimen TB 5 clearly proves that the fixed ramule was pinnulated. Arm fragment no. 97689 (cf. textfig. 21) gives a proof that the first brachial plate in the ramule to become entirely free from the ventral roofing structure, bears a pinnule. So pinnulation in fact is most dense. It is unknown how many pinnulars formed a pinnule. A series of at least four pinnulars were seen to constitute a pinnule (cf. textfig. 21 A). The first pinnular is generally somewhat thicker than the succeeding ones; it is about twice as high as wide. Whereas all the other pinnulars are equal in size and about three times as high as wide. Separate pinnulars have strongly rounded backs. Nothing is known about the nature of their ventral sides and the presence of ambulacral plates due to the fact that in no specimen could isolated pinnulars be found.

**Regeneration.** A very remarkable skeletal structure has been observed in the specimen 6418, which is figured in textfig. 16 A. A fixed ramule comes off at the left side of the figured half-ray, whereas the main arm trunk is situated at the right side. Between both arm parts a completely closed bud-like structure occurs. It apparently represents the place where a ramule ought to be. If the position of the fixed ramule of this ray is compared to other fixed ramules of the same specimen, it is found that its position is lower than elsewhere. This implies that the bud-like structure may occupy already the place of the second ramule. Its position then is abnormal in the sense that it seems to be in contact with the dorsal cup. In order to explain this structure one may perhaps suppose that the second ramule and probably a small part of tegmen and radial series were broken off in life. The bud-like structure then could be considered as a ramule in course of regeneration. The feature of regeneration is well known among recent crinoids, and there are no reasons to suppose that fossil crinoids were not able to regenerate parts of their organism. But another question arises. The specimen DH-1036 has eight well-developed arm bases, one very small and one missing. The very small and the missing arm belonged to the same radial series. The place where the missing arm should be is filled in with irregularly arranged plates, lying in a depression passing on to the tegmen. It is reasonable to suppose that the missing arm and a small part of the tegmen have been broken off and that the wound is filled in by new skeletal tissue. But the accompanying arm of the same radius did not develop. Perhaps one may even suppose that the damage was caused when the individual was young. But anyhow the question as to why the arm did not regenerate remains. Was it impossible for *Trybliocrinus* to regenerate a whole arm? Was it impossible to regenerate an arm during immaturity? Or perhaps has the radial nerve cord so badly been damaged that regeneration did not succeed?

**Stem.** Schmidt's description of the stem of *Trybliocrinus* (1932, p. 14) was mainly devoted to the vessel-system within it, so some additional remarks have to be made. Longitudinal sections reveal that the composition of *Trybliocrinus* stems is somewhat variable. External views suggest that the stem is

composed of a regular alternation of one nodal and one or three internodals. Externally the nodals may be distinguished by the presence of rims or nodes all around the plates. Some of the longitudinal sections fully confirm this. The stem-fragment 97698 shows a regular alternation of one thicker nodal with three thinner internodals. Other sections however, as f. e. 97697, prove to lack a distinct differentiation of nodals and internodals, but some columnals may be interpreted as nodals through the presence of thickened rims around their external margins.

The columnals are simply cylindrical plates, their thicknesses remain constant up to the edge of the very wide axial canal. The internal margins of the columnals bordering the axial canal passes into five small processes not occupying the whole thickness of the plates. A transverse section through the stem at the level of the facets of the columnals shows a circular axial canal not a pentalobate one (Pl. VIII, fig. 12): all the vessels projecting from it towards the exterior of the stem. The section through the middle of a columnal on the contrary shows a pentalobate outline of the axial canal (cf. Pl. VIII, fig. 13).

Our observations regarding the vessel-system fully confirm Schmidt's remarks. It is evident that the vessels are in open connection with the axial canal but lack a communication with the exterior. The axial canal itself is believed to be of coelomic origin, so that the columnar vessel-system may be thought as to have the same coelomic origin. Its ontogenetic origin and physiological function also is similar to that of the gonioporoids of the cup-wall and the lacunar vessel-system in the tegmen. All these sorts of vessels are penetrations of the coelomic cavity in between the skeletal elements. They differ also in nature from the vessel-system within the tegmen plates.

The basal part of the stem is produced into a root-like structure with many cirri, apparently for the attachment of the specimen to the bottom. The cirri may attain lengths of at least 15 cm. They are composed of simple cylindrical plates, as high as wide (4 mm) and pierced by a round axial canal of 1 mm in diameter. Cirri frequently are grouped together in a trunk and they may divide dichotomously (cf. Pl. X, fig. 4).

*Ontogeny.* W. E. Schmidt was the first to mention (1932, p. 7—9) some special features relating the growth of the basal region in *Trybliocrinus* specimens. His observations led him to the assumption that the rosette-like structure formed by the basals was subject to a higher growth-rate than the radial series.

Ubaghs (1956, p. 556—560) in discussing the growth in the basal concavity in *Polypeltes granulatus* has also mentioned the fact that the stem covers an unusual number of proximal cup plates. This number increases with the size of the individuals. Ubaghs concluded that this is due to allometric growth of the proximal cycles of cup plates. These cycles would contract toward the dorsal pole of the cup causing a space problem there, that could only be solved by the resorption of the basals and partly even the radials. In his opinion such a way of growth exists not only in *Polypeltes* but even in *Hadrocrinus* and *Trybliocrinus*.

In order to find a conclusive answer to the questions, a series of twenty isolated bases of *Trybliocrinus* cups were selected from a larger population. These forms all differ in diameter of the stem, ranging from 3 mm in the smaller individual to 21 mm in the largest specimen. It is believed that such a series represents a growth series, although it is realized that this is not necessarily true. The specimens in fact have been taken at random from the larger population

of *Trybliocrinus* and there is a chance of course that such a series as we took from the population does not represent anything particular or may even represent something else (i. e. an evolutionary series). Nevertheless this series will be regarded as a series of different growth stages, because the difference in size is best explained by difference in age of the animal at death. The diameter of the stem is taken to indicate the age of the specimens since no better age indicator is available. In textfig. 23 only five representatives of this series are figured and all drawn at equal diameter of the stem for better comparison of changes during ontogeny. From left to right they are arranged with increasing diameter of the stem, so at decreasing magnification. The upper series of figures shows external views of the specimens, the lower series the corresponding internal views.

Four major tendencies may easily be distinguished in the upper series of figures.

(i) During growth the stem covers the proximal circles of cup plates in a progressive way until IBrr and iRR completely disappear, thus raising considerably the number of plates in contact with it. In specimen 97665 the circle of the radials projects completely beyond the stem, only the five radials are in contact with it. In specimen 97680 about half the radials are covered and the lower tips of iRR1 touch the stem, so raising the total number of plates in contact with it to ten. In specimen 97646 ten plates still surround the stem but the place of the radials is taken by the IBrr1; the iRR are half covered by the stem. Specimen 97663 shows still a higher number of plates in contact with the stem. The distal tips of iRR1 are still free but the second-range iRR may even touch it. The IBrr1 are about half-covered. Finally specimen 97647 shows disappearance of iRR1 and the almost complete disappearance of IBrr1, so bringing IAxx closer to the stem. The number of plates in contact with the stem in such stages may rise up to sixteen, if the anal interradius is differentiated.

(ii) In connection to the first mentioned tendency the plates become smaller relative to the diameter of the stem.

(iii) The next feature in textfig. 23 is the fact that the plates tend to change their shapes from more or less isometric in young forms to elongated in older ones. Comparing specimen 97665 to specimen 97647 as extremities of the series one observes that the younger form has about isometric iRR, whereas in older stages these plates are distinctly elongate, the heights exceeding the widths. If one compares the only primaxil of specimen 97680 to those in specimen 97647 the difference is striking.

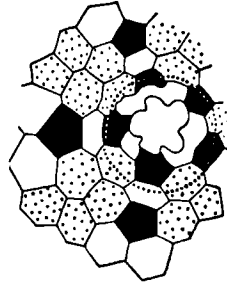
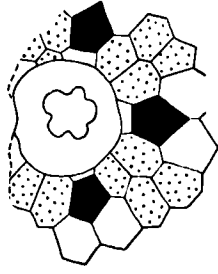
(iv) The axial canal becomes larger in proportion to the stem diameter.

It is supposed that the four mentioned tendencies may be explained by assuming variation in growth-rates for the proximal cycles of cup plates. In order to check this assumption, measurements have been made of various dimensions and ratios of the cup, the results of which are given in Table II. This table lists the criteria in order of increasing stem-diameter ( $R_0$ ). The trends in all of these criteria have been compared to the values of  $R_0$  and tested for their significance. Rank-correlation tests<sup>1)</sup> were used in order to find whether definite conclusions may be drawn about these trends. In the table  $x$  indicates the deviation in the normal distribution in terms of the standard deviation of relative rankings. Where the number of observations is greater

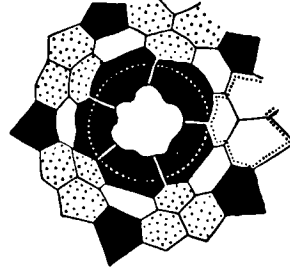
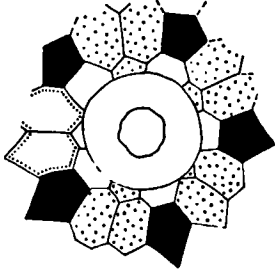
<sup>1)</sup> For the ranking method applied here the reader is referred to M. G. Kendall, 'Rank correlation methods' 1st. ed., (1948, pp. 37—42), London, Griffin Cy.



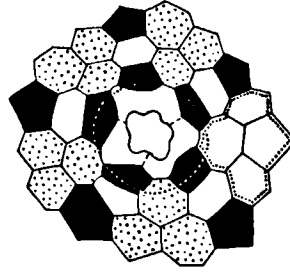
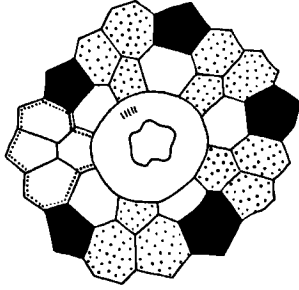
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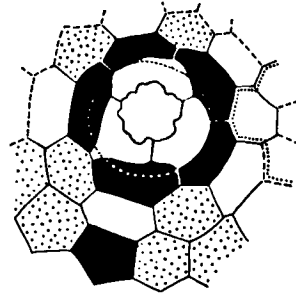
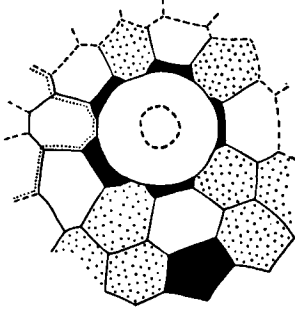
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97680



97665

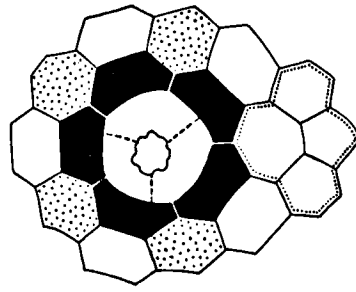
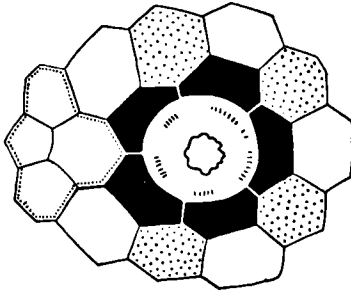


Fig. 23. *Trybliocrinus Flatheanus* Geinitz. — Two series of five diagrams (upper series in external view, lower series in internal view), showing the changes during ontogeny. From left to right specimens no's 97665, 97680, 97646, 97663, 97647 (coll. Mus. Geol. Min., Leiden).

Table II

Cat. no.	R <sub>0</sub>	R <sub>1</sub>	R <sub>2</sub>	R <sub>3</sub>	R <sub>4</sub>	R <sub>5</sub>	R <sub>6</sub> —R <sub>1</sub>	R <sub>7</sub> —R <sub>1</sub>	R <sub>8</sub> —R <sub>2</sub>	a	b	c	d	e
TB 4a	12.2	23.6	36.6	51.8	13.0	15.2	18.2	23.6	19.0	14.4	16.0	19.0	14.4	16.0
97666	17.7	23.0	38.6	57.0	15.6	18.4	14.0	—	23.0	15.3	15.0	23.0	15.3	15.0
DH 1043	20.2	28.8	49.8	71.0	21.0	21.2	18.5	31.5	24.7	21.0	23.0	24.7	21.0	23.0
TB 4b	21.0	32.7	52.3	76.8	19.6	24.5	15.5	31.2	17.5	23.5	23.0	17.5	23.5	23.0
97665	24.2	47.0	79.8	—	32.8	—	27.6	43.8	30.2	32.8	—	30.2	32.8	—
TB 4d	27.5	41.0	69.5	95.2	28.5	25.7	25.6	37.5	25.0	27.5	28.3	25.0	27.5	28.3
TB 4e	30.5	44.7	80.2	115.2	35.5	35.0	25.0	42.2	27.0	31.9	34.7	27.0	31.9	34.7
TB 4c	32.0	45.0	65.0	89.0	20.0	24.0	22.0	31.0	20.0	22.0	—	20.0	22.0	—
97664	35.2	40.0	71.8	—	31.8	—	23.2	43.0	27.0	31.2	—	27.0	31.2	—
97680	41.4	49.2	92.5	125.0	43.3	32.5	28.0	57.0	36.0	38.5	44.0	36.0	38.5	44.0
97678	45.2	51.0	77.7	127.0	26.7	49.3	30.0	43.5	34.0	—	42.0	34.0	—	42.0
97679	50.6	61.5	102.5	155.3	41.0	52.8	30.7	59.7	37.0	42.0	53.0	37.0	42.0	53.0
97677	55.0	—	95.5	144.5	—	49.0	32.3	62.0	37.5	42.0	55.8	37.5	42.0	55.8
97646	63.2	—	101.0	158.0	—	57.0	34.0	61.2	40.4	45.0	58.4	40.4	45.0	58.4
97661	64.8	83.2	140.0	—	56.8	—	35.0	—	60.0	66.0	—	60.0	66.0	—
97662	65.0	79.0	173.0	—	—	—	33.5	—	55.0	—	—	55.0	—	—
97649	75.2	—	103.5	175.0	—	71.5	—	62.0	35.0	—	70.0	35.0	—	70.0
97663	78.4	—	108.4	186.3	—	77.9	—	57.0	31.6	—	79.8	31.6	—	79.8
97648	80.2	—	160.0	232.5	—	72.5	—	68.5	38.0	53.0	73.0	38.0	53.0	73.0
97647	87.5	—	102.5	185.0	—	82.5	—	54.0	40.7	—	77.7	40.7	—	77.7
x	4.11	4.77	5.04	3.44	4.78	4.14	3.62	3.72	4.26	4.75	—	—	4.26	4.75
P	.000 04	.000 02	.000 000 5	.000 6	.000 002	.000 04	.000 3	.000 2	.000 02	.000 002	—	—	.000 02	.000 002
regression coefficient	0.72	0.90	0.34	0.43	0.54	0.68	0.86	0.51	0.86	0.72	—	—	0.68	0.86
confidence interval	0.52—0.93	0.79—1.02	0.17—0.52	0.17—0.71	0.44—0.65	0.51—0.86	0.72—1.01	—	—	—	—	—	—	—

than ten the distribution of  $x$  may be assumed to be of the statistic Normal type. The value of  $P$  is the two-sided exceedance-probability such that an observation would fall outside the range from  $-x$  to  $+x$ . This means that the ranking correlation found could only occur by chance with the probability  $P$ .  $P$  is usually quoted as a fraction of 1 so that  $P$  0.001 signifies the probability of the arrangement occurring by chance once in 1000 samples of this type. As in standard statistical practice values of  $P = 0.01$  and  $0.05$  are taken to represent the limits of significance and probable significance respectively. The computation of these tests involve the calculation of regression-coefficients which relate the various measurements quantitatively, and these will be used to discuss the variations of growth-rates.

The first two tendencies may be explained by assuming a lower growth-rate for the proximal cycles of cup plates than for the stem. In order to check this assumption measurements have been made of radii of the stem, radii of the first cycle of cup plates (including the radials), radii of the second cycle (including IBrr1 and iRR1) and radii of the third cycle (including IAxx and second-range iRR). These measurements have been taken from the centre of the specimen to the top of the radials, first primibrachs and primaxils respectively (cf. textfig. 24). Measurements of stem radii are indicated as  $R_0$  in table II and textfig. 24, those of the first cycle as  $R_1$ , the second cycle as  $R_2$  and the third cycle as  $R_3$ . The values of table II are the mean values of five (or sometimes less) measurements that could be taken from the five rays of each specimen.  $R_2$ -measurements of the rays only possessing a first primibrach are included.  $R_1$ -measurements of the rays only possessing one radial are included.

The first thing that may be concluded from the rank-correlation tests is that  $R_1$ ,  $R_2$  and  $R_3$  measurements, if arranged with increasing values of  $R_0$  show perfect positive trends ( $P$  0.000 04, 0.000 02 and 0.000 000 5 respectively). These trends only can be explained by assuming regular growth during ontogeny. This is particularly important to note for  $R_1$  since these plates (radials) are expected to be subject to active reduction.

Once the regular growth of the three proximal cycles of cup plates has been established, it is of interest to compare the growth-rates of the different cycles to that of the stem. For this purpose the increase of the heights of the second and third cycles are compared to the increase of the stem. The height of the circle of IBrr1 and iRR1 is indicated as  $R_2 - R_1$  in table II, the height of the circle of IAxx and second-range iRR as  $R_3 - R_2$ . Rank-correlation tests showed the trends in  $R_2 - R_1$  and  $R_3 - R_2$  measurements to be significantly positive ( $P$  resp. 0.000 6 and 0.000 002). A rank-correlation test was done for the  $R_1 - R_0$  measurements as well, but no trend can be established in these measurements. This is most probably due to the fact that only a few items are available. Moreover, the arrangement of the radials in some specimens is not quite regular. It was impossible to study  $R_4 - R_3$  measurements since too many of the specimens examined lacked plates of the fourth cycle.

The regression of  $R_2 - R_1$  and  $R_3 - R_2$  on  $R_0$  has been studied. It is assumed that the regression can be expressed by a straight line. The lines have been drawn in textfig. 25. The regression coefficient of  $R_3 - R_2$  on  $R_0$  is 0.90 (limits of 90 % confidence interval: 0.79—1.02), that of  $R_2 - R_1$  on  $R_0$  is 0.72 (limits of 90 % confidence interval: 0.52—0.93). This indicates that the height of the second cycle is best estimated as increasing with 72 % of the growth rate for  $R_0$ , whereas the height of the third cycle is best estimated as increasing with 90 % of the growth rate for  $R_0$ .

These results suggest that the proximal cycles of cup plates grow at a lower

rate than the stem does. The growth rates for the different cycles could be lower if more proximal to the stem. For the first cycle of the radials no exact percentage could be estimated, but its growth rate could be expected to be still lower than the rates for the third and second cycles. One is even inclined

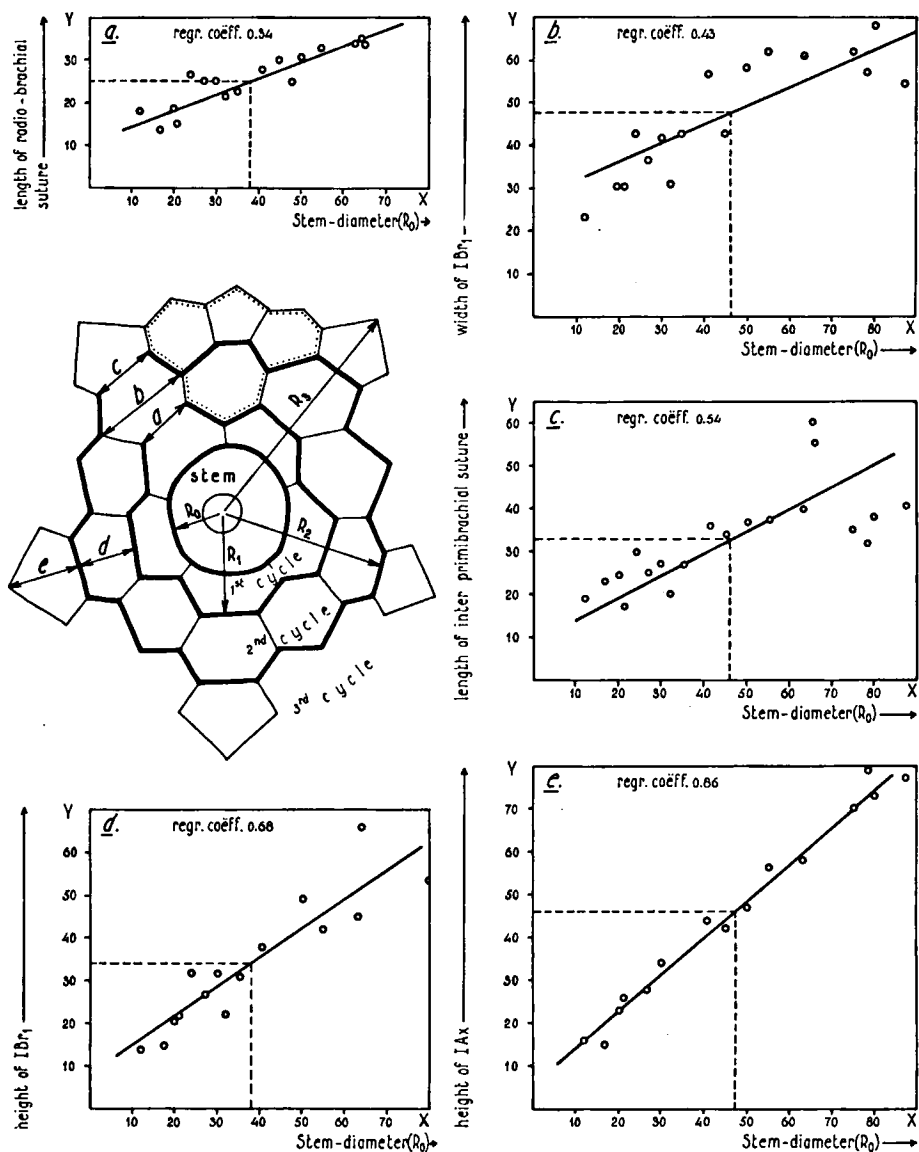


Fig. 24. Diagrams illustrating the relative growth of various dimensions of cup plates in *Trybliocrinus Flatheanus* (explanation see text).

to suppose that for the fourth cycle of cup plates a growth rate equal to that for the stem is to be found.

The difference between the two regression coefficients of the second and third cycles on  $R_0$  has been tested, but the significance of the difference cannot be established ( $t = 1.32$  with 25 degrees of freedom,  $P = 0.20$ ). There is not sufficient evidence to assert that the third cycle of plates was growing more rapidly than the second cycle of plates. The growth rates for both cycles, with some confidence, may be held as lower than that for the stem. The lower growth rates seem to be restricted to the first three cycles and perhaps to be progressive in proximal direction.

The question arises whether one must speak of an abnormal growing stem or of an abnormal growth-zone in the cup. Since there is slight evidence that lower growth rates in the cup may fade out in distal direction, this would mean that in more distally situated cycles of cup plates growth rates should be equal to that for the stem. In such a case the major part of the cup and the stem

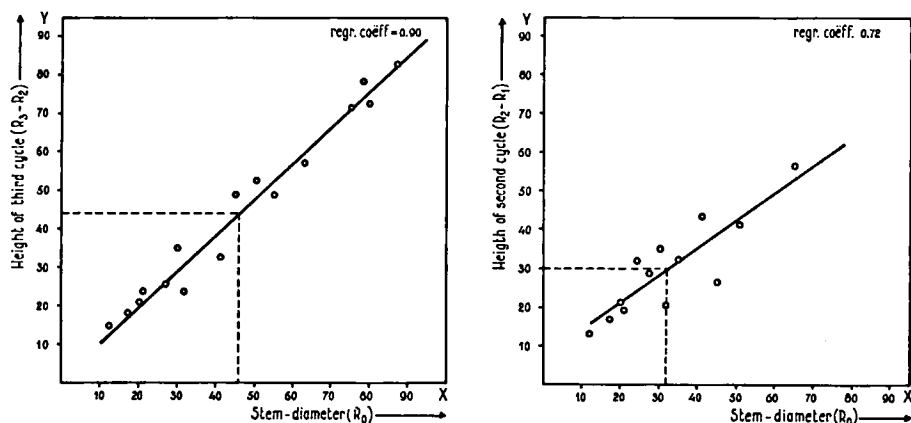


Fig. 25. Diagrams illustrating the relation of growth between second and third cycles of cup plates to the stem diameter in *Trybliocrinus Flatheanus* (explanation see text).

grow at the same rates. The proximal cycles are to be regarded than as exceptionally slow growing. The feature of a zone of lower growth rates in the proximal part of the cup fully explains what could be expected from the figures. It means that active reduction (resorption) of the plates can be rejected.

Some additional evidence to this point of view can be found from the internal surfaces of the examined specimens as shown in the lower figures of textfig. 23. The outline of the stem has been marked by a dotted line. The figures show that the radials at the internal surface of the cups do not contract so fast as they do in the external parts. The specimens 97646 and 97663 have radials that project beyond the stem outline at internal surfaces of the cup, whereas in external views the radials cannot be observed. Even in the largest specimen 97646 the radials occupy almost the whole of the internal side of the columnar region. Moreover, the deeply weathered specimen 97663 shows that the radials are still well developed. Basals have been found in nearly all well-preserved specimens. Even the largest specimen 97647 (although not perfectly preserved) shows major parts of the basals.

In connection with the first mentioned tendency, it appears that the plates of the proximal cycles of cup plates become smaller in relation to the stem.

In absolute terms these plates do not become smaller but larger as can be observed from the individual measurements in the table. The positive trends in all the measurements of cup plates can only be explained by assuming growth for these plates. The regression coefficients with their 90 % confidence intervals show that all growth rates of cup plates are lower than the  $R_0$ -rate. This fully illustrates that these plates do not grow as fast as the stem and must be gradually covered by it.

The next feature to be tested is the differentiation in shape of these plates from isometric in young individuals to elongated in older ones. Table II gives values of the width of the suture between radial and first primibrach (*a*), the greatest width of the first primibrach (*b*), the width of the suture between first primibrach and primaxil (*c*), the height of the first primibrach (*d*) and the height of the primaxil (*e*). Rank correlation tests showed the trends in all of these dimensions to be significantly positive ( $P = 0.000\ 04$ ;  $0.0003$ ;  $0.0002$ ;  $0.000\ 02$  and  $0.000\ 002$  respectively). Regression of these measurements on  $R_0$  gives coefficients of 0.34, 0.43, 0.54, 0.68 and 0.86 respectively.

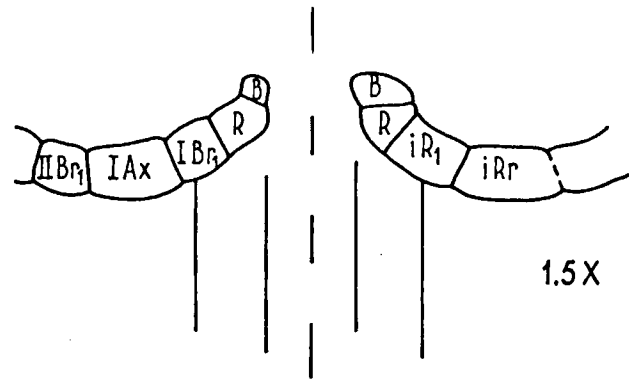
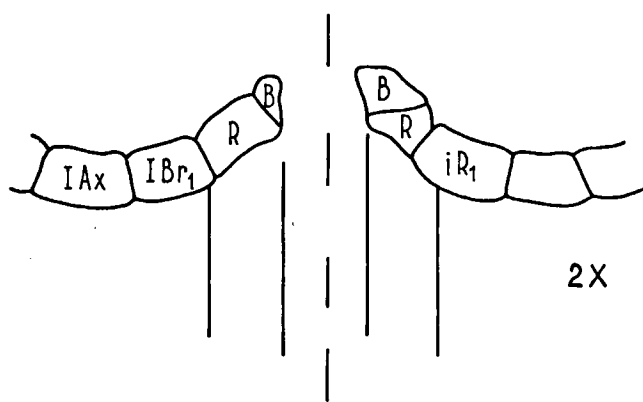
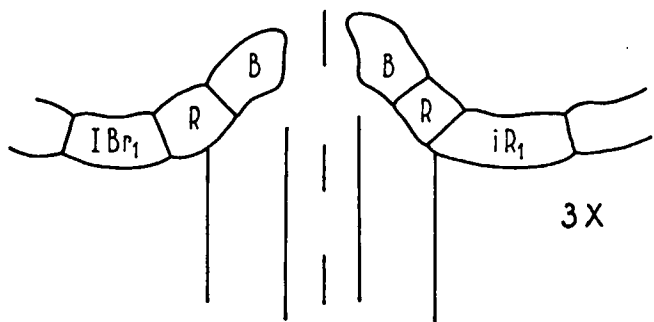
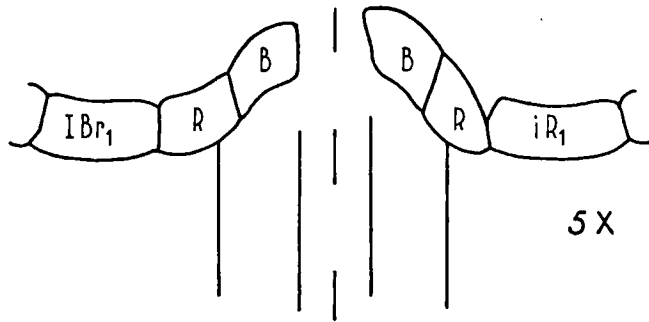
These coefficients suggest two things. (1) The widths of the plates are best estimated as ranging from 34 % to 54 % of the  $R_0$ -rate, whereas the best estimates for the heights of the plates are much higher, ranging from 68 % to 80 % of  $R_0$ -rate. One is inclined to conclude that growth in height exceeds that in width; such a phenomenon would fully explain the change in form of the plates during ontogeny. However, the confidence intervals indicate that such a conclusion is not justified on the basis of this sample. (2) The relative growth rates, both for heights as well as for widths, are higher for dimensions in more distal proportions. This phenomenon, once more, suggests that abnormal low growth in the cup plates is progressive in proximal direction. However, the confidence intervals, here too, indicate that such a conclusion is not justified on the basis of this sample. Textfig. 24 gives regression lines for the different height and width measures of the plates.

The general picture of ontogenetic growth in *Trybliocrinus* is probably best demonstrated by figure 26. The diagrams in this figure show some transverse sections through basal regions in *Trybliocrinus* cups, based entirely on the measurements and on observations both at internal and external sides of the cup. In the smallest specimen the central elevation is mainly formed by the three basals. In the larger stages the RR and even the IBrr1 and iRR become involved in the formation of the central elevation. The diagrams show perfectly the gradual displacements of the proximal cup plates relative to the stem. These plates change the direction of their facets from diverging to converging toward the central axis. The whole zone of proximal thecal elements becomes involved in the formation of the central elevation.

It is reasonable therefore to conclude that the lower growth in the proximal part of the cup is focused on the formation of the rosette-like structure on top of this elevation. In fact this structure becomes more and more differentiated during ontogeny.

Some final remarks on the ontogeny of the basal part of the *Trybliocrinus* cup have to be made. Our investigations proved the presence of a zone of low growth rates in the proximal part of the dorsal cup, including at least the

Fig. 26. Diagrams showing reconstructions of transverse sections through the base of *Trybliocrinus Flatheanus* specimens at different growth stages.



three cycles of thecal elements. It is suggested moreover that the growth-rates in this zone are lower if more proximal in position and further that growth for the height of the plates could exceed that for the width. It is very interesting to compare these results with the preliminary remarks of Ubaghs (1956, p. 560) on the ontogeny of the *Polypeltes* cup. His observations led him to the supposition that the very small size of the proximal thecal plates in the basal concavity was the result of an allometric growth. The facts from *Trybliocrinus*' ontogeny probably underline this assumption. He further believed that — in absolute terms — the proximal cup plates were smaller in older individuals than in the younger ones. He referred to his textfigures 2 A and 2 B (specimens Ec 12.035 and Ec 6.151 resp.), for which he states that magnification is about 7.5 times. But on p. 555 he mentioned as the diameter of the stem (D) in Ec 12.035 a diameter of 7 mm and for Ec 6.151 of 9 mm. In his figures 2 A and 2 B these dimensions are magnified to 39.5 and 46 mm respectively or a magnification of 5.6 and 5.1 times respectively. The real heights for IBrr1 in both figures as estimated from these magnification-rates then would be 2.7 and 2.6 mm respectively. It is doubted if this difference is significant and may be attributable to active contraction of the proximal cycles of cup plates as considered by Ubaghs (p. 560). This active contraction of the proximal cycles of cup plates to the dorsal pole of the cup in his opinion leads to a lack of space near the median pole of the cup. This lack of space is thought to be solved by complete reduction of the basals and even partial resorption of the radials.

It is noted however that as long as plates are subject to growth they cannot actually contract towards the dorsal or median pole of the cup, because their outer margins are expanding instead of contracting. The figure of contraction is only a relative figure, derived from the way in which allometric growth is presented. For example in our textfig. 23, 26 such a contraction of proximal cycles of thecal elements can be seen, but only as a result of the fact that the magnifications are so chosen that the stem appears to be stable. In fact both the stem and the proximal cycles of cup plates are in expansion but the stem much faster than the cup plates. So (at least in *Trybliocrinus*) it is not necessary to introduce such a figure as active resorption at the dorsal or median pole of the cup to solve problems there.

Ubaghs' fig. 2 A and 2 B possibly give some more indications implying that the ontogeny of *Polypeltes* is not quite comparable to that of *Trybliocrinus* as described here. The proximal cup plates of *Polypeltes* may be thought to be subject to allometric growth, but some difference may exist. In the smaller specimen Ec 12.035 the plates have a much more elongated outline compared to the larger Ec 6.151 where plates are more isometric in shape. This may indicate an opposite tendency to what has been shown for *Trybliocrinus*. It could mean that allometric growth exists in the sense that the growth for the width exceeds that for the height. Growth for the height then would be extremely low. Another possibility is that Ec 6.151 does not represent a more advanced growth stage, despite the fact that the diameter of its stem is larger than in Ec 12.035. If this is true the cup-plates then would have been subject to growth rather than to reduction (2.6 mm in younger 6.151 IBrr and 2.7 mm in older 12.035 IBrr). The growth for the heights of the plates then would exceed that for the width, changing the shape of the plates from isometric to elongated. Thus exactly the same tendencies would be found for *Polypeltes* as was shown to exist in *Trybliocrinus*.

*Remarks.* Ubaghs (1956, p. 568) thoroughly discussed the morphological criteria of the systematic position of the genera *Trybliocrinus*, *Hadrocrinus* and



*Polypeltes*, grouped by him in the family Polypeltidae. Among his list of diagnostic characters the allometric growth of the basal part of the dorsal cup received much attention. The present study reveals that such an 'allometric' growth has to be interpreted as linear growth at low rates, and proves at the same time that basals (at least in *Trybliocrinus*) are not subject to active resorption. In many specimens basals have been found to be located on the top of the internal central elevation forming a rosette-like structure, exactly as has been drawn by Schmidt (1932, p. 8, fig. 4).

The first indications of abnormal growth in the base of the cup are from Springer (1921, p. 11, textfig. 4; Pl. 2, fig. 1). He had previously noted the fact that in *Hadrocrinus discus* the stem covers the radials. He considered the basals to be atrophied because in his figured specimen basals were only observed as small notches. Ubaghs (1956, p. 557, 558; textfig. 2 A, 2 B) came to exactly the same conclusion for *Polypeltes* as Springer for *Hadrocrinus*. Both authors formed their opinion on the fact that in external views of specimens with detached stems the basals were found to lack or only present as small "remnants", whereas radials in external view were observed to be indented by the lobes of the axial canal. But it must be realised however that our knowledge of the bases in both *Polypeltes* as *Hadrocrinus* is restricted to the exterior side of the cup. Since the interior side of *Trybliocrinus* is better understood it must be held possible that in *Polypeltes* as well as in *Hadrocrinus* basals did not really atrophy but were displaced on to the top of the central elevation. The result of 'allometric' growth is not only the progressive covering of thecal elements by the stem but also the inclination of the proximal cycles of cup plates, moving them from a horizontal position. As a consequence of this progressive inclination and progressive covering the basals become situated entirely inside the cup.

It is believed that these considerations throw some new light on the systematic position of *Himerocrinus* as well. This genus has been assigned to Dolatocrinidae by Ubaghs (1953, p. 742), from which typical representatives it distinctly differs not only in size but mainly by the incorporation of large numbers or brachials, interradians and interbrachials. It is not fully understood why *Himerocrinus* has been separated even in family from *Hadrocrinus*, to which genus it once belonged. *Himerocrinus* agrees in most of its essential characters to the polypeltids. What formerly appeared to be different was the assumption that basals were not atrophied and the fact that radials are not covered by the stem. But from Springer's figures of *Himerocrinus* (1921, Pl. 3, fig. 2, 3; Pl. 4, fig. 2, 4) some important phenomena are easily learned. Examination of the specimen Pl. 3, fig. 3 shows that basals project slightly beyond the stem and the pentagonal outline of basal circllet is visible. Further the diameter of the stem is 12 mm, whereas the widths of the radials range from 13.5—15.0 mm; the width of the radials thus definitely exceeds that for the stem. Lastly the position of the radials does not deviate much from horizontal. The larger specimen Pl. 3, fig. 2 does not show the outline of basal circllet; the stem is 18 mm in diameter, whereas the width of the radials is but 12—13 mm. The stem here distinctly is wider than the radials; radials even seem to be reduced in size, if compared to the spec. fig. 2. Lastly the radials in the larger specimen are in a much more inclined position. Exactly the same differences exist between the specimens Pl. 4, fig. 2 and fig. 4. If the specimens Pl. 3 fig. 2 and Pl. 4 fig. 2 really are larger than the other two (one cannot be sure because Springer did not indicate the scale of figures) both these features can be wholly explained by assuming allometric growth for the proximal cycles of cup-plates. Allometric growth does not make it necessary that the proximal

cycles gradually become covered by the stem. Strong inclination of the cycles towards the interior may allow them to escape from covering by the stem.

So in this supposed 'allometric' growth *Himerocrinus* closely corresponds to the polypeltids but other similarities also exist. Springer's Pl. 3 fig. 4 clearly shows the presence of three unequal basals forming an elevation towards the interior, exactly as has been found in young specimens of *Trybliocrinus*. In the explanation of Pl. 4 fig. 1, Springer mentioned the presence of pits at the corners of the plates of an eroded specimen. The pits indeed are clearly visible in his figure. Later, in 1932, W. E. Schmidt (p. 16) called such pits gonioporoids, that now are regarded as diagnostic for *Trybliocrinus*. It seems advisable not to separate *Himerocrinus* from the polypeltids, to which group of crinoids it indeed has its most strong affinities. In our opinion *Himerocrinus* has to be assigned to that family. The main difference with other members of polypeltids is the reduction in number of interrachial and interbrachial plates in favour of abundant brachial plates.

If *Himerocrinus* is considered a polypeltid the essential characters of that family must read: very large theca, with 'allometric' growth-zone near the base of the cup leading either to inversion in position or to covering of the proximal cycles of cup plates by the stem; BB three, unequal, in immature specimens forming a central internal elevation, to which formation the proximal cycles of cup plates may become involved as a result of allometric growth; incorporation of many brachial elements in the cup by which interrachial and interbrachial areas may occupy large areas in the cup; tegmen low; biserial arms, typically simple or weakly branching without axillary plates; large cylindrical stem with wide pentalobate axial canal.

It appears then that *Trybliocrinus* is an aberrant polypeltid, mainly in its specialized arm structure. This type of arm is only comparable to that of *Rhipidocrinus* as has been previously pointed out by Breimer (1960, p. 257). Arms of both genera have stout rami provided with biserial ramules placed in alternating order along the main arm. The rami in *Trybliocrinus* are biserially arranged, those of *Rhipidocrinus* monoserial. The fixed ramules of *Rhipidocrinus* regularly are placed at the outsides of the radii, because they come off from IIAxx. Fixed ramules in *Trybliocrinus* may perhaps be somewhat variable in position because they do not originate from an axillar plate. It must be stated however that the resemblance of these arm structures has to be attributed to convergence. *Rhipidocrinus* is dicyclic, whereas *Trybliocrinus* is monocyclic.

The arms of *Trybliocrinus* have some slight resemblance to the arms of an undetermined genus of the Eifel, figured by Schmidt (1932, fig. 62 A, B) in the presence of a biserial ramus with biserially arranged ramules. But in the German species the ramus is strictly biserially arranged with a perfect median zigzag line. Separate brachial series leading to the ramules and intervening between two lower series of brachials as in *Trybliocrinus* do not occur in this species. So its structure is not fully comparable to that of *Trybliocrinus*. Schmidt (1932, p. 218) mentioned the similarity of this arm structure to that of *Ctenocrinus*, but in his opinion such a strict biserial arrangement for the ramules could not occur in *Ctenocrinus*. However, such an alternating position of brachials really exists in the proximal parts of the rami of *Ctenocrinus* specimens (cf. Ubaghs, 1958, Pl. V fig. 2). Alternation of brachials is soon lost in that genus, brachials become placed at equal levels and distad the both rami even separate. So the arm structure of this German specimen is comparable neither to *Ctenocrinus* nor to *Trybliocrinus*. Its configuration suggests a close lateral fusion of two rami of

different half-rays, as is typical for advanced melocrinids. If this is true its affinity is mainly to representatives of melocrinids and not to polypeltids. *Trybliocrinus*' arm structure cannot be explained by lateral fusion of different half rays. There seems to be a morphological gap between arm structure of melocrinids and that of *Trybliocrinus*. The lack of comparable structures among older monocyclic camarates makes it impossible at the moment to learn the phylogenetic or ontogenetic origing of this arm structure. In fact the phylogenetic origin of the polypeltids remains as obscure as it was before.

## Superfamily PLATYCRINICAE Austin & Austin 1842

When trying to classify Spanish Devonian Platycrinicae some considerable difficulty was met with regard to the exact stress to be laid upon some rather unusual characters found among them.

First of all the position of the smaller basal was found to be either left anterior or posterior. The left anterior position is somewhat more frequent. Other positions as just these two were not met with. The position of the smaller basal is extremely variable in that it does not show any correlation with any other characters. It seems to be noteworthy that even no correlation exists between the differentiation of posterior interradius and the posterior position of the smaller basal.

The posterior position of the smaller basal, although not unusual among Spanish Devonian Platycrinicae, is found to be quite exceptional among other members of this group. The only posterior positions were found among specimens of *Neoplatycrinus dilatatus* from the Permian of Timor.

The left anterior position of the smaller basal may be regarded as normal in Platycrinicae. It is highly characteristic for platycrinids and most hapalocrinids have it in the same position. But the hapalocrinids especially have their smaller basal in aberrant positions. In *Lyonocrinus* it has a quite unusual left posterior position. The inconsistency of the position of the smaller basal with no one other character led us to regard this feature as of no higher category than the species level.

A second peculiarity of the Spanish Devonian Platycrinicae was met with in the differentiation of the posterior interradius. Three very small plates rest on the upper facets of l. and r.post. RR, the central one pentagonal. The anus is separated from these three small plates, from adjoining l. and r.post. IBrr and post. O by a group of minuscule elements, sometimes perhaps forming a weak protuberance. This arrangement of plates invariably was observed among all specimens examined.

The above mentioned composition is believed to be very similar to that in the *Pleurocrinus mucronatus* group of species as defined by J. Wright (1938, p. 270; 1955, p. 265): "anus lateral in position, separated from post. RR by a small, usually pentagonal iR truncated at the upper margin and resting below on the shoulders of l.post. R and r.post. R. This posterior iR is generally small when compared with the median iR of other interradii. Two or more very small plates may occasionally intervene between it and the anal opening". Judging from his illustrations of species belonging to this group, it appears that a number of very small plates surrounds the anus separating it from both iRR and tegmen plates.

The differentiation of the posterior interradius is believed to be a primitive character, since it is already seen in Silurian forms such as *Lyonocrinus bacca* and *Pleurocrinus spinosus* (cf. p. 123, footnote).

The fact that this primitive characteristic of differentiation of the anal interradius invariably occurs in all Spanish Devonian Platycrinicae leads us to the assumption that this phenomenon is of a higher category than a specific feature, although perhaps not significant enough to differentiate families.

In our opinion the tegmen provides the most important characters for grouping the species of Platycrinidae. Much emphasis is placed on the fact that in the tegmen radial or first axillar ambulacrals may have been differentiated, so that the ambulacra are to be regarded as subtegmenal. The presence of a small axillar first primibrach and two secundibrachs per half ray with trunking of the arm bases is consistent with this type of tegmen structure. Modified axillar ambulacrals have special function of covering these arm trunks.

Another type of tegmen structure is presented by tegmens with suprattegmenal ambulacra intervening between the orals, that lack a differentiated axillar ambulacral. In such forms two primibrachs occur as well as a number of secundibrachs. Arms are not grouped together. It is believed that these characters provide the best possible criteria for separating the families of Platycrinidae.

The taxonomic study of Spanish Devonian Platycrinidae is based on this valuation of characters. Further explanation is given on p. 134.

Family HAPALOCRINIDAE Jaekel 1895  
Genus CANTHAROCRINUS Breimer gen. nov.

*Genotype.* *Cantharocrinus minor* sp. nov.

*Remarks.* The genus *Cantharocrinus* is erected to include two hapalocrinid species resembling *Amblacrinus* not only in general composition of the theca but especially in the suprattegmenal ambulacra leading to a subtegmenal mouth and the absence of modified first axillar ambulacrals, but differing from it by the differentiation of both posterior interradius and posterior oral and by a possible posterior position of the smaller basal. Although it is not yet fully realized what stress must be laid upon the differentiation of the posterior side, it is believed that its structure provides important characters in classification. *Cantharocrinus* in this respect preserves a primitive character absent in non-Spanish Devonian hapalocrinids. The aberrant position of the smaller basal is believed to be of less diagnostic value. It is found to be rather variable among hapalocrinids. No correlation exists between posterior positions of smaller basals and differentiation of posterior sides.

The following species are to be included within the genus *Cantharocrinus*:

*C. minor* sp. nov.

*C. simplex* sp. nov.

The species *C. minor*, although unusually small among hapalocrinids is designated the genotype mainly because it has its smaller basal in the normal l.ant. position.

*Diagnosis.* A genus of the family Hapalocrinidae, characterized by l.ant. or post. position of smaller basal; two primibrachs, first one slightly incorporated; one arm to the ray; differentiated post. interradius; tegmen with five triangular orals, posterior one differentiated; suprattegmenal ambulacra but subtegmenal mouth; absence of modified first axillar ambulacrals. Arms and stem unknown.

*Distribution.* The genus is still only known to occur in Spanish Lower and Middle Devonian Strata.

*Cantharocrinus minor* Breimer sp. nov.

Pl. XI fig. 5—7

*Holotype.* The specimen 97700 in the collection of the Rijksmuseum van Geologie en Mineralogie at Leiden (Holland).

*Paratypes.* The specimens 97701 and 97702 in the same collection.

*Locus typicus.* The northern slope of the hill on which the church of the village of Colle, near Sabero (prov. of León) is built.

*Stratum typicum.* Top beds of the La Vid shale formation, corresponding to the Lower Emsian.

*Diagnosis.* A *Cantharocrinus* species characterized by l.ant. position of smaller basal; high somewhat turbinate dorsal cup, composed of flat, smooth plates with non-depressed sutures; restricted tegmen, occupying only a small part of the ventral surface of the theca, hardly visible in side view; wide ambulacra with four series of ambulacrals (adambulacrals and covering pieces); posterior oral spiny.

*Distribution.* The species is only known with certainty from the type locality at Colle. It may be possible that it occurs in San Fenolleda, near Grado in Asturias in the Ferroñes deposits (L. Emsian). A single specimen has been found there but it lacks the greater part of the tegmen.

*Description.* The general form of the theca is somewhat turbinate; the dorsal cup gradually expanding in diameter, the tegmen very low, hardly visible in side view. The outline of the theca is rounded viewed from below, but subpentagonal from above. The dimensions for the description will be taken from the mature specimens 97700 and 97701. No. 97702 is a young specimen, that will be discussed below. The total height of the theca, oral spine included, is 8.7—9.3 mm. The cup alone is 6.7—7.5 mm high and has a maximum width of 7 mm at the level where the arms become free. It is composed of flat and smooth plates with non-depressed sutures.

*Basals* three, unequal, smaller one l.ant. in position. Outline of basal circlet pentagonal. The circlet is not constricted and fairly high; the basals 1.5—2 mm in height if measured along the surface. The place for the attachment of the stem is not excavated. The holotype preserves a part of the last columnar. It has a diameter of about 2.5 mm and is circular in outline. Coarse radial ribs are observed on the articulation-facet.

*Radials* five, in lateral contact all around the cup. The radials are by far the larger plates of the theca, that is mainly composed by them. The l.post. R and r.post. R are wider than other radials, that are 4 mm high and 3.5 mm wide. The facets for the reception of the primibrachs occupy a half to two-thirds the width of the radials. In l.post. R and r.post. R they are pushed aside. The upper left and right margins of the radials are truncated for the contact with interrarial plates.

The first primibrachs are incorporated in the dorsal cup. The young paratype 97702 preserves a single second primibrach, that is axillary and free from the dorsal cup. IBrr1 are horseshoe-shaped. Their position is inclined toward the tegmen, where they make contact with the orals. Laterally they come in full contact with the interrarial plates. The primibrachs are visible from above. At its ventral margin the primibrach is excavated by an U-shaped ambulacral groove, in free contact with the ambulacral grooves on the tegmen.

*Interrarial plates* are relatively large. In normal interrarii only one such a plate occurs. It is an elongated six-sided plate, 2.3 mm high and 1.2 mm wide, placed in exactly the same position as the primibrachs and appearing in ventral view. The plate rests on the shoulders of the underlying radials, is in lateral contact with the primibrachs and at its upper facets meets with an oral.

The posterior interrarius is differentiated. Below the anus three

small plates occur, the central one pentagonal and flanked by two lateral, more or less rectangular plates. Each of these three plates is much smaller than the hexagonal iRR of other interradia. Additional plates surround the ventrally placed anus and separate it from the overlying post. oral and adjoining primibrachs. The structure of the posterior interradius of the holotype makes it probable that the anus was placed at the top of a protuberance of many small plates. The differentiation of the posterior interradius makes it wider than normal interradia. The adjoining l. and r.post. IBrr are pushed aside, whereas the post. oral is slightly pushed forward.

The tegmen is small, occupying only the half of the ventral surface. The exact structure and composition of the tegmen only can be observed after

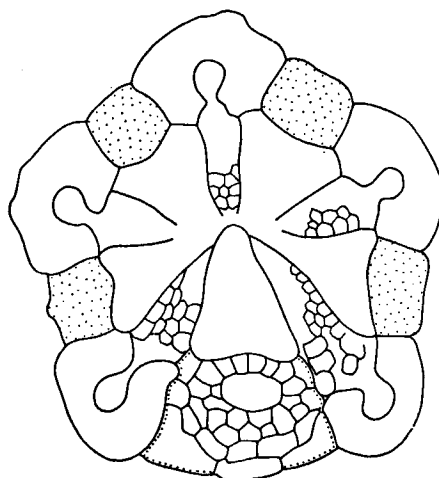


Fig. 27. Diagram showing the arrangement of plates in the tegmen of *Cantharocrinus minor*. Holotype of the species, from the La Vid formation, Colle, León (coll. Mus. Geol. Min., Leiden, no. 9770).

emerging the specimens under glycerin and studying them under the microscope (cf. textfig. 27). The tegmen is partly composed of five small orals without ornamentation. The posterior oral is wider, due to the fact that it has to cover the wide, differentiated posterior interradius. The plate bears a large spine. It is slightly pushed forward, so centrally entering in contact with all of the other orals. The outer margins of the oral are bifid, the tips in contact with primibrachs, the indented parts in contact with the interradials. The orals are only in lateral contact near the centre of the tegmen. In external view they appear to be separated by wide ambulacra running from the primibrach towards the centre, but not reaching this point. Ambulacra are covered by four series of plates, all alternating. The lateral series are composed of larger plates and are regarded as adambulacral, the central series have but very small plates that are regarded as covering pieces. There is no proof that orals closed underneath the ambulacral grooves. It remains uncertain whether ambulacra are suprattegminal, but the mouth is subtegminal, covered by the central parts of the orals.

*Cantharocrinus simplex* Breimer sp. nov.

Pl. XI fig. 8—11

*Holotype.* The specimen 97699 in the collection of the Rijksmuseum van Geologie en Mineralogie at Leiden (Holland).

*Locus typicus.* 3 km east of Argovejo, in the pass between that village and Remolina (Prov. of León).

*Stratum typicum.* The top beds of the Santa Lucia limestone formation. According to P. Comte these beds belong to the cultrijugatus-zone and correspond to the lowermost Couvinian (M. Dev.).

*Diagnosis.* A *Cantharocrinus* species characterized by post. position of smaller basal; basal excavation for the reception of the stem; comparatively flat plates with slightly depressed sutures; orals occupying a large part of the ventral surface of the theca and even visible in side view; narrow ambulacra with only two series of small elongated ambulacrals (covering-pieces).

*Distribution.* The species is only known from the type locality at present.

*Description.* The total height of the theca is 13.6 mm, of which the dorsal cup occupies 11.4 mm (measured from the base to the top of iRR) so leaving only 2.2 mm for the height of the tegmen. The cup distad gradually expands in diameter and attains its greatest width of 12.4 mm at the level where the arms came off. The tegmen occupies a large part of the ventral surface of the theca; its width is up to 10 mm. The theca is composed of smooth plates with only slightly depressed sutures. The outline of the cup is rounded when viewed from below. In top view the theca appears as subpentagonal.

*Basals* three, unequal; smaller one posterior in position. The outline of the slightly constricted basal circlet is pentagonal. The base is excavated by a depression of max. 4 mm in diameter for the attachment of the stem. The stem itself probably was cylindrical. The basal circlet is relatively low; the height of the basals, measured along the surface is but 2—2.7 mm.

*Radials* five, in lateral contact all around the cup. The radials constitute the larger part of the cup. The plates are not all alike; l.post. R and r.post. R are wider than other RR. The height of the radials is 5.5 mm. The width for smaller RR is 5.5—6 mm; for the larger ones 7 mm. Along the interradial and radio-basal sutures the plates are somewhat raised, in places even produced into a tubercular edge. The facet for the reception of the first primibrach is narrow, but 3.2—3.8 mm wide. In l. and r.post. R the facets are displaced resp. to the left and the right. Radials are truncated at l. and r. upper margins for the contact with interradial plates.

*First primibrachs* have been found to be incorporated in the dorsal cup. The plates are horseshoe-shaped and only 1 mm thick. They are placed in a slightly inclined position, so that they may be seen when viewed from above (see textfig. 28). IBrr are not only in contact with the underlying radials, but with adjoining interradials and overlying orals as well. At its ventral margins the primibrach is excavated by a V-shaped ambulacral groove, that is in free contact with the ambulacral grooves on the tegmen.

*Interradial plates* are fairly large. In normal interradia only one such a plate occurs. It is hexagonal, higher than wide (4.8 × 2.9 mm), resting on the shoulders of the underlying radials. iRR are in lateral contact with the adjoining primibrachs are placed in the same inclined position. At their upper margins they come into contact with the indented edge of the overlying oral.



The posterior interradius is differentiated. Below the anus at least three small plates occur, the ventral one pentagonal, only 1 mm wide and high, flanked by two lateral, more or less rectangular plates. Some additional plates probably surrounded the anus, separating it from the overlying larger post.oral and adjoining l. and r.post. IBrr1. The differentiation of the posterior interradius makes it wider than normal interradii. The adjoining l. and r.post. IBrr are pushed aside, whereas the post. oral is slightly pushed forward. It is possible that the anus was situated at a short protuberance of many small plates.

The *tegmen* (cf. textfig. 28) is well developed, occupying a large part of the ventral surface of the theca. It is mainly composed of five prominent, sub-triangular plates provided with a median riblet. The posterior oral is wider, its median rib is more prominent. It is believed that this must be regarded in connection to the differentiation of the posterior interradius that it covers. The

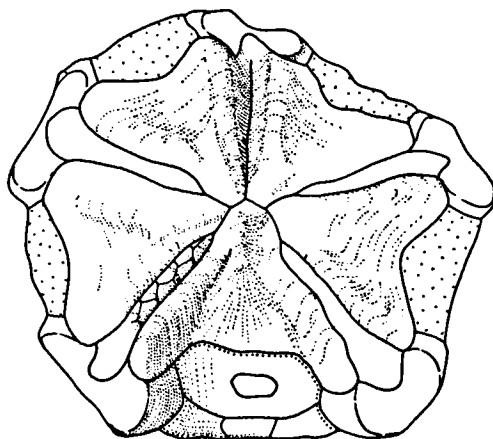


Fig. 28. Diagram showing the arrangement of plates in the tegmen of *Cantharocrinus simplex*. Holotype of the species, from the Santa Lucia formation near Remolina, León (coll. Mus. Geol. Min., Leiden, no. 97699).

plate is slightly pushed forward, so that it enters into contact with all of the other orals. The outer margins of the orals are bifid, indented for the contact with the underlying interradiial plates. Each tip of an oral is in contact with a ventral edge of different primibrachs. The orals are not in lateral contact (except for the most central part of the tegmen) at least in the external view. Along the edges of the orals narrow ambulacral grooves are present, running from the primibrach towards the centre, but not reaching this point. Ambulacral grooves are covered with a double series of alternating ambulacral plates (covering pieces) of elongated form. It is proved that the orals close beneath the ambulacral grooves. At ant. side the covering plates are missing and the interoral suture is visible at the bottom of the groove. So the ambulacra are distinctly supra-tegmenal, but the mouth is subtegmenal, covered by the central parts of the orals.

*Comparison of species.* The species *C. minor* and *C. simplex* are readily distinguished. The first one is much smaller, has a non excavated base, a restricted tegmen with ambulacra composed of four series of plates. The latter is the larger, easily recognizable by its more inflated form, excavated base, large orals and narrow ambulacra composed of but two series of covering plates.

The smaller basal in *C. minor* is in the usual l.ant. position whereas in the holotype of *C. simplex* it is situated posterior. This difference provisionally is held as a character separating both species, but it may equally well be found that the position of the smaller basal is variable in both species. This seems true since the smaller basal in the Permian species *Neoplatycrinus dilatatus* is variable in position, occurring either l.anterior or posterior. Not too much weight should be laid on this character.

Hapalocrinidae cf. *Culicocrinus nodosus* (J. Müller, 1852)

Pl. XI, fig. 1—4

- 1855 *Platycrinus nodosus* Wirtgen & Zeiller — J. Müller in Wirtgen & Zeiller, p. 15, Pl. 6, fig. 2, 3  
 1855 *Culicocrinus nodosus* Wirtgen & Zeiller — J. Müller, p. 22—25, Pl. 8, fig. 1—4, Pl. 9, fig. 1  
 1887 *Culicocrinus nodosus* Wirtgen & Zeiller — Follmann, p. 125, 126  
 1895 *Culicocrinus nodosus* J. Müller — Jaekel, p. 39—40  
 1926 *Culicocrinus nodosus* (Wirtgen & Zeiller) — Springer, p. 51; Pl. 11, fig. 3, 3a  
 1941 *Culicocrinus nodosus* (J. Müller) — W. E. Schmidt, p. 37, Pl. 7, fig. 1, 2a—6; textfig. 5 A  
 1943 *Culicocrinus nodosus* (Wirtgen & Zeiller) — Bassler & Moodéy, p. 382

*Material.* The Museo del Instituto geológico y minero de España at Madrid has six specimens (no. TB 69) of this species, one of them with the ventral side preserved (no. TB 69a). Locality and horizon of these specimens are unknown. But there is another specimen (no. TB 70) coming from Orzonaga (León) of Lower Devonian strata, probably Emsian in age.

*Description.* The description is mainly based on the complete theca no. TB 69a. The dorsal cup is inflated, about as high as wide, the tegmen is low to almost flat. The height of the dorsal cup is 10 mm, the greatest width of 12 mm is in the middle of the cup. The dorsal cup is constricted at its distal edge. The width of the tegmen is only 6 mm; its height does not exceed 2 mm.

*Basals* three, unequal; smaller one l.ant. in position. Outline of basal circlet pentagonal. The base is excavated by a shallow depression of 4.5 mm in diameter for the attachment of the stem that apparently was cylindrical. The excavation in the base is surrounded by a weak rim. The height of the basals, measured along the surface is 2.9—4.0 mm. The smaller B is provided with a central node or spine, the larger BB have two nodes or spines. The nodes are placed at regular distances along the basal circlet.

*Radials* five, in lateral contact all around the cup. The RR are by for the largest plates of the theca, the dorsal cup is mainly composed by the RR. The height of the plates is about 6 mm; the width about 6.5 mm, measured along the surface. The external surfaces of the radials are distinctly curved. About half the height of the plates occur two fairly large nodes or spines. The distal edge of the radials rather sharply curve inwards, so giving the distal part of the cup a constricted outlook.

*Brachial series* comprise two primibrachs per ray. The first primibrach is a low (1 mm), but very wide (4.5 mm) plate. It rests with a wide facet on the preceding radial. IBr1 is in lateral contact with the small interr radial plates. It must be regarded as definitely fixed to the dorsal cup. The r.post. IBr1 is the only preserved brachial plate of the ray. It is in contact with post. O and postero-right O. The facet for the reception of the IAx is a shallow depression with a ventral U-shaped ambulacral groove leading to the tegmen. The second

primibrach is axillar, wide triangular, generally not in contact with the interradial plates because it is less wide than IBr1. In l.ant. and l.post. rays the first secundibrachs are preserved. They enter in contact with the first primibrach and probably even with the interradial. So the IBrr are considered as fixed to the dorsal cup.

**I n t e r r a d i a l p a t e s** are placed in alternating positions with the radials, resting on their distal facets. iRR are merely small elements, 3 mm high, 1.3 mm wide, typically elongated. Only one iR occurs in normal interradia. The plates are inclined, so they can be seen when viewed from above. Interradials are in lateral contact with the IBrr1 and partly even with IIBrr1. Along their ventral facets they make contact with the orals.

The **p o s t e r i o r i n t e r r a d i u s** is differentiated. Three plates occur below the anus, the central one pentagonal and only 1 mm wide and high, the two lateral ones are rectangular and still smaller. The anus is situated somewhere between this row of plates and the post. O. The opening in the posterior interradius is very large (2 mm in diameter) so that it seems possible that some interradial plates may have been broken off.

The **t e g m e n** is composed of five orals only. OO are in contact with iRR and either with IBrr1 or IIBrr1. The orals are in close lateral contact, but along their facets occur grooves connecting with the ambulacral grooves of the brachials. Ambulacral plates have not been found covering the grooves. They now appear open, admitting to view the interoral sutures in their bottoms. The post. O is slightly larger than other OO. A kind of median rib must have been present on it. Towards the centre of the tegmen it is produced into a spine or node. The central tips of other OO have nodes as well.

*Remarks.* The specimens under consideration, and especially the figured specimen TB 69a resemble strikingly the German species *Culicocrinus nodosus*. The convex nature of the radials and the node-pattern are believed to be highly diagnostic for that species (W. E. Schmidt, 1941, p. 40). The base in the Spanish specimens is somewhat higher than usual among German representatives of the species. In this feature they are related perhaps to *C. inventriosus*, but in the latter species the radials are not strongly curved.

But although the affinity to *C. nodosus* is so striking, some major difference exist as well. Firstly the fact that the posterior interradius is differentiated. The only known figure of the posterior interradius in *C. nodosus* is Müllers Pl. 8 fig. 1 (1885). The anus is situated in a notch of the posterior oral and is separated from the radials by just one interradial plate. So any trace of differentiation of the posterior interradius in *C. nodosus* seems to be absent. Among other species of *Culicocrinus* such a differentiation is unknown as well<sup>1)</sup>.

The differentiation of the posterior interradius in the supposed Spanish *Culicocrinus* species is completely different from that in the German representatives of the genus but exactly the same as in Spanish Devonian genera of the Platycrinidae.

Next difference with *C. nodosus* specimens is found in the ambulacral grooves that run superficially along the interoral sutures in the tegmen. Such grooves have never been mentioned not figured for *C. nodosus*, in which species orals are always closely abutting. Ambulacral grooves on the interoral sutures have been figured for *Ambulacrinus rosaceus* in Müller, 1855, pl. 7 fig. 5a; Wachsmuth.

<sup>1)</sup> The species *Culicocrinus ? spinosus* Springer, 1926 (Pl. 11 fig. 4, a—c) from the Silurian of Tennessee in fact has some anal structures but it is arranged now under *Pleurocrinus* (cf. p. 138 of this paper).

& Springer, 1897, pl. III fig. 14 and Springer, 1926, pl. 11 fig. 2. Such grooves have been found in *Cantharocrinus simplex* and even in *Eutelecrinus fritillus* (cf. De Marez Oyens, 1940, pl. II fig. 4). Both in *Amblacrinus* and *Cantharocrinus* the grooves are superficial because the orals join beneath them, the interoral suture visible at the bottom of the groove when the covering pieces are stripped off.

Another character found in *Oenochoacrinus* may perhaps led to another interpretation of *Culicocrinus*. It is the presence of strongly modified axillar ambulacrals covering the arm bases. Müller's fig. 2, Pl. VIII, 1855 suggests that such larger radially disposed plates may have been situated on the indented edges of the orals covering the proximal brachials. If this is true the Spanish supposed Culicocrini are certainly not congeneric with the German Culicocrini but are merely a product of convergence.

### Family PLATYCRINIDAE Austin & Austin 1843

#### Genus OENOCHOACRINUS Breimer gen. nov.

*Genotype.* *Oenochoacrinus princeps* sp. nov.

*Remarks.* The genus *Oenochoacrinus* is erected to include platycrinid species with a composition unknown up to now among members of that family. *Oenochoacrinus* species agree in some of their characters with the Spanish genus *Cantharocrinus* as described in this paper: i. e. the possible posterior position of the smaller basal and the differentiation both of the posterior interradius and posterior oral. But the tegmen of these species is of quite unusual composition. It is composed of five orals in close apposition and five larger plates, radial in position, alternating with them. It is believed that these plates represent "radial dome plates" and have to be regarded as modified first ambulacral plates that have an axillary function. As a consequence the ambulacra of these species are subtegminal, as well as the mouth. It is believed that this tegmen structure has much in common with that of *Neoplatycrinus* from the Permian of Timor.

The following species are to be included within the genus:

*O. princeps* spec. nov.

*O. pileatus* spec. nov.

*O. scaber* spec. nov.

*O. princeps* is chosen the type-species, because it is best known and has its smaller basal in the usual platycrinid position.

*Diagnosis.* A genus of the family Platycrinidae, characterized by l.ant. or post. position of the smaller basal; typically one primibrach, axillary; two arms to the ray; differentiated post. interradius; tegmen mainly composed of ten plates: five pentagonal orals, posterior one differentiated, alternating with five large modified first axillar ambulacrals; subtegminal ambulacra. Arms biserial; stem unknown.

*Distribution.* The genus is still only known to occur in Spanish Lower and Middle Devonian strata.

*Oenochoacrinus princeps* Breimer spec. nov.

Pl. XII fig. 1—6

*Holotype.* The specimen TB 65a in the collection of the Museo del Instituto geológico y minero de España at Madrid.

*Paratypes.* The specimens TB 65b and TB 65c in the same collection.

*Locus typicus.* Le Velilla (province of León).

*Stratum typicum.* The type-level cannot exactly be determined since museum specimens constitute the only known representatives of the species and the labels do not indicate the exact stratigraphical formation. The specimens are undoubtedly of Devonian age.

*Diagnosis.* An *Oenochocrinus* species characterized by l.ant. position of smaller basal; high turbinate dorsal cup, strongly lobed in its upper portion, composed of flat, smooth plates; high conical tegmen with spiny orals and elongated first ambulacrals.

*Material.* The species is exclusively known from museum specimens that belong to the collection of the Museo del Instituto geológico y minero de España. Next to the types two specimens no. TB 66 from Orzonaga (León), two specimens no. TB 67 from Cerecedo (León) and five specimens of unknown provenance are housed in that collection.

*Description.* The general form of the theca is turbinate; the dorsal cup gradually expanding in diameter until the level where the arms come off. In that region the cup is strongly lobate. The tegmen is unusual high for hapalocrinids and plainly visible in side view. The total height of the theca, oral spine included is 16.3 mm. The height of the dorsal cup, measured from the base to top of the iRR is 11 mm; the tegmen so is about 5 mm high. The width of the cup in antero-posterior direction is 11.5 mm. Ornamentation only has been found on the tegmen. The measurements are taken from the holotype.

*Basals* three, unequal; smaller one in l.ant. position. Outline of basal circlet pentagonal; its height 2.8—3.2 mm, if measured along the surface. The facet for the attachment of the stem is circular, 3.7 mm in diameter.

*Radials* five, in lateral contact all around the cup. The radials are relatively small, 4 mm high and 5 mm wide, except for l.post. R and r.post. R that are 6.5 mm wide, owing to the fact that they support the wider differentiated posterior interradius. The facets for the reception of the primaxil (= IBr1) is 3 mm wide. In l.post. R and r.post. R they are pushed aside, in order to make place for the wide post. interradius. The upper left and right margins of the radials are truncated at the contact with interradiial plates.

The first primibrach is axillary, six-sided. It is 3 mm wide and but 1.2 mm high, in lateral contact with the iRR and along its upper facets with IBr1 and a small iiBr. The plate is incorporated in the cup.

The first secundibrach is still incorporated in the dorsal cup by sutures with iRR and IAxx. Two IBrr1 of the same ray are not in lateral contact but separated by a small triangular iiBr that even separates the IBrr1. The brachials that succeed IBrr1 are regarded as having been free, they are arranged strictly biserially. After six pairs of biserially arranged secundibrachs the arm divides (r.post. radius of paratype TB 65c). The ventral side of the brachials has a rounded ambulacral groove. All the biserially arranged secundibrachs have facets for pinnulars (cf. textfig. 29).

*Interradiial plates* are very elongated elements, 3.5 mm high and 1 mm wide. In normal interradii only one such plate occurs. The plate rests on the shoulders of the underlying radials. It is just in contact with IAxx and over its full length with IBrr1. Its upper margin rests against the overlying orals. The interradials lie in depressions between the lobes formed by the arm

trunks. Their position is slightly inclined toward the tegmen, so they appear in the upper view.

The posterior interradius is differentiated. Three small plates occur below the anus, the central one pentagonal and flanked by two lateral rectangular plates. Each of these three plates is much smaller than the iRR of other interradii. This is particular clear in the paratype TB 65. In the holotype the anus appears to be a minute opening, separated from adjoining brachials and posterior orals by many minute elements of irregular arrangement. This structure suggests that the anus was surrounded by an integument reinforced with small plates. The posterior interradius is clearly not protuberant. The differentiation of the posterior interradius makes it wider than the other interradii. The adjoining l. and r.post. arm trunks are pushed aside, whereas the posterior oral is pushed slightly forward.

The tegmen (cf. textfig. 29) is mainly composed by five large pentagonal

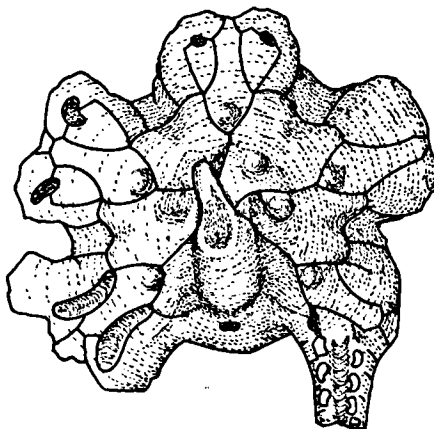


Fig. 29. Diagram showing the arrangement of plates in the tegmen of *Oenochocrinus princeps*. Holotype of the species, from Emsian strata near La Velilla, León (coll. Mus. Inst. Geol., Madril, no. TB 65a).

orals placed in close apposition. The posterior oral is differentiated and pushed forward by the anal structures. It is in contact with all other orals. Each oral bears a long spine; the spine of the post. oral is more prominent and surrounded by the four other spines. The orals alternate with five wedge-shaped plates, radial in position, that partly intervene between them. Each of these plates is provided with a single node. They occupy a large part of the ventral side of the arm trunks. In some trunks these plates are flanked by two smaller distinctly ambulacral plates, because they cover the ambulacral grooves of the underlying secundibrachs. Two ambulacral grooves of different half-rays meet under the wedge-shaped plates. The ambulacra are thought to unite there and to run subtegminally under the edges of the orals. So that the function of these wedge-shaped plates is that of an axillar ambulacral, specially modified for that function. The groups of three plates are interpreted as modified cover-plates attached to the tegmen.

*Oenochoacrinus pileatus* Breimer spec. nov.

Pl. XII fig. 7—9

*Holotype.* The specimen 97708 in the collection of the Rijksmuseum van Geologie en Mineralogie at Leiden (Holland). The theca has only three orals preserved.

*Paratypes.* The specimens 97709 and 97710 in the same collection. The paratypes have preserved only the tegmens.

*Locus typicus.* The types come from the village El Millar, near Pola de Gordon (Prov. of León).

*Stratum typicum.* The top of the Santa Lucia limestone formation. According to Comte the upper beds of this formation belong to the cultrijugatus-zone and correspond to the Lower Couvinian (M. Devonian).

*Diagnosis.* An *Oenochoacrinus* species characterized by post. position of smaller basal; heavy plated theca with constricted base, deeply excavated for the reception of the stem; swollen radials; very prominent tegmen with large, swollen first axillar ambulacrals, deeply intervening between the orals.

*Description.* The general form of the theca is somewhat cylindrical, with constricted base and flattened tegmen. The total height of the theca is 14.6 mm of which no less than 5 mm is for the height of tegmen. The width of the dorsal cup, measured in antero-posterior direction is 12.1 mm; the cup thus is slightly wider than high. The tegmen occupies the whole ventral surface (of the theca) and even a part of the lateral sides of the theca. It rests as a cap on the cup (hence the name). Ornamentation of the plates of the theca seems to be absent. Measurements for the description have been taken from the holotype.

*Basals* three unequal; smaller one post. in position. The basal circler is constricted, pentagonal in outline, fairly high (each B 3.5 mm in height) and deeply excavated for the reception of the stem. The stem itself probably was cylindrical and pierced by a narrow circular axial canal.

*Radials* five, in lateral contact all around the cup. Normal radials are 6 mm wide and but 4.5 mm high. The thickness of the radials is considerable: ca 2.5 mm. The l.post. R and r.post. R are wider than other interradii owing to the fact that they support the differentiated posterior interradius. The radials are swollen elements and the radio-basal and interradiial sutures are depressed. The facets for the reception of the first brachial is wide: up to 4.8 mm. The upper left and right margins of the radials are truncated for the contact with interradiial plates.

The first brachial plate, as preserved in the l.post. radius of the holotype appears to be a very low triangular plate only in contact with the underlying radial and not in lateral contact with the adjoining iRR. This primaxil is succeeded by a pair of large secundibrachs in contact with radials, interradians and orals. The ventral side of the brachials is excavated by a narrow but deep ambulacrual groove.

*Interradiial plates* are fairly large, hexagonal plates, 4 mm high and 3 mm wide. In each normal interradius one such a plate occurs. It is placed perfectly vertical, so does not appear in a view from above. The plate rests on the shoulders of the radials below; they come in lateral contact with brachial elements and along their upper sutures with the overlying oral.

The posterior interradius is differentiated. Three small plates occur below the anus, the central pentagonal and flanked by two lateral plates.

Each of these three plates is much smaller than the iRR of other interradia. The anus is merely a minute opening surrounded by a few smaller elements that separate it from the adjoining brachials and posterior oral. The anal structure certainly is not protuberant and the anus consequently is placed laterally in the theca. Although the posterior interradius is differentiated its dimensions are not much larger than those of other interradia. The l.post. and r.post. arm-bases are hardly pushed aside, but the posterior anal is pushed forward somewhat.

The tegmen forms a structure that largely roofs over the cup, plainly visible in side view (cf. textfig. 30 and pl. XII fig 9). The central part of the tegmen is composed of five pentagonal orals, placed in close apposition. The posterior oral is larger and slightly pushed forward, so that it makes contact with all other orals; it has a central riblet. The lateral margins of the orals

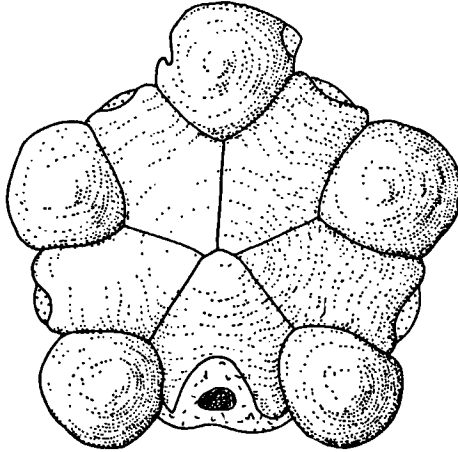


Fig. 30. Diagram showing the arrangement of plates in the tegmen of *Oenochocrinus pileatus*. Paratype of the species, from the Santa Lucia formation, El Millar, León (coll. Mus. Geol. Min., Leiden, no. 97710).

are bifid, indented for the contact with the interradial plates. The tips of two different orals are in contact with the ventral edges of the underlying brachials; the tips firmly close over the ambulacral groove of the brachials. The orals alternate with five very prominent bulbous plates, radial in position and rather deeply intervening between them. These plates are preserved in the paratypes. They must have been in contact not only with the orals but with the underlying brachial plates as well. They cover the ambulacral groove that passes subtegminal below the orals. At the lateral sides of these plates ambulacral notches were found, proving that the ambulacral grooves of an arm came in from both sides. So it must be concluded that the laterally incoming grooves united underneath these plates and ran further under the orals as one groove towards the subtegminal mouth. In this way these plates can only be interpreted as axillary ambulacral plates, specially modified for that function. They are regarded as being fully homologous with radical 'dome plates' as defined by Wachsmuth & Springer. They provide further proof that the interpretation as "modified first axillary ambulacrals" is correct.



*Oenochocrinus scaber* Breimer spec. nov.

Pl. XIII fig. 3—5, 10, 11

*Holotype.* The specimen 128 D/1 in the collection of the Museo del Instituto geológico y minero de España at Madrid.

*Locus typicus.* Although the holotype comes from Aleje, near Cistierna (León), the village of Colle is designated the type-locality because most of the specimens were found there and the stratigraphical occurrence of the crinoid fauna's is best known from that locality.

*Stratum typicum.* The top beds of the La Vid shale formation. According to Comte these beds correspond to the Lower Emsian (L. Dev.).

*Diagnosis.* An *Oenochocrinus* species characterized by a variable position of the smaller basal; very high dorsal cup, strongly ornamented; base with a rim, surrounding the facet for attachment of the stem, occasional presence of two primibrachs; small restricted tegmen, not visible in side view.

*Material.* Next to the holotype the following specimens in the collection of the Museo del Instituto geológico y minero de España at Madrid are referred to the species: 10 specimens no. 128 D from Aleje (León), 15 specimens no. 129 D from Colle (León) of which two with tegmen, 7 specimens no. 130 D from Corniero (León) of which three with tegmen.

*Description.* The theca of these specimens is mainly composed by the dorsal cup; the tegmen occupies only the half of its ventral surface. The height of the dorsal cup is 13 mm, its width 14 mm, measured in antero-posterior direction. The outline of the cup, if viewed from below is circular to slightly rounded. The top view is only a little lobate. The measurements for the description are taken from the holotype.

*Basals* three, unequal. In the holotype it is l.ant. in position but in one of the Colle specimens it was found to be in posterior position. The basal cirlet is pentagonal in outline, very high (each B 4.5—6 mm in height) and rapidly expanding in diameter. A rim surrounds the place where the stem was attached. The basal cirlet shows an ornamentation of nodes and riblets in an irregular pattern.

*Radials* five, in lateral contact all around the cup. RR are very high plates, some of them even higher than wide (7.5 × 6 mm). Only l.post R and r.post. R are as wide as high. The radials are placed perfectly horizontally. The facets for the reception of the brachials are up to 4 mm wide. The upper most left and right margins of the radials are truncated for the reception of the interradials. The ornamentation of the radials principally is the same as on the basals, but there seems to be a diagonal trend in the pattern of nodes and riblets.

*Two primibrachs* occasionally may be present. Frequently only one small triangular first primibrach is present. The r.post. ray of the holotype has two primibrachs whereas all other rays have but one. If only one axillar primibrach is present, the overlying first secundibrachs are in contact with the radial and the adjoining interradials. When two primibrachs are present it is found that the first one is irregular of form and size; it may be in lateral contact at both sides with the adjoining interradials, but it may lose one or even both of these contacts, and the overlying first secundibrachs then intervenes. After

one or two secundibrachs of a half-ray the arrangement of these plates becomes biserial.

Interradial plates are unusually small, six-sided, higher than wide ( $3.2 \times 2.1$  mm). The plates rest on the shoulders of the underlying radials. They generally are in lateral contact with the first secundibrachs and occasionally with the first primibrach. The position of the iRR is strongly inclined toward the tegmen, where it is in contact with the oral.

The posterior interradius is not preserved. Some indications however lead us to the conclusion that it must have been differentiated. Firstly the l. and r.post. RR are wider than other RR and the facets for the brachials are pushed aside, exactly as has been found among all other hapalocrinids with differentiated posterior interradia. Secondly the upper edges of l. and r.post. R

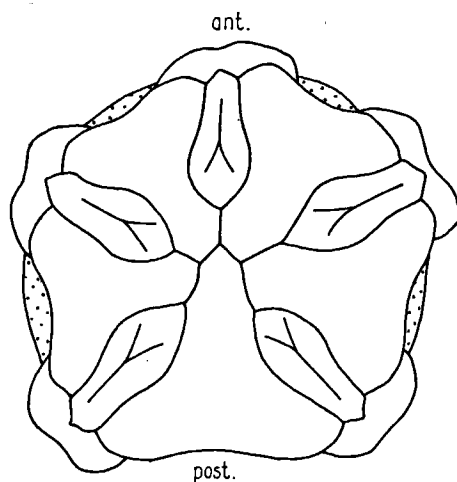


Fig. 31. Diagram showing a reconstruction of the tegmen in *Oenochocrinus scaber*. Based on the holotype, from Emsian strata near Aleje, León (coll. Mus. Inst. Geol. Min., Madrid, no. 128 D/1).

of the holotype not only have an incision for an overlying interradial plate but even two more sutures, apparently for the contact of more interradial plates. These features rather point to the assumption that the posterior interradius must have been differentiated.

The tegmen is merely a small and flat structure, occupying only half the ventral surface of the theca. It does not appear in side view. In all the specimens that preserve parts of the tegmen, it is crushed. The holotype is still the best specimen for the study of the tegmen. All the plates are preserved but they are not in their correct relative positions. Ten plates can be distinguished of which five must be oral plates and five must represent the modified first axillar ambulacrals. The posterior oral — although damaged — seems to be differentiated. The postero-right oral is still in contact with the underlying interradial. This plate is pentagonal and bears a median riblet at its central part. At left-anterior side of the tegmen an axillar ambulacral is found to be in its place. It is perfectly radial in position and wedge-shaped. It must have intervened very deeply between the orals. The presence of these ten plates proves that the tegmen is comparable with those of other *Oenochocrinus* species.

*Oenochoacrinus?* spec.

Pl. XII fig. 10—11; Pl. XIII fig. 1—2

Four specimens, now in the collection of the Rijksmuseum van Geologie en Mineralogie at Leiden (Holland) (nrs. 97704—97707) coming from the top beds of the Santa Lucia limestone near Remolina (León) are not sufficiently well preserved to allow their classification. The specimens resemble *Oenochoacrinus pileatus* in general form and composition. The orals are in close apposition so that the ambulacra must be subtegmenal. Orals are pentagonal and there is a small notch between the adjacent orals in which a first axillar ambulacral might have been situated. But no such a plate is preserved in any of the specimens, so that one cannot be sure of their place among *Oenochoacrinini*. The specimens further differ from *O. pileatus* by the l.ant. position of the smaller basal and the less prominent orals.

*Comparison of species.* The three species of *Oenochoacrinus* as described in this paper are easily recognizable. *O. princeps*, the genotype, distinguishes itself from its relatives mainly by the strongly lobed edge of the dorsal cup and by the high conical tegmen with its strongly spineriferous orals. The composition of the tegmen is similar to *O. scaber*, especially in the mode of differentiation of the axillar ambulacral, that is produced into a wedge-shaped element.

*O. pileatus* is distinguished by its inflated theca with excavated base. But the main difference with the other species is the way in which the axillar ambulacra have developed. These plates are produced into large domes alternating with the smaller orals and covering the arm bases.

*O. scaber* is mainly characterized by its ornamentation that is absent in other species of this genus.

## GENUS PLATYCRINUS Miller 1821

*Platycrinus* spec. (ex gr. *bollandensis* Wright 1938)

Pl. XIII, fig. 6—9, 12—14

J. Wright, 1938, p. 270; J. Wright, 1955, p. 265.

*Material.* The specimens no. 97712 and 97713 deposited in the Rijksmuseum van Geologie en Mineralogie at Leiden (Holland). The specimens were found at Rabanal de los Caballeros (near Cervera de Pisuerga, Province of Palencia) in the Lower Carboniferous. According to Van Ginkel (oral communication), who is studying the fusulinid fauna of this limestone member, the age of this limestone is of Middle or Upper Namurian date.

*Description.*

	97712	97713
Total height of theca	19.6	19.6
Height of dorsal cup	10.1	11.3
Height of tegmen	9.5	8.3
Diameter of tegmen	19.2	21.7
Diameter columnar socket	ca. 5	ca. 5
Height of radials	8.2	8.3
Width of radials	11.2	12.1

The circle of basals is pentagonal in outline; horizontally disposed. The basals are fused together; interbasal sutures are not visible. The largest width of the base is 13—14 mm; viewed from the side the basals are just visible. The base is excavated by a shallow depression for the reception of the stem. Last columnars must have been circular in outline.

Radials five, all alike, in lateral contact all around the cup. Radial circlet is nearly vertically disposed. Interradial sutures and radio-basal sutures depressed (especially in spec. 97713). Radials provided with rugose type of ornament. The facets for attachment of the proximal brachials occupy two thirds the width of the radials. The primaxil is merely a very small triangular plate, surmounted by the first secundibrachs, that enter in contact with the underlying and adjoining interradians.

Each interradius has a fairly large hexagonal iR1, in lateral contact with IIBrr1 and along its upper edges in contact with the tegmen plates. The plates rest upon the shoulders of the underlying radials. The posterior interradius is not differentiated. The post. iR is equal to other iRR. It is separated from the anus by only a single range of plates.

The tegmen is composed of about 30—40 plates, without any trace of individual differentiation. All plates alike, ca 3 mm in diameter. The top plate of the tegmen in 97712 is eccentric, situated somewhat l.post. from the centre. The tegmen in 97713 is slightly crushed. The anus is situated at the posterior edge of the tegmen, plainly visible in top view, separated from post. iR by only a single row of plates. While preparing the tegmen of 97712 it appeared that the tegmen plates had a fine pustular ornament. The tegmen itself is a low arching structure on the dorsal cup.

*Remarks.* It is believed that the two specimens of the Lower Carboniferous of Rabanal belong to the *bollandensis*-group of *Platycrinus*-species. The group is defined by Wright (1955): "Anus a simple opening, sometimes more or less protuberant, on the upper surface of the tegmen. In the posterior interradius, the middle IR resting on the shoulders of LPR and RPR is usually hexagonal in shape, and while it may be slightly larger or smaller, it does not differ much in size from the corresponding plates in other interradii. A variable number of plates intervene between this plate and the anal opening. The anal opening is always entirely visible in ventral view".

The characters of the posterior side of the Spanish specimens are undoubtedly those of this group. It is a difficult question whether it is a new species or falls within the range of variation which might occur around the holotype of one of the species already described. Many *Platycrinus* species are based upon very few specimens. Any information on the range of individual variation is absent. One might suggest however that the species is new because of its age. But it is realized that such easily may be overestimated. The other Rabanal specimen classified now as *Pimlicocrinus latus*, although of Namurian age, undoubtedly is conspecific with representatives of this species in the Tournaisian of the British Isles. A similar phenomenon may be the case in this *Platycrinus* species. It is preferred therefore not to describe it as a new species, but merely to discuss its affinities, mainly for stratigraphic purposes.

The Spanish specimens have affinities with *P. conglobatus* and are comparable in many features with *P. invertielensis*, *P. Smythi* and *P. directus*.

In *P. conglobatus* the cup plates are smooth (although they have a granular ornament in very young individuals), the plates are separated by shallow grooves

and the anus is situated high up in the posterior interradius. In contrast, the Rabanal species has a rugose ornament on the cup, the grooves are deep and the anus is separated from the post. iR by only one row of plates.

*P. invertielensis* is found with *P. conglobatus* and differs only in possessing a rugose ornament on the cup plates. The tegmen is unknown and it is not certain whether the species should be referred to *Platycrinus* or *Pleurocrinus*. It differs from the Rabanal species because the lower edge of the RR are straight instead of being curved.

*P. directus* is similar in the shape of the cup and it has the same pustular ornament on the tegmen as the Rabanal species. The tegmen of *P. directus* is very low and forms lobes along the base of the arms, and in this respect is different from the Rabanal species.

*P. Smythi* is a small form (probably young), which has a similar shape and ornament of the dorsal cup. The tegmen is unknown. It differs from the Rabanal species, *P. conglobatus* and *P. invertielensis* because the interradiial plate does not appear to penetrate between the upper parts of adjacent radial plates.

#### GENUS PLEUROCRINUS Austin & Austin 1843

*Pleurocrinus* spec. (ex gr. *coplownensis* Wright 1938)

Pl. XIV, fig. 1—4

J. Wright, 1938, p. 271; J. Wright, 1955, p. 265.

*Material.* A complete preserved theca, no. TB 84 in the collection of the Museo del Instituto geológico y minero de España at Madrid. Two larger but badly crushed specimens no. TB 85 in the same collection. Exact locality of the specimens is unknown. Their age is either Devonian or Carboniferous.

#### *Description.*

	TB 84
Total height of the theca	10.3
Height of dorsal cup	5.7
Height of tegmen	4.6
Diameter of tegmen	ca. 11.0
Height of radials	4.0
Width of radials	6—7

The form of the dorsal cup is more or less prismatic with truncated base. Viewed from below its outline is pentagonal. The constituent plates are smooth. The arm-bases are trunked together and come off horizontally. The tegmen is low, composed of irregularly arranged convex plates.

The circle of basals is pentagonal in outline, horizontally disposed. The basals probably are fused together, interbasal sutures are hardly visible. The largest width of the base is 8.2 mm, measured in antero-posterior direction. The outer edges of the basals are just visible in side view. The place of attachment of the stem is not well visible. It was only very slightly excavated if at all for the reception of the stem.

Radials five, in lateral contact all around the cup. The radials are vertically disposed, forming the sides of the cup; their lower edges are visible in basal view. Radials not all alike: the ant. R and antero-lateral RR are 6 mm wide, the postero-lateral RR are wider. The plates are all typically wider than

high, strongly indented at their upper edges for the reception of the first primibrach. The arm-facets are only half as wide as the radials. The region of the radio-basal sutures is depressed, forming a wide groove around the base. The interrarial sutures are not markedly depressed, except the suture between l.post. R and r.post. R, which is deeply depressed so as to form a gully connecting with the anus.

*I n t e r r a d i a l* plates are barely distinguishable. The upper left and right angles of the radials are not markedly bevelled for contact with an interrarial plate. In each interradius a small, more or less hexagonal plate alternates with the radials, but it does not project between them. The posterior interradius is wider than the other interradii. It is slightly depressed. The anus opens directly in this depressed area, so that it is not plainly visible from the side, but only in an oblique view. The anus is situated directly at the upper margins of the l.post. R and r.post. R; there is no anal plate intervening between the radials and the anus. The anus has direct contact with the gully between the posterior radials.

The first *p r i m i b r a c h* is axillar, very much wider than high. The plate is situated nearly vertically or slightly sloping inward. It has a strongly rounded back, that is in contact with several tegmen plates. The overlying pair of first secundibrachs is low, still being in contact with the tegmen plates, but not with the radials. The group of proximal brachials is trunked together. The arms must have come off nearly horizontally. The total number of free arms is ten.

The *t e g m e n* is a flat structure, composed of many irregularly arranged plates without differentiation of ambulacrals and interambulacrals. Orals are not distinguishable. The tegmen plates are convex or even slightly nodose. The arm bases are covered with elongated rhomb-shaped cover plates resting on the ventral sides of the underlying pair of first secundibrachs.

*Remarks.* It is beyond doubt that the specimens described here possess the essential characters of the *coplowensis*-group of *Pleurocrinus* species, as defined by Wright (1955): 'The anus is in a lateral position directly above the posterior RR, with no intervening plates.' Our species differs from all other species referred by Wright to his *coplowensis*-group by (1) the position of the anus in the more or less depressed posterior interradius, plainly visible only in an oblique view, (2) the truncated base and (3) the depressed gully-like suture between l.post. R and r.post. R. It is noted that *Pleurocrinus* species from Timor, belonging to the *coplowensis*-group, have a somewhat depressedly situated anus. It may be that the present species is new. It is not established as a new species since only one complete theca and that probably young, is known, which lacks the arms and the stem. Moreover, nothing is known about individual or ontogenetic variation.

#### *Systematic relations of the Platycrinicae*

The study of Spanish Platycrinicae forced us to investigate the real meaning of some of the peculiar characteristics found among them. The considerable modification of tegmen plates alternating with orals in *Oenochoacrinus* and the peculiar mode of differentiation in the posterior interradius led us to a more detailed study of this group. It seemed that the tegmen structure is of greater interest than all other characters in the systematic study of Platycrinicae. It is even believed that the tegmen structure is strongly related to the composition of

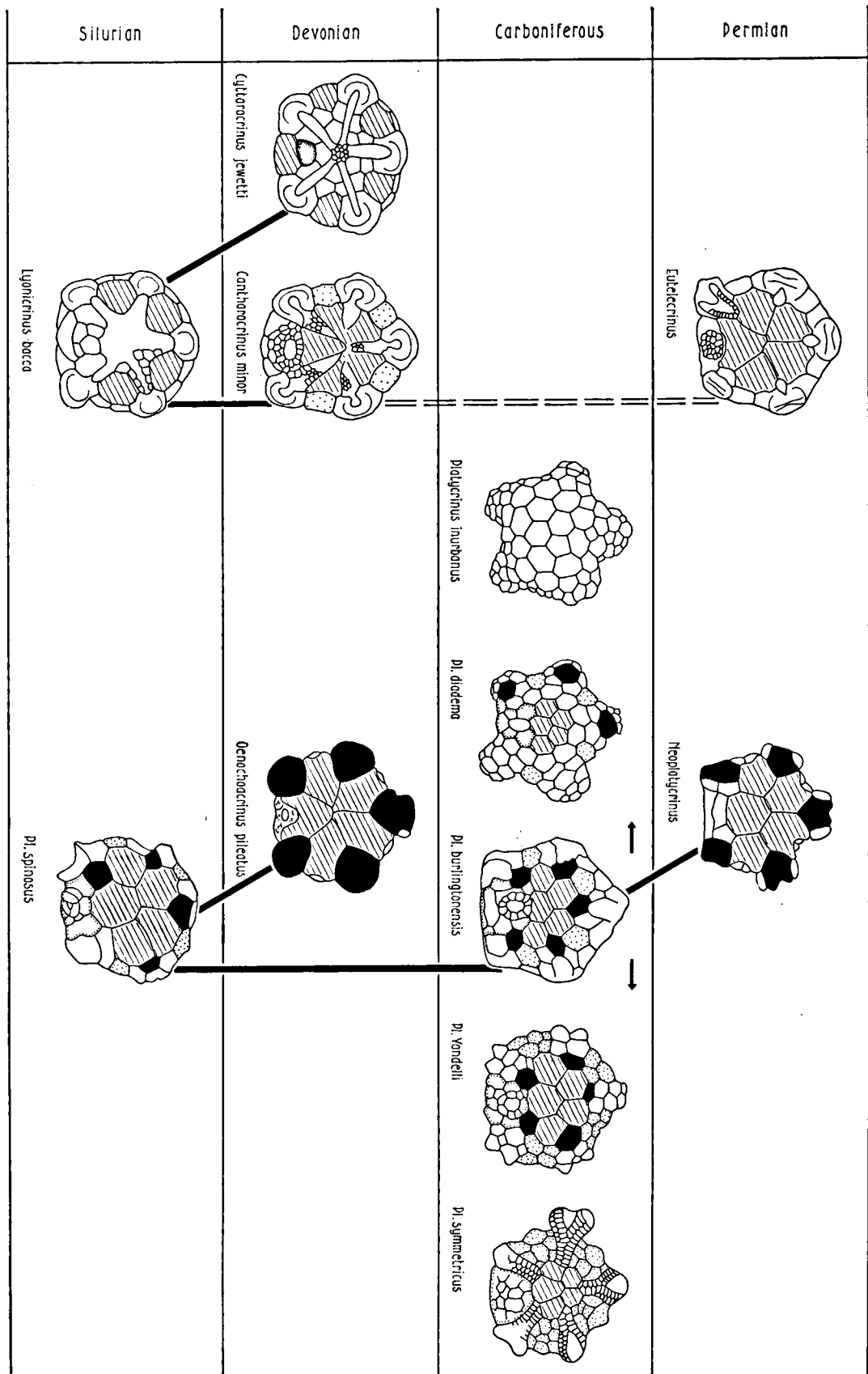


Fig. 32. Diagram showing the morphological relations of some of the Platycrinidae. (explanation see text).

arm bases. These two characteristics provide the best idea of how to differentiate genera and species in this group of crinoids. We can fully agree with a statement of Laudon & Severson (1953, p. 532): "Since the cup of *Platycrinites* is essentially stabilized, we believe that the most important criterion available for specific differentiation is the nature of the tegmen". Their statement in our opinion does not only apply to specific categories but even to the supra-specific categories.

Some new interpretation, partly based on notes among the literature on Platycrinicae, will be suggested and perhaps may lead to a somewhat unusual view of the real morphological trends in this group of crinoids. The morphological relationship of the ventral sides in thecae of the Platycrinicae is presented in textfig. 32.

If we return to the tegmen structure of *Oenochoacrinus* and especially to *Oe. pileatus* (which species is drawn in textfig. 30) its tegmen is found to be arranged in a strict pattern of ten plates: five well developed and modified orals in close apposition in the peristomal area, alternating with large "dome-plates", which partly intervene between them. (The term "dome-plates" is taken here as an exclusively descriptive one.) The anterior "dome-plate" of paratype 97710 of *Oe. pileatus* distinctly shows an "ambulacral notch" at its left side for the reception of the ambulacral groove of the incoming arm, whereas at the right side of the same "dome-plate" this notch is filled in by an individual plate that can only be interpreted as a small ambulacral. It appears that ambulacra came in at both sides of the large "dome-plate" and must have met somewhere beneath it. If this is true the plate must be characterized as being a greatly modified coverplate, occupying a strict radial position alternately with the orals.

An arrangement of tegmen plates as in *Oenochoacrinus* appeared at first to be rather unusual among Platycrinicae although some forms seem to possess similar tegmens. One of the most important representatives of these forms is *Neoplatycrinus*. After careful examination of museum specimens of *Neoplatycrinus dilatatus* from the Permian of Timor deposited in the Rijksmuseum van Geologie en Mineralogie at Leiden (Holland) it became evident that the tegmen structure of this genus could throw some light on the interpretation of the tegmen in *Oenochoacrinus*. It seems that the tegmen of *Neoplatycrinus* represents the same morphological stage as in *Oenochoacrinus* and also that these genera have much more in common. Some specimens of *Neoplatycrinus* were observed to possess a posteriorly situated smaller basal (exactly as occurs in *Oenochoacrinus*) although the left anterior position of that basal is much more common among the *Neoplatycrinus* species.

The tegmen of *Neoplatycrinus* shows basically the same organization as in *Oenochoacrinus*. It is mainly composed of five very prominent closely apposing orals and five basically pentagonal plates, strictly radial in position, alternating with the orals. In Wanner's figs. 39 and 42, Pl. VI, 1937, some *Neoplatycrinus dilatatus* species are viewed from lateral sides. Ambulacral notches appear to be situated in the pentagonal plates which alternate with the orals. Two such notches occur in each of these plates. They cover the ambulacral grooves in the different IIBrr1 below them. In figs. 40 and 41 of the same plate ambulacral notches are not only found to occur at both sides of the pentagonal plates but in two small plates flanking them as well. The amount of ambulacral openings per ray in such specimens is raised to four. An interpretation of the larger pentagonal plates and the pairs of flanking plates seems to be justified.

A separate tegmen of *Neoplatycrinus dilatatus* (see textfig. 33) could after preparation be studied from the internal side. The orals proved to project into



the interior by means of swollen structures. The pentagonal plates are situated in between these processes. Pentagonal again are plates flanked by two smaller plates. It appears that two larger ambulacral grooves flanked by two smaller ambulacral grooves are present in these plates. The limits between the four grooves are formed by sharp rims (textfig. 33). In the orals such grooves are not found. The four grooves must have met somewhere near the point where the pentagonal plates intervene with the orals. All the structures on the inside of the tegmen suggest that the ambulacra came in at the lateral sides of the pentagonal plate, hang on it (probably with the aid of the oral processes between them) and were free (probably as a tube) from those plates and towards the mouth. So one can only conclude that these larger pentagonal plates are ambulacral plates with a sort of axillary function for the reception of the

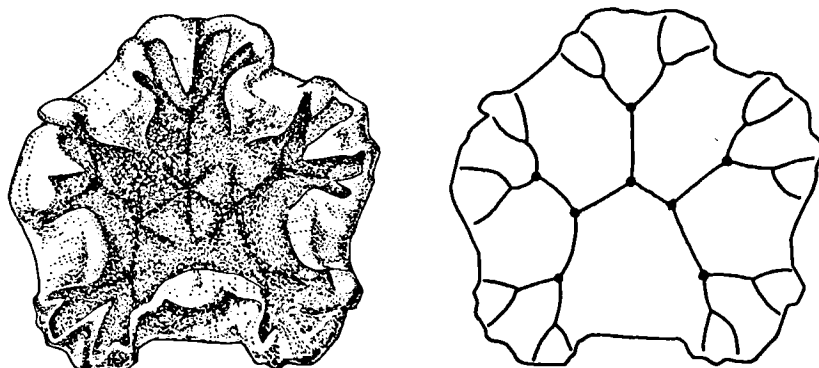


Fig. 33. Diagrams showing the internal aspect of an isolated tegmen of *Neoplatycrinus dilatatus*. Right hand figure shows arrangement of the plates. Specimen from the Permian of Timor (coll. Mus. Geol. Min., Leiden no. 101647).

ambulacra. The term "first axillar ambulacrals" will be applied in further descriptions to indicate the larger ambulacrals alternating with the orals and occupying strictly radial positions. These plates have now proved to be present in both *Oenochoacrinus* and *Neoplatycrinus*. The presence of such plates means that ambulacra in these two genera are *subtegminal*.

The ontogeny of *Neoplatycrinus dilatatus* as described by Wanner (1937, p. 78; textfigs. 1—7) is fully confirmed by our own observations. It proves that the first axillar ambulacrals are already present in the smallest known specimens with but two ambulacral openings. The plates were observed there as minuscule elements just roofing and separating the two ambulacral grooves of the underlying IIBrr1. During ontogeny the first axillar ambulacrals develop greatly until they even intervene between the orals and must definitely be regarded as incorporated in the tegmen. In this stage the first axillar ambulacrals are flanked by two smaller ambulacrals, the total amount of ambulacral openings per ray is raised to four. It is believed that this is the adult stage of *Neoplatycrinus dilatatus*. By far the most specimens show this stage of development. Among species formerly regarded as *Neoplatycrinus major* (which species was withdrawn by Wanner (1937) in favour of the view that these forms represent adult or old stages of *Neoplatycrinus dilatatus*) six ambulacral openings per ray were met with. Consequently additional very small ambulacrals are introduced in the tegmen. But

these fifth and sixth ambulacral openings belong with small fixed ramules of biserial arrangement. This seems to point to the conclusion that the arm structure of *Neoplatycrinus* must have been similar to that of *Plemnocrinus* or *Eucladocrinus*. In the present view however it is still open to question whether *Neoplatycrinus major* constitutes an independent species or not.

From our present knowledge of the tegmen in *Oenochoacrinus* and *Neoplatycrinus* some conclusion may be drawn, that will be helpful in the interpretation of the tegmens of other Platycrinidae. (1) The tegmen has a basic pattern of ten plates: five orals, interradial in position, and five first axillar ambulacrals, radial in position, alternating and partly intervening with the former. (2) During ontogeny the orals first and then the first axillar ambulacrals become modified to take their part in the formation of the tegmen. (3) As a consequence the ambulacra in the theca are subtegmenal. (4) The presence of well developed first axillar ambulacrals is consistent with the presence of a small triangular primaxil and two well developed secundibrachs per half ray. (5) The first axillar ambulacrals have a function in covering the base of the arm trunk that is the consequence of this arrangement of proximal brachials.

When trying to review the whole literature on the tegmens of Platycrinidae it was found that the pattern of principally ten plates occurred in many more species than was believed first. First of all it seemed possible to interpret the tegmen of *Culicocrinus* ? *spinosus* as described by Springer, 1926, p. 51; Pl. 11, fig. 4, 4a—c, from the Niagaran (U. Sil.) of Tennessee in the same way as indicated above (Springer's figure is reproduced on the present textfig. 32). Five larger orals are distinguishable, the posterior one pushed in between the others. But some more plates occur in the tegmen. The plates are radial in position, pentagonal and situated alternately with the orals (at r.post. side such a plate is not distinguishable in Springer's figure). It is believed that *C* ? *spinosus* has a tegmen which has an analogous composition as was described now for *Neoplatycrinus* and *Oenochoacrinus*. It seems true at least that the plates alternating with the orals — although perhaps not specially modified — may be interpreted as topographically homologous with the first axillar ambulacrals in the two mentioned genera. Perhaps they are even analogous with them if they possessed the same function covering the incoming ambulacra. In any case the ambulacra are subtegmenal.

It is not understood why Springer referred his species — although with much doubt as to its generic affinities (p. 51) — to *Culicocrinus*. The species perhaps is best placed under *Pleurocrinus*. Springer himself, together with Wachsmuth, described such forms as f. e. *Platycrinus burlingtonensis* and made many valuable observations on the real interpretations of tegmen plates in that genus (1897, p. 103). If the tegmen of *P. burlingtonensis* is examined from Wachsmuth & Springer's Pl. LXIX, fig. 3c (1897) and their remarks on p. 103 (1897) are considered one can only conclude that the tegmen of the Burlington species (reproduced here in textfig. 32) has the same topographical homologues as were already known to exist among *Oenochoacrinus*, *Neoplatycrinus* and *Pleurocrinus spinosus*.

The "set of large plates in the tegmen, radially disposed and occupying the regions between the orals and the arm bases" were called radial dome plates by Wachsmuth & Springer and firstly interpreted as "actinal representative of the radials". Such a view is to a certain extent underlined by the ontogeny of *Neoplatycrinus* and the occurrence of specially modified "radial dome plates" in *Oenochoacrinus pileatus*. Wachsmuth & Springer in 1897 turned to another interpretation of their radial dome plates in defining them (p. 103) as "highly

differentiated covering pieces". It is believed that the composition of the tegmen in *Oenochocrinus* and the new interpretation of the tegmen in *Neoplatycrinus* as described now are fully consistent with Wachsmuth and Springer's later interpretation of radial dome plates as highly differentiated covering plates. One even may hold that they provide new evidence in support of their later interpolation.

In support of their new interpretation of radial dome plates Wachsmuth & Springer referred to the different compositions of tegmens among Mississippian *Platycrinus* species. A morphological series was proposed by them to underline their view. This series consists of *Platycrinus burlingtonensis*, *P. Yandelli* and *P. symmetricus*. The series is reproduced in our textfig. 32. The first morphological stage is represented by the tegmen of *P. burlingtonensis* that is now considered to be composed of plates topographically homologous to those found elsewhere to compose the tegmen. From this stage it is but a short step to *Platycrinus Yandelli*. Five orals are easily distinguishable in this species, the posterior one pushed in between the others. First axillar ambulacrals are only slightly larger than succeeding ambulacrals, but they still occupy a strict radial position alternating with the orals. In the anterior ambulacral the first axillar ambulacral is not developed. It appears there as an ambulacral equal in size and shape as the succeeding ones. Compared with *P. burlingtonensis* there is a tendency to lose the differentiation of the first axillar ambulacrals, parallel with a tendency to incorporate more and more ambulacrals and interambulacrals into the tegmen. The textfig. 32 of *Pl. Yandelli* is reproduced from Wachsmuth & Springer's fig. 6c, Pl. LXVI, 1897.

An extreme stage in the line of the first mentioned trend is represented by *P. symmetricus* in which species five larger orals are differentiated. First axillar ambulacrals apparently did not develop. Many interambulacrals are incorporated whereas the ambulacra occupy clearly limited strips on the tegmen. The ambulacra are suprattegminal (cf. textfig. 32 as reproduced from Wachsmuth & Springer's pl. LXIX, fig. 1c; 1897). The tendency to lose the differentiation of first axillar ambulacrals and the introduction of many ambulacrals and interambulacrals noted in *P. Yandelli* seems to be complete in *P. symmetricus*. This trend apparently results in a perfect differentiation of ambulacrals in well defined strips that represent suprattegminal ambulacra of rather delicate structure.

We assume that in *P. burlingtonensis* the ambulacra are subtegminal and further that there is indeed a tendency towards the loss of differentiation of the first axillar ambulacrals making all ambulacral alike. This implies a tendency to bring the ambulacra into a suprattegminal position which means perhaps that protection of ambulacra by firm elements was lost.

The morphological trend with *Platycrinus symmetricus* as an and member is rather unusual among Platycrinicae and probably confined to the North American continent. Only a few forms were reported to be similar in composition to *P. symmetricus*. Laudon, Parks and Spreng (1952, p. 573) reported the similarity of *P. sunwaptensis* to this species, but unfortunately did not figure the tegmen. Laudon & Severson (1953, p. 532) mention the fact that immature forms of *P. bozemanensis* are so similar to *P. symmetricus* that they cannot be separated from it.

Much more frequently we find forms that apparently protect the ambulacra, either by (1) differentiation of firm and large orals and first ambulacrals that keep the ambulacra subtegminal or by (2) gradual loss of any differentiation of tegmen plates that grow out to ill-defined tegmen plates forming a competent structure for the protection of ambulacral grooves. Forms belonging to these

two groups can be placed in a morphological series in the way shown in our textfig. 32. Such a series recommences with *P. burlingtonensis* but now a trend towards loss of differentiation of tegmen plates appears in which axillar ambulacra may occasionally play a rôle. It is believed that this morphological development is the usual one among Platycrinidae of the European and Mediterranean area, not only in the Carboniferous but even in Permian times.

The basic stage again is that of a species similar to *P. burlingtonensis*. This stage is not only found in American *Platycrinus* species but it is met with in European *Pleurocrinus* species such as f. e. *P. mucronatus* (J. Wright, 1956, pl. LXXIV, fig. 12) and to a somewhat lesser degree in *P. coronatus* (J. Wright, 1956, pl. LXXII, fig. 7; textfig. 128) from the Lower Carboniferous of England and Germany respectively.

The next stage in the first mentioned trend can be found in *Pleurocrinus diadema* (cf. J. Wright, 1956, pl. LXX, fig. 1, reproduced here, textfig. 32) in which the topographical homology of the plates still can be detected but the plates themselves all are more or less alike and are apparently stout structures. In this species even some axillar ambulacra are slightly differentiated but while incorporating more elements in the tegmen they remained in a lateral position, the ambulacral separating them from the orals.

The last stage in this series in which all trace of arrangement and differentiation is lost is most abundantly represented by forms of the Lower Carboniferous of England. This stage is reproduced in textfig. 32 by *Pleurocrinus inurbanus* as illustrated by J. Wright, 1956, pl. LXXIII, fig. 16. But it is found among much more *Pleurocrinus* species, such as:

- Pleurocrinus tuberculatus* (J. Wright, 1956, pl. LXXII, fig. 13)
- Pleurocrinus grandis* (J. Wright, 1956, pl. LXXIII, fig. 5)
- Pleurocrinus coplowensis* (J. Wright, 1956, pl. LXXIII, fig. 10, pl. LXIX, fig. 11)
- Pleurocrinus ellipticus* (J. Wright, 1956, pl. LXXIII, fig. 19)
- Pleurocrinus rugosus* (J. Wright, 1956, pl. LXXIII, fig. 23, 27)
- Pleurocrinus Wanneri* (J. Wright, 1956, pl. LXXIII, fig. 30)

This morphological trend is not confined to *Pleurocrinus*. The following British species show the same development:

- Platycrinus fermanaghensis* (J. Wright, 1956, pl. LXIX, fig. 14, pl. LXX, fig. 12)
- Platycrinus externus* (J. Wright, 1956, pl. LXXI, fig. 2)
- Platycrinus bellmanensis* (J. Wright, 1956, pl. LXXI, fig. 15, 19)
- Platycrinus insulsus* (J. Wright, 1956, pl. LXXII, fig. 15)
- Platycrinus westheadi* (J. Wright, 1956, pl. LXXII, fig. 19)
- Platycrinus pileatus* (J. Wright, 1956, pl. LXXIV, fig. 8)
- Platycrinus expansus* (J. Wright, 1956, pl. LXIX, fig. 18)

Representatives of this stage in the Permian of Timor are:

- Pleurocrinus Goldfussi* (Wanner, 1916, pl. C, fig. 2c) and
- Platycrinus Wachsmuthi* (Wanner, 1916, pl. C, fig. 7b, 9b)

North American representative are:

- Pleurocrinus eminulus* (Wachsmuth & Springer, 1897; Pl. LXVIII, fig. 13c)
- Platycrinus hemisphericus* (Wachsmuth & Springer, 1897; Pl. LXVI, fig. 1d)
- Plemnocrinus beebi* (Kirk, 1946; Pl. 65, fig. 3) and species of *Eucladocrinus* and *Brahmacrinus*.

These two different modes of organisation of the tegmen are found among Carboniferous platycrinids, when representatives of this family were most abundant and had their widest expansion. The two lineages both deal with an incorporation

of many more plates in the tegmen than was the case in older representatives of the group. Loss of all differentiation of the tegmen plates apparently for protection of the food gathering system seemed to be frequently applied. It even persisted in Permian times. In addition, extreme differentiation of orals and ambulacrals with exclusion of axillar ambulacrals leaving the ambulacra as fragile structures on the tegmen is found to be an exception.

Up to now we have only dealt with the composition of the tegmen in genera as *Pleurocrinus*, *Platycrinus*, *Oenochocrinus*, *Eucladocrinus*, *Plemnocrinus*, *Brahmacrinus* and *Neoplatycrinus* which are believed to constitute the typical platycrinids. Among Platycrinidae many forms occur with tegmens that are now thought to be composed according to a different morphological plan and to follow separate morphological developments. In fact we only deal with hapalocrinids here.

The Spanish genus *Cantharocrinus* was found to possess characters that could only be placed with difficulty amongst the others. Five orals are differentiated between which the ambulacra intervene, although not to the centre of the tegmen. The posterior interradius is differentiated. If *Cantharocrinus* is considered a true hapalocrinid its tegmen must be compared to that of other hapalocrinids. Tegmen structures now available for comparison are known from *Amblacrinus*, *Culicocrinus*, *Lyonicrinus*, *Cyttarocrinus* and fragmentary from *Cordylocrinus*. The tegmen of *Amblacrinus* is here held as being very similar to that of *Cantharocrinus*. The tegmen of *Culicocrinus* with its five closely abutting orals today has to be considered a form of doubtful affinity, since nobody knows whether larger modified axillar ambulacrals could occur in it. Müller's fig. 2, Pl. VIII (1855) suggests that such a plate could have been situated in the notched edges of the orals, covering the pits between the IBr1. The form therefore will be excluded from our present considerations. On the contrary it is believed that such forms as *Eutelecrinus* and *Plesiocrinus* show some strange affinity to the hapalocrinids. The morphological relations are illustrated in textfig. 32.

The Niagaran (U. Sil.) species *Lyonicrinus bacca* possesses a very different tegmen structure to the contemporary *Pleurocrinus spinosus*. The tegmen structure in our textfig. 32 is reproduced from Springer's pl. 11 figs. 11 and 13; 1926. The posterior side in this species is differentiated, the anus lying at the end of a short protuberance. The tegmen has four larger plates, interradiial in position and at times partly interbrachially disposed. It is not completely certain whether these plates have to be considered as orals, but it is agreed, with Springer (1926, p. 50), that the plates are "analogous in position to orals" and that "this is probably the proper term for them". Ambulacra are suprattegmenal, largely intervening with the orals and leading to a central space (peristome) that even might have had an open mouth. If this interpretation is correct a remarkable feature of this species is that the orals are pushed aside and even may become interbrachially situated, to make room for the wide and prominent ambulacra that are flanked with series of adambulacrals and must have been closed by covering pieces. Ambulacra are suprattegmenal and prominent; orals not prominent and pushed aside.

*Cantharocrinus* has some affinity to *Lyonicrinus*. The posterior side is still differentiated, the anus may have been situated on a protuberance. The orals however are more prominent and even meet in the centre. They do not permit the ambulacra to penetrate suprattegmenally to the mouth, which is placed subtegmenally. Ambulacra may have four series of plates. Compared with *Lyonicrinus* there is a tendency to keep the orals at the centre and to bring the mouth and even parts of the ambulacra below the orals.

The systematic position of the Permian genus *Eutelecrinus* is a remarkable one since it seems possible to consider it a morphological end product in the lineage *Lyonicrinus*—*Cantharocrinus*. The orals in *Eutelecrinus* are kept in a perfectly abutting position, covering the mouth and major parts of the ambulacra, which are brought into a subtegmenal position. Wanner's fig. 31, Pl. VI, 1937, reproduced in our textfig. 32 is of special interest in that it shows the ambulacrum of the l.post. ray in a specimen of *Eutelecrinus Welteri*. It proves that ambulacra had two series of small side pieces meeting at the interoral suture. Ambulacra actually project beneath the orals, thus occupying a subtegmenal position. The anus is covered with a group of small plates. The supposed morphological series *Lyonicrinus*, *Cantharocrinus*, *Eutelecrinus* might be interpreted as a lineage in which the orals gradually are kept in a more "primitive ontogenetic" stage, apparently again for the protection of the ambulacra. The three mentioned genera and probably all other hapalocrinids form a group of crinoids in which specially modified first axillar ambulacrals do not play a rôle and in which there was no gradual introduction of extra elements into the cup.

The genus *Cyttarocrinus* might be considered a sort of off-shoot from the supposed lineage mentioned above, in which anal structures reduced, bringing the anus directly into the tegmen. Ambulacral grooves in this genus extend from the brachials to the centre of the tegmen. The mouth is covered by ambulacral plates at the very centre of the tegmen. Five large plates occur, disposed more or less interbrachially. The plates were considered interradians by Goldring (1954, p. 9) but it seems possible to interpret them as orals. They are unusually large for interradians and were observed to bear spines as frequently do orals. An objection against this view perhaps is that the arms then would be in an epioral position. If an interpretation of these plates as orals is correct it means that orals are strongly pushed aside to enter in a position almost between the brachials, even bringing the anus in an epioral position, while the apical space is filled with some additional interambulacrals. The genus then has to be regarded a sort of morphological off-shoot from the postulated main trend.

The present considerations on the morphological relation of the elements forming the oral surface in the Platycrinidae may provide valuable characteristics for the taxionomical interpretation of both hapalocrinids and platycrinids. It is believed further that a close connection exists between the composition of the tegmen and the organization of the arm bases. These two characters are used now to separate hapalocrinids from platycrinids.

(1) The fundamental arrangement throughout the Paleozoic in the composition of the tegmen in the family of the Platycrinidae is to be found in the basic pattern of five orals, alternating with axillar ambulacrals or topographical homologues of them. From this pattern both in Devonian and Permian times a form is derived with greatly modified first axillar ambulacrals. Whereas during Carboniferous times a tendency towards incorporation of more elements in the cup with a complete loss of differentiation of the plates is the main feature. In all platycrinids (except the symmetricus-lineage) the ambulacra are protected subtegmenal structures.

The other important character to which Ubaghs (1953, p. 743) has already alluded is fully consistent with these trends in tegmen composition. It is a fact that the arm base in the Platycrinidae is typically formed by only one, frequently (except for *Plemnocrinus*) very small triangular and axillar first primibrach with only two secundibrachs, that still are in contact with the calyx. The bases of the arms are trunked together in this way. These arm-bases are

frequently covered by axillar ambulacrals. In our opinion these two characters belong together and are of utmost importance for identification of platycrinids. The genera *Oenochocrinus* and *Neoplatycrinus*, at first glance so different from Carboniferous platycrinids, in our opinion belong indisputably with them. The forms are interpreted as specialized platycrinids in which first axillar ambulacrals were subject to considerable modification. It is believed that they do not correspond to an irreducible type of tegmental organization, since their tegmens can be thought to be derived from other platycrinid tegmens.

(2) On the contrary hapalocrinids show completely different characters. The tegmen is mainly composed of five orals. Ambulacra show a tendency to become covered by the orals that themselves tend to remain in an apposed apical position. Incorporation of large quantities of tegmen plates is unknown and no loss of differentiation of tegmen plates has been observed. In this family first primibrachs may be well developed and are followed by a second axillar primibrach. The number of secundibrachs is usually larger than in platycrinids. The proximal brachials are not in close contact with the calyx and the arm bases consequently are not trunked. Generally only two arms per ray exist, that may even remain unbranched (*Lyonicrinus*, *Clematocrinus* and *Cordylocrinus*). In connection to these structures axillar ambulacrals are not differentiated.

(3) As a consequence of these considerations the systematic position of *Culicocrinus*, *Eutelecrinus* and *Plesiocrinus* within the Platycrinidae is, in our opinion, uncertain.

*Culicocrinus* may perhaps be a platycrinid if it can be proved to possess modified axillar ambulacrals. The presence of two primibrachs points to affinity with the hapalocrinids, but these two plates are usually well incorporated in the cup.

*Eutelecrinus* has a similar position. Genetic relations of this Permian genus with the older hapalocrinids are most uncertain since no Carboniferous hapalocrinids are yet known. But some strange affinities to the hapalocrinids do exist. All *Eutelecrinus* species have large rounded facets for the reception of apparently well developed primibrachs, fully equal to those observed among other hapalocrinids (*Lyonicrinus*, *Cantharocrinus* and *Cyttarocrinus*). Wanner's figures of *Eutelecrinus* quite frequently show a horizontal bar in the facet that served in the articulation of the arms. Such a bar was reported by Goldring from *Cyttarocrinus* (1954, p. 9). On his figure 27, Pl. VI, 1937 a specimen of *Eutelecrinus fritillus* appears, possessing a large first axillar primibrach. Such a larger primaxil is attached to a specimen of *Eutelecrinus Welteri* as well. An objection against placing *Eutelecrinus* among hapalocrinids may be found in that there is only one primibrach. But this primaxil is so unusually large and well developed (in contrast to true platycrinids where it is generally very small) that one must conclude from it that the arms of *Eutelecrinus* could not have been trunked together as was the case in typical platycrinids. The ambulacra of *Eutelecrinus* still may partly intervene between the orals (cf. Wanner's fig. 2—19; Pl. VI, 1937 of *Eutelecrinus poculiformis* specimens) or even be fully suprategmental as in the specimen of *Eutelecrinus fritillus* as described by De Marez Oyens (1940, p. 299, 300; Pl. II, fig. 4). These positions of ambulacra indicate an affinity to hapalocrinids since this situation of ambulacra on the edges of the orals is known from *Cantharocrinus simplex*, some specimens of *Amblacrinus* and in cf. *Culicocrinus nodosus* from Spain.

Summarizing the characteristics of Platycrinidae are thought to be:

(1) solid tegmen, with ambulacra primitively protected by well developed orals,

alternating with axillar ambulacrals, that may become specially modified; tendency towards loss of differentiation of tegmen plates while incorporating large numbers of interambulacrals in the tegmen during apogee in Carboniferous times.

- (2) typically only one small axillar primibrach and two secundibrachs that trunk the arm bases together and keep them in contact with the cup.

The genera to be included in this family: *Pleurocrinus* (Sil.-Perm), *Platycrinus* (Dev.-Perm), *Oenochocrinus* (L. and M. Dev.); *Brahmacrinus* (L. Carb.), *Plemnocrinus* (L. Carb.), *Eucladocrinus* (L. Carb.), *Neoplatycrinus* (Perm). The position of *Eutelecrinus* and *Plesiocrinus* in this family is doubtful.

The characteristics for Hapalocrinidae are thought to be:

- (1) tegmen primitively with suprattegminial ambulacra (and probably open mouth) tending to sink below the closer apposing orals in ultimate members.
- (2) tegmen without differentiation of axillar ambulacrals and without incorporation of interambulacrals in the tegmen.
- (3) usually well developed primibrach and a number of secundibrachs; arms not trunked together.

The genera to be included in this family: *Lyonocrinus* (U. Sil.), *Clematocrinus* (U. Sil.), *Cordylocrinus* (U. Sil.-M. Dev.), *Bogatocrinus* (Sil. or L. Dev.), *Thallocrinus* (L. Dev.), *Hapalocrinus* (L. Dev.), *Cyttarocrinus* (L.-M. Dev.), *Cantharocrinus* (L.-M. Dev.), *Amblacrinus* (M. Dev.). The position of *Culicocrinus* in this family is not perfectly certain.



Sub-class INADUNATA Wachsmuth & Springer 1885  
Order DISPARIDA Moore & Laudon 1943  
Family IOCRINIDAE Moore & Laudon 1943

*Myelodactylus* spec.

Stem fragments of this interesting crinoid have been found in the Santa Lucia-limestone near Correcillas (León) and in the Portilla-limestone near Valdoré (León). The fragments are distinguishable by their three-sided outline and the rows of facets for the cirri. The fragment 97736 (Rijksmuseum van Geologie en Mineralogie, Leiden) is almost identical to the stem fragment of *Myelodactylus canaliculatus* from the Middle Devonian on the Eifel as figured by Sieverts Doreck (1953, Pl. 4, fig. 1a, 1b).

It is of interest to note that the genus *Myelodactylus* has a rather wide paleogeographical range. Sieverts Doreck (1953, p. 78) reported its occurrence in the Eifelian of Maroccó. It is now also known to occur in Spanish Lower and Middle Devonian strata.

Family SYNATHOCRINIDAE S. A. Miller 1889

*Storthingocrinus Haugi* Oehlert 1896, nomen dubium

*Storthingocrinus labiatus* W. E. Schmidt 1932, nomen dubium

*Remarks.* Two species from Devonian strata of N.W. Spain have been referred to *Storthingocrinus* Schultze, 1867: *S. Haugi* by Oehlert in 1896 and *S. labiatus* by W. E. Schmidt in 1932. Oehlert obtained three specimens, which actually are housed in the Oehlert collection of the École nationale supérieure des Mines at Paris. Schmidt's specimens have to be regarded as lost. Both species were described from very imperfect material, all the specimens were composed of basals and radials only. A new specimen, comparable with those of Oehlert and Schmidt, has been found near Remolina (province of León) in the uppermost beds of the Santa Lucia limestone formation (L. Couvinian) together with some hapalocrinids. The specimen is stored in the collection of the Rijksmuseum van Geologie en Mineralogie at Leiden (Holland) under no. 97711. It is composed of three unequal basals and a circlet of five equal radials. The facets on the radials occupy the whole width of these plates. This new specimen, as those of Oehlert and Schmidt, actually is not easily classifiable, due to the lack of the tegmen. Oehlert's argument in referring his specimens to *Storthingocrinus*, and so separating them from the platycrinids, was that the composition of the patina resembled that of *Storthingocrinus* and that the radial facets occupy the full widths of the radials, leaving no place for interradials. The absence of interradials itself is not sufficient proof to separate a species from the platycrinids. Such an absence is known in that family from *Neoplatycrinus*. An assignment to *Storthingocrinus* could only be justified if the tegmen of the specimen had been preserved. The patina alone must not be classified, it leads to unnecessary confusion. Such confusion was already demonstrated by the fact that W. E. Schmidt

placed his species *S. labiatus*, and even the whole genus *Storthingocrinus* with the platycrinids, although most authors before him placed the genus in the family Synbathocrinidae (Wachsmuth & Springer, 1886, p. 89, 95; Zittel, 1879, p. 365; Bather, 1900, p. 152 and Jaekel, 1921, p. 90). In fact these cups are not clearly divisible from platycrinids. One must keep in mind moreover, that weathering could affect radial facets, making them to appear wider than in unweathered specimens. A last argument against referring the cups under discussion to *Storthingocrinus*, is the fact that they occur together with the newly discovered fauna of hapalocrinids, that was formerly completely unknown in Spain. From a morphological point of view there is not enough reason to separate the fragments of Oehlert and Schmidt from the hapalocrinids, although their radial facets are wider than in representatives of that family. However, a distinct proof that they belong to the hapalocrinids cannot be obtained. Their systematic position can not be determined from the dorsal cups only. Definite species diagnosis never can be taken from them even if new perfectly preserved material should become available. A part of the original material has also been lost already. For all these reasons I propose a status of *nomen dubium* for *Storthingocrinus Haugi* and *Storthingocrinus labiatus* and to exclude them for further use in systematic paleontology. The Int. Comm. on Zoological Nomenclature is requested to suppress the specific names *Haugi* Oehlert, 1896 and *labiatus* W. E. Schmidt, 1932 under the Plenary Powers.

Order CLADIDA Moore & Laudon 1943

Sub-order CYATHOCRININA Bather 1899

Family AMPHERISTOCRINIDAE S. A. Miller 1889

Genus VASOCRINUS Lyon 1857

S. S. Lyon, 1857, p. 485; E. Kirk, 1929, p. 7; Bassler & Moodey, 1943, p. 722; Moore & Laudon, 1943, pp. 51, 108, 133; G. Ubaghs, 1953 (in Piveteau III), p. 750.

*Genotype* by subsequent designation of E. Kirk (1929, p. 8): *Vasocrinus valens* Lyon, 1857.

*Diagnosis.* A genus of the family Ampheristocrinidae characterized by a sub-turbinate to somewhat bowl-shaped dorsal cup, composed of relatively thin plates; inward curving radials whose upper portions form a marginal platform around the periphery of the tegmen, except in the posterior interradius; broadly horseshoe shaped arm facets, allowing the arms considerable upward movement; axial canal separate from the food groove; stout proximal arm portions, horizontally disposed or somewhat inclined, either upward or downward; low tegmen, composed of small plates, madreporite probably present; round stem, pierced by a five-sided canal.

The genus diagnosis has been drawn up by Kirk (1929, p. 8). The formulation of the generic diagnosis given here is essentially that of Kirk, although some of his supposed generic characters have been omitted. He quoted the presence of three anal plates within the dorsal cup. This is not characteristic for *Vasocrinus* only, but for all the members of the family Ampheristocrinidae. This character also is of family level. Ubaghs (1953, p. 750) rightly quotes it in the family diagnosis. The next feature he included within the generic diagnosis was a tendency toward the suppression of the food groove in the anterior radius. Among the newly found Spanish material, which undoubtedly belongs to *Vasocrinus*, no such a tendency was ever met with. The individuals possessing this character are a single specimen of *Vasocrinus sculptus* (Kirk, 1929, p. 12) and a specimen

of *V. turbinatus* (Kirk, 1929, Pl. 2, fig. 2). The suppression of the food groove in the anterior radius is rather exceptional and probably of no diagnostic value at all. Lastly Kirk's statement concerning the ornamentation has been omitted from the genus diagnosis because this character is believed to be of specific level only. A good deal of variation exists in ornamentation.

*Distribution.* The genus *Vasocrinus* occurs in Northern America (*V. valens*, *V. turbinatus* and *V. sculptus*) where it is restricted to the Middle Devonian. In Germany it occurs in Lower Devonian (*V. canaliculatus*) and Middle Devonian strata (*V. stellaris* and *V. ? sulcosutura*). Stratigraphic distribution in Spain includes Lower and Middle Devonian rocks (*V. valens*, *V. turbinatus*, *V. stellaris* and *V. cf. sculptus*).

*Vasocrinus valens* Lyon 1857

Pl. XIV, fig. 5—7

1857 *Vasocrinus valens* Lyon — Lyon, p. 485, Pl. IV, fig. 3, 3a

1929 *Vasocrinus valens* Lyon — Kirk, p. 8, Pl. I, fig. 4—10

1943 *Vasocrinus valens* Lyon — Bassler & Moodey, p. 722

*Holotype.* The specimen figured by E. Kirk, 1929, Pl. I, fig. 7—9.

*Locus typicus.* The quarry near Beargrass Creek, Louisville, Kentucky, USA.

*Stratum typicum.* Jeffersonville limestone (of Onondaga age) Middle Devonian.

*Diagnosis.* A species of the genus *Vasocrinus* Lyon, 1857 characterized by a wide, conical dorsal cup, about twice as wide as high, composed of smooth, slightly convex plates.

*Material.* Rijksmuseum van Geologie en Mineralogie at Leiden (Holland): the specimen 97724 from the uppermost beds of the Santa Lucia limestone formation (L. Couvinian) at El Millar near Pola de Gordon (León); the specimens 97725 and 97726 from the upper part of the La Vid shale formation (Emsian) at Colle (León).

<i>Description.</i>	sp. 97724	Holotype (cf. Kirk, 1929, p. 9)
Height of the cup	8	9
Diameter cup (antero-post.)	13.5	15.5
Diameter stem	5.6	4.6
Height IBB	1.7	1.6
Height BB	5	4.7
Average width BB	5.6	6
Average height RR	4	4.5
Average width RR	7	7.3
Average width arm facet	4	4.3

The three specimens available are well preserved, not weathered, but all lack the stem, arms and tegmens. The dorsal cups are complete, except the posterior side of spec. 97724. The cups are widely conical, nearly twice as wide as high. The cup plates are smooth and very slightly convex. The older specimens 97725 and 97726 have shallow pits at the places where three sutures unite.

Infrabasals five, pentagonal, all equal. They are horizontally disposed. Only their distal tips are visible from the side. The infrabasal cirlet is pierced by an axial canal of 1.5 mm in diameter and pentagonal in outline. Basals five, post. B and postero right B seven-sided, the other ones six-sided. Radials five,

alternating with the basals. Radial circlet interrupted at posterior side for reception of anal plates. The r.post. R is pushed to the right and is situated on top of postero right B. The distal parts of the radials curve inward so as to form a marginal platform round the ventral side of the theca, interrupted at posterior side. Arm-facets occupy half the width of the radial. The articulation surface has a subvertical position, either inclined upward or even slightly downward. The center of the facet is pierced by a round axial canal, separated from the food groove, that itself is roofed over by covering plates. The anal plates are absent in 97724, but the two other specimens have three anal plates incorporated within the dorsal cup. The radianal is five-sided; it rests on post. B and postero right B; it is in lateral contact with r.post. R and the anal plate; it supports the right tube plate. The anal plate is large, situated in the level of the radials; it has about the same height as these plates. It is incorporated within the dorsal cup by sutures with post. B, l.post. R, RA and rt. The right tube plate is situated somewhat above the level of the radials, in contact with r.post. R and A.

*Discussion.* The specimens 97724—97726 have only very slight differences. Their proportions, dimensions and composition is identical to those of the holotype. The infrabasal circlet seems to be less prominent and composed of non-swollen plates. The type of sculpturing of the specimens 97725 and 97726 with their shallow depressions at the angles of the plates is not very different from the plate surface in the type material. Only the weak ribs passing from plate to plate are slightly wider in the Spanish specimens, so contrasting somewhat more with the depressed plate angles. However, there seem to be not enough criteria to separate our specimens from the species *V. valens* Lyon, 1857.

*Vasocrinus turbinatus* Kirk 1929

Pl. XIV, fig. 8—10

1929 *Vasocrinus turbinatus* new species — Kirk, p. 13, Pl. 2, fig. 1—4

1943 *Vasocrinus turbinatus* Kirk — Bassler & Moody, p. 722

*Holotype.* The specimen figured by Kirk, 1929, Pl. 2, fig. 1—3. It is in the Springer collection of the U. S. Nat. Museum.

*Locus typicus.* Louisville, Kentucky, USA.

*Stratum typicum.* Jeffersonville limestone (Onondaga) — Middle Devonian.

*Diagnosis.* A species of the genus *Vasocrinus* Lyon, 1857 characterized by a relatively high, conical dorsal cup, about as wide a high; basals with elevated surfaces near the centres of the plates.

*Material.* The specimen TB 76 in the collection of the Museo del Instituto geologico y Minero de España at Madrid, from Devonian strata of León. Exact age and locality undetermined.

<i>Description.</i>	TB 76	Holotype.
Height of dorsal cup	12.1	15
Diameter of dorsal cup (ant.-post.)	14.9	16.5
Diameter of stem	5.9	5.4
Height of IBB	2.2	2.6
Height of BB	5.8	5.8
Average width of BB	6.1	6.3
Average height of RR	5.2	4.1
Average width of RR	7.1	7
Average width of armfacet	3.8	4.5

The present specimen is fairly well preserved, only partly weathered, but it lacks the stem, arms and tegmen. The dorsal cup is complete, however. The last columnar is still attached to it. The cup is subturbinate, its sides gradually diverging from the base to the armfacets.

The last stem fragment has a circular outline, it is pierced by a large pentalobate axial canal. Infrabasals five, all alike, only their outer surfaces just visible in side view. Basals five, post. B and postero right B seven-sided, the other ones six-sided. The centre of the outer surface of the basals is elevated, so as to form a blunt node. Radials five, alternating with the basals. Radial circlet interrupted at posterior side for reception of the anal plates. The r.post. R is situated with a fairly large suture at the upper left shoulder of postero right B. The distal parts of the radials curve inward so as to form a narrow marginal platform around the ventral side of the theca. The arm-facets occupy about half the width of the radials and are nearly vertical. The facet is pierced by a round axial canal, separated from the food groove. Covering plates, roofing over the groove are not preserved. The radianal is a fairly large plate, even larger than the anal plate. It is five-sided in outline, at its upper margin just truncated for the contact with the right tube plate. The contacts with r.post. R and post. B are long. The surface of the radianal is elevated, just as in the basals. The anal plate is six-sided, relatively small, not attaining the same height as in the adjoining l.post. R. It is incorporated within the dorsal cup by sutures with post. B, l.post R, RA and rt. The right tube plate is very small, just resting on the radianal. The sutures with r.post R and anal plate are but very short.

*Discussion.* The specimen TB 76 is of the same proportions and composition as the type specimen of *V. turbinatus*. The only difference is that the basals in the Spanish specimen have more elevated centers, even produced into blunt nodes. It seems trivial however, to separate the specimen from *V. turbinatus* because nothing is known on the individual variation around the type and single specimen. Moreover, weathering is able to change the appearance of the cup considerably. It is quite possible that both the American and Spanish specimens had identical plate surfaces.

*Vasocrinus stellaris* (Schultze 1867).

Pl. XIV, fig. 11—14

1867 *Poteriocrinus stellaris* nov. sp. — Schultze, p. 161, Pl. V, fig. 2

1895 *Parisocrinus stellaris* L. Schultze spec. — Jaekel, p. 67, fig. 17

1929 *Vasocrinus stellaris* (Schultze) — Kirk, p. 8

1943 *Vasocrinus stellaris* (Schultze) — Bassler & Moodey, p. 722

*Holotype.* The specimen figured by Schultze, 1867, Pl. V, fig. 2. It is probably in the Springer collection of the U. S. Nat. Museum.

*Locus typicus.* Gerolstein (Eifel).

*Stratum typicum.* The exact horizon is not indicated by Schultze. Jaekel (1895, p. 67) states that it comes from Middle Devonian strata.

*Diagnosis.* A very small species of the genus *Vasocrinus* Lyon, 1857 characterized by two or three anal plates in the dorsal cup, very convex to tumid cup plates; ornamentation of fine ribs, passing from plate to plate.

*Material.* The specimen TB 75 in the collection of the Museo del Instituto geologico y minero de España at Madrid, from undetermined strata of Devonian age near Orzonaga (León).

*Description.*

	TB 75
Height of dorsal cup	6.3
Diameter of cup (ant.-post.)	8.4
Diameter of stem	2.1
Height of IBB	0.7
Height of BB	2.5
Average width of BB	3.2
Average height of RR	3.4
Average width of RR	4.3
Average width of arm facet	2.4

The specimen is beautifully preserved, unweathered. Only the posterior part of the tegmen is somewhat crushed. Stem and arms have been broken off. The cup is rather high, relative to its width; the form is somewhat bowl-shaped. It is composed of convex plates. From the elevated centre of a plate fine riblets pass to all adjacent plates. The outline of the stem is circular. The form of the axial canal is not distinguishable. The infrabasal cirlet is very low, only the outer tips of the five equal basals are visible in side view. Basals five, about equal in size, six-sided, except the postero right one that is seven-sided. It is unusual for vasocrinids that the post. B is six-sided. The post. B in this specimen has no suture with the anal plate. The basals are the most convex plates of the cup. Radials five, alternating with the basals. Radial cirlet interrupted at posterior side, where anal plates are intercalated. The r.post. R is a smaller than the RR; it is not markedly pushed aside. The distal parts of the radials bend over and inward forming a broad platform at the ventral side of the theca, bordering the tegmen. The arm-facets of the radials occupy about half the width of the radials and are nearly vertical. The facet is pierced by a round axial canal, separated from the foodgroove. The parts of the radial separating the axial canal from the foodgroove meet along the center line with a suture. This was observed in the r.ant. R. The groove itself is roofed over by covering plates. Only two small anal plates are incorporated within the dorsal cup. The radianal appears as a quadrangular plate, in contact with post. B, postero right B, r.post. R and anal X, but it has a very small contact with l.post. R; so strictly speaking the plate is five-sided. The anal X is situated between l.post. R and r.post. R, but is separated from the post. B by the lateral contact of l.post. R and radianal. A large part of the ventral side of the theca has been preserved (cf. textfig. 34). The anal tube and the postero right part of the tegmen have been broken off. The marginal shelf formed by the upper inward curving edges of the radials is wide, leaving only a little space for the tegminal structure proper.

The tegmen is a perfectly flat and firm structure. The ambulacral grooves are covered by two series of covering plates, placed in alternating order. About three or four pairs of these plates cover the ambulacral groove in the radial. The central tegminal space is filled with about 20 small pieces, irregularly arranged, one of them much larger than the others. Its position is somewhat posterior to the center of the tegmen. Its proportion and position suggest that this plate could have been a madreporite. A surface with pores is not distinguishable due to the partial crushing of the upper surface of the plate. It is logic to suppose that this plate is a madreporite, since such plates have been described from *V. sculptus* and *V. stellaris*.

*Discussion.* The specimen TB 75 agrees in all its essential characters with the

type, as described and figured by Schultze, 1867, p. 161, Pl. V, fig. 2. It is of exactly the same proportion, composition and ornamentation. The basals of the Spanish specimen are perhaps somewhat more convex than in the holotype. The tegmen of our specimen cannot be compared to that of the holotype because that specimen has no tegmen. However, the tegmen of the specimen described by Jaekel, 1895, p. 67 and figured in textfig. 17 can be compared with it. If Jaekel's figure is exactly drawn and the specimen not compressed, the following differences exist. The tegmen in Jaekel's specimen occupies a larger area of the ventral surface of the theca and is composed of comparatively smaller and more numerous plates. The bordering platform is consequently narrower. The base of the anal tube is much stouter than it could have been in the Spanish form. This may be due to the fact that in this specimen both anal X and the right tube plate support the tube, whereas in the Spanish specimen only an

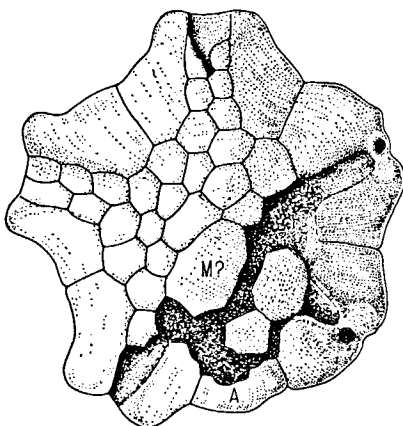


Fig. 34. Diagram showing the arrangement of plates in the tegmen of *Vasocrinus stellaris*. Specimen from Emsian strata near Orzonaga, León (coll. Mus. Inst. Geol., Madrid, no. TB 75).

anal X supports the anal tube. Last difference is met with in the fact that the madreporite in Jaekel's specimen is far larger.

It is difficult to understand what stress must be laid on these differences, since nothing is known on the individual variation that could occur around the holotype. It seems however, that these differences must not be overestimated. They are probably not of specific level. The specimen TB 75, therefore, is referred to *Vasocrinus stellaris*, at least provisionally, until more is known about individual variation.

*Vasocrinus* spec. cf. *V. sculptus* Lyon 1857.

Pl. XIV, fig. 15—17

*Material.* The specimen TB 77 in the collection of the Museo del Instituto geológico y minero de España at Madrid. The specimen is of Devonian age, but exact locality and stratigraphic horizon are unknown.

*Description.*

	TB 77
Diameter of cup (ant.-post.)	20.3
Average width BB	7.2
Average height of RR	7.5
Average width of RR	9.5
Average width of arm facet	3.5

The specimen is of large size. Its diameter exceeds that of any other vasocrinid. The upper part of the theca, including the complete ventral side, is preserved. The base of the cup, the anal tube and the arms are broken off. The form of the cup in the lateral view must have been widely conical or bowl-shaped. In ventral view it appears as pentagonal. The cup plates have an ornamentation with sharp ribs, passing from plate to plate, accompanied by sharp nodes, grouped in pairs of two, one at each side of a suture.

The basal circlet lacks its lower portion. There are five basals, all about equal in size. The post. B and postero right B must have been seven-sided, the other ones six-sided. Radials five, alternating with the basals. The l.post. R and r.post. R are smaller than the other radials, their facets are not placed centrally. The distal parts of the radials bend over inwards, forming a broad platform at the ventral side of the theca, bordering the tegmen. The arm facets are very small, occupying about one third the width of the radial. The facets are situated almost vertical. From the facets a pair of sharp ribs pass to the adjoining radials, where they meet the facets of these plates. The median part of the facet is pierced by a relatively wide, round axial canal. The canal itself is separated from the foodgroove. The bottom of the ambulacral groove in the l.ant. R shows a suture. The ambulacral groove is bordered by sharp outstanding edges, apparently for the attachment of covering plates, that are not themselves preserved. Three anal plates are incorporated within the cup. The radianal is comparatively large, five-sided. It rests on post. B and postero right B, it is in lateral contact with the anal X and r.post. R and supports the right tube plate. The anal X lies in the circle of the radials, resting on post. B and radianal. It has lateral contacts with l.post. R and right tube plate. It supports three further tube plates. The right tube plate is still within the circle of the radials. The anal X is succeeded by a row of three plates; the left plate of this row is still in contact with l.post. R. The base of the anal tube is preserved. It has a diameter of about 6 mm. The tube is situated somewhat left of the posterior side and must have been directed to the left.

The tegmen is completely preserved (cf. textfig. 35). It is composed of only a few, irregularly arranged plates with very slightly convex surfaces. One larger plate, situated posterior to the centre of the tegmen, perhaps may be interpreted as a madreporite. Covering plates are not preserved. It is perfectly clear that the ambulacral grooves become covered by some special large plates, each of them radial in position and forming a highly arched structure over the grooves. The edges of the food grooves in these plates are produced into a sharp rim, continuous with the rims bordering the groove in the radials. It seems possible that the proper ambulacra are sub-tegmenal which could explain the firm appearance of the tegmen plates.

*Discussion.* The specimen TB 77 has all the essential characters of *Vasocrinus*. Its form and ornamentation greatly resemble that of *Vasocrinus sculptus* (cf. Kirk, 1929, Pl. II, fig. 7—10). The ornamentation of our specimen however, is somewhat



more complex through the presence of groups of additional nodes. This specimen does not show whether the sharp ribs or carinae really represent sharp folds in the thin cup plates as they do in *V. sculptus*. Some further difference may exist in the fact that the arm facets are narrower, occupying only one third of the width of the radial instead of half the width as in the type of *V. sculptus*. The other specimen described by Kirk (1929, p. 11) has narrow arm facets of 3 mm in radials of 8 mm wide. The most striking difference however, is to be found in the structure of the tegmen and the position of the ambulacra. No specially modified plates in radial position for the reception of the ambulacra are known from *V. sculptus*, at least Kirk does not mention them. His fig. 8, Pl. II, 1929 is not suitable for a detailed comparison with our textfig. 35. The tegmen of *V. sculptus* could be a weak structure with a large dominant knoblike madreporite,

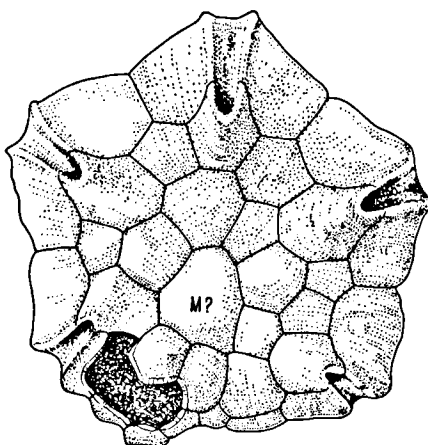


Fig. 35. Diagram showing the arrangement of plates in the tegmen of *Vasocrinus* spec. cf. *V. sculptus* (coll. Mus. Inst. Geol., Madrid, no. TB 77).

whereas in our specimen it is a firm tegmen with a smaller madreporite, if one is present at all.

The differences mentioned, in our opinion could be of specific category. The specimen TB 77 therefore is not referred to *V. sculptus*. It could belong to a new species, although one is not established yet, because only one fragmentary cup is available.

Family BARYCRINIDAE Jaekel 1918  
Genus SITULACRINUS Breimer gen. nov.

*Genotype.* *Situlacrinus costatus* spec. nov.

*Diagnosis.* An inadunate crinoid genus, belonging to the family Barycrinidae Jaekel, 1918 characterized by a pentalobate stem (at least in the proximal portion) with a wide five-lobed axial canal, composed of alternating internodals and nodals; nodals formed by five different plates; high conical dorsal cup; two anal plates in the cup: a small quadrangular rA and a larger aX at the level of the radials; wide arm facets on the radials; two low and wide primibrachs, second

axillary; primibrachs fixed to the cup by series of very small interradial plates; low tegmen, filling the small place between the stout arm bases; no differentiation of ambulacral and interambulacral plates; large polygonal madreporite; small lateral anal tube. Mode of bifurcation of arms unknown.

*Distribution.* The genus is only known to occur in the Lower Devonian (Emsian) of the province of León (Spain).

*Situlacrinus costatus* Breimer spec. nov.

Pl. XV, fig. 1—6

*Holotype.* The specimen 97728 in the collection of the Rijksmuseum van Geologie en Mineralogie at Leiden (Holland).

*Paratype.* The specimen 97729 in the same collection as the holotype.

*Locus typicus.* The northern slope of the hill on which the church of the village Colle (province of León) is built.

*Stratum typicum.* The top beds of the La Vid shale formation, corresponding to the Lower Emsian (L. Dev.).

*Diagnosis.* A species of the genus *Situlacrinus* characterized by strongly ribbing of the cup plates.

This character is interpreted as of specific level as usual in crinoids. The further true specific characters cannot be very well separated from the generic diagnosis, since this species is still the only one known.

*Material.* (1) Rijksmuseum van Geologie en Mineralogie at Leiden (Holland): three specimens no. 97728, 97729 and 97730, from Emsian La Vid formation at Colle (León); one specimen no. 97727 from Emsian La Vid formation at Villayandre (León). (2) Museo del Instituto geológico y minero de España at Madrid; nine specimens no. 125 D from Emsian La Vid formation at Colle (León).

*Description.* In most specimens only dorsal cups and small proximal portions of stem and arms are preserved. The types preserve parts of the tegmen. The dorsal cup is composed of heavy plates, 2—3.5 mm thick. Its outline from the side is conical, the height is approximately equal to the width: 11—12 mm for mature specimens. The ornamentation exists of very strong ribs, passing from the elevated centres of the plates onto adjoining plates. There are no ribs passing laterally from basal to basal, nor from radial to radial. The spaces between the ribs — mainly the interbasal and interradial sutures — appear as depressed areas.

The stem is five-lobed, at least in its proximal portion; pierced by a rather wide pentagonal axial canal, the lobes of which occupy a radial position. The stem is composed of alternately a nodal and an internodal plate, the sutures between them being dentate. Articulation facets of fine crenellae have been observed bordering the nodals. Each nodal is composed of five equal joints. Weakly developed sutures have been found between the joints. The individual parts of the stem segments have an interradial position.

The infrabasal cirlet is 3 mm high, composed of five equal and pentagonal infrabasals, plainly visible from aside. The basals are well developed, 5—6 mm high. The post. B and postero-right B are seven-sided, the other ones six-sided. The interbasal sutures are deeply depressed. The radials are five-sided plates:

5 mm wide and 4—4.5 mm high. The facet for the first primibrach is wide and placed nearly horizontal, it occupies nearly the entire width of the radial. Its real morphology cannot be studied, due to weathering of most of the facets. At the adoral side of the radial is a small semi-circular groove.

Two anal plates are incorporated within the dorsal cup. A very small quadrangular radianal plate rests on the shoulders of the post. B and postero-right B. Its position is nearly inferradial: the r.post. R has a small suture with it at its lower left corner. The anal X is larger than the radianal, situated in the radial circlet between l.post. R and r.post. R, but it is smaller than the radials. It is probably pointed at its upper edge and could have been followed by two or perhaps three tube plates. A right tube plate is not present in the dorsal cup.

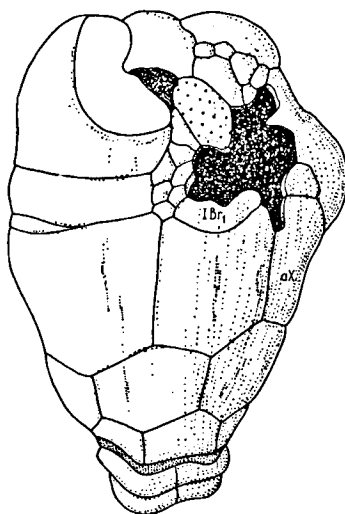


Fig. 36. Diagram showing a group of small interradial plates in *Situlacrinus costatus*. Note contacts of the interradials with IAx and madreporite (coarsely dotted). Holotype of the specimen, from the La Vid formation, Colle, León (coll. Mus. Geol. Min., Leiden, no. 97728).

The left anterior ray of the holotype has three primibrachs preserved. The first one is an extremely small lens-shaped plate, not attaining the same width as the underlying radial. The overlying second primibrach is nearly as wide as the radial, but 1.8 mm high. It comes in contact with the radial, lateral from the first primibrach. The third primibrach is pentagonal and axillar; its height is 3.5 mm, its width equal to that of the preceding brachial. In most other specimens with attached brachials, the very small lens-shaped first primibrach is absent, so one might think that the second primibrach is usually the axillary one. Secundibrachs have not been found in any of the specimens. Judging from the facets on the primaxil the secundibrach immediately following the primaxil still must have been coarse with rounded backs and a narrow semi-circular axial groove.

A highly interesting feature is shown in the holotype. A group of very small plates is intercalated between the primibrachs of the l.ant. and l.post. ray. These plates are not only in contact with the first primibrachs but even with the primaxil. (cf. textfig. 36).

Parts of the tegmen are preserved in the types, that have been figured in textfig. 37. There is no differentiation of ambulacral and interambulacral plates. The tegmen is lobed and occupies the small place that is left over by the very strong arm-bases. Its centre is formed by a large polygonal plate. This plate in both specimens shows very distinctly the pores of tubelets present in the plates. The large plate can only be interpreted as a madreporite. It is accompanied at its right side by another large plate of which the homology is uncertain. Orals do not seem to be differentiated. Groups of small, irregularly arranged plates surround these two larger plates, forming a lobed structure in contact and bordering the upper edge of the primaxil. The tegmen is at a high level (the upper facets of the primaxils) and projects between the primibrachs, connecting them laterally. In fact we can say that the proximal brachials are incorporated

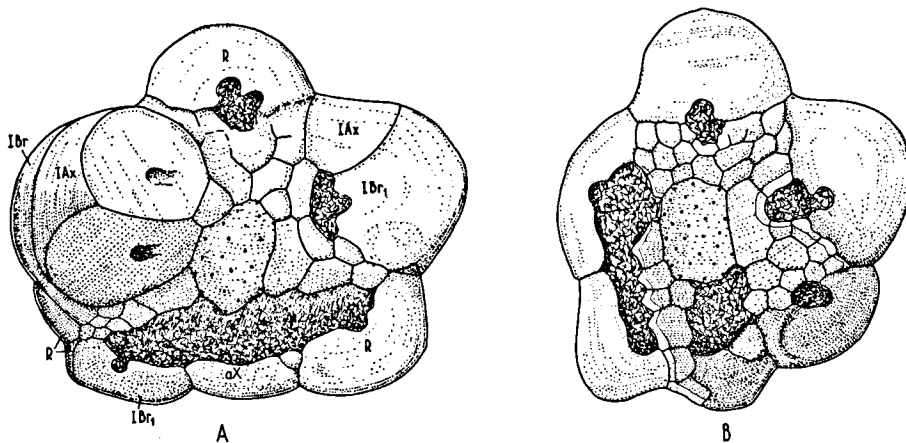


Fig. 37. Diagrams showing the arrangement of plates in the tegmen of *Situlacrinus costatus*. (A) holotype of the species, from the La Vid formation, Colle, León (coll. Mus. Geol. Min., Leiden, no. 97728). (B) paratype, from the La Vid formation, Colle, León (coll. Mus. Geol. Min., Leiden, no. 97729).

within the theca. At least the thecal cavity is enlarged by interradially situated plates between the proximal brachials and the high place of attachment of the tegmen plates. Such enlargement of the thecal cavity could be useful if it is kept in mind that the thecal cavity is reduced by the very thick plates of the proper patina.

*Remarks.* The dorsal cup of *Situlacrinus* resembles that of *Botryocrinus* and could easily be mistaken for that if arms and tegmen are not preserved. Both genera have two anal plates among which a small quadrangular radianal. Moreover, species as *Botryocrinus pachydactylus* and *B. sentosus* have cups closely comparable with that of *Situlacrinus costatus* by having the heavy radiating ribs on the cup plates.

The question arises what the relation between *Situlacrinus* and *Cosmocrinus* (syn. *Costalocrinus*) is<sup>1</sup>). Both genera have cups with a quadrangular radianal

<sup>1</sup>) The generic name *Costalocrinus* Jaekel 1918 seems to be an objective synonym of *Cosmocrinus* Jaekel, 1898. Jaekel established *Cosmocrinus* for the reception of *Poteriocrinus dilatatus* Schultze, 1867, *Cyathocrinus ornatissimus* Hall, 1843 and *Cosmocrinus Holzapfeli*

and the strong radiating ribs on the cup plates. *Cosmocrinus* may be separated definitively from *Situlacrinus* by its relatively narrow arm-facets that make it impossible for the proximal brachials to be connected laterally by interrarial plates. Moreover, there seems to be an extra plate at the internal side of the posterior interradius in the cup of *Cosmocrinus* (cf. Schultze, 1867, Pl. V, fig. 5c).

*Situlacrinus* cannot belong with the Botryocrinidae since it is shown to possess a large madreporite and it is proved that it could have only a comparatively delicate anal tube. This places *Situlacrinus* not only apart from the Botryocrinidae but even outside the whole suborder of the Dendrocrinina because madreporites do not occur in this group. Such plates are to be found among members of the Cyathocrinina under which suborder *Situlacrinus* has its true systematic position. It bears closest resemblance to the family of the Barycrinidae into which it is provisionally placed.

Among members of the Barycrinidae *Situlacrinus costatus* is a highly interesting form, both from a morphological as from a stratigraphical point of view. It is the first representative to be described from the Devonian of Europe. *Barycrinus* and *Pellecrinus* are restricted to Mississippian strata of the North American continent. Kirk (1929, p. 16) states however that undescribed species of *Pellecrinus* occur in the Middle Devonian of North America.

The most outstanding characters of *Situlacrinus* are: (1) the special organisation of the stem, (2) the thick cup plates, (3) the high conical dorsal cup, with the coarse bifurcating ribs, (4) the presence of small interrarial plates, connecting the two (or three) stout primibrachs with both the tegmen and the dorsal cup.

The composition of the stem, being divisible longitudinally into five interrally disposed sections is known from *Barycrinus*. Meek & Worthen (1868, p. 339) mention of, without stating what position the separate joints occupy. Wachsmuth & Springer (1880, p. 324, Pl. I, diagram fig. 3) figured the proximal columnal. The figure was incorrect (Wachsmuth & Springer, 1886, p. 148) because the sections of the column are interrarial and the sutures radial. Statements referring to the outline of the stem are rather contradictory. Some authors state that it is circular, others that it is pentagonal. The axial canal is at least wide and obtusely pentagonal. It seems that the stem of *Situlacrinus* is fully comparable with the stem of *Barycrinus*.

The thick cup plates are characteristic both for *Barycrinus* as for *Situlacrinus*. According to Kirk (1929, p. 15) the cup plates of *Pellecrinus* are relatively thin.

A difference between *Situlacrinus* at the one hand and *Barycrinus* and *Pellecrinus* at the other hand is the form of the dorsal cup and its ornamentation. It is low globose in *Barycrinus* and *Pellecrinus*, whereas it is highly conical in *Situlacrinus*. The arm facets of *Barycrinus* slope outward, making the arms spread out. Whereas in *Situlacrinus* the facets are horizontal, so that the arms must have been vertical. The ornamentation in *S. costatus* is similar to that in *Pellecrinus* spec. (if this species belongs to *Pellecrinus* at all) as described by Laudon, Parks and Spreng (1952, p. 546, pl. 56, fig. 1, 2).

Jaekel, 1898. Jaekel did not designate a genotype, but applying the rule of the Int. Comm. *Cosmocrinus dilatatus* is to be chosen as the genolectotype. *Cosmocrinus ornatissimus* was made the genotype of Goldring's genus *Hallocrinus*. So *Cosmocrinus* is essentially the genus to include only *C. dilatatus* and its close relative *C. Holzapfeli*. There was no need to erect the genus *Costalocrinus* for quite the same two species.

The most remarkable feature, highly interesting from a morphological point of view, is the fact that small interrachial plates intervene between the primibrachs, connecting them with cup and tegmen extending the thecal cavity upwards. Such an enlargement of the thecal cavity is unknown from *Barycrinus*. (In the figure of *Cyathocrinus protuberans* (= *Barycrinus bullatus*) as given by Hall, 1858, pl. 18, fig. 9, two small plates have been drawn between the primibrachs. It is not known exactly what these plates represent, because nothing is stated about them in the text and the accuracy of the drawing cannot be ascertained). An enlargement of the thecal cavity, as apparently exists in *Situlacrinus* is a rare feature among inadunate crinoids. Archaic forms as *Ristnacrinus* and *Ectenocrinus* have enlarged thecal cavities by lateral junction of the proximal brachials. *Cupulocrinus* and *Ottawacrinus* extend their thecal cavities by a flexible tegment enforced with minute irregular plates between the proximal brachials. A definite group of interrachial plates between the proximal brachials as in *Situlacrinus* seems to be unique among Cyathocrinina. Some poteriocrinids (as f. e. *Rhabdocrinus*) have definite patterns of interrachial plates between the very low proximal brachials.

Mainly because of the presence of interrachial plates, a large madreporite and a delicate anal tube *Situlacrinus* is held as an independent genus. It shows some affinity with flexible crinoids as in fact *Cupulocrinus* and *Ottawacrinus* do as well. There is a possibility that *Situlacrinus* was derived from *Cupulocrinus* by further reduction of the radialian, reduction of the number of primibrach; and further development of perisomal plates.

#### Family CYATHOCRINITIDAE Roemer 1855

##### *Cyathocrinites* spec.

Pl. XV, fig. 9, 10

*Material.* The specimen TB 74 in the collection of the Museo del Instituto geológico y minero de España at Madrid, from Emsian La Vid shale formation at Colle (León).

*Description.* Dorsal cup small, bowl-shaped, 7 mm high and 11 mm wide. Cup plates with heavy folds, passing from plate to plate, in between which depressed areas occur. Infrabasal cirlet very low, the five equal infrabasals just visible in side view. The circle is pierced by a rather wide, probably five-sided axial canal. Basals relatively small (3 mm high and 3.5 mm wide), six-sided, except post. B, being truncated above for support of anal X. Radials fairly large, not all of the same dimensions. The ant. R, l.ant. R and r.ant. R are 4 mm high and 6 mm wide, with an articular facet for the arm occupying  $\frac{4}{5}$  the width of the plate. The l.post. R and r.post. R are smaller and situated slightly inclined to the posterior side; the arm facets in these plates occupy nearly the entire width of the plates. L.post. R and r.post. R are in lateral contact with the very large (4 mm high and 3.5 mm wide) anal plate, that rests immediately on post. B and is placed in line with it. Major parts of the arms are preserved. They are composed of monoserially arranged brachials. Bifurcation is isotomous as far as can be judged. The proximal arm portions are rather stout, but distad the arms gradually become more delicate. Only two primibrachs occur, the second axillary. The plates are very much wider than high. Secundibrachs two to four, slightly wider than high. Arms bifurcate three or even four times. Pinnules were not observed. The tegmen is not exposed. The stem is broken off.

*Remarks.* The specimen described above certainly belongs to the genus *Cyathocrinites* Miller, 1821. Its composition is clearly of that genus. In fact the dorsal cup has the same composition as exists in the dendrocrinoid genus *Imitatorcrinus* Schmidt, 1934, but both forms differ considerably in arm structure. Arms of *Imitatorcrinus* branch only once and are pinnulated. So our form is not referable to that genus.

It is not easily possible to assign our specimen to any species already described. The genus *Cyathocrinites* occurs in strata from Gothlandian to Permian age and includes about hundred species. Unfortunately the Devonian species are all inadequately described in scientific literature. Some of them are only listed, or consist of stem- or other fragments. Many of those names have probably to be regarded as nomina dubia. Further revision of the species of the genus *Cyathocrinites* and especially the Devonian ones, is required before we could state whether our species may be referred to any valid species or is to be regarded as new. Anyhow, it seems that the specimen from Colle distinguishes itself by its wide articulation facets on the radials, the wide primibrachs and the low number of secundibrachs. In the meantime it is described and figured here for the stratigraphic and palaeogeographic value that it may have. It forms an interesting element of the crinoid fauna from Colle.

#### Family CODIACRINIDAE Bather 1899

##### *Codiocrinus* spec.

Pl. XV, fig. 15

*Material.* (1) École nationale supérieure des Mines at Paris: one specimen (no. 11) in the Verneuil collection, from "Sabero, R. de León." This most probably indicates the village Colle. It would then be of Emsian age. (2) Rijksmuseum van Geologie en Mineralogie at Leiden (Holland): one specimen no. 97731 from the base of the Santa Lucia limestone formation (Emsian) near Villayandre (León).

*Description.* Globose dorsal cups of very small size. Both specimens lack stem, arms and tegmen. The height of the dorsal cups is no more than 9–10 mm. The greatest diameter (10 mm) is at the level of the radio-basal sutures.

Infrabasal circlet pentagonal in outline, composed of three unequal infrabasals; the smaller ones rhomb-shaped; the two others widely pentagonal. The infrabasal circlet is just visible from aside. The basals are large five- or six-sided plates, the height is 5.5 mm, the width 4.5 mm. The radials are five-sided plates, all alike, height 4–4.5 mm, width 5.5–6 mm. All radials are alike, the circlet is uninterrupted. The facets for the brachials occupy about  $\frac{3}{4}$  of the width of the radial in spec. 97731, but in the other specimen nearly the entire width of the radials. The upper edge of the radial is slightly indented by the facets. Anal plates do not occur in the cup. Ornamentation is not observed.

*Remarks.* The two specimens are undoubtedly referable to *Codiocrinus* Schulze, 1867. The absence of anal plates, the presence of three unequal infrabasals and the globose form of the cup are the unmistakable characters that conclusively place our specimens into that genus. They differ from the specimens described by Schulze (1867, p. 143, Pl. III, fig. 9, 9a–b) as *Codiocrinus granulatus* by the lack of the granulate ornament and by the wider arm facets. They agree

with *Codiocrinus Schulzei* by the lack of ornament and the rather wide arm facets, but *C. Schulzei* is much larger and composed of thin plates.

A restudy of the specimen described and figured by Oehlert, 1896, p. 827, Pl. XXVI, fig. 8 (actually housed in the Ecôle nationale supérieure des Mines at Paris) reveals that this specimen probably is not conspecific with the type of *Codiocrinus granulatus*. Oehlert's specimen is poorly preserved. Although it has in fact some granulation, it lacks the prominent granular ornament with accompanying rib-structures characteristic for the type specimen. It may be that Oehlert's specimen is conspecific with the two forms described in the present paper, and that the Spanish species of *Codiocrinus* has to be described as new. This would require some better preserved specimens than are available at the present day.

### Family CUPRESSOCRINITIDAE Roemer 1855

#### Genus CUPRESSOCRINITES Goldfuss 1831

*Genotype.* *Cupressocrinites crassus* Goldfuss, 1831.

*Synonyms.* *Procupressocrinus* Jaekel, 1918 and *Aviadocrinus* Almela & Revilla, 1950. For the systematical position of the last mentioned genus see p. 163.

*Diagnosis.* The diagnosis for this genus has recently been revised by Sieverts Doreck (1953, p. 83). It reads now:

"A genus of the family Cupressocrinitidae characterized by five-sided symmetrical cup without anal X; rectilinear distal edge of R, over its whole width occupied by the radial facet; wide axial canal, incorporated as a rule within upper parts of RR, proximal Brr and pinnulars; arms composed of 3—50 Brr forming a pyramid; heavy brachials with parallel lower and upper surfaces and with deep ventral groove, hyperpinnulated from Br2. Pinnules able to coil, their basal segments roofing over the ventral groove in a way similar to covering plates; large, horizontally disposed orals; slitt- or pore-formed gonopores; delicate, polygonal plated anal tube. Stem four-sided, three-sided or round, with three to four peripheral canals; thick, encrusting root. Ambulacral covering plates and perisome plates unknown".

*Distribution.* The genus *Cupressocrinites* occurs in Devonian strata, predominantly of Middle Devonian age. The geographical distribution as far as now known suggests an area of distribution limited to Eurasia. Most abundant occurrence is within the western European region (Germany, Spain, Belgium, England).

#### *Cupressocrinites Sampelayoi* (Almela & Revilla 1950)

Pl. XVI, fig. 4, 5

1950 *Aviadocrinus sampelayoi* nov. g., nov. spec. — Almela & Revilla, p. 55, pl. III, fig. 1—3  
1953 *Aviadocrinus sampelayoi* Alm. & Rev. — Sieverts Doreck, p. 85

*Holotype.* The specimen figured by Almela & Revilla 1950, pl. III, fig. 1 is here designated as the holotype. It is in the collection of the Instituto geológico y minero de España at Madrid, cat. no. 1554.

*Paratype.* The specimen figured by Almela & Revilla 1950, pl. III, fig. 2 is designated here as the paratype because it contributes to the species diagnosis.

*Locus typicus.* Mount El Cueto, 1 km SW of Aviados (León).



*Stratum typicum.* The upper part of the Portilla limestone formation, corresponding to the Givetian (M. Dev.).

*Diagnosis.* A small species of the genus *Cupressocrinites* Goldfuss, 1831, characterized by a conical dorsal cup; basals visible from the side, provided with vertically situated nodes; robust arms composed of 1 articular and 2 large, highly compound brachials, provided along each side with 20—25 pinnular sockets; axial canal at adoral side of the arms open throughout the length of the arms; ligamentary articulation between Br2 and Br3; all thecal plates with linear ornament, parallel to the sides of the plates. Stem with rounded triangular outline and trilobate axial canal. Pinnules and orals unknown.

*Material.* (1) Museo del Instituto geológico y minero de España, Madrid: the original material of Almela & Revilla, consisting of 4 specimens from the Portilla limestones at Aviados. (2) Rijksmuseum van Geologie en Mineralogie, Leiden, Holland: 2 complete thecae no. 97714 and 97715, apparently of young individuals, from Mount Las Peñotas, 2 km SE of Llama de Colle (León) in the Portilla limestone; 1 specimen 97716 from the type locality, consisting of a dorsal cup, with polished surfaces at the proximal part of Br3; 1 specimen no. 97717 from the type locality, consisting of an isolated last brachial; some fragments no. 97718 from the type locality.

*Remarks.* New collecting work in the province of León yielded some new specimens of this interesting species. The species is restricted to the Portilla limestone (Upper Givetian). The level where it occurs is the Portilla  $\beta$ -series of P. Comte (1945, p. 361), characterized a. o. by cupressocrinids. The present species occurs not only at Aviados, but is now known to occur in Mount Las Peñotas as well. The new material has made it possible to give some additional description of the species.

*Supplementary description.* The stem of *C. Sampelayoi* is not round but rounded triangular. The stem fragment of the holotype is broken off obliquely making the fracture plane to appear as round. But looked along the direction of the longer axis of the stem, the outline is distinctly rounded triangular.

The basals are visible in side view. The paratype shows vertically disposed nodes, one on the center of each basal. The radials are very wide five-sided. The external surface has a somewhat elevated centre extending into ridges that run to the upper left and right angles of the plates. The internal facet of the radial has two vertically disposed ridges in between which the open axial groove is situated (cf. fig. 38 A). The upper articular surface of the radial is unknown.

The second brachials of the specimen 97716 has been sectioned. The sections reveal that the axial canal is open throughout the length of the plate. Textfig. 38 B, C gives two sections through that brachial plate. The exact number of pinnular sockets in the second brachial is unknown.

The third brachials may become very high. The isolated last brachial cat. no. 97717 is figured on pl. XVI, fig. 5. The axial groove is distinctly visible. It narrows and shallows towards the distal tip of the plate. The number of pinnular sockets in this specimen is about 25. The pinnules must have been placed quite close to each other, particularly near the top of the arms. The form of the brachial in the adult 97717 is different if compared to the younger form 97715. Textfig. 38 D, E shows the younger last brachial to possess a more or less horizontal upper surface forming a kind of hood, whereas in the adult last brachial the top of the plate has grown out more and more to form

an open structure. The same difference is known from *C. minor* (cf. Schultze, 1867, pl. II, fig. 12a and 12c). The lower surface of the last brachial cat. no. 97718 shows crenellae, apparently for ligamentary articulation with the preceding brachial (cf. textfig. 38 F).

*Systematic position.* As the most outstanding characters of *Cupressocrinites Sampelayoi* we must regard:

(1) The two highly compound hyperpinnulated brachials (up to 25 pinnules at both sides of a brachial). (2) The open axial canal in the arm passing into an open groove at the adoral side of the radial. (3) The three-sided axial canal

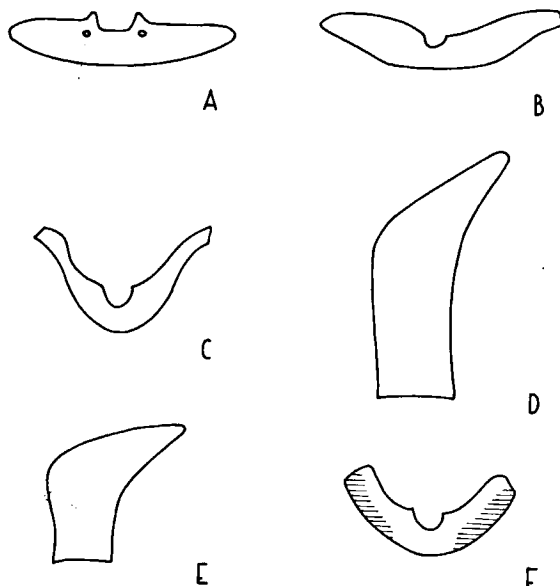


Fig. 38. *Cupressocrinites Sampelayoi* (Almela & Revilla). — Morphology of thecal elements. (A) Section through distal part of a radial. Specimen from the Portilla formation, Aviados, León (coll. Mus. Geol. Min., Leiden, no. 97718/1). (B) Section through proximal part of a second brachial. Specimen from the Portilla formation, Aviados, León (coll. Mus. Geol. Min., Leiden, no. 97716). (C) Section through the distal part of the same brachial as in B. (D) Outline of a terminal brachial in an adult specimen, from the Portilla formation, Aviados, León (coll. Mus. Geol. Min., Leiden, no. 97717). (E) Outline of a terminal brachial in a young specimen from the Portilla formation, Las Peñotas, León (coll. Mus. Geol. Min., Leiden, no. 97715). (F) Lower surface of a terminal brachial, showing areas with crenellae for ligamentary articulation. Specimen from the Portilla formation, Aviados, León (coll. Mus. Geol. Min., Leiden, no. 97718/2).

in the rounded triangular column. (4) The growth lines parallel to the plate boundaries. (5) The conical form of the dorsal cup.

It seems impossible to use this group of characters to separate the species *C. Sampelayoi* generically from *Cupressocrinites* as Almela and Revilla did. It is certainly true that these five characters occur in a group of species most closely related to *C. Sampelayoi*. This group includes *C. gibber*, *C. minor*, *C. Urogalli* and *C. inflatus*. But this group of species is still variable in character. *C. gibber* and *C. minor* are the closest relatives of *C. Sampelayoi* in respect to the composition

of the arms. But with regard to stem, dorsal cup and ornament it has more affinity with *C. inflatus* and *C. Urogalli*. *C. Urogalli* is the only one of the group with four peripheral canals in the stem. *C. inflatus* is the only one lacking the highly compound brachials (composed of up to 25 segments). *C. gibber* is the only one that lacks the special ornament parallel to the sides of the plates. *C. minor* is the only one with low depressed cup.

On the other hand the five *Sampelayoi* characters are not confined to the group of species related to this species. The open axial canal in the arm passing into an open groove at the adoral side of the radial is known from *C. hieroglyphicus* as well (cf. Schultze, 1867, pl. I, fig. 3b). The groove in the adoral side of the radial in *C. inflatus* may be closed or nearly closed so to form a true canal (cf. Schultze, 1867, pl. I, fig. 2d). The occurrence of highly compound brachials does not seem to be restricted to certain species or even individuals. *C. gibber* perhaps has only one such a very compound brachial ( $d_2$ ), the others may be of usual composition for *Cupressocrinites*.

There is extreme variability in the occurrence of these characters. None of the groups of species exclusively possess these characteristics. This may indicate that all the discussed characters are of specific level only. So there is no reason to group *C. Sampelayoi* and its allies in a separate genus. All their essential characters are known from other *Cupressocrinites* species as well. The genus *Aviadocrinus* Almela & Revilla, 1950 is put therefore into synonymy with *Cupressocrinites* Goldfuss, 1831.

Sieverts Doreck's suggestion (1953, p. 85) to group *C. Sampelayoi* as a subgenus under *Cupressocrinites* cannot be followed. Her own diagnosis for *Aviadocrinus* (p. 85) gives no decisive answer how to characterize that genus or subgenus. The diagnosis does not quote any character not already included within her diagnosis for *Cupressocrinites* (p. 83).

*Cupressocrinites inflatus* Schultze 1867.

Pl. XVI, fig. 1

*Material.* A complete crown (cat. no. 97719) and two dorsal cups with articulars and first pinnulated brachials (cat. no. 97720) from the Portilla limestone formation of Mount Las Peñotas (León) stored in the collection of the Rijksmuseum van Geologie en Mineralogie at Leiden (Holland) are attributed to this species.

*Description.* Dimensions of specimen 97719:

Total height of the crown	45.6 mm
Width at distal edge of dorsal cup	15.4—17.3
Height of dorsal cup	9.4
Height and width of Br <sub>2</sub>	7.1—9.6/6.3 (lower and upper sutures)
Height and width of Br <sub>3</sub>	8.7—6.1
Height and width of Br <sub>4</sub>	7.2—5.5
Height and width of Br <sub>5</sub>	6.7—4.9
Height and width of Br <sub>6</sub>	4.7—4.1
Height and width of Br <sub>7</sub>	3.2—3.2 (at lower suture)

The stem is round or rounded triangular in outline. It is pierced by a wide three-lobed axial canal. Its diameter is about 5 mm.

The cup is high and conical. All the circles of plates composing the cup are visible from the side. Ornamentation has not been observed on any of the cup plates. The cup plates themselves are relatively flat. Their proportions are of the usual cupressocrinitid type. The upper side of the dorsal cup, including orals, adoral sides of the radials, articulatory structures on the upper edge of the radials, are unknown.

The arms are composed of one low quadrangular articular and six compound brachials, higher than wide. The plates have a distinct linear ornament of striae, parallel to the sides of the brachials. The aboral surfaces of the brachials have a sharp V-shaped outline as viewed from above. As seen in side view the brachials show curved backs (cf. textfig. 39). The curvature is sometimes produced into a very blunt and coarse node in the centre of the plate. The adoral sides of Brr2 in specimen 97720/1 shows a deep and narrow open groove along the median line of the plates (cf. textfig. 39). Any trace of ligamentary articulation between the brachials is absent. Pinnules are unknown.

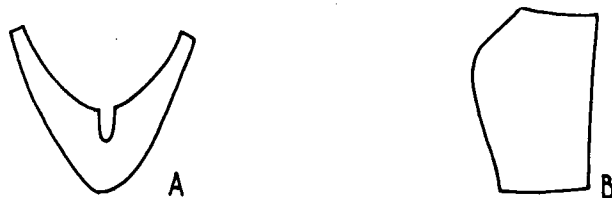


Fig. 39. *Cupressocrinites inflatus* Schultze. — (A) Section through the distal part of a second brachial with deep, open axial groove. Specimen from the Portilla formation, Las Peñotas, León (coll. Mus. Geol. Min., Leiden no. 87720). (B) Outline of a fourth brachial in lateral view. Specimen from the Portilla formation, Las Peñotas, León (coll. Mus. Geol. Min., Leiden, no. 97719).

*Remarks.* The specimens of *Cupressocrinites inflatus* from the Portilla limestone formation in León agree in all their essential characters to the figure and descriptions of Schultze (1867, p. 137). They have a very strong affinity to the specimen 1867, pl. I, fig. 2h. This specimen is only half as large as our specimen (at least if it is figured at natural size) but its form, proportions and ornamentation is strikingly similar to the Spanish representative. The high brachials especially make the two specimens to appear very similar.

The present record of *Cupressocrinites inflatus* from Spain is not the first one. Oehlert (1896, p. 825) mentioned the presence of a radial plate of a cupressocrinitid specimen coming from the Santa Lucia area, comparable with the one figured by Schultze, 1867, pl. I, fig. 2f. The radial described by Oehlert is characterized by an open groove along its aboral side and by the linear ornamentation at its external surface.

*Cupressocrinites* spec. aff. *C. Townsendi* (König 1825)

Pl. XVI, fig. 6, 7

*Material.* (1) Verneuil collection of the Ecôle Nationale Supérieure des Mines, Paris: specimens no. 10 from unidentified Devonian strata near Ferroñes (Asturias). The specimen is here figured on Pl. XVI, fig. 7. (2) Rijksmuseum van Geologie en Mineralogie, Leiden, Holland: the specimen 97721 from the base of the Portilla limestone (Givetian), 2 km N of Cremenés near Riaño (León).

The specimen is figured here on Pl. XVI, fig. 6. (3) The specimen described and figured by Bergougnieux (1938, p. 63—68, fig. 1) from the Caldas limestone (Givetian) near Caldas (Asturias).

*Description.*

	Ferroñes (Verneuil 10)	Cremenes (97721)	Caldas (Bergougnieux)
Height-width of Br1	9.3—23.1	13.3—22.3	13—25
— Br2	9.0—18.7	11.1—22.9	11—23
— Br3	7.9—16.7	9.9—21.6	8—19
— Br4	6.6—15.8	8.5—16.8	7—17
— Br5	6.1—13.2	6.8—14.1	7—16
— Br6	5.5—12.8	7.1—12.4	7—15
— Br7	5.2—11.4	6.8—10.5	7—13
— Br8	5.1— 9.7	7.2— 9.1	7—11
— Br9	4.6— 6.4	5.8— 8.6	6—8

The specimens are very large cupressocrinitid crowns. The total height in the Caldas specimen is no less than 104 mm, of which 90 mm is occupied by the arms. This specimen is the only of the present three possessing a dorsal cup. The cup has a flattened base. Basals are barely visible from the side. The cup plates are swollen. The largest diameter of the cup (at the base of the arms) is 6 cm (Caldas), 4 cm (Ferroñes) and is estimated 4.5—5 cm in the Cremenes specimen. Ornamentation is unknown from the cup plates.

The arms are high structures, composed of nine elements, the articulars not included. Each brachial is wider than high; the width gradually decreasing distad. Interbrachial sutures are straight. Along the median line of each arm is a distinct dorsal ridge, borne on the first compound brachial, occupying half the width of the succeeding brachials, but completely occupying the most distal brachials. The latter have perfectly V-shaped dorsal sides. In summit view the crown appears as five-lobed. Ornamentation is not observed. The specimen from Ferroñes is the only unweathered specimen and its plates seem to be smooth.

*Discussion.* The first specimen of this Spanish species was described by Bergougnieux (1938, p. 63) and assigned to *C. elongatus*. Affinities were believed to exist with *C. Townsendi*, *C. crassus* and *C. elongatus*. Bergougnieux rejected an assignment of his specimen to *C. Townsendi* mainly because that specimen has 14 brachials. The number of brachials in cupressocrinitid species however, is extremely variable. A comparison with the cup of *C. Townsendi* is impossible since the latter structure is unknown from that species. Some idea of the possible proportions of the crown in *C. Townsendi* is given by Bather's reconstruction of the badly crushed holotype. It appears there that the greatest width is above the dorsal cup, at about the level of the third compound brachial. One may doubt however, whether such a character is of specific significance. Evidently Bergougnieux's form cannot belong to *C. crassus* because the latter has much too different brachials. But the affinity to *C. elongatus* is not so strong as Bergougnieux was inclined to believe. He makes no mention of one of the most typical characteristics of *C. elongatus*, namely its granular ornament. Goldfuss (1839, p. 331) previously mentioned this type of ornament as highly diagnostic.

The dorsal cup in many specimens of *C. elongatus* (a.o. no's. 19619 and 16920 Geol. Mus. Leiden, which specimens have been used for comparison) is fairly high, conical or bowlshaped, but with the basals visible from the side. The cup plates are not swollen as in the specimen from Caldas. The number of brachials is larger (12—20). Last *C. elongatus* is smaller in diameter, generally two to three centimeters, except for the specimen from Dasberg, B. M. E. 15471, referred to by Bather (1914, p. 400).

It appears now that the form from Caldas has essentially the same character as the specimens from Ferroñes and Cremenés. They are regarded to be conspecific. It is still hardly possible to trace their real diagnostic characteristics. They all agree by having 9 compound brachials, wider than high and of essentially the same proportions. Ornamentation seems to be absent. The cup is extremely low, basals not visible from aside.

The affinities of this species are doubtful. An assignement to *C. Townsendi* seems unjustified for the moment, since so little is known from that species. The form and proportions of the brachials are about the same, however. The variation in number of brachials is unknown. *C. Townsendi* may definitely be different if other specimens are smooth. Bather (1914, p. 398) mentioned the presence of coarse anastomosing rugae. Such ornament could not be proved to exist in the other Spanish specimens. There are certainly some affinities with *C. elongatus*, but the Spanish specimens are not conspecific with the latter. Some resemblance certainly exists to the specimen figured by Schultze, 1867, pl. II, fig. 2 as *C. Schlotheimi* var. *alta*.

The arms are of equal proportions. The form of the brachials and presence of a median dorsal ridge makes this specimen to look very similar. But the number of compound brachials is larger (12) and the cup is higher, even conical.

*Cupressocrinites* spec. cf. *C. Schlotheimi* (Steininger 1831)

Pl. XVI, fig. 2, 3

1947 *Cupressocrinus crassus* Goldf. — Melendez, p. 296, fig. 164

*Material.* The specimen no. 96 in the Palaeontological Collection of the Universidad Central de Madrid. It comes from Middle Devonian rocks near Perlorá (Asturias).

*Description.*

	Univ. Centr. Madrid Cat. no. 96	Geol. Mus. Leiden Cat. no. 19618
Total height	61	52.8
Height dorsal cup	15	14.2
Diameter dorsal cup	39	34
Height-width Br1	8.3—23.1	10.2—21.4
— Br2	6.4—20.2	7.3—19.1
— Br3	5.8—19.1	5.4—16.2
— Br4	5.6—18.3	4.9—13.3
— Br5	5.2—16.7	4.4—10.9
— Br6	4.9—14.3	3.6— 9.8
— Br7	6.5—11.2	5.1— 7.2

The general outline of the theca is more or less egg-shaped. If viewed from below the cup appears as sub-pentagonal. The top view is not markedly lobed, but nearly round. The stem is not preserved.

The dorsal cup is fairly high, bowl-shaped, composed of flat plates without ornamentation. The basals are 12—13 mm high and 16 mm wide. They are just visible in side view. The radials are large, pentagonal; 12 mm high and 24 mm wide. The articular is 2.5 mm high. The arms are composed of seven brachials (in one ray an eighth small terminal brachial is even present).

The dimensions of these plates are given above. The interbrachial sutures are not straight, but slightly curved downward near the middle of the plates. The median parts of the proximal brachials have a rather sharp ridge, fading out after four or five brachials. The distal brachials have gently rounded back sides. Traces of ornamentation in the arms are absent.

*Remarks.* The present specimen has been figured by Melendez in his Textbook of Palaeontology (1947, p. 296) and classified as *C. crassus* Goldfuss. His figure is a reconstruction of the specimen. He based his reconstruction on the assumption that the distal part of the arms were broken off. So in his figure the specimen appears with eleven brachials, although in fact only seven (eight) are present. The specimen cannot be referred to *C. crassus*, because the brachials lack the marginal structures characteristic for that species. In fact the closest relative seems to be a specimen from Gerolstein (Eifel) stored in the collection of the Rijksmuseum van Geologie en Mineralogie at Leiden (Holland), cat. no. 19618. It is classified as *C. Schlotheimi*. This specimen is figured here (Pl. XVI, fig. 3) for comparison with the Spanish form. Its form, composition and proportions to a large degree agree with the specimen from Perlora. The first brachial is somewhat larger and the decrease in width of the brachials slightly more abrupt as in the Spanish specimen.

One may ask whether an assignment of these two specimens to *C. Schlotheimi* is justified. The species is highly variable, but the variability is mostly concerned with the ornamentation of the theca. The number of brachials could be variable. Schultze (1867, p. 132) mentioned a variation between 2 to 12. The occurrence of just two brachials is only known from *C. Schlotheimi* var. *minor*. This variety was regarded an independent species by Bather (1919, p. 133). The presence of a comparable form in Spain (*C. Sampelayoi*) seems to support this conclusion. A total of 12 brachials is known from *C. Schlotheimi* var. *alta*. This variety however, differs from all other members of the species, not only in the number of brachials, but by its tall arms, high conical dorsal cup with non-swollen basals as well. Perhaps this variety has to be regarded as a species. Schultze (1867, p. 133) mentioned the fact that this form is extremely constant. *C. Schlotheimi* var. *hybridus*, var. *granulosus* and var. *spinosus* cannot be used for judgement of variability of the number of brachials since only dorsal cups are known of these varieties, at least in scientific literature. The forms most closely related to the type material have arms composed of 4—6 brachials only, each bearing a coarse node or spine. The cups are low with flattened base. The basals are swollen. The ornamentation exists of linear striae parallel to the plate boundaries. The Spanish form and its supposed German relative differ from the typical *C. Schlotheimi* by the presence or seven (eight) brachials, by the lack of ornamentation and the non-swollen basals, by the presence of a short, sharp ridge on the proximal brachials. This form probably has to be described as a new variety of *Cupressocrinites Schlotheimi*. It is however premature to

do this here, as it would require a thorough restudy of all the German material. This could even entail a complete revision of the cupressocrinitid species.

*Cupressocrinites* spec.

*Material.* (1) Museo del Instituto geológico y minero de España at Madrid: specimen 83 D from the Portilla limestone (Givetian) of Mount Las Peñotas (province of León). The specimen is incomplete. Only the dorsal cup and the proximal brachials are preserved. (2) Rijksmuseum van Geologie en Mineralogie at Leiden (Holland): some isolated brachials and radials from the Portilla limestone (Givetian) of Mount Las Peñotas (province of León).

The fragments under consideration very much resemble at first glance, the thecal elements of *C. inflatus* from the same locality. The brachials are equally V-shaped if viewed from above. But they cannot belong to that species since the axial groove at the adoral side of the brachials is roofed to form a real axial canal. This canal must have run through the entire length of the arm. Terminal brachials still show closed axial canals to the very top of the arm. An isolated radial plate shows the presence of an axial canal at the internal side of the plate. The outer surface has a linear ornament parallel to the sutures. The fragments are not amenable to specific classification. They may however, belong to a species in general habitus resembling *C. inflatus*.

Two isolated, but crushed, dorsal cups, no. 97723, stored in the collection of the Rijksmuseum voor Geologie en Mineralogie at Leiden (Holland) also coming from Las Peñotas, perhaps belong to the same species as the fragments described above. They have wide axial canals, accompanied by four peripheral canals. The stem was probably round. They are not suitable for comparison with specimen 83 D because not all the elements to be compared are present.

Sub-order DENDROCRININA Bather 1899

Family DENDROCRINIDAE S. A. Miller 1889

*Bactrocrinites* spec.

Pl. XV, fig. 7, 8

*Material.* The specimen TB 73 in the collection of the Museo del Instituto geológico y minero de España at Madrid, from the Emsian La Vid formation at Colle (León).

*Description.* A very elongated dorsal cup with flat tegmen. The cup is composed of flat and smooth plates. The outline of the theca in summit view is oval, although this feature may be exaggerated somewhat by lateral compression of the specimen. The stem and arms are not preserved.

The total height of the cup is 22 mm, its diameter at the upper edge of the cup is 14 and 9 mm respectively. The largest width of the cup (15.5 mm) is at the level of the radio-basal sutures. The five, equal and pentagonal infra-basals are very high: 9 mm. The width is only 5 mm. The basal circlet, equally, is high; the height of the basals is no less than 8.5—9.5 mm; their width 6—6.5 mm. These plates are almost parallel-sided, hexagonal in form, except the posterior and postero right ones, these being seven-sided. The two circlets of



infrabasals and basals form a gradually flaring part of the cup wall. This is in contrast to the radial cirlet, whose plates curve inward. Consequently the greatest width of the cup is at the level of the radio-basal sutures. The radials are comparatively small pentagonal plates, wider than high, their greatest width at a low level in the plate, height 4.5 mm, width 6.5 mm. The l.post. R is situated somewhat lower than the other radials, whereas the r.post. R is placed a little higher. Both the posterior radials are slightly smaller than the other ones, due to the arrangement of the anal plates. The facets for the articulation of the arms occupy almost the entire width of the radial. The morphology of the facets cannot be observed, partly due to the weathering of the facets themselves, partly because the first primibrachs still rest on them. The IBr1 is a cylindrical plate of 1.5 mm high, distinctly wider than high. Two anal plates are incorporated within the dorsal cup: the radianal and the anal X. The radianal is four-sided, about 4 mm high and wide. Its position is inferradial, it lies below the r.post. R and rests on post. B and postero-right B; it has a lateral contact with the anal plate. The five-sided anal plate (4 by 4.5 mm) is placed in superposition to the post. B. It lies at the same level as the l.post. R, or somewhat lower than the other radials. Its upper right corner is truncated for the contact with the r.post. R. The anal supports certainly one and probably even two tube plates. The base of the anal tube is preserved. Its diameter is only 3 mm, so that it must have been a feeble structure. The tegmen is preserved. It was certainly a flat and rather competent structure, because it was formed of a few, rather heavy plates (probably orals). It is impossible to obtain details of the tegmen structure because of its poor state of preservation.

*Remarks.* Four genera of dendrocrinids have species with such remarkably elongated cups as the present specimen. All are of Devonian age and occur either in N. America or Europe or in both regions. These genera are *Bactrocrinites*, *Atractocrinus*, *Sigambrocrinus* and *Kalpidocrinus*. The last two genera can be readily excluded for the assignment of our specimen. They differ by having no radianal incorporated within the dorsal cup. *Atractocrinus* differs in the fact that the anterior radial is smaller than the other ones and probably by its atrophied anterior arm. The specimen TB 73 is referred to *Bactrocrinites* Schnur, 1849, because it has all the essential characters of that genus. Specimen TB 73 has to be placed apart from the known *Bactrocrinites* species. None of the described species has an incurving circle of radials. Some of the species are much smaller (*B. Reimanni*, *B. onondagensis*, *B. tenuis* and *B. Jaekeli*). In size it is only comparable with *B. fusiformis* and *B. Mülleri*. It seems not impossible that the Spanish specimen belongs to a different species, with affinity to *B. fusiformis* and *B. Mülleri*.

*Lasiocrinus* ? spec.

Pl. XV, fig. 11, 12

*Material.* The specimen TB 72 in the collection of the Museo del Instituto geológico y minero de España at Madrid, from the Emsian La Vid shale formation at Colle (León).

*Description.* A conical dorsal cup, laterally compressed. Proximal portions of arms and stem are preserved. The cup is composed of flat and smooth plates.

A small piece of the stem of only 3 mm height is preserved. It is rounded five-sided in outline; its composition is: nodal — internodal — nodal etc. The

diameter of the stem is 4 mm. The height of the dorsal cup is 9.5 mm. The diameters are 14 and 7.5 mm respectively. The infrabasal circlet is composed of five, equal, pentagonal plates, as high as wide: 4 mm. The basals are fairly large, almost regularly hexagonal plates, 4.5—5 mm high. The post. B and postero-right B are seven-sided because they support the radianal. The radials are five-sided plates, wider than high, 4 by 6 mm. The articulation facets occupy the full width of the radials. The facet itself cannot be studied because one or more primibrachs are preserved at all radii. The IBrr are of equal width to the radials and only 2 mm high. The radianal is a small quadrangular plate, more or less inferradial in position. The anal X is five-sided, situated in the circle of the radials between l.post. R and r.post. R. It is of the same size as the radials. It supports a large tube plate, that itself is succeeded by two plates, next to the other.

*Remarks.* The assignment of our specimen TB 72 to *Lasiocrinus* Kirk, 1914 is doubtful. It rests mainly on the fact that the dorsal cup is of identical composition as the type species of that genus (*L. scoparius*) and that the arm facets occupy the full width of the upper facet of the radials. It is realized that the dorsal cup of *Lasiocrinus* cannot be distinguished from the cup of *Antihomocrinus* Schmidt, 1934 (cf. Schmidt, 1934, p. 78). Even the outline of the stem is of no diagnostic value (cf. Goldring, 1948, p. 26, 27). The difference between the two genera is confined to the arm structure, that separates them even at familiar rank. (cf. Moore & Laudon, 1943, p. 55, 52 and Ubaghs, 1953, p. 751, 752). The arms of *Lasiocrinus* are heterotomous, whereas the arms of *Antihomocrinus* are isotomous. The only character taken from the Colle specimen and used for generic assignment is the very wide arm-base characteristic for *Lasiocrinus*. Schmidt's diagnosis for *Antihomocrinus* states that the arm facets do not extend over the full width of the radial. So generic assignment of the present specimen is difficult. The cup could even belong to *Dictenocrinus* as well (cf. Schmidt, 1941, p. 146, fig. 38b).

#### Sub-order POTERIOCRINITINA Jaekel 1918

#### Family POTERIOCRINITIDAE Roemer 1855

#### *Cromyocrinus* spec. aff. *C. simplex* Trautschold 1867

Pl. XV, fig. 13—15

*Material.* The specimen 97732 in the collection of the Rijksmuseum van Geologie en Mineralogie at Leiden (Holland) from the Moscovian Cotarasso limestone near Herreruella (province of Palencia).

#### *Description.*

Height of the dorsal cup	18.4
Largest diameter of the cup	25.1 (at radio-basal suture)
Diameter at upper edge of the cup	23.3
Diameter of the stem	4.0
Thickness of cup plates	ca 5 mm

The dorsal cup is globose, composed of heavy, thick plates. The sutures are superficial. The thecal plates have a very fine tuberculate ornamentation. The stem, arms and tegmen are unknown.

Infrabasals five, all alike, pentagonal. The infrabasals flare upward, making them visible in side view. Their total outline is nearly perfectly pentagonal. The place of attachment of the stem is round or slightly rounded pentagonal, 4 mm in diameter and slightly depressed. Basals five; post. B and postero-right B seven-sided, the other ones six-sided. The plates are as wide as high, ca. 13 mm, they are about the largest plates in the cup. Radials five, five-sided, situated nearly vertical or very slightly inclined inward. The width of the radials is 12.5 mm, the height 6.5—7.5 mm. The facets on the upper edges of the radials are horizontally disposed and extend over the full width of the plates. The facets are provided with longitudinal ribs and fossae for the attachment of muscles and ligaments. Three anal plates are incorporated within the dorsal cup. The radianal is a large oblong plate, 8.1 mm long and 6.6 mm wide, penetrating rather deeply between post. B and r.post. R. The anal X is very small (only 4.4 mm wide), five-sided and situated in the circle of the radials. It rests on the post. B with a small suture only. It has larger sutures with l.post. R and RA. Only a small contact with a right tube plate exists. The right tube plate is broken off. Its position was partly above the level of the radials. It has a very small suture with the radianal plate.

*Remarks.* The specimen from Spain is a typical *Cromyocrinus* by its globose form, flaring infrabasals, wide arm facets and the presence of three anal plates within the dorsal cup. It differs from *Ulocrinus* Miller & Gurley only by the possession of three anal plates.

Specific assignment is difficult. This is partly caused by the fact that we have only one specimen at hand, partly by the fact that specimens from the Russian Moscovian have quite a distinctive state of preservation. The latter are preserved in a very fine, whitish sort of limestone, that makes the Russian cromyocrini look very different. Many specimens of *C. simplex* in diverse museums could be studied for comparison with the Spanish form. From both this study as well as from the description of Trautschold (1867, p. 10, Pl. III, fig. 1—4) it appears that the radials have either a horizontal position or are slightly inclined inward; the basals are either disposed nearly horizontal or flare somewhat upward, making them visible in side view. With respect to organisation, dimensions and position of the thecal plates our specimen could fall within this variation of *C. simplex*. The only difference with this species is the ornament of very fine tubercles. *C. simplex* is perfectly smooth, with only an extremely fine ribbing along the sutures. So it seems that the Spanish form cannot be assigned to *C. simplex*.

The Spanish form differs from *C. geminatus* because in this species the infrabasals are horizontally disposed and the radials bend very sharply inward near their distal edges. The species *C. ornatus* has quite a different ornamentation, namely a rather coarse radial ribbing of the cup plates. *C. nuciformis* is higher than wide, the infrabasals very sharply flare upward, the basals are about 1.5 times as high as wide, the radials sloping inward, the anal X and rt are very small, there is no ornamentation. Our specimen has affinity with *C. grandis*, especially in that the ornamentation is identical. But *C. grandis* has a much larger cup, wider than high.

It seems possible that the present form represents a Spanish species, different from all other species described heretofore. Description of this species, that is believed to have strong affinities with *C. simplex*, is not justified with only one incomplete specimen at hand.

## GENUS PARADELOCRINUS Moore &amp; Plummer 1938

*Paradelocrinus* spec. 1

*Material.* The specimen 97733 in the collection of the Rijksmuseum van Geologie en Mineralogie at Leiden (Holland), from the Upper Visean griotte near Tarna Pass (León).

It is a low, truncated bowl-shaped poteriocrinid, with reduced infrabasal circlet, nearly completely covered by the round stem, not visible from the side. Only the top of the five basals are visible in side view. The thick radials flare outward, the arm facets occupy the entire width of the plates and distinctly slope outward. There is no anal plate in the cup. If viewed from below the cup is round in outline.

*Paradelocrinus* spec. 2

*Material.* The specimen 97734 in the collection of the Rijksmuseum voor Geologie en Mineralogie at Leiden (Holland), from Moscovian deposits at Mudá, near Cervera de Pisuerga (province of Palencia).

It is a low, truncated bowl-shaped poteriocrinid with depressed infrabasal circlet. The infrabasals are not visible from the side and only the top of the basals appear in side view. The radials are situated vertically and the arm facets occupy the entire width of the plates. There is no anal plate in the cup. If viewed from above the cup appears as rounded.

*Remarks.* The nearest relative of these two cups in Spanish Carboniferous strata, is the specimen described by Barrois, 1882, p. 315, Pl. XVI, fig. 2 from the "Assise de Lena" (Moscovian) at Sebarga (Asturias). It is not known where the latter specimen is lodged at the moment. The specimens 97733 and 97734, are certainly not conspecific and are provisionally referred to *Paradelocrinus*. They have a cup with a composition also known from *Erisocrinus*, *Sinocrinus*, *Encrinus*, *Protencrinus* and *Stachyocrinus*. Moore & Plummer (1939, p. 151) state: "The form of the cup in *Sinocrinus* is bowl-shaped rather than truncated cone-shaped, and the infrabasals flare gently upward, being visible in side view of the cup. *Encrinus*, which occurs in Triassic strata, lacks any trace of an anal plate, even on the inner border of the radial facets. *Protencrinus* is distinguished by the generally lower and relatively broader character of the cup and by the reduction in the size of the basals, so that they do not touch one another laterally. *Stachyocrinus* is thus far reported only from the Permian of Timor. Neither its basals nor its infrabasals can be seen in side view of the cup." Our specimen could belong either to *Erisocrinus* or to *Paradelocrinus*. An assignment to *Paradelocrinus* is preferred because the outline of the cups in summit view is rounded, the sides of the cup are moreover regularly rounded. The assignment to *Paradelocrinus* is not beyond all doubt. It is not known whether a small part of an anal plate occurs at the inner border of the cup in our specimens.

## CONCLUSIONS

### 1. *General remarks*

Collecting Spanish Crinoids was started by the Rev. Joseph A. Townsend during a journey through Spain in the years 1786 and 1787. In his "Icones Fossilium Sectiles" (1825) Charles D. E. König described a specimen collected by Townsend as "*Encrinus Townsendi*". It was the first description of a Spanish crinoid. No reports on collecting work are known until 1850, in which year Casiano de Prado worked out the local geology of the Sabero District. The famous locality at Colle is then mentioned for the first time in scientific literature. De Verneuil is the first to have published on a crinoid from Colle. He described *Pradocrinus Baylii* in honour of Casiano de Prado, who sent him the crinoids. From this time collecting of crinoids must have been nearly continuous although only a small part of the collections were described. Geinitz published his description of *Trybliocrinus* in 1867, Oehlert his report on the Devonian fossils of the Santa Lucia District in 1896 and W. E. Schmidt his article on some Lower Devonian crinoids of Asturias in 1932. Bassler & Moodey (1934, p. 75) listed the number of crinoid species as known from that time. The list quotes the following Devonian crinoid species:

*Codiocrinus granulatus* Schultze, 1867  
*Cupressocrinites Townsendi* (König, 1825)  
*Hadrocrinus hispaniae* W. E. Schmidt, 1932  
*Megistocrinus* ? *bifrons* W. E. Schmidt, 1932  
*Megistocrinus Waliszewskii* Oehlert, 1896  
*Orthocrinus planus* W. E. Schmidt, 1932  
*Periechocrinites Baylii* (De Verneuil, 1850)  
*Platyhexacrinus Kegeli* W. E. Schmidt, 1932  
*Saccocrinus* ? *intrastigmatus* W. E. Schmidt, 1932  
*Storthingocrinus Haugi* Oehlert, 1896  
*Storthingocrinus labiatus* W. E. Schmidt, 1932  
*Trybliocrinus Flatheanus* Geinitz, 1867

Three of these species are in fact unrecognizable and here treated as *nomina dubia* : *Orthocrinus planus*, *Storthingocrinus Haugi* and *Storthingocrinus labiatus*. The specimen classified as *Codiocrinus granulatus* is probably not conspecific with the types of that species, but it at least belongs to that genus. *Hadrocrinus hispaniae* is a synonym. From the twelve Devonian species listed by Bassler & Moodey only seven were well-established species. Bassler & Moodey do not quote the specimen classified by Bergougnieux (1938) as *Cupressocrinites elongatus*. Subsequent to Bassler & Moodey's index three papers on Spanish crinoids appeared: Rodriguez Mellado (1949) on an *Orthocrinus* specimen now designated the holotype of *Orthocrinus robustus*, Almela & Revilla (1950) on *Aviadorcrinus Sampelayoi* and Sieverts Doreck (1951) on *Iberocrinus multibrachiatus*. The total number of well-established species was increased to ten by their works.

As the result of the present study the faunal list of Spanish Palaeozoic

crinoids now includes 56 species, distributed over 32 genera. A total number of five new genera and sixteen new species have had to be erected. Fourteen previously described genera are reported for the first time to occur in Spain, either from new species or from species not yet sufficiently known so as to permit definite species description. Six previously described species are now known to occur in Spain as well and mentioned as such for the first time.

Silurian crinoid faunas are unknown in Spain. Crinoids occur abundantly however, in Lower and Middle Devonian strata. Carboniferous crinoids are rare. Out of the total of 32 genera of crinoids now known from Spain, no less than 25 genera (43 species) are confined to Devonian strata, whereas only 7 genera (9 species) occur in the Carboniferous system. Four species are of uncertain age.

As judged from the palaeogeographical distribution of species, the Spanish crinoid fauna is a strict local fauna. Out of the 56 species 32 received the definite status of a valid species with specific names, types and diagnoses. The great majority of no less than 26 out of these definitely established species are confined to Spain, only 3 to the Western European region and but 3 are of worldwide occurrence. Twenty four species are still of uncertain affinity or insufficiently known.

From the point of view of the palaeogeographical distribution of the genera, another picture is obtained. Out of the total amount of 32 genera to occur in Spain, but six genera are confined to Spain, nine to Western Europe (including Marocco) and seventeen genera occur at both sides of the Atlantic. So the majority of genera occurring in Spain is of wider distribution than Spain or Western Europe.

From a systematical point of view, the picture obtained is a rather peculiar one. Flexible crinoids seem to be absent or only very poorly represented. Inadunates include only 10 genera (18 species), whereas the camerates are represented by no less than 22 genera (38 species). Among camerates, diplobathrids are rare, only 7 species, whereas monobathrids form the dominant part of the Spanish Devonian fauna: no less than 31 species. Among inadunates the majority of forms belongs to the Cladida: 17 species, whereas only one species of Disparida is known.

## 2. *Stratigraphical and Palaeogeographical remarks*

### *Devonian*

The most abundant Devonian crinoid faunas occur in the Province of León. The Devonian of Asturias is far less rich in crinoids; only the Lower Devonian yielded some specimens. The Devonian crinoids of Palencia are confined to only one species. Conclusions concerning the succession of Devonian crinoids best can be taken from the Devonian system in León. The stratigraphic sequence of strata and the faunal succession of brachiopods in this area are fairly well known since P. Comte (1936, 1959) worked out a time-stratigraphic correlation. The stratigraphical column of Devonian rocks is presented in textfig. 40. The crinoid faunas are located in four different levels, indicated in textfig. 40 as Crin 1 to Crin 4. These four different faunas will be discussed independently. A correlation with the Asturian fauna seemed to be possible.

### *Emsian (L. Dev.)*

The oldest known crinoid fauna comes from the red detrital limestone band, highly organogene, at the top of the La Vid formation. This horizon is indicated

# DEVONIAN OF LEÓN

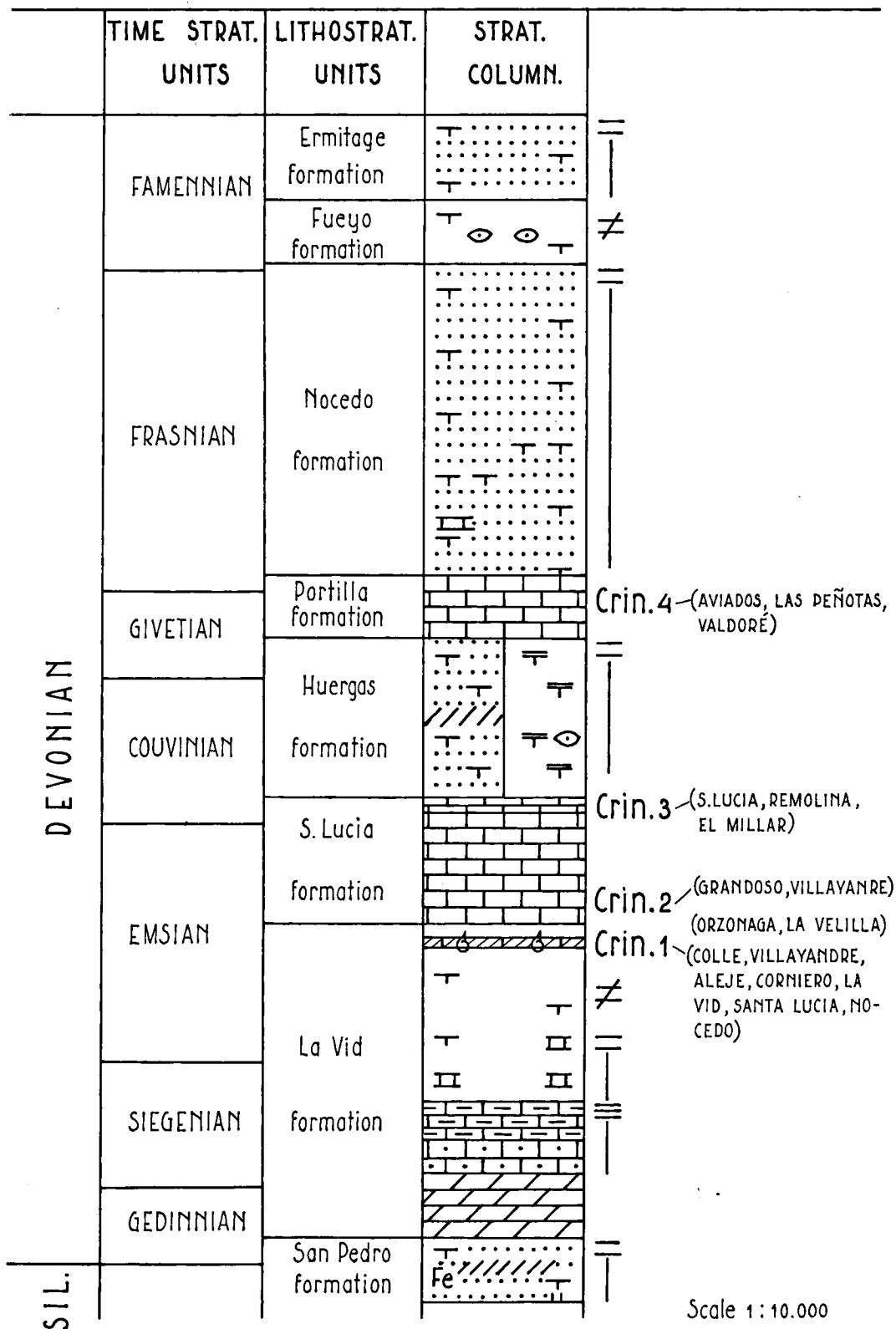


Fig. 40. Stratigraphic column of the Devonian in the province of León (after P. Comte). Crinoid occurrences indicated at the right hand side of the column.

as Crin 1 in textfig. 40. Crinoids of this level are most abundant at Colle, but are known from fossiliferous localities at Villayandre, Aleje, Corniero, La Vid, Santa Lucia and Nocado as well. According to P. Comte, the accompanying brachiopod fauna of this stratum is of Emsian age. The list of crinoids of this bed includes following 15 species <sup>1)</sup>

- C *Diamenocrinus* spec.
- C *Orthocrinus* spec.
- C, Vi, LV *Pradocrinus Baylii* De Verneuil, 1850
- C, Vi, LV, SL, N *Pyxidocrinus collensis* spec. nov.
- C *Pyxidocrinus latus* spec. nov.
- C, LV *Stamnocrinus intrastigmatus* (W. E. Schmidt, 1932)
- C, Vi *Trybliocrinus Flatheanus* Geinitz, 1867
- C *Cantharocrinus minor* gen. nov., spec. nov.
- C, A, Co *Oenochocrinus scaber* spec. nov.
- C *Vasocrinus valens* Lyon, 1857
- C, Vi *Situlocrinus costatus* gen. nov., spec. nov.
- C *Cyathocrinites* spec.
- Vi, C *Codiocrinus* spec.
- C *Bactrocrinites* spec.
- C *Lasiocrinus* ? spec.

The second level in which crinoids occur is formed by the basal beds of the Santa Lucia limestone formation. This horizon is indicated as Crin 2 in textfig. 40. Crinoids of these beds mostly occur at Grandoso (in the immediate vicinity of Colle) but are known from Huergas and Villayandre as well. According to P. Comte the accompanying fauna of these strata is still of Emsian age. The list of crinoids of this level includes the following four species <sup>2)</sup>

- G *Orthocrinus elongatus* spec. nov.
- H, G *Pithocrinus ovatus* spec. nov.
- H, G *Pithocrinus spinosus* spec. nov.
- G, Vi *Corocrinus* ? *grandosensis* spec. nov.

In the Museo del Instituto Geológico y minero de España at Madrid many museum specimens are stored, labelled as coming from Orzonaga (prov. of León). This locality is a small exposure of Devonian rocks surrounded by unconformable Stephanian strata of conglomerates, sandstones and coal seams. When trying to recollect fossils from this locality, only poorly preserved fragments of crinoids were found. The stratigraphic sequence of strata in this relatively small outcrop consists of shales and marls with overlying limestones. The fauna itself is composed of the following elements:

- Macarocrinus* ? spec.
- Orthocrinus robustus* spec. nov.
- Orthocrinus elongatus* spec. nov.
- Pradocrinus Baylii* De Verneuil, 1850
- Pithocrinus ovatus* spec. nov.

<sup>1)</sup> C = Colle, Vi = Villayandre, LV = La Vid, A = Aleje, Co = Corniero, SL = Santa Lucia, N = Nocado. Only the fossiliferous localities in León are indicated.

<sup>2)</sup> G = Grandoso, Vi = Villayandre, H = Huergas. Only the fossiliferous localities in León are indicated.



*Pyxidocrinus collensis* spec. nov.  
*Trybliocrinus Flatheanus* Geinitz, 1867  
 cf. *Culicocrinus nodosus*  
*Oenochoacrinus princeps* gen. nov., spec. nov.  
*Vasocrinus stellaris* Lyon, 1857

The elements of this fauna clearly point to the conclusion that they are of Emsian age and form an assemblage of the combined faunas from horizons Crin 1 and Crin 2: top La Vid formation and base Santa Lucia formation. This would be in full agreement to what has been found at the locality itself. The species *Pradocrinus Baylii*, *Pyxidocrinus collensis* and *Trybliocrinus Flatheanus* are elements of the top La Vid formation (level Crin 1), whereas *Orthocrinus elongatus* and *Pithocrinus ovatus* belong to the Crin 2 fauna in the base of the Santa Lucia limestone. The other elements of this fauna, *Macarocrinus* ? spec., *Orthocrinus robustus*, cf. *Culicocrinus nodosus*, *Oenochoacrinus princeps* and *Vasocrinus stellaris*, are not known from other fossiliferous localities. So all that can be stated about their age is that they could have originated either from crinoid horizon 1 or horizon 2 and consequently are to be placed in the Emsian.

A same thing has happened with museum specimens collected at La Velilla (prov. of León), stored in the Museo del Instituto Geológico y minero de España at Madrid. The specimens are of the following species:

*Pithocrinus ovatus* spec. nov.  
*Pyxidocrinus collensis* spec. nov.  
*Stamnocrinus intrastigmatus* (W. E. Schmidt, 1932)  
*Trybliocrinus Flatheanus* Geinitz, 1867  
*Oenochoacrinus princeps* gen. nov., spec. nov.

This is again an assemblage collected from crinoid levels 1 and 2. Field survey at La Velilla proved that both La Vid and Santa Lucia formations are present at that locality. No well preserved crinoids were found at La Velilla when trying to re-collect there. *Pyxidocrinus collensis*, *Stamnocrinus intrastigmatus* and *Trybliocrinus Flatheanus* are elements of the top La Vid crinoid fauna, whereas *Pithocrinus ovatus* is known to occur in the basal beds of the Santa Lucia limestone formation. *Oenochoacrinus princeps*, here again, as in Orzonaga, is from Emsian rocks but the exact level is not defined.

Emsian crinoids are known from Asturias as well. They have been found from fossiliferous localities at Arnao (Cape La Vela, Santa Maria del Mar, Fenolleda, Moniello and Torrestio). The rocks from which these crinoids have been collected were cited as "Calcaire d'Arnao" in older literature (a.o. Barrois, 1882), but P. Comte refers to this series of red calcareous shales, marls and intercalated limestones as the Rañeces complex. According to him the age of this formation corresponds to the Emsian. Crinoids from the localities mentioned above include following species:

*Pterinocrinus decembrachiatus* spec. nov.  
*Pradocrinus Baylii* De Verneuil, 1850  
*Pyxidocrinus collensis* spec. nov.  
*Pyxidocrinus latus* spec. nov.  
*Pithocrinus ovatus* spec. nov.  
*Pithocrinus* aff. *spinosus* spec. nov.  
*Stamnocrinus intrastigmatus* (W. E. Schmidt, 1932)  
*Trybliocrinus intrastigmatus* Geinitz, 1867

With the exception of the two *Pithocrinus* species this assemblage is fully equal to that of the first crinoid level at the top of the La Vid formation in León. It is not known whether *Pithocrinus*' occurrence in Asturias is different from that in León, since no complete Asturian fauna is known comparable to that of the higher Emsian level in León.

It is not impossible that the specimen from the Devonian of Burgos, known as *Pyxidocrinus San-Migueli* (Astre, 1925) is of Emsian age. Most of the *Pyxidocrinus* species in Spain are to be placed in the Lower Devonian.

The total Emsian crinoid fauna from N.W. Spain (León and Asturias) consists of 25 species listed below<sup>3)</sup>:

- A *Pterinocrinus decembrachiatus* spec. nov.
- L1 *Diamenocrinus* spec.
- L1 or L2 *Macarocrinus* ? spec.
- L1 or L2 *Orthocrinus robustus* spec. nov.
- L2 *Orthocrinus elongatus* spec. nov.
- L1 *Orthocrinus* spec.
- A, L1 *Pradocrinus Baylii* De Verneuil, 1850
- A, L1 *Pyxidocrinus collensis* spec. nov.
- A, L1 *Pyxidocrinus latus* spec. nov.
- A, L2 *Pithocrinus ovatus* spec. nov.
- A, L2 *Pithocrinus spinosus* spec. nov.
- A, L1 *Stamnocrinus intrastigmatus* (W. E. Schmidt, 1932)
- L2 *Corocrinus* ? *grandosensis* spec. nov.
- A, L1 *Trybliocrinus Flatheanus* Geinitz, 1867
- L1 *Cantharocrinus minor* gen. nov., spec. nov.
- L1 or L2 cf. *Culicocrinus nodosus*
- L1 or L2 *Oenochoacrinus princeps* gen. nov., spec. nov.
- L1 *Oenochoacrinus scaber* gen. nov., spec. nov.
- L1 *Vasocrinus valens* Lyon, 1857
- L1 or L2 *Vasocrinus stellaris* (Schultze, 1867)
- L1 *Situlacrinus costatus* gen. nov., spec. nov.
- L1 *Cyathocrinites* spec.
- L1 *Codiacrinus* spec.
- L1 *Bactrocrinites* spec.
- L1 *Lasiocrinus* ? spec.

The discovery of this Emsian crinoid fauna adds much to our knowledge of Lower Devonian crinoids, both from a stratigraphical as from a palaeogeographical point of view. Without doubt this Emsian fauna is the richest one among the Spanish faunas, both in number of individuals and in number of species. The camerates form the dominant part of the fauna. They have 18 species, all of them numerous in individuals. Some camerate species (*Pyxidocrinus collensis* and *Trybliocrinus Flatheanus*) are even known from about a hundred of specimens. The number of individuals of the other camerate species is large when compared to the 7 inadunate crinoid species forming the rest of the same fauna. Out of the 25 species now known from Emsian rocks, only five received definite specific description by previous authors: *Pradocrinus Baylii*, *Stamnocrinus intrastigmatus*, *Trybliocrinus Flatheanus*, *Vasocrinus valens* and *Vasocrinus stellaris*. No less than

<sup>3)</sup> A = Asturias, L1 = fauna top La Vid formation in León, L2 = fauna base Santa Lucía formation in León.

12 new species and three new genera have had to be erected. 7 species are not yet sufficiently known to allow specific arrangement, among which 4 inadunates. Many of them are now known for the first time to occur in Spain.

The monobathrid genera *Pterinocrinus*, *Diamenocrinus* and *Macarocrinus* are reported from Spain for the first time. The new species *Pterinocrinus decembrachiatus* is the only element of the Emsian fauna being restricted to Asturias. The monobathrid *Orthocrinus* was previously recorded from Spain by W. E. Schmidt from the unrecognizable species *O. planus* (here treated as nomen dubium). Other Emsian Orthocrini proved to constitute the new species *O. elongatus* and *O. robustus*. The latter species survived into Couvianian times.

No less than five genera (*Pradocrinus*, *Pyxidocrinus*, *Pithocrinus*, *Stamnocrinus* and *Corocrinus*) belong to the Periechocrinidae, of which only *Pradocrinus* was formerly known to occur in Spain. It is no exaggeration to state that the discovery of the true morphological relations of the periechocrinid genera was greatly aided by the knowledge obtained from the Spanish Devonian representatives of this family. The available generic name *Pyxidocrinus*, frequently misunderstood by previous authors because it was proposed as a conditional name, is now used for reference of the new species *P. collensis* and *P. latus*. The genus is definitely erected with *Actinocrinus prumiensis* as the type-species. Although *Pyxidocrinus* has a German species as the type it is essentially a Spanish genus. Strangely enough it is only now reported for the first time as occurring in Spain, although specimens of this genus were among the earliest collections of Spanish crinoids. The genus *Pithocrinus* has been emended, the arms have been described for the first time. Although *Pithocrinus* has an American type it is essentially a Spanish genus. *P. ovatus* and *P. spinosus* are referred to it as new species, but *P. intrastigmatus* (W. E. Schmidt, 1932) is excluded and made the type-species of the new genus *Stamnocrinus*. This genus includes two more species, not yet sufficiently known as to allow of definite description. The new Emsian species *Corocrinus ? grandosensis* is provisionally referred to this genus because it possesses characters unknown up to now from *Corocrinus*.

*Trybliocrinus Flatheanus* is redescribed in great detail. The species *Hadrocrinus hispaniae* Schmidt, 1932 is placed into synonymy with it. *T. Flatheanus* is still the only known species of this genus. It seems that the distribution of *Trybliocrinus* is restricted to Spain.

Among Emsian crinoids from Spain, hapalocrinids and platycrinids proved to be highly interesting from a morphological point of view. The Spanish Platycrinicae are characterized by differentiated posterior interradii and aberrant positions of the smaller basals. Even the specimens very similar to the types of *Culicocrinus nodosus* are distinguished by differentiation of the posterior interradius. The new hapalocrinid genus *Cantharocrinus* with *C. minor* spec. nov. as the type-species makes its first appearance in Emsian times. The stratigraphical distribution of the genus covers the lower part of the Couvianian as well. It is still only known to occur in Spain. The new platycrinid genus *Oenochoacrinus* with *Oenochoacrinus princeps* spec. nov. as type-species and *Oe. scaber* as one of the cotypes appeared for the first time in Emsian rocks but survived into the lower Couvianian. It is still known only from Spain. The genus is erected for platycrinids with a tegmen composed of five orals and five modified first axillar ambulacrals. The genus is shown to possess affinity with the Permian genus *Neoplatycrinus*. The better understanding of modified first axillar ambulacrals, as a character consistent with the presence of only one first primibrach and two secundibrachs in trunked arm bases, led to a review of the morphological

relations of genera in the Platycrinidae. A suggestion for their evolution on the basis of detailed morphological comparison could be worked out.

The affinity of the Emsian fauna from Spain with those of North America and West Germany is expressed by the first record of *Vasocrinus* species from Spain: *Vasocrinus valens* Lyon, 1857 and *Vasocrinus stellaris* (Schultze, 1867). *V. valens* is one of the species that survived into the lower Couvinian.

Among the few specimens of inadunate crinoids now known from the Emsian of Spain, the new genus *Situlacrinus* with *S. costatus* spec. nov. as type-species proved to be a highly interesting inadunate. It is a form with such an unusual character as the enlargement of the thecal cavity by incorporation of a small number of interradians. The genus is placed provisionally among the Barycrinidae. It would be the first Devonian form and the first record of that family from Europe.

Other inadunate species from Emsian rocks are *Cyathocrinites* spec., *Codiocrinus* spec., *Bactrocrinites* spec. and *Lasiocrinus* ? spec. Only *Codiocrinus* was formerly known from Spanish Devonian strata.

Study of the palaeogeographical distribution of species within the NW Spanish area, reveals that only one species (*Pterinocrinus decembrachiatus*) is restricted to Asturias. It is not known whether the species occurs any higher than the Emsian. Seven species occur in both regions: *Pradocrinus Baylii*, *Pyxidocrinus collensis*, *Pyxidocrinus latus*, *Pithocrinus ovatus*, *Pithocrinus spinosus*, *Stamnocrinus intrastagmatius* and *Trybliocrinus Flatheanus*. A large majority of no less than 17 species, however, seem to have been restricted in distribution to the province of León. But three species out of the total 25 species have wider distribution than Spain. *Culicocrinus nodosus* and *Vasocrinus stellaris* are known from Germany, whereas *Vasocrinus valens* was reported from North America.

The study of the stratigraphical distribution of species within the NW Spanish area reveals that only 2 out of the total 25 species (*Orthocrinus robustus* and *Vasocrinus valens*) survived into the Couvinian. All other species are restricted Emsian forms, as far as their stratigraphical distribution in Spain is concerned. 14 species are even confined to the top of the La Vid formation (see table III), four confined to the base of the Santa Lucia formation, four species (from the locality at Orzonaga) are from a not determined level in the Emsian.

The palaeogeographical and stratigraphical distribution of the species show that the Lower Devonian crinoid fauna is composed of elements stratigraphically restricted to the Emsian and geographically restricted to NW Spain. But it would be false to say that this fauna has no affinities with the Devonian crinoid faunas outside Spain. An entirely different picture is obtained if the distribution of the genera is considered. The 25 Emsian species are distributed over 19 genera of which only 5 are restricted to Spain (*Pradocrinus*, *Trybliocrinus*, *Cantharocrinus*, *Oenochoocrinus* and *Situlacrinus*). All other 14 genera are distributed over Western Europe and/or North America. The affinity of the Emsian fauna of Spain with the Lower Devonian faunas from Germany is somewhat more strongly expressed than the affinity with the North American crinoid faunas. Not less than 6 genera (*Diamenocrinus*, *Macarocrinus*, *Orthocrinus*, *Pyxidocrinus*, *Culicocrinus* and *Codiocrinus*) occur both in Germany and in Spain, although their species in both regions are different. On the other hand only 3 genera (*Stamnocrinus*, *Pithocrinus* and *Corocrinus*) occur both in Spain and in North America but with different species. The affinity of the Spanish Emsian fauna with those of the North American continent and Western Germany is still underlined by the fact that one genus (*Vasocrinus*) has species in common with

TABLE III  
STRATIGRAPHICAL DISTRIBUTION OF DEVONIAN CRINOID SPECIES  
IN NW SPAIN.

	Emsian		Couvinian	Givetian
	Top La Vid f	Base S. Lucia f.	Top S. Lucia f.	Portilla f.
<i>Pterinocrinus decembrachiatus</i>	x			
<i>Diamenocrinus spec.</i>	x			
<i>Orthocrinus spec.</i>	x			
<i>Pradocrinus Baylii</i>	x			
<i>Pyxidocrinus collensis</i>	x			
<i>Pyxidocrinus latus</i>	x			
<i>Stammocrinus intrastigmatus</i>	x			
<i>Trybliocrinus Flatheanus</i>	x			
<i>Cantharocrinus minor</i>	x			
<i>Oenochoacrinus scaber</i>	x			
<i>Vasocrinus valens</i>	x		x	
<i>Situlacrinus costatus</i>	x			
<i>Cyathocrinites spec.</i>	x			
<i>Codiacrinus spec.</i>	x			
<i>Bactrocrinites spec.</i>	x			
<i>Lasiocrinus ? spec.</i>	x			
<i>Orthocrinus robustus</i>		x	x	
<i>Macarocrinus ? spec.</i>		x		
cf. <i>Culicocrinus nodosus</i>		x		
<i>Oenochoacrinus princeps</i>		x		
<i>Vasocrinus stellaris</i>		x		
<i>Orthocrinus elongatus</i>		x		
<i>Pithocrinus ovatus</i>		x		
<i>Pithocrinus spinosus</i>		x		
<i>Corocrinus ? grandosensis</i>		x		
<i>Pithocrinus Waliszewskii</i>			x	
<i>Cantharocrinus simplex</i>			x	
<i>Oenochoacrinus spec.</i>			x	
<i>Oenochoacrinus pileatus</i>			x	
<i>Myelodactylus spec.</i>			x	x
<i>Pyxidocrinus ? bifrons</i>			x	
<i>Platyhexacrinus Kegeli</i>			x	
<i>Cupressocrinites Townsendi</i>				x
<i>Cupressocrinites Sampelayoi</i>				x
<i>Cupressocrinites aff. Schlotheimi</i>				x
<i>Cupressocrinites inflatus</i>				x
<i>Cupressocrinites spec.</i>				x

N. America and W. Germany. Four genera (*Pterinocrinus*, *Bactrocrinites*, *Lasiocrinus* and *Cyathocrinites*) occur at both sides of the Atlantic.

From all this may be concluded that the Spanish Emsian crinoid fauna could have belonged to an area in which intermigration with German faunas at the one side and North American faunas at the other side was possible. This has already been postulated by previous authors (see R. C. Moore, 1953, p. 53). It is worth noting that representatives of Lower Devonian crinoid genera in Spain and even in Germany have their relatives in Middle Devonian times in North America. *Pithocrinus* is a Lower Devonian crinoid in the Middle Devonian of Michigan. *Corocrinus*, *Lasiocrinus* and *Bactrocrinites*, already to be found in the Lower Devonian of Spain, all have species in the Middle Devonian of the state of New York, *Pterinocrinus* even in the Upper Devonian of New York. *Vasocrinus* is known from the Middle Devonian of Kentucky and *Stamocrinus* occurs in Middle Devonian rocks of Indiana. It seems that some affinity exists between the Lower Devonian crinoid fauna of NW Spain with the Middle Devonian faunas of the region West-Central New York, Ohio, Kentucky, Indiana and Michigan.

If intermigration was possible and if some affinity between faunas at both sides of the Atlantic can be found, it would be surprising that important genera and even whole families of crinoids are unknown in the Lower Devonian of Spain. Lower Devonian flexible crinoids seem to be entirely absent in Spain (with the exception of one unclassifiable fragment not described in the present monograph). Nevertheless, a genus as f. e. *Eutaxocrinus* is an important flexible form both in North America and Western Germany. One would have expected it to occur throughout the Atlantic region. Spanish Lower Devonian inadunates are scarce. In North America however, they form a large part of the fauna. *Botryocrinus* and *Decadocrinus* are important genera with many species. Numerous members of the Cyathocrinina are represented there. In Western Germany the inadunates even form the dominant part of the fauna. *Antihomocrinus*, *Botryocrinus*, *Dictenocrinus*, *Dicirrocrinus*, *Eifelocrinus*, *Gastrocrinus* and *Propoteriocrinus* are important genera, but they are entirely absent in Spain. Spanish Lower Devonian crinoids are abundant, but important groups of camerates are unknown. The widely distributed superfamily of the Melocriniticae, very well known from the Silurian of Gotland and North America and from the Devonian of North America and West Germany are absent from the Lower Devonian of Spain.

#### *Couvinian* (M. Dev.)

The next Spanish crinoid fauna comes from the top of the Santa Lucia limestone formation. This horizon is indicated as Crin 3 in textfig. 40. Crinoids of this horizon were found at Santa Lucia (León), El Millar (León) and Remolina (León). According to P. Comte the accompanying brachiopod fauna (*Cultrijugatus* Zone) is of Lower Couvinian age. The list of crinoids of this level includes following species<sup>1)</sup>;

- SL *Orthocrinus robustus* spec. nov.
- SL *Pithocrinus Waliszewskii* (Oehlert, 1896)
- R *Cantharocrinus simplex* gen. nov., spec. nov.
- R *Oenochoacrinus* spec.
- EM *Oenochoacrinus pileatus* gen. nov., spec. nov.
- EM *Vasocrinus valens* Lyon, 1857
- C *Myelodactylus* spec.

<sup>1)</sup> SL = Santa Lucia, R = Remolina, EM = El Millar, C = Correcilla.

Couvianian crinoids from Asturias are rare. They are only known from the Moniello limestone formation at Arnao (Cape El Mugaron). The species included are:

*Pyxidocrinus bifrons* (W. E. Schmidt, 1932)  
*Platyhexacrinus Kegeli* (W. E. Schmidt, 1932)

So the total number of Couvianian species in NW Spain is nine, of which but two persistent forms from the Emsian (*Vasocrinus valens* and *Orthocrinus robustus*). This Couvianian fauna is too small to allow definite conclusions concerning its true affinities. This is further underlined by the fact that no less than three species are new: *Orthocrinus robustus*, *Cantharocrinus simplex* and *Oenochoacrinus pileatus*. The geographical distribution of the genera *Oenochoacrinus* and *Cantharocrinus* is moreover restricted to Spain. *Vasocrinus valens* and *Orthocrinus robustus*, as persistent species, could perhaps indicate similar affinities both to Western Germany and North America as was established for the Emsian crinoid fauna. *Pithocrinus Waliszewskii* is the last representative of its genus in Spain. The *Myelodactylus* species is an element of worldwide occurrence.

*Givetian* (M. Dev.)

The last crinoid fauna in the Devonian system of León is from the middle part of the Portilla limestone formation. This horizon is indicated as Crin 4 in textfig. 40. Crinoids of this level are most frequent in Mount Las Peñotas, but occur in Aviados and Cremenés as well. According to P. Comte the age of the accompanying brachiopod fauna is Givetian. The list of crinoid species of this horizon is as follows<sup>2)</sup>:

A, LP *Cupressocrinites Sampelayoi* (Almela & Revilla, 1950)  
 LP *Cupressocrinites inflatus* Schultze, 1867  
 Cr *Cupressocrinites* aff. *Townsendi* (König, 1825)  
 LP *Cupressocrinites* spec.  
 V *Myelodactylus* spec.

In Asturias two more cupressocrinitids are known from Givetian limestones near Caldas and Perlora:

C *Cupressocrinites Townsendi* (König, 1825)  
 P *Cupressocrinites* aff. *Schlotheimi* (Steininger, 1831)

The total list of six Givetian species quotes:

*Cupressocrinites Townsendi* (König, 1825)  
*Cupressocrinites Sampelayoi* (Almela & Revilla, 1950)  
*Cupressocrinites* aff. *Schlotheimi* (Steininger, 1831)  
*Cupressocrinites inflatus* Schultze, 1867  
*Cupressocrinites* spec.  
*Myelodactylus* spec.

The genus *Cupressocrinites* was formerly only known to occur in Spain from *C. Townsendi* (König, 1825) in the first description of a Spanish crinoid species. The genus *Aviadocrinus* Almela & Revilla, 1950 is put into synonymy with *Cupressocrinites* Goldfuss, 1831 because all the essential characters of its

<sup>2)</sup> A = Aviados, LP = Las Peñotas, Cr = Cremenés, V = Valdoré, C = Caldas, P = Perlora.

type-species *A. Sampelayoi* occur dispersed among other *Cupressocrinites* species. Although small the fauna permits the conclusion that it has close affinity with the well known Middle Devonian cupressocrinitid faunas of Western Germany. It is supposed however, that the Spanish cupressocrinitids are somewhat younger than the bulk of the German ones. The palaeogeographic distribution of the cupressocrinitid fauna of Germany and Spain is restricted to the Eurasian region. Cupressocrinitids have never been reported to occur on the other side of the Atlantic.

#### *Frasnian* (U. Dev.)

The only known Frasnian crinoid from Spain constitutes the new species *Lenneocrinus ventanillensis* from near Ventanilla in the province of Palencia. The generic name *Lenneocrinus* was available but it is used now for definite erection of the genus with the German Givetian species *L. cirratus* Jaekel, 1918 as type-species. The Spanish representative of the genus is younger than its German relative. It is the first time that a *Lenneocrinus* species has been reported from Spain.

#### *Famennian* (U. Dev.)

The only known Spanish crinoid of Famennian age is a dorsal cup, probably of a flexible crinoid, found in a red nodular limestone near the pass of Somport (Pyrenees). The specimen is stored in the collections of the Geological Institute, University of Utrecht (Holland). The specimen is not well enough preserved to permit specific arrangement, but it is mentioned here for stratigraphical information only.

#### *Uncertain Devonian*

The exact stratigraphic horizon of four species, constituted by museum specimens only, is unknown. The species are however, most probably of Devonian age:

*Gennaeocrinus* spec. cf. *G. nyssa*  
*Vasocrinus turbinatus* Kirk, 1929  
*Vasocrinus* spec. cf. *V. sculptus*  
*Griphocrinus ovetensis* spec. nov.

#### *Carboniferous*

Most of the Carboniferous crinoids have been found in the Spanish province of Palencia, but a few come from León and Asturias.

The only known Visean crinoid is *Paradelocrinus* spec. from the province of León.

Namurian species are found near Rabanal de los Caballeros (Palencia) and Sabero (León).

S *Nunnacrinus stellaris* (De Koninck & Le Hon, 1854)  
 R *Pimlicocrinus latus* J. Wright, 1943  
 R *Aorocrinus* spec.  
 R *Platycrinus* spec. ex gr. *bollandensis*

The *Nunnacrinus* and *Platycrinus* species are representatives of genera with worldwide distribution. The palaeogeographical distribution of the genus *Pimlicocrinus* as now has become known was not restricted to England but extended



over Spain during the Namurian. The genus is now reported for the first time from Spain. The stratigraphical distribution of the species *Pimlicocrinus latus*, which is known from the Lower Carboniferous Limestone in England, ranges up to the Namurian. The *Acrocrinus* species may indicate some connection with North America.

Moscovian species were found between Mudá and Herrerueta (MH) in the province of Palencia from the Cotarrazzo-limestone. One species is known from Asturias (A):

- A *Pimlicocrinus* spec.
- MH *Iberocrinus multibrachiatus* Sieverts Doreck, 1951
- MH *Cromyocrinus* spec. cf. *C. simplex* Trautschold, 1867
- MH *Paradelocrinus* spec.

The genus *Pimlicocrinus* even survived in the Moscovian of Asturias and Marocco. *Iberocrinus multibrachiatus* seems to be restricted to Spain in geographical distribution. The presence of the genus *Cromyocrinus*, now reported for the first time from the Moscovian of Spain, points to the conclusion that some affinity may have existed between the Spanish Moscovian crinoids and the Russian fauna. The *Paradelocrinus* species may indicate some connection with North America, but this is not beyond all doubt.

Crinoids of uncertain Carboniferous age are *Pleurocrinus* spec. ex gr. *coplownensis* and a third species of *Pimlicocrinus*.

Concluding it must be stated that the Spanish Carboniferous crinoid faunas are too small and are much too scattered to allow definite palaeogeographical conclusions.

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# PLATES

PLATE I

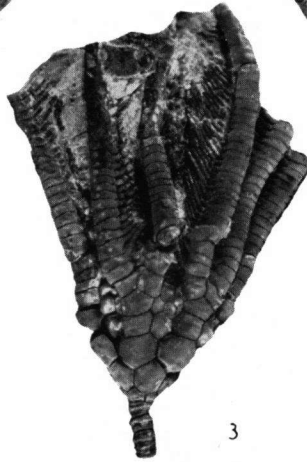
- Fig. 1—2 *Griphocrinus ovetensis* spec. nov. Holotype p. 15  
 Specimen in the collection of the Instituto de Geología Aplicada at  
 Oviedo (Asturias).  
 Devonian of Grado (Asturias).  
 Fig. 1 right posterior view; fig. 2 left anterior view.  $\times 1$
- Fig. 3 *Pterinocrinus decembrachiatus* spec. nov. Holotype p. 12  
 Specimen DH 1070 coll. Mus. Nac. Ciencias Nat. Madrid.  
 Lower Devonian of Arnao (Asturias).  $\times 1\frac{1}{2}$
- Fig. 4—6 *Orthocrinus* spec. cf. *Orthocrinus elongatus* spec. nov. p. 22  
 Specimen TB 71 coll. Mus. Inst. Geol. Min. Madrid.  
 Devonian of Orzonaga (León).  
 Fig. 4 anterior view; fig. 5 posterior view; fig. 6 ventral view.  $\times 1\frac{1}{2}$   
 (see also Pl. III, fig. 10)
- Fig. 7—9 *Diamenocrinus* spec. p. 9  
 Specimen 126 D coll. Mus. Inst. Geol. Min. Madrid.  
 Lower Devonian of Colle (León).  
 Fig. 7, 9 lateral views; fig. 8 basal view.  $\times 1$
- Fig. 10—12 *Macarocrinus* ? spec. p. 13  
 Specimen TB 62 coll. Mus. Inst. Geol. Min. Madrid.  
 Devonian of Orzonaga, near Matallana (León).  
 Fig. 10 posterior view; fig. 11 basal view; fig. 12 lateral view.  $\times 1.5$



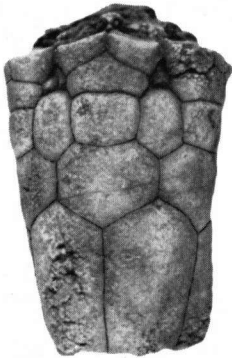
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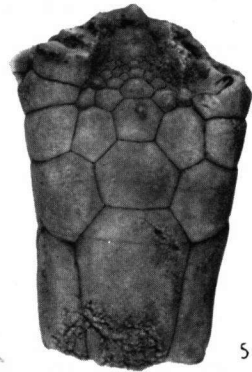
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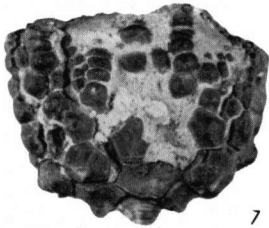
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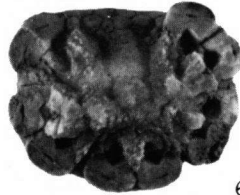
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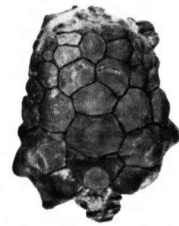
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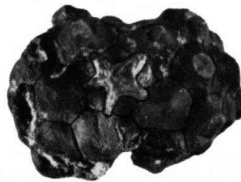
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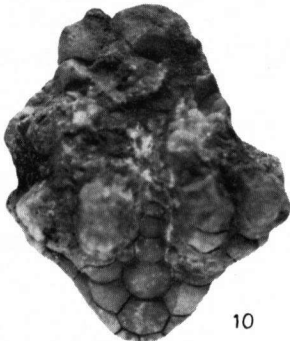
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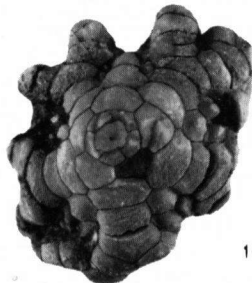
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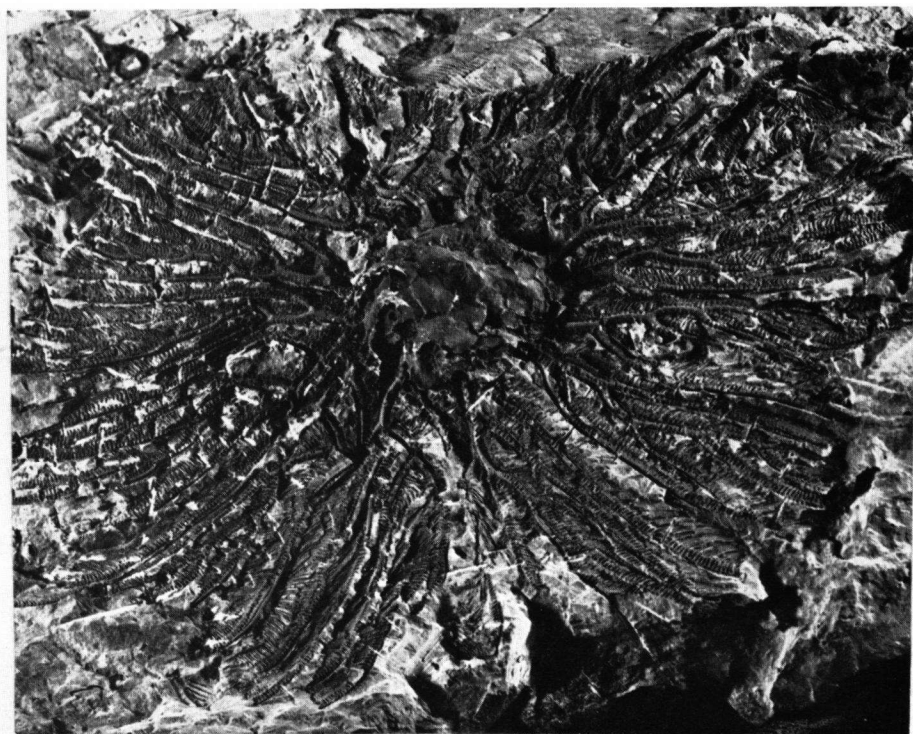
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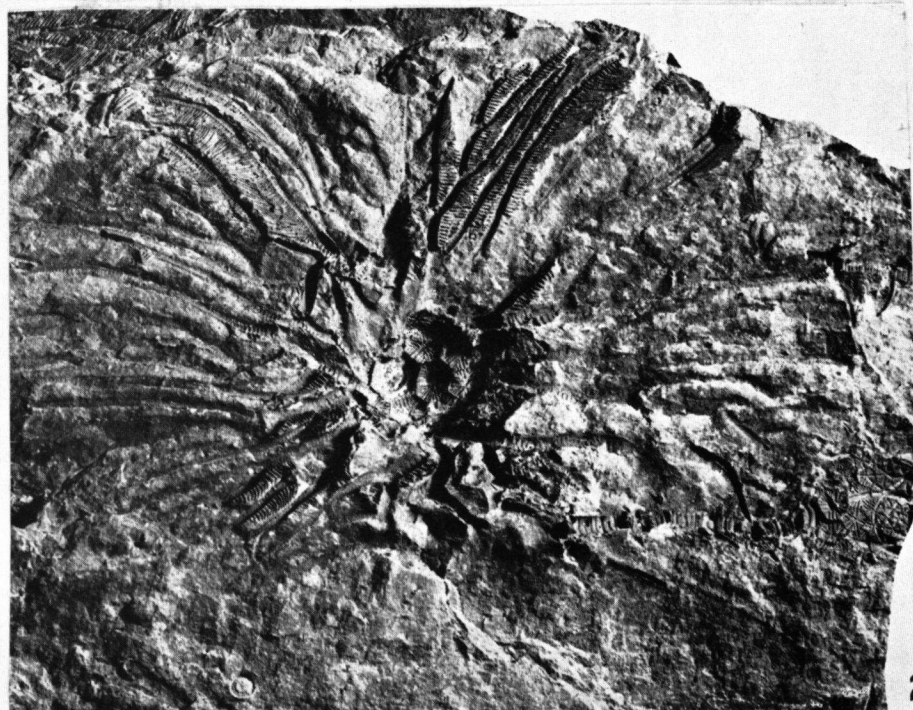
PLATE II

Fig. 1—2 *Lenneocrinus ventanillensis* spec. nov. Holotype  
Specimens 97507 and 97508 (forming part and counterpart) in the coll.  
Rijksmus. Geol. Min. Leiden.  
Frasnian shales of Ventanilla (Palencia). × 1  
Note second specimen in right part of fig. 2; enlarged photographs of  
this specimen on Pl. III, fig. 11, 13.

p. 30



1



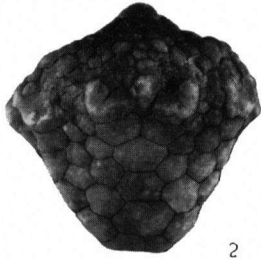
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PLATE III

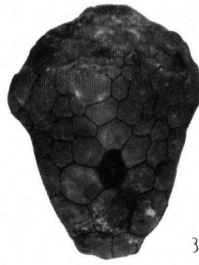
- Fig. 1 *Orthocrinus* spec. (nov. ?) p. 23  
 Specimen no. 96 D coll. Mus. Inst. Geol. Min. Madrid.  
 Emsian deposits of Colle (León).  $\times 1\frac{1}{2}$
- Fig. 2—7 *Pradocrinus Baylii* De Verneuil, 1850 p. 27  
 Series of six specimens showing change of proportions during ontogeny.  
 All specimens figured at same total height.  
 Heights of specimens actually are 9.4; 15.7; 19.3; 26.3; 42.7; 79.3 mm  
 respectively.  
 fig. 2 specimen TB 55 coll. Mus. Inst. Geol. Min. Madrid,  
 fig. 3 specimen TB 80 coll. Mus. Inst. Geol. Min. Madrid,  
 fig. 4 specimen 97512 coll. Rijksmus. Geol. Min. Leiden,  
 fig. 5 specimen TB 81 coll. Mus. Inst. Geol. Min. Madrid,  
 fig. 6 specimen 97510 coll. Rijksmus. Geol. Min. Leiden,  
 fig. 7 specimen 107 D coll. Mus. Inst. Geol. Min. Madrid.
- Fig. 8 *Pradocrinus Baylii* De Verneuil, 1850 p. 27  
 Specimen 107 D coll. Mus. Inst. Geol. Min. Madrid.  
 Lower Emsian deposits of Colle (León).  
 Figure shows tegmen of the specimen.  $\times 1$
- Fig. 9 *Pradocrinus Baylii* De Verneuil, 1850 p. 27  
 Specimen in the collection Rijksmus. Geol. Min. Leiden.  
 Lower Emsian deposits of Colle (León).  
 Isolated cup plate showing ornamentation.
- Fig. 10 *Orthocrinus elongatus* spec. nov. Holotype p. 21  
 Specimen 97503 coll. Rijksmus. Geol. Min. Leiden.  
 Upper Emsian Santa Lucia limestone of Grandoso (León).  $\times 1$
- Fig. 11 *Lenneocrinus ventanillensis* spec. nov. p. 30  
 Specimen 97507 coll. Rijksmus. Geol. Min. Leiden.  
 Frasnian shales of Ventanilla (Palencia).  
 Plasticine cast of the specimen figured Pl. II, fig. 2.  
 See also fig. 13 of this plate.  $\times 1\frac{1}{2}$
- Fig. 12 *Orthocrinus* spec. p. 19  
 Specimen 97502 coll. Rijksmus. Geol. Min. Leiden.  
 Lower Couvinian Arnao limestone of Arnao (Asturias).  
 Ventral portion of dorsal cup from the type-locality of *Orthocrinus*  
*planus* (nomen dubium) at Cape El Mugaron at Arnao (Asturias).
- Fig. 13 *Lenneocrinus ventanillensis* spec. nov. p. 30  
 Specimen 97507 coll. Rijksmus. Geol. Min. Leiden.  
 Frasnian shales of Ventanilla (Palencia).  
 Posterior side of small specimen on the same slab as the holotype,  
 figured Pl. II, fig. 2 and Pl. III, fig. 11.



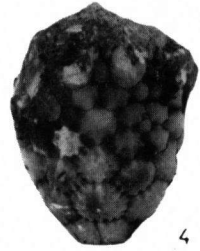
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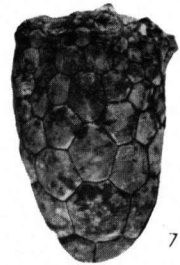
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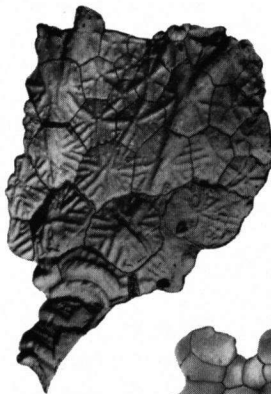
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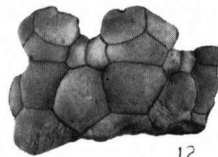
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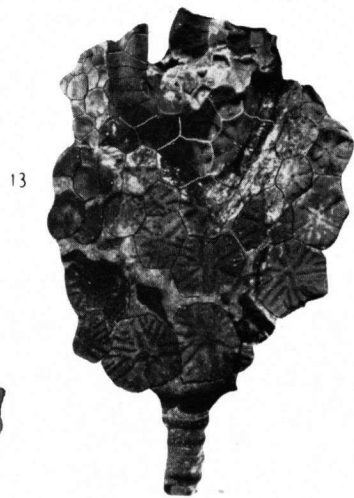
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PLATE IV

- Fig. 1 *Pithocrinus* spec. p. 47  
Specimen 97533 coll. Rijksmus. Geol. Min. Leiden.  
Upper Emsian Santa Lucia limestone of Grandoso (León). × 1
- Fig. 2 Arms of *Pithocrinus ovatus* spec. nov. p. 47  
Specimen 97534 coll. Rijksmus. Geol. Min. Leiden.  
Upper Emsian Santa Lucia limestone of Grandoso (León). × 1
- Fig. 3 Arms supposed to be of a young specimen of *Pradocrinus*. p. 27  
Specimen 97587 coll. Rijksmus. Geol. Min. Leiden.  
Lower Emsian La Vid shales of Colle (León). × 2½
- Fig. 4 *Stamnocrinus* spec. p. 65  
Specimen 97598 coll. Rijksmus. Geol. Min. Leiden.  
Red calcareous shales of Emsian age of Arnao (Asturias).  
Crushed specimen, showing posterior and left posterior sides with strong  
radial ornamentation of cup plates. × 1
- Fig. 5 *Stamnocrinus intrastigmatus* (W. E. Schmidt, 1932) Topotype. p. 59  
Specimen 97594 coll. Rijksmus. Geol. Min. Leiden.  
Red calcareous shales of Emsian age of Arnao (Asturias).  
Crushed specimen showing distinct anal tube. × 1

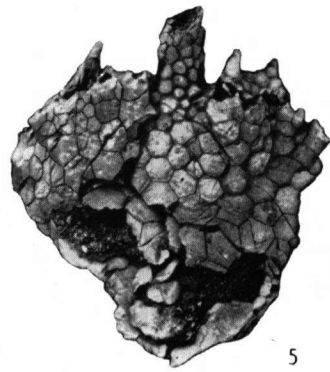
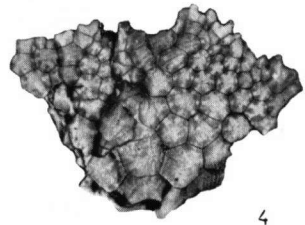
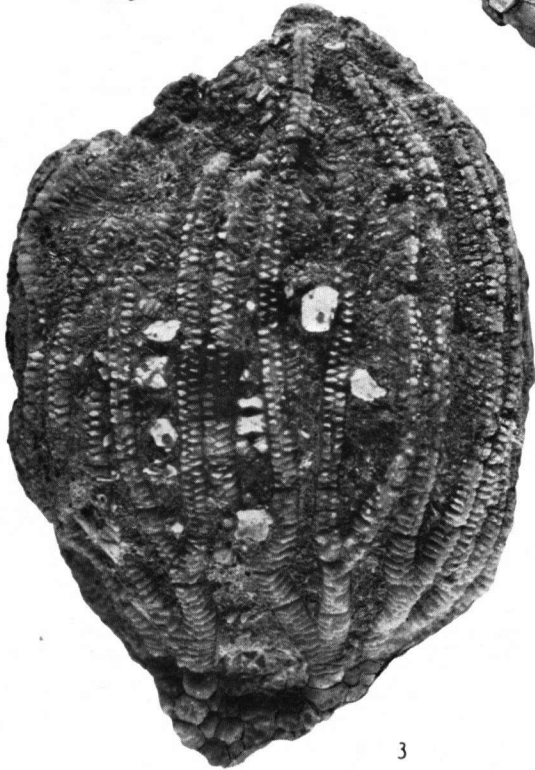


PLATE V

- Fig. 1—2 *Pithocrinus spinosus* spec. nov. Holotype p. 54  
 Specimen 97526 coll. Rijksmus. Geol. Min. Leiden  
 Upper Emsian Santa Lucia limestone of Grandoso (León).  
 Fig. 1 lateral view; fig. 2 tegmen. Natural size.
- Fig. 3 *Pithocrinus spinosus* spec. nov. p. 54  
 Specimen 97528 coll. Rijksmus. Geol. Min. Leiden.  
 Upper Emsian Santa Lucia limestone of Grandoso (León).  
 Lateral view,  $\times 1$
- Fig. 4 *Pithocrinus spinosus* spec. nov. p. 54  
 Specimen 97532 coll. Rijksmus. Geol. Min. Leiden.  
 Upper Emsian Santa Lucia limestone of Grandoso (León).  
 Lateral view of specimen clearly showing the spiny nature of the cup  
 plates.  $\times 1$
- Fig. 5—6 *Pithocrinus ovatus* spec. nov. p. 47  
 Specimen TB 42 coll. Mus. Inst. Geol. Min. Madrid.  
 Emsian deposits of Grandoso (León).  
 Summit and lateral views of isolated tegmen showing stout subcentral  
 anal tube and larger nodose tegmen plates.  $\times 1$
- Fig. 7—11 *Pithocrinus ovatus* spec. nov. Holotype p. 47  
 Specimen 97737 coll. Rijksmus. Geol. Min. Leiden.  
 Upper Emsian Santa Lucia limestone of El Millar (León).  
 Fig. 7 posterior view; fig. 8 antero right view; fig. 9 left anterior  
 view; fig. 10 tegmen; fig. 11 basal view. Natural size

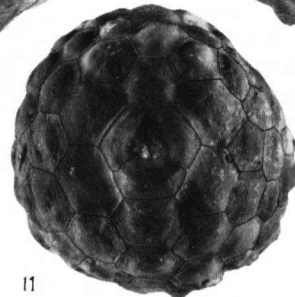
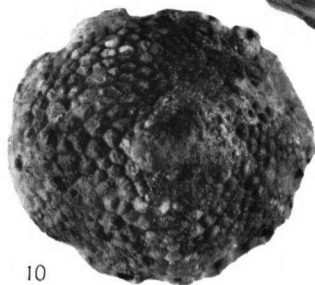
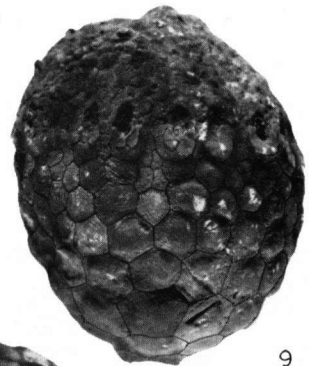
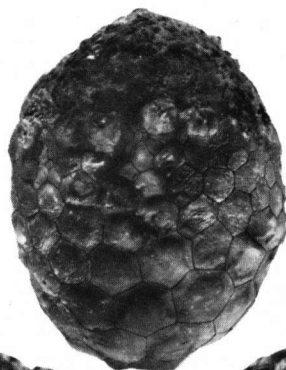
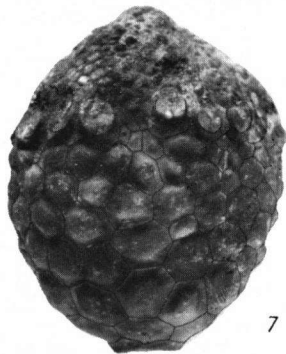
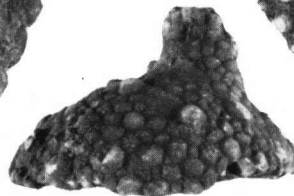
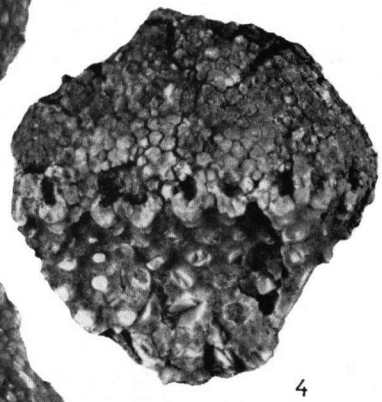
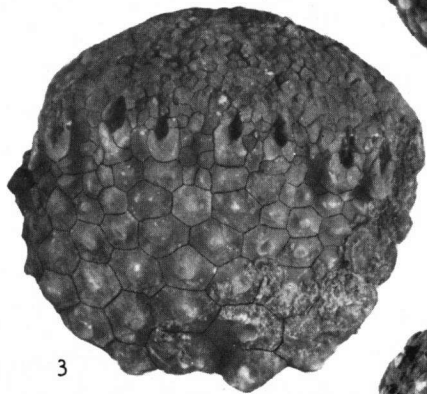
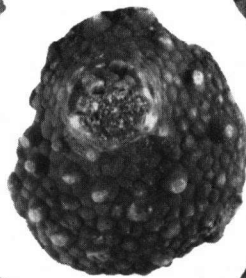
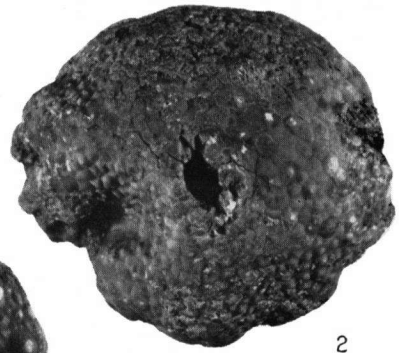
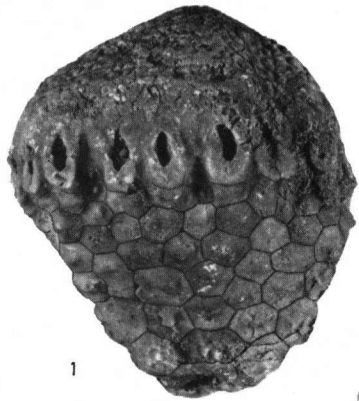




PLATE VI

- Fig. 1—5 *Pyxidocrinus collensis* spec. nov. Holotype p. 35  
 Specimen 97539 coll. Rijksmus. Geol. Min. Leiden.  
 Lower Emsian La Vid shale formation at Colle (León).  $\times 1$   
 Fig. 1 posterior view; fig. 2 posterior view, perpendicular to cup wall;  
 fig. 3 left anterior view; fig. 4 basal view; fig. 5 tegmen.
- Fig. 6 *Pyxidocrinus collensis* spec. nov. p. 35  
 Specimen 97580 coll. Rijksmus. Geol. Min. Leiden.  
 Lower Emsian La Vid shale formation at Villayandre (León).  
 Specimen shows aberrant radius.  $\times 1$
- Fig. 7 *Pyxidocrinus collensis* spec. nov. p. 35  
 Young specimen TB 54 coll. Mus. Inst. Geol. Min. Madrid.  
 Lower Emsian La Vid shale formation at Colle (León).  
 Specimen shows aberrant posterior interradius with two iRR succeeding A.  $\times 1\frac{1}{2}$
- Fig. 8 *Pyxidocrinus collensis* spec. nov. p. 35  
 Young specimen TB 54a coll. Mus. Inst. Geol. Min. Madrid.  
 Lower Emsian La Vid shale formation at Colle (León).  
 Specimen shows tegminal spines and radial ornamentation of cup plates.  
 $\times 1\frac{1}{2}$
- Fig. 9—14 *Pyxidocrinus latus* spec. nov. Holotype p. 40  
 Specimen TB 58 coll. Mus. Inst. Geol. Min. Madrid.  
 Lower Emsian La Vid shale formation at Colle (León).  
 Fig. 9 anterior view; fig. 10 basal view; fig. 11 posterior view; fig. 12  
 right side view; fig. 13 tegmen; fig. 14 left side view.  $\times 1$

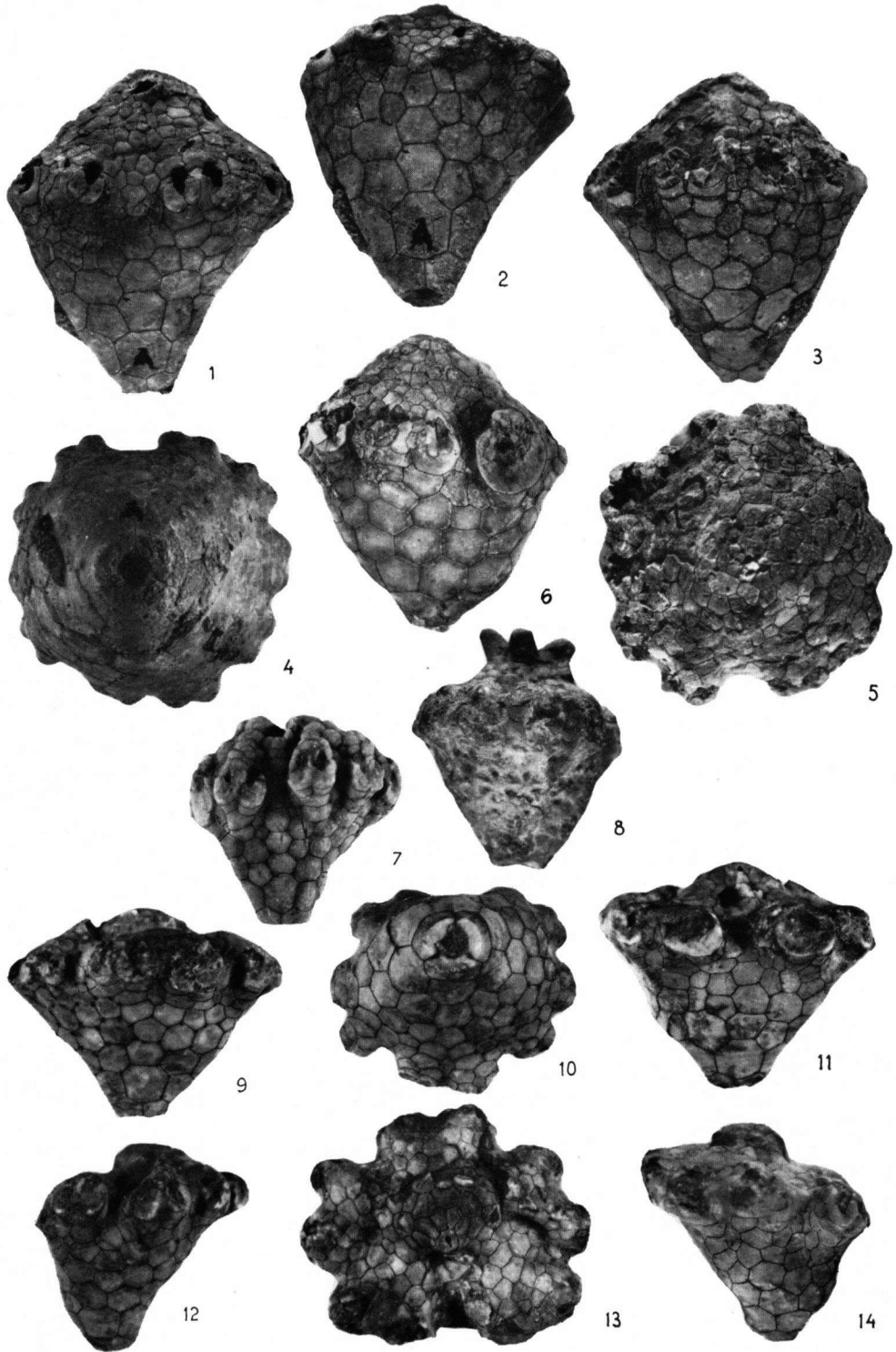


PLATE VII

- Fig. 1—5 *Stamnocrinus intrastigmatus* (W. E. Schmidt, 1932) p. 59  
 Specimen TB 46 coll. Mus. Inst. Geol. Min. Madrid.  
 Emsian deposits at Colle (León).  
 Fig. 1 right anterior view; fig. 2 tegmen; fig. 3 anterior view; fig. 4  
 posterior view; fig. 5 basal view.  $\times 1$
- Fig. 6 *Stamnocrinus intrastigmatus* (W. E. Schmidt, 1932) p. 59  
 Specimen DH 1075 coll. Mus. Nac. Ciencias Nat. Madrid.  
 Specimen shows the spines on the tegmen.  
 Unknown provenance.  $\times 1$
- Fig. 7 *Stamnocrinus intrastigmatus* (W. E. Schmidt, 1932) p. 59  
 Very large specimen 77 D coll. Mus. Inst. Geol. Min. Madrid.  
 Emsian deposits, probably of Colle (León).  
 Specimen shows very wide interradiial areas.  $\times 1$
- Fig. 8—12 *Corocrinus ? grandosensis* spec. nov. Holotype p. 67  
 Specimen TB 45 coll. Mus. Inst. Geol. Min. Madrid.  
 Upper Emsian Santa Lucia limestone of Grandoso (León).  
 Fig. 8 basal view; fig. 9 tegmen; fig. 10 right posterior view; fig. 11  
 posterior view; fig. 12 left anterior view.  $\times 1\frac{1}{2}$

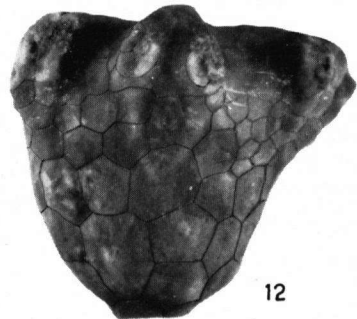
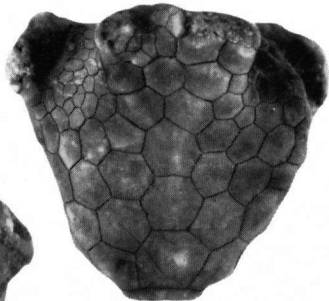
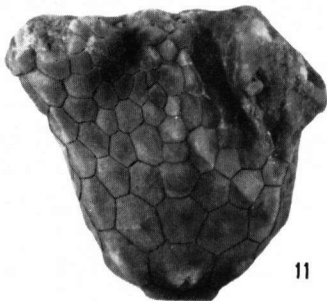
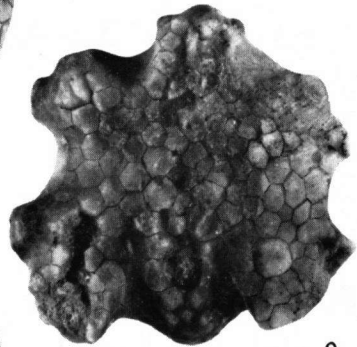
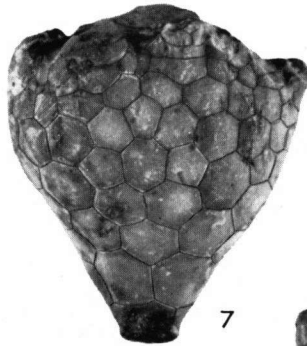
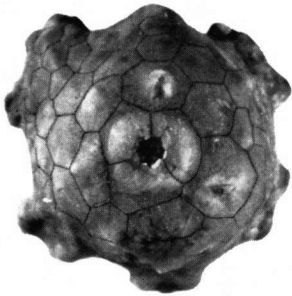
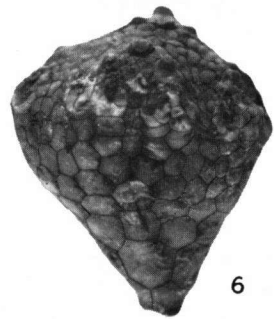
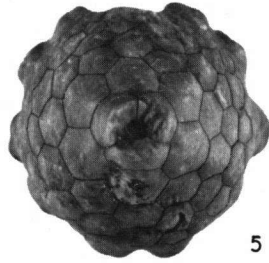
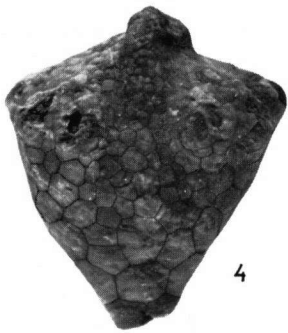
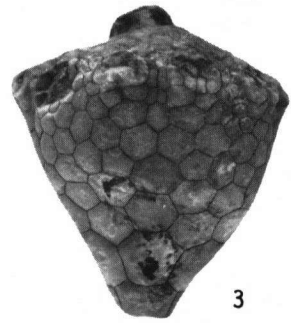
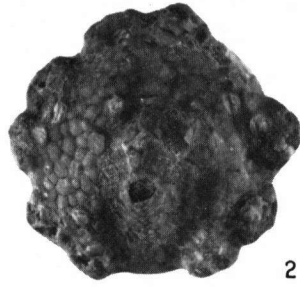
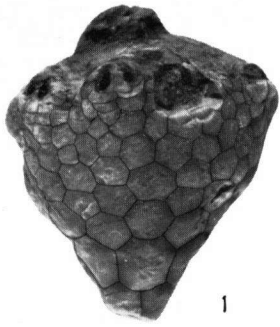


PLATE VIII

- Fig. 1—4 *Iberocrinus multibrachiatus* Sieverts-Doreck, 1951 p. 75  
 Specimen TB 64 coll. Mus. Inst. Geol. Min. Madrid.  
 Westfalian of Mudá-Valdebreto (Palencia).  
 Fig. 1 anterior view; fig. 2 posterior view; fig. 3 basal view; fig. 4  
 tegmen.  $\times 2$
- Fig. 5—6 *Aorocrinus* spec. p. 78  
 Specimen 97600 coll. Rijksmus. Geol. Min. Leiden.  
 Namurian of Rabanal de los Caballeros (Palencia).  
 Fig. 5 basal view; fig. 6 right anterior view.  $\times 2$
- Fig. 7 *Nunnacrinus* ? *stellaris* (De Kon. & Le Hon, 1854) p. 78  
 Spec. no 101 coll. Laboratorio de Paleontología, Universidad Central  
 de Madrid.  
 Lower Carboniferous of Sabero (León).  $\times 2$
- Fig. 8—10 *Pimlicocrinus latus* J. Wright, 1943 p. 80  
 Specimen 97601 coll. Rijksmus. Geol. Min. Leiden.  
 Namurian of Rabanal de los Caballeros (Palencia).  
 Fig. 8 tegmen; fig. 9 lateral view; fig. 10 basal view.  $\times 2$
- Fig. 11 *Pimlicocrinus* spec. 2 p. 83  
 Specimen TB 83 coll. Mus. Inst. Geol. Min., Madrid.  
 Age and locality unknown.  
 Basal view.  $\times 1.5$
- Fig. 12—13 *Trybliocrinus Flatheanus* Geinitz, 1867 p. 86  
 Specimen 97696 coll. Rijksmus. Geol. Min. Leiden.  
 Lower Devonian of Arnao (Asturias).  
 Fig. 12 section through the stem at intercolumnar facet, showing radial  
 canal system.  $\times 2$   
 Fig. 13 section through the stem in a columnar. Note pentalobate out-  
 line of axial canal.  $\times 2$

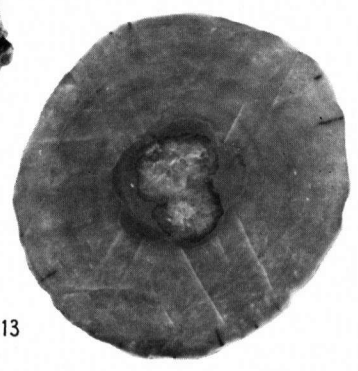
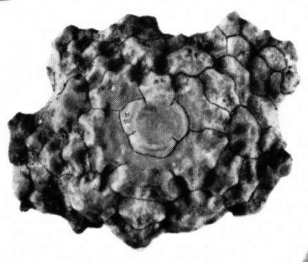
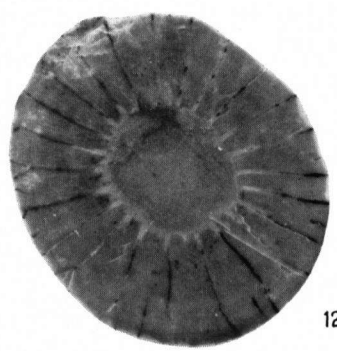
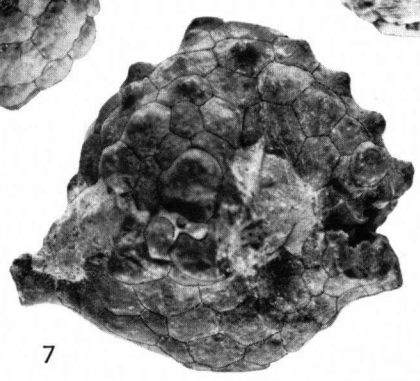
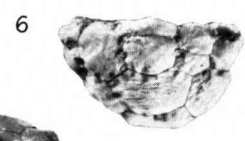
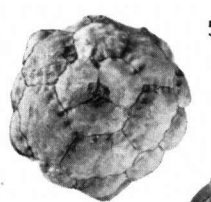
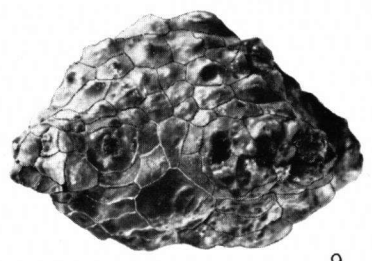
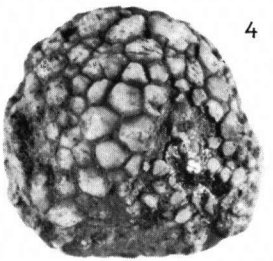
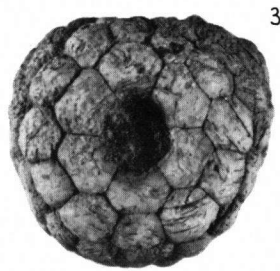
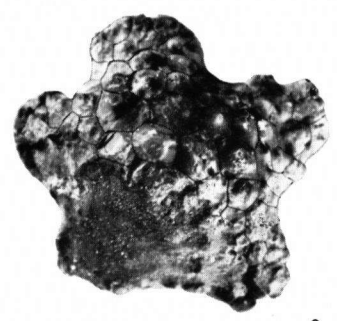
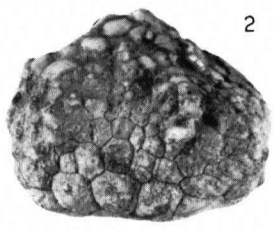
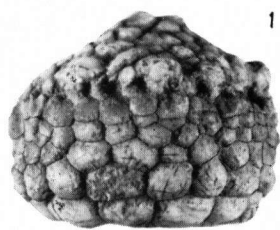
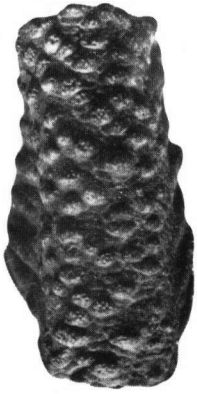


PLATE IX

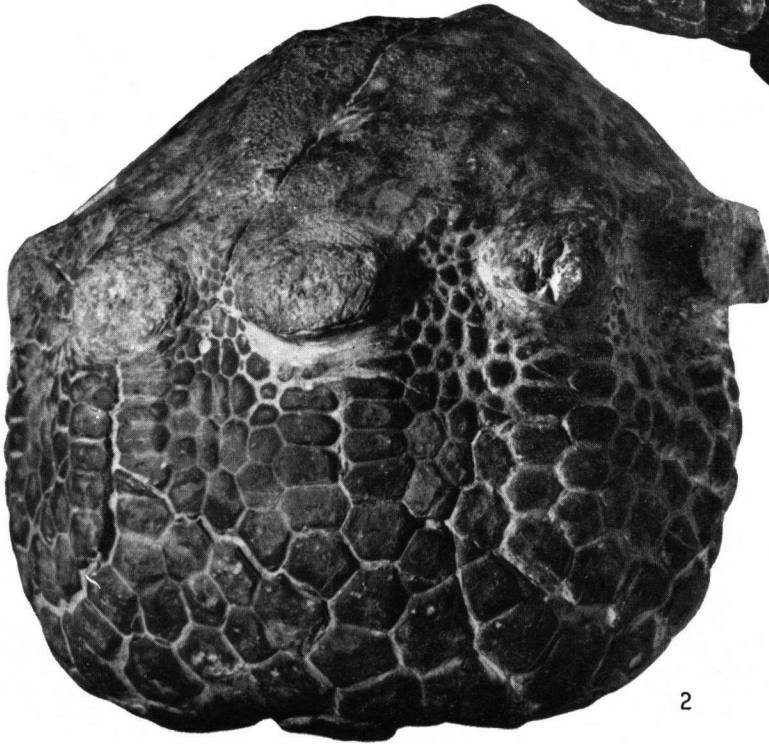
- Fig. 1—2 *Trybliocrinus Flatheanus* Geinitz, 1867 p. 86  
Specimen 2.393 coll. Mus. Inst. Geol. Min. Madrid.  
Lower Devonian of Arnao (Asturias).  
Fig. 1 and 2 lateral views. Natural size.
- Fig. 3 *Trybliocrinus Flatheanus* Geinitz, 1867 p. 86  
Specimen 97692 coll. Rijksmus. Geol. Min. Leiden.  
Lower Devonian of Arnao (Asturias).  
Portion of an arm in dorsal view. Note special type of ornamentation  
of the brachials.  $\times 2\frac{1}{2}$
- Fig. 4 *Trybliocrinus Flatheanus* Geinitz, 1867 p. 86  
Specimen 87 D coll. Mus. Inst. Geol. Min. Madrid.  
Lower Emsian of La Vid (León).  
Stemfragment. Note openings of radial canal system in weathered right  
part of the figure.  $\times 1$
- Photographs 1 and 2 Pablo Yagüe, Madrid.



3



1



2



4



PLATE X

- Fig. 1 *Trybliocrinus Flatheanus* Geinitz, 1867 p. 86  
 Specimen 97689 coll. Rijksmus. Geol. Min. Leiden.  
 Lower Devonian of Arnao (Asturias).  
 Oblique view of main arm trunk with pinnulated ramules.  
 Note stratified roof over ambulacral groove.  $\times 3$
- Fig. 2 *Trybliocrinus Flatheanus* Geinitz, 1867 p. 86  
 Specimen 97691 coll. Rijksmus. Geol. Min. Leiden.  
 Lower Devonian of Arnao (Asturias).  
 Lateral view of distal arm portion; ramules broken off; roof over ambulacral groove shown at left side of the figure.  $\times 3$
- Fig. 3 *Trybliocrinus Flatheanus* Geinitz, 1867 p. 86  
 Specimen TB 5 coll. Mus. Inst. Geol. Min. Madrid.  
 Lower Devonian of Arnao (Asturias).  
 Young specimen with arms attached. Natural size.
- Fig. 4 *Trybliocrinus Flatheanus* Geinitz, 1867 p. 86  
 Specimen TB 36 coll. Mus. Inst. Geol. Min. Madrid.  
 Lower Devonian of Arnao (Asturias).  
 Proximal trunk of the stem with long cylindrical cirri.  $\times \frac{1}{2}$
- Fig. 5 *Trybliocrinus Flatheanus* Geinitz, 1867 p. 86  
 Specimen 97694 coll. Rijksmus. Geol. Min. Leiden.  
 Internal aspect of tegmen, showing very large plates, alternating with very small ones.  $\times 1$
- Fig. 6 *Trybliocrinus Flatheanus* Geinitz, 1867 p. 86  
 Specimen 97690 coll. Rijksmus. Geol. Min. Leiden.  
 Lower Devonian of Arnao (Asturias).  
 Dorsal aspect of distal arm portion.  $\times 3$
- Fig. 7 *Trybliocrinus Flatheanus* Geinitz, 1867 p. 86  
 Specimen 6417 coll. Escuela de Minas, Madrid.  
 Lower Devonian of Arnao (Asturias).  
 Oblique view of specimen with arm bases attached.  $\times \frac{2}{3}$   
 Photograph Pablo Yagüe, Madrid.



1



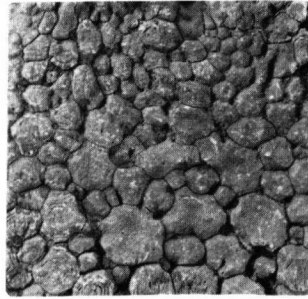
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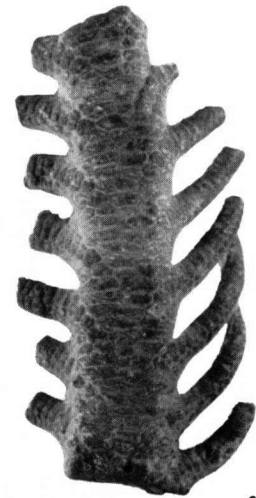
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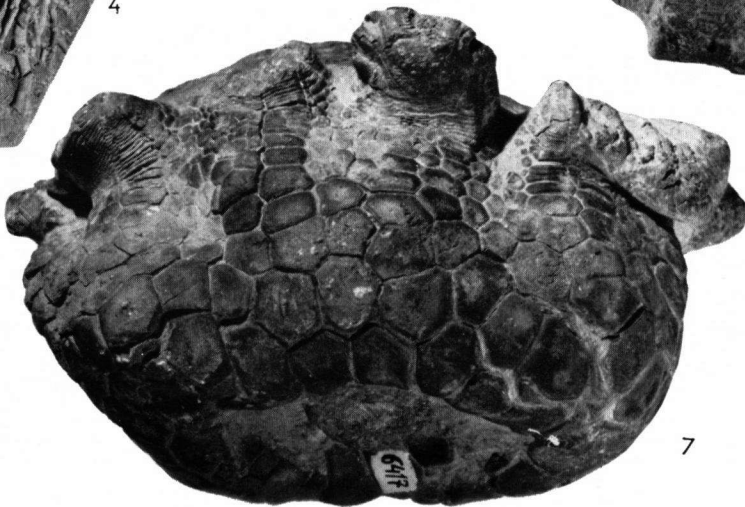
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PLATE XI

- Fig. 1—4 Hapalocrinidae cf. *Culicocrinus nodosus* p. 122  
Specimen TB 69a coll. Mus. Inst. Geol. Min. Madrid.  
Unknown provenance.  
Fig. 1 basal view; fig. 2 tegmen; fig. 3 posterior view; fig. 4 postero  
left view.  $\times 3$
- Fig. 5—7 *Cantharocrinus minor* gen. nov., spec. nov. Holotype p. 117  
Specimen 97700 coll. Rijksmus. Geol. Min. Leiden.  
Lower Emsian of Colle (León).  
Fig. 5 antero right view; fig. 6 tegmen; fig. 7 posterior view.  $\times 4$
- Fig. 8—11 *Cantharocrinus simplex* gen. nov., spec. nov. Holotype p. 120  
Specimen 97699 coll. Rijksmus. Geol. Min. Leiden.  
Lower Couvinian of Remolina (León).  
Fig. 8 basal view; fig. 9 tegmen; fig. 10 posterior view; fig. 11 right  
posterior view.  $\times 4$

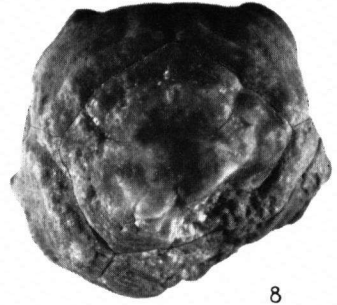
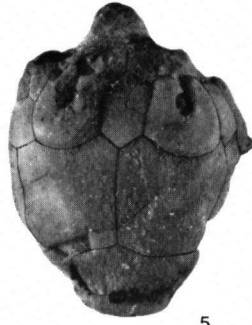
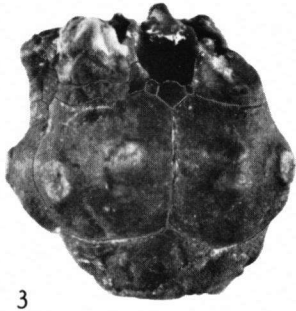
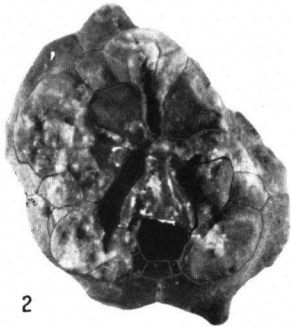
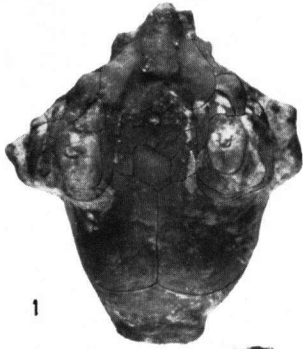
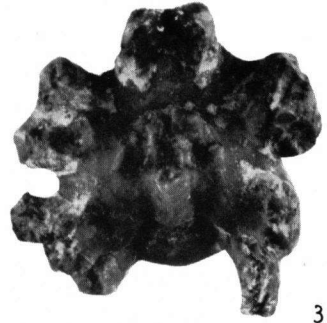


PLATE XII

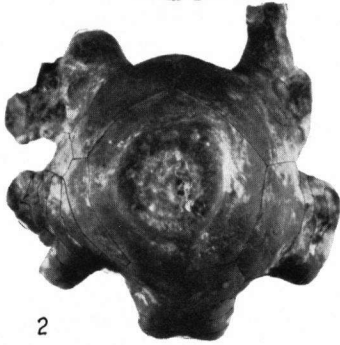
- Fig. 1—4 *Oenochoacrinus princeps* gen. nov., spec. nov. Holotype p. 124  
 Specimen TB 65a coll. Mus. Inst. Geol. Min. Madrid.  
 Devonian of La Velilla (León).  
 Fig. 1 posterior view; fig. 2 basal view; fig. 3 tegmen; fig. 4 anterior  
 view.  $\times 3$
- Fig. 5—6 *Oenochoacrinus princeps* gen. nov., spec. nov. Paratypes p. 124  
 Specimens in the collection Mus. Inst. Geol. Min. Madrid.  
 Devonian of León.  
 Fig. 5 lateral view of spec. TB 65b; fig. 6 posterior view of spec.  
 TB 65c.  $\times 2\frac{1}{2}$
- Fig. 7—9 *Oenochoacrinus pileatus* gen. nov., spec. nov. Holotype p. 127  
 Specimen 97708 coll. Rijksmus. Geol. Min. Leiden.  
 Lower Couvinian of El Millar (León).  
 Fig. 7 basal view; fig. 8 tegmen; fig. 9 postero right view.  $\times 3\frac{1}{2}$
- Fig. 10—11 *Oenochoacrinus* ? spec. p. 131  
 Specimen 97704 coll. Rijksmus. Geol. Min. Leiden.  
 Lower Couvinian of Remolina (León).  
 Fig. 10 posterior view; fig. 11 tegmen.  $\times 3\frac{1}{2}$



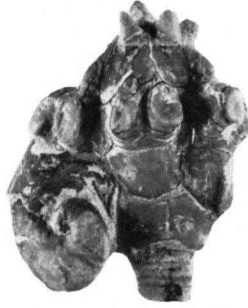
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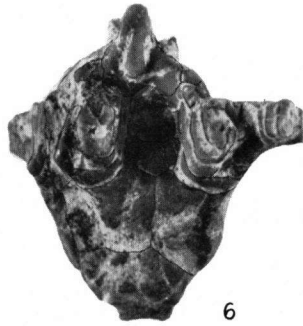
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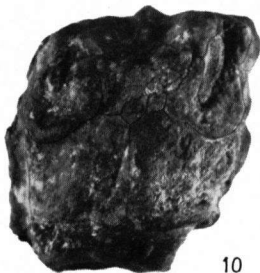
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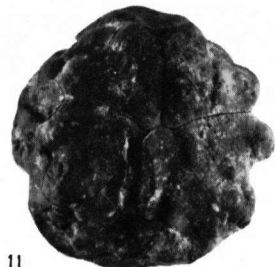
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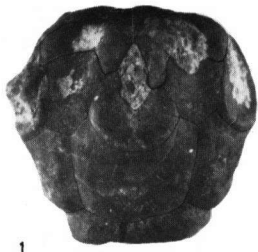
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PLATE XIII

- Fig. 1—2 *Oenochoacrinus* ? spec. p. 131  
 Specimen 97705 coll. Rijksmus. Geol. Min. Leiden.  
 Lower Couvinian of Remolina (León).  
 Fig. 1 anterior view; fig. 2 basal view. × 3
- Fig. 3—5 *Oenochoacrinus scaber* gen. nov., spec. nov. Holotype p. 129  
 Specimen 128 D1 coll. Mus. Inst. Geol. Min. Madrid.  
 Devonian of Aleje (León).  
 Fig. 3 tegmen; fig. 4 right anterior view; fig. 5 posterior view. × 3
- Fig. 6—9 *Platycrinus* spec. (ex gr. *bollandensis* Wright, 1938) p. 131  
 Specimen 97713 coll. Rijksmus. Geol. Min. Leiden.  
 Namurian of Rabanal de los Caballeros (Palencia).  
 Fig. 6 basal view; fig. 7 left anterior view; fig. 8 posterior view; fig. 9  
 tegmen. × 1
- Fig. 10 *Oenochoacrinus scaber* gen. nov., spec. nov. p. 129  
 Specimen 129 D coll. Mus. Inst. Geol. Min. Madrid.  
 Lower Emsian of Colle (León).  
 Tegmen. × 3
- Fig. 11 *Oenochoacrinus scaber* gen. nov., spec. nov. p. 129  
 Specimen 130 D coll. Mus. Inst. Geol. Min. Madrid.  
 Devonian of Corniero (León).  
 Anterior view. × 3
- Fig. 12—14 *Platycrinus* spec. (ex gr. *bollandensis* Wright, 1938) p. 131  
 Specimen 97712 coll. Rijksmus. Geol. Min. Leiden.  
 Namurian of Rabanal de los Caballeros (Palencia).  
 Fig. 12 basal view; fig. 13 postero right view; fig. 14 tegmen. × 2



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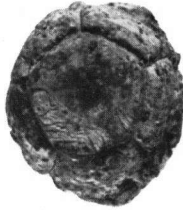
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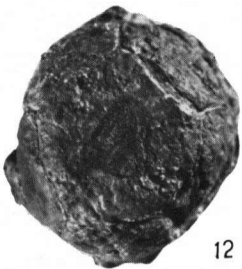
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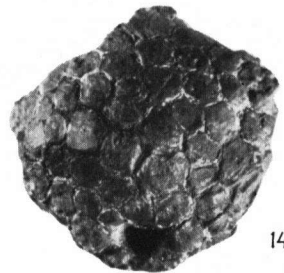
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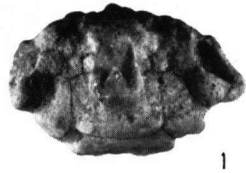


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PLATE XIV

- Fig. 1—4 *Pleurocrinus* spec. ex gr. *coplowensis* Wright, 1938 p. 133  
 Specimen TB 84 coll. Mus. Inst. Geol. Min. Madrid.  
 Unknown provenance.  
 Fig. 1 lateral view; fig. 2 basal view; fig. 3 posterior view; fig. 4  
 tegmen.  $\times 2$
- Fig. 5—7 *Vasocrinus valens* Lyon, 1857 p. 147  
 Specimen 97724 coll. Rijksmus. Geol. Min. Leiden.  
 Lower Couvinian of El Millar (León).  
 Fig. 5 posterior view; fig. 6 basal view; fig. 7 lateral view.  $\times 2$
- Fig. 8—10 *Vasocrinus turbinatus* Kirk, 1929 p. 148  
 Specimen TB 76 coll. Mus. Inst. Geol. Min. Madrid.  
 Unknown provenance.  
 Fig. 8 posterior view; fig. 9 basal view; fig. 10 lateral view.  $\times 2$
- Fig. 11—14 *Vasocrinus stellaris* (Schultze, 1867) p. 149  
 Specimen TB 75 coll. Mus. Inst. Geol. Min. Madrid.  
 Devonian of Orzonaga (León).  
 Fig. 11 posterior view; fig. 12 basal view; fig. 13 tegmen; fig. 14  
 lateral view.  $\times 4$
- Fig. 15—17 *Vasocrinus* spec. cf. *V. sculptus* Lyon, 1857 p. 151  
 Specimen TB 77 coll. Mus. Inst. Geol. Min. Madrid.  
 Unknown provenance.  
 Fig. 15 lateral view; fig. 16 tegmen; fig. 17 basal view.  $\times 2$



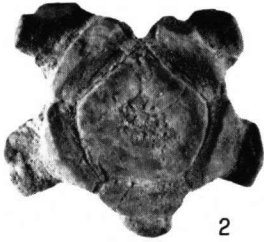
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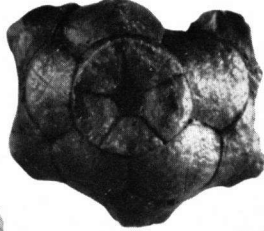
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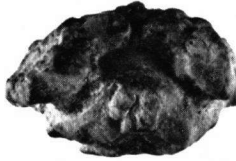
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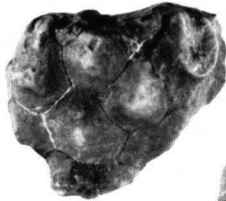
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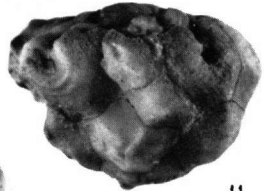
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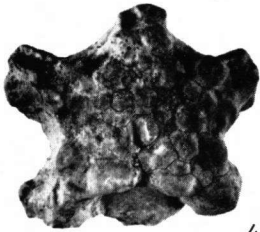
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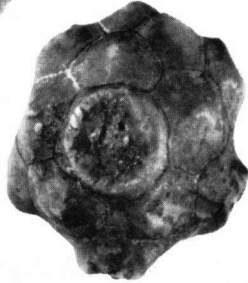
8



11



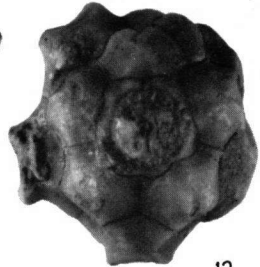
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9



10



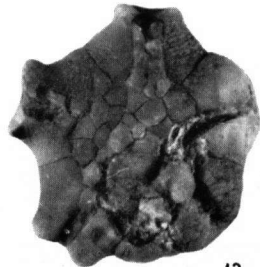
12



15



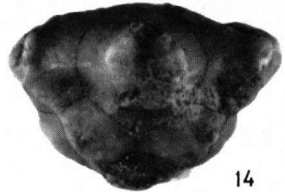
17



13



16



14

PLATE XV

- Fig. 1, 3, 4, 6 *Situlacrinus costatus* gen. nov., spec. nov. p. 154  
 Specimen 97727 coll. Rijksmus. Geol. Min. Leiden.  
 Emsian of Colle (León).  
 Fig. 1 lateral view; fig. 3 posterior view; fig. 4 summit view of  
 dorsal cup; fig. 6 basal view.  $\times 4$
- Fig. 2, 5 *Situlacrinus costatus* gen. nov., spec. nov. Paratype p. 154  
 Specimen 97729 coll. Rijksmus. Geol. Min. Leiden.  
 Emsian of Colle (León).  
 Fig. 2 posterior view; fig. 5 tegmen.  $\times 4$
- Fig. 7, 8 *Bactrocrinites* spec. p. 168  
 Specimen 96 D coll. Mus. Inst. Geol. Min. Madrid.  
 Emsian of Colle (León).  
 Fig. 7 posterior view; fig. 8 lateral view.  $\times 1\frac{1}{2}$
- Fig. 9, 10 *Cyathocrinites* spec. p. 158  
 Specimen TB 74 coll. Mus. Inst. Geol. Min. Madrid.  
 Emsian of Colle (León).  
 Fig. 9 lateral view; fig. 10 posterior view.  $\times 1\frac{1}{2}$
- Fig. 11, 12 *Lasiocrinus* ? spec. p. 169  
 Specimen TB 72 coll. Mus. Inst. Geol. Min. Madrid.  
 Emsian of Colle (León).  
 Fig. 11 lateral view; fig. 12 posterior view.  $\times 2$
- Fig. 13, 14 *Cromyocrinus* spec. cf. *C. simplex* Trautschold, 1867 p. 170  
 Specimen 97732 coll. Rijksmus. Geol. Min. Leiden.  
 Moscovian of Herrerueta (Palencia).  
 Fig. 13 posterior view; fig. 14 basal view.  $\times 1\frac{1}{2}$
- Fig. 15 *Codiocrinus* spec. p. 159  
 Specimen 97731 coll. Rijksmus. Geol. Min. Leiden.  
 Emsian of Villayandre (León).  
 Lateral view.  $\times 3$

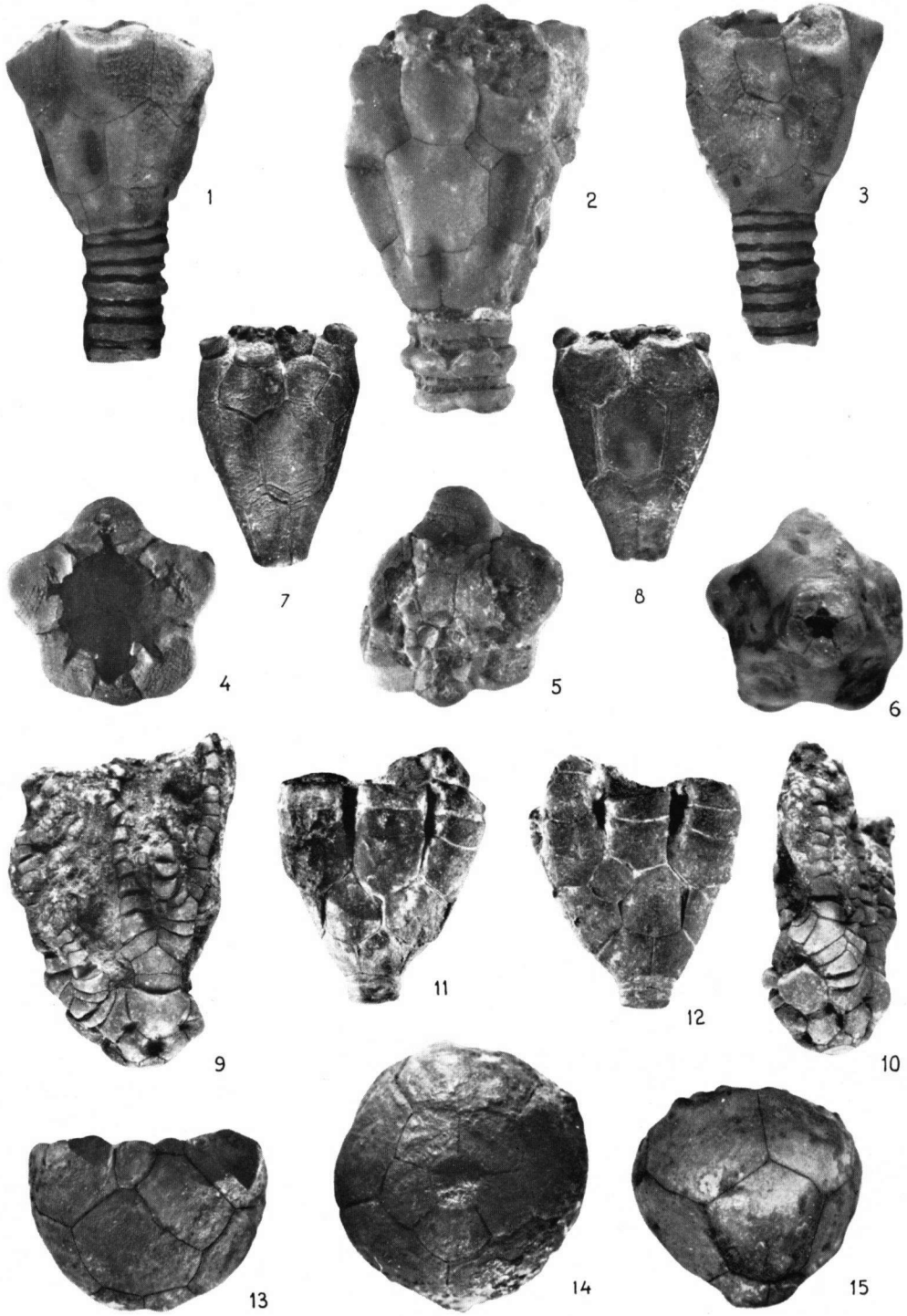


PLATE XVI

- Fig. 1 *Cupressocrinites inflatus* Schultze, 1867 p. 163  
 Specimen 97719 coll. Rijksmus. Geol. Min. Leiden.  
 Givetian of Mount Las Peñotas (León).  
 Lateral view. Slightly enlarged.
- Fig. 2 *Cupressocrinites* spec. cf. *C. Schlotheimi* Steiniger, 1831 p. 166  
 Specimen no. 96 coll. Univ. Central Madrid.  
 Middle Devonian of Perlorá (Asturias).  
 Lateral view.  $\times 1$
- Fig. 3 *Cupressocrinites* spec. cf. *C. Schlotheimi* Steiniger, 1831 p. 167  
 Specimen 19618 coll. Rijksmus. Geol. Min. Leiden.  
 Middle Devonian of Gerolstein (Eifel).  
 Lateral view.  $\times 1$   
 Figured for comparison with the specimen fig. 2 of this plate.
- Fig. 4 *Cupressocrinites Sampelayoi* (Almela & Revilla, 1950) p. 160  
 Specimen 97714 coll. Rijksmus. Geol. Min. Leiden.  
 Givetian of Mount Las Peñotas (León).  
 Lateral view.  $\times 1\frac{1}{2}$
- Fig. 5 *Cupressocrinites Sampelayoi* (Almela & Revilla, 1950) p. 160  
 Specimen 97717 coll. Rijksmus. Geol. Min. Leiden.  
 Givetian of Aviados (León).  
 Internal view of last brachial, showing open axial groove.  $\times 1\frac{1}{2}$
- Fig. 6 *Cupressocrinites* spec. cf. *C. Townsendi* (König, 1825) p. 164  
 Specimen 97721 coll. Rijksmus. Geol. Min. Leiden.  
 Givetian of Cremenes (León).  
 Lateral view.  $\times 1$
- Fig. 7 *Cupressocrinites* spec. cf. *C. Townsendi* (König, 1825) p. 164  
 Specimen no. 10 Verneuil collection Ecôle des Mines, Paris.  
 Devonian of Ferroñes (Asturias).  
 Lateral view.  $\times 1$

