The stalk joints of recent Isocrinidae (Crinoidea)

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Synopsis

The stalk joints of recent genera representative of the crinoid family Isocrinidae have been observed with the scanning electron microscope. This study indicates that the detailed morphology of the symplexial and synostosial articulations has taxonomic significance. *Neocrinus* and *Hypalocrinus* differ from the other genera by many characters. They have affinities with the fossil *Balanocrinus* group. Such a study is of interest for comparison between the fossil and recent taxa with respect to the variability of the external morphology of the stalk.

Introduction

Many fossil species of stalked crinoids have been described from dissociated parts of their columns, their calyces and arms being unknown. When a primarily fossil family includes recent representatives, it is very important for palaeontological studies to have detailed descriptions of the stalk joints of the modern species. With this in mind I have observed columnal facets of recent Isocrinidae under the scanning electron microscope. An earlier study (Roux, 1974) suggested that the microstructural organization of the pentalobate stalk joints has taxonomic significance. To confirm this possibility, I have selected mature columnals of all the recent genera and of four species of the genus *Metacrinus*. The following Isocrinidae are described:

Metacrinus nobilis Carpenter
M. rotundus Carpenter
M. angulatus Carpenter
M. wyvillei Carpenter
Cenocrinus asterius (Linnaeus)
Endoxocrinus parrae (Gervais)
Teliocrinus springeri (Clark)
Diplocrinus alternicirrus (Carpenter)
Annacrinus wyvillethomsoni (Jeffreys *in* Wyville Thomson)
Neocrinus blakei (Carpenter)
N. decorus (Wyville Thomson)
Hypalocrinus naresianus (Carpenter)

All the specimens used belong to the zoological collections of the British Museum (Natural History), except for that of *Annacrinus wyvillethomsoni*, which is from the Muséum National d'Histoire Naturelle, Paris.

Main morphological features of stalk joints

The heteromorphic column of the isocrinids is composed of varying numbers of internodal

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columnals between single larger columnals differentiated as nodals and bearing cirri. The joint between two successive internodals is usually a symplexy; that is it has interlocking radiating ridges (culmina) and grooves (crenellae), each matching culmen and crenella making a crenula, the crenulae of each joint together making a crenularium. The distal joint of each mature nodal is a synostosis, having facets with smooth surfaces. These are the two main kinds of articulation in the columnals of this family. I have never observed syzygial articulations (in which the ridges of the crenularium correspond to elevations of the apposed facet). The term syzygy has been misapplied by many previous authors to the distal articulations of the nodals. Some symplexial or synostosial articulations have one facet with a concave surface corresponding to a convexity of the opposing facet, especially in synostoses where the distal facet of the nodal is often concave; such a modified joint is a symmorphy. The terminology used here for the morphology of stalk joints mainly follows that of Moore *et al.* (1968 : 14–16).

The microstructure of the endoskeleton is very important for a detailed description (Roux, 1970, 1974, 1975; Macurda & Meyer, 1975). The mesoderm secretes a mesh-like stereom with either a regular organization of parallel galleries (α-stereom) or a variable irregular one (β-stereom). The spiculate origin of this meshwork of calcite is evident during growth (Fig. 3A); exceptionally spicules become visible within the occluded axial canal of a synostosis (Fig. 8A, C, E).

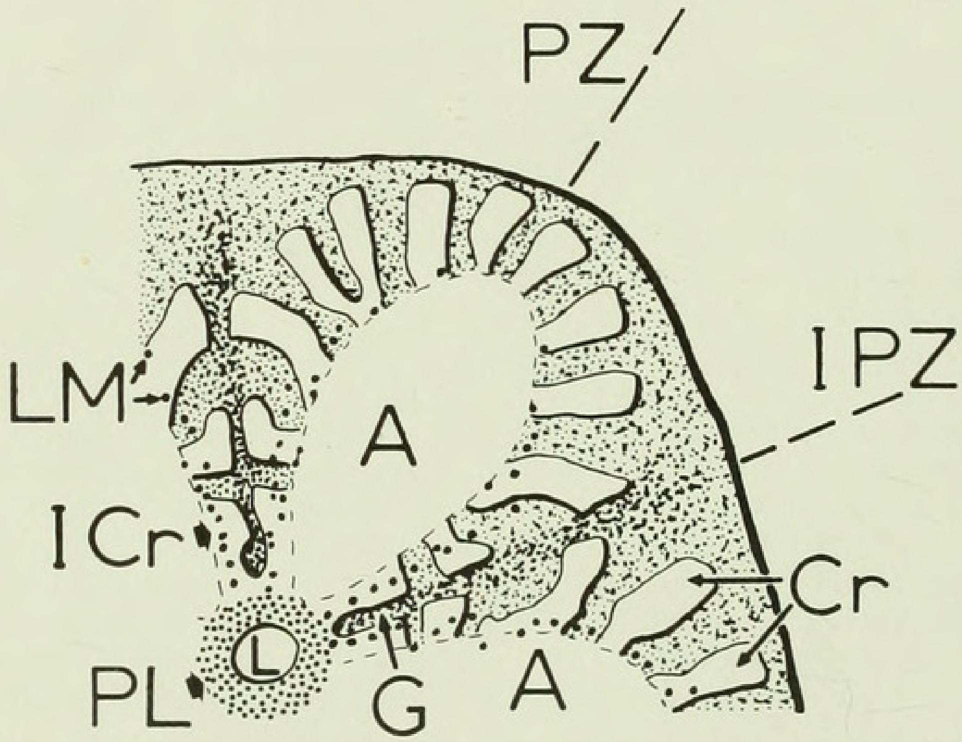

Fig. 1 Morphology of a stem joint of an isocrinid. A: areola, Cr: crenulae, ICr: inner crenularium, IPZ: interpetaloid zone, PZ: petaloid zone, G: axial groove, L: lumen, LM: large meshes, PL: perilumen.

Symplexial articulations have a pentalobate crenularium around five petaloid areolae (petaloid zones or petals).

The α-stereom is the microstructure of petaloid zones and the β-stereom of interpetaloid zones. The areola has a lanceolate or triangular shape. It may reach the outer edge of the facet (in an open crenularium, Fig. 2A) or may not (closed crenularium, Fig. 2B). A transverse section of a facet clearly shows the microstructural organization of the columnal (Fig. 2). The α-stereom of the areola takes various forms, a thin calcite meshwork with diamond-shaped meshes (Fig. 3D), or with polygonal or round meshes (Fig. 3E, F). Each end of the crenularium is formed of α-stereom with a few wider meshes. Such meshes are always visible on facets (of symplexies or synostoses) and in transverse sections; sometimes they are evenly distributed around the areola. The areolae of the fossil isocrinid *Isselicrinus subbasaltiformis* possess many such meshes (Fig. 3C) but I have never found this texture in the areolae of the recent species described here. The inner part of the symplexial crenularium is frequently differentiated, when its surface is flatter with a thickened stereom (Fig. 4B). The axis of an interpetaloid zone often appears as a line where crenulae adjoin (Fig. 5B), or as a β-stereom groove (Fig. 5A). When the perilumen is clearly differentiated it consists of a massive covering of calcite (Fig. 5E) or sometimes of a granulose surface with little meshes (Fig. 4F).

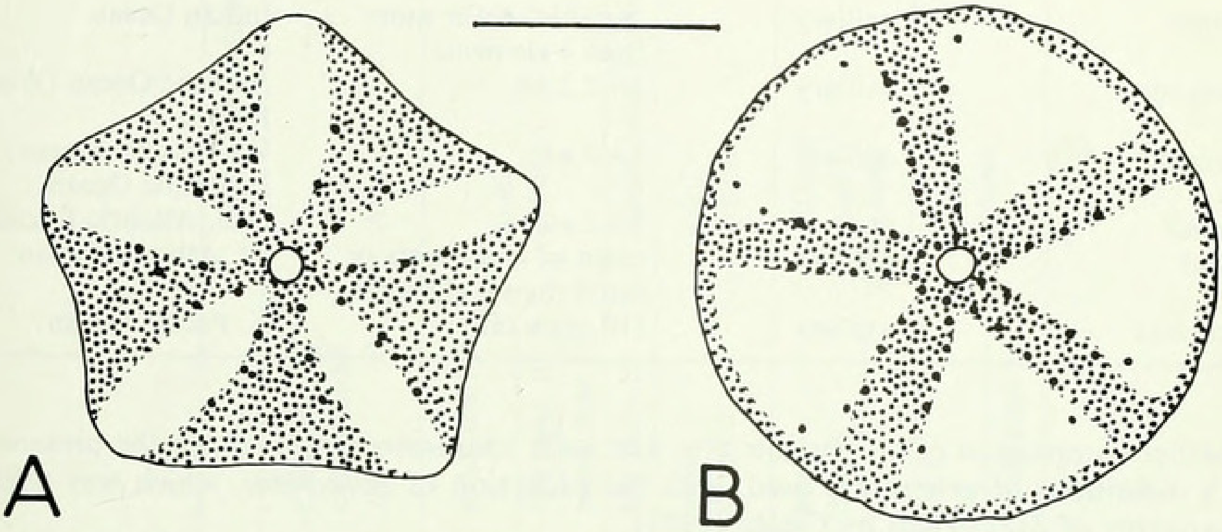

Fig. 2 Microstructural organization of a columnal in transverse section. (A) *Diplocrinus alternicirrus*; (B) *Hypalocrinus naresianus*. (Scale: 2 mm)

Synostosial articulations are secondarily ankylosed joints derived from a primary symplexial pattern in the proximal part of the column (Roux, 1974). A special stereom (synostosial stereom) with small meshes fills up the interarticular space (Fig. 3B). The greater part of the whole facet is overgrown with this stereom. The reduced crenularium has two forms: the first one (Fig. 7A) with a true synostosial stereom, the other one (Fig. 7B) with a thicker calcite stereom (like the syzygial stereom). Sometimes a radial groove (Fig. 7D) or simply a microstructural differentiation along a radial line (Fig. 7E) marks the interpetaloid axes. Applying the terminology of Moore *et al.* (1968), such a synostosis is often not a true zygosynostosis but corresponds with a crypto-symplexial pattern. Into the axial canal grows a secondary β-stereom with large meshes (axial synostosial stereom) of varying development (Fig. 8). Sometimes it fills the whole lumen; the new lumen is then often pentalobate and the axes of the petals are the interpetaloid axes of the facet. The complex axial canal of Palaeozoic crinoid columnals is probably not homologous with the occluded axial canal in isocrinid synostoses. Consequently, a few of the morphological terms of Moore *et al.* (1968) are not used here (e.g. jugulum, spatium, claustrum).

In the present paper I have not dealt with the biometry and growth of the stereom of each species but have simply described the detailed morphology of mature stem joints. However, it is important to bear in mind the ontogenetic evolution during growth of the column from the calyx to the distal part of the stalk. My purpose here is an initial comparison between the main features of the stalk joints of different taxa of isocrinids, to show their taxonomic significance.

Taxonomic significance of Isocrinid stalk joints

According to A. H. Clark (1923), the recent genera of this family are primarily distinguished by characters derived from the post-radial division series (Table 1). However, he used characters of the stalk to differentiate between the two genera *Diplocrinus* and *Annacrinus*. Although Clark thought that no fossil species are congeneric with recent ones, Rasmussen (1961) refers several Cretaceous species to recent genera. Notably he regards *Neocrinus blakei* as a recent representative of the fossil genus *Isocrinus* but in my opinion there is insufficient proof of this relationship

Table 1 Recent genera of Isocrinidae (after Clark, 1923).

Genus	I Br 2	II Br and following division series	Geographical range
Metacrinus (including *Saracrinus*)	not axillary	variable; often more than 6 elements	E. and S.E. Pacific Ocean
Cenocrinus	axillary	variable; outer series of more than 6 elements	Atlantic Ocean (West Indies)
Teliocrinus	axillary	variable; never more than 4 elements	Indian Ocean
Endoxocrinus	axillary	1 + 2 3 ax	Atlantic Ocean (West Indies)
Diplocrinus	axillary	1 + 2 ax	W. Atlantic Ocean; E. Pacific Ocean
Annacrinus	axillary	1 + 2 ax	N.E. Atlantic Ocean
Neocrinus	axillary	often of 4 elements or more than 4 elements	W. Atlantic Ocean
Hypalocrinus	axillary	[10 arms only]	E. Pacific Ocean

and further comparison of all possible arm and stalk characters is needed. In the present paper, Clark's definitions of genera are used, with the exception of *Saracrinus*, which was referred to the synonymy of *Metacrinus* by Gislén (1927).

The taxonomic significance of the characters provided by stalk joints is evident if we compare the division series of the arms of different genera. Several aspects of the morphology of symplexial facets make it possible to recognize different taxonomic levels of affinity (Table 2). These agree with the relationships between genera derived from Clark's (1923) key. This is not clear for synostosial characters (Table 3), the taxonomic weight of which is more often at the specific level. This is a consequence of the secondary modification of stalk joints from symplexies to synostoses. In the four species of the genus *Metacrinus* observed here, the facets of the symplexial joints appear rather different at first glance, in spite of all the main characteristic textures which they have in common. The apparent generic significance of differences in synostosial morphology found in *Cenocrinus*, for instance, is probably due to our insufficient knowledge of such monotypic genera.

An analysis of common characters (Table 4) including all the main aspects of arm division, symplexy and synostosis highlights several points concerning the affinities of the species studied here:

(1) In 31 cases, the number of common characters between two genera is less than five. The most important contrast is between *Neocrinus–Hypalocrinus* and the remaining genera (26/31 cases) and the second is between *Diplocrinus–Annacrinus* and *Metacrinus*. *Neocrinus* and *Hypalocrinus* both have stalks with strong affinities with the fossil *Balanocrinus*-group (see Roux, 1970), especially *Hypalocrinus*. During mesozoic times the stalk joints of crinoids having affinity with *Isocrinus* and those affiliated with *Balanocrinus* were very different. This observation reinforces my doubts about Rasmussen's view (1961) that *Neocrinus blakei* is congeneric with fossil species of *Isocrinus*. However, it *is* likely that *Neocrinus blakei* and *N. decorus*, the type-species of *Neocrinus*, belong to distinct genera since they have only four symplexial characters in common. A detailed study of the crowns of these species is necessary to solve this problem.

(2) The two main groups of modern Isocrinidae seem to possess two opposite patterns of symplexial joints, for instance *Metacrinus* and *Diplocrinus* on the one hand, as opposed to *Neocrinus blakei* and *Hypalocrinus naresianus* on the other.

(3) The genus *Metacrinus* is particularly well defined. *M. nobilis* and *M. rotundus* have the strongest affinities, while *M. wyvillei* is slightly different from *M. nobilis*, *M. rotundus* and *M. angulatus*. The analysis confirms the necessity of abandoning *Saracrinus* A. H. Clark (type-species *M. nobilis*), proposed by Gislén (1927). According to Clark (1923), *M. wyvillei* and *M. rotundus* belong to *Metacrinus* sensu stricto (*M. wyvillei* being the type-species) while *M. nobilis* and *M.*

Table 2 Taxonomic significance of symplexial characteristics.

<table>
<tr><th rowspan="3">Taxa</th><th colspan="3">Areola:</th><th colspan="2">Crenularium</th><th colspan="2">Interpetaloid zone</th></tr>
<tr><th>Mesh shape</th><th colspan="2">Overall shape</th><th rowspan="2">Outer edge of petaloid zone</th><th rowspan="2">Crenulae of one petaloid zone</th><th rowspan="2">Axis</th><th rowspan="2">Inner part</th></tr>
<tr><th>Predominating stereom</th><th>On facet</th><th>Transverse section</th></tr>
<tr><td>Metacrinus nobilis</td><td rowspan="9">polygonal or round</td><td rowspan="5">lanceolate</td><td rowspan="9">lanceolate</td><td rowspan="2">closed</td><td rowspan="2">more than 10</td><td rowspan="4">axial groove</td><td rowspan="5">differentiated</td></tr>
<tr><td>Metacrinus rotundus</td></tr>
<tr><td>Metacrinus wyvillei</td><td>slightly open</td><td>less than 10</td></tr>
<tr><td>Metacrinus angulatus</td><td>closed</td><td>more than 10</td></tr>
<tr><td>Cenocrinus asterius</td><td>slightly open</td><td>less than 10</td><td>closed axial groove</td></tr>
<tr><td>Endoxocrinus parrae</td><td>pear-shaped</td><td>closed</td><td rowspan="2">more than 10</td><td rowspan="2">axial groove</td><td rowspan="7">undifferentiated</td></tr>
<tr><td>Teliocrinus springeri</td><td rowspan="4">lanceolate</td><td rowspan="3">open</td></tr>
<tr><td>Diplocrinus alternicirrus</td><td rowspan="2">less than 8</td><td rowspan="3">without axial groove</td></tr>
<tr><td>Annacrinus wyvillethomsoni</td></tr>
<tr><td>Neocrinus blakei</td><td rowspan="3">diamond-shaped</td><td rowspan="2">pear-shaped</td><td>slightly open</td><td rowspan="2">8–11</td></tr>
<tr><td>Neocrinus decorus</td><td>pear-shaped</td><td rowspan="2">closed</td><td rowspan="2">axial groove</td></tr>
<tr><td>Hypalocrinus naresianus</td><td>triangular</td><td>triangular</td><td>more than 11</td></tr>
</table>

Table 3 Taxonomic significance of synostosial characteristics.

<table>
<tr><th rowspan="2">Taxa</th><th colspan="2">For one petaloid crenula</th><th colspan="2">Occluded axial canal</th><th rowspan="2">Main stereom on interpetaloid zone and crenularium</th></tr>
<tr><th>Number of culmina</th><th>Number of large meshes</th><th>Nature of in-filling</th><th>Secondary lumen</th></tr>
<tr><td>Metacrinus nobilis</td><td rowspan="3">less than 10</td><td rowspan="2">more than 10</td><td rowspan="4">meshwork</td><td rowspan="4">small</td><td rowspan="7">synostosial stereom</td></tr>
<tr><td>Metacrinus rotundus</td></tr>
<tr><td>Metacrinus wyvillei</td><td rowspan="2">less than 30</td></tr>
<tr><td>Metacrinus angulatus</td><td rowspan="3">10–15</td></tr>
<tr><td>Cenocrinus asterius</td><td>irregular width</td><td>spicules</td><td>large</td></tr>
<tr><td>Endoxocrinus parrae</td><td>25–30</td><td rowspan="2">meshwork</td><td rowspan="2">small</td></tr>
<tr><td>Teliocrinus springeri</td><td rowspan="3">less than 10</td><td>6–10</td></tr>
<tr><td>Diplocrinus alternicirrus</td><td rowspan="2">irregular width</td><td>spicules</td><td rowspan="2">often fill in</td><td rowspan="5">syzygial stereom</td></tr>
<tr><td>Annacrinus wyvillethomsoni</td><td>meshwork</td></tr>
<tr><td>Neocrinus blakei</td><td>variable or wanting</td><td rowspan="3">10–15</td><td rowspan="3">spicules</td><td>very large</td></tr>
<tr><td>Neocrinus decorus</td><td rowspan="2">10–15</td><td>large</td></tr>
<tr><td>Hypalocrinus naresianus</td><td>small</td></tr>
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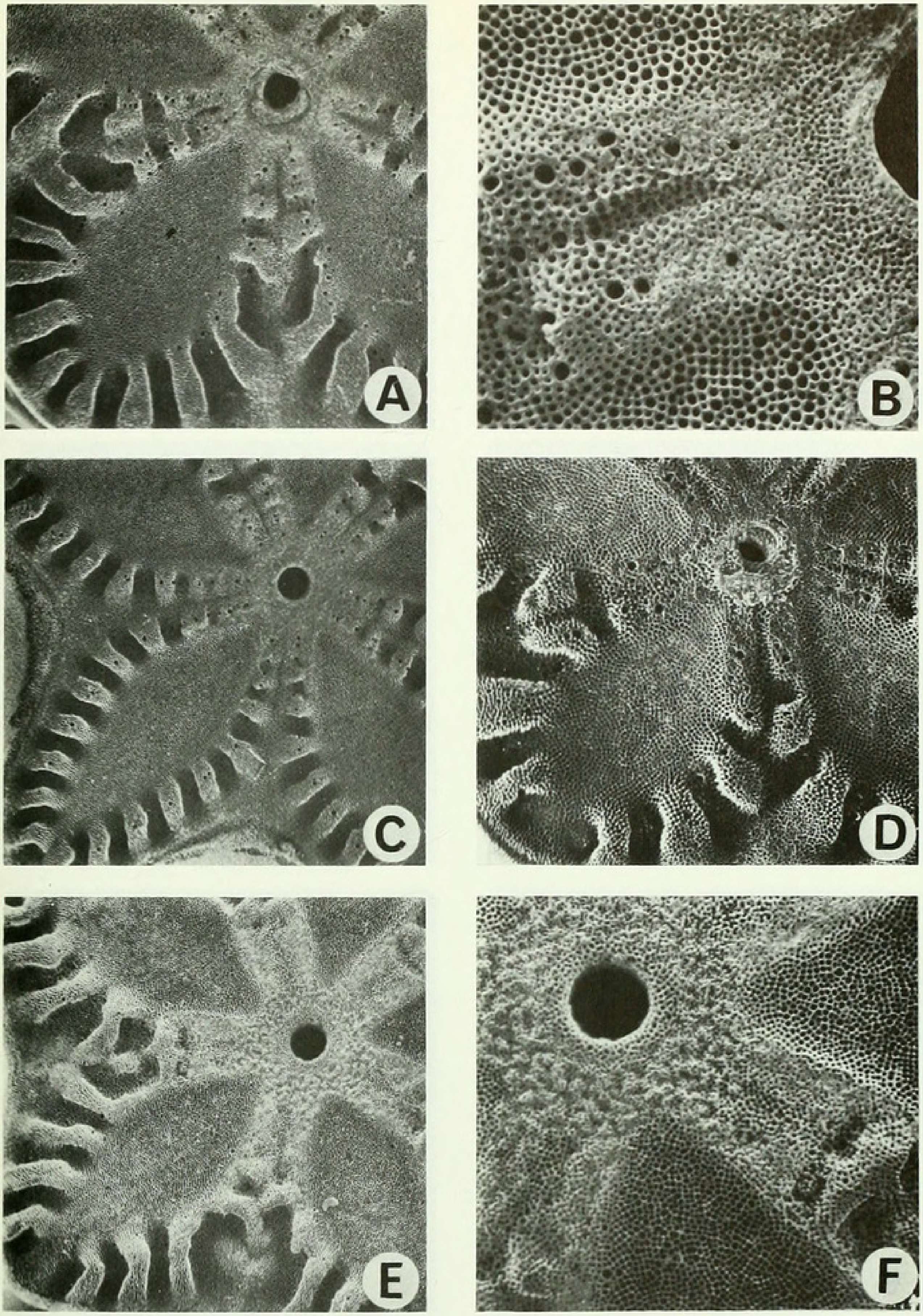

Fig. 3 Stereom of stem joints. (A) *Neocrinus decorus*, α-stereom of the crenularium in growth, showing the spiculata origin of the meshwork, $\times 750$; (B) *Metacrinus nobilis*, synostosial stereom, $\times 800$; (C) *Isselicrinus subbasaltiformis* from the Eocene London Clay, the α-stereom of symplexial areola with numerous large meshes, $\times 200$; (D) *Hypalocrinus naresianus*, α-stereom of symplexial areola with diamond-shaped meshes, $\times 800$; (E) *Metacrinus wyvillei*, α-stereom of symplexial areola with polygonal meshes, $\times 800$; (F) *Endoxocrinus parrae*, α-stereom of symplexial areola with round meshes, $\times 800$.

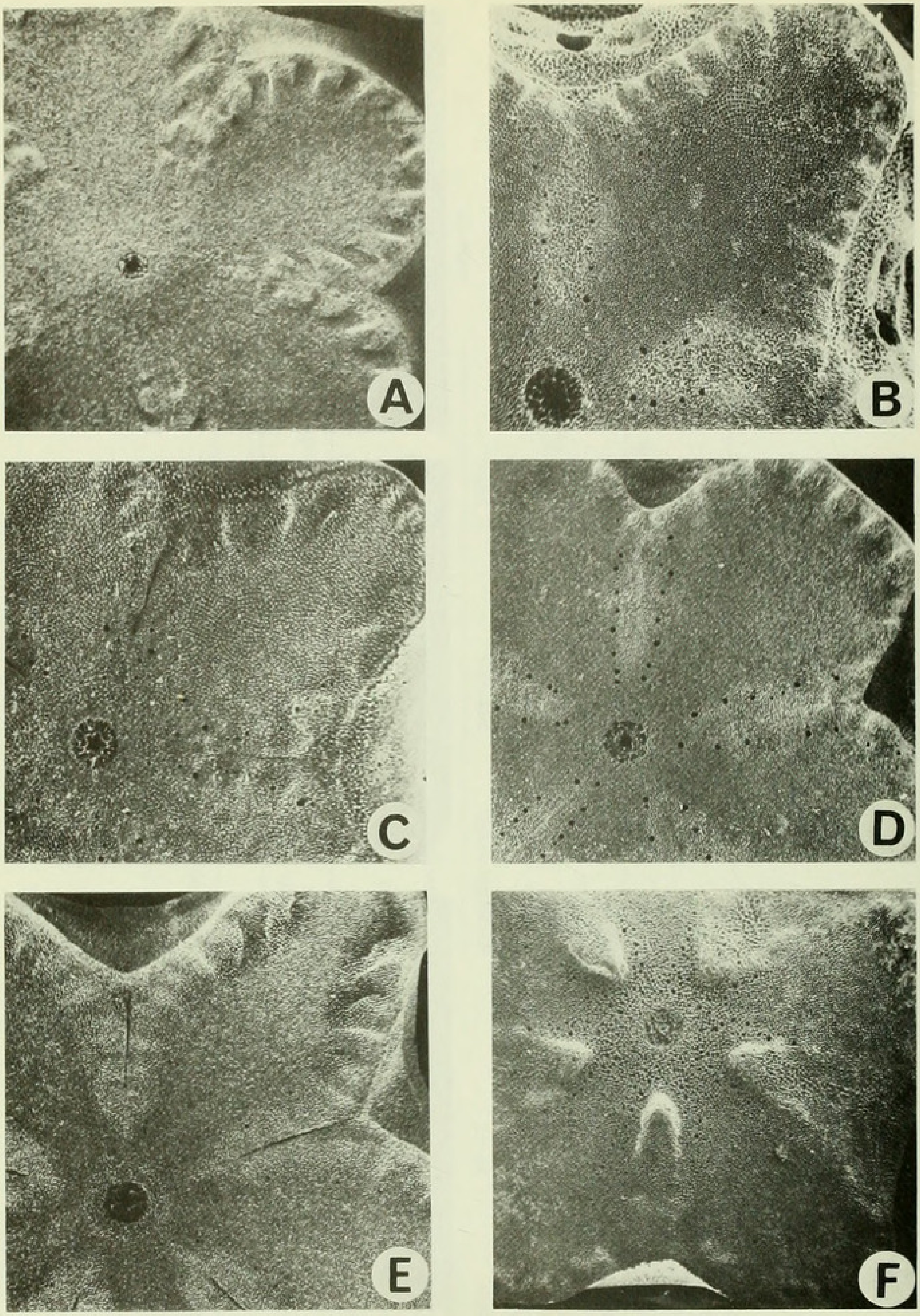

Fig. 4 Symplexial stem joints. (A) *Metacrinus rotundus*, × 18; (B) *Metacrinus rotundus*, inner crenularium with axial groove, × 125; (C) *Metacrinus angulatus*, × 18; (D) *Metacrinus wyvillei*, × 35; (E) *Cenocrinus asterius*, × 18; (F) *Cenocrinus asterius*, inner crenularium with closed axial groove and granulose perilumen, × 45.

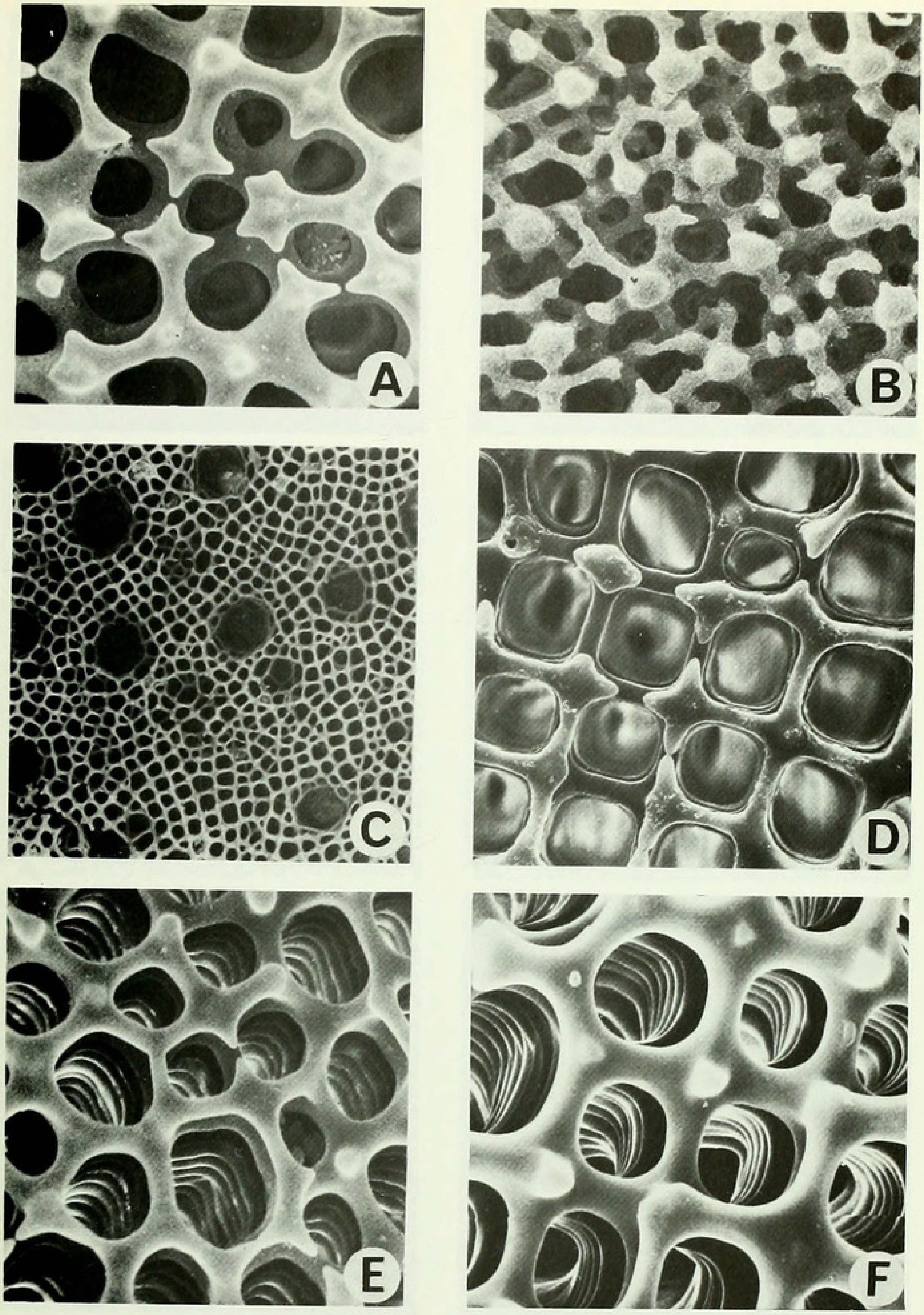

Fig. 5 Symplexial stem joints. (A) *Endoxocrinus parrae*, note the large axial groove of the interpetaloid zone, × 50; (B) *Neocrinus blakei*, × 40; (C) *Neocrinus decorus*, × 30; (D) *Hypalocrinus naresianus*, × 25; (E) *Teliocrinus springeri*, × 45; (F) *Diplocrinus alternicirrus*, × 15.

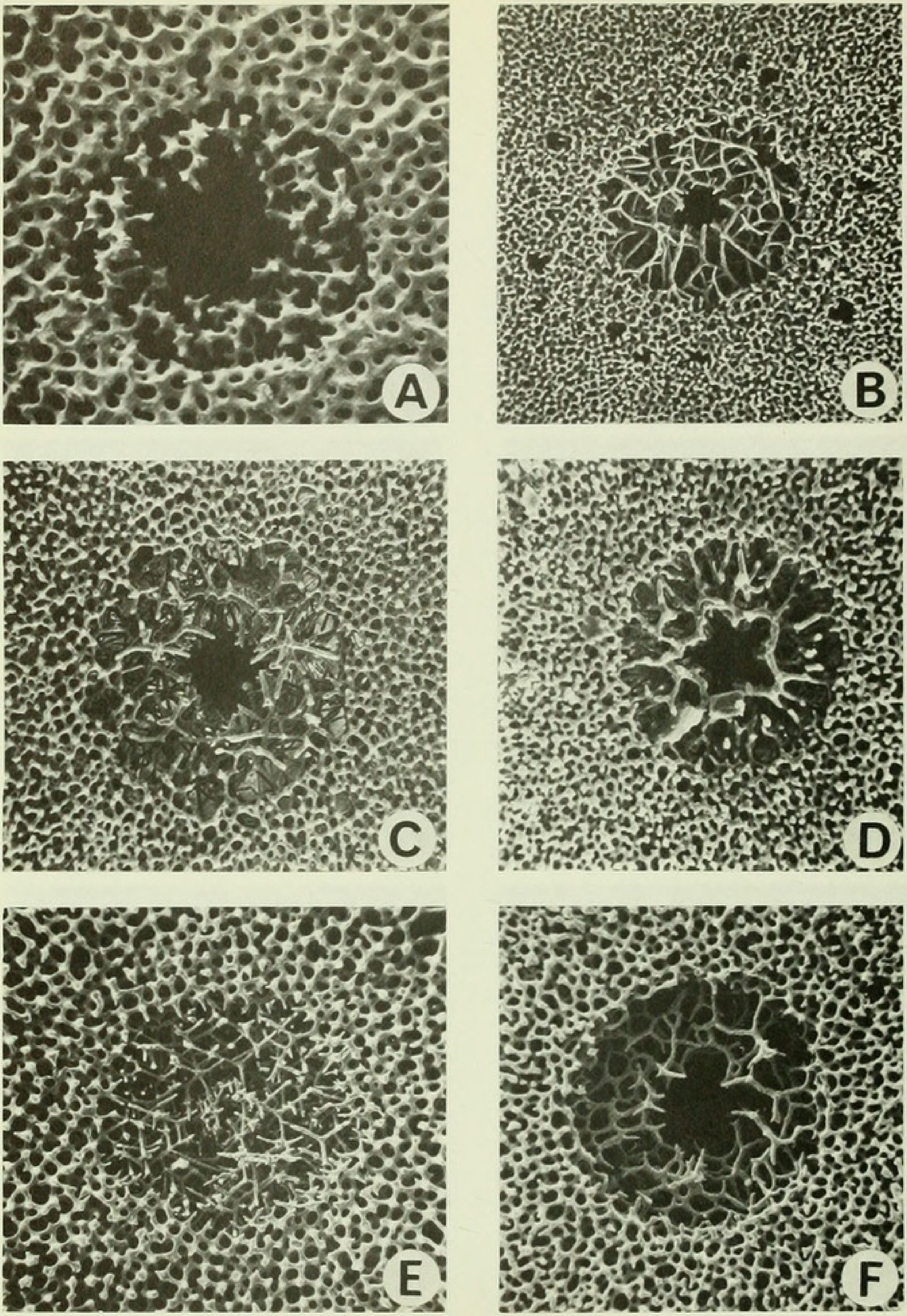

Fig. 6 Synostoses, general view. (A) *Cenocrinus asterius*, × 18; (B) *Neocrinus decorus*, × 35; (C) *Metacrinus wyvillei*, × 30; (D) *Hypalocrinus naresianus*, × 25; (E) *Teliocrinus springeri*, × 30; (F) *Diplocrinus alternicirrus*, radial symmorphy of interpetaloid zones, × 20.

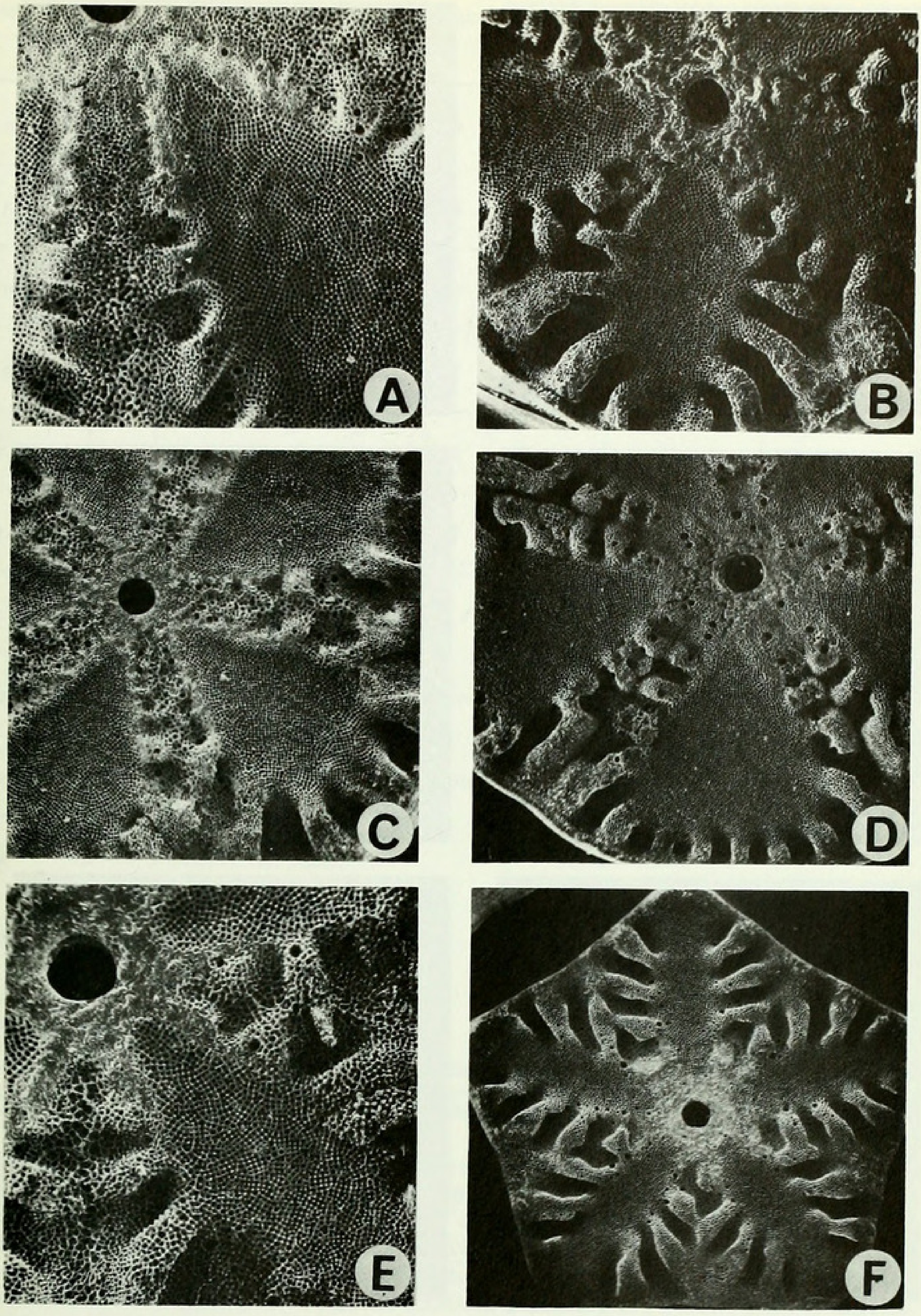

Fig. 7 Synostoses, crenularia and interpetaloid zones. (A) *Teliocrinus springeri*, crenularium with predominating synostosial stereom, × 80; (B) *Hypalocrinus naresianus*, crenularium with predominating syzygial stereom, × 80; (C) *Neocrinus blakei*, interpetaloid zone with predominating syzygial stereom, × 150; (D) *Metacrinus nobilis*, interpetaloid zone with an axial groove, × 150; (E) *Metacrinus angulatus*, interpetaloid zone, × 100; (F) *Diplocrinus alternicirrus*, symmorphial interpetaloid zones, × 50.

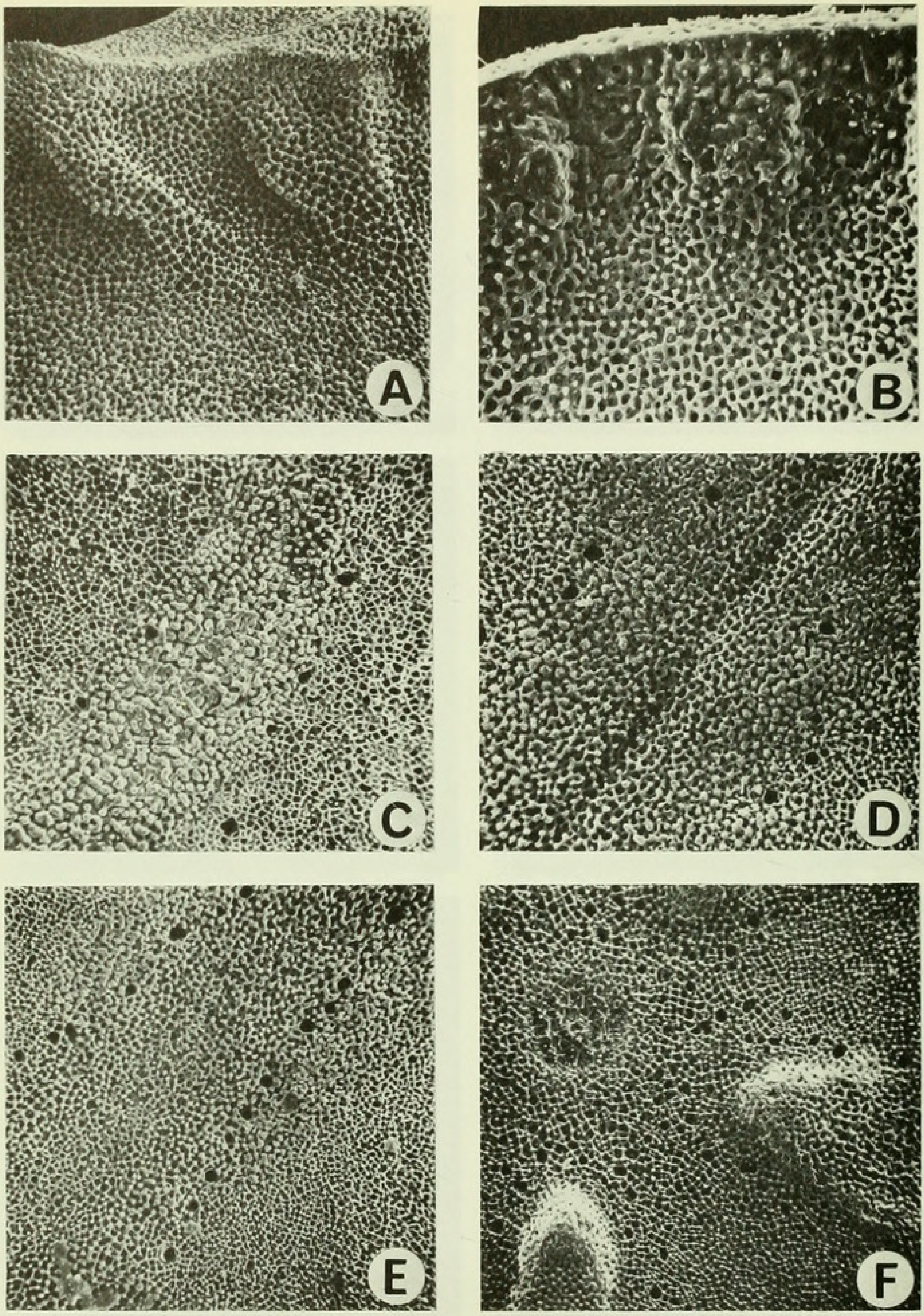

Fig. 8 Synostoses, axial canals. (A) *Cenocrinus asterius*, × 180; (B) *Metacrinus nobilis*, × 100; (C) *Hypalocrinus naresianus*, × 160; (D) *Metacrinus wyvillei*, × 150; (E) *Diplocrinus alternicirrus*, × 160; (F) *Teliocrinus springeri*, × 160.

Table 4 Characteristics common to different genera of Isocrinidae.

	H. n.	*N. d.*	*N. b.*	*A. w.*	*D. a.*	*T. s.*	*E. p.*	*C. a.*	*M. a.*	*M. w.*	*M. r.*	*M. n.*	
M. n.	0/1/3 **4**	0/0/2 **2**	0/0/1 **1**	1/2/3 **6**	1/1/3 **5**	1/3/5 **9**	1/3/5 **9**	2/1/4 **7**	3/3/7 **13**	3/4/5 **12**	3/5/7 **15**		*M. nobilis*
M. r.	0/1/3 **4**	0/0/2 **2**	0/0/0 **0**	1/2/2 **5**	1/1/2 **4**	1/3/4 **8**	1/3/5 **9**	2/1/4 **7**	3/3/7 **13**	3/4/4 **11**			*M. rotundus*
M. w.	0/1/1 **2**	0/0/1 **1**	0/0/1 **1**	1/1/2 **4**	1/0/2 **3**	1/3/3 **7**	1/4/3 **8**	2/1/6 **9**	3/4/5 **12**				*M. wyvillei*
M. a.	0/1/1 **2**	0/0/1 **1**	0/0/0 **0**	1/1/2 **4**	1/0/2 **3**	1/3/3 **7**	1/4/3 **8**	2/1/4 **7**					*M. angulatus*
C. a.	1/0/2 **3**	1/0/3 **4**	1/1/2 **4**	2/1/2 **5**	2/2/2 **6**	2/1/2 **5**	2/1/2 **5**						*C. asterius*
E. p.	1/2/1 **4**	1/1/2 **4**	1/0/1 **2**	2/1/3 **6**	2/0/3 **5**	2/2/3 **7**							*E. parrae*
T. s.	1/1/1 **3**	1/0/1 **2**	1/0/1 **2**	2/1/4 **7**	2/0/4 **6**								*T. springeri*
D. a.	1/2/1 **4**	1/2/1 **4**	1/2/2 **5**	3/4/6 **13**									*D. alternicirrus*
A. w.	1/1/1 **3**	1/1/1 **3**	1/1/2 **4**										*A. wyvillethomsoni*
N. b.	2/3/2 **7**	3/3/4 **10**											*N. blakei*
N. d.	2/4/2 **8**												*N. decorus*
H. n.													*H. naresianus*

At the left, detailed numbers of common characteristics, from the top to the bottom for each pair of species: arm, synostosis, symplexy. For synostoses and symplexies characteristics are as in Tables 2 and 3. For arms, they are: IBr 2 ax, division series beyond the first and IBr 2 biconvex shaped (*Neocrinus* and *Hypalocrinus*).

angulatus fall within *Saracrinus*. However, this view is not in accordance with many of the facts, notably the characters provided by the stalk joints.

(4) The main differences between *Metacrinus* and *Cenocrinus* are derived from the synostoses (though these are perhaps not of generic significance) and more importantly the position of the first axillary (at IBr 2 in *Cenocrinus*; beyond IBr 3 in *Metacrinus*). Besides the stalk synostoses, members of the two genera have evident affinities, especially *M. wyvillei* and *C. asterius*, the respective type-species.

(5) *Endoxocrinus* and *Teliocrinus* are clearly distinct genera.

(6) *Diplocrinus* and the monotypic *Annacrinus* possess more common characteristics than do *Metacrinus wyvillei* and the three other species of *Metacrinus* studied. *Annacrinus wyvillethomsoni* can be likened to a *Diplocrinus* adapted for life on mud substrates and is also geographically isolated. Accordingly, it seems best to reduce *Annacrinus* to the rank of a subgenus of *Diplocrinus*.

Key to the recent genera of Isocrinidae based on the morphology of the symplexial stalk joints

1	α-Stereom of areolae predominantly with polygonal or round meshes; transverse section of columnal with lanceolate areas of α-stereom	2
–	α-Stereom of areolae predominantly with diamond-shaped meshes; transverse section of columnal with triangular or pear-shaped areas of α-stereom	6
2	Inner part of the crenularium differentiated, outer end closed or slightly open . . .	3
–	Inner part of the crenularium undifferentiated	4
3	Axial groove always present on each interpetaloid zone	***Metacrinus***
–	Closed axial groove on each interpetaloid zone; perilumen granulose . . .	***Cenocrinus***
4	Outer end of the crenularium closed; areolae slightly pear-shaped; 12–14 crenulae to each petaloid zone; interpetaloid axial grooves present	***Endoxocrinus***
–	Outer end of the crenularium open; areolae always lanceolate	5
5	10 or more crenulae in each petaloid zone; interpetaloid axial grooves present .	***Teliocrinus***
–	Less than 8 crenulae in each petaloid zone; no interpetaloid axial grooves	***Diplocrinus*** (including ***Annacrinus***)
6	Less than 11 crenulae in each petaloid zone; areolae lanceolate or pear-shaped . . .	7
–	More than 11 crenulae in each petaloid zone; areolae triangular . . .	***Hypalocrinus***
7	Areolae lanceolate; crenularium slightly open; no interpetaloid axial grooves present	***Neocrinus* 1**
–	Areolae pear-shaped; crenularium closed; interpetaloid axial grooves present	***Neocrinus* 2**

Synostoses of the material examined

(From the collections of the British Museum (Natural History) unless specified.)

Genus *METACRINUS* (including *Saracrinus*)

Metacrinus rotundus Carpenter (Figs 4A, B, 9).
MATERIAL. Japan, B.M. reg. no. 1921.10.4.43–48.
SYNOSTOSES (Fig. 9). More than 40 large meshes in each petaloid zone: outer edge of the facet round: radial symmorphy.

Metacrinus nobilis Carpenter (Figs 3B, 7D, 8B, 10).
MATERIAL. Timor, 1932.12.25.3–5.
SYNOSTOSES (Fig. 10). 30–40 large meshes in each petaloid zone; a few large meshes around the axial canal, loose meshwork extending into the axial canal.

Metacrinus angulatus Carpenter (Figs 4C, 7E, 11).
MATERIAL. Kei Islands, *Challenger* st. 192, 85.3.30.15, para- or syntype.
SYNOSTOSES (Fig. 11). 25–30 large meshes in each petaloid zone; facet stellate, small crenulae at the tip of each petaloid zone, large meshes on a regular line between the petaloid zone and the interpetaloid zone.

Metacrinus wyvillei Carpenter (Figs 3E, 4D, 6C, 8D, 12).
MATERIAL. Kermadec Islands, *Challenger* st. 170A, 85.3.30.16, syntype.
SYNOSTOSES (Fig. 12). Less than 15 large meshes in each interpetaloid zone; secondary lumen stellate with sharp outlines of calcite.

Genus *CENOCRINUS*

Cenocrinus asterius (Linnaeus) (Figs 4E, F, 6A, 8A, 13).
MATERIAL. Saba Island, West Indies, 84.6.20.1.
SYNOSTOSES (Fig. 13). Large meshes of very irregular width, synostosial areola pear-shaped; thick and irregular spicules extending into the axial canal; secondary lumen large.

Genus *ENDOXOCRINUS*

Endoxocrinus parrae (Gervais) (Figs 3F, 5A, 14).
MATERIAL. No details, probably West Indies.
SYNOSTOSES (Fig. 14). 25–30 irregular large meshes in each petaloid zone; dense meshwork extending into the axial canal.

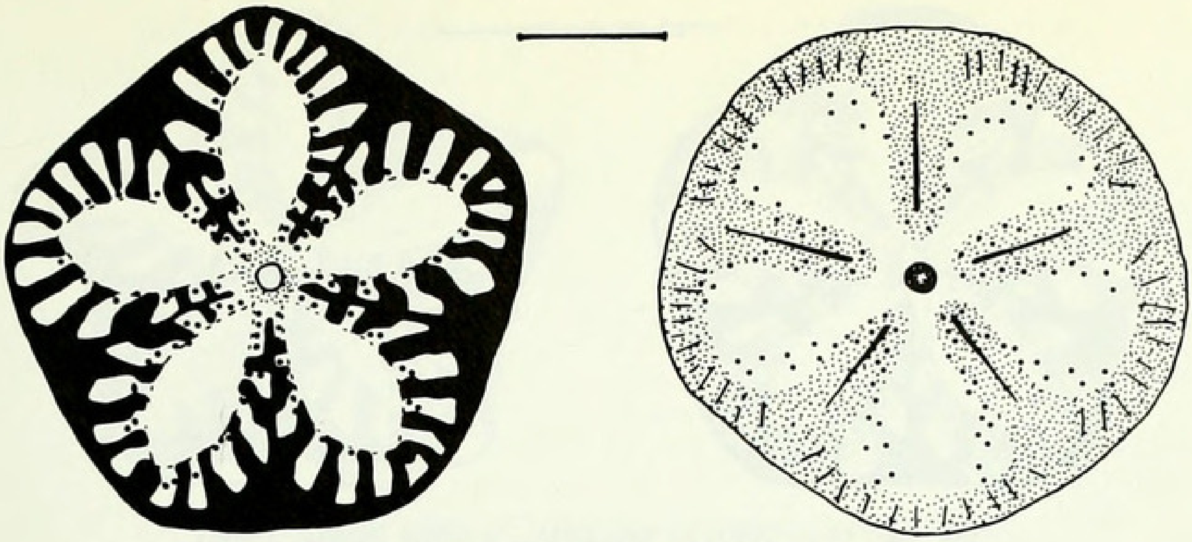

Fig. 9 Stem joints of *Metacrinus rotundus*. (Scale: 2 mm)

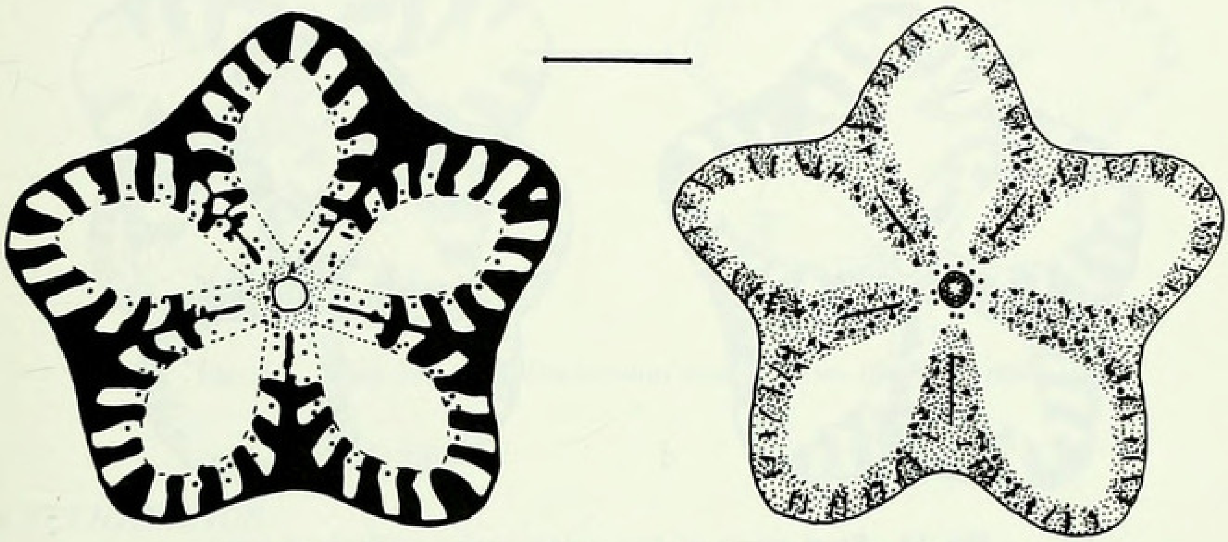

Fig. 10 Stem joints of *Metacrinus nobilis*. (Scale: 2 mm)

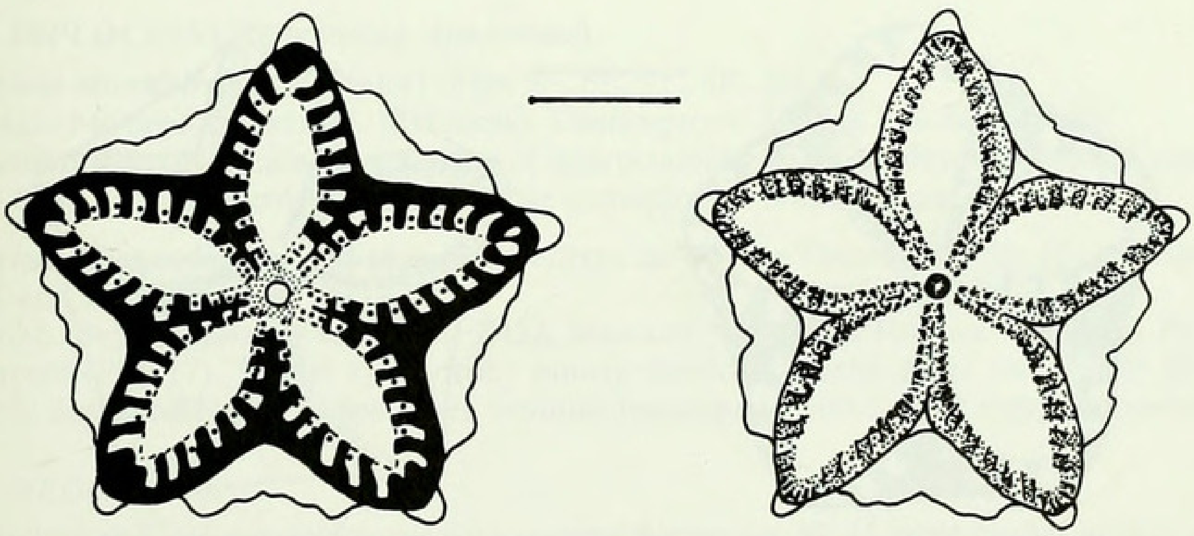

Fig. 11 Stem joints of *Metacrinus angulatus*. (Scale: 2 mm)

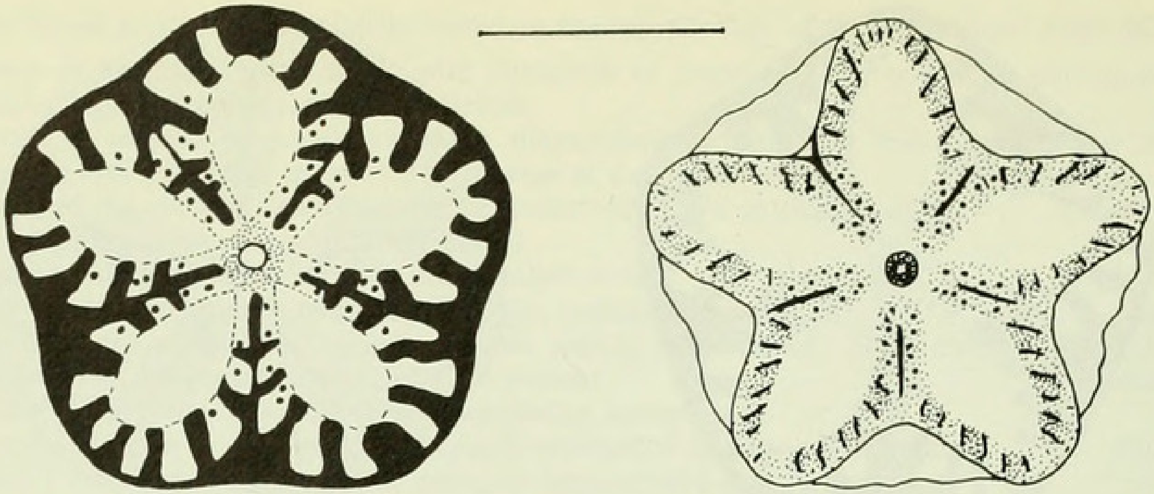

Fig. 12 Stem joints of *Metacrinus wyvillei*. (Scale: 2 mm)

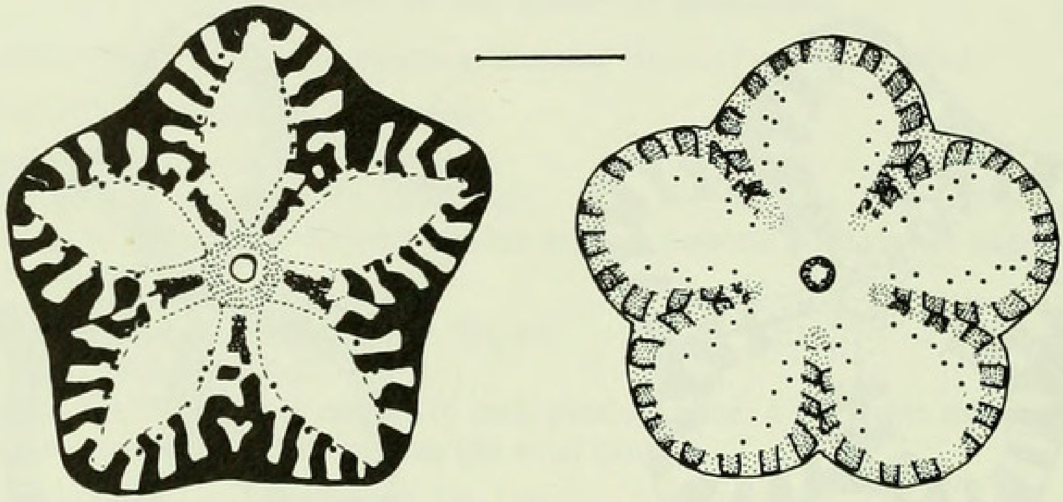

Fig. 13 Stem joints of *Cenocrinus asterius*. (Scale: 2 mm)

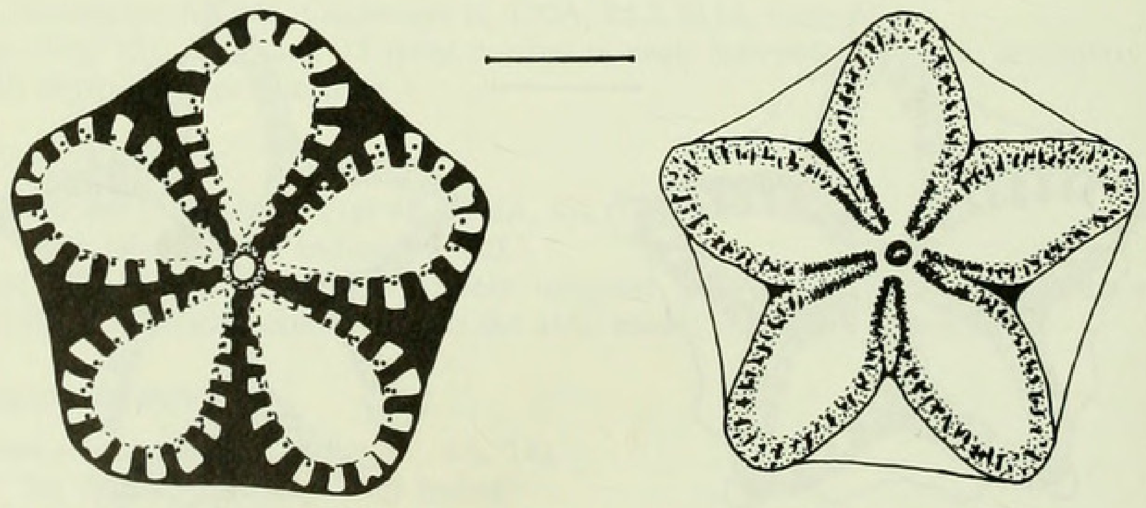

Fig. 14 Stem joints of *Endoxocrinus parrae*. (Scale: 2 mm)

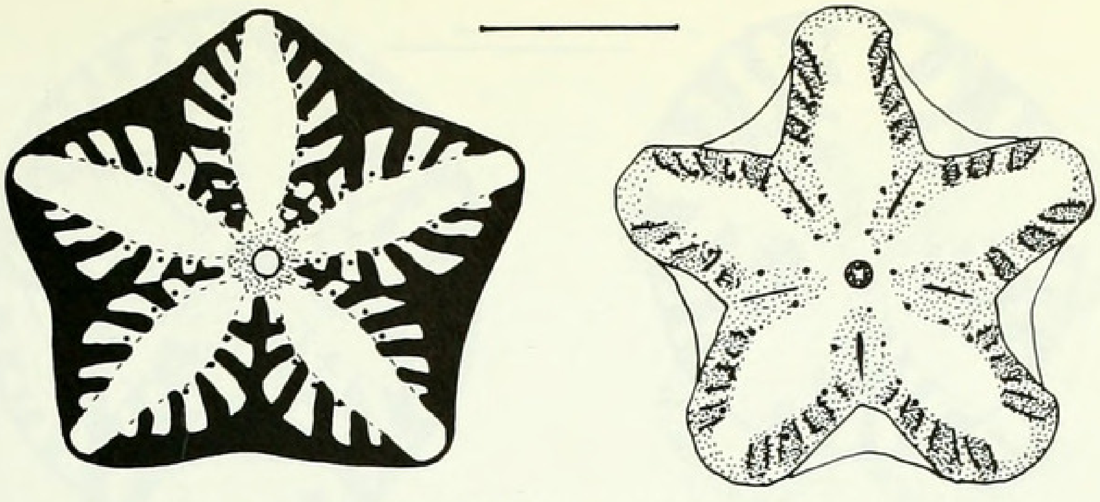

Fig. 15 Stem joints of *Teliocrinus springeri*. (Scale: 2 mm)

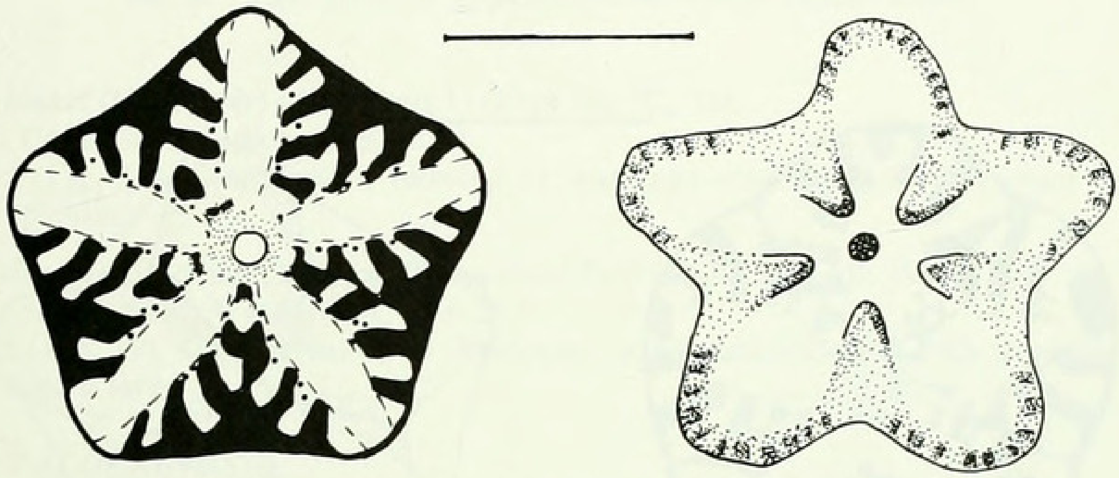

Fig. 16 Stem joints of *Diplocrinus alternicirrus*. (Scale: 2 mm)

Genus *TELIOCRINUS*

Teliocrinus springeri (Clark) (Figs 5E, 6E, 7A, 8F, 15).
MATERIAL. Madras, 1932.12.25.2.
SYNOSTOSES (Fig. 15). 10 or less large meshes in each petaloid zone: general symmorphy well developed.

Genus *DIPLOCRINUS* (including *Annacrinus*)

Diplocrinus alternicirrus (Carpenter) (Figs 5F, 6F, 7F, 8E, 16).
MATERIAL. Meangis Islands (N. Moluccas), *Challenger* st. 214, 85.3.30.22, syntype.
SYNOSTOSES (Fig. 16). Radial symmorphy of interpetaloid zones well developed; axial canal completely filled by thin spicules; small crenulae consisting of thick syzygial β-stereom.

Diplocrinus* (*Annacrinus*) *wyvillethomsoni (Jeffreys *in* Wyville Thomson) (Fig. 17; see also Roux, 1971 and 1974).
MATERIAL. Bay of Biscay, *Thalassa* st. Z452, Muséum National d'Histoire Naturelle, Paris.
SYNOSTOSES (Fig. 17). Radial symmorphy poorly developed; axial canal completely filled with relatively dense meshwork, a few outer crenulae rectangular with a thick syzygial stereom.

Genus *NEOCRINUS*

Crenularium and interpetaloid zones with syzygial β-stereom, 10–15 large meshes in each petaloid zone of synostoses.

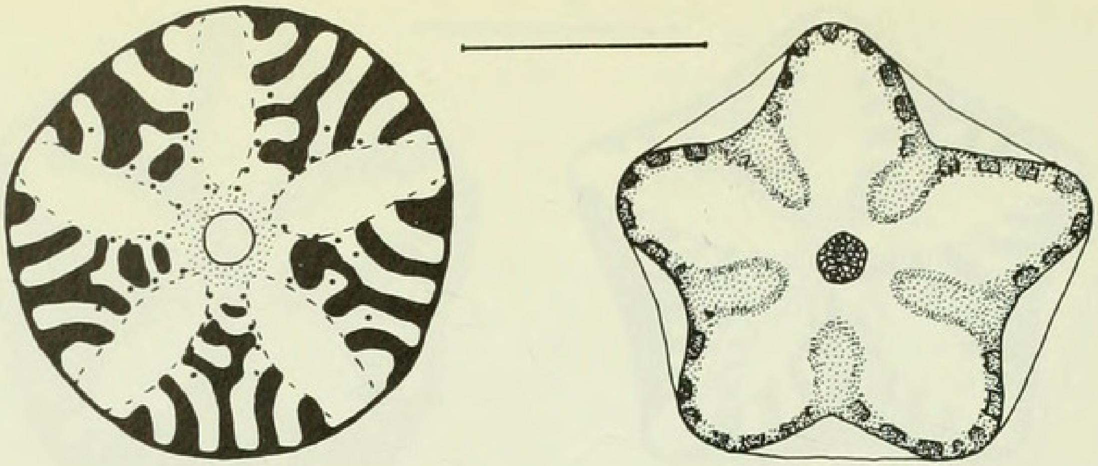

Fig. 17 Stem joints of *Diplocrinus* (*Annacrinus*) *wyvillethomsoni*. (Scale: 2 mm)

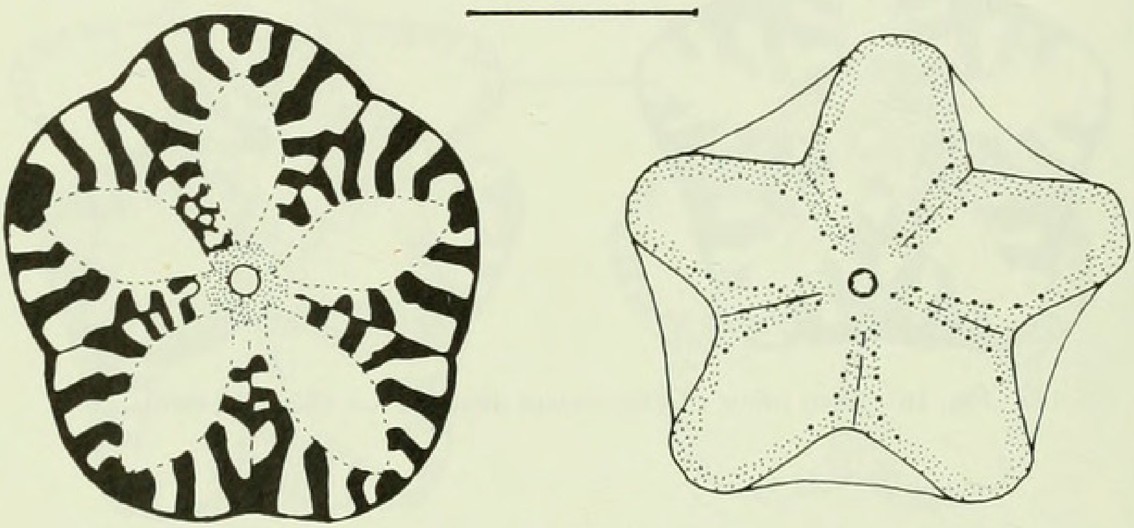

Fig. 18 Stem joints of *Neocrinus blakei*. (Scale: 1 mm)

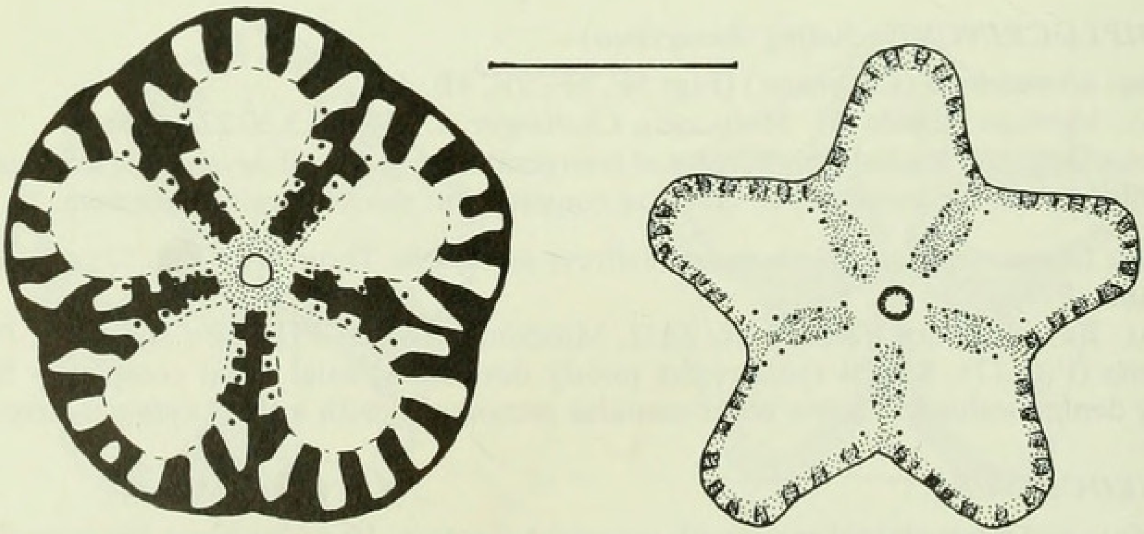

Fig. 19 Stem joints of *Neocrinus decorus*. (Scale: 2 mm)

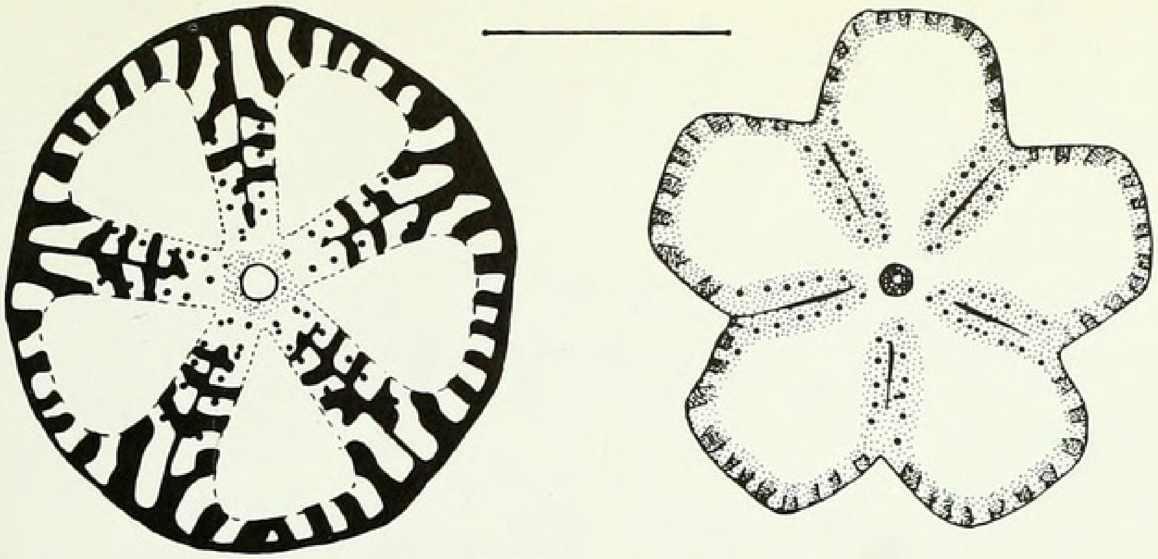

Fig. 20 Stem joints of *Hypalocrinus naresianus*. (Scale: 2 mm)

Neocrinus blakei (Carpenter) (*Neocrinus* 1) (Figs 5B, 7C, 18).
MATERIAL. Cuba, West Indies, 1939.6.15.1.
SYNOSTOSES (Fig. 18). Crenularium reduced or wanting; axial canal largely open with a few secondary spicules.

Neocrinus decorus (Wyville Thomson) (*Neocrinus* 2) (Figs 3A, 5C, 6B, 19).
MATERIAL. Saba Island, West Indies, 84.6.20.5.
SYNOSTOSES (Fig. 19). Crenularium well developed; axial canal filled in with irregular spicules; secondary lumen large.

Genus ***HYPALOCRINUS***
(Main characters like *Neocrinus*)

Hypalocrinus naresianus (Carpenter) (Figs 3D, 5D, 6D, 7B, 8C, 20).
MATERIAL. Timor, 1916.6.20.6.
SYNOSTOSES (Fig. 20). Crenularium well developed; axial canal filled in with dense spicules; secondary lumen small.

Conclusions

The characters of the stalk joints of the Isocrinidae are of taxonomic significance. The symplexial articulations indicate relationships between species belonging to the same genus, or affinities between different genera, independent of variations in external morphology. This conclusion is very useful for the study of comparative morphology of both recent and fossil genera. According to the characteristics shown by the stalk, it is likely that *Hypalocrinus naresianus* could be regarded as a recent representative of the mesozoic genus *Balanocrinus*, the crown of which is so far unknown. However, the converse presence of the fossil genus *Isocrinus* in the recent fauna is not supported by the present evidence. This problem will be reviewed later. More detailed studies are necessary to confirm differences or affinities between the various taxa of the Isocrinidae. I plan next to observe the facet ontogeny from proximal to distal in the stalk and from young to senile specimens and to relate the results to similar studies on the joints of division series and arms.

Finally a new classification suggested by the stalk joint characteristics is given below.

Family **ISOCRINIDAE**
Subfamily I
genus ***Metacrinus*** (*sensu* Carpenter)
type-species: *M. wyvillei*

genus ***Cenocrinus***
type-species: *C. asterius*
genus ***Teliocrinus***
type-species: *T. springeri*
genus ***Endoxocrinus***
type-species: *E. parrae*
genus ***Diplocrinus***
subgenus ***Diplocrinus*** (*Diplocrinus*)
type-species: *D.* (*Diplocrinus*) *maclearanus*
subgenus ***Diplocrinus*** (*Annacrinus*)
type-species: *D.* (*Annacrinus*) *wyvillethomsoni*

Subfamily II
genus ***Hypalocrinus***
type-species: *H. naresianus*
genus ***Neocrinus* 1** (not synonym of fossil *Isocrinus*)
type-species: *N. blakei*
genus ***Neocrinus* 2** (*Neocrinus sensu* Rasmussen)
type-species: *N. decorus*

New names are not given for subfamilies I and II or for *Neocrinus* 1 and 2 because the diagnoses should include detailed studies of arm joints.

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