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The Phylogeny of Sea-Stars

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THE PHYLOGENY OF SEA-STARS

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[Plates 50 and 51]

CONTENTS

(1) The rod-shaped skeletal virgalia of lower Palaeozoic somasteroids are homologues of the major skeletal elements of modern asteroids and ophiuroids.

(2) The major skeletal elements of asteroids differentiate along growth gradients which show progressive alterations in strength and direction, such that the various families can be arranged in a sequence. Soft structures differentiate in a similar manner, and yield a similar sequence. Fossil evidence indicates the older end of the sequence, which can accordingly be oriented chronologically.

(3) On this basis, the Luidiidae prove to be the most archaic surviving asteroids; they are referable to the order Platyasterida, hitherto known only from lower and middle Palaeozoic fossils. Thus the soft-part characters of the Platyasterida can now be determined, and the relationship of the order to other orders of asteroids is clarified.

(4) Growth gradient patterns show that Luidiidae probably arose from somasteroids, by a series of changes which can be specified. The extant asterozoan *Platasterias* occupies an early position in the inferred sequence, and detailed study confirms its archaic structure, showing it to be a somasteroid, though one clearly related to luidiid asteroids.

(5) It is established that the earliest asteroids had:

(*a*) Dominant *transverse growth gradients in the arm, the entry of dominant longitudinal* growth gradients being a post-platanasterid change.

(*b*) No anus, and no intestine, these structures being of post-luidiid origin, at the astropectinid grade of evolution.

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(*c*) Non-suctorial tube-feet, the development of suckers being a post-astropectinid change.

(*d*) Small, double ampullae, inherited from a pre-asteroid ancestry (identified with platasteriid somasteroids). Subsequent enlargement of the ampullae coincided with the permanent invagination of the ambulacral furrow, which occurred at the platyasterid grade of evolution, with simultaneous enlargement of the tube-feet. The single ampullae of Porcellanasteridae are thus a specialized simplification of formerly double ampullae and, being of post-luidiid origin, cannot be primitive.

(*e*) A marginal madreporite (i.e. at the edge of the disk).

(6) The mode of origin of ophiuroids from lower Palaeozoic somasteroids is deduced by methods similar to those used for finding the origin of asteroids. These predict the existence of ophiuroids with pinnate skeletal structure. Dissection confirms this, and both living and extinct ophiuroids are found to have skeletal elements homologous with virgalia. Examples are illustrated.

(7) Pinnate skeletal structure is shown to be fundamental in all asterozoans, since it occurs in all somasteroids, and has been inherited from somasteroids by both asteroids and ophiuroids.

(8) When the soft structures of ophiuroids are correlated with skeletal structures, the following inferences emerge:

(*a*) Gastric caeca must originally have extended into the arm in ophiuroids, because this is true of the surviving somasteroid *Platasterias*, and is also true of asteroids.

(*b*) The gonads must have originally been confined to the arms, arranged in approximately paired sequence along either side of the dorsal coelomic canal, because this condition is found to be primitive in other asterozoans.

Since these conditions are fulfilled in the extant genus *Ophiocanops*, this ophiuroid came under suspicion as an archaic form. Dissection of its endoskeleton confirmed its archaic character, for it agrees in all major features with the zeugophiurine Oegophiurida, hitherto thought to have become extinct in the upper Carboniferous. *Ophiocanops* is accordingly recognized as a surviving member of the Oegophiurida, and its distinctive soft-part characters may now be attributed to that order. There are no bursae, no genital plates, no dorsal or ventral arm-plates, no oral shields, no radial shields, and the madreporite is marginal.

(9) The foregoing data show which characters of asteroids and ophiuroids are ancient, and which are late, secondary features evolved after the differentiation of these two subclasses from their common somasteroid ancestry. The two categories of characters are listed.

(10) Of the characters found to be ancient, all are shared with pinnulate Pelmatozoa, and have no near parallel in any other group of echinoderms. The embryonic structure of the asterozoan disk closely matches that of the crinoid calyx; it includes a centrodorsal plate, five basals, five radials, and sometimes also five infra-basals.

(11) Somasteroids show transitional characters between other asterozoans and some pinnulate pelmatozoan stock, which must have resembled biserial crinoids. The somasteroid virgalia are considered to be homologues of crinoid pinnular ossicles, both being essentially rod-shaped elements, produced in similar pinnate growth gradients, and bearing a double row of cover-plates on the adoral surface. But whereas the cover-plates of crinoids border a food-groove placed on the pinnule itself, in the somasteroids the cover-plates are normally folded outwards, so as to guard a food-groove between the pinnule-like structures (metapinnules), between which an interpinnular integument has also developed. In the extant somasteroid *Platasterias* the cover-plates are erectile, and in the erect condition closely simulate those of crinoids, forming a double series along the adoral surface of each metapinnule.

(12) Since somasteroids are themselves antecedent to other asterozoans, it follows that all star-shaped echinoderms (Asterozoa) constitute a single phylogenetic stock, unrelated to any other echinoderms save pinnulate pelmatozoans.

(13) Embryological data suggest that asterozoans evolved from a pentacrinoid stage of development of some pinnulate pelmatozoan, as a consequence of a dislocation of the main radial growth gradient at the junction of the radial calycinal plate and the first brachial ossicle. The dislocation was such that the first brachial ossicles were deflected adorally. Comparative anatomy shows that subsequent dislocations of the transverse (i.e. pinnular) growth gradients caused the second virgalium in each metapinnule to be ejected from the growth axis to which it belonged, to become the occluded superambulacral ossicle; in post-astropectinid asteroids this occluded ossicle usually is aborted, and it is unknown at present in any ophiuroid. In the final phases of evolution in both

asteroids and ophiuroids the dislocations of transverse axes are so severe as to result in their complete disintegration, the ossicles now falling under the control of dominant longitudinal gradients.

(14) Crinoids are the only Pelmatozoa which show structure comparable to that of Asterozoa. Their characters can be segregated into two groups, namely (*a*) those which are shared with somasteroids, and (*b*) those which are shared with other, more generalized and archaic pelmatozoans, such as eocrinoids or cystoids. Crinoids can therefore be considered as late pelmatozoans which have:

(i) retained the original meridional patterns of growth in the calyx, as an inheritance from earlier pelmatozoans, and

(ii) acquired in addition five radially directed, divergent axes of growth in the horizontal plane, leading to the outgrowth of arms and, later on, to the secondary acquisition of pinnules.

Somasteroids would then be a further term in this progression, in which the first character is diminished, and the second exploited. All Asterozoa would therefore be derived (through somasteroids) from crinoids, or some crinoid-like group of Pelmatozoa.

(15) In sharp contrast, the growth gradients of the echinozoan echinoderms (i.e. Echinoidea, Holothuroidea, and probably also Ophiocistiodea) are comparable only with those of ancient, pre-crinoid pelmatozoans. All these have either meridional, or quite disordered, growth gradients. None has radial divergent components. The Echinozoa are accordingly viewed as archaic derivatives of a still more ancient globoid pelmatozoan stock.

(16) The conventional association of the Echinozoa with the Asterozoa, under one head, namely the subphylum Eleutherozoa, is now unacceptable. The characters attributed to the Eleutherozoa are in reality shared only by demonstrably late groups of Asterozoa, and demonstrably early groups of Echinozoa. The subphylum Eleutherozoa is polyphyletic, and must be abandoned as a formal unit of classification. Instead, two subphyla, Asterozoa and Echinozoa, are indicated.

(17) Auricularia and pluteus larval stages of those echinoderms known to possess them cannot reflect broad phylogenetic relationships, because they imply a closer relationship between ophiuroids and echinoids, than between ophiuroids and asteroids, and this is demonstrably false. Such larvae must therefore have arisen as secondary phases of development, presumably as responses to the demands of planktonic life during temporary food-gathering stages of development.

Introduction

The Asterozoa, or star-shaped echinoderms, may be regarded as a natural taxon, comprising the somasteroids, asteroids and ophiuroids. This view, supported by Spencer (1951), is based on fossil evidence which is now so abundant and so detailed as to permit no alternative arrangement of these groups. However, their structure differs so widely from that found in other echinoderms that the origin of the Asterozoa has long presented 'a mystery which none has yet been able to penetrate' (Ubaghs 1953).

In this memoir a possible solution is derived through the analysis of the arrangement of the skeletal elements in fossils and living forms, correlated with the evidence of soft structures. The method leads to the recognition of surviving members of archaic groups hitherto known only from Palaeozoic fossils. Their incorrect classification until now was due to the fact that fossils had been described from only the endoskeleton, whereas living asterozoans have been classified mainly on the external features. The study is the sequel to an earlier analytical critique in which it was argued that phylogenetic inferences based on larval forms of echinoderms were at complete variance with those suggested by fossils (Fell 1948). Although morphological data were assembled for some 12 years, no significant advance was made until recently, when it was possible to make the major inference that *Platasterias* (a rare west American asterozoan) exhibits growth gradients identical with those of Ordovician somasteroids. When material was obtained, dissection showed that

Platasterias is in fact a surviving somasteroid (Fell 1962, 1962*a*), though clearly related to luidiid asteroids. Armed by new evidence yielded by *Platasterias*, it was possible to review the previous work, and to develop a theoretical treatment, here set out. It permits the

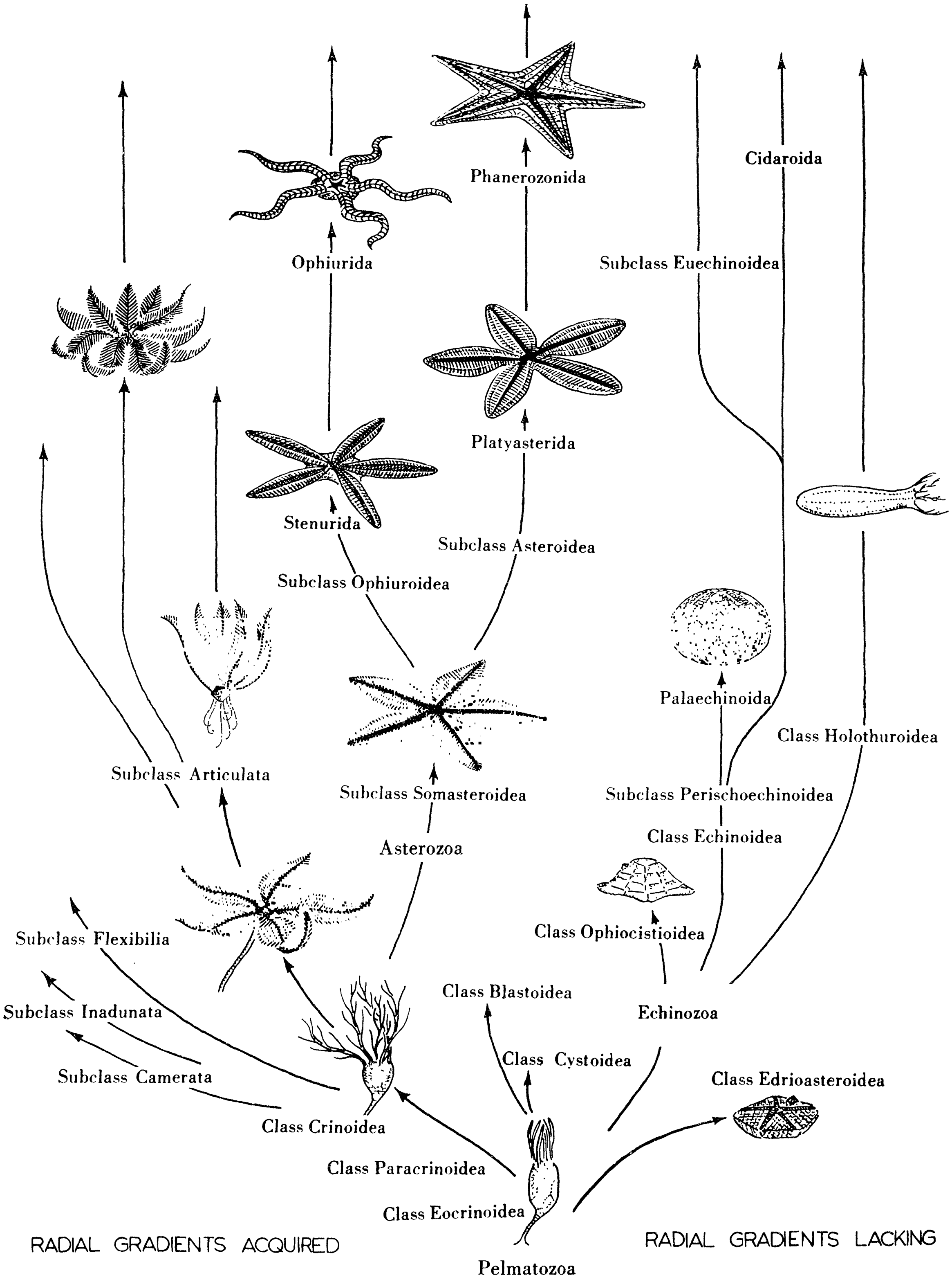

FIGURE 1. Inferred phylogenetic relationships of asterozoan and echinozoan echinoderms.

recognition of other surviving members of supposedly extinct groups, and also implies that sea-stars are more nearly related to sea-lilies than they are to sea-urchins and holothurians. These conclusions, which cut across the conventional classification of echinoderms, are interpreted in figure 1. The diagram does not claim to present established facts, but does give a general picture of the kind of interrelationships suggested by morphology.

Chronology

The geological record, as at present known, is too incomplete for exact dating of the inferred differentiations. On the one hand it implies the extinction of groups at horizons above which fossils are not recorded, yet living representatives have been found; on the other, it implies explosive differentiations at horizons below which earlier phases are still unknown. Consequently, most of the 'ages' here assigned to taxa, or to morphological changes, are based on the primary evidence itself, and expressed by terms such as pre-asteroid, post-stenurid, post-astropectinid, etc.

ORIGIN OF THE ASTEROIDEA

Since Spencer (1951) first distinguished the Somasteroidea as a separate subclass of the Asterozoa, it has been generally recognized by palaeontologists that the Asteroidea must have arisen from these ancient forms (Ubaghs 1953; Fell 1959, 1960, 1960*b*; Moore 1960). Spencer himself pointed to *Archegonaster* as a possible intermediate form, which suggested how virgalia may have been transformed into adambulacral and marginal (inferomarginal) plates of asteroids. Details of the successive morphological changes implied by this theory have remained obscure, however, because the origin of the asteroid buccal apparatus was incompletely known, and *Archegonaster* is comparable more with specialized phanerozonid asteroids, such as the Goniasteridea, whereas it seemed improbable that such forms could have been the first asteroids.

It has been generally agreed that the more primitive extant asteroids are the three families in which the tube-feet lack suckers. There has, however, been no agreement as to which of these groups might be the oldest, though the Astropectinidae are usually so regarded. The other two families, namely Luidiidae and Porcellanasteridae, are evidently related to Astropectinidae, sharing numerous characters not found in other asteroids.

Dissections showed that some astropectinid genera, such as *Proserpinaster* (figure 2*A*, *C*), and some luidiids, have highly distinctive elongate, rod-shaped superambulacral ossicles, rather forcibly recalling the intermediate virgalia of *Archegonaster* (illustrated by Spencer 1951, p. 102, Figure 9). Assuming that they might possibly represent virgalia, I tentatively eliminated the porcellanasterids from the supposed primitive assemblage, for such ossicles do not occur in that family. As afterwards appeared, this step would in any case have followed at the next isolation, for the growth gradients of porcellanasterids are demonstrably secondary. Parenthetically, it may be noted here that before the significance of the growth gradients was appreciated, an attempt was made to treat the porcellanasterids as primitive, on the grounds that in this family the ampulla of the tube-foot is simple, whereas in all others it is double; the attempt led nowhere, and the reason for its failure became apparent when small, but double, ampullae were found in *Platasterias*, showing that a double ampulla had already developed in late somasteroids, and must have been acquired from them by the first asteroids. Thus the simple ampulla of porcellanasterids must be a secondary simplification.

Having discarded the porcellanasterids, work was now restricted to Luidiidae and Astropectinidae. A study of the arrangement of the skeletal ossicles, and other structures, showed that Astropectinidae exhibit the same growth gradients as do other asteroids, whereas the Luidiidae differed from all other asteroids, and resembled somasteroids and ophiuroids. This means that Luidiidae can be set apart from the other families of Asteroidea, and their distinctive character is one shared with the other two subclasses of Asterozoa, obviously significant evidence of their generalized nature. Accordingly, the Astropectinidae could now be discarded, and closer attention paid to the luidiid genera.

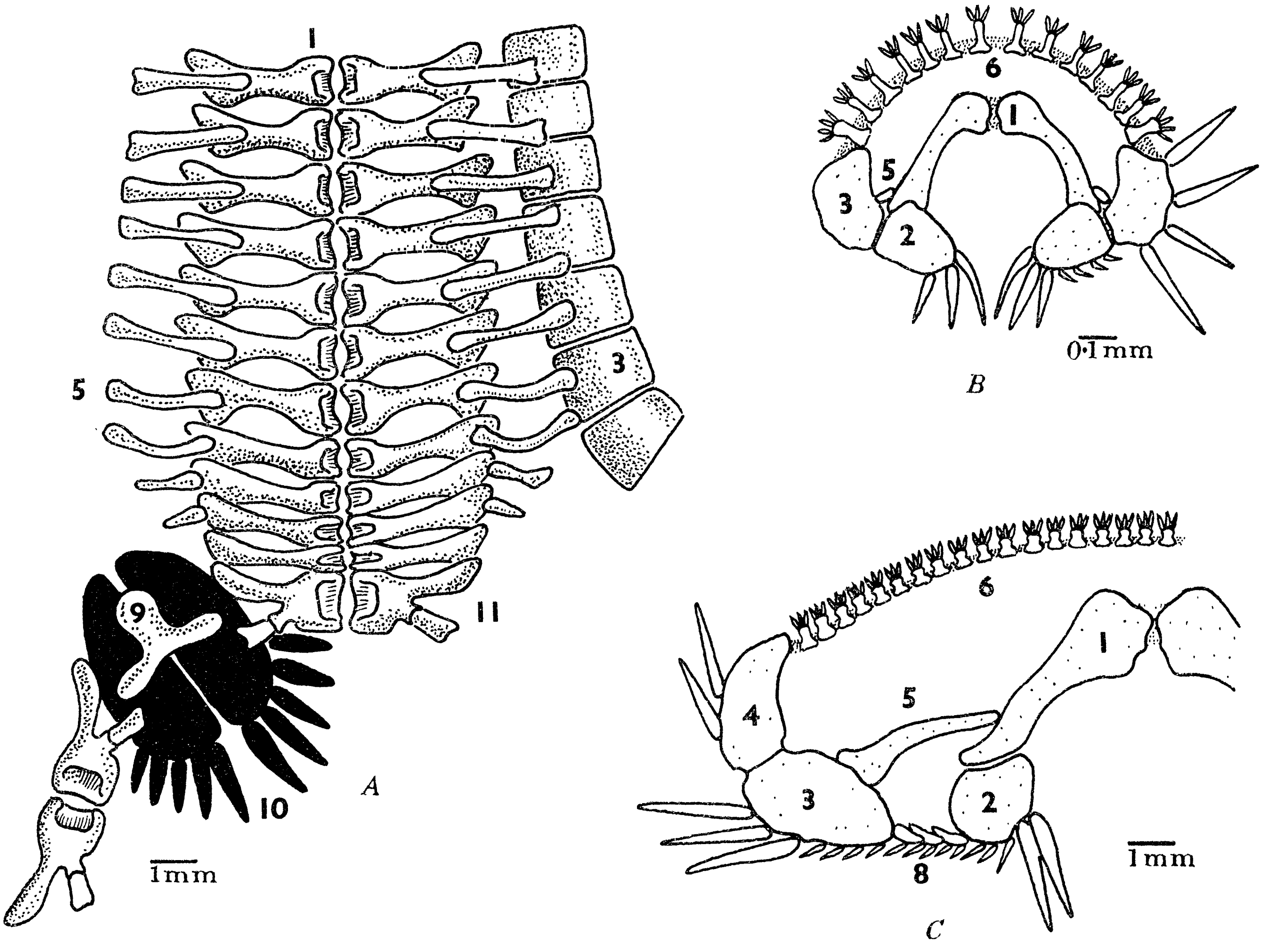

FIGURE 2. *A*, *Proserpinaster neozelanicus* (Mrtsn.) (×6) aboral (internal) aspect of ventral arm-skeleton, the actinal intermediate plates omitted. *B*, *Luidia neozelanica* Mrtsn. (×45) transverse section of extreme arm-tip, showing embryonic features. *C*, *Proserpinaster neozelanicus* (Mrtsn.) (×6) transverse section of mid-arm. 1, amb-ossicle; 2, adambulacral plate; 3, inferomarginal plate; 4, superomarginal plate; 5, superambulacral ossicle; 6, aboral body-wall; 7, inferomarginal spines; 8, actinal intermediate plates; 9, T-shaped internal jaw-plate; 10, oral plates and oral spines; 11, compound (double) amb-ossicle, shown later in this paper to comprise nos. 2 and 3, amb-1 being incorporated into the angle-plate.

Here it is appropriate to define the growth gradients observed in asterozoans, and the fields produced by their interaction.

Morphology and embryology both point to the existence of two intersecting systems of growth gradients in the post-embryonic stages. The two systems combine in three different ways, according to their respective strengths and relative directions. The three fields so produced are illustrated diagrammatically in figure 3. But, before discussing the fields, we must consider the two gradient systems separately.

One system comprises parallel (or weakly convergent) linear gradients, which run longitudinally along the arm, following the radius itself (in the case of the main axial gradient), or a parallel adradial course (in the cases of the subsidiary lateral gradients). These gradients cause the major skeletal elements to differentiate in longitudinal rows, along which homologous elements are serially repeated (figure 3*C*). The main radial gradient differentiates the ambulacral ossicles, as well as such soft structures as the radial nerve ganglia, the radial water-vessel and its appendages. The gradient immediately adjacent to the midline differentiates a similar series of adambulacral plates. If superambulacral ossicles are present, they are differentiated along an occluded lateral gradient (i.e. one that is deflected upwards, so as to lie at a higher level within the arm, and not externally visible). The next more marginal gradient differentiates the innermost longitudinal series of actinal intermediate plates; there may be other, weaker gradients producing other rows of actinal intermediate plates, and extending for successively shorter distances along the arm. Then follows a powerful outer gradient which differentiates the marginal ossicles along the entire length of the arm.

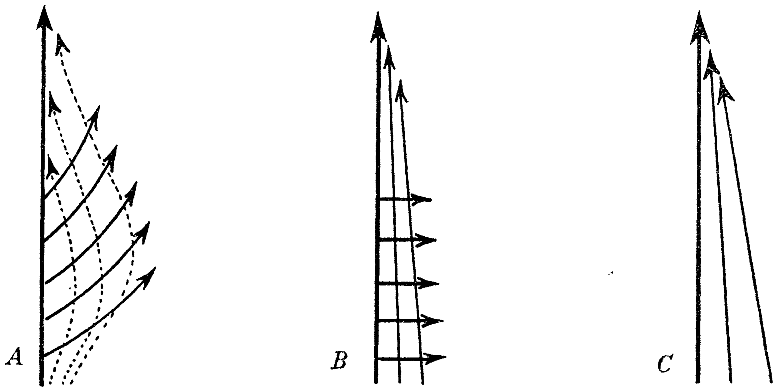

Figure 3. Schematic simplification of the three major growth gradient fields found in the arm of asterozoans; major gradients in heavy lines, subsidiary ones in broken lines. *A*, somasteroid type, also found in pinnulate crinoids; *B*, ophiuroid and platyasterid type; *C*, astropectinid and post-astropectinid type.

The other system comprises transverse gradients, emerging from the main radial axis like spars on a mast, or the pinnae of a fern-frond, each transverse gradient arising from one ambulacral ossicle. Thus the transverse gradients exactly match the ambulacral ossicles in number and disposition. Ossicles are differentiated along the transverse gradients in the following sequence, from within outwards: adambulacral, superambulacral (if present), actinal intermediate plates, marginals. Thus, if both systems are developed equally, the same skeletal plates are influenced by them simultaneously.

However, the two systems intersect and interact, and if one system should predominate over the other, the weaker gradients suffer distortion, or compression, or may be obliterated.

The most powerful gradient (and the first to be established after metamorphosis) is the main radial longitudinal axis. It seems to arise during development from the region of the hydrovascular ring-vessel, and the first sign of its existence is the outgrowth of the five diverging rudiments which become the radial canals and lead therefore to the consequent formation of the arms themselves.

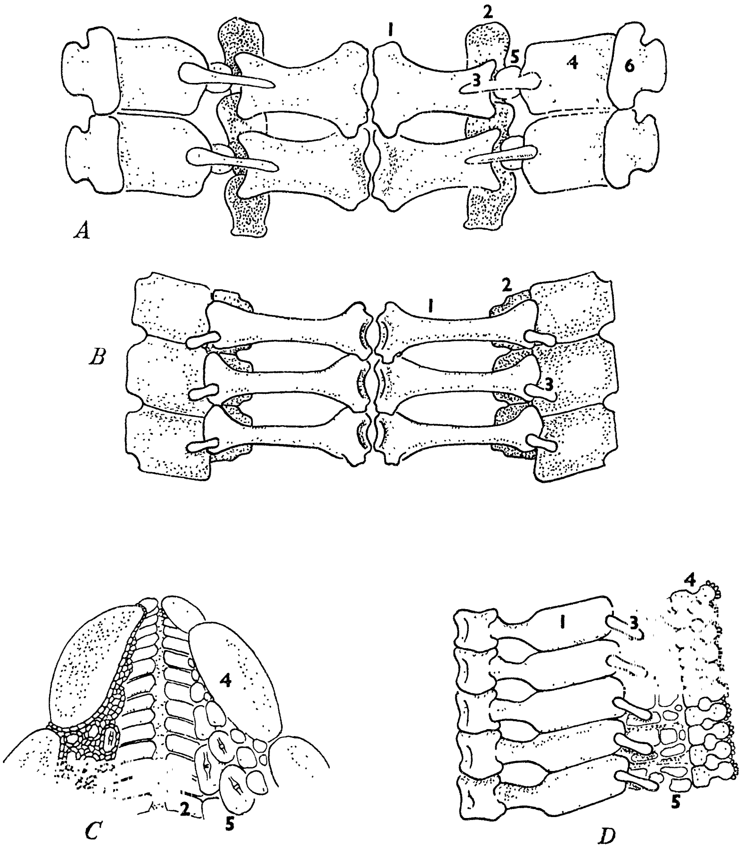

Figure 4. Progressive dislocation of transverse gradients in the asteroid arm, exemplified by: *A*, *Luidia* (internal aspect) (×4); *B*, *Astropecten* (internal aspect) (×4); *C*, *Pentagonaster* (adoral aspect, granulation removed on right side) (×4); *D*, *Leptychaster flexuosus* (internal aspect) (×4). 1, amb-ossicle; 2, adambulacral plate; 3, superambulacral ossicle; 4, infero-marginal plate; 5, actinal intermediate plate.

As stated above, all Asterozoa can be grouped into three major assemblages, according to the form the fields assume. These three categories are as follows:

Group 1. Both gradient systems are present in the arm, but the pinnate gradients dominate the field (figure 3*A*). Thus the skeletal ossicles form transversely elongate rods (virgalia), arranged in transverse or transversely oblique rows. There is at the same time more or less evidence of arrangement in longitudinal series, the latter depending on the relative strength of the longitudinal gradients. Fossils show that this is the earliest asterozoan pattern, and only somasteroids exhibit it, though strong traces of it can be found in some of the more archaic types of asteroids (figure 4), as also in some euryaline ophiuroids (figure 12*A*, *C*, *E*). It is fully developed in the surviving somasteroid *Platasterias*, a circumstance which contributed to its recognition as such, when its other somasteroid features were still unknown (figure 18, plate 51, facing p. 429).

Group 2. Both gradient systems are present, but the longitudinal gradients predominate over the transverse ones (figure 3*B*). The skeletal ossicles thus form short transverse rows, simulating segments. The longitudinal rows, on the other hand, are very conspicuous, the ossicles themselves generally being more or less elongated in the direction of the longitudinal gradient, and the whole arm rather elongate and slender. Nearly all ophiuroids show these features, usually very markedly, and one group of asteroids, the Luidiidae (figures 4*A*, 5*F*), among extant forms, and also the Palaeozoic Platanasteridae (figure 5*E*).

Group 3. Longitudinal gradients dominate the arm and, on external inspection, appear to be the only ones present (figures 3*C*, 4*C*), but dissection of the internal skeleton always reveals traces of transverse gradients. The latter do not extend beyond the superambulacral plate (figure 4*B*, *C*), and usually not beyond the adambulacral plate. Actinal intermediate plates are usually present, and are arranged in longitudinal rows; they are sometimes also arranged in oblique series, but these latter are unrelated to the transverse gradients which produce the ambulacrals and adambulacrals. Marginal plates also form longitudinal rows. They are developed independently of other series (figures 4*C*, *D*, 5*G*). Transitional forms occur in Astropectinidae, suggesting that Group 3 arose from Group 2 through an initial dislocation of the transverse gradients, the dislocation becoming progressively severe.

The oldest fossil Asterozoa have gradients of the type defined as Group 1. This type is found in all three subclasses. It is therefore reasonable to infer that it is the original pattern, and that the others were derived from it. If this was so, then Group 2 must have arisen from Group 1, and Group 3 from Group 2.

The postulate may now be tested. For, when the soft parts are correlated with the gradient characters (i.e. skeletal arrangements, since these are observable in fossils), we should obtain progressive series for these too. Should only random groupings of soft-part characters emerge, the original postulate might still be correct, but would remain suspect.

To perform the test, the taxa must first be arranged in such a manner as will yield the gradient sequence Groups 1, 2 and 3. The extinct Platanasteridae can be inserted in the appropriate place in the series, because their detailed skeletal arrangement is known. The following sequence is obtained:

Complete transverse growth gradients
  Group 1
    1. Chinianasteridae (uniform virgalia)
    2. Platasteriidae (dissimilar virgalia)
      } Somasteroidea (amb-furrow not permanently invaginated)
  Group 2
    3. Platanasteridae (petaloid arms)
    4. Luidiidae (strap-shaped arms)
Transverse gradients disrupted
  Group 3
    5. Astropectinidae (superambulacrals well developed)
    6. All other asteroids (superambulacrals lost or vestigial)
      } Asteroidea (amb-ossicles erected to produce a permanent furrow)

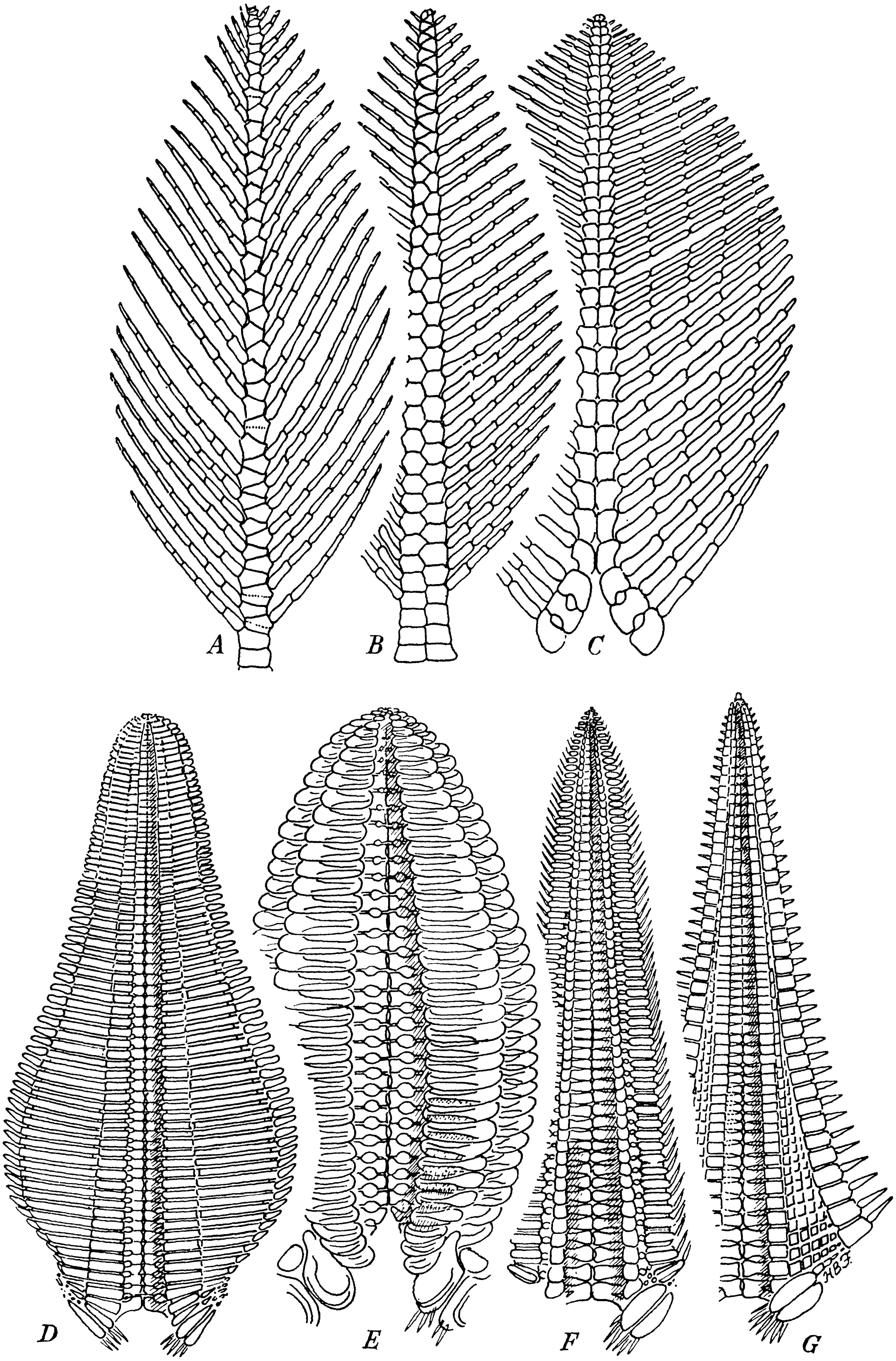

FIGURE 5. Crinoid and asterozoan arms arranged to show progressive transformation of growth gradients from dominant transverse components to dominant longitudinal ones, with ultimate disruption of transverse gradients (in *G*) and entry of actinal intermediate elements. *A*, monoserial crinoid; *B*, biserial crinoid; *C*, chinianasterid somasteroid; *D*, *Platasterias*; *E*, *Platanaster* (after Spencer 1919); *F*, *Luidia*; *G*, *Plutonaster*.

Correlating the soft-part characters against the above table, we find: The anus is lacking throughout the first four divisions, and first occurs in the Astropectinidae; tube-feet throughout the first five divisions are non-suctorial, and suctorial types occur only in division 6; superambulacral ossicles appear in division 2, when the virgalia become dissimilar, persist through divisions 3, 4 and 5, to disappear in division 6; food-grooves, which are present between the rows of virgalia (metapinnules) in divisions 1 and 2, become transformed into respiratory fascioles in the Luidiidae, persist as recognizable vestiges in Astropectinidae and Porcellanasteridae (of division 6), thereafter disappearing.

TABLE 1. TIME SEQUENCE OF MORPHOLOGICAL DIFFERENTIATIONS IN THE EARLY EVOLUTION OF THE ASTEROIDEA

morphological differentiation	group in which first occurred	morphological time-scale
	Pre-asteroid phases	
interpinnular grooves established. Cover-plates turn outwards	unknown	pre-chinianasterid
terminal plate established. Three metapinnules enter jaw. Virgalia differentiate into V-1, V-2, etc.	Platasteriidae	post-chinianasterid
	Asteroid phases	
amb-ossicles erected on V-1, to produce permanent asteroid furrow (origin of asteroids)	Platanasteridae	post-platasteriid pre-luidiid
arms lose petaloid form. Interpinnular grooves respiratory only and vestigial. Pedicellariae appear. Raptorial feeding	Luidiidae	post-platanasterid pre-astropectinid
aboral anus and intestine develop. Disk expands. Metapinnules undergo partial disruption, with transverse gradient reaching only V-2. Interpinnular grooves lost or vestigial. Entry of actinal intermediate plates in several longitudinal series broadens arm-base	Astropectinidae	post-luidiid: anus arises after initial differentiation of Astropectinidae, so it is not an original feature of family, and is lacking from some members
disappearance of the superambulacral (occluded V-2)	Porcellanasteridae, and probably independently in other stocks	post-astropectinid
tube-feet develop suckers	? Hudsonasteridae	post-astropectinid
valvate pedicellariae develop	Goniasteridae (*sensu lato*)	post-astropectinid
forcipulate pedicellariae develop	? Brisingidae	post-astropectinid
secondary reduction of marginal plates	several lines independently	post-phanerozonid

Other characters also prove to be co-ordinated: a terminal plate is lacking in division 1, first appears in division 2, and thereafter persists; actinal intermediate plates are lacking from division 1, appear as minute and irregular rudiments in division 2, persist as somewhat larger and more regular elements in the luidiids, become progressively more conspicuous in the various genera of Astropectinidae, and extremely conspicuous in post-astropectinid groups; petaloid arms are very conspicuous in divisions 1 and 2, become less conspicuous in division 3, and vanish with the Luidiidae, never to reappear.

Thus the hypothesis receives overwhelming support, and we may accordingly interpret the sequence as a chronological table. Now, since there are no reasons for supposing the extinct Platanasteridae would depart from the sequence in respect of their (unknown) soft structures, and there is every reason for thinking that they would conform with the other groups, we may leave them in the position assigned, and infer their soft parts on the basis of the extant Luidiidae, and the extant platasteriid—the forms which lie on either side of the Platanasteridae.

The fossil record shows that the inferred differentiations had all occurred by lower Ordovician times, yet the oldest known asterozoans date only from the Tremadoc (uppermost Cambrian or lowermost Ordovician). Hence the conventional geological time-scale is too coarse to express the inferred chronological sequence of morphological differentiations. Therefore a 'morphological' time-scale must be introduced, as set out in table 1, which summarizes the conclusions drawn.

The fossil Hudsonasteridae are placed at the foot of the table, for their growth patterns are of Group 3 type. Such forms are too specialized to have much relevance to the origin of asteroids, and the table does not go beyond this grade of differentiation. Pre-asteroid differentiations are included for convenience, since they show the source of some of the characters already present in the earliest asteroids (Platanasteridae); the pre-asteroid data are derived from a later part of this memoir (Somasteroidea, p. 393).

SURVIVING PLATYASTERIDA

The relationship of the Luidiidae to the Platanasteridae requires mention. As is now apparent, the Luidiidae must be exceedingly archaic forms. Their growth gradients set them apart from all other extant asteroids, and it had been my intention to propose a separate order for their reception. In discussion with Mr C. W. Wright, of London, the similarity of Luidiidae to *Platanaster* was realized. The latter genus (from the Ordovician) had been placed by Spencer (1951) in a separate order, Platyasterida. Reference to Spencer's (1919, Figure 115) diagram of the arm discloses that the ambulacral ossicles are erected to form a permanent furrow, whilst the growth gradients are of Group 2 type. Hence the order Platyasterida comprehends the Luidiidae; the order may now be more precisely defined, as follows.

Order **Platyasterida** Spencer, 1951

Diagnosis. Asteroids in which complete transverse growth gradients occur in the arm, producing transverse rows of skeletal ossicles which match the ambulacral ossicles in number and position.

Included families. Platanasteridae (arms petaloid), and Luidiidae (arms linear, strap-shaped).

The structure of *Platasterias*, among somasteroids, and of *Platanaster* and *Luidia*, among asteroids, indicate the homologies between somasteroid virgalia and asteroid plates; these homologies are stated on p. 405, under Ophiuroidea. The other major skeletal elements are those of the buccal apparatus. In Luidiidae and Astropectinidae the mouth skeleton involves two proximal pairs of ambulacral ossicles (figure 2*A*), together with an interradial element (oral plate), and an occluded T-shaped ossicle lying in the interradius. The homologies of these structures can be determined by comparison with *Chinianaster* (see p. 400). As shown later, the somasteroid buccal skeleton is derived from three basal metapinnules of the arm; since it can be shown that all the elements in the luidiid and astropectinid jaw are homologues of elements found in the somasteroid jaw, it follows that the asteroid buccal apparatus is a further modification of three original metapinnules of the arm.

Some Luidiidae show persistent loss and regeneration of parts of the arm, so much so that specimens almost always have unmatched arms, with several phases of regeneration occurring in the one arm. The same is observed in *Platasterias*. In both cases, when regeneration is taking place, some dislocation of the transverse gradients may be seen at points proximal to the sites of injury. Possibly the transverse gradients are disturbed by the severe stimulation of longitudinal gradients when the greater part of an arm has to be replaced. Perhaps the ultimate suppression of transverse gradients in post-luidiid asteroids was induced by excessive stimulation of the longitudinal gradients in persistently regenerative ancestral forms.

Schuchert's (1915) belief in the archetypal nature of the Hudsonasteridae cannot be maintained for, as stated above, the gradients are of a secondary, post-astropectinid type. *Hudsonaster* and allied genera somewhat resemble juvenile stages of extant Oreasteridae. In the latter family a large interradial plate, resembling that seen in Hudsonasteridae, seems to represent an occluded and fused pair of interradial marginal elements, though in some cases it may be an enlarged actinal intermediate plate or, on the aboral side, a calycinal plate. Certainly the retention of calycinal plates in the disk of Hudsonasteridae is not in itself evidence of archaic structure, for all asterozoans whose development is known have these plates in the young stages, and some retain them in the adult stage; this may be true even in families of quite late differentiation, such as Ophiuridae among ophiuroids, and Zoroasteridae among asteroids.

In seeking the origin of asteroids from somasteroids, then, the critical group is not the Hudsonasteridae, but the Platyasterida; and fortunately we have living representatives of the order in the Luidiidae. The next step is to examine more closely the relationship between Luidiidae and somasteroids.

Structure of somasteroids

Somasteroids are extremely flattened asterozoans exhibiting growth gradient fields of the type here termed Group 1 (figures 3 and 9). The arm-skeleton has a frond-like structure, in which elongate rods called virgalia are arranged in transverse rows, termed metapinnules. Each metapinnule arises from the abradial margin of one of the paired ambulacral (or brachial) elements which comprise the arm-axis. The structure as a whole, therefore, is comparable with that of a biserial crinoid (figure 5*B*, *C*). The virgalia form the walls of interpinnular food grooves (figure 18, plate 51, and figure 8*A*) which apparently convey ciliary water-currents to the radial food-groove, and thence to the mouth. The ambulacral ossicles are either block-like, as in the genus *Chinianaster*, where they resemble brachial ossicles of crinoids; or they may develop a lateral wing, in which case the major (i.e. transverse) axis of the ambulacral lies almost horizontally, in the same axis as the metapinnule which it bears, as in the family Villebrunasteridae (figure 6*B*) and the extant genus *Platasterias* (figure 8*E*). The radial food-groove underlies the ambulacral ossicles. In *Platasterias*, and probably in some at least of the fossil genera, a muscular mechanism

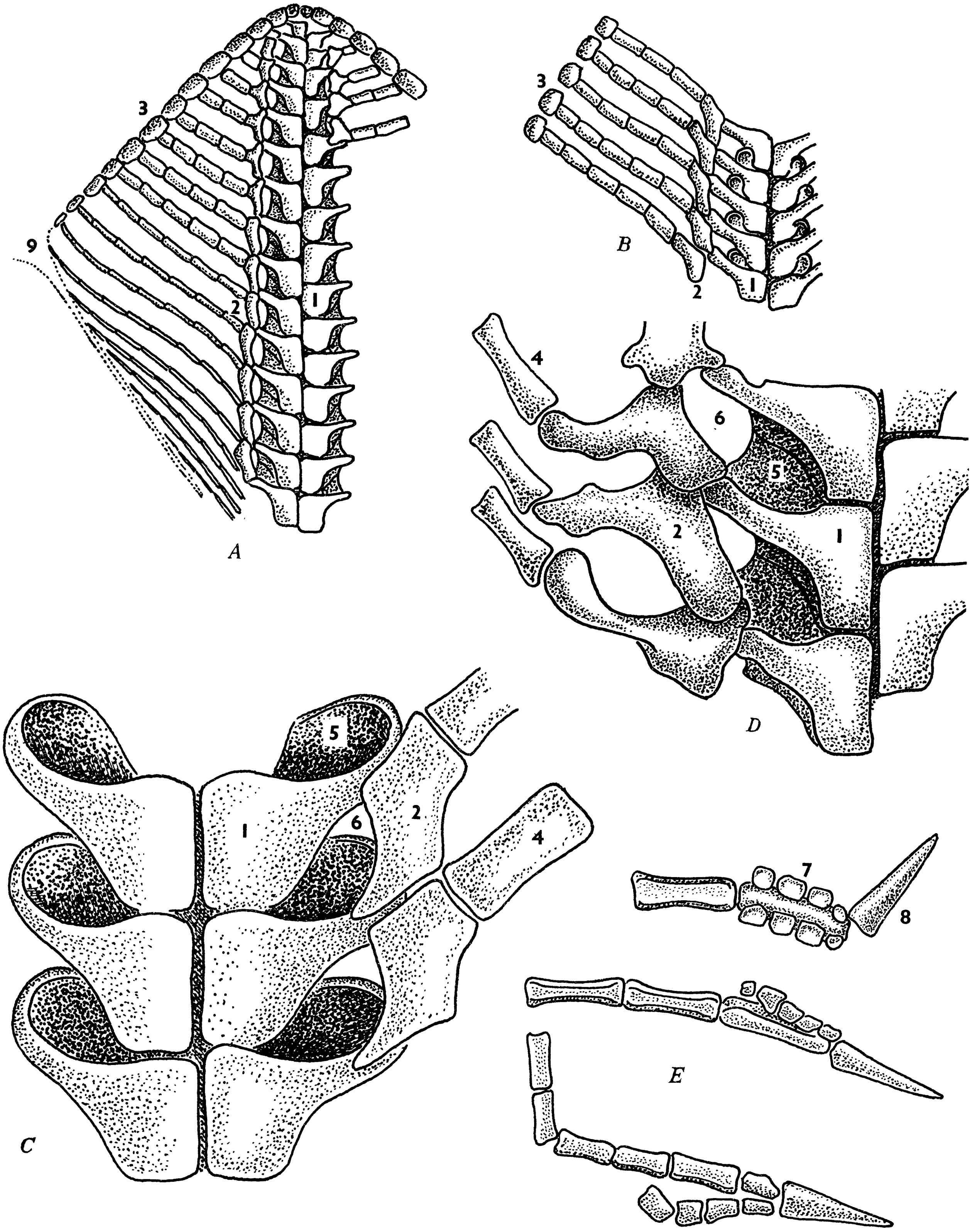

FIGURE 6. Structure of Ordovician somasteroids, from latex positive moulds of original material in the University of Lyon. *A*, *D*, *Ampullaster ubaghsi* Fell; *B*, *C*, *Villebrunaster thorali* Spencer. *E*, *Chinianaster levyi* Thoral. *A*, holotype, PS 193, interpretation of arm-skeleton, in ventral aspect (×5); *D*, detail near arm-tip, same specimen (×20). *B*, paratype, ES 5, interpretation of arm-skeleton near arm-tip (×6); *C*, holotype (part of ES 5, which bears two specimens), interpretation of structure of mid-arm region (×15); *E*, metapinnules showing cover-plates, traced from photographs of parts of ES 1 (all ×8). All material examined by courtesy of Professors H. Gauthier and G. Ubaghs. 1, capitulum of ambulacral; 2, adambulacral virgalium; 3, marginal virgalia; 4, second virgalium; 5, shelf of cupule; 6, internal (presumed ampullar) passage of cupule; 7, cover-plates; 8, terminal radiole; 9, interradial cleft.

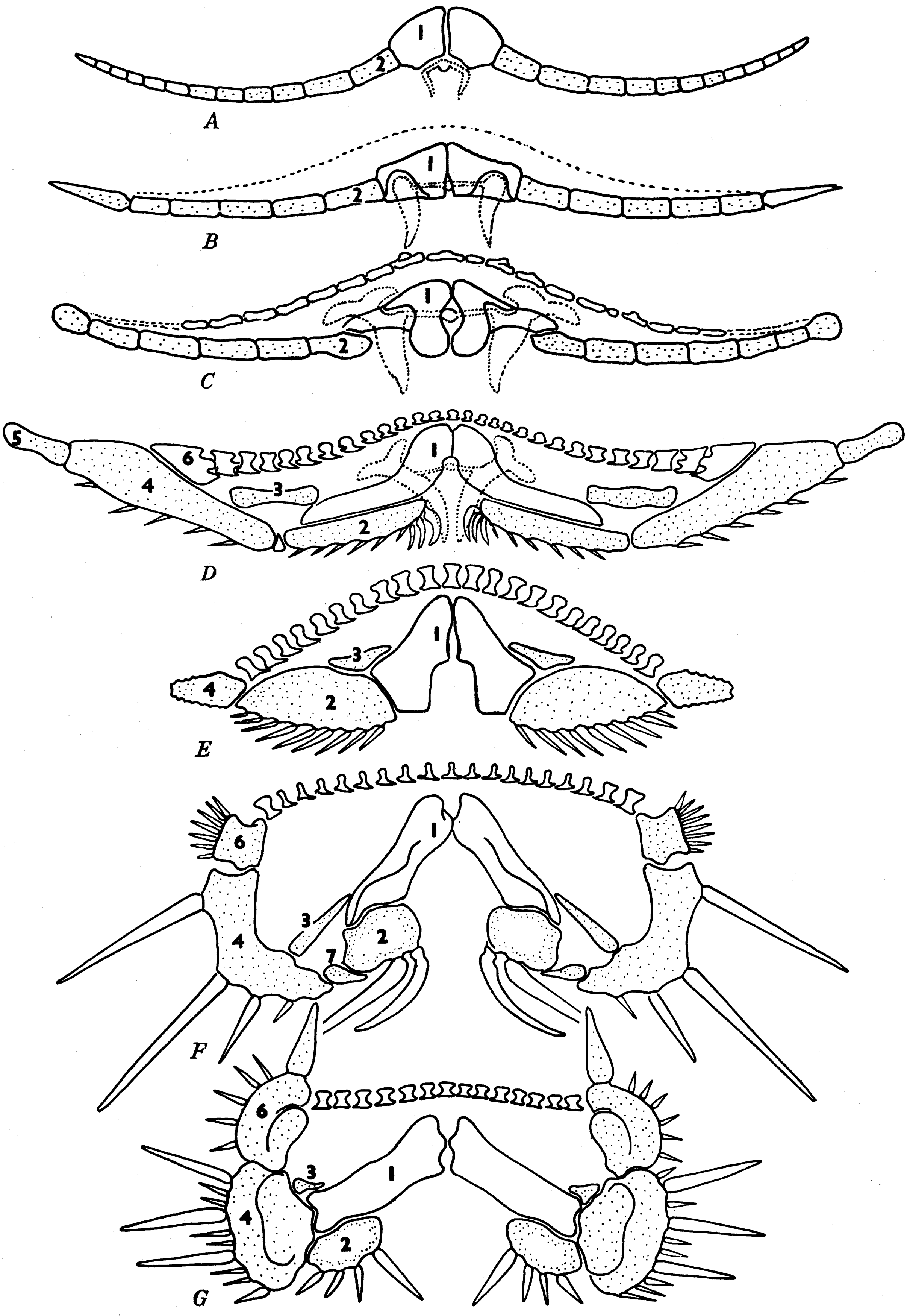

Figure 7. Cross-sections of arms of astroradiate echinoderms. *A*, biserial crinoid; *B*, *Chinianaster* (× 8); *C*, *Ampullaster* (× 10); *D*, *Platasterias* (× 4); *E*, *Platanaster* (× 6) (after Spencer 1919); *F*, *Luidia* (× 4); *G*, *Astropecten* (× 4). 1, ambulacral (brachial in *A*); 2, virgalium-1, adambulacral; 3, virgalium-2, superambulacral; 4, virgalium-3, inferomarginal; 5, virgalium-4, marginal radiole; 6, superomarginal paxilla or plate; 7, actinal intermediate (intercalary) plate. The stages shown illustrate phases in arm-evolution in somasteroids and asteroids, prior to the development of suctorial tube-feet, the amb-ossicles becoming erected in *E*, with perfection of the buttress-skeleton in *F* and *G*. See also table 1.

permits temporary erection of the ambulacral ossicle, with its associated proximal virgalium, to form an inverted-V, homologous with the ambulacral furrow of asteroids. In the extant genus *Platasterias* there are small, simple, non-suctorial tube-feet, and similar structures have recently been found in *Chinianaster* (Ubaghs & Fell, unpublished). In *Platasterias* there is a small, but double, internal ampulla (Fell 1962), and the skeletal structure of *Ampullaster*, and that of the distal half of the arm in *Villebrunaster*, implies a similar development of an internal ampulla in these Ordovician genera (figure 6*A* to *D*, 7*C*, *D*). In *Platasterias* there is a blind gut which sends gastric caeca into the arms, and it is probable that a similar structure occurred in the fossil genera. Although some genera of somasteroids could be considered as primitive asteroids, *Chinianaster* is so generalized as to permit interpretation as a primitive ophiuroid also. Spencer (1951) treated the somasteroids as a separate subclass of the Asterozoa, of equal rank with asteroids and ophiuroids, a view which has much to support it, and is here adopted. It is clear, however, that hard and fast lines can no longer be drawn between the three subclasses, and whatever subdivision be adopted, the result is inevitably somewhat artificial.

The Cambro–Ordovician genus *Chinianaster* is evidently the most generalized somasteroid, as also the oldest and most generalized asterozoan so far discovered (figure 11*A*, *B*, *D*, *E*). The other early Ordovician genera *Villebrunaster*, *Ampullaster* and *Archegonaster* are more comparable with asteroids (figures 6, 7). The extant genus *Platasterias*, while quite closely comparable with luidiid asteroids, shares with *Chinianaster* some features apparently lost by the other genera named, and in other features is more comparable with the villebrunasterid genera; it is therefore a remarkably generalized form. Until recently our knowledge of somasteroids was based almost entirely on the work of Spencer (1951), who first recognized the somasteroids as an independent assemblage of asterozoans. Subsequent study, made possible by the generosity of Professor Georges Ubaghs, University of Liège, and with the co-operation of Professor H. Gauthier, University of Lyon, has required considerable modification of the classification of somasteroids. A concise summary of the new data can be given in the form of a systematic key to the included taxa, as follows:

Key to the families of Somasteroidea

1 (6) Arms petaloid, hence a deep interradial cleft extending from the ambitus to the perignathic region (figures 6*A*, 11*D*).

2 (3) Tube-feet finely plated, tapering, non-suctorial, housed in an external cupule carried on the adoral surface of the block-like capitulum; cupule large, located at the same level as the first virgalium, making it impossible for any internal ampulla to develop (figure 11*A*). No superomarginal, inferomarginal or adambulacral virgalia differentiated. Virgalia bearing a flange, on either side of which lie two series of flattened cover-plates (figure 6*E*), the terminal virgalium forming a hinged, free, acuminate radiole; no median adoral series of spinules on the virgalia. No lateral wing on the ambulacral. Food-groove probably defined only by the tube-feet. Chinianasteridae Spencer (restricted)

3 (2) Tube-feet unplated, housed in an incomplete cupule between adjacent wings of successive ossicles (at least on distal half of arm); internal ampullae able to develop (at least on distal half of arm). Virgalia differentiated as adambulacral,

intermediate and marginal elements, though in general retaining a transversely elongate form. Adambulacral virgalium placed at a lower level than the ambulacral wing, forming the abradial margin of the housing for the tube-foot which, except in the proximal segments in some forms, rests upon a shelf on the abradial side of the capitulum, with provision for internal communication of an ampulla. Food-groove defined by the adradial margin of the adambulacral virgalium (figure 6*A* to *D*; figure 7*C* to *D*).

4 (5) No marginal radioles. Virgalia mainly in the form of delicate vertically placed plates, forming the walls of the interpinnular grooves, but apparently lacking cover-plates. Proximal cupules completely enclosing base of tube-foot, carried on the adoral surface of the capitulum (at least, in *Villebrunaster*); all other cupules sunken between the lateral wings of the ambulacra, incomplete on the abradial side, leaving an opening above the adambulacral virgalium through which an internal ampulla presumably developed (figure 6*C* to *D*). Water-vessel enclosed between the capitula, but communicating with the tube-feet between the ambulacral ossicles. First ambulacral (angle-plate of jaw) with an incipient interradial wing (figure 8*C*). No occluded superambulacral virgalium (figure 6*A* to *E*, *G*). Villebrunasteridae Fell

5 (4) Inferomarginal virgalia each bearing a cylindrical hinged radiole (terminal virgalium). Virgalia robust, transversely elongate, differentiated as four elements in each row; the adambulacral and inferomarginal elements forming vertical plates, which also form the walls of the interpinnular grooves; the occluded second virgalium (superambulacral) and terminal virgalium rod-like (figure 8*A*, *E*). Adambulacral and inferomarginal virgalia (and intermediate virgalia when developed) bearing a flange on either side of the adoral surface, on which lie two series of flattened cover-plates, held in a web, and capable of erection (figure 18, plate 51) and depression (figure 10*C*, *D*), covering the interpinnular groove when depressed. Ambulacrals capable of temporary erection by the action of an adductor muscle; bound to the adambulacral virgalia by synarthry, the adambulacrals therefore being erected with the ambulacrals, and moving upon a fulcrum at their abradial extremity; thus producing a temporary furrow of asteroid type. When not erected, the adambulacral lies in the horizontal axis of its metapinnule, forming part of the general adoral surface of the arm (figure 18). Platasteriidae Caso

6 (1) Adjacent arms fused proximally, with consequent loss of the interradial cleft and petaloid outline, the general form of the body becoming pentagonal. Virgalia differentiated as in Villebrunasteridae, but the marginals large and block-like, forming a continuous series across each interradius. Ambulacrals probably erectile, together with their adambulacrals; cupule provided with a direct means of internal communication for the ampulla. Cover-plates unknown (? absent). Archegonasteridae Spencer

Of the numerous divergences from Spencer's (1951) account which are apparent in the foregoing analysis, the more important (namely, the distinctive characters of the

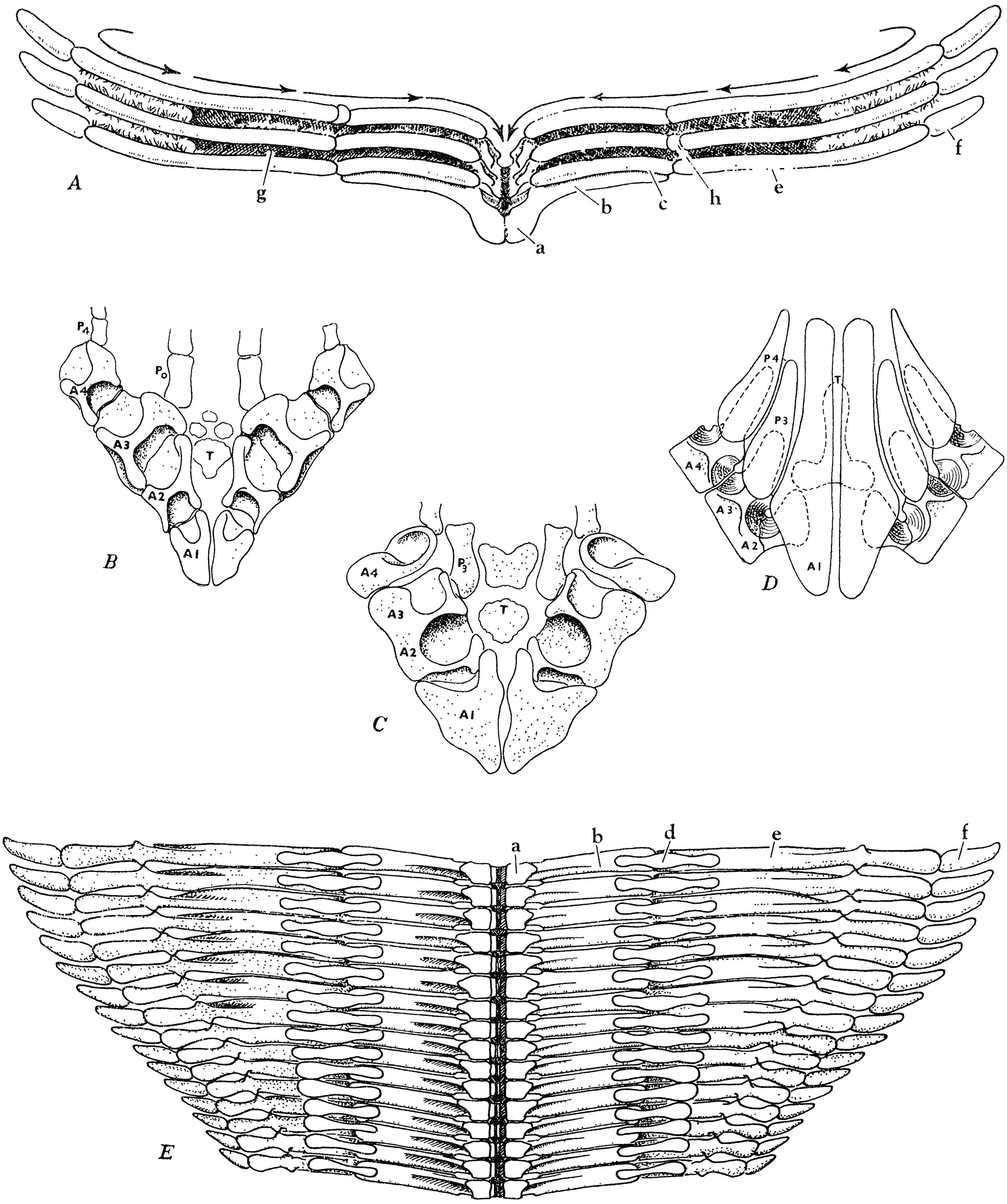

FIGURE 8. *A*, *E*, virgalia in *Platasterias*; *A*, in adoral aspect, showing intervening fasciolar grooves between metapinnules, after removal of cover-plates, inferred water-currents indicated by arrows (× 4); *E*, internal aboral aspect (× 4): *a*, capitulum of amb-ossicle; *b*, its wing; *c*, virgalium-1, adambulacral; *d*, virgalium-2, superambulacral; *e*, virgalium-3, inferomarginal; *f*, virgalium-4, marginal radiole; *g*, interpinnular groove; *h*, intercalary virgalium. *B*, *C*, *D* jaw in ventral aspect in young *Chinianaster* (× 12) (*B*); in young *Villebrunaster* (× 18) (*C*); in *Platasterias* (adult) (× 8). Abbreviations: A 1, first ambulacral, jaw angle-plate; A 2, A 3, second and third ambulacrals, united in syzygy; P_3, P_4, third and fourth metapinnules, P_3 being an oral pinnule (P_0) in *B*; T, tegminal or T-plate(s).

Villebrunasteridae) have already been discussed elsewhere (Fell 1963), and fuller descriptions, with photographs, are planned for separate publication. The probable mode of origin of the Archegonasteridae (from Villebrunasteridae) has also already been indicated elsewhere (Fell 1963), and further discussion of these rather specialized somasteroids is not relevant to this memoir. A general description of the skeleton of *Platasterias*, an extant somasteroid, has recently been given (Fell 1962, 1962*a*), and the only features which require further consideration here are those upon which subsequent work with the fossil material has thrown a new light, calling for some modification of the views earlier expressed. The most important of new data are those related to the early development of *Chinianaster* and *Villebrunaster*, some very significant evidence now being available.

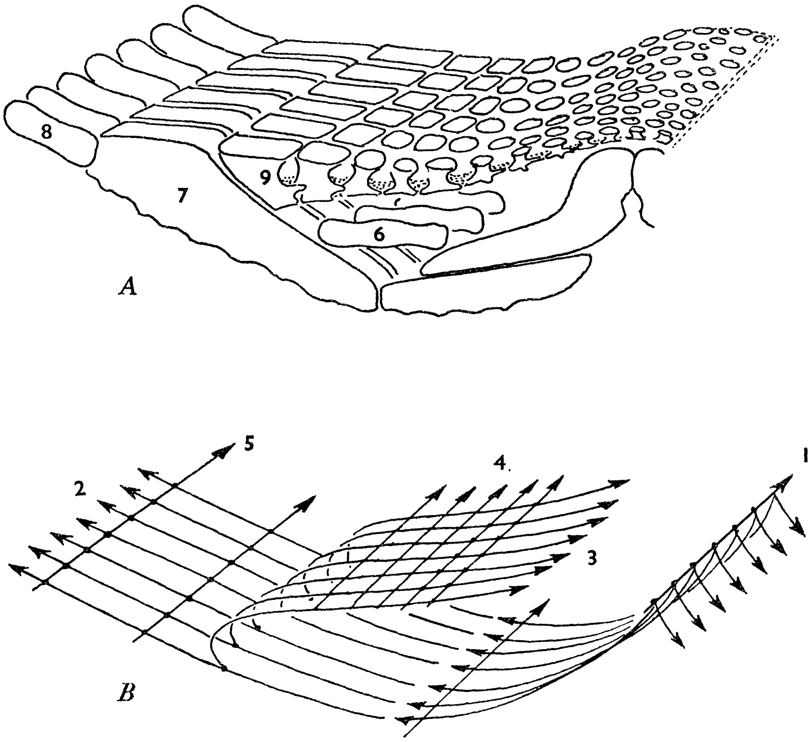

Figure 9. *Platasterias latiradiata*. *A*, block diagram of skeletal elements of mid-arm; *B*, inferred gradient field. 1, main radial (longitudinal) gradient; 2, transverse gradients of metapinnules; 3, dorsolateral adradial gradients of paxillae; 4, longitudinal dorsal paxillar gradients; 5, longitudinal marginal gradient; 6, superambulacral ossicle; 7, inferomarginal elements; 8, terminal virgalium; 9, outer paxilla, or superomarginal element.

In the collection of somasteroids from the lower Ordovician of St Chinian, now held at the University of Lyon, are several imprints and counter-imprints of juvenile stages of both *Chinianaster* and *Villebrunaster*. The most important of these are catalogued as No. 555 (coll. Lignières), a young *Chinianaster*, R *ca*. 7 mm, not seen by Spencer; and No. 563 (coll. Lignières), a young *Villebrunaster* of about the same size, also not seen by Spencer. In addition, a further juvenile specimen of *Chinianaster* exists, No. ES2 (coll. Thoral), apparently examined by Spencer. The elucidation of these specimens will require further work, particularly the young *Villebrunaster*, but sufficient study and photography has now been carried out to permit the interpretation of the jaw region in *Villebrunaster*, and an almost complete reconstruction of the young *Chinianaster* (figures 17, plate 50; 8*B* to *D*, 11*E*).

A full account of the photographic method employed need not be given here, since it is not relevant to the general subject-matter under discussion, and will in any case be reported elsewhere. It will suffice to state that the fossils, though greatly distorted, are almost complete, and show the ossicles in their natural association. They exhibit most aspects of the surfaces of the ossicles in considerable detail. In order to obtain a single comprehensive view in one aspect (internal aboral aspect being chosen for the first survey, here reported), it was necessary to make a series of negatives of various portions, by photomicrography. From these were selected six negatives which exhibited all available parts in uniform aspect; and from these six a series of prints enabled a photo-mosaic to be assembled, which was rephotographed to yield the single picture reproduced in figure 17, plate 50. Details were elucidated by oblique views not here given.

As is evident from figure 17, and the explanatory diagram (figure 11*E*), the ambulacral ossicles of the juvenile stage of *Chinianaster* are relatively very much more massive in the earlier phase of growth than they are in the adult stage (figure 11*D*); they resemble, in fact, the brachial ossicles of a biserial crinoid. The structure and mode of origin of the jaw is clearly demonstrated, three pairs of ambulacrals being involved (the first to third, labelled A1, A2 and A3 in figures 8*B*, 11*E*). The angle-plate of the jaw is formed from the first ambulacral, but slightly modified. The mouth-frame, not hitherto known in any fossil somasteroid, is seen to be formed from a syzygy of the second and third ambulacrals (the line of syzygy can be demonstrated in oblique photographs, the syzygy being also proved by the duplication of cupules on the ventral surface, seen in figure 8*B*). The syzygy carries a conspicuous ridge, on the outer end of which is a facet for the articulation of the enlarged metapinnule carried by the mouth-frame (P_0). Some extraordinary points of similarity to crinoid structure are at once evident. These are (*a*) the first metapinnule appears to be movable, and by its enlargement invites direct comparison with the oral pinnule of a crinoid, being probably an accessory feeding organ, and (*b*) the oral pinnule is carried on the outer element of the syzygy, the second ambulacral having none. This invites direct comparison with crinoids, where the corresponding terminology would describe the syzygy as being of the normal type, the hypozygal carrying no pinnule, and the epizygal carrying a well-developed one.

The disk was covered adorally by plates, which may be termed tegminal plates. The madreporite was not found, but is shown (in figure 11*E*) in the position it occupies in the lectotype (an adult). There are apparently no terminal plates, though the last pair of ambulacrals enclose a passage for the water-vessel, and may possibly represent an incipient terminal plate. In the photograph (figure 17, plate 50) it has not been possible to include the terminal ambulacrals, as these were embedded end-on in the matrix, and were not accessible for photography in the aspect chosen.

Figure 8*C* shows the jaw structure in young *Villebrunaster*. It is directly comparable with that in *Chinianaster*, but the angle-plate (ambulacral-1) is larger, and has developed an incipient interradial wing. The virgalium of the epizygal is of normal type for the genus, namely an adambulacral, and no free pinnule could have been present.

Figure 8*D* shows the jaw of *Platasterias* in the same aspect (i.e. adoral). It is clearly comparable with *Villebrunaster*, the second and third ambulacrals being united in syzygy, and the angle-plate evidently comprising the first ambulacral, which has now developed a conspicuous interradial wing, and has moved somewhat out of the general ambulacral alinement. Thus it points to an erroneous feature of the homologies drawn in my recent paper on *Platasterias* (Fell 1962*a*), in which it was inferred that the angle-plate of the jaw is an adambulacral element. It also seems probable that the T-shaped plate of *Platasterias* (and some phanerozonid asteroids) is derived from occluded tegminal plates, not from a metapinnule as previously inferred. It is obvious that the analogous odontophor in some Palaeozoic asteroids (e.g. *Platanaster*) cannot be homologous with the T-shaped plate, being rather an occluded inferomarginal, as already inferred (Spencer 1919).

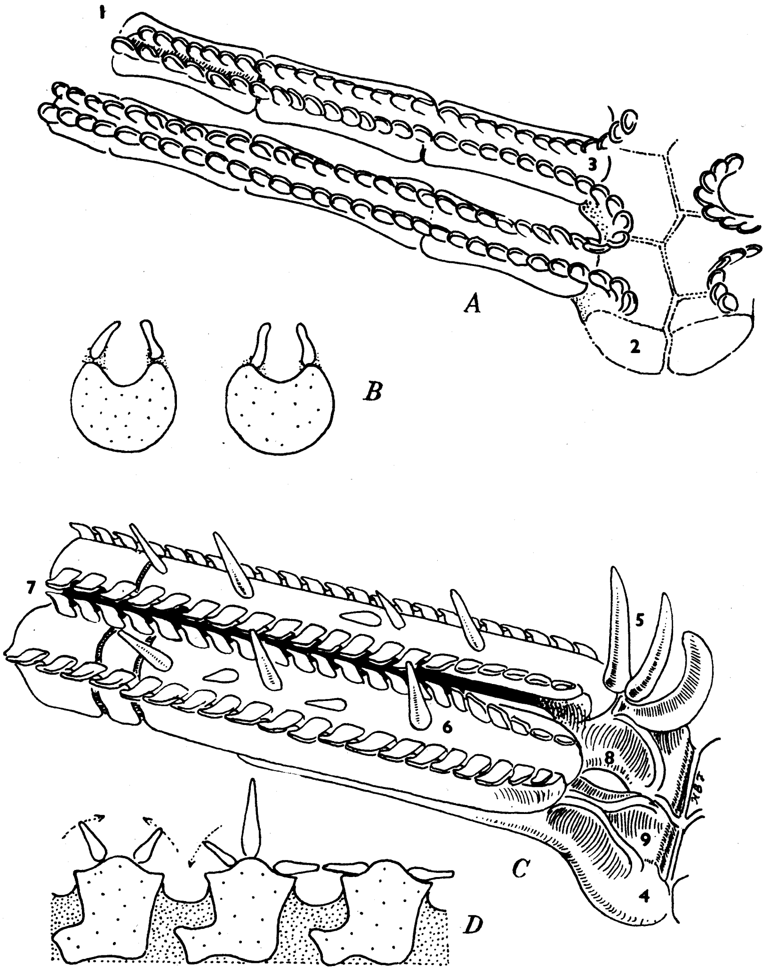

Figure 10. Comparison of pinnate structure of the arm in a biserial crinoid (*A* and *B*) with that in *Platasterias* (*C* and *D*), obliquely adoral aspects being shown in *A* and *C*, and transverse sections of pinnules and metapinnules in *B* and *D*, integument dotted. 1, pinnular; 2, brachial; 3, pinnular food-groove; 4, ambulacral ossicle; 5, adambulacral spines; 6, ventral spinule; 7, interpinnular groove; 8, cupule; 9, alveolus of adductor muscle which erects amb-ossicles to form temporary furrow.

It is hoped to extend this photographic method to the other fossil somasteroid material now under investigation, and to report further results in a later contribution. It has not been possible as yet to devise any means for checking whether the distal ambulacral ossicles in young *Chinianaster* do in fact lie opposite one another (as shown), or whether

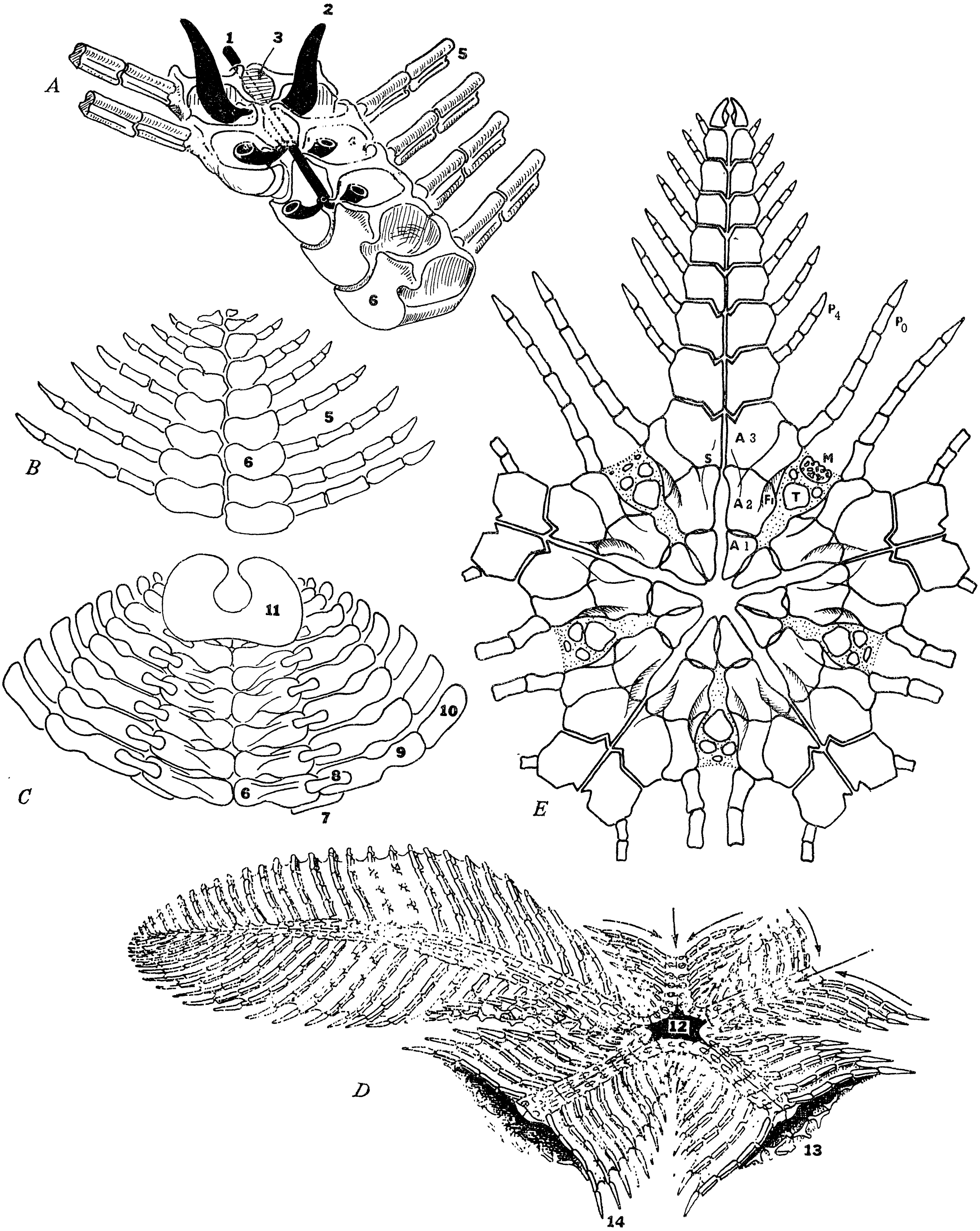

FIGURE 11. *A*, *B*, *D*, *E*, *Chinianaster levyi*, restored on the basis of material in the University of Lyon collection. *C*, *Platasterias latiradiata*. *A*, adoral aspect of axial skeleton, showing also adjacent virgalia and the tube-feet, as inferred (× 18). *B*, arm-tip of adult *Chinianaster* showing alternating ossicles in this region (× 18). *C*, corresponding region in *Platasterias*, 81st to 88th metapinnules in specimen examined, in aboral (internal) aspect (× 18). *D*, inferred appearance of *Chinianaster* (adult), in adoral aspect, arrows indicating water-currents (inferred) (× 3); details of jaw-structure omitted. 1, radial water-vessel; 2, tube-foot; 3, adductor muscle; 4, cupule; 5, virgalia; 6, amb-ossicle; 7, virgalium-1; 8, virgalium-2; 9, inferomarginal, and 10, its radiole (i.e. virgalia-3 and -4); 11, terminal plate; 12, mouth; 13, aboral body-wall; 14, marginal radioles. *E*, juvenile *Chinianaster*, key diagram for figure 17, plate 50. A 1, A 2, A 3, first, second and third ambulacrals, the second and third united in syzygy at S; P_0, oral pinnule; P_4, fourth metapinnule; T, tegminal plate; M, inferred madreporite (based on adult) (× 11).

they alternate, as in the distal part of the arm of its adult stage (figure 11*B*) and in Villebrunasteridae (figure 6*A*, *B*). The nature of the mid-radial surface of the ossicles does, however, imply that some sliding of the ossicles occurred during growth; post-mortem separation of the left and right series of each arm is attributable to the firmness of the zig-zag synarthries between successive ambulacrals of the same series, and it seems highly probable that the so-called 'buccal slits' of Spencer's (1951) account are due entirely to such post-mortem change.

Origin of the Ophiuroidea

Palaeontologists have for long agreed that ophiuroids must be related to asteroids, since their skeleton suggests this, and the two groups show markedly increasing similarities, the further back they are traced (Gregory 1900; Schuchert 1915). Zoologists have expressed differing views. Mortensen (1927), the leading echinoderm systematist and embryologist of his day, acknowledged that ophiuroids and asteroids must be related, and placed the two groups in proximity in his text-books, despite the fact that their larvae are very different. Most other authors of zoological texts have accepted the views of embryologists who held that the similarity of the pluteus larvae of ophiuroids and echinoids indicates a phylogenetic relationship between these two groups, to the exclusion of the asteroids, where no pluteus larva occurs. Numerous anatomical similarities between ophiuroids and asteroids have not been adequately discussed, and stress has been laid on certain differences, despite the fact that these differences vanish when fossils are taken into account. This treatment was opposed by Fell (1948), chiefly on the grounds that fossil evidence of asteroid-ophiuroid affinity is conclusive, and cannot be overlooked; accordingly the differences between the larvae must be due to independent larval evolution, and do not reflect phylogeny.

Following the definition of the subclass Somasteroidea by Spencer (1951), it became apparent that somasteroids must have been the common ancestral forms from which asteroids and ophiuroids arose, a view adopted by Ubaghs (1955) and Fell (1959, 1960).

Now that *Platasterias* is seen to be a somasteroid, and *Luidia* a platyasterid, it is possible to consider the evidence of their soft parts and growth gradients, and thus to view the problem in a new and much clearer light.

The following features of ophiuroids occur in *Platasterias* and also in Luidiidae, and are thus common to all three groups of Asterozoa, and must be part of their common somasteroid legacy:

(1) Absence of an anus, intestine and intestinal caeca.

(2) Non-suctorial tube-feet

(3) Compound growth gradient fields in the arm, with intersecting longitudinal and transverse axes.

None of these features occurs in archaic grades of echinoids, with which ophiuroids should show affinity if they are interrelated. The first and third characters occur in no echinoid; the second occurs only in specialized echinoids, known to have arisen during the late Mesozoic.

Therefore ophiuroids (which are known fossil in the lowermost Ordovician) are likely to have acquired the three characters listed, not from any common ancestor shared only

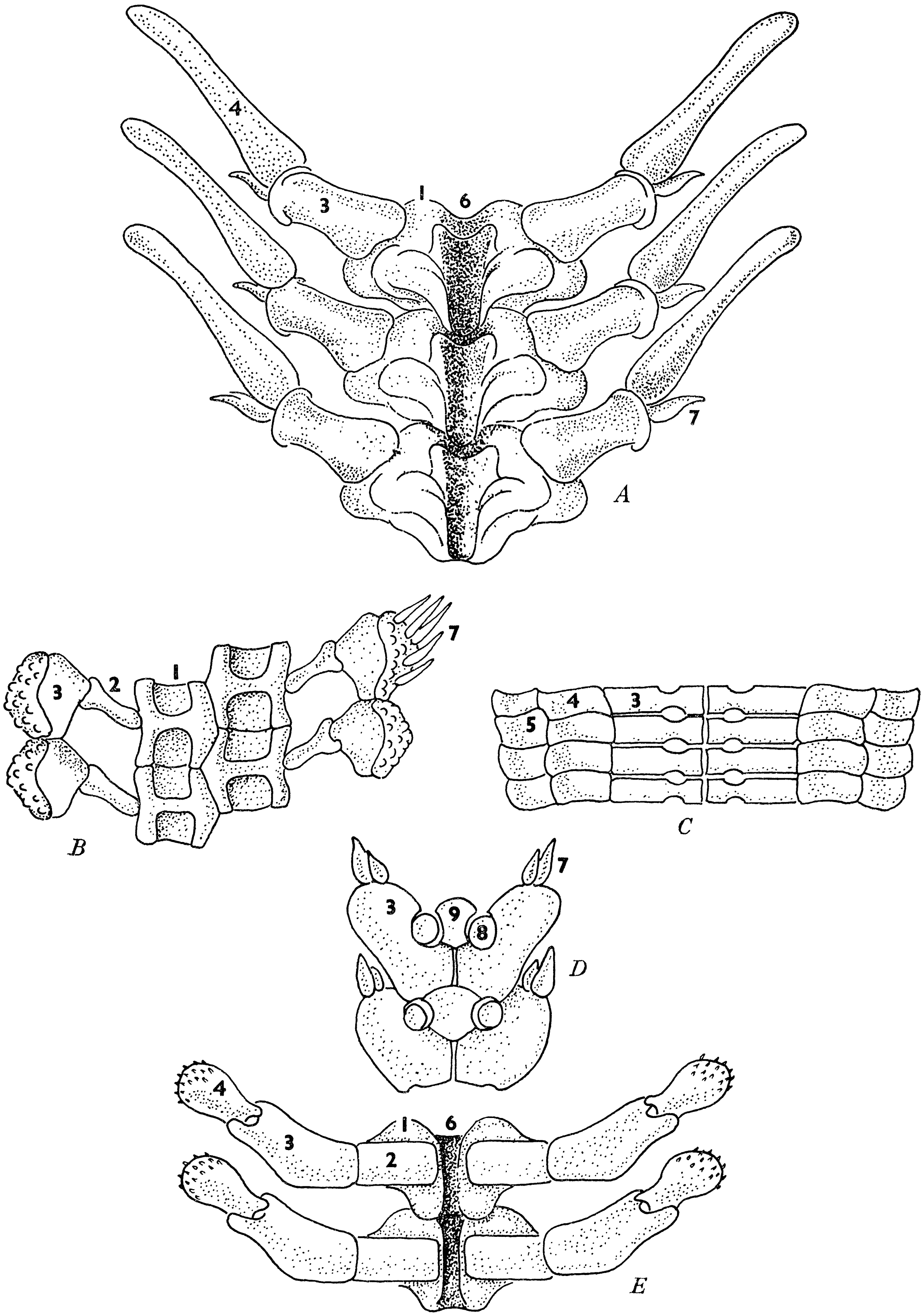

FIGURE 12. Pinnate structure in Ophiuroidea. *A*, *Asteronyx loveni*, dissection of arm-skeleton in adoral aspect (×10). *B*, *Eophiura bohemica* (×3·5) (after Spencer 1951); *C*, *Astrophyton*, arm-base (after Lyman 1882) (×3). *D*, *Ophiuraster symmetricus* (×20); *E*, *Trichaster palmiferus* (×6). Abbreviations: 1, amb-ossicle (vertebra); 2, virgalium-1 (sublateral); 3, virgalium-2 (lateral); 4, virgalium-3 (lateral radiole in *A* and *E*); 5, virgalium-4; 6, hyponeural groove; 7, lateral (secondary) spines; 8, tentacle-scale; 9, ventral arm-plate. Specimens of *Trichaster* and *Asteronyx* received from University Zoological Museum, Copenhagen.

with echinoids, but from some common ancestor shared with Platasteriidae and Luidiidae. This ancestry can only have been the early Palaeozoic somasteroids.

If that premise is correct, archaic ophiuroids must have had virgalia arranged to form metapinnules. Such forms have not been recognized. Do they exist?

The metapinnules of somasteroids are joined by integument, with only the distal virgalia free. Similarly in asteroids, the structures equivalent to metapinnules (namely, the transverse rows of skeletal plates in Luidiidae) are completely united by integument to adjacent structures. Hence, if metapinnules occur in any ophiuroids, they would doubtless be obscured by integument. Since most systematic work on ophiuroids has hitherto relied upon external structures, metapinnules would be in all probability overlooked.

To search for virgalia in the numerous extant genera would be impracticable without some prior guidance, but data given recently (Fell 1960*b*) suggest that only three extant families could be considered relevant, for the characters of all the others would seem to preclude the likelihood of rod-shaped elements occurring in the arm-skeleton. Material being immediately available of two of these families, the Trichasteridae and Asteronychidae, dissections were first carried out on representative genera.

In several genera clear evidence of pinnate structure was found, with virgalia arranged in metapinnules of the expected pattern. An example is *Asteronyx* (figure 12*A*). The homologies of the virgalia with the skeletal elements of typical ophiuroids can be indicated precisely, as in figure 12*D*. The homologies with the virgalia of somasteroids and archaic asteroids can also be determined, but this requires prior comparison with structures known in lower Palaeozoic ophiuroids, especially the Stenurida. Here, the radial food-groove retained the open condition seen in somasteroids, and the ambulacral ossicles were not yet fused to form vertebrae; an example is *Eophiura* (figure 12*B*). Evidently the sublateral plate of Stenurida is virgalium-1 (the adambulacral of asteroids). If so, the lateral plate must be virgalium-2, and not the homologue of the adambulacral of asteroids (as hitherto supposed; Ludwig 1882; Fell 1941). Has virgalium-1, the sublateral, been retained in any modern ophiuroid? A systematic search has disclosed that a rod-like skeletal body lies on either side of the (fused) ambulacral elements, between the latter and the lateral plate (virgalium-2), in the genus *Trichaster* (figure 12*E*). This rod-like element must surely be virgalium-1, that is, the stenurid sublateral plate. But no such structure occurs in *Asteronyx* (figure 12*A*) nor, for that matter, in any other genus so far investigated; thus, virgalium-1 must have been lost in modern ophiuroids, with rare exceptions, such as *Trichaster*. Therefore the apparent first virgalium of *Asteronyx* must really be virgalium-2; therefore the elongate rod-like body carried by the latter is probably virgalium-3. This virgalium-3, however, resembles in form and disposition the terminal radiole of *Platasterias*, already shown to be virgalium-4. Have we therefore lost count of a virgalium in ophiuroids? On present evidence, it is impossible to say; but since the superambulacral of asteroids (virgalium-2) disappears without trace after its occlusion, the same process might have occurred in ophiuroids. Consequently the homologies of all the ophiuroid virgalia cannot yet be exactly specified, though the uncertainty is merely one of detail. The fundamental fact, namely that virgalia and metapinnules of somasteroid type occur in ophiuroids, is clear.

The result is far-reaching; for it means that the ophiuroid arm-skeleton must have been derived from an original pinnate archetype, the lateral plate of modern ophiuroids being the last vestige of its metapinnule. Just as subsidiary marginal spines develop in *Platasterias* above and below the marginal radiole (i.e. virgalium-4), so also in *Asteronyx* the distal virgalium (whether it be V-3 or V-4) is accompanied by a smaller cluster of spines. In the evolution of the sheathing lateral plate of later ophiuroids these smaller spines must have become gradually indistinguishable from the original terminal virgalium, just as occurred also in the case of the virgalium and spines carried on the inferomarginal virgalium of Luidiidae.

As regards the buccal apparatus, it is already known from earlier work (Ludwig 1882, *et auctt.*) that two pairs of lateral elements enter the jaw, with their corresponding ambulacral elements. It follows that the same interpretation applies to ophiuroids as for *Platasterias* and the archaic asteroids, to wit, the buccal skeleton is of pinnate derivation. Here, however, we can identify only two metapinnules; whether or not an additional proximal metapinnule has been occluded, or any analogue of the T-plate of other asterozoans, cannot at present be determined. Further embryological or palaeontological work may provide the answer.

A LIVING OEGOPHIUROID

It is widely stated in standard works that ophiuroids differ from asteroids in having the reproductive organs restricted to the disk region, and in lacking extensions of the gut into the arms. However, this is not so; as long ago as 1917 Matsumoto had reported extensions of the gonads into the arms in *Astroceras* and *Trichaster*; the same was reported for *Euryale* by Fedotov (1926), and Mortensen (1933) gave fuller details for other genera. All Euryalidae (*sensu* Fell 1960) probably have this feature, and it is also characteristic of the Asteroschematidae. Further, Mortensen (1932) defined a new family, the Ophiocanopidae, on the basis of the rare Indonesian species *Ophiocanops fugiens*, in which he had found that the gonads occur in approximately paired series along the arms (being absent from the disk), and a caecum of the stomach extends along the dorsal coelom of each arm.

Now, the present study shows that these must be archaic characters, for they occur in Luidiidae among asteroids, and at least the second character occurs in somasteroids (the gonads in *Platasterias* were not preserved, or undeveloped, in material so far examined). Therefore *Ophiocanops* became suspect as a possible relict of Palaeozoic ophiuroids; but published information on its endoskeleton was insufficient to make any comparison with fossils. No specimen being available in New Zealand, I sought the help of Dr F. Jensenius Madsen, Universitetets Zoologiske Museum, Copenhagen (in which museum Mortensen's material is held). Through his kindness, part of Mortensen's material from Jolo was sent to me. Dissection and microtomy confirmed Koehler's (1922) and Mortensen's (1932) observations, and also enabled the skeletal structure to be worked out. The latter shows that *Ophiocanops* is a surviving member of the Oegophiurida, an order of Ophiuroidea previously known only from lower and middle Palaeozoic horizons. It can now be inferred, therefore, that the unique soft-part characters of *Ophiocanops* are in reality the characters of the order Oegophiurida. There are no genital plates, and no genital bursae. The absence of genital plates in fossil oegophiurids implies a similar lack of bursae. The

Palaeozoic fossils exhibit an arm devoid of dorsal or ventral arm-plates; the same is true of *Ophiocanops*, where the shape and arrangement of the lateral plates (i.e. virgalia, as already shown) exactly matches the fossils. The fossils had seemed to suggest an arm of flattened form, since the lateral plates of either side are divergent and widely separated, hinged upon their corresponding ambulacral (vertebral) elements. The same skeletal arrangement occurs in *Ophiocanops*, but the arm is not at all flattened, in fact it is cylindrical; this is because a large dorsal coelom, and the gonads, overlie the axial skeleton, whilst the hyponeural groove is roofed over by integument on the underside. Presumably the same would be true of the fossils. Accordingly the following revised and expanded definition of the order Oegophiurida is now proposed:

Order **Oegophiurida** Matsumoto, 1915
(syn. Oegophiurina Spencer, 1951; Ubaghs, 1953)

Hyponeural groove covered by soft integument, to form a relatively spacious epineural canal, not closed over by ventral arm-plates. Disk covered by naked skin, or granulated skin, or by imbricating scales. Ambulacral ossicles alternate or opposite, fused to form vertebrae or separate. Madreporite primitively lateral, but tending to move ventrally. No oral shields. No radial shields. No dorsal or ventral arm-plates. No genital plates. No bursa. Paired serial gonads arranged approximately segmentally along the proximal two-thirds of the arm. Gastric caeca entering the arms.

Hitherto known from lower Ordovician to upper Carboniferous, but now also known from the extant family Ophiocanopidae.

Ophiocanops, on account of the well-developed vertebrae, falls in the suborder Zeugophiurina. The more precise systematic status of the genus may be assessed from the following key:

Suborder **Zeugophiurina** Matsumoto, 1929
(nom. corr., ex Zeugophiuroidea Matsumoto, 1929; syn.,
Zeugophiuricae Spencer, 1951; Ubaghs, 1953)

Ambulacral ossicles opposite, fused or separate. Middle Ordovician onwards.

Key to the known families

Disk small; arms elongate, slender, streptospondylous. Madreporite marginal.
Distal angles of jaw of normal proportions. One enlarged, dorsally placed, partly hollow primary arm-spine, supporting the dorsal skin of the arm, and protecting the dorsal coelom, gonads and caeca. Four smaller ventrolateral arm-spines, whereof the two lowermost form crotchets of euryaline type. Extant. Indonesia. Ophiocanopidae Mortensen, 1932

(Comprising the single known genus and species *Ophiocanops fugiens* Koehler, 1922; holotype Cat. No. 41080 U.S.N.M., U.S. National Museum, Washington).

Madreporite ventral. Distal angles of jaw elongate. Single hollow arm-spine. Upper Devonian of North America. Klasmuridae Spencer, 1927

Disk large; arms robust, zygospondylous or partly so.
Arm-spines needle-like, parallel to arm-axis. Silurian to lower Carboniferous Furcasteridae Spencer, 1925

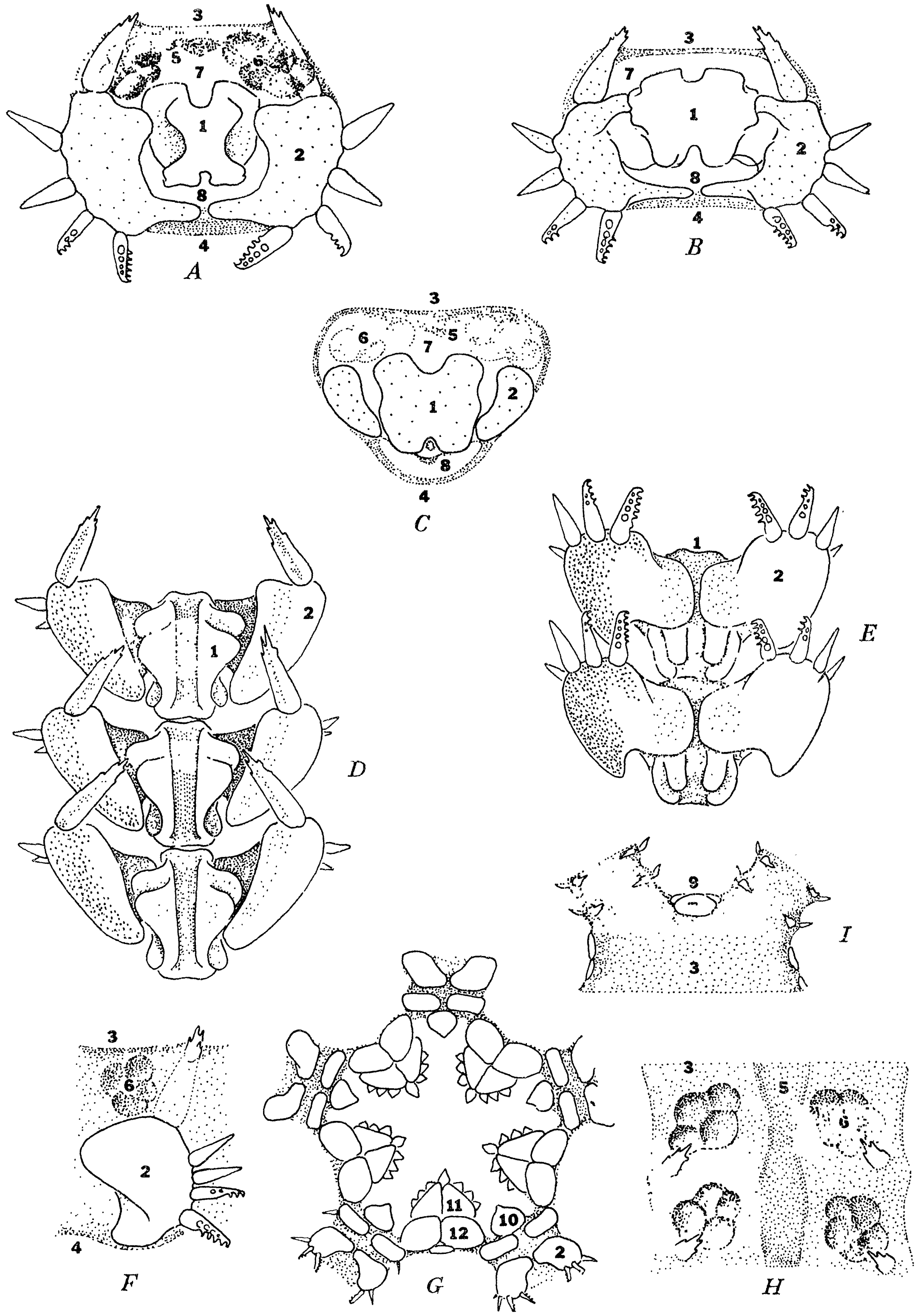

Figure 13. *Ophiocanops fugiens* (Order Oegophiurida), skeletal anatomy and related soft parts. *A*, distal aspect, transverse section of arm proximad (× 40); *B*, proximal aspect, distal arm-joint beyond reproductive and gastric region (× 7·5); *C*, transverse section through posterior (proximal) part of basal arm-joint (× 40); *D*, dissection of skeleton, aboral (internal) aspect, after removal of gonads and other dorsal soft parts (× 40); *E*, adoral (external ventral) aspect of arm, after removal of ventral muscle-band (× 40); *F*, lateral aspect of arm (× 40); *G*, disk, adoral aspect (× 10); *H*, aboral aspect of arm partly cleared with KOH, but not dissected (× 40); *I*, aboral aspect of disk (× 10). *I* and *G* based on Koehler (1922); all other data from material made available by University Zoological Museum, Copenhagen. 1, amb-ossicle (vertebra); 2, lateral plate; 3, aboral (dorsal) body-wall; 4, ventral muscle-band; 5, dorsal gastric caecum; 6, gonad; 7, dorsal coelom; 8, epineural canal; 9, madreporite; 10, radial ventral plate of buccal apparatus; 11, oral plate; 12, adoral plate.

Arm-spines not needle-like, inserted on a lateral flange, inclined obliquely to the arm-axis. Middle Ordovician to lower Devonian. Cosmopolitan.

Hallasteridae Spencer, 1925

The evident relationship between Ophiomyxidae and Ophiocanopidae suggests that the former family may have been an early derivative of Ophiocanopidae; this, if so, would be in accordance with Matsumoto's conclusion (Matsumoto 1915) that Ophiomyxidae are an archaic group. Since, however, strong evidence of pinnate structure is found in the Euryalina, as recorded above, it seems equally clear that some Euryalina are also archaic forms. As Mortensen (1932) indicates, the vertebral articulation of *Ophiocanops* is broadly of the streptospondylous (i.e. typically euryaline) type, whereas the arrangement of the arm-spines is ophiurine rather than euryaline. These facts suggest that both Euryalina and Ophiurina are derived from an oegophiurid stock, near to that which includes the Ophiocanopidae.

Mortensen (1932), whose researches did not encompass the fossil ophiuroids, was surprised and baffled by the whole structure of *Ophiocanops*. Never having encountered any living genus with so simple a disk (figure 13*G*, *I*) he was led to attribute its simplicity to secondary reduction and loss of the oral shields, radial shields, and other elements. He then supposed that the reduction of the disk had compelled the development of the brachial gonads and brachial caeca (figure 13*A*, *C*, *F*, *H*). Not realizing that the disk characters match those already known from the fossil oegophiuroids, he did not closely investigate the skeleton of the arms, and his sections (Mortensen 1932) show only the soft parts. As seen in the figures here given, the brachial skeleton is restricted to ambulacral and lateral elements, but both are extremely well differentiated, and relatively massive. The lateral plates have a medially directed wing (figure 13*A*, *B*, *E*), which, however, does not meet its fellow on the midline, save at one restricted region. Thus sections cut so as to lie outside the plane of the medial wings disclose an almost completely naked arm (figure 13*C*). The gonads lie above or between the lateral plates (figure 13*A*, *C*, *F*) always in the large dorsal coelom. The epineural canal, formed by the overgrowth of muscular integument below the hyponeural groove, are relatively large, as would be expected in a form of such antiquity as oegophiurids. The whole skeletal anatomy, both of the arm itself, and of the disk, is in complete accordance with the known characters of oegophiurids, and were *Ophiocanops* known only as a fossil it could not have been classified in any group other than the Oegophiurida. This being so, I find it quite unacceptable to attribute all its characters to secondary simplification and transformation, since this implies a complete reversal of the known evolutionary sequence of ophiuroids.

In reality, far from exhibiting secondary simplification, *Ophiocanops* shows quite archaic and generalized features. One of the most interesting is the marginal (dorsolateral) position of the madreporite (figure 13*I*). This character is known in no other living ophiuroid, and was evidently lost prior to the differentiation of the order Ophiurida. On the other hand, a marginal madreporite characterizes the order Stenurida, the earliest and most somasteroid-like ophiuroids, and also occurs in those somasteroids where the madreporite is known, and in some archaic asteroids. It is evident that this must be the original condition, and that in ophiuroids the madreporite has moved ventrally, to lie outside the adoral plates, whilst in asteroids it has tended to move dorsally towards the centre of the disk. It is significant that in none of the Echinozoa is the madreporite known to have occupied a marginal (i.e. ambital) position.

Another generalized character would appear to be found in the single radial plate which occupies the jaw-angle at the base of the arm. A corresponding structure is seen in some species of *Astroceras* (Family Euryalidae *sensu* Fell (1960), syn Trichasteridae *sensu* Mortensen (1933)). In *Astroceras*, therefore, the first arm-joint often has the appearance of having two ventral arm-plates, namely the radial oral plate, and the true ventral plate proper to the first arm-joint. The plates which thus resemble ventral arm-plates, but are evidently not true ventral arm-plates, must serve as valvate structures helping to close the gaping jaw (figure 13*G*). The radial oral plate evidently develops as the first sign of an incipient mid-ventral gradient, along which ventral arm-plates are subsequently differentiated in post-oegophiurid ophiuroids. The accompanying table 2 indicates the inferred sequence of some of the differentiations discussed above.

TABLE 2. SEQUENCE OF MORPHOLOGICAL DIFFERENTIATIONS IN EARLY EVOLUTION OF OPHIUROIDS

morphological differentiation	group in which first occurred	morphological time-scale
	Pre-Ophiuroid phases	
Virgalia stabilized as V-1, V-2, V-3 and V-4, in longitudinal and transverse gradients. Jaw established. Madreporite marginal. Brachial serial gonads. Brachial gastric caeca	Somasteroidea	post-chinianasterid and pre-stenurid
	Ophiuroid phases	
V-1 becomes sublateral. Interpinnular grooves lost. Disk sharply demarcated from narrow arms. V-2 now dominant virgalium, with secondary spines	Stenurida	pre-oegophiurid
amb-ossicles tend to fuse in opposite pairs. Radial food-groove (hyponeural groove) sealed by soft muscular integument, to form 'epineural canal', but no ventral (or dorsal) arm-plates	Oegophiurida	post-stenurid and pre-ophiocanopid
bursa evolves. Gonads enter disk. Genital plates develop. Gastric caeca disappear from arm. Ventral arm-plates appear, and seal off the epineural canal, now reduced to a vestige	Ophiomyxina	post-ophiocanopid and pre-euryaline
vestiges of V-1, V-3 and V-4 still persist in some genera. Vertebrae streptospondylous. Gonads may enter arm, but never as serially repeated organs. Dorsal arm-plates lacking. Bifurcation of arm frequently occurs	Euryalina	euryaline
V-2 only recognizable virgalium, now transformed into lateral plate. Dorsal arm-plates evolve, conspicuous tentacle-scales usually present. Vertebrae usually zygospondylous	Ophiurina	ophiurine

So far as concerns the finer details of ophiuroid phylogeny, nothing in the foregoing discussion would seem to invalidate the general sequence adopted in a recent synoptic treatment of the group (Fell 1960*b*), except the consequential transfer of the Ophiocanopidae from Ophiurida to Oegophiurida.

Ophiuroids, like early somasteroids and platyasterid asteroids, must have had originally a very small disk, a feature still exhibited by the surviving somasteroid *Platasterias*, the surviving Luidiidae and by ophiuroids such as the Ophiocanopidae and Asteronychidae. Initially, however, the disk was only indistinctly demarcated from the arm-base. The closure of the radial food-groove (i.e. hyponeural canal), and its conversion into the 'epineural canal' is evidently a secondary, and exclusively ophiuroid, phenomenon, linked with increasing agility of the arm, and a change in food-gathering habits. The involvement of the tube-feet in the vertebral ossicle in the adult stage of modern Ophiurida is also a secondary feature of that order, as a result of a telescoping of the main radial gradient during post-larval development. Spencer (1951) attributed the loss of the cupule, and the consequent involvement of the tube-foot with the vertebra, to the increasing flexibility of the arm itself, following the evolution of vertebrae from the fusion of paired ambulacral plates; fossil evidence re-inforces embryological evidence in this matter. The general homologies of the disk-plates of young ophiuroids with calyx-plates of crinoids, postulated by Ludwig (1882), have been accepted, save for minor differences, by all embryologists who have since studied the question.

Summarizing. No fundamental differences exist between ophiuroids and other asterozoans, and it is misleading to stress the differences between ophiuroids and asteroids in an attempt to establish some connexion between ophiuroids and echinoids. Ophiuroids, like asteroids, must have arisen from somasteroids, and since *Pradesura* has been found in the Tremadoc (Ubaghs, personal communication, 1962), ophiuroids differentiated from somasteroid ancestors not later than uppermost Cambrian times. All Asterozoa are closely related, forming a natural homogeneous assemblage, having no near connexion with the other so-called eleutherozoan classes.

Origin of the Asterozoa

In seeking the ancestry of Asterozoa, crucial evidence is supplied by the somasteroids, the oldest and most generalized forms. Collateral evidence is given by those characters widely shared among Asterozoa, both in embryonic and adult stages.

The following characters, restricted to one or other asterozoan groups of demonstrably late derivation, must be discarded from further consideration: suctorial tube-feet, highly developed ampullae, and an elevated ambulacral furrow (all found only in late asteroids); a closed radial groove, or epineural canal, and fused vertebral elements (late ophiuroids only); a naked disk (always preceded in development by a calycinal system of plates); longitudinal adradial growth gradients (secondary conditions derived from original pinnate transverse growth gradients); sharply demarcated slender arms; continuous marginal ossicles; interradial gonads confined to the disk; a sac-shaped unbranched stomach, an intestine, and aboral anus.

The following archaic characters remain, either known to be shared by all archaic asterozoans, or so widely shared among living asteroids and ophiuroids as to imply their inheritance from a common ancestry:

(1) Growth gradient fields of the type designated Group 1, resulting in pinnate structure and the production of petaloid, flattened arms.

(2) Arms with the radial nerve and radial water-vessel placed on the adoral surface of the axial skeleton.

(3) A double series of brachial axial elements (ambulacral elements) which, in the oldest forms either alternate, or give evidence of an original alternating condition; this alternating arrangement itself giving evidence of probable derivation from a still earlier uniserial condition, in which wedge-shaped axial ossicles must have carried a pinnule on the broader (outer) edge.

(4) Serially repeated rod-shaped, or approximately rod-shaped, elements, the virgalia, bearing a double row of webbed cover-plates, resembling the pinnular food-groove of a crinoid; the webs and cover-plates overhanging the interpinnular space, roofed by interpinnular integument.

(5) A disk-region which, in the younger stages of development at least, was covered by a centro-dorsal plate, usually surrounded by a ring of five basals, surrounded in turn by a ring of five radials; these plates covering and enclosing the entire disk at the time of their differentiation.

(6) Ciliary feeding, mediated by pinnately arranged fasciolar grooves, leading into the radial food-groove, and thus to the mouth.

All terms in this residual occur in somasteroids or, in the case of (5), are universal in other Asterozoa, and may be attributed to somasteroids until the contrary is demonstrated. Accordingly, the whole complex may be collectively termed the *somasteroid residual.*

Review of the included classes of the phylum Echinodermata shows:

(*a*) Crinoidea share the entire somasteroid residual.

(*b*) No term of the residual is shared by any other class.

Have the shared characters arisen entirely independently in Crinoidea and Somasteroidea through parallel adaptation to similar functional needs, or do they indicate a phylogenetic relationship?

The only functional needs shared by the two groups are those related to ciliary feeding, for in other respects they differ. Crinoids are either anchored by an aboral stem or are free-swimming; somasteroids are neither, being motile benthic forms. Crinoids direct the adoral surface upwards, to obtain plankton or plankton-fall as food; somasteroids direct it downwards. Now, ciliary feeding occurs in other echinoderm classes. Some of these adopt the posture of asterozoans, with the mouth turned downwards (spatangoid echinoids, for example). Others lie on the side, employing oral tentacles for ciliary feeding (dendrochirote holothurians). Fossil groups such as cystoids and blastoids were attached by the aboral apex, or an aboral stem, and relied upon brachioles for securing plankton; edrioasteroids collected plankton in the ambulacral food-grooves which coursed spirally upon the upper surface, thus increasing the collecting area. Yet none or these shares the complex mechanism shared by crinoids and somasteroids, though the functional needs seem to be the same. Hence the remarkable similarities between crinoids and somasteroids can only imply phylogenetic affinity; the classification system would collapse if the resemblances were dismissed as due to convergence, and much lesser resemblances used to unite groups not otherwise proved to be related.

If, then, crinoids and somasteroids are phylogenetically related, three possible relationships are available (1) crinoids and somasteroids arose from a common ancestry not shared by other echinoderms, (2) somasteroids arose from crinoids, or (3) crinoids arose from somasteroids. The last of these can be dismissed, since the fossil record shows that crinoids arose from earlier and more generalized pelmatozoans. Of the two remaining alternatives, both are possible, but since the fossil record shows that pinnulate crinoids evolved on several occasions, independently, from non-pinnulate crinoids, the second alternative would seem the more plausible. However, if the first alternative be preferred, the result is little different, for it implies a common ancestor differing little from a crinoid.

The hypothesis demands an explanation of the differences between crinoids and somasteroids, of which the most serious is the complete absence from the crinoid arm of an aboral body-wall, an extension into the arm of the perivisceral coelom, the development of brachial extensions of the stomach, and jaws.

Though it is conceivable that a viable form might arise from a crinoid, in which the pinnules were first united by integument alone, it is unlikely that this could have led to somasteroids. Were such interpinnular webs effective (or at least, not disadvantageous) existing comatulids might be expected to provide examples; in fact, few show the feature at all, and in none is there an extensive webbing; the Notocrinidae are an example. Even if interpinnular webs are postulated, it is hard to see by what means the perivisceral coelom and gut-caeca might have entered the arm. More serious still, no explanation would be offered of the origin of the somasteroid buccal apparatus. The latter, since it is of pinnulate origin, would necessarily arise on the *aboral* side of the stomach. Hence, any attempt to derive a somasteroid from a crinoid collapses, if it is based on adult anatomy.

An entirely different result emerges if attention be directed instead to the post-larval embryonic stages. As already seen, the evolution of the arm in Asteroidea has involved progressive dislocations of transverse growth gradients, and subsequent translocation of skeletal elements into new positions. In the post-luidiid phase the transverse gradient (already dislocated by the occlusion in the aboral direction of the second virgalium), suffers a further dislocation at the junction of V-1 and V-3, resulting in a sliding process, by which the inferomarginals (V-3) move out of their respective gradients. This dislocation permits the growth of a longitudinal series of actinal intermediate plates between the marginals and the adambulacrals. The dislocation of the transverse gradient between V-1 and V-3 permitted the interpolation of a new series of plates which effectively occupy the gap left by the occlusion of V-2.

Although direct evidence of the soft parts of Ordovician somasteroids is lacking, it is possible to explain the origin of such structures as brachial gastric caeca, and the brachial extensions of the perivisceral coelom, by postulating a dislocation of the main radial gradient in each arm—at the level of the first ambulacral ossicle. The dislocation may be envisaged as arising (as doubtless the others did) through a relatively minor alteration in a normal process of development.

In figure 14*A* is shown in diagrammatic vertical section the pentacrinoid stage of a feather-star of the pentametrid (5-armed) type. Figure 14*B* is the comparable stage in development of an asterozoan, oriented in the same way. In the crinoid embryo, the first brachial ossicle rests directly upon the calyx (on the radial plate), through which pass both the meridional gradient of the calyx itself and the radial gradient of the arm, intersecting in the sagittal plane. In the young asterozoan, on the other hand, the homologous ossicle in the embryo (amb-1) is displaced adorally, and will later contribute to the future buccal apparatus of its side of the radius. Thus, an intervening space is left between the proximal amb-ossicles and the calyx-plates. Through this gap the periviseral coelom begins to grow out along the radius, carrying with it the outgrowing caecum of the archenteron, and pushing before it the aboral wall of the radial margin of the calyx.

By some process such as this the first Asterozoa probably arise from crinoids. During development, the proximal brachial ossicles must gradually have lost their direct connexion with the radial calyx-plates, tending to move adorally. Once such dislocation became permanent, the asterozoans would be established as an independent group.

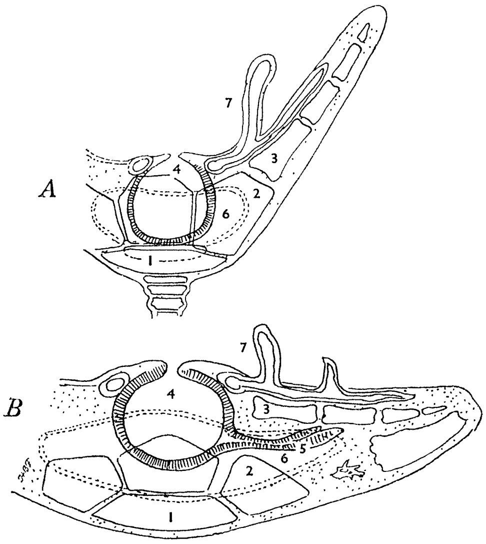

Figure 14. Comparison of pentacrinoid stage (*A*) of a crinoid, with (*B*) equivalent stage of an asterozoan, in vertical optical section, to illustrate inferred dislocation of main radial gradient in *B*, and consequent structural capacity to permit outgrowth of perivisceral coelom and caeca into arm. 1, centrodorsal; 2, radial calycinal plate; 3, first brachial (or amb-1); 4, archenteron; 5, caecum; 6, perivisceral coelom; 7, tube-foot. Discussion in text.

Evidence of a dislocation of the main radial gradient can be observed in the post-larval development of extant asterozoans. All published accounts of the development of the skeleton show that there is a gradual migration of the proximal ambulacral elements from an initial position on the main axis of the arm, to a secondary position nearer the mouth, the first two pairs of amb-ossicles, plus their adjacent virgalia, actually contributing to the jaw. The general accounts of the process (Ludwig 1877–82; Fewkes 1887–88; Murakami 1940–41; Fell 1941) seem to be of wide application, consistent with what can be seen in the young stages of any species of asterozoan. It is notable that the terminal plate is not part of the calyx, originating independently, and absent from the earliest somasteroids. The carinal plates of asteroids, and the dorsal plates of ophiuroids, are also late structures, not homologous with any brachial ossicles of crinoids.

Stürtz (1886, 1893) separated the fossil asteroids into major groups, according to whether the amb-ossicles are opposite or alternate. Gregory (1900), however, showed that this classification is artificial and self-contradictory, for opposite amb-ossicles have arisen independently in various fossil genera. Within the somasteroids both conditions occur.

Archegonaster and juvenile Chinianasteridae have alternating amb-ossicles; *Platasterias* has opposite ossicles, and they are opposite in the mature part of the arm in *Villebrunaster*. In biserial crinoids, the amb-ossicles (i.e. brachial ossicles) form opposite pairs, and the pinnules are consequently opposite; this condition is known to have arisen from a preceding stage in which the ossicles were alternate. The alternating condition, in turn, is known to have arisen from a still earlier stage in which monoserial ossicles occurred (figure 5), a condition still exhibited by the surviving groups of crinoids. The original condition in somasteroids must also have been monoserial, the alternating and opposite arrangements evolving in the same way as in crinoids. In ophiuroids, too, the alternating condition is found in Palaeozoic fossils (figure 12*B*), but the later ophiuroids all have opposite amb-ossicles. In the oldest ophiuroids, the Stenurida, the skeletal structure is comparable with that of Luidiidae, differing only in the arrangement of the amb-ossicles; hence it is probable that the alternating condition, seen in some Palaeozoic asteroids, is older than the opposite condition seen in others. Thus, the state of the amb-ossicles, whether monoserial, alternating or biserial, is merely a morphological grade of differentiation. It is analogous to the grades of jaw structure in Echinoidea, where Durham & Melville (1957) have recently proved that the camarodont condition originated independently in several unrelated lines of descent; the old order Camarodonta, being polyphyletic, has had to be abandoned as a formal unit of classification, and similar considerations apply in the present case.

Fossil crinoids show that pinnules differentiated relatively late in phylogeny, arising independently in several different groups of crinoids, in the lower Palaeozoic. In embryos of crinoids, as might be anticipated, pinnules do not arise until after the brachial ossicles have formed; they are at first quite short, and grow out like twigs from the main brachial axis, new pinnular ossicles being added distally. The arrangement of virgalia in Chinianasteridae implies the same manner of growth. In the embryo, the arm would already have carried an extension of the perivisceral coelom, and the outgrowing caeca, before the pinnules would develop. Thus the pinnules would automatically differentiate in the ventral body-wall. In *Chinianaster*, as also *Platasterias*, the distal pinnular elements project beyond the margin of the arm, indicative of the persistent strength of transverse gradients in these archaic asterozoans, a feature doubtless inherited from crinoid forebears.

In somasteroids the aboral skeletal elements are rod-shaped or more or less triradiate or quadriradiate, with or without an elevated tabulum. In Chinianasteridae they formed a mesh, without obvious transverse arrangement, recalling the less specialized Spinulosida. *Platasterias* has well-formed paxillae, with the quadriradiate portion embedded in the aboral body-wall, the elevated tabulum projecting above it; this was doubtless the archetypal structure of the paxilla in phanerozonid asteroids. Did such paxillae arise *de novo*, or were they derived from pre-existing structures? A possible answer is given by *Platasterias*, where the paxillae of the disk are small and irregularly arranged (as in Chinianasteridae), whereas on the arms they are larger, especially near the margins, and also form distinct transverse series, matching the metapinnules in number and arrangement (figure 9*A*). The growth gradients are evidently as shown in figure 9*B*, and the pattern suggests that these larger paxillae are perhaps distal virgalia whose gradient is deflected adradially on the aboral surface. This would not, of course, imply that the aboral body-wall itself arose by adradial growth from the margin, for this would plainly be impossible, and in any case conflicts with embryological evidence. All that might be inferred is that the gradients are carried in any soft tissues which happen to lie across their course and, being deflected around the edge of the arm, cause the paxillae to differentiate as if they were virgalia. The cross-section of a *Platasterias* paxilla is decidedly similar to that of a chinianasterid virgalium. A similar but weakened manner of arrangement of paxillae is seen in Luidiidae. In the post-luidiid families, however, the dislocation of transverse gradients is so severe that the paxillae usually show little sign of transverse arrangement at all. The complete absence of these structures from the arms of ophiuroids is doubtless due to the narrowness of the arm, and the consequent dominance of a single longitudinal radial gradient on the aboral side. On the disk, on the other hand, some ophiuroids show tabulate disk-plates which strikingly recall paxillae, and many in addition carry spinules.

The calyx in Asterozoa and crinoids

Early embryological studies by Agassiz, Ludwig and Sladen demonstrated eighty years ago that in young asteroids and ophiuroids the disk is initially enclosed within a series of plates which are directly comparable with the calyx of crinoids. Subsequent studies by Fewkes (1888), whilst confirming the earlier work, led to some uncertainty as to the exact homologies (though Fewkes did not deny the homologies). Later, Gregory (1900), who had carried out no embryological work himself, denied all the inferred homologies, and stated that the 'irregularity' of the calycinal plates of ophiuroids 'discredits their supposed homology with the three circlets of plates in the calyx of a crinoid. It is only natural that among the many variations in the grouping of the dorsal plates of ophiuroids, that one or more pentamerous rings should be more conspicuous than the rest' (Gregory 1900, p. 269). In his extremely brief discussion of this surprising view, Gregory considered adult and juvenile phases without discrimination, and his comment is illustrated by a diagram of *Ophiopyrgus* in which the plates are incorrectly identified (radial elements are termed 'basals', and a succeeding ring of interradially placed elements are termed 'radials'). More recently Mortensen (1912), Murakami (1940, 1941) and Fell (1941) have published further data, but no general review of the question of homology or otherwise of the calycinal plates with those of crinoids has been given. In the interim since Gregory's appraisal of the earlier work, a very extensive body of scattered data has accumulated, from which it is now evident that every species of asterozoan for which the young stage is known has a well-developed calyx, and that the plates develop in a well-defined pattern. It is therefore to be assumed that a calyx is characteristic of the whole class, and that probably all species exhibit it.

Fewkes's uncertainty as to the exact homologies arose from the fact (unknown to him) that the species he and his predecessors had studied belong to late groups of Ophiuroidea and Asteroidea, where the skeleton has acquired secondary plates. Fewkes, for lack of data, was unable to distinguish primary and secondary plates, for this requires a knowledge of the chronological sequence in which the taxa appeared. Gregory's misunderstanding, on the other hand, arose from his failure to distinguish juvenile and adult phases, the original calyx-plates of young stages being confused with interpolated secondary plates in the adults.

The following review is based on young material of many genera present in expedition collections examined in connexion with other work, but also draws upon numerous isolated records in the literature, not individually specified here.

Clark (1921) demonstrated that the pentacrinoid stage of all comatulids (for which the development is known) exhibits a calyx superficially of monocyclic type, there being a centrodorsal, surrounded by five interradial basals, in turn surrounded by five radials. An example is *Promachocrinus* (figure 15, 1 and 4), an Antarctic polybrachiate genus where, none the less, the pentacrinoid stage is of pentametrid symmetry. The basal elements are always occluded in extant comatulids, regressing during development, and ultimately sliding under the centrodorsal. The stage at which the basals are occluded varies, and in some genera it occurs relatively early, as, for example, *Eumorphometra* (figure 15, 3 and 6). Thus, at otherwise corresponding stages of development, the calyx may present either one or two cycles of plates, the variation merely expressing differences in activity on the radial and interradial meridional gradients. Infrabasals are sometimes found in pentacrinoid stages (Clark 1921), though they are always very small (figure 15, 11) and are inserted between the basals and centrodorsal as a later intercalation, and subsequently resorbed, or fused to the centrodorsal. Thus the calyx in comatulids is really dicyclic, though superficially monocyclic; the infra-basals are vestigial, form after the basals, and are soon lost.

In all ophiuroids for which caliciferous stages are known (several hundred species) the disk is provided with a complete calyx, comprising a centrodorsal and five radial plates. This is true of families which in the adult have a completely naked disk, such as the Asteronychidae and Ophiomyxidae, as well as of families which have a plated disk in the adult stage; invariably there is a complete calyx in the early stages of development. In many ophiuroids the calyx lacks the interradial basal elements, examples being *Ophiomyxa* (figure 15, 12) and *Ophiomastus* (figure 15, 9). The form of the calyx varies from a rounded dome, as in most genera, to a subconical dome, as in *Ophiosteira* (illustrated in Fell 1961, Figure 7, p. 68). In *Ophiopyrgus wyvillethomsoni* the calyx has the same shape as in a crinoid, with a conspicuous cylindrical centrodorsal, carrying an aboral excrescence simulating a vestigial or broken stem-columnal (which it may actually be); the holotype of this Tongan species is held in the British Museum (Nat. Hist.), and was recently re-examined at my request by Miss Ailsa Clark, whose notes and sketches are the basis of the figures here given (figure 15, 2 and 5). *Ophiopyrgus* is similar to the postulated transitional form between crinoids and asterozoans. Many ophiuroids develop basals, for example, the genus *Ophiosteira* (figure 15, 7), and these may persist into the adult stage, as in the genus cited, and many others of the family Ophiuridae. Infra-basals are not known to develop in ophiuroids.

In most ophiuroids the calyx is transitory, the plates being either resorbed or lost among a host of intercalary plates which arise around or between them. In many, however, the calyx-plates can still be recognized in the adult stages, and are then termed 'primary' plates; they often suffer more or less displacement, if the meridional plates in which they lie are still active. Thus many species show, in the adult, a centrodorsal at the centre, but the primary radial plates have moved midway towards the ambitus, or into some other intermediate position, with smaller, secondary plates wedged between them. Specific

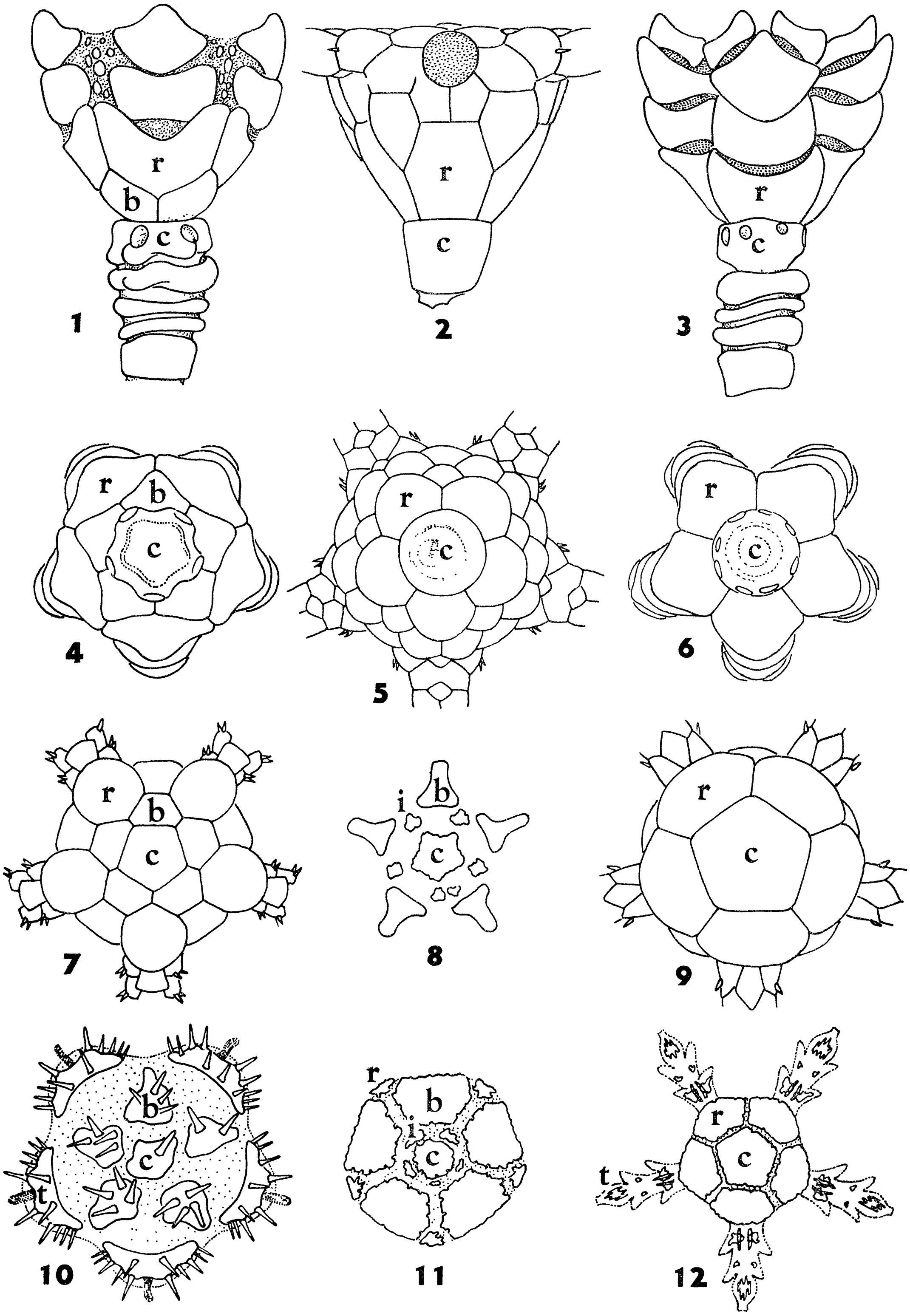

FIGURE 15. The calyx in astroradiate echinoderms. 1, 4, *Promachocrinus kerguelensis* (× 12), 2-year pentacrinoid stage, from material taken by the Trans-Antarctic (New Zealand) Expedition; 2, 5, *Ophiopyrgus wyvillethomsoni* (× 10), from holotype in British Museum (Nat. Hist.), sketched by Miss Ailsa M. Clark; 3, 6, *Eumorphometra aurora* (× 12), pentacrinoid stage almost ready for liberation, from material taken in the Ross Sea by the New Zealand Oceanographic Institute; 7, *Ophiosteira echinulata*, immature specimen with basals still conspicuous (× 6); 8, 10, *Asterina* sp. (× 15); 9, *Ophiomastus stellamaris* (× 30); 11, infra-basals in early pentacrinoid stage of comatulid; 12, *Ophiomyxa* sp. (× 15), juvenile. 1, 2 and 3 viewed in lateral radial aspect; all others in aboral aspect. b, basal; c, centrodorsal; i, infra-basal; r, radial; t, terminal plate.

differences may depend on such variations in meridional gradient activity; thus, in *Amphiura complanata* Koehler (1914) shows that the radials have moved out into widely spaced positions, between which lie numerous secondary scales, and Fell (1951 *a*) illustrates the same circumstance in *Hemilepis abernethyi*; again, in *Amphiura amokurae* Mortensen (1924) records a similar case. From the same genera species may be selected which illustrate the complete loss of the calyx, for example, *Hemilepis kinbergiensis*, or *H. griegi*, and *Amphiura belgicae*; again, in the related genus *Monamphiura*, the calyx may persist with little alteration in the adult state, as in *M. heraldica*, or only the centrodorsal may persist, as in *M. annulifera*. Numerous comparable cases exist.

Data, such as those just cited, were interpreted by Gregory (1900) as meaning that basals and radials represent enlarged plates of varying origin, belonging to any one of various cycles about the apex. Had he examined consecutive stages in any one species, the error of this interpretation would have been obvious. The plates are exact homologues, do not belong to various cycles, but move into various positions as a purely secondary phenomenon.

In the families with a naked disk, shown in this memoir to be primitive, the calyx develops as a complete structure, enclosing the whole disk, in no way differing from that of other ophiuroids; the condition in young specimens of *Ophiomyxa* is shown in figure 15, 12; Mortensen (1912) has illustrated a somewhat later stage in *Asteronyx*, where the calyx is still entire. Before the adult stage is reached, the entire structure vanishes, without trace. Now, the fossil record shows that dorsal arm-plates did not evolve till late in the phylogeny of ophiuroids. The structures are lacking, or at best only very imperfectly developed, in Asteronychidae and Ophiomyxidae. Yet all members of these families have well-developed ambulacral ossicles, which at first appear as paired, independent elements, as in asteroids and somasteroids; only later do they fuse in pairs to form vertebrae. The data therefore indicate that the radial gradient in the crinoid, which passes outwards through the radial plate of the calyx, and into the arm, produces brachial ossicles, and the latter must be the homologues of the ambulacral ossicles of asterozoans, not of dorsal arm-plates. Hence, in the young stages of *Ophiomyxa* and *Asteronyx*, the homologues of the brachial ossicles of crinoids are located at a deeper level in the arm, because the ambulacral ossicles themselves are displaced adorally. The lateral plates are the virgalia, as shown earlier in this paper. Now we arrive at the explanation of Fewkes's embarrassment, for the amphiurid he studied is a member of a family far removed from the Palaeozoic ophiuroids, differing *inter alia* in having a series of dorsal (and ventral) arm-plates. Fewkes thus observed the successive differentiation along the radius of a series of dorsal plates resembling the radial plates, but carried on the arm. Since he realized that these could not be homologues of the brachials of crinoids, he was at a loss as to whether the radial plate of the calyx was really such, or only an innermost member of the dorsal arm-series. The problem is here resolved, for there are no dorsal arm-plates in *Asteronyx* and *Ophiomyxa*, yet the radial plate is fully developed, and its gradient continues distally as the ambulacral series. It would be desirable to know the young stage of *Ophiocanops*, since we have in this genus a surviving member of a Palaeozoic group; however, in the light of the data here presented, it may be predicted that it will have a calyx similar to that of *Asteronyx* and *Ophiomyxa*, and that no trace of dorsal plates will be found in continuation of the radial element. This inference could be tested if young stages of *Ophiocanops* can be found on corals in Jolo.

The evidence here presented shows that Ophiocanopidae and Asteronychidae must be ancient forms, the one an oegophiurid, the other having virgalia of pinnate type, though it is a member of the Euryalina. Since *Ophiocanops* is obviously related to the Ophiomyxidae, all three families are to be regarded as archaic. All have a soft, naked disk in the adult stage. This, then, gives the explanation of why we do not find a calyx in Palaeozoic fossil ophiuroids. Evidently ancient ophiuroids had the calyx only in the young stage, and it was lost in the adult—just as is still the case in the three families mentioned, where no other disk skeleton forms, apart from radial shields in the Asteronychidae and Ophiomyxidae. The radial shields, however, are not part of the calyx. Their development in Euryalina shows that they arise from an adradial series of platelets equal in number and position to those segments of the arm which have been incorporated into the disk below. Thus they are homologous with the dorsal arm-plates of the rest of the radius; as indeed their arrangement in many ophiuroids suggests, for the basal dorsal arm-plates are often split into two portions, right and left. This in turn means that the late Palaeozoic Aganasteridae (the first of the suborder Ophiurina to appear in the fossil record) have been incorrectly interpreted as giving evidence of the late appearance in phylogeny of elements of the calyx in ophiuroids. The radial shields, supposedly part of the calyx, and present for the first time in Aganasteridae, permit no such interpretation; they are late structures, in no way connected with the calyx. I do not doubt that the young Aganasteridae had a calyx of the same type as *Asteronyx*, or indeed any other ophiuroid and that it was exclusively found in the young stages, and lost in the adult, just as in living ophiuroids.

It is not necessary to consider the asteroids at such length, for very similar reasoning applies throughout. The fundamental calyx of the asteroid is that illustrated for *Asterina* in figure 15, 10; similar calices are seen in all other genera examined. The only significant differences from ophiuroids lie in the absence of radial elements, and the dominance of the basals. In later stages, just as in crinoids, infrabasals are interpolated (figure 15, 8) and then lost again. The terminal plates are conspicuous, but, as seen from evidence already presented in this memoir, and illustrated in figure 11, the terminal plate is of post-chinianasterid (and pre-platyasterid) origin, and is therefore not part of the calyx. As regards the dorsal mid-radial elements of the arm, customarily called carinals in asteroid systematics, these are clearly secondary for the same reason that the dorsal arm-plates of ophiuroids are secondary. They are not homologous with the radials of crinoids or of ophiuroids, and are lacking from Luidiidae and other archaic families of asteroids. Since Fewkes and Sladen worked on *Asterina* and *Asterias*, both genera of late and specialized families, the same confusion arose as to the homologies of the carinals as had disturbed the interpretation of the calyx plates of ophiuroids. The true brachial elements are, of course, not the carinals but the ambulacrals, and their virgalia always begin at the adambulacral element.

We remain in ignorance of the calyx in any somasteroid, but this unfortunate hiatus will be of short duration, since it will not be difficult to obtain the necessary stages of *Platasterias*. It can hardly be doubted that a typical calyx will be found in the young stage. One juvenile specimen of *Chinianaster* (University of Lyon, Coll. Lignières, No. 563) does not exhibit the aboral surface, but the fact that such juvenile specimens occur as fossils gives us good grounds for anticipating that suitable material will be found if it is sought, since the matrix is capable of recording such delicate impressions as those the calyx would leave.

Summarizing, it will be evident that the Asterozoa possess a well-developed calyx, entirely comparable with that of crinoids, and of such other pelmatozoans as have a similar theca. On the other hand, there is no real calyx at all in echinoids or holothurians. The structure of the body in these forms can be compared only vaguely with that of crinoids or asterozoans, and is more directly related to that of the armless pelmatozoans; this is illustrated by the former arguments as to the systematic status of the archaic genus *Bothriocidaris*, now considered to be an echinoid, but regarded by Mortensen as a cystoid. Structures at the apex in modern echinoids have been compared (to my mind, inadmissibly) with the calyx plates of asterozoa. The similarity is only slight, the mode of development is different; and much more important, the similarity vanishes the further back in time one ranges, so that the earliest known echinoids are not comparable at all. Thus *Aulechinus* has one interradial madreporite, and no other regularly arranged apical plates; *Bothriocidaris* has a radial madreporite. The distinctive characters of the apex of later echinoids are lacking, and so vague are the boundaries between the ancient echinoids and holothurians that the genus *Eothuria* was originally described by MacBride & Spencer (1939) as a holothurian, but is now regarded as probably an echinoid. Whilst indicative of a probable close relationship between early holothurians and early echinoids, the very confusions which have occurred (in recent years) between cystoids, echinoids and holothurians serve to accentuate how widely these forms differ from early asterozoans. It is true we do not know the larval stages of either the Chinianasteridae or the ancient Perischoechinoidea, but the information at our disposal does not point to any conceivable near connexion between these groups. On the other hand, all that we know about asterozoa and crinoids leads to the inference that a calyx is a fundamental feature of these two groups.

Virgalia and pinnulars

The virgalium can now be defined as an elongate calcite skeletal element, formed in linear series along a transverse growth gradient, which originates in the axial (ambulacral) region of the arm; one transverse gradient is based upon each ambulacral ossicle, and consequently the series of virgalia are repeated successively along the arm, corresponding exactly in number and arrangement with the ambulacral ossicles themselves. Thus, if the ambulacral ossicles are alternate, as in Archegonasteridae, the rows of virgalia are alternate; and if the ambulacral ossicles are opposite, as in *Villebrunaster*, *Platasterias* or *Luidia*, the rows of virgalia are opposite. The virgalia of each series are essentially similar, but the distal members become smaller, so that the series tapers towards the tip of each series. In the less specialized asterozoa, particularly the Villebrunasteridae, and to a lesser extent the Platasteriidae, the transverse rows of virgalia are at first short at the base of the arm, further out become progressively longer, and then shorten again. The outline of the arm is therefore petaloid (figure 11*D*, and figure 17, plate 50).

The metapinnules of Asterozoa invite comparison with the pinnules of Crinoidea; and the definition of the virgalium here given is such as could include the pinnular ossicle of crinoids. However, the differences between these structures cannot be lightly glossed over. Two possible objections to the homology may be suggested (1) that pinnulars are differently shaped from virgalia, the former carrying a food-groove on the adoral surface, the latter having a 'tram-rail' form, with no groove on the adoral surface, and (2) that virgalia are elements of ossicular rows which are always united by integument to adjacent rows, whereas pinnulars are elements of free pinnules. Neither objection seems fundamental.

Reference to figure 11*A*, confirms the 'tram-rail' form of virgalia in their earliest known occurrence (in Chinianasteridae). They have essentially the same form in *Platasterias* (figure 10*D*). But their subsequent fate in Asteroidea and Ophiuroidea, as set out in the earlier parts of the present memoir, show the extreme plasticity of these elements, which become converted into rods, blocks, flat plates, or spines, or even into investing curved lateral plates, as in ophiuroids. The homologies of these various derived structures are unquestionably with virgalia. Thus the initial 'tram-rail' shape is not to be regarded as a fundamental feature of the virgalium itself, for it is subject to alteration.

Now, in all asterozoans the initial form of any skeletal structure during development is retained at the tip of the arm (or pinnate branch), as observed by Jackson (1889, 1903). The same is true of all crinoids (Clark 1921). Thus we may interpret the more or less cylindrical form of the distal virgalia of somasteroids as indicating the initial form of all the virgalia. Hence it would appear that a virgalium was initially a cylindrical rod without other surface features, formed serially in a pinnule-like row.

Considering now the crinoids, the same is seen to be true of the pinnular. It is invariably a cylindrical rod when it first appears during development, it invariably retains this form in the distal pinnules of the arm, and such changes as may occur in its shape are found only in the older, and more basally placed pinnulars. In many crinoids (perhaps half of all known existing species) the pinnular retains this essentially cylindrical form throughout life (see Clark 1921, for numerous examples); and in those which depart from it, the addition of the adoral ambulacral furrow, dorsal spines, or keels, etc., are clearly secondary features.

Further, in pentacrinoid stages of comatulids, the pinnulars—as also the brachials—retain the cylindrical form till near the end of the second year of life (in those genera where the duration of pentacrinoid life is known). The furrow in these cases is carried by soft tissue only, resting upon the cylindrical ossicle, and not affecting its shape. In *Promachocrinus* and *Eumorphometra* the cylindrical form of all arm-elements is most pronounced during the first 2 years, and *Promachocrinus* never develops a food-groove on the pinnular ossicle, even in the adult (which is large), and only a very feeble groove on the brachial ossicles. Yet, despite the absence of the groove, other specializations, such as dorsal spines and a deeply embedded nerve-strand occur. Thus the pinnular is not fundamentally a grooved ossicle; probably its primitive form is cylindrical.

As for the objection that pinnules are fundamentally free structures, whereas rows of virgalia (metapinnules) are united by integument—this view presupposes that no intermediate stage could exist, and ignores the fact that the pinnules in the Antarctic Notocrinidae have more or less tegumentary links with the tegmen and with the brachial axis (the gonads being even transferred to the brachial elements in consequence). Besides, there are numerous similarities between metapinnules and pinnules. Both result from the presence of gradients of Group 1 type, found in no other echinoderms. Metapinnules like pinnules, either alternate or lie opposite in pairs, and in both cases the alternatives depend on whether the brachial axial ossicles alternate or are biserial. In both cases cover-plates, webs and fasciolar grooves are supported by the major elements. Such similarities may well be due to homology.

The earliest Asterozoa must have had the following characters:

(1) General structure resembling a pentametrid comatulid.

(2) Pinnules joined by integument in the basal part of the arm.

(3) Growth gradients of the same type as in crinoids and somasteroids, i.e. Group 1.

(4) Fasciolar grooves in the integument between pinnules, with coverplates and webs capable of bending outwards to cover the grooves, as in *Platasterias*.

(5) Gonads at the base of the ray, probably repeated serially on either side, as in comatulids, and archaic asterozoans.

(6) Small disk, petaloid arms, depressed body, and body outline as in chinianasterid somasteroids and comatulids.

(7) Alternate (or even monoserial) brachial ossicles.

(8) Radial water-vascular tubes developed along the adoral side of the brachial ossicles, but possibly with simple branches traversing the proximal virgalia, along their adoral surfaces. The madreporite laterally placed at the edge of one interradius.

(9) A blind gut, with incipient caeca entering the arm-base between the radial calycinal elements and the proximal brachials.

(10) Posterior dorsal coelom entering the arm-base.

(11) No pedicellariae.

Such 'protosomasteroids' are at present unknown, but may be expected from Cambrian horizons, and may well have persisted into much later periods.

It might be objected that a postulated derivation from a free-swimming crinoid, or comatulid-like crinoid implies derivation from a specialized stock. But since the most plausible explanation of the origin of a somasteroid from a pelmatozoan involves alterations in development in a pentacrinoid stage, not in an adult stage, the objection that free-swimming forms are specialized loses most of its weight. Besides, it is of course equally acceptable to derive the somasteroid from a stalked stock, and the presence of what may be a rudiment of a stalk on the centrodorsal plate of *Ophiopyrgus* (an extant ophiuroid, figure 15) shows that it is not altogether ruled out that existing asterozoans may yet be found with a pentacrinoid stage.

Thus it is not necessary, in my view, to infer that a somasteroid must have originated from a comatulid. It could have arisen from the pentacrinoid stage of either a stalked or free-swimming form; but having once arisen, it would *resemble* a comatulid.

The fact that pinnulate crinoids are not known to have preceded somasteroids in the fossil record is a legitimate criticism; but not one, I think, which should be allowed to weigh too heavily. The sudden appearance in Europe and North America of highly evolved stocks during the lower Ordovician (and Tremadoc) is a reflexion, not so much of sudden evolution or sudden creation, as rather of a change in the environment, permitting colonization by forms which had evolved elsewhere. The arrival of the lower Ordovician forms may well have coincided with some physical change, such as the inferred flooding of Europe at that time by epeiric seas. Could it not be more reasonable to infer that in other regions, such as the Indo-Pacific, pinnulate stocks were present in late Cambrian times? Efforts should be made to find suitable facies in late Cambrian rocks in the Indo-Pacific region, before any categorical statements are made that crinoids are of later origin than somasteroids. However, in deference to the fossil record as it is known at present, it must be admitted that somasteroids, and the earliest ophiuroids of somasteroid-like groups, had already differentiated by the uppermost Cambrian or lowermost Ordovician, whereas true crinoids are not known from rocks older than lower Ordovician. Just how significant such negative evidence may be is sufficiently obvious from the present memoir, which reports living members of the Platyasterida, Oegophiurida and Somasteroidea, all which groups have until now been considered extinct since the middle Palaeozoic, merely because the fossil record does not report their existence after the Carboniferous. Similarly the record is likely to be equally unreliable as to the dates of first appearance of these, and other, groups. Where the fossil record is so woefully incomplete, as in the three instances cited, morphology proves a surer guide to relationship, and hence to inferred ancestry. I am therefore unable to attach much weight to the mere absence of fossil crinoids from Cambrian rocks when other data imply that such fossils can be expected. Future research may well fill the hiatus.

General considerations

The major phylogenetic trends of Somasteroidea, Ophiuroidea and Asteroidea can be analyzed and expressed as a series of progressive modifications of two systems of growth gradients, and both systems can be traced to their origin in some pentametrid branch of the Crinoidea or their immediate relatives. A natural classification of the asterozoans can now be derived on the basis of the growth gradients, which are preserved in the plate-arrangement of the adult, and can thus be read with equal facility in fossils and extant forms. The larval stages, on the other hand, have followed an independent clandestine evolution, related to special demands of the planktonic phase in the life-history of those echinoderms with such phases.

A far-reaching result of the whole preceding discussion is that asterozoans represent a post-crinoid evolutionary development, and are the youngest of the echinoderm groups. On the other hand, the Echinoidea and Holothuroidea cannot be so regarded, and their origin must be sought elsewhere.

Pre-crinoid phases

It is at present impossible to make any precise inference as to the origin of crinoids, but it has never been seriously disputed that their ultimate ancestry lies among the earliest pelmatozoans, and must have comprised forms similar to cystoids or eocrinoids. The same conclusion emerges when the analytical method here used is applied to the problem.

As shown already in this memoir, crinoids share a large group of characters with somasteroids, the so-called *somasteroid residual* defined on p. 412. When this residual is subtracted from the sum-total of crinoid characters, there remains a further residual which comprises essentially those generalized characters possessed by archaic, attached pelmatozoans with a globoid body in which the primary (and only) gradients are meridional. The analysis can be taken no further (though, of course, it can be expressed in more detailed anatomical terms), for at this point the fossil record fails. We can only assume that it will eventually be traced among the archaic, bilaterally symmetrical homalozoans, namely the carpoids.

The Pelmatozoa would therefore appear to form two major groups, an earlier one having no definite gradients, or meridional gradients only, and a later one in which radial gradients appeared, causing the outgrowth of the arms. If the characters of holothurians and echinoids are now examined, they will be seen to fall into a relationship with the former, but not with the latter. An archaic echinoid, for example, may be considered as a kind of early pelmatozoan in which the meridional gradient patterns have been fully expressed, and the body re-oriented, so that the adoral surface is directed downwards, and the anus has migrated to the aboral pole. Holothurians may be considered in the same light. Ophiocistioids seem to represent an intermediate grade, in which the anus is not yet at the aboral pole. Of the fossil history of the holothurians we know next to nothing. Of that of the echinoids, on the other hand, a relatively rich documentation is available; and this has been explored in great detail, notably by Mortensen (1928–51) and more recently by Durham & Melville (1957). The early history of the echinoid test gives evidence of much instability in the nature of the meridional gradients, especially as regards the numbers of vertical columns of plates in the ambulacral and interambulacral areas. This is only what would be expected in a group which has apparently relied entirely upon permutations of meridional gradients for its evolution. Probably similar consideration would apply to the holothurians, could we but find well-preserved fossils. At no stage is there evidence of arm-structure ever having occurred in any of the echinozoans, and this may be attributed to the lack of radial axial gradients.

General phylogeny

The analysis has now reached the point where its results appear in sharp contrast against those opinions which are still generally in vogue. For, just as appeared for the post-larval embryological data set out above, so also does it appear from the whole comparative anatomical review here presented, the Asterozoa and Crinoidea form a natural sequence, derived from an earlier pelmatozoan stock; but the Echinozoa, on the other hand, form a separate grouping, possibly derived from the same early pelmatozoan stock. This result contradicts the idea of a 'subphylum Eleutheroza' (a grouping which comprises Asterozoa and Echinozoa, and is supposedly contrasted with the Pelmatozoa). Since the concept of the Eleutherozoa is so widely accepted (and has indeed been adopted in my own work hitherto), it will be necessary to examine the basis of it in some detail.

The last decade has seen a broadening in our knowledge of the earliest asterozoans, and this in turn was the natural outcome of a half-century's research on Palaeozoic echinoderms. Although imperceptible at the time, but much clearer now in retrospect, every advance in our knowledge of archaic asterozoans, both of ophiuroids and asteroids, as well as somasteroids, has accentuated the similarities between them and crinoids, whereas every advance in our knowledge of archaic echinoids has shown how dissimilar they were to asterozoans and crinoids.

Until now, the Eleutherozoa have been credited with the following common characters, thought also to distinguish them from Pelmatozoa:

(1) An aboral anus (the absence of an anus from ophiuroids being explained as a secondary loss).

(2) Suctorial tube-feet with ampullae (ophiuroids being regarded as aberrant, as also late echinoids, where the tube-feet are respiratory).

(3) No trace of crinoid arm-structure.

(4) No trace of pinnate food-grooves, webs and cover-plates.

(5) Ciliary feeding unknown (save as a secondary feature in late echinoids, and in some ophiuroids and a few asteroids).

(6) Jaws.

(7) A single madreporite, instead of multiple hydropores.

(8) No stalk, the adoral surface being directed downwards.

(9) Pedicellariae (unknown, however, in ophiuroids and holothurians).

(10) Dermal spines (radioles).

(11) Bilaterally symmetrical larvae.

A drastic review of these supposed 'Eleutherozoan' characters is now inevitable.

Anus

There is no anus in archaic asteroids, nor in any ophiuroid, nor is it known in any somasteroid. An aboral anus occurs as a late acquisition in post-luidiid asteroids. On the other hand, fossils show that an aboral anus is a fundamental character of echinoids, present in the earliest forms. All holothurians have an aboral anus.

Suctorial tube-feet and ampullae

Suctorial tube-feet, which occur in all the early morphological grades of echinozoa, are completely lacking from all except late phases of asteroid evolution. That they appear so widespread among existing asteroids is merely due to the fact that the most successful and aggressive littoral asteroids comprise late derivatives of earlier stocks which had originally lacked suctorial tube-feet. The ampulla, on the other hand, is much more widespread, since it occurs in all asteroids, in late somasteroids (Platasteriidae, where however it is small), and may possibly have occurred as an external structure in early somasteroids and perhaps even in the cupule of Palaeozoic ophiuroids. The evidence indicates that the ampulla underwent an increase in size after the erection of the asteroid furrow, and the perforation of the interossicular foramina, permitting the entry of the ampullae into the brachial coelom. The small size of the ampullae in *Platasterias*, and their complete absence from all extant ophiuroids, suggests that they are not fundamental characters of asterozoans, but are more likely to be secondary structures evolved after the asterozoa had differentiated as a separate group. In the Echinozoa, the evidence points entirely the other way. Here, the earliest condition we know, that of the regular forms, such as *Aulechinus*, shows a large well-developed ampulla. Forms such as *Aulechinus* exhibit the transitional stages between an external ambulacral canal, such as occurs generally in echinoderms, and the secondary internal canal, as occurs in all later echinoids. Such resemblances as are seen between *Aulechinus* and Asterozoa do not seem to imply any close relation between echinoids and asterozoans, but merely reflects their common descent from an ancient generalized pelmatozoan which had an external radial ambulacral canal. The fact that no ampulla occurs in the earliest asterozoans, and stages in its evolution can be traced in the asteroid line alone, shows that the ampulla has evolved independently in asteroids and echinoids, long subsequent to the separation of their ancestral stocks. In later echinoids, when the ampulla is small, it is clearly a secondary condition achieved in late phases, notably the irregular echinoids, where suctorial tube-feet have been lost, following a change in feeding and respiratory habits. Neither suctorial tube-feet nor ampullar structure can be cited as fundamental eleutherozoan characters therefore, since they have evolved independently in the Asterozoa and Echinozoa. In figure 16 are illustrated known stages in the evolution of the tube-foot in asterozoans, prior to the appearance of the sucker. The condition in a young developing pentacrinoid stage of a crinoid is illustrated in figure 16*A*; here, the tube-feet (tentacles) alternate, since the arm is uniserial in all known extant species, but it is obvious that in the extinct forms with biserial arms the tube-feet would have been paired. There is at first only one tube-foot opposite each pinnule, the other tube-feet being added later as the pinnular vessel grows outwards. When this is compared with a somasteroid such as *Platasterias* (figure 16*B*) it is not difficult to envisage how the asterozoan condition could arise, by

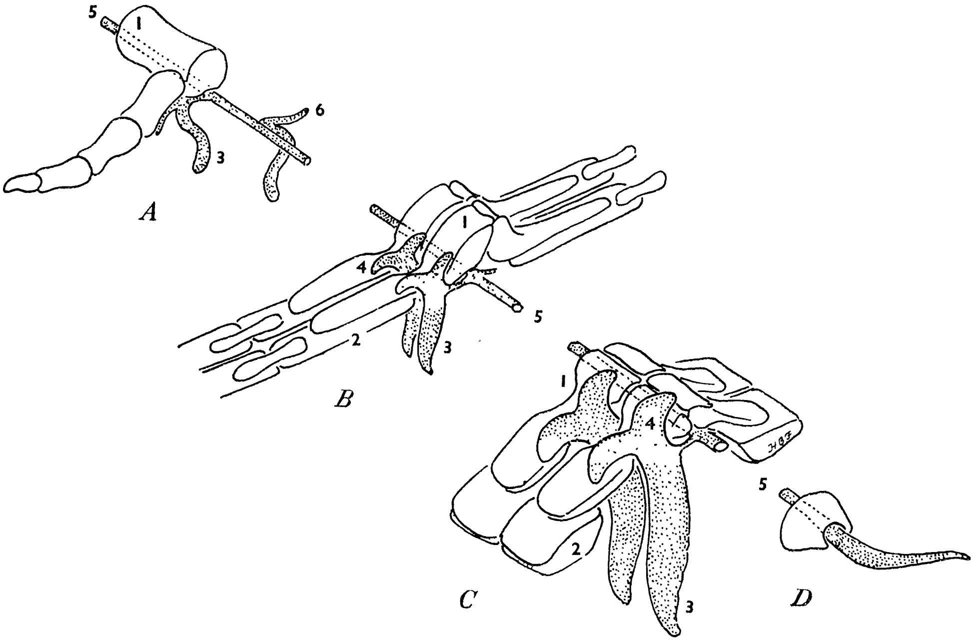

FIGURE 16. Tube-feet and related structures in: *A*, developing pentacrinoid stage of comatulid; *B*, *Platasterias*; *C*, *Luidia*. The asteroid terminal plate is represented in *D*, with projecting extension of radial water-vessel, simulating a tube-foot. Description in text. 1, brachial (ambulacral) ossicle; 2, adambulacral plate; 3, tube-foot (tentacle); 4, ampulla; 5, radial water-vessel; 6, rudiment of pinnular water-vessel.

suppression of the rudiment which would produce the pinnular vessel (or its conversion into the ampulla itself, perhaps), and by the insertion of the ampulla between the adjacent ambulacral wings. The condition in fossil somasteroids is inferred to have been like that shown in figure 11*A*, where the whole tube-foot evidently rested in the cupule; there was no internal ampulla in Chinianasteridae, as evidenced by the lack of a perforation between adjacent amb-ossicles (figure 11*B*), but the manner in which the perforation arose can be inferred from *Platasterias* (figure 11*C*), where a small hole appears between adjacent amb-ossicles in the early stages of development near the arm-tip. In figure 16*C* is shown the condition in the Platyasterida (*Luidia*), after the erection of the ambulacral furrow; the whole tube-foot is larger, since more space is available for its accommodation, and it is now called upon to serve as a collecting agent for gross detrital scavenging and predation; consequently the ampulla has enlarged to accommodate the larger volume of hydrocoel fluid required by the tube-foot. Successive stages in the process, in which the suctorial condition is reached, can be understood without further illustration in the present context.

The foregoing suggestions offer a reasonably acceptable interpretation of the origin of the asterozoan tube-foot from a structure such as is exhibited in the tentacles of crinoids. At the same time it will be seen that it is unreasonable to derive the asterozoan tube-foot from the type present in early echinoids, for in order to do this, we must first postulate that the ampulla and suction-cup are lost, and then postulate that they gradually evolve again in accordance with the sequence in which we now realize they appeared in asterozoans.

Crinoid arm-structure

A pattern of gradient fields produces in the somasteroids an arm-structure which closely parallels that of crinoids, and is found in none of the echinozoans. The gradual transformation of this pattern, from that seen in somasteroids, to the derived, and superficially dissimilar, pattern seen in ophiuroids and asteroids, has been demonstrated in the present memoir, and shown to be due to progressive changes in gradient fields in growing tissues. Thus the lack of crinoid-like arms in modern asteroids and ophiuroids is a purely secondary condition. The crinoid-like features of the arm in early asterozoans are sufficiently evident in figures 6 and 11, and in figure 17, plate 50. On the other hand, no echinozoan has ever been found to have arms of any shape or form, nor anything even remotely similar to them.

Pinnate food-grooves, webs and cover-plates

These structures are shared in common by somasteroids and late pelmatozoans and the probable mode or derivation of the somasteroid pattern from the crinoid pattern has been outlined in this paper. The somasteroid grooves can in turn be recognized in the respiratory fascioles of luidiid asteroids. Pinnate food-grooves, with associated webs and cover-plates, do not occur in any other echinoderms. Analogous grooves and cover-plates occur in some blastoids and edrioasteroids, but they are clearly of independent origin, since they have no relationship to pinnate arm-structures, and are carried directly by the ambulacral plates of the meridional gradients in those animals. Among the Echinozoa there is nothing remotely comparable to pinnate food-grooves, and webs with or without cover-plates are also quite unknown.

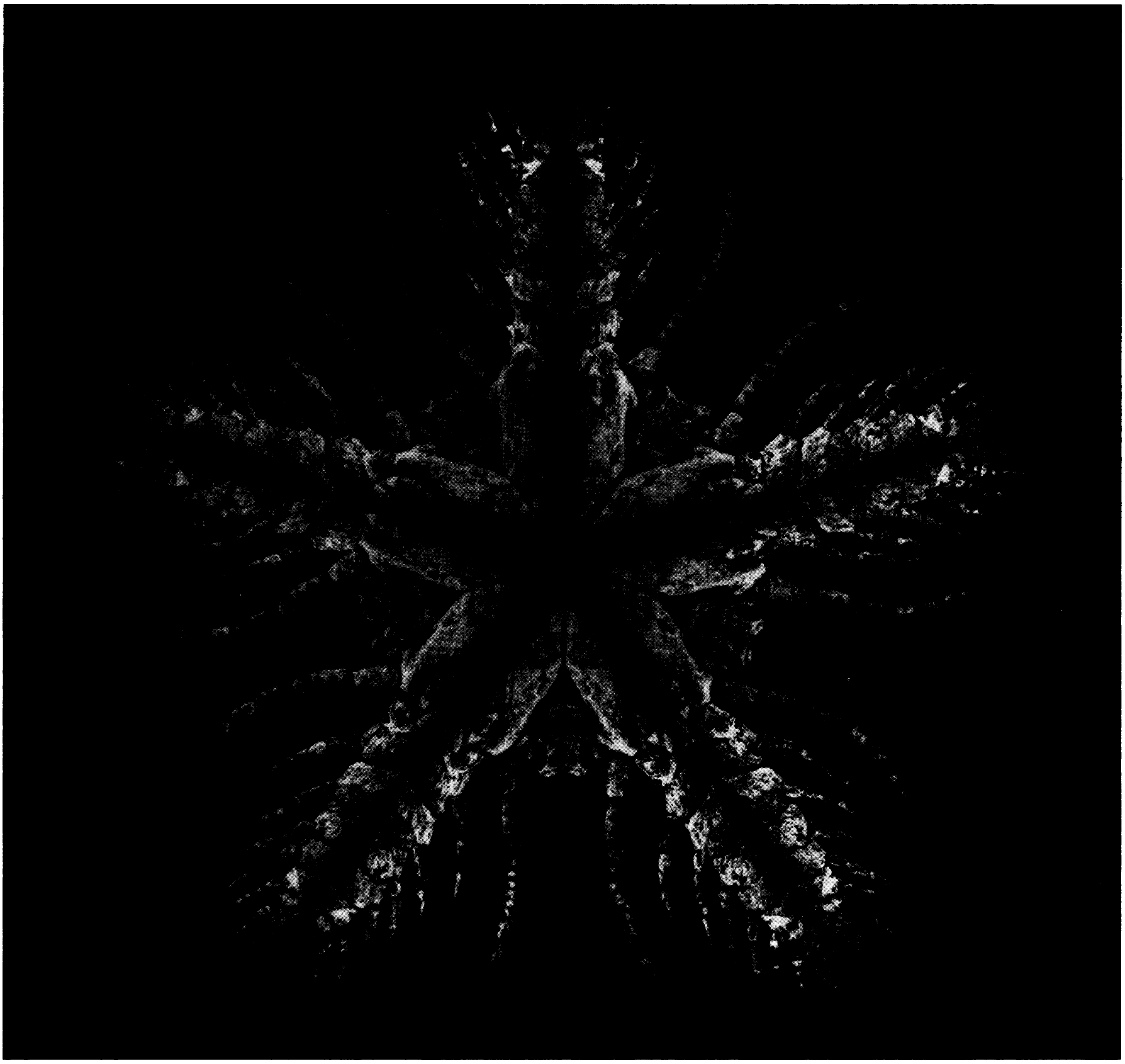

FIGURE 17. *Chinianaster levyi* Thoral (Chinianasteridae, Somasteroidea), juvenile stage, R 7·0 mm. Mosaic photographic reconstruction of skeleton in internal aspect, based on six negatives obtained from specimens 555 (coll. Lignières) and ES 2 (coll. Thoral), in the University of Lyon collection; material studied by courtesy of Professors H. Gauthier and G. Ubaghs. (Magn. × 14.) For identification of structures, see figure 11*E*. Photography M. D. King and the author.

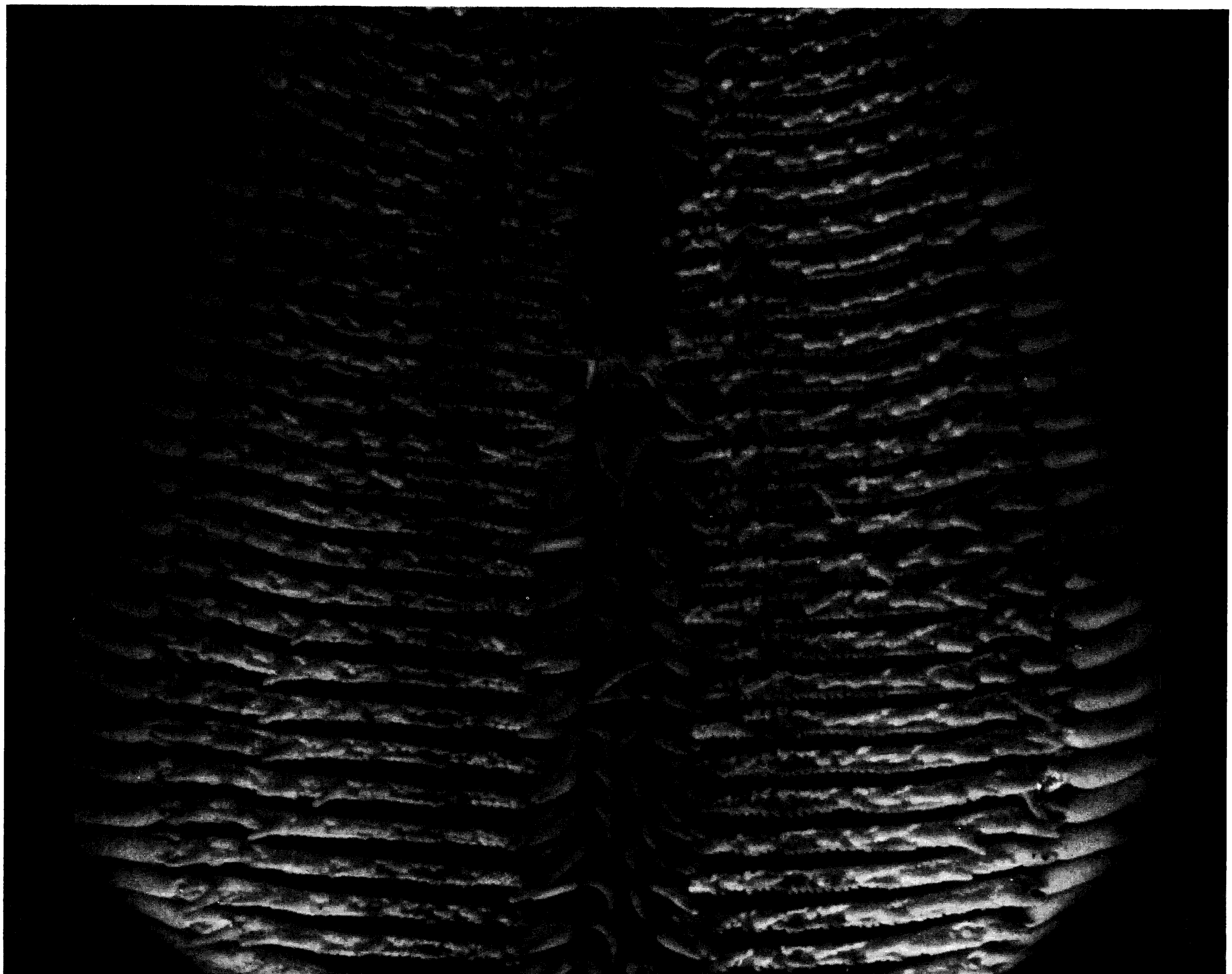

FIGURE 18. *Platasterias latiradiata* Gray. Adoral aspect of proximal part of one arm. In this specimen the webs and cover-plates are erected, exposing the interpinnular grooves. (Magn. × 6). Material from Corinto, Nicaragua, *Velero III* Station 962-39, May 1939, courtesy F. C. Ziesenhenne, Allan Hancock Foundation. Photo: M. D. King.

Ciliary feeding

Somasteroids show that ciliary feeding is a fundamental feature of the earliest asterozoans, and that it was established on a pinnate plan. It closely matches the mechanism found in crinoids. Its absence from most modern asteroids and from many ophiuroids is clearly secondary. On the other hand, the only echinozoans which possess ciliary feeding mechanisms are demonstrably late forms, in which the mechanism has been secondarily acquired, following the adoption of spatangoid features, in the late Mesozoic. Further, the ciliary mechanisms in echinoids comprise ribbon-like bands which meander across the surface of the meridionally-symmetrical test, whereas pinnately arranged bands or grooves are completely unknown. Thus, whereas ciliary feeding was the initial mechanism in asterozoans, and was subsequently lost, in echinozoans it was lacking from the original forms, and was subsequently acquired by certain groups, and then only in a way completely unlike asterozoans.

Jaws

As shown here, the asterozoan jaw arose from the transformation of three pairs of proximal ossicles on each arm-base. The structure seen in modern ophiuroids and asteroids is demonstrably derived from that seen in somasteroids, which in turn is derived from an earlier crinoid-like pinnule structure. In echinozoans, on the other hand, the jaw structures betray at no stage a pinnulate structure, and were simpler and fewer in the early echinozoans than in the later ones. The history of the buccal apparatus in echinoids is already well known, and offers no comparable features to those seen in asterozoans. In each case the buccal apparatus has evolved independently, and along different lines, from different beginnings.

Madreporite

A madreporite may replace or incorporate hydropores in various pelmatozoan groups. In the somasteroids, where the madreporite is at present known only from some genera, it lies near the margin of the disk, and as indicated above (p. 409) the madreporite has subsequently moved adorally in ophiuroids, and more or less adapically in asteroids. In holothurians it is usually internal, and lies in an interradius, near the adoral region. In the earliest echinoids it is either radially or interradially placed, but is always adapical. Such diverse conditions do not indicate more than the variability of the structure. The notion that pelmatozoans have only hydropores and that 'eleutherozoans' have always a madreporite, is incorrect; some ophiuroids have hydropores in each interradius, and some pelmatozoans have a madreporite.

Aboral stalk and orientation

The secondary loss of the stem occurred in many groups of pelmatozoa independently. Some of the free forms thus produced may even have become benthic creeping forms, oriented with the adoral surface directed downwards (e.g. *Edriocrinus*), though this is not certain. Most free crinoids have evidently adopted a comatulid mode of nektonic life. The somasteroids suggest, by their symmetry and other features, an ancestry linked with some pentametrid free-swimming crinoid, with more or less tendency towards biserial arms. Such an ancestor would be stalked only in the earliest post-larval stages, and it is easy to envisage the loss of the pentacrinoid stage in descendant groups. To deny any relationship between somasteroids and crinoids, merely on the grounds of there being no stalk in somasteroids, would be unreasonable. Changes in orientation have occurred frequently, and are of no broad phylogenetic significance; they are related to feeding habits. Thus, the gorgonocephalid and related ophiuroids, irrespective of whether the arms are branched or simple, have the adoral surface directed upwards, as in crinoids; they rest upon the sea-floor, scooping the plankton from the water in exactly the same way as in crinoids. On the other hand, the carnivorous euryalids creep about the surface of antipatharian corals, browsing on the polyps; and yet again the long-armed related genera climb antipatharians, or 'fish' the surrounding water, oriented so that the adoral surface lies on one side and the aboral on the other, with the ambitus of one side directed downwards; sea-floor photographs illustrating these habits have been published by Fell (1961). Numerous other examples can be cited of change of orientation. Suffice it to note that asterozoans which are habitually oriented with the adoral surface downwards are those forms in which the pinnate arm structure has vanished through secondary changes, and those which exhibit the pelmatozoan orientation are forms in which more or less evidence of pinnate structure can be found. The earliest somasteroids were presumably able to feed in either position, and may even have been capable of swimming like feather-stars. No such capabilities are exhibited by the earliest echinoids nor, indeed, by any echinoids, since their fundamental structure prohibits this.

Pedicellariae

The comparative anatomy of pedicellariae in asterozoans is now relatively well understood. The structures arose from modified spinules or granules, and numerous stages in the various evolutionary sequences are known from extant asteroids. Pedicellariae are unknown from the somasteroids and are lacking from some of the most archaic types of asteroid. They are unknown from ophiuroids (such structures as have erroneously been termed pedicellariae in that group being in reality crotchets). Thus pedicellariae are a secondary acquisition in asterozoans, and occur only in certain asteroids of late origin. In Echinozoa, pedicellariae occur only in echinoids, and exhibit an evolutionary sequence entirely independent of that seen in asteroids. Clearly they have arisen independently in the groups which have them and, like larval forms, are not related to broad phylogenetic groupings. Their detailed anatomy differs in asteroids and echinoids, and their similarities seem attributable to parallel evolution in response to similar needs.

Radioles

Somasteroid anatomy shows that primary marginal radioles in ophiuroids and asteroids have arisen from distal virgalia. Other dermal spines and spinules are late developments in asterozoans. Dermal spines and spinules occur as discrete skeletal elements in some crinoids (e.g. *Monstrocrinus* where they resemble cidaroid radioles, and *Acanthocrinus*); they have arisen independently in such cases. Radioles occur universally in echinoids, but are lacking from holothurians. The evidence indicates independent origin of these structures in the various classes.

Bilaterally symmetrical larvae

The unreliability of larval forms in echinoderms as a basis for broad phylogeny has been discussed elsewhere (Fell 1948); and the inductions which have led to the isolation of various archaic forms here reported could never have been drawn on the basis of larval evidence. Echinoderm larvae must have followed independent clandestine evolution, in response to temporary planktonic food-gathering phases in the life-history, and do not reflect the relationships of the classes. To infer that ophiuroids are more closely related to echinoids than to asteroids, as their larvae would imply, is too preposterous to warrant further serious consideration (Fell 1962).

CONCLUSIONS

Crinoids and asterozoans present a uniform progression, in which the main pattern of growth of the body is at all times dominated by five, divergent radial axes (giving rise to the arms); and whereas the earliest asterozoans retain the pinnate pattern of subsidiary transverse axes of growth, emerging from the main radial axis, the later grades of differentiation show a gradual transformation into patterns in which longitudinal series of structures become predominant, and eventually obliterate the transverse axes. The fate of subsidiary structures, such as food-grooves, cover-plates, tentacles and tube-feet can be traced, and found to be correlated with the changes in the major skeletal elements.

On the other hand, the echinoids, holothurians (and probably also the Ophiocistioidea) comprise an entirely distinct assemblage, in which dominant, divergent radial axes never arise, but instead are replaced by a meridional pattern of growth, more comparable with that of archaic globoid pelmatozoans, at a pre-crinoid grade of evolution.

Thus, the assemblage termed Eleutherozoa, which includes all asterozoans as well as echinoids, holothurians and ophiocistioids, is a heterogeneous grouping, made up of at least two dischronous stocks, one of pre-crinoid derivation, the other of post-crinoid derivation. It is polyphyletic, and the characters supposed to be shared by Eleutherozoa are either those shared by all radiate echinoderms, or are shared only by demonstrably late groups of Asteroidea and demonstrably early groups of Echinoidea. In addition to including stocks not closely related, the Eleutherzoa excludes those pelmatozoans which must be more closely related to asterozoans than asterozoans are to the echinoids and holothurians. The taxon Eleutherozoa is therefore unacceptable as a formal unit of classification, for it conceals the relationships between excluded and included classes.

These conclusions can be given taxonomic expression if the subphylum Eleutherozoa is abandoned, and replaced by two subphyla, as indicated in the following table:

- Subphylum Echinozoa
  - Classes Echinoidea, Holothuroidea, Ophiocistioida, Helicoplacoidea
- Subphylum Asterozoa
  - Class Stelleroidea (with subclasses Somasteroidea, Asteroidea and Ophiuroidea)

Formal diagnoses need not be given here, since they are sufficiently indicated in the preceding paragraphs.

The inferred interrelationships are suggested in figure 1, which may be regarded as a visual presentation of the main results of this inquiry. The Helicoplacoidea, the discovery of which was announced after this paper went to press (Durham & Caster 1963), may be regarded as an early Cambrian echinozoan stock, which would lie on figure 1 near the inferred bifurcation of Edrioasteroidea and Echinozoa.

Appendix

Conspectus of extant Asterozoa herein referred to fossil taxa

The foregoing analysis confirms the natural relationships between Somasteroidea, Asteroidea and Ophiuroidea implied by the classification adopted by Spencer (1951), in which all three taxa are treated as subclasses of a single class Asterozoa. In its broad outlines, the classification used by Spencer is found acceptable; but the definition of the Order Platyasterida is modified to include reference to the dominant transverse and longitudinal gradients occurring in the arm; and the status of Spencer's Order Hemizonida is considered dubious, pending further investigation, for its included families appear to represent both astropectinid and post-astropectinid grades of development.

The conventionally accepted criteria, said to distinguish Ophiuroidea from Asteroidea, such as the sharp demarcation between arms and disk, absence of caeca and gonads from the arms, madreporite on the adoral side, a covered ambulacral groove, non-suctorial tube-feet, and lack of pedicellariae, all collapse when account is taken of Palaeozoic groups now found to survive in existing seas. Ophiuroids and asteroids are closely related, but the two groups may be distinguished by the permanent erection of the amb-ossicles to form an invaginated furrow in asteroids, and the absence of an invaginated furrow in ophiuroids; in both groups the longitudinal gradients are predominant in the arm. Somasteroids have dominant transverse gradients, and the amb-ossicles are not permanently erected to form a furrow, nor is there any tendency to form fused vertebrae. These distinctions are considered insufficient to justify separation of Ophiuroidea and Asteroidea as separate classes.

Class ASTEROZOA

Subclass Somasteroidea

Content as defined by Spencer (1951), but with the addition of the following living representative:

Family Platasteriidae Caso, 1945, as defined by Fell (1962*a*): with single included genus and species *Platasterias latiradiata* Gray, 1871, tropical west American coasts.

Subclass Ophiuroidea

Content as defined by Fell (1960*b*), but Ophiocanopidae to be removed from Order Ophiurida, and transferred to Order Oegophiurida:

Order Oegophiurida Matsumoto, 1915
  Suborder Zeugophiurina Matsumoto, 1929
    Family Ophiocanopidae Mortensen, 1933, as redefined herein, with single known included genus and species *Ophiocanops fugiens* Koehler, 1922, Indonesia, sublittoral.

Subclass Asteroidea

Content substantially as defined by Spencer (1951)

Order Platyasterida Spencer, 1951, as redefined herein. The extant Luidiidae are all to be transferred to the order.

Family Luidiidae Verrill, 1899

Revised diagnosis: Platyasterida in which the arms are elongate, tapering and strap-like, flattened above and below. Differing from Platanasteridae in lacking petaloid arms. Known at present only from existing seas, but it is probable that fossils have been erroneously referred to '*Astropecten*'.

As here understood, the family comprises nine genera, which differ in relatively minor features, and may perhaps warrant no higher status than that of subgenera of *Luidia*. Except for the permanent erection of the amb-ossicles, Luidiidae exhibit numerous similarities to somasteroids, and warrant much more detailed study.

Included genera

1. *Luidia* Forbes, 1839 (restricted)

Syn. *Hemicnemis* M & T, 1840.

Type species: *Asterias ciliaris* Philippi, 1837.

Included species: *ciliaris* Philippi; *sarsi* D & K; *elegans* Perrier; *africana* Sladen; *sagamina* Döderlein; *asthenosoma* Fisher; *orientalis* Fisher; *superba* A. H. Clark; *porteri* A. H. Clark; *neozelanica* Mortensen, 1925; *aciculata* Mortensen (var. of *sagamina* fide Madsen); *atlantidea* Madsen.

Incertae sedis: *californica* Perrier; *chefuensis* Grube; *debilis* Grube.

2. *Integraster* Döderlein, 1920

Type species: *Luidia integra* Koehler, 1910.

The species tend to link *Luidia* and *Quinaster*, a circumstance which has hindered the subdivision of *Luidia*. The irregular arrangement of the paxillae in *heterozona* and *barimae* makes these species difficult to classify.

Included species: *integra* (Koehler); *avicularia* (Fisher); *heterozona* (Fisher); *barimae* (John & Clark).

3. *Quinaster* Döderlein, 1920

Type species: *Luidia quinaria* von Martens, 1865.

Included species: *quinaria* (v. Martens); *amurensis* (Döderlein); *hardwickii* (Gray); *inarmata* Döderlein; *longispina* (Sladen); *prionota* Fisher; *yesoensis* (Goto).

4. *Penangaster* Döderlein, 1920

Type (and only known) species: *Luidia penangensis* de Loriol, 1891.

5. *Denudaster* Döderlein, 1920

Type species: *Luidia denudata* Koehler, 1910.

Included species: *denudata* (Koehler); *gymnochora* (Fisher); *moroisoana* (Goto).

6. *Petalaster* Gray, 1840

Type species: *Petalaster columbia* Gray, 1840 (redescribed by A. M. Clark, 1953, with synonymy).

Included species: *columbia* Gray; *tessellata* (Lütken); *clathra* (Say); *ferruginea* (Ludwig); *foliolata* (Grube); *marginata* (Koehler).

7. *Senegaster* Döderlein, 1920

Type (and only known) species: *Asterias senegalensis* Lamarck, 1816.

8. *Alternaster* Döderlein, 1920

Syn. *Armaster* Döderlein, 1920.

Type species: *Asterias alternata* Say, 1825.

As here understood *Alternaster* includes *Luidia armata* Ludwig, which was made the type of *Armaster* by Döderlein (1920); *Alternaster* thus corresponds to the 5-armed division of the *alternata*-group of Döderlein and later writers.

Included species: *alternata* (Say); *barbadensis* (Perrier); *convexiuscula* (Perrier); *scotti* (Bell); *variegata* (Perrier); *bellonae* (Lütken); *armata* (Ludwig); *ludwigi* (Fisher); *phragma* (H. L. Clark); *rosaurae* (John and Clark); *quequenensis* (Bernasconi).

9. *Maculaster* Döderlein, 1920

Type species: *Luidia maculata* M & T, 1842.

Included species: *maculata* (M & T): *aspera* (Sladen); *hystrix* (Fisher); *magnifica* (Fisher); *hexactis* (H. L. Clark); *mauritiensis* (Koehler); *savignyi* (Audouin); *sibogae* Döderlein; *australiae* Döderlein; *varia* (Mortensen).

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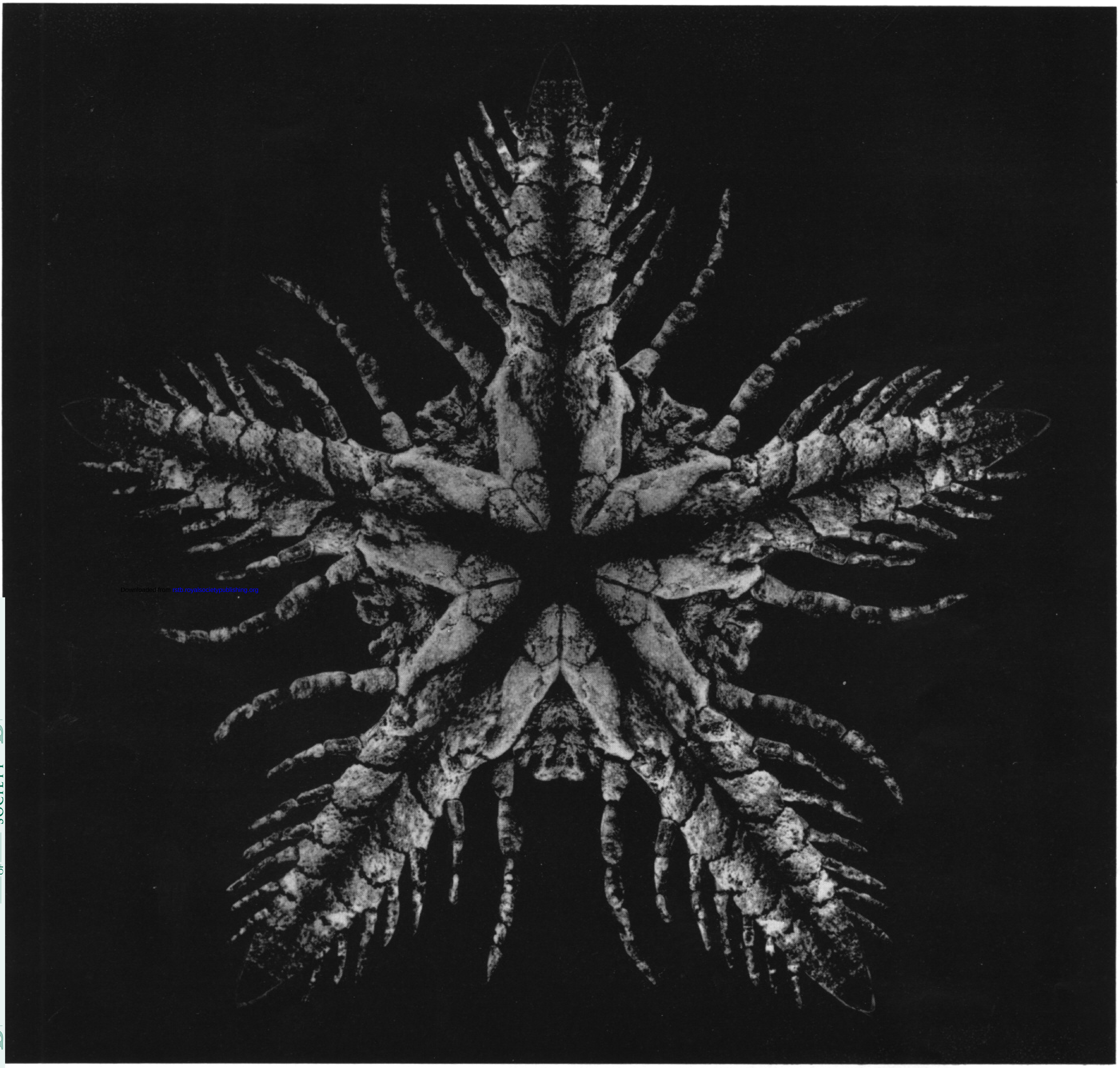

FIGURE 17. *Chinianaster levyi* Thoral (Chinianasteridae, Somasteroidea), juvenile stage, R 7·0 mm. Mosaic photographic reconstruction of skeleton in internal aspect, based on six negatives obtained from specimens 555 (coll. Lignières) and ES 2 (coll. Thoral), in the University of Lyon collection; material studied by courtesy of Professors H. Gauthier and G. Ubaghs. (Magn. × 14.) For identification of structures, see figure 11*E*. Photography M. D. King and the author.

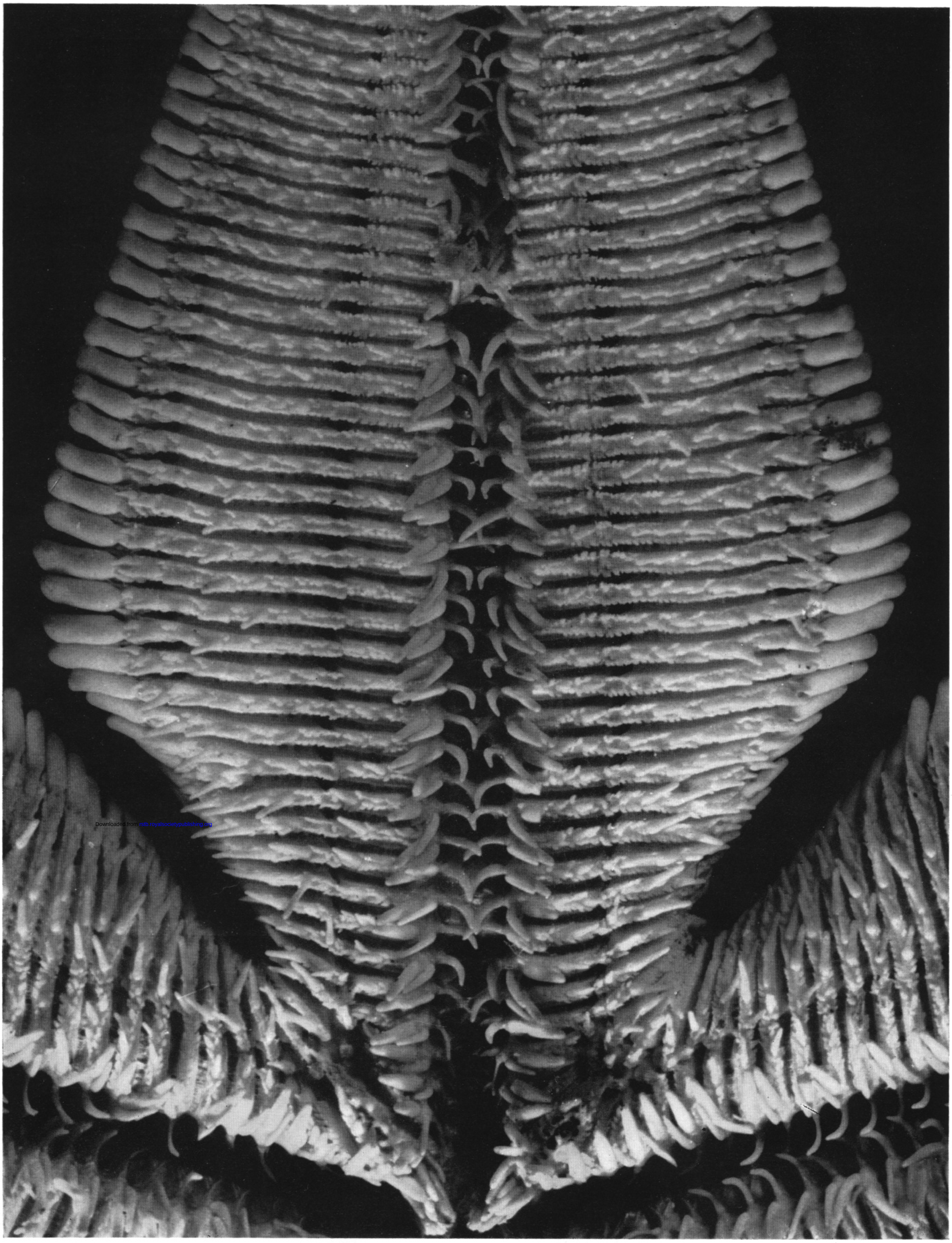

FIGURE 18. *Platasterias latiradiata* Gray. Adoral aspect of proximal part of one arm. In this specimen the webs and cover-plates are erected, exposing the interpinnular grooves. (Magn. × 6). Material from Corinto, Nicaragua, *Velero III* Station 962-39, May 1939, courtesy F. C. Ziesenhenne, Allan Hancock Foundation. Photo: M. D. King.