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Pages 1-16, Plates 1-4, Text-figures 1-8

A LIVING SOMASTEROID, *PLATASTERIAS LATIRADIATA* GRAY

By H. Barraclough Fell

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A LIVING SOMASTEROID, *PLATASTERIAS LATIRADIATA* GRAY

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ILLUSTRATIONS

ABSTRACT

Platasterias latiradiata GRAY, hitherto supposed to be an aberrant luidiid asteroid, is shown to have fundamentally the same structure as the Cambro-Ordovician Somasteroidea, and must accordingly be referred to that group of Asterozoa. The pinnate character of the skeleton of the somasteroid arm, first elucidated by SPENCER (1951), is shown to extend also to the external alimentary-respiratory system, and to have been the basis from which the asteroid morphological features arose, by successive changes in axial gradients during development. Features not conserved in fossil somasteroids include paired erectile webs on either side of the inter-pinnular fasciolar grooves, incorporating serially arranged cover-plates, closely simulating those of crinoids. The buccal skeleton, though approximating that of asteroids, is demonstrably of pinnate structure, which is elucidated. Enlarged external cupules accommodate the tube-feet when retracted, and the supposed evidence of external ampullae in fossil somasteroids is considered to have been a misinterpretation. SPENCER's inferred homologies between somasteroid virgalia and asteroid adambulacral and marginal plates are confirmed, and the superambulacral plate is also shown to be an occluded virgalium. A series of adductor muscles between the ambulacral plates permits partial, temporary erection of a shallow furrow, approximately of asteroid type; the triangular depressions in which these muscles are inserted are represented by corresponding structures in *Chinianaster,* and accordingly it is considered that a shallow, temporary furrow must have been erected during feeding activity in at least some Paleozoic Chinianasteridae. The family Platasteriidae Caso is redefined. Possible derivation of all astroradiate extant echinoderms from crinoids is postulated, on the basis of the marked resemblances to crinoids now evident in somasteroids.

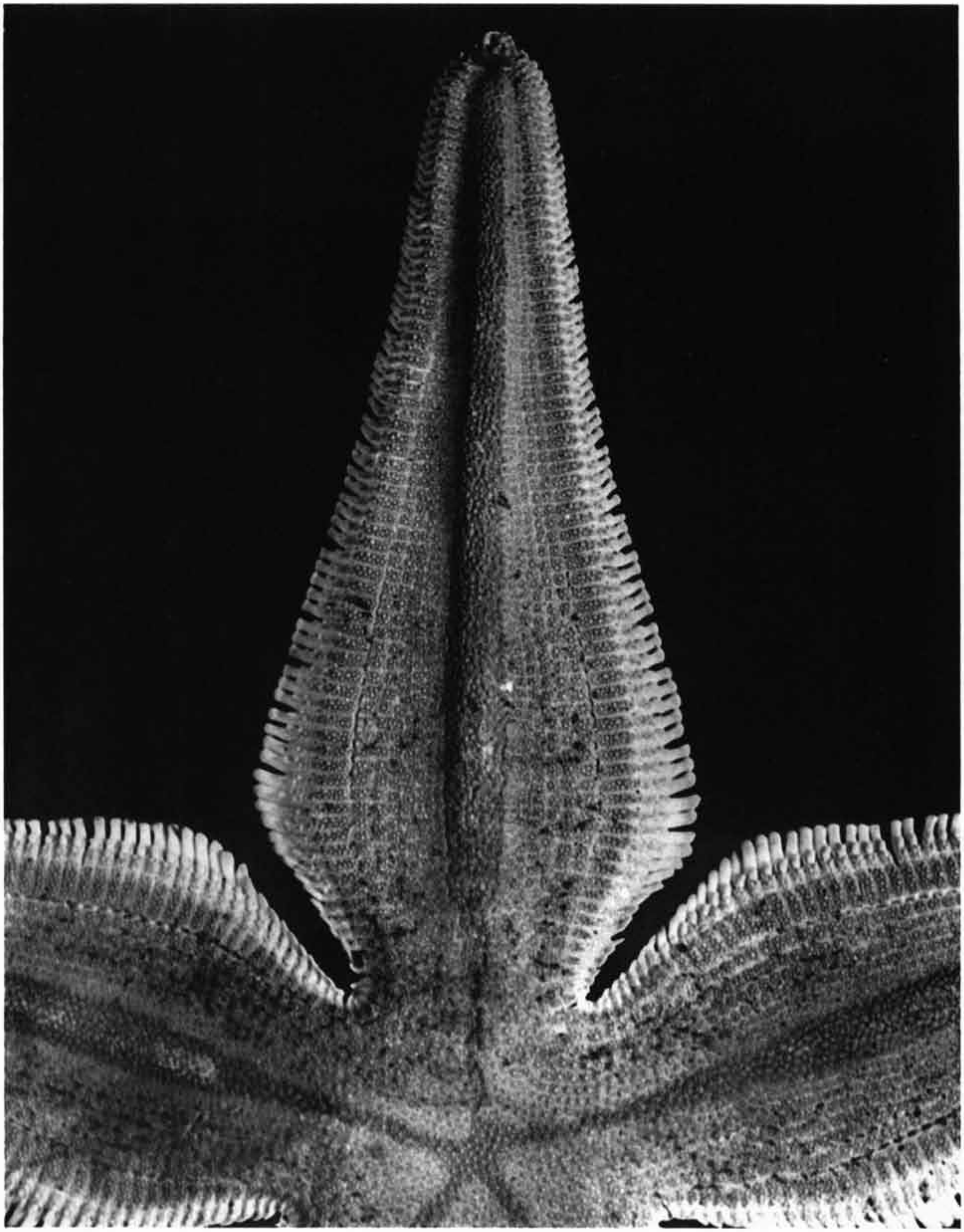
INTRODUCTION

As recently announced, *Platasterias latiradiata* is a surviving member of the Somasteroidea, an archaic group of star-shaped echinoderms hitherto thought to have become extinct early in the Ordovician Period (FELL, 1961). A brief account of the analytical method by which the affinities of the animal were first realized has already been given (FELL, 1962). This contribution is limited to brief discussion of the major features of somasteroid anatomy, as illustrated by *Platasterias,* with the stress mainly upon endoskeletal structures of paleontological significance. A more detailed discussion of axial gradients and their theoretical implications will be presented elsewhere.

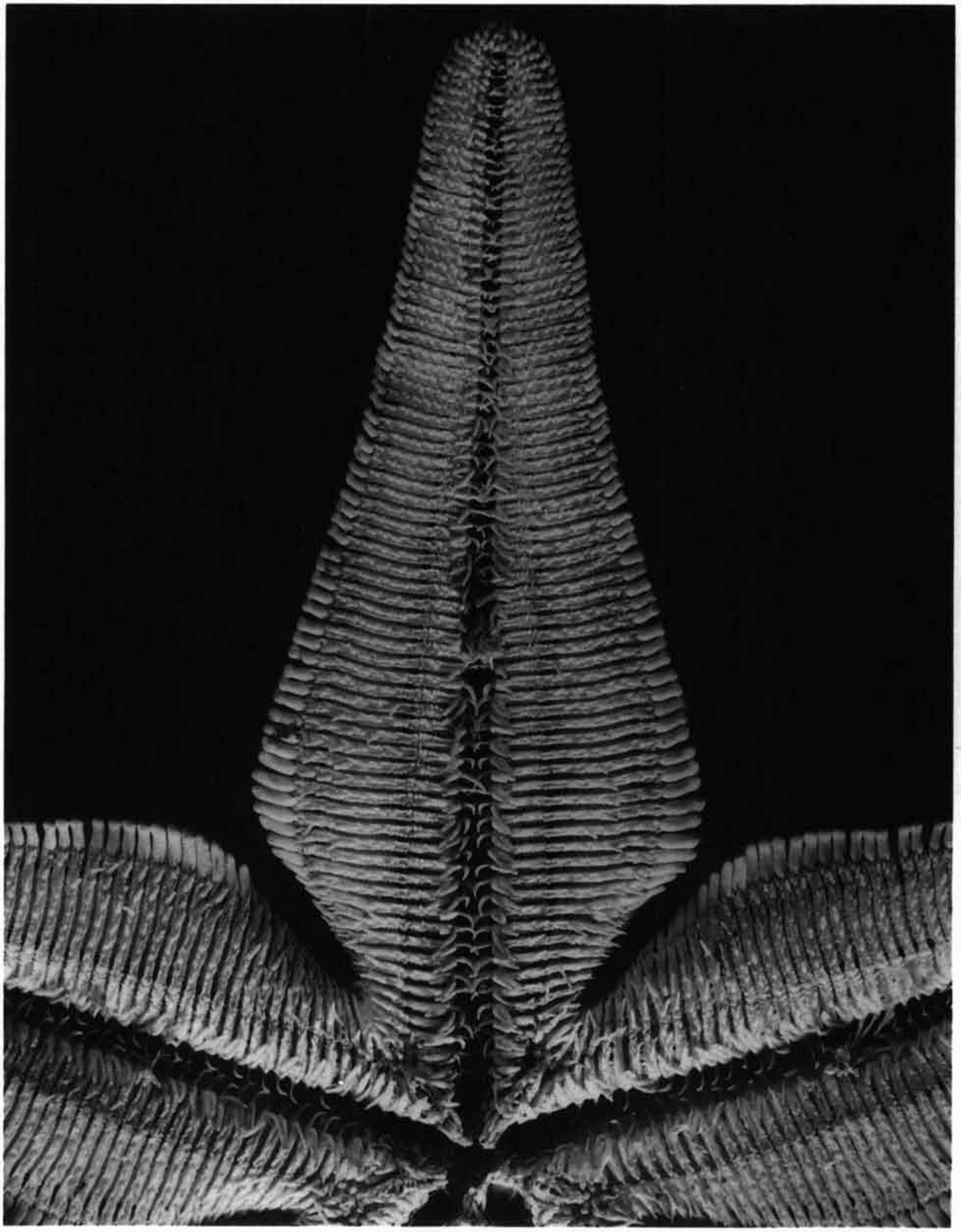
Somasteroids differ from all other echinoderms in having an extremely flattened, star-shaped body, in which the skeleton of the arms resembles that of biserial arms of crinoids, the former being built of elongate rods (called virgalia) arranged in obliquely transverse rows on either side of the axial series of ambulacral ossicles. The rows of virgalia in the more unspecialized somasteroids are arranged like the pinnules of a biserial crinoid arm, and form the adjacent walls of intervening grooves, which apparently convey water-currents to the radial food-groove, and thence to the small, central mouth. The ambulacral ossicles are not erected to form an inverted-V, as in asteroids, but are placed in a more or less recumbent attitude; thus the radial furrow is not invaginated into the arm, but is merely a shallow, narrow groove underlying the ambulacral ossicles. As can now be inferred from the living example, a Y-shaped depression on the median aspect of the ambulacral ossicles houses a transverse adductor muscle, capable of producing a partial, temporary elevation of the median ventral surface of the arm, during selective detrital feeding; the presence of similar Y-shaped depressions in at least *Chinianaster,* among the lower Paleozoic members, suggests that this muscle, and the mode of feeding it facilitates, may be a more generalized character of early somasteroids. As we can also infer from the living example, somasteroids are characterized by having simple tube-feet, without suckers, and a blind gut resembling that of ophiuroids and luidiid asteroids. SPENCER (1951) regarded the somasteroids as ancestral to both asteroids and ophiuroids, and ranked them as a subclass of Asterozoa. This view is supported, but *Platasterias* is clearly seen to lie near the line of descent which led to luidiid asteroids.

EXPLANATION OF PLATE 1

FIGURE 1. *Platasterias latiradiata* GRAY. Aboral aspect of disc and one arm. Specimen from Corinto, Nicaragua, Allan Hancock Foundation, *Velero III* Station 962-39, 2-5 m, 4 May 1939. R, 64 mm., r, 11 mm. Photo M. D. KING.



FELL — Living Somasteroid



Fell — Living Somasteroid

Photographs accompanying this paper were made by M. D. KING, Victoria University of Wellington. Text-figures (except Figures 1-3) were drawn by me.

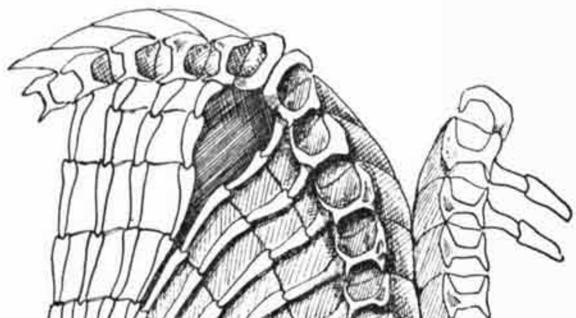


FIG. 1. *Chinianaster levyi* THORAL (Chinianasteridae), Lower Ordovician, France, ×4.5 (after Spencer, 1951).

MATERIAL EXAMINED

Platasterias latiradiata GRAY, 1871, was described on the basis of a single specimen from Tehuantepec, Oaxaca, in southern Mexico. The holotype is preserved in the British Museum of Natural History, London, and a portion of it was examined early in the present investigation through the courtesy of the Museum, and of Miss AILSA M. CLARK, the curator of the Department of Echinoderms. Subsequently, five more or less complete specimens were received from the Allan Hancock Foundation, University of Southern California, by courtesy of Captain F. C. ZIESENHENNE. This latter material, all in dried condition, was obtained off Corinto, Nicaragua, in shallow water. The presence of fine sand-grains in the fasciolar grooves of both the Tehuantepec and Corinto material suggests that the species normally frequents soft, sandy botom, the recorded depth being 2 to 5 m. Although very little museum material exists, and most of it derives from one *Velero III* station, it seems likely that the species is local, rather than rare.

BODY SHAPE

The highly characteristic outline of the body in *Platasterias* (Pls. 1, 2) is due to the petaloid form of the arms, which are narrow basally, broaden rapidly, and then narrow again distally; as a consequence, the bases of the arms are separated by deep, narrow interradial fissures, the disc being confined to a relatively small central area. Whereas no asteroid is known to have a body of this form, it is characteristic of the chinianasterid somasteroids (Figs. 1, 2) and is evidently an original feature of somasteroids, since the Chinianasteridae are the least specialized members of the group. Among other echinoderms, only crinoids possess petaloid arms. In the more specialized somasteroids, for example *Archegonaster* (Fig. 3), the body assumes a pentagonal outline, and the virgalia are partly stabilized as adambulacral, intermediate and marginal elements. *Platasterias* exhibits stabilization of the virgalia, but in other respects is evidently much more primitive than *Archegonaster,* from which it differs widely in general appearance.

In dorsal aspect each arm presents a mid-radial ridge (Pl. 1) caused, not by any underlying ambulacral furrow, but by the massive capitula of the ambulacral ossicles themselves. The older descriptions (GRAY, 1871, *et auctt.*) refer to a longitudinal ventral carina on either side of the mid-radius. This puzzling feature, unknown in other extant Asterozoa, is now seen to be caused by a fulcrum, upon which the adductors of the ambulacral plates operate, and it marks

EXPLANATION OF PLATE 2

FIGURE 1. *Platasterias latiradiata* GRAY. Adoral aspect of disc and one arm of specimen illustrated in Plate 1. Photo M. D. KING.

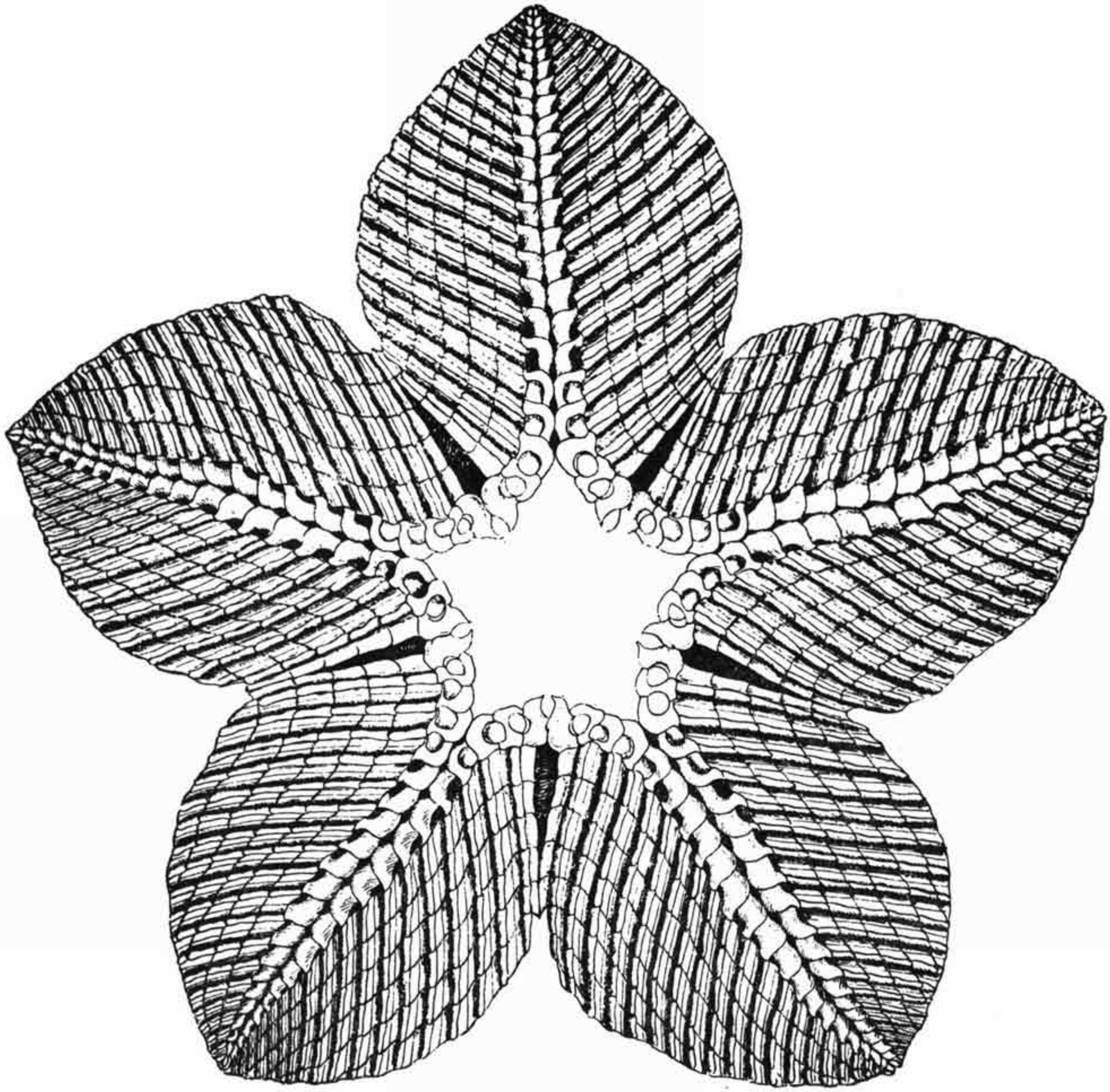


Fig. 2. *Villebrunaster thorali* Spencer (Chinianasteridae), uppermost Cambrian-Lower Ordovician (U. Tremadoc-Basal Arenig), southern France, ×5 (after Spencer, 1951).

the outer limit of that part of the arm which, in asteroids, is invaginated.

ARM STRUCTURE

The essentially pinnate arm structure of all somasteroids is well illustrated in *Chinianaster* (Fig. 1), *Villebrunaster* (Fig. 2), and *Archegonaster* (Fig. 3) among Paleozoic forms; the corresponding features are immediately evident in *Platasterias* by inspection of Plates 2, 3 and 4, and Figures 4,*A* and 5. Less conspicuous, though clearly demonstrable, is the persistence of pinnate structure to the very base of the arm (Fig. 6), and its involvement in the formation of the jaws.

The axial skeleton of the arm comprises the ambulacral ossicles, arranged here, as in all known Asterozoa, in a double series. The ambulacral ossicles occur throughout the arm in opposite pairs (Figs. 4-6). A similar arrangement is illustrated by Spencer (1951) in *Villebrunaster;* it was evidently found also in *Chinianaster,* though some dislocation may have occurred in the holotype after death (Fig. 1). SPENCER (1951) seemed to think that the ambulacral ossicles in these forms were more or less alternate; his figures (including photographs) do not support this view, but suggest rather that any alternating condition in fossils is due to post-mortem effects. Indeed, the structure of the individual ambulacral ossicles in *Platasterias* so closely matches that in *Chinianaster,* that there can hardly be any doubt that both must have been arranged in the same way, in order to accommodate the adductor muscles, whose impressions are quite evident in SPENCER's figures. It follows, therefore, that opposite ambulacral ossicles occurred in at least some of the Chinianasteridae, as also in *Platasterias,* and that the distinctly alternating condition seen in *Archegonaster* can not be more than a familial character of the Archegonasteridae. However, general morphology suggests that paired opposite ambulacral ossicles are derived from an earlier stage in which the ossicles alternate; and these again, may have arisen from a still earlier (and as yet unknown) uniserial condition, in the same way that biserial-arm crinoids arose from uniserial ancestors. These speculations, however, must be reserved for discussion in a more appropriate context.

SPENCER (1951) drew attention to four important characters of the ambulacral ossicles of somasteroids which, taken together, distinguish them from those of all other Asterozoa. These are:

(1) The ossicles are not erected to form an ambulacral furrow. Instead, they lie in a recumbent position, covering only a very narrow and shallow radial food-groove.
(2) The tube-feet emerge from broad basin-like structures (here termed alveoli), interpreted by SPENCER as perhaps locating external ampullae.
(3) The ossicles more or less enclose the radial water-vessel (especially in *Villebrunaster,* less strongly in *Chinianaster*).
(4) The three proximal pairs of ambulacral ossicles are involved in forming the jaw.

It may be added here that, without realizing its significance, SPENCER illustrated a fifth distinctive feature, namely the conspicuous Y-shaped ridges between adjacent alveoli. The meaning of these structures is indicated below.

All five features are clearly exhibited by *Platasterias,* and are readily understood by reference to the illustrations here given. The characters will be discussed in the order in which they are listed above.

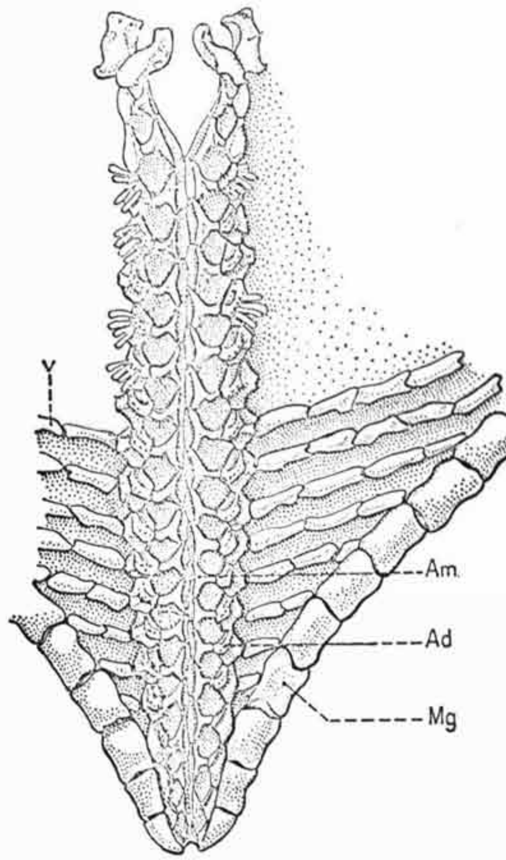


FIG. 3. *Archegonaster pentagonus* SPENCER (Archegonasteridae), Lower Ordovician, Czechoslovakia, ×3 (after Spencer, 1951). [Explanation: Virgalium, *V*; ambulacral, *Am;* adambulacral, *Ad;* marginal, *Mg.*]

(1) The normal recumbent attitude of the ossicles is seen in transverse sections at the base of the arm (Fig. 4,*B*), in a regenerating arm (Fig. 7,*C*), and in the oblique ventral aspect of the arm (Pl. 4). As a direct result of their recumbent attitude, the region corresponding to the asteroid furrow ("2—2," in Pl. 4) is not invaginated; the apparent furrow "1—1," in Pl. 4) is therefore the homologue of the radial food-groove of crinoids, and corresponds to only the uppermost recess of the asteroid furrow. In *Platasterias* a partial erection of the ambulacral ossicles is possible, through the action of a series of short transverse adductor muscles (Fig. 4,*B*, "11"). One such muscle occurs between each pair of ossicles, and it takes its origin on either side in the depressed fork of the Y-shaped ridge, which lies between adjacent alveoli. The structure is visible in the dissected upper arm of Plate 3, as also in Figure 7,*A* (where it is labelled "8"). On the left hand arm-base of Plate 3 such partial erec-

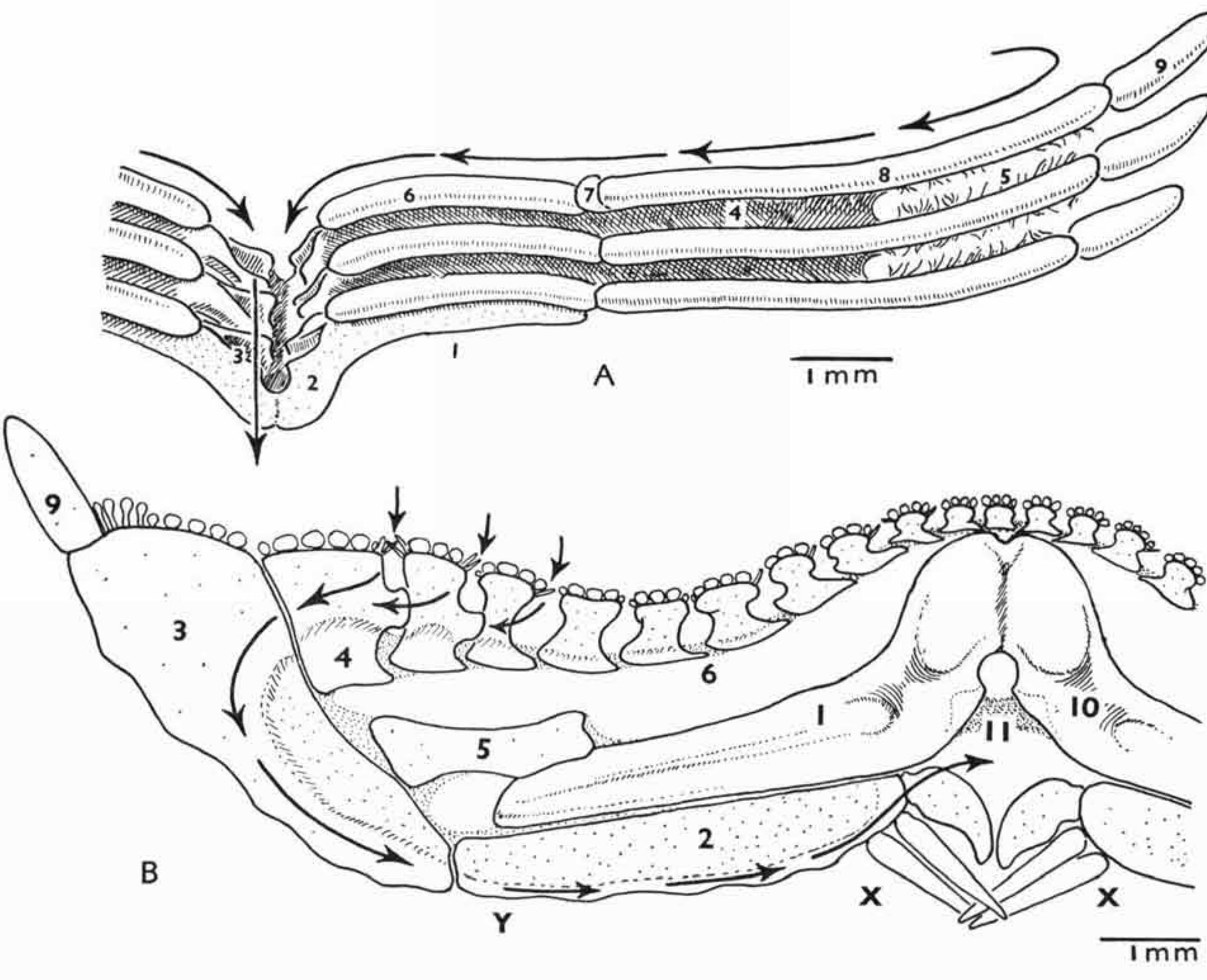


FIG. 4. *Platasterias latiradiata* GRAY (Platasteriidae), drawn from holotype.—*A*. Virgalia in ventral oblique aspect. [Explanation: Arrows indicate inferred direction of ciliary currents of the pinnately arranged fasciolar channels; *1*, wing of ambulacral ossicle; *2*, capitulum; *3*, depression for adductor muscle of ambulacral ossicles; *4*, fasciolar channel; *5*, microspines of fasciole; *6*, virgalium-1 (adambulacral); *7*, intercalary virgalium (actinal intermediate); *8*, virgalium-3 (marginal, homologue of inferomarginal); *9*, distal virgalium (marginal radiole); virgalium-2 is the occluded superambulacral plate, not seen here.]—*B*. Transverse section of arm at level of sixth row of virgalia, where the margin is upturned on account of the apposition of adjacent arms at the interradius. [Explanation: *1*, Recumbent ambulacral ossicle; *2*, virgalium-1 (adambulcral); *3*, virgalium-3 (marginal); *4*, superomarginal paxilla, which forms no part of the marginal skeleton; *5*, occluded virgalium-2 (superambulacral ossicle); *6*, aboral body wall; *9*, distal virgalium (marginal radiole); *10*, basin of tube-foot; *11*, adductor of ambulacral ossicles, for raising mid-ventral surface slightly upon the fulcrum at point marked Y. Note, the somasteroid ambulacral furrow, marked X-X, corresponds to only the upper part of the asteroid furrow. The whole mid-ventral area between the point Y and its corresponding point on the side of the arm is the homologue of the asteroid furrow, which is not elevated in somasteroids, save under the action of the adductor muscles. Direction of the inferred water-currents indicated by arrow. Microspines are probably ciliated.]

tion is evident. Reference to Figure 4,*B* shows that near the point marked "Y" on this section there is a movable fulcrum between the adambulacral virgalium (marked "2") and the marginal virgalium ("3"). Specimens from Corinto had evidently been selectively feeding upon small amphipods, which are present in the stomach; in one case an amphipod is preserved midway along a radial food-groove. It is evident that during such selective feeding the furrow is temporarily raised in the manner indicated, for otherwise there would not be room in the shallow and narrow food-groove for the passage of food of this order of size. The adambulacral armature is mobile, and is evidently brushed aside as the amphipod is pushed along

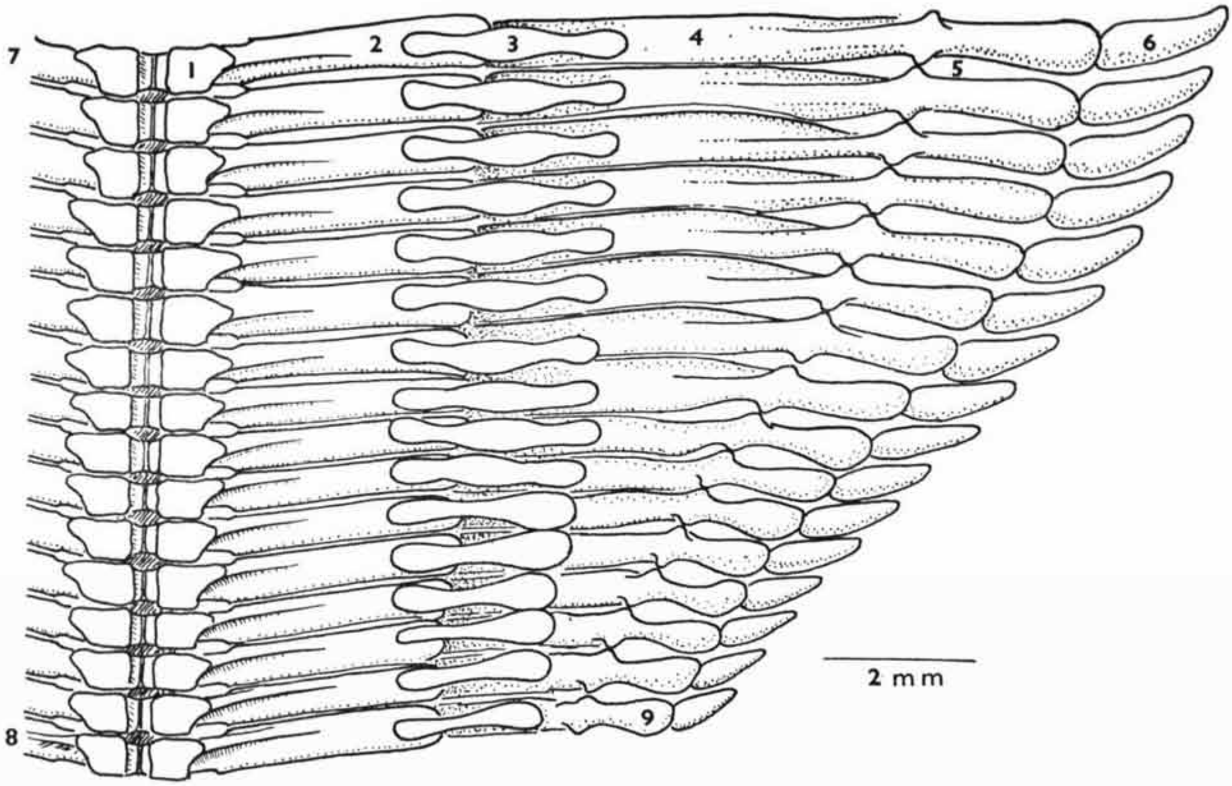


FIG. 5. *Platasterias latiradiata* GRAY (Platasteriidae), drawn from specimen from Corinto, Nicaragua. Ventral skeleton of arm-base, in internal aspect, of region from marginal-4 to marginal-19 (corresponding to ambulacral-8 to ambulacral-23). [Explanation: *1,* Capitulum of ambulacral-23; *2,* its wing; *3,* virgalium-2 (superambulacral ossicle) of metapinnule-23; *4,* virgalium-3 (marginal) of same metapinnule; *5,* fasciolar region; *6,* virgalium-4 (marginal radiole) of metapinnule-23; *7,* ambulacral-23; *8,* ambulacral-8; *9,* marginal-4 (i.e., virgalium-8 of metapinnule-8).]

the groove by the tube-feet. Since identical Y-shaped structures are observable in SPENCER's figures of *Chinianaster* (Fig. 1) it may be inferred that a similar muscle occurred in at least this genus among the fossils, and that selective detrital feeding must have been possible. It is self-evident that the extreme flattening of fossil Chinianasteridae is partly an artifact produced by pressure, and that in life the axial region of the arm was slightly elevated into a temporary furrow during feeding. Thus we have the explanation of one hitherto baffling character of the fossils, in which the pinnate food-grooves seemed to lead into no obvious radial groove; this difficulty was particularly marked in *Archegonaster* and *Villebrunaster,* where we may also assume a probable mechanism of the kind which now seems quite definite in *Chinianaster*.

(2) Basin-like structures between adjacent ambulacral ossicles are conspicuous in *Archegonaster* and *Chinianaster,* and have hitherto been interpreted as accommodating supposed external ampullae. However, the small, bifurcate ampullae of *Platasterias* are internal, and yet enlarged cupules of precisely the same type are present. It is obvious that the cupule merely houses the tube-foot when it is retracted (for example, when an amphipod is being pushed across it by the neighboring tube-foot on the distal side); there are no grounds for attributing any other function to the structure in the fossils. Thus, external ampullae are not known to be a character of somasteroids (though they may have occurred). The cupules are well seen in the upper arm of Plate 3, alternating with the Y-shaped ridges, just as in the fossils.

(3) Inspection of Figure 4,*B* shows the partial enclosure of the radial water-canal, which is housed in the tubular groove overlying the adductor muscle. When the adductor muscle is active, the enclosure becomes almost complete.

(4) Three proximal pairs of ambulacral ossicles are involved in the formation of the jaw (Fig. 6).

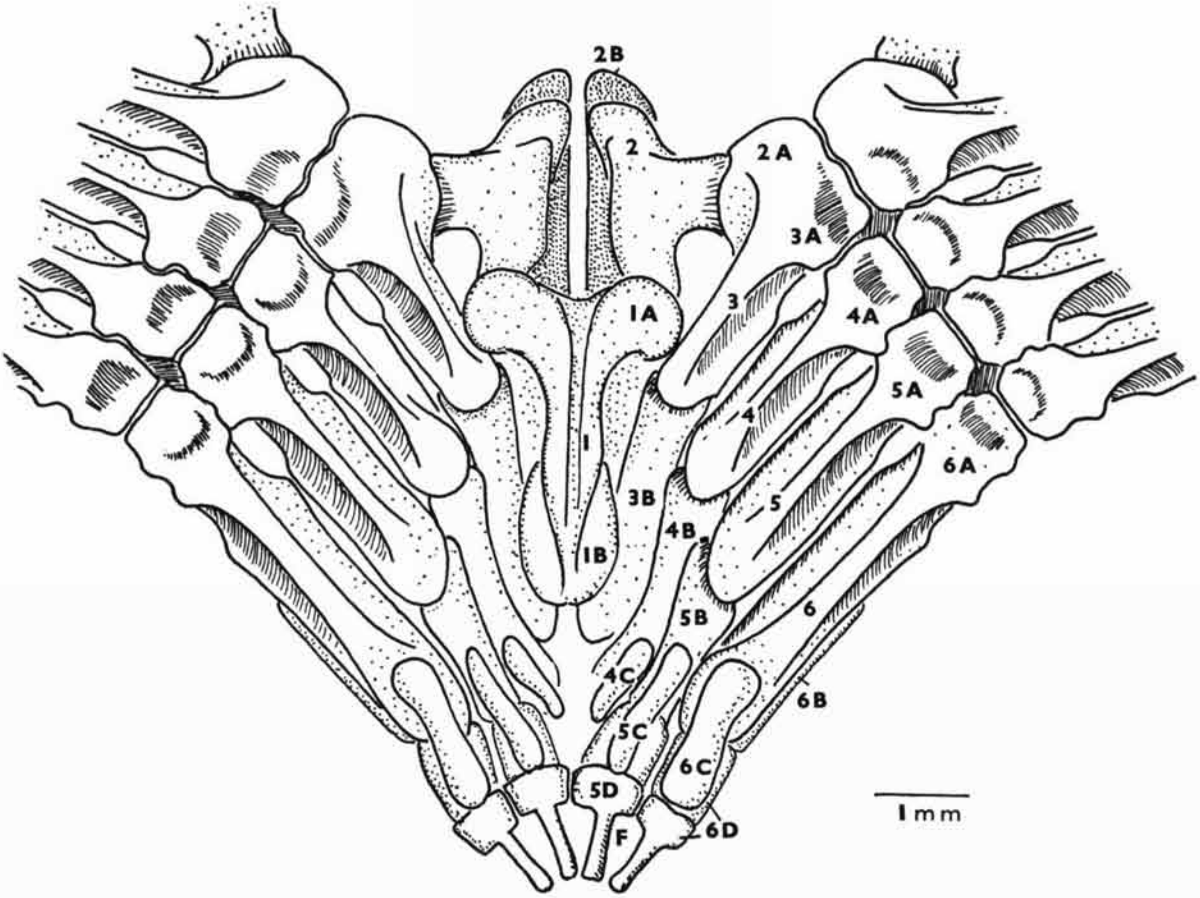


Fig. 6. *Platasterias latiradiata* Gray (Platasteriidae), drawn from same specimen as for Figure 5. Buccal skeleton and arm-base, in internal aspect. [Explanation: *1-6,* Wings of first to sixth ambulacral ossicles; *1A-6A,* their capitula; *1B-6B,* adambulacral virgalia of the metapinnules corresponding to ambulacrals-1-6; *4C-6C,* superambulacral virgalia of metapinnules-4-6; *5D-6D,* marginal virgalia of metapinnules-5-6. For explanation of homologies, see text.]

The complexity of the structure requires separate description (p. 12).

(5) The Y-shaped ridges have already been discussed under (1) above.

It will be seen, thus, that in all major structural features the ambulacral ossicles of *Platasterias* match those of the Paleozoic genera, and differ from those of asteroids. Further, the soft-part anatomy of the associated structures in *Platasterias* provides a simple explanation of the functioning of the somasteroid radial groove in both fossil and extant examples, and shows that some limited measure of selective detrital feeding is combined with the microphagous ciliary mechanism.

One rather pronounced difference in the ambulacral plates of *Platasterias* lies in the development of the long slender wing carried on the outer margin of the ossicle (seen in Figure 4,*B*, "1," and in Figure 6). This is undoubtedly to be regarded as an asteroid feature, and its development in some somasteroids evidently made possible the ultimate erection of the ambulacral plate upon the adambulacral virgalium, and thus led to the asteroid condition. In *Platasterias,* when the adductor muscle raises the ambulacral ossicles during selective detrital feeding, the adambulacral virgalium is obliged to rise too, since it is bound to the wing by fibrous tissue for the whole of its length; in asteroids, on the other hand, the wing of the ambulacral ossicle rests with only its distal end upon the (quite short) adambulacral element, and the relation of the structures is such as to make the erection of the ambulacral element a permanent condition, from the earliest embryonic differentiation of the skeleton.

It is noteworthy that in the younger part of the arm in *Platasterias* (Fig. 7,*C*) the ambulacral ele-

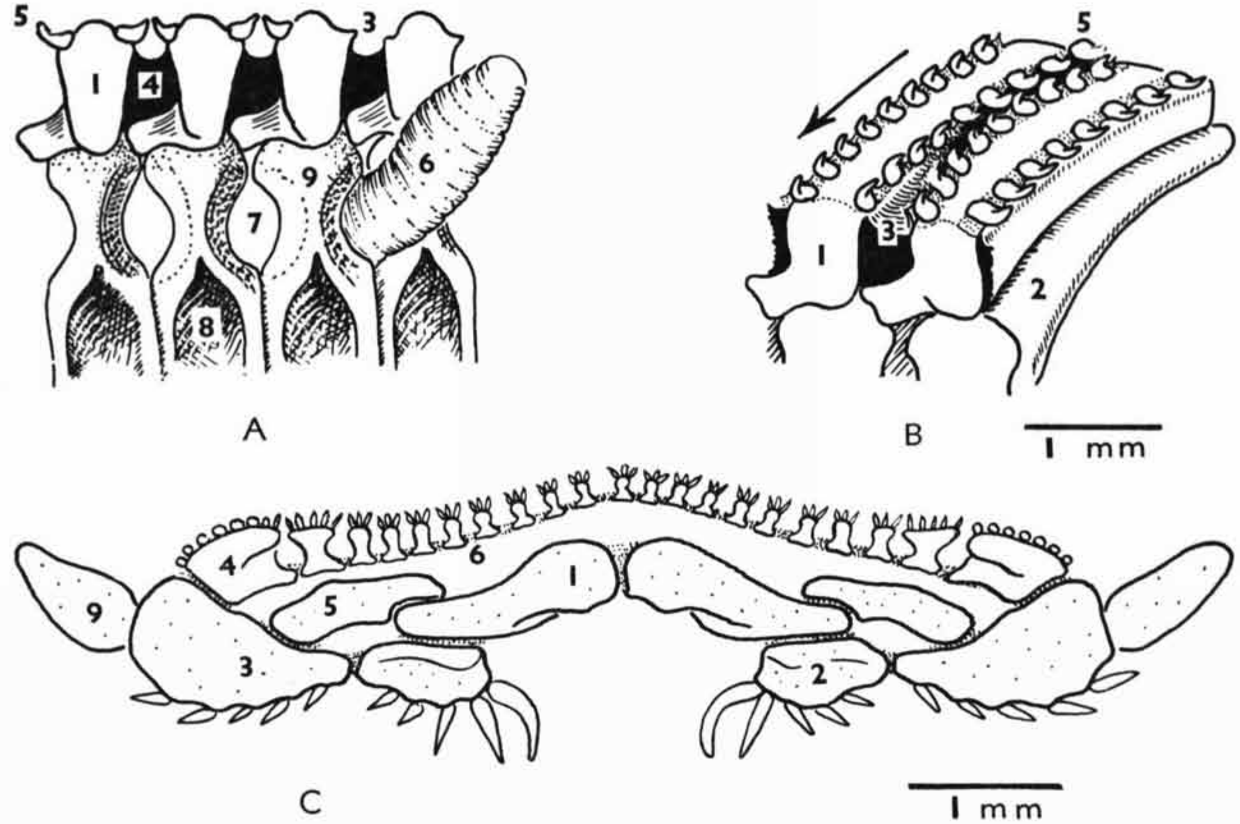


FIG. 7. *Platasterias latiradiata* GRAY (Platasteriidae), drawn from holotype.—*A*. Furrow aspect of furrow-wall, as seen in a small mirror inserted at 45° angle into the furrow. [Explanation: *1*, Virgalium-1 in end aspect; *3*, fasciolar channel; *4*, muscle between adjacent virgalia; *5*, cover-plate guarding fasciolar channel; *6*, tube-foot; *7*, basin; *8*, depression for adductor muscle; *9*, end aspect of wing of ambulacral ossicle.]—*B*. Block diagram, in oblique ventral aspect, of part of adjacent virgalia and fasciolar channels. [Explanation: *1*, Virgalium-1 (adambulacral); *2*, wing of ambulacral ossicle; *3*, fasciolar channel, artificially exposed by raising the two rows of valvate cover-plates which are held in a continuous web; *5*, cover-plates and webs in normal position, concealing fasciolar channel; direction of inferred water-current indicated by arrow.]—*C*. Transverse section of arm near tip, in a region of regenerating arm 8 mm. in diameter, the youngest stage observed. [Explanation as for Figure 4*B*.]

ments are much shorter, and quite horizontal, as in the fossils. The adductor muscle is not yet functional in this part of the arm, where the skeletal anatomy would make any kind of erection quite impossible.

METAPINNULES

The rodlike elements which form obliquely transverse rows, matching the ambulacral ossicles in number and in position, may be compared with the pinnular elements of crinoids, and the rows themselves may be compared with the pinnules. To facilitate description, and to underline the parallel which seems to exist between the pinnule and the row of virgalia, it is here proposed to introduce the term **metapinnule** for such a row of virgalia. The metapinnules are to be numbered from the base of the arm outward, as are pinnules in crinoids. The individual elements of a metapinnule, for which SPENCER's (1951) term virgalia is already available, are numbered serially from the radial (i.e., proximal) end outward. The virgalia thus correspond to the pinnulars of crinoid pinnules.

In *Villebrunaster* and *Chinianaster* the number of virgalia in each metapinnule varies with the position of the metapinnule (Figs. 1, 2). The same is true of *Archegonaster* (Fig. 3), though here the variation is of a different character, conditioned by the pentagonal form of the body. In *Platasterias* the number of virgalia is fixed, and clearly the condition foreshadows that which is seen in Luidiidae among asteroids. The only variation observed concerns the presence or absence of an accessory (intermediate) element just distal from the innermost (adambulacral) virgalium. An external view of the metapinnules is seen in Figure 4,*A* (after dissection), and Figure 5 illustrates the internal aspect; sectional views are seen in Figure 4,*B*, and in Plate 4. It seems rather evident from Figure 5 that the rodlike superambulacral ossicles ("3") are probably occluded virgalia, and this inference is supported by sections of the embryonic part of an arm which is regenerating (Fig. 7,*C*). In the latter, the disposition of the ambulacral ossicle is such as to imply that it has become wedged between the first virgalium (adambulacral) and the superambulacral element. In other words, the superambulacral element must be the second virgalium. No younger stage has as yet been investigated. As already stated (FELL, 1962), it was the occurrence of rodlike superambulacral ossicles in certain astropectinid and luidiid forms which first led to the suspicion that superambulacral plates might really represent virgalia, for they presented some resemblance to the intermediate virgalia of *Archegonaster,* and were found to share the same axial gradients as the adambulacral and marginal plates in Luidiidae. Thus, these plates played a critical part in the first steps which led ultimately to the isolation and recognition of *Platasterias* as a somasteroid.

The logical nomenclature for the virgalia of any metapinnule in *Platasterias,* and the corresponding homologies with asteroids, will be as follows: virgalium 1=adambulacral; virgalium 2=superambulacral plate; virgalium 3=marginal (inferomarginal); virgalium 4=marginal radiole.

Owing to the exceptional length of the wing of the ambulacral ossicle in *Platasterias,* it seemed plausible that the wing might represent a proximal virgalium, fused to the original ambulacral ossicle (which would in that case correspond only to the capitulum of the ossicle). However, no evidence in support of this view has been obtained, whereas the development of the ambulacral ossicle, as seen in Figure 7,*C*, yields rather strong evidence against it. Accordingly, in the foregoing description, the wing has not been counted as a virgalium.

The virgalia, in addition to providing the fundamental unit for the entire endoskeleton (apart from the axial skeleton and paxillae) also play an important part in the formation of the pinnate fasciolar food-grooves, which evidently serve the functions of microphagous feeding and of respiration. Before describing these, however, it will be more convenient to trace the metapinnules into the base of the arm, and so elucidate the buccal skeleton.

BUCCAL SKELETON

As will now be shown, the entire buccal skeleton of *Platasterias* has been derived from the pinnate skeletal system, involving the three proximal pairs of ambulacral ossicles in each arm, together with their associated metapinnules.

Casual inspection of the ventral surface of the arm-base in *Platasterias* (Pl. 3) suggests that the paired oral plates are merely the somewhat enlarged adambulacral virgalia of the first metapinnule. Dissection of the internal surface of the jaw-region, however, discloses that this is not so, and that the real situation is more complex (Fig. 6). The pinnate structure of the arm continues without significant alteration (apart from a reduction in size of the distal virgalia) so far as the innermost marginal. As can be seen from Figure 6, this is the outer element of the metapinnule of the fifth ambulacral ossicle. It is clear, from inspection, that the next row of plates represents the fourth metapinnule, which develops no marginal element, but terminates in an internal superambulacral element (Fig. 6 "4C"). Continuing proximally, we reach the third metapinnule, now reduced to only one element (Fig. 6, "3B") which is the adambulacral virgalium; this element is the short adambulacral which lies next to the oral plates, and appears in ventral aspect (Pl. 3) to be the second

EXPLANATION OF PLATE 3

FIGURE 1. *Platasterias latiradiata* GRAY. Ventral skeleton after exposure by dissection, seen in external aspect from below. Photo by M. D. KING. [Explanation: *1,* alveolus of tube-foot; *2,* Y-shaped ridge enclosing depression for origin of adductor muscle of ambulacral plates; *3,* interradial fasciolar groove between oral virgalia; *4,* oral virgalium (second metapinnule); *5,* oral armature; *6,* mouth; *7,* fasciolar food-groove; *8,* adambulacral virgalium of fifteenth metapinnule; *9,* marginal virgalium of same metapinnule; *10,* distal virgalium of same metapinnule; *11,* adambulacral armature; *12,* adambulacral virgalium with cover-plates still *in situ,* protecting food-grooves on either side. The longer edge of the field measures 25 mm.]

FELL — Living Somasteroid

FELL — Living Somasteroid

adambulacral, which it is not. The capitulum (Fig. 6, "3A") of the third ambulacral ossicle is fused to that of the second ambulacral, as in luidiid and astero-pectinid asteroids. The wing of the second ambulacral (Fig. 6, "2") is a discrete element, again as in luidiid and astropectinid asteroids, and is directed inward to rest upon the oral plate of its side (Fig. 6, "2B"). The latter can therefore be recognized as the adambulacral virgalium of the second ambulacral; it is thus the vestige of the second metapinnule. The remaining structures, forming a T-shaped compound plate in the interradius, can easily be recognized as the occluded first ambulacral plates of either side (Fig. 6, "1," "1A"), to which are fused distally two small elements, one on either side (Fig. 6, "1B") corresponding to the adambulacral element of the first metapinnule. Earlier in the investigation a similar T-shaped plate was found in the jaw-apparatus of luidiid and some asteropectinid asteroids; here, however, its reduction has been carried further, and when the plate was originally noticed, it was thought to represent only the first ambulacral elements, fused together. The function of the plate, obscure in luidiids and astropectinids, is obvious enough in *Platasterias,* where it is relatively larger; it serves for the origin of musculo-fibrous tissue which unites the two oral elements to it, and thus strengthens the otherwise fragile, bipartite jaw. In asteroids, on the other hand, the greater development of the oral plates renders the T-shaped element superfluous, and it is accordingly reduced or, more generally, lost altogether. The homologies of the three ambulacral elements taking part in the jaw, with the three ambulacral elements observed by SPENCER in fossil somasteroids, is evident. The entry of the adambulacral virgalium of the second metapinnule into the jaw-structure to form the oral plate, is an advanced feature, obviously leading to asteroids and ophiuroids. The relatively simple state of the jaw, however, is underlined by the uniform appearance of all the adambulacral elements externally visible, and by the fact that fasciolar grooves and covering webs, with cover-plates, extend unaltered throughout the entire series; thus an unpaired fasciolar groove occurs between the two oral plates (Pl. 3).

It will be observed that the general principles by which the arm-structure has been modified to give rise to the jaw-structure present remarkable parallels to that which is already known to have occurred in ophiuroids. Evidence will shortly be presented elsewhere showing that the structure of the arm of certain ophiuroids is fundamentally pinnate, as in somasteroids, and that the condition seen in other ophiuroids is a specialization of the earlier pinnate pattern. The whole pattern of skeletal development in all Asterozoa—somasteroids, asteroids, and ophiuroids—is therefore considered to be fundamentally the same, namely, the pinnate pattern initiated by crinoids (FELL, 1962a).

PINNATE FASCIOLAR GROOVES

SPENCER (1951) inferred from the structure of Chinianasteridae that a system of fasciolar food-grooves, set between the adjacent metapinnules, led into the radial food-groove, and he drew a parallel with the observed tegumental fascioles in the asteroid *Porania,* which is known to be a potentially microphagous form, when detrital food supplies fail. The structure of *Platasterias* confirms SPENCER's inferences, for such food-grooves exist, and the ciliary mechanism is probably located on the microspines placed on the anterior and posterior faces of the free portions of the marginal virgalia (Fig. 4,*A*, "5"). The proximal half of the marginal virgalium, and the whole of the adambulacral virgalium, is united by muscle to the corresponding structures of the adjacent metapinnules. This muscle forms the roof of the food-groove.

A supposed difficulty in SPENCER's interpretation lay in the apparent lack of any floor to the food-groove unless, indeed, the Chinianasteridae lay upon the aboral surface, with the oral surface directed upward, to receive the plankton-fall.

EXPLANATION OF PLATE 4

FIGURE 1. *Platasterias latiradiata* GRAY. Arm in oblique ventral aspect, partially dissected to expose skeleton. Holotype, from Tehuantepec, southern Mexico, now in the British Museum of Natural History, London. The region shown extends from the sixth to the twelfth marginal, plus regenerating portion. Photo by M. D. KING. [Explanation: *1-1,* radial food-groove; *2-2,* uninvaginated region which in asteroids is erected into the furrow; *3,* recumbent ambulacral ossicle; *4,* adambulacral virgalium; *5,* marginal virgalium; *6,* distal virgalium; *7,* aboral body-wall. Portion shown measures 20 mm. across.]

This difficulty is now seen to be imaginary. The food-grooves do in fact possess a floor. It is formed by two longitudinal webs which link a series of cover-plates on either side of each food-groove (Pl. 3 and Fig. 7,*A*,*B*). The webs are erectile, and when erected, occupy the same position as, and closely simulate, the food-grooves of the pinnules of crinoids. Such erected webs are visible on the arm shown in ventral aspect in Plate 2. Their detailed structure has not yet been investigated, but the fact that they can be raised and lowered implies a muscular mechanism and suggests that a nerve strand may perhaps traverse the ventral surface of the metapinnule. The general likeness to crinoids is astonishing. Between the two rows of cover-plates on each metapinnule, there is an irregular series of median spinules, forming a ventral armature. The three furrow-spines represent a specialization of such spinules. On the other hand the so-called marginal spine (in earlier descriptions of *Platasterias*) is an entirely different structure, for it is obviously the distal virgalium of the metapinnule itself. A similar situation exists in the ophiuroid genus *Asteronyx* (FELL, 1962a).

NUTRITION

It is apparent that two types of nutrition occur in *Platasterias* and, in the light of the foregoing discussion of the ambulacral structure and its musculature, the same two types of nutrition must have occurred in the Paleozoic chinianasterids. These are:

(1) Microphagous ciliary feeding, performed by the action of the pinnate food-grooves. The currents of water (indicated by heavy arrows in Figure 4) would enter between the lateral paxillae, traverse the food-groove, be directed into the radial food-groove, and so pass to the mouth. The mobile flattened furrow-spine seen in Figure 4,*B* probably acts like a baffle; if placed at a 45° angle it would automatically direct the current towards the mouth. The water-current would also subserve the function of respiration, especially as it passed over the tube-feet.

(2) Selective detrital feeding, in which small amphipods (no larger than can pass along the radial food-groove) are captured by the tube-feet, and passed along the groove to the mouth. As noted above, one specimen from Corinto is preserved in which an amphipod is held in this position, and several specimens are seen to have an amphipod within the jaws. This would be the limit to which "carnivorous" feeding could extend, the relatively small mouth making it impossible for voracious feeding of the general asteroid type to occur. In general, this second type of feeding is directly comparable with what is found in many ophiuroids, save that in these latter, the mobile arms are the food-gathering agents, rather than the tube-feet.

ABORAL SKELETON

Little is known of the aboral skeleton of fossil somasteroids. SPENCER (1951) has described three-radiate and four-radiate structures, with an elevated central column, scattered in the aboral integument. He compared them, most inappropriately, with the triradiate spicules which occur in embryonic echinoids. The latter structures, which actually occur in all embryonic echinoderms, are in no way comparable, since they are minute sclerites which subsequently fuse to form the crystalline mesh of the adult plates. The structures observed by SPENCER in fossil somasteroids ought to have been termed paxillae, and on first inspection, they are seen to be directly comparable with the four-radiate paxillae of *Luidia*, the central elevation being the tabulum of the paxilla, characteristically elongate in this genus (Fig. 7,*C*). The more common type of paxilla in the paxillose phanerozonid asteroids is that illustrated in Figure 7,*B*, where the base exhibits no radiate structure, and the tabulum is shorter and more robust. Before *Platasterias* had been examined in the present investigation, I had already come to the conclusion that the Luidiidae are the most archaic surviving asteroids, and accordingly the similarity between the aboral paxillae of luidiids and chinianasterids was readily understandable. *Platasterias* conforms to the essential plan of luidiid paxillar structure, but in the part of the arm adjoining the marginals, the paxillae are much enlarged (Fig. 7,*A*). The central paxillar spinules are converted into granules. In the outer part of the arm (Fig. 7,*C*) the paxillae are slender, four-radiate or five-radiate, and closely resemble the structures described for fossil somasteroids. The outermost paxilla is the evident homologue of the superomarginal of *Luidia*, and hence of all other asteroids. Thus the luidiid paxilla is seen to be a direct inheritance from somasteroid ancestors, and the basis from which all other aboral skeletal structures of asteroids can easily be derived (Fig. 8).

There remains the madreporite, an element of the aboral skeleton in *Platasterias*. It is small in the material at my disposal, and covered by granules, simulating a paxilla. Further information cannot at this stage be given, as the madreporite is better considered in connection with the water-vascular system, which has not yet been investigated. The anatomy of the soft parts, without direct paleontological significance, is reserved for a later contribution.[1]

SYSTEMATIC POSITION

Brief discussion of the paleontological significance of the hard parts of *Platasterias* has been included in the appropriate contexts above, and more extended consideration must be withheld until the whole study is more advanced. It will be recognized that the affinities of *Platasterias* lie so close to the Cambro-Ordovician Chinianasteridae that there can be no doubt that it is a somasteroid, and thus the oldest known asterozoan hitherto discovered in any extant fauna. As already suggested (FELL, 1962), *Platasterias* is best regarded as falling in a distinct family, for which the name Platasteriidae CASO, 1945, is available, and the definition of the family is to be revised in the following sense:

Family PLATASTERIIDAE Caso, 1945

Somasteroids with petaloid arms, separated by deep interradial fissures; with biserial, opposite ambulacral ossicles; with the virgalia stabilized as adambulacral, superambulacral, marginal and terminal elements; and with a buccal apparatus derived from three proximal ambulacral ossicles and their associated metapinnules. Type, and only known, genus: *Platasterias* GRAY, 1871.

From the Cambro-Ordovician Chinianasteridae, to which they are most closely related, the Platasteriidae differ in the stabilization of the virgalia, and the entry of metapinnular elements into the jaw.

Before concluding this preliminary memoir, it would be apropriate to pay tribute to the perspicacity of the late W. K. SPENCER, upon whose researches our previous knowledge of somasteroids was almost entirely based, and who first defined the group. Having regard to the fragmentary impressions upon which SPENCER worked, it is quite astonishing that he was able to demonstrate the essential characters of somasteroids so clearly and, as now seen, so accurately, even to the extent of muscle-impressions, whose nature could not then be understood. The overwhelming superiority of paleontological methods, over embryological speculation, is obvious; for only the former revealed the underlying pinnate morphology of the oldest asterozoans, and has made possible its recognition in modern ophiuroids and asteroids. None of these facts had been elicited by embryological methods, and the phylogeny postulated on the basis of larval forms is preposterously divorced from the plain facts of the fossil record and of comparative anatomy.

[1] Planned for publication by the British Museum of Natural History, London.

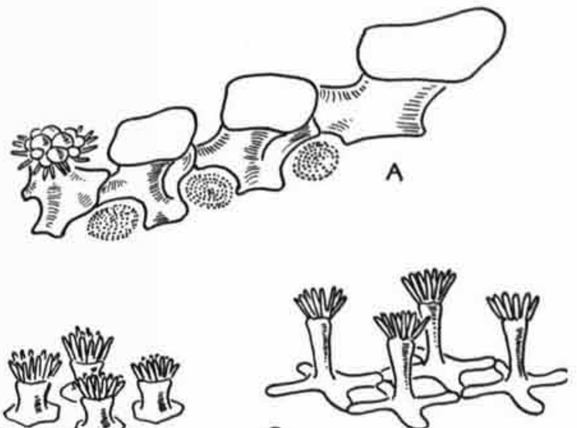


FIG. 8. Paxillae of asterozoans.—*A. Platasterias latiradiata* GRAY (Platasteriidae)—*B. Psilaster acuminatus* (Astropectinidae).—*C. Luidia neozelanica* (Luidiidae).

Many features of *Platasterias* and, as now seen, of somasteroids in general, clearly foreshadow asteroids, and a good case can be made for reducing the group to an order of Asteroidea. At the same time, however, as SPENCER pointed out, somasteroids can also be considered as representing a pre-ophiuroid phase of asterozoan evolution. My own investigations strongly support SPENCER's views. Thus, despite the asteroid-like features of somasteroids, it seems preferable to maintain SPENCER's classification of the class Asterozoa, in which he recognized three subclasses, the Somasteroidea, the Asteroidea and Ophiuroidea. A fuller discussion of the topic will be given elsewhere.

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ADDENDUM

Since the foregoing was written, I have been able, through the kindness of Professor GEORGES UBAGHS, Université de Liège, to examine latex molds of the original types of *Chinianaster* and *Villebrunaster*. There are no marginal elements in *Chinianaster;* Figure 1, here reproduced from SPENCER (1951), is therefore partly in error, for the metapinnules terminate each in a free, acuminate radiole, as in *Villebrunaster*. The condition is thus nearer to *Platasterias* than was supposed. The ambulacral ossicles are essentially opposite, as inferred above, though they become alternate at the arm-tip, and are alternate in a young specimen. The virgalia are comparable in form to pieces of a tram-rail, having a flattened base, and a flanged keel; thus they too are more comparable with *Platasterias* than was apparent from SPENCER's account. Details will be given elsewhere.