

SOMASTEROIDEA, ASTEROIDEA, AND THE  
AFFINITIES OF *LUIDIA* (*PLATASTERIAS*)  
*LATIRADIATA*

by DANIEL B. BLAKE

**ABSTRACT.** Important changes in the taxonomy and phylogenetic interpretation of stellate echinoderms were proposed during the 1960s by H. B. Fell; certain of this author's ideas are re-evaluated. Fell argued that the extant west American sea star *Platasterias latiradiata* Gray is a surviving member of the otherwise Palaeozoic Somasteroidea. The extant family Luidiidae was considered primitive among true asteroids and it was included with the Palaeozoic family Palasteriscidae in the order Platysterida. The skeletal arrangement of *Platasterias* and *Luidia* was interpreted as having been derived with relatively limited change from a currently unknown Cambrian crinoid ancestry. It is argued here that *Platasterias* is not a somasteroid but a subgenus of *Luidia*, and the Luidiidae is returned to the large living order Paxillosida. The origin of the morphology of *Luidia*, including *Platasterias*, is related to sea star behaviour and habitat rather than a crinoid ancestry. The Luidiidae is not considered to be of major importance in delineating asteroid phylogeny.

SEVERAL papers published during the 1960s by H. B. Fell (1962*a, b*; 1963 *a-c*; 1967) developed a series of stimulating and intriguing hypotheses on stellate echinoderm phylogeny that significantly altered viewpoints of the history of these organisms. Certain of these ideas are reconsidered in this paper.

Prior to Fell's work, three classes or subclasses were recognized among stellate echinoderms: the Asteroidea (sea stars or starfish), Ophiuroidea (brittle stars or serpent stars and basket stars), and the Somasteroidea, the last a taxon of primitive echinoderms then considered to be restricted to lower and middle Palaeozoic rocks. Relationships among the groups were unclear. Because of disparate early development, many biologists (e.g. Hyman 1955) believed the ophiuroids and asteroids had independent origins, and were only secondarily similar in certain features. These workers found (and still find) it undesirable to combine ophiuroids and asteroids in formal higher taxa below the phylum level, e.g. the class Stelleroidea and subphylum Asterozoa *sensu* Spencer and Wright 1966.

Other workers, stressing the fossil record, were of the opinion that the two living groups shared a common origin, and that their ancestors or near ancestors could be recognized among the fossil somasteroids. Further, Fell (e.g. 1948) considered that the developmental arguments for separating the asteroids from ophiuroids were unconvincing. These workers tend to believe that the two should be combined in a phylogenetically unified higher taxon below the phylum level (e.g. Spencer and Wright 1966).

In his work on phylogeny, Fell developed a number of interrelated topics: (1) the nature of the Somasteroidea; (2) the relationships among the extant sea stars *Platasterias*, *Luidia*, the remaining asteroids and the Palaeozoic Somasteroidea; (3) the relationship between the extant ophiuroid *Ophiocanops* and the Palaeozoic ophiuroids; and (4) the phylogenetic relationships among somasteroids, asteroids, and ophiuroids. Fell proposed a hypothesis for the origins of stelleroids from an inferred crinoid ancestry, suggested a sequence of evolutionary events leading from the Somasteroidea to the Ophiuroidea and Asteroidea, and transferred a number of living taxa to groups previously considered to be of exclusively Palaeozoic occurrence. These included the family Luidiidae from the Paxillosida to the Platysterida, both within the Asteroidea; the genus

*Platasterias* from the Asteroidea (Paxillosida) to the Somasteroidea; and the ophiuroid *Ophiocanops fugiens* to the Oegophiurida from the Phrynophiurida. Fell's re-evaluations were enthusiastically received by some workers, but a number of his ideas were challenged, including the arguments for the derivation of asterozoans from crinoids, by Philip (1965), answered by Fell (1965); the affinities of *Ophiocanops*, by Hotchkiss (1977); and the affinities of *Platasterias* by several workers (e.g. Madsen 1966; Blake 1967, 1972, 1973; Pearse 1969; Algor 1971).

A survey of textbooks and papers published during the later 1960s and 1970s shows a continuing uncertainty as to how *Platasterias latiradiata* should be treated, yet the question of affinities of the species is an important one. Not only is a living fossil intriguing simply as a survivor, but its existence raises questions on the nature of evolutionary processes. Further, once ranked as a 'living fossil', a species will become the basis for reconstruction of the biology of its presumed close fossil relatives, a fact illustrated by Fell's (1962*b*, p. 2) explanation of purpose for one of his papers: 'This contribution is limited to brief discussion of the major features of somasteroid anatomy, as illustrated by *Platasterias*.' *Platasterias* as a somasteroid clearly will strongly influence interpretations of stellate echinoderm biology and history.

The concern of this paper is primarily with the second of the four topics cited above, the nature of *Platasterias* and the Luidiidae. Other problems in the nature of relationships among stellate echinoderm groups are in need of restudy, but these ideas are beyond the purposes of this paper.

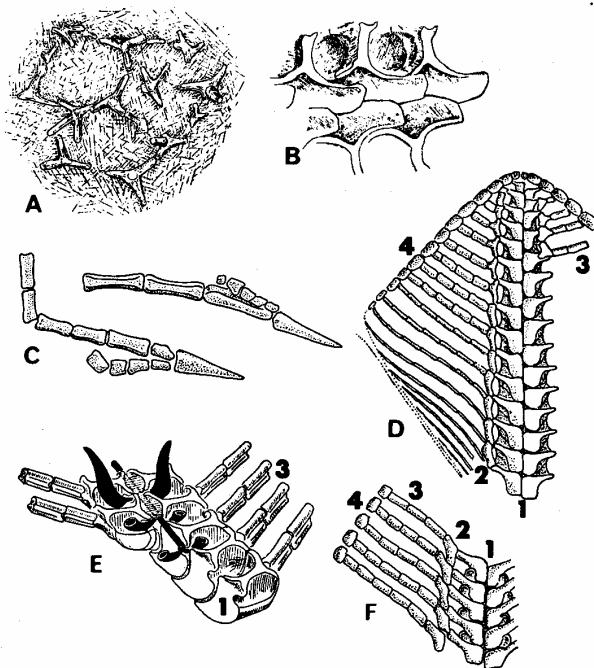
I will argue that *P. latiradiata* should be considered a subgenus of *Luidia*, itself a genus unequivocally included in the Asteroidea (rather than the Somasteroidea) by Fell (1963*a*). Assigning *Platasterias* as a subgenus of *Luidia* does not in itself challenge Fell's ideas on somasteroid/asteroid phylogeny; *Luidia* (including *Platasterias*) might still be the primitive extant asteroid with many features, as outlined by Fell, derived with little modification from the somasteroids. In re-evaluating the taxonomic and phylogenetic position of the monogeneric Luidiidae, I will next argue that there is no clear connection between Palaeozoic somasteroids and the luidiids (including *Platasterias*), and that the Luidiidae should be transferred from the order Platysterida to the order Paxillosida. A functional, rather than phylogenetic, hypothesis for the origin of luidiid morphology is proposed.

#### SOMASTEROIDEA

The concept of the Somasteroidea originated with Spencer (1951) and evolved with the work of Fell (1962*a, b*; 1963*a-c*; 1967), Spencer and Wright (1966), and McKnight (1975). In spite of this effort, the group is difficult to characterize and therefore comparisons between somasteroids and other organisms are difficult as well. Relevant fossils are in need of restudy and reillustration. I have based the following diagnosis on the literature (and not original study of the fossils), and I believe it represents the fossil somasteroids as pictured by those workers who include *Platasterias* in the taxon. In keeping with the arguments presented here, however, I have removed characters derived from *Platasterias* only. Although such a diagnosis logically follows arguments for transfer of *Platasterias*, a concept of the Somasteroidea is necessary for the comparisons that follow.

##### Subclass Somasteroidea Spencer, 1951

Asterozoans in which the axial skeleton consists of ambulacrals in a double series, usually paired but apparently alternating in some species. Each ambulacral gives rise to a transverse series of ossicles; in apparently primitive species, these ossicles are similar and rod-like elements termed virgals, but in more advanced species the virgals are differentiated into adambulacrals, marginals, and related ossicles. A permanent ambulacral furrow or groove is lacking so that the long axis of the ambulacral is approximately linear and horizontal, and the ossicles essentially lie in the plane of the remaining ossicles of the oral surface. The adambulacral (or first virgal) (different spellings of 'virgal' and its plural form have been used; I have followed Spencer and Wright 1966) generally abuts the lateral (abradial) margin of the ambulacral, or overlap is slight. In some species the ambulacrals probably could be raised to form temporary ambulacral furrows. A large or small radial channel for the radial water canal is present along the oral margin of the line of juncture of pairs of ambulacrals, or it is more or less enclosed by the ambulacrals. The tube-feet are seated in broad basins which in some species communicate to the body cavity. Jaw ossicles are differentiated, but odontophores are lacking. Open



TEXT-FIG. 1. Morphology of the Somasteroidea, modified slightly after Spencer (1951) and Fell (1963a). A, abactinal arrangement of *Sturzaster marstoni* (Salter), morphology considered by Spencer to be close to that of *Chinianaster*; Spencer (1951, p. 95). B, ambulacrals of *Arcegonaster pentagonus*; Spencer (1951, p. 104). C, metapinnules with cover plates, *Chinianaster levyi*; Fell (1963a, p. 394). D, interpretation of arm of *Ampullaster ubaghasi*, view of oral surface; Fell (1963a, p. 394). E, reconstruction of a part of the arm of *Chinianaster*, water vascular system darkened; Fell (1963a, p. 402). F, interpretation of arm, near tip, of *Villebrunaster thoralis*; Fell (1963a, p. 394). Key: 1, ambulacrals; 2, adambulacrals; 3, virgals; 4, marginals. Illustrations courtesy of H. Barraclough Fell and the Royal Society.

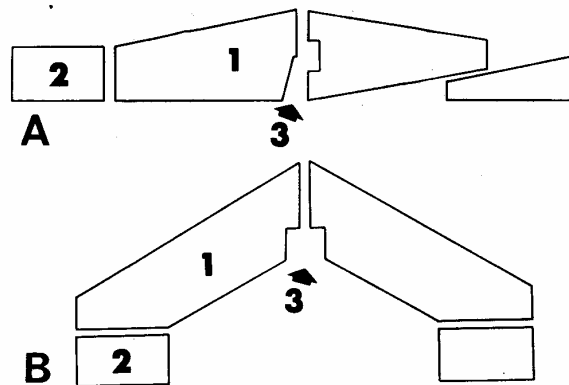
buccal slits might be present at the mouth frame in at least some species. Aboral ossicles are paxilliform, with delicate tetradiate bases. Encrusting ossicles or spinelets are present at least on some ossicles of the ventral surface. Over all, the skeleton beyond the ambulacrals is quite delicate (text-fig. 1).

*Discussion.* Most of these characters are also expressed among species assigned to the Asteroidea, but critical to the concept of the Somasteroidea is an ambulacral/adambulacral arrangement in which an ambulacral furrow or groove is lacking (text-fig. 2). Spencer (1951, p. 88) says in reference to somasteroids that '... these first stages show no sign of an ambulacral furrow', and Fell (1963a, p. 389) used the development of a furrow or groove as the basic character separating somasteroids from asteroids. The ambulacral groove or furrow is different from the ambulacral channel for the radial water canal; for further discussion, see under ambulacral column arrangement.

In somasteroids the abradial margin of the ambulacral either abuts the adradial side of the adambulacral (first virgal), or the ambulacral can overlap the adambulacral to a very limited extent (text-fig. 2). In his discussion of somasteroids, Fell (1963a, p. 393) says 'Each metapinnule arises from the abradial margin of one of the paired ambulacral (or brachial) elements . . .'. The long axis of the ambulacral is approximately horizontal and the basin for the tube-foot lies close to the plane of the oral surface.

In true asteroids the ambulacral rests on the aboral surface of the adambulacral, rather than laterally adjacent to it (text-fig. 2). In addition, the axis of the adradial end of the ambulacral is oblique to that of the general ambulacral/adambulacral articulation surfaces. These arrangements produce a permanent furrow with the basin for the tube-foot elevated.

McKnight (1975) argued that the lack of an odontophore is an important character unifying somasteroids. The odontophore is a small, unpaired typically T-shaped ossicle present between members of a jaw ossicle pair. It appears to brace and thus strengthen the jaw apparatus, and its phylogenetic development might reflect the changing food habits suggested by Spencer (1951), away from the small particle feeding inferred for somasteroids to the large particle feeding present in many living asteroids.



TEXT-FIG. 2. Stylized diagrams oriented transverse to arm axes, showing arrangement of 1, ambulacrals, and 2, adambulacrals in A, somasteroids (*Chinianaster* arrangement to left, *Ampullaster* to right), and B, asteroids. The overlap of the ambulacral on the adambulacral in *Ampullaster* is very small; compare to text-fig. 1D. 3, radial water channel. Based on work of Spencer (1951) and Fell (1963a), especially the latter's fig. 7, p. 395.

#### COMPARISONS BETWEEN *PLATASTERIAS*, FOSSIL SOMASTEROIDS AND TRUE ASTEROIDS

*Platasterias* is compared to fossil somasteroids and living asteroids, especially *Luidia* as traditionally recognized, in the following somewhat overlapping sequence: (1) over-all body form; (2) nature of the skeleton; (3) ambulacral column arrangement; (4) growth gradients; (5) other morphologic features; (6) feeding. Fell's view of *Platasterias* as a somasteroid was derived in large part from his evaluation of ambulacral column arrangement and growth gradients. A discussion of the taxonomic positions of *Platasterias* and *Luidia sensu* Fell therefore must wait until section 4. Each section begins with a summary of the ideas of Spencer (1951), Fell (1962a *et seq.*), and Spencer and Wright (1966) and continues with my comments. I have tried to include all major arguments on *Platasterias*, but the discussion is not comprehensive on other topics, such as the morphology

TABLE 1. Changes in the distribution of important characters in the inferred somasteroid/asteroid phylogeny, as envisaged by H. B. Fell. The diagram was prepared by the writer, based on his reading of Fell (1963a, pp. 389 ff.; 1963b) and it is intended as an aid to understanding Fell's ideas of the major events in his inferred phylogeny (represented by the sequence 1 through 6) rather than as an exact character distribution summary. Dotted lines mean a character is present in only some members of a division, and minor exceptions occur. For example, although the family is not entered separately, the Porcellanasteridae lack an anus and suckorial tube-feet, whereas other sea stars, such as certain *Astropecten* and *Asterias* species, have subpetaloid arms. Notes: (1) virgals similar in Division 1, dissimilar in Division 2; (2) development of actinals becomes stronger through the sequence; (3) no entry in Fell (1963a) for this division. The terminal is the unpaired ossicle at the distal tip of the arm.

Among somasteroids, the monogeneric Chinianasteridae was considered primitive, based largely on the presence of undifferentiated virgals and robust ambulacrals, and the absence of communication pores between ambulacrals for ampullae. Next in the sequence, but not separated from the Chinianasteridae in Fell 1963a, came the Villebrunasteridae, including *Villebrunaster* and *Ampullaster*. Here, virgals are differentiated and pores, inferred for internal ampullae, were present. *Platasterias* (Platasteriidae) was considered to have common features with both the Chinianasteridae and the Villebrunasteridae but appeared to be about at the villebrunasterid grade based on the inferred differentiation of the virgals, and the presence of internal ampullae (1963b, p. 144). The monogeneric Archegonasteridae, not included in the table, was considered to be an advanced somasteroid, specialized in body shape and lack of interradial slits, metapinnule reduction, and development of the robust marginals. True asteroids originated with development of a permanently erect ambulacral furrow.

ASTEROIDEA	Group 1	1. Chinianasteridae	complete transverse gradients	petaloid arms	virgals <sup>1</sup>			feeding fascioles		
		2. Platasteriidae								
	Group 2	3. Platanasteridae				terminalis	superambulacrals		ω	non-suctorial tube feet
		4. Luidiidae	furrow erect					actinals		
	Group 3	5. Astropectinidae						respiratory fascioles		
		6. Most other asteroids								anus

of the fossils. Fell's (1963a, b) major ideas on somasteroid/asteroid phylogeny are summarized in Table 1.

McKnight (1975) modified the concept of the Somasteroidea and transferred five Palaeozoic genera to this taxon. His modification is included here, but I did not attempt to re-evaluate somasteroids in light of the transferred taxa because properties of these genera were not incorporated in, and do not appear to bear directly on, Fell's ideas on the position of *Platasterias* and *Luidia*.

1. Over-all body form

Spencer (1951, p. 91) described somasteroids as having a large central body in which the arms are parts of the oral surface, i.e. '... the arms are just beginning to be differentiated'. Fell (1963a) described somasteroids as extremely flattened but, more important, as asterozoans with petaloid arms. Fell (1963a, fig. 5) presented a sequence of diagrams illustrating the inferred transformation of arm shape beginning with the petaloid arm of a monoserial crinoid, and ending with the triangular

arm of the extant astropectinid *Plutonaster*. The petaloid arm of *Platasterias* was placed by Fell between the petaloid arms of a chiniansterid somasteroid and a somewhat weakly petaloid platanasterid asteroid. Petaloid arms thus were considered to be subdued in the most primitive of Asteroidea, the fossil Platysterida, and they are absent from later groups.

Spencer (1951) did not consider the somasteroids to be flattened, rather he saw them as flexible, noting (p. 93): 'At one time the body is strongly compressed, at another the body of the same species is well rounded.'

*Discussion.* *P. latiradiata* is a relatively flat species, but such a body shape is not restricted to somasteroids, e.g. see such extremely flattened living asterinids as *Anseropoda* and *Stegnaster*.

Although the arms of *Platasterias* are strongly petaloid and the disc deeply notched interbrachially (Pl. 20, fig. 1), comparable shapes are known elsewhere, albeit more weakly developed. Examples include *Astropecten regalis* (Pl. 20, fig. 2) (Paxillosida) and *Asterias forbesi* (Forcipulatida) (Pl. 20, fig. 8). Inferomarginals in *Astropecten regalis*, like those in *Platasterias*, are transversely elongate (Blake 1973, pl. 14) and the body is flattened. These similarities among taxonomically widely separated species suggest convergence as an alternative hypothesis for origin of body shape, perhaps under conditions such as those suggested by Madsen (1966): 'I assume the petaloid arms in *Platasterias* (brought about by the transverse elongation of the adambulcralia and inferomarginalia) to be secondary adjustment to a life on a shifting sandy bottom (and perhaps a primarily ciliary method of feeding).' Fell (1962a, p. 634) noted that the extreme narrowness of the ambulacral furrow in *Platasterias* is suggestive of the fossil somasteroids, although he observed that this could be secondary. Narrow furrows occur in other modern taxa, for example, the Ophidiasteridae (Valvatida) and the Echinasteridae (Spinulosida).

## 2. Nature of the skeleton

Spencer (1951) considered *Chinianaster* and *Villebrunaster* to be the primitive somasteroids. In these genera he recognized three types of ventral ossicles: the ambulacrals arranged in a double row, the mouth angle ossicles, and the rod-like intermarginals or virgals arranged in transverse series extending from each ambulacral ossicle. Fell used the term 'metapinnules' for the rows of virgals, after the inferred homologous pinnules of crinoids. In more advanced somasteroids the morphologically simple virgals became differentiated to form marginals, adambulacrals, and other ossicles.

## EXPLANATION OF PLATE 20

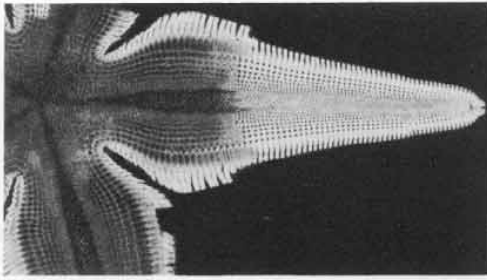
Figs. 1, 5, 6, 10, 12. *L. (Platasterias) latiradiata* (Gray). 1, over-all aboral view showing petaloid arms, alignment of abactinals, and similarity in marking to that of *L. clathrata*, see Pl. 22, × 1. 5, lateral view of inferomarginal, furrow left, row of processes are articular facets linking successive inferomarginals, × 9. 6, adambulacral, proximal view, furrow right; one muscle groove (upper, light arrow) and one articular facet (lower, dark arrow) marked; these and other structures correspond in positions with similar structures in *L. clathrata*, fig. 4 (see Blake 1972, 1973; Heddle 1967 for further discussion). 10, aboral view of cleared arm showing enlarged superomarginal row (arrow) arising at terminal, as in *L. clathrata*, see fig. 9, × 3. 12, aboral view of uncleared arm showing abactinal ossicle and granule development, compare to *L. clathrata*, fig. 11, × 3.

Fig. 2. *Astropecten regalis* Gray. Oral view showing petaloid arms and well defined marginal spines (arrow), × 1.

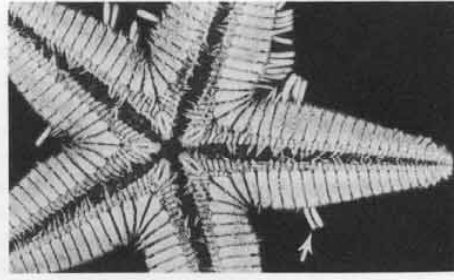
Figs. 3, 4, 9, 11. *Luidia clathrata* (Say). 3, lateral view of inferomarginal, furrow left, × 9. 4, adambulacral, inclined proximal view, furrow right, see discussion for fig. 6, above, × 9. 9, inclined aboral view of cleared arm, see discussion for fig. 10, above, × 3. 11, aboral view of uncleared arm, see discussion for fig. 12, above, × 3.

Fig. 7. *Luidia neozelanica* Mortensen. Lateral view of inferomarginal, compare with figs. 3, 6; note outline and lack of articular facet row in this species; see text for further discussion, × 9.

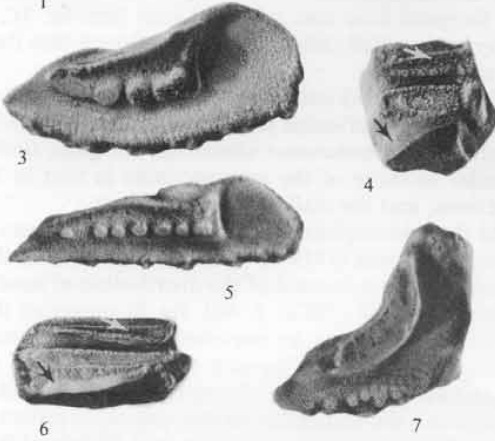
Fig. 8. *Asterias* sp. Aboral view showing petaloid arms in which an interbrachial notch (arrow) nearly reaches the madreporite, × ½.



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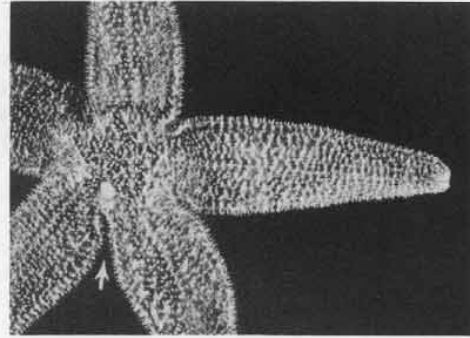
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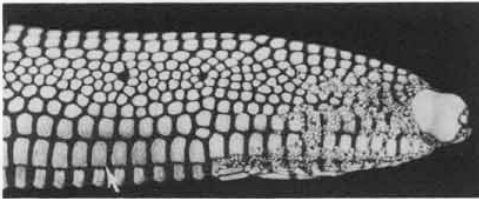
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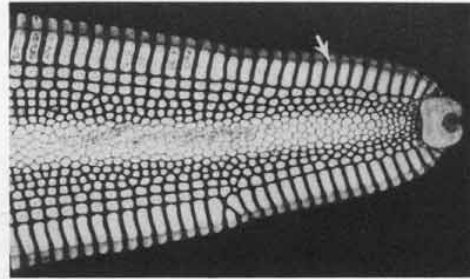
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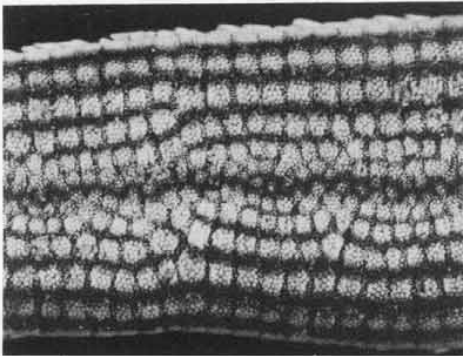
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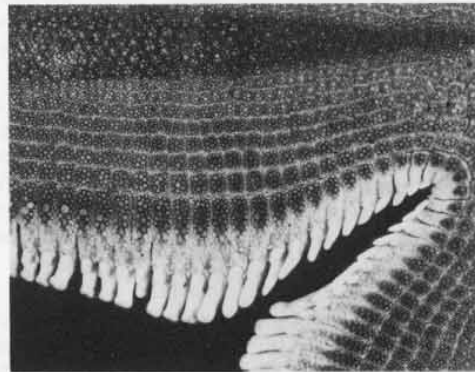
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10



11



12

BLAKE, living sea stars

The change in terminology marks this differentiation. Some virgals were partially (Archegonasteridae) or completely lost (Archophiactinidae) (Spencer 1951).

Spencer (1951) did not describe marginals in *Villebrunaster* from his relatively incomplete material, but Fell (1963*b*, p. 144) pointed out that these ossicles can be recognized in more complete specimens. Fell (1962*b*, p. 66; 1963*a*, p. 396) further noted that there are no adambulacrals, superambulacrals, or inferomarginals in *Chinianaster*. The metapinnules of *Chinianaster* terminate in a free radiole, as in *Villebrunaster* (Fell 1962*b*, p. 16). These patterns are important in interpreting *Chinianaster* as the primitive somasteroid, and *Villebrunaster* as a second step in somasteroid evolution.

The ambulacrals of somasteroids (text-fig. 1) were described as stout and block-like, or a lateral wing is developed; they form a sheath or channel for the radial water vessel. The virgals are rod-like and form the walls of channels separating successive metapinnules. The virgals of *Villebrunaster* were described (Fell 1962*b*, p. 16) as having a flattened base and a flanged keel (text-fig. 1*C*, *E*) and thus were seen as similar to those of *Platasterias*, but Fell (1963*a*, p. 422) cautioned that these ossicles proved morphologically plastic in later evolution.

The abactinal skeleton of fossil somasteroids (text-fig. 1*A*) consists of an open meshwork of paxilliform ossicles, each consisting of a slender, vertically oriented axial stalk bearing a number of elongate basal flanges. Fell (1962*b*, p. 14) noted that *Chinianaster* abactinals are quite similar to those of *Platasterias* and *Luidia* but less similar to those of the astropectinids in that in the latter the base is disc-like and lacks basal projections, and the stalk is relatively stout.

In living sea stars, an unpaired ossicle termed the odontophore is found between members of an oral ossicle pair. In certain Palaeozoic asteroids, Spencer (1919 in 1914–1940) concluded that this ossicle was derived from an occluded inferomarginal, but because of the distribution of ossicles about the jaw region in *Chinianaster* and *Villebrunaster*, Fell (1963*a*, p. 401, fig. 8) suggested that in *Platasterias* an analogous T-shaped ossicle was derived from an occluded, non-metapinnular tegmental ossicle. McKnight (1975), however, argued that an odontophore (and, presumably, the analogous T-shaped ossicle as well) is lacking from adult somasteroids. Stressing the significance of the absence of this ossicle McKnight (1975) transferred the Helianthasteridae and three genera of the Taeniactinidae to the Somasteroidea from the Spinulosida *sensu* Spencer and Wright (1966). The somasteroid skeleton beyond the ambulacral column was described by Spencer (1951, p. 93) as 'slightly built'.

*Discussion.* The primary similarity between *Platasterias* and fossil somasteroid ossicle form seems to be in transverse elongation, and, perhaps, the development of keel- and flange-shaped ossicles, as in *Chinianaster* and, to some extent, *Platasterias*.

Virgals differentiated as marginals are absent from *Chinianaster*, the inferred primitive somasteroid (Fell, 1963*b*, p. 144). Those of *Villebrunaster* (text-fig. 1*F*), representing the inferred next phylogenetic step (Fell, 1963*b*), are rather simple cylinders elongate parallel to the arm axis. They are not transversely elongate as is the case in *Platasterias* (Pl. 20, fig. 5; Pl. 21, figs. 2, 5) and as presumably would be true in a primitive somasteroid under strong influence of transverse gradients (see below). Illustrated ambulacrals (Fell, 1963*a*, figs. 5, 6; text-fig. 1, herein) of fossil somasteroids are relatively robust with a broadened adradial head and an abradial wing deflected distally, whereas those of *Platasterias* (Pl. 21, fig. 2) are wide and short, lacking the broadened head. In over-all outline, the ambulacrals of *Platasterias* thus seem to be more primitive even than those of *Chinianaster* (although ambulacrals were not considered to be derived from virgals). *Chinianaster* lacks differentiated adambulacrals, whereas those of *Villebrunaster* (Fell 1963*a*, fig. 6; text-fig. 1, herein) apparently are simple ossicles elongate parallel to the arm axis, rather than transversely elongate as is the case in *Platasterias* (Pl. 20, fig. 5; Pl. 21, fig. 5). There are no known fossils of adambulacral shape similar to those of *Platasterias*.

In contrast, ossicle morphology of *Platasterias* is very close to that of *Luidia clathrata*, differing significantly only in degree of transverse elongation (Pl. 21, figs. 1, 2; text-fig. 3). The abactinals, marginals (Pl. 20, figs. 3, 5) and adambulacrals (Pl. 20, figs. 4, 6) are particularly similar. This is true not only of the form itself, but also of the complex articulation structure arrangement of the



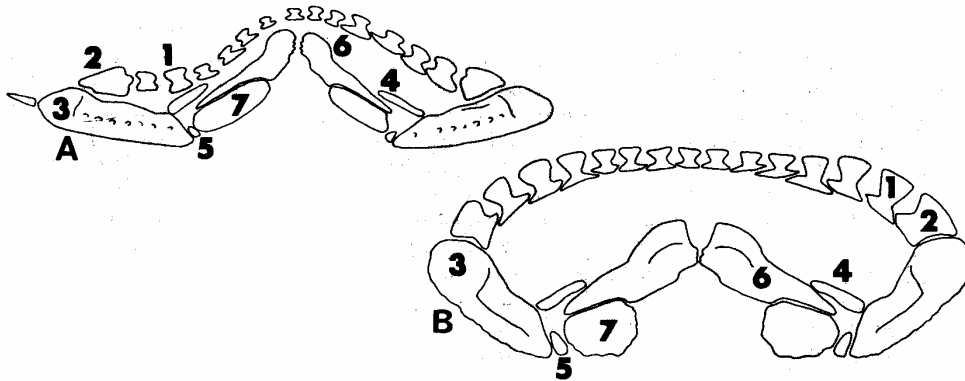
ambulacral column, involving both ambulacrals and adambulacrals (Blake 1972, 1973). The abactinal surface of the adradial end of the ambulacral is truncated in *Platasterias*, but the basic form of these ossicles is the same as in *Luidia*. Fell (1962*b*) stressed the presence of a Y-shaped groove on the actinal surface of the ambulacral of *Platasterias*, pointing out that the structure also occurs on fossil somasteroids, and he suggested that the associated muscle is used to temporarily elevate the ambulacral furrow. This muscle depression, however, occurs on all modern asteroids.

Fell (1962*b*, p. 7) also noted in *Platasterias* that the tube-feet emerge from a broad, basin-like depression. The transverse section of the middle of the long axis of the ambulacrals of most asteroid species (except, for example, the compressed ossicles of certain asteriids and asterinids and the delicate ossicles of the pterasterids) is cylindrical, hence a broad, basin-like depression is typical of most species.

Algor (1971) pointed out that *Platasterias* has the ambulacral system characteristic of modern asteroids, and he concluded that *Platasterias* is in no way primitive. Algor (1971) differentiated between ancient and modern asteroids on the basis of articulation structures across the furrow, arguing these muscles and facets were weakly developed in Palaeozoic taxa compared to the sturdy patterns seen in living species. Algor's sample of the Palaeozoic species was too small, for sturdy articulation structures comparable to that of modern species *do* occur, e.g. in *Promopalaester magnificus* (Miller) and *P. dyeri* Meek. Important, however, is that *Platasterias* is constructed in the same pattern as *Luidia*, rather than in the weakly articulated manner described for the somasteroids.

Superambulacrals are present in both *Platasterias* and *Luidia* but they have not been reported from fossil somasteroids. Inferomarginals of both *Platasterias latiradiata* and *L. clathrata* are step-shaped with overlapping, multifaceted contact points (Pl. 20, figs. 3, 5) (Blake 1973). The superomarginals are relatively large in *Platasterias* but their basic form is the same as those of *L. clathrata*. Arrangement and basic morphology of mouth frame ossicles are essentially the same between *P. latiradiata* and *L. clathrata*, although the odontophore is absent from fossil somasteroids (McKnight 1975). Distal arm ossicles, which are not transversely elongate, are essentially identical between *P. latiradiata* and *L. clathrata*, and much closer to each other than they are to those of species belonging to any other genus.

Fell (1962*b*, p. 15) suggested that the abactinals of *P. latiradiata* are similar to those of *L. neozelanica*, however, paxilliform abactinals occur in all of the living sea star orders except the Forcipulatida. A survey of the diagrams of Fisher (1911) shows that basal projections are present



TEXT-FIG. 3. Cross-sections of arms of A, *Luidia (Platasterias) latiradiata*; and B, *Luidia (Petalaster) clathrata*. In life, arms are flexible and ossicle orientations vary with behaviour; inferomarginals can be more steeply inclined to the horizontal than shown here or in Pl. 21, fig. 1. Key: 1, abactinals; 2, superomarginals; 3, inferomarginals; 4, superambulacrals; 5, actinals; 6, ambulacrals; 7, adambulacrals.

in abactinials of taxonomically diverse species and that the slender abactinials illustrated for several of the spinulosidan families (e.g. Solasteridae, Korethrasteridae, Pterasteridae) are closer to Spencer's somasteroid illustration (1951, fig. 5) than are those of *Platasterias* or *Luidia*. The abactinials of *P. latiradiata* and *L. clathrata* are very similar to each other, however.

Similarities extend to exterior morphology as well (Pl. 20, figs. 1, 11, 12; Pl. 22), as was demonstrated by Madsen (1966) for *P. latiradiata* and *L. marginata*.

I have argued on the basis of skeletal morphology that *P. latiradiata* clearly is very close to *L. clathrata*, but shows only relatively minor similarities to fossil somasteroids. Fell dissected specimens of *Luidia*; if the similarities are this strong, why was he not struck by them as well? I believe the answer lies in the species of *Luidia* available to Fell for dissection. For forty-three species of *Luidia*, Döderlein (1920) recognized ten subgenera and four supra-subgeneric taxa he termed 'groups', each group named for a representative species. Döderlein (1920, p. 223) presented a phylogenetic interpretation of *Luidia* in which he suggested that the Clathrata Group was primitive and gave rise to both the Quinaria and Alternata Groups; the Ciliaris Group was in turn derived from the Quinaria Group.

In external appearance, species of the four groups are superficially similar to one another, whereas the ossicle morphology of the members of the Ciliaris Group is quite distinct from that of the other three (Blake 1973); I suspect that if the external morphology of the Ciliaris Group were as distinct as the skeletal morphology, this group would be recognized as a separate genus.

In his discussions Fell placed little emphasis on the species available to him for study, but in an illustration of abactinials (1962b, p. 15) and an arm tip in cross-section (1963a, p. 386) he does note that his drawings were based on *L. neozelanica*. This species had not been described at the time of Döderlein (1920), but it has since been referred to the Ciliaris Group (Clark 1953; Fell 1963a, p. 433). Further, Fell's (1963a, p. 395) drawing of the cross-section of a *Luidia* arm shows a crescentic inferomarginal outline typical of the Ciliaris Group, rather than the step-shape typical of the marginals of the other three groups (Pl. 20, figs. 3, 5, 7). Madsen (1966) assigned *Platasterias* to *Petalaster*, a subgenus of the Clathrata Group; although I recognized *Platasterias* at the subgeneric level because of its distinctive shape, I agree with Madsen's inclusion of the species in the Clathrata Group.

Fell thus appears to have based his comparisons between *Luidia* and *Platasterias* on a species inferred to be well removed in phylogenetic position (Döderlein 1920) and distinct in ossicle morphology (Blake 1973) from those *Luidia* species which are suggested to be closest to *P. latiradiata* (Madsen 1966).

### 3. Ambulacral column arrangement

Although not in his diagnosis, Spencer (1951, p. 88) noted that '... these first stages ...' (in reference to somasteroids in general) '... show no sign of an ambulacral groove ...'. Spencer did describe a '... shallow channel ...' (p. 102) along the midradius of *Archegonaster*, and '... a deep channel ...' (p. 98) in *Chinianaster*. Spencer (1951) cited his 1914 paper for illustration of the channel. In a drawing of an asteroid arm in cross-section, Spencer (1914 in 1914-1940) showed that the ambulacral channel refers to the axial notch for the radial water canal. The channel is thus a structure distinct from the ambulacral furrow or groove. Although the ambulacral channel is deep in *Chinianaster*, the basins for the tube-feet are '... placed almost in the oral plane'. If an ambulacral furrow is present, as in asteroids, the ambulacrals are arched and the basins for the tube-feet are raised above the oral surface of the animal.

In Fell's discussions, whether or not the ambulacral furrow is at most temporarily erect (somasteroids) or permanently erect (asteroids) is essential to the notion of somasteroids and *Platasterias* as a somasteroid. The change from temporarily to permanently erect was selected as the point at which the pre-asteroid phase gave way to the asteroid phase (1963a, p. 391).

Fell described a well-developed 'lateral wing' on the ambulacral of *Platasterias*. This 'wing' provides attachment for the musculature extending to the first virgal (i.e. the adambulacral) that permits temporary erection of the ambulacral ossicle to form an inverted V-shaped groove considered homologous with the asteroid furrow. The ossicle arrangement in *Platasterias* was considered to be asteroid-like and leading toward the asteroid grade of organization (1962b, p. 10). Although recognizing that in *P. latiradiata*, the wing extends over the adambulacral in the manner found in asteroids, Fell (1963a, p. 393) considered '... 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 Villebrunasteridae . . . . In asteroids, the adambulacrals are below the abradial end of the ambulacrals and the basins for the tube-feet permanently raised above the substrate.

The channel for the water canal in *Platasterias* was considered partially enclosed by the ambulacral ossicles, much as in the Palaeozoic fossils.

*Discussion.* Interpretation of the ambulacral ossicles is important to the idea of a temporarily erectable furrow (Pl. 21, figs. 1, 2; text-fig. 3). In *Platasterias*, the impression of a linear, nearly horizontal ambulacral ossicle is conveyed by the broad 'lateral wing' of the ambulacral, but important to the nature of the furrow is the angle between the axis of the ambulacral/adambulacral articulation and the axis of the adradial portion of the ossicle. The ambulacral/adambulacral articulation axis is approximately horizontal in the relaxed living sea star (although capable of broad adjustment; see Heddle 1967) and therefore the angle the adradial end of the ossicle makes to the articulation axis reflects the relaxed, permanent furrow development. From a number of medial arm ossicles of mature specimens that I measured on a binocular microscope stage, this angle is approximately 20° in *L. clathrata*, 30° in *P. latiradiata*. The size of the angle depends on the precise points selected for measurement, but the critical idea is that in *Platasterias*, as in *Luidia*, these two axes are not parallel; a permanent furrow is present in both. Fell's sketches (1963a, p. 395), although presumably not intended to be precise, do accurately reflect approximate relationships, and the presence of a furrow in both.

In a figure description, Fell (1962b, p. 13) suggested that the outer, oral surfaces of the adambulacrals, as seen in *Platasterias*, are erected into the furrow at the asteroid grade. Although these faces are pulled toward one another as any sea star closes the furrow, the surfaces are not erect in the furrow in asteroids and remain directed toward the substrate in the relaxed animal. As is true of other surface ossicles, the adambulacrals bear spines on their surficial faces. Both *Platasterias* and other sea stars have approximately vertically oriented adradial side faces on the adambulacrals.

Equally important to ambulacral ossicle orientation is the nature of the ambulacral/adambulacral articulation structures, for, as noted above, the same facets and muscle depressions, arranged in approximately the same proportions, can be recognized in both *Platasterias* and *Luidia* (Pl. 20, figs. 4, 6) (Blake 1972, 1973), as well as in other asteroids. Both sea stars must be capable of approximately the same movements; Heddle (1967) described how this musculature and articulation can be used in locomotion and digging, and in a different genus I (Blake 1981) have argued that these structures can be used in righting, interpretations that seem appropriate for *Platasterias* as well as *Luidia*. The broad lateral wing, as suggested by Madsen (1966) for the inferomarginals and adambulacrals, is a part of the morphology of *Platasterias* adapted to its habitat of a shifting, sandy bottom.

As noted by Fell (1962b, p. 7), the radial water canal in *Platasterias* occupies a channel along the arm axis (Pl. 21, fig. 1) much as in certain somasteroids. A similar channel, however, occurs in *L. clathrata* (Pl. 21, fig. 2) as well as in other asteroids (e.g. *Asterias*), hence the feature is not of taxonomic value among living sea stars.

#### 4. Growth gradients

Spencer (1951, p. 91) described the interambulacrals, or virgals, as arranged in linear series at an angle to the ambulacral row with a single series arising at the abradial edge of each ambulacral. The development of virgals provided the basis for the families recognized by Spencer: in the Chinianasteridae, ossicles occupy the entire oral surface apart from the ambulacrals and mouth; in the Archegonasteridae, virgals occur only distally on the arms, and virgals are lacking from the Archophiactinidae.

Fell (1963a) developed his ideas of growth gradients in asterozoans about this transverse alignment of oral surface ossicles. Growth gradients were considered to be parallel or weakly convergent lines along which morphologic structures were aligned. Growth gradients were envisioned as

arranged in two series, one set parallel to the arm radius and a second, lateral set subperpendicular to the first. The ambulacral ossicles, nerve ganglia, and radial water vessel were aligned along the main longitudinal gradient, the adambulacrals along the first lateral gradient, and so on.

Each row of virgals was termed a metapinnule, and each represents a transverse gradient. The influence of either longitudinal or transverse gradients could be stronger; where transverse gradients dominated, metapinnule ossicles were aligned, whereas these ossicles were offset transversely but aligned longitudinally as the longitudinal gradients became dominant. The differentiation of the typical asteroid oral surface ossicles from the morphologically similar virgals was associated with the inferred declining influence of transverse gradients: the adambulacral from virgal 1, the superambulacral from virgal 2, the marginal from virgal 3, and the marginal radiole, from virgal 4 (Fell, 1963a, pp. 392, 405).

Transverse gradients dominate in primitive somasteroids (e.g. *Chinianaster*) but gradually lose their influence; longitudinal gradients dominated in *Astropecten* and phylogenetically later asteroids. The transverse gradients were ultimately derived from the inferred crinoid ancestor, hence the metapinnule from the crinoid pinnule.

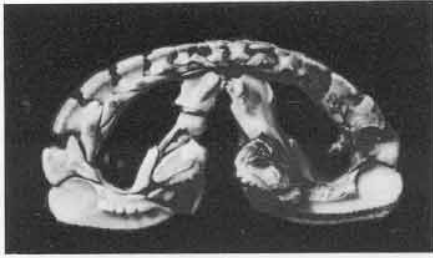
Members of ambulacral pairs apparently alternate across the arm axis in certain fossil somasteroids (Spencer 1951, p. 102) much as the brachials alternate in biserial crinoids. This similarity of arrangement contributed to Fell's view of a close relationship between crinoids and stelleroids (Fell 1963a, p. 415). In *Platasterias* the transverse gradients were considered clearly recognizable (Pl. 21, fig. 5), although the ossicles are equally clearly equated with their inferred homologues in asteroids.

Ossicle alignment was the sole criterion provided for recognition of gradient type. Most post-Palaeozoic sea stars have few to many ossicles on the oral surface between the adambulacral and inferomarginal series: these are the so-called actinal intermediates of Fell's terminology, or more simply, actinals (text-fig. 3). Actinals typically form a more or less tightly packed mosaic, they are similar to one another in shape, and although a broad size range can be present, size changes are gradational across the surface. The ossicles thus are perceived as forming parallel rows of a single orientation, or, frequently, intersecting rows, one of which is oriented more or less parallel to the arm axis, the other radiating obliquely from the furrow toward the animal margin. Dominant orientation of rows can be consistent within taxa; Hotchkiss and Clark (1976) used the arrangement of these ossicles to separate the *Asteropseidae* from the *Poraniidae*.

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#### EXPLANATION OF PLATE 21

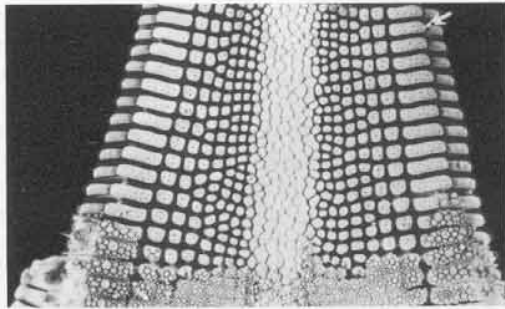
- Figs. 1, 4, 6. *Luidia clathrata* (Say). 1, transverse view of arm, ossicles identified in text-fig. 2; see note with text-fig. 2,  $\times 3$ . 4, inclined aboral view of arm showing alignment of lateral abactinals with superomarginal row (arrow); alignment is lost in midarm area; some spinelets are still in place,  $\times 3$ . 6, oral surface of arm showing alignment of inferomarginals (arrows), actinals, and adambulacrals. Tube-feet are visible along arm axis,  $\times 3$ .
- Figs. 2, 3, 5. *L. (Platasterias) latiradiata* (Gray). 2, transverse view of arm, ossicles identified in text-fig. 2,  $\times 4$ . 3, aboral view of arm showing alignment of lateral abactinals with superomarginal (arrow) row; alignment is lost toward midarm region,  $\times 3$ . 5, oral surface of arm showing alignment of ossicles, enlarged marginal radioles; arrow indicates inferomarginals,  $\times 3$ .
- Fig. 7. *Asterias* sp. Aboral view of interior of oral surface of arm showing alignment of ossicles in radial series, see discussion in text; arrows indicate ambulacrals,  $\times 3$ .
- Fig. 8. *Archaster typicus* Müller and Troschel. Oral surface of arm showing well-defined fascioles (arrow) between inferomarginals. Pits in some adambulacrals are for pedicellariae. Note similarity of lateral spines with those of *L. (P.) latiradiata* and *Astropecten regalis* (Pl. 20, fig. 2),  $\times 3$ .
- Fig. 9. *Dermasterias imbricata* (Grube). Oral surface of arm showing ambulacral spines (arrows) crossing over furrow axis, in function forming furrow cover plates,  $\times 3$ .



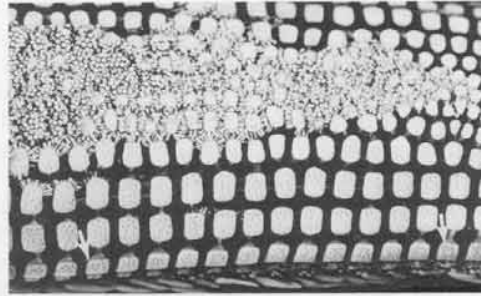
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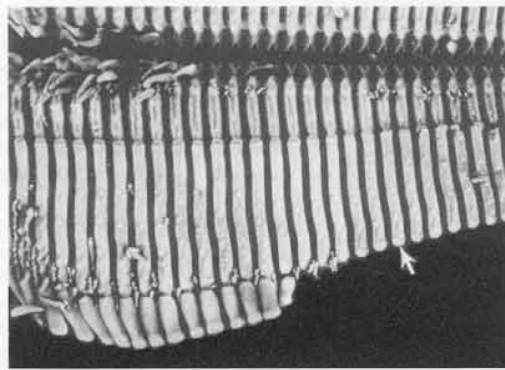
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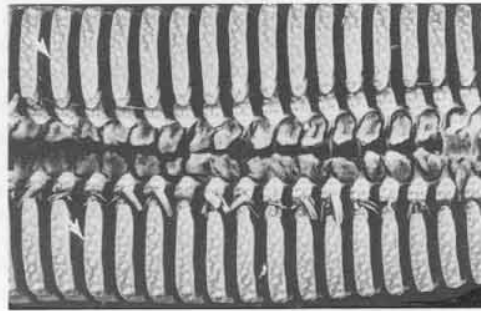
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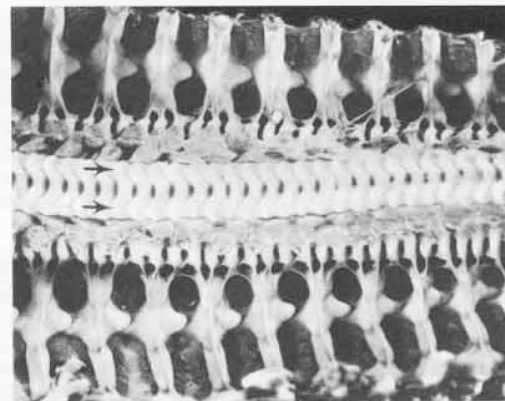
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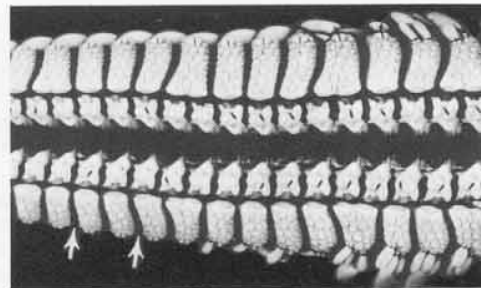
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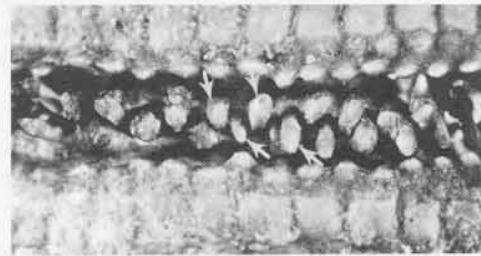
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Certain authors have interpreted the oblique arrangement of actinals in true asteroids as reflecting transverse growth gradients *sensu* Fell, but Fell himself equivocated on the origins and significance of these ossicles. In reference to the astropectinid and later stages of evolution, Fell (1963a, p. 389) said '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.' The inferred phylogenetic history of these ossicles was described as well (Fell 1963a, p. 391): 'Actinal intermediate plates are lacking from division 1 (i.e. Chinianasteridae, see Table 1, herein), appear as minute and irregular rudiments in division 2 (i.e. Platasteriidae), persist as somewhat larger and more irregular elements in the luidiids, become progressively more conspicuous in various genera of the Astropectinidae, and extremely conspicuous in post-astropectinid groups.' In suggesting that actinals were absent at the chinianasterid grade but appeared at the platasteriid grade, Fell implied that these ossicles are derived but appeared very early. In addition, Fell (1963b, p. 144) stated that the virgals in *Platasterias* had stabilized at four elements (identified above) not including actinals.

Fell (1963a, p. 387), however, also stated, 'Ossicles are differentiated along the transverse gradients in the following sequence, from within outwards: adambulacrals, superambulacrals (if present), actinal intermediate plates, marginals.' Elsewhere, Fell (1962a, p. 635) referred to actinals as 'accessory virgalia'; in the figure description (Fell 1962b, fig. 4a), the actinal was labeled 'intercalary virgalium (actinal intermediate)' and again (1963b, abstract) the metapinnule was referred to as differentiated into the actinal intermediate, as well as the other ossicle types. Although he apparently was uncertain as to how to treat these ossicles in *Platasterias* and *Luidia*, Fell's strongest statements seem to be that the actinals were secondary, and not derived from virgals.

In order to understand Fell's interpretation of *Platasterias* and the nature of the Somasteroidea, it is necessary to consider the several steps Fell (1963a) used to select the groups of extant sea stars he inferred to be primitive, and the phylogenetic sequence selected to connect fossil somasteroids to living species. Among living sea stars, Fell limited his search for the primitive group to the Luidiidae, Astropectinidae, and Porcellanasteridae because 'It has been generally agreed that the more primitive extant asteroids are the three families in which the tube-feet lack suckers' (1963a, p. 285). Of the three, the porcellanasterids were tentatively eliminated because they lack superambulacrals, one of the ossicles inferred to be homologous with the virgals of somasteroids.

More important to Fell's (1963a, p. 385) phylogenetic ideas was the concept of growth gradients. Among living sea stars, transverse rows are most clearly defined in the Luidiidae, less so (because the two systems of gradients were seen as changing influence gradually) in the Astropectinidae and Porcellanasteridae. As Fell had recognized the strongly developed transverse gradients in the lower Paleozoic somasteroids, their development in the Luidiidae permitted recognition of this group as primitive among living families. The gradients are weaker but present in the Astropectinidae (Fell, 1963c, p. 467), which was then next in the phylogenetic sequence. The Porcellanasteridae is specialized in a number of features, and was therefore third in the sequence.

Isolation of *Platasterias* as a somasteroid began with the realization that this genus '... exhibits growth gradients identical with those of Ordovician somasteroids' (Fell, 1963a, p. 383). Fell then obtained specimens of *Platasterias* for dissections; this work led to the assignment of *Platasterias* to the Somasteroidea, as well as to the refinement of a phylogenetic sequence extending from somasteroids through several steps of asteroid evolution (see Table 1). The phylogenetic sequence was based on a variety of characters and emphasized morphology of the fossils but not their stratigraphic position because the fossils appeared through an interval of strata inferred to be too brief to permit recognition of phylogenetic sequence based on stratigraphic sequence (1963a, p. 385). Fell (1967, p. 580) pointed out, however, that his phylogeny is consistent with what is known of the stratigraphic sequence.

In summary, gradient recognition depends upon ossicle alignment. A continuing, gradual decline in transverse gradient influence and a concomitant increase in the influence of longitudinal gradients was suggested to have occurred during somasteroid/asteroid phylogeny.

*Discussion.* As pointed out by Fell, the ambulacrals, adambulacrals, superambulacrals, and marginals are aligned in both *Platasterias* and *Luidia* (Pl. 21, figs. 5, 6). Although *Luidia* typically has a cluster of larger spines at the abradial ends of the marginals (Pl. 22, figs. 1, 9) rather than

a single larger radiole, as in *Platasterias* (Pl. 21, fig. 5), the positions of the spines on the marginals are the same. Although only a single large spine occurs on each *Platasterias* marginal, numerous smaller spines are present, and further, number of spines apparently is not important, as is shown by the variation found among *Luidia* species. Presence of a single marginal radiole in the petaloid species *Astropecten regalis* (Pl. 20, fig. 2) argues for the convergent evolution of marginal spine reduction. Because there is no difference in ossicle alignment between *Platasterias* and *Luidia*, this character cannot be used for taxonomic separation (although ossicle proportions do differ).

A more serious problem arises from the arrangement of the actinals and abactinals. These ossicles in *Luidia* and *Platasterias* are relatively stout, and the actinals and the lateral two to four rows of abactinals in *Platasterias* and the Clathrata Group species of *Luidia* are aligned with the four ossicles (Fell, 1963a, pp. 392, 405) of the transverse series (Pl. 20, figs. 1, 9-12; Pl. 21, figs. 3-6). Abactinal alignment with the marginals is weaker toward the middle of the abactinal surface and among the other *Luidia* groups (*sensu* Döderlein 1920) in general. A single row of actinals is present in most species of *Luidia*, including members of the apparently primitive Clathrata Group (Döderlein 1920), but extra series are present among the Alternata Group.

In some manner, the arrangement of the actinals and abactinals must be accommodated with ideas on transverse gradients because the alignment satisfies the criterion of transverse gradient recognition. Fell (1963a, p. 415) recognized the problem presented by the abactinals and noted that these ossicles were not aligned in the primitive Chinianasteridae. He suggested (p. 416) that in *Platasterias* the gradients would seem to be carried into the soft tissues in their path, and that caused '... the paxillae to differentiate as if they were virgalia'. The alignment was thus considered secondary. Fell also (1963a, p. 389) pointed out that actinal intermediates (i.e. actinals) are aligned in transverse series in various astropectinid and phylogenetically (*sensu* Fell 1963a) later sea stars.

For discussion purposes, I have accepted the following hypotheses from Spencer's and Fell's papers: (1) that asterozoans were derived from a crinoid ancestry, so that the primitive asterozoan had radial rows of virgals; (2) that somasteroids are the primitive asterozoans and gave rise to the asteroids; (3) that abactinals were present in the primitive somasteroid (because Spencer 1951, described them in the earliest known taxa). If (1) or (2), as now understood, were rejected, then the phylogenetic hypothesis using growth gradients could not be maintained. If (3) were rejected, then the fossil record is misleading and where it is misleading can be interpreted only using external criteria.

Beginning with these assumptions, abactinal alignment seen in *Platasterias* and *Luidia* can be considered either primitive and present in the first somasteroid, or derived and appearing after the first somasteroid grade. The actinals of *Platasterias* and *Luidia* can be considered either as primitive and homologous with virgals, or not. If primitive, then their alignment must be primitive, i.e. they are a part of the primitive transverse gradient. If secondary, their alignment must be secondary as well (i.e. their alignment could not be part of a primitive transverse gradient if the ossicles themselves did not occur in the primitive species). Where I treat the actinals as primitive, I will treat the specific actinal arrangement seen in *Platasterias* and *Luidia* (i.e. a single actinal row) as secondary because of the distribution of these ossicles in the accepted (see above) primitive somasteroid.

First, if we accept both abactinal arrangement and actinal ossicles as seen in *Luidia* as primitive, then the fossil record is incomplete and misleading. The abactinal pattern reported in somasteroids, including *Chinianaster*, the inferred primitive genus, is an open meshwork of light paxilliform ossicles (Spencer 1951, p. 91). If a hypothesis of declining influence of transverse gradients is to be followed, then the abactinal arrangement seen in *Platasterias* and *Luidia* must have been derived from some unknown pre-chinianasterid somasteroid, and retained while other characters (including ossicle differentiation) were evolving toward the asteroid grade. This means that known fossil somasteroids had to be off the main line of somasteroid evolution because their abactinal fields had already attained a derived, open meshwork state (text-fig. 1A; Pl. 21, fig. 3), a condition not reached in surviving asteroid evolution (*sensu* Fell) until after the level of the Paxillosida. Following the implications further because the abactinals of *Luidia* and *Platasterias* are sturdy, the primitive abactinal condition in somasteroids likely was sturdy as well, and the relatively fragile ossicles of known

fossils represent derived states. Thus, taxa with the relatively sturdy arrangement are unknown from the fossil record, whereas the relatively fragile ones were preserved. Finally, the fossil record itself becomes unreliable in that although most oral surface ossicle distributions in known fossils are considered to represent primitive conditions, the abactinal arrangement is considered secondary for reasons external to the fossils themselves.

As to the actinal surface ossicles, their reduction sequence in known somasteroids began with a full oral surface field (*Chinianasteridae*), continued through an intermediate step in which ossicles were present only distally on the arms (*Archegonasteridae*), and ended with complete elimination of these ossicles (*Archophiactinidae*) (Spencer 1951). Thus the presence in *Platasterias* and most *Luidia* of a single row extending the entire arm length must represent a lineage separate from known fossils because they match neither any known fossils, nor the known reduction sequence.

The second approach is to assume, as Fell did, that abactinal alignment and actinal ossicles are secondary. This path, however, also yields difficulties because it requires extension of the transverse gradients on to the aboral surface at the time the influence of these gradients is hypothesized to be declining and the longitudinal gradient influence increasing. Because the row of actinals also becomes aligned with adjacent adambulacrals and marginals, we must hypothesize alternating rows of increasing and decreasing influence of transverse gradients (i.e. adambulacrals, decreasing; actinals, increasing; marginals and marginal radioles, decreasing; abactinals, increasing). Even if we were to argue that abactinals represent an ossicle system separate from crinoids and not derived from them, and therefore not primitive in somasteroids, the problem of alignment is not resolved. Abactinals do occur in an open meshwork pattern in the known primitive somasteroid (*Chinianaster*), and *Platasterias* was considered to be approximately at the *Villebrunaster* level of organization, at a post-*Chinianaster* pre-*Archegonaster* somasteroid grade. Transverse gradients are hypothesized to be declining in influence during this sequence, yet in *Platasterias* these gradients had to be extending their influence on to a new area of the body.

Further, because transverse alignment can be secondary among some ossicle systems, it might also be secondary among all others. *Platasterias* therefore does not readily fit into a somasteroid/asteroid phylogeny based on growth gradients. This does not challenge the hypothesis as applied only to known fossils.

Primitive and derived states could be rearranged so that abactinal alignment is considered primitive and actinals derived, or vice versa, but this only combines inherent difficulties in different ways.

It would be possible to argue the large actinal field was not lost in the connecting links between somasteroids, luidiids, and remaining asteroids, but this alternative removes *Platasterias* and *Luidia* from the main line of asteroid evolution, for there is no known platasteriid or luidiid, fossil or living, with the appropriate morphology (i.e. well-defined fascioles, and a large actinal field). *Tethyaster* is an astropectinid that comes quite close to this morphology, and indeed Jangoux (1975) argued that this genus is in many ways intermediate between *Luidia* and *Astropecten*. The marginal fascioles in *Tethyaster*, however, are relatively small, and the development of fascioles also was important in Fell's hypothesis, serving as feeding and respiration channels.

In any event beginning with the assumptions of Spencer (1951) and Fell (1962a *et seq.*), and assuming either that abactinal alignment and actinal occurrence is primitive or secondary, known fossil and modern taxa permit no application of the hypothesis of growth gradients to somasteroid/asteroid phylogeny that does not require ignoring important aspects or morphology. In essence, alignment is too extensive in *Platasterias*, more extensive than in the fossil somasteroids, and this calls for explanation other than phylogenetic inheritance from a crinoid ancestry. Such an origin is suggested below, under a functional explanation for alignment in *Luidia*.

As noted earlier here, individual ambulacral column and marginal ossicles of *Platasterias* are transversely more elongate than are those of the fossil somasteroids. Again, *Platasterias* is showing an inferred primitive trait more strongly than it is seen in the earliest known somasteroids, and therefore an explanation other than inheritance of a primitive condition is demanded.

##### 5. Other morphologic characters

*The nature of the mouth frame.* In modern sea stars, all ambulacral pairs are united across the furrow by muscles and articular structures. In the somasteroids, Spencer argued that the proximal ambulacrals (three pair in *Chinianaster*) were not linked across the furrow, resulting in broad, V-shaped openings termed buccal slits. These slits, however, are likely to have resulted from post-mortem events. Spencer (1951, p. 100) argued that ambulacrals of certain small *Chinianaster* were pulled apart after death, and Fell (1963a, p. 403) suggested that the buccal slits of Spencer



resulted from such changes. The ossicles of the buccal slits in *Archegonaster* apparently show no significant, distinctive morphologic characters (Spencer, 1951, fig. 9) as might be expected of ossicles that form the margin of an opening rather than an articulated double column. Minor differences are illustrated in these ossicles, but near-oral ambulacral column ossicles also are somewhat distinctive in certain living sea stars (e.g. the Astropectinidae).

*Arrangement of spinelets, along the fasciolar margins.* In *Platasterias*, a series of small spinelets, termed cover plates by Fell, line the edges of the adoral surfaces of the marginals and adambulacrals. These spinelets were described as being held in a web and, when depressed, they cover the fasciolar grooves between subsequent metapinnules or transverse gradient series (1963a, p. 397). The arrangement was inferred derived from the crinoid ancestor, but differs in closing over the interpinnular groove rather than over the pinnule surface, as in crinoids. The cover plates in *Platasterias* were seen as protecting the fasciolar or feeding grooves.

A similar arrangement is found in *Luidia*, *Astropecten*, and other sea stars, although the ossicles in these taxa typically are more slender, i.e. spine-like, and much more numerous than in *Platasterias*. As in *Platasterias*, these ossicles can be depressed over the furrows. I was unable to recognize true webbing in preserved specimens of *Luidia* (although such a covering is present in *Goniopecten*, suborder Cribellina, order Paxillosida), but a mucus covering is present that in dried specimens available to me can extend to the tips as well as between adjacent spinelets. The dense, overlapping arrangement of many spinelets provides an effective cover for the fasciolar furrow. Various sea stars, e.g. *Dermasterias imbricata* (Pl. 21, fig. 9), are capable of pulling the sides of the furrow (i.e. the adambulacrals) together and arching the furrow spines over the furrow. Functionally, these are cover plates and such plates are widely distributed among the Asteroidea.

The arrangement found in *Platasterias* could be readily derived from that of *Luidia* by reduction of spine number and minor changes of spine shape. Arrangement of fasciolar spinelets therefore provides little justification for significant taxonomic separation of *Luidia* and *Platasterias*.

*Superambulacrals.* Fell (1963a) argued that the superambulacrals of *Platasterias* and *Luidia* are occluded second virgals. This explanation of origins is plausible, however, superambulacrals are unknown in fossil somasteroids but they are present throughout the Luidiidae and Astropectinidae. This distribution can only serve to isolate the fossil from the extant sea stars, not link them in a single phylogenetic sequence.

*Soft parts.* *Platasterias* has a blind gut with caeca extending into the arms, an arrangement Fell (1963a, p. 396) thought probably existed in fossil somasteroids. In addition, *Platasterias* has small, simple non-suctorial tube-feet considered similar to those in *Chinianaster* (Fell 1962c, p. 474) and small, double internal ampullae also inferred to be similar to those in Ordovician somasteroids. *Luidia*, like *Platasterias*, has simple, non-suctorial tube-feet, double ampullae, and a blind gut with caeca extending into the arms.

#### 6. Feeding habits

Spencer (1951, p. 87) emphasized feeding behaviour in his tripartite division of stelleroids: 'The grouping of starfish adopted here is based upon the activities of the arms, especially during feeding.' The asteroids were seen as carnivores on larger organisms, primitive ophiuroids were believed adapted for feeding on small particles on or in the bottom, and the somasteroids inferred to have lived on planktic particles (in the suggested relatively primitive genus, *Villebrunaster*) or particles from the surface sediment layers (in the suggested advanced somasteroid *Archegonaster*).

Fell also stressed observed and inferred feeding behaviour in his phylogenetic sequence. He (1962a, p. 14) suggested two types of feeding are present in *Platasterias*, 'microphagous ciliary feeding', and 'selective detrital feeding'. In the former, particles of food were believed to be conveyed in water currents along the fascioles to the arm radius, then proximally toward the mouth. In specimens of *Platasterias* available to him, Fell observed amphipods in the mouth and in a food groove; he suggested that the amphipods were collected by the tube-feet and passed to the mouth.

He inferred that this would be the limit of carnivorous feeding, because of the relatively small mouth of *Platasterias*. A specimen of *Platasterias* in the U.S.N.M. collections has a foraminiferan, small snail, and arthropod fragments in the mouth area; the presence of this small prey does not appear fortuitous.

As observed by Fell (1963a), *Astropecten* and especially *Luidia* (Pl. 21, fig. 6) are living species with quite similar fasciolar furrows extending between the marginals and ambulacrals, yet these are voracious predators of other echinoderms, molluscs, and arthropods. Although suspension feeding has been suggested for both (Fenchel 1965, for *Luidia sarsi*; Gemmill 1915 and Gislén 1924 for *Astropecten*), Feder and Christensen (1966) doubt this behaviour occurs in these genera. The furrows in both, as Fell (1963a, p. 391) observed for the Luidiidae, are probably respiratory in nature. In contrast, taxonomically diverse genera in which suspension feeding has been observed do not possess fasciolar furrows (e.g. *Henricia*, Spinulosida, Rassmussen 1965, ossicles are aligned in this genus, yielding unobstructed channels between ossicle rows; *Oreaster*, Valvatida, Halpern quoted in Anderson 1978; unidentified Brisingidae, Forcipulatida, Pawson 1978). Fell recognized the differences in function between the fascioles of the modern sea stars and that inferred for the somasteroids and assumed the function changed with the evolution of the asteroid grade.

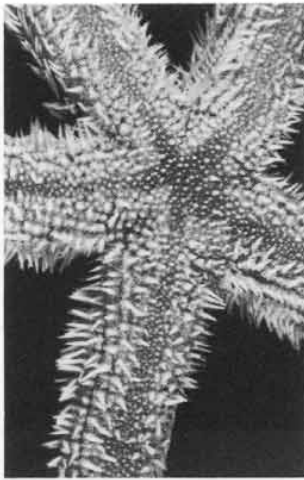
Suspension feeding is difficult to document without direct observation. Gislén (1924) found surface ciliary currents to be widespread in sea stars and therefore the potential for ciliary feeding as well, although the currents flow away from the oral area in some species. Gislén (1924), however, considered the functions of the currents to be largely for respiration and cleaning, although he did observe some capture of particles.

The size of the mouth does not provide a useful guide to potential prey size limits, as suggested by Fell for *Platasterias* (1962b, p. 14), for both *Astropecten* and typical *Luidia* species, although

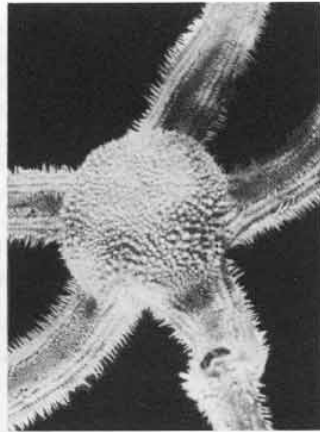
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#### EXPLANATION OF PLATE 22

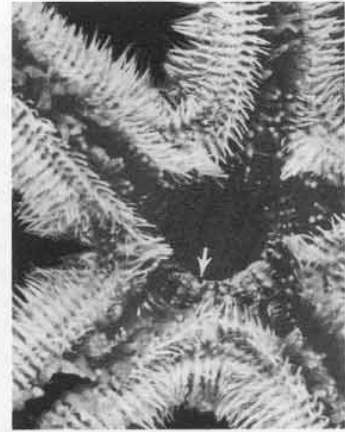
- Fig. 1. *Luidia alternata* (Say). USNM 7528. Inclined view of disc region of specimen not distorted by food; specimen in alcohol,  $\times 1$ .
- Figs. 2, 3. *Luidia alternata* (Say). USNM 7528. 2, inclined aboral,  $\times \frac{1}{2}$ ; and 3, oral view,  $\times 1$ , of individual containing unbroken corona of *Lytechnius varegatus* (Lamarck). The peristome of the echinoid (arrow, pointing to gill slit) is centred on that of the sea star. The sea star major radius is 140 mm, relaxed minor radius 20 mm, and height 15 mm. The echinoid corona diameter about 50 mm, height 25 mm. All dimensions approximate. Spines and organic materials are missing from the echinoid but pieces of the Aristotle's Lantern are present. The echinoid thus apparently was dead or nearly so at time of ingestion and it had been consumed and presumably was soon to be expelled at time of collection. In alcohol.
- Figs. 4, 5. *Luidia clathrata* (Say). USNM E17599. 4, view into disc; and 5, lateral view of fragmentary individual, radius about 100 mm, containing a specimen of *Moira atropos* (Lamarck), length about 40 mm. The echinoid is now incomplete (arrows point to remaining coronal plates) but the aboral surface of the sea star retains the form of the sea urchin, hence the echinoid was complete when ingested. Fine lines beyond the echinoid plates are its spines; the echinoid apparently was ingested alive, or very recently dead; specimen is dry,  $\times 1$ .
- Fig. 6. *Luidia clathrata* (Say). USNM 8442. Inclined aboral view of specimen, radius about 110 mm, containing *Moira atropos*, length about 40 mm. Spines are retained on prey,  $\times 1$ .
- Figs. 7, 8. *Luidia clathrata* (Say). USNM E3268. 7, aboral view; and 8, oral view of sea star containing a broken but not distorted *Mellita quinquesperforatus* (Leske). The spines are missing from the echinoid. Sea star radius about 150 mm, that of the echinoid is about 50 mm. Aboral ossicles of the sea star are distorted from life position, beyond the edge of the sea star in a relaxed state (arrow); the aboral surface of the sea star was partially opened after collection. Compare colour marking with that of *L. (P.) latiradiata*, Pl. 20, fig. 1; specimen is dry,  $\times \frac{1}{2}$ .
- Fig. 9. *Luidia clathrata* (Say). Oral view of mouth area of specimen not distorted by food; specimen is dry,  $\times 1$ . *Luidia* can consume particles of dimensions many times greater than the 2 or 3 mm mouth diameter, and of volumes greater than that of the relaxed disc. Much caution is needed in interpreting possible food particle size in fossil organisms with flexible bodies.



1



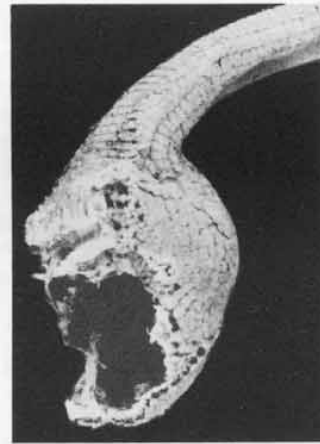
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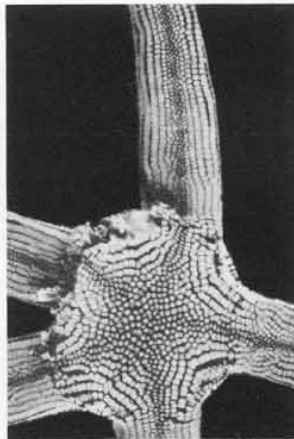
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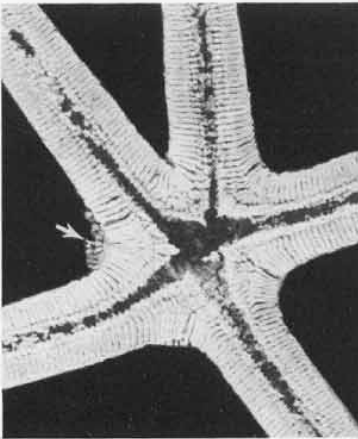
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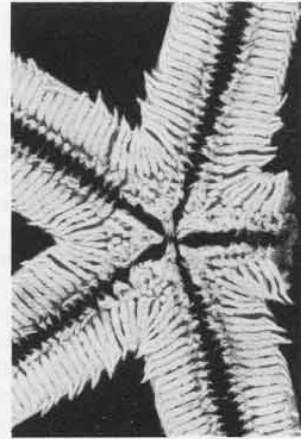
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8



9

BLAKE, sea star *Luidia*

effective predators, also have relatively small oral frames. The lack of importance of mouth size is clearly seen in a series of *Luidia* specimens in the U.S.N.M. collections (Pl. 22). In each example illustrated, the size of the ingested echinoid exceeds that of the relaxed diameter of the disc. Peristome size, measured in related *Luidia* specimens of comparable sizes, is 2 to 3 mm; oral spines mounted around the mouth of the sea star overlap over the peristomial opening. Occurrence of large prey in a number of specimens clearly demonstrates the behaviour is not unusual. *Astropecten*, too, is capable of feeding on relatively large prey organisms (Clark 1962, pl. xiii).

Thus, *Luidia* has fasciolar grooves similar to those of both *Platasterias* and presumably of the ancient somasteroids, but there is no clear evidence that either *Platasterias* or *Luidia* make use of suspension feeding and therefore the presence of fascioles in Palaeozoic somasteroids provides no morphologic evidence of suspension feeding in these organisms. The presence of very large prey in *Luidia* means that mouth and body size provide no clear guide to food particle size in echinoderms with a loosely articulated skeleton, including the Palaeozoic somasteroids.

#### Summary

*Platasterias* is very close to typical species of *Luidia* in all characters except those related to the transverse elongation of ossicles, and similar to Palaeozoic somasteroids only in ways it is also similar to *Luidia*. Greater differences in ossicle morphology, except for this transverse elongation, are seen between species of the Ciliaris Group of *Luidia* (*sensu* Döderlein 1920) and Clathrata Group (*sensu* Döderlein 1920) than are seen between *Platasterias* and the Clathrata Group of Döderlein. I therefore consider (Blake 1972) *Platasterias* to be a subgenus of *Luidia* assignable to the Clathrata Group, and not a somasteroid as suggested by Fell. As noted above, Madsen (1966) carried this interpretation one step further, for he did not believe *Platasterias* warranted subgeneric recognition. Summary comparison among sea star taxa is provided in Table 2, with *Porania* included as an example of an asteroid well removed from the Luidiidae.

If *Luidia* were to be extensively subdivided, perhaps along the lines suggested by Döderlein (1920), then *Platasterias* could be recognized at the generic level, but on a morphologic basis, it still would have to be included in the same family as other *Luidia* species. *Luidia*, as noted by Fell (1963a), clearly is a member of the Asteroidea.

### THE NATURE OF *LUIDIA*

#### *The affinities of the Luidiidae*

In his work, Fell assumed the sea stars with nonsuctorial tube-feet, and in particular the astropectinids and luidiids are primitive among extant sea stars. I agree with this interpretation but, although consensus might lean toward the families cited, no general agreement has ever been reached.

Mortensen (1922), noting that few authors had commented directly on the question of primitive position, queried the then-active sea star workers as to their opinions. W. K. Fisher, H. L. Clark, and R. Koehler all considered the astropectinids to be primitive, as did Mortensen himself, whereas Döderlein thought the asterinids were primitive. Earlier, Perrier (1884) argued the forcipulates were primitive on inferred directions of pedicellariae evolution.

Most active sea star taxonomists list the Paxillosida first in their faunal lists, seemingly thereby implying an inferred primitive position, but as A. M. Clark pointed out to me (pers. comm.), this is simply because they are following Fisher (1911).

In this diagnosis of the Platysterida (including the Palasteriscidae and Luidiidae), the only character listed by Fell (1963a, p. 392) was the development of transverse growth gradients. Spencer and Wright (1966) expanded upon the diagnosis, but most features listed by these authors also apply to members of the Paxillosida. They did include the presence of a single row of marginals in the Platysterida. Although relatively small in *Luidia* compared to those in, for example, *Astropecten*, superomarginals are present in *Luidia* (Pl. 20, figs. 9, 10), recognizable on the basis of position of origin at the terminal (see criteria listed by Blake 1978), and by size among primitive

(*sensu* Döderlein 1920) *Luidia* species. This leaves only the transverse gradients to unite the Luidiidae with the Palaeozoic Palasteriscidae, but this character, as discussed above, appears unreliable. Based on illustrations provided by Spencer (1919 in 1914–1940), however, *Luidia* and the Palasteriscidae are distinct in ossicle morphology, and fascioles apparently are lacking in the fossil family. In addition, they are separated by a Devonian to Miocene interval.

The Luidiidae, however is similar to the Astropectinidae in many soft and hard part characters, as summarized by Fisher (1911), Fell (1963a), and other workers; included here are the nature of the paxillae and other ossicles, and the presence of non-suctorial tube-feet. Following McKnight (1977), I therefore have herein returned the Luidiidae to the Paxillosida.

A partial revised classification of the stellate echinoderms based on Spencer and Wright (1966), McKnight (1975) and the arguments presented here is provided below. For comparative purposes, the equivalent classification of Spencer and Wright (1966) is also included.

Revised classification:	Spencer and Wright (1966):
Class Somasteroidea	Class Stelleroidea
Order Goniactinida	Subclass Somasteroidea
Family Chinianasteridae	Order Goniactinida
Family Villebrunasteridae	Family Chinianasteridae
Family Archegonasteridae	Family Villebrunasteridae
Family Archophiactinidae	Family Platasteriidae (includes <i>Platasterias</i>
Family Helianthasteridae	<i>latiradiata</i> )
Class Asteroidea	Family Archegonasteridae
Order Platyasterida	Family Archophiactinidae
Family Palasteriscidae	Subclass Asteroidea
Order Paxillosida	Order Platyasterida
Suborder Hemizonina	Family Palasteriscidae
Suborder Diplozonina	Family Luidiidae
Family Luidiidae (includes <i>Luidia</i>	Order Paxillosida
( <i>Platasterias</i> ) <i>latiradiata</i> )	Suborder Hemizonina
Family Astropectinidae	Suborder Diplozonina
Family Porcellanasteridae	Family Astropectinidae
Suborder Cribellina	Family Porcellanasteridae
Class Ophiuroidea	Suborder Cribellina
	Subclass Ophiuroidea

*The gap in the fossil record of the Platyasterida sensu Fell 1963a*

The fossil record does not support an inference that the lineage leading to *Luidia* has endured nearly unchanged from the Palaeozoic. The order Platyasterida *sensu* Fell (and Spencer and Wright 1966) includes three genera assigned to two families: *Platanaster* (M. Ord.) and *Palasteriscus* (L. Dev.), both belonging to the Palasteriscidae, and *Luidia* (Mio.-Rec.), belonging to the Luidiidae. There is thus a gap from Lower Devonian to Miocene in the inferred record of the order. At first inspection, this appears trivial because of the sketchy record of sea stars, but I believe it becomes more important when this record is carefully considered.

Among post-Palaeozoic sea stars, *Astropecten* and its close allies have a relatively good fossil record. This record seems to result from body structure, habitat, and habits. The sea stars have relatively stout marginal frames and at least *Astropecten* frequently lives in shallow waters on unconsolidated substrates, and burrows beneath the surface. The relative abundance of *Astropecten* as fossils does not necessarily result from a greater, enduring abundance (although they are very common today), but from where and how individuals live. *Luidia* lives in similar environments, and it too is a burrower; although the marginal frame is not as stout as in *Astropecten*, the inferomarginals of many species are comparable to those in *Astropecten*, and sturdier than those of the Asteriidae, a family known from the Jurassic and whose representatives are also sometimes found in similar habitats.

TABLE 2. Comparison of somasteroids and asteroids. Criteria available do not permit separation of *Platasterias* as a somasteroid. *Porania* (Poraniidae) is taxonomically distant from the somasteroids but still has many features in common with them. Data in part from Fell (1963a).

	ossicle alignment	ambulacral furrow	super-ambulacral	terminal	tube feet
somasteroids	primarily transverse in some, others longitudinal	not erect	absent	present or absent	?
<u>L. (Platasterias)</u>	both transverse and longitudinal	erect	present	present	non-suctorial
<u>Luidia clathrata</u>	both transverse and longitudinal	erect	present	present	non-suctorial
<u>Porania</u>	primarily longitudinal	erect	absent	present	suctorial
other asteroids	primarily longitudinal	erect	present or absent	present	non-suctorial and suctorial

	anus	body shape	feeding habits
somasteroids	?	petaloid to large oral disc	inferred suspension or small particle bottom feeder
<u>L. (Platasterias)</u>	absent	petaloid	carnivore
<u>Luidia clathrata</u>	absent	small disc, strap-shape arms	carnivore
<u>Porania</u>	present	large oral disc	suspension feeding, other
other asteroids	present or absent	varied	varied

*Luidia* is a common genus, with sixty or more species (many described since Döderlein 1920) widely distributed in temperate to tropical seas; further, individuals commonly are abundant. Individuals of most species of *Luidia* are relatively large and would not be readily overlooked in the fossil record. *Luidia superba* specimens have been reported from the Galapagos Islands with major radii up to 415 mm and an arm breadth at the disc edge of 60 mm (Downey and Wellington 1978). The absence of a fossil record for platysterids (*sensu* Fell) from Devonian to Miocene certainly is not conclusive evidence that they were not present, but because structurally comparable sea stars known from similar environments do have long records, the absence of *Luidia* or its relatives requires explanation.

*A functional explanation for the transverse alignment of ossicles in Luidia*

Fell argued that the body plan of *Luidia* is the direct phylogenetic heritage of Cambrian crinoids; in effect, that functional explanations of the morphology of these contemporary, mobile carnivores, living with their oral surfaces toward the substrate, are to be sought in ancient, attached suspension-feeding organisms living with their oral surfaces directed into the water column. I believe an explanation for the *Luidia* body plan can be developed that is more closely linked to the life needs of sea stars.

The arms of *Luidia* are very flexible in part because they are narrow and low and in part because the alignment of ossicles yields essentially a segmented pattern in which each radial row of ossicles is relatively weakly connected to adjacent rows. This arrangement weakens toward the middle of the aboral surface of the arm, where the abactinals are too small to interfere with flexibility.

The value of flexibility to *Luidia* can be correlated with preferred food and habitat. *Luidia* is a predator on larger solitary organisms—molluscs, arthropods, and other echinoderms—in which long, flexible arms are useful for the manipulation of prey. *Luidia* is commonly an inhabitant of shallow, often agitated, bottoms and, further, it frequently burrows into the substrate. Arm flexibility is useful for burrowing (Heddle 1967) and also for righting (Blake 1981).

*L. (P.) latiradiata* shares the ossicle arrangement of traditional *Luidia* species, and it, too, is an active predator (see above), but in it the demands of environment (Madsen 1966) might have dominated the need for maximum arm flexibility.

A superficially similar transverse alignment is seen in *Asterias* and other asteriids in the rows of arm ossicles immediately lateral to the furrow columns (Pl. 21, fig. 7). The ancestry of the Asteriidae is unknown, and therefore it is not known when this alignment evolved, but asteriids, like *Luidia*, are active predators with a need for relatively flexible arms.

Another hypothesis for ossicle alignment in *Luidia* and *Astropecten* can be based on the burrowing habits of these sea stars combined with the respiratory current flow described by Gislén (1924). Although surface currents appear typical of sea stars, deep fascioles seemingly are restricted to burrowers. These channels, combined with their cover spinelets, should provide protection from sediment interference for the current flow. Alignment of ossicles and their intervening channels in turn would permit a more efficient water flow than that possible in a species with an irregular arrangement of ossicles. Surface-dwelling species presumably would suffer less from current disruption and, in them, furrows generally are lacking.

*Archaster* is an extant genus superficially very similar to *Astropecten* in both form and habit. It too has relatively deep fascioles (Pl. 21, fig. 8), but only between the infero-, and not the superomarginals. *Archaster*, however, is an atypical member of the Valvatida rather than the Paxilloidea, as is *Astropecten*. It is possible that *Archaster* was derived directly from an *Astropecten*-like source but the skeletal morphology in this genus does not seem to support such an idea; convergence resulting from habitat similarities is a preferable hypothesis.

Thus, both the alignment of ossicles in the arm and the grooves between the aligned ossicles seem subject to convergent evolution; use in any phylogenetic scheme must be made with great care.

#### SUMMARY

*Platasterias latiradiata* Gray is removed from the Somasteroidea and assigned at subgeneric rank to the genus *Luidia* of the monogeneric asteroid family Luidiidae; *Luidia (Platasterias)* therefore should not be singled out as a model for the reconstruction of the biology of early stellate echinoderms. Reasons for the transfer of *L. (Platasterias)* are: (1) The single distinctive feature of the Palaeozoic somasteroids seems to be the absence of a permanent ambulacral furrow. In contrast the adambulacral/ambulacral arrangement in *L. (P.) latiradiata* is the same as that found in *L. clathrata* and essentially as in all other living asteroids; a true furrow is present in *L. (P.) latiradiata*. (2) Individual ossicle morphology and ossicle and muscle arrangement of *L. (Platasterias)* are easily within a reasonable range of variation for *Luidia*. Although many (but not all) ossicles of *L. (P.) latiradiata* are proportionately broad, they are morphologically closer to the Clathrata Group species of *Luidia* than these ossicles are in turn to the Ciliaris Group species of *Luidia*. (3) A reconstruction of phylogenetic history based on ossicle alignment (growth gradients) requires important reversals of direction of evolution in order to enable fossil somasteroids and extant *L. (Platasterias)* and other luidiids to fit the hypothesis. (4) Two important ossicle types, the odontophore and superambulacral, are present in *L. (Platasterias)* and other extant sea stars, but they apparently are absent from the fossil somasteroids. (5) Although *L. (Platasterias)* has a petaloid arm shape suggestive of that of certain crinoids, weakly developed petaloid arms are present in

other taxonomically widely separated sea star taxa; the character is subject to convergence. (6) Known food habits of *L. (Platasterias)* suggest similarities to those of typical *Luidia* species and not to those habits inferred by Spencer (1951) for the fossil somasteroids. (7) Available data suggests soft-part morphology of *L. (Platasterias)* is essentially that of a typical *Luidia*.

The Luidiidae is transferred from the otherwise Paleozoic order Platysterida to the common post-Paleozoic Paxillosida.

The origin of the transverse alignment of ossicles in *Luidia* (including *Platasterias*) is ascribed to habits and habitats of the sea star. This ossicle arrangement enhances arm flexibility, useful to an active, burrowing predator living in shallow, often turbulent, environments. The presence of deep furrows between aligned ossicle series also provides an open channel, unimpeded by sediment, for the flow of respiratory water currents.

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D. B. BLAKE

Department of Geology  
 University of Illinois  
 245 Natural History Building  
 1301 W. Green St.  
 Urbana, Illinois 61801  
 U.S.A.

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