

THE ARM STRUCTURE AND MODE OF FEEDING OF THE TRIASSIC CRINOID *ENCRINUS LILIIFORMIS*

by R. P. S. JEFFERIES

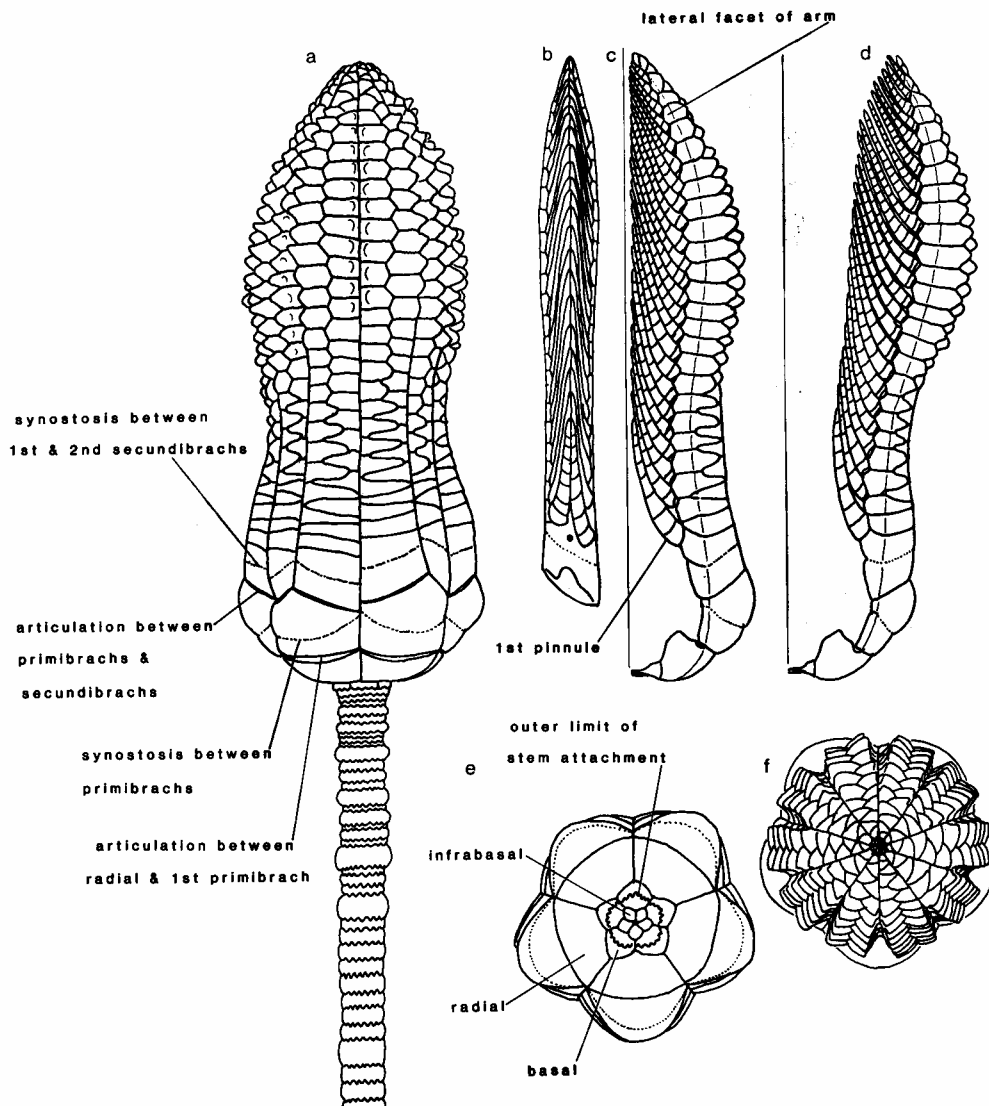
ABSTRACT. A characteristic ornament of alternating ridges and grooves (pectinate ornament or *kammartige Ornamentierung* of Hagdorn, 1982) exists on the interpinnular surfaces of *Encrinus liliiformis* Lamarck from the German Oberer Muschelkalk (Upper Anisian to Ladinian). These ridges and grooves run transverse to the length of the pinnule and in life would have formed a very large number of microscopic interpinnular channels. These channels would probably have been ciliated and suggest that *E. liliiformis*, unlike most other crinoids, was at least in part an active filter feeder, i.e. produced its own feeding currents, by active ciliary beat through the interpinnular channels. Passive filtration of bottom currents, like that observed in Recent crinoids, may also have been used, particularly near the tips of the arms.

ZUSAMMENFASSUNG. Eine charakteristische Ornamentierung (kammartige Ornamentierung von Hagdorn, 1982) befindet sich auf den Ober- und Unterseiten der Pinnulae von *Encrinus liliiformis* Lamarck aus dem deutschen Oberen Muschelkalk (Oberanisien bis Ladinium). Sie besteht aus alternierenden Rücken und Furchen, die die Länge der Pinnula quer überkreuzen und die beim lebenden Tier eine große Anzahl mikroskopischer, zwischen den Pinnulae gelegener, Röhren gebildet haben würden. Allem Anschein nach waren diese Röhren bewimpert und alles deutet darauf hin, daß *E. liliiformis*, zumindest zum Teil, sich (ungleich anderen Crinoiden) als aktiver Filterfresser nährte, d. h. erzeugte seine eigenen Filter-Strömungen mittels aktiven Wimperschläges in den interpinnularen Röhren. Passives Filtrieren der bodennahen Strömungen des Wassers, wie oftmals bei rezenten Crinoiden beobachtet, war wahrscheinlich auch an der Nahrung beteiligt, besonders in den distalen Teilen der Arme.

THE German Triassic crinoid *Encrinus liliiformis* Lamarck from the Oberer or Hauptmuschelkalk is one of the most famous species of fossil crinoid. It was well described in a classic monograph by Beyrich (1858), the growth of its stem was studied by Aldinger (1928), and countless other works have mentioned it – thus Biese (1934) listed 778 previous references. More recently Linck (1954) and Hagdorn (1978) have published important field observations on the species and Seilacher *et al.* (1968) have discussed the mechanics of the stem. Nevertheless it is the pinnular ornament which provoked this paper. Although mentioned by Hagdorn (1982, p. 15) under the name of comb-like or pectinate ornament (*kammartige Ornamentierung*), it has not previously been described. Pectinate ornament suggests a new interpretation of how the species fed.

E. liliiformis is conventionally placed in the family Encrinidae of the paraphyletic suborder 'Poteriocrinina' of the paraphyletic subclass 'Inadunata' (Moore *et al.* 1978, p. 720). Unlike most inadunates, however, it lacks an anal plate or plates, and for this reason may be closely related to the latest common ancestor of extant crinoids. Indeed Simms (1988, p. 271) regards the Encrinidae as the most crownward plesion in the stem group of the Crinoidea. In this paper I shall not further discuss the systematic position of *E. liliiformis* nor consider how widespread the presumed mode of feeding may have been. Stratigraphically *E. liliiformis* is one of the youngest known inadunates.

I am grateful to Herr Hans Hagdorn, of Künzelsau, Württemberg, who supplied material of *E. liliiformis* from his own collection and thus encouraged me to trespass on his own intellectual field. Dr David Hardwick, of Imperial College, London, kindly discussed the species with me from a hydrodynamic viewpoint.

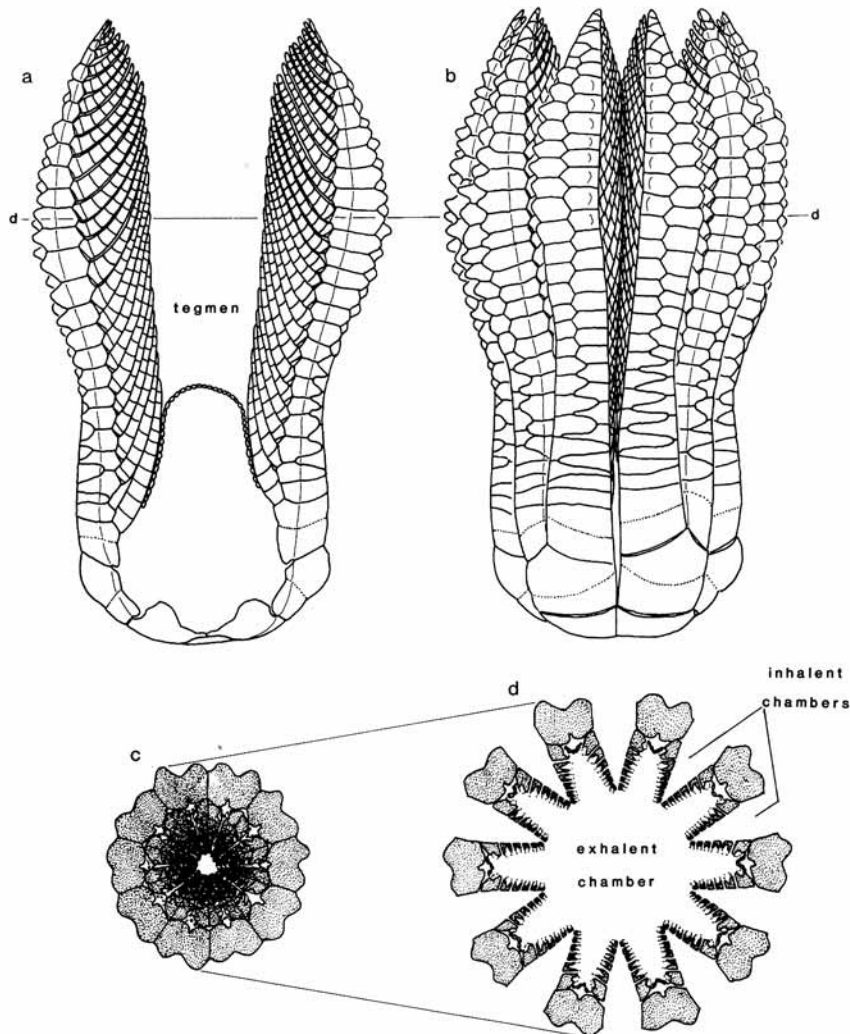


TEXT-FIG. 1. *Encrinurus liliiformis*. General reconstruction of anatomy. a, Lateral aspect of theca and upper part of stem. b, An arm in closed position seen from the central axis of the theca. c, Lateral aspect of arm in closed position. d, Lateral aspect of arm when partly opened. Note that the upper pinnules have become slightly separated from each other because of the outward warping of the lower part of the arm, whereas the lower pinnules all remain in close contact. e, Theca in basal aspect. f, Theca from above when closed. Note the small circular gap remaining between the tips of the arms.

ANATOMICAL DESCRIPTION

'Upper' and 'lower' in what follows, whatever the part being described, will consistently refer to the crown of the crinoid orientated stem-downwards by convention. 'Right' and 'left', with respect to an arm, refer to the sides of the arm seen from outside by the observer. For a general description of crinoid morphology see Ubaghs (1978).

In outer shape (text-fig. 1a; Pl. 53, fig. 3) the crown of *E. liliiformis* resembles an unopened tulip



TEXT-FIG. 2. *Encrinus liliiformis*. Reconstructions to show the effects of opening. *a*, Lateral aspect of partly opened theca, omitting the nearest two radii and the five arms farthest from the observer. The tegmen is shown inflated upwards so as to block the gaps which would otherwise exist at the bases of the pinnule series of adjacent arms. *b*, Lateral aspect of the partly opened theca. It is likely that the theca could open somewhat wider than this (cf. text-fig. 5). *c*, Section through theca at level d-d (in text-figs. 2a, b) with theca completely closed. The thecal space at this level is almost entirely filled by pinnules except for a central axial region. *d*, Section through d-d to show how, on opening, the series of pinnules remained in contact with those of adjacent arms by their tips. Thus ten inhalent chambers would be separated from a central exhalent chamber which, in transverse section, would have the form of a ten-pointed star.

but with a constriction or waist situated about one third of the height from the base. The stem was without cirri and was often cemented down by an attachment disk or root (Pl. 53, fig. 2). Hagdorn (1978) has found these roots *in situ* where they help to form the framework of small reefs. Often, however, the stem broke during the life of the crinoid. When this happened, the animal frequently survived the breakage long enough to form a new rounded end to the truncated stem (Linck 1954, p. 233).

As to the plates of the crown, there are five small infrabasals entirely hidden by the stem

attachment and five basals small enough to be invisible in lateral aspect (text-fig. 1a). Five large radials alternate with the basals and each carries a muscular articulation with the respective first primibrach. The junction between first and second primibrach is an immobile synostosis and the second primibrach is an axillary. By means of a pair of muscular articulations, separated by a summit in perradial position, each premaxillary is connected with a pair of undivided arms, thus making ten arms in all.

In each arm the first two secundibrachs are uniserial and joined by an immobile synostosis. More distally, the secundibrachs become biserial in arrangement. However, this biseriality is more quickly evident internally than externally. For on the outside approximately the first seven secundibrachs are uniserial (text-fig. 1a), whereas seen from inside the third and fourth secundibrachs already alternate. The lower secundibrachs, in the externally uniserial region, are joined to each other by obvious muscular articulations with recognizable emplacements for the aboral ligament, interarticular ligament and the adoral muscles. In this region, therefore, successive ossicles could presumably move slightly relative to each other, bending inward by the contraction of the muscles or outward by elastic contraction of the aboral ligaments. Such movement, however, could not have represented more than a slight warping of the externally uniserial region. More distally, where the secundibrachs are strongly biserial both inside and out, the junctions between successive plates must have been immobile, or almost so, though vestigial traces of the various regions of the muscular articulations are always visible between the plates. In the upper part of this fully biserial region each brachial plate carries a rounded knob externally. Still more distally, towards the tip of each arm, the plates have no such knobs and tend once more to a uniserial arrangement.

The ten arms could shut tightly in life, judging by the fact that the fossils are usually preserved in this condition. The tips of the arms are rounded, however, rather than pointed, so a small, approximately circular or decagonal area would always have remained open distally (text-fig. 1f). At the sides of each arm the brachial plates carry wide lateral facets which represent surfaces of contact with the neighbouring arms when the crown was tightly shut (text-fig. 1c).

How wide the crown could open in life is an important problem. Opening would mainly happen by elastic contraction of the aboral ligaments between the radial plates and the first primibrachs, and between the axillary plates and the first secundibrachs, although there would also be, as already suggested, outward flexing of the externally uniserial region of the arm and perhaps of the proximal part of the biserial region also. It is impossible, however, to estimate accurately the maximal angle of bending which occurred at each of the joints involved and so no precise conclusions can be drawn from the anatomy as regards the maximal gape.

Preservation of the fossil is more informative in this respect. Most of the complete fossils are rather tightly closed or slightly ajar. The closure is presumably the result of muscular contraction at death by burial – whether burial resulted from a sudden influx of mud or, as Hagdorn (1978, p. 62) has suggested, was sometimes caused by falling crown-first into the mud when the stem broke. If these complete fossils were trying to close themselves when they died, it is likely that, in this extremely common species, those now recorded as being widest open would indicate the normal

EXPLANATION OF PLATE 53

Encrinurus liliiformis. Except for fig 3, horizon and locality unknown, presumably Obermuschelkalk, Germany.

All specimens photographed optically and coated with ammonium chloride.

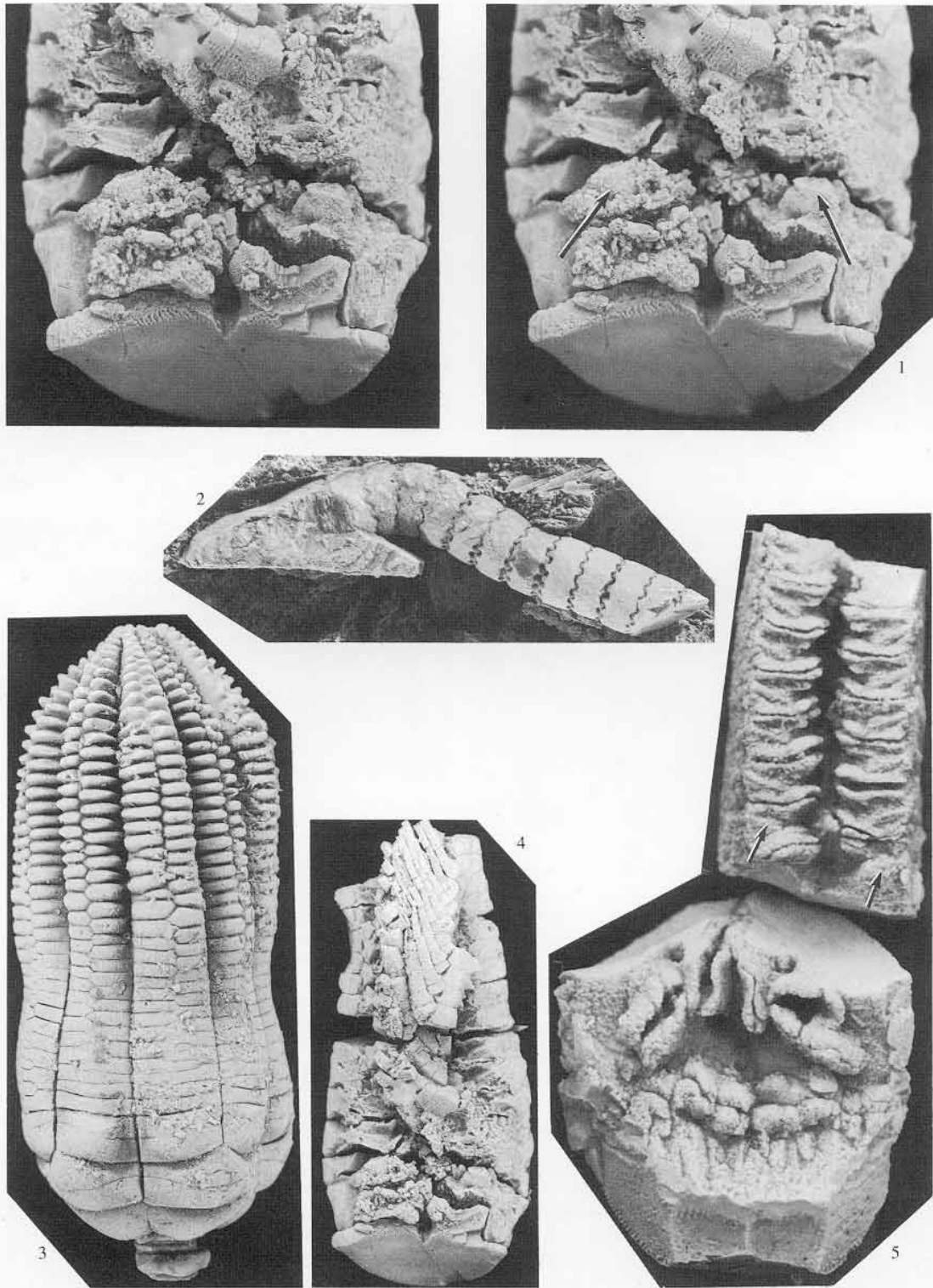
Figs. 1 and 4. BM(NH) E5284. Internal surface of arm with pinnules and integument plates still partly in place.

Fig. 1, stereopairs of lower part, $\times 4.2$. Fig. 4, whole of the incompletely preserved arm, $\times 2.1$. Note the scattered integument plates and the bases of the lowest pinnules (arrowed) which, unlike more distal pinnules, have a rounded lower surface with no pectinate ornament.

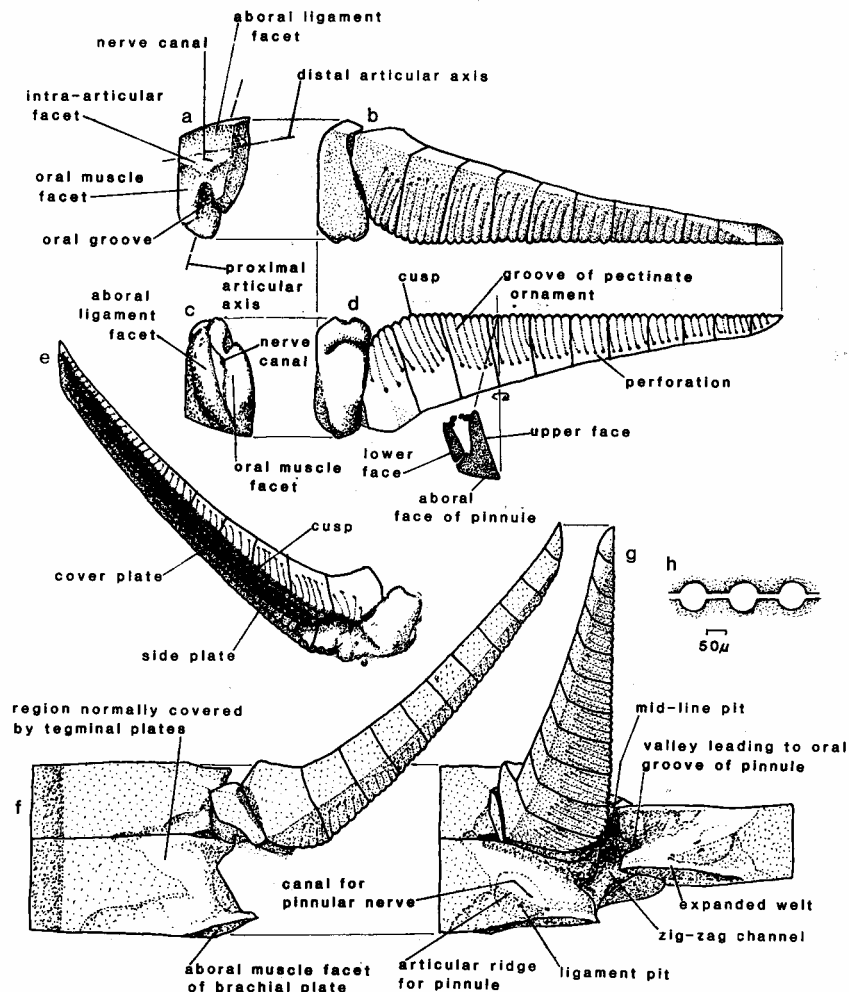
Fig. 2. BM(NH) 75854. Obermuschelkalk, Wilhelmshöhe near Schwäbisch Hall, Württemberg, Federal Republic of Germany. Holdfast on the end of the stem, $\times 1.55$.

Fig. 3. BM(NH) E53243. General view of theca and arms, $\times 1.5$. Compare text-fig. 1a.

Fig. 5. BM(NH) 1216. Part of theca and basal part of one arm in interior aspect, $\times 6.4$. The boss (arrowed) which carried the immobile lowest pinnule has no articular ridge.



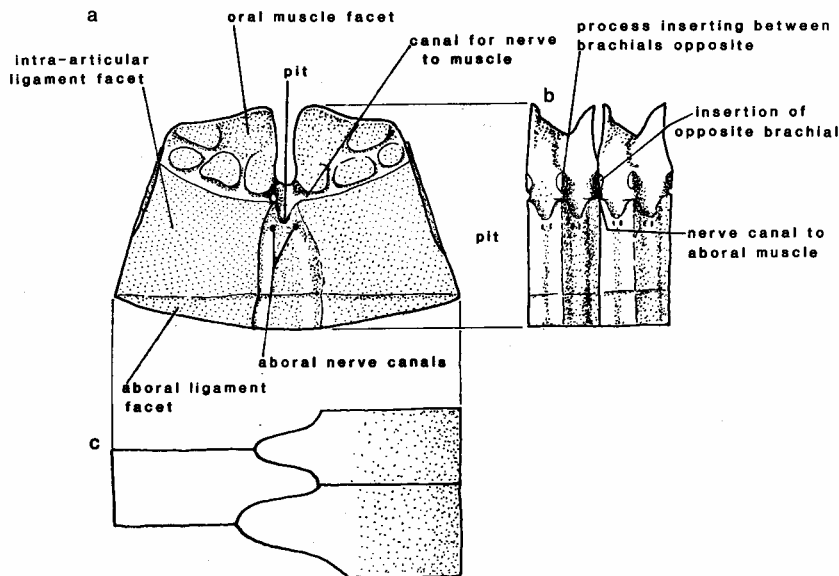
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TEXT-FIG. 3. *Encrinurus liliiformis*. Reconstruction of one pinnule and three brachial plates from the base of the fully biserial region (secundibrachs 7, 8 and 9). See also text-fig. 4. a, Distal aspect of first pinnular plate. b, Lower aspect of pinnule. c, Proximal aspect of first pinnular plate. d, Upper aspect of pinnule and transverse section. e, Adoral aspect of pinnule. f, Lateral aspect of pinnule in relation to brachial plates. g, Pinnule in relation to brachial plates seen from central axis of theca. h, Diagrammatic section of the interpinnular channels between two adjacent pinnules. The section is approximately perpendicular to the channels and parallel to the length of the pinnules.

widest extent of opening in life. Linck (1954) had a very deep knowledge of the species and believed, on these grounds, that the specimen in text-fig. 5 (traced from his photograph) was approximately in the natural position of greatest gape in life (*natürliche Lebensstellung*), and I accept this result since it seems plausible from the anatomy. Modern crinoids, when feeding, open much more widely than this and form a filtration fan, often extended transverse to a horizontal current as recorded for the Recent isocrinid, *Cenocrinus asterias*, by Macurda and Meyer (1974) (text-fig. 6 herein). If *E. liliiformis* could not open wide in this manner, it probably gathered food by some method other than, or supplementary to, passive filtration. As explained later, pectinate ornament of the pinnules suggests what this method was.

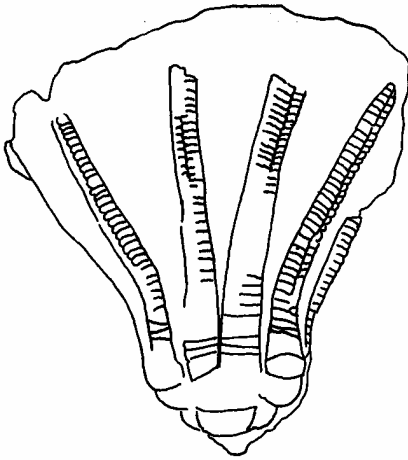
The internal skeletal anatomy of the arms and attached pinnules is complex (text-figs. 2-4). Every



TEXT-FIG. 4. *Encrinus liliiformis*. Reconstruction of three brachial plates (secundibrachs 7, 8 and 9). See also text-fig. 3. a, Distal aspect. b, Medial aspect of secundibrachs 7 and 9. c, External aspect.

brachial plate of an arm (i.e. every secundibrach) bears a pinnule except for the lowest one (the first secundibrach) and the highest one (the last secundibrach). When the crown is closed (text-figs. 1a-c; Pl. 53, fig. 3) the pinnules of a single arm, together with the brachials to which they are attached, form a 36° prism. The somewhat rounded acute edge of this prism is formed by the distal ends of the pinnules and almost coincides with the long central axis of the crown. Thus, when the crown is closed, its upper part is almost entirely filled by ten such prisms, one for each arm, in side-by-side contact with each other, as shown in text-fig. 2c. (This fact was already known to Miller 1821.) When the crown was closed the pinnules and brachials on one side of an arm presented a continuous flat mosaic formed by the facets on the brachial plates and by coplanar facets on the pinnular plates. This flat mosaic made tight contact with a similar flat mosaic on the adjacent arm.

Text-figs. 3 and 4 give a reconstruction of some brachial plates from the lower part of the biserial region (the 7th, 8th and 9th, secundibrachs) together with one of the attached pinnules. In distal aspect (text-fig. 4a) the surfaces of the brachials reveal areas for the aboral ligament, for the interarticular ligament and for the muscles of the adoral region of the arm. A zig-zag channel (text-fig. 3g) along the mid-line of the arm separates the muscular fields of the left side of the arm from those of the right. A pair of canals for the aboral nerves exists near the mid-line of the arm, aboral to the zig-zag channel, in the region where right and left brachials overlap (Pl. 54, fig. 9). Exactly in the mid-line is a series of pits (one pit for each suture between brachials) which extend from the floor of the zig-zag aborally almost far enough to reach the paired aboral nerve canals. From near each pit a branched groove extends on each brachial plate from out of the mid-line to right and left along the aboral margin of the muscular region. Each such branched groove corresponds to a similar groove in the facing surface of the adjacent brachial, so that the two grooves together (text-fig. 4c) would form a branched canal. By comparison with *Antedon* (W. B. Carpenter 1884), this canal probably carried a nerve supply to the appropriate adoral muscle. It is likely that this nerve supply arose from the aboral nerve, or nerve pair, passed invisibly into the nearly mid-line pit and thence entered the branched canal. The mid-line pits were recorded in *E. liliiformis* by Beyrich (1858, e.g. pl. 1, fig. 8) and are also known in related inadunates such as *Pentaramicrinus* and *Erisocrinus* (Ubahgs 1978, p. T167). They probably represent aboral extensions of the aboral coelomic canal of



TEXT-FIG. 5. *Encrinurus liliiformis*. Theca in probable position of widest opening during life. Traced after Linck (1954, fig. 5, p. 229).

the arm, the greater part of this coelomic canal being lodged in the zig-zag channel. As already mentioned, there could have been very little movement between the interlocked brachial plates of the region reconstructed in text-figs. 3 and 4. Contraction of the muscles could at most have produced a slight outward flexing.

The adoral face of each brachial is complicated in shape (text-fig. 3g; Pl. 53, fig. 5). An articular ridge for the pinnule extends obliquely upwards and outwards in the lower part of each brachial. A semi-elliptical field below this ridge represents the position of the aboral ligament, which connected the brachial with the first pinnular plate, and there is a deep ligament pit in this field situated near the mid-length of the articular ridge. A canal for the aboral nerve or nerves to the pinnule is located just above this pit. A rather vaguely marked area on and above the ridge would represent the emplacement of the interarticular ligaments and the adoral muscles of the pinnular articulation. Expanded welts along the upper and lower (proximal and distal) edges of each brachial served to enlarge the fields of the adoral muscles connecting the brachial plates. In the adoral surface of each brachial, a short valley leaves the mid-line zig-zag channel and would have been filled in life by a branch of the coeliac canal, passing into the appropriate pinnule.

The pinnule itself (text-fig. 3) is not uniform along its length – it tapers distally and the first two pinnular plates are markedly different from the rest and from each other. A transverse section

EXPLANATION OF PLATE 54

Encrinurus liliiformis. Stereoscan photographs. Horizon and locality unknown for all specimens figured, presumably Obermuschelkalk, Germany.

Fig. 1. BM(NH) E70107. Lower surface of two opposite pinnules to show the cusps, grooves and perforations of the pectinate ornament, $\times 32$.

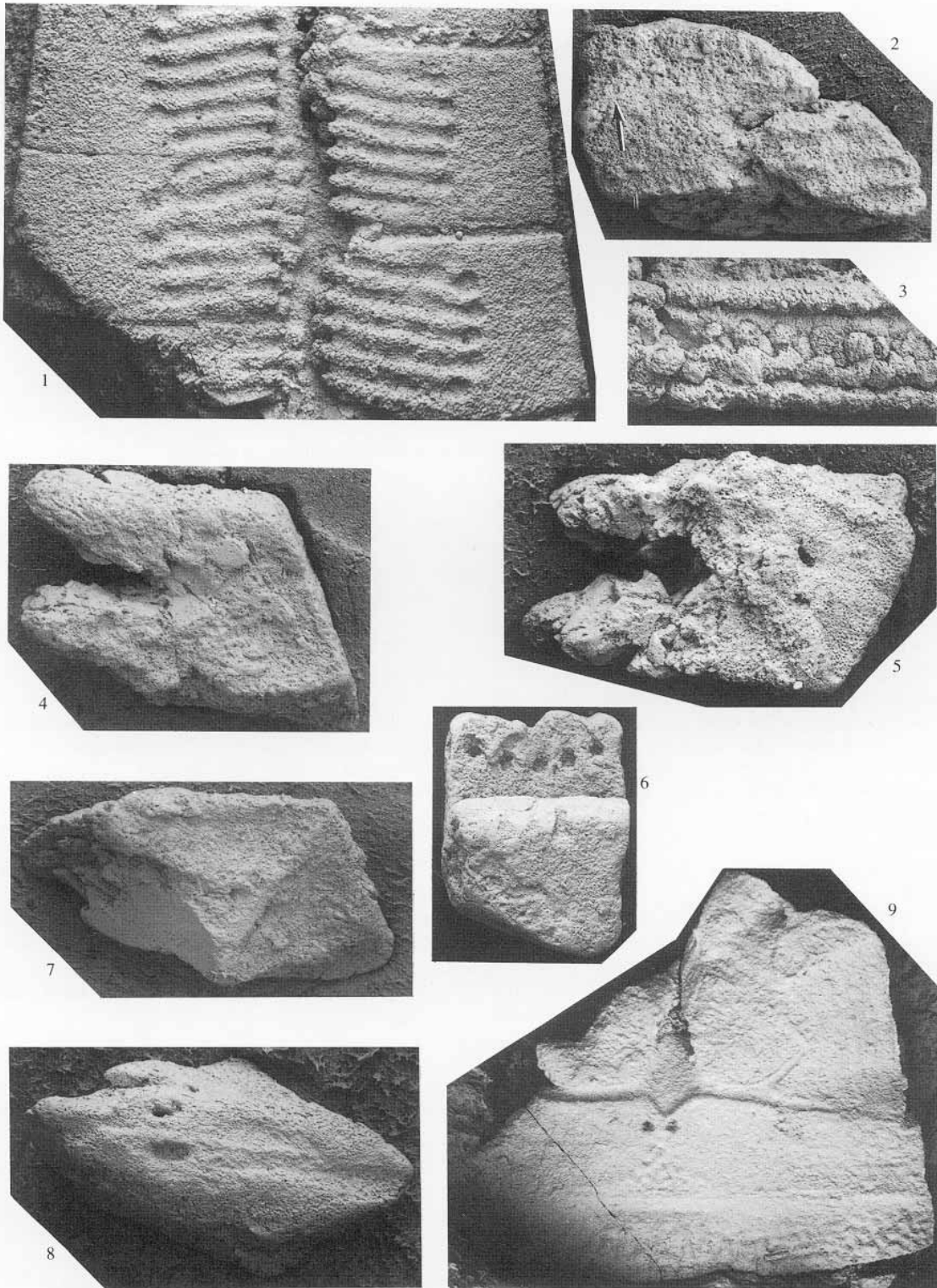
Figs. 2, 4, 5. BM(NH) E5284. Second pinnular of IIBr₅ in upper, distal and proximal aspects respectively, $\times 25$. Note the presence in fig. 2 of a transverse ridge (arrowed), the pinnular groove and two cusps of the pectinate ornament. The proximal face (fig. 5) shows an articular surface with an emplacement for the aboral ligament, whereas the distal surface (fig. 4) lacks these features.

Fig. 3. BM(NH) E70107. Oral face of a pinnule to show cover plates and U-shaped side plates, $\times 31$.

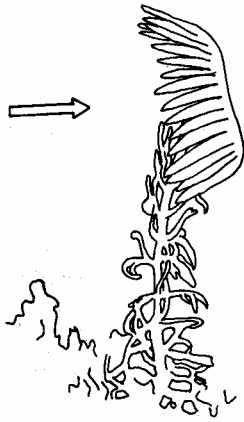
Fig. 6. BM(NH) E5284. Pinnular plate from near the mid length of a pinnule, oral surface upward, $\times 31$. The wall of one side of the oral groove has broken away, showing the medial face of the opposite wall with the perforations associated with pectinate ornament.

Figs. 7 and 8. BM(NH) E5284. First pinnular of IIBr₅ in distal and proximal aspect, $\times 26$. Compare text-fig. 3.

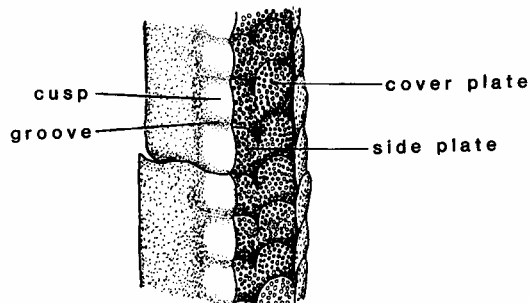
Fig. 9. BM(NH) 70107. Brachial plate from near the base of the biserial region seen in proximal aspect, $\times 15$. Compare with text-fig. 4a. Note the branching groove for the nerve to the adoral muscle, the median pit, aboral nerve canals, aboral and interarticular ligament facets.



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TEXT-FIG. 6. *Cenocrinus asterius* extended across a bottom current for passive feeding. The arrow shows the approximate direction of the bottom current. Traced after Macurda and Meyer (1974, fig. 1b).



TEXT-FIG. 7. *Neocrinus decorus* (Wyville Thomson). Parts of two pinnular plates with associated side plates and cover plates. Note the crenulation of the adoral edges of the pinnular plates. Distal is upward. $\times 34$.

through the middle of a pinnule is trapezium-shaped, the upper and lower surfaces of the pinnule corresponding to the parallel sides of the trapezium. The aboral face of the pinnule, i.e. the face farthest from the mid-line of the arm, makes an acute angle with the upper face and an obtuse angle with the lower face (Pl. 54, fig. 4; transverse section in text-fig. 3d). The aboral face of the pinnule would make contact with pinnules of the adjacent arm when the crown was closed. The fourth face of the trapezium-shaped cross-section, nearest the mid-line of the arm, is the adoral face of the pinnule. It is formed by four series of platelets, i.e. a pair of adambulacral or side plates, U-shaped in plan, and a pair of ambulacral or cover plates, circular in plan (Pl. 54, fig. 3). The concavities of the U-shaped side plates open towards the mid-line of the pinnule and may each have housed a tube foot in life. Covered by these little plates and excavated in the pinnular plates, there is a deep V-shaped adoral pinnular groove which in life was filled by the soft parts of the pinnule.

When the crown was closed, each pinnule would be in tight contact with its upper and lower neighbours. The approximately plane upper and lower surfaces of each pinnular ossicle allowed this tight contact, just as the plane aboral face of the pinnules allowed close contact with the corresponding faces of the pinnulars of the neighbouring arm.

The pectinate ornament which is the main subject of this paper is found on the upper and lower surfaces of a pinnule (Pl. 53, fig. 1; Pl. 54, fig. 1). The ornament consists of alternating flat-topped ridges and hemicylindrical grooves, each ridge and groove being approximately transverse to the length of a pinnule, and thus approximately parallel to the sutures between the pinnular plates. Very approximately, grooves are about $50 \mu\text{m}$ wide and $25 \mu\text{m}$ deep, and the flat-topped ridges that separate them are about $50 \mu\text{m}$ wide. There are some four to six grooves on the upper, or the lower, surface of each pinnular plate. The ridge between two grooves ends adorally in a cusp so that the edges of the adoral pinnular groove are scalloped. The aboral end of each groove (farthest from the mid-line of the arm but always some distance from the aboral surface of the pinnule) is connected to a perforation which passes through the plate to the internal cavity of the pinnular (text-fig. 3b, d, g; Pl. 54, fig. 6). On each pinnular plate the perforations are arranged in an arc so that the

grooves nearer the middle of a plate are longer than those nearer the proximal and distal end of the plate (text-figs. 3b, d; Pl. 54, fig. 1).

The cusps on the adoral edges of the pinnular plates, and thus the ridges which end in the cusps, alternate with the side plates of the adoral surface of the pinnule (text-fig. 3e; Pl. 54, fig. 3). These plates alternate, in their turn, with the adjacent cover plates, and the cover plates on either side of a pinnule alternate with each other. The grooves on the lower surface of a pinnular plate are therefore approximately equal in number to the grooves on its upper surface and also equal in number to the plates in each cover-plate and each side-plate series.

Pectinate ornament somewhat resembles the crenulation of the adoral edges of the pinnular plates recorded by P. H. Carpenter (1884, Pl. 37, fig. 24; text-fig. 7, herein) in the Recent isocrinid *Neocrinus decorus*. Indeed it could have arisen by an evolutionary exaggeration of just such a crenulation. In *N. decorus*, however, there are no perforations, the cusps coincide with the side plates, rather than alternating with them, and similarly, the cover plates are opposite, rather than alternate, to the side plates.

The surface of contact between any pinnule and its overlying neighbour would therefore have been interrupted by channels perpendicular to the length of the pinnule (text-fig. 3h). These channels would, in the extreme cases, be either circular or semicircular in section – they would be circular if a groove on one pinnule coincided with a groove on the overlying pinnule, and they would be semicircular if a groove on one pinnule coincided with a ridge on the overlying pinnule. If a groove partly coincided with a ridge and partly with a groove, then the channel would have had a more complicated shape. If circular in section, the diameter of the circle would have been about 50 μm , minus the thickness of any cell layer on the surface of the skeleton. Within an order of magnitude the diameter therefore agrees with those of: (1) tunicate gill slits, which are commonly 25 μm wide (Jefferies 1973, p. 440); (2) the gill slits of amphioxus, which are about 40 μm wide (Bone 1961, fig. 20); or (3) the pore canals in the tegmen of *Antedon*, which are about 60 μm wide (Hamann 1889, p. 94). All these channels are ciliated, their diameter being equal to slightly more than twice the length of the contained cilia. I therefore suggest that the grooves of the pectinate ornament of *E. liliiformis* were likewise ciliated and served to pass water from outside the pinnules to the space contained between the right and left sets of pinnules of a single arm. The perforation at the adoral end of each groove may have carried a nerve by which the ciliary activity of the channel was controlled. Since the grooves on all pinnules are almost equidistant from each other, the crinoid would be able, by adjusting the mutual position of adjacent pinnules, to ensure that nearly all of the channels were circular in section, and this was probably the normal condition since it would be best for ciliary pumping.

The two most proximal pinnular plates of each pinnule, as already said, are individualized. The first pinnular plate, in particular, is of very complicated shape. Its proximal face (text-fig. 3a; Pl. 54, fig. 8) is traversed by a ridge which articulated with the ridge on the connected brachial plate. Below this ridge the first pinnular shows an area for the attachment of the aboral ligament and above it two areas for the attachment of adoral muscles, though one of these areas (that farther from the mid-line of the arm) is much larger than the other. The adoral groove of the pinnule, continuous with that on the attached brachial, passed near the mid-line of the arm onto the proximal face of the first pinnular. The distal face of the first pinnular plate (text-fig. 3a; Pl. 54, fig. 7) is clearly divided, by an articular ridge and other sculptural complications, into areas for an aboral ligament, for intra-articular ligaments and for adoral muscles. A canal is present, near the centre of the distal face, for the aboral pinnular nerve, and there is a strong V-shaped groove in the adoral face of the first pinnular plate. The articular ridge on the distal surface of the first pinnular plate, unlike the articular ridge on the proximal surface, is approximately vertical in orientation (relative to the total crown in the conventional orientation). Thus, again in the conventional orientation of the arm, the proximal articulation of the first pinnular plate would rock the pinnule outwards (away from the mid-line of the arm) and downwards. But the distal articulation of the first pinnular would rock the remainder of the pinnule (the second and more distal pinnulars) approximately horizontal, i.e. directly away from the mid-line of the arm.

The second pinnular plate in most ways resembles more distal ones except for the above-

mentioned muscular articulation on its proximal surface (Pl. 54, fig. 5). No such articulation exists on the distal surface (Pl. 54, fig. 4). An additional difference from the others is that the aboral face (the surface farthest from the mid-line of the arm) is irregularly pentagonal in shape (text-fig. 3f), rather than rectangular. The pentagonal shape is due to the fact that the upper edge of this aboral face is raised into a point which separates two facets on the upper surface (text-fig. 3c, e, f; Pl. 54, fig. 2). The upper and lower faces of the second pinnular carry several grooves of the pectinate ornament together with the associated perforations, cusps and inter-groove ridges.

The cover and side plates of the pinnules do not continue more proximally than the pinnules. Instead the zig-zag channel excavated in the mid-line of the brachial plates was covered in life with a loose integument plated with circular plates like those of the tegmen (Pl. 53, figs. 1 and 4).

There is no sign of genital swellings on any of the pinnules – the adoral surface of the pinnule is always completely covered by uniform series of cover and side plates over the pinnular groove. It seems most unlikely that the gonads of *E. liliiformis* were in the pinnules. More probably they were situated beneath the tegmen, or else near the mid-line of each arm as in the Recent crinoid *Cyathidium* (Cherbonnier and Guille 1972; Fechter 1973). If situated near the mid-line of the arms, they would have been covered by the loosely plated integument of that region.

The first or lowest pinnule of every pinnule series was different from the others in several respects. Thus, firstly, its lower surface was convex rather than flattened and it was without pectinate ornament (Pl. 53, fig. 1). This results from the mere fact that there was no pinnule beneath it. Secondly, there was no muscular articulation proximal to the pinnule – rather the contact with the brachial is by a concave surface on the most proximal pinnular plate fitting over a convex surface on the adjacent brachial (Pl. 53, fig. 5). Thus the first pinnule, unlike higher ones, would not rotate outwards and downwards about a proximal articulation when the arm opened. A muscular articulation existed between the first and second pinnular of the first pinnule, but this would allow rotation of the pinnule only in the direction towards, or away from, the mid-line of the arm.

Higher pinnules are also not all identical. Thus (1) they differ in length according to the space inside the crown; and (2) the pectinate ornament is more obvious in lower pinnules than higher ones since the grooves become shorter in higher pinnules – indeed the highest pinnules completely lack pectinate ornament.

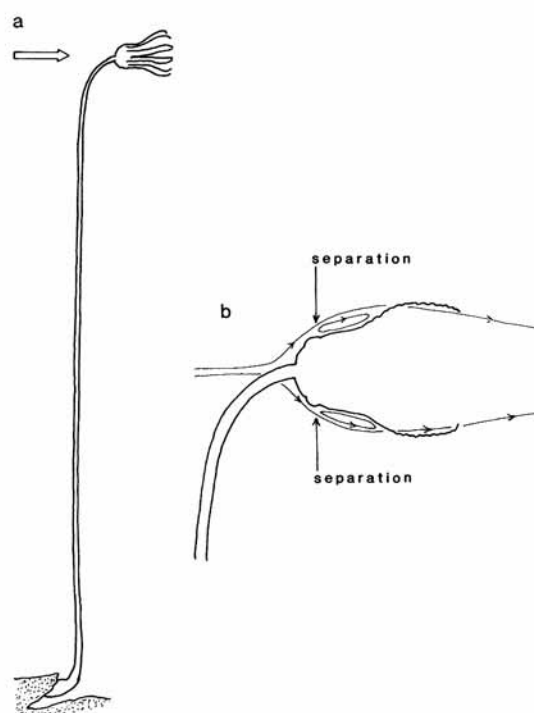
The tegmen of *E. liliiformis* is not well known. I was unable to dissect it completely, but it was covered with loose plates, sometimes bearing pores (hydropore canals). Probably the ambulacral grooves did not open on the surface of the tegmen, seeing that they did not emerge in the mid-line of the arms.

As concerns the stems, Hagdorn (1978) has observed stem bases *in situ* attached to bivalve molluscs and to each other to form small reefs. He noted that the surface of attachment is seldom horizontal and sometimes vertical, but that the lower part of the stem (Pl. 54, fig. 1) is shaped so that the stem runs vertical after a short distance (text-fig. 8). Seilacher *et al.* (1968) deduced that the upper part of the stem was more flexible than the lower part. This is demonstrated, in particular, by a specimen recorded by Linck (1954) which, in its upper part, had fallen across another stem and was strongly curved over it in consequence. The total length of the animal (holdfast, stem and crown included) was recorded by Linck (1954, pl. 51, p. 232) as 1.37 m, implying that the stem was about 1.3 m long. All this suggests that, when rooted to the bottom, the greater part of the stem would have been vertical. However, the flexibility of the higher part of the stem also suggests that, like Recent crinoids, the crown would orientate itself with the central axis horizontal, parallel to any bottom current, as suggested in text-fig. 8.

FUNCTIONAL INTERPRETATION

How the crown opened is important to the functional morphology of *E. liliiformis* in general, and of pectinate ornament in particular. Text-figs. 1b–d and 2a show the likely positions of the pinnules on the arms when the crown was closed and when it was somewhat open. On opening, the aboral ligaments of the brachial plates and of the radial articulations would contract and the pinnules of

EXT-FIG. 8. *Encrinus liliiformis*. To show probable life habit. a, General view of attached animal based on complete individual figured by Linck (1954, pl. 51) with the stem attached as shown by Hagdorn (1978, g. 6·82) and the theca trailing down-current as in *Encrinus asterius* of text-fig. 6. The total length of the stem and theca is 1·37 m. b, Enlarged view of theca to show probable current regime. Assuming a theca with $l = \text{diameter} = 0\cdot025 \text{ m}$, a current velocity of $v = 0\cdot05 \text{ m/sec}$, and a dynamic viscosity for sea water of $\nu = 10^{-6} \text{ m}^2/\text{sec}$, the Reynolds number $R = lv/\nu = 1250$. At this value of R , flow will be turbulent, with separation of the boundary layer from the theca approximately as indicated. There will be a regime of eddies and mixing near the bases of the arms, just downstream of the separation. The pair of eddies as shown will represent a condition averaged over time. The instantaneous condition will be more complicated with numerous much smaller eddies and mixing of water. The interpinnular channels, being best developed near the arm bases, would drain off water from this slowly moving, strongly turbulent region. No attempt has been made to reconstruct the flow near the central axis of the theca.



in arm would rotate away from the mid-line of the arm and downwards (by articulation between brachial and first pinnular plates) and away from the mid-line of the arm (by articulation between the first and second pinnular plates). There would have been no movement of the lowest pinnule on its brachial plate. Also, outward warping between the brachial plates of the lower part of the arm, especially in the externally uniserial region, would tend to rotate higher pinnules away from the lower ones and thus to open gaps between them (cf. text-figs. 1c, d). The downward rotation of the pinnules on their articulations with the brachials, on the other hand, would tend to close the spaces between pinnules. Probably this closure was tightest in the lower parts of the arms, where the pectinate ornament was best developed. Here the tight closure would produce interpinnular channels. Higher up the arm, the outward flexing of the arm in the biserial region would tend to separate the pinnules from each other. Consequently, the lower pinnules would be pressed closer together than the higher pinnules.

As neighbouring arms opened away from each other, the articulation of the pinnules with the brachial plates, and of the first pinnular plates with the second, would cause the pinnules to rotate outwards, away from the mid-line of the arm on which they sat. In consequence, except near the tips of the arms, the left pinnule series of an arm would remain in contact by the tips of the pinnules with the adjacent right pinnule series of the next arm, as shown in text-figs. 2b, d. Thus there would be ten external chambers (text-fig. 2d), presumably inhalent, each of which would be separated, by a pair of walls (or rather palisades) constructed of pinnules, from a single internal chamber, presumably exhalent. This internal chamber would resemble a ten-pointed star in transverse section. When the crown was open, a gap would remain at the base between the left pinnule series of one arm and the right pinnule series of the neighbouring arm. This gap was probably plugged, however, by upward dilation of the tegmen (text-fig. 2a). Thus separation between the inhalent chambers and the exhalent chamber, except by way of gaps between adjacent pinnules in the same pinnule series, would be complete.

Where pectinate ornament existed on the pinnules, it would, as already mentioned, produce

innumerable tube-shaped channels between the pinnules. Through these channels, ciliary currents would actively move water from the inhalent to the exhalent side of the pinnule series. Indeed, the presence of channels with this function is the only reasonable explanation for the existence of pectinate ornament. Food particles brought with the feeding current through the interpinnular channels would be captured on the downstream side of the pinnules by tube feet, as is normal for Recent crinoids (cf. Nichols 1960).

The differences between higher and lower pinnules (i.e. between those on the distal and proximal parts of an arm) need particular explanation. As already mentioned, these differences are of two sorts: (1) the length of the pinnules varies according to the space available inside the crown; and (2) pectinate ornament is better developed on the lower pinnules than on the higher ones, and in the highest pinnules is lacking altogether.

The weakness or absence of pectinate ornament on the higher pinnules was probably for several reasons. Firstly, as shown in text-fig. 2b, when the crown was moderately open the pinnule series of neighbouring arms would be widely separated from each other near the arm tips and so would not have functioned well by the ciliary mechanism. Secondly, as the arms opened, the pinnules would rotate downwards in the crown so as to remain in contact with the pinnules beneath them and thus to be piled on top of the lowest, almost immobile pinnule. Under these conditions, the average spacing between higher pinnules, as already implied, would be greater than between lower pinnules. And if pinnules were not in contact, the ciliary pumping mechanism could not have functioned. Thirdly, at the Reynolds numbers likely with *E. liliiformis*, there would be a system of eddies and mixing in the proximal region of the arms (text-fig. 3). The slowly moving water in this region could easily have been diverted through the interpinnular channels by ciliary action, which would not be true of the rapidly flowing water that hit the tips of the arms. Fourthly, under these same conditions, the tips of the arms, being in relatively rapid water, could have functioned in the normal crinoid manner by passive filtration, without ciliary pumping.

Often, as already mentioned, the stem broke near the base but the animal survived. Such individuals would have no means of attachment to the sea bottom unless the stem were extensively buried as an anchor. They would therefore have found it difficult to feed by passive filtration in a horizontal current and probably could not have opened wide enough to feed by the slow fall of plankton in a plankton rain. Perhaps these rootless individuals rested with the central axis of the crown vertical, with the base of the crown on the mud of the sea floor and with the stem extending horizontally beneath the surface of the mud as an anchor. In such a position the animal could feed entirely by active filter feeding, drawing ten feeding currents into the inhalent chambers between the arms and expelling an exhalent current vertically upward along the central axis of the crown.

I suggest, therefore, that *E. liliiformis* fed partly by producing its own feeding current. This would be caused by ciliary beat through the interpinnular channels and sometimes would have entirely replaced passive filtration. In other words, pectinate ornament, whose existence implies the presence of these interpinnular channels, was evolved as part of a mechanism for active ciliary pumping.

REFERENCES

- ALDINGER, H. 1928. Das Stielwachstum bei *Encrinus liliiformis*. *Zentralbl. Miner. Geol. Paläont.* B, 202–207.
- BEYRICH, H. E. VON, 1858. Über die Crinoiden des Muschelkalkes. *Abh. preuss. Akad. Wiss.* 1–49, pls. 1–2.
- BIESE, W. 1934. Crinoidea triadica. *Foss. Cat. Animalia* 66, 1–255.
- BONE, Q. 1961. The organization of the atrial nervous system of amphioxus (*Branchiostoma lanceolatum* (Pallas)). *Phil. Trans. R. Soc.* B 243, 241–269.
- CARPENTER, P. H. 1884. *Report upon the Crinoidea collected during the voyage of H.M.S. Challenger during the years 1872–76. Pt. I. General morphology, with description of the stalked crinoids.* Vol. 11, pp. 442, 62 pls.
- CARPENTER, W. B. 1884. On the nervous system of the Crinoidea. *Proc. R. Soc.* 232, 67–76.
- CHERBONNIER, G. and GUILLE, A. 1972. Sur une espèce actuelle de crinoïde crétacique de la famille Holopodidae: *Cyathidium foresti* nov. sp. *C. r. hebd. Séanc. Acad. Sci., Paris*, D 274, 2193–2196, pl. 1.
- FECHTER, H. 1973. *Cyathidium meteorensis* spec. nov., ein neuer Crinoide aus der Familie Holopodidae. *Helgoländer wiss. Meeresunters.* 25, 162–169.

- HAGDORN, H. 1978. Muschel/Krinoiden Bioherme im Oberen Muschelkalk (mo 1, Anis) von Crailsheim um Schwäbisch Hall (Südwestdeutschland). *Neues Jb. Geol. Paläont. Abh.* **156**, 31–86.
- 1982. *Chelocrinus schlotheimi* (Quenstedt) 1935 aus dem Oberen Muschelkalk (mo 1, Anisium) von Nordwestdeutschland. *Veröff. Naturk. Mus. Bielefeld*, **4**, 1–33.
- HAMANN, O. 1889. *Beiträge zur Histologie der Echinodermen. Heft 4 (Schluss-heft). Anatomie und Histologie der Ophiuren und Crinoiden.* 160 pp., 12 pls, Fischer, Jena.
- JEFFERIES, R. P. S. 1973. The Ordovician fossil *Lagynocystis pyramidalis* (Barrande) and the ancestry of amphioxus. *Phil. Trans. R. Soc. B* **265**, 409–469.
- LINCK, O. 1954. Die Muschelkalk-Seelilie *Encrinus liliiformis*. *Naturw. Mschr. d. Naturk. Heimat*, **62**, 225–235, pls. 49–56.
- MACURDA, D. B. and MEYER, D. L. 1974. Feeding posture of modern stalked crinoids. *Nature, Lond.* **247**, 394–396.
- MILLER, J. S. 1821. *A natural history of the Crinoidea or lily-shaped animals, with observations on Asterias, Euryale, Comatula and Marsupites.* 150 pp., 50 pls., Frost, Bristol.
- NICHOLS, D. 1960. The histology and activities of the tube-feet of *Antedon bifida*. *Q. Jl. microsc. Sci.* **101**, 105–117.
- SEILACHER, A., DRODZEWSKI, G. and HAUDE, R. 1968. Form and function of the stem in a pseudoplanktonic crinoid (*Seirocrinus*). *Palaeontology* **11**, 272–282, pl. 48.
- SIMMS, M. 1988. The phylogeny of post-Palaeozoic crinoids, 269–284. In PAUL, C. R. C. and SMITH, A. B. (eds.) *Echinoderm phylogeny and evolutionary biology*. Liverpool Geological Society and Clarendon Press, Oxford. 373 pp.
- UBAGHS, G. 1978. Skeletal morphology of fossil crinoids, pp. T58–T216. In MOORE, R. C. and TEICHERT, C. (eds.) *Treatise on invertebrate paleontology. Part T, Echinodermata 2*. Vol. 1, xxxviii + 401 pp., Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas.

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