FORM AND FUNCTION OF THE STEM IN A PSEUDOPLANKTONIC CRINOID (*SEIROCRINUS*)

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ABSTRACT. The position of crowns and stems in the rock indicates that *Seirocrinus subangularis* lived attached to floating logs in spite of its unusual size. The distribution of weight and flexibility along its stem is inverse to most other crinoids, but corresponds to the assumed habitat. A few general growth gradients seem to control this and other adaptive modifications of the crinoid stems.

FUNCTIONAL morphology is a most important tool in the interpretation of specialized forms that deviate ecologically from their relatives. Such deviation may be expressed by an unusual shape, as in the case of rudist pelecypods (Vogel 1960), richthofeniid brachiopods (Rudwick 1961), or *Pygope* (Vogel 1966). In other forms, an unusual mode of life is indicated by their regular occurrence in types of facies in which we would not normally expect to find them.

The case to be discussed in this paper is of the latter type. Its main object is a 4·50 × 7 m. slab which was found in the Posidonia Shales (Lias ϵ) of Reutlingen a hundred years ago and has been one of the major attractions of the Tübingen Museum since (Pl. 48, fig. 1). It contains about fifty exceptionally large specimens of *Seirocrinus subangularis* (Miller), the more common crinoid species found in the bituminous shales. F. A. Quenstedt (1868), who gave a most complete description of these fossils, referred to them as 'Schwabens Medusenhaupt'. *Seirocrinus subangularis* (long stem), as well as the rare species *Pentacrinus briareus* Miller (short stem with dense cirral fur) are regular elements of the Posidonia Shale fauna. Many beautiful specimens have been obtained by museums and private collectors from the famous Hauff workshop at Holzmaden. *Isocrinus*, though common in other members of the Lias, has never been found in these shales.

The fact that the two crinoids occur in a black shale of apparent euxinic origin becomes understandable if we think of the specimens still attached to driftwood. Even so, some uncertainty remains whether they were exclusively pseudoplanktonic or whether they could survive benthonically after the log had eventually settled to the bottom.

The pseudoplanktonic model becomes particularly critical in the Medusenhaupt specimen: about fifty calyces with an average diameter of 80 cm. and stems of more than 15 m. in length must have formed a considerable load and may have taken years to grow to this size. Could this all happen on a drifting log? After all, the layer of stagnant bottom water might have troubled only the juvenile individuals, while older ones had stems long enough to hold the calyces above the interface. Did *Seirocrinus* ever make use of this possibility? Or, viewed in another way: ought such slabs to be displayed with the crinoids standing up, as is customary, or hanging down? The burial position will give us a clue to this basic ecological question.

[Palaeontology, Vol. 11, Part 2, 1968, pp. 275–82, pl. 48.]

1. *Mode of life derived from biostratinomic evidence*

While in most Holzmaden specimens of *Seirocrinus* the calyces lie on their sides, the Medusenhaupt crowns spread their arms radially. In this position two geopetal orientations are theoretically possible: the arms either cover the stem or are overlain by it, depending on whether stem or calyx reached the floor first.

The Medusenhaupt slab—as is usual with Posidonia Shale fossils—was prepared from the lower side (Quenstedt 1868, p. 18) because the upper one would be less well preserved. Knowing this, we can readily confirm that each crown lies *underneath* its respective stem and must have touched the bottom first. Subsequent tilting of the stems did not change the original position of the arms on the mud, but it often made the arms break near their bases when the calyx tipped over together with the stem (Pl. 48, fig. 2).

Using simple laws of superposition, we can also disentangle the whole colony (text-fig. 1). It seems that the crinoid stems grew bundled over most of their length, with only the calycal parts of the stems having some individual freedom.

As the trunk sank, it must have drifted slightly to the right. This drift aligned the settling stems, while it was too weak to disarrange the radial position of the arms. At two stages, however, sinking exceeded the drift and made the stems settle in broad loops.

Conclusion. The Medusenhaupt crinoids were attached to some floating object throughout life. Their crowns hung down and were the first parts to touch the bottom when the float sank.

2. *Functional morphology of the stem*

(*a*) *Paradigms*. If, then, *Seirocrinus* was pseudoplanktonic, we should expect it to deviate in certain respects from regular crinoids. *Encrinus liliiformis* (Lamarck) for instance, a familiar Middle Triassic crinoid, would have suffered from lethal deficiencies when placed on a drifting log. Its calyx, instead of hanging down in the sea water, would probably have floated at the surface—if we accept Linck's (1954; 1965, p. 138) conclusion that detached *Encrinus* drifted along the bottom in an upright position. But even if it could somehow adjust its buoyancy to an inverse position it would break off in the first storm. The basal part of its stem, breakable even under bottom conditions, would be much too stiff to withstand the tension that any wave would cause between calyx and float.

Buoyancy of the *calyx* would seem to control the upright position of rooted sea-plants and animals most effectively. Still, we have no record whether attached crinoids of the present use this principle, i.e. whether calyces sink to the bottom or float up when

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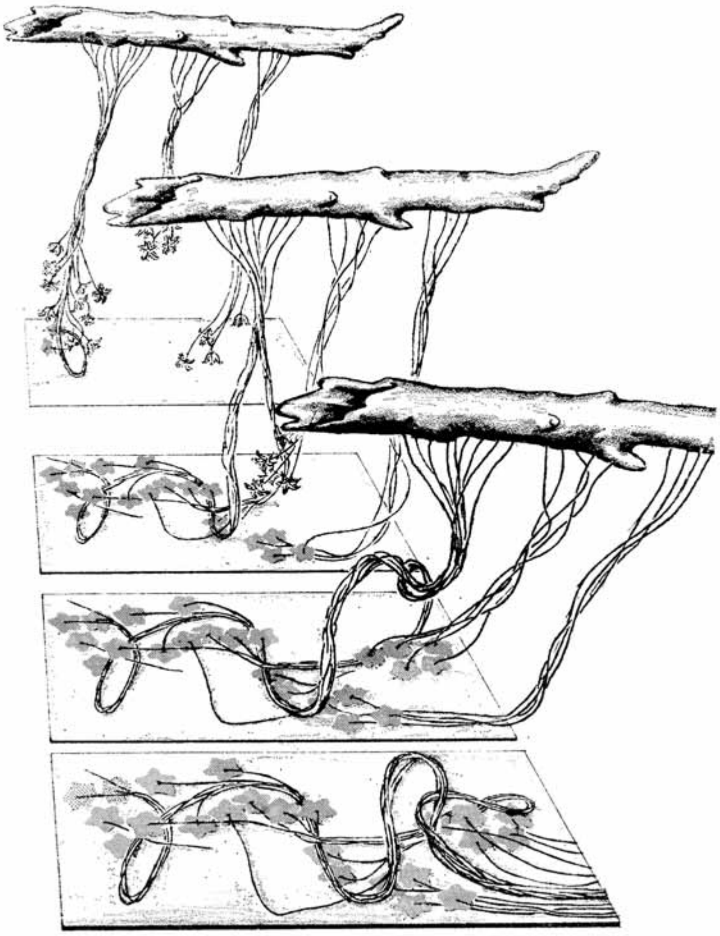
EXPLANATION OF PLATE 48

Fig. 1. Colony of *Seirocrinus subangularis* (Mill), ('Schwabens Medusenhaupt' of Quenstedt) mounted in the Geological Institute of the Tübingen University. Authors as scale.

Fig. 2. The arms, seen from below, spread radially and underlie the respective stems. This indicates that the arms touched the bottom first and the stems fell over them.

Fig. 3. Normal gradation in crinoid stems (*Encrinus liliiformis*; after Linck 1954, pl. 1): rhythmic alternation of internodal generations, still pronounced near the calyx, smoothes out towards the roots.

Figs. 4–5. In *Seirocrinus* stems gradation is reversed: fig. 5, although showing more pronounced alternation, is taken 9 m. further away from the calyces than fig. 4 in the same bundle.



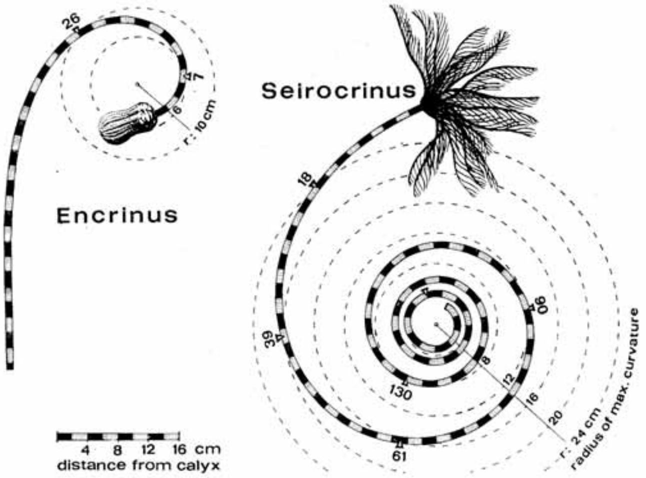
TEXT-FIG. 1. Settling of the colony as inferred from the final arrangement on the slab. Figure drawn as a mirror image to facilitate comparison with Plate 48, fig. 1.

clipped off their stems. The question of how buoyancy may be expressed in calycal morphology is therefore premature.

The effect of an inverse attitude on *stem* morphology should be easier to recognize because of the relative simplicity of its functional framework. The paradigm of a buoyant calyx would require the stem to be heavy and stiff near the root, light and flexible near the calyx. In the pendant model, as suggested for *Seirocrinus*, weight and flexibility should grade in the opposite direction.

Both relative weight and flexibility can be studied in fossil crinoid stems. Thin columnals with wide intercolumnal spaces would have resulted in low specific weight, while high and massive columnals made the stem heavier. The degree of flexibility on the other hand is recorded by the maximum curvature of different parts of complete specimens.

(*b*) *The stem of* Encrinus liliiformis. There is no doubt that the immature calycal parts were lighter than the massive basal sections of the *Encrinus* stem. Flexibility, measured from the beautiful slabs excavated by Linck (1954), decreased in the same direction (text-fig. 2).



TEXT-FIG. 2. uses the maximum bend observed in some fairly complete stems of *Encrinus* and *Seirocrinus* as an expression of the original flexibility distribution.

In *Encrinus* flexibility is high near the calyx and disappears towards the root which serves as a rigid column to support the calicular parts.

In *Seirocrinus* flexibility grades in the opposite direction. In terms of growth gradients, this may be due to limited accretionary growth and strong intercalation. In a functional sense it may express the stress distribution in a stem that hung from a floating log. (Measured on specimens in Tübingen Museum; Kat. Nr. 1325/1.)

The causes are obvious. Here, as in all crinoids, new nodals were formed as thin discs at the base of the calyx. Columnal growth was concentrated initially at the rim, leaving a saucer-shaped depression in the articulating surface. Secondary columnals (internodals) then developed in the protected space (Biese 1927, Aldinger 1928). After about four generations intercalation of new internodals ceased, but accretionary growth of individual columnals continued, flattening the articulation surfaces and rounding the slightly pentagonal outline. As a result of the process, the distinction between different generations of columnals, so obvious near the calyx, is lost towards the root (Pl. 48, fig. 3).

Both intercalation of additional columnals and accretionary growth in the axial direction increase the length of the stem, but have a different effect on its flexibility: while intercalation maintains the flexibility, accretion diminishes it.

Only the root zone may at first have retained some of its original flexibility. In this zone accretionary growth was radial rather than axial. Thereby the columnals remained fairly thin without appreciable reduction of articulations per unit length. However the original crenulation became exaggerated towards the periphery and an over-all callous cortex eventually was added to fuse the root columnals into a rigid and heavy base for the rest of the stem.

(*c*) *Stem differentiation in* Seirocrinus. *Seirocrinus* and other pentacrinid stems are easier to analyse. Not only do we know a larger number of fairly complete and well-preserved specimens, but the fact that nodals bear cirri while internodals do not, allows one to trace and measure nodal cycles well into older parts of the stem, where internodals have grown to the same size.

Growth and form, compared to the *Encrinus* stem, are completely different:

1. The 'young' aspect with hierarchic cycles of smaller and larger columnals is not restricted to the calycal end but extends over the whole stem. Moreover, alternation is more pronounced, and the stems become narrower away from the calyx (Pl. 48, figs. 4–5).
2. As far as internodes can be recognized, their length as well as the number of columnals per internode continues to increase geometrically towards the base (text-fig. 3). By projecting the observed growth rate, an internode of about 250 cm. and 1,023 columnals would be reached at about 20 m. from the calyx.
3. This trend does not continue indefinitely. Complete specimens (particularly the one figured by Müller 1963, fig. 511) show that axial growth, as in the *Encrinus* stem, decreased again near the root. In this part the cirri become stronger and densely crowded—in spite of the fact that we are dealing with the oldest part of the stem. There must have been a rapid decrease of internodal intercalation towards the base, to the point where internodals are lacking altogether.

In the case of *Seirocrinus*, the basal growth retardation did not increase flexibility, but had another functional effect: the concentration of nodals produced a dense tuft of cirri acting as a hold-fast to the driftwood.

As a whole, the stem of *Seirocrinus* meets the requirements set up in our paradigm: weight decreases and flexibility increases towards the root (text-fig. 2).

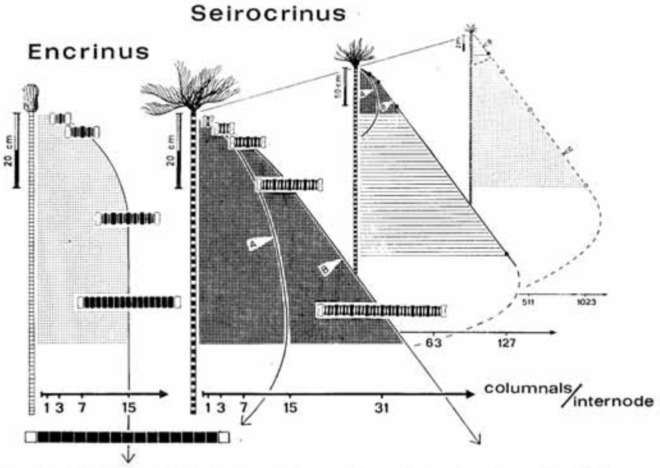
Conclusion. Weight and flexibility of the *Seirocrinus* stem grade inversely to *Encrinus*, as required by the pendant versus buoyant paradigm.

3. *Growth gradients and countergradients in the crinoid stem*

Comparing the two examples one feels that, no matter how different crinoid stems may appear, their basic morphology can be described in terms of a few common *growth gradients*:

1. *Longitudinal growth by intercalation*

(*a*) *Gradient*. Because the number of internodals increases with age, the internodes become longer with increasing distance from the calyx.



TEXT-FIG. 3. Longitudinal growth by intercalation and accretion of columnals (white = nodals; black = internodals).

Encrinus. Initial growth by intercalation stops after a few generations of internodals. Accretionary growth continues, however, so that all generations reach the same size. (Measurements made at Lauffen Cement Factories.)

Seirocrinus. Columnals never become uniform in size and seem to reach an unlimited number of generations. Close to the root, however, the internodes are increasingly shorter and a dense tuft of cirri bursts from the crowded columnals.

The three diagrams use different scales. Curves (A, B, C) are based on following specimens:

(A) Müller 1963, fig. 511 (Humboldt University, Berlin);
(B) Tübingen Museum (Kat. Nr. 1325/1);
(C) Large slab (Pl. 48, fig. 1).

Of these specimens, only (A) was complete. In the other two the deflection of the curve near the root is inferred.

(*b*) *Countergradient*. The rate of internodal intercalation is accelerated from the older to the younger parts of the stem, so that the number of internodals decreases again in the older parts of the stem close to the root.

The curves in text-fig. 3 result from the two gradients.

2. *Longitudinal growth by accretion*

(*a*) *Gradient*. Accretionary growth of the columnals is a function of time and increases away from the calyx.

(*b*) *Countergradient*. Similar to internodal intercalation, longitudinal accretion accelerates in younger parts of the stem, i.e. away from the root.

3. *Radial growth*

(*a*) *Gradients*. Primary control of nodal diameter lies in the generating area at the base of the calyx. The size of the nodals in turn determines the diameter of the initial internodals. A stem exclusively controlled by calicular growth would thicken from the base towards the calyx.

(*b*) *Countergradients*. Secondary modifications are brought about by accretionary growth in radial direction. As this growth is another time rate problem, it works in the opposite sense and tends to produce a trunk-like stem tapering from base to calyx.

The resultant of the two gradients is shown by the actual stems, which in most cases thicken at both ends.

4. *Callous overgrowth* may cover several columnals. It is used to add non-flexible structures such as anchors or lobes to the root.

This or a similar set of growth gradients should theoretically allow the crinoid stem to adjust to a variety of functional situations by speeding or slowing any one relative to the others. The flexibility in particular may thus be varied, or cirri concentrated, in different parts of the stem.

A species in which the root eventually acts as a trunk will thus emphasize gradients 3 (*b*) and 4 (*Encrinus*), while in the prehensile roots of some crinoids the same gradients are suppressed in order to retain the original state of a tapering and highly flexible tendril.

Conclusion. Similar to what we know from higher plants, a few general growth gradients seem to control a variety of adaptive modifications of the crinoid stem.

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Addendum

Dr. Jefferies (London) has kindly brought to our attention a note by the late J. F. Jackson (*Geol. Mag.* **103,** 365–6, 1966), stating that *Pentacrinus briareus* in the Lyme Regis Lias is regularly found *underneath* the lignitized driftwood to which it was attached. This fact further supports our conclusions.

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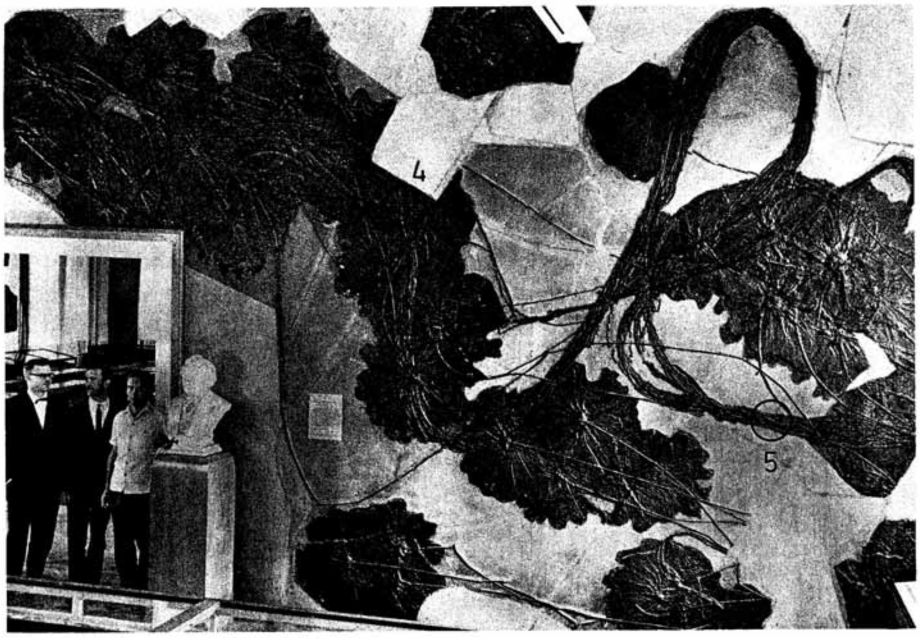

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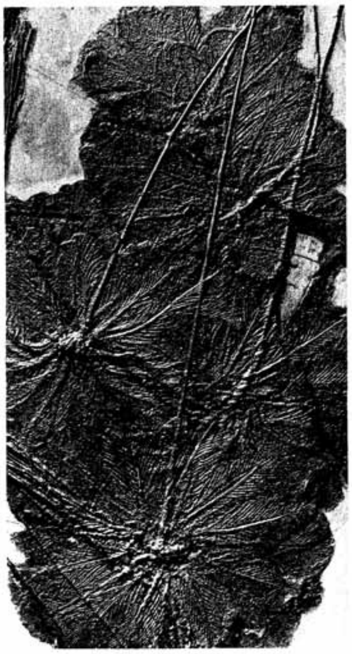

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