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SYMMETRY PLANES OF PALEOZOIC CRINOIDS

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ABSTRACT

The homocrinid *(E-BC)* plane of bilateral symmetry in the crown of some monocyclic inadunate and flexible crinoids is postulated to be a relict expression in adults of the dorsoventral symmetry plane of the doliolarian, free-swimming, larval stage.

Ubaghs (1953) has defined three planes of bilateral symmetry in the crowns of Paleozoic crinoids. The most widely prevalent of these is the so-called madreporite (M) plane of Bather. The other two planes, called homocrinid and heterocrinid symmetry planes by Ubaghs, are most common in the monocyclic inadunates, order Disparida.

1) The madreporite plane of bilateral symmetry passes through the *A* ray and *CD* interray, which by definition is the anteroposterior plane of the adult crinoid (Fig. 1). Virtually all camerate and flexible crinoids, as well as most inadunates, display this *A-CD* plane of bilateral symmetry. In most crinoid groups the mouth, anus, and other openings (e.g., hydropore, gonopore, or madreporite) lie in the *A-CD* symmetry plane.

2) Several families of disparids display the homocrinid plan, in which a plane of bilateral symmetry passes through the *E* ray and the *BC* interray (Fig. 2). This symmetry plane attains fullest expression in the bent-crown disparids, the Calceocrinidae, in which the crown is bent to one side over the stem, in the *E-BC* plane (Moore, 1962; Brower, 1966).

3) The third (heterocrinid) symmetry plane is found only in the disparid families Heterocrinidae and Anomalocrinidae and passes through the *D* ray and *AB* interray. This latter plane clearly is derived from the homocrinid plane by fusion of the two compound radials of the *B* ray (Fig. 3).

Recent studies by us of new Permian crinoids from southern Nevada have revealed that two new genera of flexible crinoids display the homocrinid plane of symmetry in the proximal part of the dorsal cup (Fig. 4-5). In fact, they furnish the first record of this symmetry outside of the disparid inadunates. One of the new forms, *Nevadacrinus,* is confidently assigned to the order Taxocrinida, whereas the other, *Trampidocrinus,* is placed with equal certainty in the order Sagenocrinida. Consequently, these flexible crinoids, distinguished by a homocrinid type of symmetry, are not judged to be closely related, even though both have a very unusual abruptly bent stem that seems to have served the same function as the bent crown of the Calceocrinidae (Lane & Webster, 1966). In both genera the *BC* basal is reduced in size, so that the *B* and *C* radials, but none of the others, are in contact with the infrabasal circlet. Because of these differences in cup-plate arrangement, we postulate that the bend in the stem results in the distal part of the column lying in the *E-BC* plane of the cup. This hypothesis cannot yet be proved directly from fossil evidence because compaction of enclosing sediment has resulted in slight crushing of the crowns and dislocation of the stems in all available specimens.

The appearance of the homocrinid symmetry plane in these distantly related crinoids suggests that there may be an underlying cause for the morphologic expression of homocrinid symmetry. It also seems significant that both the calceocrinids and the Permian flexible genera have the usually straight longitudinal adult dorsoventral axis of the crinoid bent to one side in the crown or proximal part of the stem. Because the cup plates that express the homocrinid symmetry surely formed early in ontogeny of these crinoids we have concluded that the most logical place to search for an

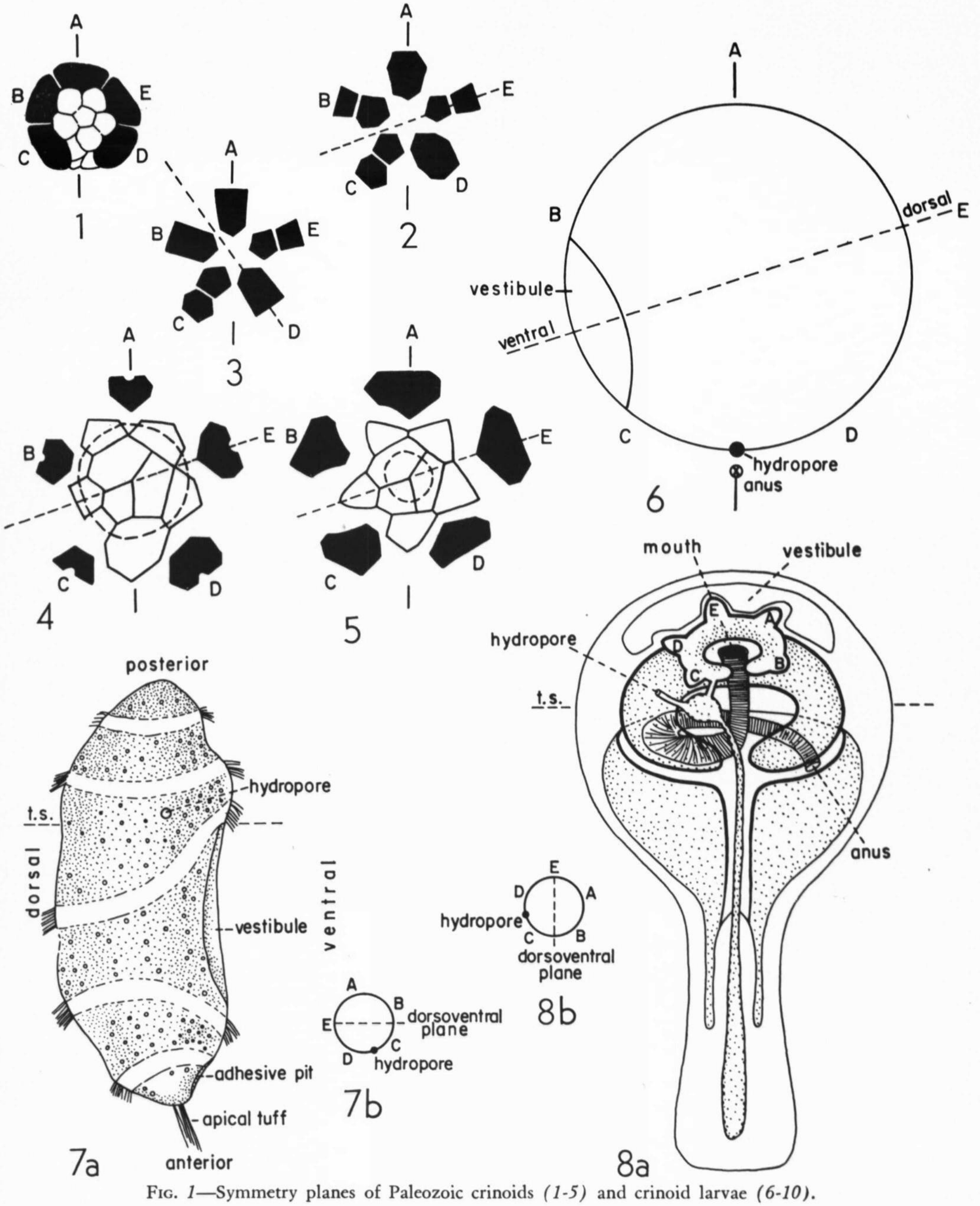

FIG. *1*—Symmetry planes of Paleozoic crinoids *(1-5)* and crinoid larvae *(6-10)*.

1. Anteroposterior *(A-CD)* symmetry plane of most Paleozoic crinoids, illustrated by *Galateacrinus* (after Moore, 1962).

2. Homocrinid *(E-BC)* symmetry plane (after Ubaghs, 1953).

3. Heterocrinid *(D-AB)* symmetry plane (after Ubaghs, 1953).

4-5. Infrabasal, basal, and radial circlets of Permian flexible crinoids, *Trampidocrinus* and *Nevadacrinus*.

6. Diagram of postulated relationship between *E-BC* plane of adult crinoid and larval dorsoventral plane.

7. Doliolarian larva of *Antedon*; *7a*, side view of larva in position of attachment (after Dawydoff, 1948); *7b*, transverse section in posterior or oral view in plane of t.s. (fig. 7a).

8. Schematic diagram *(8a)* of crinoid larva after rotation and prior to opening of anus and transverse section *(8b)* of larva in plane of t.s. (fig. *8a*).

[*A, B, C, D, E* are Carpenter ray designations. Solid lines at top and bottom of figures mark *A-CD* plane, dotted lines *E-BC*, or in Fig. *3*, the *D-AB* plane; figures *1-5* are dorsal (aboral) views of adults, radials black.]

explanation of the symmetry plane is in the early larval stages of living crinoids.

In the ontogeny of living crinoids the doliolaria is the free-swimming larval stage which immediately precedes settlement, attachment, and metamorphosis of these echinoderms (HYMAN, 1955). In the doliolaria a pronounced anteroposterior axis is recognized, with a tuft of cilia and an adhesive pit for attachment at the anterior end, and developing viscera of the crown at the posterior end (Fig. 7a,b). A depression on one surface, the vestibule, marks the mid-ventral side of the larva. During the free-swimming stage a hydropore opens outward near the posterior end of the larva, on the left side of the vestibule (when the larva is viewed from the posterior end). The hydropore in this position remains open during subsequent stages of development. The larva settles and attaches by the adhesive pit, so that the original anterior end of the larva becomes the aboral end of a subsequent pentacrinus larval stage in which the stem becomes attached to the substrate. The posterior end of the doliolaria ultimately becomes the oral side of the adult crinoid, farthest from the substrate. The viscera have been developing in the posterior (now oral) part of the larva during the attachment stage, and the vestibule and hydropore are now both near the oral pole of the doliolaria. During further development the larva undergoes rotation in which the original ventral vestibule closes and shifts from the side to the top of the larva, assuming an oral position. Internally the viscera shift in similar manner, so that rotation occurs in a ventral-toward-dorsal direction in terms of original doliolarian orientation.

After rotation the originally distinct dorsoventral plane of the doliolaria becomes largely obliterated and pentagonal symmetry is more pronounced. During rotation the hydropore remains open, and though slightly affected by visceral shifting, it holds the same relative position as before rotation. The mouth opens in a central location at the top of the attached larva and the digestive tract elongates, curving around to the left until it makes almost a complete circle (Fig. 8a,b). Ultimately, the anus opens in the same interradius as the hydropore. As here depicted (Fig. 8a), the digestive tract has not yet established its complete, twisted course.

When the anus opens below the hydropore, the posterior interray of the adult crinoid is well defined by these two openings to the exterior. The hydropore has not shifted position appreciably since it first appeared in the free-swimming doliolaria, and so the *CD*, or posterior, interray of the adult crinoid must lie to the left of what was the original dorsoventral plane of the doliolaria prior to rotation (Fib. 6). Because the hydropore, now in the adult *CD* interray along with the anus, was originally to the left of the vestibule, and the hydropore is not affected by rotation, the larval vestibule prior to rotation must have been situated in the area of the adult *B* and *C* rays. We postulate that the *E-BC*, or homocrinid, symmetry plane of the adult crinoid corresponds to the larval dorsoventral symmetry plane, and that the adult *E* ray was dorsal and the *BC* interray ventral in larval orientation. Insofar as we can determine this is the first time it has been possible to relate confidently the pentamerous symmetry of adult crinoids to the bilateral symmetry of the free-swimming larva.

In the unrelated crinoid groups that develop a pronounced bend in the usually straight dorsoventral axis of the adult crinoid, the bending seems always to take place in the *E-BC* plane. The development of the homocrinid symmetry plane in the crown or stem of these adult crinoids must be an expression of the original dorsoventral plane of their larvae. Therefore it follows that the homocrinid plane is a relic of the larval condition in flexible and inadunate crinoids, and that the larvae of these two extinct subclasses must have been similar, in some respects at least, to the larvae of living articulate crinoids.

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