# Fossilized Viscera in Primitive Echinoderms

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The increasing biological focus in paleontology has improved our insight into such matters as the timing of major evolutionary events (*1*), the nature of evolution and extinction (*2*), and the detailed anatomical and physiological characteristics of members of many fossil and extant taxonomic groups (*3–5*). Much of this information has come from studies of specimens and faunas that are preservational oddities (*6*). Thus extraordinary preservation, ranging in scale from organelles in microscopic algae to entire digestive and nervous systems in macroinvertebrates (*6, 7*), has permitted important syntheses of neo- and paleobiological data.

Echinoderms, which have an extraordinarily rich fossil record dating from the Late Precambrian, have been the focus of such synthetic studies (*7–11*). The phylum illustrates a striking decline in taxonomic diversity from 20 classes in the Paleozoic to only four classes extant (*5, 9, 12*). Ancient members of the group may have close affinities (at least embryologically) with the earliest protochordates. Thus thorough knowledge of the paleobiology of echinoderms may have broad implications for biological reassessments of other phyla.

Naturally, most information on echinoderm visceral anatomy has been derived from living individuals. Much of these data have been extrapolated directly to fossil forms without question. Our new data refute several widely accepted anatomical assumptions about extinct echinoderms and are critical for understanding the biology, classification, and inferred evolution of this phylum. A formal, systematic revision of the phylum must integrate the new paleovisceral information with information on the visceral anatomy of living forms.

## Background

In 1858, Billings (*13*) said that "not a single specimen [of fossil cystoid] retaining even a vestige of soft parts will ever be discovered." Views that discount the possibility of retrieving pertinent visceral data directly from fossils persist to this day. Contrary to Billings' prediction, significant paleoviscera have been found in five classes of fossil echinoderms (Table 1). In addition, the consistent structural relations between the paleoviscera and commonly preserved skeletal features in these five classes allows anatomical interpretations to be made about many other extinct classes. We have made detailed visceral anatomical reconstructions for ten of the 17 extinct classes of Paleozoic echinoderms and also more generalized reconstructions characterizing two major groups of predominantly extinct taxa (subphyla I and II) and a third group comprising most of the living forms (subphylum III) (Fig. 1 and Table 1).

Perhaps the most detailed reports of fossilized viscera in echinoderms are those by Haugh (*7*). Fossilized features include the gut, several coeloms, and the nervous systems of extraordinary specimens of Paleozoic camerate crinoids, a common fossil group (Figs. 1A and 2, A, C, and F). Secondary calcification and silicification sustain the remarkable three-dimensional preservation of the internal anatomy. The superb fidelity is possible because a spicular endoskeleton supported the organs in these fossils. Modern echinoderms also secrete a spicular network in their internal tissues, but in most instances it is insufficiently rigid to readily maintain the shape of the organs after death. The extreme rarity of visceral preservation in the fossil record indicates that biomineralization of viscera has always been weak. Haugh (*7*) found fossilized visceral organs that have no known close morphological counterparts in extant echinoderms. Neither the convoluted perigastric coelom around the gut nor the interradially disposed subdermal coelom (Figs. 1, A and B, and 2 and 3) are present in living echinoderms (*14*). The general plan of the camerate gut (Fig. 1A) also differs markedly from that in living crinoids. Conversely, the nervous systems are very similar (*7*).

*Summary*. Fossilized visceral organs in ancient echinoderms have anatomical features that were not inferred from the anatomy of extant relatives. The unique visceral anatomy of extinct echinoderms demonstrates the need to integrate paleontological and neontological analyses in order to fully evaluate this and other morphologically complex phyla. Comparative analysis of the visceral anatomy of extinct and extant echinoderms necessitates regrouping these animals into three new subphyla. Similar analyses for other metazoan groups could yield equally significant results.

## Preservation of Viscera

Calcitic and ferrous filling of the interstices of the spicular framework (permineralization) and subsequent recrystallization of the high-magnesium calcite spicules resulted in the unusual three-dimensional preservation of the organs. In Schopf's (*15*) terminology, this involves cellular permineralization followed by duripartic preservation. In some instances (as in certain camerate crinoids and blastoids), duripartic preservation includes a third-order replacement of the secondary calcite by microcrystalline silica (chert).

Another characteristic of visceral preservation in fossil echinoderms is the presence of uncommon opaque iron minerals in the calcified or silicified walls of the organs (Figs. 2, B and F, and 3, D, E, and G). Usually, only the outline of the organ is represented by bacteriologically induced pyrite ($FeS_2$) deposition (*6, 16*), yet this kind of sulfide mineralization is rare in the echinoderm specimens described here. X-ray analysis with a scanning electron microscope in the energy-dispersive mode revealed iron silicate, iron carbonate, and iron oxide associations. Petrographic analysis of thin sections indicated the probable existence of three opaque iron mineral complexes:

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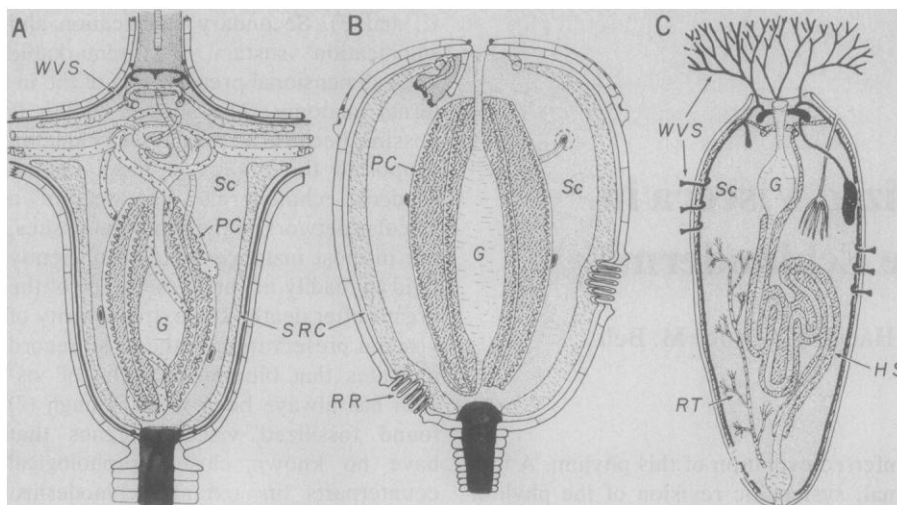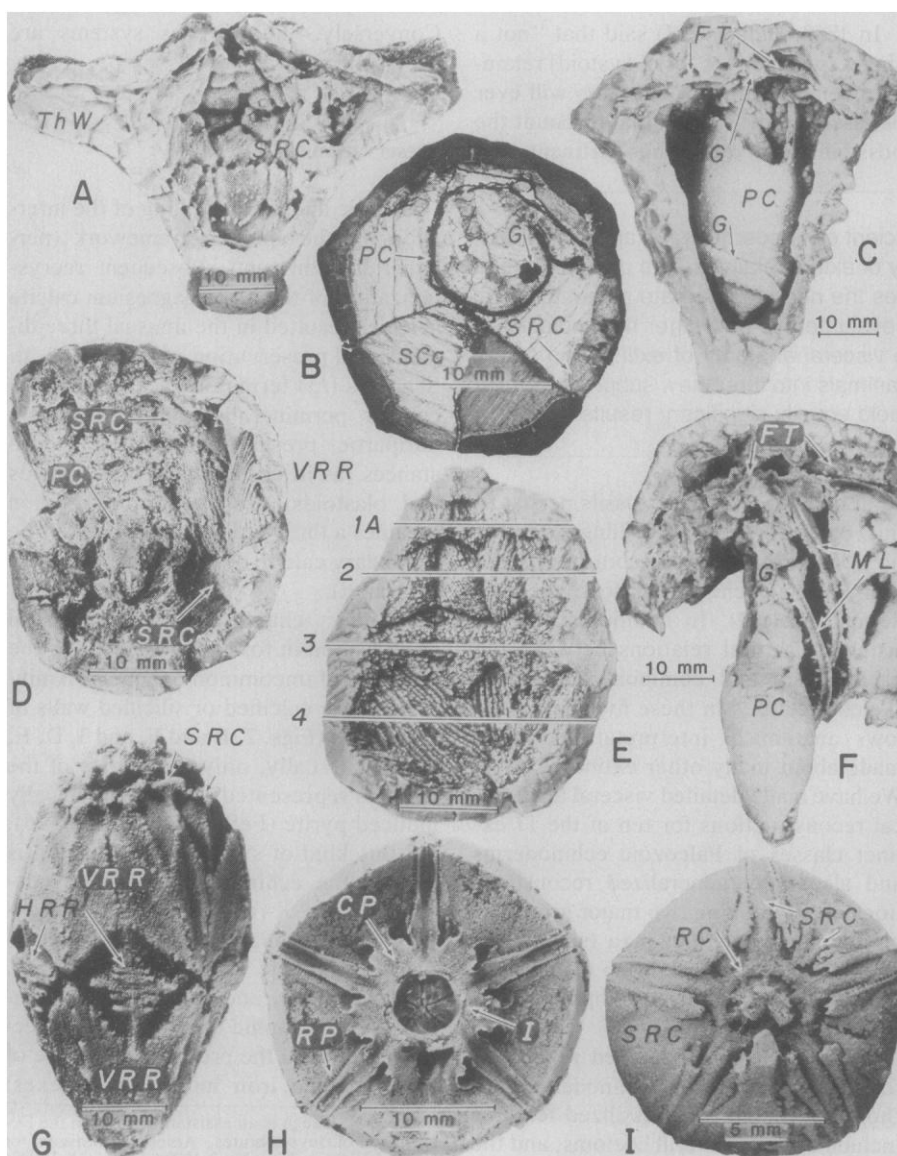
Fig. 1. Diagrammatic plans of the informal subphyla of echinoderms: (A) subphylum I, represented by a camerate crinoid; (B) subphylum II, represented by a rhombiferan cystoid; and (C) subphylum III, represented by a holothurian. Abbreviations: $G$, gut; $HS$, haemal system; $PC$, perigastric coelom; $RR$, respiratory rhomb; $RT$, respiratory tree; $Sc$, somatocoel; $SRC$, subdermal respiratory coelom; and $WVS$, water vascular system.

chamosite (complex iron silicate), siderite (complex iron carbonate), and goethite (complex iron oxide) (17). This mineralization suggests a relatively closed microenvironment caused by the tightly closed echinoderm theca, which limited the influx of reactants from the enclosing mud and overlying water column. This contrasts with the relatively open geochemical system that is responsible for completion of the more common ferrous mineralization sequence leading to pyritization of fossilized viscera. These two distinctive modes of "iron fossilization" involve differences in $p$H and oxidation states, as regulated by organic decay and relative availability of ionic iron, sulfate, carbonate, silica, and elemental sulfur (18, 19). Biologically focused laboratory and field studies dealing with decay-induced carbonate and iron silicate formation provide modern biogeochemical analogs for our fossil situation (20, 21).

Laboratory experiments with decay-induced carbonate precipitation in clams (20) indicate the following necessary sequential events: (i) generation of organic acids; (ii) presence of $CaCO_3$ and a high concentration of $Ca^{2+}$ from acidic dissolution; (iii) gradual rise in $p$H (from 5.7 to 8 or 9) caused by formation of ammonia and nitrogenous bases through degradation of protein; and (iv) carbonate precipitation from a supersaturated solution through intensive bacterial reduction of $SO_4^{2-}$ to $H_2S$:

$$2CH_2O + SO_4^{2-} + Ca^{2+} \rightarrow$$
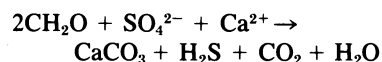$$CaCO_3 + H_2S + CO_2 + H_2O$$



Fig. 2. Three-dimensional fossilized viscera in primitive echinoderms. (A) Camerate crinoid, *Eutrochocrinus christyi* (Mississippian). (B) Thin section of the rhombiferan cystoid *Caryocrinites ornatus* (Silurian) photographed in polarized light. (C) The camerate crinoid *Teleiocrinus liratus* (Mississippian) showing extraordinary three-dimensional, silicified preservation of virtually all the spicularized viscera. (D) Hollow specimen of the rhombiferan cystoid *C. ornatus*, with no sparry calcite development. (E) Another hollow specimen of *C. ornatus*, with minor sparry calcite development, and cut at four locations for thin sections as illustrated in Figs. 4, A to D, and 3F. (F) Silicified camerate crinoid, *Actinocrinites verrucosus* (Mississippian), with perigastric coelom broken to illustrate the thin medial line of iron mineralization in the wall. (G) Dolomite internal mold of the visceral cavity of *C. ornatus*, illustrating casts of the respiratory rhombs and subdermal respiratory coelom. (H) Visceral cavity of the upper half of a hollow silicified specimen of the spiracular blastoid *Nucleocrinus verneuilli* (Devonian); respiratory hydrospires are missing. (I) Silicified specimen of the spiracular blastoid *Schizoblastus sayi* (Mississippian), with respiratory

viscera around the hydrospires. Abbreviations: $CP$, coelomic platform of the ring commissure ($RC$); $FT$, food tubes; $G$, gut; $HRR$, horizontal respiratory rhomb; $I$, impression of perigastric coelom; $ML$, median line of iron mineralization; $RP$, respiratory pore; $SCa$, secondary calcite; $SRC$, subdermal respiratory coelom; $ThW$, thecal wall; and $VRR$, vertical respiratory rhomb.

Both the permineralizing calcite of the spicular frameworks and the siderite of the opaque iron mineralization could have been generated in this manner, with the calcite spicules forming a nucleation substrate. Decay-induced generation of the primary iron silicate, chamosite, has been found to occur in shallow marine environments where it forms in fecal pellets and decaying organisms (21). In this milieu, chamosite is typically associated with goethite (probably formed by oxidation). The organically generated chamosite may comprise up to 60 percent of the unconsolidated sediment in which pyrite is lacking or minor. Similarly, the relatively closed microenvironment of an echinoderm theca would restrict the availability of organic matter, sulfate, iron, and elemental sulfur so that in concert with bacterial action and high carbonate activity, geochemical conditions would favor the formation of chamosite rather than pyrite. Little is known of the sequence of the steps leading to the formation of chamosite, but the initial reactants are probably a siliceous "mixed gel" (19). Chamosite and siderite are commonly shrouded by a yellowish-brown secondary oxidation "halo" of goethite (Fig. 3E). This suggests that the final phase of iron mineralization took place under oxidizing conditions. Chamosite also tends to be associated with goethite and siderite in Phanerozoic sedimentary iron formations (18, 19).

Iron permineralization and secondary calcification combined to preserve internal food tubes, the digestive tract, and the wall of the perigastric coelom. This is best seen in specimens of the rhombiferan cystoid Caryocrinites ornatus (Figs. 2B and 3, D, E, and G) and in many specimens of camerate crinoids (Fig. 2, C and F). This localization of ferrous permineralization indicates that the feeding system and gut provided a direct avenue of diffusion for iron and other reactants from the surrounding sediment. The porous subdermal coelom of the cystoids also received iron permineralization as a result of diffusion through the respiratory rhombs (Fig. 3, C to G). In contrast, the subdermal coelom in camerate crinoids lacks iron minerals because there are no porous thecal respiratory structures to permit diffusion. Breimer and Macurda (22) reported mineralization of internal structures associated with respiratory hydrospires in Devonian blastoids, but were puzzled as to their nature. Thin-section analyses of calcified specimens and studies of chert molds and casts revealed the same structures in several genera of Devonian and Carboniferous blastoids (Fig. 2, H and I). Clear-

ly, the structures represent the remains of the subdermal respiratory coelom.

The suite of minerals comprising the fossilized viscera of echinoderms indicates that the processes leading to visceral preservation may have proceeded in the following manner. As decay began, organic acids, ammonia, and nitrogenous bases were trapped in the porous spicular framework (Fig. 3B) of a given organ. These rapidly reacted with the externally derived ions entering through the gut and respiratory rhombs, thereby confining deposition of primary chamosite, siderite, and calcite to the spicular frameworks. This primary permineralization episode added to the rigidity of the organs and reduced their permeability. Thus the main avenues of diffusion became effectively sealed so that potential sulfide mineralization was prematurely terminated. In some instances the permineralization bonding was so effective and seemingly so rapid that mi-
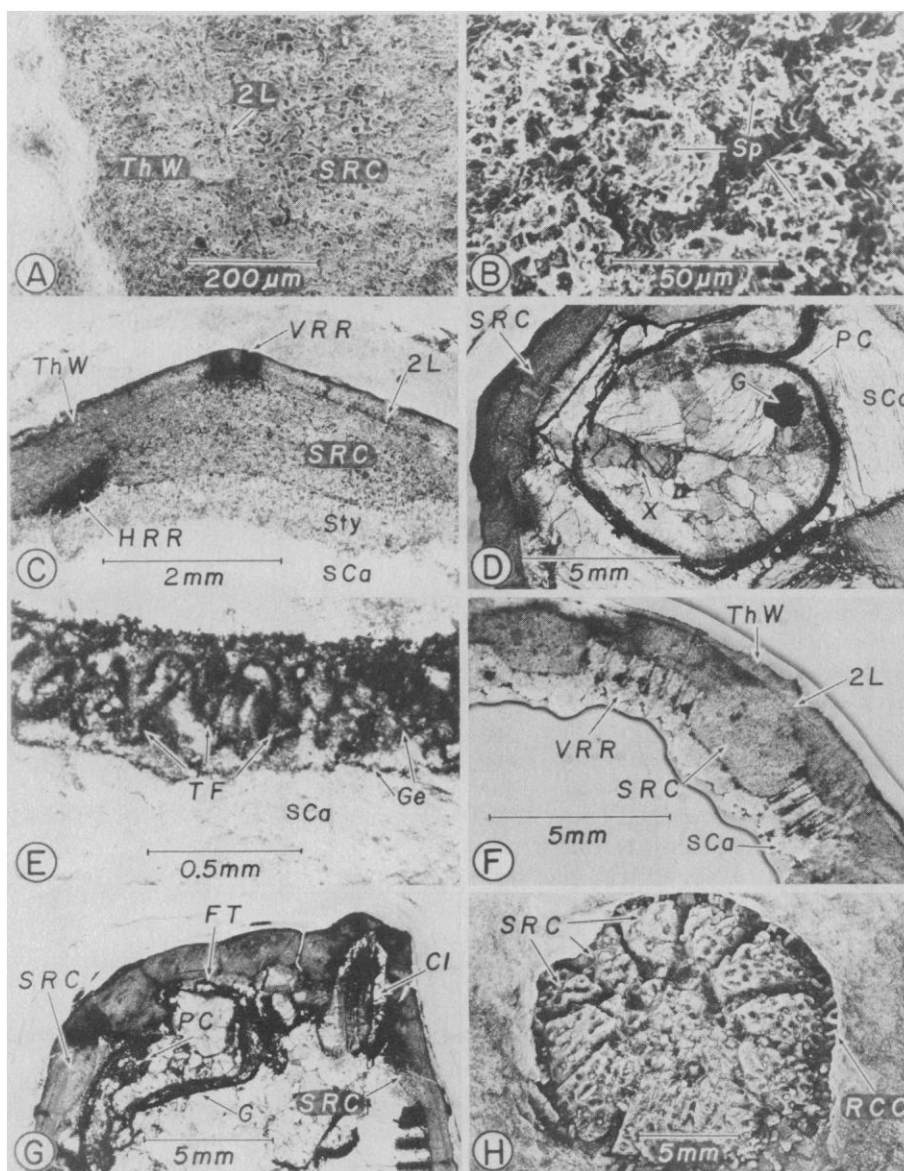


Fig. 3. Structural details of fossilized viscera. (A) Scanning electron micrograph of a cross section of the C. ornatus thecal wall and subdermal respiratory coelom delimited by the double line (2L). (B) Scanning electron micrograph of spicules of the subdermal respiratory coelom of C. ornatus. (C) Thin section of C. ornatus illustrating various respiratory viscera and the development of stylolitic (Sty) and sparry calcite. (D) Detailed view of the perigastric coelom of C. ornatus (thin section). Note that the perigastric coelom delimits areas of calcite that are out of optical phase, indicating separate crystallization. (E) Ferruginated tissue folds in the wall of the perigastric coelom of C. ornatus (thin section). (F) Detailed view of the respiratory rhombs and coelom of C. ornatus in a thin section diagrammed in Fig. 4D. (G) Remarkable preservation of viscera in the upper part of a specimen of C. ornatus (thin section). (H) Ironstone internal mold of a diplopore cystoid (Ordovician), showing casts of respiratory viscera. All thin sections were photographed in polarized light. Abbreviations: Cl, cloaca; RCC, respiratory canal casts; Sp, spicules; TF, tissue folds; X, optical extinction cross; and Ge, goethite. See legend to Fig. 2 for other abbreviations.

Table 1. Systematic reevaluation of echinoderm classes based on preserved viscera and inferred relations between viscera and commonly preserved skeletal details. Classification of Cyclocystoidea, Ophiocistoidea, and Cycloidea is indeterminate. Taxa now judged to be invalid are Lepidocystoidea (= Eocrinoidea), Camptostromatoidea (= Edrioasteroidea), Cymoidea (= echinoderms of unknown rank and affinities), and Calcichordata (= Homoiostelea and Stylophora).

| Subphylum I | Subphylum II | Subphylum III |
|---|---|---|
| Edrioblastoidea | Blastoidea* | Echinoidea (extant) |
| Crinoidea* (extant) | Parablastoidea | Stelleroidea (extant) |
| Edrioasteroidea* | Diploporita* | Holothuroidea (extant) |
| Helicoplacoidea | Rhombifera* | |
| | Eocrinoidea | |
| | Paracrinoidea | |
| | Ctenocystoidea | |
| | Homostelea | |
| | Homoiostelea | |
| | Stylophora | |

*Paleoviscera have been found in specimens of this class.

nute tissue folds were preserved in the wall of the perigastric coelom (Fig. 3E). Finally, sparry calcite grew from the inner surfaces of the permineralized organs, as is indicated by minor stylolitic calcite growth (Fig. 3C) and by the discordant optical orientation of the sparry calcite in various spaces. For example, in *Caryocrinites ornatus* the "extinction cross" of the calcite in the perigastric coelom is out of phase with the extinction zones of the surrounding visceral cavity (Figs. 2B and 3D). As the sparry calcite developed, a slight oxidation of the primary chamosite and siderite produced the translucent yellow-brown goethite oxidation halo in the adjacent spar (Fig. 3E). Many of the specimens examined are still partly hollow "geodes," indicating that the theca became so impermeable to interstitial solutions that spar development ceased far short of filling the visceral cavity (Fig. 2E). In some specimens the spar development was so slight that the permineralized three-dimensional perigastric coelom and subdermal coelom can be viewed directly (Fig. 2D).

The opaque iron minerals are confined to a very thin medial band (Fig. 2F) in the wall of the perigastric coelom of silicified camerate crinoids. Fossilization proceeded here in the same manner as in calcified specimens, but the additional third-order replacement of calcite by chert caused the opaque iron minerals to be diagenetically concentrated.

## Subdermal Respiratory Coelom

The subdermal coelom (Fig. 2, A, D, and I) is of special taxonomic and functional interest because it is unknown in extant echinoderms. This extensive interradial coelom is found in camerate crinoids, rhombiferan and diploporite cys-

toids, blastoids, eocrinoids, and other common extinct classes of Paleozoic echinoderms. Thus the subdermal coelom typifies members of subphyla I and II (Fig. 1, A and B). In the camerate crinoids (subphylum I), the subdermal coelom forms an inner lining or plexus (7, 14) that shrouds the other viscera (Fig. 2A). Orally, it divides to form a series of interradial straplike extensions that connect to a circumoral ring commissure. In
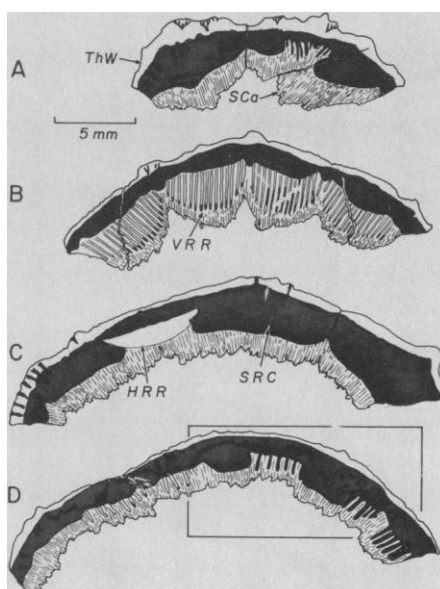


Fig. 4. Camera lucida drawings of thin sections cut at widely spaced intervals in the rhombiferan cystoid *C. ornatus* (see Fig. 2E). (A) Section through the upper subdermal respiratory coelom and the tips of the upper bank of vertical respiratory rhombs (section 1 in Fig. 2E). (B) Section through the center of the upper bank of vertical respiratory rhombs (section 2 in Fig. 2E). (C) Section through the equator of the specimen and the horizontal respiratory rhombs (section 3 in Fig. 2E). (D) Section through the center of the lower bank of vertical respiratory rhombs (section 4 in Fig. 2E). The rectangle outlines the area shown in Fig. 3F. See Fig. 2 for abbreviations.

the cystoids and blastoids (and presumably in other classes of subphylum II), the morphology of the subdermal coelom is similar, except that it is associated with a variety of thecal respiratory organs (Fig. 2, D, E, G, H, and I; Fig. 3, C. F, G, and H) (14). This coelom functioned as the chief respiratory organ in these groups—in the absence of an external hydraulic water vascular system (Fig. 1C), which serves this function in living echinoderms (23).

The morphology of the subdermal coelom has been established by examination of specimens that were preserved in different ways. The diversity of preservation modes allows determination of three-dimensional shape, spatial relations among organs, and preservational matters such as recrystallization, dolomitization, and distortion. The clearest view of the coelomic respiratory system is provided by exceptional hollow specimens (Fig. 2, D and E) with a permineralized three-dimensional subdermal network. For example, vertically broken hollow specimens of *Caryocrinites ornatus* show subdermal structures, respiratory rhombs, and varying degrees of sparry calcite development. Many of these specimens were photographed and then sectioned at widely spaced, predesignated intervals (Fig. 2E) so that thin-section detail (Figs. 3F and 4) could be compared directly to corresponding three-dimensional details of internal surfaces recorded in the photographs (Fig. 2E). Specimens were also sectioned serially at approximately 350-micrometer intervals to permit construction of enlarged three-dimensional models.

With this technique, several details were demonstrated. A biologically mineralized zone—commonly regarded as the thecal plating of the organism—actually consists of two optically distinct layers (Figs. 3, C and F, and 4). The thin outer layer is characterized by uniform thickness, dense calcite stereom, and little if any disseminated ferrous permineralization. [This is the true thecal wall, composed of skeletal plates (Fig. 3, A, C, and F).] The inner layer, with highly variable thickness, porous (but permineralized) stereom, and disseminated iron mineral grains (Fig. 3, A, B, C, and F), is the subdermal network. The latter sharply contrasts with the clear sparry calcite secondarily precipitated in the thecal cavity (Figs. 3, C and F, and 4). The boundary that delimits the thecal wall from the subdermal coelom shows as a double line both in petrographic thin sections and in scanning electron micrographs (Fig. 3, A and C). At high magni-

fication, the much greater porosity of the inner layer is seen to be the result of the spicular nature of this zone (Fig. 3B). The spicules are round in cross section and retain their own characteristic echinodermal stereomic porosity (Fig. 3B) (24). The cross-sectional profiles of the inner layer are consistent among specimens and are correlated with the developmental patterns of respiratory rhombs. Thus these subdermal structures cannot be regarded as part of the thecal plating, or merely as secondary calcite growths (25). Similar studies of dolomite and chert steinkerns of diploporite cystoids and of blastoids clearly show the presence of a morphologically similar subdermal coelom (Figs. 2, H and I, and 3H).

## Biological Significance of
## Fossilized Viscera

Paleontologists have begun to explore diverse biological topics in order to gain better insight into evolutionary processes, extinction, paleoecology, paleophysiology, and systematics (2-5). Quite properly, they have turned to living organisms for biological analogs (26). This paradigmatic approach has contributed much, but it is not self-sufficient and tends to overemphasize the modern analogs. The "dinosaur renaissance," based on extant mammalian rather than extant reptilian analogs, is perhaps the most popular current example of the need for detailed paleobiological input (27). The unusual visceral anatomy described here is of major import because it permits the elimination of several neontological misconceptions about primitive echinoderms and because it underscores the necessity for a comprehensive biological and systematic reappraisal of the phylum.

Echinoderms attained their greatest diversity early in the Paleozoic Era (before 400 million years ago), and have dwindled to only four classes. Study of fossilized internal viscera of ancient echinoderms shows that the four living classes are not fully representative of the anatomical diversity of the phylum. Three living classes comprise one subphylum, and living representatives of the fourth class are extensively modified, obscuring their original coelomic construction. The fact that only one body plan has prospered suggests that it is fundamentally more effective and became totally dominant. The survival of only four classes of echinoderms in itself suggests significant biological differences between living and extinct forms. Additional paleoanatomical information shows that, contrary to common belief (5, 11, 28), a water vascular system is absent in many extinct echinoderm classes and that pentameral symmetry is neither primitive nor universal throughout the phylum. The survival of anatomically atypical highly ranked taxa might also characterize other metazoan phyla.

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