PART S

ECHINODERMATA 1

GENERAL CHARACTERS

HOMALOZOA—CRINOZOA (EXCEPT CRINOIDEA)

By H. H. Beaver, K. E. Caster, J. W. Durham, R. O. Fay, H. B. Fell, R. V. Kesling, D. B. Macurda, Jr., R. C. Moore, Georges Ubaghs, and †Johannes Wanner

---

VOLUME 1

CONTENTS

[Volume 1, p. i-xxx, 1-296; Volume 2, p. 297-650]

INTRODUCTION

By Raymond C. Moore

The unit of the *Treatise* designated as Part S (Echinodermata 1) has been very long in preparation, for initial agreements of contributing authors selected to produce some of the sections date back to the late 1940's. By 1952 typescript and illustrations (or directions for making them) had been completed by at least one author, Professor Johannes Wanner, whose death occurred in July, 1956. Others who promised to care for important sections found that they could not produce them and thus after several years new assignments had to be arranged. *Treatise* authors receive no financial compensation for their work and consequently only such persuasion as I can muster eventually leads to desired accomplishments.

We are especially indebted to collaborators who completed work on tasks accepted at relatively late dates: 1) Georges Ubaghs in 1959 for a chapter on general characters of Echinodermata (completed March, 1961, revised 1962, 1963, 1964, 1965); 2) K. E. Caster in 1959 for "carpoid" classes (Homoiostelea completed December, 1966); 3) H. B. Fell in 1960 for chapter on echinoderm ontogeny (completed October, 1961, revised 1962); 4) R. O. Fay and H. H. Beaver in 1960 for morphology and systematic descriptions of blastoids (nearly completed July, 1961, revised 1962, 1963, 1964, 1965); 5) R. V. Kesling in 1962 for chapters on cystoids and paracrinoids (completed December, 1962, and January, 1963); 6) Georges Ubaghs in 1963-64 for chapters on Homostelea, Stylophora, and Eocrinoidea (completed July, November, December, 1965); and 7) D. B. Macurda, Jr., in 1966 for discussion of the development and hydrodynamics of blastoids (completed February, 1966).

It is appropriate to draw attention to the very large amount of basic research which is demanded from authors of *Treatise* volumes, for work by them is far from merely compilative in nature. Of course, the vast sum of information recorded in zoological and paleontological literature needs to be surveyed, digested, and organized, but additional to this are challenges to conduct important new studies. What are the most significant morphological features of each discriminated animal group and how do these bear on improvements in taxonomy? Do advancements in techniques of fossil preparation and discoveries based on new materials or critical new investigations of old contribute to better understanding of relationships that bear on classification and interpretation of phylogeny and evolution? Readers of chapters published in *Treatise* Part S assuredly will find that the various authors have responded to such challenges.

In many ways the echinoderms included in Part S are "difficult" groups in that all are extinct, some having vanished from the earth not less than 500 million years ago and the latest near the end of Permian time, approximately 200 million years before the present. None are closely related to surviving echinoderms. Accordingly, we should not be surprised to find that paleontologists have differed in interpreting and classifying them. Described genera have been shifted back and forth among different recognized classes and orders. They include some forms now considered to be crinoids and cyclocystoids.

Treatise Part S distinguishes many more taxa of homalozoans and crinozoans (exclusive of crinoids) than have been recognized previously. This is indicated by the following tabulation of genera and families in echinoderm groups equivalent to the 11 classes (not including crinoids) given in the present volumes.

Genera and Families Recognized in Treatise Part S Compared to Those in Some Earlier Publications

Source	Genera	Families
Zittel, 1896	63	15
Bather, 1900	94	27
Jaekel, 1918	99	36
Springer, 1913	109	23
Cuénot and Bergounioux, 1953	139	38
Bassler & Moodey, 1943	159	35
Gekker, 1964 (1965)[1]	106	34
Treatise Part S, 1967	273	71

[1] Incomplete listing because consideration mostly confined to Soviet Union.

Data of this sort are inadequate as a measure of expanding knowledge but they reflect it partly.

In my opinion, the most valuable contribution of *Echinodermata 1* is its survey of general characters and ontogeny observed in the phylum and delineations of morphological attributes of the crinozoan and homalozoan classes treated.

The introductory chapters by Ubaghs and Fell serve excellently for cross-tying the divergent outlooks of neozoologists and paleozoologists in studies of echinoderms, providing readily comprehensible information that each of these groups should have. It may be noted that UBAGHS (p. *S*8, Fig. 2,5,6) rejects interpretation of echinoids advanced by MOORE and FELL (*Treatise* p. *U*120-125, Fig. 100, 106). The disagreement is allowed to stand.

I commend to all readers the exceptional body of new information, including new illustrations, contained in the chapters on cystoids, blastoids, eocrinoids, and "carpoid" classes. The many kinds of advancement in knowledge speak for themselves. Although short and added at last moments, interesting new classes named Lepidocystoidea and Camptostromoidea are contributed by DURHAM. In overall view, the fossils considered in Part S demonstrate the present incompleteness in comprehension of early echinoderms and they emphasize both the need and the opportunities of future investigations in this field.

REFERENCES

Bassler R. S., & Moodey, M. W.

1943, *Bibliographic and faunal index of Paleozoic pelmatozoan echinoderms:* Geol. Soc. America, Spec. Paper 45, vi+734 p.

Bather, F. A.

1900, *The Pelmatozoa—Cystidea, Blastoidea:* in A treatise on zoology, E. R. Lankester (ed.), pt. 3, p. 38-93. Adam & Charles Black (London).

Bergounioux, F. M.

1953, *Classe des blastoïdes:* in Traité de paléontologie, Jean Piveteau (ed.), v. 3, p. 629-650, fig. 1-36, Masson et Cie (Paris).

Cuénot, Lucien

1953, *Classe de hétérostélés, classe des cystidés:* in Traité de paléontologie, Jean Piveteau (ed.), v. 3, p. 599-628, 43 fig., Masson et Cie (Paris).

Gekker [Hecker], R. F.

1964 (1965), *Klass Carpoidea, Klass Cystoidea, Klass Blastoidea, Klass Eocrinoidea, Klass Paracrinoidea:* in Osnovy paleontologii, Yu. A. Orlov (ed.), Iglokozhie, etc., p. 23-28, 30-54, fig. 5-10, 14-50, Izdatelstvo "Nedra" (Moskva).

Jaekel, Otto

1918, *Phylogenie und System der Pelmatozoen:* Paläont. Zeitschr., v. 3, p. 1-128, fig. 1-114.

Springer, Frank

1913, *Pelmatozoa:* in Text-book of paleontology, adapted from K. A. von Zittel, C. R. Eastman (ed.), p. 144-243, fig. 226-346, Macmillan (London).

Zittel, K. A.

1896, *Echinodermata:* in Text-book of palaeontology, C. R. Eastman (ed.), p. 122-250, fig. 217-402, Macmillan (London).

GENERAL CHARACTERS OF ECHINODERMATA

By GEORGES UBAGHS

[Université de Liège, Belgium] [I am much indebted to RAYMOND C. MOORE for translating my manuscript and for valuable criticism. Also I acknowledge helpful suggestions received from H. BARRACLOUGH FELL and J. WYATT DURHAM, together with the loan of some unpublished manuscripts prepared by them. My sincerest thanks are expressed for this assistance.]

CONTENTS

INTRODUCTION

The echinoderms comprise one of the most important and best-characterized of all invertebrate phyla. They are marine, benthonic (or exceptionally pelagic) Metazoa, living in an attached position or free, but never colonial. Also, they may be defined as enterocoelic, nonsegmented coelomates, without differentiated head or brain, bilaterally symmetrical fundamentally, but modified by asymmetry introduced by atrophy of some organs of the right anterior side of the body and corresponding overdevelopment of organs of the left side. Three characters serve to distinguish them easily: (1) radial symmetry (typically pentamerous), secondarily imposed on larval asymmetry; (2) an endoskeleton formed of plates or distinct ossicles, composed of crystalline calcite deposited in an organic mesenchymatous network displaying a reticulate microstructure and distinctive crystallographic properties; (3) a water-vascular system of sacs and canals of coelomic nature opening outward in a pore and giving rise to numerous small projections on the surface of the body. Finally, they lack any sort of differentiated excretory apparatus.

Several of the characters just enumerated are not constant or, at least, invariably observable. Thus, the presence of a water-vascular system, though probable, has not been recognized certainly among all fossil echinoderms. The endoskeleton may be much reduced or even completely absent among some rare holothuroids. Radial symmetry does not affect the endoskeleton of certain archaic forms (?machaeridians, "carpoids"), or it may be that this radial symmetry is lost or obscured by secondary developments of adaptive character which have affected the organism; one may recognize examples of this in most classes. Despite these variations, the definition above given suffices to constitute a diagnosis for the phylum.

Echinoderms have a structure very unlike that of other zoological groups. Nevertheless, they are by no means an isolated assemblage in the animal kingdom. The **tornaria** larva of Enteropneusta so strikingly resembles the auricularia stage of starfishes and of holothurians that MÜLLER (1850) accepted it as a larval echinoderm. Various workers have suggested that echinoderms are related to the Stomochorda and in lesser degree to the Pogonophora and Chordata. Most modern classifications express such relationships. However, metamorphoses that echinoderms undergo in the course of their ontogenetic development, as well as their general organization, prove that they stand considerably apart from any other phylum. The existence from earliest Cambrian time of types that appear to possess all essential attributes of the group and to represent at least three different classes indicate strongly that their origin belongs to the extremely remote past. One cannot doubt that the echinoderms comprise one of the most ancient and best-individualized invertebrate phyla.

The echinoderms are also one of the most highly diversified phyla, since they include five classes of present-day groups (Crinoidea, Holothuroidea, Echinoidea, Asteroidea, and Ophiuroidea—the last two often combined with Somasteroidea, as a single class, Stelleroidea — and other extinct classes (according to chosen mode of classification), which are restricted to Paleozoic rocks (?Machaeridia, Homostelea, Stylophora, Homoiostelea, Eocrinoidea, Paracrinoidea, Cystoidea, Parablastoidea, Blastoidea, Edrioblastoidea, Edrioasteroidea, Cyclocystoidea, Helicoplacoidea, Ophiocistioidea, Lepidocystoidea, and Camptostromatoidea). All these forms are so different in appearance that, as BATHER has remarked, no commonly used vernacular name is available to indicate them collectively. The term Echinodermata, introduced by J. T. KLEIN in 1734 for application to the test of sea urchins, is a scientific word constructed from two Greek words, *echinos,* hedgehog or urchin, and *derma,* integument or skin; this name is based on the spiny nature of the covering of many of these animals. It was not until 1789, however, that BRUGUIÈRE established the order of the *"Vers èchinodermes"* for the two genera *Echinus* and *Asterias* recognized by LINNÉ, still placing the third genus recognized by LINNÉ, *Holothuria,* under *"Vers mollusques."*[1]

The existence of a generally well-developed calcareous endoskeleton explains the richness of echinoderm remains in all geological systems from the Ordovician onward. Indeed, certain rock formations are largely composed of their remains. Besides this, the close relationship of the echinoderm endoskeleton, which faithfully forms a framework for the body, with other systems of organs provides very special interest for studies of the paleontological records concerning this phylum. Reconstruction of the endoskeleton of a fossil echinoderm commonly serves to give reliable indication of its original form and by appropriate analyses permits recognition in certain measure of its mode of life and biologic relationships.

In the natural world of today, echinoderms are numerous and varied. Exclusively marine and usually stenohaline, they are unknown as primary fossils in fresh-water deposits. Some species occur in such large numbers that they are among the most characteristic organisms of diverse animal populations. Echinoderms are found in all seas, in all latitudes, on all types of sea bottoms, and at all depths from the littoral zone to oceanic abysses. Oceanic expeditions have collected representatives of the phylum, chiefly Holothuroidea, at depths ranging to more than 10,000 meters (Philippines Trench). Almost exclusively, the echinoderms belong to the vagile or sessile benthos; only a few forms—both living and fossil—have become pelagic or pseudoplanktonic. Finally, they enjoy generally an important role in the economy of the ocean, both as consumers of great quantities of other animals and organic detritus and in themselves serving as food sources of various animals, including man.

Inasmuch as outstanding comprehensive reviews of our knowledge of echinoderms have been given recently by CUÉNOT (1948) and HYMAN (1955), the present chapter is confined to subjects that are judged to be particularly significant for understanding of the paleontology of echinoderms.

---

[1] The echinoderms have received many names. The following list, without pretending to be complete, probably contains the main ones: Centroniae PALLAS, 1766; Vers èchinodermes BRUGUIÈRE, 1789; Radiaires èchinodermes LAMARCK, 1801; Cératodermaires DE BLAINVILLE, 1822; Echinoderma LATREILLE, 1825; Echinodermata FLEMING, 1828; Cyclozoa echinoderma *(partim)* EICHWALD, 1829; Echinodermaires DE BLAINVILLE, 1830; Cirrhodermaires DE BLAINVILLE, 1833; Enteractinozoa BRONN, 1860; Annuloida *(partim)* HUXLEY, 1869.

MORPHOLOGY

SIZE, SHAPE, LIFE POSTURE, AND MAIN DIVISIONS OF BODY

The echinoderms are animals of small to large size, but never microscopic. The smallest and the largest of their representatives belong probably to the crinoids: fossil species of crinoids are reported to have possessed stalks longer than 20 meters, whereas others had their visceral mass enclosed in a tiny cup of a few millimeters in diameter.

The body of echinoderms may show a great diversity of shapes. It is spheroidal, discoid, ovoid, or cordiform in echinoids; it is flattened, pentagonal, or more generally star-shaped in stelleroids, with a central disc which either passes progressively into five projections called arms or rays (Asteroidea) or is sharply set off from long, slender flexible arms, simple or branched (Ophiuroidea); it is cucumber-shaped or vermiform and generally capable of considerable changes of shape in holothuroids; it is usually prolonged by a peduncle or stem, and provided with more or less branched arms in crinoids; it resembles a flower bud in blastoids; it is ovoid or spheroidal in most cystoids, discoid in edrioasteroids; it is depressed in "carpoids," with simple contour or, on the contrary, strange, complicated, and very asymmetrical outlines.

Crinoids and most extinct classes are typically attached directly or by a stalk with the face carrying the mouth, termed **oral face**, directed upward and the opposite or **aboral face** turned downward. "Carpoids" were free; most of them rested horizontally on the substratum, with probably their food-catching apparatus and anal opening directed upward. Holothuroids generally lie upon one side that consists of a flattened creeping surface; their mouth is at one end of the body and the anus at the other. Asteroids, ophiuroids, and echinoids move about on their oral surface, which is strongly differentiated from the aboral surface.

Typically, the body of echinoderms is divided into five rays, arms, grooves, or zones that diverge radially or meridionally from the mouth and carry rows of **tentacles** or podia (sing., podion, from Greek, signifying foot) belonging to the water-vascular apparatus. Since the series of podia or **tube feet** are ordinarily arranged like trees along an avenue, sectors of the body bearing these organs have been named **ambulacra** (Latin, sing., **ambulacrum,** signifying promenade bordered by trees). The mid-line of each ambulacrum is termed **radius** (pl., **radii**); it corresponds to the trace of a plane passing through the oral-aboral axis of the body and dividing the ambulacra into two equal parts. Each structure **(ray)** bisected by this plane is indicated as **radial,** or more exactly as **perradial.** In similar manner, the five sectors **(interrays)** comprised between the five ambulacra are termed **interambulacra** and their mid-lines are designated as **interradii**; organs and structures located between two adjacent radii are **interradial.** In all regularly pentamerous echinoderms, an interradius invariably lies opposite to a radius.

SYMMETRY

The subject of symmetry among echinoderms involves much complexity, and study of it calls for consideration of development of this charatcer in the course of ontogeny. The early larval stage of the classes Asteroidea, Ophiuroidea, Echinoidea, and Holothuroidea outwardly exhibits a bilateral symmetry that may be considered fundamental and primitive—that is to say, derived from the common hypothetical ancestor of the phylum. However this symmetry is by no means perfect, for unequal development of the right and left coeloms gives a structural asymmetry to the larva from its beginning, defining one of the dominant traits in morphology of the echinoderms. But this asymmetry, in spite of its early appearance and great morphological importance, is secondary. Reasons for this conclusion will be presented subsequently.

On this asymmetry of the larva, the pentamerously radial symmetry, so characteristic of the phylum, comes to be imposed. Genetically, the latter is therefore secondary. Moreover, it is neither perfect nor complete,

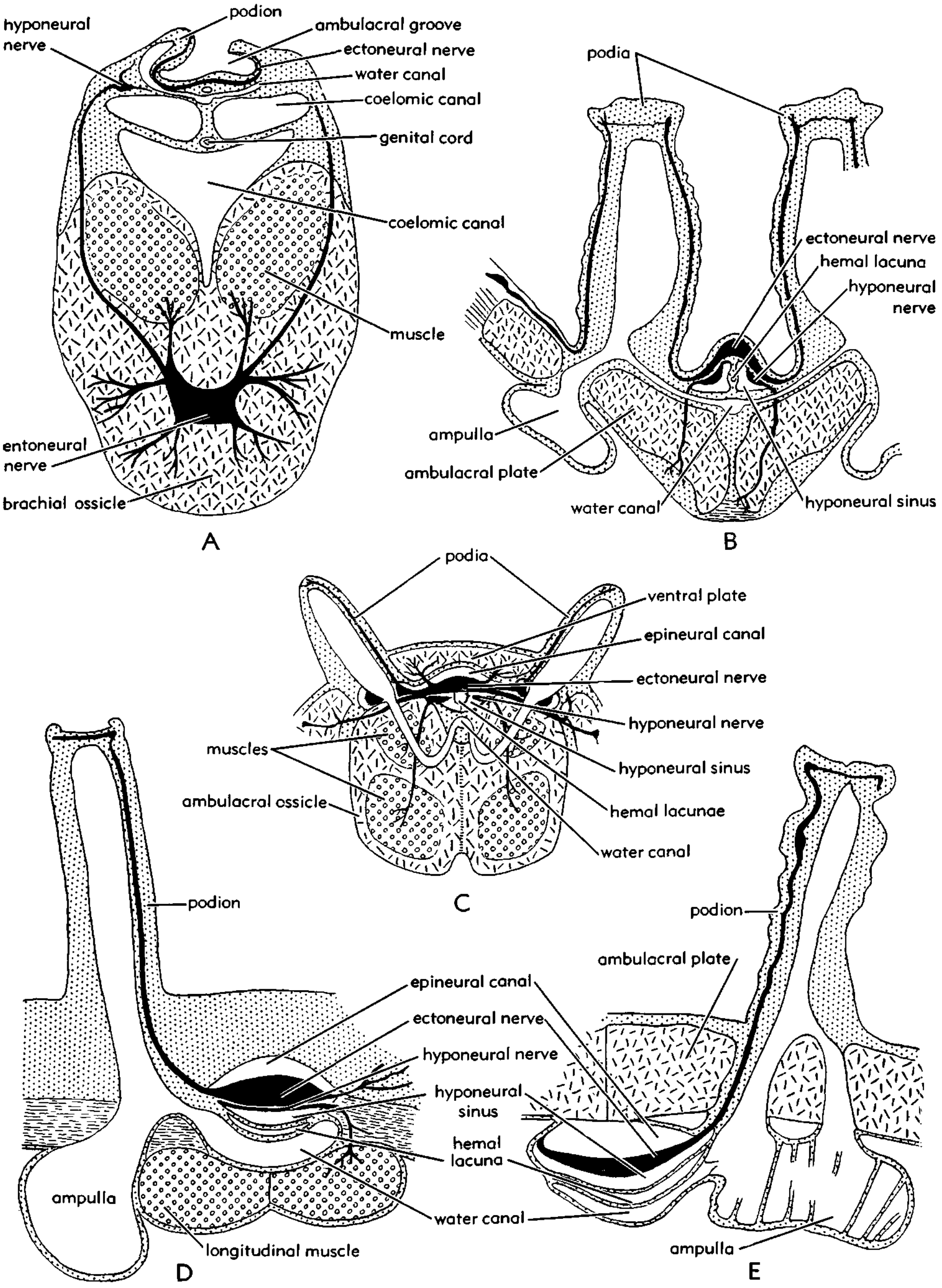

FIG. 1. Comparison of radial structures (sections of ambulacrum) in different echinoderm groups.——*A*. Crinoid.——*B*. Asteroid.——*C*. Ophiuroid.——*D*. Holothuroid.——*E*. Echinoid (Ubaghs, n).

since all echinoderms have organs or structures entirely escaping from any pentaradial arrangement. No trace of radial symmetry is ever found in the endoskeleton of archaic echinoderms such as the "carpoids." Variations of diverse sorts—mutations, atrophies, reduplications of radii—may disturb pentamerism and secondarily produce tetramerous, hexamerous or polymerous forms, as well as others that lack any discernible radial symmetry. Finally, not to be overlooked is the fact that in certain lines a radial symmetry of another order may have been acquired independently.

These alterations, however, do not hinder pentaradial symmetry from comprising one of the most striking traits in the structure of most echinoderms. In the adult, this symmetry is responsible for the remarkably uniform plan manifested in the general disposition of the food grooves, the ectoneural nervous system, the hyponeural coelomic system, the circulatory or hemal (blood) system, the water-vascular system, and the axial endoskeleton of the rays. The parallelism of these structures (Fig. 1), so extremely different in their nature and origin, comprises one of the very prominent features of echinoderm architecture.

Pentaradial symmetry, as we have said, is by no means perfect. It is disturbed by a more or less evident bilateral symmetry, which should be recognized at once as having no relationship to the fundamental bilaterality of the early larval stage. The larva, which undergoes metamorphoses or follows a more or less direct development to the adult stage, tends to acquire a new median plane which does not coincide with that identified previously. Therefore, the definitive bilateral symmetry of the organism is secondary in relation to that of the larva from which it was derived.

Comparison of different types of echinoderms reveals in addition that the bilaterality of adult individuals, when sharply defined, is of adaptive nature and that the plane of symmetry is not always the same in different groups. In certain classes several planes of symmetry may be distinguished, which are unrelated to others; many examples may be observed. We will see also that, within the limits of a single class, a same structure—for instance, the anal opening—may allow recognition of several distinct planes by its diverse positions. It is even true that the organs or parts of the body of certain echinoderms present differently oriented symmetries.

These remarks suffice to show that we may not attribute to bilaterality of echinoderms, such as appears in the adults, any far-reaching morphologic significance. In some respects, choice of a plane for orientation and comparison of classes in the phylum is arbitrary and does not postulate real homologies between the parts that receive the same orientation. For instance, the interambulacrum containing the anus or the **madreporite** (a skeletal perforated plate connecting the water-vascular system with the sea water) is not necessarily homologous throughout the phylum. Yet it is convenient to have some system of reference allowing comparison between the classes. The plane passing through the oral-aboral axis and the madreporite (or better the **hydropore** in very young echinoderms, i.e., the primary pore connecting the water-vascular system with sea water through the medium of the most anterior coelomic pouches on the left side) may furnish such a reference. This plane is designated as the **madreporite plane** or **M plane** of BATHER (Fig. 2,*2-6*). According to the nomenclature proposed by P. H. CARPENTER (1884) (Fig. 2,*1*), the ray opposite to the interray containing the hydropore is designated by the letter *A*, the other rays being then indicated by *B, C, D, E,* in clockwise direction when the animal is placed with its mouth upward. The interrays are designated by the letters of rays that bound them *(AB, BC, CD, DE, EA)*. The hydropore in the postlarval growth stages occurs in interray *CD*, as generally does also the madreporite in the adult.[1]

---

[1] Other systems of nomenclature for rays and interrays have been proposed. Echinoid specialists commonly use a numeration proposed by LOVÉN (1874), based on the antero-posterior plane of irregular echinoids. Starting from the interambulcrum containing the anus and going in clockwise direction in oral view, they designate the ambulacra by roman numerals *I* to *V* and the interambulacra by arabic numerals *1* to *5* or by listing the adjoining ambulacra (Fig. 2,*6*). Thus the interambulacrum following ambulacrum I in clockwise direction is designated as *1* or *I-II*. Generally it is admitted that ambulacrum *I* in echinoids corresponds to ambulacrum *B* of CARPENTER's system, but FELL & MOORE (1965) correlate *I* with *D* for reasons which are given in Part U of the *Treatise*. The same symbols have been employed by JAEKEL (1895) and some other specialists for attached echinoderms, but taking as a reference the interambulacrum containing the hydropore and gonopore. As a consequence, ambulacrum *I* of JAEKEL's system becomes

ambulacrum *D* in CARPENTER's system. Finally, BATHER (1900) proposed directional terms that have been commonly adopted by workers on fossil crinoids and other attached forms. The organism is placed in its natural position with mouth upwards and is viewed from the anal side; the anal interambulacrum is called **posterior** and the opposite ambulacrum **anterior**; right and left corresponds with the right and left of the observer; the other rays (or interrays) are then termed **right anterior**, **right posterior**, **left anterior** and **left posterior**; compared with CARPENTER's system, anterior ray corresponds to *A* ray and posterior interray to *CD* interray.

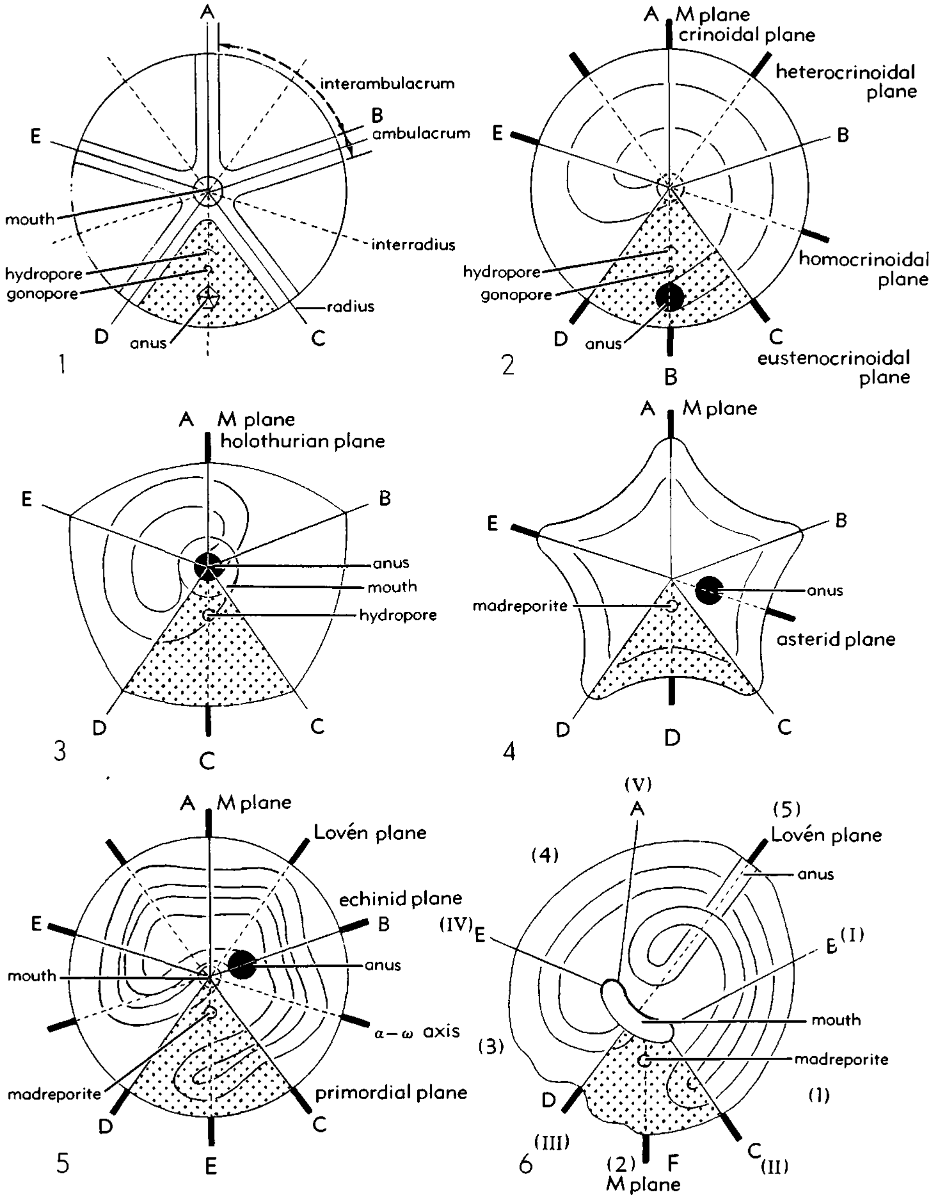

FIG. 2. Disposition of rays in relation to other structure in different echinoderm groups, all viewed from oral side (Ubaghs, n).——*1*. Orientation of generalized echinoderm according to nomenclature of rays proposed by P. H. CARPENTER. ——*2-6*. Various planes of symmetry observed in *(2)* crinoids and other attached radiate forms, *(3)* holothuroids, *(4)* asteroids, *(5)* regular echinoids, and *(6)* irregular echinoids (with LOVÉN's numerical designations in parentheses). [Explanation: Dotted area shows interambulacrum containing hydropore or madreporite.]

Among most crinoids and many other attached echinoderms a prominent plane of bilateral symmetry is typically determined by the mouth, anus, hydropore (if present) and the apical pole. This is the plane, called **crinoidal plane** (CUÉNOT, 1948) (Fig. 2,*2*), which in modern crinoids contains the first pore for passage of water and the first embryonic indication of the gonad. It is also in this plane, or immediately adjacent to it that among many cystoids, edrioasteroids, and archaic crinoids, one or two supplementary pores open; these are respectively interpreted as hydropore or gonopore, or a combination of both. The crinoidal plane thus coincides with the madreporite plane as defined above.

Other more or less evident planes of bilateral symmetry may exist among attached echinoderms. Thus the crown of some disparid crinoids tends to become more or less symmetrical in relation to a plane passing through the *E* ray and *BC* interray **(homocrinoidal plane)** or through the *D* ray and *AB* interray **(heterocrinoidal plane)** or through *C* ray and *AE* interray **(eustenocrinoidal plane)** (Fig. 2,*2*). The mouth of certain comasteroid crinoids is displaced toward the *AB* interray, accompanied by modification of the opposite *D* ray. Among cystoids and eocrinoids, the anus may be shifted so as to open in an interray (*AB* or *BC*) other than that characterized by the occurrence of a hydropore; this then determines an anal plane distinct from that of the crinoidal plane. Finally, the basal circlet of the theca commonly presents a local bilateral symmetry in which the plane may not coincide with the bilaterality of the remainder of the body.

In holothuroids, the body, elongated along the oral-aboral axis, is generally differentiated into a "ventral" flattened surface, on which the animal creeps, and an opposite arched "dorsal" surface (Fig. 2,*3*). The *A, B,* and *E* rays, forming the trivium, occupy the "ventral" surface; the *C* and *D* rays comprise the bivium on the "dorsal" surface. The median ambulacrum *(A)* of the trivium and the opposed mid-dorsal line clearly define a plane of symmetry known as the **holothurian plane** (CUÉNOT, 1891). This plane passes through the external orifice (gonopore) of the single genital gland, the "dorsal" mesentery in which the gonad is included and among forms retaining it in the adult stage, through the hydropore or madreporite. It is therefore considered as probably equivalent to the crinoidal plane and madreporite plane.

Several planes of bilateral symmetry have been recognized in echinoids. The madreporite plane seems generally to be identifiable by the eccentric position of the madreporite which mostly occurs in the *CD* interray (in irregular echinoids, it may migrate during early development into the *AB* interray, but this is of course a secondary feature). On the other hand, in most echinoids, the anus does not open exactly at the aboral pole; rather, it is found in the *B* ray or *AB* interray. These two positions permit determination of two anal planes. The first, known among some Regularia *(Salenia, Heterosalenia),* defines a **salenian plane** (CUÉNOT, 1948), also known as the **echinid plane** (CUÉNOT, 1891), passing through the *B* ray and *DE* interray so as to make an angle of 72 degrees with the madreporite plane (Fig. 2,*5*). The second determines the appearance of another anal plane oriented in the *D* ray and *AB* interray; the angle made by this plane with the madreporite plane is then 36 degrees. CUÉNOT (1891) has designated this as the **Lovén plane** (Fig. 2,*5,6*). It is recognized as having chief importance for orientation of echinoids. In particular, the bilateral symmetry so clearly manifested exteriorly and interiorly in numerous irregular echinoids (clypeasteroids, spatangoids) is developed in relation to this plane; their body tends to show differentiated functional anterior and posterior extremities and their ambulacra are divided into a trivium *(C, D, E)* and a bivium *(A, B),* which, according to adopted premises, are different from the trivium and bivium of holothuroids. As applied to sea urchins, the Lovén plane takes precedence over all others in its relation to organization of these echinoderms.

During ontogeny, however, in both regular and irregular echinoids, the newly metamorphosed urchin shows a bilateral arrangement of the plates of the apical system according to a plane corresponding neither with the madreporite plane nor the Lovén plane. Similarly, on the oral side, the skeletal and water-vascular systems appear more symmetrical with respect to this plane than to all others. Called **primordial plane** by von Übisch (1913), it makes an angle of 90° with the plane of symmetry of the larva and passes through the *C* ray and *EA* interray (Fig. 2,5). During further growth, all morphological trace of this symmetry is lost, except nearly always in the crystallographic orientation of the genital plates that encircle the aboral pole (Raup, 1965).

Lovén (1874) in discussing the morphology of echinoids has pointed out the existence of a distinctive axis (designated α-ω) passing through the *E* ray and *BC* interray (Fig. 2,5).

Among Asteroidea, the madreporite, located on the aboral side of the body in the adult, defines the *CD* interray, but the anus in all species possessing this vent opens more or less excentrically in the *BC* interray on the aboral side. One then may define an anal plane (**asterid plane** of Cuénot, 1891) which is distinct from the madreporite plane, making an angle of 72 degrees with it. But, as Asteroidea are almost perfectly radiate animals, these two planes have practically no morphological significance.

Among ophiuroids, one of the interradially situated plates (buccal or oral shield) covering the jaws acts as a madreporite, being pierced usually by a single pore. As this pore, however, cannot generally be recognized on the outer side, orientation is hardly determinable externally.

Finally, the presence in an interray of certain ophiocistioids of a madreporite or a pore interpreted as a hydropore and gonopore, or a combination of these two, allows orientation of these echinoderms according to the madreporite plane. An anal vent occurs in the same interray on the aboral side of at least one genus.

The preceding discussion leads to the following conclusions: 1) fundamental bilateral symmetry of the larva, disturbed by asymmetric development of the anterior right and left halves of the body, cannot be identified in adults; 2) pentamerously radial symmetry is secondary and superposed on the larval asymmetry; 3) bilaterality determined in young postmetamorphic individuals (and *a fortiori* in adults) by the hydropore, madreporite, anus, or any other structure is secondary with respect to fundamental larval symmetry; 4) the selection of any one plane as a plane of reference for orientation of all the classes is more or less arbitrary, and homologies based on such comparisons are judged as not being proven; 5) varied influences may produce bilateral symmetries of a third order, which in some species acquire a great importance and even may obscure other symmetries.

BODY WALL

The body wall of all echinoderms comprises three layers; an **external epithelium** or **epidermis,** a thick **median layer (conjunctive, muscular,** or **calcareous)** and an **internal epithelium (endothelium** or **peritoneum)** lining the coelomic cavities.

The external epithelium, generally covered by a very thin superficial cuticle, exhibits a rather variable organization with respect to its place of occurrence and the form considered. It may be relatively thick, formed of long, narrow, nearly threadlike cells, among which commonly neurosensory cells and glandular mucus cells are intermixed. On the other hand, it may be extremely thin, showing no definite cellular organization, and it may even disappear in adults of certain forms and in certain parts of the body. Locally, or over its entire surface, it may possess a covering of cilia producing vibratile currents capable of carrying particles toward the mouth or food grooves, or, on the other hand, toward the exterior; these currents play an important role in nutrition and in cleaning the test, as well as in respiration probably. At the base of the epithelium and more or less clearly differentiated from it, is a nervous stratum of variable thickness that forms part of the ectoneural nervous system. The external epithelium continues into the median layer, or more rarely it is found separated from it by a delicate basal membrane.

The median layer, as we have noted, consists of muscular tissues, conjunctive noncalcified **(mesenchyme)** tissues, and calcareous tissues.

(1) **Muscle fiber,** produced by differentiation of a single mesodermic cell, displays

the same characters in all classes. It is smooth, straight, or faintly wavy, sharply terminated at its extremities, and provided with a lateral nucleus. Striated muscle fibers have been distinguished among a certain number of echinoids. In the body wall, the musculature occurs under the dermis; it is well developed among holothuroids, which have a readily deformable body, but hardly perceptible among echinoids, enclosed by a rigid endoskeleton. Crinoids possess a special tissue designated as ligamentary, between the skeletal plates. It has a connective function and is shown to be formed of parallel hyaline nucleated fibers that intermingle at their two extremities with the organic network of skeletal ossicles; this tissue, probably elastic, seems to have some contractile ability.

(2) **Noncalcified mesenchyme** is composed of a fundamentally noncellular substance, amorphous or fibrillar, gelatinous or more or less firm, with disseminated, rounded or star-shaped connective cells and enclosing numerous nucleated fibers.

(3) **Calcareous tissue,** found in all echinoderms, except a few holothurians, is one of the most important features of the phylum. Its histologic constitution and crystallographic properties serve to establish the unity of the group and allow identification under the microscope of the smallest skeletal fragment.

Universally, where mesoderm exists in the body, but especially in the body wall itself, certain of its cells have the ability to secrete calcium carbonate. As a result, a skeleton is produced and this consequently is an endoskeleton. The endoskeleton, generally well developed, is composed of plates, ossicles, spicules, microscopic pieces, and integumentary appendages such as spines. It is to be understood that in life the external appendages, like the main skeleton, are clothed with epidermis and a thin layer of dermis, although this covering may rub off from prominently projecting parts.

The plates and ossicles of the main skeleton generally bear spines, knobs, granules or other projections. Particularly important are the spines to which the name of the phylum refers. Among the extant forms they occur in asteroids, ophiuroids, and echinoids, but they were also present in at least some species of most extinct groups. They are of various shapes and structures, and they have many functions, such as protection, locomotion, digging, burrow-building, production of currents, and brooding the young. Detailed descriptions will be found in chapters devoted to the different classes.

Worthy of special mention are the **pedicellariae,** which are tiny, grasping organs of various sorts, found only in starfishes and sea urchins. Typically they consist of two or several jaws, articulated proximally, and mounted on a movable stalk of varied length; the jaws and at least in part the stalk are supported by internal calcareous pieces. According to their types, they act as defense weapons or cleansing organs and they assist in capturing small prey.

Throughout its entire thickness the calcareous tissue consists of a spongy or reticulated mass. Exceptions to this fundamental rule include nonreticulate spicules, described from most extant classes, and the teeth of echinoids, formed by fusion of a series of nested cones. During life, all of the pores and small canals of the mineralized parts are filled up with mesodermic tissue. This is easily demonstrated by decalcifying a skeletal piece of a living echinoderm; the decalcification produces an organic residue pierced by holes that correspond to the calcareous elements removed by the acid. Thus the skeleton of echinoderms is composed of two interlocked networks, one composed of mineral substance **(stereom)** and the other of organic matter **(stroma).** While the stroma is continuous throughout the body wall, the stereom, comprising distinct skeletal pieces, is discontinuous.

The stroma may occupy as much as 60 percent of the volume of a particular skeletal element. It generally consists of an essentially amorphous material, less commonly fibrillar, with numerous interspersed mesodermic cells and in some instances black pigments and excreted granules. Permeable to nutritive fluids, it serves for nutrition of the calcareous network, repairing it when damaged and restoring it when a skeletal part has been lost. This intimate relation between stroma and stereom explains how the skeletal pieces enlarge during development of individuals and how the parts remain alive throughout the animal's

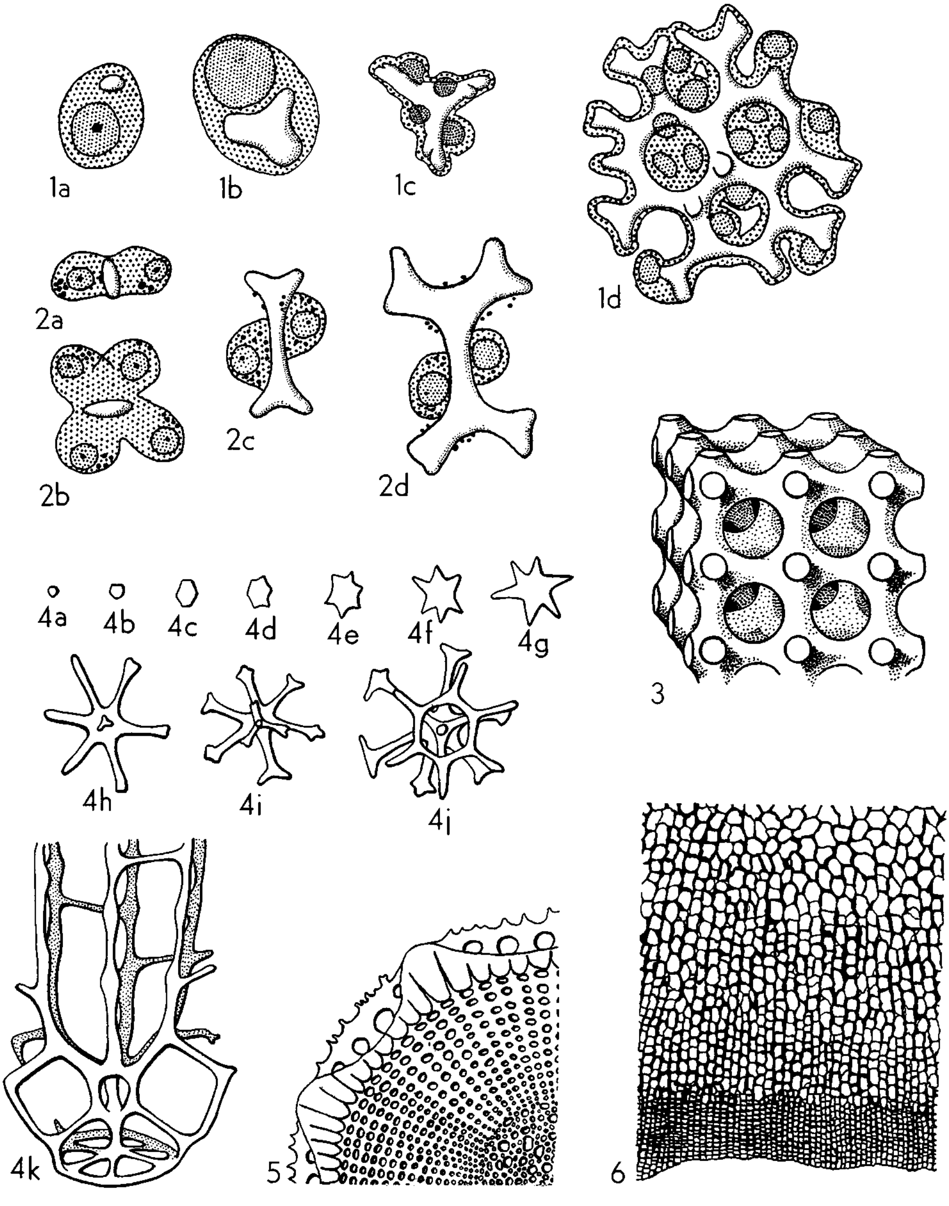

Fig. 3. Formation and biologic structure of echinoderm endoskeleton.——*1a-d*. Stages in development of plate of young ophiuroid, *Amphipholis squamata* (Chiaje); *1a,b*, ×1,280; *1c,d*, ×640 (Woodland).——*2a-d*. Stages in development of ossicles of *Cucumaria* sp. (holothuroid), ×750 (Woodland).——*3*. Regular stereom in cup plate of *Holopus rangi* d'Orbigny (crinoid), ×55 (P. H. Carpenter).——*4a-k*. Formation of typical echinoid spine, ×800 (Gordon).——*5*. Part of cross section of spine of *Stereocidaris japonica* (Döderlein) (echinoid), ×40 (Mortensen).——*6*. Closely set and less compact stereom in cidaroid spine, ×30 (Bather).

existence. Commonly they show growth lines which may demonstrate peripheral excretion of calcium carbonate without requiring, as wrongly supposed by some, an internal resorption. On the other hand, in some echinoderms, the lime-producing cells also have the power of resorbing and redepositing calcium carbonate so that the form and structure of the skeletal changes with growth of the animal. Finally, stereom and stroma are adapted to functions of particular skeletal elements; their network structure varies in different parts of an individual (Fig. 3,*5,6*), as well as from one species to another. These variations are related to the dimensions, form, and mode of grouping of meshes in the network. In addition, the existence of isostatic lines of stress may simulate conditions seen in the spongy bones of mammals.

The endoskeleton is secreted by lime-secreting cells of the mesenchyme (Fig. 3, *1a-d*). Each reticulate element is initiated by forming a calcareous granule on the inside of a single cell, the granule becoming transformed rapidly into a trifid spicule. This spicule enlarges and bifurcates at its extremities, while other lime-depositing cells join in making the secretion. The bifurcations fuse at their points of contact so as to form a fenestrated small plate. This increases along all of its periphery by the production and fusion of numerous branches, developed in all special directions. Thus, from repeated branchings and fusions is developed a three-dimensional network of more or less regular nature (Fig. 3,*3*) in which the meshes include calcite-producing cells joined in a syncytium.

In most holothuroids, the main endoskeleton consists of microscopic calcareous spicules scattered in the connective tissues, chiefly in the superficial layers of the dermis. A compact skeleton, with stereom and stroma, as in other echinoderms, is to be found only in a ring of plates encircling the pharynx, in the madreporite and in five small "teeth" occurring in some genera around the anus or within its rim. The spicules occur in a great variety of shapes (rods, crosses, plates, anchors, wheels) and are useful in identifying species. Generally an holothurian spicule begins as a minute rod between two or more secreting cells. The rod takes an X-shape by forking of its extremities, and repeated forkings and fusion of the branches result in production of a fenestrated plate, which subsequently is variously transformed into definite ossicles (Fig. 3,*2a-d*). The primordial rod of an anchor forks at one end only and the wheel-like spicules start as minute discs on which the spokes differentiate by notching of the margins. The lime-secreting cells that have produced a spicule then migrate and the spicule remains isolated in the soft tissues.

Spines are formed (Fig. 3,*4a-k*) somewhat differently from plates and spicules. In a typical echinoid spine, for instance, the primordial granule develops into a six-rayed star, the branches of which divide at their extremity, meet those of neighboring rays and thus form a complete ring that constitutes the base of the spine. A process grows vertically from the center of the star and gives rise to three branches which grow outward and upward, divide at their free end, and fuse to form a hexagonal ring more or less parallel to the base. From this ring vertical prongs are sent out which are joined by cross bars at more or less regular intervals and the whole structure elaborates to form the spine shaft. Spines in asteroids originate in about the same way.

The chemical composition of the endoskeleton of living echinoderms, as determined by studies of Clarke & Wheeler (1922), is that of a limestone (71 to 95 percent calcium carbonate) having a moderate content of magnesium carbonate in ionic substitution. The proportion of magnesium carbonate (3 to 15 percent) seems mainly to be determined as a function of the temperature, individuals of warm seas being more magnesian than those of cold seas. Generally present, in addition, are small quantities of phosphate and calcium sulfate, salts of alumina, and iron, as well as traces of strontium, barium, copper, zinc, manganese, cobalt, nickel, cadmium, and some other elements.

Each unit part of the skeleton of every echinoderm comprises a single crystal of calcite. This rule seems to have only a few isolated exceptions and is supported by all optical evidence. However, X-ray data suggest that each skeletal element is actually a composite of tiny crystal units, which are nearly parallel in the *c* direction. In that case, the optical measurements would represent orientations of large crystal aggregates (Garrido & Blanco, 1947; Nissen, 1963; Raup, 1965).

In the living organism, the stereom does not show the characteristic cleavages of the calcite, because of its latticed structure and the presence, in the meshes of the calcareous network, of the organic stroma. But, after fossilization, the stroma generally is replaced by secondary calcite, which invariably is oriented crystallographically with the calcite of the skeleton and thus makes evident its cleavages. Fossilization does not modify the original orientation of the calcite unless the mineral was completely dissolved and reprecipitated.

The crystallography of echinoderm calcite has been mainly studied by Kirchner (1929) on crinoids, Schmidt (1925) and Panning (1933) on holothuroids, Merker (1916), Schultz (1935), and Raup (1959, 1960, 1962) on echinoids. The crystallographic orienttaion seems to be more varied than was formerly supposed. For instance in echinoids, recent studies by Raup have revealed that most species conform to one or two types, according to orientation of the *c* axes of the coronal plates, the *c* axes being either uniformly perpendicular to the plate surface or tangential to the plate surface and aligned longitudinally (aboro-adorally) on the test. Exceptions are found in some cidaroid genera in which ambulacral plates have perpendicular *c* axes and interambulacral plates have tangential *c* axes, whereas in other forms the orientation is modified as a function of growth of the individual, since it may pass, for instance, from perpendicular in the first-formed ambulacral plates (located near the oral pole in the adult) to tangential in the youngest ambulacral plates (near the aboral pole) within the limits of a single column of an adult individual. According to present knowledge, such *c*-axes orientation patterns are constant at the species and genus levels, mostly also at the family and even order levels.

Also, in the apical system of sea urchins, distribution of crystal orientations shows a strong bilateral symmetry, which nearly always is identical with the primordial plane of von Übisch (Lucas, 1953; Jesionek-Syzmanska, 1959; Raup, 1965).

The functional significance of these crystallographic data is not understood. It has been suggested that crystal orientation of the coronal plates of echinoids may be useful in building curved plates (Raup, 1962) or in controlling the amount of light that can pass through the test (Raup, 1959, 1962). In the echinoid apical system, the arrangement of *c* axes may serve the organism as a navigational aid (Raup, 1965).

The skeletal tissue of echinoderms often has been compared with the bones of vertebrates. Assuredly there are analogies between them, but only analogies, for the stereom of echinoderms differs from bone in three essential characters, (1) its typically calcareous, nonphosphatic chemical composition, (2) the intracellular, rather than extracellular, formation of spicules, and (3) its very characteristic crystalline properties.

NERVOUS SYSTEM

The five classes of living echinoderms show a common pattern in the gross morphology of their nervous system. This is somewhat artificially described as composed of three related systems, namely the **ectoneural, hyponeural,** and **entoneural** systems, located at different levels within the body; all three are affected by radiate symmetry.

ECTONEURAL SYSTEM

The **ectoneural** or **oral system** consists of a subepithelial nerve plexus, and five radial cords united around the esophagus by a nerve ring. The subepithelial, mainly sensory, nerve plexus lies just beneath the epidermis of almost the whole body. It may thicken locally, where special activity is required, as, for instance, at the tip of some tube feet or at the base of echinoid spines. Among crinoids (Fig. 1,*A*) and asteroids (Fig. 1,*B*) the five radial cords and the ring around the esophagus have a superficial place immediately under the epidermis and they are in direct continuity with the general subepithelial plexus. Among ophiuroids (Fig. 1,*C*), holothuroids (Fig. 1,*D*), and echinoids (Fig. 1,*E*), they underlie a tubular noncoelomic cavity **(epineural**

canal). As in crinoids and asteroids, the radial nerves of ophiuroids, holothuroids, and echinoids are still joined to the subepithelial plexus of the body wall by connecting branches. In all living representatives, the nerve ring around the esophagus gives off nerves into the digestive system and into buccal podia (ophiuroids) or tentacles (holothuroids) where such structures exist.

HYPONEURAL SYSTEM

The **hyponeural** or **deep oral system,** primarily motor in function, lies aborally to the preceding. It is found among all extant echinoderms except echinoids that lack a masticatory apparatus. In crinoids, it consists of a ring round the esophagus and two longitudinal nerves, lying laterally, in each arm (Fig. 1,*A*); these branches supply the musculature of the water vessels, pinnules, etc. In holothuroids (Fig. 1,*D*) each radial nerve cord is divided by a longitudinal partition into an outer (ectoneural) and an inner (hyponeural) part, the latter supplying muscle fibers of the body wall; there is no hyponeural nervous ring. Among asteroids (Fig. 1,*B*), the hyponeural system is represented by paired nerves **(Lange's nerves)** lying internal to the ectoneural radial cord, and by five interradial thickenings in the floor of the ring sinus that lies aboral to the main nerve ring; the Lange's nerves supply the lower transverse muscles between the ambulacral ossicles. Among ophiuroids (Fig. 1,*C*), a thin membrane separates an outer thick ectoneural and an inner thin hyponeural system in the nerve ring and in radial nerves; it is from the hyponeural system that the nerves to the muscles that extend between the ambulacral ossicles are given off. Finally, the hyponeural system is represented in echinoids having a masticatory apparatus by five centers radially located on the aboral surface of the main ring; these centers send nerves to the muscles activating the masticatory apparatus.

ENTONEURAL SYSTEM

The **entoneural** or **aboral system** is the main motor system in crinoids. It is joined to an apical ganglionic nervous mass surrounding a coelomic cavity divided into five chambers (chambered organ); this nervous mass presents the characters and functions of a nerve center; from it a nervous sheath proceeds into the axial canal of the stem and axial nerve cords are given off to the arms; these cords are connected with each other by ring commissures within the theca that envelopes the viscera. Except for holothuroids, an entoneural system exists also in the other classes, but it is not known whether this is exactly equivalent to that of the crinoids. Moreover, it is more or less continuous with the hyponeural nervous system.

The echinoderms possess few sharply defined sensory organs. However, they are known to be sensitive to touch, to light, to odors, to quality of the water, and to orientation. Tactile sensibility is furnished by the podia, radioles, pedicellaria (or microscopic claws of echinoids and asteroids) and by the integuments themselves, often rich in cells considered as touch or chemical receptors. Light-sensitive receptors exist in holothuroids, asteroids, and echinoids. Certain holothuroids have statocysts and the sphaeridia of echinoids possibly serve for orientation of these organisms.

DIGESTIVE SYSTEM

Mouth and anus of nonradiate echinoderms are located at or near opposite extremities of the body in Stylophora and Homoiostelea, but they are near each other at the same end in Homostelea.

In radiate echinoderms, the mouth invariably is found in the oral surface and generally at its center, at the point of convergence and ending of the ambulacra. It is secondarily displaced from the center along the *A* radius or toward the *AB* interray in certain crinoids and forward along the *D* radius in spatangoid echinoids. It opens directly to the exterior, but in numerous Paleozoic fixed echinoderms it may become secondarily internal by development of a tegumentary ceiling.

The anus has a much more variable position. It is never located at the aboral pole in fixed forms, but generally is found in the upper or adoral half in the *CD* interrays, typically located laterally in cystoids, blastoids, eocrinoids, and paracrinoids, and on the oral face in crinoids and edrioasteroids; among crinoids it may occur secondarily at the center of the oral face, whereas it migrates toward the *BC* interray or *AB* interray among a few cystoids and eocrinoids. It opens at or near the aboral pole in holothuroids and some regu-

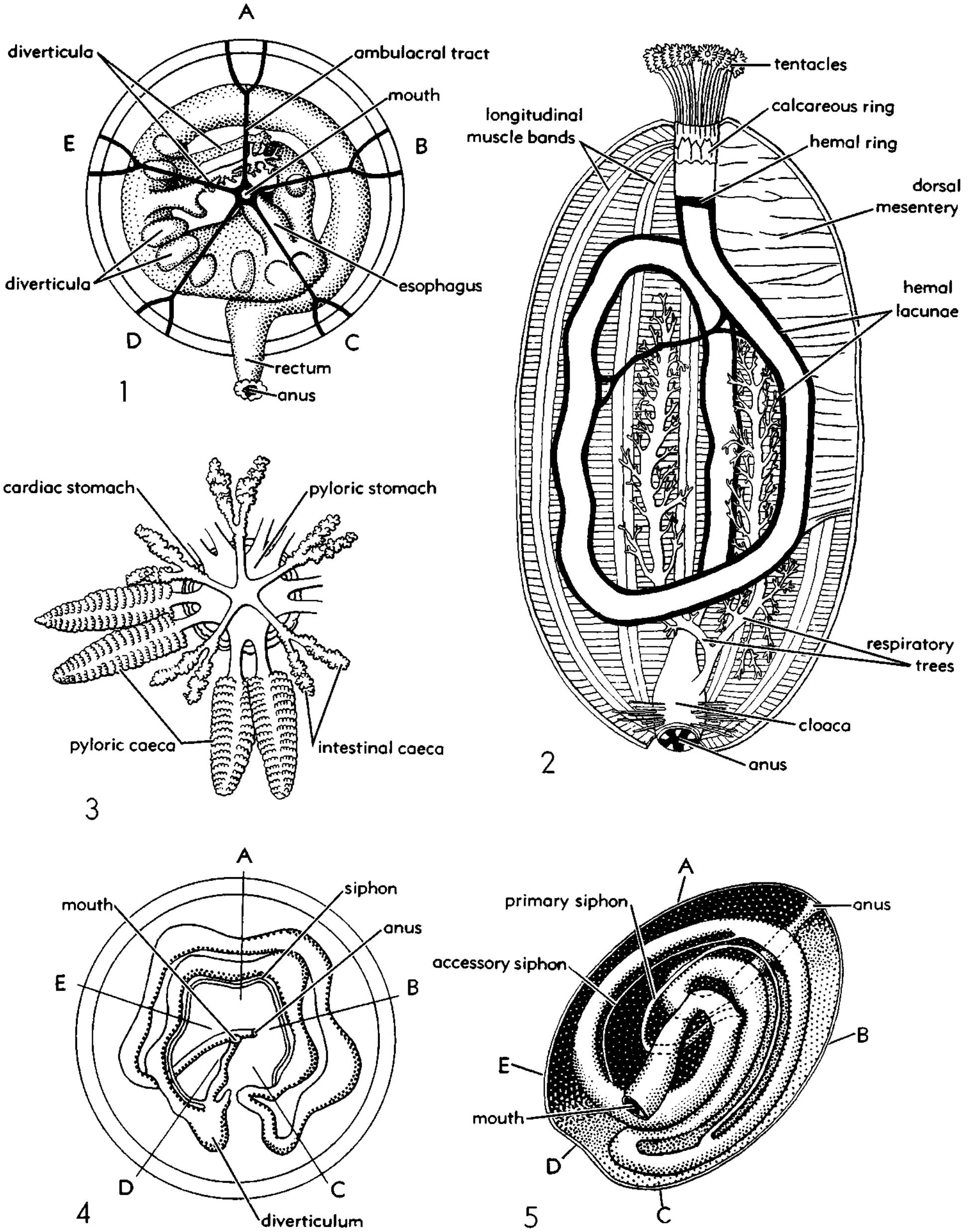

FIG. 4. Digestive systems of echinoderms.——*1.* Crinoid *(Antedon),* showing many diverticula (Chadwick).——*2.* Holothuroid, with respiratory trees and hemal system (main lacunae, solid black) (Ludwig).——*3.* Asteroid *(Culcita)* (Hamann & Ludwig).——*4.* Regular echinoid *(Echinus)* (Cuénot).——*5.* Irregular echinoid *(Brissus)* (Cuénot). [Orientation according to P. H. CARPENTER's nomenclature, except *2* and *3.*]

lar echinoids. It is aboral but somewhat excentric in other regular echinoids (*E* ray or *AB* interray) and most asteroids (*BC* interray). In a few ophiocistioids where it is known, it is aboral, located near the margin or at mid-distance between center and margin. It is lateral or on the oral side in irregular echinoids and invariably in the *AB* interray. It is lacking in somasteroids, ophiuroids, and certain asteroids which discharge excrements through the mouth.

The digestive tract consists of a more or less elongate tube, spirally enrolled in a clockwise direction (the organism presenting its oral face to the observer) in attached echinoderms, holothuroids, and very young echinoids. In adult echinoids, it is extended and this extension more or less masks the preceding arrangement. The stelleroids have a short straight digestive tube with a pronounced stomach enlargement, subdivided in asteroids by a horizontal constriction into two portions.

The digestive tube is differentiated more or less clearly into an esophagus, stomach, intestine, and rectum. It is modified by adjoined appendices that perform particular functions or simply augment secreting surfaces: diverticula of crinoids (Fig. 4,*1*); gastric brachial caeca of asteroids, somasteroids, and the ophiuroid *Ophiocanops* (Fig. 4,*3*); diverticulum and siphons in many echinoids (Fig. 4,*4*,*5*); and respiratory trees of holothuroids (Fig. 4,*2*). In general, cords or mesenterial bands composed of two peritoneal layers attach the digestive tube to the body wall; but, although present in the embryo, they are generally more or less lacking in adults.

COELOM

The general cavity of echinoderms of coelomic origin forms a large free space, except in crinoids, where it is secondarily filled by strands and membranes of connective tissue.

This cavity, carpeted by peritoneum, encloses the principal organs of the body, especially the digestive tube and the gonads (except in living crinoids where the gonads have migrated to the arms, or more generally their appendages, the pinnules). It extends broadly into the arms of asteroids, narrowly into those of ophiuroids, and by four canals into those of crinoids. It is traversed by mesenteries or strings diversely placed between the viscera and walls. Partitioning may serve partly or completely to isolate small compartments, such, for example, as the **perivisceral spaces** and cavities of the chambered organ in crinoids, the **peripharyngeal sinus** of echinoids and holothuroids, the **periesophageal sinus** of asteroids and ophiuroids, the **periproctal sinus** of echinoids, the **perianal sinus** of echinoids and holothuroids, and the **aboral** or **genital sinus** in the form of a pentagon ring in asteroids, ophiuroids, and echinoids, which furnishes for each gonad a genital branch.

The general cavity is by no means the only one that may be of coelomic origin. Likewise derived from the coelom, as proved from their development and the fact that they are lined by peritoneum, are the **axial sinus,** the **hyponeural sinuses,** the **madreporic vesicle,** and the **water-vascular system.** Because of its importance, this last will be discussed in a special section.

The **axial sinus** of crinoids comprises a vertical space enclosed by the ring of the digestive tube and surrounding the esophagus orally. Also, it contains a characteristic elongated organ, the **axial gland,** to be described presently. Some authors report that in holothuroids the axial sinus disappears during ontogeny, whereas in echinoids it is lacking entirely. Among asteroids (Fig. 5,*1*,*2*) and ophiuroids, it contains, in addition to the axial gland, an essential component of the water-vascular system known as the **stone canal**; thus in stelleroids it comprises a complex of cavities and organs, the **axial complex,** enclosed in an interbrachial septum of the *CD* interray or intimately joined to it. At its aboral extremity the axial sinus communicates with the ampulla of the stone canal, located on the internal face of the madreporite, and it ends in the genital or aboral sinus already mentioned. At its oral extremity, it opens into a large **circumoral ringlike sinus** that lies on the aboral side of the nerve ring surrounding the mouth. In asteroids this sinus is divided by an oblique partition into internal and external rings. The axial sinus opens into the internal ring, which thus appears as an extension of the axial coelom.

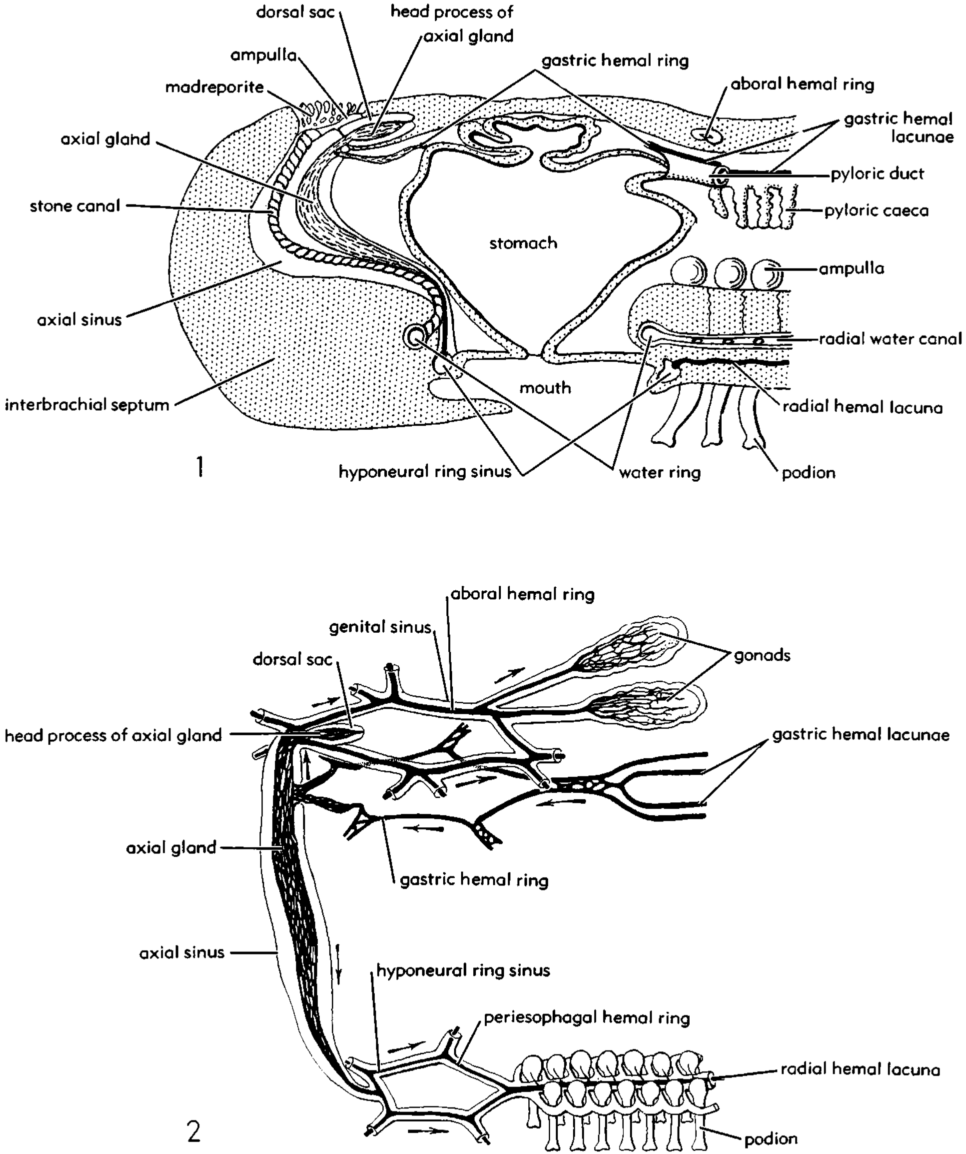

FIG. 5. Axial complex, hyponeural, and hemal systems in asteroid (Ubaghs, n).——*1.* Sagittal section through *CD* (left) interray and *A* ray (mod. from Cuénot).——*2.* Scheme of axial complex, hyponeural and hemal systems.

The **hyponeural sinuses (hyponeural sinus system)** consist of a group of tubular cavities forming typically and essentially, a **circumoral sinus,** from which lead five **radial sinuses** located on the aboral face of the five radial nerve cords (ectoneural) (Fig. 5). These radial sinuses may give off transverse branches that penetrate the podia. The ensemble of tubes has often been considered as constituting a second circulatory system designated **perihemal** (also **pseudohemal** or **perilacunar**), because tubules of this sinus system encloses distributional lacunae of the hemal system or are closely

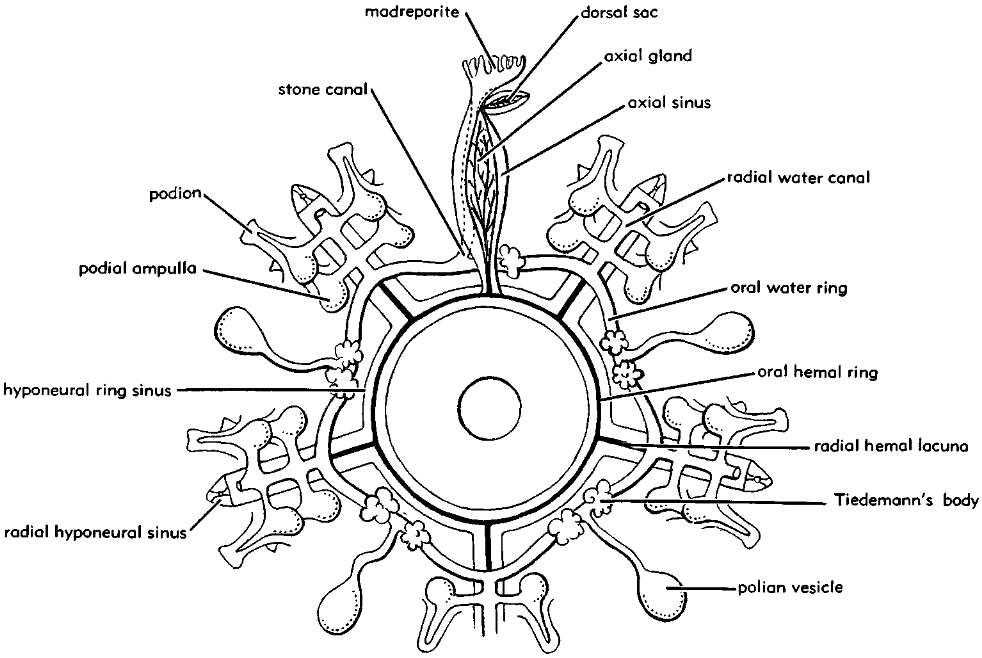

Fig. 6. Organization of water-vascular, hemal, and hyponeural-sinus systems in asteroid (diagram.) (Ubaghs, n).

associated with them. In reality, between the entire hyponeural sinus system, which is of coelomic nature, and the hemal (blood) circulatory system, formed of spaces developed in the mesenchyme, there exists only a simple physiologic analogy resulting from the fact that the hyponeural sinuses, like all coelomic cavities, contribute somewhat to the functions of nutrition, respiration, and excretion of the tissues.

The **madreporic vesicle** or **dorsal sac** of echinoids, asteroids (Fig. 6), and ophiuroids envelops the aboral part of the axial organ already mentioned. We shall refer to it again in later discussion.

The coelomic cavities are carpeted by an endothelium which ordinarily is ciliated. In the liquid contained by the cavities are numerous free cells or **coelomocytes,** classifiable according to morphologic types and varied functions; they are amoebocytes, capable of wandering through all the tissues and acting as carriers of food, as calcigenous cells, as phagocytes, and as bearers of waste products. Hemocytes (red nucleated globules with hemoglobin) exist in holothuroids.

WATER-VASCULAR SYSTEM

The **water-vascular** or **ambulacral system** is one of the most characteristic features of echinoderms. It essentially represents a hydraulic mechanism and consists of an assemblage of canals, which we have seen are part of the coelom. The system includes the following structures: 1) **oral water ring** with the **polian vesicles** and other accessory organs; 2) **radial water canals** from which arise lateral branches leading to special evaginations of the body wall comprising the **tube feet** or **podia**; and 3) **stone canal** with the **hydropore** or **madreporite.**

The oral water ring may be considered as the central part of the system. It surrounds the esophagus (Figs. 6, 7). Among echinoids it is slightly displaced inward by development of the masticatory apparatus and in holothuroids by that of the pharyngean bulb. As a rule, it bears the large pedicellate vesicles known as **polian vesicles,** located interradially and probably serving to maintain the turgescence in the apparatus. These vesicles are lacking in crinoids and echinoids; among ophiuroids four

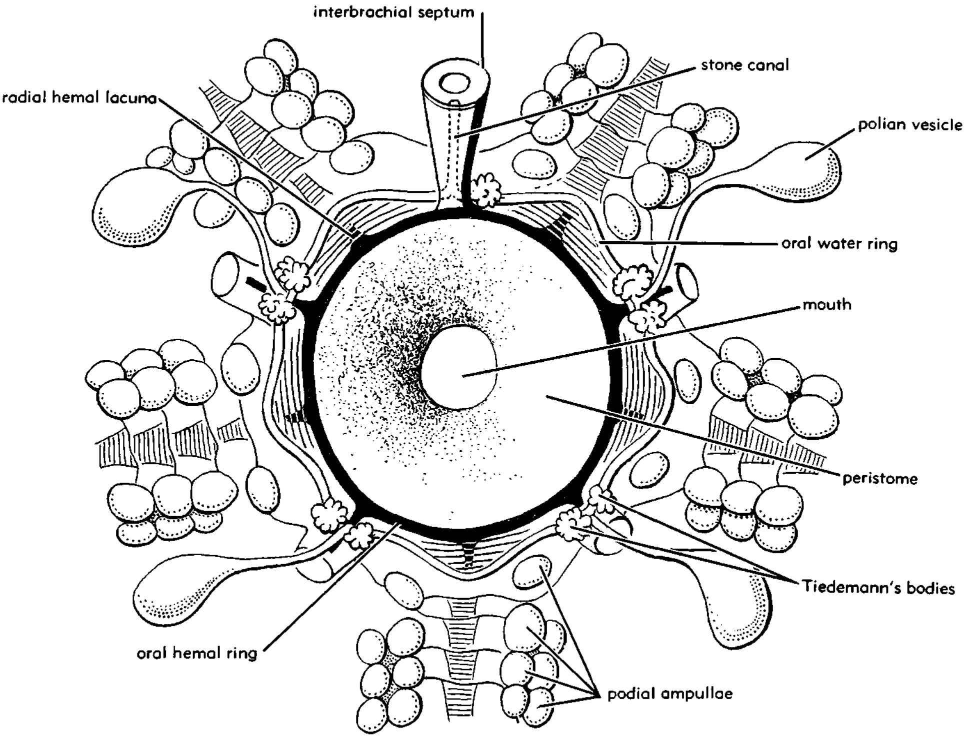

FIG. 7. Internal view of peristomial region of *Asterina gibbosa* (PENNANT) (asteroid), showing water-vascular and hemal systems, ×10 (Cuénot).

such vesicles normally occur, and in asteroids there are generally five, but in holothuroids the number is highly variable (one to more than 50). Connected with the oral ring or related to it, some lymphoid organs are found in echinoids forming the so-called **spongy body** or **spongy ring,** that is penetrated by caecal diverticula given off by the oral ring; in asteroids, the interradial **Tiedemann's bodies,** of unknown function, enclose tubules that terminate blindly but open into the oral ring.

The oral water ring gives off five radial water canals (Fig. 6) located aborally with respect to the hyponeural coelomic sinus and hemal lacuna (Fig. 1). Among holothuroids and echinoids, the canals and accompanying radial structures lie in the inner part of the body wall (holothuroids) or on the inner surface of certain plates of the endoskeleton (ambulacral plates) which are closely associated with the water-vascular apparatus. Among crinoids and stelleroids, on the other hand, they are external to the brachial (crinoids) or to the ambulacral endoskeleton (stelleroids), resting in a ventral groove (ambulacral groove) open to the exterior, except in ophiuroids where it is secondarily closed by soft integument or by ventral arm plates and transformed into an epineural canal. (In living and probably fossil somasteroids, there is no permanent ambulacral groove, but a muscular mechanism permits temporary erection of the ambulacral plates to form an open furrow, homologous with the ambulacral furrow of asteroids).

Throughout their course the radial water canals give off (to right and left) branches that end in the ambulacral tube feet or podia. In crinoids, each branch divides into three smaller branches that give rise to three podia or tentacles. The podia are found in all living classes, and probably were present in most, if not all, of the extinct groups. They exhibit a truly remark-

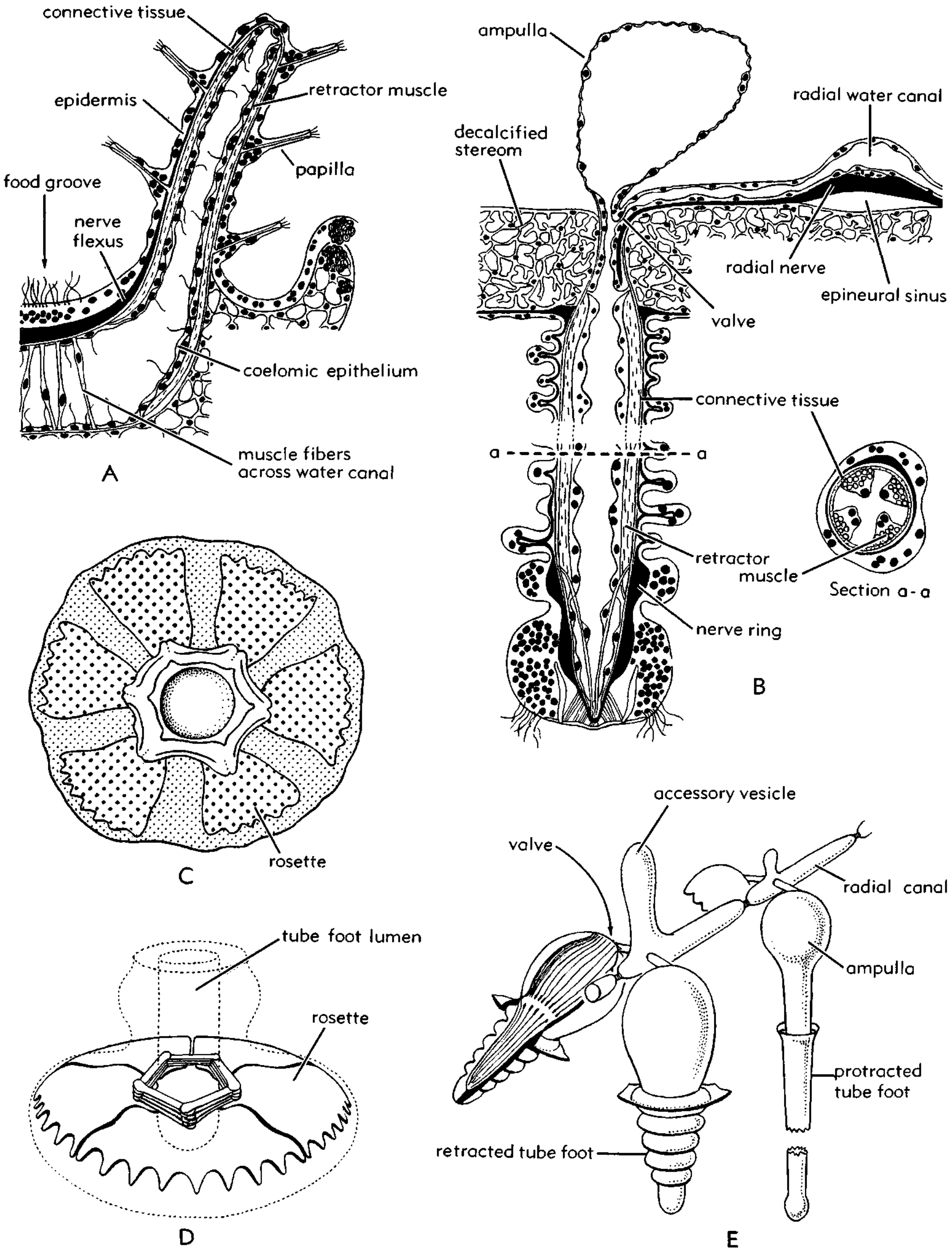

FIG. 8. Structure of tube feet.——*A*. Longitudinal section of tube foot of *Antedon bifida* (crinoid) (Nichols).——*B*. Longitudinal section of suckered tube foot and radial water canal of *Echinocyamus pusillus* (echinoid) (Nichols).——*C, D*. Structure and arrangement of skeletal elements in disc of suckered tube foot of *Echinus esculentus* (echinoid) (Cuénot, Nichols).——*E*. Diagram of part of radial water-vascular system of *Amphiura filiformis* (ophiuroid) (Buchanan & Woodley).

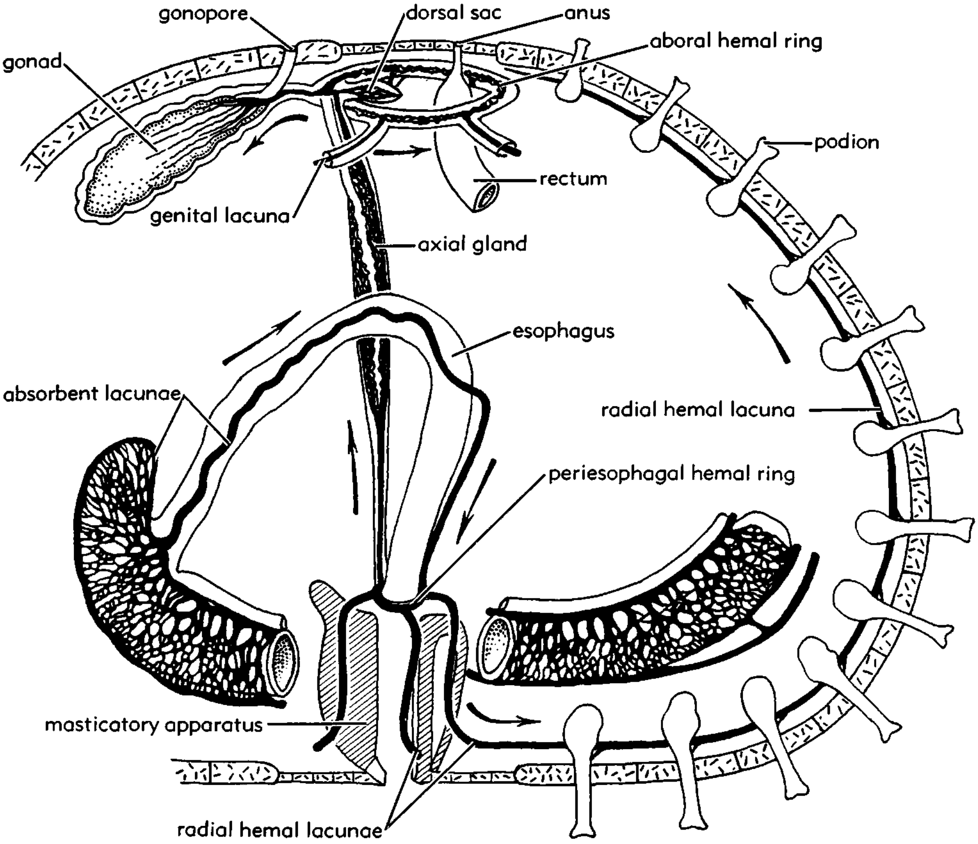

FIG. 9. Scheme of hemal system in regular echinoid (mod. from Cuénot).

able polymorphism that corresponds to their varied functions as feeding, respiratory, locomotory, burrow-building, or sensorial organs. Yet they are constructed according to the same basic plan. Each tube foot comprises (from outside to inside) an epidermis, which is continuous with that of the rest of the body, a nervous plexus, a conjunctive layer, a layer of longitudinal muscle fibers, and a flat vibratile endothelium that covers the internal cavity or lumen (Fig. 8,*A,B*). The nervous plexus is thickened on one side to form the longitudinal tube foot nerve, and generally at the distal and proximal ends to form nerve rings. The conjunctive layer may contain a spicular endoskeleton of its own; the collagen connective tissue of which it is made up constitutes the framework of the tube foot. The longitudinal muscular fibers are retractor muscles, apparently serving also for bending the tube foot. The cilia of the endothelium lining the lumen in many forms are arranged in two longitudinal bands which, as they are beating in opposite directions, determine a circulation of coelomic fluids in the internal cavity.

In crinoids and ophiuroids, the epidermis of the tube feet is raised at intervals into papillae which contain mucous cells and sensory elements (Fig. 8,*A*). Secretion of mucus is brought about in the crinoid papilla by the contraction of a single longitudinal muscle fiber, and in the ophiuroid papilla probably by a flattening of the epidermis resulting from normal protraction of the tube foot (NICHOLS, 1963).

In many holothuroids, echinoids, and asteroids, the free end of the podia is expanded into a disc having the properties of a sucker, serving for locomotion and feeding. In asteroids, the main framework of the sucker consists of connective tissue; in echinoids, it comprises a complicated calcite skeleton, consisting of a terminal rosette of five or more ossicles, and a series of much smaller ossicles arranged around the tube-foot lumen (Fig. 8,*C,D*); in ophiuroids, the skeleton supporting the disc is generally made up of a single ossicle. Adhesion in holothuroids is obtained by the stickiness of mucus secretions from cells belonging to the epidermis of the disc. In asteroids and echinoids, the sucker is operated by special muscles which create a suction when they contract. As the functioning and structure of the suctorial tube feet are different in the three classes just mentioned, one may conclude that they have evolved independently.

The podia of holothuroids, echinoids, asteroids and of the only known surviving member of the somasteroids (*Platasterias*) are each provided with an internal contractile vesicle, the **ampulla** (Fig. 6, 7). The wall of the ampulla consists of an inner coelomic epithelium, a sheath of muscles (antagonistic in action to the retractor muscles of the tube foot), commonly a thin layer of connective tissue, and a flat covering peritoneal endothelium. When the ampulla contracts, the tube foot is protracted by hydraulic pressure. A valve at the point where the branch from the radial water canal ends into the tube foot prevents ambulacral fluids from flowing back into the rest of the system (Fig. 8,*B,E*).

Since the ampulla is internal and the tube foot external, their union is effected by a canal extending through the body wall (holothuroids) or passing through a pore (generally doubled in echinoids) that lies between the ambulacral plates or perforates them (Fig. 9). The existence of similar pores in fossil forms suggests the former presence of ampullae.

In groups lacking ampullae, such as crinoids and ophiuroids, other devices may be functional equivalents of the ampullae (Fig. 8,*A,E*). In crinoids, muscle fibers stretch across the cavity of the radial water canal, except along its axis; when the muscle fibers contract, they first divide the canal into a series of compartments; then they reduce the volume of each compartment and force out the ambulacral fluid to the tube feet (NICHOLS, 1960). In ophiuroids, the radial water canal may be also constricted at intervals, but this is done by muscular sphincters; as no muscle fibers traverse the canal, it is elasticity of its walls that forces fluid back to the tube feet. Moreover, the musculature of each tube foot is differentiated into two systems, one in the long distal part of the tube foot and the other in the proximal part of it, which is more or less swollen; these systems seem to be antagonistic and the proximal part acts as an ampulla; a valve cuts off the ampulla and its tube foot from the water radial canal. In species with considerable power of podial protraction, the radial canal bears nonmuscular vesicles which are housed in special cavities in the ambulacral ossicles and probably takes excess fluid when the tube feet retract (BUCHANAN & WOODLEY, 1963; NICHOLS, 1963).

Now, to return to the oral ring, we find that into this opens (in the *CD* interray) a canal, secondarily multiplied in some echinoderms, called the **stone canal,** because calcareous spicules generally encrust its conjunctive wall. This canal opens outward in a vibratile funnel, the **hydropore,** or it connects with the internal face of a perforated calcareous plate, the **madreporite,** generally through the medium of a rather large collecting space, called the **ampulla** (Fig. 5,*1*). This ampulla maintains definite connections with the axial sinus, as already indicated. The presence of a hydropore or madreporite is the only indication that permits conclusion as to the existence of the water-vascular system in several extinct classes such as the cystoids or the eocrinoids. In most holothuroids the madreporite is internal, its pores opening into the coelom. This condition is secondary, for in the larva the water tube opens externally. In some forms, the hydropore of the madreporite may be secondarily multiplied.

HEMAL SYSTEM

The elements of the mesenchyme are throughout the body separated from one another by interstitial spaces that form a plexus of interconnected lacunae known as the **hemal** or **lacunar system.** At some points these lacunae are enlarged as canaliform passageways organized in a complicated network of channels and sinuses. The absence of an internal endothelial lining and the fact that their wall is composed essentially of connective tissue prove that they are neither part of the coelom nor true vessels but simple cylindroid spaces. The latter form a system particularly evident in holothuroids and echinoids but less clearly defined, perhaps, in other classes (Fig. 9). In such echinoderms, one may recognize, at least typically, the following principal parts: 1) a **periesophagal hemal ring** or an oral annular plexus closely associated with the nervous, hyponeural, and water-vascular oral rings; 2) five **radial hemal lacunae,** leading from the hemal ring and accompanying (beneath each of the ambulacra) the hyponeural radial sinuses and the radial hydrovascular canals with branches given off by the radial lacunae in the direction of the podia; 3) **absorbent lacunae** of the digestive tube, opening also into the hemal ring, developed as a network on the surface of the digestive tube; 4) springing from the hemal ring in the *CD* interray, another lacuna that penetrates the **axial gland** considered by some authors as a center of the entire lacunar system; 5) at the outlet of this organ, the just-mentioned lacuna reformed into a channel that centers an **aboral hemal ring**; and 6) the **genital lacunae** developed from this aboral ring but lost by branching in the conjunctive wall of the gonads. Finally, to the hemal lacunae one or several lymphoid organs may be joined, filling perhaps a purifying function.

AXIAL GLAND

The axial gland or organ (termed also ovoid gland, brown gland, heart) occurs in all modern echinoderms except holothuroids, which are said to have none or at most a poorly developed one. It is an organ closely related morphologically and functionally to the hemal system.

The axial gland is a vertically elongated mass, covered by peritoneum and formed of lacunar connective tissue. As FEDOTOV (1924) has shown, it is composed in echinoids and stelleroids of an oral and aboral portion. Among asteroids and ophiuroids, the oral part is enclosed in the axial sinus (Fig. 5, 6), placed in a longitudinal fold of the wall in contact with the stone canal in the *CD* interray; it represents one of the components of the **axial complex** of these organisms. Among echinoids (Fig. 9), it is also in close contact with the stone canal but not enclosed in a coelomic cavity; on the other hand it contains an irregular cavity, lined by endothelium, and therefore of coelomic origin. The aboral portion of the axial gland is well developed only among ophiuroids; in the two other classes mentioned it is reduced to a digitiform appendage (Fig. 5, 6, 9); in all it is enclosed in another coelomic cavity, the **dorsal sac or madreporic vesicle,** reported to have a contractile wall.

The axial gland of crinoids is an elongated body consisting of tubules of glandular epithelium set in conjunctive tissue and covered exteriorly by peritoneum; it occurs inside the axial sinus. The gland is prolonged at its aboral extremity by a conjunctive cord located in the axis of the chambered organ (portion of the general coelom surrounded by the aboral nerve center) and it continues inside of the stem; at its adoral extremity it enters into close relation with the oral plexus of the hemal system. According to CUÉNOT, the axial gland of crinoids is not homologous to that of other echinoderms, but this view is not generally accepted.

REPRODUCTIVE SYSTEM

The genital organs originate in the wall of one of the compartments of the general cavity. The facts that in ontogeny of living echinoderms the first indication of the genital apparatus makes appearance in the same interray as that containing the anus and hydropore, and further, that among numerous ancient echinoderms, one finds in the same place a single orifice interpreted as a gonopore, lead to the conclusion that originally echinoderms possessed a single gonad, opening in the *CD* interray. This primitive condition is retained by the holothuroids. Among all other classes the genital organs are multiplied and have been affected by pentameral radial symmetry. They are primarily interradial structures, though they are located in the arms of adult asteroids and of some ophiuroids, and in the arms or, more generally, in the genital pinnules (appendages of the arms) of crinoids.

In asteroids and ophiuroids, they are connected by an annular stolon enclosed by a hemal lacuna surrounded by a coelomic sinus; the same arrangement is seen in crinoids, where the genital cords, similarly sheathed, traverse the arms and penetrate into the central visceral mass, where they are lost. The genital cords uniting the gonads disappear in adult echinoids.

The sexes of echinoderms ordinarily are separate, although certain species of holothuroids and ophiuroids are hermaphroditic. The sexes cannot be distinguished on external characters except in species (known in all classes) that show anatomical features designed for care of the young and in cases, quite rare, of sexual dimorphism observed in echinoids, asteroids, and ophiuroids.

An asexual mode of reproduction by spontaneous fission of the body has been observed in a few holothuroids, asteroids, and ophiuroids. This may have relation to the great power of regeneration manifested in all echinoderms following accidental injuries, spontaneous eviscerations (holothuroids) and autotomies (Crinoidea, Asteroidea, Ophiuroidea), observed among many.

ONTOGENY

SEGMENTATION AND GASTRULATION

The eggs of echinoderms are small and poor in deutoplasm (Fig. 10,*A*), although a rather large number of species, particularly those that incubate their young or attach their eggs to foreign bodies, produce large eggs filled with yolk (vitellus).

As a general rule, cleavage is complete, almost equal, and of the radial type (Fig. 10,*B*,*C*). It results in the formation of a coeloblastula, ordinarily covered by long flagella (Fig. 10,*D*,*E*), and later this is transformed by invagination (emboly) into a gastrula (Fig. 10,*F*). At this stage, or even in the blastula stage, the embryo throws off its ovular envelope and becomes a free-moving pelagic larva.

From the beginning of gastrulation, some isolated cells become detached from the wall of the gastrular invagination (archenteron) and invade the blastocoel. They are mesodermal elements which have the aspect and serve the function of a mesenchyme. This indicates that the mesenchyme of echinoderms is of entodermal origin and thus is an entomesoderm. Not uncommonly, however, blastoderm cells migrate into the blastocoel before gastrulation and form a localized or diffused basis of an ectomesoderm, within cells of which occur calcareous granules destined to form the larval skeleton. A **primary mesenchyme** (Fig. 11) derived from the blastoderm, or true mesenchyme, appears then to exist in echinoderms, as well as a **secondary mesenchyme** derived from the archenteric wall (Fig. 11,*C*). Since these two mesenchymes shortly lose their identity, however, it is not possible to delineate their respective roles in morphogenesis.

FORMATION AND FIRST DEVELOPMENT OF COELOMS

An evagination from the upper surface of the archenteron soon becomes separated into the form of a closed sac (doubled in some forms) (Fig. 11,*D*; 12), the cavity of which is the **coelom,** thus produced by enterocoely.[1] This sac, when unpaired, becomes divided into two vesicles which are symmetrically placed on each side of the part of the archenteron that persists (Fig. 12,*B*). Theoretically at least, each of these two vesicles becomes divided into three successive compartments, that in anterior position being termed the **axocoel,** that in the middle known as the **hydrocoel,** and the posterior compartment known as the **somatocoel** (Heider, 1912) (Fig. 12,*C*,*D*). As a rule, however, the division is incomplete except in the left half of the body, only the posterior coeloms being invariably

---

[1] In species with large, yolk-rich eggs, the archenteron may remain rudimentary. The coelom then may open through slitlike gaps in the mesenchyme (schizocoely). Development of this sort in echinoderms is almost universally regarded as secondary. [See, however, *Direct Development* in the chapter by Fell, p. S77.]

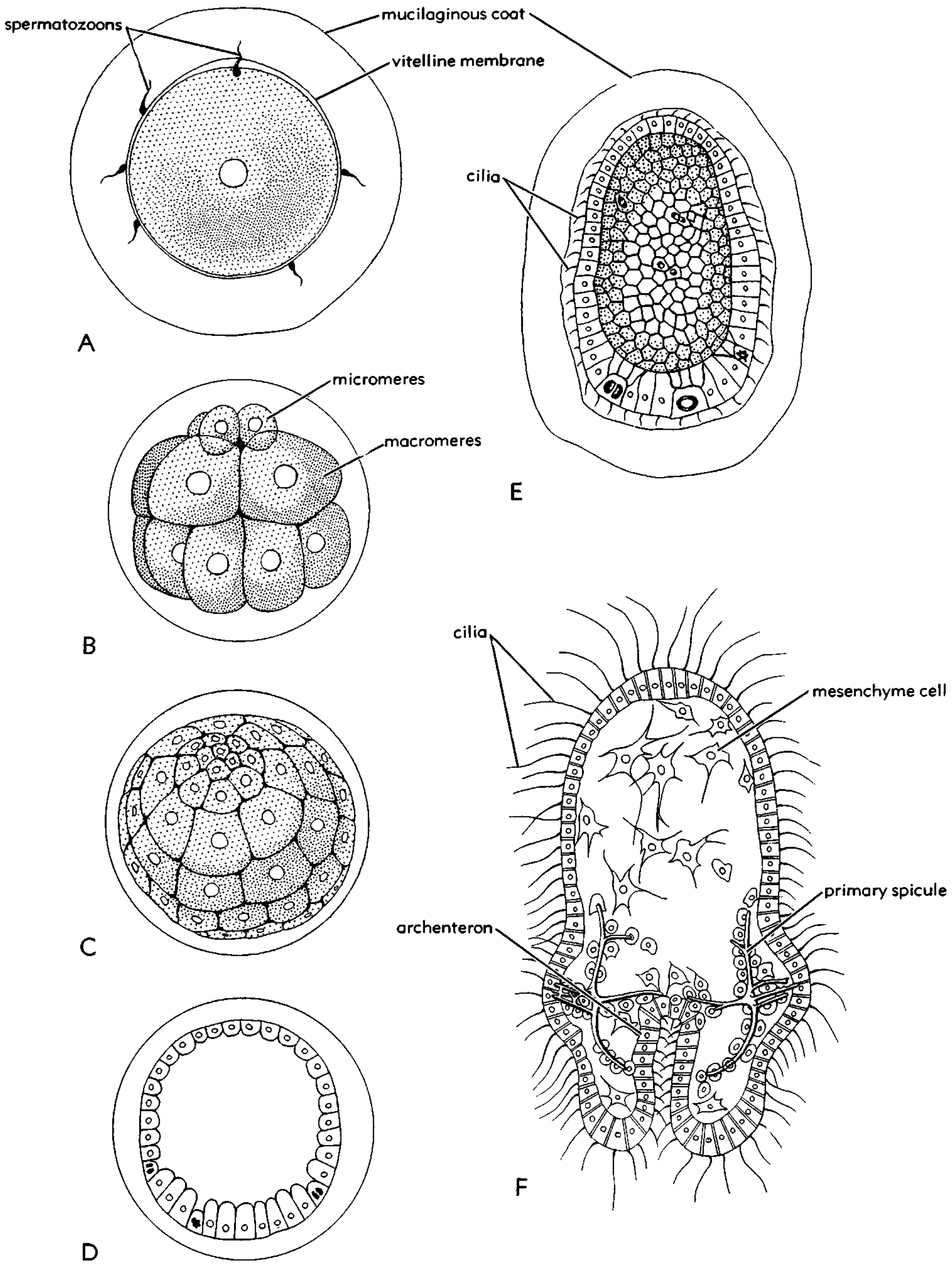

FIG. 10. Early ontogenetic stages of *Echinocyamus pusillus* (echinoid) (Théel).——*A*. Mature ovum at moment of impregnation, with one spermatozoon entering yolk and vitelline membrane beginning to separate, ×410.——*B*. Cleavage stage with 16 cells, ×400.——*C*. Later cleavage stage, at about three hours after fecundation, ×400.——*D*. Optical section through coeloblastula seven hours after fecundation, ×300.——*E*. Same at 13 hours after fecundation, ×300.——*F*. Optical section through gastrula changing into larva, 40 hours after fecundation, ×275.

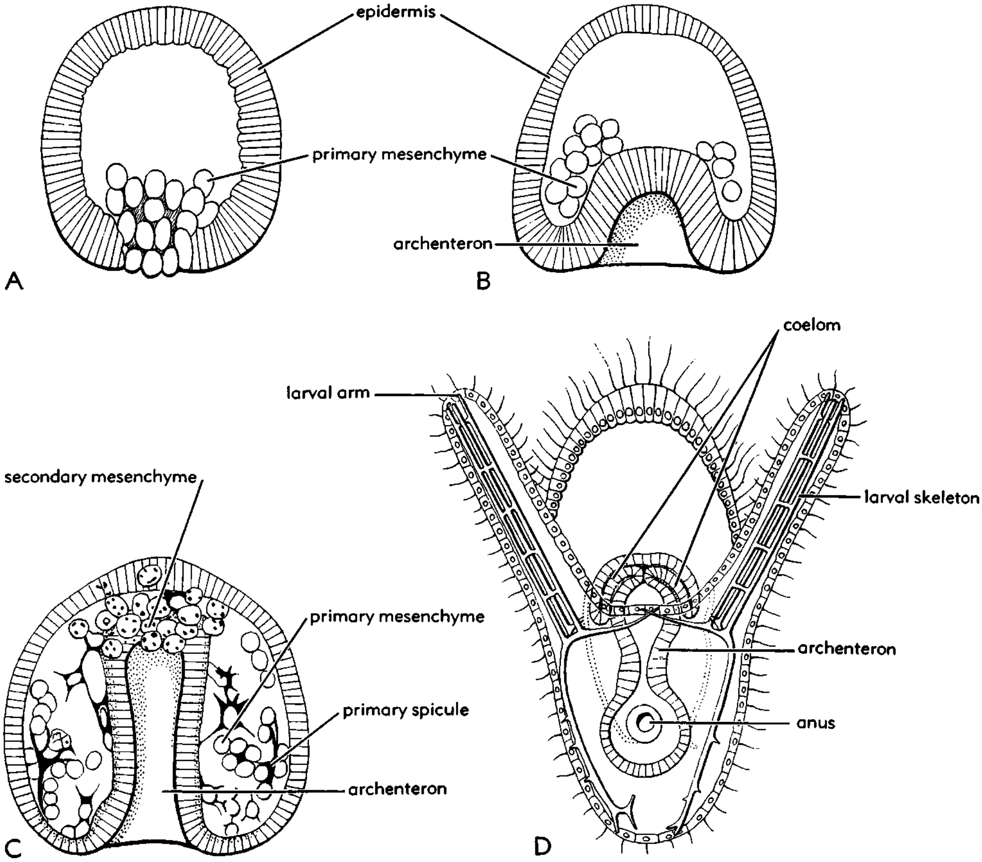

FIG. 11. Optical sections showing three stages *(A-C)* in formation of gastrula and mesenchyme of *Paracentrotus lividus* (echinoid) (Boveri); and young pluteus larva *(D)* of *Echinocyamus pusillus* (echinoid) showing formation of coeloms, ×270 (Théel).

paired; the right hydrocoel is ordinarily absent or represented only by a transitory rudiment, whereas the right axocoel (absent in holothuroids and crinoids) remains much less developed than the left one. Moreover, the separation of the axocoels and hydrocoels is by no means always sharp and they may more or less function as though they constituted a single unity. We see, then, that the embryo exhibits a profound **asymmetry** which appears very early, since it is already manifest in initial stages and even in the nonsegmented egg of some species. This is considered to be **secondary asymmetry,** however, because abnormal larvae are known that show either a division of the coelom as perfect on the right as on the left side or the development of the functional hydrocoel, not on the left but on the right side.

The ultimate fates of the diverse coelomic compartments are very dissimilar. The left axocoel remains in direct communication (except among crinoids where communication is established later on) with the left hydrocoel by means of a canal **(stone canal)** while it gives off a tubelike diverticulum **(hydroporic canal)** that opens dorsally on the left side in an orifice **(hydropore).** It is seen, then, that the hydrocoel, lacking a pore of its own, can communicate with the outside only by means of the axocoel. The right axocoel regresses, but not without having budded off a small contractile vesicle that will become, as observed later, the **dorsal sac** or **madreporic vesicle** of the axial organ. While normally the right hydrocoel, when present, plays no part in organogenesis, the left hydrocoel develops to form the water-vascular system of the adult (whence

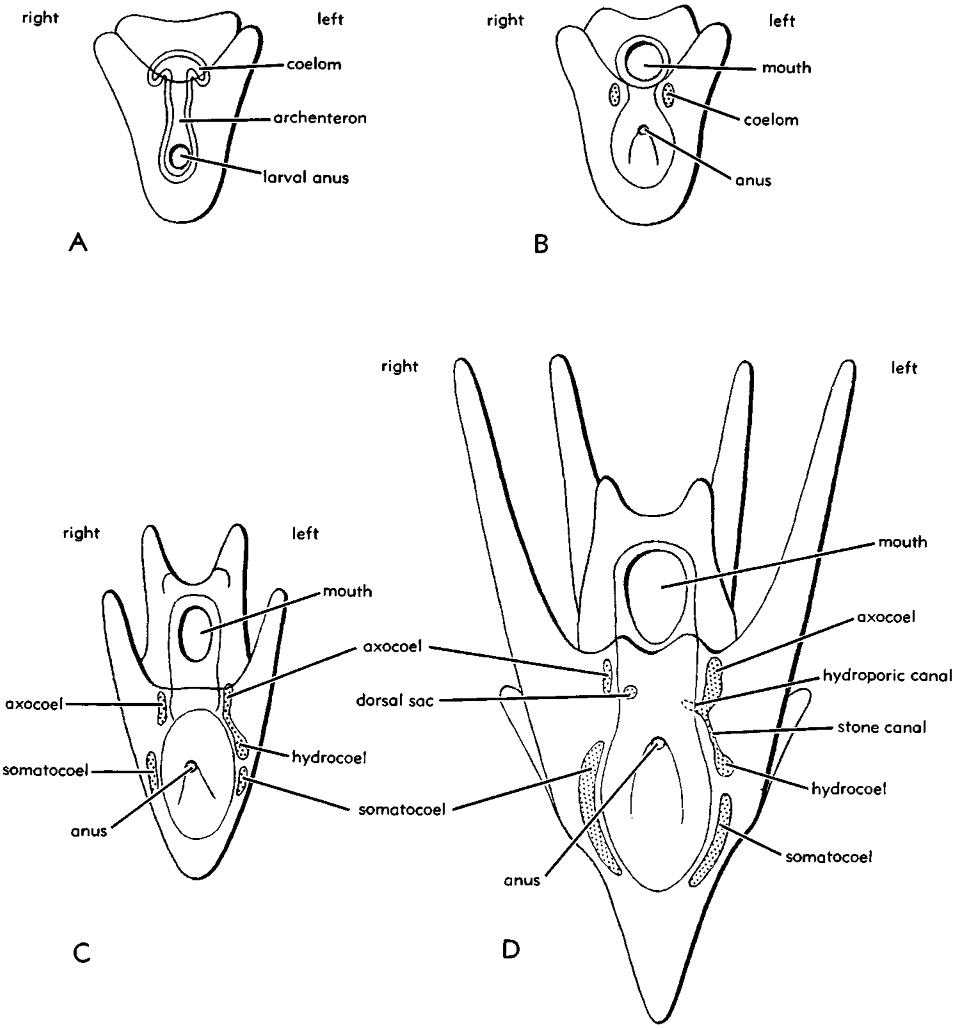

FIG. 12. Formation and first evolution of coeloms in echinoid larva (diagram.) (von Übisch).

its name). The two somatocoels, both well developed (but the left generally larger than the right) have symmetrical positions in some but strongly asymmetrical in others; where they adjoin, their walls combine to form the **principal mesentery.**

The different function allotted to each of the coelomic compartments proves that division of the coelom in no way corresponds to segmentation in the strict sense. Further, it is not accompanied by segmentation or repetition in series of any of the body structures. The mesoblast especially shows no fundamental tendency to give rise to somites. Therefore, HYMAN (1955) is entirely correct when she insists on the nonsegmented nature of the echinoderm body.

LARVAE

Notwithstanding the strong asymmetry of its coelomic elements, the embryo becomes transformed into an externally symmetrical larva. The part of the archenteron not involved in forming the coelom becomes the larval digestive tube, entirely formed of entoderm. The blastopore, which remains open (except in crinoids, where

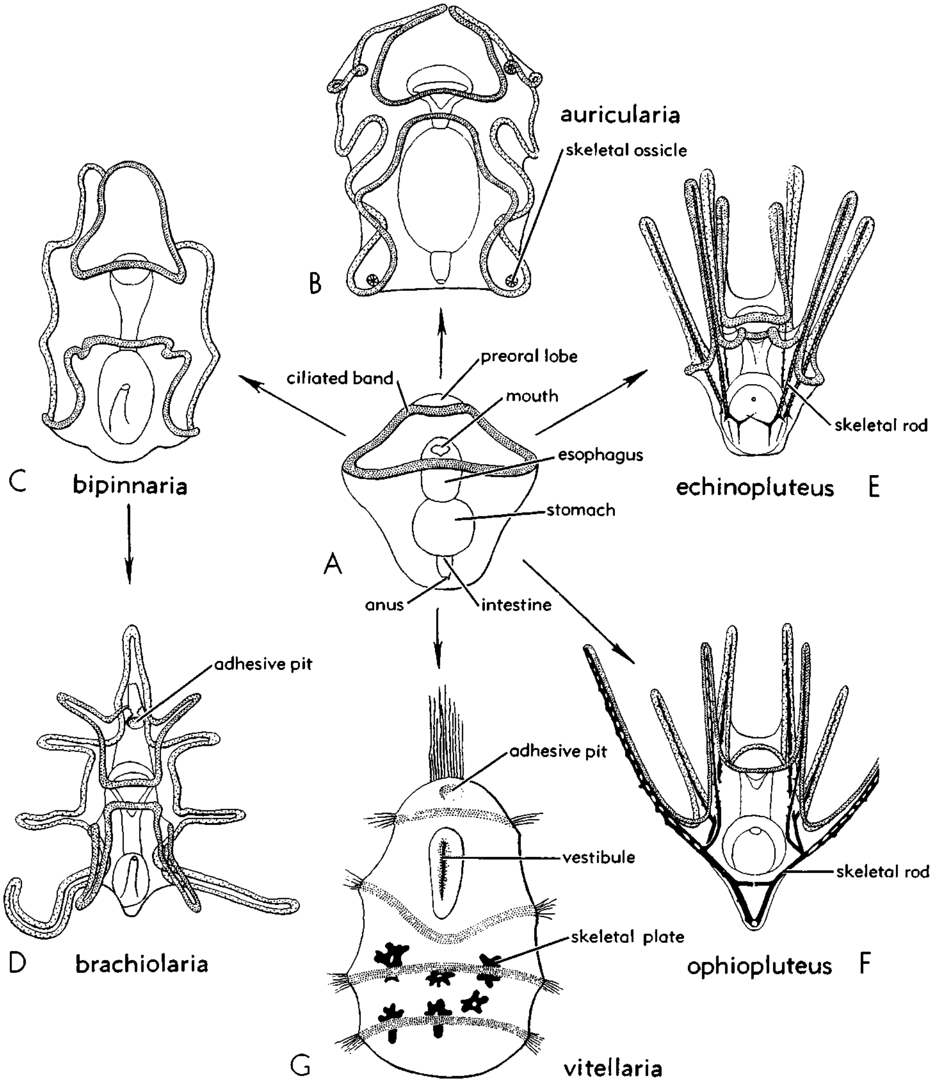

FIG. 13. Morphological relations between theoretical dipleurula larva *(A)* and other echinoderm larvae *(B-G)* (Ubaghs, n).

it is closed), becomes the larval anus and this serves to place the echinoderms among true Deuterostomia. The other extremity of the archenteron curves backward and opens to the exterior by way of the **mouth.** The appearance of this new orifice determines the **ventral face** of the larva, to which the anus, at first apical, soon becomes transferred. Finally, the digestive tube, which has become curved inward dorsally, is divided into an esophagus, a stomachic expansion, and an intestine (Fig. 13,*A*).

On the initially ovoid ventral face of the larva, a shallow, saddle-like depression is formed that encloses the mouth but leaves the anus outside of its limits. Accompanying disappearance of general ciliation, an ectodermic rim provided with flagella or cilia is produced, completely surrounding the ventral depression, following all of its sinuosities. The portion of the larval body in front of the mouth comprises the **preoral lobe.** A sensory plate, provided with nerve elements and sometimes a tuft of cilia, may be differentiated at its apex. The larva, thus characterized, belongs to the dipleurula stage of development (Fig. 13,*A*). Noteworthy is the absence of any sort of nephridial apparatus. It is active and feeds on microplankton.

Truthfully, this so-called **dipleurula** stage has no real existence, for, as shown by MÜLLER (1848), it rather represents the common characteristics or the basic pattern of the diverse sorts of swimming larval forms which externally are strongly differentiated from one another and highly varied as to the order and degree of development of their internal structures. They provide for the dispersal of species having very restricted powers of locomotion in adults and are to be regarded as special adaptations.

These larave, considered formerly as distinct organisms, have received special names; they are: **auricularia** of the Holothuroidea (Fig. 13,*B*), **bipinnaria** (Fig. 13, *C*) and **brachiolaria** (Fig. 13,*D*) of the Asteroidea, **echinopluteus** (Fig. 13,*E*) of the Echinoidea, and **ophiopluteus** (Fig. 13, *F*) of the Ophiuroidea. All have characteristic small lobes on the surface and many exhibit very long projections (larval arms), which in ophiopluteus and echinopluteus are supported by a very complex larval skeleton; this skeleton is only slightly developed in auricularia and entirely lacking in bipinnaria and brachiolaria.

Another type of larva exists in crinoids, certain holothuroids and a few ophiuroids. They are the barrel-shaped larvae or **vitellaria** (Fig. 13,*G*) of FELL, characterized by their subcylindrical form, as well as opacity of their walls (owing to presence of deutoplasm), complete absence of arms, and replacement of the continuous ciliated band by several ciliated or flagellated parallel belts. The barrel-shaped larva, which is only slightly active and cannot feed itself, is generally considered as a larval dipleurula profoundly modified by coenogenetic characters.

We may notice finally that the free larval phase characteristic of the **indirect development** of echinoderms may be much altered or (a single case known) entirely omitted, development working in a condensed manner termed **direct development**; this may be observed in the ontogeny of species having large yolk-rich eggs. Since ordinarily, however, direct development is accompanied by appearance of structures characteristic of the larvae, one admits generally that it is secondary as compared to indirect development.

METAMORPHOSIS

GENERAL CHARACTERS

The transformation **(metamorphosis)** of the larva into the definitive young organism, is effected in various ways that cannot be described here. Discussion is limited to consideration only of fundamental aspects of metamorphosis and principal features of organogenesis.

Metamorphosis of crinoids and numerous asteroids is preceded by fixation of the larva to the substratum, whereas the larvae of other echinoderms are transformed while continuing to swim about. The whole body of the larva of holothuroids participates in the formation of adult structures; among other echinoderms, a larger or smaller part of this larval body is rejected or resorbed.

In agreement with HEIDER (1912), several phases may be distinguished in metamorphosis of the echinoderms.

ASYMMETRIC PHASE

After an initial larval phase characterized by a more or less perfect bilateral symmetry (Fig. 14,*1a,b*), an **asymmetric phase** appears. We have already taken account of the preponderant development of the left anterior coeloms in the embryo. At beginning of the metamorphosis, the mouth, which was located in the mid-ventral plane of the larva, tends to be shifted toward the left side of the body (Fig. 14,*2a,b*). This displacement, very slight in holothuroids and ophiuroids, amounts to nearly 90 degrees in asteroids and echinoids, among which the mouth becomes actually lateral in position. When the larval mouth turns into the definitive mouth, the displacement is real; but the larval mouth and esophagus may also be replaced by a mouth and esoph-

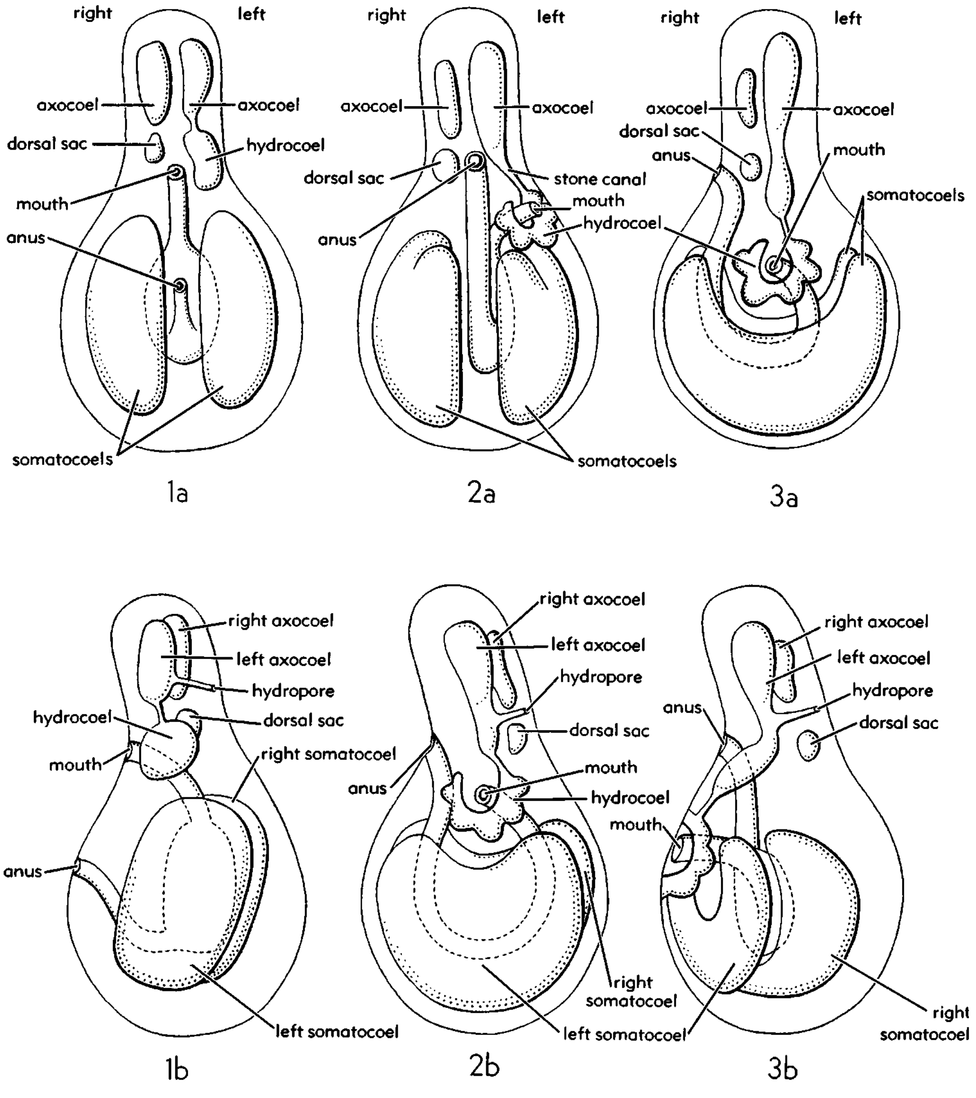

FIG. 14. First phases of metamorphosis in echinoderms (diagram.), upper row showing larvae from ventral side and lower row from left side.——*1a,b.* Initial symmetrical phase.——*2a,b.* Asymmetrical phase.——*3a,b.* Phase of secondary symmetry (Heider).

agus newly formed on the left side of the larval body, as especially seen in echinoids and asteroids. Whatever the way this change is accomplished, it produces a leftward deviation of the front part of the digestive tube, very characteristic of all echinoderms. As for the anus, whether it remains in the mid-plane of the body, being pushed strongly forward, or, as is generally the case, undergoes a shift toward the right, its displacement is in a direction opposite to movement of the mouth. The digestive tube takes then the form of a loop turned around on itself.

The displacement of the mouth carries with it the left hydrocoel, which acquires a horseshoe shape and tends to grow around the esophagus. Likewise, the two somatocoels take on a crescent shape, with development of terminal horns that play an im-

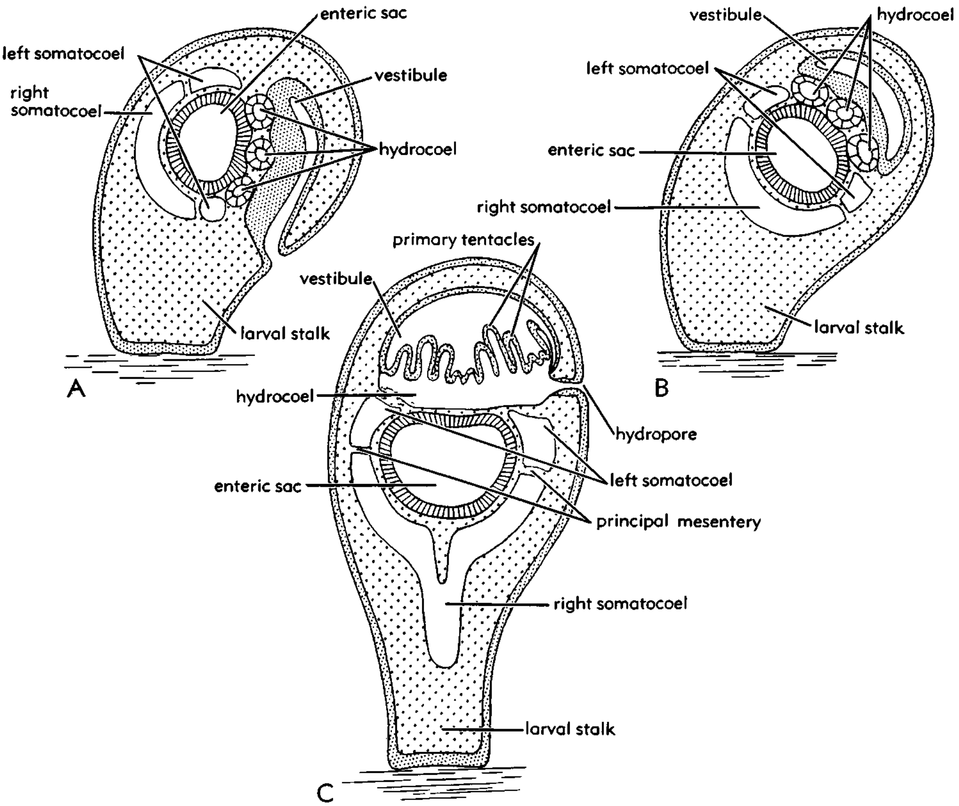

Fig. 15. Diagrammatic sections showing successive stages (*A-C*) of elevation among crinoids (mod. from Barrois).

portant role in organogenesis, as we shall observe.

The larva, arrived at this stage, no longer presents a bilateral symmetry. It has become asymmetrical. A new median plane, marked by the mouth and hydrocoelic crescent, tends to be distinguishable, however. This does not coincide with the midplane of the larva but makes a more or less large angle with it, which in asteroids and echinoids may attain approximately 90 degrees (Fig. 14,*2b*).

PHASE OF SECONDARY SYMMETRY

The phase of asymmetry is followed by one in which **secondary symmetry** is developed. The mouth tends to return to the ventral surface and to recover more or less the medioventral position that it occupied in the dipleurula larva (Fig. 14,*3a,b*). This return, however, is accompanied by displacement of the hydrocoel and the two somatocoels. All together, this amounts to what Heider has termed a torsion of the entire visceral complex around the longitudinal axis of the larval body, so that the median plane of the echinoderm in course of development comes to coincide with the primitive mid-plane of the larva. However, the symmetry thus produced does not correspond to the primitive bilateral symmetry. The digestive tube is no longer found in the median (sagittal) plane of the dipleurula larva, but rather extends in its frontal plane; the principal mesentery is not now dorsoventral but is also frontal; the originally left somatocoel is moved to the oral side, while the originally right one becomes aboral.

ELEVATION AND FLEXION

The further course of development differs among the classes of echinoderms. We will

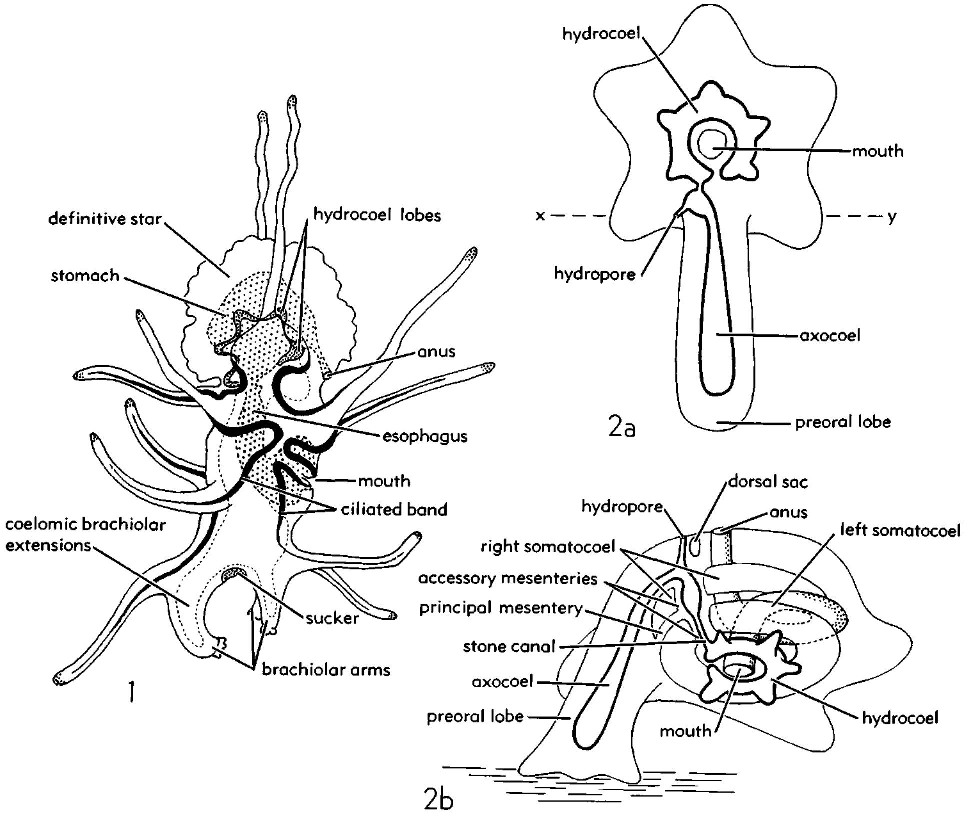

FIG. 16. Early stages in asteroid development.——*1*. Brachiolaria of *Asterias forbesi* in attached position, from left side, with definitive star formed from larval posterior region presenting its oral face to observer (Mead).——*2a,b*. Successive stages of flexion among asteroids, showing transverse axis *(x-y)* around which flexion operates (diagram.) (mod. from Heider and Dawydoff).

here consider only crinoids and asteroids having fixed larvae, because of phylogenetic significance commonly accorded to these larvae.

Among crinoids, and especially comatulids (a very specialized group but the only one for which we have knowledge of development), the larva becomes fixed by an adhesive pit carried on the ventral surface of the anterior part of its body, and this part thus becomes the attached or aboral surface, while the morphologically posterior part of the larva, with all its organs concentrated in it, turns 90 degrees about a transverse axis so as to become oriented toward the upper pole, now the free oral end of the larva (Fig. 15). The two somatocoels and the mesentery between them (principal mesentery) are disposed horizontally. Their crescentic form is accentuated and their blind extremities become located in the neighborhood of what was the original mid-ventral line, forming two short vertical mesenteries termed **accessory mesenteries.** HEIDER has used the term **elevation** for this process by which the fixed larva becomes erect and takes the inverted vertical position characteristic of crinoids and other fixed echinoderms.

On the other hand, HEIDER has designated as **flexion** (bending) the morphogenetic movements of asteroids which pass through a fixed stage. Here also the echinoderm body turns around a transverse axis in relation to the preoral lobe which assures temporary fixation of the organism (Fig. 16). This movement is accomplished in an opposite sense to that of crinoids, however; it bends the body toward the provisional peduncle (flexion), turning first the mouth toward it and then deflecting the body downward (Fig. 16). By this displacement, the organ of fixation comes to be planted on the side of the mouth that forms the oral face of the young starfish, whereas in crinoids it is inserted at the center of the aboral face. The anus appears subsequently on the aboral face and the somatocoels, by reason of their location with respect to the digestive tube, become distinguished as hypogastric (left) and epigastric (right). The principal mesentery is also disposed horizontally and the junction of their terminal projections produce accessory mesenteries perpendicular to the principal mesentery (Fig. 16,*2b*). These accessory mesenteries are important, for they determine the madreporite interray *(CD)* and are closely associated with the axial sinus (derived from the left axocoel), as well as the axial organ (mesenchymentous origin), the madreporic vesicle (derived from the right axocoel), the stone canal, and the madreporite; in brief, they are the seat of the axial complex.

ROTATIONS

Internal morphogenetic movements of rotational nature may be produced in the course of ontogenetic development of echinoderms. For example, in certain asteroids a rotation of the hydrocoelic ring has been described with displacement in a clockwise direction, accompanied by an opposite displacement of the aboral parts of the arms. Among holothuroids, the hydrocoelic ring undergoes a rotation that modifies relations of the radial canals and radii.

PENTARADIAL SYMMETRY

Fivefold radial symmetry is introduced in the echinoderm organism in the course of development by very special evolution of the left hydrocoel (see below) and by its morphogenetic influence on neighboring regions, serving to determine a final identical distribution of food grooves (or epineural canals), ectoneural radial cords, endoskeletal structures joined to the ambulacral apparatus, and hyponeural canals.

DEVELOPMENT OF PRINCIPAL ORGANS

VESTIBULE

In the larvae of all echinoderms, except asteroids, a deep ectodermal invagination is formed in front of the mouth, sheltering development of the first radial structures of the water-vascular apparatus. This is the **vestibule** (improperly called amniotic sac in echinoids) (Figs. 13; 15; 17,*B,C*).

COELOMS

Right axocoel. A small vesicle, termed **dorsal sac** or **madreporic vesicle,** located beneath the madreporite and enclosing the aboral extremity of the axial organ is derived from the right axocoel, either directly or through the medium of mesenchyme.

Left axocoel. Derived from the left axocoel are: 1) the hydroporic canal, 2) a small ampulla located at its junction with the stone canal, 3) the **axial coelom** or **sinus,** and 4) in asteroids, the internal ring of the circumoral sinus (the external ring being hyponeural, i.e., produced by the left somatocoel).

Right hydrocoel. In normal echinoderm larvae, the right hydrocoel disappears without taking any part in organogenesis.

Left hydrocoel. The water-vascular system, including all its dependent structures, is derived from the left hydrocoel. The original left hydrocoelic vesicle, very early in development, is bent into a horseshoe shape around the esophagus and tends to be closed in a complete ring (future **oral ring** of the water-vascular apparatus). Five diverticula representing the five **primary tentacles** (forerunners of the radial canals) are extended from the outer border of the hydrocoel vesicle. These five tentacles push back the subjacent integument (floor of the vestibule where this structure exists) and acquire in this way their ectodermic covering; thus the radii begin to be defined. On the other hand, the oral ring preserves its relations with the exterior by means of the larval stone canal and the left axocoel. Regression of this latter, however, permits the placement of the stone canal and hydroporic canal of the larvae end to end. In this way, finally, the water-vascular system opens directly to the exterior and at the junction of the two canals a small ampulla, as we have seen, may persist as a remnant of the left axocoel. The polian vesicles and Tiedemann's bodies, like the radial canals, are outgrowths of the oral ring. The podia are developed as evaginations from the radial canals.

Somatocoels. We have seen that the two somatocoels are displaced in such manner that the right becomes the aboral (epigastric) part of the principal coelom or general cavity of the adult and the left the adoral (hypogastric) part (Figs. 15; 16,*2a,b*). We have observed also that the principal mesentery is disposed horizontally and that terminal horns of each produce, on meeting, the accessory mesenteries perpendicular to the principal mesentery (Fig. 16,*2b*).

The right (aboral) somatocoel presents little complication; among crinoids it sends into the mesenchyme which invades the cavity of the stem, the five tubes of the **chambered organ**; these tubes, from the beginning of metamorphosis, are separated from the cavity in which they are developed. The left (oral) somatocoel produces in the interradii caecal evaginations that come to be placed above the hydrocoel ring, themselves joined in a ring and giving rise to the ensemble of the hyponeural sinus. The left somatocoel also participates in forming the **genital coelom** of free forms and among echinoids produces between the five lobes of the hydrocoel five diverticula (the dentary sacs), which represent the primordium of the masticatory apparatus (called Aristotle's lantern).

DIGESTIVE TUBE

The digestive tube of the definitive echinoderm organism is more or less developed from that of the larva. Among crinoids, the cavity of the digestive sac, closed in the larva, connects to the exterior by an esophagus produced by meeting through the hydrocoel ring of an ectodermic diverticulum and an entodermic diverticulum produced by its wall; only later on is the anal opening developed within the madreporic interradius near the hydropore. Among holothuroids, the digestive tube of the larva becomes that of the adult, but the larval anus (blastopore) disappears and the definitive anus is opened near the site of the blastopore without an ectodermic invagination. In asteroids and echinoids the larval mouth closes, and the larval esophagus, mostly resorbed, is replaced by an esophagus produced by an evagination of the stomach on the original left side of the larva through the hydrocoel ring; in asteroids this evagination opens directly to the outside; in echinoids it joins an ectodermic invagination which it meets; in various groups the new anus is produced (very belatedly) on the aboral face. In the ophiuroids, the larval anus and intestine become atrophied and entirely disappear; the mouth of the adult may be derived directly from the larval mouth or in some species may be a newly developed feature; a part of the larval esophagus seems to persist and to give rise to the definitive esophagus.

HEMAL SYSTEM AND AXIAL ORGAN

The hemal (or blood lacunar) circulatory system is produced by the mesenchyme. The axial gland is produced from connective tissues accumulated along the wall of the axial sinus in the accessory mesentery, surrounded by a fold of the wall of this sinus. Its aboral portion is intimately related to the madreporic vesicle (derived from the right axocoel), which surrounds it like a hood; in addition, it communicates (though secondarily) with the genital stalk, the origin of which we shall see is quite different.

GENITAL ORGANS

In the larvae of crinoids, a transitory first indication of the gonad appears in the principal mesentery close to anus and hydropore—accordingly in the madreporic interradius. This primordial structure is replaced by that of the definitive gonad, which seemingly lacks relation with the first. This second structure is differentiated from the aboral vertical or accessory mesentery in close association with the peritoneum of the right somatocoel. It gives rise to a compact cellular cord which migrates into the arms where it buds off the true gonads.

Among holothuroids, the genital structure makes appearance and develops in the dorsal mesentery in the neighborhood of the stone canal and in contact with the left

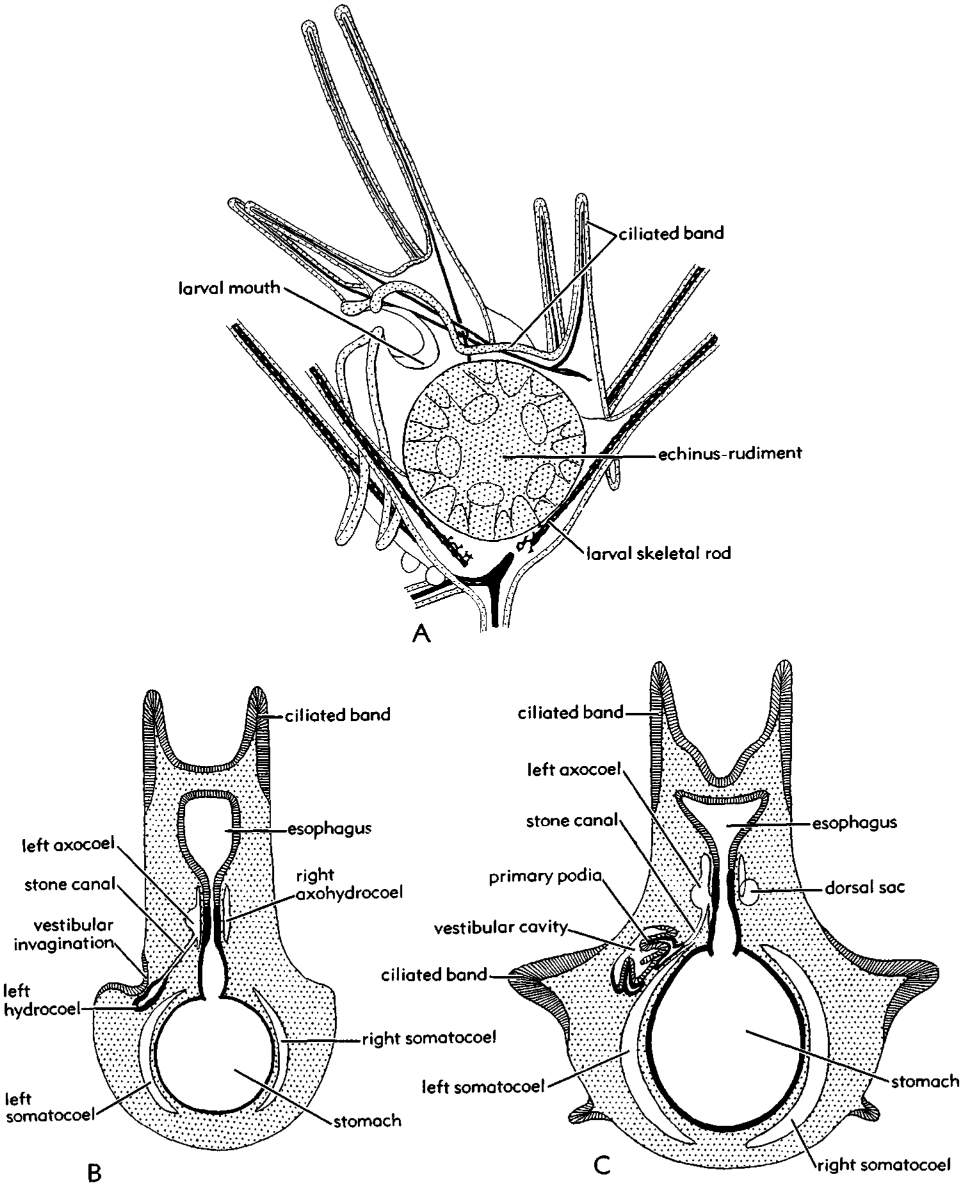

FIG. 17. Larval stages of echinoids.——*A*. Fully formed echinopluteus of *Arbacia punctulata* (LAMARCK) seen from left side, showing echinus rudiment (stippled area), ×100 (Gordon).——*B,C*. Diagrammatic frontal section through echinoplutei showing development of echinus rudiment on left side of larva (Macbride).

somatocoel, therefore with almost the same morphologic position as the gonad of crinoids.

In other echinoderms, one finds the first genital cells in the aboral (vertical) accessory mesentery, located in the madreporic interray (*CD* interray) and in close relation with the wall of the left somatocoel. After its differentiation this structure gives rise to a cellular cord, the genital stolon or stalk. This cord pushes toward the aboral surface inside a coelomic evagination of the left somatocoel so that a space, completely separated from the coelom that produced it, becomes a genital sinus. The genital stalk, with its coelomic envelope, forms a ring beneath the aboral pole and from this ring the true gonads are budded off into the interradii.

ENDOSKELETON

The first indications of the definitive endoskeleton appear before, during, or after metamorphosis. In echinoids, calcium carbonate of the pluteus larval rods is used for construction of the elements. We have already noted how the secretion of endoskeletal ossicles is produced by lime-depositing cells in the mesenchyme.

Comparable, but not necessarily homologous, development is found in the living echinoderms, except the holothuroids, producing a somewhat similar arrangement of plates around the apex of young echinoderms (Fig. 18). This arrangement persists more or less undisturbed in the adult stages of crinoids and echinoids but in the majority of ophiuroids and asteroids the primary plates are either resorbed or lost among a host of intercalary plates which arise around or between them. Among crinoids, around the larval stem, appear two cycles of five plates, both interradial in position, encircling the viscera: an aboral cycle of **basal** plates and an oral cycle of **oral** plates; generally also, inserted between the basals and the stem, are three to five small radially located plates, the **infrabasals,** that soon are resorbed or fused with the proximal skeletal piece of the stem or **centrodorsal.** Somewhat later on, five **radial** plates arise in the radii between the basals and the orals, prior to the outgrowth of the arms from the periphery of the oral surface. As the arms grow, **brachial plates** are formed in linear succession with the radials.

Among asteroids, on the aboral side of the young star, one may observe, around a **central plate,** five conspicuous interradial plates or basals, one of which incorporates the hydropore; there are no plates equivalent to the radials of crinoids and ophiuroids, but in later stages, just as in crinoids, infrabasals are introduced between central and basals, and then lost again. Early in the development appear also five radially located plates, the **terminals,** which, when the animal grows, move distally to the extremity of the arms, where they surround the terminal tentacle. The first **ambulacrals** are laid down on the oral side of the young star in close relation with the hydrocoel lobes and the first pairs of podia.

Among ophiuroids, the primary skeleton of the aboral side consists of a **central plate** and five **radials,** many species develop also a circle of interradially located **basals** between the central and the radials. Five **terminals** appear early; they are carried away to the arm tips. **Vertebrals,** representing fused ambulacrals, are secreted immediately adoral to the terminals; in adults, they constitute an internal row of ossicles supporting the arms.

Among echinoids, five interradial plates, termed **basals** or **genitals,** appear on the dorsal surface of the pluteus, and on the outer side of the primary podia, which they later surround, develop five radially situated **terminals** or **oculars.** Genitals and oculars remain in close contact, making a special system of plates (called the **apical system**) around the aboral end of the test in the adult. One of the genitals embraces the hydropore and becomes the **madreporite.**

GROWTH AFTER METAMORPHOSIS

The growth stages following metamorphosis and ending in the adult organism have very great interest for paleontologists. First, this is because they are the only ontogenetic stages that can be collected from geologic formations, but also it is because growth stages reveal important morphologic changes in endoskeletal elements—changes in form, proportions, number, placement, and topographic relations—and these changes may especially illuminate problems relating to homology and phylogeny.

An interesting application of CHILD's concept of axial gradients to the growth patterns exhibited by the endoskeletal elements and the soft parts more directly related to the endoskeleton of echinoderms recently has been made by FELL (196). He has shown that two major patterns of dominant gradients are to be recognized among echinoderms: a meridional pattern as exemplified in echinoids and holothuroids, a radial pattern as exemplified in crinoids and stelleroids. In young echinoids and young holothuroids, during metamorphosis, the hydrocoel encircles the esophagus, and sends five meridional water tubes which encircle the body cavity. Thereafter the endoskeleton, the nervous system, and part of the coelom differentiate under the same influence, and the whole body becomes more or less globose. In young crinoids and asterozoans, on the other hand, the five primary tentacles, which become the radial canals, instead of growing meridionally, are radiating more or less horizontally from the oral ring, carrying the body wall, coelom, nervous system, and the largest part of the endoskeleton with them, and resulting in a star-shaped body with arms. Then transverse growth gradients emerge from the main radial gradients, giving a pinnate structure to the arms, as well exemplified by the pinnulate arms of crinoids or the frondlike arms of somasteroids.

PHYSIOLOGY

Movements of echinoderms are provided by the podia, spines, or work of muscles. The podia are especially utilized by holothuroids, echinoids, and asteroids, but their locomotive function is weak or lacking in ophiuroids and entirely absent in crinoids. Only echinoids make use of spines for locomotion; otherwise these may serve many functions such as digging, burrow-building, protecting, harboring the developing larvae or as tactile and defensive organs. Creeping movements are effected in certain holothuroids by the general musculature of the body wall, while muscles interposed between the endoskeletal pieces govern movements of the rays of ophiuroids and the arms of crinoids; in the last-mentioned group, action of these muscles combined with the antagonistic action of ligamentary fibers may result in swimming or creeping motion (Comatulida).

LOCOMOTION

The locomotive function of the podia has been especially well studied in the asteroids by J. E. Smith (1948). The movements of protraction, retraction, and bending of each podion are controlled by a motor nerve located in the neck of the ampulla and connected with Lange's nerves and radial nerves. When the animal is moving, podia are extended first in the direction of locomotion until attached by their terminal sucker disc to the substratum, and then shortened in a backward direction so as to carry the animal forward. After contraction, the podia relax their adhesion and extend forward again. Progress of the animal requires that activities of the podia be coordinated. This coordination is accomplished by the radial nerves and the nerve ring, although a certain degree of coordination exists among the podia of an isolated arm. Presumably, a coordination center is located at the junction of each radial nerve with the nerve ring. Each center controls the longitudinal muscles that work unilaterally in a given direction, but the center that directs activity of the arm placed in the direction of forward progress exercises a temporarily dominant action. Thus, direction of movement is determined by the particular center having control at a given moment.

Individual movements of the radioles or spines of echinoids are governed by the action of muscles attached to their base and locally controlled by nerve-fiber bundles of the subepidermic system. The indispensable coordination of their movements in locomotion, however, is assured by the radial nerves.

NUTRITION

Most echinoderms are nourished by minute food particles (plankton and detritus), but some are active predators or scavengers which ingest large particles or capture living prey. They display a large array of feeding mechanisms, none of which are restricted to any particular group; furthermore each group, including many species, may use several ways of getting food.

MUCOCILIARY MECHANISMS

Among crinoids, powerful play of vibratile cilia produce centripetal currents that transport mucus-imbedded food particles along the ambulacral grooves toward the mouth. The tube feet produce and spread a mucus net in the surrounding water; then they collect the net loaded with food particles and discharge it into the groove. The same type of nutrition occurred probably in most, if not all, fossil-attached echinoderms. Among stelleroids, microphagous ciliary feeding, performed by the action of pinnate food grooves, is a fundamental feature of somasteroids. Some asteroids, e.g., *Porania, Ctenodiscus*) feed also by the mucociliary method, the food particles being entangled in mucus strands that are carried into the digestive tract. In many living starfishes, mucus protects the surface of the body and serves to collect small particles which may be carried by ciliary currents into the mouth. The mucociliary method of feeding has been also described among clypeasteroid and spatangoid echinoids; in numerous species mucus secretion and ciliary currents on the surface of the body are part of the feeding mechanisms.

TENTACULAR MECHANISMS

As just mentioned, tentacles or tube feet play an essential role in catching food particles in crinoids. Many holothuroids living in crevices or buried in mud entangle plankton and fine particles by means of the sticky tentacles surrounding the mouth; at intervals, the tentacles are thrust into the mouth and the adhering food is wiped off and ingested. Some ophiuroids are plankton-feeders, fishing with tube feet extended from the arms as they are swept through the water. Possibly the "carpoid" echinoderms used a similar feeding method.

INGESTION OF BOTTOM MATERIAL

Many holothuroid species push bottom material into the mouth with the buccal tentacles and burrowing forms swallow the mud in large quantity as they crawl along. The heart urchins (spatangoids) live buried in sandy bottoms. By means of specialized tube feet of the buccal region, they explore the walls of their burrow and catch small particles which are directed to the mouth. The digestive tract of the many species examined is invariably stuffed with bottom material. Most ophiuroids appear to be selective detritus-feeders, burrowing in the soft substrate for organic material. The starfish *Ctenodiscus* (see above) feeds primarily on mud particles which are stuck together with mucus and are carried along special grooves between the marginal plates to the podia and then to the mouth. Its stomach is generally distended with swallowed mud.

SCRAPING

Numerous echinoids equipped with strong teeth nibble on plants or masticate mostly sessile and encrusting animals. Similarly, some starfishes feed on coral polyps or sponges.

CAPTURE OF PREY

Most asteroids are predators, feeding on bivalves, gastropods, crustaceans, polychaetes, other echinoderms, sponges, and the like. Some swallow their prey whole, but others evert their stomach through the mouth and digest the captured animal externally. Most of the starfishes which feed in this way are able to capture bivalved molluscs, which are too big to be swallowed. To open the shell they use strong but intermittent pulls on the valves by means of their podia and they insinuate their stomach through tiny gaps between the valves. The use of toxins to produce relaxation of the adductor muscles of the prey is a possibility that is not yet supported by conclusive evidence. Many ophiuroids are carnivorous, preying on small worms and crustaceans, less commonly on young echinoderms and mollusks. The seizing of prey may be effected by an arm loop and the carrying of it to the mouth either by coiling of the arm or by the podia. The gorgonocephalids, which have extremely ramified and flexible arms, form an open bow-net in which small swimming animals become entrapped.

CIRCULATION

The coelomic cavities, including those of the water-vascular system, are carpeted by an endothelium, generally ciliated, vibratile movements of the cilia assuring slow circulation of internal fluids. Since echinoderms are generally in osmotic equilibrium with their environment, these fluids have a composition very close to that of sea water, except that they include products of metabolism and may contain numerous floating coelomocytes of varied sorts that perform diverse functions. These cells penetrate all tissues and all organs and one may find them also in the hemal system. Throughout the body, the liquids of internal cavities show a large degree of homogeneity.

The fact that the hemal system shows its greatest development in connection with the digestive tube and, further, that this system exhibits close relationships with important organs such as the podia and gonads, seems to indicate that it plays a considerable role in the distribution of the products of digestion. Recently, BOOLOOTIAN & CAMPBELL (1964) have demonstrated that a pulsating vessel occupying the lumen of the axial organ and terminating aborally in a compartmented contractile chamber pulses several times a minute and thus moves coelomic fluid from the perivisceral cavity into and throughout the hemal system of the sea urchin *Strongylocentrotus purpuratus*.

The cavities of the water-vascular system, which is involved in locomotory, feeding, respiratory, and burrowing activities, enclose a liquid that differs very little from the coelomic liquid. Observations of *Strongylocentrotus purpuratus* have shown that a direct communication exists between the lumina of the axial organ and the stone canal which contracts simultaneously with the pulsating vessel of the axial organ. The rhythmic contraction of this vessel, together with pulsating of the stone canal, may be important in moving fluids throughout the entire water-vascular system (3a).

RESPIRATION

Echinoderms possess a few specialized organs that function for respiration. Some gaseous exchanges can be effected through the body wall when it is sufficiently thin, as among certain holothuroids, or by means of local infolds or outfolds of this wall. Infolds (invaginations) include: 1) the ten **pouches** or **branchial sacs (bursae)** of ophiuroids, opening toward the exterior by slits placed along the bases of the arms and constantly traversed by water currents maintained by ciliary action and (in some species) by body movements that pump water in and out; 2) probably also the **hydrospires** of blastoids; and 3) the **pore rhombs** of rhombiferan cystoids. Outfolds (evaginations) are represented by: 4) the **podia** (see below); 5) the **papulae** or dermal gills of asteroids, which are simple or divided pockets that project exteriorly between plates of the skeleton, each enclosing a diverticulum of the general body cavity; 6) the external **gills** of echinoids (except cidaroids and irregular echinoids), containing branches of the peripharyngeal coelom; and 7) the organs (possibly like papulae) which probably covered the **diplopores** of diploporitan cystoids and the **sutural pores** and **epispires** of eocrinoids and some other archaic forms.

The digestive tube also may play a role in respiration. This is especially so in the case of the holothuroids (except Elasipodida and Apodida) which possess two very thin-walled, extremely ramified tubes, the respiratory trees, originating in the rearmost (cloacal) part of the digestive tube and extending into the general body cavity. By rhythmic contractions, the respiratory trees are alternately filled and emptied of water introduced into the cloaca through the anus. The rectum of living crinoids, enclosed in a conical projection **(anal tube)** developed on the oral surface of the animal, offers comparable activities; it alternately takes in and ejects sea water, thus producing a current that may be presumed to have some respiratory functions. Among certain fossil crinoids, the anal tube is enormously developed, its endoskeleton being provided with numerous perforations or very thin-walled infolds through which exchange between the exterior environment and the interior medium could be effected.

In most echinoderms which lack special respiratory structures, the tube feet are probably the main organs to have a respiratory function. In such asteroids as *Asterias,* half respiratory exchange takes place through the tube feet. When they are extended, the walls of the tube feet become extremly thin, and exchanges of gases take place between the sea water and the fluid filling the lumen; when the tube feet are retracted, exchanges take place between the fluid of the ampullae (or other internal parts of the water-vascular system if ampullae are lacking) and the fluids of the general body cavity. Maintenance of a current within the tube feet and ampullae is therefore advantageous: in many tube feet two bands of cilia, beating in opposite directions inside the lumen, and in most echinoids two canals connecting each tube foot and its ampulla are features of probably respiratory significance.

In many forms, especially in burrowing species, respiration (and other functions such as nutrition and sanitation) is greatly assisted by ciliary currents on the body surface or by special devices. For instance, in the phanerozone starfishes, the dorsal surface is covered by closely set plates, the **paxillae,** that consist of raised ossicles, each with a crown of more or less movable spinelets; these spinelets when lying horizontally form a covering under which an open space is maintained for purpose of respiration, feeding, and excretion. In the asteroid family Pterasteridae, the spinelets are united by a membrane; they form the outer roof of a brooding chamber that is aerated by pumping of water. In echinoids of the order Spatangoida, closely set minute spines, the **clavulae,** that carry longitudinal bands of cilia and occur in narrow tracts, or **fascioles,** create water currents that assist in respiration, feeding, and removing of foreign particles.

EXCRETION

Echinoderms possess no excretory system, although the function of excretion may seem to be quite active. Waste is generally evacuated by the coelomocytes or by cells having large capacity as phagocytes, the principal exits being by way of the podia, stone canal, madreporite (especially in echinoids), papulae of asteroids, pouches of ophiuroids, digestive tube, gonads, and respiratory trees of holothuroids. This eliminative action, however, does not always suffice to rid the organism entirely of its waste products; the deposition of melanoid pigments in the tissues, a feature which becomes more pronounced with increasing age, may be related also to an excretory activity. Most nitrogenous matter excreted by echinoderms occurs in the form of ammonia, with little urea and purines and only traces of uric acid; large quantities of amino acids are loosed also.

BIOCHEMISTRY

Studies in comparative biochemistry have led to formulation of conclusions of phylogenetic character. We will here consider only problems introduced by the distribution of phosphagens and sterols in animal groups, including echinoderms.

PHOSPHAGENS

Until a few years ago, it was believed that most invertebrates possessed a type of phosphagen (arginin phosphate), whereas vertebrates have another kind (creatin phosphate). The presence of phosphocreatin and phosphoarginin both in echinoderms and stomochordates seemed then to indicate that these groups were connected with one another and with the Chordata. We know now that other phyla (Porifera, Sipunculoidea, Annelida) also show this character and that the distribution of phosphagens in several phyla is by no means constant; instead, it varies among related genera, among species of the same genus, and even in different organs of the same animal. Consequently, the type of phosphagen found in a given phylum cannot be regarded as a useful criterion in considering phyletic relationships.

STEROLS

According to the nature of their contained sterols, echinoderms examined to date may be divided into two large groups: one, characterized by the presence of delta-7 sterols, comprises the asteroids and holothuroids; the other, characterized by the presence of delta-5 sterols, includes the ophiuroids, echinoids, and crinoids. This grouping is conformable to that suggested by comparative characters (excluding crinoids) of larval forms belonging to these classes. It is seen to be completely discordant with other evidence, however, especially that based on comparative anatomy and paleontology, according to which the asteroids and ophiuroids are much more closely related to one another than either of them to the echinoids.

PHYLOGENY

Remains of authentic echinoderms are found throughout the geologic column from the Lower Cambrian upward. The oldest known representatives of the phylum, already diversified and showing essential characteristics of the group, throw no light on the affinities and origins of the echinoderms, or on the manner in which their essential organization has been developed. Embryology (and in smaller degree comparative anatomy) provide more precise evidence bearing on these questions, which calls, however, for great caution in interpretation.

AFFINITIES OF ECHINODERMS

Retention of the blastopore or its emplacement as the definitive anus and the enterocoelic formation of the coelom accompanied by its division into three pairs of sacs, are characters generally considered to comprise a trustworthy basis for assignment of echinoderms with deuterostomian invertebrates, which include (in addition to echinoderms) the Stomochorda (or Hemichorda), and perhaps the Pogonophora. Inclusion of the Chordata (Protochordata and Vertebrata) in this assemblage presents another problem foreign to present considerations.

The most probable relationships of echinoderms are, in the judgment of many zoologists, with the Stomochorda (Enteropneusta, Pterobranchia, ?Graptolithina). The early larval stage of echinoderms (dipleurula larva), in fact, offers striking similarities with the tornaria larva of Enteropneusta, for these have the same general aspect, including: 1) similar placement of the circumoral ciliated band, 2) the same emplacement of the apical sensory plate, 3) the same shape and subdivisions of the digestive tract, 4) the same mode of appearance and division of the coelom, 5) identical presence of a coelomoduct with asymmetrical external orifice connecting the anterior coelom with the exterior, 6) the same general behavior of the dorsal pulsatile vesicle (madreporic vesicle of echinoderms, cardiopericardial vesicle of Stomochorda) developed from the anterior coelom, and finally, 7) absence in both of any sort of nephridial apparatus. If, moreover, the ambulacral system of echinoderms—the most distinctive feature marking these organisms—is to be compared with any other structure, it is with the lophophore of Pterobranchia, since both are derived from the middle coelom and both one and the other have the form of coelomic tentacle-bearing evaginations. Such complete resemblances can hardly be construed as fortuitous. They suggest real affinities existing between the Stomochorda and Echinodermata, but beyond this, alignment together is not justified, because the nature of complex modifications impressed on the latter in the course of their metamorphoses and the fact that no close comparison between adult echinoderms and other groups of the animal kingdom is possible sufficiently prove that at a certain stage in their history the echinoderms became radically and definitively separated from the ancestral type that possibly united them with the Stomochorda. It seems evident, moreover, that all adult echinoderms, both living and fossil, as well as larvae, in so far as we know them, are much too specialized to have been able, through later evolution, to give rise to another phylum.

Numerous authors have noted or now admit the possibility of genetic relationships between chordates (Protochordata and Vertebrata) and echinoderms. We will not undertake here a review of arguments, mainly based on embryological and biochemical considerations (see above) advanced in favor of this hypothesis. If we refer to it, it is because certain authors have judged that among some Paleozoic echinoderms indication of a common parentage between these two phyla can be found. GREGORY (1934, 1951) has drawn attention to the resemblance that exists between the theca of the stylophorans *Placocystites* or *Mitrocystella* and the body covering of a

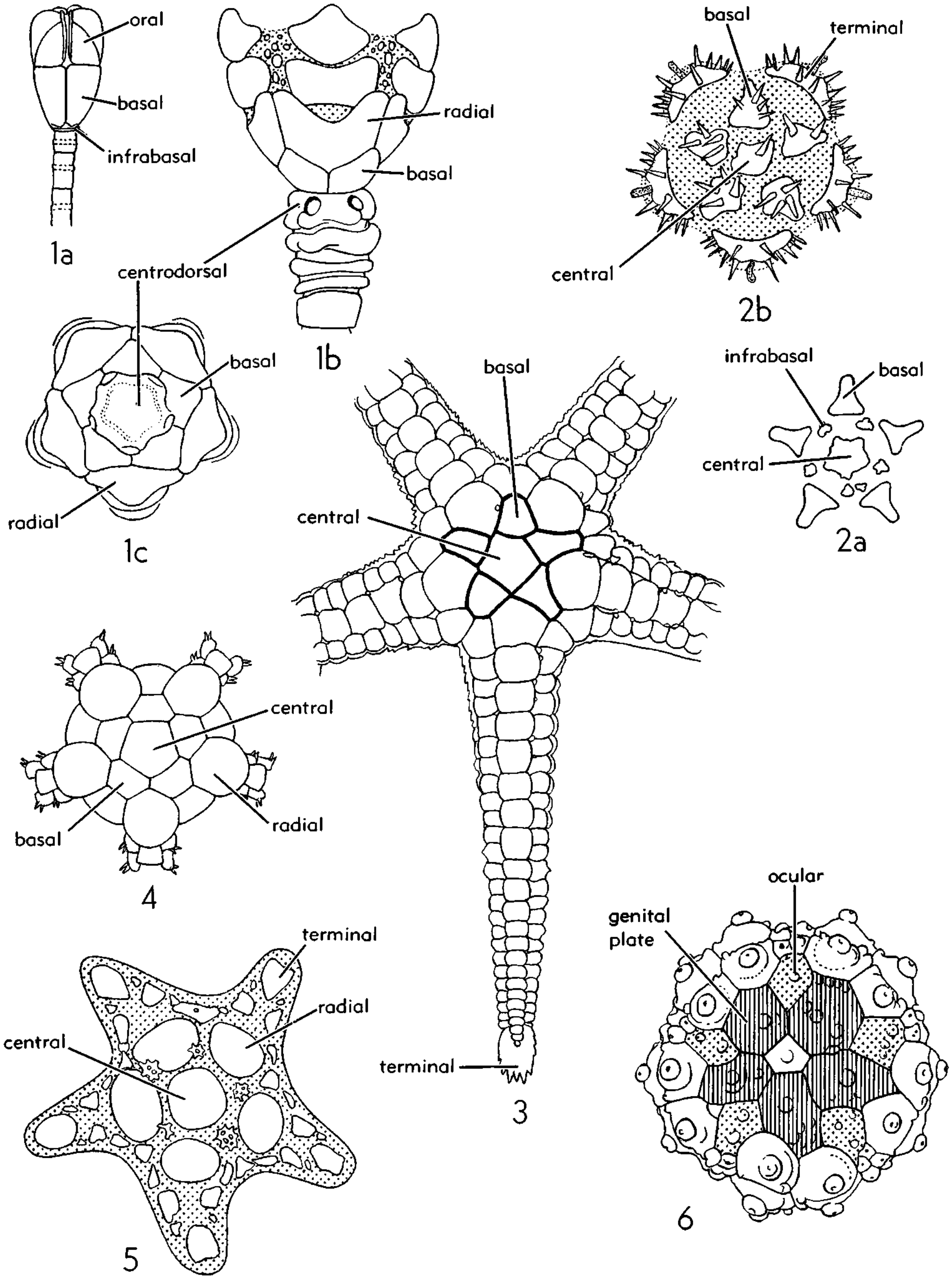

Fig. 18. Comparison of aboral endoskeletons of echinoderms.——*1. Promachocrinus kerguelensis* (crinoid); *1a,* very young larva, ×48 (Clark); *1b,c,* lateral and dorsal views of 2-year pentacrinoid stage, ×8 (Fell).——*2. Asterina* sp. (asteroid); *2a,b,* two stages, ×10 (Fell).——*3. Cnemidaster wyvillii* (asteroid), ×3 (Sladen).——*4. Ophiosteria echinulata* (ophiuroid), immature specimen, ×4 (Fell).——*5. Amphipholis squamata* (ophiuroid), very young individual, enl. (Cuénot, after Ludwig).——*6. Austrocidaris canaliculata* (echinoid), immature specimen, ×26 (Lovén).

Devonian ostracoderm, *Drepanaspis*. In the view of GISLÉN (1930), the asymmetries in organization of the "carpoids," especially in the position of the multiple orifices of the upper face of *Ceratocystis* and *Cothurnocystis,* offer close resemblances with the asymmetries and arrangement of the branchial slits of *Amphioxus* larvae. These comparisons are based either on superficial analogies or on erroneous interpretations of the "carpoid" organization. Equally objectionable is the assertion by SPENCER (1938) that the polygonal canaliculated plates of certain cystoids (e.g., *Aristocystites*) closely resemble the bony scales (tesserae) in the armor of ostracoderms or the view of CASTER & EATON (1956) that plates of the stylophoran *Paranacystis* exhibit a microstructure like that of the superficial layer of plates of the ostracoderm *Procephalaspis oesolensis.* As a matter of fact, the plates of echinoderms and tesserae of ostracoderms show entirely different histologic structure, quite aside from the fact that the bones of vertebrates and stereom of echinoderms have fundamental distinctions that should not be forgotten.

ORIGIN AND DEVELOPMENT OF ECHINODERM ORGANIZATION

The origin of echinoderms and the manner in which their organization (structure) has developed have been subjects of numerous speculations. For the ancestor and for representatives of initial phases in the history of the phylum rather widely diverse pictures have been proposed. Figures 19-20 represent some of these. The best-known, almost classic representation is the dipleurula, a hypothetical pre-echinoderm stage which should be reproduced in ontogeny (Fig. 13,*A*). All these representations help in understanding the genesis of the organization of echinoderms; this is their virtue. There is trouble, however, in distinguishing in them the part that is purely speculative from well-justified interpretation of facts. It seems more in accord with modern scientific procedures to be limited by interrogating in critical manner the diverse sources of our information and by drawing from them guidance in efforts to clarify somewhat initial phases in the history of the phylum.

The important foundation of common characters presented by the first ontogenetical stages of living forms and the organization of the only zoological group to which one may usefully compare echinoderms—that is to say, the Stomochorda—lead us to agree that echinoderms are derived from free bilaterally symmetrical forms with three pairs of coelomic pouches (or perhaps only two pairs, for division of the anterior two pairs is not always sharp) and that these pouches are developed by unequal division of a pair of sacciform evaginations of the archenteric wall. We may still agree that from the beginning the three (or two) pairs of coeloms were more or less well differentiated and, as in the Pterobranchia, of quite different size. Also generally acceptable is the conclusion that the coeloms in each pair were probably equally developed from the beginning, although in Recent larval forms only the left anterior coelom undergoes a complete division. As we have seen, certain observations from embryology require that we regard this asymmetry as secondary. Nevertheless, it constitutes a fundamental ontogenetic character which controls all stages of development, and which may be traced back to the egg. This precocity and its organogenetic importance leads to query as to whether the bilateral symmetry of the ancestral forms was not already disturbed. In any case, asymmetry must have been acquired very early by the phylum.

As an indication of this, we find no fossil echinoderms possessing two hydropores, which would allow the conclusion that two functional hydrocoels existed. The endoskeleton of "carpoids" and helicoplacoids, which probably may be considered as the most primitive of all known echinoderms, since they have no radial symmetry, lacks bilateral symmetry; although in some "carpoids" it tends to acquire a certain bilaterality, this never masks its profound and multiple asymmetries. If, then, a pre-echinoderm symmetrically bilateral stage existed, it could only have been well before the beginning of Cambrian time. It is surprising, then, that WHITEHOUSE (1941) judged that in an enigmatic Middle Cambrian fossil of

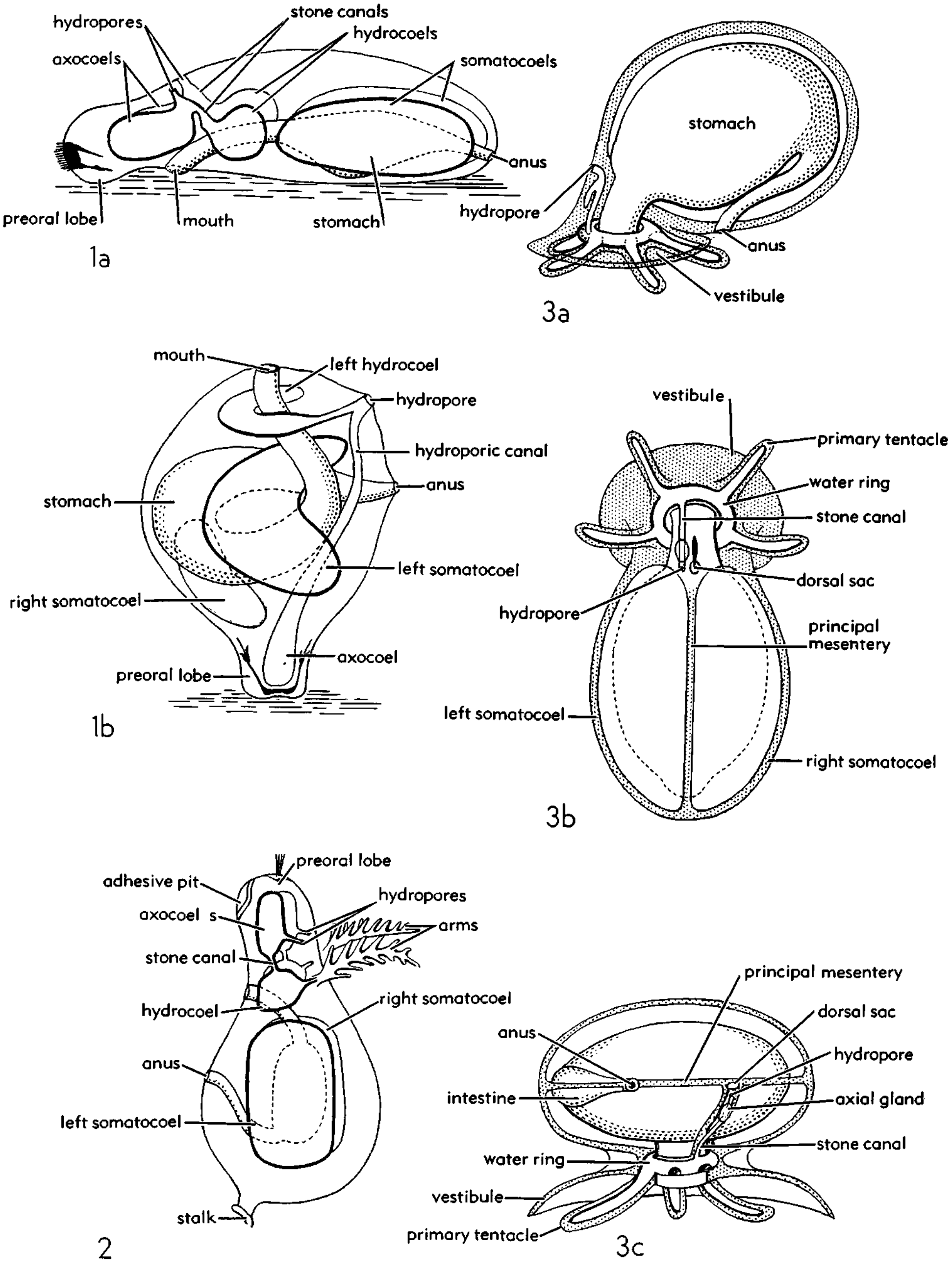

FIG. 19. Theoretical reconstructions of echinoderm ancestor.——*1.* Dipleurula ancestor; *1a,b,* from left side and after fixation (primitive pelmatozoic ancestor) (Bather).——*2.* Dipleurula ancestor (Heider).——*3.* Pentactaea ancestor; *3a-c,* from left side, dorsal view, and after torsion to radial stage (half of vestibule and two tentacles supposedly removed) (Bury).

Queensland *(Peridionites)* he had found a form corresponding morphologically to the stage of dipleurula in larval development of the phylum, a quite erroneous and improper interpretation, as shown clearly by GISLÉN (1947), HYMAN (1955), NICHOLS (1962), and others.

In order to explain the morphologic and ontogenetic peculiarities of echinoderms, it is commonly supposed that their ancestors have passed through a fixed stage. This condition refers to (1) the radial organization of the adults, (2) the asymmetrical development of many structures, (3) the rotations and torsions undergone by organs during ontogeny, (4) the possession of a calcareous well-developed endoskeleton necessary to protect a sessile organism, and (5) the fixation that actually precedes or accompanies the metamorphosis of the larvae of crinoids and numerous asteroids and that one generally agrees to recognize as having great phylogenetic importance.

In order to explain the preponderant development of organs belonging to the left half of the body, at expense of those of the right half, and the displacement of the mouth to the left of the larva, diverse authors (BÜTSCHLI, LANG, BATHER, VON ÜBISCH) have supposed further that fixation was effected by the right part of the anterior extremity or that the ancestral forms came to rest on the right side of the body or became fixed with that side (GISLÉN).

As a consequence of this, it is supposed that (1) the preoral part of the body became elongated in a peduncle, undeveloped or entirely lost in most free echinoderms; (2) the mouth was displaced toward the left and eventually to the morphologically posterior pole; (3) the principal organs underwent a torsion by which the originally left side became the oral part of the developed organism, and the originally right side, the aboral part; (4) the structures in the right anterior part of the body were reduced, with preponderant compensatory growth of the left half. In summation, if we follow the most generally accepted interpretation, the event marking the origin of the echinoderm phylum would have been adaptation to a sessile or sedentary mode of life.

This hypothesis, of course, cannot be founded on present paleontological evidence. As a matter of fact, the "carpoids" and the Helicoplacoidea, which are probably the most primitive known echinoderms, were not attached to the sea bottom. But this does not imply that their ancestors were not fixed. It does simply show that, if a fixed stage ever existed in the common history of the phylum, this stage must belong to such remote past that it is unlikely that it could be represented in the fossil record. It is true that certain Ordovician cystoids (e.g., *Aristocystites*) have been considered sometimes (BATHER, 1900, 1901, 1929) as presenting the structure of this primordial form forecast by theory. But it appears more and more evident that cystoids in general and the Aristocystitidae in particular comprise a specialized group that does not possess this generalized organization from which could be derived the basic structure of *all* other echinoderms.

The above theory is almost entirely founded on ontogenetic considerations. It postulates that the changes which occur in the development of Recent echinoderms possess, at least to some extent, a recapitulative significance. It must be noted, however, that (1) the morphologic orientation and asymmetry of the embryo are found to be already determined in the egg of certain echinoderms, then *before* any development; (2) all traces of a fixed stage have disappeared from the ontogeny of holothuroids, echinoids, ophiuroids, and even many asteroids; (3) the fixation of asteroid larvae is regarded by some zoologists as a cenogenetic specialization without phylogenetic significance; (4) the attachment of the crinoid and asteroid larvae takes place in the middle line (not on the right side) of the anterior part of the larval body; (5) the appearance of a protective endoskeleton probably results less from a special cause such as the discovery of the bottom by direct ancestors of echinoderms than from a more general factor responsible for the production of skeletal structures in many unrelated invertebrates in late Precambrian time or at about the beginning of the Paleozoic Era.

The appearance and development of radial symmetry in echinoderms generally is also attributed to adaptation for a fixed

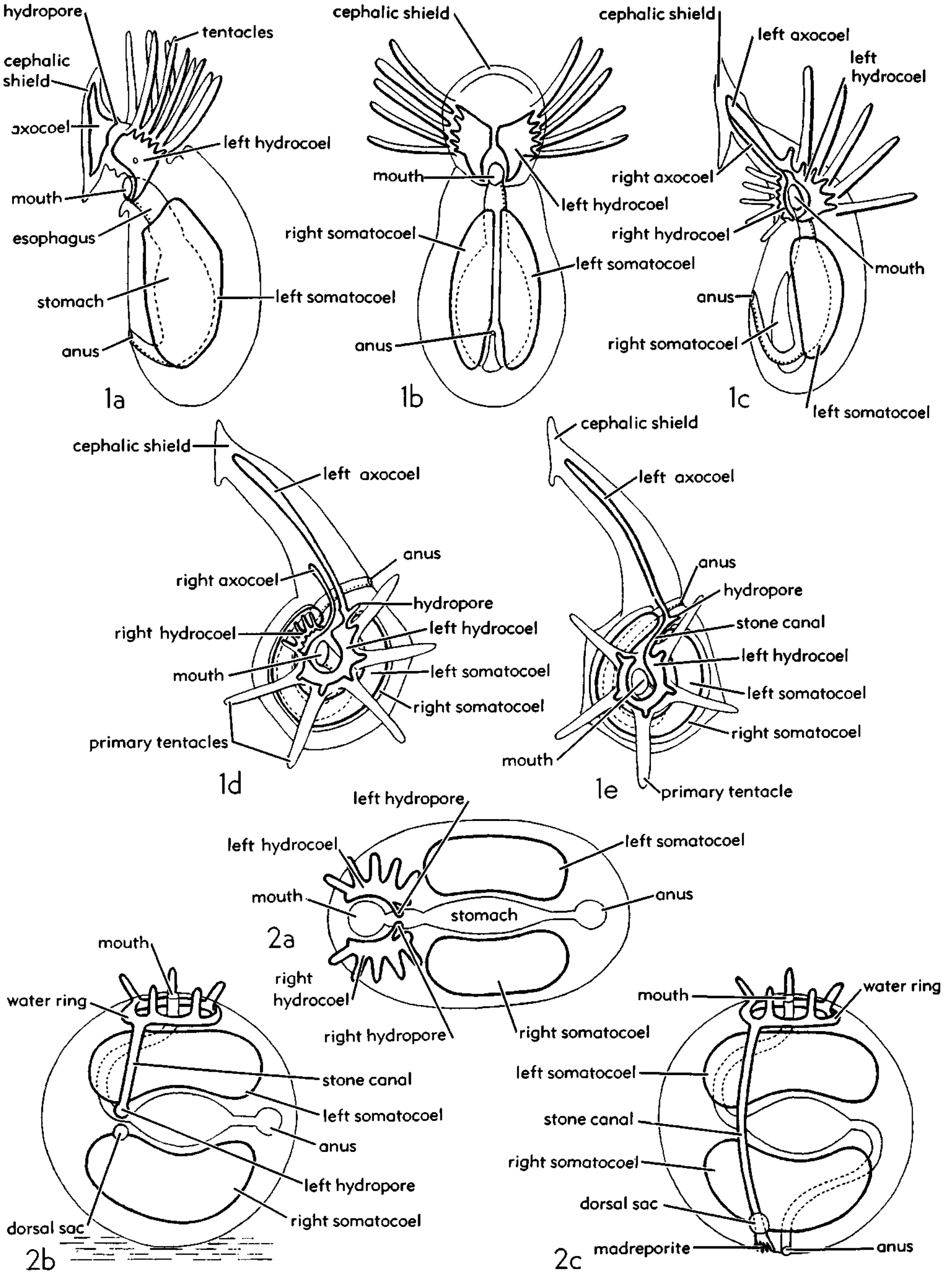

FIG. 20. Theoretical reconstructions of echinoderm ancestor (continued).——*1. Cephalodiscus*-like ancestor; *1a,b,* from left side and ventral view; *1c-e,* progressive stages in transformation to echinoderm, from left side (Grobben).——*2.* Echinoderm ancestor; *2a,* free-living bilateral form, ventral view; *2b,* radial condition after fixation; *2c,* echinoid condition, again free-living (von Übisch).

mode of life. Such a conclusion is not obligatory, however, since fixed organisms exist which are not radial and radial organisms are found, which, like the ctenophores, probably never have been sessile. In addition, radial symmetry of the echinoderms is superimposed in the course of ontogeny on asymmetry of free-swimming, as well as fixed, larvae. For the rest, if a fixed mode of life is attributed to ancestors of the echinoderms, it is not so much for explaining their radial symmetry as for taking account of the hypertrophy in growth of the left side as compared to the right side, correlated with torsions shown by the organs in the course of metamorphosis. What embryology suggests appears to be entirely different. It indicates that radial symmetry is introduced by development of the left hydrocoel and by the morphogenetic modifications that this part of the coelom exercises on other organs, as well shown by RUNNSTRØM (1918). Now the left hydrocoel develops the water-vascular apparatus, which in initial stages of its growth is represented by the five primary tentacles and resembles the lophophore of pterobranchs. At most, we can suppose that fixation of the free bilaterally symmetrical ancestor by the right anterior part of the body and accompanying reduction of the right hydrocoel provided the conditions needed for the left hydrocoel to grow around the esophagus into a ring from which proceeded the five primary radial structures. In this way, we may recognize the possibility of some indirect relation between radial symmetry and the presumed passage through a fixed stage during the history of the phylum, but all the same nothing in this assumption explains why the left hydrocoel acquired a fivefold (rather than a three-, four-, or sixfold) organization.

BATHER (1900, 1901, 1929), followed by HEIDER (1912), has maintained the view that the pentamerous condition of the echinoderms must have been preceded by a triradiate condition of the subvective system. This opinion is based on interpretation of a morphological series consisting of certain attached fossil echinoderms (cystoids) and on some theoretical considerations. Initially, three food grooves (three arms, according to HEIDER, two primitive lophophores and a third added later) would be spread out on the theca diverging from the mouth, one in a direction opposed to the anus, and the other two on each side of the mouth; the development of a groove on the posterior side would have been prevented by the presence of anus and hydropore. Eventually, the two lateral grooves would be divided, increasing the number of alimentary furrows to five. These grooves, fringed by tentacles (podia) produced from the left hydrocoel, would gradually lengthen outward. Other coelomic extensions would accompany them, serving as blood vessels, while the ciliated epithelium covering the floor of the grooves would produce the five radial ectoneural cords. The tentacles would remain as small soft structures, or contrariwise, would be enlarged and come to be supported by endoskeletal plates. The ciliated grooves would then be extended along these giant podia developed as brachioles. Finally, this pentactiny, at first superficial, would have gradually affected internal organs and eventually the whole organism.

Two sorts of objections may be opposed to these considerations. The first is that they find no support in embryology. The other objections are based on paleontology. A triradiate condition of the subvective system observed in a very small number of fossil echinoderms, represents a secondary character, without doubt. Archaic fixed forms show an important range of variation in the number of brachioles and food grooves. Moreover, the cystoids to which BATHER referred comprise a strongly specialized group preceded in time by other classes, namely that of the helicoplacoids, "carpoids," edrioasteroids, and eocrinoids. Now, only one food groove starts from the mouth in helicoplacoids, and in mitrate, cornute, and solute carpoids. The edrioasteroids exhibit a well-defined pentamerism from the time of their first appearance in the Lower Cambrian and the eocrinoids possess multiple brachioles generally distributed in five groups. We may add that in all earliest known representatives of the blastoids, crinoids, stelleroids, echinoids, and ophiocistioids, pentaradial symmetry is already very well developed. This indicates that paleontology offers no solution to the problem of the origin of the pentamerous condition in echinoderms. In fact most representations of the source stock of echinoderms admit the existence in it of either two tentacles-bearing arms, as in *Rhabdopleura* (HEIDER) (Fig. 19,*2*), or a group of five tentacles (*Pentactaea* of SEMON and of BURY) (Fig. 19,*3a-c*), or two groups of tentacles, one right and the other left (BÜTSCHLI, GROBBEN, VON ÜBISCH) (Fig. 20,*1-2*).

The entirety of the preceding consideration brings out more what is not known than what is known. It is true that the phylogenetic phases that we have tried to trace must belong much farther back in geological time than the earliest terrains found to contain fossils. Interpretations based on embryology cannot, for the most part, be confirmed by this evidence; in no case should they be considered as a certainty. The phylogenetic theories, even the most ingenious, may be useful as working hypotheses, but one cannot minimize the important part of speculation which they contain.

ORIGIN AND INTERRELATIONS OF ECHINODERM CLASSES

The differentiation of classes among echinoderms belongs to Precambrian time, or, at least, was accomplished during the earliest Paleozoic. Remains of Helicoplacoidea, Edrioasteroidea, and Eocrinoidea are found in the lower half of the Lower Cambrian. Slightly later, but still in the Lower Cambrian, occur two genera (*Camptostroma* and *Lepidocystis*) which may represent two other classes. In Middle Cambrian, other major groups are recorded: Homostelea, Stylophora, along with the enigmatic Australian forms *Cymbionites* and *Peridionites*. Homoiostelea, Crinoidea, Stelleroidea and Ophiocistioidea are first observed in the Uppermost Cambrian or in the Lower Ordovician. All other classes of echinoderms, including Holothuroidea (identified by isolated spicules), are known from the Middle or Upper Ordovician onward, and no new class has been introduced since the close of that period.

Next, we may observe that these classes, from the time of their appearance in the geologic record, are generally well delimited in fundamental and distinctive characters. The assignment of a fossil to one of these classes is rarely doubtful if its morphology has been adequately elucidated. It is true that forms reputed to be intermediate between the defined classes exist, for they combine certain structural characters considered as distinctive of the different classes. But these so-called intermediate forms, although relatively numerous among early echinoderms, are only morphological intermediates; none of them indicate true phylogenetic links between the classes (REGNÉLL, 1960). The origin of the classes is unknown.

Another very important observation relates to the great antiquity of the architectural plan on which each of the echinoderm classes is constructed. The earliest crinoids and first echinoids, for example, exhibit structural organization essentially similar to that of living crinoids and echinoids. Without doubt, in the course of phylogeny of each of these groups, important transformations that represent functional and morphological adaptations to different modes of life have been introduced as response to ecologic conditions. But fundamental anatomical plans have remained unchanged throughout the history of these classes. Even structures as complex as the Aristotle's lantern of echinoids may be traced back to the very distant past.

Extreme antiquity of essential structures of the classes is matched by like antiquity of their main systematic divisions. As soon as they appear, the "carpoids" are represented by three classes (Homostelea, Homoiostelea, Stylophora) and the cystoids by their two orders (Rhombifera, Diploporita); the Crinoidea (already in the Middle Ordovician) by three of their four subclasses (Camerata, Inadunata, Flexibilia); the Echinoidea by two of their orders (Bothriocidaroida, Echinocystitoida); the Stelleroidea, by their three subclasses (Somasteroidea, Asteroidea, Ophiuroidea). This so-very-early diversification carries far back in time the actual origin of the classes and shows that their differentiation must be much earlier than the moment represented by actual remains found in rock strata.

Another observation seems worthy of record, namely, that from the time of their appearance in the stratigraphic record, the echinoderms have been distributed into two large groups according to their habits with respect to environment—free forms, such as the mitrate and cornute "carpoids," stelleroids, and echinoids, and attached forms, such as the crinoids, cystoids, and blastoids. Already in earliest Cambrian time, free-living (helicoplacoids) and sessile forms (eocrinoids, edrioasteroids) were represented. The attached mode of life is generally referred to as **pelmatozoic**[1] (from *Pelmatozoa,* a term proposed by LEUCKART, 1848, and meaning animal, *zoon,* provided with a stalk, *pelma*) and the free mode of life as **eleutherozoic** (from *Eleutherozoa*, a name introduced by BELL, 1891, and meaning animal that moves freely, *eleutheros*). Typically pelmatozoic mode of life characterizes those echinoderms which, during the whole or at least the early portion of their existence, are attached either directly by the aboral surface or by an aboral jointed stalk; their oral surface is directed upward; their podia serve primarily as food-catching organs, their regimen is microphagous and their ambulacra, acting as food-grooves, carry food particles to the mouth by mucus-ciliating mechanisms; their anus generally opens on the oral surface or laterally, but never aborally. On the other hand, adoption of a free-living or eleutherozoic habit means that the animal develops locomotor mechanisms and a mode of nutrition which generally is nonciliary; the oral surface is directed downward or is located at one end of the body (holothuroids); the anus, if present, is typically aboral.

Customarily such contrasting characters as those just mentioned have been used as a basis for a division of the phylum Echinodermata into two subphyla, the Pelmatozoa and the Eleutherozoa. It has become more and more evident, however, that this grouping is less supported by real genetic affinities than by structural and functional analogies. Pelmatozoan and eleutherozoan characters have probably arisen independently, and at different times, in various echinoderm groups. Therefore, it does not seem possible to build a natural classification on the basis of the described characters alone (FELL, 1963, 1965).

Evidence furnished by comparative anatomy, embryology, and paleontology suggests that symmetry and patterns of dominant gradients of growth, which may be considered as innate features initially independent of the environment, probably constitute a better criterion for grouping of the classes in more comprehensive units. On such grounds, for subphyla[2] recently have been recognized by FELL (1965). They have been adopted in the present *Treatise,* as indicated in the following table.

Subphyla of Echinodermata

Subphylum HOMALOZOA. Echinoderms without radial symmetry and with fundamentally asymmetrical body. Included classes: HOMOIOSTELEA, HOMOSTELEA, STYLOPHORA (these three classes collectively called "carpoid" echinoderms), and possibly MACHAERIDIA.

Subphylum CRINOZOA. Echinoderms with radial symmetry, showing a partial meridional pattern of growth tending to produce an aboral cup-shaped or globoid plated test (theca) and a partial radially divergent pattern of growth forming appendages (brachioles or arms) which carry exothecal extensions of feeding ambulacra. Included classes: BLASTOIDEA,

---

[1] More rarely, statozoic (from Statozoa, a name coined by BELL, 1891, and meaning animal which is stationary, *statos*).

[2] Many other groupings of echinoderm classes have been proposed in the past. Most of them deserve no more than historical interest. Some seem worth recording because they have played a part in shaping basic concepts of the present classification. In the famous work in which he demonstrated that the echinoderms are to be regarded as a main division of the animal kingdom, LEUCKART (1848) divided the phylum into three classes, termed Pelmatozoa (including *"Cystideen"* and *"Crinoideen"* as orders), Actinozoa (including *"Echiniden"* and *"Asteriden"* as orders) and Scytodermata (including Holothuriae and Sipunculida as orders). In 1891, BELL proposed a rather complicated classification, in which the term Eleutherozoa (used for the first time) is opposed to the term Statozoa (practically a synonym of Pelmatozoa). This procedure seems to have initiated the dualistic division into Pelmatozoa and Eleutherozoa, popularized by BATHER (1899, 1900) and adopted in most treatises and textbooks published subsequently. In presenting his classification, BATHER was fully aware of the phylogenetic heterogeneity of the Eleutherozoa, but he judged the Pelmatozoa to comprise a closely related group. In 1929, however, he recognized the nonpelmatozoan nature of the "carpoids" (invariably placed among the Pelmatozoa until then) and recommended that they should be separated (along with the Machaeridia) from all other echinoderms. This led WHITEHOUSE (1941) to propose a new subphylum, Homalozoa, for both the "carpoids" and the machaeridians. On the other hand, ZITTEL (1895), following HAECKEL, recognized three subphyla—Pelmatozoa, Asterozoa, and Echinozoa, distributing the free-living echinoderms in two subphyla instead of one. A similar grouping was advocated by JAEKEL (1918), MATSUMOTO (1929), and especially by FELL (1962), who furnished evidence of the fallacious nature of the presumed significant similarities of the eleutherozoans.

Crinoidea, Cystoidea, Edrioblastoidea, Eocrinoidea, Parablastoidea, Paracrinoidea, and Lepidocystoidea.

Subphylum Asterozoa. Echinoderms with radial symmetry, showing a radially divergent pattern of growth which produces projecting rays and a star-shaped body. Included class: Stelleroidea, containing subclasses Somasteroidea, Asteroidea, and Ophiuroidea.

Subphylum Echinozoa. Echinoderms with radial symmetry, meridional pattern of growth producing an essentially globoid body, but no arms or projecting rays. Included classes: Cyclocystoidea, Echinoidea, Edrioasteroidea, Helicoplacoidea, Holothuroidea, Ophiocistioidea, and Camptostromatoidea.

The stratigraphic distribution of the subphyla and classes of the Echinodermata is shown graphically in Figure 21. However, this diagram has not been redrawn to include newly recognized classes defined by Durham—the curious Camptostromatoidea (L.Cam.), added to the Echinozoa, and Lepidocystoidea (L.Cam.), assigned to the Crinozoa. Also, the Holothuroidea possibly range into the Ordovician.

MAIN DIVISIONS OF ECHINODERMATA

HOMALOZOA

The subphylum Homalozoa—a term proposed by Whitehouse (1941) and meaning flat *(homalos)* animal *(zoon)*—comprises the exclusively fossil group (Middle Cambrian to Middle Devonian) of "carpoid" echinoderms and perhaps the enigmatic Machaeridia (Fig. 21).

As stated previously, the Homalozoa lack any trace of radial symmetry, a feature the importance of which had already been emphasized by Bather (1930), who proposed to divide the Echinodermata into two contrasted groups: the Echinoderma bilateralia comprising the "carpoids" and Machaeridia, and the Echinoderma radiata, containing all the other echinoderms. If the concept is sound, the term "bilateralia" is inappropriate, for it fails to recognize another of the most important features of these echinoderms, namely, their fundamental asymmetry.

The Machaeridia were marine animals with body enclosed in an elongate, bilaterally symmetrical shell composed of an even number of longitudinal columns of plates. They have been referred to the Mollusca, Annelida, Arthropoda, and (because their plates are composed of crystalline calcite showing, in at least one genus, the cleavage characteristic of echinoderms) to the Echinodermata. Among echinoderms, they have been regarded either as a distinct group representing an early offshoot from the echinoderm stem (Bather) or as isolated parts of the body of forms belonging to other classes. On this last hypothesis, some of them have been considered as the stem of "carpoids" (Woodward), the cover plates enveloping the spines of mitrate "carpoids" (Pope), or the tube feet of ophiocistioids (Nichols).

If the assignment of Machaeridia to Echinodermata remains an open question, the same doubt regarding the "carpoids" would not be permissible, for (1) their stereom is formed of crystalline calcite displaying the reticulate microstructure characteristic of this phylum, and (2) most of them possess an ambulacral groove organized according to the typical echinoderm pattern.

The "carpoids" have been and still are commonly classed with the pelmatozoan echinoderms. No morphologically intermediate forms are known between them and the other echinoderms, however. They constitute a very isolated group, characterized primarily by their asymmetry, on which radial symmetry has never been imposed. This lack of radial symmetry is probably related to the fact that their water-vascular system did not produce five primary tentacles, but sent only one extension into a single ambulacrum, which may be looked upon as an unpaired lophophore structure. All of them are depressed and they seem to have experienced some sort of eleutherozoic existence. They probably belong to another and apparently much more primitive adaptive radiation than those that produced the radiate echinoderms.

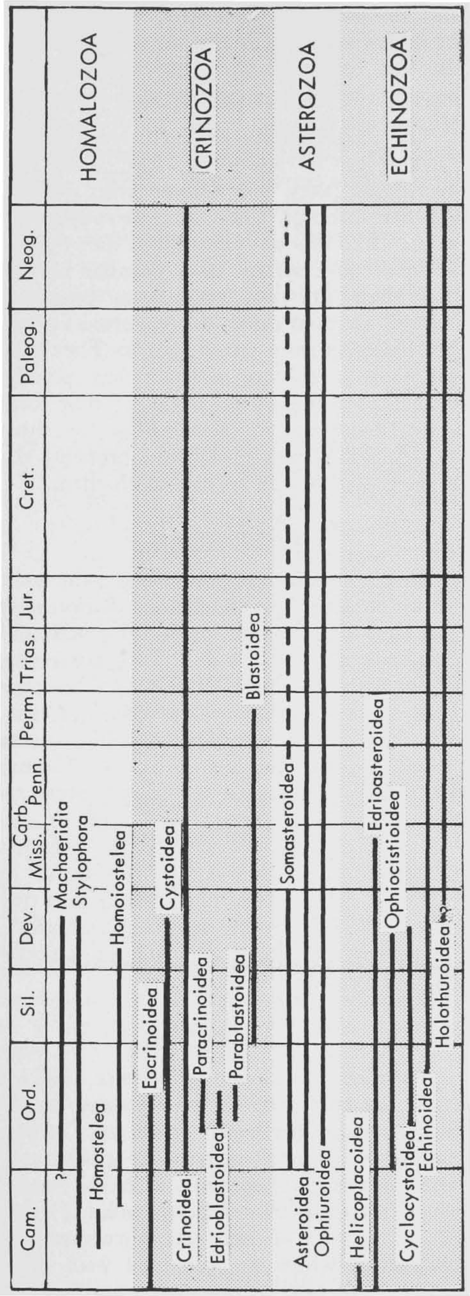

FIG. 21. Stratigraphic distribution of subphyla and class of Echinodermata (Ubaghs, n). [Added groups include the echinozoan class Camptostromatoidea (L. Cam.) and crinozoan class Lepidocystoidea (L. Cam.).]

The "carpoids" were first recognized as an independent class by JAEKEL (1901), who divided it later (1918) into four orders: Cincta, Cornuta, Mitrata, and Soluta. To these, GEKKER (1938) added the new order Digitata to include *Rhipidocystis*. Now it appears that this assemblage is quite heterogeneous. Firstly, *Rhipidocystis* differs from all other "carpoids" in having strongly developed brachioles and other crinozoan features; it seems preferable to place it among the Eocrinoidea (UBAGHS, 1961). Secondly, whereas the Cornuta and the Mitrata present the same basic organization, they differ as much from the Cincta and Soluta as the two latter differ between themselves. These orders, except the two first ones, are so widely apart that relationships between them cannot be satisfactorily proven. They may represent unrelated, or at least remote, remnants of an early preradiate echinoderm stock. Therefore, it seems better to treat them as separate classes: Homostelea, containing the Cincta; Homoiostelea, comprising the Soluta; and Stylophora, grouping together the Cornuta and Mitrata.

CRINOZOA

The Crinozoa, a name proposed by MATSUMOTO (1929), are echinoderms which are 1) affected in varying degree by radial (generally pentamerous) symmetry; 2) typically characterized by a globoid, pyriform, or cup-shaped body (theca) enclosing the visceral mass or the main part of it, and 3) provided with food-gathering appendages which are either simple exothecal projections (brachioles of noncrinoid Crinozoa) or evaginations of the body wall carrying extensions of the coeloms and various systems of organs with them (arms of crinoids). In the theca, the meridional pattern of growth appears dominant, whereas in the food-gathering appendages (particularly the arms of crinoids), it is the radially divergent pattern which is prevalent. Crinozoa are attached more or less permanently to the substrate, either directly by their aboral surface, or more generally by an aboral jointed stalk. Their oral surface is typically directed upward. Their podia serve primarily as food-catching organs; their regimen is microphagous and their ambulacra act as food grooves. The anus generally opens on the oral surface and, though it may be found on the side of the theca, is never strictly aboral. All members of this subphylum, except crinoids, are exclusively Paleozoic.

The subphylum Crinozoa, as here defined, corresponds to the subphylum Pelmatozoa of many other classifications, except that it does not include the "carpoids," which are classified among the Homalozoa, and the classes Edrioasteroidea and Cyclocystoidea, which are transferred to the Echinozoa. As so restricted, it comprises eight classes: Eocrinoidea, Paracrinoidea, Cystoidea, Blastoidea, Parablastoidea, Edrioblastoidea, Lepidocystoidea, and Crinoidea. Such classes seem to have unequal value, whether one considers numbers of their representatives, diversity within each group, distribution in geologic time, or importance in stratigraphic paleontology. To judge them according to purely morphological criteria, certain classes, such as the Crinoidea and Blastoidea, seem to form natural groups having well-defined morphological attributes, but others may well represent artificial or heterogeneous assemblages.

EOCRINOIDEA

The oldest known crinozoans are Lower Cambrian members of the Eocrinoidea (Fig. 21). This group, introduced by JAEKEL (1918) as a subclass of the Crinoidea, was elevated to class rank by REGNÉLL (1945). It comprises heterogeneous assemblage of genera, some of which are still inadequately known. Though the organization of at least many of their representatives is essentially cystoid-like, they differ from typical cystoids either in their entire lack of thecal pores or in the presence of sutural pores which are basically different from the diplopores and pore rhombs of the true cystoids. On the other hand, most of their so-called crinoidal features are demonstrably homoplastic resemblances—especially one cannot homologize their brachioles with the arms of crinoids. Therefore, it does not seem possible to refer eocrinoids to the Cystoidea, as now restricted, and still less to the Crinoidea. Thus, it appears convenient to regard them, at least provisionally, as a separate class. Remains of Eocrinoidea have not been found in terrain younger than Middle Ordovician.

PARACRINOIDEA

The Paracrinoidea are exclusively Middle Ordovician in age (Fig. 21). Like the eocrinoids, they are neither true cystoids nor true crinoids. Their theca is constructed mainly like that of cystoids, but they possess a thecal pore system of a peculiar nature, and their uniserial or biserial pinnulate "arms" seem to differ as well from cystoid brachioles as from crinoid arms. They may represent a line of development parallel with that of these groups or they may form an artificial entity. Recognition of them as a separate class constitutes probably the most practical way to deal with them.

CYSTOIDEA

The Cystoidea comprise one of the most important classes of the Crinozoa. Formerly they included in addition to all noncrinoid Crinozoa, the "carpoids," Edrioasteroidea, and Cyclocystoidea. Nowadays, the class generally is restricted to noncrinoid Crinozoa that possess special pores piercing the thecal skeleton (diplopores, pore rhombs) and biserial brachioles; radial symmetry affects their food grooves and, only in advanced members, the thecal plates. Patterns of growth are dominantly meridional in many of them. They are divided into two orders, the Rhombifera and the Diploporita, of unknown origin, which may have developed independently.

BLASTOIDEA

Blastoidea are a fairly distinct class of Crinozoa characterized by 1) their highly developed pentamerous symmetry, 2) prevailing meridional pattern of growth, 3) uniformity of arrangement of their 18 to 21 thecal plates in four definite cycles, 4) specialized nature of their recumbent ambulacral areas, which are provided with great many small biserial brachioles, and 5) particularly distinctive structures and localization of their hydrospires (calcareous infolds of the thecal wall which hang into the body cavity beneath each ambulacrum). They are known from Silurian to Permian (Fig. 21). It has been maintained mainly by JAEKEL (1918) and REGNÉLL (1945) that the blastoids should be considered as a subclass or order of the Cystoidea, especially because the hydrospires may be regarded as a variety of thecal pores and because biserial brachioles are present in both groups. While thecal pores and biserial brachioles exist also in many Eocrinoidea, the distinctiveness of the Blastoidea as a whole and the very special structure and arrangement of their hydrospires make it desirable to separate the group as a class, as now usually is done.

PARABLASTOIDEA

The Parablastoidea are a very small group erected by HUDSON (1907) (as an order of the Blastoidea) for the Middle Ordovician (Chazyan) genus *Blastoidocrinus* BILLINGS (Fig. 21). This form, which recalls the Blastoidea in many respects, differs from them in important features, such as number of thecal plates and structure of the ambulacra. Of unknown ancestry and descent, these echinoderms may well represent an aberrant and unsuccessful offshoot of an early blastoid stock.

EDRIOBLASTOIDEA

The Edrioblastoidea contain so far a single genus, *Astrocystites* WHITEAVES, from the Middle Ordovician of North America (Fig. 21). This genus, of an exclusively meridional pattern of growth, differs from all other Crinozoa in lacking arms and brachioles and in having ambulacral pores, as in the Edrioasteridae, a family of Edrioasteroidea. It is separated, however, from typical members of this class in being provided with a well-defined jointed stem and in having a theca superficially like that of blastoids. Customarily it has been placed among the Edrioasteroidea, but FAY (1961) erected a new class, the Edrioblastoidea, to receive it.

CRINOIDEA

The Crinoidea constitute the most diversified class of the Crinozoa. They are stalked or (but secondarily) stalkless pentamerous echinoderms. Their theca, reduced to an aboral cup covered orally by a vault or tegmen, bears radially outspread food-gathering arms, which generally are branched. Therefore, the theca alone retains the meridional pattern of growth. The arms differ fundamentally from brachioles of noncrinoid Crinozoa. Whereas brachioles are simple external processes of the theca supported by their own small endoskeletal pieces, crinoid arms are evaginations of the body wall containing extensions of the food grooves, coelom, and nervous, water-vascular, hemal, and reproductive systems, and they are supported by plates directly continuous with the radial plates of the theca. The fact that crinoid arms and the brachioles of noncrinoid Crinozoa are not homologous renders particularly puzzling the problem of the origin of the crinoids. They first appear in the Lower Ordovician with all of their essential features, and no morphological intermediates are known which suppress or reduce the gap existing between them and older, more primitive crinozoans. The crinoids, like other classes of Crinozoa, flourished especially during the Paleozoic Era, contributing in large areas to the formation of thick sedimentary deposits. Since the Early Triassic, they have been represented only by the Articulata, one of the four subclasses which may be distinguished among them (Fig. 21).

The morphologic and phylogenetic hiatuses that separate the classes of the subphylum Crinozoa from one another are probably not of the same importance. Some are widely apart, whereas others seem to be somewhat closely allied. The precise origin of all of them is unknown and their interrelationships are very puzzling. Yet the unity of general crinozoan organization supports judgment that the classes may be derived from a common, though uncertain, source belonging undoubtedly to the very distant past. The eocrinoids sometimes have been interpreted as such a possible source. This concept finds support in the fact that they precede known representatives of other classes in time. They may indeed contain ancestors of the cystoids, from which some of them are kept apart by rather artificial distinctions. But possible relationships with other classes, and particularly with the crinoids, remain purely conjectural. The so-called crinoidal features of eocrinoids seem generally based on superficial resemblances.

One does not know any intermediate between eocrinoids and crinoids, or between eocrinoids and paracrinoids, blastoids, parablastoids, and edrioblastoids. It must be emphasized that the time of origin of all classes, each of which possesses its distinctive features from first appearance in the geological record, must be much more remote than it is presently known. The problem of origins remains an open question.

ASTEROZOA

The Asterozoa are radiate free echinoderms that possess a depressed, pentagonal or star-shaped body, consisting of a central disc and typically five rays or arms. This shape results from the fact that growth operates in the horizontal plane along five radially divergent axes around the oral pole, and not, as in Echinozoa, along meridional directions. As a rule the mouth is inferior and always central in position. The tube feet are restricted to the undersurface of the rays. The radial water canals and other radial structures lie on the oral side of the ambulacral plates.

They comprise the asteroids, ophiuroids, and somasteroids. Among modern animals, the asteroids and ophiuroids constitute two well-separated groups, to which most zoologists accord the rank of class. The ophiuroids, however, after metamorphosis, pass through an asteroid stage, characterized among other things by an aboral skeleton closely comparable to that of a juvenile asteroid. Comparative anatomy also shows that the two groups are constructed essentially on the same plan and indicates, with the full support of paleontology, that they converge toward the same source (somasteroids) from which the segregation of asteroid and ophiuroid characters seems to have developed in progressive, divergent manner. It appears, therefore, advisable to consider the somasteroids, asteroids, and ophiuroids as subclasses of a single class, the Stelleroidea, rather than as separate classes.

Some zoologists, in opposition to this view, completely separate the ophiuroids from asteroids so as to align them with the echinoids. This is based on 1) resemblance of the ophiopluteus and echinopluteus larval stages, 2) the existence of a vestibule in the larvae of echinoids and vestiges of it in the larvae of ophiuroids, whereas this structure is absent in the larvae of asteroids, 3) the presence of an epineural canal (instead of the open ambulacral furrow of asteroids) in echinoids and ophiuroids, and 4) observation previously noted that the sterols of ophiuroids (at least of examined species) belong to the same type as those of studied echinoids, whereas the sterols of asteroids are of a different type. These arguments do not seem to be convincing. Indeed, they lend to embryologic and biochemical analogies a phylogenetic meaning that remains to be demonstrated, and they overlook allowance of the possibility that the common features just mentioned between ophiuroids and echinoids could have been acquired independently. As a matter of fact, they strongly conflict with all other evidence, such as that derived from postlarval ontogeny, morphology, and paleontology. Paleontological observations, in particular, suggest a very clear morphological convergence of ophiuroids and asteroids in the direction of a common source, whereas comparison of the history of ophiuroids and echinoids shows that the two groups have followed very distinct pathways since their known initial appearance.

Jaekel (1918), Bather (1901, 1915), and others have postulated the Edrioasteroidea as a possible source of the Asterozoa. It is the nature of their ambulacral furrows, the presence of pores interpreted as ambulacral pores, and the absence of free arms and brachioles that seems to bring them nearer the asterozoans in the same degree as these characters separate them from crinozoans. Besides, the first edrioasteroids considerably precede in time the earliest known asterozoans, and if some of them were firmly attached to the substratum, others could have simply rested on the sea bottom. However this may be, the transformation of an edrioasteroid into an asterozoan would have implied very considerable structural and adaptative modifications, as shown by Bather (1915) with considerable ingenuity. This hypothesis, we must say, has not received the confirmation that discovery of the most ancient known stelleroids by Spencer (1951) should have furnished in its support. Contrariwise, as demonstrated by Fell (1963), the endoskeleton of archaic asterozoans has a fundamental pinnate structure entirely different from that shown by edrioasteroids. If, therefore, some superficial resemblance exists between edrioasteroids and asterozoans, it seems to be ascribed to convergence, rather than genetic relationship.

According to FELL (1963), analysis of the growth patterns exhibited by the endoskeletal elements and related soft structures in fossil and extant stelleroids allows recognition of the original characters of the class. These characters, as illustrated by somasteroids, are exclusively crinozoan. They indicate that the Asterozoa must have arisen from some pinnulate crinozoan stock, namely from some pinnulate crinoid. Indeed, the oral skeleton of the arms of somasteroids resembles that of a pinnulate arm of crinoids to some extent. It is built of elongate rods *(virgalia)* arranged in obliquely transverse rows on either side of the axial series of ambulacral ossicles, as are pinnular ossicles to the brachial ossicles of crinoids. The rows of virgalia form the lateral walls of intervening grooves, protected by cover plates inserted on adjacent virgalia. In these grooves ciliary activity conveys water currents to the main radial groove, and thence to the mouth. Thus, a microphagous ciliary feeding, involving pinnately arranged food grooves, is found in archaic asterozoans, as in pinnulate crinoids.

The analogy is admittedly great, but, to my mind, of a rather superficial nature. Virgalia and pinnulars differ in many respects. The pinnate food grooves of somasteroids have not the same organization as those of the pinnules of crinoids, for 1) they are not carried *on* the virgalia, but lie *between* them; 2) they are not accompanied by extensions from the water-vascular and other systems of organs or cavities as are the food grooves of the pinnules of crinoids, but are just ciliated furrows; 3) they are not small arms, like the pinnules of crinoids, which morphologically are dwarfed arms, and 4) they are apparently of a primary origin, whereas the pinnules of crinoids are demonstrably of secondary origin. Many other and important differences exist between the general anatomy of somasteroids and that of crinoids, and earliest known representatives of the two groups, associated in the same Lower Ordovician beds, far from showing a closer resemblance, appear more distinct than their extant relatives. However appealing they may be, such explanations as those given by FELL remain hypothetical to a large extent, and as long as one has to rely only on them, it seems advisable to reserve judgment.

ECHINOZOA

Echinozoa are typically radiate echinoderms, with a cylindrical, ovoid, fusiform, pyriform, globose, cordiform, or discoid body. Divergent radial axes of growth never arise, but a meridional pattern of development appears to be a fundamental feature of the subphylum. The Echinozoa differ radically from the Asterozoa in their complete lack of outspread rays and from Crinozoa in never having feeding appendages, such as the arms of crinoids or brachioles of cystoids projecting from the body. Most of them are free-moving, but some, like the cyclocystoids and edrioasteroids, are pelmatozoic animals. According to the classification adopted in the present *Treatise,* they comprise seven classes—Helicoplacoidea, Holothuroidea, Ophiocistioidea, Cyclocystoidea, Edrioasteroidea, Camptostromatoidea, and Echinoidea.

HELICOPLACOIDEA

Helicoplacoidea comprise a few genera from the Lower Cambrian *Olenellus* zone of California, Nevada, and Canada. They were free-living echinoderms, characterized by a fusiform (when expanded) to pyriform (when contracted) spirally coiled and heavily plated body, with an expansible and flexible test and with oral and apical poles at opposite extremities. The lack of arms, shape of the body, the origination of new plates from the apical pole and the free-living character suggest that these echinoderms are related to the subphylum Echinozoa. They differ however from all other known Echinozoa by the presence of generally single ambulacrum—a character which they share with the "carpoid" echinoderms Stylophora and Homoiostelea—the spiral arrangement of both the ambulacral and "interambulacral" columns of plates, and the nature of the ambulacrum, covered by a pavement of small plates. Podial pores arranged in a row on each side of the ambulacrum which indicate the presence of an internal "radial" water vascular canal have recently been recognized. The origin of Helicoplacoidea is unknown and their relation with other echinoderms problematical. They may well represent an aberrant offshoot from some Precambrian echinoderm stock.

EDRIOASTEROIDEA

The Edrioasteroidea appear also in the Lower Cambrian, with all of their typical features (Fig. 21). Their origin is not known. They are pelmatozoic echinoderms, and it is in the subphylum Pelmatozoa that they have been included customarily. They differ however from most representatives of this now rejected subphylum in having a purely meridional pattern of symmetry —they lack arms, brachioles, or protruding rays—and in having ambulacral pores which suggest the existence of tube feet provided with ampullae, as in many echinozoans and asterozoans. Besides, they are stemless, or at least never have a typical stem, such as characterizes crinoids and cystoids; some of their earliest representatives may even have rested loose on the sea bottom. In some dendrochirote holothuroids the pharyngeal skeleton is not unlike the calcareous oral ring and the associated ambulacral plates of some edrioasteroids—an analogy regarded by Fell (1965) as suggesting that the Edrioasteroidea, like the Holothuroidea, descended from a common echinozoan stock. The inclusion of edrioasteroids in Pelmatozoa has been questioned by Matsumoto (1929), Lameere (1931), and Fell (1965), who consider that their pelmatozoan features are purely secondary responses to adoption of a sessile mode of life. Reasons for including them (and Cyclocystoidea) in the Echinozoa are given in Part U of the present *Treatise*.

HOLOTHUROIDEA

The origin and relationships of the other classes included in the subphylum Echinozoa offer problems for which no satisfying answers have been given. From a morphological point of view, the holothuroids, which do not move about on their oral surface and have only a single gonad, are unlike other free-living radiate echinoderms which travel on their oral surface and exhibit a genital system (at least in Recent representatives) influenced by radial symmetry. The Holothuroidea are identified as primitive in having only a single gonad and the observation that their gonopore and hydropore have retained original positions in the *CD* interray. The fact that their ambulacra are closed does not indicate any particular relationship, since this feature has been independently acquired in ophiuroids and echinoids. Comparative study of the internal endoskeleton of the pharyngeal region of dendrochirote holothurians suggests, however, that this endoskeleton possibly represents invaginated remnants of ambulacral ossicles similar to those found in some edrioasteroids (Fell, 1965). Nevertheless, the existence of real connections between these two classes remains hypothetical, since the paleontological history of the Holothuroidea is very inadequately known.

ECHINOIDEA

Echinoids form a well-defined group and no known representatives, fossil or living, exhibit features suggesting close relationships to any other class of echinoderms. As rightly observed by Durham & Melville (1957), the ancestral form of echinoids should have evolutionary potentialities able to produce in the Late Ordovician two types as different as *Bothriocidaris* and *Aulechinus*. This observation requires reference of the origin of the class to such a remote time that knowledge of it is at present conjectural. Diverse hypotheses have been formulated, such as derivation of the echinoids from edrioasteroids, from a primitive holothurian stock, or from diploporite cystoids. Each of these hypotheses has received appropriate critical review and none appears convincing at the present time.

OPHIOCISTIOIDEA

The class of the ophiocistioids include five genera, exclusively Paleozoic, the general organization of which does not seem expressed by that of other echinoderm classes. An affinity of the ophiocistioids with ophiuroids has been suggested by several authors, but the points of similarity between the two groups are demonstrably superficial. The resemblance to archaic echinoids seems somewhat greater, but it is with the very young echinoids, in process of metamorphosis or just after metamorphosis, that they show the most remarkable likeness. One may question whether they are not neotenic Echinozoa. Yet the differences from other classes are such as to warrant the appropriateness of regarding the ophiocistioids as a distinct group that became extinct without leaving known descendants.

REFERENCES

Bather, F. A.

(1) 1901, *What is an echinoderm?:* City London Coll. Sci. Soc., Jour., v. 8, p. 21-23.

(2) 1929, *Echinoderma:* in the Encyclopaedia Britannica, 14th edit., p. 895-904, University Press (Cambridge, Eng.).

———, Gregory, J. W., & Goodrich, E. S.

(3) 1900, *The Echinoderma:* in E. R. Lankester, A treatise on zoology, v. 3, p. 1-344, A. & C. Black (London).

Boolootian, R. A., & Campbell, J. L.

(3a) 1964, *A primitive heart in the echinoid Strongylocentrotus purpuratus:* Science, v. 145, p. 173-175, 4 text fig. (1 fig. on cover).

Clark, A. M.

(4) 1962, *Starfishes and their relations:* 119 p., 16 pl., 30 text fig., British Museum (Nat. History) (London).

Clarke, F. W., & Wheeler, W. C.

(5) 1922, *The inorganic constituents of marine invertebrates:* U.S. Geol. Survey, Prof. Paper 124, 62 p.

Cuénot, Lucien

(6) 1891, *Études morphologiques sur les échinodermes:* Arch. Biologie, v. 11, p. 313-680.

(7) 1948, *Anatomie, éthologie et systématique des échinodermes:* in P.-P. Grasse (ed.), Traité de zoologie, v. 11, p. 3-275, text fig. 1-312, Masson et Cie (Paris).

Dawydoff, Constantin

(8) 1948, *Embryologie des échinodermes:* in P.-P. Grasse (ed.), Traité de zoologie, v. 11, p. 277-363, Masson et Cie (Paris).

Delage, Yves, & Hérouard, Edouard

(9) 1903, *Les echinodermes:* in Traité de zoologie concrète, p. 1-495, Le Soudier (Paris).

Durham, J. W., & Caster, K. E.

(10) 1963, *Helicoplacoidea, a new class of echinoderms:* Science, v. 140, p. 820-822, text fig. 1.

Fell, H. B.

(11) 1948, *Echinoderm embryology and the origin of chordates:* Biol. Reviews, v. 23, p. 81-107.

(12) 1965, *Early evolution of the Echinozoa:* Harvard Univ., Museum Comp. Zoology, Breviora, v. 219, p. 1-17, text fig. 1-13.

Gekker [Hecker], R. F. (ed.)

(13) 1964 (1965), *Iglokozhie, gemikhordovye, pogonofory, i shchetinkochelyustnye:* in Yu. A. Orlov, Osnovy paleontologii, 383 p., 48 pl., 324 text fig. (Moscow). [*Echinoderms, hemichordates, pogonophores and chaetognaths.*]

Heider, Karl

(14) 1922, *Ueber Organverlangerungen bei der Echinodermen-Metamorphose:* Deutsch. Zool. Gesell., Verhandl., Jahresv. 22, p. 239-251.

Hyman, L. H.

(15) 1955, *The invertebrates: Echinodermata:* vii +763 p., 280 text fig., McGraw-Hill (New York, Toronto, London).

Lameere, August

(16) 1931, *Précis de zoologie:* v. 2, 456 p., Doin (Paris).

Lang, Arnold

(17) 1894, *Lehrbuch der vergleichenden Anatomie der Echinodermen und Enteropneusten:* 4. Theil, von Lang's Lehrbuch der vergleichenden Anatomie der wirbellosen Thiere, p. 871-1198, Fischer (Jena).

Ludwig, H., & Hamann, O.

(18) 1889-1907, *Echinodermen:* in H. G. Bronn's Klassen und Ordnungen des Thier-Reichs, v. 2, Abt. 3, Buch 1-5, p. 1-1602, C. F. Winter (Leipzig).

MacBride, E. W.

(19) 1906, *Echinodermata:* in S. F. Harmer, & A. E. Shipley (eds.), Cambridge Natural History, v. 1, p. 425-623, text fig. 185-296, Macmillan (London). [Reprinted, 1909.]

Matsumoto, Hikoshichirô

(20) 1929, *Outline of a classification of the Echinodermata:* Tohoku Univ., Sci. Repts., ser. 2 (Geol.), v. 13, no. 2, p. 27-33.

Moore, R. C.

(21) 1954, *Echinodermata: Pelmatozoa:* in Status of invertebrate paleontology, B. Kummel (ed.), Harvard Univ., Museum Comp. Zoology, Bull., v. 112, no. 3, p. 125-149, 8 text fig.

(22) 1960, *Echinodermata fossils:* in McGraw-

Hill Encyclopedia, p. 363-372, McGraw-Hill (New York).

———, Lalicker, C. G., & Fischer, A. G.
(23) 1952, *Invertebrate fossils:* 766 p., 451 text fig., McGraw-Hill (New York).

Müller, A. H.
(24) 1963, *Lehrbuch der Paläozoologie, Bd. II Invertebraten, Teil 3, Arthropoda 2—Stomochorda:* xvii+698 p., 854 text fig., Gustav Fischer (Jena).

Nichols, David
(25) 1962, *Echinoderms:* 200 p., 26 text fig., Hutchinson Univ. Library (London).

Piveteau, Jean (ed.)
(26) 1953, *Traité de paléontologie,* v. 3, *Les formes ultimes d'invertébrés. Morphologie et évolution:* 1063 p., text fig., Masson et Cie (Paris).

Raup, D. M.
(27) 1965, *Crystal orientation in the echinoid apical system:* Jour. Paleontology, v. 39, p. 934-951.

Regnéll, Gerhard
(28) 1945, *Non-crinoid Pelmatozoa from the Paleozoic of Sweden:* Lunds Geol.-Mineral. Inst., Medd., v. 108, viii+255 p., 15 pl., 30 text fig.
(29) 1960, *"Intermediate" forms in early Palaeozoic echinoderms:* Internatl. Geol. Congress, Rept. XXI Session, Norden, pt. 22, p. 71-80 (Copenhagen).

ECHINODERM ONTOGENY

By H. Barraclough Fell

CONTENTS

GENERAL FEATURES

Development in echinoderms may be indirect, involving pelagic, bilaterally symmetrical, larval forms, or more or less direct, with the larval stage either reduced or omitted. Of the extant classes, only the Echinoidea are characterized by being predominantly of the type with indirect development. The main features of development and the interrelationships of echinoderm larvae were elucidated by Johannes Müller (30), who demonstrated that four chief types of larvae exist, and that in each the final larval form arises from a preceding simpler form, now known as the **dipleurula.**

The fundamental plan of development is represented in Figure 22. The dipleurula arises from the preceding gastrula stage by the formation of a ciliated (or vibratile) band (Fig. 22,*1*) which forms a closed loop about the mouth. A simple alimentary canal is present, comprising stomodeum, archenteron or stomach, and proctodeum; the anus is generally, but not invariably, formed from the blastopore. In its subsequent development the dipleurula undergoes a transformation varying in accordance with the systematic position of the parent species.

In the Echinoidea and Ophiuroidea, the development of paired processes, or arms on either side of the body, upon which the ciliated band becomes extended, leads to formation of the simple **pluteus** (Fig. 22,*2*). Further development of paired arms, strengthened by internal calcareous rods, leads to the final larval forms, distinguished by Mortensen (1898) as **echinopluteus** and **ophiopluteus.**

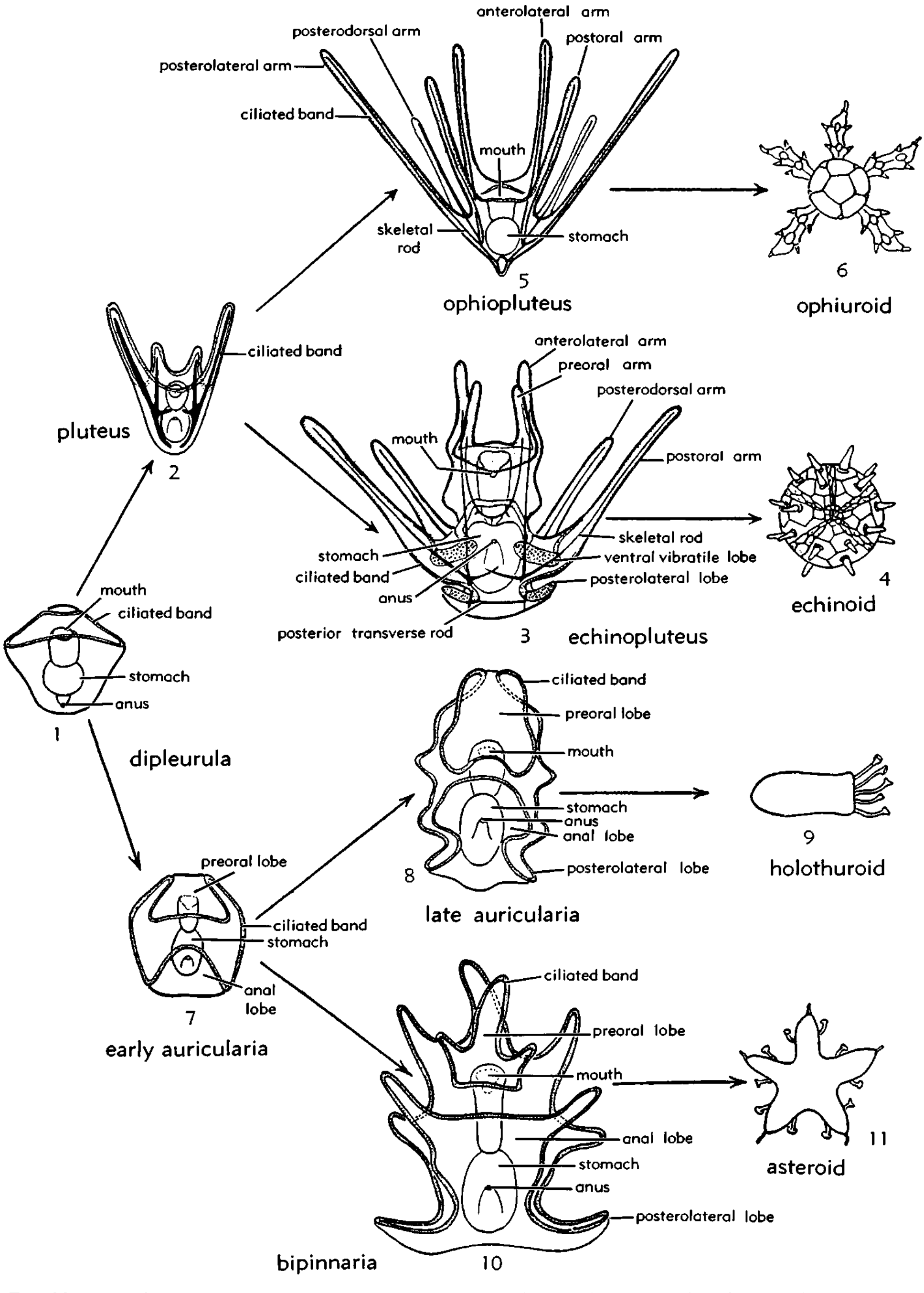

Fig. 22. General scheme illustrating relationships between bilaterally symmetrical larvae of echinoderms inferred from their morphology. *1,* Dipleurula; *2,* pluteus; *3,* echinopluteus, which metamorphoses into *4,* young echinoid; *5,* ophiopluteus, which metamorphoses into *6,* young ophiuroid; *7,* early auricularia; *8,* fully developed auricularia, which metamorphoses into *9,* young holothuroid; *10,* bipinnaria, which metamorphoses into *11,* young asteroid (8).

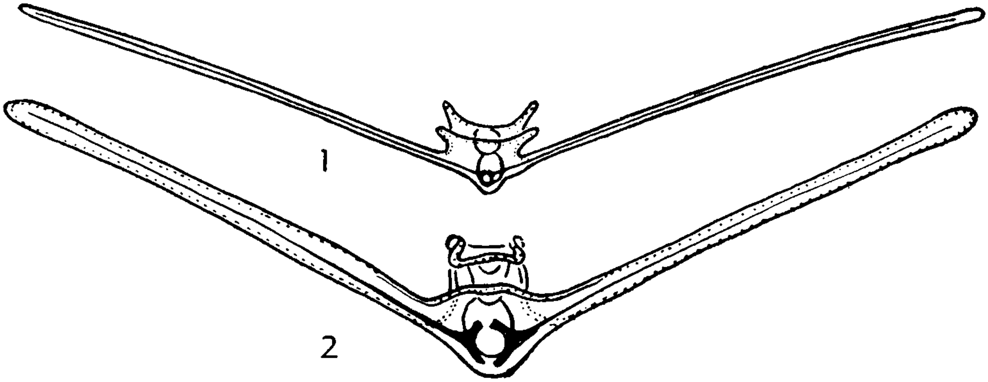

FIG. 23. Convergent larval forms. *1*, Ophiuroid, *Ophiothrix;* *2*, echinoid, *Diadema* (8).

The echinopluteus usually possesses four pairs of arms (Fig. 22,*3*), though more or fewer may be present in certain forms. The four principal pairs of arms comprise two anterior pairs, the anterolateral and preoral pairs, and two posterior pairs, the postoral and the posterodorsal pairs. In addition, at the extreme posterior end of the body are commonly found a pair of posterolateral processes, which may be elongated to form distinct posterolateral arms. Anterodorsal arms occur in certain forms as a still further complexity (compare Fig. 29,*11*, a spatangoid echinopluteus). These various arms are supported by slender calcareous rods, which may form a mesh about the archenteron at their inner extremities within the body; commonly a special posterior transverse rod is formed between the posterolateral processes. Certain portions of the ciliated band may become thickened dorsally and ventrally to form the paired dorsal and ventral vibratile lobes; or these may become separated from the main band to form prominent epaulets (see Fig. 29,*7*).

The ophiopluteus (Fig. 22,*5*), if fully developed, is of rather similar appearance, having four pairs of arms, which, however, do not correspond altogether to the four pairs commonly present in the echinopluteus. It is usual that the most prominent and enduring arms are those termed the posterolateral pair, which MORTENSEN has shown to be homologous with the posterolateral lobes of the normally formed echinopluteus. The other arms are the anterolateral, postoral, and posterodorsal pairs, respectively. The preoral arms of the echinopluteus are not represented. The internal skeleton takes the form of a pair of calcareous rods in the body, each sending branches into the four arms on its corresponding side; the posterior transverse rod is not represented.

In larvae of the Holothuroidea and Asteroidea no comparable development of paired arms occurs. Initially the dipleurula becomes rather barrel-shaped (Fig. 22,*7*), and the ciliated band is thrown into folds in an anterior and posterior loop. Further sinuous growth of the ciliated band leads to the characteristic larval forms designated as **auricularia** in holothurians and **bipinnaria** in asteroids.

The auricularia (Fig. 22,*8*) is characterized by the formation of two lobes bordered by the folded ciliated band, the preoral lobe anteriorly, and the anal lobe posteriorly, the latter bearing the anus. The mouth lies in a depression on the ventral side, between the preoral and anal lobes. Smaller posterolateral lobes occur in the same relative position as in the preceding larvae.

The bipinnaria is much more variable in structure. In some, especially primitive starfish, it is scarcely distinguishable from the simple auricularia. More frequently the sinuous lobes of the ciliated band become drawn out into prominent arms (Fig. 22,*10*) which, however, lack skeletal rods. Consequently, they are not rigid and are utilized as flexible swimming organs. Posterolateral lobes are usually found as in the auricularia. Median arms often appear anteriorly to the mouth, on the preoral lobe. It is usual for the bipinnaria stage to be followed by what is termed a brachiolaria larva, distinguished principally by the development of median sucking arms (or disc) anterior to the mouth, by means of which the larva may become temporarily attached.

Metamorphosis in each case involves either discarding or absorbing the paired larval structures, while a secondary radial symmetry is initiated through encirclement of the gut by the five lobes of the hydrocoel.

The embryology of crinoids, so far as known, does not include a comparable bilaterally symmetrical larva, and the mode of development is so different that it cannot be treated in the scheme just outlined. Many echinoderms other than crinoids also undergo development of an entirely different character from the basic plan described above. In species with large yolky eggs the larva is commonly a simple cylindrical form with a number of transverse ciliated bands. This type, which is sluggish and does not take food, has been termed the **vitellaria.** It is formed variously, and the internal organogeny differs according to the class. Echinoderm larvae occasionally grow to a considerable size. Thus the bipinnaria of *Luidia sarsi* reaches a length of 2.4 cm.

The above facts offer interesting problems. The general occurrence of a pelagic bilaterally symmetrical dipleurula stage in four of the existing classes has been interpreted as a recapitulation of the hypothetical dipleurula form from which all echinoderms are supposed to have descended. This view has not been seriously questioned and remains acceptable to taxonomists and embryologists alike. But beyond this point matters are less clear. Are the succeeding larval stages to be interpreted in the same light? If so, we would be led to conclude that ophiuroids and echinoids, with their similar pluteus stages, are more closely related to each other than to any of the remaining classes. Neither taxonomic nor paleontological evidence supports such a deduction. The only alternative is to regard the characteristic postdipleurula larval stages as digressions from the original path of development, which have arisen independently in the various classes. They may have arisen in response to the need for a temporary food-gathering stage as a preliminary to further development; for they almost invariably arise from eggs which are deficient in yolk and cytoplasm.

A more specific examination of modes of echinoderm development also leads inevitably to the conclusion that special larval evolution has occurred, often quite independently of natural groupings, as the following cases illustrate.

It is instructive to compare the larval development of an ophiuroid such as *Ophiothrix* with that of echinoids of the genus *Diadema.* The echinopluteus of the latter is greatly modified through unusual development of the postoral arms and reduction of the other arms, so that it superficially resembles an ophiopluteus (Fig. 23). This case, in which adults conspicuously distinct and only remotely related possess surprisingly similar larval forms, permits of only one interpretation: convergent embryonic evolution has occurred in the echinoid, which temporarily resembles an ophiuroid stage.

Even more striking is the case of the vitellaria larva (Fig. 24). This characteristic cylindrical larva with ciliated annulations, derived from a yolky egg, occurs in three classes, holothurians and crinoids commonly, and ophiuroids rarely. Although GRAVE (17) regarded this larva as representing an original primitive form, this view has received much less attention than it deserves.

Divergent evolution in larval development is also strikingly illustrated throughout the phylum. In ophiuroids, for example, quite diverse modes of development occur (Fig. 25). The case of *Amphiura* is illustrative. Two closely related species of this genus develop so differently that, were the adults unknown, the young stages could hardly be recognized as belonging to the same class, certainly not to the same genus. Nor is this an isolated case, for examples can be found in other genera, such as *Ophiura.*

The conclusion to be drawn from such data is that embryos and larvae of echinoderms are extremely plastic, often exhibiting convergence, divergence, and adaptation susceptible to evolutionary modifications of structure which may act quite independently of the adult stage. Ancestral structure cannot be deduced from such forms.

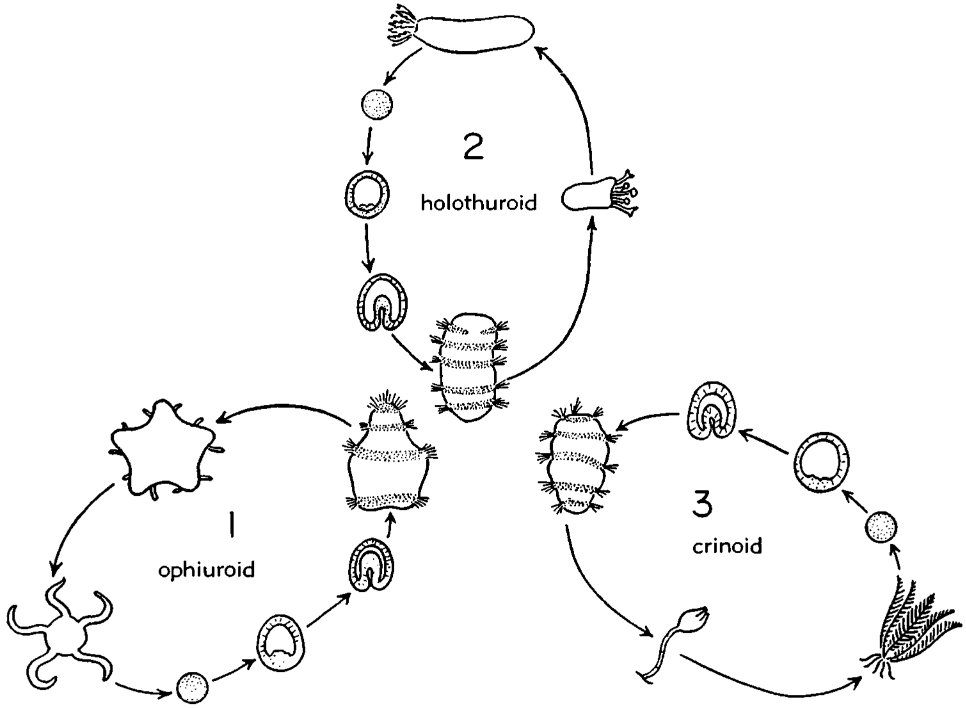

FIG. 24. Convergent patterns of development in unrelated echinoderms. *1*, Ophiuroid (*Ophioderma*); *2*, holothuroid (*Cucumaria*); *3*, crinoid (*Antedon*). In each the larva is a banded vitellaria, which is a widely shared larval form now known to occur in three families of ophiuroids, most holothuroids, and four families of crinoids (8).

LARVAL FORMS AND PHYLOGENY

The auricularia larva presents close and striking resemblances to the tornaria larva of some enteropneusts; the enterocoelous development of the coelom parallels that found in primitive chordates. Hence echinoderms and chordates have long been regarded as related groups. This conclusion, though well established in the literature, is hardly as well grounded on fact, and at present is in dispute.

The significance of similarities in the larvae of echinoderms and protochordates may be viewed in the following context. If the echinoderms are arranged to express their inferred relationships on the basis of their larval similarities and differences, the result places the ophiuroids near the echinoids, and apart from the asteroids. But this totally disagrees with evidence from paleontology and morphology, both of which indicate that ophiuroids and asteroids are closely related taxa. Further, the paleontology of echinoids, at least as well known as that of any other group of animals, indicates that echinoids have followed an entirely independent development since the early Paleozoic. On the other hand, ophiuroids and asteroids share common early Paleozoic ancestors. Therefore, the resemblances between larvae of echinoids and ophiuroids, striking though they may be, can be the result only of convergent larval evolution. Similarly, differences between the larvae of ophiuroids and asteroids, certainly very great differences, must be the result of a secondary larval divergence, because the fossil history of these two groups shows a common derivation at a later date than the divergence of the other groups of echinoderms. It follows inevitably therefore that within the phylum Echinodermata larval characters are no guide to phylog-

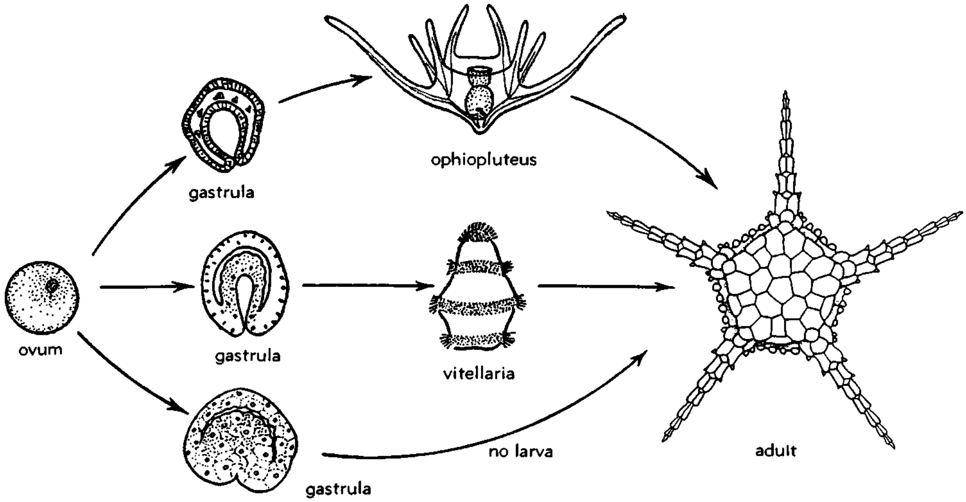

FIG. 25. Divergent patterns of development in ophiuroids. Above, with ophiopluteus larva, as in Ophiothricidae, some Amphiuridae, Ophiocomidae, and some Ophiuridae. Middle, with vitellaria larva, as in Ophiodermatidae, Ophionereidae, and some Ophiuridae. Below, with no larval form, as in Ophiomyxidae and probably most (or ?all) Phrynophiurida (Fell, n).

eny, and, indeed, run contrary to phylogeny. Since ontogeny does not reflect phylogeny within the phylum, it is obviously inadmissible to try to extrapolate beyond the phylum, or to infer phylogenetic affinity between hemichordates and echinoderms solely because the auricularia closely resembles the tornaria. The foregoing analysis, with detailed evidence, has been put forward by FELL (8) and subsequently has been accepted and supported on other grounds by N. J. BERRILL (3). E. MARCUS (21), although differing from FELL in believing that indirect development must be prototypical for echinoderms and protochordates, agreed that the asteroids and ophiuroids must be closely related, and that broad phylogenetic conclusions therefore cannot be drawn on the basis of their larvae. MARCUS, like FELL, considered any embryological or biochemical theory implying that some groups of eleutherozoan echinoderms are more closely related to enteropneusts and vertebrates than the four classes of the former are to one another, to be necessarily absurd. HYMAN (18) has dissented from this view, but failed to account for the evidence of intermediate forms which link ophiuroids with asteroids. HYMAN grouped the extant eleutherozoans together, as their larval similarities suggest, and concludes that the "arrangement recently adopted by paleontologists (e.g., UBAGHS, 1953), according to which asteroids and ophiuroids derive from a common somasteroid ancestor and hence are to be united into one class, must be somehow wrong." HYMAN further stated that FELL's views are based on modified ontogeny in forms with yolky eggs and shortened development; in point of fact, FELL arrived at his conclusions from a consideration of every species of echinoderm for which the development had been investigated, and his reasoning depends almost entirely on larval evidence, as stated clearly by him in 1948, and as summarized above. In the present context it is unnecessary to list the very numerous cases that were then adduced, since a full documentation is available in the work cited (8).

Phylogenetic influences have also been drawn from certain biochemical data which have been held to support the view that echinoderms and chordates are related taxa. As they have a direct bearing on the problem discussed in this chapter, a brief summary is appropriate here.

Biochromes are organic pigments which occur in all echinoderms. D. L. Fox (14) defined three principal groups: (1) echino-

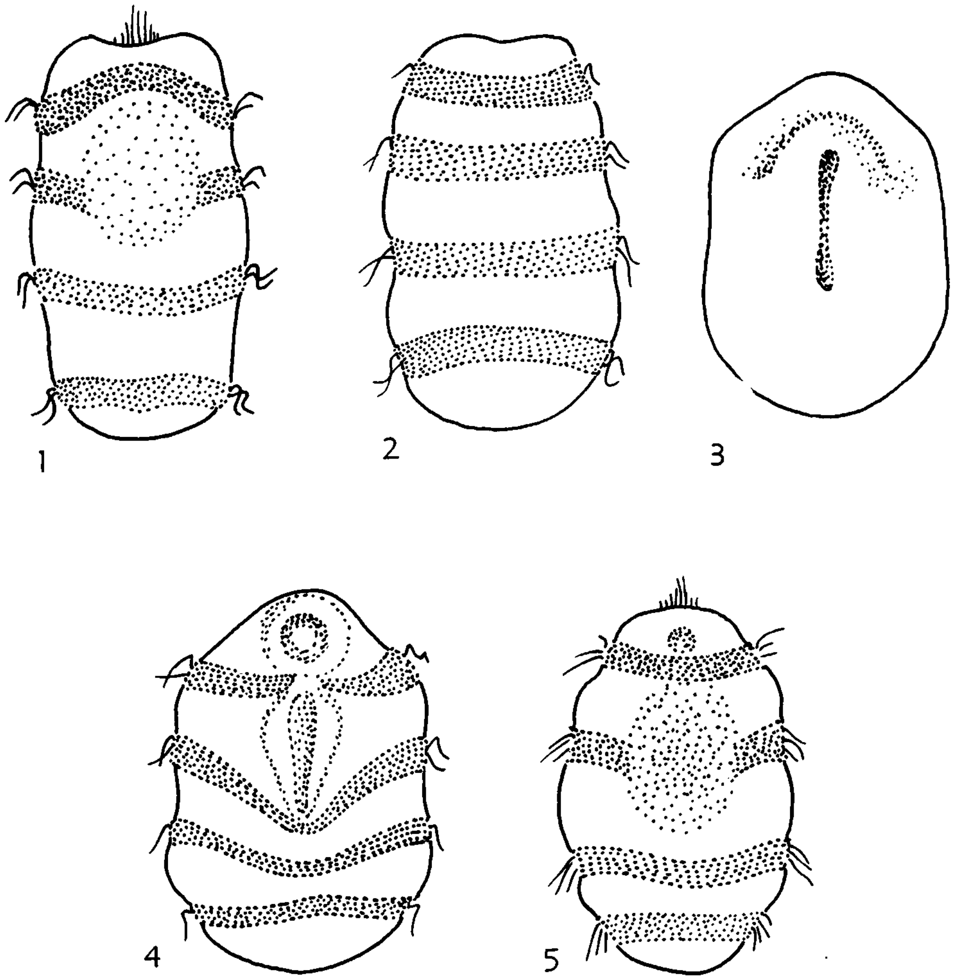

FIG. 26. Vitellaria larvae of comatulid crinoids.—*1. Tropiometra carinata* (LAMARCK), Tropiometridae, ×160 (23).—*2. Heterometra savignyi* (J. MÜLLER), Himerometridae, ×240 (28c).—*3. Notocrinus virilis* MORTENSEN, Notocrinidae, ×24 (28a).—*4. Isometra vivipara* MORTENSEN, Antedonidae, ×75 (23).—*5. Compsometra serrata* (A. H. CLARK), Antedonidae, ×160 (23).

chromes (including spinochromes), purple, red or green naphthoquinones known only from sea urchins and some homopterous insects; (2) dark melanoids which occur in ophiuroids, sea urchins and holothurians; and (3) carotenoids, which occur in the integument of all echinoderms. They are typically red or orange, but if conjugated with a protein they may be green, blue, or purple. Alcohol denaturizes the protein, so that the carotenoid reverts to red or orange.

Phosphagens are of two types in echinoderms (1). These are arginine phosphate in crinoids, asteroids, and holothurians; creatinine phosphate in ophiuroids; and both types in echinoids. Creatinine phosphate is also reported from hemichordates and vertebrates, whereas arginine phosphate is known from mollusks and arthropods. HYMAN (18) has accepted these results as supporting the theory that echinoderms are related to chordates. FELL (8) considered the biochemical evidence inconclusive, not only because it conflicts with paleontological evidence, but also because it is self-contradictory. Thus, echinochromes occur in insects and in echinoids, yet not in any other echinoderms; sterols of one type occur in echinoids and ophiuroids, and a similar type in orinoids, whereas sterols of a different type occur in asteroids and holothurians. MARCUS (21) has pointed out that ophiuroids and echinoids cannot possibly be more closely related to vertebrates than to other eleutherozoan echinoderms, yet such is the implication of the occurrence of arginine phosphate. Phylogenetic speculation based on such data would result in chaos.

To summarize, although one may postulate that the dipleurula stage of Asteroidea, Ophiuroidea, Echinoidea, and Holothuroidea recapitulates a common ancestral dipleurula, it is no longer possible to regard any of the other types of echinoderm larvae as anything but specialized forms that lack broad phylogenetic significance.

If larval stages of echinoderms are interpreted as recapitulating ancestral stages, the conclusions reached are seriously discordant with other evidence. Therefore, it is unsafe to base phylogenetic interpretations on larval stages alone.

LARVAL TAXONOMY

Researches leading to the conclusion that definite relationships can exist between the structure of adult echinoderms and that of their larvae have been carried out by MORTENSEN (23-29). Thus, in the Echinoidea, the extant orders and frequently families can be characterized by the nature of the echinopluteus. To a lesser extent a similar relation is seen in the other classes. These results, in conjunction with other relevant studies, are summarized in the following survey.

Subphylum HOMALOZOA

Nothing is known of the embryonic development of organisms classed as Homalozoa or whether a larval form occurred in any of these Paleozoic forms.

Subphylum CRINOZOA

Our knowledge of embryonic (prelarval and larval) development in crinozoans is restricted to the single surviving class, Crinoidea, and even here we have no information on the mode of development in any group other than the Comatulida, among the Articulata. In all cases so far investigated, the larva has proved to be the vitellaria. This is a transversely ringed cylindrical form, similar to the doliolaria, which follows the auricularia stage of a holothurian, but differs in arising directly from the late gastrula, as the primary larva of a yolk-laden embryo. Representative crinoid larvae are illustrated by forms classed in the suborder Oligophreatina.

Suborder OLIGOPHREATINA

Larvae of two families (Fig. 26,*1*,*2*) are known. In *Tropiometra* (Tropiometridae) four transverse bands are seen on the body. *Heterometra* (Himerometridae), although having very small eggs (diam., 0.15 mm.), yield a typical vitellaria.

Suborder MACROPHREATINA

The Macrophreatina (Fig. 26,*3*-*5*) include *Notocrinus* (Notocrinidae) which has a vitellaria with uniform ciliation, lacking definite bands, and which arises in a viviparous genus. Another genus, *Isometra* (Antedonidae) is also viviparous and yet yields a temporary larval stage, as does *Notocrinus*, having fully developed ciliated bands, in addition. Two other genera of the Antedonidae, *Compsonetra* and *Antedon*, are known to have banded vitellariae, the former with four bands, the latter with four or five bands.

Subphylum ASTEROZOA
Class STELLEROIDEA
Subclass SOMASTEROIDEA

As yet, nothing is known of the embryonic development or larval in this subclass. However, the extant genus *Platasterias* may be expected to yield data very shortly.

Subclass ASTEROIDEA

The larva, if present in development, is initially at least, always a bipinnaria. A more complex larval form, the brachiolaria,

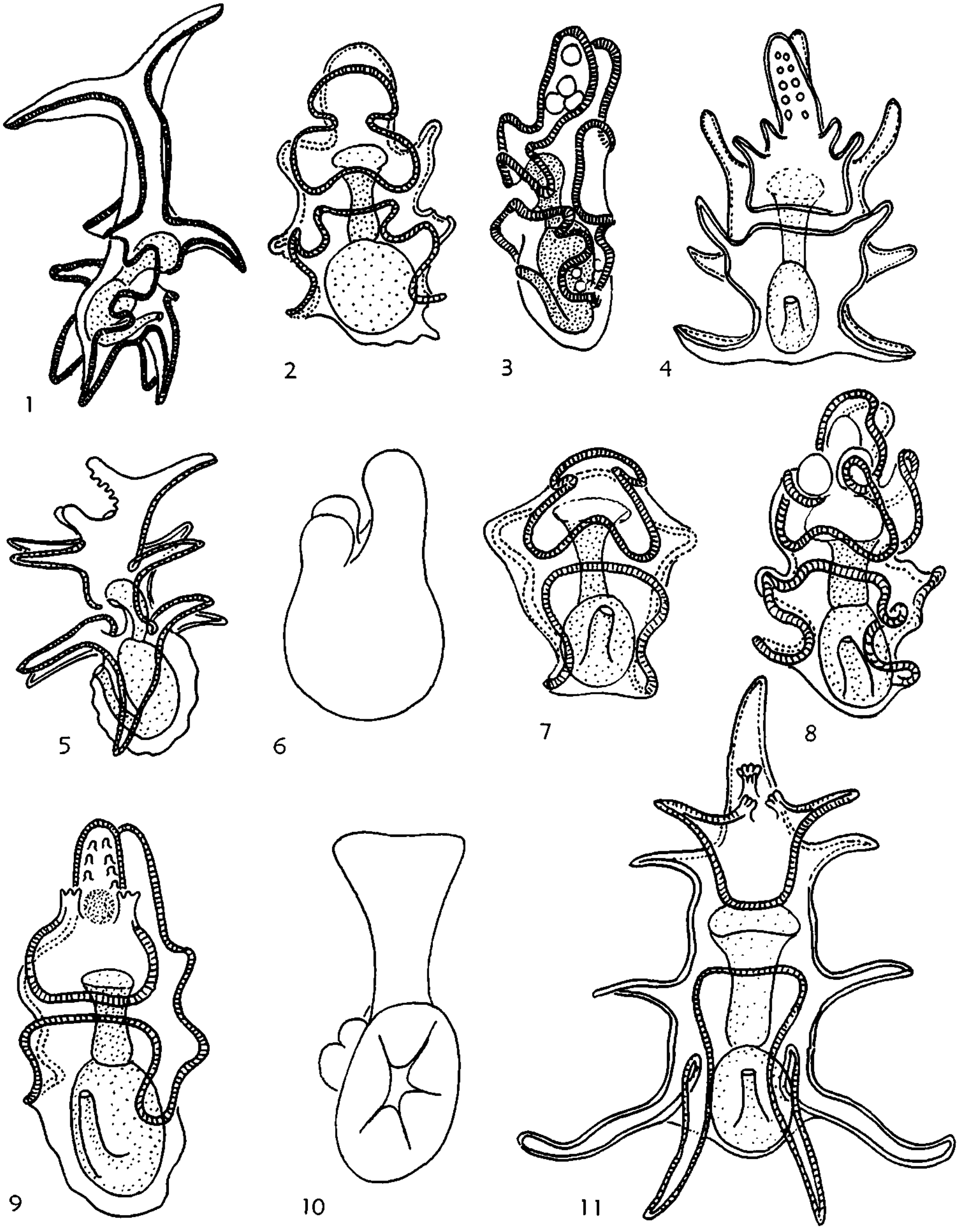

Fig. 27. Larvae of asteroids; bipinnariae *(1,2,7)* and brachiolariae *(3-6, 8-11)*.—*1. Luidia* sp. (*?sarsi* Düben & Koren), Platyasterida, Luidiidae, ×18 (15).—*2. Astropecten scoparius* Müller & Troschel, Paxillosina, Astropectinidae, ×48 (24).—*3. Archaster typicus* Müller & Troschel, Valvatina, Archasteridae, ×72 (28a).—*4. Pentaceraster mammillatus* (Audouin), Valvatina, Oreasteridae, ×30 (28c).—*5. Linckia multifora* (Lamarck), Valvatina, Ophidiasteridae, ×38 (28c).—*6. Fromia ghardaqana* Mortensen, Valvatina, Linckiidae, ×30 (28c).—*7. Asteropsis carinifera* (Lamarck), Valvatina, Poraniidae, ×90 (24).—*8. Acanthaster planci* (Linné), Spinulosida, Acanthasteridae, ×72 (28a).—*9. Patiria pectinifera* (Müller & Troschel), Spinulosida, Asterinidae, ×60 (24).—*10. Echinaster purpureus* (Gray), Spinulosida, Echinasteridae, ×30 (28c).—*11. Asterias rubens* Linné, Forcipulatida, Asteriidae, ×12 (26).

usually follows. The order Platyasterida (with the sole surviving family Luidiidae) and the family Astropectinidae in the order Phanerozonida both stand apart from all other known asteroids; in so far as known the larva never proceeds beyond the bipinnaria stage. All other asteroids appear to possess a brachiolaria, though this may be much reduced in cases of direct development (28c). Variations in larval development of asteroids, in so far as they can be correlated taxonomically, may be summarized in the following way.

Order PLATYASTERIDA

Although this order until recently was supposed to be extinct, it is now realized that the Luidiidae are members; accordingly, the characteristic larva of that family may throw more light on the origin of asteroid larval forms than was formerly realized (Fig. 27,*1*).

The general characters of the *Luidia* larva appear to include a more or less pronounced elongation of the anterior part (median lobes) and the total absence of brachiolarian arms and sucking disc. This larva differs from that of *Astropecten* in its more developed arms and elongation of the median lobes.

The development is known in three species of *Luidia*—one five-armed and two seven-armed—the latter showing considerable disturbance of normal calyx symmetry immediately after metamorphosis.

Order PHANEROZONIDA

Suborder PAXILLOSINA

Representatives of the Paxillosina are grouped in three families (Fig. 27,*2*).

Astropectinidae. The larval forms of five species of *Astropecten* are known with certainty and all are so similar as to be scarcely distinguishable. MORTENSEN (23) concluded that the Astropectinidae possess a distinctive larva, which is bipinnaria having the special characteristics of broad, round anterior lobes. There is no brachiolaria. The larval body is completely absorbed during metamorphosis. Of other genera, *Psilaster* (with yolky eggs) and *Ctenodiscus* and *Trophodiscus* (brood-protecting forms), are all presumed to have no larva.

Porcellanasteridae. Nothing is known of the development, but at least forms with large yolky eggs (e.g., species of *Ctenodiscus*) may be inferred to have direct development.

Benthopectinidae. Nothing is known of the development, but forms such as *Pontaster,* with yolky eggs, probably have direct development.

Suborder VALVATINA

Here, as also in the orders Spinulosida and Forcipulatida, a brachiolaria larval stage apparently is the normal sequel to a preliminary bipinnaria larva (Fig. 27,*3-7*); if the brachiolaria stage is not developed, then at least a vestige of the stage seems to occur. However, direct development may occur at all grades.

Archasteridae. The brachiolaria stage occurs in *Archaster*.

Goniasteridae *(sensu lato):* No larval forms are definitely associated with any member of this large family; the occurrence of large yolky eggs in *Hippasteria, Ceramaster,* and *Mediaster* suggests that in some species, at least, direct development probably occurs. Unpublished observations by J. FREEMAN CLARK show that the eggs of *Hippasteria phrygiana* rise to the surface after release, a fact which suggests that the deep-water genus spends the initial part of its life at the surface.

Oreasteridae. *Pentaceraster* is known to have a bipinnaria followed by a brachiolaria of the type in which a series of papillae occurs along sides of the ventral lobe, with a short series along the brachiolaria arms (which do not have a terminal crown of papillae). *Culcita* probably has a similar development.

Ophidiasteridae. The type genus *Ophidiaster* is known to include a bipinnaria, at least in its life history; with a brachiolaria probably following, but this is not yet certain. *Fromia* has yolky eggs, and very much modified brachiolaria, but is able to swim, however. *Linckia* passes through an initial larval stage very similar to that of *Luidia,* but later this (bipinnaria) gives place to a brachiolaria of seriopapillate type, as in *Pentaceraster.*

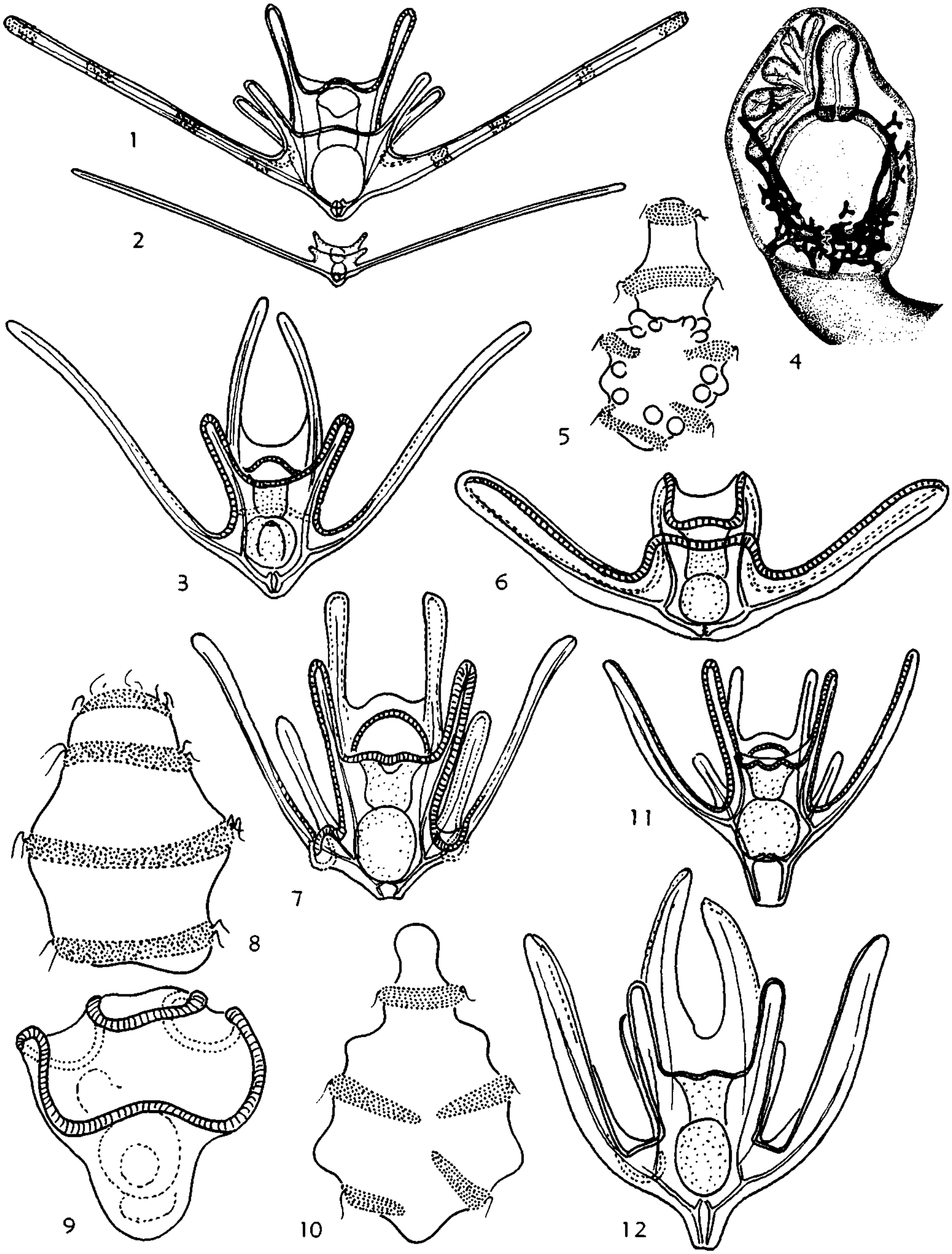

FIG. 28. Larvae of ophiuroids, ophioplutei *(1-4, 6,7,9,11,12)* and vitellariae *(5,8,10)*. All belong to order Ophiurida, larvae being unknown from other orders.—*1,2*. Ophiothricidae; *1, Ophiothrix savignyi* (MÜLLER & TROSCHEL), ×72 (28c); *2, Ophiothrix* sp., ×22 (24).—*3,4,* Amphiuridae; *3, Icalia filiformis* (O. F. MÜLLER), ×60 (28a); *4, Amphipholis squamata* (DELLE CHIAJE), ×144, vestigial pluteus with embryonic attachment to parental bursa (7).—*5,* Ophionereididae; *Ophionereis squamulosa* KOEHLER, ×48 (24).—*6,7.* Ophiocomidae; *6, Ophiocoma echinata* (LAMARCK), ×90 (28a); *7, Ophiocomina nigra* (ABILDGAARD), ×60 (28a).—*8.* Ophiodermatidae; *Ophioderma brevispinum* (SAY), ×78 (17).—*9-12,* Ophiuridae; *9, Ophionotus hexactis* (E. A. SMITH), (lobes of ciliated band not always so conspicuous), ×90 (24); *10, Ophiolepis cincta* MÜLLER & TROSCHEL, ×90 (28c); *11, Ophiura texturata* LAMARCK, ×60 (28a); *12, Ophiura albida* FORBES, ×60 (28a).

Poraniidae. *Porania* has a development similar to that of *Pentaceraster*, with seriopapillate brachiolaria. *Asteropsis* is known to have at least a bipinnaria, and in all probability it includes also a brachiolaria of seriopapillate type.

Order SPINULOSIDA

Representatives of the Spinulosida are illustrated in Figure 27,*8-10*.

Acanthasteridae. *Acanthaster*, with small eggs (0.1 mm.), includes both bipinnaria and brachiolaria larval stages in the life history.

Asterinidae. *Patiria* is known to include bipinnaria and brachiolaria (of seriopapillate type) in the life span and it includes at least two species. Very probably a similar sequence occurs in *Patiriella,* though as yet only the bipinnaria stage has been demonstrated in the New Zealand species; in an Australian species of the genus *(P. exigua)* a shortened development occurs, with vestiges of brachiolarian processes; a similar shortened development is seen in the European *Asterina gibbosa*.

Pterasteridae. Shortened development occurs in some species of *Pteraster* and *Hymenaster*, the young normally retained within a dorsal marsupium, opening to the exterior by an osculum. Unpublished observations by Fu-Shiang Chia indicate, however, that on the northwest coast of the USA *Pteraster tesselatus* is a nonbrooding species, laying large yolky eggs (diam. 1.2-1.6 mm.), from which a free-swimming ciliated modified brachiolaria develops; metamorphosis is completed within one month of fertilization (Chia, personal communication).

Echinasteridae. Shortened development is characteristic here. Some species of *Henricia* protect the brood, and have no larval stage at all; others have yolky eggs and a modified brachiolaria larva, and the same circumstance has been reported in *Echinaster*.

Solasteridae. Shortened development of echinasterid type occurs here.

Order FORCIPULATIDA

The Forcipulatida are illustrated by Figure 27,*11*.

Asteriidae *(sensu lato)*. The normal pattern of development, if fully expressed, apparently includes a bipinnaria stage, followed by a brachiolaria of the terminopapillate type. Genera include *Asterias, Marthasterias, Orthasterias,* and *Pisaster*. A bipinnaria at least is known to occur in *Coscinasterias, Evasterias,* and *Pycnopodia;* in many genera (e.g., *Leptasterias*), brooding is performed, and no larval stages are produced.

CONCLUSIONS

The foregoing survey implies that the bipinnaria must be the older type of larva among asteroids, and the more widespread occurrence of the brachiolaria can be no more than a reflection of the fact that extant asteroids belong mainly to the specialized, later groups of asteroids which are now dominant surviving forms. The brachiolaria stage was probably evolved at about the same time that suctorial tube feet first arose in the (postastropectinid, postporcellanasterid) phanerozonid asteroids. The older views maintained by MacBride (20a), that the brachiolaria is the original larva and represents a stalked pelmatozoan ancestry, cannot be maintained.

Subclass OPHIUROIDEA

As stated above, the typical larva of ophiuroids is the ophiopluteus, though development in very many cases is direct, without a larva; and in a number of cases the larva is the vitellaria, of the same type as occurs in Holothuroidea and Crinoidea. The following is a systematic survey of embryological data so far known.

Order STENURIDA

Development unknown, all extinct.

Order OEGOPHIURIDA

Although now known to have a living representative in the Indonesian genus *Ophiocanops* (Ophiocanopidae), the development is at present unknown.

Order PHRYNOPHIURIDA

Suborder OPHIOMYXINA

Ophiomyxidae (Fig. 28). No larva is known, development being absolutely direct, in at least two species without slightest vestige of larva. Viviparous forms with direct development include species of *Ophiomyxa, Ophioscolex.*

Suborder EURYALINA

Gorgonocephalidae. *Astrochlamys,* and probably *Astrothorax,* includes viviparous species, with presumably direct development. Species of *Gorgonocephalus* probably have direct development, with young stages feeding in alcyonarian polyps, but it is possible that some free-swimming stage (?gastrula) occurs.

The development of the other three families is virtually unknown, though believed to be direct.

Order OPHIURIDA

Hemieuryalidae. *Ophiochondrus* is viviparous, but nothing is known as to the existence or otherwise of a larval stage.

Ophiacanthidae. *Ophiacantha* (five species) and *Ophiomitrella* (five species) are both known to be viviparous, probably without larval stages.

Ophiothricidae (Fig. 28,*1,2*). Species of *Ophiothrix* have ophiopluteus larvae in which the posterolateral arms form a long pair of rods, much larger and more conspicuous than other rods; also, during and after metamorphosis, these long arms remain unresorbed, and are eventually thrown off after metamorphosis.

Ophiactidae. The ophiopluteus is well developed and peculiar in having a double recurrent calcareous rod; only the type genus *Ophiactis* has been studied.

Amphiuridae (Fig. 28,*3,4*). Well-developed ophiopluteus, though in some species assuming the peculiar form (previously known as "*Ophiopluteus mancus*") in which the posterodorsal arms are missing; viviparity, and consequential direct development, occurs in *Amphipholis* (two species), *Amphiodia* (one species), *Amphiura* (three species), *Monamphiura* (seven species), *Icalia* (two species), *Pandelia* (one species), *Nullamphiura* (two species).

Ophionereididae (Fig. 28,*5*). A vitellaria larva occurs in *Ophionereis squamulosa,* and another species of *Ophionereis* is viviparous; otherwise, the development is unknown.

Ophiocomidae (Fig. 28,*6,7*). Extremely broad arms are evidently characteristic of the ophiopluteus of *Ophiocoma.* This feature is not seen in *Ophiocomina.* Both genera have enlarged ciliated lobes at the bases of the two posterolateral arms, but some evidence of the same feature occurs in *Ophiura,* so it is not, in itself, distinctive of the family Ophiocomidae. It is possible that *Ophiocomina* is wrongly classified with the Ophiocomidae, and should this prove to be the case, then presumably the broadened arms will be the main familial character.

Ophiodermatidae (Fig. 28,*8*). The only larva so far known from the family is the vitellaria, first described for *Ophioderma brevispina* by GRAVE (14); similar larvae have since been found in American waters, and are provisionally attributed to other species of *Ophioderma.* In other genera of the family direct development occurs, associated with viviparity, namely in *Cryptopelta* (two species), *Pectinura* (two species), and *Ophioconis* (one species).

Ophiuridae (Fig. 28,*9-12*). A variety of larval forms, and of modes of development, occur in the Ophiuridae (i.e., Ophiolepididae auctt.). A larva of vitellaria type characterizes *Ophiolepis.* An auricularia-like larva (however, with traces of rods of a pluteus-type arm skeleton) is characteristic of *Ophionotus*; this is apparently never free-swimming, as the development is completed within the bursa in the one species *(O. hexactis)* in which this peculiar larva has been observed (Fig. 28,*9*). As in other hexamerous and polymerous forms, the symmetry of the calycinal system is seriously disturbed in the newly metamorphosed form. A normal ophiopluteus occurs in the various species of *Ophiura,* but its range of variation is so great between species of the genus that one might well suppose them to belong to different families, as MORTENSEN (28a) has commented. Viviparity, with consequent direct or partly direct development, is known in a considerable number of genera of this family, namely *Ophiotjalfa, Ophiolebella, Ophioceres, Ophiozonella, Ophiomages, Ophiosteira, Ophiurolepis,* and *Ophionotus,* each with a single species, and *Ophiura, Amphiophiura, Stegophiura,* each with two species.

Subphylum ECHINOZOA
Class ECHINOIDEA

In the Echinoidea larval evolution seems to have occurred subsequently to separation of the main orders and families. Within relatively small groups larval evolution has followed similar trends, so that characteristic larvae occur in various subgroups, where the young stages may follow similar ontogenies; but such independent evolution tends to obscure the phylogenetic relationships between the class as a whole and the other classes.

Order CIDAROIDA

Until 1937 the development of cidaroids was known only very incompletely, and no general conclusions could be drawn as to its nature. The genera *Cidaris* and *Eucidaris* had been studied. In addition, MORTENSEN had shown that the development of *Phyllacanthus parvispinus* is probably direct. In 1937 MORTENSEN (28b) published his account of *Eucidaris metularia,* and the following year (28c) that of *Prionocidaris baculosa,* which was studied through metamorphosis. The two latter accounts are the most important, and together with the earlier data enabled the conclusion to be drawn that a distinctive cidaroid larval form exists (Fig. 29,*1*). This is an echinopluteus characterized by very long, smooth fenestrated postoral and posterodorsal rods, by having the posterior transverse rod provided with long, slender median processes dorsally and ventrally, and by strong development of the ciliated lobes. A larval muscular system is present in the two latter species, enabling the two pairs of long arms to be moved backward and forward, and no doubt this feature is also generally characteristic of the cidaroid larva.

A further feature of morphological interest is that in the newly metamorphosed urchin of *Prionocidaris* a pluriserial interambulacrum occurs, as in Palaeozoic echinoids. The supernumerary plates are later resorbed, as in *Archaeocidaris.*

Order DIADEMATOIDA

Knowledge of the development of these is due mainly to MORTENSEN (Fig. 29,*2,3*). Four species belonging to *Diadema* and *Echinothrix* have been investigated. The larvae of these have proved to be types earlier described under the name *Echinopluteus transversus* (24), the parental form being at that time unknown. This is notable for great development of the postoral arms, other arms being absent save for small anterolaterals which may be present. The larva thus strongly resembles an ophiopluteus. The ciliated band is not strongly developed, in sympathy with reduction of the arms, and no vibratile lobes or epaulets are observed. Other skeletal peculiarities do not need to be specified here.

Order ARBACIOIDA

The development of three species of the genus *Arbacia* has been studied (Fig. 29,*4*). The arbaciid larva has a basket skeleton at first. In its second stage of development a posterior transverse rod is present, ending in a pair of long posterolateral arms which are similar to the other arms. Postoral and posterodorsal rods are fenestrated. Large ventral and dorsal lobes occur, but no epaulets.

Order PHYMOSOMATOIDA

The development of *Stomopneustes* is known to resemble that of the Echinometridae as noted subsequently.

Order TEMNOPLEUROIDA

Temnopleuridae. In this family the development is known for species of *Temnopleurus, Temnotrema, Mespilia,* and *Salmacis.* In the first stage no basket structure of the skeleton is seen. In the second stage (Fig. 29,*5*) a posterior transverse rod is formed and short branched posterolateral rods may or may not issue from it. Four vibratile epaulets are found, but no vibratile lobes. The arms commonly present a highly characteristic bloated appearance (24).

Toxopneustidae. Among genera belonging to this group the species of *Toxopneustes, Lytechinus, Nudechinus, Tripneustes, Sphaerechinus,* and *Pseudocentrotus.* The echinopluteus of this assemblage possesses in its first stage a short body, usually with a basket structure of the skeleton. In its second stage (Fig. 29,*6*) a posterior transverse rod is introduced. Postero-

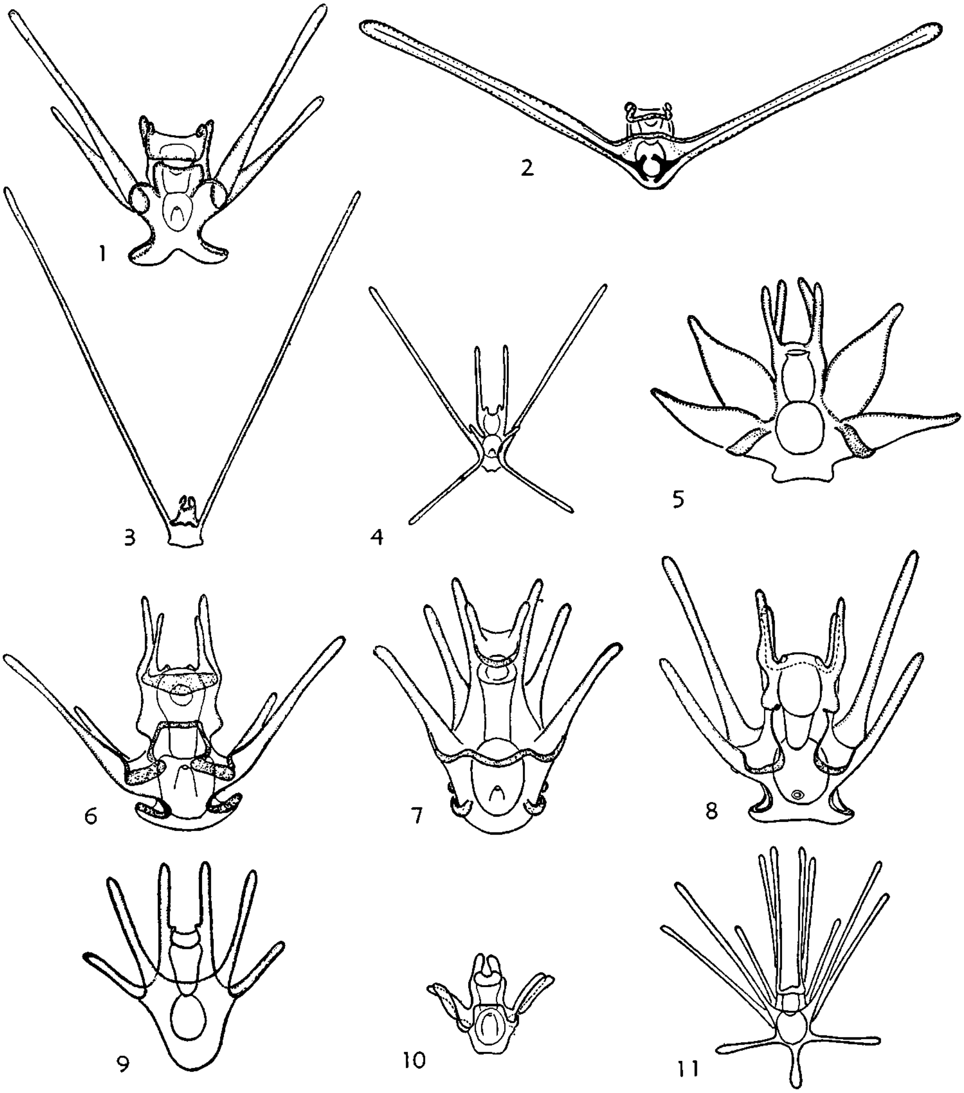

FIG. 29. Echinopluteus larvae of echinoids.—*1. Prionocidaris baculosa* (LAMARCK), Cidaroida, Cidaridae, ×30 (28c).—*2. Diadema setosum* GRAY, Diadematoida, Diadematidae, early larva, ×42 (28a).—*3.* Same, later stage (28b).—*4. Arbacia stellata* (BLAINVILLE), Arbacioida, Arbaciidae, ×24 (24).—*5. Mespilia globulus* (LINNÉ), Temnopleuroida, Temnopleuridae, ×30 (31).—*6. Lytechinus variegatus* (LAMARCK), Temnopleuroida, Toxopneustidae, ×42 (24).—*7. Echinus esculentus* LINNÉ, Echinoida, Echinidae, ×60 (24).—*8. Echinometra lucunter* (LINNÉ), ×54 (24).—*9. Arachnoides placenta* (LINNÉ), Clypeasteroida, Arachnoididae, ×48 (24).—*10. Apatopygus recens* (MILNE-EDWARDS), Nucleolitoida, Apatopygidae, ×30 (24).—*11. Echinocardium cordatum* (PENNANT), Spatangoida, Loveniidae, ×22 (28a).

lateral arms and vibratile lobes occur, and epaulets are seen at the bases of the four main arms. The rods of the main arms may be either simple or fenestrated (24). *Strongylocentrotus,* now placed in a family by itself, has a development similar to that of the Toxopneustidae.

Order ECHINOIDA

Echinidae. The larval development of echinids is known for species of *Echinus, Psammechinus, Paracentrotus, Parechinus,* and *Sterechinus.* In its first stage the larva has a short body, usually with a basket structure of the skeleton. In the second stage (Fig. 29,*7*) a posterior transverse rod is present; posterolateral and vibratile lobes occur, and also epaulets at bases of the four main arms; the rods of the main arms may be either simple or fenestrated.

Echinometridae. The development is known for species of *Echinometra, Colobocentrotus, Heterocentrotus, Evechinus, Heliocidaris,* and *Echinostrephus.* The development of *Heliocidaris erythrongramma* is direct, or partially so. The echinometrid larva has in the first stage a short, obliquely truncate body supported by a complex basket structure. In its second stage (Fig. 29, *8*) a posterior transverse rod is present. Posterolateral and vibratile lobes occur, but no epaulets. The rods of the main arms are fenestrated (24).

Order CLYPEASTEROIDA

The development is known of 15 species belonging to the genera *Clypeaster, Fibularia, Echinarachnius, Peronella, Arachnoides, Fellaster, Encope, Mellita, Astriclypeus, Laganum,* and *Echinodiscus* (Fig. 29, *9*). In the clypeasteroid larva the body skeleton forms a prominent basket structure of distinctive character. This commonly takes the form of a large, complex, fenestrated plate in the posterior end of the body.

Order CASSIDULOIDA

MORTENSEN's (24) account of *Apatopygus recens* suggests affinity between its larval development and that of the clypeasteroids. The fully developed larva is as yet unknown, but MORTENSEN's oldest stage is illustrated (Fig. 29,*10*).

Of the other surviving Cassiduloida, the development is unknown.

Order SPATANGOIDA

The spatangoids are characterized by possessing a highly distinctive echinopluteus which bears a median unpaired armlike process (Fig. 29,*11*). In addition, the anterodorsal arms are well developed. MORTENSEN (24) has further suggested that it may ultimately be found that the families Spatangidae and Brissidae have distinctive larvae, as from the data available it appears that the former possess posterolateral arms, whereas the latter lack these structures. The genera which have been studied include *Spatangus, Lovenia, Echinocardium, Moira, Brissus, Brissopsis,* and *Meoma.*

SUMMARY OF ECHINOIDS

It may be inferred from the foregoing discussion that larval evolution of the echinopluteus must have occurred subsequent to separation of the main orders and families of echinoids, and within any one group of echinoids larval evolution has followed similar trends. Thus, within relatively small groupings it is true to say that the young stages of related species show similar ontogenies. It is obvious that, with independent larval evolution occurring simultaneously in the many orders and families of echinoderms in general, the phylogenetic relationship between major groups, such as the classes, will become ever more and more obscured in so far as it is reflected in embryology. In his main study, MORTENSEN (24) wrote as follows:

> The Echinopluteus affords the greatest diversity of forms of all Echinoderm larvae, and several well-marked types are to be distinguished. It does not immediately appear which of these represents the more primitive type. Considering, however, the fact that the larvae in which the body skelton in the first stage forms a basket structure, and which have in their second stage a posterior transverse rod and more or less developed posterolateral processes are characteristic—so far as we know—of the Cidarids, Diadematids and Arbaciids, that is to say of the more primitive forms of Echinoids, it can hardly be disputed that we have to regard this larval type as the more primitive form. Consequently the larval type characteristic of the family Echinidae s. str., with the elongated, club-shaped body rods, with the recurrent rod rudimentary or absent, and without a posterior transverse rod or posterolateral processes, is highly specialized. It is therefore not at all justifiable to make this larval type represent the Echinoid larva in general as is done in most text-books.
>
> Characteristic of the larval body of the primary type are the vibratile lobes; in the more specialized types, the larva of the Echinidae s. str., and of the Spatangoids, these lobes have disappeared, while the Clypeastroid larvae have retained them to some degree. A further specialization from the lobes are the epaulets occurring in the higher types of the Regularia.
>
> Both the vibratile lobes and the epaulets evidently serve to increase the floating power of the larva. This object is attained to a still higher de-

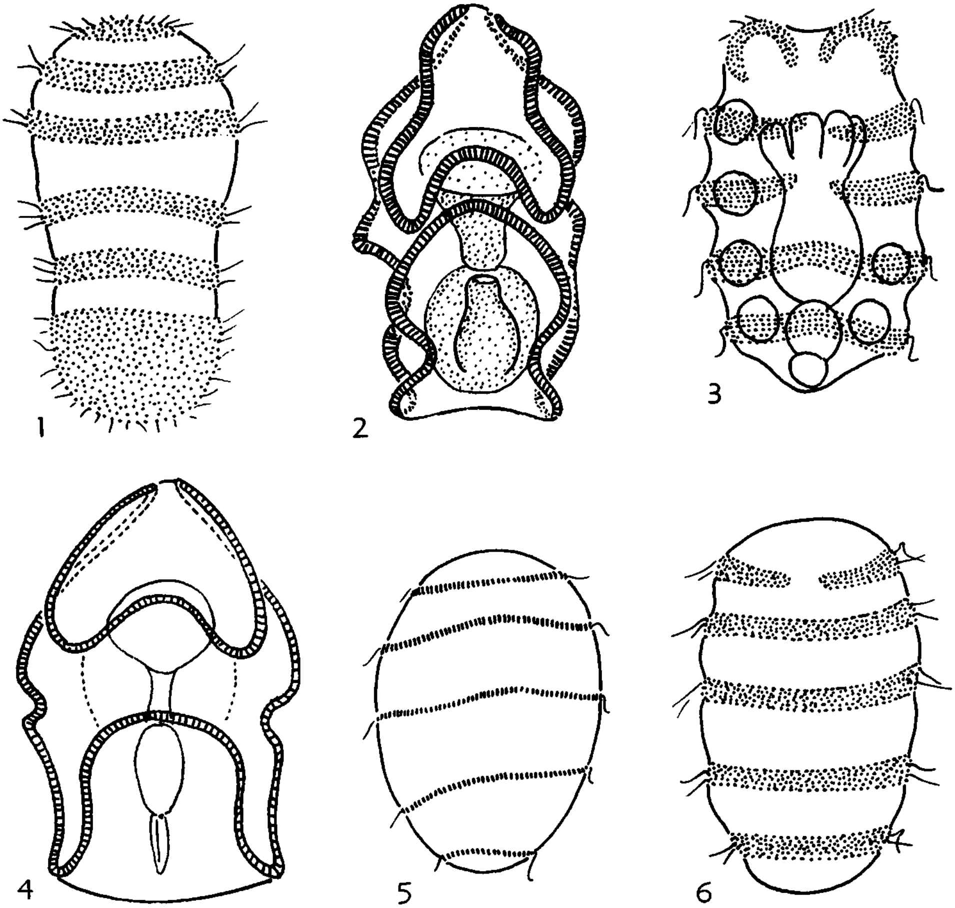

Fig. 30. Vitellaria larvae (doliolaria) *(1,3,5,6),* and auricularia larvae *(2,4)* of holothuroids.—*1.* Dendrochirotida, *Cucumaria planci* von Marenzeller, Cucumariidae, ×135 (32).—*2.* Aspidochirotida, *Stichopus californiensis* (Stimpson), Stichopodidae, ×56 (24).—*3.* Aspidochirotida, *Holothuria impatiens* (Forskål), Holothuriidae, metamorphosing doliolaria derived from a preceding auricularia stage, ×75 (28c).—*4-6.* Apodida, Synaptidae; *4, Opheodesoma grisea* (Semper), ×90 (28c); *5, Synaptula vittata* (Forskål), ×60 (28c); *6, Labidoplax* sp., ×75 (28c).

gree in several larval forms of Regular Echini and Clypeastroids in which muscles connect the lower ends of the rods of the four main arms, so that these arms become actively movable. These larvae, when floating, keep the four main arms in a more or less horizontal position, raising them when disturbed. This is not yet an active swimming movement, the muscular apparatus being too simple for performing regularly repeated movements. Only one Echinoid larva appears to be able to swim actively, viz., the remarkable Echinopluteus transversus (of Diadematidae), in which a complicated muscular system has developed, the body-skeleton being most extraordinarily adapted for serving as a support to the muscles. . . .

As regards the skeleton it is a noteworthy fact that the fenestrated rods represent a primary structure, as must be concluded from the fact that this type of rods (always confined to the four main arms) is found in the larvae of the more primitive forms. . . .

Class HOLOTHUROIDEA

The larval forms of holothurians are either vitellariae or auriculariae, and the occurrence of transitional stages between the auricularia and a secondary larva (doliolaria or pupa), in which the ciliated loops are gradually transformed into transverse rings, shows that no sharp distinction between the vitellaria and auricularia is to be made (Fig. 30). This is significant, for in the other classes of echinoderms the vitellaria seems to stand as an independent form, lacking transitional stages to link it with other larval types. In many holothurians the development must be quite direct, no larval form having ever been reported. The following paragraphs present a review of the known evidence.

Order DENDROCHIROTIDA

The only larvae reported from dendrochirotes are vitellariae, either of the annulated doliolaria type, or uniformly ciliated cylindrical forms; auriculariae are unknown (Fig. 30,*1*).

Cucumariidae. *Cucumaria planci* and other species have a transversely ringed vitellaria which is independently formed as the primary larva, not as the doliolaria of an auricularia. Other species of *Cucumaria* (e.g., *C. saxicola, C. frondosa*) are ciliated all over, evidently comprising a form of vitellaria derived directly from the late gastrula. No larva at all occurs in *Thyone.* In both *Thyone* and *Cucumaria* viviparity occurs.

Psolidae. In *Psolus phantapus* a uniformly ciliated vitellaria occurs. Viviparity occurs in *Psolus, Psolidium,* and *Thyonepsolus.*

Rhopalodinidae, Phylloporidae. No reliable information is available on the development of these families.

Order ASPIDOCHIROTIDA

An auricularia is known to occur in some aspidochirotes, with transversely annulated doliolaria stages occurring at metamorphosis. Otherwise, the development appears to be direct (Fig. 30,*2,3*).

Synallactidae. The development is unknown in these deep-water forms, but the prevalence of large yolky eggs suggests that direct development is probably usual.

Stichopodidae. An auricularia is known for *Stichopus californicus.*

Holothuriidae. Auriculariae of simple type occur in *Microthele* and *Holothuria impatiens.* Absolutely direct development occurs in *H. floridana.*

Order MOLPADIIDA

The only larva recorded is a vitellaria in *Paracaudina.*

Order ELASIPODIDA

Larval development is unknown in any of the five families of the order.

Order APODIDA

The widest range of larval forms occurs in this specialized order, with vitellariae and doliolariae, auriculariae (elaborate in some), as also direct development (Fig. 30, *4,5*).

Synaptidae. Larvae may occur, but in some genera they are omitted. An auricularia (with subsequent doliolaria) arises in species of *Synaptula, Opheodesoma grisea,* and *Labidoplax digitata.* Partially direct development occurs in *Leptosynapta inhaerens,* where a vitellaria arises (despite the small size of the eggs in that species). A vitellaria also occurs in *Labidoplax buski.* Coelomic incubation is known to occur in species of *Synaptula.*

Chiridotidae. Coelomic incubation occurs in species of *Chiridota, Trochodota,* and *Taeniogyrus.* No other information is on record as to mode of development, or larvae.

Myriotrochidae. Although nothing is recorded on the development of this family, the large planktonic "Auriculariae nudibranchiatae" are presumably referable to it, for the wheel-shaped deposits illustrated by CHUN (1896) appear to be of myriotrochid type, having numerous spokes (D. L. PAWSON, pers. commun., unpubl.).

DIRECT DEVELOPMENT

Until recently it had come to be generally assumed that all typical echinoderms have an indirect mode of development; however, a survey of the known embryological data of particlular faunas indicates that no special mode of development can be taken as the general rule for the phylum. The egg of echinoderms is liable to undergo changes in volume. Increase of volume is directly related to increase in cytoplasm and its product, the yolk material. Such increases have led to direct development. Increase in cytoplasm and yolk has not greatly affected the cleavage process, which is almost always total. A distinction between micromeres and macromeres frequently results. With increasing cytoplasm, the wall of the blastula becomes thicker, and in extreme cases the blastocoel is reduced to a vestige in the animal hemisphere. The mesenchyme fails to separate as such, but projects as a solid mass into the blastocoel. Invagination is reduced to a solid inpushing of cells, and epiboly may ensue. The archenteron may become vestigial, in which case the definitive enteron is excavated in the solid endoderm by splitting. The enterocoel becomes reduced or lost, and the coelom and its adjuncts may arise by schizocoelous splitting in mesenchyme.

It may be regarded as reasonably proven that the accumulation of yolk and cytoplasm in the egg is in some way responsible for suppression of the larval form. The salient features of the sequence of reduced larvae studied above are (1) a progressive reduction in size and number of the paired larval arms, followed by loss of the arm skeleton; (2) an increase in the amount and importance of mesenchyme, within which ultimately the coelom is excavated in place of coelomic pouches from the enteron; and (3) bilateral symmetry is lost completely. The order in which these reductions occur, in terms of increasing yolk mass, suggest progressive inhibitions in metabolism along the axes of a bilaterally symmetrical body. By convergent evolution among echinoderms with yolky eggs, a special vitellaria larva has arisen independently in Holothuroidea, Ophiuroidea, and Crinoidea. The vitellaria is characterized by its barrel shape, and the transmutation of the ciliated band into annuli. In the Crinoidea this is the only larva yet known.

In Ophiuroidea a succession of stages in reduction of the ophiopluteus may be seen, suggesting a recession backward in time of the moment at which metamorphosis is initiated. In extreme cases the gastrula itself becomes radially symmetrical and the larva is completely lost. Viviparity is of interest in echinoderm reproduction owing to the modifications of development which usually accompany its occurrence. Commonly eggs of viviparous species are large and yolky. The relationship between parent and young is often extremely intimate, with marsupia forming in the mother, an embryonic attachment developing, and even nutritive substances sometimes being supplied to the embryo by the parent. Larval stages are vestigial or suppressed altogether.

Among asteroids simple brood protection is illustrated by *Calvasterias suteri* from New Zealand. The eggs are laid and the numerous young are carried in a large cluster about the mouth, apparently in the later stages living as commensals. In the astropectinid *Leptychaster kerguelensis,* the young stars are hatched in the oviducts and later adhere to re-entrant angles between rays of the parent. *Leptasterias groenlandica* is reported to hatch its young in its stomach, a very surprising circumstance. In species of *Echinaster,* the young are carried in the ambulacral grooves with the side of the arms folded over them. More complex conditions are seen in *Pteraster* and *Hymenaster* where a dorsal marsupium occurs, held up by modified paxillae and opening dorsally by a special osculum. A marsupium is known also in *Granaster nutrix*. In the starfish *Anasterias antarctica* the embryo is joined to the parent by an attachment.

In ophiuroids all degrees of brood protection and viviparity are found; the condition is very common in Antarctic species, of which MORTENSEN (29) recorded 31 as viviparous. A very interesting example has been recorded in Britain by SMITH (33) who found numerous young individuals of *Ophiothrix fragilis* clinging to the spines and tube feet of adults, larger young ones occurring separately in the parental bursae. As the species has nonyolky eggs and well-developed pelagic larvae, this is an unexpected instance that indicates how viviparity might arise in such forms. SMITH regarded the occurrence as equivalent to natural crevice sheltering. In truly viviparous ophiuroids the eggs are usually large, and either many young may be found in the bursa (e.g., *Ophiomyxa brevirima,* from New Zealand, 4) or several (e.g., *Pectinura cylindrica*), or only a few (e.g., *Amphipholis squamata*). The last-mentioned species, as others of the same genus, is notable in having an embryonic attachment to the parent. This structure is not nutritive; there are reasons for believing that a nutritive fluid is secreted by the bursal wall (7).

In comatulid crinoids, where the eggs are large and rich in yolk, as a general rule the young adhere to and develop on pinnules of the parent. In some species, however, the eggs are free (e.g., *Tropiometra carinata, Antedon petasus*). True viviparity, involving special marsupia, is found in Antarctic crinoids (e.g., *Isometra vivipara, Phrixometra nutrix*). In *Notocrinus virilis* it appears that the young are nourished by an albuminous secretion from the wall of the marsupium (23).

Similar degrees of brood protection and of viviparity are observed in the holothurians, where the incidence in Antarctic species is as pronounced as in other echinoderm classes. In the simplest type the embryos merely rest on the surface of the body. In other species small alveoli may form in the integument, enclosing the eggs. In some the eggs develop within the oviducts, or within the coelom. In others an invagination or evagination of the body wall forms a marsupium. Genera showing viviparity include *Cucumaria, Thyone, Psolus,* and *Phyllophorus* among Cucumariidae, and *Chiridota, Synaptula,* and *Leptosynapta* among Synaptidae.

Since echinoids are distinguished from other echinoderms by possessing generally small eggs and pelagic larvae, viviparity is necessarily of limited incidence in this class. Among cidarids *Goniocidaris umbraculum,* of New Zealand, carries the young in the partly sunken peristome, covered over by oral spines, thus forming a marsupium. In other cidarids the spines of the apical part of the test form a marsupium. Among the spatangoids the sunken petals frequently serve as marsupia, as in *Schizaster, Hemiaster,* and others. In Antarctic genera a sexual dimorphism of the test is a consequence of this condition.

It is clear that brood protection and viviparity can influence development considerably. Larval stages can be effaced or at least reduced. New embryonic organs may evolve, such as the attachment stalks between embryo and parent. New modes of nutrition may arise, involving a change from ingestion of planktonic food in a functional alimentary canal to surface absorption of fluid material by the outer epithelia of the embryo. Yet in these the end result is the same—an adult echinoderm arises quite as typical of its group as an oviparous form. Here, then, is one more illustration of the potency of evolution in acting upon embryonic stages without significantly affecting the adult.

GROWTH GRADIENTS AND PHYLOGENY

The foregoing discussion, based entirely on larval forms, leads to a purely negative result, since the only deduction possible is that larval forms in echinoderms are specialized and cannot throw any direct light upon the question of origin and interrelationships of the various groups included within the phylum. This situation was apparent by 1948 (8).

A more positive approach subsequently has become possible as a result of detailed studies of growth patterns and growth gradients, particularly the postmetamorphic changes which the skeleton undergoes during its development. The results have been reported in a series of papers (Fell, 9-13), which cover a program of comparative studies carried out over the past decade. A brief summary of the conclusions is relevant in the present context, as it provides a general frame of reference within which echinoderm larvae can be viewed.

The analysis begins with asterozoans, is then extended to pelmatozoans, and thence taken forward to echinozoans. The following are the main steps in the inquiry.

(1) The rod-shaped skeletal structures known as **virgalia,** which occur in lower Paleozoic somasteroids, can be shown to be direct homologues of major skeletal elements in modern asteroids and ophiuroids, and the homologies can be specified.

(2) The axes along which the major skeletal elements differentiate in asteroids are found to show progressive alterations in strength and direction, so that the various

families can be arranged in a sequence. Direct fossil evidence indicates the older end of the series, which accordingly can be oriented in time. When the soft structures are correlated, they, too, fall in a progressive linear sequence, coordinated with the hard parts. The inferred chronology may therefore be accepted as an initial working hypothesis.

(3) Using this frame of reference, progressive eliminations enable the most archaic asteroids to be isolated. The final residual group proves to comprise the Luidiidae, the members of which are shown to be surviving representatives of the order Platyasterida, hitherto known only as lower and middle Paleozoic fossils. The order can thus be more precisely defined, the soft structures inferred, and its relationship to other asteroids indicated.

(4) Proceeding from this basis, the inference is drawn that the Luidiidae probably arose from somasteroids through certain hypothetical changes which can be specified. However, the extant asterozoan *Platasterias* ought, on the evidence of its recorded structure, to fall in an early position within the inferred sequence. Detailed study of the structure of *Platasterias* has confirmed its archaic nature and showed it to be a surviving representative of the supposedly extinct somasteroids, though at the same time clearly related to luidiid asteroids. Thus all inferences up to this juncture have been confirmed, and they can therefore be transferred to the working data.

(5) It was thereby established that (a) The oldest asteroids had dominant transverse growth axes in the arm, causing *inter alia* the skeletal plates to lie in transverse rows, and that therefore the entry into the arm of dominant longitudinal growth axes must have been a post-luidiid change. (b) The oldest asteroids had no intestine or anus, the appearance of these structures being a post-luidiid change, coinciding with the astropectinid grade of evolution. (c) The oldest asteroids had nonsuctorial tube feet, the appearance of suckers being a post-astropectinid change. (d) The oldest asteroids had small, double ampullae, inherited from a pre-asteroid ancestry (identified with platasteriid somasteroids), and the subsequent enlargement of the ampullae coincided with the permanent invagination of the ambulacral furrow, which occurred at the platyasterid grade of evolution, with simultaneous enlargement of the tube feet. (e) The single ampullae of Porcellanasteridae are thus a specialized simplification of formerly double ampullae and, being of post-luidiid origin, cannot be primitive. (f) The madreporite was originally placed at the margin of the disc.

(6) The mode of origin of ophiuroids from lower Paleozoic somasteroids can now be deduced, in accordance with theoretical methods used for the asteroids. These predict the existence of ophiuroids with the same pinnate skeletal structure as occurs in archaic asteroids. This inference, tested by dissection of the internal skeleton in representatives of extant families, has been confirmed, and surviving (as well as extinct) genera with pinnate structure have been isolated; further, the homologies of the skeletal elements with somasteroid virgalia have been demonstrated in detail.

(7) Accordingly pinnate structure of the skeleton is shown to be fundamental to all asterozoans, that of ophiuroids and of asteroids being inherited directly from somasteroid precursors.

(8) Next, the soft structures of ophiuroids are to be correlated with the inferred sequence of skeletal changes, as was done in the case of the asteroids. Study of this sort has led to the following inferences. (a) Gastric caeca must once have extended far out into the arms of ophiuroids, for this condition is found in all asteroids and has been demonstrated in the somasteroid *Platasterias*. (b) The gonads in ophiuroids originally must have been confined to the arms, arranged in approximately paired series along either side of the dorsal coelomic canal, for this condition is shown to be primitive in other asterozoans. Since all these conditions are known to occur in the extant genus *Ophiocanops,* this ophiuroid immediately came under suspicion as an archaic form, possibly wrongly classified. Investigation of the endoskeleton of this genus immediately confirmed that it is, in fact, archaic, and agrees in every major feature with that already known in the zeugophiurine Oegophiuroidea, hitherto supposedly extinct since the Late Carboniferous. Accordingly, *Ophiocanops* was rec-

ognized as a surviving representative of the Oegophiurida, and its distinctive soft-part characters could be interpreted as characters of that order. There are no bursae, no genital plates, no dorsal or ventral arm plates, and the madreporite is situated at the margin of the disc.

(9) Drawing upon all the foregoing data, one can now determine which characters of ophiuroids and asteroids are of ancient origin, and which are of late, and therefore secondary, origin, subsequent to differentiation of the two groups from their common somasteroid ancestry. The secondary features can be isolated and catalogued.

(10) Extracting this isolate from overall characters of the Asterozoa, one obtains a residue which yields the inferred original characters of ancient asterozoans. The residual morphological attributes include certain soft-part characters, as well as numerous features related to the skeletal system, and these may be amplified by direct reference to the extant somasteroid *Platasterias* and its fossil precursors, the Chinianasteridae. They prove to comprise characters which are exclusively pelmatozoan, having no near parallel in any known group of echinoderms other than pinnulate crinoids. The embryonic structure of the asterozoan disc conforms fundamentally to that of the crinoid calyx,[1] the plates initially comprising a centrodorsal, five basals, five radials, and in some infrabasals also. Interpinnular grooves in somasteroids are inferred to have arisen from an earlier pelmatozoan condition, in which the food grooves were originally carried on the pinnules. The transformation is attributed to a change in the attitude of the cover plates of the food groove, which turned outward so as to overhang the interpinnular space, with a simultaneous development of interpinnular integument. Pinnular ossicles of crinoids are therefore considered to be homologues of somasteroid virgalia, since both are essentially rod-shaped elements produced in identical pinnate axial sequences, and bearing a double row of cover plates on the oral surface. In the surviving somasteroid *Platasterias* the cover plates (and their supporting webs) are erectile, and in the erected condition apparently return to their ancient attitude, simulating a (nonfunctional) food groove on the pinnule.

(11) Somasteroids are thus interpreted as a group transitional in character between other Asterozoa and Crinozoa and are thought to have arisen from some pinnulate pelmatozoan stock, which cannot at present be precisely identified. The approximate nature of the inferred pelmatozoan ancestry is indicated, however, and points to a pinnulate crinoid. The characters of the hypothetical "protosomasteroid" fall very near to those of a biserial crinoid. Since somasteroids themselves are antecedent to other asterozoans, it follows that all star-shaped echinoderms constitute an independent genetic stock, with no relationship to any other group of echinoderms except pinnulate pelmatozoans.

(12) Embryological data are utilized to derive an hypothesis accounting for the manner in which asterozoans might have arisen from a pelmatozoan ancestry similar to pinnulate crinoids. The hypothesis postulates an initial dislocation in adoral direction of the main radial growth axis at the junction of the radial calycinal plate and the first brachial ossicle. The dislocation is inferred to have arisen in a pentacrinoid stage of development of some pinnulate pelmatozoan. Evidence that such dislocation has occurred in the past is adduced from the embryology of extant asterozoans. The dislocation is comparable in nature, though greater in magnitude, to that exhibited in the transverse growth axes of *Platasterias,* where the second virgalium in each metapinnule is occluded, and thus ejected from the growth axis in which it initially belonged, to become the superambulacral ossicle; in postastropectinid asteroids the occluded element vanishes, and the general dislocation of the entire transverse growth axis is initiated, or even completed.

(13) Extending the analysis to crinoids, their somasteroid-like features have been isolated and catalogued. The residual characters are of ancient, generalized type, like those of eocrinoids or cystoids. Crinoids thus seem to be late pelmatozoans which have (a) retained the original meridional

---

[1] The homology of asteroid and ophiuroid primary plates with the calyx of crinoids, and their fundamental difference from the apical system of echinoids, has been demonstrated by MORTENSEN, *Systematiske Studier over Echinodermlarver,* 1897, p. 169.

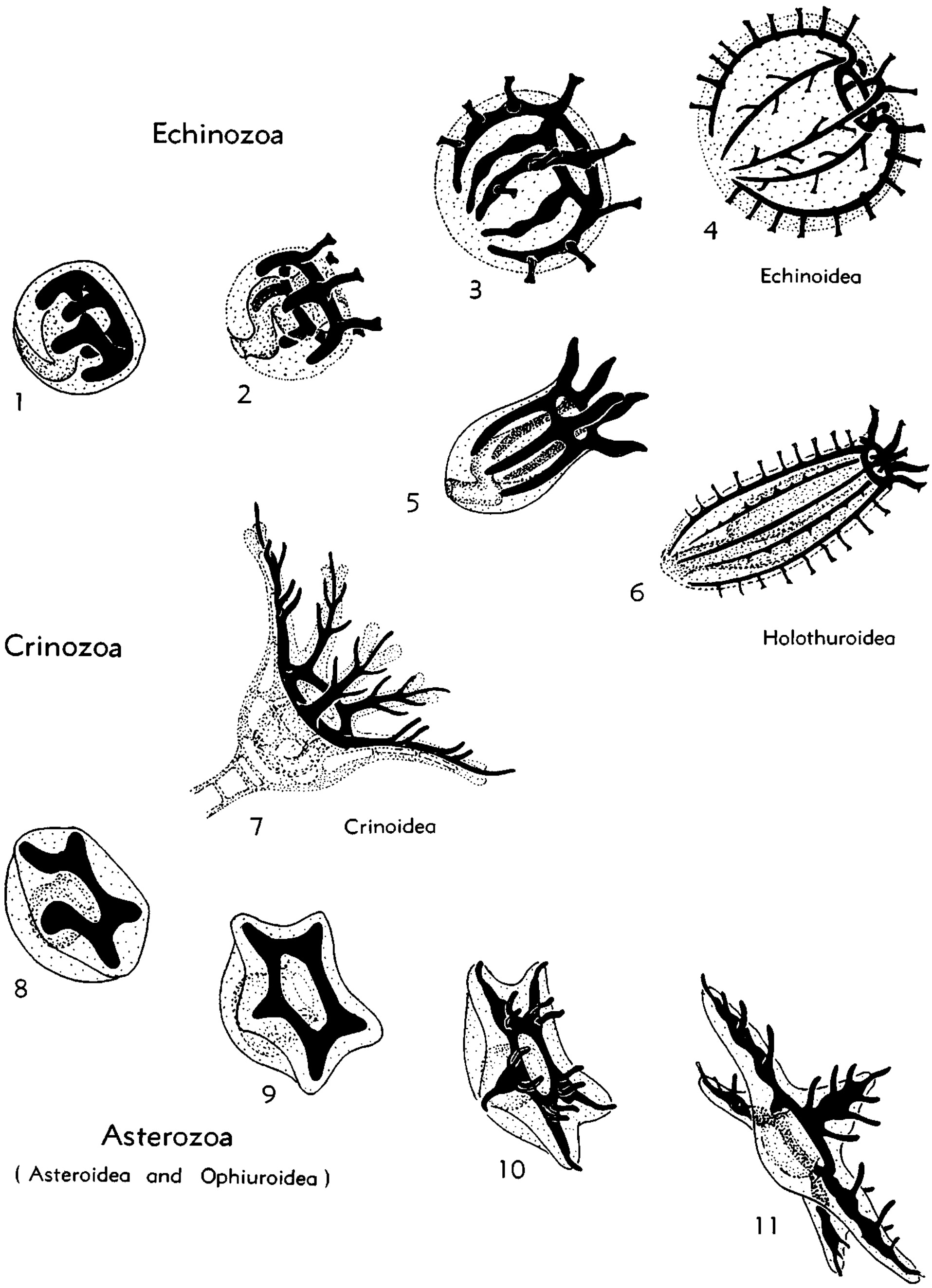

FIG. 31. Major patterns of growth gradients initiated by the hydrocoel during metamorphosis and immediately following it (hydrocoel shown in solid black). Echinozoa *(1-6)* display meridional patterns, whereas Crinozoa *(7)* and Asterozoa *(8-11)* exhibit divergent radial patterns (10) (Fell, n).

patterns of growth in the calyx, as an inheritance from early pelmatozoans; (b) in addition, acquired five, radially directed, divergent axes of growth, leading to the outgrowth of arms and, later on, to secondary acquisition of pinnular subsidiary axes. Somasteroids represent a further term in this progression, in which character (a) is diminished, and (b) is exploited.

(14) The axes of growth of early pelmatozoans are closely comparable with those of echinozoan groups (echinoids, ophiocistioids, holothurians). All are either meridional patterns, or quite disordered. None have radial divergent components.

(15) The Echinozoa are viewed accordingly as archaic derivatives of a still more ancient globoid pelmatozoan stock, the Ophiocistioidea perhaps representing transitional forms. The Echinozoa can have no closer relationship to the Asterozoa than that implied by their derivation ultimately from common ancient globoid pelmatozoans. On the other hand, the Asterozoa present numerous fundamental resemblances to Crinoidea, so great as to imply a close genetic affinity. Consequently, the conventional association of Asterozoa and Echinozoa under one head (Eleutherozoa) is unjustified. The characters supposedly shared by eleutherozoans are, in fact, shared only by demonstrably late groups of Asterozoa, and demonstrably early groups of Echinozoa. The subphylum "Pelmatozoa" is polyphyletic, and must be abandoned as a unit of formal classification.

Figure 31 illustrates the two major patterns of dominant gradients which we may recognize in echinoderms. The upper diagrams show the essentially meridional pattern established in young Echinozoa. The hydrocoel, during metamorphosis, encircles the gut, and then sends out five meridional water tubes which traverse the body. The whole skeleton and nervous system thereafter differentiates under the same meridional gradients. The lower diagrams show the contrasted pattern of dominant radial gradients, found in the Crinoidea and in the Asterozoa. Instead of growing along meridians, the five water tubes are thrust radially outward in the horizontal plane, carrying the body wall and coelom with them, and thus they produce the divergent, radiating arms. The whole skeletal and nervous system differentiates thereafter under the control of such dominant radial gradients, with the calyx alone retaining the ancient meridional system, inherited from the oldest known fossil pelmatozoans. Thus, it now appears that these postlarval gradient systems are a better clue to the phylogeny of post-Cambrian echinoderms. The conventional classification which groups echinoids, holothurians, starfishes, and brittle stars in one assemblage, set apart from crinoids, cannot possibly accommodate the facts as now known.

(16) These inferences, though based mainly on postlarval embryology and comparative morphology, are not entirely dependent on such data, for the fossil record supports them in most respects. The major phylogenetic differentiations here deduced are provisionally dated as not later than Tremadocian time, though some may have been earlier (fossil evidence being inadequate). Persistent transitional forms may be expected at later horizons. In one respect the fossil evidence at present diverges from these results in that the hypothesis predicts the existence of mid-Cambrian pinnulate pelmatozoans, whereas such forms have not yet been found earlier than the Early Ordovician; however, such negative evidence need not be treated as significant until an exhaustive search has been made for pinnulate pelmatozoans in (for example) Indo-Pacific sediments of Cambrian age, and of suitable facies.

(17) The pluteus and auricularia larval stages of echinoderms known to possess them cannot be indicative of phylogenetic affinities, for they imply relationships which are demonstrably false. The larvae may have arisen as a response to similar temporary food-gathering phases in the life-histories of groups not closely related. The evolution of such phases awaits clarification. On the other hand, the ontogeny of the postlarval stages is entirely consistent with morphological evidence from adult echinoderms and with paleontological evidence.

REFERENCES

Baldwin, E., & Yudkin, W. H.

(1) 1950, *The annelid phosphagen: with a note on phosphagen in Echinodermata and Protochordata:* Royal Soc. London, Proc., ser. B, v. 136, p. 614-631.

Bather, F. A.

(2) 1923, *Echinoderm larvae and their bearing on classification:* Nature, v. 111, p. 397.

Berrill, N. J.

(3) 1955, *Garstang's Theory:* in The origin of vertebrates, chap. 6, p. 40-49, Clarendon Press (Oxford).

Chun, C. A.

(4) 1896, *Biologische Studien über pelagische Organismen. II. Auricularia nudibranchiata:* Bibl. Zool., v. 19, no. 1, p. 53-76, pl. 3-4.

Fell, H. B.

(5) 1941, *The direct development of a New Zealand ophiuroid:* Quart. Jour. Micro. Sci., v. 82, p. 377-441, pl. 20-22.

(6) 1941, *Probable direct development in some New Zealand ophiuroids:* Royal Soc. New Zealand, Trans., v. 71, p. 25-26.

(7) 1946, *The embryology of the viviparous ophiuroid Amphipholis squamata (Delle Chiaje):* Same, v. 75, p. 419-464.

(8) 1948, *Echinoderm embryology and the origin of chordates:* Cambridge Philos. Soc., Biol. Reviews, v. 23, p. 81-107.

(9) 1962, *A living somasteroid, Platasterias latiradiata Gray:* Univ. Kansas, Paleont. Contrib., Echinodermata, Art. 6, 16 p., 4 pl., 8 text fig.

(10) 1962, *A classification of echinoderms:* Tuatara, v. 10, p. 138-140.

(11) 1962, *Evidence for the validity of Matsumoto's classification of the Ophiuroidea:* Seto Marine Biol. Lab., Publ., v. 10, pt. 2, p. 145-152.

(12) 1963, *The evolution of the echinoderms:* Smithsonian Inst., Ann. Rept. 1962, p. 457-490, pl. 1-3.

(13) 1963, *Phylogeny of sea-stars:* Royal Soc. London, Philos. Trans., ser. B, v. 246, p. 381-435, fig. 1-18.

Fox, D. L.

(14) 1953, *Animal biochromes and structural colours:* xiii+378 p., illus., Univ. Press (Cambridge, Eng.).

Garstang, Walter

(15) 1894, *Some bipinnariae from the English Channel:* Quart. Jour. Micro. Sci., v. 35, p. 451-460, pl. 28.

Gemmill, J. F.

(16) 1923, *Echinoderm larvae and their bearing on classification:* Nature, v. 111, p. 47-48.

Grave, Caswell

(17) 1900, *Ophiura brevispina:* Johns Hopkins Univ., Biol. Lab., Mem., v. 4(5), p. 83-100, pl. 1-3.

Hyman, L. H.

(18) 1955, *Phylogenetic and comparative considerations [of echinoderms]:* in The invertebrates. IV. Echinodermata, p. 691-705, McGraw-Hill (New York).

Lieberkind, Ingvald

(19) 1920, *On a starfish which hatches its young in its stomach:* Vidensk. Medd. Dansk. Naturh. Foren., v. 72, p. 121-126.

MacBride, E. W.

(20) 1921-23, *Echinoderm larvae and their bearing on classification:* (a) Nature, v. 108 (1921), p. 529-530; (b) Same, v. 111 (1923), p. 47.

Marcus, Ernest

(21) 1958, *On the evolution of animal phyla:* Quart. Review Biology, v. 35, pt. 1, p. 24-58.

Mortensen, Theodor

(22) 1898,

(23) 1920, *Studies in the development of crinoids:* Carnegie Inst., Dept. Marine Biol., Papers, v. 16, p. 1-94, 28 pl.

(24) 1921, *Studies of the development and larval forms of echinoderms:* p. 1-266, 33 pl., Gad-Carlsberg (Copenhagen). [Contains bibliography of descriptive and comparative echinoderm embryology up to 1920.]

(25) 1922-23, *Echinoderm larvae and their bearing on classification:* (a) Nature, v. 110 (1922), p. 806-807; (b) Same, v. 111 (1923), p. 322-323.

(26) 1924, *Pighude:* Danmarks Fauna, v. 27, p. 1-274.

(27) 1927, *On the post-larval development of some cidarids:* Acad. Royale Sci. & Lettr. Danemark, Mém., v. 11, pt. 5, p. 369-387.

(28) 1931-38, *Contributions to the study of the development and larval forms of echinoderms:* (a) Parts I-II, Same, ser. 9, v. 4, pt. 1 (1931), p. 1-39, pl. 1-7; (b) Part III, Same, ser. 9, v. 7, pt. 1 (1937), p. 1-65, pl. 1-15; (c) Part IV, Same, ser. 9, v. 7, pt. 3 (1938), p. 1-59, pl. 1-12.

(29) 1936, *Report on the Echinoidea and Ophiuroidea:* Discovery Repts., v. 12, pt. 1, p. 199-348, 9 pl.

Müller, Johannes

(30) 1846-55, K. Akad. Wiss. Berlin, Abhandl.

Onoda, Katsuzo
(31) 1936, *Notes on the development of some Japanese echinoids:* Japanese Jour. Zoology, v. 6, pt. 4, p. 637-654, pl. 10-14.

Selenka, Emil
(32) 1876, *Zur Entwickelung der Holothurien:* Zeitschr. Wiss. Zoologie, v. 27, p. 155-178.

Smith, J. E.
(33) 1938, *Occurrence of young Ophiothrix fragilis within the genital bursa of the adult:* Nature, v. 141, p. 554.

Ubaghs, Georges
(34) 1953, *Classe des Stelleroides (Stelleroidea):* in Jean Piveteau, Traité de Paléontologie, v. 3, p. 777-842, Masson (Paris).

CRINOZOANS

By H. H. BEAVER, J. W. DURHAM, R. O. FAY, R. V. KESLING, D. B. MACURDA, JR., R. C. MOORE, GEORGES UBAGHS, and †JOHANNES WANNER

In addition to chapters on cystoids, paracrinoids, edrioblastoids, parablastoids, blastoids, and eocrinoids, the description and discussion of lepidocystoids given in the Addendum (p. S627) belong in this section. Crinoids are allotted entirely to Part T of the *Treatise.*

CYSTOIDS

By ROBERT V. KESLING
[Museum of Paleontology, University of Michigan]

CONTENTS