

of the hand pale except the outer finger, while the lower side of the hand has the colour of the outer side of the arm. Boulenger\* seems to be the only author who has hitherto understood the hand in this animal correctly, having had the opportunity of observing it in the living state; he has noticed the position of the hand with the fingers superposed, the inner fingers only touching the ground, and the colourless condition of the inner (*i. e.* upper) side, though he has not remarked that in the latter respect this frog resembles most others. A most interesting addition to the brief biological account given by Boulenger we owe to Leslie†, who states that *X. laevis* is essentially aquatic in its habits, that it, unlike other frogs, feeds only in the water and forces its prey into its mouth by means of its hands, which act as a pair of claspers‡; its mode of locomotion on land is by difficult and awkward crawling and leaping, and when at rest it never assumes a sitting posture, and the back never appears humped. Even Leslie has made a slight mistake, saying that in the breeding male "the *palmar* surface and inner side of the forearm acquire a black horny layer;" this structure is found on the *back* of the hand, as is the case with our frogs and toads.

XXIV.—*On the Arrangement and Inter-relations of the Classes of the Echinodermata.* By Prof. F. JEFFREY BELL, M.A.

HAVING recently had to attempt the formulation of exact diagnoses of the various living classes of the Echinodermata, I have been led to consider closely the claims of the present current classification into Pelmatozoa and Echinozoa. The moment we look at the matter from the phylogenetic point of view we find ourselves involved in a very maze of difficulties. Are the stalked derived from the unstalked forms or *vice versa*? If the group Echinozoa is natural, how intimate are the relations of the Holothurians to the other skeleton-bearing forms with remnants at least of a calycinal area? What are the points, other than the non-fixed condition, which unite

\* Proc. Zool. Soc. Lond. 1887, p. 563.

† "Notes on the Habits and Oviposition of *Xenopus laevis*," Proc. Zool. Soc. Lond. 1890, p. 69.

‡ Perhaps the great process on the centrale, the process *x*, &c. are connected with this peculiar use of the hands; and it is probable that we shall some day learn that *Pipa* behaves in a similar way.



the groups of the Echinozoa among themselves? Are some of the so-called Cystidea nearer to Crinoids than others are to Echinoids? Unless the Holothurians are primitive forms, how is one to imagine the means by which they reacquired their primitive (or more worm-like) characters? The "Cystids" are undoubtedly primitive, and yet how can that condition be shown in any scheme of classification which separates them from the Holothurians? And, finally, how with current views, can one draw up exact, consistent, and inclusive diagnoses?

Forced by considerations of this kind to examine afresh the classification of Echinoderms, I have been led to some conclusions which I should like to have an opportunity of putting—and I will do it as concisely as I can—before those who are interested in questions of this kind. In the preparation of my notes I have been greatly aided by the knowledge and criticism of my colleagues, Mr. F. A. Bather and Mr. J. Walter Gregory, of the Geological Department of the British Museum, which have been freely extended to me; various faults, both of omission and commission, have in consequence been avoided; for such as remain in this paper I must ask to be alone responsible.

In what follows I do not propose to cite to any extent the names of those numerous writers who have in the last decade reopened various questions in the systematic or phylogenetic classification of the Echinodermata; for the facts with which I am going to try and defend what is new in the classification to be proposed are all perfectly well known. It is only in the way of looking at them that there is, I imagine, anything novel.

(a) *The Relation of the Holothurioidea to the rest of the Echinodermata.*

The following characters seem to be of weight:—

1. There is no system of plates corresponding to those that form the "calycinal area" in other Echinoderms; hence the group may be said to be non-caliculate.

2. The genital apparatus is not disposed quinquerradially; in all other Echinoderms the gonads are either arranged along the rays or, when they fuse, in the interradii—they may, in a word, be said to be *actinogonidiate*, whereas the Holothurian, with its bilaterally symmetrical or asymmetrical gonad, is *anactinogonidiate*.

These two characters appear to me to be of very great



significance; it would be interesting to discover to what extent they are correlated. Although the Holothurian is as truly actinoneural and actinangiote as any other Echinoderm, this actinism, so frequently pentamerism in character, has not influenced the generative system. For the moment we will leave open the question whether this is a primitive or a secondary character. We can well imagine that the development of a calyx—early acquiring, *Tiarechinus* would lead us to suppose, a large size,—if itself actinal in arrangement, would do much to impress actinism on all the systems of the body.

However, be that as it may, Holothurians are non-caliculate and anactinogonidiate, and so far they differ from all other Echinoderms known to us.

3. The musculature of the body-wall is well developed and consists of longitudinal and circular muscles; the latter may be brought so far under the influence of actinism that they are not continuous as in *Synapta*, but are broken at the rays.

Like all other characters, this must either have been inherited or secondarily acquired; we may be sure that an ancestor of the Echinoderms possessed it, so that the Holothurians have either inherited it or their ancestors lost it and they reacquired it. Between these probabilities it is not, I think, difficult to make a choice.

4. There is a system of infundibular organs which it is hard to imagine are not the homologues of the nephridia of many Vermes. Or

5. There is a system of cæcal outgrowths from the proctodæum which recall the proctodæal cæca of *Bonellia* and other Gephyrea.

Recent researches in the morphology of the nephridial systems of Vermes, and especially Mr. Beddard's discovery of anal nephridia in *Acanthodrilus multiporus*, are sufficient to justify the speculation that the Vermian ancestor of the Echinoderm was provided with a diffused nephridial system, of which it is justifiable to suppose part was inherited by the Synaptidæ and part only by the other Holothurians.

6. The water-vascular system is always continued into circumoral tentacles, but not always into those similar structures on the body generally which may be called podia\*; so far, and *pace* Prof. Ludwig, there is an apodous and a pedate stage among Holothurians.

\* It can only be due to the unfortunate habit of using cumbrous periphrases that the name suggested by Bronn ('Thierreichs,' ii. p. 383) has not been adopted; it is the least objectionable of any proposed name for the tube-feet.



7. The specialized "heart," "ovoid gland," or "plexiform gland" is not developed.

This, if the Holothurians are primitive among the Echinoderms, was only to be expected.

8. The larva is simple, and, on the whole, the mode of reproduction is less complicated than in other classes.

The position, then, that the Holothurians are primitive forms is spoken to (1) by the possession of characters certainly possessed by its ancestor, and (2) by the absence of characters seen in other Echinoderms, and evidently differentiations of structures developed after the ancestor of the Echinoderm had become separated from the ancestors of other phyla \*.

(b) *The Relations of the remaining Echinodermata among themselves.*

But while Holothurians are non-caliculate and anactinogonidial, all other Echinoderms are caliculate and all that we know are actinogonidial. Considering the irregularity of the actinism of some Cystids, such as, say, *Atelecystis Forbesi* or *Caryocystis*, we may reasonably suppose that some of them were anactinogonidial. We have then caliculate and non-caliculate groups, and of the former there were in all probability some that were anactinogonidial.

The pelmatozoic condition, to which Leuckart was the first to draw attention, was by him regarded as the actual or potential possession of a stalk; but this connotation has become altered. By Pelmatozoa we have recently meant

\* The argument from habitat is not of itself of much value, but it may have a cumulative force, coming after those which I have already adduced; and the fact that Holothurians have been found in brackish water may fairly be stated thus—they are not so differentiated as to be unable to live in any medium other than salt water. The ancestors of our existing archaic forms must surely have dwelt along a shore-line such as that described by Dr. von Kennel ('Arbeiten aus dem zool.-zoot. Inst. in Würzburg,' vi. p. 276):—"In diesem Wasser nun, für dessen Qualität als Süßwasser ich freilich keine anderen Kriterien habe, als den Pflanzenwuchs und das Gefühl der Zunge, da ich leider keine Analysen ausführen lassen konnte, herrscht ein merkwürdiges Thierleben. Zahllose Frosch- und Krötenlarven bedecken in schwarzen Klumpen den Boden oder hängen an den Wasserpflanzen, Unmassen von Mückenlarven verschiedener Gattungen schwimmen theils frei, theils sitzen sie an der Unterseite der Blätter und Steine, die im Wasser liegen, Libellenlarven und Wasserkäfer, sowie kleine Tauchwanzen, tummeln sich lebhaft herum, und mitten darunter ebenso massenhaft, wenn nicht in grösserer Zahl, Mysis, Nereiden und kleine Quallen, zusammen mit Palaemoniden und eine kleine Atyaart, zu schweigen von den kleinen rhabdocoelen Turbellarien, &c."



Echinoderms fixed by their aboral pole. It is among the Caliculata only that the question of pelmatozoism arises.

But it is the next to be faced, for, although the Holothurians exhibit clear signs of affinity with the primitive Echinoderm derived from a generalized worm, the "Cystids" show no less definitely that they are extremely archaic forms. It is stated by Barrande that *Lichenoides* had no stalk, and there is a general agreement among students of the group that there were some of the so-called Cystids that were never fixed and had not fixed ancestors. In other words, there were apelmatozoic and pelmatozoic Cystids.

Pelmatozoic	} Actinogonidial.		Cystidea.
Apelmatozoic			Cystidea.
Anactinogonidial.		Holothurians.	Cystidea.
		Non-Caliculate.	Caliculate.

The relations of the forms are shown objectively in the accompanying table. The rearrangement of the Cystidea has long been recognized as a serious want.

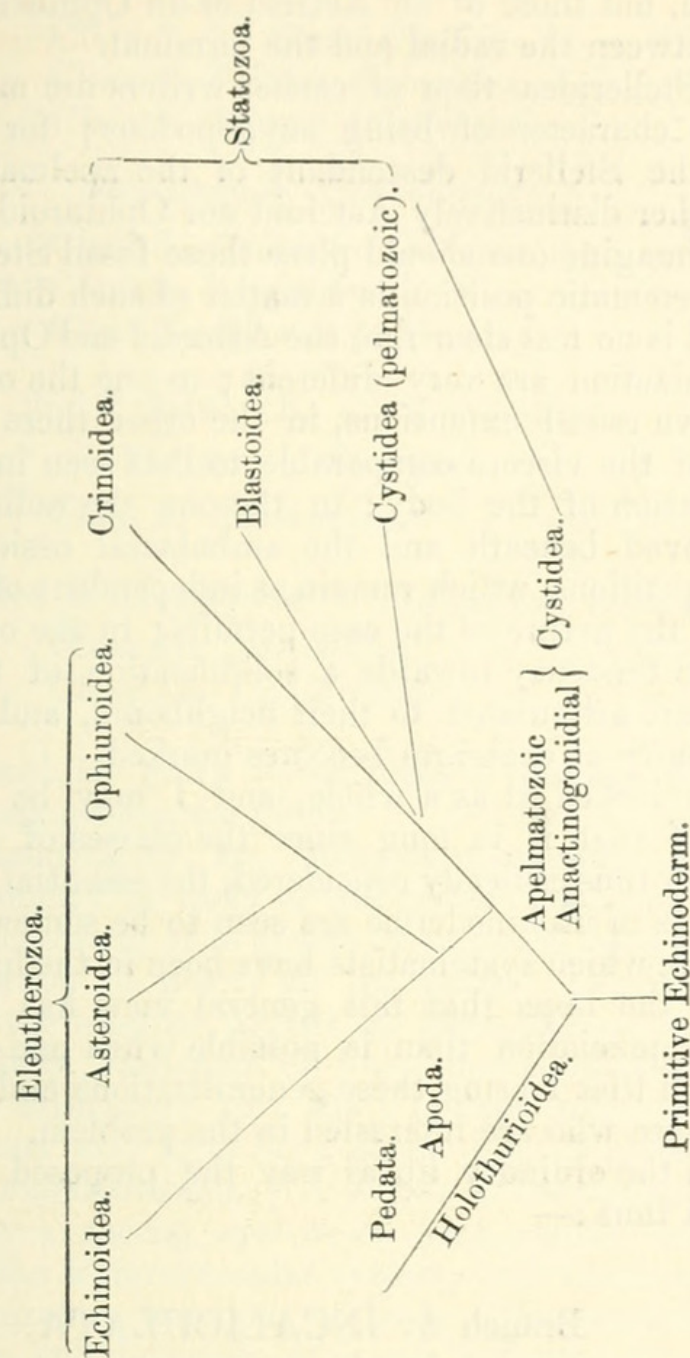
The apelmatozoic actinogonidial Cystids divide into two main branches: one leads to the strictly pelmatozoic forms, that is forms that were fixed or had ancestors that were fixed; the other leads to the Echinoidea, Asteroidea, and Ophiuroidea; the former may be called the Statozoa, the latter the Eleutherozoa.

Of the relations *inter se* of the pelmatozoic series I propose to say nothing more\*; but there remain a few generalizations to be made regarding the rest, or the Echinozoa in the sense of some authors. When, however, we have said that they are apelmatozoic and actinogonidial (which is also true of some of the other series), we have said about all that is true of them, save that they are eleutherozoic. When we come to see in what they differ we cannot find sufficient justification for their union under the common name Echinozoa, as a mark distinguishing them from all other Echinoderms.

\* I suppose no morphologist will be bold enough to say whether *Marsupites* or the irregular Blastoids are primarily or secondarily free forms.



# Phylogeny of the Echinodermata.



The typical arrangement in an Echinoid is that the ambulacra extend from the mouth to the boundaries of the calycinal area; in Asteroids and Ophiuroids the great development of additional plates causes the ambulacra to be confined to the oral aspect of the body. I am unable to find a very satisfactory term for this arrangement, but I propose, provisionally at any rate, to speak of it as zygopodous in the Urchin and azygopodous in the Starfish. Whatever we do, we must be careful not to use the term brachiate; for the arms (brachia) of a Crinoid are formed by addition to the



free edge, but those of an Asterid or an Ophiurid by intercalation between the radial and the terminal.

The Stelleridea then of earlier writers are marked by the common character of being azygopodous; for a time, no doubt, the Stellerid descendant of the apelmatozoic Cystid was neither distinctively Asteroid nor Ophiuroid; and at this stage I imagine one should place those fossil Stellerids whose exact systematic position is a matter of such difficulty.

But it is no less clear that the Asteroid and Ophiuroid types of organization are very different; in one the organs of the body have radial extensions, in the other there is a concentration of the viscera comparable to that seen in the external conformation of the body: in the one the radial extensions are grooved beneath and the ambulacral ossicles are mere serial repetitions, which remain as independent of their neighbours as the nature of the case permits; in the others there is a marked tendency towards a solidification of the arm, the ossicles are articulated to their neighbours, and the physiological unity of each arm becomes marked.

When looked at as a whole, and I may be permitted to point out that it is long since the classes of Echinoderms have been thus critically considered, the essential characters of the groups of Echinoderms are seen to be somewhat different from those which systematists have been in the habit of using. It is in the hope that this general view has led to a more correct appreciation than is possible when one class alone is considered that I bring these generalizations and speculations before those who are interested in the problem.

Put in the ordinary linear way the proposed arrangement will read thus:—

## Branch A. INCALICULATA.

### Stage *a*. ANACTINOGONIDIATA.

#### Class. 1. *Holothurioidea*.

## Branch B. CALICULATA.

### Stage *a*. ANACTINOGONIDIATA.

#### Class 2. Some *Cystidea* (?).

### Stage *β*. ACTINOGONIDIATA.

#### 1st Sub-branch. *STATOZOA*.



Sub-stage i. Apelmatozoic.

Class 3. ? "Some *Cystidea*."

Class 4. ? Some *Crinoidea*.

Class 5. ? Some *Blastoidea*.

Sub-stage ii. Pelmatozoic.

Class 6. *Crinoidea* (s. s.).

Class 7. "*Cystidea*."

Class 8. *Blastoidea* (s. s.).

2nd Sub-branch. *ELEUTHEROZOA*.

Division i. *Zygopoda*.

Class 9. *Echinoidea*.

Division ii. *Azygopoda* (s. *Stelleridea*, s. em.).

Class 10. *Asteroidea*.

Class 11. *Ophiuroidea*.

Precision will be given to our ideas if concise definitions of these various groups are given.

The Echinodermata are Metazoa Coelomata in which bilateral symmetry is early or altogether lost, but may be secondarily acquired; it is generally replaced by a quinqueradial disposition of nearly all the parts. The integument and some of the internal organs are strengthened by a crystalline deposit of carbonate of lime, mesodermal in origin, plexiform in structure; this may remain microscopic and spicular, or part may form macroscopic rods or plates or give rise to a continuous skeleton. A section of the coelom becomes modified into a special system of sacs, canals, and tubes, which form the water-vascular system, and have an ambulatory or respiratory function, or both. The sexes are generally separate, and development is rarely direct.

They are almost exclusively marine in habit.

The Incalculata are Echinodermata in which no system of plates set alternately along and between the rays is developed in the aboral region.

The Anactinogonidiata are Echinodermata in which the vascular and nervous, but not the digestive or reproductive, systems exhibit quinqueradial symmetry.

The Caliculata are Echinodermata in which the skeleton is always, in part at least, formed of plates, some of which are set in rows, alternately radial and interradiat, round a single central plate.

The Actinogonidiata are caliculate Echinodermata in which



the generative organs are radial in position or have undergone fusion and become interradial.

The Statozoa are actinogonidiate caliculate Echinodermata in which the oral surface of the body looks upwards, the body is temporarily or permanently fixed, the podia have a respiratory function only, and the anus opens on the oral surface. They may (pelmatozoic) or may not (apelmatozoic) have or have had a stalk.

The Holothuroidea are non-caliculate, anactinogonidial, apelmatozoic Echinoderms, in which the skeletal system is spicular or irregular; the musculature of the body-wall is well developed, and the mouth is surrounded by a circlet of never very numerous tentacles communicating with the water-vascular system; this is or is not provided with podia. The mouth and anus are at or near the opposite ends of a generally elongated body. A few are hermaphrodite and a few have been found in brackish water.

The Eleutherozoa are actinogonidiate caliculate Echinodermata in which the oral surface of the body looks downwards, the power of locomotion is retained, and the podia are often locomotor in function; the anus, if present, varies in position.

The Zygopoda are Eleutherozoa in which the podia extend more or less uninterruptedly from the calycinal to the oral region.

The Azygopoda are Eleutherozoa in which the podia are all or nearly all on the oral surface of the body only, and are separated by terminal plates from any contact with the calycinal area.

The Echinoidea are caliculate, actinogonidial, eleutherozoic, zygopodous Echinoderms, in which the calycinal area may be very extensive, reduced, or greatly metamorphosed; the gonads are unpaired and interradial; the body is perfectly rounded, more or less flattened, or bilaterally symmetrical, and is more or less covered by spines which may be long, stout, and strong, or present every stage of reduction to such as are fine and silky. They are all proctuchous, but the anus is not always opposite the mouth. Respiration partly by gills and partly by the podia, which may be specially modified.

The Asteroidea are caliculate, actinogonidial, eleutherozoic, azygopodous Echinoderms, in which there is an open ambulacral groove. The stellate form of the body is often well marked and the rays prolonged into "arms," which vary in their proportional length to the diameter of the disk. The digestive system, which is rarely aproctous, and the genera-



tive share in the stellate disposition of the organism. Pentameric repetition is more often exceeded in this than in any other class, and asexual reproduction from a part of the body is by no means uncommon. Respiration diffuse.

The Ophiuroidea are caliculate, actinogonidial, eleutherozoic, azygopodous Echinoderms, in which there is no distinct ambulacral groove. The "arms" are sharply marked off from the disk, are very rarely more than five in number, and are sometimes elaborately branched. The digestive system, which is aproctous, and the generative are confined to the area of the disk, as is also the specialized respiratory apparatus, which takes the form of deep clefts.

The Crinoidea are caliculate, actinogonidial, statozoic Echinodermata, provided with branching articulated arms. In a number of forms the stalked condition is larval only or it is altogether lost; the power of locomotion is often re-acquired. The aboral nervous system is highly specialized. Gonads developed in the arms. Five or more water-pores establish a communication between the coelom and the exterior.

It is not necessary for the purpose I have in view to offer definitions of the Cystidea or Blastidea; perhaps a palæontologist will oblige.

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XXV.—*Descriptions of some new Geophilidæ in the Collection of the British Museum.* By R. I. Pocock.

[Plate XII.]

**Geophilidæ.**

*Henia athenarum*, sp. n. (Pl. XII. fig. 1.)

*Colour* ochraceous; head and maxillipedes darker.

*Body* robust, more attenuate anteriorly than posteriorly.

*Head* small, wider than long, wider behind than in front, with convex sides; frontal plate indistinct.

*Antennæ* of moderate length, filiform, evenly thick throughout, shortly hairy, the segments narrower at their base, the apical segment ovate and longer than the penultimate.

*Maxillary coxæ* wide, narrowed posteriorly, chitinous lines conspicuous and complete, the anterior border crescentically excavated; *feet* short and stout, not attaining, when





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