

X.—*The Morphology and Evolution of the Ambulacrum in the Echinoidea* *Holactypoida.*

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INTRODUCTION.

During the course of the work upon which the following pages are primarily based, the need for an ever-increasing width of scope has continually arisen. In its original conception the paper was to treat of the structure of the *Holactypoida* alone. Gradually the inevitable comparisons extended their range, until in its final form the work deals more or less completely with the ambulacral structure of all the orders of the Echinoidea, and includes far more argument of a general type than was first intended. Nevertheless, the original title has been retained. As in a map designed to show the position of a town, a large area of the surrounding district must needs be included, so that the roads which lead to, from, or past the place can be distinguished; thus, too, the relative position of the Holactypoid ambulacrum in the morphogenesis of Echinoid ambulacra can only be appreciated by description of the homologous structures which preceded, succeeded, or diverged from it in the course of evolution. Thus the title, though far from comprehending all the matter subjoined to it, is apt, in that it indicates the central topic towards which all the others converge and contribute.

In the study of the Echinoidea, the ambulacra and their associated structures have always been recognised as affording taxonomic evidence of great value. Not only do the "avenues" of pores attract attention, in denuded tests, by their distinctness and diversity, but the extensions of the water-vascular system to which they give passage are concerned with many vital functions. Ambulacral plates are among the first to appear during the metamorphosis of an Echinoid pluteus, and the development of ambulacral projections from the hydrocoel marks an early stage in larval life. An ambulacrum consists of an even number of columns of plates (usually two), each one of which is perforated for the transmission of a "tube-foot." There are thus two features, more or less interdependent, that are available for study in fossil forms—the plates and the pores. But it is only within the last five decades that any consistent attempts at an understanding of the plating-structure of the Echinoid corona have been made; and even now systematic writers most frequently limit their descriptions of the ambulacra to the nature of the pores and the distribution of the ornament.

The tracing of sutures in the ambulacra of fossil Echinoids is usually attended with some difficulty, and is always in large measure dependent upon the preservation of the material. There are, however, few cases where no trace of ambulacral structure can be detected, and even in them the application of any granular stain, with or without etching, will often resolve the sutures. By the use of a mixture of alcohol and glycerine, recent forms may be made to yield the secret of their plate arrangement without retaining any permanent traces of the reagent. As a last resource, stereo-sections viewed in polarised light between crossed nicols will almost always show the outlines of the several plates by reason of the varied orientation of the calcite.

LOVÉN and DUNCAN were the pioneers in "osteological" investigation of Echinoid tests. The majority of the figures in the "*Études sur les Échinoidées*" (LOVÉN, 1875) are detailed analyses of coronal structure in a great diversity of forms, both recent and fossil. The "*Revision of the Genera and Great Groups of the Echinoidea*" (DUNCAN, 1889) was based mainly upon previous studies of ambulacral structure made by its author. The works of these two writers gave a great impetus to truly morphological study of the Echinoidea; points of morphological importance are rarely emphasized in publications bearing a date earlier than 1875.

The present paper is divided into two parts. The former comprises a summarised account of the known characters of the ambulacra in the regular Echinoidea, followed by discussion of various aspects of ambulacral structure and the principles involved in its development. The concluding sections of this part consist of a comparison between the functions and structures found in regular and irregular Echinoids, and so serve as a statement of the evolutionary problems whose solution is likely to be found in the annectant order of the *Holectypoida*. The second part is concerned chiefly with detailed description of the ambulacra of representative species of that order, after which follows an attempt to ascertain the course of ambulacral evolution which is thereby indicated.

There remains the seemly and pleasant duty of recording the names of those fellow-workers who have given help in the completion of this study. Those Echinologists, dead and living, who have unwittingly contributed towards the work by their writings, are mentioned throughout the text, and recorded in the list of literature at its close. Much of the morphological work has necessarily been done upon material in the writer's collection, since the investigations often resulted in the destruction or mutilation of the specimens. Most of those that have survived are now in the palæontological collection of University College, Reading. But among those geologists and palæontologists who have willingly afforded opportunity for the examination of their private collections, or of those entrusted to their charge, especial mention must be made of Messrs. G. E. DIBLEY, J. W. JACKSON, L. RICHARDSON, Prof. W. J. SOLLAS, Messrs. LL. TREACHER, T. H. WITHERS, and G. W. YOUNG. To Dr. F. A. BATHER, Dr. H. L. CLARK, Mr. J. COTTREAU, Prof. L. DOLLO, Dr. R. T. JACKSON, Mr. J. LAMBERT, Dr. G. STEFANINI, Mr. P. THIÉRY and DOM A. VALETTE gratitude is due for the gift or loan of copies of their own and other publications to which access would otherwise have been difficult or intermittent. My thanks are extended to Dr. G. HICKLING and Mr. D. M. S. WATSON for their ever-patient attention to sometimes wearisome expositions of my views, and for the stimulus of their frank and fraternal criticism. Lastly, for that critical and sympathetic encouragement that is so necessary for one whose work is carried on in relative isolation, I rejoice to place on record my indebtedness to Drs. F. A. BATHER, R. T. JACKSON and H. WOODWARD. Particularly during the time when most of the manuscript was written, when mental depression was almost inevitable owing to the

chaotic state of the world, the stimulating approval of these masters of research was especially helpful.

PART I.—(1) THE EVOLUTION OF AMBULACRAL STRUCTURE IN THE REGULAR ECHINOIDEA.

(a) *Preliminary Note.*

In this section a summary is given of the general characters of ambulacral structure in the corona of the Regular Echinoidea. The account is only to a small degree original, and to a less extent exhaustive. It is necessary, however, to prefix a *résumé* of this kind to the morphological and morphogenetic considerations of the succeeding sections. Although but few of the observations recorded are new, it is believed that the facts already known are here first collected into a coherent scheme, and that they are interpreted in a fresh manner.

For the ambulacral characters of the Palæozoic Echinoids, I have relied almost entirely on JACKSON'S "Phylogeny of the Echini" (1912). The account of these structures in the other Regular orders has been gathered from a very large number of sources.

The classification adopted for the post-Palæozoic forms is that given by GREGORY (1900). Although the more recent taxonomic system of JACKSON (1912) is available, and in some respects preferable, it has proved more satisfactory to treat of the morphology of the ambulacra in association with the older scheme. This is doubtless due to the close accord between GREGORY'S classification and that of DUNCAN (1889); the latter was based mainly on ambulacral characters. The section was originally written out on JACKSON'S system, but the result abounded in repetition and failed to bring out the morphogenetic facts clearly. Whether this was due to defects in the classification, or to the existence of numerous lines of parallel development, is a matter that cannot profitably be considered here. Systematic discussion is out of place in a paper devoted to purely morphological topics; especially since reference to non-Holactypoid orders is merely incidental to the main purpose of the work.

(b) *Bothriocidaris.*

Bothriocidaris is not merely the oldest Echinoid known but morphologically it approximates remarkably to the theoretical phylembryo of the class. It is necessary, therefore, that the ambulacral characters of this interesting form should be understood, before their subsequent modifications can be co-ordinated. Thanks largely to the work of JACKSON, such knowledge is now available. The descriptions and figures given by him (1912, pp. 53 and 240, Plate 1), supply the evidence upon which the following summary is based.

The ambulacral areas are each built of two columns, composed of a few high hexagonal plates which alternate in position with one another, and with those of

the contiguous interambulacral columns. It is hardly too sweeping an assertion to make that, save for the presence of podial pores in the ambulacrals, the corona is practically undifferentiated into ambulacral and interambulacral areas. Belief in the archaic quality of the Bothriocidaroid ambulacrum is supported (as has been shown by JACKSON, LOVÉN, and others) by the early ontogenetic phases of the ambulacra of many diverse types of Echinoids. The post-larval *Goniocidaris canaliculata* so exquisitely figured by LOVÉN (1892, Plate 2, here adapted, Plate 61, fig. 2), may be regarded as typical of this line of evidence. Further, as JACKSON has remarked (1912, p. 60), those ambulacral plates of advanced Spatangoids which have become obsolescent owing to loss of function by their podia, tend to revert to proportions and relations to the interambulacrals, strikingly similar to those found in Bothriocidaris.

In Plate 61, figs. 2-6, a series of ambulacra showing "Bothriocidaroid" characters is given. All the figures are brought to the same size, regardless of the actual dimensions of their originals. Figs. 2, 3, and 4 illustrate early ontogenetic phases in species representing the diverse orders of Cidaroida, Clypeastroida and Spatangoida. In the case of *Goniocidaris* and the adapical region in *Mellita*, the adult ambulacrals are utterly different in proportions from the neanic plates. In *Brissopsis* this difference is not so marked, owing to the (probably) regressive character of Spatangid ambulacra. This quality is clearly indicated by the two adult ambulacra of Spatangid genera shown in figs. 5 and 6. In all these figures it will be noted that "Bothriocidaroid" characters are indicated, not merely by the shape of the ambulacrals, or the disposition of the pore-pairs, but to a large degree by the alternation of the ambulacral and interambulacral plates. Such a series, which might be very greatly extended, seems to establish the fundamental nature of the Bothriocidaroid ambulacrum so firmly that it may be considered proved in default of contrary evidence.

For the purpose of the present paper it is unnecessary to enter into a discussion as to the origin and homologies of the Echinoid ambulacrum as such. Whether the ambulacral plates are modified from some Diploporitan Cystid ancestor, or are homologous with any parts of Asteroid or Blastoid ambulacra, matters little in a description of so advanced a structure as the Holectypoid corona. It is sufficient to accept the Bothriocidaroid ambulacrum as a "fait accompli," and to start from that as a basis. It seems, therefore, safe to assume that the primitive ambulacrum, from which all other Echinoid ambulacra were derived, possessed the following essential qualities:—

- (i) Each area consisted of two columns of similar plates.
- (ii) Each plate was hexagonal in shape, and at least as high as broad.
- (iii) The number of plates in each column was no greater than that in the interambulacral column.
- (iv) The pore-pair was situated centrally in each plate, and the pores of a pair were superposed, the line of podial perforations thus being practically straight from the apex to the peristome.

(c) *The Palæozoic Echinoidea.*

The earliest available evidence for an enquiry into the subsequent modification of Bothriocidaroid structures is found in the Upper Silurian. During the intervening period of Echinoid evolution at present unrepresented, two changes of far-reaching importance were initiated in the ambulacra. The four genera known from the Silurian are Palæechinus (Plate 61, fig. 7), Koninckocidaris, and the rather anomalous Palæodiscus and Echinocystites. With the exception of the last-named, these genera have ambulacra of closely similar types. The areas are very much narrower in proportion to the interambulacra than in Bothriocidaris, and the individual plates are low and lath-like in form. The areas are straight, so that the perforations for the podia constitute long lines of mechanical weakness, aggravated by their great numbers and close approximation. Owing to the reduced height of the plates, the number present in each column is enormously increased, and at the same time alternate interlocking with the still large interambulacral plates is impossible. So far from the maintenance of such rigid stability of the test, the interambulacral plates were able to slide across the ambulacra along the adradial sutures, in conformity with the general coronal flexibility.

Such long straight zones of weakness in the corona clearly required considerable modification if their owners were to survive. Granting the need for a greater number of podia than could be accommodated in the Bothriocidaroid ambulacrum, a remedy which inevitably produced great mechanical disadvantages was of doubtful merit. The ambulacrum of Palæodiscus, and to a less degree that of Palæechinus and Koninckocidaris, contained a very large proportion of "sutural tissue" as compared with stereom; and the plates themselves were drilled by the podial pores in a continuous line comparable with the perforation of a sheet of postage stamps with a corresponding liability to rupture.

Even at this early stage of Echinoid evolution, an attempt to circumvent the weakening effect above indicated is to be found in the ambulacrum of Echinocystites. The ambulacral plates in this genus are arranged in four columns; so that, for a given number of pores, the height of each plate is doubled in comparison with Palæodiscus. Moreover, the podial perforations are thereby arranged in more distant series. The phase of ambulacral development reached by Echinocystites was almost exactly repeated in lower carboniferous times by Lovenechinus (Plate 61, figs. 10, 11, and 13); and it is closely copied by *Echinocardium cordatum* (Plate 69, figs. 4 and 5) at the present day. It may be regarded either as a special type of "plate-crushing," with the production of alternate demi- and occluded-plates, and the complete suppression of primaries, or as the first stage in the development of "klasma-plates." Whether there is any real distinction to be maintained between the two alternatives is doubtful.

There are three Echinoid genera that arose in the Devonian: *Lepidocentrus*,

Pholidocidaris, and Lepidesthes. These three types represent very clearly two distinct morphogenetic trends as regards the ambulacra. In *Lepidocentrus*, the simple, narrow ambulacra are constructed on practically the same lines as those of the three Silurian genera first considered. The plates of each column are all primaries, and are reduced to very slender proportions. All the disadvantages attached to the "Palæechinoid" ambulacrum are here maintained and even increased. The other genera, *Pholidocidaris* and *Lepidesthes* (Plate 61, fig. 12), mark a great and irretrievable advance along the lines of modification first shown in *Echinocystites*. At least six columns of plates occur in each area in *Pholidocidaris*, and eight in Devonian species of *Lepidesthes*; and the areas themselves show a considerable increase in proportionate width.

During the Carboniferous and Permian periods, the style of ambulacral structure, initiated by *Echinocystites* and elaborated by *Pholidocidaris* and *Lepidesthes*, was maintained and amplified in such forms as *Lepidesthes extremis*, with sixteen columns, *Melonechinus* (several specimens) with twelve, and *Meekechinus elegans* with twenty, in an area. This multiplication of ambulacral columns (harmonising with similar developments in the interambulacra) resulted in the widening of the areas back to and beyond their proportions in *Bothriocidaris*, and at the same time gave passage to enormous numbers of podia. In any but flexible tests, such a multiplicity of sutures and perforations would have involved impracticable fragility; and with the on-coming of rigidity in Permo-Triassic times, this highly specialised character completely disappeared. The ambulacra of *Meekechinus* afford a striking illustration of the often fatal exuberance of evolutionary activity associated with races of animals in the early stages of their existence.

The majority of post-Devonian "Perischoechinoidea" adopted or maintained the more static type of ambulacral structure shown in *Lepidocentrus*. *Hyattechinus* (Plate 61, fig. 8), in spite of the peculiar specialisation of its podial pores, has uniformly simple ambulacral plates. Most of the genera, however, show signs of an endeavour to counteract the weakening effect of a narrow, much-sutured ambulacrum, although the attempts are more moderate than those shown by *Echinocystites*. In some genera, such as *Lepidocidaris* (Plate 61, figs. 15 and 16), *Maccoya* (Plate 61 fig. 9), *Lepidechinus* and *Perischodomus*, premature efforts at "plate-crushing" are seen, similar in many respects to that developed in so many of the Euechinoidea, particularly in the phyllodes of the "Cassiduloida." The plates tend to become cuneiform rather than lath-shaped, and some are excluded altogether from the adradial or perradial lines, and in rare cases from both. All these early, halting experiments in the direction precipitately taken by *Lepidesthes* seem to have met with the fate normal to precocity, and did not endure beyond the Palæozoic era. They are morphologically interesting, as illustrating the failure of a structural tendency which, revived with certain modifications, proved eminently efficient and successful at a later date.

In this connection the relation between "klasma-plates" and the products of "crushing" in Euechinoid ambulacra may be considered. The essential distinction between the scaly, multiporous ambulacra of such a form as *Melonechinus*, and the equally complex adoral parts of the areas of *Heterocentrotus* (see Plate 64), consists in the greater development of occluded plates, and the absence of true combination in the former. It seems reasonable to suppose that the ambulacra of *Echinocystites*, *Maccoya* (Plate 61, fig. 9), and *Lovenechinus* are morphogenetically ancestral to the complicated areas of *Melonechinus* and *Lepidesthes*. In the case of *Lovenechinus* (Plate 61, figs. 10 and 11), the young plates are ontogenetically and morphogenetically simple, and gradually attain some degree of occlusion during growth. An acceleration from the mid-zonal characters of *Lovenechinus* would lead inevitably in the direction of the formation of "klasma-plates." Thus it may be presumed that the apparently distinct columns of such plates that occur in the *Melonechinus* series were derived by over-development of the more restrained complication shown in the simpler types.

In passing, it may be remarked that the ambulacrum of *Lovenechinus*, in its highest state of development, is almost identical in structure with the petaloid part of Area III in *Echinocardium cordatum*. A comparison of Plate 61, figs. 10 and 11, with Plate 69, fig. 5, will make this resemblance clear. A point of morphogenesis of extreme interest is thereby indicated. *E. cordatum* is one of the most highly specialised, as it is one of the latest, of the Spatangidæ, which, for reasons indicated in Section 2 (e) below, has had occasion to develop secondary ambulacral complexity. It has carried out this development along strictly "Perischoechinoid" lines. Hence, if *E. cordatum* be regarded as phylogerontic (a reasonable hypothesis), the recrudescence of phylobrephic structure seems to imply that reversionary tendency in racial old-age that has been aptly termed "second-childhood." In a recent paper, L. F. SPATH (1919) draws attention to the fact that the suture of *Indoceras baluchistanense*, NOETLING, with 37 lobes and 38 saddles, recalls the "acme of specialisation among Triassic Ammonites." He argues that this, one of the last of the Ammonites, fails to reveal gerontic characters, and ascribes the sutural elaboration to environmental conditions. By a similar argument, *Lovenechinus* should have been a burrower in the sand like *Echinocardium*, but such a supposition appears grotesque, in view of its general structure. May not *Indoceras* afford another illustration of imperfect atavism in a gerontic form?

In certain Carboniferous genera, of which *Archæocidaris* (Plate 61, fig. 14) may be considered typical, an entirely different modification appears. The individual ambulacral plates retain the simple "Palæodiscoid" arrangement and proportions, while the whole area becomes sinuous in its course. This quality has an advantage over the other experiments in that, while the number of plates may be very considerable, the much-sutured areas (and the much-perforated pore-fields) no longer constitute straight cleavage lines in the corona. So long as the ambulacra were composed of widely-sutured plates, and were devoid of the superficial cementing

influence of large tubercles transgressing the sutures, the quality developed in *Archæocidaris* represents the best obtainable result, at least as regards the mechanical strength of the test.

In respect of its ambulacral structure, *Archæocidaris* bears a relation to post-Palæozoic Echinoids similar to that borne by *Bothriocidaris* to the class as a whole. The earliest Euechinoids (the *Cidaroida*) all possessed narrow, sinuous "Archæocidaroid" ambulacra, and the morphogenetically young plates of these areas in practically all Regular Euechinoids are simple, lath-like primaries.

(d) *The Cidaroida.*

The Permo-Triassic epoch, during which so many changes of a fundamental character occurred in the evolution of most groups of animals, saw the extinction of all forms of Echinoidea other than those with "Archæocidaroid" ambulacra. At the same time, with the stereotyping of the "Euechinoid" pattern, the corona progressively lost its flexible nature, becoming almost perfectly rigid by Liassic times. A detailed and interesting account of this change is given by BATHER (1909, pp. 250-256). Relative rigidity of the test-fabric constitutes almost the only important difference between *Cidaris* (*sens. lat.*) and *Archæocidaris*. In the ambulacra the condition of sinuous, narrow areas built wholly of primaries, introduced in the Carboniferous genus, was maintained with scarcely any modification in the early *Cidaridæ*; and, save for a lack of imbrication and the presence of increased granular ornament, persists unchanged in the living members of the group.

The plating of the ambulacra, although always primary, is not in every case regular. In *Paracidaris florigemma* (Plate 62, fig. 1) and several other *Cidaridæ* with strongly sinuous areas, strict alternation of the columns is interrupted where the curve is sharp. An additional plate is incorporated into the column with convex curvature. This does not imply dissimilarity in the number of plates in the two columns of an area, since such supernumerary plates occur in each column alternately. Such a development is obviously a mere adaptation to the shape of the area, but its appearance suggests a problem and a comparison.

If the usually accepted view of the growth of the *Cidaroid* ambulacrum is correct, the ambulacral plates pass in a gradual stream from the apex to the peristome, where their advancing front is resorbed, the whole process suggesting comparison with the movement and fate of a glacier. The interambulacra perhaps undergo a similar movement, but not at the same velocity. Such a streaming of the columns would mean that any individual ambulacral plate would at some time occupy a position at the convex curve of its column, and subsequently descend to a straighter region, eventually reaching the concave curve. Since the plates in the convex portion are specially modified (in some species) to fit their surroundings, and similar plates never occur in other parts of the columns, it is clear that a very great amount of resorption and sutural readjustment would be necessary if the streaming actually occurs.

Probably the production of the extra plates does not begin until relatively late in ontogeny; it has been detected only in adapical parts of the ambulacra, where the curvature is most marked.

Reference to Plate 62, fig. 3 (*Salenia*), will show that in the small and retarded group there illustrated, the entire ambulacrum (excepting the morphoneanic region) may be composed of plates alternately related to one another exactly like those at the corners of the *Cidaroid* ambulacrum. In spite of the gently curved course of the *Saleniid* areas, there is no special connection between the plating and the curvature; but it is a point of some importance that a quality occurring locally (probably as a morphogerontic feature) in some *Cidaridæ* is regional and persistent in the *Saleniidæ*. Again, in *Hemicidaris intermedia* (Plate 62, fig. 14), the ambulacrals situated between the adapical primaries and the triple compounds tend to group themselves into a *Saleniid* pattern. This is most regular in the left-hand column of the specimen figured; there it is plainly associated with the formation of "dyad" compounds.

In the *Diplocidaridæ* (Plate 62, fig. 2), two interesting modifications of the normal *Cidaroid* structures appear. The pore-pairs are biserially arranged, probably under the influence of the same mechanical necessity that produced complexity in the Palæozoic Echinoidea. It may be remarked in this connection that this family includes species whose average dimensions are considerably greater than those of the *Cidaridæ*: this may well be connected with the reduction of fragility achieved by the displacement of the podial pores. The plates are alternate in character in correspondence with the pore-pairs. Those plates which have adradial pores are relatively high (particularly in the perradial tract), and support granules that are practically secondary tubercles. The plates with perradial pores are low, and support very minute granules only. In the case figured by DE LORIO, and here copied, there is reason to believe that the perradial suture is incorrectly represented. I have been unable to examine species of *Diplocidaris* in which sutures could be detected, but it seems inevitable that the relations of the plates of the columns should be similar to those of *Salenia*. In any case, the plates of *Diplocidaris* are grouped into potential dyads, although there is no true combination. The *Diplocidarid* ambulacrum thus bridges the morphogenetic gulf between the *Cidaroida* and such simple *Diademoida* as the *Saleniidæ* and the Triassic (?) *Diadematidæ* described by BATHER (1909, p. 254).

The usually dissociated condition in which fossil *Cidaridæ* are found, and the ready collapse of dried recent specimens, show that the ambulacra produce serious lines of weakness in the test, in spite of their sinuous course. As is shown in Section 2 (e) below, *Cidaris* has but feeble powers of adhesion by means of its podia, relying more on its long radioles for protection and entanglement. No advance which involved exposure to rough treatment by waves or adversaries was possible for an organism endowed with so mechanically unsound a fabric.

In ambulacral structure, as in most other morphological features, the *Cidaridæ* have maintained that conservatism of type that characterises the root-stocks of most

classes of animals; and this fact alone is sufficient reason for the reference of all more elaborate developments back to the Cidaroid ambulacrum as a starting-point.

(e) *The Diademoida*.*

The non-Cidaroid Euechinoidea Regularia comprise a large and varied series of forms which have been, on the whole, markedly progressive in evolution from their inception in Triassic times to the present day.* While differing from the Cidaroida by many obvious characters, the Diademoida show a steadily increasing contrast in their ambulacral structure. The areas become wider than in Cidaris, lose their sinuous character, and come to support tubercles equal in size to those of the interambulacra. Moreover, a considerable increase in the number of podia in a column (and thus inevitably of plates) is achieved; and hence the mechanical difficulties incumbent upon the Palæozoic Echinoidea demand solution anew. The displacement of the pore-pairs from a uniserial course is essential if any strain is to be applied to the test in their neighbourhood, and the more advanced Diademoida can exert the function of podial adhesion to a remarkable degree. This necessity for the multiseriate arrangement of the pores involves corresponding displacement or irregular development of the plates. But instead of producing a multicolumnar area like that of *Lepidesthes*, the reaction of the Diademoid type has resulted in a far higher degree of strength than that attained by the Cidaroida. The plates become massed together into varying groups; the amount of sutural tissue between the components of a group is much reduced; and the welded plates are bound together by the extension over their outer surfaces of the closely-knit stereom of one or more large tubercles. The compound plates thus formed function mechanically as simple, high, multiporous plates of more than Bothriocidaroid strength and proportions, often alternating regularly with the contiguous interambulacra after the manner of those of the Ordovician prototype.

(i) *The Calycina*.—This group of Echinoids was one of the earliest of the Diademoida to appear, and has retained very constant characters up to the present day. Possibly represented in the Trias (see BATHER, 1909, p. 100), it is one of the best known sub-orders in the scanty Echinoid fauna of the Lias. Due probably to the generally small size of the species, the group is morphogenetically much retarded in practically all respects, and in none more than in the ambulacra. The *Acrosaleniidæ*, although the earlier family to appear, comprise rather larger forms than the *Saleniidæ*, and are somewhat more advanced in ambulacral structure. It will, therefore, be simpler to consider the latter family at the outset, since its characters, though due to phyletic retardation or regression, are the more primitive from the standpoint of morphology.

Salenia (Plate 62, fig. 3) has narrow, sinuous ambulacra which rarely support

* I retain the old-established name for this order and its sub-divisions to avoid confusion, since GREGORY'S classification is here adopted. This does not imply disbelief in the rational and legal superiority of JACKSON'S term, "*Centrechinoidea*."

ornament of a larger type than granules, although a few small tubercles may occur near the peristome. The morphoneanic plates near the apex are simple primaries for a short distance, though they resemble the plates of *Diplocidaris* in that they are alternately largely and minutely granulate. From a point not far from the ocular plate to the peristome margin, these plates become grouped into dyads by the perradial reduction of the minutely granulate ambulacra, but there are rarely any demi-plates present, and true combination is restricted to the adoral parts of the areas. I have never seen any triads in the various species of *Salenia* and *Peltastes* that I have examined, so that the few compound plates that exist in the family seem to be of the simplest possible type. Such a condition is comparable with that found in "*Diadematoïd ambulacrum* α " from the Trias of BAKONY figured by BATHER (1909, Plate 69, fig. 215), and so may be considered to be truly primitive. Whether the simplicity in the case of the *Saleniidæ* is due to retardation or actual regression is uncertain; a further discussion of the question will be found in Section 2 (f), below.

Acrosalenia (Plate 62, fig. 4) shows a considerably more advanced type of structure than *Salenia*, although the ambulacra are still far from complex. In spite of minor specific differences, all of the lower Oolitic forms that I have examined have essentially the same qualities. The ambulacra of *Acrosalenia* have been described by various writers, a summary of whose views is given by THIÉRY (1911, pp. 4—6). That author gives drawings of four species (*A. spinosa*, *A. lycetti*, *A. lamarcki*, and *A. patella*), showing clearly, though somewhat crudely, the type of structure which, according to my experience, is universal in Lower Oolitic forms. (In Corallian types, according to DE LORIO (1890), a greater development of triads and demi-plates occurs than in Bathonian species.) Adapically there is a considerable sequence of simple primaries in straight columns, the number of such plates varying with the species and perhaps with individual age. The granulation of the apical plates is somewhat irregular, but on the whole the largest ornament is found on every third plate. Adorally to these primaries the plates become grouped into dyads, each pair separated by a normal solitary primary. Below the ambitus triads of the "Diademoid" type appear, the intervening primaries having become intimately associated with the pairs adapical to them. Demi-plates are rare, but each triad is very nearly "Arbacioid" in character, the median component being much expanded perradially. Although the plates are grouped almost throughout the area in some species, I believe that there is never any real combination except on the adoral surface.

(ii) *The Diademina*.^{*}—This sub-order contains the families Orthopsidæ, Diadematiidæ, Pedinidæ, Diplopodiidæ, Phymosomatidæ and Echinothuriidæ. The Orthopsidæ, as their name implies, have ambulacra of extreme simplicity. The family as defined by Gregory ranges from the Lias to the present day; the modern representative, *Aspidodiadema*, being a deep water, probably regressive, type. The

^{*} This and the following sub-order are considered in inverse sequence to that adopted by GREGORY. Morphologically and chronologically, the *Diademina* are earlier than the *Arbacina*.

ambulacral plates are all primaries, and alternate regularly along the perradial suture. The ornament, however, is more elaborate than that of the Cidaroida, and shows that the plates are grouped in a manner corresponding with that of the simpler parts of the *Acrosaleniid* ambulacrum. In *Orthopsis* (Plate 62, fig. 5) fairly large secondary tubercles occur on every third ambulacral, and are so situated that they extend almost equally over two contiguous plates whose dividing suture passes under the mamelon. These two plates are more or less thoroughly combined into dyads, and between each pair intervenes a solitary primary which is not combined. This condition, as the ambulacrum of *Acrosalenia* shows, is preliminary to the development of triads. The *Orthopsidæ* thus resemble the *Calycina* in the stage of ambulacral development attained; and like that group, have been persistent in range and conservative in structure.

The *Diadematidæ* and *Pedinidæ* (which are united by JACKSON under the name of *Centrechinidæ*) show the typical "Diademoid" type of ambulacral plating, although many genera possess somewhat greater complexity in parts of the areas. There is always a considerable number of primaries in the adapical parts of the ambulacra, and these are normally tuberculate on every third plate in preparation for subsequent combination. Towards the peristome the adoral member of a triad is liable to become separated from the perradial suture, thus producing a partially "Arbacioid" result. It is, however, very rare to find a true "Arbacioid" plate, though such do occur sporadically. In many Oolitic and Cretaceous genera, such as "*Plesiadiadema*" and "*Placodiadema*," the compound plates at the mid-zone or above it are occasionally built of four, five, or even more, components. Usually, all the combined plates are primaries, but in a few cases one or more of them may be demi-plates. The recent forms are normally "Diademoid." The irregularity of the compounds in the Upper Jurassic and Lower Cretaceous genera is particularly interesting, since it was during that time that the family *Phymosomatidæ* probably arose from a Diademoid stock. As that family has persistently complex compounds, the occurrence of similar developments in numerous *Diadematid* genera seems to imply the existence of morphogenetic plasticity throughout the group, preparatory to the specialisation of a new type.

Among the *Pedinidæ*, *Stomechinus* and *Astropyga* show points of considerable morphological interest in the structure of their ambulacra; while *Noetlingia*, if the genus is rightly to be included in this family, presents an unique type of specialisation. In *Stomechinus* (Plate 62, fig. 7) normal "Diademoid" triads are the chief ingredients of the areas, but they are often ill-defined. "Arbacioid" compounds are practically never found. But the tuberculation of the ambulacra is somewhat sporadic, except in the adoral parts, with a tendency to repetition on every sixth plate rather than on every third. This feature gives a result that could readily be transformed into the condition found in *Astropyga*. It is a matter of much difficulty to determine the degree of combination attained in *Stomechinus*, but, after the examination of many

naturally and artificially "weathered" specimens, I incline to the opinion that the plates are merely grouped on the adapical surface, and do not enter into true combination until the ambitus is reached. *Astropyga* (Plate 62, figs. 8 and 9) has normal "Diademoid" triads adapically and adorally, but in the mid-zone (which extends for some distance in both directions from the ambitus) these triads are definitely united in pairs to produce hexads, or "super-compounds." This tendency, which is found in such diverse genera as *Acrocidaris*, *Stomopneustes*, *Echinus*, *Tripneustes*, and probably *Heterocentrotus*, seems to mark the furthest stage in ambulacral combination that is reached by any Echinoid. *Astropyga* represents the culmination of "Diademoid" structure. Discussion of the aberrant genus *Noetlingia*, which LAMBERT (1906) associates with *Stomechinus*, is deferred to the purely morphological arguments in Section 2 (d). It is sufficient here to note that the greater part of each ambulacrum consists of dyads with intervening occluded, uncombined plates, in which the pore-pairs are obsolescent. Adorally, the ambulacra are comparable with the simple parts of those of *Acrosalenia*, having dyads separated by simple primaries.

The *Diplopodiidæ* (Plate 62, fig. 6) have the peculiar quality (shared with the *Phymosomatidæ*) of biserial pore-pairs adapically; but, apart from the inevitable irregularity of the transverse sutures of the plates in that region, they do not seriously differ from the Oolitic and Cretaceous *Diadematidæ*. In one further respect, however, *Diplopodia* shows a distinct bias in the direction of *Phymosoma*. The compound plates are usually tetrads or pentads in the mid-zone, and the extra component or components are normally demi-plates intercalated between three normal "Diademoid" primaries. The plates in the biserial parts of the areas are more or less clearly grouped into triad, tetrad, or pentad series, but rarely, if ever, show signs of being truly combined.

The *Phymosomatidæ* (Plate 62, fig. 13) show many interesting ambulacral features. The adapical pore-pairs are usually biserial (though to a less extent than in *Diplopodia*), and the compound plates of the mid-zone are normally pentads built of three "Diademoid" primaries with two contiguous intercalated demi-plates. The compounds near the peristome are tetrads hardly distinguishable from those at the mid-zone of *Diplopodia*. Perhaps the actually proximal plates may be triads. There can be little doubt that, morphologically, the *Phymosomid* ambulacrum was derived by the amplification of an area constructed on the *Diplopodiid* pattern. It is a point of importance to note that, in spite of the greater complexity of the compounds in *Phymosoma*, the actual number of ambulacral plates in each column is very considerably less than in *Diplopodia* or *Stomechinus*. Clearly, simple "plate-crushing" cannot have been the chief factor in the determination of the structure. The course of the sutures within the compounds is instructive. They all tend to converge to the mamelon of the tubercle, while the perradial ends of the demi-plates are usually buried beneath it. The sutures of the primary constituents

are very suggestive of those of the Arbaciidæ, especially below the mid-zone. However, the plates always reach the perradial suture. Lastly, the Phymosomid pentads alternate very regularly with the contiguous interambulacrals, so that the compound plates have attained proportions and relations which recall those of the simple plates of Bothriocidaris.

The anomalous group of the Echinothuriidæ, which arose in the Corallian with *Pelanechinus*, and is represented by several living genera, is probably reversionary in character. The imbrication of the coronal plates invites comparison with the Palæozoic Echinoidea, but it is hardly possible that any direct phyletic connection can unite the two series. The ambulacra are composed of dissociated triads for the greater part of their length. Towards the peristome the reduced ambulacrals assume a remarkable resemblance to "klasma-plates," although their disposition is altogether unlike that in the Palæozoic forms. In both groups the parallelism of ambulacral structure may safely be ascribed to adaptation for coronal flexibility.

(iii) *The Arbacina*.—This sub-order contains the two families Hemicidaridæ and Arbaciidæ, which may be roughly defined as Mesozoic and Cainozoic groups respectively. In Hemicidaris (Plate 62, fig. 14) the adapical parts of the ambulacra are truly Cidaroid in character, being narrow, sinuous, almost devoid of tubercles, and built wholly of primaries. JACKSON considers this to be a regressive quality, but, for reasons given in Section 2 (f), I incline to consider it truly primitive, although perhaps retarded. About midway between the apex and the peristome the plates begin to be associated into groups of two or three, the middle one (in the latter case) bearing a tubercle. Gradually, as the area is traced adorally, these triads become welded together into true compounds, and often one (rarely both) of the outer components becomes squeezed out from the perradial suture. When demi-plates occur, the compound takes on the "Arbacioid" character recognised by DUNCAN, the central, tuberculate member of the triad retaining its primary nature. In those triads which support the less prominent tubercles, the structure of the compounds is typically "Diademoid." DUNCAN (1885, *b*) has figured a case of the production of a tetrad in *H. intermedia*, but my experience shows this to be an exceptional, and probably accidental, quality. In the case that DUNCAN illustrated, the adapically succeeding compound is a dyad; so that, as he recognised, the adoral member of this compound has become attached to the wrong group. Such an abnormality is of interest, as showing a possible way by which polysynthetic compound plates may have originated. A somewhat analogous case is shown in the two lowest compounds in fig. 14. It is noteworthy that in Hemicidaris the pore-pairs tend to be arranged in an arcuate plan on each compound plate. Figures and descriptions of the ambulacral structure of many species of Hemicidaris are given by DE LORIO (1890). In one form, *H. mondegoensis* (here Plate 62, fig. 12), the compounds of the mid-zone are double, and they are Diademoid in character, corresponding with those of *Astropyga*. In *H. valleti* (DE LORIO, 1890, Plate 14, fig. 2, *b*) a type of "Arbacioid"

structure closely similar to that of *Tetrapygyus* occurs. The mainly "Diademoid" triads of *Acrocidaris* (Plate 62, fig. 11) seem usually to be grouped into super-compounds at the mid-zone. The ambulacrum of *Glypticus hieroglyphicus* (Plate 62, fig. 15), according to LAMBERT and THIÉRY (1908, p. 24), shows an unusual type of triad formation. Each compound plate is built of an adapical demi-plate, a median primary that is almost a demi-plate, and a perradially expanded adoral primary. Such a structure suggests the development of dyads made of unequal primaries (the presumed primitive type of compound plates), which almost crowd out the intervening solitary plates before they unite with them. Codiopsis, according to DE LORIOI (1890), has similar ambulacra, and the structure of *Noetlingia* is possibly analogous.

The *Arbaciidæ* form a well-defined family of Tertiary date. In *Cœlopleurus* (which was studied in great detail by DUNCAN and SLADEN, 1885, *b*), the greater part of each ambulacrum is made up of triads of ideally "Arbacioid" type, *i.e.*, of a central primary and two demi-plates let into its adoral and adapical margins respectively. In *Arbacia* and *Tetrapygyus* (Plate 63, fig. 1) a higher degree of complexity is reached. But few uncombined plates occur adapically. These are followed by typical "Arbacioid" triads alternating with individual plates which, whether primaries or not, are distinct from the compound plates. This condition is almost exactly paralleled in the ambulacrum of *Hemicidaris valleti*, de Loriol. At or near the ambitus these independent plates become incorporated into the triads adoral to them, thus producing tetrads; but over the greater part of the adoral surface the compounds are built fairly constantly of five elements. The "Arbacioid" plan is none the less evident, although the adoral demi-plate becomes disconnected from the adradial suture, and constitutes an "included plate." This most instructive type of ambulacral structure is further discussed in Section 2 (c), below. *Leptarbacia* (Plate 62, fig. 16), a Cretaceous genus recently introduced by CLARK and TWITCHELL (1915) has a superficially complex ambulacral plating that is probably similar in essentials to that of *Tetrapygyus*. It is not possible to tell from the figures and descriptions available whether the small demi-plates are free or combined, but from a consideration of their sutural relations the former condition seems the more likely. It is equally uncertain whether this small Cretaceous form should be classed with the *Arbaciidæ*.

(iv) *The Echinina*.—This group of the *Diademoida* corresponds very nearly with the division *Camarodonta* proposed by JACKSON, the only genus differently placed by that author being the recent *Stomopneustes*. There are four families, of which the *Temnopleuridæ* arose in the Cretaceous period, while the *Triplechinidæ*, *Strongylocentrotidæ*, and *Echinometridæ* are of Cainozoic date. The two families first named show a remarkable constancy of ambulacral structure (see Plate 63, fig. 2). Triads of the "Echinoid" pattern (two primaries enclosing a demi-plate, or one primary with two unequal demi-plates adapical to it) build practically the entire

area from apex to peristome. A modification of this character is found in *Tripneustes* among the Triplechinidæ. Here, as DUNCAN and SLADEN showed (1885 *a*, Plate 5, fig. 4), in "*Hipponoë*" *proavia*, from the Indian Miocene, the triads unite in pairs with such intimacy that often a complete triad may become a "compound demi-plate." This combination of compounds, already seen in several genera, is here associated with a great increase in the relative width of the ambulacra and a corresponding horizontal disposition of the triserial pore-pairs. In the only two specimens of the recent *Tripneustes esculentus* that I have examined, this complex condition is only spasmodically developed, hardly more than in gerontic examples of *Echinus esculentus*.

The two families Strongylocentrotidæ and Echinometridæ develop considerably greater complexity than those described above, and, in the case of the latter group, attain the highest degree of ambulacral specialisation found among the Euechinoidea. Strongylocentrotus, the type of the former family, has, when adult, tetrad and pentad compounds in a practically continuous series from the apex to the peristome. Just near the adoral ends of the areas a few normally "Echinoid" triads remain. LOVÉN (1875, Plate 17) has described a series of ontogenetic stages in "*Toxopneustes*" *droebachiensis*. At 3 mm. diameter the adoral half of the ambulacrum is built of triads, succeeded adapically by one tetrad, one pentad, and a few uncombined primaries. In later stages all fresh compounds in this species are pentads; hexads occur in some others. As development proceeds the primitive triads lose all visible traces of the sutures of their components, although in most cases the original elements can still be distinguished by their diverse optical orientation. Here, as in many other genera, ontogeny shows the morphogenetic relation between polysynthetic compounds and the simpler types. The ambulacrum of Strongylocentrotus may be considered to bear the same relation to that of *Echinus* as the tetrads and pentads of *Tetrapygus* do to the triads of *Cœlopleurus*.

The four genera of the Echinometridæ, *Parasalenia*, *Echinometra*, *Heterocentrotus*, and *Colobocentrotus* (omitting the doubtfully placed *Stomopneustes*) present an interesting sequence of ambulacral specialisation. I have not examined specimens of *Parasalenia*, but to judge from the figures given by COTTREAU (1913, Plate 2) of *P. fontannesii*, that species seems to have strongly arcuate triads throughout the ambulacra. If this is a constant feature, *Parasalenia* is evidently the simplest, as it is the earliest of the Echinometridæ. In *Echinometra lucunter* (Plate 63, fig. 3), the compound plates on the adapical surface are usually made of five elements, including two primaries along the apical and orad margins. Below the ambitus most of the compounds are tetrads, but just near the peristome there are indications of the existence of "Echinoid" triads. *Echinometra* is thus closely comparable with Strongylocentrotus as regards its ambulacral structure and morphogeny. In *Heterocentrotus mammillatus* (Plate 64, figs. 1-5) the enormously high compounds with their arcuate pore-series are built of varying numbers of elements, but always

include two primaries (which may become almost or quite occluded locally) in the "Echinoid" position. In the gerontic specimen figured the highest compound at the mid-zone consists of 18 plates, while the average number of elements to a compound is about 11. The construction of the plates is more fully discussed in Section 2 (d), below, but it may be remarked here that there is some reason to suppose that these elaborate compounds owe much of their complexity to the union of two somewhat modified "Strongylocentrotid" pentads. The demi-plates all meet under the mamelons of the main tubercles (except adapically), whose unsutured and compact substance clearly serves to reinforce the lath-like plates at their place of union. Near the peristome the pore-fields broaden at the expense of the perradial tracts, and the arcs of pores take on an almost horizontal disposition. There are rarely any primary plates left in that region, all being compressed into included, occluded, or demi-plates. Some of the plates occasionally become so reduced that their pore-pairs may be obsolete or entirely absent. In *Colobocentrotus atratus* (Plate 64, fig. 6) the plating is essentially similar to that just described, but the average number of plates in a compound is nine. There is a far greater displacement of the pore-pairs, the arcs being practically biserial adapically, and an almost "phyllodal" arrangement obtaining near the peristome.

It would be difficult to find a more complete contrast than that between the ambulacra of the genera last mentioned and those of *Bothriocidaris*. Nevertheless, in *Colobocentrotus*, and still more in *Heterocentrotus*, the proportions of the polysynthetic compounds are not very different from those of the simple plates of the Ordovician prototype; while the compounds alternate more or less regularly with the contiguous interambulacra. With the reduction of sutural tissue and the reinforcement due to the tubercles, the compounds are mechanically at least as strong as the high, hexagonal primaries. They may be actually stronger, for the calcite of the components is not all orientated the same way, so that there are no straight cleavage-lines across the compound plates. With the displacement of the pore-pairs from straight lines, the strain on the plates becomes fairly evenly distributed. By virtue of their efficient ambulacral structure, the Echinometridæ can successfully withstand the onslaught of the wildest breakers, and seem deliberately to select the most exposed reefs for their abode. So that in this family the problem of multiplication of podia without accompanying weakness of the corona has been solved, and solved triumphantly.

(2) THE CHARACTER AND SIGNIFICANCE OF AMBULACRAL COMPLEXITY.

(a) Terminology.

In the course of the work upon which this paper is based, it has been found necessary to introduce a few terms in addition to those already in use, and to re-define others with greater precision. The Echinoid ambulacrum has usually been studied

as a belt of pores, tubercles, and granules, rather than as a region of special plating-structure, and the terminology employed by the relatively few authors who have taken the latter view is in some respects inadequate. As far as concerns the terms already in use, the standard fixed by BATHER (1909, pp. 61-62) is here followed. That, as well as the original terminology of DUNCAN, and new expressions here introduced, may be briefly summarised as follows :—

(i) An ambulacrum (or ambulacral area) consists of two columns of plates called ambulacrals (or ambulacral plates) in the Euechinoidea. The columns are styled *a* and *b* in accordance with LOVÉN's orientation (LOVÉN, 1875). The ambulacrals are numbered 1, 2, 3, etc., counting from the border of the peristome adapically. (Ideally, plate '1' should be the original member of a column, but in cases where resorption occurs during ontogeny, the proximal remaining plate must receive this number, in default of evidence as to the exact number lost.) When compound plates occur they may be similarly designated A, B, C, etc. Each ambulacral is normally perforated by a pore-pair (often enclosed in a peripodium). The belt of pore-pairs extending down an ambulacral column is called the pore-field, or poriferous-tract. If the pore-field is occupied by a continuous series of directly superposed pore-pairs, the latter are said to be uniserial. If the pore-pairs are arranged in obliquely transverse series, they are described as biserial, triserial, and multiserial, according to their grouping. If they form curved belts partially enwrapping the bases of large tubercles, they are arcuate.

(ii) An ambulacrum possesses three main sutures: the adradial (where the ambulacrals meet the contiguous interambulacrum); the perradial (the line of contact between the two columns of an area); and the transverse, which separates the plates in each column. Every ambulacral that extends across the full breadth of a column will normally possess five sutures: the adoral-transverse, adradial, adapical-transverse, apicad-perradial, and orad-perradial. For the sake of brevity, the double terms may be reduced by the omission of the words "transverse" and "perradial."

(iii) Ambulacrals may be (A) simple, grouped or compound; (B) primary or reduced.

(A) A simple ambulacral is usually a primary, and so has the five sutural margins noted above. Even if it should be reduced, it is suturally independent of the contiguous plates. Grouped ambulacrals are those which are associated into potential compounds, but lack the intimate sutural union that characterises those structures. They are intrinsically simple. A compound ambulacral usually resembles a simple one in its sutural boundaries, but consists of two or more ambulacrals firmly bound together by a reduction of the amount of sutural tissue between them (in extreme cases by ankylosis), the whole functioning as a multiporous individual plate. There is frequently a large tubercle on each compound, so situated as to reinforce the union of the components, but such tubercles are not invariably present. If two (or more) compounds become united in a manner similar to that by which they are formed from

simple plates, the result may be termed a super-compound. According to the number of ambulacrals incorporated, compounds may be described as dyads, triads, tetrads, pentads, etc. Compounds may be built entirely of either primary or reduced plates, but usually include both types. A complete compound plate may occasionally become reduced.

(B) A primary ambulacral is one which extends from the perradial to the adradial sutures of its area (*i.e.*, across the whole width of its column). It may be a simple plate, or may be part of a compound. A reduced ambulacral is one which does not extend across the whole width of its column. There are three types of reduced plates:—(α) Demi-plates, which have an adradial suture, but no perradial ones; (β) occluded plates, which take part in the perradial suture, but do not reach the adradial; and (γ) included plates (*endoplaques* of LAMBERT) which touch neither the adradial nor the perradial sutures, and are bounded by curved transverse sutures only. For some Palæozoic Echinoidea, the term *klasma-plates* is applied to the polygonal ambulacrals that agree with included plates in their relation to the longitudinal sutures of the areas. Whether the plates of the multi-columnar Palæozoic ambulacra are homologous or not with the reduced plates of elaborate Euechinoid areas, they are so different in shape and disposition that the use of a distinct term is necessary for the latter structures. Reduced plates are commonly united (with or without primaries) into compound ambulacrals, but they need not be so combined.

(iv) Ambulacral plate-complexity is considered to occur (A) when the transverse sutures of simple plates are not straight, or are deflected from a horizontal direction, (B) when compound plates are developed, and (c) when reduced ambulacrals appear. The term is intentionally vague, and does not presuppose any one determinant, or crushing due to any one cause or set of causes. For the Euechinoidea, it may be employed as a general term to express the condition of ambulacra which are unlike those of the Bothriocidaroida or simpler Cidaroida. The significance of the term is further discussed in the following section.

(b) *The Origin of Compound Ambulacral Plates.*

In the analysis of ambulacral terminology given above, one matter is involved which demands fuller consideration. It will be noticed that the phenomenon of "plate-crushing" is regarded as independent of, though often involved in, the process of the building of compound plates. The importance of maintaining this distinction is best illustrated by reference to a controversy which loses all meaning when the difference between combined plates and those which are merely grouped, distorted, or reduced is recognised. DUNCAN, to whom the first satisfactory account of elaborate ambulacral structure is to be credited, regarded the production of distorted and reduced ambulacrals as caused solely by "growth-pressure." It is possible that he included in that expression the pressure due to the expansion of

individual plates subsequent to their inception; but undoubtedly the chief type of "growth-pressure" to which he referred was that exercised by the production of new plates at the ocular-margins, and the consequent orad shifting of the columns. Dealing only with the Regular Echinoids, DUNCAN found one coincidence that naturally confirmed him in his view. The Cidaroida, in which the advancing ambulacrals can pass on to the peristome-membrane, undergoing resorption and redeposition in the process, show little or no distortion of the plates. The Diademoida, in which the development of the perignathic processes on the proximal ambulacrals demands stability in the latter, almost invariably show some degree of complexity. In the former case, the newly formed ambulacrals press against a yielding and movable column of plates; in the latter, against a column rigidly fixed adorally. It may be assumed that a mechanical explanation at once so obvious and so inevitable, must contain a large element of truth. LOVÉN, who frequently differed from DUNCAN in the interpretation of Echinoid structures, was completely in agreement with him in this matter. BATHER (1909, pp. 253-254) also expresses his belief in the influence of this type of growth-pressure on the production of complex ambulacral structure.

In the course of research into the ambulacral characters of the Irregular Echinoids, I have never found any reason to doubt the accuracy and adequacy of DUNCAN's explanation of the origin of reduced plates. On the contrary, in every case where complex ambulacral plating has been observed, his contention has been confirmed, and no alternative has seemed possible. So complete has been, and is, my belief in the power of "growth-pressure" (in DUNCAN's sense) for the production of elaborate plating in ambulacra, and even in interambulacra (HAWKINS, 1916), that I have been sceptical of the existence of any other force that could be so employed.

LAMBERT (1900), in the course of a study of the earlier Diademoida, put forward the view that compound plates are due to the influence of large tubercles overlapping the sutures. As far as the Diademoida alone are concerned, this explanation is fully as reasonable as that of DUNCAN. In the Cidaroida there are no large tubercles on the ambulacra, and no compound plates occur. Indeed, in one respect, LAMBERT's view receives greater support from the Diademoid structures than does that of DUNCAN. In such forms as *Hemicidaris*, the non-tuberculate adapical parts of the ambulacra are built of primaries, and the production of compound plates practically coincides with the appearance of large tubercles near the ambitus. On the other hand, the adapical parts of the ambulacra of *Heterocentrotus* (Plate 64, fig. 1) show a degree of complexity quite disproportionate to the size of the tubercles.

In the course of investigation into ambulacral structure, two very constant features have compelled me to adhere to DUNCAN's explanation, and to doubt the importance of tubercle-growth as a factor in the production of complexity. The first quality, which is noticeable chiefly in Diademoid ambulacra, is the tendency of the sutures to *converge* towards the tubercle. This character, which is quite

apparent in "Diademoid" triads, becomes most impressive in such polysynthetic compounds as those of *Heterocentrotus* (Plate 64, fig. 2). The tubercles attract, rather than repel, the sutural lines. Such a condition is incompatible with the view that the growing tubercles exert any kind of "pressure," whereby the plates on which they stand increase in area at the expense of their neighbours. The second character appears chiefly among the Irregular Echinoids. Without multiplying cases, it is sufficient to draw attention to the unusual complexity of structure in the anterior petal of *Echinocardium* (see HAWKINS, 1913, and Plate 69, figs. 4 and 5, of this paper). The granulation of that area is even finer than that of the rest of the adapical surface of the test; certainly, no excrescence worthy of the name "tertiary-tubercle" occurs there. So that it becomes obvious that plate-complexity, in a great degree of elaboration, can be developed quite independently of the presence of large tubercles.

However, with larger and more intimate acquaintance with the ambulacra of most families of Echinoidea, Regular and Irregular, I have reached the conclusion that both of the apparently contradictory explanations of complexity are correct. The distortion and reduction of plates is, in its inception at least, due to "growth-pressure" in DUNCAN'S sense. But distortion and reduction does not, of itself, produce compound plates. These are associations of reduced or unreduced, compressed or uncompressed, plates which are usually, and always primitively, grouped around, and bound together by, one or more large tubercles. Simple "growth-pressure" may cause the resorption and modification of stereom to almost any extent, but seems not to affect the thickness of interstitial sutural tissue. Indeed, if this organic film is instrumental in the growth of the plates (an undoubted fact), it will also be employed as an agent of resorption, and so must be maintained if the plates are undergoing that process. In compounds this placogenous membrane becomes so attenuated that the stereom of contiguous components is practically continuous. Indeed, near the peristome, all traces of sutures are often destroyed, a development analogous to "syzygy" uniting the compounds into apparently homogeneous plates.

Reverting to the principle of ambulacral development traced in Section 1 above, it may be stated that plate-crushing has for its chief purpose the accommodation of great numbers of podia within pore-fields of limited length, and incidentally the displacement of the pore-pairs from a straight line. On the other hand, plate-combination is designed to strengthen the intrinsically weak ambulacral areas, by a reduction of sutural tissue and a binding together of the several plates. It is clear that either of these processes may develop independently of the other, although the most efficient structures result from their united influence.

(c) *The First Phases of Plate-complexity.*

JACKSON (1912, p. 59) has shown that the complexity of kasma-plating in Palæozoic Echinoidea is produced by a "drawing-out process of plate movement."

It is certain that this process, in its full effect, gives results that are strikingly unlike any features found among the Euechinoidea. But, in its earlier stages, the dislocating influence of "drawing-out" produces conditions which may be surprisingly like those attained in later types. For example, the ambulacral structure of *Lovenechinus missouriensis* (Plate 61, figs. 10 and 11) is locally identical with that of the anterior petal of *Echinocardium cordatum* (Plate 69, figs. 4 and 5). Again, the triple grouping of the ambulacrals in *Lepidocidaris* (Plate 61, figs. 15 and 16) results in an arrangement differing merely in the proportions and ornament of the plates from that of the adoral parts of the areas of the Pygasteridæ. The case of *Lepidocidaris* seems especially noteworthy, since triple arrangement is adopted without any accompanying development of overlapping tubercles. It shows that, whether the growth of tubercles does or does not influence the association of Diademoid ambulacrals, their triad quality could have been acquired independently.

There is no trace of combination in the ambulacral plating of the Palæozoic Echinoidea. This may perhaps be due in part to the absence of large tubercles on the ambulacra. But since coronal flexibility was characteristic of the majority of the forms, dissociation rather than combination of plates would naturally be more effective. The absence of true compounds makes comparison of Palæozoic ambulacra with those of the Diademoida (other than the Echinothuriidæ) unprofitable, but makes their correspondence with complex areas in the Irregular Echinoidea the more striking. In addition to the two cases of resemblance mentioned in the preceding paragraph, reference may be made to the similarity between the displaced triads of an advanced "Cassiduloid" phyllode (*e.g.*, *Catopygus*, see HAWKINS, 1911, Plate 8, fig. 9) and the klasma-plates of such a form as *Melonechinus springeri* (JACKSON, 1912, p. 59). The two sets of structures are not quite identical, as in the previous cases, but are sufficiently alike to deserve comment. If to these agreements in complexity is added the very constant correspondence in simplicity shown by the "Bothriocidaroid" ambulacrals of parts of most non-Holectypoid Irregular ambulacra, the conclusion seems inevitable that there is some morphogenetic link between the two series of structures. This is probably to be found in the principle of phylogerontic atavism. The later Spatangidæ owe most of their characters to degeneration, or at least reduction, when their Cidaroid ancestry is realised. Even their symmetry may be compared, superficially, with that of a "Dipleurula," and their habits of life are not those of a robust group. Thus, if the Irregular Echinoids represent a course of evolution descending from the acme of the class, their ambulacra would naturally tend to show morpho-gerontic features, and so to revert in some manner towards a more primitive structure. That this principle is involved in their retention of "Bothriocidaroid" plates has been indicated by JACKSON (1912, p. 57), but it is peculiarly interesting to find that so elaborate a structure as that of Area III in *Echinocardium cordatum* has its prototype in *Lovenechinus* in the Palæozoic era. Even the relatively simple plating of the

petals of Clypeaster compares more closely with "Perischoechinoid" than Diademoid structure.

The simple primaries of the Cidaroid ambulacrum are often faintly cuneiform, but this is obviously an adaptation to the sinuous course of the area, and can be ignored in the present enquiry. Even in the Cidaroida, however, such forms as *Paracidaris florigemma* and *Diplocidaris* show signs of coming complexity. In *Paracidaris* the regular alternation of the ambulacral columns is broken at the sharper corners of the areas, and in *Diplocidaris* the ornament of the plates becomes diverse, finely tuberculate primaries alternating with minutely granulate ones. In the latter case it is almost permissible to regard the ambulacra as composed of grouped, though uncombined, dyads. There is no complexity in the sense of distortion of the sutures, but there is very little difference between the plating of the ambulacra of the *Diplocidaridæ* and those of the *Saleniidæ*, where dyad grouping is typical.

A very interesting and instructive account of the ambulacra of the earliest Diademoida adequately known is given by BATHER (1909, p. 254). It appears that in some Triassic types the only appreciable differences between Cidaroid and Diademoid ambulacra consist in the presence of peripodia and small tubercles on the latter. BATHER was unable to trace the transverse sutures throughout their extent, but his figures certainly justify his remark that "the plates appear equal in size." The tubercles are slightly irregular in disposition, but tend to occur on alternate ambulacrals, overlapping beyond the plates on which they are mainly based. This last character distinguishes the ambulacral structure from that of the *Diplocidaridæ*, but approximates it to the *Saleniid* type. It is worthy of note that in these forms, so far as is known, there is hardly any development of ambulacral elements in the perignathic girdle. We have, then, in the earliest known Diademoida, ambulacra that are almost perfectly Cidaroid in plating, but which show some progress in details of surface ornament.

The rarity and obscure preservation of Triassic and Liassic Echinoids make them the least known faunal series in the class, and, in spite of the work of BATHER and LAMBERT (1900), there is not yet available much material for a study of the chronological beginnings of plate-complexity. It may, however, be inferred that the Triassic ambulacra, though not comprising distorted or compound plates, show a condition that would easily resolve itself into the formation of dyads. The very constant occurrence of this simplest type of grouping in the small and retarded *Saleniidæ* lends support to the belief that the earliest phase of complication united the ambulacrals into pairs of primaries. In *Acrosalenia* the greater part of the ambulacrum is made up of alternate dyads and simple primaries. The introduction of the intervening simple plates is difficult to account for, but a similar condition at a further stage of complexity is seen in *Tetrapygyus* and perhaps in *Heterocentrotus* (see p. 414). By the association of the simple plates with one or other of the contiguous compounds, triads would result. In *Noetlingia*, which is probably

regressive in ambulacral structure, the dyads persist, and the odd simple plates are growing obsolete. JACKSON (1912, p. 117) records as regressive variants two specimens of *Echinus affinis*, in which the apical portions of the ambulacra are built of dyads.

For Echinoids generally, both Regular and Irregular types, triads are the predominant kinds of compound plates. In the Irregular forms, save for obviously secondary developments in the petals of some genera, a triad character may be said to be universal, although true combination is never found. A deduction from this fact would suggest that the Exocyclic Echinoidea were not differentiated from their Endocyclic ancestors before the latter had attained the "triad-stage" of ambulacral specialisation.

Tetrapyrgus niger (Plate 63, fig. 1) shows clearly the gradual production of tetrads from an arrangement of alternate triads and simple plates. It seems reasonable to postulate that more elaborate compound plates are similarly developed by the accretion of previously independent plates to already compound nuclei. The teratological specimen of *Echinus esculentus* described below (Section 2 (d), Plate 63, figs. 8, 11, and 13) is particularly interesting in this connection. Where supernumerary plates appear *between* the compounds they fail to become united with their neighbours, and are apparently gradually resorbed (figs. 8 and 11). Where such a plate has been developed *within* a compound it becomes incorporated into it by true combination, producing a "Strongylocentrotid" tetrad instead of the normal "Echinoid" triad.

In the examination of recent material it is relatively easy to determine the quality of the sutures between ambulacral plates. When the corona has been stained and etched, the unreduced sutures stand out as marked lines intensely coloured, while those separating the components of a true compound plate are either excessively delicate or are indicated by differences of the stereom mesh only. But in the case of fossil material, it is almost impossible to be certain of the nature of a suture. I am of the opinion that the sutures within compound plates in fossils are never displayed by natural or artificial etching, and can only be recognised by their influence on surface relief or ornament. On the other hand, the normal sutures that separate simple or compound plates, being filled in by a secondary mineral film, are liable to be made apparent by differential solution, preferably by the weather. Such satisfactory preparation of the specimen must inevitably be rare; and it is generally restricted to small regions in any one corona.

Examples of Diplopodia and Stomechinus that have undergone natural etching have convinced me that the presence of tubercles extending across more than one plate is not a certain indication of true combination. In both these genera all the ambulacral sutures near the apex seem to have the same width and "solubility," although the plates are well grouped into triads or more elaborate associations with superimposed tubercles. Towards the ambitus and adorally, only the main sutures seem capable of exposure by solution, so that their true compounds may be presumed to exist.

In the least elaborate, and chronologically earliest, types of compound plates, whether dyads or triads, the components are always primaries. It is therefore safe to assume that plate reduction did not appear before compound plates had been evolved. In a normal "Diademoid" triad the three primary components are not equal in size, nor are their transverse sutures straight, but their departure from simplicity is not associated with appreciable reduction in their average area. They are not *crushed* plates in any sense of the word. Rather the arcuate nature of their transverse sutures seems to indicate a convergence towards the tubercles of the compounds so that they may benefit by the cementing influence of the compact stereom of the mamelons. An additional determinant may be the departure from uniserial arrangement of the pore-pairs.

In the Regular Echinoids that retain some degree of simplicity in their ambulacra, the first indication of "crushing" always occurs near the adoral ends of the areas. This does not imply that the compound plates of those regions are more elaborate than elsewhere (the reverse is the case), but that their components are there distorted or reduced. This condition is most clearly seen in the simple Diademoida, such as *Hemicidaris*, in which the supra-ambital ambulacrals are practically Cidaroid, but it is none the less made manifest in more advanced types by the intensity of pore-congestion towards the peristome. It is thus safe to assume that the first *place* for the development of plate-complexity in Regular ambulacra is near to the adoral extremities of the areas. From that region the effect of crushing may extend adapically (both in ontogeny and phylogeny) until there is not a simple ambulacral left in the area. Indeed, in the Echinidæ and Echinometridæ, many of the new plates developed at the oculo-ambulacral suture seem fore-doomed to reduction, and never take on a simple character. This acceleration of the development of reduced plates in late post-larval growth in highly specialised types is strictly analogous morphogenetically to the introduction of elaboration into early larval ontogeny recognised by BEECHER.

(d) *The Capacity and Limits of Plate-complexity.*

(i) *The Production of Reduced Plates.*—DUNCAN was the first to recognise and classify the types of arrangement that occur in compound ambulacrals in the Regular Echinoidea. Three of the chief groupings of components are modifications of triads: the Diademoid, Arbacioid, and Echinoid types. It will tend towards clearness in the succeeding arguments if the interrelation of these three styles of combination is first considered.

The chronologically earliest, and morphologically simplest, type of triad is the Diademoid, in which the three components are all primaries, with a tendency for the apical and oral plates to be lowered ad- and per-radially, and for the median plate to be consequently hour-glass shaped. The boss of the tubercle (when one is present)

is situated on the median plate, and its scrobicule extends across the reduced sutures on to the other two components. This character is certainly of common occurrence in the Diadematidæ, but is rarely maintained without modification in most genera of that family. Towards the peristome one or both of the external components become separated from the perradial suture, as a result of excessive lowering of the perradial parts of the plates. There is thus developed a more or less complete approximation to the Arbacioid type. In that class of triad the median component, while low adradially, becomes relatively very high perradially, and alone possesses the perradial sutures of the compound. The apical and oral plates are reduced into demi-plates. In the majority of cases these demi-plates do not taper away gradually in a perradial direction, but retain their full height until they reach the tubercle, and then are abruptly truncated, their sutures turning through a right, or even an acute, angle. The perradial expansion of the median component is not, therefore, due to the extension of the tubercle, but is probably to be ascribed to the need for a reduction in the quantity of suturing in the area. The position of the tubercle and of the perradial limits of the demi-plates suggests that their coincidence is not accidental, but that the tubercle binds the three components together as in the Diademoid triads.

The derivation of the Arbacioid type of compound from the Diademoid scarcely requires argument: not only is it the logical sequel to the tendency started in the latter type, but within the limits of a single area the transition can be traced. The type may be elaborated in two different ways. In *Arbacia* itself, and in such forms as *Tetrapygyus* and *Goniopygyus*, tetrads or more complex compounds may be developed by the incorporation of new plates introduced *between* the original triads; much in the same way that the triads themselves probably originated from alternate dyads and simple plates. In such genera as *Leptarbacia* (Plate 62, fig. 16) and *Pedinopsis*, this process seems clearly indicated, and to judge from the figures of the former given by CLARK and TWITCHELL, the resulting tetrads and pentads are not truly combined adapically. At least the compounds have ill-defined transverse sutures, similar to those in the adapical parts of the areas of *Tetrapygyus* (Plate 63, fig. 1). In the latter case, the extra plates may be traced adorally, and are seen to enter gradually into true combination. The other type of elaboration is shown in its extreme development by the "Phymosomoid" compound, where hexads and occasionally heptads are formed by the introduction of extra demi-plates *within* the body of the compounds. This type leaves the two external components in their "Arbacioid" or sometimes "Diademoid" relations. The same method is employed in the more elaborate derivations of the Echinoid type.

The Arbacioid type is certainly older, and apparently simpler than the Echinoid. In the latter a completely contrasted structure is seen, for the median plate becomes reduced to a demi-plate (usually of very small dimensions), while the adapical and adoral components tend to retain their primary character. In the majority of cases,

a fully developed Echinoid triad consists of a broad low apical demi-plate, a minute median demi-plate projecting somewhat into the interambulacrum, and an oral primary which extends for the whole height of the compound in the perradial tract (see Plate 63, fig. 2).

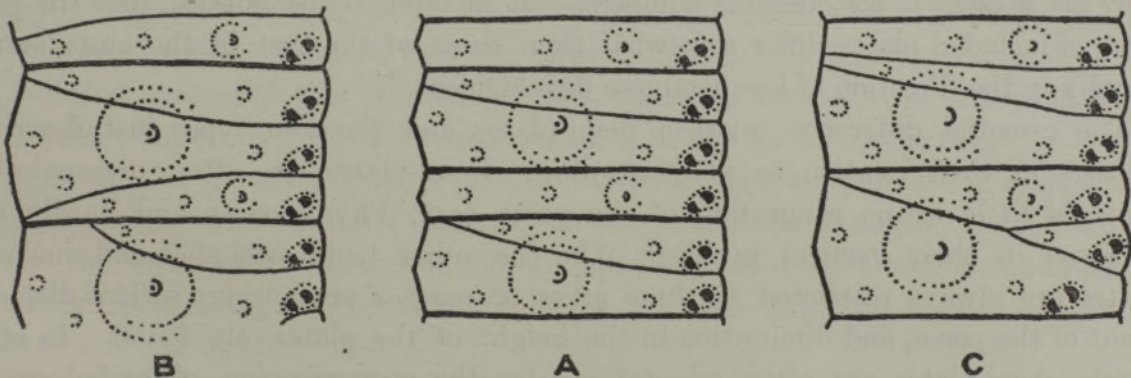
Starting from a normal Diademoid triad, with a centrally constricted median component, it is easy to imagine that further constriction would cause the transverse sutures of the median plate to meet. Such a phenomenon would produce an adradial demi-plate, but would also leave a perradial, imperforate occluded portion. Such a feature does not occur in reality—I have never seen even a teratological specimen with such an anomaly. Hence, if the median demi-plate has been produced in the manner above indicated, the greater part of the adoral transverse suture of the median plate (*i.e.*, of the adapical transverse suture of the adoral plate) must have entirely disappeared. The other possible interpretation of the median demi-plate is that its bounding sutures, and the single suture which extends from it perradially, are actually the complete two sutures of the original median primary, that plate having become lowered to the degree of extinction in its perradial portion. Such a hypothesis would involve a complete reversal of the Diademoid tendency, and is thus improbable.

Assuming that the former suggestion as to the origin of the demi-plate is correct, it would be expected that some evidence of its truth might occur in teratological, if not in normal cases. The large and otherwise perfectly normal specimen of *Echinus esculentus* from which Plate 63, fig. 10, has been drawn, seems to supply such evidence. Occasional triads are still in the retarded (or regressive) Diademoid condition, with the constriction of the median plate strongly marked. A considerable sequence of compounds in the same area are, as it were, upside down in structure. The transverse suture which separates the two external components slopes adorally instead of adapically, sometimes reducing the oral component to the condition of a demi-plate, leaving the entire perradial suture to the apical component. Here, surely, for some inexplicable reason, the adapical transverse suture of the median "Diademoid" plate (*i.e.*, the adoral transverse suture of the apical plate) has disappeared. Plate 63, fig. 10, in which three separate compounds from one column are placed together, shows more clearly than any further description the apparent relation between Diademoid and Echinoid triads.

The importance of this argument lies in its corollary. In the majority of Regular Echinoidea the compound plates owe some of their character to the destruction of part of a suture. Hence, if the argument is sound, plate-complexity is capable of obliterating sutures. This is not quite comparable with the "syzygous" union of some plates near the peristome in many advanced Regular forms, for there it is usually possible to trace the original limits of the components by the optic orientation of their calcite or by differences in the stereom-mesh. No such tests resolve the surviving primary of an Echinoid triad. The fact that the morphoneanic plates at

the apicad ends of the ambulacra in such advanced genera as *Echinus* or *Heterocentrotus* are developed in a reduced state is probably due to accelerated and compressed recapitulation, in which the stages in the attainment of the reduction have been omitted. In this connection it is appropriate to refer to the existence of the "biporous ambulacrals" around the Spatangid peristome. The principle enunciated above implies that it is *possible* that these might originally have been two plates, although it would be premature to attempt any conclusion on the subject here.

There is another possible method of derivation of the Echinoid triad which, though morphologically simple, seems less in accord with observed facts than the one indicated above. It is at least probable that the Diademoid triad was developed by the addition of an intervening simple plate to a Saleniid type of dyad. In such a primitive compound, the apicad member of the pair is usually the smaller, and may occasionally be reduced. If the intercalated plate were to become combined with the dyad *adapical* to it (and to undergo the reduction which commonly befalls such plates), an approximately Arbacioid triad would result. If, on the other hand, the extra plate were to be attached to the dyad *adoral* to it, an Echinoid triad would inevitably be produced. The very constant reduction of the apicad component of an Echinoid triad, though less in degree than that suffered by the median plate, would be in accord with such a theoretical origin for the compound. Text-fig. 1 shows in



TEXT-FIG. 1.—Diagram showing a possible (but improbable) method of derivation of the Arbacioid (B) and Echinoid (C) types of triads from the Acrosaleniid (A) condition of alternating dyads and monads. All the figures show a progressive increase in elaboration from above downwards.

diagrammatic fashion the possible derivation of the three types of triads from an Acrosaleniid condition of alternate dyads and simple plates. There are, however, two serious difficulties involved in such an explanation. Firstly, the Arbacioid structure may be, and often is, derived *through* the Diademoid, and so need not be traced back to the Acrosaleniid type; while the frequent abnormalities found in Echinoid triads illustrated in Plate 63, fig. 10, are only intelligible if taken as regressive variants pointing to a Diademoid origin for the compounds. Secondly, the Echinoid type of triad seems not to have appeared before Cretaceous times, while the

increase from dyads to triads had been established long before that period. The question of the morphogeny of the Echinoid triad needs fuller investigation before any solution can be attempted. The problem is, however, foreign to the purposes of the present study.

Except in the ambulacra of the Echinometridæ, *occluded* plates are rarely developed among the Regular Echinoidea outside the regions of peristomial pore-crowding. They seem to be an inevitable product of complex-arcuate or highly multiserial pore-series. Such grouping causes two or more pore-pairs to occur in practically a transverse line, and the plates bearing the perradiad pores have perforce to disappear before reaching the adradial suture. Even so, it is remarkable how the plates of the inner series seem to cling to the adradial suture, although they may be reduced to strips of calcite of hardly greater height than that of the sutural tissue. In the phyllodes of the "Cassiduloida" (*sens. lat.*) such occluded plates are commonly found, and they form an important proportion of the elaborate anterior petal of *Echinocardium cordatum*.

Included-plates are still more exceptional among the Regular Echinoidea. They may be defined as demi-plates which have become occluded. The aberrant genus *Noetlingia* and the Echinothuriidæ are the only types in which such plates constitute an important part of the ambulacra. They occur sporadically in *Heterocentrotus*, especially towards the peristome. In the petal of area III of *E. cordatum* they are present in considerable numbers. It is often to be noticed that the pore-pairs of included plates differ somewhat from those of the rest of the ambulacrum, usually in the direction of less complete development.

The essential difference between demi-plates and the two types just described consists in their relation to pore-crowding. Demi-plates are often present when there is little or no congestion of the pores (*e.g.*, *Phymosoma*), and hardly any decrease in their vertical interval. On the other hand, occluded and included plates are always restricted to those areas or parts of areas where serious displacement of the pores, and diminution in the height of the plates, are found. In other words, demi-plates are often adaptations for the strengthening of ambulacra by reduction in the amount of sutural tissue; occluded and included plates for the multiplication of podia. The latter types are therefore to be ascribed to "plate-crushing" in its literal sense.

In this connection a fresh question arises. If plates can be materially reduced in size by crushing, can this process be carried to its extreme, and plates, with their podia, be crushed out of existence (*i.e.*, totally resorbed)? Such a process would, in some measure, be an over-specialisation, since the crushing that might achieve it seems designed to multiply, not to reduce, the number of pore-pairs. Nevertheless, there seems to be substantial evidence in favour of the view that ambulacrals may be obliterated by crushing. In the large and otherwise normal *Echinus esculentus* described below (Plate 63, fig. 14), certain pore-pairs are situated well out in the

interambulacra near the ambitus in two of the areas. In every case these displaced pore-pairs belong to the median demi-plates of the triads. In some of the compounds affected the demi-plates are very minute, quite imperforate, and strongly projecting beyond the normal line of the adradial suture. In one case the demi-plate is absent, the compound being built of the apicad and orad members only. In this case, although the podia have survived, the condition suggests that some of the reduced ambulacrals have undergone more or less complete resorption on account of abnormally intense crushing. In the specimen shown in Plate 63, fig. 12, a whole triad shows signs of approaching destruction.

In *Noetlingia boulei* (Plate 63, figs. 4 and 5), according to LAMBERT (1906, p. 11), the adoral parts of the ambulacra consist of dyads (with an apicad demi-plate) alternating with variously distorted simple plates. At and above the ambitus the dyads are maintained almost unaltered, but the alternating "monads" are reduced to very small included plates. The suggestion made above (p. 392), that these intervening plates, having missed incorporation with the compounds (otherwise normal Echinoid triads might have resulted), prove out of harmony with the system of plating adopted, and tend to become obsolete—seems consistent with the evidence afforded by the abnormal *Echinus* shortly to be described. The pore-pairs that perforate the included plates are so minute that NOETLING (1897, p. 15), in founding the genus (*subnomine* *Protechinus*), remarked that "the pores are seemingly arranged in groups of two . . .; the third pair, however, is so much reduced that it is hardly visible." Later he uses the term "obsolete" to describe the condition of the included pore-pairs. In *Noetlingia*, then, there seems reason to believe that one set of plates, together with its series of podia, is in process of destruction.

Lastly, in the gerontic *Heterocentrotus* described below, there are in some of the compounds undoubted included plates which are so reduced that they do not extend beyond the bosses of the tubercles, and are quite imperforate. Other included plates of rather more complete preservation show the pore-pairs in various stages of resorption or blocking.

In view of these facts, it seems legitimate to propound a second principle, viz., that plate-crushing is capable of obliterating ambulacral plates, with or without the corresponding destruction of their podia.

The third and last phase of plate-complexity that need be mentioned here is the reduction and combination of compound plates, forming super-compounds. This condition occurs in many groups of the Diademoida, and its gradual development can be traced in the ambulacra of large specimens of *Echinus esculentus*. It represents the highest type of ambulacral complexity, although a super-compound of one genus need not include as many pore-pairs as a normal compound of another. I have never seen a case where more than two compounds become united, but there seems no reason to doubt the possibility of the occurrence of "super-triads."

(ii) *Detailed Description of the Structure of the Ambulacra in Echinus and*

Heterocentrotus.—The three chief effects of plate-complexity that have been indicated in the preceding paragraphs, together with certain details of less general application, can best be illustrated by the description of definite cases of ambulacral elaboration. Whether these cases are normal or teratological is immaterial, since even disease cannot induce the development of impossible structures, and features abnormal in one group of organisms may prove to be the rule in another.

(α) *Echinus esculentus*.

After the examination of several hundreds of specimens of this abundant species, from various British localities, and of sizes varying from 3 mm. to about 140 mm. in diameter, the most enduring impression gained is that of wonder at the remarkable uniformity of structure displayed in the ambulacra. When it is realised that a moderately large example has ten ambulacral columns, each composed of some 230 plates (*i.e.*, about 2,300 ambulacrals in all), grouped into about 77 compounds (*i.e.*, about 770 triads in all), the scope for variation, or at least for irregularity, in so lavish a repetition of similar structures is manifest. But specimen after specimen can be carefully studied without the discovery of any trace of abnormality in a single plate. Even in cases where some serious accident or disease has deformed or otherwise modified other coronal structures, the ambulacra are often perfectly normal. Moreover, irregularities in the disposition of the tubercles and granules of the perradial tracts are by no means always accompanied by structural disturbances. Plate 63, fig. 2, shows a typical ambulacrum drawn from a specimen of 106 mm. diameter. At the two extremities of the area the compounds are typical "Echinoid" triads in DUNCAN'S terminology, having two unequal primaries enclosing a small demi-plate. The greater part of the area is composed of plates in which the apical primary is reduced, and, indeed, this condition deserves the name "Echinoid" more truly than the young, partially developed state found adapically and adorally. Very rarely, chiefly in the adoral region, one or both of the external members of a triad may be occluded, but the occlusion is never profound, and usually occurs on the outer surface of the test only.

It seems fitting to prefix the above remarks to the rest of this sub-section, because without them the impression might be gained that ambulacral abnormality is common in *E. esculentus*. The reverse is the case, but in a discussion of the capacities of plate-complexity, the reaction to cases of irregularity demands fuller description, and is more instructive.

By far the most frequent variant in triad-formation in *E. esculentus* is the inversion of the course of the median transverse suture already discussed above (see Plate 63, fig. 10). According to my experience, this abnormality is even commoner in *E. norvegicus* and *E. acutus*, but is very rare in *Parechinus miliaris*. Next in order of frequency is the reversionary "Diademoid" plate, in which the resulting structure sometimes has partly "Arbacioid" characters. These two relatively unimportant

variations very commonly occur in areas that include more profound abnormality, but they may be independent of any such disturbing influence. They may appear in any part of a column, and their development in one area or column does not necessarily imply that they are to be found in other areas of the same corona. In no case have "Diademoid" or "inverted" triads proved to be associated with irregularity in the disposition of the pore-pairs, and they certainly do not involve either greater or less compression than that exercised upon normal compounds. Finally, neither type need show any discrepancy in ornament from the others. Both are best intelligible if regarded as manifestations of morphogenetic atavism, the regression being often instigated by the existence of some other irregularity of development.

Plate 63, figs. 6 and 7 illustrate the gradual production of super-compounds (akin to those of *Astropyga*) at the mid-zone in gerontic specimens. The example shown in the former figure is actually somewhat precocious in this respect. It is only 70 mm. in diameter, while the stage of "super-combination" that it has reached is usually not attained until the diameter is about 90 mm. The gradual production of compound demi-plates, and the influence (if any) of the major tubercles on the process, are so plainly shown by a comparison of the figures that further verbal description is unnecessary.

Turning now to cases of true abnormality; a few types have been selected as showing features helpful to the present discussion. All cases due to repair of injury, or associated with other coronal abnormality, have been excluded. Of the figures given in this connection, four (Plate 63, figs. 8, 9, 11, and 13) are drawn from the ambulacra of a single specimen. Unfortunately the corona (from Port Erin, Isle of Man) had undergone very rough treatment before I acquired it. It was one of a set exhibited for sale to tourists, and had been scraped with a knife to remove the radioles, with the result that most of the tubercles are broken. Also, the contents of the test had been violently extracted through the peristome with the same implement, so that the ambulacra are incomplete adorally. Hence it is impossible to attach their correct numbers to the plates. Beyond a reconstruction of the broken tubercles (whose bases were still apparent) there is nothing in the figures that is not perfectly clear in the specimen.

Fig. 8 shows a portion of area IV about midway between the ocular plate and the ambitus. In column *a* one, and in column *b* two contiguous, supernumerary plates occur between the normal triads. These plates, as the nature of their sutures shows, are in no way combined with their neighbours, nor (in column *b*) with one another. All are reduced to demi-plates, and the apicad supernumerary in *b* has a distinctly smaller pore-pairs than usual. It is noteworthy that in all three cases the pore-pairs are situated well away from the adradial suture, although normally the peripodia of the demi-plates impinge upon that line. There seems to have been a spasmodic increase in the rate of production of new plates at the ocular margin, so that some were built in excess of the requirements of the triads. In their subsequent

history, these extra plates have become reduced, and seem threatened with resorption. It may be surmised that, had such a development occurred in a type less established than *Echinus*, tetrads might have been formed; and such a modification might well have come to be adopted as a permanent feature.

Fig. 9 (Plate 63) illustrates the condition of area I in the same specimen, at about the same horizon of the corona. Column *b* is here perfectly normal, but two aberrant features occur in column *a*. At X there is an intercalated demi-plate precisely similar to that of column *a* in area IV. At X' a very curious modification appears. At first sight the three plates marked seem to constitute an "Arbacioid" triad. Actually, however, the three plates are quite uncombined. Here a disturbance in the sequence of plate development at the ocular has resulted in an attempted "parallel variant" in the Arbacioid line. But, owing to their incongruous disposition, the plates have failed to unite into a compound.

Fig. 11, from area I below the ambitus, shows perhaps the most striking, and certainly the most interesting, of the abnormalities present in the specimen. A supernumerary, uncombined plate is *included* along one of the main transverse sutures. It is of such small dimensions that its surface is almost covered by the very reduced peripodium, while its pore-pair is almost obsolete. Occurring, as it does, below the ambitus, this plate was developed earlier in the life of the *Echinus* than the similarly additional plates of the adapical surface shown in figs. 8 and 9. It is reasonable to suppose that it shows the condition to which, in course of time, they would have been brought. It is evident that complete destruction of the surplus plate is imminent. Again, this small, minutely perforated, included plate, is strictly comparable with the inner series of plates in *Noetlingia*. The explanation of the ambulacral structure of that curious genus offered above (p. 392) is supported, if not actually confirmed, by this abnormality in *Echinus*.

Fig. 13, from the adoral part of area III, shows the intercalation of a surplus demi-plate at X, converting the compound into an apparently normal "Strongylocentrotid" tetrad. In this case the extra plate has definitely combined with its neighbours, but it is reduced in size, and its pore-pair is disproportionately small.

Fig. 12, which is taken from the ambital part of area III of another specimen, shows a comparable, though different, type of irregularity. At X a whole triad is in course of destruction. The two external components are both occluded, and have much reduced pore-pairs, while even the demi-plate is adradially lowered in comparison with those of normal triads. On counting the plates in the two columns of the area, it is found that *a* has three more than *b* (214 and 211 respectively). There is thus one triad too many in column *a*, and the one figured seems to have been selected for resorption so that plating and pressure may be equalised.

By far the most interesting abnormality that I have seen in the ambulacra of *E. esculentus* is that illustrated in Plate 63, fig. 14. While bearing some resemblance to that described by CHADWICK (1914), it differs in the otherwise complete regularity

of the corona. The specimen (in the collection of Ll. TREACHER, Esq., F.G.S.) is a large one of about 120 mm. diameter, and is slightly more thickly tuberculate than usual. Areas II and IV both have extraordinarily congested pore-fields, the development of ambulacral plates having been abnormally rapid. A portion of area IV from the ambitus towards the peristome is here figured; the corresponding section of area II is essentially similar in character. In column *a*, plate 57 to 65, are normally combined into three triads. The "triad" 66-68 contains two plates only—the median demi-plate (67) is wanting. But out in the interambulacrum, at a distance from the adradial suture greater than the width of the pore-field, there is a pore-pair differing from the normal merely in size, position, and the absence of a peripodium. The next triad is normal, except that the apicad component is occluded. Compound 72-74 has the median demi-plate much reduced, and its pore-pair, failing to find accommodation in its normal position, is partly in the interambulacrum. The next triad is inverted and the succeeding one normal. Triad 81-83 is inverted, and the small median plate projects far out interradially; perhaps the incidence of the transverse interambulacral suture encouraged this displacement. After the next four triads (normal, inverted, normal, normal), plate 96-98 shows a condition like that of 72-74, but here the demi-plate retains its full breadth. The decrease in its height has driven the pore-pair across the adradial suture. Several occluded plates occur in the column between Nos. 105 and 111.

In column *b*, plate 64-66, has a minute imperforate demi-plate, whose pore-pair is well out among the interradiat tubercles. Plate 112-114 shows the condition found twice in the adjacent column, the reduced demi-plate being insufficient to contain the whole of its pore-pair. An anomaly in the numbering of the plates will be noted. While in both columns plates 57 are very nearly on the same horizon, plate 112 of column *a* is considerably lower (*i.e.*, nearer the peristome) than the corresponding plate in *b*. This means that there are more plates in *a* than in *b* in the region figured. The extra plates seem to exist in the whole triad 108-110, where a condition of occlusion precisely like that shown in Plate 63, fig. 12 occurs, except for the maintenance of the size of the pore-pairs. It is noteworthy that there are three pore-pairs displaced in *a*, and only two in *b*.

In this most remarkable specimen, unusual rapidity of plate development in two ambulacra is manifest in the crowding of their pores. The consequence has been an exertion of "growth-pressure" (in DUNCAN'S sense) to an unusual degree. This pressure has not reduced the size of the pore-pairs, but has disorganised the plates. Those ambulacrals in which the peripodia are normally perradiat in position have frequently become occluded, and those with adradiat pore-pairs have been more or less extruded from the area. These demi-plates are so reduced that they cannot contain their pore-pairs, and in one case a plate, of whose previous existence there can be no reasonable doubt, has totally disappeared. The influence of "growth-pressure" is surely indicated here; no other explanation of the phenomena seems possible. The

interambulacral position of the extruded pore-pairs is particularly interesting in view of the normal extension of podia over the interambulacra in the Clypeastroida.

(β) *Heterocentrotus mammillatus*.

An unusually large, gerontic individual of this species has enabled me to trace the later phases of complication in an ambulacrum which is the most highly specialised known among Regular Echinoidea. The test of the specimen is exceedingly thick; and, since it readily separated into its component plates, it has been possible to compare the arrangement of the plate-sutures on both sides of the corona, and to trace their course across the adradial suture-face. Stereo-sections have been prepared of various fragments, so that the appearances on the surface have been checked by a study of the stereom-mesh and of the optic orientation of the plates.

The pore-pairs are arranged in strongly curved arcs (much more so externally than internally), which tend to become biserial towards the apex. The apicad and orad pores of the compounds are practically in the perradial tract except near the ambitus. Towards the peristome the pore-pairs become massed together so that the peripodia are almost in contact, and no order in their arrangement can be determined by superficial examination. The general structure of the compound plates is much elaborated beyond that of an Echinoid triad, but that basis is none the less apparent. The largest plate of a compound is the orad member, the second largest is usually the apicad (normally occluded) and the remainder are either demi-plates or included. The perradial suture is made up entirely of the edges of the two external components, as in the Echinoid triad.

In Plate 64, fig. 1, the adapical part of Ambulacrum I is drawn. In spite of appearances, the plating-structure is in many ways more complex here than lower down in the area. This point is noteworthy in view of the feeble development of the tubercles. It is difficult to define with confidence the limits of all the compounds, since the plates are, on the whole, grouped rather than combined. In column *a* the apicad compound, presumably limited adorally by the large occluded plate bearing a small tubercle, has five demi-plates in addition to the main component. The apicad margin of this column is the oculo-ambulacral suture, so that the last-formed plate is clearly a demi-plate at its inception. The succeeding compound seems to have three plates reaching the perradial suture. The small apicad occluded plate I consider to be comparable with the additional plates between the triads in *Tetrapyrgus*, while the low primary is the true apicad component. There are six demi-plates between this and the tuberculate orad primary. The next compound shows a similar supernumerary plate, followed by a much reduced occluded apicad member. The orad plate of this compound is also occluded, and ten demi-plates intervene. The characters of the fourth compound from the apex are normal, and one demi-plate has become occluded (hence being an included plate). Included plates, sometimes with obsolescent pore-pairs, begin to figure largely in the fifth compound, which is

only partly shown in the figure. Column *b* is very similar to *a*, but the second plate down seems strangely simple in composition, comprising four demi-plates only, in addition to the external components.

Fig. 2 (Plate 64) shows the mid-zone, where the large tubercles, abundant smaller ornament, and semicircular arcs of pores make up a design unrivalled for beauty among the Echinoids with which I am acquainted. The sutures are clearly visible, except on the mamelons (where they do not exist at the surface, but have been inserted on evidence supplied by sections), and the regularity of the structure is surprising, in view of its extreme complexity. Sixteen demi-plates (18 components in all) represent the fullest degree of combination in this specimen. In the largest compound of column *b*, the third demi-plate from the adoral margin has its pore-pair almost obliterated by the growth of a minor tubercle on the adradial part of the plate. The only occluded plates in this region are the external components.

In fig. 3 the congested area of pores near the peristome is shown. Traces of sutures appear here and there among the peripodia, and show clearly on the bosses of the main and secondary tubercles. On several of the large tubercles, the outlines of included, imperforate plates are very sharply defined, but I should have hesitated to insert them had not sections confirmed this peculiar feature. Great as is the number of pore-pairs in this region, it is inferior to the number of plates; several have been lost during ontogeny. In the two lowest tubercles on which sutures can be seen, it will be noticed that there are two sutures on the perradiad sides of the bosses. Reference to fig. 5 shows that these tubercles rest upon two compound plates, thus producing more or less definite super-compounds.

In fig. 5 part of the corresponding region of another area of the specimen is shown in section. The section was taken as near to the exterior surface as the irregularities allowed. The effect of excessive crushing in the production of occluded and included plates, both with and without pores, is very clearly displayed. The influence of the tubercle as a "binder" is also obvious. The pore-pairs are seen to be disposed in double, almost transverse, arcs in each compound, and the distribution of the sutures suggests a "double Strongylocentrotid" origin for the plates. The transverse sutures, which roughly bisect each polysynthetic plate, are almost identical in character, so far as they extend, with the transverse sutures that bound the compounds. So that it is possible that a "Heterocentrotid" compound is really a more or less modified "Strongylocentrotid" super-compound.

Fig. 4 represents the surface of the greater part of the adradial suture. The main sutures of the compounds are indicated by thick lines, which are produced beyond the exterior edge, otherwise the figure is in no way diagrammatic. It will be observed that the arrangement of the sutures undergoes great alteration between the two surfaces of the test. Many plates that are demi-plates externally prove to be included internally, and some that are superficially occluded are true primaries within. On the whole, there is a tendency for a reduction in the number of plates

that reach the adradial suture internally, consequent on the curvature of the corona. This must be due to "growth-pressure"; it cannot well be caused by tubercle growth. The simple and direct course of the sutures of the proximal orad compounds, sheltered as these are behind the projecting perignathic processes, seems equally conclusive in this respect. The earliest formed plates preserved there have been protected by the process from the downward drive of the advancing column, while those near by, devoid of this shelter, are intensely crushed and deformed. The view that plate-complexity in the *Diademoida* is largely due to the impact of the plates upon the rigid perignathic girdle thus receives notable support.

The detailed study of the two types of ambulacra just described has supplied much of the evidence on which the preceding section was based. It also shows, to my mind, that "growth-pressure" is a real force in the determination of ambulacral complexity, although the influence of tubercles as central reinforcements in compound plates is none the less marked. Lastly, a comparison of the ambulacra of *Echinus* and *Heterocentrotus* shows that the latter are much modified developments from the former, the chief difference consisting in the incorporation of additional demi-plates within the bodies of the compounds. *Phymosoma* stands in a comparable relation to *Diadema* or *Arbacia*.

As a summary of the results reached in the last two sections, the following theory of the origin of ambulacral complexity may be put forward. The first phase of complication consisted in the grouping of the ambulacrals into pairs (dyads) of primaries, which gradually became combined by the transgression of tubercles over their common suture. Later, non-tuberculate simple primaries appeared alternately with the dyads, and these gradually became attached to (usually) the compound adoral to them. This produced the "Diademoid" triad, of which the "Arbacioid" is but an exaggerated type. Such triads could be amplified in two ways. In one case, further incorporation of alternating simple plates, in a manner similar to that above described, gave the "Tetrapygyus" tetrads or pentads. In the other, addition of extra plates between the components of the triad resulted in the "Phymosoma" hexads or heptads. By a modification of the Diademoid triad, involving the destruction of one of the internal transverse sutures of the compound, the "Echinoid" triad arose. This type is usually complicated (when amplification occurs) by the intercalation of internal plates (after the "Phymosoma" manner), giving rise to "Strongylocentrotid" and "Heterocentrotid" polysynthetic compounds. Adapically, in *Heterocentrotus*, there seem to be indications of a "Tetrapygyoid" addition of new plates between the compounds, but this is a very exceptional occurrence in the *Echinina*. The grouping or combination of the ambulacrals is often quite unassociated with any increase in the number of plates in a column, and seems designed primarily as an aid to the mechanical strength of the area. Even demi-plates are frequently manifestations of the need for suture-reduction rather than evidence of compression. On the other hand, occluded and included plates are invariably restricted to those

areas or parts of areas where the pore-pairs are congested, and their presence serves as an indication of the incidence of "growth-pressure" in its widest sense.

(e) *The Relation between Plate-structure and Function.*

The functions of the podia of the Echinoidea are various, and are probably rarely exercised singly. Perhaps their most constant purpose is to afford means for the aëration of the fluids in the vascular systems of the body. But, in the Regular Echinoidea, this possibly primitive function is more or less subordinated to the adhesive and ambulatory uses of the podia. That this adaptation was progressively acquired in the course of the specialisation of the group seems likely, and it is perhaps rendered more feasible in the Diademoida by the presumed respiratory function of the external or peristomial "branchiæ." These tufted extensions of the water-vascular system are apparently largely concerned with the regulation of hydrostatic pressure during mastication, but their branchial designation is almost certainly appropriate in some degree.

Nothing definite can be ascertained as to the chief uses of the podia of *Bothriocidaris*; but it may be suggested that the sparse distribution and small numbers of the "tube-feet" would not make them efficient as organs of locomotion or adhesion. In *Cidaris* the absence of peristomial "branchiæ" may imply that the respiratory function of the podia is of first importance; certainly the adhesive function is but feebly developed. JACKSON (1914, p. 141) remarks that "in collecting *Eucidaris* [*tribuloides*] one simply picks them up, and in no case observed did the animal cling to the ground by its tube-feet." The same author (*loc. cit.*, p. 142), writing of *Centrechinus* [*Diadema*] *setosus*, states that "the tube-feet have only the slightest hold on the sea-floor, so that specimens can be picked up . . . without any perceptible resistance." *Diadema* has the peristomial "branchiæ" well-developed, so that the lack of power in its podia seems not to be attributed to their pre-occupation with a respiratory function. On the other hand, JACKSON (*loc. cit.*, p. 154), referring to *Echinometra lucunter*, explains that "this species clings tenaciously to the rock, and has to be pulled off from the rock with some effort." The same remark would apply equally to *Echinus* or *Strongylocentrotus*. Although specimens can be dislodged from the rock with fair ease in a surprise attack, their power of adhesion when alarmed is such that their collection with ungloved hands is painful and uncertain. Often they will cling so tenaciously that the podia are torn asunder before the adhesive suckers give way. The inference from these observations is obvious. Those forms that can exert strong powers of adhesion are precisely those which have compound plates where the degree of combination is complete, the components are reduced, and the pore-pairs multiseriate. Hence the production of compound plates, and the plate-crushing associated with multiseriate pore-pairs, are adaptations towards the adhesive function of the podia. If *Cidaris* were to resist removal with an energy approaching that exerted by *Echinus*, the weak, simple ambulacrals would be torn from the corona.

So that plate-complexity, both in combination and crushing, seems to be necessary for the exercise of the most vital podial functions in forms which, like the higher Diademoida, inhabit tidal zones of the sea-floor, and, in their search for clear water, prefer wave-swept rocks where little shelter can be obtained. For such purposes, the number of podia and the strength of the ambulacra could hardly be too great; and from the Triassic period to the Holocene the record of ambulacral evolution in the Regular Echinoidea has been one of steadily progressive elaboration, culminating in the marvellous complexity of the areas in the higher Echinometridæ of the present day.

In Regular Echinoids, all the ambulacra, throughout their entire length, have much the same function and type of structure. Adhesion is practised most often in the neighbourhood of the peristome, and there the degree of plate-complexity is greatest; but the difference is in degree only. In the Irregular Echinoids a far more varied use is made of the ambulacra, in spite of the almost complete transfer of locomotor function to the radioles, and of the absence of opportunities for adhesion in a sand-burrow. Generally speaking, a characteristic ambulacrum of a mature Irregular form consists of three, sometimes of four, sections. Adapically petals are developed, and through these respiratory podia protrude. Near the peristome, phyllodes or their equivalents give passage to podia which are mainly sensory, although in the "Cassiduloida" some adhesive function seems to persist. In those advanced Spatangoida (Prymnodesminæ) which have subanal fascioles, a few long, probably prehensile, podia project from the ambulacrals thereby enclosed. For the rest, the podia are reduced to mere filaments (inevitably in some measure respiratory and sensory) which are of relatively little functional value.

It is obvious that the branchial podia of the petals are of such importance that their numbers must be maintained, and can with advantage be increased. But at the same time the exercise of their function does not involve the corona in any mechanical strain. The ambulacral plates in the petals are usually simply "Cidaroid" in nature, but in Clypeaster (Plate 68, fig. 7) and Heteraster (Plate 69, fig. 2) their multiplication is achieved by the introduction of reduced plates. The reason for the introduction of complexity in Clypeaster can hardly be physiological, since related genera (such as those of the Scutellidæ) with even more plates have low, simple primaries only.

In the case of *Heteraster oblongus* (Plate 69, fig. 2) a peculiarly interesting feature of ambulacral development is found. Areas II and IV are petaloid only in the columns (*a* and *b* respectively) that are in a posterior relation; the adjacent columns are more or less obsolete in the "Bothriocidaroid" manner. Roughly twice as many ambulacrals occur on the adapical surface in the petaloid as in the non-petaloid columns. The plates of the former series are, when fully developed, alternately demi-plates and primaries, so that the perradial suture is not affected by the difference in plating on its two sides. In *Spatangus purpureus* (Plate 69, fig. 1) a similar discordance occurs, but it consists in the incorporation of only one additional plate in

each column concerned. (The demi-plate in area V of the specimen figured is apparently fortuitous, and does not represent any numerical irregularity in the plating.) There could hardly be a clearer illustration of the adaptive purpose of plate-complexity than that afforded by *Heteraster*, but perhaps the most important morphological feature shown is that of the disparity of plating in the columns of one area. In such a form as *Echinocardium cordatum* (Plate 69, fig. 4) it is obvious that the production of new plates proceeds at a different rate at Ocular III from that at the others. But in *Heteraster oblongus* ambulacrals (*i.e.*, podia) are produced with different frequency in two columns which spring from the same ocular plate. Such irregularity is occasionally met with as a teratological feature in the Regular Echinoidea (see Section 2 (d), *Echinus*), but it is most remarkable to find it adopted as a normal, and clearly satisfactory, condition in this form. Its appearance is presumably to be ascribed to the budding-out of podial vessels from the radial water-canal at different rates on its two sides. Thus it would appear that the character of ambulacral plating is intimately connected with, and indeed determined by, the growth of the water-vascular system. To the activity of budding from the radial canal all other features of ambulacral development are secondary and subsequent.

The condition of ambulacrum III of *Heteraster* is equally instructive. In a very irregularly triserial way some of the podial pores are petaloid, and others more or less obsolete, or, at least, not specially modified. Those plates which contain petaloid pores are adradially expanded at the expense of the less specialised ambulacrals, and the latter are usually almost (though rarely quite) occluded. It may be suggested that *Heteraster* shows a stage in Spatangoid evolution in which the branchial function is beginning to leave the anterior petal, but is still partly exercised there. In any case, the resulting structure is remarkably similar to that found in many of the Palæechinidæ (*c.f.*, Plate 61, fig. 9, Maccoya), and it is reasonable to regard it as an expression of reversionary development, in a sense working back from the "Cidaroid" towards the "Bothriocidaroid" condition of plating. A somewhat analogous structure, without accompanying difference in the pore-pairs, occurs in the so-called "*Ananchytes texana*," CRAGIN (Plate 69, fig. 3).

In the more specialised Spatangidæ, the respiratory function tends to become restricted to the podia of the paired lateral petals, probably owing to the risk of damage incurred by large podia situated anteriorly in a burrowing animal. In most of these types (*e.g.*, *Spatangus*, Plate 69, fig. 1) the petal of area III becomes morphologically and functionally degenerate; but in a few, such as *Heteraster* (*vide supra*) and *Echinocardium cordatum* (Plate 69, figs. 4 and 5) it assumes an unwonted secondary complexity. In particular, the intra-fasciolar part of that area in *E. cordatum* shows a degree of complexity unattained by any other post-Palæozoic Echinoid with which I am acquainted, although in its plate-relations and absence of combination it is strangely reminiscent of some "Perischoechinoid" areas (see p. 384). A comparison of Plate 69, fig. 5, with Plate 61, figs. 9, 10, and 11, shows

that area III of *E. cordatum* is practically a structural repetition of the ambulacra of *Maccoya* and *Lovenechinus*. According to MACBRIDE, the very numerous podia which emerge through this part of the anterior ambulacrum have a definitely prehensile function, being extruded to the surface of the sand with intent to capture and drag down small organisms, and to keep the vertical tunnel clear of obstructions. The extreme tenuity of the test of *E. cordatum* probably determines the intensity of complication produced by this most interesting secondary development. Morphologically it is comparable with some of the types of secondary adaptation discussed by DOLLO (1910). Morphogenetically it is of great importance, as proving that the rate of production of new plates in an ambulacrum may differ in one and the same area according to the stage in ontogeny reached by the individual. In passing, it may be noted that the internal fasciole of *E. cordatum* seems to act as a limit to the production of complex plating in the ambulacra, and that two of the lateral areas (I and V) have demi-plates in the small parts of them included within the fasciole. Other species of the genus have no corresponding complexity, and it seems reasonable to presume that this species should be considered generically distinct, as it is morphologically peculiar.

Phyllodes and hypophyllodes (see HAWKINS, 1911) seem invariably to contain some degree of complexity, and the complication is always reminiscent of triad-formation, although no true combination occurs. Normally one in every three of the plates in these regions tends to become occluded, while the other two, in extreme cases (*e.g.*, *Catopygus*) become demi-plates. I have nothing of importance to add to the conclusions reached in the paper referred to above, on this matter. It may, however, be remarked that the triple series in the phyllodes are in harmony with the normal disposition of plates and pores in the simpler *Diademoida* (and in the *Holactypoida*), and that they probably represent an original structure; whereas the complexity of petal III in *Echinocardium cordatum* (with no particular numerical sequence in composition), or the alternating demi-plates of the Clypeastrid petal, are as evidently secondary developments. It is regrettable that the true structure of a phyllode is usually very difficult to determine, especially in fossil forms; but such intended structural representations as those given by CLARK and TWITCHELL (1915), and most other authors, for Cassiduloid phyllodes are either imaginary or based upon imperfect observation. In the Spatangidæ, where no true phyllodes exist, the podia nearest to the peristome seem to possess a function akin to that of taste. The plates through which these sensory podia pass are normally lower than the succeeding relatively obsolete plates, but they rarely attain "Cidaroid" proportions.

The posterior ambulacrals of areas I and V which are enclosed within the subanal fasciole of some Spatangidæ always show some approximation to the "Cidaroid" type, but this is more often due to an increase in breadth than to a decrease in height.

In all non-Holactypoid Irregular Echinoidea the ambulacral plates that are not

situated in any of the special regions above described show a more or less complete reversion to the "Bothriocidaroid" character. They become (or rather remain) high, hexagonal, and alternate with the interambulacra, with superposed pores in each peripodium (when the pores are double); and they differ from the ambulacra of *Bothriocidaris* merely in thickness and in the orad position of the peripodia. In many of the Clypeastroida these plates are imperforate, the pores being scattered over the adjoining interambulacra. This anomalous condition is discussed in Section 3 (c), of the second part of this paper. There can hardly be any doubt that these practically functionless ambulacra are in a morphogenetically gerontic, reversionary phase comparable with that generally ascribed to the sutures of *Prionotropis*, or the shape of *Baculites*, among the Cephalopoda. It is interesting to find some structures showing a late stage of obsolescence in types so apparently specialised as the Irregular Echinoidea. But there is at least as much reason to suppose that a Spatangid is degenerate as to consider it progressive.

To summarise the foregoing remarks, it may be stated that three main types of ambulacral complexity occur in the Irregular Echinoidea, although plate-combination is never found. The triserial complication of the phyllodes seems morphogenetically continuous with that of the simpler Diademoid ambulacra. The complexity of the petals of *Clypeaster* (and of the lateral petals of *Heteraster*) is clearly a secondary development designed to increase the number of branchial podia. The extreme elaboration of the anterior petal in *Echinocardium cordatum* is as certainly a secondary adaptation to accompany a secondarily acquired prehensile podial function.

Since the *Holectypoida* occupy a systematic position intermediate between the Regular and Irregular Echinoidea, and are probably in many ways phylogenetically annectant, the transition in ambulacral structure between that of the simpler Diademoida and that of the Spatangoida and other Irregular Orders should be traceable, in part at least, in that group. It is the main purpose of the second part of this paper to indicate those features in the Holectypoid ambulacrum which serve to link together, in some measure, the extremely divergent structures that have been contrasted above. There can be no doubt that the Irregular Echinoidea are descended from one or more Regular stocks; and while this does not necessarily imply that their line of descent passed through the *Holectypoida*, the retarded evolution of that Order, and the approximation to the Regular type that it shows in most features, suggest that the morphogenetic phases of ambulacral change may be there represented.

(f) "*Localised Stages*" in Ambulacral Structure.

Detailed study of the adult and developmental characters of the ambulacral areas of many types of the Echinoidea serves to confirm, in a general way, the application of the law of "localised stages," stated and elaborated by JACKSON (1899, 1912). But in the interpretation of the effects of the operation of this law, I am often unable

to follow that author, and the present seems a suitable occasion on which to point out the influence and the limitations of the principle as it affects ambulacra.

Every ambulacral plate may be considered to have a life of its own, in many ways independent of that of the organism to which it belongs. It is originated in the placogenous tissue at the orad margin of the ocular plate, and gradually becomes dissociated from its place of inception by the birth of its later brethren. To some degree this movement of the ambulacral is due to the gradual increase in height of the corona, the oculars moving upwards rather than the coronals moving down. But there is in most, if not in all, cases a definite orad progression of the coronal plates under the influence of the pressure exerted by those developed later. The rate of production of new plates may vary in different areas, and at different periods of growth in the same area. JACKSON'S statement that the plates nearest to the peristome are the earliest formed, while those towards the apex are of later development, is as unassailable as the stratigraphical axiom of the order of superposition of sedimentary strata.

In the Palæozoic Echinoidea and Cidaroida, where the ambulacral plates undergo little alteration during their progress, save perhaps in size and ornament, it is reasonable to regard each column as consisting of three regions—an orad portion built of plates formed early in the ontogeny of the urchin, a mid-zone of mature plates, and an apical part made of plates which are formed late in ontogeny, but are morphogenetically young. In the region first-named, the plates will retain recapitulatory simplicity; in the second, they will show the "full-character" for the species; and in the third (apart from features due to acceleration), will again tend towards simplicity. In so far as the determination of "localised stages" is applied to these groups of Echinoids, it proves both accurate and instructive. But an attempt to recognise similar stages in the Diademoida or Irregular Orders encounters considerable difficulties. In the Diademoid ambulacra, as has been shown above, "growth-pressure" of the advancing columns, and "combination" aided by the development of tubercles, react persistently and with cumulative effect on the ambulacral plates throughout their existence. Although the massed, deformed, and sometimes almost destroyed, plates around the peristome in such a type as *Heterocentrotus* are, from the standpoint of age, the earliest formed in ontogeny, it cannot be imagined that they retain any traces of the primitive simplicity proper to such plates. Though young ontogenetically, they are old morphogenetically, and the vicissitudes through which they have passed have modified them so completely that they have no original features left. In advanced forms, such as the Echinina, some of the ambulacra are "born" reduced (by morphogenetic acceleration), but this applies only to the new plates of adult individuals. The first post-larval plates are always either "Bothriocidaroid" or "Cidaroid" in character, but in the course of morphogeny these very plates are liable to undergo extreme reduction or complication.

Again, there can be no doubt that the orad ambulacra of a Spatangid have

retained essentially the proportions and details with which they were first endowed (owing to morphogenetic stagnation). But in a "Cassiduloid" these orad plates are concentrated into complex phyllodes, albeit they were precisely similar to those of the Spatangid at their inception. The low, "Cidaroid" or complex plating of a petal is not so primitive in character as the high, hexagonal plating at the mid-zone, in spite of the "youth" of the plates in the former region. It must in justice be admitted that JACKSON (1912, p. 57) does not cite the Irregular Echinoidea as illustrating his law of "localised stages of development"; but he considers the Diademoida (Centrechinoidea) to be bound by it, and by his application of the principle to such types as *Hemicidaris* and *Salenocidaris* gives an interpretation of their ambulacral structure with which I am unable to agree.

Concerning the ambulacrum of *Hemicidaris*, JACKSON says (*loc. cit.*, p. 56) "Passing dorsally [*i.e.*, adapically], we may pass from compound plates into an area of simple plates *which have dropped all attempts at fusion.*" Later, in respect of *Salenocidaris miliaris*, he writes:—"There is a single primary plate ventrally [*i.e.*, adorally], succeeded by one compound plate, which is again succeeded by simple plates throughout the area, *a case of extreme reversion.*" (In both quotations the italics and words in square brackets are mine.) It seems reasonable to ask for the evidence that the simple plates of the *Hemicidarid* ambulacrum ever made any "attempt at fusion," actually or phyletically, which attempt they have subsequently "dropped." To my mind, JACKSON'S contention in this matter, as in that of *Salenocidaris*, could be tenable only on the assumption that development into compound plates is an *original* feature of the components—an utterly unwarrantable hypothesis. He himself admits the obvious fact that newly-formed ambulacrals are typically "Cidaroid" in character, and that any degree of complication they may subsequently assume is acquired during their later individual development.

In phylogeny, as in morphogeny, elaboration in the direction of combination or reduction first appears in the oldest plates of the areas (the orad plates), and if this condition does not extend up the area (*i.e.*, adapically) for any considerable distance, the deduction must surely be drawn that, unless the contrary can be proved, a relatively primitive stage of evolution is represented. As phylogenetic specialisation proceeds, elaboration of structure progressively affects the younger ambulacral plates, until in extreme cases it is impressed upon them at their very inception. The single primary on the peristome margin of *Salenocidaris* is in no way antagonistic to this view. It has retained its relatively primitive simplicity because it has been preserved from crushing by the perignathic process (which is largely based upon it), and has had no reason for combination owing to the absence of large tubercles on its outer surface. The succeeding plates have been jammed against its immovable apical margin, and support the largest tubercles found in the ambulacrum. Such seems equally to be the interpretation of the orad plates of *Heterocentrotus* described above.

As a result of the foregoing considerations, and of facts that will appear during

detailed description of the *Holotypoid* ambulacrum, I am inclined to doubt the applicability of the "law of localized stages" to the separate plates of any but "Perischoechinoid" or *Cidaroid* forms. Nevertheless, in respect of the composition of compound plates in the *Diademoida*, the principle seems well established and plainly illustrated. The number of plates in a compound is determined once for all when all plates in the column (or part of a column) have become combined. No subsequent development can detach components from one compound to add them to another; so that, unless the (clearly mistaken) view of A. AGASSIZ (1874, p. 642) is adopted, and new plates are supposed to be produced elsewhere than at the ocular margin, the number of components in each compound is fixed, however much alteration in size and shape may befall them. Hence, in such a form as *Strongylocentrotus*, the oral triads, followed in regular apical sequence by tetrads, pentads and hexads, affords a striking proof of JACKSON'S law. *Heterocentrotus*, in which the most numerically elaborate compounds occur at the mid-zone, is in truth a genus showing reversion in its old age. There the latest formed "young" ambulacrals do not attain such complexity of combination as was reached by previously formed plates when they were of that age.

In the Irregular Echinoidea, apart from the inevitable character that the newly formed ambulacrals are morphologically neanic, the great variety of functional adaptation or lack of utility so modifies the plates during their individual "lives" that no morphogenetic regularity can be traced. In the several areas of one *Spatangid*, plates which have originated synchronously at their respective oculars may show every degree of morphological variety, from an almost "Bothriocidaroid" retardation to the highest degree of complexity. Moreover, in different types of Irregular Echinoids, the first formed plates may either retain their primitive nature (*Spatangidæ*) or acquire extreme complexity ("Cassiduloida"); while the last formed plates may maintain their primitive characters (area III of *Spatangus*), or almost at once attain elaborate specialization (area III of *Echinocardium cordatum*). It is the localised function, not a common and fundamental principle, which determines the stage of development of any particular ambulacral plate in the Irregular Echinoidea.

PART II.—(1) THE STRUCTURE OF THE AMBULACRA IN THE HOLECTYPOIDA.

This small group of the Echinoidea has undergone many taxonomic vicissitudes between the period (early in the last century) when its few known representatives were called "Galerites," and 1889, when DUNCAN raised it to the rank of an Order. At the present time it is, perhaps, orthodox to consider it a sub-order "*Holotypina*" of the Gnathostomatous Irregular Echinoids. However, in a long series of papers in the 'Geological Magazine,' and elsewhere, I have persistently followed DUNCAN in allowing the *Holotypoida* full ordinal rank. This is not the place to discuss the reasons that have induced me, with ever-increasing conviction, to maintain the distinction between the *Holotypoida* and the *Clypeastroida*; but it may be submitted,

by way of explanation, that these two sections of the "Gnathostomata" are as distinct in structure as the Cidaroida and Diademoida among the Regular forms, and are similarly related in phylogeny. If the latter groups are to be ordinally distinguished, uniformity of classification should apply a similar distinction to the former.

With regard to the internal classification of the Order, the grouping of genera and families here employed is but little modified from that given in a former paper (HAWKINS, 1912, *b*), with the incorporation of the alterations suggested in later essays.* For reasons that will appear in the sequel, I have separated the Holectypidæ from the Discoidiidae. The affinities of this newly erected family are more towards the Pygasteridæ than the true Discoidiidae—it cannot therefore remain as a sub-family of the latter group, but is hardly to be transferred to the Pygasteridæ. Full separation seems the only alternative. Similarly the Lanieriinæ (see HAWKINS, 1913, *b*), which possess a curious combination of the characters of Coenholectypus and Conulus, cannot be safely affiliated with either group, and must be regarded as a distinct family. To counterbalance this new subdivision of the Order, it is proposed to group the considerable number of morphologically and systematically confusing genera that include Pyrina, Pseudopyrina, Conulus, Globator and Echinonæus into one family, to which Amblypygus is provisionally attached. Whatever may be the real or fancied differences between the genera concerned, the ambulacral structure of all of them is so nearly identical that further discussion of this apparently reactionary change is needless here.

For convenience of reference the classification here employed is subjoined, but it must be regarded as tentative, and in some cases admittedly inadequate or unnatural. A revision of the classification must be postponed until the completion of the morphological studies of which the present paper is one.

Order : HOLECTYPOIDA.

Family I : PYGASTERIDÆ. Lias to Cretaceous.

Sub-family i : PYGASTERINÆ.

Genus 1 : *Plesiechinus*, Pomel. Type, *Pygaster macrostoma*, Wright.

Genus 2 : *Pygaster*, Agassiz. Type, *Clypeus semisulcatus*, Phillips.

Genus 3 : *Macropygus*, Cotteau. Type, *Pygaster truncatus*, Agassiz.

Sub-family ii : PILEINÆ.

Genus 1 : *Pileus*, Desor. Type, *Pygaster pileus*, Agassiz.

Genus 2 : *Anorthopygus*, Cotteau. Type, *Nucleolites orbicularis*, Grateloup.

Family II : HOLECTYPIDÆ. Lower Jurassic to Upper Cretaceous.

Genus 1 : *Holectypus*, Desor. Type, *Echinites depressus*, Leske.

Genus 2 : *Coenholectypus*, Pomel. Type, *Discoidea macropyga*, Desor.

Genus 3 : *Coptodiscus*, Cotteau and Gauthier. Type, *C. noemice*, Cotteau and Gauthier.

* For the application of the terms *Pygaster* and *Plesiechinus*, see HAWKINS, 1917.

Family III : DISCOIDIIDÆ. Cretaceous.

Genus 1 : *Discoidea*, Agassiz. Type, *D. subucula*, Leske.

Section, *D. cylindrica*, Lamarck.

Family IV : LANIERIIDÆ. Cretaceous and (?) Eocene.

Genus 1 : *Discholectypus*, Pomel. Type, *Hoelectypus meslei*, Gauthier.

Genus 2 : *Lanieria*, Duncan. Type, *Echinoconus lanieri*, Cotteau.

Family V : ECHINONÆIDÆ. (?) Upper Jurassic to Recent.

Sub-family i : ECHINONÆINÆ.

Genus 1 : *Pyrina* (*sens. lat.*), including *Globator* and *Pseudopyrina*.

Genus 2 : *Echinonæus*, Van Phelsum. Type, *E. cyclostomus*, Leske.

(?) Genus 3 : *Micropetalon*, Agassiz and Clark. Type, *M. purpureum*, Agassiz and Clark.

Sub-family ii : CONULINÆ.

Genus : *Conulus*, Leske. Type, *C. albogalerus*, Leske.

(?) Sub-family iii : AMBLYPYGINÆ.

Genus 1 : *Amblypygus*, Agassiz.

(?) Genus 2 : *Conoclypus*, Agassiz.

Order : HOELECTYPOIDA.

There are certain ambulacral characters that occur persistently in all members of the *Hoelectypoida*, affording useful diagnostic features in the Order. These characters may be summarised as follows :—

(a) The ambulacra are straight, lanceolate, and narrow, with the greatest width at or near the ambitus. They are usually flush with the level of the surrounding parts of the corona, but may be very faintly inflated. Their ornament is identical in character with that of the interambulacra, but differs in disposition.

(b) The ambulacral plates are numerous and low. In Jurassic types, the majority of the ambulacra are simple primaries (ornamented in triple series); in most Cretaceous and later types reduced plates occur in considerable numbers, often almost throughout the areas. There is always some structural complexity, and this is typically concerned with the production of "triad-grouping." No true compound plates seem to be developed.

(c) The pore-fields are narrow, and situated for the most part close to the adradial margins of the areas. The pore-pairs are usually uniserial, but are apt to become triserial near the peristome (particularly in *Conulus*), and in a few cases may be regularly biserial (*Pileus*), or irregularly multiserial (*Discoidea cylindrica*) in other parts of the areas. In Jurassic forms the pores of the adapical surface are usually somewhat larger than those of the adoral surface—these proportions are typically reversed in Cretaceous and later groups. In the former case, especially in the *Pygasterinæ*, a feebly sub-petaloid tendency is found; but the disparity of the pores of a pair is always slight, and there are no defined limits to the region in

which it occurs. In the Amblypyginæ, a definitely petaloid quality is developed. There is a fairly constant reduction in the average size of the pores from Jurassic to Cretaceous times, but the pores are always paired, and almost always enclosed in peripodia.

It is worthy of comment that in this three-fold analysis of the Holectypoid ambulacrum, the majority of the features prove to be essentially identical with those of the simpler Diademoida. In three details only is any marked difference found; (a) the ambulacra are relatively narrower than is usual in the Diademoida (although in some cases, *e.g.*, *Salenia* and *Heterocidaris*, much narrower areas occur than in any of the *Holectypoida*), (b) the ambulacral plates are never combined (though always partially grouped into triads), and (c) the pores may be slightly dissimilar, or else exceptionally minute. These three points of difference are overshadowed by the many features of similarity; indeed, the first two are more apparent than real, and might almost be cited as *resemblances* to the more primitive Diademoid ambulacra.

Family I: PYGASTERIDÆ.

The general characteristics of the Pygasterid ambulacrum may be summarized as follows:—

(a) The ambulacra are symmetrically lanceolate and, though narrow, are proportionately wider than in the adults of other families. The perradial tracts are commonly inflated, but to a small degree only. The tubercles of the adapical surface are small and widely spaced, those of the adoral surface larger (particularly in respect of their scrobicules), while near the ambitus they are congested in such a manner as to become polygonal. Their arrangement is very regular, consisting of repetition on every third plate.

(b) The ambulacral plates are low, simple primaries over the entire adapical surface; although they become distorted in the region of crowded tubercles, and often become grouped towards the peristome, they retain their primary character with very rare exceptions over the adoral surface. When grouping of the plates occurs, the triad principle is always adopted. The plates tend to increase in height from the ambitus to the peristome, whether grouping affects them or not.

(c) The pore-fields are narrow, often slightly sunken adapically. The pores of each pair are separated by a very narrow space (occupied by a granular excrescence), and the outer pore is usually very near to the adradial suture, if not actually in contact with it. Adapically the pore-pairs are in very close uniserial sequence (except in *Pileus*); they become even more congested at the ambitus, without departing from the uniserial order; adorally they are more widely separated, and may show obscure triserial arrangement (well marked in *Pileus*). In most genera the pores are slightly dissimilar on the adapical surface, the outer pore being elliptical or ovoid in shape, while the inner pore is circular or crescentic. In all cases the apical pores are

distinctly larger than those at the ambitus or on the adoral surface. All the pore-pairs are enclosed in peripodia, but these are well-defined only on the adoral surface.

Sub-family i: PYGASTERINÆ.

There are no ambulacral characters of a general nature in this sub-family which need be added to those given above.

Genus 1: *Plesiechinus*, Plate 65, figs. 1 and 2.

The type of this genus, *P. macrostoma* (Wright) is rare and not well known. Thanks to Mr. L. RICHARDSON, I have been able to make a sufficient study of the ambulacra of two specimens to determine that their structure is essentially identical with that in *P. ornatus* (BUCKMAN). The specific distinction between the two forms is but slight, and the justification for the retention of *P. macrostoma* as a distinct species rests more on stratigraphical than on morphological evidence. *P. ornatus* (usually miscalled "*Pygaster semisulcatus*"), which occurs at a considerably lower horizon (*η murchisonæ*), is, like most abundant forms, exceedingly variable in shape and ornament. One variety only (*P. conoideus*) has been named, but there are at least six others in my collection that are equally worthy of separation.—However, none of the differences in shape, ambital angle, or ornament seem to be associated with any important modifications of ambulacral structure, so that the following description holds good for all forms of this protean species and, I believe, is essentially true for the genus:—

(a) The Ambulacra.—Areas II, III, and IV are straight, and of almost exactly the same length. Areas I and V are more or less curved adapically owing to the great width of the periproct and the wide separation of the posterior oculars. They are also slightly shorter than the others, since the apical system is a little excentric posteriorly. The areas are all regularly lanceolate, but except in the apicad and orad quarters, their adradial margins are very nearly parallel. The inflation of the perradial tract is well marked in some varieties, faint in others, but is always present and never considerable.

The ornament is dense, like that of the interambulacra, consisting of primary and secondary tubercles, and variously sized granules. In young forms the tubercles occur in single rows down each column, placed nearer to the pore-fields than to the perradius, and situated on every third plate. In older examples a second, inner row of tubercles appears, placed nearer to the perradius than the earlier series, and situated on the plates immediately adoral to the originally tuberculate ones. This tubercle series never seems to extend more than half the distance from the ambitus to the apex or peristome. In fully developed specimens a third perradiad row occurs in the immediate vicinity of the ambitus. It is usually rather sporadic, and its tubercles rarely attain the dimensions of those of the other rows; very commonly

they are developed in one column only. These tubercles are usually situated on the plates that do not support members of the other two series, but they are rather irregular in distribution, and may sometimes be developed on the plates bearing tubercles of the first series. On the adapical surface the tubercles are relatively small, but their shallow scrobicules always extend across the apicad transverse sutures of the supporting plates, and not infrequently encroach slightly upon the contiguous orad plate. On the adoral surface the tubercles increase in height, but the bosses are not much greater in diameter than above. The scrobicules, however, become much wider and more deeply excavate; often they meet one another, and are then separated by a low, smooth ridge. Towards the peristome, where tubercles of the first series alone persist, the scrobicules become disproportionately large and take on an elliptical shape with the longer axis longitudinal; the bosses rise abruptly from the scrobicules, and are placed near the orad foci.

(b) The Ambulacral Plates.—From the ocular margin to a point slightly below the ambitus, the plates are simple primaries, alternating regularly in the two columns. Though constantly low, they diminish steadily in height in the direction named, becoming lath-like, with somewhat distorted transverse margins, in the region where the tubercles are most densely congregated. This condition extends to a point at rather less than one-quarter of the distance from the ambitus to the peristome. In the remaining three-quarters of the adoral parts of the areas, the plates increase rapidly in height, though undergoing a fresh diminution quite near the peristome. They are, on the average, twice as high in this region as on the adapical surface. Corresponding with this change in proportions comes a departure from simplicity. A fairly regular (though rarely perfect) grouping takes place, in such a manner that the transverse sutures meet the perradial line in groups of three. This result is attained largely by the perradiad lowering of the plates apicad to those bearing the tubercles of the first series. These plates may occasionally become demi-plates, but they are rarely much separated from the perradial suture. It is worthy of note that such demi-plates are more frequent, and better defined, in areas I and V (the short ambulacra) than in the others. A careful study of the grouping of the plates in this region shows that there are really two separate zones. One exists in that (apicad) portion where the second tubercle series occurs, the other (orad) where there are only the main tubercles. In the former zone, the plates which support the perradiad (second-series) tubercles are perradially expanded, while the other two, though both primaries, are low. In the latter, the plates bearing the tubercles of the first series are expanded, while the other two remain low, or may even be reduced. The meeting of these two discordant grouping-systems is usually marked by the presence of one or more pairs of normally alternating primaries (see X in Plate 65, fig. 2).*

* A similar drawing of the adoral part of the ambulacrum of *P. ornatus* is given by LOVÉN (1888). My figure was drawn quite independently of his, and the close correspondence between the two shows how constant are the ambulacral characters in this species.

That the distortion of the plates in the former zone is due to the presence of the perradiad series of tubercles can hardly be doubted, but it is noteworthy that distortion is the only feature there; there is no reduction. In the latter zone the plate-grouping seems to have a more fundamental origin. Although the expanded plates are again those that support large tubercles, it is clear that the reduction of other plates is quite unnecessary for the accommodation of these tubercles. Indeed, the reduction does not become appreciable until the transverse suture affected has passed or even crossed the boss. Again, tubercles with scrobicules transgressing the sutures even more widely occur on the adapical surface, with no accompanying disturbance of the plating. In this orad region of plate-grouping we have an almost perfect repetition of the alternate dyads and simple plates found in *Acrosalenia* (Plate 62, fig. 4), with the sole difference that no true combination occurs in *P. ornatus*. The fact, noted above, that demi-plates are most marked in this region in areas I and V (where the actual number of plates in these shorter areas is the same as that in the others) suggests that the plate-reduction (and grouping) is due to "growth-pressure" rather than to any direct influence of the tubercles. On the other hand, the relatively great height of the plates seems inconsistent with compression in the ordinary sense. The grouping extends into the peristomial invagination, and usually only one pair (rarely two) of normally alternating primaries occurs on the margin.

There is reason to believe that the proximal peristomial ambulacra are really the first coronals of the areas. There are traces of slight marginal resorption, and probably the extension of the branchial incisions has modified the plates adradially. But since the primordial single interambulacral plate is constantly preserved, and the ambulacra project into the peristome at least as far as the interambulacra, it seems probable that no actual destruction of plates has occurred. This argument holds good for the whole Order.

(c) The Pore-fields.—The pore-pairs are perfectly uniserial, from the apex to the region where true plate-complexity begins. Over the inner half of the adoral surface they become progressively triserial towards the peristome. The pairs situated on the non-tuberculate "monads" are shifted in a perradiad direction (though but slightly), while those of the other two pairs retain their adradial positions. Thus the disposition of the pore-pairs is not typically triserial, but might be described as showing an interrupted uniserial sequence, with every third pair out of the straight line. This condition, though apparently trivial, distinguishes the orad parts of the pore-fields of *Plesiechinus* from those of *Acrosalenia* and other *Diademoida*, and makes them comparable with the phyllodes of the *Nucleolitoida* and *Cassiduloida*. It is perhaps legitimate to describe this part of the *Plesiechinid* ambulacrum as an incipient phyllode, not worthy of the name *hypophyllode* (see HAWKINS, 1911, p. 260), but none the less suggestive of the quality so named. The pores of the adapical surface are usually faintly dissimilar, the inner one being

circular or gibbous, the outer one slightly elliptical. No condition that could be termed *sub-petaloid* is attained, but the character of the pores is suggestive of incipient petaloid structure, much in the same way that their disposition adorally is pre-phyllodal. There is little change in the size of the pores throughout the length of the areas, but they are always similar ambitally and adorally. In the latter region they may diminish in size in some cases, and the pore-pairs always become widely spaced, in contrast with their crowded disposition elsewhere. Roughly, two-thirds of the pore-pairs are situated above the ambitus:—the average figures (taken from all five areas, in 25 specimens of varying size) being 63·1 per cent. adapical, 36·9 per cent. adoral. Since the corresponding lengths of the areas average 58·5 and 41·5 respectively, there is a real excess of podia on the adapical surface. Moreover, the zone of ambital crowding extends for a short distance on to the adoral surface, and this tends to obscure the very considerable disparity in numbers and spacing of the pores on the two surfaces of the test. It is of interest to recall in this connection that the tendency in Diademoid ambulacra is to produce congestion near the peristome, while that in the Irregular Echinoids (especially in the Spatangidæ) is to reduce the adorally situated podia both in numbers and function. *Plesiechinus* undoubtedly conforms more to the latter condition, though retaining ambulacral structure which is essentially similar to that of the early Diademoida.

(d) Abnormalities.—In the very numerous examples of *P. ornatus* that I have examined, only one case of abnormality has been noticed. This is exactly identical with the malformation shown in *Pygaster macrocyphus* (Plate 65, fig. 6), and its description may be postponed until that species is considered. Trifling irregularities in the proportions of the ambulacral plates are frequent, but those that have been observed never obscured or interrupted the normal plating structure. In one specimen, the operations of a boring parasite have caused the secretion of a kind of callus over the outer surface of the test in the part affected, and, although this has involved the obliteration of two contiguous pore-pairs, it is not a development that demands consideration in the present enquiry.

Genus 2: *Pygaster*, Agassiz, Plate 65, figs. 3, 4 and 6.

This typically Upper Jurassic genus, which attains its fullest development in the Corallian, is in great need of systematic revision. The type, *P. semisulcatus* (PHILLIPS), (long miscalled "*P. umbrella*"), is the only Corallian species recognized by name from Britain, but there are at least two others from that horizon that are relatively abundant, especially in the South of England. Numerous examples of these three forms (chiefly in the Oxford Museum), and the co-type of *P. macrocyphus* (WRIGHT), from Boulogne, have afforded the evidence from which the ambulacral characters of the genus have been deduced. They all agree in essentials, and, for the sake of uniformity, the actual description has been drawn up from a fine specimen of the genotype (from the typical locality, Malton) now in the

collection of the Geological Department, University College, Reading, No. 804. This specimen is very closely similar in size, form and ornament to the lectotype in the British Museum (see HAWKINS, 1917), and, in so far as can be determined, agrees absolutely with it in ambulacral structure. The latter specimen cannot, for obvious reasons, be maltreated by the staining and other preparatory processes to which the former has been subjected.

(a) The Ambulacra.—The areas differ from those of *Plesiechinus* in two respects only. They are relatively wider (to a small degree only) at the ambitus, and, indeed, over most of the adapical surface; and they taper towards the peristome through their whole adoral extent, instead of retaining almost the full width for some distance below the ambitus. Their ornament is different in detail, though similar in general nature and distribution. On the adapical surface the tubercles are relatively small; they increase rapidly in size at the ambitus, and become disproportionately large towards the peristome. There the scrobicules are very wide, practically circular, with small, central bosses, quite unlike the elliptical areolæ of *Plesiechinus* with their excentric tubercles. In the neighbourhood of the ambitus, the second series of tubercles attains dimensions fully as great as those of the first series, so that, although a third series is only very feebly developed, there is far more congestion of the tubercles than in *Plesiechinus*, and most of the scrobicules are sharply polygonal in outline.

(b) The Ambulacral plates, Plate 65, figs. 3 and 4.—On the adapical surface the ambulacra in *Pygaster* are similar in proportions and characters to those similarly situated in *Plesiechinus*. Towards the ambitus they become even lower than in the latter genus, and their transverse sutures tend to be sinuous. Just below the ambitus somewhat irregular triad-grouping appears, clearly due to the presence of perradiad tubercles. This superficial dislocation of the transverse sutures is closely analogous with that found in *Plesiechinus*, but it comes on considerably further from the peristome than in that genus. It persists for about half the length of the adoral part of the area, but its orad limit is again further from the peristome than in *Plesiechinus*. This difference in plating is to be correlated directly with the difference of tuberculation between the two genera. In the parts of the ambulacra between the orad end of the dislocated plates and the peristome a surprising contrast from the *Plesiechinid* condition is found. Although the main tubercles are larger in *Pygaster*, the plate-structure is almost perfectly simple. Occasionally an imperfection of alternation of the columns occurs, but there is no suggestion of a triad-grouping of the plates—they are all primaries, and usually simple ones. The ambulacra of *Pygaster* have lost all traces of *Diademoid* structure, although their ornament still retains the primitive ternary arrangement. This regressive simplification constitutes, to my mind, one of the most definite diagnostic characters of the genus, and of itself would be sufficient to warrant the recognition of generic distinction between *Pygaster* and *Plesiechinus*. Since almost

all Jurassic Irregular Echinoids retain some traces of triad-arrangement near the peristome, *Pygaster* proves, in this respect, to be more advanced towards the Spatangid character than any of its contemporaries—a somewhat unexpected condition.

(c) The Pore-fields.—The pore-pairs are uniserial almost throughout. Quite near the peristome a faint tendency to triserial arrangement occurs, but it is not so pronounced as in *Plesiechinus*. The pores of the adapical surface are markedly dissimilar, particularly towards the apical system. The outer pores are elliptical, and the inner usually quite circular. Although it would hardly be correct to describe the pore-fields as sub-petaloid, the tendency towards that condition is considerably greater than in *Plesiechinus*, while the restriction of dissimilarity to a part of the adapical surface only serves to emphasise the suggestion of an incipient petal. In *P. macrocyphus* (Plate 65, fig. 6), from the Kimmeridgian, it is hardly possible to avoid the term sub-petaloid in a description of the pore-fields. Certainly, such a designation is more appropriate in that case than when applied to *Galeropygus*, and many even of the later *Nucleolitidæ*. The pores of the adapical surface in *Pygaster* are considerably larger than those of the adoral region, and show a progressive diminution in size when traced from the apex to the peristome. They are much smaller adorally than in *Plesiechinus*, and are not so widely spaced. There is a similar ambital congestion in both genera. In the specimen of *P. semi-sulcatus*, on which the foregoing description is chiefly based, 55·4 per cent. of the pore-pairs are on the adapical, and 44·6 per cent. on the adoral, surfaces respectively. Closely similar percentages have been calculated in several species of the genus. It is somewhat surprising to find a greater approximation to evenness of distribution of the podia in *Pygaster* than in *Plesiechinus*, especially since the ambulacral structure in the latter genus is more “Diademoid” than in the former.

(d) Abnormalities.—The number of specimens belonging to this genus that have been studied is far inferior to that in the majority of genera here described; and, perhaps as a consequence of this, no abnormalities of any kind have been observed save in one specimen, the cotype of *P. macrocyphus* (Plate 65, fig. 6). In that case, area II shows a particularly good example of an irregularity of development that is not at all uncommon in the *Holectypoida* and *Cassiduloida*. The present seems a suitable occasion for giving a description of this abnormality, although it seems to be of a kind that involves few morphogenetic points of interest. In the specimen here figured, at a point almost midway between the ocular and the ambitus, area II becomes rapidly narrowed for about six plates, and in the next six recovers its full width. At the narrowest point the area has only about half the width proper to the region. Both columns are affected alike, and the plates of both become cuneiform (narrowing adradially) where the constriction is most complete. At the region of maximum constriction there is an exceptionally large tubercle situated exactly over the perradial line. No traces of sutures can be detected on the boss;

and, in other cases, none can be found by methods that expose all the surrounding sutures clearly. One or two structurally single plates reach right across the area, bearing pore-pairs at both (adradial) ends. There can be little doubt that originally the perradial suture was continuous, and that the two columns have been subsequently united by anchylosis or syzygy. The cause of this type of abnormality is obscure. It may occur at any point in the length of an area, and, in a specimen of *Holectypus hemisphaericus* that I have examined, it occurs twice in one area, on the adapical surface and just below the ambitus. Since all the ambulacra are narrow at their inception, it might result from the failure of some of them to widen during growth, but the presence of the central tubercle, and the symmetrical constriction of both columns, seem to indicate that the irregularity is inborn in the plates. There is never any sign of accidental fracture, or of corresponding imperfections in other parts of the corona. In one case (of *Holectypus hemisphaericus*) the constriction occurs in two areas (I and V) at the same horizon just below the ambitus, but in all other observed cases it affects one area only. As noted above, I have seen it in one specimen of *Plesiechinus ornatus* and one of *Pygaster macrocyphus*. It occurs in fifteen out of some hundreds of specimens of *Holectypus hemisphaericus*, and in one out of several score of *H. depressus*. I have not found it in Discoidea or Conulus, in spite of the great quantities of material representing those two genera that have passed through my hands. It has been noticed in two cases in *Galeropygus agariciformis*, one of *Hyboclypus gibberulus*, two of *Nucleolites scutatus*, and one of *Clypeus sinuatus*. In all these cases the structure is identical with that described above, and must surely be ascribed to the same cause, whatever that may be. A constriction, similar save in the absence of the median tubercle, affects part of the petal of area II in a specimen of *Echinolampas* from the (?) Miocene of Persia, recently sent me by Mr. H. Woods. I have not found any comparable abnormality in any of the Spatangoida. It is regrettable that no clue to its origin and meaning is as yet forthcoming.

Genus 3: *Macropygus*.

I have been unable to obtain sufficient material for the study of the ambulacra of *M. truncatus*, which has not been found in Britain. From the few specimens seen, and reference to published figures, it would appear that the structure of the areas is very nearly the same as that in *Pygaster*. There is no indication of triad grouping adorally, nor do the pore-pairs depart seriously from a uniserial sequence. In one respect there is a marked difference from *Pygaster*, and even from *Plesiechinus*. The pores are minute throughout, with little or no dissimilarity on the adapical surface. The tentative efforts at petaloid structure that are characteristic of nearly all the Jurassic *Holectypoida* seem to have been abandoned in this, as in other Cretaceous genera in the order.

Sub-family ii: *PILEINÆ*.

The two genera here associated in this sub-family are so grouped for convenience. It is more than doubtful that any close relationship links *Pileus* with *Anorthopygus*. The position of the periproct is almost the only feature of importance that they have in common; and any lines of descent from a *Pygasterine* origin towards the truly Irregular type must needs have passed through such a phase. *Anorthopygus* is very possibly a descendant of *Macropygus* while, on stratigraphical evidence, *Pileus* must have some other ancestry. Neither of the genera has been studied under satisfactory conditions. *Pileus* is not known from the British Corallian; while *Anorthopygus*, though represented in the British Cretaceous fauna, has been found only in the Haldon Hill remanié and the Hibernian Greensand, and specimens showing details of the surface of the test have yet to be discovered. I am, therefore, unable to add to the exiguous accounts of the ambulacra of the two genera that have been published.

Genus 1: *Pileus*.

This rare and large form is unique in the order in having the pore-pairs arranged biserially throughout the adapical parts of the ambulacra. The zig-zag series of pores resemble those of *Diplocidaris* or *Diplopodia*. They agree with the pore-pairs of *Diplocidaris* in the homogeneity of the pores, and their large, elliptical shape. But their peculiar disposition is not associated with any diversity of plate structure, so that in that respect they are more like those of *Diplopodia*. It is an interesting and suggestive coincidence that the appearance of the biserial adapical pores of *Pileus* should occur in the Corallian, during which period the comparable development in *Diplopodia* arose. Whether the development is adaptive to some special circumstances incidental to life on a coral-reef, or is a case of (somewhat remote) synchronous parallelism, cannot well be determined. The "diplopodous" condition of the apical pores in *Heterocentrotus* and *Colobocentrotus* lends some support to the former alternative, although many of the Cretaceous *Diplopodiidæ* were certainly not reef-dwellers. On the adoral surface the pores of *Pileus* are quite minute, and not biserial, but they remain somewhat congested throughout. They are triserial over a large part of this surface, the triplets becoming progressively more oblique as they approach the peristome. DE LORIO (1890, p. 116) describes the pore-pairs as "grouped in little arcs of three or four pairs." Quadriseserial arrangement would probably be a local and individual irregularity. The whole of the adoral surface is densely covered with tubercles (as many as four series of tubercles occurring on each ambulacral column at the ambitus), and that feature, coupled with the triserial arrangement of the pore-pairs, suggests that some plate-complexity may occur (either intrinsic or tubercle grouping), but no descriptions or drawings give any evidence on this point.

Genus 2: *Anorthopygus*.

This Cenomanian genus has thickly tuberculate ambulacra, like *Pileus*, but no other resemblance occurs in the areas. The pores are minute and practically uniserial throughout, closely resembling those of *Macropygus*. LAMBERT (1911, p. 74) states that in *A. michelini* "the ambulacrum is entirely composed of primaries," but does not indicate whether any irregularity of alternation occurs between the columns. On a flint mould of *A. orbicularis* from Haldon the indications point to a perfectly "Cidaroid" disposition of the plates throughout, but it is unsafe to rely upon the somewhat obscure evidence afforded by it, especially since sutural irregularity due to tubercle growth is often far less marked within the test than on its outer surface. Nevertheless, all available evidence suggests that in *Anorthopygus* the simplification of plating initiated by *Pygaster* has been carried to its conclusion. According to COTTEAU (1859, p. 178) the pore-pairs become "a little oblique" near the peristome, but they may have a like disposition in *Pygaster* without any accompaniment of disturbance in the plating.

Family II: HOLECTYPIDÆ.

In spite of the diversity in structure and ornament of the three genera at present constituting this family, the ambulacral characters are remarkably constant. Even the important advance marked by the redevelopment of the posterior gonad in *Coenholectypus* is unaccompanied by any morphogenetic acceleration in the ambulacra. Since the only appreciable departure from the usual plating character occurs in a species usually identified with the genotype of *Holectypus*, it will suffice here to indicate the structure normal to the family without detailed reference to the several genera. In *Holectypus hemisphaericus* (Plate 65, fig. 8), one of the earliest species of the family and one attaining an average size, the ambulacra differ from those of the almost contemporaneous *Plesiechinus* only in dimensions and the absence of subpetaloid tendencies. Occasional demi-plates may occur in the region of "Acrosaleniid" plating, and the complication near the ambitus due to tubercle crowding is usually less marked than in the larger genus. There is a considerable range of variation in the number of grouped triads present, some specimens having only two such groups in each column, while others of the same size may have as many as six. It is perhaps worthy of note that when the amount of grouping is small, the degree of reduction of the plates is more intense. In the distribution of the pore-pairs (i.e., plates) on the corona, *H. hemisphaericus* shows a fair correspondence with *P. ornatus*. Fifty-six specimens of almost the same dimensions from one locality (Burton Bradstock, Dorset), and from the same hemera (*schloenbachii*) gave an average of 34.2 per cent. of pores on the adoral surface, as compared with 36.9 per cent. similarly situated in *Plesiechinus*. It should be noted, however, that this average figure is deduced from a series in

which the extremes are so far separated as 28.3 and 39.4 per cent. Perhaps a biometric study of this character in larger numbers of specimens might show the existence of more than one lineage.

The small *H. depressus* from the Inferior Oolite (presumably the type of the genus) is essentially similar to the species described above, as regards ambulacral structure, but there is a tendency for the plates of the adoral surface to be rather higher near the peristome. As a result, the pore-pairs of that region are widely spaced, but a compensating congestion occurs near the ambitus, so that the average percentage of plates on the adoral surface remains about the same. All other species of *Holectypus* and *Coenholectypus* that I have been able to study; except the one about to be described, are remarkably constant in the resemblance of their ambulacral structures to those of *H. hemisphaericus*.

The common species from the Cornbrash, which is usually called *H. depressus*, is superficially remarkable for the great size that it may attain. Specimens with a diameter of about 50 mm. are frequently met with, while the Inferior Oolite species rarely exceeds half those dimensions. The form is probably that named *H. striatus* by D'ORBIGNY, but since a systematic discussion would be out of place here, I prefer to call it *H. "depressus"* without prejudice to later specific determinations. A casual inspection of the ambulacra of this form shows that there is a great number of very low plates, with crowded pore-pairs, on the adapical surface, and a strange paucity of them, with widely spaced, somewhat large pore-pairs, adorally. The crowded primaries pass round and a little below the ambitus, but give place to high, almost "Bothriocidaroid" plates at the point where grouping begins. Plate 65, fig. 7, indicates this feature in an average specimen, while Plate 65, fig. 9, shows a somewhat extreme case. The plating-structure of the complicated region is seen to be essentially like that of *H. hemisphaericus* or *Plesiechinus*, but the proportions of the plates are extremely different. The average percentage of plates and pores on the adoral surface (calculated from all five areas in 12 specimens) is 24 per cent., but even this low figure does not adequately express the condition, since a considerable part of the area just adoral to the ambitus is occupied by crowded primaries. Only among such specialized Echinoids as *Clypeus sinuatus* or the simpler Spatangidæ can a similar distribution of the ambulacrals be found. But *C. sinuatus* has highly developed petals, whereas there is very little disparity in the apical pores of *H. "depressus."* It is doubtful whether this transference of the podia to the adapical surface (without any demonstrable change in their function) has any phylogenetic significance, but morphogenetically it seems explicable as a precipitate, but incomplete, progress in the direction followed more gradually by most Irregular Echinoids, and towards the goal that has been reached by the most advanced Spatangoida.

Family III : DISCOIDIIDÆ.

Although this family includes but a single genus (according to present systematic grouping), the ambulacral structure developed within its limits is more diverse, and in many respects more elaborate, than that of any other family in the Order. For those reasons detailed description is necessary; while the undoubted phyletic affinity between the family and the Clypeastroids lends an unusual interest to its morphological peculiarities. In a general way, the genus *Discoidea* may be divided into two sections, comprising small and large species respectively. POMEL (1883) distinguished the latter section by the name *Pithodia*, but later authors have rarely, if ever, accepted this genus. I am convinced that some such separation of the two groups is both convenient and natural, but, to avoid systematic discussion, I prefer here to refer to the two sections as *Discoidea cylindrica* and "the other Discoidiidae." The latter group includes *D. subucula*, the genotype, and, as far as my experience goes, all other species save *D. cylindrica*. Unfortunately, the small forms that conform to the type in essentials are extremely difficult to examine. This difficulty is partly due to their small size, but it is exaggerated by the extraordinarily thick granulation of their tests. Staining is an almost inevitable preliminary to the tracing of sutures, especially in small forms, and the linear arrangement of the minor ornament causes innumerable spurious suture-lines to appear under such circumstances. Out of several hundreds of specimens of *D. subucula* I have only one example in which (in one area only) it is possible with certainty to trace the sutures throughout the ambulacrum, and a similarly unique test of *D. dixonii* has been selected from 75 specimens. It has, however, been possible in the case of both species to detect the sutures here and there, and on every such occasion the structure has proved very nearly identical with the corresponding sections of the complete areas. In no other species of this group have I been able to trace the ambulacral sutures, and it is only on the evidence supplied by the disposition of the pore-pairs that I have concluded that such forms as *D. favrina* and *D. decorata* are akin to *D. subucula* rather than to *D. cylindrica*.

Species 1 : *D. subucula* (Plate 67, fig. 1).

(a) The Ambulacra.—The areas of this small species are very regularly lanceolate in outline, conforming in this respect, as in many others, to the Jurassic rather than to the Cretaceous quality. Small forms are often retarded in morphogeny, and, considered alone, *D. subucula* affords a striking illustration of that principle. The ornament is disposed in much the same manner as that of *Holactypus*, but tubercle-series additional to the main one are usually sporadic.

(b) The Ambulacral Plates.—Reference to the figure will show how closely in accord with the plating of the Jurassic *Holactypoida* is that of *D. subucula*. Adorally the plates are grouped into triads, as in *Plesiechinus*, but the grouping

extends further from the peristome in the small Cretaceous species, since none of it seems to be due to tubercle-growth. In this respect alone is any advance apparent. Although some of the reduced plates are almost separated from the perradial suture, I have never seen a definite demi-plate in this species. At the ambitus, and for some way up the adapical surface, the plates are low, crowded primaries resembling those of *Holectypus*, but over the apicad half of that region they become relatively high. Were the species to be considered alone, this marked feature of the apicad ambulacra might reasonably be regarded as a retention of morphoneanic characters due to the small size of the corona, but the description of *D. dixonii* which follows shows that it is an expression of some more important tendency.

(c) The Pore-fields.—The podial pores are uniformly minute, and seem perfectly homogeneous. Near the peristome they tend to depart from a uniserial sequence, but there is no definite triserial arrangement. In the specimen figured, 42·6 per cent. of the pores are on the adoral surface, and this seems to be approximately their average distribution. Such a percentage is quite out of keeping with those in *Holectypus*, or even in *Plesiechinus*, but is similar to that in *Pygaster*. It shows a tendency towards an equalisation of the distribution of the podia that points in a direction definitely away from the Spatangidæ. It is, however, more reasonable to consider the area as consisting of three parts—an adapical region of few pores, an ambital region of crowded pores, and an adoral region of less crowded, but still close pore-series situated in a zone of complex plates.

Species 2: *D. dixonii* (Plate 67, fig. 2).

This small species which is sometimes identified with *D. minima*, is abundant in the lower part of the Middle-Chalk zone of *R. cuvieri*. In size, ornament and general characters it is very similar to *D. subucula*, almost the only superficial distinction being the relative inflation of the ambitus. It is therefore reasonable to suppose that *D. dixonii* is a late development from the *D. subucula* stock, and that it should show the trend of morphogenetic evolution therein. That the latter supposition is justified is clear from a comparison of Plate 67, figs. 1 and 2. The specimen of *D. dixonii* from which fig. 2 is taken, has practically the same diameter as the *D. subucula* analysed in fig. 1. The two figures are thus similarly enlarged, and show comparative features of unexpected interest. The more obvious difference between the two ambulacra may be expressed by the number of plates in the columns. While in column *a* of *D. subucula* there were 75 plates, in that of *D. dixonii* there are only 46. The inflation of the supra-ambital parts of the test in the latter species probably accounts for the low percentage (39·1) of plates on the adoral surface.

Throughout the area the plates are much higher than in *D. subucula*, and there is but a faint tendency to ambital congestion. But while the plates are fewer and more primitive in proportionate height, the amount and degree of complexity is much

greater in the later species—*D. dixonii*. Grouped plates extend from the peristome to a region well above the ambitus, and much-reduced demi-plates are the rule rather than the exception. Indeed, the adoral part of the ambulacrum is extraordinarily like the greater part of the area in *Conulus* (fig. 3), and even more like that of a young *Echinonæus* (fig. 5). The apical plates, on the other hand, are not only primaries, but are almost “Bothriocidaroid” in character, showing a considerable progress along the line of simplification indicated in *D. subucula*. The ambulacrum of *D. dixonii* thus exhibits two apparently opposite qualities, an advance in complication and a regression in plate-production and form. Such a combination of structures seems explicable as a tendency towards the Fibulariid character (see below, Section 3 (c)), and the adoral part of the area certainly suggests affinity or parallelism with the Echinonæid ambulacrum.

Section : *Discoidea cylindrica* (Plate 66).

This large and well-known species has a considerable range (approximately coinciding with the Cenomanian), and appears to have two distinct forms. Specimens from the Upper Greensand are usually relatively small, and almost always have markedly cylindrical tests. In the Chalk Marl depressed or hemispherical forms are perhaps more abundant, but large specimens from that horizon are usually cylindrical. In the zone of *H. subglobosus* cylindrical tests, often attaining a very large size, are normal for the South of England, while the depressed type, commonly of relatively small diameter, seems more characteristic in Lincolnshire. Opinion is divided as to whether the “*forma vulgaris*” (LOVÉN) and the “*forma depressa*” are distinct species. It has been claimed that differences occur in the structure of the perignathic girdle, but I believe that these are not constant. The alternative view that the cylindrical forms are gerontic is somewhat discounted by the prevalence of small cylindrical specimens in the Upper Greensand, and by the occurrence of depressed tests of greater diameter than some that are cylindrical at higher horizons. Except for inevitable difference in the percentages of plates on the two surfaces of the test, I have been able to find no definite differences in the ambulacral characters in the two forms, and hence associate them under the same name for the purpose of the present paper.

(a) The Ambulacra (Plate 66, figs. 1, 4, 5, and 6).—The outlines of the ambulacra show a distinct, and in some measure a progressive, departure from the lanceolate type. The greatest breadth is usually a little above the ambitus, and is attained (from the ocular margin) by a very regular increase. From the region where the adoral surface becomes flat a rapid diminution in width sets in, and the areas taper with straight margins to the peristome. In cylindrical forms there is a tendency for the part just above the ambitus to be locally widened (fig. 4), while in depressed specimens the sides of the areas are either parallel or even concave in that region (figs. 1, 5, and 6). Ornamentation (Plate 66, figs. 2 and 3) is sparse except at the

ambitus, but there it becomes exceedingly dense both on the ambulacra and inter-ambulacra. In no observed cases do the tubercles transgress the transverse sutures, and their "triseriate" arrangement is often imperfect, although always recognisable. Adorally the tubercles tend to occur on every alternate primary, as in *Echinus*. Towards the peristome a line of prominent granules occurs down each column between the pore-fields and the adradial sutures (fig. 3), one granule rising from each plate with great regularity. It is clear that the ornament, from its small scale and frequent lapse, cannot be held responsible for the intensity of the plate-complexity.

(b) The Ambulacral Plates.—Complexity in a degree unknown in other Holectypoida, and, indeed, in other Irregular Echinoidea, characterises the plating of the ambulacra over their whole adoral extent, and affects the plates for a variable, but always considerable, distance above the ambitus. The original of Plate 66, fig. 1 (in the Manchester Museum), is a large specimen, with a diameter of 57 mm., and, though merely labelled "Lower Chalk," was almost certainly collected from the *H. subglobosus* zone. Adorally a few primaries persist, but even these are more or less grouped. Then follow two triad-groups (similar to those of the adoral surface of *D. dixonii*) in the Echinonoid stage, consisting of a large adoral primary, a small demi-plate, and a low adapical primary. In succeeding groups the last-named plate becomes a demi-plate, normally larger than the original demi-plate, and, with considerable irregularity, this condition is maintained as far as the ambitus. The irregularities consist, in the main, of "super-grouping" or the lapse of one demi-plate. Occasionally, tetrad-grouping appears, often in such a position that it compensates for a plate lacking in a contiguous group. The demi-plates are, in almost all cases, exceedingly minute, and near the ambitus, where their height is reduced very seriously, they are hardly adequate for the inclusion of their pore-pairs. Above the ambitus the congestion of plates is rapidly reduced, but complexity persists, albeit of a type differing from that normal to the adoral surface. Fairly regular alternation of primaries and *single* demi-plates occurs, the number of primaries gradually increasing in an apical direction. Although the adapical region is largely composed of regular, fairly high, primaries, occasional spasmodic complexity may often appear (twice in the case figured), without any visible reason or connection with the main grouping-systems. These precocious reduced plates have a peculiar interest when compared with the structures of such phylogenetically distinct forms as *Galeropygus* and many other Nucleolitidae, where occasional (usually single) demi-plates may occur at a considerable distance adapically from the hypophyllode or phyllode. The three specimens illustrated in figs. 4, 5, and 6 were selected from individuals found at different horizons, but with the same ambulacral length. They are here reproduced to show the small, but important, zonal modifications that occur in the species. Fig. 4, from an Upper Greensand (cylindrical) specimen, shows the greatest degree of ambital congestion, and has complexity extending for some distance above the ambitus. Even in the latter region the grouping is approximately

on the triad-plan. There are no precocious demi-plates. In fig. 5, from a Chalk-Marl (depressed) specimen, a considerable series of grouped primaries, followed by several "Pyrinid" groups, occurs between the peristome and the normal region. The congestion near the ambitus is less marked than in the previous case, but complexity is carried further up the area, and one series of precocious plates exists. The apical primaries are proportionately higher than in the Greensand type. The original of fig. 6, a depressed example from the *H. subglobosus* zone, shows an unusual regularity of structure on the adoral surface, and an almost complete suppression of grouped primaries and "Pyrinid" groups near the peristome. In this specimen there are no precocious plates, nor do supra-ambital single demi-plates occur, but this feature is almost certainly due to the youth of the specimen. Since it was of the same size as the Greensand form, while the average size of specimens from the *H. subglobosus* zone is almost twice as great, it can hardly be doubted that this example has not attained full development. Fig. 1 is drawn to the same magnification, and shows the characters normal to adults from this horizon. In spite of this probable difference, one striking contrast can be seen between the Greensand and "Grey Chalk" forms. In the former a fair number of primary plates persist near the peristome, in the latter very few. This character is not perfectly regular in occurrence (as fig. 1 shows), but the average condition of the ambulacra of the two types is none the less indicated in figs. 4 and 6. It is noteworthy that in the latter form triad-grouping hardly extends above the ambitus, both in the young (fig. 6) and in the adult (fig. 1); but in the latter it is partly represented by "dyad-grouping," a condition rarely found in the *varians*-zone forms, and never, so far as my experience goes, in those from the Upper Greensand.

(c) The pore-fields.—The pores are minute and similar throughout. On the adapical surface they are uniserial, and placed very near to the adradial sutures. At and just below the ambitus they become extremely congested, and take on a quite intense triserial arrangement, which may be locally either biserial or quadriserial according to irregularities in the plating. Below the zone of congestion the pore-fields become almost straight again, and a uniserial sequence (with faint traces of triserial arrangement here and there) persists to the peristome margin. The pore-fields converge more rapidly than the adradial sutures (see Plate 66, fig. 3), and each adradial tract supports a row of prominent granules, one to each plate. The exiguous proportions of the demi-plates, which are hardly adequate for the inclusion of the pore-pairs, become thus emphasized by the occupation of much of their surface by ornament.

(d) Abnormalities.—The frequent irregularities that are indicated in figs. 1, 4 and 5 on the adoral surface seem to call for no special comment. It would be remarkable if so intensely complex a plating-system were carried out with perfect precision, especially since the relatively simple ornamentation is subject to much disturbance. However, in view of the almost mathematical accuracy with which triad combination

occurs in the Triplechinidæ, it is perhaps legitimate to suggest that the irregularity so prevalent in *D. cylindrica* may be an expression of morphogenetic plasticity. The occurrence of dyad grouping above the ambitus in adult forms of late geologic age I regard as a regular gerontic feature of great significance; its presumed meaning will be discussed in Section 3 (c), below.

There is, however, one type of irregular development which, whether normal or not, seems suitable for description here. A well-marked case is illustrated on Plate 66, fig. 7. This example is by no means unique, for out of 30 specimens from the same zone (*S. varians*) that I have examined, 13 show a character identical in style and localisation though much less clearly defined. The specimen (in the collection of G. E. DIBLEY, Esq.) is a small, depressed form, telescoped by pressure adorally, accidentally truncated adapically, and much encrusted with organisms. The ambulacra are very well preserved above the ambitus, excepting area II, which is largely obscured by a Plicatula. In accord with the character normal for the zone, plate-complexity extends considerably above the ambitus, but for an unequal distance in the different areas. In ambulacra I and V regular triad-grouping is followed by a fair series of "Pyrinid" or kindred plates. In area IV (and, by analogy with other specimens, in II also), there are fewer of the "Pyrinid" groups, while in area III there are none. The zone of complexity reaches nearly half-way up the adapical surface in I and V, and hardly a quarter of the distance in III. Area IV (and probably II) agrees fairly with I and V in this respect, but the extent of the complexity falls a little short. The anterior ambulacrum of *D. cylindrica* is in no way different in length, ornament or pore-characters from the other areas, and yet it very frequently differs from them in plating. This difference (rarely so marked as in the specimen figured) seems always to lie in a greater simplicity, as expressed by the number of ungrouped primaries on the adapical surface. I have never seen a specimen in which any of the other areas showed this quality. Slight as the irregularity is, it seems worthy of record partly on account of its frequency, and chiefly because it affects the anterior ambulacrum. In the Spatangidæ this area is almost always different from the rest, usually in a striking manner. In "Heart-Urchins," however, the heteronomy of area III is clearly associated with bilateral symmetry, and it is curious to find a similar tendency in *D. cylindrica*, where the radial symmetry produces an almost hemispherical test. There is no reason to believe that the feature was extended or even maintained in any near relatives or descendants of the species, so that it would appear to be a case of obscure parallel variation appearing at a time when such phyletically distinct groups as the *Toxaster* and *Holaster* series were developing a similar quality as an essential part of their structure.

Family IV: LANIERIIDÆ.

The two genera *Lanieria* and *Discholectypus*, represented each by a single species, constitute a most peculiar group. Recently (HAWKINS, 1913 b) I redescribed the

former genus from some of the original material, so that it is unnecessary to give more than a brief indication of the ambulacral structure. In practically all morphological features both genera seem to be typical Holoctypidæ, and could almost be placed in the genus *Coenholectypus*, but in their ambulacral structure they are closely similar to the Echinonæidæ. I am convinced that their real affinities are with the former family, and that the appearance of Echinonæid ambulacral plating is a result of parallel evolution. Their ambulacral structure could be easily attained by amplification and elaboration of the Holoctypoid plating; but the introduction of a posterior genital plate, with a functional fifth gonad (wanting in the Echinonæidæ) would involve the adoption of improbable methods of evolution on the other alternative.

Family V: ECHINONÆIDÆ.

The Echinonæidæ possess the most complete complication of ambulacral structure found among the Irregular Echinoids, although the degree of reduction of the plates is not so intense as that locally developed in *D. cylindrica*, *Echinocardium cordatum*, or those forms that have true phyllodes. In the extent of the grouping, in the regularity of triad-structure in all genera, and in the remarkable absence of individual variation or abnormality, the family may be compared with the Triplechinidæ, which appeared at about the same period. Among many hundreds of specimens of *Conulus* that I have examined, not one showed disturbances of ambulacral plating (except of a trivial nature) unaccompanied by the effects of accident or disease. This perfection of development becomes the more striking when it is realised, that no single ambulacrum of *D. cylindrica* has been seen in which unbroken triad-sequence occurred. Even in *Amblypygus*, where the proportions of the plates vary from long laths in the petaloid regions to almost "Bothriocidaroid" plates adorally, the normal plan of two unequal primaries enclosing a demi-plate is quite constant in all specimens and drawings that I have seen.

The systematic grouping of the Cretaceous Echinonæidæ is in a state of great confusion. LAMBERT (1911) has discussed and dismembered the genus *Pyrina*, but it is difficult to follow his meaning in regard to the separation of the various genera involved. Generic distinctions appear to be based largely on the "obliquity of the peristome," but since all the forms in the family with which I am acquainted have oblique peristomes (not excepting the species of *Conulus*), there seems a lack of precision in the various diagnoses. *Conulus* can be distinguished from the forms usually called *Pyrina* by its ambulacral characters, as will be shown below, but I am sceptical as to the merits of such genera as *Globator* and *Pseudopyrina*. However, for the present purpose it will be sufficient to use the term "*Pyrina*" (*sens. lat.*) for all the Cretaceous forms that cannot be referred to *Conulus*, since these species, with Echinonæus of later periods, seem practically identical as regards the structure of their ambulacra.

Sub-family i: ECHINONÆINÆ, (Plate 67, figs. 4-10).

Save for a few ontogenetically young plates near the peristome, and a slightly greater number of morphogenetically young plates near the apical system, the whole ambulacrum is built of plates arranged in triad-groups similar (except in combination) to the triads of *Echinus*. An orad primary of considerable height is followed by a much-reduced demi-plate, succeeded by an apicad primary, which, in the adult, is extremely slender. I have never seen a case in which this apicad primary became reduced. In a young *Echinonæus*, the transverse suture that separates the two primaries of a triad-group is usually directed in an orad and adradial direction, so that the apicad primary is cuneiform, tapering perradially. This condition is normal (at least on the adapical surface) in the adult stage of *Conulus*; but in *Echinonæus*, and still more in "*Pyrina*," this transverse suture tends to become truly horizontal in direction. The perradial suture assumes a stiffly zigzag course, that may be described as "battlemented."

The pores are minute and similar throughout, except in *Micropetalon* (see below), and are practically uniserial. The pore-fields tend to converge towards the perradial suture near the peristome, as in *Discoidea cylindrica*, but it is rarely that any triserial arrangement can be detected. In connection with the pore-pairs of this sub-family, an interesting point arises. The orad biporous plates that characterise the ambulacra of all Atelostomatous Irregular Echinoidea are certainly not present in the Pygasteridæ and Holectypidæ, and have not been recognised in *Discoidea* or *Conulus*. LOVÉN (1875, Plate 14, fig. 128) shows a curious feature on one proximal plate in *Conulus rhotomagensis*, the two pores of the pair being widely separated. Were it not that the podial pores of *Conulus* are always paired, the condition that he illustrates might well be taken as representing a "biporous ambulacral" bearing, like that of a Spatangid, two single pores. It is usual to regard *Echinonæus* as a form with biporous ambulacrals, but the careful drawings made by WESTERGREN (1911) show that, if such structures are present, they possess quite anomalous features. In Plate 67, figs. 8, 9, and 10, copies of WESTERGREN's drawings are given, showing ontogenetic stages in the growth of the proximal parts of the ambulacra. In the very young stage (fig. 8) the vestigial perignathic process obscures the pores, but there is no sign of any "biporous" plate. In a later phase (fig. 9), when the processes have disappeared, there are normal pore-pairs in each proximal plate. But the small peristomial grooves (? vestigial branchial incisions), which notched each column in the earlier stage, are now reduced to one, which makes a small inlet into the margin of the plate which, according to LOVÉN's law, should be biporous in a Spatangid or Cassiduloid. In the adult (fig. 10) this notch has disappeared as such, and three pores, two evidently paired, perforate the plate in question. WESTERGREN shows no case of a "biporous" plate in *Echinonæus*, in which there are two pore-pairs, and, from a study of the scanty material at my disposal, I agree with him that the "biporous ambulacral" includes one pore-pair and an odd single

pore. May not this latter be the enclosed relic of the surviving "branchial incision"? In the Collyritidæ, and other forms that have persistent pore-pairs, the biporous plate contains two complete pairs, each in a peripodium, so that there is a definite difference between a normal biporous ambulacral and the analogous structure in *Echinonæus*. On the evidence available, I am inclined to answer the question asked in a previous sentence in the affirmative, and to suggest that *Echinonæus* has no true biporous ambulacrals.

The case is otherwise in the small, unique form described by AGASSIZ and CLARK (and redescribed by WESTERGREN) as *Micropetalon purpureum*. In that form (here Plate 67, fig. 4) there is a perfectly definite biporous plate in each area, normally provided with two pore-pairs. There are, however, serious doubts as to the systematic validity of *Micropetalon*. It may be, as WESTERGREN suggests, a post-larval stage in the development of some other type. The character of its ambulacral plates resembles that of the young *Echinonæus* (fig. 5) far more than that of the adult (fig. 6), and conforms fairly closely to that of *Conulus*. The faintly sub-petaloid character of the apicad pores, and the relatively large size of the tubercles, also point to the youthfulness of the specimen. I should be inclined to regard *Micropetalon* as an early stage in the development of some non-Holactypoid descendant of the Amblypyginæ, but more evidence is required before such a suggestion can be given in any but a speculative sense.

Sub-family ii: CONULINÆ. (Plate 67, figs. 3, 11, and 12.)

As regards plating-structure, the ambulacra of *Conulus* agree with those of the Echinonæinæ very closely, particularly with those of the young *Echinonæus* (fig. 5). The relative height of the plates, and the usual obliquity of the course of the internal transverse sutures of the triad-groups serves to distinguish the structure from that of "Pyrina," both features apparently resulting from less advanced (or more regressive) evolution. It is usually very difficult to distinguish the sutures on the adoral surface, owing to the great congestion of ornament; primary and secondary tubercles, granules and "glassy tubercles" occurring in great profusion. I have never found a specimen in which weathering has displayed the sutures on this surface, although such aids to investigation are frequent on the adapical surface; but there seems no reason to believe that true combination occurs. The original specimen from which fig. 3 was drawn was partly decorticated, so that in places the sutures are drawn from impressions on the internal mould. The original of fig. 12 is the only one in which, by artificial etching and staining, I have been able to display the sutures with any clearness, but there is no reason to doubt that it is perfectly typical. In fig. 11 a retarded primary (cuneiform) replaces the usual demi-plate in one case. Such a development recalls the "Diademoid" triads sometimes found in *Echinus*, but it is of very rare occurrence.

Near the peristome the pore-pairs, which are elsewhere perfectly uniserial, become

very strongly triserial in arrangement, the character being emphasised by the existence of well-marked depressions in which the oblique series are situated. As far as the pore-pairs are concerned, this arrangement is suggestive of incipient phyllode-structure, but there is no accompanying change in the nature of the plating. Nevertheless, this triserial plan of the proximal pore-pairs seems to constitute a sound distinction between *Conulus* and "Pyrina." It is most definitely marked in *C. albogalerus* among British species, and seems to progress in intensity as the genus is traced upwards through the zones of the chalk. But even the low-zonal forms of *C. subrotundus* and *C. (?) rhotomagensis* have quite clearly triserial pores.

Sub-family iii: AMBLYPYGINÆ.

The genus *Amblypygus*, which bears a close superficial resemblance to the *Echinolampidæ*, has typical "Pyrinid" ambulacral plating. But in the character of its podial pores it marks a great and systematically embarrassing advance from the *Holectypoid* condition. Over the greater part of the adapical surface the pores are completely heterogeneous, with the result that a fully petaloid character is produced. There is no complementary phyllodal development adorally, and the oblique peristome compares with that of *Echinonæus*. It is, however, solely on the nature of its ambulacral plating (as beautifully portrayed by DUNCAN and SLADEN, 1884), that I venture to include the genus among the *Holectypoida*. The apparently nearly related *Oligopygus*, according to CLARK and TWITCHELL (1915), has primary plates only, but these are irregular in shape, and often imperfect in alternation. The possible phyletic position of the sub-family is further discussed in Section 3 (c) below.

(2) THE ASCERTAINED AND PROBABLE FUNCTIONS OF THE HOLECTYPOID AMBULACRUM.

It is clear that any conclusions as to the uses of the tube-feet of the *Holectypoida* must be almost entirely hypothetical. In one case only, that of *Echinonæus*, is there a possibility of actual observation of habits and habitat; and the value of this exiguous evidence is seriously reduced by the dissimilarity in general structure between *E. cyclostomus* and the Jurassic *Holectypoida*, and might be altogether denied by those who do not follow the present writer in the inclusion of the genus within that Order. There are, however, two lines of argument, based upon independent series of observations, from which the possible ambulacral functions can be deduced with some measure of confidence. On the one hand, the known association of certain functions with definite types of structure in recent forms may be employed, by inverse argument, as a basis for the indication of the purposes of the ascertained structures of the *Holectypoid* ambulacrum; and on the other, a recognition of the lithological qualities of the deposits in which the fossils are found will afford a clue to the opportunities for the exercise of various podial

functions available for Echinoids living under the environmental conditions thus determined. The substantial agreement between the conclusions to be drawn from these independent arguments must assuredly indicate that they represent a reasonable approximation to the true solution of the problem. The results obtained have important bearings on the morphogenetic arguments which conclude the paper, so that the subjoined paragraphs are introductory to that section, and at the same time are a direct sequel to those of Section 2 (e) of Part I.

Echinonëus cyclostomus, according to H. L. CLARK (as quoted by WESTERGREN, 1911, p. 42), lives among stones and weed at about low-water mark. In Jamaica it inhabits a "sand-flat within the reef," buried in the sand under fragments of broken coral-rock. "In rare instances, specimens were found clinging to the rock" by the adapical tube-feet. "The tube-feet of *Echinonëus* are used to hold sand-grains and particles of dirt close against the test." "Both spines and tube-feet appear to be used in locomotion." It is clear from this account that *Echinonëus* has no great powers of adhesion by its podia, but rather seeks sheltered lagoon water; even there its habits are markedly retiring.

The Pygasteridæ show a progressive simplification both of pores and plating-structure. The close series of slightly dissimilar pore-pairs on the adapical surface in Lower Jurassic forms seem to represent rudimentary petals; while the more widely spaced, similar pore-pairs of the adoral surface, set in plates that show some degree of complexity (albeit none of combination) seem more adapted for the usual adhesive function. The distribution of the pores on the test, with the greater number on the adapical surface, might be taken as an indication that the respiratory function was the more important, especially as the adoral plate-complexity does not attain that true combination which alone can strengthen the areas in their resistance to strain, while the pore-pairs are hardly displaced from an uniserial arrangement. In *Pileus*, on the other hand, the markedly biserial character of the apical pore-pairs might suggest an adaptation to mechanical effort; but this suggestion would be qualified by the nature of the pores, which, though similar, are large and elliptical, two features that are quite unlike those found in the pores that transmit adhesive podia in the Regular Echinoidea. Perhaps the apical podia of *Pileus* were equally respiratory with those of *Pygaster*, the leaf-like podia being of a somewhat different shape. The podial pores are strikingly like those of the petals of the Spatangidæ, but much more densely crowded. The biserial grouping may be a device for the accommodation of great numbers of podia which, if in a continuous series, would be too closely packed for efficient aëration. On the adoral surface the small, strongly triserial pore-pairs certainly suggest the exercise of adhesion by their podia—a function which life among coral-reefs would demand in so large a form as *Pileus* if any exposure to wave-action was incurred. In the Cretaceous members of the family the pore-pairs are minute and practically similar and uniserial throughout, while there is little, if any, complexity in the ambulacral plating.

There is thus no indication of any special adaptation for respiratory purposes (podia cannot avoid performing that function to some degree), and the small size of the pores would suggest that the slender podia that passed through them could not have possessed any great power of adhesion. Perhaps the crowded ornament of *Macropygus* and *Anorthopygus* (indicative of abundant and fairly massive radioles) may be associated with ambulacral failure in this respect.

As far as can be ascertained from the facts of geological distribution, the *Pygasteridæ* appear to have been exclusively inhabitants of shallow water, and probably to have been restricted to the littoral zone. Their remains are found in the limestones and sandstones only in the Lower Oolites, and although *Pygaster macrocyphus* occurs in the Kimmeridgian, it is not found in the Kimmeridge Clay. On the whole, the clays of the Oolitic period represent the deposits of more open water than the sands or oolitic and coralline limestones, many of which are of almost inter-tidal origin. The distribution of the Cretaceous members of the family gives similar evidence. Both *Macropygus* and *Anorthopygus* are to be collected only in the "Greensand" facies of the Cretaceous deposits. The latter genus is, so far as present experience goes, restricted in Britain to the Haldon Hill drift and the Hibernian Greensand, never having been found in the chalk proper. It is thus reasonable to claim for the *Pygasteridæ* as a whole a general habitat not very different from that of *Echinonæus* and most of the *Clypeastroida*. The absence of true petaloid developments in the extinct family may be considered as an indication of imperfect adaptation to surroundings different from those of its Regular ancestors. Although the earlier *Pygasteridæ* show a tendency to develop suitable ambulacral modification, the attempt was not maintained, and the family died out in Cretaceous times with podia that had largely lost their earlier adhesive function and failed to acquire a new one.

Most of the suggestions made for the *Pygasteridæ* hold good for the *Holectypidæ*. There is less indication of any petaloid qualities in the apical podia, though this is in some degree compensated by the great numbers of apparently tubular podia that were retained on the adapical surface. On the other hand, a considerable reduction in the numbers on the adoral surface was thereby brought about, and the few podia that occurred in that position in such an extreme case as that of *Holectypus depressus* in the Cornbrash, although situated in grouped plates, would be insufficient to enable their owners to resist any violent disturbing influences. The marked crowding of the pore-pairs that occurs near the ambitus in most forms of the family is probably directly associated with the exercise of special functions by the podia of that region. In forms with flat adoral surfaces that lived on relatively smooth sand, the podia near the peristome would have little freedom for action of any kind, while the sharp ambital angle would remove the apical podia from any normal contact with materials to which they could adhere. Only at the ambitus would freedom and adhesion be practicable. Moreover, podia so situated

could use the sensory qualities that are always potentially present in them with the same success and advantage that attach to antennæ in other animals. The latter function is, perhaps, the more probable for the ambital podia, since the ambulacral plates of that region are, by their congestion, less suited than usual to withstand mechanical strain. In view of the inadequacy, either of numbers or arrangement, of the podia for the adhesive efforts required for locomotion, that function would devolve upon the radioles of the adoral surface, and it is suggestive to find that the tubercles below the ambitus are disproportionately larger than those adapically placed. The Holoctypidæ would seem, therefore, to have adopted the Clypeastroid or Spatangid mode of progression, and to have left their podia to perform the two inevitable functions of respiration and sensation, without any specialization for those purposes of a kind that affected the character of the pore-pairs. The geological distribution and probable habitat of the Holoctypidæ are both very similar to those of the Pygasteridæ.

In a discussion of the podial functions of the Discoidiidæ, it will be sufficient to consider the extreme case of *D. cylindrica*. The smaller species differ in ambulacral characters only in degree, and the differences will not, therefore, affect arguments of this kind, although they may prove to be of great importance in morphogenetic considerations. An outstanding feature of the ambulacra of *D. cylindrica* is the extraordinary numbers, and extreme congestion, of the plates and pores. In proportion to its size, the corona of this species shows vastly greater plate-complexity, and considerably greater pore-crowding, than that of any other Echinoids, excepting, perhaps, some of the later Palæozoic types. Both qualities are at their maxima on or about the ambitus, so that there is a similarity in that respect to the Holoctypidæ. The plentiful development of demi-plates, and the departure from uniserial sequence of the pores, might perhaps be taken to imply adaptation for an adhesive function, but I believe that such a view would be mistaken. In the first place, there is no combination of the complex plates, so that the poriferous tracts, already weakened by the very numerous and close-set perforations, are rendered still more fragile by the concentration of sutural tissue that results from the congested structure. Secondly, the pores are exceedingly minute, so that the podia must have been mere filaments; and, although this character might be counteracted in some degree by their great numbers, such slender proportions do not occur in those podia of recent forms that exhibit any adhesive efficiency. Lastly, *D. cylindrica* must have lived in surroundings which, in the latter part of the history of the species at least, would make podial locomotion practically impossible. Marly ooze, such as that which surrounded the species in Lower Chalk times, would render abortive the most vigorous efforts at progression by such means. The concentration of large tubercles around the ambitus seems to point to the radioles as the chief locomotive organs. The biserial (or, rather, irregularly multiserial) arrangement of the pores near the ambitus seems comparable with the analogous displacement of the

apical pores of Pileus, designed in this case to prevent the crowded, filamentous podia from becoming entangled in one another; and even to ensure that the pore-pairs, small though they are, shall be separated by bars of stereom. But, if a locomotor function is denied to the tube-feet of *D. cylindrica*, there is an undoubted difficulty in finding a cause for the extraordinary numbers of podia developed, especially on the adoral surface. That surface is so flat, save for the small but deep peristomial invagination, that it must have been very nearly in contact with the ooze of the sea-floor, so that its podia could hardly be of service for respiration. In the absence of any closely comparable structures in living forms, an attempted explanation must needs be conjectural, and it is in that sense that the following sentences must be read. An organism living on an ooze-surface must inevitably be normally microphagous in habits, even if it be endowed with jaws that could be used if occasion offered. It would therefore be an advantage to the animal to have abundant means of selecting nutritious particles from among the mass of inedible material over which it passed, so that the very numerous, slender adoral podia of *D. cylindrica* may have performed the function usually ascribed to those of phyllodes or to the ragged tube-feet that surround the peristome of a Spatangid. Added to this sensory activity there might well be a feebly prehensile function in the podia, so that they could pick up and pass to the mouth those particles that had been selected. The rapid convergence of the pore-pairs towards the peristome, and the palisade of large granules (presumably supporting a row of small radioles) along each adradial tract, might be adaptations to such a "Pelmatozoic" habit of feeding. The suggestion is made with the less diffidence on account of the remarkable character of the anterior ambulacrum of *Echinocardium cordatum*. In that advanced Spatangid (Plate 69, figs. 4 and 5) the plating of the petaloid region of area III is even more elaborate than that of Discoidea, and the podia that project from it are used, according to MACBRIDE, to catch small prey, and pass it down the anterior sulcus to the mouth. Whatever may have been the true functional uses of the podia of *D. cylindrica*, I believe that the elaborate plating-structure is the expression of a morphogenetic trend of great importance (see Section 3 (c)).

There is every reason to believe that the ambulacra of the Echinonēinæ were employed similarly to those of Echinonēus. The identity of structure gives *primâ facie* support to such a view, and the restriction of the forms here grouped under the name "Pyrina" to littoral facies of the Cretaceous deposits affords confirmation. The habitat of Conulus was undoubtedly different from that of Echinonēus. The earlier species, such as *C. rhotomagensis*, may have inhabited shallow water not far from the coast, but the later forms, typified in this country by *C. subrotundus* and *C. albogalerus*, are abundant only in those zones of the chalk which seem to have accumulated in relatively deep and open water. The extreme rarity of specimens of Conulus in the zone of *Holaster planus* seems to indicate that the genus had definitely abandoned shallow water by that time. The

markedly triserial arrangement of the adoral pore-pairs, though unaccompanied by any special plating-structure, invites comparison with the phyllodes of other groups. There is not the same structural need for displacement of the pore-pairs as exists in the ambital parts of Discoidiid ambulacra, so that the adoption of a triserial grouping would seem to be associated with some local functional peculiarity. That such an activity was connected with feeding habits would appear likely from its restriction to the podia bordering the peristome; and this assumption would apply equally to phyllodes. Possibly the proximal orad tube-feet of *Conulus* were used partly for retaining the food which the enfeebled jaws could masticate but slowly, and partly for "tasting" the material collected. Such uses would be closely akin to those believed to be made of the phyllodal podia in the Cassiduloids; and it is perhaps more strange to meet with no such provision in the other Echinonëidæ than to find it in this group. The rudiments of phyllodal plating-structure are present almost throughout the ambulacra of *Conulus*, and, if the genus had any phyletic descendants, true phyllodes could readily have been developed from the already triserial parts of the areas.

To summarise the foregoing arguments:—The Pygasteridæ alone of the Jurassic *Holactypoida*, seem to have begun to develop branchial podia in rudimentary petals, but even this family abandoned the attempt in the Cretaceous period. The Holactypidæ and Discoidiidæ have ambital congestion of pores, probably associated with the sharpness of the distinction between the two surfaces of the test, which reduced the opportunities for normal functional activity of the podia except at the margin. *Discoidea cylindrica* shows an extraordinary multiplication of podia, without any evidence of their local specialisation, and may have used those of the adoral surface for the transference of food particles to the mouth after the manner of *Echinocardium cordatum*. The Echinonëidæ, with evenly distributed podia, employ the tube-feet in such feeble expressions of adhesion as the retention of small rock-particles as a protective covering for the test (with subordinate locomotor function), while *Conulus* shows some slight tendency towards phyllodal specialisation. Probably the exercise of a respiratory function was the chief use of the Holactypoid podia, although the absence of special petaloid development shows that it was only adopted incidentally. The Jurassic types had greater powers of adhesion than the Cretaceous forms, while the only living type has adopted the burrowing habits associated (in the Spatangidæ) with an almost complete loss of adhesive power in the podia.

(3) THE EVOLUTION OF THE HOLECTYPOID AMBULACRUM.

In this, the concluding section of the paper, the facts, principles and hypotheses that have been described and enunciated in the foregoing pages are combined in an endeavour to determine the morphogenetic relations existing between the ambulacra of the *Holactypoida* and those of other orders. In arguments of this nature it is inevitable that a high proportion of the personal element should be introduced, but pains

have been taken to restrain it. Principles of evolution that have an application over far wider fields than that of ambulacral morphogeny are involved. Further, it is practically impossible to exclude occasional phylogenetic arguments, although these are subordinated to morphogenetic considerations. The various trends of evolution indicated are not of necessity lines of phylogeny; in many cases, however, there is reason to believe that the two "genealogies" are parallel if not coincident.

(a) *Within the Order.*

With one exception, all manifestations of ambulacral complexity in the *Holectypoida* show some degree of "triad-grouping." The exception (*Discoidea cylindrica*) is only partial, for the bulk of the complication is triadic, although liable to frequent irregularity. It is thus clear that a fundamental uniformity of ambulacral morphology underlies the evolution of the whole group.

There are four chief modifications of ambulacral plating in the Order:—These may be named from their earliest known possessors as the Plesiechinid, Pygasterid, Pyrinid and Discoidiid (exclusive of small species). The probable relations between the four types can be considered first. The Plesiechinid type (Plate 65, figs. 1 and 7; Plate 67, fig. 1), which consists of orad triad-grouping with but little plate-reduction, and simple primaries (apart from tubercle interference in early forms) throughout the ambital and adapical regions, occurs in the Pygasterinæ, (?) Pileinæ, Holectypidæ, and *Discoidea subucula*. Since Plesiechinus is in all respects the least "Irregular" genus of the order, and also the earliest, it seems certain that this quality may be taken as morphogenetically primitive. The Holectypidæ show no other type of structure, but some forms of the Pygasteridæ, and most of the Discoidiidæ, present differences which result, presumably, from the modification of the Plesiechinid type.

The Pygasterid type (Plate 65, fig. 3), in which plate-grouping, except for that under the influence of the tubercles, is almost absent, occurs only in the later Pygasteridæ. The ornament is still "triadic," but the plating has become simplified. Such a change was undoubtedly reversionary, whatever may be the views held as to the immediate ancestry of the *Holectypoida*, since there can be no doubt that some Cidaroid form was on their line of descent; and, although the ornament retains "Diademoid" characters, the plating of the orad parts of the ambulacrum of *P. semisulcatus* is essentially Cidaroid in quality. The structure is closely comparable with that of *Orthopsis*, and the remarks of BATHER (1909, pp. 108–109) on that genus are interesting in this connection. Such simplification could hardly be expected to precede further elaboration, so that the Pygasterid type of ambulacrum must be considered to indicate a side-line of evolution divergent from the main trend of morphogenesis in the *Holectypoida*.

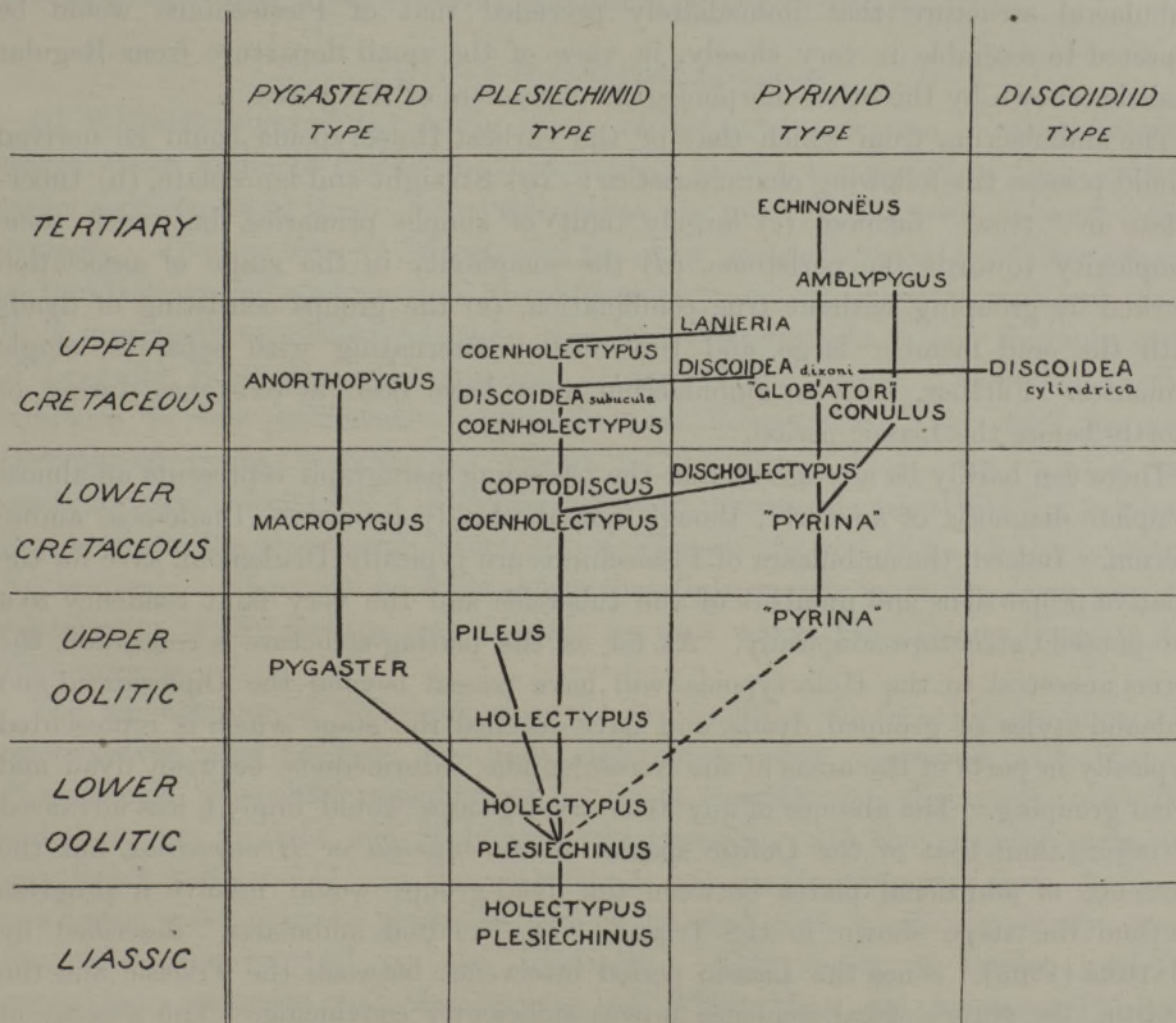
The Pyrinid type (Plate 67, figs. 2–12), which consists of very regular triad grouping on an approximately "Echinoid" plan, with the persistent development of a demi-plate in each group, is seen in its simplest expression in *Discoidea dixonii*, and is

universal and regional in the ambulacra of the Lanieriidae and Echinonaidae. The occasional production of demi-plates in the triad-groups of Plesiechinus, and their more frequent occurrence in the Holectypidae, would seem to indicate that the morphogenetic descent of the Pyrinid ambulacrum passes from the latter family through the stage represented in *D. dixonii*. This does not, however, imply that the Echinonaidae are phyletically descended from the smaller Discoidiidae; a direct sequence from the Holectypidae, or perhaps from the *Plesiechinus*-stock, is more probable, with the Discoidiidae in a parallel line of evolution. It is interesting to note that the Pyrinid type of grouping is the most static of ambulacral structures in the order. Not only do most of the later members possess it, but cases of irregularity in its development are very rare. This is surprisingly in agreement with the condition found among the Regular Echinoidea, where the "Echinoid" type of combination characterises a very large series of Cretaceous and Recent forms, and seems less liable to abnormality than any other type. The two sets of structures are, moreover, practically synchronous in their appearance, both occurring for the first time (in a definite form) in the Lower Cretaceous. This suggests that morphological evolution of the ambulacra may have proceeded at the same rate (with difference in the quality of plate-combination) in the two homogenetic but otherwise very divergent orders of Diademoida and *Holectypoida*. The appearance of true "Pyrinid" structure in the Lanieriidae, which seem to be a small group of forms phyletically descended from the Holectypidae, and quite independent of the Echinonaidae, may indicate a third parallel line; but, on the other hand, the family may be related to the smaller Discoidiidae.

The Discoidiid type (Plate 66) is remarkable for its extreme complexity and dual nature. The plate-grouping on the adoral surface and ambitus is essentially "triadic," and to judge from the morphogenetic sequence shown in the oral parts, would seem to be the result of intense acceleration from an incompletely Pyrinid structure such as that of *D. dixonii*. It is thus traceable back to the Plesiechinid type. But in the gerontic forms, particularly from the upper part of the Lower Chalk, the occurrence of alternate primaries and demi-plates is too constant and regular to be regarded as the product of abnormality. In a very large cylindrical specimen from the zone of *H. subglobosus* (text-fig. 3, p. 463), in the collection of G. E. DIBLEY, Esq., which was not available when Plate 66 was drawn, column α shows no less than 14 demi-plates alternating (with one exception) with single primaries. They are followed adapically by a curious recrudescence of simple triad grouping in this case, but that is unusual. This development is something new in the order, and is clearly quite independent of the ancestral triad-character of the other cases of complexity. It involves only those plates which, in all but fully developed Pyrinid types, are still primaries, and thus is restricted as a regular structure to the adapical surface. It has no known morphological ancestry or descent within the limits of the order. The frequent, and often extreme, irregularity of the

normally "triadic" portions of the areas is also worthy of comment. Although lapses from perfection might be naturally expected in so elaborate and congested a structure, the fact remains that no such irregularity occurs in those Echinoids whose complexity approximates to that of *D. cylindrica*. It seems explicable only as an expression of the morphogenetic instability which might be associated with transition from one stage of complexity to another, but that other is plainly not an Holectypoid type.

The foregoing considerations may be summarised in the following diagram, which, it may be well to repeat, is not intended to represent true phyletic connections, although these are probably indicated approximately :—



TEXT-FIG. 2.—Table showing the inter-relations of the four types of ambulacral structure in the *Holectypoida*. The middle line in each column represents a more or less static evolution; divergences from it indicate progression or reversion. The line ending in *Discoidea cylindrica* should not pass through *D. dixonii*, but arise independently in *D. subucula*.

(b) *Pre-Holectypoid Evolution.*

In the light of the descriptions and arguments given in Part I of this paper, the search for the morphogenetic "ancestry" of the Holectypoid ambulacrum is soon successful. Such an inquiry becomes narrowed down to the problem of the origin of the Plesiechinid type of ambulacrum, since, if the conclusions in the foregoing section are correct, the ambulacral qualities of the Holectypoida can be traced back, directly or indirectly, to that type of structure. Since Plesiechinus itself is the earliest, or one of the earliest, of the order to appear, and is undoubtedly the most primitive in general characters, the nature of the search is still further simplified. The type of ambulacral structure that immediately preceded that of Plesiechinus would be expected to resemble it very closely, in view of the small departure from Regular qualities shown by the other morphological characters of the genus.

The ambulacrum from which that of the earliest Holectypoida could be derived should possess the following characteristics :—(a) Straight and lanceolate, (b) tuberculate in "triad" fashion, (c) largely built of simple primaries, but with some complexity towards the peristome, (d) the complexity in the stage of association marked by grouping without true combination, (e) the groups consisting of dyads with the oral member large and tuberculate, alternating with separate, single primaries. Further, such an ambulacrum must have been in existence during or shortly before the Liassic period.

There can hardly be any doubt that the preceding paragraph represents an almost complete diagnosis of an early, though not absolutely primitive, Diademoid ambulacrum. Indeed, the ambulacra of Plesiechinus are typically Diademoid, save for the relative proportions and numbers of the tubercles and the very faint tendency to a sub-petaloid structure adapically. As far as the plating-structure is concerned, the forms ancestral to the Holectypoida will have passed beyond the Diplocidarid and Saleniid styles of grouped dyads, and have reached the stage which is represented typically in parts of the areas of the Acrosaleniidæ, intermediate between dyad and triad grouping. The absence of any true triad-groups would imply a less advanced structure than that of the Oolitic species of *Acrosalenia* or *Hemipedina*, but the presence of additional plates between the dyad-groups would involve a progress beyond the stage shown in the Triassic "Diademoid ambulacra" described by BATHER (1909). Since the Liassic period intervenes between the Triassic and the Oolitic, the chronological sequence proves sufficiently convincing. The absence of combination, even at the peristome, and the great preponderance of ungrouped ambulacrals in the areas, are further features that demand a less specialised origin than those known in Oolitic Diademoida.

In view of the history of the development of ambulacral structures sketched in Part I, it may be confidently stated that the Plesiechinid ambulacrum must have been evolved from an area which was definitely Diademoid, but which was less

advanced in the *amount* of complexity than that of the Saleniidæ, and less advanced in the *degree* of complexity than that of Oolitic forms of Hemipedinæ or Acrosalenia. As far as ambulacral characters alone are considered, almost any Liassic Diademoid might be expected to possess the requisite quality, and it would be premature here to attempt to determine the actual genus, or even the family, most likely to have given rise to the *Holectypoida* by direct descent.

It is interesting to note, in view of the conservatism of the *Holectypoida*, that the incorporation of the single primaries with the dyad-groups is postponed until the Cretaceous period; while the resulting triad-groups, which resemble those of *Echinus* in many respects, retain this originally separate plate as a primary in all groups except those of the elaborate ambulacra of *Discoidea cylindrica*.

(c) *Post-Holectypoid Evolution.*

(i) While the time of the origin of the *Holectypoida* occurred in stratigraphical stages whose Echinoid faunas are inadequately known, the period of their specialisation corresponds to those rock-systems that are most replete with palæontological evidence. There is thus an opportunity for more precise knowledge of the relation of the Holectypoid ambulacrum to contemporary and subsequent ambulacral types. It is important to realise, however, that the *Holectypoida* is not the only order of Irregular Echinoidea that appeared in the Liassic period. Omitting further reference to the problematical Loriolella (see FUCINI, 1904), at least one non-Holectypoid genus, *Galeropygus*, occurs in the Upper Lias. In view of this stratigraphical association, it is necessary first to discuss the possibilities of relationship between the ambulacral structures of *Plesiechinus* and those of the primitive Nucleolitoida. There can be little doubt that *Galeropygus* bears the same phyletic relationship to *Nucleolites* and *Clypeus* as that which *Plesiechinus* bears to the *Holectypoida*.

The ambulacrum of *Galeropygus agariciformis* (Plate 68, fig. 1) shows important resemblances, and no less important differences, when compared with that of *Plesiechinus*. The chief resemblances consist of the following characters:—(a) The ambulacra are straight and fairly regularly lanceolate; (b) the adapical parts are very feebly sub-petaloid; (c) the ambulacrals are simple primaries from the apex to a region quite near the peristome; (d) in the orad parts where complexity occurs the plates are grouped on the triad-plan. This series of similar qualities undoubtedly suggests that *Galeropygus* and *Plesiechinus* are homogenetic, even if they are not more intimately connected. The main points of difference are as follows:—(a) The areas of *Galeropygus* are proportionately very narrow throughout their extent; (b) The sub-petaloid adapical parts comprise plates of more slender proportions than those towards and below the ambitus; (c) These “mid-zonal” plates are almost “Bothriocidaroid” in shape; (d) The orad region of complexity is more concentrated, and more elaborate, constituting a well-marked hypophyllode; (e) The

tubercular ornament is fine-grained and diffuse, with but obscure traces of a "triadic" sequence. All of these differences might be regarded as accelerations from the Plesiechinid condition, even if, according to the general plan of ambulacral morphogeny, they present regressive qualities. There would be nothing surprising in a stock (such as that initiated by Plesiechinus) which was in the main conservative, giving rise to a side-branch of more active evolutionary character. Indeed, the rate of acceleration of the Discoidiidae and Echinonoidae in Cretaceous times was, as regards the ambulacra, far more rapid in many respects than that which could have produced Nucleolitid from Plesiechinid structures. As far as stratigraphical evidence is available, Plesiechinus and Galeropygus are practically synchronous in appearance. This fact, while not excluding the possibility of the derivation of the latter through the former, is perhaps more suggestive of their contemporaneous origin from a common stock. At least it shows that the differentiation of the Plesiechinid type cannot have progressed far before the Galeropygus-series arose. While recognising that the direct evidence as to the phyletic relationship between the two genera is fairly evenly balanced, I incline to the view that the Nucleolitid stock diverged from the Holoctypoid after the latter had definitely separated from the Diademoida. This opinion is not based upon ambulacral characters alone, and so cannot be discussed in detail in this place, but it receives considerable support from some features shown in the ambulacra of Nucleolitidae that are more advanced than Galeropygus. From a phylogenetic standpoint the two alternatives are so similar that they cannot have much significance, but morphogenetically considered they would introduce the operation of somewhat different principles.

In Plate 68, figs. 2 and 3, the ambulacra of two Oolitic species of the Nucleolitidae are analysed. It is plain that there are two features in which these late descendants of Galeropygus show marked, but varying, advances beyond the stage of ambulacral specialisation reached by that early form. The petals become more pronounced and at the same time more restricted. The hypophyllodes also become more definite, both in their apical limits, their plating-structure, and the dislocation of their pore-pairs. Whereas the petal of *Nucleolites scutatus*, from the Corallian, is more completely developed than that of *N. quadratus*, from the Cornbrash; the hypophyllode of the older type is far more elaborate than that of the Upper Oolitic species. Except for the absence of expansion and depression, the oral parts of the ambulacra of *N. quadratus* merit the name of phyllodes, while those of *N. scutatus* show very little reduction of the plates. This tendency towards a simplification of plate-complexity in *N. scutatus* is particularly suggestive when its results are compared with the truly extraordinary structures of Trematopygus (Plate 68, fig. 4). There can hardly be any uncertainty as to the close relationship between Trematopygus and Nucleolites. The two were originally classed under the same generic name, and even now some authors accept Trematopygus merely as a sub-genus of Nucleolites. The only species that I have been able to study in detail is *T. faringdonensis*. The

species occurs in one facies only of the well-known Aptian "Sponge-Gravels" of Coxwell, but the peculiar lithological nature of that deposit is admirably adapted for the display of Echinoid sutures. Secondary additions of calcite have been deposited on all available calcareous bases, and elsewhere (finally over all) a thin film of dark-red iron oxide has been spread. This process has raised the surfaces of the coronal plates well above their original levels, and has left the sutural lines unfilled. By gently scraping the surface and rapidly cleaning with hydrochloric acid, it is possible to make the plates appear white, while the sutures are left sharply defined as dark-red lines. I know of no conditions of fossilisation better calculated to make the tracing of sutures at once easy and certain. There is, therefore, no room for doubt that the ambulacral structure illustrated in fig. 4 is absolutely the true one, except in the part where the lines are dotted, and even there the indications of sutures are reasonably plain. I have studied six specimens, and the structure of all of them was practically identical. Morphologically, it is interesting to note that the amount of plate-complexity is greatest in area III, which is the shortest, and least in the longest areas I and V. But the character of the complexity is most unexpected. The relations of the plates are surprisingly like those that characterise *Conulus*; and, to make the comparison with Holectypoid structure more complete, two triad-groups in area IV are precisely similar to those that occupy the greater part of the adoral surface of *Discoidea cylindrica*. When the correspondence in geological age between *Trematopygus* and the early Echinonēidæ and Discoidiidæ is taken into account, a further coincidence appears. To suggest that there is any close phyletic link between *Conulus* and *Trematopygus* would be absurd, but some explanation of their remarkable ambulacral similarity must be forthcoming. In the first place, it is suggested that the extended range of plate-complexity is a result of continuation of the simplification of the hypophyllode indicated in *Nucleolites scutatus*. The degree of concentration of the hypophyllode has become lessened, and its nature more diffuse. But at the same time a great increase in the number of plates affected by complexity has occurred, so that, in this respect, *Trematopygus* would be related to *Nucleolites* much as the Echinonēid type of ambulacrum is to the Plesiechinid. (As an additional correspondence, the oblique shape of the peristome in *Trematopygus* may be cited.) The principle of parallel and synchronous morphogenesis in homogenetic groups is abundantly illustrated by Palæontology, but it is usually restricted to phyletic series of considerable intimacy. If the Nucleolitid series be presumed to have branched off from the Holectypoid stock, the ambulacral structure of *Trematopygus* seems explicable on that principle, though remaining none the less surprising. But if *Galeropygus*, which must surely be claimed as the parent of the Nucleolitidæ, were evolved from some Diademoid ancestor independently of Plesiechinus, the appearance of typically Holectypoid structures in its descendants would hardly be credible. Much more study of the ambulacra of the Nucleolitoida is needed before the suggestions made above can be considered proved, but they seem

to be the only ones possible, in the light of facts and morphogenetic tendencies as yet known.

A somewhat similar, though far less extraordinary, feature is illustrated in Plate 68, fig. 5. *Clypeus sinuatus* has petals in the most complete stage of development attained in the Jurassic period (see Plate 68, fig. 6), and also possesses well-developed phyllodes. But, in the parts of the ambulacra that intervene between the two specialised extremities, the characters shown are distinctly *Holactypoid*. The pore-pairs are triserial, and the tuberculation is very regularly repeated on every third plate. The plates concerned are tending to revert to *Bothriocidaroid* proportions, showing a considerable difference from those similarly situated in *Galeropygus*, and with this reversionary character there appears a regularity of ornament and disposition of the pores that strongly recalls the corresponding features in many *Holactypoida*. In this case, however, regression towards the characters of the ancestral *Diademoid* ambulacrum would probably produce a comparable effect, so that *Clypeus*, considered alone, does not afford very clear evidence as to the relation between the *Holactypoida* and *Galeropygus*.

In connection with these arguments, a strange, but very commonly found detail in the construction of the ambulacra of *Galeropygus*, deserves mention. At a point about midway between the ambitus and the apical plate of the hypophyllode, a solitary demi-plate is often present. It is in areas I and V that this occurrence is most frequent, and in columns Ia and Vb the reduction of the demi-plate is most complete. There is no associated change in the position of the pore-pairs, and the feature appears, in the light of present knowledge, to be a purely gratuitous introduction of complexity. It will be noticed that a comparable development of demi-plates occurs distally in the hypophyllode of *Nucleolites scutatus* (Plate 68, fig. 3), but in that case it is clearly associated with the adoral specialisation. The demi-plates of *Galeropygus* would excite no surprise if they were only occasionally present as trifling imperfections of plating; but their frequent appearance, and symmetrical distribution, seem to indicate that they introduce a real problem for solution. As to the nature of that solution, I am unable to express an opinion.

(ii) The only group of Irregular Echinoidea which is incontestably related in phylogeny to the *Holactypoida* is that of the *Clypeastroida*. But there are two other great series of forms, the *Spatangoida* and the "*Cassiduloida*," which show ambulacral characters that can be compared with those developed in the *Holactypoida*. The following note on the use of the ordinal terms mentioned is necessary, although the questions involved cannot be discussed in detail. In DUNCAN'S classification (followed by SLADEN and JACKSON in both editions of the American translation of ZITTEL), the term *Cassiduloidea* was employed, as a sub-section of the *Spatangoida*, to include all those non-*Holactypoid* Irregular Echinoids that are neither *Echinocorythidæ*, *Clypeastroids*, nor "*Heart-Urchins*." Under this heading, the groups which contain *Conulus*, *Pyrina*, and *Amblypygus* were comprised. These

forms are here transferred to the Holectypoida. The remainder of the sub-Order was composed of the "Echinobrissinae," Cassidulidæ, and Collyritidæ. GREGORY (1900) included in the sub-order Asternata much the same series of forms, with the exception of the Conulus-group and the Collyritidæ, which were relegated to the Holectypina and Sternata respectively. Deleting those genera that are here classed with the *Holectypoida*, GREGORY'S two families of Echinonöidæ and Nucleolitidæ, with the addition of the sub-family Clypeina [e] of the Cassidulidæ, comprise most of the Jurassic and Lower Cretaceous non-Holectypoid genera, while the remainder of his Cassidulidæ includes Upper Cretaceous and Tertiary types. The former group is, I believe, entirely distinct from the latter in phylogeny, as in many important points of morphology, and I propose that the two sections should be styled "Nucleolitoida" and "Cassiduloida" respectively. (The Collyritidæ would probably constitute an aberrant family of the former order.) The name Spatangoida is here restricted to those families (except the Collyritidæ) which GREGORY classed as "Atelostomata Sternata." The classification proposed may be summarised as follows, the family names being kept, as far as possible, in agreement with those applied by GREGORY :—

Order : NUCLEOLITOIDA . . .	Nucleolitidæ.
	Clypeidæ.
	Catopygidæ.
	Collyritidæ.
Order : CASSIDULOIDA . . .	Cassidulidæ.
	Echinolampidæ.
	Eolampidæ.
Order : SPATANGOIDA . . .	Echinocorythidæ.
	Spatangidæ.
	Palæostomidæ.
	Pourtalesiidæ.

These three orders are all characterised by the presence of some degree of petaloid structure in their ambulacra. In the Nucleolitoida, the leaf-like appearance of those parts of the areas is due to a real dissimilarity of the pores. This feature is shown in an extreme degree in *Clypeus* (Plate 68, fig. 6), where the outer pores are in the form of elongated slits, and the inner ones small and round. In a rudimentary condition, this character is met with in *Galeropygus* and *Plesiechinus*, and it is almost obsolete in the Collyritidæ. In the Cassiduloida and Spatangoida, the petals are usually more restricted in extent than in the older order, and derive their appearance from a wide separation of the pores, with or without a superficial groove connecting the pores of a pair. The pores are practically similar, and often differ from those of the extra-petaloid regions merely in their greater separation and size (see Plate 69, fig. 1). Most of the Clypeastroida have pores of this quality, so that

the slit-like pores of the Nucleolitoida seem to be almost restricted to Mesozoic Echinoids, and to have attained their fullest development (in such genera as *Clypeus* and *Pygurus*) in the Oolitic period.

(iii) It will be most convenient, in returning to morphological arguments after the foregoing systematic digression, to consider the relation between the *Holactypoid* ambulacrum and that of the *Spatangoida*, before discussing the *Cassiduloida*.

The *Spatangid* ambulacrum is typically composed of primaries throughout, and these are mostly of a *Bothriocidaroid* type (with very reduced pore-pairs), except in the petals and peristomial regions. Not infrequently occasional demi-plates may occur in the petals, especially when these are curved (see Plate 69, figs. 1 and 2); and, in some cases, more or less elaborate secondary complication may be developed in the anterior ambulacrum (Plate 69, figs. 2-5). The morphogenetic position of such ambulacra has been discussed in Part I, Sections 1 (c) and 2 (e). There is never, so far as I am aware, any definitely triserial structure either in normal or specialised areas in this order. Since the *Spatangoida* do not appear before the uppermost Jurassic stages, it seems an inevitable supposition that they must be phylogenetically descended from either the *Holactypoida* or the *Nucleolitoida*. Their independent origin from any Regular stock is rendered improbable by the definite progress in an exactly opposite direction that had been made by the *Diademoida* by that time. As regards the ambulacra, there is a far closer apparent accord between the *Nucleolitoida* and the *Spatangoida* than between the latter and the *Holactypoida*, but in neither case is there much approximation. The *Nucleolitoida* have petals, but these are constructed on a different plan from those of the *Spatangoida*; it is more possible to compare the adapical pores of *Pileus* with those of a *Spatangid* petal than those of a *Nucleolitid*. The *Spatangoida* have specially constructed regions around the peristome, recalling in position, and probably agreeing in function with, the phyllodes of the *Nucleolitoida*, but there is no trace of phyllodal plating-structure. The oral plates of the *Spatangid* ambulacrum are only less *Bothriocidaroid* than those of the ambitus. Both orders have "biporous" ambulacrals, and this may possibly prove to be a feature that really unites them in spite of the great differences in other respects. But the *Echinonoidæ* seem to show a stage in what may be regarded as a secondary method of the production of this character.

There is one morphological feature in the ambulacra of the later *Pygasteridæ* which may possibly serve to link the simplified *Spatangid* plating with the inevitably more complex structures that preceded it. *Pygaster* itself shows an almost perfect abandonment of plate-complexity towards the peristome (Plate 65, figs. 3 and 4), and there is reason to believe that the Cretaceous genera *Macropygus* and *Anorthopygus* were even more completely simple in this respect. This may seem a very small point of resemblance, and insufficient to serve as a basis for morphogenetic or phylogenetic argument; but the fact remains that the later

Pygasteridæ are the only Echinoids of the Upper Jurassic and Lower Cretaceous periods in which a tendency to ambulacral simplification is seen. The Collyritidæ apparently achieved a similar result in Bajocian times. The correspondence in the structure of the apical system of Anorthopygus and that of the Spatangoida (see HAWKINS, 1912, *a*), adds considerably to the bulk of the evidence that makes reasonable the tentative suggestion that there may be a tendency towards the Spatangoid type in the simplification of the Pygasterid ambulacrum.

(iv) There is more evidence for the formulation of an hypothesis as to the morphogenetic relations between Holectypoid and Cassiduloid ambulacra. Were it not for the Pycinid nature of its ambulacral plating, Amblypygus would naturally be classed as a primitive Echinolampid with rudimentary phyllodes. If Amblypygus had no petals, it would almost inevitably be included among the Conulinæ. Further, Conulus has a strongly triserial arrangement of pore-pairs around the peristome which could be modified into a true phyllode by trifling addition to the complication already present in the plates. By slight modifications in the nature of the pore-pairs, and by a gradual simplification of the ambulacral plating (two morphogenetic processes that certainly occurred during the evolution of the *Holectypoida* themselves), the ambulacrum of the Echinonæidæ could readily have given rise to that of the Cassiduloida. Amblypygus seems to show the modification of the apical pores, while Conulus has structures preliminary to the modification of the oral pores. All that is needed to complete the history of the transformation is a case in which the plating is in process of simplification. That such evidence will be found in Cretaceous or Lower Tertiary Cassiduloida I am confident. In spite of the superficial resemblance between many of the Cassiduloida and Nucleolitoida, in both ambulacral and other structures, there seems reason to believe that it must be ascribed to the principle of heterogenetic homœomorphy. If the suggestions as to the qualities of Micropetalon, given in Section 1 of this part of the paper, should prove to be correct, that small form would serve as an ontogenetic support to the belief in the derivation of the Cassiduloida through the Echinonæidæ.

(v) It is but rarely that such relative certainty as to the phyletic connection between two orders can be found as that which, by universal consent, obtains in the case of the *Holectypoida* and Clypeastroida. The actual family from which the latter group arose is definitely indicated. GREGORY (1900) emphasized this transition in correcting the indefensible generic term "Echinites" of DUNCAN into the suggestive name of "Protocyamus." His correction was no more legitimate than the original name, since *Discoidea subucula*, the type of the proposed genus, is already the type of Discoidea. But the significance of the name stands. The characters of the apical system alone are sufficient to bind the Discoidiidae very closely to the Clypeastroida, but there is abundant confirmatory evidence.

Nevertheless, in the matter which concerns the present work, there is a discordance in ambulacral structure in the two groups that, at first sight, seems

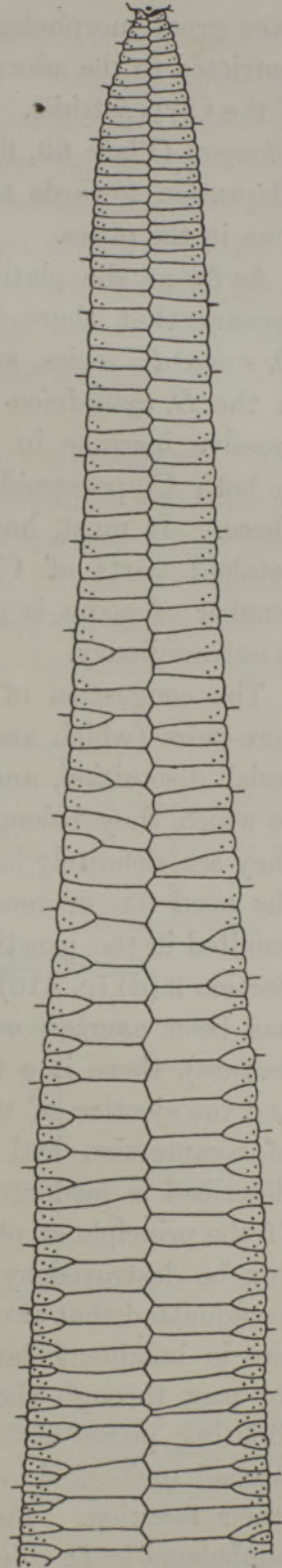
almost sufficient to outweigh the many similarities. Between the intensely complex ambulacral plating of the larger Discoidiidae and the "Bothriocidaroid" ambulacrals Clypeaster, and between the minute apicad pores of the Cretaceous family and the highly developed petals of the Tertiary group, a great gulf seems to exist. When to these differences is added the anomalous distribution of the non-petaloid pores of the Clypeastroids, scattered as they are over ambulacral and interambulacral plates in defiance of the rules governing the structure of all other Echinoids, it is seen that there is a serious morphogenetic problem if the phylogenetic sequence is to be upheld. It is with surprise, not unmixed with satisfaction, that I have been able to trace the connection between the Discoidiid and Clypeastroid ambulacra in such detail that the morphogenetic relationship between the two sets of structures would need to be postulated even without the support of arguments based on other features.

The modifications of ambulacral structure found among the Clypeastroida are capable of reference to three types. The first, which may be termed Fibulariid, shows short and not very marked petals containing large, similar pores set in distant series owing to the considerable height of the plates; and more or less "Bothriocidaroid" other parts, in which each plate is perforated by numerous minute pores, either arranged in transverse linear series near the apicad margin, or occurring in congested groups. The podial pores seem to be restricted to the ambulacral areas. The remaining two types, Scutellid and Clypeastrid, resemble one another (and differ from the Fibulariid) in the great elaboration of the petals, the typically "Bothriocidaroid" shape of the other ambulacrals, and the dissipation of the extra-petaloid pores over the interambulacral areas. The Scutellid type has petals composed of very great numbers of excessively slender primaries; in the Clypeastrid type the corresponding plates are of greater height, and are arranged on the plan of alternating primaries and demi-plates (see Plate 68, fig. 7). In all three types there are two features that are constant in character though not in quality. The pores of the petals are very nearly similar, the petaloid effect being attained by the wide separation of the individuals of a pair, and the occurrence of a well-marked superficial groove passing from one to the other along the transverse suture. The extra-petaloid pores are exceedingly minute (rarely visible except in stained or sectioned specimens), and are unlike those of any other series of Echinoids in their departure from the "one plate, one pore-pair" principle of distribution.

The Fibulariid and Scutellid types are alike in the simplicity of their plating, and the latter is clearly the morphogenetic outcome of intensification of the tendencies present in the former. In plating-structure, the Clypeastrid ambulacrum is almost unique, and the regular alternation of primaries and single demi-plates is very different from any familiar types of ambulacral complexity. Both Fibulariid and Clypeastrid types occur in the Lower Eocene, if not in the Upper Cretaceous;

the Scutellid type is slightly later in appearance. It is, therefore, necessary to seek for morphological "ancestors" for the first two types only. The extreme difference between the sparsely plated ambulacra of *Fibularia* and the crowded and complex petals of *Clypeaster* makes it difficult to believe that these two types could have arisen at one and the same time from a common ancestral type; although, in default of evidence to the contrary, such a suggestion might be made.

In the Discoidiidae there are two well-marked types of ambulacral structure, which appear to show divergent morphogenetic trends. On the one hand, the small forms typified by *D. subucula*, and succeeded by *D. dixonii*, have relatively simple ambulacra with a tendency to the development of increasing simplicity adapically, and increasing complication adorally. *D. dixonii* (Plate 67, fig. 2) has high apicad ambulacrals, and Pyrinid ambital and adoral plates. The shape and proportions of the apicad plates are very closely analogous with those of *Fibularia*. But the complex triad-grouping of the rest of the ambulacrum of *D. dixonii* is (or appears to be) in violent contrast to the "Bothriocidaroid" plating of the corresponding regions of all Clypeastroids. None the less, I am convinced that the contrast is more apparent than real, but the reasons for this belief will be better indicated in a discussion of the other Discoidiid type in its relations to the Clypeastrid. In *D. cylindrica* (Plate 66) the apicad plates seem to retain more or less "Cidaroid" proportions, while those at and below the ambitus possess complexity and congestion of a remarkable kind. In high-zonal forms, and especially in gerontic individuals, a considerable sequence of the plates of the adapical surface assumes the plan of alternate primaries and demi-plates. The fine specimen (58.2 mm. in diameter, 41.9 mm. in height, collected by G. E. DIBLEY, Esq., from the zone of *H. subglobosus* at Oxted) from which the accompanying text-fig. 3 is taken, is the largest example of the species that I have seen. (The original of Plate 66, fig. 1, has a diameter of 57 mm.) It also shows the longest continuous series of alternate primaries and demi-plates that I have detected, although there is an almost complete absence of the sporadic precocious apicad complexity that is usual in large specimens from this horizon. It is a striking fact, and one that must surely



TEXT-FIG. 3.—Ambulacrum V of a gerontic specimen of *Discoidea cylindrica*, from the apex to the ambitus, showing the great development of "Clypeastrid" primaries and demi-plates.

have great morphological significance, that such a type of structure is absolutely restricted to the adoral surface of the later members of this species and the petals of the Clypeastridæ. The similar plating of some parts of the petals of *Heteraster oblongus* (Plate 69, fig. 2) is hardly comparable, since in that case it is clearly an adaptation towards the accommodation of more plates in one column of the area than in the other.

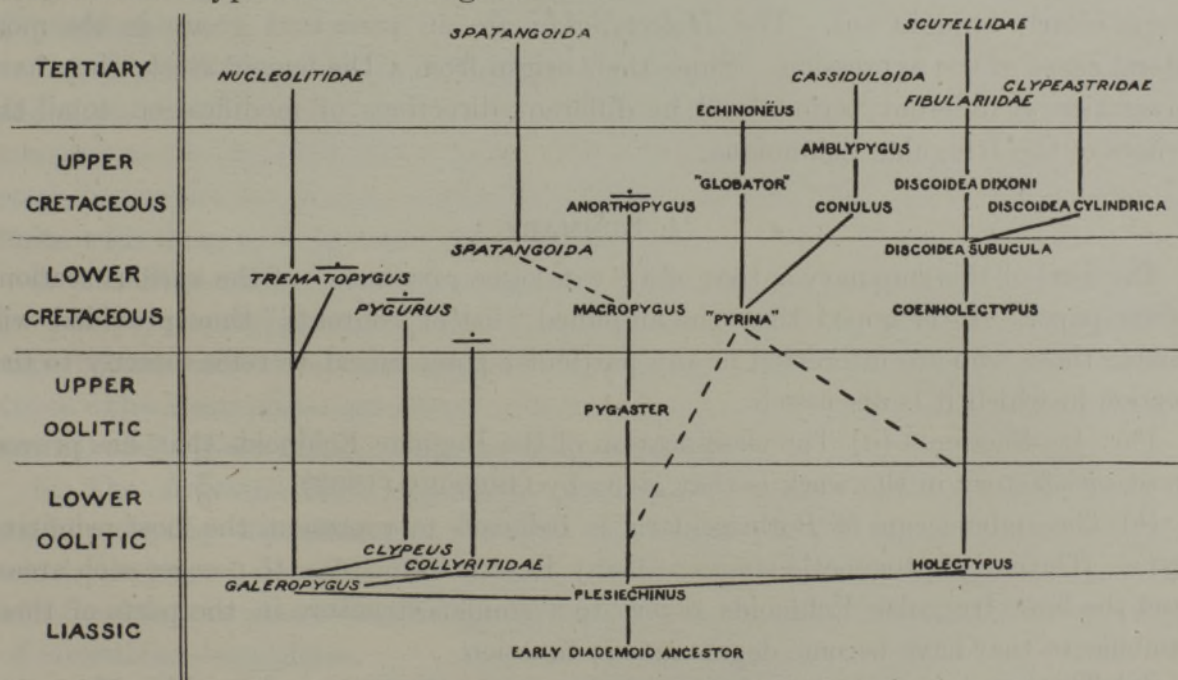
As far as the plating of the apicad parts of the ambulacra is concerned, it thus appears that there is a tendency towards the Fibulariid type shown in the *D. subucula* series, and an equally marked tendency towards the Clypeastrid type in the *D. cylindrica* series. In both lineages of the Discoidiidae there is a progressive increase in the complication of the adoral parts of the ambulacra, while in both Clypeastroid groups plate-simplicity seems to be present in its ultimate phase. It must, however, be borne in mind that the simplification of the extra-petaloid parts of Clypeastroid ambulacra is more apparent than real, for the number of podia is greatly in excess of that of the plates, and their distribution is extraordinary.

The congestion of the ambital ambulacrals in *D. cylindrica* is such that the pore-pairs (which are very minute) are compelled to take on an irregularly multi-serial disposition, and even so are scarcely to be accommodated within the plates to which they belong. Many of the demi-plates of that region are so small that they are definitely inadequate to contain the peripodia. It may be presumed that the need for, or tendency towards, the production of great numbers of podia has resulted in the exertion of "growth-pressure" on the plates involved. In Part I, Section 2 (*d*) (p. 410), it has been shown that when comparable excessive pressure has been exerted on the ambulacrals of *Echinus esculentus* (as a teratological feature), there is a tendency towards the complete destruction of the demi-plates, and the ejection of their pore-pairs into the adjacent interambulacra. The degree of compression and reduction in the areas of the specimen of *Echinus* there described is moderate in comparison with that normally developed in *D. cylindrica*. If the principle of plate-complexity stated on p. 407 is sound, and ambulacral plates can be destroyed by excessive compression and consequent reduction, then it must be admitted that two-thirds of the ambulacrals of the ambital region in *D. cylindrica* are in imminent danger of obliteration. On their resorption the podia would need to pass through the test in some neighbouring part, while the removal of the limiting plates with which they were originally associated would enable them to spread unchecked over as wide a region as was compatible with the exercise of their function. Further, the nature of the plating of the adoral parts of the ambulacra in *D. cylindrica* is such that the primary plates would show characteristic "Bothriocidaroid" proportions if the minute demi-plates were destroyed.

The number of minute, dissipated pores that perforate a Clypeastrid corona is very great; and, whether they are in pairs or not (a question to which I have been unable

to find a reliable answer), is in excess of the proportionate numbers of pore-pairs in the Discoidiid ambulacrum. But since podia are produced by "budding" from the radial canal, and those of Clypeastroids are, in many cases, developed from branches of that vessel rather than from the main trunk, there seems no logical limit to the rate of their increase when once the rule of association with separate plates has been broken. Although at the outset it would have seemed rash, if not utterly speculative, to suggest that the complex areas of *D. cylindrica* are the direct morphological predecessors of the apparently simple areas of Clypeaster, the various tendencies of ambulacral development that have been indicated throughout the paper all seem to make such a suggestion not only reasonable but inevitable.

It is unlikely that ontogenetic study of recent types of the Clypeastroida would make it possible actually to trace the destruction of the Discoidiid ambulacrals. When once simplicity of plating had been acquired in morphogeny, ontogenetic acceleration would speedily tend to drop the vestigial production of the demi-plates, and the only indication of the previous existence of such structures would appear in the great numbers of podia in proportion to the plates. This indication is maintained in all Clypeastroids throughout life.



TEXT-FIG. 4.—Table showing the relation of the ambulacral structure of the *Holoctypoida* with that of the other irregular orders. When generic names are used, the genera are intended to serve as types of structure, and no necessary phyletic association is involved. A transverse line with a dot above indicates the termination of a morphogenetic series

The ambulacra of the Clypeastroida thus seem to have a double morphogenetic origin. The Fibulariid type can be traced back to the later members of the *Discoidea subucula*-series, while the Clypeastrid type has its forerunner in

D. cylindrica. Again, the petaloid parts of the Clypeastroid types are structurally simple, although a peculiar type of restrained complexity occurs in those of the Clypeastridæ; but the extra-petaloid parts have been simplified (as regards plating) by the somewhat heroic method of the destruction of most of their constituent plates, and the scattering of their pores. The attainment of the "Bothriocidaroid" stage of reversion in Spatangid ambulacra has involved a corresponding reduction in the numbers of podia; it is doubtful whether the comparison of the high, hexagonal ambulacrals of Clypeaster with those of Bothriocidaris is justifiable. So far from showing true reversionary simplification, the ambulacra of the Clypeastroida represent an ultimate phase of plate-complexity, which gives a deceptive appearance of simplicity.

This section, and the whole paper, can be best closed by an attempt to express the conclusions reached in the form of a morphogenetic table (text-fig. 4).

It is at least probable that many of the connecting lines in the "tree" have a real phylogenetic meaning; but it is unlikely that lines of descent calculated from a single series of data will in all cases coincide with the true course of phyletic evolution. In spite of the many uncertainties involved in the diagram, one point seems clearly brought out. The *Holactypoida* are an annectant group in the most literal sense of the expression. Since their origin from a Diademoid stock, they have given rise, at different periods and by different directions of modification, to all the orders of the Irregular Echinoidea.

4. SUMMARY.

The form of this summary is that of a "catalogue raisonnée" of the various sections of the paper. It is hoped that the amplified "list of contents" thus provided will enable those who are interested in any particular point raised to refer directly to the section in which it is discussed.

Part I.—Section 1 (*a*) The classification of the Regular Echinoids that has proved most satisfactory in the work is that given by GREGORY (1900).

(*b*) The ambulacrum of Bothriocidaris is believed to represent the most primitive type. The early ontogenetic stages of many Recent forms seem to possess such areas, and the later Irregular Echinoids revert to a similar structure in the parts of their ambulacra that have become degenerate in function.

(*c*) The trend of evolution of the ambulacrum in the early and Regular Echinoids was two-fold. The number of podia (*i.e.*, plates) was more or less steadily increased from their scarcity in Bothriocidaris, and the plating-structure had consequently to be adjusted to allow of multiplication without the development of coronal fragility. In the "Perischoechinoida" there were two distinct lines of ambulacral morphogenesis—the "Palæechinoid," in which the plates retained their disposition in two columns and became much lowered, and the "Melonechinoid," in which "klasma-plating" produced multicolumnar areas, suited to the requirements of flexible tests, but impracticable

for rigid ones. By a flexing of the areas, the Palæechinoid type became modified into the "Archæocidaroid" type, which is essentially like the true Cidaroid type of later periods. Klasma plates are believed to be essentially similar to the reduced plates of elaborate Euechinoid ambulacra, and to have assumed their peculiar arrangement under the same influences that produce a like distribution of the ambulacrals of the Echinothuriidæ. Attention is drawn to the remarkable similarity between the simpler klasma-plating of some Palæozoic Echinoids and the secondary complexity that occurs in area III of *Echinocardium cordatum*. It is suggested that the latter development marks a reversionary tendency in the Spatangidæ no less than the "Bothriocidaroid" nature of the obsolete ambulacrals of that family.

(d) The Cidaroid type of ambulacrum represents the best obtainable result, as regards mechanical strength, when the plates are multiplied but not specially modified. All Euechinoid ambulacra can be traced back to this stage of development, unless they are so reversionary that they exhibit only Bothriocidaroid plating. Incipient complexity is found in the strongly curved ambulacra of Paracidaris, and incipient diversity of ornament and size (almost amounting to grouping) occurs in the Diplocidaridæ.

(e) i. Typical Saleniidæ have "dyad-groups" (which may become dyad-compounds adorally) almost throughout the area, thus showing but a small morphogenetic advance on the Diplocidarid condition. The Acrosaleniid ambulacrum shows a further stage in complexity; simple, uncombined plates occur between the dyads, and usually unite with them to form triads below the ambitus.

ii. The Diademina show "Acrosaleniid" triads in typical cases, but these compounds (or groups) often tend towards an "Arbacioid" structure. In several forms two triads may become united to form hexad "super-compounds." In many Upper Jurassic types extra demi-plates are added within the compounds, and this condition becomes normal and regular in the Cretaceous Phymosomatidæ.

iii. The Arbacina have typically "Arbacioid" triads, but these are liable to modification by the same two processes that affect the Diademoid compounds from which they are believed to be derived. The compounds may be elaborated by the addition of extra plates to their apical margins, as an alternative to the incorporation of interstitial demi-plates.

iv. The Echinina with "Echinoid" triads show a remarkable constancy of structure, although tendencies to the production of "super-compounds" occur. In the Strongylocentrotidæ and Echinometridæ the incorporation of interstitial demi-plates is progressively carried to a high degree of elaboration. The many plated multiporous compounds of Heterocentrotus have Bothriocidaroid proportions and relations, more than Bothriocidaroid strength, and include a vastly greater number of podia; they represent the successful solution of the problem of podial multiplication without coronal weakness.

Section 2 (a) Slight additions and modifications are made in the terminology applied to ambulacral structures.

(b) A distinction is drawn between "grouped" and "combined" plates. The former phase of complexity is preliminary to the latter; it is characterised by the maintenance of the transverse sutures of the plates without reduction of sutural tissue. The controversy as to the cause of the production of compound plates is considered, and the conclusion is reached that while the *reduction* of plates is to be ascribed to "growth-pressure" (DUNCAN) of various kinds, *combination* is almost always dependent originally upon the growth of large tubercles (LAMBERT), which serve to bind the components together. While "combination" is progressively intensified in the Regular Echinoidea, it is believed to be absent from the Irregular forms, where "grouping" (often very elaborate in character) represents the highest degree of complexity attained.

(c) The first phase of plate-complexity is marked by a grouping of previously simple primaries into dyads, followed by their combination. Subsequently (or perhaps before combination is complete), alternate simple plates appear between the dyads, and these gradually unite with the dyads adoral to them, forming Diademoid triads. More elaborate compounds (or groups) may be produced by a repetition of this process (*e.g.*, Arbacia), or by the intercalation of extra plates (usually reduced) within the compounds (*e.g.*, Phymosoma or Heterocentrotus).

(d) The production of demi-plates is ascribed to an attempt to reduce the quantity of sutural tissue in a compound rather than to actual compression. On the other hand, occluded and included plates appear to result from the operation of "growth-pressure." A detailed analysis of certain abnormal developments in the ambulacra of Echinus shows (i) that sutures can be obliterated by intense "crushing"; (ii) that plates may become gradually resorbed under the influence of the same force, their podia either undergoing atrophy or being driven into the interambulacra; and (iii) that in so stereotyped a style of structure as the "Echinoid," plates that are introduced between the compounds suffer reduction and ultimate resorption, while those introduced into a compound may be incorporated to form permanent tetrads like those of Strongylocentrotus. A similar analysis of the ambulacrum of a gerontic Heterocentrotus seems to indicate that the high, complex compounds of this form are really super-compounds of a Strongylocentrotid pattern, increased and modified.

(e) It is shown that, in the Regular Echinoids, plate-complexity is always present in those forms which have strongly adhesive podia, and that the two conditions seem to vary in direct proportion. Complication in the ambulacra of the Irregular Echinoids is always associated with those parts of the areas that possess important functional value. According to the distribution of utility, the rate of production of plates may vary in the different areas (*e.g.*, *Echinocardium cordatum*), or even in the separate columns of one area (*e.g.*, *Heteraster oblongus*). Ambulacral complication in

the Irregular forms seems never to result in combination, and usually produces structures closely similar to those of the simpler Palæozoic types.

(f) It is argued that JACKSON'S principle of "localised stages of development" has only a partial application to ambulacra of post-Palæozoic Echinoids. The ontogenetically early plates may become much modified by pressure, and so lose their originally simple character. However, in the actual composition of compound plates the principle seems to hold good. In the Irregular Echinoids the principle fails almost completely to account for the observed structures. The apical plates of a Spatangid petal are in a far higher state of development than those of the mid-zone, and the oral-plates of a Cassiduloid phyllode are even more complex, though ontogenetically young. In these forms, "localised function" is the determining factor in the morphogeny of ambulacrals.

Part II.—Section 1. Detailed descriptions of the ambulacra of representative genera and species of the *Holectypoida* are given. There are four main types of structure in the order. The "Plesiechinid" type has "Acrosaleniid" triad-groups adorally, with some more or less irregular grouping in the region of maximum tuberculation. This type occurs in *Plesiechinus*, the *Holectypidæ*, and *Discoidea subucula*. The "Pygasterid" type has completely simple structure (save for ornament and ambital "tubercle-grouping"). It occurs only in the later *Pygasteridæ*. The "Pyrinid" type recalls the "Echinoid" triads of many Regular Echinoids, and has triad-groups (with one demi-plate) almost throughout the area. It occurs in an incomplete phase in *Discoidea dixonii*, and in full development in the *Lanieriidæ* and the *Echinonoidæ*, including *Amblypygus*. The "Discoidiid" type is confined to the series of forms specifically united as *D. cylindrica*. It shows extreme "triad" complexity adorally (usually carried out with marked irregularity), and, in gerontic forms from high zones, a tendency to the development of alternate primaries and demi-plates on the adapical surface.

Section 2. In the Jurassic *Pygasteridæ* feeble attempts at the development of petals were made, but they were abandoned by the Cretaceous members of the family, and do not occur in the other families. It is considered doubtful, however, that the *Holectypoid* podia could exert a strong adhesive power, in view of the practically uniserial arrangement of the pores and absence of plate-combination. The congestion of pores near the ambitus is believed to indicate the concentration of podial functions to that region, and these functions would be largely sensory, especially in Cretaceous forms which lived on loose sand or ooze. It is suggested that the extremely crowded, and strongly convergent, filamentous podia of the adoral parts of the *Discoidiid* ambulacra may have served to pass food-particles from the ambitus to the mouth. The *Pyrinid* podia are known to have some slight adhesive powers, but these are chiefly employed in holding small objects as a protective cover for the test.

Section 3. i. The *Plesiechinid* type of ambulacral structure is regarded as primitive for the order. By a steady simplification the *Pygasterid* type must have

evolved from it. The Pynid type can be seen to develop from the Plesiechinid in such a sequence as that of *Discoidea subucula* and *D. dixonii*, but is not likely to have been derived through those species. The Discoidiid type is evidently an elaboration of an incomplete Pynid type, and its extreme variability in detail (a feature strongly contrasting with the general characters of Echinoid ambulacra, however elaborate), is believed to indicate morphogenetic instability preceding fresh modification.

ii. The Plesiechinid type is almost identical in essential characters with the structure shown in *Acrosalenia*, and marks an intermediate stage between the formation of dyads and that of triads. Such a morphogenetic phase will have been general among Liassic (especially Lower Liassic) Diademoida; so that, on ambulacral evidence alone, the origin of the Holoctypoid ambulacrum can only be definitely traced to an early Diademoid form.

iii. A new classification of the non-Holoctypoid Irregular Echinoids is proposed. While the ambulacra of *Galeropygus* (the earliest Nucleolitoid) might well have arisen from Diademoid types independently of the Holoctypoida, the characters shown by later modifications in the order (especially by *Trematopygus*) are believed to indicate that the Nucleolitoid line of evolution branched from that of Plesiechinus. There is little evidence as to the relation of the Holoctypoid ambulacrum with that of the Spatangoida (*sens. str.*), but it is noteworthy that the later Pygasteridæ, alone of Upper Jurassic Echinoids, show that progressive simplification of ambulacral plating which must have preceded the development of the Spatangid ambulacrum. The Cassiduloid ambulacrum is believed to be traceable to that of *Conulus* (nearly through that of *Amblypygus*), and the hope is expressed that stages in simplification of plating will be found in Eocene forms. Micropetalon is believed to be an early ontogenetic stage of some Cassiduloid, showing mainly Echinonæid features. The Clypeastroida show two distinct types of ambulacra, the Fibulariid (leading to the Scutellid) and the Clypeastrid. The former is directly foreshadowed in the later species of the small Discoidiidæ, while the latter is clearly derived from the Discoidiid ambulacrum. The anomalous scattering of the podial pores in the Clypeastroida is ascribed to the destruction of their containing plates by an overdevelopment of "plate-complexity," and the apparently "Bothriocidaroid" ambulacra of their adoral surfaces are thus not analogous with the similar plates in other Irregular groups. While in all other Irregular Orders the evolution of the ambulacra has been in the main reversionary, in the series Plesiechinus—*Discoidea*—Clypeastroida, it has followed lines similar in many respects to those normally taken in the Diademoida. While *Heterocentrotus* shows the culmination of plate-complexity with combination, *Clypeaster* represents the acme of plate-complexity without combination carried to the ultimate phase of plate-destruction.

5. REFERENCES TO PUBLICATIONS QUOTED.

The following list does not include a tithe of the papers and books which have been utilized in the course of the work. But it would have entailed the construction of a catalogue of unwieldy length and of little value, had the titles of all the papers that have been consulted been incorporated. Only those publications, to which specific reference is made in the preceding pages, are catalogued here:—

- (1) AGASSIZ, A., 1874. "Revision of the Echini.—Part IV," 'Mem. Mus. Comp. Zool.,' Harvard, No. 7.
- (2) BATHER, F. A., 1909. "Triassic Echinoderms of Bakony," 'Res. wissenschaft. Erforsch. Balatonsees,' Bd. 1, Teil 1, Pal. Anhang.
- (3) CHADWICK, H. C., 1914. "Note on an Imperfectly Developed Specimen of the Sea Urchin (*Echinus esculentus*)," 'Proc. Zool. Soc.,' 1914, pp. 65–68.
- (4) CLARK, W. B., and TWITCHELL, M. W., 1915. "The Mesozoic and Cenozoic Echinodermata of the United States," 'U. S. Geol. Survey, Monogr.,' vol. 54.
- (5) COTTEAU, G., and TRIGER, J., 1859. 'Échinides du Département de la Sarthe, considérés au point de vue Zoologique et Stratigraphique (1855–1859).'
- (6) COTTREAU, J., 1913. "Les Échinides Néogènes du Bassin Méditerranéen," 'Ann. Inst. Océanogr.,' pp. 1–193, Plates 1–15.
- (7) DOLLO, L., 1910. "La Paléontologie Éthologique," 'Bul. Soc. Belge Géol. Pal. et Hydr. Mém.,' Tome 23, pp. 377–421, Plates 7–11.
- (8) DUNCAN, P. M., 1885 (A). "On the Anatomy of the Ambulacra of the Recent Diadematidæ," 'J. Linn. Soc. Zool.,' vol. 19, pp. 95–114, Plate 5.
- (9) *Idem*, 1885 (B). "On the Structure of the Ambulacra of some Fossil Genera and Species of Regular Echinoidea," 'Q. J. Geol. Soc.,' vol. 41, pp. 419–453.
- (10) *Idem*, 1889. "A Revision of the Genera and Great Groups of the Echinoidea," 'J. Linn. Soc. Zool.,' vol. 23, pp. 1–311.
- (11) DUNCAN, P. M., and SLADEN, W. P., 1884. "Description of the Fossil Echinoidea from the Khirthar Series of Nummulitic strata in Western Sind," 'Pal. Indica,' ser. 14, vol. 1, Part 3, pp. 109–246, Plates 21–38.
- (12) *Idem*, 1885. (A) "A description of the fossil Echinoidea of Western Sind," Fasc. 5. The Gaj series (Miocene) 'Pal. Indica,' ser. 14, vol. 1, Part 3, pp. 273–367, Plates 44–55.
- (13) *Idem*, 1885. (B) "On the family Arbaciadæ," Gray.—Part I. "The morphology of the test in the genera *Cælopleurus* and *Arbacia*," 'J. Linn. Soc. Zool.,' vol. 19, pp. 25–57, Plates 1 and 2.
- (14) FUCINI, A., 1904. "*Loriolella ludovici*, Mgh. Nuove genere di Echino irregolare," 'Ann. Univ. Tosc.,' Pisa, vol. 24, pp. 1–9, Plate 1.
- (15) GREGORY, J. W., 1900. "The Echinoidea [in] Lankester's Treatise on Zoology," vol. 3.

- (16) HAWKINS, H. L., 1911. "On the Structure and Evolution of the Phylloides in some fossil Echinoidea," 'Geol. Mag.,' Dec. 5, vol. 7, pp. 257-265, Plate 13.
- (17) *Idem*, 1912. (A) "On the evolution of the apical system in the *Holactypoida*," 'Geol. Mag.,' Dec. 5, vol. 9, pp. 8-16, Plate 2.
- (18) *Idem*, 1912. (B) "The Classification, Morphology, and Evolution of the Echinoidea *Holactypoida*," 'Proc. Zool. Soc.,' 1912, pp. 440-497.
- (19) *Idem*, 1913. (A) "The Anterior Ambulacrum of *Echinocardium cordatum*, Penn.; and the origin of compound plates in Echinoids," 'Proc. Zool. Soc.,' 1913, pp. 169-181, Plate 26.
- (20) *Idem*, 1913. (B) "On *Lanieria* (Duncan) a remarkable genus of the *Holactypoida*, with a preliminary note on the tendencies of Echinoid evolution," 'Geol. Mag.,' Dec. 5, vol. 10, pp. 199-205.
- (21) *Idem*, 1916. "A remarkable structure in *Lovenia forbesi* from the Miocene of Australia," 'Geol. Mag.,' Dec. 6, vol. 3, pp. 100-105.
- (22) *Idem*, 1917. "Morphological studies on the Echinoidea *Holactypoida* and their Allies.—I. Systematic discussion of the genera *Pygaster*, Agassiz, and *Plesiechinus*," Pomel. 'Geol. Mag.,' Dec. 6, vol. 4, pp. 160-168.
- (23) JACKSON, R. T., 1899. "Localised Stages in Development in Plants and Animals," 'Mem. Soc. Nat. Hist.,' Boston, vol. 5, No. 4.
- (24) *Idem*, 1912. "Phylogeny of the Echini, with a revision of Palæozoic Species," 'Mem. Soc. Nat. Hist.,' Boston, vol. 7.
- (25) *Idem*, 1914. "Studies of Jamaica Echini," Carnegie Inst., Washington, No. 182, pp. 139-162, Plate 1.
- (26) LAMBERT, J., 1900. "Étude sur quelques Échinides de l'Infra-Lias et du Lias," 'Bull. Soc. Sci.,' Yonne, vol. 53, Part 2, pp. 3-57, Plate 1.
- (27) *Idem*, 1906. [In M. BOULE and A. THEVENIN.] "Paléontologie de Madagascar," Part 1, 'Ann. de Paléont.,' Tome 1, pp. 10-14.
- (28) *Idem*, 1911. "Étude sur les Échinides crétacées de Rennes les Bains et des Corbières," 'Mem. Soc. Sci. Aude,' Tome 22, pp. 66-183, Plates 1-3.
- (29) LAMBERT, J., and THIÈRY, P., 1908. "Révision des Échinides jurassiques du Département de la Haute-Marne," 'Bull. Soc. Nat. Haute-Marne,' Année 5, No. 20, pp. 1-32, Plate 4. [Correct pagination unknown.]
- (30) DE LORIOI, P., 1890-91. "Description de la Faune Jurassique du Portugal. Embranchement des Échinodermes," 'Comm. Trav. Geol.,' Portugal.
- (31) LOVÉN, S., 1875. "Études sur les Échinoidées," 'K. Svensk. Vet.-Akad. Handl.' Band 11, No. 7.
- (32) *Idem*, 1888. "On a Recent Form of the Echinoconidæ," 'Bihang K. Svensk. Vet.-Akad. Handl.,' Band 13, Afd. 4, No. 10.
- (33) *Idem*, 1892. "Echinologica," 'Bihang K. Svensk. Vet.-Akad. Handl.,' Band 18, Afd. 4, No. 1.

- (34) NOETLING, F., 1897. "Fauna of Baluchistan," vol. 1, Part 3. "Fauna of the Upper Cretaceous (Maëstrichtien) Beds of the Mari Hills," 'Pal. Indica,' ser. 16, pp. 1-79, Plates 1-23.
- (35) POMEL, A., 1883. "Classification Méthodique et genera des Échinides vivants et fossiles," Alger.
- (36) SPATH, L. F., 1919. "Notes on Ammonites," 'Geol. Mag.,' Dec. 6, vol. 6, pp. 27-35.
- (37) THIÉRY, P., 1911. "Notes sur quelques Échinides," 'Bul. Soc. Hist. Nat., Haute-Marne, Tome (?) 1, pp. [1-7 ?], Plate 1.
- (38) WESTERGREN, A. M., 1911. "*Echinoneus* and *Micropetalon*," 'Mem. Mus. Comp. Zool.,' Harvard, Sci. Res. "Albatross," vol. 15, pp. 41-68, Plates 1-31.

6. EXPLANATION OF PLATES 61-69.

All the figures have been drawn by the author. The lack of artistic merit that may result from this is compensated by the accuracy with which the structures are indicated. The tracing of sutures, particularly in fossil Echinoids, is a faculty that can be acquired only by long experience, and to the uninitiated is full of pitfalls and uncertainties. An attempt has been made to arrange the figures in such an order that they afford a pictorial record of the stages of specialization in the ambulacra of the Echinoidea. Most of the drawings are considerably magnified, but the actual degree of enlargement is immaterial in the majority of cases. Where it has any significance, the magnification can be ascertained by reference to the text. Those figures that are copied from other works are not necessarily identical with their originals in every detail, but are faithful reproductions of the parts with which the present paper is concerned.

PLATE 61.

- Fig. 1.—Ambulacrum III of *Bothriocidaris archaica* (from JACKSON, 1912, Plate 1, fig. 1, *pars*). This figure includes the peristomial ambulacrals, which are not clearly separable from those of the corona.
- Fig. 2.—Ambulacrum III of a very young *Goniocidaris canaliculata* (adapted from LOVÉN, 1892, Plate 2, figs. 7, 8 and 9).
- Fig. 3.—Ambulacrum III of young *Mellita hexapora* (modified from LOVÉN, 1875, Plate 49, fig. 241, *pars*).
- Fig. 4.—Ambulacrum III of very young *Brissopsis lyrifera* (from LOVÉN, 1875, Plate 37, fig. 218, *pars*).
- Fig. 5.—Ambulacrum III of *Echinocorys sulcatus* (from LOVÉN, 1875, Plate 24, fig. 181, *pars*).
- Fig. 6.—Ambulacrum III of *Spatangus purpureus* (from LOVÉN, 1875, Plate 36, fig. 208, *pars*).

- Fig. 7.—Ambulacrum of *Palæechinus quadriserialis* (modified from JACKSON, 1912, Plate 30, fig. 3, *pars*).
- Fig. 8.—Ambulacrum of *Hyattechinus beecheri* (modified from JACKSON, 1912, Plate 26, fig. 1, *pars*).
- Fig. 9.—Part of ambulacrum of *Maccoya burlingtonensis* (from JACKSON, 1912, Plate 33, fig. 2, *pars*).
- Fig. 10.—Adapical part of ambulacrum of *Lovenechinus missouriensis* (from JACKSON, 1912, Plate 42, fig. 3).
- Fig. 11.—Internal view of adoral part of ambulacrum of the same species (from JACKSON, 1912, Plate 42, fig. 5).
- Fig. 12.—Adapical part of ambulacrum III of *Lepidesthes colleti* (from JACKSON, 1912, Plate 71, fig. 1, *pars*).
- Fig. 13.—Detail of ambulacrum of *Lovenechinus* near mid-zone (from JACKSON, 1912, Plate 42, fig. 2).
- Fig. 14.—Part of ambulacrum of *Archæocidaris rossica* (from JACKSON, 1912, Plate 12, fig. 9).
- Fig. 15.—Part of ambulacrum of *Lepidocidaris squamosa* near mid-zone (from JACKSON, 1912, Plate 17, fig. 12).
- Fig. 16.—Part of ambulacrum of the same species, near mid-zone (from JACKSON, 1912, Plate 17, fig. 3).

PLATE 62.

- Fig. 1.—Part of ambulacrum (between the ambitus and the ocular plate) of *Paracidaris florigemma* (Univ. Coll., Reading, No. 23). Showing the intercalated plates on the convex columns adapically, where the curvature is sharp.
- Fig. 2.—Part of ambulacrum of *Diplocidaris verrucosa* (from DE LORIO, 1890, Plate 8, fig. 27A). The perradial suture is probably incorrectly drawn.)
- Fig. 3.—Ambulacrum of *Salenia texana* (from CLARK and TWITCHELL, 1915, Plate 12, fig. 1F).
- Fig. 4.—Ambulacrum of *Acrosalenia* (generalized from several species, and from THIÉRY, 1911, Plate 1, fig. 12).
- Fig. 5.—Adoral part of ambulacrum of *Orthopsis occidentalis* (from CLARK and TWITCHELL, 1915, Plate 17, fig. 1D, *pars*).
- Fig. 6.—Ambulacrum III of *Diplopodia versipora* (Univ. Coll., Reading, No. 519).
- Fig. 7.—Ambulacrum III of *Stomechinus bigranularis* (Univ. Coll., Reading, No. 201).
- Fig. 8.—A “super-compound” of *Astropyga radiata* (from DUNCAN, 1885, *a*, Plate 5, fig. 9).
- Fig. 9.—Internal view of three plates of the same species (from DUNCAN, 1885, *a*, Plate 5, fig. 10).

- Fig. 10.—Part of ambulacrum of *Tripneustes proavia*, showing a “super-compound” (from DUNCAN and SLADEN, 1885, *α*, Plate 48, fig. 4, *pars*).
- Fig. 11.—Ambulacral plates of *Acrocidaris nobilis* from the mid-zone and adoral surface. The former is a super-compound (from DE LORIOL, 1890, Plate 14, fig. 8).
- Fig. 12.—Ambulacral plates from near the mid-zone in *Hemicidaris mondegoensis*. The plates are all primaries, and are grouped, but apparently not combined, into super-compounds (from DE LORIOL, 1890, Plate 13, fig. 12).
- Fig. 13.—Ambulacrum III of *Phymosoma koenigi* (Univ. Coll., Reading, No. 653).
- Fig. 14.—Part of ambulacrum III (mid-way between ambitus and apex) of *Hemicidaris intermedia* (Univ. Coll., Reading, No. 517).
- Fig. 15.—Ambulacrum of *Glypticus hieroglyphicus* (after LAMBERT and THIÉRY, 1908, fig. 2).
- Fig. 16.—Part of ambulacrum of *Leptarbacia argutus* (from CLARK and TWITCHELL, 1915, Plate 16, fig. 1D, *pars*).

PLATE 63.

- Fig. 1.—Ambulacrum of *Tetrapyrgus niger*, drawn from an etched specimen and partly from thin sections. Adapically uncombined plates separate the “Arbacioid” triads. Towards the ambitus these plates become incorporated into the compounds. Adorally the compounds are tetrads, in the mid-zone typically pentads.
- Fig. 2.—Ambulacrum of an adult *Echinus esculentus*, drawn from an etched specimen. Normal “Echinoid” triads throughout.
- Fig. 3.—Ambulacrum of *Echinometra lucunter*, drawn from an etched specimen. The oral compounds are apparently triads, followed adapically by tetrads and pentads. These last types persist to the ocular plate. Save in proportions, this figure would equally illustrate the ambulacrum of *Strongylocentrotus*.
- Fig. 4.—Part of ambulacrum of *Noetlingia boulei* above the ambitus (modified from LAMBERT, 1906, p. 13, fig. 9).
- Fig. 5.—Adoral part of ambulacrum of the same species (modified from LAMBERT, 1906, p. 12, fig. 8).
- Fig. 6.—Mid-zone of ambulacrum III of *Echinus esculentus*, 70 mm. in diameter, showing the first phase in the production of super-compounds.
- Fig. 7.—Mid-zone of ambulacrum III of another specimen, 105 mm. in diameter. Certain triads have become separated from the perradial suture, being compound-demi-plates and components of super-compounds.
- Fig. 8.—Part of ambulacrum IV (mid-way between ocular and ambitus) of abnormal *E. esculentus*. At X additional demi-plates occur between the normal

triads. They are provided with fully-developed sutures, and are in no sense combined with the neighbouring plates. The two in column *b* have slightly reduced pore-pairs.

Fig. 9.—Part of ambulacrum I (mid-way between ocular and ambitus) of the same specimen. At X a similar plate to those found in fig. 8 occurs. At X' an "attempt" at "Arbacioid" structure appears, but the two demi-plates are not combined with the intervening primary.

Fig. 10.—Three plates from one column of ambulacrum of *E. esculentus*, showing a normal "Echinoid" triad, a regressive "Diademoid" triad, and an "inverted Echinoid" triad. The plates are drawn disproportionately high for the sake of clearness; they are not otherwise diagrammatic.

Fig. 11.—Part of ambulacrum I (below the ambitus) of the same specimen as that represented in figs. 8 and 9. An intercalated occluded plate (uncombined, and with an obsolescent pore-pair) occurs along the transverse suture separating two normal triads. This is probably a late stage of the abnormalities marked X in figs. 8 and 9. It compares remarkably with *Noetlingia* (figs. 4 and 5).

Fig. 12.—Part of ambulacrum III of a different specimen of *E. esculentus*, at the mid-zone. A surplus triad is in process of obliteration.

Fig. 13.—Part of ambulacrum III of the specimen figured in figs. 8, 9 and 11, midway between ambitus and peristome. At X an intercalated demi-plate makes its compound "Strongylocentrotid." The supernumerary plate is surrounded by reduced sutures, having entered into true combination with its neighbours.

Fig. 14.—Part of ambulacrum IV, from the ambitus adorally, of a large abnormal specimen of *E. esculentus*, in the collection of Ll. Treacher, Esq. For description, see p. 410).

PLATE 64.

Fig. 1.—Adapical part of ambulacrum of a gerontic specimen of *Heterocentrotus mammillatus*.

Fig. 2.—Mid-zone of the same ambulacrum.

Fig. 3.—Adoral part of the same ambulacrum.

Fig. 4.—Part of the surface of the adradial suture of the same area, showing the difference in the arrangement of the plates on the two surfaces of the test.

Fig. 5.—Section of the adoral part of another area from the same specimen, with the plate-boundaries traced between crossed nicols. The dotted circles mark the positions of the tubercles. The pores are somewhat differently placed from their external positions, owing to the obliquity of their passage through the test.

Fig. 6.—Two compounds from the orad part of the ambulacrum of *Colobocentrotus atratus*, drawn from a section viewed between crossed nicols. Slightly diagrammatic.

(For description of all these figures, see p. 412, *et seq.*)

PLATE 65.

Fig. 1.—Plan of ambulacrum IV of *Plesiechinus ornatus*.

Fig. 2.—Detail of adoral parts of ambulacrum IV of *P. ornatus* (Univ. Coll., Reading, No. 120). The X marks the position of the few simple plates that separate the two series of grouped plates. The apicad grouping is influenced by the tubercles; the orad grouping is like that of *Acrosalenia*.

Fig. 3.—Plan of ambulacrum II of *Pygaster semisulcatus* (Univ. Coll., Reading, No. 804).

Fig. 4.—Detail of adoral parts of area I in the same specimen. In the apicad part of the figure "tubercle-grouping" is present, but adorally the plating is like that of *Orthopsis*.

Fig. 5.—Adapical ambulacrals of *Pileus pileus* (from DE LORIO, 1890, Plate 21, fig. 1E).

Fig. 6.—Portion of the adapical part of ambulacrum II in *Pygaster macrocyphus* (co-type, Brit. Mus. Coll.), illustrating the type of abnormality commonest in Jurassic Holectypoida.

Fig. 7.—Plan of ambulacrum V of *Holectypus "depressus"* (Cornbrash).

Fig. 8.—Detail of adoral parts of ambulacrum IV of *H. hemisphaericus*. The plating is closely similar to that of *Plesiechinus*.

Fig. 9.—Detail of adoral parts of ambulacrum V of a Cornbrash *H. "depressus"* (a different specimen from that shown in fig. 7). The plating, though still Plesiechinid in plan, is remarkable for the great height of the ambulacrals.

PLATE 66.

Discoidea cylindrica.

Fig. 1.—Plan of ambulacrum of a specimen from the "Lower Chalk," Folkestone (Manchester Mus., No. L7740). Above the ambitus considerable numbers of "Clypeastrid" demi-plates occur, and adapically sporadic precocious complication appears.

Fig. 2.—Detail of the supra-ambital part of ambulacrum III of a small conical form from the "Lower Chalk."

Fig. 3.—Detail of mid-adoral part of ambulacrum I of a large cylindrical form showing unusual regularity.

Fig. 4.—Plan of ambulacrum II of a specimen from the Upper Greensand (Univ. Coll., Reading, No. 806).

Fig. 5.—Plan of ambulacrum III of a specimen from the *S. varians* zone (Manchester Mus., EARWAKER Collection).

Fig. 6.—Plan of ambulacrum IV of a specimen from the *H. subglobosus* zone (Collection of G. E. DIBLEY, Esq.).

(The three preceding figures are drawn to the same magnification, all the specimens having ambulacra of about the same length. Hence the original of fig. 6 is a younger form than that of fig. 4.)

Fig. 7.—Supra-ambital parts of all five ambulacra of a specimen from the *S. varians* zone (Collection of G. E. DIBLEY, Esq.). Area III is unlike the others in its greater simplicity. A large *Plicatula* obscures part of area II.

PLATE 67.

Fig. 1.—Plan of ambulacrum V of *Discoidea subucula*. The apical plates are rather high, but otherwise the structure is like that of *Plesiechinus*.

Fig. 2.—Plan of ambulacrum I of *D. dixonii* (*R. cuvieri* zone). The magnification is the same as that in fig. 1. The apical plates are exceedingly high and "Fibulariid," while those of the adoral surface are comparable with those of *Conulus*.

Fig. 3.—Plan of ambulacrum II of a small globular specimen of *Conulus albogalerus* (top of *M. coranguinum* zone).

Fig. 4.—Plan of ambulacrum III of *Micropetalon purpureum* (modified from WESTERGREN, 1911, Plate 29, fig. 6).

Fig. 5.—Plan of ambulacrum II of a young specimen of *Echinonæus cyclostomus* (from WESTERGREN, 1911, Plate 6, fig. 1, *pars*).

Fig. 6.—Plan of ambulacrum II of adult *E. cyclostomus* (from WESTERGREN, 1911, Plate 7, fig. 1, *pars*).

Fig. 7.—Part of ambulacrum of "*Pyrina*" *parryi* (from CLARK and TWITCHELL, 1915, Plate 27, fig. 1F).

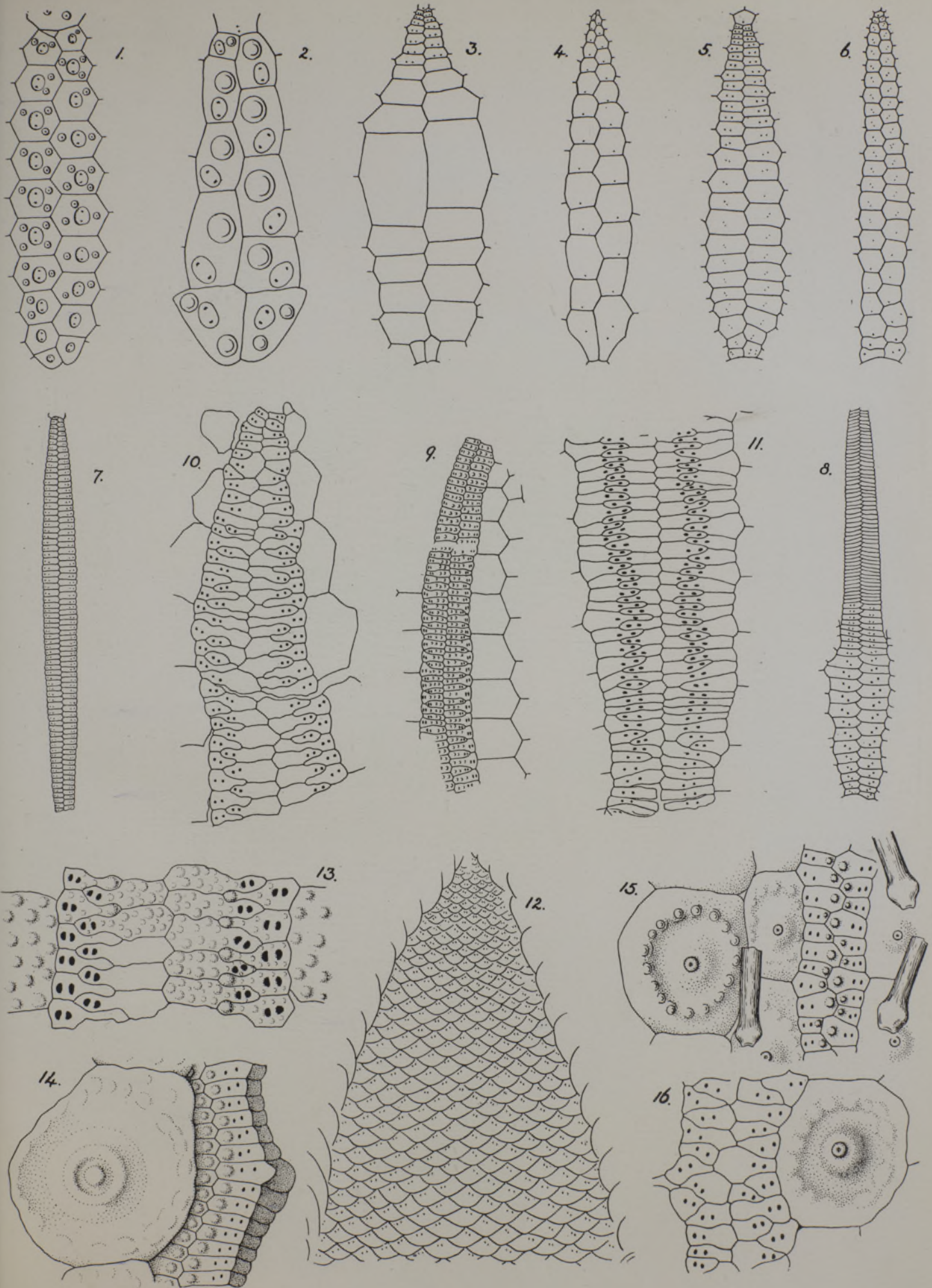
Fig. 8.—Adoral part of ambulacrum of very young *Echinonæus* (from WESTERGREN, 1911, Plate 11, fig. 6).

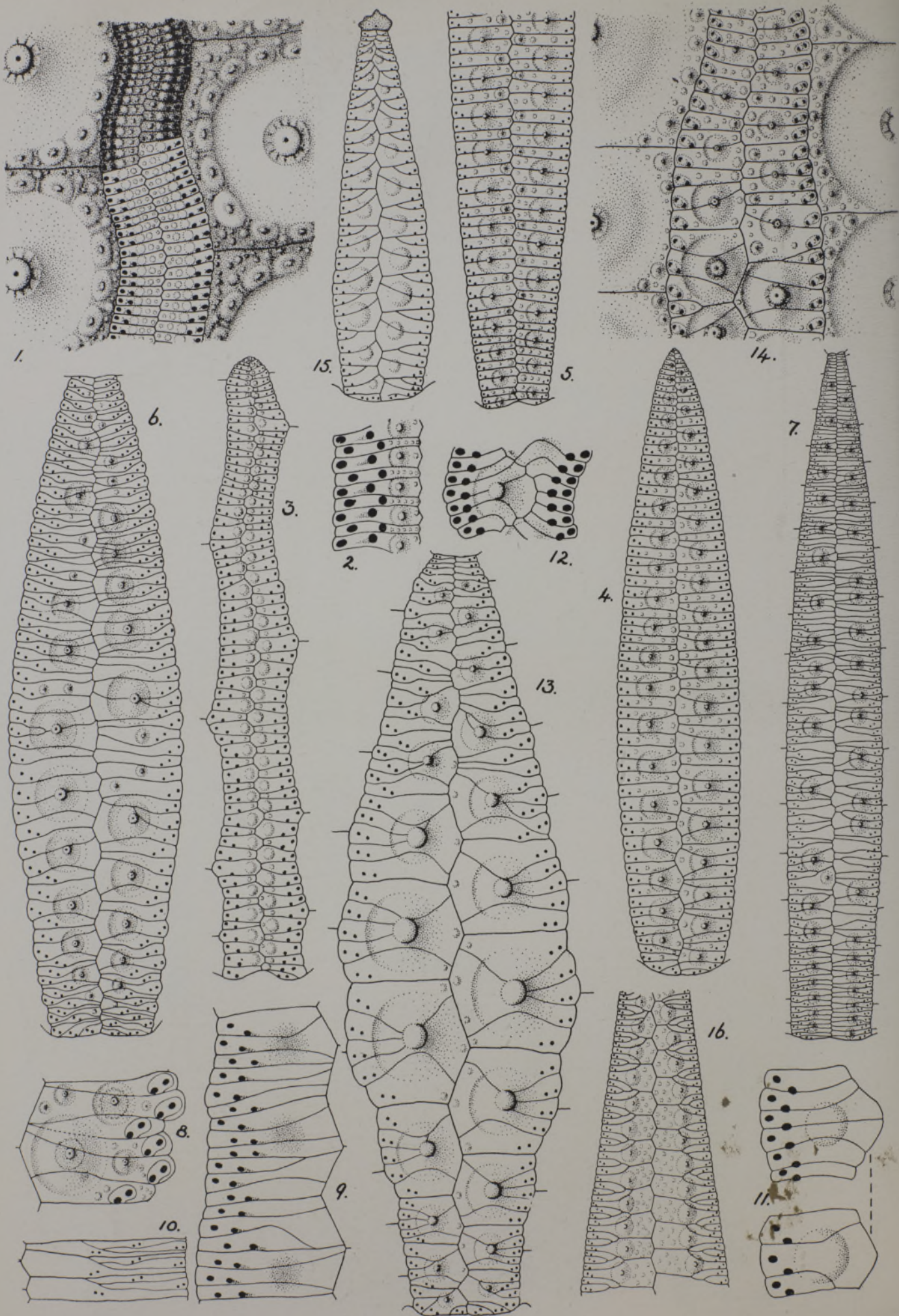
Fig. 9.—Adoral part of ambulacrum of young *Echinonæus* (from WESTERGREN, 1911, Plate 13, fig. 7).

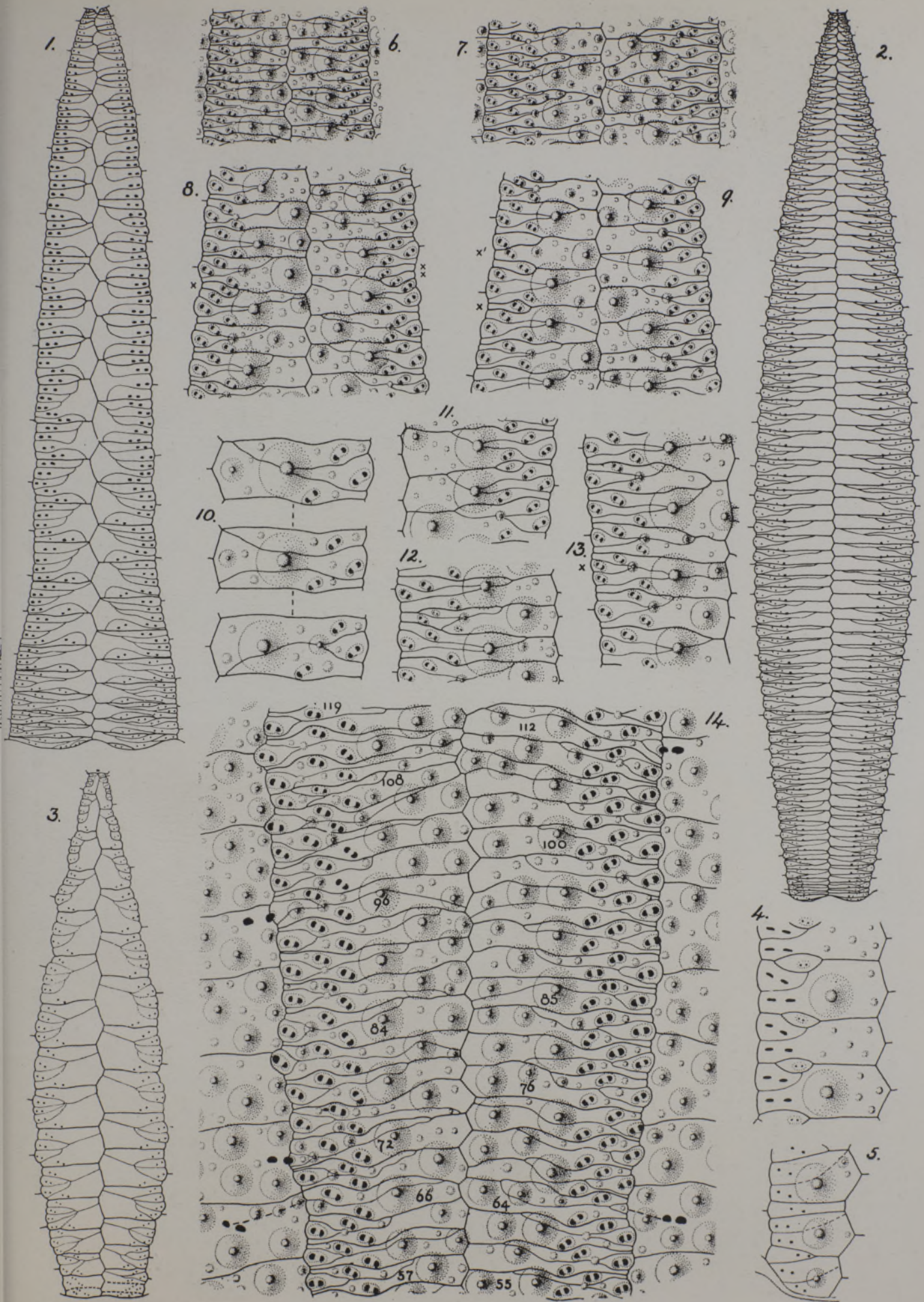
Fig. 10.—Adoral part of ambulacrum of adult *Echinonæus* (from WESTERGREN, 1911, Plate 13, fig. 2).

Fig. 11.—Detail of adapical part of ambulacrum II of *Conulus albogalerus* (Univ. Coll., Reading, No. 803).

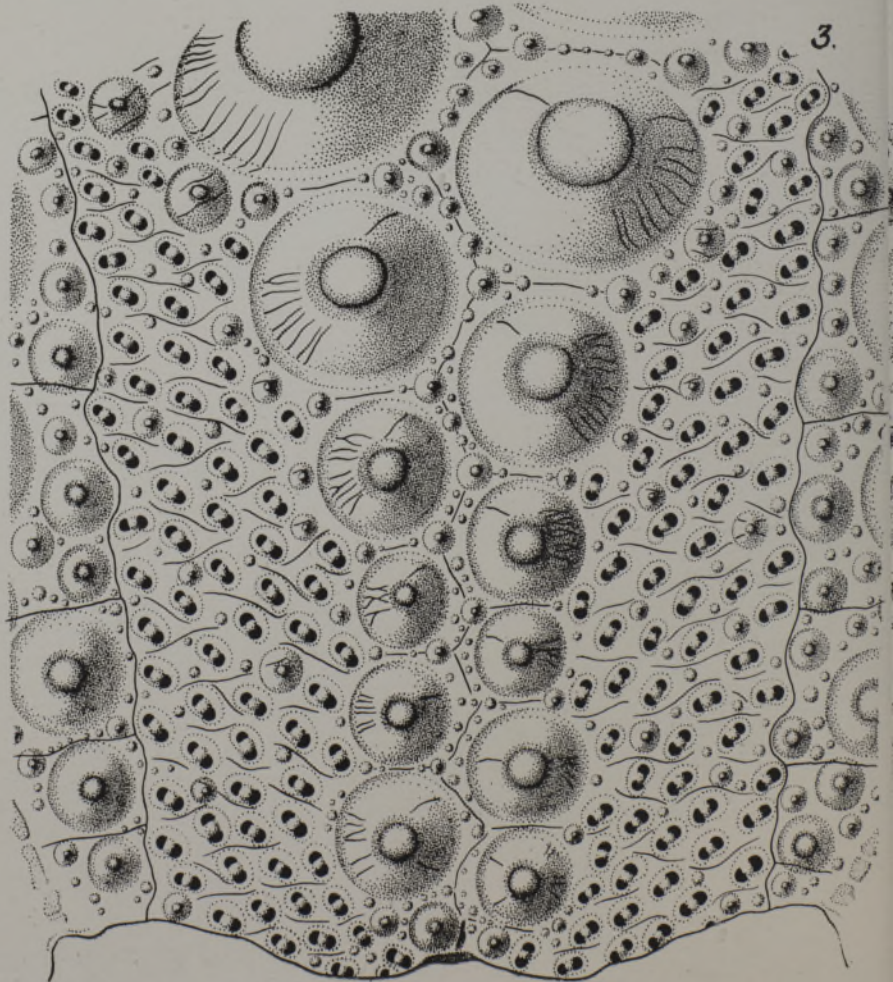
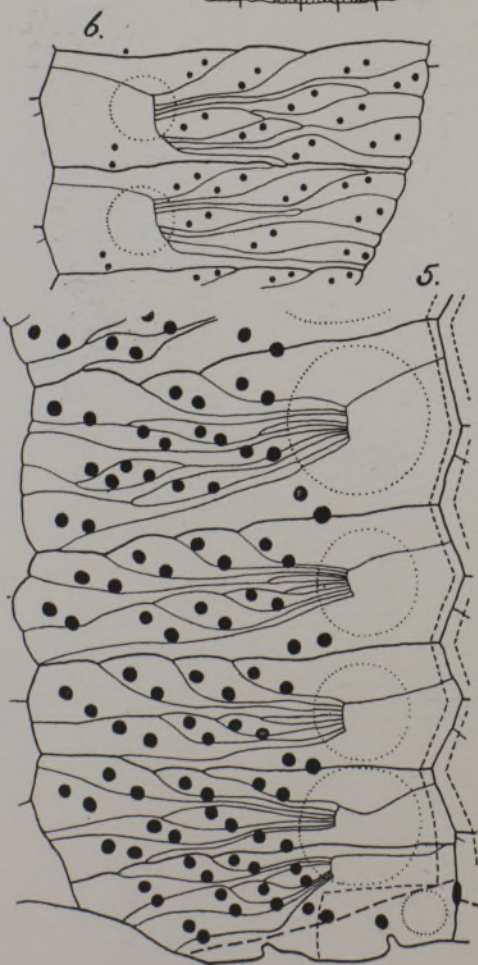
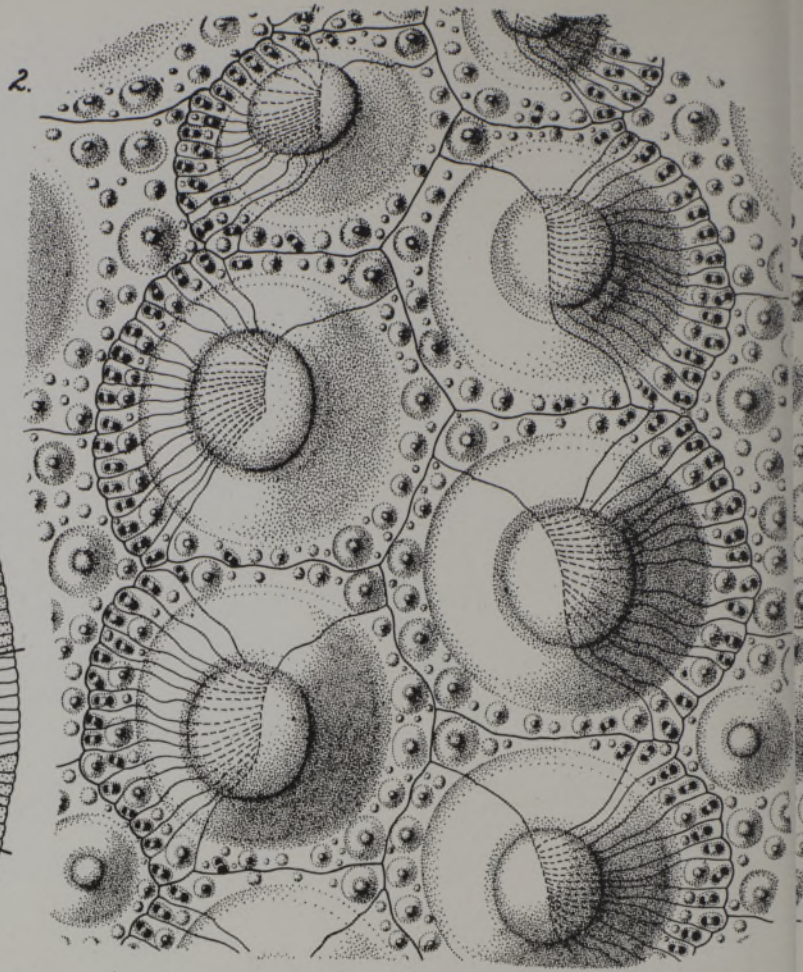
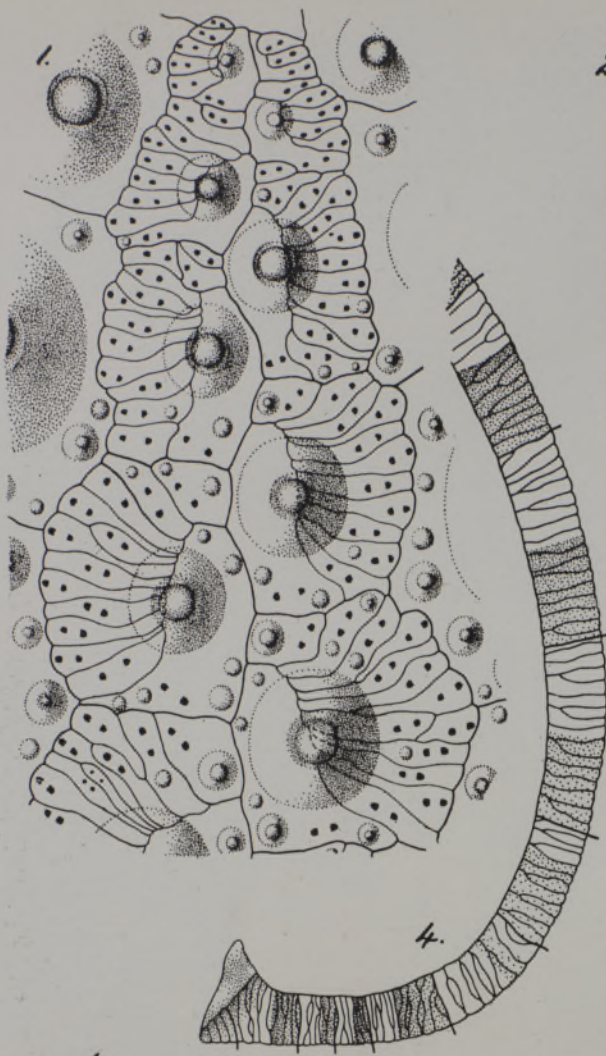
Fig. 12.—Detail of adoral part of ambulacrum V of a different specimen of *C. albogalerus*, less highly magnified. The pore-pairs are triserial, and situated in oblique grooves, near the peristome.

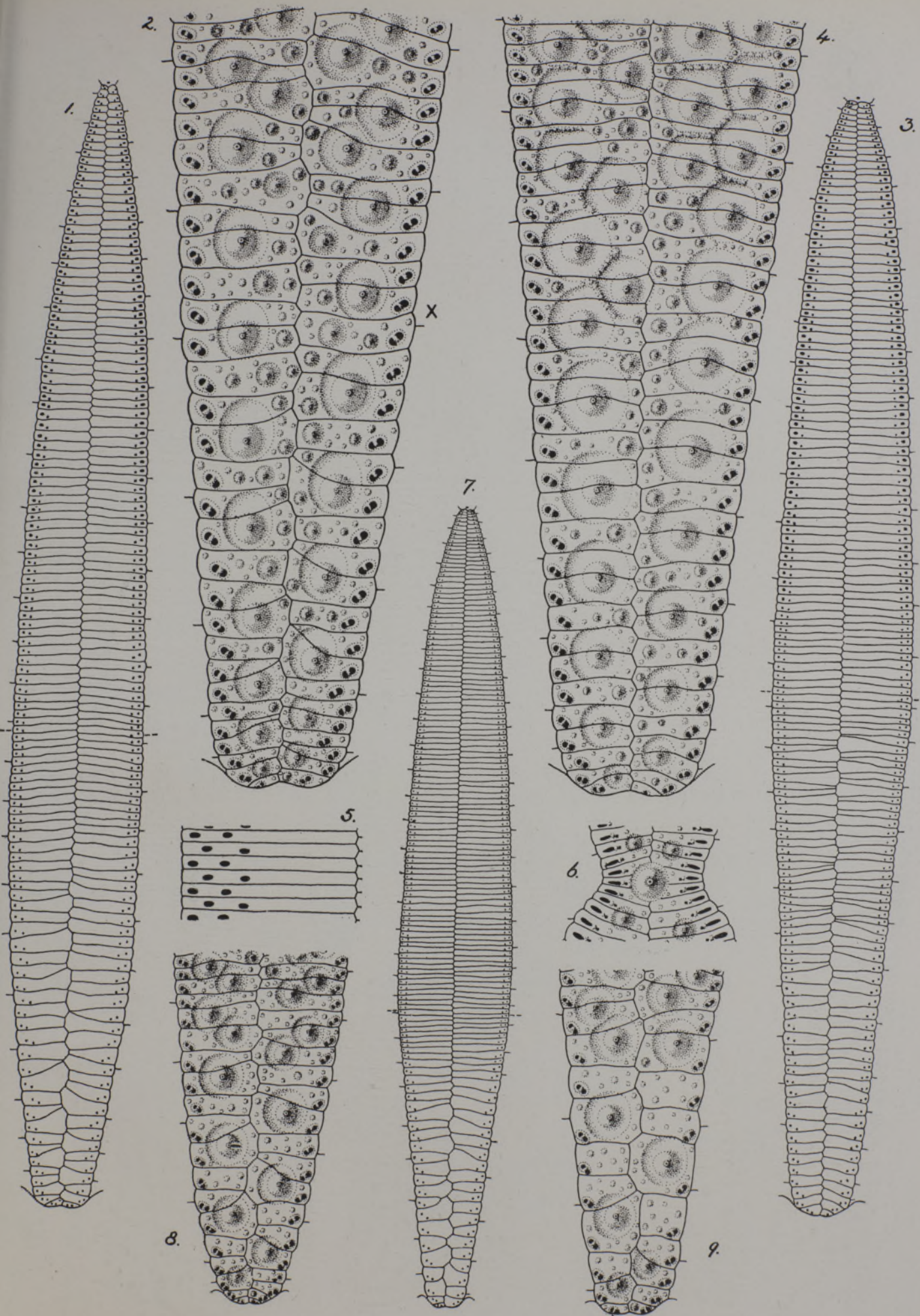


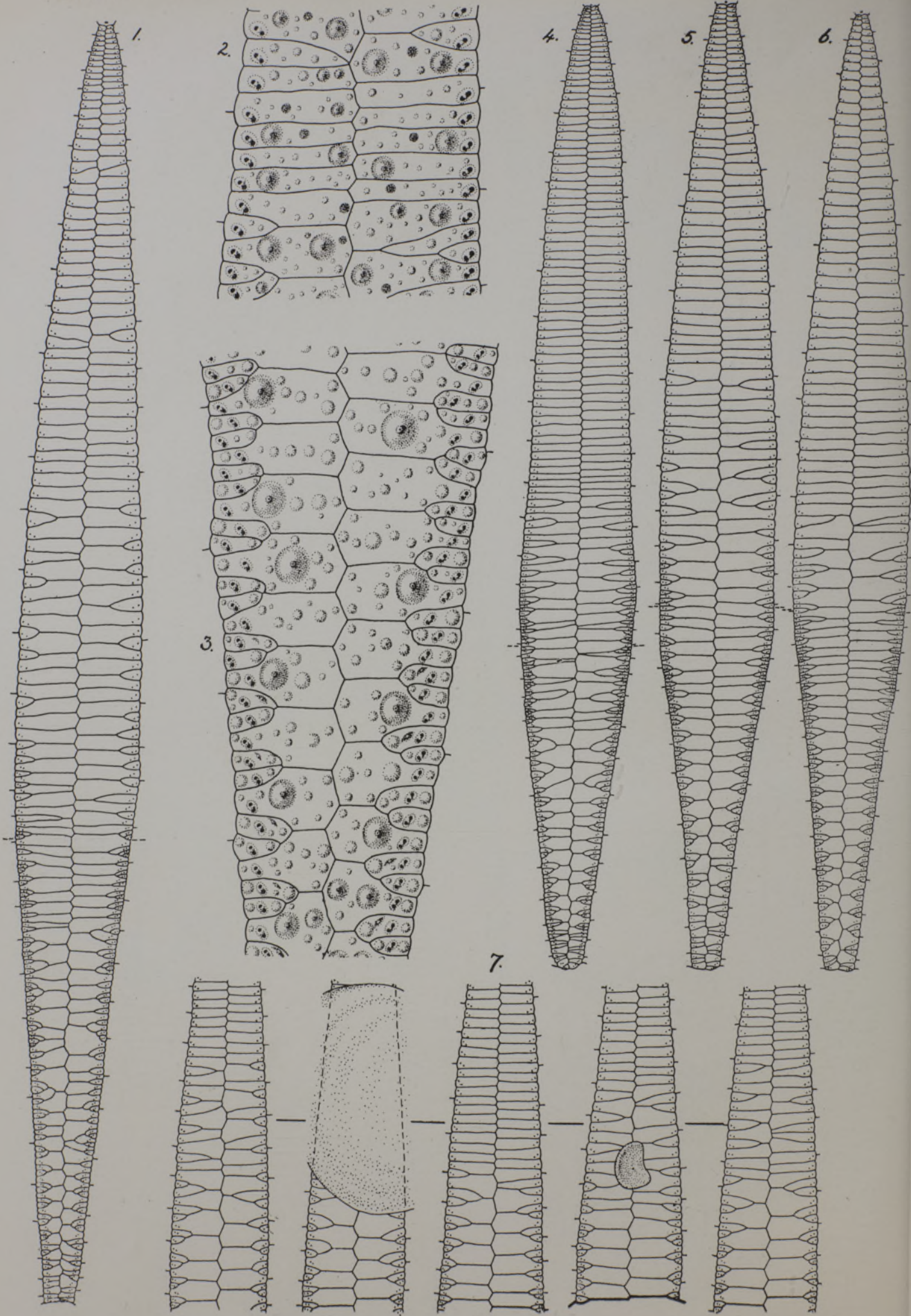


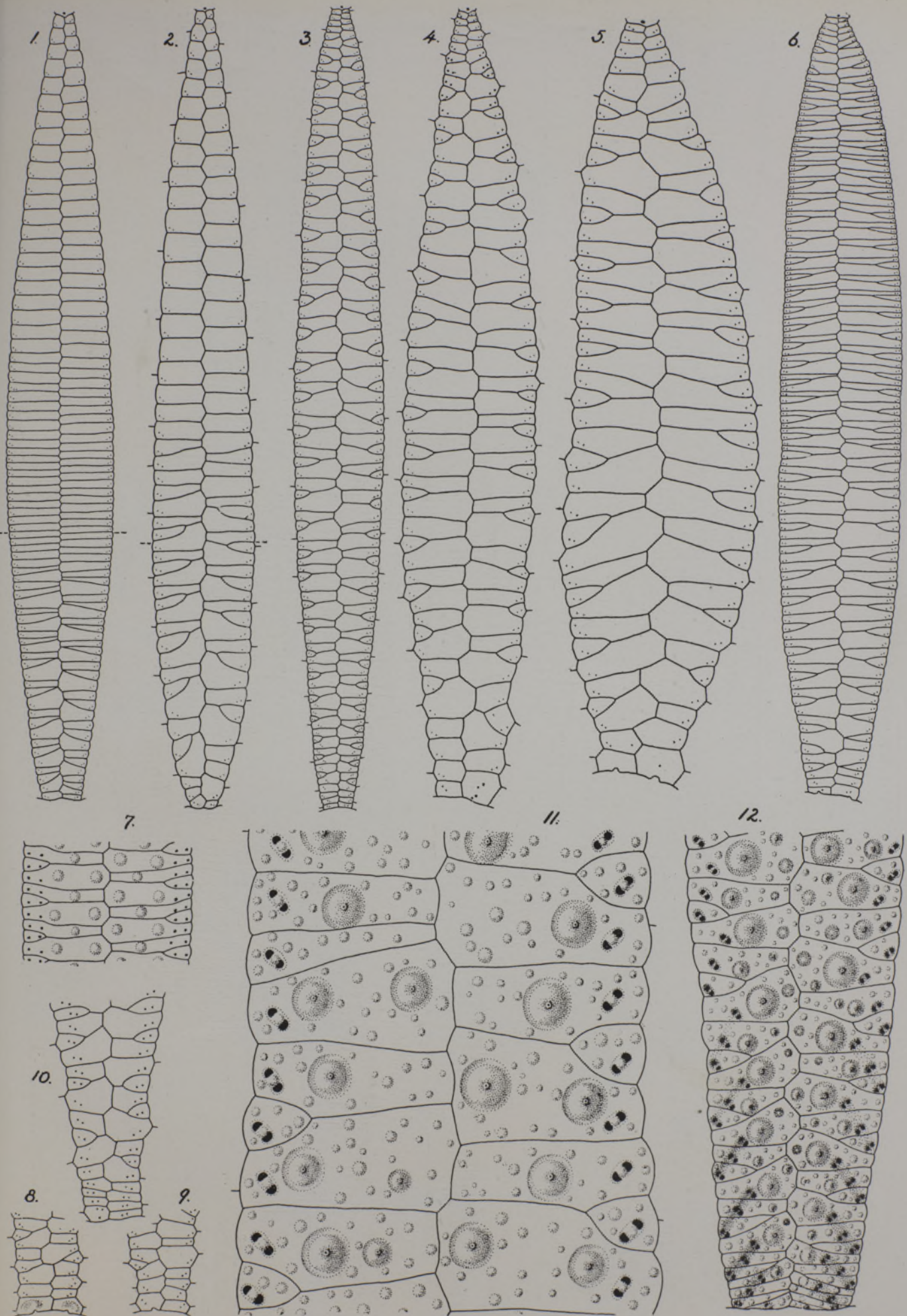


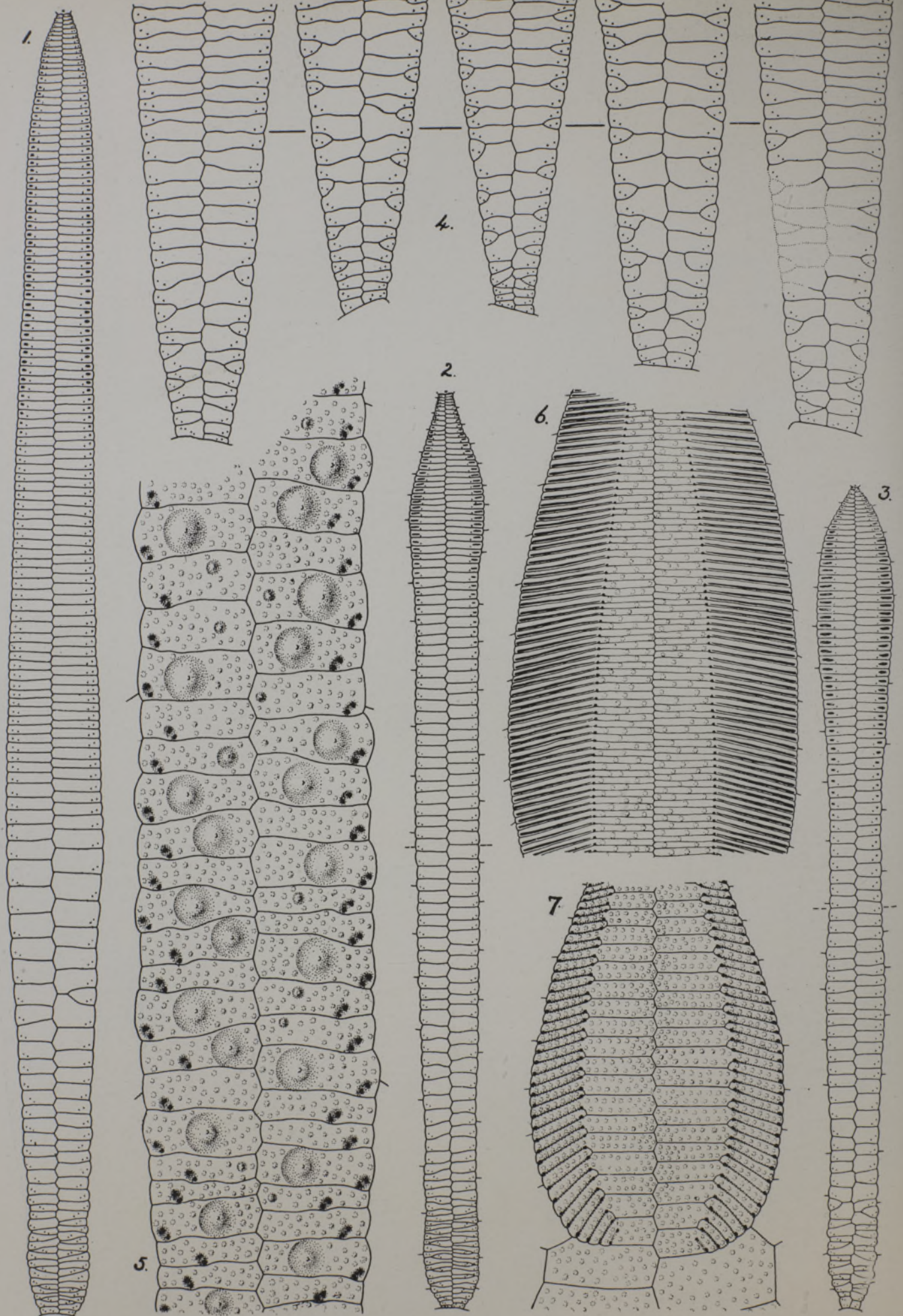
Hawkins.











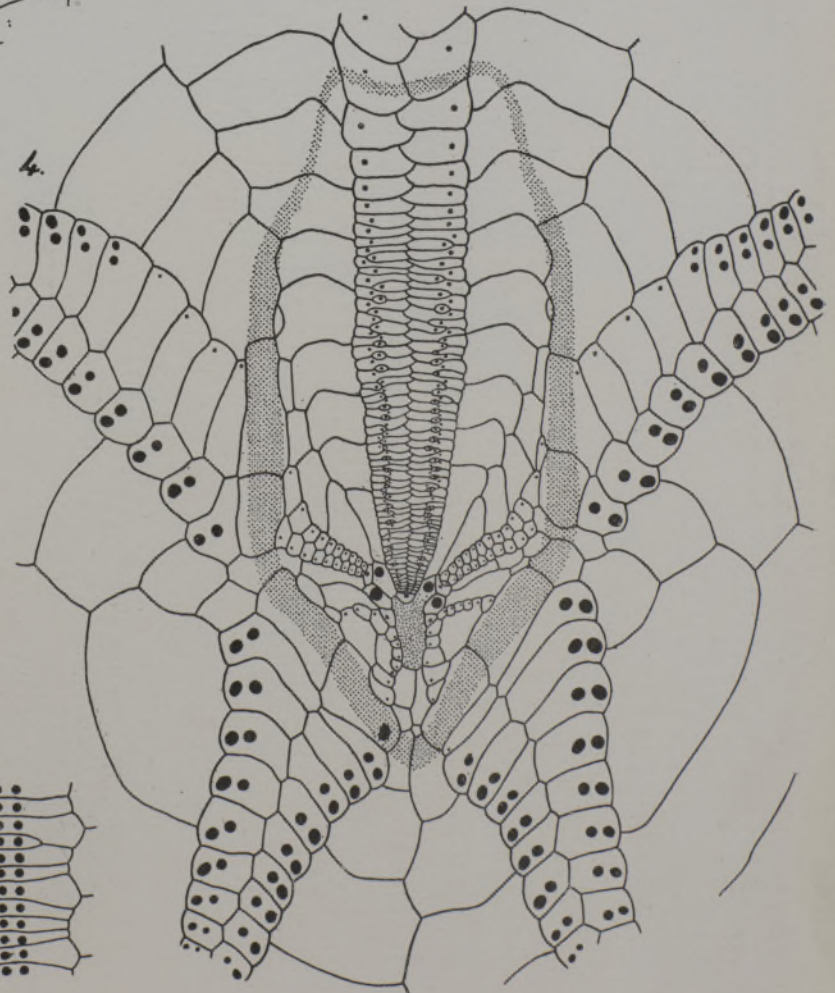
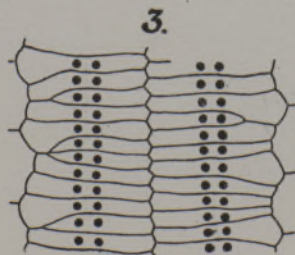
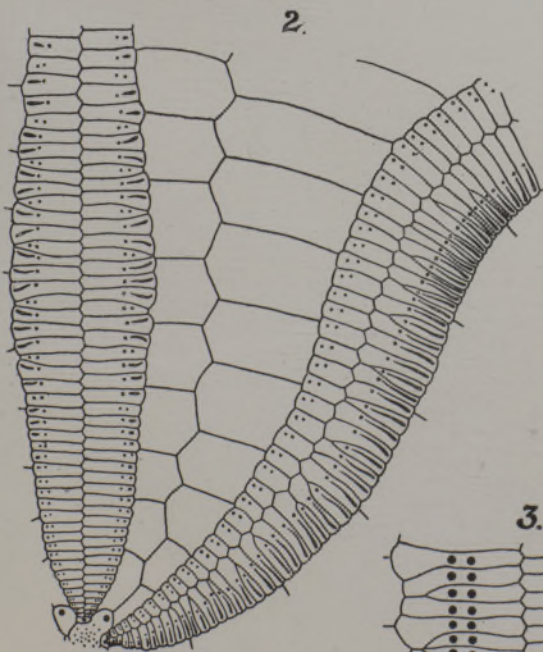
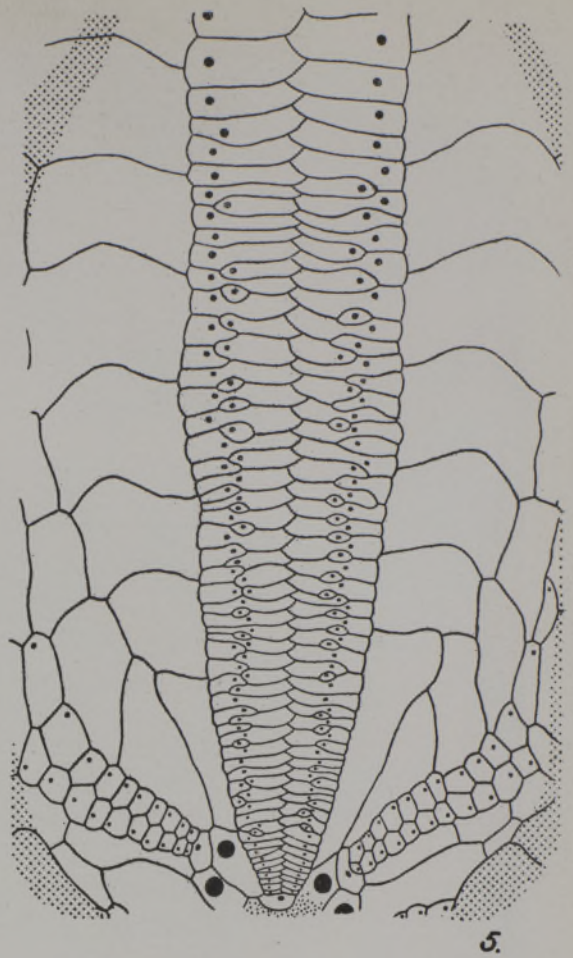
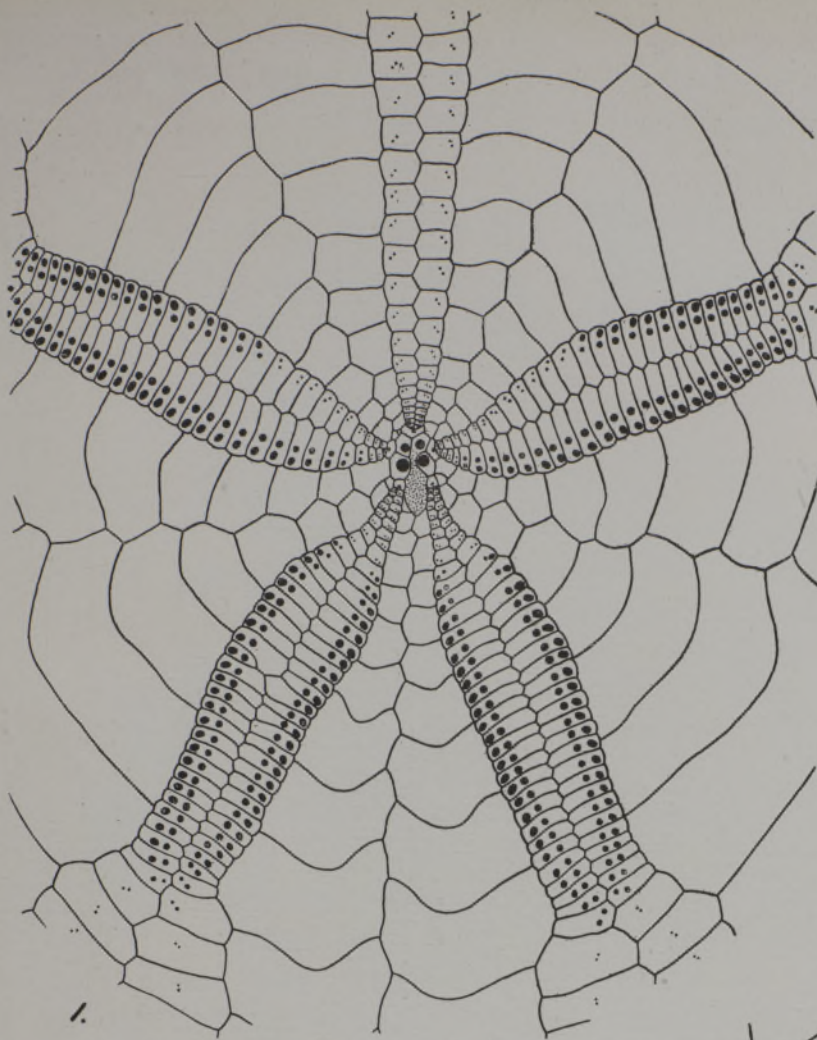


PLATE 68.

- Fig. 1.—Plan of ambulacrum II of *Galeropygus agariciformis*. The apicad pores are hardly sub-petaloid. There is a hypophyllode adorally.
- Fig. 2.—Plan of ambulacrum V of *Nucleolites quadratus*, showing a marked, but restricted, petaloid character adapically, and a complex hypophyllode adorally.
- Fig. 3.—Plan of ambulacrum IV of *N. scutatus*, showing a more advanced petaloid character and a simple hypophyllode with apicad demi-plates.
- Fig. 4.—Adoral parts of all five areas of *Trematopygus faringdonensis*, showing an extremely diffuse hypophyllode, resulting in structure like that of *Conulus*. The complexity is least in areas I and V (the longest), and greatest (reaching above the ambitus) in area III (the shortest). In column 4, a two plate-series show remarkable similarity to the structure of *Discoidea cylindrica*.
- Fig. 5.—Detail of mid-adoral parts of ambulacrum II of *Clypeus sinuatus*, showing the "triserial" arrangement of tubercles and pores.
- Fig. 6.—Detail of part of the petal of ambulacrum V of *C. sinuatus*, showing the disparity of the pores and simplicity of the plating. (Only the coarser ornament is inserted.)
- Fig. 7.—Detail of part of the petal of ambulacrum I of *Clypeaster* sp. (Univ. Coll., Reading, No. 638), showing the similarity of the pores and the nature of the demi-plates.

PLATE 69.

- Fig. 1.—Adapical part of the test of an adult *Spatangus purpureus* (drawn from an etched specimen). Ambulacrum III has Bothriocidaroid plating throughout. In some columns of the petals a disturbance in the sequence of the plating occurs, and in one case a demi-plate appears, but in the main the petaloid regions are built of Cidaroid plates.
- Fig. 2.—Ambulacra III and IV of *Heteraster oblongus* (drawn from a weathered and stained specimen, Univ. Coll., Reading, No. 812). Area III has irregularly arranged alternations of petaloid and non-petaloid pores, the plates bearing the latter being more or less occluded. Area IV has petaloid pores in one column, non-petaloid in the other. The plates of the former are alternately primaries and demi-plates, those of the latter are approximately Bothriocidaroid primaries. There are nearly twice as many plates in the petaloid column as in the other.
- Fig. 3.—Part of ambulacrum (?III) of "*Ananchytes texana*," Cragin (from CLARK and TWITCHELL, 1915, Plate 35, fig. 2, c). A similar development to that of area III in fig. 2, but with homogeneous pores.

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Fig. 4.—Adapical part of the test of an adult *Echinocardium cordatum* (drawn from an etched specimen). The parts of areas I, III, and V enclosed by the fasciole have complex plating-structure.

Fig. 5.—Area III of the same specimen, more highly magnified. Compare with Plate 61, figs. 10 and 11 (*Lovenechinus*). The resemblance suggests morphogerontic reversion even in complexity.