[From The American Journal of Science, Vol. XXXIV, September, 1912]

JACKSON ON THE PHYLOGENY OF THE ECHINI.

By Charles Schuchert.

(Contributions from the Paleontological Laboratory, Peabody Museum, Yale University, New Haven, Conn., U.S.A.)

Art. XXIII.—*Jackson on the Phylogeny of the Echini;** A synopsis by Charles Schuchert.

In this monumental monograph are established the phylogeny and classification of the Echini, including young and adult, fossil and living types, and "based on the sums of the characters and not on single characters." The volume also contains a revision of all Paleozoic Echini.

The splendid and fully illustrated work is dedicated to the great echinologist, Alexander Agassiz, and to Alpheus Hyatt, "my beloved master and friend, whose principles of research are the keynote of this memoir." Hyatt's principles are the stages in development, senescence, acceleration, and parallelism, and it has been Jackson's constant aim to compare these stages with the characters of more or less closely associated types.

Jackson began to study Echini in 1896 and during the past seven years he has devoted most of his time to a detailed study of the species and genera of this class of Echinoderma. He assembled in his private collection more than 40,000 specimens of Recent and Mesozoic Echini in all stages of growth, actually studying more than 50,000 specimens, so that he might thoroughly understand the Paleozoic species and their phylogenetic relations to the later forms. That he has succeeded the volume bears abundant evidence, for no class of invertebrates, as a class, has been wrought out with more care and philosophic insight.

One of the most important features of the work is a new method of determining ontogenetic stages of growth by noting how the plates are introduced ventrally, and in the localized stages among the plates dorsally. Echini are a particularly good class to study phylogenetically, because they have so many parts, all of which must be taken into consideration. This mass of detail furnishes constant checks and when all are in accord proves the accuracy of the resulting phylogenetic scheme.

Geological Occurrence.

Aldrovanus in 1618 was the first to figure a fossil echinoid from the Paleozoic and curiously one of the rarest of species and the oldest geologically, *Bothriocidaris globulus.*

The author recognizes 24 genera of Paleozoic Echini and of these but 4 are new to paleontology (*Hyattechinus*, *Lovene-*

* Phylogeny of the Echini, with a revision of Palaeozoic species; by Robert Tracy Jackson. Mem. Boston Soc. Nat. Hist., vii, quarto, 491 pages, 76 plates, and 258 text figures, Jan., 1912.

chinus, *Meekechinus*, and *Pholidechinus*). Of good species there are 119 and of these 23 are new. Of *incertae sedis* and *nomina nuda* there are 3 genera and 34 named forms.

Ordovician.—The oldest and most primitive Echini occur in the Middle Ordovician of Esthonia, Russia, where the genus Bothriocidaris is found with 3 exceedingly rare species (1 in the Jewe and 2 in the Lyckholm formations).

Silurian.—The oldest American representative of the class was recently found in the Rochester shale of New York (*Koninckocidaris silurica*, n. sp.). In the Llandovery of England occurs *Maccoya phillipsiae*, while the lower Ludlow has furnished *Palaeodiscus ferox* and *Echinocystites pomum*.

Devonian.—Germany has in the Middle and Upper Devonian Xenocidaris (3 species), *Eocidaris laevispina*, and Lepidocentrus (3). In the Upper Devonian of New York is found *L. drydenensis*. In England occur *Lepidesthes devonicans* and *Pholidocidaris acuaria*.

Lower Carboniferous.—The Lower Carboniferous is the period of greatest development of Paleozoic Echini and in America alone there are 50 good species, with 31 more in Europe. In the Millsap formation of Colorado occurs *Miocidaris cannoni*, a new species and the oldest stratigraphically of the Cidaridæ, the stock that gave rise to Mesozoic and later Echini. Archaeocidaris has 10 American species and 12 other forms occur in Europe. Other genera in America are Lepidocidaris (1 species), Lepidocentrus (1), Hyattechinus (3), Pholidechinus (1), Palaeechinus (1), Maccoya (2), Lovenechinus (4), Oligoporus (5), Melonechinus (11), Lepidechinus (3), Perischodomus (1), Lepidesthes (6), Pholidocidaris (1).

Upper Carboniferous.—"In the Upper Carboniferous the Palaeozoic Echini have dropped out with extreme suddenness and relatively few species are known." Archaeocidaris has 17 species in America and 2 in Europe. The only other form is the American *Lepidesthes extremis*, n. sp.

Permian.—The cidaroid *Miocidaris keyserlingi* occurs in Germany and England. Of Archaeocidaris there is 1 species in America, 1 in India, and 1 in Australia. The only other form is the American *Meekechinus elegans*, n. sp.

Types of variation defined.

Jackson states that next to stages in development variation is an extremely important subject as a basis in phylogenetic determinations. Echini are especially valuable on which to study variation, because in them variation can be so definitely expressed. It is seen in the introduction of columns, number of plates in a row, number of oculars that reach the periproct, etc.

"In order to appreciate variation it is of fundamental importance to be familiar with the characters of the associated species and genera of a case in hand, and also the developmental characters of the same. Variation may be fairly classified under five more or less distinct heads:

"1. *Arrested variation*, in which the variant retains characters seen in its own young and typical of the adults of more primitive allies, but characters which are usually eliminated in development. . . .

"2. *Progressive variation*, in which the variant has characters not typical of the species, but which are further evolved on the direct line of differential development, and are seen typically in more evolved nearly allied species or genera. . .

"3. *Regressive variation*, in which the variant takes on characters of the adult of some simple and more primitive type of the group. Such characters are not necessarily a repetition of youthful characters but may go back to a remote ancestry. An arrested variant in a sense is one form of regressive variation, but a regressive variant includes much more than arrested variation. To distinguish them, an arrested variant is one that has developed to a certain point as usual, and then failed to take on the later added characters typical of the species, so that, although an adult, it has immature characters. A regressive variant is one that has attained full characters and then in later life has reverted to youthful or primitive characters as an individual variation, or it is a variant that from youth has primitive characters not normally seen in the development of the species. . . .

"4. *Parallel variation* is where a character is taken on exceptionally which may be compared with characters normally occurring in some type of the group not closely connected, so that it cannot be genetically compared. . . .

"5. *Aberrant variation* is where a character is taken on which is quite abnormal, not to be correlated with the typical condition in associated forms" (pp. 18, 19).

Comparative Morphology.

Significance of abnormal symmetry.—Echini are remarkably constant in their pentamerous system, but Jackson found 71 variant individuals or on an average "a little more than one to a thousand. The variants are partially or completely trimerous, tetramerous, and hexamerous. . . . The ocular plates seem to exert a controlling influence in the building up of the corona, as below and in immediate contact with the oculars originate the coronal plates, both ambulacral and interambulacral. In connection with each ocular is developed a whole ambulacrum, and, in addition, a half-interambulacrum

on either side. That is, while an ambulacrum originates on the ventral border of an ocular, each interambulacrum may be considered as composed of two halves, the plates of which originated on the left or right of the area in contact with the adjacent oculars. If this is true, then the loss of an ocular would cause a failure to develop of the plates that normally went with it, also an abnormal position of an ocular should cause an abnormal distribution of the associated coronal plates" (35, 36).

The "variations from the pentamerous symmetry can all be considered as monstrosities" (50).

Ambulacral areas.—The ambulacrum "is the most essential feature of a sea-urchin, and has a first importance in classification and morphology, on account of the varied structure that it presents" (53).

Interambulacral areas.—"The interambulacrum in Echini functions chiefly as a space filler and a bearer of spines and pedicellariae. The spines serve for protection and more or less in locomotion, and pedicellariae as grasping, cleansing, and protective organs. In spite of this secondary physiological importance, the interambulacrum forms a large part of the test of the sea-urchin in most types, and is of very great interest, especially in Palaeozoic genera. The interambulacral plates originate in direct contact with the ocular plates and quite independently of the genitals. . . .

"The full differential characters of the interambulacrum as of the ambulacrum are expressed at the mid-zone of the adult. Here are usually found the full number of columns of plates characteristic of the species, also the typical tubercles, spines, imbrication, or other characters which go to make up the specific description. The ventral border in the basicoronal zone represents the earliest formed plates and the youth of the individual, as far as it can be gathered from the study of an adult specimen, though the actually first formed plates may have been resorbed in development. Passing dorsally, with later added plates, new characters may come in until we get the full differential features developed at or about the mid-zone. Dorsal to the mid-zone we pass into the area of young last formed plates which have not yet acquired the full characters. Or again dorsally, we may find senescent features in the loss of columns of plates. Passing from the basicoronal row dorsally, we find in most Palaeozoic types, and many post-Palaeozoic as well, stages in development strongly marked, which stages can be correlated with the adult condition of simpler genera or simpler species within the genus. The interambulacrum in Echini has from one to fourteen vertical columns of plates in each of the five areas, which represents the least and greatest number known at present. There are

intermediate grades representing every step between this least and greatest specialization of the area, and it is a matter of great interest to follow the progressive series as represented by stages in development, and by adult types, to see how the progressive differential structure is built up. As the plates of the ventral border are the oldest or first formed of any plates seen in an individual specimen, and as the later added plates succeed one another as we pass dorsally, it might be thought that we could read stages in development as expressed by rows and columns of plates with ease and certainty, and such can be done in many types . . . Complications may come in, however, especially resorption of the base of the corona by encroachment of the peristome cutting off part of the ventral plates, and also rarely resorption within the corona, as exceptionally in Arachnoides, or differential growth of associated plates, which may separate plates originally in contact (Echinarachnius)" (62–4).

Base of the corona.—"The characters of basicoronal interambulacral plates are the more striking and may be stated in brief. Where no plates have been removed by resorption, there is a single plate at the ventral border of the interambulacrum. The primitive type of this character is Bothriocidaris, which continues to build a single column. This same character of a single plate ventrally, but succeeded by two plates in the second row, is characteristic of the young of all modern regular Echini. . . . In the adult of most regular Echini the single plate and probably more have been resorbed by the advance of the peristome (Eucidaris). In the Palaeechinidae with many columns of plates, apparently only one plate has been resorbed, when we find two plates in the basicoronal row, . . . or in the Archaeocidaridae, several rows of plates may have been resorbed, and we find four plates in the basicoronal row. . . .

"In Bothriocidaris the basicoronal row consists of two high hexagonal ambulacral plates with pores superposed in each ambulacral area and one interambulacral plate in each interambulacral area. This same character is seen in young cidarids, young Strongylocentrotus, and Echinus, young Salenia, Arbacia, and Phormosoma. It is, I think, fair to call this a primitive character, and it represents what I (1896) described as the protechinus stage. The protechinus stage is comparable in other groups of animals to the protoconch of cephalous Mollusca, what I (1890) described as the prodissoconch of Pelecypoda, and to Beecher's (1901) protegulum of Brachiopoda and protaspis of Trilobita. All are referable to what I termed (1890) the phylembryonic stage in development, a stage in which the differential characters of the class are established in ontogeny" (69–71).

Oculars and genitals.—"An ocular plate in Echini overlies an ambulacrum wholly and the two adjacent interambulacra in part on either side. Immediately on the ventral borders of the oculars all coronal plates originate. It seems that at this point the tissues exist which give rise to new plates. . . The five oculars are always present barring the excepted Pourtalesia. The genitals overlie the interambulacra in part, but not the lateral borders of the same, and never reach the ambulacra. In some cases the genitals may not reach the interambulacra. Five genitals are typically present, but the posterior genital may be wanting (spatangoids) or one absent as an aberrant variation. . . .

"In the ancient Bothriocidaris the oculars are exceptionally large, relatively to the size of the animal; on the other hand, the genitals are exceptionally small, relatively the smallest of all known Echini. . . .

"No pores have been observed in genital plates in Bothriocidaris. It is possible they did not have genital pores, as such are wanting in the young of Recent Echini; more likely they were present, but do not show in external view . . . Also no pores have been observed in ocular plates of Bothriocidaris. . . .

"Genital and ocular plates are rare in Palaeozoic types, yet excepting the Echinocystoida I am able to show them in all families other than the Archaeocidaridae and in most genera. After Bothriocidaris just considered, the leading character in the Palaeozoic is for all the oculars to reach the periproct, and to cover the ambulacra and in part the interambulacra on either side. Also the genitals reach the periproct, are larger than the oculars, and cover the interambulacra in part, but not wholly, because the lateral borders of the interambulacra abut against the next adjacent ocular on either side." In Paleozoic Echini, as a rule, "the ocular plates are imperforate. . . . In post-Palaeozoic Echini ocular plates have one pore not always visible externally (Salenia, Arbacia) and very rarely a second pore may exist as a variant. I have seen only two or three such" (86–89).

Systematic value of oculars.—"A close study reveals characters of importance to general morphology, to the evolution of the group, to the relation of the species in the genus and related genera, and to geographical distribution. Ocular plates present an excellent systematic character which has been largely overlooked. . . .

"Early in my studies of these plates it was seen that they had an important bearing, and observations were made on all available specimens of regular Echini, Mesozoic and Recent. In the fossils this is not always easy, as for purposes of study, all five oculars and genitals must be observed, and they are

frequently lost in fossils. I have succeeded, however, in making observations on something over 50,000 regular Recent and Mesozoic specimens representing 133 species. . . . The reason for making so many observations was that while the character of a species is usually gathered correctly from five or ten specimens, the variations seen in a large number present interesting data for comparative study. . .

"In Mesozoic regular Echini the dominant character is for all the oculars to be exsert, or excluded from the periproct. In the Recent regular Echini the young also have all the oculars exsert. In the adult all the oculars may be exsert or one or more be insert. While the exsert character of the young is like the Mesozoic, the becoming insert in development is the taking on of a character which in this respect is directly comparable to the dominant character of the Palaeozoic. . . .

"As becoming insert is a progressive character with development, species in a genus that have the greatest number of ocular plates insert may be considered in this respect more evolved than other species which have a less number (Arbacia, Echinometra). Also, as a matter of variation, individuals that have fewer oculars insert than is characteristic of the species may be considered arrested variants, and those that have more plates insert than is typical may be considered progressive variants. Such variants can frequently be compared directly with related species or genera where the fewer or greater number of oculars insert is a typical specific character (Centrechinus). Specimens of a given species from different localities present often quite striking differences as regards the number of plates which are insert, those from one locality having typically fewer oculars insert than those from a different locality. Such variation with locality may well be considered as indicating incipient species, as, where there is a difference, specimens from one locality must be more progressive or less progressive than those from another. . . .

"The number of oculars insert has been spoken of by previous writers as if it were a concurrent of age, and the largest specimens had the most oculars insert. My observations are directly opposed to this view. All the evidence goes to show that the full number of oculars that are to become insert are developed early in the life of the individual, and apparently later no change in this respect takes place. A series of specimens half the mature size or larger may in most species be safely accepted as showing the mature characters as regards oculars. This is on the basis of observations on 11,500 specimens of *Strongylocentrotus dröbachiensis*, all from one locality, Dumpling Islands, the specimens varying from very young to adult, and all measured and tabulated as later

described. With few exceptions it was found that the larger individuals in a species are typical as regards ocular plates, and that variations, both arrested and progressive, are more frequent in smaller individuals, often half grown as regards size" (90–1).

Genital pores.—"In very young Echini genital pores do not exist. . . Typically, in post-Palaeozoic regular Echini there is a single genital pore within the confines of each genital plate. . . . In the Ordovician Bothriocidaris genital pores are unknown. . . . In other Palaeozoic Echini genital plates typically have more than one pore to a plate. There may be two or three . . or there may be three to five in a plate. . . . Instead of a few pores there may be numerous genital pores to a plate, even as many as ten or eleven. . . . It is possible that in types where fine madreporic pores are unknown, some of the larger pores served as madreporic openings. Otherwise all the pores in genital plates doubtless connected with genital glands, as in Recent Echini with accessory pores" (170–172).

Secondary value of genitals in classification.—"As seen from these studies, the genital plates have nothing to do with the interambulacrum, which develops on either side of the oculars. The genitals typically possess genital pores, and one of them possesses madreporic pores, but both of these structures may pierce other parts of the test. Genital plates may, therefore, be considered as structures of secondary importance, of much less morphological value than are the oculars" (173).

The lantern.—"It is believed that the structure of the lantern is of great value in systematic classification, and that the structure of its several parts presents characters that are of ordinal or subordinal value. As Dr. Mortensen pointed out (1904), the structure of the teeth, keeled or unkeeled, is 'a very important character, though it has hitherto received very little attention.' Besides the teeth there are other features of value. Briefly stated, the essential points are: teeth grooved or keeled; epiphyses narrow, or wide and united by suture; the top of the pyramids, as seen when the epiphyses are removed, a smooth floor, or pitted; foramen magnum deep, or shallow; angle of outline of the lantern depressed or erect; compasses present or absent" (177).

Classification.

The class Echinoidea Jackson defines as follows:

"The Echini, though possessing a wide range of structure, may be described as animals possessing alimentary, reproductive, nerve, and water vascular systems within an enclosing superficial pentamerous skeleton which bears movable spines. There are from two to twenty columns of plates in each of the

five ambulacral areas and from one to fourteen columns of plates in each interambulacral area. New coronal plates are formed at the ventral border of the five ocular plates, ambulacral pores pass through ambulacral plates, rarely (clypeastroids) in part between plates. The peristome in all but the Exocycloida bears from one to many rows of ambulacral plates, with or without non-ambulacral plates. There are five oculars (apparently in part or wholly wanting in some of the Pourtalesiidae), and five genitals or fewer, the whole being fused into a mass in certain types of Exocycloida. The genitals typically have each one or more pores as exits of the five interradially situated reproductive glands. In addition, typically, madreporic pores exist in genital 2, but are not recognizable in most Palaeozoic forms. The periproct is more or less plated, situated within the oculogenital ring, or in irregular types outside of that area; the anus is in the periproct. The masticatory lantern is composed of forty pieces (or clypeastroids thirty pieces); it is wanting in adult spatangoids. Respiratory organs consist of Stewart's organs, peristomal or ambulacral gills. Locomotion is effected by ambulacral feet or by spines, or both" (200).

A key to the classification of the Echinoidea is given on pages 201 to 208. Other keys to the species of Paleozoic Echini are given under the systematic descriptions.

Ancestors of Echini.—The author states that Echini "make no close approach to other classes of the Echinodermata. . . . What the ancestor of the Echini as a class was is unknown, but it might fairly be sought amongst the Cystoidea" (200).

Basis of classification.—All Echini recent and fossil are classified by Jackson on the basis of "the structure of the adult and the development of the same. . . . no single character has been followed." The characters taken into consideration are: the ambulacrum, interambulacrum, coronal imbrication, basicoronal plates, ventral resorption of corona, ocular and genital plates, periproct, peristome, Aristotle's lantern, perignathic girdle, spines and tubercles, gills and sphaeridia. "The relative value of these parts naturally differs in different groups of the Echini" (199).

The protechinus.—"The most primitive type of Echini, I believe emphatically, is Bothriocidaris. This view is based on the simplicity of its structure, and especially on the close comparison of this structure with that seen in the very young of all geologically later Echini known and the youthful characters retained at the ventral border in the adults of many types" (208).

"Each interambulacrum of Bothriocidaris consists of a single column of plates, which is represented by a single plate at the ventral border of the interambulacra in the young of all other

Echini. . . . there is ample proof that the interambulacrum begins with a single plate, as shown by Lovén (1874), and Mortensen (1903). . . . This structure with less evidence I correlated (1896) as a stage in development with the single column of plates in Bothriocidaris, naming it the protechinus stage. As Palaeozoic types with many columns of interambulacral plates begin at the ventral border, the young, with a single plate representing a single column, and later add their several columns during development, it seems that Bothriocidaris throws great light on the numerous columns there existent" (210).

Order Bothriocidaroida.—Of Echini the oldest and most primitive order is the Bothriocidaroida, found in the Middle Ordovician of Esthonia. The only genus, Bothriocidaris, has 3 very small species, with 10 columns of hexagonal ambulacral plates, each with a pair of centrally placed podial openings, and but 5 columns of interambulacrals which may have small spines. Plates not imbricate. Periproct within the oculo-genital ring, which consists of 5 very large oculars and 5 very small genitals. Jaws present. It is out of this stock, the protechinus stage, that all regular Echini have evoluted as follows :

Later Echini.—"The feature of Palaeozoic Echini is that they have more than two columns of plates in each interambulacral area. This is true of all known forms excepting Bothriocidaris and Miocidaris as far as the latter occurs in the upper Palaeozoic. Gregory (1897), Sollas (1899), and others have assumed that the most primitive form of Echini had many columns of interambulacral plates in an area, and several authors have considered Palaeodiscus as the most primitive known type. On this basis evolution would entail a loss of such parts, as our modern types all have two columns of interambulacral plates in an area. The evidence of development and adult structure is opposed to this view. At the ventral border of the young of all known modern types, and at the ventral border of the adult where not removed by resorption, we find a single primordial plate in each interambulacral area succeeded in the second row by two plates. There is no evidence in development of a larger number of columns dropping out to two in any known living form, or indeed, in any fossil form excepting as seen in senescence (Perischocidaris), and in the little known Tetracidaris of the Cretaceous. I, therefore, consider the Echini usually classed as the Euechinoida, with a geological range from the Lower Carboniferous to Recent inclusive, and comprising the orders Cidaroida, Centrechinoida, and Exocycloida as next related to Bothriocidaris. This view is based on structure and development. I am well aware of the intervening [great] geological gap, but can only appeal to the rarity of all forms in the Silurian and Devonian to account for the absence of intermediate types. . . .

"The order Cidaroida is placed as directly derived from the Bothriocidaroida without known intermediate forms. The Cidaridae as regards the structure of the young and adult are the least removed from Bothriocidaris of any known echinoid, living or fossil. The young have high hexagonal ambulacral plates with the pores of the pore-pairs superposed. Each interambulacrum has a single plate ventrally, succeeded by two plates in the next row. The peristome has a single row of primordial ambulacral plates which are like those of Bothriocidaris excepting that in that type there are two peristomal rows. The base of the corona has not yet been resorbed, exactly like adult Bothriocidaris. In young cidarids the genitals are large and oculars small and exsert, unlike Bothriocidaris. . . . The Cidaroida present distinctly a combination of Palaeozoic with modern characters" (211–2).

Order Cidaroida with 10 columns of simple ambulacral plates and 10 of interambulacrals. Coronal plates rarely imbricate. Represented in the Paleozoic by Miocidaris (1 species in the Permian Zechstein) of Germany, and another in the Millsap of Colorado. Order well represented from early Mesozoic time to Recent. Out of the Cidaroida was developed the

Order Centrechinoida, where the ambulacral plates are usually compounded of demi-plates. The stock arose in the Triassic and continued to Recent. This order divides into 3 new suborders: (1) *Aulodonta* (Triassic to Recent), with teeth of the lantern grooved, and with epiphyses narrow and not meeting in suture over the foramen magnum (Hemicidaridæ, Aspidodiadematidæ, Centrechinidæ, and Echinothuriidæ); (2) *Stirodonta* (Jurassic to Recent), with the teeth keeled and with narrow epiphyses (Saleniidæ, Phymosomatidæ, Stomopneustidæ, and Arbaciidæ); (3) *Camarodonta* (Cretaceous to Recent) with keeled teeth and wide epiphyses meeting in suture over the foramen magnum (Temnopleuridæ, Echinidæ, Strongylocentrotidæ, and Echinometridæ). The last named suborder is the most specialized of modern regular Echini.

Order Exocycloida, or the irregular Echini, developed out of the Stirodonta in the Jurassic and persists to Recent. Here the periproct is always outside of the oculo-genital ring and lies in interambulacrum 5. "Assuming a monophyletic origin for the group, the three suborders present a striking series of structural departures from the regular Echini from which they doubtless originated. Considering the characters of the group as a whole in brief, the compound ambulacral plates and peristomal gills of the Holectypina and the auricles of that group and the Clypeastrina, the existence of keeled teeth, where teeth are known, and the presence of sphaeridia, are all characters which unquestionably associate the Exocycloida with the Centrechinoida and not with the Cidaroida, where these structures

are non-existent. Mr. Agassiz (1909) has shown that in the young of the spatangoid Echinoneus a well developed lantern exists. This discovery is of the greatest interest and importance, as previously teeth were unknown in this group. . . . Looking back to the Centrechinoida, we find that this type of lantern exists only in the suborder Stirodonta. Further, the attachment of muscles, as stated, occurs only in Arbacia and probably other members of its family. . . . I therefore consider the Exocycloida as connected with the Arbaciidae, probably through some early common ancestral stock" (217–8). The Exocycloida have 3 suborders: *Holectypina* (Jurassic to Eocene) with the ambulacral plates compound or simple and with the ambulacral areas not petaloid dorsally; *Clypeastrina* (Cretaceous to Recent) with more or less flattened tests, ambulacral plates simple and the areas petaloid dorsally, while the lantern is highly modified; *Spatangina* (Jurassic to Recent) with the ambulacral plates simple and the areas commonly petaloid dorsally but with no lantern nor perignathic girdle in the adults.

Order Plesiocidaroida, an aberrant and imperfectly known stock restricted to the Triassic (Tiarechinus), in which the periproct is central but the genitals are large and occupy most of the dorsal surface. There are 2 columns of ambulacrals and 3 of interambulacrals. Plates not imbricate. Base of corona not resorbed. "It is not closely affiliated with any other group" (220).

Order Perischoechinoida, arose in the Bothriocidaroida at least as early as the Silurian and persisted into the Permian. Corona and periproct regular in form and position, with from 2 to 20 columns of plates in each ambulacral area and from 3 to 14 in each interambulacral area. No perignathic girdle, the lantern muscles attaching directly to the base of the interambulacral plates. Embraces the families

Archaeocidaridæ (Eocidaris, Archaeocidaris, Lepidocidaris), with 2 columns of ambulacrals and 4 to 8 of interambulacrals, plates thin and imbricating, base of corona resorbed, and primary spines large; Devonian to Permian.

Lepidocentridæ (Koninckocidaris, Lepidocentrus, Hyattechinus, Pholidechinus), with 2 columns of ambulacrals and 5 to 14 of interambulacrals, plates thin and imbricating, base of corona not resorbed, and all of the spines small; Silurian to Mississippian.

Palaeechinidæ or Melonitidæ (Palaeechinus, Maccoya, Lovenechinus, Oligoporus, Melonechinus), with 2 to 12 columns of ambulacrals and 3 to 11 of interambulacrals, plates not imbricate, some resorption of base of corona, only small secondary spines; Silurian to Mississippian.

In this family the genealogical relations of the genera are

clearly evinced by the structure and development of the ambulacra, an entirely new method of getting ontogenetic stages of growth (231).

Lepidesthidæ (Lepidechinus, Perischodomus, Perischocidaris, Proterocidaris, Lepidesthes, Pholidocidaris, Meekechinus), "one of the most specialized of all groups of Echini," with 2 to 20 columns of ambulacrals and 3 to 13 of interambulacrals, plates imbricating and no resorption of base of corona, primary spines small; Devonian to Permian.

Order Echinocystoida (new), arose in the same stock that gave rise to Perischoechinoida but is an offshoot from a common early stock. Irregular in form with the periproct apparently eccentric in an interambulacrum. From 2 to 4 columns of ambulacrals and 8 to 9 of interambulacrals. Plates thin and imbricating, with the spines small. Lantern typically echinoid, but no perignathic girdle. Families Palaeodiscidæ (Palaeodiscus) and Echinocystidæ (Echinocystites).