SUGGESTED GROWTH PATTERN IN THE MISSISSIPPIAN (CHESTER) ECHINOID *LEPIDESTHES FORMOSA* MILLER

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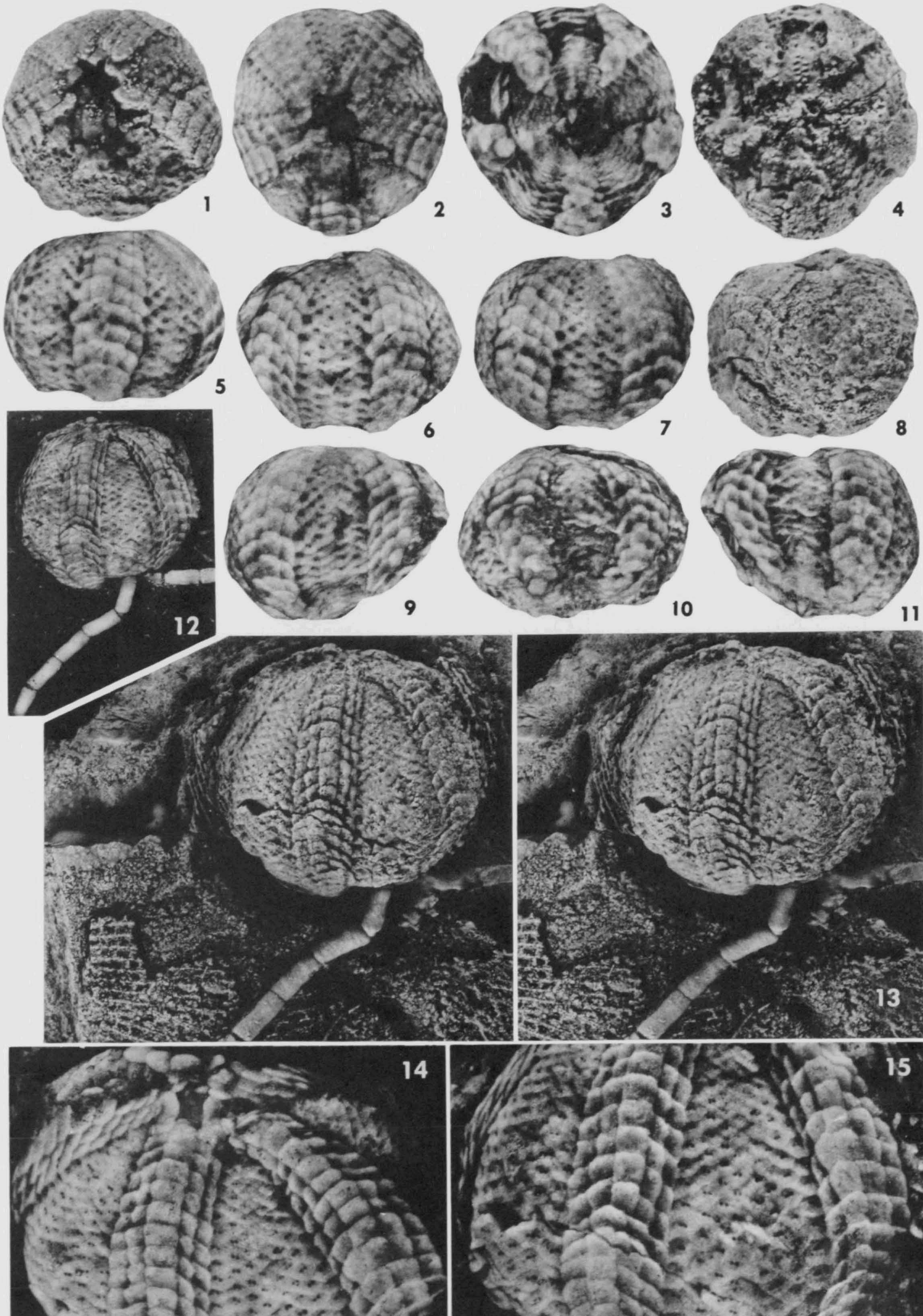
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SUGGESTED GROWTH PATTERN IN THE MISSISSIPPIAN (CHESTER) ECHINOID *LEPIDESTHES FORMOSA* MILLER

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Abstract—Two small and immature specimens of *Lepidesthes formosa* Miller from the Golconda Formation near Anna, Illinois, are well preserved for Paleozoic echinoids. In the larger, each interambulacrum shows four columns orally and five columns aborally; near midzone each ambulacrum has eight columns. In the smaller specimen, interambulacra attained only the four-column stage and ambulacra the six-column stage at midzone; all circumoral plates of this tiny echinoid are ambulacral.

In the aboral section of the larger specimen, exposed areas of individual ambulacral plates were measured by camera lucida and polar planimeter. These data seem to indicate how ambulacral plates, from their inception at the boundary of the apical system, came to occupy their regular arrangement in the oral half of the ambulacrum. Apparently, young plates were soon added to lateral columns; those which could not occupy these preferred positions passed rapidly downward meridionally and gradually shifted laterally to take their places in the eight columns typical of the species. Interambulacral plates were much wider and larger than ambulacral plates when formed, but they grew slower.

INTRODUCTION

A curious little fossil was sent by Harrell L. Strimple to Robert V. Kesling for examination in November, 1965. Partly embedded in a small slab, it was subspherical, about a centimeter and a half in diameter, with five meridional bands of plates enclosing lanceolate areas of tiny imbricated plates. One pole appeared to be set upon a thin stem of very long columnals.

Careful cleaning and submersion in xylol revealed double pores in the tiny plates, thereby clearing all our doubt as to the nature of the fossil. The apparent stem proved to be no part of the specimen at all, but echinoderm fossicles embedded in freak juxtaposition to the oral pole of the echinoid.

In February, 1966, Strimple found and sent another specimen, even smaller than the first and scarcely larger than a pea, measuring only about 7 mm in diameter. This baby echinoid is nearly spherical, remarkably complete; only slight distortion in one ambulacral area and (apparently) absence of some genital plates in the apical system prevent it from being "perfect." It shows the mouth region to be surrounded by a band of ambulacral plates; interambulacra began later with insertion of single plates.

In studying ambulacra of the larger specimen, a composite drawing was made of the aboral section of an ambulacrum by camera lucida. Areas of individual plates were measured by polar planimeter. These areas were assumed to be proportional to the age of the plates, thus affording an opportunity to speculate on the

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Explanation of Plate 154

All figures ×5 except as noted)

Figs. *1–15*—*Lepidesthes formosa* Miller *1–11*, very young specimen, SUI 12382; *1,4,8*, coated with ammonium chloride; all others submersed in xylol. *1,2*, inclined aboral and aboral views, presumed madrepore plate located below periproct. *3,4*, ora views, in xylol showing some teeth and circumoral band of ambulacral plates. *5*, lateral view of interambulacrum 4; *6*, lateral view of ambulacrum IV; *7,8*, lateral views of ambulacrum V; *9–11*, lateral views of ambulacra I, II, and III. *12–15*, half-grown specimen, SUI 12381; *13*, coated with ammonium chloride; all others submersed in xylol. *12*, lateral view, ×2; *13*, lateral stereogram, ×3; *14,15*, lateral and inclined aboral views.

manner in which ambulacral plates, originating one at a time, come to occupy eight regularly arranged columns in the middle section of the ambulacrum.

Our sincere thanks to Mr. Karoly Kutasi for needed assistance in photography, and to Mrs. Helen Mysyk for typing the manuscript.

SYSTEMATIC PALEONTOLOGY

Order ECHINOCYSTITOIDA Jackson
Family LEPIDESTHIDAE Jackson, 1896
Genus LEPIDESTHES Meek & Worthen

Lepidesthes MEEK & WORTHEN, 1868, p. 522.
Lepidestes NEUMAYR, 1881, p. 151.
Hybochinus WORTHEN & MILLER, 1883, p. 331.

Type species.—*L. coreyi* Meek & Worthen, 1868, p. 525.

LEPIDESTHES FORMOSA Miller

Pl. 154, figs. 1–15; text-figs. 2,3,4

Lepidesthes formosus MILLER, 1879, p. 41, pl. 8, fig. 4; MILLER, 1889, p. 258; KEYES, 1895, p. 184; JACKSON, 1896, p. 210; KLEM, 1904, p. 25.

L. formosa JACKSON, 1912, p. 418, pl. 66, figs. 4–7; pl. 68, figs. 3–14; KIER, 1965, text-fig. 4.

non L. formosa TERMIER & TERMIER, 1950, p. 102, pl. 231, fig. 21.

Description of specimen SUI 12381.—Corona partly embedded in matrix, undoubtedly flattened on buried side; exposed part subspherical (pl. 154, fig. 13), about 15 mm in diameter at midzone and about 12 mm between poles. Two ambulacra and two interambulacra well preserved. Each interambulacrum about 3.4 mm wide at midzone; greatest width of ambulacrum about 4.9 mm; hence, by geometric construction, original diameter computed to have been about 13.5 mm.

Interambulacrum composed of five columns in aboral half and four in oral half (pl. 154, fig. 15). Aborally, middle column widest (as exposed), about 1.1 mm, laterally overlapping adjacent columns of ambulacra (pl. 154, fig. 14). All interambulacral plates imbricating aborally, as characteristic for genus. Approximately 120 plates in each interambulacrum.

Ambulacral plates small, about 220 in each ambulacrum, imbricating orally. Largest plates at midzone, there arranged in eight columns, as characteristic for adults of species (pl. 154, figs. 14,15). Well below midzone, only four columns present. Each plate scalelike rather than hexagonal; very young aboral plates measuring about .06 mm^2 in area, those at midzone nearly .30 mm^2. Paired pores for tube feet; each pore pair nearly astride midplane of plate, regardless of location of plate in ambulacrum. Lateral columns of ambulacra overlapped by interambulacrals, probably by as much as one-fourth their area; these columns distinct nearly to apical end. In young (aboral) section, median plates distinctly smaller than lateral plates at same latitude (text-fig. 2; pl. 154, fig. 14).

Apical region with plates somewhat disarranged. Three oculars nearly in original positions, large, subrectangular to trapezoidal; pores not seen. Genital plates not clearly exposed.

Description of specimen SUI 12382.—Corona free of matrix, canteloupe-shaped, its diameter at midzone about 7 mm and its height about 6 mm (pl. 154, figs. 1–11). At midzone, ambulacra slightly narrower than interambulacra, the former averaging 2.1 mm and the latter 2.2 mm (pl. 154, figs. 5–11). By geometric reconstruction, original diameter computed to have been 6.9 mm.

Interambulacra composed of four columns each at midzone and above (pl. 154, fig. 2). Plates imbricating aborally and laterally, as usual in genus (pl. 154, fig. 5). Primordial plate of each interambulacrum separated from peristome by narrow band of circumoral ambulacral plates about 0.3 mm wide. Two plates in each second row, three each in next two or three rows (pl. 154, fig. 3); these early-formed plates apparently ankylosed in part, their junctions indistinct. Thickness of interambulacral plates decreasing markedly near midzone, within the four-column stage (pl. 154, figs. 6–11). One interambulacrum shorter than others to accommodate large plate, presumed to be madrepore, at its aboral end. About 60 plates in each interambulacrum.

Ambulacral plates small, scalelike, about 100 to each ambulacrum, imbricating orally. Paired pores visible near middle of most plates. Definitely six columns in each; one ambulacrum with a row perhaps containing seven columns at midzone; specimen seems to have died at stage when seventh column was being formed. Circumoral band of somewhat irregular plates (pl. 154, fig. 3). Four columns in each ambulacrum at level of insertion of primordial interambulacrals. Ambulacrum tapering aborally to very narrow contact with ocular plate.

Peristome ringed by crenulate area (pl. 154, fig. 4), with parts of teeth visible in mouth. Periproct with four ocular plates preserved and still aligned with ambulacra (pl. 154, fig. 2). Each ocular large, trapezoidal, its inner corners rounded; adjacent oculars nearly in contact. Except for madrepore, no indication of an intervening genital plate in narrow re-entrant between oculars. Large quadrate plate atop one interambulacrum interpreted as madrepore, nearly as wide as total interambulacrum and set

TABLE *1*.—MEASUREMENTS AND RATIOS OF SPECIMENS OF *LEPIDESTHES*

Measurements in millimeters. *h*, height as measured from specimen; *d*, diameter as determined by geometric reconstruction of *Amb* and *iAmb*, areas at midzone; *Amb*, width of *Amb* area at midzone; *iAmb*, width of *iAmb* area at midzone; BM, British Museum; BSNH, Boston Society of Natural History; MCZ, Museum of Comparative Zoology, Harvard; UC, University of Chicago; UI, University of Iowa; UMMP University of Michigan Museum of Paleontology. Data assembled from published measurements, illustrations, and actual specimens.

Species/Specimen	No. Ambulacral columns	*h*	*d*	*Amb*	*iAmb*	*Amb/iAmb*
L. wortheni Jackson	8					
BSNH 11601 (holotype)		36	24	9.2	5.8	1.6
MCZ 3171		60	37	14.2	8.8	1.6
F. Braun Coll.		—	38	14.4	9.0	1.6
L. formosa Miller	8					
SUI 12382		6	7	2.1	2.2	1.0
SUI 12381		14	14	4.9	3.4	1.4
UC 6604 (holotype)		33	31	12.0	7.0	1.7
L. coreyi Meek & Worthen	10–12					
UMMP 149		45	34	12.5	8.7	1.2
F. Braun Coll.		57	44	17.0	10.5	1.6
L. colletti White	16					
UC 6340		37	28	12.0	5.0	2.4
BM E10677		39	30	13.0	5.5	2.4
MCZ 3177		51	31	14.0	7.0	2.0
UC 6641		47	33	15.0	7.0	2.1
MCZ 3176		70	56	24.0	10.0	2.4
MCZ 3179		70	58	26.0	9.0	2.9
MCZ 3178			61	27.0	10.5	2.6

lateral and distal to an ocular (pl. 154, figs.1,2); no pores or perforations observed, but an area ornamented with small papillae.

Remarks.—The two specimens described here are the smallest reported for the species, yet they are remarkably well preserved and contribute to an understanding of ontogeny.

The holotype (University of Chicago Museum 6604) is the largest specimen known; its height was recorded as 33 mm. By geometric reconstruction based on measurements of its illustrated ambulacra and interambulacra at midzone, its original diameter is computed to have been 30.7 mm. In addition to this specimen, Jackson (1912, p. 420) reported twenty in the Springer Collection and two others in the U. S. National Museum.

In a revised description of *Lepidesthes formosa*, Jackson (1912, p. 419) stated that ambulacra were twice as wide as interambulacra. Our measurements of illustrations of the type agree with his reported 12 mm for each ambulacrum and 7 mm for each interambulacrum. This ratio is 1.7, as compared with 1.0 and 1.4 in the small specimens described here (table 1).

Jackson (1912) discovered that circumoral plates in this species are all ambulacral. He also said (1912, p. 419) that in the mouth region "the primordial interambulacral plate is apparently in the basicoronal row, with two plates in the second row, three in the third, and four in the fourth"; the fifth column, he stated, originated below midzone. We cannot discern the basal plates in the larger specimen at hand. In the smaller, however, the circumoral plates are ambulacrals, intervening between primordial and interambulacrals and peristome.

The smaller specimen reached only the four-column stage of interambulacral development. In the larger, the discontinuity between four and five columns occurs near the middle of the interambulacrum (pl. 154, fig. 13). A count of plates (compare text-figs. 4D and 4E) indicates that the smaller specimen died just about the time the fifth column was due to form. The four-column stage may have persisted longer in some individuals than in others, however; a specimen in the Springer Collection, 8042, has four columns in an interambulacrum as far aborally as preserved (Jackson, 1912, pl. 66, fig. 7).

The small echinoid, being exceptionally well preserved, was examined rigorously for cyclic repetition of features, such as described by Devriès (1959). The ambulacral and interambulacral plates received particular attention, but no "spiral" occurrences could be detected.

Occurrence.—Both echinoids illustrated here are from the Upper Mississippian Haney Shale of the Golconda Formation, Chester Series, exposed in a road cut east of Anna, Union County, southern Illinois; road cut on north side of Illinois 146 one-half mile east of the junction with

Interstate 57, in NE¼, sec. 30, T. 12 S., R. 1 W., Dongola Quadrangle. Specimens collected by Harrell L. Strimple in 1965.

Previously reported specimens are from the Kaskaskia Group in Pulaski County, Kentucky; Mississippian strata cropping out in Sloan's Valley, Pulaski County; and the Chester Group at Huntsville, Alabama. Repository and catalogue numbers of specimens are given by Jackson (1912, p. 420). Possibly, all these occurrences are from the Glen Dean Formation in Kentucky and its equivalent in Alabama; in that case, the echinoids are all slightly younger than the two specimens described here.

Illustrated specimens.—The University of Iowa, SUI 12381 and SUI 12382.

GENERAL GROWTH IN ECHINOIDS

Origin of plates.—There is no reason to doubt that plates of Paleozoic echinoids originated in the same manner as those of living echinoids. In her definitive work on echinoderms, Hyman (1955, p. 500) stated,

> More and more ambulacral and interambulacral plates form, to the aboral side of those already present, between the latter and the apical system, so that the corona gets more and more extensive, while the apical system of plates, which at metamorphosis covers the entire aboral surface, comes to cover a smaller and smaller area of surface.

Referring to Paleozoic echinoids, Jackson (1912, p. 52) said, "In the corona, the new plates, both in the ambulacral and interambulacral areas, are always added dorsally, in immediate contact with an ocular plate."

Growth of plates.—In contrast to the general agreement on the origin of plates, two strongly opposing views have been presented on the manner in which plates change after formation. The nature of growth and reduction of individual plates has important bearing on the ontogenetic development of ambulacral and interambulacral areas in *Lepidesthes.*

According to one concept, each plate is subjected to continuous growth by outer secretion and inner resorption. As championed by Jackson (1912, p. 51):

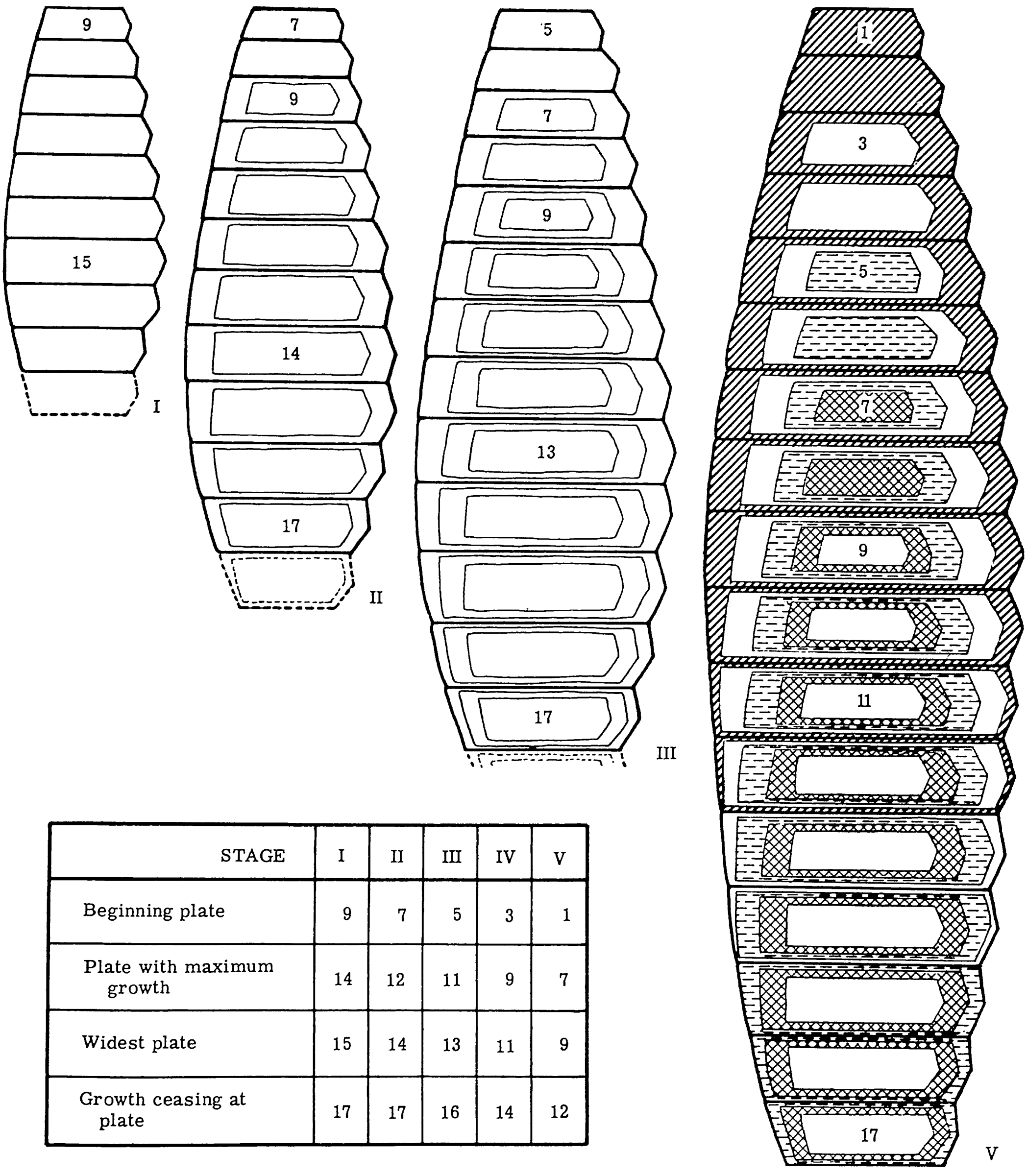
> As the parts are internal they are capable of being added or resorbed at any part throughout the life of the individual. . . . The individual plate of the test grows by a constant addition to the exterior and resorption of the interior, which latter is composed of open lattice-like or trabecular tissue. . . . Sectioning a sea urchin plate, we find no trace of its earlier shape or character within, any more than we find the traces of a young femur within in sectioning the femur of an adult dog.

By the opposing concept, each plate retains exact evidence of older stages, enveloping them with successively younger additions. Becher (1914, p. 310) reported that the central part of the plate, the earliest formed, contains a small area of regularly developed trabecular fabric, secreted in the period preceding mechanical stress from abutting plates. Around this core lies the peripheral suture structures, he continued, which become thicker with progressive growth. This peripheral growth is directed both distally and inwardly, so that the whole plate develops a deep cavity on its inner face, a cavity that becomes filled with undifferentiated secondary skeletal material. This arrangement was further described by Becher (1916, p. 17–23; 1924, p. 184–97) and by Deutler (1926, p. 120–21; fig. A). The meshes of the filling material display much too regular a pattern to have arisen by partial resorption of skeletal tissue, as supposed by Jackson (Deutler, 1926, p. 121).

Despite Jackson's generalization to the contrary, clear traces of the earlier form of plates, tubercles, and spines were found and illustrated by Deutler (1926, pls. 4–9). In fact, with special preparation, growth rings of separate plates in *Echinus esculentus* could be counted and correlated. Thereby, Deutler (1926, pl. 3) was able to establish the amount of growth in each of several successive stages in all plates of an interambulacrum. A generalized diagram based upon his observations and illustrations is offered in text-figure 1. Deutler also studied growth patterns in ambulacral plates and adjacent interambulacrals.

Details of echinoid growth established in Deutler's very important and basic work need not be elaborated here. It suffices to summarize his findings and illustrate them in our text-figure 1:

(1) New plates are added at the aboral end of interambulacra and ambulacra. The number added decreases as the animal grows older.
(2) Increase in number of plates does not occur regularly; a new plate is not always formed at the onset of a new growth interval.
(3) Interambulacral (and perhaps ambulacral) plates grow most rapidly in the first growth stage.
(4) With increasing age of the animal, interambulacral growth becomes restricted to ever fewer plates lying at the aboral side.
(5) Initial growth is primarily meridional. The older it gets, the less a plate grows in meridional direction.
(6) Growth in width increases until the plate is largest of the column. If the plate gets still older, its growth increments gradually decrease and finally cease.



STAGE	I	II	III	IV	V
Beginning plate	9	7	5	3	1
Plate with maximum growth	14	12	11	9	7
Widest plate	15	14	13	11	9
Growth ceasing at plate	17	17	16	14	12

TEXT-FIG. *1*—Growth and development of living echinoid interambulacral column, illustrated in four of five hypothetical stages. Based on actual growth increments established in *Echinus esculentus* Linneaus by Deutler (1926, pls. 3–6).

(7) Maximum growth increment in width is found at least two plates aboral to the largest plate of a growth stage.

Interambulacral-ambulacral growth rates.—Different versions have been presented for relative growth rates in interambulacra and ambulacra. Lovén (1892, p. 18) believed that ambulacral plates glide down relative to interambulacrals. Alexander Agassiz (1904, p. 100) echoed this theory, referring to a "constant flow of the coronal plates onto the actinal system more rapid in the ambulacral zone than in the interambulacral area." Jackson at first (1896, p. 232) declared, "This gliding downward I confess I cannot see in any of the types studied," but later he also came to this conclusion, stating (1912, p. 86) that "ambulacrals flow downward between the interambulacrals and pass as if discharged through the outlet of a river on to the buccal membrane."

On the other hand, Deutler (1926, p. 142,146) found no evidence that the ambulacral plates moved relative to the adjacent interambulacrals in Recent echnoids. In fact, the zigzag suture between them seemed to him strong evidence that movement could not take place. Deutler did find that the two kinds of plates had different growth rates. Maximum increment in width, he reported (p. 146), is attained earlier in the young ambulacral plates than in adjacent interambulacrals of the same age; his findings were based upon actual growth rings found in sectioned plates of one specimen. He concluded (1926, p. 136) that growth zones of interambulacrals and adjacent ambulacrals coincide.

Plate resorption.—Another question of general echinoid growth concerns the possible resorption of plates in the circumoral region. Lovén (1892, p. 25) spoke of "reabsorption of calcareous tissue which from an early period is at work at the aboral margin of the fixed corona." Agassiz (1904, p. 71) found that plates in the peristome region become resorbed. Deutler (1926, p. 59; pl. 3, fig. 1) described and illustrated such elimination of plates. Even in a very young *Echinus esculentus*, 32 mm in diameter, he detected resorption at work on interambulacral plates (1926, p. 160, text-fig. H). The necessary enlargement of peristome to accommodate the larger mouth as the animal increases in size is accomplished in two ways, according to Deutler: the plates bordering the region may grow by increments or some plates around the margin may be resorbed. Actually, he found evidence that both processes operated in *Echinus*.

Absolute growth.— Living echinoids grow very rapidly at first and taper off toward old age. Numerous studies of *Strongylocentrotus droebachiensis* (O. F. Müller), the common green urchin, were summarized by Swan (1961, p. 426). Individuals in June of the settling year attain a diameter of $\frac{1}{2}$ to $1\frac{1}{2}$ mm; at the end of the first year, they averaged 8 to 10 mm; at the end of the second year, 24 to 26 mm; third year, 40 to 42 mm; fourth year, 46 to 54 mm; and fifth year, 52 to 60 mm. Mean values show that annual growth factors are successively 9.0, 2.8, 1.6, 1.2, and 1.1.

GROWTH IN *LEPIDESTHES* AND RELATED GENERA

The pattern of growth of interambulacral and ambulacral plates worked out by Deutler can be applied to many echinoids. But *Lepidesthes* and other genera of the order Echinocystitoida, as well as those of the order Palaechinoida, have more than two columns of ambulacral plates. *Lepidesthes grandis* Kier, for example, has characteristically 20 columns at midzone of each ambulacrum; no species of *Lepidesthes* has less than eight such columns at maturity. Furthermore, in *Lepidesthes* and related genera, the ambulacrum has a narrow junction with the apical system, apparently with sufficient room for one or at most two plates to be secreted. For plates introduced one at a time to transfer into eight or more columns requires more adjustments and complexities than those which form in one column and move orally in that column. Hence, generalizations based on Deutler's observations cannot fully explain growth and development of the total ambulacrum in multicolumned echinoids.

Echinoids developed two processes, it seems, whereby an ambulacrum or interambulacrum expanded with age: (1) peripheral growth or each plate as it moved down along a meridian, and (2) lateral shifting of plates to occupy new meridional positions. The first process prevails in *Echinus esculentus* interambulacra, as described by Deutler (1926) and others. It is also the dominant process information of interambulacra in *Lepidesthes*. The second process, involving lateral components of movement in the downward migration of plates, is met in the ambulacra of *Lepidesthes* and other multicolumned Paleozoic echinoids. In reality, all genera show combinations of the two processes, as will be pointed out below.

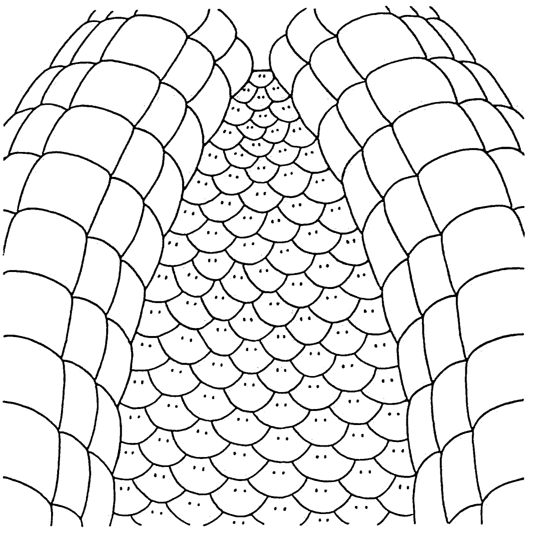
Some misunderstanding arises on the manner in which multicolumned interambulacrals are added in Paleozoic echinoids, apparently stemming from a numbering system introduced by Jackson in 1896 and continued in his 1912 and 1929 articles. In *Melonites*, *Hyattechinus*, and other echinoids with more than two columns of interambulacrals, Jackson found it convenient to apply numbers to the columns for reference. The first plate at the *oral* end of the area was designated 1, and those in one lateral column of plates above it were likewise called 1; of two plates normally present in the next row, the unassigned plate and those in the lateral column above it became 2; of three plates in the third row, the unassigned middle plate and plates of the column above (alongside plates of column 1) were called 3; similarly, the unassigned plate of the fourth row and those of the column above (alongside column 2) became known as column 4; etc. Thus, an interambulacrum of seven plates at midzone would have, from one side to the other, columns 1, 3, 5, 7, 6, 4, 2. As a means of locating a particular plate for reference, this system had utilitarian value; but it conveyed the impression that whole columns of plates formed simultaneously, first on one side of the interambulacrum and then on the other. This, of course, is not so. The final arrangement in columns is the end product of development and adjustment of plates, not an original feature.

Illustrating one of Jackson's applied numbering diagrams, Schindewolf (1954, p. 99) noted that a Carboniferous urchin might have as many as fourteen vertical columns, as compared to only two in modern urchins. The evolution, he declared was completed "in einem einzigen Schritt auf frühen Jugendstadien." Such a conclusion requires strong qualification and explanation.

Ambulacral growth.—If it is at all possible to investigate development of the total ambulacrum in *Lepidesthes formosa*, certain assumptions are necessary: that all plates in the aboral section were of equal size at inception, that growth proceeded at about the same rate in each plate, and that exposed areas are proportional to total plate size. Thereby, it would follow, the size of a plate in this region (as exposed) is proportional to its age. At midzone and below, of course, plate increments decrease and finally cease, so that plates in the oral region are definitely smaller than those at midzone. For basic information, measurements were made of individual plates. First, the aboral section of an ambulacrum of specimen SUI 12381 was reconstructed. Camera lucida drawings were made of plates in the three well-exposed ambulacra of this small echinoid. The outermost ambulacrum (pl. 154, fig. 14) was selected as the least distorted; where preservation defects were apparent, the drawing of this ambulacrum was supplemented and altered to incorporate plate outlines from comparable positions in other ambulacra. The composite diagram is text-figure 2.

Polar planimeter measurements of plate areas on the composite diagram, converted to square millimeters, were plotted at sites of plate centers and lines of equal areas were drawn (text-fig. 3a). These lines were smoothed and adjusted to ambulacral symmetry (text-fig. 3b); such regularity, one suspects, may not be common in actual development. If the basic assumptions are correct, then these lines of equal plate areas reveal the growth pattern of the ambulacrum as a whole. Where lines are closely spaced, plates usually did not move rapidly, growing to their larger size with little migration; conversely, where lines are far apart, plates usually progressed down the ambulacrum at a rapid pace, having insufficient time to attain much increase in size.

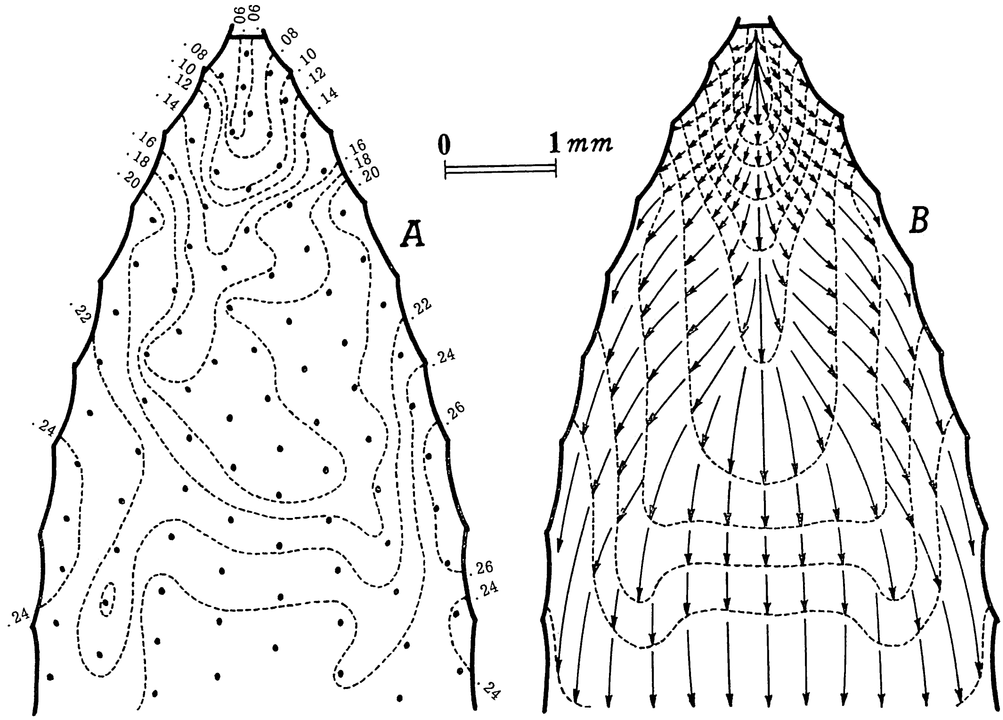
With this interpretation, the lateral columns appear to be the first formed. Rather large plates lie at the aboral ends of these columns, indicating that the side positions were soon filled by plates which maintain their place in the columns. Small plates extend in a meridional tongue down the middle of the ambulacrum (text-fig. 3a); having failed to find vacant places in lateral columns, these plates passed rapidly down the corridor between them.



TEXT-FIG. 2—*Lepidesthes formosa* Miller. Composite plate diagram of aboral part of ambulacrum in specimen SUI 12381, based primarily on middle ambulacrum of specimen as exposed (pl. 154, fig. 14) but supplemented with data from other ambulacra.

Is size of plate (as exposed) in aboral region really proportional to age?—Inasmuch as our whole interpretation of ambulacral growth in *Lepidesthes* is based upon the assumption that the exposed parts of plates in the aboral region bear a direct relationship to age, such assumption must come under considerable scrutiny. Dr. Porter M. Kier of the United States National Museum (letter dated 15 April 1966) writes, "I personally do not believe that you can assume that plate age is proportioned to plate size, so that I rather question your conclusions." Dr. Kier points out that only part of the ambulacral plate is exposed, due to imbrication, and that the amount covered may be more in some places than in others. Dr. David M. Raup, first reviewer of this paper, raises similar objections.

Actually, two questions are involved here. First, is the exposed part proportional to the total size of the plate? In some crushed and distorted specimens we have examined, the answer must be definitely no; one could no more determine size relationships from the visible parts than one could in the case of a pile of discarded shingles. It was for this reason that only a specimen retaining what seems to be its original subspherical shape was selected for study. In it, we think, the angle of imbrication is nearly constant



TEXT-FIG. 3—*Lepidesthes formosa* Miller. *A*, analysis of text-figure 2; dots represent centers of plates; dashed lines represent exposed areas of ambulacral plates as measured by polar planimeter (labeled in values of mm^2); it is presumed that 25% of marginal plates is covered by interambulacral imbrication. *B*, hypothetical pattern of ambulacral growth based on text-figure 3*A*; dashed lines are lines of equal size (and presumably equal age) of individual plates; arrows indicate mean directions and vectors of plate movements. Scale shown between figures.

in the region considered and the exposed part is approximately proportional to total size of plate. Exceptions, as pointed out, are the lateral columns, which are strongly overlapped by interambulacral plates.

The second question, is plate size in *Lepidesthes* and similar echinoids proportional to age? We base our assumption that this relationship holds true in the aboral region of *Lepidesthes* upon the established verity in the two-columned ambulacra of living echinoids. We have no incontestable "proof" in Paleozoic echinoids that one plate did not grow at expense of its neighbors, or that plates were not of different sizes at their inception.

Of particular value and bearing would be a perfectly preserved *Lepidesthes*, each plate of which could be removed entire and polished to show growth rings. Some day such a specimen may be found and examined, clearing many doubts about the growth process.

For the present, we deem that imbrication produced only minor and insignificant differences in size of exposed plates within the aboral part of the ambulacrum in SUI 12381, and we attribute major differences to age. From our data we can only suggest how *Lepidesthes* grew.

Ambulacral/interambulacral growth.—Let us consider the matter of relative ambulacral/interambulacral growth during ontogeny. Quite obviously, an abrupt change occurs very early in the life history, for at first *all* plates are ambulacral, as has been shown in *Lepidesthes formosa* (Jackson, 1912, pl. 68, fig. 3; herein, pl. 154, fig. 3) and in *L. alta* (Kier, 1958, p. 19, pl. 7, fig. 4); at that time the ratio of ambulacrum to interambulacrum is infinity. With introduction of the first ("primordial") interambulacral plates, the ratio is still quite large, around 4. Thereafter, the change in ratio is not clear cut. From published descriptions and figures, we may conclude that at least by the time an individual of *Lepidesthes* is half-grown it has attained the specifically characteristic number of columns of ambulacral plates at mid-zone.

From measurements of four specimens of *Lepidesthes colletti* White, Jackson (1912, p. 425) stated, "These measurements show that the ambulacra are twice as wide as the interambulacra or wider, and are proportionally wider in large specimens than in small ones." From the measurements assembled in our table, 1 there does seem to be a general increase in most species of *Lepidesthes*, but increase in ratio is not always directly correlated with increase in diameter. Perhaps, the exceptions are caused by distortion in preservation rather than original size. Nevertheless, the ratio seems to be constant in such species as *Lepidesthes wortheni* Jackson.

Text-figure 4 presents a hypothetical growth series leading to the larger of the specimens of *Lepidesthes formosa* illustrated herein. The three youngest stages, all preceding the six-column ambulacral stage, were reconstructed on the basis of plates preserved in the oral region of specimen SUI 12382 (pl. 154). Available evidence indicates that from the introduction of its primordial plate (text-fig. 4A), the interambulacrum increases in relative size until it is about as wide as the ambulacrum (text-fig. 4D), and thereafter decreases until in adults it is only a little more than half as wide as the ambulacrum.

Different directions of imbrication in ambulacra and interambulacra may have developed to keep the units distinct. Although in the aboral region the ambulacral plates shifted laterally to attain the characteristic eight columns, no ambulacral plate of *Lepidesthes* has been observed intruding into an interambulacrum. It would seem imposssible for plates to cross over the boundary from either side, just as it would be impossible to interleaf cards in two stacks held at right angles. Whatever pressures were generated during growth, they were resolved within the confinement of a particular sector of the corona.

Plate resorption.—Circumoral plate resorption seems not to have been significant in *Lepidesthes* and multicolumned echinoids. Jackson first reached this conclusion in 1896 (p. 237) when he reported no or very slight resorption of corona in Lepidesthidae. He made an even stronger stand in 1912 (p. 71), stating,

> In Palaeozoic Echini with imbricate plates and many interambulacral columns, there is no resorption, and therefore the primordial interambulacral plate is retained in the adult, as in . . . *Lepidesthes.*

As already mentioned, Jackson illustrated a specimen of *Lepidesthes formosa* with the circumoral ring composed entirely of ambulacral plates. The same situation prevails in the small specimen illustrated herein (pl. 154, fig. 3). Kier (1958, p. 19) established that the oral region in *Lepidesthes alta* is similarly constructed. If resorption took place at all, it involved only a very few of the first-formed plates.

Absolute growth.—The exact age of reported specimens of *Lepidesthes formosa* must remain highly conjectural. Yet if this species grew at approximately the average rate recorded for the living *Strongylocentrotus droecbachiensis* by Swan (discussed above), and if the lagrest reported specimen of *L. formosa* at about 31 mm diameter is assumed to be a fifth year adult, then the two described here at diameters of 7 and 14 mm would have died at ages of one and two years respectively.

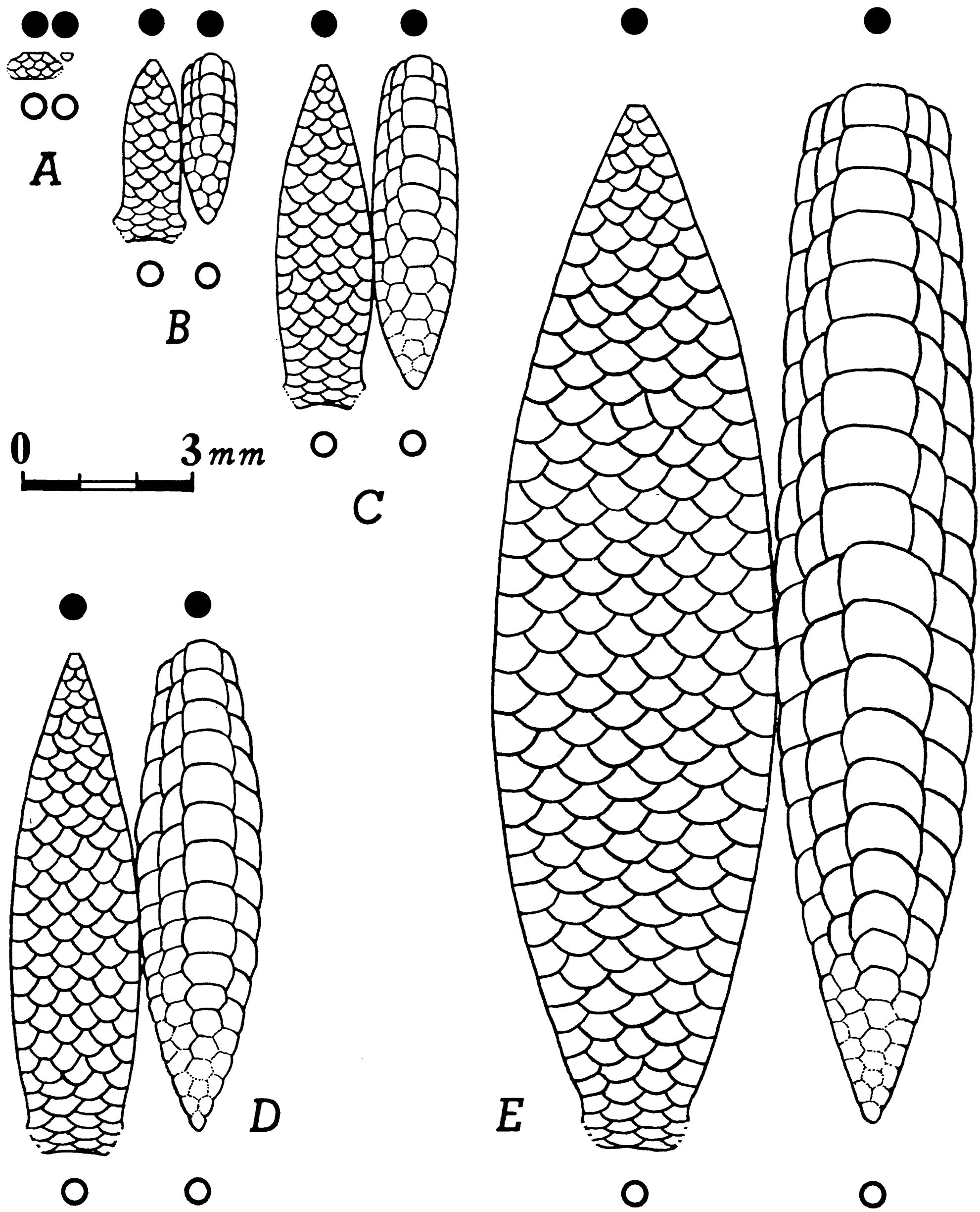
Conclusions.—Major changes in the ambulacral growth pattern of *Lepidesthes* and related multicolumned echinoids took place at: (1) introduction of interambulacral columns, at which time plates of each ambulacrum were distributed in about four columns, (2) introduction of the fifth ambulacral column, (3) introduction of the sixth ambulacral column, etc.

Minor adjustments occurred: (1) at midzone during youthful stages, when additional interambulacral columns were added, changing the shape of the ambulacral sector, and (2) in the aboral part of the ambulacrum continuously throughout the animal's growth as each plate migrated downward to secure its position in a column.

Both peripheral increments and lateral shifting of plates appear to have entered into ontogenetic increase in size. Overall, for each ambulacrum and interambulacrum of ten-columned echinoids (including all living forms), lateral shifting was simply an oscillation between two columns. peripheral increments were more significant, giving rise to the ambulacral/interambulacral ratio at midzone and to shape of the adult corona. For those areas in multicolumned echinoids, however, lateral shifting was more complex and important, ultimately determining the number of columns at midzone.

Ontogeny in *Lepidesthes formosa* involved three distinct phases: (1) development of ring of ambulacral plates around the apical disk, delimiting the peristome region, (2) establishment of interambulacra, which from inception as five little primordial plates increased until they formed a quinquepartite buttressing framework about as extensive as the ambulacra, and (3) gradual relative decrease of interambulacra in favor of ambulacra. The definitive number of adult columns in both ambulacra and interambulacra were formed near the end of the second phase. Growth by plate increments, we think, predominated in phases one and three and seems to have been the only factor operating orad to midzone throughout ontogeny, albeit slowly. On the other hand, growth by lateral shifting of plates was most in evidence in phase two but continued to be significant in ambulacra between apical disk and midzone of the corona.

We have no satisfactory answer to a very fundamental question. How were plates able to



TEXT-FIG. 4—*Lepidesthes formosa* Miller. Juvenile growth stages, showing typical ambulacrum (left) and interambulacrum (right) in selected statges; black spots mark centers of periprocts and circles mark centers of peristomes. *A–C*, hypothetical stages of very young individuals, at inception of primordial interambulacral plates (*A*), at beginning of five-column stage of ambulacrum (*B*), and at six-column stage of ambulacrum (*C*); based upon oral parts of specimen SUI 12382 (pl. 154, figs. 3,4). *D*, six-column stage of ambulacrum, based upon specimen SUI 12382 (pl. 154, figs. 1–11). *E*, eight-column stage of ambulacrum, based upon specimen SUI 12381 (pl. 154, figs. 12–15); although less than half the diameter of the holotype of the species, this specimen shows full column development in both ambulacra and interambulacra. Further growth involves increase in ambulacral/interambulacral width ratio and relative decrease in width of oral ends of ambulacra.

shift laterally, coming to fit against different adjacent plates in the process?

Probably, other species of *Lepidesthes* and related multicolumned echinoids went through similar ontogenies, but information is insufficient to uphold such generalization at this time.

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