CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

UNIVERSITY OF MICHIGAN

VOL. XIV, No. 15, pp. 265–276 (3 pls.) NOVEMBER 14, 1958

CYCLIC PATTERN OF AMBULACRAL COVERING PLATES IN *DISCOCYSTIS LAUDONI* AND ITS TAXONOMIC IMPLICATION

BY

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VOLUME XIV

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8. A New *Tempskya,* by Chester A. Arnold. Pages 133–142, with 3 plates and 1 figure.
9. A New and Unusual Species of the Ostracod Genus *Herrmannina* from the Middle Silurian Hendricks Dolomite of Michigan, by Robert V. Kesling. Pages 143–148,with 1 plate.
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12. A Middle Devonian Species of the Ostracod Genus *Antiparaparchites,* by Robert V. Kesling. Pages 191–200, with 1 plate.
13. Infrabasals in the Crinoid *Opsiocrinus* Kier, by Porter M. Kier. Pages 201–206, with 1 plate.
14. Fossil Crabs from Guam, by Robert V. Kesling. Pages 207–263, with 12 plates.
15. Cyclic Pattern of Ambulacral Covering Plates in *Discocystis laudoni* and its Taxonomic Implication, by George M. Ehlers and Robert V. Kesling. Pages 265–276, with 3 plates.

VOL. XIV, No. 15, pp. 265–276 (3 pls.) NOVEMBER 14, 1958

CYCLIC PATTERN OF AMBULACRAL COVERING PLATES IN *DISCOCYSTIS LAUDONI* BASSLER AND ITS TAXONOMIC IMPLICATION

BY

GEORGE M. EHLERS and ROBERT V. KESLING

CONTENTS

INTRODUCTION

THE arrangement of the covering plates in the edrioasteroid *Discocystis laudoni* Bassler is cyclic. The plates on one side of each ambulacrum are disposed in repeated cycles of six, and they are offset by half a cycle from those on the opposite side. In fact, the pattern is remarkably similar to the intricate design described for *Lepidodiscus squamosus* (Meek and Worthen) by Kesling and Ehlers (1958, pp. 927–29), so much so that *L. squamosus* appears to be more closely related to *Discocystis laudoni* than to other species of *Lepidodiscus*. According to present classification, *Discocystis* differs from *Lepidodiscus* only in the nature of its interambulacral plates. Such a separation may be questioned, because another genus of the family Agelacrinitidae, *Agelacrinites*, includes one species with mosaic and another with imbricating interambulacral plates. A reconsideration of generic criteria is certainly suggested.

Discocystis laudoni was originally described very briefly by Bassler (1936, p. 21) as follows:

> This fine species, the types of which were collected and presented by Dr. L. R. Laudon, of Tulsa University, is readily distinguished by its narrow, well-developed long ambulacra curving decidedly throughout their length. In *D. sampsoni* and *D. kaskaskiensis* the ambulacra are comparatively straight for the first third of their length and then curve rather abruptly. In other features these three species show the generic characters very uniformly.

Bassler made no mention of the pattern of the ambulacral covering plates in *D. laudoni,* and his original figures (1936, Pl. 3, Figs. 7–8) do not show it.

Only the two cotypes have been described. They are catalogued in the United States National Museum (USNM) as No. S3886. In this paper one cotype, which is nearly free of matrix, is referred to as No. S3886*a*. The peristomial region and the proximal parts of ambulacra IV and V are not preserved, but this specimen is of particular interest because the aboral side, which reveals that the ambulacral flooring plates are uniserial, is exposed. The other cotype, which is attached to the matrix on its aboral side, is referred to as No. S3886*b*. It lacks the distal parts of ambulacra II, III, and IV but has the peristomial region very well preserved. Fortunately, the features absent in the one are present in the other. Hence, all significant characteristics of the species can be studied in the two types.

The two cotypes were difficult to photograph. The plates in both are white and the weathered limestone matrix is also white. Although each of the sutures between the plates could be discerned by lighting the specimen at some particular angle, it was impossible to obtain a single exposure that showed all of them clearly. The procedure we used was one which had been found useful in accentuating the sutures in other echinoderms. The specimen was soaked in a dilute solution of brown ink for several hours and then washed thoroughly. Unlike readily available commercial inks of other colors, in brown ink the pigment is extremely fine and disseminated. When the ink dries, the color remains evenly distributed. In the edrioasteroids, the ink solution soaked into the weathered limestone matrix between the plates, but readily washed off the surface of the plates. The matrix along the sutures was faintly stained in the process. The specimens were then submersed in xylol and photographed, see Plates II and III. The only disadvantage of accentuating sutures by this method is that any small particles of matrix adhering to the surface of a covering plate will also be stained. Prolonged washing in dilute ammonia will remove nearly all traces of the ink stains.

We sincerely appreciate the efforts of Dr. G. Arthur Cooper and Dr. Porter M. Kier, of the United States National Museum, who arranged the loan of the cotypes.

PATTERN OF AMBULACRAL COVERING PLATES

A prominent zigzag central line between the plates on one side and those on the other is the most conspicuous feature of the covering plates of the five ambulacra in *Discocystis laudoni.* This line begins at the peri-

stomial region and extends to the end of the long, curved ambulacrum. Bordering the central line, the margins are raised, strongly emphasizing its zigzag course (Pl. I, Figs. 1, 3), and the apparent angles of the line are rather irregularly serrate (Pl. II, Figs. 1–2). Only a very few of the plates have serrate edges, and most of the serrations are at their junctions.

In the proximal part of each ambulacrum, the central line is nearly straight, and the plates on each side of it are irregularly polygonal (see Pl. III). Throughout the rest of the ambulacrum, however, the central line is zigzag and the plates on each side are fairly regularly cyclic (Pl. II, Figs. 1–2). With few exceptions, each cycle is composed of six plates. Of these, the first, second, fourth, and sixth plates extend from the central line to the edge of the ambulacrum; in typical cycles, the third and fifth plates do not.

The first plate is small and short. It is located where the zigzag central line is near the edge of the ambulacrum. In some cycles this small plate is rectangular, but in others it is trapezoidal or pentagonal; in a few, it is deeply indented to fit around the apex of the central line. The second plate is typically subpentagonal. It is bounded by the edge of the ambulacrum, the first plate, the central line, the third plate, and the distal part of the fourth plate. In shape it varies somewhat from one cycle to another. The third plate is small. It fits between the proximal parts of the second and fourth plates and borders on the central line. In most cycles it is triangular, but in some, in which the adjacent part of the central line is serrate, it is subrhombic.

The fourth plate is the longest and largest and has nearly the same shape in each cycle; it is much less variable than any of the others. The sides are parallel and more or less perpendicular to the edge of the ambulacrum, but the shape of its proximal end depends upon the configuration of the adjacent part of the central line; it may be straight, bluntly tapering, sharply acuminate, or, in rare cases, indented. The fifth plate is almost a mirror image of the third and is situated between the fourth and sixth plates; the sixth plate is a mirror image of the second.

The plates on the other side of the ambulacrum are arranged in similar cycles, but are offset by half a cycle so that the first plate on one side is directly opposed to the fourth plate on the other side.

In addition to its general curvature and distal tapering, each ambulacrum is slightly convex at the first plate of each cycle and slightly concave at the fourth plate. In most cycles, the distal edges of the second, fourth, and sixth plates fit against three sides of a very short but broad, trapezoidal plate of the interambulacrum.

Although the cyclic arrangement of ambulacral covering plates in

Discocystis laudoni is like that described in *Lepidodiscus squamosus* (Meek and Worthen) by Kesling and Ehlers (1958), the following differences were noted: (1) the plates in *L. squamosus* vary much less from one cycle to another than do those in *D. laudoni;* (2) the edges of the ambulacra in *L. squamosus* are not sinuous like those in *D. laudoni;* (3) the limbs of the central zigzag line are regularly serrate in *L. squamosus;* (4) in *L. squamosus* the plates form a smoothly vaulted convex cover across the ambulacrum, but in *D. laudoni* the margins of the plates are prominently raised along the edges of the zigzag central line; (5) in *L. squamosus* the proximal end of the long fourth plate is typically blunt, but in many cycles in *D. laudoni* it is rather sharply acuminate; and (6) the third and fifth plates in each cycle are rarely if ever triangular in *L. squamosus,* whereas they are commonly triangular in *D. laudoni.*

OTHER FEATURES OF THE SPECIES

Several characteristics of *Discocystis laudoni* that were not mentioned in the original description are shown in the two cotypes. They are the covering plates of the peristome, the plates in the anal pyramid, a supernumerary ambulacrum (in No. S3886*a*), and a structure in the posterior interambulacrum that may be a genital pore. A brief discussion of these features is offered below.

Covering plates of the peristome.—Irregular, polygonal plates cover the anterior half of the peristome and meet those that cover the posterior half along a transverse serrate line. This line extends from the junction of the central lines of ambulacra I and II on the left to that of ambulacra IV and V on the right (Pl. III). At its center this transverse line is joined by a posterior extension of the central line of ambulacrum III. Such an arrangement is also present in *Lepidodiscus squamosus,* as described by Kesling and Ehlers (1958).

The peristomial region in *Discocystis laudoni* is like that in *L. squamosus;* it is strongly asymmetrical with the left half much narrower than the right. The covering plates in the right posterior region form a conspicuous arcuate slit, the left half of which is roughly parallel to the transverse serrate line across the middle of the peristome; the right half is parallel to the proximal part of ambulacrum V. This slit in *D. laudoni* corresponds to a line in the right posterior part of the peristome in the holotype of *Lepidodiscus squamosus* along which the plates are caved in. The arcuate shape of the slit in *D. laudoni* suggests that it was an opening into the peristome, and its position strongly indicates that it is the hydropore. The plates between the slit and the transverse line form a shallow trough

(Pl. I, Fig. 3). Posteriorly, the slit is bounded by large, broad covering plates.

Plates in the anal pyramid.—The original figures of the cotypes (Bassler, 1936, Pl. 3, Figs. 7–8) are retouched in the anal region, so that No. S3886*a* appears to have seven nearly equal, subtriangular plates arranged like segments of a circle, and No. S3886*b* appears to have eight similar plates. Our examination of the types does not confirm such an arrangement or number of plates. In each specimen, the anal pyramid is nearly circular, gently convex, with the shape of a low dome. Each pyramid contains plates of at least two conspicuous sizes and shapes: large subtriangular plates and narrow, elongate, lanceolate plates. Whereas the triangular plates vary only slightly in width of base and in height, the lanceolate plates vary greatly, particularly in length.

Excluding the small plates around the periphery, in No. S3886*a* the anal pyramid has 20 plates (Pl. II, Fig. 2). Of these, 10 are subtriangular, 9 are lanceolate, and one is small and subrhombic. Only one of the subtriangular plates extends to the center of the pyramid; two of them, situated in the anterior part of the pyramid, are in contact throughout their length, but the others are wholly or partly separated by the lanceolate plates, which radiate outward from the center. The two lanceolate plates in the left anterior region are much shorter than the others. The small subrhombic plate, near the center of the pyramid in a posterior position, is bordered by one subtriangular plate and three lanceolate plates.

In No. S3886*b* (Pl. III) the anal pyramid has only 19 plates; it lacks the small subrhombic one present in the other cotype. In this specimen, the two adjacent subtriangular plates lie in the posterior part of the pyramid, rather than in the anterior, as in No. S3886*a*. Furthermore, only one of the lanceolate plates is conspicuously shorter than the rest, and that one is situated on the right side. None of the subtriangular plates extends to the center.

Supernumerary ambulacrum.—In No. S3886*a*, ambulacrum II bifurcates near the middle of its length (Pl. I, Figs. 1–2). Each branch has ambulacral covering plates with the same cyclic arrangement as that in the proximal part of the ambulacrum. One branch lies on the oral surface of the theca, and the other branch curves over the edge onto the outer edge of the aboral side. Although the distal part of ambulacrum II is not present in No. S3886*b* for comparison, we assume that the supernumerary ambulacrum in No. S38886*a* is in reality an anomaly, as are those known in other species of edrioasteroids.

Genital pore.—A genital pore has not been established in edrioasteroids. In the cystoids, however, a conspicuous opening of the theca, supposed to

have served as a genital pore, has been recognized for many years. In most cystoids, such a "pore" lies in the posterior interambulacrum between the anal opening and the mouth. In No. S3886*b* there is a structure in the posterior interambulacrum that has the general form of a pore, and its position suggests that it may have been the genital pore. This feature lies to the right of the anal pyramid (Pl. III). The posterior interambulacrum has a polygonal depressed area, apparently where one or more large interambulacral plates are missing from the specimen, which contains an elongate, narrow opening bordered by plates. The bordering plates are much smaller than those in the adjacent area. In No. S3886*a*, the corresponding area is covered by one large polygonal plate.

Our knowledge of edrioasteroid anatomy and morphology is far too meager at this time for us to decide whether this opening and plate arrangement were normal for the species or were anomalous—caused perhaps by an injury during the life of the animal. It appears to us, however, that this area was formerly covered over by a large interambulacral plate as in No. S3886*a*. With the exception of the flooring plates of the ambulacra and the plates framing the peristome, no other structures in erdioasteroids are known in which the outer plates of the oral surface are directly underlain by additional plates. It seems credible, therefore, for this to be a genital pore, which opened below a protective interambulacral plate and connected with some kind of duct leading out between the interambulacral plate and the subthecal plates. The groove anterior to the opening may have formed such a duct.

TAXONOMIC IMPLICATION

Since the ambulacral covering plates of *Discocystis laudoni* markedly resemble those in *Lepidodiscus squamosus*, both in shape and cyclic arrangement, the description (Kesling and Ehlers, 1958) of the plates in *L. squamosus* would need very little modification to apply to those of *D. laudoni*.

In contrast to this pattern, the ambulacral covering plates in other species assigned to *Lepidodiscus* are not arranged in cycles. In *L. alpenensis* Bassler, for example, the plates on one side alternate with those opposite, varying only in a gradual decrease in size toward the distal end of the ambulacrum. All the plates have nearly the same shape. Most of the ambulacral covering plates in *L. ephraemovianus* (Bogolubov), as shown in Hecker's figure (1940, Fig. 3), also have a simple alternation. Although a serrate central line is present in each ambulacrum, it is formed by the apices of the plates on one side fitting between those on the other.

Because the arrangement of ambulacral covering plates of *Lepidodiscus squamosus* so closely resembles that of its Mississippian contemporary, *Discocystis laudoni,* but differs so markedly from those of other species that have been assigned to *Lepidodiscus,* one does well to question whether the generic distinction between *Lepidodiscus* and *Discocystis* is real. As noted above, the genus *Discocystis* has been separated from *Lepidodiscus* on the basis of mosaic, rather than imbricating, interambulacral plates. Bassler (1936, p. 20) wrote of *Lepidodiscus* as having "Theca with the curvature of the ambulacra as in *Discocystis,* namely, four rays to the left and one to the right, but differing in the presence of strongly imbricating interambulacral plates."

Is this mosaic or imbricating nature of the interambulacral plates generically significant? We believe not. *Lepidodiscus squamosus* and *Discocystis laudoni* both have discoidal thecae, the same curvature of ambulacra, relatively small peristomial regions, long curved ambulacra, peripheral plates imbricating but not fused to form a rigid ring, and a similar intricate pattern of ambulacral covering plates. In each species, ambulacrum V curves to the right and terminates very close to the anal pyramid, and ambulacrum I extends around the distal half of ambulacrum V. The two species agree in all characteristics except one, the nature of the interambulacral plates. They appear to be related closely enough to be assigned to one genus. *Lepidodiscus,* described by Meek and Worthen in 1868 (p. 357), has priority over *Discocystis,* described by Gregory in 1897 (p. 131), but the synonymy of the two genera must be decided by careful study of the type species of *Discocystis, D. kaskaskiensis* (Hall).

A comparison of two other species is pertinent. *Agelacrinites hamiltonensis* Vanuxem, the type species, and *A. southworthi* Bassler demonstrate the extent of variation in interambulacral plates that can exist in one genus. Whereas Bassler (1936, pp. 15–16) did state of *Agelacrinites,* "This genus . . . is readily recognized by its five long, narrow, much curved ambulacra, two of which (4 and 5) bend to the right, and three (1, 2, 3) to the left, and by the sculptured, mosaic interambulacral plates," in the original description of *A. southworthi* (1936, p. 16), nevertheless, he wrote, "The interambulacral plates, which are large, smooth, and imbricating, differ markedly from the sculptured polygonal, very slightly overlapping plates of the genotype." We do not question that *A. southworthi* is congeneric with *A. hamiltonensis;* both have discoidal thecae, the same curvature of ambulacra, relatively small peristomial regions, long, narrow ambulacra, and peripheral plates more or less fused to form a rigid ring. However, the generic character of "sculptured, mosaic interambulacral plates" does not apply to *A. southworthi.* Since both

mosaic and imbricating plates occur in species of *Agelacrinites,* separation of *Lepidodiscus* and *Discocystis* only on the basis of a difference in interambulacral plates is difficult to justify.

The pattern of ambulacral covering plates, which is complex in many edrioasteroids, deserves more serious taxonomic consideration than it has hitherto received. We find it difficult to believe that the cyclic patterns in *Lepidodiscus squamosus* and *Discocystis laudoni* evolved independently and became so remarkably similar by convergence. The development of additional ambulacral covering plates and changes in their size, shape, and arrangement seem to be more significant than the degree of proximal overlap in the interambulacral plates.

Before any revisions in the classification of edrioasteroids can be proposed, however, the pattern of ambulacral covering plates must be studied in well preserved specimens of all species. This is a monumental task. Furthermore, the differences observed must be evaluated in conjunction with other features of the edrioasteroids, such as the pattern of peristomial covering plates, curvature of the ambulacra, shape of the theca, and nature of the peripheral plates. Perhaps relationships will also be revealed by the pattern of plates in the anal pyramid, although this now appears to vary greatly within each species. As shown in *Agelacrinites southworthi,* the current classification does not provide a reliable key at the generic level. Some criteria now being applied are dubious; others should be carefully appraised.

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Received for publication April 4, 1958

PLATES

EXPLANATION OF PLATE I

(All figures × 2)

PAGE

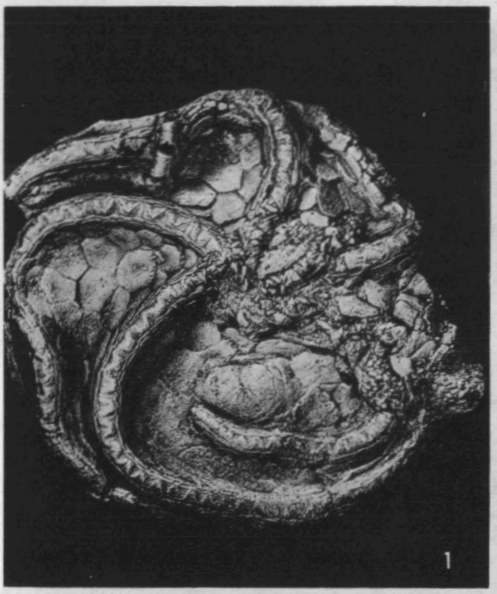
Discocystis laudoni Bassler 268

FIGS. 1–2. Oral views of cotype (USNM No. S3886) No. S3886*a*.

FIGS. 3–4. Oral views of cotype (USNM No. S3886) No. S3886*b*.

In Figures 1 and 3 the specimen was coated with a thin sublimate of ammonium chloride to emphasize the form of various plates; in Figures 2 and 4, it was submerged in xylol to show the sutures between plates more clearly.

PLATE I

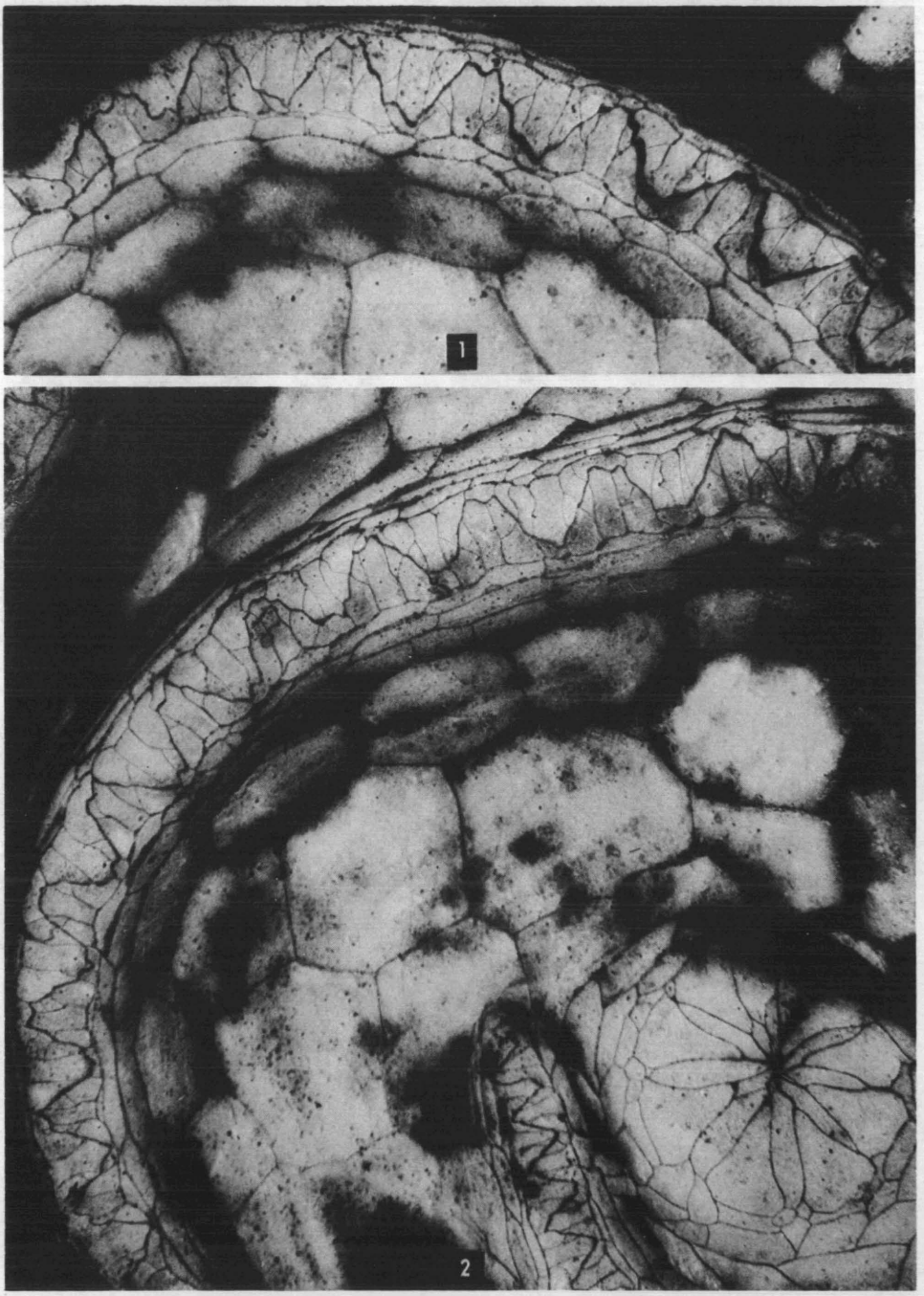

1


2


3


4

PLATE II



EXPLANATION OF PLATE II

(All figures × 6)

FIG. 1. Oral view of part of ambulacrum II, showing the arrangement of the ambulacral covering plates. Cotype S3886*a*.

FIG. 2. Oral view of part of ambulacrum I, the anal pyramid, the terminus of ambulacrum V (lower center), and a short segment of ambulacrum II (upper left). Cotype S3886*a*.

In both instances, the specimen was photographed while submersed in xylol.

EXPLANATION OF PLATE III

(Figure × 5)

PAGE

Discocystis laudoni Bassler 268

Oral view of the peristomial region, proximal parts of the ambulacra, the anal pyramid, and the terminus of ambulacrum V (lower left). No. S3886*b*.

The specimen was photographed while submersed in xylol.

PLATE III