Article XVI.—THE JURASSIC AMMONITE FAUNA OF CUBA
BY MARJORIE O'CONNELL, Ph. D.
PLATES XXXIV TO XXXVIII
INTRODUCTION

In 1910 Dr. Carlos de la Torre of the University of Havana announced the discovery of Jurassic ammonites at Viñales in the Province of Pinar del Rio, western Cuba. No species were described and the generic identifications appear to have been incorrect, leading to a mistaken correlation of the formations at Viñales with those of the Upper Jurassic (Kimmeridgian) of Mazapil, Mexico. In the summers of 1918 and 1919 Mr. Barnum Brown made an extensive collection of ammonites from Viñales and numerous other localities in Pinar del Rio, the material thus obtained revealing a large and varied fauna sufficient to determine an accurate zonal succession and make possible a detailed correlation with synchronous formations in Mexico and Europe. Besides this material I have also had for study some sixty-odd specimens sent to me by Dr. Mario Sanchez Roig of Havana, to whom I wish to express my thanks for his courtesy and generosity. Dr. la Torre gave to Mr. Brown some unlabelled specimens from his type locality and these I have identified. Dr. T. W. Stanton, of the United States Geological Survey, kindly loaned me his own collection of ammonites from the Kimmeridgian and Portlandian of Mazapil, while from Professor A. W. Grabau, of the Palaeontological Museum of Columbia University, I secured the loan of some very fine specimens of the genus Idoceras, also from Mazapil. I have thus been enabled to compare the Cuban and Mexican faunas and to determine their true relations.

In the present paper I shall describe only a small part of the entire fauna, selecting a few species which conclusively establish the fact that the rocks formerly supposed to be of Kimmeridgian age really belong to the Upper Oxfordian. I have studied the material from the point of view of ontogeny, dwelling upon the biological principles illustrated in the development of these ammonites. The stratigraphy, field relations, correlations and palaeogeography will be taken up in a more extended report which is now in the course of preparation, and in which will be included the descriptions of many more genera and species, together

with faunal lists for the successive palæontological zones of the Jurassic. All of the types described below are from the material collected by Mr. Brown and are in the collections of the Department of Geology and Invertebrate Palæontology of The American Museum of Natural History.

While this paper was in the editor's hands, preparatory to publication, there appeared among the agricultural reports of Cuba a paper entitled 'La Fauna Jurásica de Viñales' by Doctor Mario Sanchez Roig, containing brief descriptions of a large number of specimens collected by him and his father. The species which I had identified for them in 1918 and 1919 are there figured and described, while the age of the formations which I determined from the fossils is also included. In addition they included certain species which are incorrectly identified as, for instance, all of those referred to the genus Idoceras and figured on Pl. x, figs. 5–7, and Pl. xi, figs. 1–5. I have seen some of the material identified by Dr. Roig as Idoceras; it all belongs to the genus Perisphinctes, as do also the specimens figured in his paper. On page 669 I have explained how a superficial resemblance of the Cuban species of Perisphinctes to the Mexican species of Idoceras may lead to incorrect identifications and to consequent errors in correlation. A misleading feature of Dr. Roig's paper is his inclusion, without quotation marks, of entire descriptions of Mexican species translated verbatim from Burckhardt's publications into Spanish, with often not a single word about the Cuban specimen, as for instance, under Haploceras fitlar on pp. 40, 41. What appears as a description of the Cuban form is actually a translation of Burckhardt's description of H. fitlar from Mazapil. Dr. Roig states nothing at all about his own material except for four measurements which he gives at the beginning. One not familiar with Burckhardt's monographs, or not having them at hand for constant comparison, would have no way of telling whether he was reading a new description of a Cuban ammonite or an old description of one from Mexico. It is only fair to state, however, that Dr. Roig labored under many difficulties, such as inadequate library facilities, lack of good collections of type material for comparison, the incompleteness of his own specimens, many of which could not be identified, and especially the fact that his own training had been primarily in medicine rather than in palæontology. His interest in natural history led him to collect vertebrate and invertebrate fossils and to make known to the scientific world some of the

1Roig, Mario Sanchez. 1920. La Fauna Jurásica de Viñales. Republica de Cuba, Secretaria de Agricultura, Comercio y Trabajo, Boletin Especial, 61 pp., 23 plates.
important organic remains of the Jurassic of western Cuba. To the naturalists of Cuba and to others who do not have ready access to Burckhardt's monographs, the careful translation of the protographs from French into Spanish will be very useful, and I know, from a personal communication, that Dr. Roig made the translations with the feeling that he was rendering a service to his Cuban and Spanish readers to whom original sources in other languages were not so available as they were to him.

Brief announcements of the stratigraphy and correlation of the Jurassic formations of Cuba were given before the Palæontological Society of America at the Baltimore meeting in 1918¹ and before the Geological Society of America at the Boston meeting in 1919.² Certain palæontological studies of the Cuban ammonites have been incorporated in a short paper originally presented at the Baltimore meeting above referred to.³

In the description of the ammonites of Cuba I have employed the nomenclature first proposed by Hyatt⁴ and later added to by J. P. Smith.⁵ Most writers on this group of invertebrates are in the habit of giving a few shell measurements and ratios for adult specimens or else they give a set of measurements for several specimens of different sizes of the same species and then make certain general statements about observed trends in shell proportions. It is well known that all ammonites change in proportions in successive stages of development but accurate quantitative data is seldom given. I have, therefore, in describing the ontogeny of the Cuban species, given actual shell measurements and calculated certain significant ratios for as many stages of growth in individual conchs as the preservation of the specimen would permit. At any point on the shell six measurements are sufficient for the determination of the size and form of the conch, these being the diameter (d), the height of the whorl measured from the venter to the line of involution with the preceding whorl (h. i.), the height measured from venter to the impressed zone (h. i. z.)—a measurement which can be made only when one has an oral cross-section—the height of the whorl above the preceding

5. Smith, J. P. 1913. Chapter on Cephalopods in Eastman Translation of Zittel's 'Text-Book of Palæontology.'
whorl \((h. p.)\) obtained by measuring the vertical distance from the venter to the line of involution of the preceding whorl, the width of the whorl \((w)\) or the greatest thickness between the lateral faces, and the width of the umbilicus \((u)\). These measurements are all given in millimeters. From these may be calculated the shell proportions which vary with growth, that is, the allometric ratios. They are \(\frac{h.i.}{d}, \frac{h.i.z.}{d}, \frac{w}{d}, \frac{w}{u}, \frac{u}{d}\) and \(\frac{h.i.}{u}\).

**DESCRIPTION OF SPECIES FROM THE OXFORDIAN**

**Perisphinctes** Waagen

In the Perisphinctidae the costae have a characteristic arrangement into groups or bundles, there being one long costa passing from the line of involution to, and usually across, the venter, while one, two, three, or sometimes more, shorter costae branch off from the long one. At repeated intervals on the conch there is a smooth groove or constriction occurring usually after every three to seven bundles of costae. A detailed study of all of the Cuban specimens belonging to the genus *Perisphinctes* showed that in each sector of the whorl bounded by two constrictions, or sphincters, the succeeding groups of costae vary one from another, there being certain definite trends in the development of individual costae as well as in their arrangement into groups. From the ontogeny of several of the species, it appears that in the earliest stages the conch is smooth; then constrictions develop; and finally simple, unbranched costae appear, filling in the spaces between constrictions. The details of the time of appearance of these morphological features will be found below (pp. 650, 676) under the description of *Perisphinctes cubanensis* and *P. plicatiloides*. The simple costae soon become branched. The process of branching expressed in terms of growth seems to indicate that the mantle of the animal grew more rapidly forward on the ventral region than on the sides and consequently it was thrown into folds more rapidly on the ventral and ventro-lateral regions than on the dorso-lateral regions. Thus, while a single fold in the mantle at the umbilical margin was sufficient to take up all the surplus forward growth of the mantle, two, three, or more folds were required to take up the growth on sides and venter. The position of these folds is shown in the conch by the arrangement of the costae, which are nothing more than the shell expression of the form of the soft parts of the animal.

In order to have a uniform and simple way of referring to the various costae I have adopted the following system of nomenclature. The conch is divided into sectors bounded by the grooves or sphincters, for which
reason I designate them intersphincterical sectors. At the beginning of each is a single, simple costa, usually a little more pronounced and thicker than the others and this is continuous across the venter, where it is often, and in adult specimens generally, double, there being no actual bifurcation but rather a thickening and broadening with a dividing line passing longitudinally across the ventral portion of the costa. This first and distinctive costa bounding each sphincter orally I have designated the orad or o costa, Fig. 1. So far as the Cuban species are concerned this costa never marks the beginning of a triad of costae but always appears alone and is then followed by the typical triad groups; and it seems to be a rather universal fact in all species of *Perisphinctes*

![Diagram](image)

Fig. 1. Diagrammatic sketch of the mode of development of costae in the genus *Perisphinctes*, showing the origin of diad and triad groups and of intercalated costae.

that the first costa in any intersphincterical sector is simple, with at most a ventral branching, and is succeeded by the more complex triads or bundles of costae. On the apicad side of each sphincter is a complex system of costae consisting of a single continuous costa (the *apicad* or *a* costa) passing from the umbilical suture on one side of the whorl uninterruptedly across the venter to the suture on the opposite side. From this costa there diverges at a point near the line of involution a second costa (*a*2) which is directed orad. With the growth of the conch the point of divergence moves ventrad and eventually a new costa (*a*3) develops, diverging from *a*1 at the line of involution. As the point of divergence of *a*2 from *a*1 migrates ventrad, the maximum strength or thickness of the *a*1 costa passes in its ventral portion to *a*2 while the ventral part of *a*1 is separated off and finally becomes a free intercalated rib, passing apicad and out of the group of costae definitely bounding the sphincter.

The letters *a*1, *a*2, and *a*3 are, therefore, used to designate the costae in the same relative position to the sphincter, *a*1 being in every case the first continuous costa apicad of the sphincter. The process of costal development is thus shown diagrammatically in Fig. 1.
Perisphinctes cubanensis, new species
Plate XXXIV, Figures 1 and 2

I have before me three fairly complete specimens of Perisphinctes which show the following range in maximum diameter: 50.7 mm., 65 mm., and 86.57 mm. The character of the final whorl of each specimen differs so markedly from that of the remaining two in form, size, and number and arrangement of costae that probably each specimen, if found in separate localities, would be described as a distinct species. Yet a careful study of the ontogeny of each conch has shown that all three specimens are closely related and that two of them represent specializations in given directions from a simple more generalized type, which I have selected as the holotype of Perisphinctes cubanensis, new species (A. M. N. H. No. 18556). The other two specimens I have designated as mutations α and β (A. M. N. H. Nos. 18557 and 18558, respectively). I have called these specialized individuals mutations in order to indicate that the modifications, whether allometric or rectigradational, are in given directions, or orthogenetic, yet I cannot be certain, from the material so far studied, whether they are true mutations in the Waagen sense showing modifications in successive horizons or whether they are variations in the Waagen sense (submutations of Grabau) showing modifications in one horizon. Since the Viñales fauna comes from nodules which contain species from two zones of the Upper Oxfordian, the three individuals under discussion might be either mutations or variations, and I have called them by the former name that there might be no confusion with the ordinary usage of variety, a term which is laxly employed and carries with it no implication of orthogenetic development such as is shown in these specimens.

The holotype of Perisphinctes cubanensis shows the greater part of six volutions, on three of which portions of entire whorls, including the venter, are visible. Very little of the shell is preserved, so that all of the characteristics and measurements noted below are for the internal mold only. Nothing can be learned of the embryonic stages of development because the protoconch is absent, nor is it possible to determine the exact position of the earliest conch stage. For this reason, in counting the number of volutions, I have arbitrarily started at the first point in the umbilicus where a whorl rises out of the central, limey matrix which conceals or replaces the protoconch. This point almost certainly does not mark the precise beginning of the first conch volution but is very close to it and serves as a convenient point of reference from which to count the
successive volutions. Since this form is monotypic, I have no additional specimens to break down for studying the protoconch and early embryonic stages of growth.

**Form and Proportions.**—The shell as a whole is rather compressed, giving the whorls an oval cross-section (except for the impressed zone), which, however, does not show any angularity at the umbilical shoulder nor along the ventral margins. The umbilical shoulder is always pronounced, though rounded, and there is thus produced a distinct umbilical zone. On the sixth volution where the whorl is more compressed and the shoulder consequently more distinct the distance between the line of involution and the point of greatest thickness of the whorl is 6.3 mm. It is highly probable that the earliest whorls were circular in cross-section (except for the dorsal in-bending of the curve caused by the impressed zone), since the ratio of width to height at the end of the third volution is 0.89, the trend in succeeding volutions being toward a smaller ratio, which shows that if at any time in the ontogeny the whorl was as wide as high, that is with a ratio of 1.00, it must have been before the third volution. In the holotype of *Perisphinctes cubanensis* the whorls increase regularly in height, having approximately the same ratio to the diameter throughout the ontogeny, for the greatest range is from 0.33 to 0.39 (see third column in Table 1). Because the increase in height is fairly constant and not progressively greater, involution is not extreme and there results a broad umbilicus which in the early whorls is approximately as broad as the aperture is high but in the later stages slowly becomes relatively broader, as is shown by the decrease in the ratio \( \frac{h.i.}{u} \) from 1.00 to 0.89 (see columns 2 and 11, and 3 and 13 in Table 1). In the early shell the width of the whorl is about one-third the total diameter, but this ratio decreases (column 9) so that at the end of the specimen the width is only one-quarter of the diameter, showing that there is a relative decrease in breadth as compared to diameter, as well as a decrease when compared to the height of the whorl. All of these progressive allometric changes in the ontogeny are set forth in Table I.
Costae and Sphincters.—In the earliest observable nepionic stage the conch is smooth, showing neither costae nor constrictions. At the end of one and a quarter volutions the first constriction or sphincter appears, the umbilicus here being 1.79 mm. wide. On the remaining three-quarters of the second volution there are two more constrictions, but no costae are discernible until one and three-quarters volutions, although they probably appear at about one and a half volutions, since apicad of that position the whorls are still smooth, as shown by the surface of a few remnants of actual shell, while where the costae are first seen they are already well developed. The critical area, unfortunately, is destroyed. The costae appear just apicad of the third constriction, the umbilicus here being 3.30 mm. wide and the whorl 5.00 mm. thick. It is to be noted that the appearance of constrictions is independent of the formation of costae, since the former appear earlier than the latter in the ontogeny, and yet, once the costae begin to develop, they always follow a definite plan of formation which heralds the appearance of a constriction and the costae never have this particular arrangement without being followed by a constriction nor, on the other hand, does a constriction ever appear which is not preceded by costae which are arranged in a different manner from that observed in intersphincterial areas. Thus, while the lines of growth are parallel to the costae, the constriction diverges pronouncedly from the direction of the principal costae, which indicates a marked ventral growth of the shell prior to the formation of

Table 1.—Allometric Changes in *Perisphinctes cubanensis*, new species

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<thead>
<tr>
<th>$d$</th>
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<td>1</td>
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<td>22.03</td>
<td>8.75</td>
<td>0.39</td>
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<td>......</td>
<td>11.00</td>
<td>7.80</td>
<td>0.35</td>
<td>0.89</td>
<td>8.80</td>
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<td>33.56</td>
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<td>9.88</td>
<td>2.52</td>
<td>0.29</td>
<td>15.78</td>
<td>9.68</td>
<td>0.29</td>
<td>0.78</td>
<td>11.74</td>
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<td>55.00</td>
<td>21.40</td>
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<td>26.90</td>
<td>16.30</td>
<td>0.29</td>
<td>0.76</td>
<td>20.50</td>
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<td>65.89</td>
<td>24.30</td>
<td>0.36</td>
<td>19.35</td>
<td>4.95</td>
<td>0.29</td>
<td>31.60</td>
<td>18.52</td>
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<td>83.47</td>
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<td>22.40</td>
<td>5.22</td>
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<td>37.27</td>
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<td>0.26</td>
<td>0.75</td>
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<td>86.57</td>
<td>29.78</td>
<td>0.34</td>
<td>23.92</td>
<td>5.76</td>
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<td>39.60</td>
<td>21.42</td>
<td>0.24</td>
<td>0.72</td>
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each constriction. This law holds throughout the ontogeny of the holotype of the species and for the two mutations and has also been observed in other species.

The arrangement of costae on either side of the third constriction is shown in Fig. 2. On the apicad side of the constriction a rather coarse costa \((a_1)\) appears, its point of origin being upon the umbilical shoulder, which is pronounced though rounded. This costa is strong and thick and gives off a branch \((a_2)\) near the line of inclusion. The \(a_3\) costa diverges near to the umbilical suture of the second volution and is directed orad diagonally across the whorl, parallel to the \(o\) costa which is simple and not very prominent. Whether or not the \(a_3\) costa gives off a branch on the ventral or lateral ventral zone cannot be determined because of the involution of the whorls. Thus the fundamental plan of sphincterdelimitation by the costae may be briefly described as follows. A simple orad costa and a complex apicad system in which costae \(a_2\) and \(a_3\) are developed, with the latter simple (or branched?). The \(a_1\) and \(o\) costae are strong, while the branches of \(a\) are weaker. As a result, the two strong costae enclose a triangular area which widens ventrally and in which are situated the weaker costae and the constriction. The last of the branches of the \(a\) system, in this case \(a_3\), and the \(o\) costa are always parallel and bound the constriction on either side. This fundamental plan can be observed in each sphincterdel costal group in this species and its mutations but in the latter onto-stages of the holotype and in the earlier ones of accelerated mutations certain modifications take place leading to increased complexity along definite lines. The modifications so far observed are in three directions: one, through the development of additional orad branches; two, through the ventral migration of the point of divergence of the older branches \((a_2, a_3, \text{etc.})\); and, three, through the increased obsolescence of the dorsal portion of the last-formed costa on the apicad side of the constriction, that is, usually, \(a_3\), or, in cases of acceleration, \(a_4\), until it appears as a free intercalated costa.

The third volution of the conch contains at least three constrictions, but the state of preservation does not permit more accurate observation. However, the specimen does show that between the \(o\) costa
of the third constriction (counting from the earliest one seen) and the $a_1$ of the fourth, there are six intersphincterial costae, the branching of which is not exposed, and the same number exists between the fourth and fifth constrictions, but between the fifth and sixth the number cannot be determined.

Half of the fourth volutions is visible in its entirety because the later whorls are broken off. Complete constrictions are thus exposed and the character of the ventral costae may be determined. What appears to be the eighth constriction of the conch occurs just orad of the beginning of the fourth volution at a point where the umbilicus is 8.38 mm. wide, the whorl 5.89 mm. thick and 5.80 mm. high. There is a single straight costa ($o$) on the orad side of the constriction (Fig. 3). On the apicad side a single, low, coarse costa ($a_1$) arises on the umbilical shoulder. At a height of 3.12 mm. from the line of involutions the $a_2$ branch diverges from the $a_1$ costa; $a_3$ in its dorsal portion merges into $a_1$, showing that it was formed very soon after $a_2$. At a height of 3.81 mm. from the line of involutions $a_3$ bifurcates, the orad branch, passing across the venter approximately parallel to $o$. On the venter this branch of $a_3$ becomes broader than other members of the $a$ system so that it appears as a slightly prominent lip emphasizing the apicad boundary of the constriction. The $a_3$ costa is strong on the dorso-lateral area until branching takes place, and then the branch becomes strong so that there is produced the appearance of an almost continuous strong costa on the apicad side of the constriction.

On the first half of the fourth volution, there are four constrictions, of which the one just described in detail is the first. Between the $o$ costa of the eighth and the $a$ system of the ninth constriction there are three lateral costae, the first of which is simple with an apicad deflection in its venter portion, the other two having one branch each which gives an appearance of bifurcation. Between the ninth and tenth constrictions are four intersphincterial1 costae, all of which are branched once, and the same is the case between the tenth and eleventh, while there are only three between the eleventh and twelfth constrictions, the costae thus

---Line of involutions

Fig. 3. Arrangement of costae at beginning of fourth volution of *Peri-

sphinctes cubanensis*, holotype A. M. N. H. No. 18556, showing increased complexity in grouping produced by repeated bifurcations.

\[\text{---Line of involutions}\]

---Line of involutions

1It is to be remembered that by this term I designate the lateral costae between the $o$ of one constriction and the $a$ system of the next succeeding one.
showing a certain amount of variation. There are three constrictions on the second half of the fourth volition, which is the last complete whorl on the holotype and which ends at a diameter of about 31.8 mm., the shell being broken away just at the point where the fifteenth constriction should appear so that only portions of the fifth and sixth volutions remain. On the last half of the fifth, which ends at a diameter of about 65.8 mm., there are four constrictions, twenty primary costae arising in the umbilical zone and fifty-five ventral costae, including the o and a as well as the intersphincterial costae. Between the first two constrictions the lateral costae are either singly or doubly branched; between the last two all are doubly branched giving the appearance of trifurcation or intercalation. The arrangement of the costae on the last quarter of the whorl is shown in Fig. 4.

On the last half of the fifth whorl the costae are well preserved on both sides and on the venter and it will be noted that they are arranged in groups of three, in which one costa passes from venter to dorsum and is strong, while two are developed on the venter only and are less pronounced (Fig. 5). Furthermore, a careful study of each group shows that there is a steady oral progression of the strong costa from group to group. Thus, on the right side of the shell the first group (I) beyond the o costa of intersphincterial group M shows costa 1 strong and continuous and deflected apicad toward the venter, with 2 and 3 weaker, 2 being attached, 3 directed towards 1, but free. In the second group (II) the greatest strength has passed to costa 2, while the point of divergence of branch 1 is weak and 3 has approached 1 dorsally. In group III the first costa has become free, 2 is still strong but bent backward, while 3 has become fully attached to 2. In the fourth group (IV), which is the a system of the next constriction, 1 has separated off and appears as a free "intercalated" costa, 2 is still directed toward 3 but is free, while the greatest strength has passed to 3 which bends apicad so much that, with additional growth on the ventral portion, two new costae appear in quick
succession. Of these, 4 is parallel to 3 except at its dorsal end where it approaches 3 and, if prolonged, would join it about midway of the lateral face of the whorl; 5 bends more strongly toward 4 and is shorter than it, but on the left side 5 actually joins 4.

The left side of the shell shows less acceleration in the orad migration of the strong costa. Thus group I' has 1 and 2 united as in group I but 3 is entirely free, not even pointing towards the strong rib. Group II' shows costa 1 just becoming free as in group II on the right side, but costa 3 is still nearly parallel. The third costa of groups I' and II', though appearing parallel to the second costa in each case, would, if
continued dorsally, join this costa near the line of involution. The third costa of group III' in its dorsal end bends toward the second costa, which is strong, and would join it, if continued, much farther from the dorsum than the third costa of the two preceding groups. This, then, may be interpreted as a progressive ventral migration of the point of divergence of the third from the second costa in the successive groups, even though, at the point of divergence, the shell is not thrown into a costal elevation. The third costae of groups I, II, and III on the right side show this same progress further along, costa 3 of group I corresponding essentially to 3 of group III', while costa 3 of group II very nearly joins costa 2 and the corresponding costa of group III actually does join. In this respect, then, the three groups of the right side represent further stages in acceleration beyond the first three groups of the left side. The fourth group (IV') of the left side or the a system is less accelerated than the group IV on the right side, costae 1, 2, and 3 of IV' corresponding essentially to 1, 2 and 3 of group III on the opposite side. Costa 1 of group IV' is free; 2 is the strong costa but is deflected apicad ventrally; 3 joins 2 at the point of deflection; 4 is still free and essentially parallel to 3; and 5 turns towards 4 but does not join it. In group IV on the right side, as already stated, costa 4 joins 3; and 5 joins 4. Again, if we prolong costa 4 in group IV' it would join the strong costa near the line of involution and costa 5 would join 4 much more dorsad than is the case in group IV on the right side. Thus again is shown the ventral migration of the point of departure of the costae on the more accelerated side, a mode of progressive change already referred to as characteristic of the orad costa of successive a systems.

In the intersphincterial sector N there are only three groups of costae instead of four, but these on the whole are more accelerated along the lines already discussed than are the corresponding ones in sector M (Fig. 5). This is not the case, however, with the first group of the right side of the N system, which is essentially like the first group of the M system, but the second group of N is parallel to the apicad part of group IV in M; that is, costae 1, 2, 3 of N-II have the same relation to one another as costae 1, 2, 3 of M-IV. Group N-III, however, is more accelerated than any group in M, for the three costae are parallel, 1 and 2 being short and free while 3 is strong but not deflected. N-III is the a system of the constriction terminating N, on the right side, but only costa 4 is preserved, this bending toward 3 but not joining it, being, therefore, more accelerated than the corresponding costa of group M-IV. On the left side of the shell, however, the series is complete, groups I' and
II' being practically the same as their corresponding groups on the right side, though slightly less accelerated. Costa 4 of group III has the character of 4 of group III, but two additional costae, 5 and 6, appear. Costa 5 is longer than 4 and parallel to it and would, therefore, if prolonged diverge from costa 3 nearer the line of involution. Costa 6 is short, its dorsal end bending towards 5 but not joining it. Taking costae 3, 4, 5, and 6 of this group, and the corresponding lines of growth of the shell which are always parallel to the costae wherever preserved, we see here an accelerated forward growth of the ventral side of the shell, this being always more rapid than the forward growth of the shell as a whole, a fact which explains the arrangement of the costae of this group. This accelerated forward growth comes to an end with the formation of the constriction, as already pointed out.

The o costa, which in all the earlier whorls is a simple, thick costa, becomes compound somewhere on the fifth volution, for it so appears at the constriction at five and a half volutions and becomes progressively more marked. This compound character is due to an interruption in the formation of the costa, the mantle fold, of which it is the shell expression, having for a short time contracted on the venter, giving rise to a groove, after which it expanded to the usual size and a costa of normal strength was formed. On the holotype these two parts of the compound costa never become independent branches but, because they are incipient branches and so appear at a rather early stage in mutation β, I have called them the o₁ and o₂ costae.

The only portion of the sixth whorl preserved is that from five and a quarter to five and a half volutions, that is, from a diameter of 78.6 mm. to one of 86.5 mm. In this space there are two constrictions which I shall designate x and y since I do not know their exact numerical position in the ontogeny. There are three groups of costae in the intersphincterial region X (Fig. 6). Group X-I on the right side corresponds almost exactly with the stage of development shown in group N-II, the acceleration being so great that instead of the maximum strength being found in the first costa as it is in group I in M and N, it has already passed to the third. Costae 1 and 2 in X-I are both free but directed towards 3, while in the next group (II) they appear to be almost parallel to 3. In this respect X-II corresponds to the first three costae in N-III. Group X-III is accelerated beyond anything observable in the N area and undoubtedly corresponds to some stage exhibited in the shell during the early part of the sixth volution, which portion, unfortunately, is missing. This last group in X is the complete a system terminating sector X and
Fig. 6. Arrangement of the costae on first half of sixth volvation of *Perisphinctes cubanensis* showing adult costal grouping, each triad consisting of one long, strong costa and two short, weaker, free, "intercalated" costae. Right side (R) more accelerated than left side (L).

Fig. 7. Tracing from the holotype of *Perisphinctes cubanensis* showing the last costae on the final whorl and the adult costal delimitation of the last constriction. Note that the new costa \(a_4\) begins near umbilical shoulder; \(a_2\) and \(a_3\) have become obsolescent dorsally appearing as free, "intercalated" costae. Same as group III in Fig. 6, \(a_1 = \text{costa } 3, a_2 = 4, a_3 = 5, a_4 = 6\).
contains six costae, of which the third is the strongest (Fig. 7). Costae 1 and 2 are essentially parallel, appearing as free "intercalated" ventral costae; 3 is deflected apicad ventrally so that the short branch 4 is in line with the dorsal portion of 3 and would join it if prolonged. Costa 5 is short and directed toward, but not joined to, 6. In N-III' the sixth costa is short while 5 is longer, extending half-way towards the dorsum, while in X-III and X-III' the strength has passed orad to 6 which is the longer costa and which extends three-fourths of the way towards the dorsum. On the left side of the whorl the first of the three X groups is slightly less accelerated than on the right, costa 2 is a little stronger than 3 and the line of continuous growth is along the former not the latter as on the right side; 3, however, is united to 2. Group X-II' is practically identical with X-II, as is also X-III' with X-III. On the orad part of the left side some of the shell is preserved towards the dorsum and the growth-lines are clearly shown paralleling the long and strong 3 costa and the shorter, weaker 6. In the shell it is seen that the sixth costa approaches much nearer the dorsum than would be supposed from what can be observed in the internal mold, which suggests that in later whorls this will become a normal long costa.

These details concerning the mode of costal development throughout the ontogeny of this species bring out the following interesting facts: (1) the costae develop in a definite and progressive manner throughout the entire conch; (2) the sphincters divide the conch into sectors in each of which the costae develop with mathematical precision and increasing complexity, the arrangement at the beginning of each sector repeating that at the middle or end of the preceding one, while the costae at the end of each sector are more advanced than those at the end of the preceding one; the definite trends in development are thus progressive in their entirety, but at repeated intervals in the life of the animal there was a resting period, a slight repetition and then a further advance; (3) there was differential acceleration on the right and left sides of the animal, showing that the mantel folds were seldom absolutely bilaterally symmetrical, one side of the mantel having been thrown into folds such as the opposite side had one-quarter or one-half of a volution before. Yet each side showed the same plan of costal arrangement and though one lagged behind the other the nicety and exactness of their correspondence is truly remarkable. The significance of this clearly demonstrated orthogenetic method of growth is more fully discussed in another paper.¹

Having considered in detail the arrangement and number of costae and the sphincterial costal systems, we may turn to the form and mode of growth of the individual costae. As we have already observed, the costae on the first four volutions begin on the umbilical shoulder, but in the last two volutions the point of origin moves dorsally, the o costa being, in general, slightly longer than adjoining costae. In those places on the fifth and sixth volutions where the shell is preserved, all costae are seen to arise directly from the line of involution, but the internal mold shows the first traces of these same costae only on the umbilical shoulder, which would lead to the supposition that, were the shell preserved throughout the later whorls, all of the costae would be found to have their inception at the lines of involution. Throughout the ontogeny the costae are directed orad at an angle of about 20° to a line passing through the centre of the umbilicus. Since the lateral costae in general develop parallel to one another, it is obvious that, being on a spiral, if a costa had an orad trend of 20° at any point and the next costa were parallel to it the second would have a direction less than 20°. This is actually the case and the costae would in time be directed less and less orad, until they became vertical to the whorl and would then bend apicad. But we have seen that prior to the formation of each constriction there is an excessive ventral growth and formation of new costae so that the general trend is restored. To be more precise, it is only the successive o costae that have the orad inclination of 20°, while the succeeding intersphincterial costae become progressively less and less inclined until the first costa of each a system averages an inclination of only about 15°. The strong apicad reflection of the costae on the umbilical shoulder is a character which is found in all of the mutations but is not confined to this species. A slight orad inflection at about the middle of the flanks is very generally, though not invariably, present. The primary costae are most sharp at the umbilical shoulder, becoming less salient and more rounded as they approach the point of branching. On the venter all of the costae have approximately the same strength, with the exception of the simple or compound o costa, which is pronounced not because it is any higher but because it is broader and thicker than the other costae. Occasionally, too, the last costa of the a system is thickened. On the later whorls the most sharp and salient costae are the longest ones of the a systems of the successive constrictions.

Wherever the venter is exposed the costae in the internal mold show a slight depression or apparent obsolescence on the median ventral line. In some places the costae are completely interrupted, in others merely
notched, while at the end of the last whorl preserved most of the costae show no weakening at all in crossing the venter. Where this obsolescence is shown there is produced a smooth, narrow ventral band. The full significance of this feature is discussed below on p. 669, but it may here be stated that the interruption is visible only on the internal mold and that in the few places where the shell is preserved on the venter the costae show no weakening. The smooth ventral band is, therefore, occasioned by the formation of a ridge on the inner surface of the shell, this ridge being due to excessive shell deposition or an internal ventral thickening which finds no expression in the outer surface.

Sutures.—As is the case with so much of this Cuban material, the preservation is such that no sutures are shown.

Comparison with Related Forms.—Since the holotype of this species is almost certainly not the conch of a fully grown individual and since no sutures are shown, comparison with other species is very difficult. It is very closely related to Perisphinctes durangensis Burckhardt from the lower beds of the Upper Oxfordian of Cerro del Volcán in Durango, Mexico. Unfortunately, Burckhardt had only a single, fragmentary specimen and his specific characteristics as to form, proportions, and costal arrangement are described from the last two whorls only. The dimensions which he gives are taken at a diameter of 123 mm., while the specimen of \textit{P. cubanensis} shows a maximum diameter of 86.37 mm. Comparisons in actual measurements and in proportions between the two species are, therefore, impossible but the form, cross-section of whorls, costal arrangement, and the mode of development of the costae bounding the sphincters may be compared and in these respects the two species are very similar.

Horizon and Locality.—Lower beds of the Upper Oxfordian; Viñales, Pinar del Rio, Cuba.

\textit{Perisphinctes cubanensis} a, new mutation
Plate XXXIV, Figures 3 and 4

Holotype (A. M. N. H. No. 18557).—This mutation is represented by a single specimen which is practically complete, except for one break, through five and a half volutions. The last whorl has been crushed and a certain amount of lateral compression has thus been brought about. Shell remains in only a few places and it is in such a poor state of preservation where it is shown that it is of little value except at the end of the specimen, where a narrow strip shows the mode of growth of one of the costae.
The conch in form, proportions and amount of involution is so similar to the holotype of *P. cubanensis* that, were it not for differences in the costal and sphincterial development, the two specimens would be considered as the same species, for they differ less from each other in these allometric characters than do many individuals which are unhesitatingly referred to a single species. Unfortunately, it is impossible to make measurements of the young stages, but between the diameters of 39.3 mm. and 65.0 mm. the actual dimensions and proportional ratios are almost identical in the two forms and they show the same directions in development. (Compare Tables 1 and 2.)

**Table 2. Allometric Changes in *Perisphinctes cubanensis* mutation a**

<table>
<thead>
<tr>
<th>$d$ mm.</th>
<th>h.i.</th>
<th>$h.i.$</th>
<th>h.i.</th>
<th>$h.i.$</th>
<th>h.i.z.</th>
<th>h.p.</th>
<th>w</th>
<th>w</th>
<th>u</th>
<th>u</th>
<th>h.i.</th>
<th>No. of volutions completed</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>5</td>
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<td>7</td>
<td>8</td>
<td>9</td>
<td>10</td>
<td>11</td>
<td>12</td>
<td>13</td>
</tr>
<tr>
<td>39.3</td>
<td>15.1</td>
<td>0.38</td>
<td>19.3</td>
<td>13.1</td>
<td>0.33</td>
<td>0.86</td>
<td>13.6</td>
<td>0.34</td>
<td>1.11</td>
<td>4½</td>
<td></td>
<td></td>
</tr>
<tr>
<td>45.5</td>
<td>16.9</td>
<td>0.37</td>
<td>22.1</td>
<td>14.4</td>
<td>0.31</td>
<td>0.85</td>
<td>15.7</td>
<td>0.34</td>
<td>1.06</td>
<td>5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>65.0</td>
<td>23.4</td>
<td>0.36</td>
<td>18.8</td>
<td>4.6</td>
<td>0.29</td>
<td>31.8</td>
<td>18.8</td>
<td>0.29</td>
<td>0.81</td>
<td>25.3</td>
<td>0.39</td>
<td>0.92</td>
</tr>
</tbody>
</table>

It will be noted that the measurements and ratios for mutation $a$ might almost be used as interpolations for *P. cubanensis*: the first two lines of figures in Table 2 would fit in between the second and third in Table 1, while the third line in Table 2 would fit in between the third and fourth in Table 3. There are, however, certain differences due to slight differential acceleration or retardation in the allometrons. For instance, if we take *P. cubanensis* as the standard for comparison, then mutation $a$ shows retardation in the retention, at a diameter of 65 mm. of the shell ratios $\frac{w}{d}$ and $\frac{w}{h.i.}$ which in *P. cubanensis* are found at some diameter between 22 and 33 mm. On the other hand, the ratios of width of umbilicus to diameter and of height of whorl to umbilicus are in mutation $a$ at 65 mm., diameter the same as are found at some diameter between 65 and 83 mm., in *P. cubanensis*. In this respect, then, mutation $a$ is accelerated. These varying rates of change furnish an excellent example of heteroëpistasis.
In costal arrangement mutation $a$ retains a primitive condition, most of the triad groups showing only one free costa, while in the adult *P. cubanensis* both of the short costae have become free. The costae bounding the sphincters in the last whorl of mutation $a$ have the appearance of homologous costae in the early stages of *P. cubanensis*, the points of divergence of the $a$ costae not having migrated very far ventrad, while the $o$ costae show no tendency toward ventral division. The whole costal plan, as well as the individual costae, show less acceleration than obtains in either *P. cubanensis* or mutation $\beta$.

The internal mold shows a ventral groove the same as in *P. cubanensis* and mutation $\beta$ and its origin is the same.

The preservation is such that no sutures are shown.

**Horizon and Locality.**—Lower beds of the Upper Oxfordian; Viñales, Pinar del Rio, Cuba.

**Perisphinctes cubanensis** $\beta$, new mutation

Plate XXXV, Figures 1 and 2

**Holotype** (A. M. N. H. No. 18558).—The third specimen in this group is rather poorly preserved and the inner whorls cannot be studied, but in its proportions it appears undoubtedly to belong to the *P. cubanensis* series, although the costae show an acceleration beyond any stage observed in the other forms. While it is impossible to count the inner whorls, it is probable that there are about five volutions represented, judging from the size.

The conch is most like that of mutation $a$, showing the same proportional deviations from *P. cubanensis* as does that mutation. The amount of involutions is approximately the same for all the specimens at the same diameter. In Table 3 are given all of the measurements that could be obtained from the specimen, together with the ratios.

**Table 3. Allometric Changes in Perisphinctes cubanensis mutation $\beta$**

<table>
<thead>
<tr>
<th>$d$ mm.</th>
<th>h.i. mm.</th>
<th>h.i. $d$</th>
<th>h.i.- h.i. mm.</th>
<th>h.i.- h.i. $d$</th>
<th>h.p. mm.</th>
<th>$w$ mm.</th>
<th>$w$ $d$</th>
<th>$u$ mm.</th>
<th>$u$ $d$</th>
<th>h.i. $u$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>5</td>
<td>6</td>
<td>7</td>
<td>8</td>
<td>9</td>
<td>10</td>
<td>11</td>
</tr>
<tr>
<td>39.7</td>
<td>14.9</td>
<td>0.37</td>
<td></td>
<td></td>
<td>19.1</td>
<td>12.7</td>
<td>0.37</td>
<td>0.85</td>
<td>13.8</td>
<td>0.34</td>
</tr>
<tr>
<td>44.7</td>
<td>15.9</td>
<td>0.35</td>
<td></td>
<td></td>
<td>21.1</td>
<td>13.2</td>
<td>0.29</td>
<td>0.83</td>
<td>18.1</td>
<td>0.41</td>
</tr>
<tr>
<td>50.7</td>
<td>17.4</td>
<td>0.34</td>
<td></td>
<td></td>
<td>23.9</td>
<td>14.3</td>
<td>0.28</td>
<td>0.82</td>
<td>20.3</td>
<td>0.40</td>
</tr>
</tbody>
</table>
From these figures we see that, when the conch is 39.7 mm. in diameter, it is almost identical in form with mutation α at a diameter of 39.3 mm. (see Table 2) and, in consequence, the acceleration or retardation in proportions which we noted when comparing mutation α with P. cubanensis, hold also for mutation β. But, while at this stage α and β are alike and both differ in the same way from P. cubanensis and while both continue as they increase in size to differ in the same directions from the primitive form, β shows a more rapid progress in ratio changes than does α, so that when β is 50.7 mm. in diameter it has very nearly the shell ratios of α at 65 mm. or is slightly in advance.

It is in the costal arrangement that mutation β differs most decidedly from the other two specimens in this group and it is possible that when more material is studied this difference will be found to be great enough to require the separation of this mutation as a distinct species. Even on the fourth volution the costae show a repeated double bifurcation and once a triple bifurcation, so that the typical triad grouping is frequently interrupted by bundles of costae arranged in multiples of two. This is well shown at the very end of the holotype in figure 1 on Plate XXXV. The o costae, wherever visible, are markedly double in character on the venter, assuming at an early stage a character which in P. cubanensis does not become prominent until the fifth volution. Since there is only a single specimen of mutation β and none of the early whorls are shown nor any sutures, its affinities are a little uncertain except as indicated by the allometric proportions.

**Horizon and Localities.**—Lower beds of the Upper Oxfordian; Viñales, Pinar del Río, Cuba.

*Perisphinctes delatorii*, new species

Plate XXXV, Figures 3; 4a, b, c; 5; 6


**Holotype** (A. M. N. H. No. 18559).—Portions of six volutions are preserved, but after the second, which is complete, only half or less of each whorl remains. During the preparation of the specimen, which was almost wholly embedded in the tough limestone of one of the nodules, the incomplete later whorls separated from each other so that the entire dorsum and venter of the fifth and sixth and the venter of the third and fourth volutions were exposed. On the first, second, and third whorls the shell is more or less preserved, but beyond these there is only the internal mold, which, however, on the dorsum of the last two
whorls has the shell from the preceding whorls still clinging to it. At three places the conch has broken along septa exposing to view the lobes and saddles.

**Form and Proportions.**—The first two whorls are smooth, evolute, and rounded on sides and venter. At the earliest point where measurements can be made, that is, in the first quarter of the third volution, the whorl is only five-sevenths as high as wide, the involution is close and the height is considerably more than the width of the umbilicus. The readings recorded in Table 4 show that the following changes in proportion take place in the ontogeny: (1) the ratio of width to height of whorl progressively diminishes from 1.40 at a diameter of 5.70 mm. to 0.84 at a diameter of 67.1 mm.; (2) the ratio of height to diameter also progressively diminishes, passing from 0.44 to 0.32 in the same diameter intervals; (3) the ratio of width to diameter decreases from 0.61 to 0.28; (4) the ratio of width to umbilicus fluctuates, but is greater from a diameter of 35 mm. on than in the earlier stages. In other words, as the conch increases in size it becomes more evolute, passing from a

<table>
<thead>
<tr>
<th>d (mm)</th>
<th>h.i. (mm)</th>
<th>h.i. (d)</th>
<th>h.i.z. (mm)</th>
<th>h.i.z. (d)</th>
<th>h.p. (mm)</th>
<th>w/d</th>
<th>w/h.i.</th>
<th>u/d</th>
<th>u/h.i.</th>
<th>No. of volutions completed</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2.50</td>
<td>0.44</td>
<td>3</td>
<td>0.32</td>
<td>5.70</td>
<td>6.28</td>
<td>0.43</td>
<td>1.18</td>
<td>4.49</td>
<td>1.09</td>
</tr>
<tr>
<td>5.70</td>
<td>3.80</td>
<td>0.40</td>
<td>3.03</td>
<td>0.32</td>
<td>5.70</td>
<td>6.28</td>
<td>0.43</td>
<td>1.18</td>
<td>4.49</td>
<td>1.09</td>
</tr>
<tr>
<td>9.50</td>
<td>4.90</td>
<td>0.37</td>
<td>5.39</td>
<td>2.06</td>
<td>7.78</td>
<td>7.88</td>
<td>0.41</td>
<td>1.04</td>
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</tr>
<tr>
<td>13.30</td>
<td>7.45</td>
<td>0.39</td>
<td>2.06</td>
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<td>9.34</td>
<td>0.41</td>
<td>1.04</td>
<td>7.10</td>
<td>1.05</td>
</tr>
<tr>
<td>19.00</td>
<td>10.18</td>
<td>0.38</td>
<td>7.75</td>
<td>2.43</td>
<td>12.80</td>
<td>12.80</td>
<td>0.38</td>
<td>1.01</td>
<td>9.34</td>
<td>0.91</td>
</tr>
<tr>
<td>26.82</td>
<td>11.8</td>
<td>0.33</td>
<td>9.80</td>
<td>2.0</td>
<td>16.3</td>
<td>16.3</td>
<td>0.33</td>
<td>1.00</td>
<td>13.8</td>
<td>0.85</td>
</tr>
<tr>
<td>35.1</td>
<td>11.8</td>
<td>0.33</td>
<td>9.80</td>
<td>2.0</td>
<td>16.3</td>
<td>16.3</td>
<td>0.33</td>
<td>1.00</td>
<td>13.8</td>
<td>0.85</td>
</tr>
<tr>
<td>67.1</td>
<td>22.05</td>
<td>0.32</td>
<td>18.65</td>
<td>3.40</td>
<td>30.5</td>
<td>30.5</td>
<td>0.28</td>
<td>0.84</td>
<td>30.7</td>
<td>0.71</td>
</tr>
</tbody>
</table>

*Table 4. Allometric Changes in *Perisphinctes delatorii*, new species*
stage where the whorls are wider than high through one where they are of equal dimensions (at 35 mm.) to one where they are higher than wide. The sides change in outline from rounded to compressed, with the result that the line of greatest width of whorl passes from the middle in the young conch towards the dorsum in the adult. It will further be observed from the data in the table that all of the ratios change more rapidly in the young than in the adult conch; thus, taking the range of the four ratios \( \frac{h\cdot i}{d}, \frac{w}{d}, \frac{w}{h\cdot i}, \) and \( \frac{h\cdot i}{u} \) from the diameter of 5.70 mm. to that of 35.1 mm. and comparing these with the corresponding ranges from 35.1 mm. to 67.1 mm., we have the following:

<table>
<thead>
<tr>
<th>Range in Diameter</th>
<th>Range in Ratio of ( \frac{h\cdot i}{d} )</th>
<th>Range in Ratio of ( \frac{w}{d} )</th>
<th>Range in Ratio of ( \frac{w}{h\cdot i} )</th>
<th>Range in Ratio of ( \frac{h\cdot i}{u} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.7—35.1</td>
<td>0.44—0.33</td>
<td>0.61—0.33</td>
<td>1.40—1.00</td>
<td>1.14—0.85</td>
</tr>
<tr>
<td>35.1—67.1</td>
<td>0.33—0.32</td>
<td>0.33—0.28</td>
<td>1.00—0.84</td>
<td>0.85—0.71</td>
</tr>
</tbody>
</table>

Costæ and Sphincters.—The first two whorls are smooth and, so far as the preservation permits of accurate observation, there are no constrictions until near the completion of one and three-quarters volutions. Here, and again at about one and seven-eighths volutions, occurs a pronounced constriction with a strong orad trend ventrally. We are able to establish beyond any doubt the early character of the whorl in this species, because the specimen shows the entire sides and venter of the first quarter of the third volution, and—a thing which is rare in this material—the shell is preserved. At the very beginning of the volution the shell is smooth and then, almost immediately, appears the third constriction which is most profound where it crosses the umbilical zone and shoulder and least marked on the venter. The whorl here is 3.2 mm. wide and 2.3 mm. high, while the umbilicus is 2.8 mm. in width. Bounding the constriction on the orad side is the first costa of the conch, thick and strong on the venter, weaker on the sides and not discernible dorsad of the umbilical shoulder. Between the third and fourth sphincters the venter and sides of the whorl are smooth except for the fine growth-lines which can be clearly seen and which, from their strong orad trend, indicate that the ventral growth was very much in excess of the dorsal, as is also shown by the fact that between these two constrictions the ventral arc measures 4 mm., the dorsal only 1 mm. On the orad side of
the first costa the shell along the umbilical shoulder is at first as smooth as it is on the sides and venter and then there appear three gentle undulations which, though faint, are distinct and show the first stages in the formation of intersphincterial costae. They are only 0.7 mm. in length and fade away imperceptibly towards the venter.

We thus see that the costae are not at first continuous, nor should we, indeed, expect them to be from the very method of their development, for the costae are but the outer and visible expression in the shell of the inner and now invisible configuration of the mantle of the living animal. The appearance of costae means that a transverse oral fold had formed at this stage in the growth of the animal. Such a fold, repeated at regular intervals throughout the life of the individual, seems in the beginning to have arisen as a mechanical adaptation, although after it had become impressed as a fixed character it continued to form even after the mechanical necessity had largely ceased to exist. We have noted that in the third revolution the shell on the venter was increasing very rapidly, while on the dorsum the rate was only one-fourth as great. On the venter the shell is smooth, indicating that the rate of shell-building just kept pace with that of the growth of the abdomen. If we suppose that on the umbilical margin the rate of shell-building lagged behind the rate of growth of the dorsum of the animal, then we would have, in the mechanical necessity for the crowding of the soft parts into the dorsal shell region, an adequate explanation of the formation of short folds to take up the surplus in growth. The explanation is suggested as one which is adequate to account for the facts observed and as one which is in accord with similar phenomena observed in other Mollusca, but, until more specimens have been studied, no general applicability can be claimed for it in other species. It is evident that folds formed in this manner for the purpose of enabling the animal to crowd its soft parts into a shell which was too small on the back would give rise to costae which, if we read their origin aright, would not pass across the venter.

The temptation is strong at this point to venture a generalization concerning the origin of costae in general, namely, that the point of inception is in the umbilical zone and that costae are at first short and developed only on the dorsal portion of the sides whence, during the ontogeny, they extend ventrad and may in time cross the venter, when they will appear as complete costae. This generalization is borne out by two other lines of evidence, the first phylogenetic, the second ontogenetic. The most primitive species of the Lower Jurassic (Liassic) genus *Psiloceras* is characterized in the adult by simple unbranching costae which
arise on the umbilical shoulder, are strong on the sides, and become faint or obsolescent on the venter. In this form which Hyatt has called *Psiloceras planorbe* var. *plicatum*¹ we have very possibly the ancestral type of the genus *Perisphinctes* and we see that the costæ which are characteristic of the neanic and ephiebic stages in *Psiloceras* have the form and mode of development which they display in the early part of *Perisphinctes* where, in less than half of a volvation, the conch passes from the smooth to the regularly ribbed form, showing thus in its ontogeny a recapitulation of the characters of the early Jurassic form. If, as has been thought, *Psiloceras* is a decadent genus and not a primitive radical of several groups, we should look for some *Psiloceras*-like ancestor of the Perisphinctinae. The ontogenetic evidence mentioned above as being in support of the general statement regarding the mode of formation of costæ is found in the life history of *Perisphinctes cubanensis* and of each of its mutations. At all times when new costæ appear they are first formed as part of the a system, and they always begin near the umbilical suture or shoulder as we have repeatedly seen.

Beyond the fourth constriction, that is, at about 2½ volutions, the shell is smooth for a short distance and then the costæ appear, stronger and slightly longer than in the preceding intersphincterial area, but not yet reaching the venter, nor even, indeed, the line of inclusion. The development is similar between the fifth and sixth constrictions, the whorl being smooth immediately orad of the o costa and then the costæ appear, faint at first but increasing in strength until the a costa is reached. Here, on the apicad side of the sixth constriction, at about three and a half volutions, there is observable the first costal branching. The a₁ costa is exceptionally thick on the umbilical shoulder and at a height of about 0.6 mm., from the line of involution a₂ diverges at a small angle and, judging from the strength of this branch and of a₁, the two pass across the venter. The formation of this new costa, not parallel to but divergent from the simple intersphincterial costæ, brings about a reduction in the differential acceleration of growth on the venter as compared to that on the dorsum, so that the angle at which the constriction bends orad is smaller than it had been up to this point. This phenomenon is, perhaps, to be explained as due to a slowing up of the shell-building power on the venter without a corresponding decrease in the abdominal growth of the animal, with the result that, confronted by the necessity of keeping itself within a shell that was not growing as fast as it was, the animal had

¹*Genesis of the Arietidae*, 1889, p. 121, Pl. 1, figs. 5, 6.
to form an additional fold in its mantle and this fold apparently extended across the venter from the very beginning of its development and did not, like the earlier folds which took up the surplus growth along the umbilical margin, die out on the sides. After the seventh constriction the specimen is broken so that it is impossible to give the absolute number of the constrictions on the later whorls.

At four and a half volutions the a system has the following arrangement: \(a_1\) is simple and strong; at the umbilical shoulder \(a_2\) which is less salient diverges from and quickly becomes parallel to \(a_1\), while ventrally the former even slightly approaches the latter. Costa \(a_3\) diverges from \(a_2\) at 4.0 mm., from the line of involution, appearing as a bifurcation of \(a_2\). From the compound \(a_2-a_3\) stem, \(a_4\) diverges at 3.4 mm. from the umbilical suture and does not attain the same strength as the other \(a\) costæ until it reaches the venter. All of the costæ of the \(a\) system become of equal strength in crossing the venter, but on the sides \(a_1\) is the strongest and the later-formed ones are weaker.

In the succeeding intersphincterial region the first costa following \(o\) is simple, the second, third, and fourth are bifurcatingly branched. In the second the orad branch is slightly stronger and bends forward; in the third the strength is a little greater in the apicad branch, with the point of divergence of the orad branch weakened, the continuity being on the apicad part of the fork. This is more marked on the fourth costa. The fifth is again simple; the sixth and seventh are bifurcatingly branched, the orad branch of the sixth being slightly the stronger, but in the seventh both branches are equal in strength. The eighth costa is bifurcatingly forked but the greater strength is in the apicad branch. The ninth costa has the character of a simple rib with an orad branch separated from it dorsally, this having the appearance of a free intercalated rib. Then follows the \(a\) system. On the whole, then, in this intersphincterial region the stronger part of the branching costa is the apicad portion, the orad branch being mostly a little weaker and in one case still distinct from the apicad. In only one costa is the reverse the case. As already shown in the ontogeny of the holotype of \(P. cubanensis\), the later whorls show a forward migration in the strength of the branches. Thus, practically all of the costæ of this intersphincterial series are in the condition shown by the first groups of later intersphincterial systems.

The \(a\) system which succeeds the group just described has the following arrangement: \(a_1\) is strong, \(a_2\), which is weaker and not so salient as \(a_1\), branches off at 4.2 mm., above the line of involution, this point, therefore, being relatively as well as absolutely more ventrad than is the
point of branching in the preceding a system; $a_3$ separates off at 2.5 mm., above the line of involution and the strength of $a_2$ continues across the venter in $a_3$; $a_4$ appears as a free costa.

The next intersphincterial system, which begins at $4\frac{3}{4}$ volutions has the following arrangement. After the usual strong costa follows a simple costa (I) with a pronounced orad deflection on the side of the whorl, a character which is found in the first costae of all the succeeding intersphincterial groups, but has not up to this stage in the ontogeny been very marked. In group II on the right side the apicad branch is free, but on the left side it is still slightly in junction with the costa as a whole, the strength of which is continued in the orad branch. Group III on the right side has the greatest strength and continuity in the orad branch, but the apicad is still weakly joined to it, while on the left side the strength of both branches is about equal. These relations hold in the succeeding costae with but slight variations. Thus, on the whole, the strengthening has passed to the orad branch, though this is not true for every costa as yet. The left side of the conch is a little more accelerated in this respect than the right.

At $5\frac{3}{4}$ volutions and on, the character is still essentially the same. The first costa of each group is simple, the other two branched (appearing bifurcated) with the strength more constantly in the forward branch, the apicad being frequently free.

**Ventral Groove.**—The last whorl of this species (Pl. XXXV, figs. 4c and 5) is of very great significance, since it provides the proof of the origin of the ventral groove seen in the internal molds of all of the Cuban species of *Perisphinctes* and noted as well in many European forms. This groove has been mistaken by some authors as identical with that present in the genus *Idoceras* and for this reason the rocks at Viñales were originally correlated with the Kimmeridgian of Mexico. The geologic significance of this apparently insignificant groove is, therefore, evident.

Because of the manner in which the individual whorls of *P. delatorii* separated during the process of preparation, I was able to see the dorsum and venter of several of them, and the last whorl fortunately retained on its dorsal surface the shell from the preceding whorl. By making a polished cross-section, shown in Pl. XXXV, fig. 5, I found that the shell is composed of two layers. The outer one, clearly formed by the edge of the mantle, showed a normal rounded venter with the costae uninterrupted, the inner, however, was thickened at the middle and must have been subsequently formed by the mantle within the body chamber. This median
thickening produced a ridge which projected inward and which would give rise to a groove in the internal mold. Thus in *Idoceras* (Pl. XXXVI, fig. 3) the costae in the shell appear bevelled down to the level of the median ventral line, while in the Cuban *Perisphinctes* they are perfectly continuous across the venter in the shell but in the internal mold there is a groove cut into the costae. Morphologically the two smooth bands which are produced are totally unrelated, the one in *Idoceras* being formed at the aperture in the shell, the one in the *Perisphinctes* occurring only in the mold and being an expression in reverse of a secondary internal thickening of the shell. This median groove has been observed in a large number of European species of *Perisphinctes*, but all of these are known only from internal molds so that the significance of the groove and its mode of origin have never been determined. Pompeckj called attention to the fact that every specimen of *Perisphinctes plicatilis* which he had seen showed a groove and he regretted that none of them had any of the shell preserved. Some European authors have suggested that the groove was due to wear on the specimen but, since it is visible on the inner whorls when the specimen is broken down, such an explanation obviously is incorrect. The groove is neither of specific nor generic value as is the smooth band in *Idoceras*, for I have observed it in many genera of the *Stephanoceratidae* as in *Dactylioceras, Stephanoceras, Grossouria, Ataxioceras*, and others. I have no explanation to offer for the reason of such a median thickening of the shell, but of the fact there can be no doubt.

**Sutures.**—The preservation is of such a nature that no sutures are visible, except in the young whorls where they are not distinctive enough to be used for specific identifications.

**Horizon and Locality.**—Lower beds of the Upper Oxfordian; Viñales, Pinar del Rio, Cuba.

*Perisphinctes plicatiloides*, new species

Plate XXXVI, Figures 1 and 2


Non

1818. *Ammonites plicatilis* Sowerby. SOWERBY, Min. Conch., p. 149, Pl. CLXVI.


1875. *Perisphinctes plicatilis* (Sowerby). WAAGEN, Jurassic Cephalopoda of Kutch, p. 189, Pl. LI, figs. 2a, b, 3; Pl. LII, fig. 3.
Among the Perisphinctinae is a single, well-preserved internal mold (holotype, A. M. N. H. No. 18560) belonging to the plicatilis group. The specimen shows about five complete volutions, but practically none of the shell is preserved. During the process of fossilization the conch was filled with calcite crystals, the inner two-thirds of the internal mold consisting entirely of crystallized calcite, around which is a thin layer of chapapote. Finally, the main external part of the internal mold is a layer, about 2 mm. thick, composed of a mixture of chapapote and calcite. The interfacial angles of the calcite crystals often intersect the sutures, making it difficult to follow them.

The chief reasons for separating this species from the typical plicatilis as well as from other forms of that group, are that the sides of the whorls are convex instead of flat and the sutures are more complex and very distinct from those in other species of the plicatilis group in having a short ventral and long superior-lateral lobe.

SYNONYMY.—So many different forms have been referred to plicatilis of either Sowerby or D'Orbigny and such conflicting statements are found in the literature concerning the characters of the real plicatilis, that it seems advisable to set down a clear statement of the facts in order that we may, perhaps, arrive at a more definite conception of this very common species.

In 1818 Sowerby figured and described Ammonites plicatilis from a formation since identified as the Upper Corallian. The holotype was an internal mold from Buckland's Collection and is now in the University Museum at Oxford. The protolog and protograph are so poor that subsequent authors have, as a rule, considered them insufficient for the definition of the species, but recently the holotype has been redescribed and refigured so that we are sure of its characters (Healey, 1904a, p.
55, Pl. ix, figs. 1, 2, text fig. 1; 1904b, Pls. lvii, lviii). It is a compressed form, with rounded venter but flat sides, the whorls in the adult being about as high as wide so that the cross-section is quadrangular with rounded corners. The involution is about one-fourth; constrictions are very faint; there are sixty-eight long costae on the whorl ending at a diameter of 96 mm. and most of these branch on the venter, a few bifurcating and rarely some remaining single. Miss Healey has given a careful drawing of the suture in the Palæontologia Universalis (1904b, Pl. lvii, T. 1b) which shows that it was very complex and consisted of three lobes in which the first dorsal one is longer than the others, while the ventral and superior-lateral lobes are of about equal length.

D'Orbigny in the Paleontologie Française (1842, pp. 509–514) redescribed A. plicatilis Sowerby including in his synonymy a large number of species which subsequent authors have again separated out as wholly distinct. His description was a composite one including the characters of the many forms which he considered to be plicatilis, but the European consensus of opinion has settled upon the illustration which he gives on Pl. cxxii in figs. 1 and 2 as the true plicatilis, the one which is to be regarded as Sowerby's species.

This idea that D'Orbigny's figures represented the true plicatilis appears to have originated with Seebach. He visited England with the express purpose of studying in the field and the museum the formations and collections of the Jurassic that he might compare them with the northwest German Jura. In his volume on the Jura of Hanover, he makes the statement that, after seeing Sowerby's types of plicatilis in the British Museum, he is convinced that that author had in mind the same species which D'Orbigny described and illustrated so much better (Seebach, 1864, p. 156). But Sowerby's type of plicatilis is only a single specimen and it is in the University Museum at Oxford so that, whatever Seebach saw, and I doubt not it was the cotypes of A. biplex Sowerby, which are in the British Museum, it was not the holotype of plicatilis. However, be this as it may, Seebach's statement has been widely accepted and many authors at present use the designation P. plicatilis (Sowerby) D'Orbigny or omit all reference to Sowerby.

Siemiradzki, on the other hand, fell into a different error. For some reason which is not made clear, he states (1898–1899, pp. 70, 249–252) that Sowerby's type of plicatilis is lost and that, the original description and figure being poor, we must rely upon the next reference in the English literature and he refers to Phillips' figure in the 'Geology of Yorkshire' (1829, Pl. iv, fig. 29). As Miss Healey has pointed out (1904a, p. 54),
this was a wrong reference, since the species illustrated is a keeled form called *Ammonites solaris* by Phillips, and Siemiradzki must have been referring to the third edition of the 'Geology of Yorkshire' (1874) in which Pl. iv, fig. 29 shows a form which is called *Ammonites solaris* (erased 1874) and receives the new designation *A. plicatilis* (replacing *A. solaris*) (1874, p. 325) but correctly referred to on p. 265 as *A. plicatilis* Sowerby where reference is given to Sowerby's Pl. 166. In the second edition of the 'Geology of Yorkshire' (1835) the illustrations are the same as in the first. Because of this error, Siemiradzki places Sowerby's species in the *Ornatenton* or Middle Kellaway instead of in the Upper Corallian where it belongs.

There can, however, be no doubt that Sowerby and D'Orbigny had two distinct forms in mind and since both have been described and figured with sufficient precision for later recognition, and particularly since there is no longer any doubt about Sowerby's holotype, by the laws of priority the name *plicatilis* must be used for forms fitting Sowerby's description, and a new name must be given to the species called *plicatilis* by D'Orbigny. The first to recognize this necessity was de Loriol (1903, p. 82) who gave the name *P. orbignii* to D'Orbigny's *Ammonites plicatilis*, a species characteristic of the zone of *Peltoceras transversarium* of the Oxfordian.

Neumann has introduced a new confusion into the synonymy by giving to D'Orbigny's *plicatilis* the name of *P. healeyi* (1907, p. 29), ignorant of the fact that in 1903 de Loriol had already, as we have seen, called it *P. orbignii*. The name *P. healeyi* would automatically, under these conditions, become dead and there would also be no reason for using Neumann's *Healeyi*-group for this and related species. But it is clear from his description and figures (1907, Pl. ii, figs. 5a, b) that the species which he has found in the *Cordatus*-beds, is different in several important points from D'Orbigny's. It is a thicker, coarser form, with broader, more widely separated costæ which, instead of passing in a straight line from the umbilicus to the flanks of the whorls, are deflected apicad on the umbilical shoulder. The involution is greater, the cross-section of the whorls is different, and the constrictions are much deeper. Moreover, Neumann's species comes from the *Cordatus*-beds of the Lower Oxfordian, D'Orbigny's from the *Transversarius*-beds of the Upper Oxfordian. The name *healeyi*, therefore, might still stand if applied to the Cetechowitz species, but Neumann's synonymy could not be accepted, particularly since he has included in it both the original *plicatilis* of Sowerby identified by later authors and species referable to D'Orbigny's *plicatilis*. 
I have before me two specimens from Germany, the one (No. 1813/3, A. M. N. H. Coll.) being just a little smaller than Sowerby's holotype, the other (No. 9822 G, Palæontological Museum, Columbia University) a little smaller than D'Orbigny's *plicatilis*. The former comes from Württemberg, the latter from Haldem, Hanover, and, while not from the typical localities, they yet show very clearly how different are the forms described by the two authors. The one which I have identified as *P. plicatilis* (Sowerby) has the same dimensions as the holotype and is to be distinguished from the Hanover specimen by being on the whole much thicker and more massive, with deeper umbilicus and more pronounced umbilical shoulder, while the costae, which are straight, in D'Orbigny's, showing no deflection on flanks or venter, are in Sowerby's species slightly deflected apicad on the umbilical shoulder and on the venter they bend orad, as well as being throughout less sharply defined. Once the two forms have been seen side by side there is no mistaking them, however large the specimen may be, for there are fundamental differences in form, involution, costal development, and sutures that separate them from the very beginning of their ontogeny and they do not converge in later stages.

We must thus recognize three distinct species in the *plicatilis* group, no two of which can be united.


*P. orbignyi* de Loriol, 1903. Upper Oxfordian—*Transversarium* beds. Protograph: de Loriol, Jura Lédonien, part 2, p. 81, Pl. xi, fig. 2.

*P. healeyi* Neumann, 1907. Upper Kellaway—*Cordatus* beds. Protograph: Neumann, Die Oxfordfauna von Cetechowitz, p. 29, Pl. ii, figs. 5a, 5b.

De Riazz has described and figured from the *Transversarium* beds of Trept a large series of specimens of the *plicatilis* group. He has designated them *P. plicatilis* Sowerby D'Orbigny (De Riazz, 1898, pp. 9–12, Pls. i–iii, figs. 1, 2, 3,); if the identification is correct, the forms should be called *P. orbignyi* de Loriol, but the specimen which he considers as the typical *plicatilis* (1898, Pl. iii, figs. 1a, b) is thicker throughout and slightly more involute than D'Orbigny's. Therefore it is not unlikely that the Trept species are variations from D'Orbigny's type, and should at least receive a variety name. This fauna of Trept is particularly interesting as providing both young and mature individuals, the *Perisphinctes* attaining to an unusual size. Thus de Riazz mentions one *plicatilis* 236 mm. in diameter. However, it is apparent that there are manifold difficulties in comparing such large individuals with D'Orbigny's holotype which was recognized to be a young form and measured only 85
mm. in diameter. Among the specimens in the *PLICATILIS* group, de Riaz has found a number which differ in one or more characters or in proportions from D'Orbigny's type, and these he has classed together simply as *P. aff. Plicatilis* d'Orb., not finding enough marked differences to found new species. Undoubtedly this group of forms which are not strictly true to type could be arranged in a number of evolutionary lines which were derived from some generalized and fundamental form by allometric or rectigradational changes or by both.

Waagen has recorded *P. plicatilis* Sowerby from the Kuntkote sandstone of Kutch in the zone of *Peltoceras transversarium* (1875, p. 189, Pl. LI, figs. 2a, b, 3; Pl. LII, fig. 3), but the specimens are like neither Sowerby's nor D'Orbigny's species, differing from both in the disposition and form of costae and in not showing the characteristic lateral compression.

**Form and Proportions.**—The conch of the holotype of *Perisphinctes plicatiloides* is only slightly involute and, in consequence, the umbilicus is broad. The venter is uniformly rounded, passing into the gently convex sides without any indication of ventro-lateral shoulders. The sides pass more abruptly, but still with a rounded contour, to the line of involution, producing a rather indefinite umbilical shoulder and a comparatively shallow umbilicus. The latter becomes proportionally broader with age as shown in column 12 of Table 5. Where the conch is approximately 35 mm. in diameter, the height and width of the whorls

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**Table 5. Allometric Changes in Perisphinctes plicatiloides, new species**

*O'Connell, Jurassic Ammonite Fauna of Cuba* 675
are about equal, but beyond this the height becomes steadily greater than the width, though, because of the convexity of the sides, the cross-section at no time appears either squarish or trapezoidal as in the typical *plicatilis*. The ratio of height of whorl to width of umbilicus becomes progressively less as does also the ratio of height of whorl to the diameter (columns 3 and 13 of the table), two changes which indicate that the amount of involution decreases with age.

**Costæ and Sphincters.**—The earliest volution of the conch appears to be smooth with strongly convex sides. As in the other *Perisphinctes* of this fauna, the first pronounced surface character to appear is a constriction which antedates the costæ. The first of these is seen just beyond one and a quarter volutions, arising apparently on the umbilical shoulder in the internal mold. These early costæ show no evidence of branching, although this might take place on the ventral portion which is, of course, invisible on account of the involution. There are about six costæ preceding the next constriction.

At about one and a half volutions the first branching in the a system occurs, the \( a_1 \) costa being very strong while its branch is less pronounced both in height and sharpness. The actual divergence of \( a_2 \) is near the middle of the flanks, but \( a_1 \) is very strong and thick below this point, suggesting that dorsally the two are confluent.

Beginning with the constriction which marks the end of the second volution, the costal arrangement in the five succeeding intersphincterial areas has certain unusual features which are most suggestive as to the origin of "bifurcations." At the beginning of the third volution two simple costæ follow the \( o \) costa and are essentially parallel to it, showing only a slight divergence ventrally such as is normal for simple, un-branched costæ. The third costa, however, bends towards the second above the umbilical shoulder, almost but not quite touching it. (See Fig. 1, p. 647.) The space between the ventral ends of the third and fourth costæ is so small as to suggest that the former remains simple on the venter, but the space between the fourth and fifth, and fifth and sixth costæ, etc., is wider, suggesting the presence of a ventral branch in each one of these. After the next constriction, the first costa is still simple, parallel, and close to \( o \), but the dorsal ends of the second and third costæ are united, their ventral portions forming two branches of equal strength, while the costæ orad of this have the position and divergence indicative of ventral branching. Thus, counting the costæ on the umbilical shoulder, we would say that the second costa is branched or "bifurcates." The next succeeding intersphincterial group shows this
same tendency carried still further. Again, if we count the costae on the umbilical shoulder, the second one shows its point of "bifurcation" moved ventrally until it is about 3.5 mm. above the line of involution, but it is still considerably below the line of inclusion. The first costa, which was simple in the preceding intersphincterial system, is now branched, the divergence occurring at about 2.7 mm. above the line of involution. It thus appears that, after branching is established, the point of divergence of the branch moves progressively ventrad until it reaches such a position that it is covered by the next succeeding whorl. At the same time, the branching habit of the costae is pushed backward in each system until all the costae branch.

In the intersphincterial system following the one just described, all of the points of divergence have moved so far ventrally as to be covered by the succeeding volution, as is indicated by the mode of divergence of the costae. Thus, the lateral costae appear to be simple, but in reality they are the compound stems of branched individuals. That such is indeed the case is clearly shown where the venter of the conch is first exposed and where all of the lateral costae divide into two branches, which, however, are entirely concealed when the succeeding whorl (which separated off during the preparation of the specimen) is placed in position.

Where the ventral portion of the final whorl preserved is first exposed, it is seen that the branching is still bifurcate, but, as in P. cubanensis, the strength of the costa passes progressively forward and as this takes place the apicad one of the two branches becomes free first on one and then on the other side of the whorl after the manner described for P. cubanensis. A third branch on the orad side of a costa occasionally is seen, forming a trifurcation, but the trifurcating type of costae is more characteristic of the last part of the final whorl where, however, bifurcation still persists in some cases.

The whorl ending at a diameter of 62.8 mm. has 42 lateral and about 84 ventral costae, which, when the simple o costae are subtracted, leaves most of the costae bifurcating and only a few trifurcating. Wherever the shell is preserved, the costae are seen to arise nearly but not quite at the line of involution, leaving a very narrow smooth band which appears wider on the internal mold because the costae seem to arise more nearly on the umbilical shoulder. The costae are strongest on the flanks, where at times they are quite salient, particularly in the younger whorls. Towards the end of the last whorl they become more rounded and less elevated. Throughout the entire conch the costae show a slight
curvature on the flanks and a faint backward deflection on the umbilical shoulder, but this is much less pronounced than in *P. cubanensis*. On the venter the costae are uniformly weaker, and there is a marked median faintness giving rise to the appearance of a median depression on the venter of the internal mold. As in the case of *P. cubanensis*, this is due to a median ventral thickening of the shell on the interior. Unfortunately, there is no place in this specimen where the shell is preserved on the venter itself, so that the exterior ventral aspect of the shell is not determinable for this species, but it is very probable that no depression or interruption of the costae is shown on the venter of the shell proper any more than it is in *P. cubanensis* and other forms where the shell is preserved. Of the internal thickening there can be no doubt, for it can be seen on one fragment of the last volution where the shell of the preceding whorl is preserved on the impressed zone.

**Fig. 8.** Suture line of *Perisphinctes plicatiloides*, new species.

Sutures.—The suture (Fig. 8) is more complex than in any other species of the *plicatilis* group. The ventral lobe is about twice as long as wide and has two long terminal branches, each of which shows numerous minor indentations. These branches constitute the siphonal saddle, which is divided by a small median lobe. The first or superior-lateral lobe is long and narrow, terminating in three pointed prongs and showing three major additional lobes on either side with many smaller indenta-
tions. This lobe extends twice as far apicad as either the ventral or second lateral lobe and is longer even than the first dorsal lobe. The second or inferior-lateral lobe is notably shorter than the first and is directed obliquely toward it. The first lateral saddle does not extend quite so far orad as the siphonal saddle, is unsymmetrically divided by many minor inflections, and is smaller than the other two lateral saddles. The second lateral saddle is long, unsymmetrical, broader than the superior lateral lobe and terminates about on a line with the siphonal saddle. The third lateral saddle is a little shorter than the first lateral saddle and is rather evenly indented on its dorsal side by the inflections of the first dorsal lobe.

The suture of *Perisphinctes plicatilooides* thus differs markedly from that of *P. plicatilis* (Sowerby) in having the first lateral lobe so much more prominent than the other lobes. In the English species the first dorsal lobe is longer than the others, while in D'Orbigny's *plicatilis* it is the ventral lobe which has the greatest length and this is the case in de Loriol's *P. orbignyi* from the Jura and Waagen's *P. plicatilis* (Sowerby) from India. Unfortunately Burckhardt was unable to prepare the sutures of the Mexican *P. aff. orbignyi* de Loriol which, from its other characteristics, appears to be the same as *P. plicatilooides*, although identity of ammonites can never be established on form alone and without the corroborative evidence of the sutures.

On account of the great dissimilarity in the fundamental suture pattern in the various European forms which are called *plicatilis* and because all differ in this respect from the Cuban species, it seems probable that the "*plicatilis group*" is made up more largely of homoeomorphic equivalents than of genetically related species. All of the *plicatilis*-like ammonites show certain similarities in form and proportions and in the arrangement of costæ, but it is well known that these characteristics are not so reliable as the sutures in determining genetic relationships and, since the sutures are so markedly different in the various species, there seems to be little justification for the grouping of these unrelated forms into a *plicatilis* series unless we do so merely for convenience in speaking of the numerous species throughout the world which have certain external features in common.

**Related Forms.**—As is the case with the other Cuban species, this finds its nearest relative in the Mexican fauna. Burckhardt has described and figured a specimen identified as *Perisphinctes aff. orbignyi* de Loriol (1912, p. 22, Pl. iv, figs. 2–4). No European *plicatilis* is so like the Cuban one in form, evolution and proportions as is this Mexican form, yet there
are certain slight differences, the most noticeable of which is in the costæ. In Burckhardt's species these are salient and are strongly curved on the umbilical shoulder, resembling, in this respect, the specimens described by DeRiaz from Trept. Both the Cuban and Mexican forms differ from D'Orbigny's in having convex instead of flat, compressed sides, the cross-section of the first two being almost identical but unlike that of the third. Burckhardt has called attention to the fact that the costæ on his specimen, which is an internal mold, are enfeebled on the median ventral line, in which respect it differs from D'Orbigny's plicatilis. This difference, I think, is only apparent, for Pompeckj, as we have seen, has stated that all of the northwest German plicatilis show the depression in the internal mold. All of the illustrations given by European authors in recent works show that a depression is present, and I doubt not but that D'Orbigny either omitted reference to this feature or else that he figured a specimen in which the shell was preserved and in which, consequently, the median furrow would not be seen.

**Horizon and Locality.**—Lower zone of Upper Oxfordian; Viñales, Pinar del Rio, Cuba.

*Perisphinctes cf. alterniplicatus* Waagen

1875. *Perisphinctes alterniplicatus* WAAGEN, Jurassic Fauna of Kutch, Palaeontologia Indica (9), I, p. 199, Pl. L, figs. 2a, b.


There is a single specimen (A. M. N. H. No. 18576) showing a quarter sector through six whorls and I have referred it provisionally to *P. cf. alterniplicatus*. Since I cannot measure the diameter, it is impossible to give any of the shell ratios, and the preservation is such that no sutures are visible, so that the identification must be made on the form of the whorls and the character of the costæ. The distinctive feature about the costæ is that a long costa on one side of the whorl, when traced across the venter, ends in a short costa instead of being continued in a long one, this arrangement producing an alternation on the two sides of the whorl which suggested the specific name *alterniplicatus*.

**Horizon and Locality.**—Lower beds of the Upper Oxfordian; Viñales, Pinar del Rio, Cuba.
OCHETOCEPAS Haug

Ochetoceras canaliculatum (von Buch) burckhardtii, new variety

Plate XXXVII, Figures 1, 2, and 3


SYNONYMY.—The specific name canaliculatus was first used in print by von Buch in 1831 for a number of small ammonites from the Coral Rag of Noschnau on the Eck near Aarau in the Swiss Jura (1831, Pl. i, figs. 6, 7, 8). He identified his specimens as Ammonites canaliculatus Münster, describing them as small, with many costæ which are ordinarily divided a little above the lateral canal; in a specimen 5 cm. in diameter he counted 48 to 52 costæ near the venter which he stated to be sharp and very finely crenulated. Oppel, who had von Buch's holotype before him as well as several specimens labelled by Münster, states that von Buch's description was not in accord with the original specimen, for the latter showed no bifurcation of the costæ, a feature which was expressly noted and figured by von Buch. The material in Münster's collection was unlabelled, while the specimens in the Bayreuth Museum described by him in 1833 as A. canaliculatus belonged to a number of distinct species from different horizons (Oppel, Jurassische Cephalopoden, 1862, p. 157). Oppel considered that the figures given by D'Orbigny were more accurate than the protograph and since he had the holotype in his possession and refigured it (loc. cit., Pl. li, fig. 3) we may accept his judgment in the matter.

D'Orbigny identified an ammonite common in the French Oxfordian as A. canaliculatus and ascribed the species to Münster (Terr. Juras., Pl. cxcix, figs. 1, 2). It would seem that D'Orbigny described and figured a form identical with von Buch's holotype, though not agreeing with that author's protolog or protograph which Oppel states are incorrect. If we accept Oppel's redescription and re-illustration of von Buch's holotype, then the species name should be credited to the latter author. At any rate, by no rule of priority could the name canaliculatus be ascribed to D'Orbigny, for if this form is the same as von Buch's his identification would simply be listed in the synonymy of canaliculatus, and if it is not the same a new name would have to be given to it, since both species belong to the same genus, Ochetoceras, and the name canaliculatus must be retained for von Buch's holotype since that has now been redescribed by Oppel. Haug, who placed this species in his genus Ochetoceras, has also given the priority to von Buch without, however, stating his reasons (1885, p. 697). According to this line of reasoning, Burckhardt should not have identified the Mexican species as O. canaliculatum
(D'Orbigny). For reasons which will be brought out as I describe the Cuban species, I consider it to be identical with the Mexican species and regard both as a variety of the European canaliculatum.

The following is a synonymy of the critical references to Ochetoceras canaliculatum (von Buch):

1831. Ammonites canaliculatus von Buch, Recueil de Planches de Petrifications Remarquables, Pl. 1, figs. 6, 7, 8.

1842. Ammonites canaliculatus Münster. D'Orbigny, Paléontologie Française, Terr. Jurassiques, p. 525, Pl. cxix, figs. 1, 2 and 6, non 3.


Form and Proportions.—There is a single well-preserved representative of this species (holotype, A. M. N. H. No. 18561) showing practically all of the shell intact which is unusual in this material. The specimen, judging from its comparatively small size and the fact that there are only about two and a half volutions present, is probably only a sub-mature individual, so that the characters and proportions which it shows are not to be considered wholly diagnostic for the species but only for the stage of development represented.

The conch is compressed and discoidal. The whorls increase rapidly so that involution is almost complete, giving, with increased diameter, a proportionally smaller and smaller umbilicus. In cross-section the whorls are about two and a half times as high as broad, the ratio decreasing with the age of the conch, as may be seen from the Table 6 (columns 2, 8, 10).

Table 6. Allometric Changes in Ochetoceras canaliculatum (von Buch) burckhardtii, new variety

<table>
<thead>
<tr>
<th>(d) mm.</th>
<th>(h.i.) mm.</th>
<th>(h.i.) (d)</th>
<th>(h.i.z.) mm.</th>
<th>(h.i.z.) (d)</th>
<th>(h.p.) mm.</th>
<th>(w) (d)</th>
<th>(w) (h.i.) mm.</th>
<th>(u) (d)</th>
<th>(u) (h.i.) mm.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>5</td>
<td>6</td>
<td>7</td>
<td>8</td>
<td>9</td>
<td>10</td>
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<tr>
<td>16.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>8.6</td>
<td></td>
<td>0.53</td>
<td></td>
<td></td>
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<tr>
<td>18.6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>8.8</td>
<td></td>
<td>0.46</td>
<td></td>
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</tr>
<tr>
<td>38.4</td>
<td>22.0</td>
<td>0.62</td>
<td></td>
<td></td>
<td>9.8</td>
<td>0.26</td>
<td>0.45</td>
<td>5.7</td>
<td>0.14</td>
</tr>
<tr>
<td>52.5</td>
<td>28.2</td>
<td>0.53</td>
<td></td>
<td></td>
<td>30.6</td>
<td>12.5</td>
<td>0.24</td>
<td>0.44</td>
<td>6.9</td>
</tr>
<tr>
<td>55.8</td>
<td>31.5</td>
<td>0.56</td>
<td>23.7</td>
<td>7.8</td>
<td>0.42</td>
<td>32.3</td>
<td>13.4</td>
<td>0.23</td>
<td>0.42</td>
</tr>
</tbody>
</table>
In shell proportions the Cuban form approaches so closely to the specimens described by Burckhardt from the upper beds of the Upper Oxfordian of Cerro del Volcan, Mexico, that there is no doubt that all belong to the same species, but each shows a greater or less degree of acceleration over D’Orbigny’s holotype, not only in proportions but in all other characters, for which reason I have given the Cuban form a distinct varietal name and have included here Burckhardt’s specimens for reasons more fully given below. A comparison of the more important shell ratios will bring out the relations existing between the European, Mexican, and Cuban species (Table 7).

<table>
<thead>
<tr>
<th>Table 7. Comparison in Allometric Ratios of Species of Ochetoceras</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ammonites canaliculatum (holotype) (European)</td>
</tr>
<tr>
<td>-----------------------------------------------</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>Ochetoceras canaliculatum (D’Orbigny) (Mexican)</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>O. canaliculatum (von Buch) var. burckhardt (holotype) (Cuban)</td>
</tr>
</tbody>
</table>

From these figures it is clear that the Mexican specimen having a diameter of 32 mm. has a cross-section of about the same proportions as those of the Cuban specimen 55.8 mm. in diameter, while that which is 55.5 mm. in diameter has the cross-section which is shown in the Cuban specimen at the place where it is only about 28 mm. in diameter. Thus the smaller of Burckhardt’s specimens is more accelerated, the larger less accelerated than the Cuban form in respect to the ratio of thickness to height of whorl, while all three are more accelerated than D’Orbigny’s holotype, for the Cuban specimen although only 55.8 mm. in diameter has almost the identical proportions as those in D’Orbigny’s which is 94 mm. in diameter, and both of Burckhardt’s specimens, though representing young individuals, are identical with, or closely approach, the proportions of the adult described by D’Orbigny.

The conch is strongly compressed, with the region of greatest thickness at about the middle of the whorl when that is 16 mm. high but changing position gradually in a dorsal direction. Where the whorl is 31.5 mm. high the maximum transverse diameter is 5.7 mm. above the umbilical shoulder, that is, at about one-fifth of the way from the umbilicus to the venter.
Dorsally the whorls end abruptly at the umbilicus where they bend down at a right angle. Where the whorl is 31.5 mm. high from umbilical suture to venter the transverse diameter at the umbilicus is 4.5 mm. On account of the close involution of the whorls, due in its turn to the very rapid increase in size, little of the early whorls is visible in the umbilical opening. Where the diameter is 55.8 mm. only 1.5 mm. of the preceding whorl is visible in the umbilicus.

One of the most striking features of the conch is a distinct lateral groove visible throughout the shell in the specimen being described. It becomes obsolescent in the last part of the final whorl which is preserved and, since the specimen is probably only a little more than half the size of the adult, it is to be expected that an ephibic conch would be entirely devoid of a definite channel although the growth-lines might well continue to bend forward in the position marked by the groove in earlier whorls. A constant centrodorsal position on the whorl is retained by the groove, the median line of which is 5.5 mm. from the umbilical shoulder when the whorl is 12.8 mm. high and 12 mm. from the umbilical shoulder when the whorl is 28 mm. high, the ratio in both cases being 0.43, showing the position of the groove to be at slightly over two-fifths of the distance from the umbilical shoulder to the venter. The groove at the beginning of the final whorl of our specimen is 0.5 mm. broad, widening to 1.5 mm. just before it loses its distinctness as a definite canal.

Where the actual shell is preserved, fine, closely crowded, radiating growth-lines are visible (Pl. XXXVII, fig. 3). On the inner flank, that is, between the umbilicus and the groove, these lines have a gentle uniform curvature forward passing from the umbilical shoulder, where they are fairly strong, towards the lateral groove. There they bend forward strongly, forming distinct lappets, which become less pronouncedly elongate as the groove becomes fainter, though still retaining a strong forward bend. On the specimen which I have it is impossible to trace the growth-lines across the groove where this is deep, but forward as it becomes obsolescent the lines may easily be followed from dorsum to venter. In the region where the groove is most pronounced the growth-lines on the outer flank, that is, between groove and venter, are moderately falsiform, the convexity forward being more pronounced than on the inner flank. Just before they reach the venter, the growth-lines become stronger and lose their convexity so that they run in a direction at right angles to the keel. There is thus produced an extremely fine carination or denticulation on either side of the keel. These two lines of ventrolateral carinations or angulations are strongly developed only in the largest part of the whorl.
Keel.—Rising up between the two angulations is a pronounced and characteristic keel with smooth flanks which converge into the finely noded central ridge of the keel (Pl. XXXVII, fig. 2). The nodes are minute, but very distinct, there being five in the space of 22 mm. where the whorl is 28.2 mm. high. The keel here rises 1.5 mm. above the ventro-lateral angulations but in the young part of the shell it is much less prominent. While the cross-section of the keel in the largest part of the conch preserved shows a decided angle between the flanks and the flat groove on either side of the keel, this is wholly absent at the beginning of this same whorl, the flanks passing convexly up to the groove at the base of the keel. Thus in the older shell there are two angles, which in the younger shell are represented by a convex and a concave curve, respectively.

The siphuncle is visible at a number of places on the specimen and measures 1 mm., in diameter at the maximum (Pl. XXXVII, fig. 2). The outer edge of the siphuncle rises above the ventro-lateral angulations, as may be seen in places where the median keel is broken away.

Costæ.—Paralleling the growth-lines are a few rather widely separated folds or costæ which are more strongly developed on the inner than on the outer flanks. These costæ appear for only a short time in the ontogeny and characterize less than one complete volution. D’Orbigny noted that his specimen was smooth (except for the lateral groove) until it attained a diameter of 30 mm. when costæ appeared and continued until a diameter of 60 mm. was reached when the costæ disappeared. I have counted with certainty ten costæ on the inner flanks of the final whorl, but while they are more numerous on the outer flank I have been unable to count them because of the poor preservation of the shell. It is clear, then, that not only in shell proportions is the Cuban specimen more accelerated than D’Orbigny’s and von Buch’s holotypes, but also in the time of appearance and disappearance of the costæ in the ontogeny as well as the period of their duration. The costæ in their curvature, arrangement and ontogenetic duration are practically identical with those in the Mexican forms described by Burckhardt.

Sutures.—At a diameter of 52 mm., the suture shows a ventral, two lateral, and two auxiliary lobes (Pl. XXXVII, fig. 3.) The portion of the ventral lobe lying in the mesal plane is undecipherable on account of the preservation; the lateral branches are well developed and lie at right angles to the keel. The first or superior-lateral lobe is slightly longer than the ventral lobe and is divided into three main branches, the middle of which has a trifurcate termination, while the two lateral ones are
bifurcate. The second or inferior-lateral lobe occupies the lateral groove, is simple, and not so deep as the first lateral lobe. The first auxiliary lobe is trifid, the second is an almost unmodified lobe with slight indentations foreshadowing a tripartite division. The first or superior-lateral saddle is divided into two unequal parts by a lobe directed dorsally, the inner portion being larger than the outer and being again subdivided by a small lobe into two branches which have trifurcate terminations. The first lateral saddle is slightly larger than the first and also bipartite. The first and second auxiliary saddles have a few simple secondary lobes but a bipartite division is not marked. The saddles are broader than the corresponding lobes but of about the same length.

Comparison with Related Forms.—This species in all of its characteristics is so similar to Burekhardt’s *Ochetoceras canaliculatum* (D’Orbigny) from the Upper Oxfordian of Cerro del Volcán, Mexico, that I do not hesitate to say that the two are identical, differing from each other by only so much differential acceleration in certain characters as any two individuals of the same species living side by side may do. The Cuban form has the same general suture pattern as the Mexican form but it is not so complicated, and the lobes are relatively broader and the entire suture shows fewer secondary inflections. Thus, in respect to the suture, the Mexican form is more accelerated than the Cuban, but in certain shell proportions it is less accelerated, while the costæ are practically identical in the two. D’Orbigny’s and Burekhardt’s species have almost identical sutures, so that the remarks which were made in the comparison of the Mexican with the Cuban species hold in comparing the French with the latter. The species described by D’Orbigny is the common wide-spread Oxfordian form which occurs throughout Europe in the zone of *Peltoceras transversarium*, and the Mexican and Cuban species are simply geographical variants. I regard this species as the best and most reliable horizon-marker in the Cuban fauna.

Horizon and Locality.—Upper zone of the Upper Oxfordian; Viñales, Pinar del Rio, Cuba.

**Ochetoceras mexicanum** Burckhardt

Plate XXXVIII, Figures 1, 2, and 3


Description of the Cuban Plesiotype

The only specimen (A. M. N. H. No. 18562) of this species so far collected from Viñales is a sub-mature individual showing two complete volutions and probably having one or one and a half volutions concealed
in the inner umbilical region. Thus the characters noted will not be those of the adult form and can be used only in identifying shells of about the same size. The specimen is well preserved, showing portions of the shell and in several places the entire keel remains intact.

**Form and Proportions.**—The conch is compressed, elliptical and closely coiled. On account of the pronounced involution the umbilicus is small and, the flanks of the whorls bending downward abruptly at the umbilical shoulder, the opening is surrounded by nearly vertical walls. Since only the last whorl is exposed enough to allow of measure-

| Table 8. Allometric Changes in *Ochetoceras mexicanum* Burekhardt |
|------------------|---------|---------|---------|---------|---------|---------|---------|---------|
| $d$ mm. | $h.i.$ mm. | $\frac{h.i.}{d}$ | $h.p.$ mm. | $w$ mm. | $\frac{w}{d}$ | $\frac{w}{h.i.}$ | $u$ mm. | $\frac{u}{d}$ | $\frac{h.i.}{u}$ |
| 1      | 2       | 3       | 4       | 5       | 6       | 7       | 8       | 9       | 10      |
| 35.0   | 19.4    | .55     | ....... | 11.8    | .33     | .60     | 5.3     | .15     | 3.6     |
| 39.3   | 21.8    | .55     | ....... | 12.3    | .31     | .56     | 6.1     | .15     | 3.5     |
| 41.0   | 23.2    | .56     | ....... | 12.7    | .31     | .55     | 6.6     | .16     | 3.5     |
| 43.1   | 24.3    | .56     | ....... | 13.8    | .32     | .56     | 6.3     | .14     | 3.8     |
| 44.7   | 24.8    | .55     | 26.7    | 14.0    | .31     | .56     | 5.5     | .12     | 4.7     |

measurements being taken, it is impossible to make any important generalization about the trend of the various allometric changes. The ratios of height to diameter and width to diameter remain about constant showing that the conch does not change much in general proportions. There is a marked increase in the amount of involution as brought out by the figures in columns 8, 9, and 10 in Table 8. The width of the umbilicus shows an absolute decrease which leads to a relative decrease in the ratio of that width to the diameter and an increase in the ratio of the height of the whorl to the width of the umbilicus.

**Lateral Groove.**—At slightly less than half-way from the umbilicus to the venter, there is a rather pronounced lateral groove which becomes fainter and shallower towards the end of the specimen (Pl. XXXVIII, fig. 3). On the inner part of the flanks numerous regularly-spaced costae are developed. They arise at the umbilical shoulder where they are faint and attain their greatest prominence at the edge of the lateral
groove. These costæ are directed obliquely orad across the sides and, at the beginning of the last whorl of the specimen, are strongly deflected orad at the lateral groove. The costæ die out in the groove and begin again on the outer flanks. In some cases it is evident from the continuity of the growth-lines that the costæ on the ventro-lateral side of the groove are continuations of those on the dorso-lateral, but there are also many additional intercalated ones. Thus, on the outer side of the groove there are 43 costæ and on the inner only 22. The costæ on the ventro-lateral area arise at the groove, are strongly deflected apicad, and then bend orad so that they have the form of a shallow sicle, concave toward the oral opening; as they approach the venter they attain their maximum height and breadth and are sharply deflected orad, the angles thus produced on the successive costæ forming a continuous abdominal angle between the ventral and lateral zones.

Keel.—The costæ end at the abdominal angle above which rises the keel. On the sides this has fine, closely crowded crenulations which terminate in minute denticulations of which I counted nine in a distance of 5.4 mm. The keel rises to a maximum height of 1.6 mm. above the siphuncle, which is shown at a number of places on the specimen and which is 1.5 mm. in diameter (Pl. XXXVIII, fig. 2).

Where the shell has been preserved, the fine growth-lines are visible giving rise to striæ parallel to the costæ. The growth-lines can be most clearly seen in the lateral groove.

Sutures.—The sutures are relatively simple, consisting of a ventral, two lateral, and two auxiliary lobes with the corresponding saddles. The ventral lobe has two rather long terminal branches which are directed obliquely apicad. The superior-lateral lobe is long and narrow with a central, trifid terminal branch, and simple secondary lobes. The second lateral lobe occupies the lateral groove, is unsymmetrical, and is shorter than the first lateral lobe. The two auxiliaries are progressively shorter and simpler. The superior lateral saddle cannot be studied on account of fractures in the specimen. The inferior lateral saddle is asymmetrical, being divided by a pointed secondary lobe into two parts, each of which is differently modified by added inflections. The three auxiliary saddles are decreasingly shorter and show a terminal division into two parts.

Comparison with Related Forms.—This species is identical with the Mexican form described by Burckhardt. The Cuban specimen is smaller than the holotype, so that there is necessarily a slight difference in shell ratios but it is no greater than would be expected. The sutures
are somewhat simpler in the Cuban form but have the same pattern and same fundamental divisions. Burckhardt has pointed out that the Mexican form is closely related to the shell called "Ammonites canaliculatus" by Quenstedt (Ammoniten des schwäbischen Jura, Pl. xcii, figs. 1–5), which is characteristic of zone β of the White Jura or the zone of Peltoceras bimmamatum. I most decidedly agree with Burckhardt that Quenstedt's species cannot be united with Ochetoceras canaliculatum as de Loriol has done (Oxfordien superieure du Jura Ledonien, p. 24), for the former species is accelerated in the mode of development of the costae and in the complexity of the sutures. The Cuban and Mexican O. mexicanum are clearly ancestral in all their characters to the "A canaliculatus" as described and figured by Quenstedt. This fact adds corroborative evidence as to the age of the beds containing O. mexicanum; it must be lower than the horizon of Peltoceras bimmamatum and this has been shown to be the case by the presence of O. canaliculatum in the same beds.

**Horizon and Locality.**—Upper zone of the Upper Oxfordian; Viñales, Pinar del Rio, Cuba.

**Ataxioceras** Fontannes

**Ataxioceras virgulatus** (Quenstedt)

Plate XXXVIII, Figures 4 and 5

1858. Ammonites virgulatus Quenstedt, Der Jura, p. 593, Pl. lxxiv, fig. 4.

1888. Ammonites virgulatus Quenstedt, Die Ammoniten, III, p. 923, Pl. c, fig. 5.


**Description of the Cuban Plesiotype**

A single somewhat crushed specimen (A. M. N. H. No. 18563) of this species was found by Mr. Brown, and I have identified three representatives of the species among the material sent by Dr. Roig. The specimen which I have figured is a little over 60 mm. in diameter, being twice as large as any of the specimens found by Burckhardt at San Pedro del Gallo. It shows about four and a half complete volutions, the last quarter of the final one being crushed. More of the shell is preserved than is usual in this Cuban material, but in places the finer surface characters are obliterated by chapapote flakes and calcite.

The conch, in the beginning, is smooth, with very convex sides and rounded venter. At about one and three-eighths volutions the first costa appears as a short fold (1 mm. long) directed orad, arising on the umbilical shoulder and passing across the flanks for about a third the distance, that is, just to the line of inclusion. The first constriction comes
in at one and a half volutions and is followed by simple, unbranched costæ which have a strong orad trend. In the intersphincterial region beyond the second constriction the first branching of costæ is seen, occurring on the umbilical shoulder. These details of the early part of the conch are shown on one side of the specimen where a portion of the first half of the third volition has broken away. Beyond this the costæ are well shown, arising a little below the umbilical shoulder and passing across the flanks diagonally and without branching. The costæ are fine, sharp, and numerous, there being thirty-two on the last half of the third volution, counted on the umbilical shoulder. On the last whorl each costa branches once about midway across the flanks, the branches as a rule remaining united so that there are few intercalated costæ.

The constrictions are numerous and well defined, but neither broad nor deep. There are nine constrictions on the fourth whorl in a little over half a volution. They occur at irregular intervals and are directed diagonally orad across the flanks of the conch.

On account of the crushing of the specimen, I could not make the usual series of measurements but can give the figures at one diameter.

\[
\begin{align*}
\frac{d}{h} &= .44 \\
\frac{h}{d} &= 44.8 \\
\frac{w}{d} &= .31 \\
\frac{u}{d} &= .28 \\
\end{align*}
\]

The ratios correspond fairly well with those for the largest specimen found by Burckhardt.

The conch as a whole is compressed, the whorls having almost flat flanks which bend down abruptly at the umbilical shoulder but which pass without any angulation into the evenly rounded venter. The umbilicus is broad, open and not deep, but yet clearly defined.

The sutures are not shown.

Horizon and Locality.—Upper beds of the Upper Oxfordian; Viñales, Pinar del Rio, Cuba.
BIBLIOGRAPHY

O'Connell, Jurassic Ammonite Fauna of Cuba


HEALEY, MAUD. 1904a. Notes on Upper Jurassic Ammonites, with special reference to specimens in the University Museum, Oxford, No. 1. Quarterly Journal Geological Society, London, LX, pp. 54-64, Pls. ix-xii. (Types refigured and redescribed: Perisphinctes plicatilis (Sow.), P. biplex (Sow.), P. variocostatus (Buckland), Olcostephanus pallasianus (d'Orb.), new var.)

1904b. Ammonites plicatilis Sowerby. Palæontologia universalis, Ser. I, Fasc. III, Pls. LVII, LVIII. (Refiguring of holotype, suture line redrawn on T 1 b of Pl. LVII.)


1866. Über die zone des Ammonites transversarius. Geognostisch-Paläontologischen Beiträge von Benecke, Schloenbach und Waagen. München. pp. 207–316. (Table showing distribution of ammonites in zone of transversarius.


1858. Der Jura. Tübingen, 842 pp., 100 plates.


Riaz, A. De. 1898. Description des Couches à Pelloceras transversarium (Oxfordien Supérieur) de Trept-(Isère), 69 pp., 19 plates.

Seebach, Karl. 1864. Der Hannoversche Jura. Berlin, 158 pp., 10 plates, map. (Map of Hannover with Jurassic outcrops.)


Fig. 2. *Perisphinctes cubanensis*, new species. Holotype: ventral view. A. M. N. H. No. 18556.

Fig. 3. *Perisphinctes cubanensis* mutation a, new mutation. Holotype: lateral view. P. 660. A. M. N. H. No. 18557.

Fig. 4. *Perisphinctes cubanensis* mutation a, new mutation. Holotype: ventral view. A. M. N. H. No. 18557.

**HORIZON:** Lower zone of the Upper Oxfordian, Upper Jurassic.

**LOCALITY:** Viñales, Province of Pinar del Río, Cuba.

All of the figures are natural size.
PLATE XXXV

Fig. 1. *Perisphinctes cubanensis* mutation β, new mutation. Holotype: lateral view. P. 662.

Fig. 2. *Perisphinctes cubanensis* mutation β, new mutation. Holotype: ventral view.

Fig. 3. *Perisphinctes delatorii*, new species. Holotype: lateral view showing portions of six volutions. P. 663.

Fig. 4. *Perisphinctes delatorii*, new species. Holotype: lateral view showing whorls separated.

(a) Portions of first four volutions, showing early stages with simple costae.
(b) Portion of fifth volution, showing costae bifurcating.
(c) Portion of sixth volution, showing adult arrangement of costae.


Fig. 6. *Perisphinctes delatorii*, new species. Holotype: view showing whorls broken along septa. Innermost whorl exposed smooth on venter.

A. M. N. H. No. 18558.

A. M. N. H. No. 18559.

A. M. N. H. No. 18559.

A. M. N. H. No. 18559.

HORIZON: Lower zone of the Upper Oxfordian, Upper Jurassic.

LOCALITY: Viñales, Province of Pinar del Rio, Cuba.

All of the figures are natural size.

Fig. 2. *Perisphinctes plicatiloides*, new species. Holotype: ventral view, showing median groove in internal mold, the coste being unchanged in direction in crossing the venter. Natural size. Compare with Fig. 3. A. M. N. H. No. 18560.

Fig. 3. *Idoceras soteloi* Burckhardt. Plesiotype: ventral view, showing orad bending of coste and their complete interruption in both shell and internal mold along the median ventral zone. Natural size. Specimen in Paleontological Museum, Columbia University.

Fig. 4. *Idoceras soteloi* Burckhardt. Plesiotype: lateral view of same specimen shown in Fig. 3. Natural size.

**Horizon:** Original of Figs. 1 and 2 from lower zone of the Upper Oxfordian, Upper Jurassic. Original of Figs. 3 and 4 from *Idoceras* zone of the Kimmeridgian, Upper Jurassic.

**Localities:** Original of Figs. 1 and 2 from Viñales, Province of Pinar del Rio, Cuba. Original of Figs. 3 and 4 from Mazapil, Mexico.

Fig. 2. *Ochetoceras canaliculatum* (von Buch) var. *burckhardtii*, new variety. Holotype: ventral view, showing outline of keel and ventral angles. Natural size. A. M. N. H. No. 18561.

Fig. 3. *Ochetoceras canaliculatum* (von Buch) var. *burckhardtii*, new variety. Holotype: lateral view enlarged about three and one-half times to show suture, growth-lines, and character of keel. A. M. N. H. No. 18561.

**HORIZON:** Upper zone of the Upper Oxfordian, Upper Jurassic.

**LOCALITY:** Viñales, Province of Pinar del Rio, Cuba.
PLATE XXXVIII


Fig. 2. *Ochetoceras mexicanum* Burckhardt. Plesiotype: ventral view, showing siphuncle in cross-section and outline of keel. Natural size. A. M. N. H. No. 18562.

Fig. 3. *Ochetoceras mexicanum* Burckhardt. Plesiotype: lateral view, enlarged about two and one-half times to show suture, character of costae, lateral groove, and keel. A. M. N. H. No. 18562.

Fig. 4. *Ataxioceras virgulatus* (Quenstedt). Plesiotype: lateral view. Natural size. A. M. N. H. No. 18563.

Fig. 5. *Ataxioceras virgulatus* (Quenstedt). Plesiotype: ventral view. Natural size. A. M. N. H. No. 18563.

HORIZON: Upper zone of the Upper Oxfordian, Upper Jurassic.

LOCALITY: Vínales, Province of Pinar del Rio, Cuba.