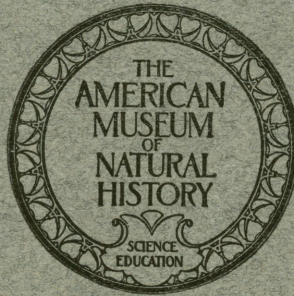


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NEW SPECIES OF AMMONITE OPERCULA FROM THE MESOZOIC ROCKS OF CUBA

By MARJORIE O'CONNELL



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INTRODUCTION

Among the material collected by Mr. Barnum Brown in 1919 in the Province of Pinar del Rio, western Cuba, are seventeen specimens and numerous fragments of the small calcareous, bivalved shells which are known as aptychi. They are the opercula with which the ammonites closed up the aperture of the conch after the animal had withdrawn into the body chamber.

So far as I know there has been only one occurrence noted of an *Aptychus* in American Mesozoic formations. Castillo and Aguilera described *Aptychus mexicanus* from the Jurassic rocks of Sierra de Catorce, San Luis Potosi, Mexico,¹ and this seems to have been a sporadic occurrence. But in Cuba there is a definite horizon which has been traced for several miles and at which nothing but aptychi and an occasional small *Haploceras* are found. The rocks consist of alternating shales and limestones with the former predominating. They are dark gray but weather light brown or almost white and show a considerable amount of iron stain. The aptychi occur on the surfaces of the shale and are well preserved, although very fragile on account of the iron impregnation. The *Aptychus* beds were discovered in the heart of the Organ Mountains in outcrops along two stream beds, the Rio San Cristobal and Rio Hondo, northeast of the town of San Cristobal and northwest of Candelaria. From the field relations and the general stratigraphy, these strata appear to be of Upper Jurassic age, but the aptychi themselves possess certain characteristics which have heretofore been found only in Cretaceous species. Until further field work can be done it is impossible to state the exact age of the beds but it must be either Tithonian or Neocomian with the palæontological evidence strongly favoring the latter.

¹Castillo, Antonio del and Aguilera, Jose G. 1895. 'Fauna Fossil de la Sierra de Catorce, San Luis Potosi.' Boletin de la Comision Geologica de Mexico, I.

HISTORY OF INVESTIGATIONS AND CLASSIFICATION OF OLD WORLD
APTYPCHI

Hermann von Meyer in his paper 'Das Genus *Aptychus*' (1831), proposed the generic name *Aptychus* for the paired plates found within the body chamber of many species of ammonites. While he did not recognize the true significance of the plates, he distinguished correctly between two different types which he described as *A. lævis* and *A. imbricatus*, each with two varieties. These have since been recognized as representatives of two large groups, the Cellulosi and the Imbricati, respectively.

There is no monographic work on *Aptychus*, the descriptions of species being scattered through the literature in short papers. Since the opercula are often found in formations containing few or no ammonites, it would be exceedingly valuable if all of the data concerning the geological range of every known species of *Aptychus*, as well as the ammonite genera to which they belong could be brought together. Such a study would have to be undertaken in Europe where *Aptychus* beds are common, for in America up to the present few representatives of this genus have been found and material is not available for carrying on researches on the subject. On page 12 below is given a short and by no means complete bibliography of the more important references dealing with the morphology and taxonomy of aptychi and the stratigraphic range of Jurassic and Cretaceous species.

The systemic position of the bivalved *Aptychus* plates was formerly a subject for much discussion and a large amount of the early literature was devoted to it. The various theories advanced concerning the type of organisms to which the aptychi belonged may be found in the contributions by Parkinson (1811), Meyer (1831), Voltz (1837), Coquand (1841), and Quenstedt (1849). It is now generally accepted that the aptychi are ammonite opercula, as is indicated by their position *in situ* in the body chamber in many specimens. Oppel has figured and described, from the Solnhofen beds of Bavaria, a large number of ammonites with aptychi in the body chamber or at the aperture (see reference on p. 13 for Oppel 1863) and other authors have recorded sporadic occurrences of aptychi *in situ* (e.g., Meyer, 1831, Retowski, 1891, 1893).

Aptychus is not a genus; it is simply a convenient term for referring to opercula when the ammonites to which they belong are unknown. When an aptychus is found *in situ* in an ammonite it does not receive a separate specific name but is known as the aptychus of that particular genus and species of ammonite. But when aptychi occur alone, as they

frequently do, with no ammonites in the same stratum, then for convenience in referring to them they are given specific names. If an aptychus thus named is subsequently found to be the operculum of an ammonite which had previously been described, the aptychus should be called by the specific name of the ammonite, while the specific name which had been used for the aptychus would become a synonym. Each species of ammonite that possessed an operculum in all probability possessed a distinctive type and, conversely, when different types of aptychi are found we may assume that they belonged to separate ammonite species.

When aptychi are sectioned they are found to be made up of three shell layers of which the inner and outer are very thin and dense, while the middle is thick and cellular or tubular (Figs. 1, 2, 4, 6). The outer and inner layers are frequently destroyed during fossilization, leaving

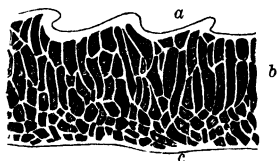


Fig. 1. Vertical section of the shell of *Aptychus profundus* Voltz, showing the three shell layers (a, b, c).

Greatly magnified. Upper Jurassic (after Meneghini and Bornemann from Zittel).

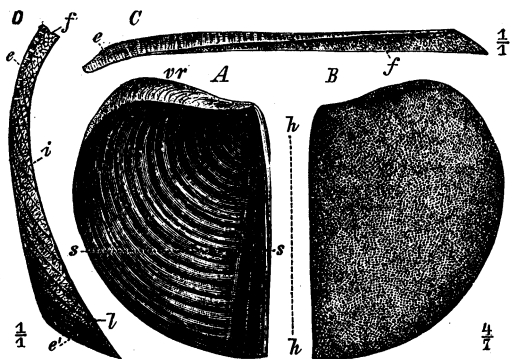


Fig. 2. *Aptychus laevis* Meyer, the aptychus of a species of *Aspidoceras*.

A. Interior view of a valve showing the growth-lines. B. Exterior of same; h-h, junction line. C. Inner edge of the valve; f, junction surface. D. Vertical section through the valve along the line s-s, of A; i, growth-lamellæ merging externally (e) but thickening toward the interior (l). Upper Jurassic, Kimmeridgian, Le Havre, France. (After Steinmann.)

the more resistant middle one. Aptychi increase in size by the addition of concentric bands of shell around the periphery. The edges of these bands, covered only by the thin outer layer, may show on the convex surface like the ends of off-lapping shingles or they may bend over each other so closely as to show only concentric lines on the external surface.

The internal surface is marked by crowded growth-lines, which are sometimes crossed by radial lines from the apex.

A classification of aptychi has gradually been evolved and, as added to and emended by Zittel (1885, pp. 402-403), now includes seven groups based on the shape and thickness of the shell, the character of the surface



Fig. 3. *Aptychus lamellosus* Voltz.

Exterior view. Upper Jurassic, Solnhofen, Bavaria. Natural size. (After Zittel.)

layer and of the lamellæ. The three most abundantly represented groups in the Upper Jurassic and Lower Cretaceous (Neocomian) are the Cellulosi, Imbricati and Punctati. The Cellulosi are forms with thick curved plates having a fine porous, convex external surface and a concave internal surface covered with fine growth-lines (Fig. 2). The Imbricati have thinner shells and usually the small posterior end is very thick. The convex surface is covered with shingle-like lamellæ, the edges of which appear like folds in some cases or like sharp knife-edges in others, the crests being separated by depressions which are rounded or angular (Figs. 1 and 3). The inner surface has concentric growth-lines. The aptychi of this group are found in various species of the Oppe-liinæ in the Upper Jurassic, especially at Solnhofen and in the Lower Cretaceous and are also found isolated in the various *Aptychus* shales and limestones. The Punctati (Fig. 4) are similar to the Imbricati except that the lamellæ overlap more closely

and the crests are bent over until they cover up the intervening hollows; the edges of the crests are marked by lines of punctæ on the external surface. The outer shell layer is thicker than in the Imbricati and the distinctness of the lines of punctæ depends upon the degree to which erosion of this layer has progressed, the punctæ being etched out when the amount of erosion is slight, but if this continues the lamellæ are worn smooth. Illustrations of these types maybe found in the works cited below, especially Quenstedt (1849) and Zittel (1885).

The *Aptychus* shale of Cuba contains three species all belonging to the Imbricati and all well represented. No other fossils have been discovered in this formation except a few small ammonites belonging to the

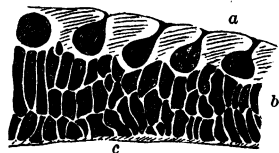


Fig. 4. *Aptychus punctatus* Voltz.

Vertical section showing three shell layers (a, b, c.). Greatly enlarged. (After Meneghini and Bornemann from Zittel.)

family of the Haploceratidæ. The determination of the age of the beds therefore depends upon the evidence offered by the aptychi themselves without the aid of the ammonites to which they belonged.

In Europe aptychi have been found throughout the Jurassic and Cretaceous of many regions. In certain localities, particularly in Bavaria in the Solnhofen beds, they are usually found *in situ* in the body chamber of the ammonite shell. Elsewhere they occur segregated in beds by themselves, as is the case in the Tithonian *Aptychus* limestones of the Alps and Apennines and in the Eo-Cretaceous or Neocomian *Aptychus* limestones of the eastern Alps.

The Imbricati, those semi-elliptical to quadratic forms with overlapping lamellæ on the convex surface and fine concentric lines on the concave surface, are the most abundant and widespread. They occur in great numbers associated with conchs belonging to the subfamily of the Oppeliinæ and to the family of the Haploceratidæ, and also alone. The Jurassic Imbricati for the most part have the lamellæ parallel to the curved periphery of the outer edge of the aptychus, as in *A. lamellosus* Voltz from the Solnhofen beds (Fig. 3). The lamellæ, in other words, extend in a continuous curve from the anterior to the posterior end, without bending back toward the apex and forming an angle on the posterior slope. All of the Jurassic Imbricati of this type may be united into the *A. lamellosus* group, including the following forms as representative species:

<i>Aptychus crassicauda</i> Quenstedt	Middle White Jura
<i>A. sparsilamellosus</i> Gümbel	Upper Jurassic (<i>Acanthicus</i> beds)
<i>A. lamellosus</i> Voltz	Upper Jurassic (Solnhofen beds)
<i>A. profundus</i> Voltz (= <i>A. imbricatus</i> Meyer)	" " " "
<i>Aptychus</i> of <i>Oppelia bous</i> (Oppel)	" " " "
" " <i>O. euglyptus</i> (Oppel)	" " " "
" " <i>O. lithographica</i> (Oppel)	" " " "
" " <i>O. thoro</i> (Oppel)	" " " "

The Cretaceous Imbricati are distinguished from those of the Jurassic in having the lamellæ bent toward the apex as they approach the line of junction (Figs. 5, 6). In some species, notably *A. didayi* Coquand, there is an acute angle formed on the posterior slope. These forms constitute the *A. didayi* group, including as representative species:

<i>Aptychus angulocostatus</i> Peters	Lower Cretaceous (Neocomian)
<i>A. didayi</i> Coquand	" " "
<i>A. lineatus</i> Peters	" " "
<i>A. pusillus</i> Peters	" " "
<i>A. seranonis</i> Coquand	" " "
<i>A. undatocostatus</i> Coquand	" " "
<i>A. insignis</i> Hébert	Upper Cretaceous (Mæstrichtian)



Fig. 5. *Aptychus didayi* Coquand.

Natural size. Lower Cretaceous, Neocomian, Central France. (After Pictet.)

The same distinction exists between the Jurassic and Cretaceous Punctati, the former having the lamellæ essentially parallel to the outer curved periphery, the latter having them bent into an angle along the posterior slope. As examples of the Jurassic species may be mentioned: *Aptychus punctatus* Voltz and *A. beyrichi* Oppel; of the Cretaceous species: *A. rugosus* Sharpe from the Mæstrichtian of England.

The species found in the *Aptychus* shales north of San Cristobal in Cuba all belong to the Imbricati and to the *didayi* rather than the *lamellosus* group. In all of them the lamellæ are bent more or less sharply on the posterior slope and turn towards the line of junction of the plates, meeting it either at a right angle, as in *A. cubanensis*, or at an acute angle toward the apex, as in *A. pimientensis* and *A. cristobalensis*, but never at an acute angle away from the apex, as in *A. lamellosus* Voltz and related species of that group. The Cuban species are altogether Cretaceous in their appearance, being most like *A. didayi* Coquand and *A. insignis* Hébert. They are smaller than the two latter and narrower than *A. didayi* but the type of lamellæ is the same in all of them. Either the Cuban species belong to the Cretaceous or else they are to be regarded as late Tithonian fore-runners of the Cretaceous types. The following new species are described from the region north and northeast of San Cristobal¹:

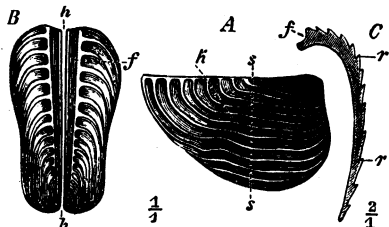


Fig. 6. *Aptychus* of *Haploceras*.

A. Side view of valve showing posterior angulation; B. Exterior of both valves. Anterior or proximal end below, posterior or distal end above. Lamellæ meet exterior junction line at right angle. *f*, triangular junction surface bounded interiorly by *h-h*, the interior line of junction (*Harmonielinie* or *Symmetrielinie*). C. Vertical section through one valve along the line *s-s* in A, showing the folds *r* off-lapping from the inner to the outer margin. Lower Cretaceous, Neocomian of Chalançon, Drôme, France. (After Steinmann.)

Species	Locality	Locality	Locality	Locality
	No. S. C. 2	No. S. C. 3	No. S. C. 4	No. S. C. 5
<i>Aptychus cristobalensis</i>	1	3		
<i>A. cubanensis</i>	5		3	
<i>A. pimientensis</i>		2		3

¹The details concerning the exact localities are given under the descriptions of the species.

DESCRIPTION OF NEW SPECIES FROM CUBA

Group of the Imbricati

***Aptychus cristobalensis*, new species**

Figures 7 and 8

DESCRIPTION OF THE HOLOTYPE (Amer. Mus. No. 19017/3).—The shell is calcareous, thin at the apex (anterior) and thick at the narrow distal (posterior) end. The length of the outer junction line is 29 mm., the greatest width 17 mm. and the cord of the peripheral arc from the distal to the proximal ends is 30.7 mm. The broad truncated end is about 10 mm. long. At the apex the three shell layers together are only 0.3 mm. thick; at the distal end the thickness is 6.0 mm.

The curved periphery is bounded by a narrow smooth shell band, which widens toward the distal end where it is perpendicular to the convex surface of the plate. Each half of the aptychus is nearly flat in the early growth stages. It becomes gently convex along the short diameter but extremely convex along a radial line at about one-third the distance between the long and short diameters. This convexity is so pronounced as to give rise to a ridge from which the shell slopes down abruptly to the external junction line (i. e., the long diameter).

At the apex of each plate there are numerous, almost invisible growth-lines, each of which marks the edge of a lamella. Each additional growth-band is broader than the preceding but the first fifteen lamellæ are so narrow as to be scarcely distinguishable to the naked eye. They are arranged like shingles except that they off-lap instead of overlap away from the apex. The last ten lamellæ are broad but only a few are continuous from end to end of the shell. The last four or five wedge out along the periphery, each succeeding one being shorter. It is in this manner that the shape of the aptychus is determined, the broadest part being in the region where all the lamellæ are present, the narrow end being occupied by only a few. The lamellæ become very thin toward the truncated proximal end and terminate nearly at right angles thereto, there being a narrow smooth band at the edge. In the opposite direction, the lamellæ show a slight offset toward the apex as they approach the convex radial ridge, and after they cross it they curve back toward the apex, ending abruptly at the junction line. This flexure is angular until the aptychus is about half-grown, the angle being slightly less than 90°. On the remainder of the shell the flexure loses its sharp angularity, becoming rounded and more open with a divergence of 110–120°.

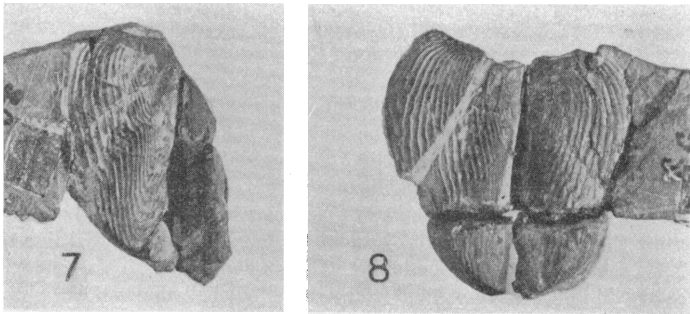
The inner, concave side of the aptychus is covered with fine concentric, evenly-spaced growth-lines about 0.1 mm. apart (Fig. 7).

DESCRIPTION OF PARATYPE No. 19017/2.—Length 30 mm., greatest width about 16 mm., cord of the peripheral arc 33.2 mm. long. Truncated proximal end about 10 mm. long, thickness of distal end 5.5 mm. Outline of two plates in juxtaposition is semi-elliptical. The junction surface is smooth and at right angles to the convex shell surface. It is triangular in shape with its apex at the point of origin of the plate whence it increases to a width of 3.2 mm. at the distal end. It is faintly concave but the three bounding lines are straight. Between the junction plate and the inside or concave surface of the aptychus there is a bevelled edge (Fig. 8).

NUMBER OF SPECIMENS.—Holotype and 3 paratypes.

ASSOCIATED SPECIES.—*Aptychus pimientensis*, new species, at locality No. S. C. 3.

LOCALITIES.—Northeast of Mt. Pimiento in Rio Hondo, 7 miles northeast of San Cristobal (locality No. S. C. 3) 3 specimens, Nos. 19017/1, 19017/2, 19017/3 (holotype); on Finca of Rafael Begoa, 9 miles north of San Cristobal in Rio San Cristobal (locality No. S. C. 2) 1 specimen of immature individual, No. 19017/4.



Figs. 7 and 8. *Aptychus cristobalensis*, new species.

Fig. 7. Oblique side view of one valve showing curvature of lamellæ on posterior slope. The interior of the other valve is shown at the right, the valve being thrust forward. Natural size. Holotype, A. M. N. H. No. 19017/3.

Fig. 8. Top view of both valves in position. Natural size. Paratype, A. M. N. H. No. 19017/2.

Comparisons.—This species belongs to the group of which *Aptychus didayi* Coquand is the most widespread European representative. It is, however, relatively narrower than that species and has much finer lamellæ, while the pronounced flexure of the lamellæ of the fullgrown shell is rounded and not angular. (See Coquand, 1841, p. 389, Pl. ix, fig. 10, and Quenstedt, 1842, p. 314, Pl. xxii, fig. 21.) It agrees very closely with the description of *A. angulocostatus* Peters (1854, p. 441) but that author did not give an illustration of his species and the European types are not accessible to me, so that it would be unsafe to identify the Cuban form with that species. *A. cristobalensis* probably belongs to a species of *Oppelia*.

Horizon of Related European Species.—*Aptychus didayi* Coquand is a characteristic Lower Cretaceous (Neocomian) species occurring throughout the Mediterranean province in southern France, in the eastern Alps, in Austria and northern Africa. (Compare Fig. 7 with Fig. 5.) *Aptychus angulocostatus* Peters is found associated with *A. didayi* in the Neocomian Wienerwald sandstone of Austria and Bohemia (Peters, 1854, p. 441; Paul, 1889, pp. 59, 175).

***Aptychus cubanensis*, new species**

Figures 9 to 14

DESCRIPTION OF THE HOLOTYPE (Amer. Mus. No. 19018/2).—Length of the junction line 17 mm.; greatest width of one valve, 9 mm. On the posterior slope the lamellæ curve to meet the external line of junction at right angles and assume their maximum size and saliency as they approach this line. The last three or four lamellæ to be formed do not extend completely around each half of the aptychus but wedge out

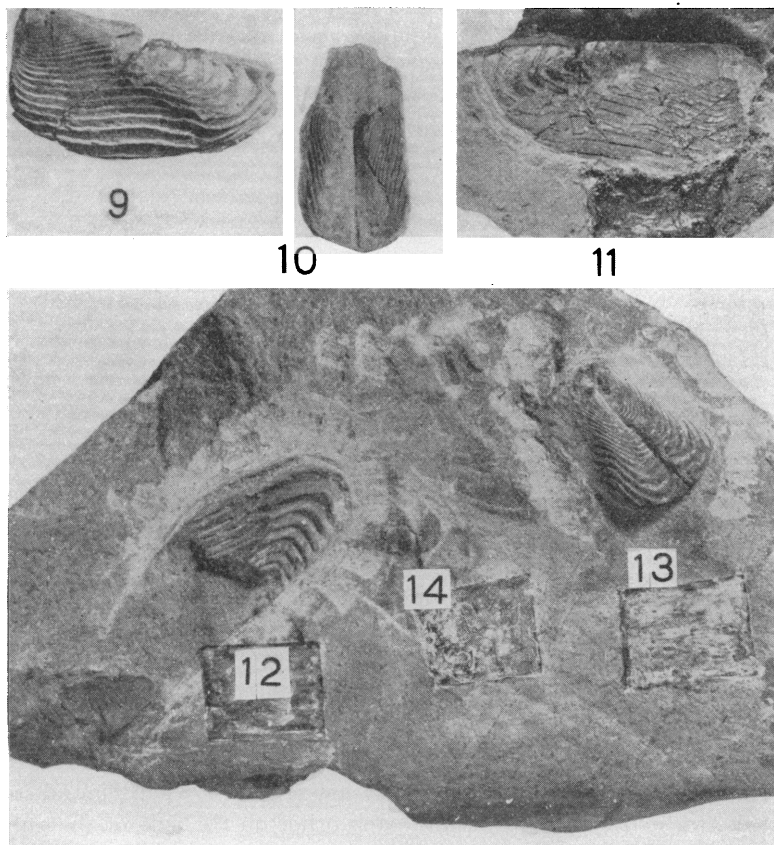
Figs. 9 to 14. *Aptychus cubanensis*, new species.

Fig. 9. Side view showing lamellæ meeting external junction line at right angles. $\times 2$. Holotype, A. M. N. H. No. 19018/2.

Fig. 10. Top view of immature aptychus with both valves in juxtaposition. $\times 2$. Paratype, A. M. N. H. No. 19018/1.

Fig. 11. Exterior. $\times 2$. Paratype, A. M. N. H. No. 19018/3.

Fig. 12. View of posterior end of a broken valve showing the lamellæ meeting external junction line at right angles. $\times 2$. Paratype, A. M. N. H. No. 19018/6.

Fig. 13. Exterior of two valves of nepionic aptychus. $\times 2$. Paratype, A. M. N. H. No. 19018/7.

Fig. 14. Exterior of immature aptychus showing two valves in juxtaposition along junction planes. $\times 2$. Paratype, A. M. N. H. No. 19018/8.

along the curved periphery. On the long anterior surface the lamellæ are thin and sharp but as they increase in size posteriorly their edges become rounded and they appear more like folds separated by channels than like overlapping knife-edges. The external line of junction is thickened and elevated and it serves to form a very definite boundary for the lamellæ (Fig. 9).

DESCRIPTION OF PARATYPES.—On Specimen 19018/7 (Fig. 13), 11 mm. long, 20 lamellæ were counted, this not being the total number since the finer ones near the apex were too small to be distinguished. The two valves are shown in contact along the junction line and when in this position the posterior slopes are horizontal, while the anterior portions are deflected abruptly downward. The outline as a whole is rhombohedral with the distal end squarish and truncated. The largest specimen (No. 19018/6), which shows only one valve, is approximately 21–22 mm. long and 10 mm. wide (Fig. 12).

The nepionic aptychus (specimen No. 19018/8) is nearly flat, showing only a slight anterior convexity. One of the plates is 3.5 mm. long and 1.8 mm. wide. Thirteen fine, concentric, continuous lamellæ could be counted, although at that early stage they appeared merely as growth-lines, the lamellar character not being visible on the surface (Fig. 14).

The interior concave side of the aptychus is covered by minute, concentric growth-lines. The middleshell layer is thin near the apex but increases posteriorly. The thickest part of the shell is at the margin on the line of the posterior ridge.

NUMBER OF SPECIMENS.—Holotype and seven paratypes.

ASSOCIATED SPECIES.—*A. cristobalensis*, new species, at locality No. S. C. 2.

LOCALITIES.—On Finca of Rafael Begoa, 9 miles north of San Cristobal (locality No. S. C. 2) five specimens, Nos. 19018/1–5; on Finca of Rafael Begoa (locality No. S. C. 4) 3 specimens, Nos. 19018/6–8.

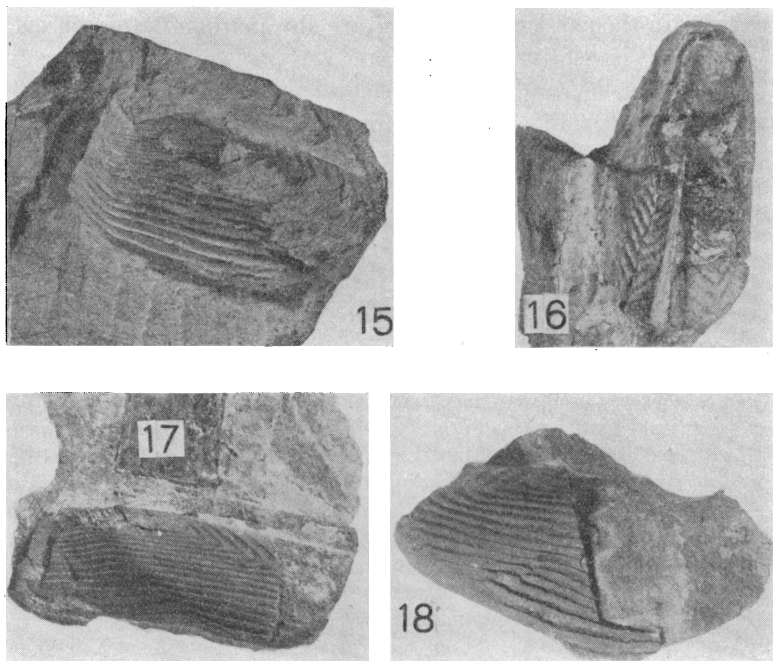
Comparisons.—The distinguishing characteristics of *A. cubanensis* are the angle of curvature of the lamellæ along the posterior ridge and their abrupt, right-angled termination at the external line of junction. These features readily differentiate it from *A. cristobalensis* and *A. pimientensis*, which are found associated with it. The thickening of the lamellæ into folds as they reach the external line of junction is also characteristic. This species appears to be almost identical with the aptychus of *Haploceras* figured by Steinmann (1907, fig. 542) from the Neocomian of Chalançon, Département of Drôme, France, (Fig. 6) except that the Cuban specimens are smaller and they are narrower when viewed from the side. The lamellæ wedge into each other on the side of the valve, while in the French species they are simple and continuous. *Aptychus cubanensis* evidently belongs to a species of *Haploceras*.

***Aptychus pimientensis*, new species**

Figures 15 to 18

DESCRIPTION OF THE HOLOTYPE (Amer. Mus. No. 19019/1). This species is small, rhombohedral in outline and with delicately etched surface features. The measurements for one valve are: length 19 mm., width 10.2 mm., length of the truncated proximal end 8.2 mm (Fig. 15).

The lamellæ are fine and close-set; they increase regularly in size and, beyond the apical portion which is broken away, 26 can be counted. The largest ones wedge out against the smooth peripheral band. There is a pronounced radial ridge on the posterior slope; on the posterior side of the ridge the lamellæ turn sharply toward the apex at an acute angle of about 30° . The junction surface is smooth, triangular, with a maximum width of 1.7 mm.; it is at right angles to the convex surface of the shell. The surfaces of all the lamellæ are finely punctate but this character is most clearly visible on the peripheral surface at the thickest part of the shell.



Figs. 15 to 18. *Aptychus pimientensis*, new species.

Fig. 15. Exterior of valve. $\times 2$. Holotype, A. M. N. H. No. 19019/1.

Fig. 16. Exterior of both valves in juxtaposition, showing triangular junction planes and posterior angulation of lamellæ. $\times 2$. Paratype, A. M. N. H. No. 19019/3.

Fig. 17. Side view of crushed specimen showing acute angulation of lamellæ. $\times 2$. Paratype, A. M. N. H. No. 19019/4.

Fig. 18. View of posterior end of one valve, showing costæ wedging out against peripheral margin and also along the side, producing characteristic *en echelon* notching. $\times 2$. Paratype, A. M. N. H. No. 19019/5.

DESCRIPTION OF PARATYPES.—Specimen No. 19019/4, which is crushed, shows the sharp angulation of the lamellæ on the posterior slope (Fig. 17). Specimen No. 19019/3 shows the two valves in contact along the junction line (Fig. 16). Specimen No. 19019/5 shows the notching of the lamellæ on the anterior slope of the ridge (Fig. 18).

NUMBER OF SPECIMENS.—Holotype and 4 paratypes.

ASSOCIATED SPECIES.—*Aptychus cristobalensis*, new species, at locality No. S. C. 3.

LOCALITIES.—Mt. Pimiento, 5 miles north of San Cristobal, Province of Pinar del Rio (locality No. S. C. 5), three specimens, Nos. 19019/1-3; northeast of Mt. Pimiento in Rio Hondo, 7 miles northeast of San Cristobal (locality No. S. C. 3), two specimens, Nos. 19019/4, 5.

Comparisons.—The most noticeable characteristic of this species is the inflection of the lamellæ at an acute angle as they approach the junction margin. This feature serves as a ready means of distinguishing *A. pimiensis* from *A. cristobalensis* in which the lamellæ are curved, not angular in their inflection. There are also more minute differences: *A. pimiensis* is relatively longer than *A. cristobalensis*, has more even and regular lamellæ, and is rhombohedral instead of semi-elliptical in shape. This species, like the others from the same beds, bears a general resemblance to *A. didayi* from which it differs primarily in shape, being rhombohedral instead of triangular, and having finer, more numerous lamellæ. It probably belongs to a species of *Oppelia*.

BIBLIOGRAPHY OF SOME OF THE MORE IMPORTANT LITERATURE ON THE GENUS *APTYPCHUS*

1811. PARKINSON, JAMES. 'Organic Remains of a Former World.' 3 vols; III, pp. 184-187. (Genus *Trigonellites* (= *Aptychus*) described p. 186; *T. lata*, p. 186, Pl. XIII, figs. 9, 12; *T. lamellosa*, p. 186, Pl. XIII, figs. 10, 11. By the strict rules of priority the name *Trigonellites* should now be used instead of *Aptychus*, but the latter name is firmly rooted in the literature and there is the further consideration that Parkinson considered the opercula to be pelecypods and the name *Trigonellites* is etymologically more appropriate for pelecypods than ammonites.)
- 1830-33. ZIETEN, C. H. 'Die Versteinerungen Württembergs.' (Good illustrations of *Aptychus lævis latus* Meyer (p. 49), Pl. xxxvii, figs. 6 and 7, showing exterior and interior and plates *in situ*.)
1831. MEYER, HERMANN VON. 'Das Genus *Aptychus*.' Nova Acta, XV, pp. 125-170. (Original description of *A. lævis*, p. 128, Pls. LVIII, LIX, figs. 6-9; *A. imbricatus*, p. 139, Pl. LIX, figs. 10-12. Structure of shell, Pl. LIX, fig. 13. Aptychi from the Lias, Pl. LX, figs. 1-7. Aptychi regarded as the shells of mollusks devoured by ammonites, p. 156.)
1837. VOLTZ, PHILIPPE LOUIS. 'Erste Notiz über das Genus *Aptychus*.' Neues Jahrb., pp. 304-312. (General resumé of opinions concerning the nature of aptychi. Voltz considered them to be ammonite opercula.)
1837. 'Zweiter Vortrag über das Genus *Aptychus*.' Neues Jahrb., pp. 432-438. (Classification of 25 species of *Aptychus*, 12 new, into Cornei, Imbricati, and Cellulosi. List of ammonite genera with which aptychi are found *in situ*.)
1841. COQUAND, HENRI. 'Mémoire sur les *Aptychus*.' Bull. Soc. Geol. France, (1) XII, pp. 376-391, Pl. ix. (Summary of previous opinions on the significance of *Aptychus* (pp. 376-386). Considered by Coquand to be genus intermediate between *Loligo* and *Sepia* (p. 387); protographs and

- protologs (pp. 387-390): *A. blainvillei*, p. 387, Pl. ix, figs. 8, 9; *A. beaumonti*, p. 388, Pl. ix, fig. 12; *A. radians*, p. 389, Pl. ix, figs. 11 and 11 bis; *A. didayi*, p. 389, Pl. ix, fig. 10; *A. seranonis*, p. 390, Pl. ix, fig. 13. List of 33 species of *Aptychus* classified and with geological horizon, pp. 390, 391.)
1841. GLOCKER, E. F. 'Ueber den Jurakalk von Kurowitz in Mähren und über den darin vorkommenden *Aptychus imbricatus*.' Nova Acta, XXIX, Suppl. 2, pp. 275-308, Pls. I-III. (Mode of occurrence of *Aptychus imbricatus* in the Jurassic of Kurowitz, pp. 285, 286, 289. Detailed description of examples of this species and of the character of the shell layers, pp. 293-306, Pl. III, figs. 1-7, 9. The species here described is synonymous with *A. punctatus* Voltz and is a typical example of the group of the Punctati.)
1846. GEINITZ, H. B. 'Grundriss der Versteinerungskunde.' (Aptychi discussed pp. 307-310; five species (not new) described.)
1849. QUENSTEDT, F. A. 'Die Cephalopoden.' (Very full descriptions of numerous previously known species, pp. 306-323. Protolog of *A. crassicauda*, p. 314, protograph, Pl. XXII, fig. 25. Of especial interest is description of *A. didayi* Coquand, p. 314, Pl. XXII, fig. 21.)
1854. PETERS, K. 'Die Aptychen der österreichischen Neocomien und oberen Juraschichten.' Jahrb. d. k. k. g. Reichsanstalt, V, pp. 439-444. (Protologs of: *A. angulocostatus*, *A. undatocostatus*, *A. lineatus*, *A. pusillus* (p. 441); *A. rectecostatus*, *A. reflexus* (p. 442); *A. aplanatus*, *A. giganteus* (p. 443). Occurrence of *A. didayi* Coquand in the Neocomian noted (p. 441). *A. latus* Voltz (p. 443), *A. depressus* Voltz and *A. profundus* Voltz (p. 444) reported from the Upper Jurassic of St. Veit and Lainz, Austria.)
1854. PICTET, F.-J. 'Traité de Paléontologie,' 2nd edit. II. (Numerous previously described species listed (p. 558), some figured Pl. XLVII, figs. 10-17. Excellent illustration of *A. didayi* Coquand, Pl. XLVII, fig. 17.)
1854. HÉBERT, E. 'Tableau des Fossiles de la Craie de Meudon.' Mém. Soc. Geol. France, (2) V, pp. 345-374. (Original descriptions of three new species of *Aptychus* from the Chalk of Meudon: *A. insignis*, p. 367, Pl. XXVIII, fig. 6; *A. obtusus*, p. 367, Pl. XXVIII, fig. 7; *A. crassus*, p. 368, Pl. XXVIII, fig. 8.)
1856. SHARPE, D. 'Description of the Fossil Remains of Mollusca found in the Chalk of England.' Pt. III, Cephalopoda. (Aptychi of the Chalk (pp. 53-58). New species described: *A. portlocki*, p. 56, Pl. XXIV, figs. 2, 3, 4, (6?); *A. gollevillensis*, p. 56, Pl. XXIV, fig. 5; *A. icenicus*, p. 57, Pl. XXIV, fig. 7a, b; *A. rugosus*, p. 57, Pl. XXIV, figs. 8a, b, and 9; *A. peramplus*, p. 58, Pl. XXIV, fig. 10.)
1858. QUENSTEDT, F. A. 'Der Jura.' (Illustrations and descriptions of a number of previously described species.)
1863. OPPEL, ALBERT. 'Ueber jurassische Cephalopoden.' Pal. Mitth. III. (Proto-graphs and protologs of many species of aptychi found *in situ* in ammonites from the Lithographic Limestone of Solnhofen. *Ammonites lithographicus*, p. 248, Pl. LXVIII, figs. 1-3; *A. thoro*, p. 250, Pl. LXVIII, figs. 6, 7; *A. steraspis*, p. 251, Pl. LXIX; *A. bous*, p. 252, Pl. LXX, fig. 1;

- A. euglyptus*, p. 253, Pl. LXX, figs. 1-5; *A. hybonotus*, p. 254, Pl. LXXI, figs. 1-3; *A. autharis*, p. 255, Pl. LXXI, figs. 4-6; *A. latus*, p. 256, Pl. LXXII, fig. 1; *A. pipini*, p. 257, Pl. LXXII, fig. 3; *A. aporus*, p. 258, Pl. LXXIII, figs. 1-3; *A. hoplisus*, p. 259, Pl. LXXIII, figs. 4, 5; *Aptychus* sp., p. 261, Pl. LXXIV, figs. 3, 4. The Solnhofen beds contain the largest Upper Jurassic *Aptychus* fauna so far known.)
1865. SCHAUROTH, CARL VON. 'Verzeichniss der Versteinerungen in Herzogl. Naturalien cabinet zu Coburg.' (Protologs and protographs of: *A. punctatus*, p. 152, Pl. iv, fig. 13; *A. exsculptus*, p. 153, Pl. iv, fig. 14. Occurrences given for *A. latus* Münster and *A. lamellosus* Münster, p. 152.)
1866. BENECKE, E. W. 'Ueber Trias und Jura in den Südalpen.' Geogn.-Pal. Beiträge, I, pp. 1-204. (*A. cf. lamellosus* Voltz and *A. cf. latus* Münster reported in *Acanthicus* beds, p. 185, *A. curvatus* Giebel, *A. cf. gigantis* Quenstedt reported from Diphyakalk (p. 192). *A. didayi* recorded as characteristic of the Biancone (Neocomian) formation, p. 135.)
1866. OPPEL, ALBERT. 'Ueber die Zone des *Ammonites transversarius*.' Geogn.-Pal. Beiträge I, Heft 2, pp. 207-316. (References to the occurrence of aptychi species, pp. 218, 234, 252, 279. Occurrence of *Aptychus didayi* in Neocomian of Algeria, p. 273.)
1867. WAAGEN, WILHELM. 'Ueber die Ansatzstelle der Haftmuskeln beim Nautilus und den Ammoniden.' Paläontographica, XVII, pp. 185-210, Pls. xxxix and xl. (Discussion of the position of the aptychus in the body chamber of ammonites, pp. 192, 193; illustrations on Pl. xl.)
1868. ZITTEL, KARL A. 'Die Cephalopoden der Stramberger Schichten.' (Discussion of characters of *Aptychus*, pp. 49-52; description of Stramberg species (pp. 52-55); *A. punctatus* Voltz, p. 52, Pl. I, figs. 15a, b; *A. beyrichi* Oppel, p. 54, Pl. I, figs. 16-19.)
1868. PICTET, F.-J. 'Mélanges Paléontologiques. IV. Fossiles de la Porte-de-France,' (*A. latus* Voltz) p. 283, Pl. XLIII, figs. 1-4) and *A. imbricatus* Meyer (p. 285, Pl. XLIII, figs. 5-10) described from the Limestone of Porte-de-France.)
1870. ZITTEL, KARL A. 'Die Fauna der Aeltern Cephalopenführenden Tithonbildungen.' (*A. punctatus* Voltz (p. 31), *A. beyrichi* Oppel (p. 32), and *A. exsculptus* Schauroth (p. 32, Pl. I, fig. 10) and Cellulose of the *latus* type (pp. 88, 89) described from the Tithonian of the Alps.)
1875. FAVRE, ERNEST. 'Fossiles du Terrain Jurassique de la Montagne des Voirons.' Mém. Soc. Pal. Suisse, II, pp. 1-78. Pls. I-VII. (Four previously known species identified in formations ranging from *Transversarium* through *Acanthicus* zones: *A. latus* (Parkinson), p. 47, Pl. VII, figs. 1-3; *A. punctatus* Voltz, p. 49, Pl. VII, figs. 4, 5; *A. sparsilamellosus* Gümbel, p. 50, Pl. VII, figs. 6-9; *A. beyrichi* Oppel, p. 52, Pl. VII, figs. 10, 11.)
1881. LORIOLO, P. DE. 'La Zone à *Ammonites tenuilobatus* D'Oberbuchsitten.' Idem, VII, pp. 1-60, Pls. I-X. (Presence of *Imbricati* recorded, p. 27, Pl. VII, figs. 6, 7, and *Cellulose*, p. 27, Pl. VII, figs. 8, 9, no species described.)
1885. ZITTEL, KARL A. 'Handbuch der Paläontologie.' II. (Classification of Aptychi, pp. 400-403, figs. 544-553.)
1885. QUENSTEDT, F. A. 'Die Ammoniten des Schwäbischen Jura.' (Illustrations and amplified descriptions of numerous previously described species.)

1890. TOUCAS, A. 'Étude de la Faune des Couches tithoniques de l'Ardèche.' Bull. Soc. Geol. France, (3) XVIII, pp. 560-629. (Occurrence of *A. punctatus* Voltz, pp. 579, 595; *A. beyrichi* Oppel, p. 580; and *A. cf. latus* Voltz noted in the Tithonian of the Alps, Carpathians, Apennines, etc.)
1891. RETOWSKI, O. 'Die Aptychen sind echte Ammonitendeckel.' Neues Jahrb., Jahrgang 1891, II, pp. 220-221 and text figure. (Description and illustration of *A. beyrichi* Oppel shown *in situ* in the aperture of *Haploceras elimatum* (Oppel).)
1893. RETOWSKI, O. 'Die tithonischen Ablagerungen von Theodosia.' Bull. Soc. Imp. des Nat. Mosc., N. S., VII, pp. 206-301, Pls. ix-xiv. (*A. punctatus* Voltz reported to be very abundant in Tithonian of Theodosia in the Crimea (p. 225); *A. beyrichi* Oppel described as *A. elimati* because found *in situ* in *Haploceras elimatum* (p. 226); *A. cf. exsculptus* Schauth rare, p. 227, Pl. ix, fig. 2.)
1893. CHOFFAT, PAUL. 'Faune Jurassique du Portugal.' (No species described. Rare occurrence of aptychi fragments in limestones of Cabaço series noted; Cellulose of the *latus* type frequent in the marl beds of the Montejunto and Abadia series of Portugal.)
1894. MICHAEL, RICHARD. 'Ammoniten Brut mit Aptychen in der Wohnkammer von *Oppelia steraspis* Oppel sp.' Zeit. d. deutsch. geol. Gesellschaft, XLVI, pp. 697-702, Pl. LIV. (Contains description of embryonic ammonites found in body chamber of *Oppelia steraspis*, both the young and mature shells having aptychi.)
1896. BLACKMORE, H. P. 'Some notes on the Aptychi from the Upper Chalk.' Geol. Mag., N. S., (4) III, pp. 529-533, Pl. xvi. (Paper deals with Upper Cretaceous aptychi only and they are considered to be opercula of belemnites. *A. rugosus*, p. 532, Pl. xvi, fig. 16, shows form very similar to Cuban species.)
1898. CRICK, G. C. 'Fossil Cephalopoda in the British Museum.' (Four Upper Cretaceous (Upper Chalk) species of *Aptychus* listed (pp. 32, 33). All previously described by Sharpe, *q. v.*)
1899. PAUL, C. M. 'Der Wienerwald. Ein Beitrag zur Kenntniss der nordalpinen Flyschbildungen.' Jahrbuch der k. k. geol. Reichsanstalt, XLVIII, pp. 53-178, Pl. I-VI, 26 text figures. (The species of *Aptychus* occurring in the Wienersandstein are recorded on pp. 58, 59, 60, 135, 141, 142, 152, 158, 175.)
1905. VETTERS, HERMANN. 'Die Fauna der Juraklippen zwischen Donau und Thaya.' Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients, XVII, pp. 223-259, Pls. XXI, XXII. (Occurrence of *Aptychus punctatus* Voltz, p. 242, Pl. XXI, fig. 4, and *A. latus* Meyer, p. 243, in the Niederfellabrunn Tithonian noted.)
1907. TOULA, FRANZ. 'Die Acanthicus-Schichten im Randgebirge der Wiener Bucht bei Giesshübl.' Abh. d. k. k. geol. Reichsanstalt, XVI, Heft 2 (Aptychi of *Acanthicus* beds, pp. 80-82, 88. Original description of: *A. cellulosalamellosus*, p. 80, Pl. XVIII, fig. 4; *A. insolidus*, p. 81, Pl. x, fig. 2. Occurrence of *A. cf. didayi* Coquand noted, p. 88, Pl. XII, fig. 6.)
1907. STEINMANN, GUSTAV. 'Einführung in die Paläontologie.' Leipzig. (Description of aptychi, pp. 319, 320; excellent illustrations, figs. 540-542.)

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