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Article VII.—PHYLOGENY OF THE AMMONITE GENUS *OCHETOCERAS*[1]

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INTRODUCTION

The family of the Harpoceratidæ includes the closely involute, discoidal ammonites which possess a smooth, noded, or crenulated keel, sigmoidal costæ and sometimes, but not always, a lateral groove or channel. The sides of the aperture have a sigmoidal curve parallel to the costæ or they are prolonged into lateral lappets, while the venter is produced into a rounded crest. The sutures are simple, with narrow digitate lobes and squarish saddles, the latter usually radial. The family ranges from the Lower Jurassic (Liassic) into the Lower Cretaceous (Comanchic).

In this family two sub-families have been recognized, the Harpoceratinæ of Zittel, including such typical forms as *Harpoceras* Waagen, *Lioceras* Hyatt and *Brasilia* Buckman, and the Oppelinæ[2] of Haug, including as representative genera *Oppelia* Waagen, *Oechotraustes* Waagen, *Streblites* Hyatt and *Creniceras* Munier-Chalmas.

Prior to the year 1885 the large group of discoidal forms possessing a lateral groove or canal, and called, therefore, the "canaliculati," had generally been assigned to the genus *Harpoceras* in the first of the two sub-families mentioned above. But in 1885 Haug in his monograph on *Harpoceras* made the suggestion that the "canaliculati" did not belong to that genus nor were they even directly derived from it, but were instead offshoots from *Oppelia*, itself a derivative from *Harpoceras*. It was, therefore, to be classed in the second sub-family, that of the Oppelinæ. He regarded *Ammonites flexuosus canaliculatus* Quenstedt (1849, 'Die Cephalopoden,' Pl. IX, fig. 5; 1858, 'Der Jura,' Pl. LXX, fig. 13), from the upper division (Oxfordian) of the Middle Jurassic beds of Germany, as the connecting link between the oldest Middle Jurassic Oppelias of the "flexuosi" group, that is, the forms with flexed or sigmoidal costæ, and the Upper Jurassic "canaliculati." For this latter group he proposed the sub-generic name *Ochetoceras*[3] (Haug, 1885, p.

[1] In working up the Jurassic fauna of Cuba collected by Mr. Barnum Brown in 1918 and 1919 it was found necessary to make a comparative study of the European, Cuban, and Mexican species of *Ochetoceras*. The present paper embodies the chief results of that study and includes brief descriptions of several new species from Cuba. The complete descriptions and illustrations will appear in a forthcoming paper on the Jurassic of Cuba.

[2] The species in this subfamily were classified on a phyletic basis by Douvillé (1913).

[3] Derivation: ὀχετός, canal, + κέρας, horn.

698); subsequent refinements in classification have shown that the name should be accorded full generic rank.

The distinguishing generic characteristic of *Ochetoceras*, as pointed out by Haug, is the sharp and angular keel which persists throughout all growth stages even to the end of the conch. This is the primary difference between *Ochetoceras* and *Oppelia*, for in the latter the keel is rounded at least on the body chamber and often throughout the entire conch. A lateral canal is sometimes present in *Oppelia;* in *Ochetoceras* it is typically present throughout the ontogeny although in some species its position is indicated by the flexing of the costæ rather than by an actual groove. Haug accepted as a satisfactory description of his new genus the characterization previously given by Zittel for the "canaliculati," namely (Zittel, 1881–'85, p. 460):

> Rather involute forms with sharpened and keeled venter and high (i.e. laterally compressed) oral aperture. Costæ falciform, strong, with the position of flexing marked by a lateral canal. Suture line very finely incised.

Geologically, *Ochetoceras* has a limited range, having been found so far mainly in the two lower divisions of the Upper Jurassic, the Lusitanian and Kimmeridgian, in each zone from the lowest part of the former (zone of *Peltoceras transversarium*) to the highest part of the latter (zone of *Aulacostephanus pseudomutabilis*), although one species ranges into the lower Tithonian (Portlandian), zone of *Oppelia lithographica.*

Geographically, it has a broad range, occurring in the Old World in England, France, Germany, Switzerland, Portugal, Spain, northern Africa, Persia, the Caucasus Mountains, and the Balkans. In the New World it has previously been known only from Mexico (Durango and Mazapil) until the new discoveries in Cuba showed it to be well represented there.

Since the genus has a limited geological and wide geographical range, it has the ideal requisites for an index fossil for the lower and middle divisions of the Upper Jurassic. Furthermore, the individual species, while having a broad geographical range, have a geological range usually limited to a single faunal zone, so that they serve excellently for the broad correlation of small stratigraphical units in widely separated regions. The succession of biozones[1] which can be recognized for the species of

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[1]A faunal zone, according to Oppel and his followers, is one of the smallest divisions of a formation determined by the presence in it of a particular unit fauna; it is a stratigraphic division defined in terms of the palæontological content. A biozone, as defined by Buckman, is "the range of organisms in time indicated by their entombment in the strata" (Geol. Mag., 1902, p. 556). The current usage of these and other chronological and stratigraphical terms is fully discussed in a paper by C. Diener, 1918, 'Die Bedeutung der Zonengliederung für die Frage der Zeitmessung in der Erdgeschichte,' Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage Band XLII, pp. 65–172.

Ochetoceras is the same in Europe and Cuba, while the strata containing the organic remains in the latter region can be divided into the same faunal zones as those established by Oppel for the Upper Jurassic of western Europe. Thus the phylogeny of *Ochetoceras* has a biological as well as a stratigraphical interest and value.

Haug divided the European species of *Ochetoceras* into the groups of *O. hispidum* and *O. canaliculatum* (Haug, 1885, p. 696). The same two groups may be recognized in Cuba and Mexico where the phyletic series contain some of the same species as occur in Europe. However, not all of the European species have been found in Cuba while, on the other hand, some species have been found in the New World which are unknown in the Old. In general, it may be said that in the Lusitanian the species are cosmopolitan and show a wide geographic range, while in the Kimmeridgian they are provincial. Thus, in the Lusitanian the same species are found in Europe, Asia, and America; in the Kimmeridgian the geographical range is more restricted and the species in various countries, though related, are different. The differences arise from specializations along certain lines such as the trend of one or more conch ratios, the triple carinations on the venter, or the distribution and arrangement of the costæ. But such specializations are not to be regarded as due to the introduction of new characters; they are rather the result of retardation or acceleration of characters already impressed upon the species in the several phyletic lines in the Lusitanian; during the Kimmeridgian the orthogenetic trends which were foreshadowed in the Lusitanian are followed out in a manner which could be predicted from a study of the ontogeny of the species in the older horizon.

DISCUSSION OF SPECIES OF DOUBTFUL AFFINITIES

Before passing to the discussion of the two main groups of *Ochetoceras* recognized by Haug and a third group which is here recognized for the first time, it may be well to note that these three groups do not contain all of the known species of the genus.[1] There are certain European forms of doubtful affinities about which too little is known for their phyletic relations to be determined unless one had access to the types, since the original descriptions and illustrations are poor or incomplete and there is too little information about the ontogeny. For instance, there is *Ammonites guembeli* Oppel (1862, p. 159; 1863, p. 197, Pl. LI, figs. 5*a-c*, 6*a*, *b*, 7*a-c;* also Quenstedt, 1885, p. 842, Pl. XCII, figs. 16, 17)

[1]Douvillé (1913) united all of the species of these three groups into the large phyletic series of *Ochetoceras* without separating out the different branches.

from the lower Kimmeridgian of Bavaria. At a very early stage the conch has nodes on the ventro-lateral angulation, while there is no median keel or lateral groove. It does not, therefore, possess the essential characters of *Ochetoceras*. At a diameter of 30 mm., however, the nodes become elongate in a radial direction and fuse into single costæ which, although of entirely different origin, appear like those of *O. canaliculatum;* instead of the lateral groove characteristic of *Ochetoceras* there is a row of fine nodes along the middle of the lateral zone. The conch proportions of *A. guembeli* at this stage are also like those of *O. canaliculatum;* thus, at a diameter of 30 mm., the height of the whorl is 15 mm., the width 7 mm., and width of umbilicus is 3–4 mm., giving the ratios of height to diameter 0.50, width to diameter 0.23, width to height 0.46, width of umbilicus to diameter 0.10 to 0.13. These ratios are almost identical with those for *O. canaliculatum* at a diameter of 90 mm. (see Table 3). After this stage the conch develops a wavy keel resembling a cock's comb. This species was used by Quenstedt as the genoholotype of *Cymaceras* (1885, p. 842), but Haug has placed it in the genus *Ochetoceras* (1885, p. 698; 1908–'11, p. 1049). However, I believe that the latter assignment is not borne out by the facts of the ontogeny, for in the earliest observable stage *A. guembeli* is not an *Ochetoceras*. If, at one stage in its development, it passes through a phase where it has an external resemblance to one of the species of *Ochetoceras* without, however, having evolved its characters in the same way as that species does, and then later develops a keel altogether at variance with the keels of all the other species of *Ochetoceras*, then *A. guembeli* is scarcely to be regarded as genetically related to *Ochetoceras*.

The same may be said for *Harpoceras* (?) *argonautoides* Mayer, var. *sulculufera* Fontannes, from the Tenuilobatus beds of Crussol, Ardèche, France, (Dumortier and Fontannes, 1875, p. 232, Pl. v, fig. 5 and Fontannes, 1879, p. 15), which is related to *A. guembeli* Oppel. There is a third aberrant species, *Ochetoceras* (?) *daghestanicum* Neumayr (Neumayr and Uhlig, 1892, p. 45, Pl. vi, fig. 1) which appears to belong in this same group, although it does not show a wavy or undulatory keel. It occurs in the Lusitanian of the Caucasus, probably in the zone of *Peltoceras bicristatum*, and is distinguished by its smooth inner flanks and its row of nodes in the position of the lateral groove in *Ochetoceras, sensu stricto*. These nodes give rise to bundles of costæ which pass ventrad. It seems not improbable that this form might have given rise to *Cymaceras guembeli* in the Kimmeridgian, for the young of that species resemble the later stages of *O.* (?) *daghestanicum*. Another specialization

from the same Lusitanian form might have given rise to *Harpoceras* (?) *argonautoides sulculufera*, also from the Kimmeridgian, but such suggestions for a phyletic series must be speculative because so little is known about the forms. However, I would not include any of these three species under *Ochetoceras, sensu stricto.*

An isolated form of doubtful affinities which does not seem to fall into any of the phyletic series is *Ochetoceras subclausum* (Oppel) (1863, p. 190, Pl. LII, figs. 3*a*, *b*). It is a small, low-whorled, smooth form occurring in the lower Lusitanian (zone of *Peltoceras transversarium*) of Switzerland and southern Germany. It has a deep lateral groove which is most pronounced at the end of the conch. On the inner whorls there is a sharp median keel, but from the middle of the body chamber to the aperture this angulation decreases and the venter becomes rounded as in *Oppelia.* The diameter of a mature conch is 32 mm., height of whorl 13 mm., width of whorl 7 mm. and width of umbilicus 7 mm., giving as conch ratios $\frac{\text{h.i.}}{\text{d}} = .40, \frac{\text{w}}{\text{d}} = .22, \frac{\text{w}}{\text{h.i.}} = .55, \frac{\text{u}}{\text{d}} = .22.$ The last whorl is loosely coiled and slants off across the preceding with the result not only that the umbilicus is increased in width but also that the spiral curve of the venter is distorted. The partial loss of the power of coiling and the loss of the keel are generally signs of onto- or phylo-gerontism, and such appears to be the case in the present instance, for *O. subclausum* was evidently a decadent species and it left no known descendants.

The upper Tithonian *Ammonites folgaricus* Oppel and the Lower Cretaceous (Valanginian) *Ammonites macrotelus* Oppel have been assigned to *Ochetoceras* by Douvillé (1913, p. 63), but they do not belong to that genus in the restricted sense.

GROUP OF *OCHETOCERAS AROLICUM*

General Characteristics.—This is a small, heterogeneous assemblage of species of doubtful affinities. It includes forms with nearly smooth conchs, on which costæ developed during the ephebic or gerontic stage. There is no lateral groove but its position is indicated either by the locus of the inner ends of short costæ on the outer flanks or by the locus of the angle of flexing of long costæ which pass from umbilicus to venter. Keel triple, with carinations of equal height or with median keel elevated. Nearly all of the species show gerontic tendencies.

TABLE 1. DIMENSIONS, PROPORTIONS AND GEOLOGICAL AND GEOGRAPHICAL DISTRIBUTION OF THE SPECIES IN THE GROUP OF *Ochetoceras arolicum* (Oppel)

Geological Age	Faunal Zone	Species	Geographical Distribution	d[2] mm.	h. i. mm.	h. i. / d	w mm.	w / d	w / h. i.	u mm.	u / d
1	2	3	4	5	6	7	8	9	10	11	12
Portlandian	Zone of *Oppelia lithographica*	*O. steraspis* (Oppel) (Cotypes)	Germany: Solnhofen, and Eichstädt, Bavaria; Württemberg Switzerland: Canton Aargau	85	50	.58	17[1]	.20[1]	.34[1]	9	10
Kimmeridgian	Zone of *Aulacostephanus pseudomutabilis*										
	Zone of *Streblites tenuilobatus*										
Lusitanian	Zone of *Peltoceras bicristatum*	*O. trimarginatum* (Oppel) (Cotypes)	Germany: Bavaria and Württemberg	51[1]	30.6[1]	.60[1]	11[1]	.22[1]	.36[1]	13[1]	.25[1]
	Zone of *Peltoceras transversarium*	*O. arolicum* (Oppel) (Cotypes)	Switzerland: Canton Aargau Germany: Baden, Württemberg and Bavaria	74	40	.54	16	.21	.40	9	.12
		O. stenorhynchum (Oppel) (Cotypes)	Switzerland: Canton Aargau Germany: Baden, Swabian Alp, Württemberg	40	20	.47	8	.18	.40	7	.16

[1]Approximate.
[2]Meaning of abbreviations: d = diameter; h.i. = height of whorl from line of involution to venter; w = width of whorl; u = width of umbilicus.

LOWER LUSITANIAN, ZONE OF *Peltoceras transversarium*

Ochetoceras arolicum (Oppel)

SPECIFIC CHARACTERS.[1]—Conch flat, discoidal, involute, with convergent lateral zones and sagittate cross-section; triple keel; in ephebic stage, faint, widely-spaced, crescentic folds on ventral half of each lateral zone. (Oppel, 1863, p. 188, Pl. LI, figs. 1*a*, *b*, 2*a*, *b*).

GEOGRAPHICAL DISTRIBUTION.—Birmensdorf, near Baden, Canton Aargau, Switzerland.

Ochetoceras stenorhynchum (Oppel)

SPECIFIC CHARACTERS.[1]—Conch strongly compressed, whorls smooth up to body chamber where faint costæ appear. Umbilicus broad with sloping sides and blunt umbilical shoulder. Venter moderately wide with three carinations of equal height. Involution decreases in gerontic stage. Body chamber occupies three-fifths of a whorl. Suture like that of *O. trimarginatum* (see below), (Oppel, 1863, p. 189, Pl. LII, figs. 1*a*, *b*).

GEOGRAPHICAL DISTRIBUTION.—Lägern, near Baden, Canton Aargau, Switzerland.

The Relation of the Species from the Lower Lusitanian

These two species are almost intermediate in generic characters between *Oppelia* and *Ochetoceras;* they have the form, general appearance, and some of the surface features of the latter genus but they do not possess the lateral groove, although its position is indicated by the ends of the costæ. The narrow venter (even in *O. stenorhynchum* it is not very wide) and the triple carinations persisting to the end of the conch indicate that these two species belong to *Ochetoceras* rather than to *Oppelia*. Both species appear to be offshoots from *Oppelia eucharis* (D'Orbigny) (1842, p. 524, Pl. CXCVIII, figs. 3, 4) which occurs in the upper Oxfordian in eastern and western France; *Ochetoceras arolicum* represents a specialization in extreme sharpening of the venter with the development of triple carinations of which the middle is the highest, while *Ochetoceras stenorhynchum* specialized towards a broader triple venter with all three carinations of equal height. *Oppelia eucharis* at a diameter of 60 mm. has the following ratios: $\frac{\text{h.i.}}{\text{d}} = .54$, $\frac{\text{w}}{\text{d}} = .20$, $\frac{\text{w}}{\text{h.i.}} = .37$, $\frac{\text{u}}{\text{d}} = .13$.

UPPER LUSITANIAN, ZONE OF *Peltoceras bicristatum*

Ochetoceras trimarginatum (Oppel)

SPECIFIC CHARACTERS.—Conch compressed; whorls smooth, except last one on which are 20 weak costæ. Umbilicus very broad, tapering outward near aperture. Suture with five short lateral lobes and saddles; first lateral lobe palmate and longer

[1]The dimensions and conch ratios are given in Table 1, p. 392.

than ventral; first lateral saddle broad and asymmetrically divided into two parts. Venter with three carinations of same height. Cross-section sagittate with lateral zones convergent. (Oppel, 1862, p. 159, Pl. L, figs. 2*a*, *b*.)

GEOGRAPHICAL DISTRIBUTION.—Bavaria and Württemberg, Germany.

The Relations of *O. trimarginatum* to Other Species

Ochetoceras trimarginatum was derived from *O. stenorhynchum* with which it agrees in sutures and type of keel. The rather great divergence in conch ratios between the two species is to be explained by the evidences of phylo-gerontism even in the older one. In both species there is a loss of the power of coiling, which produces an increasingly wider umbilicus, whereas in normal series the involution increases with the age of the individual. This particular sign of gerontism is observable in all individuals of each species, so that it is an evidence of onto-gerontism, and it also obtains in successive species, so that is indicative of phylo-gerontism. In *O. trimarginatum* the umbilicus is one-fourth the diameter in width, being thus considerably broader than in any other species in any series. The *stenorhynchum-trimarginatum* branch was evidently decadent; it was confined to the Lusitanian, having no known descendants, and the geographical distribution was restricted to the regions of the Swiss and Swabian Jura.

UPPER KIMMERIDGIAN, ZONE OF *Aulacostephanus pseudomutabilis*, AND LOWER TITHONIAN (PORTLANDIAN), ZONE OF *Oppelia lithographica*

Ochetoceras steraspis (Oppel)

SPECIFIC CHARACTERS.—Whorls compressed, high and thin. Umbilicus narrow. Conch smooth until half grown; in later stages covered with numerous thin costæ which, on inner part of flanks, are very faint and are directed obliquely orad either in a straight line or in a sigmoidal curve and, on outer part of flanks, have a falciform curvature; at the middle of the lateral zones the costæ are flexed at a sharp angle. In early stages venter tricarinate, in later stages unicarinate. (Oppel, 1863, p. 251, Pl. LXIX, figs. 1–9.)

GEOGRAPHICAL DISTRIBUTION.—Solnhofen and Eichstädt, Bavaria, and Württemberg, Germany; Lägern, near Baden, Canton Aargau, Switzerland.

The Relation of *O. steraspis* to Other Species

The young of *O. steraspis* is smooth and in all respects like *O. arolicum* at a diameter of 40 mm. (see Oppel, 1863, Pl. LXIX, figs. 3*a*, *b*, and compare with Pl. LI, figs. 1*a*, *b*). In the adult *O. arolicum* a few widely spaced costæ appear; by acceleration their time of appearance is

TABLE 2. DIMENSIONS, PROPORTIONS AND GEOLOGICAL AND GEOGRAPHICAL DISTRIBUTION OF THE SPECIES IN THE GROUP OF *Ochetoceras hispidum* (Oppel)

Geological Age	Faunal Zone	Species	Geographical Distribution	d[2] mm.	h. i. mm.	h. i. / d	w mm.	w / d	w / h. i.	u	u / d
1	2	3	4	5	6	7	8	9	10	11	12
Kimmeridgian	Zone of *Streblites tenuilobatus*	*O. hispidiforme* (Fontannes) (Holotype)	France: Crussol, Ardèche	39	19.9[1]	.51	10[1]	.26	.51	7[1]	.18
		O. semimutatum (Fontannes) (Holotype)	France: Crussol, Ardèche	30	16.5[1]	.55	11.1[1]	.37	.67	4.5[1]	.15
Lusitanian	Zone of *Peltoceras bicristatum*										
	Zone of *Peltoceras transversarium*	*O. mexicanum* Burckhardt (Holotype)	Mexico: Cerro del Volcán, Durango	62	35	.56	19	.30	.54	10	.16
		(Plesiotype)	Cuba: Viñales, Pinar del Rio. *	44.7	24.8	.55	14.0	.31	.56	6.5	.14
				41.0	23.2	.56	12.7	.31	.55	6.6	.16
				35.0	19.4	.55	11.8	.33	.60	5.3	.15
		O. pedroanum Burckhardt (Holotype)	Mexico: Cerro del Volcán, Durango	35	18	.51	11.5	.32	.63	6.5	.18
		O. hispidum (Oppel) (Cotypes)	Germany: Bavaria, Württemberg Switzerland: Aargau France: Voirons in Savoie	44	23	.52	16	.36	.69	8	.18

*Bracketted readings are for dimensions at successive stages on the same specimen.
[1]Calculated from the ratios.
[2]For meaning of abbreviations see p. 392.

pushed back in the ontogeny of *O. steraspis* and they have become a more deeply impressed and persistent character. The specialization, in this as in the other end members of the phyletic series of *Ochetoceras*, is the trend toward multiple costæ.

GROUP OF *OCHETOCERAS HISPIDUM*

GENERAL CHARACTERISTICS.—This is a small group comprising forms with broad, inflated whorls, thick, coarse costæ, a broad umbilicus and a noded keel. All of the species have been founded upon incomplete specimens so that the characters of the late ephebic and gerontic stages are unknown. The specific descriptions are for individuals ranging from 30 to 60 mm. in diameter and for conchs of that size the following ratios may be considered as characteristic of the group (see Table 2, p. 395).

The height of the whorls is always slightly over, but never much in excess of one-half the diameter (range 0.51—0.56); the width of the whorls is about one-third the diameter, being, with one exception, 0.30 or over (range 0.26—0.36); the ratio of width to height is over 0.50, (range 0.51—0.69), in most instances over 0.55; the range of the ratio of width of umbilicus to diameter is 0.14 to 0.18. The following trends in proportion are shown in both ontogeny and phylogeny: the relative height remains practically constant so far as can be observed; the relative width as compared both to diameter and to height shows a tendency to decrease, while the relative width of the umbilicus is remarkably constant. These facts indicate that the chief change in proportions which the species of this group undergo is the modification of the relative width of the whorls. This allometric trend is both ontogenetic and phylogenetic. Thus, the whorls are markedly inflated in the early stages of primitive species but they become flatter in the later stages, and similarly in *O. hispidiforme*, the final representative of group, the whorls at a diameter of only 39 mm. are relatively more compressed than they are at a greater diameter in any of the species from an earlier horizon.

The keel is low, denticulated or noded, bounded by smooth concave zones but no true channels, and not markedly triple, although in most species subdued lateral angulations develop between the lateral and ventral zones.

The sutures are known only in the species of the lower Lusitanian; they are simple with shorter lobes and saddles, the latter usually broader, the former narrower, than in the group of *Ochetoceras canaliculatum*.

LOWER LUSITANIAN, ZONE OF *Peltoceras transversarium*

Ochetoceras hispidum (Oppel)

SPECIFIC CHARACTERS.[1]—Whorls broad, umbilicus wide. Lateral groove broad and deep, not crossed by costæ. Cross-section of whorls broad oval. On inner flanks, between groove and umbilicus, coarse, straight, evenly-spaced costæ with oblique orad trend; on outer flanks, between groove and venter, costæ nearly straight, slightly curved orad, unbranched, club-shaped with thick end near venter. No intercalated costæ. Keel simple with no lateral carinations; large median nodes, one corresponding to each costa. (Oppel, 1863, p. 193, Pl. LII, figs. 2*a*, *b*.)

GEOGRAPHICAL DISTRIBUTION.—The species occurs in Bavaria, Württemberg, and southern Baden, Germany; in Canton Aargau, Switzerland (Oppel, 1863, p. 193; Quenstedt, 1885, p. 840, Pl. XCII, figs. 9–11), and in Savoie, eastern France, (Favre, 1875, p. 27, Pl. II, fig. 8). *O. hispidum*, therefore, is confined to the type regions of the European Jurassic, to eastern France, northern Switzerland and southwestern Germany.

Ochetoceras mexicanum Burckhardt

SPECIFIC CHARACTERS.[1]—Whorls high and moderately broad. Costæ straight, oblique orad on inner flanks, coarse, slightly curved, strong, club-shaped, occasionally branching on outer flanks. Keel finely noded and bounded by shallow lateral channels and subdued lateral carinæ. Suture: five broad lateral saddles, four narrow, elongate, digitate lateral lobes. (Burckhardt, 1912, p. 7, Pl. II, figs. 8–12; O'Connell, 1920, p. 686, Pl. XXXVIII, figs. 1–3.)

GEOGRAPHICAL DISTRIBUTION.—Cerro del Volcán, Durango, Mexico; Viñales, Province of Pinar del Rio, Cuba.

Ochetoceras pedroanum Burckhardt

SPECIFIC CHARACTERS.[1]—Whorls rather thick and only moderately high. Lateral groove broad, deep and sharply defined. Costæ on outer flanks robust, not branched. Umbilicus broad. Cross-section of whorls elongate oval. Keel finely noded; bounded by low ventro-lateral angulations. Suture: six lateral saddles, six lateral lobes; ventral lobe a little shorter than first superior; lateral saddles asymmetrically divided into two parts. (Burckhardt, 1912, p. 9, Pl. I, figs. 13–17.)

GEOGRAPHICAL DISTRIBUTION.—Cerro del Volcán, Durango, Mexico.

The Relation of the Lower Lusitanian Species

Ochetoceras mexicanum occupies an intermediate position between the species of the *O. hispidum* group and those of the *O. canaliculatum* group, but is undoubtedly a derivative of the former. It is not improbable that *O. mexicanum*, described from a specimen 62 mm. in diameter, represents the adult stage of *O. pedroanum*, described from an incomplete specimen only 35 mm. in diameter. The holotypes of these spe-

[1]Dimensions and conch ratios are given in Table 2, p. 395.

cies came from Mexico. But in Cuba occurs a single specimen of *O. mexicanum* nearly 45 mm. in diameter and the conch proportions and general characters which it shows at a diameter of 35 mm. are nearly identical with those of *O. pedroanum* at that diameter, while as it increases in size it approaches the proportions of the Mexican *O. mexicanum*. The sutures in both species are similar and both have subdued tricarinate noded keels, although the lateral carinations are not very pronounced. *O. pedroanum* itself is so near to *O. hispidum* in all of its characters and proportions as to be regarded as a probable variation of that species, the differences between the two being such as are to be expected in forms widely separated geographically.

Lower Kimmeridgian, Zone of *Streblites tenuilobatus*

Ochetoceras semimutatum (Fontannes)

Specific Characters.[1]—Whorls strongly compressed. Costæ thick and straight on inner flanks, club-shaped, curved and occasionally branched on outer flanks. Keel noded; median carination bounded by faint lateral carinations. (Fontannes, 1879, p. 17, Pl. II, fig. 9.)

Geographical Distribution.—Crussol, Ardèche, France.

Ochetoceras hispidiforme (Fontannes)

Specific Characters.[1]—Whorls relatively low and greatly compressed. Ratio of width to height of whorl only one-half. Umbilicus broad. Costæ coarse, straight and oblique on inner flanks, club-shaped, falciform and bifurcate on outer flanks.

Geographical Distribution.—Crussol, Ardèche, France.

The Phyletic Trends in the *O. hispidum* Group

The most variable conch ratio is that of width to height of whorl. Since the relative height as compared to the diameter remains nearly constant in onto- and phylo-stages, while the relative width decreases, it is evident that the width to height ratio for the whorl is essentially a function of the width. In *O. mexicanum*, in which more onto-stages can be studied than in any other species of the group, the decrease in the width to height ratio is clearly shown. The same decrease appears in the phylogeny, *O. hispidum*, the oldest species, having the highest ratio, *O. semimutatum*, the youngest species, the lowest ratio. Furthermore, the change in ontogeny from a broad to a narrow, strongly compressed whorl takes place more rapidly in later than in earlier species, showing that this change in proportion has been accelerated. Thus, the

[1]Dimensions and conch ratios are given in Table 2, p. 395.

TABLE 3. DIMENSIONS, PROPORTIONS, AND GEOLOGICAL AND GEOGRAPHICAL DISTRIBUTION OF THE SPECIES IN THE GROUP OF *Ochetoceras canaliculatum* (Buch)

Geological Age	Faunal Zone	Species	Geographical Distribution	d[4] mm.	h. i. mm.	h. i. / d	w mm.	w / d	w / h. i.	u mm.	u / d
1	2	3	4	5	6	7	8	9	10	11	12
Kimmeridgian	Zone of *Aulacostephanus pseudomutabilis*	*O. zio* (Oppel) (Holotype)	Germany: Württemberg	41	21	.51	8	.19	.38	6	.14
	Zone of *Streblites tenuilobatus*	*O. neohispanicum* Burckhardt (Holotype)	Mexico: Durango	70	39	.55	16[1]	.22[1]	.41[1]	11	.15
		O. vicente dentatum, new variety (Holotype)	Cuba: Constancia, Pinar del Rio	46	25.8	.56	13.1	.28	.50	5.7	.12
		O. vicente, new species (Holotype and Paratype)	Cuba: San Vicente, Pinar del Rio *	69.2 42.9 36.5	37.3 23.8 19.3	.54 .53 .53	20.4 12.6 10.4	.29 .29 .29	.55 .53 .54	9.5 6.6 5.7	.13 .15 .16
		O. canaliferum (Oppel) (Holotype)	Germany: Wurttemberg Switzerland: Aargau France: Crussol, Ardèche	76	43	.56	15	.19	.34	9	.11
		O. palissyanum (Fontannes) (Cotypes)	France: Crussol, Ardèche	54 46	28.6[3] 23[3]	.53 .50	9.7 10[3]	.18? .22	.34 .44	8.1[3] 8.2[3]	.15 .18
Lusitanian	Zone of *Peltoceras bicristatum*	(Cotypes)	Germany: Württemberg and Bavaria Switzerland: Aargau	61.0	31.0	.51	16.0	.26	.51	9.0	.15
		O. semifalcatum (Oppel) (Plesiotype)	Cuba: Constancia, Pinar del Rio *	61.0 47.4	31.3 24.7	.51 .52	15.8 12.1	.26 .25	.50 .49	9.6 7.7	.15 .16
		(Plesiotype)	Cuba: Rio Hondo, Pinar del Rio *	56.0 42	29.0 23.2	.52 .55	14.3 11.3	.25 .26	.49 .49	8.2 5.3	.14 .13
		(Cotypes)	France: Marans in Charante Inférieure, etc. Germany: Swabian Jura, etc. Spain, Portugal, the Balkans	55	27.5[3]	.50	9.9[3]	.18	.36	8.8[3]	.16
		O. marantianum (D'Orbigny) (Plesiotype)	Cuba: Constancia, Pinar del Rio	23.3	11.8	.50	6.7	.29	.57	5.1	.21
	Zone of *Peltoceras transversarium*	(Holotype)	Cuba: Viñales and Constancia, Pinar del Rio	55.8 55.5	31.5 31.0	.56 .56	13.4 16.0	.23 .29	.42 .51	7.5 8.0	.13 .14
		O. canaliculatum (Buch) var. *burckhardti* O'Connell	Mexico: Cerro del Volcán, Durango	32.0	18.5	.57	8.0	.25	.43	5.0	.16
		O. canaliculatum (Buch)	Switzerland: Aargau France: Rhone Valley Germany: Württemberg, etc. England, Spain, Portugal, Persia, northern Africa.	90.[2]	52.6	.56	21.6	.23	.43	12.2	.13

*Bracketted readings are for dimensions at successive stages on the same specimen.
[1]Approximate.
[2]Dimensions given by D'Orbigny (1842, p. 525).
[3]Calculated from ratios.
[4]For meaning of abbreviations, see p. 392.

lower Lusitanian *O. mexicanum* has a height to width ratio of .30 at a diameter of 62 mm., but the lower Kimmeridgian *O. hispidiforme* has attained a corresponding ratio of 0.26 at a diameter of only 39 mm., which indicates that it probably had the same ratio as *O. mexicanum* when it was only about half the size of that species.

In respect to the type of costæ and mode of branching the trend is toward an increase in the number of costæ with a concomitant decrease in coarseness and a bifurcation of the ventral ends. The costal trends in this phyletic series are parallel to those which are observed in the *O. canaliculatum* group (see below, p. 409). For example, *O. hispidiforme* bears the same relation to *O. hispidum* as *O. marantianum* does to *O. canaliculatum*, the development of the analagous costal branching taking longer in the *O. hispidum* than in the *O. canaliculatum* group. (See Table 5.)

GROUP OF *OCHETOCERAS CANALICULATUM*

GENERAL CHARACTERISTICS.—This group includes highly involute species with thin, flat whorls having a cuneate cross-section and flat convergent lateral zones. In general the umbilicus is relatively smaller than in the *O. hispidum* group, ranging from 0.11 to 0.16 (0.12 to 0.15 most characteristic), while in the *hispidum* group the range is from 0.12 to 0.18, with 0.16 to 0.18 as most characteristic. The most distinctive conch ratio for the group is that of width to height, which is seldom as great as one-half and may be as small as one-third, with a maximum range of 0.34 to 0.57 and a characteristic range for adult forms of 0.36 to 0.49. Height of whorls slightly over one-half the diameter, with a range of 0.50 to 0.56; whorls narrow, with a ratio range of 0.18 to 0.29. The venter is generally tricarinate; median keel finely noded. Lateral groove narrow, usually not sharply defined, persistent in ontogeny, becoming faint in onto- and phylo-gerontic stages. Costæ on inner flanks widely spaced, oblique orad, straight; on outer flanks numerous, falciform, crowded. In later onto- and phylo-stages costæ branch ventrally and there are fine, short, intercalated costæ. Sutures simple in early, but more complex in later, phylo-stages, where the lobes are long, narrow, and deeply incised, and possess a slender, pointed termination; the saddles are broad and squarish.

LOWER LUSITANIAN, ZONE OF *Peltoceras transversarium*

Ochetoceras canaliculatum (Buch)

SPECIFIC CHARACTERS.[1]—Compressed, involute, with flat or slightly convex, convergent lateral zones. In the adult, height of whorl a little over one-half, width

[1]Dimensions and conch ratios given in Table 3.

one-quarter, of the diameter; ratio of width to height less than one-half (0.43). Lateral groove dorsad of median lateral line; shallow, but persistent. On inner flanks faint folds, few in number; on outer flanks, sickle-shaped, unbranched costæ, concave orad, not continuous with folds on inner flanks. Costæ impersistent in ontogeny, conch smooth before and after costate stage. Triple keel throughout ontogeny. (Buch 1831, Pl. I, figs. 6–8; D'Orbigny, 1842, Pl. CXCIX, figs. 1, 2; Oppel, 1862, Pl. LI, fig. 3; O'Connell, 1920, pp. 681–682.)

GEOGRAPHICAL DISTRIBUTION.—Western, central and southern Europe, eastern Asia, northern France.

Ochetoceras canaliculatum burckhardti O'Connell

VARIETAL CHARACTERS.—Conch compressed, discoidal. Whorls increase rapidly; umbilicus small, deep, with vertical walls. Cross-section cuneate, slightly bulging, two and one-half times as high as wide; height decreases with age; greatest width at about middle of whorl. Lateral groove present from earliest observable stage to end of conch, becoming obsolescent before beginning of body chamber; crossed at intervals by folds. Median keel high and angular with flat bounding zones and sharp ventro-lateral angulations; fine nodes present throughout. Indistinct straight folds on inner flanks; few widely-spaced crescentic costæ on outer flanks for one or two volutions of neanic or ephebic stages; conch almost smooth after a diameter of 50 mm. Sutures simple; at least four lateral lobes, short, broad, with palmate terminations; saddles squarish with asymmetric tripartite division. (O'Connell, 1920, p. 686, Pl. XXXVIII, figs. 1–3.)

GEOGRAPHICAL DISTRIBUTION.—Viñales, Laguira and Constancia, Province of Pinar del Rio, Cuba; Cerro del Volcán, Durango, Mexico (*vide Ochetoceras canaliculatum* (D'Orbigny), of Burckhardt, 'Faunes Jurassiques, etc.,' 1912, p. 5, Pl. I, figs. 1–7).

The Relations of the Lower Lusitanian Species

As we have already seen (p. 387 above), Haug regarded *Ammonites flexuosus canaliculatus* Quenstedt from the lowest Oxfordian (zone of *Quenstedticeras lamberti*) as the connecting link between the *flexuosi* Oppelias and the true *Ochetoceras canaliculatum*. The adult of Quenstedt's species has a noded keel and the position of the lateral canal is indicated by the flexing of the costæ, although no actual canal is developed. But another character is present which seems to preclude this species from the direct line of descent of the Canaliculati, namely, the rows of spines on the ventro-lateral angulations. These are not present in the young of any of the Upper Jurassic Canaliculati as they should be in accordance with the law of recapitulation. Quenstedt referred to Buch's illustration of *flexuosus* in which the ventro-lateral nodes are very pronounced (Buch, 1831, Pl. VIII, fig. 3) and his own illustration shows the same feature (Quenstedt, 1858, p. 531, Pl. LXX, fig. 13).

Wepfer in his retroactive revision of the Oppelias (1913, p. 39) rightly called attention to the fact that the costæ in Quenstedt's species thicken ventrally in a way which is not to be expected in a form ancestral

to the Canaliculati and he also pointed out that in the latter the external lobe is nearly as long as the first lateral lobe, while in the Flexuosi there is a marked difference in length between the two, the lateral accessory branch of the external lobe being much shorter than the first lateral lobe. For these reasons Wepfer seeks the ancestor of the Canaliculati not in the Flexuosi but in the form originally described by Quenstedt as *Ammonites canaliculatus fuscus* (1849, Pl. VIII, figs. 7–9), later as *A. fuscus* (1885, p. 634, Pl. LXXV) from the Brown Jura ϵ. But *A. fuscus* also does not seem to fulfill the theoretical requirements for an ancestral form, since the young of *O. canaliculatum* is not like the adult of *A. fuscus*.

Douvillé has made a better suggestion in deriving *Ochetoceras canaliculatum* from *Oppelia henrici* (D'Orbigny) from the zone of *Cardioceras cordatum* and this in turn from *Oppelia hersilia* (D'Orbigny) from the zone of *Quenstedticeras præcordatum* of the Oxfordian (Douvillé, 1913, p. 62). D'Orbigny gave a brief description of *O. hersilia* (1850, p. 351) but did not figure the form. De Loriol has identified a large series of specimens from the *Creniceras renggeri* beds (=zone of *O. præcordatum*) from the Bernese Jura as *O. hersilia* (1898, p. 11, Pl. I, figs. 7–13) and these forms seem to be clearly ancestral to *O. henrici* from the next higher zone, while the latter with its simple flexed costæ, triple keel and foreshadowed lateral canal, serves admirably as the direct ancestor of *Ochetoceras canaliculatum*. This relation is also brought out by other phyletic facts. The young of *Ochetoceras canaliculatum* is smooth up to a diameter of 10 or more millimeters and in this respect it recapitulates with acceleration the smooth stage which lasts in *Oppelia henrici* up to a diameter of 25 mm. The latter species even in the adult does not develop a true lateral canal and this *henrici* stage is recapitulated very early in *Ochetoceras canaliculatum*.

When the conch proportions of the various species under discussion are considered, it is seen that the adult Oxfordian Oppelias have the proportions found in earlier stages in the Lusitanian and Kimmeridgian species of *Ochetoceras*. (See Table 4.)

The transition from the *Oppelia* into the *Ochetoceras* type took place by the slow development of a lateral canal at the angles of flexing of the costæ, and the change from a narrow cuneate venter into a tricarinate venter. The phyletic trends in conch proportions observable in the Upper Jurassic species of *Ochetoceras* were clearly established in the late Middle Jurassic Oppelias. It is also clear from a comparison of the figures in Tables 2 and 4 that the *hispidum* and *canaliculatum* groups are distinct.

TABLE 4. COMPARISON OF THE ALLOMETRIC PROPORTIONS IN THE MIDDLE JURASSIC OPPELIAS AND THE UPPER JURASSIC CANALICULATE DESCENDANTS

Species	Palæontological Zone	d mm.	h. i. mm.	h. i. / d	w mm.	w / d	w / h. i.	u mm.	u / d
Ochetoceras zio (Oppel)	Zone of *Aulacostephanus pseudomutabilis*	41	21	.51	8	.19	.38	6	.14
Ochetoceras neohispanicum (Burck.)	Zone of *Streblites tenuilobatus*	70	39.0	.55	16.0	.22	.41	11	.15
Ochetoceras canaliculatum burckhardti O'Connell	Zone of *Peltoceras transversarium*	55.8	31.5	.56	13.4	.23	.42	7.5	.13
Oppelia henrici (D'Orb.)	Zone of *Cardioceras cordatum*	90	....	.55	....	.21	.38	....	.14
Oppelia hersilia (D'Orb.)	Zone of *Quenstedticeras præcordatum*	81	....	.54	....	.22	.40	....	.18

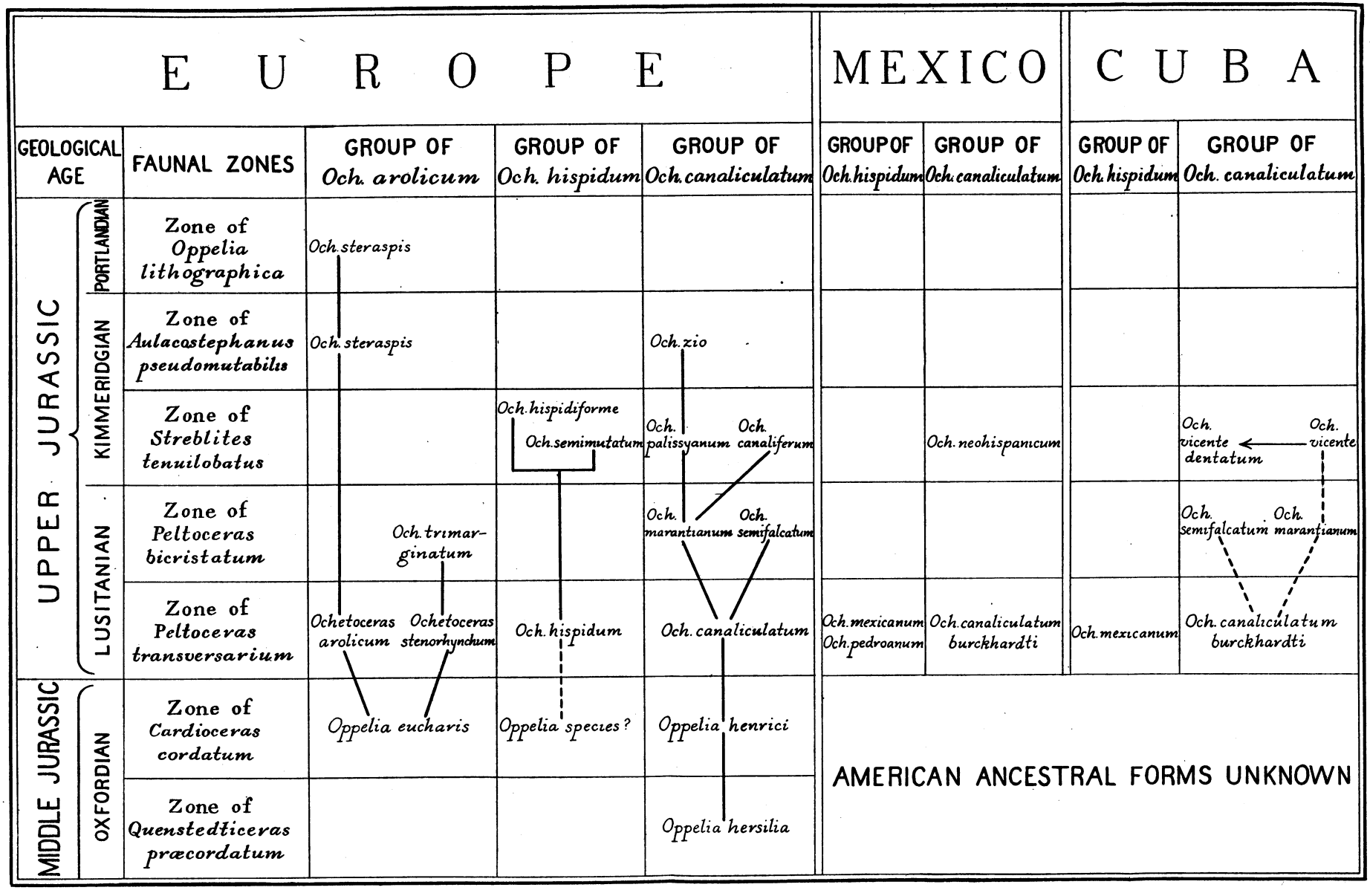

TABLE 5. PHYLOGENY OF EUROPEAN AND AMERICAN SPECIES OF *Ochetoceras*

They are distinguished not only by their different types of surface sculpture but even more especially by their proportions, the species in the *hispidum* group being relatively thicker whorled, having higher ratio of width to diameter and width to height, than those in the *canaliculatum* group. It will be seen (Table 4) that these proportions were established in the ancestors of the latter group in Middle Jurassic time. All of these facts show that Oppel was correct in describing *O. hispidum* and *O. canaliculatum* as distinct species and that Haug's division of the Canaliculati into two major groups derived from these species was essentially sound.

The variety of *canaliculatum* which occurs in Cuba and Mexico is to be regarded simply as a geographical variant of the widespread European form. The Cuban, Mexican and European representatives all show differential acceleration in one or more characters. Thus the suture in the Mexican and European forms is more accelerated than in the Cuban; the number, arrangement and duration of the costæ are the same in the Mexican and Cuban forms, both of which in these respects show acceleration over the European representatives. The American forms are accelerated in respect to the width to height ratio of the whorls, the young in the American variety having the proportions of the older stages of the European species.

UPPER LUSITANIAN, ZONE OF *Peltoceras bicristatum*

Ochetoceras marantianum (D'Orbigny)

SPECIFIC CHARACTERS.[1]—Conch strongly compressed; whorls with little convexity, sagittate cross-section. Profound lateral groove. Dorsad of groove a few irregular costæ; ventrad of groove falciform costæ, many of which divide into two branches at one-third their height. Umbilicus straight. Venter narrow, keel sharp. (D'Orbigny, 1842, p. 533, Pl. CCVII, figs. 3–5).

GEOGRAPHICAL DISTRIBUTION.—In Germany (Swabia, Franconia), in Switzerland (Canton Aargau), in France (the Rhone Valley, Haute-Marne, Yonne, the Aquitanian Basin), in Spain (Aragon), in Portugal, and in the Balkans (Dobrudscha), at Constancia, Pinar del Rio, Cuba.

The single specimen of *Ochetoceras marantianum* found in Cuba is of a young individual only 23 mm. in diameter; its proportions are somewhat different from those of D'Orbigny's holotype, as would be expected, but the typical division of the costæ is shown.

[1]Dimensions and conch ratios given in Table 3.

This species is in the direct line of descent from *O. canaliculatum* showing a specialization toward increased lateral compression and the bifurcation of the costæ. Whether or not the Cuban representative of *O. marantianum* belonged to the European fauna or was independently derived from *O. canaliculatum burckhardti* cannot be determined.

Ochetoceras semifalcatum (Oppel)

SPECIFIC CHARACTERS.[1]—Conch moderately flat; whorls one-half the diameter in height and one-quarter in width; ratio of width to height one-half. Venter tricarinate; median keel sharp and finely noded. Lateral groove weak; in gerontic stage obsolescent. Dorsad of groove costæ are fine, straight, directed orad; ventrad of groove costæ are bent apicad in a sickle-shaped curve concave orad; are continuous across flanks, but become very weak on dorsal side of groove, while on ventral side they branch near the venter. (Oppel, 1863, p. 194, Pl. LII, figs. 6, 6*a*; Haug, 1885, p. 697.)

GEOGRAPHICAL DISTRIBUTION.—Württemberg, Bavaria, and the Swiss Jura in Europe. Rio Hondo and Constancia, Province of Pinar del Rio, Cuba.

The Cuban material shows nearly all stages of the ontogeny, thus augmenting our knowledge of the species considerably. One specimen is the same size as Oppel's holotype, the measurements of the two varying by less than one millimeter at a diameter of 61 mm. near the end of the body chamber. In the early ephebic stage the conch has almost the same proportions as are exhibited in the late ephebic stage of *O. canaliculatum* (Buch) and of *O. canaliculatum burckhardti* O'Connell (see ratios in Table 3). Not only in actual measurements and proportions does *O. semifalcatum* recapitulate the stages passed through by *O. canaliculatum*, but the mode of development of the keel and costæ is repeated with the result that a young conch of the former species is identical in appearance with a mature conch of the latter. Haug regarded *O. semifalcatum* as a member of the *O. hispidum* group (1885, p. 697), but a study of the ontogeny of the former species, which was not possible with the European material but has been made possible by the discoveries in Cuba, reveals the fact that there is no convergence of characters toward an *O. hispidum* stage. On the contrary, the conch becomes relatively thinner as the ratio of width to height of whorl decreases and the lateral zones are not inflated as in *O. hispidum* but become flatter in the earlier onto-stages, while there is a concomitant decrease, instead of an increase, in the relative width of the umbilicus. These facts are illustrated in a young conch from Rio Hondo (see Table 3): at a diameter of 42 mm. the width of the umbilicus is identical with, and the other ratios

[1]Dimensions and conch ratios given in Table 3.

are very near to, the corresponding ratios in *O. canaliculatum* at a diameter of 90 mm.; every conch ratio of the adult of the older species is recapitulated in the half-grown conch of the geologically younger species. *O. semifalcatum* appears to have been a specialization as a side branch in late Lusitanian time, both in the European and American faunas, but was not in the direct line of descent leading to the Kimmeridgian species. The contemporaneous *O. marantianum* was the one from which the succeeding species were derived. (See Table 4, p. 402.)

Lower Kimmeridgian, Zone of *Streblites tenuilobatus*

Ochetoceras palissyanum (Fontannes)

Specific Characters.[1]—Conch very compressed, discoidal; whorls one-half of the diameter or more in height but less than one-fourth in width; ratio of width to height less than 0.45. Umbilicus shallow and rather broad. Lateral groove broad, shallow, poorly defined. Dorsad of groove costæ are irregularly spaced, of unequal strength, oblique orad, slightly curved; ventrad of groove costæ are numerous; many branch once or twice and they bend sharply orad in approaching the venter. Venter unicarinate, not noded; median keel sharp, passing into lateral zones without interruption by ventro-lateral carinations. (Dumortier and Fontannes, 1875, p. 230, Pl. v, fig. 6, and Fontannes, 1879, p. 18, Pl. II, fig. 10.)

Geographical Distribution.—Crussol, Ardèche, France.

This species was clearly derived from *O. marantianum* by specialization in the direction of multiple branching of the costæ near the ventral margin. In the latter species most, but not all, of the costæ show two branches; in *O. palissyanum* all of the costæ show two or three branches, and there are fine, short intercalated costæ besides. In dimensions and proportions the two species are practically identical.

Ochetoceras canaliferum (Oppel)

Specific Characters.[1]—Whorls high and very narrow. Umbilicus small. Lateral groove narrow, distinct. Dorsad of the groove are a few folds strongly inclined orad and somewhat curved; ventrad there are nine or ten strong, crescentic costæ passing from groove to venter, while between them are large numbers of fine, short costæ—fully 200 on the last whorl—which are strongly bent orad near the venter. Keel sharp, low, may be triple but not so described. (Oppel, 1856, p. 686; 1863, p. 195, Pl. LII, figs. 4*a*, *b*.)

Geographical Distribution.—Württemberg, Germany and near Baden, Canton Aargau, Switzerland.

Ochetoceras vicente, new species

Specific Characters.[1]—Conch moderately flat; height of whorls about twice the width and one-half the diameter. Lateral zones flat, converging rapidly ventrad. Cross-section of whorls sagittate. Involution three-fourths; umbilicus broad. Venter

[1]Dimensions and conch ratios given in Table 3.

tricarinate; median keel high, faintly denticulate, bounded by two gently concave channels and ventro-lateral carinations. Lateral groove definite in early stages, obsolescent in gerontic stage. Costæ ventrad of groove simple, curved, crowded in young; in the half-grown conch short, fine, oblique costæ appear along the ventro-lateral angulation between the long costæ; in gerontic stage some of the long costæ become faint near lateral groove, others split ventrally into several branches, all becoming less distinct and prominent. Dorsad of groove are a few irregularly spaced folds with pronounced growth lines between them; folds increase in number on last whorl but decrease in distinctness. Sutures complex, crowded, modified by numerous small inflections throughout; six lateral lobes and saddles; lobes terminate in single point with many small accessories and are broader than saddles.

GEOGRAPHICAL DISTRIBUTION.—San Vicente, Province of Pinar del Rio, Cuba.

Ochetoceras vicente dentatum, new variety

VARIETAL CHARACTERS.[1]—Proportions and surface features practically the same as in *O. vicente* except that the fine intercalated costæ are not so numerous. Sutures simpler and less crowded. Distinguishing feature is the strongly noded keel.

GEOGRAPHICAL DISTRIBUTION.—Constancia, Province of Pinar del Rio, Cuba.

THE RELATIONS OF *Ochetoceras vicente*

This species is the analogue in the Cuban fauna of *O. canaliferum* in the European fauna. In its early stages *O. vicente* recapitulates all of the conch proportions of *O. marantianum* and its more remote ancestor, *O. canaliculatum burckhardti*. Thus at a diameter of about 43 mm. it has nearly the same proportions as the latter has at a diameter of 55.5 mm. (see Table 3). Since the adult stage of *O. marantianum* is unknown in the Cuban fauna, comparisons must be made with the European representative of that species. *O. vicente* retains until the early gerontic stage the same ratio of width to height and this is primitively high, being over 0.50, and such as characterizes the species in older geological horizons as well as the earlier onto-stages of species in younger horizons. The involution increases with age, as in all species in this group. On the whole, the adult proportions indicate retardation. Specialization, therefore, has taken place not in trends in proportions but in the type of costal development, just as in the contemporaneous and analogous European species.

The costæ show a similar recapitulation of the successive phylo-stages: in the young of *O. vicente* they pass through *canaliculatum* and *marantianum* stages. At a diameter of 40 mm. the *canaliferum* stage begins with the appearance near the ventro-lateral angulation of fine, short, oblique costæ of the same type as those occurring in the ephebic and gerontic stages of *O. canaliferum*.

[1]Dimensions and conch ratios given in Table 3.

The sutures are crowded and complexly incised but their fundamental plan is of the *canaliculatum* type.

O. vicente dentatum retains the more primitive, finely-noded condition of keel which is characteristic of *O. marantianum*.

Ochetoceras neohispanicum Burckhardt

SPECIFIC CHARACTERS.[1]—Conch strongly compressed; whorls high and narrow with sagittate cross-section. Lateral groove faint and narrow. Dorsad of groove are faint striations and folds directed obliquely orad; ventrad of groove are falciform costæ of unequal strength, some amounting to coarse folds, the remainder being fine. Between the long costæ are striations of various lengths. Ventrad the costæ branch. Keel low, sharp, not triple. (Burckhardt, 1912, p. 46, Pl. x, figs. 1–3, 7.)

GEOGRAPHICAL DISTRIBUTION.—Cerro del Volcán, San Pedro del Gallo, Durango, Mexico.

This is the American analogue of *O. palissyanum*. The chief line of specialization in both forms is in the arrangement and number of costæ, the trend in both being toward finer and more numerous costæ with intercalated striations and ventral branching. The proportions in both species are similar but *O. neohispanicum* is not so strongly compressed as *O. palissyanum*.

UPPER KIMMERIDGIAN, ZONE OF *Aulacostephanus pseudomutabilis*

Ochetoceras zio (Oppel)

SPECIFIC CHARACTERS.[1]—Conch greatly compressed; whorls thin and high, cuneate in cross-section. Venter thin, unicarinate. Narrow lateral groove. Dorsad of groove, coarse radial plications; ventrad of groove, thick, falciform, simple costæ numbering 16 on last half whorl, and between every two of these, three or four finer costæ not extending to the groove but reaching the venter where they bifurcate. (Oppel, 1863, p. 196, Pl. LII, figs. 7*a–c*.)

GEOGRAPHICAL DISTRIBUTION.—Württemberg, Germany.

This species is a direct descendant of *O. palissyanum*, with which it agrees in proportions and from which it differs by the bifurcation of the small costæ; it represents the final stage of specialization in the multiplication of the costæ ventrad of the lateral groove. *Ochetoceras zio* was founded upon a single specimen, which is the only known representative of this phyletic series in the upper Kimmeridgian rocks.

GENERAL SUMMARY

The genus *Ochetoceras* is confined to the Lusitanian, Kimmeridgian, and lower Tithonian (Portlandian) divisions of the Upper Jurassic and was derived from the Middle Jurassic *Oppelia*. The numerous species

[1]Dimensions and conch ratios given in Table 3.

are found to fall into three phyletic series: (1) the series of *Ochetoceras arolicum;* (2) the series of *O. hispidum;* (3) the series of *O. canaliculatum.* In addition, there are a few forms of doubtful affinities. It is impossible to trace all of the species of *Ochetoceras* back to a single ancestral species of *Oppelia;* rather does it seem that the various phyletic series arose independently from distinct species of *Oppelia.* Douvillé pointed out that there were certain orthogenetic trends visible in the Oppelias and that *Ochetoceras* was derived from the branch in which there was a trend toward a narrow venter. Thus in the late Middle Jurassic (Oxfordian) several Oppelias developed narrow, tricarinate venters and lateral canals; from these forms the three or more branches of *Ochetoceras* developed. The *arolicum* branch is distinguished from the other two branches by its retention of the primitively smooth, *Oppelia*-like lateral zones in most onto-stages. The *hispidum* and *canaliculatum* branches are distinguished one from the other by the fundamentally divergent conch proportions and the character of the costæ of the species in each, the *hispidum* branch containing broad-whorled, coarsely costate species, the *canaliculatum* branch including compressed, high-whorled, finely costate species. The two groups cannot, therefore, be united under *O. canaliculatum* as Wepfer and others have tried to do.

The same trends in development are visible in all three series as the phylogeny is traced from the lowest Lusitanian to the Portlandian. These trends are: (1) a progressive diminution in the ratio of width to height of whorl and width of whorl to diameter; (2) a progressive diminution in the coarseness of the costæ; (3) the branching of the primary costæ at their ventral ends and finally the branching of the intercalated costæ or striæ. These trends have been observed in the onto-stages of all species in which it has been possible to study the ontogeny, so that they are onto- as well as phylo-trends; they are observable especially in the Kimmeridgian species, for in them the onto-stages of the more primitive Lusitanian forms are recapitulated. In terms of growth, these definite directions of development indicate that the adult primitive species were relatively thick-whorled forms, while the descendants in later faunas became progressively thinner and more compressed, although they still retained in their earliest onto-stages the proportions of their ancestors. (These facts are more apparent in the *hispidum* and *canaliculatum* series. Little is known about the ontogeny of any of the species in the *arolicum* series except that all of them show evidences of gerontism and therefore do not strictly adhere to the trends observable in normal, robust species.) In all of the primitive species the mantle of the animal

was nearly smooth or else thrown into coarse folds during a part of the life-time of the individual, the early stages of all primitive forms being smooth as in the ancestral *Oppelia* stock. In the descendants, the mantle folds became a more enduring feature; they were stronger, lasted longer, and were crowded back in the ontogeny. It may be suggested that the introduction of many costæ, of multiple branching, and of numerous intercalations, was in direct reponse to the crowding of the mantle into the smaller body cavity which was produced by the lateral compression of the whorls.

All of the trends which have been observed appear to be orthogenetic, for they are followed by all except decadent species in all of the phyletic series and in all of the phylo-stages. They must have been independent of environment, since they obtained in the species of the Asiatic, European, and American faunas, which by no means enjoyed uniform living conditions. The Cuban fauna, for instance, is a dwarf fauna as compared to that of the Swiss and German Jura—the dwarfing having been due to unfavorable bionomic influences—yet the species of *Ochetoceras* show exactly the same onto- and phylo-trends as do those of central Europe. The end members of all of the phyletic series arrived at nearly the same stage of development at the end of two geological epochs. Thus in the *arolicum* series *O. steraspis* from the upper Kimmeridgian and Portlandian is the analogue of *O. zio* in the *canaliculatum* series from the same horizon. In the lower Kimmeridigan we find that, in the *canaliculatum* series, *O. vicente* of Cuba is the analogue of *O. canaliferum* of Germany, Switzerland, and France, while *O. neohispanicum* of Mexico is the analogue of *O. palissyanum* of France. In the *O. hispidum* series *O. hispidiforme* of France is the lower Kimmeridgian analogue of *O. mexicanum* of Cuba and Mexico and all of these are related to the ancestral *O. hispidum* as *O. marantianum* of France and Cuba is related to the ancestral *O. canaliculatum* of Europe and America. The species of the *O. hispidum* series never passed beyond the stage of simple branched costæ to the stage of multiple branching and intercalation, which illustrates the fact that the inherent force which controls orthogenetic trends is more powerful or works more rapidly in some phyletic series than in others.

The phylogeny of the European groups of *O. hispidum* and *O. canaliculatum* was worked out in part by Oppel, Haug and Douvillé but has been modified in the present paper, as shown in Table 5. The relations of the European species in the *O. arolicum* group and of the Mexican and Cuban representatives of the *O. hispidum* and *O. canaliculatum* groups are here set forth for the first time.

BIBLIOGRAPHY OF SELECTED REFERENCES[1]

BUCH, LEOPOLD VON. 1831. 'Recueil de Planches de Pétrifications Remarquables.' Berlin, 20 pp., 8 plates.

BURCKHARDT, CARLOS. 1912. 'Faunes Jurassiques et Cretaciques de San Pedro del Gallo.' Instituto Geologico de Mexico. Boletin num. 29, 264 pp., 46 plates.

D'ORBIGNY, ALCIDE. 1842. 'Paléontologie Française. Terrains Oölitiques ou Jurassiques.' Tome I. Paris.' 642 pp. Atlas, 1842–49, 234 plates.

1850. 'Prodrome de Paléontologie.' Vol. I. Paris. (Protograph of *Ammonites hersilia*, p. 351.)

DUMORTIER, E. AND FONTANNES, F. 1875–76. 'Description des Ammonites de la zone à *Ammonites tenuilobatus* de Crussol (Ardèche) et de quelques autres fossiles Jurassiques nouveau ou peu connus.' Mémoires de l'Académie des sciences, etc. de Lyon, XXI, pp. 187–341, Pls. I–XXI.

DOUVILLÉ, ROBERT. 1913. 'Esquisse d'une Classification Phylogénique des Oppeliidés.' Bulletin de la Société Géologique de France, (4) XIII, pp. 56–75.

FAVRE, ERNEST. 1875. 'Description des Fossiles du Terrain Jurassique de la Montagne des Voirons (Savoie).' Mémoires de la Société Paléontologique Suisse, II, 77 pp., 7 plates.

FONTANNES, FRANCISQUE. 1879. 'Description des Ammonites des Calcaires du Chateau de Crussol, Ardèche. (Zones à *Oppelia tenuilobata* et *Waagenia beckeri*).' Lyon. 122 pp., 13 plates.

HAUG, ÉMILE. 1885. 'Beiträge zu einer Monographie der Ammonitengattung *Harpoceras*.' Neues Jahrbuch für Min., Geol., und Pal., Beilage Band, III, pp. 585–722, Pls. XI, XII.

1908–11. 'Traité de Géologie, II Les Périodes géologiques.' Paris.

LORIOL, PERCEVAL DE. 1898. 'Étude sur les Mollusques et Brachiopodes de l'Oxfordien Inférieur ou zone a *Ammonites renggeri* du Jura Bernois.' (Accompanied by a stratigraphic notice by Professor E. Koby). Mémoires de la Société Paléontologique Suisse, XXV, 115 pp., 7 plates.

NEUMAYR, MELCHIOR, AND UHLIG, VICTOR. 1892. 'Ueber die von H. Abich im Kaukasus Gesammelten Jurafossilien.' Denkschriften der kaiserlichen Akademie der Wissenschaften. Math.-naturw. Classe, LIX, 122 pp., 6 plates.

O'CONNELL, MARJORIE. 1920. 'The Jurassic Ammonite Fauna of Cuba.' Bull. Amer. Mus. Nat. Hist., XLII, pp. 643–692, Pls. XXXIV–XXXVIII.

OPPEL, ALBERT. 1856–58. 'Die Juraformation Englands, Frankreichs und des südwestlichen Deutschlands.' 857 pp., map. Stuttgart.

1862–1863. 'Palæontologische Mittheilungen aus dem Museum des königlichen bayerischen Staates.' Stuttgart, 1862. Part III, 'Ueber Jurassische Cephalopoden.' Pp. 127–266, Pls. XL–LXXIV.

QUENSTEDT, FRIEDRICH AUGUST. 1858. 'Der Jura.' 842 pp. Tübingen.

1885. 'Die Ammoniten des schwäbischen Jura.' Stuttgart. 1140 pp. Atlas, 1883–85, 126 plates.

[1]A complete bibliography of all reference works consulted will be published in the longer paper on the 'Jurassic of Cuba' to appear later.

ROLLIER, LOUIS. 1909. 'Phyllogénie des Principaux Genres d'Ammonoides de l'Oolithique (Dogger) et de l'Oxfordien.' Archives des Sciences Physiques et naturelles, (4) XXVIII, pp. 611–623.

WEPFER, EMIL. 1913. 'Die Gattung Oppelia in süddeutschen Jura.' Palæontographica, LIX, pp. 1–68, Pls. I–III.

ZITTEL, KARL. 1881–85. 'Handbuch der Palæontologie.' Abteilung I, Band II.