A Description of new species of Zeuglodont and of Leathery Turtle from the Eocene of Southern Nigeria

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18. A Description of New Species of Zeuglodont and of Leathery Turtle from the Eocene of Southern Nigeria.

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(Plates I. & II.*)

Two small collections of vertebrate remains from the Ombialla District of Southern Nigeria have recently been received by the British Museum, one having been sent by Sir Frederick Lugard, G.C.M.G., the other by Sir John Eaglesome, K.C.M.G. The sternum of a large carinate bird included in the latter collection has already been described †, and it is now proposed to give a short account of some remains of a Zeuglodont Whale and of a Turtle belonging to the so-called Athecate group.

Pappocetus lugardi, gen. et sp. nov.

Portions of the lower jaws of a Zeuglodont are included in both collections, and, although in both cases incomplete, the specimens to some extent supplement one another, so that the structure is fairly clear. The most complete specimen (M 11414, referred to as specimen A) consists of the imperfect left ramus wanting the articular and angular regions, but united with a considerable portion of the anterior region of the right ramus including the hinder part of the symphysis (Pl. I. fig. 1). Portions of five teeth are preserved on the left side and of two on the right. The bones were embedded in an intensely hard pyritous clay, including many fragments of molluscan shells. This may be regarded as the type-specimen.

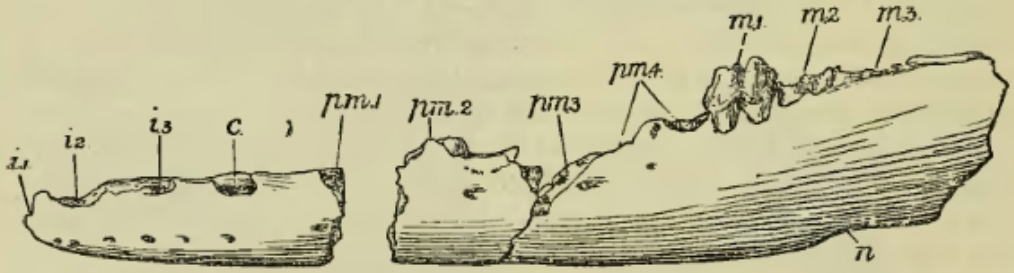
The other specimen (M 11086, specimen B) is a left ramus of a mandible broken into three pieces (text-fig. 1). The anterior of these bears the sockets for the incisors, canine, and front half of the single-rooted pm_1. Behind this a length of about 2·5 cm., which must have carried the posterior half of pm_1 and anterior half of pm_2, is wanting. The length missing is estimated by comparison with specimen A, which belonged to an individual of nearly the same size. The two other fragments unite below, but, unfortunately, the portion of the alveolar border bearing pm_3 is lost. The hinder piece bears the basal portion of the very large pm_4, and following this without interval are the three molars, of which the first is nearly complete, the second is represented by the roots only, while the third, which had not yet emerged, has been exposed by cutting away the bone; the articular and angular regions are missing.

* For explanation of the Plates see p. 319.

† Proc. Zool. Soc. 1916, p. 519.

The outer face of the mandibular ramus is convex from above downwards, the convexity being most marked in the symphysial region, which extends back to the level of the anterior root of pm_3; in *Prozeuglodon* it does not seem to extend beyond the hinder end of pm_2. The symphysial surface itself bears a strongly rugose surface for union with the opposite ramus, the rugosities being most strongly developed posteriorly: the union between the two rami must have been much stronger than in *Zeuglodon* or *Prozeuglodon*, where the symphysial surfaces bear only a few straight and slightly developed longitudinal rugosities. Behind the symphysis the inner face of the ramus is convex from above downwards immediately beneath the alveolar border, but towards the ventral edge becomes gently concave in the same direction. The ventral border is nearly straight from before backwards as far as beneath the hinder end of m_2, where it turns somewhat upwards for a short distance and then continues in the original direction, so that at this point a slight step-like prominence is formed (text-fig. 1, *n*). The posterior portion of the ramus is lost in both specimens. In its general form the mandibular ramus is very similar in form to those of *Prozeuglodon* and *Zeuglodon*, but at the same time is distinguished from them by being more massively constructed and by the presence of the slight step in the ventral border referred to above.

Text-figure 1.



Left ramus of mandible of *Pappocetus lugardi*, gen. et sp. nov.

n, step-like notch on lower border (M 11086). About $\frac{1}{6}$ nat. size.

Teeth.—So far as can be ascertained the dental formula of the mandible was I. 3, C. 1, Pm. 4, M. 3—the full Eutherian dentition. Of these, I_1 is represented in specimen B by the socket only; this is situated at the extreme anterior end of the jaw and was separated from its fellow of the opposite side by a very thin wall of bone only. The tooth must have been directed forwards and somewhat upwards. I_2 and I_3 are represented in the same specimen by their broken bases, which are somewhat wider, from before backwards than from side to side, and appear to have possessed a slight keel on the anterior border. Of the incisors I_2 is much the largest, the longitudinal diameter of its base being about 27 mm., while in I_3 this measurement is only 13 mm.; I_1 was about the same size at I_3. This relatively large size of I_2 seems to be characteristic of this genus, not occurring in

Prozeuglodon or *Zeuglodon*. I_2 follows immediately behind I_1, but between it and I_3 there is interval of about 23 mm. The canine is separated from I_3 by a diastema of 30 mm.; it is represented by its broken base, which shows that it was about the same size as I_2, and was probably somewhat compressed from side to side with an anterior angle; like the incisors it was directed forwards. Behind and a little to the outer side of the lower canine there is a slight depression in the outer surface of the jaw, presumably for the reception of the point of the upper canine. Pm_1 is represented by the anterior half of its broken base in specimen B, and by its socket only in specimen A; it is separated from the canine by an interval of about 45 mm., and was considerably compressed laterally, its long diameter being about 30 mm., the transverse only 14. The remaining teeth are all represented in one or other of the specimens by their more or less broken crowns. Pm_2 is preserved in specimen A only, where it is present on both sides, following pm_1 at an interval of 19 mm. It is a two-rooted tooth, the greatest length of which is 37 mm., while its greatest width above the front of the posterior root is 13 mm. So far as can be made out, the compressed crown formed a single cusp without accessory serrations. Both the anterior and posterior borders of the crown are blunt and rounded; at the base of the crown there is a well-marked constriction and on the inner side there is a slightly developed cingulum. The enamel is much roughened, being raised into knotted ridges, which for the most part run vertically. On the posterior lobe of the tooth the enamel ridges of the outer and inner side meet, forming a keel which is situated rather more on the inner than on the outer side of the crown.

Pm_3 is represented in specimen B by its roots only, but in A is present on both sides, that on the left being nearly complete. It is a long, laterally compressed two-rooted tooth, the length of the crown being 53 mm., its greatest breadth only 15 mm. The crown forms one large cusp, the anterior slope of which is shorter and steeper than the posterior. On the anterior border there seem to have been no accessory cusps, but on the posterior there are two with perhaps a rudimentary basal cusp just above the cingulum, which is well developed on the postero-internal side; it is also distinctly marked on the outer and less clearly on the inner face of the tooth. The summit of the main cusp has undergone considerable wear, which also extended down the anterior edge; the top of the upper accessory cusp is also worn.

Pm_4 is unfortunately represented in specimen B by its two roots only, while in A the crown is very imperfect. It was even more strongly compressed laterally than pm_3, and from before backwards was considerably the longest tooth in the series, measuring 59 mm. in this direction, while from side to side the greatest width (above the posterior root) is only 18 mm. It consisted of a main anterior cusp, which may or may not have borne small accessory cusps, and a posterior heel-like cusp which

is broken but which seems to have had a cutting-edge. There is a distinct cingulum round the whole crown, but it is much more strongly developed at the posterior end. The enamel, except near the base of the crown, is smoother than in pm_3, perhaps partly through wear. The posterior root is considerably the larger.

The first molar (Pl. I. fig. 2) is present in both specimens, though in each case the summit of the main cusp is wanting; it is much smaller than pm_4 with which it is in contact; its antero-posterior length is 44 mm. and its width (above the anterior root) 18·5 mm. The crown formed a cutting-blade consisting of a large anterior and a smaller posterior lobe, both inclined a little backwards. On the outer face of the posterior lobe there is a well-marked surface of wear produced by shearing against the upper tooth and extending down to the cingulum. This latter is well marked and is most prominent at the hinder border of the tooth. Immediately above the cingulum on the antero-internal side of the tooth the enamel is raised into a group of small rounded tubercles, a line of which is continued up on the antero-internal face of the main cusp towards its summit. The general surface of the enamel is raised into faint irregular ridges, which, increasing towards the unworn edges of the hind cusp, give them the appearance of being finely crenulated.

In specimen A m_2 is only just emerging, while in B, though more advanced, the tooth is not fully in place; in both specimens it is imperfectly preserved, but, so far as can be seen, was quite similar to m_1. In specimen A it can be seen that the posterior edge of the main cusp is raised into a number of crenulations, which pass on the sides into irregular ridges of enamel.

M_3 was not cut in either specimen, but in B it has been partly exposed and its form seems to be like that of the other molars. The molars and the last premolar form a closed series.

The collection also includes an isolated single-rooted tooth (M 11087) with a conical crown, probably one of the incisors of this species (Pl. I. fig. 3). The inner face is somewhat flattened, and is limited anteriorly by a well-defined ridge. The posterior surface of the tooth has the enamel raised into numerous irregular more or less vertical ridges of enamel, the outer one being the best defined and running up to the summit of the crown. There is a slightly developed cingulum, most marked on the inner and posterior faces.

Another specimen probably belonging to this species is an imperfect axis vertebra (M 11089), without the neural arch and lateral processes (Pl. I. fig. 4). The odontoid is a blunt prominence, oval in section; it has a longitudinal ridge on its upper surface and a slight dimple-like depression on its anterior end. From the base of the odontoid the lateral surfaces for the atlas slope strongly backwards, widening as they go; their upper edge is marked by a strong ridge, behind which the stout pedicle of the neural arch arises, inclining to its fellow of the opposite side. The posterior

surface of the centrum is nearly flat, and between its lateral edge and the broken base of the transverse process is a well-marked concavity. The ventral surface has a strong prominence in the middle line, deepening towards its posterior border. In the middle line on the dorsal surface, on its posterior half, is a deep circular pit—probably the nutritive foramina opened into it. A similar depression has been noticed on the axes of a Cave-Bear and of the Creodont *Apterodon*; probably it is found elsewhere, but it is not seen in two axis vertebræ of *Prozeuglodon*. Compared with the axis of *Protocetus* as figured by Fraas*, this specimen has a blunter odontoid, the lateral surfaces for the atlas slope more strongly backwards, and the posterior surface is much wider in proportion to its depth. In *Protocetus* the centrum is about as long and has a similar ventral prominence. In *Prozeuglodon* † the whole vertebra is shorter, the ventral ridge is indicated only by a slight posterior prominence, and the surfaces for the atlas do not slope so much backwards. The length of the centrum and the backward slope of the atlantal surface, the width of the posterior surface and the ventral prominence, seem to be primitive characters, approximating to what is seen in the Carnivore-Creodont group.

This new Zeuglodont, for which the name *Pappocetus lugardi* is suggested, is especially interesting on account of the Carnivore-like characters of the teeth, which seem to point to a Creodont-Carnivore ancestry as was suggested by Fraas from his study of the Middle Eocene genus *Protocetus* ‡. Unfortunately in this animal only the upper dentition is known, but probably the lower teeth were not very unlike those now described. To this relationship with the Creodonts some objections have recently been raised by Matthew and Gregory §, who point to a number of characters which seem to indicate that the Zeuglodonts may have branched off from the primitive Insectivora, perhaps from some such form as the Eocene *Pantolestes*, a type which, at any rate, shows that some of the early members of the order attained a considerable size and became adapted to an aquatic life ‖. Attention is also drawn to the remarkable superficial similarity in the form of the Zeuglodont skull to those of some of the Centetidæ, notably *Hemicentetes*. This similarity is also particularly noticeable in the form of the mandible, in which even so small a point as the step-like notch on the ventral border is present, though farther back. In the structure and arrangement of the teeth there seems to be nothing that altogether excludes the possibility of such a

* Fraas, "Neue Zeuglodonten aus dem unteren Mitteleocän vom Mokattam bei Cairo," Palæont. Abhandl. Bd. x. (1902–5), p. 211, pl. ii. figs. 2–5.

† Andrews, Catal. Tertiary Vertebrata of the Fayum (1906), p. 254, text-fig. 82 B–D.

‡ Palæont. Abhandl. n. s. Bd. vi. (1904), p. 199.

§ "The Orders of Mammals," Bull. Amer. Mus. Nat. Hist. vol. xxvii. (1910), p. 414.

‖ Memoirs of the Amer. Mus. Nat. Hist. vol. ix. (1909), p. 523.

relationship, and it is interesting to note that probably the ancestors of the Centetidæ lived in Africa in early Tertiary times, and it is there also that the Zeuglodonts probably originated.

Cosmochelys dolloi, gen. et sp. nov.

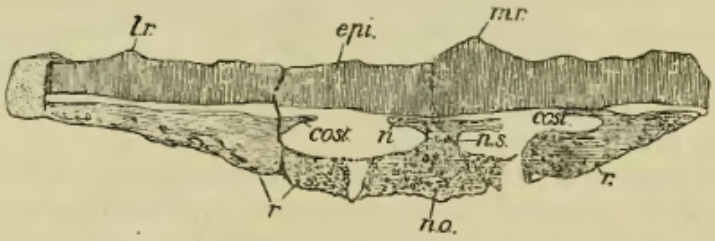
The second specimen (R 4338) now described consists of portions of the central region of a carapace belonging to a Chelonian referable to the so-called Athecæ, to which belong the recent Leathery Turtle, *Dermochelys coriacea*, and the Tertiary genus *Psephophorus* to which the present form seems to be most nearly allied. This specimen was presented to the Museum by Sir John Eaglesome, K.C.M.G. Unfortunately, the fragments seem to have been picked up at random, so that much has been lost; but, nevertheless, it has been possible to join a certain number of pieces, which together make up a portion of the carapace measuring about 37 cm. long by 27 cm. wide. On the right side of this the upper portions of five ribs are preserved and on the left three, corresponding to the posterior three on the right side. In the case of these three posterior ribs, the upper portion of their articular ends are preserved, articulating with the neural arches. These bore neural short spines, to the upper ends of which the remnants of the disappearing neurals are joined. The whole outer surface of the carapace is covered by a thick armour of epithecal plates, corresponding to the shell of *Dermochelys*.

This epithecal shell may be described first. As in *Dermochelys* it consists of several rows of longitudinally keeled plates separated by a mosaic of smaller plates without ridges. The keeled plates forming the median dorsal ridge are roughly hexagonal and elongated in a longitudinal direction; they present much the appearance of the neurals of a thecal carapace. The keeled plates of the two upper lateral rows are seen also to be irregularly hexagonal, but shorter than those of the median row. Two or three isolated keeled plates (Pl. II. fig. 3), to which the outer points of ribs are adherent, are much larger than the rest and are nearly quadrate in outline: they were probably near the margin of the carapace and are thinner than the central plates. The exact number of keeled ridges cannot be determined, but there were at least seven. The central part of the carapace preserved shows a median and two lateral ridges, while the large (? marginal) plates above referred to bear another, and others may have been present, since it is unknown how much of the carapace is missing between the outer part of the main fragment and the margin; the distance must have been considerable to allow for the narrowing of the broad ribs towards their outer pointed ends. In *Dermochelys* a median and three lateral ridges are present, seven in all, but Völker * thinks that probably there were originally nine.

* Völker, "*Dermochelys coriacea*," Zool. Jahrbücher (Anatomie), vol. xxxiii. (1913), p. 477.

The plates filling the intervals between the ridges are smaller than the keeled plates and of more irregular forms (Pl. II. fig. 2). So far as can be seen, between each pair of ridges there are only two rows of these plates, except that here and there a small irregular plate may be intercalated. This comparatively small number of intermediate plates seems to be a primitive character, since in *Psephophorus* and *Dermochelys* there is a progressive increase in their numbers: in *Psephophorus* there were at least six rows and in *Dermochelys* they are very numerous. The epithecal plates are very thick and massive; in the median row the thickness of the lateral portions is about 10 mm., while at the ridge it may be as much as 16 mm. In the lateral plates above noticed, the general thickness has decreased to 7 mm. or, at the ridge, 9 mm. According to Seeley *, the plates of *Psephophorus* may attain a thickness of nearly 10 mm., but are usually thinner. The outer surface of the plates is beautifully sculptured, with a series of irregular tuberosities in the middle bordered by ridges more or less radially arranged, and running to the margin which is usually bevelled off, so that the suture between neighbouring plates runs at the bottom of a groove. In *Psephophorus* also the surface of the plates is sculptured, but the ornament appears to consist of radial ridges only and to be less pronounced than here. Probably in life the outer surface was covered by a leathery skin, or possibly by horny plates, though this does not seem likely. The presence of this strongly marked ornament seems to show that this Turtle was not adapted for rapid motion through the water, but was probably a littoral or even a swamp-living form like *Trionyx*. It is unfortunate that nothing is known of the plastron.

Text-figure 2.



Transverse section through epithecal and thecal shell of *Cosmochelys*.

cost., costal plate; *epi.*, epithecal shell; *l.r.*, lateral ridge of ditto; *m.r.*, median ridge of ditto; *n.*, neural plate; *n.a.*, neural arch; *n.s.*, neural spine; *r.*, rib. ½ nat. size.

The thecal skeleton, so far as preserved, consists of the remnants of the costals and neurals. The costal plates are confined to the upper end of the ribs, where they are fairly well developed,

* Seeley, "Note on *Psephophorus polygonus* v. Meyer," Quart. Journ. Geol. Soc. vol. xxxvi. (1880), p. 406.

projecting forwards and backwards so as to unite with one another in a short suture; external to this they narrow rapidly to the edge of the broad and strongly developed rib. Towards the middle line of the carapace the costals are free from the ribs for a short distance, forming flanges which project towards the vestigial neurals, but do not reach them. In this respect the degree of reduction is intermediate between what is seen in *Protostega* and *Archelon*, in which the greatly reduced costals still meet the neurals and unite with one another, and in *Dermochelys*, where the upper borders of the costals, though marked by a distinct ridge, do not form flanges projecting towards the neurals, which are, in fact, absent or perhaps in part represented by the bilobate upper ends of the neural spines; moreover, in *Dermochelys* the costals do not unite with one another. The upper ends of the ribs are thick and no doubt had a considerable articulation with the vertebral centra, but this region is abraded and only the portion articulating with the neural arch remains. The distance between the heads of the ribs of opposite sides is about 33 mm. The most anterior of the ribs preserved appears to be curved backwards towards the rib behind and to have had the costal plate on the hinder side only: this was, probably, the first rib. The outer free portion of the other ribs is very broad and strongly developed.

The neural arch bears a short stout neural spine, to the upper end of which is attached a thin, flat, table-like neural, which projects on either side for about 7 mm., but remains separated from the upper edge of the costal by an interval of 10 mm.

In the figure (Pl. II. fig. 4, text-fig. 2) the relations of the costals, neurals, ribs, and neural arches to one another and to the epithecal shell is well shown. It will be noticed that the median ridge of the epithecal shell is not immediately above the middle line of the underlying neural, but in the crushing that has been undergone has been displaced to one side. This probably indicates that in life the epithecal and vestigial thecal shells were separated by a considerable layer of soft tissue now represented by a thin film of matrix only.

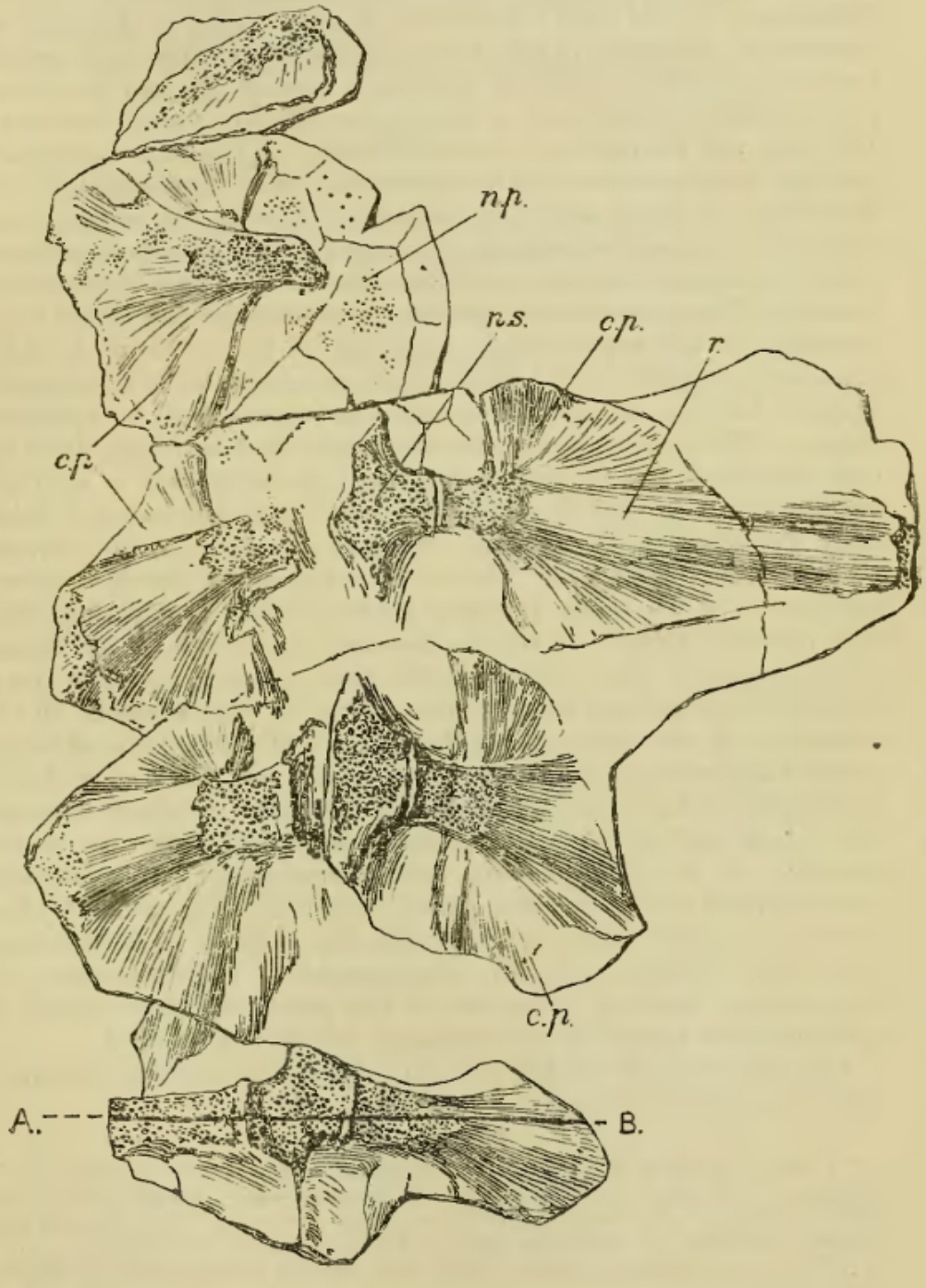
Of the remainder of the skeleton nothing is yet known. It is greatly to be desired that engineers and others who are on the spot where excavations are opened, would collect all the fragments that are exposed, especially in tropical localities like Nigeria, where fossils once uncovered are rapidly disintegrated and cuttings very soon overgrown and rendered inaccessible. Of course, it would be still better if, when such works are in progress, a skilled collector could be present to see that nothing was lost.

The Chelonian above described approaches most nearly to *Psephophorus*, but, as pointed out, differs from this in several respects, notably in the arrangement of the plates on the epithecal shell, and it is therefore referred to as a new genus *Cosmochelys*, the specific name being *Cosmochelys dolloi* in honour

of Professor L. Dollo, who has done so much to elucidate the history of this group of Chelonians.

This specimen is of especial interest, because it appears to help

Text-figure 3.



Inner surface of part of carapace of *Cosmochelys* (R 4338). $\frac{1}{3}$ nat. size.

c.p., costal plate; *n.p.*, median epithecal plate; *n.s.*, neural arch; *r.*, rib.
A–B, line of section shown in text-fig. 2 and Pl. II. fig. 4.

to fill up one of the gaps in the series of forms which end in *Dermochelys*. According to Dollo's * view, the Cheloniidæ and related forms, which no doubt were derived from littoral and, more remotely, from terrestrial types, underwent a reduction of their thecal armour in consequence of their becoming more and more adapted to pelagic life; this reduction seems to have culminated in the later Cretaceous, in such forms as *Allopleuron*, *Protostega*, *Archelon*. Dollo then supposes that some such pelagic form re-adopted a littoral or perhaps a swamp life and that these new conditions rendered a protective armour again necessary. This was not formed by a re-development of the thecal skeleton, but by the formation of an epithecal armour external to it. Whether, as Dollo seems to believe, this was an entirely new formation or resulted from the increased development of epithecal elements already present, as Völker, Hay, and others think, is not certain. The presence of epithecal elements in the neural and probably in the supramarginal regions of the shell of *Archelon* gives some support to the latter view, especially as it is generally agreed that the marginals of all Chelonians are of epithecal origin. However this may be, it appears that in forms like that now described a very strong epithecal skeleton with a strongly sculptured outer surface was developed outside the reduced thecal shell, and this could only have been of use to a littoral or even partly terrestrial animal. This stage in the series should theoretically occur in the early Tertiary period, and it is precisely from this horizon (Lower or Middle Eocene) that *Cosmochelys* comes. It is supposed that subsequently this or some similar form returned to a pelagic mode of life, which in turn resulted in the reduction of the epithecal skeleton. In the Oligocene-Miocene genus *Psephophorus*, this has not advanced very far, and is chiefly manifested in the multiplication of the number of plates between the ridges and in the less strongly developed sculpture of the surface. In the culminating form, *Dermochelys*, the reduction has advanced so far that the plates of the carapace are very thin, smooth, and very numerous between the ridges: in the plastron they have almost entirely disappeared. Unfortunately, in *Cosmochelys* nothing is known of the plastron, either thecal or epithecal, but probably the epithecal was well developed.

The discovery of further remains of this interesting Chelonian will be awaited with great interest.

* Dollo, "Première Note sur les Chéloniens oligocènes et néogènes de la Belgique," Bull. Mus. roy. d'Hist. Nat. de Belgique, tom. 5 (1888), p. 59. Also "Sur l'Origine de la Tortue Luth (*Dermochelys coriacea*)," Bull. Soc. roy. des Sciences médicales et naturelles, 1901. Also "*Eochelone brabantica* .... et l'Evolution des Chéloniens marins," Bull. Acad. roy. des Belgique, 1903, p. 792, and other papers.

Lists of papers relating to the origin of the Athecæ are given by Versluys, Report Brit. Assoc. 1913 (Birmingham), p. 806; and by Völker, on "Ueber das Stamm, Gliedmassen-, und Hautskelet von *Dermochelys coriacea*," Zoologische Jahrbücher (Anatomie), vol. xxxiii. (1912–13), p. 543.

EXPLANATION OF THE PLATES.

Plate I.

Pappocetus lugardi, gen. et sp. nov.

Fig. 1. Mandible, outer side. (Type-specimen M 11414.) $\frac{1}{3}$ nat. size.
2, 2*a*. Outer and inner aspects of first molar of specimen M 11086. $\frac{2}{3}$ nat. size.
3. ? Incisor (M 11087). Nat. size.
4. Anterior face of imperfect axis vertebra (M 11089). $\frac{1}{2}$ nat. size.

Plate II.

Cosmochelys dolloi, gen. et sp. nov. (Type-specimen R 4338.)

Fig. 1. Outer surface of middle portion of epithecal shell. $\frac{2}{3}$ nat. size.
2. Outer face of intermediate plates of epithecal shell. Nat. size.
3. Outer face of two lateral plates of epithecal shell. $\frac{2}{3}$ nat. size.
4. Vertical transverse section through thecal and epithecal shell. Nat. size.

c.p., costal plate.
c.r., central ridge.
ep., epithecal shell.
l.r., lateral ridge.
n., neural plate.
n.sp., neural spine.
r., rib.